ECOLOGY OF THE *OLEARIA COLENSOI* DOMINATED SUB-ALPINE SCRUB IN THE SOUTHERN RUAHINE RANGE, NEW ZEALAND.

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***Olearia colensoi* in flower.**

Reproduced from a lithograph by Walter Fitch in Flora Novae-Zelandiae (J.D. Hooker 1852). Source: Alexander Turnbull Library in New Zealand Heritage, Paul Hamlyn Ltd

ABSTRACT

The *Olearia colensoi* (leatherwood or tupari) dominated southern Ruahine sub-alpine scrub is the largest continuous area of sub-alpine asteraceous scrub in New Zealand - the result of a lowered treeline due to climatic conditions characterised by high cloud cover, high rainfall, and high winds and the absence of high altitude *Nothofagus* species.

Meteorological investigation of seven sites in the southern Ruahine found that altitude alone was the main environmental determinant of climatic variation, particularly temperature regime. Temperatures varied between sites at a lapse rate of 0.61°C $100m^{-1}$ while daily fluctuation patterns were uniform for all sites. Rainfall increased with altitude over the Range at a rate of $3.8mm\ m^{-1}$. Cloud interception, unrecorded by standard rain-gauges, adds significantly to total 'rainfall'.

Vegetative phenology of *Olearia colensoi* is highly seasonal and regular with an annual growth flush from mid November to January. Leaf litter production in *Olearia colensoi* formations is high ($4.864\ t\ ha^{-1}\ yr^{-1}$), in comparison with world averages for cool temperate forest conditions ($2.5\ t\ ha^{-1}\ yr^{-1}$), and is higher than some lowland forest systems in New Zealand. The high rate of litter production is the main contributor to the build up of the Takapari Peaty Loam on the southern Ruahine plateau regions (accumulating at up to $0.33mm\ yr^{-1}$).

Olearia colensoi is an irregularly heavy (mast) flowering plant. Floral primordia are initiated in the summer / autumn preceding anthesis and the degree of flowering is correlated with the temperature regime at that time. Flowering in individual plants can occur in successive years. *Olearia colensoi* mast flowering / seeding appears to be a consequence of synchronised floral initiation during favourable (above average temperature) summers when adequate carbohydrate reserves are available. The evolutionary basis for this synchronisation may involve predator satiation, as a selective pressure, in combination with other 'efficiencies of scale' such as pollination success.

Phytosociological investigation of vegetation data from 34 plots in the southern Ruahine, Mt Taranaki, Westland and western Tararua Range, analysed using multivariate classification and ordination techniques, demonstrated that the southern Ruahine is significantly different from other leatherwood areas in New Zealand. Regional differences in species composition were apparent but the main differentiation was a high (91% mean) cover of *Olearia colensoi* in the southern Ruahine. Ordination analysis indicates that the southern Ruahine leatherwood communities are particularly homogeneous.

Southern Ruahine *Olearia colensoi* formations are continuously regenerating. Areas of canopy opened by disturbance or die-back are replaced by *Olearia colensoi* without any intermediate successional vegetation. There are currently no impediments to *Olearia colensoi* regeneration and no indications that *Olearia colensoi* will not continue as the dominant vegetation cover, regardless of possible climate change and animal population fluctuations.

Natural forest decline accelerated by introduced browsing animals has allowed a down-slope range expansion of *Olearia colensoi* to occur during the last forty years. Much of the higher altitude *Libocedrus* forest in the southern Ruahine has been replaced by *Olearia colensoi*. The *Olearia colensoi* formation now appears to have reached its maximum range and apart from localised increase is likely to remain relatively constant in extent in the foreseeable future.

The extent of dominance over such a large area of sub-alpine scrub by a single habitat-specific (wetter-cloudier sub-alpine) species is an ecological feature unmatched elsewhere in New Zealand and renders the southern Ruahine a nationally significant ecological area.

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CHAPTER 1

INTRODUCTION

THE SOUTHERN RUAHINE SITUATION

The southern Ruahine Range (Fig. 1.1) has the largest continuous area of *Olearia colensoi* Hook.f. (Tupari or leatherwood*) sub-alpine scrub in New Zealand (DoC 1992). *Olearia colensoi* virtually totally dominates the southern Ruahine sub-alpine zone which probably represents the most extensive single area of monospecificly canopied sub-alpine scrub of any species in New Zealand.

Sub-alpine scrub is common as localised shrubland in association with tussock grassland in most high mountain areas of New Zealand, but more extensive areas are restricted geographically. The southern Ruahine is one of only three North Island sites to be mapped as a distinct 'sub-alpine scrub' vegetation class in 'The Vegetative Cover of New Zealand' (Newsome 1987). The majority of sub-alpine scrub sites occur in the Central Westland District of the South Island. The three North Island sites, Tongariro National Park, Raukumara Range and southern Ruahine together with the South Island sites total some 96,000 ha (Newsome 1987). A further 88,000 ha of sub-alpine scrub mixed with indigenous forest includes areas on Mount Taranaki, Raukumara Range and the Tararua Range in the North Island and a number of South Island sites. Though not included in the above scrub classes areas of leatherwood scrub also occur on Stewart Island (Wilson1987).

Sub-alpine scrub is composed of a number of community types ranging from *Dracophyllum* dominated heaths to Asteraceous scrubs (leatherwood) (Dawson 1988, Wardle 1991). The southern Ruahine, Raukumara Range, Central Westland, Mount Taranaki and Stewart Island have the largest areas of leatherwood scrub communities. On Mt Taranaki the leatherwood is dominated by *Brachyglottis elaeagnifolia* (*O. colensoi* being absent); the other leatherwood areas are dominated to varying extents by *O. colensoi*. Of all these areas the southern Ruahine is the largest ($\approx$45 km^2) continuous sub-alpine scrub formation dominated by *O. colensoi*, *B. elaeagnifolia* occurring only as a secondary component more prominent on recently disturbed sites

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* As the common name 'leatherwood' is also used for other Asteraceous sub-alpine shrubs, some of which occur in the same area, botanical names have been used throughout when referring to species; where the term leatherwood has been used it refers to the vegetation formation as a whole including other species. Nomenclature follows Allan (1961), Moore & Edgar (1970) and Connor & Edgar (*nomina nova* 1987).

such as road and track cuttings. All these large sub-alpine scrub areas have in common the absence of high altitude *Nothofagus* forest and the tree line is consequently lower than normal (Dawson 1988). In the southern Ruahine *O. colensoi* has been increasing in abundance since the Taupo eruption ≈1819 years ago, as evidenced by pollen profiles (Lees 1986). The success of *O. colensoi* is one of the most prominent features of the southern Ruahine Range.

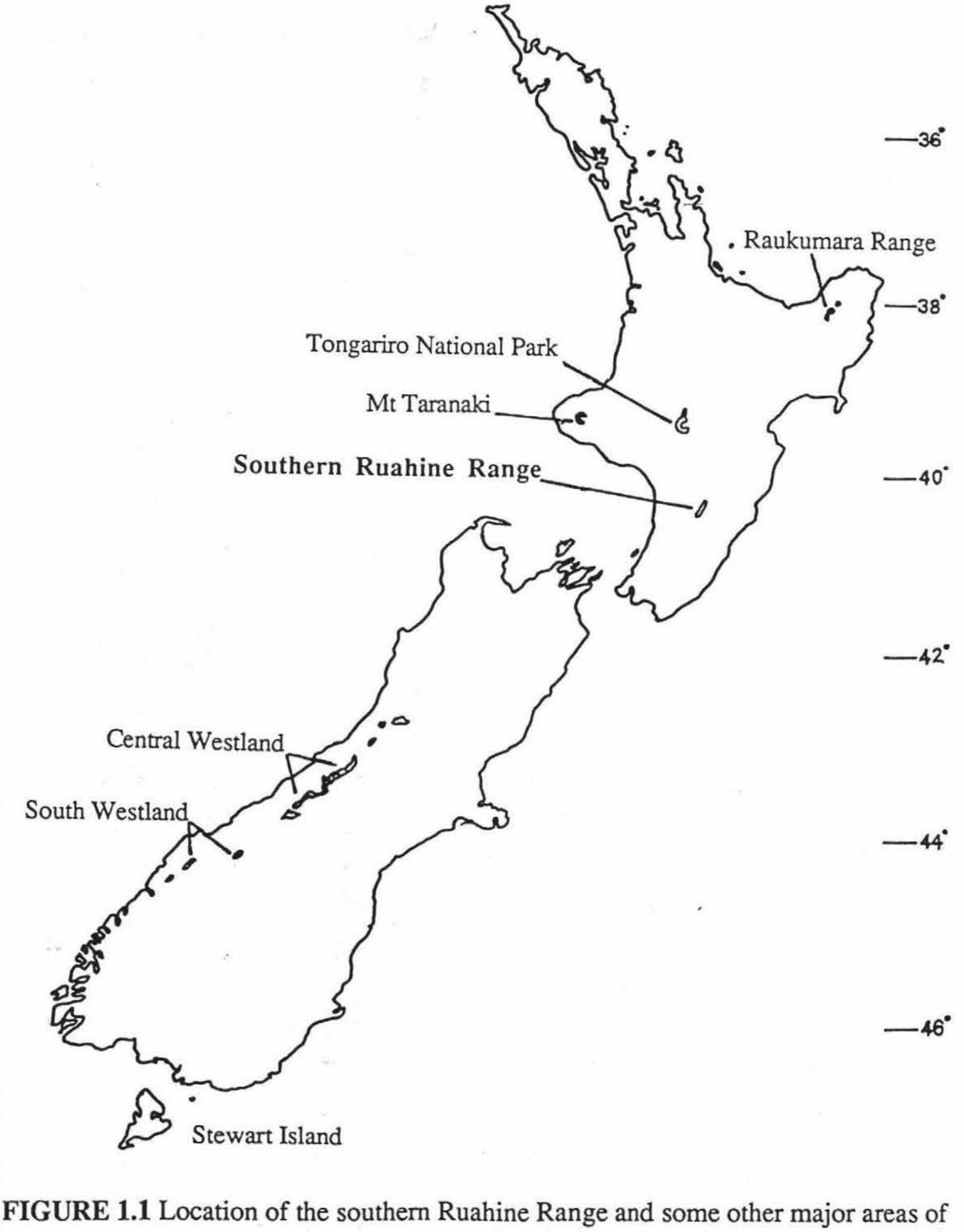

FIGURE 1.1 Location of the southern Ruahine Range and some other major areas of sub-alpine scrub in New Zealand.

Olearia colensoi

Olearia colensoi is a tall, broadleaved, evergreen, asteraceous shrub endemic to New Zealand (Fig. 1.2). It was first described by J.D. Hooker in 1853 from Mount Hikurangi material provided by William Colenso in 1844; subsequently three varieties have been described (Allan 1961). The variety *colensoi* occurs north of 43°S, the variety *argentea* south of 43°S, and variety *grandis* on Stewart Island and some southern islands (Wardle *et al.* 1971) (Fig. 1.3).

Olearia colensoi is abundant on the wetter mountains of New Zealand where in the absence of *Nothofagus* species it is often dominant at the treeline. On drier mountains it is absent or confined to exceptionally moist sheltered habitats such as deep gorges (Wardle 1986). It is extensively dominant in the subalpine zone in high rainfall areas on the axial ranges of the North Island, the westernmost ranges of the South Island, and on Stewart Island (Wardle *et al.* 1971). In the North Island it is found on the Raukumara, Huiarau, Ruahine, Tararua and Rimutaka Ranges. In the South Island it is abundant on the western side of the island but rare on the drier eastern side (Eagle 1986). In Central Westland *O. colensoi* dominates on sites with impeded drainage, shaded southerly aspects, and on the fog-bound westernmost ranges (Wardle 1991).

FIGURE 1.2 *Olearia colensoi* in flower; photo taken in late January 1990 at Wharite Peak (920m). Pappus hairs are visible and achenes are starting to be shed .

In the mountains *O. colensoi* is a closely branched shrub up to 3 metres tall; at its southern range, where it occurs down to sea level, it grows as a tree up to 10 metres in height (Eagle 1986). *Olearia colensoi* has light-brown papery bark, the branchlets are covered in woolly buff coloured hairs. The leaves are thick and densely tomentose abaxially with white to buff coloured hairs. The disc florets are yellow or deep red (Eagle 1986). *Olearia colensoi* has the ability to spread vegetatively (Wardle *et al.* 1971). Layering is more common on steep slopes where plants commonly lie down-slope with branches and stems taking root at points of ground contact. Sexual reproduction is however more common and successful seeding has been recorded over most of its altitudinal range in the Tararua Range (Field 1968). Flowering is irregular resulting in heavy flowering and seeding (mast) years every three to five years.

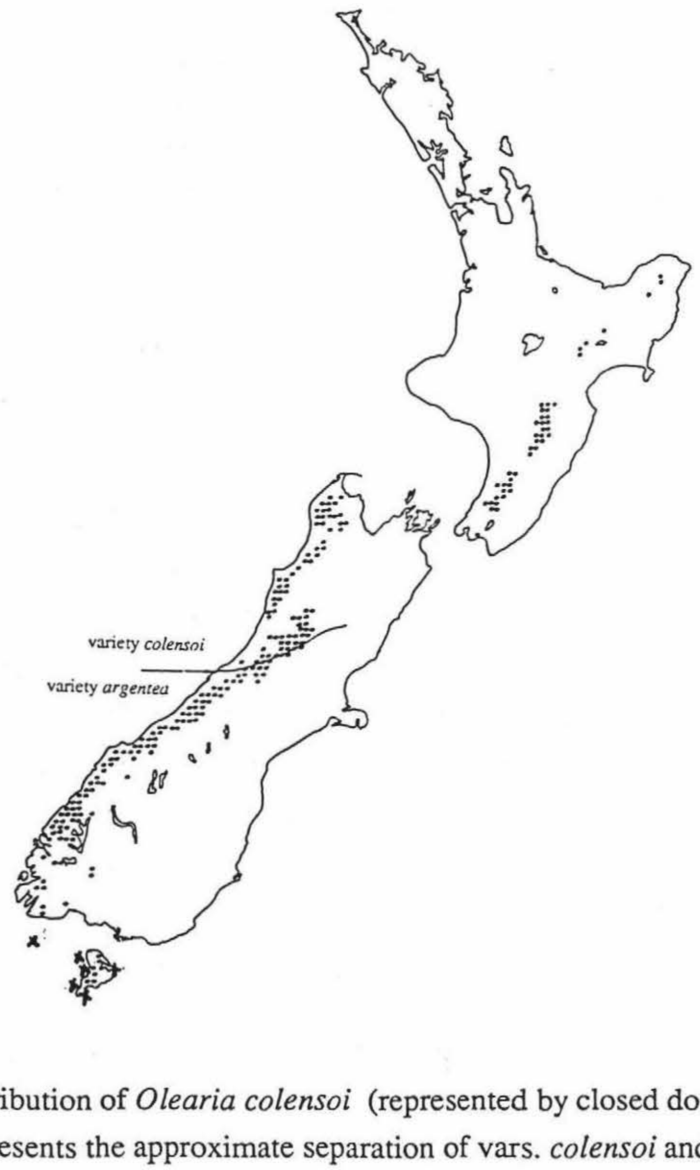

FIGURE 1.3 Distribution of *Olearia colensoi* (represented by closed dots). The line drawn at 43°S represents the approximate separation of vars. *colensoi* and *argentea*. *O. colensoi* var. *grandis* is represented by 'x' and occurs only on Stewart Island and some southern islands. (Adapted from Wardle *et al.* 1971).

Vegetation change in the southern Ruahine

A number of vegetational dissimilarities exist between the southern Ruahine and northern areas of the Range, particularly in the upper altitudinal limit of a number of tree species (lower for *Dacrydium cupressinum, Podocarpus hallii, Libocedrus bidwillii, Halocarpus biformis,* and higher for *Weinmannia racemosa*). A major vegetational dissimilarity is the virtual absence of *Nothofagus* from the southern Ruahine. Isolated pockets of low altitude *N. solandri* var *solandri* occur on the western side of the range and *N. fusca* in the very north (Takapari Peak-upper Tamaki area) but *N. menziesii* and *N. solandri* var *cliffortioides* are completely absent.

In the southern Ruahine leatherwood has spread down-slope over the last 30-40 years and has been considered to behave as an opportunistic weed (J.P. Skipworth *pers.comm.*). The increase in leatherwood abundance is part of extensive vegetation change that has occurred throughout the southern Ruahine since the 1920s (Cunningham 1979). This change has been particularly apparent in the montane *Weinmannia racemosa* forests where widespread die-back occurred during the 1950s to 1970s. Decline in *Libocedrus bidwilli* and *Halocarpus biformis* formations have also been significant (Elder 1965) and have been replaced in part by down-slope spread of *O. colensoi.*

The Ruahine forests were considered to be generally in good heath prior to 1920 (Cunningham 1977, 1979). Since 1920 deer, possums and goats have had a 'profound and deleterious effect on the forests throughout the range' (Cunningham 1979). Possums were first liberated in the range in 1893 and red deer in 1908. A number of subsequent liberations occurred with deer liberated at Delaware in 1922 and goats at Opawe in 1925 (James 1973). Introduced animals, possums in particular, were held by most workers to be the prime causal agent in the *Weinmannia racemosa* forest deterioration and its subsequent replacement by a mixed low vegetation of *Pseudowintera colorata, Cyathea smithii, Rubus cissioides, Histiopteris incisa, Cortaderia* and *Microlaena avenacea* (Cunningham 1979). Decline of *Libocedrus bidwilli* and *Halocarpus biformis*, however, was not as easily explained as these were not highly preferred browse species and did not suffer the same degree of animal damage. Decline in *Libocedrus bidwilli* and *Halocarpus biformis* had been noticed before the population explosions of animals occurred and was thought to be the result of long term climatic change (Elder 1965).

Since a 1982 paper by Veblen & Stewart on *Metrosideros umbellata-Weinmannia racemosa* die-back in Westland there has been greater acceptance of factors other than animal browse being involved in forest dieback. Natural stand dynamics were seen as the underlying predisposition for forest die-back, possums being only one of a number of possible triggering factors in processes that could have occurred without them. Natural stand dynamics involves the synchronous establishment of trees on disturbed sites which gives rise to even aged stands, the trees in these stands reaching old age and a senescent stage simultaneously. These trees are then more susceptible to fungal pathogens, insects, droughts, severe frosts, and browsing, and it only requires one or a combination of these factors to trigger widespread mortality.

Forest dieback has now been studied in a number of different forest types through out New Zealand, and has generally been attributed to natural phenomena; often drought induced (Hosking & Hutchinson 1986, 1988, Skipworth 1983, Jane & Green 1986, Allen & Rose 1983). Three major drought periods have been identified as the instigating factor in forest dieback episodes in some parts of the Ruahine and elsewhere in the North Island (Grant 1984, Jane & Green 1986). These were in 1907-08, 1914-15 and 1945-46; of the three the 1914-15 drought had the most severe effect. A drop in the timberline in the Waipawa basin (central Ruahine) is attributed to the 1914-15 drought (Grant 1984), the area between the old and new treeline having been filled by leatherwood (predominantly *O. colensoi*) with some *Chionochloa.* These forest die-back events in *Weinmannia, Libocedrus* and *Halocarpus* have generally resulted in a lower tree line in the southern Ruahine, which has allowed the proliferation of shrub species particularly *Pseudowintera colorata* and *O. colensoi.* It is this range expansion of *O. colensoi* that has been particularly apparent and has contributed to the already extensive sub-alpine scrub noticeable for its virtual monotypic canopy structure and impenetrability.

The southern Ruahine has in the last fifty years passed through dramatic periods of erosion and vegetation change which have presented problems to land managers and scientists alike in attempting to unravel cause and effect. Interpreting the current complex vegetational patterns and the processes that have brought these patterns about is an essential prerequisite for management planning.

The leatherwood situation in the southern Ruahine poses a number of ecological questions:

> What features of the southern Ruahine have allowed the current large sub-alpine scrub zone to develop and expand?
>
> What factors of the vegetative strategy of *O. colensoi* have allowed it to succeed as a virtual monocultural species?

What are the phenological characteristics of mast flowering in *O. colensoi* and does this masting behaviour contribute to the success of *O. colensoi* ?

Is the southern Ruahine significantly different from other sub-alpine scrub areas?

AIMS OF THE STUDY:

This research focused on autecological and synecological aspects of *O. colensoi* and its success in the southern Ruahine.

The aims of this study were:

-to explain the competitive success of *O. colensoi,* by examining the autecology of *O. colensoi,* in particular :

- phenology of vegetative growth and flowering
- the factors that impinge on floral initiation and anthesis
- the phenomena of mast flowering, and how this may be linked to the reproductive success of *O. colensoi.*

-to interpret some of the changes that have occurred in the leatherwood scrub, particularly at the ecotone between the leatherwood formation and the 'vestigial' *Libocedrus-Halocarpus* forest formations, as a step toward understanding community processes at work in the southern Ruahine, and in particular the successional status of *O. colensoi* .

-to make predictions of the future status and changes in the subalpine vegetation, whilst accounting for the dominance of *O. colensoi* in the southern part of the Ruahine range.

-to compare the southern Ruahine leatherwood communities with other leatherwood formations to evaluate the ecological significance of the southern Ruahine situation.

This research is presented in the following chapters. Chapter 2 describes the southern Ruahine in detail. Chapter 3 presents the results of investigations into localised climatic conditions for seven sites in the southern Ruahine, used in the interpretation of floral phenology. The autecological investigations into *O. colensoi* focus on vegetative growth and productivity (Chapter 4) and floral phenology and other aspects of the reproductive success of *O. colensoi* (Chapter 5). Synecological aspects of leatherwood formations are then considered (Chapter 6) followed by a general discussion of the role of *O. colensoi* in the southern Ruahine (Chapter 7).

CHAPTER 2

THE SITE - THE SOUTHERN RUAHINE RANGE

The southern Ruahine Range has a number of physical, climatic and vegetational characteristics that set it apart from the rest of the Ruahine Range (Elder 1965) and most other mountain areas of New Zealand. This chapter describes the geography, geology, soils, vegetation and human history of the area. Climate and weather in the southern Ruahine are discussed in Chapter Three.

LAND TENURE

Most of the southern Ruahine Range (down to 500 metres) is within the Ruahine Forest Park gazetted in 1976. Since 1987 the park has been administered as a 'Conservation Park', under section 61 of the Conservation Act 1987, by the Department of Conservation (currently by the Hawke's Bay Conservancy).

GEOGRAPHY

The southern Ruahine is part of the chain of North Island axial ranges stretching from Cook Strait through the Tararua, Ruahine and Kaweka Ranges to the Central Volcanic Plateau (Fig 2.1). The southern Ruahine area is well defined by natural topographical features that separate it from the rest of the Ruahine Range. The area is a long plateau tilted away from an abrupt scarp in the east to a less defined scarp in the west and runs north from the Manawatu Gorge to the Pohangina Gorge and the Apiti-Norsewood saddle. The highest point is Takapari Peak at 1257m. The range decreases in average height southwards to Wharite Peak at 920m before dropping off into the Manawatu Gorge. The topography of the area has been described by Mosley (1977) as rapidly down-cutting, with deepening valleys from removal of support from the toes of the valley slopes and exhibiting a youthful unstable topography.

GEOLOGY

The bedrock in the southern Ruahine range consists of non-schistose sediments (greywacke) of Triassic-Jurassic age that are part of the Torlesse Supergroup (Marden 1981). The rocks are mostly interbedded grey sandstones and siltstones with dark argillites, and less commonly sandstones and mudstones, detrital conglomerates, limestones, cherts and volcanic associations (Marden 1981).

Geologically the Ruahine is a relatively young mountain range, with intense faulting and shattering of already folded strata. The rate of uplift may have been as high as 4.5mm per year over the last 0.8 million years (Boellstorf & Te Punga 1977). The greywacke rocks characteristic of the area are easily eroded and this in conjunction with the high rainfall climate renders the southern Ruahine Range inherently prone to erosion (Cunningham 1978).

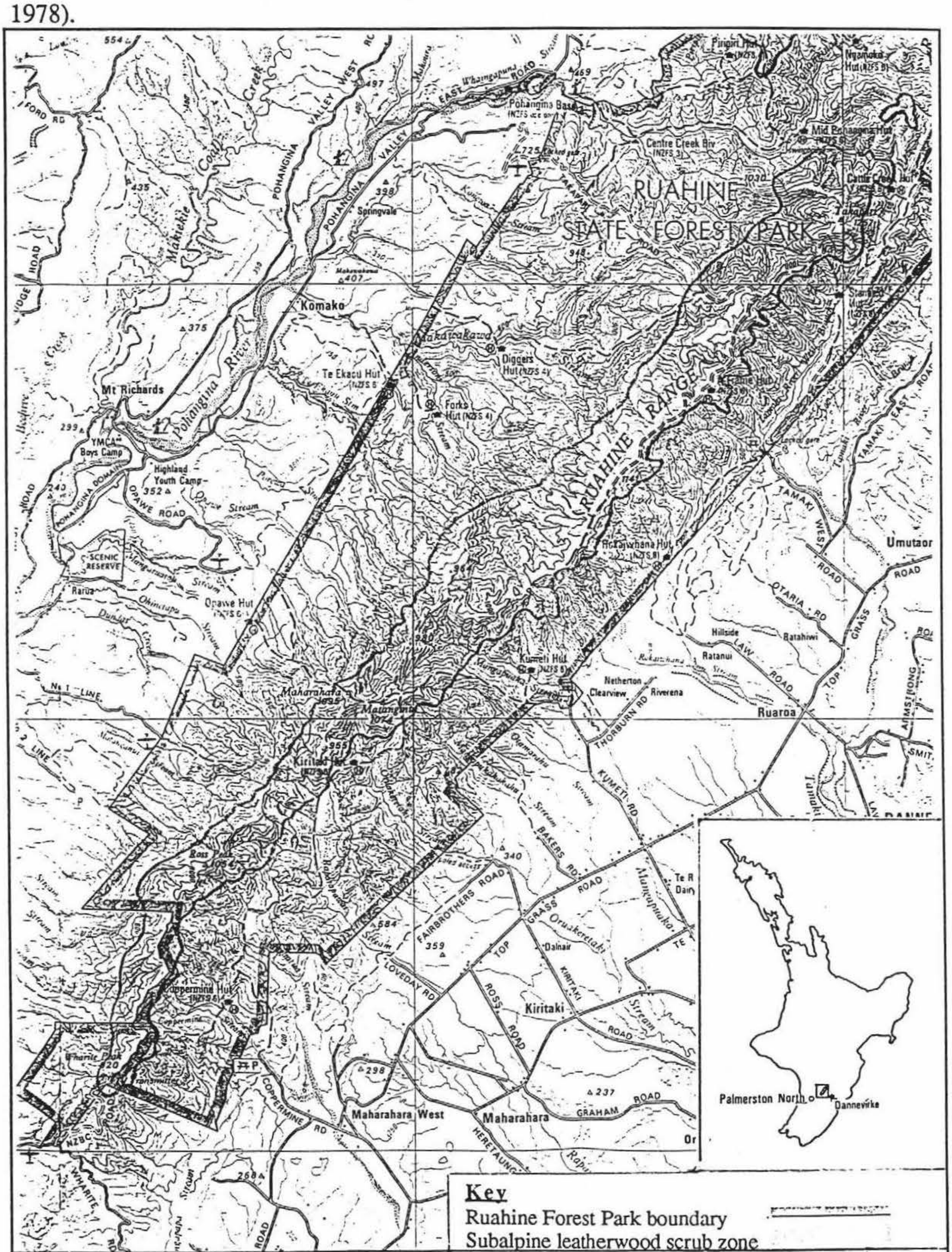

FIGURE 2.1 Map of the southern Ruahine Range study area showing principal place names and features mentioned in the text. Base map NZMS 274/5 1984 Ruahine State Forest Park NZ Forest Service & Dept Lands & Survey

SOILS

The soils of the Ruahine Range occur on a number of parent materials, ranging from peat with tephric loess to basement greywacke, and including loess derived from greywacke, colluvium, scree deposits and shattered greywacke fault zones. These together with a variety of slope classes and variations in rainfall give a complex soil pattern, the profile development of these soils being controlled by past and present erosion events (Hubbard 1981).

The distribution of soils in the southern Ruahine shows a relationship to topography and elevation (Hubbard 1981). Well-drained stony silt loam soils occur on low river terraces. Gravelly, infertile soils prone to scree and slip erosion occur on the steeper mountain slopes, and organic soils occur on the plateau surface in the centre of the study area at elevations over 1000m; these soil types have been described by Hubbard (1981) as follows:

Ruahine steepland soils; occur at elevations of up to 1100m on greywacke parent material (Hubbard 1981). Rijkse (1977) describes the profile as generally shallow and stony, liable to severe slip and scree erosion. Some of these soils are under forest.

Renata silt loam and Renata hill soils; occur over the same elevation range as the Ruahine steepland soils but are formed in a loess unit, derived from greywacke, over lying a greywacke basement. The Renata silt loam has an iron pan at depth and supports forest.

Rimutaka steepland soils; extend to the highest elevations in the southern Ruahine Range, experiencing annual rainfall of 2300mm or more. The profile is strongly leached, and typically shallow with a thin mottled B horizon and also supports forest.

Takapari peaty loam and Takapari hill soils; occur at elevations of 1070 to 1370 metres with rainfall of greater than 2300mm per year, and a cold climate (mean annual soil temperature less than 8°C), This peaty loam has formed in a loess unit capping the gently rolling greywacke plateau of the southern Ruahine. Organic matter has built up slowly under *Olearia colensoi* vegetation. Some peat bogs occur in hollows and depressions in the plateau supporting *Chionochloa.*

Soils of the Takapari Plateau leatherwood area

The upper plateau of the southern Ruahine Range is stable with little or no mass movement (Hubbard *et al.* 1980). The tephrostratigraphy and erosional history of a deep profile of Takapari Peaty Loam at the Delaware ridge was examined by Hubbard *et al.* (1980). The profile showed a thin continuous layer of coarse ash at 60 cm depth which was identified as Taupo pumice (eruption date 1819±70 yrs B.P.). Another layer of thin continuous ash at 87cm was identified as Waimihia Formation (3420±70yrs B.P.) From the ash markers it is inferred that soil above 87cm has accumulated over the last 3440 years. During the 1600 years between the two eruptions 27cm of soil accumulated and 60 cm of soil has accumulated in the last 1800 years since the Taupo eruption. Prior to 3440 years ago either no soil development occurred or it was subsequently lost through erosion; Hubbard *et al.* (1980) suggested that the present period of soil formation initiated with peat accumulation over greywacke bedrock at about 3440 years ago. This was followed by a period of increased loessial deposition dominated by tephric material. Loessial additions then declined and organic accumulation continued as the main addition to the soil profile through to the present day. Their conclusion is that of erosional stability on the plateau for the last 4600 years with widespread stripping of the summit prior to that time due to the prevailing climatic conditions.

HUMAN IMPACTS

William Colenso was the first European to travel in the Ruahine Range. His routes when travelling from Hawkes Bay to the Rangitikei were variously through the Northern Ruahine or via the Manawatu Gorge guided by local Maori (Colenso 1884). Colenso heralded in an era of European activity that was to have strong impacts on the southern Ruahine. Land settlement and clearance for farming saw the removal of forest well up on to the flanks of the range to around 500 metres in both the east and west. Further inroads into the area were made in localised areas through logging, stock grazing and accidental burning. For the sub-alpine zone direct human impacts have tended to be confined to roading and tracking with the occasional spot fire. An extensive road was bulldozed into the southern Ruahine in the 1970s. This road travels up the Delaware ridge and then south along the main range for some ten kilometres. Current human activity is predominantly recreational hunting and tramping.

Some of the biggest impacts humans were to have on the area were via the introductions of browsing animals, such as deer, possums and goats, together with rabbits and hares which moved in from other areas. Red deer were liberated between 1908 and 1922 and several liberations of possums were made on both sides of the range from 1893 to the late 1920s (Oaks 1983). Animal numbers built up in the range leading to peaks in possum populations in the early 1950s and in deer about the same time (Cunningham & Stribling 1978). Canopy defoliation became apparent at this time and the density of animals and their effects on the vegetation became a concern.

At the same time as animal populations peaked and damage to vegetation became apparent, the range entered a period of increased erosion. The increased sediment loads of the rivers and deposits of gravel outwash onto farmland caused concern and prompted the Catchment Boards, Soil and Water Conservation Authority and the Forest Service to implement plans to try and stem the erosion. Strategies for animal control were implemented and attempts to revegetate slip areas were made. These revegetation attempts centred on the use of exotic species (Thomas 1984) and led to the introduction of a number of species which have now themselves caused some concern, particularly *Pinus contorta.*

VEGETATION

Vegetationally the southern Ruahine can be defined in three main altitudinal vegetation belts: podocarp-hardwood forest, *Weinmannia* forest (or its scrub replacement), and leatherwood (sub-alpine) scrub. Two smaller vestige formations also occur locally, namely *Libocedrus-Halocarpus* forest and *Chionochloa* tussock areas (Elder 1965). Podocarp-hardwood forest occupies the lower slopes on both sides of the range giving way, with increase in altitude, to what was once *Weinmannia racemosa* forest which in turn merges into leatherwood scrub with areas of *Halocarpus biformis*. In the north of the southern Ruahine *Nothofagus fusca* begins to replace *Weinmannia racemosa* on the middle slopes (Elder 1965). The leatherwood scrub is dominated by *Olearia colensoi*, its lower range margin intergrading in places with *Halocarpus biformis* and *Libocedrus bidwillii* which Elder (1965) considered to be the vestiges of a once prominent *Libocedrus /Halocarpus* forest. The other vestige formation of *Chionochloa pallens* occurs on Takapari interspersed with *Olearia colensoi* and on exposed ridges on Maharahara as well as some grassed basins of *Chionochloa rubra* on the plateau between Takapari and Maharahara (Elder 1965).

Vegetational dissimilarities between the southern Ruahine and northern areas of the range include a drop of 150m in the upper limit of a number of species particularly *Dacrydium cupressinum, Podocarpus hallii, Libocedrus bidwillii, Halocarpus biformis, Brachyglottis elaeagnifolia, Coprosma foetidissima* and *Chionochloa conspicua* (Elder 1965). *Weinmannia racemosa* however reaches a higher altitude than further north. *Nothofagus* species are absent from the upper slopes of the southern end of the Ruahine. *Weinmannia* forest or *Libocedrus bidwilli* and *Halocarpus biformis* formed the tree line in the absence of beech.

Changes in the vegetation have been marked since 1950. Elder (1965) had difficulty in describing the vegetational belts of the southern Ruahine because of this state of change, and changes have continued since his description. The following account uses his description as a base line against which the current vegetation is described.

LOWER ZONE (350m to 700m): *Dacrydium cupressinum -Metrosideros robusta* forest. Before 1950 large emergent *Dacrydium cupressinum* and *Metrosideros robusta* trees characterised this zone which can be subdivided into two sub-altitudinal zones; 350-600m and 600-700m. In the 350-600m zone *Beilschmiedia tawa* is a common component that has increased in extent. *Metrosideros robusta* has however been declining in extent since 1950 probably due to the depredations of possums which preferentially browse it. Emergent *Dacrydium cupressinum* remain as the main physiognomic feature of this zone. There is an abundance of lianes and epiphytes particularly *Ripogonum scandens*. Small isolated pockets of *Nothofagus solandri* var. *solandri* occur below 400m in the west above the Pohangina valley.

MIDDLE ZONE (700-920m): *Weinmannia* forest
This altitudinal zone has undergone the most dramatic change with virtual collapse of this forest throughout the southern Ruahine and replacement by a tangle of shrubs and tree ferns. Prior to 1950 *Weinmannia racemosa* was the dominant canopy species in this zone. *Prumnopitys ferruginea* was an associated species in the lower part of this zone and *Podocarpus hallii* in the upper part. Emergent podocarps still remain in some areas while the *Weinmannia* component has all but disappeared from many areas. *Libertia pulchella*, *Luzuriaga parviflora* and *Leptopteris superba* were characteristic associated species both before and after the *Weinmannia* collapse. The current physiognomic vegetation types tend to be dominated by *Pseudowintera colorata* scrub with some *Olearia colensoi* areas in the upper regions, mixed *Pseudowintera-Cyathea-Coprosma* scrub in lower regions, and localised *Fuchsia* scrub in some steeper gullies.

UPPER ZONE (900m and above): The sub-alpine (leatherwood) scrub
Almost the entire crest of the southern Ruahine is occupied by leatherwood scrub. Of the two species commonly described as leatherwood and often found occurring together it is *Olearia colensoi* that is the virtual monospecific dominant. Elder (1965) describes *Brachyglottis elaeagnifolia* (the other leatherwood species) as being more dominant at lower altitudes. Today *Brachyglottis elaeagnifolia* is most common in the lower part of the zone but only becomes dominant on recently disturbed sites such as track and road cuttings.

Two other vegetation types that warrant a description are the *Libocedrus/Halocarpus* forest and *Chionochloa* grassland. These are vestigial formations that Elder (1965) describes as 'mere ghosts' of their former extent. *Libocedrus/Halocarpus* forest approaches dominance at around 900m in some areas of the southern Ruahine particularly the Delaware Ridge. Other areas of similar altitude at Opawe and Pretender have virtually totally died out. *Chionochloa* grassland occurs as scattered areas on the highest peaks (Takapari and Matanginui), where *Chionochloa pallens* grows interspersed with *Olearia colensoi*. On the Takapari plateau a number of tussock basins exist dominated by *Chionochloa rubra*. These basins are mostly quite small in extent the largest being about 1.5 hectares but appear to be vegetationally stable.

A full list of vascular species occurring in the southern Ruahine sub-alpine zone is contained in Appendix 1.

CHAPTER 3

CLIMATE OF THE SOUTHERN RUAHINE RANGE

INTRODUCTION

Climate is a dominant factor in the ecology of mountain forests (Baumgartner 1980). It governs tree regeneration, stand formation and structure, species composition, growth habit of plants and biomass production. The atmospheric environment also has the ability to severely damage individual plants during all phases of their life cycle (Baumgartner 1980). This chapter reviews the data already published on the climate of the Ruahine Range and then presents the results of an investigation into site specific meteorological conditions in the southern Ruahine Range, focusing on sites studied for vegetative and floral phenology in later chapters.

The day-to-day weather of the Ruahine range is produced by a regular series of anticyclones and depressions moving eastward off the Tasman sea (Burgess 1989). The predominant wind flow is westerly. Winds are affected by the range causing deflections and local funnelling; wind speed increases through gaps such as the Manawatu Gorge.

The majority of anticyclones passing over the area have centres just to the north of the North Island; thus the predominant airflow reaching the range is between north-east and south-west. The westerly air-streams are lifted over the Ruahine Range and a build-up of cloud and associated orographic rainfall can spread westward from the ranges to the coast and also spill over the range to the east (Burgess 1989). West to north-west air-streams usually bring showers, or moderate rain falls if a front also occurs in the flow (Burgess 1989). Strong westerly flows occur at any time of the year but are the strongest in the spring (September -November) persisting for 4-5 days (Burgess 1989). North to north-east air streams run mostly parallel to the range, giving warm cloudy weather with some rain or drizzle. East to south-east air-streams often bring heavy rainfalls in the range and to the east of the range, while the western side is more sheltered. South to south-east air-streams bring cold unstable showery weather over the range (Burgess 1989).

The following account summarises records (predominantly from Burgess 1989) of wind speed, rainfall, and frequency of rain-days for Wharite Peak Meteorological Station (in operation form 1966 until 1986) and compares these with the Palmerston North DSIR

Meteorological Station which is later used as the reference station for site comparisons within the southern Ruahine.

Wind

The wind direction and speed over the greater Manawatu area is strongly modified by the Ruahine and Tararua ranges and the Manawatu Gorge. North westerlies are persistent through the Manawatu Gorge and especially at Wharite Peak where they occur for over 50% of the time (Fig. 3.1). After north westerlies and westerlies the next most common winds in the range come from an easterly quarter.

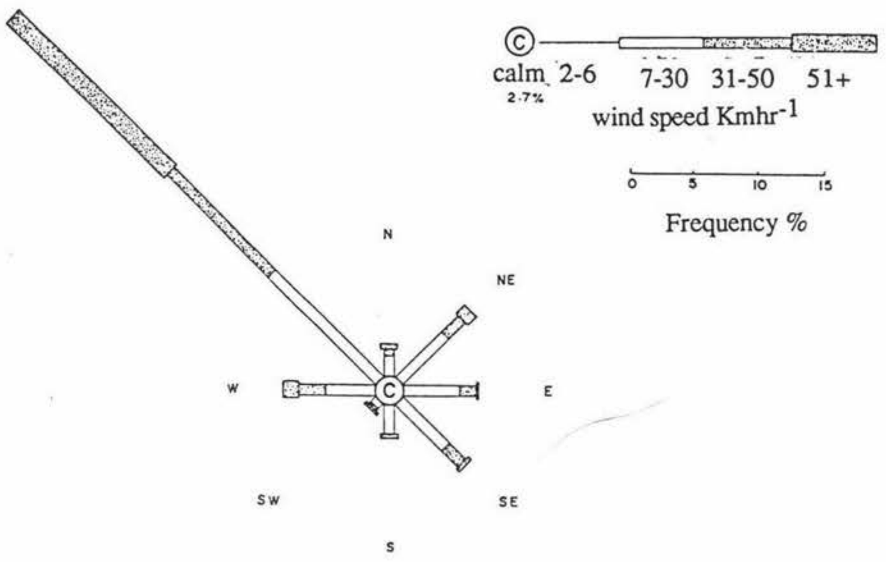

FIGURE 3.1 Wind rose for Wharite Peak Meteorological Station at 914m for the years 1966-1976, showing prevailing surface winds and mean daily wind speeds (adapted from Cunningham 1978 and Burgess 1989).

At Wharite Peak mean wind speeds are among the highest recorded for any meteorological station in New Zealand. The mean daily wind speed at Wharite (1966-1980) is 44 km hr^{-1}, while exposed coastal and lowland areas in the Manawatu have average wind speeds of 15 -18 km hr^{-1} and Palmerston North (DSIR) averages 11 km hr^{-1} (Fig 3.2). Wind speed has a large local variation in the range due to the complexities of the local terrain. The strongest winds at Wharite occur in the spring but the seasonal variation in wind speed is small (Fig 3.2). In most lowland and coastal areas gales (mean wind speed over a ten minute interval of >63 km hr^{-1}) occur on average on 3 to 7 days per year; at Wharite Peak they occur on average on 80 days per year (Burgess 1989). Thompson (1982) estimated gales to occur 17 % of the time in the ranges. Winds of gale force can persist for periods of a week or more in the range. High wind gusts are most frequent over exposed ridges and summits, especially when perpendicular to the wind. At Wharite they exceed 90 km hr^{-1} on 133 days a year compared with 10 days per year for coastal Manawatu.

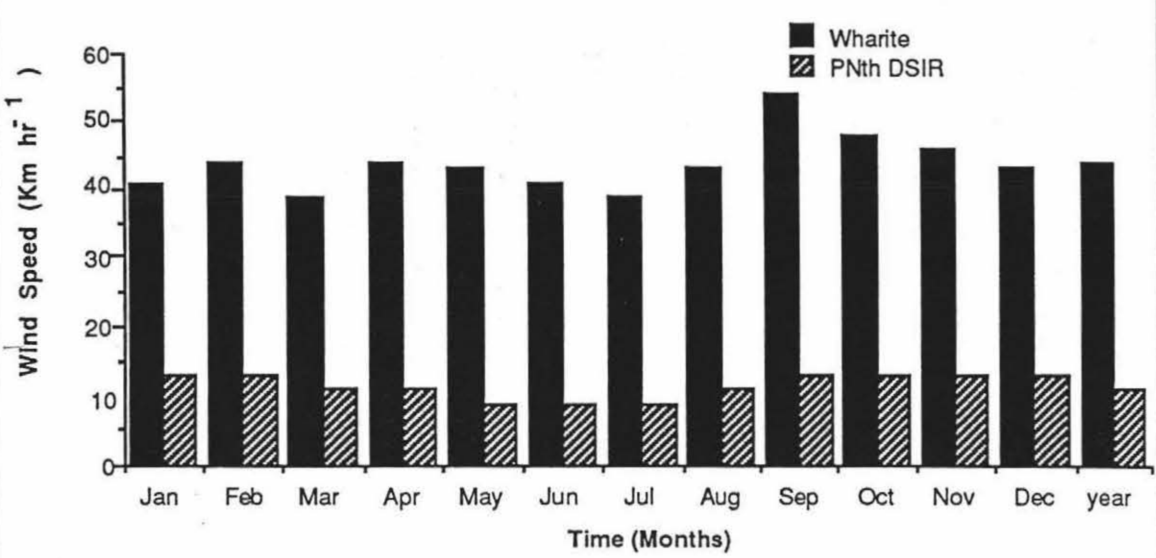

FIGURE 3.2 Mean daily wind speed (km hr^{-1}) per month and per year for Wharite Peak (1966-80) and Palmerston North DSIR (1928-84) Meteorological Stations (data from Burgess 1989)

Precipitation, Fog, Cloud and Humidity

The Ruahine Range lies in a south-south-westwards direction; thus regions in its lee to the east are significantly drier and sunnier than those on the west of the range exposed to the predominant westerlies.

Annual rainfall totals in the southern Ruahine Range are over twice those recorded for lowland Manawatu and increase with increasing altitude (Table 3.1). Monthly rainfall shows less seasonality than lower sites (Fig 3.3). Rainfall of greater than 1mm day^{-1} occurs on average on 195 days a year at Wharite peak (Fig 3.4) and hail occurs on average on 2.8 days per year (Burgess 1989). Snow occurs on average 2-3 days each month from June to August at Wharite, totalling some 15 days per year. The highest recorded number of snow days occurred in 1976 (21 days).

Fog is reported for 220 days each year at Wharite. The high fog/cloud levels are a distinctive feature of the southern Ruahine (Burgess 1989).

Wharite records a lower average vapour pressure than lower altitude Manawatu sites and higher average relative humidity (Burgess 1989).

TABLE 3.1 Total annual rainfall from four sites in the southern Ruahine Range and for Palmerston North DSIR

site	altitude (m)	total annual rainfall (mm)	years	source
Palm Nth DSIR	30	991	1951-80	Burgess 1989
Wharite Peak	920	2165	1951-80	"
Delaware Ridge	945	2083	1976-86	Manawatu-Wanganui Regional Council
Traverse Hut	1065	3169	1976-86	"
Divide Repeater	1140	3590	1976-86	"

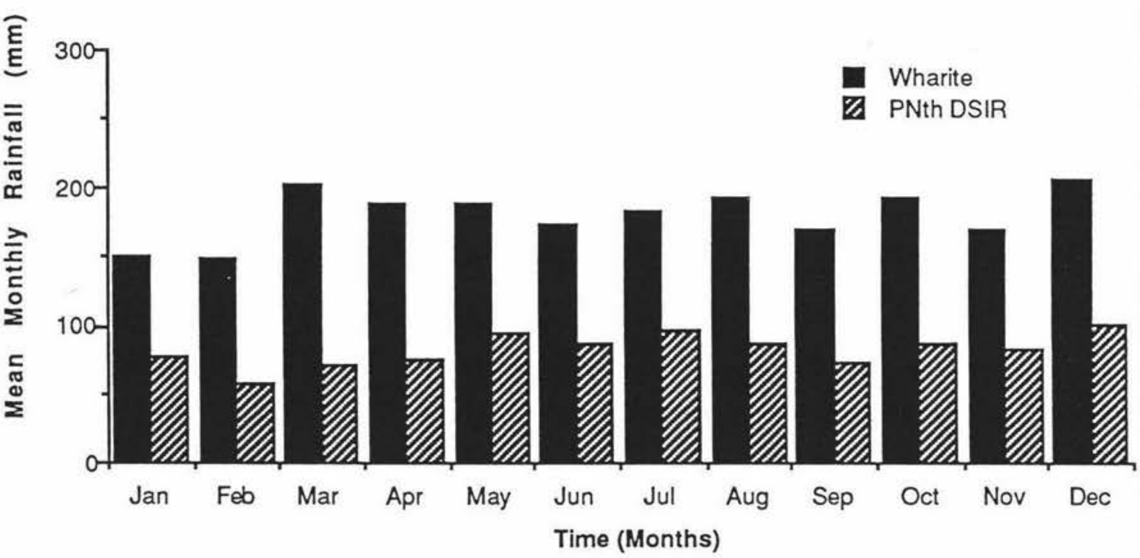

FIGURE 3.3 Average monthly rainfall (mm) during 1966-80 at Wharite Peak and Palmerston North DSIR Meteorological Stations. Average annual rainfall for this period was 2165mm at Wharite and 991mm at Palmerston North (data from Burgess 1989).

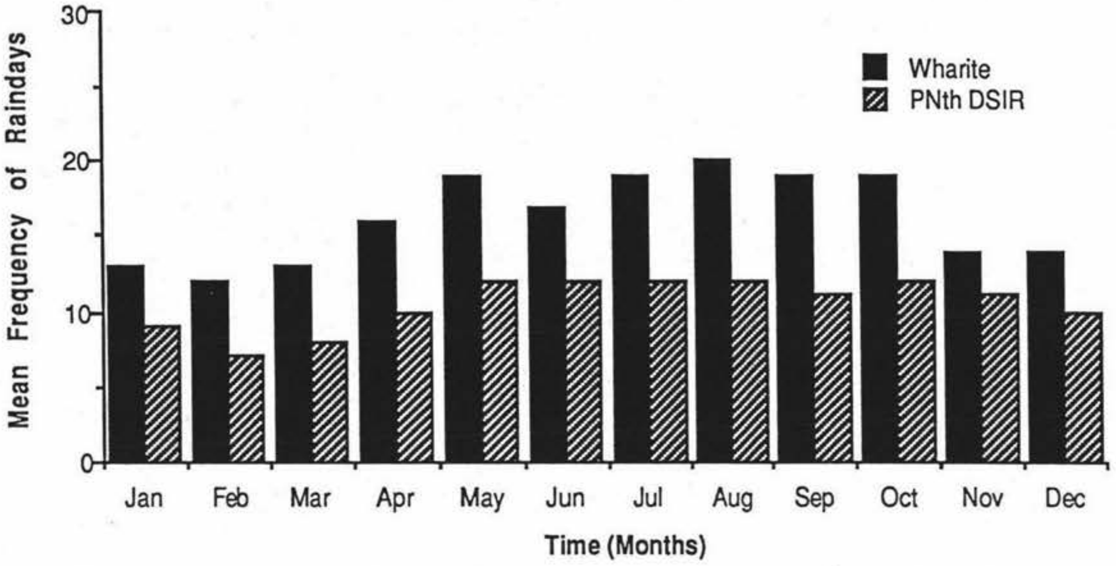

FIGURE 3.4 Mean monthly frequency of rain-days (>1mm day^{-1}), during 1966-80 at Wharite Peak and Palmerston North DSIR Meteorological Stations (data from Burgess 1989)

Temperature

Mean air temperatures decrease at the rate of approx 0.6°C for every 100m increase in altitude. Frosts can occur at any time of the year in the range (Burgess 1989).

METHODS

In order to obtain site specific meteorological information for interpreting phenological and phytosociological data, seven meteorological stations were set up in the southern Ruahine sub-alpine zone and monitored for one year.

Meteorological stations were set up at seven of the thirteen permanent plots described in greater detail later in Chapter 4). Five of these sites were in the Takapari area and were placed in a west-east sequence traversing the range thus giving an altitude-aspect sequence; the other two were on Wharite to give a geographical perspective over the southern Ruahine (Fig 3.5). The plots ranged from 1090m in the west to 1170m on the crest of the plateau and down to 1085m on the eastern side in the Takapari area, and 900m and 890m in the Wharite area (Table 3.2).

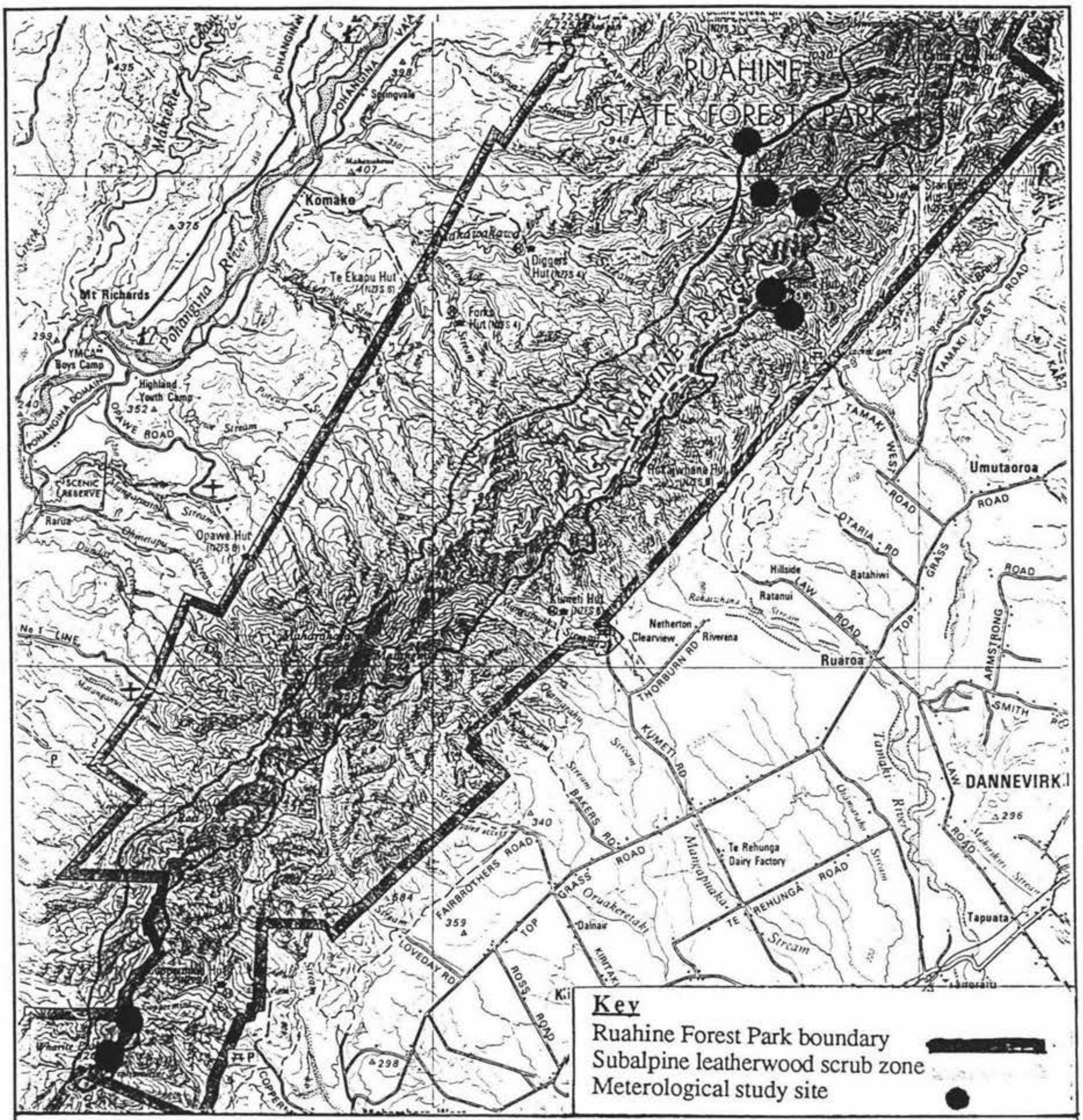

FIGURE 3.5 Location of seven meteorological study sites in the southern Ruahine Range. Base map NZMS 274/5 1984 Ruahine State Forest Park NZ Forest Service & Dept Lands & Survey

TABLE 3.2 Site details of the seven meteorological stations in the southern Ruahine. Grid references refer to map series NZMS 260 T23.

Station	Location	Grid ref	Alt (m)	Aspect
1	Takapari	655209	1090	140
2	Takapari	668197	1170	190
3	Takapari	678195	1175	270
4	Takapari	669175	1085	110
5	Takapari	672172	1000	40
6	Wharite	536024	890	90
7	Wharite	537028	900	170

At each site a modified Stevenson screen was set up 1.2m above ground level to house standard monthly thermohygrographs (Casella and Kato) with bimetallic temperature sensors and hygroscopic hair humidity sensors (temperature accuracy ± 1.5°C, humidity accuracy ± 5% over 20-90% relative humidity range). Four minimum-maximum mercury thermometers were placed at each site, one in the screen, one outside the screen at 0.5m height, and two buried at 25cm depth in the soil. Instruments were recorded over a full calender year from February 1990 to March 1991, at as close to monthly intervals as logistics allowed.

Temperature regimes

Monthly minimum-maximum records from the series of min-max thermometers were plotted and compared for all sites.

Daily minimum-maximum temperatures were transcribed from the thermohygrograph charts. The screen thermometer was used to calibrate the charts from the recorded temperature at chart placement and removal. Some problems were encountered with turntable stoppage on some of the Thermohygrograph machines due to the high humidity and cold conditions. This created gaps in the continuity of the records at some sites. To circumvent this discontinuity, comparative analysis of the site data was conducted in two parts.

- Data from those periods when <u>all</u> machines where functioning correctly (49 days) were analysed and compared for all sites. Average minimum, maximum, and daily mean temperatures were calculated and compared between sites and against other site attributes (altitude, aspect, slope)
- Temperature records from the DSIR Palmerston North Meteorological station were used as a base line to calculate the daily average difference in minimum, maximum, and mean temperatures between the DSIR station and each of the Ruahine sites for all days for which records existed. Comparative analysis of between-site differences was then conducted using these averages.

Precipitation

A series of rain gauges was set up at each of the meteorological station sites. Gauges were of cylindrical design with a mouth opening of 150mm and a height of 750mm. Additional compact glass storage gauges were deployed at some sites; these had a mouth opening of 19.5mm and a storage capacity of 375cm^3 (equating to a recording capacity of 1280mm of precipitation). An oil film was used in both types of gauges to prevent evaporative loss. At site 4 (Table 3.2, Fig 3.5) three gauges were set up to investigate differences in capture of precipitation between vertical and inclined gauges to estimate the amount of precipitation arriving at an inclined angle due to the prevailing wind rather than vertically. One gauge was vertical, one was inclined 20^{o} from vertical and facing west and one was inclined 20^{o} from vertical and facing east.

Wind / Exposure

Tatter flags were set up at each site. Tatter flags have been used as an inexpensive effective way of measuring exposure by measuring the fraying rate of a standard square of cotton material (Rennie 1980, Rutter 1968). Standard flags (380 x 310mm) were used to the specifications outlined in Rennie (1980). Modification of the pole design by addition of a metal vane was made part way through the study to try and overcome problems of flags wrapping around the supporting pole.

RESULTS

Temperature regimes

All sites showed consistent variation in temperature regimes. The timing of daily fluctuations in temperature was almost identical over all sites, however the actual temperature and the magnitude of the movements (e.g., minimum / maximum) varied consistently between the sites (Fig. 3.6).

The difference between the yearly average minimum and maximum temperatures of each of the southern Ruahine sites and Palmerston North (DSIR) over the full 360 days of recording showed consistent variation between sites and was significantly positively correlated with altitude ($r=0.99, p>0.001$ and $r=0.98, p>0.001$ respectively) (Fig. 3.7). The difference in daily minimum temperature between Palmerston North and the southern Ruahine increased at a faster rate than the difference in daily maximum temperature (Fig. 3.7).

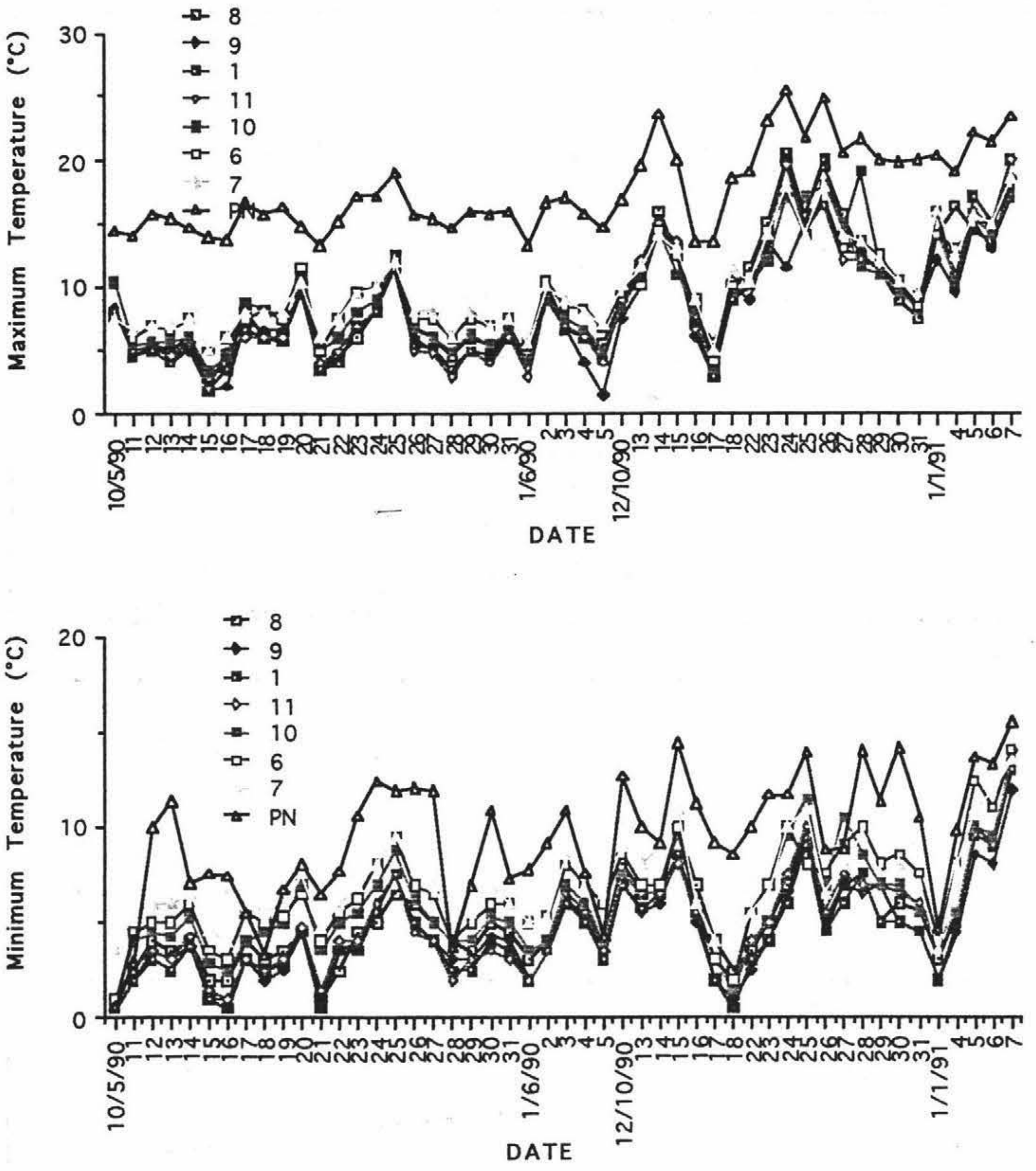

FIGURE 3.6 Mean daily minimum (lower graph) and maximum (upper graph) temperatures for the seven southern Ruahine meteorological sites during the 49 days when all machines were functioning correctly; as an example of site variability. Palmerston North DSIR Meteorological Station included for comparison.

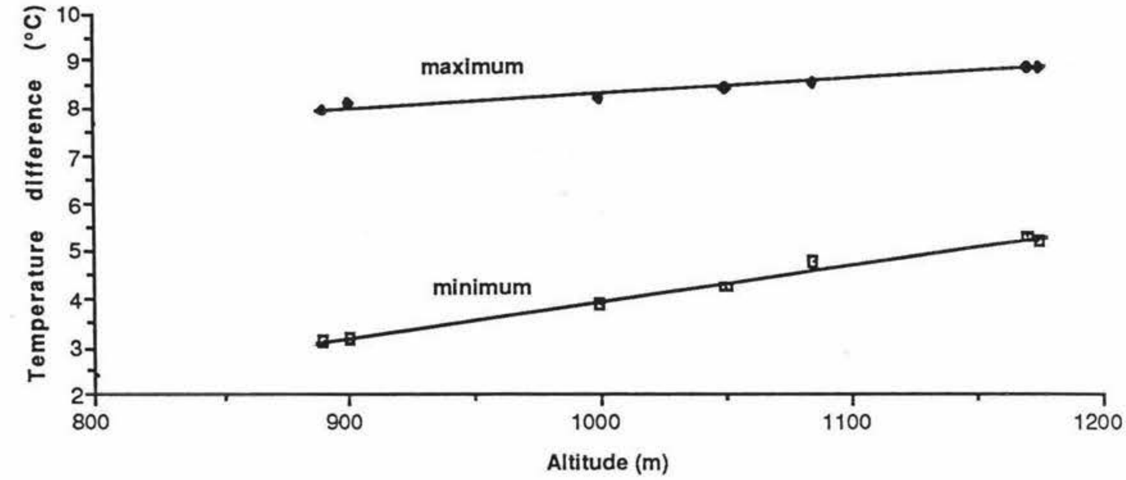

FIGURE 3.7 Difference between the yearly average minimum and maximum temperatures of each of the southern Ruahine sites and Palmerston North (DSIR) in relation to altitude.

The lapse rate of mean temperature between the Ruahine meteorological stations and Palmerston North was constant at 0.61°C per 100m. The average minimum and maximum temperature however lapsed at different and changing rates. The maximum temperature lapse rate decreased with increasing altitude and the minimum temperature lapse rate increased with increasing altitude (Fig. 3.8).

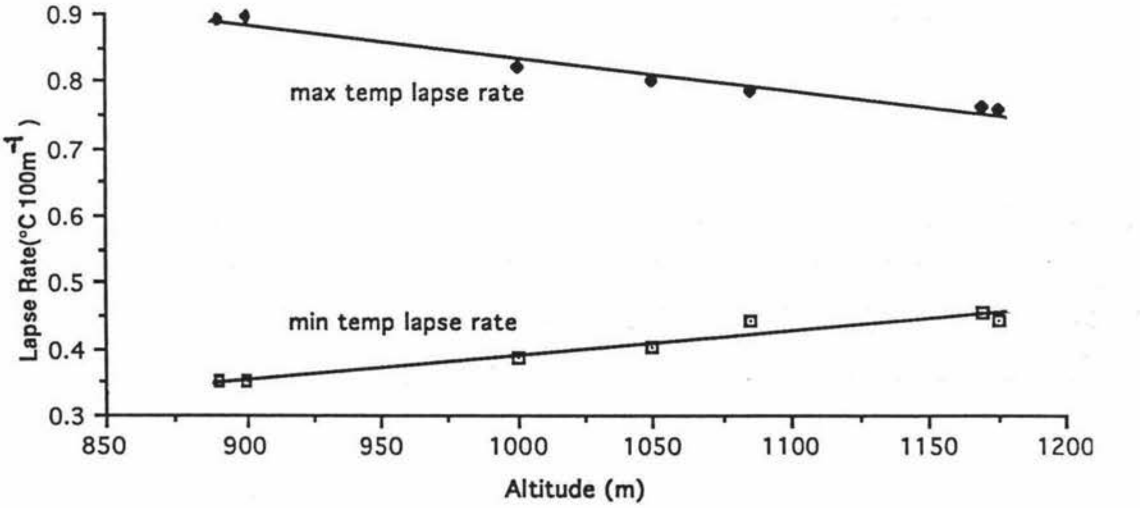

FIGURE 3.8 Maximum and minimum temperature lapse rates (°C $100m^{-1}$) between the study sites and Palmerston North (DSIR) Meteorological Station at 33 metres altitude. Mean lapse rate is constant at 0.61°C.

Precipitation

Mean rainfall increased with altitude between stations, ranging from 1665mm at 900m to 2703mm at 1170m (Fig 3.9), an increase of 3.8mm m^{-1}. The glass storage gauges at Site 4 showed marked differences in precipitation collected depending on the angle and direction of inclination. The gauge inclined 20^{o} (from vertical) to the west collected on average 80% more precipitation then the gauge inclined 20^{o} to the east, and 66% more than the vertical gauge.

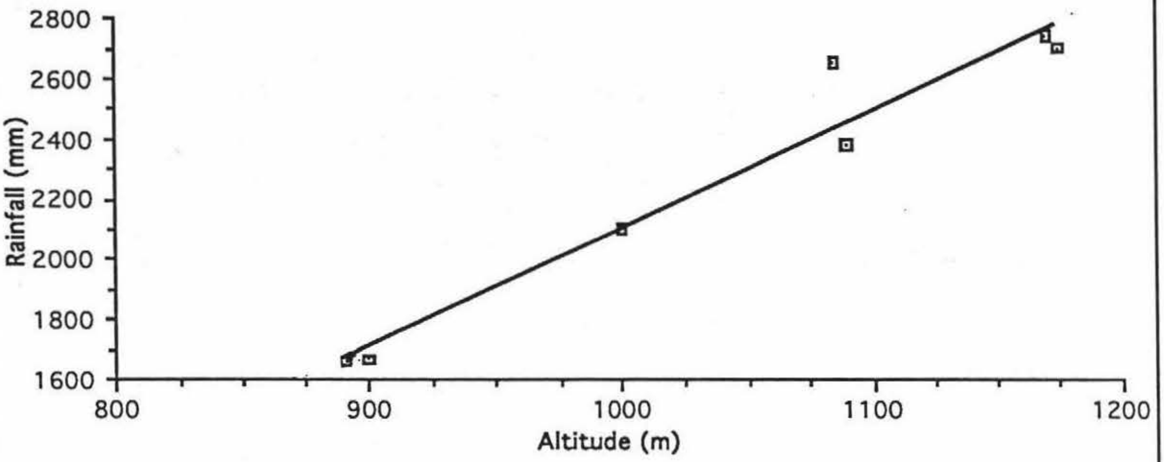

FIGURE 3.9 Mean annual rainfall for seven meteorological stations in the southern Ruahine, recorded from March 1990 - March 1991.

Wind / Exposure

Results from the tatter flags were inconclusive due to the inability of the flags to cope with the extremes of wind and humidity encountered in the range. When wet the cotton flags wrapped around the support post and would set solid in this position if dried by the wind, not unfurling even with subsequent re-wetting. Modified flag poles had a metal vane attached to prevent the cotton flag wrapping; this placed too great a strain on the mounting point and on the stainless steel support rod causing these to bend and on the most exposed site the rod snapped in two.

Wind troughs in the leatherwood canopy running in parallel lines perpendicular to the prevailing wind direction are common in the southern Ruahine and are even discernible on high altitude aerial photos. In the most exposed sites the 2-3m wide troughs have physical breaks in the canopy where foliage has died. The troughs and breaks in the canopy advance in an easterly direction as the wind cuts in to the canopy along the break. The canopy along the western edge of the break does regenerate and so the break effectively moves slowly eastward giving the leatherwood canopy a wave appearance (Fig 3.10).

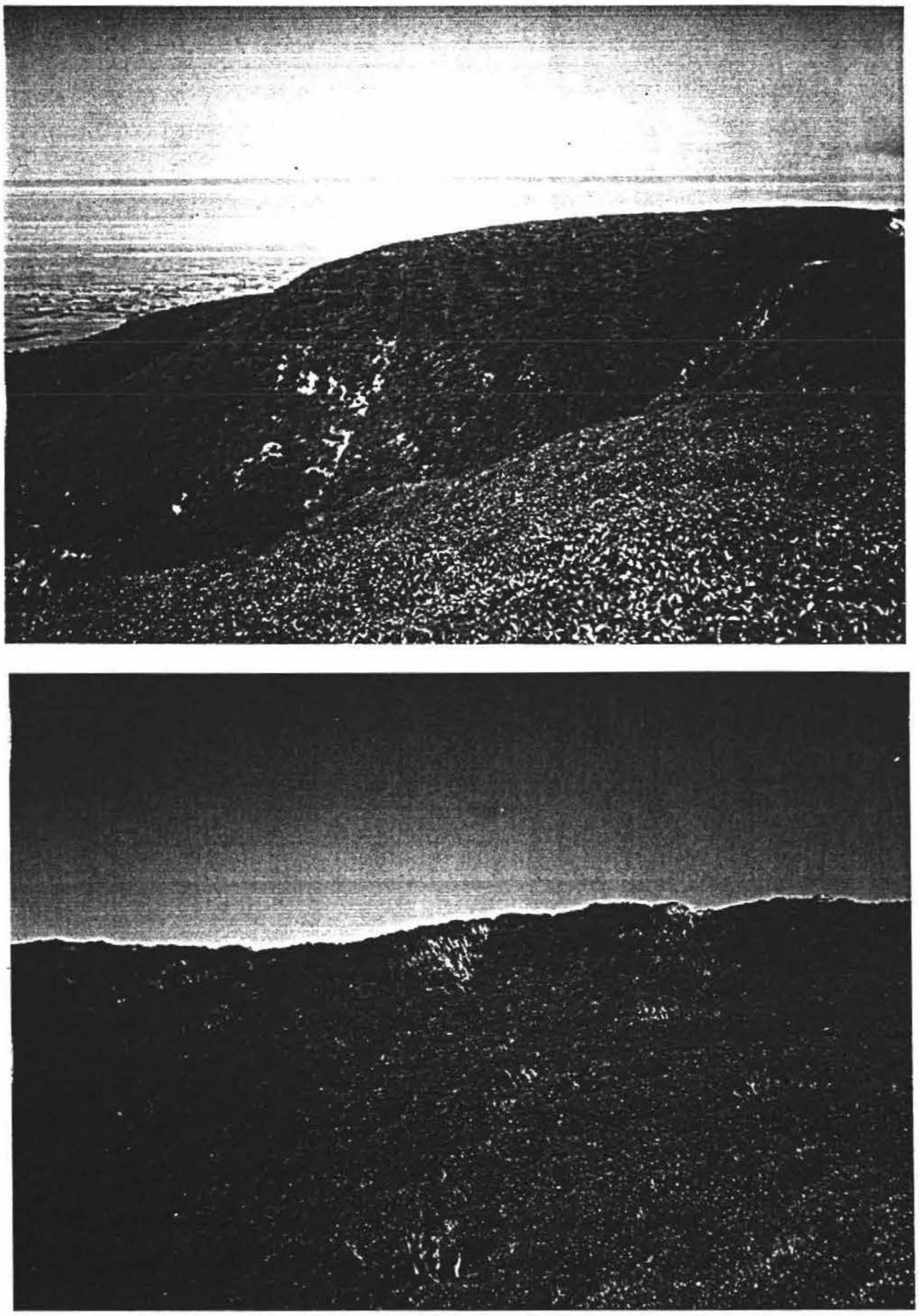

FIGURE 3.10. Wind caused 'waves' in the leatherwood canopy on the Takapari Plateau at 1170m. Troughs and breaks in the canopy can be seen running in parallel lines perpendicular to the prevailing (North-West) winds. The lower photo is a close up of the same site.

DISCUSSION

New Zealand has been broadly classified into three categories based on annual precipitation and fog/cloud cover and temperature (McCracken 1980). The southern Ruahine and the other main sub-alpine scrub areas of Mt Egmont, Mt Ruapehu, the Tararua ranges and the South Island West Coast, especially south of Arthur's Pass, all fall in the group of very high annual precipitation (2500 to 8000 mm) with long periods of cloud, fog and drizzle.

There is generally a lack of information on climate in the mountains of New Zealand (McCracken 1980). Much of the available mountain climate information stems from short term biological investigations. The longest running collection of mountain climate data comes from the Craigieburn Range starting in 1961 and is summarised by McCracken (1980). The annual mean lapse rate in the Craigieburn Range was 0.66 °C with the lowest lapse rates in the winter (0.42°C) and highest in the spring and summer (0.85°C in September).

The lapse rate of temperature calculated between two South Island meteorological stations (Black Birch at 1396m and Jordan at 305m - a 1091m difference) also had a mean lapse rate of 0.6 °C per 100m (Coulter 1967). The difference was much greater in summer than in winter and much greater for temperature maxima than for minima, the lapse rate being 0.9 and 0.8 for maximum and minimum respectively in summer and 0.8 and 0.3 in winter (Coulter 1967). Such recorded differences in minimum and maximum lapse rates have been little used, most studies only consider mean temperature lapse rates. The lapse rates found in the southern Ruahine concur with the results from these two South Island mountain areas. The differences in maxima and minima lapse rates are marked in the southern Ruahine and it would seem that these differential rates have a significant effect and provide information for more accurate interpretation of temperature effects in relation to plant growth phenomena. It is likely that minimum temperature thresholds, rather than mean or maximum daily temperature, are the main influence on plant growth phenomena.

Temperature differences between meteorological sites in the southern Ruahine were consistent with altitudinal differences at a lapse rate of 0.61°C $100m^{-1}$. Variations of topography, aspect, slope and consequent exposure, between sites, had no significant effect on the temperature regimes recorded. All seven sites, regardless of site physiography or aspect, showed the same trends in temperature fluctuations differing only in the magnitude of the temperatures. The southern Ruahine sub-alpine zone is then relatively uniform in respect to temperature regimes.

There was no detectable west-east gradient in rainfall over the sites measured, probably due to the narrowness of the range in the southern Ruahine and insufficient altitudinal difference between the western and eastern sites. A west-east gradient does exist at lower altitudes especially further north where the range is wider and higher creating a distinct rain-shadow to the east. Precipitation generally increases with altitude (Baumgartner 1980). The high frequency of cloud in the southern Ruahine, as well as adding significantly to total precipitation (Cunningham 1978), is most likely inhibiting plant growth through lowered light levels and influencing species distribution. Cloud and fog intercepted by plant foliage is a source of precipitation not recorded by standard rain gauges which are designed to catch falling droplets. It has been shown on some sites that the total annual precipitation can be more than doubled when fog is included (Grunow 1963 in Cunningham 1978, Lambrechtsen & North 1973). The results from the inclined rain gauges support these observations as it appears the gauge inclined to the west was intercepting water droplets (rain and cloud/fog) that were moving horizontally with the prevailing westerlies. The rainfall in the southern Ruahine is high when measured by standard rain gauge techniques but could be up to 66% higher when cloud interception is taken into account.

The southern Ruahine is extremely windy; this is apparent to any one working in the area and is borne out by meteorological records from Wharite Peak The attempt to quantify exposure differences between the sites using tatter flags failed due to the persistent high winds and high humidity conditions. Two sites where the stainless steel rod supporting the flags was bent or snapped corresponded with those subjectively assessed as the most exposed, due to a combination of increasing altitude and westerly aspect. Wind effects can be seen in the leatherwood canopy were parallel lines of canopy dieback are visible running perpendicularly to the prevailing wind direction. These striations are also visible in aerial photos of the leatherwood. Examination of these lines seems to indicate that the wind effects create these breaks in the canopy which advance in an easterly direction as the wind cuts in to the canopy along the break. The canopy along the western edge of the break does regenerate and so the break effectively moves slowly eastward with the prevailing wind much like a wave through water or a mobile sand dune.

The high winds, high cloud cover and high rainfall combine with the mountain temperature regime to produce climatic conditions more extreme than could be expected for the altitudinal and latitudinal range of the area. These extreme climatic conditions are the dominant factor in determining the type of vegetation cover and species composition in the southern Ruahine and are the main limiting factors of plant productivity in the Range.

CHAPTER 4

VEGETATIVE PHENOLOGY & PRODUCTIVITY

INTRODUCTION

Total biomass (living and dead material above and below ground) is often the most direct expression of how effectively a community occupies its site (Wardle 1991). Few total biomass studies of New Zealand vegetation have been published however, partly due to the difficulties in obtaining such data. Litter production is a component of total biomass that is easier to record and is often used as a measure of productivity (Bray & Gorman 1964, Lonsdale 1988).

In this chapter phytomass, litter production, stem radial increment and aspects of shoot phenology of *Olearia colensoi* were investigated.

METHODS

Thirteen permanent plots were established in the southern Ruahine sub-alpine scrub zone during February 1989. These plots were used to monitor aspects of vegetative phenology (this chapter) and floral phenology (Chapter 5). The plots were in three areas, Takapari, Maharahara, and Wharite (Fig. 4.1). Altitude and aspect sequences were established in the Takapari and Maharahara areas where plots were placed at the lower altitude limit of the leatherwood scrub zone on both western and eastern sides of the range and at middle and upper altitude sites. Two plots were established on the main divide in the Wharite area .

Restricted random placement was used for all plots, whereby plots were sited randomly within selected altitudinal-aspect areas. Three plots (T1, M2, and M3, Fig 4.1) were 10x10 metres and the remaining ten were 10x5 metres in size. For comparative purposes all plot data was standardised to $50m^2$.

The following environmental factors were recorded at each plot :

altitude
aspect
slope
physiography (face, ridge, spur, gully, knob, flat)

All canopy *Olearia colensoi* within the plot were tagged. The following measurements were taken for all individuals in the year they flowered:

basal circumference
length of plant (from initial rooting point, along the stem, to top of canopy)
height of plant (perpendicular distance from ground level to the top of the canopy)
spread of plant canopy (down slope and across slope)
number of terminal shoots (counted for some plants and estimated, from the average number of shoots per unit area of canopy for others)

ANNUAL SHOOT GROWTH

Six plants of *Olearia colensoi* and four of *Brachyglottis elaeagnifolia* from Wharite (two plants of each) and an altitudinal sequence on the Delaware Ridge, were used for measurement of annual shoot extension growth, leaf production, leaf senescence and bud formation. Single shoots from the crown of each plant were tagged and measured at monthly intervals (with extra recording during the growth flush as visits allowed) from August 1989 to December 1990.

The following parameters were measured:

length of internode (current leaf whorl to previous leaf whorl)
number of leaves
length of apical bud (until leaf opening)
length (base of petiole to leaf tip) and breadth of all leaves.

The basal diameter, height, length and spread (down slope and across slope) of canopy and number of shoots on each plant were also recorded.

Dissections of apical buds at intervals over the course of a year were carried out to determine the timing of leaf and floral initiation.

ANNUAL WOOD INCREMENT

Dendrometer bands were established on four individual *Olearia colensoi* at three sites (T1, W1 and W2) in February 1989. Bands were constructed from 0.3mm thick aluminium sheet. Readings were taken at intervals during the study. Discs and increment cores were taken from *Olearia colensoi* plants for aging and calculation of annual wood increment.

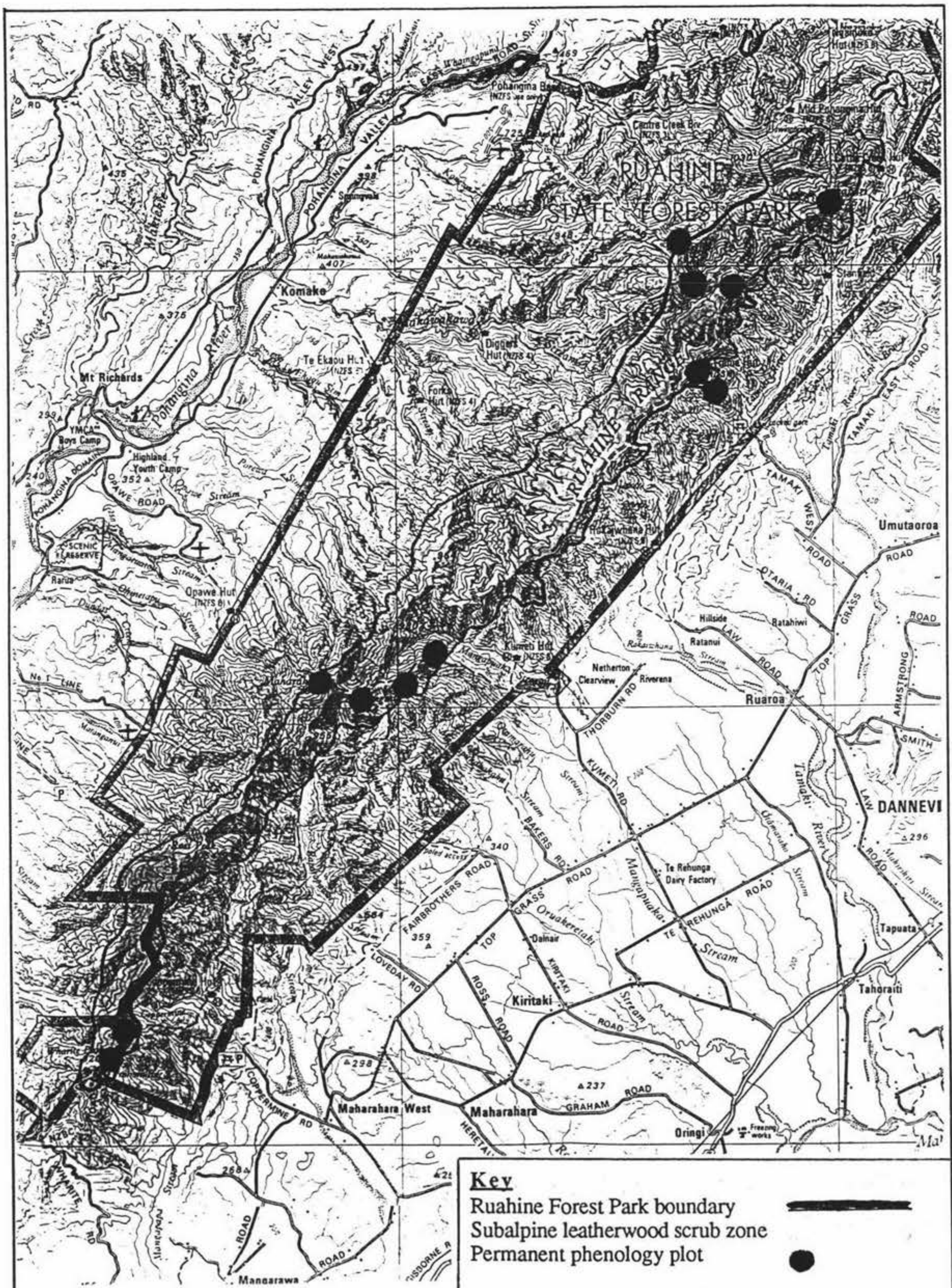

FIGURE 4.1 Map of the southern Ruahine study area showing distribution of permanent plot sites. For physical and vegetative details of sites see Table 4.1

ANNUAL LITTER PRODUCTION

A series of litter traps were installed during May 1989. Two replicate traps were installed at seven of the permanent plots (W1, W2, T1, T2, T3, T4, and T5). The plastic traps were 9 litres in volume, with a mouth opening of 0.0479m^2 (247mm diameter), and depth of 250mm. Traps had drainage holes in the base to allow water to escape. Traps were placed beneath the canopy, attached to props to prevent movement, and with the trap mouth 250mm off the ground to prevent collection of leaves displaced laterally from the litter layer by wind. Traps were emptied at approximately monthly intervals over a 24 month period. Litter collected was oven dried in paper bags at 98°C for 48 hours. The litter, separated into leaf and stem, was weighed after drying.

In order to calculate the amount of litter normally present beneath *Olearia colensoi*, duplicate 30 x 30cm samples of litter were collected from the scrub floor at litter trap sites W1 and W2. The litter from the subplots was oven dried at 98°C then weighed.

PHYTOMASS

Total dry weight phytomass data was recorded for four *Olearia colensoi* plants in May 1989. The plants were selected at random from the leatherwood zone. Plants were excavated with attempt made to retain the root system intact while excluding foreign root matter. Plants were separated into constituent parts (leaves, stems and roots) and air dried at 25°C for three months. Four samples of stem and leaf material were oven dried at 98°C for three days while equivalent sized samples were air dried for three months after which a comparison was made to determine if any difference in final dry weight was discernible using air drying as opposed to oven drying.

Samples of *Olearia colensoi* canopy (30 x 30 cm areas) were harvested from three plants at Wharite in August 1990. The shoots from these plants were separated into stem, current season's leaves (1yr) and the previous season's leaves (2yr). Number of leaves of each age per shoot, number of main apical shoots, number of lateral shoots, length and width of the previous seasons shoot extension growth, length and width of the current resting bud, and the phyllotactic direction (clockwise / anti-clockwise) of the leaves on the shoots were recorded. Samples were then oven dried at 98°C and weighed.

RESULTS

Density of *Olearia colensoi* per plot varied from 5400 to 17600 plants ha^{-1} (0.54 - 1.76 plants m^{-2}) (Table 4.1). Density and size of plants was correlated with altitude. Plant density increased (R=0.6 p≤.0 025, Fig 4.1) and plant height decreased (R=0.74 p≤.0 005, Fig 4.2) with increasing altitude. There was no significant correlation with aspect or slope. Density of *Brachyglottis elaeagnifolia* plants decreased with increasing altitude (R=0.74 p≤.0 005, Fig 4.3).

TABLE 4.1 Physical and vegetative characteristics of thirteen permanent phenology plots established in the southern Ruahine. Grid references refer to map series NZMS 260 T23. *O. col = Olearia colensoi*, *B. elae = Brachyglottis elaeagnifolia*

Plot	Location	Grid ref	Alt (m)	Aspect	*O. col* ha^{-1}	*B. elae* ha^{-1}	Height	Veg description
M1	Maharahara	610111	854	60	8400	1200	2.43	leatherwood /*Pseudopanax*
M2	Maharahara	602107	999	75	7200	0	2.18	uniform leatherwood
M3	Maharahara	592014	1022	270	15200	200	2.23	uniform leatherwood
M4	Maharahara	583108	961	270	9200	400	2.59	leatherwood /*Pseudopanax*
T1	Takapari	655209	1090	140	9800	0	1.97	leatherwood & remnant *Libocedrus/Halocarpus*
T2	Takapari	668197	1170	190	13800	0	1.63	uniform leatherwood
T3	Takapari	678195	1175	270	7200	200	1.97	uniform leatherwood
T4	Takapari	669175	1085	110	11000	0	1.95	uniform leatherwood
T5	Takapari	672172	1000	40	11200	400	3.05	leatherwood / *Pseudopanax*
T6	Takapari	694206	1050	325	16000	0	2.56	uniform leatherwood
T7	Takapari	699216	1255	12	17600	0	1.16	leatherwood some *Chionochloa/Phormium*
W1	Wharite	536024	890	90	5400	400	2.29	uniform leatherwood
W2	Wharite	537028	900	170	6600	600	2.39	uniform leatherwood

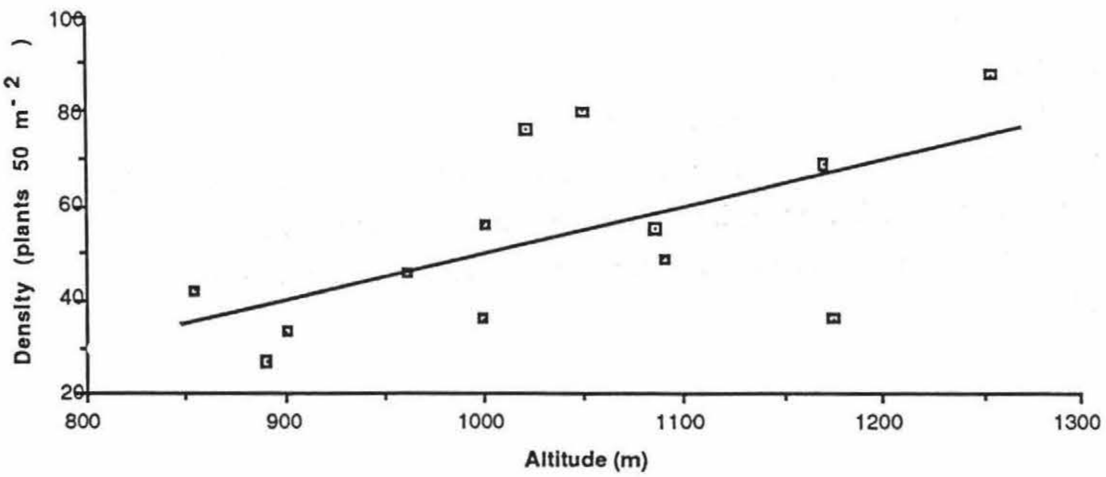

FIGURE 4.1 Density of *Olearia colensoi* plants per 50m^2 with increasing altitude. (R=0.6, p≤ 0.025)

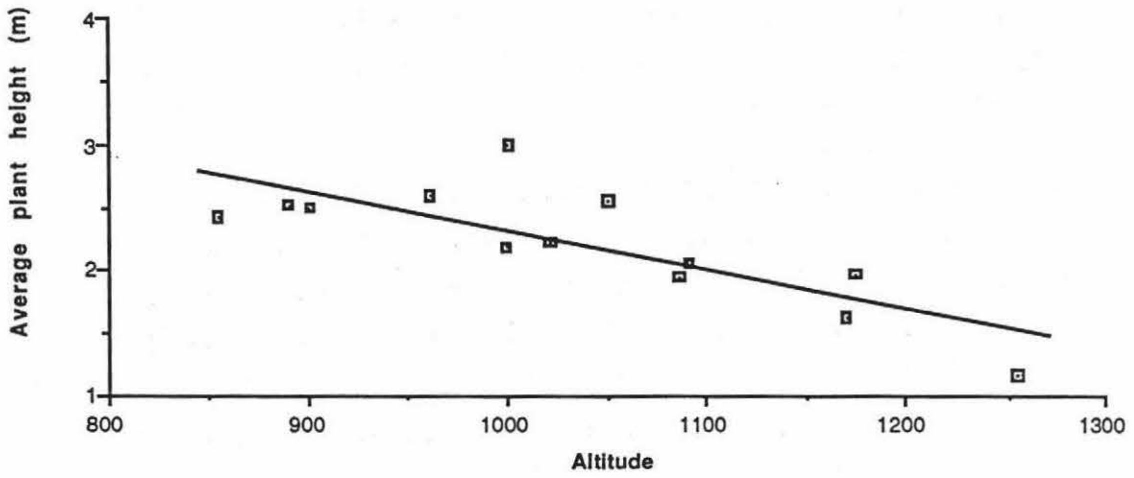

FIGURE 4.2 Height of canopy *Olearia colensoi* plants at each plot with increasing altitude (R=0.79, $p \leq 0.001$)

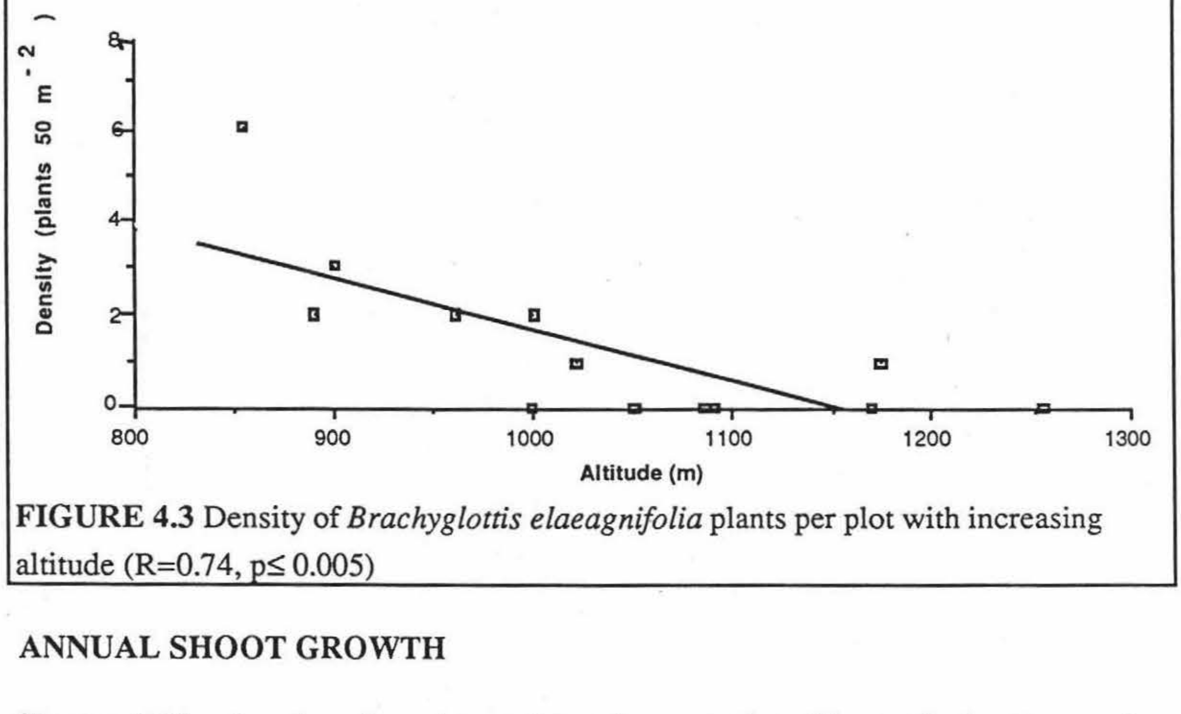

FIGURE 4.3 Density of *Brachyglottis elaeagnifolia* plants per plot with increasing altitude (R=0.74, $p \leq 0.005$)

ANNUAL SHOOT GROWTH

Shoots of *Olearia colensoi* produce a determinant number of leaves during the growing season, the average being six. These leaves open in a single growth flush from November to January. When the new season's leaves are fully expanded the previous season's leaves begin to yellow and senescence continues culminating in leaf fall at an average leaf age of 16 months, most of the previous season's leaves falling from January to June (a retention time of 14 to 19 months). Exposure of the site does however affect leaf retention time with longer retention in more sheltered situations. The canopy of *Olearia colensoi* is confined to a 10-15 cm dense layer of foliage at the extremities of the branches with on average two seasons of leaf production present. Leaf number produced per year per shoot is uniformly consistent on individual plants and varies from four to seven with six being the average.

Olearia colensoi terminal buds became visible at the axil of the current leaf whorl in January. After this initial growth they increased only marginally in length over the winter and began extension growth in October. The first leaves started unrolling in late November (Fig. 4.4a) and all leaves had completed extension growth by the beginning of January (Fig. 4.4b). Slight discrepancies in height for some leaves from one recording to the next (decreases) resulted from the difficulty in exactly defining the base of the petiole in developing leaves.

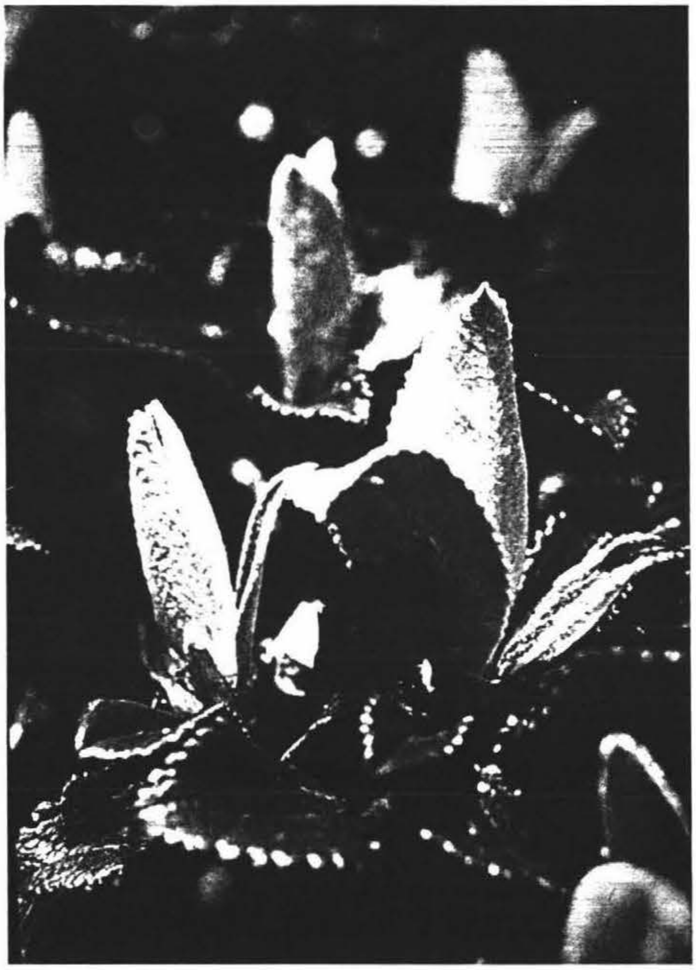

FIGURE 4.4a Shoot of *Olearia colensoi* in late November with leaves emerging from the apical bud. The white abaxial tomentum is visually striking at this stage.

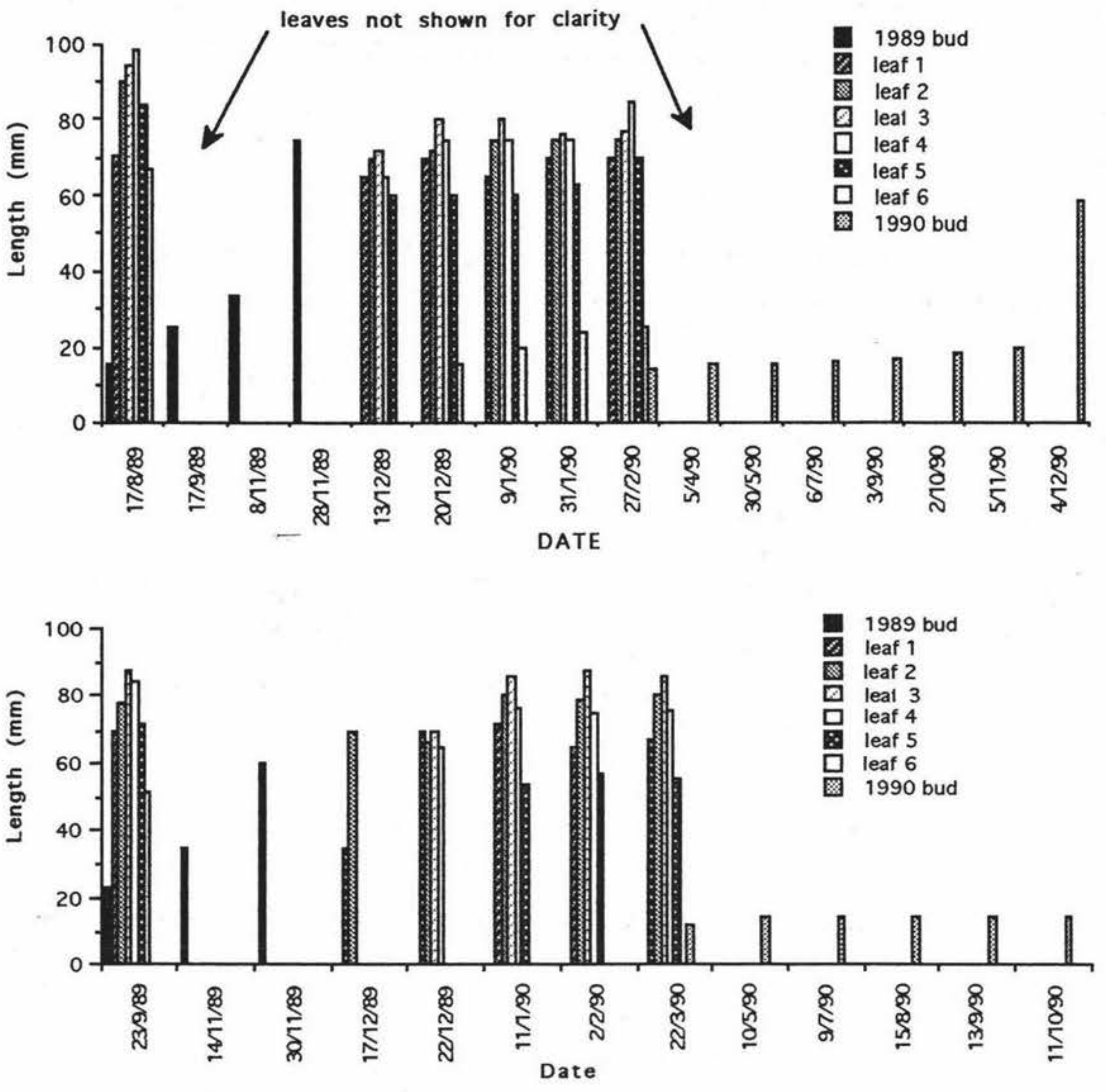

FIGURE 4.4b Bud elongation and leaf length for two of the monitored *Olearia colensoi* plants representative of those measured. The upper graph being Plant 1 from Wharite at 920m and the lower graph Plant 6 from Takapari at 1050m. Recording was over one year from Spring 1989 to Spring 1990. Shoot phenology (bud and leaf development) represented as change in leaf and bud length over time.

SHOOT DISSECTION

Shoots of *Olearia colensoi* produce on average six leaves per season. The leaves are preceded on the shoot by, on average, ten bud scales. Only one growth flush occurs per season; thus there is a repetitious annual cycle of initiation of ten bud scale primordia followed by six leaf primordia. At the beginning of January nearly all bud scale primordia have been initiated. Leaf primordia initiation begins soon after. In June all bud scale and leaf primordia are present in the over-wintering bud. Floral buds also over-winter with a similar number of bud scales present, and all capitula (six on average) of the raceme present.

ANNUAL WOOD INCREMENT

Dendrometer bands for four plants recorded an average radial wood increment of 2.2 mm year^{-1} (3.9, 1.5, 2.6, 1.0 mm radius increase respectively).

Measurement of discs and increment cores of *O. colensoi* gave average ring increments of 2.4 mm per annum (n=7 std dev=0.51)

ANNUAL LITTER PRODUCTION;

For the two year period June 1989 to June 1991 leaf litter fall per trap per year ranged from 3.476 t ha^{-1} to 7.632 t ha^{-1}, with the average being 4.864 t ha^{-1} (Std dev=1.198)(Table 4.2). Seven of the fourteen traps also caught some stem material; the average for all traps was 0.249 t ha^{-1}. Timing of litter fall shows higher fall rates in the months January to June, with the lowest fall rates from July to December (Fig 4.5). Total litter fall was not significantly correlated with altitude (R=0.31, p< 0.1)

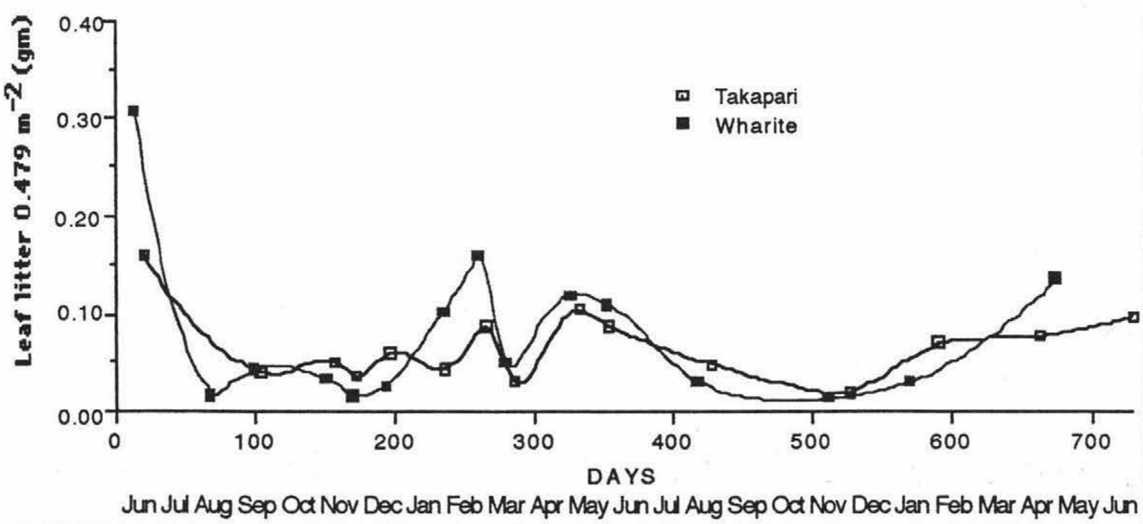

FIGURE 4.5 Average daily *Olearia colensoi* leaf litter fall for the period 12/6/89 to 3/6/91. Plotted as the daily average fall since the previous visit (visit intervals were not equivalent in length). As visit times for Wharite plots did not coincide with the Takapari plots they have been plotted separately. Smooth curve fitted.

TABLE 4.2 Annual litter fall for all litter traps for the periods 14/6/89 - 3/6/91 at Takapari and 12/6/89 - 7/4/91 at Wharite. a & b = duplicate traps.

	Dry weight of litter fall ($t\ ha^{-1}\ yr^{-1}$)			
Litter trap	Leaves	Twigs	Other	Total
T1 a	4.439	0.303	0.107 moss	4.849
T1 b	4.764	0	0	5.062
T2 a	4.018	0.298	0	4.316
T2 b	4.484	0.419	0	4.903
T3 a	4.127	0	0	4.127
T3 b	3.751	0	0	3.751
T4 a	4.945	0	0	4.945
T4 b	3.831	0	0	3.831
T5 a	6.458	1.135	0	7.809
T5 b	6.606	0.847	0	7.453
W1 a	5.492	0.094	0	5.586
W1 b	4.066	0.382	0	4.448
W2 a	7.632	0	0	7.632
W2 b	3.476	0	0	3.476
Mean	4.864	0.249	0.107	5.22

It was possible to compare litter fall from the canopy with the quantity of litter on the scrub floor and with potential litter fall derived from the phytomass measurements. The 30 x 30 cm samples of the litter layer beneath plots W1 and W2 gave an average of 12.611 $t\ ha^{-1}$. This was higher than the average of 6.671 $t\ ha^{-1}$ litter calculated from the litter collected beneath the plants excavated for phytomass determination.

Potential *Olearia colensoi* litter fall calculated from the phytomass plants was 2.759 $t\ ha^{-1}\ yr^{-1}$ (55% of the mean annual leaf production of 5.0175 $t\ ha^{-1}$ [based on 45% weight difference between dry-weight samples of photosynthetically active one year leaves and leaves of comparable size caught in litter traps]). Potential litter fall calculated from harvested 30x30 cm samples of *Olearia colensoi* canopy was 3.493 $t\ ha^{-1}\ yr^{-1}$ (55% of 6.352 $t\ ha^{-1}$). Ground leaf litter at (12.611 $t\ ha^{-1}$) represented 4.6 and 3.6 years of leaf litter fall respectively for the two calculations (discounting decomposition weight loss of the litter). Litter turn over (decomposition) is at least three times slower than litter production based on these calculations.

PHYTOMASS

BIOMASS OF HARVESTED *OLEARIA COLENSOI* PLANTS

There was no significant difference in final dry weight of samples air dried at 25°C for three months and those dried at 98°C for three days. The majority of the biomass of the four excavated *Olearia colensoi* plants consisted of stem and branches (60% average) (Fig. 4.6). Roots, one year old leaves, and two year old leaves constituted on average 21.9%, 8.2% and 3.3% respectively of the total plant biomass. Size and age of the harvested plants varied (Table 4.3) accounting for some of the variation in dry weights. Using the biomass data recorded an estimate of total biomass per hectare was derived by extrapolation from the canopy area of each plant. The average total *Olearia colensoi* biomass in the southern Ruahine calculated this way was 62.458 t ha^{-1} (range 40.102 - 103.063 t ha^{-1}). Leaf litter added another 6.871 t ha^{-1} to bring the total estimated average phytomass of the leatherwood area to 69.349 t ha^{-1}. A second estimation using the average biomass of the four plants multiplied by the average density of plants from the permanent plots gave an estimation of 76.115t ha^{-1}. The four plants harvested were less than average age and size (Table 4.3) therefore total biomass calculations are probably an underestimation.

FIGURE 4.6 Dry weight of constituent parts of four *Olearia colensoi* plants from the southern Ruahine. See table 4.3 for size parameters and altitude of the plants.

TABLE 4.3 Size parameters of four *Olearia colensoi* plants harvested from the southern Ruahine for phytomass determination. Weight of constituent parts are given in Fig. 4.6.

	Height (m)	Spread (m)	Basal Dia (mm)	Age	Altitude (m)
plant 1	1.5	1.5 x 1.5	75	21	890
plant 2	1.8	1.8 x 2.6	55	22	1141
plant 3	1.1	1.1 x 0.9	50	20	1120
plant 4	1.5	1.0 x 2.4	85	25	1090

30 x 30 cm harvested canopy areas of *Olearia colensoi*

The average 1 year leaf weight of the three plants sampled was 6.351 t ha^{-1}, and 2 year leaf 0.761 t ha^{-1} the average weight of the shoot increment (stem between the 1 year and 2 year leaf whorls) was 1.501 t ha^{-1}. In total 80 shoots were recorded of which 63% had an anticlockwise phyllotactic direction and 37% clockwise.

Of these three plants comparison in terms of site exposure showed the following trends;

the more sheltered plants have

-greater number of leaves per shoot

-lower number of shoots

-greater number of 2 yr leaves present

-greater average leaf wt

DISCUSSION

The leatherwood formations of the southern Ruahine represent one of the densest areas of any sub-alpine scrub in New Zealand and probably the densest area of *Olearia colensoi* averaging 10,661 stems ha^{-1}. The density of similar height leatherwood scrub at Peg leg Flat dominated by *Brachyglottis bennettii* (*Olearia colensoi* being absent) was recorded at 2600 stems ha^{-1} (Haase 1986). The size and density of *Olearia colensoi* is significantly correlated with altitude- size decreasing and density increasing with increasing altitude.

Leaf primordia have been noted as present in the over-wintering buds of *Olearia colensoi* (Wardle *et al.* 1971). Adult shoots have a single growth flush starting around mid October; buds begin to open late November and leaves are fully expanded by early January (Wardle *et al.* 1971). New over-wintering buds of adult shoots begin to form as soon as the old buds open in the spring. Occasionally buds open in the same summer to produce lammas (prematurely expanding) shoots (Wardle *et al.* 1971). Cambial growth (wood increment) begins about the same time as shoot growth, is at a maximum after shoot extension growth has stopped, and continues on into May (Wardle *et al* 1987). Wood increment rates given by Wardle *et al.* (1971) were 10-20 growth rings per cm (1.7-2.5 mm per year) and annual shoot growth is 4-10 cm per year (Wardle 1963). This compares with *Olearia colensoi* plants in this study measured for annual growth and plants aged by ring counting which had average ring increments of 2.4mm per year.

The timing of maximum litter fall recorded from the litter traps agrees with the observations of growth phenology from the tagged plants. The rate of leaf litter fall found in this study is high when compared with other forest ecosystems (Table 4.4). The average litter fall for leatherwood (4.864 t ha^{-1}) is twice that of some lowland podocarp/broadleaf forests and is closer to that of tropical forests than that expected for subalpine vegetation. Leaf litter fall is within the range of tall mangrove forest which is considered to be one of the more highly productive of forest communities in New Zealand (Knox 1983).

Lonsdale (1988), in a statistical examination of the litter fall data from 389 natural forest sites world-wide, produced predictive models for litter fall. The best models were based on latitude and latitude plus altitude but an F-test comparing the two suggested that altitude could be dropped from the model (Lonsdale 1988). The best predictive model was then based solely on latitude and is;

$\log Y = -0.0090L+0.80$ (where Y is litter-fall and L is latitude)

Using the Lonsdale model the predicted leaf litter fall for the southern Ruahine at latitude 40° Sth is 2.754 tonne ha^{-1} considerably lower than the 4.864 tonne ha^{-1} average over the two years studied.

TABLE 4.4 Comparison of leaf litter fall rates from the southern Ruahine leatherwood with other forest types in New Zealand and the predicted leaf litter fall rate using the Lonsdale model of relationship to latitude.

Forest type	Location	Latitude	Leaf litter fall ($t\ ha^{-1}$)	**Predicted**	Reference
Podocarp-rata-broadleaf	Orongorongo Vly	41°21`S	3.07-3.39	**2.678**	Daniel 1975
Nothofagus truncata	Silverstream	41°09`S	2.14-6.91	**2.698**	Miller 1963
Nothofagus solandri var *cliffortioides*	Craigieburn	43°07`S	1.75-3.71	**2.588**	Wardle 1970
Lowland podocarp /broadleaf	Orongorongo Valley	41°21`S	2.328-3.097	**2.678**	Cowan *et al* 1985
podocarp/hardwood forest	Hochstetter	42°27`S	3.649	**2.615**	Levett *et al*. 1985
hard beech forest	Granville	42°19`S	4.132	**2.624**	Levett *et al*. 1985
Avicennia marina	Auckland	36°48`	2.72-5.62	**2.943**	Woodroffe 1982
Arctic-Alpine forests			0.7		Bray & Gorman (1964)
Cool temperate forest			2.5		Bray & Gorman (1964)
warm temperate forest			3.6		Bray & Gorman (1964)
equatorial forest			6.8		Bray & Gorman (1964)
20 Topical forests			5.400		Golley 1978

The Lonsdale model does appear to underestimate potential leaf litter fall in some New Zealand forest situations, particularly Westland lowland forests where the oceanic influences probably lessen the effect of the higher latitudes. However the difference between the predicted and actual leaf litter fall for the southern Ruahine is much larger than the underestimation for other forests. There is also a greater than expected difference between low altitude sites of comparable latitudes and the study area. There seems to be no definable relationship between altitude and leaf litter fall in the forests of the world but there is to total litter fall (Lonsdale 1988). This seems to be the case in the southern Ruahine. There is a negative correlation between plant height and altitude which is probably a combination of exposure contributing factors setting the optimum height plants can obtain in the prevailing conditions. Thus while total litter fall is not correlated with altitude, total plant production is expected to decrease with increasing altitude as the annual wood increment is less, resulting in smaller plants. It could be that the relatively even leaf production over the altitudinal range is a consequence of differences in resource partitioning, a greater proportion going into leaf production instead of stem increase for which there is less advantage as altitude increases.

Such a high level of litter production is unexpected for a subalpine situation. Litter breakdown, while not specifically measured, is not expected to proceed very fast under the cooler conditions that prevail in the subalpine situation with consequent limitations on soil microbial activity. The high litter fall together with slow decomposition could account for depth of peaty loam soil beneath leatherwood on the plateau of the range (in places up to 1100mm deep). Litter samples indicate that litter on average represents the accumulation of 3.6 years; this calculation does not take into account decomposition loss and thus is an under representation of the time of accumulation. The shallow fibrous root system of *Olearia colensoi* forms a matt 2-3cm deep directly beneath the litter layer and above the soil surface; this seems to indicate that the root system is effectively moving up through the litter layer as it accumulates and a reasonably high proportion of the leaf litter passes through the root zone without recycling and adds to the formation of the peaty loam that develops under established *O. colensoi*.. Over the last 1800 years ≈1mm of soil has formed every three years on the southern Ruahine plateau.Leatherwood has most likely been the dominant vegetation on the plateau over that time and has been the major contributor to the soil accumulation through its high leaf litter production. Total biomass estimates for the leatherwood formation are not high in comparison with lowland forest situations where tree trunk biomass is the greatest contributor. The high leaf production of *O. colensoi* however indicates that the total productivity of leatherwood in comparison to lowland forest is not as great as the difference in total biomass would indicate.

CHAPTER 5

FLORAL PHENOLOGY AND REPRODUCTIVE ABILITY OF *OLEARIA COLENSOI*

INTRODUCTION

Anthesis in *Olearia colensoi* occurs in the spring (October- November), with seed ripening completed by February and most seed (achenes with pappus) shed by the end of March. Flowering in *Olearia colensoi* does not occur every year. Heavy flowering and seeding years (mast years) occur once every 3-5 years (Field 1968, Wardle *et al.* 1972).

Intermittent prolific flowering (hereafter referred to as mast flowering) occurs in many indigenous New Zealand species from a wide range of families (Table 5.1) and is characteristic of many forest tree species world wide (Harper 1977, Silvertown 1987). Floral initiation in these mast seeding plants occurs in the preceding summer or autumn to that in which anthesis occurs (Mark 1970). It is generally held that widespread floral initiation occurs only in a summer with above average temperatures (ie the summer preceding anthesis). Mast seeding may be related to years when adequate resources are available, intervening seed-less years occurring because trees take time to recover from reproductive effort (Silvertown 1987). Alternatively, such seeding may be a response to predator satiation (Janzen 1971, Silvertown 1987), or an adaptation to maximise reproductive efficiency (Norton & Kelly 1988). It is possible these factors operate in combination (Allen & Platt 1990).

To examine whether the success of *Olearia colensoi* in the southern Ruahine is linked to its flowering behaviour and reproductive ability, aspects of floral phenology of *Olearia colensoi* were studied, particularly the characteristic mast flowering pattern. Permanent floral phenology plots were established and data collected over three seasons to quantify flowering periodicity and intensity for known individuals over a range of sites with differing environmental variables. Some of the assumptions related to mast flowering in *Olearia colensoi* were tested. Seed viability and germination rates were investigated.

TABLE 5.1 Some indigenous New Zealand plants exhibiting masting phenomena.

Genus/species	Reference
Angiosperms	
Nothofagus (all N.Z. species)	Wardle 1984
Nothofagus solandri	Allen & Platt 1990
Chionochloa rigida	Connor 1966, Mark 1965
Aciphylla	Campbell 1981
Celmisia viscosa, C. lyallii	Mark 1970
Phormium cookianum	Brockie 1986
Olearia colensoi	Wardle *et.al.* 1971
Olearia ilicifolia	Haase 1986b
Beilschmeidia tawa	West 1986
Metrosideros umbellata	Wardle 1971
Brachyglottis bennettii	Haase 1986b
Cordyline australis	Mark 1970
Schefflera digitata	Mark 1970
Cortaderia	Connor 1966
Astelia	Wheeler 1966
Gautheria	Armstrong 1964
Pseudowintera colorata	"
Eleaocarpus dentatus	"
Toronia toru	Godley 1975
Pomaderis	Allan 1961
Gymnosperms	
Dacrydium cupressinum	Norton *et.al.* 1988
podocarps 3 spp	Beveridge 1973

METHODS

FLORAL PHENOLOGY

Thirteen permanent plots were established in the southern Ruahine sub-alpine scrub zone during February 1989 and are described in detail in Chapter 4. These plots were used to monitor aspects of vegetative phenology (Chapter 4) and floral phenology (this chapter). The plots were in three areas, Takapari, Maharahara, and Wharite (Fig. 4.1). Altitude and aspect sequences were established in the Takapari and Maharahara areas where plots were placed at the lower altitude limit of the leatherwood scrub zone on both western and eastern sides and at middle and upper altitude sites. At Wharite two plots of similar altitude were established. The 810 tagged plants in the thirteen plots were monitored for floral phenology over three seasons 1988/89, 1989/90 and 1990/91. All plants that flowered during this time and the number of racemes they produced were recorded. Numbers of flowering and non-flowering *Brachyglottis elaeagnifolia* were also recorded in each plot.

Temperature data collected from the meteorological stations (Chapter 3), and supplemented by the DSIR meteorological station in Palmerston North, was used to investigate the relationship between the summer monthly mean temperature of the previous season with the number of plants flowering and intensity of flowering.

INFLORESCENCE CHARACTERISTICS, SEED VIABILITY AND GERMINATION IN *OLEARIA COLENSOI*

Six mature racemes (material permitting) were collected from each flowering plant each season to record capitulum and floret number, measure raceme length, and test seed viability and germination potential. As well as the above plants, six heavy flowering plants selected in January 1989 from Wharite and Takapari Plateau sites were assessed for seed viability and germination potential. Whole racemes collected from individual plants were air dried for 2-3 days in paper bags to allow excess moisture on the racemes to dissipate and achenes to loosen on the capitula. Each sample of racemes from the individual plants were then scored for length of raceme (base of peduncle to top of upper capitulum), number of capitula per raceme, and average number of achenes per capitulum. All seeds (achenes) were removed from all capitula and 100 seed samples from each plant were manually sorted into viable (filled) and non viable (empty) by prodding each seed, viable seed being firm under the probe and non-viable seed collapsing (this was checked by dissection). Those damaged by insect predation were counted as non-viable seeds (approximately 5%). Full seeds were weighed.

Three germination experiments were conducted. The first was a germination trial of viable seed from the six heavy flowering plants set up 5 weeks after harvesting in January 1989. The second experiment tested germination of seed from the same plants after 5 months storage in the dark at 5^{o}C. The third test was conducted after the 1989/90 seed harvest and involved all flowering plants from which sufficient viable seed was available. In all germination trials seeds were placed on moist filter paper in covered petri dishes held at room temperature and in subdued light. Germination was recorded over ten weeks.

RESULTS

FLORAL PHENOLOGY

In total 192 of the tagged plants (23.7%) flowered at some time during the three seasons studied. In 1988/89 plants flowering per plot ranged from 0 to 48.5%; in 1989/90, 0 to 60.6%; and in 1990/91 0-9.1% (Table 5.2).

All plots except T1 and T7 showed an increase in number of plants flowering between the years 1988/89 and 1989/90, and all plots (except plot T1 which had no flowering plants throughout) showed a decrease in plants flowering between 1989/90 and 1990/91 (Table 5.2). Sites with the greatest number of flowering plants were M3, W2, M4 and T5.

TABLE 5.2 Percentage of *Olearia colensoi* plants flowering at thirteen permanent plots in the southern Ruahine over three seasons, 1988/89, 1989/90 and 1990/91.

Plot	Location	Altitude	No of canopy plants 50m^{-2}	% *Olearia colensoi* plants flowering 1988/89	1989/90	1990/91
M1	Maharahara	854	42	14.3	26.2	4.8
M2	Maharahara	999	37	15.1	21.9	0
M3	Maharahara	1022	70	7.9	19.7	0
M4	Maharahara	961	46	30.4	41.3	4.3
T1	Takapari	1090	49	0	0	0
T2	Takapari	1170	69	0	5.8	0
T3	Takapari	1175	37	9.6	13.7	0
T4	Takapari	1085	55	3.6	20.0	1.8
T5	Takapari	1000	56	16.1	48.2	3.6
T6	Takapari	1050	80	3.8	18.8	0
T7	Takapari	1255	88	5.7	2.3	0
W1	Wharite	890	27	3.7	51.9	7.4
W2	Wharite	900	33	48.5	60.6	9.1

Of the total 810 tagged plants, 10.5% flowered in 1988/89, 21.7% in 1989/90 and 1.9% in 1990/91. Most of those plants that flowered in 1988/89 flowered again in 1989/90 (Table 5.3) while only low numbers flowered in 1990/91.

Intensity of flowering of individual plants (racemes per plant and racemes m^{-2} of canopy area) in 1988/89 was correlated with intensity of flowering in 1989/90 ($R=0.489$, $p\leq0.001$ and $R=0.275$, $p\leq0.005$ respectively).

Average flowering intensity (number of racemes plant^{-1}) increased from 1988/89 to 1989/90 and then decreased markedly from 1989/90 to 1990/91 (Table 5.3). Of the 74 plants that flowered in both 1988/89 & 1989/90, 27% produced more inflorescences in 88/89, 65% more in 89/90 and 11% the same amount in both years.

Seventeen *Brachyglottis elaeagnifolia* plants occurred over the 13 plots. In 1988/89 eleven (64.7%) of these plants flowered compared to five (29.4%) in 1989/90 and none in 1990/91.

TABLE 5.3 Percentage of 810 tagged *Olearia colensoi* plants flowering for the possible yearly combinations 1988/89 to 1990/91. Plants that flowered in only one season are represented along the diagonal of the matrix (eg 1988/89x1988/89 at 1.5%).

	1988/89	1989/90	1990/91	Total plants flowering %	average no. racemes plant^{-1}
1988/89	1.5	8.1	0.0	10.5	12
1989/90		12.2	0.25	21.7	16
1990/91			0.4	1.9	2.5
1988/89 & 1989/90			1.1		

ENVIRONMENTAL CORRELATES OF FLOWERING IN *OLEARIA COLENSOI*

The number of plants flowering over the three seasons of the study had a significant negative correlation with altitude in 1989/90 and 1990/91 but not 1988/89 (Table 5.4) and showed no, or only weak, correlation to aspect or slope. The intensity of flowering per plot (racemes m^{-2} of plot area) showed significant negative correlation with altitude for all years (Table 5.4) but no correlation with aspect or slope. The intensity of flowering (racemes m^{-2} of canopy area) showed no significant correlation with altitude, aspect or slope in any year.

Amount of flowering was not significantly correlated with the size of the plants (canopy area or stem size)

TABLE 5.4 Correlation of percentage of plants flowering per plot (50m^{2}) and flowering intensity per plot (racemes 50m^{-2}) with altitude for the three seasons of the study.

	Flowering Plants 50m^{-2}		Racemes 50m^{-2}	
	R	p	R	p
1988/89	0.51	$p \leq 0.1$	0.74	$p \leq 0.005$
1989/90	0.77	$p \leq 0.005$	0.75	$p \leq 0.005$
1990/91	0.77	$p \leq 0.005$	0.7	$p \leq 0.01$

Temperature

The percentage of plants flowering per season showed indications of a trend with the average summer month (Dec-Feb) temperature of the previous season. The relationship was most apparent between mean December temperature of the previous season and percentage of plants flowering (Fig 5.1).

Meteorological investigation (Chapter 3) showed that the Ruahine temperature regime over a year (March 1990 - March 1991) varied between sites and with Palmerston North DSIR Meteorological Station consistent with an altitudinal response of decreasing temperature with increasing altitude. Long term meteorological data for the southern Ruahine is confined to the years 1966-1986 for Wharite Peak. As the Ruahine temperatures were significantly correlated with Palmerston North temperatures (mean difference 0.61°C $100m^{-1}$), long term meteorological data from Palmerston North was used for examining the relationship of temperature and flowering in the Ruahine.

Examination of the average summer month temperature for the Palmerston North DSIR Meteorological Station from 1967 -1991 showed seven seasons (potential floral initiation times) when mean temperature was greater than 0.5^{o} above the long term average (Fig 5.2). Records do not exist to confirm the degree of flowering prior to 1987

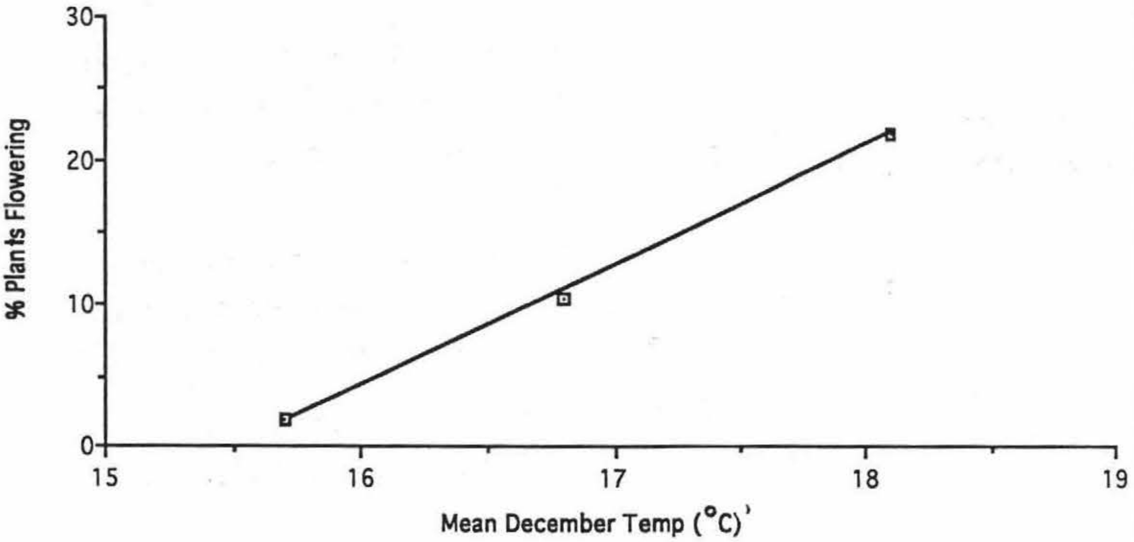

FIGURE 5.1 Percentage of plants flowering per season in relation to the average December temperature of the previous season for the years 1988/89, 1989/90 and 1990/91. Temperature data from Palmerston North DSIR Meteorological Station (30m).

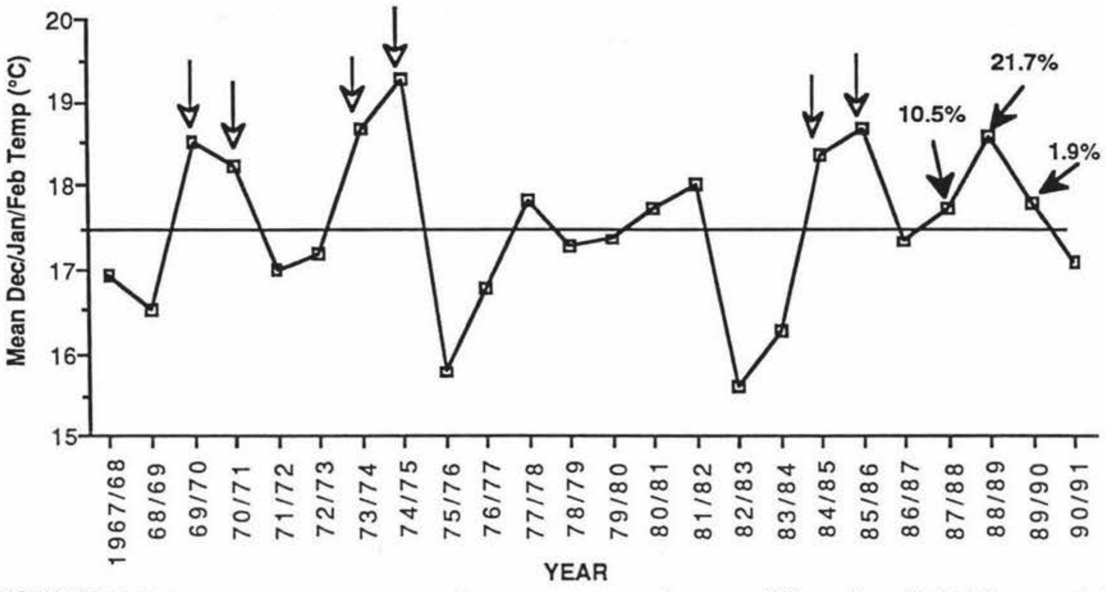

FIGURE 5.2 Average summer month temperatures (mean of Dec, Jan & Feb) recorded at Palmerston North DSIR Meteorological Stations for the years 1967-1990. The long term temperature average is shown as a horizontal line. Degree of flowering (the following year) associated with this temperature regime is given as percent of plants flowering for the years 1988-1990. Potential inductive seasons prior to 1988 are indicated with open headed arrows, although records do not exist to confirm the degree of flowering following those years.

INFLORESCENCE CHARACTERISTICS, SEED VIABILITY and GERMINATION IN *OLEARIA COLENSOI*

For the years 1988/89 and 1989/90 the mean raceme length was 9cm and the mean capitulum number per raceme was 4.6 (Table 5.5) The average number of achenes per terminal capitulum was 38(n=17) and 33(n=30) in 1988/89 and 1989/90 respectively.

Percent viable seed from all plants in all years was low as was the percent germination (Table 5.5). The average viable seed weight for all plots was 0.00285g (1988/89 & 1989/90)

Maggot-chewed seed amounted to 5% of all seed of plants 1 to 6 and similar percentages of the other plants which were not scored for maggot activity.

TABLE 5.5 Raceme measurements, percentage of viable seed (filled) and percent germination of viable seeds for; A. six heavy flowering plants in 1989 and B. percent viable seed for all plots over the 1988/89 and 1989/90 seasons. * = not recorded

	raceme length (cm)	ave capitulum No /raceme	% viable seed	ave wt viable seed (gm)	% germination	% germination after 5 months at 5^0C
A. 6 plants 1988/89	*	*	6.2	*	1.6%(n=948) (33%of viable)	0.7%(n=2438) (11%of viable)
B. 1988/89 (59 plants)	8.6	4.2	3.2	0.0029	*	*
1989/90 (46 plants)	9.5	4.9	5.2	0.0028	0.25%	*

DISCUSSION

INFLORESCENCE CHARACTERISTICS, SEED VIABILITY AND GERMINATION IN *OLEARIA COLENSOI*

Germination rates of *Olearia colensoi* seed in this study were very low. While this may be lower than in the field the proportion of viable seed is also low, such that even if all viable seeds germinated this would still represent a low proportion of the total seed crop. It is probable that viable seed numbers and germination rates are higher for *Olearia colensoi* in mast years as this has been found to be the case in other masting species (Norton *et al.* 1988). Even if viability and germination rates did not increase the sheer number of seeds produced in a mast year would likely be enough to ensure sufficient regeneration. There is at least no failure to produce enough viable seed to ensure replacement and colonisation of new areas in the southern Ruahine as seedlings are prolific in many areas along tracks and road sides and on prostrate moss-covered stems within the scrub. These seedlings tend to be of even aged cohorts, probably resulting from previous mast seeding years. Seed of *Olearia colensoi* is not long lived and no seed bank exists. Instead there appears to be a bank of large numbers of *Olearia colensoi* seedlings growing on low epiphytic bryophyte mats, particularly on prostrate stems of *Olearia colensoi* ; these seedlings make little growth beneath closed canopies but are released on canopy opening.

MAST FLOWERING

Mast flowering occurs in a number of New Zealand plants (Table 5.1). Floral initiation in most mast flowering species occurs during the previous summer/autumn. Floral initiation in the season before flowering (often early in the growing season) is reported for many overseas alpine species, not all of which exhibit mast flowering (Billings and Mooney 1968). Autumn initiation is common in alpine plants in New Zealand (81 of 100 alpine species examined from 18 families, Mark 1970) and again is not confined to mast flowerers. For alpine plants it has been suggested that floral primordia form during the previous season as an adaptation to ensure completion of the reproductive cycle in the short growing season of the alpine situation(Mark 1970).

A mast or heavy flowering year in *Olearia colensoi* is generally one in which over 50% of mature plants flower (Wardle *et al.* 1972). In non-mast years plants either do not flower at all or the number of plants flowering, and the intensity of flowering (inflorescences per plant) is low. All three seasons of this study were non mast years when defined by greater than 50% flowering. Flowering did however occur in all three seasons and some individuals flowered in consecutive years; thus flowering in *Olearia colensoi* is not an 'all or nothing' response.

Environmental triggers of mast flowering

It is generally held that widespread floral initiation in masting species occurs only in a summer with above average temperatures (ie the summer preceding anthesis). Heavy flowering in *Nothofagus* occurs at irregular intervals averaging three to five years apart, and an association between prolific flowering and hot, dry summers in the preceding season has been implicated (Wardle 1984). Wardle (1984) identified flowering years in 1935, 1938, 1944, 1951, 1953 and 1955; these seasons were each preceded by summers which were hotter and drier than normal. These same years were identified by Field (1968) as summers in which initiation would have been possible in *Olearia colensoi* in the Tararua Range and the limited records available confirmed flowering after three of these summers. In *Chionochloa rigida* flowering occurs most commonly at three year intervals and is often coincident with flowering in *Nothofagus* (Connor 1966). The average summer month temperatures of the previous season (Dec-Feb) are implicated as the triggering factor to the degree of flowering in any one season. The trend found in this study between flowering and previous summer average temperatures (especially December mean temperature) is in accord with this contention but conclusions are limited by the small number of seasons available.

It appears that over the 1988/89 and 1989/90 seasons two partial flowering years occurred in succession as the result of two partially inductive preceding summers . The intensity of flowering of each plant over these two seasons was not high. Many plants had only one raceme per plant whereas plants are capable of bearing 3-4 racemes on most shoots when flowering heavily (*pers. obs.*). Intensity of flowering (racemes per unit area) decreases with altitude. Mean temperatures decrease with altitude at a lapse rate of 0.61°C $100m^{-1}$ and the range (min to max) decreases as well (Chapter 3); therefore it requires more consistently warmer days at higher altitude to raise the mean temperature 1° above the long term mean at higher altitudes than it does at lower altitudes. This may account for the observed decrease in plants flowering and intensity of flowering with altitude as the inductive summer temperatures were not greatly above the long term mean. In an exceptionally warm summer floral initiation (and subsequent flowering intensity the following season) would likely be more even over the altitudinal range as all altitudes would experience temperatures sufficiently greater than their long term mean to trigger floral initiation.

The evolutionary basis of mast flowering

Three main hypotheses have been advanced to explain masting behaviour. One hypothesis (predator satiation hypothesis), argues that extreme variation in crop size (masting), may increase a plant's fitness because it reduces the proportion of seeds eaten by animals (Janzen 1971, Silvertown 1987). Another hypothesis is that climatic conditions suit seed production better in some years than in others and that intervening seed-less years result because trees take time to recover from the effort of reproduction (Resource availability hypothesis)(Silvertown 1987). The third hypothesis argues that reproductive efficiency is increased in mast years through 'economies of scale' (large episodes of reproduction having more chance of success than small ones), be it due to predator satiation or wind pollination efficiency or some other factor (Norton & Kelly 1988). The hypotheses are discussed in the following sections.

Predator Satiation Hypothesis

The predator satiation hypothesis argues that seed predators consume a large proportion of small seed crops but they cannot consume a tree's entire crop in a mast year. Hence the probability of a seed escaping predation is greatest when crops are large. It would not be advantageous for the plant to produce large crops regularly because predators would build up numbers from one year to the next on succeeding bumper crops. The seed predators that exert the strongest selection in favour of masting are likely to be monophagous seed parasites (Keen 1958). The hypothesis predicts that there should be a negative relationship between the probability of a seed being eaten and the size of the current seed crop in a masting species and this has been confirmed by foresters for a number of species (Silvertown 1987). It has been noted that individuals in some species exhibit the masting habit more intensely than others in the same geographical region which led to investigation of whether the masting habit was most pronounced in those tree populations where seed predation was strongest. Silvertown (1980) found that five of the seven most heavily preyed-upon species he studied showed the masting habit; of eight which suffered lower seed predation only two showed very variable seed production. Examples exist of different populations of the same species geographically isolated so that one population has its major insect seed predators absent, and the other predators present. The predator-free population does not show the masting habit but the predated population does (Silvertown 1987). It follows from this argument that trees with fleshy fruits and animal-dispersed seeds would not be expected mast but should produce fruit regularly. The seeds in such fruits generally pass through the gut intact so if masting occurred it would prevent efficient seed dispersal by 'satiation' of the dispersal vector. Most North American forest trees with non-fleshy dispersal units mast to some degree, while most of those with fleshy dispersal units do not (Silvertown 1980).

A corollary of predator satiation may be pollinator satiation for those species with animal pollination vectors. This would be more so for plants with specialist pollinators which may be unable to exploit the number of flowers presented in a mast year resulting in lower pollination rates. It is likely then that mast behaviour is more common in wind pollinated plants. Many prominent masting genera are wind pollinated (eg. *Nothofagus, Fagus, Quercus, Pinus*).

Resource Availability Hypothesis

Summer / autumn initiating plants are often producing floral initials at the same time as extension growth of the current season's shoots. High levels of carbohydrate are needed for floral initiation (Krammer & Kowsoski 1979). Thus the competing demands on photosynthate from both floral initiation and vegetative growth suggests that optimum conditions for photosynthesis are necessary to produce adequate nutriment for floral initiation to occur. In a mast year, flower maturation and seed development would also be occurring over the period of floral initiation, and would be competing with both vegetative growth and floral initiation. The high photosynthate demands in a mast year are therefore likely to preclude floral initiation (and consequently flowering the following season) preventing two mast years occurring in succession.

Economies of Scale Hypothesis

The validity of predator satiation as an explanation for mast seeding in rimu has been questioned by Norton & Kelly (1988) who observed that six mast years, out of 15 examined, occurred immediately after other mast years. They suggested that reproductive efficiencies of scale associated with synchronous male and female reproductive effort may be an important selection pressure favouring masting. In particular (for rimu) wind pollination would be more efficient in mast years resulting in higher seed set. They found a high correlation between female cone initiation (total seedfall) and pollination efficiency (percentage sound seed).

Resource Availability or Predator Satiation in *Olearia colensoi* ?

For *Olearia colensoi* the critical time over which the temperature regime affects floral initiation has been recorded as December and January (Field 1968). This is the same time as extension growth of the current season's shoots for which high levels of carbohydrate are needed. The competing demands on photosynthate from both floral initiation and vegetative growth require optimum conditions for photosynthesis to produce adequate carbohydrate reserves for floral initiation to occur. The high photosynthate demands in a mast year likely preclude floral initiation (and consequently flowering the following season) preventing two mast years occurring in succession. It has however been observed that some flowering does occur in non-mast years (Field 1968), though this information is mostly anecdotal. This study confirmed the ability of individual plants to flower in successive years, and the intensity of flowering (racemes per plant) in 1988/89 was significantly correlated with intensity of flowering in 1989/90. The intensity of flowering in these years was most likely much less than in a mast year however; thus the consecutive flowering observed may have occurred because nutrient reserves were not depleted in the first season as they would be expected to be in a mast year. The six heavily flowering plants selected for seed collection in 1988/89 (Table 5.5) all flowered again in 1989/90, but at reduced levels (quantitative data not recorded). The plants from the floral phenology plots that flowered in 1988/89 mostly flowered at a higher intensity (racemes per plant) in 1989/90 and this corresponded to the warmer summer in the season prior to 1989/90 (the initiating period). The intensity of flowering of the phenology plot plants was lower than that of the six heavily flowering seed plants in 1988/89. It does appear then that heavy flowering limits the intensity of flowering in the following season even though environmental conditions at the time of floral initiation in the autumn preceding the second season may be more conducive to formation of primordia (higher average summer temperature). Whether the reduced flowering is due to reduced floral initiation, which would be occurring at the time of fruit maturation in December/January, or to the inability of floral initials to develop due to lack of carbohydrate (ie initials effectively abort) is not known but it is most likely the former and could possibly be determined by bud dissections from the same plants spanning mast and non mast years.

Does mast seeding follow mast flowering automatically?

In *Nothofagus* a lack of seed after prolific flowering has been noted and attributed to extreme frosts or wet conditions that have prevented seed development (Poole 1948, 1965, Wardle 1970, Mansen 1974 Wardle 1984). Mast seeding does not therefore always follow mast flowering. Failure of the seed crop in such cases may allow mast flowering to occur in consecutive years if carbohydrate reserves are not further depleted through seed development.

Age effects on flowering

Approximate age of *Olearia colensoi* plants can be inferred from basal diameter. The amount of flowering (racemes /plant) was correlated with the basal diameter of the plant in the 1989/90 season only. Non-flowering plants were not measured in this study; however non-flowering plants appeared to have an age range similar to that of the flowering plants. Thus age alone was not considered to be a factor in the 76.3% of tagged plants that did not flower at any time during the study. There has been no investigation of the length of a juvenile stage, if any, in *Olearia colensoi* but plants are able to flower at relatively young ages in some circumstances. A 30 cm (approximately five year) sapling of *Olearia colensoi* transplanted form 900m in the Ruahine to 30m at Palmerston North in the winter of 1989 flowered in the 1990/91 season. The shift to a lower altitude and the consequent exposure to a higher average temperature (≈+6.9°C) over the 1989/90 summer may in this case, have promoted floral initiation. Flowering in plants of this size was not observed in the field.

Brachyglottis elaeagnifolia occurred only sparsely as a secondary component of some of the plots in the southern Ruahine. Most of the *Brachyglottis elaeagnifolia* recorded flowed in the 1988/89 but not in the subsequent two years. It does not therefore seem to be in synchrony with *Olearia colensoi*, but the number of plants in the plots was too low to draw any significant conclusions as to its normal floral phenology pattern.

Individual plants as genetic mosaics

A hypothesis put forward by Gill (1986) is that plants with extensively branching architecture are actually colonies of many heritable genotypes. The genetic diversity is generated by the accumulation of developmental mutations arising spontaneously in the meristems of proliferating modular parts. Each module produced by an apical meristem, being meristimatic, is highly mutagenic. The developmental mutations are expressed somatically and also inherited through the gametes produced on these modules.

In this study plants were recorded and measured on an individual basis. While this is an advance on anecdotal observations of flowering on a community scale, it is possible that information is still being missed in that individual plants may behave more as a population of branches rather than a single entity. Branches of woody plants may behave as individuals in terms of competition with other branches on the same plant; this competition may extend to a genetic selection level thus conferring an adaptive advantage to a long lived woody species (ie the individual can effectively evolve even to the point of a change in genome through the mutational ability of indeterminate apical meristems). In terms of seasonal variation in flowering it may be informative to investigate flowering on a per branch basis; some branches may flower heavily one year but not the next while another branch may flower instead. Individual flowering whether by plant or branch is less important that flowering success and survival of the population. At a population level studies of flowering per unit area of canopy rather than per individual are probably more informative.

Conclusions

Mast flowering in *Olearia colensoi* cannot be simply explained by resource availability or predator satiation alone. *O. colensoi* mast flowering/seeding appears to be a consequence of synchronised floral initiation during favourable (above average temperature) summers when adequate carbohydrate reserves are presumably available. The evolutionary basis for this synchronisation may involve predator satiation as a selective pressure, but it is most likely acting in combination with other efficiencies of scale such as pollination success.

Temperature appears to be the main controlling factor in floral initiation and subsequent flowering but is most likely tempered by carbohydrate reserves and energy balances within the plant.

Seed viability and germination percentages in *Olearia colensoi* were low in this study but are expected to be higher in mast years. Reproduction by seed is in any case not limiting.

The total fecundity of a plant is determined by a hierarchy of components which may be adjusted in different ways in different species (Silvertown 1987). While the reproductive processes of *Olearia colensoi* alone do not explain its success in the southern Ruahine, its reproductive behaviour in combination with its other life history strategies have contributed to the success and expansion of the leatherwood formation in the southern Ruahine.

CHAPTER 6

SYNECOLOGY OF LEATHERWOOD

PHYTOSOCIOLOGY OF THE SOUTHERN RUAHINE LEATHERWOOD SCRUB AND COMPARISON WITH OTHER LEATHERWOOD AREAS.

INTRODUCTION

Sub-alpine scrub formations in New Zealand have not received extensive ecological investigation, partly due no doubt to the inaccessibility and the inhospitable prevailing weather conditions of many of the areas concerned, the impenetrability of the scrub itself, and the absence of any commercial basis or environmental concerns for sub-alpine scrub to drive such research. Scrub of all types is often viewed as second rate vegetation and treated with disdain due to the impediments it poses to free travel, but sub-alpine scrub has significant intrinsic and ecological features as well as direct soil and water conservation values that warrant greater appreciation and understanding. Fortunately, from a conservation point of view, most sub-alpine scrub areas, unlike lowland scrub, have not suffered directly from the exploitive human practices of farming or forestry and are now predominantly protected (except from introduced animals, recreational pursuits and mining applications) within the Conservation Estate managed by the Department of Conservation.

On the southern Ruahine tops the extensive sub-alpine scrub is dominated by a visually striking continuous cover of leatherwood* (Chapter 1). Apart from scattered individuals of other canopy shrubs or small trees, such as *Brachyglottis elaeagnifolia, Halocarpus biformis* and *Pseudopanax simplex*, the scrub is virtually totally dominated by *Olearia colensoi.* The southern Ruahine has over the last 70 years undergone considerable vegetation change to which the leatherwood zone has not been immune. By all accounts the most significant change in the leatherwood formation has been an increase in extent, particularly a down-slope expansion (J.P. Skipworth *pers. comm.*).

To examine vegetation patterning, community structure and regeneration dynamics of the southern Ruahine sub-alpine zone, a phytosociological analysis was undertaken. The southern Ruahine was then compared to four other leatherwood areas (Mount Taranaki, South Westland, Central Westland and Tararua Range) to assess the ecological significance of the southern Ruahine leatherwood formation.

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* Leatherwood is a general term applied to *Olearia colensoi* and a number of other tree daisy species especially *Brachyglottis elaeagnifolia.* In this study the term leatherwood is only used for the vegetation type and species are referred to by botanical name.

METHOD

Phytosociology

A phytosociological evaluation was carried out using randomly placed quadrats within which a number of vegetational and environmental parameters were measured.

In order to objectivity decide on the quadrat area to be used, two nested plot series were established, one at Wharite at 870 m and one at Takapari at 1130m. The nested plots increased geometrically in size from 0.25m^2 to 128 m^2. Number of species present for each incrementally increasing plot area was recorded to generate species area curves (number of species occurring plotted against plot area). The species area curves were used to calculate the optimum plot size to ensure recording at least 90% of species present in the area.

In total thirty four 5x5m phytosociology plots were recorded from the southern Ruahine and other leatherwood areas (Fig 6.1).

Southern Ruahine

In the southern Ruahine twenty one plots were placed randomly above the 700 metre contour, corresponding to the lowest altitude at which individual *Olearia colensoi* commonly occur in the southern Ruahine. Using randomly generated map co-ordinates, plots were mapped on 1: 50,000 topographical maps. In the field the position of the plot grid reference was located as near as possible on the ground and the final position of the plot determined by random placement (a random number of meters less than 20 along a random direction). Using this randomly defined point as the plot centre a square 5x5m plot was set out with the sides of the plot parallel and perpendicular to the slope.

Other leatherwood areas

Thirteen 5x5m plots were recorded from other leatherwood regions. These plots were placed in a restricted random manner to sample representative areas of leatherwood in those regions. Six of these plots were on Mount Taranaki, three plots were on Mount Fox (south Central Westland), three in the Camp Creek catchment of the Alexander Range (Central Westland) and one on Table Top (western Tararua Range) (Fig 6.1).

Environmental Parameters Recorded

At all plots in all regions the following environmental parameters were recorded:

altitude
aspect (along line of maximum slope)
slope (maximum)
physiography (face, spur, ridge, knob, flat, gully)
exposure (3 point scale; high, medium, low)

parent material
drainage (subjective assessment; good, poor)
soil depth (mean of 4 random probes to bed rock)

Vegetation Parameters Recorded

For the southern Ruahine plots the number of individuals and percent cover of all vascular species was recorded in three height / life spectra categories as follows;

Seedling	: less than 15cm in height
Sapling	: greater than 15cm in height but not reaching the canopy
Canopy	: within the scrub canopy or emergent above it

Average height of the canopy (mean of four random points) was also recorded.

For the plots from other regions, percent cover of all vascular species and average height of the canopy was recorded.

Southern Ruahine Leatherwood Ecotones

Community structure was examined at the ecotone between the southern Ruahine leatherwood formation and the vestigial *Halocarpus / Libocedrus* formation in two areas; Delaware Ridge (1090m) and Wharite (824m). Increment cores of live and standing dead trees and shrubs were taken to determine age of plants for interpretation of past vegetation changes. DBH or basal diameter and height measurements were recorded for cored trees and neighbouring plants.

Analysis

The species percent cover data from all plots was analysed by classification (Euclidean Distance with Ward Minimum Variance Clustering) in the computer programme SYSTAT (Wilkinson 1990) and ordination by DCA (Detrended Correspondence Analysis) using the computer programme CANOCO (ter Braak 1988).

The southern Ruahine plots were also analysed separately by classification (Euclidean distance and Ward Minimum Variance Clustering) and CCA (Canonical Correspondence Analysis; ter Braak 1986) again using the programmes SYSTAT and CANOCO. CCA was used to infer the ecological structure of the leatherwood communities in the southern Ruahine by relating environmental variables to the analysis.

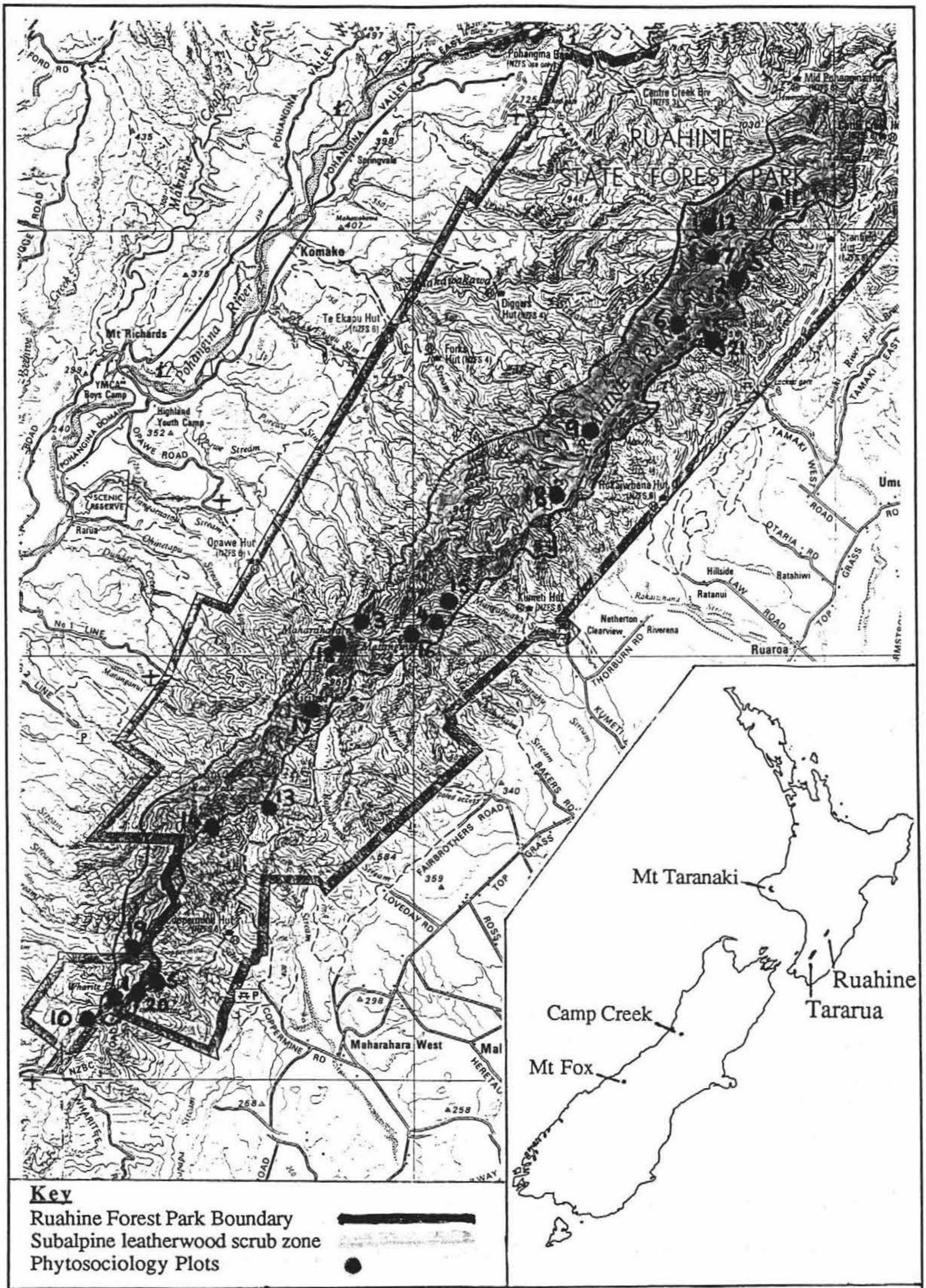

FIGURE 6.1 Location of the phytosociology plots within the southern Ruahine. The other areas examined (Mt Taranaki, Mt Fox, Camp Creek and Tararua Range) are shown on the insert map. Plots were random (Ruahine) or restricted random (other regions) 5x5 m square quadrats.

RESULTS

Minimal Area Plots

The species area curve generated from the nested plot data at 870m on Wharite increased from 3 species at 1 m^2 to 26 species at 128 m^2. The nested plots on the Takapari plateau at 1130m generated a species area curve that increased from 4 species at 1 m^2 to 19 species at 128 m^2 (Fig 6.2). The plot size that yielded 90% of the total species occurring in the largest area examined was 16m^2 for Takapari and 32m^2 for Wharite. As the Wharite site at 870m represented the lower range of the leatherwood zone (where species diversity was greater) and the Takapari site at 1130m the more normal altitudinal range of leatherwood, the mean (24m^2) of these two areas was taken as the sample area that would adequately sample the main leatherwood communities while still being logistically feasible in the dense scrub conditions. As 25m^2, represented by a 5x5m plot, was close to this mean it was used as the standard plot size.

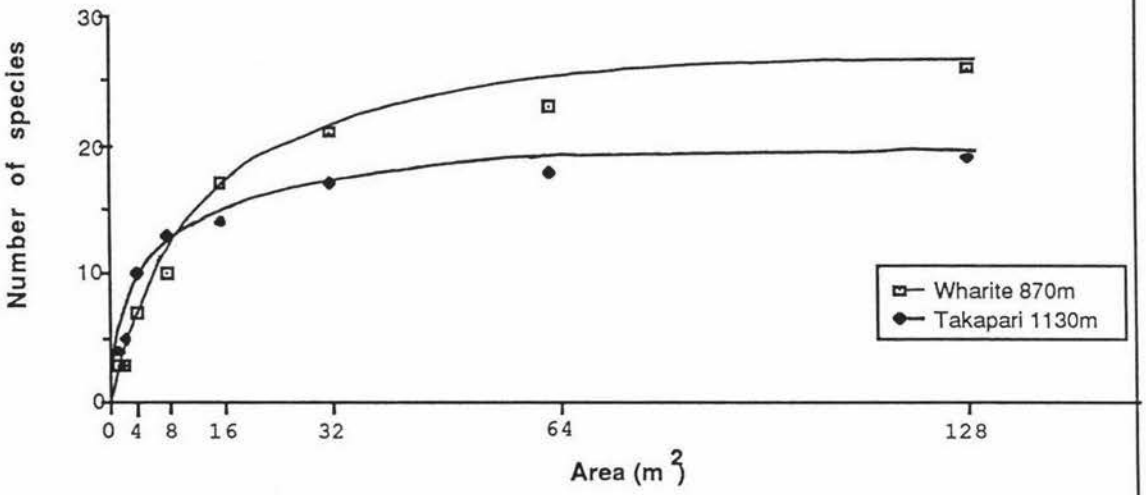

FIGURE 6.2 Species-area curves generated from two geometrically increasing nested plot sequences in the southern Ruahine leatherwood; Wharite at 870m and Takapari Plateau at 1130m.

Phytosociology

The average number of species recorded per 25m^2 plot for all regions was 16 (range 8 - 24). The averages for the different regions were; Ruahine 16.9 (n=21), Egmont 16 (n=6), Central Westland 16 (n=3), south Central Westland 10 (n=3) and Tararua 18 (n=1). Species diversity (No. of species per plot) in the Ruahine leatherwood plots declined with increasing altitude ($R=0.56$ $p<0.005$). Canopy height declined with increasing altitude and exposure. Soil depth was variable as were other environmental parameters (Table 6.1)

TABLE 6.1 Environmental parameters, dominant canopy species, average canopy height and number of seedlings and saplings of *Olearia colensoi* for Leatherwood plots from five regions. Plot prefixes are as follows; R = Ruahine, E = Mt Taranaki, F = Mt Fox, CC = Camp Creek and T = Tararua (see fig 6.1 for locations). Species are shown by the first three letters of their binomials (see table 6.2 for full species names)

Plot	Altitude	Aspect	Slope	Phys	Soil depth	Dominant sp+%cover	Canopy height (m)	Seedlings / saplings $25m^{-2}$
R1	870	270	16	ridge	300	Ole col 83%	2.5	66
R2	1130	89	35	face	400	Ole col 88%	2.1	400
R3	1040	25	55	face	267	Ole col 85%	2.3	52
R4	900	160	35	face	595	Ole col 48%	2.4	180
R5	800	120	50	spur	247	Ole col 31%	3.0	136
R6	1030	20	24	face	311	Ole col 100%	2.5	503
R7	1140	140	2	face	417	Ole col 78%	2.0	510
R8	1062	350	22	face	545	Ole col 92%	2.5	71
R9	1090	210	6	plateau	390	Ole col 96%	2.1	83
R10	820	310	25	spur	510	Cop pav 50%	1.8	0
R11	1030	330	44	face	207	Ole col 95%	3.3	7
R12	1060	340	30	spur	465	Ole col 94%	2.6	40
R13	800	160	18	ridge	498	Psew col 45%	2.2	4
R14	808	180	20	spur	437	Psew col 25%	2.0	1
R15	854	60	9	ridge	412	Ole col 80%	2.4	190
R16	1016	75	15	face	280	Ole col 100%	2.2	123
R17	1055	270	15	spur	350	Ole col 95%	2.2	180
R18	946	270	20	ridge	390	Ole col 90%	2.6	120
R19	890	90	5	ridge	450	Ole col 90%	2.3	255
R20	900	170	10	ridge	395	Ole col 95%	2.4	360
R21	1000	40	15	ridge	380	Ole col 90%	3.1	180
E1	1050	18	5	face	*	Psed col 50%	2.5	*
E2	1160	140	5	face	*	Bra ela 50%	2.3	*
E3	1281	50	10	spur	*	Bra ela 50%	1.8	*
E4	1400	50	15	face	*	Bra ela 50%	1.2	*
E5	1312	150	10	face	*	Dra lon 50%	1.0	*
E6	1200	180	10	ridge	*	Bra ela 80%	1.5	*
F1	1113	280	30	ridge	250	Ole col 30%	2.8	*
F2	1045	280	22	ridge	450	Ole col 50%	2.3	*
F3	991	250	25	ridge	*	Ole col 70%	2.5	*
CC1	1129	260	40	face	*	Dra lon 25%	2.4	*
CC2	1204	300	45	face	*	Dra uni 60%	2.6	*
CC3	1122	290	38	spur	*	Ole col 70%	2.5	*
T1	976	240	35	face	*	Ole col 40%	2.5	*

Plot R9 (Fig.6.3) is typical of the leatherwood community of the Takapari plateau where at 1090 m the leatherwood appears to have been stable for many generations. At this plot the average height of the scrub is 2.1 metres. The average soil depth is 390mm on a south-west slope of 6°. *Olearia colensoi* is the only canopy species present with 95% cover (5% open canopy). Density of canopy *Olearia colensoi* plants is 1.64 plants m^{-2} while the density of seedlings and saplings is 4.84 m^{-2}. Twelve other subcanopy or ground dwelling vascular plant species occur in the plot but their total cover is only 24%, 70% of the floor cover being litter. The leatherwood belt is some 3 kilometres wide at this point and of uniform composition (Fig.6.4).

Plot E3 (Fig 6.5) is typical of the main leatherwood belt on Mount Taranaki where at 1281m the 1.5m canopy is dominated by *Brachyglottis elaeagnifolia*, *Dracophyllum longifolium* and *Coprosma pseudocuneata* (50%, 30% and 20% cover respectively).

Plot F1 (Fig 6.6) is typical of the leatherwood belt on Mount Fox where at 1113m the 2.8m canopy is dominated by *Dracophyllum longifolium* and *Olearia colensoi* (50% and 30% cover respectively).

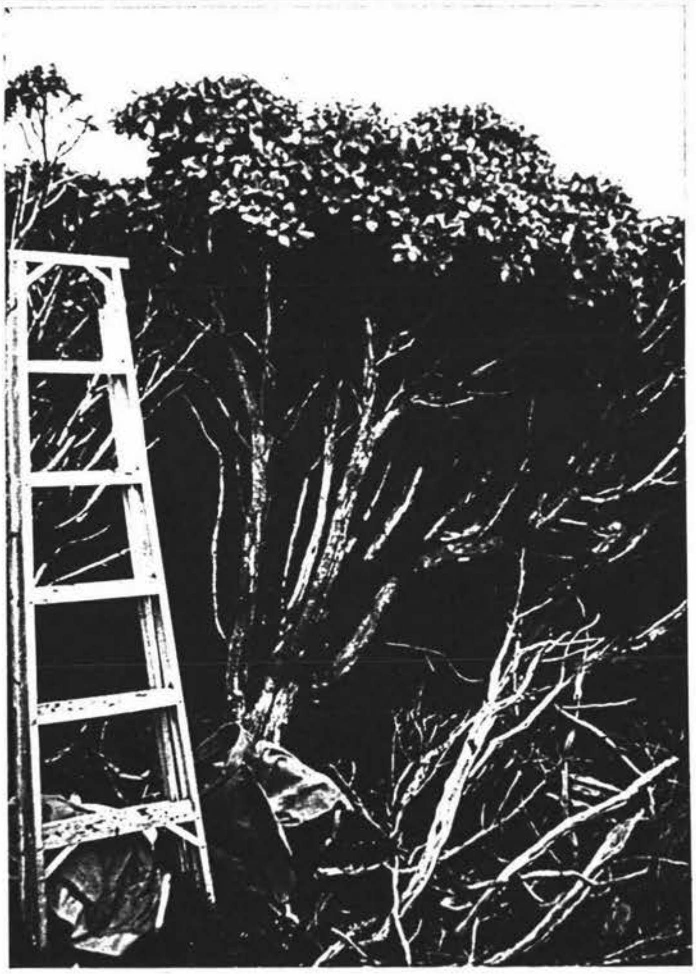

FIGURE 6.3 Southern Ruahine leatherwood from the track side in the vicinity of Plot R9 at 1090m, typical of the leatherwood on the Takapari plateau where *Olearia colensoi* dominates the 2.1m high canopy.

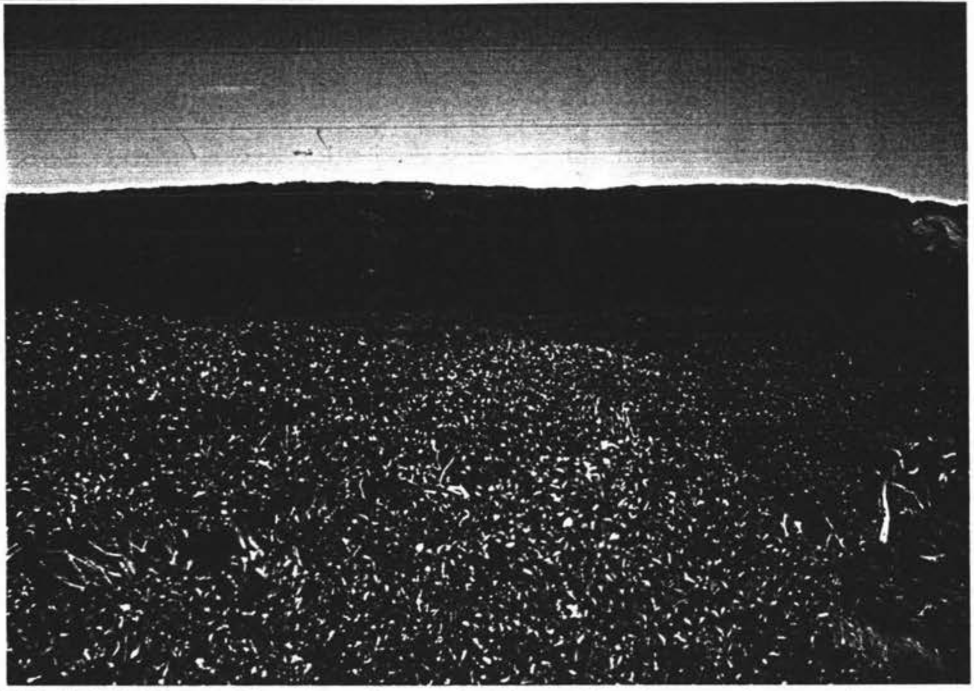

FIGURE 6.4 Uniform *Olearia colensoi* dominated leatherwood extensive on the Takapari plateau.

FIGURE 6.5 Mount Taranaki leatherwood at 1281m where the 1.5m canopy is dominated by *Brachyglottis elaeagnifolia*, *Dracophyllum longifolium* and *Coprosma pseudocuneata* (50%, 30% and 20% cover respectively)

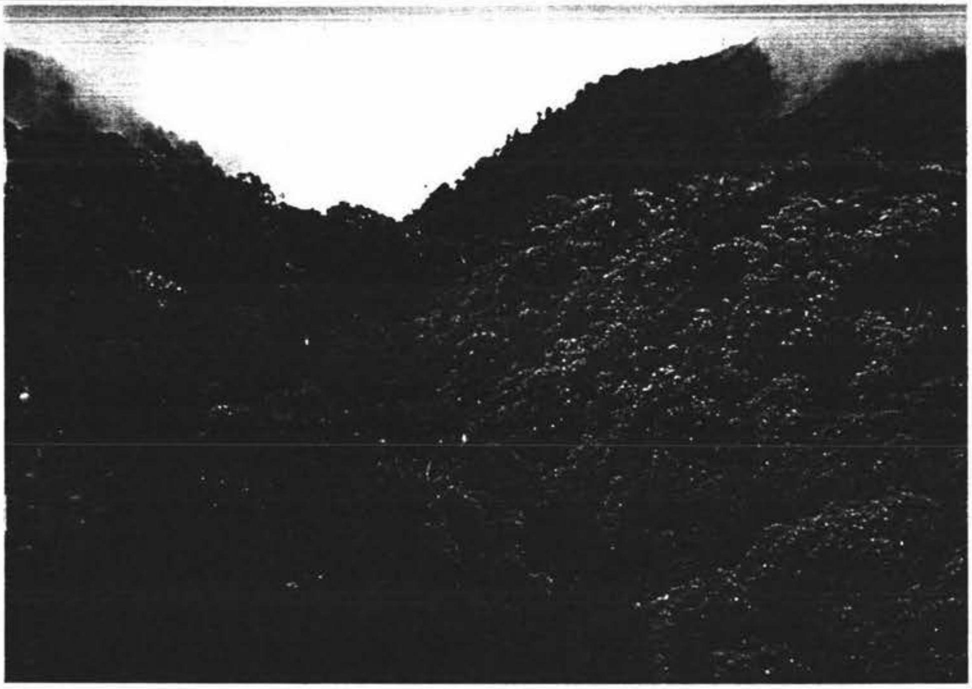

FIGURE 6.6 Typical leatherwood on Mount Fox where at 1113m the 2.8m canopy is dominated by *Dracophyllum longifolium* and *Olearia colensoi* (50% and 30% cover respectively) Some *Dracophyllum traversii* also noticeable.

Classification of leatherwood communities

The cluster analysis (Euclidean Distance, Ward Minimum Variance) was examined at the four group level (Fig. 6.7). The groupings corresponded with geographical regions with some exceptions. Two plots grouped with plots from outside their geographical region: plot F3 and R4 (Fig 6.7, see Fig. 6.1 for sites). Plot F3 grouped with the main group of Ruahine plots. F3 was the most similar of all the Westland plots to those of the Ruahine in that it had a high (70%) cover of *Olearia colensoi* and a low cover of *Dracophyllum* species, this together with low diversity (only 8 species present) resulted in F3 clustering with the main Ruahine group. Plot R4 grouped with the Fox and Tararua plots due in the main to a 33% cover of *Brachyglottis elaeagnifolia* * which was the highest recorded for any Ruahine plot. It also had higher than average cover of *Leptopteris superba*, *Polystichum vestitum* and *Coprosma foetidissima* which contributed to its disassociation from the other Ruahine plots. Two Ruahine groups

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*In this study *Brachyglottis elaeagnifolia* and *B. bennettii* are treated as the same species in accordance with the opinion of A.P. Druce that they are varieties of the same species (*B. rotundifolia.*) For ease of use in figures and in tables *B. elaeagnifolia* has been used to cover both species.

emerged from the dendrogram: a smaller group of four lower altitude ecotone plots and the larger closely branched group of plots from the main altitudinal leatherwood zone.

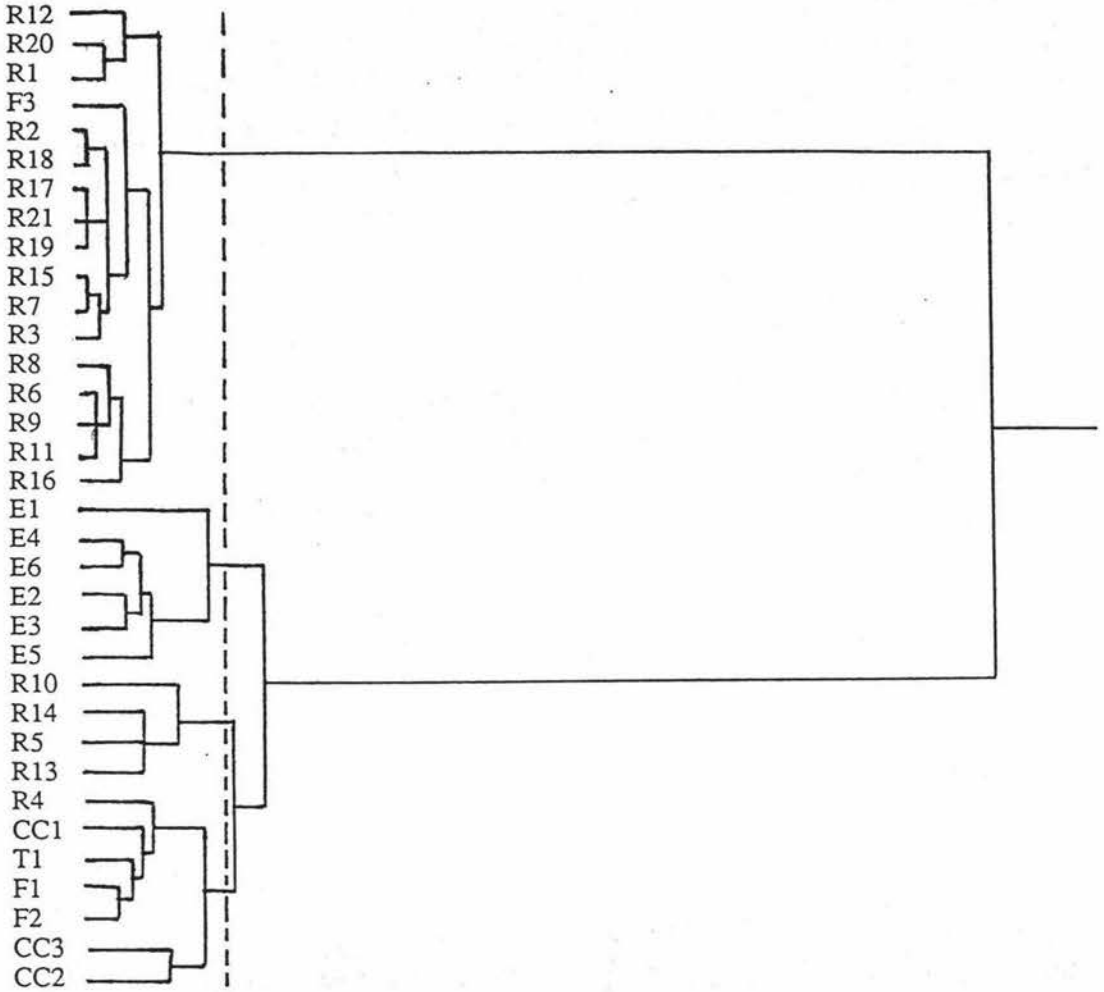

FIGURE 6.7 Dendrogram of leatherwood plots from all regions clustered using Euclidean Distance and Ward Minimum Variance in the programme SYSTAT. Plot prefixes are as follows; R = Ruahine, E = Mt Taranaki, F = Mt Fox, CC = Camp Creek and T = Tararua (see Fig 6.1 for locations)

The groupings generated by the classification correspond well with plot distribution in the DCA ordination (Fig 6.8). The Southern Ruahine plots grouped into two with one much larger group forming a tight cluster to the lower left of the ordination. The smaller Ruahine group consisted of four plots all from low altitudes (800-820m) and was influenced by the occurrence of a number of forest dwelling species to be seen in the upper left of the species DCA ordination (Fig 6.9). Plots forming the larger Ruahine group were all of higher altitude (854-1140m) and with a much greater cover of *Olearia colensoi* (85% compared to 16% average for the lower altitude plots). All the Mt

Taranaki plots grouped together in the dendrogram and formed a distinct cluster to the right of the ordination. The altitudinal range of these plots was 1050m to 1400m and although the dominant species were the same in most plots some variation in cover and co-occurring species were apparent (Table 6.2). The Tararua plot fell intermediate on the ordination between the Ruahine and most of the Westland plots but grouped as a best fit with two of the Mt Fox plots, plot CC1 and the Ruahine 4 plot, in the dendrogram. Two of the Camp Creek plots (CC2 andCC3) formed the smallest group.

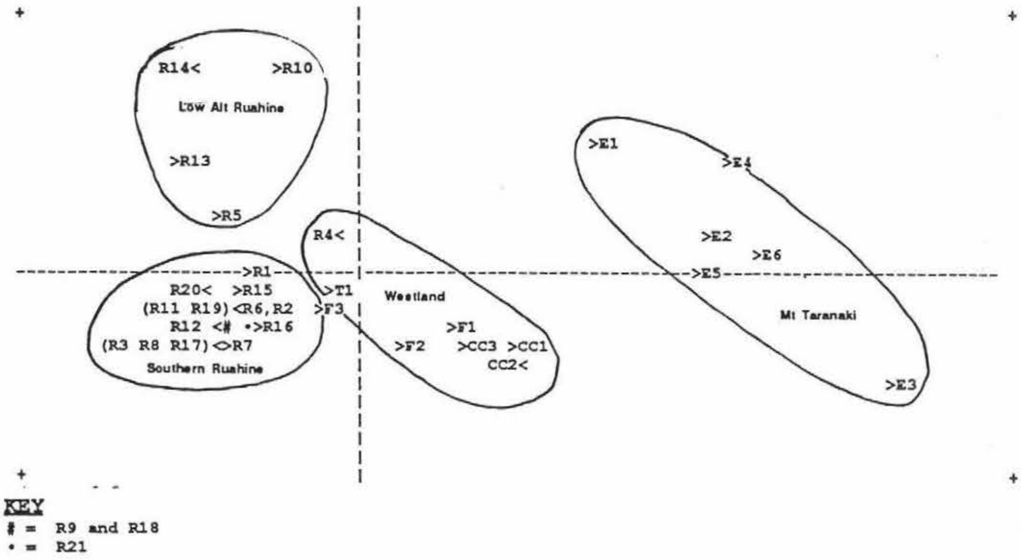

FIGURE 6.8 Detrended Correspondence Analysis ordination of leatherwood plots from all regions. Plot abbreviations are: E = Mount Taranaki, F = Mt Fox (South Westland), CC = Camp Creek catchment (Central Westland), T = western Tararua Range, R = southern Ruahine. Axis 1 is horizontal, axis 2 is vertical. The exact position of plots in the ordination is occupied by the pointers (<,>,^) Cluster analysis groups are indicated.

```
                                 |                                          KEY
                                 |                                          1 = GEN SP
        >MET FUL                 |                                          2 = NER CIL
                                 |                                          3 = UNC SPB
                     RUB CIS     |                                          4 = GRAMITI
           >CYA SMI  ^>BLE FLU   |                                          5 = OLE ARB
        >MET DIF                 |                                          6 = COP FOE
                                 |                                          7 = CHI FLA, DRA TRA, CYATHOD
  ASP BUL <>MYS SAL      >MULENBE       >POD HAL
                                 |
                  >BLE DIS       |
                                 |                             >COP TEN, CAR ARB
       >CLE SPP                  |                                                >CHI RUB
             >LUZ PAV            |     >COP PAV
                                 |
             >PSEWCOL            |      GRI LIT <>BLE MIN             >CORYBAS      >CAS VAU
                >CYC PEN         |                  >UNC SPA
             >MIC AVI            |                             >PSEPCOL
           >LIB PUL  >PSE SIM    |                                             >CORIARI
             >LIB IXI            |            >MYR DIV
                          >DIC SQU                                            >GAH PRO
         UNC SPC <  V 6 >LEP SUP |
                    WEI RAC      |                                       >BRA ELE
              >PRU FER      BLE CAP  >AST NER                                   >PSE ANO  >CEL GRA
-------------------->POL-VES---^-|-->GAU-SP----------------------------------------------------------------
                    BAREGRD <5 >EPI SPP                                       >CEL GLA, FORSTER
         HYEMENO <  3    4 >FUC EXC
     SCH NIT < 1,2>(MEL LAN, PIT RIG)                                                         >GAU DEP
     LIB BID <  V  >OLE COL      |
               (SCH ALL, STE LLA)|   >OLE LAC        COP PSE < >ANI ARO                        >DRA LON
         CHI CON <>HAL BIF       |  PHO COO <>PTE BAN                                      >LYC FAS
                                 |  COP SER <    >7      ARC TRA
                                 |            >PIT CRA      ^    >OUR MAC
                                 |         DRA UNI < >CEL ARM
                                 |                   >CHI PAL                          (HEB STR, HEB ODO)<
                                 |
```

FIGURE 6.9 Detrended Correspondence Analysis ordination of species from all plots from all leatherwood regions. Species are shown by the first three letters of their binomials (see Table 6.2 for full species names). The exact position of species in the ordination is occupied by the pointers (<,>,^)

Plots and species when arranged in order of their of their DCA scores (Table 6.2) showed a unimodal response of species to environmental factors as indicated by the elliptical shape oriented on the diagonal from top left to lower right (Jongman, ter Braak and van Tongeren, 1987). Species in the leatherwood formations that have their ecological optima in leatherwood communities with a dominant *Olearia colensoi* component form a large group in the centre of the table. The species most commonly associated with *Olearia colensoi* in the main leatherwood belt in the southern Ruahine are in order of decreasing percent cover; *Astelia nervosa*, *Hymenophyllum* species, *Microlaena avenacea*, *Polystichum vestitum*, *Psedowintera colorata*, *Psedopanax simplex*, *Coprosma parviflora*, and *Brachyglottis elaeagnifolia*. (Table 6.2).

TABLE 6.2 Leatherwood plots from five regions showing species percent cover per plot. Species and plots are arranged in order of their DCA scores. The 4 main groups generated by the Classification dendrogram are defined by vertical lines. Species characteristic of *Olearia colensoi* dominated leatherwood communities form the large central portion of the table. Plot prefixes are as follows; R = Ruahine, E = Mt Taranaki, F = Mt Fox, CC = Camp Creek and T = Tararua (see Fig 6.1 for locations)

	E3	E6	E4	E2	E5	E1	CC2	CC1	CC3	F1	F2	R4	T1	F3	R21	R16	R6	R2	R1	R15	R19	R11	R9	R7	R18	R17	R3	R8	R20	R12	R10	R5	R14	R13
Hebe stricta	30			20		15																												
Hebe odora	2	5																																
Dracophyllum longifolium	30	2	2	5	50	5		25	2	50	40		<1	5																				
Celmisia gracilenta	1		1																															
Gaultheria depressa	1			1																														
Lycopodium fastigiatum	1				1																													
Cassinia vauvilliersii	2		15		10																													
Pseudopanax anomalus		1			1																													
Chionochloa rubra			15																															
Coriaria plumosa			1		1																													
Gahnia procera				1																														
Celmisia glandulosa					1																													
Fostera tenella					1																													
Brachyglottis elaeagnifolia	50	80	50	50	40	35	50	10	1			33	15		5		2	3	2	2	1	2			1				1		1	1		
Corybas macranthus				1		1																												
Ourisia macrophylla	2		1		1		5	1	1																									
Anisotome aromatica	1		1		1		1			1																								
Coprosma tenuifolia						20																												
Carmichaelia arborea						1																												
Pseudopanax colensoi	5	2		15		50	1	1						4		1			2	2	1	1								1				
Coprosma pseudocuneata	20	15		20	30	1	40	15	45	20	20		5					1					1	<1										
Archeria traversii								10																										
Chionochloa pallens							15		1																									
Uncinia spA	1	1		1		30		1				<1				1	3		5	<1	1		2					<1			1			
Celmisia armstrongii							1	1	1																									
Dracophyllum uniflorum							60	20	50																									
Blechnum minus						20	40						5		1					1					1						5			
Cyathodes fasiculata								1			1																							
Chionochloa flavescens							1	2	1	5																								
Dracophyllum traversii								20	5		5			6																				
Griselinia littoralis		1				20							1				1			1	2	<1						<1		<1			1	1
Pittosporum crassiuscula									4																									
Myrsine divaricata		1		5		20						6	1	4	1	1	1	4					1	<1	2		1	<1						
Pterostylis banksii						1																					1							
Phormium cookianum								8	4	10	4		2				1	1										<1		<1		11		
Coprosma serrulata							2	1		5	8																							
Podocarpus hallii		1				15														1												1	11	
Astelia nervosa	1	1	1	1	5	50		10	1	20	15	5	20	20	1	20	7	3	6		5		3	4		1	1		1		4	5		
Coprosma paviflora			30	5	1	1						3			1		4	5		2		2	4	1	1	1	<1	2	1	4	50			
Olearia lacunosa							5				8			4																				
Gaultheria sp					1		50	1		4	4		5								1										5	3		
Epilobium sp		1				1									1		3																	
Blechnum capense	1	1		1	5				10		6	3		2			2		5		5	<1	2				4	7		3	9	5	<1	1
Olearia arborea				1		1							1				4																	
Dicksonia squarosa												4																				1		
Fuchsia excortica				1											1		3																	
Mulenbeckia australis					1							<1																	1		4		<1	
Gramittis spp				1		1					1	<1			1	1				1	1	<1	1			1	<1	1	1	1				<1
Leptopteris superba												33					3	3				1			5							1	1	4
Blechnum fluviatile												<1																			3			
Coprosma foetidissima												18	15		1					5	1								1			7		8
Pseudopanax simplex		2	1	5	1	1						8	1		1		5	4		5	1	10		<1	1	2	1	1	1	8	9	12	18	1
Rubus cissoides																				1											9			
Polystichum vestitum												26			1	1	5	9	4	2		3			10		<1	3		84	3		1	2
Uncinia spB												1	5		1	1	<1	6	1	<1	1	<1	1	2	1	1	1	1		<1	1	1		1
Weinmannia racemosa												2	1							2												2		1
Olearia colensoi							15	20	70	30	50	48	40	70	90	100	100	88	83	80	90	95	96	78	90	95	85	92	95	94		31	1	35
Blecnum discolor																			4	1											20	2		6
Halocarpus biformis								5													1				5		16			20			1	
Pittosporum rigidum																		6																
Melicytus lanceolata																	6																	
Nertera ciliata																	<1			<1														
Cyclosorus peniga																														1	1			
Uncinia spC															1		2	3			1	1			1					1	3	2		
Hymenophyllum spp						1	10					9	1		1	1	9	1	4		1	6	9	<1		1	3	14	1	10	1	2	1	4
Chionochloa conspicua													2														5			1				
Stellaria decipiens																	<1						<1											
Schizeilema allani					1																						4	1		4			<1	<1
Gentiana sp																		1		1				<1			1					<1		
Prumnopytis ferruginea																				2														1
Luzuriaga parviflora									5											1	1				1						1	3	3	
Schizeilema nitens																1	2						8		1	1		19						
Pseudowintera colorata												6	1		1		<1	3	21	1	1	6			1				10	7	19	15	25	45
Microlaena avenacea												1					1		11	5	5		3		1				20	5	16	9	11	25
Libertia ixiodes																																1		
Libocedrus bidwillii																												<1		19		1		
Cyathea smithii																					1								1		8		18	3
Libertia pulcella																				1	1											8	1	1
Myrsine salicina																			<1												18	7	24	35
Asplenium bulbiferum																						<1											1	
Metrosideros fulgens																																	5	
Metrosideros diffusa																																	4	3
Clematis paniculata																																		<1
				Mt Taranaki						Westland													Southern Ruahine									Low Alt Ruahine		

The CCA of Ruahine plots with biplot of environmental variables (Fig 6.10) shows that the first axis of the ordinations corresponds principally to altitudinal differences between plots. Lower altitude plots at the lower altitudinal range of *Olearia colensoi* occur on the right of the ordination and are characterised by those species to the right of the CCA of species (Fig 6.11). Environmental variable biplot scores are plotted as arrows on the ordination. The direction of the arrow indicates the direction of maximum change of that variable, and the length is proportional to the rate of change. Environmental variables with long arrows are more strongly correlated with the ordination axes than those with short arrows, and therefore are more closely related to the community variation shown in the ordination (Ter Braak 1987). Most of the Ruahine plots form a tight cluster close to the centre of the ordination and represent plots from the optimal range of *O. colensoi*.

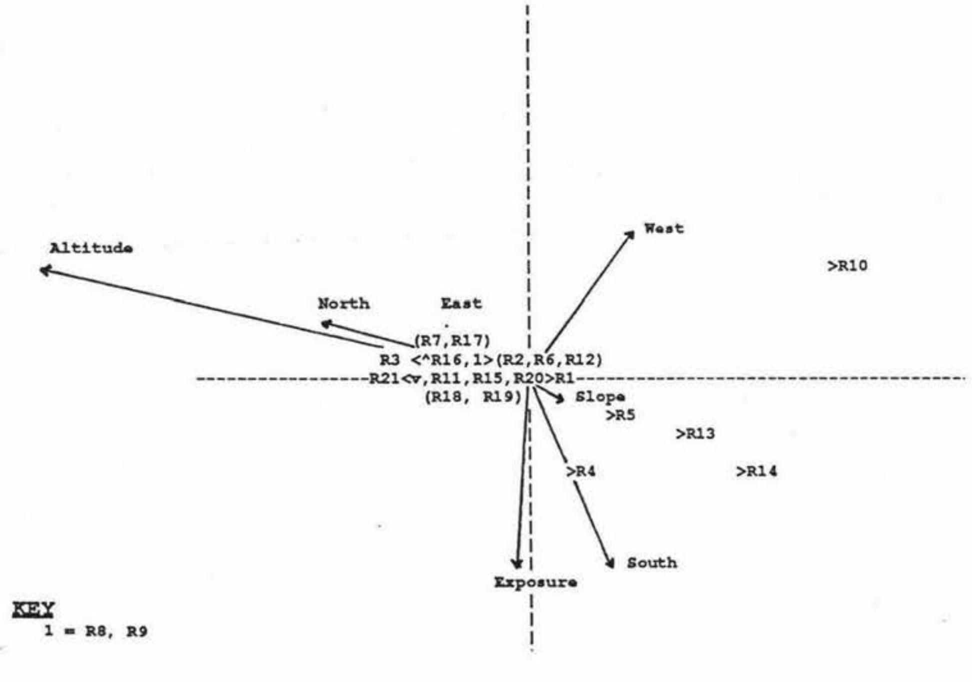

FIGURE 6.10 Canonical Correspondence Analysis of southern Ruahine plots and environmental variables (arrowed). The direction of the arrow indicates the direction of maximum change of that variable, and the length is proportional to the rate of change. The longer the arrow, the stronger the correlation with the ordination axes. Exact position of plots in the ordination is occupied by the pointers (<,>,^)

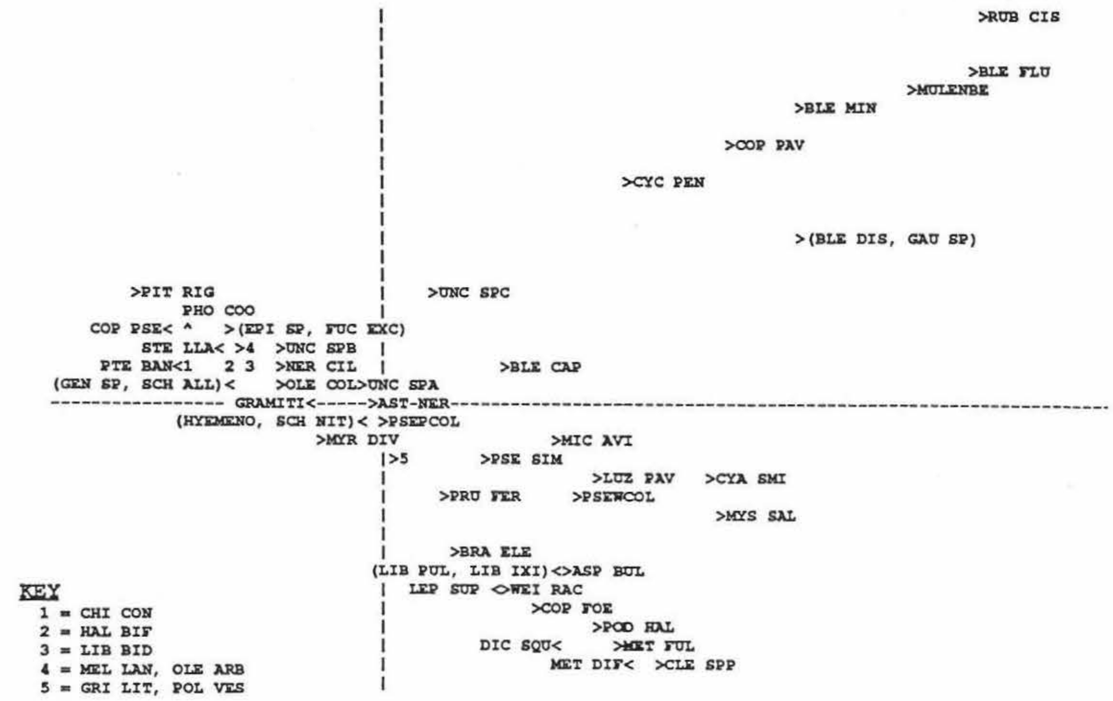

FIGURE 6.11 Canonical Correspondence Analysis of species from the southern Ruahine plots only. Species are shown by the first three letters of their binomials (see table 6.2 for full species names). Exact position of species in the ordination is occupied by the pointers (<,>,^)

Leatherwood Ecotones

Increment cores at the *Halocarpus/Libocedrus* ecotone

The average age of both dead and healthy *Libocedrus* trees in the ecotonal regions currently under decline is 294 years (Table 6.3). The *Olearia colensoi* canopy shrubs in these areas are on average 37 years old. Scattered older *O. colensoi* individuals occur in these areas that are up to 200 years old (Fig 6.12) while the average age of *O. colensoi* in the more typical leatherwood communities is 67 years (Table 6.3).

TABLE 6.3 Height, DBH (Basal diameter for shrubs) and age (established from increment cores) of ecotone *Libocedrus* and *Halocarpus* , and *Olearia colensoi* in the southern Ruahine.

Species	Location	Altitude(m)	Height(m)	DBH(mm)	Age	Health
Libocedrus bidwilli	Delaware Ridge	1090	11	334	168	good
	Delaware Ridge	1090	11	270	226	good
	Wharite	800	7.5	336	198	good
	Wharite	824	13	560	694	dead
	Wharite	885	4	400	204	dead
	Wharite	885	4.5	318	203	dead
	Wharite	885	12	500	418	declining
	Wharite	885	11	520	288	good
	Wharite	890	4	388	262	dead
	Wharite	890	3.2	286	283	dead
				Average	**294**	
Halocarpus biformis	Takapari	1075	1.8	194	278	dead
	Takapari	1075	2.0	175	264	declining
	Takapari	1075	2.2	318	318	good
	Delaware Ridge	1090	8	344	335	good
	Delaware Ridge	1140	1.78	155	224	good
	Wharite	824	7	426	348	good
				Average	**295**	
Main Leatherwood Zone						
Olearia colensoi	Tamaki	1000	3	160	48	good
	Tamaki	1085	2.2	235	77	good
	Wharite	900	3	155	67	good
	Wharite	900	2.7	145	72	good
	Wharite	900	2.6	135	69	good
				Average	**67**	
Ecotone						
Olearia colensoi	Delaware Ridge	1090	5.5	400	200	good
	Delaware Ridge	1090	2.1	82	37	good

FIGURE 6.12 The leatherwood /*Libocedrus -Halocarpus* ecotone on the Delaware Ridge at 1090m (upper photo) and on Wharite at 824m (lower photo). On the Delaware Ridge dead and aged *Libocedrus* / *Halocarpus* and scattered old (200yr) *Olearia colensoi* (arrowed), overtop a younger (30-37yr) leatherwood formation.

DISCUSSION

Minimal Area

Typical sizes of plots to be used for analysing different vegetation types can be found in most vegetation ecology texts. Values ranging from $100m^2$ for forests to $20\text{-}50m^2$ for various scrub types are commonly quoted (Mueller-Dombois 1974). The optimal size will depend on the particular vegetation being sampled. Minimal area curves provide a means of deciding on plot sizes in an objective way and are particularly useful in previously unsampled or variable vegetation. Because of the density (impenetrability) of the leatherwood scrub subjective assessment of plant diversity, and plot sampling area required, could tend toward underestimation. The $25m^2$ plot size determined from the species area curves ensured that the plot size used would record 90% of the likely occurring species over the main altitudinal range of the leatherwood formation. This plot size was however barely manageable in the dense scrub conditions.

Phytosociology of leatherwood

The average number of species occurring in plots from the different geographical areas is very similar; therefore species diversity of the different areas is not significantly different but species composition and cover is (Table 6.2).

The results of the classification concur in the main with geographical regions. Minimum Variance Clustering was used to produce the dendrogram and is useful when plots are suspected to come from homogeneous classes (Pielou 1984). Only two plots transgress regional boundaries in the dendrogram (Fig 6.11). One of the main features influencing the clustering of plots is the percentage cover of *Olearia colensoi*. The Mount Taranaki sites have no *Olearia colensoi* and fall well to the right on axis one of the DCA ordination. The Ruahine plots group on the left of axis one while the Westland sites fall in between. The one Tararua site falls intermediate between the main Ruahine group and the Westland sites in the ordination and groups with the Westland sites in the dendrogram; thus while the Tararua plot had similarities in species composition to the southern Ruahine, due to its relatively close proximity, there were differences in community structure that in total were more similar to the Westland leatherwood areas. Logistic constraints prevented further plots being recorded from the Tararua Range. Leatherwood in the northern Tararua Range is thicker and more similar to the southern Ruahine than the Western Tararua. The Fox 3 site groups with the main Ruahine group and is a reflection of its high *O. colensoi* cover, the highest recorded for the Westland sites. The extent of continuous areas in Westland with this degree of *O. colensoi* cover appear however to be limited (*pers. obs.* and deduction from *pers.comm.* R. Stocker).

Mount Taranaki was included in the study because of its extensive leatherwood zone which in the absence of *O. colensoi* is instead dominated by *Brachyglottis elaeagnifolia*. In other areas these two species commonly occur together but their altitudinal range is not identical. The differences in distribution and dominance are likely due to a combination of; altitudinal preference, browse resistance / palatability, and site colonisation / habitat preferences. Clarkson (1986) compared the North Island distribution of *O. colensoi* and *B. elaeagnifolia* and found *O. colensoi* lacking on recent volcanic soils while *B. elaeagnifolia* flourished on them. In the southern Ruahine leatherwood, *B. elaeagnifolia* is more common at lower altitudes (Elder 1965) and on suitable sites can grow below the altitudinal range of *O. colensoi* . Areas in the southern Ruahine dominated by *B. elaeagnifolia* are small and confined to previously disturbed sites, as on the road berm of the Wharite Peak road from 700m to 880m.

No exotic species were recorded in any of the plots although some adventive weeds were present along track sides and in disturbed areas. The main leatherwood belt when left undisturbed is comparatively immune to exotic plant invasion

The CCA of southern Ruahine plots shows a strong correlation of the first axis with altitude which is the main environmental variable influencing the community structure. The bulk of the Ruahine plots form a tight cluster in the centre of the ordination. Those plots that fall outside this main cluster are from the lower altitudinal range of *O. colensoi*. The analysis indicates that the main leatherwood belt of the southern Ruahine is particularly homogeneous. Only at lower altitudinal zones does species composition and cover change enough to be distinguishable by ordination.

Ecotones

Olearia colensoi appears to have been the dominant stable vegetation on the Plateau regions of the southern Ruahine for thousands of years. At lower altitudes it has increased in density over the last 30-50 years with the demise of the montane *Weinmannia racemosa* forest and the high altitude forest species, particularly *Libocedrus* and *Halocarpus* and their attendant sub-canopy species of *Pseudopanax colensoi*, *P. simplex*, *Coprosma foetidissima* and other preferentially browsed species. An example of this type of vegetation change can be seen at 1090m on the Delaware ridge (Fig 6.12). At this site the current vegetation consists of scattered tall 300 year old *Libocedrus* and *Halocarpus* with some individuals of *Cordyline indivisa* and *Pseudopanax simplex*, and one very large (5.5 metre high, 33cm basal diameter) 200 year old *Olearia colensoi* plant. Beneath these taller plants there is a thick, uniform, 2.5 metre high canopy of 30-37yr old *Olearia colensoi* plants. The best interpretation of the events leading to this current situation is that a once intact *Libocedrus / Halocarpus* canopy has deteriorated over the last fifty years due to decline of the mature trees and hastened by the destruction of the understorey by introduced animals. The original, probably dense, understorey of species such as *Pseudopanax colensoi*, have all but been removed by browsing animals; possums, deer and goats. With the deterioration of the understorey and the death of some of the canopy trees the canopy would have become very open and fragmented, allowing the severity of wind effects on the remaining trees to increase, further hastening the decline. A few *Olearia colensoi* plants were growing as subcanopy species in the original *Libocedrus/Halocarpus* forest. These plants were not preferentially browsed and survived while the other subcanopy species declined. These large *Olearia colensoi* individuals contributed to the seed source which enabled *Olearia colensoi* to opportunistically establish in the gaps created by the subcanopy destruction. This animal-induced collapse would have occurred some thirty to forty years ago (based on the age of the *Olearia colensoi* plants that currently occupy the site) and this corresponds with the accepted dates of peak animal numbers in the southern Ruahine (early 1950's for possums and deer, Cunningham 1978) .

In contrast with these ecotone areas the main belt of leatherwood in the southern Ruahine is particularly uniform. Plot R9 (Fig.6.3) is typical of the leatherwood community on the Takapari plateau where at 1090 m the 2.1m leatherwood appears to have been stable for many generations. *Olearia colensoi* is the only canopy species present with 95% cover (5% open canopy). All other subcanopy or ground dwelling vascular plant species have a total cover of only 24%. The leatherwood belt is some 3 kilometres wide at this point and leatherwood of similar composition stretches as far as the eye can see.

Conclusions: Leatherwood in New Zealand

While there are overall similarities in the leatherwood areas of New Zealand there are major differences in species composition and relative dominance of key species. The Mt Taranaki leatherwood stands out for its lack of *O. colensoi* and high *B. elaeagnifolia* cover. Westland sites have localised areas of high *O. colensoi* cover but co-dominant *Brachyglottis bennettii* and *Dracophyllum* species also have high cover values and other canopy forming species such as *Olearia laucunosa* and *Olearia ilicifolia* are also common. The southern Ruahine stands out from the other areas in the dominance of the canopy by *O. colensoi* with an average cover value of 91% over its optimal range (42% for Westland and Tararua, and 0% for Mt Taranaki). Few other canopy forming species are present in the southern Ruahine leatherwood. *Dracophyllum* species particularly are virtually absent whereas they are a common canopy shrub in the other leatherwood areas. The southern Ruahine is unique not only in the extent of the leatherwood zone but also in the community composition of the leatherwood. The leatherwood community in the southern Ruahine is particularly homogeneous as the cluster and ordination analysis showed.

CHAPTER 7

GENERAL DISCUSSION

The southern Ruahine leatherwood zone is the longest continuous leatherwood area in New Zealand (DoC 1992) and is the dominant feature of the North Manawatu Gorge Ecological District. Because of this the zone has been recognised as a potential Ecological Area in the current Ruahine Forest Park Management Plan (DoC 1992) in an effort to afford the area appropriate protection status. As well as the size of the leatherwood zone the southern Ruahine is unique in the degree of dominance by one species: *Olearia colensoi*. No other leatherwood area in New Zealand has the same degree of dominance by *O. colensoi* over such a large area. To many people however the leatherwood zone and *O. colensoi* in particular is considered a nuisance due to its impediments to free travel. In this sense leatherwood suffers from the lack of understanding that other habitats such as swamps and wetlands have experienced in the past.

The extensive sub-alpine zone in the southern Ruahine and equivalent areas on Mount Taranaki and in Central Westland are all areas of disjunction in the distribution of *Nothofagus*. In the absence of the high altitude *Nothofagus* species (*N. menziesii* and *N. solandri* var *cliffortioides*) the treeline is lower than normal and an extensive subalpine scrub zone occurs above the treeline (Dawson 1988). Local depressions of the treeline can also occur due to high incidence of fog (Dawson 1988). Where absence of beech and high incidence of fog/cloud occur together, as in the southern Ruahine, Taranaki and Westland, the broadest belts of subalpine shrubland are found. While the nomenclature of treelines is poorly standardised (Wardle 1981) the term 'subalpine' is used by some to imply that the potential treeline lies at the upper limit of these shrublands and that it is the local climatic conditions and absence of suitable species such as *Nothofagus* that allows a lower altitude range for the scrub species.

Hypotheses to explain the position and occurrence of treelines centre on summer environmental conditions as they influence carbon fixation, shoot growth, and shoot maturation (Wardle 1981). Above the approximate position of the 10°C isotherm for the warmest month mean temperature, plant growth is limiting and trees will not persist (Tranquillini 1978, Wardle 1974). In the Ruahine, January is the month with the highest mean temperature. Temperature data collected during this study and calibration of long term data from Wharite Peak and Palmerston North indicate that the 10°C isotherm for January in the southern Ruahine occurs at ≈1250m (based on a lapse rate of 0.61°C per

100m). The actual treeline varies between 850 to 1050m, considerably lower than the potential treeline.

The absence of *Nothofagus* from large areas is often attributed to failure to recolonise after massive deforestation caused by glaciation (Westland) or vulcanism (Central North Island) (Wardle 1984). Zotov (1938) suggested that the frequent cloud cover favours subalpine scrub at the expense of *Nothofagus* by reducing light levels to a point where beech seedlings are not competitive. Wardle (1986) tested this hypothesis. Using satellite photos he found no convincing correlation between cloud cover and forest type, though the distribution of individual species was related to climatic factors. *O. colensoi* showed highly significant correlations with respect to precipitation. The absence of *O. colensoi* from the volcanic mountains Egmont, Tongariro and Ruapehu was however unrelated to climatic parameters.

There are then two major factors associated with broad sub-alpine scrub zones in New Zealand

- the absence of the two tree line forming *Nothofagus* species (*Nothofagus menziesii* and *Nothofagus solandri* var *cliffortioides*)
- and a high precipitation, high cloud cover climatic regime

The southern Ruahine has both of these conditions and is unique in the physical extent of the sub-alpine zone over which these conditions predominate. The narrowness of the range and relatively low height of the peaks contributes to the breadth of the leatherwood area as the subalpine belts from both sides of the range effectively meet at the top to form one continuous subalpine zone. The meteorological data presented in Chapter 3 confirmed existing records that the southern Ruahine is one of the cloudiest and windiest areas of high rainfall in New Zealand. The high cloud cover is probably one of the most significant factors in allowing the leatherwood zone to proliferate. High cloud cover effectively increases the total precipitation, maintains high humidity conditions and decreases average light intensity levels, factors of competitive advantage to *O. colensoi* . Treeline *Nothofagus* with its slow rate of spread has possibly not yet had the opportunity to disperse into the southern Ruahine since the last Pleistocene ice retreat, some 14,000 years ago, when the vegetation of the region was most likely confined to shrub / grassland, forests being excluded by the cold climatic conditions. The high cloud cover could also actively inhibit *Nothofagus* establishment in the area through the inability of the seedlings to compete at low light levels.

The southern Ruahine has then a combination of characteristics operative over a large area that are conducive to the establishment of an extensive sub-alpine scrub zone. The other unique aspect of this scrub in the southern Ruahine is its virtual total dominance by *O. colensoi* While *O. colensoi* is a major component of similar sub-alpine scrub associations in the west of the South Island it does not attain such total dominance and is absent from the scrub associations of the volcanic mountains of the North Island (Mounts Taranaki, Tongariro and Ruapehu). On Mount Taranaki *Brachyglottis elaeagnifolia* is the dominant species. *B. elaeagnifolia* also occurs in the southern Ruahine but only occurs frequently at lower altitudes and on disturbed sites such as track and road sides. The road to Wharite Peak is an example where *B. elaeagnifolia* dominates the road berm from 700 to 900 metres. Absence of *O. colensoi* from Mount Taranaki has been though to be a consequence of the competitive advantage of *B. elaeagnifolia* on young soils of volcanic origin (Clarkson 1986). There should however be some sites on the volcanic mountains that could support *O. colensoi* and it is possible, though perhaps unlikely given its wind dispersed seed, that *O. colensoi* has not yet dispersed onto these mountains since their relatively young origins.

Olearia colensoi possesses a set of attributes that enable it to thrive in subalpine conditions characterised by high precipitation, high cloud cover and high winds. It has a characteristic shrub form with multiple branches arising from close to ground level to form a uniform spread of canopy. It has a compact dense foliage layer concentrated on the outside of the plant leaving the interior leafless. Leaf turn-over is high resulting in high leaf litter production, higher than some lowland forest systems. Annual wood increment in shrubs is generally expected to be less than in forest trees which have greater stem biomass (height and girth generally being greater). In a tree carbon products of photosynthesis are deposited as wood giving incremental height and girth increase, both being required to support the canopy at a height commensurate with its habitat preferences and the height of competing trees. The same heights attained by forest trees are inappropriate in high wind, low temperature regimes where the shrub forms are more successful. The shrub strategy may involve less wood increment but higher leaf turnover resulting in net carbon assimilation at much the same level as forest at lower altitudes. When comparing total annual carbon fixation it is possible that the leatherwood scrub is not greatly lower in productivity that lowland forest and most likely no less productive than forest at the same altitudes. While trees are effectively accumulating carbon in wood, leatherwood shrubs (through high leaf litter production) effectively deposit carbon in peaty soils (especially on gentle slopes where erosional loss is minimal). This appears to be the situation on the Takapari plateau where peaty soils have been accumulating over greywacke bed rock for the past 8000 years (Hubbard & Neall 1980). Pollen profiles indicate that *O. colensoi* has been present throughout this time and has increased since the Taupo eruption (1820 yrs B.P.) (Lees 1986) and it is probable that much of this peaty soil build-up has been the product of leatherwood leaf litter production. High leaf turnover may also be a consequence of a harsh environment. young leaves of *Agrostis capillaris* photosynthesise better before full expansion (G.L. Rapson *pers comm.*) Young leaves of *O. colensoi* may also be most productive when young, quickly losing efficiency after the first season in the harsh conditions, possibly in combination with shading from the new seasons leaves which must form a tight wind resistant canopy.

Olearia colensoi plants have a shallow fibrous rooting system; most of the extensive fibrous mat of roots is directly beneath the litter layer but above the soil itself. Fibrous root mats also arise adventitiously beneath epiphytic bryophyte mats and even 'internally' in the stem when involutions of the stem decay, a quite common occurrence. Most of these fibrous root systems then are effectively above the actual soil level and could enable the plants to cope with soils prone to water-logging. The high precipitation conditions in the area often bring about prolonged periods of water saturated soils. Under most conditions the plant may be able to obtain sufficient water uptake from the bryophyte mats and directly beneath the litter layer. In times of severe water deficit however these fibrous shallow root systems would be unable to cope as the bryophyte mats and litter layer desiccate. The strategies which enable the plant to cope with ombrogenous, water logged conditions render the plant drought-prone. This vulnerability is probably reflected in the xeromorphic features of the leaves which have a thick abaxial tomentum enabling better control of transpirational losses during water deficit periods as well as during the strong and persistent winds that can occur in the sub-alpine area.

Olearia colensoi has an ability to propagate vegetatively especially on steeper slopes where down-slope layering occurs and this has been identified as a successful means of reproduction (Field 1968, Wardle *et al* .1972). Sexual reproduction is however the norm and in the southern Ruahine there appear to be no impediments to flowering and seed set and dispersal over the full altitudinal range of *O. colensoi*. Flowering in *O. colensoi* is however irregular, a feature commonly associated with many temperate forest tree species world wide. It is not therefore a feature unique to subalpine conditions or to shrub habits. Autumn floral initiation (an associated feature of mast flowering) can be construed as having adaptive value in a short subalpine growing season by allowing anthesis to occur early in spring thus allowing time for fruit development and maturation before the onset of winter. Autumn initiation however, is also not confined to subalpine or shrub habits; thus it would seem the floral phenology of *O. colensoi* is not of special relevance to its success in the southern Ruahine or elsewhere. Irregular heavy flowering is correlated with summer weather conditions of the previous season; whether this is due to a requirement for conditions conducive to the build-up of carbohydrate reserves necessary for successful flowering, or is simply a cue for the plants to synchronise their flowering as the predator satiation theorists would hypothesise, is debatable. *Olearia colensoi* does have fruit predators in the form of a Dipteran fly larvae that eats achenes within the capitula, so could benefit from mast flowering as a predator satiation mechanism. What ever the adaptive significance of mast flowering it is probably less significant than other factors in contributing to the success of *O. colensoi* in the southern Ruahine.

Leatherwood in the southern Ruahine has increased its altitudinal range over the last 50 years consequent to the decline in areas of *Libocedrus bidwillii* and *Halocarpus biformis*. and demise of the *Weinmannia racemosa* forest. The lowering of treelines in the southern Ruahine can still be seen today with *Libocedrus* and *Halocarpus* giving way to leatherwood shrubland. Spread of *O. colensoi* down-slope is more a consequence of filling out or increasing in abundance at lower altitudes, where individual *O. colensoi* were already present as part of the subcanopy prior to the *Libocedrus* decline. With the collapse of the canopy species (*Libocedrus*, *Halocarpus* and *Pseudopanax*), *O. colensoi* has been able to increase in abundance. The decline in *Libocedrus* and *Halocarpus* and the collapse of the *Weinmannia racemosa* forest with consequent lowering of the tree line is a phenomenon widespread through the southern Ruahine but not confined to the Ruahine Ranges. Similar situations also occurring in areas as diverse as the Kaimai Range and Westland. The natural stand dynamics decline of high altitude forest species in the southern Ruahine has allowed *O. colensoi* to increase in abundance at its lower altitudinal range.

On the summit of the plateau in the southern Ruahine the indications are that leatherwood has been in existence for many generations; pollen data indicate *Olearia* has been regenerating for a long time on the same site (Lees 1986). Phytosociological investigation of the main leatherwood zone (Chapter 6) indicates this area of leatherwood is in a state of continuing renewal. As old *O. colensoi* plants die, either singularly or in patches, they are replaced directly by young *O. colensoi* plants. Plots in this area with dominant *O. colensoi* canopies have high numbers of seedlings and saplings present in what amounts to a seedling bank from which immediate recruitment is possible following any opening of the canopy.

Mixed tussock-leatherwood areas occur at some localities in the sub-alpine zone of the southern Ruahine (Takapari Peak, Takapari Plateau and Matanginui Peak); on the peaks the predominant tussock is *Chionochloa pallens* while basins of *Chionochloa rubra* are found on the Takapari plateau area. These tussock areas were mentioned by Elder in 1965 and have been examined at intervals by Mr A.P. Druce over a number of years from 1966-1989 (see Appendix 1 for species list). The wetter areas are dominated by

Chionochloa rubra and some are very old bogs that are too wet to support leatherwood scrub. The *Chionochloa pallens* areas have fluctuated in extent and from earlier accounts it appears they have generally been declining (Elder 1965). The *Chionochloa rubra* areas appear, however, to have remained relatively stable in area for hundreds of years. Some movement of the margin has occurred and can be observed in a number of areas today with leatherwood spreading into the tussock areas. This may however be isolated fluctuations caused by localised disturbances by man and animals or seasonal fluctuations (establishment in dry years-decline in wet years) rather than a change in the equilibrium of the original tussock and leatherwood communities.

The decline of the *Weinmannia racemosa*, *Libocedrus bidwillii* and *Halocarpus biformis* forest has been accelerated by the introduction of animals (deer and possums). The clearance of the lowland forest must also have had an effect, if not on direct factors such as seed source then on changing climatic factors such as cloud, rainfall and wind. Long term stability in the leatherwood at lower altitude is dependent on the consequent regeneration, if any, of *Libocedrus* and *Halocarpus*. Forests of this kind may require disturbance events to allow regeneration to occur (Veblen & Stewart 1982b) or at least change in climatic conditions. Areas of *Halocarpus* and *Libocedrus* that have now died out may well have been even aged stands that had developed in a drier period with lower cloud incidence, while the present climatic conditions are more conducive to scrub formation than forest. If the predicted trend of global warming occurs the consequences in the Ruahine are likely to be increased cloud cover and rainfall due to increase in moisture-laden westerlies from off the Tasman Sea. If cloud incidence and rainfall are to increase above present levels then it is likely that *O. colensoi* will maintain its competitive advantage and increase even further at its current lower altitudinal limit. In the Wharite area between 880-950m *O. colensoi* and *Pseudowintera colorata* are the predominant species together with an associated ground flora. Long-term floristic composition in this area is harder to predict but it would appear *O. colensoi* will increase in this area particularly in the windier cloudier sites. Floristic composition over the next 50 years will also be affected by fluctuations in animal numbers in the Ruahine Range. Indications are that deer and possum numbers are increasing in the range at present. Deer have an impact on the leatherwood formation by opening tracks and browsing buds and petioles in the winter when feed becomes more scarce. Hares and rabbits are present in the range at relatively high numbers; their effects of browsing leatherwood (again petioles and buds) tends to be confined to track sides and roadsides and is especially noticeable in the winter months. Possum browse of *O. colensoi* was only rarely observed but possums did browse heavily on *Brachyglottis elaeagnifolia* (some individuals were totally defoliated on Wharite during the winter of 1990). While increasing animal numbers are unlikely to alter the *O. colensoi* dominance on the range, floristic composition of associated species will change with deer and possum increase. More palatable species such as *Pseudopanax* will not be able to maintain populations with higher animal numbers.

The southern Ruahine vegetation is not static, the young orogenic origin and fluctuating climatic conditions have seen considerable vegetation changes; introduced animals and humans have also had an impact on the vegetation cover altering the direction of vegetation change. These changes are still occurring and are particularly noticeable at the ecotone between *O. colensoi* and the *Libocedrus/Halocarpus* formations. These changes are complex ecological events - the product of the autecological features of the plants involved, their competitive and regenerative abilities, changing climatic and edaphic conditions, and more recently introduced animal browse regimes and associated disturbance. In management terms it is not possible, and is in any case inappropriate, to attempt to manage an area as if it were a static vegetative entity. Change is an inherent feature of all vegetative systems, some changing faster than others so that changes on a time scale greater than human life spans give the impression of stability. In the Southern Ruahine vegetation changes will continue. Management practices in this area should concentrate on minimising the influence of human-introduced factors that impinge on normal processes of change. In this regard the most important management requirement is the control of introduced animals. Introduced animals have been a considerable problem in the area in the past and will continue to be so. Total eradication of deer and possums is unfortunately not a viable option but every attempt to keep numbers as low as possible should be made. Recreational hunting of deer will probably continue to be the main means of control particularly due to the accessibility of the area from the townships of Ashhurst, Woodville, Dannevirke, Feilding and Palmerston North. Possums however pose a greater problem for control with the collapse of the fur industry and loss of incentive for private hunters.

Direct human impacts on the area have generally been less severe than those of animals; however damage has occurred. Roading and tracking will probably be the main impacts in the future. An extensive road was bulldozed into the leatherwood area in the 1970s, ostensibly for hunting access and caused considerable damage in some areas. Any further roading in the area would be inappropriate. The current road and walking track system provide ample access to the area for hunters, trampers and others. Maintenance of the road and tracks should be confined to the minimum to avoid excessive disturbance of the vegetation.

THE PAST, PRESENT AND FUTURE OF *OLEARIA COLENSOI* AND THE LEATHERWOOD FORMATION IN THE SOUTHERN RUAHINE RANGE

The physical characteristics of the southern Ruahine have produced a large area of sub-alpine attributes even though these altitudes would normally support forest at these latitudes. An extensive sub-alpine scrub belt has formed that is virtually totally dominated by *O. colensoi. Olearia colensoi* is well adapted to climatic conditions of extreme cloud, wind and high precipitation. The ability of *O. colensoi* to establish and flourish in high rainfall regimes seems to give it a competitive edge over other plants. Its shallow fibrous root system that mats on the soil surface and arises adventitiously beneath epiphytic bryophyte mats, enables it to cope with often waterlogged soils. A consequence of this shallow rooting system however is a susceptibility to drought episodes. Even after mortality through such events *O. colensoi* has a propensity to regenerate directly, without intervening seral vegetation sequences. Forest decline this century has allowed a down-slope range expansion of *O. colensoi* to occur. There are no impediments to *O. colensoi* regeneration and no indications that *O. colensoi* will not continue as the dominant vegetation cover in the foreseeable future, regardless of possible climate change and animal population fluctuations. *Olearia colensoi* is not an uncommon plant in the wetter New Zealand mountains; it has a wide geographical distribution and is not under threat of major decline. In the southern Ruahine *O. colensoi* is extremely abundant, this abundance over a relatively large area (≈45 sq km) for a plant that can be considered habitat specific and limited (wetter/cloudier sub-alpine altitudes) is an ecologically significant feature unrepresented elsewhere in New Zealand and is worthy of recognition by designation of the area as an Ecological Zone within the Ruahine Forest Park.

APPENDIX

Vascular Plant species
recorded from the southern
Ruahine leatherwood zone.

Amended from a list by Mr A.P. Druce
Botany Institute DSIR

* denotes adventive species

indigenous species	177
hybrid groups	9
adventive species	24

GYMNOSPERMS

Halocarpus biformis
Libocedrus bidwillii
Podocarpus hallii x *P. nivalis*
Prumnopytis feruginea

DICOT TREES

Aristotelia serrata
Fuchsia excorticata
Griselinia littoralis
Pseudopanax colensoi s.s.
*P. simplex (*incl *P.simplex* var *sinclairii)*

DICOT SHRUBS

Aristotelia fruticosa var. *suberecta*
Brachyglottis repanda s.s.
B. elaeagnifolius
Cassinia leptophylla var. *(C. vauvilliersii)*
Coprosma depressa
C. foetidissima
C. perpusilla ssp. perpusilla
C. pseudocuneata s.s.
C. sp. (a) (unnamed; incl. in *C. parviflora)*
C. sp. (b) (*C. parviflora* var. *dumosa)*
*C. sp. (*c) (unnamed; aff. *C. cheesemanii*)
Cyathodes empetrifolia
Dracophyllum longifolium var. *septentriale*
D. recurvum
D. longifolium x *D. recurvum*
Gaultheria rupestris (incl. *G. subcorymbosa*)
G. sp. (unnamed; incl. in *G depressa var. novae-zelandiae*)
G. rupestris x *G.* sp.
Hebe odora s.s.
Hebe subalpina var. (*H. truncatula)*
Melicytus alpinus s.s.
Myrsine divaricata s.s.
M. nummularia
Olearia arborescens
O. colensoi var. *colensoi*
O. ilicifolia
O. arborescens x *O. ilicicfolia*
Pentachondra pumila
Pimelea buxifolia
Pittosporum rigidum var. *rigidum (incl. P.rigidum* var. *maius)*
Pseudowintera colorata

DICOT LIANES

Muehlenbeckia australis
Rubus cissoides var. *cissoides*

ASTERACEOUS HERBS

Abrotanella caespitosa
Brachyscome radicata var. *radicata*
Celmisia gracilenta var.
C. incana (incl. *C. discolor*)
C. gracilenta x *C. incana*
**Cirsium arvense*
**C. palustre*
**C. vulgare*
**Conyza* sp.
Craspedia minor var. *minor* (incl. *C. major*)
**Crepis capillaris*
Gnaphalium gymnocephalum
G. limosum s.s.
G. mackayi s.s.
G. ruahinicum
G. sphaericum
Helichyrsum filicaule
**Hypochoeris radicata*
**Leontodon taraxacoides*
Leptinella sp.
**Mycelis muralis*
Raoulia glabra
R. tenuicaulis (incl. var. *dimorpha* and var. *pusilla*)
**Senecio jacobaea*
S. minimus
**S. sylvaticus*
**Sonchus asper*
**Taraxacum officinale* s.l.

DICOT HERBS (OTHER THAN ASTERADS)

Acaena anserinifolia
Aciphylla colensoi var. *colensoi*
Anisotome aromatica
Cardamine sp. (a) (*C. debilis* agg.)
C. sp. (b)
Drosera arcturi
Epilobium alsinoides s.s.
E. brunnescens s.s.
E. chlorifolium
E. cinereum
E. cockayneanum
E. insulare
E. pedunculare
E. nummularifolium
**E. obscurum*
E. pernitens
E. rotundifolium

E. sp. (unnamed; incl. in *E. brunnescens* ssp. *minutiflorum)*
Euphrasia cuneata
Forstera tenella
Gentiana sp. (unnamed)
Geranium microphyllum
Gonocarpus aggregatus
Hydrocotyle heteromeria
H. moschata
Kelleria sp. (*Drapetes laxus)*
Liparophyllum gunnii
Montia fontana s.s.
Myosotis venosa
M. sp. (*M. forsteri* agg.)
Nertera balfouriana
N. ciliata
N. depressa (incl. *N. cunninghamii)*
Oreomyrrhis colensoi s.s. (incl. var. *hispida* and var. *multifida*
Ourisia colensoi
O. lactea ssp. *drucei*
O. colensoi x *O. lactea*
Oxalis magellanica agg.
Pratia angulata agg.
Psychrophila novae-zelandiae
Ranunculus membranifolius
Schizeilema allanii
S. nitens
Stellaria decipiens (incl. *S. parviflora)*
Urtica incisa
Viola filicaulis
V. cunninghamii

MONOCOT TREES

Cordyline indivisa

MONOCOT HERBS (OTHER THAN ORCHIDS, GRASSES, SEDGES, RUSHES)

Anaphalis sp. (*Helichrysum bellidoides* s.s.)
Astelia fragrans
A. linearis var. *novae-zelandiae*
A. sp. (unnamed; aff. *A. nervosa)*
Libertia pulchella
Luzuriaga parviflora
Phormium cookianum

ORCHIDS

Aporostylis bifolia
Chiloglottis cornuta
Corybas macranthus
Prasophyllum colensoi
Pterostylis montana
P. renosa

GRASSES

Agrostis sp. (c.f. *A. perennans*)
**A. capillaris*
**Anthoxanthum odoratum*
Chionochloa conspicua ssp. *cunninghamii*
C. pallens var.
C. rubra var.
C. conspicua x *C. rubra*
C. pallens x *C. rubra*
Cortaderia fulvida
**Dactylis glomerata*
Deschampsia tenella
Deyeuxia aucklandica
Dichelachne crinita
**Festuca arundinacea*
Hierochloe recurvata
H. redolens
**Holcus lanatus*
**Lolium perenne*
Microlaena avenacea
Rytidosperma gracile
**Poa annua*
P. breviglumis
P. pusilla
P. sp. (undetermined)

SEDGES

Carex dissita
**C. ovalis*
C. sp.
Carpha alpina s.s.
Gahnia procera
Isolepis habrus
I. pottsii
Oreobolus pectinatus
Schoenus pauciflorus s.s.
Uncinia sp. (a) (unnamed)
U. astonii
U. caespitosa
U. clavata
U. filiformis
U. fuscovaginata var. *fuscovaginata*
U. gracilenta
U. silvestris (syn. *U. affinis)*
U. uncinata
U. sp. (b) (unnamed; af. *U. nervosa)*
U. sp. (a) x *U. fuscovaginata*

RUSHES

Centrolepis ciliata
Empodisma minus
Juncus antarcticus
**J. articulatus*
J. australis
**J. bufonius*
**J. effusus*
J. gregiflorus
J. novae-zelandiae
J. pusillus
J. sarophorus
Luzula migrata
L. subclavata
L. sp. (unnamed; incl. in *L. picata* var. *limosa)*

FERNS

Asplenium flaccidum s.s.
Blechnum discolor
B. fluviatile agg.
B. penna-marina
B. minus
B. procerum
B. sp. (*B. capense* agg.)
Grammitis magellanica ssp. *nothofageti*
Cyathea smithii
Histiopteris incisa
Hymenophyllum multifidum
H. malingii
H. peltatum
H. rarum
H. sanguinolentum agg.
Hypolepis rufobarbata
Leptopteris superba
Paesia scaberula
Polystichum vestitum

LYCOPODS

Lycopodium fastigiatum
L. scariosum
L. varium (incl. *L. billardierei* and *L. novae-zelandicum)*

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