

MODELLING RELATIONSHIPS BETWEEN ENVIRONMENT AND CANOPY COMPOSITION IN SECONDARY VEGETATION IN CENTRAL NORTH ISLAND, NEW ZEALAND

Summary: Relationships between composition of secondary vegetation and environment were studied in central North Island, New Zealand. A classification procedure was used to identify broad compositional groups which included forest, broadleaved scrub, shrub-fernland, sclerophyllous scrub and shrubland, and tussock-shrubland. Generalised additive models (GAMs) were used to examine relationships between species' distributions and mean annual temperature and rainfall, stand age, distance from intact forest, slope, topography, and drainage. There were marked differences in the environmental relationships of individual species. We conclude that temperature and rainfall have a dominant role in determining succession after disturbance at a regional scale, but distance from intact forest, topography, slope and solar radiation, become important at local scales. Variation unaccounted for by these environmental factors is most likely linked to historical factors such as variation in disturbance and/or grazing and browsing regimes. Intervention by managers will probably be required in the future if the current diversity of secondary vegetation in central North Island is to be maintained.

Keywords: Secondary succession; disturbance; environmental factors; classification; plant community analysis; Generalised Additive Models.

Introduction

Although most of the central North Island could be expected to support tall forest, deforestation by early Polynesian occupants was so extensive that by the time European settlement began (c. 1840) the area occupied by secondary fernland, grassland, and scrub (>650 000 ha) was similar to the area of forest (McGlone, 1983; Rogers, 1994). Frequent burning continued in European times, but is poorly documented.

Large areas of secondary vegetation were converted to plantation forest from the 1920s onwards, and once problems associated with micronutrient deficiencies were solved in the late 1930s, further large areas were converted to pastoral use (Molloy, 1988).

As a result of these landuse changes, secondary vegetation in the central North Island is now mostly confined to publicly owned land managed for conservation purposes. Here, it presents a challenge to managers charged with preserving representative flora and fauna, particularly as the general exclusion of fire in recent decades is resulting in displacement of seral communities and their associated distinctive flora and fauna by forest species. In this study we test to see whether there are consistent relationships between vegetation composition, environment, and

time since disturbance at a regional level of study. Such information will form an essential foundation for the conservation management needed if these distinctive elements of the central North Island landscape are to be preserved.

Study Area

The study area covers a 2.5° range of latitude (37° 05' - 39° 37') and 1.5° range of longitude (175° 35' - 177° 05') in the central North Island (Fig. 1). Complex landforms reflect both tectonic and volcanic processes (Healy, 1982). Uplifted ranges of Mesozoic sandstone, argillite, and conglomerate lie along the eastern and western margins of the study area, rising to elevations of 1700 m and 900-1000 m, respectively. Between these, an extensive down-faulted volcanic zone has produced numerous eruptions over the last 300 000 years (Froggatt and Lowe, 1990). Andesitic strato-volcanoes occur in the south of this zone, but vulcanism in the centre and north-east has produced predominantly rhyolitic tephra to form extensive ignimbrite plateaux. To the north, Miocene and Pliocene andesites and rhyolites form the Coromandel Range, rising steeply to 750-850 m. Small areas of Pliocene marine sandstone and siltstone occur in the far south of the study area.

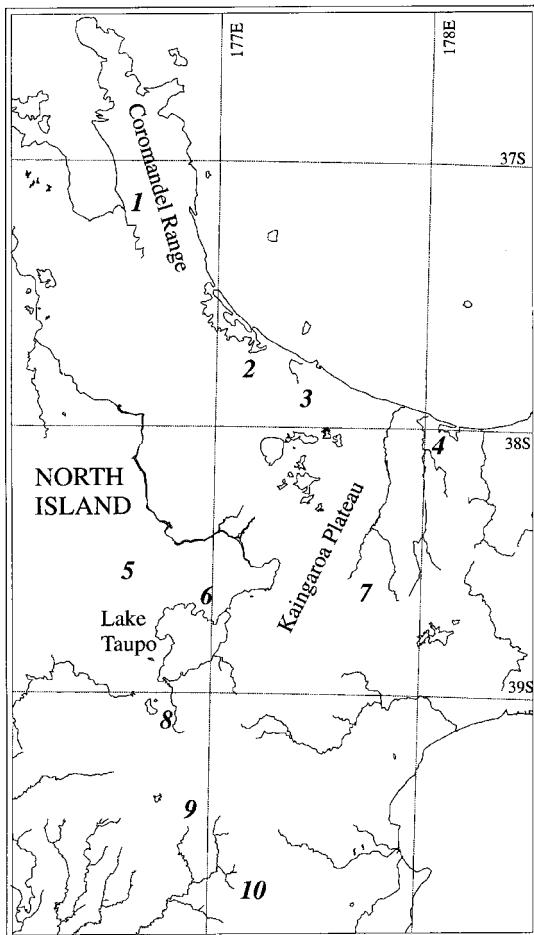


Figure 1: Study site locations - 1 - Coromandel; 2 - Te Puke; 3 - Paengaroa; 4 - Whakatane; 5 - Pureora; 6 - Taupo; 7 - Whirinaki; 8 - Rangipo; 9 - Moawhango; 10 - Ruahine.

The climate of the study area is generally cool and moist, with mean annual temperatures ranging from 8 °C at high elevation in the south-west to 15 °C at sea-level in the north (New Zealand Meteorological Service, 1985a). Differences between the mean daily temperatures of the warmest and coldest months are approximately 10 °C. Frosts are a significant feature of the extensive central basins and plateaux. For example, on average they occur on over 100 days per year on the Kaingaroa Plateau, with extreme minima reaching -15 °C (New Zealand Meteorological Service, 1983). Rainfall is generally equable throughout the year, and varies from 4800 mm yr⁻¹ on sites above treeline in the

south to slightly below 1200 mm in parts of the Taupo basin, but increases again to c. 2500 mm on the north-eastern coastal hills and on the Coromandel Range (New Zealand Meteorological Service, 1985b).

Three major soil groups occur in the study area (Molloy, 1988). The most extensive group are deep, weakly weathered and relatively infertile, coarse-textured pumice soils formed on rhyolitic tephra. Finer textured volcanic loams occur on andesitic and older rhyolitic ashes mainly in the south; those formed on andesitic parent material are more fertile than those on rhyolite. Volcanic clays occur on the much older andesitic and rhyolitic parent materials of the Coromandel Range. On the predominantly steep land sites remaining in indigenous vegetation, these clays are often heavily podzolised and of low fertility.

Early successional vegetation in central North Island is generally dominated by mixed broadleaved shrublands, *Leptospermum scoparium*¹, and/or *Pteridium esculentum* (Ure, 1950; McQueen, 1961), but on cold and/or frosty sites these give way to *Dracophyllum* spp. and tussocks such as *Poa cita* and *Chionochloa rubra* (Atkinson, 1981; Leathwick, 1987; Smale, 1990; Rogers and Leathwick, 1994).

Methods

Site selection

Sites were selected using a three-stage, stratified sampling scheme, designed to obtain data from as many combinations of environmental conditions and stand ages as possible. Conceptually, this is "sampling for pattern" as described by Eberhardt and Thomas (1991), except that we aimed to maximise the environmental rather than the spatial dispersion of plots.

First, 10 extensive study sites (Fig. 1, Table 1), each containing a range of secondary vegetation, were selected so as to sample the range of climates occurring in the region. Average mean annual temperature (Table 1) ranged from 13.6 °C at Coromandel in the north to 7.8 °C at the Ruahine site, and mean annual rainfall from 1250 mm at the Taupo site to 2550 mm at the Rangipo site. Second, at each study site, sampling strata of obviously different disturbance ages were tentatively identified

¹ Botanical nomenclature follows Cheeseman (1925), Allan (1961), Connor and Edgar (1987), Webb, Sykes and Garnock-Jones (1988), and Brownsey and Smith-Dodsworth (1989).

Table 1: *Locations and characteristics of the 10 study sites.*

	Coromandel	Te Puke	Paengaroa	Whakatane	Pureora	Taupo	Whirinaki	Rangipo	Moawhango	Ruahine
Latitude (S)	37° 05'	37° 49'	37° 57'	38° 03'	38° 30'	38° 40'	38° 43'	39° 10'	39° 30'	39° 37'
Longitude (E)	175° 40'	176° 13'	176° 22'	177° 05'	175° 35'	175° 50'	176° 35'	175° 47'	175° 52'	176° 10'
Mean annual temperature (°C)	13.6	13.1	13.4	13.5	11.1	11.4	10.3	8.8	9.5	7.8
Mean annual rainfall (mm)	2200	2150	1850	1700	1800	1250	1600	2550	1500	2150
Predominant soil-forming parent material	Miocene andesites, Pliocene rhyolites	Holocene rhyolitic ash	Holocene rhyolitic ash	Holocene rhyolitic ash	Holocene rhyolitic ash	Holocene rhyolitic ash	Holocene rhyolitic ash	Holocene andesitic/rhyolitic ash	Holocene andesitic ash over Pliocene marine sandstone /siltstone	Holocene andesitic ash over Triassic greywacke /siltstone
No. plots	54	15	18	23	23	19	24	27	27	26
Range of disturbance ages	7-145	20-60	8-75	12-75	47-100	15-90	54-95	30-95	17-70	43-65
Grazing animals	Feral goats, pigs	Feral goats, deer, pigs	?	Domestic stock	Feral deer, pigs	Feral deer, pigs, goats	Feral deer, pigs	Feral deer	Domestic stock/feral deer	Feral deer
Range of distances to intact forest (m)	20-600	100-750	250-750	20-200	50-300	10-15 km	20-710	0-600	40-3500	10-1300
Composition of adjacent forest	Conifer/broadleaved	Conifer/broadleaved	Conifer/broadleaved	Conifer/broadleaved	Conifer/broadleaved	Conifer/broadleaved	Conifer/broadleaved	<i>Nothofagus</i>	<i>Nothofagus</i>	Conifer/broadleaved

using aerial photographs of a range of ages in conjunction with information from both written and oral historical sources. Third, the vegetation and site conditions were described at a number of sites in each stratum, with sites chosen to sample the available range of elevation, slope, aspect, and topographic position. Where the terrain, size of disturbance event, and vegetation allowed, sites were located at fixed intervals along transects, with interplot distances varying depending on the size of the disturbance patch. In small disturbance patches this was sometimes not practical, and plots were subjectively located to sample the available range of environments.

Site description

Vegetation at each site was described using reconnaissance plots (Allen and McLennan 1983). Plot radii were varied so as to encompass a minimum of *c.* 30 canopy plants, in practice varying from 2 m in fernland and grassland up to 10 m in tall secondary forest. Canopy cover (*sensu* Atkinson, 1985) was estimated for each of the species present using the cover scores of Bailey and Poulton (1968), i.e., 1: 0-1%; 2: >1-5%; 3: >5-25%; 4: >25-50%; 5: >50-75%; 6: >75-95%; 7: >95-100%.

The topography at each plot was classified using the nine-unit landform model of Dalrymple, Blong

and Conacher (1968). Units encountered in this study, and their corresponding predominant slope and geomorphic processes, were (i) interfluvial: 0-1° slope and at top of hillslope sequence - dominant geomorphic process is vertical water movement; (ii) seepage slope: 2-3(-10)° slope - lateral water movement; (iii) convex creep slope: maximum of 45° slope - transportation of material by soil creep; (v) transportational mid-slope: 26-35° - transportation of material by mass movement; (vi) colluvial foot-slope: redeposition of material by mass-movement; (vii) alluvial toe-slope: redeposition by alluvial processes. Drainage was described using the seven-step scale of Taylor and Pohlen (1970), i.e., from "0" = very poorly drained, to "6" = excessively drained. Qualitative notes were taken on soils.

Information on disturbance regime

Information on ages of disturbance events (particularly fires) was obtained for each stratum from sections or cores taken from marginal trees (Druce, 1957), aerial photographs, and historical records. This was supplemented and cross-checked by increment cores or cross sections taken from a number of the largest woody canopy plants in each plot. Estimated stand ages were mostly between 10 and 100 years. Distances from the nearest intact

forest large enough to act as a significant seed source for forest species, were measured either on the ground or from aerial photographs. Although maximum distances were mostly less than 1 km, at the Taupo site they were 10-15 km, reflecting the extensive deforestation in this area.

Analysis

Where possible, indirect gradients such as altitude and slope were converted prior to analysis into direct gradients with which they are strongly correlated (e.g., temperature and rainfall) and which have a more direct effect on plant growth (Austin and Smith, 1989). For example, estimates of mean annual temperature were derived for each plot from its altitude, latitude, and distance from the coast using the regression equations of Norton (1985). Rainfall was estimated for each plot from a grid of climate estimates derived from splined surfaces fitted to rainfall station data (Mitchell, 1991). Use of slope to obtain estimates of absolute minimum temperature would have been desirable but was not possible. For this reason, slope was included in the analysis as a raw variable.

Vegetation-environment relationships at a broad community level were investigated by dividing plots into groups of similar composition using the divisive classification technique of two-way indicator species analysis as implemented in TWINSPAN (Hill, 1979). Pseudospecies cut levels were set so that each cover value, i.e., 1-7, was treated as a separate

pseudospecies - see Hill (1979) for details. The environmental relationships of the resulting groups were then investigated using analysis of variance to test the significance of differences in each environmental variable between groups.

More detailed individual analyses of the environmental relationships of 16 widespread canopy dominants were undertaken using the non-parametric regression technique of generalised additive models (GAMs - Hastie and Tibshirani, 1990; Yee and Mitchell, 1991) as implemented in S-Plus (Venables and Ripley, 1994). This technique differs from more conventional generalised linear models (GLMs - McCullagh and Nelder, 1983) in that relationships between species abundance and each continuous environmental variable (e.g., temperature) are defined using a continuous regression function whose shape is determined from the data using a scatterplot smoother. Along with GLMs, the technique allows ready analysis of data with non-normal error distributions. Our regression models used a logistic link function and binomial error term (McCullagh and Nelder, 1983), and predicted percentage canopy cover from estimates of stand age and environment, using species cover scores converted to the percentage midpoints of their respective cover classes. Models were developed using a forward step-wise procedure (Nicholls, 1989). Because of their strongly skewed distributions, slope and distance values were transformed to square root and log₁₀ respectively.

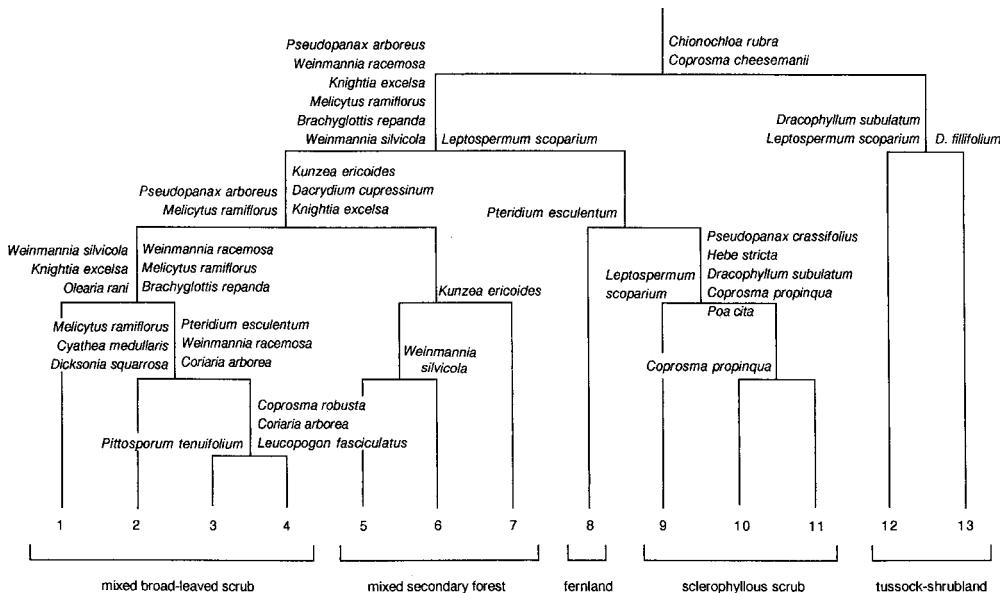


Figure 2: Dendrogram showing relationships between the 13 plot groups, with indicator species shown for each division.

Results

Major secondary communities

Five broad groupings containing 13 plot groups were recognised from the TWINSPAN classification (Fig. 2, Table 2), i.e., mixed broadleaved scrub (groups 1-4), mixed secondary forest (5-7), shrub-fernland (8), sclerophyllous scrub and shrubland (9-11), and tussock-shrubland (12, 13). Significant differences were found between the 13 groups for all the continuous environmental factors (Fig. 3). Differences in mean annual temperature were the most pronounced, followed by differences in rainfall, stand age, distance from intact forest, and slope.

Mixed broadleaved scrub groups occupied sites with stand ages of c. 25-60 years. They exhibited a moderate bias towards warm sites, but occurred over a wide rainfall range. The widespread occurrence of suppressed *Pteridium esculentum* in the understorey in all four groups, suggests that they have arisen by invasion of fernland by broadleaved species, and on some sites also by treeferns. Scrub dominated by *Weinmannia silvicola*, *Pseudopanax arboreus*, and *Blechnum* sp. 1 (group 1) occurred only at the Coromandel site, where it occupied warm, high-rainfall sites generally close to intact forest, and mostly on andesitic substrates. Individuals of taller forest species such as *Knightia excelsa* and *Olearia rani* were scattered throughout, and seedlings of many forest species were common in the understorey. Scrub dominated by *Pseudopanax arboreus* and *Meliccytus ramiflorus* (group 2) occurred on sites of similar temperature to the previous group, but with lower rainfall and intermediate distances from intact forest, mainly at the Te Puke and Paengaroa sites. It showed a strong bias towards transportational midslopes and colluvial footslopes. Other common species included *Brachyglottis repanda*, and the treeferns *Cyathea medullaris* and *Dicksonia squarrosa*. Scrub dominated by *Pseudopanax arboreus* and *Weinmannia racemosa* (group 3) occurred on cooler, drier sites than the two previous groups, and generally at greater distances from intact forest. It was widespread, occurring at the Te Puke, Taupo, and Pureora sites, mostly on convex creepslopes and transportational midslopes. *Pittosporum tenuifolium* was locally co-dominant either on steep sites or sites with very little slope. Scrub dominated by *Coriaria arborea* and *Pseudopanax arboreus* (group 4) occupied sites of similar environment, but occurred almost invariably on sites with bare mineral soil, i.e., unweathered Taupo tephra close to the lake margin at the Taupo study site, and steep talus slopes at Te Puke. *Coprosma robusta*, *Leucopogon fasciculatus*, and *Pteridium esculentum* were also locally abundant.

The mixed secondary forest groups had the oldest mean stand ages, and occurred close to intact forest. Forest dominated by *Dacrydium cupressinum*, *Weinmannia racemosa*, and *Pseudopanax crassifolius* (group 5) occurred on sites of moderate temperature and rainfall at the Pureora site, where it generally formed a marginal belt around the primary forest. A wide range of other species typical of primary forest were present both in the canopy and understorey. Forest dominated by *Weinmannia silvicola* (group 6) occurred only at Coromandel, occupying warm, high rainfall sites on steep slopes, generally close to intact forest. Although generally of low diversity, given the very high dominance of *W. silvicola*, young *Dacrydium cupressinum* and *Knightia excelsa* were scattered throughout in low numbers. *Kunzea ericoides* forest (group 7) occurred over a wide geographic range and under contrasting environmental conditions; at Coromandel (higher rainfall) it occurred exclusively on recent, fine alluvium on river terraces, but at Whakatane and Whirinaki (lower rainfall) it occupied steeper hill slopes. Other species locally present included *Weinmannia racemosa*, *Knightia excelsa*, and *Leptospermum scoparium*. Seedlings of forest species such as *Dacrydium cupressinum* and *Dacrydium dacrydioides* were common in the understorey.

Shrub-fernland dominated by *Pteridium esculentum* and *Leptospermum scoparium* (group 8) occurred mostly at Paengaroa, Moawhango, and Coromandel, at the latter largely restricted to andesitic substrates. It had the youngest mean stand ages, and occurred at moderate-to-long distances from intact forest. A number of adventive species, e.g., *Lotus pedunculatus*, *Erica lusitanica*, and *Hakea salicifolia*, were common in this group, along with a range of smaller shrubs such as *Coprosma robusta* and *Pomaderris ericifolia*.

Leptospermum scrub (9) formed the largest but floristically most simple group, with *Leptospermum* often the only canopy species. It was widespread; at Coromandel it was dominant either on the infertile podzolised soils formed under the former *Agathis australis* dominant forest on rhyolitic substrates, or on stony alluvium, at Whakatane and Moawhango it occurred on sites which were once in pasture, and at Whirinaki it occurred on an extensive, once forested, rolling ignimbrite plateau. Although the mean stand age for this group was relatively young, the group includes plots at the Moawhango site with stand ages of 80 years or more, and in which regeneration of forest species has been severely limited by the poor dispersal ability of the *Nothofagus solandri* var. *cliffortioides* dominant in the adjacent primary forest. Scrub dominated by *Leptospermum*, *Kunzea*, and *P. crassifolius* (group 10) had older mean stand ages, and occupied sites which were generally

Table 2: Composition of the 13 TWINSPAN plot groups. The percentage occurrence and mean canopy cover (calculated from cover-class mid-points) of prevalent species (sensu Curtis, 1959) are shown for each group. Minor occurrences of species are shown by a '+'.

	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dacrydium cupressinum</i>			+		100(30.1)	57(3.4)	+		+	+			
<i>Prumnopitys ferruginea</i>					40(0.2)								
<i>Weinmannia silvicola</i>	100(39.5)	+				100(65.0)							
<i>Olearia rani</i>	44(2.6)	+	+			+	+						
<i>Knightia excelsa</i>	44(2.6)	+	+		60(4.2)	57(5.1)	37(4.1)		+				
<i>Cyathea dealbata</i>		+				+	26(1.8)						
<i>Elaeocarpus dentatus</i>			+		40(0.2)								
<i>Pseudopanax arboreus</i>	78(14.2)	71(24.3)	100(34.7)	72(15.8)	80(7.2)	71(2.1)	+	+	15(1.5)	+			
<i>Blechnum sp. 1</i>	56(14.5)	+	42(9.3)	+		+	+	+	+	+		+	
<i>Coprosma robusta</i>	44(1.8)	+	+	72(7.6)				30(2.1)	+	+			
<i>Dicksonia squarrosa</i>	+	35(3.1)	+		40(2.0)		+	+	+				
<i>Meliccytus ramiflorus</i>		88(18.4)	+	+									
<i>Cyathea medullaris</i>		53(9.0)	+	+		+							
<i>Brachyglottis repanda</i>		47(2.5)	21(1.7)	+		+	+						
<i>Coriaria arborea</i>		+	+	91(19.5)		+	+			+			
<i>Litsea calicaris</i>		29(6.9)	+										
<i>Aristotelia serrata</i>		29(3.6)	+	+				+		+			
<i>Weinmannia racemosa</i>		+	74(16.9)	45(6.7)	100(28.5)		37(7.2)	+					
<i>Leucopogon fasciculatus</i>	+	+		54(8.0)		+	+	+	+	27(4.1)			
<i>Pseudopanax crassifolius</i>			+		100(17.1)	+		+	+	82(8.9)		+	
<i>Kunzea ericoides</i>	+	+	+	+			100(55)	+	14(1.2)	55(14.6)			+
<i>Pittosporum tenuifolium</i>		+	52(5.2)				26(0.6)		+	64(2.3)	+	+	
<i>Phyllocladus trichomanoides</i>					40(0.7)		+		+				
<i>Carpodetus serratus</i>	+	+			+		+	+	11(1.9)				
<i>Hebe stricta</i>			+	+			+	+		+	80(3.5)		
<i>Hakea salicifolia</i>		+	+					30(2.9)					
<i>Pteridium esculentum</i>	+		52(7.6)	45(12.1)	+		+	96(48.9)	18(1.1)	+	+		
<i>Lotus pedunculata</i>								30(3.2)	+				
<i>Pomaderris ericifolia</i>				+				22(5.8)					
<i>Erica lusitanica</i>			+					43(5.8)	+	+			
<i>Gaultheria antipoda</i>			+	+	+		+	+	+	64(4.9)	+		+
<i>Phormium tenax</i>								+		36(0.9)	+		
<i>Coprosma sp. (t) (Eagle, 1982)</i>										55(13.1)	+		+
<i>Coprosma propinqua</i>								+		+	50(18.1)		
<i>Leptospermum scoparium</i>	33(4.5)	+	26(3.6)	36(3.3)	+	28(7.5)	31(5.9)	78(19.2)	100(69.2)	73(26.6)	50(2.4)	70(22.4)	
<i>Holcus lanatus</i>								+			40(5.6)		+
<i>Dracophyllum subulatum</i>										64(3.6)	80(28.1)	96(29.8)	+
<i>Poa cita</i>										40(2.4)	+		
<i>Cassinia vauvilliersii</i>												48(4.5)	+
<i>Festuca novae-zelandiae</i>												39(1.1)	
<i>Pentachondra pumila</i>												39(1.4)	
<i>Lycopodium fastigiatum</i>										40(2.1)	+		+
<i>Anthoxanthum odoratum</i>								+	+				33(1.1)
<i>Hypochaeris radicata</i>										40(0.9)	+	30(0.2)	
<i>Rytidosperma gracile</i>										40(2.2)	+		
<i>Chionochloa rubra</i>												96(17.7)	100(25.7)
<i>Celmisia spectabilis</i>												26(2.8)	63(7.5)
<i>Coprosma cheesemanii</i>												78(4.3)	78(10.3)
<i>Poa colensoi</i>										+		52(0.8)	78(4.1)
<i>Gaultheria novae-zelandiae</i>												+	30(1.5)
<i>Hierochloa redolens</i>												+	59(4.1)
<i>Dracophyllum filifolium</i>													93(30.6)
# plots	9	17	19	11	5	7	19	23	73	11	10	23	39
Mean annual temp. (°C)	13.5	13.3	11.8	11.9	11.1	13.3	12.8	12.8	11.6	10.5	11.0	8.9	7.8
Mean annual rainfall (mm)	2213	1960	1610	1600	1825	2240	1775	1920	1970	1755	1775	2560	2175
Slope (°)	16.9	17.9	16.5	18.2	12.8	24.1	15.1	15.8	13.2	8.2	4.8	6.1	11.3
Age (yrs)	56.1	55.8	43.3	33.1	94	65.3	70.3	22.1	39.6	63.5	50.7	53.5	56.2
Distance (m)	161	913	7193	8255	110	76	106	569	702	469	201	244	375

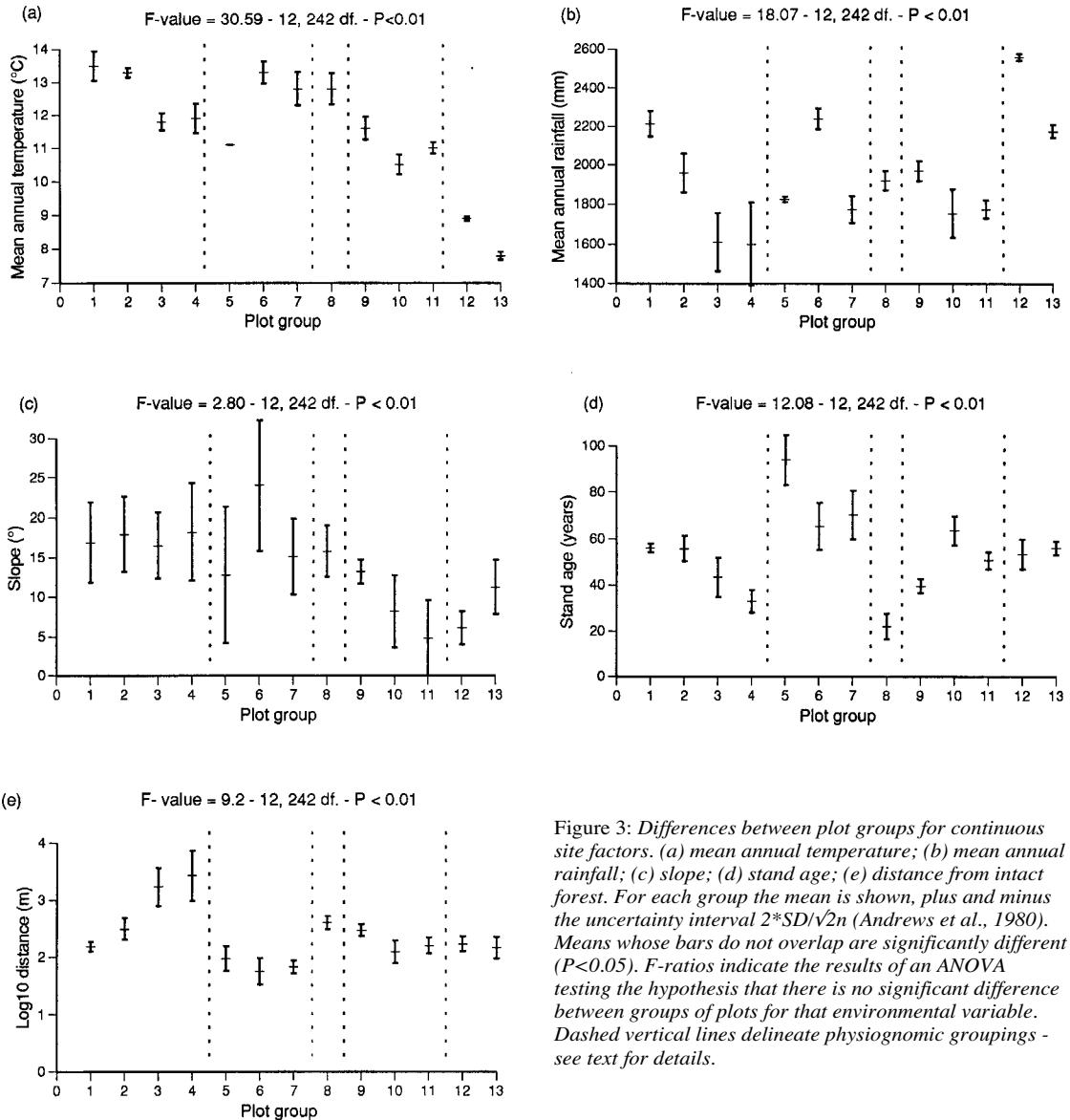


Figure 3: Differences between plot groups for continuous site factors. (a) mean annual temperature; (b) mean annual rainfall; (c) slope; (d) stand age; (e) distance from intact forest. For each group the mean is shown, plus and minus the uncertainty interval $2 \cdot SD / \sqrt{2n}$ (Andrews et al., 1980). Means whose bars do not overlap are significantly different ($P < 0.05$). F-ratios indicate the results of an ANOVA testing the hypothesis that there is no significant difference between groups of plots for that environmental variable. Dashed vertical lines delineate physiognomic groupings - see text for details.

cooler, drier, and closer to intact forest than the previous group. It occurred predominantly on gently sloping sites at Whirinaki and Pureora. Other widespread species present included *Pittosporum tenuifolium*, *Dracophyllum subulatum*, and *Gaultheria antipoda*. Shrubland dominated by *Dracophyllum subulatum*, *Coprosma propinqua*, and *Hebe stricta* (group 11) occurred at Whirinaki and Pureora, occupying sites with the lowest mean slope of any group. On the flattest of these sites

Dracophyllum subulatum was often the only shrub present, and grew as scattered individuals among grasses, lycopods, and lichens, other shrub species only becoming common as slope increased.

The two tussock-shrubland groups occupied cool, wet climates, occurring almost exclusively at Rangipo and Ruahine. Tussock-shrubland dominated by *D. subulatum*, *Leptospermum*, and *Chionochloa rubra* (group 12) occupied sites with little slope at Rangipo. Other widespread species included

Coprosma cheesemanii, *Cassinia vauvilliersii*, and *Poa colensoi*. Tussock-shrubland dominated by *Dracophyllum filifolium* and *Chionochloa rubra* (group 13) occurred only at the Ruahine site, where the climate is cooler but drier than at Rangipo. Other important species included *Hierochloa redolens*, *Poa colensoi*, and *Coprosma cheesemanii*.

Environmental relationships of major species

Mean annual temperature and stand age were fitted as significant terms in all the species regressions (Table 3). Relationships between mean annual temperature and species cover varied widely, but were generally curvilinear. Topography, rainfall, distance from intact forest, and slope were also included as significant terms in regression models for many species.

Three species, *Leptospermum scoparium*, *Kunzea ericoides*, and *Pteridium esculentum*, are predicted to occur over large parts of the temperature range (Fig. 4). *Pteridium* reaches highest cover on recently disturbed transportational mid-slopes at around 10.5 °C, under moderately high levels of rainfall, with steep slope, and distant from intact forest (Figs. 4-6). Even in the most ideal conditions, it is generally displaced by woody species by around 50 years. *Leptospermum* has a bimodal responses to temperature reflecting its widespread occurrence on colder sites, and its more local distribution on warmer sites (Whakatane and Coromandel study

areas) where it occurred either in grazed pasture, or in the absence of grazing, on older, infertile soils, or on recent but very stony soils. It reached high levels of cover across all landform units. On cool sites it often persists for up to 100 years, but on warmer sites is gradually replaced by other broadleaved trees and shrubs from about 50 years on. *Kunzea ericoides* also has a bimodal relationship with temperature, but with highest levels of occurrence reached on warm, low rainfall sites with older disturbance ages and close to intact forest; the age at which it appears increases as temperature decreases.

A number of species occur only on warm sites (> c. 11 °C). *Knightia excelsa* reaches greatest cover on interfluvial sites with old disturbance ages, and under high rainfall. *Meliclytus ramiflorus* was most abundant on sites with high temperatures, where it reaches greatest cover on colluvial foot-slopes with moderate to high solar radiation. *Pseudopanax arboreus* occurred over a wide range of ages, reaching its greatest cover on sites with moderately high rainfall, intermediate slopes, and distant from intact forest. In contrast, *Pseudopanax crassifolius*, although occurring in stands of similar age to *P. arboreus*, reached greatest cover close to intact forest, and with a strong bias towards gently sloping seepage slopes. Cover of *Weinmannia racemosa* increases steadily with age since disturbance to reach high levels of cover, particularly on mid and upper landform units with low solar radiation. *Weinmannia silvicola* differed in occurring on the warmest sites under high rainfall

Table 3: Significance of components in final GAM regressions relating species canopy cover to environment and time since disturbance. Table values indicate scaled changes in deviance (distributed as for an F-statistic) resulting from dropping each component from the regression. Interactions, where fitted, are indicated by letters representing each factor combined with an asterisk, e.g., T*A indicates an interaction term between temperature and age.

Species	Mean annual temp.	Mean annual rainfall	Stand age	Distan. intact forest	Slope	Solrad.	Topo.	Drain.	Interactions	Residual mean deviance
<i>Carpodetus serratus</i>	7.03	-	5.35	23.59	5.28	-	12.3	-	D*A	1.43
<i>Chionochloa rubra</i>	364.9	-	9.05	11.4	-	7.70	8.23	-	SR*A, SL*A	1.44
<i>Coprosma cheesemanii</i>	200.91	6.58	12.79	14.02	23.42	6.58	4.75	6.58	D*A	0.71
<i>Dacrydium cupressinum</i>	17.60	5.90	12.60	32.14	23.13	-	6.35	-	T*A	0.65
<i>Dracophyllum filifolium</i>	794.65	-	30.13	26.42	27.59	-	-	-	D*A	0.85
<i>D. subulatum</i>	47.74	17.38	12.56	-	7.65	11.58	7.05	-	T*A	5.20
<i>Knightia excelsa</i>	52.12	4.53	108.52	-	-	-	15.11	6.41	-	2.31
<i>Kunzea ericoides</i>	3.77	15.90	2.62	11.70	-	-	4.18	-	T*A	11.50
<i>Leptospermum scoparium</i>	17.88	-	4.91	4.70	3.21	-	-	3.93	D*A, T*A	40.31
<i>Meliclytus ramiflorus</i>	40.60	-	6.57	6.84	-	-	25.01	6.81	D*A, T*A	1.16
<i>Pittosporum tenuifolium</i>	11.87	-	5.28	28.63	10.12	4.12	3.39	-	T*A, D*A	1.43
<i>Pseudopanax arboreus</i>	28.70	4.82	9.74	19.72	5.37	-	3.85	-	T*R	10.72
<i>P. crassifolius</i>	82.78	2.38	26.38	3.03	-	17.06	32.60	12.85	D*A	0.63
<i>Pteridium esculentum</i>	10.63	3.39	14.40	2.39	6.58	-	5.44	-	T*A, SL*A	15.81
<i>Weinmannia racemosa</i>	27.23	-	11.11	17.36	-	2.40	7.54	-	T*A	5.34
<i>W. silvicola</i>	1237.7	734.4	119.25	-	175.21	20.40	25.79	54.31	-	1.68

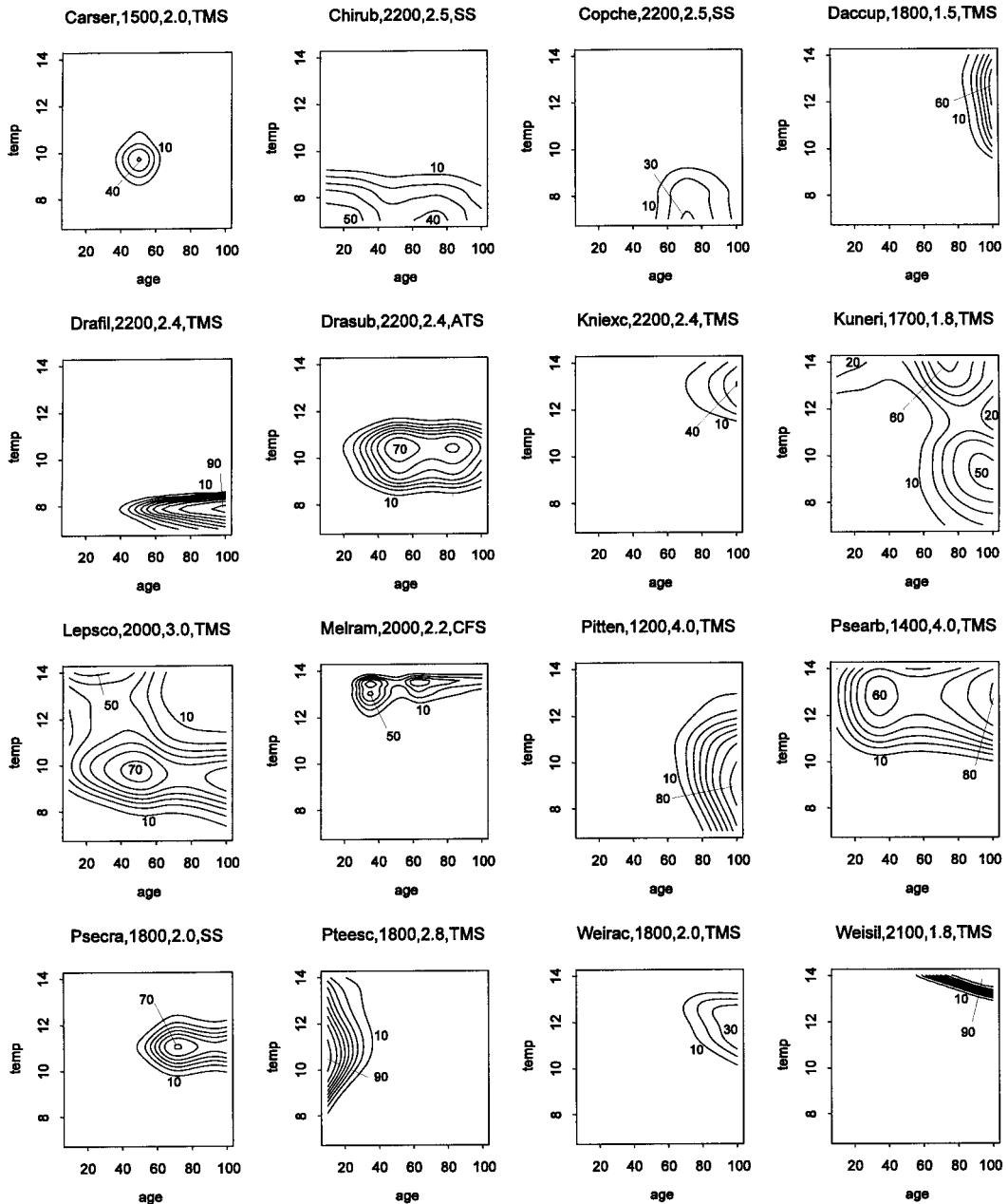


Figure 4: Predicted canopy cover for major species in relation to stand age and mean annual temperature. Abbreviated species names consist of the first three letters of the generic and specific names, and are listed in full in Table 3. Rainfall, $\log(\text{distance})$, and topography were set at the optimum indicated by inspection of fitted values for the respective regression analyses; values chosen are indicated along with the abbreviated species name displayed above each graph. Topographic classes are as follows: IF - interfluvial; SS - seepage slope; CCS - convex creep slope; TMS - transportational mid-slope; CFS - colluvial foot-slope; ATS - alluvial toe-slope. Slopes were set to the mean for each chosen topographic class, and drainage was set to "well drained".

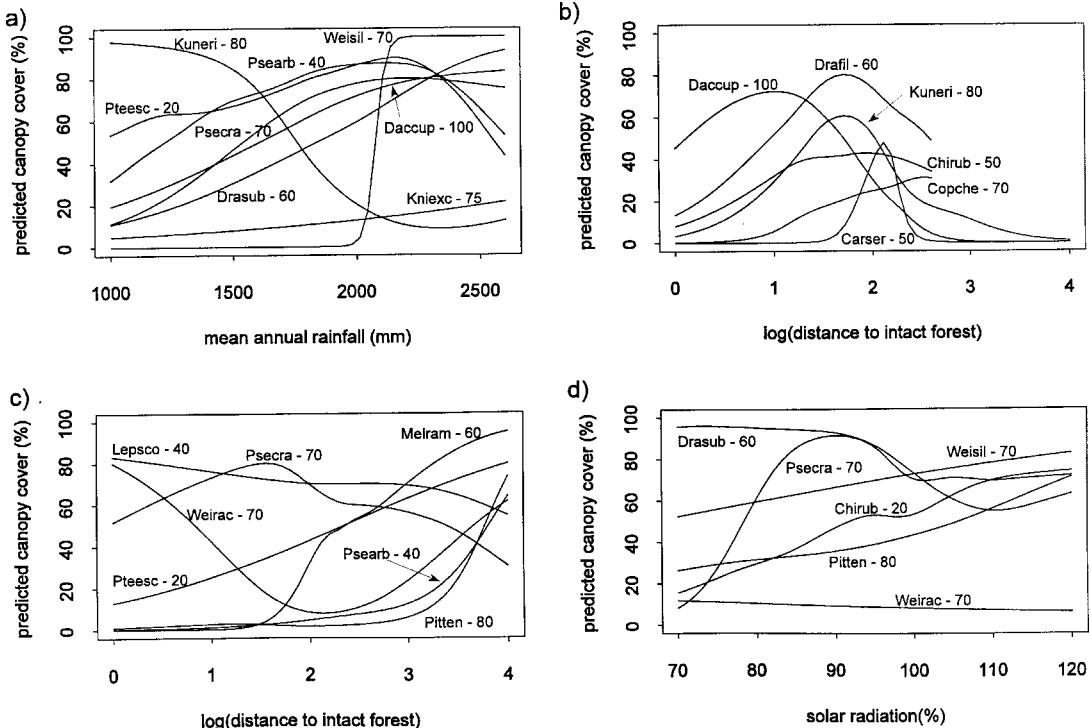


Figure 5: Predicted canopy cover for major species in relation to (a) rainfall, (b) and (c) distance from intact forest, and (d) solar radiation - percentage of radiation received on a flat site. Values for other variables were set as follows: temperatures were set at the optima suggested from Fig. 4; ages were set at the level at which maximum cover occurred in Fig. 4, adjusted where necessary to allow variation along the x-axis to be adequately displayed - values are given after the abbreviated species name; values for other variables were set as in Fig. 4.

(>c. 2200 mm), reaching highest cover on steep transportational midslopes with high solar radiation.

Fewer species are restricted to sites with intermediate temperatures (c. 8-11 °C). *Dacrydium cupressinum* reaches highest levels of cover on sites with little slope, and with the oldest stand ages, declining dramatically in cover at distances greater than 40-50 m from intact forest. *Carpodetus serratus* occurs at intermediate ages, reaching greatest cover on convex creep slopes with low to intermediate rainfall, and close to intact forest. *Pittosporum tenuifolium* occurs on sites most distant from intact forest, with greatest abundance reached either on flat or very steep sites with high solar radiation. *Dracophyllum subulatum* occurs at intermediate disturbance ages, reaching greatest cover on alluvial toe-slopes with little slope, and increasing in cover as rainfall increases.

Three species are dominant on the coolest sites (<c. 9.0 °C). *Chionochloa rubra* reaches highest cover on interfluves which have been recently

disturbed, are distant from intact forest, and have little slope and high solar radiation. However, it persists longest on sites with low solar radiation. *Coprosma cheesemanii* reaches greatest levels of cover at around age 70 years on gently sloping seepage slopes and colluvial toe-slopes. On cool, high rainfall sites, *Dracophyllum filifolium* increases steadily in cover with increasing age since disturbance, to become dominant on most sites from age 50 yr onwards. Exceptions are either sites having little slope, or those close to intact forest, where other species replace it with time.

Discussion

This study clearly demonstrates the wide range of compositional variation which occurs in both space and time in the secondary vegetation of central North Island, and which results from the widely varying responses of the dominant species to both

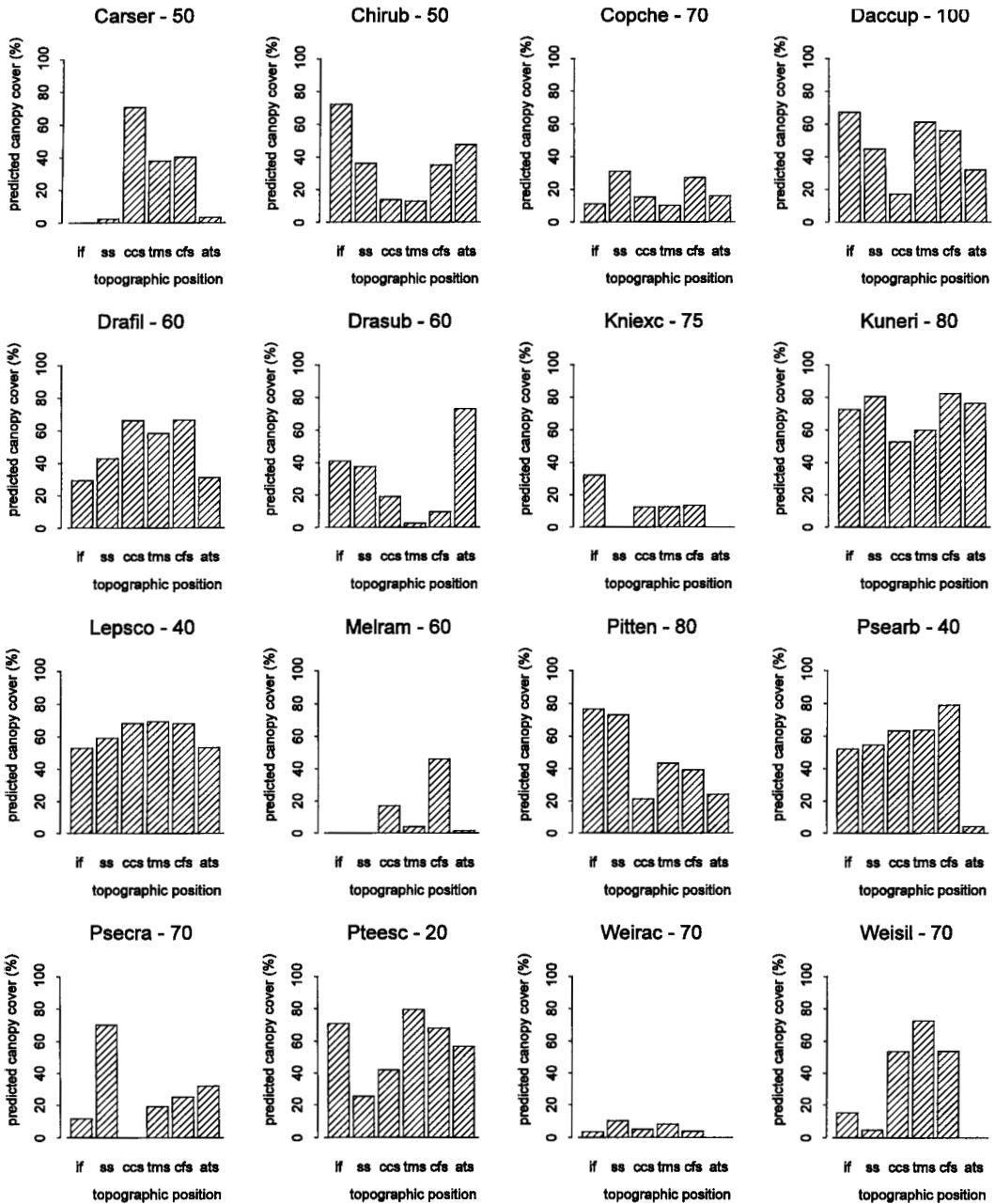


Figure 6: Predicted canopy cover for major species in relation to topography. Values indicate the predicted cover at the age displayed after the abbreviated species name for each graph. Values for other variables were set as in Fig. 4. Topographic classes are as follows: IF - interfluvial; SS - seepage slope; CCS - convex creep slope; TMS - transportational mid-slope; CFS - colluvial foot-slope; ATS - alluvial toe-slope.

disturbance and environment. This variation is least marked in early-successional vegetation, which is generally dominated by varying mixtures of two species of wide-environmental tolerance but contrasting physiognomy, i.e., the shrub *Leptospermum* and the fern *Pteridium*; the only other widespread dominant in early succession, the tussock *Chionochloa rubra*, occurs only on the coolest sites. However, with time, there is a progressive increase in regional differences in composition as a wide range of other species, mostly with more specific environmental requirements, become established, a trend which is also apparent in other studies of this nature (e.g., Christenson and Peet, 1984). This subsequent successional development is most rapid in warmer climates, and particularly where *Pteridium* is the dominant pioneering species; on such sites broadleaved species invade to form shrubland from as early as 20 years onwards. Compositional change occurs much more slowly where *Leptospermum* or *Kunzea* are dominant, i.e., mostly on cooler sites. Where relatively pure *Leptospermum* or *Kunzea* canopies have formed, further development appears to be often associated with large-scale senescence of these species, leading to their replacement by conifers and broadleaved species which have developed in the sub-canopy, provided there are adequate seed sources adjacent. The slowest changes predictably occurs on the coolest sites, where even 50 years after fire, stands are still dominated by low-statured shrubs such as *Dracophyllum* spp., and species typical of high forest are still rare.

The role of environment

Results, particularly from the GAM analyses indicate that although age since disturbance is an important determinant of the abundance of individual species, it is also strongly determined by a range of environmental factors operating over various spatial scales. Of these, temperature emerges as that with the strongest correlation; plot groups in the TWINSPAN classification were most strongly separated in relation to temperature, and temperature was dominant in most of the GAM regressions. Its most obvious effect is in determining the range of species potentially able to occur at any particular site through its fundamental control of several plant life processes (e.g., Woodward, 1987). However, it is also an important factor controlling the rate of successional development, with return to forest vegetation generally much more rapid on warm than cold sites as already noted.

In terms of spatial scales, temperature is generally more important at a regional rather than

local scale, i.e., differences in overall temperature regime and consequently vegetation are likely to be less marked between closely adjacent study sites than between sites which are widely separated in space. An important exception to this is the influence of extreme events such as frost, which although widely correlated with average daily temperatures, are also strongly influenced by topography, and hence can show very marked variation over very small spatial scales (Leathwick, 1987), giving rise to dramatic local changes in vegetation, e.g., local dominance by the tolerant *Dracophyllum* spp. in so-called "frost-flats" with only very slow invasion by other woody species (Smale, 1990).

Of the other environmental factors, rainfall is important at broad spatial scales influencing species distribution at a regional level both through its direct effects on soil moisture availability, and its more indirect effects on soil development. Its effects are generally less important than temperature, reflecting the ready availability of soil moisture in most months of the year in all the study areas. In contrast, slope and topography, as a consequence of their greater variability over small spatial scales, function at a much more local level, influencing both microclimate as already indicated, and local variation in soil properties and moisture availability. For example, stable ridge soils can be expected to be less fertile than those on lower slope positions subject to periodic inputs of colluvium or alluvium (Campbell, 1973; 1975; Gerard, 1981); those on mid-slopes are likely to be more variable, depending on the periodicity of mass-movement. Soils in upper slope positions are also likely to be more drought prone than those on lower slope positions, and this can produce marked local variation in vegetation composition (McQueen, 1961).

The importance of distance from intact forest stems from its influence on availability of seed for later successional species (Rogers and Leathwick, 1994). Species more typical of mature forest such as *Dacrydium cupressinum* have greatest cover close to intact forest, while those occurring at longer distances either have small, easily dispersed seeds (e.g., *Pseudopanax arboreus*, *Melicicytus ramiflorus*), or are able to withstand recurrent disturbance through vegetative resprouting (e.g., *Pteridium esculentum*, *Chionochloa rubra*).

How predictable are these successions?

Although the strength of the correlations between individual species abundance and both environment and time, indicate that the regional variation in secondary vegetation composition has a strong predictable component, the relatively high residual

mean deviances for some species, and particularly for the early successional *Pteridium* and *Leptospermum*, indicate that factors additional to those we analysed are also important determinants of species distribution and abundance. Examination of our data and review of relevant literature suggests that improvement of these models would probably require additional information on disturbance regimes, browsing/grazing regimes, and/or soil fertility as follows.

Fire, the dominant disturbance agent at most of our sites, could be expected to vary in intensity, extent, periodicity, and the time of year at which burning occurred, and such variation is likely to have a profound effect on species composition (e.g., White, 1979; Heinselman, 1981; Sousa, 1984). For example, frequent burning is likely to favour dominance of *Leptospermum* over *Kunzea*, because the former retains its seed in woody capsules for several years, but the latter sheds its seed as soon as it ripens (Burrell, 1965). Similarly, frequent burning is likely to favour species able to vegetatively resprout after fire, e.g., *Pteridium* (Cremer and Mount, 1965), *Chionochloa* (Wardle, 1991), and *Weinmannia racemosa* (Druce, 1957), and extensive burning is likely to favour species with fine wind-dispersed propagules, e.g., *Pteridium*, *Leptospermum*, *Kunzea*, and *W. racemosa*.

Marked differences could also be expected in grazing influence at our study sites varying both in time and space, and have potential to profoundly affect successional rates and pathways, both in the early (e.g., Silvester, 1964; Wardle, 1991) and later stages of succession (e.g., Payton, Allen and Knowlton, 1984). In our study area, for example, *Leptospermum* is likely to have been favoured at the expense of *Pteridium* in areas subject to grazing by domestic stock (Guthrie-Smith, 1953; Clarke, 1960; Grant, 1967; Wardle 1991).

Finally, although we made no measurements of soil fertility, our observations indicated that although *Leptospermum* is widespread as a pioneer on colder sites (c. 9–12 °C mean annual temperature), it is unlikely to compete with *Pteridium* on warmer sites in the absence of grazing, except where soils are either infertile (older, leached rhyolitic substrates) or have physical limitations to growth such as stoney or bouldery substrate.

Management implications

The diverse and dynamic nature of central North Island secondary vegetation elucidated by our results will in time pose a dilemma for conservation managers, who, up until now, have been reluctant to regard planned human disturbance as a tool to be used

for the maintenance of species and community diversity (Rogers and Leathwick, 1994). But given both the inevitable progress towards high forest, and the frequent focus in the reserves network on primary forest at the expense of secondary vegetation, it seems likely that with time much of the diversity currently exhibited by secondary vegetation in central North Island will be lost without some form of human intervention. This inevitability will present a dilemma to conservation management staff who in many cases are also responsible for public education to minimise destruction of reserves by uncontrolled fire. Although fire is widely used for conservation management in other countries, e.g., Australia, its use as a conservation management tool in New Zealand is generally neither documented nor understood. For this reason progress towards managed use of fire, if it occurs at all, will require careful consideration of a wide range of issues, including public perceptions and use of conservation lands, problems with weed invasion, and risks of ecosystem degradation.

Statistical considerations

A study such as this presents a major challenge in sampling design, not only because of the limited number of study sites which were available to be sampled, but also because of the finite number of disturbance events, sometimes only 2 or 3, which occurred at each study site. Two inadequacies can be identified in the data as a consequence. First, although the sampling design used was designed to maximise the number of environmental combinations sampled, the final dataset was far from balanced in a statistical sense, with many combinations of environmental variables sampled by only one or two plots and some not at all. Second, because sampling had to be clustered in a limited number of study sites, values for some variables, e.g., temperature and rainfall, were also strongly clustered. Although superficially this resembles pseudoreplication (e.g., Hurlbert, 1984), it more accurately reflects the varying scales over which different environmental variables are spatially autocorrelated, with temperature and rainfall, in particular, generally varying only a little over small distances, *cf.*, variables such as slope and topography. Although the exact consequences of this on the regression analysis are difficult to assess, comparison of fitted values from the GAM analysis with the raw data points confirms that these regressions have functioned robustly as a tool for summarising the complex interactions between vegetation composition and environment observed in the data. However, as with any regression analysis, extrapolation should not be attempted beyond the environmental domain from

which the original data were collected, and given the potential for confounding effects from other species not encountered in this study, should probably also be limited in their application to central North Island.

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