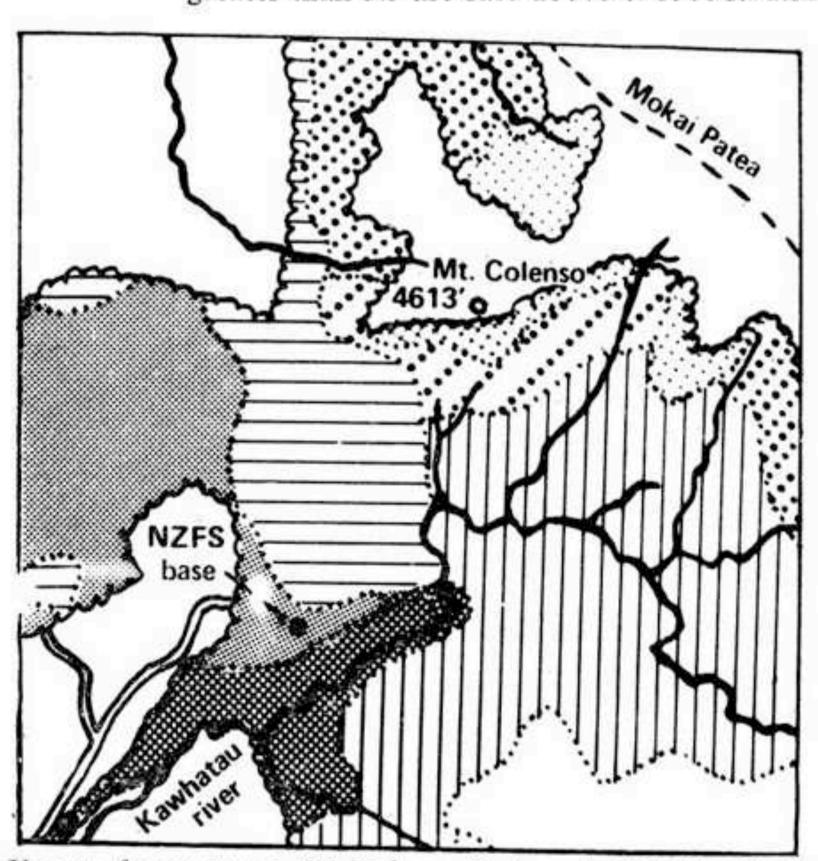
COLENSO VEGETATION OF MOUNT STUDIES THE ON NEW ZEALAND

FOREST CONTINUUM THE

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SUMMARY: Plotless methods were used to sample four forest stands situated at different altitudes on Mount Colenso, Ruahine mountain range, North Island, New Zealand. The altitudinal distributions of the main woody species are described graphically. All species have overlapping altitudinal ranges, so that no clear altitudinal 'belts' can be distinguished. The forest composition is regarded as a continuum showing gradual variation from diverse mixed (podocarp-beech) forest on the terraces of the Kawhatau river (c. 2000 ft. above sea level), through red beech (Nothofagus fusca) dominated forest at intermediate altitudes, to Libocedrus/ Dacrydium forest at the upper limits of tree growth (c. 4000 ft. a.s.l.). The splitting of this continuum into forest types defined by canopy dominants is briefly discussed. Tree seedling populations show a decrease in specific diversity, though not in total numbers, with increasing altitude. A significant decline in soil pH with altitude is demonstrated. Surface soils with a pH greater than 5.5 are rare above c. 3500 ft. a.s.l. but frequent at lower altitudes.



Introduction

This paper presents a quantitative description of the forest vegetation on the slopes of Mount Colenso which face the Kawhatau Valley. It is introductory in nature, and will be followed by a more detailed account of the population structure, dispersion and regeneration of red beech (Nothofagus fusca) (Ogden 1971).

Mount Colenso is an outlier of the Mokai Patea range with an altitude of 4,613 ft. a.s.l., and it is situated on the western side of the main Ruahine mountain range approximately 15 miles east of Taihape (see Elder 1965; Map 1). It is one of the most westerly and easily accessible peaks in the Ruahine mountains. Elder (1965) summarised the geological, historical and climatic data available for the western Ruahines and described and mapped the vegetation. Detailed forest type maps are at present being prepared by the New Zealand Forest Service (Fig. 1).

Fieldwork was carried out from the Kawhatau base hut of the New Zealand Forest Service. The

Key to forest types (McKelvey, P. J., and Nicholls, L. J. 1957)

G6 Kaikawaka-Pink Pine (Libocedrus bidwillii-Dacrydium biforme)

J4 Red Beech-Mountain Beech-Kaikawaka (Nothofagus fusca-N. solandri var. cliffortioides-L. bidwillii)

J5 Mountain Beech-Kaikawaka

K3 Red Beech

K7 Red Beech-Mountain Beech

I1 Red Beech-Rimu (N. fusca-Dacrydium cupressinum)

14 Rimu-Miro-Matai-Red Beech-Black Beech (D.cupressinum-Podocarpus ferrugineus-P.spicatus-Forest margin

Road River

N. fusca-N. solandri var. solandri)

FIGURE 1. Forest types on Mt. Colenso (J. L. Nicholls, pers. comm.)

hut is situated above the Kawhatau River (2,169 ft. a.s.l.) at the foot of a forested spur, up which a track runs to the summit of Mount Colenso. The extensive flat area around the base hut carries mixed beech/podocarp forest which has been selectively milled. Below this flat the land slopes steeply to the Kawhatau River, the slope being interrupted by long and narrow terraces. The terraces show little evidence of disturbance, but a few larger trees have probably been removed. The steep spur above the base hut carries red beech forest, and at about 3,000 ft. a.s.l. it levels out to climb gently to the upper limit of the red beech. Here again, the slope is steeper and covered with a narrow belt of forest dominated by Libocedrus bidwillii and Dacrydium biforme (Libocedrus/Dacrydium Forest). This grades rapidly into an equally narrow belt of subalpine scrub and *Phormium colensoi*. The summit ridge carries Chionochloa tussock grassland with patches of Hebe and Cassinia.

METHODS

Fieldwork was carried out in February of 1969 and 1970. Three stands of vegetation, situated at altitudes of 2,100 ft. a.s.l. (stand 1), 2,750 ft. (stand 2) and 3,250 ft. (stand 3), were chosen for detailed study in 1969, and a fourth stand was added at 3,650 ft. a.s.l. in 1970. Also in 1970, the presence of different species was recorded at 100-foot altitude intervals between the Kawhatau River (Flying Fox) and the summit of Mount Colenso.

Each stand was square and about one hectare (2.471 acres) in area and was sampled by the point-centred quarter method (Cottom and Curtis 1956; Greig-Smith 1964). An approximately regular grid of 25 points, each 25 paces apart, was recorded in each stand. On steep or uneven terrain covered with dense vegetation accurate measurement of stand area and location of points is difficult, and, in consequence, the accuracy of density estimates is affected. Mark and Esler (1970) have shown that this method usually overestimates basal area, and may under-estimate density. However, if all that is required is adequate coverage of stand area and an unbiased sample of the species present, chosen without any preconceptions, the method is satisfactory.

At each sampling point, the nearest tree in each of four 90° quadrants was identified, and its circumference and distance from the point was

measured. This provided data for 100 trees in each stand. The minimum trunk diameter recorded was two inches (5.1 cm.) at approximately four feet (1.2 m.) from the base (2 in. d.b.h.). In the case of trunks forked near the ground measurement was normally made below the fork.

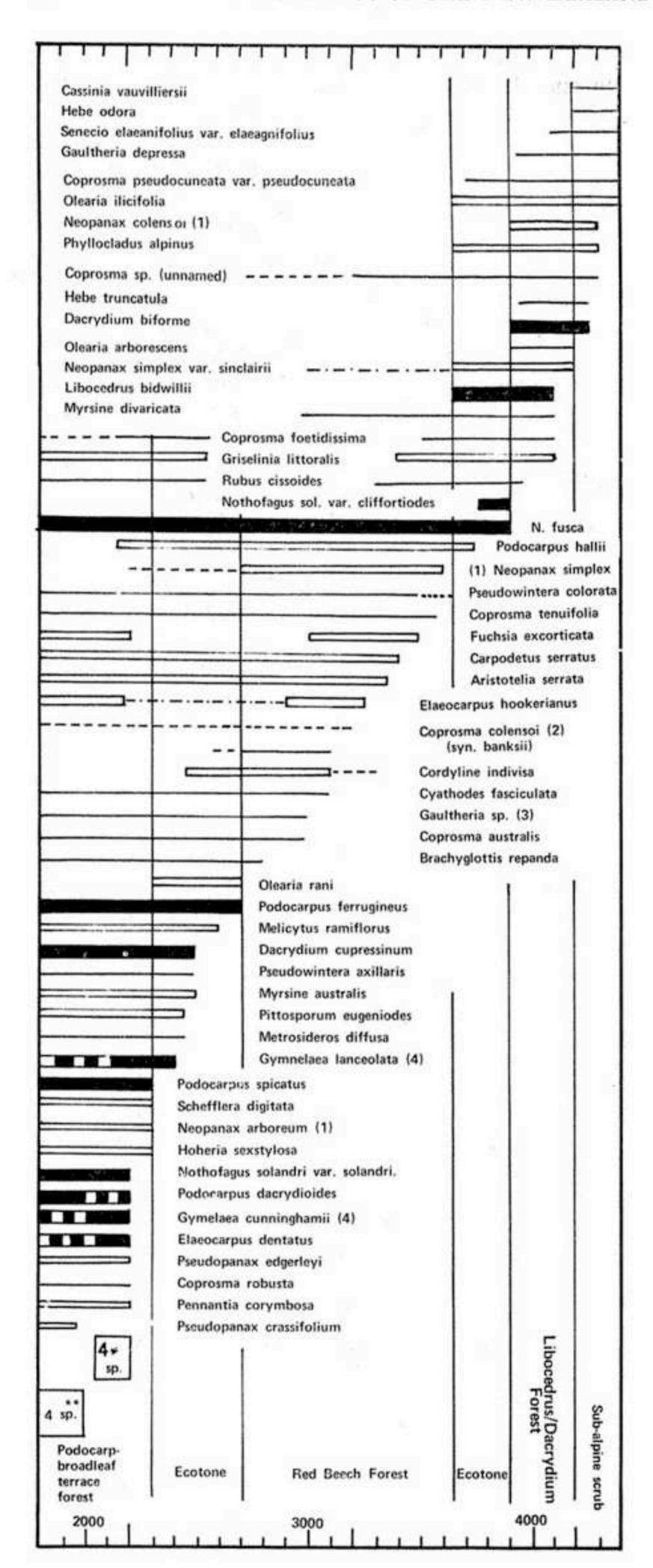
In each stand enumerated in 1969, seedling numbers were counted in quadrats of four square metres. These were placed in a similar way to the points for the tree enumeration but on an independent grid. In stand 3, 25 quadrats were counted, in stand 2, 24 and in stand 1, 14. Seedlings were defined as young trees less than 45 cm. in height. Information on individuals greater than 45 cm. in height but less than 2 inches (5.1 cm.) d.b.h. ("saplings") was obtained from stand 1 only by running three belt transects across the stand and recording the numbers of each species in 75 continguous quadrats of about 4.5 square metres.

No detailed examination of the soil of each stand was attempted, but soil profiles were examined and pH recorded at different altitudes.

RESULTS

I. The altitudinal distribution of individual species. The altitudinal distributions of the 64 woody species identified are recorded in Fig. 2. These have been arbitrarily classified as canopy, subcanopy and shrub species although some are known to change their growth form considerably with altitude. In general, the upper altitudinal limit of each species is more clearly defined than its lower limit. This is due to a tendency for stragglers to occur in forests at altitudes lower than those in which the species is most commonly found. The lower limit of many of the species (e.g. Pseudowintera colorata; Fuchsia excorticata) is certainly at a lower altitude than the lowest investigated (1,800 ft. a.s.l.).

All species show overlapping altitudinal ranges, so that no clear-cut altitudinal 'zones' or 'belts' can be distinguished even if canopy species only are considered. Thus, the forests on the Kawhatau spur form a continuum of overlapping species distributions — from mixed beech/podocarp forest on the terraces, through red beech dominated forest at intermediate heights and into Libocedrus/Dacrydium forest near the tree-line. Libocedrus/Dacrydium forest is separated from the red beech forest below by a zone in which mountain



beech (Nothofagus solandri var. cliffortioides) occurs, and merges gradually into the Olearia, Hebe and Cassinia scrub above. This scrub, in turn, gives place gradually to tussock grasses and herbs. Division of this continuum into communities with ecotones between (Fig. 2) is arbitrary, albeit convenient for descriptive purposes.

There was a marked decline in the diversity of woody species with increasing altitude. In the mixed terrace forest, 44 species were recorded, and of these 20 were not found higher than 100 feet above the base hut. Red beech forest, on the other hand, contained only 22 species, none of which was entirely restricted to it, and most of which were present also in the mixed forest of the terraces. In Libocedrus/Dacrydium forest only 14 species occurred, and most of these were not found below the Libocedrus/beech ecotone; only two were found on the terraces. Only 11 species of woody plants were recorded from the subalpine scrub above 4,000 ft., but large herbs (Chionochloa, Phormium, Aciphylla, etc.) were abundant.

The altitudinal distribution of the ferns and herbs studied is similar to the continuum seen in the canopy trees and shrubs (Fig. 3). Diversity also decreases with increasing altitude. For the central Ruahines, Elder (1965, Appendix 2) records 14 fern species which are common below 3,000 ft. a.s.l., five between 3,000 and 4,000 ft. and only two above 4,000 ft. There is, however, an increase in the number of herb species present as one passes from forest to tussock. The composition

Figure 2. Altitudinal distribution of Canopy
Sub-canopy Shrubs and lianes — on the
Kawhatau spur of Mt. Colenso.

Dashed bars and lines imply status uncertain, probably present but rare, dot/dash lines imply present but rare, dots seedlings only observed. *Single observations of Melicytus lanceolatus, Parsonsia heterophylla, Melicope simplex, Neopanax anomalum; **Hebe stricta, Rubus schmidelioides, Myrsine salicina, Neomyrtus pedunculatus. Nomenclature is after Allan, H. H. (1961) Flora of New Zealand (Vol. 1). Several name changes have taken place as follows: (1) Neopanax now transferred to Pseudopanax; (2) Coprosma banksii is regarded as a form of C. colensoi; (3) Specimens of Gaultheria could not be ascribed to any sp., although some were probably G. antipoda; (4) Gymnelaea, now Nestegis.

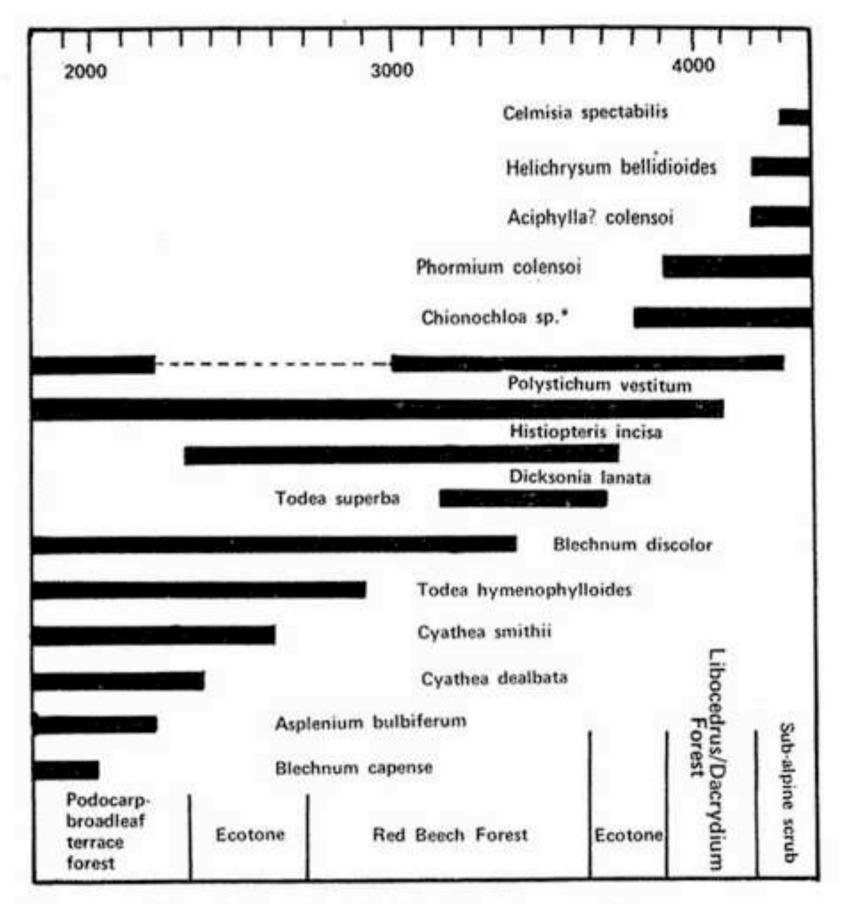


FIGURE 3. Altitudinal distributions of some common ferns and subalpine herbs on the Kawhatau spur of Mt. Colenso.

of the tussock grasslands of Mount Colenso appears to be typical of the central Ruahines (see Elder 1965, list 5a).

2. The altitudinal gradient of soil types

The terrace soils are mainly deep sandy loams, without clearly marked horizons, which are yel-

lowish brown in colour and become paler with depth. The soil surface is usually covered by a layer of decaying leaves over a dense root mat. Greywacke pebbles are abundant on the lower terraces. On the steeper parts of the spur above the base hut, the underlying fragmented greywacke is exposed in places. Here soils are generally yellowish or brown, shallow and stony with a thin layer of leaf litter. Beneath extensive areas of Dicksonia lanata, slowly decaying fronds form a thick surface layer.

The flat parts of the spur above 3,200 ft. a.s.l. have a darker and deeper soil with angular greywacke fragments below and occasional iron mottling which increases with altitude. In the tussock grassland, surface soils are usually peaty and sometimes bleached below the peat with rusty patches at 2 to 3 ft. depth (60–90 cm.). The soils on the Mokai Patea are often deep and probably aoelian in origin (Moar, N. T. pers. comm.).

A total of 98 pH recordings was made in 1969 and 1970 at many different locations. These show considerable variation of soil pH within the range of 4.2 to 6.5 even over small areas. Table 1 summarises these results and illustrates a general decrease in the pH of surface soils with increasing altitude. This effect is statistically significant ('t' for comparison of samples taken between 2,060 and 2,169 ft. a.s.l. with those taken between 2,750 and 3,250 ft. a.s.l. =2.702 (P<.02); for comparison of samples taken between 2,060 and 2,169 ft. a.s.l. with those taken between 3,750 and 4,400 ft. a.s.l. 't'=4.434 (P<.001). Surface soils with a pH greater than 5.5 appear to be rare above about 3,500 ft. a.s.l. but are frequent at lower altitudes.

TABLE 1. Means and standard errors for soil pH at different altitudes and depths on Mt. Colenso

	Sample depths (cm.)							
Altitudinal range of samples	Description of sites		0-15 Mean and standard			>15 Mean and standard		
(feet a.s.l.)		n*	error	range	n	error	range	
4400	Chionochloa tussock grassland							
to	Dacrydium/Libocedrus forest and	7	5.03 ± 0.13	4.6 - 5.4	11	5.27 ± 0.19	4.6 - 6.3	
3750	Nothofagus solandri var. cliffortioides ecotone							
3250	N. fusca forest. Mainly beneath							
to	Pseudowintera colorata in stands	37	5.34 ± 0.08	4.2 - 6.5	6	5.37 ± 0.13	5.1 - 5.9	
2750	2 and 3							
2169	Kawhatau base clearing and							
to	beneath Pseudowintera in stand 1.	24	5.65 ± 0.06	4.9 - 6.5	13	5.15 ± 0.05	4.9 - 5.5	
2060	Mixed beech-podocarp forest.							

^{*} n=number of samples

^{*} Mainly C. pallens. Some C. rubra was recorded higher and C. conspicua was present rarely in Red Beech Forest.

TABLE 2. L	Description	of	stand	S
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Stand	Altitude (ft. a.s.l.)	Mean density of trees per stand (ha)	Slope	Vegetation type
4	3650	536	Variable, mainly gentle	Near upper limit of red beech and into Libocedrus ecotone
3	3250	911	Mainly flat	Red beech
2	2750	803	Very steep	Red beech
1	2100	1322	Terrace flat below base hut	Mixed red beech — Podocarpus

Associated with the altitudinal pH shift is a gradual change in profile. The proportion of organic matter in the surface layers, and their water retention capacity, increases with altitude. Above 4,000 ft. a.s.l., a mor type of peat occurs, and pH tends to increase lower in the profile. In flushed situations, for example near tarn outflows, the pH of the deeper layers may be above 6.0. At altitudes below 2,500 ft. a.s.l., on the other hand, a mull type of humus overlies the root-mat and pH decreases with depth ('t' for comparison of pH recordings from above 15 cm. depth with those from below 15 cm. at lower altitudes (2,060–2,169 ft. a.s.l.) = 5.108; P<.001).

3. The quantitative composition of the forest at different altitudes

The four stands studied in detail are briefly described in Table 2. More detailed information on species composition is included in Tables 3 and 4

The estimated mean tree density (Table 2) varies from 536/ha, in stand 4 to 1,322/ha, in stand 1. The difference between these two extremes of density is due mainly to the abundance of *Pseudowintera* species in the understorey of stand 4. The stand data confirm the general reduction in number of species with increasing altitude, and indicate the way in which the proportions of

TABLE 3. Tree species frequencies in the 100 trees sampled in each stand and basal areas of each species relative to the total basal area of all trees in the stand

Species (arranged in descending order of	Frequencies per 100 trees Stand				Relative basal areas Stand			
altitudinal range)	1	2	3	4	1	2	3	4
Coprosma pseudocuneata				11		<u> </u>		2.0
Olearia ilicifolia		-		3	-	_	-	3.6
Phyllocladus alpinus		-	1	1	200	-	10000	< 1.0
Myrsine divaricata	-		-	15		-	-	1.1
Griselinia littoralis	1	11	25	21	< 1.0	1.8	14.1	32.3
Nothofagus fusca	8	47	21	37	50.0	94.6	78.6	58.6
Neopanax simplex var. sinclairii	_	1		12	_	< 1.0		2.1
Podocarpus hallii		3	_		200	1.2		
Pseudowintera colorata	45	9	14		5.3	< 1.0	< 1.0	
Fuchsia excorticata	10	10	22		4.6	< 1.0	4.8	Manager 1
Coprosma spp.*	5	1	1		< 1.0	< 1.0	< 1.0	
Carpodetus serratus	5	2		***	1.2	< 1.0	-	
Aristotelia serrata	3	5	16		< 1.0	< 1.0	1.8	
Elaeocarpus hookerianus		3			< 1.0	< 1.0		-
Cyathodes fasciculata	3	3			< 1.0	< 1.0	30,000	-
Podocarpus ferrugineus	4		-	A. 1444	10.8		****	
Melicytus ramiflorus	5	2	-		12.3	< 1.0		-
Cyathea (2 spp.) *	4	-	***	*****	3.5			* ****
Dacrydium cupressinum	1				9.9	-	-	-
Pseudowintera axillaris	1		-	-	< 1.0	+	+	
Myrsine australis	3			W-100	< 1.0	*******	Arteman	2,000
Pittos porum eugenioides	ĩ		4 1000		< 1.0	11000	1	2.00
Pennantia corymbosa	1		****		< 1.0	-		
Unidentified (dead)	_	3	1			< 1.0	< 1.0	
Number of species	17	12	6	7	17	12	6	7

^{*} Coprosma spp. were not identified in 1969, but most of those here recorded were broad-leaved species. Cyathea dealbata and C. smithii.

different species shift with altitude. It should be noted that the 'importance values' (Table 4) are defined rather differently from usual. 'Importance values' can be misleading, insofar as they combine in one figure two or more distinct attributes of the vegetation. Although the population structure of a species may be quite different in two stands, it may have similar 'importance values' (e.g. red beech in stands 3 and 4). 'Importance values' are generally of use in providing a single figure allowing easy comparison of species in a number of stands. However, their interpretation is difficult unless the measures which they combine are also given (Table 3).

Table 4. 'Importance values' (% Frequency + Rel. basal area) of all species with relative basal areas greater than one in at least one stand

	'Importance value' Stand						
Species	1	2	3	4			
Olearia ilicifolia	_		_	6.6			
Coprosma pseudocuneata	-	-		13.0			
Neopanax sim. var. sinclairii	_	_	-	14.1			
Myrsine divaricata	_	_	-	16.1			
Griselinia littoralis	2.0	12.8	39.1	53.3			
Nothofagus fusca	58.0	141.6	99.6	95.6			
Aristotelia serrata	4.0	6.0	17.8				
Fuchsia excorticata	14.6	11.0	26.8	_			
Pseudowintera colorata	50.3	10.0	14.0	-			
Podocarpus hallii		4.2					
Carpodetus serratus	6.2	3.0		_			
Melicytus ramiflorus	15.3	3.0		-			
Podocarpus ferrugineus	14.8	-		-			
Dacrydium cupressinum	10.9						
Cyathea (2 sp.) *	7.5	-		-			

* C. dealbata, C. smithii

Stand 4 differs markedly from the other three, having only red beech and Griselinia littoralis in common with them. Stands 1, 2 and 3 have five species in common, although the relative importance of these species changes from stand to stand. Stand 2 is remarkable for the high degree of dominance shown by red beech (importance value =141.6, maximum possible, in monoculture =200), while stand 1 lacks marked dominance by any of its many species. In this stand, a few large red beeches, and numerous small Pseudowintera colorata forming dense understorey thickets, have similar high importance values. The high density of P. colorata may indicate past milling or grazing. There are a few stumps of felled trees on the terrace, but careful inspection suggested that few, if any, trees have been removed from within stand 1.

Red beech is by far the 'most important' species if all stands are considered. Its maximum 'importance value' is on the steep slope of stand 2, and below this its population declines as other species increase in abundance. Beech occurs at a high density between 2,700 and 3,700 ft. a.s.l., although in different parts of this range it seems to have very different population structures. Griselinia littoralis was the only other species to occur in all stands. Its maximum 'importance value' was reached near the upper limit of red beech where there were many large old trees, but none less than 6 in. (15 cm.) d.b.h. was recorded. Like Aristotelia serrata, it declined in importance with decreasing altitude. Griselinia seedlings were often abundant beneath mature trees in all stands, but saplings and young trees were very rare. This species is selectively grazed by deer (Holloway et al. 1963; Wardle and Hayward 1970), which probably explains its apparent regeneration failure.

Pseudowintera colorata and Fuchsia excorticata show a marked decline in abundance on the steep slopes of stand 2. These species appear to favour the deeper, damper soils on flatter parts of the spur (stand 3) or on the terraces (stand 1). In the eastern Ruahines, populations of both these species and of Griselinia littoralis have changed in abundance, distribution and age structure since c. 1940 coinciding with increasing numbers of browsing mammals (Elder, pers. comm.). Podocarpus hallii and Elaeocarpus hookerianus occurred only in stand 2. The remaining species listed in Tables 4 and 5 tend to fall into two groups — those restricted to stand 4 and those restricted to, or most common in, stand 1.

4. Seedling and 'sapling' densities (Table 5)

Average regeneration (all spp.) per m² showed no significant differences in the three stands on which counts were made. The overall mean seedling density was 12.7 ± 2.0 seedlings/m². This is equivalent to approximately 10^5 seedlings per stand. However, mean values obscure some real differences in the regeneration pattern between stands (Fig. 4). Patchiness of distribution was greatest on the steeply sloping stand 2 and least on the terrace (stand 1). Low density areas on the slope were almost always associated with a dense cover of *Dicksonia lanata* or *Histiopteris incisa* (see also Elder 1965, p. 24). *Dicksonia lanata* formed large patches, especially in stand

2. Beneath the fern tussocks, a dry layer of dead fronds several inches deep may hinder the germination and establishment of tree seedlings. Dense patches of seedlings were frequently composed mainly of one species—particularly Griselinia littoralis—and were usually close to the parent tree. The generally less patchy distribution of seedlings in stand 1 can perhaps be related to its even topography and to the larger number of species present. The increase in species diversity with decrease in altitude shown by the seedling community parallels that recorded for

Table 5. Seedling densities

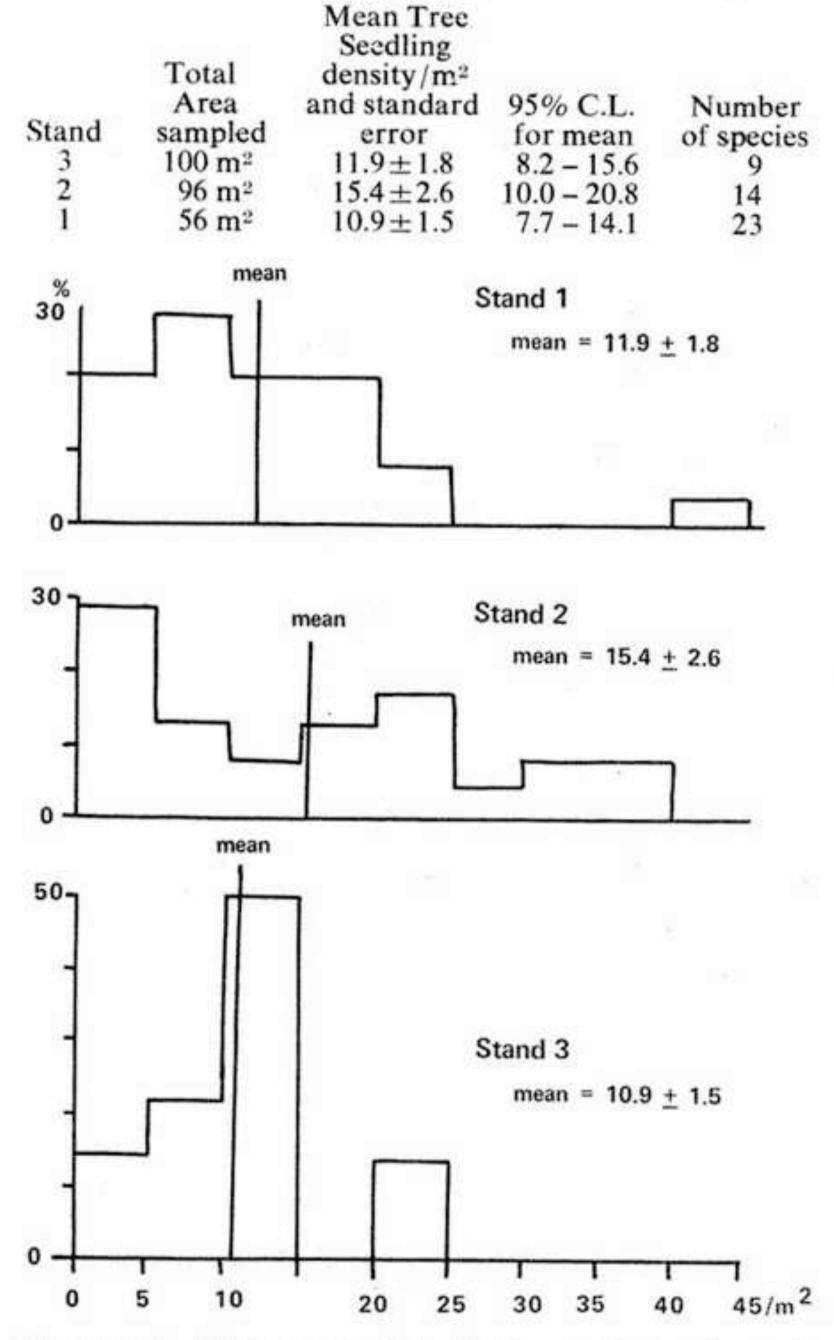


FIGURE 4. Frequency distributions of number of seedlings/m². Figure refers to all seedling species.

mature trees. (In 1970, a more detailed analysis of the density and distribution of red beech seed-lings was undertaken. The results will be reported separately.)

Saplings were only enumerated in stand 1. Pseudowintera colorata was the most common, occurring in dense patches which excluded most other species. It was estimated that there were approximately 8,000 saplings in stand 1, of which 6,000 were P. colorata. Of the 18 other species recorded, only Aristotelia serrata and Coprosma spp. (mainly C. australis) had a frequency above 10% in 75 quadrats.

The distribution of species across the terrace was interesting. On two transects running completely across the terrace (160 m.) Pseudowintera colorata formed dense stands in the central portion, but towards the riverside edge of the terrace there was a marked increase in the number of species. Of the 19 species recorded, 17 were found within 21 m. of the terrace edge, and seven species, including podocarps and beeches, were recorded as saplings from this area only. Coprosma spp. were almost confined to this marginal zone. Whether this is a local effect (the transects were only 18 m. apart) or a more general one, associated for example with increased light penetration or differences in soil drainage pattern towards the edge of the terrace, is not known. It was noticed that soil properties did appear to change along the transect; around the foot of the slope leading to the higher terrace the surface soil was stonier than elsewhere, presumably due to pebbles eroded from the bank above.

The frequency distribution of saplings per quadrat was tested for goodness of fit to a Poisson curve with a mean value of 4.59 saplings/quadrat. Observed and expected values differed significantly when tested with χ^2 , showing a very significant departure from randomness (P<.001). The data thus confirm the empirical observation that saplings are distributed in patches of high density, with low density areas between.

DISCUSSION

Classification of forest vegetation into 'forest types' and the imposition of boundaries between them is necessary both for the description and management of a forest area. Objective methods of making such classifications have been developed (Williams and Lambert 1959). However,

OGDEN: THE FOREST CONTINUUM

once a system of classification has been adopted it tends to influence the eye of the observer, such that the vegetation under consideration tends to be categorised into one unit or another. In this way a misleading impression of the nature of the boundaries between different categories of a classification ('communities') may arise. Also, there is a tendency for sampling to be biased towards those 'homogenous' areas which the worker considers typical, so that transitional areas are neglected. The data presented in this paper suggest that the forest communities of the western Ruahines intergrade, so that the construction of boundaries between them must be arbitrary.

The same conclusion was also expressed by Elder (1965) in a discussion of the altitudinal distribution of the physiognomic species in the Ruahine mountains. "The most striking feature of high-country vegetation is its stratification into well marked altitudinal belts, and the examination of these is the most obvious line for investigation of distribution." Elder then states, "... there was a suspicion that there had been a tendency to lump groups of species into belts on rather too arbitrary a basis", and later "In averaging out [the altitudinal ranges of different species] it became clear that the representative species are not grouped in altitudinal zones, but appear in an overlapping gradation."

An objective description of the forests must take into account the general lack of clear-cut boundaries. If empirical classification is to be employed, it seems better to recognise a few main communities with broad ecotones between them, than to split the continuum into a large number of arbitrary segments. The concept of the continuum, and the ordination methods of the Wisconsin school (Bray and Curtis 1957), seem very suitable for application to these highly diverse forests.

Although no 'diversity indices' (Williams 1964) have been calculated, the data reveal a gradual decrease in the number of woody species with increasing altitude. From this fact alone one might expect the boundaries between forest types to be more easily defined at higher altitudes. The 'tree-line' is a good example of a vegetational boundary which is usually fairly obvious, although nevertheless arbitrarily defined.

In discussing the forests of the Tararua mountains, Holloway et al. (1963) state that "maximum variety exists in the forests of the foothills and

deep valleys, at altitudes not exceeding 1,500 feet, on the deepest, most fertile and least erodible soils. On these sites, there are a score of forest types distinguished by varying combinations of dominants". The same pattern exists in the Ruahines.

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