REGENERATION PATTERNS IN BEILSCHMIEDIA TAWA-DOMINANT FOREST AT ROTOEHU

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ABSTRACT

Regeneration in gaps and under closed high canopy, representing the gap and mature phases of the forest growth cycle, was investigated in two small areas within forest dominated by **Beilschmiedia tawa** (A. Cunn.) Kirk (tawa) at Rotoehu in the North Island of New Zealand. Significant differences in regeneration occurred between phases, and within phases diameter distributions varied among species. These results suggest differing replacement strategies among species, largely reflecting differences in shade-tolerance. Of the four major regenerating species, shade-tolerant tawa and **Dysoxylum spectabile** (Forst. f.) Hook. f. (kohekohe) commonly develop to advanced stages beneath closed canopies; relatively intolerant **Litsea calicaris** (A. Cunn.) Kirk (mangeao) and **Knightia excelsa** R. Br. (rewarewa) seldom do, apparently requiring gap formation for development to maturity. In the area where tawa and kohekohe were co-dominant in the canopy, they tended to replace each other, thus maintaining their co-dominance.

In forests where the gap phase is important, replacement trends may best be gauged from gap regeneration alone. Of the indices of species' relative importance tested, four juveniles of largest diameter appeared the most appropriate predictor of future canopy occupation in gaps.

INTRODUCTION

There has been increasing interest in recent decades in the processes by which forest canopies are replaced and in ways of predicting future canopy composition and elucidating successional trends. Although several modes of canopy replacement are recognised, in many forests the gap phase is of vital significance as part of the forest growth cycle (Whitmore 1975). The occurrence of a mosaic of patches at different stages of maturity (Watt 1947) is characteristic of forests in which gap phase replacement, i.e., colonisation of openings, is occurring.

In this study, we examined regeneration in two phases, "gap" and "mature", of the forest growth cycle in Rotoehu State Forest where "patchiness" suggested that gap phase replacement might be important. The "gap phase" is defined here as the relatively brief period during which the gap is receptive to colonisation, from the time of its formation to the development of a seedling/sapling thicket (often with scattered poles) consisting of surviving advance growth and new recruits. The "mature phase" may be defined as the period when the final canopy trees at any given site have reached the predominant canopy height (cf. Cousens 1974).

Initially centred on two long-established (1957) 0.4-ha ecological transects* with known histories, sampling was extended to forest in the vicinity. This paper presents data on gap and understorey regeneration, draws conclusions about the regeneration strategies of major canopy species in Rotoehu Forest, examines indices of species importance as predictors of future canopy composition, and tentatively indicates successional trends in the areas studied.

BACKGROUND

Rotoehu Forest lies in the central Bay of Plenty, 22 km south-west of Te Puke, and occupies the undulating to dissected eastern portion of the Kaharoa Plateau. Soils are Tarawera gravels, recent volcanic soils which overlie deep deposits of Kaharoa Ash and earlier tephra and are therefore droughty in summer. Climate is sunny and sheltered, with a rather variable annual rainfall of *c.* 1700 mm. About 70 ground frosts occur per year (Nicholls 1969; Wards 1976).

Before logging, the forest comprised mostly scattered rimu (*Dacrydium cupressinum* Lamb.) emergent over dense hardwood tiers dominated by tawa and pukatea (*Laurelia novae-zelandiae* A. Cunn.) on valley floors, and tawa, kohekohe, and kamahi (*Weinmannia racemosa* L. f.) elsewhere (Types D3 and D4; McKelvey & Nicholls 1957). Between 1934 and 1959 it was logged for podocarps and, to a varying extent, hardwoods also. It showed evidence of widespread cultural interference during the Polynesian era, with early seral kamahi-rewarewa stands apparently grading into later successional stages scattered throughout.

Introduced red deer (*Cervus elaphus* L.), pigs (*Sus scrofa* L.), and brush-tailed possums (*Trichosurus vulpecula* Kerr) were common for several decades until the late 1950s but are now considerably reduced owing to sustained hunting and intermittent poisoning and trapping (J. R. Leathwick, pers. comm.).

The areas examined in the study lie 16–18 km inland at altitudes of 250–350 m. Both carry tawa-dominant forest and podocarps are virtually absent because of the earlier logging. Area 1 lies on steep terrain in the more dissected eastern sector of the forest (GR 025213). Kamahi was a significant codominant in 1957 when the transects were established, while kohekohe was confined to broader ridges and was relatively insignificant (Table 1). The area was logged for podocarps and tanekaha (*Phyllocladus trichomanoides* D. Don) between 1937 and 1939, and showed considerable evidence of logging disturbance. Area 2 lies on undulating terrain in the Pongakawa Ecological Area (GR 983243). Kohekohe and mangeao were significant canopy components in 1957 while kamahi was of only minor importance. Although the locality was logged for podocarps in 1942–43 and tawa in 1947 there was no clear evidence of logging within the area studied.

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* New Zealand Forest Service Ecological Transects 8 and 9.

TABLE 1—Forest canopy composition (%) in 1957*

	Relative density	Relative dominance	Importance value†
Area 1			
Tawa	61	62	62
Kamahi	20	17	19
Rewarewa	8	8	8
Others‡	11	13	12
Area 2			
Tawa	46	50	48
Kohekohe	23	16	19
Mangeao	12	21	16
Others§	18	13	16

* Greater than 20 cm d.b.h.o.b.; in Ecological Transects 8 and 9

† Average of relative density and relative dominance

‡ Including mangeao

§ Including rewarewa

Since 1957 there has been extensive kamahi mortality in both areas, creating in Area 1 a gap phase of unusually large dimensions. Mortality in other species has been much less, in tawa and kohekohe suggesting all-aged populations in demographic equilibrium.

Three modes of death and decay are common in Rotoehu Forest: standing death and disintegration *in situ,* standing death and subsequent windsnap, and windsnap of live trees. Windthrow appears to be uncommon. These processes account for single trees and, through the "domino effect", small groups of trees, producing canopy gaps of varying sizes. Very small gaps may be filled simply by the lateral expansion of crowns of adjacent trees. More often, however, canopy replacement occurs from the pool of surviving regeneration or from new recruits.

METHOD

Data Collection

Only discrete, clearly definable gaps caused by identifiable species ("gapmakers") and of broadly determinable age were assessed (Table 2). In estimating age, transect records as well as degree of decay were used. Gap area was defined as the polygon enclosed by the boles of "edge trees" (those whose crowns overlap to form the upper canopy around the gap) and measured by the product of the largest distance across the gap and the largest distance perpendicular to this.

Multiple-tree gaps were subdivided into single-tree "subgaps" in proportion to the basal areas of gapmakers. In practice this was achieved by proportioning distances between adjacent gapmakers.

In each gap or subgap numbers of stems of canopy species less than 2.5 cm d.b.h. were recorded by species in two height classes: 1–2 m, and greater than 2 m. Diameters

TABLE 2—Characteristics of gaps and understorey plots

	Area 1		Area 2	
	Gap	Understorey	Gap	Understorey
Number of gaps/understorey plots	10	15	21	22
Number of subgaps	16		21	
Mean gap age (yr) with range	12 3–24		11 0–25	
Mean gap area (ha) with range	0.025 0.008–0.066		0.010 0.001–0.035	
Mean understorey plot area (ha) with range		0.010 0.002–0.020		0.011 0.003–0.027
Gapmakers/canopy species (No. subgaps and understorey plots)				
Tawa	5	6	7	6
Kohekohe	0	2	10	7
Kamahi	7	0	0	0
Mangeao	0	3	4	3
Others	4	4	0	6

of all stems of canopy species greater than 2.5 cm diameter were recorded. Marginal stems whose boles were within the defined gap but crowns outside were not included. Vegetative shoots of tawa edge trees were included.

Regeneration of canopy species was examined under a similar number of canopy trees of major species, taking care to avoid edge trees. Areas of understorey plots were defined by edge trees, as in gaps.

The prevalence of gaps on ridges in Area 1 resulted in an inevitable topographic bias in sampling, with gaps concentrated on ridges and understorey plots on surrounding slopes. No such bias occurred in Area 2, with its more uniform topography.

Data Analysis

Density-diameter distributions for the major regenerating canopy species were derived for both gap and understorey phases and plotted on semilogarithm paper. Several single indices of relative importance were derived for each species for each gap or understorey plot. Indices were then averaged over all plots in each phase. The indices used were:

(1) Relative density (DEN) – the proportion of all stems made up by each species;

(2) Relative dominance (DOM) – the proportion of total basal area made up by each species;

(3) Importance value (IV) – the average of DEN and DOM;

(4) The proportion of the largest four juveniles made up by each species (L4);

(5) Single largest juvenile (L1).

Differences between indices were assessed by significance tests. An assumption inherent in classical parametric tests is that variables are normally distributed. As this assumption was felt unlikely to hold, non-parametric tests were used. The Mann-Whitney test (Lehmann 1975) was used to assess the effects of age and size on gap composition (after classifying gaps into two age- and two size-classes) and for comparing the means of two populations (e.g., gap and understorey). The Kruskal-Wallis test (Lehmann 1975) was used for comparing means of several populations (e.g., in testing the effect on regeneration of different gapmaker species), and 2 $\times$ 2 contingency tables were used for testing the single largest juvenile index.

RESULTS

Gapmaker/Canopy Species and Gap/Understorey Composition

Gaps formed by kohekohe and tawa in Area 2 showed a significant reciprocal relationship (i.e., each species tended to replace the other) between gapmaker and gapfiller as indicated by density, importance value, and dominance (Table 3). Tawa-created gaps contained similar proportions of tawa and kohekohe juveniles, while kohekohe-created gaps contained tawa in much greater abundance. Kohekohe was more abundant than tawa under canopy trees of both species but, as discussed later, may be substantially reduced after gap formation in this particular area.

TABLE 3—Reciprocal replacement between tawa and kohekohe in Area 2 (percentage of tawa or kohekohe to all juveniles)

Index	Gapmaker/ canopy species	Gaps Gapfiller T	K		Understorey Juveniles T	K	
L1	T	57	29	NS	33	50	NS
	K	85	10	NS	29	57	NS
L4	T	54	39	NS	12	67	NS
	K	75	14	NS	29	50	NS
DOM	T	45	41	*	14	66	NS
	K	78	14	*	35	47	NS
IV	T	41	40	**	9	72	NS
	K	74	10	**	20	54	NS
DEN	T	37	39	**	5	78	NS
	K	60	8	**	9	62	NS

T = tawa
K = kohekohe

NS = not significant
* = significant at p = 0.05
** = significant at p = 0.01

Gap and Understorey Composition

All the major canopy species were well represented as juveniles in both areas (Table 4) except kamahi which was currently failing almost entirely to regenerate even on tree ferns or fallen logs, favoured established sites in many localities (Wardle 1966; A. E. Beveridge, pers. comm.). However, species proportions differed markedly between juvenile and canopy populations, except for the gap phase in Area 2. In Area 1 this results partly from the extreme scarcity of kamahi regeneration and the gross over-representation of rewarewa as juveniles compared to canopy individuals.

Juveniles of the four major regenerating species occurred significantly in both gap and understorey phases. A wide range of light regimes occurs under high forest, however, and observation suggests that mangeao and rewarewa tend to occur in light wells in the understorey whilst tawa and kohekohe are more widely distributed.

Slopes of diameter distributions (Fig. 1) reflecting growth-rates and survival in various size-classes are similar for both phases in each species, in most instances approaching the negative exponential distribution. The effect of release on suppressed juveniles of these species has been investigated previously in 0.08-ha plots established in 1958 on a valley floor 1.5 km north of Area 2 (N.Z. Forest Service 1962). A later assessment showed generally increased survival and growth rates after release, although tawa also survived well in suppressed conditions and kohekohe, approaching its regional altitudinal limits in Rotoehu Forest (Nicholls 1969), suffered considerable damage from frost after release.

TABLE 4—Comparison of mean indices of gap and understorey composition

	Gaps						Understorey					
	L1	L4	DOM	IV	DEN	ST†	L1	L4	DOM	IV	DEN	ST
Area 1												
Tawa	44	25	31	19*	7**	230*	57	58	57	49*	42**	940*
Kohekohe	6	8	4	3	2	80	20	13	12	10	8	260
Rewarewa	31	38	49*	62**	75**	3100*	13	18	23*	34**	44**	1600*
Mangeao	13	23	13	13	13	520**	10	10	8	7	6	100**
Other	6	5	4	2	1*	80*	0	0	0	0	0*	13*
Total						4000						2900
Area 2												
Tawa	74	62**	62**	56**	49**	760**	41	24**	27**	19**	11**	270**
Kohekohe	14	26*	25*	26**	26**	780**	36	55*	50*	58**	67**	2600**
Rewarewa	7	7	7	9	12	300*	5	10	10	11	13	400*
Mangeao	5	3	5	8	11	350	14	9	10	9	8	310
Other	0	0	0	1	1	80	5	2	4	3	1	50
Total						2300						3600

* = significant at p = 0.05
** = significant at p = 0.01
† ST = stocking in stems/ha

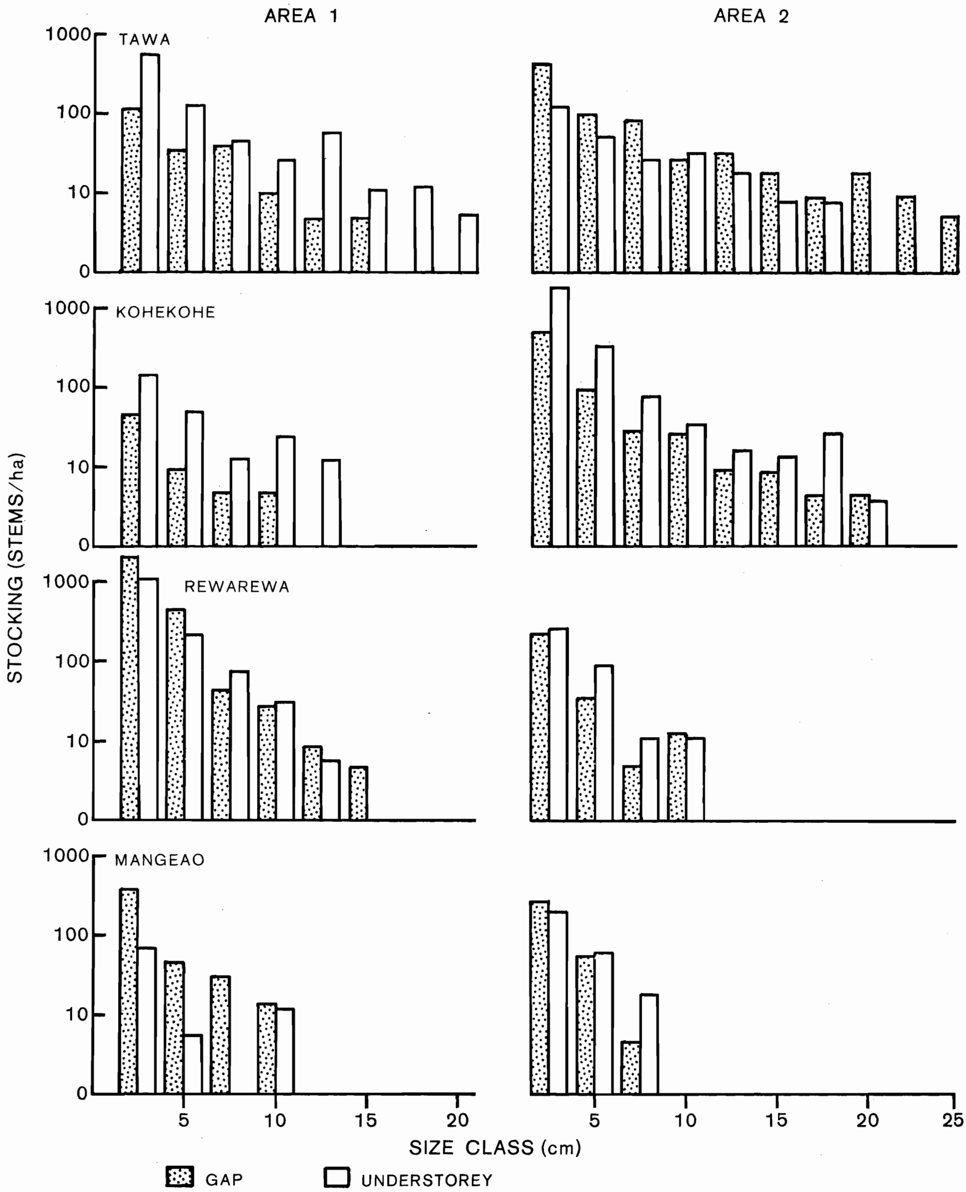

FIG. 1—Diameter distributions of the major regenerating species in gap and understorey plots in the two areas.

In the present study, tawa and kohekohe have generally flatter diameter distributions than mangeao or rewarewa, being better represented as larger stems in both phases. In tawa, at least, this is likely to reflect lower mortality rather than faster growth rates. Kohekohe was much more abundant, particularly in the smallest size-classes, in understorey than in gaps in Area 2 (Table 4) where it was an important canopy component. A similar trend was apparent in Area 1, although numbers were too small to show significant differences. Frost damage after release is a likely explanation.

The relative paucity of tawa of all sizes in gaps as opposed to understorey in Area 1 probably reflects the topographic bias in sampling, and the species' patent sensitivity to exposure and drought (Knowles & Beveridge 1982) – factors operating more strongly on ridges (where most gaps occurred) than elsewhere in the area. It may also reflect logging disturbance, more obvious on ridges than elsewhere. In Area 2, however, tawa of most sizes was better represented in gaps than under high forest. In the presumed absence of sampling bias, this suggests that development of "advance growth" tawa accelerates as canopy trees senesce (Knowles & Beveridge 1982) and crown decline sets in (Gatsuk *et al.* 1980; authors' unpubl. data) allowing increased light penetration beneath the canopy.

Juveniles of mangeao and rewarewa were more abundant in gaps than elsewhere in Area 1. In spite of sampling bias, the particular abundance of the two smallest size-classes, for rewarewa especially, suggests definite colonisation of gaps by these species.

Indices of Species' Relative Importance

The relationship between mean and standard deviation for each index and population (species, study area, and phase) is shown in Fig. 2. Standard deviation is strongly influenced by the mean, approaching zero for smaller and larger means and reaching a maximum at a mean of *c.* 50. Clear differences in precision exist between indices. Importance value and density are the most precise, largest juvenile the least; largest four juveniles and basal area lie between them. From the curves in Fig. 2, the standard method of obtaining sample sizes required to detect significant differences between two means was used to produce Fig. 3. Although this assumes use of the t-test, non-parametric tests would require similar sample sizes.

It is apparent from Fig. 3 that the number of gaps (or understorey plots) required to identify differences between populations in proportions of major species is about 20 in each population. In the present study, sample sizes used were adequate to detect differences between understorey and gap regeneration, but inadequate to identify any but the strongest relationships between regeneration and gapmaker or canopy species.

Differing patterns of indices among species (Table 4) reflect differences in diameter distributions (Fig. 1). Indices reflecting basal area, i.e., relative dominance (DOM), largest four juveniles (L4), and largest single juvenile (L1), give high values in species relatively well-represented as large juveniles, e.g., tawa, while density (DEN) gives high values in species relatively well-represented as smaller juveniles, e.g., rewarewa. In forest where major regenerating species have similar diameter distributions (e.g., tawa and kohekohe in Area 2), therefore, the choice of index used to predict future canopy composition is less crucial than in forest where distributions differ markedly (e.g., tawa, mangeao, and rewarewa in Area 1).

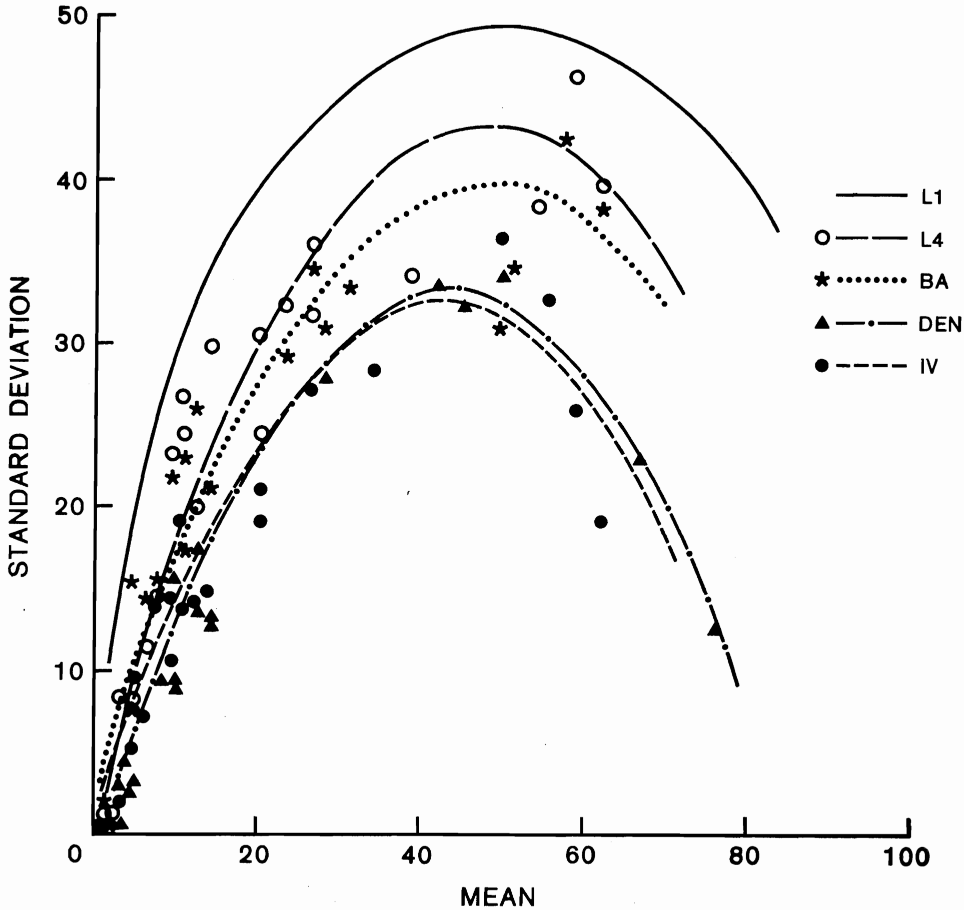

FIG. 2—Relationship between mean and standard deviation for different indices. The L1 curve is calculated from the relationship between mean and standard deviation for a binomial variable. For the other indices, means and standard deviations are plotted for each species in each of the four categories sampled (gap, understorey × Area 1, Area 2) together with quadratic regression curves.

DISCUSSION

This preliminary investigation of regeneration patterns in two small areas of tawa-dominant forest at Rotoehu was confined to the gap and mature phases of the forest growth cycle. The transition from mature to gap phase involves the maximum disturbance in juvenile growing environment and probably, therefore, the greatest change within a given time period in juvenile populations. Further changes in composition are

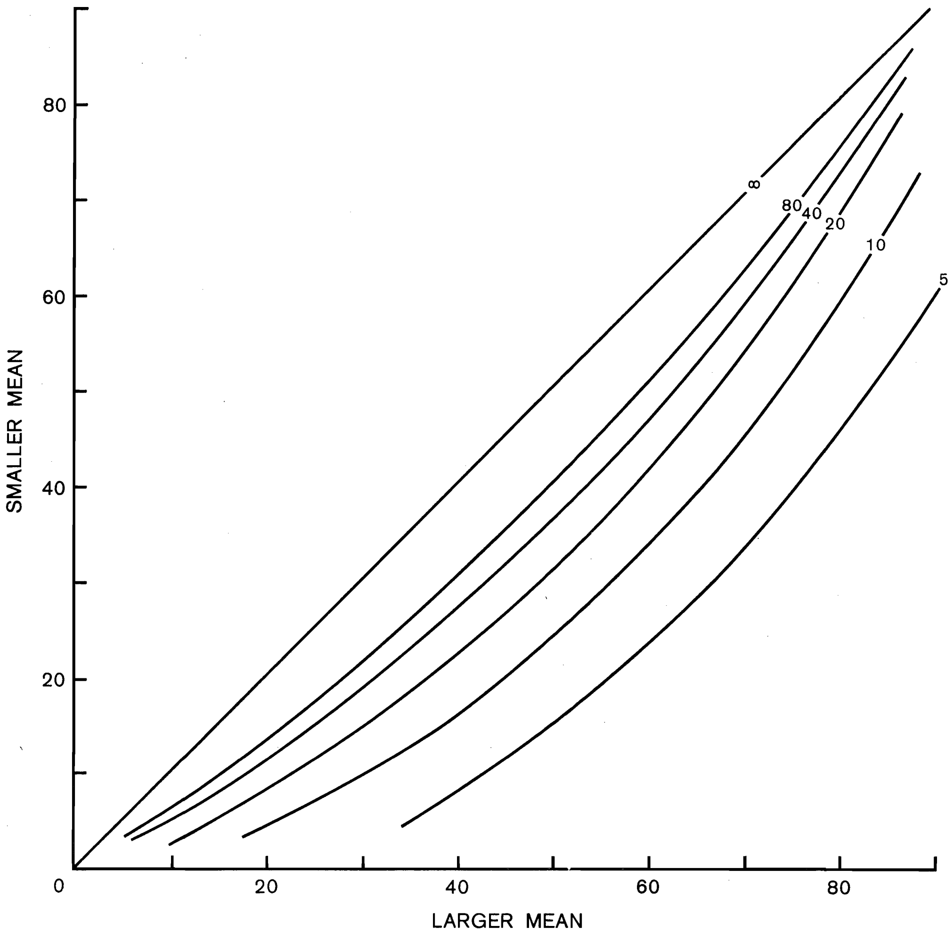

FIG. 3—Curves show sample sizes required from each population to detect significant ($p = 0.05$) differences between their means, using DEN or IV indices. For DOM or L4 use twice this size and for L1 use four times this size. Use twice the above sizes to detect significant differences at $p = 0.01$.

likely to occur, however, during the building phase of the forest growth cycle (Cousens 1974).

The reciprocal replacement evident in Area 2 between kohekohe and tawa would seem to favour tawa with its stronger tendency to self-replacement; the predominance of tawa in the existing canopy suggests that reciprocal replacement has operated in the past. A wider sample would determine whether this is a more widespread phenomenon or merely a local anomaly. It is outside the scope of this paper to examine possible mechanisms behind such a replacement pattern; suffice it to say that it is a feasible explanation for the continued co-existence of these species. Reciprocal replacement as a means of maintaining co-dominance has been described in North American beech-maple woods (Fox 1977; Runkle 1981; Woods 1979).

The differing composition of gap and understorey regeneration, and the markedly different diameter distributions among major regenerating species in each phase suggest distinct differences in their regeneration strategies, largely reflecting differences in shade-tolerances. Regeneration of shade-tolerant tawa develops to advanced stages in the understorey beneath a light or deteriorating angiosperm canopy (Knowles & Beveridge 1982) and usually survives gap formation. Kohekohe behaves similarly, but may be substantially reduced after gap formation on colder sites by frost damage. Maintenance of both species in the tawa-dominant areas of Rotoehu Forest, where the gap phase is widespread and an obviously important part of the forest replacement process, appears to depend largely on advance growth surviving gap formation.

Mangeao and rewarewa, however, seldom attain large pole size in the understorey in tawa-dominant forest here*. Although they generally survive gap formation, there is also evidence in Area 1 of gap colonisation, particularly by rewarewa. These species appear to be significantly gap-dependent, i.e., require gap formation for development to maturity.

Divergences between gap and understorey populations in both areas are therefore of considerable significance, and mean that understorey regeneration alone may be a misleading indicator of replacement trends. In forests where the gap phase is an important part of the canopy replacement cycle, replacement may be gauged more reliably from gap regeneration than from understorey regeneration alone or from total regeneration.

The value of indices of species' relative importance as predictors of future canopy occupation at any site does not appear to have been adequately addressed. A suitable index will be accurate, precise, and free from bias. It seems reasonable that, on average, one tree is replaced by another and that in this instance, with similar survival and growth rates in "released" conditions (except possibly kohekohe), the single largest juvenile in a gap is the most likely future occupant of that growing space. This index has been used, with modification, by several workers (e.g., Fox 1977; Brewer & Merritt 1978). It also seems likely that the ultimate occupant of any gap will be amongst the largest few juveniles present in the gap phase. The index of largest four juveniles (L4) is more precise than L1, obtainable with similar rapidity and, like L1, favours species such as tawa with good representations of larger stems. Although more precise still, the other indices of dominance, density, and importance value require much greater sampling effort and favour species such as rewarewa with high proportions of smaller stems. The largest four juveniles thus appears to be the most appropriate predictor of future canopy composition of the five indices tested, in situations where similar survival and growth rates in gaps obtain. It is applicable only to single-tree gaps so its use requires subdivision of multiple-tree gaps into single-tree subgaps.

The L4 index in gap regeneration suggests that current replacement trends in Area 1 will lead to a canopy rather different from the present one; rewarewa in particular appears likely to become more prominent, and kamahi to disappear altogether.

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* They commonly do in the lighter-canopied kamahi-rewarewa stands (A. E. Beveridge, pers. comm.)

In Area 2, however, gap composition as gauged by L4 approximates current canopy composition, although mangeao appears likely to decline and kamahi to disappear altogether.

CONCLUSIONS

The approach used here, of quantitative assessment of regeneration in two successive phases of the forest growth cycle, goes some way toward elucidating forest dynamics in the manner proposed by Webb *et al.* (1972). Current regeneration appears to be reproducing a forest similar in structure and composition to the surrounding one in one of the two areas studied. All the predominant canopy species regenerate continuously under high forest, although mangeao and rewarewa appear to attain canopy stature only intermittently as gap formation and the absence of other, well-developed, advance growth allow. The diameter distributions of tawa and kohekohe approach the negative exponential curve; those of mangeao and rewarewa do so only in seedling/sapling sizes, and are erratic in largest sizes (data from Ecological Transects 8 and 9). Further clarification of these aspects of forest dynamics in Rotoehu Forest must await more extensive studies, ideally embracing all phases of the forest growth cycle.

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