

# REGENERATION PATTERNS IN MONTANE CONIFER/BROADLEAVED FOREST ON MT PUREORA, NEW ZEALAND

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## ABSTRACT

Regeneration in montane *Podocarpus hallii* Kirk/*Weinmannia racemosa* L.f. (Hall's totara/kamahi) forest on Mt Pureora, central North Island, New Zealand, was sampled in the three phases of the forest growth cycle. Average age differed significantly between the gap (12-year), building (67-year), and mature (227-year) phases. Diameter growth rates were similar amongst major canopy species, but significantly faster during the gap and building phases (0.31 cm/year) than the mature phase (0.19 cm/year).

Two broad patterns of successional change were evident between phases, some species populations (e.g., small-leaved *Coprosma* spp., tree ferns) increasing during the gap phase and declining thereafter, and others (e.g., Hall's totara, kamahi, *Griselinia littoralis* Raoul (broadleaf), *Myrsine salicina* Hook.f. (toro)) increasing during the building phase. *Pseudowintera colorata* (Raoul) Dandy (horopito), although a gap invader, was prominent throughout. Replacement strategies reflect differing shade tolerance, relatively intolerant species being gap invaders and those with intermediate tolerance establishing during the building phase. Because canopy dominants mostly establish later in the succession ("building-phase replacement"), gap composition alone is not a reliable indicator of future canopy composition in this forest type.

Gap-maker/gap-filler and canopy/understorey relationships suggest that a regeneration cycle involving alternation of podocarps and broadleaved trees, similar to that described from nearby lowland forest, may be operating. Although no unequivocal disruption of natural replacement processes in major canopy species is evident, other studies show that progressive impoverishment of lower tiers by introduced browsing mammals is occurring here.

**Keywords:** montane forest; conifer/broadleaved forest; gap phase; building phase; mature phase; replacement strategy.

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## INTRODUCTION

Montane conifer/broadleaved forests, occurring above the altitudinal limit of canopy rimu (*Dacrydium cupressinum* Lamb)\* and dominated by kamahi, occur widely on mountains in the central North Island where beeches (*Nothofagus* spp.) are rare or absent. Despite their widespread occurrence, these forests have received only descriptive attention to date, on a national (e.g., Nicholls 1976; Wardle 1991) or regional scale (e.g., McKelvey 1963; Atkinson 1981; Clarkson 1986; Leathwick *et al.* 1988). Broadly similar forests in the central western South Island have been affected in recent decades by extensive dieback, prompting intensive studies of their dynamics (e.g., Veblen & Stewart 1982; Stewart & Veblen 1982). Apart from that of Ogden *et al.* (1991) there have been no comparable studies in similar forests in the central North Island.

The forest growth cycle—i.e., the process by which canopy trees are replaced—is traditionally considered to consist of three contiguous phases, “gap”, “building”, and “mature” (Watt 1947). The gap phase is considered here to be the period when canopy openings are receptive to colonisation, the building phase as the period after canopy closure when survivors of the ensuing seedling/sapling thicket attain canopy status, and the mature phase as the following period when the canopy remains intact. In this study we examined regeneration in each of these phases in montane conifer/broadleaved forest on Mt Pureora, central North Island, in order to (1) determine the composition of the three phases, (2) determine factors affecting the composition of each phase, (3) assess the regeneration strategies of the major canopy species, and (4) analyse current successional trends.

## STUDY AREA

Mount Pureora, a symmetrical andesitic cone reaching 1170 m a.s.l., lies at the northern end of the Jurassic greywacke Hauhungaroa Range (Grindley 1960), 20 km north-west of Lake Taupo, in the Pureora Ecological District. The basement geology is overlain by numerous tephra deposits, the most recent being 0.5–1 m of Taupo Tephra (Pullar 1973; Froggatt & Lowe 1990). Soils are podsolised yellow-brown pumice soils of low natural fertility (Rijkse & Wilde 1977).

Climate is cool-temperate and humid within the montane zone, with a mean annual rainfall of 1600–2400 mm. Rainfall is relatively constant, but with a marked winter maximum. Mean annual temperature is approx. 9°C, with a January (midsummer) mean of approx. 14°C and a July (midwinter) mean of approx. 4°C (New Zealand Meteorological Service 1985; Norton 1985). Snow falls occasionally during winter and spring, but does not lie for long.

Within the lower montane zone (approx. 860–1080 m) the predominant vegetation is Hall's totara/shrub hardwood forest (McKelvey 1963), consisting at lower altitudes of scattered to locally abundant Hall's totara and occasional miro (*Prumnopitys ferruginea* (D. Don) de Laub.) emergent at 15 m or more over a canopy of kamahi with some broadleaf, tauheowheo (*Quintinia acutifolia* Kirk.), and subcanopy toro (Leathwick *et al.* 1988), the subject of this study. At higher altitudes totara is barely emergent over a dense wind-roof canopy at approx. 9 m dominated by kamahi, with broadleaf, haumakaroa (*Pseudopanax*

\* Nomenclature follows Allan (1961) and Connor & Edgar (1987)

*simplex* (Forst.f.) Philipson), and stinkwood (*Coprosma foetidissima* J.R. et G.Forst.). Horopito dominates the understorey throughout.

Upper montane low forest dominated by haumakaroa, stinkwood, and broadleaf occurs above approx. 1080 m, grading into subalpine scrub dominated by stinkwood, threefinger (*Pseudopanax colensoi* (Hook.f.) Philipson), and haumakaroa (Leathwick *et al.* 1988).

Introduced red deer (*Cervus elaphus* L.) and brushtailed possum (*Trichosurus vulpecula* Kerr) have been present in significant numbers for only about 30 years, but are now common. Feral pigs (*Sus scrofa* L.) have probably been present for at least 150 years, but only in small numbers. Feral cattle (*Bos taurus* L.) were present earlier in the century but have now died out (McKelvey 1963; Broome & Krzystyniak 1985).

Human impact on the study area has been negligible. A fire about 70–80 years ago (McKelvey 1963) destroyed about 70 ha of forest on the eastern side of the mountain; the original forest cover is now replacing itself.

Predominant modes of death and decay vary among species. Most of the few dead Hall's totara encountered were uprooted, while standing death was common in kamahi (often followed by windsnap) and broadleaf (usually followed by disintegration *in situ*).

## METHODS

### Data Collection

One hundred and twenty-nine temporary plots were placed along transects following contours between about 920 m and 960 m a.s.l. on the north-eastern, western, and south-western sides of the mountain, covering the three phases of the forest growth cycle. Only discrete, definable gaps caused by identifiable species ("gap-makers") were used. Actual canopy gap area—in contrast to the "expanded gap" of Runkle (1982)—was estimated by measuring the longest distance across the gap and the longest distance perpendicular to this. In an area of extensive canopy collapse on the south-western side of the mountain, square plots of average canopy gap size (0.006 ha) were placed in the centre and at the edge of gaps. In order to examine the relationship between previous or existing canopy species and regenerating species, plots in building-phase forest were placed in discrete, definable, sapling thickets that had clearly been occupied by the crowns of previous canopy trees, while plots in mature forest were defined by the area under the crowns of individual trees; in both sorts of forest, areas were measured as for gaps. Regeneration was sampled under a similar number of trees of each of the predominant canopy species (Hall's totara, kamahi, and broadleaf).

In all plots, numbers of established seedlings (<2.5 cm dbh, >1 m high) were recorded by species, along with the diameter of larger stems (>2.5 cm dbh). Epiphytic stems rooted below 2 m were recorded. In gaps, several of the largest seedlings of gap colonisers present, e.g., wineberry (*Aristotelia serrata* (Forst.) Oliver) and small-leaved *Coprosma* spp. (Ogden *et al.* 1991) were felled at the base and sections were removed for sanding and aging, in order to obtain a minimum estimate of gap age. In building-phase plots, several of the largest stems present were also felled at the base and sections removed to determine patch age. In mature plots, a selection of saplings (2.5–10 cm dbh) and trees (>10 cm dbh) of major species, including the largest stems present, were sectioned or cored at 1.4 m to ascertain mean annual

(i.e., over the life of the plant) and current diameter growth rates (i.e., in the last decade), lifespans, and patch age. Species, diameters, and mode of death—i.e., windthrow, windsnap, standing death—of gap-makers were also recorded. Discs and cores were sanded, and growth rings (assumed to be annual) were counted under a binocular microscope. All canopy species sampled have slightly distinct to distinct growth rings (Meylan & Butterfield 1978).

A sample of 11 felled saplings and small trees (3–15 cm dbh) of major canopy species (Hall's totara, kamahi, broadleaf, toro, and tawheowheo) showed an average mean annual height increment of 15 cm (range 10–18 cm). Similar growth rates have been recorded in planted and natural Hall's totara seedlings growing under a light overstorey (G. A. Steward, pers. comm.). A somewhat more conservative estimate of annual height growth (12 cm) was used to estimate average time to reach breast height (12 years), which was added to age at coring height to obtain estimates of total age in cored trees.

To determine the proportion of forest in each phase, eight line transects each approx. 600 m long, were sampled in the study areas; the length of transect in each phase was measured.

### Analysis

Diameter frequency histograms of major species were derived for each of the three major phases in the forest growth cycle.

Diameter-at-breast-height *v.* age relationships were fitted using the Gompertz function (Ratkowsky 1983)  $dbh = A \cdot \exp(-\exp(-B(\text{Age}-C)))$  where A, B, and C are fitted parameters.

Density and total basal area of plots were tested against patch age. Logistic regressions for each major species of the proportion of density and of basal area contributed by that species were fitted for plots in the gap and building phases. The following terms were fitted, in the given order:

age	to test for any increase or decrease in the proportion;
age <sup>2</sup>	to allow for species which peak, then decrease in importance with age;
phase	fitted as a dummy variable to test for any sudden change as the forest progresses from gap to building phase, as distinct from gradual changes with age;
gap-maker	fitted using dummy variables, to test whether the regenerating species are affected by the previous (gap) canopy species;
area	tested for gap phase; plots in the area of extensive canopy collapse were tested using a dummy variable.

For plots in the mature phase, the significance of canopy species was tested using dummy variables.

The data analysis program GENSTAT (Lawes Agricultural Trust 1987) was used to perform this analysis. Significance of each factor was tested using the mean scaled deviances of models including and excluding the factor, the ratio of which approximates an F distribution.

A principal components analysis (PCA) on the proportions of density and of basal area of the major species was performed to identify associations between species within plots. Correlations among variables in compositional data are inevitable because they are restricted to sum to unity. To overcome this problem, the PCA was performed after applying a

transformation (Aitchison 1985) consisting of the logarithm of each proportion divided by the log of the geometric mean of all proportions. Where species were not present in a plot, they were designated as having a proportion of 0.01.

## RESULTS

### Characteristics of Gap, Building, and Mature Plots

Mean estimated plot age—i.e., age of the largest stem—differed significantly ( $p < 0.05$ ) between gap, building, and mature phases (Table 1). The overall mean age of mature plots is under-estimated, because of under-estimation of ages of the largest kamahi and broadleaf trees, which invariably have false trunks formed by the fusion of descending roots. Although the age ranges of building and mature plots overlapped slightly, most of the latter were older than any building plots. Excluding gap plots in the area of extensive canopy collapse, the mean area of gap and mature plots was similar, but 2–3 times that of building-phase plots. The latter is more likely to be a sampling artefact than a reflection of any real difference in patch size between phases. Mature plot area (= crown area of the individual canopy tree) did not vary with overstorey species.

### Growth Rates

Diameter growth rates in all species together were significantly faster (approx. 160%) in gap and building phases than in mature forest (Table 2). Amongst individual species, only in Hall's totara and kamahi were growth rates significantly faster ( $p < 0.05$ ) in the building than the mature phase, although a similar trend was evident in the other species. No significant differences in diameter growth rate between species were apparent.

Although diameter *v.* age functions of all species followed a similar general trend (Fig. 1), the average size and age at which growth rates peak varied markedly between species. Emergent Hall's totara reaches its maximum diameter growth rate at approx. 55 cm dbh, (approx. 210 years). Canopy kamahi (32 cm, 100 years), broadleaf (15 cm, 40 years), tawheowheo (12 cm, 60 years), and subcanopy toro (6 cm, 50 years) peak earlier.

TABLE 1—Characteristics of gap, building, and mature phase plots in Hall's totara/ kamahi forest on Mt Pureora.

Phase	Gap	Building	Mature
Number of plots	50	36	43
Age (years)			
mean (SE)	12 (1)*	67 (3)	227 (17)†
range	1–24	30–105	77–652
Area (ha)			
mean	0.006	0.002	0.005
range	0.001–0.02	0.001–0.006	0.001–0.01
<b>Previous or present canopy species (number of plots)</b>			
Hall's totara	9	2	15
Kamahi	23	20	12
Broadleaf	7	13	16
Others	6	1	0
Unknown	5	0	0

\* Minimum gap age

† Mature age almost certainly under-estimated

TABLE 2—Diameter growth rates (cm) as periodic mean annual increment (1981–91) of major canopy species in gap, building, and mature phases in Hall's totara/ kamahi forest on Mt Pureora (standard errors in parentheses)\*

Species (No. samples)	Phase					
	Gap		Building		Mature	
Hall's totara ( <i>n</i> =50)	0.19	(0.04)	0.30	(0.03)	0.19	(0.03)
Kamahi ( <i>n</i> =48)	[0.28]		0.34	(0.04)	0.16	(0.01)
Broadleaf ( <i>n</i> =17)	[0.47]		0.33	(0.04)	0.26	(0.05)
Toro ( <i>n</i> =19)	[0.36]		0.27	(0.04)	0.19	(0.03)
Tawheowheo ( <i>n</i> =14)	[0.37]		0.29	(0.06)	[0.23]	
All species ( <i>n</i> =148)	0.31	(0.03)	0.31	(0.02)	0.19	(0.01)

\* Square brackets indicate inadequate sample size

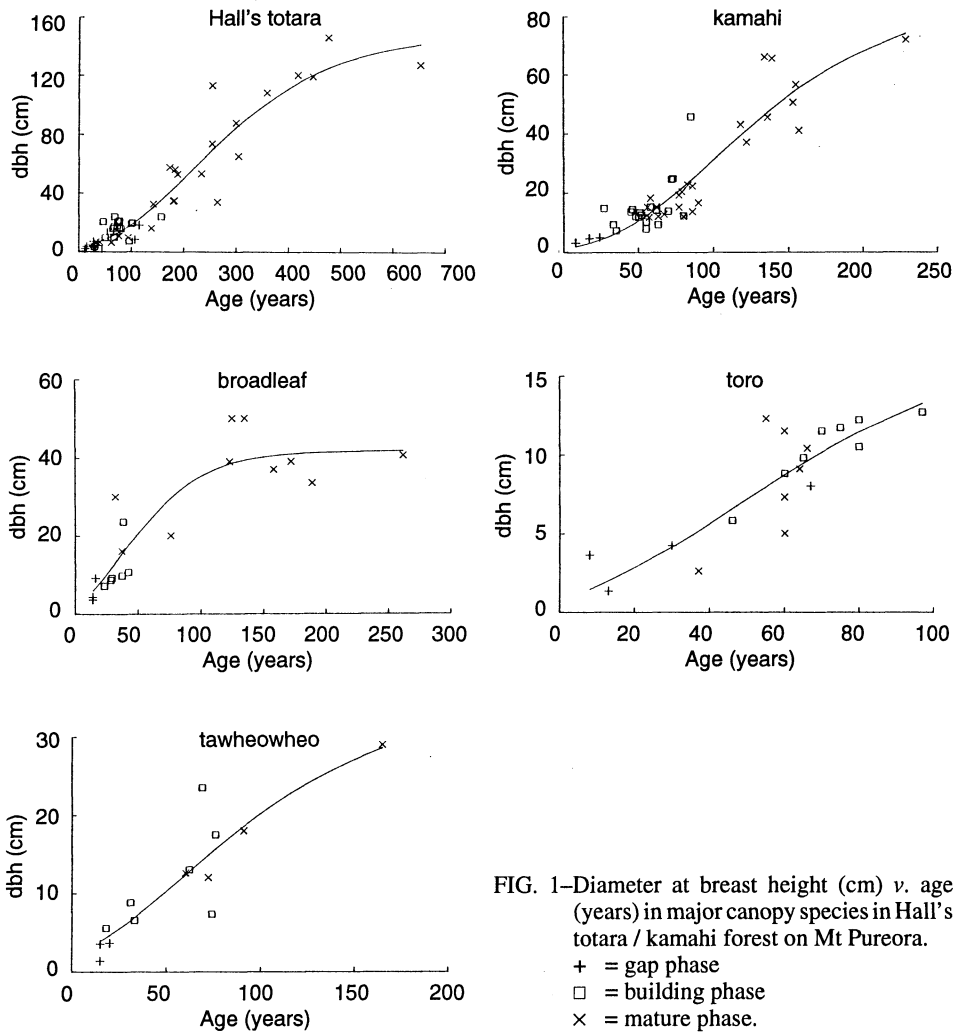


FIG. 1—Diameter at breast height (cm) v. age (years) in major canopy species in Hall's totara / kamahi forest on Mt Pureora.

+ = gap phase  
 □ = building phase  
 x = mature phase.

### Composition of Gap, Building, and Mature Phases

All the current major canopy species were well represented as juveniles (subcanopy individuals), with the possible exception of kamahi and toro (Tables 3 and 4, Fig. 2). Regeneration in kamahi is largely epiphytic, and since juveniles rooted more than 2 m above ground level were not sampled, kamahi may be somewhat under-represented in this study.

All major and some minor species showed significant change in both relative density and basal area of juveniles with patch age. Hall's totara, kamahi, toro, and tawheowheo increased ( $p < 0.01$ ) in both relative density and basal area. Broadleaf increased in relative basal area only ( $p < 0.01$ ). Horopito and tree ferns decreased in both relative density ( $p < 0.01$ ,  $p < 0.05$  respectively) and relative basal area ( $p < 0.01$ ). Putaputaweta (*Carpodetus serratus* J.R. et G.Forst.) decreased in relative density ( $p < 0.01$ ), increasing then decreasing ( $p < 0.01$ ) in relative basal area. For most species, the change with patch age was gradual rather than showing a sudden discontinuity during the transition from gap to building phase. The exception was broadleaf which showed a marked increase in relative basal area ( $p < 0.01$ ) at the beginning of the building phase.

Hall's totara juveniles were more prominent under kamahi and broadleaf, and less so under canopy of their own species (density  $p < 0.05$ ; basal area  $p < 0.01$ ). Kamahi basal area was higher in gaps formed by totara, and lower in those formed by itself and by broadleaf ( $p < 0.01$ ). Broadleaf was more prominent in gaps formed by kamahi and less so in those formed by totara (density and basal area  $p < 0.01$ ); the reverse was true in the understorey of mature forest (basal area  $p < 0.05$ ). The basal area of broadleaf was higher in larger gaps ( $p < 0.05$ ), while that of tree ferns was lower ( $p < 0.01$ ). Regeneration did not differ appreciably between normal gaps and plots in abnormally large gaps.

Two broad patterns of change within species populations, as indicated by logistic regression predictions standardised to sum to 100% of density (Fig. 3) and basal area (Fig. 4), are evident between gaps, building phase, and mature forest. The first group, comprising *Coprosma* spp. (mostly *C. aff. parviflora* and stinkwood), tree ferns (mostly soft tree fern, *Cyathea smithii* Hook.f.), putaputaweta, and wineberry, increases during the gap phase and declines thereafter. Diameter distributions are initially positively skewed, and remain so or become more symmetrical. Horopito shows the same sort of pattern, though less strongly, remaining prominent throughout the forest growth cycle. It maintains a positively skewed diameter distribution, suggesting continuing regeneration. The second group, comprising Hall's totara, kamahi, broadleaf, toro, and tawheowheo, increases during the building phase. Diameter distributions are erratic in the three major species, initially positively skewed and later more symmetrical in toro, and positively skewed throughout in tawheowheo.

The first axes of the PCA ordination are similar in both gap/building and mature phases (Table 5), explaining 25% and 21% of the variance respectively. In the gap and building phases the first axis is significantly correlated with age ( $r = 0.54$ ,  $p < 0.01$ ,  $n = 85$ ), indicating two species associations: horopito plus tree ferns in younger forest *v.* the four major canopy trees in older forest. The second axes are also similar, except for the position of kamahi, explaining 22% and 19% of the variance respectively.

### Changes in Density and Basal Area Over Time

Density of regeneration (subcanopy plants over 1 m tall) showed an overall though non-significant decline with age. Average basal area at gap formation is approx. 8 m<sup>2</sup>/ha

TABLE 3—Mean density (stems/ha) of subcanopy individuals >1 m high in gap, building, and mature phases in Hall's totara/ kamahi forest on Mt Pureora.  
P.h. = Hall's totara, W.r. = kamahi, G.l. = broadleaf.

Regenerating species	Previous or present canopy species													
	Gap					Building					Mature			
	P.h.	W.r.	G.l.	Other	Overall	P.h.*	W.r.	G.l.	Other*	Overall	P.h.	W.r.	G.l.	Overall
Hall's totara	104	105	119	88	104	0	662	175	1136	658	43	158	352	184
Kamahi	104	112	119	44	95	1147	1081	350	1136	929	200	70	144	138
Broadleaf	15	75	0	73	54	0	132	35	0	84	14	18	0	16
Toro	192	112	0	88	131	0	309	595	1136	680	372	175	288	278
Tawheowheo	30	97	178	176	120	0	860	140	0	500	100	70	144	105
Horopito	2841	3719	2556	2748	2966	1147	2889	2484	4545	2767	1987	3349	2047	2461
Small-leaved coprosmas	488	687	416	485	519	0	618	280	1136	678	300	316	256	291
Wineberry	30	388	59	118	149	0	0	0	0	0	57	0	32	45
Putaputaweta	533	164	119	147	241	0	66	140	0	103	214	140	96	150
Tree ferns	799	866	178	602	612	0	596	525	0	560	157	403	464	341
Others	562	515	595	382	514	191	1279	770	0	747	658	386	320	454
<b>Total</b>	5698	6840	4339	4951	5505	2485	8492	5494	9089	7706	4102	5085	4143	4463

\* Less than five plots



TABLE 4—Mean basal area (m<sup>2</sup>/ha) of subcanopy individuals >1 m high in gap, building, and mature phases in Hall's totara/ kamahi forest on Mt Pureora.  
P.h. = Hall's totara, W.r. = kamahi, G.l. = broadleaf.

Regenerating species	Previous or present canopy species													
	Gap					Building					Mature			
	P.h.	W.r.	G.l.	Other	Overall	P.h.*	W.r.	G.l.	Other*	Overall	P.h.	W.r.	G.l.	Overall
Other														
Hall's totara	0.07	0.47	0.06	0.00	0.15	0.00	6.59	3.14	7.55	5.76	0.02	0.33	4.78	1.71
Kamahi	0.16	0.19	0.04	0.00	0.10	22.21	5.64	3.69	16.02	11.89	2.60	0.78	2.05	1.81
Broadleaf	0.00	0.06	0.00	0.06	0.04	0.00	2.16	0.00	0.00	1.08	0.76	0.27	0.00	0.51
Toro	0.28	0.36	0.00	0.55	0.40	0.00	3.30	5.68	12.21	7.07	2.41	1.20	2.87	2.16
Tawheowheo	0.02	0.04	0.06	0.76	0.22	0.00	4.47	0.94	0.00	2.70	2.55	0.94	0.26	1.25
Horopito	4.04	3.81	1.47	1.16	2.62	0.00	7.39	6.31	0.00	3.43	4.40	2.66	2.35	3.14
Small-leaved coprosmas	0.14	0.25	0.16	0.23	0.20	0.00	1.94	1.04	2.32	1.77	0.45	0.05	0.45	0.31
Wineberry	0.01	0.08	0.00	0.01	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Putaputaweta	0.42	0.08	0.00	0.05	0.14	0.00	0.10	1.20	0.00	0.65	1.91	0.96	0.60	1.16
Tree ferns	4.38	5.44	0.00	5.78	3.90	0.00	7.41	6.85	0.00	7.13	3.15	0.96	6.73	3.61
Others	0.58	0.30	0.87	0.27	0.51	0.00	0.98	1.76	0.00	0.92	0.55	0.13	0.95	0.55
<b>Total</b>	<b>10.10</b>	<b>11.08</b>	<b>2.66</b>	<b>8.87</b>	<b>8.31</b>	<b>22.21</b>	<b>39.98</b>	<b>30.61</b>	<b>38.10</b>	<b>42.40</b>	<b>18.80</b>	<b>8.28</b>	<b>21.04</b>	<b>16.21</b>

\* Less than five plots

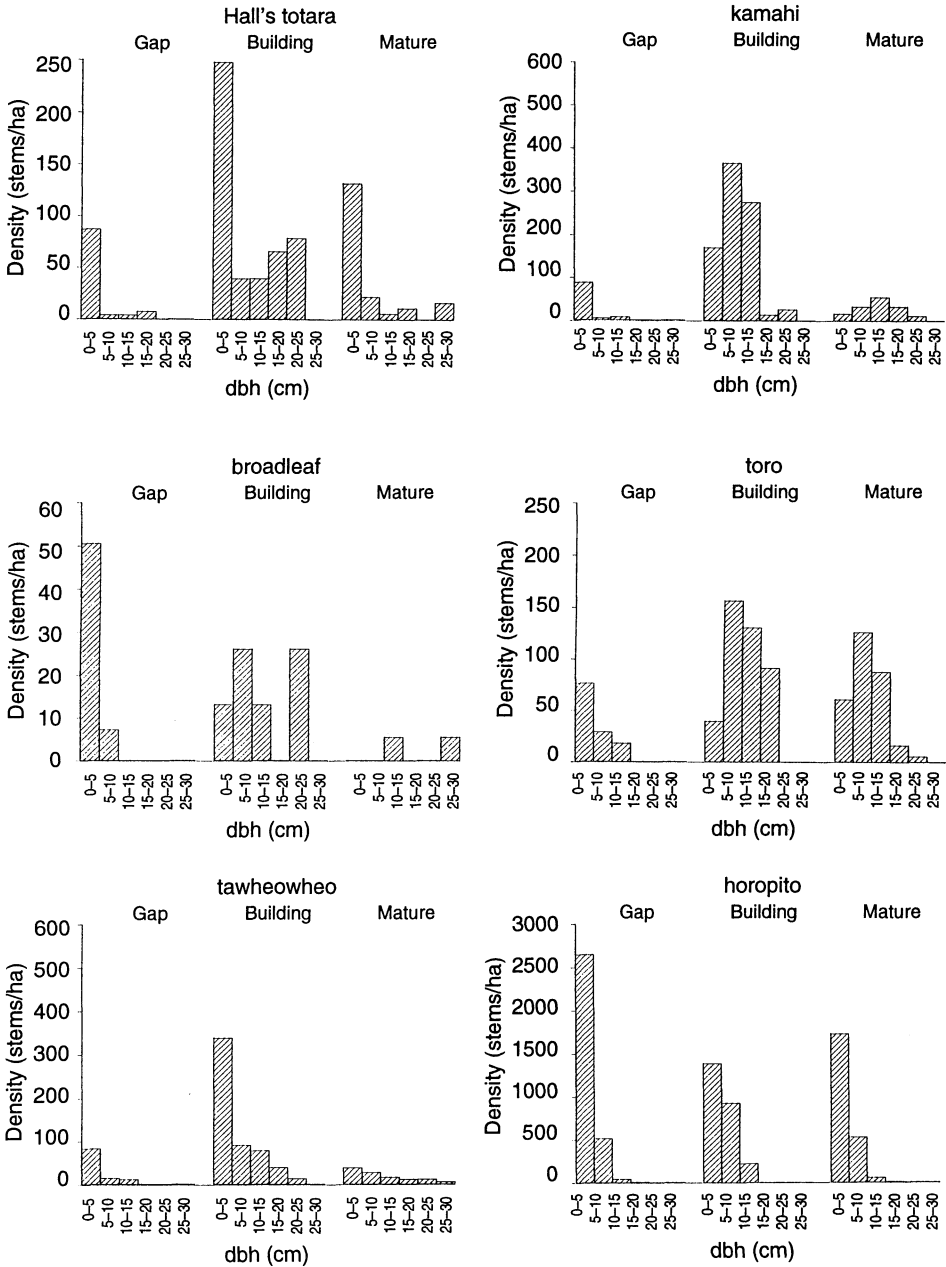


FIG. 2—Diameter distribution of major species in different phases of the forest growth cycle in Hall's totara / kamahi forest on Mt Pureora.

(Fig. 5), and comprises mostly horopito and tree ferns surviving from the preceding forest. Basal area increases rapidly during the building phase, at approx. 0.6 m<sup>2</sup>/ha/annum, and is significantly (p<0.05) positively related to age in a linear fashion; no non-linear effect was

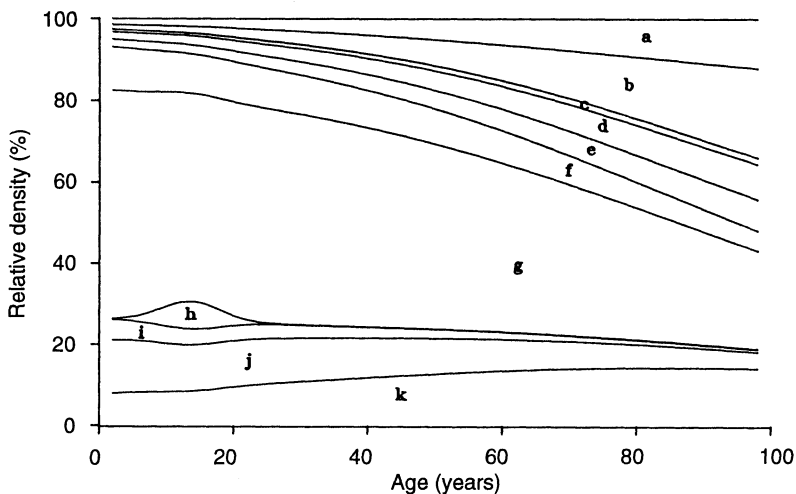


FIG. 3—Changes in relative density of major species during gap and building phases in Hall’s totara / kamahi forest on Mt Pureora. a = tawheowheo, b = kamahi, c = broadleaf, d = Hall’s totara, e = toro, f = small-leaved *Coprosma* spp., g = horopito, h = wineberry, i = putaputaweta, j = tree ferns (mostly *Cyathea smithii*), k = others as follows: *Coprosma grandifolia*, *C. tenuifolia*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Elaeocarpus dentatus*, *E. hookerianus*, *Fuchsia excorticata*, *Geniostoma rupestre*, *Leucopogon fasciculatus*, *Melicytus lanceolatus*, *Myrsine divaricata*, *Neomyrtus pedunculata*, *Nestegis cunninghamii*, *Pennantia corymbosa*, *Phyllocladus alpinus*, *Prumnopitys ferruginea*, *P. taxifolia*, *Pseudopanax anomalus*, *P. crassifolius*, *P. colensoi*, *P. edgerleyi*, *P. simplex*, *Pseudowintera axillaris*, *Schefflera digitata*.

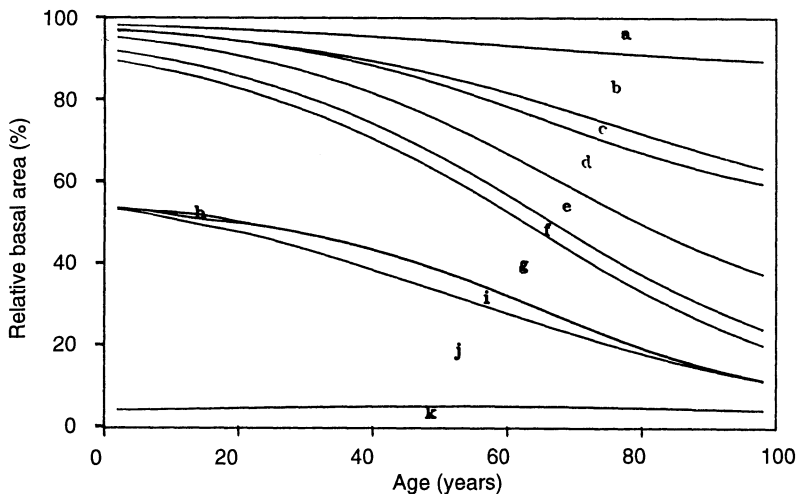


FIG. 4—Changes in relative basal area of major species during gap and building phases in Hall’s totara / kamahi forest on Mt Pureora. Symbols as in Fig. 3.

TABLE 5—Principal axes (eigenvectors) of a principal components ordination of proportions of major species in gap/ building and mature phases in Hall’s totara/ kamahi forest on Mt Pureora.

Regenerating species	Axis			
	1		2	
	Gap/building phases		Mature phase	
Hall’s totara	-0.26	-0.11	-0.11	-0.03
Kamahi	-0.26	+0.33	-0.14	-0.08
Toro	-0.21	+0.31	-0.14	+0.49
Tawheowheo	-0.31	-0.09	-0.45	+0.29
Horopito	+0.40	+0.53	+0.24	+0.45
Small-leaved coprosmas	+0.01	-0.62	+0.21	-0.52
Wineberry	+0.04	-0.01	0	+0.08
Putaputaweta	+0.15	-0.27	+0.14	-0.20
Tree ferns	+0.72	-0.07	+0.66	+0.08
Others	-0.11	+0.16	-0.43	-0.37
Percentage of variance explained	25		16	
			21	
			19	

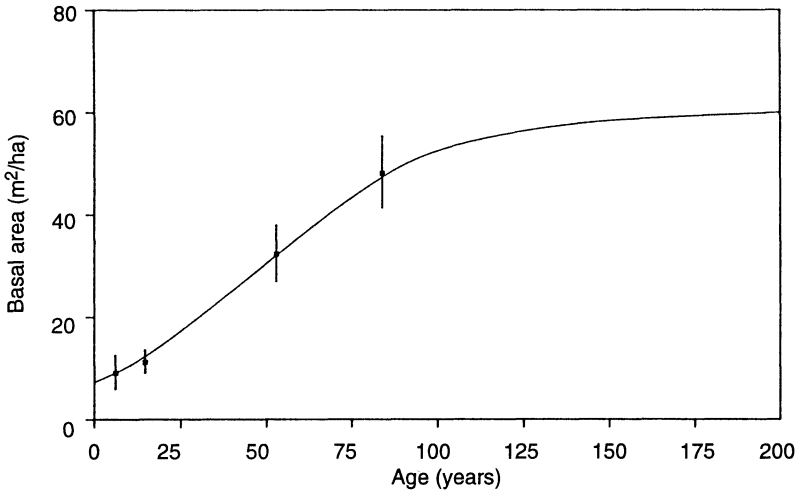


FIG. 5—Change in basal area (m<sup>2</sup>/ha) with time (years) since gap formation in Hall’s totara / kamahi forest on Mt Pureora (pooled plot means, with standard errors). Equilibrium basal area (60 m<sup>2</sup>/ha) from 0.4-ha long-term plot in the locality includes canopy trees. Curve fitted by eye.

detectable. Unpublished data from a 0.4-ha long-term plot in the locality indicate that basal area at dynamic equilibrium in this forest type is approx. 60 m<sup>2</sup>/ha, around 90% of which is attained about a century after gap formation. Mature forest is likely to attain a somewhat greater basal area, since equilibrium forest, although predominantly mature, includes all three phases.

### Proportion of Forest in Gap, Building, and Mature Phases

Estimated percentages of forest area in each phase (Table 6) show considerable variation between transects, indicating a large-scale mosaic of patches of different age. High percentages in the gap and building phases in some of them indicate not only extensive recent canopy collapse, but also similar collapse within the past century in other places.

TABLE 6—Estimated percentage of Hall's totara/ kamahi forest on Mt Pureora in gap, building, and mature phases (standard errors in parentheses).

Canopy species (mature phase only)	Gap	Building	Mature
Hall's totara			31.5 (4.5)
Kamahi			33.2 (2.1)
Broadleaf			16.4 (1.6)
Others (mostly toro, tawheowheo, and miro)			18.8 (4.5)
<b>Total</b>	11.5 (1.6)	29.0 (4.1)	59.5 (4.6)
<b>Range</b>	5.0–16.7	11.2–44.3	43.5–79.9

## DISCUSSION

Age estimates indicate that the gap phase lasts for some two to three decades on average, and the building phase for about a further seven. Thus, a century or so after gap formation, predominant canopy height has been reached. Basal area accumulates rapidly during the building phase—approx. 0.6 m<sup>2</sup>/ha/annum, a rate similar to that in lowland indigenous forests, e.g., nearby tawa (*Beilschmiedia tawa* (A.Cunn.) Kirk)-dominant forest (Smale *et al.* 1987) and secondary kauri (*Agathis australis* (D.Don) Lindl.) forest (Burns & Smale 1990). A lower predominant canopy height indicates a lower rate of biomass accumulation.

The oldest Hall's totara cored was estimated to be 652 years old, kamahi 229 years old, and broadleaf 262 years old. Maximum diameters attained, along with periodic mean annual growth rates in the three phases, suggest a maximum lifespan in Hall's totara of approx. 750 years, and approx. 450 years in kamahi; "normally attainable ages" (Harper & White 1974) are likely to be somewhat lower. Wardle (1991) also gives 450 years for the maximum lifespan of kamahi; greater ages (approx. 700 years) have been estimated in south-east Otago (Smith *et al.* 1985). With its capacity for vegetative renewal, similar growth rates, and similar maximum diameters, broadleaf probably has a similar lifespan to kamahi. Thus, canopy residence times are likely to be up to approx. 350 years for kamahi and broadleaf in this forest type, but considerably longer (up to approx. 650 years) for Hall's totara. Senescent broadleaf commonly replaces itself epiphytically *in situ*, thus prolonging site occupation and canopy residence indefinitely. Maximum diameters attained and growth rates suggest maximum lifespans for tawheowheo of approx. 225 years, and approx. 100 years for toro; data in the study by Dobson (1977) suggest a similar maximum lifespan for toro.

Estimated percentages of forest in the gap and building phases, together with their average duration, suggest average forest turnover times—rates of gap formation at any given site—of approx. 250 years. Mean annual diameter growth rates here and mean diameters of larger

(>30 cm dbh) canopy trees in the long-term plot suggest that this is a reasonable estimate of turnover time. Thus, average canopy residence times may be much shorter than the maxima outlined above. Stewart *et al.* (1991) pointed out that such estimates are highly sensitive to the estimated time for gap closure. Reasonably robust estimates of phase duration indicate that the broadleaved matrix of this forest type has a somewhat similar canopy lifespan to that of lowland tawa-dominant forests (Forest Research Institute 1987).

Amongst major canopy species, Hall's totara establishes early during the building phase (i.e., in old gaps), with little effective regeneration in the understorey of mature forest. Although seedlings occur in significant numbers there, they are mostly strongly suppressed, and appear to require canopy thinning or opening for development to maturity (*see* Beveridge 1973). The microclimatic conditions prevailing under senescing groves of gap-invading species such as small-leaved coprosmas are presumably ideal for the establishment and early growth of this species. Typically, diameter growth rates accelerate through the building phase, reaching a peak some time after emerging above the general hardwood canopy. Herbert (1980) reported a similar growth pattern in rimu in uneven-aged lowland dense podocarp forest near the study area.

Kamahi invades gaps to a limited extent, but mostly establishes epiphytically (*see also* Wardle 1966; Clarkson 1986; Lusk & Ogden 1992) later during the building phase, with some subsequent self-thinning (Stewart & Veblen 1982). Like Hall's totara, kamahi does not regenerate effectively under mature forest; the seedlings and saplings that occur are invariably strongly suppressed and seldom, if ever, reach the canopy. Diameter growth rates accelerate during the building phase, peaking some time after predominant canopy height is reached. Lusk & Ogden (1992) reported similar growth rates in uneven-aged, lowland dense podocarp forest at Horopito, approx. 90 km south of the study area, though peaking somewhat earlier during the sapling stage. Sample sizes are small, yet broadleaf too appears to show a similar pattern to kamahi, establishing to a limited extent in gaps but also establishing epiphytically later in the building phase. In mature forest, epiphytic regeneration of broadleaf occurs in the crowns of senescing canopy trees, particularly of its own species. Diameter growth rates peak early. Both kamahi (Beveridge 1973; Lusk & Ogden 1992) and broadleaf establish on subsoil in gaps, as on the upturned root-plates of windthrown trees, while soft tree fern, in spite of its persistent skirt of dead fronds, is an important epiphytic host for these species later on. Seedlings and saplings of Hall's totara, kamahi and broadleaf were frequent in 3-m-high small-leaved coprosma scrub that had developed after fire 40–50 years earlier in Hall's totara-kamahi forest on Mt Pureora (McKelvey 1963).

Tawheowheo also invades gaps to a limited extent, but mostly establishes later during the building phase; diameter growth rates peak early. Toro does not regenerate effectively under healthy mature forest either, establishing to a limited extent in gaps but mostly later during the building phase; diameter growth rates peak early during the mature phase. Dobson (1977) reported an apparently all-aged toro population developing under a largely senescent kamahi forest on coastal dunes in north Westland.

Amongst subcanopy and understorey species, horopito is prominent in the understorey of mature forest, but also invades gaps to a significant extent, with some subsequent self-thinning during the building phase. Maximum diameters of approx. 12 cm and mean annual diameter growth rates (approx. 0.06 cm) indicated by a small sample of felled saplings

suggest a maximum lifespan of approx. 200 years. Together with a “reverse J” diameter distribution in mature forest, this indicates that regeneration occurs in the understorey of high forest, especially in better lit areas such as at the margins of overlapping crowns and under the thinning canopies of senescent canopy trees.

Tree ferns (mainly soft tree fern), small-leaved coprosmas (mainly *C. aff. parviflora* and stinkwood), and, to a lesser extent, putaputaweta (*see also* Lusk & Ogden 1992) and wineberry are also prominent gap invaders, declining during the building phase. The decline in tree ferns may be due partly to self-thinning (Campbell 1990) and partly to smothering by taller-growing trees, especially epiphytes growing on them; lifespans are unknown. Maximum diameters in small-leaved coprosmas of approx. 14 cm and mean annual diameter growth rates of 0.25 cm suggest natural lifespans of approx. 60 years; overtopping by taller trees is also likely to be a factor in their demise. Putaputaweta’s lifespan is unknown, but is unlikely to be much longer than 100 years (cf. 150–250 years—Ogden *et al.* 1991); wineberry lives for less than 30 years (Wardle 1991). Apart from wineberry, these species persist in significant numbers in the understorey of mature forest, with some continuing establishment, especially towards the end of the mature phase as canopy trees senesce. In similar montane forest on Mt Hauhungatahi, approx. 75 km south of the study area, horopito and soft tree fern are the most important species in gaps (Ogden *et al.* 1991).

This and other studies (e.g., June 1982; Stewart & Veblen 1982; Williams & Buxton 1989) indicate that the major canopy species in this forest type (Hall’s totara, kamahi, and broadleaf) have intermediate shade tolerances, while horopito, the major understorey species, is more shade-tolerant. Amongst minor canopy species, toro also has intermediate shade tolerance, while tawheowheo may be more light-demanding. Thus, the variety of replacement strategies here reflects the variety of shade tolerances. Relatively intolerant—i.e., light-demanding—species such as small-leaved coprosmas are primarily gap colonists. Species with intermediate tolerance, e.g., the three main canopy species, mostly establish during the building phase (earlier for totara, later for predominantly epiphytic kamahi and broadleaf). More shade-tolerant species, e.g., horopito, can establish and grow to maturity in the understorey of mature forest.

In contrast to lowland tawa-dominant forests (e.g., Smale & Kimberley 1983) and beech forests (e.g., Stewart *et al.* 1991), where canopy dominants either survive gap formation as advance growth or colonise gaps (gap-phase replacement), gap composition here is not by itself a reliable indicator of future canopy composition. Future canopy dominants mostly establish later in the forest growth cycle by means of what may be termed “building-phase replacement”. Secondary succession operates, albeit on a miniature scale, within the overall forest mosaic, with early successional species apparently facilitating (*sensu* Pickett *et al.* 1987) the entry of canopy dominants by providing a suitable microclimate (Hall’s totara) or substrates for epiphytic establishment (kamahi and broadleaf); they in turn later inhibit the early successional species. More specifically, gap-maker/gap-filler and canopy/understorey relationships suggest a regeneration cycle in which Hall’s totara tends to be replaced by either kamahi or broadleaf; kamahi in turn tends to be replaced by broadleaf or totara, and broadleaf by totara. Beveridge (1973) described a somewhat similar cycle in lowland podocarp/kamahi/shrub hardwood forest in the region, in which tree ferns (*Dicksonia squarrosa* Forst.f.) Swartz) invading gaps formed by windfallen podocarps, mostly rimu, are replaced epiphytically by kamahi, which in turn are replaced by podocarps growing up

beneath them. Senescent hinau (*Elaeocarpus dentatus* (J.R. et G.Forst.) Vahl) and black maire (*Nestegis cunninghamii* (Hook.f.) L.Johnson) also act as nurses for podocarps (Herbert 1986).

Hall's totara is a preferred food of possum, and kamahi is a major constituent of possum diet where both are present (Coleman *et al.* 1985). Broadleaf is unpalatable to possums but highly palatable to deer (Wardle 1974), while kamahi and Hall's totara are relatively unpalatable to deer. The coincidence of the presence of introduced browsing mammals here with the average duration of the gap phase (approx. 30 years) makes the full impact on these species difficult to discern at present. However, most major canopy species appear to be regenerating successfully; possible exceptions are toro, a preferred food of possum (Fitzgerald 1981), and kamahi. In both species a dearth of seedlings is apparent, although in the latter this may reflect a predominantly epiphytic establishment mode rather than a real regeneration gap. Significant changes in subcanopy and understorey composition have already been brought about here in the past 30 years by introduced mammals, with the reduction of some highly palatable species like haumakaroa and stinkwood, the local extinction of others (e.g., threefinger), and a concurrent increase in unpalatable horopito and soft tree fern (Williams 1991). Highly palatable species originally represented some 25% of density but less than 5% of basal area in a long-term 0.4-ha plot here.

Species such as pate (*Schefflera digitata* J.R. et G.Forst.) and *Coprosma tenuifolia* Cheesem. which are still common in the understorey of similar forest on Mt Egmont (M.C.Smale, pers. obs.), where ungulates are rare, are now largely epiphytic on Mt Pureora, occurring terrestrially only at deer-inaccessible sites such as on bluffs and in large canopy gaps smothered by lawyer (*Rubus cissoides* A.Cunn.). The growing space vacated by highly palatable species has been largely occupied by horopito, whose abundance reflects its ability to survive gap formation and grow in a wide range of light regimes, enhanced since the introduction of browsing mammals by its extreme unpalatability. Hence, although the present canopy is more-or-less being maintained, subcanopy and understorey composition is being steadily impoverished. The implications of this continuing shift in lower-tier composition—from shorter-lived species to relatively long-lived horopito, and tree ferns—for the future regeneration of canopy species are unclear.

Cohort senescence is occurring locally in extensive groves of similar-sized (and probably similar-aged) kamahi trees, creating in places a gap phase of enormous dimensions (pers. obs.). These groves may have developed after a widespread exogenous disturbance, probably catastrophic windthrow, several centuries ago, in turn initiating an endogenous disturbance now. Unlike Hall's totara, kamahi and, to a lesser extent, broadleaf regenerate abundantly on recently devastated sites (Stewart & Veblen 1982). Large patches of forest in the building phase indicate that extensive collapse is not a new phenomenon, but has been occurring for at least a century, long before the arrival of browsing mammals. The same phenomenon occurs widely in montane rata (*Metrosideros umbellata* Cav.)-kamahi forests on steepplands in the central western South Island, where mass movement is a common exogenous disturbance (Stewart & Veblen 1982). The predominance of kamahi in this forest type probably reflects aspects of its reproductive biology such as prolific seed production, effective wind dispersal, and its ability to establish on a wide range of terrestrial and epiphytic sites (Wardle 1966). These give it a competitive advantage over Hall's totara (probable seeding periodicity, lower seed production, and reliance on terrestrial establishment) and



broadleaf (lower seed production, future reliance on epiphytic establishment) under a wide range of disturbance regimes, especially large-scale ones. The similarity between regeneration in normal gaps and in areas of extensive canopy collapse suggests that similar successional pathways operate in both instances.

The approach used here, of quantifying regeneration in three phases of the forest growth cycle, supports the following responses to most of the classic questions about forest dynamics posed by Webb *et al.* (1972). The regenerating species are reproducing a forest similar in structure and composition to the surrounding one; McKelvey's (1963) view that the forest is replacing itself, made before the impact of introduced mammals had become apparent, is still valid. The emergent and canopy species mostly establish during the building phase of the forest growth cycle, i.e., in old gaps, and thus regenerate intermittently at any given site but continuously over the forest as a whole. The ability of two of the canopy dominants to regenerate epiphytically reduces their susceptibility to damage from introduced terrestrial browsing mammals. Diameter distributions over all phases are erratic in Hall's totara and broadleaf, bell-shaped in kamahi and toro, and "reverse J" in tawheowheo and horopito. Diameter growth rates are faster during the gap and building phases than in mature forest; height growth rates may be expected to follow a similar trend. In the longer term, the continuing influence of introduced arboreal and terrestrial browsing mammals may significantly alter the regeneration patterns described in this paper.

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