

**STUDIES ON THE VEGETATION OF MOUNT COLENZO,
NEW ZEALAND**

**4. AN ASSESSMENT OF THE PROCESSES OF
CANOPY MAINTENANCE AND REGENERATION
STRATEGY IN A RED BEECH (*NOTHOFAGUS FUSCA*)
FOREST**

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SUMMARY: Information on diameter frequency distributions and spatial patterns, together with estimates of diameter growth and mortality, are used to draw up regeneration balance sheets for three stands of red beech (*Nothofagus fusca*) on Mount Colenso, New Zealand. Because large canopy gaps are a feature of these forests, attention is directed particularly to their future status. It is concluded that, in the short-term, a further opening of the canopy is likely in the higher altitude forest. This forest appears to have developed following catastrophic destruction, and its predominantly even-aged red beech population may be still undergoing competitive thinning. At lower altitudes uneven-aged forest is likely to maintain its present canopy structure. Simple mathematical predictions based on the Leslie Matrix Model indicate that, in the longer term, the present population has the potential to colonize the larger gaps in all the stands. However, such predictions do not take account of the observed lack of suitable micro sites for seedling survival in the centres of large gaps.

Small canopy gaps created by the fall of one or two trees are a consequence of the regeneration strategy in uneven-aged stands. The varying ages and spatial distributions of such gaps lead to considerable variation in size class frequency distribution from place to place. The strategy of individual replacement in "stable" forests, which generates small gaps of varying duration, may render such forests particularly susceptible to invasion by other species.

INTRODUCTION

The different tree species comprising mixed forests show differences in reproductive strategies which are related to the various roles they play: as canopy dominants, shade-tolerant understorey species or light-demanding "gap-fillers". These different strategies involve different seed and dispersal characteristics, different spatial distributions, and different growth and mortality rates for the various age classes into which tree populations may be divided (Whitmore, 1974). Consequently, species with different roles have differently-shaped ages and

size-frequency distributions (e.g. Jones, 1956; quoted by Longman and Jenik, 1974). Clearly, it is necessary to know what these characteristic distributions are before supposed departures from them can be used as evidence for the stability or otherwise of the population in question.

Many studies have considered a negative exponential frequency distribution to be "normal" for multi-aged populations (Meyer, 1952), and have compared the observed size-frequency distribution, at least intuitively, with this. Deficiencies in the smaller size classes are then taken as evidence for inadequate recruitment to the adult population. Such "regeneration gaps" must be distinguished from "canopy gaps", which are simply breaks in the canopy.

A distinction can also be made between populations in which individual replacement takes place and those in which stand replacement is the rule.

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In the former the death of a mature individual is a pre-requisite for the survival of another to maturity. In so far as decaying red beech logs in small canopy gaps are strongly favoured regeneration sites for red beech (Ogden, 1971b; June and Ogden, 1975) this is the "normal" process in undisturbed red beech forest on Mt. Colenso. In general, large areas of species with this strategy might be expected to show the negative exponential type of population age structure already mentioned. In cases where whole forest stands are replaced by an even-aged population following some large scale disturbance on the other hand, a paucity of individuals in smaller size classes will result as the stand ages. Recruitment is followed by a long period in which mortality preponderates as self-thinning processes operate (White and Harper, 1970).

Many New Zealand forest trees show "regeneration gaps" which have been accounted for in various ways by different authors (Cameron, 1954; Holloway, 1954; Widdowson, 1960; Wardle, 1963). Such gaps may, however, at least in some cases, be a consequence of regeneration strategies based on whole stand replacement* (Ogden, 1971b). Red beech may respond to different external environments by either individual or stand replacement strategies. Once an even-aged structure has developed in such a light-demanding species there will be a tendency for it to be maintained through several "cycles" of regeneration even in the absence of another "synchronising event". Finally, it should be noted that observed size (d.b.h.)-frequency distributions variously distort the true age distribution in the population.

This paper analyses the rates of regeneration in

*The synchronicity of such gaps over wide geographical areas poses other questions which are not dealt with here.

a forest dominated by red beech but with large canopy gaps which frequently contained few or no younger trees. Data on diameter-frequency distributions, spatial patterns, growth and mortality rates were combined in simple mathematical models with the aim of predicting the future state of the canopy.

METHODS AND ASSUMPTIONS

Three stands in forest dominated by red beech at Mount Colenso, Ruahine Range (1760 05' E, 390 45' S), covering an altitudinal range of 950 to 1080 m a.s.l., were selected for study. The vegetation of the area has been described by Ogden (1971a), and the stands studied are the same as those previously described by June and Ogden (1975).

The circumferences of all live red beech individuals above 2 m in height were measured within a selected area of each stand (1.23 ha in Upper Stand, 0.41 ha in Middle Stand and 1.04 ha in Lower Stand). Height and proximity to other trees and canopy gaps were also recorded for each individual. The population was divided into seedlings, saplings, sub-canopy trees and canopy trees (Table 1). The circumferences and positions of recognisable dead red beech trees greater than 10 cm in diameter were also noted. Canopy cover percentage was estimated by vertical sightings at 396 points along transects in each stand. Canopy gaps were recognised where there was no cover from the foliage of canopy trees for a minimum of 2 m horizontal distance in any direction.

Stem sections and cores from 25 cm above ground were taken for counting annual growth rings. Four years were added to the age estimate to allow for seedling growth to this height. A linear regression relationship between stem size and estimated age was used to calculate the mean diameter growth rate and the age limits for each size class.

TABLE 1. *Attributes of the four sections of the red beech population.*

	Seedlings ¹	Saplings	Sub-canopy trees	Canopy trees
Size criteria	5-200 cm in height	200 cm height < 10 cms dbh	10-24 cm dbh or > 24 cm but shorter than the upper canopy: not necessarily over-shadowed	> 24 cm dbh and reaching the upper canopy
Age range (years)	2-20	20-60	60-200	100-450
Mortality per annum	13.4%	1.0%	0.6%	0.6%

¹ Data for "established" seedlings, June and Ogden (1975).

Estimating the parameters of the population model

Estimates of the growth and mortality rates of canopy and sub-canopy trees are subject to certain limitations imposed by the sampling procedure. Processes with a high intrinsic variance, such as growth rate per individual or per age class, require an enormous sampling effort if narrow confidence limits are to be placed on them. Similarly, mortality rates, at least of larger individuals, cannot be reliably estimated from a short period of observation. When an estimate of a long-term stochastic phenomenon, such as mean mortality rate, is required, the safest approach appears to be to make several independent estimates from different bases. In view of these considerations, average growth and mortality rates, based on all three stands, were calculated for the four main sections of the population. Size class frequency distributions, on the other hand, are not subject to the same sampling limitations, and were not averaged.

The number per hectare in each size class, diameter growth rates and mortality rates were used to produce a balance sheet for stand regeneration showing the estimated annual input and output for each major section of the population. After allowing for mortality, the number of individuals growing out of each section becomes the input to the next section. Mortality rates of the seedling population are discussed in June and Ogden (1975); only the "established seedlings" are considered here as these constitute the "pool" from which the larger size classes are recruited. Sapling input was based on an estimate of 0.4% of the established seedling population growing into the sapling class each year (June and Ogden, 1975).

In estimating mortality rates for the sapling and sub-canopy classes allowance must be made for their spatial pattern, as this influences mortality. The self-thinning process which operates within sapling clumps, such as those deriving from dense seedling populations on rotten logs, ensures that only one individual per clump will eventually become a canopy dominant. Although occasionally more than one member of a clump may reach the canopy, the smaller members are more or less suppressed. They occupy canopy space which could potentially be filled by a single dominant canopy tree. Such clumps are, therefore, regarded as individuals for the purposes of the model. Moreover, the light-demanding nature of red beech means that only clumps situated in canopy gaps are likely to contain individuals which will be recruited to the next size class, while clumps developing beneath the shade of sub-canopy and / or canopy trees will contribute only to the mortality figures, unless the fall of a nearby tree

places them in the open. In the following discussion "potentially successful" individuals are those which will be recruited to the next size class. They comprise isolated individuals (more than 2 m from other trees) and the largest individual from each clump within a canopy gap. Clumps were defined as groups of individuals growing within 2 m (horizontally) of each other. "Potentially successful" saplings and sub-canopy trees are assumed to reach the canopy. Although this is usually the case, it does not invariably occur, but nor do trees not defined in this way invariably succumb, and it is assumed that these two low probabilities balance each other. The following calculations show how sapling mortality was calculated.

In all three stands a total of 109 "potentially successful" and 192 other ("surplus") saplings were enumerated. The "potentially successful" individuals will all become recruited to the sub-canopy class within 40 years, which is the age range of saplings. These 109 saplings can be equated to the 62% of existing sub-canopy trees which are "potentially successful" and the remaining 38 % of "surplus" sub-canopy trees must therefore be derived from "surplus" saplings. Thus, 67 "surplus" saplings will survive and the remainder (125) represent the expected mortality over a 40 year period which can be converted to an annual rate.

Sub-canopy trees were assumed to grow into the next diameter class within 30 years, the age range of each diameter class; some were allocated to canopy status according to the present proportions of canopy and sub-canopy trees in that diameter class (Fig. 1). Sub-canopy trees may therefore pass through several size classes before they reach the canopy. For example, there are 16 "potentially successful" sub-canopy trees in the 10-20 cm dbh size class in the Upper Stand and 43.7% of the 20-30 cm dbh class are canopy trees. Hence the annual rate of recruitment of "potentially successful" trees to the canopy from the 10-20cm dbh class is $16 \times 0.437/30 = 0.23$ trees per annum. This calculation was repeated for each sub-canopy size class, and the results pooled to give the canopy input for each stand.

Mortality rates for canopy and sub-canopy trees were estimated from observations of trees dying in the study stands during 1972 and those thought to have died in the previous year. An estimate was also obtained from the exponential section of the combined size-frequency distribution from all stands. Knowing the average time taken for a tree to grow from one size class to the next (based on mean diameter growth rate) and assuming that the exponential rate of decline of numbers in successive

diameter classes is unchanged as trees pass through the size classes, then the number of trees dying in a given time interval can be calculated (Wardle, 1970). In the absence of contrary data, an average mortality rate was accepted for canopy and sub-canopy trees, although it is recognised that some patchiness still exists in these age groups, and consequently that "potentially successful" trees may have a somewhat lower mortality. The death of a canopy individual which is one of a clump may have negligible effect on the long-term canopy structure, as the lateral branch growth of its neighbours rapidly fills the gap.

Predictions

Predictions of population trends are based on an interpretation of the data in Figure 3, and on analyses using a modified version of the Leslie Matrix Model of Hartshorn (1975). The flow diagram (Fig. 3) includes no "feed-back" from mature trees to the seedling population (but see June and Ogden, 1975), while for the Matrix Model an estimate of this feedback is required. The model has been reviewed by Usher (1972) and details are not presented. Given an initial size class frequency distribution, and estimates of fecundity, growth and mortality rates for each class, the model defines the contribution which any size class makes to all other size classes in a unit time period. Two estimates were made, for each stand, of the average annual contribution per mature tree to the established seedling pool. These estimates were made by dividing the number of established seedlings/ha (June and Ogden, 1975) by (1) their approximate modal longevity (5 years) or (2) their approximate maximum longevity (20 years), and then by the number of canopy and sub-canopy trees/ha. The second estimate is considered to be unrealistically small (Enright and Ogden, in prep.). The model was run twice for each stand with these different estimates of the annual contribution of mature trees to the established seedling pool and the mortality and transfer rate data in Table 1 and Figure 3.

It must be stressed that predictions of future states based on this model, or simply on the data in Figure 3, are probabilistic. Moreover, they cannot be any better than the estimates of the population parameters on which they are based. We admit the limitations of the latter, and consequently regard our predictions as no more than hypotheses which future study should aim to test. Even with accurate estimates of mortality, growth rate etc., we can predict no more than *potential* future states, as stochastic processes, such as catastrophic storms, insect attack, fire etc., are not included in the model

(except in so far as their occurrence in the past has influenced our estimates of the population parameters). For this reason, and because the population parameters themselves will change as the canopy changes, we have restricted our predictions to a span of time well within the possible longevity of the species.

RESULTS

Stand structure

Large canopy gaps were a feature of all stands and resulted in a relatively low percent canopy cover (Table 2). Gaps were up to 40 m in width and 0.07 ha in area and were filled with thickets of shrubs (*Pseudowintera colorata*, *Griselinia littoralis*, *Fuchsia excorticata* etc.), tangles of *Rubus*, occasional saplings and small trees of red beech and dense swards of ferns, mainly *Dicksonia lanata*. In the Middle Stand most red beech saplings were found in clumps around the margins of large gaps, whereas in the other stands the saplings were scattered in small clumps throughout the stand. On average, 52 percent of saplings and 42 percent of sub-canopy trees were located in gaps, which, on average, occupied only c. 30 percent of the study area (Table 2). Individuals with potential to form a canopy are thus preferentially located in gaps.

TABLE 2. Canopy and basal area characteristics of red beech in the three stands.

Stand	Canopy characteristics		Total basal area (m ² /ha)	
	% cover	Height range (m)	Live trees	Dead trees ¹
Upper	88	14-19	41.4	30.4
Middle	64	21-22	46.5	37.9
Lower	62	21-25	50.3	31.5

¹ Dead trees include fallen logs and dead stumps.

While the canopy diameters of most red beech canopy trees ranged from 6-8 m, some heavily branched trees, usually around the margins of canopy gaps, had diameters twice these dimensions. The basal area of living trees was low (41.4 to 50.3 m²/ha) compared with other recorded values for *Nothofagus* forest in New Zealand. For example, 73.5 m²/ha for a red beech stand in the Routeburn Valley (Westerskov and Mark, 1968) and from 46 to 69 m²/ha (mean = 57.3 m²/ha) for closed stands of *N. solandri* (Wardle, 1970). The highest basal area recorded by Franklin (1967) in beech forest was 80.8 m²/ha. Live basal area was not directly pro

portional to percentage canopy cover. There was also a large basal area of dead trees, and stumps and fallen logs of red beech in various states of decay were found in all parts of the stands.

Size structures

The size-frequency distributions had a different form in each stand (Fig. 1). The Upper Stand was numerically dominated by small canopy trees, the Middle Stand by saplings, and the Lower Stand was intermediate in structure with a higher proportion of sub-canopy and large trees. Some of the modal peaks found in adjoining areas (Ogden, 1971a) were present. The wide variation in growth rates between individual trees (Fig. 2) means that the size structures

can only be interpreted as age structures in a general way.

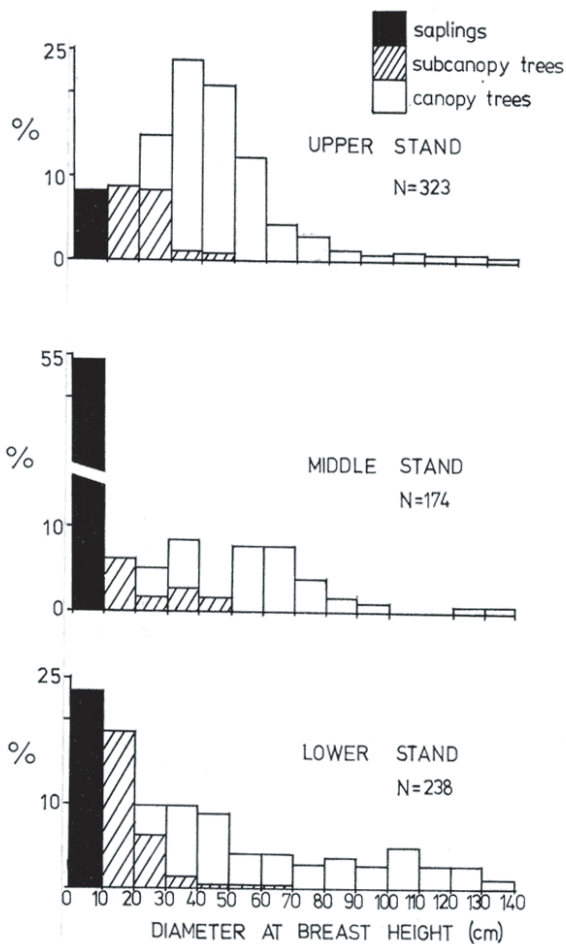


FIGURE 1. Frequency distributions of red beech stem diameters on Mount Colenso.

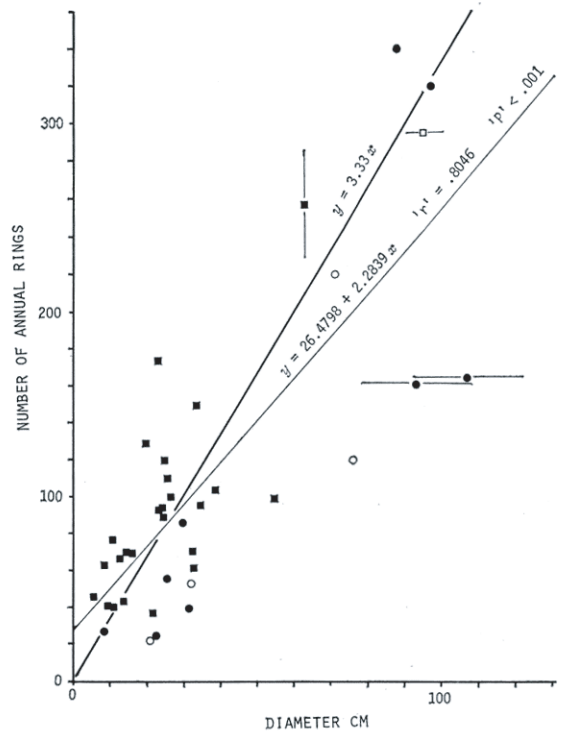


FIGURE 2. The relationship between age and diameter for red beech on Mount Colenso and elsewhere in the North Island. Points with vertical or horizontal bars attached indicate counting or diameter measurement uncertainty. The regression line $y = 26.4798 + 2.2839x$ is based on all the data. The regression $y = 3.33x$ assumes a mean annual growth of 0.3 cm/yr. Solid squares: Mt Colenso, 914-1112m; Solid circles: Mt Colenso, 640-661 m; Open circles: Makaroro Valley, Ruahines, 701-1036 m (N. Elder, pers. comm.); Open square: Mt Ruapehu, c. 914 m (I. Atkinson, pers. comm.).

Growth and mortality rates

The mean growth rate of 25 trees sampled between 900 and 1100 m within and adjacent to the study stands was 0.28 cm/yr with a standard deviation of 0.14 cm/yr. This has been rounded off to 0.3 cm/yr and used in the regeneration model for both canopy and sub-canopy trees. The line corresponding to this growth rate is shown passing through the origin in Figure 2, which also shows the best linear regression line fitted to the data. The equation defining this line

was not used to estimate age because it was thought to be unduly influenced by two large trees from a lower altitude than the study area.

Although, in common with other *Nothofagus* species, the growth rates of red beech show considerable differences from region to region, in anyone area the relationship between age and diameter is statistically significant and approximately linear over most of the life of the tree (Ogden, 1978). No allowance was made for the effect of altitude on growth rate in the regeneration mode], mainly because the stands studied overlapped altitudinally and covered a total range of only c. 130 m. Variation in growth rates between trees in anyone stand exceeds the estimated 0.104 cm/yr due to the altitudinal difference between the upper and lower stands (Ogden, 1978).

The mean mortality rate for sub-canopy and canopy trees is 0.6 % p.a. (Table 3). There was no evidence of large scale mortality resulting from drought, insect attack or wind-throw during the study period; only isolated trees died. These mortality estimates can be compared with the few published estimates for New Zealand trees. Wardle (1970) gives values of 3 % for 75-85 year old, 1.2 % for 175 year old and 0.08% for 275 year old stands of *N. solandri* undergoing self-thinning. In mixed-aged stands of the same species a mean annual mortality < 1.73 % p.a. must apply to the older half of the population (Wardle, 1970). The same author (1974) mentions mortality rates of "one percent or less" for mountain beech (*Nothofagus solandri* var. *cliffortioides*) and Elder (cited by Wardle, 1970) recorded 2.3 % p.a. in an even-aged mountain beech stand while it passed from 70 to 87 years old, and 0.6% over the following 10 years.

TABLE 3. Mortality estimates for red beech trees.

	% Mortality per annum	
	Sub-canopy trees	Canopy trees
1971 mortality	0.6	0.9
1972 mortality	0.0	0.0
Estimates from size structure	1.1	0.8
Mean	0.6%	0.6%

The regeneration model and predictions of future states

The estimated inputs and outputs for each section of the population in the three stands are shown in Figure 3. The mortality rates in this figure are

derived from averages over all stands, so that differences in the dynamics of the stands tend to be averaged out. The considerable differences in size class frequency distributions between the different stands are the dominant feature of the model. Taking only the "potentially successful" individuals as contributing to regeneration in each stand, the immediate trends in canopy replacement can be deduced. Canopy replacement is inadequate in the sense that output from it (mortality) slightly exceeds input to it in the Upper and Middle Stands, but is adequate in the Lower Stand. The imbalance between input and output is not large, however, and a 0.2 % lowering of the tree mortality rate would reverse the trend in the upper two stands. Moreover, if "surplus" trees are allowed to contribute to the canopy the imbalance is negligible.

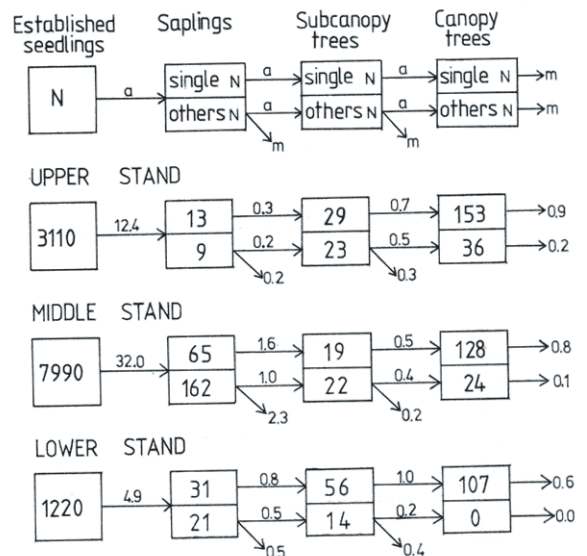


FIGURE 3. Regeneration model for red beech showing the annual input and output for each section of the population. *N* refers to the number of individuals per hectare. *a* to the transfer rate (number per hectare per annum) and *m* to the mortality rate (numbers per hectare per annum). Single *N* refers to the number of "potentially successful" individuals.

Sapling numbers will increase rapidly in all stands because recruitment from the seedling class considerably exceeds losses due to growth and mortality. Total sub-canopy numbers can be expected to increase only in the Middle Stand. No significant change can be expected in the Lower Stand, but an initial decrease seems probable in the Upper Stand.

Although the regeneration model is not designed to allow extrapolation of replacement trends beyond 30 years (the minimum time span used in estimating transfer and mortality rates) the predicted changes in sapling and sub-canopy numbers can be used for indicating the potential trends in canopy replacement in the longer term, assuming that other parameters of the model do not change. Thus, after c. 30 years the predicted decline in sub-canopy trees in the Upper Stand will result in a further opening of the canopy. In the other stands, however, increased recruitment to the sub-canopy seems likely to lead to the gradual filling of the canopy gaps. Over a longer time span (c. 70 years), the expected increase in sapling numbers will result in an increase in canopy recruitment in all the stands, as the present day saplings begin to reach the canopy.

The results of the analyses using the Leslie Matrix Model confirmed those given above, and are not presented in full. The dominant latent root of the matrix (λ) is equal to the natural log of 'r', the intrinsic rate of natural increase, so that a value of 1.0 indicates a stable population, and values above and below 1.0 respectively expanding and declining populations. In five of the six analyses run with estimates of the estimated ratio of seedlings becoming established annually to mature trees ranging from 0.36 to 8.28, the dominant latent root was close to, but above, 1.0 ($\lambda = 1.0118 + 0.00417i$) suggesting that a slow expansion of the population will occur in all stands. The only exception, a dominant latent root of 0.99962, occurred in one of the analyses of the Lower Stand data and indicated that here recruitment to the established seedling class must exceed 0.4 per mature tree per year for long term canopy maintenance.

DISCUSSION AND CONCLUSIONS

The red beech forest on the slopes of Mount Colenso has a relatively low basal area, frequent canopy gaps and abundant fallen logs. These circumstances might appear ideal for immediate seedling survival and growth, and canopy restoration in the longer term. The analyses reported here, overall, support that conclusion. When all stands are considered together the population appears capable of replacing itself and at least maintaining the present canopy structure. However, we must note that the balance between canopy gains and losses is precarious and variable from place to place. This conclusion and the following field observations and theoretical argument suggest that some of the larger canopy openings will be slow to close.

Comparison of the numbers and distribution of saplings and sub-canopy trees with the spatial extent

of the canopy gaps in the field indicates that complete closure of the existing gaps is not possible in the near future. Indeed, the upper forests, where the uni-modal size-frequency distribution suggests that a stand replacement strategy is in operation, a temporary increase in the extent of the gap phase seems probable. Gaps which exceed the canopy height in mean diameter are frequently occupied by a dense ground cover of *Dicksonia lanata* which totally prevents seedling establishment (June and Ogden, 1975). Except near their margins, suitable microsites cannot be created in such gaps by the fall of adjacent trees, so that they have a degree of permanence not found in smaller openings. The latter exist for a variable, and sometimes prolonged, length of time as a consequence of (1) the importance of the rotting log microsite in red beech establishment, and (2) the difference between the life span of the canopy trees and time taken for a log to decompose.

June (1974) has estimated that log decomposition takes 80-300 years. On average we might expect fallen logs to be "available" to red beech seedling colonisation for a lesser period of time. As this time is less than the longevity of the mature trees, it follows that in anyone small area there will be periods when suitable log microsites are rare or absent. During these periods the non-canopy trees, survivors from earlier seedling clumps, are suppressed and die off progressively. If they are all dead before a canopy opening occurs in the area, then the opening is likely to be long-lived, because of the time needed for suitable mossy log microsites to be formed and colonised. But if some sub-canopy trees or saplings remain, then presumably one or more of them fills the gap relatively quickly. Small scale heterogeneity of canopy structure and local discontinuities in size class distributions seem inevitable with such a system.

The differences between the stands have been partially obscured by the use of average values for some parameters of the model. However, the existing structural characteristics are quite clear. The Upper Stand size class frequency distribution is similar to that previously reported for an adjacent area (Ogden, 1971b) and indicates that it has arisen following destruction of the previous forest at this altitude. Elder (1965) has commented on catastrophic climatic events in other parts of the Ruahine Range. Some of the present canopy gaps in the upper forests may be remnants from this time; the heavily branched form of their marginal trees suggests that the openings have existed for a century or more. In contrast, the canopy gaps in the lower stands are bordered by relatively narrow-crowned trees.

In four stands from altitudes between 830 and 1030 m (Middle and Lower Stands and stands 2 and 3 of Ogden, 1971a) bi- or tri-modal frequency distributions occur. The altitudinal range of the stands included in this study (950-1080 m) is hardly sufficient to test Ogden's (1971b) suggestion that a slow, downwards altitudinal migration of the red beech population is in progress or has recently occurred. The canopy and sub-canopy components of the Upper Stand appear more vulnerable than those of the Middle and Lower Stands, but this is probably a function of the stand replacement strategy, so that the results do not clearly support the hypothesis of recent downhill migration. On the other hand, nor do they rule out that possibility.

We conclude that the regeneration process in 'undisturbed' red beech forest will generate a mosaic of various age structures, with a paucity of individuals in particular age categories in particular areas at particular times. Small canopy gaps are an essential feature of this regeneration system, and will be temporary at anyone location. The larger gaps in the forests of Mount Colenso will, however, remain a feature of these forests for several generations, although our analyses of the present recruitment and mortality rates indicate a gradual increase in the numbers of red beech, suggesting that the gaps will eventually be healed. Our earlier conclusion (June and Ogden, 1975) that the seedling population size will be maintained at or above its present level in future is pertinent here.

In a wider context we speculate that the openness of red beech forest may render it relatively susceptible to invasion by other species, which, by closing the gaps, may eventually oust the former dominant. In times of changing climate and forest tree population migrations, such as have occurred during the Holocene period, an alternative strategy would have clear advantages for such a vulnerable species. Periodic massive production of small seeds, and the high light requirements of its seedlings, pre-adapt red beech for migration to new open areas. Establishment and survival on moist, bare mineral soil in such areas is almost as good as on rotting logs, and the growth rates of the young trees may be higher (Franklin, 1965). Relatively even-aged pioneer populations have jog-normal size-frequency distributions indicating that self-thinning processes occur in them over a long time scale. In contrast, in undisturbed multi-aged populations where individual replacement is operating the self-thinning (selective) process becomes restricted to very localised seedling and sapling patches. As, in the absence of further disturbance, the former type of forest will gradually change into the latter, so also will it

gradually become more susceptible to invasion by competitors.

ACKNOWLEDGMENTS

We would like to thank Christopher June, the technical staff of the Botany and Zoology Department, Massey University and the New Zealand Forest Service for their assistance.

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