STUDIES ON THE VEGETATION OF MOUNT COLENSO NEW ZEALAND

2. THE POPULATION DYNAMICS OF RED BEECH

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SUMMARY: The population structure of red beech (*Nothofagus fusca*) is described for four forest stands situated at different altitudes on Mount Colenso. Data on red beech seedling densities and frequency distributions of living and dead tree diameters (d.b.h.) are presented. Red beech seedlings are shown to be more numerous, and on average larger, on decaying red beech logs than elsewhere. This seedling site preference could lead to a 'regeneration cycle', and explain the 'regeneration gaps' and bimodal d.b.h. frequency distributions commonly found in red beech forest in the Ruahine ranges. A comparison of the population structure in the four stands suggests that the red beech population may be undergoing a slow downhill migration. However, the apparent scarcity of saplings at higher altitudes does not necessarily imply a declining population in that area; it may be due to the long-term cyclic nature of population replacement following a catastrophe. Past browsing by deer and periodic mast production are thought to have had little effect on the population structure of red beech trees on Mount Colenso.

INTRODUCTION

Mount Colenso is situated on the western side of the Ruahine mountain range about 15 miles east of Taihape. The forest vegetation of the western side of the mountain was described in the first paper in this series (Ogden 1971). Red beech (*Nothofagus fusca*) is the dominant canopy species between c. 2,300 and 3,700 ft. a.s.l. Above the red beech forest there is *Libocedrus bidwillii/Dacrydium biforme* forest with *N. solandri* var. *cliffortioides* occupying the ecotone. At its lower limit, on the terraces of the Kawhatau river, the red beech forest merges gradually into a more diverse type which contains *Podocarpus ferrugineus* and *Dacrydium cupressinum*. The forest vegetation as a whole forms a continuum of changing composition with altitude.

Holloway's controversial hypothesis of recent (1200 ± 200 A.D.) climatic deterioration in New Zealand (Holloway 1954) is based to a large extent on population data for several of the dominant forest trees of the South Island. Gradual replacement of podocarp dominated forest (*Podocarpus* and *Dacrydium* spp.) by beech (*Nothofagus* spp.) is inferred from comparisons of the relative proportions of dead stumps, overmature trees, poles, saplings and seedlings of these species. The tacit assumption made is that it is possible

— within reasonable limits — to tell the relative ages of individuals of these species simply by looking at them, i.e. from trunk diameter, amount of dead wood and other features. If this assumption is admitted then a description of the relative numbers of individuals of different sizes provides a rough indication of the age structure of the population. Age structure has long been used by animal ecologists for assessing whether or not a given population is stable, declining or increasing, but plant ecologists have been slow to employ the method — except in this simplified intuitive form.

Although much of the evidence for climatic change comes from other species of *Nothofagus* (*N. solandri* var. *cliffortioides* and *N. menziesii* in particular), Holloway remarks that "the distributional peculiarities of red beech in the forests of the far south, and its behaviour in the southernmost red beech dominant stands, are explicable only in terms of regional climatic deterioration unfavourable to this species". Elder (1963), discussing evidence for recent climatic change in the forests of the North Island, states that "Red beech shows a tendency to retreat in the Ruahine range mid-altitude forest which would match a retreating timberline". Although he admits that the pattern is not clear, he observes that "the most definite

evidence of a change in conditions affecting red beech comes from the inland Patea area". This area is immediately north of Mount Colenso. In the Tararua mountains "the upper limit of red beech is usually marked by a preponderance of old trees and a scarcity of regeneration, indicating that in the recent past the climate at these altitudes has become unfavourable for red beech" (Franklin 1967).

Thus, comments by several forest ecologists suggest that red beech populations in New Zealand may be declining or undergoing a downward altitudinal migration. Elder (*pers. comm.*) has observed red beech apparently invading lower altitude communities (e.g. podocarp forests) and considers this phenomenon to be especially common near the limits of its present distribution in the Ruahines. His observations parallel those of Holloway for other species of beech in the South Island. If altitudinal migration is indeed occurring, this should be reflected in a shift in population age structure with altitude. This paper describes an attempt to demonstrate such a shift in the red beech forest of Mount Colenso, and to explain the mechanisms of individual replacement, or population maintenance, in stands situated at different altitudes.

METHODS

The fieldwork was carried out from the Kawhatau base hut of the New Zealand Forest Service (2,169 ft. a.s.l.) during February 1969 and 1970. The methods employed in 1969 have already been described (Ogden 1971). Circumferences of red beech trees were measured during plotless sampling of three one-hectare stands situated at 2,100 ft. a.s.l. (stand 1), 2,750 ft. a.s.l. (stand 2) and 3,250 ft. a.s.l. (stand 3). In 1970, comparable information was obtained from a fourth stand situated at 3,650 ft. a.s.l. (stand 4). Also in 1970, several quadrats were marked out in each stand; all red beech trees, fallen logs and stumps greater than 6 in. (15 cm.) circumference (1.9 in. or 5 cm. d.b.h.) in these quadrats were measured. This procedure provided an unbiased sample of red beech trees and was continued until about 70 live trees had been measured in each stand. A note was made of the proximity of each live tree to the nearest dead tree.

In 1969, seedlings of all species in all stands were counted on a regular grid of four square

metre quadrats. In 1970, a more detailed study of the distribution, densities and heights of red beech seedlings was made in relation to ground cover. For this purpose, three classes of ground cover were recognised:

(i) *"Logs"* — red beech logs and stumps in various stages of decay;

(ii) *"Bare areas"* — leaf litter or moss covering ground surface with no low herbaceous cover; and

(iii) *"Fern"* — dense ground cover of any type, usually *Polystichum vestitum, Dicksonia lanata,* or *Histiopteris incisa.*

An estimate of the relative amount of each type of ground cover was obtained by recording the type at every point on a regular grid of point locations. On each ground cover class except "logs", red beech seedlings were counted in 4 m² quadrats. This procedure was impractical on logs and stumps where a 2 m. long segment of trunk was used as the sampling unit. The average surface area of these was estimated at 3.6 m². Seedlings in each quadrat were classified according to height. In 1970 this type of sampling was carried out in all stands except stand 3 where only a visual inspection was made.

Two other investigations of seedling populations were made in an area between stands 3 and 4. In the first study, all beech seedlings growing on one large log were measured, and several of them were marked with metal tags for future measurement. In the second study, the heights of all red beech seedlings were recorded on a transect 1.8 m. wide; a note was also made of whether or not they were growing on logs. The transect was continued until 50 seedlings growing on logs had been measured.

RESULTS

1. Seedling regeneration

In 1969, seedling densities were estimated from quadrats placed without reference to the nature of the ground surface. In contrast, in 1970, densities were estimated on each of the four types of ground cover recognised. The relative amounts of the different types of ground cover are shown in Table 1, and the estimated seedling densities in Table 2.

Most red beech seed falls during March and April, and germination takes place between March and November (Kirkland 1961) or over a longer

period: Franklin (*pers. comm.*) records a peak of germination between October and December with some seed germinating 18 months after shedding. Consequently, the seedling population counted represents those which have survived from previous seed crops either as dormant seed or as seedlings. Seedling densities were greatest in stand 4 where the canopy is low and relatively open and the forest floor mossy and strewn with decaying logs. Stand 2, with the next greatest density, slopes steeply, so that the canopy tends to be open. Rotting logs occupy about 30% of the ground cover and *Dicksonia lanata* much of the remainder. Stands 1 and 3 have relatively low seedling densities and are characterised by being level with a dense understorey of *Pseudowintera colorata* and tangles of *Rubus*.

TABLE 1. *Relative proportions (%) of different types of ground surface cover in different stands*

Type of Ground Cover	Stand 1	Stand 2	Stand 3	Stand 4
(1) "Logs"	25	30	—	25
(2) "Bare"	55	20	—	45
(3) "Fern"	20	50	—	30

TABLE 2. *Estimated red beech seedling densities in different stands*

Type of Density Estimate	Stand 1	Stand 2	Stand 3	Stand 4
No. /ha. (1969)	2,000	23,000	5,000	—
No./ha. (1970)	2,000	24,000	—	103,000
No./m² (over whole stand)	0.2	2.3	0.5	—
No./m² ('present' quadrats only)	0.8	3.9	2.5	—
Relative density (i.e. as % total density of all spp.)	1.6	14.9	4.2	—
Frequency %	21	58	20	—

Seedling densities from 23,000/ha. (stand 2) to 103,000/ha. (stand 4) are not excessive for red beech forest. Kirkland (1961) recorded an average seedling density of 210,000/ha. during a mast year in North Westland. Survival of these seedlings over the first few months varied from 10 to 48%; in another study area, survival of seedlings over a three-year period ranged from 17 to 55% and seedlings survived better under deep shade than in the open. In all four stands the seedling population appears to be quite adequate for red beech regeneration. For example, if the present seedling

population was to completely replace the mature tree population in each stand, less than 1% of the seedlings would be required to survive to maturity in stand 4, and less than 5% in stand 1. Stands 2 and 3 would fall between these values.

TABLE 3. *Estimated red beech seedling densities under different types of ground cover in Stand 4*

Type of Ground Cover	Average Seedling density/m²	No. of 4m² quadrats
(1) "Logs"	18	4
(1) "Bare"	12	7
("Bare" not close to "Logs")	6)	
("Bare" adjacent to "Logs")	19)	
(3) "Fern"	0.1	5

Seedlings were distributed unevenly and highest densities were found on and around fallen logs and decaying stumps. These observations are illustrated in Table 3. In addition, seedlings growing on and around logs tended to be larger than those elsewhere (Tables 4 and 5). Although these data refer only to stand 4, counts made in other stands gave similar results. In stand 1, beech logs were rare and seedlings were associated with logs of other species, or on bare ground beneath an open canopy.

TABLE 4. *Height frequency distributions (%) of red beech seedlings under different types of ground cover in Stand 4*

Type of Ground Cover	Height classes in cm. 0–15	16–30	31–45	46–60	Total number measured
(1) "Logs"	50	41	8	1	263
(2) "Bare" (Including bare areas adjacent to logs)	64	34	2	0	330

TABLE 5. *Association between red beech seedlings (of different height classes) and logs*

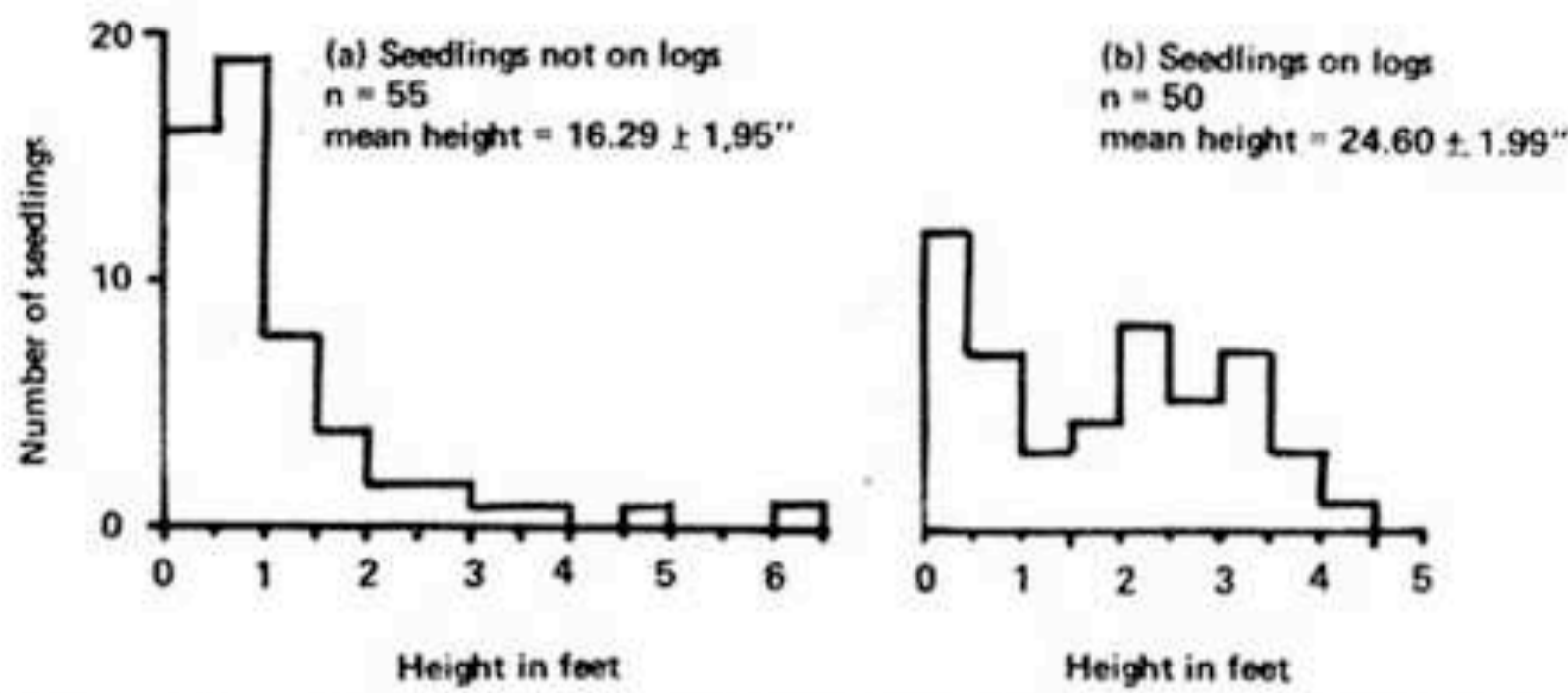| Height Classification	Number of Seedlings On logs	Not on logs	Chi square	'P'
greater than 15 cm	39	39		
equal or less than 15 cm	11	16	0.3697	>0.05
greater than 30 cm	31	20		
equal or less than 30 cm	19	35	5.9027	<0.05
greater than 60 cm	24	8		
equal or less than 60 cm	26	47	12.3005	<0.001

FIG. 1. *Frequency Distributions of Seedling Heights. Note: Comparison of means: d=2.97, P<0.01. For explanation of 'd' see Bailey, 1959.*

The association between logs and seedlings becomes progressively more significant as larger sized seedlings are counted (Table 5, Fig. 1). This suggests that either growth rates are faster on logs, or else the log allows for the continued survival and growth of a greater proportion of the periodic seedling crop.

2. *Association of mature trees with dead logs and stumps*

In stand 4, living trees are often growing on dead stumps or fallen logs. This is to be expected from the pattern of seedling regeneration. The result is a clumped distribution, with small groups of living trees, usually two to four, forming loose aggregates on old stumps. Frequently, the smallest member of such a clump is standing dead. The mean range in diameter of trees occurring together in such clumps is considerably less than the overall diameter range within the stand (9 in. compared to 32 in.). Table 6 shows that in stand 4 almost all living trees were more or less closely associated with dead tree stumps, while in stands 2 and 3 only about half the trees were thus associated. In stand 1 dead trees were absent.

3. *Frequency distribution of diameter classes of living and dead trees*

Stand 4, near the upper altitudinal limit of red beech, appears to have a fairly even-sized population of trees (Fig. 2). Living trees with a d.b.h. greater than two feet are uncommon, although dead logs and stumps more than twice this diameter may be found. At some time in the past the red beech population of this stand was composed of larger trees than it is now. In contrast, stands 2 and 3 have irregular or bimodal frequency
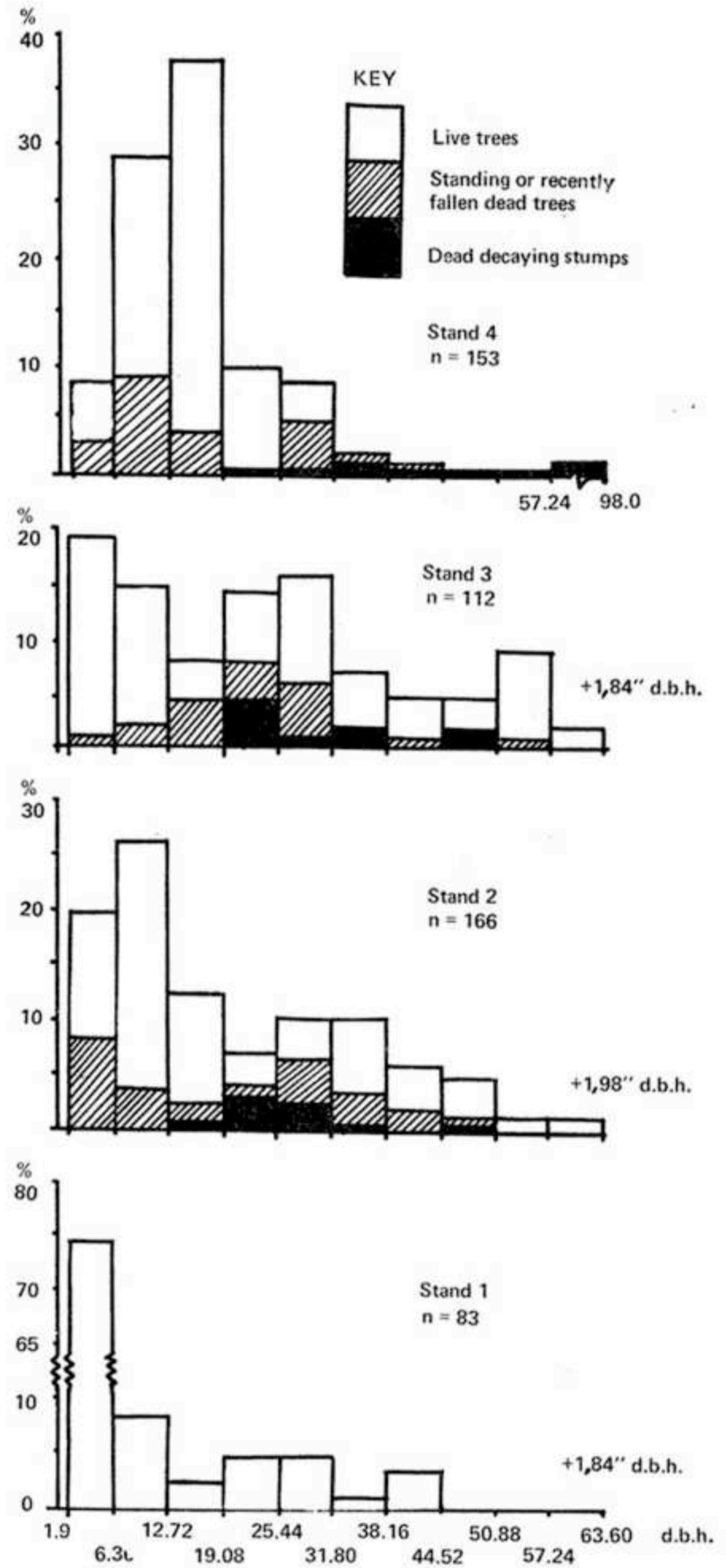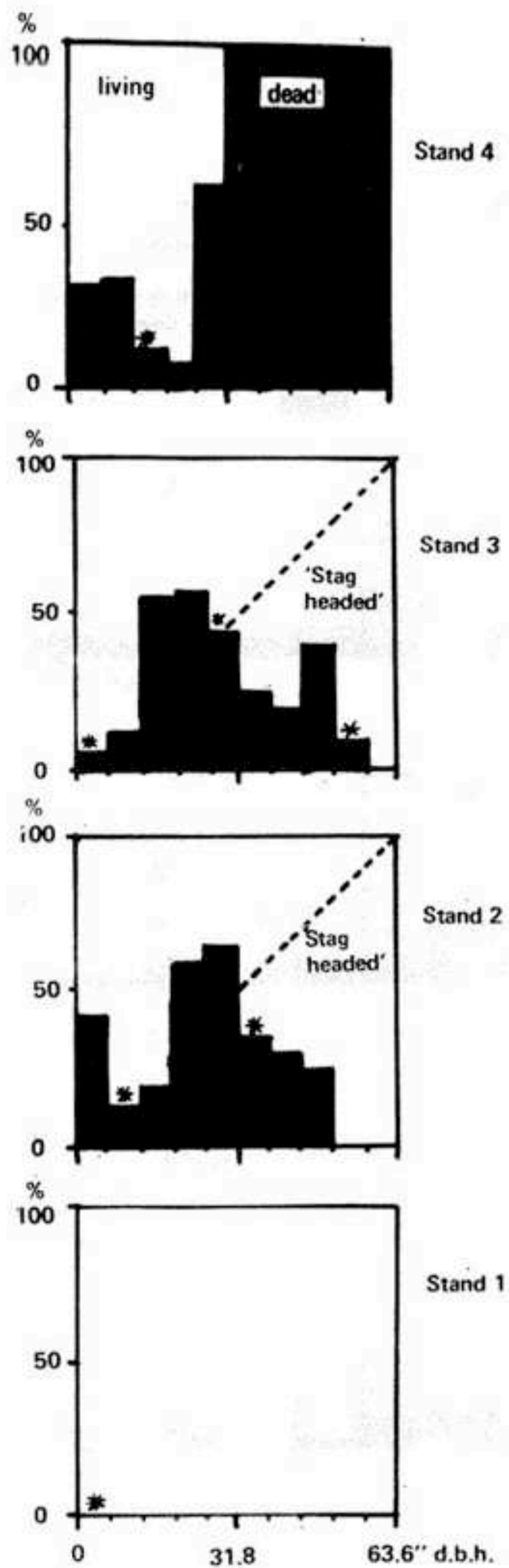

FIG. 2. *Frequency Distributions of Red Beech Diameters on Mount Colenso. Diameter classes are 6.36" intervals, equivalent to 20" circumference.*

distributions. In all stands the modal classes for dead trees immediately precede those for living trees, suggesting that dead trees are commonest in size classes just smaller than the modes (Fig. 3). In the low altitude stand 1, dead beech trees and stumps are absent, seedlings are relatively rare, and the population is composed mainly of young trees and saplings which are very patchily distributed. If the living tree data for all four stands are combined, the resulting frequency distribution (Fig. 4) suggests a stable population structure; despite local variations, there is no reason to believe that the red beech population in the area as a whole is undergoing any decline or expansion.
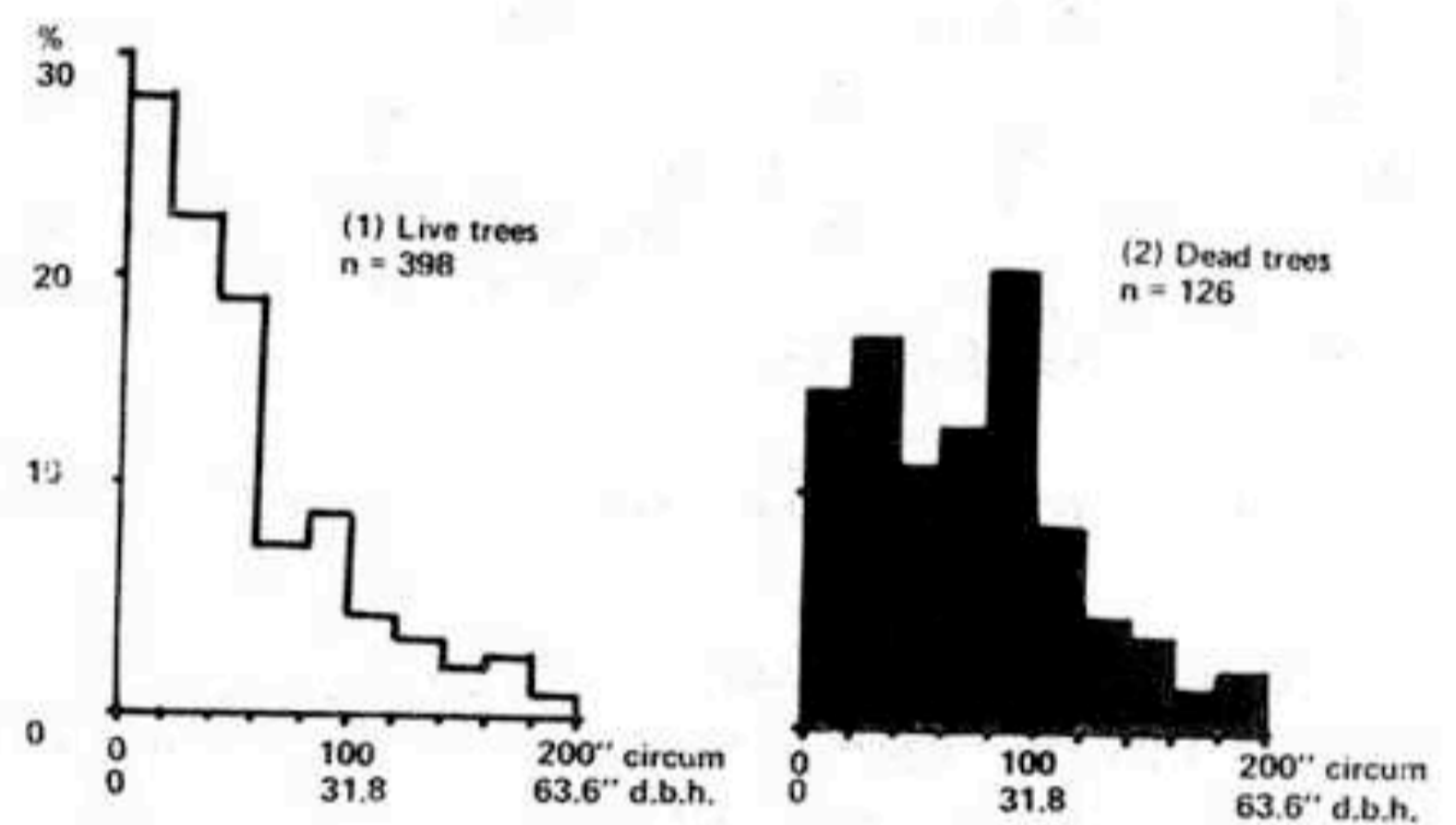

FIG. 4. *Frequency distributions of 'live' and 'dead' Red Beech in all stands on Mount Colenso.*

FIG. 3. *Relative proportions of 'live' and 'dead' trees in each diameter class on Mount Colenso. Shaded area represents proportion of dead trees in each size class.*
* Indicates modal classes of d.b.h. frequency (see Fig. 2).

TABLE 6. *Association between living and dead red beech in stands situated at different altitudes on Mt. Colenso*

Stand	Altitude (ft. above sea level)	(1) On	(2) Very close	(3) Close	(4) Associated	(5) Not associated
4	3650	35	49	7	91	9
3	3250	9	15	22	46	54
2	2750	5	19	24	48	52
1	2100		No dead stumps observed			100

Explanation of columns (1) to (5):
(1) Living tree growing on the dead stump or log.
(2) Living tree growing within an area described by the buttress roots of the dead stump.
(3) Living tree growing within an area of fallen beech logs, but not so close as (1) or (2).
(4) The sum of (1), (2) and (3).
(5) All other living beech trees.

DISCUSSION

1. The age/diameter relationship

In order to interpret d.b.h. frequency distributions in terms of the past history of a stand we must assume that stem diameters are reasonably reliable indicators of relative age. This assumption is probably justified for any one species in any one stand provided that size classes are not divided too finely and interpreted too closely (Daubenmire 1968). The age/diameter relationship is, however, sensitive to site conditions and it is not safe to assume that trees of one diameter in one stand are the same age as trees of the same diameter in another stand. Cameron (1959) obtained approximately linear relationships between age and diameter for several New Zealand forest trees, but the slopes of his regressions for any one species differed in different forest types. Wardle (1969, Fig. 32) illustrates the same situation for *Nothofagus solandri*. Franklin's (1965) data for red beech growing in an even-aged unthinned stand suggest a gradually declining growth rate after about 40 years. His data indicate that a tree of 10 in. d.b.h. is approximately 45 years old, while a tree of 15 in. d.b.h. is about 90 years. Other data given by Franklin for stands subjected to various thinning treatments all suggest that average growth rates are less than this. Franklin records the effects of dominance and suppression in red beech stands, stating that "while the trend is decreasing diameter growth with age, at any given time, with trees up to 6 in. d.b.h., larger trees grow at a faster rate than smaller ones". A few ring counts done by Elder (*pers. comm.*) in the Ruahines do not fit Franklin's curve — for example, the timbers of the Makaroro bridge, 30 in. diameter with only 120 rings, and a tree in the upper Makaroro, 28 in. d.b.h. with 220 rings.

In virgin forest, growth rates may vary widely even over quite small areas. The largest trees in a stand may not be the oldest — simply those which have had the most favourable growing conditions. Wherever there are groups of trees of the same species, intra-specific competition will cause skewing of the d.b.h. frequency without influencing the underlying age frequency distribution. Thus, the d.b.h. frequency distribution is the product of age, site factors, and competition, and must be interpreted with caution.

An investigation of the age/diameter relationship of red beech on Mount Colenso has been commenced, but as no ring counts are yet available, d.b.h. classes can be considered only as very approximate relative age classes of trees, in any one stand, and age comparisons between stands can be made only in general terms.

2. The regeneration cycle of red beech on Mount Colenso

Red beech seedlings are commoner on decaying red beech logs than elsewhere. Moreover, the seedlings on such logs tend to be larger than those growing elsewhere. As a small seedling group established on a mossy log gradually develops, the individual seedlings and young saplings must come into competition. Eighteen trees cannot stand on the square metre which supported 18 seedlings. The distribution of heights of seedlings in the group becomes skewed as a few larger individuals suppress the majority. Smaller seedlings die either through shading or root competition or some other cause. This 'elimination process' may be thought of as a selection pressure against the smallest members of a group, no matter how large they may be. Eventually the group becomes reduced to two or three large trees. If the population is composed of a series of such groups, all of which started growth at approximately the same time, distribution of sizes is likely to be approximately normal or, at least, monomodal. However, due to the continuously changing nature of inter- and intra-group relationships and densities, the 'elimination process' will be imperfect and a number of smaller trees will survive to skew the frequency distribution. In such a population, composed predominantly of small groups of roughly equal age, the death of the smallest member in a large number of groups may represent the removal of a large proportion of individuals from one size class. Depending on the class interval chosen, this class could be that immediately smaller than the living modal class. There must be a relationship between clump size and homogeneity on the one hand and the proportionate effect of removal of the smallest individual in the clump on the other. For example, if the individuals in a series of identical clumps of four trees are allocated by pairs to two adjacent classes, then removal of the smallest individual in each group represents a 50% reduction in the frequency of the smaller of the two classes. This process of 'clump thinning' seems likely to account for the position of the modal peaks for dead trees in all

stands (Fig. 2), and for the proportionate distribution of dead matter in different d.b.h. classes (Fig. 3). In general, in all stands, a large proportion of dead trees are found in d.b.h. classes just smaller than modal classes for living trees.

If the observed seedling preferences and the suggested competitive thinning processes are correct, it follows that one red beech tree is likely to grow where another has fallen. If many trees fall simultaneously, as seems to have been the case in stand 4, a population develops which has a relatively even age structure. Such a young vigorous population may inhibit further recruitment for many years creating a 'regeneration gap' in the age distribution of mature trees. Notwithstanding continuous mortality as a result of intragroup competition, it seems likely that mature individuals in such even-aged stands may begin to degenerate at more or less the same time. In this way, once a 'regeneration cycle' was started, it could perpetuate itself for a few generations. Thus, populations may occur which are composed of two, or possibly three, different generations with the relatively rare survivors from the older generation separated from the younger by a 'regeneration gap'. The distinctness of the different generations would be in part a function of the severity of the synchronising catastrophe, and in part a function of the time which had elapsed since its occurrence. Wardle (1969) has described in detail similar self-prepetuating 'regeneration cycles' in mountain beech (*N. solandri* var. *cliffortioides*) forests. This hypothesis could account for the origin of the live diameter frequency distribution, and explain the relationship between peaks for dead and living trees in stands 2 and 3.

Thus a single process could explain the d.b.h. frequency distributions observed in all stands. Moreover, it is possible that the present condition of the different stands is the result of a single catastrophe acting with different severity at different altitudes. At a date in the past, represented by a diameter range between 12 and 30 in. d.b.h., most of the larger trees in stand 4 died. The mossy decaying remains of these ancient giants are still strewn over the forest floor, and they form an ideal seed bed. The evidence suggests a severe storm which felled all the larger trees at least 100 years ago. The event would have been followed by regeneration, both from seedlings and saplings already present and later from seedlings growing on the fallen trunks and splintered stumps

themselves. Superficially even-aged red beech stands composed of 'released' trees (i.e. those present before the catastrophe) and 'post release' trees (i.e. those germinating after the catastrophe) have been demonstrated by Kirkland (1961). The regenerating red beech population in stand 4 must have been patchily distributed — higher density clumps being associated with fallen trunks and stumps. Thinning within these clumps would reduce their density by gradually eliminating the smaller trees. This would lead to a distribution of small groups, within which all individuals were of a similar diameter class (similar age). This is precisely the situation in stand 4 at present. Moreover, as tangible evidence of the continuance of competitive processes, the smallest member of a group is frequently standing, unbranched and dead. On average, in stand 4, the members of a group of three, four or more trees fall into only two diameter classes (Fig. 2).

A catastrophe sufficient to impose an even age structure in stand 4 would probably also have destroyed a large number of trees in stands 2 and 3. Growth rates are probably faster at lower altitudes, so that the second mode in stands 2 and 3 may correspond to the first mode in stand 4. The first mode in stands 2 and 3 would then represent the second generation following the catastrophe. That not all the original pre-catastrophe population in these stands was destroyed is suggested by the presence of large living (though usually overmature and "stag headed") trees; these form a third mode in stand 3. The suggestion of a single catastrophe occurring over 100 years ago, which was of greater severity at higher altitudes, must be regarded as speculative until ring counts are available, but the stump-clump regeneration pattern on which it is based is clearly demonstrable, at least in stand 4.

3. *Evidence for altitudinal migration of the red beech population*

One of the aims of this investigation was to gather data relevant to the question of altitudinal migration in red beech. Downhill movement has been suggested by several workers whose remarks are quoted in the introduction to this paper. The following discussion reviews certain aspects of the germination requirements of the species and relates these to its pioneering ability. The population structure of the species at high altitudes is compared with that at lower altitudes.

While the seedlings of red beech are shade *persistent*, they are not shade *tolerant* insofar as they are not likely to develop and become recruited to the mature tree population in shady situations. Also, young seedlings are particularly vulnerable to desiccation (Kirkland 1961). The light and moisture requirements of the seedlings thus provide an explanation of the 'regeneration cycle' by giving a greater chance of survival to those individuals which germinate on mossy logs in small canopy gaps. The same requirements apparently also give the species the ability to pioneer open areas on alluvial deposits on valley floors. Such riparian red beech stands are frequently even-aged. They are common in the Ruahines and Tararuas, and they are thought to originate from water-borne seeds (Preest 1963). According to Morris (1959), red beech forest reaches its maximum development on alluvial flats and low terraces where soil fertility and drainage are optimal. These sites contrast markedly with the steep skeletal soils, such as those of stand 2, in which red beech forest is most extensive (Franklin 1965).

Stand 1 is mixed podocarp-beech forest on a terrace some 200 ft. above the Kawhatau river. Its red beech population is unlikely to have originated from water-borne seed. However, its population structure, and the absence of any dead logs or stumps, strongly suggests a pioneer population. The saplings and young trees are concentrated towards the edge of the terrace where the land slopes steeply towards the Kawhatau, and the canopy is more open. In this area, red beech appears to be invading the mixed terrace forest, particularly along its steep margin, but the process is slow, being limited by the rarity of suitable sites for seedling establishment.

Thus, at the lower altitudinal limits of the species distribution on the Kawhatau terraces, dead logs are absent, and the living population is composed predominantly of young trees. In contrast, at 3,650 ft. (stand 4), near the upper altitudinal limits of the species, large dead logs are a conspicuous feature of the forest floor, and, although seedlings are abundant, saplings are extremely rare. Superficially then, the present appearance of the forest suggests a decline of population at high altitudes accompanied by invasion of the lower forest communities. The frequency distribution of d.b.h. in stand 4 cannot, however,

be considered good evidence of a retreat. It may simply indicate that insufficient time has elapsed since the destruction of the former giants for the new generation to have achieved the old size. A few standing dead trees in larger size classes (25–44 in., Fig. 2) are the only evidence suggesting that the dominant individuals in the present population have reached their maximum size. Absence of saplings is to be expected from what is understood of the dynamics of regrowth following catastrophe; it does not mean that the forest cannot replace itself.

However, several independent lines of evidence suggest that the timber-line in the Ruahines is descending. Elder (1965) cites several instances of buried timber above the present tree-line and mentions large old bushes of *Olearia colensoi* on Mount Colenso well above the present upper margin of the sub-alpine scrub.* In *Libocedrus/ Dacrydium* forest the conspicuous pattern of old trees with no replacement in sight is taken as further evidence of retreat (Elder 1963). On Mt. Colenso this forest occupies a narrow belt between 3,900 and 4,200 ft. a.s.l. Gnarled and thick boled old trees with only a few living branches remaining are characteristic of this region. Only lower on the mountain, in and adjacent to stand 4, were young conical trees found. Further evidence of timber-line retreat is given by Wardle (1969) who states "in the mid-Ruahine range the bush-line of mountain beech has apparently disintegrated recently . . .".

When the suggestions that mature red beech trees in stand 4 are no longer as large as they once were, and that invasion of non-riparian low altitude forest is ocurring in stand 1 are taken together with the evidence of tree-line retreat and the previously quoted comments of Holloway (1954), Elder (1963) and Franklin (1967), it seems safe to conclude that a slow downhill migration of the red beech population is in progress. Superimposed upon this movement on Mount Colenso may be regeneration cycles stemming from a relatively recent catastrophe. Even in the absence of such a catastrophe, population decline at high altitudes might be a slow process, because the dying trees provide favourable sites for their own replacement.

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* These are still present.

4. Seedling population and 'regeneration gaps'

Widdowson (1960) has described an age frequency graph for red beech in the north-eastern Ruahines which shows two 'regeneration gaps'. The elder of these gaps was dated between 1930 and 1940 and correlated with the maximum red deer population in the area. The second gap (1948–53) was also thought to be due to an increase in deer numbers. However, Holloway et al. (1963) report that, in the Tararuas, "sufficient seedlings or saplings (of red beech) escape or survive browsing for replacement of normal canopy losses". Several authors consider red beech to be relatively resistant to deer browsing (e.g. Wardle and Hayward 1970) although it is certainly eaten when deer are present in large numbers.

Judging from the growth rates of red beech given by Franklin (1965) and Elder (pers. comm.), heavy browsing between 1930 and 1940 could have produced a 'regeneration gap' which would be revealed now as a paucity of trees in the range 5–12 in. d.b.h. Figure 2 provides no evidence of such a gap on Mount Colenso. Even if the first 'low' on all the frequency histograms is to be ascribed to deer browsing, the second gap in stand 3 (38–51 in. d.b.h.) and the 19–25 in. gap in stand 2 must have originated before deer were present in any numbers (1930). Being situated near the timber-line, stand 4 is most likely to have received heavy use by deer. Today there are some signs of deer (e.g. browsed shoots of Griselinia littoralis), but red beech seedlings show no signs of damage. The rarity of saplings and poles in this stand is to be expected if the regeneration system described is correct. Moreover, with a cyclic regeneration pattern in which a substantial proportion of the population are of a similar age, recruitment to the mature tree population might take place only periodically with long intervals in which seedlings rarely became saplings or poles. Thus, even if severe depletion of the seedling population took place over several years it might have only slight influence on the pattern of recruitment. Wardle (1969) has pointed out that in even-aged stands of Nothofagus solandri an absence of seedlings does not necessarily indicate that the stands are deteriorating.

By precisely the same arguments, it can be concluded that heavy seeding (mast years), occurring on average every five years (Kirkland 1961),

will not produce corresponding d.b.h. frequency peaks in later years. Mast years are, however, an important part of the regeneration system; they probably provide most of the seedling population which then survives in various degrees of suppression for several years until it is replenished. In European Fagus sylvatica, a large proportion of the annual seed crop may be eaten by forest rodents, so that periodic heavy seeding offers obvious advantages, but the selective advantage of the habit in Nothofagus fusca in New Zealand is not so clear. If periods in which large-scale recruitment from seedlings to saplings and poles occurs are separated by many years in which competition and mortality preponderate, then mast years and seedling persistence are to be viewed not as periodic extravagances, but as a means of conserving seed while ensuring that a replacement population is always available. Mast years must also be of importance in the invasion of new areas forming an important part of the migratory equipment of the species.

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