"The Germination, Growth and Survival of Red Beech (Nothofagus fusca) Seedlings in relation to Forest Regeneration."

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ABSTRACT

The population structures of three stands of red beech forest in the N.W.Ruahine Range are described. Seedling establishment, growth and survival is studied by means of tagged seedlings in permanent plots. Three microsite types are identified, the rotting wood microsite being the most favourable for seedling growth and survival. No seedlings survive under the extensive fern layer. Light compensation points for 1st year seedlings are 1.9% and 3.9%. Light intensities in some microsites are below the compensation point. Seedlings have established at least every 2 - 3 years in the past and seedling establishment is not solely dependent on the occasional mast seed years. A model combining estimates of densities, survival rates and mortality rates predicts that the size of the seedling population will be maintained.

Regeneration appears to be effective only in the ridge-top stand. Large canopy gaps containing few saplings and seedlings occur in all stands. Seedling numbers are limited by the availability of suitable microsites and this in turn reduces the rate of regeneration.

CHAPTER I. INTRODUCTION

Nothofagus forest covers much of this country's mountainous land where it has an important protective function in stabilizing the soil and controlling flooding. It also forms part of the unique aesthetic and recreational appeal of the mountains. Deterioration in the condition of Nothofagus forest was noticed soon after the introduction of browsing mammals (Cockayne, 1926) and continues to give concern in many areas (N.Z.Forest Service, 1972). This deterioration is considered to be largely due to the removal of seedlings by browsing so that replacement of canopy gaps and colonization of slip-faces is retarded or prevented. Trampling by animals also damages the forest floor (McKelvey, 1959). An extensive campaign is being conducted to control the introduced animals, of which red deer and opossums are the most important. Studies of forest regeneration are necessary to assess the effects of animal control and other management programmes, and to predict future trends in the condition of the forests.

The aims of this study were (1) to quantitatively describe a red beech (Nothofagus fusca) population and (2) to determine the mechanisms of regeneration in this population. Regeneration refers to the replacement of the canopy trees by younger members of the same population. The state of regeneration is usually assessed by relating the frequency and size range of the immature individuals to the amount of canopy space being created by dying and senescent trees. Assumptions are made about the likelihood of the immature individuals present growing and surviving in sufficient numbers to fill the canopy gaps. Direct assessment of the state of regeneration requires a long period of observation and has seldom been done.

Emphasis was placed on the population dynamics of the seedling part of the red beech population. Seedlings represent the input of individuals necessary to maintain the population structure. Seedling success may be determined by competition with other plant species or with older members of the red beech population.

Of the possible environmental factors involved in this competition, light intensity was studied in detail. Attention was also given to the possibility of allelopathic interactions involving phenolic compounds.

From a knowledge of seedling dynamics obtained over a short period, and from a description of the present population structure, (including mature trees), it was hoped to obtain an overall view of red beech regeneration.

CHAPTER II. THE STUDY AREA

Mount Colenso is situated on the western edge of the Mokai Patea plateau in the north-western Ruahine Range. Three forest stands of one hectare each were studied. Details are given in Table 1. below.

Table 1.

Stand	Description	Aspect	Average slope	Altitudinal range (metres above sea level)
Upper	slope	W.S.W.	44°	1042 - 1112
Middle	broad ridge-top with some flat areas	S.	20°	1012 - 1046
Lower	slope	W.S.W.	42°	915 - 988

The stands are situated on a long ridge which rises from the Kawhatua River and runs in a northerly direction to the summit of Mt Colenso (1401 m. a.s.l.). Fig.1. shows the study area with the position of the stands.

The forest composition of this ridge has been described by Ogden(1971a). The study stands are located in the part of the altitudinal continuum where Nothofagus fusca is the sole canopy tree. Podocarpus hallii is an occasional sub-canopy tree. The most abundant shrub species are Griselinia littoralis and Pseudowintera colorata, with Fuchsia extortica also abundant in the Middle Stand. Shrubs are infrequent except in the large canopy gaps where they occur in thickets, often covered with Rubus cissoides. A dense fern cover occupies most of the ground layer, Polystichum vestitum, Histiopteris incisa and Dicksonia lanata being the main species.

Occasional seedlings or saplings of Libocedrus bidwilli, Phyllocladus alpinus and Nothofagus solandri are found in the Upper Stand. These three species are present as canopy trees above the zone of red beech forest. N.Solandri seedlings (about 20) were also found throughout the Middle Stand, and one was found in the Lower Stand. No mature N.solandri trees were found in the Middle or Lower Stands, the nearest known trees being approximately 600 m. distant to the north on an exposed ridge above the red beech forest, and also at about the same distance to the east.

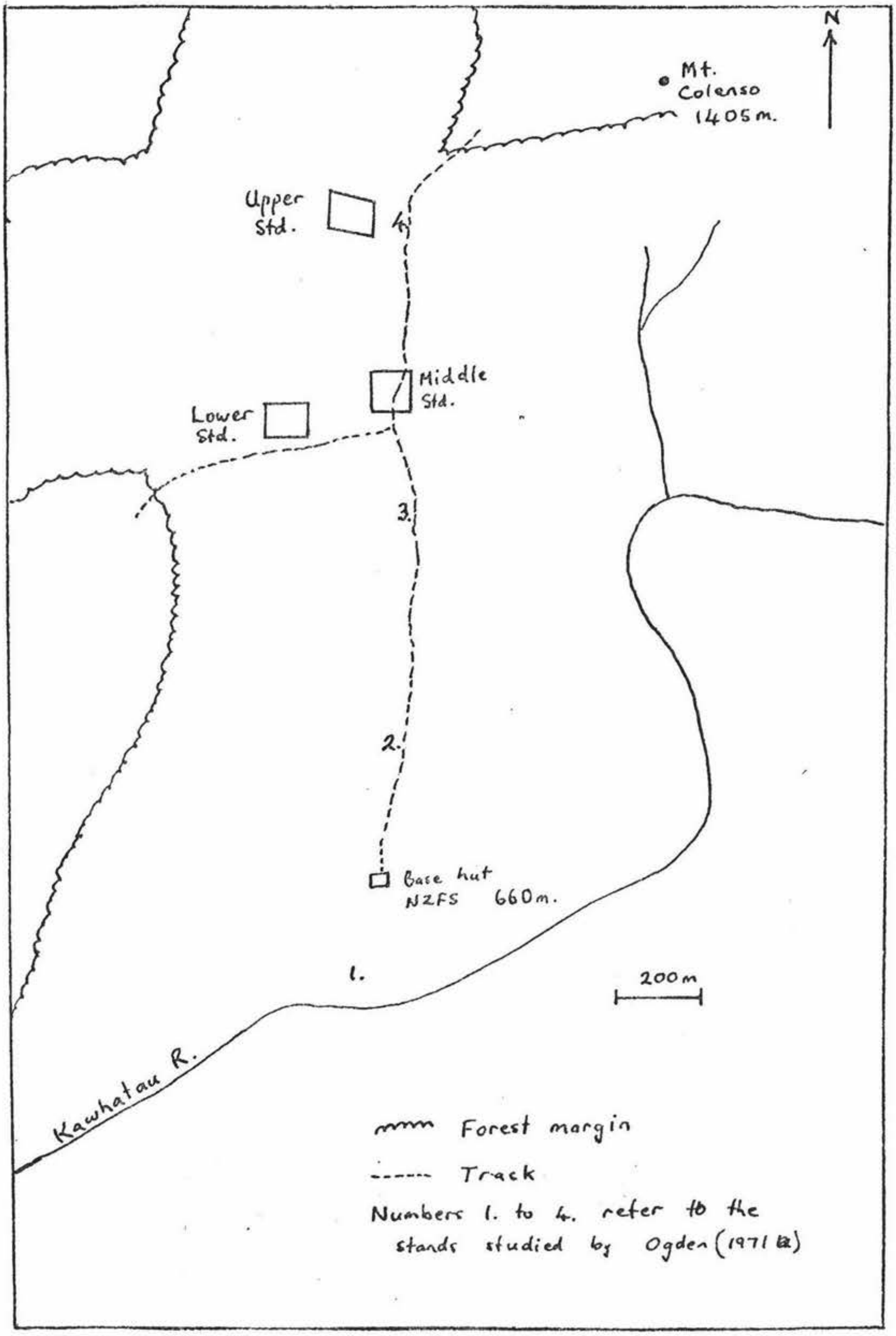


Fig 1. Sketch Map of Study Area.

The presence of seedlings and saplings of canopy species from a higher altitudinal zone in the red beech forest suggests a possible future change in the composition of this forest. Replacement of N.fusca by P.alpinus, L.bidwilli and N.solandri would be consistent with the downward migration of these species.

SOILS

The soil type for the area is the Ruahine Stony Silt Loam, derived from greywacke (Gibbs et.al., 1968). The soils were briefly described by Ogden (1971a).

CLIMATE

The climate of the region was described by Garnier (1958) as cool and superhumid. The prevailing wind is westerly. Rainfall is approx. 1524 mm (60 inches), (Maunder and Browne, 1972). A rain gauge at a farmhouse (2100 ft. a.s.l.) approx. 1500 m to the south-west of the study area gave an average rainfall of 1324 mm (52.11")for the years 1962 to 1972, with a range from 1011 mm to 1673 mm (A.C.Watkins, pers. comm.). Daily minimum temperature was also recorded by Mr Watkins for the same period. Mean monthly figures for rainfall and minimum temperature are given in Appendix. 1. There were an average of 8.2 snow-falls per year in the period 1962 to 1972. Snow fell throughout the year (except January and February) but was heaviest and most frequent between June and September. In a heavy snow-fall occuring on the 18 August 1972 branches were broken off canopy trees and saplings were pushed over and sometimes uprooted under the weight of snow.

HISTORY

The study area lies on the boundary between State Forest No. 75 and unoccupied Crown Land to the west. This Crown Land was formerly privately owned as part of Colenso Station. The study area has not been disturbed by fire, grazing or timber extraction (J.H.Dorrian, pers.comm). Private land to the west was milled and cleared for farming in the 1920's (A.C.Watkins, pers.comm).

INTRODUCED ANIMALS

Elder (1965) describes the spread of introduced animals and their effects on the vegetation in the Ruahine Range.

(i) Red Deer.

Red deer were liberated at Matapiro to the north-east of the Range in 1883 and spread southward along the Range. A liberation was made at Kawhatau (close to the study area) in 1908 and deer were first observed on Mokai Patea in 1910. To the north of Mt.Colenso there was a high population by the mid 1920's and the forest floor had been bared. A rapid southward shift occurred between 1933 and 1935, and was noted particularly at the head of the Waipawa River which is opposite Mt.Colenso. Widdowson (1960) records a population peak in the north-eastern part of the Range (between the Ngaruroro and Makaroro Rivers) in about 1930.
Kean and Newcombe (1937) travelled along the upper part of the Kawhatau River, the Waikamaka valley and part of Mokai Patea in 1937, and reported signs of heavy browsing by deer. N.sol.var cliffortiodes, Blechnum capense and Polystichum vestitum and a number of shrub species were being eaten or ring-barked. Damage was most evident on river flats, and also in hillside beech forest on the eastern edge of lower Mokai Patea. Shooting operations against deer were begun in 1938. By 1945 the deer population in the northern Ruahine Range had noticeably decreased and a general decline continued.
Since 1958 shooting has been concentrated in the most erosion-prone catchments. Vegetation recovery was evident in some areas by 1955. Deer were plentiful in the study area in 1966, but have become scarce since 1968 with increased hunting resulting from the shifting of the Forest Service base hut to the Kawhatau (J.H.Dorrian, pers.comm.) Private hunting for venison has also increased recently. During 1972 only occasional signs of deer were seen but there was some browsing of Griselinia littoralis. The historical record indicates an increase in the deer population in the study area from 1910, with a peak population being reached between the mid 1920's and 1945, most likely in the middle of this period. A decline in population associated with the removal of palatable plants followed. The population has been maintained at a low level since 1968 by intensive hunting.

(ii) Opossums.

Opossums appear to have become established in the Ruahine Range since the 1920's although their occupation of high altitude beech forest was not noted until later (1943 - 1955 in some parts of the Range). The population appeared to be high throughout the study area. Opossums are hunted for skins in some years. Evidence was found of opossum browsing of the N.fusca canopy. Twigs of yellow leaves were observed throughout the canopy in late April. By winter the leaves had turned brown, and the twigs were found to be ring-barked. Bark had been removed from twigs 1/16 to 1/2 inches in diameter, although there was usually bark left on one side of the stem. Similar damage has been described for N.fusca and N.solandri var cliffortiodes in the Ruahine Range and attributed to opossums (Grant, 1956).

(iii) Goats.

Goats were established on the main range, east of Mt. Colenso by 1954 (Elder, 1965). It is not recorded when they were first present in the vicinity of Mt. Colenso. The number of goats in the study area was reduced by shooting in 1965. They are now present in low numbers in the lower altitude beech-podocarp forest adjacent, and are occasionally seen in the study area (J.H.Dorrian, pers.comm.). No goats were observed in the study area in 1972.

(iv) Pigs.

Wild pigs were observed about the bush edge on the northern Mokai Patea by Newcombe and Kean (1937). None have been recorded in the study area.

Period of Study

65 days were spent on field work between December, 1971 and January, 1973. Observations were made at least once a month.

Chapter III THE SEEDLING POPULATION

Section 1 INTRODUCTION

The seedling is generally the most vulnerable stage in the life cycle of a forest tree with the exception of the seed. Seedling establishment is critical for the maintenance of the forest community, or in the colonization of an open area by forest. In this study emphasis has been placed on the seedling section of the population because of the importance of seedlings in population maintenance, and also because seedlings are more amenable to study than are mature trees.

A seedling is arbitrarily defined here as a plant up to 2m tall; this corresponds to a diameter at breast height (d.b.h.) of 1.8 to 2.5cm and an age of approximately 20 years. The N.Z.National Forest Survey definition is an individual above 15.2cms in height and up to 2.5cm d.b.h. (Masters et al, 1957). Individuals in the next size category are referred to as saplings.

Large numbers of red beech seedlings arising from the 1971 mast seed year were present in the study area in 1972. These are referred to as '1st year seedlings', and the remainder of the seedling population as 'established seedlings'.

The following questions were considered.

(1) How many seedlings are present?
(2) What is the rate of input from germinating seed?
(3) At what rate are seedlings dying?
(4) What are the growth rates of seedlings and at what rate are seedlings reaching the next size class?
(5) In what microsites do seedlings grow?
(6) What environmental factors are likely to control seedling growth and survival?
(7) What is the role of the seedling population in the mechanisms of regeneration?

The forest floor offers a variety of microsites for seedling establishment. Three main microsite types were identified:

(I) under a dense fern canopy.
(II) on bare ground.
(III) on rotting red beech wood.

Studies were made on the relative importance of each microsite to the seedling population and, by experimental modifications of the microsites, of the factors which affect seedling growth and survival. Light intensity, an important factor in the control of plant growth, was selected for detailed study. Measurements of the light intensities on the forest floor were made, a productivity experiment using potted seedlings in the forest was carried out and a controlled experiment involving different light intensity levels was performed under garden conditions. A preliminary study was made of the role of phenolic allelochemicals which may affect seedling growth.

The basic approach was to make monthly measurements of seedling numbers and size in quadrats placed in each microsite type. Seedlings were aged to determine the population age structure and also growth rates over a longer period than the one year of study. The seed input for 1972 was measured using seed trays.

Section 2 SEED PRODUCTION

Methods

Observations were made of flowers, cupules and seeds present on the ground and in the foliage from Dec. 1971 to Jan. 1973.

Two 10' x 6' sheets of plastic were laid down as seed traps in the Middle Stand. The litter was collected from 7 March to 16 May 1972 and examined for seeds.

Seeds were collected from the litter and moss layers on the forest floor in Dec.1971 and April 1972 and examined for embryos.

Results.

No flowers or seeds were seen on trees from Dec. 1971 until Dec. 1972 when a few flowers appeared. No seed was collected in the traps and no seeds containing embryos were found in the litter (106 were examined closely). The previous year (1971) had been a heavy mast year judging from the large numbers of newly germinated seedlings and empty seeds on the ground.

Discussion.

Following a heavy mast year, seedfall was negligable in 1972 and was likely to be so again in 1973. This confirms other observations of large fluctuations in Nothofagus seed production in successive years (Poole 1948, Wardle 1970a).

The history of seed production in the Ruahine Range is poorly recorded. A heavy mast year in 1936 for red beech throughout its range was reported by Poole (1948), and, in the vicinity of the study area, by Newcombe and Kean (1937). The next mast year recorded was in 1949 (Poole 1955, Greenwood 1951), followed by another in 1955 (Elder 1965). A Forest Service file (F.S. 28/1/3/2) indicates a good seed year for red beech in the eastern Ruahines in 1963 (J.L.Nicholls, pers. comm.). The heavy flowering preceeding the 1971 mast year was noticed on Mt.Colenso by A.C.Watkins (Pers.comm.) who had not seen such flowering since 1955. Elder (1965) mentions a four or five year interval between mast years in the Ruahine Range. From these records it appears that heavy seed production occurred in the study area in 1936, 1949, 1955 and 1971, and possibly in 1963. In the intervening years there were presumably some light seed falls and some years with no seed fall.

Section 3. GERMINATION: AN EXPERIMENTAL SOWING

As there was no seedfall in 1972, seeds obtained from elsewhere were sown by hand in a number of plots in order to determine the relationship between the number of seeds falling on the ground and the numbers germinating.

Methods.

Red beech seed collected in 1971 in Westland was obtained from the N.Z.Forest Service, Wellington. The seed was divided into 60 lots each weighing 2.80gm and containing 398.8 ± 6.3 seeds (mean with standard deviation). 20.6% of the seeds were viable (tetrazolium test) which gives 82 ± 1.4 viable seeds per lot.

One lot of seed was broadcast by hand over a 1m x 0.5m section of 60 of the permanent plots (see Section 5), including all microsite types and treatments. First year seedlings were removed from the oversown area unless already tagged. Sowing was done in late Feb. and early March 1972, which is just prior to the usual time of maximum seed fall (Wardle 1970a, Kirkland 1961). Plots were checked for newly germinated seedlings at monthly intervals and seedlings were tagged as they germinated.

Results.

Only 5 seeds germinated in Dec. 1972 and Jan. 1973 on log and bare microsites. Little further germination could be expected after January. (Section 5). Assuming that the 5 seedlings counted originated from the sown seed, they represent only 0.02% of the total number, or 0.06% of the viable seed.

Discussion.

The number of germinating seedlings is too small for analysis. The germination % is low compared with other studies; for example, Kirkland (1961) found a 0.3 to 4.6% germination for red beech, and 0.0 to 18.3% for hard beech on litter in north Westland. Franklin (1971) records a germination of 0.0 to 38.8% for silver beech in Southland.

An average seed fall of 4922 sound seed per m^2 was recorded for a mast year in N.solandri in the Kaweka Ra. Wardle (1970a).

The germination of 0.06% would therefore produce 3 seedlings /m^2 in a comparable seed year. However much higher seedling densities were recorded, (see Section 5), with a maximum of 236 seedlings /m^2. Therefore, the 1971 seed fall must have been remarkably heavy (in the order of 100,000 sound seed per m^2) or the germination % higher (about 2.0%). The latter is more likely.

Section 4. SEEDLING MICROSITES.

Three main types of microsite were recognised; 'fern', 'log' and 'bare'. These were distinguished as follows:-

(a) Fern microsite: a complete ground layer of fern fronds of *Polystichum vestitum*, *Dicksonia lanata* or *Histiopteris incisa*.

(b) Bare microsite: ground surface covered with litter or moss, or with bare mineral soil; occasional small ferns, herbs or woody seedlings (e.g. *Griselinia littoralis*, *Coprosma* spp, *Rubus cissoides*.) present in the ground layer.

(c) Log microsite: surface of fallen red beech logs; covered with a dense moss layer, herbs, woody seedlings or ferns, or a bare wood surface. The most common moss species are *Rhizogonium minioides* (Hook.) Schimp., *Hypnum cupressiforme* Hedw., *Dicranoloma grossialare* (C.M.) Dixon, *Ptychomnion aciculare* (Brid.) Mitt. and *Acrocladium auriculatum* (Mont.) Mitt.

A fourth microsite type includes rotting red beech stumps and branches and rotting wood adjacent to stumps. Areas of this microsite, although favourable sites for red beech seedlings, were not sufficiently extensive for the establishment of plots.

All microsites exist under a variety of canopy conditions which range from open canopy gaps to dense shrub and tree layers.

Experimental modification of microsites.

Microsites were altered in order to study the factors affecting seedling survival and germination. Root competition from trees and shrubs in bare microsites was removed by cutting the roots leading into a plot (trenching).

Competition from shrubs and other cover in log and bare microsites was removed by cutting off these plants. The different components likely to be effective in competition from the fern layer were distinguished by the removal of the fronds, litter or roots and rhizomes of the ferns present.

Methods.

(1) Bare microsite: trenching.

A 25cm deep trench was dug around the plot, cutting off all roots leading into the plot. The trench was refilled with soil. It was redug in Oct. 1972.

(ii) Bare microsite: Pseudowintera removal.

Plots with a complete cover of Pseudowintera colorata were cleared by removing the shrubs at ground level.

(iii)Log microsite: removal of cover.

All the ferns, shrubs and seedlings (except red beech seedlings) were removed from 1 x 1m plots (N.B.all other plots 2 x 1m or 4 x 0.5 m.)

(iv) Fern microsite: frond removal.

All live fronds were cut at ground level and removed.

(v) Fern microsite: litter removal.

All loose surface litter and dead fronds were removed by hand. This destroyed any red beech seedlings present. Litter was removed throughout the year as necessary.

(vi) Fern microsite: rhizome removal.

The rhizomes and mat of fern and tree roots were dug out and discarded. This left bare mineral soil which was then firmed by foot.

Results.

Results for seedling survival are included in Section 5. Treatments (v) and (vi) were done in anticipation of a seed fall and for the experimental sowing (Section 3.)

Microsite Frequencies.

Methods.

The microsite type was identified at a number of regularly spaced points.

Four transects, 25m apart, were used in each stand. There were 99 points along each transect, 33 of them on the line of the transect and 3m apart and the remainder 3m on either side of these points. This gives 396 points per stand. At each point a rod was held vertically from the ground and the type of microsite assessed. The presence of shrub or red beech canopy directly above each point was determined by standing at the point and looking directly upwards. This method gives only an approximate and subjective measure of the extent of large gaps in the canopy.

Microsite descriptions have been given previously. Rotting wood apart from logs was also recognised. The following additional details were recorded:

Fern microsite:	predominant species
Bare microsite:	Presence of moss, litter or bare mineral soil; presence of overhanging shrub canopy.
Log microsite:	presence of fern, herbaceous or woody cover growing on the log; presence of moss, litter or bare wood.

Results and Discussion.

Microsite frequencies are given in Table 2.

The fern microsite is the most common, especially in the Lower Stand where the high frequency of fern is complimented by a low frequency of the bare microsite. There is a significant proportion of the rotting wood microsite in all stands.

Further details of the microsites are given in Tables 3, 4 and 5. A large proportion of the log and bare microsites have some cover (shrub or fern) which is likely to inhibit seedling growth. The mossy ground layer, which is very favourable for seedling survival (see Section 5), is infrequent in the bare microsite but common in the log microsite. The Upper Stand is more likely to be favourable for seedlings than the other stands because there is more moss and less cover in both log and bare microsites.

The widespread occurence of Dicksonia lanata which is unpalatable to deer and opossums (Elder, 1965) may be a result of this fern spreading following browsing of competing ground layer species. Blechnum discolor is also browse resistant. Polystichum vestitum is eaten under intense browsing pressure by deer (Kean and Newcombe, 1937; Wardle, 1961) but is relatively common.

Results for tree canopy cover are given in Chapter IV.

Soil Properties of log and bare microsites.

There are likely to be many differences between the log and bare microsites in soil properties. The bare microsite has a normal soil, with a litter layer (0 to several cms deep), a thin humus layer containing tree roots, and a deep mineral soil (a stony silt loam). The log microsite usually has a litter or moss layer overlying a layer of rotten wood. Below this layer of soft rotten wood (which may be less than 1 cm thick) the wood may be sound and inpenetrable to roots. In this case the seedling roots run along near the surface of the log and reach the ground where possible. Sometimes the log may be soft and well decayed to its centre.

Table 2. % frequencies of the main microsite types, for each stand.

	Upper Stand	Middle Stand	Lower Stand	Average
Rotting wood:				
- log	11.2	12.8	8.1	10.8
- other	9.9	7.3	7.6	8.3
- total	21.1	20.1	15.7	19.1
Bare	21.8	27.6	5.3	18.4
Fern	57.1	52.3	79.0	62.5

Table 3. Bare microsite, % frequencies of cover types.

	Upper Stand	Middle Stand	Lower Stand	Average
Overhanging shrub cover	23.3	82.7	71.4	58.1
Ground surface:				
litter	82.6	93.6	100.0	89.9
bare mineral soil	5.8	4.6	0.0	4.6
moss	11.6	1.8	0.0	5.5

Table 4. Log microsite, % frequencies of cover types.

	Upper Stand	Middle Stand	Lower Stand	Average
Overhanging cover	38.6	72.5	69.4	59.1
Ground surface:				
litter	31.3	50.0	45.2	41.8
bare wood	16.9	20.0	16.1	17.8
moss	51.8	30.0	38.7	40.4

Table 5. Fern microsite, Species composition (% frequencies).

	Upper Std	Middle Std	Lower Std
Dicksonia lanata	70.5	59.1	97.1
Polystichum vestitum	21.0	26.0	2.9
Histiopteris incisa	6.3	10.1	0.0
Blechnum discolor	2.2	1.1	0.0
Cyathea smithii	0.0	3.9	0.0

Colonization of logs by red beech seedlings after they have fallen to the forest floor can be rapid. Some of the logs felled during selective milling in an area below the Lower Stand had seedlings up to 1.5 m tall growing on them in 1973, 20 years after felling.

The mineral content and pH of samples of mineral soil (bare microsite) and decomposed wood (log microsite) were tested (Table 6).

Table 6. Soil test results for mineral soil and decomposed wood.

	Mineral soil	Wood
pH	5.25 ± 0.5	4.25 ± 0.2
Minerals (ppm)*		
Ca	3	5
K	7	8
P (Truog)	1	3
Mg	17	27

* Soil test by Ministry of Agriculture and Fisheries for pooled samples collected in Middle Stand.

The log microsite would appear to be a more fertile medium for plant growth.

The mineral soil and rotten wood also probably differ in their water retention capacity and in other physical properties. Other chemical differences are discussed in Section 9.

Section 5. SEEDLING NUMBERS.

Establishment of permanent plots

A number of permanently-marked plots were used to follow trends in seedling densities and growth.

Plots were established in each stand in Jan. and Feb. 1972 and visited monthly until Jan. 1973. The plot dimensions were 2 x 1 m, or 4 x 0.5 m when located on fallen logs.

Quarter or smaller sections of the plot were used for some measurements; in one section all seedlings were counted. Plot corners were marked with wire or aluminium pegs, or 6 inch nails in the case of logs. The plot boundaries were located by placing a 2 m pole between corners.

Plots were situated along 100 m transects running parallel and 25 m apart. There were four transects in each stand. Plots were positioned at random along the transects. A limited number of suitable log and bare sites were available; these were located, then the required number of plots allocated at random. Treatments were also allocated randomly once the plots were chosen. Plots were chosen without reference to the overhanging canopy so that for any plot, a shrub or tree layer may or may not be present.

Details of the plots are given in Tables 7 and 8. Log microsite plots were located on recognisable rotting logs at least 0.5 m in diameter and 4 m long. Recently fallen logs with an undecomposed wood surface were not chosen. There were either one or two replications of each plot type per transect, giving 4 or 8 replications per stand. For modification treatments additional unmodified plots were established as controls in some cases.

Table 7 Numbers of permanent plots

	Unmodified plots			Modified plots
	Microsite type			
	Log	Bare	Fern	
Upper Std	9	8	8	4
Middle Std	6	6	4	6
Lower Std	4	4	4	12
	19	18	16	22

Total = 75

Table 8 Details of modified permanent plots (showing numbers of plots).

Upper Std	trenching	4
Middle Std	*Pseudowintera* removal	4
	removal of cover (log)	2
Lower Std	frond removal	4
	litter removal	4
	rhizome removal	4

Tagging of seedlings.

First year seedlings were tagged with 6 inch long sections of galvanised wire which were looped around the stem of the seedling and stuck in the ground with one end protruding. Thus tags could be located by touch as well as sight. Individual seedlings were not recorded separately.

Established seedlings were tagged by means of a numbered square of aluminium attached by wire to the stem.

Monthly Measurements.

(a) First year seedlings.

All tagged seedlings within a marked section of a plot were located and counted. This section ranged from 1 m x 0.5 m (0.5 m^2) to 0.25 x 0.25 m (0.063 m^2) in size. Newly germinated seedlings could be identified as untagged individuals and from appearance. Additional seedlings outside these sections were counted in some plots.

(b) Established seedlings.

The heights of tagged seedlings to be nearest 0.5 cm were measured.

For all seedlings observations were made on insect predators, browsing damage, possible causes of death and of phenological events such as bud break and growth flush.

Seedling Densities.

Methods.

(i) First-year seedlings.

Data are from the counted sections of permanent plots as described above.

(ii) Established seedlings.

A stratified-random sampling method with 1 m^2 quadrats was used to estimate stand densities. Sampling was done along transects parallel to the edge of each stand. A random point was chosen along each 14 m section of the quadrat and the nearest available 1 m^2 quadrat of each microsite type (log, bare and fern) located and counted. Quadrat shape was either 1 x 1 m or 2 x 0.5 m, quadrat size being limited by the availability of sufficiently large areas of the log and bare microsites. Care was taken to find any logs obscured by vegetation. Five transects per stand were sampled. Seven 14 m sections per transect were taken giving a total of 21 samples per transect. Altogether there were 107 samples for each of the three microsite types.

Additional data were obtained from the permanent plots.

Results.

(i) First-year seedlings.

Densities are presented in Tables 9 and 10 and the raw data in Appendix Table 2. Additional plot data were incorporated in the Feb. 1972 estimate (Table 10). Densities at the probable time of germination (Nov.1971) were obtained by extrapolation of the survivorship curves back to this date (Fig 2). These density estimates, together with microsite frequencies (Section 4) were used to obtain the total number of seedlings in each stand (Table 11). Mean seedling densities (no. of seedlings per m^2) for each microsite were multiplied by the area in each hectare estimated to be covered by that microsite. The proportions of the total seedling numbers found in each microsite are given in Table 12, and for mossy and non-mossy surfaces in Table 13.

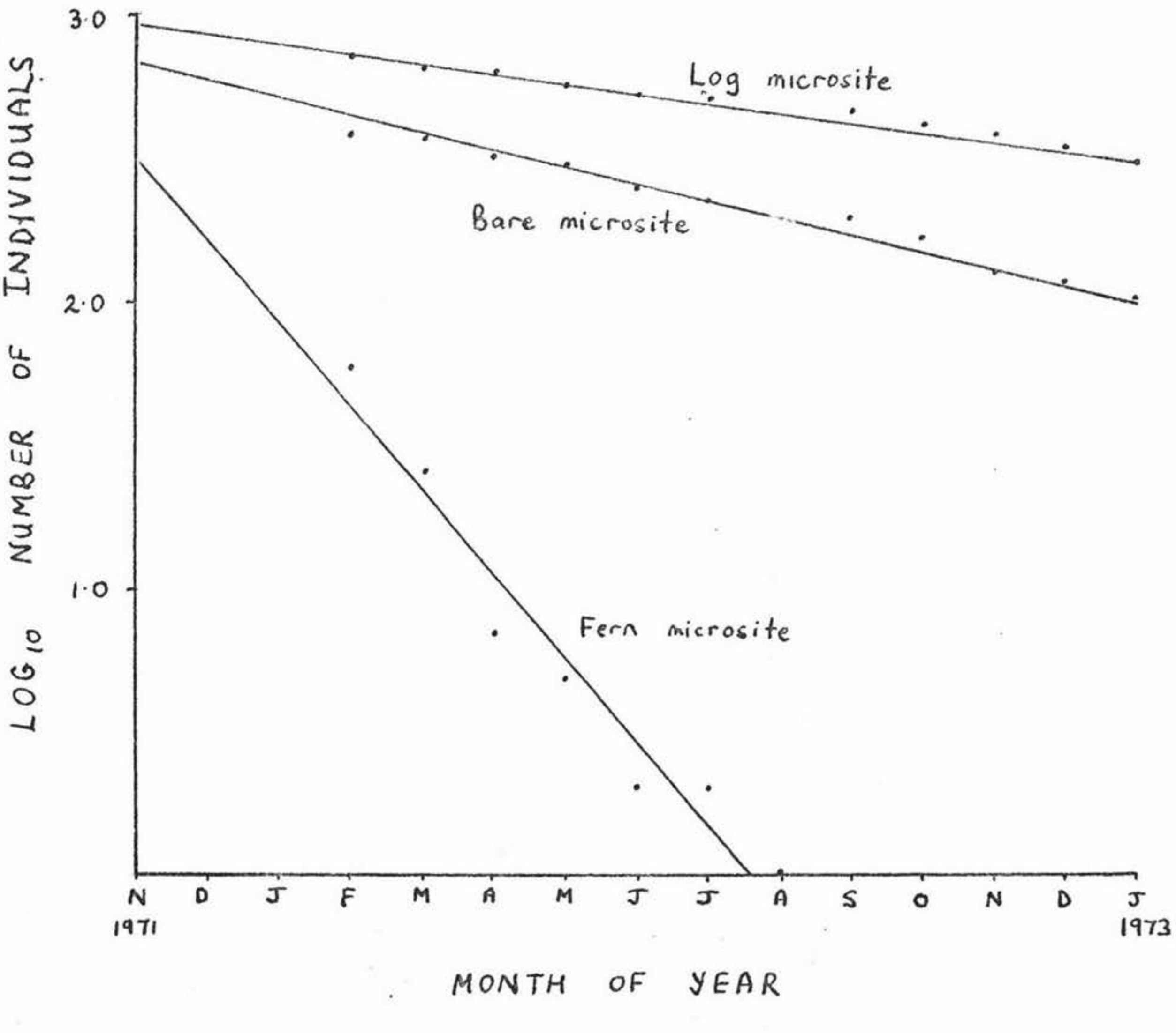


FIG. 2 Survivorship of first-year seedlings.

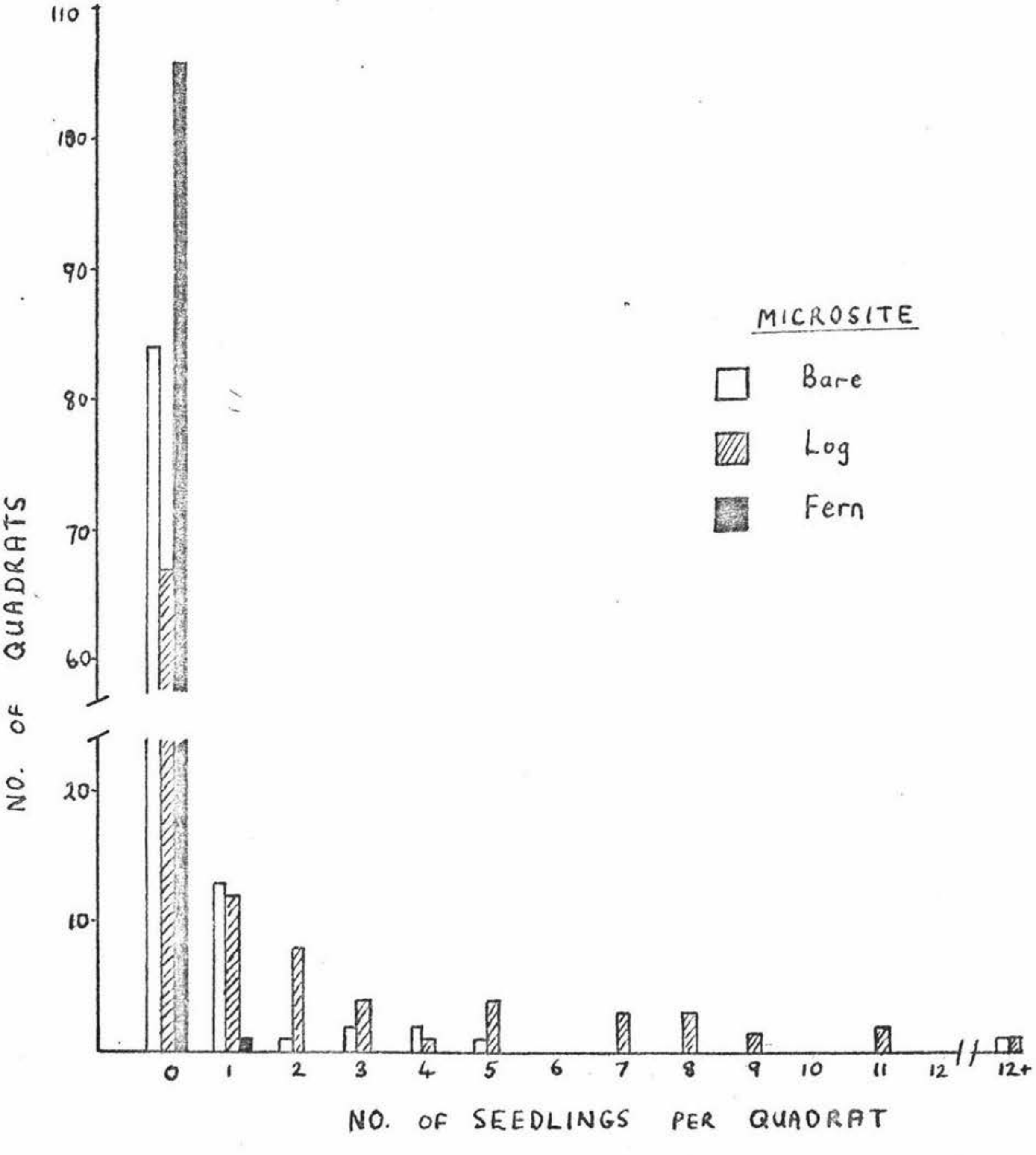


FIG. 3 Frequency distribution of established seedlings in random quadrats.

Highest densities are found in the log microsite and the lowest in the fern microsite. The Upper Stand has the highest densities for both the log and bare microsites, and the Lower Stand the highest for the fern microsite. One year after germination and following the disappearance of all seedlings in the fern microsite the greatest proportion (85%) of the seedlings occur in the log microsite. Total seedlings numbers vary considerably between the stands and are greatest in the Upper Stand.

(ii) Established seedlings.

Seedling densities for each microsite and in each Stand were obtained from random sampling (Table 14), and from permanent plots (Table 15). Higher densities were obtained from permanent plots (Table 15) which probably reflects a bias in the location of the plots.

The frequency distribution of seedling numbers per quadrant for the random sampling is given in Fig. 3 using combined data for the three Stands. For both log and bare microsites the departure from a Poisson distribution is significant (Chi - squared P0.01), the departure from randomness being greater for the log microsite.

The mean seedling density is highest in the log microsite and very low in the fern. The Middle Stand has the highest densities for all microsites, and the Lower Stand the lowest.

Table 9 Densities of 1st year seedlings (no. of seedlings per m^2).

	Initial (Feb.1972)	Final (Jan. 1973)	No. of 0.5 m^2 plots sampled.
Log microsite			
Upper Std	89.3	50.9	9
Middle "	50.4	17.2	5
Lower "	62.0	36.0	5
mean	70.2	38.1	

Table 9 cont.

Bare microsite			
Upper Std	53.0	12.3	8
Middle "	16.0	1.3	6
Lower "	31.7	10.0	7
mean	38.1	8.4	
Fern microsite			
Upper Std	3.4	0.0	10
Middle "	5.5	0.0	4
Lower "	16.5	0.0	4
mean	6.7	0.0	

Table 10. Densities of 1st-year seedlings at Feb. 1972 (with additional data) and at probable time of germination (Nov. 1971).

Log microsite	Density at Feb. 1972 (No. per m^2)	No. of $0.5m^2$ plots sampled.	Estimated Density at germination (average only).
Upper Std.	82.8	12	
Middle Std	55.4	10	
Lower "	67.8	9	
			85.1
Bare microsite			
Upper Std.	35.6	16	
Middle "	9.7	12	
Lower "	23.6	11	
			46.9
Fern microsite			
Upper Std.	2.4	14	
Middle "	3.0	8	
Lower "	17.1	19	
			36.8

Table 11. Total numbers of 1st-year seedlings per hectare

	Microsite			Total
	Log	Bare	Fern	
Nov. 1971				
mean	162,500	86,300	230,000	478,800
Feb. 1972 *				
Upper Std.	174,700	77,600	13,700	266,000
Middle "	111,400	26,800	15,700	153,900
Lower "	106,400	12,500	135,100	254,000
mean.	130,800	39,000	54,800	224,600
Jan. 1973				
Upper Std.	107,400	26,800	0	134,200
Middle Std.	34,600	3,600	0	38,200
Lower "	56,500	5,300	0	61,800
mean.	66,200	11,900	0	78,100

* data from Table 10.

Table 12. Proportions of seedlings in the different microsite types (as percentages)

	Log		Bare		Fern	
1st-year seedlings	Feb. '72	Jan. '73	Feb. '72	Jan. '73	Feb. '72	Jan. '73
Upper Std.	65.7	80.0	29.2	20.0	5.1	0.0
Middle "	72.4	90.6	17.4	9.4	10.2	0.0
Lower "	41.9	91.4	4.9	8.6	53.2	0.0
mean	58.2	84.8	17.4	15.2	24.4	0.0

Established seedlings*	(at May, 1972)		
Upper Std.	67.8	32.2	0.0
Middle "	70.0	28.0	2.0
Lower "	88.5	11.5	0.0
mean	71.3	27.5	1.2

* at May, 1972.

Table 13. Proportions of 1st-year seedlings on mossy and non-mossy surfaces as %. (observations made in Jan. 1973).

	Mossy	Bare wood or litter
Log microsite*	98.9	1.1
Bare microsite*	64.4	35.6

* significantly greater proportion on mossy surface. (1% level)

Table 14. Established seedling densities from random sampling in May, 1972. (mean No. per m^2 and 95% confidence limits).

	Microsite		
	Log	Bare	Fern
Upper Std.	1.00 (0.23 - 1.77)	0.46 (0.12-0.80)	0.00
Middle "	*2.78 (1.54-4.02)	*0.81 (0.0-1.99)	0.03
Lower "	0.69 (0.15-1.23)	0.26 (0.00-0.56)	0.00
mean	1.49	0.51	0.01
Maximum density recorded	13	21	1

*significantly different from other Stands (5% level)

Table 15. Established seedling densities from permanent plots, in May, 1972

(mean no. of seedlings per m^2 and 95% confidence limits)

	Microsite.		
	Log	Bare	Fern
Upper Std.	3.82 (0.91-6.71)	0.50 (0.25-0.74)	0.00
Middle "	*12.56 (11.38-13.74)	1.15 (0.55-1.75)	0.13
Lower "	2.50 (0.0-5.66)	0.50 (0.28-0.72)	0.00
mean.	5.82	0.75	0.02
Max. density recorded	28	7	1
No. of 2 m^2 quadrats	17	26	28

*significantly different from other stands (1% level).

Table 16. Total numbers of established seedlings per hectare, (at May, 1972)

(means with 95% confidence limits in brackets).

	Microsite			Stand total
	Log	Bare	Fern	
Upper Std.	2110 (490 - 3730)	1000 (260 - 1740)	0	3110
Middle "	5590 (3100 - 8080)	2240 (0 - 5490)	160	7990
Lower "	1080 (240 - 1930)	140 (0 - 300)	0	1220
mean	2930	1130	50	4110

Total numbers of established seedlings in each Stand were calculated as for 1st-year seedlings (Table 16).

Estimates for the total no. of seedlings per hectare stand range from 240 to 13,700 (95% confidence limits). The Middle Stand has the largest number of seedlings.

The proportions of the established seedling population found in each microsite are shown in Table 12.

(b) Seedling Survivorship

(i) 1st-year seedlings

Methods.

The monthly counts for the three stands (Appendix Table 2) were combined. Data from modified plots, with the exception of the trenching treatment plots, were excluded. Population decay rates were then determined by plotting numbers of seedlings (on a logarithmic scale) against time of year, and fitting linear regression lines. From these regressions the half-lives can be calculated, and, by extrapolation, the time for the population to become extinct. The half-life of the population is the time taken for the population size to decrease by one half during a period of exponential decline.

Results

The combined data for the monthly counts are given in Table 17, together with monthly mortality rates. The decay rates for the three microsites are given in Fig. 2 and the derived data in Table 18.

Table 17. Combined monthly counts of 1st-year seedlings.

Month (Feb. 1972 to Jan. 1973)

	F	M	A	M	J	J	A	S	O	N	D	J
Log microsite	711	681	633	587	541	512	-	483	460	429	399	369
Bare "	428	373	326	301	256	229	-	202	174	145	133	111
Fern "	61	26	7	5	2	2	-	0	0	0	0	0

% mortality.

Log microsite		5.2	7.0	7.3	7.8	3.3	3.8*	3.8	4.8	6.7	7.0	7.5
Bare "		12.8	12.6	7.7	14.9	10.5	5.9	5.9	13.9	16.7	8.3	16.5
Fern "		57	73	28	60	0	50	50	-	-	-	-

* estimated from Sept. counts.

Table 18. Decay rates of 1st-year seedling populations.

	Half-life (months)	Time for extinction of population in one hectare (years). *
Log microsite	12.5	18.8
Bare "	5.8	7.7
Fern "	1.1	1.5

* time taken from Feb. 1972; using total seedling population of 130,800 for log, 39,000 for bare and 54,800 for the fern microsite (Table 11.)

Microsite decay rates differ markedly, the half-life for the log microsite being about 12 times that for the fern microsite. Smith (1971) recorded half-lives for tropical forest seedlings ranging from 3 to 19 months for different species.

Only three newly germinated seedlings were found throughout the study period; these occurred in March, 1972.

Mortality rates over the period of observation (11 months) were calculated (Table 19). The monthly mortality rates have been given in Table 17.

Annual mortality rates are highest for the fern microsite (100% in all cases) and lowest for the log microsite (40 to 66%). The highest mortality occurs in the Middle Stand. Of the experimental treatments, the trenching and frond removal gave overall mortality similar to the controls. However, the monthly data for the frond removal (Appdx. Table 2) indicates greater survival up to the end of the year. Removal of competing species (all cover on logs, Pseudowintera colorata on bare microsites) resulted in a greater mortality of red beech seedling.
Much of this mortality occurred in the first month after the removal of cover.

The highest rates of mortality occurred during Autumn and Summer; the lowest mortality was in the Winter.

Causes of Mortality

It was usually impossible to ascertain which cause or combination of causes of mortality was effective. Many seedlings disappeared without trace between the monthly sampling periods. The following causes of mortality were identified.

Table 19. Annual mortality of 1st-year seedlings.

	Initial no.	Final no.	% mortality
Log microsite			
Upper Std.	386	229	40.7
Middle "	126	43	65.9
Lower "	155	90	41.9
mean			45.7
Cover removal	32	2	93.7
Bare microsite			
Upper Std.	212	49	76.9
Middle "	487	4	91.5
Lower "	111	35	68.5
mean			79.6
Trenching	113	23	79.7
Pseudowintera removal.	52	1	98.1
Fern microsite			
Upper Std.	17	0	100
Middle "	11	0	100
Lower "	33	0	100
mean			100
Frond removal	40	0	100

(a) Dessication. The leaves and stem become brown. In exposed situations in canopy gaps the leaves are small and red before death. Mortality apparently resulting from dessication was observed during Summer, Autumn and Spring. It occurs in seedlings rooted in moss or mineral soil as well as in those with roots confined to the surface litter layer.

Dessication appears to be the major cause of death for first-year seedlings.

(b) Disease. A stem wilting, probably of fungal origin, was noted.

(c) Low temperature. Leaf damage and loss of leaves occurred following frosts in Winter. In some cases, only the stem remained green and a terminal bud gave rise to new leaves from October onwards.

(d) Defoliation by insects

(e) Mechanical. Includes uprooting and trampling by birds and opossums, erosion of exposed mineral soil and smothering by leaf litter or fallen branches.

(ii) Established seedlings.

Method

Mortality rates over 11 months were calculated from observations made on tagged seedlings.

Results.

The average mortality rate is 13.4% (Table 20) and is slightly higher for the seedlings in the bare microsite. This is equivalent to a half-life of 4.8 years.

All deaths recorded were in the period September to January, with most occurring in December. Die-back of terminal shoots occurred throughout the year. Much die-back and loss of leaves occurred during Winter, although the seedlings affected did not finally appear dead until the Spring or early Summer.

There was occasional defoliation by a leaf-roller caterpillar. Insect galls containing a Cecid larva (M.Kay pers.comm.) were found in the shoot apexes in Summer and Autumn. These occurred in 11.3% of the tagged seedlings and usually involved the death of the infected apex.

No browsing by animals was noticed during the study period. A number of seedlings have a stunted form and many of these (8.4% of all seedlings) appear to be trimmed off to a certain height above the ground. This appearance is consistent with browsing by deer or goats.

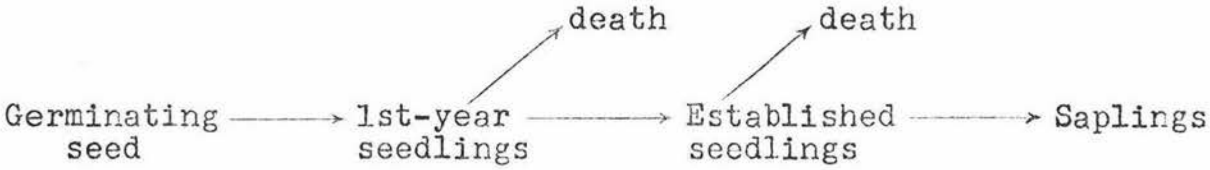
Table 20 Mortality of established seedlings in permanent plots from Feb. 1972 to Jan. 1973.

	Initial No.	Final No.	% Mortality
Log microsite	189	165	12.7
Bare "	42	35	16.8
Fern "	1	1	0
Total	232	201	13.4

(c) A Population Model

A simple, deterministic population model was developed to predict changes in the seedling population size.

The model involves recruitment by seed germination, death and growth into the sapling size class. It can be represented as follows.



The following information was used.

Input from seed-fall (1971 mast year):
478,800 seedlings per ha. (Table 11),
consisting of 162,500 on log microsites,
86,300 on bare microsites,
230,000 on fern microsites.

Mortality, 1st-year seedlings:
half lives of 12.5, 5.8, 1.1 months for seedlings on log, bare, fern microsites respectively (Table 18)

Established seedlings
Density: 4110 per ha. (Table 15)
Mortality: 13.4% per annum (Table 20). The mortality for 11 months is taken as an annual figure.
Recruitment to saplings: 0.4% per annum (see Section 6)

The total number of seedlings present per ha. for each year was calculated:

Total no. of seedlings= No.surviving from previous year. + input from seed germ when appropriate.

The number of seedlings surviving from the previous year is found by subtracting the number of deaths over that year from the numbers of seedlings present in the previous year. Mortality is calculated separately for established seedlings and for 1st-year seedlings on the different microsites. First-year seedlings were regarded as established seedlings when their density had dropped to 5000 per ha. When this point was reached they were added to the pool of established seedlings.

Various patterns of seed fall were used. The evidence for the Ruahine Range suggests a period of from 6 to 16 years between heavy mast years with some seedfall in some of the intervening years (Section 2).

Model I	One mast year of 1971 size every 10 years.
Model II	as for Model I and with one partial mast year (33.3% of 1971 size) at the 6th year of a 10 year cycle.
Model III	as for model I and with two partial mast years (10% of 1971 size) at the 5th and 8th years of a 10 year cycle.

Additional assumptions made were:

(i) The seedling populations decline exponentially, i.e. with a constant mortality rate with changing density. Mortality rate may in fact be density dependent and decline with decreasing seedling density.

(ii) The mortality rates observed over one year are typical of a longer period. Climatic and biotic differences from year to year could alter the mortality rate. Mortality rates may be higher following mast seed years (Hett, 1971).

(iii) The microsite proportions don't change with time.

Results.

Total seedling numbers calculated over a 10 year period are plotted in Fig. 4 for the three models. The population declines rapidly following the heavy mast year recorded in 1971. With no additional seed-fall (model I) the total population size declines slightly from 4110 to 3870 seedlings per ha. over the 10 year period. However, with additional though smaller seed-falls in the intervening years, the population size increases. Two smaller seed years (Model III) leads to a higher population (12,450 per ha.) than the single intermediate seed year (Model II) which produces a final population of 9350 seedlings per hectare.

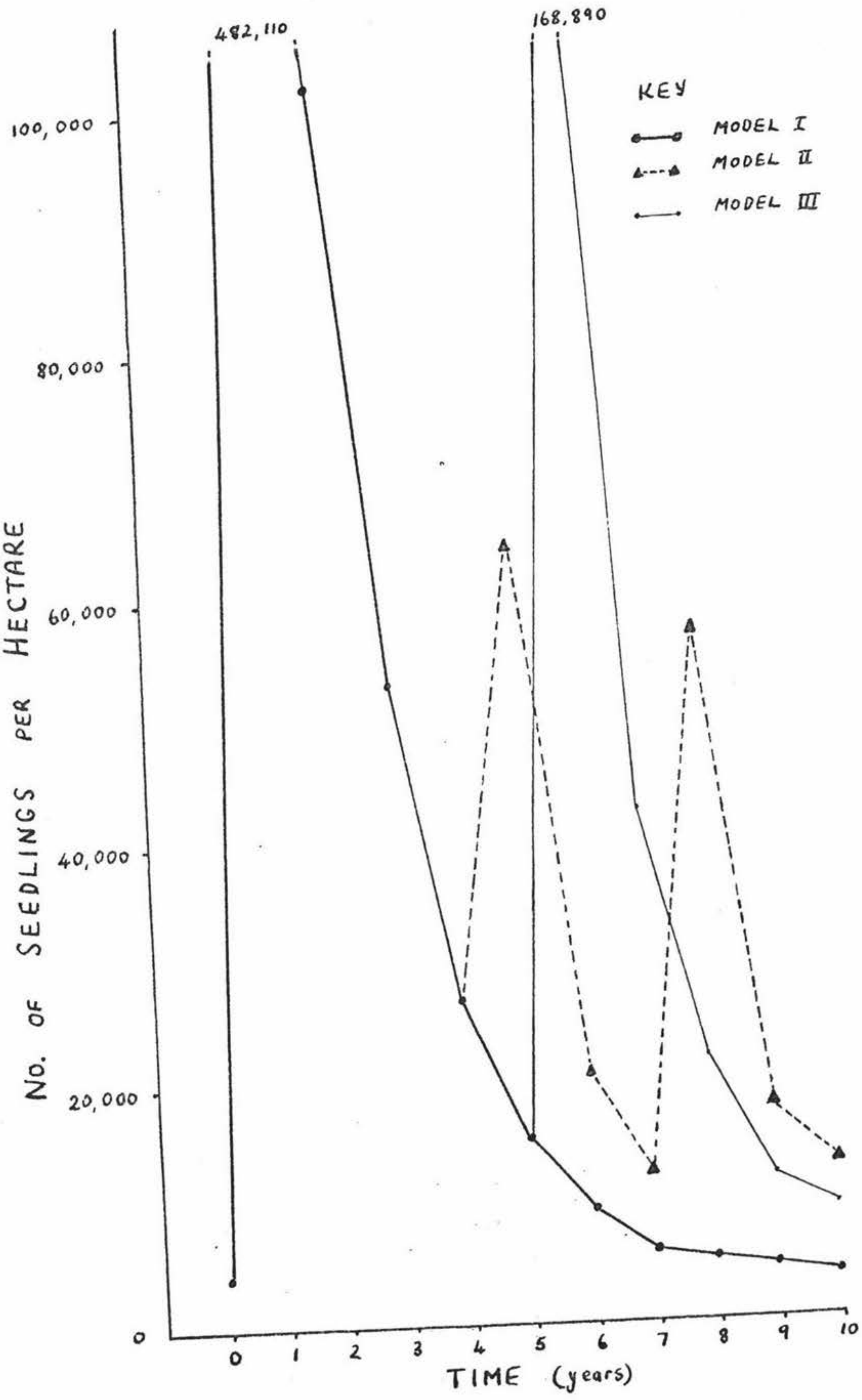


FIG. 4 Predicted changes in the size of the seedling population.

Section 6. Seedling height and diameter

The range of seedling size was studied with the use of heights and stem diameters as measures of size.

Methods

Seedling height was measured to the nearest 0.5 cm and stem diameter at 5 cms above the ground was measured to the nearest 0.1 mm using calipers. Height and diameter measurements were obtained from the 232 tagged seedlings in permanent plots and additional measurements were made during density sampling in May, 1972.

Results.

Average monthly height increments were calculated for all tagged seedlings (Table 21). Most growth occurred from Spring through to Autumn and in Winter there was an overall decline in height caused by dying back of the terminal shoots. Bud break was first noticed in mid-October. Maximum growth occurred in November-December and in March, corresponding to two periods of growth flush. Growth rates were greater in the log microsite and the Middle Stand has higher rates than the other stands. Maximum rates per annum for individual seedlings were 17.0 cms (bare microsite) and 18.5 cms (log microsite).

Mean heights and diameters at May,1972 are given in Table 22 and the frequency distributions for height and diameter in Figs. 5 and 6. First-year seedlings are not included in this data.

Table 21. Growth rates of established seedlings: mean monthly height increments per seedling (mm).

	Month of year (Feb. 1972 to Jan. 1973)												
	F	M	A	M	J	J	A	S	O	N	D	J	Total growth
Log microsite													
Upper Std.	5.6	7.7	-6.5	-0.4	-1.0	-1.0	-	0.9	-0.4	0.7	11.0	-0.7	17.3
Middle "		5.4	5.5	5.8	3.9	0.7	-	-3.4	2.3	9.3	6.2	6.7	45.0
Lower "		14.8	4.8	-0.8	-1.6	1.0	0.2	-2.2	-4.6	4.4	4.1	7.9	32.6
mean	5.6	8.3	0.6	1.7	0.6	0.8	0.2	-1.3	-0.5	4.5	7.7	3.7	30.2
Bare microsite													
Upper Std.	3.1	3.9	0.3	-2.1	-5.3	-1.5	-	1.3	1.7	6.1	1.1	3.6	8.9
Middle "		6.3	6.3	1.8	-2.9	-0.3	-	0.0	-2.8	9.1	6.1	-2.1	25.0
Lower "		5.0	6.6	-3.8	0.0	0.0	0.0	-2.5	0.0	-2.5	6.3	2.5	15.0
mean	3.1	5.2	3.5	-0.5	-3.4	-0.8	0.0	0.3	-0.6	7.1	3.9	0.9	16.7

Table 22. Mean heights and diameters of established seedlings in May, 1972 (with std.deviations; N = 387 for log microsite and 125 for bare microsite).

	Height (cm)	Diameter (mm)
Log microsite		
Upper Std.	35.4 ± 35.7 *	3.34 ± 3.73 *
Middle "	53.4 ± 45.7	5.13 ± 4.89
Lower "	31.9 ± 33.3 *	2.51 ± 2.06 *
mean	38.0 ± 37.4	3.66 ± 3.89
Bare microsite		
Upper Std	13.4 ± 6.3 *	1.55 ± 0.69 *
Middle "	51.2 ± 48.4	4.03 ± 3.91
Lower "	16.2 ± 12.3 *	2.04 ± 2.15
mean	25.7 ± 32.7	2.53 ± 2.56

* significantly different from Middle Std (1% level).

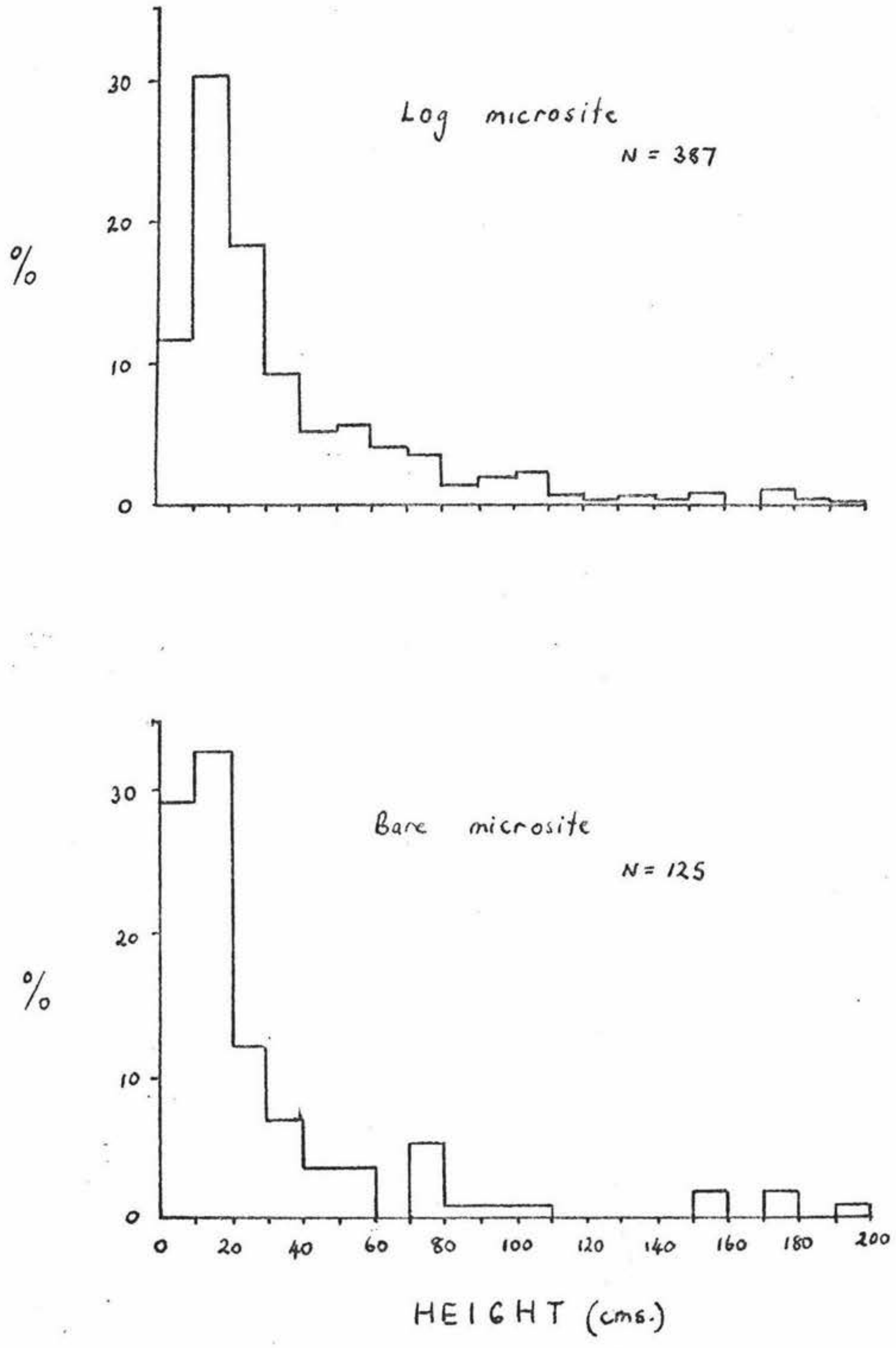


FIG. 5. Height frequency distributions for established seedlings.

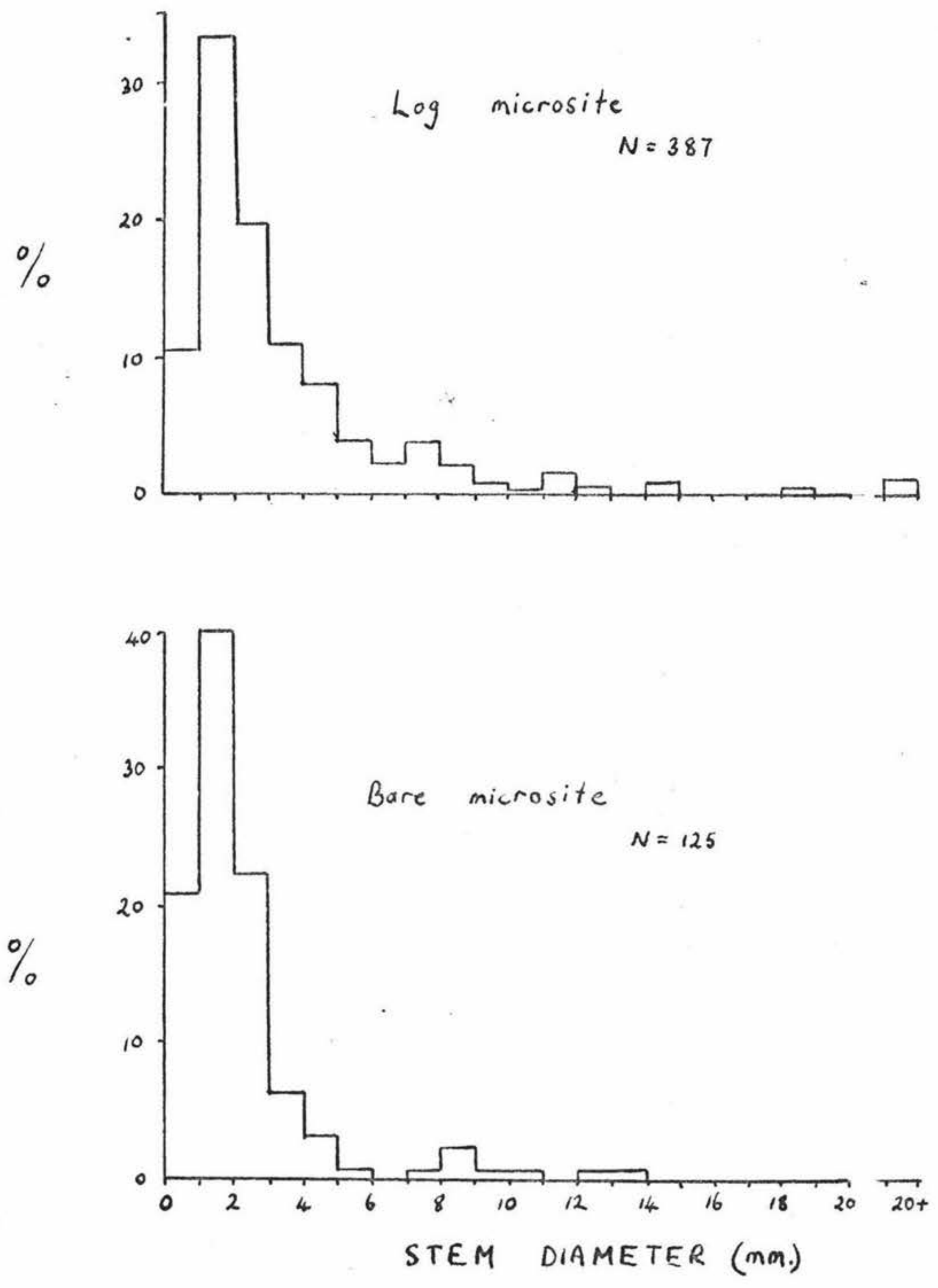


FIG. 6 Stem diameter frequency distributions for established seedlings

Seedlings are significantly larger in the Middle Stand, and seedlings in the log microsite have a significantly greater (1% level) diameter and height than those in the bare microsite. The height and diameter frequency distribution for both microsites approximate an inverse J-shaped form (Meyer, 1952), but with fewer seedlings than expected in the smallest size class * and more than expected in some of the larger classes. In fact, there is some evidence of 3 or 4 model size classes for the log microsite and 2 for the bare microsite.

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* Inclusion of data for 1st year seedlings would make the distribution closer to the J-shaped form.

<u>Discussion</u>.

Each modal class could represent a different age group derived from the widely-spaced heavy mast years. This possibility will be examined further in Section 7

The J-shaped form of the size distribution suggests a stable, uneven-aged stand capable of maintaining its structure (Meyer and Stevenson, 1943). Numbers in each successive size class decrease as mortality proceeds. The number of seedlings attaining the maximum seedling size will depend on the amount of input from seed and on mortality rates throughout the seedling stage. This number is of interest as it represents the output from the seedling population into the mature tree population. Referring to the seedlings in the largest size in the height distribution (190 - 200 cms) and assuming that they are all capable of growing to 200 cms in one year, a maximum of 2 seedlings per hectare (0.4% of this sample) become saplings in one year. This output from the seedling population is low compared with an estimated annual loss of 13.4% of the seedlings due to mortality (Section 5).

Section 7. Seedling Ages.

Methods.

A sample of 60 seedlings obtained during density sampling in May, 1972 were aged by counting growth rings in the stem. Sections were obtained from the base of the stem, stained for lignin with aniline sulphate and examined at 63x and 252x with a compound microscope. Difficulty was encountered with acentric stem growth, partial rings and indistinct rings, but generally each ring was assumed to represent one year's growth. Four year old red beech seedlings grown at Massey University were found to have four growth rings. N.solandri var cliffortoides produces one ring per year in a subalpine habitat (Wardle, 1963).

Uncertainty in the ring counts is approximately ± 2 years, or ± 1 year for the youngest seedlings.

Results.

The age frequency distribution is given in Fig. 7. It cannot be directly compared with the size-distributions (Figs. 5 & 6) since the aged seedlings were not a random sample of the population. Fig. 7 demonstrates a series of peaks in the age distribution which can be dated as 1969, 1967-66, 1964, 1962, 1959, 1954 and 1952, though not with certainty as to the exact year. The oldest seedlings (22 years) dates from 1950. Most take approximately 16 years to reach the sapling size class (2 m in height).

The height - age relationship (Fig.8) shows that there is much variability in growth rate. Growth rates are higher in the log microsite and for the Middle Stand

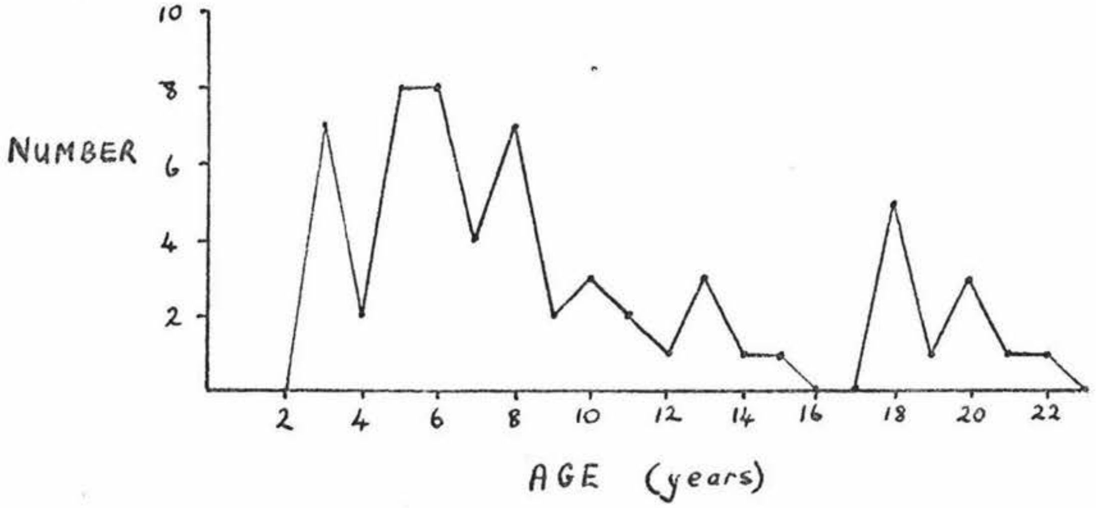

FIG. 7 Age distribution of established seedlings, N = 60.

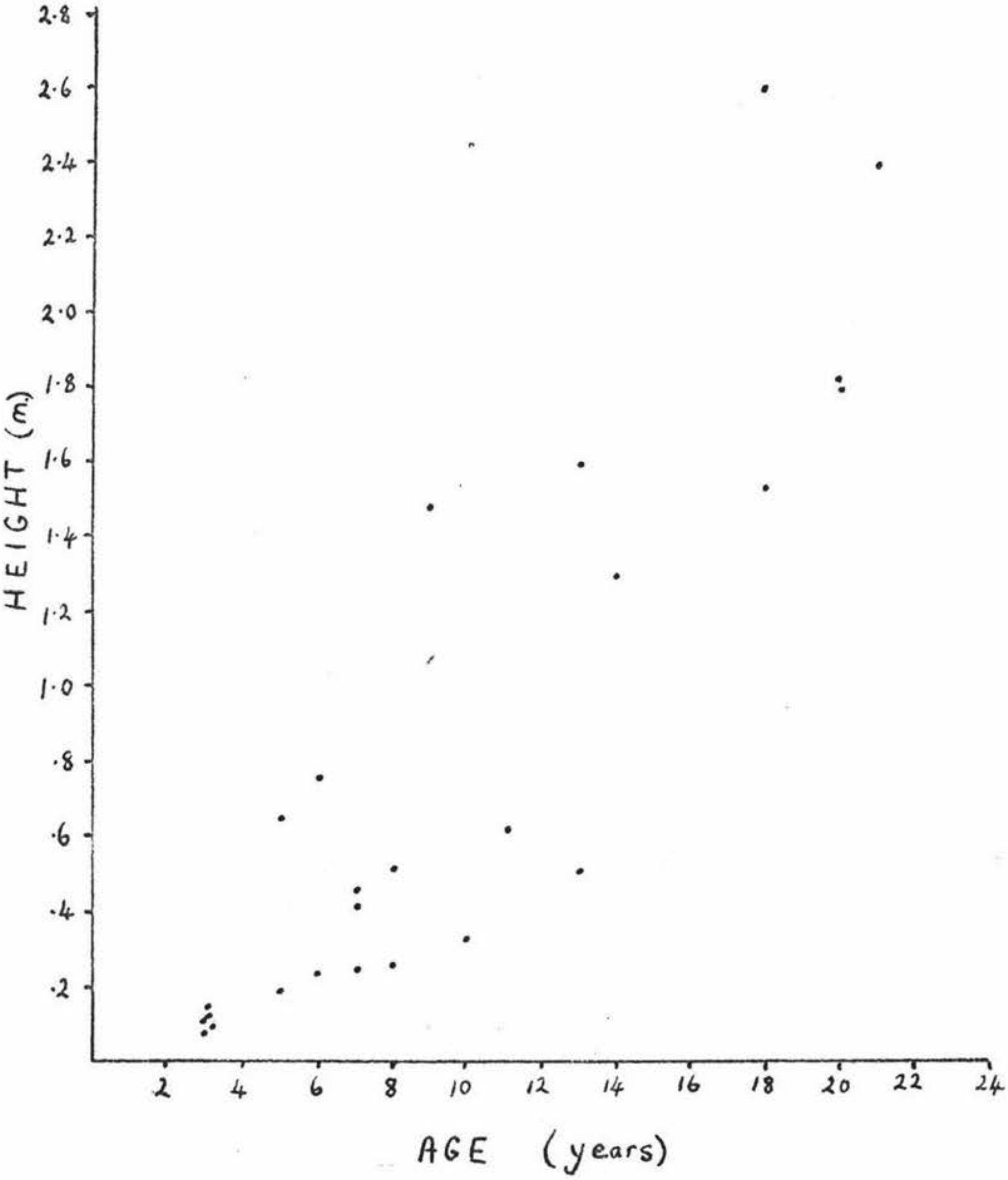

FIG 8. Relationship between seedling height and age.

Table 23. Diameter growth rates of established seedlings.

	Rings per mm diameter (means with std. deviations)	No. of seedlings.
Log microsite		
Upper Std	3.44 ± 1.33	10
Middle "	1.99 ± 1.02 **	16
Lower "	2.55 ± 0.85 *	14
mean	2.42 ± 1.19	
Bare microsite		
Upper Std.	4.09 ± 0.89	10
Middle "	2.58 ± 1.36 **	7
Lower "	3.19 ± 0.58	3
mean	3.43 ± 1.22	

* significantly different from Upper Std - 5% level

** " " " " " - 1% level

(Table 23). The lowest rates are found in the Upper Stand for the bare microsite.

Discussion.

The seedling population appears to consist of a number of even-aged groups, separated by two or more years. This age structure is not clearly reflected in the size structure which is a result of differences in individual growth rates. Seedlings of the same age develop a range of sizes. Some of the variability can be accounted for by location (Stand) and some by microsite (Table 23).

An age structure comprising a number of even-aged groups could originate in the mast seeding behaviour of red beech, or, with a steady seed fall, from failure of seedling establishment at germination in some years. Seedling establishment is not likely to fluctuate drastically in view of the variety of microsites available for germination and the lack of extreme climatic fluctuations from year to year. There is good evidence of large fluctuations in seed fall from year to year (Section 2). The historical record shows that heavy seed production probably occurred in the study area in 1936, 1949, 1955 and 1963 with lighter seed falls in some of the intervening years. The data of Fig. 7 show age groups dating from 1964 and 1954 which could be derived from the 1963 and 1955 mast years. No seedlings were dated to before 1950. There is evidence in the age distribution of two mast years since 1963 - 1966 (or 1967) and 1969. No seedlings became established in 1970, the year before the heavy mast of 1971.

Overall, the evidence from the seedling age distribution, published records of mast years and observations on seed fall in 1972 and 1973 suggests that significant numbers of seedlings became established every two or three years and that very few establish in some years.

A study of sugar maple seedling populations, (Hett, 1971) has shown that the number of viable seeds produced each year does not affect the number of seedlings establishing. In years of high seed input mortality rates are higher than in years of low input. Sugar maple, like red beech, has large fluctuations in seed production from year to year.

Section 8. The effects of light intensity on seedling growth and survival.

(a) Light intensities of seedling microsites.

Light intensities found in the different microsites were measured by photochemical and photoelectric methods. The aim was to determine the light intensity range for each microsite type and also the lowest relative light intensity (r.l.i.) at which seedlings were found. All measurements were made in the Middle Stand.

(i) Photochemical method.

Anthracene in benzene solution decomposes in light and the amount of anthracene decomposing can be used as a measure of the amount of light received by the solution (Dore, 1958). The method is cheap and convenient and is useful as it gives an integrated measurement of light intensity. The main limitation is the insensitivity to photosynthetically active radiation in the visible range, the main adsorption peak of anthracene being 350 nm. (ultraviolet). This would not be important for obtaining relative intensity values unless a spectral shift between the visible and ultraviolet occurs as light passes through leaf canopies. These is some evidence that ultraviolet light is transmitted through canopies relatively less than visible light (Robertson, 1966) and this would affect the validity of the results. However, much of the light received by the forest floor consists of sunflecks of unfiltered, direct light (Evans, 1956).

Methods

Sealed glass tubes (volume 4.6 mls.) containing a saturated anthracene solution in benzene were placed on the ground in a number of selected microsites, with and without red beech seedlings, in the study area. Tubes were placed horizontally and aligned east-west.

Several tubes were kept in a light-proof box as zero light controls. A 100% r.l.i. control was obtained from tubes placed in an elevated position in a large clearing below the study area. A total of 74 tubes were placed from 1000 to 1030 hours on 22 Jan. 1973 and collected at 1200 hrs. the next day. The weather during this 26 hr. period was cloudy with occasional sunny periods. The period of exposure was judged on the basis of trial runs under similar weather conditions.

After collection of the tubes, the concentration of anthracene remaining was measured with a spectrophotometer at 350 nm. Transmittance is proportional to the amount of light received by the tubes.

Results.

Relative light intensity values were calculated and expressed as a % of the mean value for fully exposed tubes (100% r.l.i. control). Systematic error for each estimate is in the order of ± 0.75%. Considerable variation was found between tubes placed together in the same location.

Results are given in Table 24.

(ii) Photoelectric method.

Methods.

Measurements were made with a portable "EEL" selenium cell photometer which measures light in the visible range. Instantaneous measurements were made in the forest on evenly overcast days between 1100 and 1300 hours. No

Table 24. Relative light intensities using a photochemical method.

Description of microsite	Relative light intensity (%)	
	mean	range
Log, in clearing (no cover)	22.5	21.0 - 24.6
Log, under canopy (no cover)	8.0	5.1 - 11.4
Log, under canopy (with cover)	3.3	0.0 - 7.7
Bare, under canopy	3.3	2.0 - 5.1
Bare, under canopy * (with shrub cover)	1.7	0.5 - 4.2
Bare, in clearing	9.4	2.0 - 12.8
Bare, in clearing * (with shrub cover)	1.3	0.0 - 2.0
Fern, under canopy *	1.5	0.0 - 4.7
Fern, in clearing *	1.6	0.5 - 2.4

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* no seedlingspresent.

Table 25. Relative light intensities using a selenium cell photometer.

	Relative light intensity (%).	
Description of microsite	mean	range
Log, in clearing	35.6	25.6 - 49.7
Log, under canopy	16.6	9.0 - 25.6
Bare, in clearing	39.5	27.1 - 65.4
Bare, in clearing (with shrub cover)**	6.0	2.2 - 14.3
Bare, under canopy	10.5	2.3 - 28.3
Bare, under canopy (with shrub cover)*	1.9	0.8 - 3.8
Fern, under canopy *	1.5	0.1 - 4.5

* no seedlings present.

**no 1st-year seedlings at intensities below 3.7%.

account is therefore taken of the occurrence of sunflecks. The reference point for the measurements, taken as 100% r.l.i., was an elevated log in a clearing which was known to be exposed to direct sunlight throughout the period of measurement.

Results.

A summary of results is given in Table 25 together with notes on seedling distribution.

The photoelectric method gives results comparable with those obtained from the anthracene method for the lower range of intensities, but not for the higher range where the values are greater than expected. The photoelectric measurements for the higher range of intensities were taken largely in direct light at midday whereas the anthracene measurements included the diffuse, reflected light that would predominate on the forest floor for the greater part of the day. Thus discrepancies can occur between instantaneous and integrated measurements of relative light intensity.

(b) Productivity of seedlings in the forest.

Potted seedlings were placed in different locations in the study area covering a range of light intensities. Growth was estimated over a short period and related to the measured light intensities at the locations. This technique has been used by Wardle (1959) in a study on *Fraxinus excelsior*.

Methods.

First-year seedlings were transplanted from the forest in May 1972 and grown under a shadeframe (relative light intensity 45% approx.) at Massey University.

On 21 Nov. 1972, 20 seedlings of comparable size and vigour were selected, 8 of which were harvested immediately (initial harvest), and the remainder transferred into 300 ml. pots in a fertilized peat-sand potting mixture. The heights and leaf breadths of the potted seedlings were measured and the seedlings placed in the study area where the pots were dug into the mineral soil and watered.

Four seedlings were placed at each of three locations, as follows -

Location (a) - under dense fern layer and under tree canopy.

Location (b) - cleared of fern layer and under tree canopy.

Location (c) - cleared area within a large tree canopy gap.

The relative light intensity (r.l.i.) at each location was determined by the photochemical method (see previous section).

Harvesting was done after 9 weeks, by which time two of the original 12 seedlings had died. Oven dry weights, together with heights and leaf breadths, were measured (final harvest).

Dry weights of the 8 seedlings of the initial harvest were used to obtain a linear regression relationship between the sum of the leaf breadths and total dry weight for individual seedlings. Thus the leaf breadth measurements were used to estimate the initial dry weights of the potted seedlings placed in the forest. Final dry weight was measured directly.

Leaf areas for initial and final harvests were obtained from a linear regression relating leaf area with leaf breadth (based on a random sample of 21 leaves). Net Assimilation Rate (NAR) for the 9 week period of the experiment was calculated for each seedling from the above data.

Results.

Mean values for height, leaf area and total dry weight increments, together with mean NAR values are presented in Table 25a. The linear relationship between NAR and the logarithm of r.l.i. (Howard, 1973[b]; Wardle, 1959) was used to determine the compensation point for growth (NAR = 0), which corresponded to a relative light intensity of 1.9% (Fig. 9). The linear regression is given by $y = 18.9x - 5.4$ where y is the NAR and x represents the logarithm of r.l.i.

Table 25a. Productivity of potted seedlings in the forest . Mean values with standard deviations are shown. Total number of seedlings = 10.

Location	(a)	(b)	(c)
r.l.i. (%)	2.2	5.3	12.8
Height increment (cm)	1.19±0.51	2.67±1.07	3.78±2.30
Leaf breadth increment (cm)	1.05±3.24	2.02±2.61	9.06±2.62
Total dry weight increment (mg)	14.2±22.4	47.9±17.8	139.0±28.4
NAR ($mg/cm^2/week$)	0.37±3.06	10.04±2.32	14.80±2.39

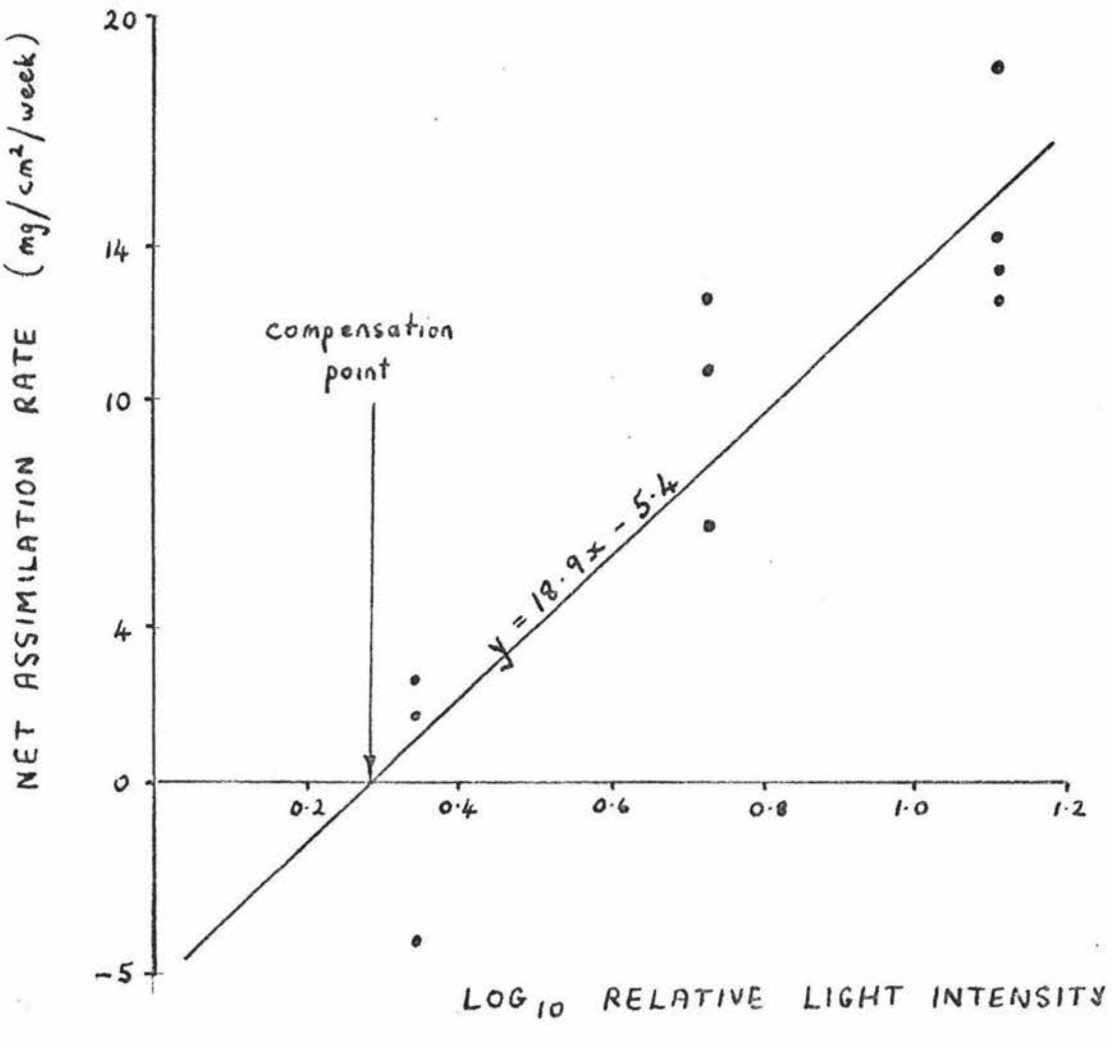


FIG. 9 Relationship between N.A.R. and relative light intensity for potted seedlings in the forest.

(c) Growth responses to light intensity: a garden experiment.

Seedlings were grown under different amounts of shade and the growth responses over most of a growing season were measured.

Methods.

Growing conditions. Seedlings were grown outside in the nursery of the Plant Materials Centre, Ministry of Works, Palmerston North. The soil, Manawatu fine sandy loam, had been fertilized and, in addition, "Rustacote" nutrient granules were applied during the experiment. Plants were kept well watered.

Seedlings. First year seedlings were collected from immediately below the study area (altitude 669m) in April 1972 and again in Sept. and Oct. 1972. They were transplanted into the garden and covered with hessian. Unbranched, healthy seedlings of uniform size were selected during collection and prior to the beginning of the experiment.

Treatments. There were four light intensity treatments as follows:

Relative light intensity	Shade material
100%	none
44%	one layer of "Silon", a black synthetic cloth.
35%	one layer of 14oz.hessian
13%	two layers of 14oz.hessian

The relative light intensities are mean values of measurements made under the shade frames with a selenium cell photometer. Measurements were made on 10 different days, three of them evenly overcast, in Nov. 1972 and Feb. 1973. The shade cloths were stretched over shade frames measuring 167.6cm by 106.7 cm and covering a seedling plot of 61 cm by 61 cm (16 seedlings at 15.2 cm spacings). The top of each frame was fixed at 30.5cm above the ground. Shade cloth covered the sides of the frame to within approx. 2.5 cm of the ground and the ends were left open to allow air circulation. Despite this, differences in exposure to wind would occur between the shade frame treatments and the 100% r.l.i. treatment. Air temperature in the 100% r.l.i. treatment was up to 2.0^{o}c higher than the other treatments on hot days, although differences were not significant at lower temperatures and surface soil temperatures also showed no differences.

Each of the four treatments was replicated three times and the replicates assigned to three randomised blocks. This gave 12 plots, each with 16 seedlings, giving a total of 192 seedlings.

Measurements. The treatments began on 19 Nov. 1972 and continued until 12 Feb. 1973, a period of 13 weeks during which there was continuous seedling growth.
The heights of all seedlings and leaf breadths of all leaves were recorded initially. A sample of 25 seedlings was collected at this time for dry weight determinations. From this sample a regression was obtained relating leaf breadth to total dry weight (for individual seedlings).

The linear regression equation obtained was:

$$y = 1.026\,x + 4.4,$$

where x = leaf breadth (mm) and y = total dry weight (mg).

Leaf breadth is the maximum breadth measured to the nearest 0.5 mm.

At the final harvest the heights of all seedlings were measured and the branching pattern recorded. Observations were made on the general appearance of the seedlings and in particular damaged plants were looked for. Some had been browsed by rabbits and these were excluded from the harvest. Plants were carefully dug up and roots washed. The presence of mycorrhiza on a small sample of plants was investigated. Following oven drying (90°c for 48 hrs) the roots, stems and leaves for each seedling were weighed. Plant parts such as dead leaves falling from the plant are not included in the final seedling weight.

Results.

Initial seedling dimensions are given in Table 25b.

Table 25b. Initial seedling dimensions (Means with std. deviations).

Height	46.5 ±	8.3 mm
Total dry weight	23.9 ±	12.6 mg
Leaf area	435.3 ±	122.5 mm^2

At the end of the experiment the range in size was considerable, with some seedlings up to 30 cm tall and some showing almost no growth. Seedlings in the 100% r.l.i. treatment had noticeably smaller and redder (sometimes bleached) leaves than the other treatments.

The degree of branching was greatest in the 100% r.l.i. treatment and least in the 13% r.l.i. treatment (Table 26)

Table 26. Number of branches per seedling (mean and std. deviation).

treatment (r.l.i.)	No. of branches
100%	4.4 ± 3.2
44%	3.5 ± 1.8
35%	4.0 ± 2.5
13%	1.4 ± 1.4 *

* significantly different from other treatments at 5% level, (other differences not significant).

Mycorrhizal roots were present on most seedlings at the time of transplantation from the forest. They were also common at the end of the experiment, although the large, rapidly growing roots were not mycorrhizal.

Most mortality occurred with the 100% r.l.i. treatment (Table 27).

Table 27. No. of seedlings dying during the experiment.

Treatment:	No.dead	No.damaged by rabbits	Remaining No.
100% r.l.i.	8	1	39
44% r.l.i.	3	1	44
35% r.l.i.	0	1	47
13% r.l.i.	4	5	39
			169 Total.

Height Growth

The Relative Growth Rates (RGR) for all seedling heights were calculated using the initial and final heights, (Table 28).

Table 28. Relative Growth Rates for seedling height.

Treatment (% r.l.i.)	RGR* (mm/mm/week).
100	0.067 ± 0.027
44	0.086 ± 0.027
35	0.086 ± 0.024
13	0.062 ± 0.027

* means and std. deviations.

Most height growth occurs under medium shade (35% and 44% r.l.i.) and the least under the denser shade (13% r.l.i.). The overall effect of light intensity on height growth is significant at the 1% level (two-way analysis of variance with unequal but proportional subclass sizes, Sokal & Rohlf, 1969).

Dry Matter Production.

Initial dry weights were estimated from the sum of leaf breadths for individual seedlings using the linear regression relationship previously obtained. Final dry weights were measured directly. Relative Growth (RGR) of all plants and for the five plants per replicate with the highest RGR were calculated (Table 29).

Table 29. The effect of light intensity on dry matter production.

Treatment (%r.l.i.)	RGR (mg/mg/week) All plants.	(means and std. deviations) Highest 5 plants.
100	0.143 ± 0.052	0.187 ± 0.028
44	0.141 ± 0.045	0.178 ± 0.021
35	0.150 ± 0.042	0.193 ± 0.016
13	0.094 ± 0.040	0.120 ± 0.017

Light intensity has a significant overall effect on dry matter production (two-way analysis of variance, 5% level of significance), the optimum growth occurring at 35% r.l.i.

The relationship between RGR and r.l.i. (Fig.10) can be used to determine the light compensation point for growth (RGR = 0). Linear regressions were calculated using the highest 5 RGR values per replicate and using all RGR values. These gave compensation points of 3.9% and 12.7% r.l.i. respectively. The full light (100% r.l.i.) treatment was not comparable with the other three treatments which have shade frames. Under this treatment the plants were subject to more wind and higher air temperatures. Mortality was also higher (Table 27) and more moribund plants were present.

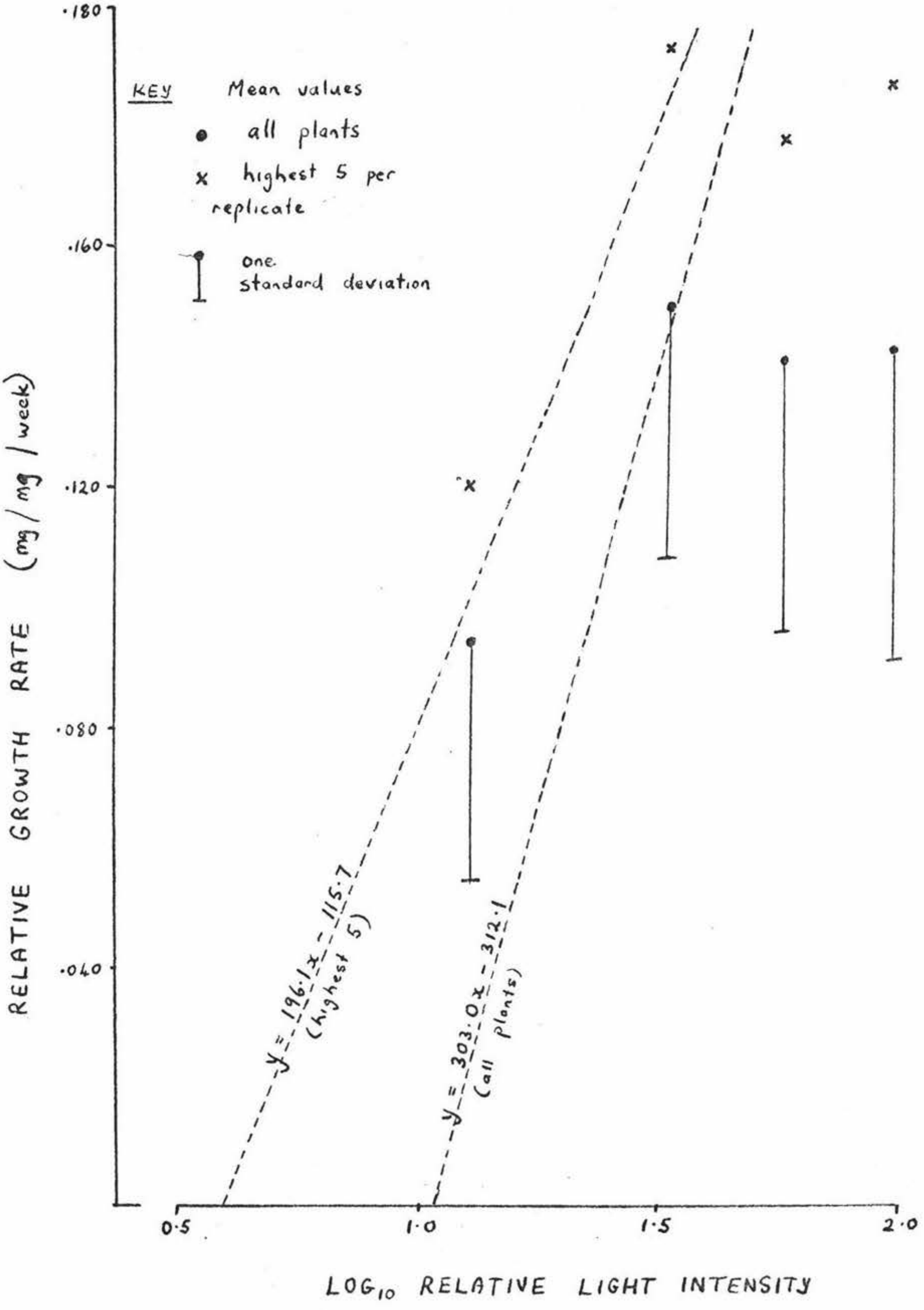


FIG. 10 Effects of light intensity on dry matter production.

Average growth was less than expected on the basis of a logarithmic relationship between growth and light intensity. Since the plants in this treatment appeared to be adversely affected by treatment effects other than light intensity, the data were not included in the linear regression analysis used to obtain the compensation point. The analysis for the highest 5 RGR values per replicate will reflect response to light intensity better than that using all plants. The former analysis reflects response under ideal growth conditions, the latter the response of a population subject to various environmental stresses, involving factors other than light intensity.

The allocation of dry matter to the main plant parts (Table 30) shows that at lower light intensities there is less allocation to the roots and more allocation to the leaves. Allocation to the stem is not affected. Thus there is some evidence for an increase in the shoot/root ratio at lower light intensities.

TABLE 30 Dry matter allocation (as % of total dry weight).[1]

	Root	Stem	Leaves	Shoot/root ratio.
Treatment (% r.l.i.)				
100	24.67 ± 5.77	28.01 ± 8.29	45.77 ± 3.60 *	3.0
44	26.24 ± 5.89 *	28.34 ± 4.57	45.23 ± 3.92 *	2.8
35	21.94 ± 5.36	29.08 ± 3.84	49.24 ± 3.29	3.6
13	23.96 ± 5.39	26.37 ± 3.30	49.61 ± 4.53	3.2

* significantly different (5% level) from the 35% r.l.i. value

[1] Mean % with std. deviations

DISCUSSION.

Seedlings are not found in fern microsites or in bare microsites with a shrub canopy. These microsites have the lowest range of light intensities recorded on the forest floor, less than 4.7%. The estimated light compensation points (1.9% from the field productivity experiment and 3.9% from the garden experiment), when compared with the microsites containing seedlings, suggest that the compensation point is raised under forest conditions. This increased light requirement may be a result of the interaction of other growth-limiting factors such as temperature, root competition and disease (Jarvis, 1964; Shirley, 1945).

The estimated compensation points (1.9 and 3.9%) fall within the 0.5 to 5% range found for a number of forest tree species (Bieleski, 1959; Okali, 1972). The only published value for Nothofagus is an estimate of 1.15% for 6 month N.cunninghamii seedlings (Howard, 1973b). N.Cunninghamii seedlings do not survive under a dense tree canopy, although light intensities recorded under the canopy were well above the compensation point (Howard, 1973a). Red beech is characterised silviculturally as a strong light demander that will survive, but not develop, under its own canopy (Franklin, 1965; Kirkland, 1961). However, factors other than reduced light intensity could account for the suppression of seedling growth beneath a canopy; for example competition for nutrients and water with the roots of canopy trees could inhibit growth.

Provided a fern canopy or a dense shrub canopy is not present, the range of light intensities found in the forest is adequate for seedling growth. Intensities in most log and bare microsites are at or near the optimum for growth (35% from the garden experiment.). Log and bare microsites situated in clearings provide the highest range of light intensities (up to 65%), with the most exposure to direct sunlight. All seedlings probably receive some direct light from sunflecks.

Responses to decreased light intensity include a reduction in branching, a slight increase in the shoot/root ratio and a decrease in height growth. These responseshave ecological significance. Less branching means fewer growing apexes and consequently more vulnerability to dieback or predator attack, while an increased shoot/root ratio could make the seedling susceptible to drought, especially if the roots have not penetrated the surface litter to the mineral soil (Jarvis, 1964).

The effects of light intensity on seedling growth and survival have only been partially examined in this study. Light intensity is but one of a complex of interacting factors that control plant growth. Light intensity has been shown to have a significant effect on the growth of red beech seedlings and to correlate with seedling distribution in the forest.

Section 9.

Allelochemicals and Seedling Growth: a preliminary study.

The ecological role of compounds that originate in one species, are released into the environment, and inhibit or promote the growth of another species has become an active field of research. Such compounds are termed allelochemicals, and the phenomenon of inhibition, allelopathy. Allelochemicals have been reported in a wide range of plant communities, including forests in moist climates (Whittaker & Feeny, 1971). Salicylic acid, which inhibits herbaceous growth beneath the crowns of *Quercus falcata* trees in South Carolina is an example for this type of forest (Muller & Chou, 1972).

The known allelochemicals are secondary plant products such as phenolics, alkaloids, terpenoids, organic cyanides and amino acids (Whittaker, 1970). Phenolic compounds are the best known water-soluble allelochemicals. Simple phenolic compounds are common in soils at concentrations up to 10^{-5} M (Whitehead, 1964; Wang et.al. 1967). The physiological effects of these compounds are numerous and include the inhibition of mineralion uptake (Glass, 1973).

To demonstrate that allelopathy is occurring it is necessary to show that:

(1) the allelochemical is released from the plant into the environment (allelochemicals can be released by volatilization or leaching from leaves and stems, by excretion from roots, or by decay of plant parts);

(2) the allelochemical inhibits the germination, growth or reproduction of the other species under natural conditions;

(3) other competitive facts are not responsible for the observed inhibition.

A common technique is to apply leachates from the inhibiting species to isolated potted plants of the other species. Using this technique, the toxic compounds in the leachate can be identified.

It must then be shown that these compounds are available in the natural situation in sufficient quantities to cause the observed degree of inhibition.

The widespread occurrence of allelopathic phenolic compounds suggested that they might be involved in the growth and survival of Nothofagus fusca seedlings.

Phenolics are present in extractives of Nothofagus species as flavononoids, polyphenols and simple phenols. (Hillis & Orman 1961; K.R.Tate, pers, comm). Other New Zealand species have been little studied.

Patchy seedling distribution, possibly resulting from allelopathy, was a feature of the study area. N.fusca seedlings were usually absent under Pseudowintera colorata and fern canopies. Bare ground was sometimes found under trees of Griselinia littoralis. However, in these cases competition involving other environmental factors such as light may be involved. Rotting logs were found to be a favourable seedling site (Section 5); yet they would be expected to have a high phenolic content as a result of lignin decomposition.

The aims of this investigation were:

(a) to identify simple phenolic compounds in shoot leachates;

(b) to quantify the phenolic content of forest soil and of shoot leachates;

(c) to determine the effects of phenolic compounds on the growth of Nothofagus fusca seedlihgs.

METHODS

(a) Identification of simple phenolic compounds.

Intact twigs from mature trees of Nothofagus fusca and Pseudowintera colorata in the study area were collected in mid December. The twigs were soaked in distilled water for four days and the resulting solution (leachate) was filtered.

The leachate was hydrolysed by refluxing in 1 M.HCl for two hours. It was then extracted with ether using a continuous extraction apparatus. The ether phase was extracted with 5% bicarbonate and the resulting aqueous phase acidified, then re-extracted with ether. The combined ether phases were dried before being made up to a small volume with methanol.

This methanol solution was used in two dimensional, thin-layer chromatography with silica gel. The first solvent was the non-aqueous phase of a 10 : 7 : 3 (v/v) benzene - acetic - water mixture (B Ac W) and the second phase 2% acetic acid (Ac).

After drying, the chromatogram was observed under ultraviolet light. Fluorescent spots were noted after fuming with NH_3. Chromatograms were sprayed with diazotized p-nitroaniline, then with 30% NaOH.

The total phenolic content of unhydrolysed leachates was measured before and after the above extractions, using Folin - Ciocalteureagent and the method of Swain & Hillis (1959). Vanillic acid was used as a standard.

(b) The total phenolic content of soil and plant extracts.

The phenolic content was determined as described above. Shoot leachates of N.fusca, P.colorata, Dicksonia lanata and Griselinia littoralis were prepared as in section (a) above. Aqueous extracts from the soil samples were prepared by mixing 50 mls. of distilled water with 50 mls. of soil and leaving for 48 hours.

The mineral soil and organic soil (rotting Nothofagus fusca wood from a fallen log) samples were pooled samples, each from two different locations in the study area. Samples of the soil used in the pot experiments (see below) were made up of 10 mls. of soil from each replicate pot.

(c) Effects of phenolic compounds on the growth of Nothofagus fusca seedlings.

Seedlings between one and two years of age were collected from the study area in October (set 1.) and November (set 2.) and transplanted into a fertilized peat-sand mix. Most seedlings appeared to have mycorrhizal roots. The two sets of seedlings were grown in a heated glasshouse for 46 and 15 days respectively before treatment. The larger seedlings from set 1. were used for litter treatments, and the smaller seedlings from set 2. for leachate treatments. In the litter treatments 10 gms. of fresh shoots of either Pseudowintera colorata or Nothofagus fusca were macerated and incorporated in the surface soil of each pot. A control had no litter added. In the leachate treatments 10 mls. of each of the four leachates (distilled water in the case of the control) were applied to the surface of each pot at approximately fortnightly intervals. There were 4 such applications. 200 ppm. ferulic and vanillic acid solutions were also used (2 mg. in each 10 ml. application). All seedlings were grown singly in pots, 5 seedlings for each treatment, in the glasshouse of the Dept. of Botany and Zoology, Massey University. Hoagland's solution was applied to all pots at the beginning of the experiment. Pots were watered by capillary feeding from a moist sand bench. Additional water was applied at the top of the pots as required and following leachate application. Plants were grown for 58 days from the first treatment to the final measurement.

Initially, the heights of all seedlings and the heights and total dry weights of a harvested subsample were measured.

At the final measurement the heights and total dry weights of all seedlings were measured. Soil pH of the potting mix was measured at the beginning of the experiment, and the pH of a pooled sample from each treatment at the end.

RESULTS AND DISCUSSION

(c) Identification of phenolics -

Details of spots detected on chromatograms of acid hydrolysates are given in Appendix Table 3.

The spots represent simple phenolic acids. Using the details given by Ibrahim & Towers (1960) for a number of common phenolic acids, three chromatogram spots were tentatively identified. These are, for N.fusca spot no.3 - gentisic acid, for P.colorata spot no.7 - caffeic acid and spot no.9 - a cis-trans isomer of sinapic acid.

The phenolic content of the final fraction from the ether extraction of unhydrolysed leachate was measured as zero, indicating that the phenolics were present in a conjugated form in the leachates. Most simple phenolics are present in living cells in a conjugated form, usually as glycosides (Harborne, 1964).

(b) Total phenolic content of soil and plant extracts - Results are given in Table 31. The range of phenolic concentration detected was 1 - 300 ppm.

Table 31. Total phenolic content of soil and plant extracts, given in parts per million.

Extract	Collection Date	Phenolic Content (ppm).
N. fusca shoots	Nov. (1972)	87
	Dec. "	110
P.colorata shoots	Nov. "	62
	Dec. "	67
D.Lanata fronds	Dec. "	257
G.Littoralis shoots	Dec. "	15
Rotting N.Fusca wood	Jan. (1973)	10.3 (average of 2 samples)
Mineral soil	Jan. "	2.5 (average of 2 samples)

Table 31 cont.
Extracts from pots.

Extract	Phenolic content (ppm)	Extract	Phenolic content (ppm
Potting mix (before planting)	2.5	D.lanata leachate	2.2
Control	2.4	G.littoralis leachate	2.2
N.fusca litter	3.0	Ferulic acid	1.9
P.colorata litter	1.9	Vanillic acid	2.0
N.fusca leachate	2.1		
P.colorata leachate	2.0		

The phenolic content of soil extracts is low and compares with reported values (Whitehead, 1964; Wang et al, 1967). 2 ppm is equivalent to 1.2×10^{-5}M vanillic acid. Phenolic contents of shoot extracts are much higher; the 257 ppm value for the Dicksonia lanata leachate is equivalent to 1.5×10^{-3}M vanillic acid. Phenolic compounds leached from the foliage during rainfall will be added to the soil. Leaching from bark and roots, and the decay of dead plant parts are other possible sources. The low phenolic level in the soil may be due to leaching, degradation by micro-organisms (Henderson, 1960), or complexing with humic acids and organic colloids (Muller & Chou, 1972). The higher phenolic level of the rotting wood 'soil' could be a result of high rates of organic decomposition, especially of lignins. Despite the higher phenolic level of the rotting wood, compared with mineral soil, the wood is the more favourable site for N.fusca seedling growth and occurrence (see Section 5.).

(c) Effects of phenolics on the growth of N.fusca seedlings -

Results of initial and final seedling weights and heights are given in Appendix Table 4. Differences between treatments are not significant at the 5% level. No difference in seedling appearance in the different treatments was noted. Soil pH (range 4.68 - 4.90) was not significantly different between treatments at the end of the experiment.

Despite the failure to demonstrate an allelopathic response in this experiment, the following points should be noted.

1. The applied leachates and phenolic acids might have an effect on seedling growth under different growing conditions.
2. The high organic content of the potting mix could lead to complexing of phenolics and micro - organism activity could cause their breakdown.
3. Even if an inhibition of mineral uptake were occuring, it need not limit seedling growth because of the abundant supply of mineral nutrients.
4. Phenolics can inhibit germination; their presence in leachates could be effective in inhibiting N.fusca germination rather than growth, and this would be important in the control of seedling numbers.

CONCLUSIONS

(a) A number of conjugated phenolic compounds are present in shoot leachates of N.fusca and P.colorata. Three simple phenolic acids were tentatively identified.

(b) Phenolics can be leached from the shoots of N.fusca and P.colorata in significant amounts. However, the total phenolic level in the forest soil is low (2-3 ppm). The total phenolic level in rotting wood is four times higher than the mineral soil.

(c) The N.fusca seedlings growing in a peat potting mix under ideal conditions are not inhibited by applied leachates and phenolic acids. The litters of N.fusca and P.colorata are also not inhibitory. Inhibition under growth-limiting forest conditions may be more likely. However, the most favourable seedling microsite, rotting wood, has a higher total phenolic level than adjacent mineral soil. Thus there is no indication that allelopathy involving N.fusca seedling growth is effective in the forest studied.

If allelopathy does occur in such a situation it is likely to be complex because there are many species involved in competition with N.fusca seedlings, growth conditions are limiting, and a large number of compounds could be involved.

SUMMARY (The Seedling Population)

Following a heavy mast year in 1971 large numbers of newly-germinated seedlings were present in the study area in 1972. Most germination probably occurred in the Spring of 1971 (Oct. and Nov.) with occasional late germination in the following Autumn. The germinating seed had survived on the ground for approximately 6 - 7 months throughout the Autumn and Winter of 1971. On the ground, the seed would be subject to decay, loss of viability and attack from herbivorous animals such as mice.[1] Some microsites may be more favourable for seed survival, for example, the mossy cover on some log and bare microsites would appear to offer suitable conditions of aeration, moisture availability and stability. However, extrapolation of the seedling survivorship trends for the three main microsite types indicates similar seedling densities at the time of germination which would mean that seed survival is not greatly affected by microsite conditions.

[1] Irregular irruptions of mice have been noticed following years of heavy beech seedfall (Elder, 1965; Wodzicki, 1950).

The estimated initial density of germinated seedlings (480,000 per ha.) is of the order expected following a heavy seed year (Wardle 1970a) and a moderate germination percentage (2 to 3%). Franklin (1971) recorded densities of silver beech cotyledonary seedlings of up to 120,000 per ha. for undisturbed microsites in the Alton Valley, Southland. Densities of 200,000 seedlings per ha. were found in red beech forest in Westland (Kirkland, 1961).

The seedling population was initially dominated numerically by 1st-year seedlings (480,000 versus 4,000 established seedlings in early 1972). However, the higher mortality rates of 1st-year seedlings compared with established seedlings mean a rapid decline in their relative importance. Decay rates for the 1st-year seedlings show the importance of microsite for seedling survival. Seedlings growing in the fern microsite (half life = 1.1 months) rapidly become extinct; none are present in the plots less than one year after germination. In contrast, seedlings in the log microsite (half life, 12.5 months), can be expected to survive in a hectare stand for up to 18 years. These microsite differences are reflected in seedling densities which are greatest for the log microsite and lowest for the fern microsite for both 1st-year and established seedlings. The log microsite increases in relative importance as seedling mortality continues, until a large proportion of the total seedling population is confined to logs (over 70% of established seedlings). Most of the remainder of the population occurs in the bare microsite. The few seedlings present in fern microsites probably occupy bare microsites recently invaded by ferns, since observations of newly-germinated seedlings under fern show that they are all ephemeral.

Development of distribution pattern.

Seedlings germinate in all microsites. As mortality occurs, they soon become confined to the limited number of log and bare microsites. From a presumably random distribution at the time of germination, the distribution pattern becomes more and more clumped. The clumps themselves may be randomly distributed, although in the case of fallen logs the distribution will depend upon the locations of trees of previous generations and the direction in which they fell.

On the available log and bares microsites, established seedlings are non-randomly distributed. This indicates that some of the available microsites are more favourable for seedling survival than others, which may result from a lack of competing species, the presence of a moss layer, well-rotten wood in the case of a log, a favourable light regime or other factors. To summarize, seedlings are confined to a limited area of scattered log and bare microsites, of which only some are favourable for red beech seedlings. It is the location of these clumps of high density in relation to canopy gaps, rather than the total number of seedlings, that is of importance in regeneration.

Seedling mortality

Mortality occurs throughout the year with most deaths during the Spring, Summer and Autumn. The exponential nature of the survivorship curves implies a constant mortality rate with time, (Antonovics, 1972). However, the mortality rate declines as densities decrease and as seedlings become larger and better established. The main causes of death seem to be associated with climatic factors, of which drought and low temperature are the most important. Seedlings must be able to survive a variety of climatic and biotic stresses in the sequence in which they occur. For example many seedlings sustaining frost damage during the Winter were unable to survive the dry periods in the following Spring.

Deer and goat browsing seems to have occurred in the past when the animal populations were much higher, but is not significant at present. Nothofagus seedlings are eaten when animal numbers are high (McKelvey, 1959; Elder, 1965), although generally they are not preferred food (Wardle et al, 1970).

The influence of competing species on 1st-year seedling survival can be both beneficial and adverse. The canopy of Pseudowintera, and the herbaceous and shrub cover of logs, appear to protect seedlings from dessication in an otherwise fully exposed situation, without reducing light below the compensation point. Removing the dense fern canopy prolongs seedling survival, probably because light intensities are raised above the compensation point as a result of the frond removal. The thick litter layer found beneath the fern canopy must decrease the chance of seedlings establishing a root system in the humus and mineral soil layers, making the seedlings very vulnerable to drought. From the trenching experiment it does not appear that root competition from mature overstorey trees affects seedling survival. The effects of trenching may, however, take longer than one year to become apparent and seedling height growth may also eventually respond to the removal of competition (Shirley, 1945).

The total number of established seedlings varies from 1200 to nearly 8000 for the three hectare stands studied. This variation can be partly explained by the availability of log and bare microsites. The Lower Stand with the lowest seedling density has the lowest proportion of these microsites. The stand with the highest density of established seedlings (the Middle Stand) is the least favourable for newly germinated seedlings. Conditions affecting seedling survival have evidently changed in the stand, which may be a result of older seedlings occupying the favourable sites and suppressing the younger seedlings.

Seedling densities given by Ogden (1971b) are generally higher than those estimated for established seedlings in this study. A density of 103,000 seedlings per ha. is given for an area which is adjacent to the Upper Stand but with an unusually extensive ground cover of moss and with much rotting wood which afford favourable seedling sites.

Combining the data for seedling input, mortality and growth in a simple population model enables some general predictions to be made about the future status of the seedling population. The amount of input into the population by seed germination appears to have an important effect on the population dynamics. Well-spaced heavy mast years with more than nine years of no seed-fall between them would lead to a decline in the population size. However, seed-fall is more regular than this, with lighter seed-falls between the heavy mast years. With the rates of mortality measured, the model suggests that such additional seed-falls would be sufficient to maintain, or even increase, the seedling population size.

CHAPTER IV THE TREE POPULATION.

Individuals over 2 m in height were included in this section of the population. Three different classes of trees were recognised: saplings (up to 10 cm diameter at breast height), subcanopy trees other than saplings, and canopy trees. Subcanopy trees do not attain the height of adjacent trees which form the upper canopy.

The aim of this study was to describe the age/size structure, spatial relationship and other features of the tree population.

SECTION 1. PHENOLOGY.

Results.

Resting buds form in the leaf axils by Autumn and bud opening and shoot elongation occur in the Spring. Bud opening continued from late Nov. (Lower Stand) to mid-Dec. (Upper Stand), and shoot elongation continued until mid-April (1972). Seedlings began elongation before the mature trees. Heavy leaf fall occurred in Jan. after the main growth flush, and also on occassions throughout the Winter.

Section 2. Size distribution

The aim was to describe size frequency distributions for the three study stands using stem circumference as a measure of tree size.

Methods.

Stem circumference to the nearest cm was measured at breast height. When large buttress-roots were present the measurement was taken above the buttresses. All live trees, stumps, standing dead trees and fallen logs were measured, although some dead trees covered with undergrowth were missed.

All trees within the Upper (1.232 ha area) and Lower (1.040 ha area) Stands, together with all trees within a 0.413 ha area in the north-east corner of the Middle Stand were measured.

The following characteristics of each tree were also noted:

(i) Site of growth -
Whether or not the tree was growing on a dead stump or fallen log.

(ii) Whether a canopy or subcanopy tree. Small trees in canopy gaps would be classed as canopy.

(iii) Growth form. The heights of a small number of trees were estimated with a Relascope instrument.

Results.

Live trees.

The size structure of live trees in the Upper Stand (Fig.11) is in the shape of a normal distribution with most trees in the 20 - 60 d.b.h. (diameter at breast height) size range. In contrast, the Middle and Lower Stands approximate the negative exponential distribution but with over-representation in the larger size classes and under-representation in the smaller classes. The Upper Stand has a single modal size class (30 - 40 cm d.b.h.); the other two Stands have two or three modal classes including the sapling class (1.5 - 10 cm d.b.h.). The Middle Stand is dominated by saplings which comprise nearly 55% of the stand population compared with only 8% for the Upper Stand.

The structures described by Ogden (1971b) for adjacent stands are similar to those described above. Stand 4 which is situated on the ridge-top adjacent to the Upper Stand has an identical modal peak but with fewer trees in the smallest and largest size classes. The Middle Stand is at a higher altitude on the same ridge-top as Stand 3, but lacks the third modal peak of Stand 3 and its second modal peak occurs in a smaller size class. The Lower Stand is not comparable with Stand 2 which is at a lower altitude and on a slope of different aspect.

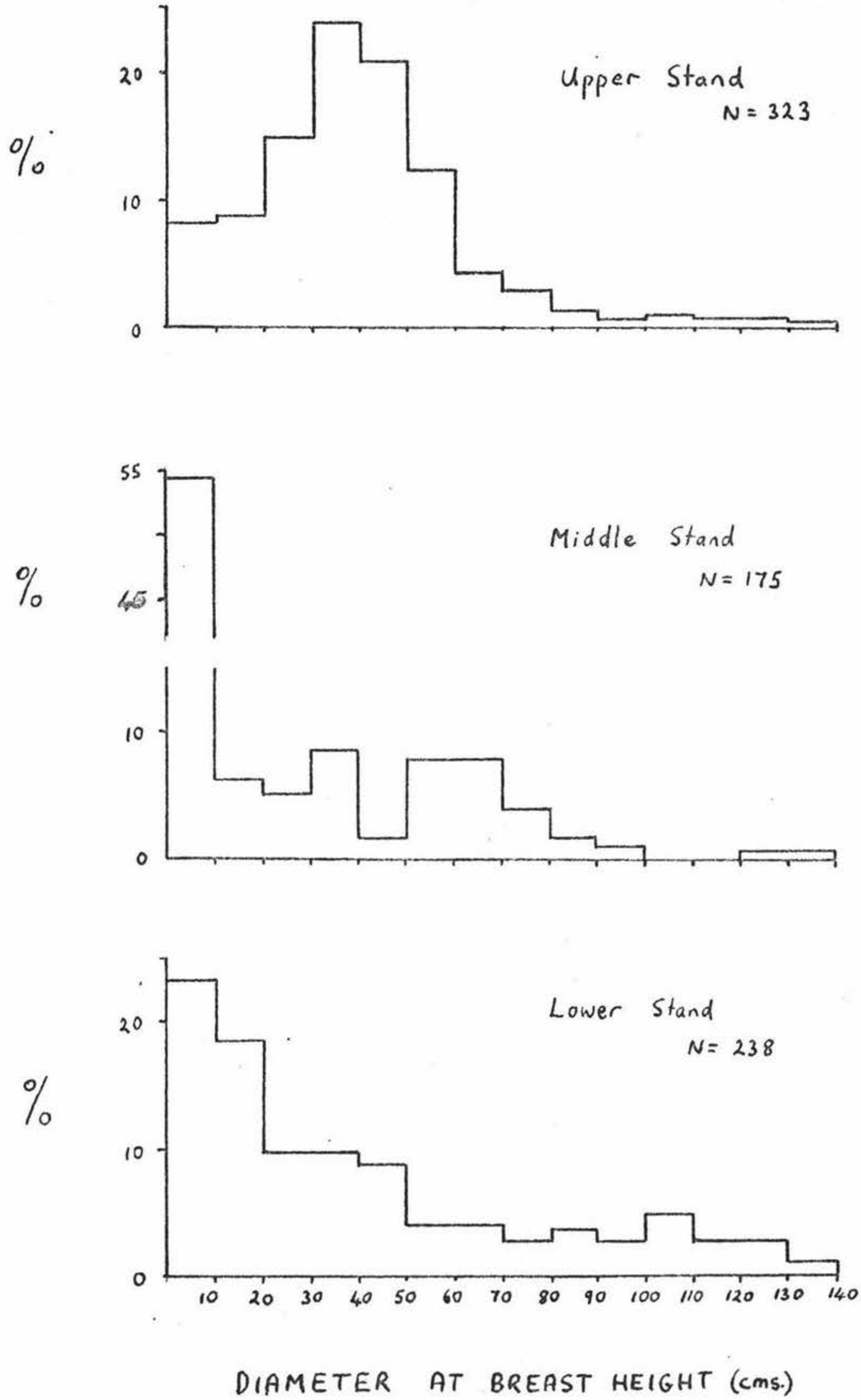


FIG. 11 Frequency distributions for stem sizes.
(Live trees)

Saplings

Saplings were divided into three equal size classes (Table 32). A lower age estimate of 16 ± 4 years was obtained from Fig 8, and an upper estimate from the age - size relationship (Fig 15). The age ranges for each size class were assigned assuming that size is proportional to age.

Table 32. Sapling size distribution.

	Circumference size class		
Stand	1.5 - 10 (cm)	11 - 20	21 - 31
Upper	12	7	7
Middle	69	14	12
Lower	18	19	18
Total	99	40	37
Age range (years)	16 - 30	30 - 43	43 - 56

Most saplings are less than 10 cm circumference, although the larger sizes are also well represented.

Dead Trees.

The size distributions for dead trees (Fig.12) differ from those for live trees. In the Upper Stand a modal class preceeds that of live trees and there is another peak, chiefly of stumps and fallen logs at 60 - 70 cm d.b.h. The other Stands have a more even distribution of sizes.

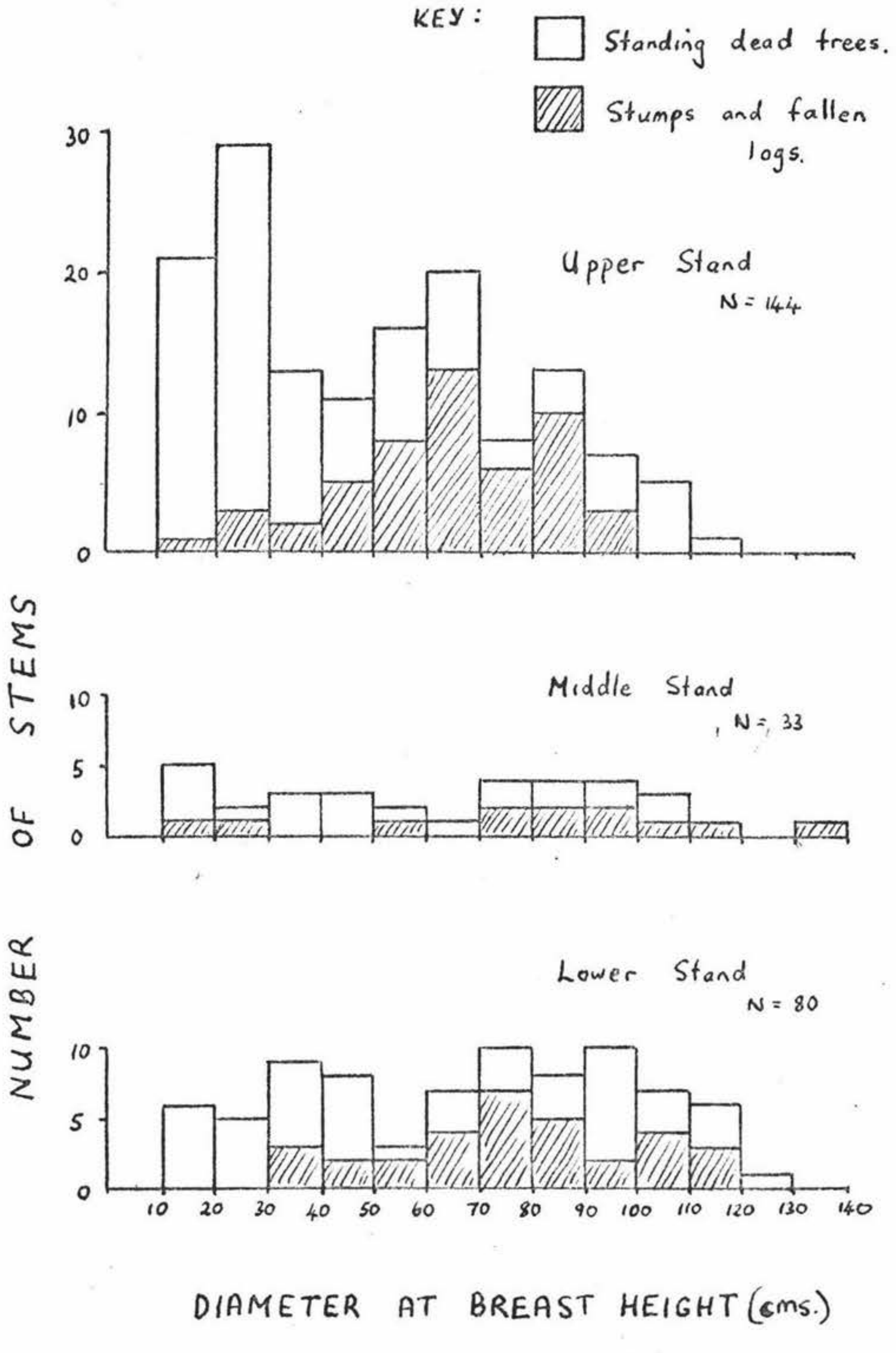


FIG. 12 Frequency distributions for dead stem sizes.

Basal Area and Tree Density.

Basal area was derived from stem circumference measurements.

Table 33. Basal Areas. (m^2/ha).

Stand	Live trees	Standing dead	Stumps & logs	Total dead
Upper	41.4	15.2	15.2	30.4
Middle	46.5	17.6	20.2	37.9
Lower	50.3	15.0	16.6	31.5

For two recently fallen trees with rotten centres only 30% of the measured basal area was living wood. Thus stand basal area as measured is likely to be an overestimate of living biomass with large trees of this nature present.

Tree densities for the three categories were derived (Table 34)

Table 34 Tree Densities (stems/ha.)

	Living				Dead		
Stand	sapling	subcan.	canopy	total	Standing	other	total
Upper	21	25	216	262	75	67	142
Middle	228	31	165	424	51	49	100
Lower	53	38	138	229	47	52	99

Canopy tree densities are low in the Middle and Lower Stands which are the most open-canopied. These Stands have higher densities of saplings and subcanopy trees.

Discussion

The significance of the size structures will be considered in Chapter V.

Each of the six stands that have been described on Mount Colenso appear to be homogeneous in terms of population structure. The stands can be considered as occupying distinct sites which differ in altitude, slope, aspect and other factors. A consideration of regeneration in an area of forest must take into account population differences associated with sites within the area.

Dead trees represent past members of the population which have not decayed completely. With a knowledge of decay rates, the dead trees can be used as an indicator of the population in the past.

Trees of all sizes die. A negative-exponential size structure for live trees would lead to a similar structure for dead trees, provided the proportion of trees dying was the same for all size classes. However, if the smaller trees took less time to decay than the larger ones, the size structure would tend to become more even with time. This may account for the relationship between the size structure of live and dead trees (Figs 11 & 12) in the Middle and Lower Stands. An alternative explanation is that % mortality is lower amongst small trees, but this is unlikely (see Section 6). In the Upper Stand a peak of standing dead preceeding the peak for live trees probably represents recently dead trees of the modal class. The second peak of stumps and fallen logs could represent a previous, even-aged generation, or could result from an accumulation of the more decay-resistant trees of this size.

The decay rate will depend upon the state of the tree at death, the position of decay and other factors. At death, some trees already have rotten centres. Small stems, which have a low wood volume, would take less time to decay than larger ones. Decay will also depend on whether the tree remains standing after death or falls to the ground; standing dead trees may decay more slowly if colonization by microorganisms, insects and other decomposers is inhibited in an exposed situation. Colonization by mosses, ferns, tree seedlings and shrubs will also contribute to the decomposition processes. Decay rates can be estimated in a number of ways:

(i) Direct observation, for example, by knowing the date of a storm or other catastrophe which killed trees. Red beech trees felled during milling below the Lower Stand 20 years ago are still mainly sound, although parts of the outer surface of some stems have decayed sufficiently to allow colonization by red beech and other seedlings.

(ii) Falling trees sometimes injure live trees in such a way that the event is recorded in the annual ring growth of the stem. This allows the date at which the tree fell to be established.

(iii) Ageing living trees growing on dead trees. An allowance must be made for the time taken for seedling establishment after the death of the tree. This can be as little as 20 years (see above). G.A.M.Scott (pers. comm.) has observed a red beech tree in the Eglington Valley, Fiordland which was estimated as 300 - 500 years old growing on a partially-rotten log. In this study, trees of up to an estimated 250 years of age have been found on rotting red beech remains, although most trees growing on rotting wood are up to 150 years (Section 3).

(iv) The average decay time can be calculated from the numbers of live and dead canopy-sized trees (30 cm d.b.h. and above) and the estimated mortality rate (Section 6). Of the 478 canopy trees enumerated in the three Stands, an average of 0.7% or 3.3 die every year. Thus the 274 canopy-sized dead trees represent the accumulation of trees dying over the past 83 years, which is an estimate of the average time for a tree to decay completely. With a mortality rate of 0.2%, this estimate is 287 years.

Taking the estimates from both the above methods, the decay time is in the range of 80 - 300 years.

Basal area is lowest in the Upper Stand, which has the most closed canopy. The open-canopied Lower Stand has a high basal area but this may be an over-estimate associated with the presence of many large senescent trees in the stand. The three Stands have low basal areas compared with other Nothofagus forest. Examples are, 73.5 m^2/ha for a red beech stand in the Routeburn Valley (Westerskov and Mark, 1968) and from 46 to 69 m^2/ha for closed stands of N.Solandri (Wardle, 1970b).

Section 3. Spatial pattern and Growing Site.

A study of the regeneration pattern requires a knowledge of the spatial relationships of trees within the stand. The position of all living and dead trees except fallen logs within a 1.232 ha stand was mapped. The resulting map can depict the pattern of a considerable area of forest which could not be viewed as a whole in the field.

Methods.

Starting with one tree in a corner of the Upper Stand the distance and direction of each successive tree was measured. Distance between trees was measured by marking off 2 m sections in a straight line along the ground using 2 m rules. The distance was read to the nearest 10 cm and the error involved was found to be ± 0.5 to 1.0 m for distances up to 14 m. Distances over 12 m were measured by a tape. Between tree direction was estimated by sighting with a Silva compass from tree centre to centre. The angle (0 to 360 degrees) was read to the nearest even-numbered angle and the error involved was in the order of ± 2 degrees. Additional tree to tree measurements were made to act as checks to the mapping procedure. Canopy gaps were approximately located. Distances from tree trunks to the edge of gaps, as well as a map sketched in the field were used to define gaps.

A scale map was drawn from the date obtained in the field (see Fig.13). The size and class of each tree is shown by a symbol.

A 104 x 120 m (1.232 ha), rhomboid-shaped area was mapped in this way.

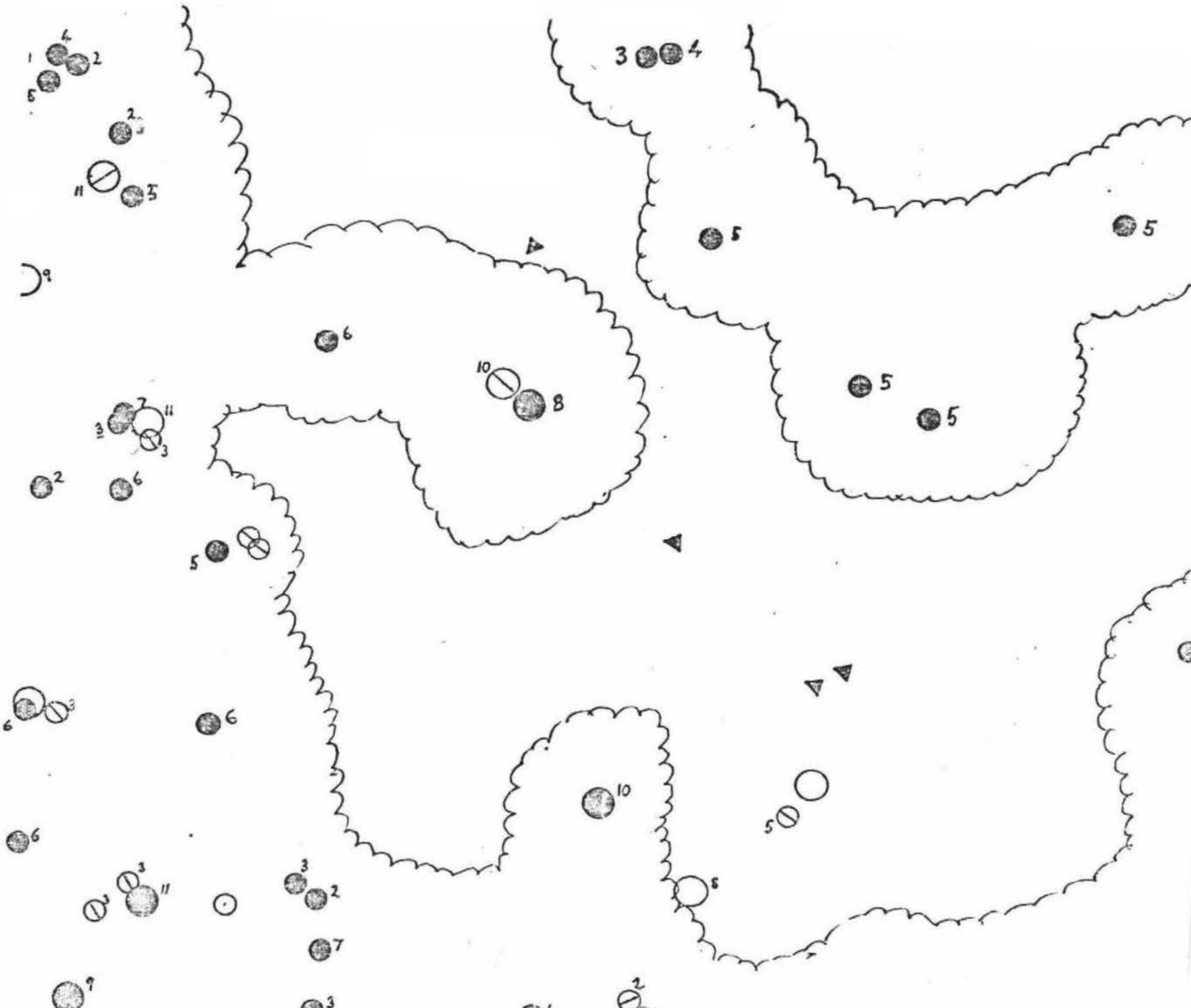
Pattern analysis, following the method of Grieg-Smith (1961), was done using all live trees in the mapped area. A grid of 1024 rhomboid quadrats, each 3.75 x 3.25 m (11.0 m^2) was used.

Fig. 13 (facing). Tree map of a section of the Upper Stand.

Scale 1 cm = 2.6 m

Key: Wavy line - Edge of canopy
Triangles - Saplings
Shaded circles - live trees
Open circles - Stumps and fallen logs
Open circles with diagonals - Standing dead trees.

Numbers refer to d.b.h.: 2 = 10-20 cms d.b.h.,
3 = 20-30 cms d.b.h., etc.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Results and Discussion.

Growing Site.

The following sites of growth can be recognised

(1) on mineral soil
(2) on fallen, rotten logs
(3) on rotten stumps or on the scattered wood beside the stump
(4) on rotten wood which is unrecognisable as stump or log.
(5) adjacent to a standing dead tree.

Growing sites were noted during circumference measuring, in particular the number of trees growing on wood (Table 35).

Table 35. Proportions of trees growing on rotten wood (as %)

Stand	Diameter class (cms, d.b.h.)									
	0-10	-20	-30	-40	-50	-60	-70	-80	-90	90+
Upper	64	39	58	48	48	35	36	22	25	0
Middle	59	29	0	60	33	21	33	14	0	0
Lower	75	48	61	33	52	20	10	14	0	0
Average	65	45	53	50	48	30	26	17	6	0

Younger trees are more commonly found on rotting wood and the proportion on wood declines as the wood decays with time. The largest tree found on wood (83 cms. d.b.h.) is estimated as 250 years old (Section 5). The proportion of trees on wood declines when the trees are over 50 cms d.b.h. (equivalent to 150 years old). Both stumps and fallen logs are favoured sites.

Over 65% of trees recruited to the sapling stage, and an even greater proportion of seedlings (Table 12), are growing on rotting red beech remains.

The regeneration of red beech is therefore greatly dependent on the growing sites produced by the death and decay of mature trees.

Position of Saplings, Mature trees and Dead trees.

Most saplings are associated with canopy gaps. Ten of the total of 26 are located in gaps and 6 within 1 m of the edge of gaps (in the Upper Stand). The remaining 10 are found beneath a closed canopy. Most saplings occur singly, the largest number in a clump being 4. (Large clumps with up to 10 saplings are common in the Middle Stand). Thirteen of the 26 saplings are in a clump or closely adjacent to canopy trees; these are unlikely to replace canopy trees. There are insufficient saplings or small trees in a position to fill the present, large canopy gaps.

Trees in the size range 10 - 20 cms d.b.h. usually occur as the smaller member of a clump of canopy trees. About a quarter are subcanopy.

Trees larger than 20 cms d.b.h. are more likely to be found singly. The largest trees are well spaced.

Stumps, logs and standing dead trees are found throughout the stand, usually in clumps. Dead trees of all sizes are found in the large canopy gaps, indicating that the formation of these gaps is recent.

Tree Clumps.

Groups of two or more trees growing close together are a feature of the stand (fig.13.), and indeed of red beech forest throughout the area (Ogden, 1971b). Three types of clump were recognised. Their nature and possible origins are described below.

(1) Associated with dead trees.

Groups of up to five live trees are found growing on the same fallen log or stump, or adjacent to a large standing dead tree. The size range of live trees in a clump can be as little as 2 cm d.b.h. difference between a group of 3 trees and up to 140 cm d.b.h. between 2 trees. The average size range in a clump is 22 cms d.b.h. which corresponds to an estimated age range of 90 years (Section 5.). The area covered by the stems of a clump is up to 4 - 6 m^2.

Different sized trees growing in a clump could be the same age and the range in size could be a result of the suppression of growth of some members of the clump. This effect has been demonstrated in even-aged populations of forest trees (Koyama and Kira, 1956).

Most clumps have one or more standing dead trees which are smaller than the live trees. These represent recently dead trees and their presence is consistent with the thinning of the smallest, and least vigorous, member of a high density clump, (White and Harper, 1970). The smallest live tree of a clump is usually subcanopy and would be the most likely tree to die next.

Pairs of live trees of up to 60 cms d.b.h. occur. Their trunks often grow close together at the base. Pairs consisting of one large live tree and a standing tree of similar size are also found. These pairs probably represent the final stages of clump thinning.

Clumps of mature trees arise from the colonization of the favourable rotting wood microsites by seedlings. Self-thinning within a clump continues over a long period and until a single large tree is left.

(2) Not associated with rotting wood.

The clumps have two or three live trees and one or more standing dead tree. The trees are larger than those in the clumps described above. These features are consistent with the clumps originating on rotting wood which has subsequently decayed away.

Pairs of well-decayed stumps are found, suggesting that the same pattern of clump development has occurred in previous generations.

A number of clumps consist of a large standing dead tree with one or two smaller, live trees growing near its base. In some cases the standing dead tree and live trees could be of the same generation, having established on the same rotten log or stump. In other cases the live trees could have established at the base of the standing dead tree following its death or near the end of its life span.

(3) Large scale clumps

The pattern analysis shows evidence of clumping at block sizes 16 and 128 (Fig.14). Although the existence of peaks in the mean square plot can be associated with high density aggregations in a stand, the interpretation of the size of these aggregations depends on the type of plant distribution (Westman and Anderson, 1970). The peak at block size 16 (area 192 m^2) could be associated with the replacement of large canopy gaps by clumps of trees. Clumps of this size can be located on the tree map and they consist of trees with a size range of up to 50 cms d.b.h. (age range 150 years). The trees are generally up to 60 cms d.b.h. If clumps of this scale represent the filling of a large canopy gap in the recent past, then colonization of the gap must have continued over a considerable period (up to 150 years). The block size 128 peak (area 1540 m^2) corresponds to the areas between the canopy gaps occupied by trees.

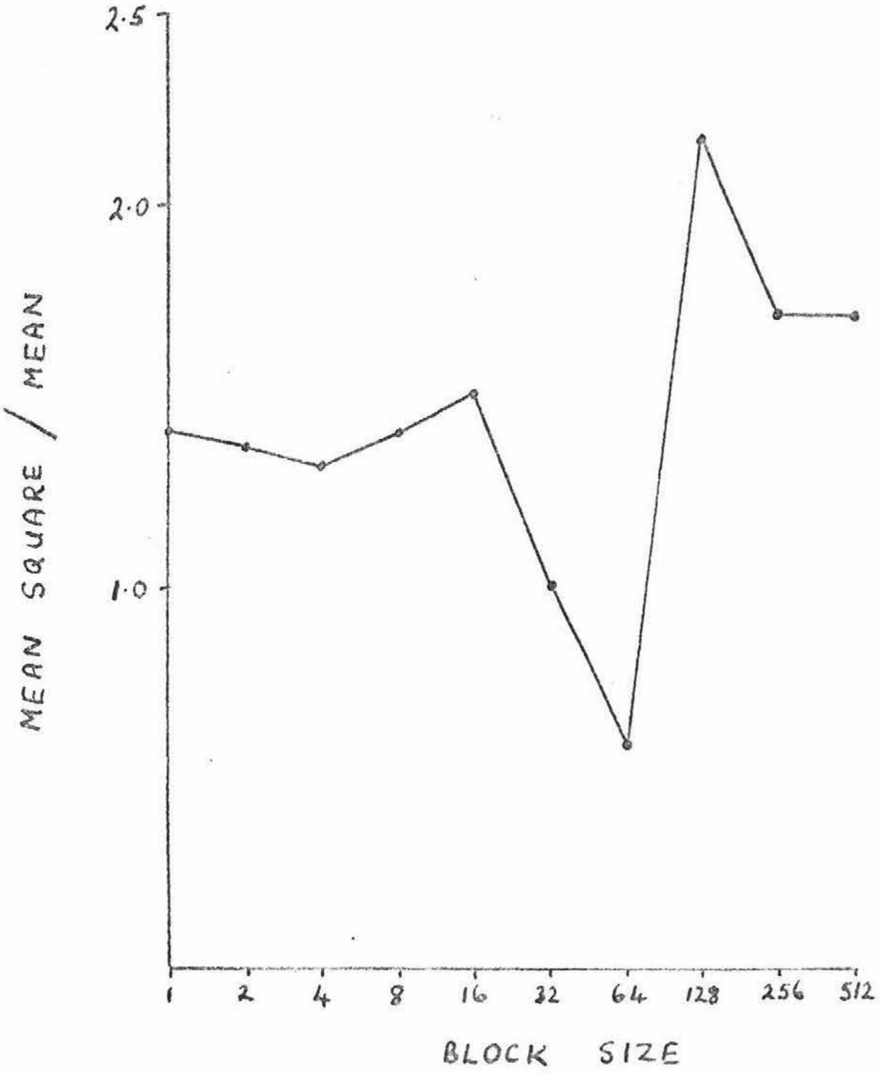

FIG. 14 Pattern analysis (Upper Stand)

Section 4. Growth Form and Canopy Cover.

Methods.

Observations on growth form and canopy dimensions were made in conjunction with circumference measuring.

An estimate of % canopy cover was obtained during transect sampling of microsites (Chpt.III, Section 4).

Results and Discussion

Canopy Cover

Table 36. % cover of tree canopy.

Stand	Transects				Average
Upper	77	93	90	93	88
Middle	64	60	73	60	64
Lower	72	50	67	58	62

The three Stands are open-canopied with large canopy gaps, especially the Middle and Lower Stands. Even in the Upper Stand gaps of up to 0.07 ha in area and 40 m in width occur (see Fig 13). There are also small gaps resulting from the death of one or several canopy trees.

Canopies of single trees are up to 16 m in diameter, with most canopies 6 to 8 m in diameter. Park (1971) described 'post stead-state' silver beech forest where gaps occupied 10 to 50% of the canopy.

Growth Form

Widely-spreading and heavily-branched trees are found in the Upper and Middle Stands, particularly around large canopy gaps. In contrast, many of the large trees in the Lower Stand have small canopies, even where there are no adjacent large trees.

Epicormic branches have developed up the main trunk of these trees. Many large trees have partially dead tops.

Stilt-like roots, as described by Cockayne (1926), are found on many small trees. These appear to develop in trees beginning growth on top of a fallen log. Roots extend to the ground on both sides of the log which then rots away.

The proportions of trees in the subcanopy category are shown in Table 37.

Table 37. Proportions of subcanopy trees (as %)

Stand	Diameter class. (cms d.b.h.)					
	0 - 10	10 - 20	20 - 30	30 - 40	40 - 50	50+
Upper	35	43	31	3	3	0
Middle	28	45	33	33	0	0
Lower	22	52	52	9	5	0
Avge.	27	48	38	8	3	0

Most subcanopy trees are in the 10 to 20 cm diameter class, although some are up to 50 cm in diameter. Most saplings are found in canopy gaps and therefore don't come within the subcanopy category. Trees usually commence growth in a canopy gap or have become canopy trees before reaching 30 cm in diameter, which means that most trees have attained the upper canopy by the age of 116 years (age estimate from Section 6.) The largest subcanopy trees are up to 50 cm in diameter.

The heights of large canopy trees range from 14 m in the Upper Stand to 25 m in the Lower Stand. There is much variation in height within this range making the upper canopy height very irregular.

Section 5. Growth Rates and Tree Ages.

Diameter growth rates were obtained by analysing annual growth ring width in stems.

Methods.

Several small trees were cut down and a stem section removed from the base. The sections were polished and the number of growth rings counted. Increment bores were also taken from 15 trees. The age estimates were based on the average ring width in the core and the diameter of the stem. Additional stem section counts from the study area were obtained from Dr. J. Ogden. Since cores and sections were taken at about 25 cm from ground level, a correction was made for the time to reach this height; four years were added to the ring counts (see Chpt III, Fig.8).

Results.

Age estimates for 24 trees, 9 of them from stem sections, are given in Fig.15. The relationship between stem size and estimated age is given by the linear regression,

$y = 1.045x - 27.3$, where y is circumference in cm and x the estimated age in years. This is equivalent to a diameter growth rate of 0.34 cm per year.

Growth rates vary considerably between individual trees, e.g. from 3.8 to 16.0 rings per cm, and can also vary greatly during the life of a single tree. Subcanopy trees grow more slowly than canopy trees. Growth rates in this sample do not show a correlation with altitude (for an altitudinal range of 915 to 1112 m).

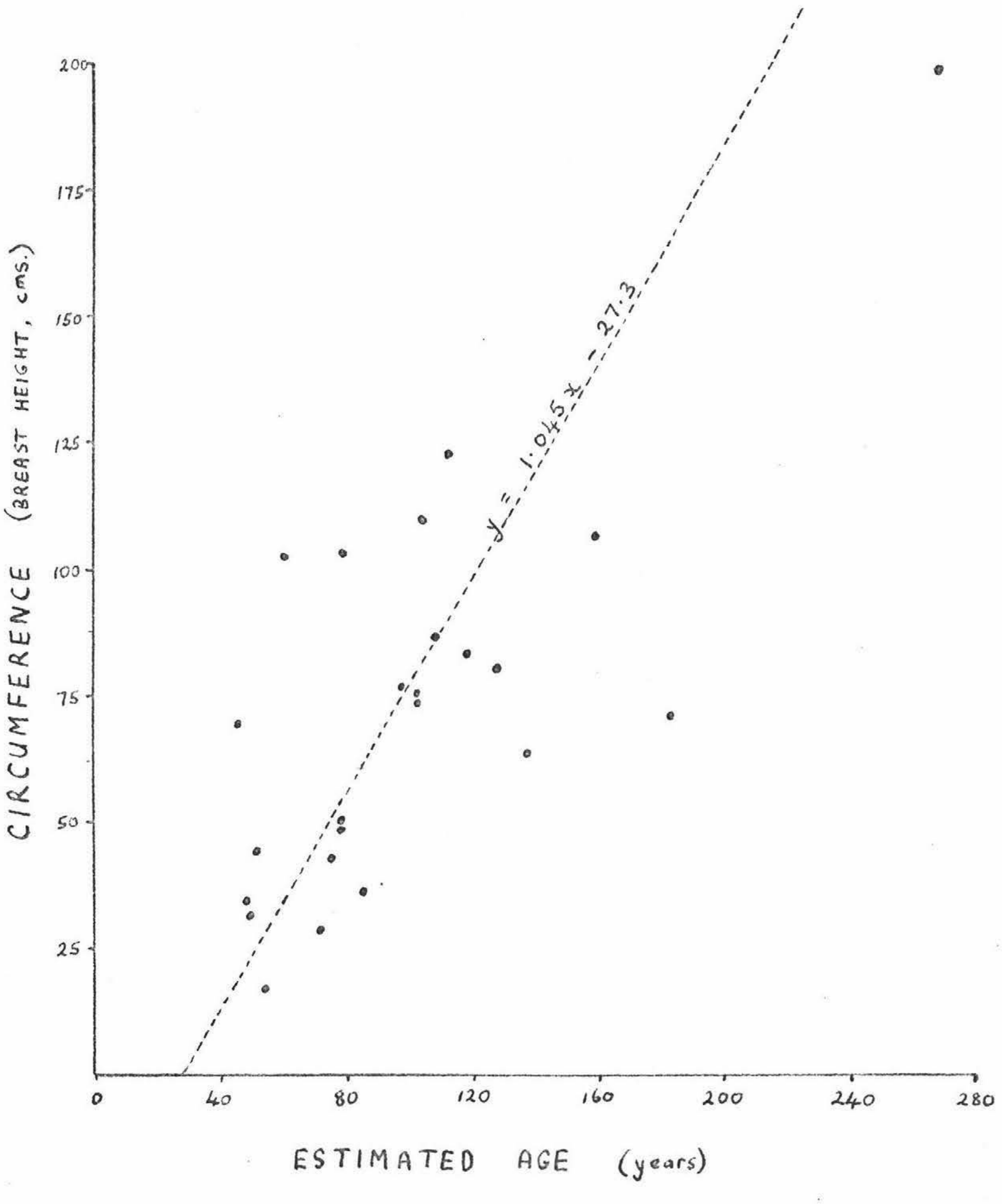

FIG. 15 Relationship between stem size and estimated age.

Discussion.

Linearity between diameter and age has been demonstrated for Nothofagus elsewhere, (Wardle 1970 b, Armstrong and Bussell, 1964). In this case, linearity is obscured by differences between individual growth rates. This variability could be related to the position of growth of each tree rather than to altitude or other site factors. The influence of neighbours on growth rate is important; trees subdominant to adjacent canopy trees have slower growth rates.

The linear regression used for estimating age is based on a small and variable sample. Consequently, estimates are in the order of ± 20 yrs for 10 cm d.b.h. and up to ± 80 yrs for the 40 cm d.b.h. and larger diameter classes (see Fig.15). Uncertainty increases with the size of the tree. This uncertainty makes interpretation of the size distributions as age distributions difficult. A distinctive age distribution will tend to be obscured by the size distribution as trees of the same age grow at different rates. However, a size distribution with modal peaks (Fig.11) is more easily interpreted as reflecting even-aged groups in the population than as a result of a slowing in growth rate at one stage in the life span.

Each diameter size class represents an age range of approx. 30 years. The maximum age in the sapling class is estimated as 56 ± 20 yrs. and the minimum 16 ± 4 years (from Fig.8). The largest tree measured, 140 cm in diameter, has an estimated age of 445 years which is in the lower range of the maximum life span of 450 - 600 yrs for red beech (Hinds and Reid, 1957).

Section 6. Mortality Rates.

Estimates of mortality rate are essential for a consideration of canopy replacement. Rates were obtained from direct observation and by indirect means.

Methods and Results.

(i) Direct Observation

No canopy trees died in 1972 in the 3 ha area contained within the three Stands studied. Two trees were blown down in 1972 in the areas adjacent to these Stands (estimated as 3 ha). This gives a mortality rate of 0.2 % per yr. for the 6 ha.

During circumference measuring (Section 2), three recently dead canopy trees with leaves and twigs still intact were noticed. Assuming that these trees died in 1971 an estimate of 0.6% mortality per yr in the three stands is obtained.

(ii) Evidence from dead material

Standing dead trees have recently died. The number of standing dead trees in each size class is expressed as a % of live trees in the next size class (this allows for tree growth: trees of the size class from which the dead trees came have subsequently grown larger). The analysis is done only for the diameter range 10 to 50 cm d.b.h. (17% of which are subcanopy), since the larger dead trees probably remain for a much longer time. The average % of dead to live trees is 33.3%, giving 1.1% mortality per yr (assuming that these trees have died over the past 30 years).

(iii) Evidence from the size structure of live trees

Assuming a stable, exponential size structure, and knowing the time needed to pass from one diameter class to the next, an estimate of expected mortality can be obtained (Wardle 1970b, p 629). Taking only the exponential section of the combined stand data (diameters of 30 cm and greater, Fig.11) and using the estimate of 30 yrs. for growth from one diameter class to the next (Section 5), 115 trees are expected to die in 30 yrs

(1.0% mortality per yr.). This estimate applies largely to canopy trees.

The mean of the four estimates is 0.7% per yr.

Discussion

The above estimates apply to normal mortality in what is assumed to be a stable population structure. Mortality rates probably vary considerably from year to year with variations in climate and consumer populations. Occasional catastrophes can produce high mortality over a short period. Without evidence obtained from a long period of observation, the above estimates can only be very approximate.

Elder (cited by Wardle, 1970b) observed mortality of 2.3% per year for 17 years and 0.6% per year for the next 10 years is an even-aged mountain beech stand.

For the whole red beech population, mortality is greatest amongst newly-germinated seedlings and decreases as seedlings become older (Chpt.III). Saplings growing in dense clumps in which thinning occurs would have a high mortality, as would larger trees subdominant to canopy trees. For the remainder of the population - trees not affected by suppression - mortality presumably remains low until the trees became senescent at the end of their life span. Few trees survive to the maximum age.

CHAPTER V. REGENERATION.

Regeneration involves the replacement of canopy trees after their death by younger individuals of the population. The processes of regeneration include,

1. (1) the death and decay of canopy trees
2. (2) the development of suitable microsites for seedlings
3. (3) seed production by canopy trees and seed dispersal
4. (4) seedling establishment, survival and growth
5. (5) growth of seedlings into mature canopy trees.

Regeneration can be represented by a simple model in which four different stages of the life cycle are considered as separate pools, each containing a number of individuals (Fig.16). The output from one pool becomes the input for the next. Individuals are affected by the processes of birth, growth and death, which are in turn influenced by a number of environmental factors such as light intensity.

Population Structure

The structure of a population can be described by the size or age frequency distribution. In the case of forest trees the distribution of breast height diameter is generally used rather than the age distribution which is difficult to obtain.

Populations tend to develop a stable age structure provided the environment is constant (Lotka, 1925). The stable structure for a forest tree population is considered to be that of a negative exponental (or J - shaped) distribution (Meyer and Stevenson, 1943). A constant input into the population (recruitment) in the form of germinating seedlings is balanced by output resulting from the death of individuals.

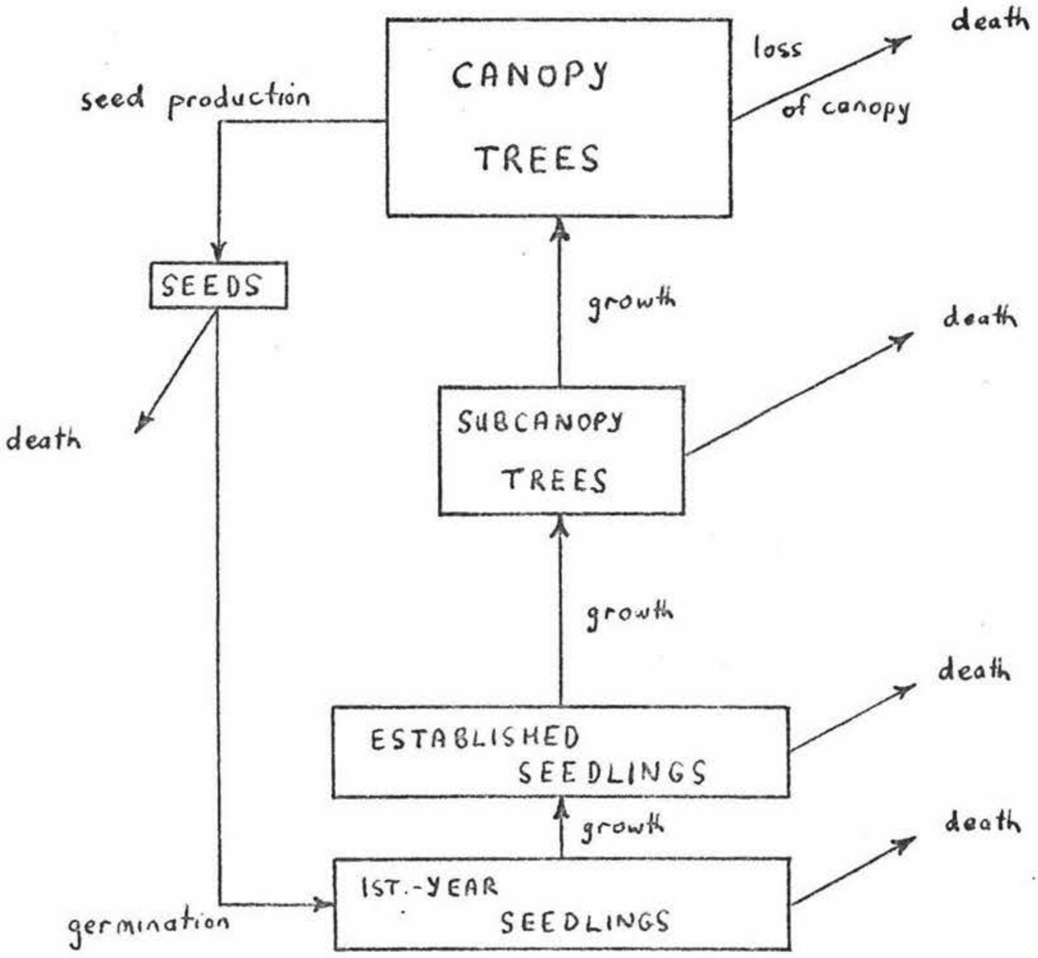

FIG. 16 Model of forest regeneration.

Mortality rates are constant throughout the population (Deevy, 1947). For each size class a certain proportion of the individuals will die and the remainder will grow into the next class which therefore contains fewer individuals. Consequently, the population structure is one of diminishing numbers in successively older age classes.

Non-exponential distributions are commonly found for tree species in undisturbed forest (Jones, 1945). These may take the form of a normal distribution, or of a distribution with two or more modal peaks. In these cases some age (or size) classes are under-represented in comparison with the stable, J - shaped distribution and some over-represented. An example of a normal distribution in Nothofagus forest is given by Ogden (1971b), and of two or three peak distributions by Westerkov and Mark (1968) and Park (1971). A lack of individuals in the smaller size classes has been noticed in Nothofagus forest throughout the Ruahine Range (Widdowson, 1960; Elder, 1965) and is referred to as a 'regeneration gap'.

Non-exponential diameter distributions probably reflect a population structure dominated by individuals of a similar age in the case of the normal distribution, or by a number of distinct age groups in the case of the multipeaked distributions. These distributions would result when a period of successful recruitment to the population is preceeded and followed by periods of no recruitment. Under-representation of an age class could be caused by heavy mortality or very rapid growth rates among individuals of that class. Wardle (1963) found these causes unlikely in the case of a regeneration gap in rimu.

The J-shaped distribution can also arise in an even-aged population at high density which is undergoing self-thinning (Koyama and Kira, 1956). An example of an even-aged red beech stand with this distribution is given by Foster (1931).

Nothofagus forest forms a stable climax over wide areas. Stable size structures are commonly found (Westerkov & Mark, 1968; Mark and Esler, 1970) and also result when stands showing nonstable structures are combined (Ogden 1971b ; Wardle 1970b). Nonstable structures may occur in an expanding population, for example during colonization of a new area, or in a declining population affected by catastrophe or internal development. The postulated deterioration of silver beech forest leading to the formation of scrub, fern, sedge and moss communities in the Tararua Range is an example of the latter (Park, 1971). Population structures could also alter as a result of long-term climatic change as proposed for South Island forests by Holloway (1954).

Types of Regeneration Pattern.

Three different patterns of regeneration in single species Nothofagus forest have been recognised.

(1) Replacement under canopy.

Seedlings, tolerant of the conditions under a closed tree canopy, are able to grow up into the canopy and replace mature trees as they die. Silver beech is able to regenerate in this way (Franklin, 1965).

(2) Gap replacement.

The formation of large gaps in the canopy with the death of individual canopy trees leads to the development of seedlings beneath the gap which eventually fill the gap. Seedlings and saplings present in a suppressed state beneath a closed canopy can rapidly respond by increasing growth if the canopy is opened (Cockayne, 1926). Gaps can also be filled by branch growth from adjacent canopy trees. Gap replacement is the common pattern in Nothofagus forest (Cockayne, 1926; Franklin, 1965).

(3) Large-scale replacement.

Large-scale regeneration may follow the destruction of a large area of canopy by fire, wind, snow, drought, parasitism, or other adversity. Elder (1965) has described destruction of beech forest by storm and snowfall in localised areas in the Ruahine Range. As with gap replacement, regeneration following a loss of canopy will be dependent on surviving seedlings or an adjacent seed source. Where recruitment following a catastrophe is complete and continues for a limited time, a dense, even-aged stand will develop. Further recruitment is inhibited until trees in the stand reach maturity and begin to die. At this point another period of recruitment is initiated and, following the replacement of all old trees of the stand, a new even-aged stand has developed.

This self-perpetuating cycle has been postulated for red beech in the study area by Ogden (1971b). The pattern may be partly obscured by the survival of some trees of the original stand or subsequent even-aged groups, giving a two or three aged structure. Examples of this structure have been described for mountain beech (Wardle 1970b) and for hard beech (Miller, 1963).

The State of Regeneration

The maintenance of population structure, and in particular the maintenance of canopy cover, will depend upon the success or failure of regeneration. A stable population will contain seedlings and saplings which are able to replace canopy trees as they die. Normally, the number of seedlings and saplings will be in excess of the number of canopy trees, which allows for mortality amongst seedlings. More seedlings will be continually added to the population by seed germination. The state of regeneration can, therefore, be superficially judged from the relative numbers of seedlings, saplings and mature trees.

Successful regeneration, however, may not rely on a large seedling 'base', and may only be necessary for short periods if the pattern of regeneration is cyclic. A regeneration cycle in Fagus forest in which seedling establishment is not successful for 150 out of the 250 years of the cycle has been postulated by Sukachev and Sylis (1964). The effective life span of a tree will determine the rate of regeneration necessary to replace itself. Thus a tree like red beech with a life span of up to 450 years need not be replaced for many centuries. In a mixed-aged forest not subject to catastrophe only those trees reaching the end of their life span need to be replaced for regeneration to be effective.

Study of Regeneration.

The rationale of most studies of regeneration is that the dynamics of the population can be deduced from the present features of the population, which are used as evidence of the immediate past and as indicators of the future. A knowledge of the size and age structure of the population (both live and dead trees), the spatial relationships between individual trees, saplings, seedlings and canopy gaps, the diameter and height growth rates, the effects of predators, and the seedling requirements is necessary in such an approach.

Direct observation over a long period of time is the ideal method of study. Permanent plots in which all individuals have been located and measured can be established and then revisited after a number of years. A permanent plot has been established in this study (the Upper Stand).

A forest stand undergoing regeneration can be viewed as a system involving the birth, growth and death of many individuals over a long period of time.

The forest is influenced by external factors such as climate and has a number of internal control mechanisms, e.g. the suppression of growth by adjacent trees. Consequently, mathematical models and computer simulation can be useful techniques in studying such a complex system.

Bosch (1971) has developed a mathematical population model for redwood regeneration which verifies the known high regenerative ability of this species. A computer simulation of the population dynamics of a mixed-species forest has been used to predict the climax state (Botkin et al, 1972).

Discussion

Processes of Regeneration

(1) Death of Canopy trees.

Trees die from a variety of causes: snow-damage, disease, browsing, dessication, drought, soil movement, etc. Mortality in the study area proceeds at a slow rate (less than 1% p.a. for canopy trees). Mortality rates would be higher for trees in clumps than for separate trees, and also for suppressed saplings and subcanopy trees. The area of canopy gap created by the death of a single tree would be about 40 m^2 for an average-sized tree and up to 150 m^2 for a large tree. The opening of a gap increases the exposure of adjacent trees which may lead to a further extension in the size of the gap with the death of trees around its perimeter. The large gaps in the study area are the result of the deaths of a number of adjacent trees. Gaps may be partially or wholly filled by the outgrowth of branches of adjacent trees. A dead tree is sometimes uprooted, but more often remains standing after death before breaking off near the base.

(2) Development of suitable seedling microsites.

Creation of a canopy gap results in a change in the microclimate of the forest floor. Light intensities are higher (chpt 3, Section 8), and with more exposure to direct sunlight, there will be a reduction in air humidity and an increase in air temperature. Soil conditions will also change, partly as a result of the death of the tree roots. Thus, conditions become more favourable for seedlings in some respects (e.g. high light intensity) and less favourable in others (e.g. more exposure to dessication). Other species may respond to the changed conditions and become the dominant ground cover, thereby reducing the chances for red beech establishment.

Aristotelia serrata, Pseudowintera colorata, Rubus cissoides and Fuchsia extortica are the predominant colonizers of gaps.

The availability of the favourable rotting wood microsite depends upon the rate of decay of the dead tree. It may take several hundred years for a stem to rot completely but a fallen log will be sufficiently decayed within tens of years (Chpt 4, Section 2). Thus, a long period is available for colonization.

(3) Seed Production.

Seedfall is irregular with massive falls every 6 to 16 years and lesser falls in some of the intervening years (Chpt 3. Section 2). The size of the seedling population would not seem to be limited by the amount of seedfall in view of the large seed output.

(4) Seedling establishment, growth and survival.

The log and bare microsites, which comprise a small proportion of the forest floor area, are the only suitable ones for seedling establishment. The more extensive fern microsite is unsuitable because light intensities are below compensation point and a thick litter layer prevents rooting in the soil.

Of the available log and bare microsites, only a few are colonized by red beech seedlings. These are generally without a cover of competing species and have a moss layer. The log microsite supports higher densities of red beech seedlings than the bare microsite and seedlings on logs grow faster and have higher survival rates in the first year of growth. The marked favourability of the log microsite could be the result of a number of factors: the elevation of logs means a better light regime, the rotting wood as a root medium has good water retention properties and high nutrient levels, the moss covering is favourable for seedling germination and seed survival. The dependence of seedlings on rotting wood suggests that the nutrient supply in the ecosystem may be limiting to seedlings, so that regeneration depends on the release by decay of the nutrients immobilized in the stems and branches of canopy trees.

Many seedling deaths are related to exposure to direct sunlight in canopy gaps. Low temperatures during Winter also appear to cause deaths and limit growth.

Deer and goats have browsed seedlings when their population numbers have been higher, but no complete destruction of seedlings in the past is evident. The composition of the undergrowth has been altered by the browsing of the most palatable species (e.g. Griselinia littoralis seedlings are absent) which may have led to the expansion of ferns and other species, especially the unpalatable Dicksonia lanata and Pseudowintera colorata. Trampling by these animals may have reduced the moss covering of bare ground.

Pattern of Regeneration.

Replacement under canopy does not appear to be the regeneration pattern. Some saplings and small trees are found under a closed canopy but they appear to be suppressed. Sub canopy trees are usually the smallest member of a clump and have presumably developed in a canopy gap with the other trees.

The evidence supports the view that gap replacement is the normal pattern. Most saplings are found within or around the perimeter of the large canopy gaps that exist. Regeneration is largely dependent on rotting wood microsites which become available with the death of canopy trees and the associated gap formation. Sapling distribution is not related to light intensity in any obvious way. Light intensities in canopy gaps are more commonly near the optimum for seedling growth, but the maximum intensities and associated exposure found in gaps would tend to limit growth. This makes the edge of a large canopy gap an ideal situation for seedlings and saplings. The results of pattern analysis (Chpt 4. Section 3) show a scale of tree aggregation equivalent to a large canopy gap, a suggestion that gaps have been successfully filled by a number of trees in the past.

From the evidence of stumps and logs within canopy gaps, the gaps formed, at the most, 300 years ago. It is more likely that they date from around 150 years ago, the time of the postulated catastrophe (see below), and up to the present.

Size Structures.

Large scale replacement following a catastrophe can be used to explain the structures of the three stands.

The Upper Stand is dominated by smaller trees which could represent an even-aged group approximately 120-180 years of age. An even-aged group could give rise to a normal size distribution as a result of variation in individual growth rates. There are relatively few large trees in the Stand (see Table 38). Thus the stand structure is consistent with a period of large scale regeneration about 150 years ago which followed the destruction of a proportion of the mature trees (the survivors still remain).

The Upper Stand is situated just adjacent to Stand 4 (Ogden, 1971b) where none of the larger trees remain and the same even-sized group forms a complete canopy. In this exposed, ridge-top site the destruction was apparently more complete and the following regeneration more successful. A severe storm which blew over trees mainly on the ridge-top may have been the cause.

The structure of the Middle Stand could result from a less devastating catastrophe (at about the same time as in the Upper Stand) which was followed by a less extensive period of regeneration represented today by two adjacent modal size peaks (Fig.11). At present a further period of regeneration is in progress.

The Lower Stand structure approximates a negative exponential distribution which indicates a constant population input over a long period. The stand is not regenerating successfully and the large canopy gaps present could have formed in the suggested catastrophe of 150 years ago but were not filled by subsequent regeneration.

Thus the occurrence of a single catastrophe can be used to explain the divergences from a stable, exponential population structure. A return to a stable structure is only apparent in the Middle Stand.

Success of Regeneration.

The complete stand population structures, together with basal area and canopy cover, are given in Table 38.

Table 38.

				Canopy trees			
Stand	1st-year seedlings[1]	Established seedlings[2]	Saplings & subcan.trees	20-70	70-140 (cms d.b.h.)	Basal area[3]	% Cover[4]
Upper	134,200	3110	46	197	19	41	88
Middle	38,200	7990	259	131	34	47	64
Lower	61,800	1200	91	88	50	50	62
Mean	78,100	4110	132	139	34		

1. from Table 11
2. from Table 15
3. living biomass, Table 33. (m^2/ha)
4. from Table 36.

In terms of numbers, the first-year seedlings dominate the population. Excluding these seedlings, most of which are short-lived, the established seedlings predominate in the remainder of the population. However, the number of established seedlings for each canopy tree, and, more importantly, the number of saplings and subcanopy trees for each canopy tree is low, (Fig.17). The Middle Stand has the largest numbers of established seedlings and saplings.

The number of seedlings and subcanopy trees is not inversely proportional to the tree basal area. This is inconsistent with the theory that regeneration is stimulated following a reduction in stand biomass below a certain level (57 m^2/ha for mountain beech, Wardle 1970 b). The Upper Stand with the lowest basal area is also the most close-canopied, although large canopy gaps without adequate saplings in them for re-regeneration are present. While regeneration appears to be most successful in the Middle Stand which could be related to the large extent of canopy gaps, the Lower Stand also has a large area of canopy gap but few seedlings and saplings.

With a knowledge of growth and mortality rates, the relative numbers in the different sections of the population can be considered more significantly. Assuming a mortality rate of 0.7% p.a. for all trees (Chpt 4, Section 6.) and a growth rate of 10 cms diameter per thirty years (Chapt.4, Section 5.), the potential input and output of the sapling class and the output from the canopy tree class were estimated (Table 39.).

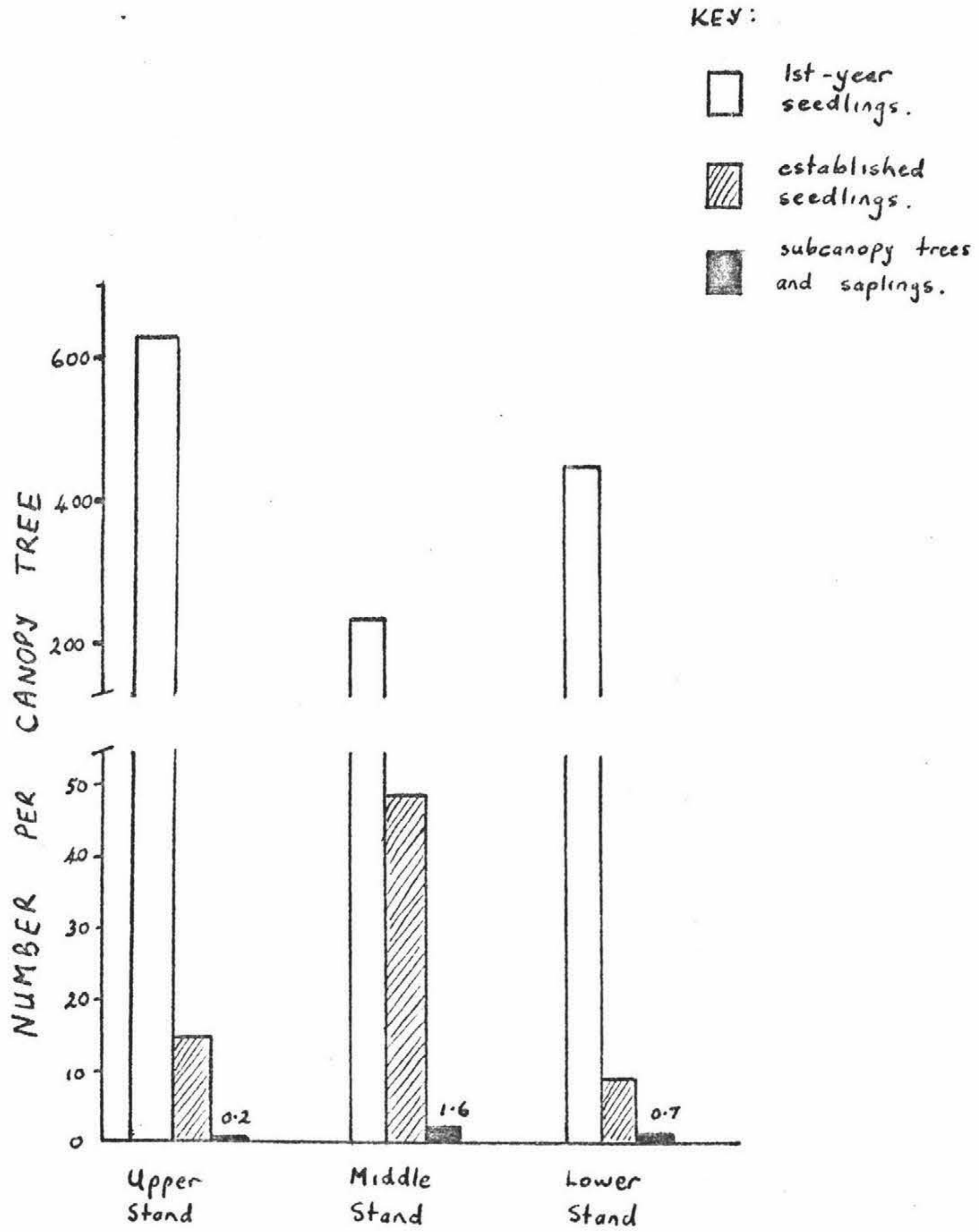

FIG. 17 Relative numbers of seedlings, saplings and canopy trees.

Table 39. Predicted sapling input in relation to canopy losses.

Stand	No.saplings[1]	Input from seedlings[2]	Sapling mortality[3]	Sapling output[4]	Canopy & subcan. tree mortality
Upper	21	373	5	16	51
Middle	230	959	48	182	41
Lower	53	146	11	42	37

1. No. per ha. from Table 32.
2. In 30 yrs and assuming 0.4% p.a. of the established seedling population grows to sapling size (Chpt. 3. Section 6).
3. 0.7% p.a. mortality in 30 years
4. In 30 yrs. Mortality losses subtracted from number of saplings present (column 1.) and assuming that all surviving saplings grow into next size class.

There is potential for an increase in sapling numbers from the growth of existing seedlings. In the Middle and Lower Stands the estimated numbers of saplings growing into mature trees exceeds the numbers of canopy trees likely to die. This is not so in the Upper Stand. Thus, regeneration is likely to be successful in the Middle Stand and, more doubtfully in the Lower Stand.

Total seedling and sapling numbers do not adequately reflect the state of regeneration since their spatial distribution is not random. Not all saplings are associated with canopy gaps and few are found in the centres of large gaps (Chpt 4, Section 3.). While all saplings are potential replacements for canopy trees, most are found in clumps or adjacent to large trees and will not survive as replacements.
In the Upper Stand half the saplings are in such a position. Referring now to the calculated sapling contribution (Table 39), only in the Middle Stand will there be adequate sapling numbers for successful regeneration.

Conclusion

At present, regeneration is not effective in the study area as is evident in the existence of large canopy gaps which are occupied by few seedlings, saplings and small trees. A ridge-top site appears to be the exception to this pattern.

The life cycle of red beech is weakest at the seedling level. Seedling, and consequently sapling, numbers are limited mainly because of the lack of suitable microsites on the forest floor. Most potential microsites are occupied by other species. Environmental factors such as light intensity also influence seedling numbers.

A long-term change in climate which has created conditions less favourable for red beech seedling and tree growth in the last 100 - 200 years could be the cause of the regeneration failure. Such a climatic change could also lead to a downward altitudinal migration, as suggested by Ogden (1971 b) for the study area. However, there is no clear sign of a retreat at the upper altitudinal limits (1185 m, 73 m above the Upper Stand), although seedlings are scarce here. At the lower limits (700 m on the southern slope of Mt. Colenso) there is no evidence of an invasion of podocarp forest. The low altitude stand described by Ogden (1971 b) as an example of such invasion had been selectively milled in the 1920's (A.C.Watkins pers.comm.), which could account for the large numbers of saplings and young trees present. The size distributions of the three study stands are not consistent with a migration, although the effects of regeneration cycles would obscure any altitudinal trends.

Deer browsing of beech seedlings has also been suggested as a cause of regeneration failure (Widdowson, 1960), but no evidence to support this was found. A small amount of browsing has occurred. The combined effects of introduced animals; seedling browsing and trampling of the soil by deer and goats, foliage browsing by opossums and seed predation by mice, must have adversely affected the regeneration mechanisms of red beech within the past 50 - 60 years. Their effects may account for present and future failure of regeneration, but regeneration was not successful before the introduction of these animals.

Appendix Table 1.

Mean monthly rainfall in mm (1961 - 1972)

J	F	M	A	M	J	J	A	S	O	N	D
108	74	93	99	111	147	132	121	113	96	102	127

Mean monthly minimum temperature (°C) (1961 - 1972)

J	F	M	A	M	J	J	A	S	O	N	D
7.5	7.1	6.6	4.1	1.9	0.4	-0.4	0.2	1.4	3.1	4.4	6.3

Appdx. Table 2. Monthly counts of 1st-year seedlings in permanent plots.

	Month of year. (from Jan.1972)												
	J	F	M	A	M	J	J	A	S	O	N	D	J
Log microsite.													
Upper Std.	402	386	376	353	344	320	305	-	288	273	259	240	229
Middle "	-	170	156	136	112	97	95	-	81	74	60	55	50
Lower "	-	155	149	144	131	124	123	121	114	113	110	104	90
Cover removal	-	32	17	15	12	8	8	-	7	5	5	4	2
Bare microsite.													
Upper Std.	212	182	159	142	137	107	98	-	86	73	60	57	49
Middle "	58	47	36	26	21	17	16	-	12	6	5	5	4
Lower "	-	111	102	91	84	77	66	61	58	54	46	42	35
Trenching	113	88	76	67	59	55	49	-	46	41	34	29	23
Pseudowintera removal	-	52	13	7	5	4	4	-	3	2	2	1	1
Fern microsite.													
Upper Std.	-	17	6	1	0	0	0	-	0	0	0	0	0
Middle "	-	11	6	2	2	2	2	-	0	0	0	0	0
Lower "	-	33	14	4	3	0	0	0	0	0	0	0	0
Frond removal	-	40	3	3	3	3	3	3	3	2	2	1	0

Appendix Table 3.

Colour reactions and R_F values of spots from 2-D chromatography of hydrolysate extracts from shoot leachates.

	UV/NH_3 colour	Nitroaniline/(1) NaOH colour	R_F value.	
			BAcW	Ac.
N.fusca extract.				
Spot No.1	purple	brown	0.86	0.55
2	red		0.18	0.64
3	blue		0.11	0.75
4	purple	red	0.08	0.68
5	blue		0.02	0.71
6	purple		0.03	0.58
7	purple		0.03	0.47
8	purple		0.45	0.03
9	red		0.60	0.06
10	purple	brown	0.59	0.17
11	bright-yellow		0.91	0.04
P.colorata extract.				
Spot No.1	purple		0.76	0.65
2	blue		0.21	0.74
3	brown	brown	0.17	0.64
4	purple	brown	0.06	0.69
5	light blue		0.00	0.73
6	blue		0.02	0.58
7	blue		0.02	0.47
8	bright blue		0.00	0.13
9	green		0.52	0.31
10	none	brown	0.00	0.59

(1) Most spots seen under UV did not stain with nitroaniline/NaOH.

Appendix Table 4

Initial heights and dry weights of N.fusca seedlings (averages and std. deviations)

	Oct. collection	Nov. collection
Height (mm.) (all seedlings)	82.8 ± 17.6 (N = 15)	47.7 ± 9.1 (N = 35)
Weight (mg.) (of subsample)	98.16 ± 57.73 (N = 5)	36.4 ± 5.96 (N = 5)

Final heights and dry weights (averages and std. deviations)

For each treatment N = 5

Litter Treatments	Height (mm)	Dry weight (mg.)
Control	246.8 ± 65.6	1054.3 ± 441.5
P.colorata litter	240.4 ± 72.2	711.3 ± 362.7
N.fusca litter	190.0 ± 28.8	975.0 ± 444.8
Leachate Treatments		
Control	102.0 ± 29.1	225.8 ± 84.5
N.fusca	105.2 ± 18.0	268.8 ± 55.6
P.colorata	123.6 ± 29.1	312.0 ± 113.6
Dicksonia lanata	95.2 ± 25.2	253.0 ± 138.9
Griselinia littoralis	114.0 ± 28.2	237.1 ± 91.7
Ferulic acid	110.4 ± 35.4	206.8 ± 81.5
Vanillic acid	112.8 ± 26.7	284.8 ± 149.1

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