STUDIES ON THE VEGETATION OF MOUNT COLENSO, NEW ZEALAND

3. THE POPULATION DYNAMICS OF RED BEECH SEEDLINGS

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SUMMARY: A population of red beech *(Nothofagus fusca)* seedlings was studied in a forest dominated by red beech but apparently with little regeneration. Estimates of the germination, growth and survival rates of seedlings growing on different microsites were obtained in three, one hectare stands over a one year period and the size and age structure of the population examined. Irregular and sometimes massive seedfalls occur but some seedlings establish at least every two or three years. The most favourable site for red beech seedling survival and growth is on rotting logs, but bare areas on the forest floor are also suitable. Extensive stands of *Dicksonia lanata* completely prevent seedling establishment. A simple model based on estimated survival rates on the various microsites and assuming certain patterns of seed input suggests that the population size is likely to be maintained or increased in the future. Little evidence was found for an adverse effect by introduced animals on the seedling population.

INTRODUCTION

The composition of red beech *(Nothofagus fusca)* forest on the western slopes of Mount Colenso has been described by Ogden (1971a). Red beech is the sole canopy species between about 840 m and 1120 m altitude. A preliminary study of red beech population dynamics suggested that downhill migration and a 'regeneration cycle' may explain the size frequency distributions in four stands (Ogden 1971b).

This paper examines the hypothesis that the red beech seedling population has a stable structure, resulting in a sustained level of recruitment to the mature section of the population. The size of the seedling population is governed by (1) input from seed dissemination, (2) the frequency of suitable microsites on the forest floor, (3) seed germination, seedling establishment and subsequent survival in such microsites, and (4) recruitment into the mature population. Estimates of seedling germination, growth and survival rates were obtained over one year. The effects on seedlings of several environmental factors, particularly light intensity and allelochemicals, were also examined (June, 1974).

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METHODS

Three, one-hectare stands were located along a ridge running south from the summit of Mount Colenso. Details are given in Table 1. The stands lie on the same ridge as stands 2, 3 and 4 of Ogden (1971b).

TABLE 1. *Descriptions of study stands.*

Stand	Aspect	Average Slope	Altitude
Upper (slope)	W.S.W.	44°	1080 m
Middle (broad ridge-top with some flat areas)	S.	20°	1030 m
Lower (slope)	W.S.W.	42°	950 m

Two seed traps were set out in the Autumn of 1972. Seeds and flowers were searched for in the litter and foliage throughout the study period. Seedlings are arbitrarily defined in this study as individuals up to 2 m in height. Red beech seedlings 2 m tall have a diameter at the base of 1.4 to 2.5 cm and an age of approximately 20 years. Large numbers of seedlings arising from the 1971 mast seed year were present. These are referred to as 'first-year' seedlings, and older seedlings as 'established' seedlings. Three main types of seedling microsite were recognised, 'log', 'bare' and 'fern', as described by Ogden (1971b). Microsites were distinguished without reference to overhead canopy conditions. Microsite frequencies in the three stands were determined by categorising the nature of the surface at 396 regularly-spaced points spaced along four transects in each stand.

Permanent plots were established in each microsite type along four transects in each stand. A total of 53 plots, each 4 m^2, were used. All red beech seedlings within demarcated sections of the plots were counted at monthly intervals. First-year seedlings were tagged so that newly germinated seedlings could be identified each month. A sample of 232 established seedlings was tagged and seedling heights measured to the nearest 0.5 cm each month. Observations were made on the possible causes of seedling mortality.

Densities of first-year seedlings were obtained from the permanent plots and established seedling densities by stratified random sampling with 1 m^2 quadrats. A random point along each 14 m of a transect was chosen and the nearest available 1 m^2 square of each microsite type sampled. There were five transects in each stand giving a total of 107 samples for each microsite. In conjunction with this sampling, established seedling heights were measured and a sample removed for age determination. Age estimates were obtained from growth ring counts of basal stem sections stained with aniline sulphate and examined under 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. Uncertainty in the age estimates is approximately ± 2 years or ± 1 year for the youngest seedlings. The period of study was from December, 1971 to January, 1973, observations being made at least once a month.

RESULTS

(a) Seed Production

No flowering or seedfall occurred in the 1971/72 summer and only a few flowers were seen in 1972/73. A heavy seedfall had occurred in 1971 judging from the large numbers of newly germinated seedlings present in December, 1971. The history of *Nothofagus* mast years in the Ruahine Range is fragmentary but heavy mast years were noticed in 1936 (Kean and Newcombe, 1937), 1949 (Greenwood, 1951), 1955 (Elder, 1965) and 1963 (N.Z. Forest Service file, J. L. Nicholls pers. comm.). Elder (1965) mentions a four or five year interval between mast years. Thus in the past 40 years heavy seedfalls have been noticed at intervals of 6 to 16 years. There were presumably light seedfalls in some of the intervening years and some years with no seedfall.

(b) Microsites

Microsite frequencies are given in Table 2. The fern microsite predominates (with *Dicksonia lanata* forming extensive stands), although there is a significant proportion of rotting wood in all stands. Fallen red beech logs become available for seedling colonization within 20 years and for up to 250 years after falling (June, 1974). A moss layer is found on 5% of the bare microsite and 40% of the log microsite.

TABLE 2. *% Frequencies of microsite types.*

	Upper Stand	Middle Stand	Lower Stand
Rotting wood	21.1	20.1	15.7
Bare	21.8	27.6	5.3
Fern	57.1	52.3	79.0

(c) Seedling Numbers

Densities of first-year and established seedlings show significant variation with stands and microsites (Tables 3 and 4). The Middle Stand has the highest density of established seedlings but the lowest density of first-year seedlings. The log microsite is the most favourable for all seedlings and one year after mast germination 85% of the surviving seedlings were found on logs. Although initially a large number of seedlings were found in the fern microsite none survived for more than one year (Fig. 1). Most first-year seedlings were found on mossy surfaces (including 99% of those in the log microsite and 64% of those in the bare microsite). The frequency distribution for established seedling numbers per quadrat obtained from random sampling shows a significant (Chi-squared $P<0.01$) departure from randomness, indicating their patchy distribution on the different microsites. Most established seedlings (71%) were found on logs.

Total seedling numbers in each stand were obtained by multiplying mean seedling densities by the area occupied by each microsite (see Table 2). First-year seedling numbers in all stands (Fig. 1) show a rapid decline over a period of 14 months from an estimated total of 478000 p.ha. at germination. By contrast, there was a mean number of 4110 established seedlings p.ha. (Table 5).

TABLE 3. *Average densities of first-year seedlings (Number p. m²).*

	Microsite		
Feb. 1972	Log	Bare	Fern
Upper Stand	85.0	37.0	2.0
Middle Stand	46.5	12.4	3.0
Lower Stand	66.6	23.6	15.6
Mean with standard error	65.4 ± 9.5	25.7 ± 4.4	8.4 ± 1.9
Jan. 1973			
Upper Stand	50.0	11.4	0.0
Middle Stand	12.9	0.6	0.0
Lower Stand	32.0	11.1	0.0
Mean with standard error	33.3 ± 8.3	8.5 ± 2.6	0.0

TABLE 4. *Established seedling densities (mean number p. m² with 95% confidence limits in brackets, at May, 1972).*

	Microsite Log	Bare	Fern
Upper Stand	1.00 (0.23-1.77)	0.46 (0.12-0.80)	0.00
Middle Stand	2.78*(1.54-4.02)	0.81*(0.00-1.99)	0.03
Lower Stand	0.69 (0.15-1.23)	0.26 (0.00-0.56)	0.00

* Significantly different from other stands ($P<0.05$).

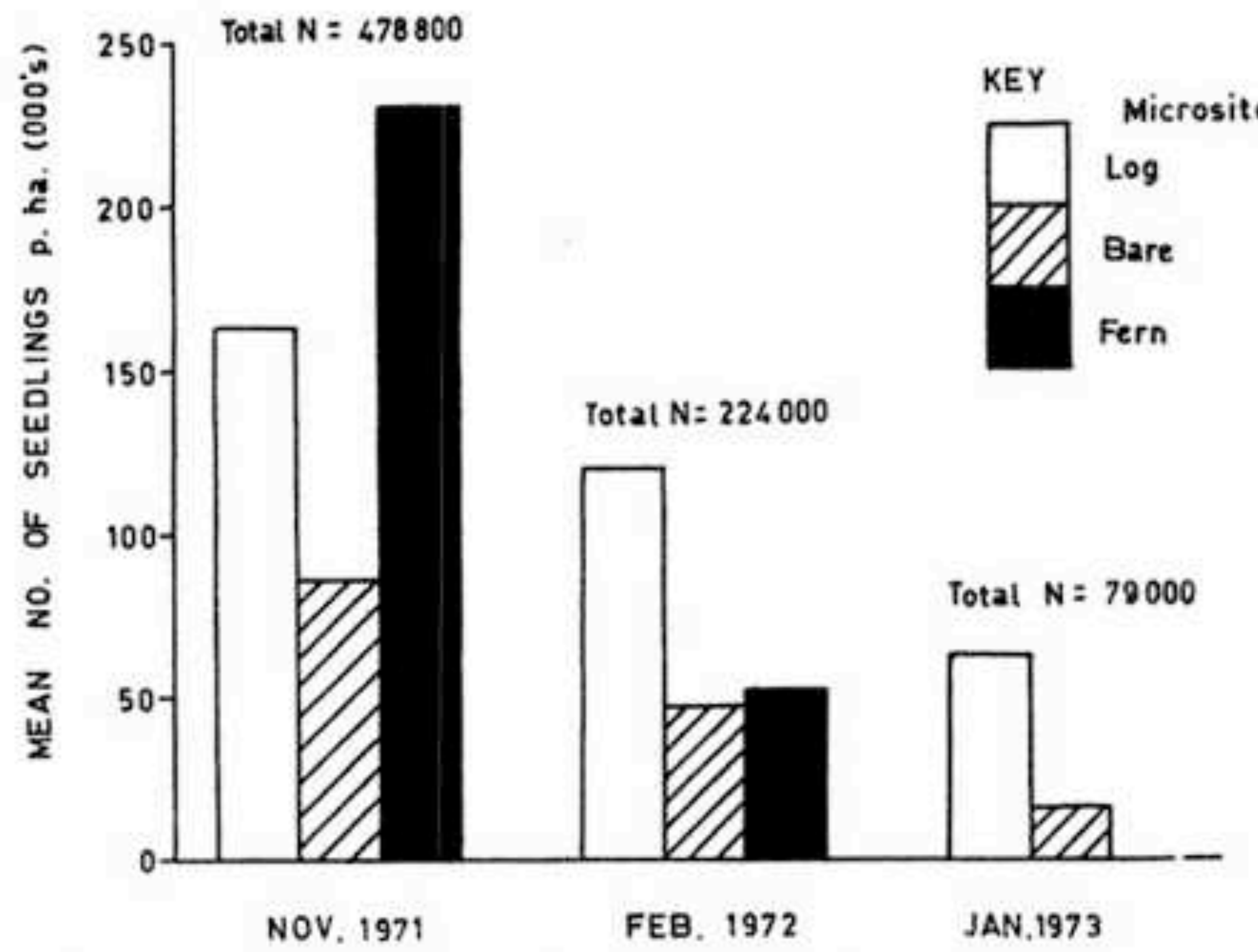

FIGURE 1. *Estimated total numbers of first-year seedlings per hectare.*

microsite were derived by fitting linear regression lines and are expressed as half lives (half life being the time taken for the population size to halve during a period of exponential decline). Survival is greatest in the log microsite and lowest in the fern microsite. Only 54% of first-year seedlings in the log microsite and 20% of those in the bare microsite survived to the end of the first year after germination. Seedling numbers at the probable peak of germination (November, 1971) were obtained by extrapolation of the survivorship curves (Fig. 2). Most mortality occurred during autumn and summer, apparently through dessication or following frost damage during the winter. Mortality rates were lowest during the winter. Other causes of death were defoliation, stem wilting, uprooting by birds which fed in the litter, and smothering by litter.

TABLE 5. *Total numbers of established seedlings per hectare (means with 95% confidence limits in brackets, at May, 1972).*

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

(d) Survivorship

Monthly counts of first-year seedlings from permanent plots gave survivorship data over a 12 month period (Fig. 2). Population decay rates for each

The tagged, established seedlings had a half life of 57 months over the study period (13.4% mortality p.a.). Survival was not significantly greater among seedlings growing on logs. Most deaths occurred in late spring following die-back and loss of leaves during winter. The apices of some seedlings were infected by a Cecid larva which caused a gall, and there was some defoliation by a leaf-roller caterpillar. No animal browsing was noticed during the study period although some seedlings had a trimmed appearance consistent with deer or goat browsing in previous years.

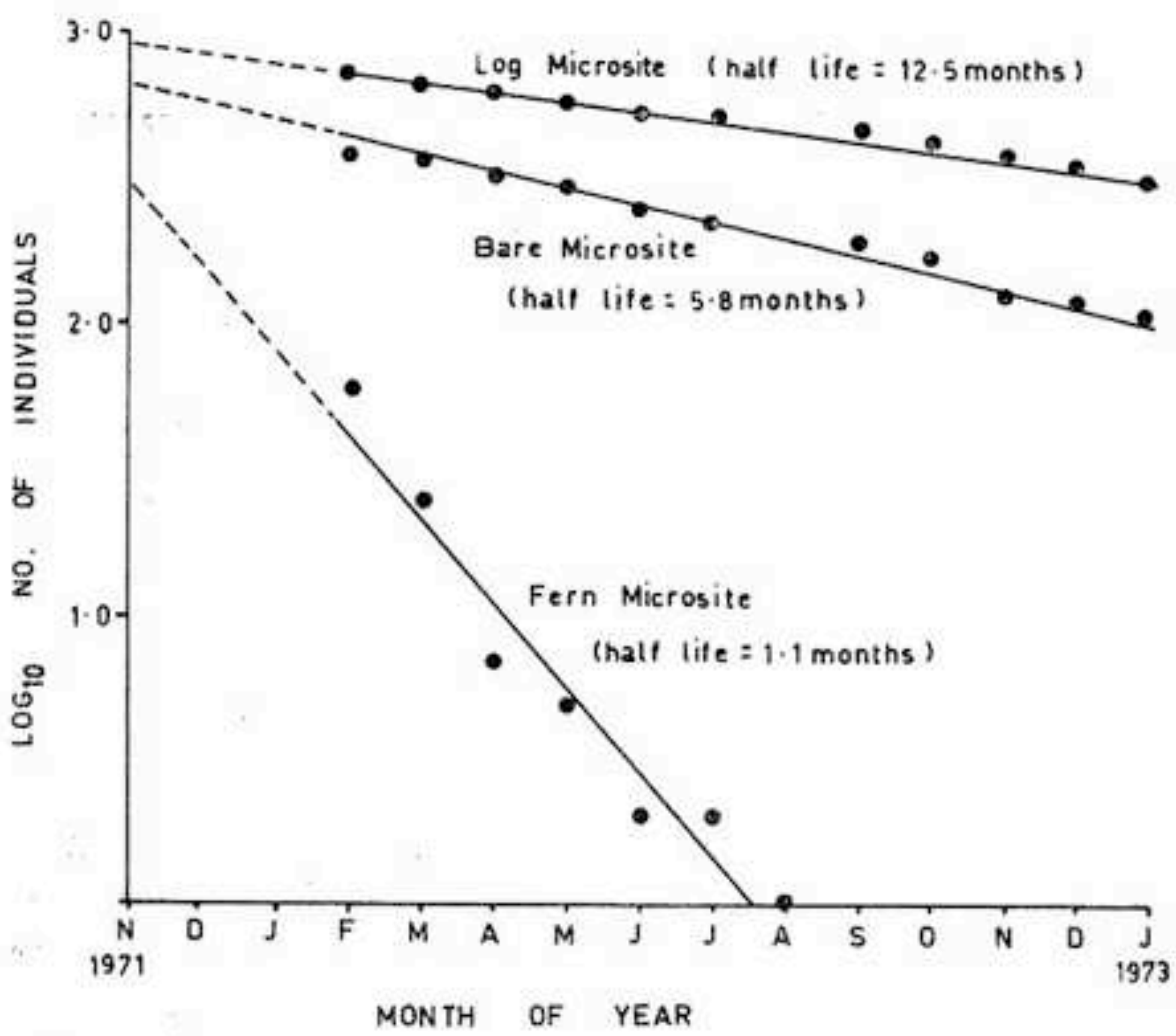

FIGURE 2. *Survivorship of first-year seedlings (tagged seedlings in permanent plots).*

(e) Seedling Growth

First year seedlings reach a height of 4 to 5 cm one year after germination. For established seedlings net height growth is 3.0 ± 1.8 cm p.a. in the log microsite which is significantly greater than in the bare microsite (1.7 ± 2.4 cm p.a., means with standard errors). However, individual seedlings grew up to 18.5 cm in height in one year. The frequency distribution for established seedling heights (Fig. 3) follows a negative exponential distribution for seedlings greater than 10 cm tall. The inclusion of first-year seedling data would continue this trend. Assuming that all seedlings in the 190-200 cm height class can grow to over 200 cm in one year, a maximum of 0.4% of the population (16 seedlings p.ha.) will become saplings in one year. This is the potential recruitment to the mature population.

(f) Seedling Ages

Ages determined by ring counts were proportional to seedling height. The oldest seedling in the sample was 22 years. Seedlings originated in all years between 1971 and 1950 with the exception of 1970, 1956 and 1955. Seedlings of the recorded mast years of 1955 and 1963 do not dominate the population.

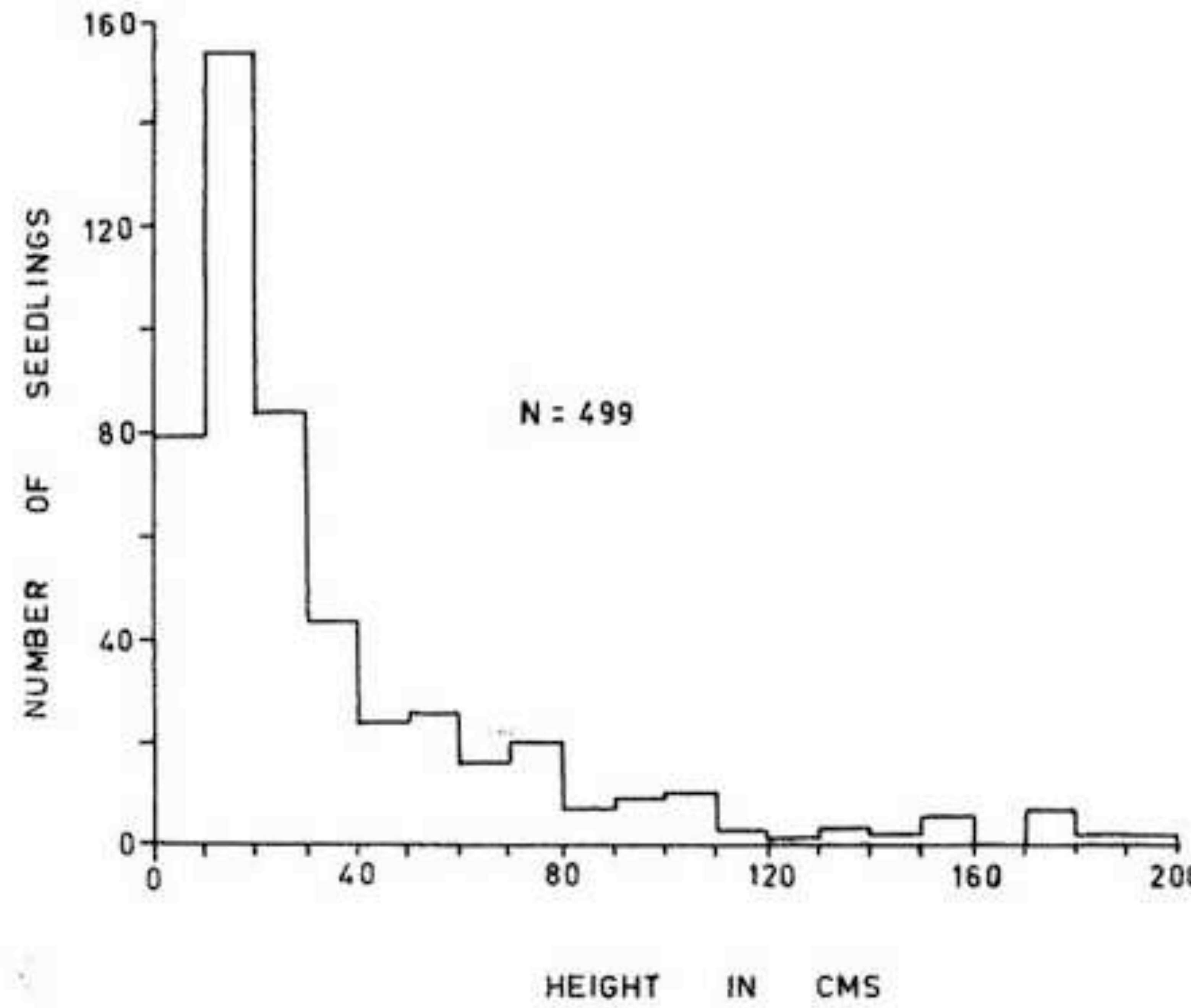

FIGURE 3. *Height frequency distribution for established seedlings (log and bare microsites).*

(g) A Population Model

A simple, deterministic population model was used to predict changes in seedling population size. It can be represented as follows:

Germinating seed → First year seedlings (↗ death) → Established seedlings (↗ death) → Saplings

For each year the total number of seedlings was calculated from the number surviving the previous year and allowing for germination, mortality and recruitment to the mature population. A constant mortality rate with changing density was assumed, except when the density of first-year seedlings dropped to an arbitrary figure of 5000 p.ha at which point they were added to the pool of established seedlings. Microsite frequencies were assumed to be constant. Two models of seed input were used to simulate the likely pattern of seedfall. Model I had one mast year of 1971 size every 10 years and Model II had two additional seedfalls 10% of the 1971 size at the 5th and 8th years of a ten year cycle. The pattern of seedling survival depicted in Figure 4 is therefore based on the mortality rates already calculated applied to the above assumptions concerning seedfall frequency and intensity.

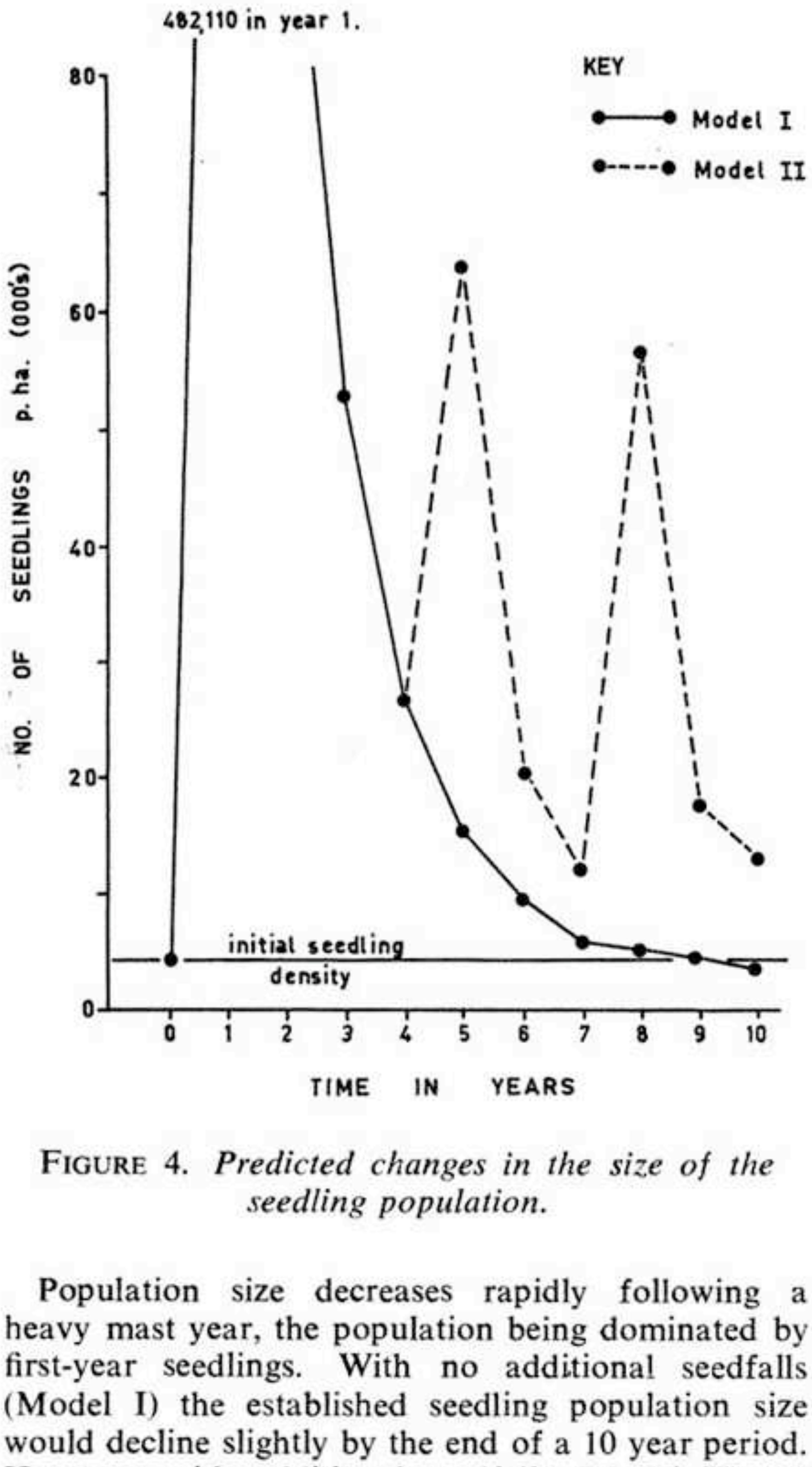

FIGURE 4. *Predicted changes in the size of the seedling population.*

Population size decreases rapidly following a heavy mast year, the population being dominated by first-year seedlings. With no additional seedfalls (Model I) the established seedling population size would decline slightly by the end of a 10 year period. However, with additional seedfalls (Model II) the population size would be maintained or increased.

DISCUSSION

Large fluctuations in seedfall occur. A massive fall in 1971 was preceded by at least one year and followed by at least two years of insignificant seedfall. However, seedling establishment is more regular than the occasional mast falls that have been recorded in the past 20 years.

A number of factors influence seedling success. Relative light intensities are below the calculated compensation points (1.9% and 3.9% in two separate determinations for first-year seedlings, (June, 1974) in almost all fern microsites and in those bare microsites with an overhanging shrub layer, usually of *Pseudowintera colorata*. Seedlings are not found where relative light intensities are less than 4.7%. Optimum light intensities for growth (35% in one determination) occur in log and bare microsites in clearings. A moss layer is particularly favourable for first-year seedlings. This may reflect its suitability for the overwintering of seed and for seedling survival during periods of drought. The litter layer present in the fern and much of the bare microsites prevents the easy rooting of seedlings in the mineral soil layers which leads to dessication during drought. The marked favourability of the log microsite, where seedlings grow faster and survive better, is presumably the result of a number of factors (June, 1974). The elevation of logs means a better light regime, the rotting wood as a root medium retains water well and has higher nutrient levels than are present in the A horizon of the soil, the prevalent moss covering is favourable for seedling germination and survival, and there are fewer competing species such as *Pseudowintera colorata* present.

Following germination of seedlings throughout the stand in all microsites, the surviving seedlings become more and more confined to a few of the log and bare microsites. Log microsites only occur where trunks and branches have fallen and bare microsites in small areas among the extensive fern layer. Areas of these microsites with other shrub and herbaceous species contain few red beech seedlings. Thus, older seedlings are only found in a small number of clumps scattered around the stand.

The size of the seedling population will be limited by seed input, the availability of suitable microsites, losses due to recruitment to saplings, and biotic and climatic factors affecting survival and growth. Input by seed germination does not appear an important limiting factor in view of the large 1971 mast seeding and evidence of earlier seed years. Suitable microsites, particularly fallen logs, are limited in extent by the availability of dead wood and the occupation of the forest floor by other species. Thus, microsite availability is an important limiting factor. Recruitment to saplings involves only a small proportion of the population. Most seedling deaths can be attributed to climatic factors such as frost and drought, although fungal and insect predators have some effect on mortality. Deer and goat browsing of seedlings is negligible at present which is consistent with the recently reduced populations of these animals. The high opossum population has little direct effect on seedlings. Elder (1965) has suggested that deer browsing has caused an increase in unpalatable plants such as *Dicksonia lanata* and *Pseudowintera colorata* associated with a reduction in palatable species in the ground and shrub layers. The most palatable species, *Griselinia littoralis*, has nearly been eliminated from the shrub layer but the palatable *Polystichum vestitum* is still a significant component of the fern flora (21% of the fern cover in all stands). In 1914, only six years after deer were liberated in the area (Elder, 1965) and well before they had reached maximum population densities (1925-1945), Aston (1913) noted extensive stands of *Dicksonia lanata* beneath beech forest in the area, a description applying to the study area today. This indicates that the limitations on microsite availability caused by the *Dicksonia* layer have not been a consequence of the deer invasion in the past 65 years. Observations on the size frequency distributions of saplings in the stands (June, 1974) confirm the conclusions of Ogden (1971b) that high deer populations in the past have not produced a 'regeneration gap' in red beech. The effect of deer may have been to reduce the extent of the moss layer on the ground through trampling, thus decreasing the favourability of the bare microsite. The combined evidence does not support the suggestion of a reduction in the red beech seedling population by deer.

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 which may be a result of older seedlings occupying the limited number of favourable microsites and suppressing the younger seedlings. Alternating periods of high and low seedling establishment are part of the 'regeneration cycles, suggested by Ogden (1971b). However, a simple mathematical model for seedling population size which uses estimates of germination, growth and survival obtained over one year from all stands predicts that the population size will be maintained or may increase in the future. The results suggest that, overall, recruitment of seedlings to the adult population is likely to be maintained at or above its present level.

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