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POPULATION STRUCTURE IN A BEECH-PODOCARP FOREST NEAR BELL HILL, WESTLAND

C.J. BURROWS, A.T. DOBSON and THIRD YEAR
PLANT ECOLOGY CLASS

Department of Botany, University of Canterbury,
Christchurch, New Zealand

ABSTRACT

In a one hectare quadrat in a Westland forest, only two of the eight most abundant tree species, *Weinmannia racemosa* and *Phyllocladus alpinus* possess populations clearly approaching balanced all-aged structure. Young stems of both species arise vegetatively. The three *Nothofagus* species present seem to exhibit group even-aged structure, but there is a wide gap between the youngest and oldest groups except in *N. solandri* where a group of tall saplings and poles occurs. Regeneration of the main dominant on the site, *Dacrydium cupressinum*, has failed almost completely. *Podocarpus ferrugineus* has a regeneration pattern like that of the beeches, with a gap between the youngest and older groups.

Three possible explanations, not necessarily completely mutually exclusive, are advanced to account for the population structure of the forest. More field study is needed to test the hypotheses.

INTRODUCTION

In August 1974, the third-year Botany Plant Ecology Class (University of Canterbury), whose members are listed at the end of the paper, marked a one hectare quadrat in a stand of mixed forest beside the Haupiri-Nelson Creek road (grid reference S52/100792, or c. 171°37'E, 42°31'S. To examine the population structure of the forest, the height and diameter classes of all trees, including juveniles, were recorded. This paper describes the results of the study and advances hypotheses to account for the observed population structure.

SITE CHARACTERISTICS

The site (Fig. 1) is at 240 metres above sea level, on a flat to gently-sloping, slightly terraced, outwash surface which dates from the Kumara 2 glacial phase (Suggate 1965). A few small, very slightly incised streams meander over the surface. The soils belong to the Okarito gley-podsol set (Gibbs *et al.* 1950) and are shallow, stony and infertile. Annual precipitation is about 250 cm.

The stand of forest has been little disturbed by human activity, unlike the surrounding area. The Haupiri-Nelson Creek road marks its eastern boundary, and recent widening for road-sealing has left leaning or fallen trees on this margin. The forest on the western and southern sides of the stand was logged

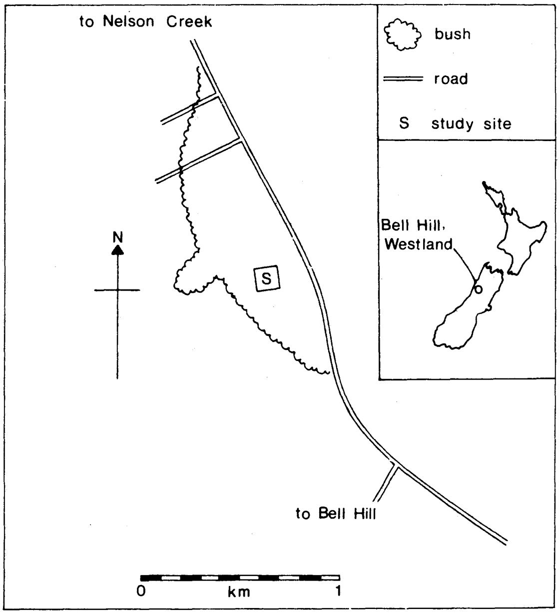

Fig. 1. Sketch map of study area.

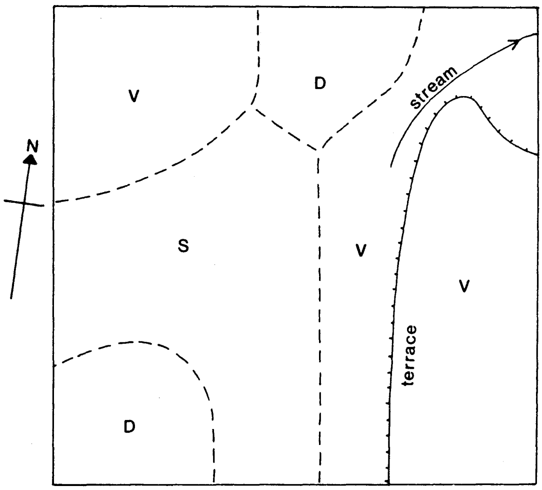

Fig. 2. Site characteristics and ground cover. Relative densities of the ground cover, which consists of shrubs and saplings of the forest trees, are given as follows: S, sparse; D, dense; V, very dense.

for rimu (*Dacrydium cupressinum*), then burnt, probably 40 or 50 years ago. Since the fire, there has been fairly dense regeneration of *Nothofagus truncata* and *N. solandri* in the burned area on this side. The northern end of the stand tails off through progressively lower forest, cut by two dirt roadways, until it ends in open sedge and scrub vegetation. The only disturbances noted in or adjacent to the quadrat were a burnt tongue of forest, on which dense beech regeneration occurs, near the northwest corner, and a few young *D. cupressinum* trees cut by an amateur axeman in the centre of the plot.

Fig. 2 shows some of the salient features of the quadrat, and its ground cover.

Farm development is planned in the area west and north of the forest stand, but it is intended that the forest stand shall receive reserve status (Mr J.A.S. Shaw, Commissioner of Crown Lands, Hokitika, pers. comm.).

METHODS

The quadrat was subdivided into strips 20 m wide, and pairs of students (one observing, one recording) worked systematically along the strips counting and measuring all individuals of one tree species. The height classes were 0.16 m - 0.60 m, 0.60 m - 1.50 m, 1.50 m - 3 m, 3 m - 6 m, 6 m - 12 m, > 12 m. Within the last three height classes the trees were counted in 5 cm diameter classes (D.B.H.). In the > 29.9 cm class, all diameter measurements were recorded. Juveniles of *N. truncata, N. fusca,* and *Weinmannia racemosa* were so numerous that they were counted on only half of the plot.

The canopy height is rather uniform, and was recorded separately. Dead trees in the various classes were noted when they could be identified, but there were relatively few present and many were unidentifiable. They were not considered further. Notes were made about general ground conditions, soils, and minor species present. A few fallen trees were sectioned for aging and a few increment cores were taken from standing trees for the same purpose. Most of the latter were in old trees with rotten hearts and were useless for obtaining tree ages.

Errors or bias in the population estimates may have arisen from the non-uniformity of the site. The northwest corner of the quadrat was noticeably wetter underfoot than other parts and approached the margin of forest which had been disturbed by fire. *Nothofagus fusca* seemed to be concentrated near the east side of the quadrat and *N. solandri* toward the north end. Misidentification of young *N. fusca* and *N. truncata* plants also may have lead to some counting errors, and the counts of juveniles of some species, which are very dense on the ground, may also be in error to an unknown extent.

RESULTS

After tabulating the population counts it was decided that only eight species were abundant enough to provide population estimates which could be used reliably, either to interpret the past history of the species on the site or to predict their future. The results are presented as histograms (Figs. 3-5). All other vascular plant species present are listed in Table 1,

TABLE 1

RELATIVE ABUNDANCE OF ALL SPECIES NOT CONSIDERED IN FIGURES 3-5

Species are listed according to the following arbitrary scale: 1 - Very sparse; 2 - Uncommon; 3 - Common; 4 - Very common - forming dense clumps.

Tree species	Abundance
Dacrydium biforme sapling, small tree.	1-2
Podocarpus hallii sapling.	1
Libocedrus bidwillii small tree (dead).	1
Elaeocarpus hookerianus seedling, sapling, small tree.	2
Griselinia littoralis seedling, sapling.	3
Metrosideros umbellata large tree.	1
Myrsine australis seedling.	1
Myrsine salicina seedling.	1
Myrsine "montana" seedling.	1
Pseudopanax crassifolius seedling, sapling, small tree.	3
Pseudopanax simplex small tree.	1
Shrubs	
Podocarpus acutifolius	2
Archeria traversii	1
Coprosma ciliata	1
Coprosma foetidissima	2
Coprosma sp. cf. *parviflora*	2-3
Coprosma pseudocuneata	1
Cyathodes fasciculata	2-3
Leptospermum scoparium	1
Myrsine divaricata	1
Neomyrtus pedunculata	4
Pittosporum crassicaule	1
Pseudopanax anomalus	1
Pseudowintera colorata	1
Climber	
Rhipogonum scandens seedling.	1
Herbs	
Libertia pulchella	1
Luzuriaga parviflora	2
Nertera dichondraefolia	3
Nertera cf. *depressa*	1
Uncinia sp.	1
Ferns	
Cyathea smithii	2
Dicksonia squarrosa (young).	2
Asplenium flaccidum (epiphyte).	1
Blechnum discolor	2
Blechnum minus	3
Ctenopteris heterophylla	1
Gleichenia cunninghamii	2
Grammitis billardieri (epiphyte).	1
Hymenophyllum multifidum	1
Hymenophyllum villosum (epiphyte).	1
Polystichum vestitum	1

TABLE 2. APPROXIMATE TOTAL BASAL AREA OF ALL TREES 3 m HIGH

Species	Basal area, dm^2
Dacrydium cupressinum	1908.6
Podocarpus ferrugineus	130.5
Phyllocladus alpinus	38.6
Nothofagus solandri	254.3
Nothofagus truncata	506.0
Nothofagus fusca	195.3
Weinmannia racemosa	506.7
Quintinia acutifolia	125.8

together with an estimate of their relative abundance. Table 2 shows the approximate total basal area of all trees > 3 m high, for each of the eight main species, calculated on midpoint values of the diameter classes.

The forest canopy ranges from 22 to 27 m in height.

DISCUSSION OF RESULTS

The height and diameter class information obtained for the eight main species can be used as an approximate index to their population age structure. If a species has a balanced population structure, many more young plants than old ones should be present. Types of tree population structure are discussed by Jones (1945).

A. *Dacrydium cupressinum* (rimu). Serious imbalance is present in the population structure. Seedlings, saplings and young poles are rare. Even among the canopy trees, the diameter classes are unbalanced, with almost all trees in the > 29.0 cm class. Ages of two mature canopy trees (assuming that growth rings are annual) are: 388 years (24.6 rings per cm of radius, from a section), and 342 years (24.1 rings per cm radius, from a core). These trees were established before about 1580 and 1630 AD, respectively. Subsequently, regeneration has failed almost completely.

B. *Podocarpus ferrugineus* (miro). Although relatively few canopy trees of this species are present, evidently there has recently been abundant establishment of seedlings and young saplings. This may be sufficient to maintain the present density of stocking of adults. A section of a mature canopy tree had 93 rings (11.1 rings per cm radius) but a subcanopy pole had 160 rings (31.3 rings per cm radius).

C. *Phyllocladus alpinus* (mountain toatoa). The vast numbers of "seedlings" and sapling stems present are a result of the vegetative mode of reproduction of this species. Stems lying along the ground give rise to numbers of vertical stems, each of which could, potentially, become a tree. Lower numbers of saplings and poles are present and there are few mature (subcanopy) trees. It is possible that the density of adults found now represents the normal reduction from an initial density of juveniles similar to that now present, but adults may ultimately be more dense than at present. A section from one mature tree gave an age of 163 years (20.4 rings per cm radius).

D. *Nothofagus solandri* (mountain beech). Although the number of seedlings, saplings and poles of this species are relatively low, the distribution in the 5.0 - 9.9 cm diameter class suggests that a surge of regeneration occurred, perhaps 30 - 40 years ago, and that this regeneration will probably be sufficient to maintain the present rather low stocking of mature canopy trees in the larger diameter classes. The age of one mature tree was 73 years (7.2 rings per cm radius), a fast growth rate compared with other species whose ages could be determined.

E. *Nothofagus truncata* (hard beech). Abundant young plants of this species are present but tall saplings and poles are rare and the mature tree component is strongly biased in favour of the larger diameter classes. Apparent group even-aged population structure is evident in many *Nothofagus* forests as a result of the accumulation of "advance growth" plants which are released only when light gaps are formed or when root competition is diminished (Kirkland 1961). The pattern in *N. truncata* on this site may represent the norm. This species is out of phase with *N. solandri*, however, in the timing of development of different aged groups. No fallen trees could be found for sectioning.

F. *Nothofagus fusca* (red beech). The density of mature trees is low and the density of young plants is probably inadequate to replace them. Otherwise the population structure resembles that of *N. truncata*). One mature tree was 94 years old (9.1 rings per cm radius).

G. *Weinmannia racemosa* (kamahi). Of all the species present (except perhaps *Phyllocladus alpinus*) this one exhibits a fairly close fit to a pattern of balanced all-aged population structure. The large number of juveniles present results, to a large extent, from vegetative reproduction from layered stems or suckers which give rise to vertical stems. No tree ages were obtained.

H. *Quintinia acutifolia* (tawheowheo). Mature trees are not abundant on the site and numbers in the younger classes (also resulting largely from vegetative reproduction) are probably adequate to replace them. No tree ages were obtained.

GENERAL DISCUSSION

The results obtained permit several conclusions to be drawn about past history and future development of the forest stand:

1. Several hundred years ago there was a period of active *D. cupressinum* regeneration resulting in its dominance on the site.

2. Unless there is a change in the regeneration pattern this species will be eliminated (or nearly so) from the site as the canopy trees die.

3. Their place will be taken over by *Weinmannia racemosa* and the *Nothofagus* species.

At least three possible but not necessarily wholly mutually exclusive causes of these processes of change may be postulated.

Firstly, the changes might be the result of invasion of the site by *Nothofagus* species. Although the beeches have inhabited the general region for about 2400 years (Moar 1971), the immediate study site is virtually on an ecotone between broadleaved evergreen forest and beech forest and invasion may have occurred within the lifetime of the existing *D. cupressinum* trees. If so, judging by the distribution patterns in adjacent areas, it is possible that *N. fusca* was the first invader, followed by the other two species. No evidence is available at present to verify an hypothesis of recent invasion by beech species. In any case there is abundant evidence nearby for failure of *D. cupressinum* regeneration in sites where no *Nothofagus* is present, a widespread feature in Westland forests (Wardle 1963). The presence of the beeches might decrease the chances of rimu regeneration but is not the primary cause.

Secondly, the changes may be the result of regional climatic change as suggested by Holloway (1954) and Wardle (1963). Wardle proposed that a likely cause of failure of *D. cupressinum* regeneration was the occurrence of periodic drought. The occurrence of a few *Dacrydium biforme* plants and one small, dead *Libocedrus bidwillii* tree within the quadrat indicate that the site may formerly have been wetter than it is now. In the remnant strip of forest to the north of the quadrat site (Fig. 1) these two species are common, in a matrix of *N. solandri* and *Phyllocladus alpinus*. This forest, in turn, gives way to pakihi bog vegetation in which *Leptospermum scoparium, Calorophus minor* and sedges are common. A dense *D. cupressinum* stand could have become established in a *Leptospermum* stand if the climate had been much wetter and subsequently became drier. Elsewhere in Westland, species like *N. solandri, P. alpinus* and *L. bidwillii* normally occur on wet sites near pakihi margins. If the drying trend continued it is likely that *D. cupressinum* regeneration, at the seedling level, would be affected by drought, especially in competition with other species in deep shade on the forest floor (cf. Cameron 1963). Elsewhere excessive shade is provided by dense growth of ferns on the forest floor (Wardle 1963) but in the present situation beech saplings and shrubs, especially *Neomyrtus pedunculata*, would have the same effect.

The third possibility is that fire has been involved in the changes although no direct evidence, such as presence of charcoal in the soil, was found. An ancient fire might have permitted *D. cupressinum* forest to develop by first inducing a *Leptospermum* community through which the rimu could emerge. The presence of the pakihi area to the north could be an indication of clearance of the forest by Polynesian or natural fires. The terrace site, though infertile, appears to be suitable for forest development given sufficient time and freedom from disturbance. No logs were found here and the pakihi vegetation is species-rich and therefore seems to have been long-established. If the suggestion is correct that this area is an ancient forest site, then the forest must have been destroyed at least four centuries ago.

Further fieldwork is needed to test these hypotheses about the causes of the dynamic population structure of the forest stand.

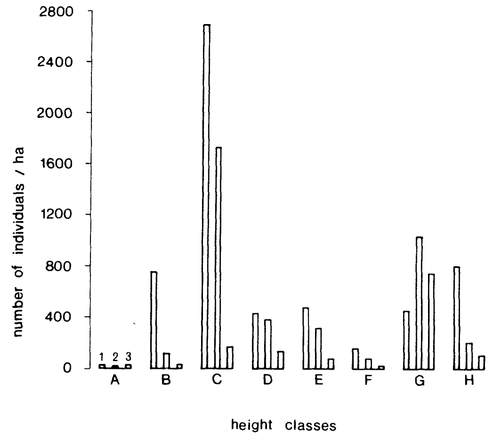

Fig 3. Young plants (<3 m high) in three height classes: 1, <60 cm; 2, 60-150 cm; 3, 150-300 cm. Species: A, *Dacrydium cupressinum*; B, *Podocarpus ferrugineus*; C, *Phyllocladus alpinus*; D, *Nothofagus solandri*; E, **N. truncata*; F, **N. fusca*; G, **Weinmannia racemosa*; H, **Quintinia acutifolia*.
* half plot only.

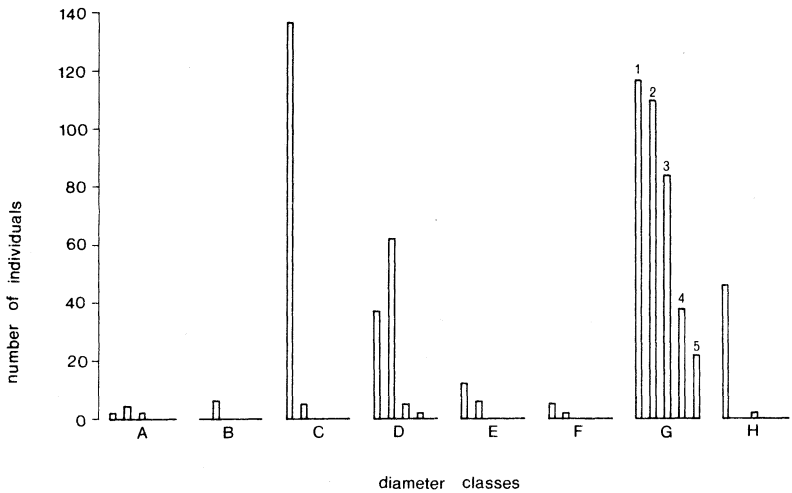

Fig. 4. Saplings and poles (3-12 m high) in five diameter classes: 1, 0-4.9 cm; 2, 5.0-9.9 cm; 3, 10.0-14.9 cm; 4, 15.0-19.9 cm; 5, 20.0-24.9 cm. Species as for Fig. 3.

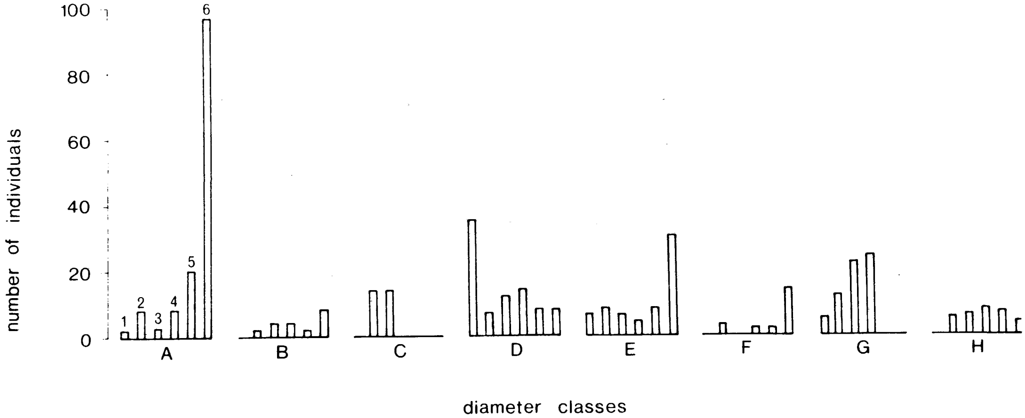

Fig. 5. Mature trees (>12 m high) in six diameter classes: 1, 5.0-9.9 cm; 2, 10.0-14.9 cm; 3, 15.0-19.9 cm; 4, 20.0-24.9 cm; 5, 25.0-29.9 cm; 6, >29.9 cm. Species as for Fig. 3.

STAGE III ECOLOGY CLASS, 1974

Lorna Bailey, Marilyn Begg, Martin Buchanan, Geoff Dangerfield, Leon Fife, Judith Gregg, Tony Guilliland, Lyn Hamilton, Gavin Hawkes, Peter Huntley, Murray Kelly, Jane Martin, Rosemary Paterson, John de Ruiter, Glenn Stewart, Bill Vandenende, Gillian Wratt.

Dr F. Schlegel-Sachs also assisted considerably with the fieldwork.

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