THE LIFE HISTORY OF MOUNTAIN BEECH

(NOTHOFAGUS SOLANDRI VAR *CLIFFORTIOIDES)*

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INTRODUCTION

The object of this paper is to summarise present knowledge of the life history of mountain beech *(Nothofagus solandri* var *cliffortioides).* This task is not as straight forward as it may seem. Mountain beech occupies a wider range of habitat than any other New Zealand tree species and it shows a corresponding range of life form, seeding habits, regenerative patterns, growth habits, growth rates, stand replacement and mortality patterns. It is a species which forms the highest timberlines in the country, growing at altitudes in excess of 1500 m as in the Wairau Valley in Marlborough. On the other hand, in Southland and Fiordland, mountain beech occurs on escarpments and rocky outcrops at sea level where it is often subjected to salt spray. With the exception of halls totara *(Podocarpus hallii),* it occupies drier sites than other New Zealand large tree species and forms monotypic stands in areas of eastern Canterbury, Marlborough and inland Otago where the rainfall may be less than 100 mm annually. In contrast, it is also a component of the stunted forest on the poorly drained and boggy pakihi sites of the West Coast where the rainfall exceeds 500 mm. In Fiordland, mountain beech occupies sites on slow weathering parent rock where the soil mantle is extremely thin; it is also a component of the scrub on the very poor soil derived from the ultra-basic rocks in the vicinity of the Dun Mountain in Nelson and the Red Hills region of South Westland.

As soils improve and the climate becomes more conducive to forest growth, mountain beech becomes progressively less important in stand composition. It fails to compete successfully with the broadleaved hardwood species, the podocarp species and even the other beech species.

This paper presents a very generalised summary of the life history of mountain beech, based primarily on the pattern which might be expected at mid-altitudes, around 900 m, in the extensive monotypic mountain beech forest east of the main divide in the South Island. However, examples encompassing the extreme variation will be given. This summary will be followed by a description of two studies which demonstrate the variation in various phases of the life history. The first study relates to seedfall and the second to the pattern of diameter growth in the post-sapling stage.

THE LIFE CYCLE

1. Flowering

Flower primordia are formed in the dormant vegetative buds during the summer preceding the one in which flowering takes place. Abundant flowering does not occur every year and appears to be dependent on the preceding summer being hot and dry. Seedlings approximately six years old have been observed in flower, but it is probable that viable seed is not produced until 25-30 years and then only when the trees are open grown.

Flowering occurs between late October and early January, the timing being largely dependent on altitude but also varying slightly between seasons. Occasionally, at low altitudes, trees have been observed to flower twice in one season — once in September and then again in March. Pollination is by wind.

2. Seedfall

Regeneration is normally from seed; though rare, vegetative propagation by layering does occur naturally, and cuttings can be struck reasonably easily under artificial conditions. Most seeds are shed between March and May. There appears to be approximately one good seed year (in excess of 50 million seeds/ha) per decade, and usually about two or three partial seed years (between 5 and 50 million seeds/ha) over the same period. The seedfall over the remaining years is negligible (cf. Manson 1974, p.27). Good seed years do not necessarily follow good flowering years — probably as a result of unfavourable weather at critical stages of development.

The quality of seedfall varies considerably from year to year and from site to site. In a good seed year over 70 percent of the seed may be capable of germination. In a poor seed year the range is from 0 to about 15 percent.

Seed dispersal is by gravity, aided by wind, and seeds do not normally travel more than about 200 m from a seed source.

3. Germination

At low altitudes in the North Island germination may occur in late autumn, but usually the seed overwinters on the ground and does not begin to germinate until September, or even as late as December at high altitudes. The best germination usually occurs in conditions of partial overhead shade and the poorest where the germination medium is exposed to full sunlight.

Seedling mortality is high in the summer and autumn following germination, especially under conditions of full sunlight. The seedlings which survive may reach 10 cm height in the first growing season, but at high altitudes near timberline they are more likely to reach only two to four centimetres.

4. Seedling Development

Seedlings which have survived the first season under conditions of partial overhead shade are capable of growth rates in excess of 45 cm per year. On the other hand, seedlings which have germinated under a moderately dense parent canopy will enter a stage of semi-dormancy. These seedlings, which are referred to as 'advance growth' may remain alive while making very little growth for up to 20 years, and possibly longer (cf. Manson 1974, p.30). The mean growth rate of 'advance growth' seedlings measured near timberline in the Craigieburn Range was around 1.5 mm per year. Even though the growth rate of these seedlings is slow, annual mortality after the first season averages only about eight percent. Once the competition from the parent trees is removed, and more light reaches the forest floor, these seedlings are capable of responding rapidly and within a year or two are difficult to distinguish from seedlings which have never gone through the quiescent stage.

5. The Sapling Stage

The growth and mortality pattern of saplings varies considerably and is related to competition from canopy trees. Progression from the seedling to the sapling stage is dependent on adequate light reaching the forest floor through canopy gaps. While the canopy remains open sapling growth is reasonably vigorous, with mortality from competition between saplings probably in the vicinity of two to five percent of all stems per year. If, however, the remaining trees from the original canopy are sufficient to close the canopy, all saplings, regardless of the stage of development, will soon show a marked reduction in growth rate and then die. Saplings of mountain beech appear to show much less tolerance of shading by the parent canopy than 'advance growth' seedlings.

In sheltered places at low altitudes, where there is little competition, mountain beech saplings may grow as much as 90 cm in one year, but under conditions of moderate overhead shading they are more likely to put on about 7-15 cm per year.

6. The Mature Tree

Saplings and poles of mountain beech retain a whip-like form with strong apical dominance and few competing side branches until they approach final height. This may take between 80 and 150 years in stands, but considerably less time in the open. From then on an increasing proportion of the growth is involved in crown extension.

The ultimate height attained by mountain beech varies considerably with site. On poorly developed soils this may be only 45 cm, while on deeper, more fertile soils it may exceed 24 m. In the Craigieburn stands at 900 m altitude tree height is generally around 20 m.

The diameter growth rate of mountain beech under stand conditions is fairly constant throughout the life of the tree but, like height, varies considerably from site to site. In the Craigieburn Range the average ring width is around 0.08 cm. At high altitudes on poor soils in Fiordland, on the other hand, it may be 0.02 cm. Trees from the margin of the stand grow considerably faster than those within and ring widths of 0.25 cm are not uncommon. Maximum tree diameter also varies. On the better sites, breast height diameters of 60 cm occur reasonably frequently and occasional trees may be 80 cm or more (cf. Manson 1974, p.30).

The maximum age that mountain beech attains is normally around 300 years, though occasional trees have been measured with up to 360 distinct growth rings. As the stand approaches maturity, the mortality rate decreases. In closed stands about 200 years old it is only about one percent or less per annum.

7. Phenology

The vegetative buds of mountain beech open from September to early December, depending on altitude, and shoot extension may continue until mid-autumn. Bud elongation may precede bud burst by as much as two months.

The annual growth cycle is complicated by the presence of two different kinds of shoots. The majority of shoots of young plants and virtually all the shoots of adult plants have limited growth — the leaves already present as initials in resting buds expand and this is followed by the formation of new resting buds. There may be several flushes of limited growth from these buds in a single season. The second kind of shoot, the leading shoot of seedlings and saplings, produces leaves continuously throughout the summer.

The leaves are generally shed during the growing season following the one in which they were produced, but occasionally leaves may be retained for two years on slower growing shoots. Peak leaf fall occurs between December and April.

8. Stand Replacement

The most extensive areas of mountain beech are on the eastern side of the main divide in the South Island and in the central North Island. In these areas, mountain beech usually forms monotypic stands, and less often occurs in various admixtures with silver beech and red beech. These forests are usually composed of mosaics of stands of one, two, or sometimes three age classes. They are seldom truly normal (mixed age). The size of these stands is variable, but frequently may be quite large — several hectares in extent. These uniform stands result from regeneration following catastrophes such as windthrow, snow-break or insect attack.

A closed stand in mountain beech forest has a basal area in the vicinity of 45-60 m^2/ha. While this basal area is maintained seedlings beneath the canopy have little chance of growing beyond the advance growth stage. If partial opening of the canopy does occur as a result of mortality of individual trees, seedlings are capable of reasonably rapid growth into the pole stage. However, expansion of the crowns of the existing trees rapidly fills the gaps, the original basal area is again achieved and the released poles eventually die. When extensive canopy opening results from catastrophe, the poles grow to form a new canopy, a basal area of between 45 and 60 m^2/ha is attained, and the uniform structure is maintained. This new stand may be single-aged or two-aged depending upon the extent to which catastrophe has destroyed the canopy.

This pattern of stand replacement does not necessarily apply to all mountain beech forest. Stands on pakihis, in forest where there is a greater variety of species and on sites where there is slow weathering parent rock close to the surface appear to show a greater range of age classes, and thus may have very different patterns of replacement.

EXAMPLES OF VARIATION

1. Seedfall

A study to demonstrate the variations which can occur in seedfall, even over short distances, was carried out in the Craigieburn Range in inland Canterbury, and at Mt Thomas some 50 km distant in the Canterbury foothills. Two lines of seed trays were established on Mt Wall in the Craigieburn Range — one at 1340 m altitude and the other some 600 m away at 1036 m altitude. A further line of seed trays was established at 500 m on Mt Thomas.

Each of the three lines is composed of eight trays spaced at 40 m intervals along the contour. All lines are on north-west aspects with similar degrees of slope. The stands at each site have similar basal areas and are not dissimilar in appearance, though at 1036 m the forest tends to be somewhat taller, and at Mt Thomas it tends to have a greater complexity of understorey species.

The trays are circular metal funnels with a catching area of 0.279 m^2 (3 ft^2) and the contents are collected monthly. The two lines of trays at Mt Wall have been used now for nine seasons and the Mt Thomas trays for eight seasons. A summary of the annual seedfall is given in Table 1.

TABLE 1. Total Seedfall and Percent of Sound Seed for Each Line of Trays and Year of Collection. Boxed Records Represent Major Seed Years, Underlined Records Partial Seed Years.

Year	1340 m		1036 m		500 m	
1965	64	0.0	10	0.0	No record	
1966	2	0.0	368	12.0	6375	33.7
1967	2791	7.0	7986	57.1	201	14.9
1968	10	0.0	68	0.0	77	10.4
1969	4764	27.4	7866	60.4	1392	35.0
1970	48	4.2	25	0.0	13	0.0
1971	23038	63.8	18614	73.8	15458	63.4
1972	661	1.8	298	6.0	90	2.2
1973	36	0.0	42	2.4	826	14.6

There has been one major seed year recorded since the study began. This was in 1971 and occurred at all three sites (Table 1). At 1340 m, 23,000 seeds fell into the trays, at 1036 m, 18,600, and at 500 m, 15,500. The percentage soundness of seed was also similar throughout, being respectively 64, 74 and 63.

At each level there have been two partial seed years. One of these, in 1969, was again common to all three lines. However, the other differed between the Mt Wall and the Mt Thomas lines, occurring in 1967 at Mt Wall and 1966 at Mt Thomas. Even where two or more lines had a partial seedfall in the same year, the percentage soundness varied considerably. At 1340 m on Mt Wall in 1967, only seven percent of the seed was sound, while at 1036 m in the same year, 57 percent was sound.

The remaining years have had poor seedfall and in some years at some altitudes virtually no seeds at all were collected. Thus in 1966 at 1340 m on Mt Wall only two seeds were collected, neither of which was sound; at 1036 m on Mt Wall, in 1965, 10 seeds were collected, only one of which was sound; and at 500 m on Mt Thomas, in 1970, 13 seeds were collected, none of which was sound (cf. Manson 1974, p.28).

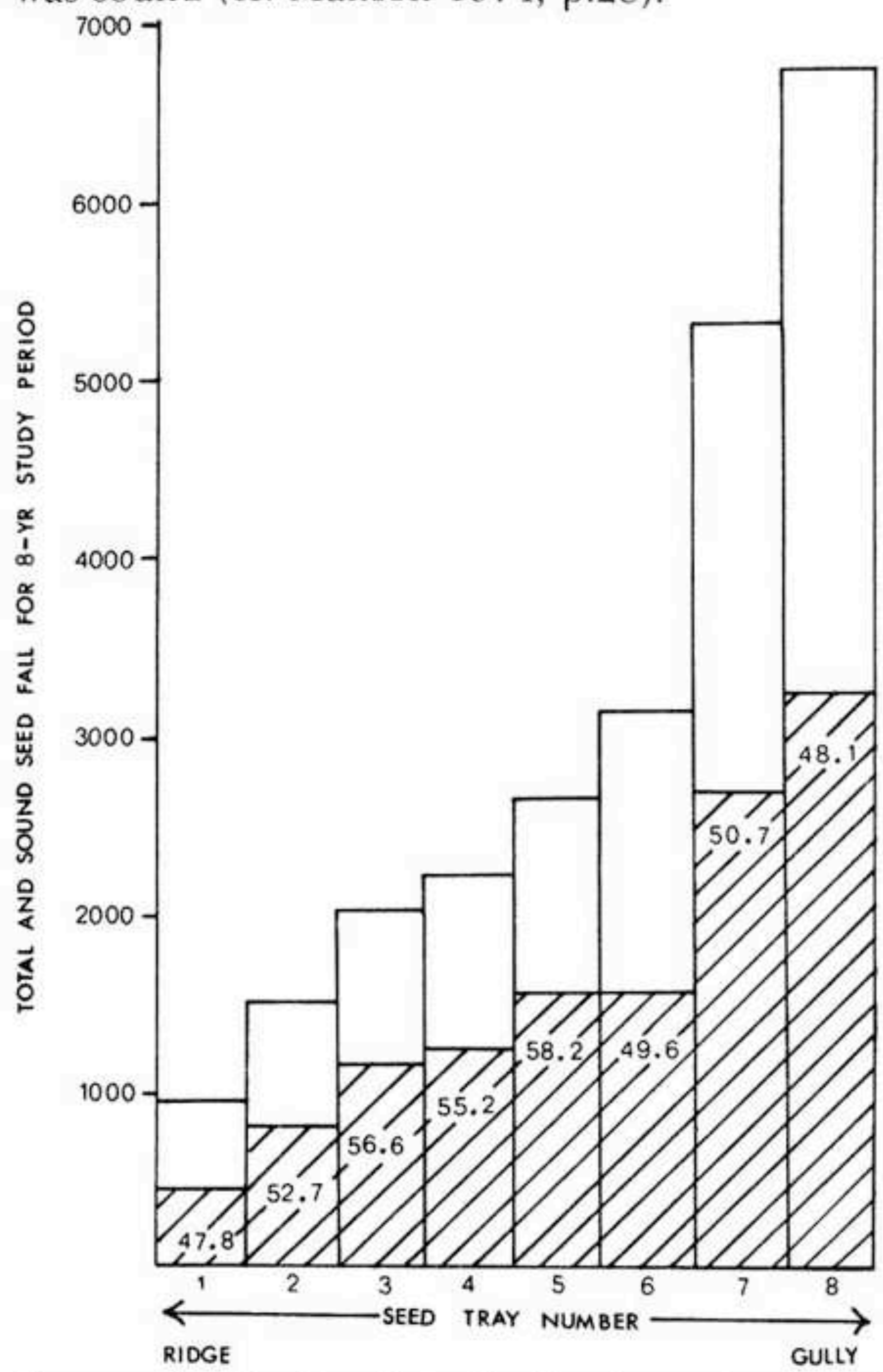

FIGURE 1. *Total seed production (open bars) and sound seed production (hatched bars) for each seed tray at Mt Thomas for the years 1966-1973. The percentage of seed which is sound is indicated in the hatched bars.*

The Mt Thomas seed trays are all on the same contour but stretch from close to a ridge top to near a small gully. Total seedfall has increased in a fairly regular manner along this gradient each year the study has been in progress. This is demonstrated in Figure 1 which shows the total seedfall for each tray for the full eight years of the study. Number of seeds collected by the trays varies from about 900 in the tray nearest the ridge to 6700 in the tray nearest the gully. In contrast with total seedfall, there is little difference in the proportion of sound seed and the trays at the extreme ends of the line collected 47.8 percent and 48.1 percent of sound seed respectively.

In summary, seedfall may vary as much as seven times even between stands only 320 m apart; there may be differences in seed years between stands which are not more than 50 km apart; and the quality of seed may vary considerably between adjacent sites sharing the same pattern of seed years.

2. Diameter Growth

This study is concerned with determining the extent of variation over short distances. As part of a larger study on stand structure, growth and replacement 124 plots were selected on a restricted random basis from the forests in the Craigieburn Range and in the Harper-Avoca tributary of the Rakaia Catchment. Half of these stands were selected between 850 and 1050 m altitude and the remaining half between 1150 and 1350 m. At each plot the three trees nearest to the plot centre in each of three d.b.h. categories (namely 0-15 cm, 15-30 cm and 30 cm) were selected.

Four increment cores of greater than two centimetres length were removed from the trunk of each tree at 1.4 m above ground level. One core was taken from the uphill side, one from the downhill side, and the other two at right angles to these. The cores were trimmed and the number of rings in the outer two centimetres of each counted. The mean number of growth rings per centimetre for each tree was then calculated. The mean was then determined for all trees in each of the 0-15 cm, 15-30 cm, and 30 cm+ categories for each of the two altitudinal zones. The results are illustrated in Figure 2.

Whereas there was little difference in diameter growth of trees in the smaller diameter class, there was a considerable difference in the larger classes. The trees from the upper zone produced only three-quarters the growth of those in the lower zone. The trees in the smaller diameter class included stems which were either struggling to gain dominance over other trees or were becoming suppressed. At this stage the limiting growth factor is interstand competition and this would outweigh the influence of climate. The larger trees were generally those which had attained dominance, the crowns would be emergent, and consequently would be under a greater influence from climate (cf. Manson 1974, p.30).

DISCUSSION

The subject of this symposium is the 'Ecology and Management of the South Island beech forests'. It has been pointed out in this paper that the species occupies a very wide range of habitat and in consequence the life history is very variable. Examples of the extent to which the life history may vary, even over short distances, have been described. No attempt has been made to indicate how these forests must be managed.

Up to now, the mountain beech forests have been managed almost exclusively for protection purposes, and this must remain the primary objective as they mostly occupy steep mountain land which, from past experience, is prone to

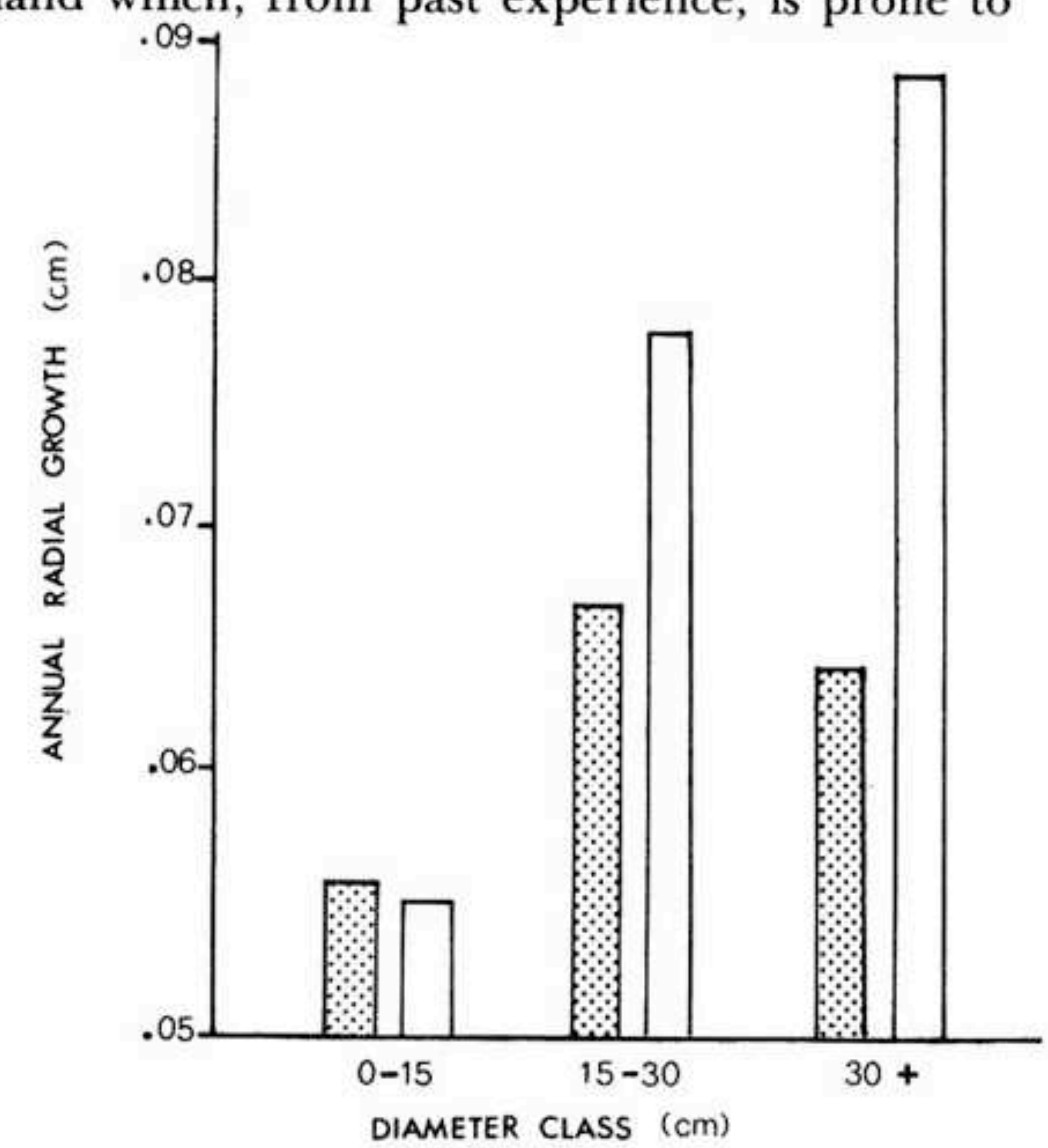

FIGURE 2. *Mean ring width in outer 2 cm of radius for trees in the 0-15 cm, 15-30 and 30 cm+d.b.h. size classes at 850-1050 m (unshaded) and at 1150-1350 m (hatched) altitude.*

accelerated erosion if much forest cover is removed. In future there may well be a justifiable demand for these forests to also provide forage for game animals, or perhaps even to be utilised for wood. However, whatever the objectives, the form which management takes will be largely dictated by the aspects of the life history which have been discussed in the text.

For example, the great variability necessitates detailed knowledge of local performances and the application of very plastic management regimes. Management practices may well have to be varied even between adjacent sites.

Any management regime dependent on the seedfall of the species rather than on advance growth for regeneration must make allowance for the marked periodicity in seeding. It may be necessary to wait four years or even longer for any significant amount of viable seed to fall.

It may prove difficult to regenerate mountain beech on areas where the parent trees have been removed (either by catastrophe or by felling), particularly if the area is large. Lack of regeneration in areas where advance growth was not present at the time of canopy removal would result from the inability of seeds to germinate and of young seedlings to survive under full light or to survive competition from herbaceous species (cf. Franklin 1974, p.18). Seed dispersal distances are short and regeneration by migration from the margins of the new forest edge would take many years. In protection forest it may be necessary to temporarily convert such areas to other species, particularly if land protection values are high (Franklin 1974, p.18). In production areas it may be necessary to consider thinning the canopy to allow advance growth to become established before felling (Franklin 1974, p.18).

These are some examples of how management practices in mountain beech forest would be dictated by aspects of the life history of the species. Other facets of the life history which would be important in determining management regimes would relate to the inability of seedlings and saplings, once released, to withstand further strong competition from the parent trees and the marked differences which occur in the growth rates of open grown trees and those which occur in stands.

REFERENCES

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