THE LIFE HISTORY OF SILVER BEECH *(NOTHOFAGUS MENZIESII)*

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INTRODUCTION

Silver beech *(Nothofagus menziesii)* is found growing in a reasonably wide range of climatic and edaphic conditions although it is excluded from lowland sites in the warmer and drier areas of the country. An upper altitudinal limit of 1430 m is reached at timberline on Mt Hikurangi and at over 1200 m in the Tararua Range and Western Nelson. The upper limit is generally below 910 m in the eastern South Island and below 980 m in Western Fiordland. Silver beech is not common below 600 m in the North Island but descends to sea level south of Paringa in the South Island (Wardle 1967). This species is highly frost and exposure resistant and is capable of regeneration and growth on extreme sites; however it is intolerant of drought conditions (Williams and Chavasse 1951). Silver beech has the greatest shade tolerance of the New Zealand beech species.

Some of the sites occupied by silver beech are obviously inferior to others, and this is reflected very clearly by the growth form. On the best sites (generally at low altitude) it may grow to a tree exceeding 26 m, but on the worst sites (generally at high altitude) it is reduced to a sprawling shrub (Wardle 1963). This paper broadly outlines the major aspects of the life history of silver beech but pays particular attention to those aspects known to be affected by increasing altitude. Increasing altitude has been used as a measure of decreasing site quality throughout this paper.

THE REPRODUCTIVE PHASE OF THE LIFE HISTORY

Only mature canopy trees in the forest community flower and produce seeds. The age at which reproduction begins has not been recorded but it will undoubtedly be found to be variable, depending on climatic conditions and the intensity of competition between trees.

1. *Flowering*

Floral primordia are formed during the summer season and over winter in the resting axillary buds of the shoots produced during that same season (Poole 1948). A dry summer season is thought to stimulate the production of floral primordia but this has yet to be substantiated for silver beech by quantitative investigation.

Although some flowering occurs every year the intensity of flowering is highly variable. Heavy flowering occurs occasionally but the records of this are inadequate to show any flowering pattern, if in fact one exists. On some sites two heavy flowering years may be consecutive (Manson unpubl.). Flowering takes place in the spring, closely following bud burst which occurs later with increasing altitude.

Pollination is by wind and nuts reach their maximum size about two months after pollination. Details of seed development are given by Poole (1950, 1952).

2. *Periodicity of Seeding*

Silver beech usually produces some viable seed every year (Poole 1948). The complete seed failures which have been recorded for other *Nothofagus* species (cf. Wardle 1974, p. 24 Table 1) occur only rarely or not at all.

TABLE 1. *Silver Beech Seed Production Takitimu Mountains 1972*

Tray pairs	Mean Alt.	Est. seeds per ha	Est. sound seeds per ha	%
1 to 3	905 m	25,116,000	5,639,140	22.5
4 to 6	789 m	21,384,480	5,477,680	25.6
7 to 9	673 m	31,951,140	13,365,300	41.8
10 to 12	557 m	42,081,260	15,709,460	37.3

Heavy seed years occur less frequently than heavy flowering years indicating that heavy flowering is not necessarily followed by heavy seeding.

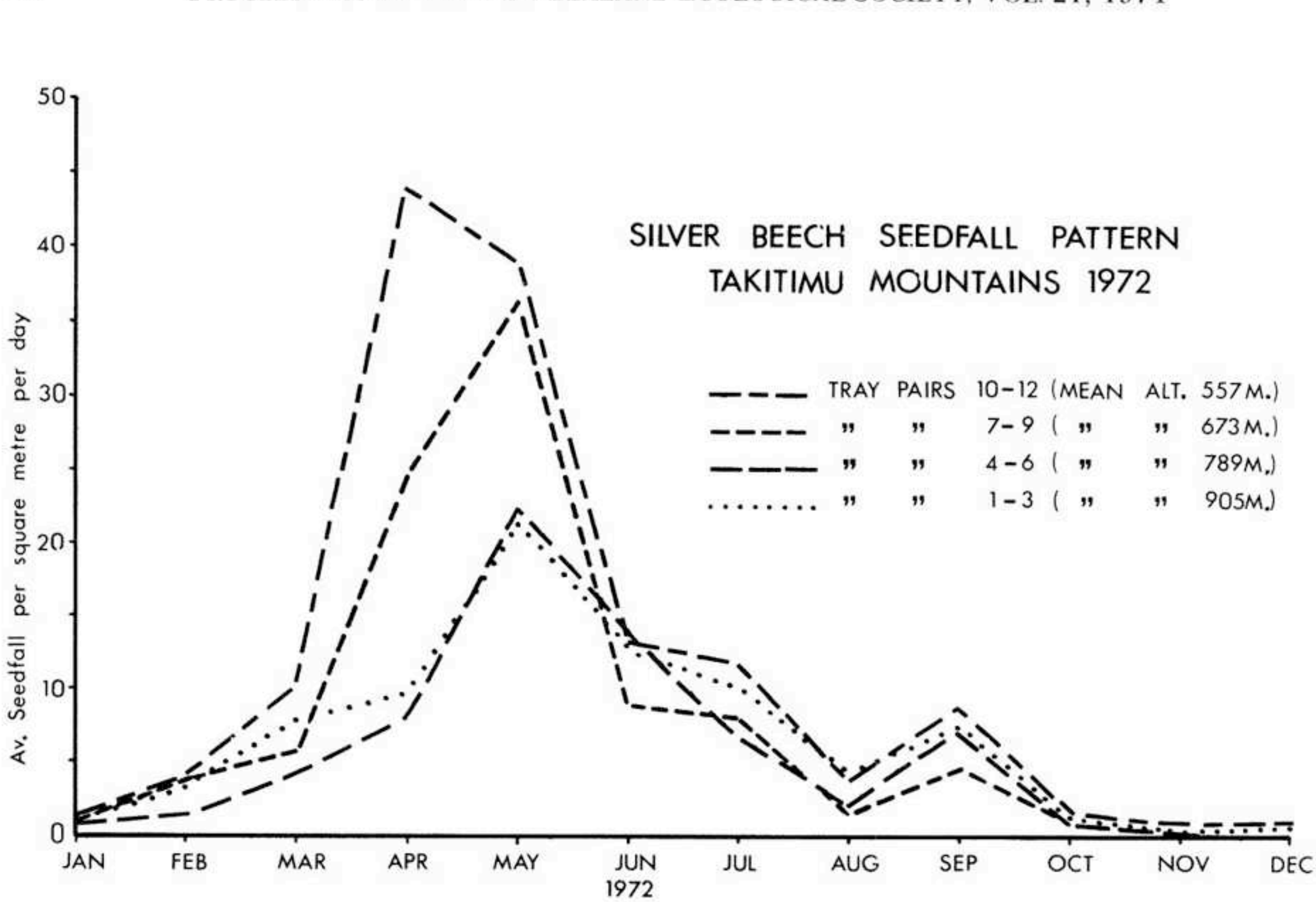

FIGURE 1. *Silver beech seedfall pattern Takitimu Mountains 1972.*

Sound seeds have been produced in the Takitimu Mountains every year since 1970. Seed and litter has been collected monthly from 12 pairs of seed trays identical to those described by Wardle (1974, p. 24). These trays are spaced evenly between 520 m a.s.l. and 945 m a.s.l. on an east facing slope.

During 1970 (a light seed year) a mean total of 70,000 sound seeds fell per hectare. Heavy seedfalls occurred in two consecutive years, 1971 and 1972, with an average in excess of 10 million sound seeds per hectare per year. This represents over 1000 sound seeds per m^2, a number far in excess of what would be needed to maintain a forest, even assuming a very low survival rate.

3. *The Effect of Increasing Altitude on Seed Quantity and Quality*

Although most of the seed is autumn shed, the month during which peak seedfall occurs can vary from year to year and from low to high altitude. During 1970 (a light seed year) the peak of seedfall was in May in the Takitimu Mountains. In 1971 (a heavy seed year) the peak occurred in April at all altitudes. The peak of seedfall occurred in April 1972 at low altitude but was delayed until May in the mid and high altitude forest (Figure 1). The month during which peak seedfall occurs is probably controlled by the time at which flowering occurs, a late spring causing a late seedfall.

Total number of seeds, number of sound seeds and seed quality decrease with increase in altitude (Table 1) (cf. Wardle 1974, p. 24 Table 1).

Only 22.5 percent of seeds falling close to timberline (945 m) during 1972 were sound, whereas on the lower slopes and close to the lower forest margin the percentage viability was nearly double this figure.

Lower seed production at higher altitude may be the result of lower flower production. The reduction in viability observed with increasing altitude may be the result of the increased susceptibility of the higher altitude forests to unfavourable conditions during flowering and seed development. Frost damage to shoots and flowers has been observed by a number of authors.

THE VEGETATIVE PHASE OF THE LIFE HISTORY

1. *Germination and Seedling Establishment*

Germination can take place immediately after seedfall (Poole 1950) but is normally delayed until October, November or December, the actual time becoming later with increasing altitude. No viable seed remains ungerminated in the soil beyond the first year after seedfall (Wardle 1967) although some apparently sound seed is still present.

Seedlings appear to thrive on a mixture of humus and mineral soil but are subject to drought on raw humus, except where summers are moist, and to washing out by rain on pure mineral soils (N.Z. Forest Service 1965, p. 115). Growth is often very slow under field conditions and seedlings seldom produce more than two to three leaves during their first year (Wardle 1967).

2. *Establishment Patterns of Regeneration*

Regeneration normally occurs in dense pockets under an open forest canopy or on the forest margins. Silver beech is also capable of vigorously colonising burns and bare mineral soils under some circumstances. Light and moisture availability have an important controlling influence on establishment.

Regeneration appears to be less abundant on high altitude sites.

3. *Seasonal Growth Patterns*

The species is inactive during the winter months. Growth resumes in the spring with bud break which becomes later with increasing altitude. In the Tararua Range in 1963-64 50 percent of buds on trees were open by 10 November at 820 m and by 4 December at 1120 m (J.A. Wardle pers. comm.); while in the Lewis Pass in 1971 extensive bud burst occurred in early November at 760 m but not until early December at 1220 m (Manson, unpubl.). These results indicate an average delay of approximately one week for every 100 m increase in altitude.

After bud burst, shoot elongation was rapid and lateral shoots had completed over 95 percent of the total season's growth by mid-January at all altitudes. Terminal shoots had two separate flushes of growth separated by about six weeks during which there was little elongation. The first flush began in late September and ended in late December (early January at 1220 m), while the second began in mid-February and concluded in late April with the formation of overwintering buds (Figure 2).

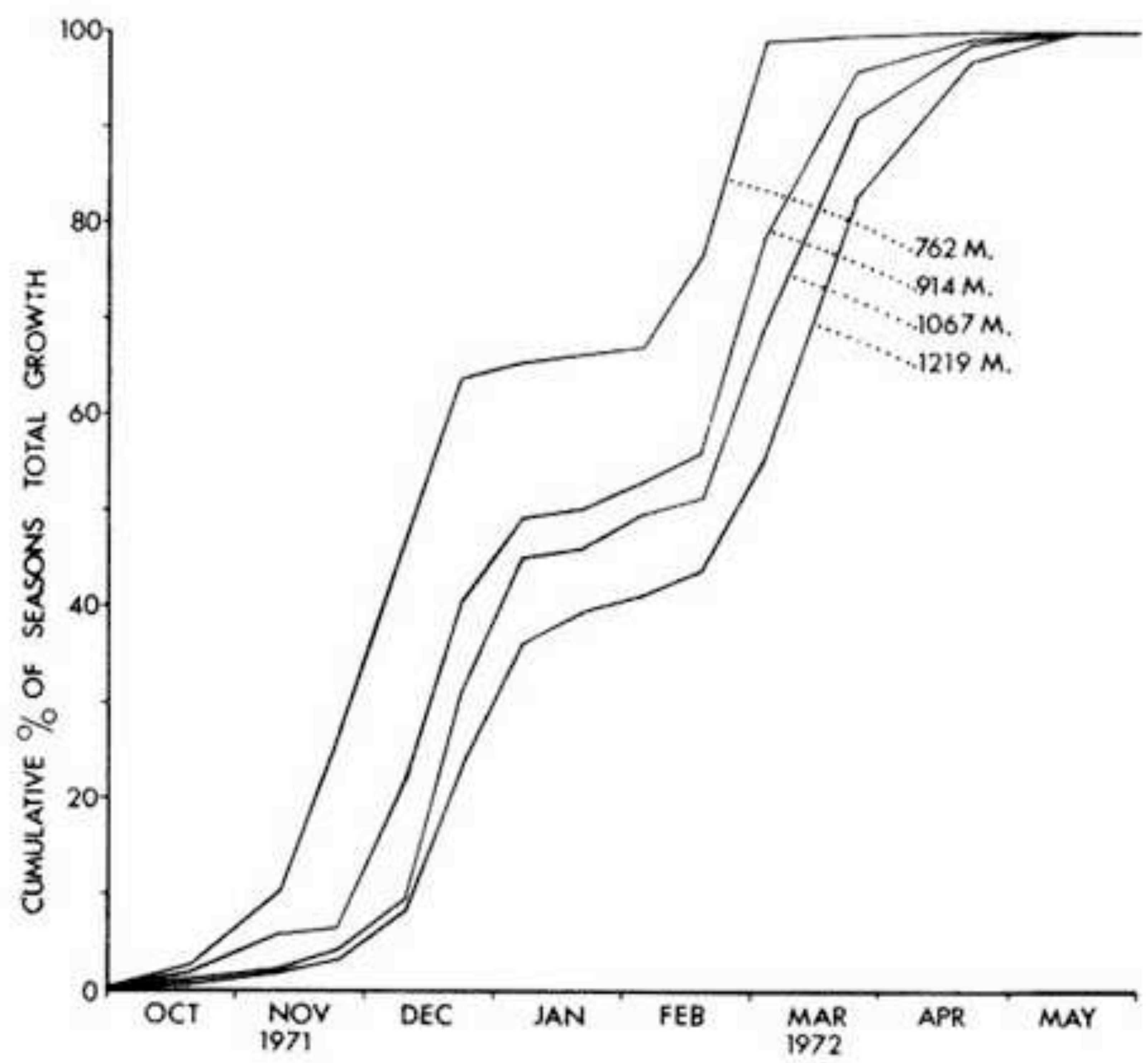

FIGURE 2. *Seasonal growth pattern for terminal shoots of 2 m tall silver beech saplings at 4 altitudes in the Lewis Pass area.*

In contrast to this, first year seedlings grow continuously throughout the season (Bussell 1968a). Bussell found that shoot growth in mature trees also is continuous throughout the season.

4. *Growth Rate of Seedlings*

The affect of light availability on the growth rate of seedlings has been demonstrated by a number of authors (Cockayne 1926, Wardle

1967) and all report an increase in the rate of growth with increased light availability.

The results of a study by Bussell (1968a) demonstrate that regeneration of different ages grows at different rates. The terminal shoots on "first year seedlings" grew an average of 12.4 cm per year, "third year seedlings" grew 7.5 cm per year and young trees ("10 years old") grew 18.3 cm per year. The value given by Bussell for "first year seedlings" is considerably larger than the 2-6.5 cm given by Wardle (1967).

Growth rate decreases as altitude increases. At 840 m in the Lewis Pass, terminal shoots of saplings two metres tall grew an average of 17.25 cm for the season while similar shoots grew an average of 10.90 cm at 1220 m. Lateral shoots on these same saplings grew an average 3.08 cm at 840 m and 3.89 cm at 1220 m.

5. *Tree Height Growth and Stand Top Height*

Hocking and Kenderine (1945) found at Rangataua Forest that between the 30th and 40th years, stand trees had an average annual height increase of 24.4 cm per year. The rate of height increase declined steadily as age increased, and between the 110th and 120th years was 6.1 cm per year. This further declined to 3.0 cm per year between the 170th and 180th years.

The results of Herbert (pers. comm. and 1973) illustrate that the mean annual height increase for silver beech trees decreases with increasing altitude.

Scott, Mark and Sanderson (1964) have recorded the decline in canopy height with increase in altitude at Lake Hankinson.

TABLE 2. *Height of Silver Beech at Lake Hankinson (Compiled from Scott* et al., *1964)*

Altitude (m)	213	305	427	610	762	899
Canopy (m)	25.6	20.1	16.8	14.0	4.3	2.7

The sharp decline in canopy height above 610 m shown in Table 2 was also recorded by Herbert (pers. comm.) in South Westland where the maximum stand height above 610 m was about 12.2 m.

The maximum stand top height is commonly 24 to 26 m on the better sites (Williams and Chavasse 1951) but it may exceed 30 m (Mark and Sanderson 1962).

Cockayne (1926) concluded that increased exposure to wind is a major factor causing decrease in canopy height with increasing altitude.

6. *The Diameter-Growth Rate Relationship*

Under stand conditions there is usually a period of retarded diameter growth. Young trees are suppressed by overhead shading by canopy trees, or by competition from other young trees if regeneration is occurring in a mosaic pattern. Under favourable conditions this period may be as short as 20 to 30 years (Hocking and Kenderine 1945) but it may last 100 years in unfavourable conditions (Herbert 1973, cf. Wardle 1974, p. 22).

On terrace sites in Fiordland trees of less than 7.5 cm d.b.h. are slow growing (about 17 rings per cm). From 7.6 cm — 15 cm d.b.h. growth rate increases to a maximum of about seven to ten rings per centimetre at 30 cm d.b.h. This is maintained until senescence.

On face sites below 610 m the growth pattern is similar but the maximum growth rate achieved is reduced to about 12 rings per cm.

Above 610 m a mean growth rate of about 18 rings per cm is applicable to trees of all size classes (Herbert 1973, cf. Wardle 1974, p. 23).

7. *The Age-Diameter Relationship*

The rate of diameter growth is extremely variable, for under ideal conditions trees may reach 66 cm d.b.h. in less than 200 years (Williams and Chavasse 1951) but on poorer sites trees may take 600 years to reach this diameter (Herbert 1973).

Stand trees grow slower than those in the open because of competition for light and possibly nutrients and moisture (Cockayne 1926).

The influence of increasing altitude on growth rate has been demonstrated by Herbert (1973) who found that trees on terrace sites in Fiordland took 330 years to reach 66 cm d.b.h. while on face sites above 610 m 600 years were required to reach the same diameter (cf. Wardle 1974, p. 23).

DISCUSSION

The information presented in this paper

illustrates that many of the stages in the life history of silver beech are variable, this variation being a reflection of the wide range of climatic and edaphic conditions that the species is able to tolerate.

Some aspects in the life history relevant to management are partially understood but there are still many gaps in our understanding of the behaviour of the species. At the present time quantitative work on seed production patterns is still in its infancy. More studies designed to record seed production over a wide range of forest and site types would lead to a better understanding of the seeding habits of the species. The relationship between climatic conditions and seed production should be investigated further.

Information on the conditions necessary for the establishment and survival of regeneration both in undisturbed forest and in areas where the canopy has been removed or damaged is limited. The relationship between canopy density and the survival rate and growth rate of regeneration needs further investigation. Information of this type combined with data on stand mortality and replacement would allow management to be more soundly based than at present.

The need for more detailed information on the life history of silver beech is clear. It is obvious however that it will be a long time before the behaviour of the species is known in sufficient detail to allow accurate predictions to be made on how it will react in any given situation or to any given treatment.

REFERENCES

BUSSELL, W.T. 1968a. The growth of some New Zealand trees, 1. Growth in natural conditions. *New Zealand Journal of Botany* 6:63-75.

BUSSELL, W.T. 1968b. The growth of some New Zealand trees, 2. Effects of photoperiod and temperature. *New Zealand Journal of Botany* 6:76-85.

COCKAYNE, L. 1926. Monographs of the New Zealand beech forests, Part 1. The ecology of the forest and taxonomy of the beeches. *Bulletin New Zealand State Forest Service* 4:67 pp

HERBERT, J. 1973. Growth of silver beech in Northern Fiordland. *New Zealand Journal of Forestry Science* 3: 137-51.

HOCKING, G.H.; KENDERINE, C.A.B. 1945. Silvicultural observations on a central North Island beech forest. *New Zealand Journal of Forestry* 5: 90-102.

MARK, A.F.; SANDERSON, F.R. 1962. The altidunal gradient in forest composition, structure and regeneration in the Hollyford Valley, Fiordland. *Proceedings of the New Zealand Ecological Society* 9: 17-26.

NEW ZEALAND FOREST SERVICE, 1965. Beech forestry in New Zealand, Volume 2. Papers contributed. (Compiled by D.A. Franklin) (Unpublished).

POOLE, A.L. 1948. The flowering of beech. *New Zealand Journal of Forestry* 5: 422-7.

POOLE, A.L. 1949. Notes on the 1949 beech seeding. *New Zealand Journal of Forestry 6:51-4.*

POOLE, A.L. 1950. Studies in New Zealand *Nothofagus*, 1. Taxonomy and floral morphology. 2. Nut and cupule development. *Transactions of the Royal Society of New Zealand* 78: 363-80, 502-8.

POOLE, A.L. 1952. The development of *Nothofagus* seed (including a preliminary account of the embryogeny, etc.). *Transactions of the Royal Society of New Zealand* 80: 207-12.

SCOTT, G.A.M.; MARK, A.F.; SANDERSON, F.R. 1964. Altitudinal variation in forest composition near Lake Hankinson, Fiordland. *New Zealand Journal of Botany* 2: 310-23.

WARDLE, J.A. 1970. Ecology of *Nothofagus solandri*, 3. Regeneration. *New Zealand Journal of Botany* 8: 571-608.

WARDLE, J. 1974. The life history of mountain beech *(Nothofagus solandri* var *cliffortioides). Proceedings of the New Zealand Ecological Society* 21: 21-6

WARDLE, P. 1963. Growth habits of New Zealand sub-alpine shrubs and trees. *New Zealand Journal of Botany* 1: 18-47.

WARDLE, P. 1967. Biological flora of New Zealand, 2. *Nothofagus menziesii. New Zealand Journal of Botany* 5: 276-302.

WILLIAMS, R.W.M.; CHAVASSE, C.G.R. 1951. The silviculture of silver beech in Southland. *New Zealand Journal of Forestry* 6: 219-35.