

GROWTH OF SILVER BEECH IN NORTHERN FIORDLAND

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ABSTRACT

The growth patterns of silver beech (*Nothofagus menziesii* (Hook. f.) Oerst.) in natural forest conditions in northern Fiordland, New Zealand, are described.

Growth rates differed significantly between some forest associations. The reasons for this were related to site quality (particularly below 610 m altitude) and the effects of altitude. Growth rate was compared for three altitude zones and found to decrease at higher altitudes.

Growth rate/diameter relationships for trees growing on < 610-m-altitude slopes and terraces followed a negative exponential curve to reach a maximum growth rate at about 40 to 50 cm diameter at breast height (d.b.h.). Trees from > 610-m-altitude slopes showed a steady increase in growth rate to a maximum at about 40 cm d.b.h. There was no reliable evidence for a decrease in growth rate in larger diameter stems.

Diameter/age relationships showed that at any given diameter, terrace trees were youngest and high altitude trees oldest. The differences in age increased with increasing diameter.

At high altitudes, a greater proportion of large trees (> 30 cm d.b.h.) fell into the 30 to 70 cm d.b.h. size classes than at low altitudes where there were more stems > 70 cm d.b.h.

The regression, $y = 0.070 (\pm 0.025) + 0.011 (\pm 0.001) X$, for bark thickness on d.b.h. was calculated.

INTRODUCTION

During the 1969-70 summer a reconnaissance survey of northern Fiordland was made by staff of the Forest and Range Experiment Station. Estimates of vegetation condition and type were obtained by sampling in temporary plots located at 135-m slope intervals along 84 altitudinal transects running from valley bottom to timberline. Starting points for the transects were located in a restricted random fashion along the stream courses. Transects followed a compass bearing representing the shortest distance plus 5° from the starting point to the top of the scrub belt (Wardle *et al.*, 1971).

The opportunity presented by this experiment layout was taken to sample growth rates of silver beech (*Nothofagus menziesii* (Hook. f.) Oerst.) in natural forest conditions in Fiordland. Increment cores were taken in plots along the transects in the southern portion of the survey area. This included all major valleys bounded by the Mystery Burn in the south and the Doon River in the north-east on the eastern side of the main

divide, and in the Windward, Irene and George Rivers, and Bligh, George, and Sutherland Sounds on the western side of the main divide (Fig. 1).

The increment cores were used to assess growth rates from the presence of annual growth rings in the most recently formed 2.5 cm of radial increment for each tree sampled. Hutchinson (1926) queried the annual formation of a single growth ring in

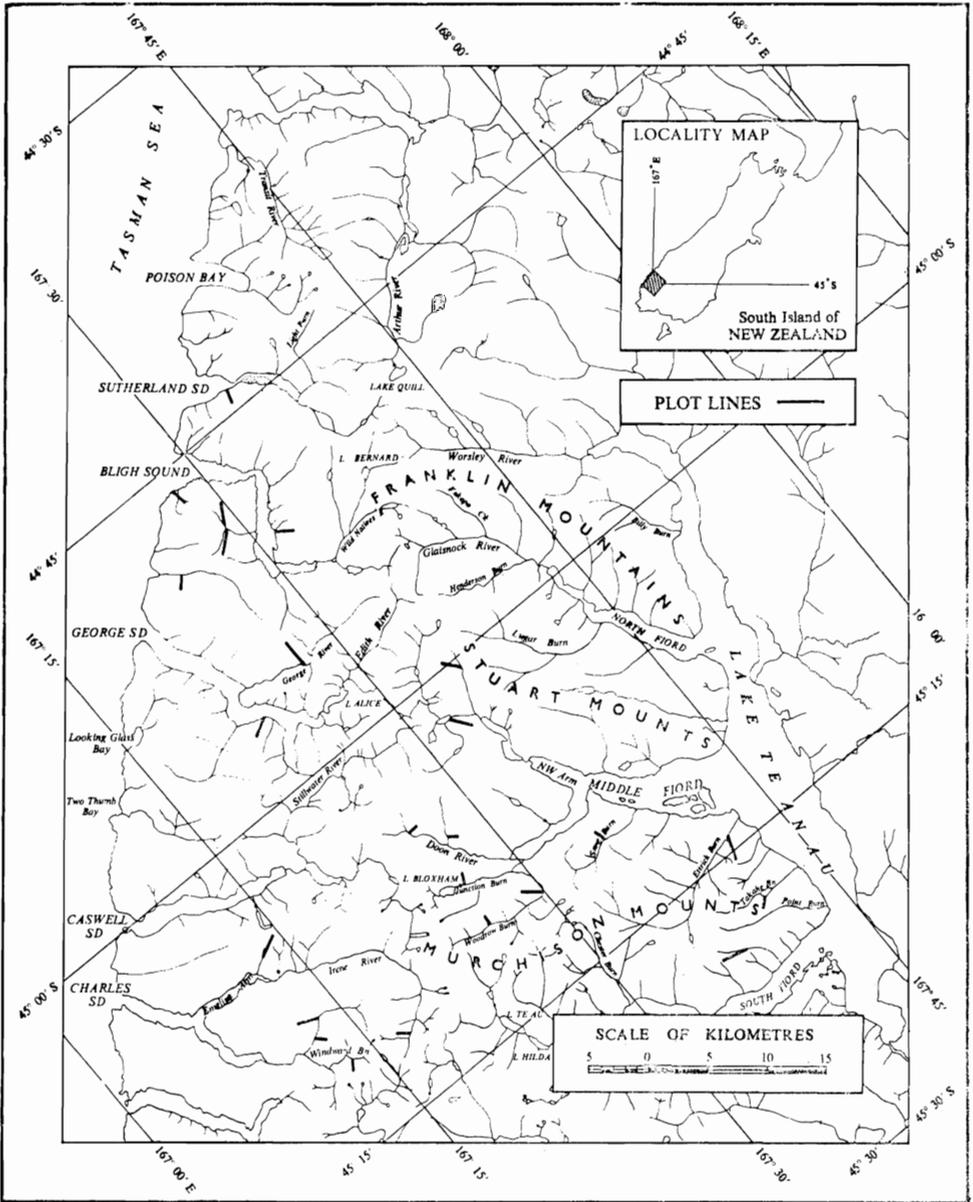


FIG. 1—Locality map and map of the survey area, northern Fiordland, showing line positions.

New Zealand trees (particularly those of taxad species) but concluded that ring formation in beech species was predominantly singular and annual. P. Wardle (1963) found that leading shoots of mountain beech seedlings and saplings tended to form an additional "false" ring but pointed out that such rings are not likely to be confused with the annual growth rings.

The terminal shoots of silver beech saplings (up to about 3.1 m in height) usually showed two growth flushes accompanied by the formation of two growth rings (Bussel, pers. comm.). No data were available for the terminal shoots of larger trees, although in lateral shoots of young and mature trees "one ring was generally formed each year" (Bussel, 1968). However, a proportion of these shoots formed an incomplete second ring.

In this investigation each obvious complete band of latewood tissue is taken to mark the completion of one year's radial growth.

METHODS

Three trees were sampled at each temporary plot. They comprised the nearest tree to plot centre in three d.b.h. classes: 5.0 to 15.0 cm, 15.1 to 30.0 cm, and 30.1 cm and over. At each plot, slope (in degrees), aspect (in degrees), soil depth, altitude, estimated stand height, and composition were measured. Soil depth was measured with a metal probe to a maximum of 45 cm and is expressed as the mean of five values taken round the centre point of each plot. Additional off-line trees were sampled on the terraces.

At each plot, cores at least 2.5 cm long were removed from each quadrant of each sample tree. All cores were removed from about 1.4 m (d.b.h.) above the upper-most visible roots, or above ground level if roots were not visible.

A total of 2,104 cores representing 526 trees of diameter classes between 5.1 cm and 163.8 cm was obtained. A flat transverse surface was cut on each core with a scalpel and the surface wetted with linseed oil. Rings were counted under a binocular microscope and the mean value in rings per 2.5 cm for the four cores representing each tree was calculated. Growth rate information from the most recently formed 2.5 cm radial increment of each sample tree was used to build up reasonably comprehensive diameter/growth rate and diameter/age estimates.

In most cores there was a tendency to obvious ring porosity which made it possible to count up to 100 rings per 2.5 cm without much difficulty.

By sampling at breast height, the time taken to reach a height of 1.4 m is ignored, so that estimates of total age and growth rate are from the time at which the tree had reached this height. The thickness of bark on each of the cores was measured (in millimetres) and a mean value calculated for each tree.

All subsequent references to diameter refer to overbark diameter at breast height.

RESULTS

Growth Rates within Forest Associations

A total of 16 associations were defined by the use of Sorensen's 'K' index of similarity and by a centroid clustering procedure (Wardle *et al.*, 1971). Most of the sample stems occurred in six associations (C₁, C₂, C₃, C₄, P₂, and M₁) (Appendix 1). Associations

M_2 and E_1 contained too few samples to be used in the statistical analysis but are included for comparison.

An analysis of variance was run using 55 trees from each of the above six associations to determine whether the mean growth rates differed. Where an association contained more than 55 sample trees the sample number was reduced to 55 using random number tables. The analysis indicated significant differences in mean growth rates between associations, and the least significant difference test was used to determine where these differences occurred (Table 1).

Mean altitude, slope, stand height, and complexity, and distribution, terrain, soil depth, and aspect were used to define some habitat and structural differences between associations (Table 1). An attempt was made to relate these to differences in growth rate.

At the 5% level of confidence, the associations can be divided into three groups according to growth rate. Silver beech in the seral association P_2 and the lower mid altitude association C_3 had the fastest growth rates. Slower growing trees were found in the low level western association C_4 and the mid altitude association C_2 , whilst the slowest growing trees occurred in the high altitude association C_1 , and association M_1 . Within associations P_2 , C_3 , C_4 , and C_2 the main habitat differences were aspect (C_3 and P_2 with an E bias, and C_4 and C_2 with a W bias), altitude (a 427-m range), and soil depth (association P_2 is restricted to sites with young, rapidly weathering, shallow soils).

Association C_1 is restricted to high altitudes, and, in common with association M_1 , frequently occurs on ridge spur sites which may be drier and less fertile than the adjacent slope sites. The generally slow growing trees in association M_2 would logically be equated with those in associations C_1 and M_1 because of their affiliation with ridge spur sites. The lower altitude association E_1 , which is confined to deep soils, is comparable in growth rate to associations C_3 and P_2 .

Significant differences in mean growth rate between associations may therefore be explained in part by differences in "site quality" (aspect, soil depth, terrain), and altitude. In the following section the effect of change in altitude on growth rate is examined.

Relationship between Growth Rate and Altitude

The mean growth rate of the three trees sampled at each site was calculated. The mean values have been used as the raw data for comparison of growth rate for a series of 76 m altitude classes (Fig. 2).

Trees growing on terraces do not fall into a continuous altitudinal gradient as do all other sample trees. Further, site conditions (soil depth, soil type, water regime) differ markedly between terrace and equivalent altitude hill sites, and for these reasons terrace-grown trees are excluded from this analysis.

Despite considerable variation about the mean values, growth rate tends to decrease at higher altitudes. Up to about 610 m the mean falls between 31 and 38 rings per 2.5 cm for all altitude classes, but from 610 m to timberline the number of rings per 2.5 cm increases to about 58.

TABLE 1—Comparison of mean number of rings per 2.5 cm for forest associations.

Association*	C ₃	P ₂	C ₄	C ₂	M ₁	C ₁	M ₂	E ₁
Mean number of rings per 2.5 cm	26.6	27.1	36.3	38.2	54.7	61.2	59.4	29.8
Standard error	± 3.2	± 1.5	± 2.4	± 2.0	± 3.2	± 3.7		
L.S.D. 5%†	-----		-----		-----			
L.S.D. 1%	-----		-----		-----			
Mean altitude (m)	395	605	185	572	490	853	530	377
Mean stand height (m)	18.7	16.1	17.9	16.6	15.5	11.3	11.5	19.9
Mean complexity	26	24	32	27	27	19	24	21
Mean slope (°)	28	26	24	32	32	31	26	26
Dominant aspect	NNE	E	NNW	NNW	ENE	N	SW	E
Terrain	Slope/terrace	Slope/terrace	Slope/terrace	Slope	Slope/spur	Slope/spur	Slope/spur	Slope
Soil depth	Variable	Shallow	Variable	Shallow/moderate	Shallow/moderate	Shallow/moderate	Moderate	Deep
Distribution	Throughout but tendency to immediately E of main divide	Throughout	W	W with tendency to NW	W	W with tendency to SW	Centred on main divide and NW	SE

* C₃ — Lower mid altitude and terrace silver beech-**Blechnum**-pepperwood forest P₂ — Silver beech-lacebark forest

C₄ — Low level western kamahi-silver beech forest C₂ — Mid altitude silver beech-**Coprosma** forest

M₁ — Mid altitude silver beech-rata-kamahi-mountain beech forest C₁ — High altitude silver beech-**Coprosma-Senecio** forest

M₂ — Mountain beech-totara-**Dacrydium** forest E₁ — Eastern mountain beech-silver beech forest

See Appendix 1 for a detailed description of these associations.

† Bars join mean values where no significant difference exists at the given levels of confidence (L.S.D. = least significant difference).

Soil depth (mean of 5 measurements):
 0-23 cm — shallow
 23.1-45 cm — moderate
 45.1 cm and over — deep

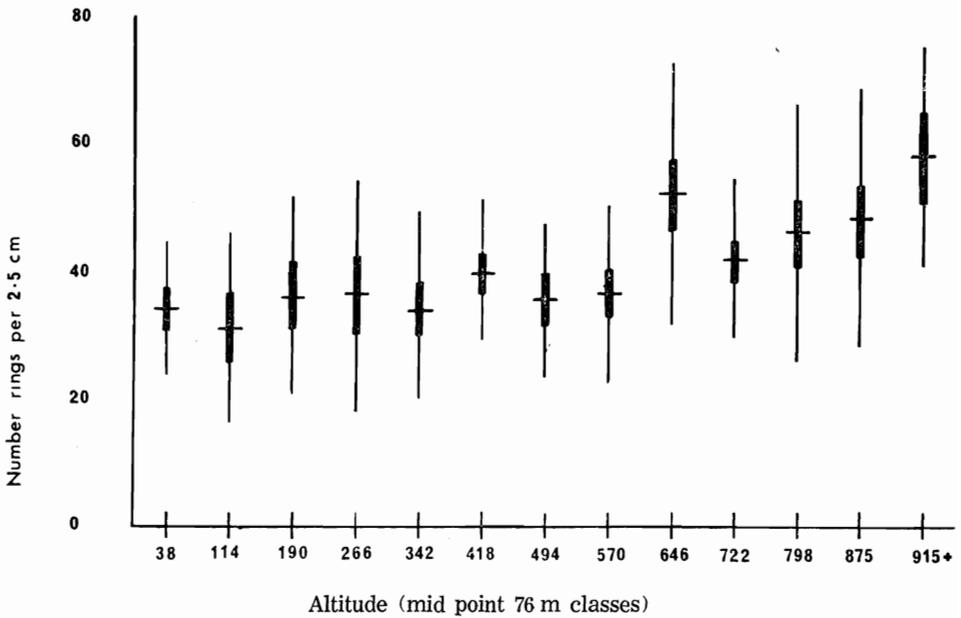


FIG. 2—The relationship between altitude and number of rings per 2.5 cm. Altitude class mid points are at 76 m (250 ft) intervals. Mean, standard error, and standard deviation are shown.

Relationship between Growth Rate and Tree Diameter

In the previous section it has been shown that growth rate decreases at higher altitudes. For this reason two altitude categories have been constructed. These comprise the relatively homogeneous < 610 m category, and the > 610 m category. Terrace trees have been placed into a third category.

Growth rate/diameter relationships have been calculated separately for each of the three categories.

Occasional trees showed much slower growth rates than the mean value for the size class or altitude category. All trees with more than 100 rings per 2.5 cm in the > 610 m category, and more than 70 rings per 2.5 cm in the < 610 m category were considered senescent or dying and have been arbitrarily excluded from the following calculations. These trees comprised about 4.5% and 5.0% of the two samples respectively. No terrace-grown trees were excluded as none could be regarded as grossly atypical in growth rate. The size class distribution of these senescent or dying trees is discussed later.

Table 2 shows the mean number of rings per 2.5 cm and the mean annual radial increment for 7.5-cm diameter classes in the three categories.

(1) Terrace Trees

Terrace trees were sampled mainly in off-line plots in the lower Windward and Irene valleys and in the lower Junction Burn valley. In addition, some lines contained one or two terrace plots.

TABLE 2—Mean growth rate (annual radial increment) and mean number of rings per 2.5 cm for terrace, and < 610 m and > 610 m altitude trees.

Diameter Class (cm)	Category								
	M.A.R.I. (cm)	Terrace M.N.R.I.	S.D.	M.A.R.I. (cm)	< 610 m M.N.R.I.	S.D.	M.A.R.I. (cm)	> 610 m M.N.R.I.	S.D.
0 - 7.5	0.058	44.0	± 6.7	0.056	45.0	± 13.4	0.051	50.5	± 18.3
7.6-15.0	0.079	32.7	± 10.7	0.064	40.6	± 14.5	0.056	45.7	± 19.4
15.1-22.5	0.094	27.7	± 7.6	0.084	30.5	± 14.8	0.056	44.7	± 17.4
22.6-30.0	0.102	24.9	± 9.5	0.074	34.4	± 16.5	0.061	42.5	± 17.0
30.1-37.5	0.147	17.3	± 8.0	0.074	34.1	± 17.2	0.064	40.0	± 21.8
37.6-45.0	0.119	21.2	± 11.3	0.086	29.5	± 17.7	0.043	57.4	± 17.7
45.1-52.5	0.160	15.9	± 8.5	0.089	28.3	± 13.7	0.056	46.3	± 19.3
52.6-60.0	0.114	22.2	± 10.0	0.099	25.7	± 14.2	0.053	46.6	± 26.8
60.1-67.5	0.122	20.8	± 3.3	0.076	33.5	± 22.8	0.061	42.2	± 13.7
67.6+	0.135	19.0	± 5.9	0.086	29.5	± 13.6	0.056	45.8	± 22.9

M.A.R.I. = mean annual radial increment

M.N.R.I. = mean number of rings per 2.5 cm

S.D. = standard deviation

The mean altitude for all terrace plots was 113 m, mean slope 2° and mean soil depth in excess of 45 cm. The number of rings per 2.5 cm ranged from 8 for two trees of 30.7-cm and 33.3-cm diameter respectively, to 54 for an 8.4-cm diameter sapling. These correspond to an annual radial increment of 0.317 cm and 0.048 cm respectively.

The diameter/growth rate relationship follows a negative exponential curve to reach a maximum mean annual radial increment of about 0.127 cm (20 rings per 2.5 cm) in the 33.9 to 48.9 cm diameter range (Fig. 3). This growth rate appears to be maintained for larger-diameter trees (Fig. 3, Table 2).

(2) *Trees Growing at Altitudes of < 610 m*

Trees in this category were sampled mainly in on-line plots. The mean altitude was 366 m, soil depth 24.9 cm and slope 24.5°. The number of rings per 2.5 cm ranged from 8 for two trees of 34.3-cm and 67.3-cm diameter respectively to 68 for a 5.3-cm diameter sapling. This corresponds to annual radial increments of 0.318 and 0.038 cm respectively.

The diameter/growth rate trend is similar to that of terrace trees, although less marked (Fig. 3, Table 2). In the 3.8- to 56.4-cm diameter range there is an increase in mean annual radial increment from 0.056 to 0.099 cm (45 and 25 rings per 2.5 cm respectively). The 60.1 to 67.5 cm d.b.h. size class shows a further decrease in growth rate but does not lie on the general curve (Fig. 3). Except for saplings in the < 7.6-cm diameter range the curve is generally parallel to that of terrace trees.

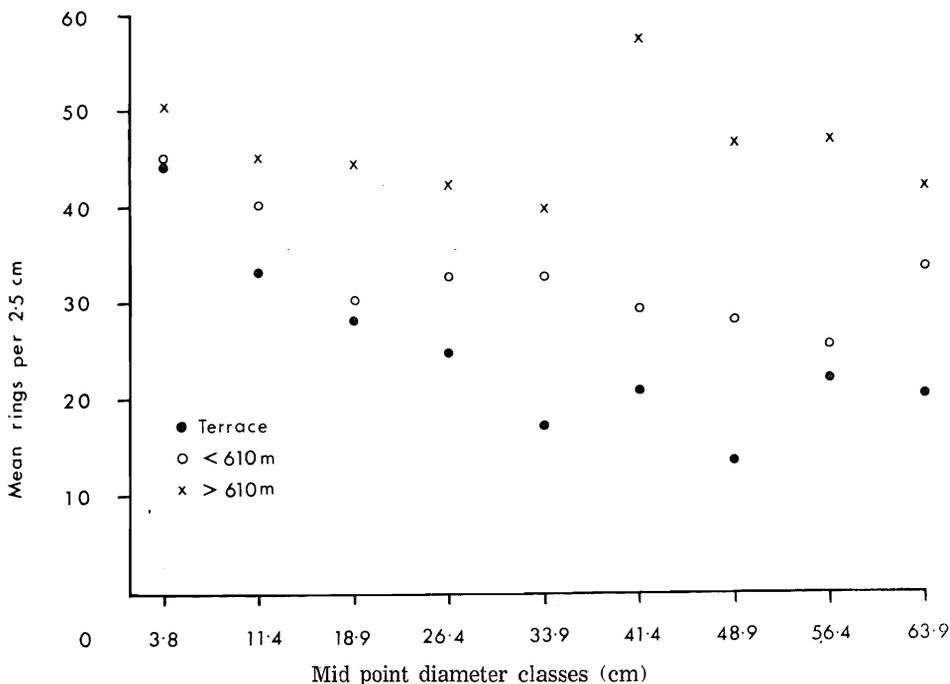


FIG. 3—The relationship between diameter and mean number of rings per 2.5 cm for terrace, and < 610 m and > 610 m altitude trees. Diameter class mid points are at 7.5 cm (3.0 in.) intervals.

(3) *Trees Growing at Altitudes of > 610 m*

Trees in this category were sampled mainly in on-line plots. The mean altitude was 778 m, soil depth 24.4 cm, and slope 31.0°. The number of rings per 2.5 cm ranged from 12 for a 48.8-cm diameter tree to 99 for a 10.7-cm diameter tree. These correspond to growth rates of 0.210 and 0.025 cm annual radial increment respectively.

The diameter/growth rate trend is less clearly defined than for terrace and < 610-m altitude trees. There appears to be a fairly regular, but small increase in growth rate up to about 34.0 cm diameter (Fig. 3, Table 2). The pattern for larger diameter trees is very irregular with wide confidence limits. However, a mean growth rate of about 0.056 cm annual radial increment (45 rings per 2.5 cm) may be applicable to trees in the larger diameter classes.

The Relationship between Diameter and Age

Diameter/age relationships have been constructed for the terrace, < 610 m and > 610 m altitude categories (Fig. 4). These estimates have been calculated on the basis of growth rate/diameter relationships, by accumulating the number of annual rings required for a 2.5 cm increase in diameter for each diameter class in the three categories.

Because of the considerable variation in individual growth rates within the respective diameter classes (all trees from strongly suppressed to dominant had an equal chance of being included in the sample) the graph has a limited, but useful, predictive value. These ages are not absolute since the period taken to reach a height of 1.4 m is not accounted for.

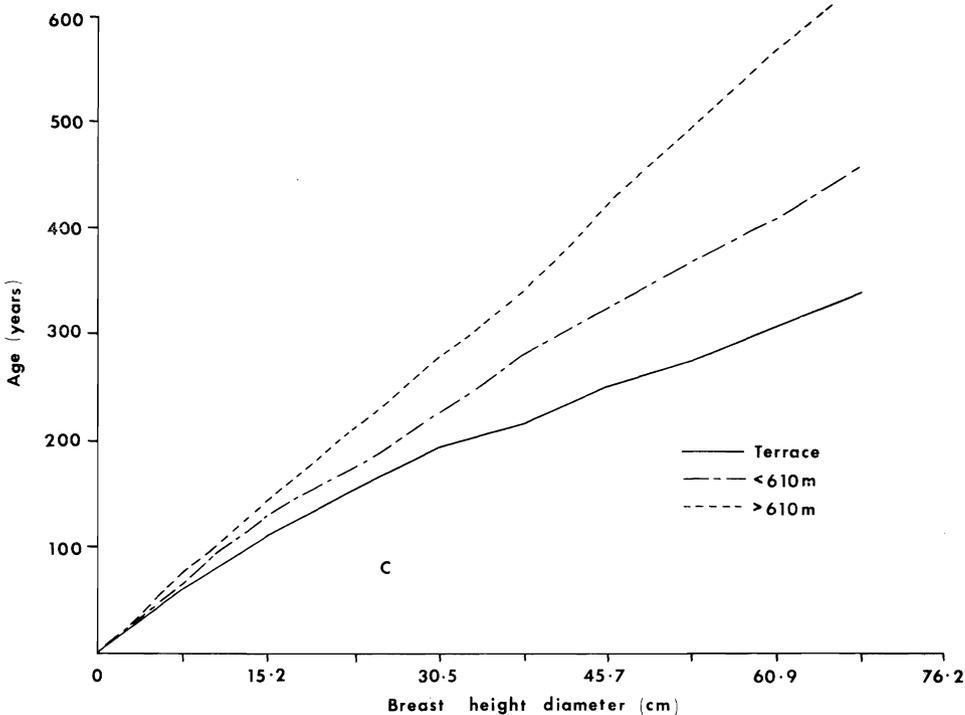


FIG. 4—The relationship between diameter and age for terrace, and < 610 m and > 610 m altitude trees.

Trees from all three categories reach a diameter of about 10 cm at 60 to 85 yr. The size attained by older trees, however, differs markedly. Terrace trees show a substantial decrease in age relative to increasing diameter. The mean age of a 33-cm diameter tree is 200 yr, a 66-cm diameter tree, 330 yr. In the > 610 m altitude category the relationship is nearly straight linear. The age of 33-cm and 66-cm diameter trees is about 300 and 600 yr respectively. For trees in the < 610 m category, the age of 33-cm and 66-cm diameter trees is about 240 and 430 yr respectively.

Slow Growing or Moribund Trees

There was no indication of a possible decrease in growth rate associated with old age in the larger diameter trees (*see* Section (3)). In addition the smallest diameter size classes invariably contained slower growing trees than the larger diameter size classes. Slower growth in the smaller diameter size classes could represent the intrinsic growth pattern of silver beech in closed canopy conditions, or could result from contamination of the sample by a large proportion of suppressed or dying (slow growing) trees.

To investigate these points, the size class distribution of trees with more than 70 rings per 2.5 cm was determined, and the percentage of the total size class sample contributed by these slow growing trees calculated (Table 3).

With the possible exception of the 40 to 50-cm size classes, there is an apparently random distribution of slow growing trees. There is again no evidence for a decrease in growth rate in the larger diameter trees, nor is there a marked increase in the proportion of slow growing trees in the smallest diameter size classes indicating decreased growth rates due to competition.

The Altitudinal Distribution of Large Diameter Trees

The randomly selected on-line trees greater than 30 cm d.b.h. were assigned to one of four diameter classes: 30-50 cm, 50.1-70.0 cm, 70.1-90.0 cm, > 90.1 cm. The altitudinal distribution of the trees in each class was then determined by allocating each tree to one of seven, 153-m altitude classes (Table 4).

In the > 915-m altitude class the largest diameter tree recorded was 69.1 cm, and, compared with lower altitudes, there was a preponderance of trees in the 30-50 cm diameter class. In the 611-m-914-m altitude range there were proportionately fewer trees with diameters exceeding 70.0 cm d.b.h. than at lower altitudes.

The stem size distribution was also compared for the six associations. The effect of increased altitude was again apparent, with the high altitude (mean 853 m) association C₁ containing no trees > 70 cm d.b.h. Trees in association M₁, growing on less fertile soils, were also concentrated in the < 70.0 cm diameter classes.

The Relationship between Diameter and Bark Thickness

All increment cores were removed with the bark intact. The bark thickness from the four cores from each tree was measured in millimetres and the mean value calculated. The regression for bark thickness on diameter was calculated for all trees from all sites.

The regression of bark thickness on diameter is represented by the expression:

$$y = 0.070 (\pm 0.025) + 0.011 (\pm 0.001) x, (r^2 = 0.73)$$

where y = bark thickness in mm

and x = breast height diameter in cm

The effect of both altitude and growth rate on bark thickness was tested. There

TABLE 3—Distribution of slow growing trees by diameter classes.

Diameter class (cm)	0— 5.0	5.1— 10.0	10.1— 15.0	15.1— 20.0	20.1— 25.0	25.1— 30.0	30.1— 35.0	35.1— 40.0	40.1— 45.0	45.1— 50.0	50.1— 60.0	60.1— +
Number of slow growing trees	2	9	6	5	7	4	1	4	5	4	2	3
% total number in class	15.4	13.6	7.6	7.6	12.7	10.5	2.8	14.8	38.5	23.5	13.3	9.7

TABLE 4—Percentages of large diameter (> 30 cm d.b.h.) trees shown for altitude classes. Class limits are at 152 m (500 ft) intervals. Maximum tree diameter recorded in brackets.

Altitude class (m)	N	Diameter b.h. classes (cm)			
		30-50	50.1-70.0	90.1+	
915+	8	75	25 (68.0)	0	0
763-914	23	65	26	5	4 (102.0)
611-762	29	55	38	4	3 (97.0)
459-610	36	61	19	14	6 (105.4)
306-458	30	50	30	10	10 (134.6)
154-305	21	62	14	14	10 (139.7)
0-153	16	56	19	19	6 (156.2)

was no significant difference in bark thickness between fast and slow growing trees, or between trees from widely differing altitudes. The highest altitude trees did tend to have a slightly greater mean bark thickness than the lowest altitude trees and the small difference that does exist is possibly due to a combination of generally slower growth and harsher environment at high altitudes.

There was no measurable difference in bark thickness between trees sampled on east and west sides of the main divide.

DISCUSSION AND CONCLUSIONS

Significant differences were found between the diameter growth rates of silver beech growing in different forest associations. Differences in diameter growth between associations at comparable altitudes may be partly explained by variations in "site quality" (aspect, soil depth, soil fertility). The comparatively depressed diameter growth in associations M_1 and M_2 can be related to soils of low fertility, indicated in M_1 by the presence of mountain beech (J. Wardle, pers. comm.) and in the M_2 by the presence of *Phyllocladus alpinus* and *Dacrydium bidwillii*. Consistently rapid diameter growth in association P_2 can be related to young, rapidly weathering soils although lack of overhead competition from the associated lacebark could be a contributory factor. Increased altitude and lower fertility soils could be responsible for the reduced growth rates found in association C_1 . These results can be compared with those of Wardle (1970) who found that diameter growth of trees in mountain beech associations could be influenced by altitude and other site factors.

The study showed that there was a decrease in growth rate of silver beech at higher altitudes. These results may be compared with those of Mark and Sanderson (1962) who found that growth rates of silver beech in the Hollyford Valley were generally more rapid below, than above, 457 m. J. Wardle (pers. comm.) found evidence for decreased growth rates in mountain beech with increased altitude in the Harper-Avoca area, although a previous study by Wardle (1970) did not show a marked correlation between altitude and growth rate.

The diameter/growth rate pattern of silver beech was shown to follow a negative exponential curve for trees growing on terraces and on slopes of < 610 m altitude. The curve was most pronounced for terrace trees, whilst high altitude trees approached a straight linear relationship. The patterns could result from strong root and light competition in the smaller size classes and probably represents the normal diameter/growth rate pattern in mixed age silver beech stands.

No evidence for any marked decrease in the growth rate of large diameter trees was found in this study. With the possible exception of the 40-50-cm size class there was a near random distribution of slow growing trees according to diameter class. Presumably growth rate falls off as individual stems become diseased and/or over-mature but it must be concluded that a constant growth rate is maintained until this stage is reached.

Diameter/age estimates showed the development of increasingly large differences in the three categories. Terrace trees became progressively larger than all other trees at a given age. High altitude trees were the slowest growing whilst trees at mid altitudes were intermediate in growth rate.

There have been few studies on the growth of silver beech in untended, natural forest conditions. However, in Woodlaw forest Williams and Chavasse (1951) counted annual rings on the stumps of felled untended silver beech. The diameter/age ranges were roughly comparable to the diameter/age estimates for terrace grown trees in the present study. In contrast Williams and Chavasse (1951), Hinds and Reid (1957), and Franklin (1965) considered that well tended stands growing under favourable conditions in Southland could produce 45 cm d.b.h. stems in about 120 yr. Hocking and Kenderdine (1945) indicated that similar growth rates were possible at Rangataua.

In this study all trees (from strongly suppressed to dominant) had an equal chance of being included in the sample. Death of trees in all size classes in natural beech stands is a continuous process (J. Wardle, pers. comm.) and, accepting that suppressed trees, i.e., trees most likely to die from the effects of competition, are slower growing than the dominants, it is possible to improve the diameter/growth rate and diameter/age relationships by a consideration of only the fastest growing trees, i.e., those trees which are likely to make up a large proportion of a given stand.

The distribution of large diameter stems by altitude and association showed that at high altitudes, and in associations growing on low fertility soils, there was a greater proportion of stems in the < 70 cm d.b.h. size classes than at low altitudes, or on more fertile soil types. In the < 610 m altitude zone (including terraces), 75% to 80% of all stems > 30 cm d.b.h. were contained in the 30 cm to 70 cm diameter classes. Above 610 m altitude, 91% to 100% of all stems were contained in the same classes. Similarly associations C₁ (high altitude) and M₁ (low fertility soils) contained greater proportions of stems in the 30- to 70-cm diameter size classes than other associations.

The indications are that at high altitudes, or under low fertility soil conditions, there are restrictions both on absolute tree size and growth rate.

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APPENDIX I

The Associations

C₁ — Silver beech-*Archeria-Senecio* forest

This is a major association in the Charles Sound area. Dominated by silver beech with a sub-canopy of *Senecio bennettii* and occasionally *Pseudopanax simplex*. Shrub tiers are generally dense and dominated by *Coprosma pseudocuneata*, *Archeria traversii*, *Myrsine divaricata*, *Pseudopanax colensoi*, and *Coprosma astonii*.

C₂ — Silver beech-*Coprosma* forest

This is an important association in the mid west and south-west. Dominated by silver beech with some rata (*Metrosideros umbellata*) and kamahi (*Weinmannia racemosa*). There is a dense sub-canopy of broadleaf (*Griselinia littoralis*), *Pseudopanax simplex*, and *P. colensoi*. Shrub tiers usually dense and dominated by the *Coprosma* species—*C. foetidissima*, *C. astonii*, and *C. colensoi*. *Pseudowintera colensoi*, *Myrsine divaricata*, and *Archeria traversii* may also be important species.

C₃ — Silver beech-pepperwood-*Blechnum* forest

This is a moderately important association throughout the survey area. The canopy is dominated by silver beech and kamahi. The sub-canopy is dense and dominated by broadleaf, putaputaweta (*Carpodetus serratus*), *Pseudopanax simplex* and lancewood (*P. crassifolium*). The shrub tiers are relatively open with main species including *Coprosma foetidissima*, pepperwood (*Pseudowintera colorata*) and occasionally *Myrsine divaricata*, *Coprosma astonii*, and *Cyathea smithii*.

C₄ — Kamahi-silver beech-*Cyathea* forest

This association is restricted to low altitudes on the western side of the survey area. The canopy is dominated by kamahi. Silver beech is generally present and there may be some rata, miro (*Podocarpus ferrugineus*), and rimu (*Dacrydium cupressinum*). The fairly dense sub-canopy consists of broadleaf, *Cyathea smithii*, *Pseudopanax simplex*, lancewood, *Schefflera digitata*, *Myrsine australis*. The shrub tiers are generally open with *Coprosma foetidissima*, pepperwood, *Coprosma colensoi*, and *Myrsine divaricata*.

M₁ — Silver beech-rata-kamahi-mountain beech forest

This association is important in the western side of the survey area and along the central ranges. The canopy is co-dominated by silver beech, rata, kamahi, Hall's totara (*Podocarpus hallii*), and mountain beech (*Nothofagus solandri* var. *cliffortioides*). There is a fairly dense sub-canopy of *Pseudopanax simplex*, *P. lineare* and broadleaf. The shrub tiers are dominated by *Coprosma foetidissima*, *C. colensoi*, and *Myrsine divaricata*.

M₂ — Mountain beech-*Phyllocladus* forest

This is a minor association only. The canopy is dominated by mountain beech with occasional silver beech, rata, Hall's totara, kamahi and pokaka (*Elaeocarpus hookerianus*). The sub-canopy consists of *Pseudopanax simplex*, *P. lineare*, and broadleaf, with a dense shrub tier of *Phyllocladus alpinus*, *Myrsine divaricata*, *Coprosma foetidissima*, and *Archeria traversii*.

P₂ — Silver beech-lacebark-*Polystichum* forest

This association occurs throughout the survey area. It forms a seral vegetation on rock debris slopes and on terraces. Silver beech is almost always present as an emergent

dominant, with a sub-canopy of lacebark (*Hoheria glabrata*) often associated with broadleaf and *Pseudopanax simplex*. The shrub tier is dominated by *Coprosma astonii* and *C. ciliata* with *Myrsine divaricata*, pepperwood, and *Coprosma foetidissima*.

E₁ — Mountain beech-silver beech-kamahi forest

This association is confined to the eastern side of the survey area. There is a canopy of mountain beech, silver beech, and kamahi with occasional miro, Hall's totara, and rata. The sub-canopy consists of lancewood, *Pseudopanax simplex*, and broadleaf. The only important shrub species is *Coprosma foetidissima*.

E₂ — Simple silver beech forest

This association is confined to the eastern side of the survey area and is the least complex of all the associations. The canopy is dominated by silver beech but mountain beech is sometimes present. The sub-canopy and shrub tiers are almost entirely composed of regeneration of these species.