DYNAMICS OF EVEN-AGED NOTHO FAGUS TRUNCATA AND N. FUSCA STANDS IN NORTH WESTLAND, NEW ZEALAND

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ABSTRACT

Untended, fully stocked, even-aged stands of Nothofagus truncata (Col.) Ckn. (hard beech) or N. fusca (Hook. f.) Oerst. (red beech) of natural and cultural origin and ranging in age from 20 to 100 years, were sampled using temporary and permanent plots on a range of sites in North Westland, South Island, New Zealand. Changes in stand parameters with age were quantified in order to assess growth of these stands, and thus gain some insight into their silvicultural potential.

Stands of each species followed a similar pattern of growth, with rapid early height and basal area increment. Mean top height reached a maximum of c. 27 m by age 100 years. Basal area reached an equilibrium of c. 41 m²/ha in N. truncata and 46 m²/ha in N. fusca as early as age 30 years. Nothofagus truncata stands had, on average, a somewhat lower mean diameter at any given age than N. fusca stands, and maintained higher stockings. Both species attained similar maximum volume of c. 460 m³/ha at age 100 years.

Keywords: even-aged stands; stand dynamics; growth; Nothofagus truncata; Nothofagus fusca.

INTRODUCTION

Species of Nothofagus (southern beech) comprise most of the forest cover of the Upper Grey, Inangahua, and Maruia Valleys in North Westland (Franklin & Nicholls 1974). These extensive forests form a considerable potential wood resource, estimated at 140 000 ha, and are amenable to intensive and extensive management for a range of wood products, especially good-quality medium-density sawn timber (Gleason 1982).

† Since deceased.

Within these forests, secondary even-aged stands of *N. truncata* and of *N. fusca*, often with appreciable admixtures of *N. menziesii* (Hook. f.) Oerst. (silver beech), commonly develop after canopy destruction through catastrophic windthrow, fire, or clearfelling (Masters et al. 1957) (Fig. 1), and in total extended over c. 2000 ha in 1952 (Conway 1952).

Although the range of *N. truncata* and *N. fusca* does overlap in places (Hinds & Reid 1957), in general they show distinct site preferences in the region (Moorhouse 1939; Morris 1959). *Nothofagus truncata* prefers ridges in dissected hill country, and better-drained sites on glacial outwash terraces; *N. fusca* prefers floodplains and the lower slopes and gullies of dissected hill country (June 1982). *Weinmannia racemosa* Lf. (kamahi) and *Quintinia acutifolia* Kirk (quintinia) are commonly associated with *N. truncata*, and *N. menziesii* with *N. fusca* (Morris 1959).
The occurrence of even-aged stands of *Nothofagus* of one or more species was noted as early as 1926 by Cockayne, who mentioned the development of large even-aged stands of *N. solandri* var. *cliffortioides* (Hook f.) Poole (mountain beech) after extensive windthrow, and of more-or-less even-aged stands of *Nothofagus* spp. after milling or fire (Cockayne 1926). Since then substantial areas of such stands (commonly termed “pole stands”) have been identified by National Forest Survey (Masters *et al.* 1957), and there have been a number of detailed descriptions of *N. fusca* in Westland (Foster 1931; Moorhouse 1939; Evans & Jackson 1972) and *N. menziesii* in Southland (Birch 1935). Other authors, including Williams & Chavasse (1951), Conway (1952), Kirkland (1961), and Wardle (1970, 1984) have discussed even-aged stands within broader contexts, as did the 1964 Forest Research Institute symposium on beech forestry (Franklin 1965). There have, however, been no detailed investigations in even-aged stands of *N. truncata*.

*Nothofagus truncata* and *N. fusca* have predominantly “gap-phase” regeneration modes in the region (June 1982); thus, forests in which they predominate are likely to consist of small even-aged patches of various ages. Even-aged stands develop after logging, and may have silvicultural potential, so their dynamics have both ecological and management implications. In this study we examined even-aged *N. truncata* stands in order to assess their developmental pattern. A range of *N. fusca* stands was also examined for comparison. Time-series data gathered over periods ranging from 12 to 15 years from permanent sample plots in other even-aged *N. truncata* and *N. fusca* stands in the same region were also used for comparative purposes.

**STUDY AREAS**

Full details of the study areas are available from the senior author.

*Nothofagus truncata*

Twenty-one study areas, mostly in the Grey Valley were examined (Fig. 2), all within the lowland forest zone (see Nicholls 1983). Soils are yellow-brown earths (steepland variants), well-drained, strongly leached, and of low to very low natural fertility, and podsols with imperfect drainage and extremely low fertility (Mew 1980). Climate is mild and superhumid; annual rainfall is relatively constant, but shows marked local variation, e.g., 2000 mm at Waimaunga and 3600 mm at Granite Creek (New Zealand Meteorological Service 1978). Data from a permanent sample plot in Hochstetter Forest were analysed.

*Nothofagus fusca*

Nine study areas in the Grey, upper Inangahua, and upper Maruia Valleys were examined. A variety of soil types occur, including yellow-brown earths and lithosols. Five localities lie in the lowland forest zone, under a mild superhumid climate; the other four areas are within the montane forest zone and have a cooler superhumid climate.

Data from permanent sample plots in four further localities in the same region, sited mostly on lithosols or recent alluvial soils within the lowland forest zone and with a mild superhumid climate were also analysed.
FIG. 2—Location of study areas and permanent sample plots. *Nothofagus truncata:*
1 = Sullivan Creek, 2 = Half-Ounce Creek, 3 = Duffers Creek, 4 = Back Creek, 5 = O'Rourkes Creek, 6 = Fitz's Gully, 7 = Upper Grey River, 8 = Ahaura River, 9 = Wallsend, 10 = Brunner Mine, 11 = Galweys Lookout, 12 = Waiuta, 13 = Sawyer Creek, 14 = Tobin Creek, 15 = Webby Creek, 16 = Inangahua Landing, 17 = Granite Creek, 18 = Bywash Creek, 19 = Orwell Creek, 20 = Frenchmans Creek, 21 = Waimaunga. *Nothofagus fusca:*
22 = Maruia River (east bank), 23 = Marble Hill, 24 = Rahu River, 25 = Station Creek, 26 = Progress Water Race, 27 = Reefton, 28 = Flagstaff, 29 = Craigieburn, 30 = Baxter Creek.
Permanent sample plots: *1 = Hochstetter (Wd 160), *2 = Staircase Creek (N50-53), *3 = Slabhu Creek (N54, 55), *4 = Oriental Creek (N56-58), *5 = Waipuna (Wd 71).
DATA COLLECTION

The 30 sites known to contain even-aged stands (from local experience, National Forest Survey mapping, or inspection of aerial photographs) were visited on the ground. Between two and five temporary, 0.04-ha, rectangular plots were placed in apparently fully-stocked portions of each stand, and diameters at breast height (1.4 m) of all stems greater than 10 cm in diameter were measured. Frequency of smaller stems greater than 1.4 m in height was recorded in 2-cm-diameter classes. At 19 sites, sectional measurements using the method described by Whyte (1971) were gathered from 12–15 selected felled stems, chiefly poles and trees (>10 cm dbh), but covering the full range of sizes present. Bark thicknesses on two radii were assessed at each measurement point on the stem using a Swedish bark gauge. "Effective" ages were obtained from examination of growth rings on smoothed discs taken from cut stumps. "Effective age" is the age of advance growth since release by destruction of the previous canopy (Kirkland 1961). Mean parameters were obtained for each stand by averaging individual plot parameters.

The permanent plots are 0.1 ha in extent, and with one exception were thinned 12–15 years after they were established. Only measurements taken in the period before thinning were used in the analysis. Where plots of similar age occurred at the same locality, stand parameters were obtained by averaging plot parameters.

CHARACTERISTICS OF EVEN-AGED NOTHOFAGUS STANDS

Even-aged stands of _N. truncata_ and _N. fusca_ are characterised by a relatively narrow range of diameters and uniform canopy height and structure. The latter allow easy identification of these stands from aerial photos. Generally, in both species a substantial proportion of the trees in even-aged stands resulting from the destruction of mature forest develop from the "advance growth" of the previous stand (Kirkland 1961). Stands resulting from the destruction of previous pole stands, however, are likely to develop largely from seedlings recruited after the disturbance (J. A. Wardle, pers. comm.). Sometimes stands contain a small proportion of canopy trees surviving from the previous stand (Fig. 3). Such trees influence stand structure and were avoided in plot establishment.

Diameter distributions of beech are initially negatively skewed, approaching a "reverse J-shaped" curve (Fig. 4). As the mean diameter of the stand increases and density decreases with age, the distribution tends towards normality, reflected in a bell-shaped curve. This indicates that while self-thinning proceeds, no further recruitment takes place, so that stands remain even-aged for at least the first 70 to 100 years.

The _N. truncata_ stands contained considerable amounts of other species, mainly _W. racemosa_, _Q. acutifolia_, and _Myrime salicina_ Hook. f. (toro), accounting on average for 60% of total density and 25% of total basal area. Increment in mean diameter for these species averaged only half that of _N. truncata_, supporting the view (Moorhouse 1939) that _W. racemosa_ and _Q. acutifolia_ are eventually suppressed by beech. Diameter distributions of _W. racemosa_ and _Q. acutifolia_ reflect those of _N. truncata_, suggesting that these species do not regenerate during the first 100 years.
FIG. 3—Two pole stands of different ages at Orwell Creek, each containing survivors of the previous forest. The older stand (right) derives from logging in c. 1902, followed by attrition of the remaining trees. The younger stand (left) derives from logging of the resulting pole stand in c. 1958, followed by windthrow of the remaining trees.

H₁ = survivor from the original forest, H₂ = survivor from the 1902 pole stand, H = hard beech (N. truncata), R = red beech (N. fusca), K = kamahi (W. racemosa), Q = quintinia (Q. acutifolia).

The lower part of the Figure represents vertical projection of crown areas on to the ground.

of the stands' life. *Weinmannia racemosa* shares the intermediate shade-tolerance of *N. truncata* in north Westland, while *Q. acutifolia* is relatively light-demanding (June 1982). Unlike *W. racemosa* and *Q. acutifolia*, diameter distributions of *M. salicina* maintained a "reverse J-shaped" curve, even at an age of 100 years, indicating continuous regeneration and considerable shade-tolerance.

*Nothofagus menziesii* was present in all but one *N. fusca* stand, as well as two *N. truncata* stands. Proportions varied enormously but showed no obvious relationship with site factors or age. In the *N. fusca* stands, however, it occupied a subdominant
FIG. 4—Diameter distributions in (upper) some **N. truncata** stands and (lower) some **N. fusca** stands.

position and so accounted for less basal area (21% on average) than its numerical importance (averaging 31%) would suggest. Mean diameter of **N. menziesii** averaged 60% that of **N. fusca**; in the three permanent plots with high proportions of **N. menziesii** for which species-specific data were available, **N. menziesii** declined sub-
stantially in terms of both relative density and relative basal area over periods of 13–15 years. Thus, *N. menziesii* appears to be progressively suppressed by faster-growing *N. fusca*. Diameter distributions of *N. menziesii* mirror those of *N. fusca* suggesting that, in spite of its relatively high shade-tolerance (Wardle 1984), no further recruitment of *N. menziesii* occurs for the first 70 years in mixed stands.

Even-aged beech stands are inherently unstable on some sites, where edaphic and climatic factors predispose them to periodic windthrow. Intraspecific competition and its associated stress, which may be aggravated by drought, also predispose them to attack by native pinhole borer (*Platypus* spp.) (Milligan 1979). Severe attack on trees over 35 cm in diameter usually kills them (Milligan 1979), so that well-stocked even-aged stands with trees greater than 40–50 cm dbh are rare (Franklin & Beveridge 1977).

**ANALYSES AND RESULTS**

**Notation**

*Individual tree statistics*  

\[ \begin{align*}
D &= \text{overbark diameter (cm)} \\
D_{1.4} &= \text{overbark diameter at breast height (cm)} \\
Bt &= \text{bark thickness (mm)} \\
Bt_{1.4} &= \text{bark thickness at breast height (mm)} \\
b_{ab} &= \text{individual tree basal area over bark (m}^2) \\
Ht &= \text{individual tree height (m)} \\
V_{ub} &= \text{individual tree volume under bark (m}^3) \\
\end{align*} \]

*Stand parameters*  

\[ \begin{align*}
\text{Age} &= \text{effective stand age (years)} \\
\text{Den} &= \text{stocking density (stems/ha)} \\
\text{MD} &= \text{mean diameter (cm) (diameter of tree of mean basal area)} \\
\text{MD}_{250} &= \text{mean diameter (cm) of the 250 largest trees/ha} \\
\text{BA} &= \text{stand basal area over bark (m}^2/\text{ha}) \\
\text{MTH} &= \text{mean top height (m) (mean height of the tree of mean diameter of the 100 largest trees/ha)} \\
\text{Vol} &= \text{total stand volume underbark (m}^3/\text{ha}) \\
\end{align*} \]

**Individual Tree Equations**

Individual tree volumes were calculated using the conic integral formula for lower sections (below 3 m), cone for the apex, and Smalian’s formula for remaining sections.

Two-way volume functions of the form

\[ V_{ub} = b_{ab} \times Ht \times \text{form factor} \]

were derived for each stand, and for each of the three *Nothofagus* species. Standard deviation was assumed to be proportional to the product of height and basal area.
Differences between form factors of species and within species of stands, were tested by ANOVA, but were not significant.

Form factors for each species are given in Table 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Form factor</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nothofagus truncata</td>
<td>0.454</td>
<td>0.004</td>
</tr>
<tr>
<td><em>N. fusca</em></td>
<td>0.453</td>
<td>0.004</td>
</tr>
<tr>
<td><em>N. menziesii</em></td>
<td>0.440</td>
<td>0.007</td>
</tr>
</tbody>
</table>

**Bark thickness**

Bark thickness was measured in 151 *N. truncata* trees in 13 study areas and, for comparative purposes, in 30 *N. fusca* trees in five study areas and 16 *N. menziesii* trees in two study areas - a total of 1119, 183, and 124 individual observations respectively. These were then analysed in relation to diameter, individual tree, and species.

Within individual trees, bark thickness increased with diameter according to the function

$$B_t = a \times D + b$$

Within species, $a$ and $b$ varied significantly ($p < 0.05$) between individual trees, but no relation with height or dbh was evident.

To minimise variance due to individual tree differences, the factor

$$F = \frac{a \times D_{1.4} + b}{B_t_{1.4}}$$

was applied to the above function, giving

$$B_t = \left( a \times D + b \right) F$$

This results in better estimates of bark thickness for *N. truncata* but not for *N. fusca* or *N. menziesii*, when bark thickness at breast height is available.

The coefficients and their standard errors and 95% confidence intervals given in Table 2 indicate similar bark thickness in all New Zealand beeches.

<table>
<thead>
<tr>
<th>Species</th>
<th>a</th>
<th>Standard error</th>
<th>b</th>
<th>Standard error</th>
<th>95% confidence interval Without F</th>
<th>With F</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>N. truncata</em></td>
<td>0.23</td>
<td>0.007</td>
<td>1.2</td>
<td>0.05</td>
<td>±1.6 ±0.9</td>
<td>±0.9</td>
</tr>
<tr>
<td><em>N. fusca</em></td>
<td>0.28</td>
<td>0.017</td>
<td>0.5</td>
<td>0.20</td>
<td>±1.6 ±2.4</td>
<td>±2.4</td>
</tr>
<tr>
<td><em>N. menziesii</em></td>
<td>0.27</td>
<td>0.021</td>
<td>0.2</td>
<td>0.25</td>
<td>±0.7 ±0.5</td>
<td>±0.5</td>
</tr>
<tr>
<td><em>N. solandri</em></td>
<td>0.23</td>
<td>-</td>
<td>0.15</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* Wardle (1970)
Stand Equations

Stand equations were derived by linear or non-linear regression methods from site means, and thus apply to average sites only; individual sites may vary considerably about them. Means from permanent plots were used to check the equations. Unless stated otherwise, all equations apply only to the total beech component of the stand. Other species are ignored.

Mean top height

Mean top height was derived for each temporarily sampled stand by obtaining stand height functions of the form

\[ Ht = 1.4 + a (1 - b D^{1.4}) \]

(Richards 1959)

and calculating the height corresponding to the mean diameter of the 100 largest trees per hectare. These and estimates of MTH from the permanent sample plots were plotted against age (Fig. 5), and a height/age function of the form

\[ \text{MTH} = a (1 - b \text{Age}) \]

derived from temporary plots by non-linear least-squares methods. Since no significant difference existed between *N. fusca* and *N. truncata* stands, one function was obtained for both: \(a = 26.9\) (s.e. 1.2), \(b = 0.964\) (s.e. 0.004).

![Graph showing mean top height vs age for *N. truncata* and *N. fusca*](image)

FIG. 5—Mean top height v. age; P indicates data from permanent sample plots.

The height/age function indicates a maximum mean top height of c. 27 m reached by an age of c. 100 years. Estimates from permanent plots generally agree with this function.

Mean diameter

A linear regression was fitted for each species for the temporary plots as follows

\[ \text{MD} = a + b \times \text{Age} \]

As the intercepts were not significant, regressions were forced through the origin (Fig. 6). Mean diameters of the permanent sample plots are included for comparative purposes. Differences between coefficients were tested for species and for stands by ANOVA.
The coefficient obtained for *N. truncata* stands was 0.24 (s.e. 0.01), and for *N. fusca* stands 0.32 (s.e. 0.02).

Mean diameter was significantly lower (p < 0.01) in *N. truncata* stands than in *N. fusca* stands of similar age, and significant differences (p < 0.01) also existed between the mean diameters of stands of similar age. The coefficients indicate that *N. truncata*, on average, attains about 75% the mean diameter at given age of *N. fusca*, as implied by Hinds & Reid (1957). Changes in mean diameter over time in permanent plots suggest that mean diameter increases at an accelerating rate over the first 20 to 40 years and then remains constant. The line which best fits the changes in mean diameter of each of these plots is

\[ MD = 0.47 \times \text{Age} - 10.5 \]

and appears to be the best available for *N. fusca* stands between c. 40 and 100 years old.

**Mean diameter of the 250 largest trees/ha**

The following equation was fitted

\[ MD_{250} = a \times \text{Age}^b \]

and the coefficients obtained for *N. truncata* stands were \( a = 3.9 \) (s.e. 1.3), \( b = 0.47 \) (s.e. 0.08) and for *N. fusca* stands \( a = 3.6 \) (s.e. 2.2), \( b = 0.53 \) (s.e. 0.17).

As with over-all mean diameter, mean diameter of the 250 largest trees/ha was significantly lower in *N. truncata* stands than *N. fusca* stands of similar age (Fig. 7).
The diminishing rate of increase over time reflects increasing competition between individuals. Individual diameter growth of dominants and codominants is likely to follow a similar pattern, as shown by Franklin (1965).

**Stand basal area**

Stand basal areas are presented in Table 3. Regression analysis of stand basal area on age was performed, and differences between species and between stands were tested by ANOVA.

<table>
<thead>
<tr>
<th></th>
<th>Beeches only</th>
<th>s.e.</th>
<th>All species</th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. truncata stands</td>
<td>41</td>
<td>2</td>
<td>54</td>
<td>2</td>
</tr>
<tr>
<td>N. fusca stands</td>
<td>46</td>
<td>2</td>
<td>47</td>
<td>1</td>
</tr>
</tbody>
</table>

No significant correlation between stand basal area and age was apparent in the temporary or in the permanent plots (Fig. 8). While mean basal area increment was not significantly different from zero, this does not exclude the possibility of a slight increase over time, as suggested by Wardle (1984) for N. solandri var. cliffortioides and N. menziesii. There were significant differences (p <0.05) in total and beech basal area between the N. fusca and N. truncata stands, and significant differences (p <0.01) also existed between stands of the same species. No correlation between basal area and site factors such as soil type was evident. This and changes in basal area in permanent plots suggest that differences in basal area between stands may reflect fluctuations in time, rather than differences in site quality. Thus, stands appear to reach their equilibrium basal area by as early as age 30 years, and to fluctuate about it thereafter. Even-aged N. truncata stands in North Westland attain a similar basal area to N. solandri var. cliffortioides forest and a moderate basal area in relation to beech forest in general (c. 48 and 57-73 m²/ha respectively – Wardle 1984), but N. fusca rather less than usual (c. 55 m²/ha – Wardle 1984).

FIG. 8—Stand basal area v. age.
**Stand density**

Given the equation $MD = b \times \text{Age}$ and constant basal area, the following necessarily holds for beech stands aged between 30 and 100 years

$$\text{Den} = \frac{a}{\text{Age}^2}$$

Coefficients derived from the mean diameter $v.$ age equation and mean basal area are as follows: for *N. truncata* stands, $a = 8.33 \times 10^6$; for *N. fusca* stands, $a = 5.44 \times 10^6$.

They indicate that *N. truncata* stands have a rather higher stocking density than *N. fusca* stands of similar age. In stands of each species, however, the equations indicate that natural thinning (which selectively removes the smaller stems in the lower dominance classes) operates with diminishing intensity as stands age (Fig. 9). For example, in *N. truncata* stands, predicted natural thinning intensity at age 40 (5% per annum) is twice that at age 80 (2.5% per annum).

**Total stand volume**

Three methods of calculating stand volume (Philip 1983) can be used in secondary beech stands. In the first, the volumes of a sample of trees from a particular stand are accurately determined from sectional measurements and a stand volume line of the form $\text{Vol} = c \times \text{BA}$ obtained. Stand volume can then be calculated directly from stand basal area.

In the second, two-way volume functions of the form $V_{ub} = a \times \text{Ht} \times D_{1.4}$ are obtained for a particular stand from sectional measurements of a sample of trees. Total stand volume is then obtained by calculating the volumes of the individual trees using this two-way volume function. The required tree heights are calculated from the height/diameter curve. The small differences in form factor obtained here for stands of different ages and on various sites suggest that this method should be fairly accurate.

The third method uses a two-way stand volume function of the form $\text{Vol} = k \cdot \text{BA} \times \text{MTH}$ necessitating only measurements of stand basal area and mean top height.
In this study, the second method was used to derive individual stand volumes. These volumes were then used to calculate the value of \( k \) for the third method. A 95% confidence interval of the factor \( k \) is

\[
 k = 0.40 \pm 0.01
\]

It is the easiest method to use but also the least accurate. Nevertheless, it enables stand volume to be determined to within c. 15% (Fig. 10).

Assuming constant basal area and using the height function, the following function necessarily holds

\[
 Vol = a(1 - b^{Age})
\]

The coefficients of volume \( v. \) age were derived from the mean top height \( v. \) age equation and mean basal area: for \( N. \ truncata \) stands, \( a = 440 \) and \( b = 0.964 \); for \( N. \ fusca \) stands, \( a = 495 \) and \( b = 0.964 \). They apply to \( N. \ truncata \) and \( N. \ fusca \) stands between 30 and 100 years old, and indicate rapid early stand volume increment, slowing down but continuing to accumulate until maximum stand height is reached, at an age of c. 100 years (Fig. 11).
DISCUSSION AND CONCLUSIONS

The predominant sampling method used here, of temporary plots in stands of different ages, has given an adequate picture of stand development. Nevertheless, it is inferior to time-series measurements in permanent plots, particularly with regard to basal area, volume, and diameter growth-rate. This is because permanent plots enable a clearer separation of temporal effects from site ones.

In this study, both species of beech attained similar height and volume growth but, on average, *N. truncata* stands had rather lower mean diameters and basal areas (beech component only) than *N. fusca* stands of similar age, and maintained somewhat higher densities.

No inverse correlation between stand height and altitude (cf. Moorhouse 1939; Conway 1952; Hinds & Reid 1957; Wardle 1984) was evident, probably because of the limited altitudinal range (c. 300 m) sampled. Neither was any correlation between height, mean diameter, or basal area, and soil type (gley podsol v. steepland yellow-brown earth) evident in *N. truncata* stands. Thus, *N. truncata* appears to grow at comparable rates on these soil types.

In both species, most stand parameters showed considerable variation between sites. Mean diameter and mean diameter of the 250 largest trees/ha at a given age varied by ±30%, presumably reflecting differences in site quality. Mean top height at a given age varied by ±20%, rather less than mean diameter; the one site with a significantly lower mean top height was in an exposed coastal locality. Basal area varied by ±30%, although indications from permanent plots are that some of this may be temporal rather than site variation. The considerable variation in volume of ±40%, primarily reflecting basal area variation, may also be partly temporal.

The earlier documentation in North Westland of the development of *N. fusca* forest by secondary (and sometimes primary) succession (Moorhouse 1939; Conway 1952) is largely confirmed, and indications are that *N. truncata* stands follow a very similar course of development. A summary of functions relating average stand parameters to age in each species is presented in Table 4, and of predicted parameters in average 50- and 100-year-old stands in Table 5. Development beyond 100 years is

<table>
<thead>
<tr>
<th>Function</th>
<th><em>N. truncata</em></th>
<th><em>N. fusca</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean top height (MTH)</td>
<td>26.9 ( (1-0.964^{Age^2}) )</td>
<td>26.9 ( (1-0.964^{Age^2}) )</td>
</tr>
<tr>
<td>Mean diameter (MD)</td>
<td>0.24 Age</td>
<td>0.32 Age</td>
</tr>
<tr>
<td>Mean diameter of the</td>
<td></td>
<td></td>
</tr>
<tr>
<td>250 largest trees/ha (MD(_{250}))</td>
<td>3.9 Age(^{0.47})</td>
<td>3.6 Age(^{0.53})</td>
</tr>
<tr>
<td>Basal area (BA)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All species</td>
<td>54</td>
<td>47</td>
</tr>
<tr>
<td>Beeches only</td>
<td>41</td>
<td>46</td>
</tr>
<tr>
<td>Stand density (Den)</td>
<td>(8.33 \times 10^6 ) Age(^2)</td>
<td>(5.44 \times 10^6 ) Age(^2)</td>
</tr>
<tr>
<td>Stand volume (Vol)</td>
<td>440 ( (1-0.964^{Age^2}) )</td>
<td>495 ( (1-0.964^{Age^2}) )</td>
</tr>
</tbody>
</table>
usually marred by pinhole borer attack resulting in extensive mortality; subsequent regeneration destroys the even-aged character of the stand (Franklin & Beveridge 1977). A generally similar pattern of early development occurs in even-aged stands of *N. solandri* which, like *N. fusca* and *N. truncata*, is relatively shade-intolerant (Wardle 1984). A study of patches at varying stages of development in virgin beech (*Fagus crenata* Blume) forest in north-western Honshu, Japan (Nakashizuka 1984), showed that this species behaves rather similarly to *N. fusca*. Stand height stabilised at c. 27 m, although at a greater age. Basal area stabilised at 46 m²/ha after about 40 years. Stand densities were c. 5800 and 440 stems/ha at 50 and 100 years, respectively. By implication, diameter growth rates must also be similar to those of *N. fusca*.

| TABLE 5—Parameters (beech component only) of “typical” secondary beech stands of two ages in North Westland |
|----------------------------------------------------------|----------------------------------------------------------|
| **N. truncata**                                             | **N. fusca**                                             |
| 50 years                                                  | 100 years                                                |
| Density (stems/ha)                                        | Density (stems/ha)                                       |
| 3300                                                     | 2200                                                     |
| Mean diameter (cm)                                        | Mean diameter (cm)                                       |
| 12                                                       | 16                                                       |
| Mean diameter of the 250 largest trees/ha (cm)             | Mean diameter of the 250 largest trees/ha (cm)            |
| 25                                                       | 29                                                       |
| Basal area (m²/ha)                                        | Basal area (m²/ha)                                       |
| 41                                                       | 46                                                       |
| Mean top height (m)                                       | Mean top height (m)                                      |
| 23                                                       | 23                                                       |
| Total volume (m³/ha)                                      | Total volume (m³/ha)                                     |
| 370                                                      | 416                                                      |

The rapid site occupation indicated by fast initial basal area and volume increments suggests that, like *N. fusca* (Gleason 1982), *N. truncata* may respond favourably to early thinning. Thus, it shares the considerable silvicultural potential of that species in some lowland forests in North Westland, but its management is likely to be subject to similar constraints.

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