# CELL WALL AND LUMEN PERCENTAGES IN RELATION TO WOOD DENSITY OF NOTHOFAGUS NERVOSA

by

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SUMMARY

Cell wall and lumen percentages were determined for vessels, fibres and rays from 10 trees of *Nothofagus nervosa* (rauli), and analysed in relation to ring number from the pith, ring width, and density. Increase in density across the juvenile wood was mainly associated with an increase in fibre wall %, which outbalanced a simultaneous increase in vessel lumen %. Decrease in density across the mature wood was associated with changes in both fibre wall and total lumen percentages. Though density varied only slightly with ring width, this was accompanied by appreciable changes in percentages of different cell types. These trends in the wall and lumen percentages of the various cell types suggest that some physical properties may vary more within the tree (or with growth rate) than is suggested by the limited variation in density that is found in rauli. There were significant between-tree variations in both density and cell types, indicating the possibility of selection for either at an early stage of tree growth.

*Key words:* *Nothofagus procera, Nothofagus alpina,* rauli, cell type percentages, wood density, specific gravity.

INTRODUCTION

*Nothofagus nervosa* (Phil.) Dim. et Mil., commonly known as rauli, is the currently accepted legitimate synonym of *N. procera* or *N. alpina* (Lennon et al. 1987). Some seed origins of rauli from Chile have been found to grow at a remarkably rapid growth rate in the United Kingdom, making the species an interesting possibility for hardwood production forestry (Christie et al. 1974; Danby 1991). There has been concern about the density and strength properties of such fast grown rauli (Brazier & Moore 1985), but recent work suggests that the influence of ring width on density is so slight as to be negligible, though statistically significant (Denne et al. 1999). However, that does not necessarily imply that growth rate has little or no influence on other aspects of rauli wood quality.

In oak, density was found to be significantly correlated with vessel lumen parameters (Zhang & Zhong 1992; Rao et al. 1997), but in rauli that relationship is not a close one, for Denne et al. (1999) found anomalies in the relation between wood den-

sity and porosity (as indicated by vessel lumen area area$^{-1}$). Data from rauli indicated that within-tree variation in density with cambial age across discs was only partially associated with variation in vessel lumen area area$^{-1}$, and between tree variation in vessel lumen area area$^{-1}$ accounted for only 45% of the variation in mean tree density.

The present work was designed to explore these apparent anomalies, by investigating the extent to which variations in density relate to changes in the proportions of cell wall and lumen of each cell type in rauli. An ultimate objective is to assess the consequences that selection for density between trees, or control of density by manipulation of growth rate or rotation length, is likely to have for physical characteristics associated with the cell structure of the wood.

## MATERIAL AND METHODS

Five trees of *Nothofagus nervosa* were sampled from each of two sites in the UK: trees from site 1 were 58 years old (grown from seed collected in Chile), and trees from site 2 were 39 years old (seed origin Malleco Forest Reserve, Chile). Further details of these sites are given in Denne et al. (1999). Since no significant differences ($p \geq 0.05$) in density, ring width, or cell-type proportions were detected between the sites, data from the two sites are treated as a single sample of ten trees.

One disc was cut from each tree at 3.6 m above ground level, and a strip 20 mm wide and 10 mm deep was taken across the minimum diameter of each disc, avoiding any visible defects. After smoothing the transverse surface with a razor blade, the width of each growth ring was measured to the nearest 0.1 mm with a travelling microscope. The strip was then divided into 3-ring blocks, and the density of each block determined as oven dry weight/green volume by the Archimedes method (Olesen 1971).

For measurements of cell wall and lumen percentages of the various cell types, transverse sections 30 μm thick were cut from blocks that included ring numbers 3, 11, 19, 25, and 35 from the pith. Methodological constraints dictated that cell percentages were determined from rings on one side of the pith, while ring width and density data were means from the same growth ring on the two sides of the pith. Abnormalities such as reaction wood or frost damage were avoided by moving tangentially to an unaffected part of the same growth ring, or (in a small minority of samples) by excluding the ring from further analyses.

Cell percentages were determined by point sampling using an eyepiece scale with a light microscope. Each ring was sampled at four positions equally spaced across the ring width: the scale (which had 11 points) was placed randomly about the centre of each of those quarters of the ring using a × 10 objective, changing to a × 40 objective to determine the type of cell underlying each point. The sampling was repeated until 110 points had been recorded from each quarter, totalling 440 points from each ring analysed from each tree. The cell types were recorded as vessel wall, vessel lumen, fibre wall, fibre lumen, ray wall or ray lumen (the amount of axial parenchyma was negligible in these samples). The proportions of each category were then calculated as percentage area per unit area.

The present data for vessel lumen percentages were found to be closely correlated with those for vessel lumen area per unit area given in the paper by Denne et al. (1999), though the previous data for vessel lumen area area$^{-1}$ tended to be about 5% lower than vessel lumen percentage from point sampling of the same growth rings. This discrepancy may be attributed to sampling method, for the automated digitiser analyses used for the earlier data for vessel lumen area area$^{-1}$ covered the whole growth ring, while the point sampling method used for the present data inadvertently excluded a region of narrower vessels which occurred towards the end of the last quarter of most rings.

Some trees had thicker cell walls (or larger cell lumens) than others, consistent across discs, and such differences between trees tended to obscure the trends in wall or lumen proportions with ring number from the pith. For that reason the data points shown in Figures 1 to 5 were transformed to compensate for between-tree differences. This transformation was done by dividing the raw data for tree 'n' by the ratio between the mean for tree 'n' and the mean of all trees for the parameter being analysed. Hence: $a_i = b_i/(c/d)$ where $a_i$ is the transformed value for the i-th ring from the pith for tree n, $b_i$ is the original value for the i-th ring of tree n, c is the mean for all rings analysed for tree n, and d is the overall mean for all rings in all trees analysed.

Transverse faces of blocks taken from rings 3 and 35 of a low (tree 1) and a high density tree (tree 9) were prepared for scanning electron microscopy (SEM) by a razor cut method. After sputter coating with gold the faces were examined at 14 kV in an Hitachi 520 SEM. Photographic images were recorded on film and are shown at matched magnifications (Fig. 6–9).

Microsoft Excel (version 4.0a) was used as data spreadsheet, Minitab 10 for analysis of variance, and Microcal Origin for the graphics and for linear or polynomial regression analyses.

RESULTS

*Variation in cell type, wall and lumen percentages with ring number from pith*

*Cell types* — As shown in Figure 1, fibre % decreased with ring number from the pith (from analysis of variance, significant at $p \leq 0.01$), mirrored by increase in vessel percentage towards the bark ($p \leq 0.002$), with no significant change in ray % ($p > 0.1$). Comparable increases in vessel percentage with distance from the pith were also found in *Salix* spp. (Taylor & Wooten 1973), *Shorea* spp. (Bosman et al. 1994) and *Eucalyptus* spp. (Hudson et al. 1998). Conversely, vessel percentage was found to decrease, and fibre percentage to increase, across discs of *Alnus glutinosa* (Vurdu & Bensend 1980) and *Betula pendula* (Bhat & Karkkainen 1981).

There was some evidence that the variation in cell types with cambial age was curvilinear in *Nothofagus nervosa*, since the change in fibre and vessel percentages across discs fitted more closely to second order polynomial curves than to the linear regressions (Fig. 2a, b). These curves suggest minimum vessel % and maximum fibre % at about 10–20 rings from the pith.
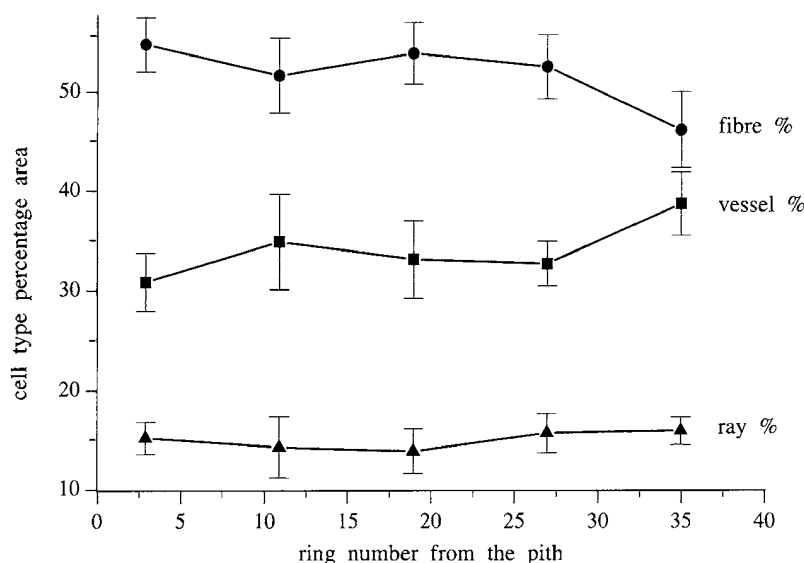
Fig. 1. Variation in fibre, vessel and ray percentage with ring number from the pith, across discs from 10 trees of *Nothofagus nervosa*. Vertical lines show twice standard error on each side of the mean.

The overall averages of cell types (Table 1) are close to those recorded for *Alnus glutinosa* stems, where mean values were vessels 28.9%, fibres 57.6%, and rays 12.9% (Vurdu & Bensend 1980). Vessel percentage was lower than that recorded for *Tilia americana* (Kollmann & Côté 1968, vessel 55.6%, fibre 36.1%, and parenchyma 12.8%) but higher than that published for several other diffuse-porous species, including *Betula pendula* (Bhat & Karkkainen 1981), *Acer pseudoplatanus* (Dodd 1985), *Shorea* spp. (Bosman et al. 1994) and *Eucalyptus* spp. (Hudson et al. 1998). In *Fagus sylvatica* the mean percentage conductive area (calculated from automatic image analyses of vessel lumens) was found to vary between 18.5% and 22.7% within the trunk of one tree (Gasson 1985), compared with the 29.3% vessel lumen for *N. nervosa* (Table 1).

Table 1. Cell type averages from ten trees of *Nothofagus nervosa*, with lumen % and wall % for each cell type. Data are from the point sampling method, and are on a % area basis. Figures in brackets are standard deviation of the means of all rings sampled.

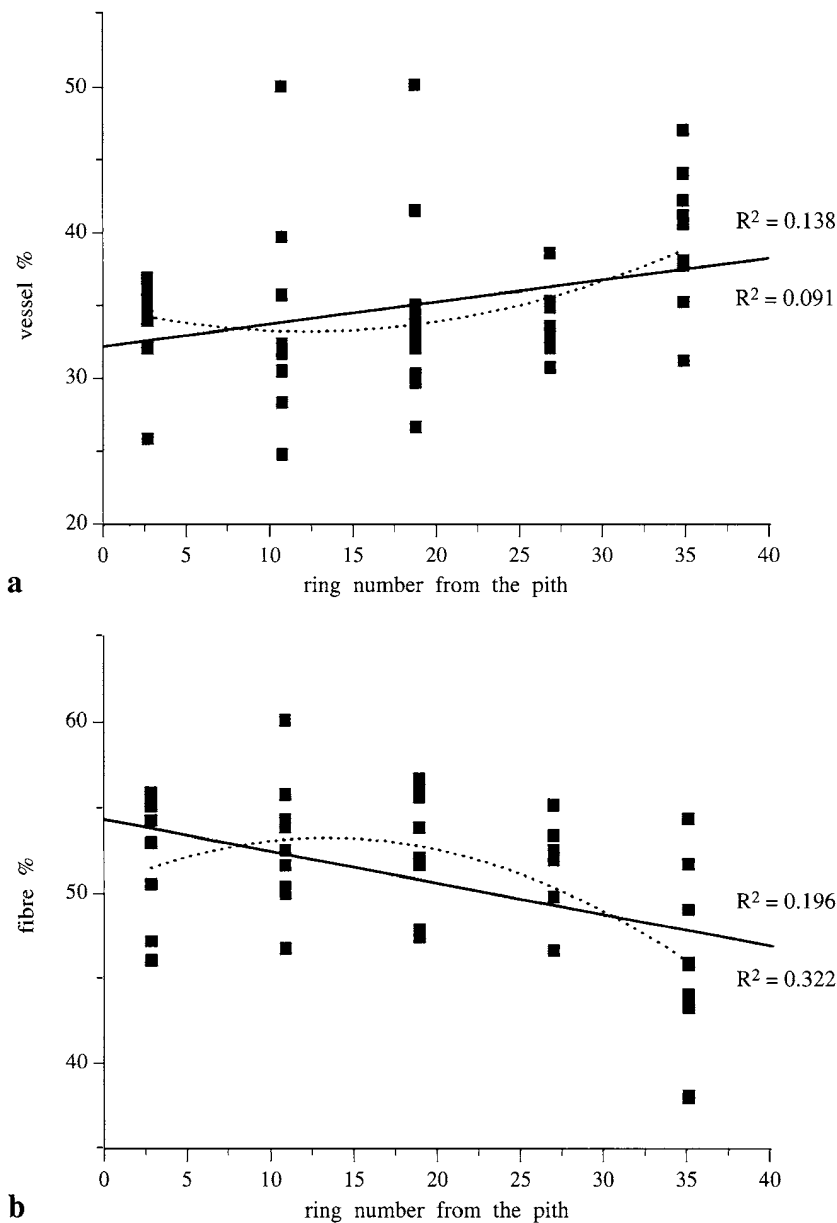|        | lumen %    | wall %     | cell type % |
|--------|------------|------------|-------------|
| vessel | 29.3 (5.1) | 4.5 (1.2)  | 33.8 (5.9)  |
| fibre  | 16.0 (3.2) | 35.0 (4.2) | 51.1 (5.8)  |
| ray    | 11.7 (3.1) | 3.5 (0.9)  | 15.1 (3.4)  |
| total  | 57.1 (3.8) | 43.0 (3.8) | 100.0       |

Fig. 2. Variation in a) vessel and b) fibre percentages across discs from 10 trees of *Nothofagus nervosa*, showing linear regression and second order polynomial curves.

*Wall percentages* — Variations in percentage wall material with ring number from the pith are shown in Figure 3a. Changes in total wall % appear to be curvilinear, reaching maximum wall % at about 20 rings from the pith (Fig. 4a). This curve was comparable to that of density (Fig. 4b), which also tended to increase to a maximum about
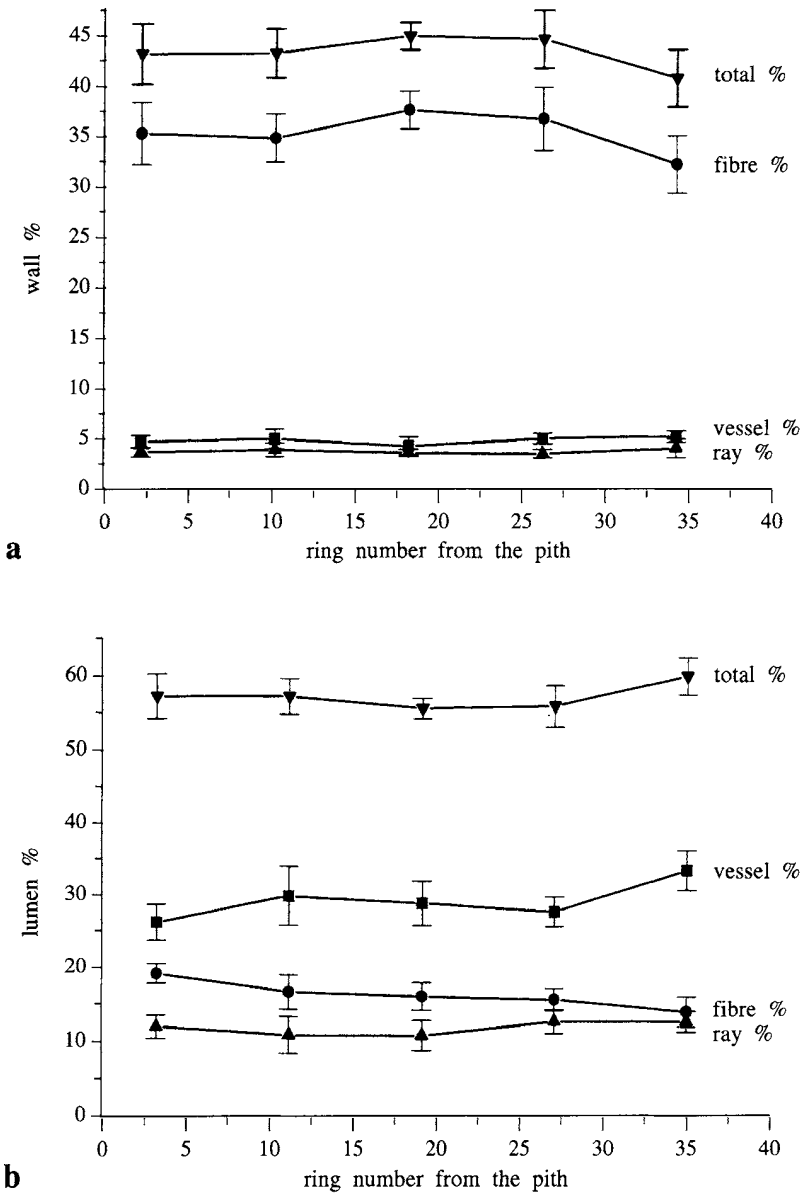
**a**



**b**

Fig. 3. Variation in a) wall and b) lumen %, of vessels, fibres, rays, and total cell types, across discs from 10 trees of *Nothofagus nervosa*. Vertical lines show twice standard error on each side of the mean.

20 rings from the pith before decreasing towards the bark. Such a relationship would be expected since the density of cell wall material has been shown to be almost constant (Kellogg & Wangaard 1969); regression analysis of the present data showed density increased linearly with total wall area % (between trees $R^2 = 0.814$). Most of
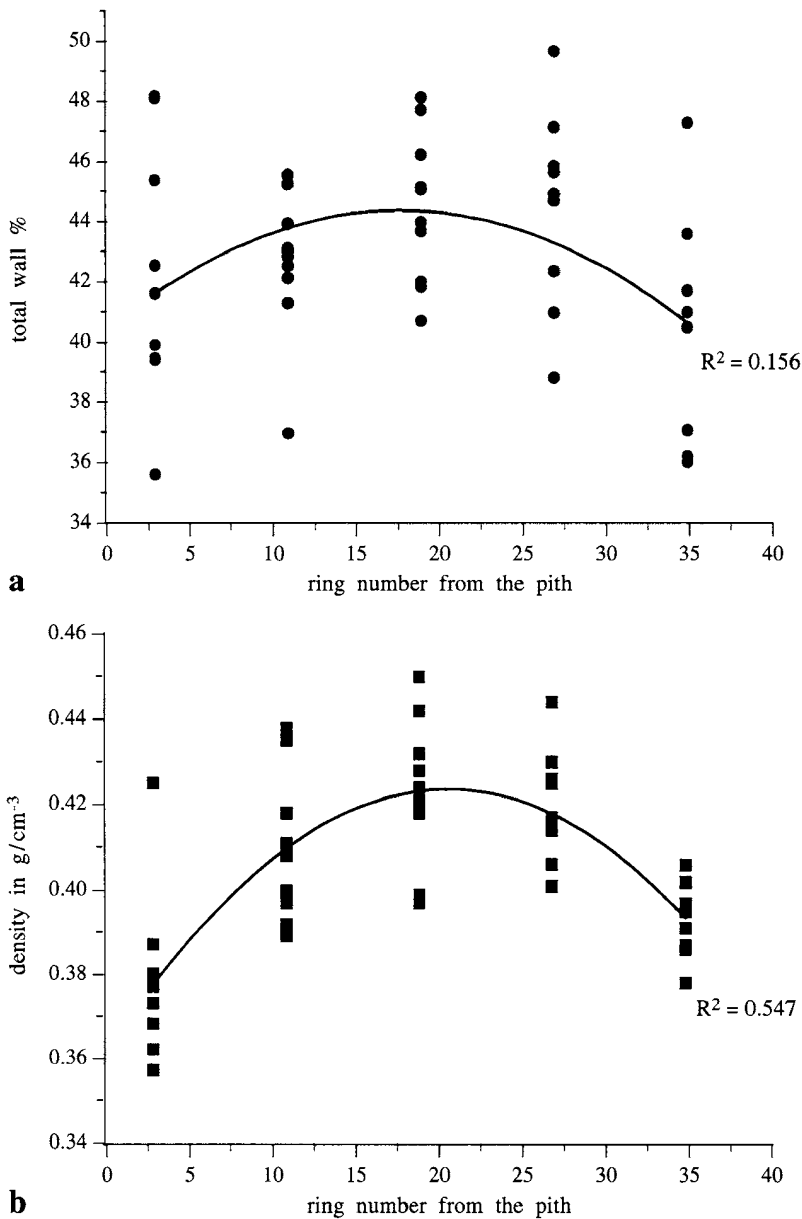
Fig. 4. Variation in a) total wall % and b) density with ring number from the pith across discs from 10 trees of *Nothofagus nervosa*.

the change in total wall % with ring number reflected variation in fibre wall % (Fig. 3a); changes in vessel wall and ray wall percentages with cambial age were insignificant (p > 0.1).
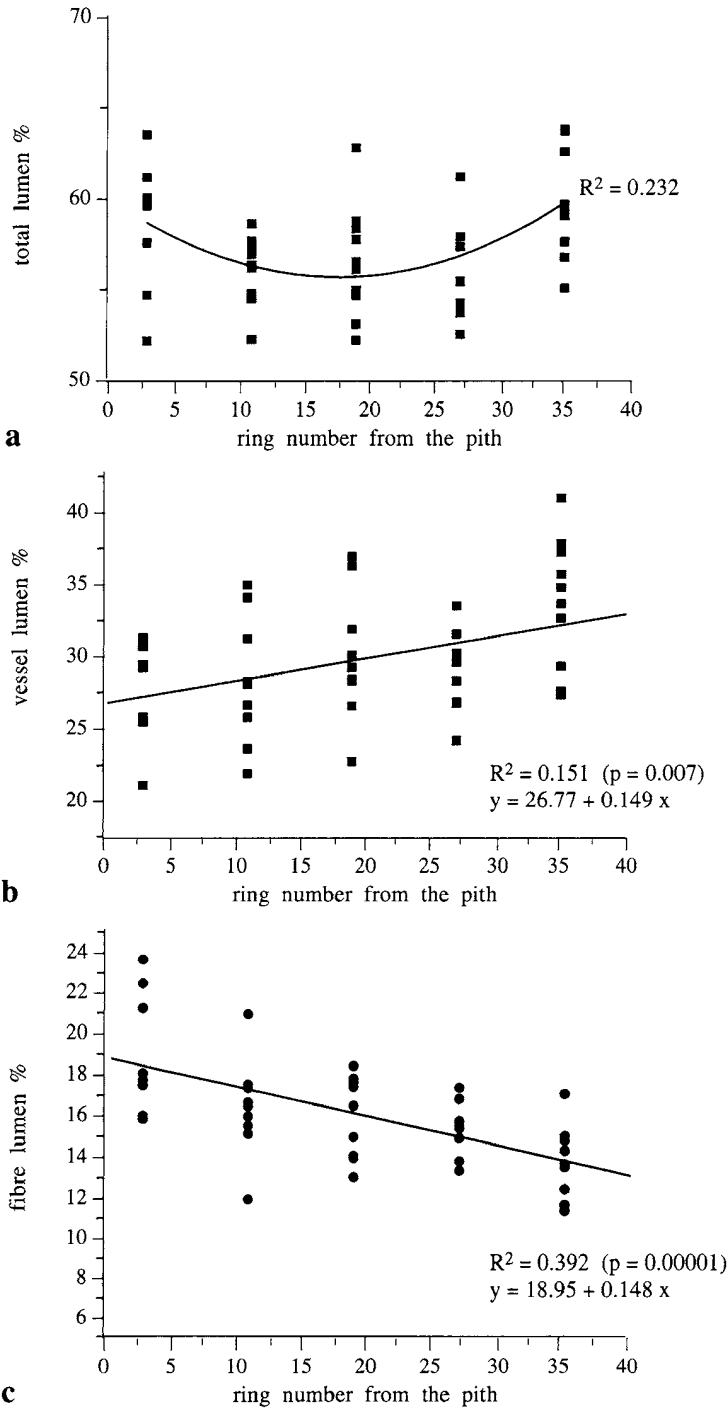
Fig. 5. Variation in a) total lumen %, b) vessel lumen %, and c) fibre lumen % with ring number from the pith across discs from 10 trees of *Nothofagus nervosa*.
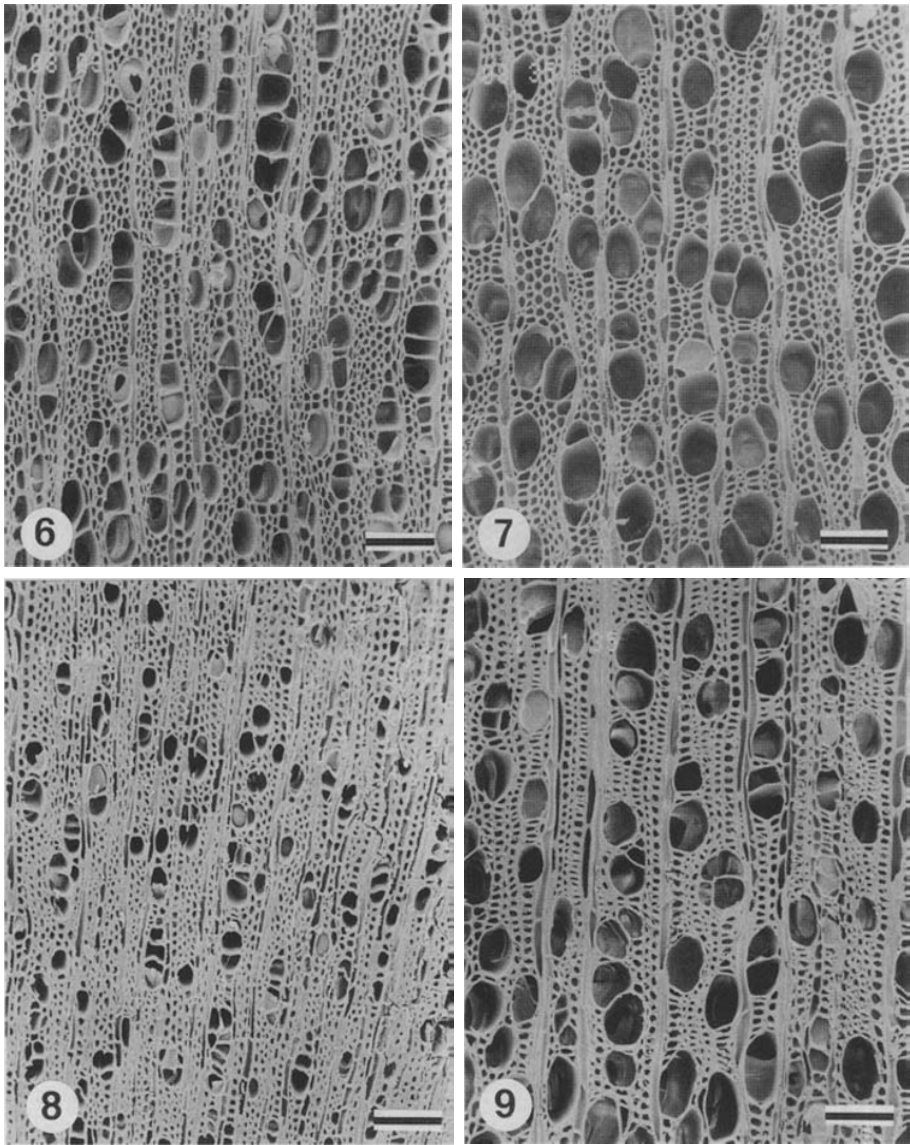
Fig. 6–9. Transverse surfaces of *Nothofagus nervosa* wood to show distribution and size of vessels, fibres, and rays. – 6: 3rd ring from the pith in tree 1. – 7: 35th ring from the pith in tree 1. – 8: 3rd ring from the pith in tree 9. – 9: 35th ring from the pith in tree 9. — Scale bars = 100 μm.
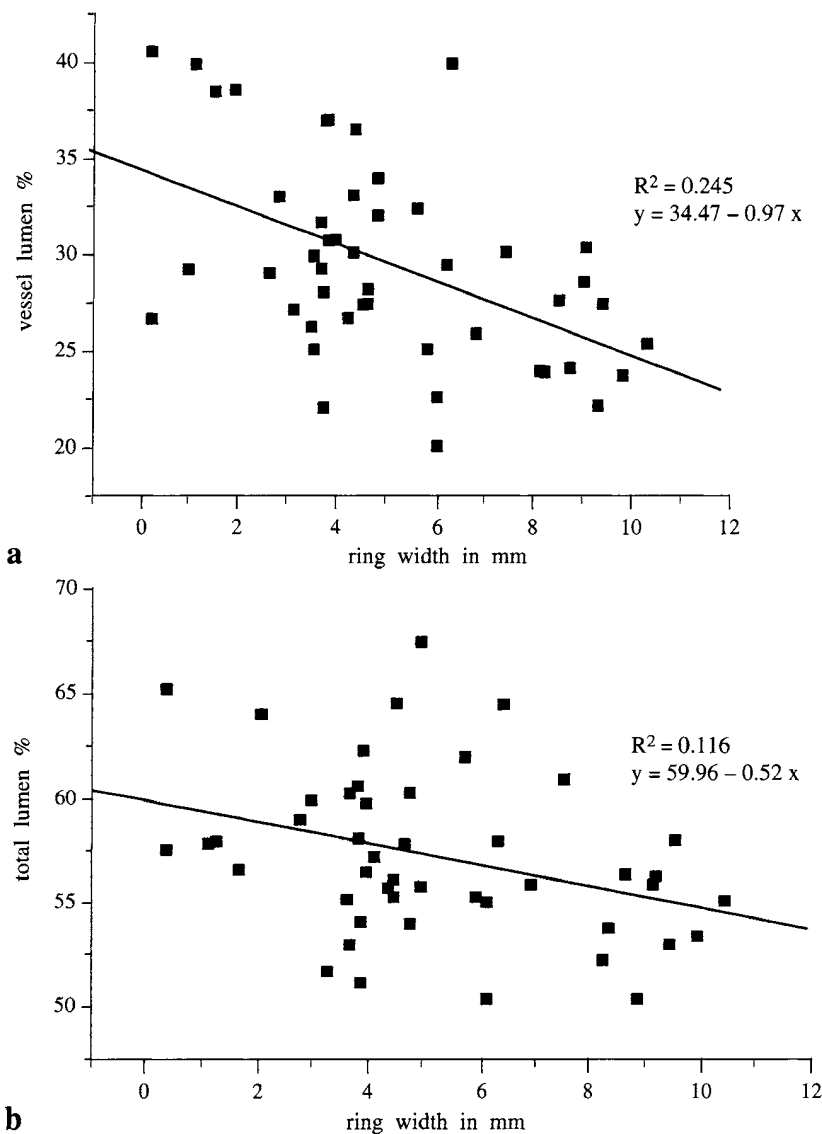
Fig. 10. Variation in a) vessel lumen % and b) total lumen % with ring width in discs from 10 trees of *Nothofagus nervosa*.

*Lumen percentages* — In contrast to changes in wall percentages, variation in total lumen % (Fig. 3b, 5a) was associated with variation in both fibre and vessel lumen % (Fig. 3b). The increase in vessel lumen % with ring number from the pith (Fig. 5b) was offset by a decrease in fibre lumen % (Fig. 5c), with no significant change in ray lumen % ($p > 0.1$). While variation in total lumen % with cambial age was curvilinear (Fig. 5a), variations in vessel and fibre lumen percentages across discs appear to be linear, for second order polynomial curves were very close to the linear regressions for both vessel and fibre lumen percentages over the range of ring numbers analysed.
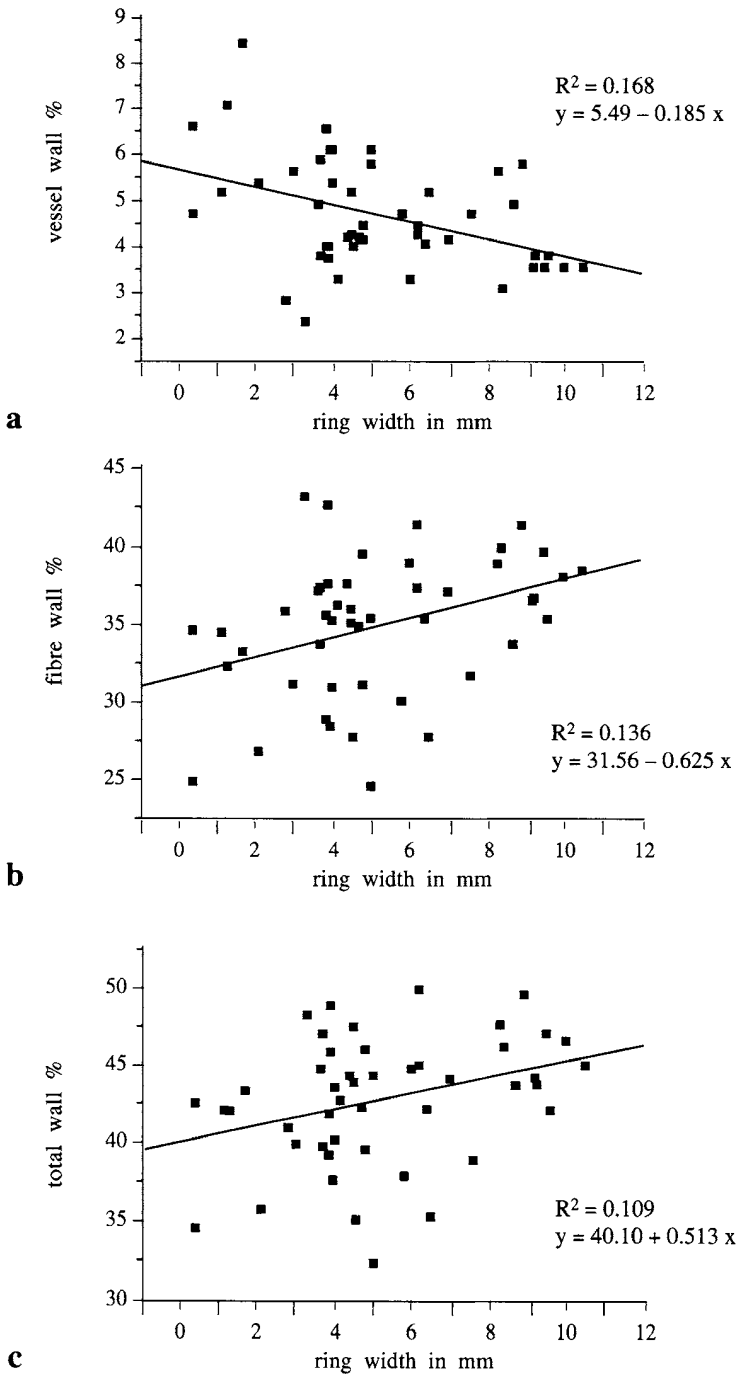
a



b



c

Fig. 11. Variation in a) vessel wall %, b) fibre wall %, and c) total wall % with ring width in discs from 10 trees of *Nothofagus nervosa*.

Mature wood (Fig. 7, 9) had larger but fewer individual vessels than juvenile wood (Fig. 6, 8). This confirms the earlier work on rauli which suggested the increase in vessel lumen percentage with cambial age was associated with increase in mean vessel lumen size, despite a decrease in vessel frequency (Denne et al. 1999).

### Variation in cell wall and lumen percentages with growth rate

Total lumen % tended to decrease with increase in ring width (Fig. 10b): the slope of that regression was less than that for vessel lumen % (Fig. 10a), since that decrease was compensated to some extent by increase in the lumen % of other elements (data not shown). Comparably, total wall % increased linearly with ring width (Fig. 11c), and the slope of that regression was less than that for fibre wall % (Fig. 11b), which was partly counterbalanced by decrease in vessel wall % with ring width (Fig. 11a).

### Variation in proportions of cell types between trees in relation to density

Mean disc density varied significantly between trees (p ≤ 0.0001), and this variation in density was more closely associated with variation in total wall % than with any of the individual cell parameters measured. Lower mean density trees had thinner fibre walls and wider vessel lumens (Fig. 6, 7) than higher mean density trees (Fig. 8, 9). However, differences in density did not seem to be consistently related to proportions of vessels, fibres or rays, though each of those parameters varied significantly between trees. For example, while density tended to increase with the proportion of fibre to vessel percentages (Fig. 12), tree 7 had an exceptionally low fibre % in relation to its density (associated with a high ray %).
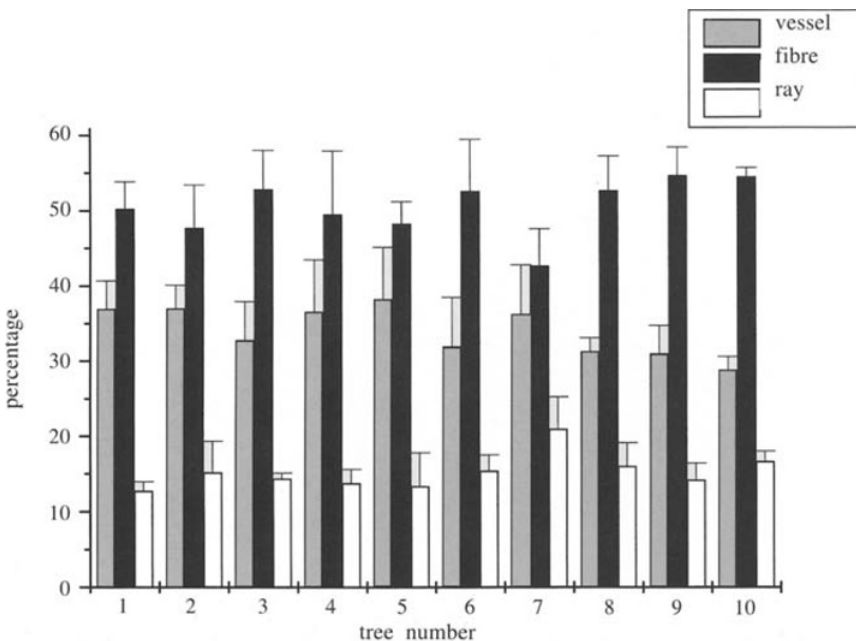


Fig. 12. Variation in cell type percentages between trees of *Nothofagus nervosa*. Trees are numbered from the lowest mean density (tree 1) to the highest (tree 10)

## DISCUSSION

Previous work on variation in the density of rauli (Denne et al. 1999) showed an apparent anomaly in that an increase in density across the first 20 rings from the pith was concurrent with an increase in porosity (measured as vessel lumen area area$^{-1}$). That anomaly was resolved as this study found an increase in total wall material (Fig. 4a) across those growth rings (Fig. 4b), largely associated with an increase in fibre wall percentage (Fig. 3a) that outbalanced the effect of a simultaneous increase in vessel lumen proportion (Fig. 5b). The subsequent decrease in density across the outer rings (Fig. 4b) can be attributed to both a decrease in fibre wall % (Fig. 3a) and an increase in total lumen percentages (Fig. 5a).

Apart from their influence through density, such changes in cell proportions may well have a direct effect on the physical properties of the wood. Thus, the relatively low fibre content implies that the percentage of 'fines' in *Nothofagus* pulp is likely to be high, and may increase with length of rotation since the fibre content diminished across mature wood with cambial age (Fig. 2b). Also, the increase in vessel content with cambial age (Fig. 2a), associated with increase in vessel size (Fig. 6–9), suggests that the surface of paper manufactured from mature *Nothofagus* wood may have a greater tendency to 'pick' than that from juvenile wood. These possibilities merit further investigation.

To take that argument further, whilst the earlier rauli data indicated a significant but slight linear increase in density with growth rate, density increasing by only 0.005 g/cm$^{-3}$ mm$^{-1}$ increase in ring width (Denne et al. 1999), the present data indicate that the influence of growth rate is greater on the cell type percentages than on density. Thus, with increase in ring width an increase in vessel lumen % was partially offset by a decrease in fibre lumen %: consequently total lumen % increased (and hence density decreased) at a slower rate than vessel lumen % with increase in ring width (Fig. 10). Similarly, the rate of increase in fibre wall % appeared to be higher than that of total wall % with ring width (Fig. 11). This too suggests that the physical properties of rauli may by influenced by silvicultural management more than is indicated by its very limited influence on density, and merits further analyses.

The highly significant differences in mean density between trees were consistent across discs from juvenile to mature wood, suggesting the possibility of genetic selection for density at an early stage. However, it seems that there is only a loose association between mean tree density and percentages of individual cell types (Fig. 12), indicating some capacity to select for proportions of cell types independent of density.

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