SHORT COMMUNICATION

Annual rings in *Beilschmiedia tawa* (Lauraceae)

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Abstract Evidence is presented that the growth rings in the wood of fast growing tawa are annual. Diameter growth rates of tawa are variable but usually 1–4 mm yr^{-1} in trees > 20 cm diameter at 1.4 m height. Tawa probably has maximum longevity in the range 300–400 years. It shows unexplained biennial fluctuations in diameter increment, a feature shared with several New Zealand tree species.

Keywords wood; annual rings; parenchyma bands; *Beilschmiedia tawa*; dendrochronology

The problem of the periodicity of growth ring formation in the wood of New Zealand tree species was first mentioned by Stewart (1905) and has since been the subject of prolonged discussion recently reviewed by Dunwiddie (1979). From this review, Dunwiddie's own work (Dunwiddie 1979), and subsequent research (Norton 1979), it seems safe to conclude that annual rings are produced by some indigenous conifers and dicotyledons in montane situations.

This conclusion agrees with the earlier conclusion of Wardle (1963), who showed that several subalpine species have predominantly annual rings. However, eccentric rings (markedly wider on some radii than on others for several years) and "double" or "false" rings (Lloyd 1963) have sometimes caused difficulty in estimating age from ring counts, and frustrated dendrochronological studies (Bell & Bell 1958, Wells 1972).

There appear to be no definitive studies on the periodicity of growth ring formation in the angiosperms forming the canopy or sub-canopy in the lowland forests of New Zealand. Meylan & Butterfield's (1978) survey shows that vessels are usually distributed throughout the growth ring (though larger early-wood vessels occur in some species) and that growth rings are "indistinct" or only "slightly distinct" in most of these species, but the frequency of ring formation is not known.

Received 6 July 1981

The rings of both tawa (*Beilschmiedia tawa* (A. Cunn.) Benth. et Hook.f. ex Kirk) and taraire (*B. tarairi* (A. Cunn.) Benth. et Hook.f. ex Kirk) are described as "slightly distinct to dinstinct" by Meylan & Butterfield (1978). They are composed primarily of fibres, with small scattered groups of vessels, and bounded by parenchyma in both species.

The rings of tawa have generally been thought to be annual (Croker 1949; Knowles & Beveridge, in press), although McKelvey (1954) expressed the opposite view, claiming that the parenchyma bands visible in cross-sections did not define annual increments. Dunwiddie (1979) illustrated lobate growth and "ambiguous parenchyma bands" in this species. No comparable studies appear to have been made on taraire. A detailed study of the growth and wood anatomy of *B. bancroftii* (Bail.) White in North Queensland by Amos & Dadswell (1950) showed that each growth period (the tropical winter) was terminated by a band of parenchyma which was initiated at the close of one growth period and completed at the beginning of the next. However, because parenchyma is formed in this species whenever growth is slowed by environmental stresses, not all such bands divide consecutive years.

In this note we present evidence that, at least under some circumstances, the parenchyma bands of tawa delimit annual increments, and can thus be used to determine the age of the tree.

Seventeen cross sections from 8 tawa trees were studied in detail, although more sections and increment cores were examined. The trees were felled in January 1981 in parts of Pureora Forest (Block A295; NZMS 1 N84 064707) which had been subject to selective logging for podocarps and tawa during

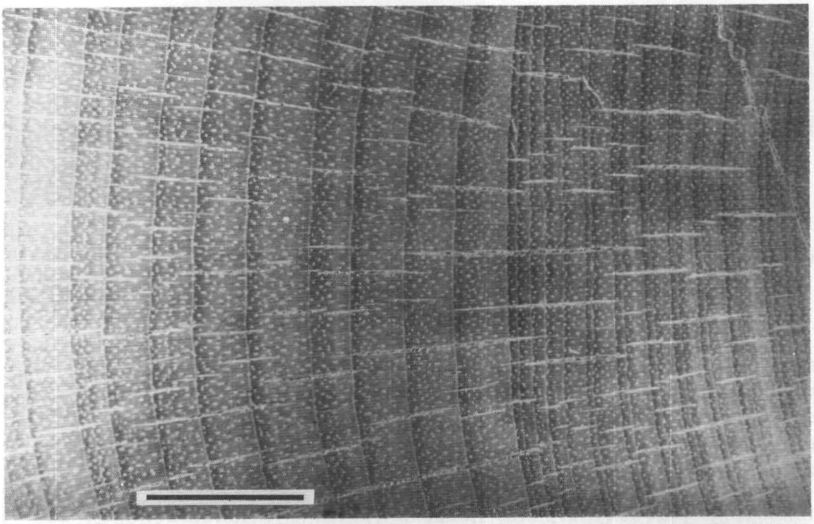

Fig. 1 Section of tawa showing the marked increase in growth rate after logging in 1961, and the biennial fluctuations in ring width before then (Bar = 1 cm).

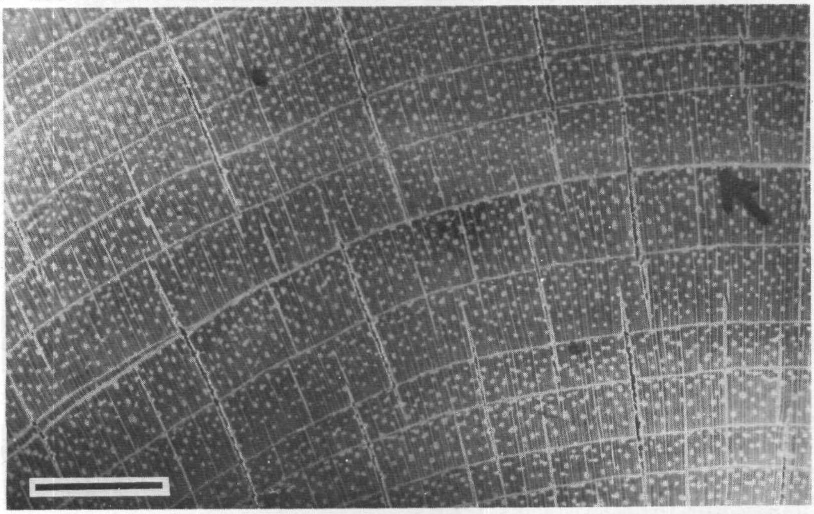

Fig. 2 Distinct annual growth rings in a relatively fast growing tawa from Pureora Forest. Arrow indicates cells distorted, possibly by frost damage, forming a false ring on the far right (Bar = 5 mm).

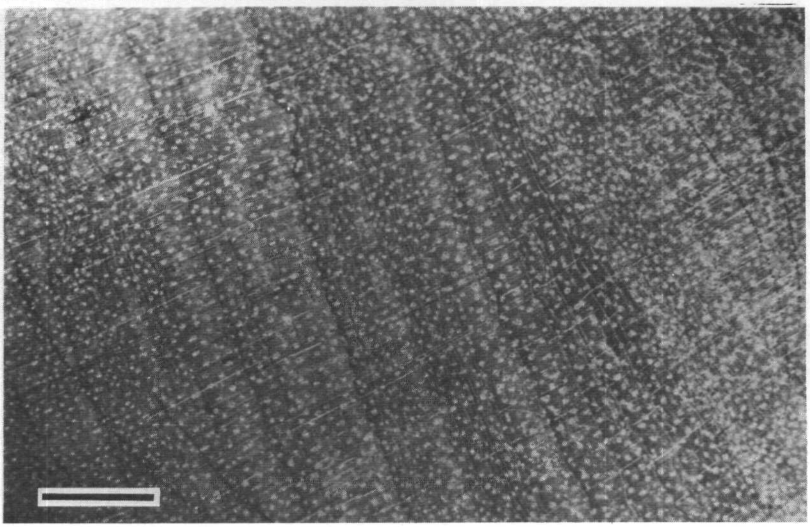

Fig. 3 Indistinct growth rings in a large taraire tree from Martin's Redoubt. (Bar = 5 mm).

Table 1 Mean growth rate of tawa and taraire. Radial increments are means from 2 radii (taraire), and 8 or more radii (tawa). Tawa trees were "released" by felling surrounding trees in 1961. Note that although the rings are narrower after 1961 in tree 296, this nevertheless represents a basal-area increase, due to the greater circumference of the trees. The only tawa tree to show a decline in basal-area increment since 1961 was UH, which was an isolated stag-headed tree. Equivalent growth periods are included for taraire for comparison. Estimated age assumes height growth at 5.01 cm yr^{-1} to height 1.4 m.

Tree identification	Diameter at 1.4 m (cm)	Estimated age (yr)	Radial increment ($mm\ yr^{-1}$)		
			Overall	1942–61	1961–80
B. tawa					
341	5.6	77	0.41	0.43	0.57
192	14.7	86	1.38	0.87	2.35
H	25.2	99	1.73	2.21	3.60
304	7.2	133	0.33	0.42	0.51
310	5.3	142	0.24	0.18	0.26
UH	43.0	156	1.74	1.94	1.47
16	21.2	192	0.65	0.80	2.37
296	38.3	202	1.09	1.96	1.77
B. tarairi					
1	60.5	298	0.93	0.83	0.79
2	64.7	341	0.94	0.71	0.50
3	43.8	246	1.04	0.43	0.48

March to September 1961 (Beveridge 1975). Since then the diameters of six of the felled trees had been monitored regularly by the New Zealand Forest Service (A. E. Beveridge, pers. comm.). Consequently, the trees studied had a known history of site disturbance and diameter growth. The study area location, vegetation, and methods are described in detail by West *et al.* (1981).

Fig. 1 demonstrates a marked increase in growth rate after "release" by the felling of an adjacent tree in 1961. When examined microscopically (× 10–40) all the trees studied from the 1961 logging trial area had 19 clear and complete growth rings from the point of "release" to the outer perimeter. Moreover, the diameters recorded for these trees in December 1961 agree closely with the present diameters to the "release" point. These results unequivocally establish the annual nature of the growth rings in these relatively fast growing trees (Table 1). In cross sections from some large old trees and small suppressed trees, eccentric growth rings occurring over several years on the same radius can result in a lobate appearance in the growth ring pattern, as illustrated by Dunwiddie (1979). Age determination was more difficult in these instances.

Fig. 1 shows the marked biennial fluctuation in ring width before 1960. Lloyd (1963) and Dunwiddie (1979) have drawn attention to this in several indigenous conifers. In *Phyllocladus glaucus* Carr. the tendency for wide and narrow rings to alternate is so pronounced that first order auto-correlation values* are often negative. The reason for this regular growth pattern is not known, but it appears to be a feature of several tree species in the North Island and to be synchronous between sites for some species (Dunwiddie 1979). This phenomenon emphasises the need for long-term phenological observations on individual trees as an important step in understanding their biology and interpreting the information retained in their annual ring-width sequences. The possibility that the paired rings actually represent two growth flushes within a single year (Lloyd 1963) cannot be ruled out, although it seems unlikely in view of the cross-dating of such patterns between sites demonstrated by Dunwiddie (1979) and the clearly annual nature of the rings since 1961 shown in the present study.

Figs 2 and 3 contrast the distinct annual rings of tawa with more-or-less indistinct growth rings in taraire. Three cross sections of the latter were obtained from recently fallen trees at Martin's Redoubt (NZMS 1 N46 & pt. N47 480220) in February 1980. Numerous parenchyma bands, and variations in wood colouring, render ring counting difficult in these specimens. However, some tawa specimens show similar features, so that the contrast illustrated may not reflect a fundamental difference between the two species. The arrow on the specimen in Fig. 2 marks a parenchyma band which forms a false growth ring elsewhere on the circumference (far right). Such false rings were not frequent on the specimens examined and could usually be easily diagnosed by tracing the ring laterally. They could cause over-estimation of ages derived from ring counts on increment cores.

Our studies on growth rates (Table 1; West *et al.* 1981) confirm the data of Smale (1981), and show that tawa growth rates are very variable, depending

*The correlation between ring width in year t and year t + 1 for all years.

on the surrounding environment. Seedlings, in particular, may grow extremely slowly for decades, and much of the "advanced growth"— the seedling population on the forest floor — is 60–80 years old. Diameter growth increases through sapling and pole classes and averages from 1 to 4 mm yr^{-1} in trees > 20 cm diameter at 1.4 m height. Using the 8 study trees and a further sample of 33 cross sections and/or cores from the same area, we obtained a significant positive relationship between the number of annual rings and diameter ($y = 2.78x + 69.72$; where y = number of growth rings, x = diameter under bark, both at 1.4 m; $n = 41$, $r = 0.7866$, $P < 0.001$) but the range of ages for any particular diameter was very wide. Consequently, it is possible to estimate the age of an individual from its diameter only very approximately. For example, the observed age of the eight trees studied in detail differs significantly ($P < 0.001$) from the expected age based on their diameters, using the regression equation. However, the results do indicate that tawa trees > 30 cm diameter at 1.4 m are over 100 years old, and that maximum longevity is probably in the range 300–400 years. The scanty data from taraire suggest similar, or greater, longevity.

In conclusion, we emphasise the predominantly annual nature of the growth rings of tawa, the slow but variable rates of growth which they reveal, and the presence of unexplained biennial fluctuations in diameter increment. Age determination may sometimes be hindered by additional bands of parenchyma which may arise in response to environmental stresses, and eccentric growth which is a feature of trees with reduced mean ring widths.

ACKNOWLEDGMENTS

We acknowledge the assistance of the New Zealand Forest Service, in particular A. E. Beveridge, R. Dale, and M. C. Smale. Mr A. Jeffs assisted with sample collection and preparation.

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