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BOLE GROWTH PATTERNS OF *PINUS RADIATA* D. DON IN RELATION TO FERTILISATION, BENDING STRESS, AND CROWN GROWTH

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Radial increment patterns were studied in 18 stand-grown **Pinus radiata** trees after thinning and fertilisation. Patterns in ring width increment along the bole were significantly correlated with bending stress, crown growth activity, and their interaction. Bending stress appeared to regulate growth in the upper 20% of the bole and crown growth factors dominated in the lower bole. No significant effect of fertilisation was found in patterns of stress or crown growth activity in any of the years analysed although a large shift in form factor associated with fertilisation was noted in one year.

INTRODUCTION

Factors controlling ring growth in tree boles have been studied extensively for over a century. Two approaches have been fruitful: one approach invokes nutritional and hormonal gradients arising as a result of physiological growth processes in the crown; the second approach involves a physiological response to a gradient of physical bending stress generated by tree sway. Detailed historical reviews of aspects of these theories may be found in Onaka (1950), Farrar (1961), and Larson (1963).

Results of recent studies suggest a possible physiological basis for the response to physical bending stress. Ethylene applied exogenously has a localised stimulatory effect on radial increment of several tree species (Neel 1971; Brown & Leopold 1973; Barker 1979). It has also been shown that bending of stems and branches increases endogenous ethylene levels in *Pinus strobus, Pyrus malus,* and *Prunus persica* (Leopold *et al.* 1972), in *Malus domestica* (Robitaille & Leopold 1974), and in *Pinus radiata* (G. Fischer, pers. comm.). Growth responses may not, however, always be comparable with responses to exogenously applied ethylene since, in one study, bending reduced diameter growth as well as elongation (Robitaille & Leopold 1974). These latter workers also noted that application of naphthalene acetic acid increased ethylene evolution. Jacobs (1954), Larson (1963), and Burton & Smith (1972) have demonstrated that guying or bending trees can influence diameter increment pattern along tree boles in several coniferous species, presumably in response to changes in bending stress patterns. Bryant (1950) and Büsgen *et al.* (1929) have shown that the relationship of bole diameter to bending stress is in accord with a beam of uniform resistance, as suggested by Metzger (1893), but this relationship represents the result of accumulated growth patterns over several years. Growth allocation patterns within a single year's sheath have not received much attention with respect to bending stresses.

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Bending stress patterns in trees are related to wind speed profiles, crown drag, and both bole diameter and wood elasticity profiles. Consequently, in any particular wind profile, a stress pattern will develop which is related, in part, to crown foliage distribution. In addition to such a direct influence on bending stress, crown variables such as size, weight distribution, and hormonal contribution also have been correlated directly to bole growth patterns (Beckwith & Shackleford 1976; Hall 1965; Onaka 1950; Labyak & Schumacher 1954).

The hormonal theory considers the actively growing apices and needles in the crown as sources of basipetally transported auxin. The physiological gradients resulting in the tree bole act to control cambial activity and cell development, ultimately determining stem form (Larson 1964). The contributions by branches to bole development have been studied by numerous authors using various kinds of pruning techniques. Labyak & Schumacher (1954) and Stiell (1969) have illustrated that the contribution of individual branches to bole growth depends on the size and position in the crown of the branch.

Thus models including either measures of bending stress or crown physiological influences on bole growth have been used independently with reasonable success in explaining bole diameters and patterns of radial increment in trees.

This paper reports results which combine detailed measurements of crown and bole attributes to generate patterns of both relative bending stress and crown physiological influence gradients. These gradients up the bole are compared with gradients in ring width increment.

METHODS

In the period February to April 1976, 18 single-stemmed final-crop quality *Pinus radiata* trees between 30 and 35 m high (planted 1957) were felled and detailed bole and crown measurements were taken. The trees were part of a thinning and fertilisation trial established by N.Z. Forest Products Ltd near Tokoroa in 1971. The plots used were thinned to an average of 490 stems/ha and fertilised with approximately 250 kg/ha of nitrogen as urea. Volume response was small in the 1971–72 growing season so plots were refertilised in 1972. Subsequently, there was a substantial volumetric response both as a result of increased diameter growth and a shift in the pattern of growth, with increased amounts of radial growth higher up fertilised boles. Height growth was not affected.

For each tree, the height of each live branch cluster (containing at least one live branch) was recorded. For these trees, the crown base was approximately 8 m high. For each branch in each live cluster, branch diameter (2.5 cm from the bole), total branch length, and age as well as yearly branch length increments were measured. A subsample of 32 branches was used to develop regression equations relating oven-dry foliage weight to branch length and age.

Each bole was sampled by taking cross-sectional discs at 1-cm taper steps in the green crown region and at 2-cm steps below the green crown. Discs were taken at mid-internodal points to avoid branch swellings. This procedure gave between 20 and 30 discs per tree. The disc surfaces were smoothed and measurements to each ring were taken along 4 radii and averaged. Profiles were plotted and any anomalies resolved by rechecking discs. Wood density (green volume, oven-dry weight) was measured on wood samples taken at 1.4 and 12 m as well as for 4 discs taken from between 20 m and the top of each tree.

Using the past branch-length growth values it was possible by subtraction to estimate past crown dimensions. This was done for each year back to the year of fertilisation response (a total of 4 years). The regression equation for foliage weight was used to estimate oven-dry weight of foliage on each branch for each year and thus the distribution of foliage weight through the crown length for each year after treatment. This relationship, based on logarithm of branch length, branch age, and their product, had an R^2 value of 0.69, and was not significantly influenced by treatment ($P = 0.05$). Analysis of residuals showed that prediction was stable for branches less than 4 m long, but was quite erratic for large older branches.

The yearly foliage weight distribution patterns were used as a basis for distributing wind loads along the crown.

Wind loading on each cluster was obtained from the relationship:

$$D_i = CK(ODF)_i\ V_i^2$$

where D_i = drag force at cluster i
C = drag coefficient (from Mayhead 1973)
V_i = wind speed at cluster i (from a profile given in Oliver & Mayhead 1974)
K = constant representing air density/2
$(ODF)_i$ = oven-dry weight foliage at cluster i.

Total wind drag on the tree was estimated as the sum of all cluster drag values. A percentage contribution by cluster was then calculated and used to distribute an arbitrary total wind load of 100 N along the crown. Papaesch (1977) measured loads on *P. radiata* trees subjected to measured wind speeds at 3 points along the stem. The ratio of the force at the upper strain point to that at the mid strain point was about 3.5. An equivalent ratio calculated for the trees in this experiment was 3.3 which supports the use of this procedure for distributing wind load.

Bending stresses in the cambial zone were calculated for bole cross sections corresponding to each cluster height using diameters obtained from stem analysis profiles, an estimated modulus of elasticity gradient obtained from the wood density profile, and the calculated drag profiles. An iterative, non-linear computer solution was used for these calculations.* The profiles were stable in configuration over a range of wind velocity profiles.

In addition to physical bending stress, a crown growth effect index was also developed. In simulating the contribution of a branch cluster, it was assumed that a reasonable representation of the relative stimulatory contribution to the bole by a cluster would be the branch length growth in that cluster during the year being considered. Onaka (1950) reported that for *Pinus densiflora* the amount of growth hormone produced by a branch was roughly proportional to the amount of growth by the branch. A similar approach has been used by Beckwith & Shackleford (1976). It was also

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* The program used for these calculations was kindly supplied and adapted by Dr J. Astley, Faculty of Mechanical Engineering, University of Canterbury, New Zealand.

assumed that the effect of a cluster on bole growth was basipetally directed in conjunction with a polar hormonal transport system and that this effect declined with distance from the cluster (Labyak & Schumacher 1954). These assumptions imply that small but rapidly elongating branches in the upper crown may exert a greater influence than larger but more slowly elongating branches in the lower crown.

Bole growth in *P. radiata* lags behind branch and terminal elongation (Jackson *et al.* 1976). Therefore, the model contains the assumption that crown elongation is completed before radial bole growth begins. A crown activity index was calculated for a number of points along the bole which correspond with data from disc measurements. The crown influence factor was calculated as:

$$\mathrm{CAI}_i = \sum_{j=i}^{N} \sum_{k=1}^{n_j} \frac{I_{jk}}{(h_j - h_i + L_{jk})^{\frac{1}{2}}}$$

where N = total number of branch clusters above a bole cross-section
n_j = number of branches in the jth cluster
I_{jk} = yearly length increment of the kth branch in the jth cluster
h_j = height of jth cluster
h_i = height of the ith bole cross-section
L_{jk} = branch length at the end of the growing season
CAI_i = relative contribution of all clusters above the ith bole cross-section to growth at the ith disc.

RESULTS

The trees selected for growth analysis conformed to final crop standards. Despite this attempt to obtain uniformity, there were differences in individual tree response. In 16 of the 18 trees analysed, response was conditioned by size before trial establishment. An analysis of covariance of the data using initial volume as a covariate showed significant differences attributable to both years from treatment as well as treatment and that a significant relationship existed between subsequent growth rate and initial tree volume. The range of growth response adjusted for initial differences is indicated in Fig. 1. Within the limits shown, individual tree growth patterns were generally homogeneous although two trees, one from each treatment, showed erratic and declining patterns of growth (see Table 3 for individual tree responses). The graphs of average growth rates adjusted for initial volume differences (Fig. 1) show that the growth rates of the fertilised and control trees are diverging. There is a suggestion in the 1974–75 data that the superiority of the fertilised trees may be beginning to decline.

Height growth was not influenced significantly by treatment (in line with the findings of Woollons & Will 1975).

The volume growth patterns were analysed by computing first-order growth components arising from changes in form (F), basal area (G), and height (H) for each tree (Table 1). These accounted for 96% of total growth. Over the 5-year period, the fertilised trees outgrew the controls by approximately 11%. Volumetrically, fertilisation over the 5-year period did not appear to influence allocation of growth

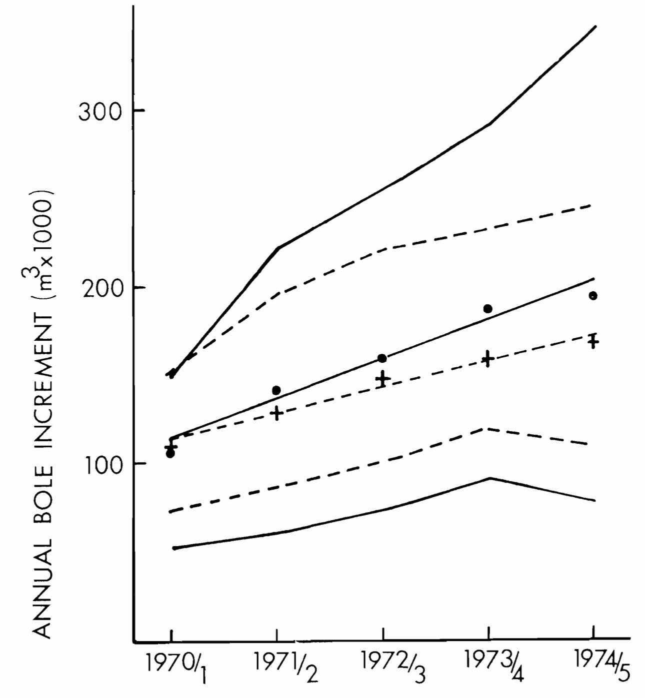


FIG. 1—Volume increment trends by treatment showing extremes (2 upper and 2 lower lines) and average (2 centre lines) responses for 9 fertilised (——) and 9 control (— — —) **P. radiata** trees.

TABLE 1—Contributions to 5-year increment by basal area (G), height (H), and form factor (F) growth components (sum of all trees)

Treatment	ΔGFH	ΔHFG	ΔFGH	Total
FERTILISER				
m^3	4.096976	2.288628	0.369624	6.755228
%	60.7	33.8	5.5	100.0
CONTROL				
m^3	3.583741	2.19012	0.334804	6.108669
%	58.7	35.8	4.4	100.0

to any sustained degree since both fertilised and control trees had near identical proportions allocated to the 3 first-order components. During 1972–73, however, there was a very large difference in allocation with form contributions dropping significantly in the control trees. During this year, form change contributed a positive 2% to total growth of fertilised trees and there was a corresponding negative 12% contribution by the form component of the controls. During the other 4 years form contributions in the control trees were higher, resulting in an overall similarity in form contributions over the period. Nevertheless, fertilisation in conjunction with thinning influenced the allocation of wood increment along the bole, particularly in one year.

This form shift of 1972–73 was analysed with reference to crown growth activity patterns and the distribution of bending stresses arising from wind acting on the crown. Barker (1978) showed a correlation between change in form factor and total upper crown growth. It was not apparent in this earlier work whether the form change resulted from a general increase in tree vigour or a change in growth pattern through the length of the crown itself. Although the base of the live crown in the years before measurement could not be accurately defined, it was thought reasonable to assume that because of the thinning, the live crown base had remained relatively stable during the 4 years after treatment. Nevertheless, because of this limitation, comparisons between treatments were only made within years.

For each tree, crown activity indices were calculated at each disc by year and by treatment as a percent of maximum index value for the year and were plotted on overlays against percentage height. Superimposing these overlays showed that patterns were very similar every year for each tree. The index increased evenly up the bole reaching a maximum at about 73% of total height (plus or minus about 10%). Above this point there was a linear decline to near zero at the top. Fertilised trees had similar patterns to the control trees even during 1972–73.

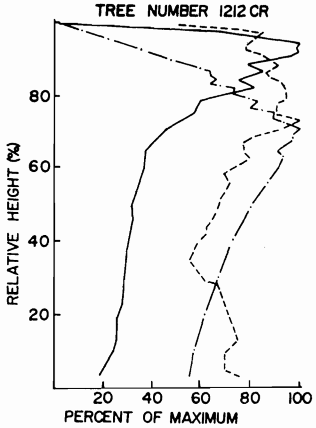
Fig. 2 shows 3 representative trees from 1974–75 from each treatment representing a range of growth rates. It is apparent that in most trees, ring widths below the height of maximum crown activity index were closely correlated with the index.

The bending deflections calculated showed that there were terminal deflections of about 1–3 m. These values were observed commonly in the field at Tokoroa. Centres of wind pressure on the crown, calculated using foliage weight and wind profiles, were between 74 and 82% of tree height. The simple assumption of a triangularly-shaped crown with a centre of pressure at 1/3 of the crown length would have given values of about 80% of total tree height.

Computed stress profiles were transformed to percent of maximum stress value for each tree and year and were plotted on overlays against relative height. On superimposing these profiles a common pattern was observed. There was a uniform bending stress or gradually increasing stress up to about 75% of the tree height. At this point, there was a very rapid increase to values 5–10 times those in the lower bole, reaching a maximum at 93% of total height. Then values dropped off rapidly to zero at the top (Fig. 2). Again, fertilisation had no influence on the vertical pattern of bending stress.

Ring width patterns were somewhat irregular but a consistent pattern emerged when they were transformed to percent maximum and plotted against percent height. Above about 30% height there was a gradual increase to a point of maximum at an average height of 90% of total height. This point of maximum ring width (HRW) corresponded quite closely with the point of maximum bending stress (HBS) in most trees (Table 2). Differences between HRW and HBS were larger in the control trees

FIG. 2—(Right) Variation of cambial bending stress (———), crown activity index (— ● —), and ring width (— — —) with height for fertilised (F) and control (C) **P. radiata** showing rapid (R), average (A), and slow (S) growth rates. 1974–75 growing season.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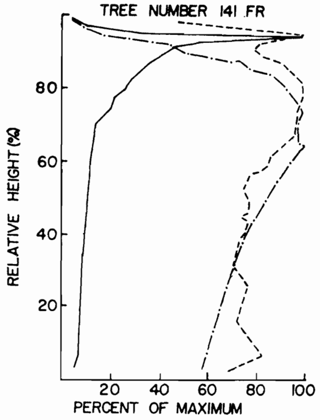
RELATIVE HEIGHT (%)
20
40
60
80
20
40
60
80
100
PERCENT OF MAXIMUM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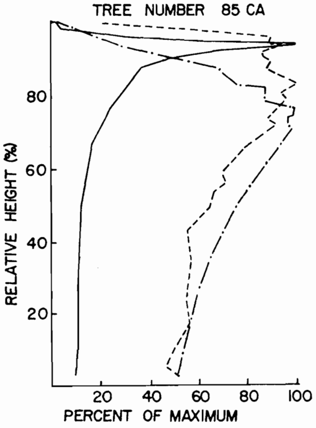
RELATIVE HEIGHT (%)
20
40
60
80
20
40
60
80
100
PERCENT OF MAXIMUM


TREE NUMBER 85 CA
RELATIVE HEIGHT (%)
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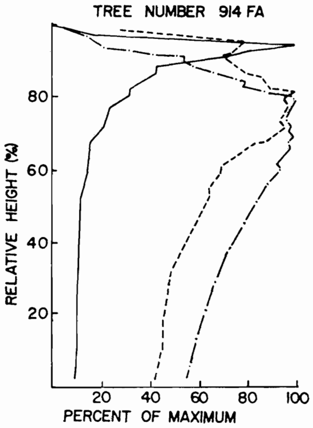
40
60
80
20
40
60
80
100
PERCENT OF MAXIMUM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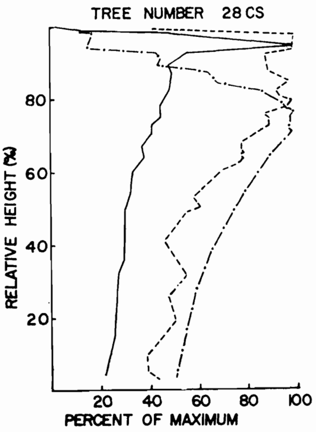
RELATIVE HEIGHT (%)
20
40
60
80
20
40
60
80
100
PERCENT OF MAXIMUM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RELATIVE HEIGHT (%)
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40
60
80
20
40
60
80
100
PERCENT OF MAXIMUM

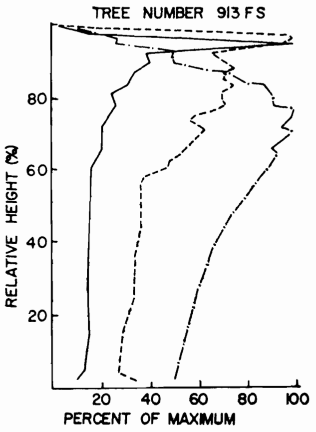

TREE NUMBER 913 FS
RELATIVE HEIGHT (%)
20
40
60
80
20
40
60
80
100
PERCENT OF MAXIMUM

TABLE 2—Height of maxima in ring widths (HRW) and bending stresses (HBS) for 18 **P. radiata** trees

FERTILISED					CONTROL				
Growth rate*	Total height	HRW (m)	HBS (m)	Diff. (HRW—HBS)	Growth rate	Total height	HRW (m)	HBS (m)	Diff. (HRW—HBS)
Av.	31.7	29.8	29.7	0.1	Slow	28.9	24.2	27.2	—3.0
Av.	30.2	28.0	28.0	0.0	Av.	30.2	24.0	28.1	—4.1
Av.	28.6	27.1	26.7	0.4	Slow	30.2	28.6	28.1	0.5
Rapid	30.2	28.6	28.2	0.4	Rapid	32.2	23.1	29.7	—6.6
Av.	31.4	25.6	29.3	—3.7	Av.	30.1	28.5	28.2	0.3
Slow	30.2	29.0	28.6	0.4	Av.	31.4	26.0	29.2	—3.2
Av.	31.6	25.2	28.9	—3.7	Slow	30.0	25.3	27.0	—1.7
Av.	31.6	29.8	29.5	0.3	Slow	28.5	27.3	26.6	0.7
Av.	33.7	32.7	32.2	0.5	Av.	30.6	29.1	28.5	0.6

* See Fig. 1

than in the fertilised trees, but this effect was not statistically significant (P = 0.05). Although the crown activity index had declined to a value of about 50% of its maximum in the upper bole region, there was no concomitant decline in ring width such as occurred in the lower bole.

When the raw data for ring widths were plotted against bending stresses, a curvilinear relationship was apparent (Fig. 3). The relationship between logarithm of bending stress and ring width gave highly significant correlations between the two variables, although the relationship was confounded by concurrent variation in the crown activity index.

When the raw data for ring widths were plotted against crown activity index, generally linear relationships were evident in the lower and middle bole (Fig. 4). In the upper bole region, where bending stresses began to change by large amounts, the relationship between ring width and crown activity index broke down.

In an attempt to assess the contributions of stress and crown activity separately, a multiple regression approach was used. Despite the limitations of the multiple regression technique used, both logarithm of bending stress and crown activity index appear to contribute significantly to the amount of radial increment measured.

For each tree during the year 1974–75, regressions of ring width on logarithm of bending stress, crown activity index, and the product of log bending stress and crown activity index were computed. The coefficients of multiple determination ranged from 0.76 to 0.97 (Table 3).

For 10 of the 18 trees, the regression coefficients for the 3 independent variables were all significantly different from zero, at least at the 0.95 level. Of the remaining 8 trees, the coefficients for crown activity index and crown activity times stress were both significant (at the 0.95 level) for 4 trees and of the remaining 4, log stress was the only significant coefficient. However, these correlations need further investigation under controlled conditions to verify whether the assumption of a linear relationship for crown activity index and a logarithmic relationship for bending stress with ring

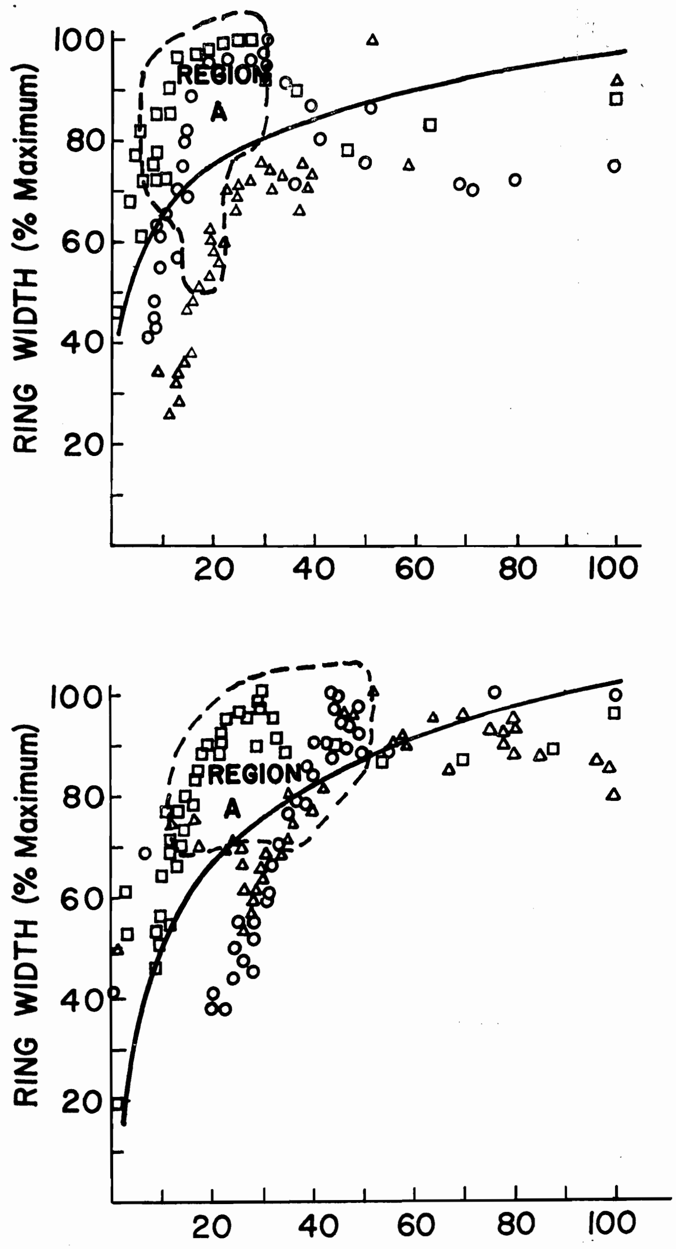
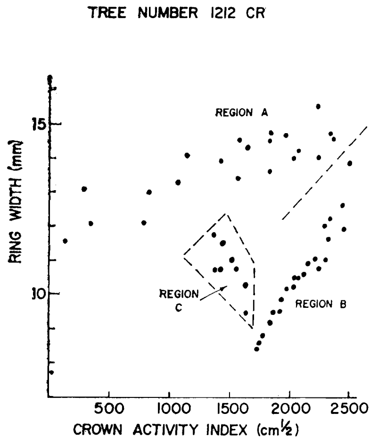
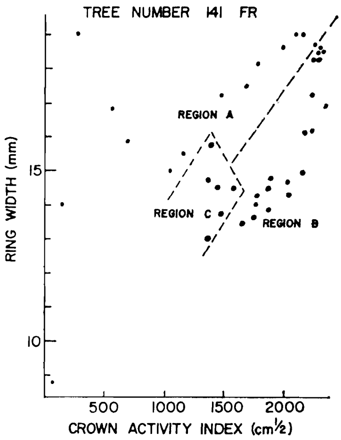
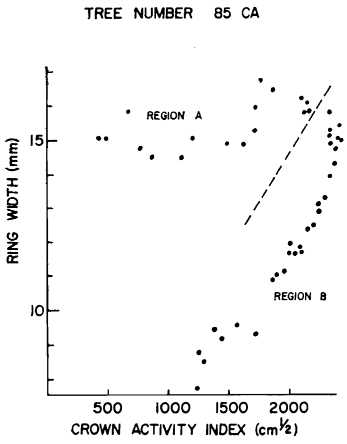
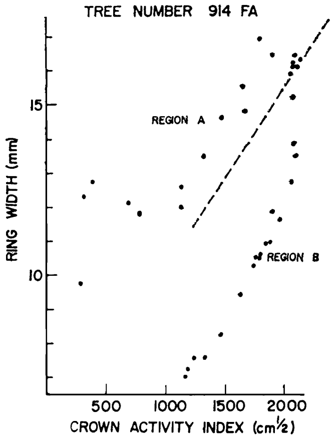


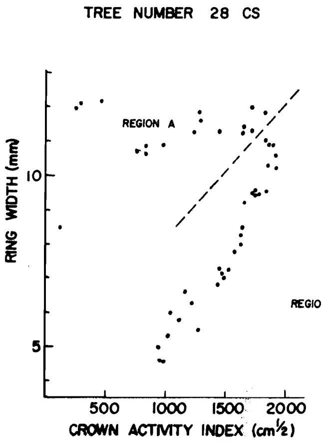
FIG. 3—Ring width in relation to bending stress for 6 representative trees with rapid, average, and slow growth rates. Top: Fertilised trees (Δ = 913, ○ = 914, □ = 141). Bottom: Control trees (Δ = 1212, ○ = 28, □ = 85). Zone of maximum crown activity (over 80%) indicated as Region A. Regressions are of form ring width = a + b $\log_e$ (bending stress). (Horizontal axis: Bending stress (% maximum).)


TREE NUMBER 1212 CR
REGION A
REGION C
REGION B
RING WIDTH (mm)
15
10
500
1000
1500
2000
2500
CROWN ACTIVITY INDEX (cm½)


TREE NUMBER 141 FR
REGION A
REGION C
REGION B
RING WIDTH (mm)
15
10
500
1000
1500
2000
CROWN ACTIVITY INDEX (cm½)


TREE NUMBER 85 CA
REGION A
REGION B
RING WIDTH (mm)
15
10
500
1000
1500
2000
CROWN ACTIVITY INDEX (cm½)


TREE NUMBER 914 FA
REGION A
REGION B
RING WIDTH (mm)
15
10
500
1000
1500
2000
CROWN ACTIVITY INDEX (cm½)


TREE NUMBER 28 CS
REGION A
REGION B
RING WIDTH (mm)
10
5
500
1000
1500
2000
CROWN ACTIVITY INDEX (cm½)

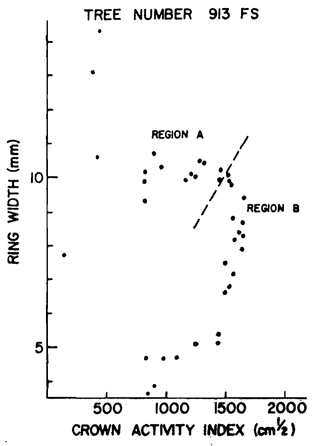

TREE NUMBER 913 FS
REGION A
REGION B
RING WIDTH (mm)
10
5
500
1000
1500
2000
CROWN ACTIVITY INDEX (cm½)

TABLE 3—Summary of regression results relating ring width to logarithm of bending stress (S), crown activity index (C), and their product (SC) for 1974–75 season. Growth rate is indicated as rapid (R), average (A), or slow (S)

Tree no. and growth rate	Probability of non-zero coeff. (%)			
	Variable			
	S	C	SC	R^2(%)
CONTROL				
87 A	81	98	100	96
84 S	69	97	98	77
212 A	67	100	100	84
21 S	100*	56	65	86
28 S	100	100	100	96
217 A	97	100	100	85
820 S	100	99	99	93
1212 R	98	100	100	76
85 A	100	100	100	97
FERTILISED				
141 R	72	99	100	78
914 A	98	93	99	94
114 A	98	78	89	76
116 S	98	99	100	89
94 A	100	100	100	75
913 S	100	100	100	94
147 A	100	100	100	82
144 A	100	22	24	97
143 S	100	46	60	85

* Probability greater than 99.99%

width is justified. A plot of residuals from this regression showed that the model fitted the data well but that there was an increased number of erratic predictions in the upper 15% of the crown region (Fig. 5).

Also, butt swell was not predicted well. Although deviations were much lower in this region than in the upper crown, a tendency to underestimate ring widths for the basal discs is evident in Figs 2 and 5, particularly in the more rapidly growing trees.

DISCUSSION

Although fertilisation prevented the sudden marked reduction in form factor noted in the controls after thinning, the effect was transitory and was most evident in one particular year. Nevertheless, in terms of the total fertiliser response, this one year form change accounted for an amount equal to 25% of the total fertiliser volume response since treatment. During this one year both basal area and height increments

FIG. 4—(Left) The relationship between ring width and crown activity index for fertilised (F) and control (C) **P. radiata** showing rapid (R), average (A), and slow (S) growth rates. Region A represents the upper bole with high variable bending stresses; Region B represents the mid and lower bole with relatively constant bending stress; Region C represents the area of butt swell.

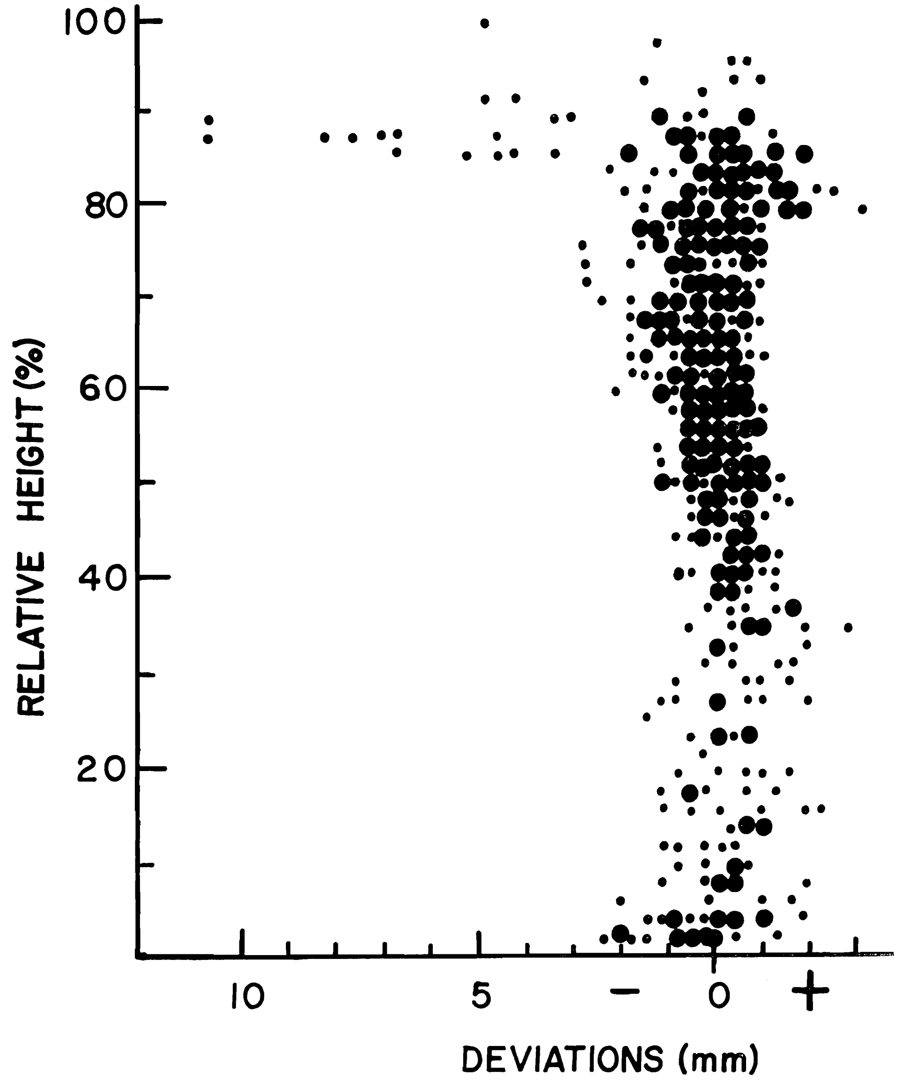


FIG. 5—Estimated ring widths minus actual ring widths of 18 **P. radiata** for the 1974-75 growing season. Large dots = Multiple data. Average ring width = 11.6 mm.

for the fertilised trees were less than those of the control (95 and 88% respectively) yet the volumetric increment of the fertilised trees averaged 108% of that of the controls.

It does not appear from the crown activity index data that the form change involved a changed pattern of growth within individual tree crowns; rather it resulted from a general increase in vigour of the entire crown region. This general increase in crown growth and vigour does not appear to have markedly influenced the patterns of bending stress either. The failure of either stress distribution or crown activity indices to show obvious shifts in relation to the fertiliser-induced shift in form factor suggests that physiological variables other than stress or crown activity related to nutrition are involved in controlling tree form. However, for each tree a high correlation was found between bending stress in the cambial region, crown activity index, their interaction, and ring width.

The general pattern of ring width in these trees was for a maximum to occur in either the second or third annual shoot back from the apex with generally wide rings between about 70 and 95% of total tree height. Although the live crown bases were at about 30% of total height, the widest rings were being laid down near the most actively growing section of the crown. These patterns are in general agreement with those found by numerous other workers (Duff & Nolan 1953; Onaka 1950; Hall 1965; Beckwith & Shackleford 1976; Burton & Smith 1972; Larson 1963, 1964, 1965), although the maximum ring width is somewhat higher in the crowns of *P. radiata* than in the other species studied.

The bending stress patterns calculated suggest that increased ring width increment in response to stress is likely to be found at about 90% of total height. Below this part of the bole, a beam of uniform resistance has developed and bending stress changes are minor in the bottom 80% of the bole region. The logarithmic relationship between bending stress and ring width found in this study correlates with other work which has shown that growth responses in *P. radiata* vary logarithmically with concentration of exogenously applied ethylene (Barker 1979). G. Fischer (pers. comm.) has found that the internal ethylene levels arising from exogenously-applied ethylene resemble those created by bending. These results strongly suggest that an ethylene-moderated growth response to bending is involved in *P. radiata*. The profiles of stress that are generated suggest that if stress-induced ethylene is active in controlling differential growth rates of the cambium, its influence will likely be in the upper crown region where stresses vary exponentially. Over the lower part of the bole, below about 85% of tree height, crown activity index appeared to be more closely related than stress to the pattern of ring width variation. However, above 85% of tree height, the relationship changed markedly. These results suggest that ring width in the upper bole is mediated chiefly by stress-related factors and growth in the lower bole is more strongly regulated by crown growth factors and distance from the crown. This supports the hypothesis of Larson (1965) that a dual active and passive system controls xylem increment. The presence of the well-defined bending stress maximum in the upper region of the bole and the correspondence between the heights at which bending stress and ring width are maximal, plus the breakdown of the ring width-crown activity index relationship in this same region reinforce the contention by Brown (1971) that deviations from a strictly passive growth allocation system in the upper bole can be explained in terms of localised bending stress patterns. However, those ring width patterns showing butt swell effects were not adequately explained by either stress or crown activity. This failure may be explainable in terms of the bending stress model used and the nature of the root system of the individual tree. The assumption of a rigidly fixed tree base that was used here is probably not justified for all trees, particularly for those that lack a pronounced tap root and have large supporting laterals near the surface. Such a root configuration could generate substantially different stress patterns in the basal region of the bole than the model that was used.

Hall (1965) has summarised a number of papers linking measures of bole growth with foliage weight distribution. However, crown weight is distributed in a pattern quite similar to the crown growth activity pattern. These in turn also resemble in general form the distribution of physical bending stresses. Separation of nutritional aspects of the crown from the hormonal contributions by branches of differing elongation rates or from the physical bending contributions arising either locally from torque effects (Quirk *et al.* 1975) or throughout the tree bole from wind flexing cannot easily be done since all three aspects are intimately related. The present study suggests, however, that in different parts of the bole, different factors are dominant in controlling ring width increment.

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