even-aged stands should be carried out at such heights as to show the same number of growth rings in each specimen (Richardson, 1961). Cores were harvested at the mid-point of the internode in which 23 complete growth rings were present in the case of the 1941 plantings, and 22 complete rings for the trees which were planted in 1942. Before removal from the tree, the ends of each specimen were marked to show the direction of the tree axis. Specimens were wrapped in polythene to minimize moisture loss pending examination.

The cores were divided into strips extending from bark to bark as follows. A cut was made parallel to the long axis of the core and at right angles to the pith direction to separate a piece in the shape of a segment of a cylinder, of 6 mm maximum thickness for use in the determination of ring width and density characteristics. Saw cuts parallel to the long axis of the core and parallel to the pith direction were made in the remainder to separate a piece 12 mm wide containing the pith, for use in the measurement of grain angles. On this piece the sawn surface at right angles to the direction of the pith was planed to serve as a datum. The relationship of this datum to the marks on the ends of the specimen showing the direction of the tree axis could be established so that angles of grain deviation were finally referred to this direction. The remains of the core provided material measuring at least 12 mm in the direction of the grain for the determination of average tracheid length.

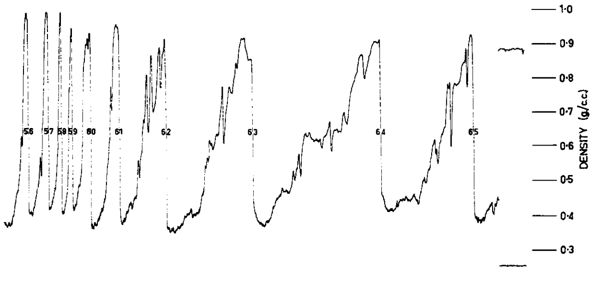
The determination of characteristics other than grain inclination was carried out using material from the shorter of the two radii of each core, as this would normally be expected to contain the least amount of compression wood. Angles of grain deviation for individual growth rings in each specimen were expressed as the mean of values from both radii.

Wood characteristics were determined for each growth ring from the 1954/55 growing season onwards as follows:

(a) Average tracheid length: A strip from the late wood was macerated and 50 whole tracheids were taken at random and measured at 40 magnifications using a projection microscope.

(b) Grain inclination: A thin sliver was peeled from the tangential face of the last-formed late wood to disclose the grain direction. The angle between this direction and the datum surface, which was related to the direction of the tree axis, was measured with an engineer's protractor.

(c) Ring width and density characteristics: The 6 mm thick segments were allowed to dry over a saturated solution of sodium dichromate to an equilibrium moisture content of approximately 8 per cent., and a precision sanding machine was used to machine a flat on the curved surface of each piece parallel to the flat face and to abrade this flat face to produce radial strips measuring $4.70 \pm .05$ mm thick in the fibre direction. The strips were irradiated from a source of soft X-rays and by the technique of Polge (1965), contact radiographs were obtained and scanned by means of a double beam microdensitometer. Individual growth rings were identified and marked on the resulting densitometric traces for each tree as in *Figure 1*. For each annual ring, the maximum and minimum excursions of density, the width of the ring components for which density values were less than 0.5 g/cc and 0.6 g/cc, and greater than 0.6 g/cc and 0.7 g/cc respectively, and the total width of the ring were read directly from the curves. The area contained between a line parallel to the abscissa and the curve was measured and used to calculate the average density for each growth ring. As the experiment involved only wood formed from 1954 onward, i. e. wood outside the eleventh growth ring from the pith, and thus not subject to heartwood formation in trees of this age (Nicholls and Dadswell, 1965), it was deemed unnecessary to treat specimens to remove resinous infiltrates.



PLOT II TREE 3

Figure 1. — The variation in optical density of the radiograph of a 4.7 mm thick strip from a *Pinus pinaster* tree. This variation pattern is directly related to variations in wood density of the strip. A linear scale of wood density is shown and is positioned by means of calibrating marks. The dormant period assumed to occur in July is a convenient place to mark the successive years of growth. This tree was from the plot thinned to 375 stems per hectare in February 1958 and treated with fertilizer in September 1961.

Results and Discussion

Data from contemporaneously formed rings were grouped and treatment means were calculated for each of the features under review. As the effect of age (distance from the pith) on wood characteristics is small in material formed outside the eleventh growth ring from the pith (see, for example, Nicholls, 1967), little effect should be apparent due to one plot being planted one year later than the other eleven. In the discussion which follows, the nominal growing season is assumed to extend from July to July.

For each characteristic, any differences resulting from the treatments under investigation should be revealed by a comparison of treatment means. During the 12 year study period from July 1954 to July 1966 three age segments are of interest in the analyses. From July 1954 until January 1958 all plots were subjected to the same conditions, and wood laid down in this interval may be used to establish norms for the various characteristics; from February 1958 until August 1961 the wood reflects the influence of different spacings; and from September 1961 onwards results should indicate the interaction effect of thinning and fertilizer application. For each feature, the variable analysed was the deviation of the value for a particular growth ring from the mean for the three years from July 1954 to July 1957.

The results and discussion for each characteristic follow:

Ring width: The patterns of variation for this feature are set out in *Figure 2*. An inspection of the graph for the unthinned trees (2500 stems per hectare), shows that in the period from 1954 to 1960 (prior to fertilizer treatment and for material 12 to 18 rings from the pith) annual increments were similar to those previously reported for wood of the same age obtained from trees of the Leiria provenance and likewise grown on a good quality site at Gnangara (Nicholls, 1967). This is a typical growth pattern for plantation-grown conifers. Following the application of fertilizer in September 1961 this group of trees showed a rapid response in stem diameter growth rate such that in a period

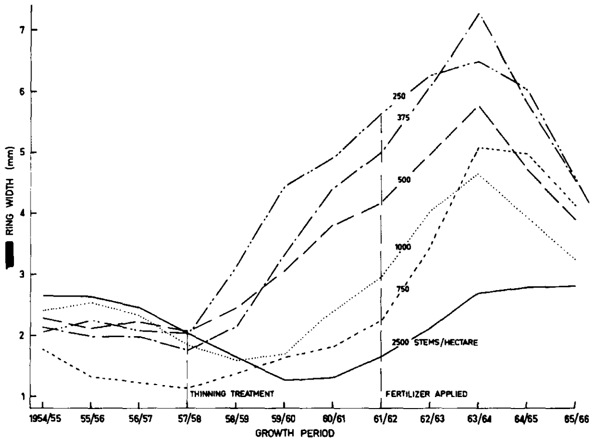


Figure 2. — The influence of thinning and fertilizer treatment on the means of ring width for groups of *Pinus pinaster* trees.

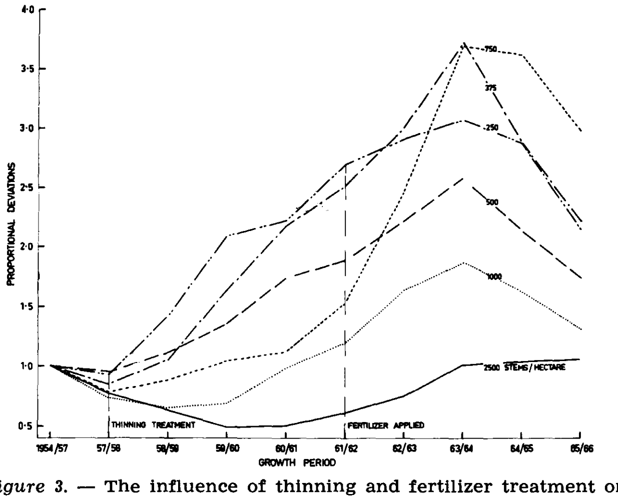


Figure 3. — The influence of thinning and fertilizer treatment on the proportional deviations from the mean for the period 1954 to 1957, of the means of ring width for groups of *Pinus pinaster* trees.

of two years ring widths were double those recorded immediately prior to treatment.

An initial examination of the data for all groups of trees indicated that the standard deviations were proportional to the means; therefore a logarithmic transformation was used in the analysis of this characteristic and trends discussed refer to the transformed data. The deviations from the mean for the period 1954 to 1957 are plotted in *Figure 3* as proportional deviations from this mean value. As the thinning treatment was completed in February 1958 it would not be expected that a systematic effect would be apparent during the remainder of the 1957/58 growing season. However in the next four years, viz. 1958/59 to 1961/62, the analyses showed a highly significant linear trend with the logarithm of thinning intensity. For the 1962/63 season the linear trend was highly significant but there was some evidence of departure from linearity, and for the remaining three growth periods to 1965/66, the trend was non-linear, indicating some interaction effect between thinning and fertilizer treatment. It appears that the greatest effect was produced when fertilizer was applied to the plots where trees had been thinned to 750 stems per hectare.

The relationship between response and thinning intensity revealed by these results confirms the findings of others (see for example, Donald, 1956; Jacobs, 1962). It should be noted however that the ring widths reported herein were measured at a nominal breast high level, and as attention has already been drawn to the increase in stem taper associated with thinning treatment, the same relative increase may not occur higher in the trees. The greatest stem diameter response due to thinning was 220 per cent. in trees from the plots thinned to 250 stems per hectare. On the basis of the present results, it is clear that at this maximum thinning intensity, growth was still limited by environmental factors. This is illustrated for example by noting that subsequent to thinning, fertilizer treatment produced a further increase in ring width in the trees from these plots.

From *Figure 2* the response in stem diameter growth due only to fertilizer treatment can be estimated from the trees on the unthinned plots. It is also apparent that there is a greater increase in ring width as a result of applying fertilizer to the plots where trees were thinned to *ca.* 750 stems per hectare. As a generality therefore, the data agree with the findings of Erickson and Lambert (1958), that a combined treatment involving both thinning and fertilizer produces greater growth rates than does either treatment alone.

It is suggested that all trees would be subject to water stress by 1957. This stress would tend to be alleviated by the thinning treatment, which also promotes increased light and reduces competition for nutrients, resulting in increased growth and an increased root system. Water stress is further reduced and growth further increased in 1961 with the application of fertilizer which assists root growth (Buchholz and Neumann, 1964). By the 1963/64 growing season however top growth has increased to such an extent that water stress is again limiting, and with possible leaching and loss of fertilizer efficacy growth rate declines in the following years in all but the unthinned trees. In this respect it would be interesting to observe the reaction to further application of fertilizer in say 1966. It is further suggested that the trees from the plots thinned to 750 stems per hectare were the most affected by water stress prior to thinning and that this condition was not markedly allayed by the thinning treatment but was relieved by the application of fertilizer so that these trees exhibited the best response to this latter treatment.

Spiral grain — Grain angles did not change significantly in magnitude or sign as a result of thinning treatment or the application of fertilizer. These findings do not conflict with conclusions from other studies which have shown that grain angles are not affected by environmental variation between trees expressed by differing growth rates (Nicholls and Fielding, 1965), or as a result of differences in site quality (Fielding, 1967).

When all data were pooled to form a grand mean the pattern of change in grain angles was similar to that previously reported (Nicholls, 1967) for trees of the Leiria provenance grown in the Somerville plantation (some 25 km to the South) and subject to the same general climatic conditions (equivalent to the standard for Perth). Although all trees exhibited a left-hand grain inclination in growth rings adjacent to the pith, approximately 20 per cent. had changed to a right-hand tilt by the end of the study period (corresponding to 23 growth rings from the pith).

Average tracheid length — The means for each group representing the separate thinning treatments are set out in *Table 1* and plotted in *Figure 4*, as deviations from the

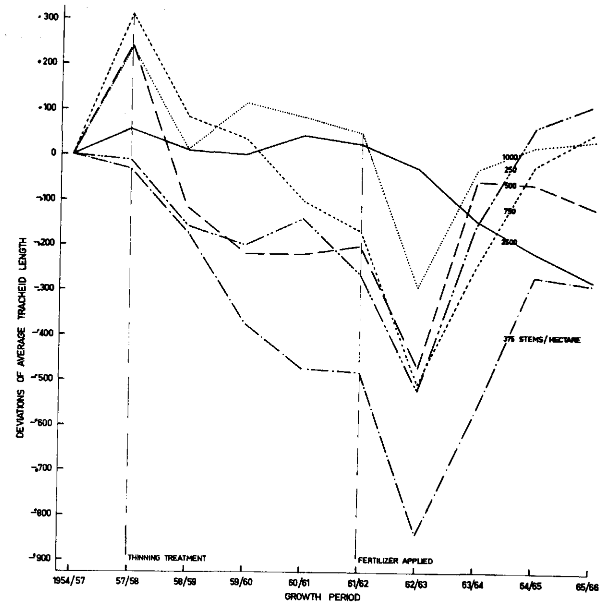


Figure 4. — The influence of thinning and fertilizer treatment on the deviations from the mean for the period 1954 to 1957, of the means of average tracheid length for groups of *Pinus pinaster* trees.

mean for the period 1954 to 1957, through the successive growth periods to 1966.

The data for the unthinned trees prior to the fertilizer treatment in 1961 are similar to those previously reported for trees of the same age and provenance grown also at Gnangara (Nicholls *et al.*, 1963). It may be seen that the application of fertilizer to the unthinned plots resulted in a steady diminution in tracheid lengths.

The analysis for this characteristic shows that the effect of thinning varies significantly from growth ring to growth ring.

The pattern in *Figure 4* for the means associated with the thinned plots for the 1957/58 growth ring, is an indication of the initial reaction to the thinning treatment, as the determinations of average length were carried out on material from the late wood which was probably laid down in April and May and the thinning treatment was completed in February. The means are seen to be in two separate groups which are significantly different from one another. Those for the trees thinned to 1000, 750 and 500

Table 1. — The means of average tracheid length through successive years from 1954 to 1966 for groups of *P. pinaster* trees subjected to various thinning intensities.

Growth period	Average tracheid length (mm)					
	Thinning intensity (stems/hectare)					
	2500	1000	750	500	375	250
54/55	4.72	4.41	4.44	4.65	4.72	4.56
55/56	4.93	4.52	4.48	4.70	4.83	4.60
56/57	4.97	4.61	4.72	4.79	4.81	4.69
57/58	4.93	4.75	4.88	4.95	4.76	4.61
58/59	4.89	4.52	4.63	4.60	4.62	4.46
59/60	4.88	4.63	4.60	4.49	4.41	4.42
60/61	4.92	4.60	4.45	4.49	4.31	4.48
61/62	4.90	4.56	4.38	4.51	4.31	4.35
62/63	4.85	4.22	4.04	4.24	3.95	4.12
63/64	4.73	4.48	4.30	4.66	4.22	4.46
64/65	4.66	4.53	4.53	4.65	4.52	4.68
65/66	4.60	4.55	4.60	4.60	4.50	4.73

stems per hectare have increased, and those thinned to 375 and 250 stems per hectare show a slight decrease with respect to the datum mean. It is suggested that the observed pattern is the net result of two effects. The immediate consequence of the thinning treatment is to increase the available light to the intermediate branches and Savina (1939, 1956) has observed an increase in cell length following such treatment. It is reasonable to assume, however, that beyond a certain thinning intensity there is no further sensible increase in light but there could be increased wind action and phototropism leading to compression wood formation and hence reduced tracheid lengths.

In the next growing season, viz. 1958/59, all residual trees showed a reduction in average tracheid length. However, the means for the plots thinned to 500, 375 and 250 stems per hectare were significantly less than those from the unthinned plots and the plots thinned to 1000 and 750 stems per hectare. At this time, in addition to the increased light, the reduced competition for soil moisture and nutrients had resulted in an increase in stem diameter growth rate, which is associated with a shortening of tracheid length (Dinwoodie, 1963; Larson, 1963 and many others). Each of the factors of light, compression wood and growth rate plays a part in determining the observed values for average tracheid length. The pattern was similar for the following growing season, but the effect of thinning to 375 stems per hectare reduced tracheid lengths to a significantly greater degree than did thinning to 500 or 250 stems per hectare. In wood formed during the 1960/61 growing season, there is evidence that thinning to 750 stems per hectare reduced tracheid lengths in the residual trees to less than those from the unthinned plots and from plots thinned to 1000 stems per hectare, and thinning to 375 stems per hectare had a significantly greater effect on tracheid length than did any other thinning intensity. This pattern was maintained during the 1961/62 growth season which includes the time when fertilizer was applied to all plots.

The effect of the fertilizer treatment is apparent in the following growth period, i. e. during 1962/63, in the form of a dramatic reduction in average tracheid length in the residual trees from all the thinned plots. It may be recalled (*Figure 3*) that the application of fertilizer also resulted in greatly increased ring width. For this growth period it is apparent from *Figure 4* that tracheid length values have separated into four groups which are significantly different from one another, such that tracheid lengths from the unthinned plots are longer than those from the trees thinned to 1000 stems per hectare and the trees from plots thinned to 375 stems per hectare have the shortest tracheids. The trees from all the thinned plots exhibited a large increase in tracheid length values during the 1963/64 growing season, but for this and the remaining period under review, the trees from the plots thinned to 375 stems per hectare continue to have tracheids which are significantly shorter than those from any other of the thinned plots.

Maximum and minimum density:

There were no significant effects of treatment for either of these variables. This is not unexpected as in a previous publication (Nicholls, in press) it was suggested that the extreme excursions of density were linked with factors of temperature. It is planned to investigate this tentative relationship at an early date.

The difference between the maximum and minimum density which is a measure of the intra-incremental uniformity was also analysed and failed to show any consistent effect of treatment.

Table 2. — The means of average density through successive years from 1954 to 1966 for groups of *P. pinaster* trees subjected to various thinning intensities.

Growth period	Mean density (arbitrary units) Thinning intensity (stems/hectare) 2500	1000	750	500	375	250
54/55	6.269	6.565	6.273	6.337	6.206	6.811
55/56	5.992	6.103	6.000	6.126	6.194	6.268
56/57	6.273	6.277	6.196	6.160	6.169	6.153
57/58	6.169	6.540	6.091	6.431	5.976	6.480
58/59	6.569	6.469	6.065	6.627	6.322	6.993
59/60	7.138	7.445	7.243	7.047	7.253	7.359
60/61	6.459	6.166	5.877	6.026	6.074	6.298
61/62	6.385	6.281	6.357	5.927	6.295	6.341
62/63	6.725	6.351	6.182	6.359	6.244	6.177
63/64	6.769	6.355	6.181	5.977	5.963	5.933
64/65	6.555	6.307	5.843	6.048	5.889	5.890
65/66	6.786	6.390	6.026	6.014	6.483	6.258

Average density:

The means for this characteristics for each of the groups of trees are set out in *Table 2*. As for ring width a logarithmic transformation of the data was used in the analyses for this variable, and trends discussed refer to the transformed data. For each of the thinning treatments, the deviations from the mean for the period 1954 to 1957 are plotted in *Figure 5* as proportional deviations from this mean value.

From *Table 2* and *Figure 5* it may be seen that for every group, there is a clearly defined peak in the 1959/60 growing season. This is similar to that previously reported (Nicholls, 1967) for *Pinus pinaster* trees grown at Somerville plantation (some 25 km further South) and subject to the same climate (that of Perth). This peak was attributed to a combination of climatic factors which favoured an increase of thick walled cells in the 1959/60 growth ring, and is assumed to influence growth in the same way insofar as the trees in the present study are concerned. Excluding this peak there was a slight increase (5½ per cent.) throughout the period of the investigation in the average density of the trees from the unthinned plots.

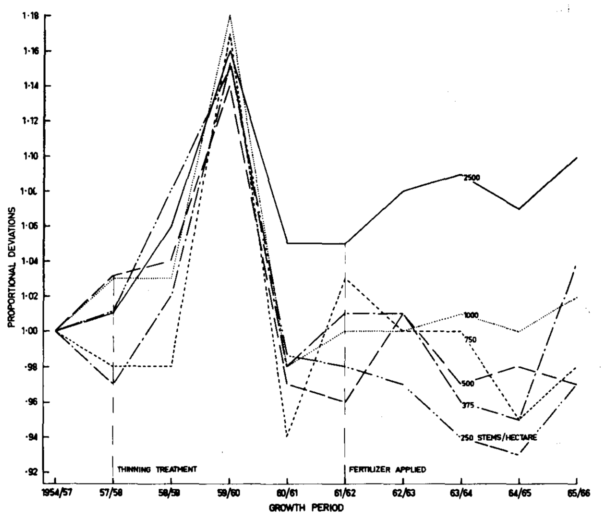


Figure 5. — The influence of thinning and fertilizer treatment on the proportional deviations from the mean for the period 1954 to 1957, of the means of average density for groups of *Pinus pinaster* trees.

For the period up to and including the 1959/60 growing season neither thinning nor thinning intensity had any significant influence on density values. There were no significant effects of treatment in the 1961/62 growing season which included the period when fertilizer was applied. During the remaining period under review density values generally remained more or less constant. However for trees from the plot thinned to 250 stems per hectare there was a steady decline in density from the 1961/62 season onward.

Generally therefore average density was unaffected or slightly reduced by treatment. This is not inconsistent with the majority of observations listed above.

Ring components: — Practically all past work dealing with the effect of silvicultural treatment on wood characteristics has been carried out using far from ideal methods of precisely estimating the early wood/late wood boundary. However recently proposed methods of determining density in relation to radiation absorption furnish a continuous record of density variation throughout the life of the trees, and besides providing information not previously available, allow the use of satisfactory alternatives to the determination of this boundary. One such approach involves a series of density levels, and the influence of a treatment is considered in relation to the change in the width of the annual ring component with density less than or greater than each level in turn. This procedure has been adopted in the present investigation using three such levels viz. 0.5, 0.6 and 0.7 g/cc. The widths of the components with density less than 0.5 and 0.6 g/cc respectively are considered and may be likened to the early wood part of the ring, and the widths of the portions with density greater than 0.6 and 0.7 g/cc are obtained and are analogous to late wood.

Figures 6 and 7 illustrate the patterns of variation for the widths of the components with density less than and greater than 0.6 g/cc respectively. A logarithmic transformation of data has been used in the analyses, and again trends refer to the transformed data. In each case, for each thinning treatment, the deviations from the mean for the period 1954 to 1957 are plotted as proportional deviations from this mean value.

From *Figure 6* it will be seen that following thinning treatment there is a significant increase in the width of the "early" wood component and this increase is more

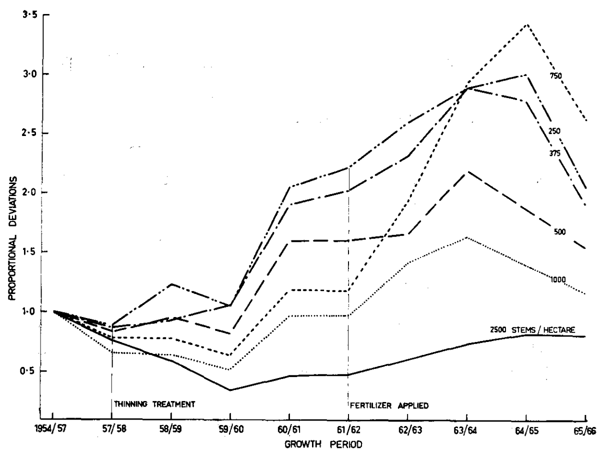


Figure 6. — The influence of thinning and fertilizer treatment on the proportional deviations from the mean for the period 1954 to 1957, of the means of the width of the ring component with density less than 0.6 g/cc for groups of *Pinus pinaster* trees.

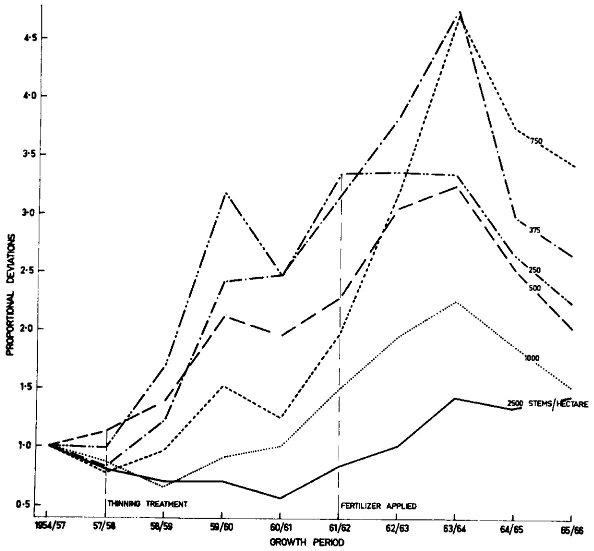


Figure 7. — The influence of thinning and fertilizer treatment on the proportional deviations from the mean for the period 1954 to 1957, of the means of the width of the ring component with density greater than 0.6 g/cc for groups of *Pinus pinaster* trees.

marked as the thinning intensity increases. A highly significant linear trend with the logarithm of thinning intensity is maintained for the next three growing seasons until the application of fertilizer in the 1961/62 season. The increase in width of the "early" wood component is maintained until the 1963/64 growth period but thereafter the width declines. The trend with the logarithm of thinning intensity however is non-linear during the last three growing seasons because of the disproportionate behaviour of the trees associated with the thinning intensity of 750 stems per hectare. The patterns for the ring component with density less than 0.5 g/cc are similar to those depicted in *Figure 6*. Reference to *Figure 3* shows that the patterns of "early" wood change are remarkably similar to those for the complete growth ring.

It may be seen from *Figure 7* that the previous remarks which are appropriate to the "early" wood would also generally apply to the "late" wood component. However in *Figure 7* there is a peak in the "late" wood width associated with the 59/60 growing season similar to, but less intense than that for average density which is shown in *Figure 5*. There is also a disproportionate tendency in the 1963/64 season to form thick walled cells in the trees from the plots thinned to 375 and 750 stems per hectare. The patterns for the ring component with density greater than 0.7 g/cc are similar to those set out in *Figure 7*.

If the ring components are considered as proportions of the growth ring, analysis reveals that for the component with density greater than 0.6 g/cc, the only effect of treatment is that the mean for the unthinned trees during the period 1962 to 1965 is significantly greater (5 per cent. level) than the mean for the thinned trees. For the component with density greater than 0.7 g/cc there is no significant effect of thinning or of thinning intensity. It is not unexpected that the treatments are found to have little effect when the ring components are considered on a proportionate basis as the influence of the treatments on the widths of the separate elements, viz. "early" wood, „late" wood and whole ring is similar.

Inspection of *Figure 1* which is the densitometric trace pertaining to a tree from a plot thinned to 375 stems per hectare provides some indication of the change in ring texture as a result of thinning and fertilizer treatment. The increase in ring width following thinning (February 1958), and to a much more marked degree after the application of fertilizer (September, 1961) is associated with an enhanced responsiveness to environmental changes and is manifest as deviations in density which are superimposed on the main annual pattern.

Conclusions

Substantial increases in stem diameter growth rate of the residual trees follow thinning and these increase with thinning intensity. However, even with the most intense thinning these responses could be augmented by treatment with super phosphate. It would be of interest to investigate the effect of a series of fertilizer applications to ascertain what improved rate of growth could be economically maintained by this means. It is interesting to note the disproportional response to the combined treatment which was seen in the trees from the plots thinned to 750 stems per hectare, and it would be of value to confirm the reasons for this excellent growth rate and to exploit fully the factors involved.

Apart from the effect on average tracheid length wood quality has not been adversely affected by the treatments. The silght decrease in mean density would not be harmful for most applications. Excluding the patterns associated with the plots thinned to 375 stems per hectare the thinning treatment has not been unduly detrimental to average tracheid length. The abrupt decrease in length following the application of fertilizer is the result of the related growth rate increase. This abrupt change can be alleviated by applying the fertilizer over a period rather than at one time but with consequent increase in the cost of application which could not be substantiated.

An interesting result of the work is the observation that improvements in growth rates resulting from these treatments are similar in both the early and late portions of the growing season.

Acknowledgements

The author wishes to thank the Conservator of Forests, Forests Department, Western Australia, for the wood specimens used in this study, and particularly Dr. E. R. Hopkins for supervising their collection.

Appreciation is also recorded of the assistance of Miss R. Logan and Mrs. J. Juricskay in the carrying out of the detailed measurements on which the results of the investigation have been based, and of the assistance of Miss N. Ditchburne, Division of Mathematical Statistics, C.S.I.R.O., in the statistical analyses and for helpful discussions relating to them.

Summary

Wood specimens from 60 trees of *Pinus pinaster* grown at Gnangara plantation, Western Australia were examined. These trees formed part of a thinning trial covering a range of thinning intensities from 2500 (unthinned) to 250 stems per hectare. Fertilizer was applied to the trees some 3½ years after thinning.

The effect on the wood of thinning and the interaction of thinning with fertilizer treatment was investigated. Stem diameter growth increased as a result of thinning and was further increased following the application of fertilizer. Neither treatment affected the incidence of spiral grain. Thinning generally reduced average tracheid length and the subsequent fertilizer treatment produced a marked reduction in this characteristic. The effect of the two treatments on the width of the ring components formed

in the early and the late part of the growing season was generally similar. The average density was slightly reduced as a result of the most intense thinning and fertilizer treatment.

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Statistical Validity of Single-Tree Plot in Forest Genetics Research

By E. C. FRANKLIN[1])

Single-tree plots have received much attention in recent literature, primarily because some researchers in forestry are proving to themselves what agricultural researchers were reporting over 40 years ago: that, because of the large amount of environmental variability on the average planting site, large block sizes result in poor statistical precision (WOOD and STRATTON 1910, BATCHELOR and REED 1918).

The single-tree plot permits minimum block sizes for a given number of entries in a complete block design. However, several arguments have been advanced against the use of single-tree plots. This discussion will center on several questions about the use of single-tree plots raised by SHIUE and PAULEY (1961) and EVANS *et al.* (1961). My purpose is to show that the theoretical arguments and experimental results presented by these authors can be interpreted in a way which suggests that the obstacles to the use of small-plot designs, single-tree plots in particular, are not as serious as is generally assumed. I am not arguing against or in favor of the use of single-tree plots, because the choice of plot size in forest genetics research usually involves many considerations other than those which are purely statistical (WRIGHT and FREELAND 1960).

Normality and Homogeneity of Error Variation

The major points made by SHIUE and PAULEY concerning plot size can be briefly summarized. In provenance and progeny tests, error variation consists of two parts: environmental and genetic. "Such genetic [error] variation, especially in the case of controlled pollination, is not necessarily distributed normally in the offspring" (SHIUE

[1]) The author is Associate Plant Geneticist at the Southeastern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Olustee, Florida.