WOOD PROPERTIES OF CLONAL RADIATA PINE GROWN IN SOILS WITH DIFFERENT LEVELS OF AVAILABLE NITROGEN, PHOSPHORUS AND WATER

J. MADDERN HARRIS, D. L. McCONCHIE and W. A. POVEY

Forest Research Institute, New Zealand Forest Service, Rotorua

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ABSTRACT

Cuttings of radiata pine were grown for six years in wooden containers set in the ground. Three clones were grown under seasonal water deficits (soil water potential —10 bars), but at other times natural soil moisture was maintained as necessary at a soil water potential of not less than —0.5 bars. Seasonal deficits were applied during the periods June-November, December-May or throughout the whole year June-May, using a factorial design. Two of the clones were also grown under four different soil nutrient conditions: (i) N deficient, (ii) P deficient, (iii) normal soil of average fertility, (iv) double topsoil with unrestricted root access to subsoil.

The effect of periodic moderate moisture stress on wood properties was to induce the formation of frequent narrow false rings. These increased minimum (earlywood) density, mean density and latewood ratio in the affected growth layers. Tracheids were also shorter in the outer growth layers of trees grown under moisture stress.

The effects of soil nutrient status on wood properties were small. Pith diameter was larger in the fast-growing trees in double topsoil than in the slow-growing trees with mineral deficiencies. The fast-growing trees also had slightly lower average wood density towards the base of the stem than the other three treatments. Phosphate deficiency produced high latewood density only in the outer growth layers.

Wood density, pith diameter and tracheid length differed consistently between clones. No effects, either clonal or environmental, were detected in development of spiral grain.

Because many of the apparent responses of wood properties to environmental stress appeared only in the outer growth layers of these young trees, it is suggested that, whenever possible studies of the physiology of xylem formation based on young-tree material should be extended to older trees in order to ensure that the same responses are obtained in outerwood formation.

INTRODUCTION

Numerous studies of radiata pine grown in New Zealand have demonstrated how widely wood properties vary under differing conditions of growth (Harris, 1965; Burdon and Harris, 1973; Cown, 1973, 1974). In approximate order of importance, the effects

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of formative age, genotype, climatic and edaphic factors, and silvicultural treatment can all be shown to influence wood properties in many ways.

Age of formation (cambial age) of the wood gives rise to the well-known gradients of wood properties from the pith outwards, so that corewood is always found to be less dense, weaker, and to contain shorter tracheids than the outerwood which is laid down later in stem development. This is the major source of variation and is easily recognised, but it is more difficult in field studies to relate overlying variations in either corewood or outerwood to the effects of environment or genotype respectively. Nor is it always simple to determine which are the most important environmental factors for practical purposes. Results often prove to be very dependent upon the system of sampling that has been used.

In an early survey of wood properties, covering 37 sites within the existing major forest areas of radiata pine, a very close correlation was found between outerwood density and mean annual temperature (Harris, 1965). Corewood density was found to be less closely, although also very significantly, correlated with mean annual temperature. It appeared that the only major deviations from these trends were to be found in forests where phosphate deficient soils resulted in wood that was denser than normal. Subsequently Cown (1977) analysed wood density and site data for 105 sites in New Zealand which had been extensively studied by Jackson and Gifford (1974). From this analysis it was concluded that wood density was most closely correlated with February temperature and July rainfall. Of the soil parameters measured, topsoil P, N and pH were the most important. Together with tree age, these factors accounted for 50% of the observed variation in wood density at any one stem position.

Quite obviously the original study which had been confined to major forested areas was inadequate to predict the responses of trees to the extremes of environment which were encountered in the more extensive study — and which may well be encountered in future plantings as forestry is required to extend its activity onto a wider range of sites. It is equally obvious that if controlled experiments are possible, these will provide better material for assessing the important environmental variables.

Looking to the future, the extension of exotic forestry into new areas, and the need to pay closer attention to the economics of silviculture, make it essential to gain a greater understanding of all wood formation processes and the various factors that influence them. If this is done wood properties can be predicted for harvests of all ages grown under all conditions. Equally it is necessary to understand the effects of environment on growth and form of trees. Two experiments set up in the grounds of FRI in 1967 were designed:

(a) to measure the effects of seasonal water deficits on the seasonal growth patterns of radiata pine cuttings from three different clones (Jackson *et al.*, 1976) and

(b) to study the effects of different N and P levels on the growth of two of these clones (Will and Hodgkiss, 1977).

During the six years of growth before trees were destructively sampled, some notable differences in growth patterns were observed (data from Jackson *et al.,* 1976; Will and Hodgkiss, 1977):

(i) Trees growing free of soil-water deficits continued to grow, in height and diameter, throughout the entire year. Height growth was fastest during spring (October/November), with a secondary peak of activity during autumn (March/April).

(ii) Drought imposed during winter/spring reduced height growth considerably in late spring, causing an apparent shift of peak growth; summer/autumn drought virtually eliminated the secondary peak of height increment.

(iii) Growth in diameter was most strongly reduced by drought imposed during summer/autumn.

(iv) Both N and P deficiencies restricted diameter growth of stem and of branches, but had less effect on stem height growth. Trees with unrestricted root growth obtained more nutrients, particularly N, and made greater stem diameter and branch growth, as well as about 10% greater height growth.

(v) Part of the decreased branch growth caused by N and P deficiencies resulted from reduction (or elimination) of the autumn flush of growth. These conditions tended to minimise retarded leader development, which was so severe in one clone when grown under high nutritional levels that leader dominance was completely lost.

(vi) N and P deficiencies resulted in shorter needles, and N deficiency in particular caused the foliage to become a lighter yellowish green.

This paper describes the wood properties of the radiata pine clones used in these experiments and examines responses in wood formation to the series of treatments imposed on trees of identical age and genotype. In describing the experiments Jackson *et al.* (1976) make the point that "It was assumed, from the outset, that there would be large clone × treatment interactions, and in the layout of the experiment clonal effects were deliberately confounded with anticipated positional effects in the plantation. This was done for reasons of economy, since the main objective was to determine the effect of . . . (treatment) . . . on the common growth pattern of selected genotypes."

MATERIAL AND METHODS

Full details of the experimental design and procedures have been given by Jackson *et al.* (1976) and Will and Hodgkiss (1977). Briefly, the trees used consisted of the three FRI clones, Nos. 450, 451 and 460 and these were planted out in 1967 as 27-month-old rooted cuttings into individual polythene-lined wooden containers set in the ground. After giving the trees one year to become established, experimental procedures were commenced in June 1968.

For the experiment dealing with seasonal soil water deficits the containers were evapotranspirometer units of 2.72 m^3 capacity spaced at 4 × 5 m. These were subjected to periodic water deficits by excluding rainfall completely from the surface of the unit (though not from the tree crown) for 6-12 months in each year. To prevent trees from dying during periods of high evapotranspiration, minimum soil moisture was maintained at 15% by volume, corresponding to a soil water potential of —10 bars. When a particular unit was not scheduled to be on a water deficit, soil moisture was allowed to fluctuate according to the amount of rain falling on the container. However, during natural drought periods soil moisture was not allowed to fall below about 40% by volume corresponding to a soil water potential of —0.5 bars.

The basic pattern of water deficits was a factorial design combining four treatments:

(i) No deficit throughout a year, June to May — (nil)

(ii) June to November (winter/spring) deficit — (w.s.)

(iii) December to May (summer/autumn) deficit — (s.a.)

(iv) Year-round deficit, June to May — (w.s.s.a.)

For the experiment dealing with nitrogen and phosphorus supply, only FRI clones Nos. 451 and 460 were used. Containers similar to those used in the soil moisture experiment were variously filled with:

(i) Sandy pumice subsoil and topsoil so as to replicate as nearly as possible the normal soil profile on the site;

(ii) Sandy pumice subsoil known to be deficient in N and P, brought in from an area 1 km away; in addition

(iii) Other open-bottomed containers with shallow sides (which therefore gave unrestricted root access to subsoil), had double the surface area of the closed containers, and thus contained double the amount of topsoil.

In January 1968 fertilisers were applied to maintain tree growth in the containers of subsoil ((ii), above), and to correct all but the deficient nutrient designated for each:

Low-N units — 10 g urea in January 1968 as a starter: 100 g superphosphate in January and October 1968, and 250 g each succeeding spring.

Low-P units — 30 g urea in January and October 1968 and 100 g each succeeding spring.

From each of the experimental trees, cross-sectional discs approximately 10 cm long and clear of branches were cut from the main stems at about the mid-point of every annual height increment. Selection of the correct sampling points was greatly facilitated by the detailed measurements that had been made on trees throughout the whole period of the experiment, and by the photographs of trees against a graticule background (Jackson *et al.,* 1976, Figs. 4-6; Will and Hodgkiss, 1977, Fig. 6). Wood samples therefore consisted of a series of discs from each tree, in the lowest of which were six annual growth layers. This number was reduced by one growth layer in each successive height increment until the final disc from the apical shoot consisted of a single year's growth.

The following measurements were then made to assess wood properties:

(i) Stem diameter inside bark, bark thickness and pith diameter were measured at each height increment.

(ii) Diametrically opposed sectors were cut from 2-cm discs at every height increment to measure wood basic density (oven-dry weight per volume green).

(iii) Radial strips of wood were prepared from the samples containing 5 and 3 annual growth layers, and these were conditioned to 10% moisture content for detailed measurement of wood density variations using the beta-ray densitometer (Harris, 1969).

(iv) Tracheid lengths of earlywood and latewood in every annual growth layer from the discs containing 5 growth layers were measured by the method of Harris (1966).

(v) Spiral grain was measured on the latewood of each annual growth layer in every sample from each tree (Nicholls, 1967).

In addition discs containing five annual growth layers were used to measure the effects of seasonal soil moisture deficits on tracheid dimensions in the 1970/71 growth layer. The regimes of moisture deficits, which were maintained by weekly watering as necessary to ensure that minimum soil moisture did not fall below 15% by volume, produced sequences of very delicate false rings resulting in an almost lamellate appearance (cf. Barnett, 1976; Jackson *et al.,* 1976, Fig. 7). This was especially noticeable in trees that had been subjected to year-round deficit.

The strips of wood prepared for densitometry were used to measure radial diameter and tangential wall thickness on 30 tracheids in each of four zones within the 1970/71 growth layer, following the method of Cown (1975). One measurement zone was five cells in from the earlywood boundary; one was five cells in from the latewood boundary; and two were located 30 cells to either side of the November/December "treatment boundary" as estimated from growth measurements made at the time.

RESULTS

Growth, Stem Morphology and Mean Wood Density Within Discs

The results summarised in Table 1 compare some features of the growth and mean wood density at each annual height increment for the three clones used to study the effects of seasonal drought. In addition, combined results for the two clones 451 and 460 are included to illustrate the effects of soil nutrient status.

Mean wood density: Clone 451 produces denser wood at all levels in the stem than clones 450 and 460. Apart from this, the various treatments had remarkably little effect: only the lower discs from the trees grown in double topsoil stand out as having low wood density.

Stem diameter: Here too the effects of treatment are less than might be expected. The vigour of trees grown in double topsoil is immediately apparent, as are the effects of phosphate deficiency in reducing diameter growth, but periodic drought treatments have apparently had little effect on stem diameter. In fact trees grown under moisture stress from June to November showed a surge of growth when re-watered in December that more than restored any reduction in increment. As Jackson *et al.* (1976) point out, "This is a curious result, and would appear to indicate that a rainfall regime with a dry spring and wet summer and autumn is more favourable for maximum basal area increment than one with good rainfall distributed throughout this period."

Bark thickness: In these young trees there is little difference in the thickness of the smooth bark that covers most of the stem, but both moisture stress and low nutrient status seem to have produced thinner bark at the butt than in the unstressed trees growing in normal soil or double topsoil.

Pith diameter: Clone 460 has slightly smaller pith than clones 450 and 451. In other respects it is clear that the most vigorous growth produces the largest pith, and amongst the stressed trees those growing in nitrogen-deficient soils have the smallest pith.

Grain angle: No consistent effects of treatment show up in grain angles.

Densitometry

Table 2 summarises measurements made with the beta-ray densitometer on samples cut from the disc containing five annual growth layers. It should be noted that the wood properties of different trees are recorded to illustrate the effects of a particular soil moisture regime over a series of treatment periods. Thus a tree on water deficit from June to November in one year might have been switched to supplemented water supply in the following year, during which time another tree of the same clone would have been used to illustrate the effects of water deficit. However, one member of each of the three clones was involved in each of the four treatments during any one period, so that clonal *representation* in a particular treatment was continuous throughout the experiment.

TABLE 1—Comparison of wood properties between three clones under periodic water stress and two clones in soils of different nutrient status

Wood Property	Clone*	Treatment	Measured at annual height increment					
			1	2	3	4	5	6
Basic Density (Kg/m^3)	450	I.s.d.	355	339	332	327	309	289
	451	I.s.d.	394	379	362	348	335	338
	460	I.s.d.	352	351	353	342	327	303
	C	Normal soil	372	362	361	335	327	296
	C	P deficient	378	360	336	324	312	280
	C	N defiicient	377	361	348	332	316	285
	C	Double topsoil	338	352	354	337	325	291
Stem Diameter (mm)	450	I.s.d.	161	128	111	83	55	32
	451	I.s.d.	167	131	105	73	50	30
	460	I.s.d.	155	122	100	79	51	28
	C	Normal soil	169	121	96	66	40	26
	C	P deficient	105	98	87	64	42	24
	C	N deficient	142	126	102	83	58	30
	C	Double topsoil	216	176	150	110	74	31
Bark Thickness (mm)	450	I.s.d.	6	4	3	3	2	2
	451	I.s.d.	9	5	4	3	2	2
	460	I.s.d.	6	4	4	3	2	2
	C	Normal soil	12	4	3	2	2	2
	C	P deficient	7	4	2	2	2	2
	C	N deficient	5	2	2	2	2	2
	C	Double topsoil	10	5	5	4	4	2
Pith Diameter (mm)	450	I.s.d.	2	5	7	8	8	10
	451	I.s.d.	3	5	6	8	9	8
	460	I.s.d.	2	4	4	6	6	6
	C	Normal soil	2	6	4	6	8	8
	C	P deficient	2	3	5	6	6	7
	C	N deficient	1	2	4	4	4	4
	C	Double topsoil	2	6	6	8	10	7
Grain Angle (°)	450	I.s.d.	5	7	5	5	4	3
	451	I.s.d.	6	5	5	5	4	4
	460	I.s.d.	6	8	6	4	2	2
	C	Normal soil	3	5	6	4	3	0
	C	P deficient	7	7	7	7	5	3
	C	N deficient	6	6	6	4	3	4
	C	Double topsoil	6	8	8	6	5	4

* Clones 450, 451 and 460 — averages for four trees in each clone.

C Results for clone 451 and 460 combined.

I.s.d. Intermittent seasonal drought.

In relating wood density to treatment at the time of wood formation, the minimum value will occur within the period June-November, whereas maximum density occurs in cells laid down in December-May, even though secondary thickening in the latewood might not have been completed until the following August (Barnett, 1971).

TABLE 2—Average* densitometric values (at 10% moisture content) for each annual increment in discs containing five annual growth layers

Densitometric Parameter	Treatment†	Density (kg/m³) at growth layer from pith 2	3	4	5
Mean Wood Density	Nil	380	410	390	440
	w.s.	370	390	450	450
	s.a.	410	430	400	440
	w.s.s.a.	410	460	470	480
	Normal	390	420	420	480
	P—	400	440	440	480
	N—	380	440	440	460
	Double	400	400	420	440
Minimum (Earlywood) Density	Nil	300	320	320	330
	w.s.	300	320	370	360
	s.a.	310	310	320	330
	w.s.s.a.	330	350	380	370
	Normal	320	300	340	360
	P—	310	350	340	340
	N—	320	340	340	360
	Double	340	360	340	350
Maximum (Latewood) Density	Nil	560	590	630	640
	w.s.	540	540	660	610
	s.a.	600	600	630	620
	w.s.s.a.	550	600	640	620
	Normal	540	560	600	600
	P—	560	620	680	690
	N—	540	630	640	620
	Double	510	560	620	580
Latewood Ratio	Nil	0.33	0.34	0.23	0.34
	w.s.	0.33	0.28	0.27	0.37
	s.a.	0.33	0.41	0.27	0.38
	w.s.s.a	0.37	0.46	0.34	0.42
	Normal	0.32	0.44	0.32	0.52
	P—	0.38	0.34	0.31	0.37
	N—	0.28	0.36	0.30	0.38
	Double	0.44	0.25	0.30	0.36

* Soil moisture treatments: average of one tree from each of three clones
Soil nutrient treatments: average of one tree from each of two clones.

† Treatment: Nil = No moisture deficit; w.s. = winter/spring deficit; s.a. = summer/autumn deficit; w.s.s.a = year-round deficit; normal = normal soil; P— = phosphate deficient; N— = nitrogen deficient; double = double topsoil, unrestricted root growth.

Mean wood density within growth layers: High mean density values are associated with year-round soil moisture deficits which have already been noted as producing multiple false rings. Lower density has been produced by the "nil" treatment in which rainfall was supplemented as necessary to prevent moisture stress.

Minimum earlywood density: Year-round deficits also produce the highest earlywood density. Here again the periodic interruptions of growth that give rise to false rings have obviously affected the full expression of vigorous earlywood development in which minimum density values normally occur.

Maximum latewood density: This parameter does not show any response to year-round water deficit: although multiple rings interrupt earlywood formation and increase mean density, neither they nor the terminal latewood give rise to wood that is denser than normal. On the other hand it is well known that phosphate deficiency increases latewood density (Harris, 1967) and it is noticeable that growth layers 4 and 5 in the low-P treatment have the highest values recorded.

Latewood ratio: The scale of this experiment was not large enough to produce reliable values for latewood ratio (Harris, 1969), but year-round water deficit shows up, as expected, with consistently high values. It is also interesting to note that all values for ring 4 are lower than the average of the two adjacent rings. Polge (1965) was one of the first to suggest that such deviations in density parameters from year to year can be correlated with climatic variables — in this case "climatic variables" which, surprisingly, have not been over-ridden by periodic drought treatments.

Densitometry of radial strips cut from discs containing three annual growth layers gave similar results. Latewood density was highest in the outer growth layer of the low-P treatment, and year-round moisture deficits resulted in high minimum density, mean density and latewood ratio.

Specific examination of the effects of moisture stress on the 1970/71 growth layer confirmed many of the general findings. The range of density within this annual growth layer was least for treatments in which moisture stress had been imposed over the period June/November. This was mainly a consequence of the high minimum (earlywood) densities already referred to in these treatments. Trees that were droughted during December/May did not show an equivalent increase in latewood density. Densitometer records for the extreme treatments (supplementary watering compared with year-round deficit) using Clone 451 are illustrated in Fig. 1.

Wood Anatomy

Tracheid length: Clone 460 tended to produce shorter tracheids than clones 450 and 451 (Table 3). Differences in tracheid length between treatments are small and inconsistent over the first three years' growth, but in year 4 and 5 the trees grown in double topsoil have consistently produced shorter tracheids than the trees grown under conditions of nitrogen or phosphate deficiency. During the same period trees grown with supplementary watering throughout the year have produced longer tracheids than trees grown under soil moisture deficits throughout the year. Similarly the more detailed examination of development within the 1970/71 growth layer (Table 4) also shows how moisture stress has generally resulted in shorter tracheids, especially in the latewood.

Transverse cell dimensions: The effects of treatment on tangential double-wall thickness

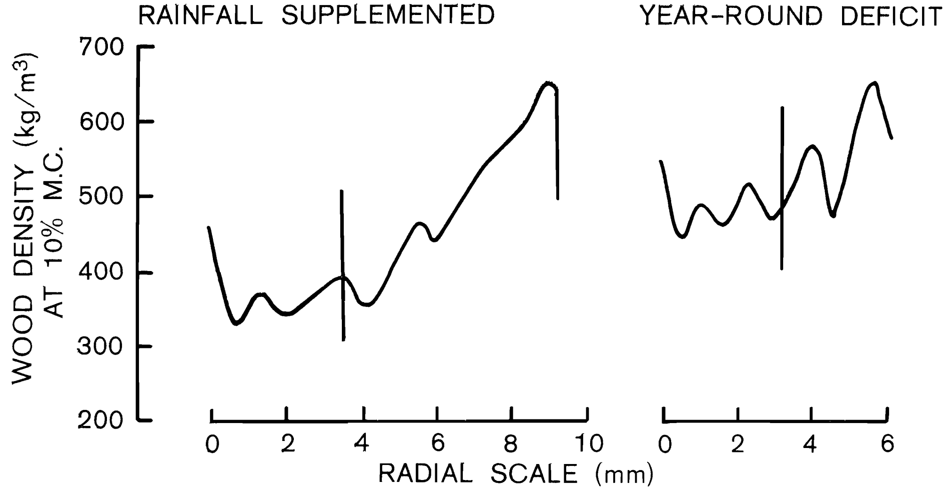

FIG. 1—Wood density across the 1970/71 growth layer; Clone 451

and radial cell diameter within the 1970/71 growth layer are summarised in Table 5. It was a feature of all three clones that trees receiving supplementary watering did not produce greatest cell wall thickness in the latewood but at the third measuring point, 30 cells from the November/December "treatment boundary". In all other treatments there was a strong tendency for wall thickness to reach maximum values in the latewood and this was so for all three clones when subject to moisture stress in the June/November period. It is difficult to explain this apparent difference between trees grown free of moisture stress and trees that had recently "recovered" from moisture stress. It may be that this feature, too, was associated with the surge of radial growth that followed re-watering.

Trees stressed in June/November also produced cells of greatest radial diameter in latewood (Table 4), and these cells were significantly larger than those in the December/ May deficit and the supplementary watering treatments (Duncan's multiple range test at the 5% level of significance). The moderate moisture stresses applied in this experiment did not, however, at any time reduce cell diameters to the degree found in false rings formed during high moisture stress under natural conditions (Jenkins, 1974). Supplementary watering did have the effect of producing cells with significantly greater radial diameter than those in the other three treatments when measured at the third point, 30 cells outside the treatment boundary.

DISCUSSION

Although none of the clones used in these experiments had been selected for their wood properties, clone 451 consistently produced denser wood than the other two, and clone 460 produced narrower pith and shorter tracheids.

Several of the effects of treatment on wood properties can be related to rate of growth. For example, rapid circumferential growth requires more frequent anticlinal division in the cambium and these tend to reduce tracheid length. Consequently shorter tracheids were formed in response to vigorous growth by trees growing in double

TABLE 3—Tracheid length in earlywood and latewood for each annual increment in discs containing five annual growth layers

Clone No.	Treatment	Tracheid length (mm) at growth layer from pith									
		1		2		3		4		5	
		ew	lw	ew	lw	ew	lw	ew	lw	ew	lw
450	Rainfall	1.5	1.6	1.6	2.0	2.2	2.2	2.4	2.8	2.9	3.2
451	supplemented	1.4	1.7	1.9	1.8	2.1	2.2	2.6	2.5	2.6	3.0
460	(Nil)	1.6	1.6	1.7	1.9	1.8	1.9	2.1	2.2	2.4	2.6
Average		1.5	1.6	1.7	1.9	2.0	2.1	2.4	2.5	2.6	3.0
450	June/November	1.6	1.7	1.8	2.1	2.1	2.3	2.1	2.4	2.6	2.9
451	deficit	1.5	1.8	1.7	2.2	2.2	2.3	2.2	2.4	2.5	2.7
460	(w.s.)	1.3	1.4	1.6	2.0	1.7	2.2	1.7	2.1	2.1	2.6
Average		1.4	1.6	1.7	2.1	2.0	2.3	2.0	2.3	2.4	2.7
450	December/May	1.4	1.6	2.0	2.0	1.9	2.0	2.4	2.5	2.3	2.5
451	deficit	1.5	1.6	1.8	2.2	1.9	2.0	2.2	2.3	2.5	2.6
460	(s.a.)	1.4	1.6	1.6	1.9	1.8	1.7	1.9	2.3	2.4	2.4
Average		1.4	1.6	1.8	2.0	1.9	1.9	2.1	2.4	2.4	2.5
450	Whole-year	1.2	1.7	1.9	2.2	2.0	2.2	2.4	2.1	2.2	2.5
451	deficit	1.6	1.7	1.7	2.1	2.1	2.2	2.2	2.3	2.4	2.6
460	(w.s.s.a.)	1.4	1.5	1.5	2.0	1.7	1.9	1.8	2.0	2.2	2.3
Average		1.4	1.6	1.7	2.0	1.9	2.1	2.1	2.1	2.2	2.5
451	Normal soil	1.4	1.5	1.6	2.0	2.2	2.2	2.3	2.4	2.6	2.8
460		1.2	1.4	1.5	1.8	1.8	1.9	1.9	2.1	2.3	2.3
Average		1.3	1.4	1.6	1.9	2.0	2.0	2.1	2.2	2.4	2.6
451	P. deficient	1.4	1.6	1.6	1.8	1.8	2.1	2.2	2.5	2.4	2.7
460	(P—)	1.5	1.6	1.5	2.2	1.9	2.3	2.5	2.5	2.5	2.5
Average		1.4	1.6	1.6	2.0	1.8	2.2	2.4	2.5	2.4	2.6
451	N. deficient	1.3	1.5	1.7	2.0	2.0	2.3	2.2	2.5	2.6	2.7
460	(N—)	1.4	1.6	1.9	2.9	1.8	2.2	2.5	2.7	2.7	3.1
Average		1.4	1.6	1.8	2.0	1.9	2.2	2.4	2.6	2.6	2.9
451	Double topsoil	1.4	1.5	2.0	2.1	2.3	2.0	2.2	2.3	2.3	2.5
460		1.4	1.4	1.6	1.6	1.7	2.0	2.0	2.2	2.1	2.2
Average		1.4	1.4	1.8	1.8	2.0	2.0	2.1	2.2	2.2	2.4

topsoil. On the other hand moisture stress reduces tracheid length, and trees growing with supplementary watering produced longer tracheids. This probably reflects the role of turgor pressure in tracheid elongation.

In trees grown under stress, whether from periodic soil water deficits or nutrient deficiency, pith diameters were smaller (particularly on nitrogen deficient soils) and bark at the base of the stem was thinner.

TABLE 4—Tracheid length (mm) within the 1970/71 growth layer

Clone No.	Treatment	Earlywood 1	2	3	Latewood 4
450	Rainfall	2.1	2.1	2.3	2.2
451	supplemented	2.1	2.2	2.4	2.3
460	(Nil)	1.7	1.7	1.9	2.1
Average		2.0	2.0	2.2	2.2
450	June/November	2.0	1.9	2.2	2.4
451	deficit	2.1	2.1	2.2	2.3
460	(w.s.)	1.6	1.8	2.1	2.2
Average		1.9	2.0	2.2	2.3
450	December/May	2.2	2.3	2.5	2.2
451	deficit	2.0	2.0	2.1	2.0
460	(s.a.)	1.8	1.8	2.1	2.0
Average		2.0	2.0	2.2	2.1
450	Whole-year	2.0	2.0	2.0	2.1
451	deficit	2.1	2.0	2.2	2.0
460	(w.s.s.a.)	1.9	1.8	2.0	2.1
Average		2.0	2.0	2.0	2.1

* Zones 2 and 3 were located 30 cells on each side of the "treatment boundary" — see Methods section.

TABLE 5—Tracheid double-wall thickness and radial diameter

Measurement areas (cf. Table 4)	Wall Thickness µm	Cell Diameter µm	Thickness Diameter %	Wall Thickness µm	Cell Diameter µm	Thickness/ Diameter %
		Nil Deficit			December/May Deficit	
1 Earlywood	6.3	34.9	18	6.6	32.5	20
2	6.4	40.3	16	6.0	40.1	15
3	6.9	42.0	16	6.0	37.2	16
4 Latewood	6.5	18.9	35	7.1	16.8	42
		June/November Deficit			Whole-Year Deficit	
1 Earlywood	5.9	35.1	17	6.4	30.8	21
2	6.5	42.5	15	6.3	32.6	19
3	6.0	39.4	15	6.4	31.2	21
4 Latewood	7.3	25.9	28	7.3	20.3	36

The most marked effect of moisture deficits on wood properties was the development of false rings, especially in trees grown under whole-year deficits. This treatment increased minimum (earlywood) density, mean density and latewood ratio within the annual growth layer. On the other hand when drought applied in the period June/November was relieved by watering in December, this had some curious and apparently long-term effects on the properties of wood laid down in the remainder of the growing season. These effects might be regarded as experimental artifacts were it not for the observation by Jackson *et al.* (1976) that cross-sectional increment is apparently greater following dry spring conditions than when rainfall is evenly distributed throughout the growing season. In trees subjected to moisture stress in June/November, cross-sectional increment catches up with that of unstressed trees during the period December/May, tracheid wall thickness continues to increase right into the latewood, and latewood tracheids are also wider than those formed under the other treatments.

Another feature of interest in these young trees was the reduced latewood ratio in the outermost growth layer but one, and the fact that this low value was consistent in all treatments whether soil moisture deficits had been applied or not. The development of latewood is often regarded as being strongly influenced by soil moisture levels (e.g. Dobbs, 1953, Paul, 1963, Lassen and Okkonen, 1969), but these results clearly indicate that other factors can exercise some control over latewood ratio whether trees are growing under moisture stress or not.

Finally, there are several features of wood development in these experiments which suggest that response to environment changes as trees grow older. An obvious example is the development of high latewood density in trees growing on phosphate deficient soils. Only the outer two growth layers show this effect. If the trees had been growing under field conditions it might have been suspected that they had exhausted available phosphorus over the first three years and that deficiency symptoms developed thereafter. In these experiments, however, phosphate deficiency which was measured at the outset (Will and Hodgkiss, 1977), had not increased significantly at the conclusion of the experiment (P. D. Hodgkiss, pers. comm.) and yet the response has still been delayed.

Similarly, response of tracheid length to treatment becomes apparent only in the outer growth layers. These observations suggest the possibility that the balance of physiological factors controlling wood properties changes with increasing cambial age, and are in agreement with previous observations that quite different correlations are obtained between environmental factors and the wood properties of corewood or outerwood (Harris, 1965; Cown, 1977). If this is so. then studies of the physiology of xylem formation based on young tree material, should, whenever possible, be extended to older trees in order to ensure that the same responses are obtained in outerwood formation.

CONCLUSIONS

The effects of soil nutrient status and periodic moisture stress on wood properties of eight-year-old radiata pine were quite minor. Although trees grown in double topsoil with unrestricted root development were very vigorous compared with those grown in containers under conditions of N and P deficiency, differences in wood properties were not marked. Pith diameter differed between clones and also directly related to tree vigour. Trees growing in N deficient soils had the smallest pith. Mean basic density was slightly lower in the butt sections of trees growing in double topsoil but the expected response of high latewood density under conditions of P deficiency was apparent only in the outer growth layers.

The chief effect of moderate moisture stress was to induce the formation of a number of fine false rings. These increased minimum (earlywood) density values in the affected growth layers, and also increased mean density and latewood ratio. Moisture stress also resulted in the production of shorter tracheids, especially in latewood.

Several of the expected effects of environment on wood properties seemed only to be beginning to show up in the outer growth layers of these eight-year-old trees. This raises the issue of different levels of response to environment in corewood as compared with outerwood (or for xylem produced by cambium of increasing age). It is therefore suggested that, wherever possible, evaluation of xylem development and physiology based on young trees should be confirmed for trees well beyond the seedling or juvenile stage before results are applied to problems of outerwood formation.

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