COMPRESSION WOOD IN *PINUS RADIATA* CLONES ON FOUR DIFFERENT SITES

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ABSTRACT

Compression wood as indicated by opacity to light was studied in 18 **Pinus radiata** clones replicated within and between four different sites. At all sites it was more prevalent in the lower bole. Differences between sites in compression wood occurrence could be related to exposure, toppling of trees after planting, and the presence of leaning trees at stand margins. It is suspected that soil phosphate deficiency reduced compression wood formation at one site. The percentage of compression wood, including very mild grades, was typically 30-45%, but differences between sites and up the stem occurred more in the amount of severe compression wood.

Between ramets of a clone at a single site the sum of lean and butt sweep up to 4.25 m from the ground was more closely related to compression wood rating than any other measured crookedness parameter.

The clones differed in propensity to form compression wood. Stems that are initially very straight or very crooked will apparently contain either little or abundant compression wood respectively. However, moderately crooked stems may straighten with strongly developed compression wood or, at the other extreme, remain crooked with only slight compression wood, depending on genotype.

At no site were sinuosity and compression wood correlated, within or between clones.

INTRODUCTION

Compression wood in conifers is normally formed in response to deviations of the shoot from the vertical. As Shelbourne *et al.* (1969) remarked, this invites the assumption that the response to a given deviation would be roughly constant between genotypes and between environments. In turn we would expect any heritable variation in compression wood formation to be a consequence of inheritance of stem crookedness.

Recent work, however, suggests otherwise. Low (1964a) obtained no close relationship between percentage of compression wood and stem deviation in *Pinus sylvestris.* Moreover, studies with young *P. taeda* (Shelbourne, 1966; Shelbourne *et al.,* 1969; Shelbourne and Stonecypher, 1971) did not reveal the expected positive association between total percentage of compression wood and stem deviations, although such a relationship was observed with respect to the percentage of severe compression wood.

On the contrary, compression wood percentage appeared to be highly heritable in itself, more so than stem straightness.

Compression wood can vary widely in severity, and its technical significance presumably depends on the severity. Certain wood properties appear to diverge progressively from those of normal wood with increasing visual grade of compression wood (Low, 1964b; Shelbourne and Ritchie, 1968), but Shelbourne and Ritchie observed an abrupt increase in cell wall checking in summerwood as visual rating increased from mild to severe. Hence, it is preferable, in any study of compression wood incidence, to recognise different grades of severity.

This paper reports a study of compression wood occurrence in a clonal trial with *P. radiata* D. Don, investigating the influence of genotype and site.

MATERIAL AND METHODS

The Experiment

This is described fully elsewhere (Burdon, 1971). Eighteen clones were replicated as cuttings within and between four sites, at Glenbervie, Whakarewarewa (Whaka), Gwavas, and Berwick State Forests. Out of the 72 possible clone-site subclasses 13 were missing, and the number of surviving ramets (trees) within the remaining subclasses ranged from one to six. A destructive assessment was made 12 years after planting.

Exposure varied considerably, being least at Glenbervie and greatest at Gwavas, where one margin of the plot was almost fully exposed to the prevailing wind. At Whaka the tree tops eventually became exposed. Incomplete surround plantings meant that some experimental trees were growing at the stand margin at Whaka, Gwavas and Glenbervie. The Whaka site was flat, others were on slopes of about 20°.

The soils differed widely in both physical properties and fertility. At Whaka and Gwavas they were sandy loams. At Glenbervie there was a clay distinguished by very low fertility, the trees growing poorly and showing typical symptoms of severe phosphate deficiency. The soil at Berwick was a loess-derived clay loam, prone to becoming waterlogged and soft in winter, with the result that many of the trees toppled after planting (J. Barber, pers. comm.).

Assessment

Before felling, lean, butt sweep, stem sinuosity and stem sweep (referred to collectively as crookedness parameters) were recorded on each tree.

Butt sweep and lean were reckoned as the net stem deviation below breast height (1.4 m), and lean between breast height and 4.25 m respectively. These deviations were measured by suspending a plumb line from the lower bark surface at the top of the appropriate part of the stem, and recording the horizontal distance between the plumb line and the bark surface at the bottom. For butt sweep this was done above any flare associated with the emergence of roots. On this basis the measurements underestimated true values by half the above-bark stem taper plus the amounts of any stem over-correction.

Stem sinuosity and stem sweep were both scored subjectively by three independent observers, recording very straight as 1, and extremely crooked as 9 (Burdon, 1971).

At felling 5 cm-thick discs were cut from the following points (cf. Burdon and Harris, 1973):

(1) breast height
(2) t_9 (i.e., nine annual growth stages down from the top of the tree), provided this was more than 0.6 m above breast height;
(3) t_7
(4) t_5

All discs were taken clear of nodal swellings, obvious compression wood associated with branch clusters, and stem deformation associated with leader breakage or dieback near the sampling point. Badly suppressed and toppled trees were rejected. From each disc another disc was cut as close as possible to 3 mm thick.

Discs were examined for compression wood using transmitted light (Pillow, 1941). Each disc was placed over a light box and kept fully moist. Compression wood appeared opaque and reddish and six visual grades of severity, denoted 0-5, were recognised:

0. Normal wood
1. Latewood patchily opaque
2. Latewood generally opaque
3. Latewood opaque, earlywood partly opaque
4. Latewood and earlywood generally opaque
5. Latewood and earlywood highly opaque

Boundaries and grades of compression wood zones were marked with indelible pencil. Zones of compression wood of widely different grades were often abutting. Where part of a disc contained numerous small patches of compression wood an average grade was assigned.

A glass plate was then placed over each disc. The disc circumference and compression wood boundaries and grades were traced on translucent paper of gauged weight. The tracing of each zone was cut out and the cross-sectional area of a zone was measured as the weight of its paper tracing (cf. Naylor, 1956).

For each disc the following parameters were calculated:

(1) Percentage total compression wood
(2) Percentage (of disc) "severe" compression wood (Grades 3, 4 and 5)
(3) Compression wood rating, namely

$$\frac{\Sigma (A \times G)}{B.A.}$$

where A = cross-sectional area of compression wood zone,
G = compression wood grade of that zone,
and B.A. = cross-sectional area of entire disc.

The last of these parameters is regarded as the most meaningful single expression of compression wood incidence.

Corresponding parameters for whole trees were estimated by summing the $\Sigma (A \times G)$ values for the breast height, t_7, and t_5 discs and dividing by the sums of the B.A. values. Trees with breast height discs missing were discarded for calculations of whole tree ratings. In those few with either t_7 or t_5 discs missing whole tree values were calculated on the basis of the two available discs.

Analysis

A two-way unbalanced analysis of variance (method of fitting constants—Snedecor, 1956, 12.17) of tree compression wood rating was used to test for differences between sites and between clones over all sites, and for clone-site interactions. Differences between sites in the residual error variances, together with the imbalance of the classification made this analysis subject to bias, particularly in respect of main effects. Accordingly, efforts were concentrated on analysing the data for one site at a time.

Within-clone relationships between whole tree compression wood parameters and crookedness parameters were studied as pooled (or average) within-clone regressions (*see* Burdon and Low, 1973). With the small clone-site subclasses multiple regression analysis was not practicable, so main interest lay in the single crookedness parameter best related to compression wood rating.

Clonal differences were tested by analysis of variance, from which clonal repeatabilities at each site were calculated as $V_C/(V_C + V_E)$, where V_C is the between-clones component of variance and V_E is the ramets-within-clones or error component (Burdon, 1971). Clonal differences in compression wood parameters are normally regarded as genotypic in origin. Assuming this, and if the clones are a random population sample, the repeatabilities may be accepted as broad-sense heritabilities.

Using the pooled within-clone regressions as the basis of a covariance correction to the between- and within-clones sums of squares for compression wood rating, the clonal repeatabilities for this rating could be obtained with an adjustment for variation in crookedness between individual trees. Clonal means adjusted thus for crookedness were also calculated.

For the regression analyses and the repeatability analyses clones with only a single value at a site were discarded, for that site.

Clonal (genotypic) correlations between characters were calculated from clonal components of variance and covariance as

$$W_{C_{(xy)}} \Big/ \sqrt{V_{C_{(x)}} \cdot V_{C_{(y)}}}$$

where $W_{C_{(xy)}}$ is the between-clones covariance component between the characters x and y, and $V_{C_{(x)}}$ is the between-clones variance component for x. The covariance components are calculated from mean cross-products in the same way as variance components are calculated from mean squares.

For purposes of presentation site means were taken as the average of all trees without regard to clonal classification. Despite the imbalance this procedure gives acceptable comparisons of sites provided clonal differences are not large.

RESULTS

General Pattern of Occurrence

Results are set out in Fig. 1. The strong development of compression wood in the lower stem is particularly evident.

Site means and coefficients of variation (means divided by standard deviations) for whole tree compression wood parameters are listed in Table 1. In respect of compression wood rating Glenbervie stands apart from the other sites; the overall analysis of

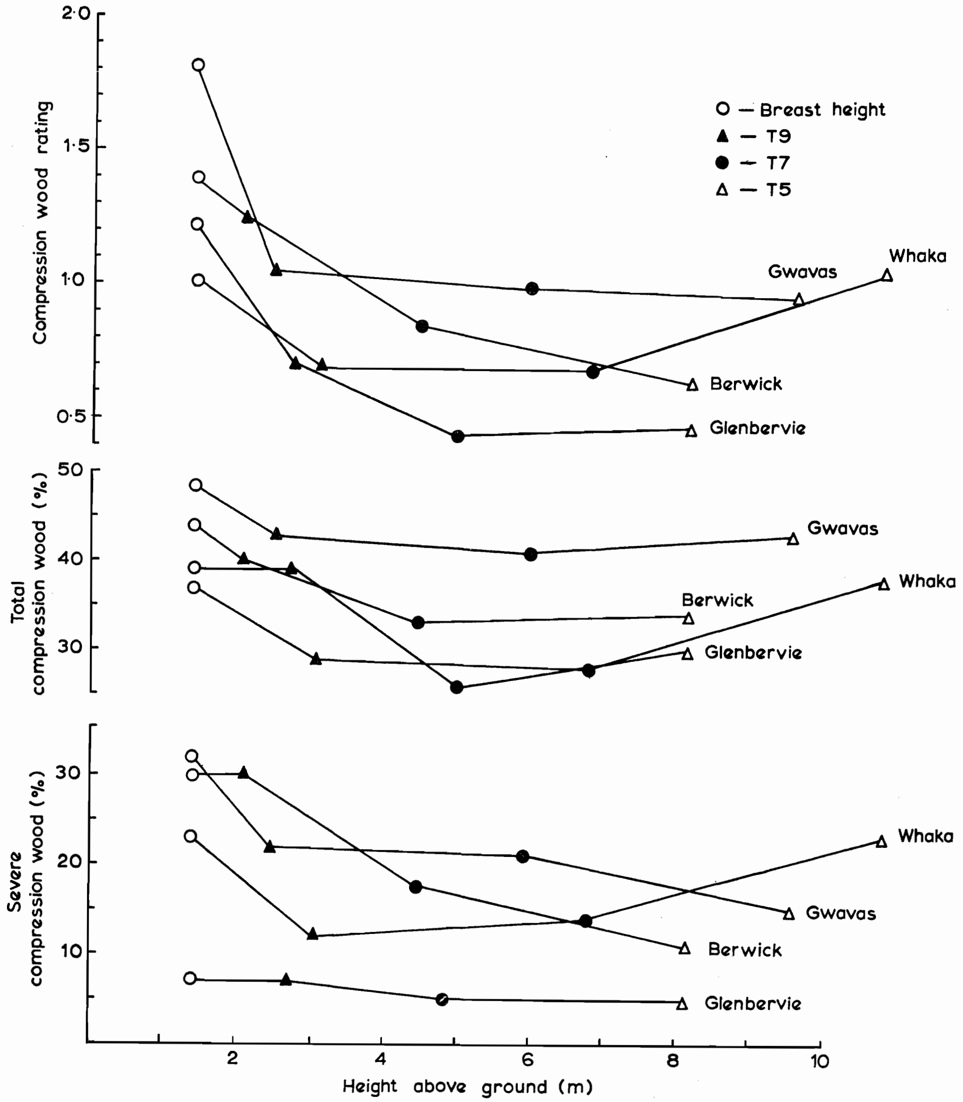

FIG. 1—Mean values for compression wood parameters at successive sampling points up the stem, by sites

variance (subject to reservations mentioned earlier) indicated very clear-cut site differences when this site was included ($P < 0.001$) but none at all when it was omitted ($F < 1$). Among trees percentage of severe compression wood varied more than percentage of total compression wood; many contained little or no severe compression wood, but a few contained large amounts. Among sites Gwavas showed the least tree-to-tree variability.

TABLE 1—Site means and coefficients of variation for tree compression wood parameters

Statistic	Compression wood parameter	Site: Glenbervie	Whaka	Gwavas	Berwick
Mean	Compression wood rating	0.60	0.94	1.15	1.09
	Percentage severe compression wood	6	23	25	22
	Percentage total compression wood	34	37	44	38
Coefficient of variation %	Compression wood rating	41	47	21	40
	Percentage severe compression wood	99	66	54	71
	Percentage total compression wood	27	27	20	27

Crookedness and Non-genetic Relationships with Compression Wood

Table 2 lists site means for each class of objectively measured stem deviation with corresponding coefficients of variation. At Berwick, in particular, and to lesser extent Whaka, the frequency distribution of lean classes was positively skewed, with a few stems showing especially large deviations from the vertical. This is reflected in high coefficients of variation.

At Gwavas, both lean and butt sweep were consistently orientated with the prevailing wind. At Berwick only the slight cases were so orientated, the rest being haphazard. Because sinuosity and sweep were assessed subjectively, rigorous comparisons between

TABLE 2—Site means and coefficients of variation for crookedness parameters

Statistic	Site	Crookedness parameter (cm deviation from vertical): Butt sweep	Lean	Lean plus butt sweep
Mean	Glenbervie	7.04	15.29	22.33
	Whaka	8.00	21.01	29.01
	Gwavas	10.08	16.23	26.31
	Berwick	8.53	11.74	20.27
Coefficients of variation %	Glenbervie	56	30	40
	Whaka	55	89	53
	Gwavas	59	42	40
	Berwick	58	124	64

sites could not be made for these characters. However, the general impression was that stems were straightest at Glenbervie and least so at Whaka and Gwavas, roughly in inverse relation to vigour.

From Tables 1 and 2 it can be seen that at the level of site means, compression wood rating closely parallelled butt sweep but not lean.

At Gwavas eight of the trees studied had grown at the stand margin, fully exposed to the prevailing wind. Despite this they had much less ($P < 0.01$) lean plus butt sweep than the remainder, the means being 14.5 cm and 26 cm respectively, as the effect of the wind had been largely offset by the tendency of edge trees to lean outwards. However, mean compression wood ratings for the two groups were identical. For further analyses these eight marginal trees were discarded.

To consider the relationship within sites Table 3 shows coefficients of determination (R^2), by sites, for the pooled within-clone regressions of compression wood rating on crookedness parameters and on breast height diameter over bark (d.b.h.o.b.). In general, the largest percentage of variation in compression wood rating is accounted for by lean plus butt sweep. This regression is significant ($P < 0.05$) at all sites except Glenbervie. For further analysis lean plus butt sweep was accepted as the best available measure of stem crookedness.

TABLE 3—Coefficients of determination (R^2), by sites, for pooled within-clone regressions of tree compression wood rating on crookedness parameters

Site	Independent variable					
	Lean	Butt sweep	Lean plus butt sweep	Stem sweep	Sinuosity	D.b.h.o.b.
Glenbervie	0.16 N.S.	0.00 N.S.	0.14 N.S.	0.28*	0.13 N.S.	0.36*
Whaka	0.27**	0.21*	0.36**	0.18*	0.02 N.S.	0.11 N.S.
Gwavas	0.15 N.S.	0.09 N.S.	0.23*	0.16 N.S.	(–) 0.04 N.S.	(–) 0.02 N.S.
Berwick	0.14*	0.26**	0.38***	0.07 N.S.	0.00 N.S.	(–) 0.07 N.S.

NOTE: N.S. denotes not significant, $P > 0.05$
* denotes significant, $P < 0.05$
** denotes highly significant, $P < 0.01$
*** denotes very highly significant, $P < 0.001$
Minus sign in brackets indicates negative regression

Although the subclasses were too small for any satisfactory tests it appears that real differences exist between clones in residual error (between-ramets) variance for compression wood rating not accounted for by the regression on lean plus butt sweep. To take an extreme example, Fig. 2 shows compression wood rating plotted against lean

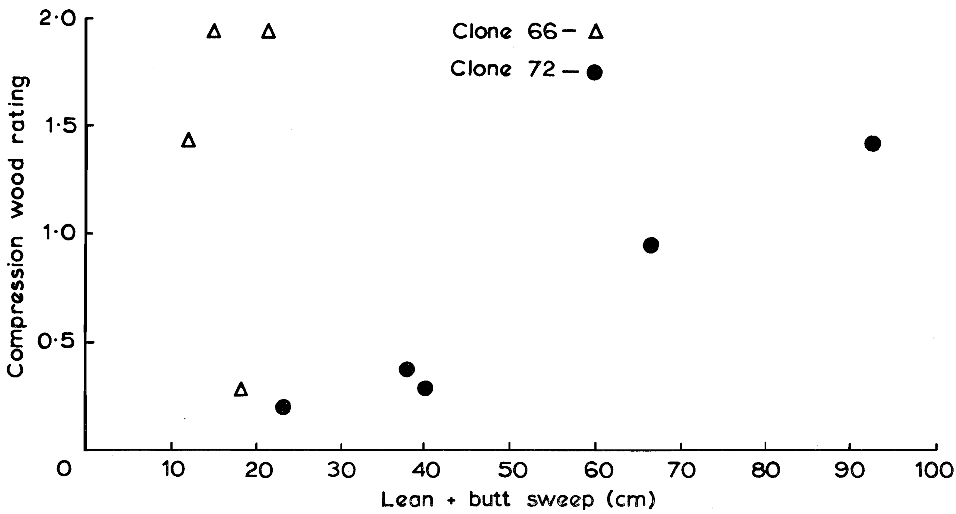

FIG. 2—Compression wood rating vs lean plus butt sweep in individual ramets of clones 66 and 72 at Whaka

plus butt sweep for individual ramets of Clones 66 and 72 at Whaka. The erratic variation of Clone 66 was repeated at Berwick, although this clone was always fairly straight. Any heterogeneity of error variance among clones is an unwelcome departure from the assumptions involved in pooling within-clone regressions and in using the pooled regressions for analysis of covariance.

Results for pooled within-clone regressions of compression wood rating on lean plus butt sweep at each site are shown in Table 4. Residual error variances were much lower at Glenbervie and Gwavas, differences being highly significant overall (Bartlett Test, $P < 0.01$). Regression slopes appear to be less at Glenbervie and Gwavas, although no significant slope differences were detected between sites (t-tests).

TABLE 4—Within-clone regression slopes of compression wood rating on lean plus butt sweep, residual error variances, residual error degrees of freedom and number of trees involved

Site	Regression slope (b)	Residual error variance	Residual error degrees of freedom	Total trees
Glenbervie	0.027	0.057	14	26
Whaka	0.047	0.139	24	34
Gwavas	0.028	0.044	20	31
Berwick	0.052	0.112	29	44

Genetic Aspects

The clonal repeatabilities of whole-tree compression wood rating and percentage total compression wood are shown in Table 5. Transforming percentages to arcsin values had little effect on calculated repeatabilities.

TABLE 5—Clonal repeatabilities of tree compression wood rating, by sites

Compression wood parameter	Site: Glenbervie	Whaka	Gwavas	Berwick
Compression wood rating	0.01 N.S.	0.08 N.S.	0.42*	0.49***
Percentage total compression wood	$\geqq 0$ N.S.	0.20 N.S.	0.27 N.S.	0.55***
Compression wood rating, adjusted for lean plus butt sweep	0 N.S.	0.41*	0.54*	0.43***

N.S. denotes not significant, $P > 0.05$
* denotes significant, $P < 0.05$
*** denotes very highly significant, $P < 0.001$

Repeatabilities for these characters at individual sampling points (t_9, etc.) were comparable with those for whole trees, and showed no clear trend, apart from being lower in the small t_5 discs. It appears, then, that no one sampling point gives optimal resolution of clonal differences. Percentage severe compression wood was not significantly repeatable at any site, possibly because of its skewed distribution. Little weight is attached to the low repeatabilities at Glenbervie, because of the comparatively weak compression wood development, the variability of tree growth, and the paucity of data.

The adjustment for lean plus butt sweep, far from eliminating significant clonal repeatabilities for compression wood rating, actually boosted them at Whaka and Gwavas. However, the estimates of repeatability cannot be accepted as strictly valid because of apparent clonal differences in residual error variance. However, a better basis for covariance correction would probably have been early stem deviation, rather than stem deviations persisting at the assessment date when righting may already have occurred. Despite these reservations it is concluded that clonal differences in compression wood formation definitely exist, whether or not they were considered in relation to stem deviation from the vertical. However, any estimates of the actual magnitude of these differences would be unsatisfactory.

Clonal behaviour over different sites appears to have been fairly consistent. Taking the analysis of variance of tree compression wood rating over all sites, for what it is worth, clone-site interactions were slight and non-significant ($F_{38, 100} = 1.4$, $P = 0.08$), while clonal differences overall were significant even on the basis of the more stringent but biased test against the interaction mean square ($F_{17, 38} = 2.4$, $P = 0.01$). With Glenbervie data omitted the results were essentially the same. The question was also studied by means of correlations between pairs of sites (excluding Glenbervie) of the mean clonal compression wood ratings (Table 6).

TABLE 6—Correlations, between sites, of clonal means for compression wood rating. Adjustments of means made on the basis of pooled within-clone regression for each site

Parameter		Sites	
		Gwavas	Berwick
Unadjusted means	Whaka	0.43 N.S.	0.48 N.S.
	Gwavas		0.48 N.S.
Means adjusted for lean plus butt sweep	Whaka	0.50 N.S.	0.53 N.S.
	Gwavas		0.69*

N.S. denotes not significant, $P > 0.05$
* denotes significant, $< P\ 0.05$

The positive values further indicate fair consistency over different sites. Without the adjustment for lean plus butt sweep the correlations are slightly weaker.

Table 7 shows adjusted mean compression wood ratings, expressed as deviations from site means, at Whaka, Gwavas and Berwick. Clone 72, which was well represented showed a much lower value at Whaka than at Gwavas and Berwick. However, at the latter sites its sinuosity was very severe. In some clones the angle of branching was visually distinctive, and the indications are that there is a positive association between adjusted compression wood rating and steepness of branching.

TABLE 7—Clonal means of compression wood ratings, adjusted for lean plus butt sweep, expressed as deviations from site means, for Whaka, Gwavas, and Berwick

Clone No.	Whaka	Site Gwavas	Berwick	Average over sites	Remarks
61	—	+ 0.26	+ 0.79	+ 0.52	
62	—	+ 0.33	+ 0.37	+ 0.35	Prone to forking and steep-angled branching
65	+ 0.18	— 0.25	—	— 0.03	
66	+ 0.61	+ 0.46	+ 0.50	+ 0.52	Steep-angled branching
67	— 0.33	0	— 0.19	— 0.17	Partly suppressed at Whaka, steep-angled branching
68	—	— 0.38	— 0.57	— 0.47	Wide-angled branching
69	+ 0.36	+ 0.06	— 0.32	+ 0.03	
71	+ 0.17	— 0.08	— 0.15	— 0.02	
72	— 0.80	— 0.21	— 0.19	— 0.40	Wide-angled branching
73	+ 0.14	— 0.37	+ 0.14	— 0.03	

Among the crookedness parameters sinuosity shows significant clonal repeatabilities within sites, although there were clearly clone-site interactions (Burdon, 1971). However, with the other crookedness parameters, which were analysed in this study, clonal repeatabilities were generally very low and non-significant. Hence of all the clonal (genotypic) correlations between compression wood rating and any single crookedness parameter only those between compression wood rating and sinuosity were potentially meaningful. In fact the estimates for these correlations were close to zero at all sites.

Another relationship was studied—within individual sites the correlation between the clonal means of sinuosity and of compression wood rating adjusted for lean plus butt sweep. The correlation coefficients (r) were -0.48, 0.25 and 0.23 at Whaka, Gwavas and Berwick respectively. None approaches statistical significance.

There was no evidence of any overall clonal relationship between wood density and compression wood rating.

DISCUSSION

Sampling at several points up the stem appears advisable for getting a reasonably unbiased estimate of stem compression wood, rather than for obtaining repeatable results.

In this study the pattern of compression wood formation can generally be related to conditions at the individual sites. The high and comparatively uniform ratings at Gwavas can be related to the exposure, which would have affected all trees to some extent. The high if rather variable ratings near ground level at Berwick reflect the prevalence of toppling. At Whaka the large tree-to-tree variation can be related to the presence of leaning trees at the stand margin. Poor nutrient status at Glenbervie may have lowered the propensity for compression wood formation there, either by a specific effect of phosphate deficiency (cf. Raunecker, 1957) or an effect of the general reduction in vigour (cf. Pillow and Luxford, 1937). The plot showed a fertility gradient, and it was the only site where, within clones, compression wood rating was positively correlated with stem diameter.

The lack of relationship among sites between compression wood rating and lean plus butt sweep (Tables 1 and 2) was surprising. However, several factors influenced the significance of the measured deviations at the respective sites. Differences between sites in stem taper, which were disregarded, must have caused bias. Taper was undoubtedly least at Glenbervie, so lean plus butt sweep would have been underestimated least there. Moreover, among sites deviations arose in differing circumstances. At Berwick the initial toppling had frequently been followed by over-correction, so the measurements represented rather inconsistent under-estimates of total stem deviation. At Whaka the average lean was inflated by some very crooked trees of Clone 72 which also had a low propensity for compression wood formation.

The behaviour of the trees on the exposed margin at Gwavas is noteworthy, compression wood ratings being high although the trees deviated little from the vertical through the effects of wind being largely counter-balanced by the tendency of marginal trees to lean outwards. That compression wood may form without appreciable deviations from the vertical is also indicated by entire growth rings of compression wood, generally in conditions favouring exuberant growth (J. M. Harris, pers. comm.). Moreover, Westing (1965) notes that any force tending to alter the established orientation of a shoot may induce compression wood formation.

Genetically, the results can be satisfactorily interpreted if compression wood formation is viewed as a mechanism to produce or restore a vertical orientation, by either or both of active righting and differential radial growth. The anomalous tree-to-tree variation in some clones, although weakening formal statistical analysis, actually supports the conclusion that genotypes differ in propensity to form compression wood. Take the behaviour of Clone 66, a "high compression wood" clone, as illustrated in Fig. 2. All trees were fairly straight, but the extremely variable compression wood ratings could be explained if some trees were straight from the outset and others initially crooked but then corrected by the strong compression wood-forming response. However, if a stem was extremely crooked initially, if a lean developed in a large stem, or if crown development was extremely asymmetrical, the righting response would doubtless be ineffective, despite abundant compression wood formation. By contrast the "low compression wood" clone, 72, showed a slow and progressive increase in compression wood rating with increasing crookedness.

Clones 66 and 72 were conspicuously straight and sinuous respectively, which by itself would suggest that sinuosity is the result of inherently weak compression wood formation rather than a cause of compression wood development. However, this cannot be entirely the case; were it so, strong negative correlations would be expected, among clonal means, between sinuosity and compression wood rating adjusted for lean plus butt sweep, but these were not obtained. Moreover, the lower compression wood ratings in Clone 72 at Whaka than at Berwick and Gwavas suggest that its extreme sinuosity at the latter sites has caused some compression wood formation.

Sinuosity is of special interest as a character which is highly heritable (Shelbourne, 1966; Shelbourne and Stonecypher, 1971; M. H. Bannister, in prep.) and is a primary criterion in plus tree selection. However, it appears to be objectionable not as a cause of compression wood, except in extreme cases, but essentially as a cause of wandering pith and of enlarged knotty cores in pruned logs.

The evidence in this experiment for the genetic basis of compression wood formation is tenuous in itself, but it corroborates the results of Shelbourne (1966) and Shelbourne *et al.* (1969). Little can be concluded, however, concerning genotype-site interactions.

This study of compression wood occurrence in relation to stem deviations applied only to wood within the first ten rings from the pith. Moreover, the relative influence of visual compression wood grade on corewood and outer-wood properties in *P. radiata* is still to be established. Thus, although the genetic variation in visually rated compression wood is better understood now, its overall technical significance is uncertain.

CONCLUSIONS

(1) Compression wood in *P. radiata* appears to be generally more pronounced near ground level than higher up the stem.

(2) Between sites and between levels on the stem the amount of severe compression wood appears to be rather more variable than total compression wood.

(3) Among sites, strong development of compression wood can be related to exposure and to toppling of trees after planting. Low soil fertility may not favour compression wood formation.

(4) At individual sites tree-to-tree variation within clones in the degree of compression

wood formation is related to lean plus butt sweep, less so to broad stem sweep and not at all to stem sinuosity.

(5) Genotypes appear to differ markedly in their propensity to form compression wood with a given deviation from the vertical.

(6) Sinuosity appears in part to reflect a low genotypic propensity for compression wood formation; only in extreme cases can it be accepted as a significant cause of compression wood formation.

(7) Trees that are initially very straight or very crooked can be expected to contain little or abundant compression wood respectively, whatever the genotypes.

(8) However, with initially intermediate degrees of crookedness, trees may either end up straight with very pronounced compression wood, or remain crooked with only slight compression wood, according to whether genotypic propensity for compression wood formation is high or low.

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