GENOTYPE AND LOCATION EFFECTS ON INTERNODE LENGTH
OF PINUS RADIATA IN NEW ZEALAND

M. J. CARSON and C. S. INGLIS*
Ministry of Forestry, Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

(Received for publication 13 October 1986; revision 18 October 1988)

ABSTRACT

Internode length of Pinus radiata D. Don in New Zealand is under strong additive genetic control, and it is an important index of the amount of clearwood yielded by unpruned trees. Variation between genotype in internode length is much greater on fertile, high-latitude sites, but rankings of genotypes are quite stable over all sites. Both multinodal (short-internode) and long-internode breeds have been developed to supply timber products for differing end-uses. Much greater yields of clearwood can be obtained from a long-internode breed, but this will be at some cost in gains for growth and form traits when compared to the most advanced multinodal tree type. It is important to match the choice of breed with the planting site, and with subsequent management of the forest crop; this will be greatly assisted when the effects of the tree breeding programme can be accounted for in existing forest planning models.

Keywords: tree improvement; selection; breeding; long-internode; multinodal; Pinus radiata.

INTRODUCTION

Clearwood from Unpruned Logs

New Zealand’s Pinus radiata resource extends over one million hectares, and will yield over 18 million m³ wood per year by the year 2000 (G. P. Horgan, unpubl. data). Most forest stands are being managed for sawlog/peeler production, with the balance of the wood going to pulp and paper, posts and poles, panel products, and reconstituted wood products. In the last 20 years, forest management practices have emphasised the production of clearwood (i.e., knot-free wood) by pruning the butt log and doing heavy and early thinning to increase diameter growth on the pruned trees (Sutton 1984). The effects of this “clearwood strategy” in reducing growth increment on a per tree basis (from pruning) and on a per hectare basis (from heavy thinning) have been assumed to be more than compensated for by the expected price premiums for long-length clearwood.

An estimated 3.2 million m³ of the annual harvest in the year 2000 will be in pruned logs, and this will yield approximately 880 000 m³ clearwood in lengths greater than 3 m (G. P. Horgan, unpubl. data).

* Present address: Carter Holt Harvey Forests Ltd, P.O. Box 17121, Auckland 5, New Zealand.
However, many of the end-uses for clearwood require lengths below 2 m, and often as short as 0.3 m. It is clear that substantial amounts of clearwood in lengths greater than 0.3 m could be produced from internodal portions of unpruned logs. The long-run supply of such clearwood will depend on both economic and biological factors. Economic factors include market demand, timber prices, location of resource, and costs of harvesting, processing, and marketing the wood. Biological factors affecting clearwood yields include the species response to local environmental factors (site fertility, water relations, solar radiation, aspect, etc.) and genotypic variation within the species. The *P. radiata* improvement programme in New Zealand has modified the expression of genetic variation in internode length to a degree that will have profound effects on future yields of internodal clearwood.

**Development of Multinodal and Long-internode Breeds**

Depending on site and genotype, *P. radiata* will normally produce from one to five branch clusters on the stem in a year's extension growth. Frequency of branch clusters of *P. radiata* is strongly inherited and the genetic variance is almost all of the additive type; a narrow-sense heritability of about 0.5 was estimated for progenies of the native populations of *P. radiata* (R. D. Burdon, unpubl. data), and Bannister (1962) estimated a heritability of 0.45 for a New Zealand land-race of *P. radiata*. Selection for a multinodal branching habit decreases internode length and produces an associated reduction in average branch size, which leads to a reduced knot size and greater suitability of the timber for construction purposes. Selection for long internodes increases average internode length, but also tends to increase average branch size to the extent that the additional yields of clearwood are at the expense of yields of construction-grade timber. Early tree improvement selections were for trees with light, flat-angled branches, which virtually necessitated selection for a multinodal tree type (the "850" clonal series).

Subsequent recognition of the potential for manipulating branching habit led to selection of two groups of "plus" trees of "multinodal" and "long-internode" types. These two contrasting tree types were expected to "fulfil the needs of all end uses: the extreme multinodal type suitable for groundwork, framing, structural plywood, and (when pruned) board grades; and the extreme uninnodal type which is particularly suited to producing boards, short clears for remanufacture and for clear veneers from short peeler bolts" (Shelbourne 1970). This division has resulted in two seed orchard breeds of *P. radiata* – the mainstream growth and form breed based largely on the multinodal "268" clonal series and the special purpose "long-internode" breed. Seed of these two breeds is now available in commercial quantities, and will soon supersede seed of the earlier "850" series, which has been planted from about 1972 to the present day.

**Coping with Options**

The ability to provide a choice of improved breeds is a new dimension for New Zealand tree breeders of the 1980s, and it provides a challenge. Where, in the past, it was sufficient to provide evidence of genetic gain and to produce seed of the single improved breed that was adapted to a category of forest sites, now the tree breeder must distinguish adequately between breeds with alternative uses, and provide forest managers with sufficient information to make a choice. That information should cover
an understanding of the behaviour of important traits in terms of genetic gain, genotype-environment interaction, correlated responses, indirect selection, and economic weights. It should also include an adequate translation of genetic gains expressed in terms of conventional selection traits to quantified estimates of growth and log quality traits that can be used directly in forest planning models. We will show how we have attempted to assist the choice of breed, using examples from a detailed study of internode length of *P. radiata* in New Zealand.

**Material**

The study of internode length involved measurements on samples of trees growing in five locations of an open-pollinated progeny test. The trial sites are described in Table 1 and are each considered to be representative of a large planted resource. The trials were originally planted in a randomised complete block design with five replicates; seedlots were arranged in family sets within replicates, and were represented in 10-tree row plots. The trials at Woodhill, Kaingaroa, and Golden Downs Forests had already been thinned to the best five trees per plot. Trees had been conservatively pruned to about 2 m height at all locations.

Three groups of *P. radiata* progenies were sampled in between 28 and 50 trees per group per site:

(a) An "850" series clonal seed orchard seedlot, representing the "850" subdivision of the growth and form breed (referred to here as the "850" group);

(b) Open-pollinated progeny of 23 plus-trees of the "268" clonal series, representing the "268" subdivision of the growth and form breed (referred to here as the "268" group);

(c) Open-pollinated progeny of eight long-internode trees, representing a "long-internode" breed.

Although the "850" series seedlot is truly representative of the available seed orchard product, the samples of open-pollinated progenies in (b) and (c) above will provide only indicative characteristics of future stands grown from growth and form and long-internode breeds.

**TABLE 1—Description of field sites used in the internode length study**

<table>
<thead>
<tr>
<th>Site</th>
<th>Description</th>
<th>Latitude</th>
<th>Site index* (m)</th>
<th>Soil type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woodhill</td>
<td></td>
<td>36°30'S</td>
<td>24</td>
<td>Recent coastal sand</td>
</tr>
<tr>
<td>Kaingaroa (a)</td>
<td></td>
<td>38°20'S</td>
<td>35</td>
<td>Recent pumice</td>
</tr>
<tr>
<td>Kaingaroa (b)</td>
<td></td>
<td>38°50'S</td>
<td>34</td>
<td>Recent pumice</td>
</tr>
<tr>
<td>Golden Downs</td>
<td></td>
<td>41°20'S</td>
<td>25</td>
<td>Weathered fluvio-glacial gravel</td>
</tr>
<tr>
<td>Otago Coast</td>
<td></td>
<td>45°50'S</td>
<td>24</td>
<td>Silty loams derived from sedimentary rocks</td>
</tr>
</tbody>
</table>

* Site index was estimated from heights taken on "850" series trees at each site, converted to height (in metres) at age 20 according to unpublished tables prepared by R. Tennent and H.E. Burkhart.
Data used to represent the "850" group and the long-internode breed at Kaingaroa came from an earlier study by C. J. A. Shelbourne and D. Briscoe (New Zealand Forest Service 1984); in their study, data for the "850" group were from a 32-tree sample at the same site as for the trees of the "268" group, but the long-internode breed was represented by open-pollinated progenies of eight clones growing in a similar trial at a different location within Kaingaroa Forest ("Kaingaroa (b)" in Table 1).

Since Shelbourne and Briscoe found that 32-tree samples of the "850" group assessed at both the Kaingaroa (a) and (b) sites were virtually identical for internode length traits, it was assumed that measurements of the long-internode breed at Kaingaroa (b) could be compared with measurements of the "268" group at Kaingaroa (a).

Sampling of trees of the long-internode breed was subject to a further complication. Trees sampled at the Woodhill, Golden Downs, and Otago Coast sites were progenies of clones for which the initial phenotypic selection placed no particular emphasis on internode length; however, on the basis of age 7 progeny assessment data, 10% of clones with longest internodes were reselected for use in this study. At the Kaingaroa (b) site, the trees sampled were progenies of clones which were both initially selected for their long-internode habit and reselected for this trait based on age 10 assessment data. As a result, the long-internode breed as sampled at the Kaingaroa (b) site might be expected to be more representative of a future seed orchard product than the samples from the other three sites.

In addition to the main comparison, the "268" group could be divided into three sub-groups comparing:

(i) A highly multinodal set of eight progenies selected on a multitrait index for general purpose use ("Sub-group 268A");
(ii) A set of seven progenies selected with major emphasis on improved growth rate and stem form and little emphasis on internode length ("Sub-group 268B");
(iii) A set of eight progenies reselected with particular emphasis on longer internodes ("Sub-group 268C").

This comparison within the "268" series aimed to determine the extent to which this existing multinodal breed could be reshaped by family selection for an altered emphasis on branching habit.

All measurements were made on trees aged between 13 and 15 years old. Usually, three or four progenies of each clone were assessed at each location. Sample trees were chosen from within two replications of each of the progeny tests. The first one or two "crop" trees encountered in a row plot of a seedlot in a replication were sampled. Trees of "crop" standard had to be relatively straight, non-malformed dominants.

**METHODS**

**Assessment**

Each sample tree was assessed for:

(a) Branching habit: 1 to 9 score, where 1 = uninodal and 9 = strongly multinodal;
(b) Internode length (to nearest 0.05 m): where the tree was climbed and measured for the height above the base of the tree to the bottom and top of each successive
branch cluster. (The base height was set at 0.2 m to allow for stump height.)
Measurements were taken up to 11.2 m height, so that internode length data would
represent the first two 5.5-m logs on each tree.

Mean internode length (MIL) and distributions of internode length were derived
from these measurements. Calculation of MIL assumed that logs would be cross-cut
at the nearest whorl to the nominal 5.5-m piece size, so that yields of clearwood would
be maximised.

Heights of between 25 and 30 trees of the sample of "850" group trees were
assessed at all four trial locations as an estimator of site quality (Table 1). Site index
may give an under-estimate of site quality for the Otago Coast location, since the
height : basal area ratio is typically much lower on Southland sites.

Statistical Analyses

Internode length data were analysed to derive MIL for each tree on a PDP 1134
computer using special software developed for this purpose. The MIL for individual
trees was analysed in an ANOVA with terms for sites, groups, and the site-by-group
interaction all as fixed effects. Correlation coefficients were calculated for relationships
among branching habit traits.

RESULTS AND DISCUSSION

Group Differences in Mean Internode Length

Mean internode lengths for the different *P. radiata* groups ranged from 0.36 m
(Sub-group 268A) to 0.49 m (long-internode) for the first 5.5-m log, and from 0.40 m
(Sub-group 268A) to 0.64 m for the second 5.5-m log, when averaged over the four
trial sites (Table 2). The long-internode breed had the longest MIL for both first and

<table>
<thead>
<tr>
<th>Site</th>
<th>First 5.5-m log</th>
<th>Second 5.5-m log</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&quot;268&quot; sub-groups</td>
<td>&quot;850&quot; group</td>
</tr>
<tr>
<td>268A</td>
<td>0.30 0.37 0.38</td>
<td>0.35 0.41</td>
</tr>
<tr>
<td>268B</td>
<td>0.37 0.42 0.46</td>
<td>0.47 0.55</td>
</tr>
<tr>
<td>268C</td>
<td>0.38 0.46 0.50</td>
<td>0.43 0.55</td>
</tr>
<tr>
<td>Group means*</td>
<td>0.36d 0.41bc 0.43b</td>
<td>0.41bc</td>
</tr>
</tbody>
</table>

* Site means followed by a different letter differ significantly in a Waller-Duncan comparison test at $p \geq 0.05$. 

TABLE 2—Mean internode lengths (MIL) for the first two 5.5-m logs for *P. radiata* groups at four New Zealand sites
second logs at all sites, while the multinodal sub-group 268A had consistently the shortest MIL; differences between these two groups were a mere 12% for the second log at Woodhill but more than 100% at the Kaingaroa site, and were statistically significant overall (Table 3).

Table 3—ANOVA comparing improved P. radiata groups at four New Zealand sites for mean internode length (MIL) in the first and second 5.5-m log height classes

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean squares</th>
<th>F value</th>
<th>Prob &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>3</td>
<td>0.2689</td>
<td>25.43</td>
<td>0.0001</td>
</tr>
<tr>
<td>Breed (group)</td>
<td>4</td>
<td>0.2136</td>
<td>20.20</td>
<td>0.0001</td>
</tr>
<tr>
<td>Site x group</td>
<td>10</td>
<td>0.0114</td>
<td>1.08</td>
<td>0.3746</td>
</tr>
<tr>
<td>Log 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>3</td>
<td>1.4871</td>
<td>69.60</td>
<td>0.0001</td>
</tr>
<tr>
<td>Breed (group)</td>
<td>4</td>
<td>0.4211</td>
<td>19.71</td>
<td>0.0001</td>
</tr>
<tr>
<td>Site x group</td>
<td>10</td>
<td>0.0741</td>
<td>3.47</td>
<td>0.0002</td>
</tr>
</tbody>
</table>

Internode lengths of the "850" group were similar to those for sub-group 268B. The "850" group has proved relatively multinodal in comparison to unimproved and mildly select seedlots in many tree improvement trials (M. J. Carson & C. J. A. Shelbourne, unpubl. data). This trend to increased multinodality has clearly accelerated with the "268" group; both parents of seed orchard progenies of "268" clones will be of the selected multinodal type (compared to only one for the open-pollinated progenies) and so "268" orchard progeny may be expected to have shorter MIL than those shown in Table 2.

The trends shown for MIL of open-pollinated progeny of "268" and long-internode clones have been confirmed in two other internode length studies involving control-pollinated families of both groups. Inglis (unpubl. data) measured internode length on the first three 5.5-m logs of a 32-tree sample of control-pollinated long-internode progeny on a central North Island pumice site. He obtained MIL of 0.51 m, 0.92 m, and 0.80 m for the first three 5.5-m log height classes, respectively, and these represent the longest values recorded for any seedlot at any site in New Zealand. In a trial comparing simulated seed orchard breeds (from controlled pollinations) J. A. Brown (unpubl. data) measured first log MIL of 0.39 m for a "268" group and 0.70 m for the long-internode breed from samples of 90 trees. A mildly select forest seedlot had an MIL of 0.54 m in the same study. Inglis (unpubl. data) also found in comparisons over four sites that the long-internode breed had branches up to 1 cm larger in diameter than unimproved trees, while an "850" seed orchard seedlot had branches about 0.5 cm smaller.

Site Variation in Mean Internode Length

Trees at the Kaingaroa site had the longest MIL (particularly for the second log), and those at Woodhill were considerably shorter than at the other three sites (Table 2). Second log MIL were longer everywhere except at the Woodhill site, which reflects the typical situation in New Zealand, with the longest internodes occurring in the 2- to 11-m
zone up the tree (Inglis, unpubl. data). The site factors controlling MIL are not well understood as yet, but there is some evidence for a weak association with latitude (i.e., longer MIL at higher latitudes) and for shorter MIL to occur where site fertility is limiting. Data from the Woodhill site fit this hypothesis quite well, since this was the northernmost site measured and its sandy soils are nitrogen-deficient.

The range of MIL between multinodal and long-internode breeds tended to increase as site means for MIL increased (Table 2); greatest expression of the trait occurred in the second log at the Kaingaroa site, where the 0.46-m difference in MIL between the two extreme groups (268A and the long-internode breed) was larger than the between-site differences found in this study and, indeed, larger than any between-site difference found by Inglis in measurements in over 120 New Zealand stands (Inglis, unpubl. data). There were moderate differences in the MIL of the sub-groups of the "268" group, indicating that reselection could be effective in reducing multinodality.

**Genotype × Environment Interaction for Mean Internode Length**

There was little evidence in this study for any major interaction of *P. radiata* breeds with different sites for mean internode length. Although the "site × group" term in the ANOVA for second log MIL was statistically significant, it was small compared to the site and breed differences and did not lead to important changes of rank for sites or breeds (Table 2). The absence of important rank interactions for internode length traits has been confirmed in many other tree improvement studies, including a recent polycross test of 104 progenies at six sites (C. J. A. Shelbourne, unpubl. data). This result is of particular importance to forest planners since it implies that sites have a predictable MIL for a given breed, and breeds have a predictable MIL at a given site.

Although the breeds rank similarly across different sites, there is evidence in Table 2 for greater gains in MIL of the long internode breed at some sites than at others (compare Woodhill means with those for Kaingaroa). This implies that deployment of the long-internode breed to these sites could lead to greater profitability.

**Correlated Responses to Changes in Mean Internode Length**

The sampling procedure followed in this study precluded the examination of genetic correlations between internode length traits and other important traits. However, these relationships are now well understood after confirmation in numerous studies. The moderate-to-strong association between multinodality and improved growth rate and stem form is illustrated in the estimates of genetic correlation obtained by Shelbourne in the 9-year-old polycross test at six sites (Table 4). At these sites (three of which are common to the internode length study), correlations of branch habit score and diameter were usually positive, and ranged up to $r_q = 0.57$ at the Kaingaroa site. There is a trend for the correlations to be weaker for the southern sites (particularly for form traits), which may indicate a relative advantage for the long-internode breed on these sites.

These correlations represent "good news" for the development of a multinodal breed, but less so for pursuit of the long-internode trait. In fact, they have had an important effect on realised gains for the "268" group and the long-internode breed for traits other
Table 4—Estimates of genetic correlation coefficients for the association of branching habit with other growth and form traits as measured in the *P. radiata* polycross progeny test on six New Zealand sites at age 9 (from unpubl. data of C.J.A. Shelbourne)

<table>
<thead>
<tr>
<th>Forest site</th>
<th>Diameter*</th>
<th>Stem straightness†</th>
<th>Malformation‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woodhill</td>
<td>0.31</td>
<td>0.56</td>
<td>N.E.</td>
</tr>
<tr>
<td>Maramarua</td>
<td>N.E.</td>
<td>0.46</td>
<td>0.31</td>
</tr>
<tr>
<td>Kaingaroa</td>
<td>0.57</td>
<td>0.51</td>
<td>0.38</td>
</tr>
<tr>
<td>Golden Downs</td>
<td>0.13</td>
<td>0.38</td>
<td>0.31</td>
</tr>
<tr>
<td>Eyrewell</td>
<td>0.33</td>
<td>0.34</td>
<td>N.E.</td>
</tr>
<tr>
<td>Berwick</td>
<td>0.22</td>
<td>0.17</td>
<td>N.E.</td>
</tr>
</tbody>
</table>

* Diameter at height 1.4 m.
† Scored subjectively on a 1–9 scale.
‡ Scored subjectively on a 1–9 scale.
§ Not estimated owing to imprecise estimates of variance for one or both correlated traits. All correlation coefficient estimates shown are calculated from variance components significantly >0, p=0.05.

than branching habit. Recent estimates of the performance of control-pollinated "268" and long-internode progenies (simulating the performance of current seed orchard breeds) at age 5–6 on five New Zealand sites showed a "268" seedlot to have 26% more volume than an unimproved seedlot, compared to only 12% for a long-internode seedlot and 13% for an "850" seed orchard seedlot (J. N. King, unpubl. data). Form differences in the same study are perhaps best expressed by the "percentage of stems acceptable for final crop"; for this trait, the "268" seedlot had 81% acceptable stems compared to 60% for the long-internode seedlot and 68% for the "850" seedlot. These figures do not tell the whole story since, for example, the long-internode breed has been developed with less intensive selection than has the "268" group. However, they do indicate the current relative rankings of the breeds on offer to forest owners and the nature of the "trade-offs" faced in choosing to plant one breed rather than another.

### Selection for Clearwood Production

Tree improvement work in New Zealand has traditionally used subjective ratings to classify genotypes for stem form and branching habit traits. Use of a nine-point score for "branching habit" has proved extremely practical, and sensitive for differentiating between *P. radiata* seedlots and families. Until recently there seemed little need to quantify the changes in internode length that resulted from use of the "branching habit" score, since these changes seemed to be moving in the right direction and we did not have sophisticated tools for evaluating the effects of change. However, the recent development of a "silvicultural stand model" (SILMOD) by the Radiata Pine Task Force (Whiteside & Sutton 1983) and its more comprehensive successor STANDBAK (Kininmonth 1987) has changed these circumstances. STANDBAK is designed to be used as a management planning tool for comparing silvicultural alternatives. It predicts stand output in terms of log quality and log yields for a specified silvicultural regime, and then estimates the profitability of the regime based on discounted growing, harvesting, and processing costs, and corresponding revenues from the sale of timber. Changes in branching habit can be simulated in STANDBAK through alteration of the "internode index" (M. J. McGregor & F. J. N. Williams, unpubl.
data) which is defined as "the sum of all internode lengths of not less than 0.6 m in a 5.5-m log length (expressed per metre of log length)". Linear correlation coefficients for correlations between "branching habit" and MIL with the internode index are all relatively high (Table 5). The model uses regression equations to predict sawn timber output in various clearwood and knotty grades (Whiteside 1982).

Table 5—Linear correlation coefficients between "branching habit" score and mean internode length (MIL) with internode index in the internode length study

<table>
<thead>
<tr>
<th>Site</th>
<th>Trees sampled</th>
<th>Correlation coefficient</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Branching habit ×</td>
<td>MIL ×</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>internode index</td>
<td>internode index</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Log 1</td>
<td>Log 2</td>
<td>Log 1</td>
</tr>
<tr>
<td>Woodhill</td>
<td>127</td>
<td>-0.63</td>
<td>-0.60</td>
<td>0.84</td>
</tr>
<tr>
<td>Kaingaroa</td>
<td>89</td>
<td>-0.45</td>
<td>-0.71</td>
<td>0.79</td>
</tr>
<tr>
<td>Golden Downs</td>
<td>151</td>
<td>-0.72</td>
<td>-0.58</td>
<td>0.80</td>
</tr>
<tr>
<td>Otago Coast</td>
<td>151</td>
<td>-0.61</td>
<td>-0.78</td>
<td>0.75</td>
</tr>
</tbody>
</table>

The "internode index" was derived from measurements in the MIL study and used as inputs to program SAWMOD (a component model of STANDPAK which predicts timber grade) (Kininmonth 1987). The "850" and "268" groups were compared with the "long-internode" breed for predicted combined yields of "No. 1 cuttings" and "Factory" grades of timber from a "typical" unpruned log. The "typical" log was assumed to be a straight 5.5-m log of 40-cm small-end diameter. Branch size index was assumed to vary with internode index, with values of 3.5 cm for the "850" group, 3 cm for the "268" group, and 5 cm for the long-internode group. Logs were sawn to Sawing Pattern 5 and timber was visually graded for maximum value using the price list for "Projected Future Export Prices" (Price List 3 in SAWMOD).

The resulting percentage yields of clear timber grades vary roughly (Table 6) in similar relation to the second log MIL in Table 2, illustrating the large effects of site and breed differences in MIL. Therefore, the use of "branching habit" as a selection trait will lead to large changes in clearwood yields of improved breeds of *P. radiata*.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Pinus radiata breeds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&quot;Growth and form&quot; &quot;850&quot; &quot;268&quot;* &quot;Long-internode&quot;†</td>
</tr>
<tr>
<td>Woodhill</td>
<td>11.0 11.0 21.6</td>
</tr>
<tr>
<td>Kaingaroa</td>
<td>37.0  24.4  54.6</td>
</tr>
<tr>
<td>Golden Downs</td>
<td>34.5  24.4  54.6</td>
</tr>
<tr>
<td>Otago Coast</td>
<td>37.0  32.1  54.6</td>
</tr>
</tbody>
</table>

* The "268" values correspond to the mean of data for sub-groups 268A, 268B, and 268C.
† Internode index inputs to SAWMOD for long-internode trees at Kaingaroa, Golden Downs, and Otago Coast were constrained at a maximum 0.5 m/m (which makes these probable under-estimates of clearwood yields).
Relative Economic Weights for Internode Length v. Growth and Form Traits

STANDPAK has provided us with a tool for evaluating the relative economic weights of differing target traits. Input values of internode index, growth rate gains, and so on, can be varied to explore the sensitivity of predictions of timber grade outturn and profitability to genetic changes. An extensive simulation study using STANDPAK was attempted to determine the economic importance of internode length relative to growth and form traits in the tree improvement programme (Carson 1988). When internode index was varied for a typical clearwood regime, percentages of sawn timber in all clear grades (from the unpruned logs) varied from about 5% for a "268" seedlot to 44% for a long-internode breed. However, although these differences in grade outturn were large, their effect on regime profitability was less than that predicted for moderate improvements (8–15%) in volume and large improvements in stem straightness. Conclusions supported the extensive use of the "268" group of the growth and form breed for most regimes (owing to its superior growth rate and stem form) and selective use of the existing long-internode breed on sites where its particular internode length and stem form attributes confer maximum advantage (Carson 1988).

Prediction of Internode Length Distributions

The distributions of internode length around the mean for a site or breed also differ dramatically according to both site and breed. Distributions (extremes of) for second log values for the "268" group and the long-internode breed on Kaingaroa sites (i.e., Kaingaroa (a) and (b) respectively – Table 1) are illustrated in Fig. 1. Although the extremes of MIL are somewhat larger than this over all New Zealand sites (ranging from MIL = 0.14 to MIL = 1.05) the distributions show similar differences to those in Fig. 1. These distributions can be used to generate internode indices of the kind used in the current versions of STANDPAK. If the distributions of internode length are known (or can be predicted) for a given breed and site combination, then yields of clearwood can be estimated for a range of silvicultural regimes. It appears that it will be possible to estimate internode length distributions from MIL, using either the known "gamma" or "negative-exponential" distributions (M. J. McGregor, pers. comm.). Mean internode length of a stand can itself be estimated from counts of clusters and height measurements, thereby dispensing with the laborious climb-and-measure techniques we have had to use till now.

CONCLUSIONS

Guidelines for Use of the Improved Breeds

Results of this study have confirmed that there is a large potential for exploiting genetic variation in internode length of *P. radiata* to dramatically increase the yields of internodal clearwood. However, use of the existing long-internode breed incurs an opportunity cost in growth rate and quality of stem form relative to the "850" and (particularly) the "268" groups of the growth and form breed. Optimal use of the long-internode breed will result from:

(a) Identifying those forest sites at which gains in internode length will be high, and relative losses in growth rate and form will be low;
(b) Tailoring the silvicultural regime to take advantage of the tree's natural advantage in producing clearwood without the need for artificial pruning (and losses in growth due to pruning).

Preliminary results indicate that the long-internode breed may have a "comparative advantage" on sheltered sites in Southland and in the Nelson/Marlborough area where MIL are long, tree form is generally good, and trade-offs in growth rate may be less than on sites with higher site index (as, for example, in the northern Kaingaroa area). The nature of these "trade-offs" at the forest/region level are becoming better understood as we assess a trial series comparing the new breeds at 12 sites (planted 1979–80).

A new trial series is currently being established which will compare the new breeds for silvicultural factors of site quality, timing of thinning, and final-crop stocking. Our preliminary recommendations for managing stands of the long-internode breed for clearwood production include:

- Maintaining initial stockings at or above 1000 stems/ha;
- Pruning to approx. height 2 m;
• Delaying thinning to a low final-stocking (200–300 stems/ha) after the second log has formed (i.e., possibly an extraction thinning);
• Making a careful silvicultural selection of final-crop stems.

There is an obvious need for more stand-size trial plantings of the long-internode breed, both to accustom forest managers to it and to provide much-needed information on its performance.

Prediction of Internodal Clearwood Yields

The development of STANDPAK and its integration with other forest planning models represent a major advance in our ability to predict the influence of log quality variables on timber yields and regime profitability. STANDPAK can be improved by replacing regression relationships based on "internode index" with equations based on MIL, enhancing our ability to predict clearwood yields. Provision of a "look-up table" of MIL for improved breeds at different forests will allow STANDPAK users to make better predictions of clearcutting yields without the need to assess MIL in their own stands. Further research on predicting MIL from site variables may lead to a model analogous to a growth model, suitable for predicting internodal clearwood on a regional or even national basis. We may eventually develop growth models that include a capability for internode length prediction.

Implications for Future Improved Breeds

Future planning in the P. radiata improvement programme requires better knowledge of how vigorously the New Zealand forest industry will pursue the option of processing and marketing internodal clearwood. The distributions of internode length are of major importance here; although the total length of clearwood in lengths greater than, say, 0.3 m may be similar for the "268" group and the long-internode breed, the former has a far larger proportion of its clearwood in short pieces (Fig. 1). If all other factors are equal, there are obvious advantages in growing clearwood in long pieces, thereby reducing the costs of recutting and increasing the flexibility of the product for meeting a range of end uses. More work is needed in determining the value of these advantages relative to the market requirements for clearwood, the costs of fingerjointing, and the availability and cost of clearwood substitutes. Only when these factors are better understood will we be able to define an optimum MIL for future improved P. radiata breeds.

In the meantime, mating of the best first- and second-generation long-internode selections is proceeding as quickly as possible, with plans to plant these families as a breeding population in 1990. Based partly on the evidence from this study of variation in MIL within the "268" group, a recent re-analysis of economic weights used in the reselection of the "268s" has led to the selection (for control-pollinated orchard use) of a smaller and less multinodal group of clones than those previously identified (M. J. Carson, unpubl. data). This group (often referred to as the "Best 16") has MIL roughly equivalent to sub-group 268B in this study. In a current project for obtaining up to 1200 new plus-trees from the New Zealand land races of P. radiata no special effort is being made to select for either extreme of branch cluster frequency.
In conclusion, internode length has been shown to be a very responsive selection trait, under strong genetic control. Site variation in internode length is large but rankings of genotypes are stable. Breeds developed in only a single generation of selection will yield markedly different proportions of clearcutting timber grades, but associated responses in growth and form traits may assume greater importance in the choice of breed to plant. This implies a critical need to better understand and quantify genetic gains. Our example involving the internode length trait merely illustrates this more general problem that will increasingly confront tree breeders as their tree improvement programmes mature. What we learn from this process will determine our future success in implementing control-pollinated orchard and clonal forestry methods of refining tree breeds.

ACKNOWLEDGMENTS

Vivienne Sutton, Charles Low, and Ian Whiteside are thanked for assisting with data analysis. We also thank Tony Shelbourne for making his data available and for refereeing comments, and John King and Rowland Burdon for refereeing comments.

REFERENCES


