THE LONG-INTERNODE BREED OF RADIATA PINE - A CASE STUDY OF BREED DIFFERENTIATION

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Abstract: Development of the long-internode breed of radiata pine in New Zealand is an example of genetic differentiation within a forest tree species to obtain a specific end-product. Radiata pine shows marked variation in the number of branch clusters formed annually, with a corresponding variation in internode length. Long internodes are commercially valuable due to greater yield of knot-free lumber in the unpruned part of the stem for a variety of products. Internode length is under strong genetic control and is highly amenable to selection. Recent sawing studies of a 28 year-old clonal test have shown that clones selected for long internodes gave much higher lumber value as US shop grades.

Breeding for internode length began in 1970 with the selection of 104 long-internode plus trees in plantations. Subsequent work includes open-pollinated progeny testing of both the first-generation selections and 74 second-generation selections, 153 crosses involving the first- and second-generation selections, and further first-generation selections in 1985. Advanced-generation selections will be made in the control-pollinated trials in 1998.

Gains in internode length entail somewhat reduced gain in the following: volume growth, branch size and stem quality. Problems in stem form are greater on highly fertile or very exposed sites. The adverse genetic correlations have led to separation of the long-internode population from the main breeding population. The goal is a tree with one or two branch clusters per year, to be grown on specific sites, with suitable silviculture. Deployment of improved stock is through control-pollinated seed of full-sib families (with the option of vegetative amplification). A clonal forestry option also exists, and is becoming more attractive as vegetative multiplication becomes less expensive.

The next major advance for the long-internode breed will be forming 2 small elite sublines of about 12 individuals each. These will have the best of the 3 distinct genetic resources available. Internode length will remain a major emphasis, with threshold values imposed for growth rate, stem form, resistance to *Cyclaneusma* needlecast, wood stiffness and spiral-grain angle. Future breeding will largely be within the sublines, allowing for unrelated crosses between sublines for production purposes.

Keywords: clear lumber, branch cluster frequency, *Pinus radiata* D. Don

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INTRODUCTION

Radiata pine (Pinus radiata D. Don) is the main commercial forestry species in New Zealand. Differentiation of tree types in terms of internode lengths has long been seen as desirable to accommodate different products (Shelbourne 1970; Carson and Inglis 1988) These include boards, structural timber, veneers, posts and poles, panel products, reconstituted wood products, kraft and mechanical pulp and paper (Carson and Inglis 1988; Kininmonth and Whiteside 1990).

Genetic improvement of radiata pine in New Zealand began in 1953 with selection of first-generation plus trees in plantations (Shelbourne et al. 1986). Early emphasis was on height, diameter, straightness, lack of malformation, small branch size and freedom from stem cones. It was seen that radiata pine varies markedly in branch cluster frequency (the number of branch clusters, from 1 to 6, formed annually), with a corresponding variation in internode length. This trait proved to be highly heritable (Bannister 1962). The major advantage of long-internode trees is in the production of usable lengths of clearwood in unpruned logs (Carson and Inglis 1988).

The main breeding programme for radiata pine, with selection for fast-growing, well-formed trees with light, wide-angled branches, provides trees suitable for structural timber (framing, etc) and, when pruned, long clear timber. This population is the main population or the `Growth and Form' breed in Carson and Inglis (1988) and Carson et al. (1990). However the selection has also driven internode length below that of unimproved plantations (Carson and Inglis 1988), which will have a marked, deleterious effect on the production of internodal clearwood. By 1970, there seemed to be justification for development of a long-internode' breed of radiata pine. This tree type was to meet the need for boards, short clears for remanufacture and clear veneers from short peeler bolts (Shelbourne 1970). Differentiated breeds (populations) were later formed for Dothistroma resistance and higher wood density (Carson et al., 1990).

Influential work by Fenton and Sutton (1968) helped promote the 'direct sawlog regime'. This used wide spacing, heavy thinning and pruning to achieve maximum clearwood production over a rotation of 25-35 years. This intensive silviculture, combined with good growing conditions and genetic improvement have contributed to rapid tree growth and greatly improved stem form in the radiata pine plantations in New Zealand. Plantation areas have increased dramatically (now 1.4 million hectares for P. radiata) but rigorous investment criteria have encouraged the harvest of ever-younger trees, as early as 20 years in one account (Macalister 1997). However very young trees have a high proportion of juvenile wood with its attendant drawbacks, such as greater twist, lower density, lower strength and poorer lumber recovery (Cown 1992). Wood quality problems are aggravated on highly fertile ex-pasture sites (Macalister 1997). There is serious concern as how an increased proportion of juvenile wood will affect New Zealand's forest products industry (Cown 1992, Macalister 1997).

During the 1990s the NZ tree improvement focus has changed from improving growth and log quality to improving specific end-product values. The tree breeder's task now adds improving juvenile wood quality (particularly stiffness and stability), to further improving a breed for increased clearcuttings. More and more plantations are being established as full-sib family blocks, and clonal forestry is being developed. It is likely that forest trees will be increasingly differentiated into 'breeds' just as agricultural and fruit crops have been differentiated into cultivars. The long-internode breed of radiata pine provides a useful case study of breed differentiation for a forest tree species.

FORMING THE LONG-INTERNODE BREED

Over 150 plus-trees with the long internode habit were selected in plantations between 1970 and 1973 (Shelbourne et al. 1986). Open-pollinated families of these selections were established as an initial breeding population. These progenies have yielded important information on the genetic control of this trait. Seventy-four second-generation selections were made in 1982 within the open-pollinated progeny tests of these first-generation selections. A further 52 first-generation long-internode selections were made in 1985. Open-pollinated seed were collected from these 52 clones to establish progeny tests (jointly with progeny of the second-generation selections) on two sites in 1987. Control-pollinated trials with 153 crosses (involving first- and second- generation clones) were planted on two sites in 1990 and will be measured shortly.

The best first- and second-generation selections remain in clonal archives. Thus the genetic resource of the long-internode breed now includes over 50 first-generation and 37 second generation selections and potential third-generation selections. For reasons described later, this population has been kept separate from the mainline (largely multinodal) breeding population.

THE MEASUREMENT AND GENETICS OF INTERNODE LENGTH

Several methods have been used to assess the long-internode trait. The most direct (but also the most time-consuming) is to measure the distances between the zones of knots associated with successive branch clusters up the stem. From these data can be derived *mean internode length* and measures of frequency of long intemodes such as *internode index* (the proportion of the log in intemodes of 60cm or greater). This has usually been measured in the first and second logs, to 5.7 and 11.2 meters (18.8 and 37 feet) respectively. A direct count of the *number of branch clusters* is another useful quantitative measure. *Branch cluster frequency* or *branch habit* can be scored subjectively on a 1 to 9 scale; this is easy to estimate and can prove a reliable indication of family rankings for the long internode habit and of internode index. Branch cluster frequency is routinely assessed in genetic trials of radiata pine in New Zealand. Heritability estimates for branch cluster frequency are given in Table 1; it is often the most heritable of the growth and form traits. High heritabilities and coeffiecients of variation were also observed for branch cluster frequency in studies of the native populations (from USA and Mexico), grown in New Zealand (Burdon 1992).

Table 1. Heritability estimates from three open-pollinated radiata pine progeny tests established in the central North Island of New Zealand.

Genetic material	Age in years	Number of families	Branch cluster frequency score		DBH		Straightness score	
			h^2_i	h^2_{hs}	h^2_i	h^2_{hs}	h^2_i	h^2_{hs}
1st generation selections[1] ("885 series")	8	467	0.33	0.67	0.21	0.56	0.21	0.56
1st gen. long-internode[2] selections ("870 series")	10	104	0.27	0.65	0.26	0.66	0.20	0.63
2nd gen. long-internode selections[1] ("883 series")	8	73	0.32	0.66	0.21	0.55	0.30	0.64

1 From unpublished data of K.J.S. Jayawickrama. Estimates based on one location.
2 From unpublished data of M.J. Carson, C.J.A. Shelbourne and C.B. Low. Estimates based on one location.
h^2_i = narrow-sense heritability on individual-tree basis, h^2_{hs} = heritability of half-sib family means

Differences in internode length between contrasting genotypes can be dramatic. The data in Table 2 are for progeny of open-pollinated highly-ranked first-generation long-internode selections, when compared with seedlings obtained from a first-generation 'Growth and Fond orchard. The largest difference was in the percentage of internodes above a given length. For example, while 45% of internodes exceeded 120 cm (48 inches) for the long-internode families, only 14% of internodes of the seed orchard progeny exceeded this length. Everything else being equal, these differences equate to large differences in the yield of long clear-cuttings.

Similar dramatic results were shown in a 12-year-old genetic gain trial with replicated block plots of 64 trees (Table 3). While controlled crosses among 'Growth and Form' trees had increased branch cluster frequency (by 1.9 points) compared with climbing select material, controlled crosses among long-internode trees had decreased branch cluster frequency by 3.0 points (a difference between the two breeds of 4.9 points). Considered in isolation, branch cluster frequency in radiata pine is a perfect trait for genetic manipulation - highly heritable, easy to assess and of major economic value.

Table 2. Comparison of the highest ranked 1st generation long-internode selections with 1st-generation 'Growth and Form' seed orchard seedlot

	Dbh in cm (and inches)	Height in meters (and feet)	Straight-ness (units)	Mean internode length in cm (and inches)	% of internodes exceeding 60 cm (24")	% of internodes exceeding 120 cm (48")
Long internode progenies[1,2]	26.2 (10.5)	16.4 (54.1)	5.94	67 (26.8)	72	45
1st generation seed orchard mix[2]	25.9 (10.4)	16.1 (53.1)	6.50	47 (18.8)	44	14

1 8 of 100 open-pollinated families, selected for internode length
2 32 trees measured
3 *from unpublished data of C.J.A. Shelboume and D. Briscoe. Trees were measured at* age *10* in *an* open-pollinated progeny test in the central North Island.

Table 3. Realized genetic gain for different seedlots, compared to climbing select (=seed tree) planting stock'.

Genetic material	Branch cluster frequency'		DBH		Straightness		% Acceptable crop trees	
	score (1-9)	Change (units)	cm (inch)	Gain (%)	score	Change (units)	Mean	Change
C.P. crosses between 1 st gen. ("870") long-internode selections	2.38	- 3.00	27.1 (10.8)	1.2	5.57	+ 0.99	52	+ 25
C.P. crosses between 1't gen. GF selections	7.28	+ 1.90	28.2 (11.3)	5.2	6.75	+ 2.17	75	+ 48
O.P. orchard mix of best 25 1 st gen. GF selections	6.33	+ 0.95	28.0 (11.2)	4.6	5.53	- 0.95	53	+ 26
Climbing select (=seed tree) seedlot	5.38		26.8 (10.7)		4.58		27	

1 Unpublished data from C.B. Low, NZFRI. Age 12 results from a trial planted in the central North Island. C.P. = control pollinated, O.P. = open pollinated. GF = Growth and Form.
2 Measured on a subjective scale (1=1 cluster per year, 9=highly multinodal).
3 Measured on a subjective scale (1=1 very crooked, 9=perfectly straight).

Despite the ease of manipulation of internode length, there are certain disadvantages associated with the long-internode habit. Examples of genetic correlations between branch cluster frequency and two major traits (diameter and stem straightness) are given in Table 4. They show that families expressing the long internode habit tend to grow slower, be more crooked and have more malformation than the Growth and Form families. This is a common finding for genetic trials of radiata pine in New Zealand. For example, it can be seen from Table 3 that the long-internode control-pollinated families were less straight (1.2 points lower) and had a lower percentage of acceptable crop trees (52 vs 75) when compared to the GF control-pollinated families. Further, long-internode trees tend to have larger diameter branches and steeper branch angles than highly multinodal trees. While it is possible to select for well-formed trees with a long-internode habit, increasing the internode length does entail some reduction in gains for growth rate, stem form and malformation.

Two points should be noted when considering the growth and form of long-internode trees. First, the long-internode habit is in low frequency in the population and it is harder to find a long-internode tree with acceptable form and growth (Shelbourne 1970). Second, many more first-generation candidates showing average to high branch cluster frequency have been selected and tested in New Zealand (over 1500 compared to 200 long-internode selections) as they comprised the main breeding population. Thus the best parents in the main breeding population have come from a far larger pool of candidates compared to the best long-internode parents.

For this and other reasons the long-internode breed has not gained market acceptance in the past. Financial analysis using the growth and log-quality model STANDPAK showed that (given a range of price lists used and numerous, conservative assumptions) the Growth and Form breed usually gave the best return (Carson 1988). The abandonment of long-internode seed orchards by the major seed company when under financial pressure meant that the supply of improved seed for the long-internode breed dwindled.

Recent realization by the forestry industry that the amount of clear cuttings from unpruned logs is much reduced in genetically improved stands has resulted in a renewal of interest in the long-internode breed, and in extending internode length in the main Growth and Form breed. Further, recent data show open-pollinated families of the best second generation long-internode clones to have comparable growth and form to families of good first-generation clones (grown on the same site), but a reduction of 1.5 units of branch cluster frequency score (Jayawickrama, unpublished data). In this case two cycles of selection within the long-internode population have achieved similar gains in growth and form to those from one cycle in the main population.

Table 4. Estimates of genetic correlation coefficients for branch cluster frequency, with three growth and form traits'.

	Genetic correlation of branch cluster frequency with		
Site	DBH	Straightness	Malformation4
Woodhill	0.31	0.56	N.E.
Maramarua		0.46	0.31
Kaingaroa	0.57	0.51	0.38
Golden Downs	0.13	0.38	0.31
Eyrewell	0.33	0.34	
Berwick	0.22	0.17	N.E[5]

1 Measured in a P. *radiata* polycross progeny test on six New Zealand sites at age 9. From unpublished data by C.J.A. Shelboume and C.B. Low. Reproduced with permission from Carson and Inglis (1988).
2 Scored on a subjective scale (1=one whorl per year, 9=highly multinodal).
3 Scored on a subjective scale (1= very crooked, 9=perfectly straight).
4 Scored on a subjective scale (1=highly malformed, 9=no malformation).
5 Not estimated due to imprecision of estimates of one or both variance components.

SITES, ESTABLISHMENT AND MANAGEMENT

Improved stock can be deployed through control-pollinated seed of full-sib families (with the option of vegetative amplification), and ultimately, through clonal forestry (Burdon 1991). If vegetative propagation is used, some physiological ageing (maturation) can be introduced. Such maturation can improve stem form in radiata pine (Menzies et al. 1991). Another approach being researched is to cross highly-ranked long-internode selections with Growth and Form selections showing outstanding form and fast growth.

There are strong site effects and management considerations in growing trees with long internodes. Trees grown on the central plateau of the North Island or at higher latitudes in the South Island tend to have longer internodes than on low-elevation sand-dune and clay soils in the northern North Island. Differences expressed among genotypes are greater on sites with good expression of the long-internode habit, and there appears to be little breed x site interaction for internode length (Carson and Inglis 1988). Stand density appears to have minor effects on internode length (Grace and Carson 1993). However, long-internode genotypes grown on fertile sites at wide spacing tend to have poor form and to grow very large branches. Long-internode trees are also susceptible to top breakage in areas with frequent strong winds. Thus it is clear that the long-internode breed needs to be targeted to appropriate sites (i.e. certain sites in the South Island and less fertile sites in the central North Island) and given appropriate silviculture (Carson and Inglis 1988). A model has been developed to predict stand mean internode length for stands of both genetically improved and unimproved P. radiata (Grace and Carson 1993).

INTERNODE LENGTH, WOOD PROPERTIES AND UTILISATION

Trees from the Growth and Form breed tend to produce wood acceptable for lower-value framing timber or pulpwood from the unpruned part of the stem (second log and upwards), especially when grown at wide spacing. In contrast, long-internode trees are commercially valuable due to greater yield of knot-free lumber (short clears) in the unpruned part of the stem for a variety of industrial uses (e.g. random width boards for US millwork industry, veneer, appearance-grade clear cuttings, fingerjointings etc). This was shown, for example, in a recent sawing and wood-properties study involving ten 28-year-old clones with two trees per clone (Beaureguard, R., Gazo, R., Kimberley, M., Turner, J., Mitchell, S and Shelbourne, C.J.A., unpublished data). The clones were selected for a range of internode length, branch size, wood density, and diameter at breast height (dbh), and representative logs were sawn into random-width boards. All boards were graded by both Western (USA) Lumber Rules and New Zealand Appearance Grades, and (after resawing to framing), by NZ Visual Framing and Australian Machine Stress Grading Rules.

Broad-sense heritabilities for dbh, branch index (largest four branches per log) and internode index (percent internode lengths > 60 cm), spiral grain and density were over 0.9. The three long-internode clones showed values per m^3 that were 30-40% higher than the value of the other seven short-internode clones. These preliminary results, based on a very small number of clones, suggest that selection for high internode index can result in large gains in grade and value for US random-width boards and NZ Appearance Grade lumber.

By contrast, only minor differences were found in machine-stress framing-grade and value between multinodal and long-internode clones. At least for this inaterial, it appeared that if branch size is controlled by relatively high stocking (350 stems/ha in this test), select clones of the long-internode breed could be used for structural timber, especially if also selected for clearwood stiffness.

FUTURE DEVELOPMENT OF THE LONG-INTERNODE BREED

The market demand for millwork lumber is predicted to remain, and recent studies have highlighted the product value associated with long-internode trees. The best second-generation selections appear to combine the long-internode habit with good growth and form. Pruning is costly in general and hard to effect on certain sites (e.g. steep areas), and major forest owners are reassessing the economic rationale for pruning (Anonymous 1997). These factors can make growing of a long-internode tree cost-effective for some growers. The tree of choice will have good (but not extreme) expression of the long-internode habit, with acceptable growth, form and wood properties.

The next major advance of the long-internode breed will be the formation in 1998 of 2 sinall elite sublines of about 12 individuals each. These will contain the best of the 3 distinct genetic resources available (about 50 available first-generation clones, 37 second-generation clones, and the 153 full-sib families). Internode length will remain a major emphasis, with threshold values imposed for growth rate, stem form, resistance to Cyclaneusma needlecast, wood stiffness and spiral grain angle. Cvclaneusma needlecast can limit productivity on some sites, while radiata pine trees with high grain spirality produce unstable lumber. Clonal tests will be used in parallel with seedling progeny tests for estimation of breeding values. Crosses among the highly selected elite clones will be suitable for immediate use in the production population. Future breeding will largely be within the sublines, allowing for unrelated crosses between sublines for production purposes.

WHAT INSIGHTS CAN THE LONG INTERNODE BREED PROVIDE?

We feel the development of the long-internode breed of radiata pine can lead to several useful insights. First, the success of the programme is largely due to a long-term commitment (over 27 years) towards this goal, with only minor modifications along the way. Second, this goal of obtaining a specific end-product for clearly defined markets was slightly ahead of its time. In this case tree breeders anticipated, rather than catered to, industry requirements. Third, the differentiation of breeds is a logical progression in the intensity of management of forests. The progression is 1) natural stands 2) unimproved plantations 3) genetic improvement of growth rate, form and adaptability and 4) specific breeds for specific products.

Fourth, the differentiation of breeds is logical where adverse genetic correlations exist. In the case of radiata pine it is difficult to achieve rapid, simultaneous improvement of internode length, growth rate and stem form; some trade-offs are inevitable. For some end uses, the added value of knot-free lumber from the long-internode material can compensate for reduced gain in growth rate, branch size and straightness; for others it would not. Fifth, a strong knowledge base (genetic parameters, economic weights, etc) is needed to make the hard choices of what traits to optimize for a given product. Sixth, appropriate use of site and silviculture play an important role in optimizing the value this breed.

CONCLUSIONS

Differentiating radiata pine into breeds or clones selected for different end-uses is possible for a variety of end-products. The early development of a long-internode breed is one example. Markets and technologies can change enormously during the time it takes to grow a crop of this species and a "portfolio" of breeds and clones of known characteristics may prove to be the most profitable in the future. However, improved juvenile wood is likely to be necessary for all purposes.

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