NEW ZEALAND'S LONG INTERNODE BREED OF *PINUS RADIATA*

K. J. S. JAYAWICKRAMA, C. J. A. SHELBOURNE, and M. J. CARSON

New Zealand Forest Research Institute Limited, Private Bag 3020, Rotorua, New Zealand.

(Received for publication 24 October 1997; revision 9 February 1998)

ABSTRACT

Pinus radiata D.Don shows marked variation in the number of branch clusters formed annually, with a corresponding variation in"internode" length (distance between branch clusters). Long internodes are commercially valuable due to greater yield of knot-free lumber in the unpruned part of the stem. Internode length is under strong genetic control and is highly amenable to selection. In a recent sawing study trees of clones selected for long internodes gave much higher lumber value as U.S. shop grades than short-internode trees.

Breeding for internode length began in 1970 with the selection of 104 long-internode plus-trees. Subsequent work included open-pollinated progeny testing of both the first-generation selections and 74 second-generation selections, making and testing 153 crosses involving 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 gains in volume growth, branch size, and stem quality. The Long Internode breed has been separated from the main breeding population. The goal is a tree with one or two branch clusters per year, to be grown on appropriate sites with suitable silviculture. Deployment of improved stock is by using seedlings or cuttings from control-pollinated seed. A clonal forestry option also exists. The next step to advance the Long Internode breed is likely to be forming two small elite sublines. Future breeding will largely be within the two elite sublines, allowing for unrelated crosses between sublines for production purposes.

Keywords: clearwood; millwork lumber; branching; branch clusters; knots; tree breeding; genetic gain; *Pinus radiata*.

INTRODUCTION

Pinus radiata is the main commercial forestry species in New Zealand. Various products are manufactured from *P. radiata*, including boards, structural timber, veneers, posts and poles, panel products, reconstituted wood products, kraft and mechanical pulp and paper (Carson & Inglis 1988; Kininmonth & Whiteside 1991).

Genetic improvement of *P. radiata* in New Zealand began in 1953 with selection of firstgeneration plus-trees in plantations (Thulin 1957; Shelbourne *et al.* 1986). It was soon clear that *P. radiata* varied from 1 to 6 in branch cluster frequency (the number of branch clusters formed annually), with occasional trees failing to form any branch clusters in some years (Bannister 1962). As branch cluster frequency increased there was a corresponding decrease in the distance between branch clusters. This distance is commonly called "internode" length by foresters, although in strict botanical terms the stem segment between branch clusters in *P. radiata* is not an internode (Bannister 1962). Branch cluster frequency soon proved to be at least moderately heritable (Bannister 1969).

The main breeding programme for *P. radiata* has emphasised selection for fast-growing, well-formed trees with light, wide-angled branches (Thulin 1957; Shelbourne *et al.* 1986). This phenotype is good for structural timber (framing, etc.) and, when pruned, knot-free timber. These selections have formed the main breeding population, from which the "Growth and Form" breed (Carson & Inglis 1988; Carson *et al.* 1990) has been selected. However, the selection has also driven average internode length below that of unimproved plantations (Carson & Inglis 1988), which reduces the yield of clearwood in unpruned logs. By 1970, there seemed to be justification for development of a separate breed of *P. radiata* with long internodes. This tree type was to meet the need for boards, short clears for remanufacture, and clear veneers from short peeler bolts (Shelbourne 1970).

In addition to the long-term emphasis on improving growth and log quality, tree breeders in New Zealand are now focusing on improving wood properties related to specific endproduct values. Improving juvenile wood quality (particularly stiffness and stability) has become a major new challenge. An increasing area of plantations is being established as fullsib family blocks, and clonal forestry is now practised on a small scale. It is likely that forest trees will be increasingly differentiated into "breeds" similar to agricultural cultivars.

This paper summarises over 27 years' work on the long-internode breed of *P. radiata* in New Zealand, targeted at appearance-grade lumber, and an early example of breed differentiation for a forest tree species. While some published information is reviewed briefly, much of the emphasis is on unpublished results from trials established by the New Zealand Forest Research Institute.

FORMING THE LONG-INTERNODE BREED

Stages in forming the Long Internode breed (Fig. 1) are outlined below.

Plus-tree Selection

Over 150 plus-trees with the long-internode habit were selected in 14- to 18-year-old plantations, in the northern part of Kaingaroa Forest, between 1970 and 1973 ("870" and "873" series—Shelbourne *et al.* 1986). In order to find sufficiently straight trees, with long internodes on the part of the stem between 3 and 16 m above ground, selectors cruised about 10 ha per tree selected. This translated to a selection intensity of one in 4000 dominant or co-dominant trees. Open-pollinated progenies of 104 of these selections were established as an initial breeding population.

A further 52 first-generation long-internode trees (part of the "885" series) were selected in 1985. These 52 were among 468 plus-trees selected in 1000 ha of 13- to 41-year-old plantations in the northern boundary of Kaingaroa Forest, equating to an intensity of one long-internode tree per 20 ha. The other criteria for selection were vigour and stem



FIG. 1–Stages in the development of the Long Internode breed of *Pinus radiata* in New Zealand, 1970–2000.

straightness. Open-pollinated seed was collected from these 52 selections to establish progeny tests (jointly with progeny of "883" series selections, *see below*) on two sites in 1987. Progeny of an additional 503 plus-trees were planted in 1988 and 1989 ("887" and "888" series); branch cluster frequency was not a factor determining acceptance in these selections.

Second-generation Selections

Seventy-four trees (the "883" series) were selected in 1982—69 within open-pollinated progeny tests of first-generation selections and five from a small control-pollinated test. These were selected from 51 of the "870" families, with one or two selections made within each of the 24 top-ranked first-generation families and only one within each of the next 27 families. Ranking of families was based on internode length, diameter, incidence of malformation, stem straightness, and crown health; selection of plus-trees within families was based on the same traits, and also the presence of cones (for intercrossing).

Advanced-generation Crossing Programme

Control-pollinated trials with 153 crosses (of first- and second- generation parents) were planted on two sites in 1990 and will be measured in 1998. These crosses were generated using 69 first-generation parents as females to produce 72 crosses with second-generation parents and 81 crosses with first-generation parents (from one to five crosses per female). In all, 143 genotypes participated in these 153 crosses. A small subset (10 families) was also propagated clonally, obtaining 123 clones in total. These were planted in 1990 on one site adjacent to the seedling trial.

Status as of 1997

The genetic resource of the long-internode breed (in clonal archives) now includes over 50 first-generation selections and 37 second-generation selections. There are also the potential advanced-generation selections, and the option of selecting first-generation "887" and "888" series parents whose progeny have long internodes, good growth rates, and acceptable form. For reasons described later, the long-internode breed has been kept separate from the main (largely multinodal) breeding population.

MEASUREMENT OF INTERNODE LENGTH

Several methods have been used to quantify internode length. The most direct, but also the most time-consuming, is to measure the length of internode between successive branch clusters up the stem. From these data can be derived *mean internode length* and measures of frequency of long internodes such as *internode index* (the proportion of the log in internodes of 60 cm or greater). This has usually been measured in the first and second logs, to 5.7 and 11.2 m respectively. A direct count of the *number of branch clusters* is another useful quantitative measure. *Branch cluster frequency* or *branch habit* is typically scored subjectively on a 1 to 9 scale, and is routinely assessed in genetic trials of *P. radiata* in New Zealand (and in trials by Australian members of the New Zealand Radiata Pine Breeding Co-operative). Although branch cluster frequency has proved a reliable trait to rank groups of families (grown together in common trials) for the long-internode habit, it is less reliable when comparing families grown in different trials and selected for different criteria (Turner *et al.* 1997).

INTERNODE LENGTH—GENETIC PARAMETERS AND GENETIC GAIN

Heritability estimates for branch cluster frequency are given in Table 1. Information on trial design and equations used, for the trials described in this section, are given in Appendices 1 to 4. Differences in internode length between contrasting progeny groups can be dramatic. The data in Table 2 are for progeny of first-generation long-internode selections, seedlings obtained from a first-generation Growth and Form orchard, and an unimproved seedlot. The largest difference was in the percentage of internodes above a given length. For example, although 45% of internodes exceeded 120 cm for the long-internode families, only 14% of internodes of the seed orchard progeny exceeded this length.

Similar dramatic results were shown in a 12-year-old genetic gain trial with replicated block plots of 64 trees (Table 3). Although controlled crosses among Growth and Form trees had increased branch cluster frequency by 1.9 units compared with "climbing select" material (climbing select = seed collected from good phenotypes in unimproved plantations), controlled crosses among long-internode trees had decreased branch cluster frequency by 3.0 units. The difference between the two breeds was thus 4.9 units. Internode lengths were not measured in this trial; however, as an indication, a perfectly uninodal tree (one cluster/year) could have internodes of 2 m on a good central North Island site, while a highly multinodal tree (six clusters/year) would have internodes of about 35 cm. Considered in isolation, branch cluster frequency in *P. radiata* is therefore a perfect trait for genetic manipulation—heritable, easy to assess, and of major economic value.

Genetic material	Age (years)	No. of families	Branch cluster frequency score		DBH		Straightness score	
			h ² i	h ² _{hs}	h² _i	h ² _{hs}	h ² i	h ² _{hs}
Native populations and								
New Zealand land race								
grown in New Zealand*								
Mainland California	8	50	0.27		0.16		0.20	
Guadalupe	8	50	0.21		0.30		0.14	
Cedros	8	50	0.20		0.27		0.14	
New Zealand land race	8	100	0.22		0.15		0.17	
First-generation selections' ("885 series")	Ť							
Site = Kaingaroa	8	467	0.33 (0.030)	0.67	0.21 (0.024)	0.56	0.21 (0.024)	0.56
Site = Pouto	8	467	0.36 (0.031)	0.70	0.22 (0.024)	0.58	0.21 (0.024)	0.57
First-generation long- internode selections‡ ("870 series")	10	104	0.19 (0.038)	0.63	0.24 (0.043)	0.70	0.28 (0.049)	0.74
Second-generation long- internode selections† ("883 series")	8	73	0.32 (0.077)	0.66	0.21 (0.060)	0.55	0.30 (0.074)	0.64

 TABLE 1–Heritability estimates from open-pollinated P. radiata progeny tests established in the central North Island of New Zealand.

* From Burdon *et al.* (1992a, Table 7). Each heritability estimate is based on plantings spread over 3 years on two locations, and is adjusted for departures from random mating. These estimates may be depressed due to being from large block units. Counts of the number of branch clusters on the stem, made at age 7, gave adjusted heritability estimates which were higher than the corresponding estimates for branch cluster frequency score: mainland 0.46; Guadalupe 0. 55; Cedros 0.31; New Zealand land race 0.49.

† From unpublished results of work by K.J.S.Jayawickrama. Each heritability estimate based on one location.

[‡] From unpublished results of work by M.J.Carson, C.J.A.Shelbourne and C.B.Low. Estimates based on one location.

 $h_{i}^{2} = narrow-sense heritability on an individual-tree basis; <math>h_{hs}^{2} = heritability of half-sib family means.$ Numbers in parentheses are standard errors of the individual-tree heritabilities.

Further details on the trials and estimation procedure are given in Appendix 1.

Although manipulating internode length is easy, the long-internode habit has some disadvantages. Some estimates of genetic correlations between branch cluster frequency and two major traits, diameter and stem straightness, are given in Table 4. They show that families with the long internode habit tend to grow more slowly, and are more crooked than families of trees selected for growth and form. This has been seen in other genetic trials of *P. radiata* in New Zealand (e.g., Burdon *et al.* 1992b). Referring again to the genetic gain trial, the long-internode control-pollinated families were less straight (1.2 points lower) and had fewer acceptable crop trees (52% v. 75%) than the high Growth and Form control-pollinated families (Table 3). Further, long-internode trees tended to show increased malformation, and had larger diameter branches and steeper branch angles, than highly

Jayawickrama et al.-Long Internode breed of Pinus radiata

	Dbh (cm)	Height (m)	Straightness (units)*	Mean internode length (cm)		Internodes > 60 cm (%)		Internodes > 120 cm (%)	
				Log 1†	Log 2†	Log 1	Log 2	Log 1	Log 2
Long-internode progenies‡§	26.2	16.4	5.94	55	91	62	83	33	58
First-generation seed orchard§	25.9	16.1	6.50	43	54	43	46	15	14
Unimproved§	24.6	15.7	4.41	48	74	52	68	20	40

TABLE 2-Comparison of internode lengths of first-generation long-internode progenies	with a first-
generation Growth and Form orchard seedlot and an unimproved seedlot.	

* Assessed on a subjective 1 to 9 scale (1 = very crooked, 9 = extremely straight).

† Log 1 = 0-5.5 m, Log 2 = 5.6-11 m.

‡ The highest ranked eight of 100 open-pollinated families, selected for internode length.

§ 32 trees measured per group.

From unpublished results of work by C.J.A.Shelbourne and D.Briscoe. Trees were measured in 1982 at age 10 in an open-pollinated progeny test in the central North Island (*see* Appendix 2). The following standard errors of the means were calculated from these data:

Dbh: 0.52 Height: 0.21 Straightness: 0.32 Mean internode length-Log 1: 2.6, Log 2: 6.1

Genetic material	Branch cluster frequency†	Dbh	Straightness‡	Acceptable crop trees (%)	
	Score Differ- (1–9) ence§ (units)	Mean Gain§ (cm) (%)	Score Differ- (1-9) ence§ (units)	Mean Differ- (%) ence§ (%)	
Bulked CP crosses between first-generation ("870") long-internode selections	2.38 -3.00 (0.091)	27.1 1.2 (0.23)	5.57 +0.99 (0.090)	52 +25	
Bulked CP crosses between first-generation Growth and Form (=GF) selections	7.28 +1.90 (0.085)	28.2 5.2 (0.21)	6.75 +2.17 (0.084)	75 +48	
OP orchard mix of best 25 first-generation GF selections	6.33 +0.95 (0.090)	28.0 4.6 (0.22)	5.53 - 0.95 (0.088)	53 +26	
Climbing select seedlot	5.38 (0.087)	26.8 (0.22)	4.58 (0.085)	27	

TABLE 3-Comparison of long-internode seedlot with other seedlots in a large-plot genetic gain trial at age 12 years*

* Unpublished results from work by C.B.Low. Age 12 results from a trial planted in the central North Island (*see* Appendix 3). CP = control-pollinated, OP = open-pollinated, Climbing select = seed from good phenotypes in unimproved plantations. Numbers in parentheses are standard errors of the means.

* Measured on a subjective scale (1 = 1 cluster per year, 9 = highly multinodal).

Measured on a subjective scale (1 = very crooked, 9 = perfectly straight).

§ Compared to climbing select.

Trial series and site	Genetic con cluster f	relation of branch requency* with	Source of information		
	Dbh	Straightness [†]			
"850" series polycross fan	nilies				
Woodhill	0.37	0.56	Unpubl. results of work by		
Kaingaroa	0.54	0.51	C.J.A.Shelbourne and C.B.Low		
Golden Downs	0.13	0.38	(age 9, 106 families)		
"885" series open-pollinat	ed Growth and	Form families			
Kaingaroa	0.18	0.43	Unpubl. results of work by		
Pouto	0.18	0.33	K.J.S.Jayawickrama (age 8, 467 families)		
"883" series open-pollinat	ed Long Intern	ode families			
Kaingaroa	0.26	0.12	Unpubl. results of work by K.J.S.Jayawickrama (age 8, 73 families)		

TABLE 4-Estimates of genetic correlation coefficients for branch cluster frequency, with dbh and stem straightness.

* Scored on a subjective scale (1 = one branch cluster per year, 9 = highly multinodal).

Scored on a subjective scale (1 = very crooked, 9 = perfectly straight).

Further details on these trials and the estimation procedure are given in Appendix 4.

multinodal trees (Bannister 1980). While we can select well-formed trees with a longinternode habit, longer internodes do entail a reduction in gains for growth rate, stem form, and malformation.

Recent data give hope for breeding fast-growing, long-internode trees showing good form. Open-pollinated families of the best five of 73 second-generation long-internode ("883") clones showed no loss in growth and form compared to families of good first-generation ("885") clones suitable for the Growth and Form breed (best five of 467, on the same site). However, the branch cluster frequency score (on a 1–9 scale) of the second-generation families was 1.5 units lower (Appendix 1, Part A). Another comparison was possible at the same site: the mean for 73 second-generation families (over 2000 trees) v. the mean for 467 first-generation families (over 11 500 trees). Once again, the "883" series means for diameter at breast height (dbh), straightness, needle retention, and percentage acceptable stems were very close to those of the "885" series; however, the branch cluster frequency was 1.5 points lower. Two cycles of selection in the long-internode population achieved similar gains in growth and form to those from one cycle in the main population.

One point should be noted regarding the growth and form of the long-internode breed. Many more first-generation candidates showing average to high branch cluster frequency have been selected and tested in New Zealand (over 2000 compared to 200 long-internode selections) as they comprised the main breeding population. Thus, the best parents in the main breeding population come from a far larger pool of candidates than the best longinternode parents.

GROWING LONG-INTERNODE TREES

Carson (1988) conducted a financial analysis using the growth and log-quality model STANDPAK and numerous conservative assumptions. Using a range of price lists, the

Growth and Form breed (the production subset of the main breeding population) usually gave a better return than the Long Internode breed. Owing to the plantation industry's strong emphasis on growing trees for pruned clearwood, the Long Internode breed did not gain market acceptance. Under financial pressure, the main New Zealand seed company abandoned long-internode seed orchards with the result that the supply of improved seed dwindled. However, the forestry industry is finding that genetically improved stands giv a lower proportion of clearwood from unpruned logs. This has renewed interest in the Long Internode breed, and more particularly in extending internode length in the Growth and Form breed.

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 *P. radiata* (Menzies *et al.* 1991). Another approach, which is being researched, is to cross highly-ranked long-internode selections with fast-growing, well-formed selections from the main breeding population.

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 those on low-elevation sand-dune and clay soils in the northern North Island. While differences expressed among genotypes are greater on sites with good expression of the long-internode habit, there appears to be almost no breed \times site interaction (involving rank changes) for internode length (Carson & Inglis 1988). Stand density appears to have only minor effects on internode length (Grace & Carson 1993). However, long-internode trees on fertile sites at wide spacing tend to have poor form and to grow very large branches, more so than highly multinodal trees. Long-internode trees are also more susceptible to top breakage in areas with frequent strong winds. Thus, this breed needs to be targeted to appropriate sites and given appropriate silviculture (Carson & Inglis 1988). A model has been developed to predict stand mean internode length for stands of both genetically improved and unimproved *P. radiata* (Grace & Carson 1993).

INTERNODE LENGTH AND UTILISATION

The implications of internode length on utilisation were discussed in detail by Shelbourne (1970). Long-internode trees are commercially valuable owing to greater yields of knot-free lumber (short clears) in the unpruned stem, and are suitable for a variety of industrial uses (e.g., random width boards for the United States millwork industry, short clearwood peeler bolts for veneer, appearance-grade clear cuttings, fingerjointings, etc.). The United States market alone absorbs more than US\$60 million per year in high-value, long-length clear and cuttings grades (Jayne 1996). Unpruned trees from the Growth and Form breed tend to produce a much smaller volume of wood suitable for such purposes. However, highly multinodal trees provide the best knot distribution pattern and knot size for framing timber, for mechanical pulp, and for chemical pulp (Shelbourne 1970).

A recent sawing and wood-properties study, involving two ramets each of ten 28-yearold clones, was reported by Beauregard *et al.* (1997). The clones were selected for a range of internode length, branch size, wood density, and dbh, and representative logs were sawn into random-width boards. Broad-sense heritabilities were over 0.9 for dbh, branch index (largest four branches per log) and internode index (percentage internode lengths >60 cm), spiral grain-angle, and density. The heritability estimates are based on a very small number of clones, and may be biased upwards because of the selection described above. However, the data did suggest that long-internode clones can yield more high-value products from unpruned logs (U.S. random-width boards in this study) than short-internode clones of the same log size.

FUTURE DEVELOPMENT OF THE LONG-INTERNODE BREED

Market demand for millwork lumber is predicted to remain high, 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 (Anon. 1997). Given pruning costs around NZ\$1 per lift per tree, 200–400 final-crop trees/ha (Maclaren 1993), and three or more lifts to the top of the first log, pruning can cost NZ\$1000/ha or more, and this cost is borne early in the rotation. These factors can make growing of a long-internode tree cost-effective for some growers. The tree of choice will have good expression of the long-internode habit, with acceptable growth, form, and wood properties.

The New Zealand *P. radiata* breeding strategy is currently under review. It is likely that the next step for the Long Internode breed will be the formation of two small elite sublines, with about 12 individuals in each subline. These will contain the best selections from the first, second, and advanced generations. 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. The option of using clonal tests (in addition to the seedling tests) will be explored. Crosses among the elite clones will be suitable for immediate use in the production population. Future breeding will be within the sublines, allowing for unrelated crosses between sublines for production purposes.

In conclusion, New Zealand's Long Internode breed of *P. radiata* has progressed considerably since its inception in 1970. Much has been learned on potential gains from selection for internode length, and the attendant effect on other traits. A valuable genetic resource has been developed which is available for New Zealand's forestry industry.

ACKNOWLEDGEMENTS

The data presented are taken from many years of work done by the Genetics and Tree Improvement group of the New Zealand Forest Research Institute. I.J.Thulin played a leading role in starting *P. radiata* improvement in New Zealand, and M.H.Bannister led early research on the patterns of inheritance. R.D.Burdon, R.Cameron, S.D.Carson, A.Firth, P.A.Jefferson, J.King, C.B.Low, M.Miller, R.I.Parr, G.Stovold, T.G.Vincent, and M.Wilcox made important contributions. R.D.Burdon, M.Dieters, L.Gea, G.Hodge, C.T.Sorensson, and T.G.Vincent made useful comments on this paper. The New Zealand Radiata Pine Breeding Co-operative has provided financial support for this programme and sites for progeny trials. Government funding for tree breeding is provided through the Foundation for Research, Science and Technology.

REFERENCES

ANON. 1997: New Zealand. Widman's World Wood Review, May 4 (5): 1,4-5.

- BANNISTER, M.H. 1962: Some variations in the growth pattern of *Pinus radiata* in New Zealand. *New Zealand Journal of Science* 5: 342–370.
- ——1969: An early progeny trial in *Pinus radiata* 1. Juvenile characters. *New Zealand Journal of Botany* 7: 316–335.
- ——1980: An early progeny trial in *Pinus radiata* 3. Characters affecting log quality. *New Zealand Journal of Forestry Science* 10: 325–342.
- BEAUREGARD, R.; GADO, R.; KIMBERLEY, M.O.; TURNER, J.; MITCHELL, S.; SHELBOURNE, C.J.A. 1997: Genotype variation in radiata pine random width board quality. Pp.53–62 in IV Proceedings of CTIA/IUFRO International Wood Quality Workshop "Timber Management Towards Wood Quality and End-Product Value", 18–22 August, Quebec City, Canada.
- BECKER, W.A. 1992: "Manual of Quantitative Genetics". 5th ed. Academic Enterprises, Pullman, WA.
- BURDON, R.D. 1991: Position statement—clonal forestry with *Pinus radiata*. Pp.187–198 in Miller, J.T. (Ed.) Proceedings of FRI/NZFP Forests Ltd Clonal Forestry Workshop, 1–2 May 1989. *New Zealand Ministry of Forestry, FRI Bulletin No.160.*
- BURDON, R.D.; BANNISTER, M.H.; LOW, C.B. 1992a: Genetic survey of *Pinus radiata*. 3: Variance structures and narrow-sense heritabilities for growth variables and morphological traits in seedlings. *New Zealand Journal of Forestry Science* 22: 160–186.
- CARSON, M.J. 1988: Long-internode or multinodal radiata pine—a financial analysis. *New Zealand Ministry of Forestry, FRI Bulletin No.115.*
- CARSON, M.J.; INGLIS, C.S. 1988: Genotype and location effects on internode length of *Pinus* radiata in New Zealand. New Zealand Journal of Forestry Science 18: 267–279.
- CARSON, M.J.; BURDON, R.D.; CARSON, S.D.; FIRTH, A.; SHELBOURNE, C.J.A.; VINCENT, T.G. 1990: Realising genetic gains in production forests. *In* Proceedings of IUFRO Working Parties on Douglas fir, Lodgepole pine, Sitka spruce and *Abies* spp.—Breeding and Genetic Resources. Session: Genetic gains in production forests. Olympia, Washington, USA.
- GRACE, J.C.; CARSON, M.J. 1993: Prediction of internode length in *Pinus radiata* stands. *New Zealand Journal of Forestry Science* 23: 10–26.
- JAYNE, V. 1996: US market wobbles? N.Z. Forest Industries 27(11): 12-14.
- KININMONTH, J.A.; WHITESIDE, I.D. 1991: Log quality. Pp.5-1 5-21 in Kininmonth, J.A.; Whitehouse, L.J. (Ed.) "Properties and Uses of New Zealand Radiata Pine". Forest Research Institute, New Zealand Ministry of Forestry, Rotorua, New Zealand.
- MACLAREN, J.P. 1993: Radiata pine grower's manual. New Zealand Forest Research Institute, FRI Bulletin No.184.
- MENZIES, M.I.; KLOMP, B.K.; HOLDEN, D.G. 1991: Optimal physiological age of propagules for use in clonal forestry. Pp.142–146 in Miller, J.T. (Ed.) Proceedings of FRI/NZFP Forests Ltd Clonal Forestry Workshop, 1–2 May 1989. New Zealand Ministry of Forestry, FRI Bulletin No.160.
- SHELBOURNE, C.J.A. 1970: Genetic improvement in different tree characters of radiata pine and the consequences for silviculture and utilisation. Pp.44–58 in Sutton, W.R.J. (Ed.) "Pruning and Thinning Practice". 16–20 March, Rotorua, New Zealand. New Zealand Forest Service, FRI Symposium No. 12.
- SHELBOURNE, C.J.A.; BURDON, R.D.; CARSON, S.D.; FIRTH, A.; VINCENT, T.G. 1986: "Development "Plan for Radiata Pine Breeding". Forest Research Institute, Rotorua, New Zealand.
- THULIN, I.J. 1957: Application of tree breeding to forestry in New Zealand. New Zealand Journal of Forestry 7: 41–46.

TURNER, J.A.; CARSON, S.D.; MANLEY, B.R. 1997: Relationship of mean internode length to breeding values for branch cluster frequency. Pp.147–154 in Burdon, R.D.; Moore, J.M. (Ed.) "Genetics of Radiata Pine". Proceedings of IUFRO Conference 1–4 December, Rotorua, New Zealand. New Zealand Forest Research Institute, FRI Bulletin No.203.

DETAILS OF TRIALS LISTED IN TABLE 1, AND ESTIMATION OF HERITABILITIES

(A) "885" and "883" series selections

The data for both series are from a trial in the volcanic plateau of the central North Island (Kaingaroa Forest, Cpt 324) on a cutover *Pinus nigra* Arn. site at 570 m elevation, at 4×4 m spacing. The trial was established with a "sets-in-replications" (SIR) design with 25 replications of 21 sets. Of these 21 sets, 18 were for "885" series families and three were "883" series families. Each set had 30 seedlots (24 or 25 families and the rest controls). Single-tree plots were used. An average of 22.4 trees/family survived to measurement. The trial was unthinned at the time of assessment (age 8) but 100% pruned to 2 m height at age 6.

For the "885" series only, data from a second site (Pouto) were available. This was at an elevation of 30 m on a sand-dune site on the west coast of the northern North Island. Prior to planting, the sand was stabilised with marram grass and then enriched with lupin. The spacing was 4×3.5 m, and a SIR design with 25 replications of 18 sets was used. Each set had 30 seedlots (24 or 25 families and the rest controls). Single-tree plots were used. An average of 23.7 trees/family survived to measurement. The trial was unthinned at the time of assessment (age 8) but 100% pruned to 2 m height at age 6. Each trial was analysed separately, and the following statistical model was used:

Trait = mean + replication + family + residual

Narrow-sense heritabilities (h_{I}^{2}) were estimated as:

$$\hat{\mathbf{h}}^2_{\mathrm{I}} = 4\hat{\boldsymbol{\sigma}}^2_{\mathrm{f}} / (\hat{\boldsymbol{\sigma}}^2_{\mathrm{f}} + \hat{\boldsymbol{\sigma}}^2_{\mathrm{e}})$$

Heritabilities of half-sib family means (h_F^2) were estimated as:

$$\hat{h}_{F}^{2} = \sigma_{f}^{2} / (\sigma_{f}^{2} + (\sigma_{e}^{2} / n))$$

With

 σ_{f}^{2} = family variance σ_{e}^{2} = error variance n = effective number of trees per family

Standard errors of heritabilities estimated according to Becker (1992, p. 48).

(B) "870" series selections

The data are taken from a progeny test at Waimihia Cpt 785 (central North Island) of 104 open-pollinated progenies for trees from the "870" selection series (M.J.Carson, C.J.A.Shelbourne, and C.B.Low unpubl. data). The trial was established in 1972 at 500 m altitude on a first-rotation site. The spacing was 4×2 m. A SIR design was used with 10 replications of four sets, each of 28 seedlots and two controls. Ten-tree row-plots were used, thinned to five trees/plot at age 6; this gave an average of 43 trees/family when measured at age 10. This was a selective thinning to favour trees with good expression of the long-internode habit. The following statistical model was used:

Trait = mean + replication + family + family*replication + residual Narrow-sense heritabilities were estimated as:

 $\hat{\mathbf{h}}^2_{\mathrm{I}} = 4\hat{\sigma}^2_{\mathrm{f}} / (\hat{\sigma}^2_{\mathrm{f}} + \hat{\sigma}^2_{\mathrm{rf}} + \hat{\sigma}^2_{\mathrm{e}})$

Heritabilities of half-sib family means were estimated as:

 $\hat{\mathbf{h}}^{2}_{\mathrm{F}} = \hat{\boldsymbol{\sigma}}^{2}_{\mathrm{f}} / (\hat{\boldsymbol{\sigma}}^{2}_{\mathrm{f}} + (\hat{\boldsymbol{\sigma}}^{2}_{\mathrm{rf}} / 10) + (\hat{\boldsymbol{\sigma}}^{2}_{\mathrm{e}} / n))$

where σ_{rf}^2 = family*replication variance

Standard errors of heritabilities were estimated according to Becker (1992, p. 48).

DETAILS OF TRIALS LISTED IN TABLE 2

The data are taken from the same "870" progeny test at Waimihia Cpt 785 as described in Appendix 1 and are unpublished results of work by C.J.A.Shelbourne and D.Briscoe. The seed orchard mix was a 1971 collection from the "850" series clonal orchard at Kaingaroa. All four sets in replications 1, 2, 3, and 4 were sampled for this study which was conducted in 1982. The first two dominant or co-dominant trees encountered were chosen (1 seedlot × 4 sets × 4 reps × 2 trees = 32). The best eight out of 100 were also sampled by picking the best two progenies per set (as identified by the 10-year assessment) and choosing the first dominant or co-dominant tree in each plot (2 progenies × 4 sets × 4 reps × 2 trees = 32). Ranking of these progenies was primarily on their branch score, with some culling for slow growth and poor bole straightness.

The trees were rated for stem straightness and diameter measured at breast height. The trees were then climbed and the height (from the base of the tree) to the bottom and the top of each branch cluster was measured, up to a height of 11.2 m. Data for internode lengths presented in Table 2 are for the first and second logs.

DETAILS OF GENETIC GAIN TRIAL DESCRIBED IN TABLE 3

The data in Table 3 are part of the results of a genetic gain trial planted in 1984 in Cpt 327, Kaingaroa Forest. The trial was planted with 10 replications of 64-tree blocks per seedlot. The trial had been thinned to 300 stems/ha before the assessment. The results presented are based on the following number of trees per seedlot:

control-pollinated Long Internode	357 trees
control-pollinated Growth and Form	412
best 25 open-pollinated Growth and Form	371
climbing select	396.

DETAILS OF TRIALS LISTED IN TABLE 4, AND ESTIMATION OF GENETIC CORRELATION

(A) "850" series polycross families

The data are taken from a progeny trial of 106 polycross families planted at six locations in 1972. The families were generated by crossing 106 first-generation "850" series clones with a 10-clone pollen mix of clones derived from North Island seed orchards. A "sets-in-replications" design was used with 10 replications at each site. The polycross progenies were divided into three sets of 25 and a fourth of 31. Five seedlings of each seedlot were individually randomised within each replicate of sets 1–3 and an average of 3.5 seedlings per family were planted in each replication of set 4. The spacing was 4×4 m. Data are presented for the three sites with the highest heritabilities for the age 9.5 measurement. Brief descriptions of these three trials are as follows:

Site	Location	Soil type	Elevation	Trees measured per family
Woodhill Cpt 225, 230, 231	West coast of northern North Island	Dune sand	20	32.2
Kaingaroa Cpt 327	Volcanic plateau, central North Island	Volcanic ash and pumice	560	43.4
Golden Downs Cpt 345	Northern South Island	Moutere gravel	670	32.8

The following statistical model was used for the analyses of data from these trials:

Trait = mean + replication + family + family*replication + residual

(B) "885" series and "883" series open-pollinated families

The same trials described in Appendix 1.

(C) Estimation of genetic correlation for all three series

- r_G = family covariance [trait 1, trait 2] / [(family variance, trait 1)^{1/2} × (family variance, trait 2)^{1/2}]
 - = additive covariance [trait 1, trait 2] / [(additive variance, trait 1)^{1/2} × (additive variance, trait 2)^{1/2}]

For the "850" polycross families these variances and covariances were unweighted averages of the four separate estimates for the four sets.