GENETIC INFLUENCE ON SECOND-LOG BRANCHING IN *PINUS RADIATA*

M. S.WATT

School of Forestry, University of Canterbury,
Private Bag 4800, Christchurch, New Zealand

J. A.TURNER

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

and E. G. MASON

School of Forestry, University of Canterbury,
Private Bag 4800, Christchurch, New Zealand

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ABSTRACT

The development of planning models, which quantify the genetic influence on branch diameter at the family level, would enable forest managers to make informed decisions regarding the management of improved breeds of *Pinus radiata* D. Don. In a preliminary study of the genetic influence on branch diameter at the family level, progeny trials of both "850" seed orchard and long-internode selection series were sampled from a compartment in Kaingaroa Forest in the central North Island of New Zealand. Second-log measurements of branch diameter and internode length were taken from 210 trees within 30 families across the "850" seed orchard and long-internode selection series. After branch index was adjusted for diameter at breast height, the residuals were regressed successively against mean internode length and branch cluster frequency breeding value at the family level.

Mean internode length was significantly correlated to branch index residuals within each selection series, but it was not correlated to branch index residuals across selection series. In contrast, branch cluster frequency breeding value was moderately correlated to branch index residuals both within and across the two selection series. The failure of mean internode length to completely account for differences in branch index between selection series suggests that forest managers may to a certain extent be able to manipulate branch index independently of internode length.

Although this study showed that branch cluster frequency breeding value was correlated to branch index residuals across selection series at the family level, these findings are preliminary. If further research shows the relationship between branch cluster frequency breeding value, and branch index holds across other selection series, inclusion of branch cluster frequency breeding value in planning models may enable the genetic influence on branch index to be quantified at a more refined level than previously possible.

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INTRODUCTION

Tree breeding research suggests that numerous traits influencing tree size and quality can be manipulated to suit specific sites, management regimes, processing methods, and markets. The tree breeding programme can produce "designer trees"—planting stock with altered quality features such as branch diameter, internode length, stem straightness, and wood density.

The development of planning models that predict the branch diameter for improved breeds would not only aid selection of the appropriate genetic stock for the site and required end-use, but also enable managers to financially quantify the influence of different management strategies on improved genetic material.

Differences in branch diameter among broad genetic groups have been quantified (Shelbourne 1970; J.C.Grace unpubl. data; J.A.Brown & M.J.Carson unpubl. data). However, differences in branch diameter for individual families have, to date, been quantified only in terms of a subjective scoring of branch cluster frequency. A national ranking of families for this selection trait has been obtained through the development of breeding values (S.D.Kumar, S.D.Carson, F.C.Burger & P.A.Jefferson unpubl. data), using subjective data available from field progeny trials. Previous work (Turner *et al.* 1997) has shown that branch cluster frequency breeding values (brBV) provide a good explanation of variation in internode length among families in the breeding programme. This study sought to extend the previous work to explore the extent to which brBV can explain family variation in branch size.

In a study comparing branch diameter among climbing select, multinodal, and long-internode selection series progeny, branch cluster frequency was identified as being significantly associated with branch diameter, after correction was made for tree diameter (Brown & Carson unpubl. data). This research indicated that families with small branches will have a high branch cluster frequency (or short internodes), a result which leaves managers little scope to manipulate branch diameter independently of internode length. An additional aim of the study reported here was to investigate whether internode length is the principal determinant of differences in branch diameter between selection series with contrasting branching habits. A residual genetic effect remaining after the influence of internode length and tree diameter have been removed would indicate that branch diameter can be manipulated to some degree independently of internode length.

The objectives of this study were to (1) establish if either mean internode length (Fig. 1) or brBV is significantly related to objective measures of branch index (Fig. 2) within two selection series of contrasting branch habit, and (2) examine if the coefficients (slope and intercept) of these within selection series relationships are significantly different between selection series.

History of New Zealand *Pinus radiata* Improvement

A brief description of the history of New Zealand *Pinus radiata* improvement is given to provide background to the selection and development of open-pollinated seed orchards producing the multinodal and long-internode material on which this study was carried out.

Fig. 1

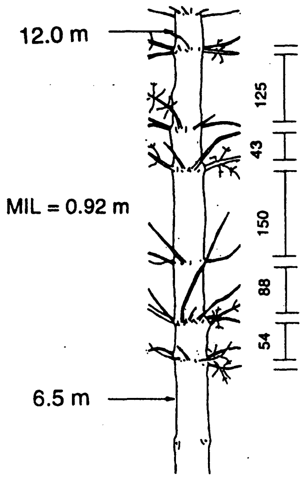

Fig. 2

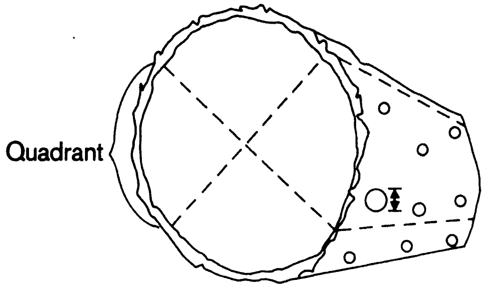

FIG. 1–Mean internode length = $\frac{\text{Sum of length (m) of internodes in branched section of log}}{\text{Number of internode lengths in branched section of log}}$

FIG. 2–Branch index (BIX) is the mean of the largest branch in each of four quadrants, for the nominated length (source: Inglis & Cleland 1982).

Earliest plantings

Earliest plantings of *P. radiata* in New Zealand were made using seed collected from Año Nuevo and Monterey, California. By 1927, importation of seed from this source for commercial plantings had ceased and New Zealand land races had subsequently developed (Vincent & Dunstan 1989). Records indicate that, from the planting boom of the 1930s until the early 1950s, seed was sourced mainly from stands within the New Zealand provinces of Manawatu and, to a lesser extent, Canterbury (Vincent & Dunstan 1989). As these initial collections took no account of parental phenotype, the seed is considered to be unimproved, and has a growth and form rating* (GF) of 1–3 (Vincent & Dunstan 1989).

Initial phenotypic improvement

Initial attempts to obtain improved seed were made during the 1950s, by felling and collecting from open-pollinated trees of phenotypically superior form (termed "felling select"), in stands approximately 40 years of age (Shelbourne *et al.* 1986; Burdon & Miller 1992). However, genetic gains arising from the felling select method were subsequently shown to be relatively poor. Introduction of the climbing select method in 1968 overcame these problems. Cone mixing was eliminated by climbing, while selection of trees in young stands (14 to 20 years) enabled higher selection standards to be met. Both climbing and felling select methods used a selection intensity of 10 to 25 trees/ha. Trees grown from seed

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* A rating assigned by the New Zealand Seed Certification Service for the Growth and Form breed, which reflects a seedlot's relative genetic worth for growth and stem form, with growth given twice as much weight as stem form (Carson 1996).

collected by the felling select method have an estimated average GF rating of 3 (Vincent & Dunstan 1989), while trees grown from the climbing select method have an estimated average GF rating of 7 (Vincent & Dunstan 1989).

Early seed orchards

Intensive selection (approximately 1 tree/100 ha) of vigorous well-formed "plus-trees" for planting in early seed orchards ("850"*) began in 1950 and continued until 1966 (Shelbourne *et al.* 1986; Burdon & Miller 1992). Plus-trees, chosen from the old crop stands planted between 1925 and 1935, were selected for a combination of the following features: straight stems, light flat-angled branching, absence of cones in the lower to mid bole, high vigour, and lack of malformation (Shelbourne *et al.* 1986). These apparently heritable features were chosen because of their perceived importance for the successful utilisation of *P. radiata* (Thulin 1957).

Using clones of the 14 phenotypically best trees from the "850" plus-tree selection, the first seed orchards were established at Kaingaroa Forest in 1957 (Shelbourne *et al.* 1986). Trees grown from these clones have an average estimated GF rating of 13. Later establishment of these "850" seed orchards at Gwavas and Kaingaroa, using the 25 and 36 phenotypically best clones, produced seed with an average estimated GF rating of 14. As these early seed orchards were open-pollinated, good isolation from genetically inferior pollen was necessary to maximise gains.

Initial difficulties experienced in production of improved seed from the "850" seed orchards indicated that the approach used was deficient in several respects. Delayed progeny testing, pollen contamination, and a lack of intensive reselection resulted in gains from "850" seed orchard seed which often did not realise the full potential of the material (Carson *et al.* 1990).

Long-internode selection

Trees for the North Island long-internode "870" breeds were first selected in the early 1970s, at an intensity of 1 tree/10 ha. Phenotypic selection criteria for clones were: freedom from malformation, stem straightness, good vigour, and uninodal branching habit. Trees with a single annual cluster of branches were initially sought. As trees with this branching habit were relatively uncommon, trees with a regular two-cluster (binodal) arrangement were more frequently selected (Fig. 3). Seed orchards were established in 1970 using the 104 parents selected. Later second-generation selections were made in the open-pollinated families and propagated into a clonal orchard (Shelbourne *et al.* 1986).

Genetic Gains of Improved Seedlots

Branch cluster frequency gains

Branch cluster frequency in *P. radiata* is under strong genetic control, with an estimated narrow sense heritability of 0.45 (Bannister 1969; Burdon & Miller 1992) and is associated

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* The number "850" is a prefix number denoting a particular series of clone. The first digit in the clonal series number refers to the regional origin of the clone (8 signifies collections carried out by the Forest Research Institute, not necessarily within one conservancy). The second digit refers to the year of selection, here 1950 (Vincent & Dunstan 1989).

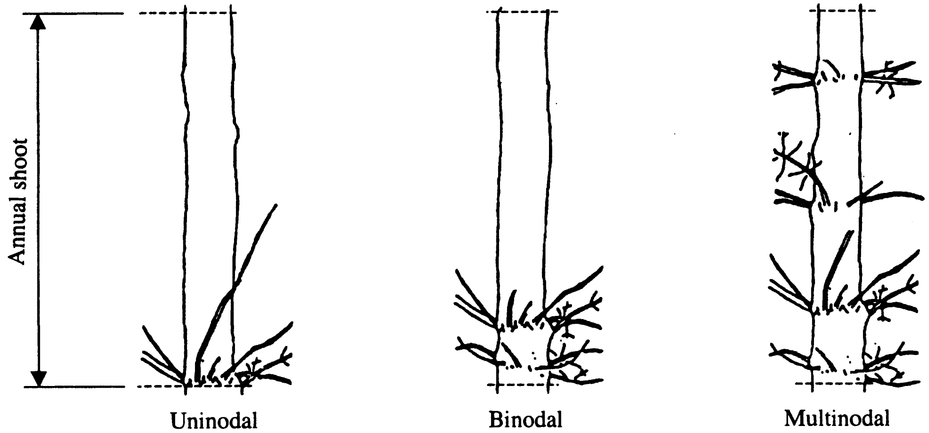

FIG. 3–Typical uninodal, binodal, and multinodal branch habit within an annual shoot.

with a "light, flat-angled branching habit" (Carson & Inglis 1988; Burdon & Miller 1992). The original selection of "850" seed orchard plus-trees for "light, flat-angled branching" will have transferred significant change in this trait to subsequent progeny. Measurement of large plot genetic gain trials at age 5 found "850" seed orchard material to have a 20% increase in branch cluster frequency score over bulk unimproved seedlots (Shelbourne *et al.* 1986). At age 12, the same trials indicated the branch cluster frequency score of the "850" seed orchard *P. radiata* to be 26% higher than that of felling select material (Sorensson & Shelbourne in prep.). In addition to increases in branch cluster frequency, "850" seed orchard progeny also have more branches on the first log than the felling select material (Cleland 1986).

Branch cluster frequency and branch cluster depth determine internode length. As well as being under genetic control, internode length is strongly influenced by site fertility and latitude, with shorter internode lengths occurring on sites with low fertility or at northern latitudes (Carson & Inglis 1988; Tombleson *et al.* 1990; Grace & Carson 1993). In a study that compared internode length across sites and genotypes, Carson & Inglis (1988) found the long internode "870" selection series had significantly longer mean internode length (MIL) than the "850" seed orchard material across all sites*. Stand stocking does not have a significant effect on internode length (Siemon *et al.* 1976 ; Grace & Carson 1993) on forest sites.

Branch diameter

(a) *Selection series comparisons*: An early study (Shelbourne 1970) investigating genetic gains from the breeding programme indicated some reduction in average branch diameter. It was found that average branch diameter of 11-year-old "850" seed orchard clones was smaller than that of the unimproved breeds by 19% in the first log and 10.7 % in the second log.

Shelbourne & D.Briscoe (unpubl. data) compared branch index (BIX) between 13-year-old trees from "850" seed orchard and long-internode "870" material to those from an

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* Sites included Woodhill, Kaingaroa, Golden Downs and Otago Coast.

unselected bulk seedlot. Compared to the "850" seed orchard material, BIX was on average 0.6 cm larger for the long-internode material. Only marginal differences (0.1 cm) in BIX were noted between the "850" seed orchard material and the unselected bulk seedlot.

(b) *Inclusion of a genetic effect in branch models*: Using data collected from selected sites throughout the country, a stand level model for predicting BIX was developed by Grace (unpubl. data), based on empirical data and assumptions about growth processes. To account for regional variation, it was found that central North Island sites were best modelled separately from all other areas.

For all regions, the model was based on the hypothesis that branches grow laterally either until they touch the crown of another tree, or are overtopped by other branches. To explain branch development in terms of this hypothesis, Grace (unpubl. data) formulated a model which predicted branch size from stocking.

The developed model comprised three components. Estimates of green crown height were made from stocking and predominant mean height at time of thinning. Whorl branch index* was then predicted from site index and either stocking or taper. Finally, BIX was predicted from whorl branch index, using equations that incorporated site index and number of branch clusters in the log length as variables.

Grace (unpubl. data) noted that the model could be applied to both "850" seed orchard and felling select material, as data collected by Shelbourne & Briscoe (unpubl. data) showed that differences in branch size between the two selection series were minor. Grace (unpubl. data) recommended, for long-internode material, that half a centimetre should be added to BIX.

R.L.Knowles & M.O.Kimberley (unpubl. data) investigated the effect of site fertility, diameter at breast height outside bark† (dbhob), stocking, site index, and genotype on second log branching. In this study empirical data were taken from 25 stands managed under direct sawlog regimes from both forest and farm sites. Their findings showed that BIX was significantly correlated to dbhob at age 20, to site index, and to genotype. It was also noted that the effects of stocking and site fertility could be explained by dbhob, provided the stand had been managed under a direct sawlog regime.

The original dataset (Knowles & Kimberley unpubl. data) was extended through the inclusion of a recently measured stand, and used to develop an empirical BIX prediction model for direct sawlog regimes (Kimberley & Knowles unpubl. data). Using site index, dbhob at age 20, growth and form factor (GF), and final thinning mean top height as variables, the model was associated with 98.5% of the variance in the dataset. It was found that branch indices of GF 14 trees were approximately 1 cm smaller than those of GF 7 trees, although the differences were strongly associated with dbhob at age 20 (Fig. 4).

(c) *Relationship between branch cluster frequency and branch diameter*: Brown & Carson (unpubl. data) compared the diameter of the largest branch from the diameter over stubs

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* Whorl branch index is the sum of the diameter of the largest branch in each quadrant of a whorl, divided by n, where n is the number of quadrants containing branches (Grace unpubl. data).

† Tree diameter at a height of 1.4 m.

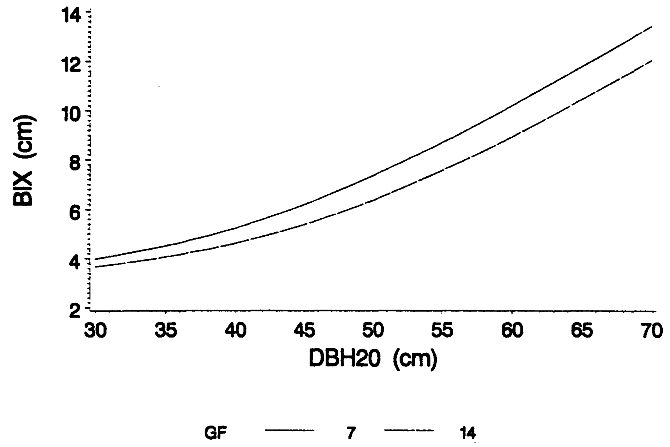

FIG. 4–Relationship of BIX to dbhob at age 20 (DBH_{20}) for GF14 and GF7 trees (source: M.O.Kimberley, R.L.Knowles unpubl. data).

(DOS) whorl within the first log, between progeny of selections from climbing select, multinodal, and long-internode material. The trees were sampled from an age 7 trial in Kaingaroa Forest, which had been planted at 1111 stems/ha and thinned to 600 stems/ha. To remove the effect of dbhob, "branch fineness" (the ratio of largest branch diameter to dbhob) was used as the dependent variable. Although the analysis indicated a strong correlation ($r^2 = 0.57$) between the number of branch clusters per log and "branch fineness", there were still small but significant differences between selection series after removal of this factor. Once the effects of dbhob and the number of branch clusters per log were removed, it was found that progeny of the long internode and climbing select material had slightly larger branches than the progeny of the multinodal selection series (Brown & Carson unpubl. data).

METHODS

Site and Trial Selection

Compartment 905, which is located within Kaingaroa Forest in the central North Island region of New Zealand, was chosen for the study. This compartment contains progeny trials of both the "850" and "870" selection series. The "850" selection series progeny trial was planted in a diallel design (Turner *et al.* 1997), which was composed of 50 families. The "870" selection series progeny trial is an open-pollinated sets in replicates design, with 104 parents (Turner *et al.* 1997), each represented by seven 5-tree-row plots.

Stand variables of both progeny trials are summarised in Table 1. Both trials received one thinning—the "850" progeny trial at an established mean top height of 1 m, and the "870" progeny trial at an estimated mean top height of 5.5 m.

Family Selection

Given the degree of association found between the number of branch clusters per log and "branch fineness" in previous work (Brown & Carson unpubl. data), it was calculated that at least 15 families within each progeny trial should be measured to adequately describe any

TABLE 1–Stand variables of the sampled progeny trials.

Selection Series	Goal	Experiment type	Year planted	Final stocking (stems/ha)	Stand ht. at thinning (m)
"850"	Multinodal	Diallel	1975	400	1
"870"	Uninodal	Sets in replicates	1972	450	5.5

possible relationship between MIL and BIX at the family level (M.O.Kimberley, Forest Research Institute, pers. comm.).

To ascertain if a relationship existed between MIL and BIX, families were sampled across the entire MIL range. MIL has been shown to be linearly related to brBV (Turner *et al.* 1997). Families within each progeny trial were separated into four quartiles, according to their brBV. Stratified sampling was used to increase the probability that families representing the extremes of brBV, and therefore MIL, were included. Using this technique, five families were randomly selected from both the bottom and top quartiles, while the other five families were selected randomly from the middle two quartiles.

A sample of seven trees was chosen to represent each family. Sample size calculations were based on MIL, as this trait is more variable than BIX (M.O.Kimberley, pers. comm.). Using second-log MIL measurements previously collected from the same trials (Turner *et al.* 1997), variation in this trait was calculated across a range of families, within both the long-internode and early seed orchard selection series. Analysis of these data showed that a sample size of seven trees per family permitted MIL to be predicted to within acceptable limits of error (standard error less than 15%) for both selection series.

Data Collection

Measurements were taken from December 1998 to February 1999. Only crop trees which had a dbhob greater than 30 cm and were free from ramicorns or basket whorls within the second log* were sampled. Dbhob of each sampled tree was measured, and cores were taken to enable calculation of dbhob at tree age 20 (DBH_{20}). Within the second log, the distance from the stump height (0.3 m) to the top and bottom of each branch cluster was measured. Using callipers, the horizontal diameter at the base of all branches within the second log was measured to the nearest millimetre. Each branch was allocated to one of four radial quadrants on the second log.

The complete dataset included measurements of 10 576 branches and 1819 branch clusters from 210 trees within the two trials.

From the data collected, MIL was calculated as the average of all internode lengths greater than 0.05 m within the second log. BIX was calculated as the mean of the largest branch in each of the four quadrants (Fig. 2) within the second log. Summary statistics of the measured trees, by selection series, are given in Table 2.

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* In this study the second log was defined as the branched zone on the tree from 6.5 m to 12.0 m (with an allowance of 0.3 m. for stump height).

TABLE 2–Descriptive statistics of the sampled trees, by selection series.

	N	Mean	Standard deviation	Min.	Max.
"850" selection series					
Dbhob age 23 (cm)	105	49.5	7.4	30.5	67.5
BIX (cm)	105	4.90	1.04	3.00	7.90
No. of branch clusters/log	105	9.4	2.4	4.0	16.0
No. of branches/log	105	52.3	12.4	20.0	85.0
MIL (m)	105	0.46	0.20	0.20	1.47
"870" selection series					
Dbhob age 23 (cm)	105	44.4	6.9	31.0	61.9
BIX (cm)	105	5.05	1.07	3.25	7.88
No. of branch clusters/log	105	7.8	2.4	3.0	12.0
No. of branches/log	105	48.8	12.3	23.0	82.0
MIL (m)	105	0.55	0.25	0.25	1.40

Data Analysis

Data analysis was undertaken using the general linear model (PROC GLM) procedure by SAS (SAS Institute 1989).

As dbhob is strongly associated with BIX (Inglis & Cleland 1982), the effect of this variable was removed by fitting a linear regression to family mean BIX for the combined dataset. Subsequent analyses at the family level used the residuals obtained after BIX had been adjusted for DBH_{20}, a dependent variable which will be hereafter referred to as BIX_{resid}.

Two separate general linear models were constructed to predict BIX_{resid}, using family level mean values of MIL or brBV. Covariance analysis was used to test for significant differences in selection series intercepts and slopes for these two models. Correlations of MIL and brBV to BIX_{resid} were assessed across selection series when there were no significant differences in selection series intercepts, and separately for each of the two selection series when significant differences in intercepts existed. To ensure that statistical assumptions* were not violated, the degree of association between independent variables was checked, and residual plots were examined for bias.

As a predictive variable, MIL does not indicate how whorls are clustered on the tree stem. For instance, a tree with an internode length of 0.8 m may have branch clusters distributed singly at uniform spacing (uninodal) along the stem or in groups of two (binodal), with longer internodal distances between the groups (Fig. 3).

The influence of branch cluster distribution on BIX was examined using a subset of the entire dataset, which included only those trees with MIL greater than 0.6 m, a length over which the binodal habit is more easily discernible from the uninodal habit. Trees were classed as uninodal if they had no internode lengths less than 0.25 m, or binodal if they had one internode length or more less than 0.25 m.

To examine whether branch cluster distribution influenced BIX after the effects of DBH_{20} and MIL had been removed, the following general linear model was constructed, at the tree level:

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* Statistical assumptions are no multicollinearity, heteroscadascity, and non-linearity

$$BIX = \alpha DBH_{20} + \beta MIL + \gamma \qquad \text{[Model 1]}$$

BIX residuals (BIX_{resid2}) obtained from Model 1 were plotted against MIL, by branch cluster distribution category (binodal and uninodal), to check if spatial distribution of branch clusters was an influence on BIX. Analysis of variance was used to statistically check for differences in BIX_{resid2} values between binodal and uninodal groups.

RESULTS

Removal of the Diameter at Breast Height (dbhob) Effect

At age 20, the linear relationship between BIX and DBH_{20} differed significantly ($p < 0.01$) between selection series (Fig. 5).

A moderate degree of association was found between DBH_{20} and BIX for both the "850" ($r = 0.74$) and the "870" ($r = 0.66$) selection series.

Plotting residuals against DBH_{20} and predicted BIX showed little apparent bias, indicating that there had been no violation of statistical assumptions.

Before additional analysis was undertaken, branch index was adjusted for DBH_{20} by fitting a linear regression to family mean branch index for the combined dataset. This dependent variable will hereafter be referred to as BIX_{resid}.

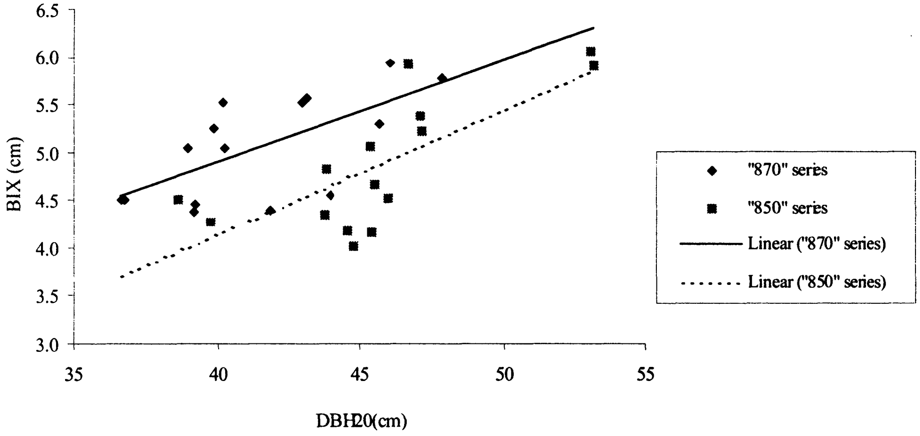

FIG. 5–Relationship between DBH_{20} and BIX at the family level, by selection series.

Influence of Mean Internode Length (MIL) on Branch Index Residuals (BIX_{resid})

The intercept of the relationship between BIX_{resid} and MIL differed significantly ($p < 0.01$) between selection series (Table 3). After adjustment was made for MIL, the "870" selection series had branch indices approximately 0.3 cm larger than those of the "850" selection series (Fig. 6).

TABLE 3–Significance of independent variables, series intercepts, and slopes. Dependent variable : BIX_{resid}

Test	Variable tested	Significance level
Independent variable	MIL	0.0001
Series intercepts	Series	0.0025
Series slopes	Series*dbhob age 20	0.7838
	Series*MIL	0.5718

Within each selection series, MIL was significantly associated with BIX_{resid}. The correlation coefficients between BIX_{resid} and MIL were 0.77 for the "870" selection series, and 0.58 for the "850" selection series. Removal of one family (circled Fig. 6) produced a non-significant relationship between MIL and BIX_{resid} for the "850" selection series.

The association between independent variables (DBH_{20} and MIL) was insignificant ($p > 0.05$), and residual plots showed little apparent bias.

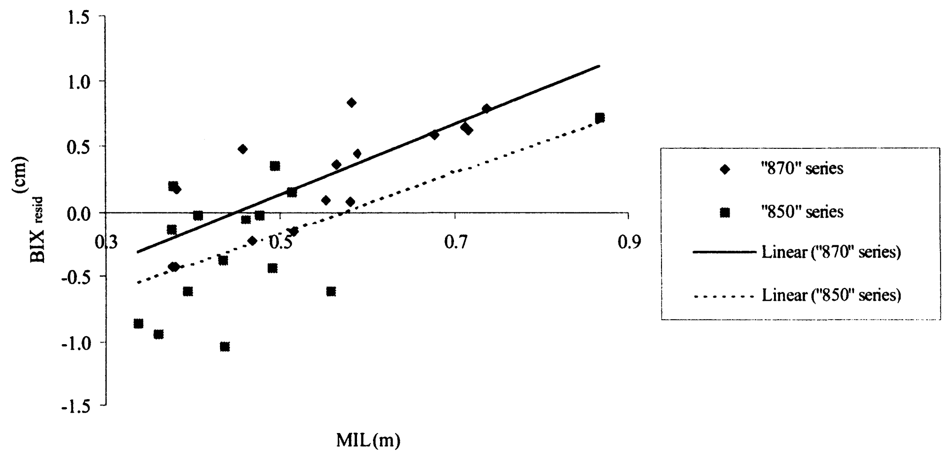

FIG. 6–Relationship between BIX_{resid} and MIL at the family level, by selection series.

Influence of Branch Cluster Frequency Breeding Value (brBV) on Branch Index Residuals (BIX_{resid})

There was a significant ($p < 0.01$) negative linear association (Fig. 7) between BIX_{resid} and brBV, which had a correlation coefficient of 0.69. There were no significant differences in either slopes or intercepts between selection series (Table 4).

Plots of actual BIX_{resid} against predicted BIX_{resid} and independent variables indicated that residuals were randomly scattered with little apparent bias. Although the two independent variables (DBH_{20} and brBV) were significantly related ($p < 0.01$), the correlation coefficient for the relationship of only 0.49, indicated a weak degree of association.

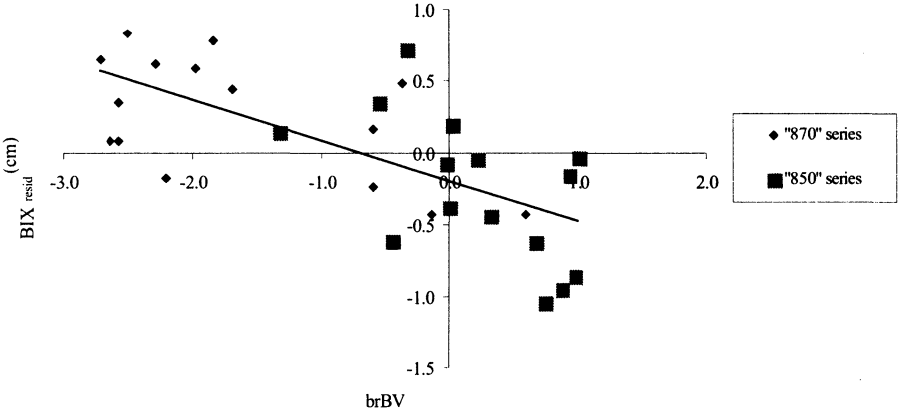

FIG. 7–Relationship betyween BIX_{resid} and brBV at the family level, by selection series.

TABLE 4–Significance of independent variables, series intercepts and slopes. Dependent variable : BIX_{resid}

Test	Variable tested	Significance level
Independent variable	brBV	0.0001
Series intercepts	Series	0.418
Series slopes	Series*dbhob age 20	0.217
	Series*brBV	0.826

Comparison of Within-tree Branch Cluster Distribution Between Selection Series

After adjustment had been made for DBH_{20} and MIL, there were significant ($p < 0.01$) differences in BIX_{resid} between selection series (Table 3, Fig. 6). To examine possible reasons for these differences, the within-tree spatial distribution of branch clusters was compared between selection series.

Within both selection series, trees were classified as either "uninodal" or "binodal". Trees with a MIL greater than 0.6 m were classified as "binodal" if they had one internode or more less than 0.25 m, and "uninodal" if they had no internodes less than 0.25 m. Selection series comparisons indicate that the "binodal" branching habit was more prevalent within the long-internode selection series (Fig. 8).

For a given MIL, "binodal" trees tended to have a larger BIX than "uninodal" trees. After BIX had been adjusted for DBH_{20} and MIL at the tree level, the residuals were separated into "binodal" and "uninodal" categories (Fig. 9). On average, BIX_{resid2} was slightly overpredicted for "uninodal" trees (residual mean = –0.07), and underpredicted for the "binodal" trees (residual mean = 0.33). However, the non-significance of these differences ($p > 0.05$) indicated that residual separation was not very pronounced. This may have reflected the limitations of the dataset and analysis in distinguishing between the "uninodal" and "binodal" branching habits.

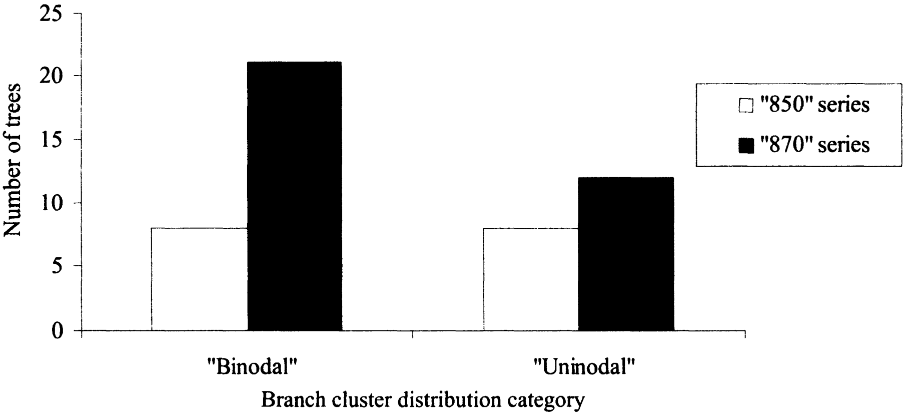

FIG. 8—Breakdown of trees with MIL over 0.6 m into branch cluster distribution category, by selection series.

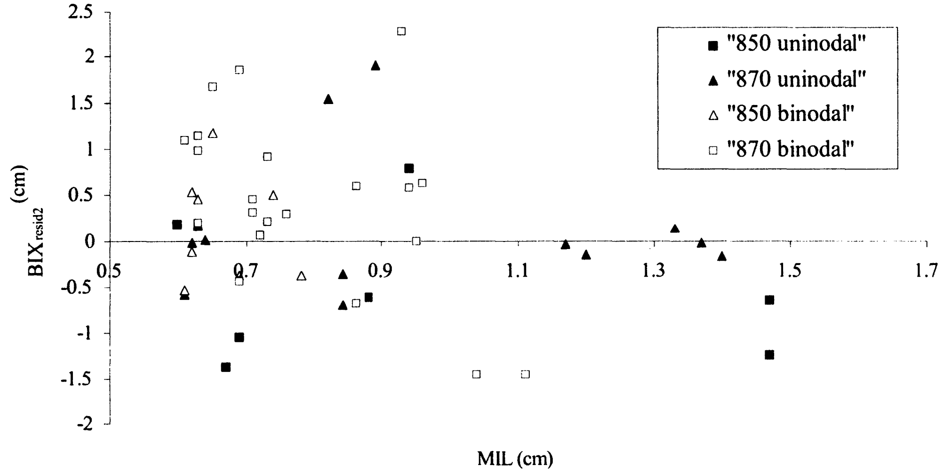

FIG. 9—BIX_{resid2} against MIL, by branch cluster distribution and selection series.

DISCUSSION

The study results have shown that, for a given dbhob, the long-internode "870" selection series had significantly larger branch indices than the "850" seed orchard selection series, a finding which is consistent with previous work (Shelbourne & Briscoe unpubl. data).

Branch cluster frequency breeding value (brBV) may be correlated with BIX across selection series, as this variable incorporated spatial measures of branch cluster distribution not included in MIL. After the effects of DBH_{20} and MIL had been removed, families within the long-internode selection series had a significantly larger BIX than those in the "850" seed orchard selection series (Table 3, Fig. 6). Results suggest this difference may be due, in part, to the greater frequency of "binodal" trees within the long-internode "870" selection series (Fig. 8) which, on average, had larger branch indices than "uninodal" trees of the same MIL (Fig. 9). While both MIL and brBV incorporated measurements of branch cluster frequency, only brBV included allowance for the spatial distribution of branch clusters. By accounting for the influence of branch cluster distribution on BIX, inclusion of brBV in the model may have enabled prediction of BIX to be made across combined selection series.

More research needs to be undertaken to assess the extent of any multicollinearity between dbhob and brBV. Although the sampled families covered almost the entire range in brBV, the range in family level DBH_{20} sampled was relatively narrow (37 to 53 cm). Further research should, therefore, check whether the relationship found between DBH_{20} and brBV is consistent across a broader diameter range.

The association of MIL and brBV with BIX may be confounded by differences in stocking between the two trials. The influence of stocking on branch size has been recognised (J.C.Grace unpubl. data; Makinen & Colin 1998). However, a number of studies have shown that stocking information could be excluded without loss of accuracy if dbhob were to be included as an independent variable (Inglis & Cleland 1982; M.O.Kimberley & R.L.Knowles unpubl. data; Makinen & Colin 1998). In accordance with these findings, an assumption underlying this study is that dbhob can be used to account for stocking differences, both within and between the selection series.

Practical Implications

After the statistical influence of dbhob at age 20 had been removed, MIL was associated with a significant amount of variation in BIX within both selection series. Adjustment for MIL significantly reduced selection series differences, from approximately 1.0 cm (Fig. 5) to 0.3 cm (Fig. 6). However, significant differences in BIX between selection series remained, possibly reflecting the fact that MIL does not account for variation in the distribution of branch clusters on the stem (binodal *v.* multinodal branch habit). The failure of MIL to completely account for differences in BIX between selection series suggests that forest managers may be able to manipulate branch diameter to a certain extent, independently of internode length.

The results showed that brBV was significantly associated with BIX (adjusted for dbhob age 20), and that the same regression equation holds for both selection series. If the relationship between BIX and brBV holds for other selection series, predictions of the genetic influence on BIX at the family level are likely to represent an improvement on past predictions made at the selection series level. Previously, branch index models have predicted the genetic influence at the selection series level, either through incorporating growth and form factor into the model (Kimberley & Knowles unpubl. data), or by using adjustments based on empirical data (Grace unpubl. data).

However, predictions of the genetic influence on BIX at the selection series level do not account for genetic variation in BIX between families within each selection series, which this study has shown can be considerable (Fig. 6). Although only preliminary, this research indicated that inclusion of brBV as a genetic modifier in planning models may enable the genetic influence on BIX at the family level to be quantified both within and between selection series.

Future Work

Although this study indicated that brBV was associated with BIX (adjusted for dbhob age 20) across two selection series, the findings are limited in many respects, as it is not known if this relationship holds for other selection series, sites, or different silvicultural treatments. Further research should examine genetic influences on branch size across a wider range of selection series. To explore the effects of site on genetic relationships with branch size, measurements of branch size would need to be taken from a wide range of trials throughout New Zealand, encompassing a diverse range of sites where *P. radiata* is grown. Silvicultural influences on the relationship between branch size and genetics would also need to be evaluated, through measurement of branch size from a range of thinning trials.

CONCLUSIONS

A moderate degree of association was found between dbhob at age 20 and branch index (BIX) for both the early seed orchard ($r = 0.74$) and long internode ($r = 0.66$) selection series. After the effect of dbhob (at age 20) had been removed statistically, families within the long internode "870" selection series had branch indices approximately 1 cm larger than those of the early seed orchard selection series.

Branch cluster frequency breeding value (brBV) was moderately ($r = 0.69$) correlated to residual branch index (BIX_{resid}, adjusted for dbhob at age 20). Once the effect of this variable had been removed there were no significant differences in family BIX between selection series.

Mean internode length (MIL) was significantly ($r = 0.58$ for "850" seed orchard selection series; $r = 0.77$ for long-internode selection series) related to BIX_{resid}, within each selection series. The relationship between BIX_{resid} and MIL differed significantly between selection series. After adjustment was made for MIL, families within the long-internode "870" selection series had branch indices approximately 0.3 cm larger than those of the "850" seed orchard selection series. This result may be due to MIL not capturing variation in branch cluster distribution on the stem (binodal *v.* uninodal branch habit) that is implicit in brBV.

Results from this study indicate that prediction of family level BIX from brBV is possible and that forest managers may to a limited extent be able to manipulate BIX independently of internode length.

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GLOSSARY

Basket whorls: Branch clusters containing numerous large branches. Above the cluster, there is a sharp reduction in stem diameter.

Breeding value (BV): A number that represents a parent's relative genetic worth compared to other parents. May represent genetic worth for a single trait or for a mix of traits, each with a specific economic value.

Branch cluster frequency score: A subjective score from 1 to 9 based on the number of branch clusters per year, where 1 = extremely uninodal, 9 = extremely multinodal for multinodal breeds, and 1 = extremely multinodal, 9 = extremely uninodal, for uninodal breeds (Carson 1991).

Branch Index (BIX): the mean of the largest diameter branch in each of four quadrants in a log (Inglis & Cleland 1982). A log is usually defined as 5.5 m length of bole.

Diallel design: Within this progeny trial design parents are divided into small 5- to 10-tree groups, and matings are done within each group.

Direct Sawlog Regime: Silvicultural regime in which the crop is thinned early to the final stocking.

Family: Denotes a group of individuals which have one or more parents in common.

Genotype: Particular assemblage of genes possessed by an individual.

Heritability: Expresses the extent to which phenotypes are determined by the genes transmitted from their parents.

Growth and form factor (GF): A rating assigned by the New Zealand Seed Certification Service for the Growth and Form Breed, which reflects a seedlot's relative genetic worth for growth and stem form, with growth given twice as much weight as stem form.

Mean internode length: $\frac{\text{Sum of length (m) of internodes in branched section of log}}{\text{Number of internode lengths in branched section of log}}$

Phenotoype: The physical characteristics expressed by a tree due to the interaction between the environment and the particular set of genes it has, i.e., its genotype (Falconer 1989).

Progeny: Seed produced from the same parent tree.

Ramicorn: A steeply angled branch which may have competed with the leader of a tree.

Selection series: Group of plus-trees identified at the same time for the same set of traits.

Site index: The mean top height (in metres) of a stand 20 years after the planting date.

Stratified sampling: Sampling technique whereby the population is divided into subpopulations (strata) of a known size, and a simple random sample is selected from each subpopulation.

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