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USE OF PHYLLOTAXIS TO PREDICT ARRANGEMENT AND SIZE OF BRANCHES IN *PINUS RADIATA*

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ABSTRACT

The location and size of branches in the tops (main stem diameter < 20 cm) of 16 *Pinus radiata* D. Don trees (26 years old) were recorded, and phyllotactic patterns in each branch cluster were described and analysed. Branch position and size within the cluster were examined in relation to ontogenetic sequence. Accurate three-dimensional branch locations were used to analyse branch azimuth and branch vertical position. Divergence angle, branch vertical position, and branch diameter within a cluster were all shown to be strongly related to position in the ontogenetic sequence. A mathematical model incorporating relationships between branch location, branch size, and phyllotactic pattern was constructed for the prediction of branch arrangement and development in *P. radiata*. The model has potential for forestry applications, particularly those involving log and timber grading, where reliable branch and knot size data are required.

Keywords: branches; mathematical models; phyllotaxy; *Pinus radiata*.

INTRODUCTION

The size and spatial arrangement of branches on a tree stem have a large effect on the quality of logs and wood products because of the problems caused by knot formation. It was suggested that a database containing descriptions of the stem features of young trees might be used to predict log quality at a future harvest (B. Rawley & W. Hayward pers. comm.), and so a project investigating *P. radiata* crown dynamics was initiated at the New Zealand Forest Research Institute in 1991. This involved a long-term programme of destructive sampling that encompassed trees influenced by a wide variety of genetic, site, and silvicultural factors (Grace *et al.* 1998).

During the course of this work, observation of the spiral patterns on *P. radiata* seed cones and stems led to a review of published work on phyllotaxy and branching and its relationship with well-established mathematical principles. Results of this review suggested that knowledge of the phyllotaxis of *P. radiata* might be useful in the construction of a spatial model of branch development and eventually in the prediction of branch location and size.

Background Information

*Morphology of **Pinus radiata** stems*

Bannister (1962) noted that the terms *internode* and *whorl* are often incorrectly applied to *P. radiata*. In this species the true internode, in its botanical sense, is the vertical separation between any two successive lateral members (branches, seed cones, or needles), and is therefore only a few millimetres in length. In botanical literature the term *whorl* is reserved for structures emerging at a common origin. *Pinus radiata* branches are separated vertically by the length of the internodes, and thus have individually distinct origins. In this report the term *cluster* is used instead of *whorl*. *Pinus radiata* trees typically produce a number of branch clusters in 1 year and are thus polycyclic. The portion of a stem consisting of a branch cluster and the section of stem below it has been variously referred to as a *stem unit* (Doak 1935), a *growth cycle* (Bollman & Sweet 1976), and a *growth unit* (De Reffye *et al.* 1995). The term *growth unit* will be used in this report. A growth unit contains a sequence of zones, each of which is characterised by a specific type of lateral member (Fig. 1). The sequence on a main stem growth unit (in order from top to base) is branches, seed cones, needles, cataphylls (sterile bracts). Seed cones are not always present since they are a feature of reproductive maturity. In mature trees they are normally borne on growth units initiated in the bud in summer and autumn, and subsequently elongated during the late winter and spring growth period (Fielding 1960; K. Horgan pers. comm.).
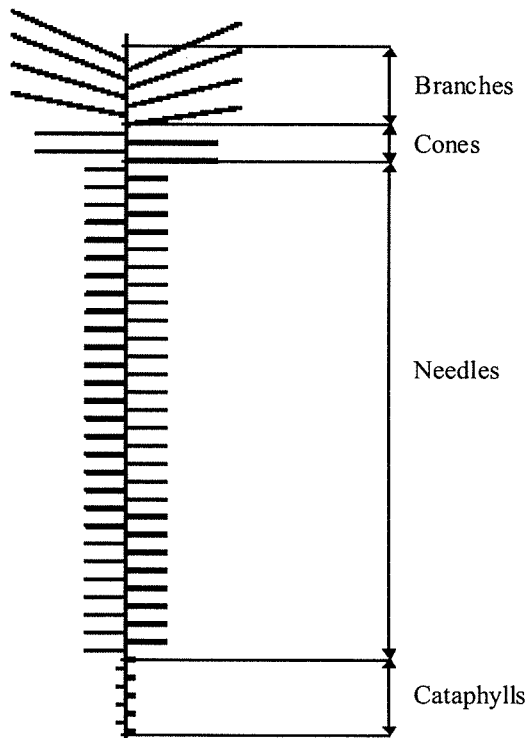

FIG. 1–Structure of a growth unit on the main stem of *Pinus radiata*.

Phyllotaxy

Phyllotaxy is the study of the arrangement of leaves on the axis of a plant. Terminology and principles of phyllotaxy have been reviewed by Stevens (1974), Boles & Newman (1990), and Stewart (1996). Zagórska-Marek (1985) collected information on a number of phyllotactic patterns observed in conifers and other species. Williams & Brittain (1984) and Jean (1988) demonstrated mathematical relationships between various phyllotactic patterns. Williams & Brittain (1984) developed a geometric model based on the "Next Available Space" theory of Snow & Snow (1932, 1933). This theory assumes that phyllotaxis is the result of competition for space by primordia after they are produced by a meristem. More recently Douady & Couder (1992) devised an elegant laboratory experiment and computer models which demonstrated a physical basis for the formation of the various phyllotactic patterns. Patterns established at the apical meristem maximise the space available to each emerging primordium and provide the basis for a stable plant architecture during subsequent growth. In *P. radiata* the growing space for each branch within a cluster will be maximised even though the number of branches in the cluster may vary. Cannell & Bowler (1978a) noted that phyllotaxis affects the distribution of vascular tissue, access to light, crown weight, and wind resistance.

Phyllotaxis of *Pinus radiata*

Pinus radiata has a spiral phyllotaxis. Primordia emerging from primary meristems in a generative or ontogenetic sequence become separated through the extension growth and diameter growth of intervening tissues into a helical arrangement. This spiral, the ontogenetic helix, develops vertically in either a clockwise (S or left-handed) or counter-clockwise (Z or right-handed) direction. The angle between two successive primordia on the ontogenetic helix is known as the divergence angle. The ontogenetic helix is not easy to discern in *P. radiata* but gives rise to other recognisable patterns known as parastichies. These are intersecting (opposed) sets of parallel helices, clearly visible on a pine cone and among scars left by scale leaves on the stem. In Fig. 2 is depicted an S ontogenetic helix connecting each primordial location, five Z parastichies which connect every fifth primordial location, and eight S parastichies connecting every eighth primordial location. This is one of the common arrangements found in *P. radiata*. Spatial distortion of an ontogenetic helix due to change in either vertical or radial growth will cause different numbers of parastichies to become apparent, even where the divergence angle remains constant.

Some features of common phyllotactic patterns are reproduced in Table 1. Although other patterns occur, they are regarded as unusual. Monojugate patterns relate to a single ontogenetic helix, and multijugate patterns are characterised by two or more ontogenetic helices. Bijugy denotes two ontogenetic helices, two primordia separated by 180° being produced at each level. Trijugy implies production of three primordia separated by 120° at each level.

The Fibonacci or primary pattern is the most commonly observed arrangement in species with a spiral phyllotaxis (Adler 1974). Numbers of opposed parastichies in monojugate primary patterns follow a sequence recognised by Leonardo Fibonacci in the thirteenth century. In this sequence, each number is the sum of the two preceding numbers. As the magnitude of the numbers increases, the ratio of two consecutive numbers rapidly approaches the Golden Ratio ($\Phi = 1.618...$) derived from the Divine Proportion identified in the fifteenth
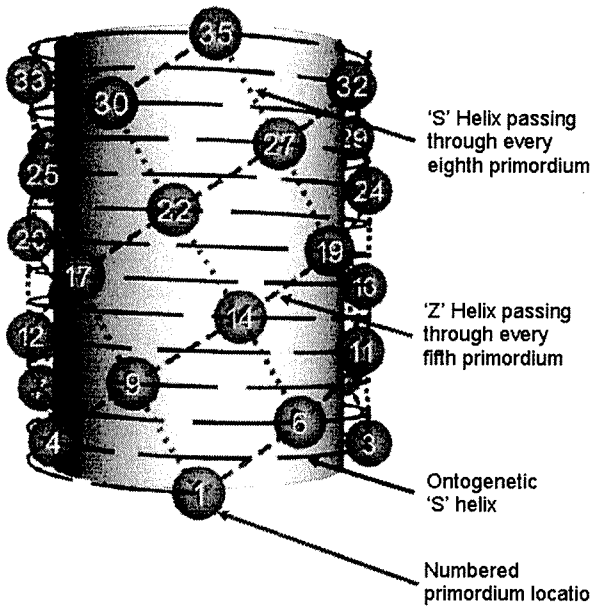
FIG. 2–Diagrammatic representation of a primordial arrangement commonly found in *P. radiata*. The arrangement of primordia in developmental sequence (here forming an S ontogenetic helix) gives rise to several subsidiary but more visible helical arrangements (parastichies). In this example five Z parastichies connect every fifth primordium (1, 6, 11...; 2, 7, 12... etc.) and eight S parastichies connect every eighth primordium (1, 9, 17...; 2, 10, 18... etc.). The 5 : 8 arrangement of opposing parastichies corresponds to the Fibonacci series 2, 3, 5, 8, 13... which defines a primary monojugate phyllotactic pattern having a divergence angle of 137.5°.

TABLE 1–Characteristics of helical phyllotactic patterns (*after* Zagorska-Marek 1985).

Phyllotactic pattern	Numbers of opposed parastichies	Theoretical divergence angle (degrees*)	Example
Monojugate pattern			
Fibonacci (primary)	2:3:5:8...	137.5	*Pinus radiata*
First accessory (secondary)	3:4:7:11...	99.5	*Sequoia sempervirens*
Second accessory (secondary)	4:5:9:14...	77.9	*Pinus halepensis*
Third accessory (secondary)	5:6:11:17	64.1	*Lycopodium selago*
Fourth accessory (secondary)	2:5:7:12...	151.1	*Pinus maritima*
Fifth accessory	3:7:10:17...	106.0	*Salix viminalis*
Sixth accessory	2:7:9:16...	158.1	*Cereus chilensis*
Seventh accessory	3:8:11:19...	132.2	*Plantago media*
Multijugate patterns			
Bijugy	2:4:6:10...	137.5/2	*Cephalotaxus drupacea*
Trijugy	3:6:9:15...	137.5/3	*Araucaria excelsa*

* Values given to nearest 0.1°.

century by Luca Pacioli. Multiplication of the number of degrees in a circle by the reciprocal of Φ gives an angle close to 222.5°. The reflex of this angle is close to 137.5° and is known as the Ideal Angle or Fibonacci Angle.

Branch azimuth

During application of phyllotaxy to consideration of branch azimuth, the vertical helix is commonly regarded as a spirally-expanded circle. For the Fibonacci pattern the theoretical divergence angle is close to 137.5°. It has been observed that many plant species including *P. radiata* demonstrate the Fibonacci sequence in their phyllotaxis and often exhibit divergence angles close to 137.5°. Cannell & Bowler (1978b) presented a computer model for the arrangement of needles on conifer shoots, based on a divergence angle of 137.5°.

MATERIALS AND METHODS

Sixteen 26-year-old trees in a breeding trial in Compartment 905 of Kaingaroa Forest were selected for destructive sampling. Eight of these originated from control-pollinated crosses between individuals with a multinodal habit. The remainder were selected from open-pollinated progeny of individuals with a uninodal habit (Table 2). Care was taken to include the whole range of mean internode length (MIL) observed in an earlier study at this site (M.S.Watt & J.A.Turner unpubl. data). Distortions of branch azimuth due to curvature of branches in the horizontal plane were avoided.

TABLE 2—Characteristics of sample trees

Habit	Family	Tree	Dbh* (cm)	MIL† (m)
Multinodal	1	1	36.1	0.35
		2	57.7	0.51
	2	3	41.4	0.46
		4	46.0	0.34
	3	5	32.9	0.35
		6	57.0	0.87
	4	7	42.2	0.80
		8	52.4	0.35
Uninodal	5	9	37.0	0.34
		10	48.6	0.71
	6	11	29.0	0.64
		12	46.3	0.38
	7	13	33.5	1.27
		14	49.3	0.48
	8	15	29.2	0.64
		16	44.0	1.55

* Diameter at breast height (1.4 m).
† Mean Internode Length.

The top section of the main stem (< 20 cm diameter) was removed from sample trees. Before each top was photographed and dissected, it was examined for annual scars left by the resting bud of the apical shoot. Individual clusters were cut out and numbered sequentially from the tree top. The number of annual rings at the base and top of each cluster was recorded. Cluster configuration was digitised using the methods of Smith & Curtis (1995) and a computer-based position tracking system (Broom *et al.* 1999) to produce a record of branch and cone locations in three dimensions. Scars in the bark around a branch were used to define the position of the branch origin at the stem pith boundary (D. Barthelemy

pers. comm.). This avoided errors associated with branch angle and stem growth. Lateral member type (branch or cone) was noted. Branch basal diameter measured adjacent to the stem but clear of the branch collar, was recorded to the nearest millimetre.

Opposed sets of parastichies were marked with a felt pen immediately below each cluster. Phyllotaxis was classified by counting the number and direction of the parastichies. The directions of the parastichies were used to define the direction of the ontogenetic helix. Clusters with seed cones appeared to have the same arrangement as other clusters, but the cones were found to obliterate the parastichies. Clusters containing seed cones were therefore excluded from further study. Altogether, 92 branch clusters were examined in detail.

The parastichies were then used to establish the ontogenetic sequence of branches from base to top of each cluster, branches being numbered in order of primordial development. In clusters with bijugate phyllotaxis, odd numbers were reserved for one ontogenetic helix and even numbers for the other. Two branches occupying the same level on different helices were therefore identified by successive numbers. Thus in a bijugate cluster with six branches numbered 1, 2, 3, 4, 5, 6, it was clear that Branches 1, 3, and 5 were associated with one ontogenetic helix, while Branches 2, 4, and 6 were associated with the other.

A pilot study (D.Pont unpubl. data) had revealed a potential problem caused by missing branches. Marking of parastichies and numbering of branches on the ontogenetic helices allowed the absence of a branch at a specific location to be clearly identified and recorded.

The collected data were used to analyse branch divergence angle, vertical separation, and relative branch size within clusters.

RESULTS

Frequency distribution of cones and branches within the sample clusters is shown in Fig. 3.
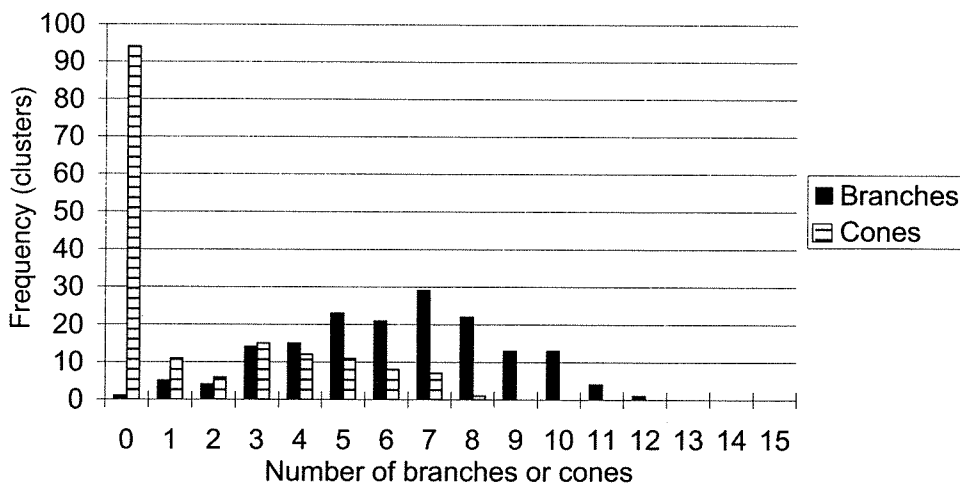

FIG. 3—Frequency distribution of branches and cones within clusters.

Phyllotaxis

Phyllotactic patterns identified in this study (Table 3) were Fibonacci (S and Z), First (S and Z) and Fourth (Z only) Accessories, and bijugy (S and Z). The Fibonacci pattern was most frequent (66% of all clusters), followed by the First Accessory pattern (12%), bijugy (9%), and Fourth Accessory (2%). Ten of the 92 clusters could not be sequenced. Trees 4, 6, and 14 each exhibited two patterns. Among the sequenced clusters, 78% had an S ontogenetic helix.

TABLE 3–Phyllotactic patterns in *P. radiata* trees sampled from a breeding trial in Kaingaroa Forest

Habit	Family	Tree	Number of clusters showing specific patterns									
			Monojugy					Bijugy		Obscure		Total
			Fibonacci		First accessory		Fourth accessory			?*	X†	
			2:3...		3:4...		2:5...	2:4...				
			S	Z	S	Z	S	S	Z			
Multinodal	1	1	9									9
		2	10									10
	2	3	7							4	1	7
		4						1		1		8
	3	5		2			2				3	3
		6		1					1			5
	4	7	6									6
		8						4				4
Uninodal	5	9	6									6
		10			7							7
	6	11				4						4
		12							3			3
	7	13	8									8
		14	3	1								4
	8	15	3								1	4
		16		4								4
		Total	52	8	7	4	2	5	4	5	5	92
		%	57	9	8	4	2	5	4	5	5	100

* Parastichies visible but ontogenetic sequence impossible to trace due to distortion.
† Parastichies not visible due to external damage.

Missing Branches

Following the ontogenetic sequence within a cluster, from the first to last branch, branches are expected to occur at regular angular intervals (the divergence angle) at the intersections of opposed pairs of parastichies. In almost one-third of the clusters, branches were not found at expected locations. Evidence of an aborted branch bud was sometimes present at those locations. In approximately 50% of these clusters, only one branch was absent (Table 4). All clusters with fewer than six branches had no missing branches. Absences were more frequent at the lower and upper ends of the cluster sequence. The numbering system used for unijugate patterns required the presence of branches in the first

TABLE 4–Numbers of clusters with missing branches.

| | No. of missing branches | | | | | | |
	1	2	3	4	5	6	Total
No. of clusters (Total = 82)	13	7	3	0	0	1	24

and last positions in a cluster, but in bijugate clusters the numbering method did not preclude absence of branches from these positions. Trees 4, 6, 8, and 12 contained bijugate clusters and in several of these a branch in one sequence did not have a corresponding branch on the other ontogenetic helix. In one bijugate cluster the branch in the last numbered sequence position was missing. Of the total number of absences, 40% were associated with the second position, and 33% with the penultimate position.

Relationship Between Spatial Arrangement of Branches and the Ontogenetic Sequence

Azimuth and divergence angle

The azimuth and the vertical position of each branch were derived from the digitised cluster configuration, and divergence angles were calculated as the difference in azimuth between each successive branch in the ontogenetic helix. Analysis of divergence angles was confined to complete clusters demonstrating Fibonacci or First Accessory phyllotaxis. Average divergence angles in these clusters were within approximately half a degree of the theoretical values of 137.5° and 99.5° respectively (Table 5). Frequency distributions of divergence angles for the two patterns were found to overlap (Fig. 4). In clusters with Fibonacci phyllotaxis, individual divergence angles were distributed evenly around the theoretical value, and most were within the range 120°–160°. No between-tree trends were apparent. Error variation among divergence angles within a cluster tended to alternate on either side of the origin, indicating that the azimuth error for each branch was independent of that of its neighbours. Any variation in azimuth was regarded as a local distortion of the overall phyllotactic pattern.

These observations suggested that the theoretical phyllotactic pattern and a fixed divergence angle would form an appropriate basis for the calculation of branch azimuth. An independent error term for each branch could be applied where appropriate. In order to test this hypothesis, the azimuth data were transformed and analysed as follows. A cumulative branch azimuth for each cluster was obtained by adding 360° for each passage of the ontogenetic helix through the origin (0°). This provided a series of increasing azimuth

TABLE 5–Divergence angles in clusters with Fibonacci or First Accessory phyllotactic patterns

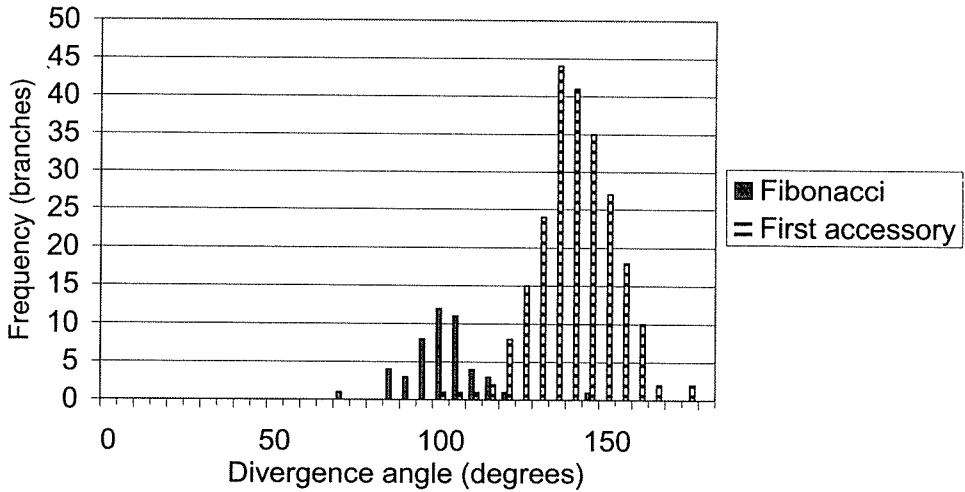| | Phyllotactic pattern | |
	Fibonacci	First Accessory
No. of observations	231	54
Minimum angle (°)	98.5	17.8
Maximum angle (°)	172.8	178.2
Mean (°)	137.92	98.97
Standard deviation (°)	11.41	19.09

FIG. 4–Frequency distribution of divergence angle in all clusters with Fibonacci (2:3) or First
Accessory (3:4) phyllotactic patterns.

values. Differences between theoretical and actual cumulative azimuth values at each branch
position were averaged for each cluster. Azimuth values for each branch were transformed
firstly by subtracting the azimuth of Branch No. 1, so that all clusters had a common origin
value (0° at the start of the sequence), and secondly by adding the average cluster difference
so that any bias due to local error in the azimuth of the first branch would be avoided.

Transformed azimuth values for branches within one phyllotactic pattern were fairly
constant over a maximum of 11 branch positions in the sequence (Fig. 5). The outlier in the
First Accessory phyllotactic pattern (Cluster 10/10) was excluded from further analysis.
Cluster 11/9 was also excluded because a single branch was found to be displaced by 70°
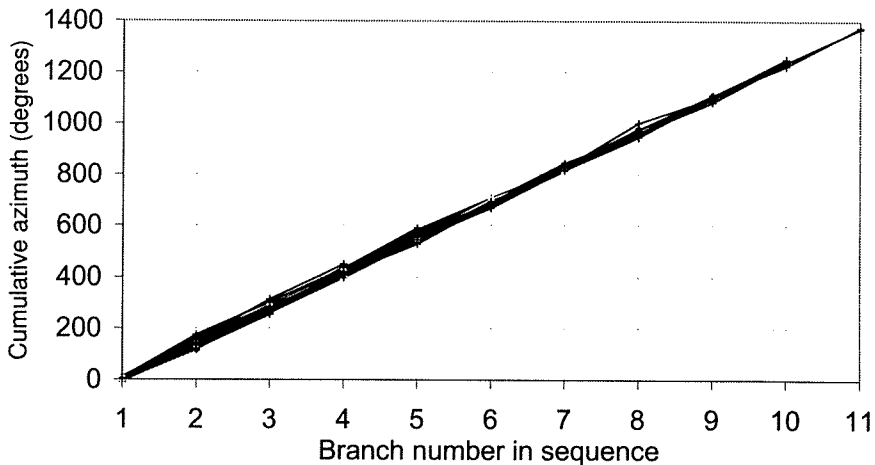from its expected position.

FIG. 5–Cumulative azimuth along the ontogenetic sequence for each cluster with Fibonacci
phyllotactic pattern.

Transformed azimuth data for each cluster were pooled by phyllotactic pattern to allow regression analysis of the linear relationship between branch azimuth and position in the ontogenetic sequence. Data for all branches were combined and the intercept was fixed to zero (Equation 1).

$$A = Sd \qquad\qquad (1)$$

where　A = branch azimuth (degrees from first branch in ontogenetic sequence)
　　　　S = branch position in ontogenetic sequence (S = 0 for first branch)
　　　　d = estimated value for divergence angle (degrees): for the Fibonacci pattern d = 137.58, for the First Accessory pattern d = 99.31.

The relationship was highly significant ($p < 0.001$). Residuals were plotted against tree number, cluster number, number of branches, position in ontogenetic sequence, azimuth, branch vertical location, branch diameter, cluster age, and cluster position in the annual shoot. No significant trends were apparent. Application of the Shapiro-Wilk test showed that residuals for the Fibonacci pattern were normally distributed. Distribution of residuals for the First Accessory pattern showed a high kurtosis value (Table 6).

TABLE 6—Results of test for normal distribution of azimuth residuals

	Phyllotactic pattern	
	Fibonacci	First Accessory
No. of observations	270	55
Mean	−0.27	0.01
Standard deviation	6.91	8.13
Skewness	−0.09	−1.20
Kurtosis	0.52	4.57
T:Mean=0	−0.65	0.01
Pr>|T|	0.52	0.99
W:Normal	0.98	0.92
Pr<W	0.31	0.002

Vertical location of branches

The vertical separation of successive branches along the ontogenetic sequence was calculated for each cluster in the Fibonacci and First Accessory data sets. An overall positive trend in the relationship between branch vertical position and ontogenetic sequence was apparent in spite of considerable variability. Errors associated with precision of measurement and digital data transformation had been anticipated and would have contributed to this variation. Variances for the two phyllotactic patterns were significantly different ($p < 0.01$).

A Student's t-test showed that the means for vertical separation of branches in the two phyllotactic patterns were not significantly different ($p > 0.05$). The two data sets were therefore combined for further analysis. A strong possibility of measurement error was known to be associated with Z helices. Six of the 46 clusters for which data were available had Z helices, and these were excluded from the data set.

Regression analysis showed a strong linear relationship ($p < 0.01$) between branch vertical location and branch position in the ontogenetic sequence (Equation 2).

$$L = Si \qquad (2)$$

where L = branch location (millimetres from first branch in ontogenetic sequence)
S = branch position in ontogenetic sequence ($S = 0$ for first branch)
i = estimated value for vertical separation: for the Fibonacci and First Accessory patterns $i = 3.49$ mm.

Analysis of the residuals for the linear regression revealed significant relationships with branch diameter, cluster age, and cluster number which were considered to be due to measurement error on larger branches. Tree number and cluster position in the annual shoot showed significant trends ($p < 0.01$ in both cases).

Application of Duncan's Multiple Range Test showed that Tree 3 had a greater mean vertical separation of branches than the other eight trees analysed, but no other between-tree differences were significant ($p > 0.05$). Vertical separation was smaller in the last cluster of the annual shoot than in the other clusters. Examination of residuals revealed that this effect, although statistically significant, was quite small. Application of the Shapiro-Wilk test showed that the residuals were normally distributed around their respective means.

Relationship Between Branch Position in the Ontogenetic Sequence and Branch Diameter

Observation of branch clusters revealed a tendency for branch diameter to increase along the ontogenetic sequence from the base to the top of the cluster, although a large amount of variation was apparent (Fig. 6). Since it was clear that no direct linear relationship existed, the significance of other relationships was explored.

Madgwick (1994, Fig. VI.19) showed that when *P. radiata* branches within a cluster were ranked in order of decreasing diameter, a strong negative exponential relationship existed between relative mean diameter and branch rank number. J. Grace (unpubl. data) observed
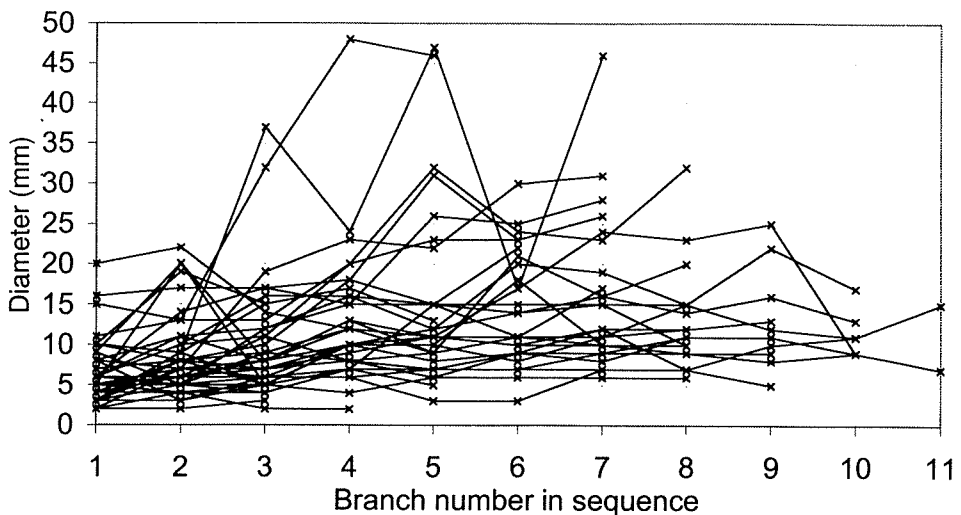

FIG. 6—Branch diameters in individual clusters.

high variability in this relationship among data for individual clusters. A sigmoid function was considered to be more appropriate for predicting relative branch diameter from three variables: branch rank number, cluster maximum branch diameter, and number of branches (Equation 3).

$$D_r = \exp(-a(R-1)^b) \qquad (3)$$

where $a = cN^d$

  $b = eM^f$

and D_r = relative branch diameter within a cluster

  R = branch rank, in decreasing order of branch diameter

  N = number of branches in cluster

  M = cluster maximum branch diameter (mm)

  $c\ d\ e\ f$ = model parameters.

The equation was modified by the replacement of branch rank number with branch position in the ontogenetic sequence, expressed in reverse order. In addition, absolute branch diameter was predicted by inclusion of maximum branch diameter as a multiplier (Equation 4):

$$D = M \exp(-a(S_{rev}-1)^b) \qquad (4)$$

where $a = cN^d$

  $b = eM^f$

and D = branch diameter within a cluster (mm)

  S_{rev} = position in ontogenetic sequence (reverse order)

  N = number of branches

  M = cluster maximum branch diameter (mm)

  $c\ d\ e\ f$ = model parameters (*see* Table 7).

TABLE 7–Parameter estimates for Equation 4

Parameter	c	d	e	f
Estimate	0.9844	−1.2800	0.6625	0.2372
Asymptotic standard error	0.3971	0.2410	0.1488	0.0539

Examination of branch diameter distributions within clusters did not suggest a need for separating the two phyllotactic patterns (Fibonacci and First Accessory) during analysis of branch diameter relationships, and data were therefore pooled. Regression analysis showed that for the combined data, the relationship expressed in Equation 4 had an r^2 value of 0.73. In order to examine the output of Equation 4 over a range of inputs, the number of branches per cluster was confined to 3, 6, 9, or 12, and maximum branch diameter to 10, 20, 30, 40, or 50 mm. The output appeared to be stable (Fig. 7). As an additional test, Equation 4 was used to predict relative branch diameter for each cluster in the data set using the actual maximum diameter and number of branches in each cluster. Predicted values were of the same order as those in the basic data set (Fig. 6).

Residuals from Equation 4 were plotted against predicted branch diameter, maximum branch diameter within cluster, branch position in the ontogenetic sequence, number of branches, age, position on shoot, tree number, phyllotactic pattern, vertical position, and azimuth. No trends were evident. Analysis of the residuals indicated that a small but

significant component was attributable to clusters with different numbers of branches. However, no consistent trend was observed for number of branches, and errors associated with individual numbers of branches were small. None of the other variables showed significant effects. Pooled branch diameter residuals were normally distributed around the mean (Fig. 8).
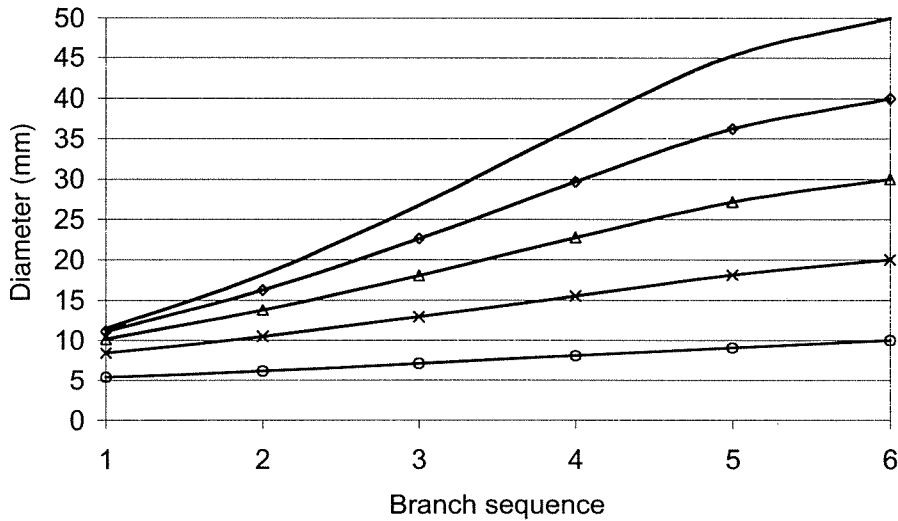
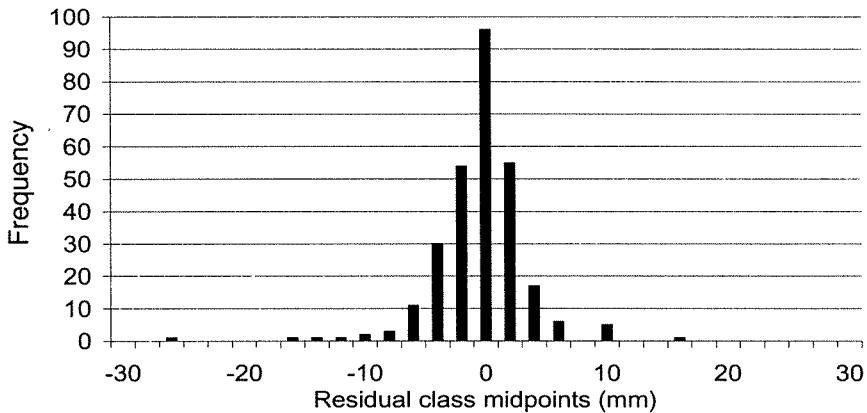FIG. 7–Effect of maximum branch diameter on output from Equation 7, for clusters with six branches.

FIG. 8–Frequency distribution of branch diameter residuals.

Relationship Between Branch Location, Branch Size, and Phyllotactic Pattern

In combination, Equations 1, 2, and 4 provided the basis for the development of a mathematical model which could be used to estimate and describe spatial relationships between branch location and size within a cluster. A computer program incorporating the

model was designed to predict the three-dimensional structure of any cluster from the following data : number of branches, divergence angle, internode length, diameter of largest branch. The inclusion of stem diameter (immediately above the cluster) and trimmed branch length allowed generation of a diagram. A comparison between diagrammatic output from this program and a photograph of Cluster 1/12 is given in Fig. 9.
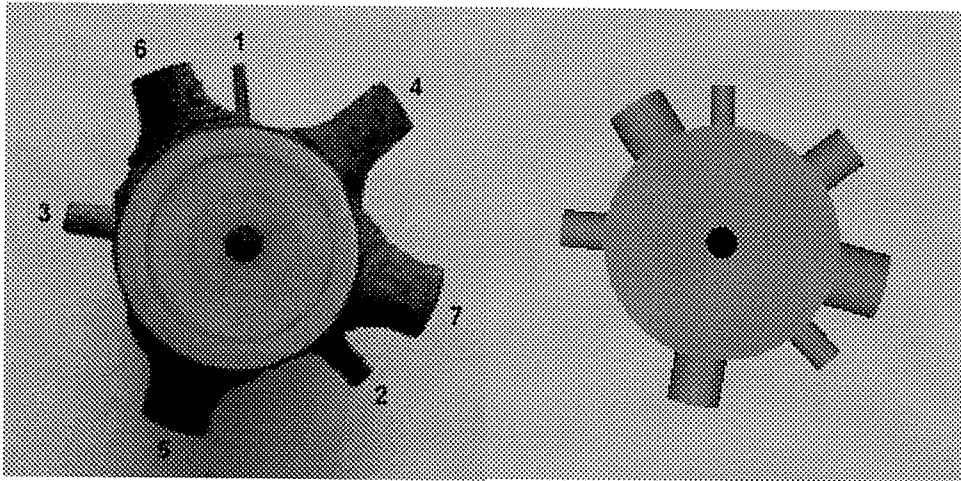

FIG. 9–Photograph of Cluster 1/12 compared to diagram of model output.

DISCUSSION

Four different phyllotactic patterns were identified in the 16 tree tops examined in this study. The Fibonacci pattern and S helix direction were found to be most frequently represented. Within trees there was a tendency for a pattern to be preserved across clusters although transitions to different patterns were observed, and were more common in specific individuals. The trees were sampled from a breeding trial, but it is likely that their characteristics are shared by other populations. Kremer *et al.* (1989) were unable to demonstrate significant differences, in terms of the proportions of the phyllotactic patterns, between populations of full-sib families in three *Pinus* species.

Almost one-third of all clusters had branches missing from the ontogenetic sequence. Boundaries between the zones in a growth unit are not always clear (Bollman 1983). Overlap of the branch zone with the needle, cone, or cataphyll zones could explain the absence of branches at the beginning and end of the cluster sequence.

Working with *P. taeda* L., Doruska & Burkhart (1994) examined the correlation of branch azimuth between clusters using circular statistics. They found that branches were distributed uniformly around the stems of whole trees and stems within branch clusters. The present phyllotactic study of *P. radiata* has demonstrated a regular arrangement of branches within clusters without resorting to circular statistics. Results support the hypothesis that in the absence of a transition to a different pattern, all primordial positions are located according to the same phyllotactic pattern and have a similar divergence angle. Regular phyllotactic patterns can be expected to result in uniform distribution of branch azimuth.

Within clusters, internode length (i.e., the vertical separation between branches) and divergence angle both tended to be constant. The slightly greater variability associated with internode length was attributable to measurement error. A more accurate estimate of mean internode length could be made by counting lateral members over a measured length of stem. Internode length was related to position of the cluster in the annual shoot, and varied with family. One of the trees had a mean internode length that was significantly greater than that of the other eight trees in the sample.

Jacobs (1936) noted that the number of primordia in a growth unit is determined in the bud and that the final length of the internode varies according to the influence of the environment on vertical growth rate. Baxter & Cannell (1978) showed that internode length in *Picea sitchensis* (Bong.) Carr. was determined by cell division rather than cell elongation and that stems with longer internodes had larger apical domes and higher rates of primordial initiation. Internode length is therefore likely to be influenced by any factor affecting primary growth including those associated with genotype, site, and climate.

Correlation between relative branch diameter within a cluster and branch position in the ontogenetic sequence is considered to reflect the development of branch dominance within the cluster. Baxter & Cannell (1978) demonstrated dominance within the annual shoot of *Picea sitchensis* where a cluster of larger branches develops at the top of the annual shoot and smaller branches are found below. Dominance effects within branch clusters were not examined. Causes of the large variation in maximum branch diameter observed between clusters in the current study have not yet been defined, but within-crown and between-crown factors could be responsible. Cluster position in the annual shoot was correlated with maximum branch diameter in the cluster, and may be a useful variable to include during the refinement of branch diameter prediction.

In this study of plantation-grown *Pinus radiata* the phyllotactic pattern established at the apical meristem was shown to persist in the spatial arrangement and size of branches within clusters in the stems of 26-year-old trees. Within a cluster, branch azimuth, branch vertical location, and branch diameter were all shown to be related to branch position in the ontogenetic sequence. In combination, these relationships provide a sound biological basis for a three-dimensional model of branch arrangement and size within the cluster.

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