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BRANCHING CHARACTERISTICS of RADIATA PINE: NUMBER and POSITION of BRANCH CLUSTERS WITHIN ANNUAL SHOOTS

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EXECUTIVE SUMMARY

Two functions within the branch model are; the number of clusters in an annual shoot; the relative position of clusters within an annual shoot.

The number and position of branches within annual shoots have been investigated using data from Kaingaroa and Southland.

The number of branch clusters within an annual shoot was found to vary between 1 and 7; and can be predicted as a function of annual shoot length and tree age. However, one function is unlikely to apply to all sites and families. The function developed needs to be tested with height growth models.

There is generally a preferred relative position of specific clusters within an annual shoot. It is debateable whether these positions are influenced by site and genetics. It is suggested that a table of mean values is implemented initially.

BRANCHING CHARACTERISTICS OF RADIATA PINE :

NUMBER AND POSITION OF BRANCH CLUSTERS WITHIN ANNUAL SHOOTS

J. C. GRACE

1. INTRODUCTION

The location and dimensions of branches encased within a stem are major determinants of timber quality. A branch model (Grace and Pont, 1997) is being developed which will simulate the location, diameter and growth of branches attached to the stem. It is proposed to link the branch model with individual tree growth models, wood property models and sawing simulators to determine the most appropriate silviculture for a stand to meet given end-use requirements, or the most appropriate end-use for a particular tree or log.

Two of the functions within the branch growth model predict:

the number of branch clusters within an annual shoot

the relative position of branch clusters within an annual shoot.

Together with a height growth model, these functions simulate the position of branch clusters along a stem.

Definition of an annual shoot

In radiata pine, an annual shoot consists of one or more growth units. A growth unit consists of a section of stem without needles, followed by a section of stem with needles, possibly followed by female cones and ending in a cluster of branches (D. Barthelemy (pers comm.)).

However, the most appropriate method to define the end of one annual shoot and the beginning of the next annual shoot is debateable (Burdon, 1994). From a biological perspective, the end of an annual shoot is marked by a zone of compressed parastichies above a branch cluster. However this zone of parastichies is considered to be formed in summer, and any autumn elongation is essentially a “head start” on the spring flush (Burdon, 1994). From a mensurational perspective, the end of an annual shoot is assumed to occur in mid-winter when height increment is at a minimum (Tennent, 1986) and at the point where the number of stem growth rings changes by one (Fig. 1).

In order to link with growth models, the mensurational definition of an annual shoot will be used in the branch model. This raises an important issue, how to allocate growth units formed during the autumn/ winter to annual shoots and where to count stem growth rings.

If autumn extension occurs, it is feasible that an annual shoot (using the mensurational definition) will not end with a branch cluster but mid-way through a growth unit, and hence the growth unit would not be completely formed until the spring. As autumn extension is considered to be a head-start on spring elongation, it is considered that such a growth unit should be considered the first growth unit in the next annual shoot.

This growth unit would have one more stem growth ring at the base of the growth unit, compared to immediately below the branch cluster. Stem growth rings should therefore be counted at the base of the cluster to ensure that the growth unit is allocated to the correct annual shoot.

Summary of previous studies

Grace and Pont (1997) summarised the relevant literature relating to the number and position of branch clusters within an annual shoot. Several factors appear to influence the number of branch clusters within an annual shoot namely: genetics, tree age, annual shoot length, relative tree size and environment.

The number of clusters formed per year appears to be under strong genetic control after the first 5-6 years (Fielding, 1960).

Jacobs (1937) indicated that tree age has a major influence on the characteristics of shoots. For fourteen year old trees, Bannister (1962) concluded that most of the variation in the number of clusters per annual shoot were due to differences between trees. Small parts of the variation could be explained by tree age and annual shoot length.

Jacobs (1938) suggested that suppression results in less clusters in an annual shoot. This was supported by Fielding (1960).

Temperature appears to influence the number of clusters in an annual shoot (Bollmann and Sweet,1976); and rainfall patterns appear to influence the relative position of clusters within an annual shoot (Bannister, 1962).

Objective

The objective of the current study is to analyse data from Experiment RO905, Kaingaroa; Compartment 905, Kaingaroa; and Taringatura, Southland to develop functions to predict:

the number of branch clusters within an annual shoot
the relative position of branch clusters within an annual shoot.

2. METHODS

During autumn 1996, thirteen 29-year-old radiata pine (planted at 3086 stems/ha in 1967) were felled from Experiment RO905. Brief details of these trees are given in Table 1. Further details relating to the sampling strategy and data collection are given in Grace *et al.* (1996).

During autumn 1997, 16 trees were felled in Compartment 905, Kaingaroa. Eight trees were from the "850" diallel planted in 1975. The other eight trees were from a uninodal progeny trial planted in 1972. In each trial, two trees from each of 4 families were sampled. The families sampled covered the range of multinodality/ uninodality in the trials. Brief details of these trees are given in Table 2. Further details, relating to the sampling strategy and data collection are given in Grace *et al.* (1998a). The family numbers (Table 2) rank each family within a trial according to their branch cluster frequency breeding values. The breeding values, themselves provide a ranking of families in terms of the frequency of branch clusters. The two trials have been ranked separately.

During spring 1997, 8 trees were felled from the "850" diallel planted in 1975 at Taringatura, Southland. These 8 trees were from the same four families that were sampled in Compartment 905, thus allowing a comparison of sites without the confounding effect of genotype. Brief details of these trees are given in Table 3. Further details relating to the sampling strategy and data collection are given in Grace *et al.* (in prep).

Table 1. Diameter at breast height (DBH), time of thinning and nominal stocking after thinning for sample trees from Experiment RO905, Kaingaroa.

Tree Number	DBH[1] (cm)	Time of thinning	Nominal Stocking after thinning (stems/ha)
1	65.8	1974 and 1983	300 /200
2	51.0	1974 and 1983	400/200
3	42.5	1974 and 1983	400/200
4	66.4	1979	200
5	53.5	1979	200
6	63.8	1976	200
7	54.8	1976	200
8	46.6	1976	400
9	33.8	1976	400
10	61.1	1974	200
11	54.4	1974	200
12	43.3	1974	400
13	33.8	1974	400

[1] DBH measured at time of felling (trees: 29 years-old).

Table 2. **Family, DBH and mean internode length (MIL) for sample trees from Compartment 905, Kaingaroa.**

Experiment	Family Code for analysis	Tree Number used in analysis	DBH[2] (cm)	MIL[3] (m)
Diallel	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

Table 3. **Family, DBH and mean internode length (MIL) for sample trees at Taringatura, Southland.**

Family code for analysis	Tree Number used in analysis	Tree DBH[4] (cm)	MIL[5] (m)
1	5	47.7	0.41
1	7	53.5	0.46
2	6	36.3	0.59
2	9	50.9	0.41
3	10	35.7	0.54
3	8	56.5	0.45
4	3	31.8	1.55
4	11	50.3	0.42

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2 DBH recorded by J. A. Turner during summer 1995 when trees were 20 years-old.
3 MIL recorded by J. A. Turner during summer 1995 when trees were 20 years-old.
4 DBH recorded by J. A. Turner autumn 1996 when trees were 21 years-old.
5 MIL recorded by J. A. Turner autumn 1996 when trees were 21 years-old.

Once the trees were felled, the base and top of each branch cluster were marked on the stem. In Experiment RO905, the visible branch angle was used to estimate where the stem and branch piths would meet, the lowest meeting point defining the base of the cluster. In Compartment 905 and Taringatura, the appearance of the bark surrounding the lowest branch was used to determine the base of the cluster. The top of the cluster was defined as the point where the highest branch emerged from the stem. The height to the base and top of each cluster were measured.

The trees were cut into discs using the markings as a guide but making certain that the base and top of a particular cluster were within the same disc. Clusters which overlapped were not separated.

The number of stem growth rings were counted on the top and bottom surfaces of the discs containing branch clusters. In most instances there are no difficulties with counting rings. There were two instances were difficulties arose. It was difficult to count stem growth rings on suppressed trees where the annual increment was very small. At the end of an annual shoot, it was sometimes difficult to determine when the inner ring disappeared.

In Experiment RO905, data were recorded on paper and notes were made when the inner ring was not so obvious. These inner rings have been included in the ring counts used in these analyses.

At Compartment 905 (apart from the last 5-6 years growth) and Taringatura, ring counts were recorded on a data logger. In Compartment 905, only clearly identifiable rings were recorded . At Taringatura, the number of clearly identifiable rings were recorded in one field. In another field, the possibility of an extra inner ring was recorded.

For the last 5-6 years growth on the trees from Compartment 905, ring counts were recorded on paper and notes made where there was a possibility of an inner ring. The number of stem growth rings were also recorded independently, for a selection of clusters, by two people who are experienced at identifying rings (Grace *et al*, 1998b). From comparing the two sets of results, it was concluded that indistinct inner rings should be counted as a ring.

The above ring count data were used to define the base and top of annual shoots, the number of branch clusters within an annual shoot, and their relative position within the annual shoot.

If the stem ring count changed from the base to the top of a disc containing overlapping clusters, it was not possible to identify which was the last cluster in an annual shoot. However it is suspected that both clusters would belong to the same annual shoot as short internodes tend to occur towards the end of the year (Bannister, 1962).

The data from Taringatura were analysed both including, and excluding indistinct inner rings. There was little difference between the results. It is therefore considered that the results from Compartment 905 are comparable with the other two sets of data even though indistinct rings were not recorded.

In Experiment RO905, it was possible to positively identify 210 annual shoots. In Compartment 905, it was possible to positively identify 141 annual shoots. At Taringatura it was possible to positively identify 99 annual shoots.

The relationship between number of branch clusters in an annual shoot and several independent variables were examined prior to developing an algorithm for predicting number of branch clusters within an annual shoot. The independent variables considered were ones that have been found, in the literature, to influence the number of branch clusters formed per year.

The relative position of branch clusters within an annual shoot were calculated and examined to determine possible methods for predicting the relative position of branch clusters within an annual shoot.

3. RESULTS - EXPERIMENT RO905

NUMBER OF CLUSTERS IN THE ANNUAL SHOOT.

The number of branch clusters within an annual shoot tends to increase slightly with the tree age at the time the annual shoot was formed. The trend is significant when all trees are considered but not generally on an individual tree basis (Table 4 and Fig. 2).

The number of clusters in an annual shoot is generally positively and significantly correlated with shoot length both on an individual tree basis and for all trees combined (Table 4 and Fig. 3).

A 3-d plot of the data is shown in Fig.4.

Table 4. Correlation between number of branch clusters in an annual shoot and both annual shoot length and tree age when the annual shoot was formed.

Tree		Number of annual shoots measured	Correlation between number of branch clusters and shoot length	Correlation between number of branch clusters and tree age
1		20	0.54 (p=0.01)	-0.007 (ns)
2		22	0.75 (p=0.0001)	0.28 (ns)
3		22	0.54 (p=0.01)	0.29 (ns)
4		23	0.28 (ns)	0.19 (ns)
5		12	0.24 (ns)	0.48 (ns)
6		12	0.60 (p=0.04)	0.42 (ns)
7		7	0.51 (ns)	0.062 (ns)
8		20	0.64 (p=0.002)	-0.043 (ns)
9		17	0.77 (p=0.0003)	0.23 (ns)
10		10	0.35 (ns)	0.24 (ns)
11		16	0.65 (p=0.006)	-0.36 (ns)
12		9	-0.07 (ns)	0.19 (ns)
13		20	0.55 (p=0.01)	0.39 (p=0.09)
all trees		210	0.46 (p=0.001)	0.20 (p=0.004)

RELATIVE POSITION OF CLUSTERS WITHIN AN ANNUAL SHOOT

All annual shoots with a given number of branch clusters were combined to determine the relative position of each cluster within the annual shoot. The mean values are shown in Table 5 and the variability in Fig 5.

Table 5. Relative position of branch clusters within an annual shoot

Number of branch clusters in the annual shoot	1	2	3	4	5	6	7
Number of annual shoots sampled	7	25	53	87	26	10	2
Cluster Number within annual shoot							
1	1.0	0.51	0.31	0.24	0.18	0.17	0.15
2		1.0	0.64	0.48	0.37	0.32	0.24
3			1.0	0.77	0.58	0.49	0.36
4				1.0	0.83	0.68	0.50
5					1.0	0.85	0.70
6						1.0	0.93
7							1.0

When there were only 2 clusters in the annual shoot, the position of the first cluster was very variable and there was no obvious "preferred position". This contrasts with Bannister's (1962) results where the first cluster tended to be towards the end of the annual shoot. A possible reason for this difference is that Bannister used the morphological definition of an annual shoot whereas the mensurational definition has been used in this study. For annual shoots with more than two clusters, there was a "preferred position" for each cluster.

Another point which needs to be considered is whether the position of one cluster influences the position of the following cluster. The correlation coefficient between the relative position of one cluster and the difference in relative position between it and the following cluster was calculated provided that the following cluster was not the end of the annual shoot and there were sufficient data (Table 6).

Table 6. Correlation between the relative position of one cluster, and the difference in relative positions between it and the following cluster.

Number of clusters in the annual shoot	3	4	5	6
Correlation coefficient between:				
Position of first cluster and difference in position between 1st and 2nd clusters	-0.33 (p=0.02)	-0.25 p=(0.02)	-0.06 (ns)	-0.59 (p=0.08)
Position of 2nd cluster and difference in position between 2nd and 3rd clusters		-0.55 (p=0.0001)	-0.47 (p=0.02)	-0.54 (ns)
Position of 3rd cluster and difference in position between 3rd and 4th clusters			-0.51 (p=0.007)	-0.60 (p=0.06)
Position of 4th cluster and difference in position between 4th and 5th clusters				-0.53 (ns)

The results (Table 6) show that there is a negative correlation between the relative position of one cluster and the difference in relative position between it and the following cluster.

4. RESULTS - COMPARTMENT 905

NUMBER OF BRANCH CLUSTERS IN AN ANNUAL SHOOT

The last 5-6 annual shoots formed have not been included in this analysis because the ring counts for clusters within these annual shoots were counted by different people at a later stage for investigating autumn extension. An advantage of excluding them from the analysis is that they provide a small independent data set for testing the model.

Trees 11, 13 and 15 were also excluded from this analysis due to the occurrence of leader replacement and difficulties with identifying stem growth rings due to the small tree size.

The number of branch clusters in an annual shoot was generally correlated with tree age when the shoot was formed for the uninodal trees but not for the multinodal trees (Table 7 and Fig. 6). A probable reason is that the multinodal trees were pruned to 6 m removing annual shoot formed before age 7-years (Fig. 6a). It was the annual shoots formed before 9 years which contribute most to the correlation for the uninodal trees (Fig 6b).

There is a positive correlation between number of branch clusters in a shoot and shoot length which is generally significant on an individual tree basis (Table 7 and Fig 7).

Table 7. Correlation between number of branch clusters and both annual shoot length and tree age when the annual shoot was formed.

Tree	Number of annual shoots	Correlation with shoot length	Correlation with tree age when annual shoot formed
Group 1 multinodal			
1	6	0.92 (p=0.01)	-0.37 (ns)
2	8	0.88 (p=0.004)	0.16 (ns)
3	10	0.71 (p=0.02)	0.44 (ns)
4	11	0.86 (p=0.0006)	0.23 (ns)
5	8	0.95 (p=0.0002)	-0.03 (ns)
6	10	0.58 (p=0.08)	0.51 (ns)
7	9	0.68 (p=0.05)	0.51 (ns)
8	9	0.95 (p=0.0001)	0.37 (ns)
Group 2 Uninodal			
9	12	0.81 (p=0.001)	-0.17 (ns)
10	14	0.53 (p=0.05)	0.50 (p=0.07)
12	16	0.85 (p=0.0001)	0.29 (ns)
14	15	0.32 (ns)	0.73 (p=0.002)
16	13	0.35 (ns)	0.66 (p=0.02)
Group 1	71	0.75 (p=0.0001)	0.20 (p=0.09)
Group 2	70	0.51 (p=0.0001)	0.41 (p=0.0004)

It is of note that trees 14 and 16, from the two most uninodal families selected, have no strong correlation between number of branch clusters and shoot length, while there is a stronger correlation between number of branch clusters and tree age.

A 3-d plot of the data is shown in Fig.8.

To investigate whether family was likely to influence the number of branch clusters in an annual shoot, the mean number of branch clusters per annual shoot was calculated (Table 8). The number of annual shoots used in the calculation varied slightly between trees. However the age range was similar. The difference in the mean number of cluster in an annual shoot was less than one between the two trees from a given family. The mean number of clusters formed per year tended to increase with increasing branch cluster breeding value as is to be expected (Fig. 9).

Table 8 . Mean number of branch clusters within an annual shoot.

Tree	Group	DBH (cm)	Number of annual shoots using complete annual shoots (sample size)	Minimum age of annual shoot considered	Maximum age of annual shoot considered	Mean number of clusters per annual shoot
1	Multinodal	36.1	6	8	17	4.0
2		57.7	8	7	16	3.5
3		41.4	10	8	17	3.4
4		46.0	11	7	17	3.7
5		32.9	8	8	17	3.2
6		57.0	10	7	16	2.5
7		42.2	9	7	15	3.6
8		52.4	9	7	15	4.3
9	Uninodal	37.0	12	9	20	4.1
10		48.6	14	5	18	3.3
11		29.0				
12		46.3	16	6	21	3.2
13		33.5				
14		49.3	15	5	21	3.3
15		29.2				
16		44.0	13	8	20	2.7

RELATIVE POSITION OF CLUSTERS WITHIN AN ANNUAL SHOOT

All annual shoots with a given number of branch clusters were combined to determine the relative position of each cluster within the annual shoot. The mean values are shown in Table 9. The variability in the position of each cluster is shown in Fig 10.

Table 9. Relative position of branch clusters within an annual shoot

Group 1 - multinodal

Number of branch clusters in annual shoot	1	2	3	4	5	6	7
Number of annual shoots observed	6	9	18	25	8	4	1
Position of cluster in annual shoot							
1	1.00	0.59	0.33	0.27	0.20	0.16	0.21
2		1.00	0.70	0.51	0.36	0.30	0.37
3			1.00	0.80	0.57	0.50	0.43
4				1.00	0.79	0.69	0.53
5					1.00	0.84	0.65
6						1.00	0.82
7							1.00

Group 2 - uninodal

Number of branch clusters in an annual shoot	1	2	3	4	5	6
Number of annual shoots observed	5	12	25	17	7	4
Position of cluster in annual shoot						
1	1.00	0.44	0.27	0.21	0.17	0.15
2		1.00	0.60	0.45	0.38	0.33
3			1.00	0.74	0.63	0.49
4				1.00	0.85	0.74
5					1.00	0.89
6						1.00

The correlation coefficient between the relative position of one cluster and the difference in relative position between it and the following cluster was calculated provided that the following cluster was not the end of the annual shoot and there were sufficient data (Table 10). The correlation was generally negative (as was the case in Experiment RO905).

Table 10. **Correlation between the relative position of one cluster, and the difference in relative positions between it and the following cluster.**

Group 1 - multinodal

Number of clusters in the annual shoot	3	4	5
Correlation coefficient between:			
Position of first cluster and difference in position between 1st and 2nd clusters	-0.57 (p=0.01)	-0.56 (p=0.003)	-0.75 (p=0.03)
Position of 2nd cluster and difference in position between 2nd and 3rd clusters		-0.31 (ns)	-0.64 (p=0.09)
Position of 3rd cluster and difference in position between 3rd and 4th clusters			-0.38 (ns)

Group 2 - uninodal

Number of clusters in the annual shoot	3	4	5
Correlation coefficient between:			
Position of first cluster and difference in position between 1st and 2nd clusters	-0.59 (p=0.001)	-0.37 (ns)	-0.07 (ns)
Position of 2nd cluster and difference in position between 2nd and 3rd clusters		-0.53 (p=0.03)	0.09 (ns)
Position of 3rd cluster and difference in position between 3rd and 4th clusters			-0.78 (p=0.03)

5. RESULTS - TARINGATURA

NUMBER OF BRANCH CLUSTERS IN THE ANNUAL SHOOT

The number of branch clusters formed per year does not change significantly with tree age (Table 11 and Fig. 11). However the number of branch clusters formed per year is significantly correlated with shoot length, both on an individual tree basis and for all trees combined (Table 11 and Fig. 12). The results for tree 3 stand out as being different from the others. In the field, tree 3 stood out as having several long internodes. This is a possible reason for the differences.

Table 11. Correlation between number of branch clusters in an annual shoot and both annual shoot length and tree age when the cluster was formed.

Tree	Number of annual shoots measured	Correlation with shoot length	Correlation with tree age
3	9	-0.04 (ns)	0.54(ns)
5	14	0.89 (p=0.0001)	-0.13 (ns)
6	13	0.89 (p=0.0001)	0.20 (ns)
7	15	0.45 (p=0.10)	0.16 (ns)
8	13	0.94 (p=0.0001)	0.02 (ns)
9	13	0.78 (p=0.002)	-0.28 (ns)
10	11	0.80 (p=0.003)	0.00 (ns)
11	11	0.73 (p=0.01)	-0.17 (ns)
all trees	99	0.69 (p=0.0001)	-0.01 (ns)

A 3-d plot of the data is shown in Fig. 13.

To investigate whether family was likely to influence the number of branch clusters in an annual shoot , the mean number of annual shoots per tree was calculated (Table 12). The number of annual shoots considered varied slightly between trees. However the age range was similar. There was no significant correlation between the mean number of clusters formed per year and branch cluster breeding value (Fig. 14). However there are too few families and trees per family to draw any definite conclusions.

Table 12. Mean number of branch clusters within an annual shoot.

Family	Tree	No. of annual shoots	Age range of annual shoots	Mean number of branch clusters in an annual shoot
1	5	14	9 to 22	3.57
1	7	15	8 to 22	3.07
2	6	13	10 to 22	2.69
2	9	13	8 to 22	3.08
3	8	13	9 to 21	3.00
3	10	11	10 to 20	3.00
4	3	9	10 to 18	2.89
4	11	11	8 to 18	3.18

RELATIVE POSITION OF CLUSTERS WITHIN AN ANNUAL SHOOT

All annual shoots with a given number of branch clusters were combined to determine the relative position of each cluster within the annual shoot (Table 13 and Fig. 15).

Table 13. Relative position of branch clusters within an annual shoot

Number of clusters in annual shoot	1	2	3	4	5	6
Number of annual shoots observed	5	25	37	24	6	2
Position of cluster in annual shoot						
1	1.0	0.53	0.36	0.26	0.19	0.13
2		1.0	0.70	0.50	0.40	0.31
3			1.0	0.80	0.61	0.50
4				1.0	0.78	0.68
5					1.0	0.83
6						1.0

The correlation coefficient between the relative position of one cluster and the difference in relative position between it and the following cluster was calculated provided that the following cluster was not the end of the annual shoot and there were sufficient data (Table 14).

Table 14. Correlation between relative position of one cluster, and the difference in relative positions between it and the following cluster.

Number of clusters in the annual shoot	3	4	5
Correlation coefficient between:			
Position of first cluster and difference in position between 1st and 2nd clusters	-0.44 (p=0.006)	-0.49 (p=0.01)	0.23 (ns)
Position of first cluster and difference in position between 2nd and 3rd clusters		-0.83 (p=0.0001)	-0.24 (ns)
Position of first cluster and difference in position between 3rd and 4th clusters			0.04 (ns)

The correlations (Table 14) are generally negative as was the case for the Kaingaroa datasets.

6. MODEL DEVELOPMENT - NUMBER OF BRANCH CLUSTERS IN AN ANNUAL SHOOT

Summary of above results

Comparing the results (Tables 4, 7, 11 and Figs 2, 3, 6, 7, 11, 12):

* the number of branch clusters in an annual shoot is generally positively and significantly correlated with shoot length.
* the number of branch clusters in an annual shoot tends to increase approximately linearly with annual shoot length.
* the number of branch clusters in an annual shoot is generally positively, but not significantly, correlated with tree age at the time the shoot was formed.
* the number of branch clusters per year initially increases with age but soon reaches a plateau. The multinodal trees show the least trend, but also there is little data available for younger ages where the trend was most obvious for the uninodal trees.
* it is of interest to note that for three of most uninodal trees sampled (Trees 14 and 16, Compartment 905; and Tree 3, Taringatura), the correlation with shoot length is less pronounced and the correlation with tree age more pronounced. This may indicate a change in strategy as trees become more uninodal.

Possible model formulation

The literature review indicated that genetics, tree age, annual shoot length, relative tree size, and environment are likely to influence the number of branch clusters in an annual shoot. The above analyses confirm that branch cluster breeding value, tree age and annual shoot length have some influence on the number of clusters formed per year. The annual shoot length at any age will be influenced by both environmental conditions and the competitive status of the tree. However, at present, there is insufficient data to consider including environmental variables or branch cluster breeding value in a predictive model.

As the number of branch clusters in an annual shoot tended to increase with both shoot length and tree age, a simple predictive model would be:

$$\text{NCLUSTER} = a\ \text{TREEAGE}^{b}\ \text{SHOOTLEN}^{c} \qquad (1)$$

where:

NCLUSTER is the number of branch clusters in an annual shoot
TREEAGE is the age (years) of the tree when the annual shoot was formed
SHOOTLEN is the length of the annual shoot (m)

I considered it was important to include TREEAGE in the model as:

there was generally a positive correlation, if not significant correlation, with tree age.

Furthermore, if TREEAGE was exculded from Eqn. 1, the residuals, from fitting the model, were correlated with TREEAGE.

Eqn.1 will need to be linked with height growth models to provide tree age and shoot length. However, stand and individual tree height models predict "average" height growth and do not account for environmental variability between years. Eqn.1, linked with a stand height growth model, may not predict the observed variability in number of clusters per year.

An alternative approach is to use a stochastic model which mimics the observed variability in number of clusters per year, but ignores the interactions with tree age and shoot length. However when linked with a height growth model, the distribution of internode lengths may not be correct (as one may have a large number of clusters in an annual shoot of average length).

Models using these two approaches have been developed, however the most appropriate formulation will need to be determined by testing these models in conjunction with height growth models.

Predictive Model

Eqn. 1 was fitted to the data from each location separately. The predicted coefficients are shown in Table 15. In each case, the residuals were not correlated with the predicted values, TREEAGE or SHOOTLEN.

Table 15. Predicted coefficients and errors from fitting Eqn. 1 to the individual datasets.

Data Set	RO905	Multinodal trees, Compartment 905	Uninodal trees, Compartment 905	Multinodal trees, Taringatura
Predicted coefficients				
a	1.01 ± 0.11	0.50 ± 0.14	0.60 ± 0.17	0.85 ± 0.22
b	0.38 ± 0.04	0.59 ± 0.11	0.52 ± 0.10	0.35 ± 0.09
c	0.70 ± 0.05	0.94 ± 0.09	0.72 ± 0.12	0.80 ± 0.08
comparison of actual and predicted number clusters				
Correct	56%	59%	51%	65%
Differs by 1 or less	93%	94%	86%	96%
Differs by 2 or less	99.5%	100%	100%	99%

The predicted number of clusters is correct over 50% of the observations, and is correct or differs by one for approximately 90% of the observations (Table 16).

Eqn. 1 is not constrained to keep the number of clusters in an annual shoot below the observed maximum of 7. However, within the range of observed shootlengths for a given tree age, the predictions are realistic.

These results indicate that the model equation provides a reasonable fit to the data. It is interesting to note that the poorest fit is obtained for the uninodal dataset. The correlation between shoot length and number of clusters was least for the most uninodal trees in the above datasets. These results may indicate that the model formulation may not be so appropriate for uninodal trees. However a larger dataset would be needed to prove/ disprove this.

To determine whether there were significant differences between these coefficients, Eqn. 1 was fitted to the combined dataset with each observation weighted according to the inverse of the number of observations for a particular group of trees. The predicted coefficients for the combined dataset are shown in Table 16.

Table 16. Predicted coefficients and errors from fitting Eqn. 1 using combined dataset.

Data Set	RO905	Multinodal Compartment 905	Uninodal Compartment 905	Multinodal Taringatura
Predicted coefficients				
a	0.86 ± 0.11			
b	0.39 ± 0.04			
c	0.76 ± 0.06			
Comparison of actual and predicted number of clusters				
Correct	50%	63%	51%	47%
Differs by 1 or less	93%	90%	90%	94%
Differs by 2 or less	99%	100%	100%	99%
Analysis of residuals by data set				
Mean residual	0.31	0.13	-0.15	-0.35
Significantly different from zero	yes	no	no	yes

A comparison of actual and predicted values (Table 16) indicated that the errors for the combined model were slightly greater than those from the individual models. The mean residual was significantly different from zero for 2 of the 4 datasets (Table 16). The correlation between residuals and predicted values, tree age and shoot length were calculated for each group of trees. There were significant correlations ($p \leq 0.5$) between residuals and predicted values, and between residuals and shootlength for the multinodal trees in Compartment 905. All other correlations were not significant.

These results indicate that a combined model for different sites and different genetic material is not applicable. This should be expected given the literature. Also, data collected by James Turner (pers comm) indicates that the number of clusters in an annual shoot will be higher in the "850" diallel at Woodhill compared with the "850" diallel in Compartment 905, Kaingaroa. However Woodhill has a lower site index. This is further evidence that the relationship between number of clusters per annual shoot and shoot length varies with site.

Stochastic Model

Assuming that the number of branch clusters within an annual shoot is random, a probability distribution for the number of branch clusters within an annual shoot was calculated for each set of data (Table 17).

Table 17. Probability distribution for the number of branch clusters within an annual shoot.

Number of branch clusters within an annual shoot	Probability of a shoot having a given number clusters			
	RO905	Multinodal trees, Compartment 905	Uninodal trees, Compartment 905	Multinodal trees, Taringatura
1	0.03	0.09	0.07	0.05
2	0.12	0.13	0.17	0.25
3	0.25	0.25	0.36	0.37
4	0.41	0.35	0.24	0.24
5	0.12	0.11	0.10	0.06
6	0.05	0.06	0.06	0.02
7	0.01	0.01	0.00	0.00

The results (Table 17) indicate that:

* Uninodal trees on the same site as multinodal trees tend to form less clusters per year. This is to be expected.

* For the same families of multinodal trees, there are less clusters formed per year at Taringatura compared to Compartment 905, Kaingaroa. This result supports that of Bollman and Sweet (1976) who found for one clone that the number of clusters formed per year was larger on the warmer of two sites.

* There tend to be more clusters formed per year in Experiment 905 compared with the multinodal trees in Compartment 905. These trees were unimproved and are considered to be less multinodal than the multinodal trees in Compartment 905. This again points to the influence of temperature as Experiment RO905 would be in a warmer location that Compartment 905.

Conclusions

Number of clusters in an annual shoot can be predicted as a function of tree age and annual shoot length. However one predictive model is unlikely to apply to all sites. It is possible that Eqn. 1 may not apply for uninodal trees.

Separate stochastic models will be needed to cover variation with genetics and site.

Both the predictive and stochastic models will need to be tested with height growth models to determine the most appropriate approach.

7. MODEL-DEVELOPMENT
RELATIVE POSITION OF BRANCH CLUSTERS IN AN ANNUAL SHOOT

Issues

Tables 5, 9, 13 show the mean relative position for each cluster within an annual shoot. One possible model is to use these tables as look-up tables.

The disadvantages of this approach are:
- it ignores the observed correlations between relative positions of consecutive clusters (Tables 6, 10, 14).
- it may tend to reduce the variability in internode lengths

The advantage of this approach is:
- it avoids developing a more complex model with limited data and little knowledge of the mechanisms involved.

It is considered that the most appropriate approach would be to implement a look-up table initially. If any obvious defects in this approach are found, a more complex model should be developed.

Model

The SAS procedure PROC GLM was used to test whether there were any significant differences, between groups of trees, in the relative position of a given cluster within an annual shoot.

When all four sets of trees were compared there were significant correlations between the relative position of clusters in annual shoots with 3 or 4 clusters. There were no significant differences when the two sets of multinodal trees were compared. Also there was only one significant correlation when the RO905 data were compared with the uninodal data (1st cluster in an annual shoot with four clusters).

Given that the trees from RO905 were not improved and therefore tend to be less multinodal, the above results indicate that relative positions may vary according to the multinodality of the trees. They also indicate that site may not influence the relative position of a given cluster.

From comparing the mean length of annual shoots with 3 or 4 clusters (approx 1.5 m) with the variability in relative position, it was concluded that the position of a cluster would generally vary by less than 20 cm if a combined table rather than an individual site table was implemented.

It was therefore considered that a combined table should be implemented initially. The values in Tables 5, 9 and 13 were averaged to produce Table 18.

Table 18 Relative position of branch clusters within an annual shoot

Number of clusters in an annual shoot	1	2	3	4	5	6	7
Position of each cluster in annual shoot							
1	1.0	0.52	0.32	0.24	0.19	0.15	0.18
2		1.0	0.66	0.48	0.38	0.32	0.30
3			1.0	0.78	0.60	0.50	0.40
4				1.0	0.81	0.70	0.52
5					1.0	0.85	0.68
6						1.0	0.88
7							1.0

Conclusion

Table 18 should be implemented initially.

Further research is necessary to determine whether the variability in the position of an individual cluster should be included within the model.

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Figure 1. **Diagram showing the effect of autumn extension on the definition of an annual shoot.**

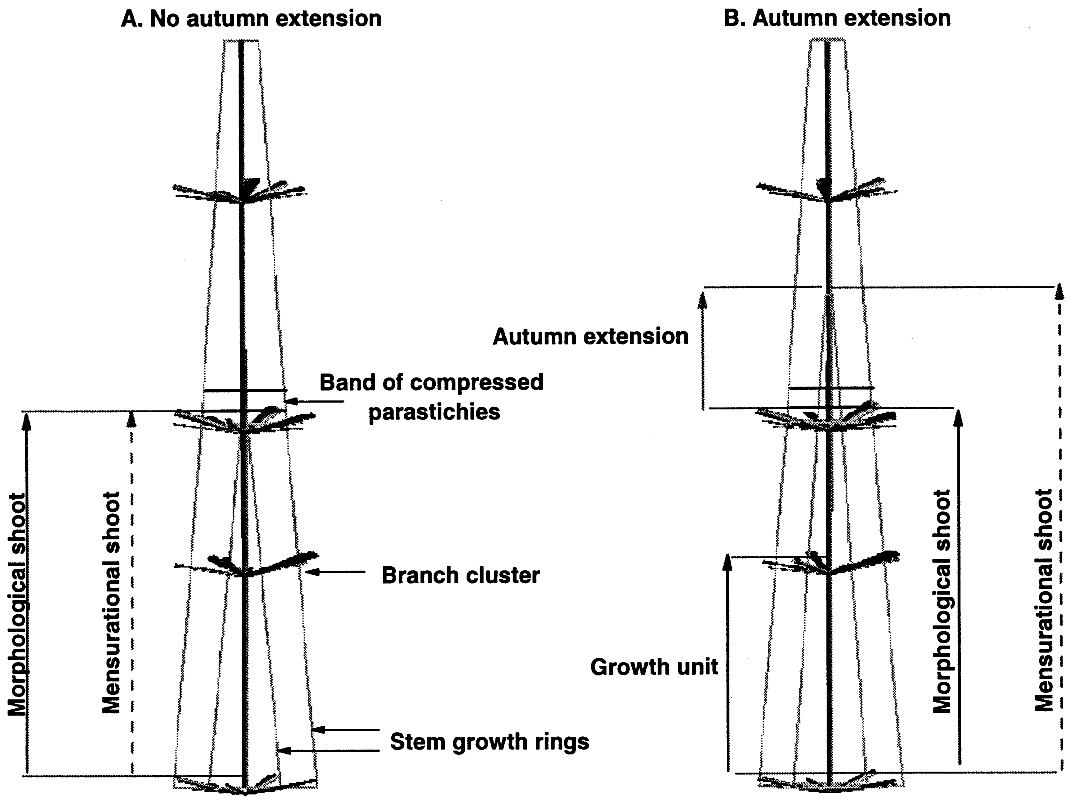


Figure 2. **Relationship between number of clusters in an annual shoot and tree age when the cluster was formed for Experiment RO905**

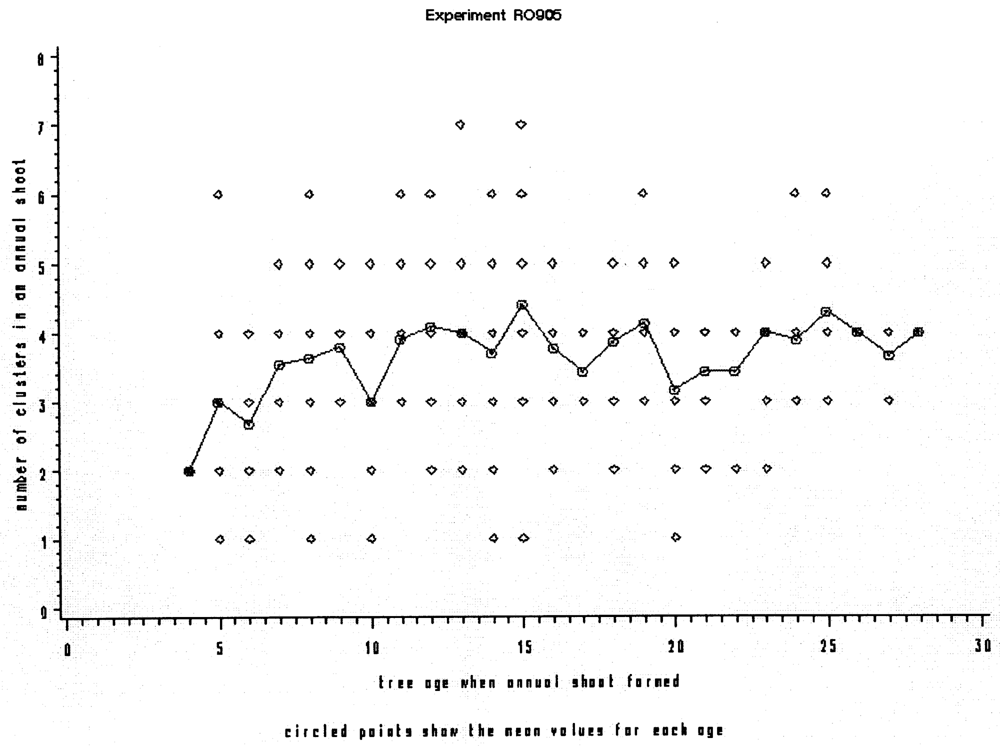


Figure 3. **Relationship between number of clusters in a shoot and annual shoot length for Experiment RO905.**

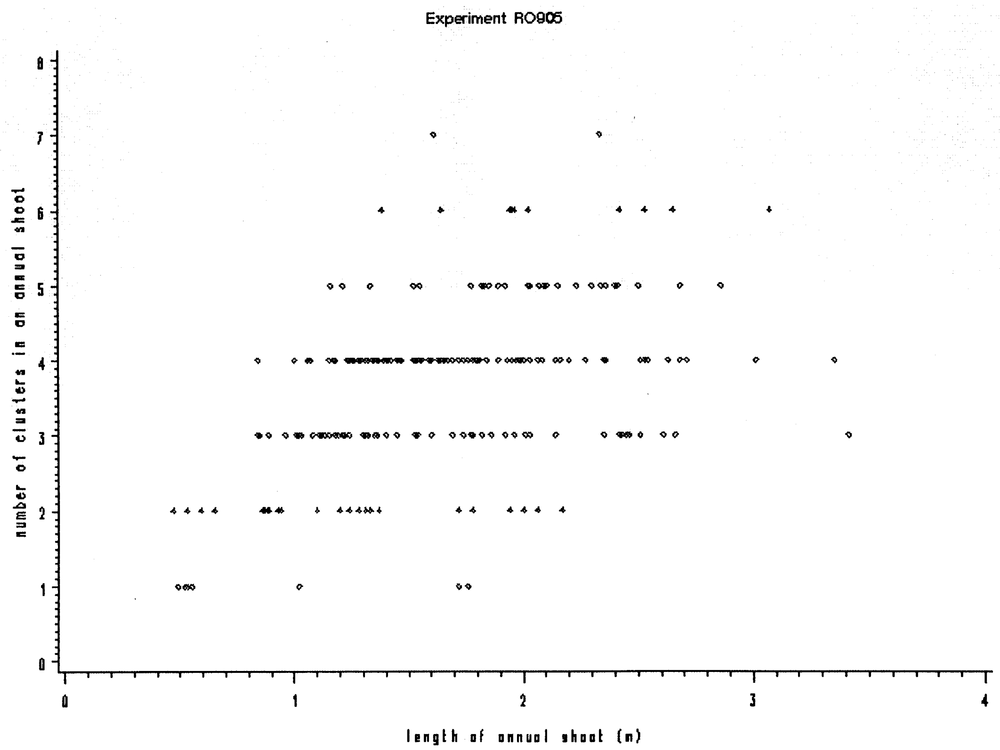


Figure 4. **3-d plot showing the relationship between number of clusters in an annual shoot, annual shoot length and tree age when the annual shoot was formed for Experiment RO905.**

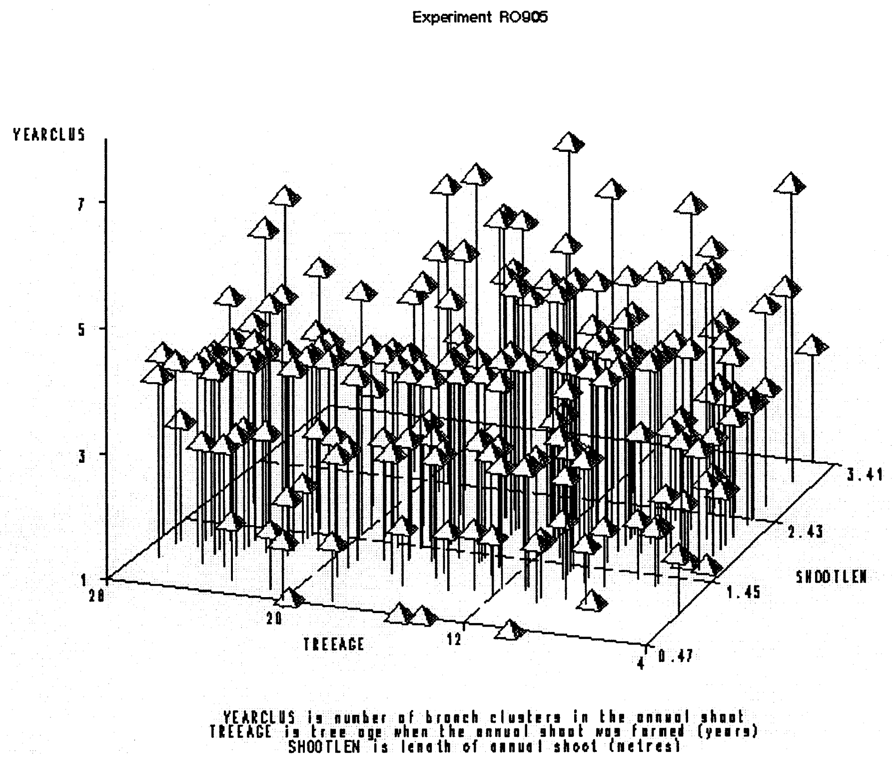


Figure 5. Relative position of branch clusters within an annual shoot in Experiment RO905.
YEARCLUS is the number of clusters in an annual shoot, CLUSTPOS is the cluster number, and RP is its relative position.

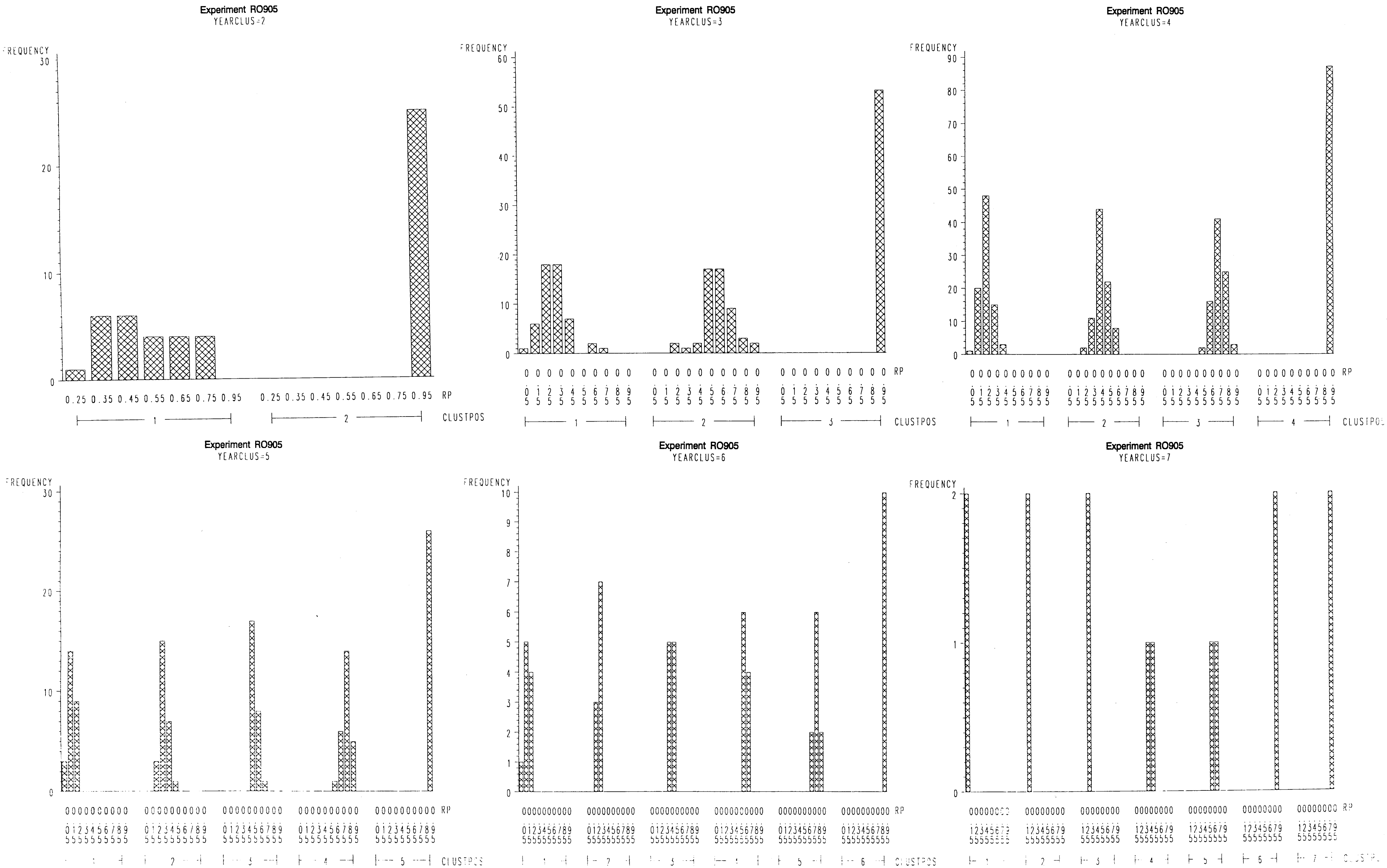


Figure 6. **Relationship between number of clusters in an annual shoot and tree age when the cluster was formed for Compartment 905.**

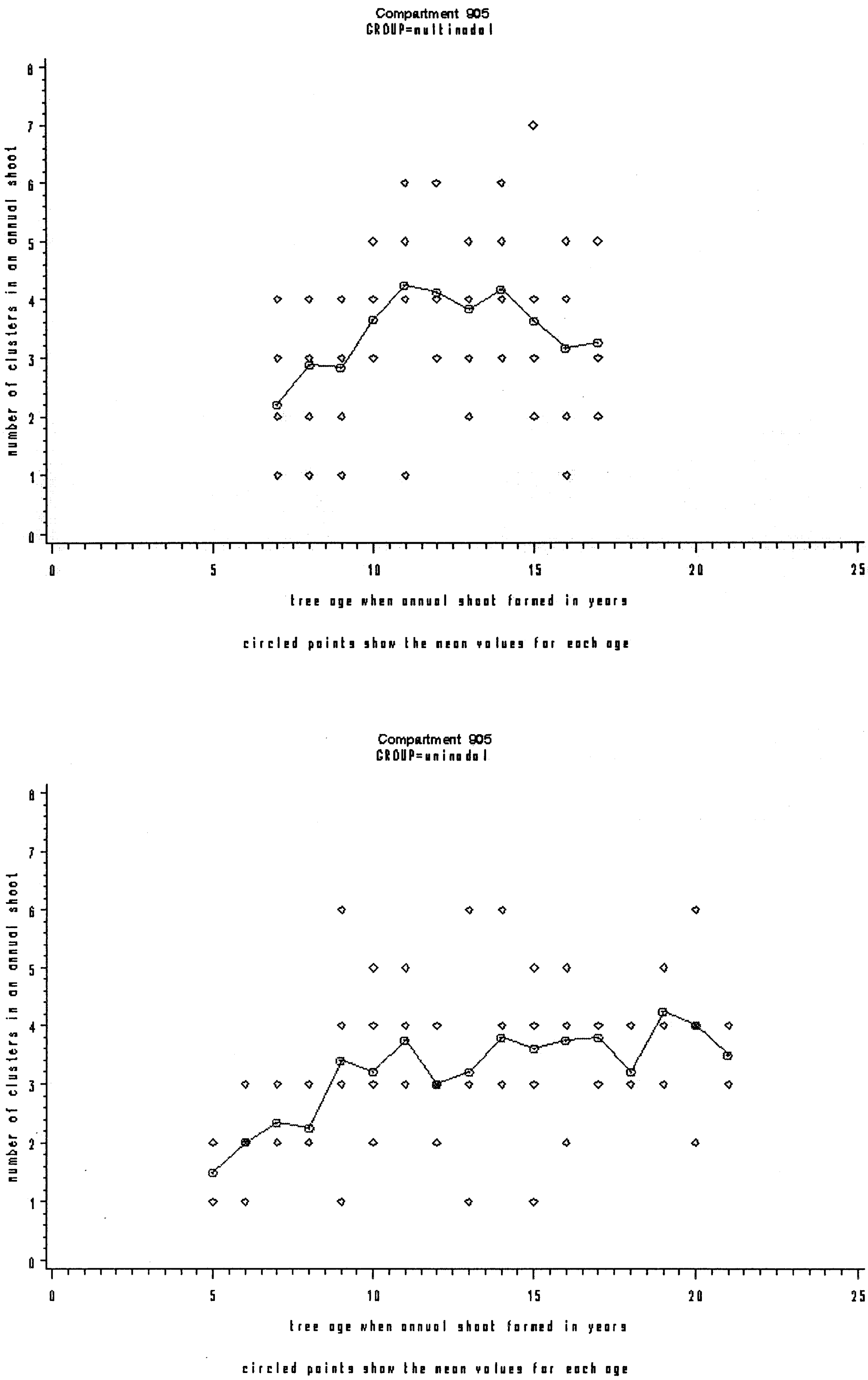


Figure 7. **Relationship between number of clusters in a shoot and annual shoot length for Compartment 905.**

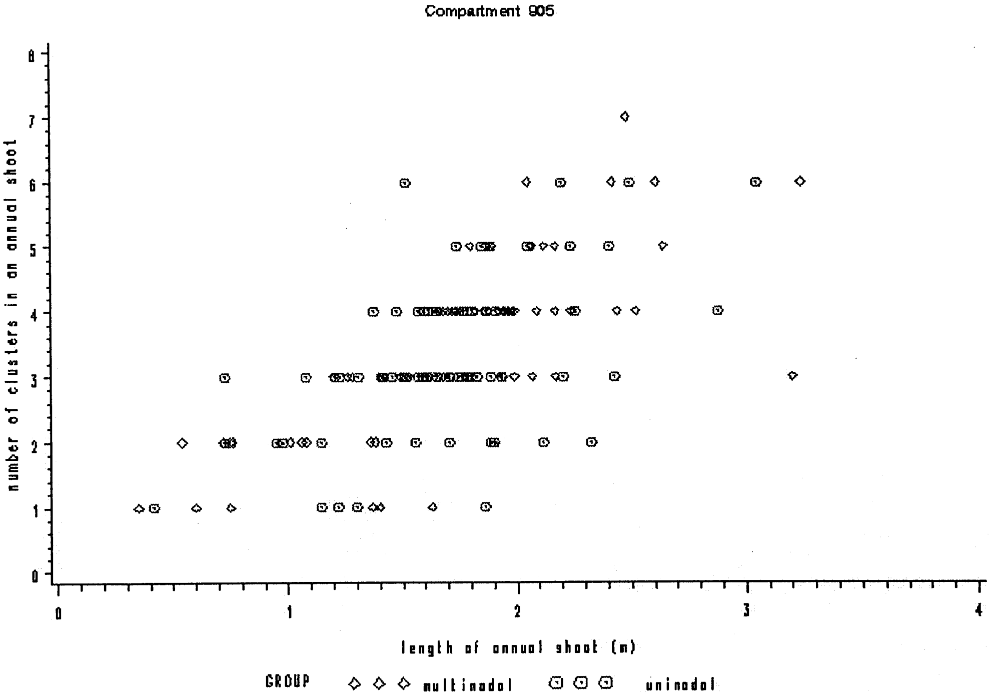


Figure 8. **3-d plot showing the relationship between number of clusters in an annual shoot, annual shoot length and tree age when the annual shoot was formed for Compartment 905.**

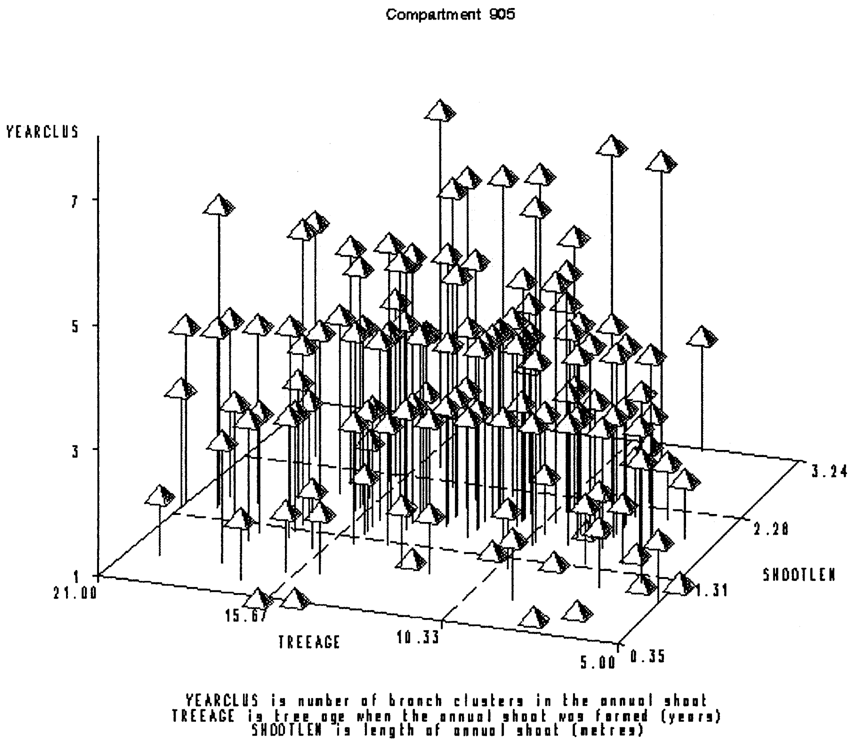


Figure 9. **Relationship between average number of clusters in an annual shoot and branch cluster frequency breeding values for Compartment 905.**

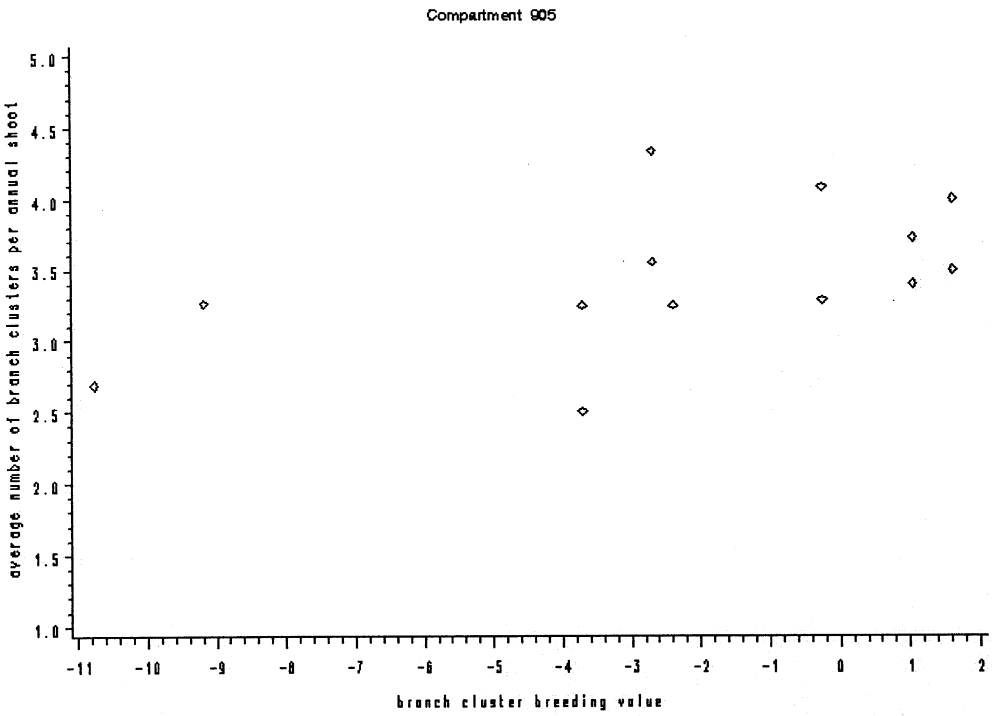


Figure 10. Relative position of branch clusters within an annual shoot in Compartment 905, Kaingaroa.
YEARCLUS is the number of clusters in an annual shoot, CLUSTPOS is the cluster number, and RP is its relative position.

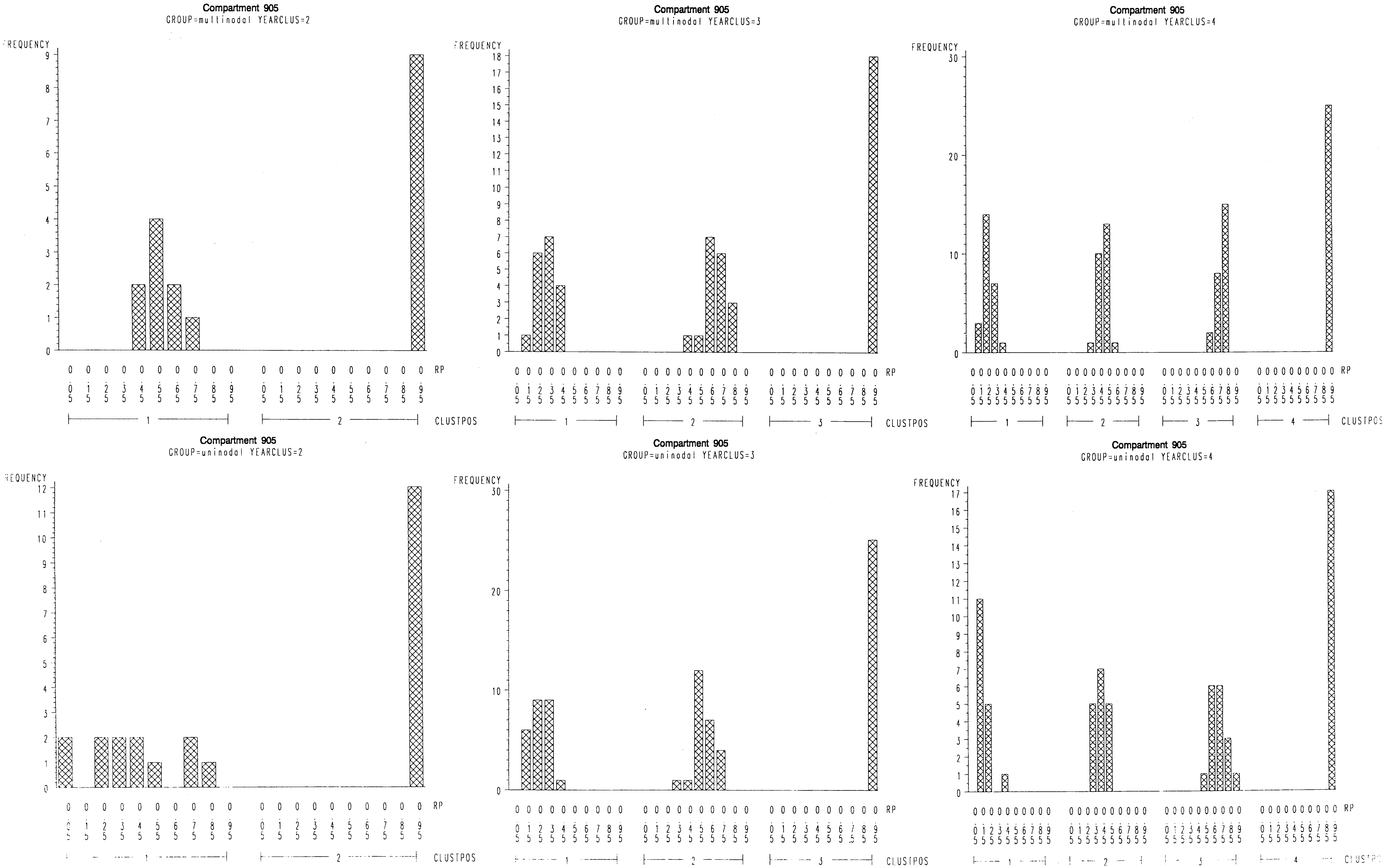
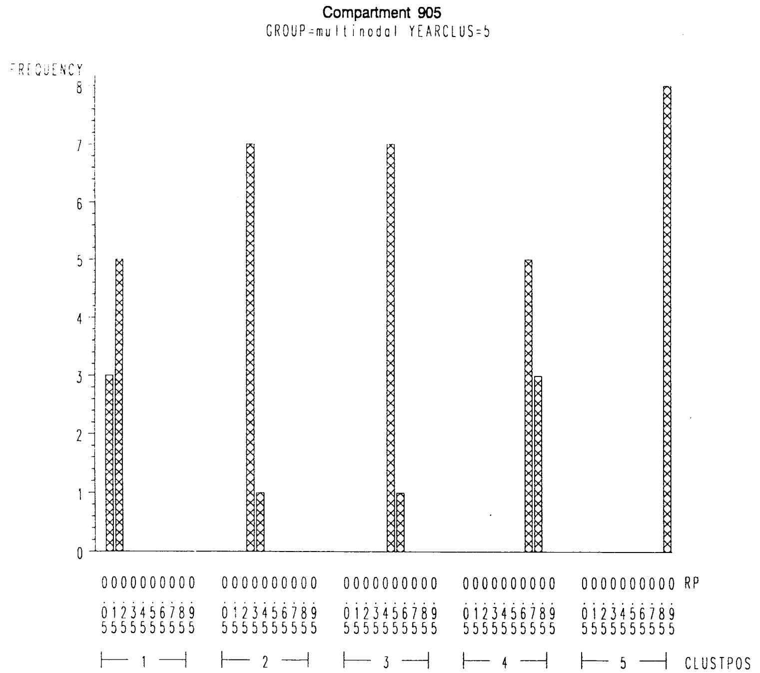
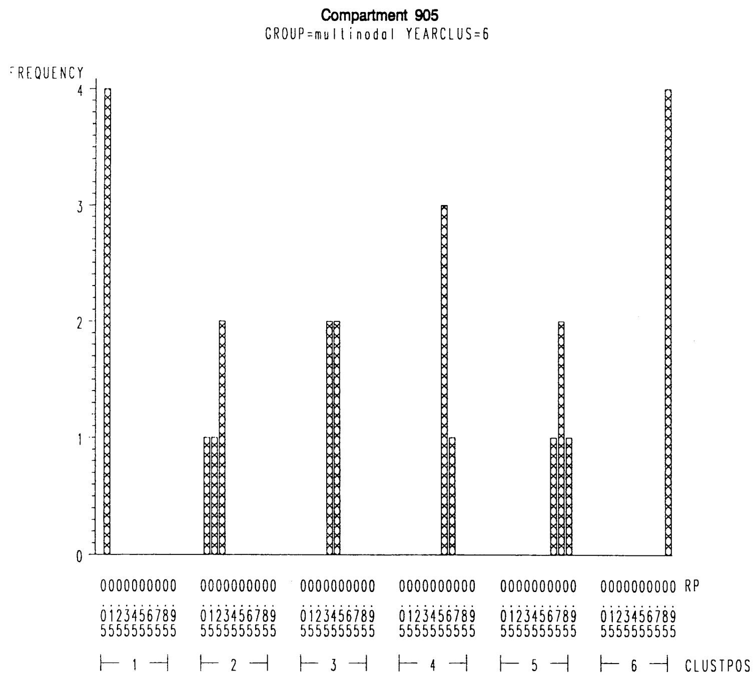
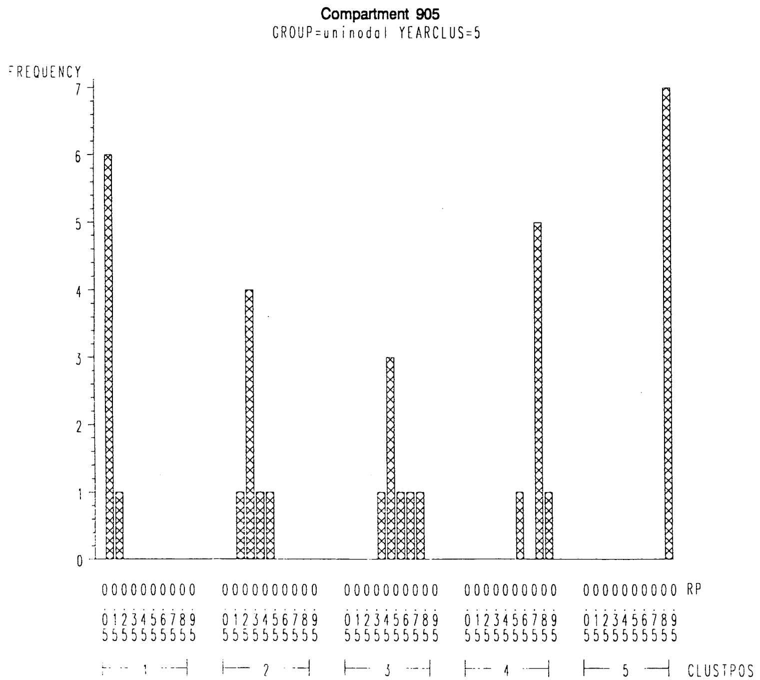


Figure 10 (continued). Relative position of branch clusters within an annual shoot in Compartment 905, Kaingaroa.
YEARCLUS is the number of clusters in an annual shoot, CLUSTPOS is the cluster number, and RP is its relative position.







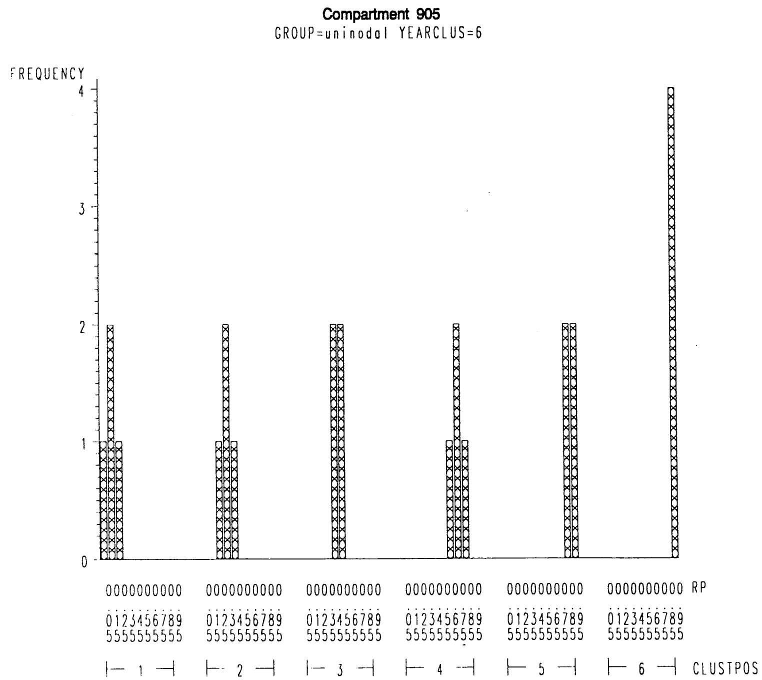


Figure 11. **Relationship between number of clusters in an annual shoot and tree age when the cluster was formed for Taringatura.**

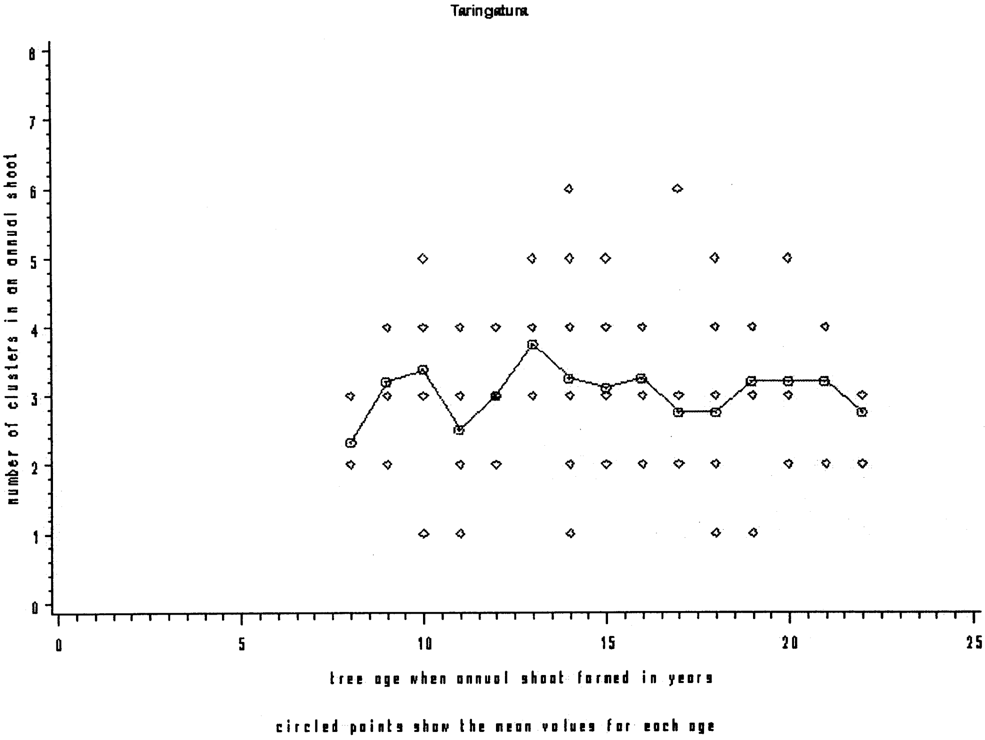


Figure 12. **Relationship between number of clusters in a shoot and annual shoot length for Taringatura.**

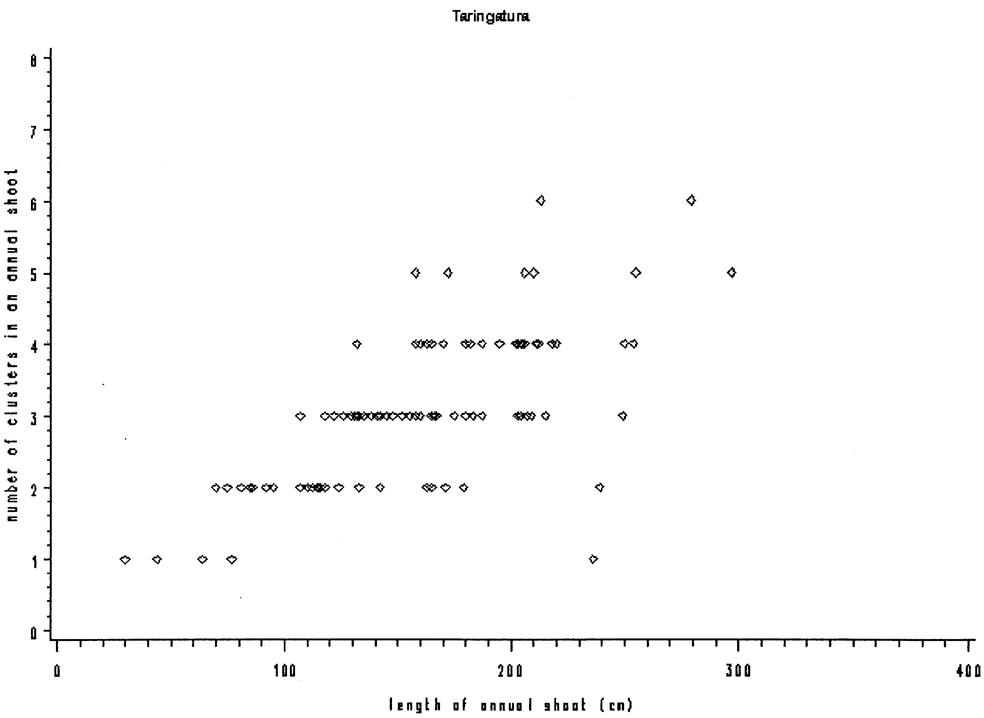


Figure 13. **3-d plot showing the relationship between number of clusters in an annual shoot, annual shoot length and tree age when the annual shoot was formed for Taringatura.**

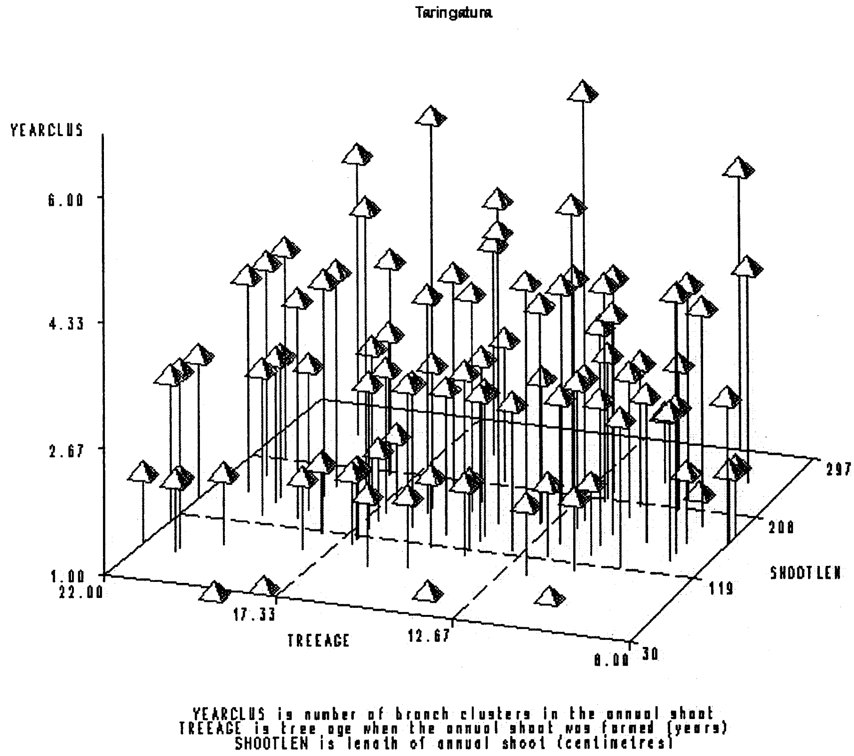


Figure 14. **Relationship between average number of clusters in an annual shoot and branch cluster frequency breeding values for Compartment 905.**

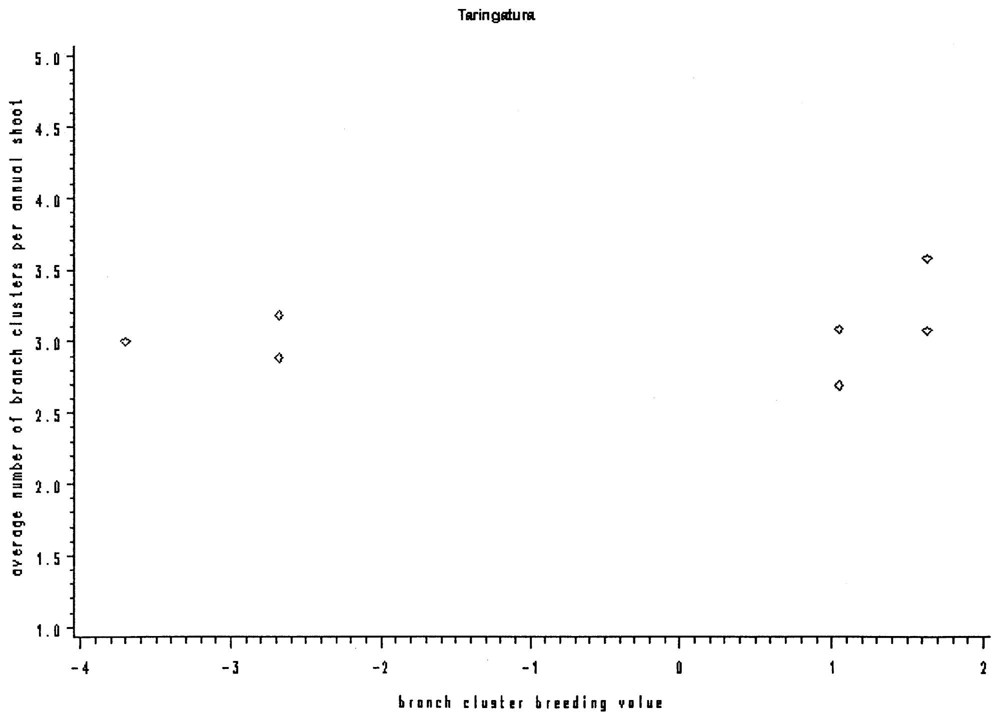


Figure 15. Relative position of branch clusters within an annual shoot at Taringatura.
YEARCLUS is the number of clusters in an annual shoot, CLUSTPOS is the cluster number, and RP is its relative position.