

**Branch Functions within
TreeBLOSSIM Version 3**

J. C. Grace

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Stand Growth Modelling Cooperative

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: This is an unpublished report and must not be cited as a literature reference.

Executive Summary

TreeBLOSSIM combines an individual-tree growth model with a branch growth model. The model is distant-independent, i.e. the actual spacing of the trees is not used in calculating either stem or branch growth. The individual-tree growth model predicts tree height development, breast-height diameter development and tree mortality. The branch model predicts the location of all branches and stem cones attached to the main stem, branch development through time, branch defects and branch mortality.

This reports documents a revision to the branch model carried out in 2004. The form of each of the 15 functions was reconsidered. Four functions remained unchanged. Four functions were refitted i.e. the form of the mathematical equation remained the same. Seven functions were revised i.e. the mathematical equation was changed. These functions are designed for GF14 seedlots and replace those documented in SGMC Report No. 108. They will be implemented in TreeBLOSSIM Version 3.

The functions documented in this report will apply to TreeBLOSSIM Version 3.

Branch Functions within TreeBLOSSIM – Version 3

J.C. Grace

Introduction

TreeBLOSSIM combines an individual-tree growth model with a branch growth model. The model is distant-independent, i.e. the actual spacing of the trees is not used in calculating either stem or branch growth. The individual-tree growth model predicts tree height development, breast-height diameter development and tree mortality. The branch model predicts the location of all branches and stem cones attached to the main stem, branch development through time, branch defects and branch mortality.

Stand Growth Modelling Report No. 108 documented the branch functions within Version 1.1 (11/06/2001) of TreeBLOSSIM. These functions remained unchanged in all later releases of TreeBLOSSIM labelled Version 1 or Version 2.

Since Version 1.1 was released:

- More radiata pine trees have been destructively sampled to provide branching data from additional sites throughout New Zealand
- PhotoMARVL data have been collected from a range of sites throughout New Zealand. These data have been compared with TreeBLOSSIM predictions, to determine the strengths and weaknesses of TreeBLOSSIM.

The objective of this report is to document a major revision of the branch functions within TreeBLOSSIM that incorporates this new knowledge. The revisions have been made using the assumption that TreeBLOSSIM is a distant-independent model. An appendix is included detailing the influence of actual tree spacing on branch size.

In the revision of each function, consideration has been given as to whether there should be one function for each growth modelling region or whether there should be a general function for the whole of New Zealand.

The functions documented in this report will apply to TreeBLOSSIM Version 3.

TreeBLOSSIM revision – Data used

Only data from sites planted with “850” seed have been used in this analysis. This will enable a better understanding of the environmental /site influences on branching. The datasets are outlined in Table 1.

Table 1. Datasets used in the revision of TreeBLOSSIM functions

Region	SiteId in Database	Trial Series	Trial Number	Latitude (°)	No. trees smpld	Sampling Strategy
Sands	6	Diallel	AK622/2	36.6	8	2 from each of 4 families
Clays	13	PSP	FR58/1	36.4	5	From given percentage points in DBH distribution.
Central North Island	3	Diallel	RO320/25	38.5	8	2 from each of 4 families
Central North Island	7	FCS	RO2098	38.3	3	1 tree from each of 3 different final crop stockings. All similar DBH at time of thinning
Hawkes Bay	8	PSP	WN235/0	39.3	3	Trees that showed stem fluting
Nelson	12	FCS	NN529/1	41.6	3	1 tree from each of 3 different final crop stockings. All similar DBH at time of thinning
Canterbury	10	FCS	CY597	43.5	3	1 tree from each of 3 different final crop stockings. All similar DBH at time of thinning
Southland	5	Diallel	SD413	46.2	8	2 from each of 4 families
West Coast	11	Diallel	WD174	42.5	8	2 from each of 4 families

* FCS = Final Crop Stocking
PSP = Permanent Sample Plot

TreeBLOSSIM structure

The branch component of TreeBLOSSIM is hierarchical in structure with functions pertaining to:

- The tree
- The annual shoot
- The branch cluster
- The branch

The functions at each level are:

Tree Level:

- Probability that a tree has reached reproductive maturity (based on 1st occurrence of stem cones).

Annual Shoot Level:

- Number of branch clusters.
- Relative position of branch clusters within the annual shoot.

Cluster Level:

- Number of branches in a cluster and stem cones in a cluster.
- Azimuthal location of branches and stem cones.
- Azimuth angle of largest branch.

Branch Level:

- Branch potential.
- Branch diameter development through time.
- Branch angle.
- Occurrence of bark encasement due to branch mortality.
- Occurrence of bark trapped above a branch that is not due to branch mortality.

Functions at the tree level

Probability that a tree has reached reproductive maturity (based on 1st occurrence of stem cones)

Comments on previous implementation and suggestions for improvements

The function predicted that trees would reach reproductive maturity from tree-age zero onwards. Our observations indicate that trees need to be a certain age before cones form. An improvement would be to develop a function with no maturity before a given tree-age.

The order in which trees became “mature” was based on their order in the imported tree list. K. Horgan (pers. comm.) suggested that tree growth rate influences cone formation.

New analysis

Methods

For each tree, FIRSTCONEAGE was calculated. This is the tree-age when the first stem cone was produced, i.e. the age at which the tree reached maturity. For each site, the relationship between tree DBH and FIRSTCONEAGE was investigated.

For each site, FIRSTMATURITYAGE (the earliest age at which a tree reached maturity) and LASTMATURITYAGE (the latest age at which a tree reached maturity) was calculated. The relationship between latitude and both FIRSTMATURITYAGE and LASTMATURITYAGE was investigated.

Results

These data showed no significant correlation between tree DBH and FIRSTCONEAGE at any site.

Both FIRSTMATURITYAGE and LASTMATURITYAGE increased with increasing latitude (Figure 1). Linear regression equations that predicted both FIRSTMATURITYAGE and LASTMATURITYAGE as a function of latitude were calculated (Figure 1). These equations (see below) were incorporated into a model that predicted the percentage of mature trees as a function of tree age and latitude (Figure 2).

Discussion

There was little data to derive this function. While these data showed no significant correlation between tree DBH at time of felling at FIRSTCONEAGE, other studies (K. Horgan, pers comm.) have suggested that the faster growing trees produce cones earlier.

It is considered that environmental variables are the underlying cause of the observed relationship between latitude and both FIRSTMATURITYAGE and LASTMATURITYAGE. Data from a wider range of sites will be needed in order to realistically predict FIRSTMATURITYAGE and LASTMATURITYAGE from environmental variables.

Implementation

The equations relevant to the implementation of this function are:

```
FIRSTMATURITYAGE = -9.477 + 0.414 * latitude;  
LASTMATURITYAGE = -15.666 + 0.718 * latitude;
```

```
if age lt FIRSTMATURITYAGE then PERCENTAGEMATURETREES = 0;  
if age gt LASTMATURITYAGE then PERCENTAGEMATURETREES = 100;
```

Between these two ages the percentage of mature trees (PERCENTAGEMATURETREES) was calculated using the formula:

$$(age - FIRSTMATURITYAGE) * 100.0 / (LASTMATURITYAGE - FIRSTMATURITYAGE)$$

The predicted shape of these equations is shown in Figure 2.

Trees reach maturity based on their position in the tree list. This was chosen on the basis that there was no significant relationship between tree DBH and FIRSTCONEAGE, and that the tree list is not usually ranked according to tree DBH.

An alternative implementation would that the age a particular tree reaches reproductive maturity based upon its 'tree potential'. This approach would allow for a relationship between tree DBH and FIRSTCONEAGE.

Figure 1. Field data used to develop model of reproductive maturity, and predicted regression equations.

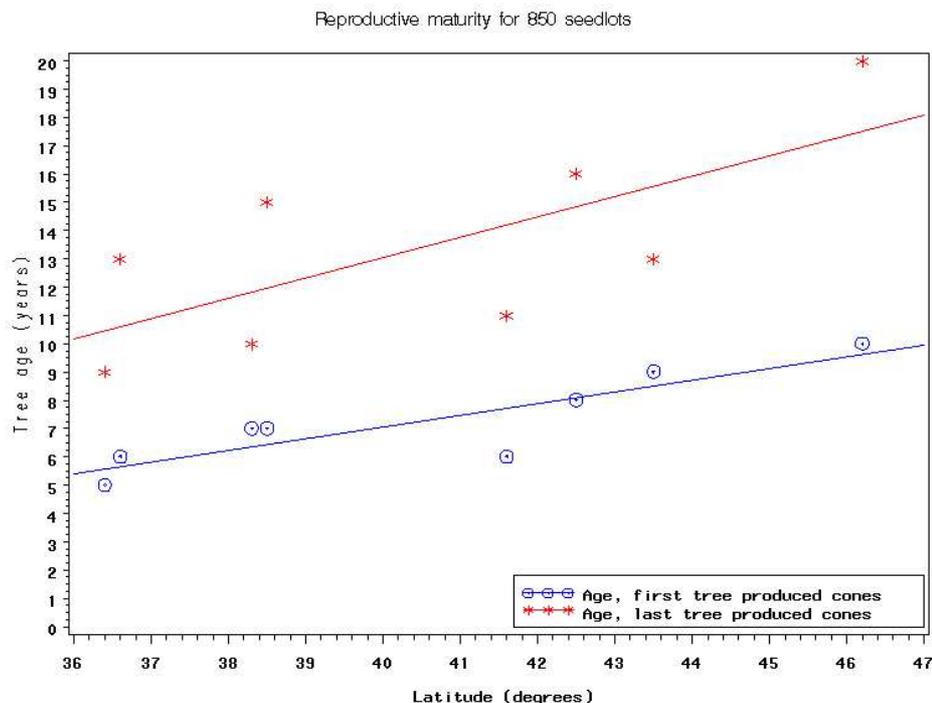
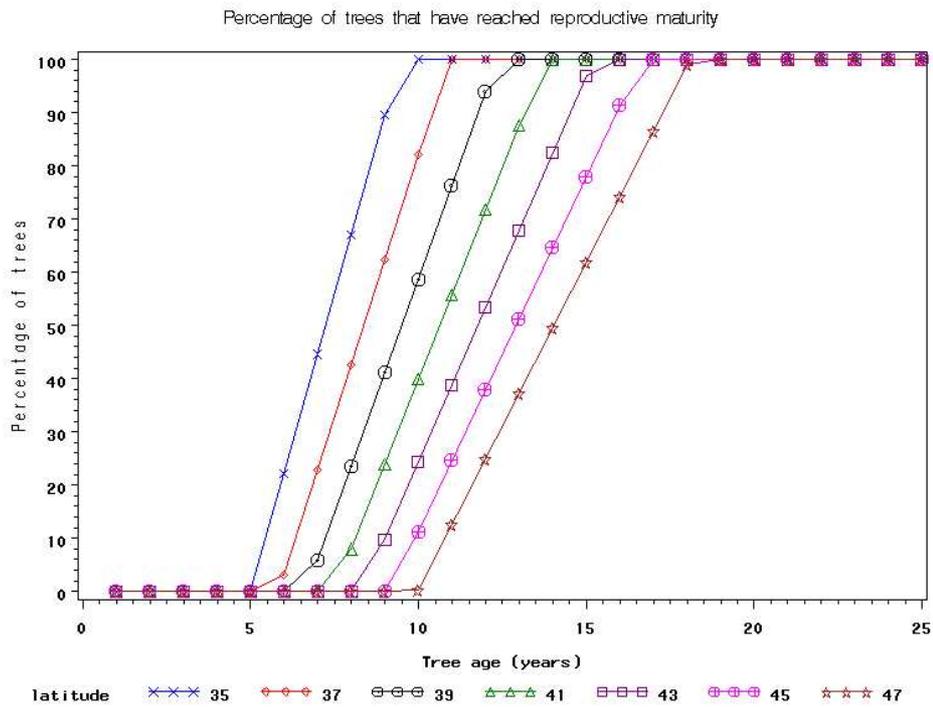


Figure 2. Model to predict reproductive maturity.



Functions at the annual shoot level

Number of branch clusters

Comments on previous implementation and suggestions for improvements

The function included in the previous implementation, predicted zero branch clusters for a zero shoot length. This resulted in zero branch clusters being predicted for very short annual shoots on young trees. Morphologically, it is possible to get annual shoots with no branch clusters when the tree is old, but not when the tree is young. Comparison of TreeBLOSSIM predictions with PhotoMARVL data, indicated that TreeBLOSSIM was predicting too many branch clusters, particularly higher in the tree.

Given the relatively short rotation length for radiata pine, an improvement would be to impose a lower and upper asymptote for the number of branch clusters in an annual shoot. Such a model would likely to be in error if one attempted to extend the rotation length.

This implies that we should find some very old radiata pine to measure in order to get the function shape correct.

New analysis

Methods

For each tree, the number of branch clusters in each annual shoot, and annual shoot length was calculated. Several different equations were investigated for predicting the number of branch clusters in an annual shoot as a function of annual shoot length and tree age.

Results

The number of branch clusters in an annual shoot is shown in Figure 3.

The following mathematical equation was considered most appropriate for predicting number of branch clusters in the annual shoot:

$$C_s = 1.0 + C_{\max} (\exp(-\exp(b - c \times L_{as}))) \times (1 - \exp(-Age_{tree} \times d))$$

where:

C_s is the number of branch clusters in the annual shoot

C_{\max} is the maximum number of branch clusters in the annual shoot

L_{as} is the length of the annual shoot

Age_{tree} is the age of the tree in years

b, c, d are model parameters.

The logic behind this formula is as follows:

There is a minimum number of clusters in an annual shoot. This is the term 1.0

There is a maximum number of clusters in an annual shoot. This is the term $C_{\max} + 1$.

The term: $\exp(-\exp(b - c \times L_{as}))$ is a sigmoidal shaped curve varying between 0 and 1. This allows the number of clusters in an annual shoot to increase with annual shoot length.

The term: $(1 - \exp(-Age_{tree} \times d))$ also varies between 0 and 1. This allows the number of clusters in an annual shoot to increase with increasing tree age.

Several options were investigated for the derivation of the model parameters (b, c, d) and C_{max} :

1. (b, c, d) and C_{max} allowed to vary by site /region
2. (b, c, d) constant across regions but C_{max} allowed to vary by site /region
3. (b, c, d) constant across regions but C_{max} predicted as a function of temperature

It was decided to implement approach 1 initially for the following reasons:

- it provided a better fit to the observed data at a regional level, and hence is better for testing whether this functional form is actually an improvement on the previous one.
- It was not known whether forest companies have access to climate data for their forests.

The predicted shape of this function is shown in Figure 4 (for 1m annual shoots) and Figure 5 (for 2m annual shoots).

Discussion

The predicted function for Site 8, (Esk Forest, Hawkes Bay) is rather different from the other sites. One possible reason is that clusters were not measured above 20-24 m due to tree damage.

If comparisons of PhotoMARVL data and model predictions, indicate that this model formulation is reasonable, then further consideration would be given to:

- generating a countrywide model, and
- predicting the maximum number of clusters in an annual shoot from the mean number of clusters in an annual shoot. This variable can potentially be estimated in the field.

Implementation

Both options 1 and 2 have been implemented. This was to enable approach 2 to be compared with approach 1. The coefficients are shown in Table 2.

Table 2. Coefficients to predict number of clusters in an annual shoot

Region	SiteId	C _{max}	b	c	d
Central North Island	3	6	2.278	1.729	0.109
Southland	5	6	1.539	1.241	0.0837
Sands	6	8	1.026	1.268	0.0994
Central North Island	7	6	1.642	1.398	0.0952
Hawkes Bay	8	6	2.210	1.370	0.306
Canterbury	10	7	1.580	1.678	0.0567
West Coast	11	7	1.213	0.846	0.134
Nelson	12	5	1.825	1.416	0.135
Clays	13	8	1.686	1.502	0.102
All regions		As for region	1.150	0.934	0.140

Figure 3. Observed variation in number of branch clusters in an annual shoot

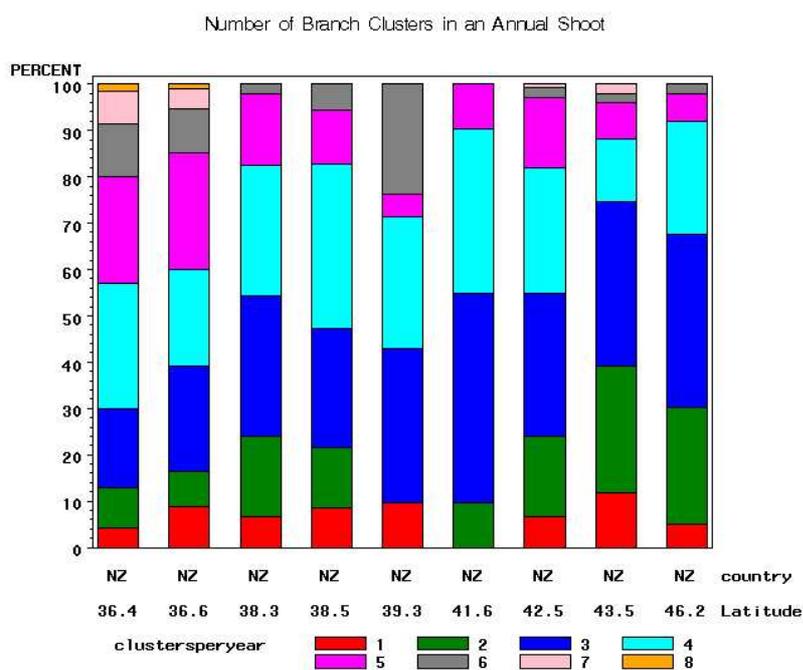


Figure 4. Model to predict number of clusters in a 1m long annual shoot.

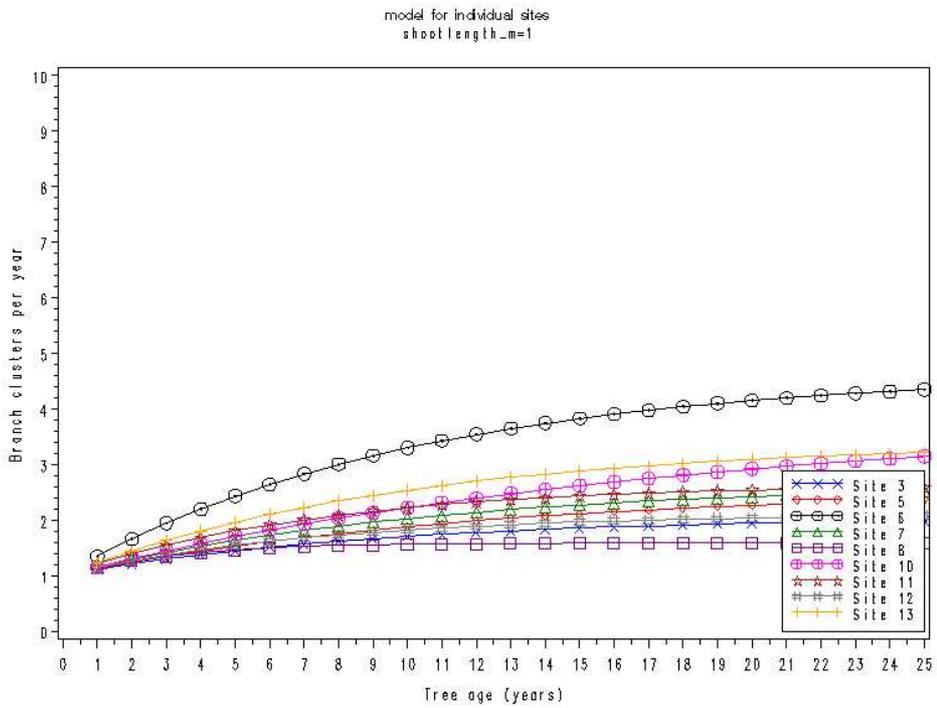
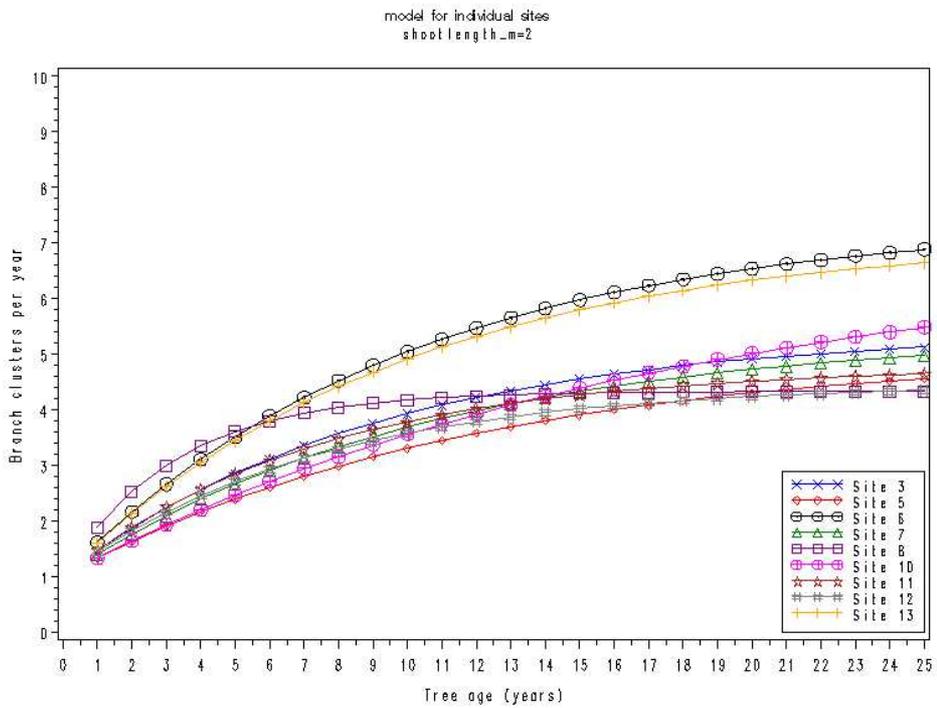


Figure 5. Model to predict number of clusters in a 2m long annual shoot.



Relative position of branch clusters within the annual shoot

New analysis

Methods

The SAS[®] procedure, PROC GLM, was used to investigate whether site influenced the relative position of cluster *I*, within an annual shoot with *J* clusters.

This procedure uses the method of least squares to fit mathematical equations to observed data. Both continuous variables (such as mean top height and basal area) and class variables (such as site and treatment) may be included in the equation as independent variables. In this case the only independent variable was the class variable 'site'.

Site was only significant in two cases (Position 1 in annual shoots with 3 clusters and Position 3 in annual shoot with 4 clusters). As site was generally not significant, it was decided to assume that site did not influence the relative position of any branch clusters. The mean position of cluster *I* within an annual shoot with *J* clusters was calculated for each site. These means were then averaged across sites.

Results

The mean values across sites are shown in Table 3.

Table 3. Relative positions of branch clusters within annual shoots

Number of clusters in the annual shoot	1	2	3	4	5	6	7	8
Position of cluster within the annual shoot								
1	1.0	0.52	0.35	0.26	0.19	0.16	0.14	0.12
2		1.00	0.70	0.50	0.41	0.32	0.31	0.22
3			1.00	0.78	0.62	0.51	0.48	0.26
4				1.00	0.81	0.69	0.60	0.45
5					1.00	0.84	0.72	0.66
6						1.00	0.86	0.79
7							1.00	0.87
8								1.0

Discussion

These values are very close to those in Report No. 108.

Functions at the cluster level

Number of branches and stem cones in a cluster

Comments on previous implementation and suggestions for future improvements

In TreeBLOSSIM (versions 1 and 2), the number of branches in a cluster and the number of stem cones in a cluster were predicted by independent functions. A consequent was a very small probability of predicting a cluster with zero branches and cones.

From a biological perspective, buds form first, and then differentiate into branches or stem cones. Hence an improvement is to predict the number of buds in a cluster, and then the percentage of buds that become cones.

There is evidence that cones tend to be absent from the last cluster in a morphological annual shoot. In collecting the data to develop TreeBLOSSIM, annual shoots have been determined based on stem ring counts. This will not be the same as a morphological annual shoot if the resting bud has expanded early (in the autumn, rather than the spring).

New Analysis

Methods and results

Graphs were plotted showing the number of branches and cones in a cluster (Figure 6), the number of branches in a cluster (Figure 7), and the number of stem cones in a cluster after tree maturity (Figure 8).

- Does site influence the number of “buds” (branches and cones) in a cluster?

Visually, the number of branches and stem cones in a cluster is affected by site (Figure 6). However observed patterns appear to be related more to the trial design than any effect of site environment. For example, sites 7, 10 and 12 (the final crop stocking trials) tend to have visually similar distribution but more branches and cones in a cluster compared with other sites. Similarly 3 of the 4 diallel sites (3, 5 and 11), have a visually similar distribution for number of branches and cones in a cluster. This suggests that the differences between sites are influenced by the genetic make-up of the trees sampled rather than environmental factors. It has therefore been assumed that there are no site differences in the number of branches and cones in a cluster.

- Does position of cluster in the annual shoot influence the number of “buds”?

2608 clusters were measured with number of “buds” ranging from 1 to 15, plus one cluster with 20 “buds”. This later was excluded from the analysis as it was suspected that two clusters had been measured as one. Of these, only 2236 could be correctly positioned within an annual shoot. 489 of these clusters were formed prior to tree maturity and 1747 after tree maturity.

An analysis using PROC GLM indicated that only a very small proportion of the variation could be accounted for by site, number of clusters in an annual shoot, and position of cluster within an annual shoot. For clusters formed after tree maturity (after site had been accounted for), neither the number of clusters in an annual shoot nor the position of the cluster within the annual shoot influenced the number of “buds” in a cluster.

- Distribution for number of branches and cones in a cluster.

Based on the above analyses, the observed cumulative probability distribution (Table 4) will be used to predict the number of buds in a cluster.

Table 4. Observed distribution for number of “buds” in a cluster.

Number of “buds”	Observed number of clusters	Cumulative probability
1	46	0.018
2	116	0.062
3	166	0.126
4	298	0.240
5	405	0.395
6	397	0.548
7	385	0.695
8	356	0.832
9	191	0.905
10	131	0.956
11	56	0.977
12	39	0.992
13	13	0.997
14	7	1.000
15	1	1.000

- Probability that a cluster with n “buds” contains m stem cones.

One possibility for a model was that each bud had an equal probability of becoming a cone (M. Kimberely, pers comm). This approach predicted that more clusters containing cones than were observed and was abandoned.

Factors that have the potential to affect the number of cones in a cluster with n “buds” include site, number of clusters in an annual shoot and cluster position within the annual shoot. There appear to be site differences (Figure 8). However the number of clusters in an annual shoot varies with site. The number of potential combinations was too great to obtain a reliable model using the SAS procedure, PROC LOGISTIC. For this reason, it was decided to use the observed probability that a mature cluster with n buds had m cones (see Table 5 and Figure 9). It is interesting to note that the probability that a cluster does not contain cones decreases as the number of buds increases.

A future approach would be to develop a “biologically-sound” model for cone formation and then test it against available data.

Table 5. Cumulative probability distribution for number of stem cones in clusters with m “buds”.

Number of buds	Number of cones	Number of observations	Cumulative probability
1	0	30	0.968
1	1	1	1.000
2	0	84	0.913
2	1	5	0.967
2	2	3	1.000
3	0	100	0.847
3	1	11	0.941
3	2	2	0.958
3	3	5	1.000
4	0	164	0.792
4	1	22	0.899
4	2	8	0.937
4	3	9	0.981
4	4	4	1.000
5	0	209	0.786
5	1	31	0.902
5	2	16	0.962
5	3	7	0.989
5	4	2	0.996
5	5	1	1.000
6	0	224	0.772
6	1	39	0.907
6	2	15	0.959
6	3	6	0.979
6	4	5	0.996
6	5	0	0.998
6	6	1	1.000
7	0	214	0.720
7	1	30	0.822
7	2	23	0.899
7	3	17	0.956
7	4	11	0.993
7	5	1	0.996
7	6	0	0.998
7	7	1	1.000
8	0	185	0.651
8	1	31	0.761
8	2	13	0.806
8	3	30	0.912
8	4	12	0.954
8	5	8	0.982
8	6	3	0.993
8	7	1	0.996
8	8	1	1.000

5. continued

Number of buds	Number of cones	Number of observations	Cumulative probability
9	0	94	0.566
9	1	16	0.663
9	2	17	0.765
9	3	10	0.825
9	4	20	0.946
9	5	7	0.988
9	6	0	0.992
9	7	0	0.996
9	8	2	1.000
9	9	0	1.000
10	0	70	0.579
10	1	5	0.620
10	2	5	0.661
10	3	13	0.769
10	4	9	0.843
10	5	9	0.917
10	6	9	0.992
10	7	1	1.000
10	8	0	1.000
10	9	0	1.000
10	10	0	1.000
11	0	19	0.365
11	1	2	0.404
11	2	2	0.442
11	3	4	0.519
11	4	5	0.615
11	5	9	0.788
11	6	6	0.904
11	7	5	1.000
11	8	0	1.000
11	9	0	1.000
11	10	0	1.000
11	11	0	1.000
12	0	10	0.278
12	1	0	0.292
12	2	1	0.306
12	3	2	0.361
12	4	5	0.500
12	5	9	0.7500
12	6	6	0.917
12	7	1	0.944
12	8	2	1.000
12	9	0	1.000
12	10	0	1.000
12	11	0	1.000
12	12	0	1.000

5. continued

Number of buds	Number of cones	Number of observations	Cumulative probability
13	0	0	0.017
13	1	0	0.033
13	2	0	0.050
13	3	0	0.066
13	4	1	0.083
13	5	3	0.333
13	6	4	0.667
13	7	4	1.000
13	8	0	1.000
13	9	0	1.000
13	10	0	1.000
13	11	0	1.000
13	12	0	1.000
13	13	0	1.000
14	0	1	0.143
14	1	0	0.200
14	2	0	0.257
14	3	0	0.315
14	4	0	0.372
14	5	2	0.429
14	6	0	0.500
14	7	1	0.571
14	8	2	0.857
14	9	0	0.905
14	10	0	0.952
14	11	1	1.000
14	12	0	1.000
14	13	0	1.000
14	14	0	1.000

Figure 6. Observed number of branches and stem cones in a given cluster.

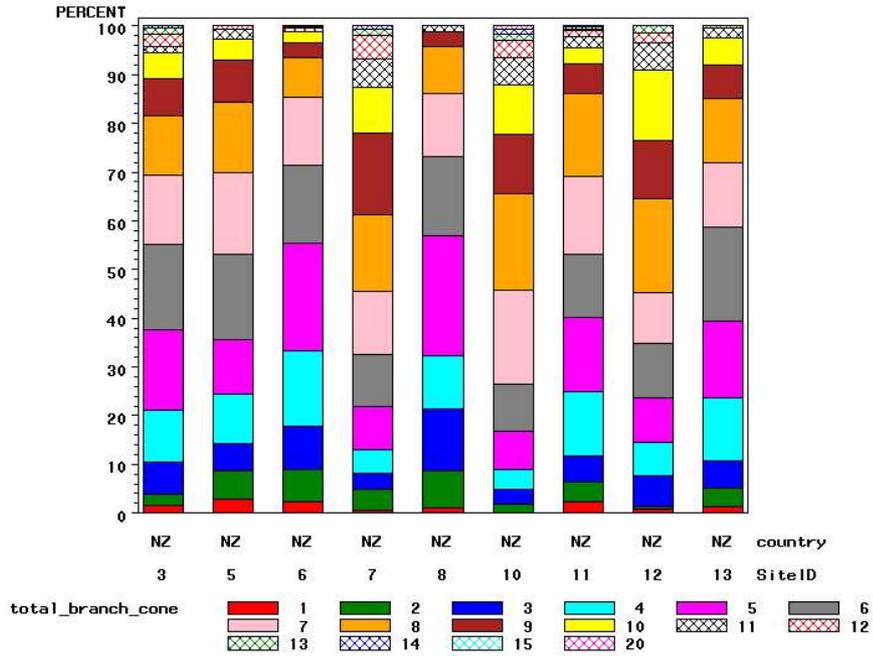


Figure 7. Observed number of branches in a cluster.

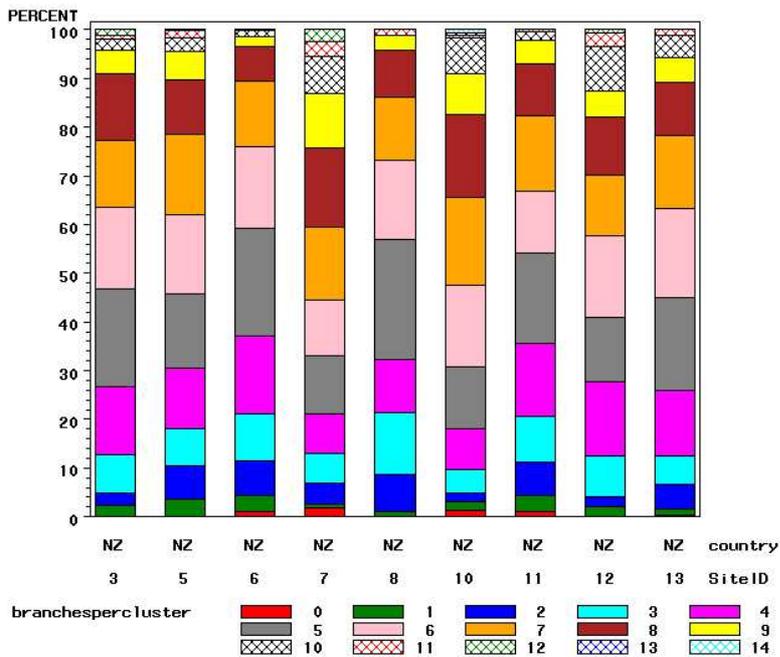


Figure 8. Observed number of stem cones in a cluster for clusters formed after tree maturity.

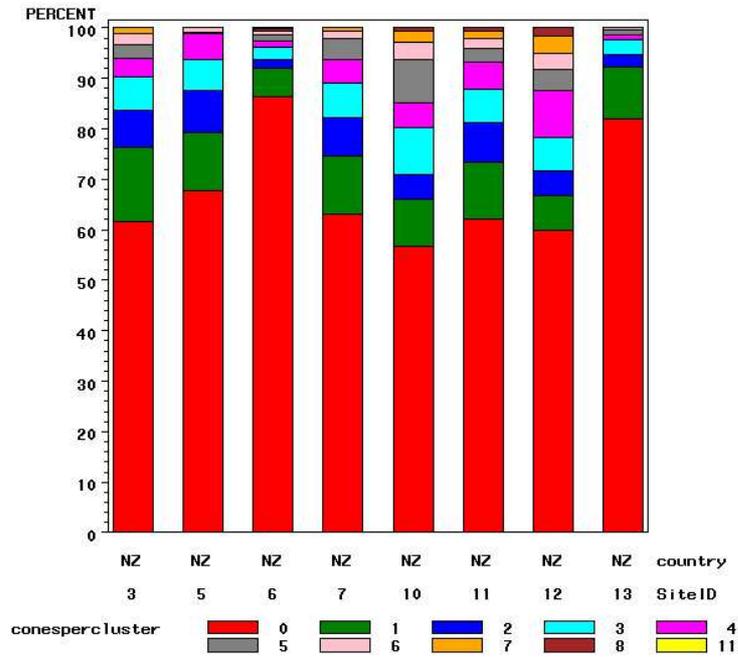
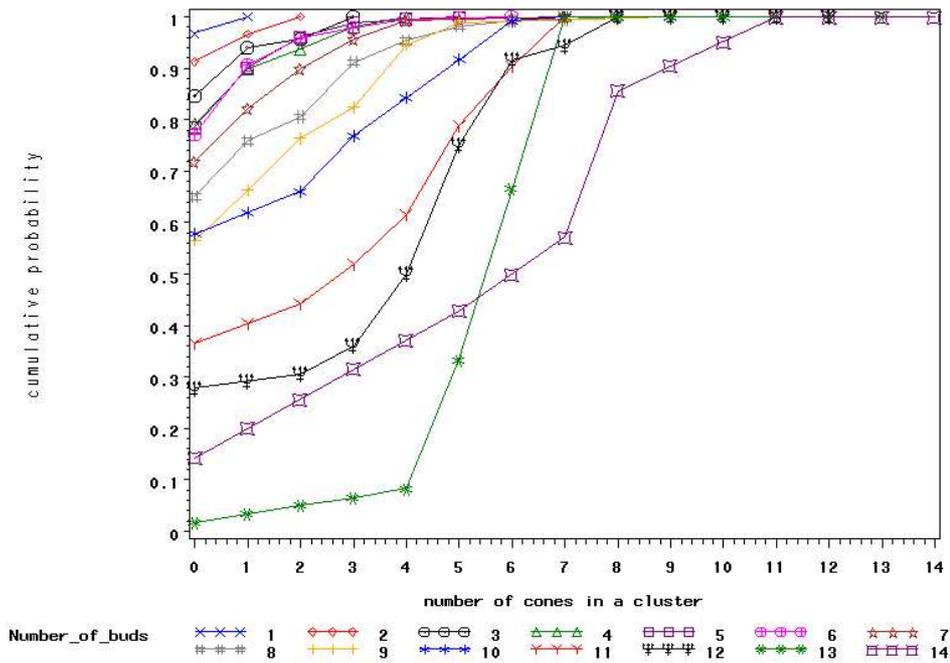


Figure 9. Cumulative probability distribution for number of cones in a cluster with n buds.



Azimuthal location of branches within a cluster

Comments on previous implementation and suggestions for future improvements

The azimuthal location of branches within a cluster is currently modelled using the 2:3 phyllotatic pattern, which means that branches are arranged in a spiral with a separation of 137.5° between adjacent branches.

This approach has a sound biological basis and will not be changed.

Azimuth angle of the largest branch in a cluster

Comments on previous implementation and suggestions for future improvements

Previous analyses showed that:

- The azimuth angle of the largest branch in a cluster was highly variable but tended to avoid South.
- The azimuth angle of the largest branch only had a small influence on timber value.

For these reasons, the azimuth angle of the largest branch in a cluster was assumed to be random in versions 1 and 2 of TreeBLOSSIM.

The analysis (Appendix 1) also supports the idea branch diameters are influenced by azimuthal position.

When data points are distributed around compass directions, circular statistical techniques need to be used. There are several distributions that can be used to model how points are clustered around different compass directions, for example the von Mises distribution and the wrapped normal distribution. The analyses (SGMC Report No. 74) indicated that a von Mises distribution would be appropriate for explaining the observed distribution of azimuth angles. However this is not as easy to implement as the wrapped normal distribution.

New analysis

Methods

The azimuth angle of the largest branch was sorted into 90° classes centred on the 4 directions: North, East, South, and West (Figure 10). Southern aspects tended to be avoided by most trees. Three trees stand out as being different - site_tree 702, 1001 and 1201. Site_tree is a unique identifier for each tree in the dataset being $100 \times \text{siteid} + \text{treeid}$.

Circular statistics were used to determine whether the azimuth angle of the largest branch was random or not (see SGMC Report No. 74 for details).

A predicted wrapped normal distribution was calculated for each tree using the observed mean vector length and mean azimuth angle.

Results

The analysis indicated that the azimuth angle for the largest branch in a cluster was significantly different from zero ($p \leq 0.05$) for all but 11 of the 45 trees considered. The mean azimuth angles tended to be close to North (between 330° and 360° , and between 0° and 30°) (see Table 6 and Figure 12). The smaller, the mean vector length (a measure of dispersion), the more likely the distribution is to be random. The data (Table 6) indicates that the trees with small mean vector lengths were often those with mean azimuth angles between 60° and 300° .

The predicted wrapped normal distributions are shown in Figure 11. The predicted wrapped normal distribution was significantly different from the observed distribution for only 6 of the 45 trees.

Discussion

The above results and those in Appendix 1 indicate that the azimuth angle of the largest branch is influenced by “North” and by the distribution of neighbours. The location of neighbours cannot be implemented in a distant-independent model, but it is suggested that a wrapped normal distribution be implemented as it is an improvement over the random distribution currently used.

It is suggested that the mean azimuth angle be set to zero as branch location is obviously influenced by North. It is suggested that the mean vector length be set to 0.40 for each tree – the mean of the observed vector lengths.

Implementation

The wrapped normal distribution is implemented by calculating random numbers from normal distribution, and then constraining the random numbers to be between 0° and 360° .

The mean vector length is converted to a measure of dispersion (equivalent to the variance) using the formulae:

```
rho = 2 * ln (meanvectorlength);  
rho = - rho;
```

where ln is the natural logarithm.

A random number from a normal distribution was calculated using the formulae:

```
a = 0 + sqrt(rho) * normal (seed);  
a = meanazimuthangle + a * 180 / 3.141592654;
```

Where ‘Normal (seed)’ is a SAS function calculating random numbers from a normal distribution with a mean of 0 and standard deviation of 1.

These random numbers are then constrained to lie between 0° and 360° using a modulus function:

```
a1 = mod (a, 360);  
a2 = a1;  
if a2 lt 0 then a2 = a2 + 360;
```

Figure 10. Observed distribution for azimuth angle of the largest branch.
 (Site_tree is 100xsiteid + treeid).

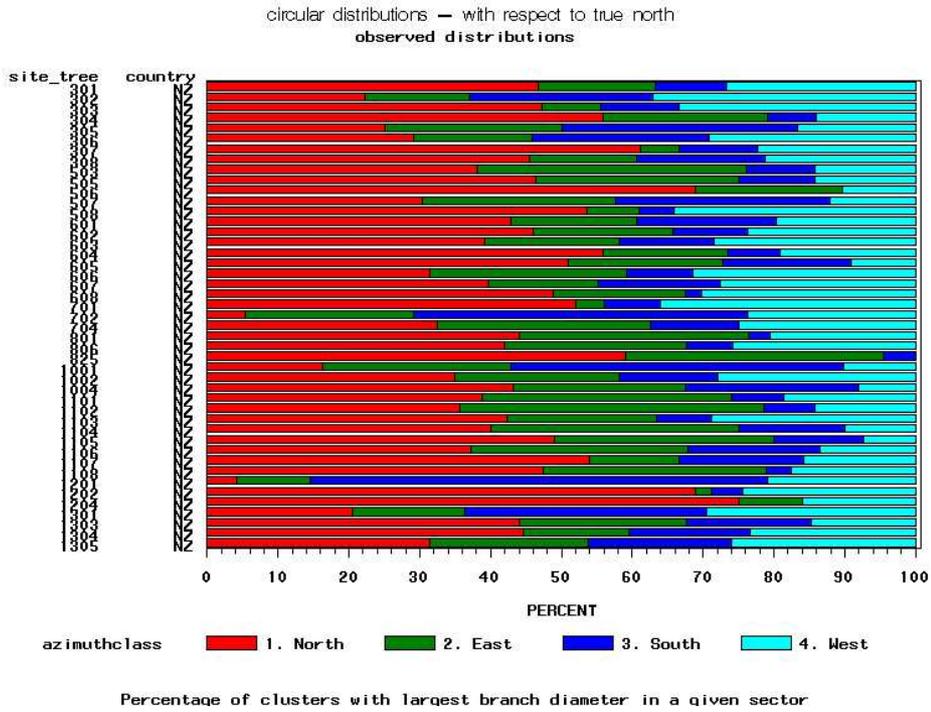


Figure 11. Predicted distribution of azimuth angles.

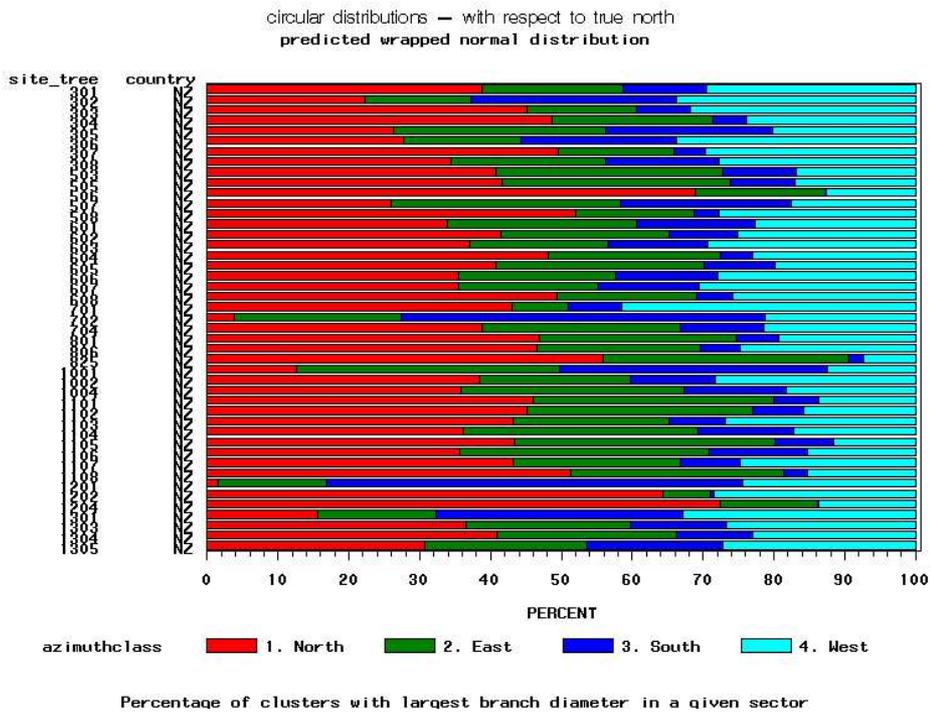


Figure 12. Relationship between mean azimuth angle and vector length for individual trees.

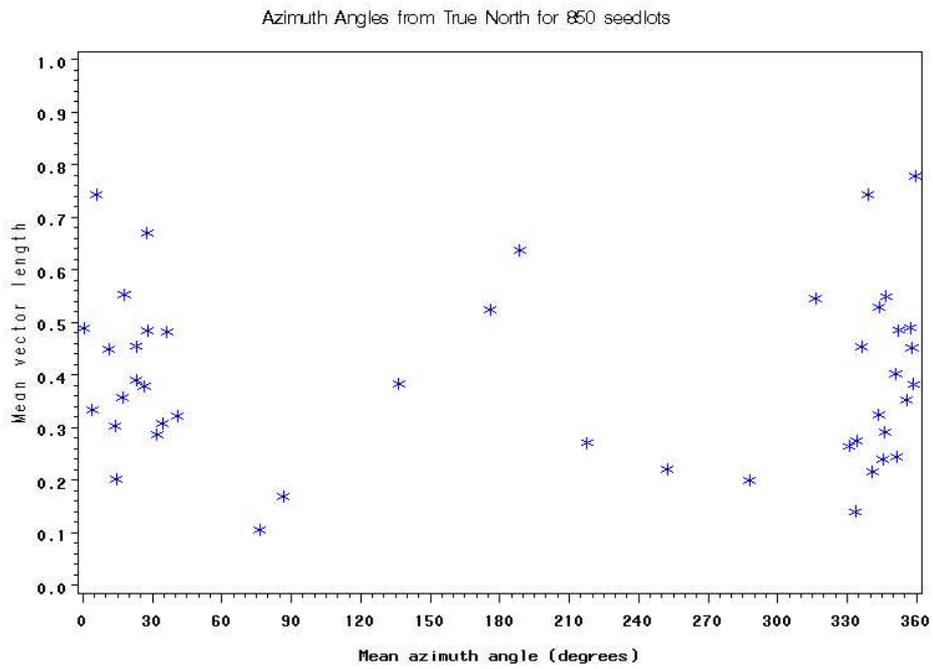


Table 6. Circular statistics for trees from 850 seedlots.

Site	Tree	Number of clusters	Mean vector length	Mean Azimuth Angle
3	1	30	0.32	344
3	2	27	0.22	252
3	3	36	0.45	336
3	4	43	0.49	357
3	5	12	0.11	76
3	6	24	0.20	288
3	7	18	0.53	344
3	8	33	0.22	341
5	3	21	0.38	27
5	5	28	0.39	23
5	6	29	0.74	6
5	7	33	0.17	87
5	8	41	0.55	347
6	1	56	0.20	15
6	2	76	0.35	356
6	3	74	0.27	334
6	4	68	0.49	0
6	5	55	0.36	17
6	6	54	0.24	346
6	7	58	0.26	331
6	8	43	0.49	352
7	1	50	0.55	317
7	2	55	0.52	176
7	4	40	0.30	14
8	1	34	0.45	11
8	6	31	0.45	358
8	25	22	0.67	28
10	1	49	0.38	136
10	2	43	0.29	346
10	4	37	0.29	32
11	1	54	0.48	28
11	2	28	0.45	23
11	3	52	0.40	351
11	4	20	0.31	35
11	5	55	0.48	36
11	6	59	0.32	41
11	7	63	0.38	359
11	8	57	0.55	18
12	1	48	0.64	189
12	2	45	0.74	339
12	4	44	0.78	360
13	1	44	0.27	218
13	3	34	0.24	351
13	4	47	0.33	4
13	5	54	0.14	334

Functions at the Branch Level

Branch Potential

Comments on previous implementation and suggestions for future improvements

The concept of a branch potential arose from the hypothesis that “each branch has a pre-determined capability for diameter growth when it is in the bud”. Each branch was assigned a “growth potential” made up of 6 “subsidiary potentials” which together determine the maximum diameter that can be attained by a branch (see SGMC report No. 108).

Comparisons of TreeBLOSSIM predictions with PhotoMARVL data have indicated that the variation in the diameter of the largest branch in a cluster predicted by TreeBLOSSIM was larger than observed on some sites. It was considered that a contributing factor would be the “cluster potential”.

Branch Position Potential

The branch potential accounts for the variation in branch diameters within a cluster. The largest branch is assigned a potential of 1. The potential of other branches is less than 1 and is determined based on their position in the phyllotatic spiral.

Methods

An equation to predict branch potentials was calculated using relative branch diameters. Relative branch diameter was plotted against branch rank for each site individually and for all sites combined. The following model, a sigmoid curve where branch potential decreases with increasing branch rank, was fitted to the combined data set.

$$P_b = \exp(-a_b \times (r-1)^{b_b})$$

where:

P_b is the branch potential

(branch potential in model; relative branch diameter in analysis)

r is the branch rank

(the largest branch in terms of diameter is assigned rank 1, the next largest branch is assigned rank 2, etc.)

a_b, b_b are predicted coefficients

The larger b_b , the more rapidly P_b decreases with increasing branch rank.

Results

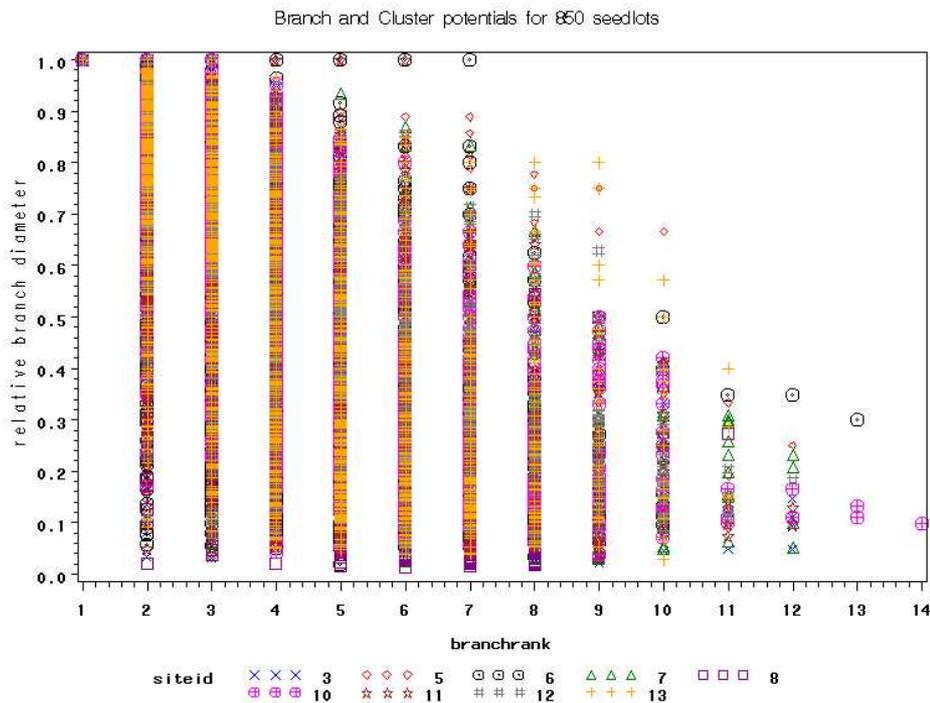
The relative branch diameter for a given branch rank was highly variable for all sites (Figure 13). The above equation is very simple and only attempts to mimic the decrease in relative branch diameter with increasing branch rank.

The predicted values of a_b and b_b were respectively, 0.25 and 0.88. These values are similar to those given in SGMC Report No. 108.

Discussion

A more detailed model would be required to explain the huge variability observed on each site. Development of such a model is considered low priority, as the relative diameters of branches in a cluster did not appear to have a major impact on timber value (see SGMC Report No. 82).

Figure 13. Observed branch potentials.



Cluster Potential

The cluster potential allows for the observed variation in the diameter of the largest branch in the cluster. For example one cluster may have large branch diameters and the following cluster small branch diameters. The reason for the variation is not known, but it is suspected that it may be related to the morphological development of the annual shoot.

The predicted model results appear to be rather sensitive to this function. In SGMC report 108, it was stated that the first two versions of TreeBLOSSIM did not predict sufficient variation between clusters. The implementation in Version 1.1 attempted to address this issue but further tests indicated that TreeBLOSSIM now predicts too much variation on some sites.

Another feature noted was that TreeBLOSSIM would predict clusters with extremely small branches. This occurred because the minimum possible cluster potential was zero.

Methods

The data required to derive the cluster potential, is a sequence of branch clusters that have developed under a common stocking and that have stopped growing in diameter. The suitable data are those from the diallel trials. All clusters where the branch age was less than 10 years were excluded to avoid growing branches.

The cluster potential, P_c , was calculated as:

Diameter of the largest branch in a cluster / (mean diameter for the largest branch in a cluster averaged over “non-growing” clusters within the tree)

The clusters within a tree were ranked according to cluster potential, and a cluster rank between 0 and 1 calculated.

For each sample tree from the diallel trials, the standard deviation for P_c was calculated. PROC GLM was used to investigate whether the standard deviation varied by site.

Cluster potential was predicted using the same approach as previously, except that a non-zero intercept was included.

$$P_c = d_c + \frac{u}{a_c + b_c \times u - c_c \times u^2}$$

where:

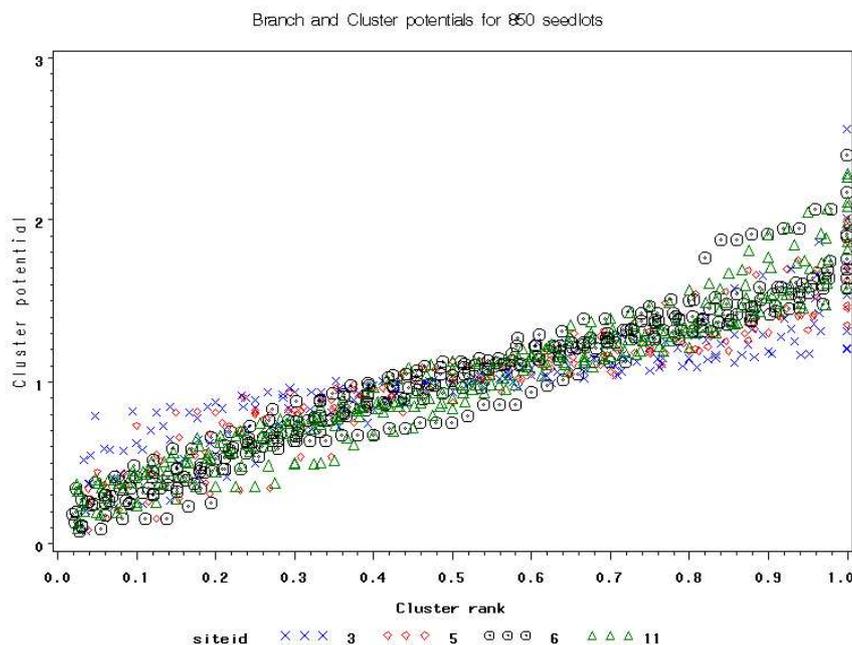
- P_c is the cluster potential
- u is cluster rank
- a_c, b_c, c_c, d_c are predicted coefficients

Results

The relationship between cluster potential and cluster rank (Figure 14) appears to vary with site. However, the PROC GLM analysis indicated that the standard deviation for cluster potential at the tree level did not vary with site. Therefore, the coefficients of the above equation were estimated using the combined data from all 4 diallel sites.

The predicted values of a_c, b_c, c_c, d_c were respectively: 0.26, 0.94, 0.58, 0.13.

Figure 14. Observed cluster potentials.



Discussion

The same approach to predicting cluster potential was used, in order to assess the effect of having one model versus model for individual sites.

Tree Potential

The tree potential has not been altered. It is calculated as follows:

$$P_t = \text{tree DBH} / \text{plot mean DBH}$$

Stocking and Site Potentials

These have not been altered as they were developed using other data (see SGMC Report No. 98) and Table 10 in SGMC Report No. 108.

Note: No data from Westland was included in the analysis in SGMC Report No. 98. The parameters for Nelson region have been assigned for the Westland region.

Genetic Potential

This is currently assumed to be 1 for all seedlots.

PhotoMARVL data from GF7, GF14 and GF 22 seedlots in the 1978 Genetic Gain Trials, indicated that seedlot only had a minor effect on branch diameter (see SGMC Report No. 119). PhotoMARVL data collected during 2003-2004 will provide further data on the variation in branching characteristics with seedlot.

The need for a varying genetic potential will be reassessed when these new data have been analysed.

Response Potential (Branch response to thinning)

This has not been modified. See SGMC Report No. 108 for details.

Branch diameter development through time

Comments on previous implementation and suggestions for future improvements

One of the reasons for developing a branch model was to be able to predict future diameters for branches given data at a given point of time.

In the previous version of the model, branch diameter was predicted as a function of branch age; and branch growth predicted the difference in diameter between two ages. Once a branch had reached its maximum diameter, the diameter was assumed to remain constant.

All the testing of TreeBLOSSIM has been carried out using non-destructive methods, so we have only been able to compare model predictions with actual data at one point in time. Comparison of TreeBLOSSIM predictions with PhotoMARVL data suggested that on average the prediction of branch diameter is reasonable.

Comparison of TreeBLOSSIM predictions with field assessment of branching in FR54 (Clays region) suggested that the zone of actively growing branches was shorter than predicted by TreeBLOSSIM. In the version of TreeBLOSSIM used for the above analysis, it was assumed that branch development in the Clays region would be the same as the Sands region. This problem might be resolved with a different model for the Clays region.

These results suggest that the functional form used to predict branch diameter is reasonable, but that there should be regional models.

New Analysis

Methods

Branch diameter increases rapidly for a number of years and then remains approximately constant. The actively growing phase is the more important. The age, A_M , at which each branch first reached its maximum diameter was calculated.

The equation used previously was fitted to the data for each branch. The equation form allows the branch to grow to a maximum diameter and then decline in diameter. To avoid the data being too heavily weighted by the non-growing phase, observations where branch age was greater than $A_M + i$ were excluded from the analysis. Various values for i were investigated.

In the implementation, the branch diameter will be assumed to be constant once the maximum has been reached. This is logical as branch diameter only changed by a few millimetres after the maximum was reached.

$$bd = \frac{A}{a_{bd} + \frac{A^2}{4 \times a_{bd} \times bd_{\max}^2}}$$

where:

- A is the branch age in years
- bd is the branch diameter (in mm) at age A
- bd_{\max} is the maximum branch diameter observed
(in the model this is replaced by the branch potential)
- a_{bd} is the model coefficient

The relationship between a_{bd} and bd_{\max} was examined for each branch to confirm that the equation used in the previous analysis was still relevant:

$$a_{bd} = \frac{b_{bd}}{bd_{\max}^c}$$

The combined model was then fitted to the data for each site. The combined model was fitted using different values of $A_M + i$.

Results

In the previous analysis, the value of c used was 0.5. Consideration was given to whether this should change by site and/or be different from 0.5. It was decided that 0.5 was an appropriate value.

The value of b_{bd} increased very slightly with increasing value of $A_M + i$. It was considered that the most appropriate value of $A_M + i$ was $A_M + 3$ as this resulted in the minimum mean residual for the whole data set combined.

The predicted values for b_{bd} (Table 7) seem quite logical. Sites where crowns were visually quite open with few dead branches had larger values of b_{bd} . A larger value of b_{bd} means that the branches grow slower. It would also mean that the actively growing part of the crown would be shorter. The value for the Riverhead (Clays) is a lot lower than the value for Woodhill (Sands), so this should resolve the observed discrepancy mentioned above.

Future research would be to relate the values of b_{bd} to site characteristics. From a visual assessment of the values, a nutritional score might be appropriate.

Table 7. Predicted values of b_{bd} for each dataset.

SiteId	Region	Forest	b_{bd}
3	Central North Island	Kaingaroa	0.600
5	Southland	Taringatura	0.633
6	Sands	Woodhill	0.789
7	Central North Island	Kaingaroa	0.728
8	Hawkes Bay	Esk	0.777
10	Canterbury	Eyrewell	0.815
11	West Coast	Mawhera	0.760
12	Nelson	Golden Downs	0.796
13	Clays	Riverhead	0.632

For the majority of observations, branch diameter was predicted to within 1cm of the observed value (Figure 15, Figure 16 and Figure 17).

The function predicts that larger branches grow for longer than smaller branches (see Figure 18 for an illustration).

The coefficient b_{bd} influences the age at which a branch reaches its maximum diameter, and the path by which the branch reaches that diameter. Figure 19 illustrates the growth of a branch whose maximum diameter is for a 50 mm for the sites with the minimum and maximum value of b_b . Figure 20 illustrates growth of a branch whose maximum diameter is for a 50 mm at site 6 (Sands) and site 13 (Clays). The model for Clays reaches the maximum quicker, should therefore improve TreeBLOSSIM predictions for FR54. This will be confirmed when the PhotoMARVL data for this site are compared with TreeBLOSSIM predictions.

Figure 15. Residuals from fitting equation to predict branch diameter.

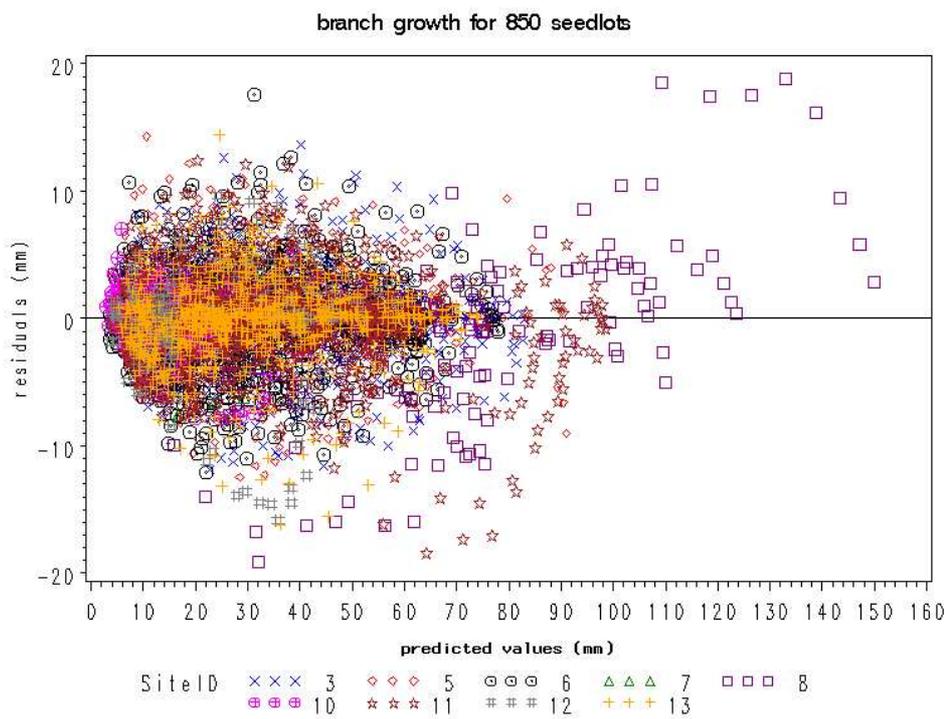


Figure 16. Residuals from fitting equation to predict branch diameter.

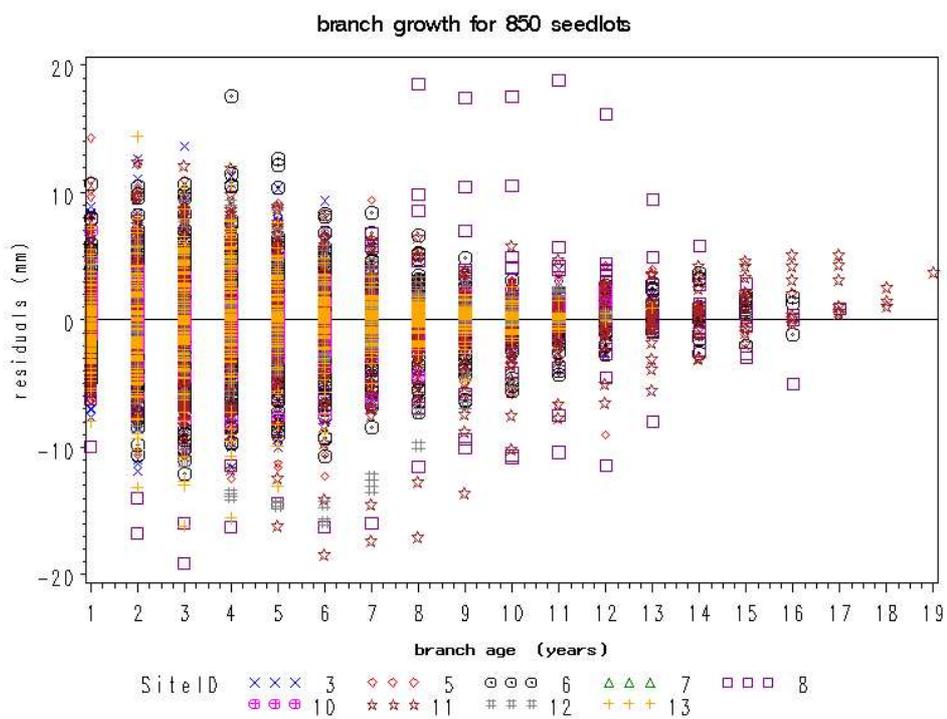


Figure 17. Residuals from fitting equation to predict branch diameter.

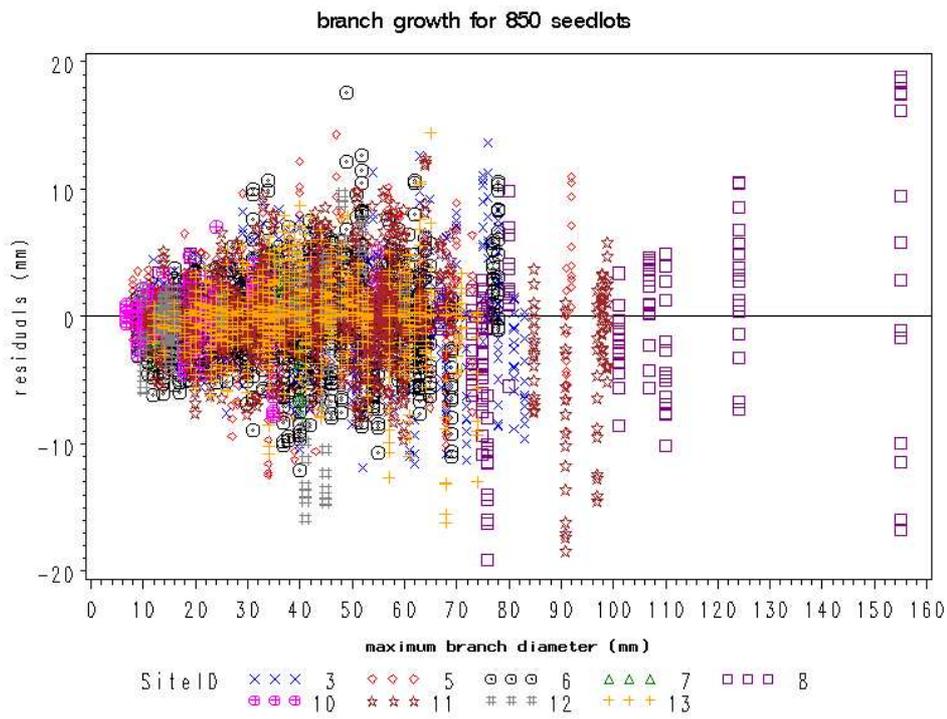


Figure 18. Illustration of model predicting branch diameter development.

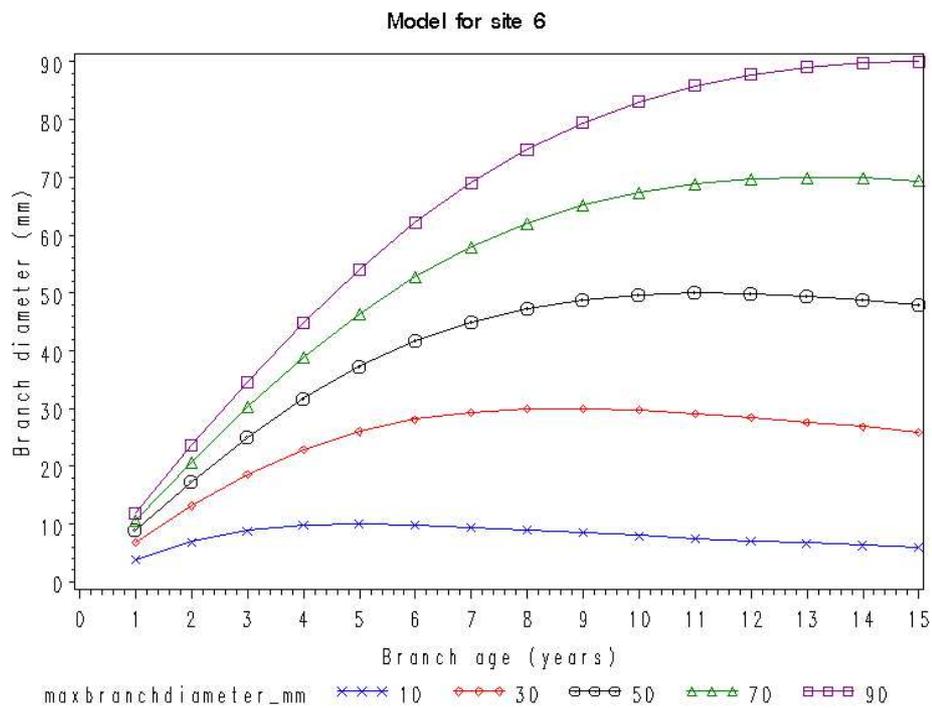


Figure 19. Illustration of model predicting branch diameter development.

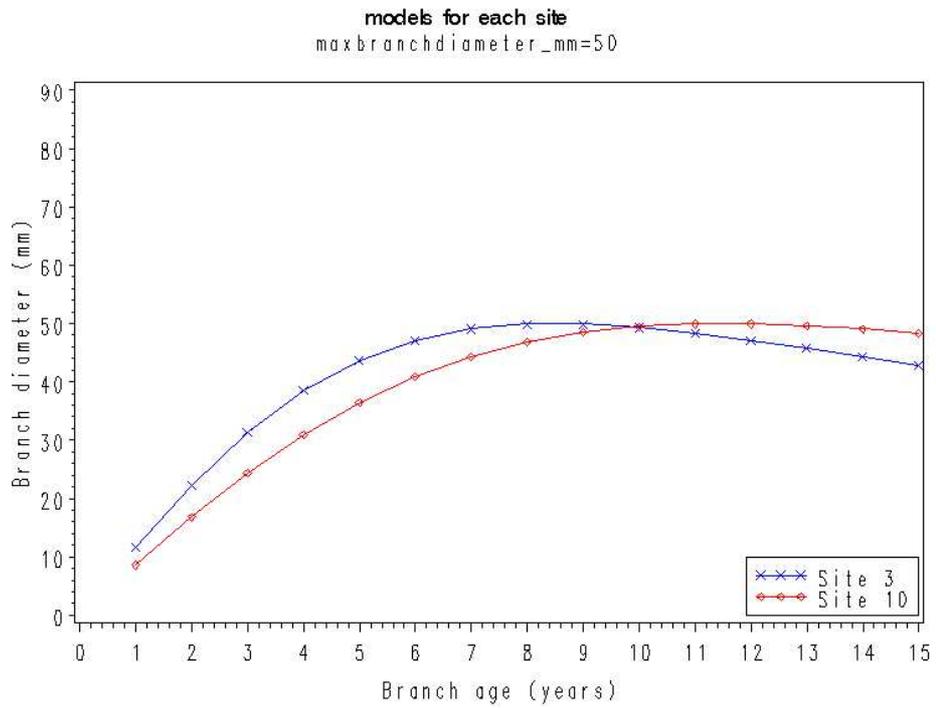
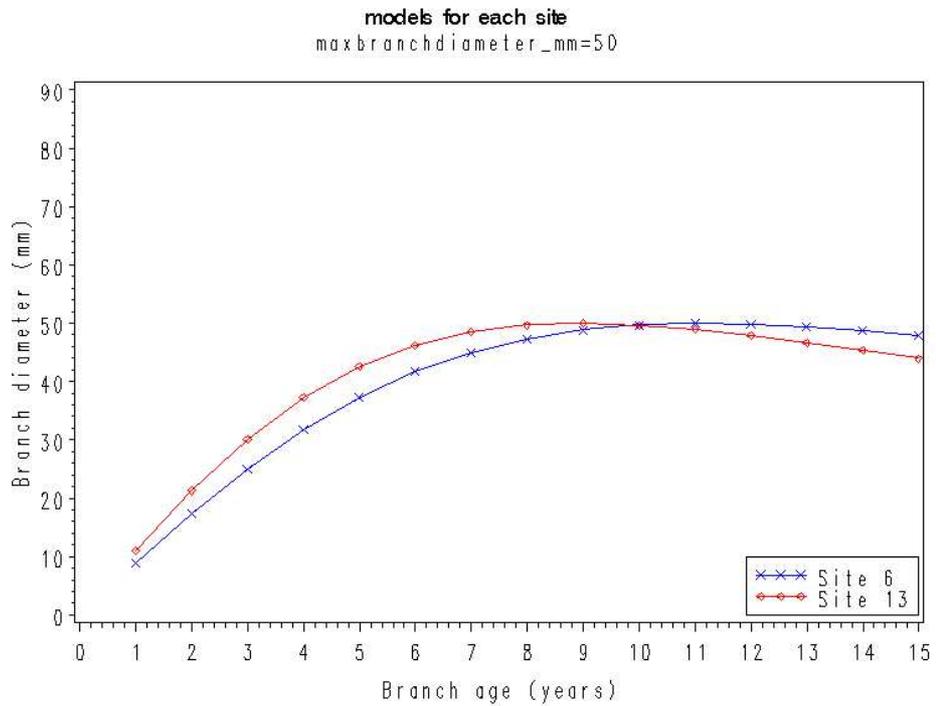


Figure 20. Illustration of model predicting branch diameter development.



Branch Angle

Comments on previous implementation and suggestions for future improvements

Several approaches have been investigated for this function. The variable calculated has been *yval*, the vertical distance, between the point of intersection of the branch and stem piths, and the position of the branch pith at the stem surface was calculated. The observed relationship between *yval* and stem radius was generally curvilinear, whereas the sawing simulator, AUTOSAW, assumes a linear relationship.

Previous functions have attempted to reproduce the observed curvilinear relationship. In this implementation, a linear relationship has been developed to provide an easier link to AUTOSAW.

New analysis

Methods

The following linear relationship was fitted to the observed data for each branch:

$$yval = a_e + b_e \times r_{stem}$$

where

yval is the vertical distance between the point of intersection between branch and stem piths and the current position of the branch pith

a_e is a predicted coefficient, that can be interpreted as a vertical offset along the stem. This is the difference between the actual and predicted point where the branch and stem piths intersect.

b_e is a predicted coefficient, that can be interpreted as the tangent of the branch angle

r_{stem} is the stem radius

Mathematical models (using PROC GLM) were then developed to explain the observed variation in a_e and b_e between the individual branches.

Results

Values of a_e and b_e were predicted for 967 branches spread across 9 sites.

The individual branch values of a_e varied widely on each site. The overall range was -55 mm to +54 mm. At a site level, the mean values varied between 2 mm (site 10) and 13 mm (site 3). While the SAS procedure, PROC GLM, indicated that there were significant differences between sites, site only explained a tiny proportion of the observed variation ($R^2 = 0.13$).

The predicted values of a_e for the individual sites are given below. In these equations a_e has been replaced by `modela`.

```

if siteid=3 then modela = 12.6;
if siteid=5 then modela = 8.3;
if siteid=6 then modela = 4.0;
if siteid=7 then modela = 6.3;
if siteid=8 then modela = 5.9;
if siteid=10 then modela = 1.9;
if siteid=11 then modela = 7.2;
if siteid=12 then modela = 11.6;
if siteid=13 then modela = 11.1;

```

These values were used in testing how well the branch angle was predicted.

From a practical point of view, the differences in a_e are considered minor. There is subjectivity in the field measurements in choosing the point where the branch and stem piths meet. This will influence the predicted value of a_e . For these reasons it is suggested that the coefficient, a_e , be set to zero within TreeBLOSSIM.

Variables considered to explain the observed variation in b_e were siteid, observed bark inclusion class, observed maximum branch diameter, and average spacing. Average spacing was calculated as $\sqrt{(10000 / \text{final stocking})}$.

The R^2 value for the GLM model that included observed maximum branch diameter observed bark inclusion class and siteid was 0.48. Only branches formed after the final thinning were included in the model that had average spacing as in independent variable. The R^2 value for the GLM model that included observed maximum branch diameter, observed bark inclusion class, siteid and average spacing was 0.47.

Average spacing was not predicted to have a significant effect on b_e . The model (including maximum branch diameter, bark inclusion, average spacing and siteid) predicted that a change in stocking from 200 stems/ha to 600 stems/ha would result in a 2° change in branch angle.

The observed bark inclusion was predicted to have a significant effect on b_e . The model (including maximum branch diameter, observed bark inclusion class and siteid) predicted that branch angle would be 19° higher for a branch with over 50% bark inclusion compared with a branch with no bark inclusion (branch angle being measured from horizontal upwards).

The maximum branch diameter was predicted to have a significant effect on b_e . The model (including maximum branch diameter, observed bark inclusion class and siteid) predicted that branch angle would be 30° higher for a 100mm branch compared with a 10mm branch.

Site was predicted to have a significant effect on b_e . The model (including maximum branch diameter, observed bark inclusion class and siteid) predicted that branch angle would vary by up to 22° between sites for a given branch diameter and bark inclusion class. Siteid 8 was quite different. If this was excluded the difference was only 12°.

The model to predict b_e is:

$$b_e = 0.08 + 0.007 * \text{maxbranchdiameter_mm} + \text{barkvalue} + \text{sitevalue}$$

The values for `barkvalue` and `sitevalue` are given below.

```

if siteid=3 then sitevalue = 0.00;
if siteid=5 then sitevalue = -0.14;
if siteid=6 then sitevalue = 0.00;
if siteid=7 then sitevalue = -0.04;
if siteid=8 then sitevalue = -0.38;
if siteid=10 then sitevalue = 0.02;
if siteid=11 then sitevalue = -0.07;
if siteid=12 then sitevalue = -0.19;
if siteid=13 then sitevalue = 0.00;

if branchbarkinclusion_0_1_2 = 0 then barkvalue=0.27;
if branchbarkinclusion_0_1_2 = 1 then barkvalue=0.36;
if branchbarkinclusion_0_1_2 = 2 then barkvalue=0.67;
if branchbarkinclusion_0_1_2 = 3 then barkvalue=0.00;

```

The overall model to predict `yval` is:

$$yval = a_e + b_e * \text{ringstemradius_mm};$$

This model was fitted to the original data. However it was not particularly good at predicting branch elevation (Figure 21). However the large errors are likely to be unimportant, as simulations (SGMC Report 82) indicated that branch angle had a low impact on value when cutting visual grades. The ability to link with AUTOSAW is a major plus for this approach. Model simulations (Figure 22 and Figure 23) indicate how branch elevation will change for a branch without bark inclusion.

Within TreeBLOSSIM itself, the coefficient, a_e , will be set to zero and the maximum branch diameter (`maxbranchdiameter_mm`) replaced by the branch potential.

Figure 21. Residuals from model predicting branch elevation.

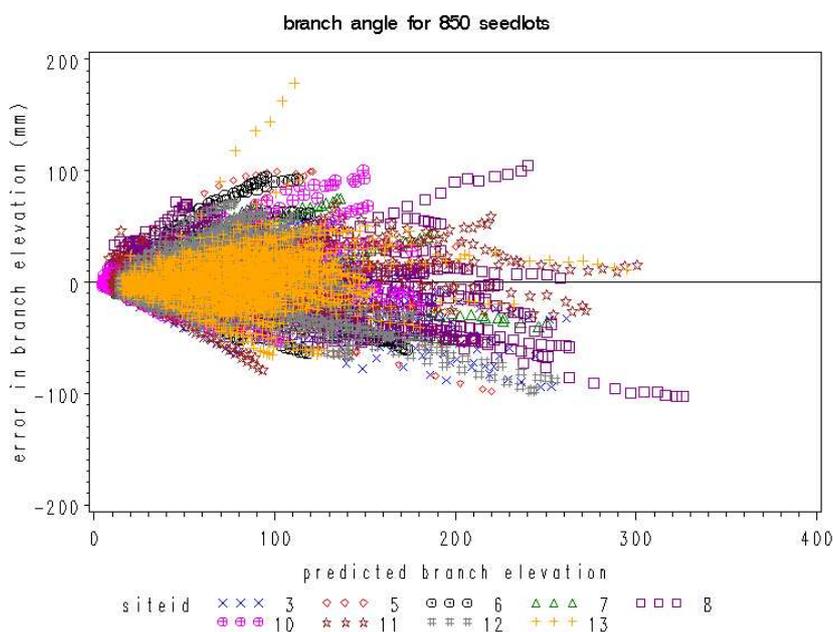


Figure 22. Variation in branch angle with stem radius for different sites when the maximum branch diameter is predicted to be 10mm.

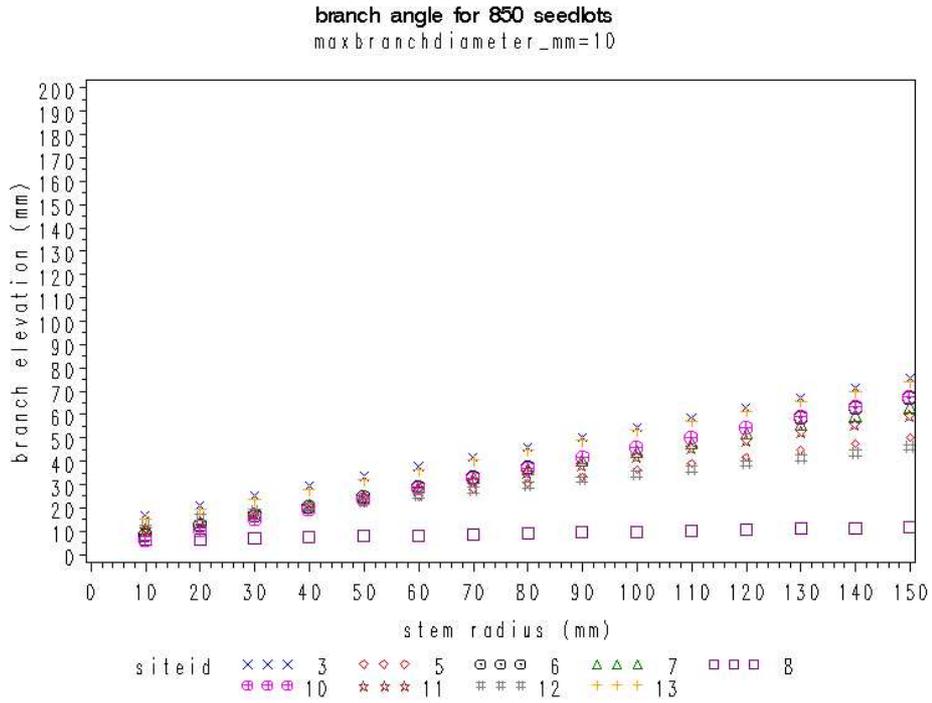
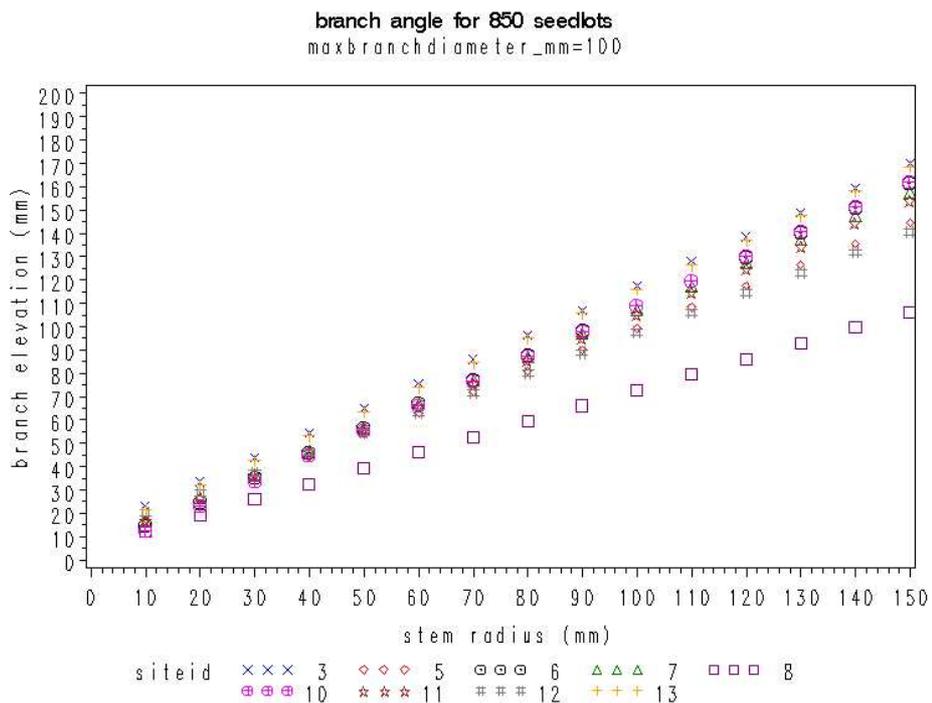


Figure 23. Variation in branch angle with stem radius for different sites when the maximum branch diameter is predicted to be 100mm.



Branch Mortality

Comments on previous implementation and suggestions for future improvements

The approach used in the previous implementation was to predict the probability a branch was dead, based on the largest diameter attained and the number of years since the branch reached that diameter. This approach has been retained.

New Analysis

Methods

The SAS procedure, PROC LOGISTIC was used to develop the model. The form of the logistic model is:

$$p_1 = i + c_{bd} \times bd + c_{pm} \times A_{pm}$$

$$p_2 = \exp(p_1) / (1 + \exp(p_1))$$

where:

bd is the branch diameter at age A_{pm} + number of years to reach its maximum diameter

A_{pm} is the number of years since the branch reached its maximum diameter

i is a predicted intercept

c_{bd} , c_{pm} are predicted coefficients

p_1 , p_2 are predicted probabilities

A branch is assumed to be dead if $p_2 \geq 0.5$

Three alternative models were considered:

1. A separate model for each site
2. One model for all sites
3. One model with separate intercepts for each site

Results

There were 6209 observations of which 1030 (17%) represented a dead branch. In all cases, the model was better at predicting the occurrence of a live branch compared to a dead branch. It was decided to implement model 3, for the following reasons:

- The percentage of observations correctly predicted was similar to model 1.
- It was considered that there were insufficient dead branches to justify the observed form of the individual site models.

The model coefficients are shown in Table 8. Observed data and model for the two extreme sites are shown in Figure 24 and Figure 25.

As an example a branch 10mm in diameter would have a 50% chance of being dead 5 years after it had reached its maximum diameter at site 13. At site 6, the same branch would have a 50% chance of being dead after 11 years.

The observed site intercepts appear to be related to observed crown structure. The more open the crown, the more negative the site intercept.

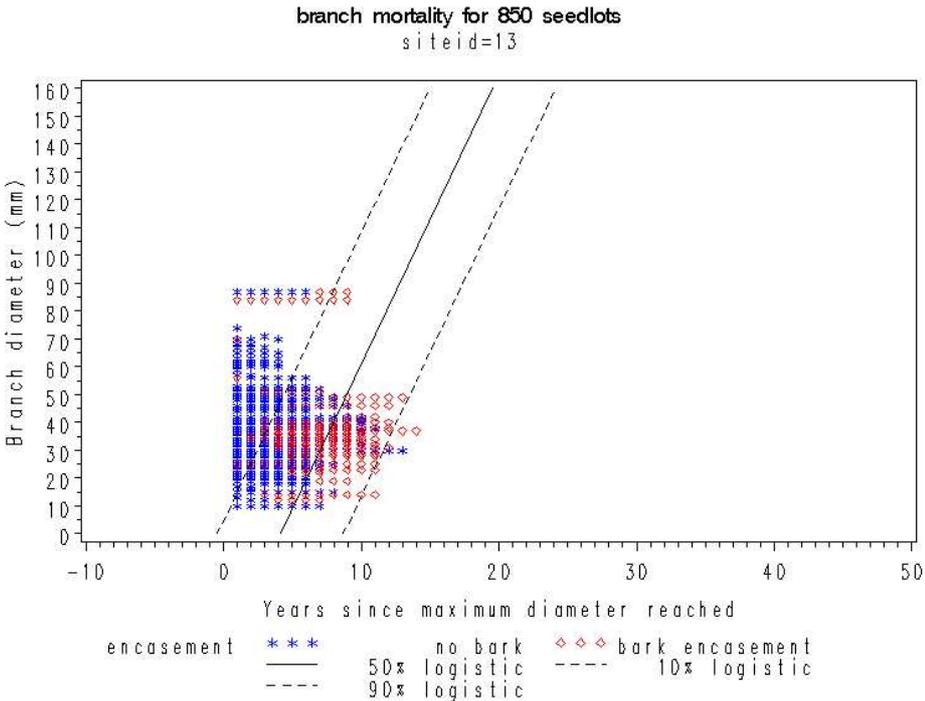
Table 8. Predicted coefficients for branch mortality model.

Coefficient label	Region	Coefficient value
c_{bd}		-0.0463
c_{pm}		0.48
Intercept – Site 3	Central North Island	-2.60
Intercept – Site 5	Southland	-3.35
Intercept – Site 6	Sands	-4.84
Intercept – Site 7	Central North Island	-2.65
Intercept – Site 8	Hawkes Bay	-2.76
Intercept – Site 10	Canterbury	-4.69
Intercept – Site 11	West Coast	-3.11
Intercept – Site 12	Nelson	-4.67
Intercept – Site 13	Clays	-1.98

Discussion

Further research is needed to be able to relate the individual site intercepts to environmental parameters.

Figure 24. Branch mortality – data and model for site 13 (Clays)



Results

The dataset consisted of 921 observations:
682 branches with no bark trapped
175 branches with up to 50% bark trapped
64 branches with over 50% bark trapped

The observed number of observations for each bark inclusion class with respect to maximum branch diameter is shown in Table 9. It can be seen that the likelihood of bark being trapped increases with increasing maximum branch diameter.

Table 9. Observed percentages for different classes of bark inclusion

Maximum branch diameter	Number of observations	Observed percentage		
		0	1	2
0 – 2 cm	183	94.0%	5.5%	0.5%
2 – 4 cm	372	82.8%	15.6%	1.6%
4 – 6 cm	264	62.5%	28.0%	9.5%
6 – 8 cm	74	41.9%	32.4%	25.7%
> 8 cm	28	21.4%	32.2%	46.4%

The logistic regression analysis indicated that both siteid and maximum branch diameter were significant. However the R^2 value was only 0.22. If site was excluded the R^2 value was 0.18, indicating that site had less influence than maximum branch diameter.

Given the small number of observations for large branches, and low R^2 values for the logistic regression, it was decided that the observed probabilities would be implemented in TreeBLOSSIM.

Discussion

It is considered that further data would be necessary to determine whether site was actually an important influence. The logistic regression analysis indicated that site 6 (Woodhill) would be most likely to have bark trapped at a given branch diameter. Given the small size of the branches at Woodhill, and the fact that only 1 of the 153 branches was classed as 2, these results seem somewhat dubious. Site 8 (Esk) was next most likely to have bark trapped. This seems more logical as 12 of the 57 branches were classified as 2.

Appendix 1.

Influence of actual tree spacing on branching characteristics of radiata pine.

Introduction

TreeBLOSSIM is a distant-independent model, i.e. the location of the tree with respect to its neighbours is not considered. In order to investigate whether actual tree spacing does influence the branching characteristics of radiata pine, data on the location of neighbours is needed. For each site, an effort was made to collect relevant data.

For sample trees that came from Permanent Sample Plots, it was assumed that the plot stem map would provide adequate data, hence data on location of neighbours was not collected. At the start of this analysis, it was discovered that several sample trees were close to plot boundaries, meaning that there was insufficient data for the analyses below.

For sample trees from diallel trials, the distance to all neighbours, within a circle of known radius, centred on the sample tree were measured. This gave an indication of local stocking for each tree. The DBH of the neighbouring trees were measured. These data were used for the analysis below.

These data were adequate where neighbouring trees were regularly spaced (Figure 26). For trees where the neighbours were irregularly spaced (Figure 27), a better strategy would be to measure the location of the nearest neighbour in 8 directions at approximately 45° intervals. This would allow realistic calculations of growing space indices.

Figure 26. Location of neighbouring trees for Tree 1 from Site 3 (Diallel Trial, Compartment 905, Kaingaroa).

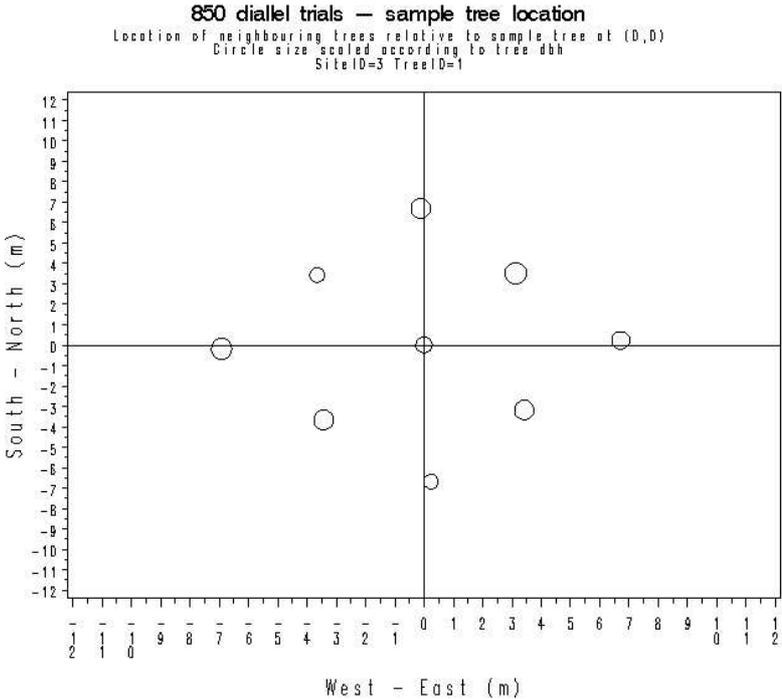
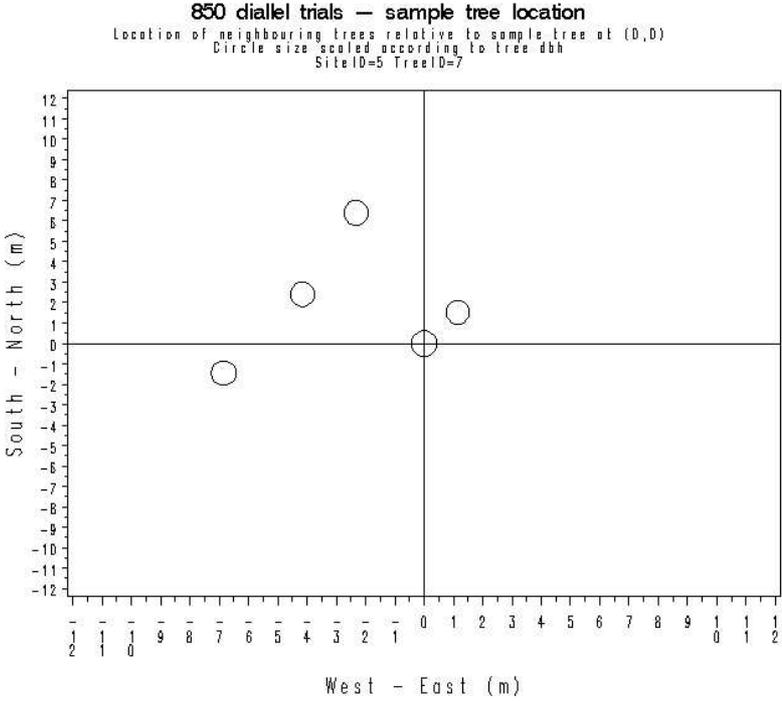


Figure 27. Location of neighbouring trees for Tree 7 from Site 5 (Diallel, Taringatura, Southland). The lack of neighbours on the south-east site is due to the fact that this tree was close to a track edge and the trees across the track were outside the set radius.



Methods

For each suitable sample tree, the azimuth range (0° to 360°) was divided into n zones, where n is the number of neighbours. The zone boundaries were placed at the azimuth location of neighbours. For each zone, the following were calculated:

- The cosine of the azimuth angle, midway between the two neighbours ($\cos(\alpha)$). The nearer the answer is to 1, the closer the zone midpoint is to North.
- The separation angle between the two neighbours (β)
- The average distance from the sample tree to each of two neighbours that form the boundary of the zone (L_{mean})
- The mean diameter of sample tree branches falling within the zone (D_{zmean})
- The maximum diameter of sample tree branches falling within the zone (D_{zmax})

The SAS procedure, PROC GLM, was used to investigate whether D_{zmean} or D_{zmax} were influenced by the position of neighbours, i.e. is:

$$D_{zmean} = f(\cos(\alpha), \beta, L_{mean})$$

$$D_{zmax} = f(\cos(\alpha), \beta, L_{mean})$$

Results

D_{zmean}

After site and tree within site had been accounted for, only $\cos(\alpha)$ was significant. The R^2 value for model including site, tree within site and $\cos(\alpha)$, was 0.55. The predicted coefficient was 2.97. This means that the value of D_{zmean} for a zone facing North would, on average, be 6 mm larger than that for a zone facing South.

D_{zmax}

After site and tree within site had been accounted for, only $\cos(\alpha)$ and β were significant. The R^2 value for the model including, site, tree within site, $\cos(\alpha)$ and β , was 0.55.

The predicted coefficients were:

$$\begin{aligned}\cos(\alpha) &: 5.76 \\ \beta &: 0.23\end{aligned}$$

The coefficient for $\cos(\alpha)$ means that the value of D_{zmax} for a zone facing North would, on average, be 12 mm larger than that for a zone facing South.

The coefficient for β means that the value of D_{zmax} 21 mm larger if the separation between neighbours was 180° (would represent an edge tree) than if the separation was 90° .

Discussion

The above results indicate that the azimuthal location of branches and position of neighbours have some influence on their diameter. The R^2 , values indicate that there are other factors that influence branch diameters.

The location of neighbours had a significant influence on the value D_{zmax} but not D_{zmean} . The analysis suggests that the value D_{zmax} would be on average 21 mm larger in an edge tree with no neighbours in a 180° , compared to a tree with neighbours separated by 90° . This result needs to be treated with caution, as there were few separation angles greater than 90° (Figure 28).

It is suggested that it would be worth sampling trees with irregular spacing of neighbours to confirm this result, and to investigate the resultant impact on wood property distributions within the stem. After such data were collected, we would be in a better position to judge the need for a distant-dependent model.

Figure 28. Distribution of observed separation angles between adjacent neighbours.

