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Title	Stable Foliage Cluster (FC), a Basic Unit of the Crown Structure of Tree Species and Its Application to Modeling of Tree and Forest Structure: Configuration of the FC Model
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Relation	Second International Symposium on Plant Growth Modeling, Simulation, Visualization and Applications (PMA 2006)
Issue Date	2006
Doc URL	https://hdl.handle.net/2115/57510
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Type	conference paper
File Information	Sumida-FCmodel-IEEE_CS_2014.pdf



Stable Foliage Cluster (FC), a Basic Unit of the Crown Structure of Tree Species and Its Application to Modeling of Tree and Forest Structure: Configuration of the FC model

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Abstract

The "foliage cluster (FC) model" shows that the size (the amount of leaves, number of yearly shoots and total twig length), turnover time, and branching (i.e., forking) structure of a twig becomes stable in the top of the crown in an oak species by forming a "stable FC" [1]. A stable FC can be treated as a basic component of the crown structure and as an alternative to individual leaf or current-year shoot. The FC model is composed of several equations approximating the branching structure of twigs. Differences in size and branching morphology among twigs are represented by differences in values of the parameters of the equations. We described details of our analyses of data taken from real twigs and applied to the equations implemented in the FC model.

1. Introduction

In closed forest canopies where there is very little space for tree crowns to exponentially expand, development of new branches is maintained by forming a "stable FC (foliage cluster)" [1]. Stable FC is an objectively and concretely definable structural unit composed of yearly shoots of several years. Once a stable FC is formed, it can retain a stable size (stable amount of leaves and twigs) with a constant turnover time of several years, while a forking branch structure is maintained inside it [1]. Hence the stable FC can be treated as a basic component of the crown structure and as an alternative to individual leaves or current-year shoots.

However, the data preparation for the FC model is somewhat complicated and requires a detailed explanation. Here, we describe the details of the morphological data analyses used in applying data to the equations implemented in the FC model. Several modeling schemes have been altered from the previous version [1] of our FC model.

2. The FC (foliage cluster) model

2.1. Model outline

The FC model simulates the development of a morphological structure of forking branches, including demographic processes of the birth, growth and death of yearly shoots. These processes were inferred from the morphology data of 0- and 1-year-old shoots of fourteen twigs sampled from mature crowns of a deciduous oak, *Quercus serrata*. The FC model is similar to Wilson's model [2], except that the stochastic processes of branch development are not implemented in the FC model.

The simulation of FC development is started with a single mother shoot. In the 1st simulation year, current-year shoots are produced on the mother shoot (Fig. 1, left). The number of current-year shoots and the length and location of each of the current-year shoots on the mother shoot are determined as a function of the length of the mother shoot. Each of these current-year shoots can become a mother shoot the next simulation year, producing several new current-year shoots as accords with their length. On the other hand, current-year shoots shorter than a "threshold length" cannot produce

any new shoots in the next simulation year, or they die before the next year. As years proceed, the number of current-year shoots per twig increases, while the number of the current-year shoots dying the next year also increases. As a result, all the lateral branches originating from the current-year shoots of the 1st simulation year die out, leaving the main axis (Fig. 1, right). After that, the number of current-year shoots of

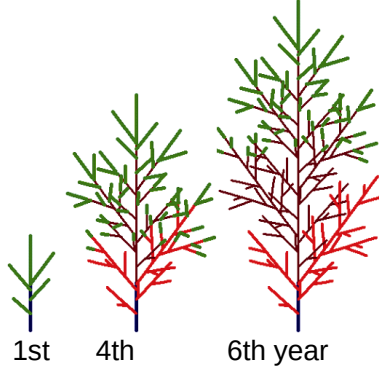


Figure 1. Branching structures at the 1st, 4th and 6th simulation years generated by the FC model. Green lines show current-year shoots (leaves not shown). At the 6th year, all the branches originating from the lateral shoots of the 1st simulation year (red lines) are dead, since they do not have any current-year shoots at distal ends.

a twig becomes stable; that is, the "stable FC" is formed. Such processes are generated using the following equations approximating twig morphology.

2.2. Mother-shoot length and daughter-shoot length

We first approximated the relationship between the length of a 1-year-old mother shoot (L_1 , cm) and that of the most distal (i.e., located at the distal end) current-year daughter shoot (L_{top} , cm) (Fig. 2a) by

$$L_{top} = L_1 - \{a_1 L_1 (L_{recur} - L_1)\}^2, \quad [\text{Eq. 1}]$$

where a_1 is a parameter concerning the curvature of the approximation curve, and L_{recur} is the "recurrent length", a constant given to each sample twig. The recurrent length is the length that satisfies $L_{top} = L_1$, which was to assume the extension growth of the main stem. Equation 1 implies that the offspring of a mother shoot shorter than recurrent length will become shorter and shorter with years (Fig. 2a).

The value of a_1 was numerically determined such that the residual sum of squares is a minimum. In determining the value of L_{recur} from the data, we first categorized the data sets of (L_1 , L_{top}) of all the 0- and 1-year-old shoots of each sample twig into those with $L_1 > L_{top}$ (i.e., mother shoot length > daughter shoot

length) and those with $L_1 \leq L_{top}$ (i.e., mother shoot length $\leq$ daughter shoot length). Then we compared the longest mother shoot length ($L_{1 \max}$) of the former category and the longest daughter shoot length ($L_{top \max}$) of the latter. Then L_{recur} of a sample twig was determined by

$$L_{recur} = L_{1 \max} \quad \text{if } L_{1 \max} \geq L_{top \max}$$

$$L_{recur} = (L_1 \text{ of the 1-year-old shoot having the daughter shoot with } L_{top \max})$$

$$\text{if } L_{1 \max} < L_{top \max}. \quad [\text{Eq. 2}]$$

Moreover, in applying Eq. 1 to the data sets, only the former category (i.e., those with $L_1 > L_{top}$) was used to reflect the tendency that daughter shoots were shorter than mother shoots if mother shoot length < recurrent length.

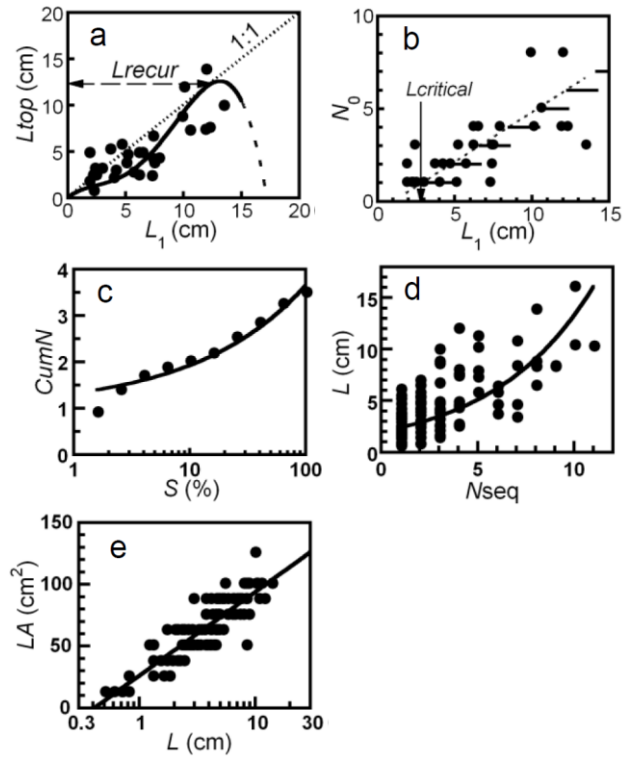


Figure 2. Equations implemented in the FC model that approximate the morphological attributes of a twig.

2.3. Number of daughter-shoots on a mother shoot

Our preliminary analyses showed that the diameter of the stem of a 1-year-old mother shoot was not a good predictor of the number of current-year shoots per mother shoot. This may be partly because stem diameters of most 1-year-old shoots ranged between

0.2 and 0.5 cm, and so diameter measurements could not be done accurately. Moreover, the sampling of the twigs was done almost once a week from mid July to late October, during which time most of the current-year shoots did not change length once they flushed, though their diameters increased; diameters for samples taken in later season would thus be greater. Hence only the length of the mother shoot (L_1 , cm) was used for the relationship with the number of current year daughter shoots on a mother shoot (N_0).

The relationship between L_1 and N_0 was approximated by applying reduced major axis regression to the data (dotted line in Fig. 2b),

$$N_0 = a_2 + b_2 L_1, \quad [\text{Eq. 3}]$$

Since the number of daughter shoot is an integer, N_0 was actually expressed by

$$N_0 = [a_2 + b_2 L_1], \quad [\text{Eq. 4}]$$

where the square brackets represent the Gauss' notation for N_0 to be an integer (solid lines in Fig. 2b), and a_2 and b_2 are those obtained by Eq. 3. When reduced major axis regression was applied to the data of the fourteen twigs sampled, the relationships, except for one twig, were all significant ($P < 0.01$). Hence the length of the mother shoot is likely to well predict the number of daughter shoots. In the relationship in Eq. 4, there is a threshold in the mother shoot length below which a mother shoot does not produce any daughter shoots, or $N_0 = 0$. This mother shoot length is called the critical length (L_{critical}), and is calculated by

$$L_{\text{critical}} = 1/b_2 - a_2/b_2. \quad [\text{Eq. 5}]$$

If the length of a current-year shoot is shorter than the critical length, it does not produce any daughter shoots the next year. In this case the current-year shoot is regarded as dying before it becomes 1 year old the next year.

2.4. Locations of daughter shoots on a mother shoot

We observed that current-year daughter shoots tended to be located more densely at the distal than the proximal part of a 1-year-old mother shoot. To represent this structure, we expressed the locations of daughter shoots on a mother shoot by percent length (S , %) from the distal ($S=0\%$) to proximal ($S=100\%$) ends of a mother shoot, and divided it into ten classes with an equal logarithm-transformed interval (i.e., from $\log(S(\%)) \leq 0.2$, $0.2 < \log(S(\%)) \leq 0.4$, . . . , to $1.8 < \log(S(\%)) \leq 2$). Then the frequency of the locations of all the daughter shoots in each of the ten $\log(S(\%))$ -classes was obtained for each of the sample twigs. Finally the frequency was transformed into the cumulative frequency ($CumN$) from the distal to the proximal ends of a mother shoot. Here, it was also

assumed that the most distal daughter shoot ($i=1$) is always located at the distal end ($S=0\%$) of a mother shoot. For the remaining $CumN-1$ daughter shoots, we assumed that they are located at S that gives an integer value of $CumN$; the most distal one ($i=1$) was assumed to be located at $S(\%) = 0$ as stated above, and so $CumN_{S=0}=1$ at $S=0$. The second distal one ($i=2$) is regarded to be located at S that gives $CumN=2$, the third one ($i=3$) at S giving $CumN=3$, and so on. The number of daughter shoots located between $S(\%) > 0$ and $S(\%) = 100$ is given by the difference between the $CumN_{S=100}$ and $CumN_{S=0}$ ($=1$), or by $(CumN_{S=100} - 1)$. Then the relationship between $CumN$ and S (Fig. 2c) was approximated by

$$CumN = a_3 S^{b_3} + 1, \quad [\text{Eq. 6}]$$

where a_3 and b_3 are parameters numerically evaluated such that the residual sum of squares is a minimum. In practice, only the value of b_3 is used to obtain the locations of daughter shoots, as is explained later.

The parameter b_3 corresponds to the changes in linear density of the daughter shoots with changing position S (or the slope of the approximation curve on a log-log plane when S is large enough). For a given number of daughter shoots N_0 on a mother shoot, if $b_3 < 1$, daughter shoots tend to be located densely around the distal end of a mother shoot: if $b_3 = 1$, they are located at a constant interval from the distal end of a mother shoot: and if $b_3 > 1$, they tend to be located densely around the proximal end of a mother shoot. With the value of b_3 and the number of daughter shoots on a mother shoot N_0 , we can determine the location (L_i , cm) of the i -th daughter shoot (counted towards the proximal end of mother shoot; $i = 1, 2, \dots, N_0$) on a mother shoot.

Note that $CumN$ is not a function of the mother shoot length L_1 but that of the relative location $S(\%)$. The number of daughter shoots per mother shoot (N_0 values) should differ depending on the mother shoot length L_1 (Eqs 3 and 4), and so $CumN_{S=100}$ (the $CumN$ value at $S=100\%$) does not always agree with the number of daughter shoots N_0 of an arbitrary mother shoot. To convert the value of $CumN$ into a value for an arbitrary mother shoot with a length L_1 , we defined a conversion factor p , a constant specific to each twig sample, as follows;

$$p = (N_0 - 1) / (CumN_{S=100} - 1) \\ = (N_0 - 1) / (a_3 100^{b_3}). \quad [\text{Eq. 7}]$$

Then the cumulative number of daughter shoots on a mother shoot with a length L_1 ($CumNL$) is given as a modified form of Eq. 6 by

$$CumNL = p a_3 S^{b_3} + 1, \quad [\text{Eq. 8}]$$

Substituting Eq. 7 into Eq. 8, we obtain

$$CumNL = (N_0 - 1) (S / 100)^{b_3} + 1. \quad [\text{Eq. 9}]$$

Equation 9 shows the relationship between the relative location S (%) on a mother shoot with a length L_1 and the cumulative number of daughter shoots at S , where it was assumed again that the most distal daughter shoot is always located at the distal end of a mother shoot (i.e., $CumNL=1$ at $S=0$). In Eq. 9 the value of a_3 in Eq. 6 has been cancelled out and only b_3 remains. The relative location for the i -th daughter shoot (S_i , %; $i=1, 2, \dots, N_0$) on a mother shoot is given by transforming Eq. 9 into the form:

$$S_i = 100 \left((CumNL_i - 1) / (N_0 - 1) \right)^{1/b_3}, \quad [\text{Eq. 10}]$$

where $CumNL_{i=1}=1$, $CumNL_{i=2}=2$, .., and $CumNL_{i=N_0}=N_0$. Note that N_0 has already been calculated from the mother shoot length L_1 by Eq. 1.

The actual location of (L_i , cm) of the i -th daughter shoot expressed as a distance from the distal end of a mother shoot with a length L_1 is then determined by

$$L_i = L_1 S_i / 100. \quad [\text{Eq. 11}]$$

2.5. Length of each daughter shoot on a mother shoot

We observed that the length of a current year daughter shoot became shorter as its location was nearer to the proximal end of the 1-year-old mother shoot. To express this structure, we assigned a number (the daughter shoot sequence number ($Nseq$); $Nseq=1, 2, 3$, etc.) to each of the daughter shoots on a mother shoot in order of occurrence from the proximal end of the mother shoot. The relationship between the daughter shoot sequence number $Nseq$ and the length of a daughter shoot (L , cm) was approximated (Fig. 2d) by

$$L = a_4 \exp(b_4 Nseq), \quad [\text{Eq. 12}]$$

where a_4 and b_4 are the coefficients of regression obtained by pooling the data of all the daughter shoots in each twig sampled. Here, the data of daughter shoots were excluded if a mother shoot had only one daughter shoot. The value of b_4 is an index of the degree of the acrotonic development of daughter shoots; that is, the lengths of proximal daughter shoots progressively shorter [3] if $b_4 (>0)$ is greater, while they are the same if $b_4=0$.

In the FC model, this relationship was used to determine the length of each of the N_0 number of daughter shoots on a mother shoot, where N_0 was obtained by Eq. 4. Hence $Nseq$ ranges from 1 to N_0 . On the other hand, the length of the most distal daughter shoot (L_{top}) has already been determined by Eq. 1. Hence, the results from Eq. 12 were used to calculate the length of each lateral daughter shoot (i.e., those other than the most distal daughter shoot) relative to that of the most distal daughter shoot on a mother shoot, that is,

$$RL = a_4 \exp(b_4 Nseq) / (a_4 \exp(b_4 N_0)) \\ = \exp(b_4 (Nseq - N_0)), \quad [\text{Eq. 13}]$$

where RL shows the relative length of the lateral daughter shoot for a given $Nseq$. Note that the coefficient a_4 in Eq. 12 has been cancelled out, and hence is not used in the FC model. The actual length of a daughter shoot (L_D , cm) is then given by

$$L_D = L_{top} RL. \quad [\text{Eq. 14}]$$

2.6. Leaf area on a current-year shoot

Finally, to estimate the leaf area of a current-year shoot (LA , cm^2), the relationship between the leaf area (LA) and the length of current-year shoot (L , cm) was used (Fig. 2e);

$$LA = a_5 \ln(L) + b_5. \quad [\text{Eq. 15}]$$

3. Future modeling

Since each parameter for the above equations in the FC model reflects a specific aspect of twig morphology, sensitivity analyses of the parameters would allow us to investigate the relationship between the morphology of twigs and the demography of yearly shoots composing the twigs. Investigations on the relationship of the variations in the values of the parameters to the local environments of twigs and twig positions in an individual, etc. would be needed before a realistic simulation of branch/tree structure development using the FC model.

4. References

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