*Original Paper*

# Foliage area distribution within a first-order branch in *Cryptomeria japonica*

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In this study, we investigated the distribution of foliage area within a first-order branch of *Cryptomeria japonica* D. Don. The Weibull distribution function fitted well to the relationship between the distance from the tip of a branch ($z$ : m) and the ratio of the foliage area from the tip to $z$ ($f(z)$ : $m^2$) to the total foliage area of the branch ($FA$ : $m^2$). A close relationship was found between the scale parameter $\alpha$ of the Weibull distribution function and the length of a branch ($BL$ : m), although the shape parameter $m$ did not significantly correlate with $BL$. Thus, the characteristics of foliage area distribution within a branch depended on the size of the branch. Moreover, $FA$ and the average foliage area per second-order branch ($FA/NS$) were significantly correlated with $BL$, and rapidly increased as $BL$ increased. The foliage area distribution a longer first-order branch would therefore be determined by the second-order branches having more foliage than a shorter first-order branch.

**Keywords**: first-order branch, second-order branch, foliage area, *Cryptomeria japonica*, Weibull distribution function

## Introduction

The quantity and distribution of foliage area within the crown play an important role in the ability of a tree to assimilate carbon, because foliage area is directly responsible for most light interception, gas exchange, and other production-related processes. Therefore, competition, growth, and self-thinning have been related to the foliage area within a crown (*e.g.* Dean and Long 1986; van Hees and Bartelink 1993; Gillespie *et al.* 1994).

In many studies, the vertical profile of light intercepted by foliage within a crown has been analyzed by the use of the "stratified clip method" devised by Monsi and Saeki (1953). Previous models based on this analysis assumed foliage to be statistically independent horizontal layers, with each layer having a uniform or random distribution of elements. However, more recent efforts have recognized the obvious clumping of crown elements in horizontal layers (*e.g.* Hashimoto and Suzaki 1982; Whitehead *et al.* 1990; Webb and Ungs 1993).

Shinozaki (1963) devised the "*Sainome* cutting method" for analyzing the three-dimensional foliage area (or biomass) distribution, and Kurachi *et al.* (1986) successfully applied this method to Japanese larch (*Larix leptolepis*). As suggested by Kurachi (1994), although the *Sainome* cutting method could accurately measure the three-dimensional foliage area (or biomass) distribution, it could not analyze the changes in three-dimensional foliage distribution with crown development, because the foliage within the crown was separated into three-dimensional cellular arrays with a constant cell size.

On the other hand, models of branch morphology have been developed by assuming deterministic or stochastic rules for changes in the branching process with crown development (for reviews see Fisher 1992; Honda 1971; Cochrane and Ford

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1978). Furthermore, some studies (Fisher and Honda 1979a, b; Ford and Ford 1990; Ford *et al.* 1990) analyzed the relations of various morphological rules to stemwood production. Although a vast amount of baseline data and analyses were required to construct the model, this approach appeared to be a powerful method for representing the change of three-dimensional foliage distribution with crown development, because crown development would be the result of interactions between many processes concerning branch morphology (Ford and Ford 1990).

In analyzing the pattern of crown development, first-order branches are an important determinant of the overall crown structure, because they are the dominant order in terms of size, and their disposition determines the arrangement of higher-order branches (Nelson *et al.* 1981). Therefore, first-order branches provide a logical basis for a model of the crown architecture, and many researchers have investigated crown development by analyzing the structure of first-order branches within the crown (*e.g.* Nelson *et al.* 1981; Hashimoto 1990; Gillespie *et al.* 1994). In these previous studies, the foliage area or weight was analyzed for the vertical distribution within a crown, but was not analyzed for the distribution within a first-order branch. Therefore, crown development in terms of the changes in the structure of first-order branches and the distribution of the foliage area within a crown cannot directly relate to each other. In this study, we therefore investigated the changes of foliage area distribution within a first-order branch with the elongation of the branch as our initial efforts to construct three-dimensional crown structures for *Cryptomeria japonica*.

## Materials

The four *Cryptomeria japonica* D. Don trees used in this study were obtained from Takiguchi *et al.* (1994). The stem of every tree had been sectioned at 1.0-m intervals from 0.2 m above ground level to the tree top, and two branches (where possible) were sampled from each 1.0-m section within a crown. Each sample branch was separated from its base and was measured for its total length (length of first-order branch, $BL$) at 0.01-m accuracy. For every second-order branch attached to a first-order branch, we then measured the distance from the tip of a first-order branch to the base of the second-order branch ($z$ : m) at 0.001-m accuracy, and the total length of foliage shoots attached to it ($L_S$ : m) at 0.001-m accuracy.

## Methods

### Estimation of foliage area

Katsuno and Hozumi (1988) found for *C. japonica* that the ratio of the foliage area ($FA_F$ : m$^2$) to the length of a foliage shoot ($L_F$ : m) was constant as

$$\frac{FA_F}{L_F} = 1.2\times 10^{-2} (\mathrm{m}^2\mathrm{m}^{-1}). \quad (1)$$

Then we calculated the total foliage area of a second-order branch ($FA_S$ : m$^2$) from the total length of foliage shoots attached to it ($L_S$ : m) as

$$FA_S = 1.2\times 10^{-2} L_S, \quad (2)$$

where $L_S=\sum_{i=1}^{N} L_{Fi}$ and $N$ was the total number of foliage shoots attached to the second-order branch.

Finally, we calculated the total foliage area of a branch ($FA$ : m$^2$) as

$$FA=\sum_{i=1}^{NS} FA_{Si}, \quad (3)$$

where $NS$ was the total number of second-order branches attached to a first-order branch.

### Weibull distribution function for describing the foliage area distribution within a branch

In many previous studies (*e.g.* Schreuder and Swank 1974; Hagihara and Hozumi 1986; Gillespie *et al.* 1994), it was suggested that the vertical distribution of leaf (or foliage) area within a crown can be successfully expressed by the Weibull distribution function. In this study, we also analyze the characteristics of foliage area distribution within a branch of *C. japonica* by using the Weibull distribution function. According to Mori and Hagihara (1991), we postulate that the foliage area density $\gamma(z)$ ($m^2m^{-1}$) within a branch at a distance $z$ (m) from the tip of the branch takes the form

$$\gamma(z)=\frac{FA\cdot m}{\alpha}\left(\frac{z}{\alpha}\right)^{m-1}\exp\left\{-\left(\frac{z}{\alpha}\right)^{m}\right\} \quad (\alpha, m>0), \tag{4}$$

where $m$ and $\alpha$ ($m$) are the shape and scale parameters of the Weibull distribution function specific to a branch, and $FA$ is the total foliage area of the branch.

From Eq. 4, the cumulative foliage area $f(z)$ existing from the tip of a branch to $z$ within a branch can be expressed as follows:

$$f(z)=\int_0^z \gamma(z)dz=FA\left[1-\exp\left\{-\left(\frac{z}{\alpha}\right)^{m}\right\}\right]. \tag{5}$$

Eq. 5 can be rewritten in the form:

$$\frac{f(z)}{FA}=1-\exp\left\{-\left(\frac{z}{\alpha}\right)^{m}\right\}. \tag{6}$$

The relationship between $f(z)/FA$ and $z$ for every sample branch was fitted to Eq. 6 with non-linear regression by using the polytope method of Okumura (1991).

When $m>1$, Eq. 4 reaches the mode of $\gamma(z)$ at position $z_M$ as

$$z_M=\alpha\left(\frac{m-1}{m}\right)^{1/m}. \tag{7}$$

As shown by van Hees and Bartelink (1993), the position of $z_M$ would be important for investigating the movement of foliage area distribution as a branch elongates and the crown develops. Therefore, the position of $z_M$ was calculated from the estimated parameters $\alpha$ and $m$ in Eqs. 6 and 7.

**Size dependence of the parameters of the model**

Hagihara and Hozumi (1986) found for *Chamaecyparis obtusa* that the scale parameter of the Weibull distribution function fitted to the vertical leaf area distribution within a crown tended to decrease as tree size increased. Mori and Hagihara (1991) also suggested for *C. obtusa* that the parameters of the Weibull distribution function fitted to the vertical leaf area distribution were changed as the stem diameter at breast height of a tree changed. Thus, the variation of such a distribution as a vertical distribution of leaf area is explained by relating the parameters of the Weibull distribution function to tree size.

According to the methods of Mori and Hagihara (1991), we therefore assessed the characteristics in the foliage area distribution by analyzing the relations of $m$, $\alpha$, and $z_M$ to branch length ($BL$) to investigate their changes with the elongation of first-order branches.

In Eq. 6, we could only give the ratio of the foliage area existing from the tip of a branch to $z$ ($f(z)/FA$). The actual foliage area distribution ($f(z)$) within a branch was determined by Eq. 6 and the total foliage area per branch ($FA$). In our previous study (Takiguchi *et al.* 1994), we found a close relationship between $FA$ and the basal area of a branch in *C. japonica*, but did not investigate the relationship between $FA$ and $BL$. Therefore, we also investigated the relation of $FA$ to $BL$ in this study.

Moreover, to investigate the characteristics in the spatial arrangement of higher-order branches and foliage shoots with the elongation of first-order branches, we analyzed the relation of average foliage area per second-order branch ($FA/NS$) to $BL$, because foliage area was directly related to foliage shoot length, as shown by Eq. 1.

## Results

The Weibull distribution function fitted well with the actual foliage area distribution within a branch, as shown in Fig. 1. Hagihara and Hozumi (1986) and Mori and Hagihara (1991) suggested for *C. obtusa* that the shape parameter $m$ of the Weibull distribution function (Eq. 6) fitted to the vertical foliage area distribution tended to change according to tree size. However, the shape parameter $m$ fitted to the foliage area distribution within a branch of *C. japonica* in this study did not significantly correlate with $BL$; the mean value was 3.37 (Fig. 2a). On the other hand, the scale

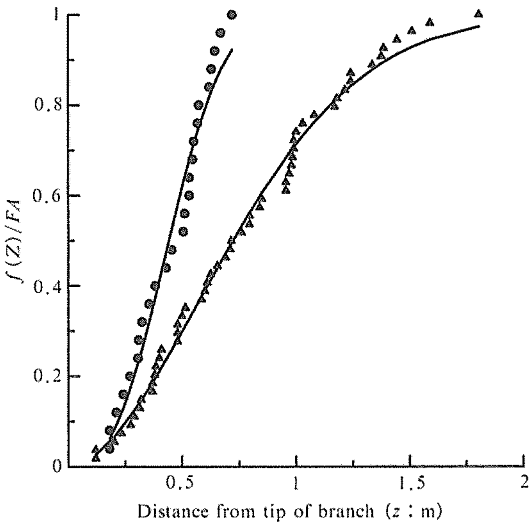


Fig. 1. Examples of the $z$-$f(z)$ relationships for two branches. $z$ is distance from the tip of the branch, $f(z)$ is the cumulative foliage area existing from the tip of the branch to $z$, and $FA$ is the total foliage area of the branch. Solid lines represent the Weibull distribution function of Eq. 6 fitted to the $z$-$f(z)$ relationships for the two branches.

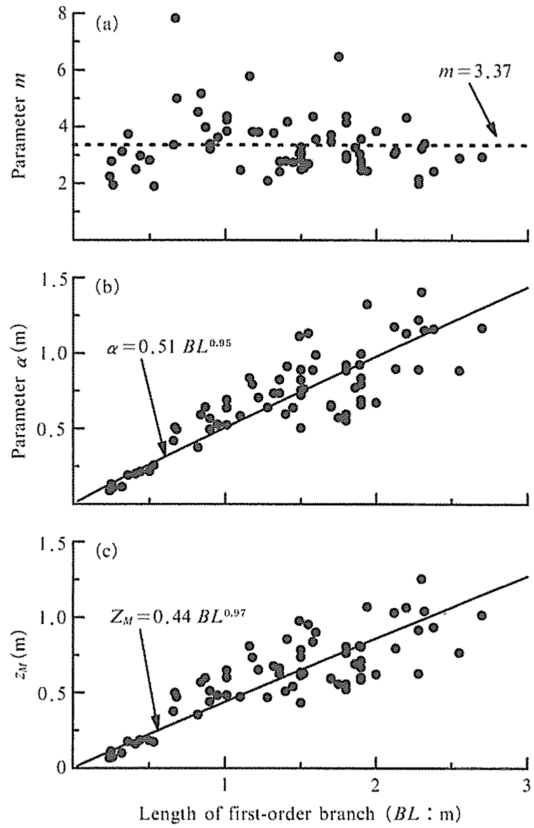


Fig. 2. The relations of (a) the shape parameter $m$ in Eq. 5, (b) the scale parameter $\alpha$ in Eq. 6, and (c) $z_M$ in Eq. 7 to the length of a first-order branch ($BL$).

parameter $\alpha$ of Eq. 6 and $z_M$ of Eq. 7 were significantly correlated with $BL$, and their relationship was expressed (Figs. 2b, c) as:

$$\alpha = 0.51 BL^{0.95} \quad (R^2 = 0.85), \tag{8}$$

$$z_M = 0.44 BL^{0.97} \quad (R^2 = 0.83). \tag{9}$$

Last, the total foliage area of a branch ($FA$) and the average foliage area per second-order branch ($FA/NS$) were significantly correlated with $BL$ (Figs. 3a, b). Their relationships were expressed as

$$FA = 0.46 BL^{2.12} \quad (R^2 = 0.82), \tag{10}$$

$$\frac{FA}{NS} = 0.015 BL^{1.81} \quad (R^2 = 0.86). \tag{11}$$

## Discussion

According to Baily and Dell (1973), the foliage area distribution characterized with the Weibull distribution function (Eq. 4) is summarized as follows: If $m < 1.0$, then the foliage area distribution is J-shaped; if $m = 1.0$, then the distribution is exponential; if $1.0 < m < 3.6$, the distribution is mound-shaped and negatively skewed; if $m = 3.6$, the foliage area is normally distributed; as $m$ increases above 3.6, the distribution becomes progressively more skewed; and as the value of $m$ tends to infinity the distribution approaches a spike. The foliage area would therefore be normally distributed before and behind the position of $z_M$, because the shape parameter $m$ was nearly equal to 3.6 independent of the length of the branch.

On the other hand, we found a close relationship between $\alpha$ of the Weibull distribution function for the foliage area distribution within a branch and $BL$, similar to that for the vertical foliage area distribution within a crown and the stem diameter suggested by Mori and Hagihara (1991). Therefore, the range of foliage area distribution within a branch showed an approximately

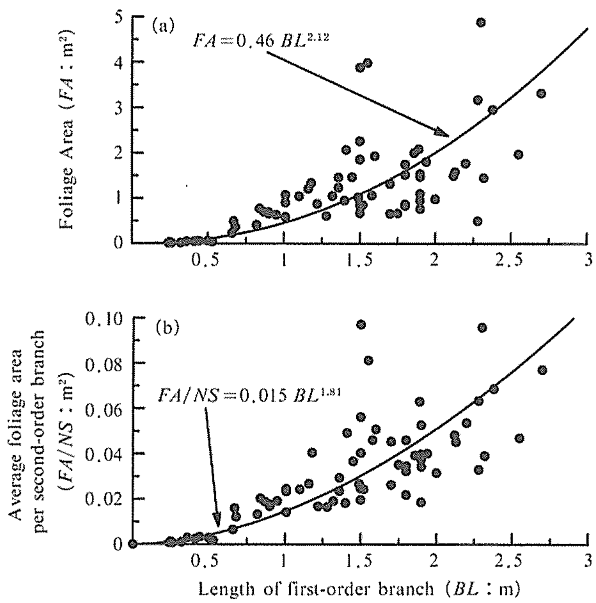


Fig. 3. The relations of (a) the total foliage area of a branch ($FA$) and (b) the average foliage area per second-order branch ($FA/NS$) to the length of a first-order branch ($BL$).

linear increase as a branch elongated, as suggested by the relationship between $\alpha$, $z_M$, and $BL$ (Eqs. 8, 9).

The relationships between $FA$, $FA/NS$, and $BL$ (Eqs. 10, 11) suggest that the rapid increase of foliage area per branch with the elongation of a branch would be caused mainly by the rapid increase of the foliage area per second-order branch. Thus, the role of second-order branches would change with the elongation of the first-order branch; *i.e.* more second-order branches that allowed higher-order branches to occupy more space rather than directly supporting the foliage shoots might exist on a longer first-order branch than on a shorter one.

As mentioned above, the characteristics of foliage area distribution within a branch or crown depended on the size of a branch or stem. For complete expression of the crown architecture of *C. japonica*, we should further investigate other characteristics of crown architecture, such as the branching structure and the size distribution of first-order branches within a crown. However, the results presented in this study offer a convenient means for easily simplifying the foliage area distribution within a first-order branch, and a logical basis for analyzing crown architecture by directly relating crown development in terms of the elongation of first-order branches to the distribution of the foliage area within the branch.

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*Tentative translation from the original Japanese title by the author of this paper.

## スギ一次枝における葉面積分布

山本一清・瀧口博之

スギの樹冠構造のモデル化の基礎的研究として，スギ一次枝における葉面積分布について検討を行った。スギ一次の葉面積分布はワイブル分布により適切に表現された。得られたワイブル分布の形のパラメータ $m$ 及び尺度のパラメータ $\alpha$ について一次枝長（$BL$：m）との関係を検討した結果，パラメータ $m$ と $BL$ の間に有意な相関は認められなかったが，パラメータ $\alpha$ については $BL$ の間に密接な相関関係が認められた。加えて，一次枝総葉面積（$FA$：$m^2$）および一次枝内の二次枝当たり平均葉面積（$FA/NS$）は $BL$ と有意な相関を示し，$BL$ の増大とともに急激に増大した。これらのことから，一次枝伸張にともなう $FA$ の増加が二次枝数の増加ではなく，むしろ二次枝当たりの葉面積の増加によるものであることが示唆された。

キーワード：一次枝，二次枝，葉面積，スギ，ワイブル分布