Structural variation in current-year shoots of broad-leaved evergreen tree saplings under forest canopies in warm temperate Japan

AKIO TAKENAKA
National Institute for Environmental Studies, 16-2 Onogawa, Tsukuba 305, Japan

Received August 26, 1996

Summary  Stem length and leaf area of current-year shoots were measured in saplings of eight broad-leaved evergreen tree species growing under a forest canopy. Stem length varied over a range of one to two orders of magnitude within each species. In all species, both the number of leaves and the mean stem length between successive leaves were greater in longer shoots. Mean leaf size and stem length were not correlated in six of eight species, and only weakly positively correlated in the other two species. Thus, total leaf area per stem increased with stem length, but not in direct proportion: leaf area per stem length was smaller in shoots with long stems and larger in shoots with short stems. I conclude that the within-species variation in the leaf-stem balance of current-year shoots is related to variation in shoot functional roles, as has been observed for long and short shoots in many deciduous tree species: shoots with long stems are extension oriented and contribute to the framework of the crown, whereas shoots with short stems serve mainly for leaf display. Among species, large differences were found in the leaf area per stem length ratio. In the species with larger leaf area per stem length ratios, leaves had narrower blades or longer petioles, or both, resulting in a reduction of mutual shading among the leaves on the shoot.

Keywords: leaf area, shoot function, shoot structure, stem length, tree architecture.

Introduction

The modular structure of trees, consisting of a number of shoots, has been well recognized (Hallé et al. 1978, White 1979, Jones 1985, Sprugel et al. 1991). Repetitive formation of shoots as modules results in a complex 3-D structure. This view has facilitated computer simulation of morphological development of trees (e.g., Honda 1971, Fisher and Honda 1977, Borchert and Tomlinson 1984, Takenaka 1994a). Physiologically, the apparently autonomous behavior of branches justifies studies at the branch level (Watson and Casper 1984, Franco 1985, Ford and Ford 1990, Sprugel et al. 1991), although integration of shoot level phenomena to the whole tree is not straightforward (Küppers 1989).

Shoots have several functions, including exploiting available space, capturing light for photosynthesis, bearing flowers and fruit for reproduction, and supporting other shoots, both mechanically and physiologically. In a tree crown, individual shoots may differ in their relative contribution to various functions: some shoots extend vigorously, whereas others remain short; some are specialized for sexual reproduction, whereas others never bear flowers; and some produce many offspring shoots, whereas others produce none. This shoot differentiation has profound effects on overall tree architecture (Hallé et al. 1978).

Shoots of some tree species show morphological differentiation (Zimmermann and Brown 1971). Short shoots are characterized by restricted extension growth of internodes. Examples are found in genera such as Acer, Corylus, Pyrus, Populus, Fagus, Betula, Larix, Ginkgo and many others (Gunckel and Wetmore 1946, Hallé et al. 1978, Jones and Harper 1987, Remphrey and Powell 1988). It has been suggested that long shoots contribute to the overall structural framework of a tree crown, and short shoots are specialized mainly for leaf display and photosynthesis (Hallé et al. 1978, Jones and Harper 1987). Increased height and crown width are caused by the extension of long shoots. Short shoots do not contribute to the increase in crown size, but do contribute to light capture in the crown.

Morphological differentiation of long shoots and short shoots has been reported for many deciduous tree species, but few evergreens (Hallé et al. 1978). This does not necessarily mean that there is no variation in shoot structure in evergreen tree species. Rather, it is possible that morphological studies have overlooked quantitative variations in shoot structure. In the present study, I hypothesized that evergreen tree species have variation in the leaf-stem balance similar to the long shoot–short shoot variation reported for many deciduous species. I studied seedlings and saplings of eight broad-leaved evergreen tree species occurring in the climax forest of warm temperate Japan. Allometric relationships between stem length and leaf area of current-year shoots were analyzed.

Materials and methods

Field measurement

The study area (30°21’ N, 130°28’ E; elevation ca. 200 m) was located in a broad-leaved evergreen forest on the west side of the island of Yakushima, in southern Japan. At the meteorological station on the island, mean annual temperature is
19.6 °C. The forest is one of the few remaining climax forests in warm temperate Japan and was declared a UNESCO World Heritage site in 1993. The major component tree species of the canopy are evergreens such as *Neolitsea aciculata* (BL) Koidz., *Litsea acuminata* (BL) Kurata, *Quercus salicina* Blume, *Ardisia sieboldii* Miq. and *Ilex torunda* Thunb. The height of the canopy trees is about 15 m.

Eight evergreen tree species were chosen for measurement: *Symlocos glauca* (Thumbs.), *S. prunifolia* Sieb. et Zucc., *Viburnum odoratissimum* Ker-Gawler var. awabuki (K. Koch) Zabel, *Myrsine seguini* Lev., *Camellia japonica* L., *Cleyera japonica* Thunb., *Litsea acuminata* and *Neolitsea aciculata* (Blume) G. Koidz. Adult trees of these species reached more than 10 m in height at the study site. Clearly distinguishable current-year shoots and an abundance of seedlings and saplings in the study area were the criteria for the choice of species. The color of stems, bud scars and branching patterns facilitated the recognition of current-year shoots. In all species, two- to three-year-old leaves were retained. Apparent differentiation of long shoots and short shoots was not observed in any species.

The structure of current-year shoots of each species was examined in November 1995, when the extension growth of the year had terminated. Three to 12 plants of each species were chosen for measurement (Table 1). To cover a range of light environments, plants growing under forest canopies with and without gaps were included. Shoots from adult trees were not sampled because of difficulty in accessing the crowns. This exclusion may have limited the range of structural variation observed within individual species.

To reveal the range of structural variation, shoots were sampled from various parts of the plants, including main axes and lateral branches, and from points high and low in the crown. The length of each shoot (from the basal point of the stem to the apex of the shoot) and the widths and lengths of all leaves on the shoot were measured. To minimize the impact on the vegetation of the site, sample shoots were not harvested. About 20 sample leaves for each species were collected after field measurement and brought to the laboratory. The images of the leaves were scanned into a computer and their areas were determined. A regression equation to estimate leaf area, based on the product of leaf length and width, was generated for each species. Coefficients of determination \( R^2 \) were larger than 0.98 for all species.

**Table 1. Broad-leaved evergreen tree species measured for the structure of current shoots.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Number of sample plants</th>
<th>Height range of sample plants (m)</th>
<th>Number of sample shoots</th>
<th>Shoot orientation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Symlocos glauca</em></td>
<td>Symlocaceae</td>
<td>9</td>
<td>0.3–3.5</td>
<td>30</td>
<td>Intermediate</td>
</tr>
<tr>
<td><em>S. prunifolia</em></td>
<td>Symlocaceae</td>
<td>6</td>
<td>0.5–2.0</td>
<td>33</td>
<td>Plagiotropic</td>
</tr>
<tr>
<td><em>Myrsine seguini</em></td>
<td>Myrsinaceae</td>
<td>7</td>
<td>0.5–2.5</td>
<td>30</td>
<td>Orthotropic</td>
</tr>
<tr>
<td><em>Viburnum odoratissimum</em></td>
<td>Cornaceae</td>
<td>8</td>
<td>0.4–4.0</td>
<td>29</td>
<td>Intermediate</td>
</tr>
<tr>
<td><em>Cleyera japonica</em></td>
<td>Theaceae</td>
<td>4</td>
<td>1.8–3.6</td>
<td>30</td>
<td>Plagiotropic</td>
</tr>
<tr>
<td><em>Camellia japonica</em></td>
<td>Theaceae</td>
<td>8</td>
<td>1.0–2.5</td>
<td>30</td>
<td>Plagiotropic</td>
</tr>
<tr>
<td><em>Litsea acuminata</em></td>
<td>Lauraceae</td>
<td>12</td>
<td>0.4–2.2</td>
<td>33</td>
<td>Orthotropic</td>
</tr>
<tr>
<td><em>Neolitsea aciculata</em></td>
<td>Lauraceae</td>
<td>3</td>
<td>1.8–3.0</td>
<td>33</td>
<td>Orthotropic</td>
</tr>
</tbody>
</table>

**Allometric analysis**

When a shoot is divided into units consisting of a single leaf and a subjacent stem segment, if the variation in the leaf area/stem length ratio of the units is not associated with the variation in the shoot length, then the shoot leaf area is proportional to the shoot length. In such a case, a log-log plot of leaf area versus shoot length will have a slope of 1. The slope will differ from 1 if the leaf area/stem length ratio within the units varies with shoot length.

In the determination of a line to represent a plant allometric relationship, it is necessary to consider error variances of both of the variables (Sackville Hamilton et al. 1995). I used the major axis method (Sokal and Rohlf 1995) to fit a line to the log-log plot of leaf area versus shoot length of each species, assuming that the error variances of the two variables did not differ significantly.

**Leaf shape parameter**

The shape of a leaf affects the degree of mutual shading among leaves on a shoot (Niklas 1988, Takenaka 1994a, Sekimura 1995). Takenaka (1994b) proposed that the mean distance of leaf area from the stem be used as a leaf shape parameter to predict the susceptibility of the leaves to mutual shading. This parameter \( D \) is normalized to leaf size by dividing by the square root of leaf area. Leaves with a narrow blade, long petiole, or both, have large values of \( D \). A computer simulation study (Takenaka 1994b) showed that shoots with leaves of large \( D \) are less susceptible to mutual shading. This is because the leaf area is less concentrated in the space around the stem than it is for leaves with small \( D \).

To investigate the relationship between the leaf-stem balance of the shoot and the leaf shape, values of \( D \) were determined for the eight tree species, using the images of leaves scanned into the computer for the leaf area measurements. The value of \( D \) was calculated by numerical integration of the
distance from every small fraction of the leaf lamina to the point of attachment to the stem.

**Results**

Lengths of current-year shoots varied over a range of one to two orders of magnitude within each species (Table 2). The shortest shoots were found mainly on heavily suppressed seedlings and in the lower parts of the crown. Shoots at the top of the main axis were often the longest.

In all species, longer shoots had more leaves (Figure 1) and longer mean stem lengths between leaves (Figure 2) than did shorter shoots. Mean area of individual leaves did not correlate significantly with shoot length, except for in *Neolitsea aciculata* and *Camellia japonica* (Figure 3).

A log-log plot of leaf area versus shoot length showed a near linear relationship for each tree species (Figure 4). Because of the greater mean stem length between leaves in longer shoots, the slopes of the lines fitted to the log-log plots were smaller than 1.0, ranging from 0.15 to 0.77 (Table 3). For seven of the eight species, 95% confidence intervals of the slope did not include 1.0. The 95% confidence interval for *Neolitsea aciculata* marginally included 1.0 (0.57–1.02).

No distinct difference in the leaf area versus shoot length relationship was found between main axes and lateral shoots in any species. Most of the shoots on the main axes showed a leaf/stem ratio similar to that of vigorously growing lateral shoots. Main axes of limited current-year growth, which were sometimes observed under a dense canopy, did not differ in leaf-stem balance from suppressed shoots from the lower part of a crown.

Within individual species, values of the leaf shape parameter ($D$) did not vary much (Table 2); the coefficient of variation (SD/mean) was less than 10% for all species. In contrast, among species, variation in $D$ was large, ranging from 1.04 in *Cleyera japonica* to 2.16 in *Litsea acuminata*.

**Table 2.** Shoot length, leaf area per shoot length (LA/SL), and relative distance of leaf area from the stem ($D$) of eight broad-leaved evergreen tree species. LA/SL was calculated for each sample shoot and then averaged for each species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Shoot length (cm)</th>
<th>LA/SL (cm)</th>
<th>$D$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td><em>Symplocos glauca</em></td>
<td>10.8</td>
<td>8.5</td>
<td>43.7</td>
</tr>
<tr>
<td><em>S. prunifolia</em></td>
<td>8.7</td>
<td>7.7</td>
<td>9.4</td>
</tr>
<tr>
<td><em>Myrsine seguinii</em></td>
<td>9.9</td>
<td>8.9</td>
<td>37.7</td>
</tr>
<tr>
<td><em>Viburnum odoratissimum</em></td>
<td>6.8</td>
<td>7.3</td>
<td>37.8</td>
</tr>
<tr>
<td><em>Cleyera japonica</em></td>
<td>6.6</td>
<td>5.0</td>
<td>10.3</td>
</tr>
<tr>
<td><em>Camellia japonica</em></td>
<td>8.1</td>
<td>5.5</td>
<td>16.2</td>
</tr>
<tr>
<td><em>Litsea acuminata</em></td>
<td>11.8</td>
<td>9.6</td>
<td>46.8</td>
</tr>
<tr>
<td><em>Neolitsea aciculata</em></td>
<td>9.2</td>
<td>6.3</td>
<td>7.8</td>
</tr>
</tbody>
</table>

Figure 1. Relationships between numbers of leaves per shoot and current-year shoot lengths. The correlation coefficient calculated for each of the species is shown with significance level (* = 5%; ** = 1%). Open circles indicate main axes. A, *Symplocos glauca*; B, *S. prunifolia*; C, *Myrsine seguinii*; D, *Viburnum odoratissimum*; E, *Cleyera japonica*; F, *Camellia japonica*; G, *Litsea acuminata*; H, *Neolitsea aciculata*. 

[Image of graph showing relationships between numbers of leaves per shoot and current-year shoot lengths for different species]
Total leaf area per shoot length varied greatly among species, ranging from 7.8 cm in *Neolitsea aciculata* to 46.8 cm in *Litsea acuminata* (Table 2). Large leaf/stem ratios were associated with both large mean leaf area ($r = 0.94, P < 0.001$) and large mean number of leaves per stem length ($r = 0.89, P = 0.003$). There was a significant positive correlation among species between mean $D$ and the mean leaf area/shoot length ratio ($r = 0.78, P = 0.03$).

**Discussion**

Although the allometric relationships among whole-tree dimensions such as height, number of leaves, stem diameter and crown width have been studied extensively (e.g., Kohyama 1987, King 1990, Niklas 1994), shoot and branch level variables have not received much attention (see White 1983).

Variation in the balance between the amount of leaves and shoot length has been observed in evergreen conifers (Carter and Smith 1985, Sprugel et al. 1996); however, it has not been considered in terms of functional differences between extension oriented shoots and leaf-display oriented shoots. Sprugel et al. (1996) reported that shoots of *Abies* species grown under sunny conditions have larger amounts of leaves per shoot length than shoots developed under shaded conditions, and concluded that such variation is apparently advantageous for the efficient utilization of light. I examined the range of variation in shoot structure of eight evergreen tree species and found that leaf area per stem length was greater for short stems than for long stems.
The observed variation in the balance between shoot leaf area and shoot length may be analogous to the morphological differentiation of long and short shoots in many deciduous tree species. Thus, the proposed functional differences between long and short shoots of deciduous trees (Hallé et al. 1978, Jones and Harper 1987) can likely be applied to the shoots of evergreen trees. Shoots with longer stems may contribute to the framework of the crown, whereas shoots with shorter stems may serve mainly for light capture.

Current-year growth of main axes tended to form shoots with long stems (Figure 2). Shoot structure apparently depends not only on the position of the shoot in the crown, but also on internal and external factors. For instance, injury to the apical meristem of main axes often stimulates extension of other shoots to replace the injured one (Hallé et al. 1978), and growth of a main axis can be suppressed under shaded conditions. Kohyama (1980) reported that restricted growth of the main axis of Abies mariesii M. T. Mast. saplings results in an umbrella-like crown shape. Flexibility in shoot formation plays an important role in the responses of total crown architecture to environmental conditions (Jones 1985, Koike 1986, Sorrensen-Cothern et al. 1993, Takenaka 1994a).

Larger total leaf area per stem length increases mutual shading among leaves on a shoot (Niklas 1988, Takenaka 1994b). However, leaves with large values of D are less susceptible to shading. Another factor that affects the degree of mutual shading is the number of leaves. Even if the shape and size of leaves and internode length are constant, an increase in the number of leaves increases mutual shading (Takenaka 1994b). In species with leaf longevity greater than a year, accumulation of leaves over years can result in severe shading. Thus, all evergreen shoots will ultimately become shade shoots. This may partially explain the absence of a clear distinction between short shoots and long shoots in evergreen tree species compared with deciduous species such as Betula, Larix, and Ginkgo. We can further hypothesize that shoots with short stems are more leafy in deciduous species compared to evergreen species.

Dispersion of leaf area away from stems may cause increased interaction among neighboring shoots. Such interaction would be reduced by low shoot density in the crown. I predict low branching frequency in species with leaves with large D and large leaf area per stem length. One of Corner’s rules (White 1983), which states that larger appendages such as leaves are associated with less ramification of the axis, agrees with this prediction.

From the viewpoint of the carbon budget of a tree, the cost for construction of shoots of different structures is of interest; however, estimation of such costs is not straightforward. In addition to the construction of the shoot itself, costs are incurred by the stem and root system that support the shoot mechanically and physiologically (Niklas 1992, Gartner 1995). Furthermore, the costs of making identical shoots can vary depending on the locations in which they sprout. A shoot further from the main stem or root system will require a greater

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope</th>
<th>95% interval</th>
<th>Intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>Symplocos glauca</td>
<td>0.33</td>
<td>(0.16, 0.52)</td>
<td>2.04</td>
</tr>
<tr>
<td>S. prunifolia</td>
<td>0.57</td>
<td>(0.44, 0.71)</td>
<td>1.25</td>
</tr>
<tr>
<td>Myrsine seguinii</td>
<td>0.15</td>
<td>(−0.15, 0.49)</td>
<td>1.96</td>
</tr>
<tr>
<td>Viburnum odoratissimum</td>
<td>0.50</td>
<td>(0.29, 0.75)</td>
<td>1.73</td>
</tr>
<tr>
<td>Cleyera japonica</td>
<td>0.36</td>
<td>(0.23, 0.51)</td>
<td>1.36</td>
</tr>
<tr>
<td>Camellia japonica</td>
<td>0.59</td>
<td>(0.45, 0.75)</td>
<td>1.51</td>
</tr>
<tr>
<td>Litsea acuminata</td>
<td>0.28</td>
<td>(−0.02, 0.64)</td>
<td>2.26</td>
</tr>
<tr>
<td>Neolitsea aciculata</td>
<td>0.77</td>
<td>(0.57, 1.02)</td>
<td>1.06</td>
</tr>
</tbody>
</table>
investment in mechanical support and transport than a shoot close to the main stem or root system. Integration of various processes and factors at the whole-plant level is indispensable for a complete cost–benefit analysis of shoot structure. Process based models of tree growth, such as those by Rauscher et al. (1990) and Pettunen et al. (1996), are promising tools for the evaluation of local processes in the context of the whole-tree.

In the present study, I focused on examining the range of variation in shoot structure. Samples were not collected to evaluate distribution patterns of shoots over the range of morphological variation, although analysis of such patterns is necessary to understand crown architecture development. Future work should address the issues of the number of shoots formed, the type of shoots formed, and the location of shoot formation. A dynamic view of the process of tree structure formation is needed in order to understand tree resource acquisition and competition among trees (King 1990, Lovell and Lovell 1985).

Acknowledgments
This work was supported by a Grant-In-Aid (No. 06304003) from the Ministry of Education, Science and Culture, Japan. I thank Dr. H. Nagashima for assistance in the field work. Dr. N. Kachi, Dr. T. Kohyama, Dr. H. Nagashima and Dr. I. Terashima are acknowledged for their useful suggestions and discussion.

References


