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Effects of leaf blade narrowness and petiole length on the light capture efficiency of a shoot

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Effects of the length : width ratio of a leaf blade and petiole length on shoot light capture were studied with computer simulation. Both a larger length : width ratio and longer petiole contributed to larger light capture per unit leaf area due to a reduced aggregation of leaf area around the stem. Other conditions being equal, shoots with narrow leaves and no petioles and those with wide leaves with petioles showed similar light capture as long as the mean distance of the leaf blade from the stem was the same. In shoots with a short internode and/or distichous phyllotaxis, however, narrow leaves contributed more to avoiding mutual shading than wide leaves with petioles. The predominance of light coming from a higher angular altitude also favored narrow leaves. The possible consequences of these results in the adaptive geometry of plant architecture are discussed.

Key words: computer simulation; leaf shape; light interception; mutual shading; petiole.

INTRODUCTION

In a shoot with multiple leaves, shading among the leaves reduces the light capture efficiency of the shoot on a per leaf area basis. Shoot morphology critically affects the degree of mutual shading. Because less light capture causes lower photosynthetic production of a plant, shoot morphology must have been under a selection pressure for less mutual shading.

If leaves on a shoot are displayed in a plane without overlapping, there is no shading among the leaves. Examples of this type of leaf display are found widely in horizontal shoots with leaves arranged in two rows on both sides of the stem (Givnish 1984). Flat or umbrella-like arrangements of leaves at the shoot tips in a whorl are also common (Chazdon 1985). In some species with these type of shoots, differentiation in petiole length among the leaves greatly decreases leaf overlap. Differentiation in the leaf inclination angle is another way to reduce mutual shading in a short shoot with multiple leaves (Niklas 1988).

In an upright shoot with leaves of identical shape, the internode length critically affects the degree of shading among leaves (Niklas 1988). The longer the internode, the larger the distance between leaves and the less the mutual shading. Another possible factor related to the degree of mutual shading is leaf shape (Horn 1971; Chazdon 1985; Niklas 1988, 1989). However, there has been no comprehensive analysis on the relationships between leaf morphology and shoot light capture. In this report, two features of leaf shape, that is, leaf blade narrowness and petiole length, are studied in relation to shoot light capture. Both a narrow blade and a long petiole are expected to reduce the degree of aggregation of leaf area around the stem and consequently, shading among the leaves. The aim of the present study is to estimate these effects of leaf shape quantitatively. Computer simulation was carried out to evaluate the light capture efficiency of a shoot because it is difficult to measure the amount of light captured by a real plant under field conditions. Moreover, computer simulation enables the manipulation of leaf shape and arrangement, which can hardly be done in real plants.

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METHODS

Model shoot

Consider the mean distance from all points on the blade of a leaf to its point of attachment to the stem. This distance can be scaled to leaf size by division with the square root of the leaf area. In this paper, the relative distance is denoted by *D*. *D* increases with increasing length : width ratio of a leaf blade and with increasing petiole length. An upright shoot with leaves of smaller *D* must be less efficient in light capture because the leaves are stuffed in a cylinder of a smaller volume around the stem and more mutual shading occurs. The value of *D* can be calculated by numerical integration of the distance from small fractions of the leaf blade to the point of attachment to the stem over the whole leaf area.

To examine the relationship between the narrowness of a leaf blade and shoot light capture, a series of leaves (B series, where B stands for 'Blade') was generated. Leaves of this series do not have a petiole. Leaves with rhombus blades with a length : width ratio of 1 : 1, 2 : 1, 4 : 1 and 8 : 1 were denoted as B_0, B_1, B_2 and B_4, respectively (Fig. 1). The corresponding *D* values (Fig. 1) cover the range of those found in a preliminary survey of leaves of 30 plant species. Most of the species had leaves with *D* values ranging from 0.8 to 1.6.

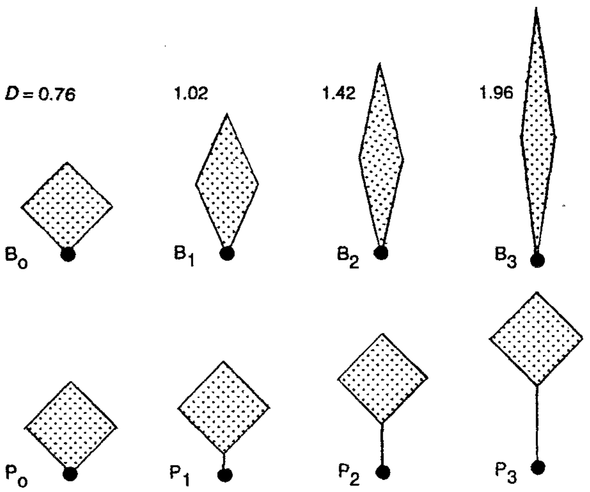

Fig. 1. Model leaves used for the simulation of shoot light capture. The basal point of a leaf at which it attaches to the stem is indicated with a closed circle. Upper row, the B series of leaves of changing length : width ratio of a leaf blade; lower row, the P series of leaves of a changing petiole length. Leaves of each pair in a column have the same value of *D* (the mean distance of the blade of a leaf from its point of attachment to the stem, scaled to the leaf area) indicated on top of each column.

Another series of leaves (P series, where P stands for 'Petiole') of different petiole lengths was generated to examine the effects of the petiole length on shoot light capture. The shapes of the leaf blades of this series are the same as that of B_0 of the B series. The leaves have petiole lengths of 0, 0.23, 0.70 and 1.25 (scaled to leaf area) and are denoted as P_0, P_1, P_2 and P_3, respectively (P_0 is identical to B_0). The lengths of the petioles were determined to make the *D* values of P_1, P_2 and P_3 the same as B_1, B_2 and B_3, respectively.

A model shoot was composed of a straight stem of infinitesimal width and 10 or 24 leaves identical in shape with constant intervals within the shoot. The leaves were arranged in three phyllotaxes: (i) spiral with a divergence of 135°; (ii) decussate (leaves are opposite, neighboring pairs crossing at a right angle); and (iii) distichous (a special case of spiral phyllotaxis with a divergence of 180°). For shoots with the spiral and distichous phyllotaxis, the internode lengths of 0.1 and 0.5 (scaled to leaf area) were chosen within the range observed in a preliminary survey of erect shoots of various species. In decussate shoots with two leaves at each node, the internode lengths of 0.2 and 1.0 were used instead of 0.1 and 0.5, respectively. Other factors expected to affect shoot light capture including shoot and leaf inclination were also varied.

Calculation of light capture

For light coming from a given direction, the amount of light captured by a shoot is proportional to the projected area of the shoot on the plane normal to the direction of light. In the present study, the projected area of the shoot was obtained by drawing images of leaves of a shoot on a graphic screen of a microcomputer and counting painted pixels.

To calculate total light capture of the model shoot under uniformly bright sky conditions, the sky was divided into nine horizontal bands of 10° width of angular altitude (0–10°, 10–20°, and so on). Along the isoaltitudinal line in the middle of each band, five points were located at regular intervals. The amount of light captured by the model shoot was calculated for each of the five points in the band and averaged. The total light capture of the shoot was obtained by summing up the received light for each band of the sky weighted with the 'area' (solid angle, more precisely) of the band.

Throughout this paper, the light capture of a shoot is expressed as a relative value to that of horizontal leaves without any mutual shading. The relative light capture (hereafter referred to as *I*) decreases with the increasing degree of mutual shading among the leaves within a shoot. When *I* is referred to as a function of leaf shape, it is written as $I(B_0)$, $I(B_1)$, and so on.

All of the computer programs for the simulation were coded with C language and executed on a 32-bit microcomputer.

RESULTS

Figure 2 shows the light capture of the model shoots with 10 or 24 leaves arranged in spiral phyllotaxis. The stem was vertical or inclined 45 °, and the leaves were horizontal or inclined 45 ° from the horizontal surface bending upward toward the zenith. For both B and P series, *I* increased with increasing *D*. *D*-dependencies of *I* for the two series were quite similar for shoots with longer internode lengths of 0.5, irrespective of the leaf number, leaf inclination and stem inclination. In shoots with shorter internodes of 0.1, $I(B_n)$ was slightly higher than $I(P_n)$ (n = 1, 2, 3). The values of *I* were higher in shoots with 10 leaves than in shoots with 24 leaves because a shoot with a less number of leaves suffers less mutual shading.

To examine the effects of the directional distribution of the light source on the *I*–*D* relationships, *I* for lights from high (60–90°), middle (30–60°) and low (0–30°) angular altitudes were calculated for vertical shoots with spiral phyllotaxis (Fig. 3). The values of *I* were higher in shoots with 10 leaves than in shoots with 24 leaves, especially for higher light directions. For each of the light conditions and leaf numbers, the degree of mutual shading was larger when light was from higher angular altitudes, which is reasonable because the leaves were distributed in an upright cylinder around the stem. $I(B_n)$ and $I(P_n)$ (n = 1, 2, 3) had similar values to each other for all the light directions, except when the internode length was short and the light came from higher altitudes. In this case, the *I* of shoots with narrow leaves (B series) surpassed those of shoots with petioled leaves with identical *D* values. In the shoots with longer internode lengths, the similarity between $I(B_n)$ and $I(P_n)$ is also expected to hold for the solar beam and non-uniformly distributed diffuse light because the similarity held irrespective of the direction of light.

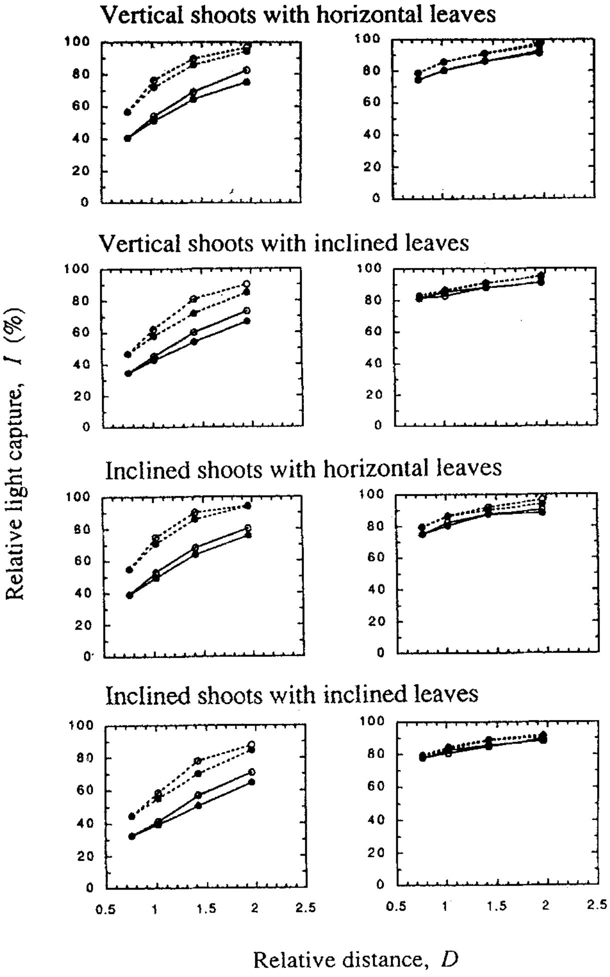

Fig. 2. *D*-dependency of *I*, relative light capture, of a model shoot with 10 (·····) or 24 (——) leaves arranged spirally (divergence angle: 135°). Shoots were vertical or inclined 45°. Leaves were horizontal or inclined relative to horizontal plane, bending 45° upward toward the zenith. Left column, shoots with a short internode (0.1); right column, shoots with a long internode (0.5). Open circles represent $I(B_n)$ (n = 0, 1, 2, 3), or *I* of shoots with leaves of the B series (changing blade shape). Closed circles represent $I(P_n)$ (n = 0, 1, 2, 3), or *I* of shoots with leaves of the P series (changing petiole length).

Phyllotaxis affected shoot light capture especially when the internode length was short (Fig. 4). Light interception was less in shoots with decussate phyl-

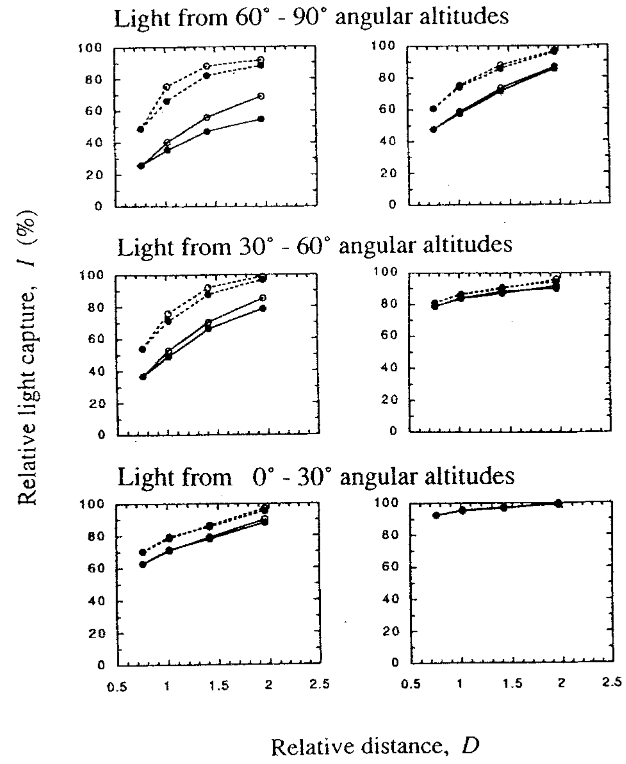

Fig. 3. D-dependency of I of a model shoot with 10 (·····) or 24 (——) leaves spirally arranged for different directional distribution of light; light from high (60–90°), middle (30–60°), and low (0–30°) angular altitudes (from top to bottom). Left column, shoots with short internode (0.1); right column, shoots with long internode (0.5). Open circles represent $I(B_n)$ and closed circles, $I(P_n)$ (n = 0, 1, 2, 3).

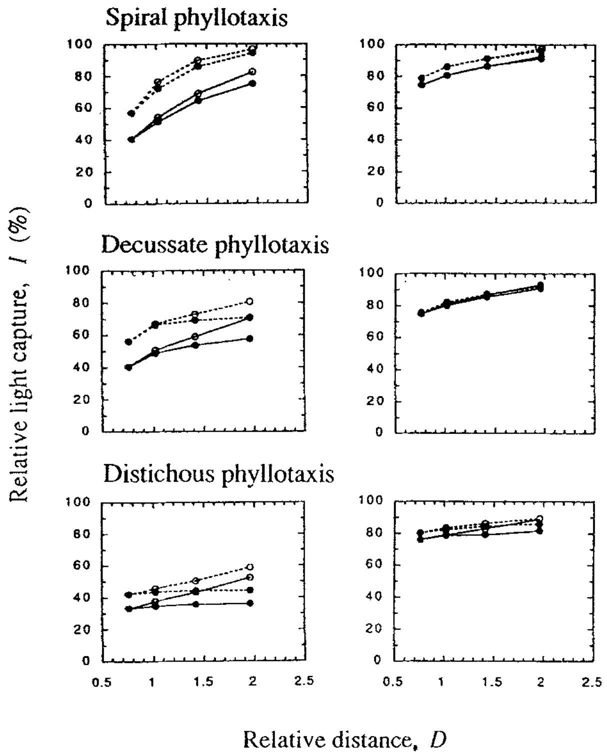

Fig. 4. D-dependency of I of a model shoot with 10 (·····) or 24 (——) leaves arranged in spiral (top), decussate (middle) and distichous (bottom) phyllotaxis. Left column, shoots with a short internode; right column, shoots with a long internode. Open circles represent $I(B_n)$ and closed circles, $I(P_n)$ (n = 0, 1, 2, 3).

lotaxis than in those with spiral phyllotaxis, and even less in those with distichous phyllotaxis. The difference between $I(B_n)$ and $I(P_n)$ was greater for decussate shoots compared to shoots with spiral phyllotaxis and even greater for distichous shoots. In distichous shoots, the addition of a petiole to the leaf blade scarcely reduced shading among leaves on the shoots.

DISCUSSION

As was expected, leaves of larger D, with a narrow blade or with a petiole, reduced mutual shading among leaves within a shoot. The similarity in light capture of shoots with leaves different in shape (narrow and not petioled *vs* wide and petioled) but identical in their D values is noteworthy. Thus, leaves of a wide range of variation in shape can be described in terms of their efficiency in avoiding mutual shading with this simple parameter. D dependencies of calculated shoot light capture were also similar in model shoots with lobate, palmate, palmately compound and pinnate leaves (data not shown).

Even though large D values benefit plants by reducing mutual shading among leaves on a shoot, greater construction costs are required for petioles or robust midribs to support long and narrow leaf blades. Moreover, in plants with branching architecture, too large a D increases shading among neighboring shoots. It is probable that these costs and disadvantages place upper limits on the range of D values of leaves of real plants.

Leaves on a vertical shoot are arranged in several rows along the stem, although the pattern is not always strictly followed. The number of rows varies among the phyllotaxes: eight rows for a shoot with spiral phyllotaxis with 135° divergence (3/8 of

360°), four for decussate shoots, and two for distichous shoots. Comparison of the light capture of model shoots of different phyllotaxes (Fig. 4) showed that shoots with fewer rows of leaves along the stem suffer more mutual shading.

Shading among leaves on a shoot can be divided into two components; shading among leaves within a row (within-row shading), and that among leaves of different rows (between-row shading). Narrow leaves contribute to higher light capture efficiency of a shoot by reducing both within- and between-row shading. Within-row shading is reduced because a leaf with a narrow blade shades the subjacent leaf less than a leaf with a wide blade does, and between-row shading is reduced because of the increased mean distance between leaves of different rows. On the other hand, petioles reduce only between-row shading by increasing the distance between rows of leaves. Within-row shading is not affected by petiole length. Thus, under conditions in which the relative contribution of within-row shading is large, light capture efficiency is expected to be higher for shoots with narrow leaves than for those with petioled leaves even when compared between leaves of identical *D* values.

The results of the present study support the above discussion. Higher light capture efficiencies in shoots with narrow leaves than shoots with petioled leaves were observed when (i) the internode length was short; (ii) light came exclusively from higher angular altitudes; and (iii) the phyllotaxis was distichous. Under all these conditions, the relative contribution of within-row shading to the overall mutual shading is large. Under the first condition, short internodes reduce the distance between neighboring leaves in a row much more than the distance between leaves of different rows. Under the second condition, vertical light is obstructed only by the superjacent leaf in the same row. Under the third condition, in shoots with fewer rows of leaves, the distance between neighboring leaves is less within a row but greater among different rows.

It can be hypothesized that under conditions (i), (ii) and (iii) listed above, plants have narrow leaves as a result of selection for higher light capture efficiency. First, plant species that invest less in stems and make short internodes are expected to have narrow light capture units. Making a longer stem is beneficial in exploiting more light resources, reducing shading among leaves on the stem, and displaying flowers more conspicuously to pollinators, but requires more investment in the stem at the expense of investment in other organs including leaves. The pattern of carbon allocation between different organs must have been subjected to strong selection pressure for optimizing the carbon budget of a plant. The investment to the stem determined by natural selection is one of the constraints for the selection of leaf shape. The analysis of shoot morphology over a wide range of plant species of different life forms and ecological behaviors is likely to reveal a correlation between the allocation pattern and leaf shape.

Second, it can be expected that plant species living mainly under light conditions in which light comes predominantly from higher angular altitudes tend to have narrow leaves. Such a light environment is widely found on forest floors under closed canopies (Reifsnyder *et al.* 1971; Takenaka 1987; Turton 1992). However, many of the herbaceous plants living on forest floors do not have elongated vertical shoots with leaves arranged along them. Rather, this prediction would be applicable to tree seedlings and saplings with lateral branches living under forest canopies. The present model considers a shape of leaves on a shoot, but the results are applicable also to shoots with flat lateral branches. It is generally observed that the light environment affects some features of the architecture of juvenile trees such as internode length and number of leaves and branches, which are closely related to light capture efficiency. In addition to these features, the shape of leaves and lateral branches is also responsible for light capture. Studies of the morphology of shrubs and juvenile trees under forest canopies have emphasized height, crown expansion and dry matter allocation among leaves and stem (Kohyama 1987; King 1990; Kohyama & Hotta 1990). The hypothesis proposed here that the shape of the light capturing area is related to light angle would provide another view of their morphology.

The third hypothesis that can be made is that plant species that show phyllotaxis with a small number of rows of leaves have narrow leaves. Plant species belonging to Gramineae and Cyperaceae might provide an example of this correlation. Narrow leaves and phyllotaxes with only two (distichous) or three rows of leaves on a shoot are common in plants of these families. Although the cause and effect relationship is not clear, this correlation of phyllotaxis and leaf shape accords with the above prediction.

Without the above conditions favoring narrow leaves, plants may have a wide range of possible leaf shape keeping the light capture efficiency unchanged. The large variation in leaf shape found in nature seems to support this view. However, the above conclusion is based on an assumption that leaves of the same *D* values call for the same amount of construction cost. Extensive measurements of leaf shapes and costs are needed to verify this assumption. If there is a substantial difference in the construction cost of narrow leaves and leaves with petioles, the more costly type of leaf must have other advantages over the less costly type.

All the above predictions of leaf shape are based solely on the light capture efficiency of a shoot. Other factors such as energy budget and water balance are also closely related to leaf shape (Givnish & Vermeij 1976; Givnish 1979, 1984, 1987). Integration of a wide range of aspects of leaf shape is needed for a more comprehensive understanding of its adaptive significance. The results of the present paper contribute to one of these aspects of the significance of leaf shape.

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REFERENCES

CHAZDON R. L. (1985) Leaf display, canopy structure and light interception of two understory palm species. *American Journal of Botany* **72**: 1493–1502.

GIVNISH T. J. (1979) On the adaptive significance of leaf form. In: *Topics in Plant Population Biology* (eds O. T. Solbrig, S. Jain, G. B. Johnson & P. H. Raven) pp. 375–407. Columbia University Press, New York.

GIVNISH T. J. (1984) Leaf and canopy adaptations in tropical forests. In: *Physiological Ecology of Plants of the Wet Tropics* (eds E. Menina, H. A. Mooney & C. Vazquez-Yanes) pp. 51–84. Dr Junk Publisher, The Hague.

GIVNISH T. J. (1987) Comparative studies of leaf form: Assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist* **106**(Suppl): 131–60.

GIVNISH T. J. & VERMEIJ G. J. (1976) Size and shapes of liane leaves. *American Naturalist* **110**: 743–778.

HORN H. S. (1971) *The Adaptive Geometry of Trees*. Princeton University Press, Princeton.

KING D. A. (1990) Allometry of saplings and understorey trees of a Panamanian forest. *Functional Ecology* **4**: 27–32.

KOHYAMA T. (1987) Significance of architecture and allometry in saplings. *Functional Ecology* **1**: 399–404.

KOHYAMA T. & HOTTA M. (1990) Significance of allometry in tropical saplings. *Functional Ecology* **4**: 515–521.

NIKLAS K. J. (1988) The role of phyllotactic pattern as a 'developmental constraint' on the interception of light by leaf surfaces. *Evolution* **42**: 1–16.

NIKLAS K. J. (1989) The effect of leaf-lobing on the interception of direct solar radiation. *Oecologia* **80**: 59–64.

REIFSNYDER W. E., FURNIVAL G. M. & HOROWITZ J. L. (1971) Spatial and temporal distribution of solar radiation beneath forest canopies. *Agricultural Meteorology* **71**: 21–37.

TAKENAKA A. (1987) Analysis of light transmissivity of forest canopies with a telephoto method. *Agricultural and Forest Meteorology* **40**: 359–369.

TURTON S. M. (1992) Understorey light environments in a north-east Australian rain forest before and after a tropical cyclone. *Journal of Tropical Ecology* **8**: 241–252.