

A simple formulation of interaction between individuals competing for light in a monospecific stand

K. HIKOSAKA,† H. NAGASHIMA,* Y. HARADA and T. HIROSE

Biological Institute, Graduate School of Science, Tohoku University, Aoba, Sendai 980-8578, Japan

Summary

1. A new method to evaluate the interaction between individuals competing for light in a monospecific stand is presented.
2. Light intercepted by a leaf of a target individual is influenced by its own leaves and those of neighbours higher in the canopy. We assume that light intercepted by the leaf is the sum of the light that penetrates the foliage of the target and the foliage of neighbours. We define the degree of the interaction as the fraction of the intercepted light that penetrated the foliage of neighbours.
3. To determine the degree of interaction, we established experimental stands of an annual, *Xanthium canadense* Mill., and measured light interception directly with light-sensitive films attached to leaves. We calculated the interaction using light absorption of individuals within the stand and of those isolated from the stand. Light interception of an individual was influenced more by its neighbours' leaves than by its own. The degree of interaction was greater in the stand of higher density.
4. The method presented here may be useful in studying the role of architectural characteristics in light competition in relation to evolutionarily stable strategies of individuals in monospecific stands.

Key-words: Evolutionarily stable strategy, light absorption, neighbour effect, plant competition

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Introduction

In many plant communities, individuals compete for resources, including light. Canopy photosynthesis models describe how light is absorbed by leaves in a canopy and used for photosynthesis (Hikosaka, Sudoh & Hirose 1999). Many authors have discussed characteristics that maximize canopy photosynthesis, such as leaf angle, leaf-area index and nitrogen allocation among leaves (Monsi & Saeki 1953; Saeki 1960; Verhagen, Wilson & Britten 1963; Hirose & Werger 1987; Evans 1993; Anten *et al.* 1995; Terashima & Hikosaka 1995; Hirose *et al.* 1997; Hikosaka & Hirose 1998; Anten, Hikosaka & Hirose 2000).

However, traits leading to maximal canopy photosynthesis at the stand level do not necessarily lead to success of an individual in the canopy. For example, the photosynthetic capacity of canopies with vertical leaves exceeds that of those with horizontal leaves, because more light passes between leaves and reaches deeper layers, resulting in more uniform distribution

of light within the canopy (Saeki 1960; Verhagen *et al.* 1963). However, horizontal leaves intercept light more than vertical leaves under light of the same intensity. Consider the appearance of a mutant with horizontal leaves in a stand of individuals with vertical leaves. Photosynthesis of the mutant would exceed that of neighbours because of its greater light absorption. Therefore, the evolutionarily stable leaf angle is expected to be more horizontal than the 'optimal' leaf angle that maximizes whole-canopy photosynthesis (Hikosaka & Hirose 1997). Similarly, an individual in a stand can increase its light interception by increasing leaf area to beyond that which maximizes the photosynthesis of the whole stand (Anten & Hirose 2001).

Several previous studies have discussed the evolutionarily stable strategy (ESS) of plants competing in dense stands, in terms of plant height (Givnish 1982; Iwasa, Cohen & Leon 1984), leaf angle (Hikosaka & Hirose 1997) and leaf area (Schieving & Poorter 1999; N.P.R. Anten, unpublished results). They suggest that the ESS solution depends strongly on the effects of neighbours on the light environment of the target. If the light environment of an individual is independent of its neighbours, the ESS solution for any trait is the same as that which maximizes the photosynthetic rate of the whole stand (Parker & Maynard Smith 1990; Hikosaka & Hirose 1997). Alternatively, if the effect of

†Author to whom correspondence should be addressed.
E-mail: hikosaka@mail.cc.tohoku.ac.jp

*Current address: Nikko Botanical Garden, Graduate School of Science, University of Tokyo, Nikko, Tochigi 321-1435, Japan

neighbours is large, the difference between the two solutions is large. Here we define 'interaction' in terms of the effect of neighbours on the light environment of a target individual.

The interaction may depend on architecture: geometrical dimensions such as the physical distance between individuals (Givnish 1982), the size of the individuals (Hikosaka & Hirose 1997), and the degree of mixing of leaves in a space (N.P.R. Anten, unpublished results). The interaction term influences the ESS solution of plant traits for competition. However, no-one has evaluated the interaction term directly. In this paper we present a simple method to quantify the degree of interaction between individuals in actual stands, which will be useful in deriving ESS solutions for light competition.

THEORY

To quantify the degree of interaction, we use the model of Hikosaka & Hirose (1997) with modifications. For simplicity, we consider a stand consisting of individuals of the same height.

Attenuation of photon-flux density (PFD) in a leaf canopy follows Beer's law:

$$I_n = I_0 \exp(-KF_n), \quad \text{eqn 1}$$

where F_n is the cumulative leaf area per unit ground area from the top of the canopy to position n in the canopy; I_n and I_0 are PFDs at n and above the canopy, respectively; and K is the light-extinction coefficient. As the difference between I_{n-1} and I_n indicates absorbed PFD between layer $n-1$ and n , the PFD received per unit leaf area, I'_n , is described as follows:

$$I'_n = KI_0 \exp(-KF_n)/(1-\sigma)^{0.5} = KI_n/(1-\sigma)^{0.5}, \quad \text{eqn 2}$$

where σ is a leaf-scattering coefficient (Goudriaan 1977).

The present model assumes that light intercepted by a leaf of a target individual is the sum of light penetrating the foliage of the target and the foliage of neighbours. We define the degree of interaction as the fraction of the intercepted light that penetrated the foliage of neighbours. The PFD on a horizontal surface at a layer n around a leaf of the target (I_{Tn}) is then described by:

$$I_{Tn} = (1-\eta)I_0 \exp(-K_T f_{Tn}) + \eta I_0 \exp(-K_N f_{Nn}), \quad \text{eqn 3}$$

where the subscripts T and N indicate the target and neighbours, respectively, and f_n is the cumulative leaf-area index above layer n over the fraction of ground area occupied by the plants. If the area and spatial distribution of leaves are identical between individuals (i.e. $f_{Tn} = f_{Nn}$), f_{Tn} is equal to F_n . η indicates the degree of interaction with neighbours ($0 < \eta < 1$). If η is large, PFD at a leaf of a target individual depends largely on neighbours. Although actual η may vary from the

top to the bottom of the canopy, η as determined by equation 3 represents a mean interaction averaged over layers for individuals in the stand. PFD intercepted by a leaf of a target individual depends on its K value (see equation 2):

$$I'_{Tn} = K_T I_{Tn} / (1-\sigma)^{0.5}. \quad \text{eqn 4}$$

If an individual is isolated from the stand, its light interception per leaf area at layer n (I'_{Ton}) is calculated from equations 3 and 4 with an assumption that $f_{Nn} = 0$:

$$I'_{Ton} = K_T [(1-\eta)I_0 \exp(-K_T f_{Tn}) + \eta I_0] / (1-\sigma)^{0.5}. \quad \text{eqn 5}$$

To determine η , in this paper we established experimental stands and directly measured light interception by leaves of individuals within the stand (I'_{Tn}) and of individuals placed isolated from the stand (I'_{Ton}). If we assume that the K_T and K_N values are equal to the K value that is estimated in the stand, and that f_{Tn} is equal to F_n , then the η value is calculated by equations 3 and 5.

Materials and methods

A broad-leaved summer annual, *Xanthium canadense* Mill., was used in the present study. This species is a competitive-ruderal and often colonizes disturbed habitats (Anten & Hirose 1998). Seeds of *X. canadense* were sown in pots of 12.5 cm diameter (1.5 l) filled with river sand on 2 July 1999 (one plant was grown in each pot). We arranged the pots uniformly to establish two stands with different densities in an experimental garden at Tohoku University, Sendai, Japan. There were 16 and 64 plants m^{-2} , respectively, for low-density (LD) and high-density (HD) stands. Water was added every day, and a commercial fertilizer, HYPONEX (Murakami Bussan Co., Tokyo, Japan), was supplied weekly at a rate of 15 mg N per pot.

To measure light interception by leaves, we used a light-sensitive film (Optleaf R-2D, Taisei-Kako, Tokyo, Japan), which contains pigment that fades as photons are absorbed. The integrated amount of absorbed photons is obtained from the change in transmittance of the film. We stapled strips of film (2 × 1 cm) on both adaxial and abaxial side of leaves of *X. canadense*, and determined light interception for each leaf. In the early morning of 23 August 1999, three potted plants were removed from each stand and placed in an open space, and films were placed on all leaves of the plants. Another three plants were randomly selected within each stand, and films were placed on all their leaves. On the evening of 24 August 1999, plants and films were collected. The transmittance of films was determined with a spectrophotometer (UV-160 A, Shimadzu, Kyoto, Japan). The weather on 22 and 23 August was cloudy and sunny, respectively. The daily PFD, determined using a quantum sensor

(Li-1000, Li-Cor, Lincoln, NE, USA), was 2.5 and 23.9 mol m⁻² day⁻¹, respectively.

The least-squares method was applied for curve-fitting with Kaleidagraph (Abelbeck Software, Reading, PA, USA).

Results

Although the same amounts of nutrients were supplied, there was a large difference in the architecture of individuals between the LD and HD stands. HD individuals were taller and developed leaf areas at higher positions (Fig. 1). However, the total leaf area of an individual was similar in the two stands. Consequently, leaf area indices of the two plots were proportional to plant density (0.77 and 3.09 m² m⁻²).

Relative photon absorption decreased exponentially with cumulative leaf-area index (Fig. 2). Some of the

top leaves that faced the sun received more PFD higher than did reference films placed horizontally outside the canopy. The pattern of light interception by individuals within the stand was described well by equation 2: $K = 0.64$ and 0.88 for the LD and HD stands, respectively.

In Fig. 2, light absorption by isolated individuals is plotted against the leaf-area index before isolation (assuming $f_{Tn} = F_n$). When compared at the same leaf-area index, isolated individuals absorbed more light. The difference in light absorption between individuals within and isolated from the stand was larger in the HD stand. This pattern was described well by equation 5 using K values obtained from individuals within the stand. The index of interaction, η , was calculated as 0.70 and 0.85 for the LD and HD stands, respectively. The larger η in the HD stand was expected because the interaction increases as the distance between individuals decreases.

Discussion

Many authors have studied the light interception of different species or individuals in plant stands, either theoretically (Rimington 1984; Sinoquet *et al.* 1990; Sinoquet & Bonhomme 1992; Wallace 1997; Wallace & Verhoef 2000) or experimentally (Ryel *et al.* 1990; Hirose & Werger 1995; Anten & Hirose 1998, Anten & Hirose 1999; Hikosaka *et al.* 1999). However, these studies did not include the effects of neighbours on light interception of target plants. The values obtained here for the interaction between individuals, η , may be used in theoretical models to derive ESS solutions, as shown by Hikosaka & Hirose (1997).

We modified Beer's law to describe light interception of isolated individuals (equation 5), although Beer's law was originally applied to a large, homogeneous canopy where leaf area was distributed randomly (Monsi & Saeki 1953). More elaborate models would be needed to describe light distribution in canopies with nonrandomly distributed leaves (Monsi, Uchijima & Oikawa 1973). However, such models become too complicated to apply to real stands. Equation 3 assumes that the target intercepts light which penetrates its own foliage and that which penetrates neighbours' foliage. Some light may come from the fraction that penetrates foliage of both the target and neighbours, but we ignored this because the amount would be small. Jackson & Palmer (1979) showed that light interception in discontinuous canopies is well described by an equation similar to our equation 5. They compared the predicted light transmission with that obtained from an experiment where the three-dimensional distributions of leaves and light were simulated, and showed a close correspondence between the two.

In modelling, we assumed a stand consisting of individuals of similar height. When a stand consists of individuals of various sizes, dominant individuals whose uppermost leaves are exposed to the top of the

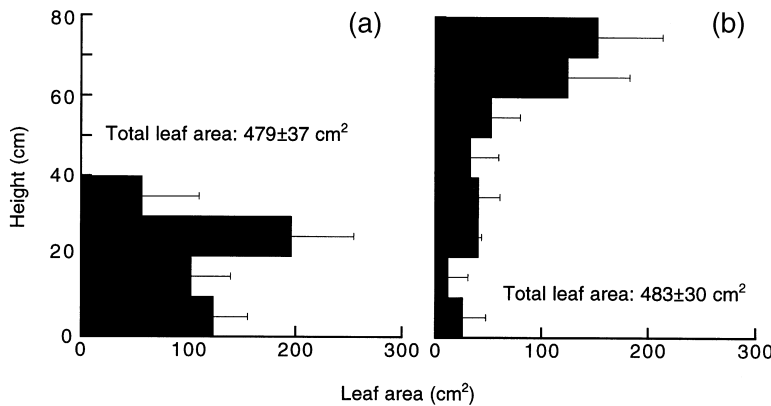


Fig. 1. Vertical distribution of leaf area of a plant in the low-density (a) and high-density (b) stands ($n = 6$).

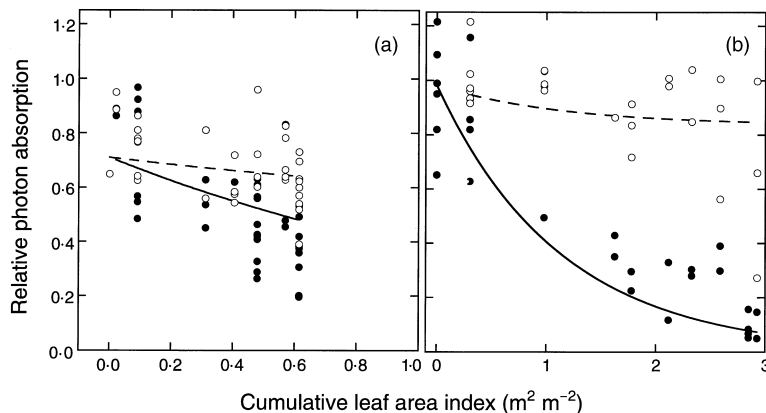


Fig. 2. Distribution of light absorption by leaves in the low-density (a) and high-density (b) stand. Values relative to the photon-flux density on the horizontal surface at the top of the canopy are shown. Open and closed symbols denote light interception of plants isolated from the stand and of those within the stand, respectively. The x axis shows cumulative leaf area per ground area (LAI) in the stand. For isolated individuals, LAIs before isolation are plotted. 1.0 of light absorption was obtained in the horizontal surface at the top of the canopy. Solid and broken lines are fitted for individuals within the stand (equation 2) and those isolated from the stand (equation 5), respectively. Solid lines are $I/I_0 = 0.71 \exp(-0.64F)$; $r = 0.62$ and $I/I_0 = 0.98 \exp(-0.88F)$; $r = 0.90$ for low- and high-density stands, respectively. Broken lines are $I/I_0 = 0.71[0.30 \exp(-0.64F) + 0.70]$; $r = 0.35$ and $I/I_0 = 0.98[0.15 \exp(-0.88F) + 0.85]$; $r = 0.37$ for low- and high-density stands, respectively.

stand should be targeted for analysis. In many stands, dominant individuals have similar heights, despite large variations in their above-ground mass (e.g. Nagashima & Terashima 1995). As most seed production in a monospecific stand comes from dominant individuals (Nagashima 1995), targeting dominants is more relevant evolutionarily.

We used a light-sensitive film to measure light absorption by leaves. Other methods have been used, e.g. quantum sensors (Hilbert & Messier 1996) and multiple layers of sepia paper (Ackerly 1992). To estimate η , we did not have to measure the light absorption of every leaf of a plant because Beer's law was assumed for light extinction in the canopy. However, light absorption of leaves showed large variation horizontally, even at the same height in the stand. In particular, at a small leaf-area index, differences in light absorption between plants within a stand and those isolated from the stand were small (Fig. 2). Many data points are necessary to determine K and η accurately.

Although η represents the degree of interaction, a larger η does not necessarily indicate that the light interception of the target is more reduced by neighbours. η indicates the contribution of light penetrating neighbours' foliage relative to light interception by the target. When η is small, light interception by a leaf of the target is affected mainly by its own foliage. Therefore, if architectural traits are identical between the target and its neighbours (i.e. $K_T = K_N$ and $f_{Tn} = f_{Nn}$), a difference in η does not influence light interception because the foliage of both target and neighbours has similar effects on the light interception of the target. However, if the target has different architectural traits from those of neighbours, light interception of the target may vary with η . If upper leaves of the target pass less light to lower layers than do those of neighbours, a large η is advantageous for light interception by the target. For example, horizontal leaves (large K) absorb more light than vertical leaves, but reduce irradiance more strongly at lower positions. When η is large, irradiance at lower positions in the target canopy is independent of the inclination of its upper leaves. Therefore, when neighbours have vertical leaves, horizontal leaves of the target will no longer have a negative effect on its lower leaves. We predicted that, within a stand, horizontal leaves are an ESS when η is large (Hikosaka & Hirose 1997). *Xanthium canadense* has horizontal leaves (Anten & Hirose 1998) with a large K , which is consistent with its large η .

Many plant traits, such as petiole length, branching and biomass allocation, may influence light competition because they can affect η . Although several authors have studied plant architecture as a mechanism to avoid self-shading in an individual (e.g. Niklas 1992; Takenaka 1994; Pearcy & Yang 1998), studies on its significance in relation to competition with neighbours have been limited (Hilbert & Messier 1996). Consider two species that have similar leaf areas, architecture and other traits related to light interception,

but differ in the length of their petioles: one species has short and the other long petioles. When these species form monospecific stands, light interception by an individual is the same in the two stands if the plant density is the same. Since long petioles do not increase light interception in a monospecific stand, they seem costly and inefficient in terms of carbon economy. However, interaction among individuals would be quite different between the two species: it would be larger in the stand of species with long petioles. We may predict that species with longer petioles will have more horizontal leaves than the species with short petioles. Species that have horizontal leaves with a long petiole would be advantageous in competition with a species having vertical leaves supported by a short petiole.

Xanthium canadense plants have long petioles. The horizontal distance from the stem to leaf tips of the largest leaves was over 20 cm (data not shown), longer than the distance between the nearest individual plants in the HD stand (12.5 cm), which might contribute to increasing η . This implies that competing species tend to have large η values even though increasing η does not necessarily raise whole-plant photosynthesis. It is important to quantify the degree of interaction between individuals in order to understand the role of plant architectural traits in competition. The method presented here will allow the role of architectural characteristics in competition for light to be studied in terms of the ESS of individuals in monospecific stands.

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