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BRIEF COMMUNICATION

Photosynthetically versatile thin shade leaves: a paradox of irradiance-response curves

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Abstract

Thick sun leaves have a larger construction cost per unit leaf area than thin shade leaves. To re-evaluate the adaptive roles of sun and shade leaves, we compared the photosynthetic benefits relative to the construction cost of the leaves. We drew photosynthetically active radiation (PAR)-response curves using the leaf-mass-based photosynthetic rate to reflect the cost. The dark respiration rates of the sun and shade leaves of mulberry (*Morus bombycis* Koidzumi) seedlings did not differ significantly. At irradiances below 250 µmol m^{-2} s^{-1}, the shade leaves tended to have a significantly larger net photosynthetic rate (P_N) than the sun leaves. At irradiances above 250 µmol m^{-2} s^{-1}, the P_N did not differ significantly. The curves indicate that plants with thin shade leaves have a larger daily CO_2 assimilation rate per construction cost than those with thick sun leaves, even in an open habitat. These results are consistently explained by a simple model of PAR extinction in a leaf. We must target factors other than the effective assimilation when we consider the adaptive roles of thick sun leaves.

Additional key words: construction cost; dark respiration rate; mesophyll; *Morus*; mulberry; net photosynthetic rate; photosyn–thetically active radiation.

The leaf-area-based irradiance-response curves of thick sun leaves and thin shade leaves clearly differ (Retter 1965, Grahl and Wild 1972, Björkman 1981). At high irradiance (I), sun leaves have large net photosynthetic rates (P_N), while shade leaves have small rates. At low I, however, shade leaves tend to have larger P_N than sun leaves. According to the area-based curves, the adaptive merit of sun leaves seems obvious: they assimilate effectively in open habitats. Conversely, the merit of shade leaves is obscure; their P_N surpasses those of sun leaves in a very narrow range of low I that is unlikely to be always found on the forest floor or under the forest canopy. For example, sunflecks, which account for a considerable part of the photosynthesis of shade leaves, have a higher I than this range (Chazdon and Pearcy 1991). Therefore, shade leaves may possess no definite merit. However, another possibility exists: the self-evident appearance of area-based curves has distracted us from the real merit of shade leaves.

We investigated the economics of sun and shade leaves to re-evaluate their adaptive roles. For this purpose, we compared the photosynthetic benefit relative to the construction cost of the leaves. Area-based curves do not reflect this cost because thick sun leaves have a larger leaf matter per area (LMA) than thin shade leaves (Larcher 1994, Lambers *et al*. 1998). Therefore, we redrew the curves using a leaf-mass-based P_N for the comparison. We measured the P_N of mulberry (*Morus bombycis* Koidzumi) seedlings and obtained mass-based curves for sun and shade leaves. Then, we confirmed the generality of the curves using previous reports and sought to elucidate them using the extinction of photosynthetically active radiation (PAR) within a leaf.

Mulberry is a pioneer deciduous tree of secondary succession that grows mainly in the montane zone of East Asia. Seeds of mulberry were collected in a secondary forest in Nikko City in June 2001. Soon after collection, the seeds were sown in plastic pots (10.5 cm diameter and

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Abbreviations: Chl – chlorophyll; I – irradiance; LMA – leaf matter per area; P_N – net photosynthetic rate; PAR – photosynthetically active radiation; R_D – dark respiration rate.

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12.0 cm depth). Seedlings emerged about 1 week after sowing. The seedlings were thinned to leave a single plant per pot. Each pot was watered with 100 cm^3 of nutrient solution (*Hyponex*, 1/200; *Hyponex*, Marysville, OH, USA) every 3 d. The seedlings were grown in an open field at the Nikko Botanical Garden. They shed their leaves in early November. In mid-April 2002, the shoots were cut at about 3 cm above the soil surface. Half of the pots were set in an open field to facilitate the development of sun leaves, while the remainder was set on a forest floor to allow the development of shade leaves. The relative *I* of the forest floor was about 2 %. In early May, new shoots began to elongate. We pruned the shoots in mid-May to leave one shoot per pot. Thereafter, the plants were again given the nutrient solution. The plants on the forest floor ceased leaf expansion by early June, while the plants in the open field continued shoot elongation. In late July, the photosynthetic rates were measured using a portable photosynthesis measurement system (*CIRAS1*; *PP Systems*, Hitchin, UK). The measurement conditions were as follows: CO_2 concentration 350 µmol mol^{-1}, leaf temperature 30 °C, and relative humidity 70 %. After the P_N was measured, the leaves were collected to measure area and dry mass. Adjacent leaves were also collected to determine the chlorophyll (Chl) content (AOAC 1984).

Mulberry tree developed typical sun and shade leaves; the sun leaves had multiple layers of palisade mesophyll cells, while the shade leaves had a single cell layer. The mean ± SD of the LMA of the sun and shade leaves was 53.7 ± 2.3 and 15.1 ± 1.0 g m^{-2}, respectively; the LMA of the sun leaves was 3.6 times greater than that of the shade leaves. Chl content per unit leaf area of the sun and shade leaves was 0.58 ± 0.08 and 0.35 ± 0.08 g m^{-2}, respectively; the Chl content of the sun leaves was 1.7 times larger. Fig. 1*A* shows the area-based PAR-response curves of the leaves. As reported previously, the dark respiration rate (R_D) and compensation *I* of the shade leaves were smaller than those of the sun leaves. The P_N values were similar at *I* of about 50 µmol m^{-2} s^{-1}. At a greater *I*, the sun leaves had a significantly larger P_N than the shade leaves. The photosynthetic capacity under PAR saturation of the sun leaves was 3.9 times larger than that of the shade leaves. This ratio was similar to that of the LMA.

Fig. 1*B* shows the mass-based PAR-response curves of the same leaves. No significant difference was observed in R_D between the two. At I <250 µmol m^{-2} s^{-1}, the P_N of the shade leaves tended to be larger than that of the sun leaves. For example, the ratio of the P_N of the shade leaves to that of the sun leaves was about 4 at 50 µmol m^{-2} s^{-1} and 2 at 100 µmol m^{-2} s^{-1}. At I >250 µmol m^{-2} s^{-1}, we found no significant difference in the P_N between the two types. Therefore, at any *I*, the thin shade leaves did not have a significantly smaller P_N per unit leaf mass than the thick sun leaves.

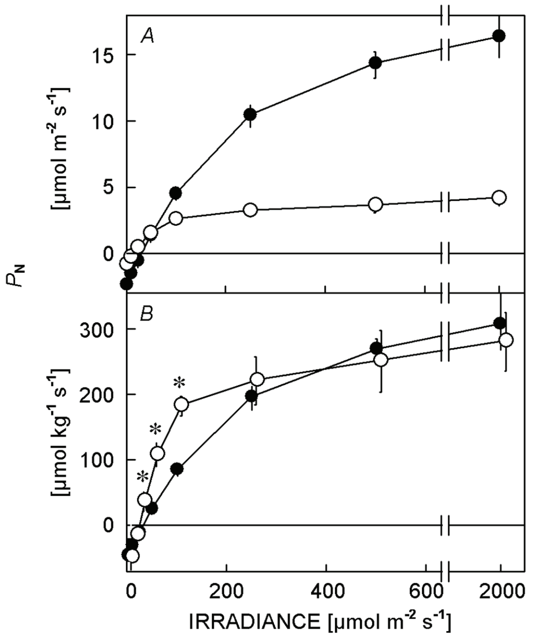

Fig. 1. Leaf-area (*A*) and leaf-mass (*B*) based photosynthetically active radiation (PAR)-response curves of *Morus bombycis*. *Closed circles* – sun leaves; *open circles* – shade leaves. Means ± SD; $n = 6$. * in *B* indicates the net photosynthetic rates (P_N) of the shade leaves that are significantly different from those of the sun leaves (two-sided *t*-test, $p<0.05$).

Both the area-based and mass-based PAR-response curves were reproduced qualitatively using a simple model, which assumes that a sun leaf is a lamination of shade leaves (Fig. 2). Based on the model prediction, we explained the shape of the measured mass-based curves with reference to PAR extinction along a transverse section of a leaf (Terashima and Saeki 1983, Nishio *et al.* 1993, Vogelmann and Han 2000). Since R_D is considered the maintenance respiration of cells (Penning de Vries 1975), the respiration is proportional to leaf mass. Therefore, the mass-based R_D of shade leaves is similar to that of sun leaves. At I <250 µmol m^{-2} s^{-1}, a large part of the incident PAR is absorbed by the upper cells (palisade mesophyll cells) of the thick sun leaves. As a result of this self-shading effect in a leaf, the lower cells (spongy mesophyll cells) of the sun leaves receive very weak PAR. Consequently, the P_N of these cells does not contribute much to the assimilation of CO_2. In contrast, incident PAR easily penetrates to the spongy mesophyll cells of the thin shade leaves. Therefore, the lower cells of the shade leaves contribute to CO_2 assimilation. The different P_N of the lower cells would cause the difference in the mass-based P_N between the sun and shade leaves at this low *I*. At I = 250–500 µmol m^{-2} s^{-1}, all the cells of the shade leaves and the upper cells of the sun leaves are *I*-saturated. Therefore, the P_N of the shade leaves does not increase with *I*. In contrast, the P_N of the lower cells of the sun leaves increases with *I* up to 500 µmol m^{-2} s^{-1} because they are not under PAR saturation due to self-shading. Therefore, the P_N of the sun leaves increases with *I* in this range. At I >500 µmol m^{-2} s^{-1}, the sun leaves do not increase P_N with increasing I because all the cells are under PAR saturation. As a result, the mass-based P_N of the sun and shade leaves become similar at high I. Therefore, the difference in the measured mass-based curves of the sun and shade leaves appears to be a logical consequence of the presence or absence of self-shading in a leaf.

The measurements and theoretical consideration indicate that sun and shade leaves have similar mass-based P_N only at high I, at which all cells are under PAR saturation. The high I does not continue all day, even on fine days in open habitat, because irradiation is low at dawn and dusk. On rainy days, I declines still more. Accordingly, the daily photosynthetic benefit relative to the construction cost of shade leaves surpasses that of sun leaves in any habitat. Therefore, even in open habitat, plants can assimilate CO_2 effectively by developing thin shade leaves with a large area if they allocate a fixed amount of material for leaves. This statement may sound paradoxical, but concurs with the general tendency for plants with a small LMA have a larger relative growth rate than those with large LMA, as LMA is the key factor affecting the relative growth rate of plants (Poorter and Remkes 1990). Although area-based light-response curves do not show a clear adaptive merit of shade leaves with a small LMA, they are considered versatile when we focus on the economics of leaf photosynthesis.

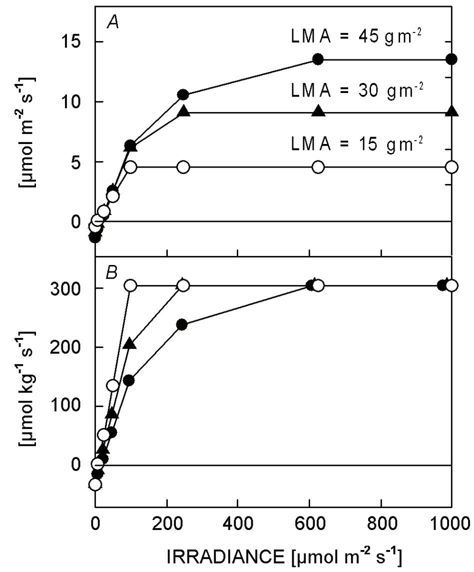

Fig. 2. Leaf-area (*A*) and leaf-mass (*B*) based photosynthetically active radiation (PAR)-response curves drawn from a model. We approximated the area-based curve of a hypothetical thin shade leaf with a leaf matter per area (LMA) of 15 g m^{-2} using the following Blackman-type curve (Blackman 1905): $Y = 0.05X - 0.5$ ($0 \le X < 100$), and $Y = 4.5X$ ($100 \le X$), where Y and X are the net photosynthetic rate (P_N) and irradiance (I), respectively. This approximation is appropriate for a thin layer (Terashima and Saeki 1985). We layered the shade leaves and calculated the P_N of hypothetical thick sun leaves with LMAs of 30 and 45 g m^{-2}, assuming that each layer absorbs 60 % of the incident PAR. The absorption efficiency was estimated from that of sun leaves of the mulberry. The model reproduced well-known features of area-based PAR-response curves of sun and shade leaves (see *A*). This suggests that a thick sun leaf is photosynthetically almost identical to laminated self-shading thin shade leaves, although structural and biochemical differences exist (Larcher 1994, Lambers *et al.* 1998). Self-shading in a leaf decreases the benefit per construction cost of the hypothetical sun leaves at relatively low I (see *B*) because lower layers within the sun leaves receive less PAR. For example, when I = 100 µmol m^{-2} s^{-1}, the hypothetical shade leaf is irradiance-saturated, but the lowest layer of the sun leaf with a LMA of 45 g m^{-2} receives I of only 16 µmol m^{-2} s^{-1}. This I is close to the assumed compensation I of each layer (10 µmol m^{-2} s^{-1}). The balance of the two curves, 45 and 30 g m^{-2} in *A*, is the P_N of the lowest layer of a sun leaf with an LMA of 45 g m^{-2}. At I >625 µmol m^{-2} s^{-1}, even this layer is light-saturated, and the benefit per construction cost of the hypothetical sun leaf coincides with that of the hypothetical shade leaf. The model helps better understand the measured curves.

To confirm this conclusion, we examined the area-based PAR-response curves of sun and shade leaves reported elsewhere (*e.g.* Grahl and Wild 1972, Björkman 1981). If we assume that the LMA of sun leaves is twice that of shade leaves, then the shade leaves in those reports are more beneficial than the sun leaves at I <250–500 µmol m^{-2} s^{-1}, which does not controvert our result. Next, we extended the comparison to interspecific differences. Koike (1988) showed that thick leaves of *Populus maximowiczii* Henry, a shade-intolerant deciduous tree, have an area-based PAR-response curve similar to that of sun leaves, and that thin leaves of *Acer palmatum* Thunb., a shade-tolerant deciduous tree, have a curve similar to that of shade leaves. On the assumption that LMA is proportional to leaf thickness, the conversion of their curves to mass-based curves shows a similar tendency. Therefore, the conversions of the reported curves support our conclusion regarding photosynthetically versatile shade leaves with small LMAs.

An important question now arises. Why do many plant species develop thick sun leaves when exposed to high I? One possible explanation is that selection pressures other than economical assimilation forced the evolution of sun leaves. If transpiration occurs in proportion to leaf area, sun leaves with large LMA can reduce transpiration per unit leaf mass. This could have an advantage in open habitat where the water budget tends to be severe. The mean breaking loads for the traction of the sun and shade leaves of mulberry tree are 251 and 55 g cm^{-1}, respectively (Okajima and Tateno, unpublished). This could be advantageous in open habitat, where leaves are subject to the wind (Thomas and Winner 2002). Moreover, in open habitat with high I, the photosynthetic inefficiency of thick sun leaves can be compensated to some extent. Therefore, the benefits of leaf thickness, *i.e.* safety, would be given priority in stressful open habitats.

Another issue remains to be resolved. In contrast to the hypothetical shade leaves in the model, the actual shade leaves of mulberry had a somewhat smaller mass-based P_N than the sun leaves at high I, although the difference was not significant (see Figs. 1*B* and 2*B*). Shade leaves, which are thought to be effective for harvesting low I, have larger Chl content and a smaller ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) content per unit leaf mass than sun leaves (Lambers *et al.* 1998). In fact, the mass-based Chl content of the shade leaves was about twice that of the sun leaves, so their absorption efficiency (about 85 %) was larger than that of the hypothetical shade leaves in the model. The smaller investment in RuBPCO to accommodate low I might cause the smaller mass-based P_N at high I.

In summary, leaves with a small LMA are thought to be omnipotent in assimilation rate per unit leaf mass. The shade leaves formed in less stressful environments have a small LMA for economy, while the sun leaves formed in stressful environments presumably increase their LMAs for safety, in a trade-off with some photosynthetic benefit per unit leaf mass.

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