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The effect of growth irradiance on leaf anatomy and photosynthesis in maple species

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Introduction

Photosynthetic response to light is different between light-demanding and shade-tolerant tree species when they are grown in high light. The light-demanding species is generally has a high carbon assimilation capacity (A_{\max}) compared to shade-tolerant species. CO₂ transfer conductance inside leaves (g_i) is one of the important factors for determining photosynthetic response to high light, because limitation of assimilation rate by g_i is comparable to that by stomatal conductance (Caemmerer and Evans 1991, Epron *et al.* 1995, Kogami *et al.* 2001). The difference in A_{\max} between light-demanding and shade-tolerant species would be related to that in g_i , since g_i is highly affected by leaf anatomy, which varies between species and between light environments.

However, some factors other than net carbon gain may determine the acclimation to high light. High light condition in temperate forests often causes a high VPD, resulting stomatal closure and depresses CO₂ assimilation rate in midday. In addition, low CO₂ assimilation rate under high light may cause photoinhibition. Increasing the ratio of leaf carbon gain to leaf water loss (water use efficiency) and enhancing a resistance to photoinhibition are particularly important strategies to acclimate high light condition.

The objective of this study was to compare the morphological and physiological responses to high light among three *Acer* (maple) species *Acer rufinerve* (light-demanding), *Acer mono* (intermediate tolerance), and *Acer palmatum* (shade-tolerant). The responses in g_i and WUE are particularly emphasized. We investigated chlorophyll fluorescence to compare the resistance to photoinhibition among the species.

Materials and methods

Seedlings of three *Acer* species were grown in an open field at the Research Institute for Bioresources, Okayama University from May 1998 to November 2000. Plants were watered four times daily and fertilized once a week with a 1/500 nutrient solution (N:P:K=5:10:5, Hyponex, USA) at 500 mL per pot.

Just after their leaves unfolded, the potted seedlings were transferred to high light (100% full sun) or moderate shade (17% full sun), and grown from April to October 1999. Leaf gas

exchange was measured from September to October 1999 for fully expanded leaves, using a system described by Hanba, Miyazawa, & Terashima (1999). Mean leaf temperature was 24.8°C, leaf-to-air vapor pressure deficit (VPD) was 750 Pa, and ambient CO₂ partial pressure in the chamber was 35 Pa. Light-saturated rate of CO₂ assimilation (A_{\max}), stomatal conductance to CO₂ diffusion (g_s) and transpiration rate (E) were measured under saturated irradiance (740 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Calculation of CO₂ transfer conductance from the substomatal cavities to the sites of carboxylation (g_i) was given by Hanba *et al.* (2001). CO₂ partial pressure in chloroplasts (C_c) was calculated using the equation $C_c = C_i - A_{\max}/g_i$, where C_i is CO₂ partial pressure in the intercellular airspaces. Determinations of anatomical and biochemical parameters were described by Hanba *et al.* (2001).

Growth experiments were repeated for *Acer mono* and *Acer rufinerve* to measure chlorophyll fluorescence. Seedlings were transferred to high light or moderate shade, and grown from April to October 2000. Leaf discs of 1.8cm² were cut from the central part of the lamina, placed on moistened filter paper under low light (10 $\mu\text{mol m}^{-2} \text{s}^{-1}$) at 25°C. Leaf discs were exposed to 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD using a Halogen light source after the initial measurement of chlorophyll fluorescence (F_v/F_m), using a portable fluorometer (Plant Efficiency Analyzer, Hansatech, Norfolk, UK). After 2h exposure to high light, leaf discs were placed in low light (10 $\mu\text{mol m}^{-2} \text{s}^{-1}$) at 25°C to monitor the recovery from photoinhibition.

Results and discussion

The increases in S_c in highlight grown plants were most pronounced in *A. rufinerve*, a light-demanding species (Fig. 1). The high leaf assimilation rate in *A. rufinerve* is expected from the high S_c , because high S_c enhances the diffusion of CO₂ from the surface of mesophyll cells to chloroplasts resulting a stimulation in A_{\max}/area (Araus *et al.* 1986, Evans *et al.* 1994, Syvertsen *et al.* 1995, Evans 1998). The high Rubisco content in *A. rufinerve* (Fig. 1) similarly suggests a high photosynthetic potential in *A. rufinerve*. However, the A_{\max}/area in highlight grown *A. rufinerve* was no larger than those in other species (Fig. 1).

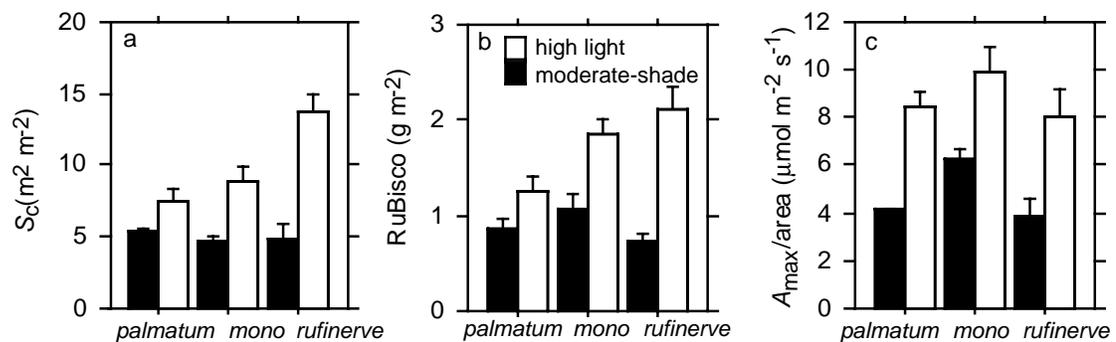


Fig. 1 Leaf traits of *Acer* species adapted to high light or moderate shade. **a**, surface area of chloroplasts exposed to intercellular air spaces (S_c); **b**, Rubisco content; **c**, light-saturated assimilation rate (A_{\max}/area). Values are mean (se).

The factors that limit A_{\max} in *A. rufinerve* grown in high light are resistances to CO₂ diffusion from the atmosphere to carboxylation sites. CO₂ conductance inside leaves (g_i) in *A. rufinerve* was no greater than those of the other species (Fig. 2). Similarly, stomatal conductance (g_s) in *A. rufinerve* was similar to the other species. As a result, *A. rufinerve* had a low CO₂ partial pressure at the carboxylation site, C_c (130 $\mu\text{mol mol}^{-1}$), compared to *A.*

palmatum ($150 \mu\text{mol mol}^{-1}$) and *A. mono* ($190 \mu\text{mol mol}^{-1}$), when measured under high irradiance (Fig. 2). This low C_c in *A. rufinerve* minimizes the increase of A_{max} in highlight grown *A. rufinerve*. Evans (1999) showed that when measured under high irradiance, lower assimilation rate in sclerophyllous leaves was accompanied by lower C_c compared to mesophyllous leaves, which is in line with our present result.

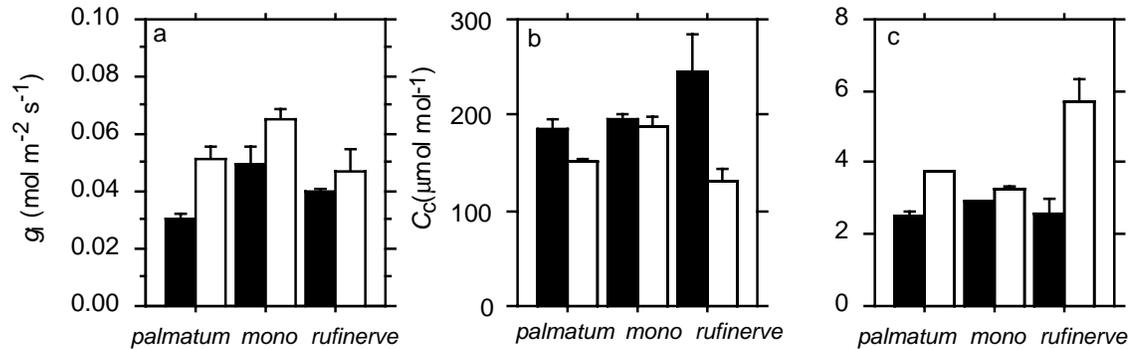


Fig. 2 Leaf traits of *Acer* species adapted to high light or moderate shade. **a**, CO_2 transfer conductance inside leaves (g_i) measured under high irradiance; **b**, CO_2 partial pressure in chloroplasts (C_c) calculated from the assimilation rate; **c**, photosynthetic water use efficiency (WUE; A/E - mmole/mol) estimated from the gas exchange measurements under high irradiance. Values are mean (se).

A significant increase in water use efficiency (WU) in highlight grown *A. rufinerve* (Fig. 2) suggests that *A. rufinerve* is more capable of accumulating carbon while using less water. In an open field in the Japanese temperate zone, maximum daily temperature in summer is so high ($29.3 - 31.5^\circ\text{C}$ from July to September 1999) that leaves may be water-stressed by increasing leaf-to-air vapor pressure difference (VPD). Many previous studies showed that increasing water use efficiency (WUE) is an important aspect of plant acclimation to drought (e.g., Ehleringer 1993, Nilsen & Orcutt 1996). Therefore, the high WUE in *A. rufinerve* is a favorable characteristic under full sun, especially when summer drought occurs.

After 2h exposure to high light, photoinhibition occurred in leaf discs from either high light or shade grown plants (Fig. 3). In leaf discs from highlight grown *A. rufinerve* were much less photoinhibited compared to highlight grown *A. mono* and shade-grown plants. Recovery in F_v/F_m was faster in highlight grown *A. rufinerve* compared to highlight grown *A. mono* and shade-grown plants. These results suggest that when grown in high light, resistance to photoinhibition would be higher in *A. rufinerve* (light-demanding species) compared to *A. mono* (intermediate shade-tolerant species).

In conclusion, among the *Acer* species, the light-demanding species *A. rufinerve* had strategies to increase water use efficiency, rather than increasing net carbon gain only, to acclimate high light. High resistance to photoinhibition in *A. rufinerve* is advantageous in high light compared to *A. mono*.

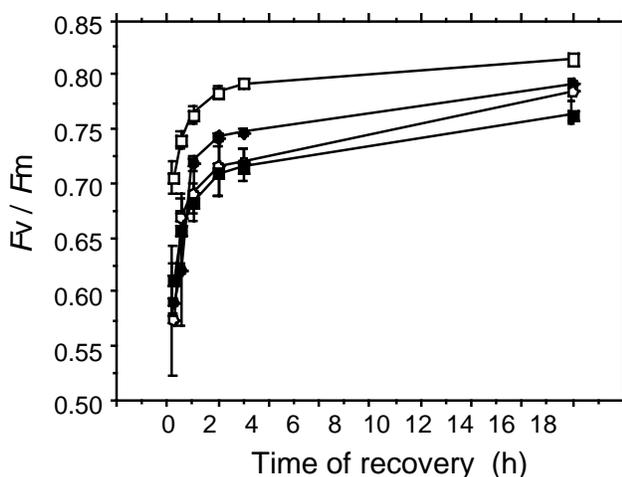


Fig. 3 Recovery in Fv/Fm of leaf discs exposed to high light. Values are mean (se) for *Acer rufinerve* (square) and *Acer mono* (diamond) grown in high light (open symbols) or moderate shade (closed symbols), respectively.

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