

Gas Exchange in *Schima superba*, a Subtropical Monsoonal Forest Tree*

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Abstract

Gas exchange characteristics for CO₂ and water vapor were measured on intact leaves of *Schima superba* Gardn. and Champ., a common, early successional tree of subtropical monsoonal forests in southern China. Plants were grown under greenhouse conditions that were controlled to mimic natural environmental conditions. At a leaf temperature of 26 °C, the compensation irradiance occurred at 0.03 mmol m⁻² s⁻¹ and by 0.7 mmol m⁻² s⁻¹ leaves were saturated by radiant energy. A net photosynthetic rate (P_N) of 10 μmol m⁻² s⁻¹ was measured at the temperature optimum (between 24 and 27 °C), but there was only a small dependence of P_N on leaf temperature between 20 and 30 °C. P_N decreased more rapidly at leaf temperatures above 30 °C, which suggests that carbon gain under field conditions may be limited by the high temperatures typically observed in the summer. Gas exchange in *Schima superba* leaves was also very sensitive to changes in the leaf to air water vapor gradient. Leaf conductance decreased from 0.12 to 0.05 mol m⁻² s⁻¹ as the water vapor gradient increased from 1.2 to 3.3 mPa Pa⁻¹. Over this humidity range, P_N decreased from 10 to 6 μmol m⁻² s⁻¹. The decrease in P_N was attributable to a decrease in intercellular CO₂. Thus under natural field conditions P_N in *Schima superba* is likely to be reduced by the temperature and humidity conditions that commonly occur during midday periods.

Much of the previous research into the gas exchange characteristics of native plants has focused on temperate and arctic species, and relatively few data are available for tropical and subtropical plants (Mooney *et al.* 1980, Medina and Klinge 1983). Of the photosynthetic studies on tropical and subtropical plants, most have focused on the role of light as a limiting factor (Bazzaz and Pickett 1980, Robichaux and Pearcy 1980, Pearcy and Calkin 1983, Langenheim *et al.* 1984) and the potential role(s) of soil drought or atmospheric humidity have received little attention.

In those tropical forests experiencing a pronounced dry season, there are indications that water availability may limit productivity. Lugo *et al.* (1978) reported a six-fold increase in diurnal carbon gain by *Exostema caribaeum* in a Puerto Rican forest during the wet season as compared to the dry season. In addition, leaf gas exchange activity appears to be sensitive to diurnal humidity changes. Fetcher (1979) and Whitehead *et al.* (1981) have reported that stomatal conductances in several rainforest species decreased in response to an increased leaf to air humidity gradient (Δw). Mooney *et al.* (1983) have shown that stomata of *Piper hispidum*, a shrub from Mexican rainforests, are also sensitive to Δw , and that increased Δw through its effect on leaf conductance does result in a reduced net photosynthetic rate (P_N).

The purpose of this study was to characterize the whole leaf-level photosynthetic responses of *Schima superba* Gardn. and Champ., which is an important subtropical forest tree in southern China. It is a dominant component of the vegetation from early successional through mature forest

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stages (Wang *et al.* 1982). Since this tree species is thought to be drought tolerant and occurs in forest stages with widely varying humidity, one of the principal objectives of this study was to determine the gas exchange responses in *Schima* to decreased humidity.

MATERIALS AND METHODS

Seedlings of *Schima superba* were collected from field locations at the Ding Hu Shan MAB Biosphere Reserve in southern China. They were transplanted to and grown in 10 liter pots in a greenhouse at the University of Utah. Greenhouse conditions were controlled so that air temperatures were 25–30 °C during the day and midday relative humidities ranged between 60 and 80 %. No additional *I* other than sunlight was supplied to the plants. All plants were watered to field saturation daily and were fertilized with Hoagland's solution weekly.

P_N and transpiration rate of intact leaves were measured using an open gas exchange system as described by Ehleringer (1983), except that CO₂ concentrations in the incoming air were mixed using mass flow controllers instead of a gas mixing pump. All gas exchange measurements were made at the University of Utah, which is at 1515 m elevation. Mean atmospheric pressure averaged 86 Pa. Calculations of gas exchange parameters were as described by Caemmerer and Farquhar (1981).

For measurements of the dependence of P_N on incident irradiance (*I*), leaves were first exposed to *I* of 1.8 mmol (photon) m⁻² s⁻¹ (400–700 nm), an ambient CO₂ concentration of 350 cm³ m⁻³, 21% O₂, a leaf temperature of 26 °C, and a leaf to air water vapor gradient (Δw) of 15 mPa Pa⁻¹. After steady state P_N was obtained, neutral density filters were inserted to reduce *I*. Steady state rates were again obtained before proceeding to the next lower *I*.

For the measurements of the photosynthetic dependence on leaf temperature, P_N was initially determined at a 25–26 °C leaf temperature. *I* was maintained at 1.8 mmol (photon) m⁻² s⁻¹, 350 cm³ m⁻³ CO₂, 21% O₂, and a Δw of 15 mPa Pa⁻¹. After steady state P_N was obtained, the leaf temperature was lowered in steps of 5 °C. After P_N at the lowest leaf had been measured, leaf temperatures were increased to 26 °C. After leaves had recovered, the leaf temperature was increased in 5 °C increments.

For the measurement of the photosynthetic dependence on intercellular CO₂ concentration, P_N was first determined at an ambient CO₂ concentration of approximately 350 cm³ m⁻³. Leaf temperature was maintained at 26 °C, incident *I* was 1.8 mmol (photon) m⁻² s⁻¹, and a Δw of 1.5 mPa Pa⁻¹. After steady state rates had been obtained the ambient CO₂ levels were decreased in steps of approximately 50 cm³ m⁻³. After the P_N at the lowest intercellular CO₂ concentration had been measured, ambient CO₂ was again increased to 350 cm³ m⁻³ and steady state values obtained before proceeding to high CO₂ concentrations.

For the measurements of the dependence on Δw , leaves were first exposed to an environment of 350 cm³ m⁻³ CO₂, *I* of 1.8 mmol (photon) m⁻² s⁻¹, Δw of 10 mPa Pa⁻¹ and a leaf temperature of 26 °C. After steady state P_N had been obtained, Δw was increased in approximately 0.5 mPa Pa⁻¹ intervals.

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RESULTS AND DISCUSSION

Photosynthesis in leaves of *S. superba* reached the compensation irradiance at $0.03 \text{ mmol (photon) m}^{-2} \text{ s}^{-1}$ and were saturated by $0.7 \text{ mmol (photon) m}^{-2} \text{ s}^{-1}$ (Fig. 1). Maximum P_N under ambient conditions was $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$, which is similar to what has previously been reported for tropical tree species (Bazzaz and Pickett 1980, Robichaux and Pearcy 1980, Medina and Klinge 1983, Pearcy and Calkin 1983). In contrast to the P_N dependence of I , the leaf conductance to water vapor was not maximal at $0.7 \text{ mmol m}^{-2} \text{ s}^{-1}$, but continued to increase slightly with I . The result was that transpiration rates continually increased with I , while the calculated water use efficiency (ratio of P_N to transpiration) decreased somewhat at I above $0.7 \text{ mmol m}^{-2} \text{ s}^{-1}$.

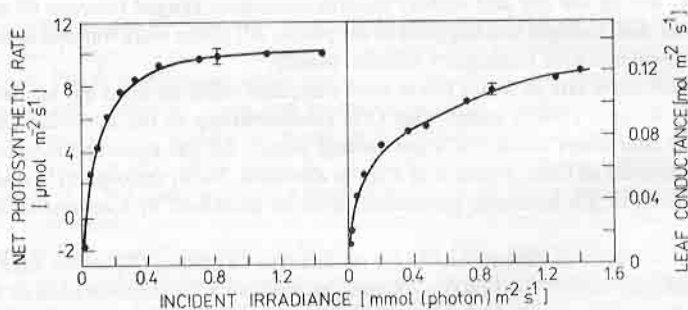


Fig. 1. Responses of net photosynthetic rate and leaf conductance to water vapor in leaves of *Schima superba* to changes in the irradiance. Vertical bar indicates ± 1 standard error about the mean.

P_N was largely independent of temperature between 20 and 30 °C (Fig. 2), with the photosynthetic temperature optimum being between 24 and 27 °C. However, P_N decreased rapidly at leaf temperatures below 20 °C and above 30 °C. Field observations of diurnal leaf temperatures show that leaf temperatures are often 30–34 °C during the growing season (Z. F. Lin, personal communication). This implies that carbon gain under field conditions may be limited by the high temperatures typically observed in the summer.

P_N in *S. superba* leaves was extremely sensitive to changes in the intercellular CO_2 concentration at all CO_2 concentrations below $350 \text{ cm}^3 \text{ m}^{-3}$ (Fig. 3). There was no indication of a transition or break point in the response curve as has been suggested by Caemmerer and Farquhar (1981).

The stomata in *S. superba* leaves were sensitive to changes in Δw (Fig. 4). Over the Δw span of 1.3 to 3.4 mPa Pa^{-1} , leaf conductance to water vapor decreased from 0.125 to 0.045 $\text{mol m}^{-2} \text{ s}^{-1}$. This 64% decrease in leaf conductance resulted in a substantial decrease in the intercellular CO_2 concentration. Since P_N by the leaves was linearly dependent on the intercellular CO_2 levels, the decrease in intercellular CO_2 level resulting from stomatal closure caused P_N to decrease from 10 to 6 $\mu\text{mol m}^{-2} \text{ s}^{-1}$.

Changes in Δw from 1.0 to 2.5 mPa Pa^{-1} over the day during the summer months are common in the monsoonal forests of China where *Schima* occurs (Huang and Fan 1982, Z. F. Lin, unpublished observations). As such, gas exchange activity in *S. superba* leaves is likely to be affected by the lower intercellular CO_2 concentrations imposed by reduced leaf conductances. Recently, Ehleringer *et al.* (1986) measured leaf carbon isotope ratios in this species in several locations, which by differences in canopy development, were thought to differ in Δw . These sites ranged from open, disturbed through closed, mature canopies. Carbon isotopic composition, which is an integrated

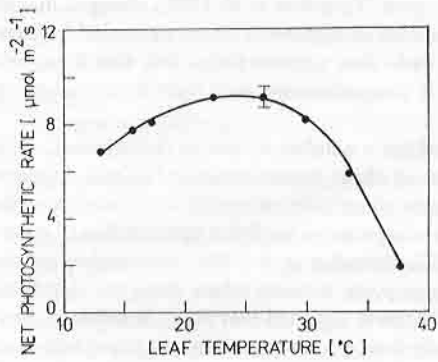


Fig. 2.

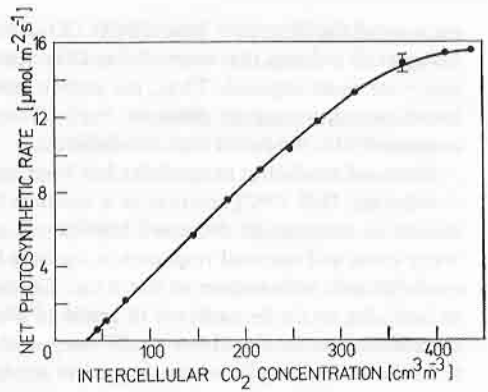


Fig. 3.

Fig. 2. The dependence of net photosynthetic rate of leaf temperature in *Schima superba*. Vertical bar indicates ± 1 standard error about the mean.

Fig. 3. The dependence of net photosynthetic rate on intercellular carbon dioxide concentration in leaves of *Schima superba*. Vertical bar indicates ± 1 standard error about the mean.

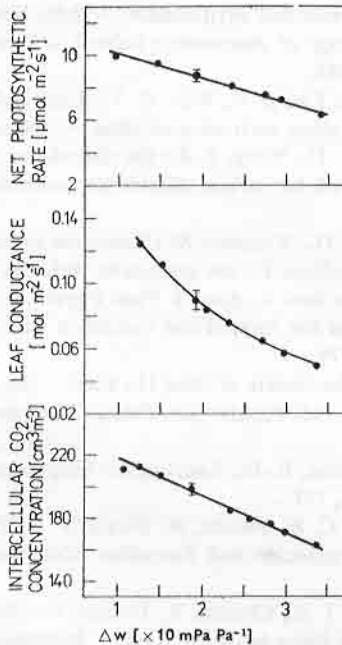


Fig. 4. The responses of net photosynthetic rate, leaf conductance to water vapor and intercellular CO₂ concentration to changes in leaf to air water vapor gradient, Δw . Vertical bar indicates ± 1 standard error about the mean.

measure of the long-term intercellular CO_2 concentration (Farquhar *et al.* 1982), changed in such a way as to indicate that intercellular CO_2 concentrations in *S. superba* leaves decreased in leaves that were more exposed. Thus, the carbon isotope ratio data support the notion that *S. superba* leaves are operating at different intercellular CO_2 concentrations and that these values are correlated with the Δw of the microhabitat.

Stomatal sensitivity to humidity has been reported for a number of species (Lange *et al.* 1971, Schulze and Hall 1982), and may be a common feature in plants from temperate habitats. Stomatal closure in response to decreased humidity is a means of reducing transpiration under potential water stress and stomatal responses to Δw have been interpreted as implying optimization of photosynthetic gain with respect to water use (Cowan 1977, Farquhar *et al.* 1980). Stomatal sensitivity to humidity might be expected in leaves of plants occupying habitats where there are significant diurnal changes in Δw . However, Mooney *et al.* (1983) have reported that *Piper hispidum*, a shrub from the humid tropics where Δw values are typically low, also has stomata which are extremely sensitive to humidity changes. The results from our study demonstrate another tropical species with humidity sensitive stomata, and it may be that this phenomenon is quite common in tropical plants.

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