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BRIEF COMMUNICATION

Photosynthetic water use efficiency in tree crowns of *Shorea beccariana* and *Dryobalanops aromatica* in a tropical rain forest in Sarawak, East Malaysia

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Abstract

Photosynthetic water use efficiency (PWUE), stomatal conductance (g_s), and water potential were measured at two different positions in the tree crown of two emergent tropical tree species (*Shorea beccariana* Burck, *Dryobalanops aromatica* Gaertn. f.). The trees were about 50 m high, in a tropical rain forest in Sarawak, East Malaysia. In both species, g_s at the upper crown position at midday was lower than at the lower crown position, even though both positions were exposed to full sunlight; the difference was greater in *S. beccariana.* Hydraulic limitation occurs in the upper crown position in both species. A midday depression was observed in the photon saturated photosynthetic rate in both species, especially at the upper crown. However, PWUE was markedly higher in the upper crown than the lower crown at midday, even though no morphological adjustment was observed in the leaves; this difference was greater in *S. beccariana.*

Additional key words: Dipterocarpaceae species; hydraulic limitation; leaf area and thickness; nitrogen; saturation irradiance; specific leaf area; stomatal conductance; water potential.

The hydraulic architecture of trees refers to the structure and properties of the water transport system that controls the balance between water supply and transpiring leaf area. Tropical tree species need to maintain a high photosynthetic water use efficiency (PWUE; P_{sat}/g_s), even at high temperatures and under strong sunlight (Mulkey *et al*. 1996). Therefore, hydraulic architecture is a major determinant of tropical canopy photosynthesis, particularly regarding leaf water status and stomatal behaviour (*e.g.* Šesták *et al*. 1985, Tyree and Zimmermann 2002).

The total hydraulic resistance between soil and leaves increases with tree height, which may limit the ability of tall trees to transport water to leaves at the top of tree crowns (Martinez-Vilalta *et al*. 2007). This restriction is known as the hydraulic limitation hypothesis (Ryan and Yoder 1997), and has often been studied focusing on leaf traits, comparing differing size and age with height (*e.g.* Koike *et al.* 2001a,b, McDowell *et al.* 2002, Kenzo

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Abbreviations: g_s – stomatal conductance; P_{sat} – photon-saturated photosynthesis; PPFD – photosynthetic photon flux density; PWUE – photosynthetic water use efficiency; SLA – specific leaf area; Ψ_{xylem} – xylem water potential.

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et al. 2006). This hypothesis also explains why the ratio of leaf area to sapwood area falls (McDowell *et al.* 2002). Because of the larger water deficits and higher temperatures, the effects of hydraulic limitation seem to be much greater for tropical emergent trees than for temperate trees.

To moderate the reduced leaf water potential and to avoid cavitation (Sperry *et al.* 1993, Hubbard *et al.* 1999, Sangsing *et al.* 2004), stomatal conductance (g_s) is reduced. This limits carbon uptake and prevents water loss through transpiration (Hubbard *et al.* 1999, Bond *et al.* 2007), which explains the midday depression in the gas exchange rate (Koike *et al.* 2001a, Grassi *et al.* 2005).

In the canopy surface of tropical trees, the conditions of strong sunlight and high temperature lead to a large vapour pressure deficit. The resultant water stress induces stomatal closure and thus inhibits photosynthetic function (Mulkey *et al.* 1996, Koike *et al.* 2001a, Kenzo *et al.* 2004, 2006). In addition, water stress is usually considered to be greater if the crown position is higher (Tyree and Zimmermann 2002).

We investigated the effect of the height of the crown position on PWUE and whether there is any specific morphological and physiological differentiation in leaves of tropical emergent trees.

The study site was located in the Lambir Hills National Park, Sarawak, Malaysia (4°12'N, 114°00'E). The climate is wet tropical, with weak seasonal changes in rainfall. Annual precipitation is between 2 100 and 3 300 mm (Kenzo *et al.* 2004), and the air temperature at the site is generally 20–35 °C. The site is comprised of a mixed lowland dipterocarp forest growing on low-nutrient sandy or clayey soil (Ashton 1982). We used an 85 m-high canopy crane with a 75 m reach for rapid and repeated sampling of foliage at two different heights from the canopies of two Dipterocarpaceae species. The canopy surface at this site was approximately 50 m above ground level. The two Dipterocarpaceae species that were included in this study are typical dominant species in Malaysian lowland forests (elevation 70–400 m) (Ashton 1982). The studied trees were three *Shorea beccariana* Burck trees (tree heights 51.8, 51.9, and 52.4 m, DBH 94.4, 94.0, and 85.8 cm, height differences between the upper and lower crown parts 9.6, 12.3, and 10.5 m, respectively) and four *Dryobalanops aromatica* Gaertn. f. trees (heights 40.6, 49.7, 47.1, and 50.1 m, DBH 52.3, 74.6, 66.6, and 63.8 cm, height differences 9.0, 10.1, 12.2, and 10.8 m, respectively). *D. aromatica* is a common dominant species on hillsides in this region (Itoh *et al.* 1995). Two exposed positions in the crown of the trees, designated upper and lower, were then selected for the tests (Table 1).

Table 1. Species differences, differences between upper and lower parts of the crown, and diurnal differences in photosynthetic water use efficiency, PWUE [µmol mmol^{-1}], stomatal conductance, g_s [kmol m^{-2} s^{-1}], xylem water potential, Ψ_{xylem} [MPa], specific leaf area, SLA [m^2 kg^{-1}], leaf nitrogen content [g kg^{-1}], leaf area [cm^2], and leaf thickness [mm]. Means±SD. Statistical differences between morning and midday values of PWUE and g_s were significant at $p<0.5$ with the exception of lower PWUE of *Dryobalanops*. At the same p, only midday Ψ_{xylem} differences of upper and lower crowns were significant. No other differences of characteristics within the crown were significantly different.

	Shorea		*Dryobalanops*	
	upper	lower	upper	lower
PWUE morning	40.80±2.16	47.06±3.26	42.60±2.67	49.26±3.53
PWUE midday	57.76±4.84	52.68±2.74	55.61±2.70	50.19±5.19
g_s morning	2.98±0.40	2.65±0.15	2.17±0.12	1.81±0.11
g_s midday	1.12±0.10	1.78±0.07	1.10±0.15	1.52±0.14
Ψ_{xylem} predawn	–0.357±0.063	–0.325±0.082	–0,491±0.057	–0.464±0.074
Ψ_{xylem} midday	–1.331±0.144	–0.958±0.152	–1.109±0.112	–0.701±0.078
SLA	431±44	424±49	589±75	552±54
N content	13.48±1.02	11.67±1.06	11.36±1.42	11.04±1.15
Leaf area	40.18±3.20	41.80±3.80	6.16±0.40	6.32±0.50
Leaf thickness	0.457±0.050	0.452±0.050	0.303±0.020	0.299±0.020

Diurnal changes in photon-saturated photosynthesis (P_{sat}) and g_s per unit leaf area, at ambient CO_2 (*ca.* 360 g m^{-3}), were measured at the two crown positions exposed to full sunlight (photosynthetic photon flux density, PPFD, of about 2 800–3 000 µmol m^{-2} s^{-1}). The predawn and midday water potentials were recorded after measurement of P_{sat} and g_s. To obtain light photosynthesis curves, we used an *LI-6400* open system infrared gas analyzer (*LiCor*, Lincoln, NE, USA). To determine P_{sat} and g_s we used an *ADC-H4a* open system infrared gas analyzer (*Analytical Development Co.*, Hoddesdon, UK). The irradiance-photosynthesis curves were obtained using the equation of Boote and Loomis (1991). The compensation irradiance (I_c) was calculated according to the formula of Kitaoka and Koike (2004). Diurnal changes in P_{sat} and g_s were measured under saturating PPFD (>1 500 µmol m^{-2}). Relative humidity and CO_2 concentration in the analyzer chamber were maintained at close to ambient conditions (relative humidity at about 60 %, CO_2 at 360 g m^{-3}) by using the automated control for the *LI-6400* system. PWUE (P_{sat}/g_s) was calculated from these values.

To estimate the water potential of the leaves, we measured the xylem pressure potential of the shoot tips (referred below as the xylem water potential, Ψ_{xylem}) using a pressure chamber (*PMS-600*, *PMS Instrument Co.*, Oregon, USA). To assess tolerance to drought, we also determined the specific leaf area (SLA). After measurement of P_{sat} and g_s, the leaves were cut and placed immediately in a cool chest in our laboratory. The leaf thickness was determined using a micrometer (*Mitsutoyo*, Tokyo, Japan). The leaf area (determined using an *LI-300*, *Li-Cor*, Lincoln, NE, USA) and leaf dry mass were measured to calculate the SLA; the leaf dry mass was obtained after drying for 2 d at 60 °C. The leaf N content was measured with a portable nitrogen detector (*Agriexpert PPW-3000*, *Satake*, Hiroshima, Japan) calibrated with a NC analyzer (*NC-900*, *Shimadzu*, Kyoto, Japan) (Ichie *et al.* 2002, Eguchi *et al.* 2006).

All data were tested for significance by one-way analysis of variance (ANOVA), using a *StatView* statistical software (version *5.0*; *SAS Institute*, NC, USA). Data collected from leaves from different trees of the same species were represented as separate data points.

There was no difference in the pattern of P_{sat} dependence on PPFD between the upper and lower crown positions of either *S. beccariana* or *D. aromatica* (Fig. 1). The initial gradient of the irradiance curves was less for *S. beccariana* than for *D. aromatica* at both crown levels. P_{sat} was 14.5 µmol m^{-2} s^{-1} for *S. beccariana* and 10.0 µmol m^{-2} s^{-1} for *D. aromatica*, and the corresponding saturation irradiances were around 1 500 and 600 µmol m^{-2} s^{-1}, respectively. The compensation irradiance (I_c) of leaves at the two crown levels was higher (about 40 µmol m^{-2} s^{-1}) in *S. beccariana* than in *D. aromatica* (about 35 µmol m^{-2} s^{-1}). In *S. beccariana*, the I_c at the lower crown position was lower than at the higher crown position, while no difference was observed in *D. aromatica*.

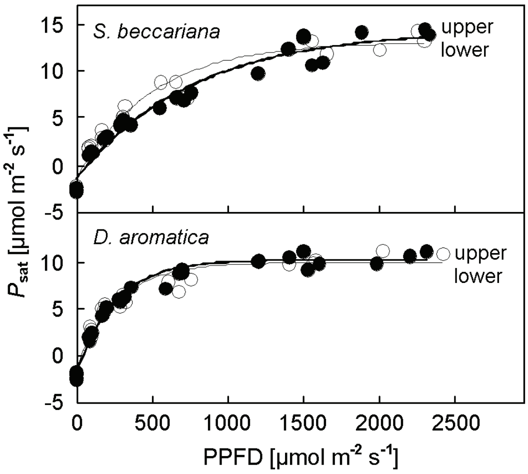

Fig. 1. Net photosynthetic rate (P_N) of two Dipterocarpaceae species in relation to irradiance. Curves were fitted using the asymptotic equation of Boote and Loomis (1993).

The mean PWUE at the upper crown level in both species was larger at midday than in the morning (Table 1). The difference in g_s between the upper and lower crown positions was larger in *S. beccariana* than in *D. aromatica*. The mean variation of g_s in *S. beccariana* and *D. aromatica* between morning and midday was 1.86 and 1.07 kmol m^{-2} s^{-1} in the upper position, and 0.87 and 0.29 kmol m^{-2} s^{-1} in the lower position, respectively.

Table 1 shows also the relation between Ψ_{xylem} at predawn and midday and at the different crown heights for the two species. Ψ_{xylem} at midday differed significantly between leaves in the different crown positions, whereas before dawn, Ψ_{xylem} values for the upper and lower crown positions were similar. For *D. aromatica* the predawn Ψ_{xylem} was –0.491±0.057 MPa for the upper crown and –0.464±0.074 MPa for the lower crown, while the predawn Ψ_{xylem} of *S. beccariana* was –0.357±0.063 MPa for the upper position and –0.325±0.082 MPa in the lower one. In contrast, the midday values of Ψ_{xylem} for *D. aromatica* were –1.109±0.112 MPa for the upper position and –0.701±0.078 MPa for the lower one. Midday values of Ψ_{xylem} for *S. beccariana* showed the similar decrease to *D. aromatica*, especially at the upper position. The variation between predawn and midday Ψ_{xylem} in the upper crown position was 0.974 MPa for *S. beccariana* and 0.618 MPa for *D. aromatica*.

Neither species showed any significant difference in SLA or N content between the upper and lower positions (Table 1). Although *D. aromatica* upper crown leaves showed a slightly larger mean leaf thickness than the lower leaves, there was no statistically significant difference in leaf area or thickness between the crown positions in either species. The individual leaf area and leaf thickness of *S. beccariana* was larger than that of *D. aromatica* ($p<0.05$).

Similar PWUE values were found in both crown positions for both species (Table 1), which was not expected because of the very high temperature and strong PPFD in the region. However, based on the morning PWUE values, the lower crown position generates more photosynthetic production than the upper crown position in the severest conditions. PWUE of light demanding species is usually high (Larcher 2004). The PWUE at midday tended to be larger at the higher crown position in each species, although *S. beccariana* has light demanding characteristics (Koike *et al.* 2001a).

In tropical emergent trees, leaf water status is a major factor in the regulation of stomatal closure in response to reductions in Ψ_{xylem} caused by strong PPFD (Larcher 2004). The value of Ψ_{xylem} was greatest before dawn in both crown levels and for both species. However, once strong sunlight reached the crown, Ψ_{xylem} in the upper crown of both species fell faster than that of the lower crown. This is due to the increase in PPFD, temperature, and VPD toward midday. Following the drop in Ψ_{xylem}, g_s also fell, especially in the upper crown position. These changes suggest that water potential declines more steeply with tree height at midday because of both frictional and hydrostatic components of water transport. An increase in stomatal limitation of gas exchange has previously been associated with tree height (*e.g.* Martinez-Vilalta *et al*. 2007).

In both studied species, reduction of water stress to maintain adequate stomatal opening was achieved by reducing g_s with increasing tree height. This tendency was clearer in *D. aromatica*, noted for its desiccation resistant characteristics (Itoh *et al.* 1995), than in *S. beccariana*.

The irradiance curve shows that *S. beccariana* has more effective photon energy utilization than *D. aromatica* (Fig. 1). Moreover, *S. beccariana* has a smaller number of leaves in the crown (data not shown), which suggests there is no differentiation between sun and shade crowns (Koike *et al.* 2001a). However, in spite of the irradiance demanding characteristics of *S. beccariana* and its high $P_{sat,}$ its PWUE was lower than that of *D. aromatica* (Table 1).

Reduced stomatal sensitivity in tall trees enables a more stable carbon uptake over the wide diurnal range of PPFD experienced (*e.g.* Šesták *et al.* 1985). This also leads to a high PWUE value. As a result of the midday increase in transpiration in the lower crown, stomatal closure occurs, preventing water loss from the upper part of various emergent species (Maruyama *et al.* 1996, Hiromi *et al.* 1999). Our data revealed that tropical emergent trees can avoid these water deficits and achieve high PWUE (Table 1).

No morphological differences in SLA or leaf thickness at the two crown positions were observed in either species. SLA is strongly correlated with leaf thickness in deciduous broad-leaved trees (Šesták *et al.* 1985, Koike *et al.* 2001a,b), with high desiccation tolerance, and also with density and leaf gas exchange (*e.g.* Niinemets *et al.* 2004). However, SLA of the two species was lower than that found in mature trees in a temperate forest (Kitahashi *et al.* 2001, Koike *et al.* 2001b). The high PWUE of the two species may be realized through a high capacity for regulation of stomata.

The leaf N content varied only slightly over the entire crown surface at our study site, and no other leaf characteristics varied with crown position (Table 1). Although there are some physiological differences between sun and shade crowns of *D. aromatica* (Koike *et al.* 2001a), the photosynthetic rate was independent of crown position. Thus the photosynthetic function of tropical emergent trees is regulated by water deficit and stomatal closure occurs in response to strong sunlight. However, no corresponding foliage features were found between the upper and lower positions in the crown (Fig. 1, Table 1).

We conclude that tropical emergent trees can adjust their water relations in line with the prevailing environment by coordinating changes in PWUE and hydraulic capacity, through regulation of g_s. In particular, the strong sunlight in tropical regions clearly affects the degree of water stress in different crown positions and at different heights of trees.

References

Ashton, P.S.: Dipterocarpaceae. – Flora Malesiana, Ser. 1, **9**: 237-552, 1982.

Bond, B.J., Czarnomski, N.M., Cooper, C., Day, M.E., Greenwood, M.S.: Developmental decline in height growth in Douglas-fir. – Tree Physiol. **27**: 441-453, 2007.

Boote, K.J., Loomis, R.S.: The prediction of canopy assimilation. – In: Boote, K.J., Loomis, R.S. (ed.): Modeling Crop Photosynthesis. From Biochemistry to Canopy. Pp. 109-140. American Society of Agronomy and Crop Science Society of America, Wisconsin 1991.

Eguchi, N., Ichie, T., Ji, D.H., Karatsu, T., Koike, T.: Accurate estimation of nitrogen concentration in deciduous tree leaves in a field study using a portable non-destructive nitrogen detector. – J. Plant Physiol. **163**: 680-683, 2006.

Grassi, G., Vicinelli, E., Ponti, F., Cantoni, L., Magnani, F.: Seasonal and interannual variability of photosynthetic capacity in relation to leaf nitrogen in a deciduous forest plantation in northern Italy. – Tree Physiol. **25**: 349-360, 2005.

Hiromi, T., Ninomiya, I., Koike, T., Ogino, K.: [Regulation of transpiration by patchy stomatal opening in canopy tree species of Dipterocarpaceae in tropical rainforest, Sarawak, Malaysia.] – Jap. J. Ecol. **49**: 83-90, 1999. [In Jap.]

Hubbard, R.M., Bond, B.J., Ryan, M.G.: Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. – Tree Physiol. **19**: 165-172, 1999.

Ichie, T., Kitahashi, Y., Matsuki, S., Maruyama, Y., Koike, T.: The use of a portable non-destructive type nitrogen meter for leaves of woody plants in field studies. – Photosynthetica **40**: 289-292, 2002.

Itoh, A., Yamakura, T., Ogino, K., Lee, H.S., Ashton, P.S.: Population structure and canopy dominance of two emergent Dipterocarp species in a tropical rain forest of Sarawak, East Malaysia. – Tropics **4**: 133-141, 1995.

Kenzo, T., Ichie, T., Watanabe, Y., Yoneda, R., Ninomiya, I., Koike, T.: Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest. – Tree Physiol. **26**: 865-873, 2006.

Kenzo, T., Ichie, T., Yoneda, R., Kitahashi, Y., Watanabe, Y., Ninomiya, I., Koike, T.: Interspecific variation of photosynthesis and leaf characteristics in canopy trees of five species of Dipterocarpaceae in a tropical rain forest. – Tree Physiol. **24**: 1187-1192, 2004.

Kitahashi, Y., Maruyama, Y., Ichie, T., Koike, T.: Water utilization of broad-leaved trees varies at different height of the same sunny crown. – Proceedings of the VIII INTECOL, Seoul 2001.

Kitaoka, S., Koike, T.: Invasion of broadleaf tree species into a larch plantation: Seasonal light environment, photosynthesis, and nitrogen allocation. – Physiol. Plant. **121**: 604-611, 2004.

Koike, T., Kitahashi, Y., Nakagawa, M., Nakashizuka, T.: Mid-day depression of photosynthetic rate in canopy trees native to Tropical Rain Forest in the Lambir Hills National Park, Sarawak, Malaysia. – Proceedings of Canopy Biology in Tropical Rain Forests. Pp. 51-56. Sarawak 2001a.

Koike, T., Kitao, M., Maruyama, Y., Mori, S., Lei, T.T.: Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile. – Tree Physiol. **21**: 951-958, 2001b.

Larcher, W.: Physiological Plant Ecology. 4th Ed. – Springer-Verlag, Heidelberg – Berlin – Tokyo 2004.

Martinez-Vilalta, J., Vanderklein, D., Mencuccini, M.: Tree height and age-related decline in growth in Scots pine. – Oecologia **150**: 529-544, 2007.

Maruyama, Y., Matsumoto, Y., Morikawa, Y.: [Water relations and morphology of *Cryptomeria japonica* leaves vary with crown position.] – J. jap. Forest Soc. **78**: 427-432, 1996. [In Jap.]

McDowell, N.G., Phillips, N., Lunch, C., Bond, B.J., Ryan, M.G.: An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. – Tree Physiol. **22**: 763-774, 2002.

Mulkey, S.S., Kitajima, K., Wright, S.J.: Plant physiological ecology of tropical rainforest canopies. – Trends Ecol. Evol. **11**: 408-412, 1996.

Niinemets, Ü., Sonninen, E., Tobias, M.: Canopy gradients in leaf intercellular CO_2 mole fractions revisited: interactions between leaf irradiance and water stress need consideration. – Plant Cell Environ. **27**: 569-583, 2004.

Ryan, M.G., Yoder, B.J.: Hydraulic limits to tree height and tree growth. – BioSciences **47**: 235-242, 1997.

Sangsing, K., Kasemsap, P., Thanisawanyangkura, S., Sangkhasila, K., Gohet, E., Thaler, P., Cochard, H.: Xylem embolism and stomatal regulation in two rubber clones. – Trees **18**: 109-114, 2004.

Šesták, Z., Tichá, I., Čatský, J., Solárová, J., Pospíšilová, J., Hodáňová, D.: Integration of photosynthetic characteristics during leaf development. – *In*: Šesták, Z. (ed.): Photosynthesis During Leaf Development. Pp. 263-286. Academia, Praha; Dr W. Junk, Dordrecht – Boston – Lancaster 1985.

Sperry, J.S., Alder, N.N., Eastlack, S.E.: The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. – J. exp. Bot. **44**: 1075-1082, 1993.

Tyree, M.T., Zimmermann, M.H.: Xylem Structure and the Ascent of Sap. – Springer-Verlag, Berlin 2002.