PHOTOSYNTHETICA 45 (2): 189-193, 2007

Midday depression of photosynthesis in *Enkleia malaccensis*, a woody climber in a tropical rainforest

A.C. TAY[*], A.M. ABDULLAH[**], M. AWANG[**], and A. FURUKAWA[***]

Graduate School of Humanities and Sciences, Nara Women's University, Kitauoya-Nishimachi, Nara 630-8506, Japan[*]
Faculty of Environmental Studies, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor Darul Ehsan, Malaysia[**]
Kyousei Science Center for Life and Nature, Nara Women's University, Kitauoya-Nishimachi, Nara 630-8506, Japan[***]

Abstract

We measured the diurnal changes in net photosynthetic rate (P_N) and stomatal conductance (g_s) of the leaves of a liana, *Enkleia malaccensis* Griff. (Thymelaeaceae), at the canopy level in the lowland tropical rainforest at Pasoh, Peninsular Malaysia. The measurements were made from a canopy walkway system, 30 m from the ground for 3 d in March 2003. P_N increased with increasing photosynthetically active radiation (PAR) before noon, though P_N was not enhanced by the strong radiation hit in the afternoon. Plotting g_s at saturating PAR (>0.5 mmol m^{-2} s^{-1}) against the vapour pressure deficit (VPD) failed to reveal a significant correlation between VPD and g_s, and g_s became very low at VPD >2.5 kPa. The relationship between P_N and g_s was fitted on the same regression line irrespective of measuring day, indicating that this relationship was not influenced by either VPD or leaf temperature (T_L). Therefore, in the liana *E. malaccensis,* an increase in VPD leads to partial stomatal closure and, subsequently, reductions in P_N and the midday depression of P_N of this plant.

Additional key words: irradiance; leaf temperature; stomatal conductance; tropical liana; vapour pressure deficit; water potential.

Introduction

As a typical tropical rainforest in Malaysia, the Pasoh Forest Reserve is rich in productivity and biodiversity (Kochummen 1997). A total of 814 woody species representing 294 genera and 78 families were recorded during a census of tree species in a 50-ha permanent research plot in the forest (Manokaran and LaFrankie 1990). Lianas (woody vines) climbing self-standing trees are a prominent feature of forest dynamics. More than ten different liana species could easily be identified by naked eye from the canopy walkway system at the Pasoh Forest Reserve. Because of their abundance, lianas can suppress tree regeneration and increase tree mortality, in addition to providing a food source and linking access between canopies for arboreal animals (Schnitzer and Bongers 2002). The biomass of lianas in tropical forest was estimated as 10 t per ha or *ca*. 2 % of the total forest biomass (Kato *et al.* 1978). However, climbing plants grow vigorously and enhance tree turnover, leading to enrichment of environmental CO_2, and thus potentially reducing the forest carbon stock in the long run (Granados and Körner 2002).

The eco-physiological study of lianas has only recently garnered attention, although these plants are abundant in forest communities, especially in tropical rainforests (Hegarty and Caballé 1991). During recent years, many emergent trees in the Pasoh Forest Reserve have been damaged by strong wind, and this damage has been exacerbated by insufficient forest management as well as nearby forest-clearing activities for developing oil palm plantations. The high fecundity of lianas disturbs forest recovery and regeneration because of their physical interference and competition for nutrient and radiant energy. Studying the photosynthetic performance of lianas, including their net photosynthetic rate (P_N) and stomatal conductance (g_s), is essential to achieve a sustainable forest management strategy. Therefore, we measured the photosynthetically active radiation (PAR), leaf temperature (T_L), P_N, g_s, and vapour pressure deficit (VPD) of *Enkleia malaccensis* for 3 d at the canopy level for establishing diurnal patterns of gas exchange in this tropical liana.

Received 14 October 2005, *accepted* 20 September 2006.
Fax: +81-742203989, e-mail: tayaichen@yahoo.com

Materials and methods

The study site was located at Pasoh Forest Reserve in the Negeri Sembilan State, Peninsular Malaysia (lat. 2˚5′N, long. 102˚18′E, 106 m a.s.l.) (Manokaran and LaFrankie 1990). The forest is categorized as a lowland tropical forest dominated by species of Dipterocarpaceae. In 1992, a canopy walkway system was created in this reserve and includes three towers, two of which are 30 m high and one 52 m high. Three 20-m walkways span between the towers at 30 m high. Measurements of P_N and g_s of a liana, *Enkleia malaccensis* Griff. (Thymelaeaceae), were made using this walkway system. The plant sampled had climbed to the top of a canopy tree, *Elateriospermum tapos* (Euphorbiaceae), by twining.

P_N and g_s in leaves of *E. malaccensis* at 30 m in height from the ground were measured on 19, 20, and 21 March 2003. CO_2 and water vapour concentrations at the inlet and the outlet of the cuvette were measured with a portable photosynthesis system (*LI-6400*, *Li-Cor*, Lincoln, NE, USA). The leaf was clamped inside leaf chamber of the portable photosynthesis system with the upper leaf surface inside the chamber fully exposed to direct sunlight. PAR was measured using a gallium arsenide sensor installed inside the chamber. This sensor was calibrated against a quantum sensor (*LI-190SB*, *Li-Cor*). The parameters P_N, g_s, and VPD were calculated using the method of Ball (1987), and the saturation vapour pressure was calculated using Richard’s equation (Field *et al.* 1989). Measurements were performed from 08:00 to 19:00 local time by inserting part of a leaf into a cuvette. The cuvette temperature was controlled using Peltier thermoelectric cooler installed to the portable photosynthesis system to follow the ambient temperature.

Water potential (Ψ) was estimated using a psychrometric method (*Tru Psi*, *Decagon Devices*, Pullman, WA, USA). A selected leaflet was cut into a strip (*ca.* 12 mm wide and 45 mm long) and enclosed within a sample cup, which was sealed with a vinyl cap. Collected samples were brought back to the laboratory and were put into a sample changer and Ψ was read.

Results

The pattern of diurnal changes of PAR was influenced by weather conditions of the measuring day (Fig. 1). Fluctuation of PAR is observed frequently in this humid tropical area. On 19 March, PAR of 1.0 mmol m^{-2} s^{-1} or greater was attained during both the morning and afternoon, although the duration of this activity was brief during the afternoon. In contrast, on 21 March, PAR greater than 1.0 mmol m^{-2} s^{-1} was observed only in late afternoon. Under these radiation conditions, however, the diurnal changes in VPD were not markedly different between these two measuring days. On 20 March, the weather was cloudy, and VPD was always lower than 2.5 kPa during the daytime.

To determine the effects of vine length and the altitude of target leaves, we measured the predawn Ψ. These values did not differ between the measuring days and were –0.57±0.02 and –0.60±0.01 MPa (n = 3) on 20 and 21 March, respectively.

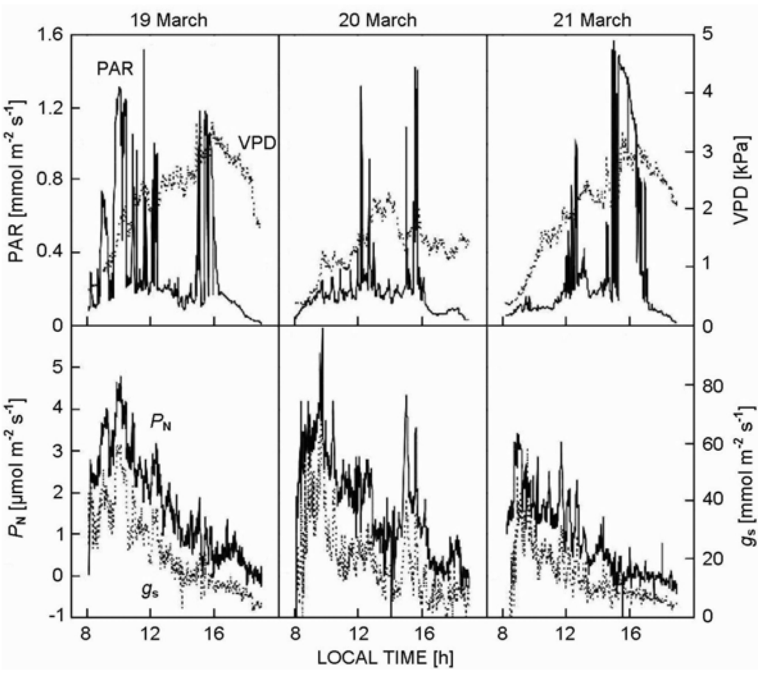

Fig. 1. Diurnal courses of net photosynthetic rate (P_N) and stomatal conductance (g_s) in *Enkleia malaccensis*. The microclimatic parameters, photosynthetically active radiation (PAR) and vapour pressure deficit (VPD), are also shown. Measurements were made in the field on the date shown in each subfigure.

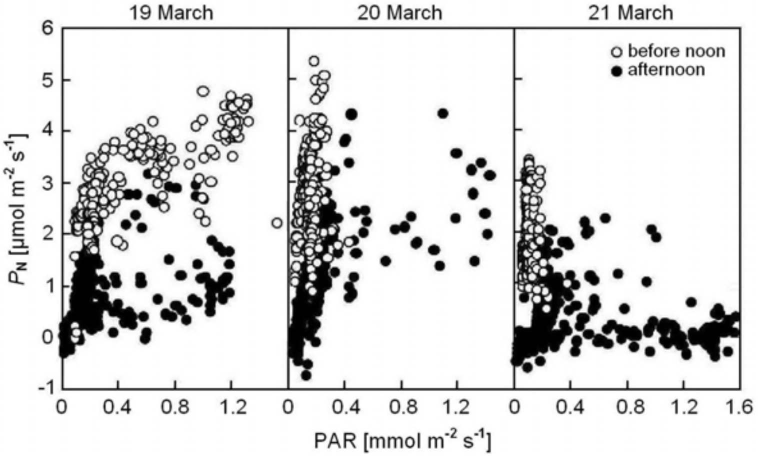

Fig. 2. Net photosynthetic rate (P_N) as a function of photosynthetically active radiation (PAR) in *Enkleia malaccensis* for three days.

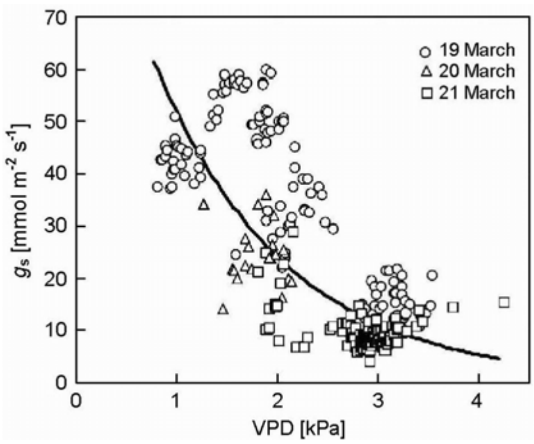

Fig. 3. The relationship between vapour pressure deficit (VPD) and stomatal conductance (g_s) in *Enkleia malaccensis* for three days.

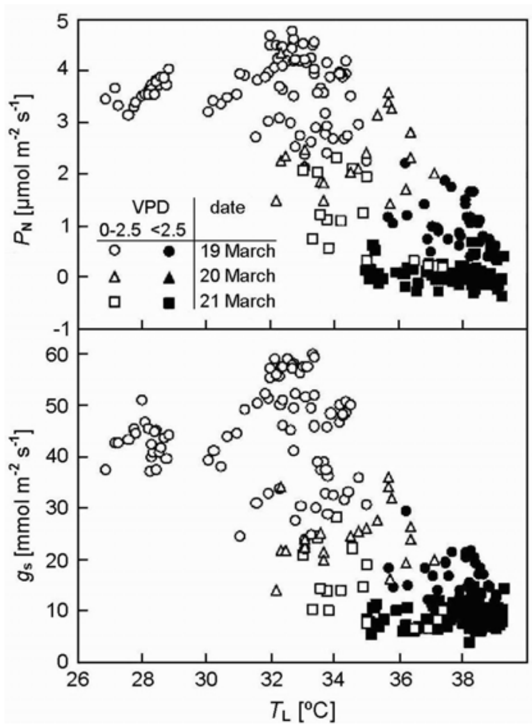

Fig. 4. Net photosynthetic rate (P_N) and stomatal conductance (g_s) as a function of leaf temperature (T_L) in *Enkleia malaccensis* for three days.

In general, PAR is the environmental factor with the most influence on photosynthesis and stomatal aperture in the field. Thus it is easy to expect that the diurnal changes of P_N and g_s will follow the changes in PAR. However, in the liana measured, the trend of diurnal changes in P_N and g_s was different from that of PAR (Fig. 1). Both P_N and g_s exhibited a similar trend over time, with decreasing rates. Midday depression of P_N and g_s occurred with no remarkable recovery, except on 20 March. P_N and g_s fluctuated throughout the day, with the highest peaks in the morning regardless of PAR variations. Before noon on 19 March, PAR increased rapidly and accelerated P_N, but the incident PAR detected that afternoon did not enhance P_N at that time. A sudden increase in PAR exceeding 1.0 mmol m^{-2} s^{-1} in the afternoon of 20 March resulted in dramatic increases in P_N and g_s, which were accompanied by spikes in these values.

To clarify the relationship between PAR and P_N, P_N was plotted against PAR by using data shown in Fig. 1 (Fig. 2). On all three days, the P_N measured in the afternoon was lower than that measured before noon at higher PAR. A dramatic decline of P_N in the afternoon was detected on 21 March, *i.e.* P_N in the afternoon of this day became negative when PAR was higher than the saturating PAR. In contrast, on 20 March, a cloudy day, P_N in the afternoon was compatible with P_N detected at higher PAR (>1.2 mmol m^{-2} s^{-1}) in the morning.

To detect the effects of environmental factors other than PAR on diurnal changes in P_N, g_s, a factor that controls the diffusion of CO_2 into intercellular air spaces, was plotted against VPD at saturating PAR (>0.5 mmol m^{-2} s^{-1}) (Fig. 3). Although the data were scattered, there was a clear tendency for g_s to decrease with increasing VPD. Most VPDs were higher than 2.0 kPa and g_s values

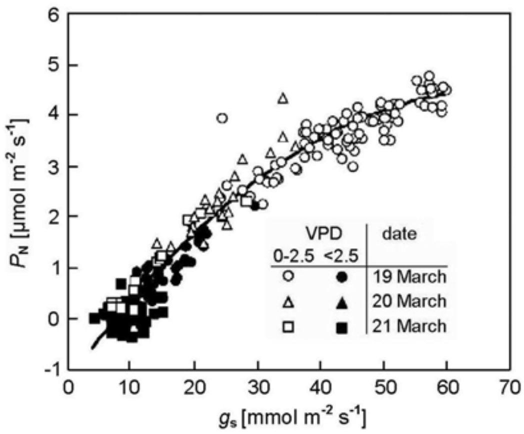

Fig. 5. The relationship between stomatal conductance (g_s) and net photosynthetic rate (P_N) in *Enkleia malaccensis* for three days.

were lower than 2.0 mmol m^{-2} s^{-1} at saturating PAR on 21 March, whereas on other two days, VPDs fluctuated from 0.8 to 3.6 kPa and g_s decreased with increasing VPD. The relationship between VPD and g_s then was calculated using the entire data set shown in Fig. 3:

$$g_s = 113\ e^{(-0.768\ VPD)}\ (r = 0.734) \quad (1)$$

This equation indicated that the midday depression of g_s in *E. malaccensis* was mainly due to VPD.

In addition to VPD, leaf temperature (T_L) is another influential environmental factor contributing to midday depression of P_N and g_s. Therefore P_N and g_s at saturating PAR were plotted against T_L (Fig. 4). P_N and g_s were optimized at T_L of 32–34 ºC. The decline in P_N or g_s at higher T_L was caused by increases in both T_L and VPD. When T_L exceeded 35 ºC, VPD became higher than 2.5 kPa and accelerated the decline of P_N and g_s.

Irrespective of VPD, the relationship between P_N and g_s was curvilinear for all measurement days (Fig. 5). During any one day of measurement, P_N and g_s correlated. The relationship between these two parameters was influenced neither by VPD nor by the measurement day. Therefore this relationship can be described by the following equation:

$$P_N = -1.27 + 0.17\ g_s - 0.0012\ g_s^2\ (r = 0.979) \quad (2)$$

Judging from the figure, a hyperbolic formula should be fitted, but no adequate equation could be obtained (insignificant correlation coefficient).

Discussion

The liana *E. malaccensis* showed a pronounced midday depression in P_N and g_s under tropical humid conditions. On a cloudy day, VPD was always lower than 2.5 kPa, and P_N was accelerated by the short duration of sunlight during the afternoon. However, when strong irradiation (PAR >1.5 mmol m^{-2} s^{-1}) occurred before noon, acceleration of neither P_N nor g_s could be detected in the afternoon.

A number of possible causes have been proposed for the midday depression in P_N and include an increase in VPD inducing the stomatal closure (Brodribb and Holbrook 2004), high temperature enhancing the photorespiration rate (Muraoka *et al.* 2000), and accumulation of high concentrations of sugars and subsequent inhibition of the photosynthetic apparatus (Sawada *et al.* 1986). However, for lianas, other factors may contribute to midday depression of P_N. According to Boyer (1974), among the resistances to the transfer of water from roots to leaves, that caused by stem was lower than those caused by other organs. Furthermore, the xylem of vines is bigger and wider than those of self-standing plants (Ewers *et al.* 1991). This characteristic of vines may reduce the resistance to the transport of water from roots to leaves, although the large diameter of xylem cells can easily lead to cavitation. If the midday decline of P_N or g_s was induced by embolism in *E. malaccensis*, no recovery would be observed. However, P_N or g_s or both recovered during the morning of the following day. Therefore, embolism might not be induced in this liana under the weather conditions during the study.

According to the CO_2 compensation concentration of *E. malaccensis* (64 μmol mol^{-1} at 35 ºC of leaf temperature, unpublished data), this liana is categorized as C_3 plant. When direct sunlight hit the leaf, leaf temperature exceeded 35 ºC, thus exceeding the reported optimal temperature for P_N in C_3 plants (Berry and Björkman 1980), although the optimal leaf temperature for P_N of this liana in the field was between 32 and 33 ºC.

Midday depression without remarkable recovery suggests that the extensive xylem of lianas reduces the resistance associated with the transport of water from roots to leaves, and easily causes cavitation leading to embolism (Herzog *et al.* 1995, Zweifel *et al.* 2000). The curvilinear relationship between P_N and g_s reveals that the increase in P_N gradually slows with increasing g_s, but it is equivocal whether changes in g_s cause or result from changes in P_N (Ishida *et al.* 1999, Roumet *et al.* 2000).

Prolonged depression of P_N and g_s in *E. malaccensis* was attributed to its long twining stem and extensive xylem. In the afternoon, marked increase of VPD due to high T_L in this liana stimulated stomatal closure with subsequent decreases in P_N and g_s regardless of high PAR. In light of these observations and considerations, the depression of P_N appears to be induced by the decline of g_s caused by the increase in VPD. Furthermore, the close correlation between depression of g_s and P_N in our study suggests dysfunction of the xylem; in other words, a shortage of water supply from the root system to leaves causes the midday depression (Brodribb and Holbrook 2004). Because of the long and twining stem and high altitude of the leaves measured in the present study, the predawn water potential was low (–0.59 MPa; the average value of 2-d measurement) and resulted in water shortage in the leaves. Thus the midday depression of P_N in *E. malaccensis* seems mainly due to increased VPD, which enhances water loss from leaves and causes stomatal closure, and not to high leaf temperature, which typically increases the photorespiration rate or influences the photosynthetic light-harvesting systems.

References

Ball, J.T.: Calculations related to gas exchange. – In: Zeiger, E., Farquhar, G.D., Cowan, I.R. (ed.): Stomatal Function. Pp. 445-476. Stanford University Press, Stanford 1987.

Berry, J., Björkman, O.: Photosynthetic response and adaptation to temperature in higher plants. – Annu. Rev. Plant Physiol. **31**: 491-543, 1980.

Boyer, J.S.: Water transport in plants: mechanism of apparent changes in resistance during absorption. – Planta **117**: 187-207, 1974.

Brodribb, T.J., Holbrook, N.M.: Diurnal depression of leaf hydraulic conductance in a tropical tree species. – Plant Cell Environ. **27**: 820-827, 2004.

Ewers, F.W., Fisher, J.B., Fichtner, K.: Water flux and xylem structure in vines. – In: Putz, F.E., Mooney, H.A. (ed.): The Biology of Vines. Pp. 127-160. Cambridge University Press, Cambridge 1991.

Field, C.B., Ball, J.T., Berry, J.A.: Photosynthesis: principles and field techniques. – In: Pearcy, R.W., Ehleringer, J., Mooney, H.A., Rundel, P.W. (ed.): Plant Physiological Ecology: Field Methods and Instrumentation. Pp. 209-253. Chapman and Hall, London 1989.

Granados, J., Körner, C.: In deep shade, elevated CO_2 increased the vigor of tropical climbing plants. – Global Change Biol. **8**: 1109-1117, 2002.

Hegarty, E.E., Caballé, G.: Distribution and abundance of vines in forest communities. – In: Putz, F.E., Mooney, H.A. (ed.): The Biology of Vines. Pp. 313-335. Cambridge Univ. Press, Cambridge 1991.

Herzog, K.M., Häsler, R., Thum, R.: Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. – Trees **10**: 94-101, 1995.

Ishida, A., Toma, T., Marjenah: Limitation of leaf carbon gain by stomatal and photochemical processes in the top canopy of *Macaranga conifera*, a tropical pioneer tree. – Tree Physiol. **19**: 467-473, 1999.

Kato, R., Tadaki, Y., Ogawa, H.: Plant biomass and growth increment studies in Pasoh forest. – Malayan Nature J. **30**: 211-224, 1978.

Kochummen, K.M.: Tree Flora of Pasoh Forest. – Forest Research Institute Malaysia, Kuala Lumpur 1997.

Manokaran, N., LaFrankie, J.V.: Stand structure in Pasoh Forest Reserve, a lowland rain forest in peninsular Malaysia. – J. trop. Forest Sci. **3**: 14-24, 1990.

Muraoka, H., Tang, Y., Terashima, I., Koizumi, H., Washitani, I.: Contributions of diffusional limitation, photoinhibition and photorespiration to midday depression of photosynthesis in *Arisaema heterophyllum* in the natural high light. – Plant Cell Environ. **23**: 235-250, 2000.

Roumet, C., Garnier, E., Suzor, H., Salager, J.-L., Roy, J.: Short and long-term responses of whole-plant gas exchange to elevated CO_2 in four herbaceous species. – Environ. exp. Bot. **43**: 155-169, 2000.

Sawada, S., Hayakawa, T., Fukushi, K., Kasai, M.: Influence of carbohydrates on photosynthesis in single, rooted soybean leaves used as a source-sink model. – Plant Cell Physiol. **27**: 591-600, 1986.

Schnitzer, S.A., Bongers, F.: The ecology of lianas and their role in forests. – Trends Ecol. Evol. **17**: 223-230, 2002.

Zweifel, R., Item, H., Häsler, R.: Stem radius changes and their relation to stored water in stems of young Norway spruce trees. – Trees **15**: 50-57, 2000.