PHOTOSYNTHETICA 46 (4): 557-566, 2008

Photosynthetic response of two tropical liana species grown under different irradiances

M.C. SANCHES* and I.F.M. VÁLIO

Instituto de Biologia, Departamento de Fisiologia Vegetal, Universidade Estadual de Campinas, CP 6109,
CEP 130083-970, Campinas, São Paulo, Brazil

Abstract

We investigated the characteristics of gaseous exchanges and chlorophyll *a* fluorescence under different irradiances in two liana species *Canavalia parviflora* Benth. (Fabaceae) and *Gouania virgata* Reissk (Rhamnaceae), both of a semi-deciduous tropical forest of Southeast Brazil. We used cultivated plants growing under irradiances of 100, 40, 10, and 1.5 % of the photosynthetic photon flux density (PPFD). Higher net photosynthetic rates (P_N) were observed during early morning under full sunlight. After this, reduced P_N values were recorded due to pronounced stomatal closure. In *Canavalia*, the gas exchange responses diminished concomitant with reduced irradiance. *Gouania* exhibited a narrower range of response, with high P_N values even at 10 % PPFD. Marked reduction of the effective photochemical yield ($\Delta F/F_m$') near midday was observed, followed by increases in the non-photochemical quenching for both species under full sunlight. Despite the common occurrence of these species in open areas of the forest, both were able to maintain relatively high P_N in shaded environments. We suggest that lianas present an intermediate physiological behaviour between shade and non-shade tolerant species.

Additional key words: acclimation to irradiance; *Canavalia parviflora*; chlorophyll fluorescence; *Gouania virgata*; liana; non-photochemical quenching; semi-deciduous tropical forest; stomatal conductance; transpiration rate; water use efficiency.

Introduction

Lianas (woody climbers) are conspicuous species in tropical forests. They are rooted in the soil and use other plants to ascend up to the canopy (Gerwing 2004). Once the lianas begin to grow on the forest floor they experience both extremes in terms of radiation quantity and spectral quality (Lee and Richards 1991). In tropical forests irradiation continuously changes in time and space. Pioneers and shade-tolerant species differ in their ability to acclimate to different irradiance. In general under high irradiances, pioneer and/or early succession species have higher net photosynthetic rates (P_N) that are followed by increases in stomatal conductance (g_s) and transpiration rates (E) when compared to shade-tolerant species (Huante and Rincón 1998, Ellis *et al.* 2000). These appropriate features are important for resource acquisition (irradiance, water, and nutrients) and protection against photoinhibition (Krause *et al.* 2001). On the other hand, below the canopy, photosynthesis is limited by low availability of sunlight, being dependent on sunflecks (Pearcy 1990). Even under such conditions, shade-tolerant species of tropical forests are able to maintain relatively high P_N and low compensation irradiance (Cai *et al.* 2005).

Although the study of lianas has increased in recent years, knowledge of their eco-physiology is still fragmentary compared to trees (Cai *et al.* 2007, Tay *et al.* 2007). Lianas reduce growth of their host trees (Pérez-Salicrup and Barker 2000), but produce nutrient-rich litter (Cai and Bongers 2007), contribute to evapotranspiration in seasonal forests (Restom and Nepstad 2001), and are an important source of food for animals (Gentry 1991).

Similar to pioneer trees, many liana species grow better in gaps and margins' forests (Putz 1984). This pattern of distribution indicates the necessity of high

---

Received 13 December 2007, *accepted* 8 July 2008.

**Present address*: Instituto de Ciências Exactas e Biológias, Departamento de Ciências Biológicas, Universidade Federal de Ouro Preto, 35400-000, Ouro Preto, MG Brazil; fax: +51 31 35591633, e-mail: sanchesmc@yahoo.com.br

Acknowledgments: We thank Dr. Carlos A. Joly for use of the portable open-system gas analyser IRGA and Dra. Rogéria P. de Souza and Dr. Eduardo Caruso Machado for help with handling the equipment. We also thank FAPESP (Fundação de Amparo a Pesquisa do Estado de São Paulo) for a fellowship to MCS. We are grateful to Dra. Maria Luiza S. Tucci for useful comments on the present work. We also thank Prof. Dr. L. Sodek for English revision and the anonymous reviewers for constructive comments on the manuscript.

irradiance for their establishment and development (Lüttge 1997), this being considered by some authors as gap-dependent pioneer species (Schnitzer and Bongers 2002). Nevertheless, seeds of some species are able to germinate and seedlings grow under the deep shade of the canopy (Nabe-Nielsen 2002, Sanches and Válio 2002). These data suggest that some mechanism of shade tolerance can be found in liana species.

Considering these features a study was made of the photosynthetic activity of two liana species, *Canavalia parviflora* and *Gouania virgata*, using daily gas exchange and chlorophyll (Chl) *a* fluorescence measurements under an irradiance gradient regime from 100 to 1.5 % of photosynthetic photon flux density (PPFD). The imposed irradiation regime is within the natural range of PPFD found in different microenvironments of the semi-deciduous tropical forest that is the natural habitat of these species (Gandolfi 2000). If radiation heterogeneity is a common aspect of the habitat occupied by lianas (Castellanos *et al*. 1999), one might expect that lianas would be plastic in their photosynthetic responses and present similar values of P_N, g_s, and E as found in pioneer species (Ribeiro *et al*. 2005).

Materials and methods

Plants examined were *Canavalia parviflora* Benth. (Fabaceae) and *Gouania virgata* Reissk (Rhamnaceae). *C. parviflora* exhibits a twiner stem, whereas *G. virgata* uses tendrils for climbing support. These species were chosen in view of their high frequency in the forest. Although adult individuals of *C. parviflora* and *G. virgata* are both widely distributed in open areas, such as forest borders, juvenile individuals of *G. virgata*, but not *C. parviflora*, are also found in the interior of the forest. Henceforth, the two species will be designated by their generic name only. Both species are native of the semi-deciduous tropical forest located in southeast Brazil (22°44′S, 47°06′W); 670 m altitude. The climate is characterized by a dry season with mild temperatures (12–27 °C) from April to September and a wet and warm season (18–34 °C) from October to March. A minimum of five plants was chosen to collect naturally dispersed fruits. Subsequently, the fruits were taken to the laboratory where seeds were removed and cleaned. Seedlings were obtained from seeds germinated in Petri-dishes at 25 °C under continuous "white" fluorescent radiation, following prior scarification. Germinated seeds were transplanted to plastic pots (700 cm^3) and maintained in the glasshouse for initial establishment. In order to obtain similar-sized plants, seeds of *Gouania* were sown before *Canavalia* seeds. The juvenile plants were then transplanted to plastic pots (3 000 cm^3) filled with a mixture of soil and sand (2 : 1) and transferred to experimental conditions.

Plants were transferred to an open area at the State University of Campinas. The plants were kept well watered during the experiments and a Hoagland solution (100 cm^3 per pot) was added every fifteen days (Hoagland and Arnon 1938). Plants of each species were randomly assigned in four groups of 20, which were disposed on benches positioned in the north-south direction. These benches were covered with different layers of neutral shade netting. An additional irradiance consisted of plants growing in full sunlight (benches without shade netting representing 100 % of irradiance). The PPFD (400−700 nm) was recorded once a day over a month, using a *LI-191SA* line quantum sensor or an *LI-190SA* quantum sensor attached to a *LI-1000* data logger (*Li-Cor*, Lincoln, NE, USA) on cloudless days near midday. The percent level in each treatment was calculated with respect to the full sun value. The average PPFD values with the standard error obtained during the experiment were: 1 728.85±62.82; 701.92±64.88; 176.19 ±17.11; 26.60±9.63, corresponding to 100, 40, 10, and 1.5 % of PPFD. The minimum and maximum temperatures for the different treatments were [ºC]: 16.0−34.5, 16.0−34.0, 16.0−31.0, and 16.0−32.0 for 100, 40, 10, and 1.5 % PPFD, respectively. In addition, air temperature and relative humidity data were obtained from a meteorological station close to the location of the experiments and used to calculate the leaf to air vapour pressure difference (Δw).

Daily time-courses of gas exchange were made on four fully expanded and healthy leaves 2−3 nodes below the shoot apex, each from a different plant. The net photosynthetic rate per unit leaf area (P_N), stomatal conductance to water vapour (g_s), transpiration rates (E), leaf temperature (T_{leaf}), and the ratio of intercellular to ambient CO_2 concentration (C_i/C_a) were determined with a portable open-system gas analyser IRGA (*LCA-4*, *Analytical Development Co*., Hoddesdon, UK) connected to a *PLC4 (B)* (6.25 cm^2) leaf chamber. The air entering the leaf chamber was drawn from a height of 3 m aboveground and passed through a 1 500 cm^3 buffer vessel to avoid fluctuation of ambient CO_2 concentration (C_a). For comparison of the P_N, g_s, and E values five leaves of different individual plants for each species were used. The data were collected in the hours of maximum P_N, g_s, and E according to the results of the daily time-courses of gas exchange measurements. Water use efficiency (WUE) was calculated as the ratio P/E at the moment of maximum P_N according to Nobel (2005). The P_N–PPFD curves were obtained for 3 leaves from different specimens growing under 1.5 % and full sunlight. These data were collected in the morning under full solar irradiation. Attenuation of PPFD at the leaf surface was achieved by covering the top of the leaf chamber with different layers of neutral shade netting. Each irradiance measurement was taken after stabilization of CO_2 readings, usually after about 2 min. All these measurements were made in the middle of the rainy season (February to March 2002).

Diurnal course of Chl fluorescence was measured with a pulse-amplitude modulated photosynthesis yield analyser (*MINI-PAM*, *Walz*, Effeltrich, Germany) equipped with a leaf clip holder (model *2030-B*) using four leaves from the same specimen used for the gas exchange measurements. The PPFD measurements were taken close to the leaf surface using a micro-quantum sensor, which was factory calibrated against a *LI-COR 190* quantum sensor (*LI-COR*, Lincoln, NE, USA). Maximum fluorescence (F_m) and minimum fluorescence (F_0) were measured in darkness before dawn and their maximal photochemical efficiency of photosystem 2 (PS2) was obtained from the formula $(F_m - F_0)/F_m = F_v/F_m$. The maximum fluorescence (F_m') and steady-state fluorescence (F) in the light-adapted state were measured at various times during the day, following the methods described by Bilger *et al.* (1995). Saturated radiation pulses of 700 ms duration were applied through a fibre-optic cable oriented at 60° to the leaf surface. The angle and distance between the leaf and the fibre-optic cable were manually adjusted and set with the leaf clip holder. For the measurements of irradiance-adapted parameters, care was taken not to shade the leaves by the fibre optic probe and the leaf clip holder. The effective quantum yield of PS2 was calculated according to Genty *et al.* (1989) as $(F_m' - F)/F_m' = \Delta F/F_m'$. Non-photochemical quenching (NPQ) was calculated according to Maxwell and Johnson (2000) as $NPQ = (F_m - F_m')\ F_m'$. The predawn measurement values of maximum fluorescence (F_m) were used to calculate this quenching parameter. The electron transport rate (ETR) through PS2 was also calculated (White and Critchley 1999) according to the equation: $ETR = (\Delta F/F_m')\ PPFD\ 0.5\ A$ where: $\Delta F/F_m'$ is the photochemical yield under irradiation; PPFD corresponds to the radiation incident at the leaf surface [μmol $m^{-2}\ s^{-1}$; 0.5 is a multiplication factor which assumes that the transport of a single electron requires the absorption of 2 quanta (White and Critchley 1999)] and A is the photon absorbance at the leaf surface for wavelengths in the range 400−700 nm. From optical property measurements, it was possible to work with a specific radiation absorbance for *Canavalia* and *Gouania* leaves. The A values varied from 0.72 to 0.91 for leaves under different irradiances (Sanches and Válio 2006).

Data analysis: For the daily time-course of P_N, E, g_s, C_i/C_a, and Chl *a* fluorescence, descriptive statistics were applied to obtain means and standard error. For comparison between two variables (irradiance×species) two-way ANOVA was used. When significant, the data were subjected to the Tukey test at the 5 % level. The P_N×PPFD curve was fitted according to Prado *et al.* (1994).

Results

Environment: The leaf-to-air vapour pressure difference reached 4.75 and 5.50 kPa under 100 and 40 % at midday for both species, whereas values of 4.50 also prevailed at midday under 10.0 and 1.5 % of PPFD (Fig. 1). The leaf temperature (T_{leaf}) for *Canavalia* and *Gouania* under 100 and 40 % PPFD was 25.5−39.0 °C. Under shade conditions (10.0 and 1.5 % PPFD) T_{leaf} values were on average 35−36 °C (data not shown).

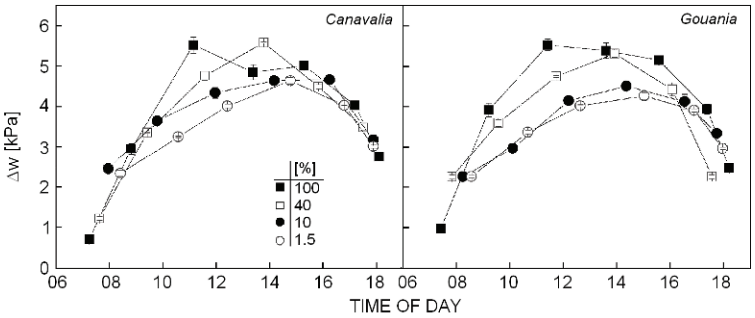

Fig. 1. Daily time-course of leaf-to-air vapour pressure difference (Δw) [kPa] in *Canavalia parviflora* and *Gouania virgata* under 100, 40, 10, and 1.5 % of photosynthetic photon flux density. Means ± SE; *n* = 4.

Diurnal courses of gas exchange and irradiance responses (Figs. 2 and 3): The P_N, E, g_s, and the C_i/C_a ratio varied amongst the two species in terms of maximal values, the midday depression period, and their behaviour under distinct irradiances. P_N reached maximum of about 6 μmol $m^{-2}\ s^{-1}$ during the morning for both species under 100 and 40 % PPFD. In *Canavalia* and *Gouania* under full sunlight the peak values of g_s were attained in the early morning, at around 07:30 h. Following this early morning peak, a drop of 80 % in g_s was observed which resulted in a reduction of E but not of P_N. As the stomata remained closed, a sharp decrease in P_N was observed near midday. This pattern was detected in both *Canavalia* and *Gouania* even though the effect was smaller in the latter species. However, due to brief recovery of g_s around 13:00 h, both species were able to modify their P_N

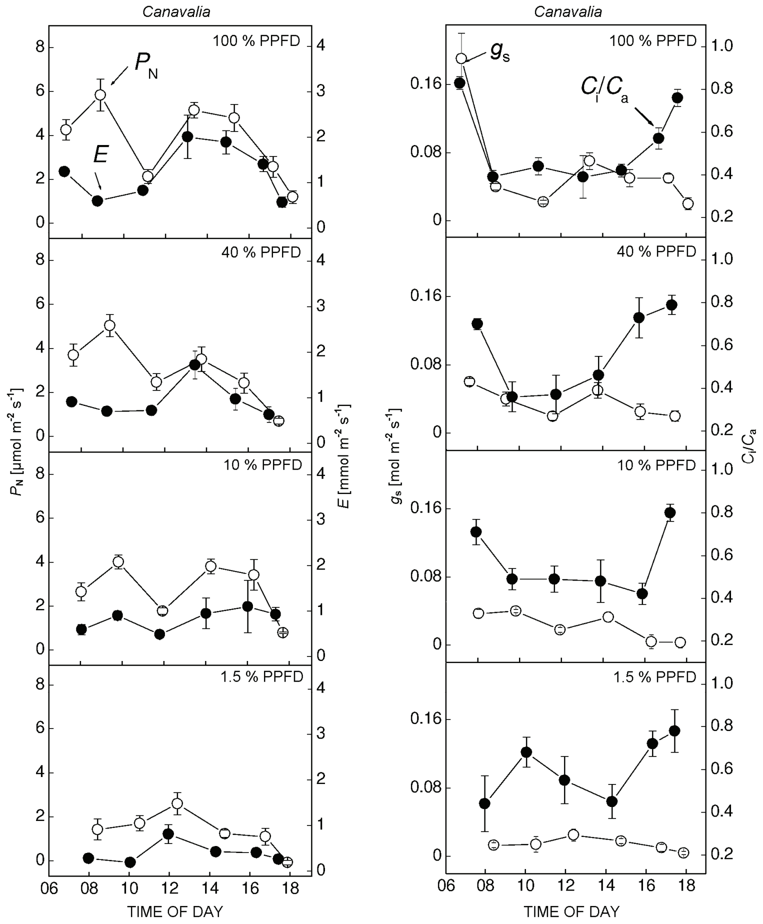

Fig. 2. Daily time-course of net photosynthetic (P_N) and transpiration (E) rates (*left column*), stomatal conductance to water vapour (g_s), and the ratio of intercellular to atmospheric CO_2 concentration (C_i/C_a) (*right column*) for leaves of *Canavalia parviflora* growing under different irradiances. Means ± SE, $n = 4$ (each replicate from different specimens).

and E exchanges, between 14:00 and 16:00 h, attaining values similar to those at early morning. The g_s values under full sunlight for *Canavalia* and *Gouania* species were severely limited by leaf-to-air vapour pressure difference (Fig. 4).

In *Canavalia* under 10 % PPFD, the higher P_N occurred between 08:00 and 09:00 h and in the afternoon between 14:00 and 16:00 h, with reductions of P_N, g_s, and E near midday. The same behaviour was observed for plants under full sunlight and 40 % PPFD. On the other hand, at 10 % PPFD *Gouania* showed increases in P_N during the morning and the maximum values occurred near to midday (Fig. 3). Overall, at 1.5 % PPFD *Canavalia* and *Gouania* showed low P_N during the day, but still under this treatment higher values were obtained near midday. The E and g_s showed a similar pattern. In general, average C_i/C_a ratios were 0.45−0.70 for *Canavalia* and *Gouania* species under all irradiances (Figs. 2 and 3).

The curve of photosynthetic irradiance response showed that both species exhibited higher photon-saturated P_N under full sunlight than under 1.5 % PPFD (Fig. 5). These curves also indicated that a PPFD of about 600 µmol m^{-2} s^{-1} was high enough to saturate P_N under full sunlight, while leaves under 1.5 % PPFD saturated their P_N at lower irradiances. In *Canavalia* the compensation irradiance was lower under full sunlight and higher under deep shade, whereas the opposite pattern was recorded for *Gouania*.

Comparison of gas exchange (Fig. 6): In *Canavalia* leaves there were significant differences in P_N, E, g_s, and WUE between plants growing at full sunlight and lower irradiances. *Gouania* sustained relatively high P_N down to 10 % of PPFD. Although both species exhibited substantial photosynthetic plasticity along the irradiance gradient imposed, *Canavalia* showed a greater range of variation in P_N than *Gouania*. Factorial analyses revealed that *Gouania* leaves achieved higher P_N than *Canavalia* under 40, 10, and 1.5 % sunlight. However, the E was superior in *Canavalia* leaves under full sunlight. In spite of the greater E observed in *Canavalia* leaves under full sunlight, the WUE was superior in this treatment when compared to *Gouania* (Fig. 6). By contrast, under deep shade (1.5 % sunlight), *Gouania* leaves were superior in WUE.

Diurnal courses of Chl fluorescence: Distinct patterns were observed in $\Delta F/F_m'$ according to the irradiance (Fig. 7). The $\Delta F/F_m'$ dropped drastically after sunrise at higher irradiances. *Canavalia* showed a strong reduction in $\Delta F/F_m'$ at midday, 0.142 under full sunlight and 0.156 under 40 % PPFD. Under the same conditions *Gouania*

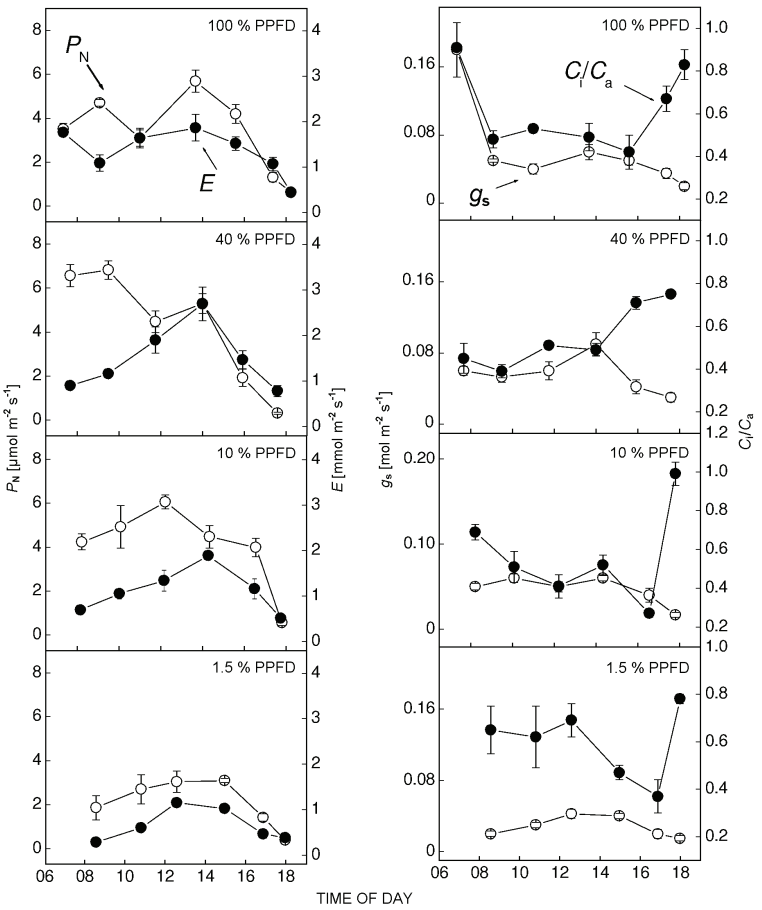

Fig. 3. Daily time-course of net photosynthetic (P_N) and transpiration (E) rates (*left column*), stomatal conductance to water vapour (g_s), and the ratio of intercellular to atmospheric CO_2 concentration (C_i/C_a) (*right column*) for leaves of *Gouania virgata* growing under different irradiances. Means ± SE, $n = 4$ (each replicate from different specimens).

exhibited somewhat higher values of about 0.228 and 0.347. At the two lower irradiances the decrease in $\Delta F/F_m$' seen at midday was much smaller than in plants grown at high irradiances. The pre-dawn measurements that correspond to the dark-adapted state showed the F_v/F_m ratio of about 0.801 for all irradiances and for both species. Under full sunlight, the daily time-course of ETR displayed two patterns. *Canavalia* showed higher ETR between 10:00 and 12:00 h followed by a decrease and subsequent recovery. On the other hand, the daily time-course of ETR in *Gouania* showed a drop between morning and midday, with the highest values at 15:00 h. Under 40 % PPFD, ETR rates were 50.25 and 60.95 µmol m^{-2} s^{-1} at early morning for *Canavalia* and *Gouania,* respectively, but the maximum values in *Gouania* leaves under 40 % sunlight were attained at 14:00 h. ETR was reduced under shade (Fig. 7). Under both full sun and 40 % PPFD, *Canavalia* and *Gouania* showed increases in NPQ up to midday and decreases during the afternoon (Fig. 7). Under the shade (10 and 1.5 % PPFD) lower NPQ values were observed during the day (Fig. 7).

Discussion

Lianas usually occupy open areas where high photon availability and high environmental variability prevail. This distribution pattern is similar to that found for pioneer tree species (Schnitzer and Bongers 2002). Nevertheless, maximum P_N values observed for the liana species were below those found for pioneer species and not far from climax species (Hölscher *et al.* 2004, Nogueira *et al.* 2004, Ribeiro *et al.* 2005). Zotz and Winter (1996) recorded values of carbon assimilation of less than 10 µmol m^{-2} s^{-1} in lianas from the Panama forest and more recently Santiago and Wright (2007) and Cai *et al.* (2007) found lower values of P_N for lianas compared with tree species. Similar results of P_N were also observed in *Enkleia malaccensis*, a twiner liana from a lowland tropical forest located in Malaysia (Tay *et al.* 2007). These values are within the range found for *Canavalia* and *Gouania*. The g_s values were also intermediates to those found in pioneer and late succession species (Juhrbandt *et al.* 2004).

Although P_N is often positively correlated to the specific leaf area (Franco *et al.* 2005) high values were not found in tropical lianas (Cai *et al.* 2007, Tay *et al.* 2007) in spite of the fact that the lianas presented a larger specific leaf area than their host trees (Salzer *et al.* 2006).

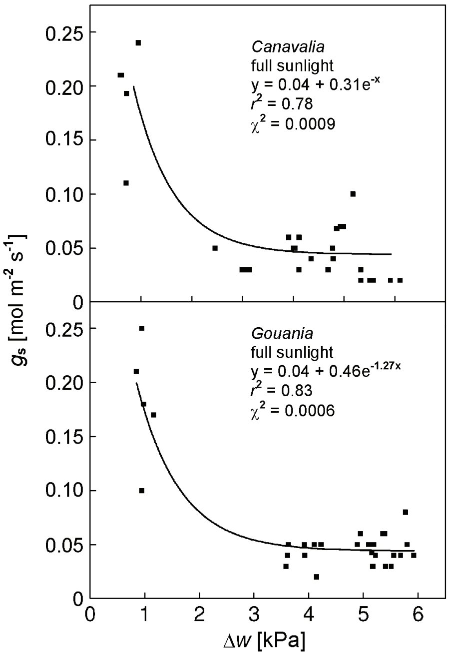

Fig. 4. Relationship between stomatal conductance (g_s) and leaf-to-air vapour pressure difference (Δw) [kPa] of *Canavalia parviflora* and *Gouania virgata* leaves under full sunlight.

Nevertheless, lianas usually produce many leaves (Putz and Windsor 1987) and are richer in nitrogen content than the trees which support them (Salzer *et al.* 2006). These appropriate traits may partially compensate the low P_N observed in *Canavalia* and *Gouania*. Lianas have lower requirements for carbon investments in support tissues than trees (Putz 1990) suggesting a lower demand of carbon for growth of this organ.

Canavalia and *Gouania* showed similar values of P_N under full sunlight, but *Canavalia* was superior in relation to *Gouania* in WUE under 40 % and full sunlight. Thus the gas exchange responses to water limitations have an important role in the acclimation of these species under high irradiance, indicating a tendency for a conservative pattern of water use (Domingues *et al.* 2007). Indeed, the decrease in g_s after its initial peak in early morning was so severe that it resulted in decreased E, but not carbon assimilation, resulting in a high WUE in *Canavalia*. As their stomata remained closed, a decrease in both P_N and C_i/C_a ratio was observed near midday, indicating that stomatal limitation was presumably the main cause of reduced P_N over this period. However, in the early afternoon, with the brief recovery of g_s, both species exhibited another increase in P_N. This result, characterized by a double peak in the daily time-course of P_N, suggests that lianas are able to carry out photosynthesis even under low C_i indicating high carboxylation efficiency in these species (Franco *et al.* 2005).

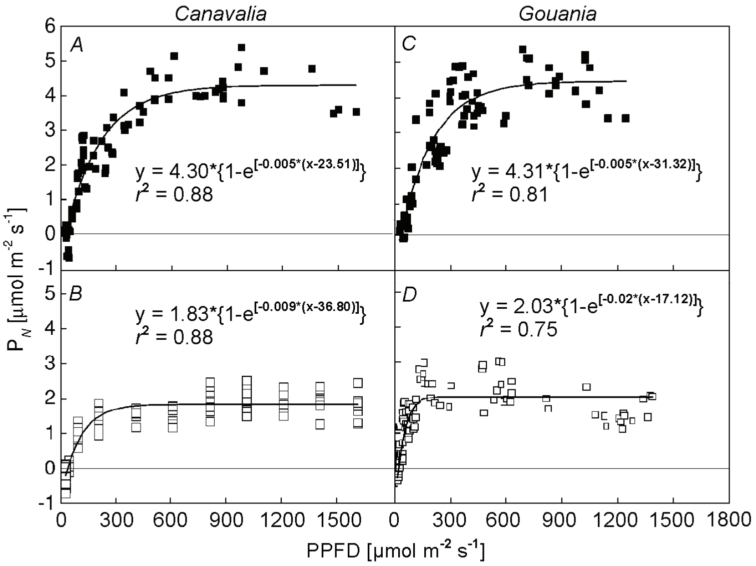

Fig. 5. Relationship between net photosynthetic rates (P_N) and photosynthetic photon flux density (PPFD) at the leaf surface of *Canavalia parviflora* (*left column*) and *Gouania virgata* (*right column*) growing under 100 (*A*, *C*) and 1.5 % (*B*, *D*) of PPFD.

It is possible that reductions of 70 % in P_N near midday in *Canavalia* and 40 % in *Gouania* relative to the maximum values attained during the day were probably the result of a combination of multiple stresses such as the high irradiance to which these species were submitted and an increase in evaporative demand. Data from the irradiance response indicate that a PPFD of about 600 μmol m^{-2} s^{-1} was enough to saturate P_N and at midday the maximum PPFD reached values above 1 800 μmol m^{-2} s^{-1}. It is unlikely that this restriction was caused by an internal reduction of the water status of the plants, since the pots were well watered before the measurements.

Our results regarding the daily time-course of g_s support the suggestion by Barker and Pérez-Salicrup (2000) that lianas limit excess water loss by leaf adaptation. This also agrees with Andrade *et al.* (2005) who discuss the reduction of water flux in lianas through stomatal closure. The stomata of leaves under full sunlight were very sensitive to the increase of leaf-to-air

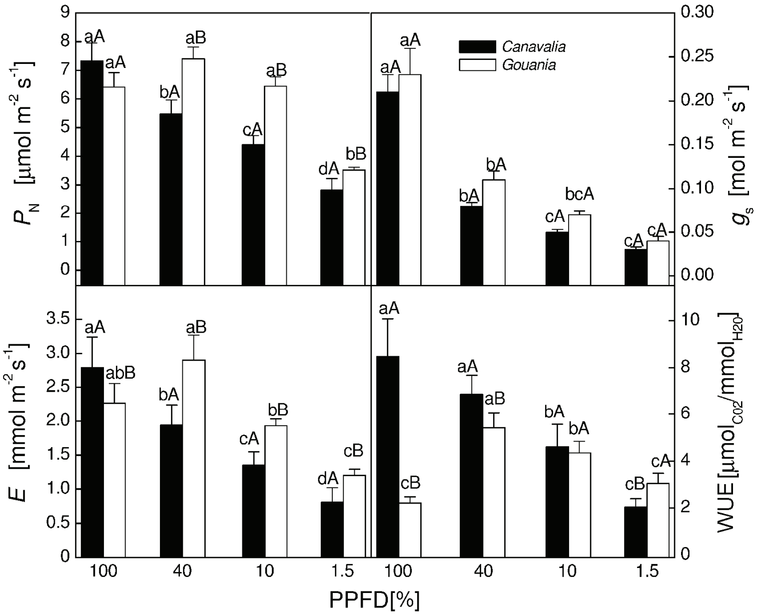

Fig. 6. Maximum values of net photosynthetic rates (P_N), transpiration rates (E), stomatal conductance (g_s), and water use efficiency (WUE) in *Canavalia parviflora* and *Gouania virgata* kept under different irradiances. *Lowercase letters* compare different irradiances and *uppercase letters* compare species. $n = 5$ (each replicate from different specimens).

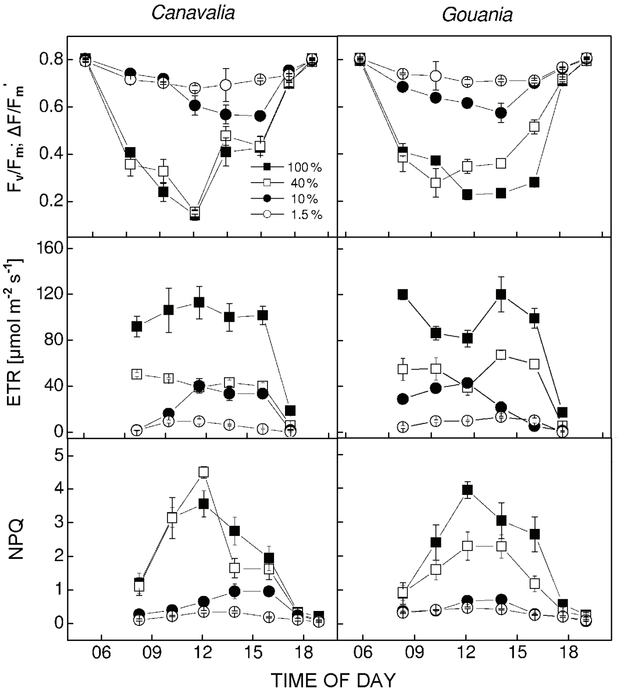

Fig 7. Daily time-course of photochemical efficiency of photosystem 2 in the dark (F_v/F_m, pre-dawn and after sunset measurements) and in the light ($\Delta F/F_m$', the remaining measurements), electron transport rate (ETR), and non-photochemical quenching (NPQ) for *Canavalia parviflora* and *Gouania virgata* leaves kept under different irradiances. Means ± SE, $n = 5$ (each replicate from different specimens).

vapour pressure difference resulting in the lowering of g_s near midday. Stomata sensitivity to humidity has been described for tropical (Castellanos 1991, Barker and Pérez-Salicrup 2000, Tay *et al.* 2007) and temperate lianas (Teramura *et al.* 1991) where stomata closure occurs in response to an increase of Δw leaf-to-air, resulting in reduced water loss, as observed in our daily time-course measurements of E. Lianas are considered heliophytes, hence a mechanism that reduces water loss during some period of the day is important for the exploitation of environments where evaporative demand is high. Restom and Nepstad (2001) comparing E between tree species and lianas in a secondary Amazon forest detected a smaller reduction of E in trees during transition from the wet to dry seasons compared with liana species. All these results suggest that lianas are incapable of maintaining high E under high temperature and full sunlight. The maintenance of high E is common in large trees with their greater capacity to store water in stems (Goldstein *et al.* 1998). The ratio between maximum diameter and sap wood volume is smaller in lianas in relation to trees (Gartner *et al.* 1990) and so a lower capacity of water storage in the stems is to be expected (Andrade *et al.* 2005). Additionally, lianas usually have proportionally a greater leaf area per unit of transverse stem area compared to trees (Ewers *et al.* 1991). Overall, these traits may have contributed to a strong control of stomatal aperture, thus preventing any hydraulic injury, such as xylem embolism.

Our results show that high PPFD was not the only factor that limits carbon assimilation. Even under more amenable irradiance the species showed a reduction of P_N during the hottest hours of the day, mainly in *Canavalia* where restrictions of 56 and 48 % of P_N were detected at 40 and 10 % of PPFD, respectively. It is possible that leaf temperatures above 35 °C can be responsible for such reductions.

Under low irradiance, the liana species presented low P_N but they were capable of keeping their stomata open for long periods. Separately or in combination, these factors could contribute to the maintenance of C_i (Pearcy 1987). Under 1.5 % of PPFD the values for CO_2

concentration inside the mesophyll (230 µmol mol^{-1}) were higher when compared to the values in plants maintained under full sunlight. Considering that the competition between the oxygenase and carboxylase activities of ribulose-1,5-bisphosphate carboxylase/oxygenase is smaller under high C_i, higher CO_2 concentration would result in an increase in the quantum efficiency, an important trait for carbon assimilation in a hot environment limited by light (Pearcy 1987, Lei and Lechowicz 1997). However, *Gouania* kept its stomata open for a longer period than *Canavalia*. Such differences in the regulation of stomatal aperture may provide evidence for better use of sunflecks within the forest by *Gouania*. This characteristic can be important for *Gouania* species, since their juveniles are also observed under the forest canopy.

In lianas a high capacity to acclimate under imposed irradiance was expected, where acclimation is considered as the difference of maximum values of P_N between high and low PPFD (Kursar and Coley 1999). Lianas exhibited lower values of P_N, g_s, and E under 1.5 % PPFD, compared to plants under full sunlight. Lower P_N in shaded plants could be due to production of thin leaves, low cellular volume per unit area, and low stomatal density, thus resulting in lower concentrations of photosynthetic enzyme and electron transporters (Lambers *et al.* 1998). *Canavalia* was able to adjust physiologically to the different irradiances by reducing its P_N in parallel with reductions of PPFD. This plasticity observed in *Canavalia* is similar to the pattern observed for pioneer species that occupy environments where local conditions are much more variable than those occupied by shade-tolerant species (Ribeiro *et al.* 2005). It is also similar to photosynthetic responses found in *Stigmaphyllon lindenianum*, a liana with a twiner stem found in the tropical forest of Panama (Avalos and Mulkey 1999). In *Gouania*, P_N was relatively high down to 10 % of PPFD and the difference of P_N between full sunlight and 1.5 % of PPFD was smaller than in *Canavalia*. To sustain a positive carbon balance under low PPFD, it is necessary to maximize the amount of absorbed photons and photochemical efficiency for CO_2 absorption and at the same time minimize carbon loss through low respiration rates (Lambers *et al.* 1998).

Gouania presented higher P_N than *Canavalia* under 10 and 1.5 % PPFD. This species showed larger specific leaf area and a significant increase of absorption efficiency (ratio between absorptance at 400−700 nm per unit of biomass in photosynthetic tissues) under equal irradiance (Sanches and Válio 2006). Such attributes could contribute to the higher P_N observed enhancing their possibilities for growth and survival in low-irradiance environments.

The daily time-course of Chl fluorescence indicated the absence of photoinhibition, since the F_v/F_m values were close to 0.8 at predawn and after sunset. This reversibility of F_v/F_m has been found in different tropical plants growing in tree-fall gaps and thus experiencing different irradiance regimes during the day (Thiele *et al.* 1998), as well as in pioneer species (Dias and Marenco 2006).

Under 40 % and full sunlight the lianas presented a marked decline of $\Delta F/F_m'$ concomitant with the peak of irradiance and small P_N around midday. Decreases of $\Delta F/F_m'$ can be considered as an adjustment to the prevailing conditions, reflecting reductions of the fraction of photon energy absorbed by Chl associated with PS2 and utilized in photosynthesis (Maxwell and Johnson 2000). In *Canavalia*, reduction of $\Delta F/F_m'$ was followed by maintenance of ETR. This suggests a detour of electron flux to another process not directly involved in carbon assimilation and could indicate the occurrence of photorespiration (Lambers *et al.* 1998). Recent research in field conditions has pointed out the importance of photorespiratory CO_2 production as a way to minimize possible deleterious effects caused by excess of photons, high leaf temperature, and reductions in C_i resulting from partial stomatal closure (Iio *et al.* 2004). Besides photorespiration, the metabolism of nitrogen, mainly nitrate reduction in the leaves or the Mehler-ascorbate peroxidase reaction could contribute as a sink for electrons generated by photochemical reactions (Franco *et al.* 2007). In *Gouania* this pattern was not clear. The ETR decreased in parallel with the reduction of $\Delta F/F_m'$ due probably to photoinhibition and a down-regulation of photosynthesis (Krause *et al.* 1995). If ETR decreases during the midday depression of P_N, this could also reflect a non-stomatal effect of P_N (Iio *et al.* 2004).

For both species the reduction in $\Delta F/F_m'$ was paralleled by an increase in NPQ. This has been considered as a protection mechanism against excessive irradiance (de Mattos *et al.* 1999). In *Canavalia* and *Gouania* the decline of photochemical efficiency was probably related to the component of fast relaxation of NPQ, through energy dissipation *via* maintenance of an electron gradient of protons across the thylakoid membrane and by dissipation of heat produced by the xanthophyll cycle (Thiele *et al.* 1998). This was evidenced by complete recovery of $\Delta F/F_m'$ after sunset (Franco and Lüttge 2002). Thus, the excess of photon energy that could be harmful to *Canavalia* and *Gouania* was dissipated as heat protecting the plants against photodamage. The NPQ in the lianas decreased with increase in shade suggesting a possible trade-off between high photochemical efficiency under low irradiance and higher protection capacity under high irradiance by energy dissipation as heat (Einhorn *et al.* 2004). The NPQ values obtained in the present study for both lianas under high irradiance are considered high and common for species from sunny environments (Bilger *et al.* 1995).

Finally, our first hypothesis that lianas would be plastic in their photosynthetic responses was partially confirmed. *Canavalia* showed plasticity in its photosynthetic activities with large changes in P_N, g_s, and E to the imposed irradiance. For *Gouania* this difference was less pronounced showing values of the P_N under full sunlight closer to those obtained in more shaded treatments. However, our second hypothesis that lianas must show similar values of gas exchanges to those found in pioneer species was not supported. Although the lianas occupy similar niches to pioneer species, their P_N and g_s values under full sunlight were closer to those found for shade-tolerant species. *Gouania* was more tolerant to shade since the values of P_N were higher and its compensation irradiance was lower than *Canavalia* at 1.5 % PPFD indicating low respiration rates. These features are appropriate for this species that is also found in more shaded environments within the forest. At 40 % and full sunlight *Canavalia* exhibited higher WUE than *Gouania.* In the seasonal tropical forest, where these plants are native, winter is characterized by pronounced drought. Therefore, high WUE is a favourable trait since it enables this species to maintain high P_N even under low g_s (Franco *et al*. 2005).

The predominance of lianas in habitats with high PPFD, such as gaps and forest borders, similar to those occupied by pioneer species, does not imply that their leaf physiological responses would be similar to such plants. Lianas must be characterized by a wide range of adaptation to the different irradiance to which they are submitted and by different requirements to shade tolerance, in the same way as tree species (Gilbert *et al.* 2006). Our findings suggest that lianas share several physiological leaf traits that are inherent to pioneer and shade-tolerant species. Both species sustained relatively high P_N under 40 and 10 % of PPFD, showing that they are capable of adjusting to heterogeneous and low irradiance. These adjustments are essential to lianas that experience pronounced variations in both spectral quantity and quality during their life histories (Lee and Richards 1991).

References

Andrade, J.L., Meinzer, F.C., Goldstein, G., Schnitzer, S.A.: Water uptake and transport in lianas and co-occuring trees of seasonally dry tropical forest. – Trees **19**: 282-289, 2005.

Avalos, G., Mulkey, S.S.: Photosynthetic acclimation of the liana *Stigmaphyllon lindenianum* to light changes in a tropical dry forest. – Oecologia **120**: 475-484, 1999.

Barker, M.G., Pérez-Salicrup, D.: Comparative water relations of mature mahogany (*Swietenia macrophylla*) trees with and without lianas in a subhumid, seasonally dry forest in Bolivia. – Tree Physiol. **20**: 1167-1174, 2000.

Bilger, W., Schreiber, U., Bock, M.: Determination of the quantum efficiency of photosystem II and of non-photochemical quenching of chlorophyll fluorescence in the field. – Oecologia **102**: 425-432, 1995.

Cai, Z.-Q., Bongers, F.: Contrasting nitrogen and phosphorous resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China. – J. trop. Ecol. **23**: 115-118, 2007.

Cai, Z.-Q., Poorter, L., Kao, K-F., Bongers, F.: Seedling growth strategies in *Bauhinia* species: comparing lianas and trees. – Ann. Bot. **100**: 831-838, 2007.

Cai, Z.-Q., Rijkers, T., Bongers, F.: Photosynthetic acclimation to light changes in tropical monsoon forest woody species differing in adult stature. – Tree Physiol. **25**: 1023-1031, 2005.

Castellanos, A.E.: Photosynthesis and gas exchange of vines. – In: Putz, F.E., Mooney, H.A. (ed.): The Biology of Vines. Pp. 181-204. Cambridge University Press, Cambridge 1991.

Castellanos, A.E., Tinoco-Ojanguren, C., Molina-Freaner, F.: Microenviromental heterogeneity and space utilization by desert vines with their host trees. – Ann. Bot. **84**: 145-153, 1999.

de Mattos, E.A., Herzog, B., Lüttge, U.: Chlorophyll fluorescence during CAM-phases in *Clusia minor* L. under drought stress. – J. exp. Bot. **50**: 253-261, 1999.

Dias, D.P., Marenco, R.A.: Photoinhibition of photosynthesis in *Minquartia guianensis* and *Swietenia macrophylla* inferred by monitoring the initial fluorescence. – Photosynthetica **44**: 235-240, 2006.

Domingues, T.F., Martinelli, L.A., Ehleringer, J.R.: Ecophysiological traits of plant functional groups in forest and pasture ecosystem from eastern Amazônia, Brazil. – Plant Ecol. **193**: 101-112, 2007.

Einhorn, K.S., Rosenqvist, E., Leverenz, J.W.: Photoinhibition in seedlings of *Fraxinus* and *Fagus* under natural light conditions: implications for forest regeneration? – Oecologia **140**: 241-251, 2004.

Ellis, A.R., Hubbel, S.P., Potvin, C.: In situ field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. – Can. J. Bot. **78**: 1336-1347, 2000.

Ewers, F.W., Fischer, 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.

Franco, A.C., Bustamante, M., Caldas, L.S., Goldstein. G., Meinzer, F.C., Kozovits, A.R., Rundel, P., Coradin, V.T.R.: Leaf functional traits of neotropical savanna trees in relation to seasonal water deficit. – Trees **19**: 326-335, 2005.

Franco, A.C., Lüttge, U.: Midday depression in savanna trees: coordinated adjustments in photochemical efficiency, photorespiration, CO_2 assimilation and water use efficiency. – Oecologia **131**: 356-365, 2002.

Franco, A.C., Matsubara, S., Orthen, B.: Photoinhibition, carotenoid composition and the co-regulation of photochemical and non-photochemical quenching in neotropical savanna trees. – Tree Physiol. **27**: 717-725, 2007.

Gandolfi, S.: História natural de uma floresta semidecidual no interior de São Paulo, SP. − PhD Thesis. Universidade Estadual de Campinas, Brazil 2000.

Gartner, B.L., Bullock, S.H., Mooney, H.A., Brown, V., Whitbeck, J.L.: Water transport properties of vine and tree stems in a tropical deciduous forest. – Amer. J. Bot. **77**: 742-749, 1990.

Genty, B., Briantais, J.-M., Baker, N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. biophys. Acta **990**: 87-92, 1989.

Gentry, A.H.: The distribution and evolution of climbing plants. – In: Putz, F.E., Mooney, H.A. (ed.): The Biology of Vines. Pp. 3-49. Cambridge University Press, Cambridge 1991.

Gerwing, J.J.: Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. – Forest Ecol. Manage. **190**: 57-72, 2004.

Gilbert, B., Wright, S.J., Muller-Landau, H., Kitajima, K., Hernandéz, A.: Life history trade-offs in tropical trees and lianas. – Ecology **87**: 1281-1288, 2006.

Goldstein, G., Andrade, J.L., Meinzer, F.C., Holbrook, N.M., Cavellier, P., Jackson, P., Cellis, A.: Stem water storage and diurnal patterns of water use in tropical forest canopy trees. – Plant Cell Environ. **21**: 397-406, 1998.

Hoagland, D.R., Arnon, D.I.: The water-culture method for growing plants without soil. − Agricultural Experiment Station Circ. 347, 1938.

Hölscher, D., Leuschner, C., Bohman, K., Juhrbandt, J., Tjitrosemito, S.: Photosynthetic characteristics in relation to leaf traits in eight co-existing pioneer tree species in Central Sulawesi, Indonesia. – J. trop. Ecol. **20**: 157-164, 2004.

Huante, P., Rincón, E.: Responses to light changes in tropical deciduous woody seedlings with contrasting growth rates. – Oecologia **113**: 53-66, 1998.

Iio, A., Fukasawa, H., Nose, Y., Kakubari, Y.: Stomatal closure induced by high vapor pressure deficit limited midday photosynthesis at the top canopy of *Fagus crenata* Blume on Naeba moutain in Japan. – Trees **18**: 510-517, 2004.

Juhrbandt, J., Leuschner, C., Hölscher, D.: The relationship between maximal stomatal conductance and leaf traits in eight Southeast Asian early successional tree species. – Forest Ecol. Manage. **202**: 245-256, 2004.

Krause, G.H., Koroleva, O.Y., Dalling, J.W., Winter, K.: Acclimation of tropical tree seedlings to excessive light in simulated tree-fall gaps. – Plant Cell Environ. **24**: 1345-1352, 2001.

Krause, G.H., Virgo, A., Winter, K.: High susceptibility to photoinhibition of young leaves of tropical forest trees. – Planta **197**: 583-591, 1995.

Kursar, T.A., Coley, P.D.: Contrasting modes of light acclimation in two species of the rainforest understory. – Oecologia **121**: 489-498, 1999.

Lambers, H., Chapin, S.T., III, Pons, T.J.: Plant Physiological Ecology. − Springer-Verlag, Berlin 1998.

Lee, D.W., Richards, J.H.: Heteroblastic development in vines. – In: Putz, F.E., Mooney, H.A. (ed.): The Biology of Vines. Pp. 205-243. Cambridge University Press, Cambridge 1991.

Lei, T.T., Lechowicz, M.J.: The photosynthetic response of eight species of *Acer* to simulated light regimes from the centre and edges of gaps. – Funct. Ecol. **11**: 16-23, 1997.

Lüttge, U.: Physiological Ecology of Tropical Plants. – Springer-Verlag, Berlin 1997.

Maxwell, K., Johnson, G.N.: Chlorophyll fluorescence – a practical guide. – J. exp. Bot. **51**: 659-668, 2000.

Nabe-Nielsen, J.: Growth and mortality rates of the liana *Machaerium cuspidatum* in relation to light and topographic position. – Biotropica **34**: 319-322, 2002.

Nobel, P.S.: Physicochemical and Environmental Plant Physiology. − Elsevier/Academic Press, San Diego 2005.

Nogueira, A., Martinez, C.A., Ferreira, L.L., Prado, C.H.B.A.: Photosynthesis and water use efficiency in twenty tropical tree species of differing sucession status in a Brazilian reforestation. – Photosynthetica **42**: 351-356, 2004.

Pearcy, R.W.: Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. – Funct. Ecol. **1**: 169-178, 1987.

Pearcy, R.W.: Sunflecks and photosynthesis in plant canopies. – Annu. Rev. Plant Physiol. Plant mol. Biol. **41**: 421-453, 1990.

Pérez-Salicrup, D., Barker, M.G.: Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. – Oecologia **124**: 469-475, 2000.

Prado, C.H.B.A., de Moraes, J.A.P.V., de Mattos, E.A.: Gas exchange and leaf water status in potted plants of *Copaifera langsdorffii*. 1. Responses to water stress. – Photosynthetica **30**: 207-213, 1994.

Putz, F.E.: The natural history of lianas on Barro Colorado Island, Panama. – Ecology **65**: 1713-1724, 1984.

Putz, F.E.: Liana stem diameter growth and mortality rates on Barro Colorado Island, Panama. – Biotropica **22**: 103-105, 1990.

Putz, F.E., Windsor, D.M.: Liana phenology on Barro Colorado Island, Panama. – Biotropica **19**: 334-341, 1987.

Restom, T.G., Nepstad, D.C.: Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia. – Plant Soil **236**: 155-163, 2001.

Ribeiro, R.V., Souza, G.M., Oliveira, R.F., Machado, E.C.: Photosynthetic responses of tropical tree species from different sucessional groups under contrasting irradiance conditions. – Rev. brasil. Bot. **28**: 149-161, 2005.

Salzer, J., Matezki, S., Kazda, M.: Nutritional differences and leaf acclimation of climbing plants and the associated vegetation in different types of an Andean Montane rainforest. – Oecologia **147**: 417-425, 2006.

Sanches, M.C., Válio, I.F.M.: Seedling growth of climbing species from a southeast Brazilian tropical forest. – Plant Ecol. **154**: 51-59, 2002.

Sanches, M.C., Válio, I.F.M.: Leaf optical properties of two liana species *Canavalia parviflora* Benth. and *Gouania virgata* Reissk. in different light conditions. – Rev. brasil. Bot. **29**: 319-330, 2006.

Santiago, L.S., Wright, S.J.: Leaf functional traits of tropical forests plants in relation to growth form. – Funct. Ecol. **21**: 19-27, 2007.

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

Tay, A.C., Abdullah, A.M., Awang, M., Furukawa, A.: Midday depression in *Enkleia malaccensis*, a woody climber in a tropical rainforest. – Photosynthetica **45**: 189-193, 2007.

Teramura, A.H., Gold, W.G., Forseth, I.: Physiological ecology of mesic, temperate woody vines. – In: Putz, F.E., Mooney, H.A. (ed.): The Biology of Vines. Pp. 245-286. Cambridge University Press, Cambridge 1991.

Thiele, A., Krause, G.H., Winter, K.: *In situ* study of photoinhibition of photosynthesis and xanthophyll cycle activity in plants growing in natural gaps of the tropical forest. – Aust. J. Plant Physiol. **25**: 189-195, 1998.

White, A.J., Critchley, C.: Rapid light curves: A new fluorescence method to assess the state of the photosynthetic apparatus. – Photosynth. Res. **59**: 63-72, 1999.

Zots, G., Winter, K.: Diel patterns of CO_2 exchange in rainforest canopy plants. – In: Mulkey, S.S., Chazdon, R.L., Smith A.P. (ed.): Tropical Forest Plant Ecophysiology. Pp. 89-113. Chapman & Hall, New York 1996.