马占相思的日光合作用和日碳固定总量研究

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摘 要 马占相思(*Acacia mangium*)是一种具有较高经济价值和生态效益的热带速生树种。为了研究其光合作用对一天内光强、温度等环境因子变化的响应,揭示其迅速生长的生理生态机制,在叶片水平上测量了马占相思在 24 h 内的净光合速率(P_n)、蒸腾速率、气孔导度(G_s)、胞间 CO_2 浓度(C_i)、每日固定碳的总量、夜间消耗碳的总量以及日间光合系统 II 光化学效率(F_v/F_m)的变化。结果显示:其净光合速率在正午降低了 14.5%;其较高的蒸腾速率和气孔导度有助于保持叶片日间较高的碳固定速率;光合系统 II 对于高光强和高温有较强的忍受度;每日固定碳的总量为 $502 \text{ mmol CO}_2 \cdot \text{m}^{-2}$,夜间碳的损失为 $54 \text{ mmol CO}_2 \cdot \text{m}^{-2}$ 。研究结果在一定程度上揭示了马占相思在热带高光强和高温条件下迅速生长的生理机制。

关键词 马占相思 叶绿素荧光 气体交换 光合作用 日碳固定总量

DIURNAL PHOTOSYNTHESIS AND CARBON ECONOMY OF ACACIA MANGIUM

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Abstract *Acacia mangium* is a fast growing tropical tree species with significant economic and ecological values. The diurnal variations of photosynthesis and daily-integrated photosynthetic CO_2 assimilation over whole photoperiods of *A. mangium* phyllode were investigated. The results showed that the photosynthetic CO_2 uptake of *A. mangium* phyllode exhibited a 14.5% decrease during midday. The PSII of the *A. mangium* phyllode was tolerant to high Photosynthetic photon flux density (PPFD) levels and high temperatures. The integrated daily carbon gain and nocturnal carbon loss of *A. mangium* phyllode was $502 \text{ mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ and $54 \text{ mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, respectively. All of these physiological traits allow *A. mangium* to take advantage of the high PPFD environment in the tropics and help this plant to realize rapid growth.

Key words *Acacia mangium*, Chlorophyll fluorescence, Gas exchange, Photosynthesis, Carbon economy

In natural environments, plants are exposed to fluctuations in air temperature, light and water availability, and atmospheric humidity during the course of a day. These interacting factors have important effects on plant physiological processes, and thus the growth of the plants (Zotz & Winter, 1996). The diurnal courses of gaseous CO_2 and water vapor exchange provided fundamental information on plant responses and adaptations to their natural growth environments. In addition, measurements of diurnal (24 h) CO_2 exchange is the most direct method to determine the primary photosynthetic productivity of leaves in the field (Zotz & Winter, 1996), which is essential for the analysis of carbon allocation and plant growth.

Diurnal changes of photosynthetic CO_2 assimilation

rate have been studied in plants growing in the temperate, Mediterranean, and subtropical climates, and a typical midday depression in the photosynthetic CO_2 uptake rate of these plant species was also reported (Lange *et al.*, 1982; Tenhunen *et al.*, 1984; Raschke & Resemann, 1986; Roy & Slalager, 1992; Faria *et al.*, 1996; Ishida *et al.*, 1999; 2001a). Several physiological responses have been used to explain the probable cause of a midday depression in photosynthetic CO_2 uptake. For instance, the decrease in stomatal conductance could result in a midday depression of net photosynthesis (Tenhunen *et al.*, 1984; Raschke & Resemann, 1986; Knapp & Smith, 1989). Another reason for the reduction of photosynthetic CO_2 uptake rate during midday could be the

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feedback inhibition of photosynthesis by carbohydrate accumulation (Foyer, 1988). It has also been reported that long periods of high PPFD (Photosynthetic photon flux density) could lead to the midday depression of photosynthetic CO_2 rates (Kuppers *et al.*, 1986). Recently, the combination of chlorophyll fluorescence measurements and gas exchange determinations in the diurnal variations of leaf photosynthesis has provided valuable insights on the regulatory mechanisms of the photosynthetic machinery under natural field conditions (Schreiber *et al.*, 1994; Faria *et al.*, 1996; Xu & Shen, 1997).

Acacia mangium is a tropical pioneer species, widely used in reforestation programs and pulp wood plantations in the humid tropics (Sim, 1986; Mok *et al.*, 2000). Juvenile plants of *A. mangium* have true compound leaves, made up of minute leaflets, which are replaced by phyllodes [expanded petioles that form simple, photosynthesizing laminae (Esau, 1965)] in older plants. The objective of the present work was to describe and analyze *in situ* diurnal CO_2 and H_2O exchange pattern and the integrated daily carbon gain and nocturnal carbon loss of *A. mangium* phyllodes, in order to assess the responses of *A. mangium* phyllode photosynthesis to diurnal variations in environmental conditions and to advance the understanding of the ecophysiological mechanism by which *A. mangium* copes with the combination of high PPFD levels and high temperatures during midday in the humid tropics.

1 Materials and methods

Seeds of *A. mangium* were pretreated and germinated according to Yu and Ong (2000), and seedlings were grown in pots (33 cm diameter, 26 cm depth) in an exposed open site in the Teaching Garden of Department of Biological Sciences, National University of Singapore.

Twenty-four hours (8:00–8:00) CO_2 and H_2O exchange of mature *A. mangium* phyllodes (250 days after sowing) were recorded at 2 h intervals with a CIRAS-1 portable differential $\text{CO}_2/\text{H}_2\text{O}$ infrared gas analyzer (PP systems, Hitchin, UK). Measurements were made in the field on three consecutive days [(27 August to 29 August, 1999) and April (24 April to April 26, 2000)], which were bright and clear with no cloud and with similar radiation and environmental conditions. Under natural day/night conditions, gas exchange rates of phyllode were determined at an airflow rate of $200 \text{ cm}^3 \cdot \text{min}^{-1}$ with *ca.* $365 \mu\text{mol} \cdot \text{mol}^{-1} \text{CO}_2$ in the cuvette, and a phyllode area of 2.5 cm^2 was enclosed in the cuvette. Day and night environmental conditions inside the cuvette were nearly i-

dentical to those plants would experience in a natural environment. Environmental variables (PPFD level, air temperatures) and physiological parameters (net photosynthetic rate, transpiration rate, stomatal conductance, intercellular CO_2 concentration, and phyllode temperature) were measured throughout the day with a CIRAS-1 infrared gas analyzer. The integrated daily carbon gain per unit phyllode area of an *A. mangium* phyllode was estimated by integrating the areas beneath the diurnal photosynthetic CO_2 assimilation curves.

The photochemical efficiency of PS II (F_v/F_m) of *A. mangium* plants was determined in parallel with the diurnal gas exchange measurements on separate phyllodes from 8:00 to 18:00 at 2 h intervals. In the field, intact phyllodes attached to the *A. mangium* plant were dark-adapted for 30 min (covered with aluminum foil, and preliminary experimentation showed that 30 min dark-adaptation was enough for F_m to reach maximal value). These dark-adapted phyllodes were excised with a sharp razor blade. With the cut-end wrapped in moist cotton, each phyllode was immediately brought back to the lab for measurement with a pulse amplitude modulation fluorometer (PAM 101-103, Waltz, Effeltrich, Germany). Minimal fluorescence, F_o , was determined at a light level lower than $0.01 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. After F_o was recorded, a 600-ms saturating light pulse ($5\,000 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) was given and F_m , maximal fluorescence, was determined. Saturating light was supplied by a Schott flash lamp (KL 1500, Schott, Mainz, Germany). The photochemical efficiency of PS II, F_v/F_m , was calculated from F_m and F_v , $F_v = F_m - F_o$ (Schreiber *et al.*, 1994).

The experiments were repeated two times in August 1999 and April 2000, respectively. The values for environmental variables (PPFD level, air temperatures) and physiological parameters (net photosynthetic rate, transpiration rate, stomatal conductance, intercellular CO_2 concentration, and phyllode temperature) were averaged over six days of measurement, as the environmental conditions were similar for these days. Each result is represented as the mean $\pm$ standard error (SE).

2 Results

2.1 Environmental conditions

The daily changes in PPFD level on a sunny day in the experimental site are shown in Fig. 1(A). The sun rose around 7:00 local time and the radiation increased quickly, so that by 10:00 the PPFD incident on the canopy of unshaded plants exceeded $1\,500 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

s^{-1} . From 10:00 to 16:00, the PPFD level was in the range of $1\,400 - 1\,700\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and it decreased to $34.7\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 18:00 (Fig. 1A). Diurnal changes in air and phyllode temperatures were shown in Fig. 1B.

Fig. 1 Diurnal courses of variation in photosynthetic photon flux density (PPFD) (A), and *A. mangium* phyllode temperature and air temperature (B)

Measurements were made on clear sunny days. The vertical bars indicate standard errors of means

The air temperature ranged from $27\ ^{\circ}\text{C}$ to $38\ ^{\circ}\text{C}$, and daytime temperature on an average was $6\ ^{\circ}\text{C}$ higher than the nighttime temperature. With the exception of midday (12:00 to 14:00), the phyllode temperature was similar or slightly lower than the air temperature. During 12:00 to 14:00, the phyllode temperature was $0.54 - 0.70\ ^{\circ}\text{C}$ higher than the air temperature (Fig. 1B).

2.2 Photosynthesis

The 24 h CO_2 exchange pattern of *A. mangium* phyllodes is shown in Fig. 2. Generally, the rate of photosynthetic CO_2 uptake (P_n) was parallel to the changes in PPFD levels throughout the day as it responded primarily to changes in PPFD levels (Fig. 1A, Fig. 2). The highest P_n of *A. mangium* phyllodes was observed at 10:00 ($19.74\ \mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and it remained high during the day. However, a slight depression (14.5%) in the P_n was observed between 12:00 – 16:00, with respect to the highest value observed at 10:00 (Fig. 2). Integrated over the whole 24 h period, the daily net CO_2 uptake was $502\ \text{mmol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, and the net CO_2 loss during nighttime was $54\ \text{mmol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{day}^{-1}$.

2.3 Stomatal conductance, transpiration rate and intercellular CO_2 concentrations

During the times when the PPFD levels were high (from 10:00 to 16:00), the transpiration rate and stomatal conductance of *A. mangium* phyllodes were also high (Fig. 3A, B). Midday depressions of transpiration rate

Fig. 2 Diurnal changes in the rate of photosynthetic CO_2 exchange of *A. mangium* phyllode
Measurements and the vertical bars see Fig. 1

and stomatal conductance were observed (Fig. 3A, B). Intercellular CO_2 concentration (C_i) peaked at 2:00, thereafter decreased, and remained constant from 10:00 to 16:00. After sunset (18:00), it increased again (Fig. 3C).

Fig. 3 Diurnal changes in transpiration rate (A), stomatal conductance (B), and intercellular CO_2 concentration (C) of *A. mangium* phyllodes
Measurements and the vertical bars see Fig. 1

2.4 Chlorophyll fluorescence

The daily changes in the F_v/F_m ratio of *A. mangium* phyllodes on a sunny day are shown in Fig. 4. It was highest at 8:00 (0.85), and it decreased to 0.77 at midday. Then it increased, and by 18:00, it reached to 0.83 (Fig. 4).

Fig.4 The daily changes in photochemical efficiency of PS II (F_v/F_m) of *A. mangium* phyllodes
Measurements and the vertical bars see Fig.1

3 Discussion

The rate of photosynthetic CO_2 uptake (P_n) was positively related to the PPFD value ($R^2 = 0.96$), indicating that PPFD was the main factor affecting P_n of *A. mangium* phyllode. The same relationship between P_n and PPFD was also reported in *Pinus pumila* (Ishida *et al.*, 2001a). The highest P_n of *A. mangium* phyllodes was about $20 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and it was observed at 10:00 when PPFD level was $1\,600 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. These results resemble those of *Eucalyptus rossii*, as a similarly high P_n of this tropical tree species ($24.4 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) was observed at about the same time of the day (Roden & Ball, 1996).

Under optimum conditions (temperature of 29°C and PPFD level of $1\,400 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), a maximal P_n of $22.46 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in *A. mangium* phyllode was documented in the laboratory (Yu & Ong, 2000). The daily average rate of photosynthetic CO_2 assimilation of *A. mangium* phyllode under natural conditions on clear sunny day was 80% of this maximal value observed in the laboratory. The extent to which the daily average rates of photosynthetic CO_2 assimilation fall below their potential maximal levels would provide quantitative information on the adaptation of plants to their natural habitats (Schulze, 1982). Thus, the higher P_n in *A. mangium* phyllode reported here shows that this plant species is well adapted to the tropical high PPFD and high temperature environment.

Midday depression in photosynthesis in tropical pioneer species has been observed (Zotz & Winter, 1993; 1996; Zotz *et al.*, 1995). For instance, during the dry season (January), the P_n of *Ficus insipida* in Panama decreased from $30 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at 9:45 to $1 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at 11:20, stayed this low for two hours (Zotz *et al.*, 1995). A midday depression in P_n for Mediterranean tree species was also widely reported (Tenhunen *et al.*, 1984; Faria *et al.*, 1996). For example,

Quercus suber underwent a 75% reduction in P_n during midday in the summer, and this midday depression in P_n was strongly correlated with the severe decline in stomatal conductance (Faria *et al.*, 1996). The simultaneous midday decrease in P_n and stomatal conductance has also been observed in *Pinus halepensis*, *Quercus coccifera*, *Juniperus phoenicea* (Martinez-Ferri *et al.*, 2000), and *Ficus insipida* (Zotz & Winter, 1995). The results obtained in this study showed that the midday depression of P_n in *A. mangium* phyllodes was small, as it only reduced by 14.5% at midday. In addition, the stomatal conductance of *A. mangium* phyllodes was high throughout the day. The lowest value of $287 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ observed at 14:00 was still higher than that of the highest stomatal conductance of *Quercus suber* (Faria *et al.*, 1996) and *Quercus coccifera* (Martinez-Ferri *et al.*, 2000). The average daytime stomatal conductance ($476 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) of *A. mangium* phyllodes was about 20 times of the stomatal conductance ($25 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) of an understory plant, *Peperomia obtusifolia* (Woerner & Martin, 1999). The highest stomatal conductance ($630 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) of *A. mangium* phyllodes was observed at 16:00. To our knowledge, only the stomatal conductances of two tropical *Eucalyptus* species were higher than this value. *E. macrorhyncha*, has a stomatal conductances of $650 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Roden & Ball, 1996); and *E. tetradonta*, has a stomatal conductances of $703 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Berryman *et al.*, 1994). Since a larger stomatal conductance increase CO_2 diffusion into leaf, the high stomatal conductance in *A. mangium* phyllode would favor carbon fixation and light utilization, although it is costly in terms of water usage. Therefore, the ability of *A. mangium* to maintain high P_n at midday is correlated with its high stomatal conductance.

In tropical environments, the combination of high temperature and PPFD level during midday might damage the apparatus of PS II. The high stomatal conductance of *A. mangium* may lower the phyllode temperature, which allows the phyllodes to maintain favorable temperatures for photosynthetic CO_2 assimilation, therefore providing a distinctive advantage in a tropical hot environment. In *A. mangium*, the high transpiration rates associated with high stomatal conductance are sufficient to prevent the phyllodes from becoming hotter than the ambient air during periods of high PPFD. Between 10:00 – 16:00, the transpiration rates of *A. mangium* ranged from 6.14 to $10.07 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and the phyllode temperature ($35 - 36^\circ\text{C}$) was lower or slightly higher (0.41°C , from 12:00 to 14:00) than the air temperature of $36 - 38^\circ\text{C}$. In comparison, the study on the diurnal gas exchange of two other tropical pioneer species (*Shorea leprosula* and

Marcaranga gigantea) in Malaysia showed that the highest transpiration rates were $5 - 5.5 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and the leaf temperature ($34 - 37^\circ\text{C}$) was higher than the air temperature of $30 - 34.5^\circ\text{C}$ during 9:00 to 16:00 (Ishida *et al.*, 1999). Therefore, it can be concluded that by maintaining phyllode temperatures close to air temperatures, *A. mangium* can sustain constant and relatively high assimilation rates throughout the photoperiod. This adaptive trait probably results in a greater net carbon gain for *A. mangium* than other species, which undergo a severe depression in photosynthetic CO_2 uptake rates during midday.

The intercellular CO_2 concentration (C_i) is an important factor in the regulation of photosynthetic CO_2 uptake rate (Mohotti & Lawlor, 2002). In this study, the stomatal conductance was large and the rate of photosynthetic CO_2 uptake of *A. mangium* phyllode was low, at 8:00, thus C_i was high in the early morning. During 10:00 to 16:00, the C_i was low, and this could be due to the decreased stomatal conductance during this time period. Furthermore, this decreased C_i would have restricted the rate of photosynthetic CO_2 uptake, and this persisted from 10:00 to 16:00.

Under natural conditions, the imbalance between energy input and energy utilization as a result of high PPFD level at midday, might lead to a decrease in the photochemical efficiency of PS II (Long *et al.*, 1994; Faria *et al.*, 1996). Simultaneous depression of PS II photochemical efficiency and P_n under natural conditions has been reported in *Quercus petraea* (Epron *et al.*, 1992) and *Quercus ilex*, *Olea europaea*, and *Eucalyptus globules* (Faria *et al.*, 1998). In this study, in addition to the 14.5% reduction in P_n of *A. mangium* phyllodes during midday, a slight decrease (8%) in the photochemical efficiency of PS II (F_v/F_m) between 12:00 - 14:00 was observed. Compared with other tropical tree species, the magnitude of this decrease in F_v/F_m of *A. mangium* was smaller. For example, it was reported that F_v/F_m decreased by 28% in *Eucalyptus macrorhyncha* (Roden & Ball, 1996) and *Planchonella obovata* (Ishida *et al.*, 2001b) during midday. In *Arisaema heterophyllum*, F_v/F_m decreased by 50% during midday (Muraoka *et al.*, 2000). Thus, a high F_v/F_m of phyllode throughout the day suggests that *A. mangium* maintains a relatively high photochemical efficiency of PS II, and this can contribute directly to the higher total carbon gain of these plants and fast growth of this species. In addition, the PS II of *A. mangium* phyllodes is relatively tolerant to high PPFD levels and high temperatures, as indicated by high F_v/F_m (0.77 - 0.83) during 10:00 - 14:00 with PPFD of $1\,500 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and temperatures of $35 - 36^\circ\text{C}$.

To determine the primary photosynthetic productivity of leaves in the field, 24 h measurement of CO_2 exchange is the most direct method (Zotz & Winter, 1996). The integrated daily carbon gain and nocturnal loss of *A. mangium* phyllodes was $502 \text{ mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ and $54 \text{ mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, respectively. Compared with other tree species, the integrated daily carbon gain of *A. mangium* phyllode is high. For example, the integrated daily carbon gain of *Ficus aurea* and *Ficus nymphaeifolia* was $202.5 \text{ mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ and $214 \text{ mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, respectively (Ting *et al.*, 1987). The nocturnal carbon loss in *A. mangium* was about 10 % of the integrated daily carbon gain; this is in agreement with the study on the 24 h courses of CO_2 exchange of leaves of eight species of tropical rain-forest plants on Barro Colorado Island, Panama (Zotz & Winter, 1993; 1996).

Furthermore, a linear relationship between the light-saturated rate of photosynthetic CO_2 uptake and the integrated daily carbon gain of the plant species was observed from the studies on the diurnal *in situ* gas exchange of eight rain-forest species (Zotz & Winter, 1993), a tropical hemi-epiphyte (*Clusia uvitana*) (Zotz & Winter, 1994), and *Ficus insipida* (Zotz *et al.*, 1995) from Barro Colorado Island, Panama, and this linear relationship could be expressed by an equation (daily carbon gain = $21.2 \times$ the light-saturated photosynthetic CO_2 uptake rate - 2.1) ($R^2 = 0.95$). In addition, Zotz *et al.* (1995) concluded that this linear relationship was quite common among plants, and it can be used in a wide range of species through extrapolating from point measurements of light-saturated rates of photosynthetic CO_2 uptake to integrated daily leaf carbon gain. However, daily carbon gain and light-saturated rates of photosynthetic CO_2 uptake might not be very closely correlated in plant species that display midday depression of photosynthesis, as the decreased midday photosynthesis might cause decreased total daily carbon gain (Zotz *et al.*, 1995). For example, in *Ficus insipida*, diurnal carbon gain was about 20% lower than that predicted by this regression method because of a strong midday depression during the dry season (January) in Panama (Zotz *et al.*, 1995). As only 14.5% midday depression of P_n was observed in *A. mangium*, this regression method could also be used to extrapolate the daily phyllode carbon gain of *A. mangium* from the light-saturated photosynthetic CO_2 uptake rate, and tropical pioneer species with high photosynthetic capacity like *A. mangium* would be expected to have a high daily carbon gain in tropical regions characterized by high radiation and high temperature.

In conclusion, *A. mangium* has high stomatal conductance, high capacities for carbon assimilation, and high light use efficiency in a tropical environment. The

PS II of *A. mangium* phyllodes is tolerant to high PPFD levels and high temperatures. The integrated total daily carbon gain in *A. mangium* is higher than other tropical pioneer species. All these physiological traits allow *A. mangium* to take advantage in tropical high PPFD environments and assist this plant in realizing fast growth.

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