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Photosynthetic performance of *Ginkgo biloba* L. grown under high and low irradiance

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Abstract

Diurnal variation in net photosynthetic rate (P_N) of three-year-old plants of *Ginkgo biloba* was studied under open, O (receiving full sunlight), net-shade, NS (40 % of photosynthetically active radiation, PAR), or greenhouse, G (25 % PAR) conditions. In all three conditions, P_N was higher in morning along with stomatal conductance (g_s), and intercellular CO_2 concentration (C_i), while leaf temperature and vapour pressure deficit were low. The O-plants exhibited a typical decline in P_N during midday, which was not observed in NS-plants. This indicated a possible photoinhibition in O-plants as the ratio of variable to maximum fluorescence (F_v/F_m) and photosystem 2 (PS2) yield (Φ_{PS2}) values were higher in the NS- and G-plants. On the contrary, stomatal density and index, chlorophyll *a/b* ratio, leaf thickness, and density of mesophyll cells were greater in O-plants. Further, higher P_N throughout the day along with higher relative growth rate under NS as compared to O and G suggested the better efficiency of *Ginkgo* plants under NS conditions. Therefore, this plant species could be grown at 40 % irradiance to meet the ever-increasing demand of leaf and also to increase its export potential.

Additional key words: chlorophyll *a* fluorescence; leaf anatomy; leaf mass; net photosynthetic rate; photoinhibition; solar irradiance; stomatal conductance; transpiration rate.

Introduction

Irradiance is the energy source for all photosynthetic organisms, which are finely tuned to harvest it efficiently. On the other hand, excess irradiance captures result in photoinhibition of photosynthesis (Long *et al*. 1994). As a result, plant has devised some sophisticated mechanisms to adapt them in irradiance environment that prevails. The adaptation of photosynthetic apparatus to the prevailing irradiance is known as irradiance acclimation of photosynthesis (Anderson *et al*. 1995). Photosynthetic irradiance acclimation involves a variety of responses, including changes in leaf anatomical (Taiz and Zeiger 1998), morphological (Boardman 1977), biochemical and photosynthetic (Chazdon and Kaufmann 1993) characteristics. There is a close relationship between the leaf characteristics and the mean irradiance experienced by the leaves. Hence irradiance distribution can be used as a predictor for spatial variation of leaf properties (Evans 1993, Pons *et al.* 1993, Anten and Werger 1996). The empirical relationships between leaf irradiance and leaf characteristics are widely used to scale up photosynthesis from leaf to canopy level (Sinquet *et al*. 2001). Leaf photosynthetic characteristics remarkably adapt to irradiance (Evans 1989) and generally, leaves developed at high irradiance exhibit higher photosynthetic capacity per unit leaf area as compared to shade leaves (Niinemets and Tenhunen 1997).

However, exposure of leaves to excessive irradiance is a well-known cause of photoinhibition, which decreases the capacity for photosynthesis in many plants (Baker and Bowyer 1994). Photoinhibition is caused by damage to the photosynthetic components and it may be short term and reversible or long term and irreversible, and is related to increased leaf temperature and to high irradiance when electron transport to acceptors is limited

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Abbreviations: Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; F_v/F_m – ratio of variable to maximum fluorescence; g_s – stomatal conductance for CO_2; LMA – leaf mass per leaf area; PAR – photosynthetically active radiation; P_N – net photosynthetic rate; VPD – vapour pressure deficit; Φ_{PS2} – quantum efficiency of photosystem 2.
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(Melis 1999). Carbon assimilation in trees under field conditions is a complex process influenced by the diurnal and seasonal changes in environmental variables. Diurnal measurements of gas exchange parameters indicate that trees often exhibit midday depression phenomenon in both net photosynthetic rate (P_N) and stomatal conductance for CO_2 (g_s) (Küppers *et al*. 1986). This is associated with high vapour pressure deficits (VPD) (Prado *et al.* 1995), high temperature (Singh *et al*. 1996), and/or strong irradiance (Palanisamy 1996). Excessive irradiance and high temperature also cause low CO_2 concentration at the carboxylation site and high proportion of photorespiration in *G. biloba* despite high ratio of electron transport to CO_2 fixation (Meng *et al*. 1999). Leaf temperature is also important for high productivity, as it affects organ growth (Tanton 1982). Studies also suggest that shade not only lowers leaf temperature but also increases humidity, which in turn increases P_N (Prado *et al.* 1995). Small VPD increases stomatal aperture (Carr 1972), causing an increased conductance to CO_2 diffusion thereby increasing availability of CO_2 for photosynthesis.

G. biloba is an ancient plant long known for its curing properties in health practice and medical care (Kleijnen and Knipschild 1992, Vesper and Hansgen 1994, Shen and Zhou 1995, Murray 1996, Laurin *et al*. 1997). Since the leaves of *Ginkgo* are used for ginkgolide extraction, successful cultivation of this plant is of economic significance. *G. biloba* is an extremely slow growing plant. Under natural temperate Himalayan condition, photosynthetically active radiation (PAR) is relatively high and extreme differences in day-night temperature prevail throughout the year. A set of conditions, under which plants could thrive well, has to be established. Therefore, we analysed the diurnal effects of different environmental factors (irradiance, temperature, VPD) on gas exchange parameters of *G. biloba* in order to scale up its growth and productivity.

Materials and methods

Plants: One-year-old plants of *G. biloba* were raised from semi-hardwood cuttings. These plants were planted during July 1999 in open field (O), net shade (NS), and under greenhouse (G; non automated and roof covered with a layer of *Agro*-net) in the campus of the Institute of Himalayan Bioresource Technology, Palampur (1 300 m a.s.l., 32°6'N, 76°33'E). The O-plants received a maximum of approximately 1 600 μmol m^{-2} s^{-1} of PAR on clear days. However, NS- and G-plants received approximately 40 and 25 % of the incident PAR, respectively. Plants were watered regularly during the summer months but irrigation was not required after the onset of monsoon rains. All the observations were taken after three years during second week of September 2002. Under all conditions, *i.e*. NS, G, and O, the measurements were made from three different plants (three leaves per plant).

Gas exchange: P_N, transpiration rate (E), VPD, g_s, air temperature, and intercellular CO_2 concentration (C_i) were measured on the attached leaves (third and fourth position) at PAR under which the plants were grown and at ambient CO_2 concentration (approximately 355 μmol mol^{-1}), by using a portable computerised open system IRGA (*Li-6400*, *LiCor*, Lincoln, USA). Measurements were made on six consecutive days, which were bright and clear with similar PAR. For all the measurements three similar, healthy, mature leaves of the each plant were selected. The measurement was repeated on three different plants in each case. These observations were also made at constant irradiance (1 000 μmol m^{-2} s^{-1}) and temperature (25 °C). P_N per unit area was determined at different PAR of 50–2 000 μmol m^{-2} s^{-1} at ambient CO_2 concentration of approximately 355 μmol mol^{-1}. CO_2 response curves were determined as ratio of P_N to C_i. These curves were generated using automatic logging system with cuvette temperature set at 25 °C and set to match the sample and reference analysers before recording each new observation. A cool PAR source (*6400-02* LED) fitted on top of the leaf chamber, capable of providing software-adjustable PAR from 0–2 000 μmol m^{-2} s^{-1} served as the irradiation source. For generating P_N/C_i curves, the CO_2 concentration in leaf chamber was reduced using a *6400-01* CO_2 injector. PAR was kept constant at 1 000 μmol m^{-2} s^{-1}. A time interval of 90 s was given to equilibrate the leaf to new conditions in each measurement. Replicates were obtained using automatic logging for each set of P_N/PAR and P_N/C_i curves.

Chlorophyll (Chl) fluorescence and Φ_{PS2} were measured with a portable pulse-modulated fluorescence monitoring system (model *FMS2*, *Hansatech Instruments*, UK) on intact, attached similar leaves, which were used for photosynthetic measurements. After 30 min of dark adaptation, F_0, F_v, and F_m were determined with 100 % of the available actinic PAR (*ca*. 3 000 μmol m^{-2} s^{-1}).

Leaf area and leaf morphology: Leaf areas of 15 fully expanded leaves from each irradiance were measured using leaf area meter *CI-203* (*QC CID,* USA). Stomatal and epidermal cell densities were estimated from surface impressions (clear enamel nail polish) with a care to avoid veins (Meidner and Mansfield 1968), by counting their number with the help of a haemocytometer (1×1 mm) under microscope at 40× magnification. Stomatal index was calculated by using formula [S/(E + S)]×100, where S and E indicate number of stomata and epidermal cells per unit area of leaf, respectively.

Chl content, leaf mass per leaf area unit (LMA), relative growth rate (RGR), and anatomical

measurements: Total Chl content was estimated from 10 leaf discs (0.79 cm^2 each) per replication obtained from randomly selected 3^{rd}-4^{th} leaves from three different plants of each irradiance condition, following the method of Pandey and Nagar (2002). Concentrations of Chl *a* and *b* in extracts were determined from absorbances at 642.5 and 660.0 nm. LMA was determined by drying 10 leaf discs (obtained as stated earlier in case of Chl estimation) at 70 °C till constant mass was achieved. The mean RGR was calculated according to Evans (1972).

Leaf segments (3×7 mm) from the middle of the lamina were fixed in FAA (formaldehyde : acetic acid : 50 % ethanol, 5 : 5 : 90) and dehydrated in a *t*-butyl alcohol series. Sections (10 μm thick) were stained with safranine-fast green, and the slides were mounted in DPX [80–10 g *Distrene* (British Resin product), 5 cm^3 dibutylphtalate, and 35 cm^3 xylene]. Thickness of epidermis and palisade and mesophyll cells was measured under *Nikon Biophot No. 78508* microscope (Japan) at 100× magnification using ocular micrometer.

Differences in the environmental variables, gas exchange, photochemical capacity, PS2 activity, and morphological and anatomical characteristics of the plants of three different irradiances were analysed using factorial Randomised Block Design (RBD) and means were tested against critical difference $p<0.05$.

Results

Environmental conditions for six consecutive days of measurements were similar (Fig. 1). PAR reached its maximum value in all conditions at midday and declined after this period (Fig. 1*A*). The leaf temperature increased with increase in PAR under all the conditions just after sunrise (except for NS), ranged maximum (30–37 °C) at midday, and declined in afternoon. The leaf temperature under G condition was slightly higher than in O- and NS-plants (Fig. 1*B*). In general, leaves of all conditions were cooler at sunrise than sunset. In O, VPD was about 1.0 kPa at sunrise, increased to 2.40 kPa at 10:00, reached a maximum value of 3.33 kPa at midday, and dropped below 1.3 kPa at sunset. Almost similar trend was found for NS-plants. However, the VPD values were little higher in G than NS and O plants, though the differences were statistically insignificant ($p<0.05$).

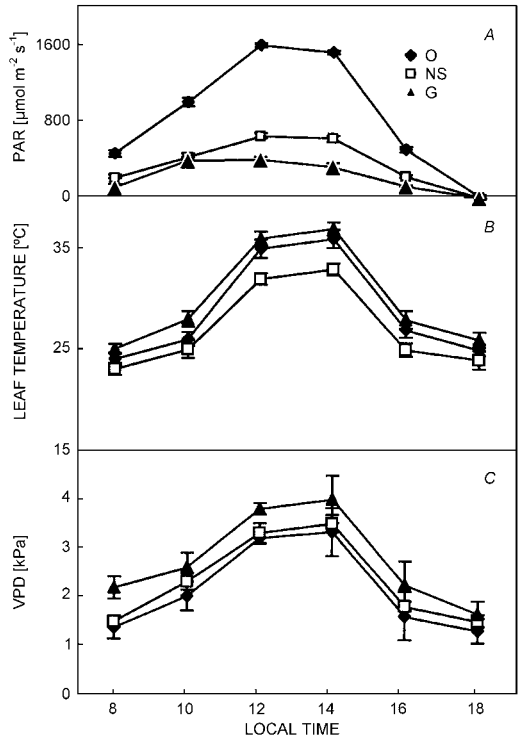

Fig. 1. Diurnal changes in photosynthetically active radiation, PAR (*A*), leaf temperature (*B*), and vapour pressure deficit, VPD (*C*) for *G. biloba* plants grown under open (O), net-shade (NS), and greenhouse (G) conditions. *The vertical bars* indicate standard errors of means.

Photosynthesis: The mean P_N values of leaves from different irradiances increased rapidly from <3.0 μmol(CO_2) m^{-2} s^{-1} to a maximum [approximately 9.0 μmol(CO_2) m^{-2} s^{-1}] between 10:00 to 11:00 (Fig. 2*A*). A progressive decrease ($p<0.05$) in P_N was observed after 12:00 in O-plants, which was less prominent in G-plants, and absent in NS-plants. Further a significant ($p<0.05$) increase in P_N was noticed in O-plants at 16:00, however, in G-plants this increase was not significant ($p<0.05$). In NS-plants a more or less constant P_N was observed up to 14:00 and a decrease followed. In general, P_N was minimal at sunset as compared to after sunrise under all the conditions.

g_s, C_i, and *E* of leaves: Initially after the sunrise g_s and C_i were maximum (Fig. 2*B*,*C*), then decreased towards midday, and again increased in late afternoon. No significant differences in g_s and C_i were observed among all the irradiance conditions. In contrast to this, *E* was minimal in the morning (Fig. 2*D*), increased towards 12:00, and drastically declined ($p<0.05$) in the late afternoon. *E* of O-plants was significantly ($p<0.05$) higher than that of NS- and G-plants.

Chl fluorescence: The Φ_{PS2} and F_v/F_m under NS and G conditions remained high (~0.8) throughout the day (Fig. 3). Under O condition, decreases in both the parameters were observed during noon ($p<0.05$) followed by a recovery in late afternoon.

Chl content, leaf morphology and anatomy, LMA, and RGR: The O-plants had significantly thicker leaves, upper epidermis, and mesophyll cells with greater LMA, stomatal density and index, and Chl *a/b* ratio (Table 1). In contrast to this, G- and NS-plants had significantly larger leaf area, Chl content, and epidermal cell density than the

O-plants (Table 1). Although NS-plants had larger leaf area than G-plants, differences between them were statistically insignificant. Significantly higher mean RGR was recorded for NS-plants followed by O- and G-plants (Table 1).

Table 1. Changes in morphological and anatomical characteristics of *Ginkgo biloba* leaves as affected by different irradiances [open (O), net-shade (NS), and greenhouse (G)]. Different letters in superscript following the values in column showed significant differences at $P<0.05$.

Plants grown under	Leaf area [cm^2]	Leaf thickness [mm]	LMA [g m^{-2}]	Stomatal density [mm^{-2}]	Epidermal cell density [mm^{-2}]	Stomatal index	Epidermis thickness upper [μm]	lower	Cell thickness mesophyll [μm]	palis.	RGR [m m^{-1} y^{-1}]	Chlorophyll content [mg m^{-2}]	*a/b*
O	8.98^{c}	0.32^{a}	1297.0^{a}	96.00^{a}	577.77^{c}	1.17^{a}	29.50^{a}	19.00^{a}	270^{a}	70^{a}	1.43^{b}	119.8^{c}	2.32^{a}
NS	13.95^{a}	0.26^{bc}	957.0^{bc}	65.60^{bc}	791.11^{b}	1.08^{b}	21.79^{bc}	16.50^{bc}	220^{bc}	65^{b}	1.52^{a}	147.0^{b}	2.15^{bc}
G	12.33^{ab}	0.25^{c}	854.0^{c}	60.80^{c}	890.71^{a}	1.07^{b}	18.24^{c}	14.50^{c}	215^{c}	61^{c}	1.40^{bc}	180.0^{a}	2.11^{c}

Discussion

Our study was conducted to assess the changes in morpho-anatomical characteristics and their influences on photosynthetic and growth performances of *G. biloba* grown under different PAR. The findings will advance our understanding for the optimisation of irradiances needed to improve productivity of *G. biloba.* Therefore the plants were grown under three different conditions for three years.

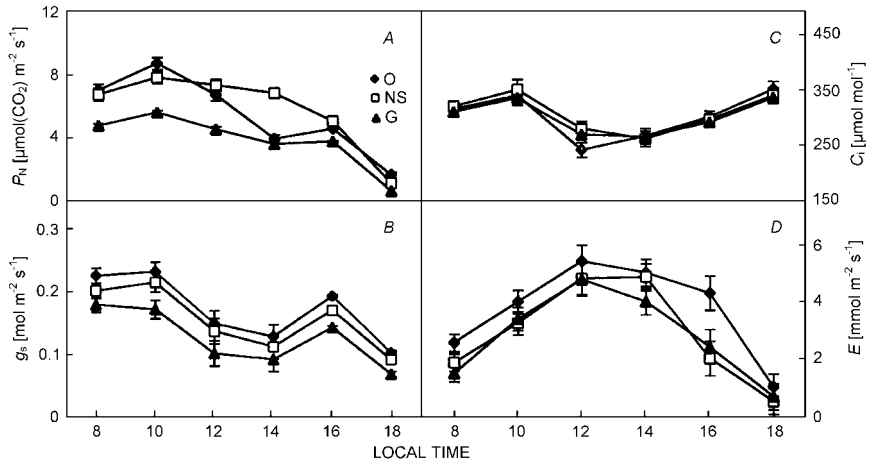

Fig. 2. Changes in net photosynthetic rate, P_N (*A*), stomatal conductance, g_s (*B*), intercellular CO_2 concentration, C_i (*C*), and transpiration rate, E (*D*) of *G. biloba* plants grown under open (O), net-shade (NS), and greenhouse (G) conditions. *The vertical bars* indicate standard errors of means.

A sharp decline in P_N at similar C_i under O-condition at midday unlike NS (Fig. 2*A*,*C*) may be due to high PAR (experienced by O-plants). This may subsequently result in stomatal and non-stomatal limitations to photosynthesis. In several cases, during midday photoinhibition the apparent carboxylation efficiency decreased while C_i remained constant (Gunasekera and Berkowitz 1992). On the other hand, the patchy stomatal closure during midday also inhibits photosynthesis (Beyschlag *et al.* 1992). A high proportion of photorespiration and low CO_2 internal conductance were observed in *G. biloba* leaves exposed to high PAR (Meng *et al*. 1999). We confirmed this from the regression of the maximum P_N measured at PAR of ~1 000 μmol m^{-2} s^{-1} which saturates P_N (measured from irradiance-response curves; data not shown) at 25 °C. In the present study, higher P_N in the morning than in the afternoon at equivalent PAR (Fig. 2*A*) reflects that leaves respond very differently to diurnal course. As the day progressed, irradiance increased to larger values, a peculiar characteristics of the Himalayan mountain system (Vats *et al.* 2002). In O-plants, P_N, F_v/F_m, and PS2 activity decreased (Figs. 2*A* and 3*A*,*B*) at noon and failed to recover back to morning rates even after significant decrease in PAR in the afternoon (Fig. 1*A*). The high irradiance or the associated increase in temperature may be the cause of decreased CO_2 assimilation in O-plants. On the contrary, NS-plants maintained higher P_N up to 14:00. An almost similar trend was noted in G-plants but P_N was significantly lower than in NS-plants (Fig. 2*A*). This finding reflects the poor carboxylation efficiency of G-plants as indicated by initial slope values (0.028±0.002) of the P_N/C_i curve (Fig. 4) which may be

consequence of lower incident PAR (<400 μmol m^{-2} s^{-1}) available to these plants throughout their growth period. This finds support in the study of Zhang *et al*. (2000) who reported that with increasing shade intensity the carboxylation efficiency, leaf area, P_N, saturation irradiance, and dry mass of *G. biloba* plants decrease. For leaves grown under low PAR, less nitrogen is allocated to soluble proteins, and amount of nitrogen in pigment-protein complexes increased from 13 to 21 % of total organic leaf nitrogen (Evans and Poorter 2001). This re-allocation of nitrogen within the leaf is important for the optimisation of photosynthesis (Hikosaka *et al*. 1998). Further, lower RGR (Table 1) of G-plants also indicates their poor efficiency to thrive well under G conditions. The decline in P_N in O-plants at midday may be due to several factors, *e.g*. high PAR causing photoinhibition, high temperature inhibiting metabolism, or larger VPD decreasing g_s and restricting the flux of CO_2 into the leaf or decrease in mesophyll conductance for CO_2 flux to the chloroplasts.

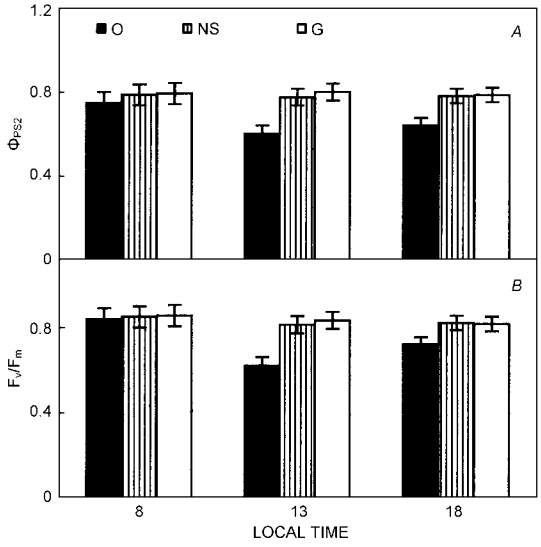

Fig. 3. Diurnal changes in Φ_{PS2} (*A*) and current photochemical capacity, F_v/F_m (*B*) of *G. biloba* plants grown under open (O), net-shade (NS), and greenhouse (G) conditions. *The vertical bars* indicate standard errors of means.

This was further confirmed by our studies conducted at constant temperature (25 °C) and PAR (~1 000 μmol m^{-2} s^{-1}), which exhibited almost similar P_N and g_s throughout the day (Fig. 5*A*,*B*). However, lower P_N and g_s in G-plants could be the consequence of higher VPD under these conditions. This is in accordance with the finding of Franks and Farquhar (1999) of a close relationship of VPD with P_N and g_s in 13 plant species including *G. biloba.* The primary symptom that not all the absorbed photons can be used for photosynthesis is a reduction in maximum F_v/F_m (Fig. 3*B*), which showed a linear correlation with the quantum efficiency of electron transport. Hence a reduction in F_v/F_m is often taken to indicate photoinhibition (Powles 1984). However, from this decrease in efficiency alone a judgement can not be made whether photoprotective or photodamaging processes are responsible. Further, photoinhibitory loss of photosynthetic capacity by inhibition of PS2 activity has been documented for plants exposed to large photon flux for prolonged periods (Baker and Boyer 1994) and this trend was also observed in our study (Fig. 3*A*).

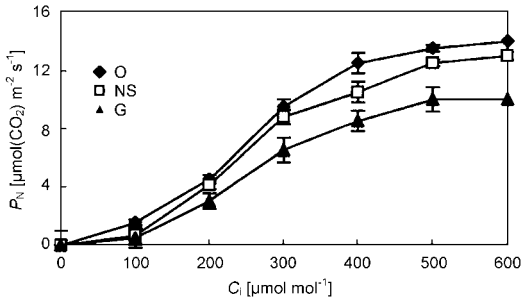

Fig. 4. Initial slope of P_N/C_i curve was 0.038 ± 0.004, 0.036 ± 0.004, and 0.028 ± 0.002 μmol m^{-2} s^{-1} per μmol mol^{-1}(CO_2) for *G. biloba* plants grown under open (O), net-shade (NS), and greenhouse (G) conditions. *The vertical bars* indicate standard errors of means.

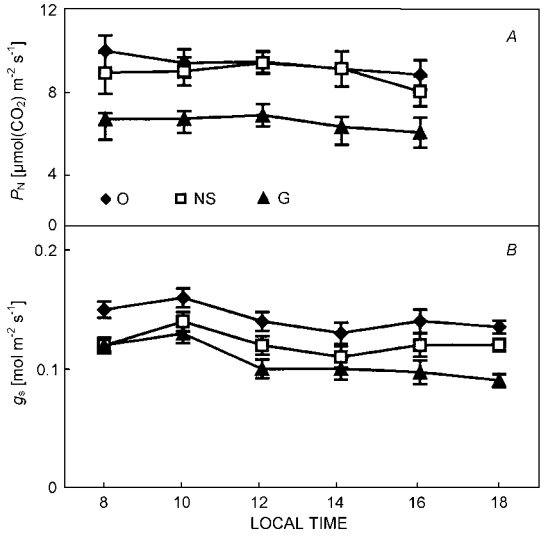

Fig. 5. Response of net photosynthetic rate, P_N (*A*) and stomatal conductance, g_s (*B*) measured at irradiance which saturated photosynthetic CO_2 assimilation (below 1 000 μmol m^{-2} s^{-1} PPFD) and at 25 °C temperature.

C_i is an important factor in the regulation of P_N and decrease in C_i after 10:00 restricted P_N (Fig. 2*A*,*C*) and the excess energy caused photoinhibition. Since P_N was lower in the afternoon, it was expected that C_i would increase at given g_s, compared to the morning. Moreover, stimulation of photorespiration by high temperature would increase C_i and decrease P_N. However, calculation of C_i is subject to a number of potential errors, parti-

cularly heterogeneity (patchiness) in g_s (Weyers and Lawson 1997).

Mesophyll (spongy and palisade) anatomy of *G. biloba* leaf varied with growth irradiance (Table 1). The thicker leaves in sun plants are due to thicker epidermis and mesophyll cell tissue (Lambers *et al*. 1998). An increase in palisade thickness along with high surface area of chloroplasts to intercellular air spaces enhances the efficiency per unit area of leaves to capture more photons (Evans 1999, Nobel 1999). The variation in leaf mesophyll anatomy with growth irradiance was most pronounced in irradiance demanding species of *Acer* (Hanba *et al*. 2002) and the notable mesophyll thickness in full sun was mainly due to thick palisade tissues. Kogami *et al.* (2001) postulated that both mesophyll thickness and low mesophyll porosity are responses of water limitation in high irradiance. Epidermal cell density of NS-plants of *G. biloba* increased with decrease in stomatal density as compared with O-plants which may be due to larger leaf area in such irradiance environment to maximise photon absorption. The reduction in Chl content in O-plant leaves, with significant change in Chl *a/b* ratio (Table 1) as compared to NS- and G-plants was most likely due to changes in both photon harvesting and electron transport components (Schiefthaler *et al.* 1999, Vats *et al.* 2002). However, further study is still needed to examine the effect of leaf anatomical characteristics on various physio-chemical parameters of *G. biloba* to maximise its productivity.

The present study suggests the possible ways of maximising the cultivation of *G. biloba* in order to scale up its productivity and export potential. *G. biloba* is an extremely slow growing plant but thrives well under shade. Hence, the present study suggests the cultivation and maintenance of these plants as bushes under tree canopies in order to attain maximum production of leaves for pharmaceutical uses.

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