Time-course of photosynthetic induction in four tropical woody species grown in contrasting irradiance habitats

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Abstract

We investigated the photosynthetic induction time-course in species of different ecological groups grown in contrasting forest irradiance environments, gap and understorey, exposed to different darkness times in order to verify the plant capacity to exploit irradiance heterogeneity. Photosynthetic induction was studied in leaves of *Bauhinia forficata* and *Guazuma ulmifolia* (early succession species, ES), and *Esenbeckia leiocarpa* and *Hymenaea courbaril* (late succession species, LS). T_{50} and T_{90} (time estimates to attain 50 and 90 % of maximum net photosynthetic rate, respectively) varied according to the time of previous exposure to darkness and growth irradiance. In both darkness times of 10 and 30 min, T_{50} was lower in the LS- than ES-species. These results, jointly with significant higher induction state of the leaves after 10 min of darkness, suggest that the LS-species has a higher potential to sunfleck utilization compared to ES-species, both grown in the understorey. After 10 and 30 min of darkness the differences between ecological groups were not clearly detected in the gap for T_{50} and T_{90}, indicating that eco-physiological characteristics of each ecological group did not influence the induction time of the species evaluated herein. Thus the capacity to show phenotypic plasticity is not exclusive to an ecological group, but it is rather a more intrinsic feature related to the differential capacity of individuals.

Additional key words: *Bauhinia*; *Esenbeckia*; *Guazuma*; *Hymenaea*; intercellular CO_2 concentration; plant eco-physiology; respiration rate; stomatal conductance; sunfleck utilization; tropical forest succession.

Introduction

In tropical forests, the formation and closure of canopy openings of different dimensions create a remarkably heterogeneous irradiance environment (Chazdon and Fetcher 1984, Kira and Yoda 1989). As a consequence, leaves are exposed to highly fluctuating irradiance changing over time that ranges from seconds to minutes or even longer. When irradiance increases after a period of low values, the corresponding increase in photosynthetic CO_2 fixation is not instantaneous and shows a time delay before the maximum rate of assimilation is achieved (Osterhout and Hass 1919, Rabinowitch 1956, Walker 1981). This delay is associated with the process of photosynthetic induction (IS), which involves activation and synthesis of various biochemical components, and with stomata movements (Pearcy 1990). Thus, IS response is dependent on several regulatory mechanisms, each working at a different time scale (Pearcy 1989, 1990). In general, the IS response to irradiance increase can be separated into two phases: an initial fast-induction phase which requires 1−2 min for completion and involves irradiance activation of some Calvin cycle enzymes and build-up of metabolic pools, particularly ribulose-1,5-bisphosphate (RuBP) regeneration (Kirschbaum and Pearcy 1988a, Sassenrath-Cole and Pearcy 1992), and a slow-induction phase, lasting 5−30 min or more, in which RuBP carboxylase/oxygenase (RuBPCO)

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Abbreviations: C_i – intercellular CO_2 concentration; ES – early succession; g_s – stomatal conductance; IS – photosynthetic induction state; LS – late succession; P_{max} – maximum net photosynthetic rate; P_N – net photosynthetic rate; PFD – photon flux density; R_D – dark respiration rate; RuBPCO – ribulose-1,5-bisphosphate carboxylase/oxygenase; T_{50} and T_{90} – time estimates to attain 50 and 90 % of maximum P_N, respectively.
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is activated and stomata open (Kirschbaum and Pearcy 1988b, Pearcy 1990). RuBPCO activation is a two-step process, involving the initial activation of activase and the subsequent activation of RuBPCO (Lan *et al.* 1992). The ability of a plant to utilize variable irradiance regimes depends on the photosynthetic induction state of the leaf (Chazdon and Pearcy 1986b, Pfitsch and Pearcy 1989) and its capacity for post-irradiation CO_2 fixation (Pearcy *et al*. 1985, Chazdon 1988), which determines the readiness of a leaf to respond to an irradiance increase.

Understanding the dynamics of photosynthetic responses to variable irradiance is of fundamental importance for explaining the ecological distribution of species and natural succession (Küppers and Schneider 1993). The degree to which a high state of photosynthetic induction can be maintained during variable irradiance partially determines the capacity of a species to exploit sunflecks within plant canopies (Pearcy 1990). These periods of high irradiance can last for a few seconds to several minutes, and can contribute from 10−80 % of daily photon flux density (PFD) received by a plant (Chazdon 1988). Photosynthesis during sunflecks may contribute to 30−60 % of the daily carbon gain, indicating that plants depend on sunflecks to maintain a positive carbon balance (Chazdon 1988). Previous works have shown that understorey plants typically exhibit photosynthetic adaptation and acclimation that allows maximization of carbon gain under such dynamic irradiance regimes (Chazdon and Pearcy 1986a,b, Ögren and Sundin 1996, Valladares *et al*. 1997).

Plant growth is not determined only by photosynthesis, but the photosynthetic utilization of photon energy plays a major role in the rain forest understorey where irradiance is frequently the most limiting environmental factor (Körner 1991, Küppers and Schneider 1993, Fetcher *et al*. 1994). Differences in photosynthetic characteristics between shade tolerant and irradiance demanding species may allow for differential utilization of the patchy radiation resource in rain forest environments (Press *et al*. 1996).

Variability in the physical environment, especially air and soil temperature, soil moisture, and irradiance in early succession (ES) habitats is higher than in late succession (LS) habitats (Bazzaz 1979). These and other differences between habitats have selected species with specific adaptations to each environment. The degree of flexibility of different species to acclimate to environmental extremes (as temperature, water, and photon availability) must itself be related to the level of environmental variation that is characteristic of the habitat in which the species is normally found (Bazzaz and Carlson 1982). Thus, ES-species might have higher physiological flexibility relative to that of species found in LS-habitats, since the former species typically inhabit environments with higher abiotic variability (Bazzaz 1979).

Based on this hypothesis we expect that ES-species would show higher CO_2 assimilation under full sunlight but not in shade. Moreover, in the understorey, it is expected that the LS-species present faster IS than the ES-ones. We analyzed the time-course of IS of four species from different ecological groups of the tropical forest succession grown in contrasting irradiance environments, with the objective of investigating the IS response in order to verify the plant capacity to exploit irradiance heterogeneity.

Materials and methods

Study site and plants: The study was carried out on a fragment of semi-deciduous seasonal forest with 5.5 ha located in Narandiba, São Paulo, Brazil (22º24’24’’S; 51º31’29’’W, altitude of 354 m). Semi-deciduous seasonal forest is typical Brazilian vegetation conditioned by a duple climatic seasonality, wet and dry season, with 20−50 % of leaf loss in the dry period. The climate is Aw type, defined as tropical with wet summer and dry winter, according to the Köppen classification. The region has a mean annual temperature of 23 ºC, mean rainfall of 1 223 mm, and a mean annual potential evaporative demand of 1 170 mm (Embrapa 2007). Irradiance in the forest gap, from 08:00 to 16:00 h, was approximately 1 600 μmol(photon) m^{-2} s^{-1} and in the understorey did not exceed 25 μmol(photon) m^{-2} s^{-1}. We studied two ES-species, *Bauhinia forficata* Link (Caesalpinoideae) and *Guazuma ulmifolia* Lam. (Sterculiaceae), and two LS-species, *Esenbeckia leiocarpa* Engl. (Rutaceae) and *Hymenaea courbaril* L. (Caesalpinoideae) (Lorenzi 1992), approximately two years old. Ten saplings of each species were planted directly in the soil of the understorey and forest gap environments, without additional use of fertilizer or irrigation, and grown in these sites for about 1 year before the measurements. The gap studied herein presents an area of 34.5 m^2, which corresponds to a small gap with canopy openness around 10 % following the classification proposed by Martins and Rodrigues (2002).

All measurements were taken in three healthy and fully developed leaves in three different individuals of each species in both forest environments. IS measurements were taken in leaves subjected to 10 or 30 min of darkness. These leaves were darkened inside the sample chamber of the open system portable infrared gas analyzer (*CIRAS-2*, *PPSystems*, UK) covered with a black cloth, reducing incident irradiance on the sampled leaf to zero (enabling an initial reading of dark respiration). After this period, leaves were exposed to a pulse of saturating PFD [1 200 μmol(photon) m^{-2} s^{-1}]. The pulse intensity was determined previously by Souza *et al*. (unpublished) through PFD-response curves, which indicated that this irradiance did not cause photo-

inhibition in these plants species.

Gas exchange: In both forest environments leaf gas exchange measurements were carried out from 09:00 to 16:00 h in healthy and fully developed leaves, from the sun exposed parts of the shoots. The measurements were recorded in three plants per species (one leaf per plant), in each environmental condition, in days with no or few clouds. Measurements of net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and dark respiration rate (R_D) were recorded using the *CIRAS-2*, at 10-s intervals, during 1 000 and 1 800 s for plants exposed to 10 and 30 min of darkness, respectively.

IS [%] was calculated as described in Chazdon and Pearcy (1986a):

$$IS\ [\%] = 100\ (P_{sat} - P_{low})\ (P_{max} - P_{low})^{-1}$$

where P_{sat} is the measured net photosynthetic rate 1 min after saturating irradiation, P_{low} is net photosynthetic rate under low irradiance, and P_{max} is the steady-state irradiance saturated photosynthesis. Photosynthetic induction curves were fitted using a sigmoid model, following Zipperlen and Press (1997).

Time estimates to attain 50 (T_{50}) and 90 (T_{90}) % of P_{max} during measurements of transient photosynthesis in saturating irradiance were obtained by fitting a sigmoid function to the induction response curves.

Data analysis: Differences in mean IS, P_{max}, and R_D among the four species growing in two contrasting forest irradiances were analyzed by a 4×2 factorial analysis of variance (two-way ANOVA). The mean values were compared by *a posteriori* Tukey test and considered significantly different at $p<0.05$.

Results

Photosynthetic induction after 10 min of darkness: In the gap, the four species analyzed showed similar final P_N after 10 min of darkness (Fig. 1). Accordingly, Fig. 2*A* indicates that there are no significant differences ($p>0.05$) in P_{max} among species in the gap. Moreover, differences in IS were not significant ($p>0.05$) (Fig. 2*A*), indicating that photosynthetic induction did not differ between the functional groups in the gap. ES-species *B. forficata* and *G. ulmifolia* attained significantly greater P_{max} ($p<0.05$) than LS-species *E. leiocarpa* and *H. courbaril* in the understorey (Figs. 1 and 2), although IS was significantly higher ($p<0.05$) in LS-species (Fig. 2*A*). Thus, following 10 min of darkness in the understorey, ES-species attained a more elevated P_{max}, however, LS-species showed faster photosynthetic induction. Differences in P_{max} between forest environments, gap and understorey, were significant ($p<0.05$) only in LS-species (Fig. 2*A*).

The g_s was higher in the gap than in the understorey for all species, although it did not show a sigmoidal response as P_N in both forest environments (Fig. 1). Species presented a steady pattern of g_s in the gap, except *G. ulmifolia*, while in the understorey there was a trend to increase throughout the IS time course in ES-species (Fig. 1).

In general, C_i did not show marked differences between forest environments and had the tendency to decrease in the IS time course when exposed to continuous saturating irradiance after 10 min of darkness in all species in both forest environments (Fig. 1). Initial C_i was similar in all species studied (about 340−380 mol mol^{-1}).

For all species studied, R_D was significantly higher ($p<0.05$) in the gap than in the understorey, even though in both forest environments there were no significant differences ($p>0.05$) among species (Fig. 2*A*).

Both estimates of T_{50} and T_{90} were higher in the understorey than in the gap for all species (Table 1), since plants required *ca*. 3−4 min to attain 50 % of P_{max} in the gap, whereas in the understorey they required *ca*. 4−10 min. In the gap, in general, both ES- and LS-species presented similar T_{50}, whereas in the understorey the LS-species presented lower T_{50}. With regard to T_{90} in the gap, *G. ulmifolia* presented higher T_{90} than the other three species. In the understorey, *H. courbaril* presented lower T_{90} than the other species, indicating a faster IS response (Table 1).

IS at 30 min of darkness: All the species studied attained greater P_N in the gap than in the understorey after 30 min of darkness (Fig. 3), although differences in P_{max} between forest environments were not significant ($p>0.05$) in all the species (Fig. 2*B*). Moreover, significant differences in P_{max} among species in both forest environments were not detected ($p>0.05$) (Fig. 2*B*). Considering IS, there were no significant differences ($p>0.05$) in both forest environments among species, but regarding forest environments all species presented significantly higher IS ($p<0.05$) in the gap, except *E. leiocarpa* which did not show significant differences ($p>0.05$) (Fig. 2*B*). All together these results indicate that after 30 min of darkness there were practically no significant differences in P_{max} and IS between ecological groups or forest environments when exposed to continuous saturating irradiance. Significant differences in R_D among species in both forest environments were not detected ($p>0.05$), however between forest environments all species presented R_D significantly higher ($p<0.05$) in the gap than in the understorey.

All species studied presented higher g_s in the gap than in the understorey (Fig. 3). The ES-species in both forest environments exhibited a sigmoid IS response for g_s hen exposed to continuous saturating irradiance after 30 min of darkness. *E. leiocarpa* practically did not show

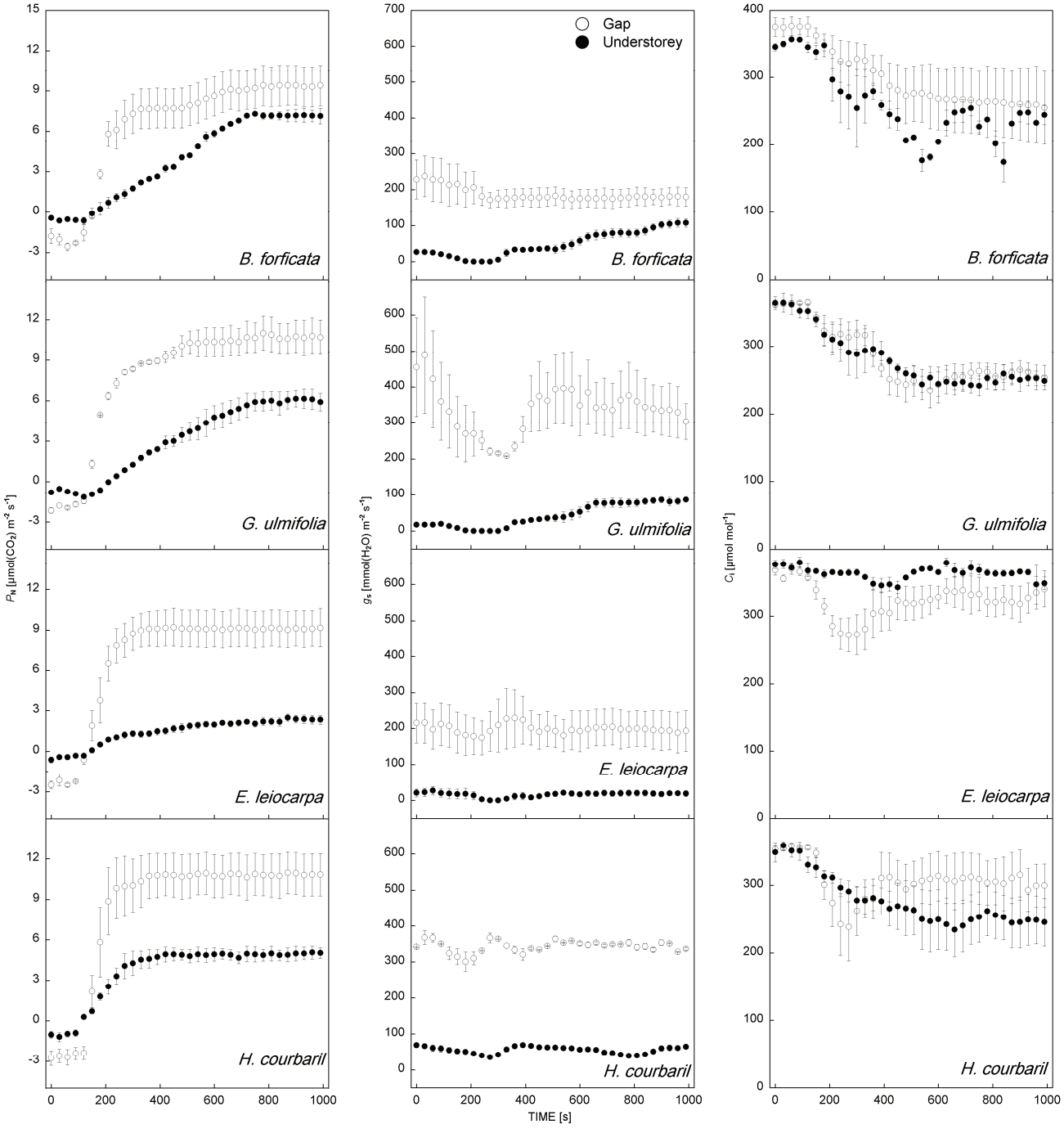

Fig. 1. Time course of the net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) in leaves of *Bauhinia forficata*, *Guazuma ulmifolia*, *Esenbeckia leiocarpa*, and *Hymenaea courbaril* grown in the forest gap (○) and in the understorey (●) after darkness time of 10 min (n = 3). Means of three replicates (n = 3); *bars* represent ± standard error.

alterations in g_s in both forest environments and *H. courbaril* presented a slow increase in g_s in the IS time course in both forest environments (Fig. 3).

After the saturating irradiance pulse, all species studied exhibited a decrease in C_i in both forest environments (Fig. 3). Initial C_i was similar in all species studied (*ca*. 370 μmol mol^{-1}), except in *G. ulmifolia* in the gap which presented elevated higher C_i (*ca*. 430 μmol mol^{-1}).

Plants required *ca*. 6−10 min to attain 50 % of P_{max} in the gap, whereas *ca*. 7−9 min in the understorey (Table 1). *B. forficata, E. leiocarpa*, and *H. courbaril* exhibited similar T_{50} in the gap, whereas in the

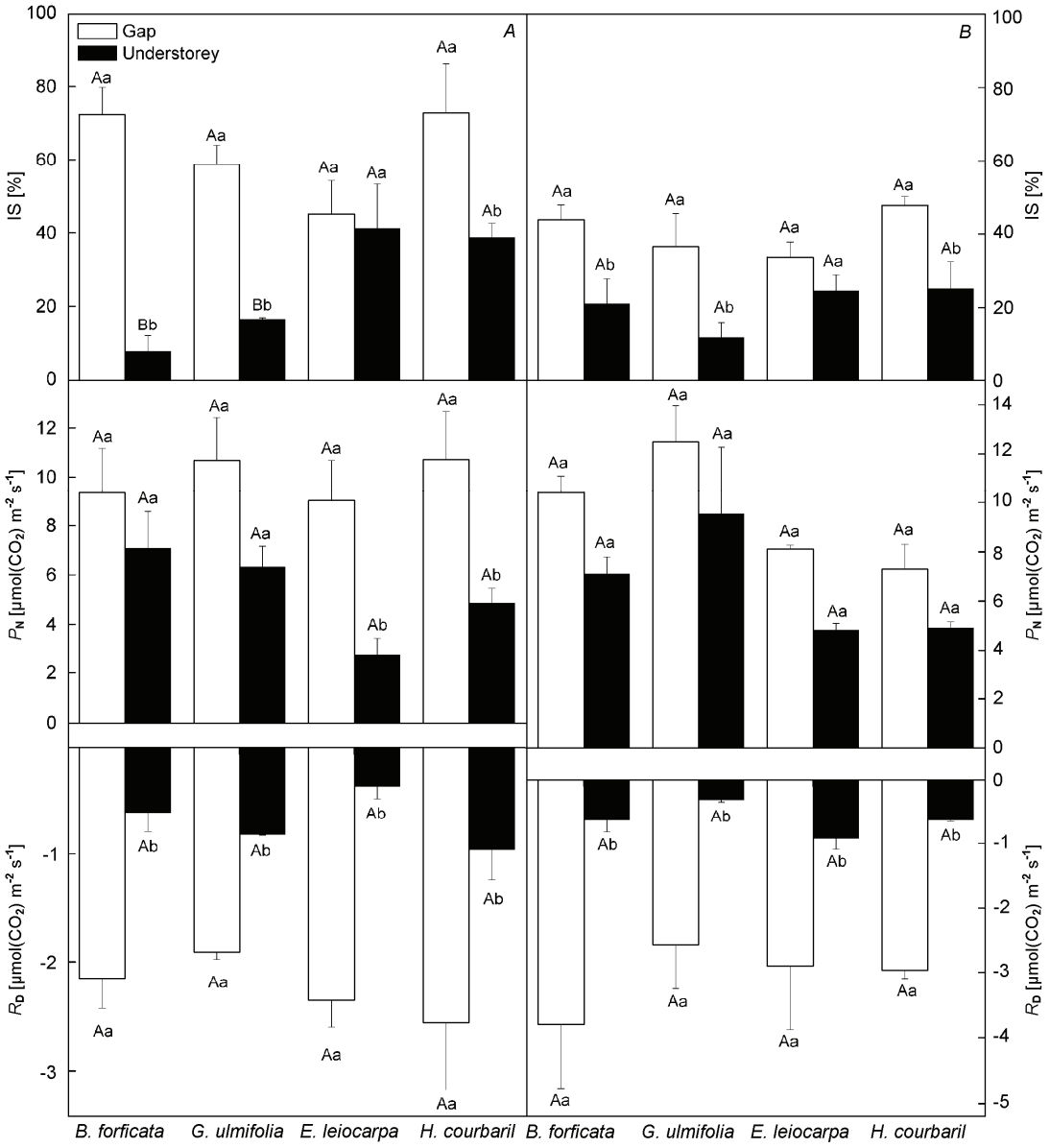

Fig. 2. Photosynthetic induction state (IS), maximum net photosynthetic rate (P_{max}), and dark respiration rate (R_D) in leaves of *Bauhinia forficata*, *Guazuma ulmifolia*, *Esenbeckia leiocarpa*, and *Hymenaea courbaril* grown in the forest gap and in the understorey submitted to 10 min (*left*) or 30 min (*right*) of darkness. *Capital letters* mean difference between species whereas *small letters* mean statistical difference between environments (p<0.05). Means of three replicates (n = 3); *bars* represent ± standard error.

understorey T_{50} was lower in LS-species than in the ES-ones (Table 1). However, pioneer species exhibited lower T_{90} when compared to LS-species.

Discussion

Previous investigations have revealed that stomata can exercise significant influence over photosynthetic induction and light-fleck use efficiency (Kirschbaum and Pearcy 1988b, Tinoco-Ojanguren and Pearcy 1992, 1993b). According to Chazdon and Pearcy (1986a), the time-courses of P_N and g_s appear nearly coincident, while C_i shows an initial drop upon irradiation and then remains relatively stable during the IS period. In our experiments, C_i followed the description of Chazdon and Pearcy (1986a), although a coordinated response between P_N and stomata opening was not always observed in either darkness times or forest environments (Figs. 1 and 3). This coordinated response was only detected in ES-species after 30 min of darkness in both forest environments (Fig. 3).

Table 1. Time estimate to attain 50 (T_{50}) or 90 (T_{90}) % of maximum net photosynthetic rate in leaves of *Guazuma ulmifolia*, *Bauhinia forficata*, *Esenbeckia leiocarpa*, and *Hymenaea courbaril* grown in the forest gap (Gap) and understorey (Us) following 10 and 30 min at darkness (n = 3). Means of three replicates (n = 3) ± standard error.

Species	Environment	Darkness time [min]	T_{50}	T_{90}
B. fortificata	Gap	10	196.13±5.55	227.27±8.69
		30	404.89±38.12	601.94±77.77
	Us	10	615.07±84.79	904.44±160.32
		30	531.95±34.04	765.06±47.27
G. ulmifolia	Gap	10	244.54±39.96	359.78±95.78
		30	541.44±147.93	798.95±224.00
	Us	10	544.20±35.95	797.96±88.23
		30	569.91±47.25	740.88±44.59
E. leiocarpa	Gap	10	202.80±8.44	252.41±12.04
		30	377.71±9.35	537.21±2.68
	Us	10	437.39±151.43	755.03±251.60
		30	464.88±66.43	1028.37±236.74
H. courbaril	Gap	10	199.67±20.23	240.39±34.73
		30	400.76±63.02	633.94±112.37
	Us	10	237.26±23.38	317.81±40.86
		30	474±1590.18	1040.53±190.71

Previous studies reported that increases in P_N after 10−12 min of the irradiance increase have generally been credited solely to subsequent increases in g_s (Tinoco-Ojanguren and Pearcy 1993a, Pearcy *et al*. 1994). We verified an increase in P_N besides of a non-simultaneous increase in g_s, mainly after 10 min of darkness (Fig. 1). These results in the photosynthetic induction course indicate that P_N has a certain degree of independence of increases in g_s, since IS responses were not limited by stomata behaviour. Moreover, before the saturating irradiance pulse, C_i was above 350 μmol mol^{-1} in all species in both forest environments and darkness periods (Figs. 1 and 3). The occurrence of a g_s-independent IS is probably due to the high initial C_i, possibly derived from respiration, which together with the current g_s should have been sufficient to support CO_2 assimilation after darkness period. Furthermore, several authors have reported that non-uniform stomata opening (*i.e.* stomata patchiness) in response to a sudden increase in irradiance might cause differences in biochemical activation throughout the leaf (Kirschbaum and Pearcy 1988b, Tinoco-Ojanguren and Pearcy 1993b, Küppers *et al*. 1999, Allen and Pearcy 2000).

In order to grow in low irradiance environments such as the forest understorey, where plants have low carbon gain (Chazdon *et al*. 1996, Strauss-Debenedetti and Bazzaz 1996), plants must minimize carbon loss trough reduction of both respiration and tissue construction costs (Givnish 1988), attaining a positive leaf carbon balance. Our data are in accordance with those previously reported since all species studied showed significant higher R_D in the forest gap than in the understorey (Fig. 2). Several authors also verified that respiration is higher in forest gap than in understorey, since higher irradiance usually implies higher metabolic rates (Ramos and Grace 1990, Fredeen and Field 1991, Han *et al*. 1999). Moreover, some studies also describe that ES-species usually show higher leaf respiration than the LS-ones (Bazzaz and Pickett 1980, Chazdon *et al*. 1996), but in our study significant differences were not detected in R_D between species in both forest environments (Fig. 2).

The higher standard error in the graphs of P_N, g_s, and C_i in both darkness times, principally for ES-species in the gap, indicates the greater variability between samples in this environment (Figs. 1 and 3). Since all gas exchange parameters showed higher standard error in the gap, we suggest that under this environment plants showed a higher variability of response compared to understorey. In this latter, more constant environment, plants possibly have a more stable metabolism, implying a smaller standard error. Accordingly, Bazzaz (1979) described that it is generally assumed that variability in the physical environment especially in air and soil temperature, soil moisture, and irradiance in ES-habitats is higher than in LS-habitats.

We found that T_{50} and T_{90} varied according to the time of previous exposure to darkness mainly in the gap, where the difference between darkness times was higher (Table 1). Such results indicate that the rate at which IS is recovered depends on the previous exposure to darkness and irradiance growth environment. As previously reported, the time required to reach full photosynthetic induction depends in part on the length of the period and PFD of low irradiance (Pons *et al*. 1992, Whitehead and Teskey 1995). The IS state of a leaf is determined by the immediate past iradiance (Pearcy and Seemann 1990) and

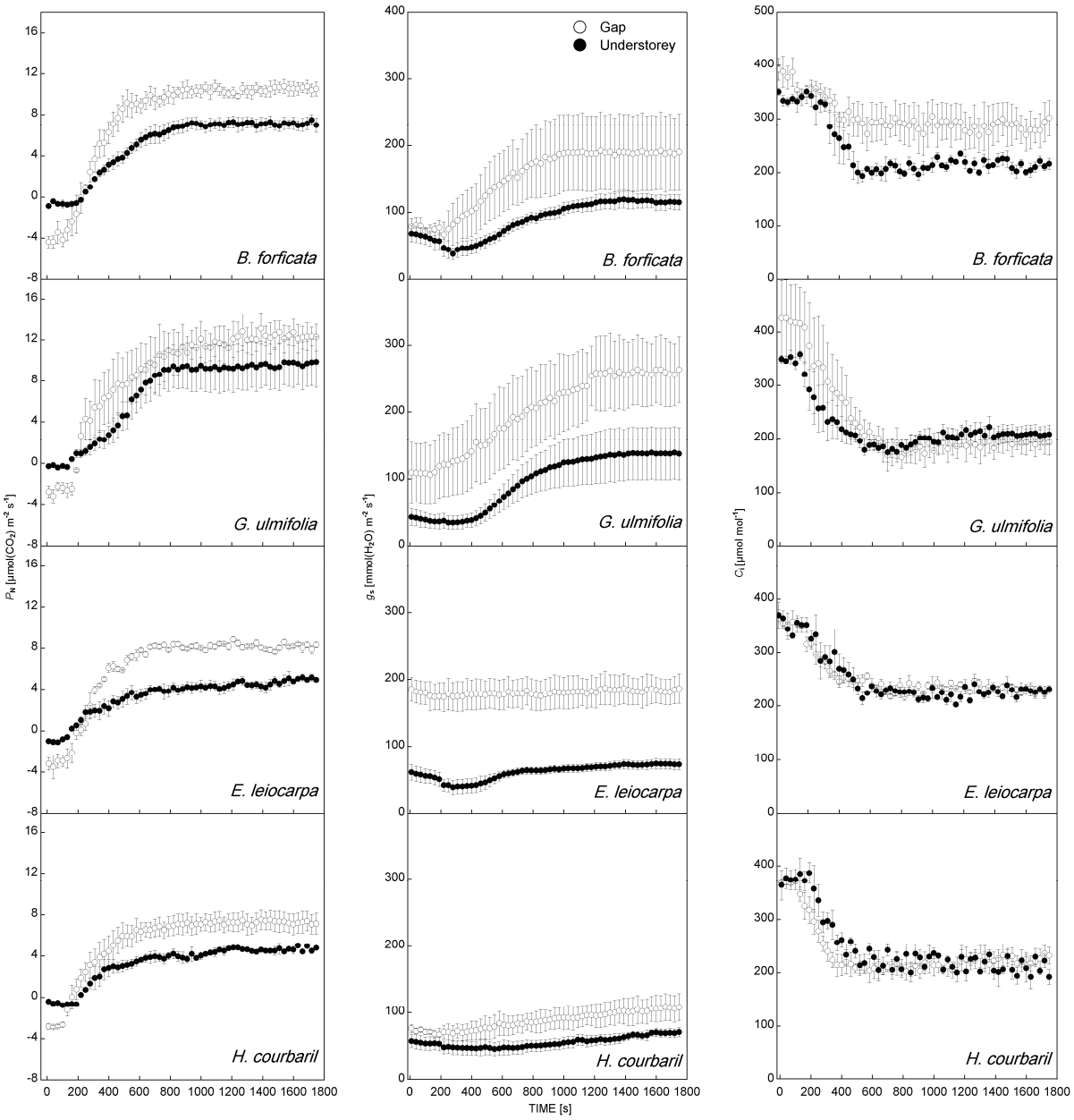

Fig. 3. Time course of net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) in leaves of *Bauhinia forficata*, *Guazuma ulmifolia*, *Esenbeckia leiocarpa*, and *Hymenaea courbaril* grown in the forest gap (○) and in the understorey (●) after darkness time of 30 min (n = 3). Means of three replicates (n = 3); *bars* represent ± standard error.

declines when an induced leaf is shaded longer than a minute or so, and can be increased by exposure of a shaded leaf to a series of sunflecks (Pearcy 1989).

Differences in T_{50} and T_{90} among plants exposed to 10 and 30 min of darkness were higher in the gap than in the understorey. This result indicates that when plants remain over a 10 or 30 min dark period, their photosynthetic apparatus demands more time to induce in the gap, whereas in the understorey estimates of T_{50} and T_{90} indicated that the photosynthetic apparatus remains induced for longer time suggesting a more rapid activation of RuBPCO, requiring less time to attain T_{50} and T_{90}. Rijkers *et al*. (2000) suggested that leaves of understorey saplings of *Pourouma bicolor*, which required the least time to reach 75 % of biochemical induction, presented a more rapid activation of RuBPCO. However, in several studies RuBPCO activity did not vary among and within species (Seemann and Kobza 1988, Tinoco-Ojanguren and Pearcy 1993b).

After 10 and 30 min of darkness the differences between ecological groups were not clearly detected in the gap for T_{50} and T_{90}, indicating that eco-physiological

characteristics of each ecological group did not influence the IS time of the species evaluated herein. On the other hand, after both darkness times, the LS-species showed lower T_{50} in the understorey indicating a faster IS. After 30 min of darkness, the ES-species showed lower T_{90} than the LS-species in the understorey, possibly related to the required eco-physiological characteristics of their typical growth environment. Therefore, although LS-species recovered the IS more rapidly, P_{max} was attained faster by ES-species (Table 1). Conversely, previous studies showed that T_{90} was short in shade-tolerant species (Kursar and Coley 1993, Chen and Klinka 1997, Valladares *et al*. 1997, Naumburg and Ellsworth 2000). Nevertheless, for some other species such as *Alocasia macrorrhiza*, *Toona australis*, *Shorea leprosula*, *Dryobalanops lanceolata*, *P. bicolor,* and *Dicorynia guianensis* in tropical environments, IS times were not affected by irradiance (Chazdon and Pearcy 1986a, Kursar and Coley 1993, Zipperlen and Press 1997, Rijkers *et al*. 2000).

After 10 min of darkness, the LS-species in the understorey showed significantly higher IS than the ES-ones (Fig. 2*A*) while after 30 min, LS presented a trend to show higher IS although the differences were not significant (Fig. 2*B*). These results of IS jointly to lower T_{50} in LS-species indicate that, after a period of darkness, this ecological group has a higher potential to exploit sunflecks compared to ES-species when both are grown in the understorey. Since sunflecks occur in short intervals, parameters such as IS and T_{50} can indicate the capacity to promptly respond to irradiance increase. Probably shade leaves maintained a higher IS longer at lower PFDs than sun leaves. Some comparative studies have suggested the latter may be capable of using sunflecks more efficiently than the previous (Chazdon and Pearcy 1986b, Chow *et al*. 1988, Küppers and Schneider 1993, Tang *et al*. 1994, Yanhong *et al*. 1994, Ögren and Sundin 1996). In agreement with this assumption, Poorter and Oberbauer (1993) and Küppers *et al*. (1996) reported that LS-species maintained a higher IS status longer than the ES-ones. In *A. macrorrhiza*, RuBPCO is 50 % deactivated after 30 min in low irradiance, whereas in *T. australis*, the shade-intolerant species, it is deactivated more rapidly (Chazdon and Pearcy 1986b). Valladares *et al*. (1997) demonstrated that understorey species showed rapid induction, since IS was significantly higher, and higher light-fleck use efficiency for short light-flecks compared to species found in clearings or small gaps. Photosynthetic utilization of sunflecks requires a quick, dynamic physiological response, which is dependent on several regulatory factors, each working at a different time scale and exhibiting remarkable variation among species and individuals grown under different irradiance (Pearcy 1990). Due to the differences in responses between plants exposed to 10 and 30 min of darkness it was possible to verify in our results that the species' capacity declines after a long period of darkness, possibly due to the inactivation of the photosynthetic apparatus. After 30 min of darkness differences between species were not marked, indicating that the photosynthetic apparatus of species from both ecological groups deactivates and requires induction to utilize photon energy efficiently.

Our results are in agreement with those reported by Valladares *et al*. (1997), who found that P_{max} and g_s were lower in understorey species than in species growing in small gaps or clearings. However, some shade-tolerant species show a significant efficiency to increase photosynthetic capacity in response to increase in irradiance availability (Chow *et al*. 1988, Turnbull 1991, Thompson *et al*. 1992). Our results show that LS-species presented elevated P_{max} in the gap and ES-ones presented elevated P_{max} in the understorey (Fig. 2), indicating high photosynthetic plasticity in species of both groups. Strauss-Debenedetti and Bazzaz (1996) state that differences in photosynthetic characteristics are generally viewed as being adaptive in nature, even if they may only reflect the constraints imposed by resource limitation. As plasticity addresses the expression of variable phenotypes under different environments (Bradshaw 1965), since both light-demanding and shade-tolerant species are capable of phenotypic plasticity, we conclude that adjustments are not necessarily related to the succession status of the species (Turnbull 1991, Popma *et al*. 1992).

Corroborating our initial hypothesis, the ES-species presented higher P_N in the gap than in the understorey, suitably with their eco-physiological characteristics, although these species had presented a high performance also in the understorey after 10 or 30 min of darkness. As expected, the LS-species presented a faster photosynthetic induction than the ES-ones in the understorey, also in agreement with their eco-physiological features. We found that, after 10 min of darkness, plants in the understorey presented a higher potential in sunfleck utilization than after 30 min, above all the LS-species. Probably after a longer darkness period the photosynthetic apparatus is partially deactivated, which tended to be higher in ES-species.

The IS time course and other parameters evaluated in the present study evidences that plant responses can be modulated by their growth environment, indicating that the physiological and metabolic state of plant species are conditioned to environmental physical factors. Species occupy distinct niches based on their abilities to respond to different environment, and the capacity to show phenotypic plasticity is not exclusive to an ecological group. It is rather a more intrinsic feature related to the differential capacity of individuals. Thus, the influence of the species ecological group derives from some distinctive characteristics of their typical habitat, which partially determines their performance when faced to adverse conditions.

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