

Network connectance and autonomy analyses of the photosynthetic apparatus in tropical tree species from different successional groups under contrasting irradiance conditions

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ABSTRACT – (Network connectance and autonomy analyses of the photosynthetic apparatus in tropical tree species from different successional groups under contrasting irradiance conditions). Biological systems are complex dynamical systems whose relationships with environment have strong implications on their regulation and survival. From the interactions between plant and environment can emerge a quite complex network of plant responses rarely observed through classical analytical approaches. The objective of this current study was to test the hypothesis that photosynthetic responses of different tree species to increasing irradiance are related to changes in network connectances of gas exchange and photochemical apparatus, and alterations in plant autonomy in relation to the environment. The heat dissipative capacity through daily changes in leaf temperature was also evaluated. It indicated that the early successional species (*Citharexylum myrianthum* Cham. and *Rhamnidium elaeocarpum* Reiss.) were more efficient as dissipative structures than the late successional one (*Cariniana legalis* (Mart.) Kuntze), suggesting that the parameter ΔT ($T^{\circ}\text{C}_{\text{air}} - T^{\circ}\text{C}_{\text{leaf}}$) could be a simple tool in order to help the classification of successional classes of tropical trees. Our results indicated a pattern of network responses and autonomy changes under high irradiance. Considering the maintenance of daily CO_2 assimilation, the tolerant species (*C. myrianthum* and *R. elaeocarpum*) to high irradiance trended to maintain stable the level of gas exchange network connectance and to increase the autonomy in relation to the environment. On the other hand, the late successional species (*C. legalis*) trended to lose autonomy, decreasing the network connectance of gas exchange. All species showed lower autonomy and higher network connectance of the photochemical apparatus under high irradiance.

Key words - dissipative structures, functional groups, high irradiance, network connectance, photosynthesis

RESUMO – (Análises de conectância da rede e autonomia do aparato fotossintético em espécies tropicais arbóreas de diferentes grupos sucessionais sob condições de irradiância contrastantes). Sistemas biológicos são sistemas dinâmicos complexos cujas relações com o ambiente apresentam importantes implicações sobre seus processos de regulação e sobrevivência. A partir destas interações pode emergir uma complexa rede de respostas que raramente são observadas pelas abordagens analíticas clássicas. Desta forma, o objetivo deste estudo foi testar a hipótese de que as respostas fotossintéticas de diferentes espécies arbóreas ao aumento da irradiância estão relacionadas às mudanças na conectância das redes de trocas gasosas e do aparato fotoquímico, assim como mudanças no grau de autonomia entre planta e ambiente. A capacidade de dissipação térmica avaliada por mudanças da temperatura foliar ao longo do dia também foi analisada, indicando que as espécies iniciais da sucessão (*Citharexylum myrianthum* Cham. e *Rhamnidium elaeocarpum* Reiss.) foram mais eficientes que a espécie tardia (*Cariniana legalis* (Mart.) Kuntze) como estruturas dissipativas. Isto sugere que o parâmetro ΔT ($T^{\circ}\text{C}_{\text{ar}} - T^{\circ}\text{C}_{\text{folha}}$) poderia ser uma ferramenta adicional para auxiliar na identificação das classes sucessionais de espécies tropicais arbóreas. Nossos resultados indicaram a ocorrência de um interessante padrão de resposta das redes e mudanças na autonomia quando as plantas foram submetidas à alta irradiância. Considerando a assimilação diária de CO_2 , as espécies tolerantes (*C. myrianthum* e *R. elaeocarpum*) tenderam a manter a conectância da rede de trocas gasosas estável e aumentar a autonomia em relação ao ambiente. Por outro lado, a espécie susceptível (*C. legalis*) à alta irradiância tendeu a perder autonomia, diminuindo a conectância da rede das trocas gasosas. Todas as espécies apresentaram menor autonomia e maior conectância da rede do aparato fotoquímico sob alta irradiância.

Palavras-chave - alta irradiância, conectância de redes, estruturas dissipativas, fotossíntese, grupos funcionais

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Introduction

In general terms, ecophysiology can be considered, *par excellence*, the science of the interactions between plant and environment upon a physiological approach (Larcher 1995). In such perspective, some conceptual considerations are needed. First of all, living systems are always open systems. They continuously exchange

material, energy and information with their environment (Schneider & Kay 1994, Mohr & Schopfer 1995). Second, living systems are systems in continuous state of change in several scales (molecular, metabolic, cellular, and morphological). Therefore, they are continuously losing energy and increasing their entropy (energy not useful to work), which must be dissipated (Mohr & Schopfer 1995, Souza *et al.* 1999). Finally, biological systems are hierarchically organized. This means that such systems cannot be fully understood if one or more elements of them are separately analyzed. Since biological systems are composed by interactive elements, such systemic interactions lead the system to display characteristics that could not be recognized in isolated elements (Mohr & Schopfer 1995, Souza & Cardoso 2003). Therefore, approaches that access and quantify system interactions, considering the networks of relationships among system elements, are required in order to improve the classical physiological methods.

Prado *et al.* (2004) and Souza *et al.* (2004) have suggested that the effects of environmental disturbances on the photosynthetic network may be evaluated through the strength of the network connectance, according to the approach suggested by Amzallag (2001). This author suggests the network connectance evaluation, a statistical method based on path analysis (Li 1975), through the analysis of the normalized correlation coefficient between network parameters. According to Amzallag (2001), the correlation coefficient can be considered not only a test of the significance, but also a measure of strength of the relationship (connection) between two parameters. The number and strength of the connections among elements in a network of an organism is directly related to the system stability (Trewavas 1986, Edelman & Gally 2001). So, a greater connectance may achieve, *a priori*, higher system stability, existing a critical threshold for the system connectance level that could negatively influence the system stability (Gardner & Ashby 1970). Thus, tighter network connectance could perform a higher level of system control, improving the system capacity to face external perturbations. Accordingly, changes in the system connectance, mostly connectance increases, could be considered as acclimatory responses to environmental disturbances.

Souza *et al.* (2004) have suggested a new approach in order to analyze the ecophysiological responses of tropical tree species to environmental changes. In that report the authors used the difference between air and leaf temperature (ΔT) to access the global dissipative capacity of plants under water deficit. In addition, Souza

et al. (2004) analyzed systemic changes in the network connectance of gas exchange, as well as the relationship of each gas exchange parameter with the environment to estimate plant autonomy in relation to the external conditions.

In the present study we considered flexibility as the plant capacity to respond to environmental changes throughout the day taking into account positive or negative relationships between physiological parameters and environmental variables. Therefore, we evaluated flexibility of response of tropical species in a wider ecological approach, considering not only “favorable” responses but also protective or restrictive responses. To accomplish this, we evaluated the autonomy (At) of the species through analysis of the correlation between physiological parameters and environmental variables. Changes of the network connectance of photosynthetic apparatus underlying such At changes were also evaluated.

In addition to water availability, temperature and nutrients, irradiance has critical influence on establishment, growth, survival and reproduction of plant species (Chazdon *et al.* 1996, Strauss-Debenedetti & Bazzaz 1996). According to spatial and temporal distribution in the forest mosaic, where plants have different capacities of surviving and developing (Pickett *et al.* 1987, Luken 1990), tree species may be separated into two main successional groups: *i*) an early successional group (pioneer and early secondary species), which has irradiance demand and *ii*) a late successional group (late secondary species), which is shade tolerant. Thus, species can be grouped according to successional groups defined on the basis of growth and shade adaptation (Bazzaz & Pickett 1980). Since early and late successional plants differ in photosynthetic characteristics, differences are expected to arise when these plants are submitted to similar conditions, especially to high irradiance (Strauss-Debenedetti & Bazzaz 1996).

The photosynthetic activity depends on both efficiency of the photochemical apparatus and stomatal control of gas exchange. However, such regulation could not be simply represented since multiple regulation pathways of stomatal aperture have been identified. They are based on the influence of intercellular CO₂ concentration, irradiance intensity (through the effect on stomatal photosynthesis), irradiance quality (through phytochrome), temperature, vapor pressure deficit and water status (water potential) of leaf tissues, concentration and cell sensitivity to phytohormones growth regulators (PGR), and the biological clock

(Farquhar & Sharkey 1982, Zeiger *et al.* 1987, Erdei *et al.* 1998, Jones 1998). In addition, the photochemical activity involves an intricate network of regulation processes that can be influenced by external factors such as temperature, water deficit and irradiance (Yordanov *et al.* 1997, Critchley 1998, Krause *et al.* 2001). Thus, the photosynthetic responses to increasing irradiance could have their understanding complemented by the approach proposed by Amzallag (2001) and Souza *et al.* (2004), since such responses result from the interactions between a very complex photosynthetic network and the environment.

Accordingly, the objective of the current study was to test the hypothesis that photosynthetic responses of tropical tree species from different successional groups under contrasting irradiance are related to changes in the network connectance of gas exchange and photochemical apparatus as well as changes in plant autonomy in relation to the environment.

Material and methods

Plant material – Based on the ecophysiological results of Ribeiro *et al.* (2005), we selected representative species from three successional groups: pioneer, early secondary, and late secondary species (Gandolfi *et al.* 1995, Martins & Rodrigues 2002). *Cariniana legalis* (Mart.) Kuntze (Lecythidaceae) is a late secondary semi-deciduous species, *Rhamnidium elaeocarpum* Reiss. (Rhamnaceae) is an early secondary deciduous tree, and *Citharexylum myrianthum* Cham. (Verbenaceae) is a semi-deciduous pioneer species (Lorenzi 1992).

Irradiance conditions - The seedlings were maintained under medium irradiance (MI) condition (34% of full sun-light) for 30 days, simulating a nursery condition. Measurements of leaf gas exchange and chlorophyll *a* fluorescence were taken at MI and after 72 h of seedling transference to the high irradiance (HI) regime (in open area located in Piracicaba, SP Brazil, 22°42' S and 47°38' W, 546 m of altitude). Air temperature, photosynthetic photon flux density (PPFD) and leaf-to-air vapor pressure difference ($VPD_{leaf-air}$) in both MI and HI conditions are shown in figure 1. Physiological evaluations (leaf gas exchange and chlorophyll *a* fluorescence) were carried out in both irradiance regimes and always in the same three plants of each species, randomly disposed in a 6 m² area, and in the same fully expanded leaf exposed to light in each plant. The measurements were taken between 7:30 and 16:30 h in intervals of 1 h (except between 11:30 and 13:30 h) in a clear day (without clouds) in each irradiance regime in August 2002. Leaf gas exchange and leaf temperature measurements – CO₂ assimilation (A, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), stomatal conductance (gs, $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), transpiration (E, $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and intercellular CO₂ concentration (Ci, $\mu\text{mol}\cdot\text{mol}^{-1}$) were taken

with a portable infrared gas analyzer working in open system (LI-6400, Li-Cor, Lincoln, NE, USA). Before measurements, the gas exchange system was zeroed using CO₂-free and H₂O_{vapor}-free air. We used a leaf chamber of 6 cm² and natural irradiance. The air entering the gas analyzer was drawn from height of 2 m above ground and passed through 10 L mixing volume before reaching the leaf chamber. Air CO₂ concentration was $360 \pm 10 \mu\text{mol}\cdot\text{mol}^{-1}$ during measurements. The capacity of leaf temperature maintenance was calculated as the difference between air and leaf temperatures ($\Delta T = T_{air}^{\circ\text{C}} - T_{leaf}^{\circ\text{C}}$) during all light period as a measure of global heat dissipation efficiency (Souza *et al.* 2004). Leaf temperature was measured using the chromel-constantan thermocouple of the LI-6400 appressed to the lower leaf surface. Chlorophyll *a* fluorescence measurements – Chlorophyll *a* fluorescence was recorded using a PAM-2000 portable fluorometer system (Walz, Effeltrich, Germany). The fluorometer was operated via a Palm-top computer (Hewlett Packard Co., Idaho, USA), which also stored the measured fluorescence data. A special leaf clip holder was used (2030-B, Walz, Effeltrich, Germany), with which the fiberoptics could be adjusted at a defined angle (60°) and a fixed distance relative to the leaf. This leaf clip holder has a micro-sensor to monitor PPFD and a thermocouple to measure lower leaf surface temperature. Measurements were taken in both light- and dark-adapted (30 min) leaves. The following parameters were assessed in order to evaluate photochemical activity: potential [$F_v/F_m = (F_m - F_o)/F_m$] and effective [$\Delta F/F_m' = (F_m' - F)/F_m'$] quantum efficiency of photosystem II (PSII) (Genty *et al.* 1989), and the apparent electron transport rate (ETR) through PSII ($\text{ETR} = \Delta F/F_m' \times \text{PPFD} \times 0.5 \times 0.84$) (Krall & Edwards 1992). Photochemical quenching [$qP = (F_m' - F)/(F_m' - F_o')$] and non-photochemical quenching [$\text{NPQ} = (F_m - F_m')/F_m'$] were calculated according to Van Kooten & Snel (1990). F_m and F_o were maximum and minimum fluorescence yields of dark-adapted leaves, respectively, and F_m' and F were maximum and steady state fluorescence yields in light-adapted state, respectively. F_o' was the minimum fluorescence yield after photosystem I (PSI) excitation by far-red light. For the calculation of ETR, 0.5 was used as the fraction of excitation energy distributed to PSII, and 0.84 was used as a general fraction of total irradiance absorbed by leaves (Demmig & Björkman 1987).

Data analysis – The experimental design was in random blocks with three replicates, where the factors were the irradiance conditions (MI and HI) and the time of day. Data were submitted to variance analysis procedures (ANOVA) and the mean values compared by the Tukey test ($p < 0.05$).

We utilized the approach proposed by Amzallag (2001) to evaluate changes in the networks of gas exchange and photochemical apparatus in each species and irradiance regime. The network connectance was assessed through the analysis of the normalized correlation coefficient (z) between two measured parameters: $z = 0.5 \ln[(1+|r|)/(1-|r|)]$, where r-values represent the regression coefficient of all measurements taken

in each day. In our study, the z-value is a quantification of the relationship between evaluated parameters related to the photosynthetic process and the environment. We separated the photosynthetic system into two regulation networks, the gas exchange network constituted by the pairs of parameters gs-A, gs-E, gs-Ci, A-Ci and A-E, and the photochemical network constituted by the relations $\Delta F/F_m' - qP$, $\Delta F/F_m' - ETR$, $\Delta F/F_m' - F_v/F_m$ and $\Delta F/F_m' - NPQ$.

The network global connectance (Cg) was calculated as the average of the z-values of each pair of parameters (Amzallag 2001). Cg value represents the level of global co-ordination of gas exchange and photochemical activity. Plant autonomy (At) was calculated as the average of z-values of all physiological parameters in relation to the photosynthetic photon flux density (PPFD), leaf-to-air vapor pressure difference ($VPD_{leaf-air}$) and temperature (T °C) in both irradiance conditions (Souza *et al.* 2004). Thus, the lower the species connectance with its surrounding environment (At value) the higher the autonomy degree will be, i.e. higher connectance between plant and environment means higher flexibility degree.

Abbreviation list – MI (medium irradiance), HI (high irradiance), PPFD (photosynthetic photon flux density), $VPD_{leaf-air}$ (leaf-to-air vapor pressure difference), A (CO_2 assimilation), gs (stomatal conductance), E (transpiration), Ci (intercellular CO_2 concentration), DT (difference between air and leaf temperatures), F_v/F_m (potential quantum efficiency of photosystem II), $\Delta F/F_m'$ (effective quantum efficiency of photosystem II), ETR (apparent electron transport rate), qP (photochemical quenching), NPQ (non-photochemical quenching), z (normalized correlation coefficient), Cg (network global connectance), At (plant autonomy), DIA (daily-integrated CO_2 assimilation).

Results

Environmental conditions – Mean solar global radiation in August 2002 (local weather station) was $14.4 MJ.m^{-2}.d^{-1}$, with an average relative humidity of 77% and maximal air temperature above 31 °C. Air temperature in HI and MI was from 21 to 39 °C, and from 21 to 36 °C, respectively. The $VPD_{leaf-air}$ varied from 0.6 to 5.3 kPa under HI, while this variation was from 0.7 to 3.8 kPa under MI. PPFD changed from 100 to $1,800 \mu mol.m^{-2}.s^{-1}$ under HI, but at MI these values varied between 50 and $600 \mu mol.m^{-2}.s^{-1}$ (figure 1). The daily-integrated PPFD was around $13.83 mol.m^{-2}.d^{-1}$ under MI and around $39.60 mol.m^{-2}.d^{-1}$ in HI.

General effects of high irradiance on photosynthesis and leaf dissipative capacity – The diurnal courses of gas exchange and chlorophyll a fluorescence were previously described in Ribeiro *et al.* (2005). Deleterious effects on photosynthesis of plants transferred from MI

to HI were sharply observed in the late successional species *Cariniana legalis*. In this species, daily-integrated CO_2 assimilation (DIA) was reduced in 47.6%, while both early successional species maintained DIA stable (table 1).

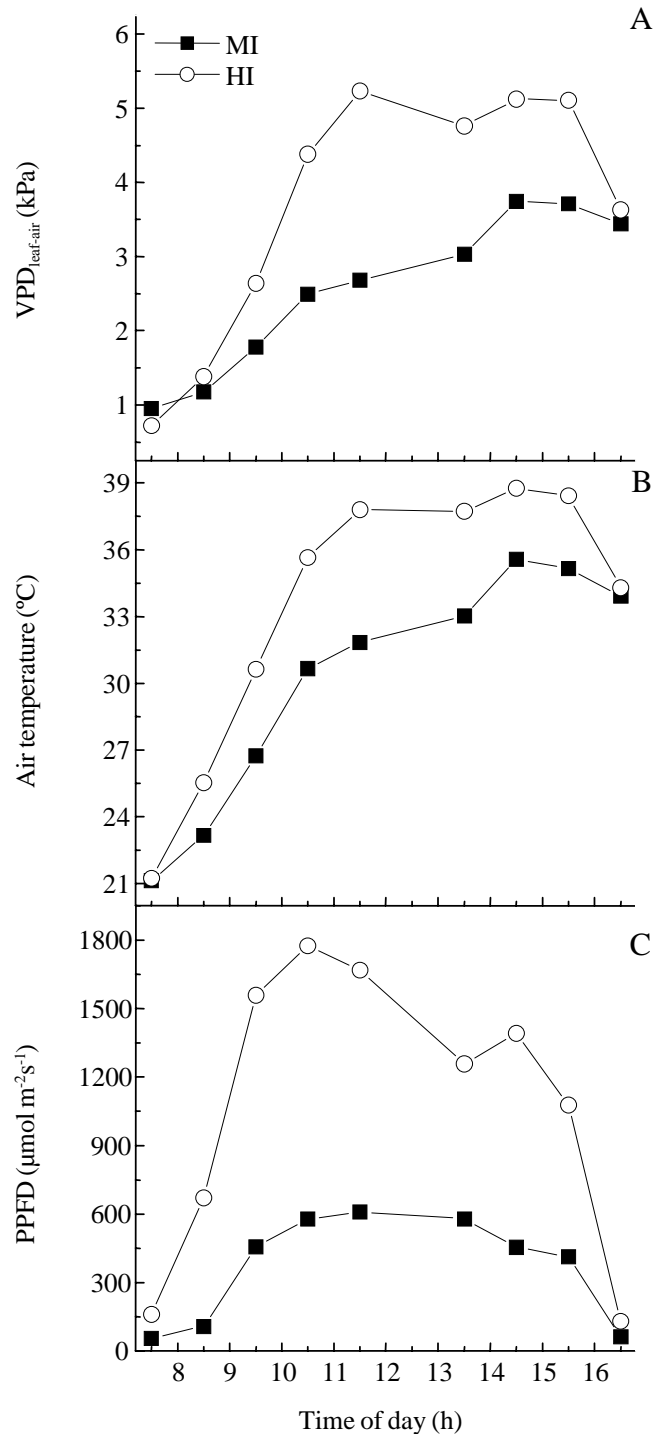


Figure 1. Daily course of leaf-to-air vapor pressure difference, $VPD_{leaf-air}$ (A), air temperature (B), and photosynthetic photon flux density, PPFD (C) at medium (MI, closed squares) and high (HI, open circles) irradiance conditions.

Table 1. Daily-integrated CO₂ assimilation and transpiration referent to the period of measurements (nine hours) of tropical tree species from different successional groups under medium (MI) and high (HI) irradiance conditions. Each value represents the mean value of three replicates. Values in the same line followed by different letters show significant difference between irradiance conditions (p < 0.05, by Tukey's test).

Successional Group	Species	CO ₂ assimilation (mol.m ⁻²)		Transpiration (mol.m ⁻²)	
		MI	HI	MI	HI
Late secondary	<i>C. legalis</i>	0.021 a	0.011 b	26.736 a	34.692 a
Early secondary	<i>R. elaeocarpum</i>	0.101 a	0.109 a	5.526 a	101.622 a
Pioneer	<i>C. myrianthum</i>	0.213 a	0.283 a	216.510 a	203.862 a

The results of ΔT analyses (figure 2) showed a higher dissipative capacity of the pioneer species as compared to the early and late secondary ones, mainly under MI. Daily mean ΔT values of pioneer, early and late secondary species were 1.420 ± 0.166, 0.247 ± 0.134, and 0.065 ± 0.156, respectively. However, the early and the late secondary species showed similar ΔT daily courses under MI condition (figure 2). Under HI, the early secondary species seems to be more efficient than the late one after 14:00 h (figure 2). In this irradiance regime, daily mean ΔT values of pioneer, early and late secondary species were 0.240 ± 0.233, -0.457 ± 0.315, and -0.897 ± 0.366, respectively. ΔT results were in agreement with transpiration rates (table 1), the main mechanism of heat dissipation.

Although all species have shown significant decreases in F_v/F_m values, markedly from 9:30 to 15:30 h, indicating photoinhibition (Critchley 1998), the late secondary did not recover the initial F_v/F_m values in both irradiance conditions (figure 3A). While pioneer and early secondary species showed dynamic photoinhibition, late secondary exhibited signals of chronic photoinhibition (figure 3A-C) (Osmond 1994). According to Critchley (1998), the maintenance of F_v/F_m values below 0.725 are indicative of photoinhibition that may cause damages to the photosystem II reaction centers. Furthermore, the late secondary species presented the highest reductions of ΔF/F_m' values throughout the day (figure 3D-F) and incapacity to dissipate the excessive energy under HI, as indicated by NPQ values (figure 4).

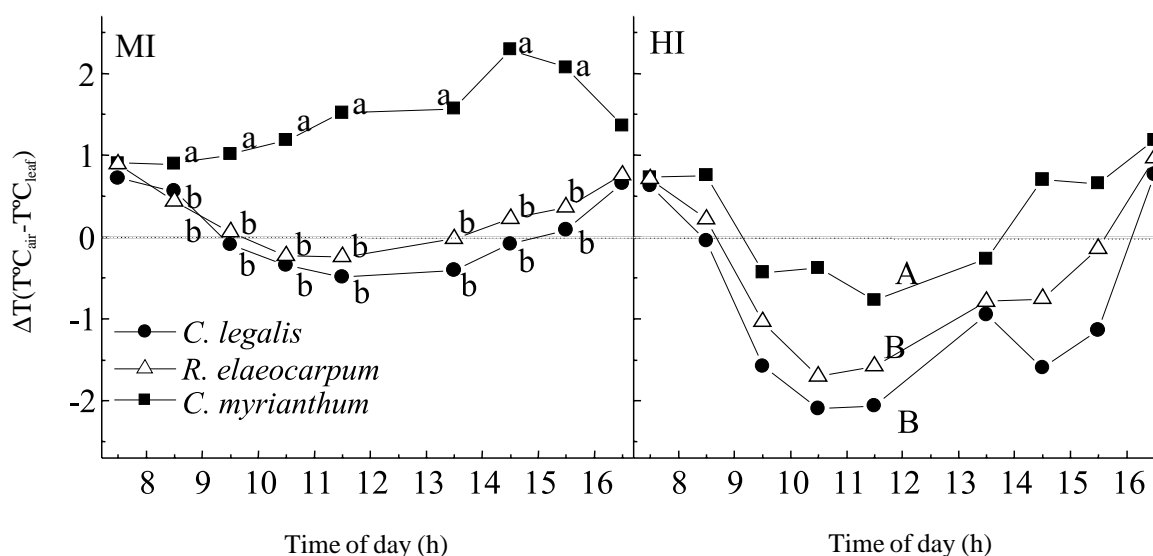


Figure 2. Daily course of the difference between air and leaf temperatures (ΔT) in *Cariniana legalis* (late secondary), *Citharexylum myrianthum* (pioneer) and *Rhamnidium elaeocarpum* (early secondary) under medium (MI) and high (HI) irradiance conditions. Each point represents the mean value (n = 3). Small letters mean statistical difference (p < 0.05 by Tukey's test) between species when the interaction species x time is significant, whereas capital letters mean difference between species (regardless time of day) when the interaction is non-significant.

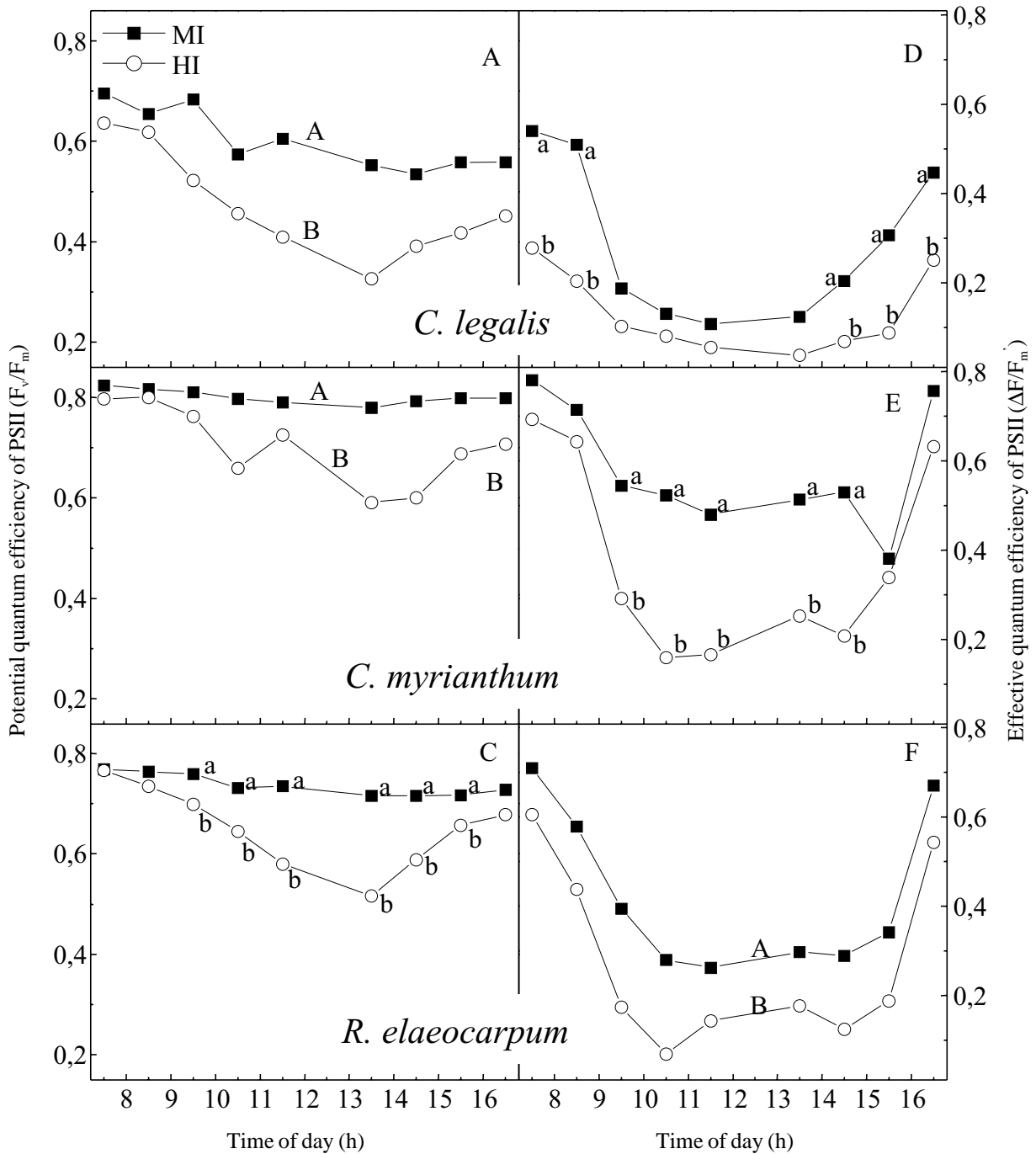


Figure 3. Daily course of potential (F_v/F_m , A-C) and effective ($\Delta F/F_m$, D-F) quantum efficiency of photosystem II in a late secondary (*Cariniana legalis*, A and D), pioneer (*Clitharexylum myrianthum*, B and E) and early secondary (*Rhamnidium elaeocarpum*, C and F) species under medium (MI, closed squares) and high (HI, open circles) irradiance conditions. Each point represents the mean value ($n = 3$). Small letters mean statistical difference ($p < 0.05$ by Tukey's test) between irradiance regimes when the interaction irradiance \times time is significant, whereas capital letters mean difference between irradiance regimes (regardless time of day) when the interaction is non-significant.

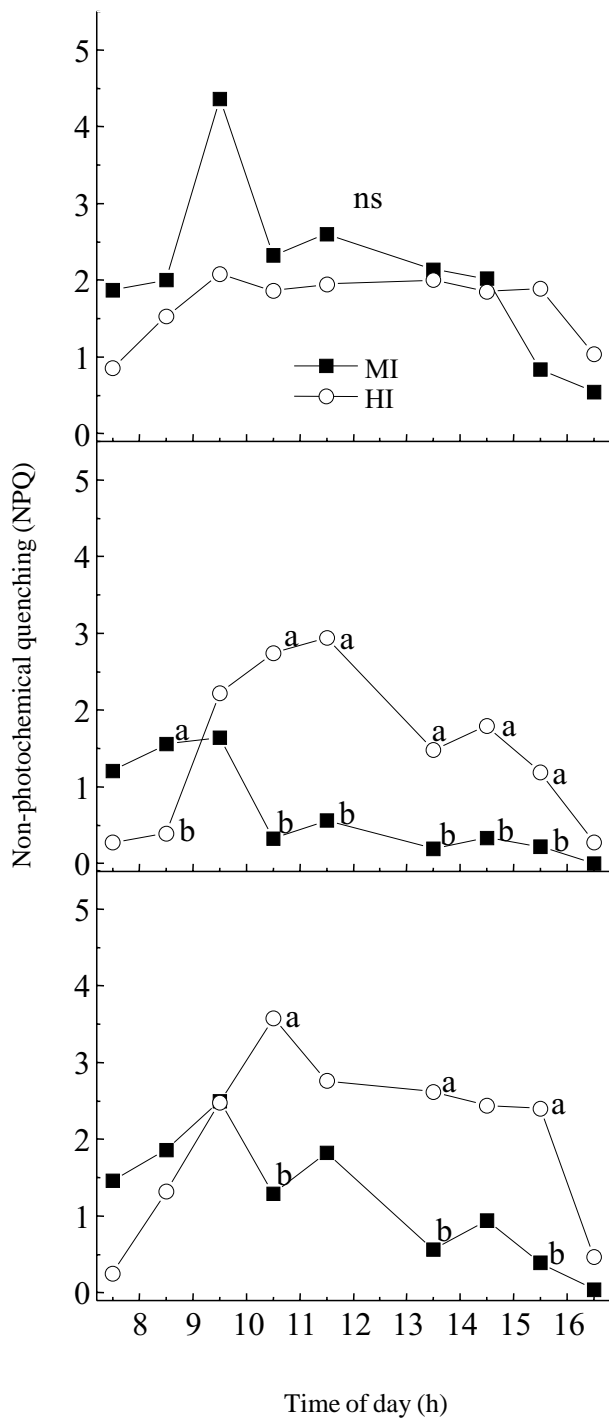


Figure 4. Daily course of non-photochemical quenching (NPQ) in a late secondary (*Cariniana legalis*, A), pioneer (*Citharexylum myrianthum*, B) and early secondary (*Rhamnidium elaeocarpum*, C) species under medium (MI, closed squares) and high (HI, open circles) irradiance conditions. Each point represents the mean value (n = 3). Small letters mean statistical difference (p < 0.05 by Tukey's test) between irradiance regimes when the interaction irradiance x time is significant. ns = non-significant difference between irradiance conditions.

A Effects of high irradiance on network connectance – Network global connectance (Cg) is related to the strength of connection in the whole network, indicating its level of control. *Citharexylum myrianthum* exhibited the highest Cg of gas exchange (Cgg), while *Rhamnidium elaeocarpum* showed the lowest Cgg value (table 2) under MI condition. When plants were transferred to HI condition, Cgg of *C. legalis* was reduced in 27.44%, while the other two species maintained Cgg values relatively stable. This Cgg reduction in *C. legalis* was mostly induced by a remarkable reduction in A-E relationship from 0.876 to 0.451 (table 2).

B A strong stomatal control of CO₂ assimilation (gs-A, p < 0.001) and transpiration rates (gs-E, p < 0.003) was observed in *C. legalis* and *C. myrianthum* under MI condition, whereas low gs-A and gs-E correlation (p > 0.5) were observed in *R. elaeocarpum*. Under HI condition, the stomatal control of gas exchange (evaluated by gs-A and gs-E) showed a sharp improvement in the early secondary species *R. elaeocarpum* (table 2). As expected, the relationship A-Ci was negatively significant (p < 0.01) for all species, with exception of *R. elaeocarpum* at HI condition. This relationship was reduced under HI in all species, mainly in *R. elaeocarpum* (table 2).

C Plant exposition to HI also affected considerably the Cg of photochemical apparatus (Cgp) (table 3). Cgp values of all species showed an increasing trend at HI, markedly in *C. legalis* and *R. elaeocarpum*. These increases were mainly due to the expressive increase of the relationship ΔF/F_m'-NPQ. This relationship was non-significant (p > 0.06) under MI, except for *C. legalis* (p < 0.02). On the other hand, all ΔF/F_m'-NPQ correlations were highly significant (p < 0.0001) under HI. ΔF/F_m'-ETR relationship was non-significant in both irradiance conditions, markedly under HI (table 3). In this environmental condition, the ΔF/F_m' was significantly reduced while ETR values did not show considerable changes (data not shown). ΔF/F_m'-qP relationship showed the same pattern of reduction under HI as observed in ΔF/F_m'-ETR, but with high and significant r-values (table 3).

In this study we have considered the relationships between physiological parameters and environmental variables as an indication of the plant autonomy degree in relation to the tested irradiance conditions. Thus, PPFD was the environmental element that presented the highest correlation with CO₂ assimilation under MI, with exception of *C. legalis* (table 4). Transpiration rates exhibited a significant correlation (p = 0.0002) with PPFD

Table 2. Correlation coefficient (r) values between gas exchange parameters (stomatal conductance = gs; transpiration = E; CO₂ assimilation = A; intercellular CO₂ concentration = Ci) and the network connectance of gas exchange = Cgg in *Cariniana legalis* = Cl, late secondary; *Cytherexylum myrianthum* = Cm, pioneer and *Rhamnidium elaeocarpum* = Re, early secondary, under medium = MI and high = HI irradiance conditions. Cgg is calculated as $C_{gg} = \sum z/n$, where $z = 0.5 \ln[(1+|r|)/(1-|r|)]$ and n is the total number of z-values. p-values are between brackets.

Irradiancecondition	Relationships	Species		
		Cl	Cm	Re
MI	gs-E	0.694 (0.0001)	0.560 (0.002)	-0.235 (0.237)
	gs-A	0.668 (0.0001)	0.790(<0.0001)	-0.009 (0.965)
	gs-Ci	-0.274 (0.167)	-0.614(0.0007)	0.502 (0.008)
	A-Ci	-0.732(<0.0001)	-0.894(<0.0001)	-0.812(<0.0001)
	A-E	0.876(<0.0001)	0.588 (0.001)	0.413 (0.03)
	Cgg	0.667	0.885	0.461
HI	gs-E	0.543 (0.003)	0.801(<0.0001)	0.449 (0.019)
	gs-A	0.524 (0.005)	0.834(<0.0001)	0.466 (0.014)
	gs-Ci	-0.140 (0.486)	-0.318 (0.114)	0.607(0.0007)
	A-Ci	-0.755(<0.0001)	-0.717(<0.0001)	-0.275 (0.165)
	A-E	0.451 (0.018)	0.908(<0.0001)	0.429 (0.026)
	Cgg	0.484	0.838	0.425

in *C. myrianthum*, and low r-values for *R. elaeocarpum* and *C. legalis* ($r < 0.47$). $VPD_{leaf-air}$ was mainly correlated with E in *C. myrianthum* ($p < 0.0001$), which also showed the highest E-T °C correlation ($r = 0.88$). In general, gs was better correlated with $VPD_{leaf-air}$, except for *C. myrianthum* that presented the highest correlation with PPFD (table 4). According to changes

in Atg values between MI and HI conditions, the relationships between physiological parameters and environmental variables trended to reduce in all species, with exception of *C. legalis*. This species showed higher Atg values under HI than in MI (table 4), suggesting that this late secondary species had lower autonomy in relation to daily environmental changes than the species

Table 3. Correlation coefficient (r) values between chlorophyll fluorescence parameters (potential and effective quantum efficiency of photosystem II = F_v/F_m and $\Delta F/F_m'$, respectively; apparent electron transport rate = ETR; photochemical and non-photochemical quenching = qP and NPQ, respectively) and the network connectance of photochemical apparatus = Cgp in *Cariniana legalis* = Cl, late secondary; *Cytherexylum myrianthum* = Cm, pioneer and *Rhamnidium elaeocarpum* = Re, early secondary, under medium = MI and high = HI irradiance conditions. Cgp is calculated as $C_{gp} = S z/n$, where $z = 0.5 \ln[(1+|r|)/(1-|r|)]$. n is the total number of z-values. p-values are between brackets.

Irradiancecondition	Relationships	Species			
		Cl	Cm	Re	
MI	$\Delta F/F_m'$	qP	0.696(<0.0001)	0.945(<0.0001)	0.665(0.0002)
		ETR	-0.332 (0.090)	-0.162 (0.421)	-0.452(0.018)
		F_v/F_m	0.471 (0.012)	0.525 (0.005)	0.408(0.035)
		NPQ	-0.453 (0.018)	-0.135 (0.502)	-0.108(0.590)
	Cgp	0.554	0.666	0.458	
HI	$\Delta F/F_m'$	qP	0.621 (0.0006)	0.696(<0.0001)	0.458(0.016)
		ETR	0.0806 (0.671)	-0.008 (0.970)	-0.057(0.778)
		F_v/F_m	0.610 (0.0007)	0.538 (0.004)	0.618(0.0006)
		NPQ	-0.774(<0.0001)	-0.859(<0.0001)	-0.816(<0.0001)
	Cgp	0.638	0.690	0.605	

Table 4. Correlation coefficient (r) values between gas exchange parameters (stomatal conductance = gs; transpiration = E; CO₂ assimilation = A) and environmental variables (photosynthetic photon flux density = PPFD; leaf-to-air vapor pressure difference = VPD_{leaf}; and air temperature = T °C) and autonomy of gas exchange = Atg in *Cariniana legalis* = Cl, late secondary; *Cytherexylum myrianthum* = Cm, pioneer and *Rhamnidium elaeocarpum* = Re, early secondary, under medium = MI and high = HI irradiance conditions. Atg is calculated as $Atg = \sum z/n$, where $z = 0.5 \ln[(1+|r|)/(1-|r|)]$ and n is the total number of z-values. p-values are between brackets.

Irradiance condition	Relationships		Species			
			Cl	Cm	Re	
MI	A	PPFD	0.119 (0.553)	0.756 (<0.0001)	0.676 (0.0001)	
		VPD _{leaf}	-0.179 (0.371)	0.035 (0.861)	-0.073 (0.716)	
		T°C	-0.131 (0.512)	0.289 (0.144)	-0.056 (0.782)	
	E	PPFD	0.314 (0.111)	0.657 (0.0002)	0.470 (0.013)	
		VPD _{leaf}	-0.015 (0.939)	0.689 (<0.0001)	0.499 (0.008)	
		T°C	0.047 (0.814)	0.880 (<0.0001)	0.519 (0.006)	
	gs	PPFD	-0.109 (0.558)	0.588 (0.001)	-0.445 (0.020)	
		VPD _{leaf}	-0.583 (0.001)	-0.168 (0.402)	-0.898 (<0.0001)	
		T°C	-0.546 (0.003)	-0.153 (0.448)	-0.911 (<0.0001)	
	HI	A	Atg	0.245	0.592	0.673
			PPFD	-0.306 (0.128)	0.410 (0.037)	0.236 (0.235)
			VPD _{leaf}	-0.234 (0.247)	-0.079 (0.702)	-0.0002 (0.999)
E		T°C	-0.222 (0.276)	0.307 (0.127)	0.029 (0.887)	
		PPFD	0.325 (0.105)	0.361 (0.070)	0.416 (0.031)	
		VPD _{leaf}	0.042 (0.837)	0.125 (0.541)	0.560 (0.002)	
gs		T°C	0.050 (0.808)	0.511 (0.008)	0.637 (0.0004)	
		PPFD	-0.291 (0.149)	0.106 (0.606)	-0.233 (0.241)	
		VPD _{leaf}	-0.652 (0.0003)	-0.414 (0.040)	-0.425 (0.027)	
		T°C	-0.649 (0.0003)	-0.037 (0.857)	-0.375 (0.054)	
		Atg	0.340	0.276	0.354	

of early successional stages under high irradiance. Thus, we can argue that the gas exchange control was reduced in *C. legalis* under HI, being this statement supported by a C_{gg} reduction of 27% in *C. legalis* (table 2).

Concerning the connections between photochemical parameters and environmental variables (Atp) (table 5), Atp values trended to increase in all species, markedly in the pioneer species *C. myrianthum*, indicating an improvement in the flexibility of photochemical responses to daily environmental changes. Nevertheless, we suppose that the lack of photochemical autonomy could also be associated to impairments due to excessive irradiance or high temperature, mainly in late secondary species.

Discussion

General photosynthetic responses – The differences in the photosynthetic responses among evaluated successional groups were in agreement with the data

reported in the literature (Bazzaz 1996, Strauss-Debenedetti & Bazzaz 1996, Ellis *et al.* 2000, Souza *et al.* 2004). Pioneer species exhibited the highest photosynthetic capacity in both irradiance conditions, since there was sufficient irradiance under MI. According to the daily courses of A (Ribeiro *et al.* 2005), the pioneer species was light saturated in both irradiance regimes, since maximum photosynthetic rates were similar. Moreover, the results of F_v/F_m showed that, although all species have shown evidences of photoinhibition under HI, *Cariniana legalis* was the only species to show chronic photoinhibition, suggesting that this species is shade-tolerant.

On flexibility of response, network connectance and dissipation – Flexibility have been defined in the current literature on evolutionary ecology as phenotypic plasticity, i.e. the plant capacity to change its phenotype in response to environmental conditions or stimuli (Novoplansky 2002, Schlichting & Smith 2002). Different successional groups have different mechanisms in order to cope with specific environmental conditions (Bazzaz & Pickett

Table 5. Correlation coefficient (r) values between chlorophyll fluorescence parameters (potential and effective quantum efficiency of photosystem II = F_v/F_m and $\Delta F/F_m'$, respectively; apparent electron transport rate = ETR; photochemical and non-photochemical quenching = qP and NPQ, respectively) and environmental variables (photosynthetic photon flux density = PPFD; leaf-to-air vapor pressure difference = VPD_{leaf} ; and air temperature = $T^\circ C$) and autonomy of photochemical apparatus = Atp in *Cariniana legalis* = Cl, late secondary; *Citharexylum myrianthum* = Cm, pioneer and *Rhamnidium elaeocarpum* = Re, early secondary, under medium = MI and high = HI irradiance conditions. Atp is calculated as $Atp = \sum z/n$, where $z = 0.5 \ln[(1+|r|)/(1-|r|)]$ and n is the total number of z-values. p-values are between brackets.

Irradiancecondition	Relationships		Species		
			Cl	Cm	Re
MI	$\Delta F/F_m'$	PPFD	-0.818(<0.0001)	-0.702 (<0.0001)	-0.881(<0.0001)
		VPD_{leaf}	-0.507 (0.010)	-0.425 (0.027)	0.366 (0.061)
		$T^\circ C$	-0.507 (0.007)	-0.443 (0.021)	-0.560 (0.002)
	qP	PPFD	-0.626(0.0005)	-0.689 (<0.0001)	-0.415 (0.032)
		VPD_{leaf}	-0.254 (0.200)	-0.416 (0.031)	-0.440 (0.082)
		$T^\circ C$	-0.261 (0.189)	-0.443 (0.021)	-0.338 (0.085)
	ETR	PPFD	0.458 (0.016)	0.673 (0.0004)	0.695(<0.0001)
		VPD_{leaf}	0.340 (0.08)	0.410 (0.034)	0.130 (0.519)
		$T^\circ C$	0.350 (0.074)	0.392 (0.043)	0.362 (0.063)
	F_v/F_m	PPFD	-0.088 (0.662)	-0.411 (0.033)	-0.317 (0.107)
		VPD_{leaf}	-0.564 (0.002)	-0.413 (0.032)	-0.321 (0.102)
		$T^\circ C$	-0.521 (0.005)	-0.288 (0.145)	-0.734(<0.0001)
	NPQ	PPFD	0.274 (0.167)	-0.158 (0.432)	0.242 (0.222)
		VPD_{leaf}	-0.255 (0.200)	-0.749 (<0.0001)	-0.535 (0.004)
		$T^\circ C$	-0.264 (0.184)	-0.443 (0.021)	-0.338 (0.085)
	Atp	0.440	0.499	0.603	
HI	$\Delta F/F_m'$	PPFD	-0.599 (0.001)	-0.843 (<0.0001)	-0.935(<0.0001)
		VPD_{leaf}	-0.681(<0.0001)	0.684 (<0.0001)	-0.710(<0.0001)
		$T^\circ C$	-0.640(0.0003)	-0.650 (0.0002)	-0.675 (0.0001)
	qP	PPFD	-0.158 (0.431)	-0.563 (0.002)	-0.356 (0.069)
		VPD_{leaf}	-0.376 (0.053)	-0.356 (0.068)	-0.065 (0.240)
		$T^\circ C$	-0.359 (0.067)	-0.384 (0.048)	-0.068 (0.736)
	ETR	PPFD	0.484 (0.010)	0.338 (0.084)	0.264 (0.184)
		VPD_{leaf}	-0.024 (0.907)	-0.173 (0.387)	0.068 (0.736)
		$T^\circ C$	-0.009 (0.966)	0.111 (0.581)	0.099 (0.623)
	F_v/F_m	PPFD	-0.212 (0.288)	-0.230 (0.248)	-0.570 (0.002)
		VPD_{leaf}	-0.624(0.0005)	-0.661 (0.0002)	-0.739(<0.0001)
		$T^\circ C$	-0.599 (0.001)	-0.439 (0.022)	-0.734(<0.0001)
	NPQ	PPFD	0.555 (0.003)	0.812 (<0.0001)	0.794 (0.0001)
		VPD_{leaf}	0.556 (0.003)	0.511 (0.006)	0.578 (0.002)
		$T^\circ C$	0.555 (0.003)	0.434 (0.024)	0.544 (0.003)
	Atp	0.486	0.570	0.615	

1980, Pearcy 1987). Accordingly, some interesting different patterns of systemic (organizational) responses to water deficit were observed between pioneer and late secondary species (Souza *et al.* 2004). While pioneer species presented increasing network connectance and decreasing autonomy as subjected to water deficit, the late secondary species showed a slight reduction in network connectance and increasing autonomy. These results, added to the analyses of the

physiological responses, indicated that the late successional species was more drought resistant than the pioneer one.

In this study, the late secondary species exhibited increasing Atp values from MI to HI conditions (table 4). Atp of *C. legalis* increased in 39% under HI due to a higher correlation of A-PPFD, A- $VPD_{leaf-air}$, and A- $T^\circ C$. The differences between Atp values of pioneer species (lower Atp value) and secondary species (higher Atp

values) under HI suggest two modes of response to high irradiance. The first mode is related to the maintenance of high photosynthetic rates, increasing plant autonomy in relation to its environment. In the second mode, plants decrease their photosynthesis in response to HI condition, losing their autonomy. The reduction of *C. legalis* autonomy was associated with a decrease (27%) in the network connectance of gas exchange (C_{gg}) under HI, while the pioneer and early secondary species maintained C_{gg} relatively stable (table 2). The reductions in C_{gg} values from MI to HI suggest a breaking down in the network connectance of gas exchange, suggesting that plants were submitted to constraining environmental conditions under HI. In addition, a reduction of C_{gg} values may suggest a lack of a full plant homeostatic capacity, indicating a non-adaptive response (Amzallag 2001, Souza *et al.* 2004).

An important issue that must be taken into account to study the occupation processes of areas exposed to high irradiance is the thermal dissipation capacity of the excessive energy. NPQ changes demonstrated to be an important mechanism of dissipation at PSII level when the species were submitted to HI. Except for *C. legalis*, the other species showed significant increases in NPQ under high irradiance. In the PSII, the excitation energy can be non-radioactively dissipated as heat, which is indicated by NPQ parameter. This transformation was higher in HI, suggesting that NPQ was an important mechanism to maintain the function of PSII (Demmig-Adams & Adams 1992). NPQ is related to the xanthophyll cycle, where the carotenoid zeaxanthin is the main pigment involved in the acceptance of energy from excited singlet chlorophyll and its dissipation as heat (Bilger & Björkman 1990, Owens 1994). In fact, the latent heat dissipative process is promoted by plant transpiration (Nobel 1999). This type of heat dissipation prevents damages caused by heat stress (Nilsen & Orcutt 1996) with obvious adaptive advantages for species in early successional stages. According to Bazzaz (1996), the high transpiration rates in early successional species may be effective in preventing superoptimal leaf temperatures when there are high radiation loads. However, there are few comparative studies to approach the question if early and late successional plants differ in relation to the dissipative efficiency. Our results based on DT values (figure 2) and transpiration rates (table 1) indicated that species of the early successional stages have more efficient dissipative capacity, which is in agreement with Souza *et al.* (2004) and supports the statement above.

The ΔT analysis refers to important theoretical questions concerning the theories of non-equilibrium thermodynamical and dissipative structures (Nicolis & Prigogine 1977, Schneider & Kay 1994). According to these theories, a biological system maintains its organization harvesting high quality energy (sun-light) from the environment, converting this energy into essential elements for its metabolism, and dissipating the energy not available to work (entropy). These processes working together produce into the organism a more organized state at the expense of global entropy increase. In such framework, the species that hold higher capacity to use solar energy by photosynthetic processes and exhibit higher dissipative efficiency, especially by transpiration, have a sharp ecological advantage in the occupation of areas with higher radiation and temperature. Thus, the measurement of leaf temperature is a suitable method to estimate the plant dissipative capacity, since the lower the system superficial temperature, the more efficient the processes of energy degradation and entropy dissipation will be (Schneider & Kay 1994, Souza *et al.* 1999, Souza *et al.* 2004).

Considering the results presented here and the results reported by Souza *et al.* (2004), we have uncovered a pattern of network responses and autonomy changes due to increasing irradiance. Evaluating the maintenance of daily CO₂ assimilation, the tolerant species to increasing irradiance (*Citharexylum myrianthum* and *Rhamnidium elaeocarpum*) trended to maintain stable the level of system network connectance and to increase the autonomy in relation to the environment. On the other hand, the late successional species (*C. legalis*) trended to lose autonomy, decreasing the network connectance of gas exchange. Taking into account the photochemical autonomy changes (Atp) under HI, all species presented higher Atp values, mainly the pioneer species *C. myrianthum* (table 5). This suggests that photochemical apparatus was more flexible to irradiance changes, since the responses of chlorophyll fluorescence (lower hierarchical level) to increasing irradiance are faster and more sensitive than gas exchange (higher hierarchical level) (Ksenzhek & Volkov 1998). Therefore, our data support the hypothesis that photosynthetic responses of tropical tree species from different successional status to increasing irradiance are related to changes in network connectances of gas exchange and photochemical apparatus and alterations in plant autonomy in relation to the environment. This observation suggests that there are some emergent

patterns involving complex metabolic networks or, in other words a, systemic pattern of response to environmental stimuli (Souza & Cardoso 2003).

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