Using network connectance and autonomy analyses to uncover patterns of photosynthetic responses in tropical woody species

Gustavo M. Souza [a,*], Rafael V. Ribeiro [b], Carlos H.B.A. Prado [c], Daniel S.C. Damineli [a,d], Agnaldo M. Sato [a], Marcelino S. Oliveira [a]

[a] Laboratório de Ecofisiologia Vegetal, UNOESTE, Presidente Prudente, SP, Brazil
[b] Centro de Pesquisa e Desenvolvimento em Ecofisiologia e Biofísica, IAC, Campinas, SP, Brazil
[c] Departamento de Botânica, Universidade Federal de São Carlos, São Carlos, SP, Brazil
[d] Departamento de Botânica, Universidade Estadual Paulista, Rio Claro, SP, Brazil

ARTICLE INFO

ABSTRACT

Daily courses of leaf gas exchange and chlorophyll fluorescence in forest gap and under-storey environments were used to build photosynthetic networks in two pioneers and two late-successional species. Photochemical and gas exchange networks were linked to each other by the relationship between electron transport rate and net CO_2 assimilation. Global network connectance (Cg), which represents the mean strength of connections within a given network, was calculated in the photochemical and gas exchange networks for both functional groups and environments. Autonomy in relation to environmental fluctuations was estimated considering the mean correlation between environmental and physiological data. Cg was consistently higher in plants under gap condition. High daily-amplitude of environmental variables in the gap induced strong connectance in photochemical and gas exchange networks regardless of functional group. Gap scenario demands network modulation with higher level of control than understorey, which would be attained by strong connections among components of photochemical and gas exchange networks. This would allow fine and fast tuning adjustments when facing highly variable and demanding environmental conditions throughout a day. As a consequence of this highly variable environment, both functional groups showed lower autonomy in the gap, where higher coupling between leaf physiology and environmental fluctuations was evident. Our results suggest that high plant–environment coupling demands high network connectance. Contrastingly, Cg was lower (especially in photochemical network) under forest understorey, promoting autonomy in a more stable environment. Our results indicate that there is a conservative pattern of photosynthesis control based on network modulation and environmental coupling. This suggests that changes in network connectance may not be specific of a functional group but rather a more general response to environmental fluctuations, strongly related to system stability. We consider this information crucial in understanding how complex adaptive systems deal with environmental fluctuations.

© 2008 Elsevier B.V. All rights reserved.

* Corresponding author. Tel.: +55 18 3229 2000; fax: +55 18 32292080.
  E-mail address: gumaia@pq.cnpq.br (G.M. Souza).

1. Introduction

Nature is organized in systems developed from the relationships among their constitutive elements. Rather than isolated components, interactions play a central role in system analysis (Ahal and Allen, 1996; Barabási, 2003; Strogatz, 2003). Plant ecophysiology can be considered, *par excellence*, a science of the interactions between plant and environment. As other living system, plants are continuously exchanging material, energy and information with their environment (Schneider and Kay, 1994; Souza et al., 2004a; Michaelian, 2005) from molecular to individual scales. Biological systems are hierarchically organized and composed by interactive elements, resulting in traits that may not be recognizable in isolated elements, i.e. high levels of organization exhibit emergent properties (Mohr and Schopfer, 1995; Souza and Cardoso, 2003; Strogatz, 2003). Thus, approaches that assess and quantify systemic interactions, considering the relationships among system elements, could play an important role in improving classical ecophysiological methods. Analyses that evaluate interactions among network components improve predictions of plant behavior under ambient environmental variation (Souza et al., 2004a).

The effects of environmental fluctuations on photosynthesis can be evaluated through the strength of connections among elements interacting in a network such as the approach introduced by Amzallag (2001). Network connectance is estimated through normalized Pearson's correlation coefficient between variables (Amzallag, 2001), a statistical method based on path analysis (Kingsolver and Schemske, 1991). According to Amzallag (2001), the correlation coefficient can be considered not only a test of significance but also a measure of strength of the relationship (connection) between two variables. The number and the strength of connections among elements in a network is strongly related to system stability (Trewavas, 1986; Edelman and Gally, 2001; Souza et al., 2005a,b). High connectance may indicate great system stability up to a critical threshold (Gardner and Ashby, 1970). Tighter networks, with strong relationships among elements, could provide high level of system control improving the capacity to overcome external perturbations. Alterations in system connectance, mostly connectance increases, could be considered an adaptive response to environmental constrains (Souza et al., 2005b). Therefore, different plant functional groups probably show distinct behavior of connectance among physiological processes in a changing environment (Souza et al., 2005a).

Evidences indicate that tropical tree species can be classified in functional groups as pioneer (early-successional) and late-successional species, on the basis of growth, shade-adaptation, leaf life span, and leaf physiological variables such as leaf gas exchange and carbon and nitrogen metabolism (Bazzaz and Pickett, 1980; Reich, 1993; Strauss-Debenedetti and Bazzaz, 1996; Nogueira et al., 2004; Ribeiro et al., 2005). Pioneer species exhibit a remarkable reduction in photosynthetic capacity (A_{max}) when grown under low photosynthetic photon flux density (PPFD), but A_{max} responds promptly to PPFD increases. In other terms, pioneers show high synchronization with environmental light availability (*sensu* Souza et al., 2005a). On the other hand, several species typical of tropical forest understorey exhibit little or no potential to raise

A_{max} in response to long term of PPFD increases (Chazdon et al., 1996; Strauss-Debenedetti and Bazzaz, 1996; Ribeiro et al., 2005), showing therefore high autonomy of A_{max}, independence of environment (Souza et al., 2005a).

In this study, we considered plasticity as the plant capacity to respond to environmental changes throughout the day, taking into account positive or negative correlations between physiological and environmental variables. To measure plasticity, we evaluated the autonomy (At) of the species through analysis of the correlation between physiological and environmental variables (Souza et al., 2004a, 2005a). Herein, autonomy represents the plant's ability to maintain stable its photosynthetic processes despite of environmental changes (Souza et al., 2004a). We suggest that photosynthetic responses to environment could have their understanding complemented by the approach proposed by Amzallag (2001) and Souza et al. (2004a,b, 2005a). Changes in network connectance of the photosynthetic apparatus likely exhibit a pattern of response to environmental changes. Specifically, we hypothesized that network connectance increases in plants growing under gap conditions in relation to those in the understorey, since the gap environment exhibits dramatic environmental fluctuations throughout the day, demanding higher control of the photosynthetic network to implement rapid responses. In addition, it was expected lower autonomy in plants inhabiting gap environments due to high degree of resource variability, which would demand higher coupling to environmental changes. Furthermore, we expect to find lower autonomy in pioneer species, which are considered to be more plastic than late-successional species (Chazdon et al., 1996; Strauss-Debenedetti and Bazzaz, 1996; Souza et al., 2005a).

2. Material and methods

2.1. Species and experimental sites

This study was carried out in a fragment of semi-deciduous forest with 5.5 ha located at Narandiba county, Brazil (22°24′24″S; 51°31′29″W, 354 m). The size of the forest gap was 34.5 m^2, corresponding to a small gap with canopy openness around 10%. Small gaps are far more frequent in tropical forest than large ones (Martins and Rodrigues, 2002).

In this study we evaluated four species from different successional groups, *Bauhinia forficata* Link (Caesalpinioideae) and *Guazuma ulmifolia* Lam. (Sterculiaceae) as light-demanding pioneer species, and *Hymenaea courbaril* L. (Caesalpinioideae) and *Esenbeckia leiocarpa* Engl. (Rutaceae) as shade-adapted late successional species (Lorenzi, 1992). They were germinated and grown in 5L pots with organic substrate under nursery conditions, at 50% of full sunlight, until 10-month-old. Then, 10 individuals of each species were planted (with a minimum distance of 1.0 m from each other) in different light environments, in a forest gap and a adjacent understorey site. They grew in these forest sites for 9 months, from March to November 2005.

Photosynthetic performances were evaluated in May (2 months after planting) and November 2005 (9 months after planting), when environmental conditions were quite different. In May (dry season), mean air temperature was 22.7 °C and

rainfall about 34 mm. The accumulated water deficiency was 54 mm as indicated by the climatic water balance calculated according to Thornthwaite and Mather (1955). In November (wet season), mean air temperature was 25.9 °C, rainfall about 116 mm, and there was no water deficiency. In the understorey, photosynthetic photon flux density (PPFD) was practically unchanged (25 μmol m^{-2} s^{-1}) along the day in both months (Fig. 1a). Diurnal-integrated PPFD ranged from 0.37 mol m^{-2} d^{-1} in May to 0.47 mol m^{-2} d^{-1} in November. Total irradiance in the understorey was underestimated since leaves evaluated therein were not exposed to sunfleck during

gas exchange measurements. Contrastingly, significant PPFD variations were recorded during daylight period in the forest gap. The highest PPFD was approximately 2000 μmol m^{-2} s^{-1} at 12:00 h (Fig. 1a). Diurnal-integrated PPFD in May was 27.9 mol m^{-2} d^{-1}, while it was 39.1 mol m^{-2} d^{-1} in November. The highest air temperature (Tair) and air vapor pressure deficit (VPD) values were also found in gap conditions, mainly between 10:00 and 14:00 h. Maximum Tair and VPD reached, respectively, 31 °C and 1.8 kPa in May, and 36 °C and 2.2 kPa in November (Fig. 1b and c).

2.2. Photosynthetic measurements

Diurnal courses of leaf gas exchange and chlorophyll fluorescence were evaluated from 8:00 to 16:00 h (in intervals of 2 h) in plants grown under gap and understorey conditions. Three plants per species and three leaves per plant were evaluated in each environmental condition in five measurements throughout the diurnal period. All measurements were recorded in cloudless days, on young but fully expanded leaves without damage, mosses or fungi.

Net CO_2 assimilation (A), stomatal conductance (gs), transpiration (E) and intercellular CO_2 concentration (Ci) were recorded with an open system, portable infrared gas analyzer (model CIRAS-2, PP-Systems, UK). On same leaves, dark respiration (Rd) was recorded after leaf dark adaptation, until gas exchange reached the steady state. Leaves were darkened inside the CIRAS-2 chamber covered with black tissue reducing PPFD to zero. All leaf gas exchange measurements were taken under natural environmental conditions (light, air temperature and humidity), since our intention was to evaluate plant performance under natural conditions. Photorespiration (Pr) was calculated according to Sharkey (1988) as follows: $\boldsymbol{v_0} = (\mathbf{A} + \mathbf{Rd})/(\mathbf{1}/\varPhi - \mathbf{0.5})$, where $\boldsymbol{v_0}$ is the rate of Rubisco (ribulose bisphosphate oxygenase/carboxylase) oxygenation, A is the net CO_2 assimilation, Rd is the respiration measured under dark conditions, and $\varPhi$ is the ratio between carboxylation and oxygenation rates of Rubisco according to Farquhar and Von Caemmerer (1982). Oxygenation rate is twice the rate of photorespiration (Sharkey, 1988).

Chlorophyll fluorescence measurements were recorded with a portable fluorescence monitoring system (model FMS 2, Hansatech Instruments, UK). Measuring light and saturating pulses were applied by a fiber-optic placed in a grooved neck at 60° of the sample plane. Maximal (F_m) and basal (F_0) fluorescence yields were measured after 30 min of dark adaptation. Variable fluorescence (F_v) was calculated as F_m minus F_0. Steady state (F_s) and maximum ($\mathbf{F'_m}$) fluorescence yields were also recorded in light-adapted tissues. Light-adapted variable fluorescence (ΔF) was calculated as $\mathbf{F'_m}$ minus F_s. The following variables were calculated in order to evaluate photochemical performance in gap and understorey conditions: potential (F_v/F_m) and effective ($\Delta F/F'_m$) quantum efficiency of photosystem II (Genty et al., 1989), apparent electron transport rate ($\mathbf{ETR} = \Delta \mathbf{F}/\mathbf{F'_m} \times \mathbf{PPFD} \times \mathbf{0.5} \times \mathbf{0.84}$) (Krall and Edwards, 1992), and non-photochemical quenching [$\mathbf{NPQ} = (\mathbf{F_m} - \mathbf{F'_m})/\mathbf{F'_m}$] (Van Kooten and Snel, 1990). In ETR estimative, 0.5 was used as the fraction of excitation energy distributed to photosystem II (PSII), and 0.84 was adopted as the fraction of PPFD absorbed by leaves (Demmig and Björkman, 1987).

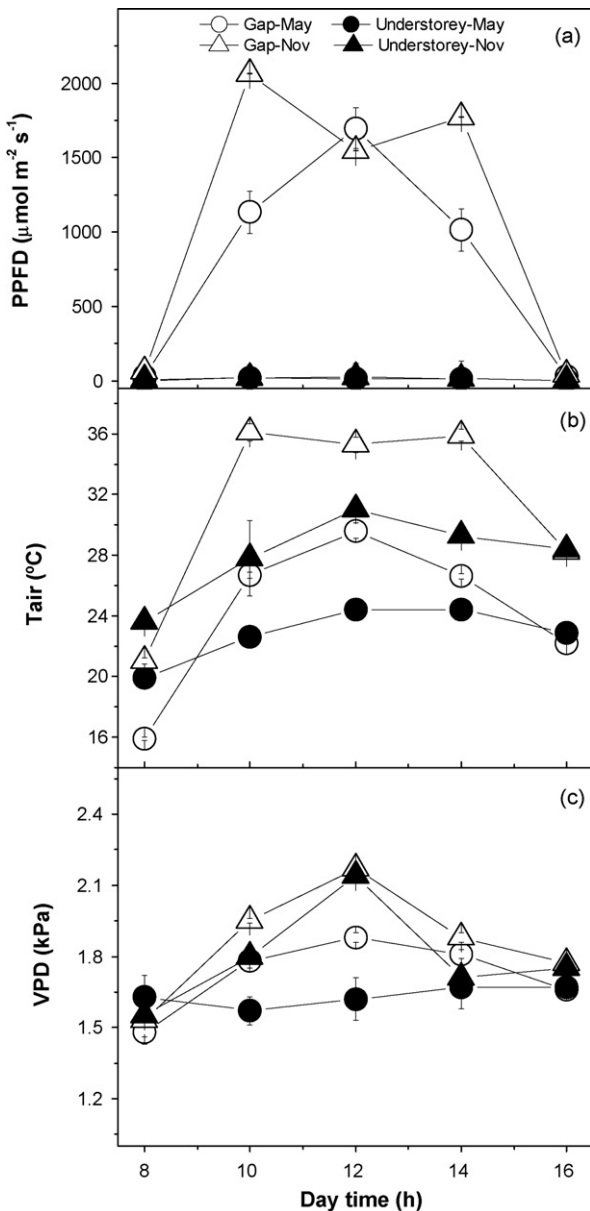**Fig. 1 – Diurnal courses of environmental variables: photosynthetic photon flux density (PPFD, in a), air temperature (Tair, in b) and atmospheric vapor pressure deficit (VPD, in c) under forest gap (open symbols) and understorey (closed symbols). Measurements were taken in both dry (May 2005, circles) and wet (November 2005, triangles) seasons. Mean values ± S.E. of 9 replications.**

2.3. Data analyses

To assess changes in the photosynthetic network, we evaluated differences in modulation of gas exchange and chlorophyll fluorescence networks when individuals were submitted to different forest environments. Modulation, here, was considered as the change in the mean strength of connections among network elements, which was measured through global connectance, Cg, following the concept and determination of Amzallag (2001). To define connectance, we specified a collection of paired variables of interest in the network. The correlation coefficients (r) between each paired variable were used to test the significance of the correlation and to measure the strength of the relationship, performing a z-transformation afterwards (Amzallag, 2001): $z = 0.5 \ln[(1 + |r|)/(1 - |r|)]$. Five points from the daily course of three individual averaged from three leaves were used to calculate r. Global network connectance (Cg) was calculated as the average of z-values formerly obtained (Amzallag, 2001). The photosynthetic process was separated into two representative networks constituted by pairs of parameters (Fig. 2). The leaf gas exchange network was composed by the following relationships: A–gs, A–E, A–Rd, A–Pr, A–Ci, Ci–gs, Ci–Pr and gs–E (adapted from Jones, 1998), and their average strength yields the global connectance of the gas exchange network (Cg_{GE}). The photochemical network was constituted by the relationships $\Delta F/F'_m$–**ETR**, $\Delta F/F'_m$–F_v/F_m, $\Delta F/F'_m$–**NPQ**, ETR–NPQ, F_v/F_m–NPQ, and F_v/F_m–ETR (Souza et al., 2005a), and their average strength yields the global connectance of the chlorophyll fluorescence network (Cg_{CF}). The ETR–A relationship linked the gas exchange and photochemical networks, and the average strength of both networks yields the photosynthetic network connectance (Cg_{total}).

Plant autonomy (At) was calculated as the average of z-values of all physiological parameters in relation to environmental variables: PPFD, VPD and Tair. Hence, lower strength of connections between physiological and environmental variables (low At value) implies in higher autonomy degree (Souza et al., 2004a). In addition, autonomy keeps an inverse relationship with plasticity since more plasticity means more change in relation to the environment.

3. Results

3.1. Diurnal courses of leaf gas exchange and chlorophyll fluorescence

Differences among gas exchange measurements taken under gap and understorey conditions were remarkable, mainly in May (Fig. 3). In May and November, pioneers growing in forest gap exhibited higher net CO_2 assimilation (A) than late-successional species, while in understorey there were no differences between successional groups (Fig. 3a–d). In November (wet season), values of stomatal conductance (gs) were higher than in May (dry season) for all species under gap conditions (Fig. 3e–h). Dark respiration (Rd) was higher in November than in May regardless of PPFD regime, and functional groups did not show significant differences throughout the day (Fig. 3i–l). Differences in Rd values between May and November could be explained by air temperature (Fig. 1b). Air temperature (Tair) in November was higher than in May, even when comparing November-understorey and May-gap (Fig. 1b). As another consequence of higher Tair, photorespiration (Pr) was consistently higher in gap than in understorey in both months and Pr values trended to be higher in November than in
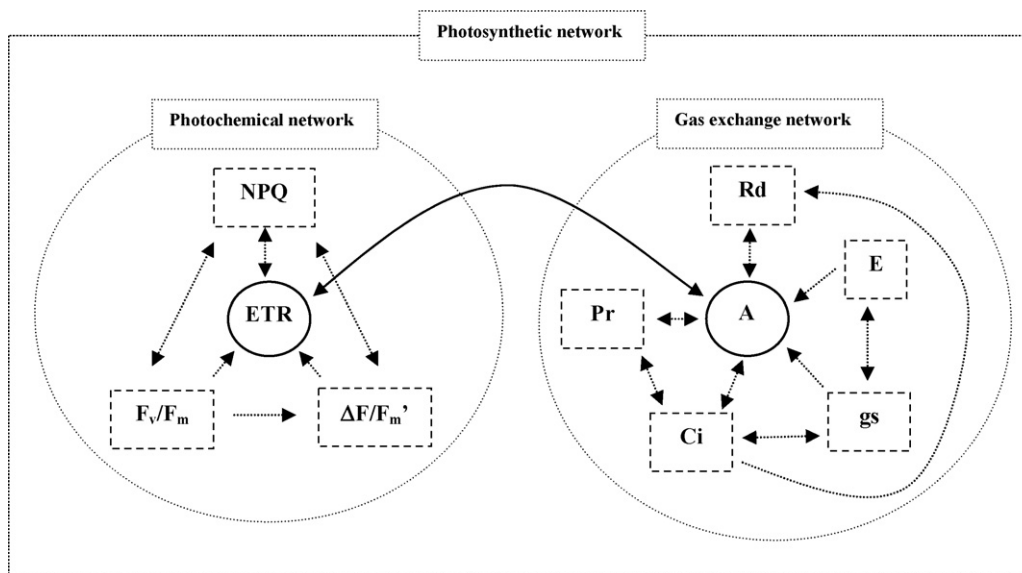
Fig. 2 – Schematic representation of photosynthetic network composed by gas exchange and photochemical networks. Gas exchange network represents relationships (dotted lines) among: net CO_2 assimilation (A); stomatal conductance (gs); transpiration (E); intercellular CO_2 concentration (Ci); dark respiration (Rd); and photorespiration (Pr). The photochemical network is constituted by the relationships (dotted lines) among: potential (F_v/F_m) and effective ($\Delta F/F'_m$) quantum efficiency of photosystem II; apparent electron transport rate (ETR); and non-photochemical quenching (NPQ). Arrows with two heads indicate mutual influence. Gas exchange and photochemical networks are linked by the A–ETR relationship (solid line).

Fig. 3 – Diurnal courses of net CO_2 assimilation (A, in a–d), stomatal conductance (gs, in e–h), dark respiration (Rd, in i–l), and photorespiration (Pr, in m–p) in leaves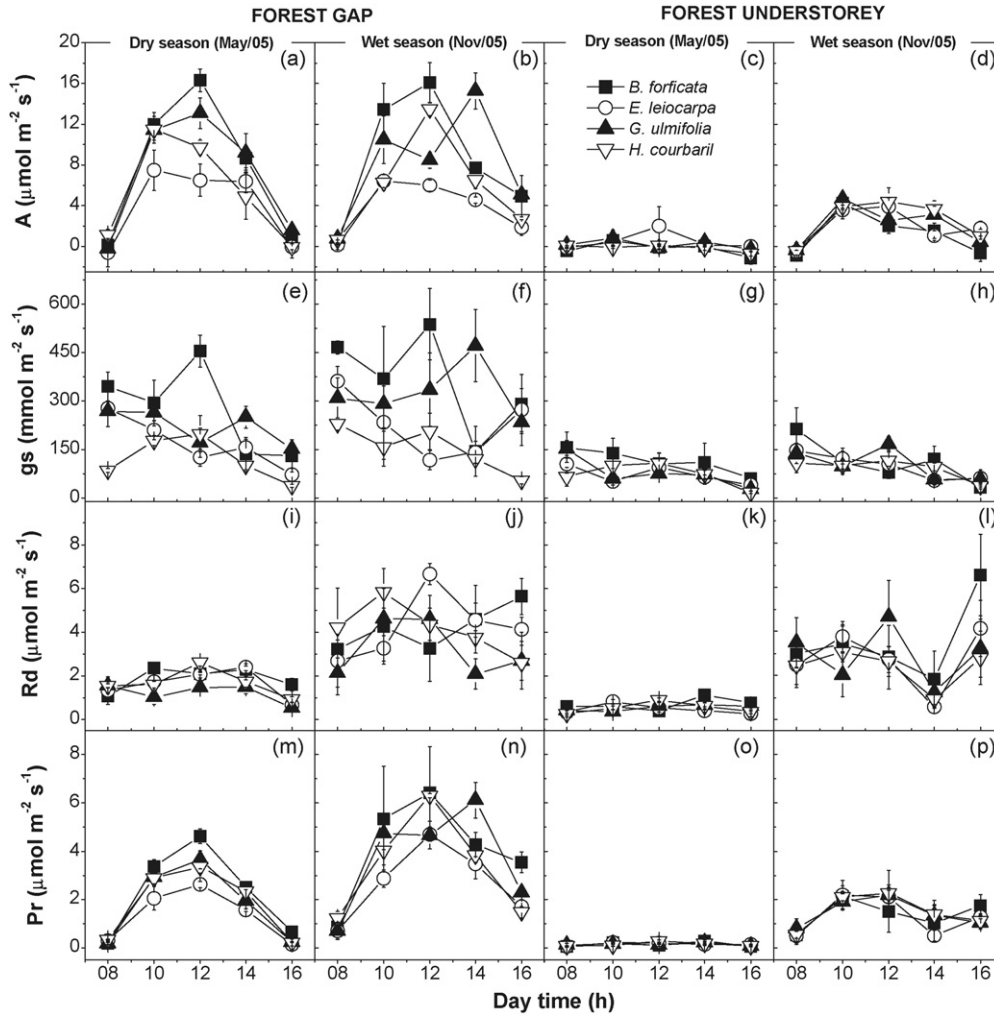 of pioneer (*G. ulmifolia* and *B. forficata*) and late-successional (*E. leiocarpa* and *H. courbaril*) tropical tree species growing under forest gap or understorey conditions. Measurements were taken in both dry (May 2005) and wet (November 2005) seasons. Mean values ± S.E. of 3 individuals and each individual averaged from 3 leaves.

May (Fig. 3m–p). However, no differences between functional groups were observed in relation to Pr (Fig. 3m–p).

Diurnal courses of chlorophyll fluorescence revealed significant differences between environments. Evidence of dynamic photoinhibition was observed under gap conditions from 10:00 to 14:00 h mainly in late-successional species *E. leiocarpa* during wet season (November), not being evident in other species in this month or in any species during May (Fig. 4a and b). In forest understorey, no differences in F_v/F_m were observed between functional groups along the day (Fig. 4c and d). In general, significant differences between functional groups in relation to chlorophyll fluorescence parameters did not take place in understorey (Fig. 4c, d, g, h, k, l, and o, p). Effective quantum efficiency of PSII ($\Delta F/F'_m$) in gap dropped from 8:00 h, when irradiance reached leaves, showing full recovery at 16:00 h when PPFD were less than 100 μmol m^{-2} s^{-1} (Fig. 1a). There was no clear difference between pioneer and late-successional species in relation to

$\Delta F/F'_m$ in both periods of evaluation. However, $\Delta F/F'_m$ was higher in May than in November, likely due to differences in daily-PPFD (Figs. 1a and 4e, f). Apparent electron transport rate (ETR) was higher in November than in May from 10:00 to 14:00 h due to higher PPFD, but no differences between functional groups were found (Fig. 4i and j). The dissipation of excessive PPFD by non-photochemical fluorescence quenching (NPQ) peaked in May (dry season) at 12:00 h in gap conditions. Except for *E. leiocarpa* at 10:00 h in November, functional groups showed similar diurnal NPQ changes and values (Fig. 4m and n).

3.2. Changes in global network connectance and autonomy

Changes in photosynthetic network connectance (Cg_{total}) showed different patterns between gap and understorey conditions. Values of Cg_{total} were consistently higher in gap
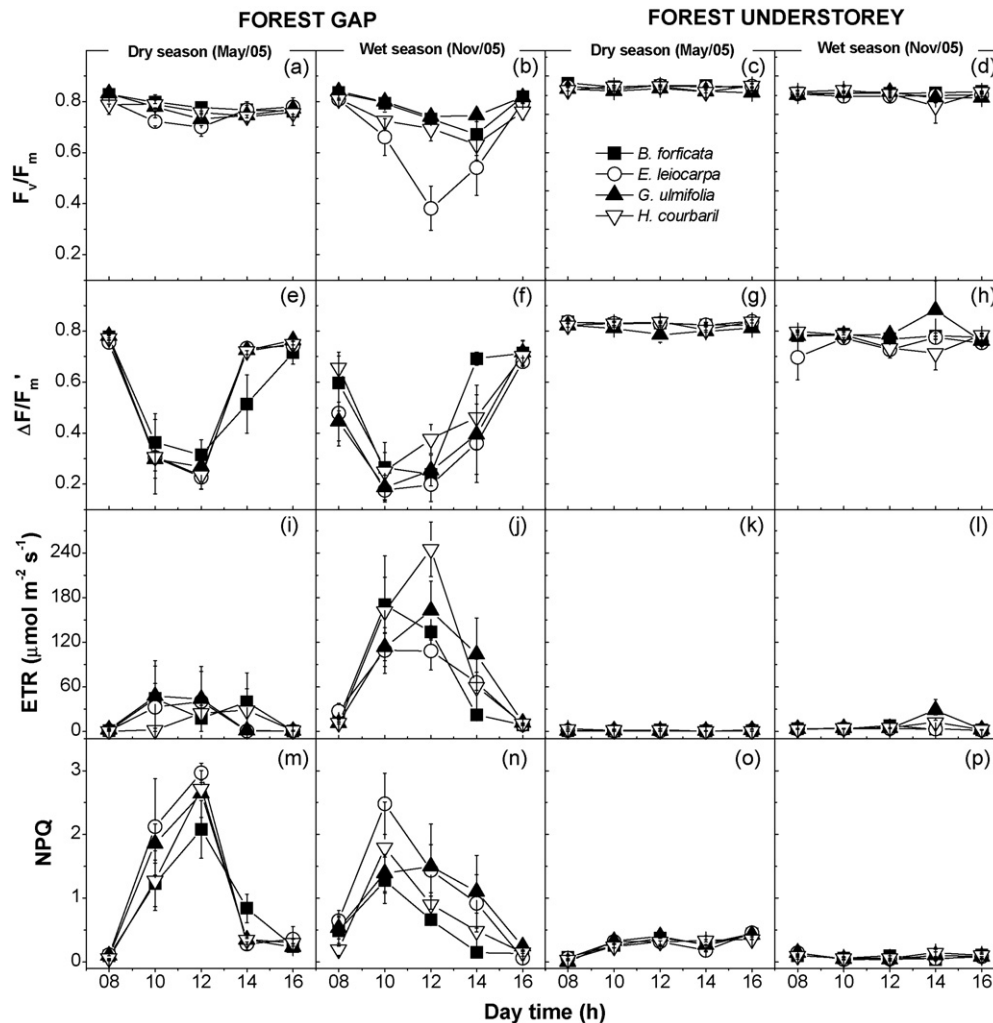
Fig. 4 – Diurnal courses of potential (F_v/F_m, in a–d) and effective ($\Delta F/F'_m$, in e–h) quantum efficiency of photosystem II, apparent electron transport rate (ETR, in i–l), and non-photochemical quenching (NPQ, in m–p) of pioneer (*G. ulmifolia* and *B. forficata*) and late-successional (*E. leiocarpa* and *H. courbaril*) tropical tree species growing under forest gap or understorey conditions. Measurements were taken in both dry (May 2005) and wet (November 2005) seasons. Mean values $\pm$ S.E. of 3 individuals and each individual averaged from 3 leaves.

than in understorey in both evaluations (Tables 1 and 2), except for *H. courbaril* in (Table 2). In May, Cg_{total} in gap was approximately 22 and 57% higher than in understorey for pioneers *B. forficata* and *G. ulmifolia*, respectively, and 45% greater in late-successional species (Table 3). However, *H. courbaril* showed Cg_{total} 17% lower in gap than in understorey in November (Table 3), because photochemical network connectance (Cg_{CF}) was remarkably higher in understorey than in gap (Table 2). Except for *H. courbaril*, Cg of photochemical and gas exchange networks were higher in gap than in understorey (Tables 1 and 2). Despite this general Cg pattern, some differences were observed between species in specific correlations. For instance, the straightforward stomatal control on CO_2 assimilation in *E. leiocarpa* was higher in understorey than in gap in May (Table 1), while in *H. courbaril* the opposite took place. A trend to higher stomatal control on transpiration was noticed in understorey than in gap in both months in all species, except in *H. courbaril* in May, suggesting

that transpiration could be under strong environmental influence under gap conditions, mostly due to high VPD.

The relationship between ETR and *A* represented the link between photosynthetic networks. For all species, in both months, the value of such link was consistently higher in the gap (Tables 1 and 2), suggesting a higher demand of electron flow to produce ATP and NADPH for supporting high values of net CO_2 assimilation (Figs. 2 and 3).

Results from autonomy analysis, which evaluates the relationship between photosynthetic and environmental changes, showed a consistent pattern of response. All species showed higher At values in gap than in understorey (Tables 4 and 5), indicating higher plasticity due to higher correlation between physiological and environmental changes. At values exhibited a mean reduction of 45% in the understorey (Table 3). This general response was present in both networks, regardless of successional status. However, specific relationships showed wide range of correlation levels (Tables 4 and 5).

Table 1 – Values of Pearson's correlation coefficient between photosynthetic parameters used to build and study connectances of photosynthetic (Cg_{total}), gas exchange (Cg_{GE}) and photochemical (Cg_{CF}) networks in late-successional (*E. leiocarpa* and *H. courbaril*) and pioneers (*G. ulmifolia* and *B. forficata*) species growing under forest gap or understorey (shade) conditions during the dry season (May 2005). 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. NPQ = non-photochemical quenching. A = net CO_2 assimilation. gs = stomatal conductance. E = transpiration. Rd = dark respiration. Pr = photorespiration. Ci = intercellular CO_2 concentration. Cg_{total} is the average between Cg_{CF} and Cg_{GE}. $P < 0.01$(*); $P < 0.05$(**); and $P > 0.05$(#).

Relationships		Late-successional				Pioneers			
		E. leiocarpa		*H. courbaril*		*G. ulmifolia*		*B. forficata*	
		Gap	Shade	Gap	Shade	Gap	Shade	Gap	Shade
F_v/F_m	$\Delta F/F'_m$	0.660*	0.630#	0.038#	0.694*	0.375#	−0.008#	0.253#	0.817*
F_v/F_m	ETR	−0.614*	0.511#	−0.190#	0.263#	−0.314#	0.132#	−0.045#	0.304#
F_v/F_m	NPQ	−0.493#	0.202#	−0.001#	−0.081#	−0.364#	−0.042#	−0.199#	−0.612*
$\Delta F/F'_m$	ETR	−0.825*	−0.105#	−0.509#	−0.240#	−0.749*	−0.197#	−0.844*	0.033#
$\Delta F/F'_m$	NPQ	−0.901*	0.233#	−0.726*	−0.234#	−0.896*	−0.105#	−0.901*	−0.340#
ETR	NPQ	0.842*	−0.066#	0.728*	−0.266*	0.817*	−0.361*	0.770*	−0.321#
ETR	A	0.566**	0.153#	0.345#	0.058#	0.751*	0.325#	0.744*	0.434#
Cg_{CF}		**0.938**	**0.296**	**0.428**	**0.289**	**0.807**	**0.172**	**0.743**	**0.480**
A	gs	−0.174#	0.572**	0.794*	0.137#	0.054#	0.110#	0.443#	0.443#
A	E	0.789*	0.827*	0.849*	0.151#	0.953*	0.095#	0.866*	0.490#
A	Rd	−0.729*	−0.040#	−0.645*	−0.342#	0.127#	0.135#	−0.601*	0.020#
A	Pr	0.513#	−0.456#	0.689*	−0.176#	0.756*	−0.814*	0.666*	−0.842*
A	Ci	−0.928*	−0.892*	−0.900*	−0.814*	−0.901*	−0.885*	−0.739*	−0.936*
Ci	gs	0.350#	−0.290#	−0.555**	−0.361#	0.325#	0.036#	0.182#	−0.297#
Ci	Rd	0.714*	0.262#	0.608*	0.219#	−0.063#	−0.120#	0.809*	0.054#
Ci	Pr	−0.618*	0.404#	−0.578**	0.038#	−0.683*	0.649*	−0.405#	0.768*
gs	E	0.086#	0.699*	0.918*	0.915*	0.156#	0.354#	0.649*	0.709*
Cg_{GE}		**0.717**	**0.628**	**0.999**	**0.462**	**0.656**	**0.465**	**0.751**	**0.693**
Cg_{total}		**0.827**	**0.462**	**0.713**	**0.375**	**0.731**	**0.318**	**0.747**	**0.586**

Table 2 – Values of Pearson's correlation coefficient between photosynthetic parameters used to build and study connectances of photosynthetic (Cg_{total}), gas exchange (Cg_{GE}) and photochemical (Cg_{CF}) networks in late-successional (*E. leiocarpa* and *H. courbaril*) and pioneers (*G. ulmifolia* and *B. forficata*) species growing under forest gap or understorey (shade) conditions during the wet season (November 2005). 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. NPQ = non-photochemical quenching. A = net CO_2 assimilation. gs = stomatal conductance. E = transpiration. Rd = dark respiration. Pr = photorespiration. Ci = intercellular CO_2 concentration. Cg_{total} is the average between Cg_{CF} and Cg_{GE}. $P < 0.01$(*); $P < 0.05$(**); and $P > 0.05$(#).

Relationships		Late-successional				Pioneers			
		E. leiocarpa		*H. courbaril*		*G. ulmifolia*		*B. forficate*	
		Gap	Shade	Gap	Shade	Gap	Shade	Gap	Shade
F_v/F_m	$\Delta F/F'_m$	0.702*	0.204#	0.273#	0.872*	0.404#	−0.253#	−0.021#	0.528**
F_v/F_m	ETR	−0.463**	−0.298#	−0.308#	−0.947*	−0.653*	−0.578**	− 0.073#	−0.469#
F_v/F_m	NPQ	−0.511#	0.282#	−0.091#	−0.584**	−0.577**	−0.478#	0.095#	−0.147#
$\Delta F/F'_m$	ETR	−0.648#	−0.233#	−0.454#	−0.807*	−0.639*	0.363#	−0.775*	−0.314#
$\Delta F/F'_m$	NPQ	−0.808*	0.001#	−0.791*	−0.266#	−0.732*	0.462#	−0.827*	−0.295#
ETR	NPQ	0.697*	−0.134#	0.364#	0.646*	0.545**	0.089#	0.559**	0.553**
ETR	A	0.739*	0.414#	0.765*	0.302#	0.549**	0.377#	0.714*	0.104#
Cg_{CF}		**0.806**	**0.231**	**0.520**	**0.897**	**0.684**	**0.401**	**0.561**	**0.372**
A	gs	−0.385#	−0.039#	0.228#	0.172#	0.149#	−0.146#	0.228#	−0.181#
A	E	0.716*	0.253#	0.714*	0.620*	0.803*	0.256#	0.787*	0.235#
A	Rd	0.503**	0.308#	0.216#	−0.146#	0.074#	−0.374#	0.165#	−0.228#
A	Pr	0.887*	0.898*	0.966*	0.893*	0.950*	0.719*	0.965*	0.652*
A	Ci	−0.829*	−0.615*	−0.823*	−0.395*	−0.673*	−0.584**	−0.551**	−0.743*
Ci	gs	0.644*	0.427#	0.185#	0.295#	0.23#	0.201#	0.376#	−0.192#
Ci	Rd	−0.601*	0.175#	−0.046#	−0.082#	−0.338#	0.523**	−0.188#	0.333#
Ci	Pr	−0.853*	−0.367#	−0.806*	−0.403#	−0.726*	−0.190#	−0.610*	−0.340#
gs	E	0.065#	0.770*	0.414#	0.809*	0.608*	0.812*	0.598*	0.849*
Cg_{GE}		**0.805**	**0.538**	**0.705**	**0.538**	**0.688**	**0.499**	**0.677**	**0.505**
Cg_{total}		**0.805**	**0.384**	**0.612**	**0.717**	**0.686**	**0.450**	**0.619**	**0.438**

Table 3 – Relative changes (%) in network features between gap and understorey environments, evidencing modulation in gas exchange (Cg_{GE}), photochemical (Cg_{CF}) and total (Cg_{total}) photosynthetic network connectance and also in the autonomy of gas exchange (At_{GE}), photochemical (At_{CF}) and total (At_{total}) photosynthetic network in late-successional (*E. leiocarpa* and *H. courbaril*) and pioneers (*G. ulmifolia* and *B. forficata*) species during the dry (May 2005) and wet (November 2005) seasons.

Network feature	Late-successional				Pioneers			
	E. leiocarpa		*H. courbaril*		*G. ulmifolia*		*B. forficata*	
	Seasons		Seasons		Seasons		Seasons	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Cg_{CF}	68.4	71.3	32.5	−72.5	78.7	41.4	35.4	33.7
Cg_{GE}	12.4	33.2	53.8	23.7	29.1	27.5	7.7	25.4
Cgt_{total}	**44.1**	**52.3**	**47.4**	**−17.2**	**56.5**	**34.4**	**21.6**	**29.2**
At_{CF}	43.8	16.4	45.2	66.7	40.2	55.4	56.0	8.7
At_{GE}	49.0	47.8	40.5	34.5	52.0	40.2	57.4	54.4
At_{total}	**46.7**	**33.4**	**42.5**	**50.8**	**46.4**	**47.8**	**56.7**	**35.9**

For instance, while in *E. leiocarpa* and *G. ulmifolia* the correlation between F_v/F_m and PPFD in May was significant in gap and non-significant in understorey, in *H. courbaril* and in *B. forficata* such correlation was non-significant in both conditions. Furthermore, while Rd and air temperature correlation in *E. leiocarpa* was significant in gap, it was not in understorey (Table 4). In *G. ulmifolia*, the opposite took place (Table 4).

4. Discussion

This study addressed two main hypotheses: (i) photosynthetic network connectance would increase in plants under gap conditions enabling higher control of the leaf's physiological network. This would be necessary to implement fast enough response since the gap environment typically exhibits dramatic environmental changes; and (ii) lower autonomy should be observed in gap environments especially in pioneer species, since they are considered to be more plastic than late-successional species. Herein, autonomy represents the ability of plant to maintain stable its photosynthetic processes despite of environmental changes (Souza et al., 2004a). In other words, in such conditions, we expect pioneers to present higher coupling to a changing environment (Chazdon et al., 1996).

The results from network connectance analyses showed a remarkable systemic response to each forest environment. Cg_{total}, Cg_{CF}, and Cg_{GE} values were consistently higher in plants under gap conditions regardless of their functional group or evaluation period, i.e. dry or wet season (Table 3), supporting our first hypothesis. According to the multiple-resource model (Chazdon et al., 1996; Strauss-Debenedetti and Bazzaz, 1996), species that experience gap events would have to show a high level of plasticity due to high daily and seasonal environmental fluctuations. Thus, the gap scenario demands a network modulation capable of maintaining photosynthetic processes under high level of control. This would be attained by physiological variables strong connected, allowing fine and fast tuning adjustments to environmental changes (Souza et al., 2005b). Hence, it was expected that pioneer would have

stronger connectance among their network components than late-successional species. However, no significant differences in Cg were observed between groups. Therefore, late-successional species showed acclimation capacity to gap conditions, with control and flexibility of photosynthetic network similar to pioneer species, regardless of their differences in maximum CO_2 assimilation and stomatal conductance (Fig. 3).

In complement to these results on network connectance, autonomy was consistently lower in the gap environment (Table 3), as we expected, since there would be a greater demand for flexibility to maintain system stability under large variation of environmental conditions.

However, lower autonomy, such as observed by Souza et al. (2005a), was not verified in pioneer rather than in late-successional species. The differences in autonomy observed by Souza et al. (2005a), instead of being inherent to functional groups, could be due to the fact that late-successional species did not have enough time to change their network organization and increase coupling with the environment. Thereupon, our second hypothesis was only partially supported. Both functional groups exhibited similar levels of plasticity under gap or understorey conditions. Moreover, despite of significant differences on leaf gas exchange, both functional groups showed fundamentally the same pattern of network modulation considering the relationships among photosynthetic variables studied herein. Therefrom, the network analysis performed in our study indicated that the systemic control of photosynthesis could be conservative regardless of species successional status.

This makes sense considering that the forest is a highly heterogeneous environment. Independently of functional group, species must be able to change their network organization to deal with the variability patterns existing therein. In fact, there is a compromise between connectance and plasticity (low autonomy). Our results indicated that plasticity likely demands high level of network connectance for attaining suitable responses under wide amplitude of environmental variation (such as in gap conditions). Values of Cg exhibited an inverse relationship with plant autonomy indicating that high level of network control is related to high plasticity.

Table 4 – Values of Pearson's correlation coefficient between photosynthetic and environmental variables used to calculate autonomies of photosynthetic (At$_{total}$), gas exchange (At$_{GE}$) and photochemical (At$_{CF}$) networks in late-successional (*E. leiocarpa* and *H. courbaril*) and pioneers (*G. ulmifolia* and *B. forficata*) species growing under forest gap or understorey (shade) conditions during the dry season (May 2005). 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. NPQ = non-photochemical quenching. A = net CO_2 assimilation. gs = stomatal conductance. E = transpiration. Rd = dark respiration. Pr = photorespiration. Ci = intercellular CO_2 concentration. Tair = air temperature. PPFD = photosynthetic photon flux density. VPD = atmospheric vapor pressure deficit. $P < 0.01$(*); $P < 0.1$(**); and $P > 0.1$(#).

Relationships		Late-successional				Pioneers			
		E. leiocarpa		*H. courbaril*		*G. ulmifolia*		*B. forficata*	
		Gap	Shade	Gap	Shade	Gap	Shade	Gap	Shade
F_v/F_m	PPFD	−0.872**	−0.115#	−0.293#	−0.294#	−0.772#	0.335#	−0.292#	0.275#
F_v/F_m	Tair	−0.882**	0.151#	−0.490#	0.201#	−0.986*	−0.346#	−0.634#	−0.565#
F_v/F_m	VPD	−0.830**	0.356#	−0.571#	0.306#	−0.945*	−0.287#	−0.595#	−0.584#
$\Delta F/F'_m$	PPFD	−0.769#	−0.942*	−0.790#	−0.425#	−0.783#	−0.747#	−0.953*	0.160#
$\Delta F/F'_m$	Tair	−0.709#	−0.617#	−0.733#	−0.038#	−0.723#	−0.854**	−0.907**	−0.583#
$\Delta F/F'_m$	VPD	−0.658#	−0.460#	−0.681#	0.102#	−0.659#	−0.882**	−0.867**	−0.539#
NPQ	PPFD	0.799#	−0.207#	0.807**	0.256#	0.812**	0.066#	0.943*	0.010#
NPQ	Tair	0.740#	0.579#	0.772#	0.931**	0.759#	0.770#	0.885**	0.797#
NPQ	VPD	0.708#	0.642#	0.791#	0.937*	0.734#	0.833**	0.900**	0.871**
ETR	PPFD	0.705#	0.518#	0.763#	0.344#	0.720#	0.719#	0.911*	0.724#
ETR	Tair	0.632#	0.330#	0.715#	−0.248#	0.651#	0.115#	0.882**	0.194#
ETR	VPD	0.548#	0.428#	0.840**	−0.166#	0.574#	0.106#	0.885**	0.195#
At$_{CF}$		**0.982**	**0.552**	**0.889**	**0.487**	**1.122**	**0.671**	**1.283**	**0.564**
A	PPFD	0.931**	0.622#	0.862**	0.673#	0.976*	0.419#	0.979*	0.761#
A	Tair	0.860**	0.553#	0.744#	−0.171#	0.927**	−0.037#	0.899**	0.198#
A	VPD	0.815**	0.620#	0.681#	−0.230#	0.900**	−0.263#	0.897**	0.012#
Rd	PPFD	0.838**	0.503#	0.827**	0.846**	0.404#	0.186#	0.827**	−0.030#
Rd	Tair	0.606#	0.222#	0.599#	0.798#	0.012#	0.657#	0.888**	−0.199#
Rd	VPD	0.693#	0.074#	0.728#	0.792#	0.197#	0.756#	0.800#	−0.097#
Ci	PPFD	−0.981*	−0.689#	−0.938#	−0.816**	−0.958*	−0.773#	−0.872**	−0.922**
Ci	Tair	−0.953*	−0.821**	−0.877**	−0.015#	−0.965*	−0.412#	−0.874**	−0.404#
Ci	VPD	−0.939*	−0.809**	−0.822**	0.105#	−0.959*	−0.205#	−0.854**	−0.239#
gs	PPFD	−0.165#	0.283#	0.860**	0.838**	−0.018#	0.044#	0.412#	0.275#
gs	Tair	−0.544#	−0.411#	0.673#	0.226#	−0.341#	−0.745#	0.151#	−0.589#
gs	VPD	−0.502#	−0.342#	0.671#	0.128#	−0.343#	−0.744#	0.239#	−0.699#
Pr	PPFD	0.981*	0.492#	0.982*	−0.923**	0.968*	0.716#	0.973*	0.688#
Pr	Tair	0.867**	0.635#	0.875**	0.547#	0.883**	0.367#	0.922**	0.502#
Pr	VPD	0.871**	0.552#	0.867**	0.530#	0.868**	0.175#	0.913**	0.294#
E	PPFD	0.911**	0.813**	0.917**	0.910*	0.965*	0.969*	0.854**	0.836**
E	Tair	0.823**	0.603#	0.847**	0.641#	0.937*	0.472#	0.808**	0.725#
E	VPD	0.767#	0.639#	0.842**	0.548#	0.909**	0.408#	0.867**	0.599#
At$_{GE}$		**1.268**	**0.647**	**1.231**	**0.733**	**1.256**	**0.603**	**1.323**	**0.564**
At$_{total}$		**1.125**	**0.600**	**1.060**	**0.610**	**1.189**	**0.637**	**1.303**	**0.564**

High Cg improves physiological control in relation to external perturbations maintaining system stability under more demanding environment, regardless plant functional group. On the other hand, under more stable conditions as in the understorey, Cg was lower, especially on the photochemical network, and leaf physiology more autonomous. Since network connectance and environmental coupling are low, these weak linkages may prevent sudden fluctuations of propagating through the network which would compromise system stability (Csermely, 2006). In short, it seems that strong links, internal or with the environment, may enhance system stability in settings where high control is needed whereas weak links, internal or with the environment, seem to promote stability when little control is needed and sudden perturbation of elevated magnitude probable. Most biological systems are probably able change the strength of their links, adapting to different environmental situations. For example, evidence supports that increases in correlation among variables are related to demand of higher physiological control. In Souza et al. (2004b) gas exchange network connectance in *Citrus sinensis*, under constant environmental conditions, changed under different VPD. Although VPD and other environmental conditions were constant, connectance was higher under higher VPD. This indicates that connectance is indeed related to physiological control, which would be required under higher VPD. In less demanding scenarios, as low VPD or low PPFD, strong correlation among variables would be unneeded and energy demanding (e.g. maintaining induction state) and could compromise system stability when facing unpredictable environmental fluctuations (e.g. sunflecks). In Souza et al. (2005b), the correlation coefficient between gas exchange variables were measured in two bean genotypes without water stress, under water deficit, and in recovery. The connection strength between A and gs consistently changed under different conditions, increasing from control to water deficit and decreasing again in recovery in

Table 5 – Values of Pearson's correlation coefficient between photosynthetic and environmental variables used to calculate autonomies of photosynthetic (At_{total}), gas exchange (At_{GE}) and photochemical (At_{CF}) networks in late-successional (*E. leiocarpa* and *H. courbaril*) and pioneers (*G. ulmifolia* and *B. forficata*) species growing under forest gap or understorey (shade) conditions during the wet season (November 2005). 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. **NPQ** = non-photochemical quenching. **A** = net CO_2 assimilation. **gs** = stomatal conductance. **E** = transpiration. **Rd** = dark respiration. **Pr** = photorespiration. **Ci** = intercellular CO_2 concentration. **Tair** = air temperature. **PPFD** = photosynthetic photon flux density. **VPD** = atmospheric vapor pressure deficit. $P < 0.01(*)$; $P < 0.1(**)$; and $P > 0.1(\#)$.

Relationships		Late-successional				Pioneers			
		E. leiocarpa		*H. courbaril*		*G. ulmifolia*		*B. forficata*	
		Gap	Shade	Gap	Shade	Gap	Shade	Gap	Shade
F_v/F_m	PPFD	−0.717#	−0.658#	−0.773#	−0.088#	−0.726#	0.727#	−0.686#	−0.815**
F_v/F_m	Tair	−0.758#	−0.886**	−0.857**	−0.192#	−0.820**	0.220#	−0.735#	−0.239#
F_v/F_m	VPD	−0.879**	−0.762#	−0.661#	0.054#	−0.824**	0.563#	−0.581#	−0.382#
$\Delta F/F'_m$	PPFD	−0.875**	−0.142#	−0.946*	−0.542#	−0.820**	0.136#	−0.597#	−0.506#
$\Delta F/F'_m$	Tair	−0.684#	0.704#	−0.823#	−0.568#	−0.575#	0.204#	−0.484#	−0.305#
$\Delta F/F'_m$	VPD	−0.686#	0.097#	−0.740#	−0.490#	−0.564#	−0.114#	−0.693#	−0.710#
NPQ	PPFD	0.825**	−0.505#	0.798#	−0.540#	0.921**	−0.587#	0.544#	−0.093#
NPQ	Tair	0.553#	−0.985*	0.672#	−0.326#	0.802**	−0.900**	0.335#	−0.414#
NPQ	VPD	0.630#	−0.697#	0.594#	−0.603#	0.806**	−0.878#	0.353#	0.105#
ETR	PPFD	0.903**	0.880**	0.710#	0.207#	0.880**	0.037#	0.722#	0.969*
ETR	Tair	0.792#	0.376#	0.694#	0.300#	0.861**	0.203#	0.629#	0.338#
ETR	VPD	0.816**	0.490#	0.903**	−0.002#	0.918**	−0.146#	0.722#	0.770#
At_{CF}		**1.046**	**0.874**	**1.071**	**0.357**	**1.147**	**0.512**	**0.700**	**0.639**
A	PPFD	0.868#	0.608#	0.684#	0.702#	0.879**	0.472#	0.804#	0.539#
A	Tair	0.887**	0.893**	0.763#	0.927**	0.913**	0.811#	0.864#	0.752#
A	VPD	0.950*	0.863#	0.956*	0.742#	0.608#	0.445#	0.971*	0.480#
Rd	PPFD	0.350#	−0.235#	0.664#	0.011#	0.581#	0.404#	−0.151#	−0.606#
Rd	Tair	0.557#	0.059#	0.370#	0.014#	0.588#	−0.122#	0.138#	−0.048#
Rd	VPD	0.821#	0.140#	0.303#	0.232#	0.786#	0.503#	−0.09#	−0.080#
Ci	PPFD	−0.862#	−0.462#	−0.725#	−0.038#	−0.905**	−0.326#	−0.953*	−0.615#
Ci	Tair	−0.876#	−0.930**	−0.863#	−0.228#	−0.934**	−0.163#	−0.912**	−0.615#
Ci	VPD	−0.955*	−0.565#	−0.972*	−0.043#	−0.763#	0.123#	−0.652#	−0.224#
gs	PPFD	−0.650#	0.260#	0.116#	0.759#	0.407#	0.731#	−0.158#	0.016#
gs	Tair	−0.806#	−0.454#	−0.200#	0.007#	0.451#	−0.107#	−0.268#	−0.719#
gs	VPD	−0.816#	−0.106#	0.006#	0.240#	0.762#	0.471#	0.169#	−0.556#
Pr	PPFD	0.779#	0.530#	0.799#	0.732#	0.908**	0.833#	0.770#	0.079#
Pr	Tair	0.875#	0.707#	0.815#	0.919**	0.959*	0.851#	0.913**	0.757#
Pr	VPD	0.954*	0.765#	0.942*	0.858#	0.754#	0.886**	0.986*	0.490#
E	PPFD	0.868#	0.579#	0.985*	0.907**	0.924**	0.914**	0.798#	0.350#
E	Tair	0.859#	0.374#	0.885**	0.682#	0.932**	0.470#	0.797#	−0.099#
E	VPD	0.742#	0.439#	0.786#	0.707#	0.803#	0.839#	0.911**	−0.210#
At_{GE}		**1.231**	**0.643**	**1.046**	**0.685**	**1.166**	**0.697**	**1.026**	**0.468**
At_{total}		**1.138**	**0.758**	**1.058**	**0.521**	**1.156**	**0.604**	**0.863**	**0.553**

both genotypes. Jalo Precoce genotype show an increase of Cg from 0.593 without stress to 0.929 under water deficit and a decrease to 0.726 in recovery. Guarumbé genotype showed an increase from 0.003 without stress to 0.775 under water stress and a decrease to 0.366 in recovery. The same was observed between other variables such as gs and E in both genotypes. In addition, in Prado et al. (2004), the connection strength between gs and E in woody Cerrado community showed higher value in dry season (0.994) compared to the wet season (0.107).

There is a long lasting debate whether pioneers or late successional species would have greater plasticity, considering the kind of environmental variability that they face (Strauss-Debenedetti and Bazzaz, 1996). Since late-successional species inhabit the understorey it is generally assumed that pioneer species are more plastic since they have to deal with variation in multiple resources (multiple resource model). Yet, even for late-successional species, it is important to change network connectance since they experience

variability in a major resource (light). Light is available in complex patterns, mainly through sunflecks, which happen usually by transitory breaches in the canopy (Chazdon et al., 1996). The intensity and frequency of sunflecks is basically unpredictable. Species inhabiting such environment would have to show high levels of photosynthetic flexibility, as proposed by the single resource model. This reinforces the view of Strauss-Debenedetti and Bazzaz (1996) that the single and multiple resource models are complementary, since late-successional species must be plastic to provide coordination of photosynthetic under sunflecks, and pioneers must be plastic to deal with variability in multiple resources. Our data is coherent with this idea since species from both functional groups were able to increase Cg and At in the gap, decreasing Cg and At in the understorey. Thus, species from both functional groups must be able to modulate their network in order to elicit suitable responses to distinct environmental variability patterns present in a forest.

Thence, our work suggests that photosynthetic network organization and autonomy patterns are not specific of a functional group but rather more general responses to environmental fluctuations, strongly related to system stability. Whereas network organization *per se* may not differentiate functional groups, the ability to change autonomy and connectance when facing perturbations may reflect differences in the homeostatic capabilities among plant species.

5. Concluding remarks

The systemic approach proposed in this study succeeded to uncover patterns of responses under contrasting environments. These responses underlying physiological networks are a result of a compromise between autonomy and connectance. Our results indicated that wide amplitude of variation in environmental conditions, such as in forest gap, demands high plasticity associated with high level of connectance in the photosynthetic network to attain suitable responses (fast and fine tuned). This casts light on the proposition that more complex dynamics provides greater stability in a changing environment, as reported in other works (Goldberger et al., 2002; Hütt and Lüttge, 2002; Souza et al., 2005b). Results supported that systemic control of photosynthesis could be conservative regardless of successional status. This reinforces the view of Strauss-Debenedetti and Bazzaz (1996) which states that the single and multiple resource model are complementary, given that species from both functional groups are able to show high plasticity, reflecting the necessity of adaptation to distinct environmental variability patterns. It is interesting to notice that the variability seen in particular parameters, as maximum CO_2 assimilation and stomatal conductance, is not accompanied by a similar amount of variability in systemic features. As stressed by Odum's classical book (Odum, 1963), the variance of the constituent parts, as CO_2 assimilation and stomatal conductance, is greater than the variance of the higher levels of organization, as is the case of network modulation features. Considering that network modulation is an emergent property of the interaction among elements, the network-like relationships (with different strengths, feed-backs and non-linear relations) among constituent parts provide regulatory properties in a higher level of organization. This could enable system stability and make variability in network features smaller than in its constituent elements.

In conclusion, we suggest that the changes in pattern of network organization are general patterns of response to environmental fluctuations, strongly related to system stability, and should be investigated further under the perspective of complexity theory, particularly addressing the stability of complex adaptive systems by means of network theory. Understanding stability in different levels of biological organization is a major issue in ecology since the stability of many ecosystems has been troubled by anthropogenic pressure (McCann, 2000). Therefore, different and complementary approaches are needed to investigate ecological stability such as diversity-stability relationships (McCann, 2000; Li and Charnov, 2001) and the allometry of energy partitioning in ecological communities (Li et al., 2004; Makarieva et al., 2004).

REFERENCES

Ahal, V., Allen, T.F.H., 1996. Hierarchy Theory: A Vision, Vocabulary, and Epistemology. Columbia University Press, New York, 206 pp.

Amzallag, G.N., 2001. Data analysis in plant physiology: are we missing the reality? Plant Cell Environ. 24, 881–890.

Barabási, A.L., 2003. Linked: How Everything is Connected to Everything Else and What it Means for Business, Science, and Everyday Life. Plume, Penguin Group, New York, 294 pp.

Bazzaz, F.A., Pickett, S.T.A., 1980. Physiological ecology of tropical succession: a comparative review. Ann. Rev. Ecol. Syst. 11, 287–310.

Chazdon, R.L., Pearcy, R.W., Lee, D.W., Fetcher, N., 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), Tropical Forest Plant Ecophysiology. Chapman & Hall, New York, pp. 5–55.

Csermely, P., 2006. Weak Links: Stabilizers of Complex Systems from Proteins to Social Networks. Springer-Verlag, Berlin.

Demmig, B., Björkman, O., 1987. Comparison of the effects of excessive light on chlorophyll fluorescence (77 K) and photon yield of O_2 evolution in leaves of higher plants. Planta 171, 171–184.

Edelman, G.M., Gally, J.A., 2001. Degeneracy and complexity in biological systems. PNAS 98, 13763–13768.

Farquhar, G.D., Von Caemmerer, S., 1982. Modelling of photosynthetic response to environmental conditions. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Encyclopedia of Plant Physiology. Springer-Verlag, Berlin, pp. 459–587.

Gardner, M.R., Ashby, W.R., 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. Nature 228, 784.

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

Goldberger, A.L., Peng, C.K., Lipsitz, L.A., 2002. What is physiological complexity and how does it change with aging and disease? Neurobiol. Aging 23, 23–26.

Hütt, M.T., Lüttge, U., 2002. Nonlinear dynamics as a tool for modeling in plant physiology. Plant Biol. 4, 281–297.

Jones, H., 1998. Stomatal control of photosynthesis and transpiration. J. Exp. Bot. 49, 387–398.

Kingsolver, J.G., Schemske, D.W., 1991. Path analyses of selection. Trends Ecol. Evol. 6, 276–280.

Krall, J.P., Edwards, G.E., 1992. Relationship between photosystem II activity and CO_2 fixation in leaves. Physiol. Plant. 86, 180–187.

Li, B.L., Charnov, E.L., 2001. Diversity-stability relationships revisited: scaling rules for biological communities near equilibrium. Ecol. Modell. 140, 247–254.

Li, B.L., Gorshkov, V.G., Makarieva, A.M., 2004. Energy partitioning between different-sized organisms and ecosystem stability. Ecology 85, 1811–1813.

Lorenzi, H., 1992. Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Plantarum, Nova Odessa, 352 pp.

Makarieva, A.M., Gorshkov, V.G., Li, B.L., 2004. Body size, energy consumption and allometric scaling: a new dimension in the diversity-stability debate. Ecol. Complex. 1, 139–175.

Martins, S.V., Rodrigues, R.R., 2002. Gap-phase regeneration in a semideciduous mesophytic forest, south-eastern Brazil. Plant Ecol. 163, 51–62.

McCann, K.S., 2000. The diversity-stability debate. Nature 405, 228–233.

Michaelian, K., 2005. Thermodynamic stability of ecosystems. J. Theor. Biol. 237, 323–335.

Mohr, H., Schopfer, P., 1995. Plant Physiology. Springer-Verlag, New York, pp. 1–20.

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

Odum, E.P., 1963. Ecology. Holt, Rinehart and Winston, New York, 152 pp.

Prado, C.H.B.A., Wenhui, Z., Rojas, M.H.C., Souza, G.M., 2004. Seasonal leaf gas exchange and water potential in a woody cerrado species community. Braz. J. Plant Physiol. 16, 7–16.

Reich, P.B., 1993. Reconciling apparent discrepancies among studies relating life span, structure and function of leaves in contrasting plant life forms and climates: 'the blind men and the elephant retold'. Funct. Ecol. 7, 721–725.

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

Schneider, E.D., Kay, J.J., 1994. Life as a manifestation of the second law of thermodynamics. Math. Comp. Model. 19, 25–48.

Sharkey, T.D., 1988. Estimating the rate of photorespiration in leaves. Physiol. Plant. 73, 147–152.

Souza, G.M., Cardoso, V.J.M., 2003. Toward a hierarchical concept of plant stress. Isr. J. Plant Sci. 51, 29–37.

Souza, G.M., Ribeiro, R.V., Santos, M.G., Ribeiro, H.L., Oliveira, R.F., 2004a. Functional groups of forest succession as dissipative structures: an applied study. Braz. J. Biol. 64, 707–718.

Souza, G.M., Ribeiro, R.V., Pincus, S.M., 2004b. Changes in network connectance and temporal dynamics of gas exchange in *Citrus sinensis* under different evaporative demands. Braz. J. Plant Physiol. 16, 119–130.

Souza, G.M., Ribeiro, R.V., Oliveira, R.F., Machado, E.C., 2005a. Network connectance and autonomy analyses of the photosynthetic apparatus in tropical tree species from different successional groups under contrasting irradiance conditions. Rev. Bras. de Bot. 28, 47–59.

Souza, G.M., Pincus, S.M., Monteiro, J.A.F., 2005b. The complexity-stability hypothesis in plant gas exchange under water deficit. Braz. J. Plant Physiol. 17, 363–373.

Strauss-Debenedetti, S., Bazzaz, F.A., 1996. Photosynthetic characteristics of tropical trees along successional gradients. In: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), Tropical Forest Plant Ecophysiology. Chapman & Hall, New York, pp. 162–186.

Strogatz, S., 2003. Sync: The Emerging Science of Spontaneous Order. Thenia, New York, 338 pp.

Thornthwaite, C.W., Mather, J.R., 1955. The Water Balance. Publications in Climatology, Drexel Institute of Technology, New Jersey, 104 pp.

Trewavas, A., 1986. Understanding the control of plant development and the role of growth substances. Aust. J. Plant Physiol. 13, 447–457.

Van Kooten, O., Snel, J.F.H., 1990. The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosyn. Res. 25, 147–150.