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Gas exchanges of two species from different successional status under greenhouse condition

Trocas gasosas de duas espécies de diferentes classes sucessionais sob condição de casa de vegetação

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ABSTRACT: Daily gas exchanges of tree species *Guazuma ulmifolia* (pioneer species) and *Cariniana legalis* (late secondary species) were measured under greenhouse condition. The main goal of this work was to verify the response of leaf gas exchange of both species to daily changes in greenhouse environmental condition. Both species showed decreased stomatal conductance (g_s) with increasing leaf-to-air vapor pressure difference (VPD) and air temperature (T_{air}). CO_2 assimilation (A) of *G. ulmifolia* was not affected by decreased g_s, while *C. legalis* showed reductions in A caused by low g_s. The effects of increasing T_{air} were higher in g_s than in A for both species. *G. ulmifolia* presented a tendency of reduction in the water use efficiency (WUE) during all day, while *C. legalis* maintained WUE relatively stable even under high VPD. The transpiration (E) of *G. ulmifolia* increased in response to increasing VPD, whereas *C. legalis* showed a reduction trend of E. The higher photosynthetic performance of *G. ulmifolia* was associated to higher values of g_s and E, supporting that physiological traits can be used to differentiate successional classes under greenhouse conditions.

KEYWORDS: *Cariniana legalis*, Ecophysiology, *Guazuma ulmifolia*, Photosynthesis, Successional classes

RESUMO: As trocas gasosas diárias das espécies arbóreas *Guazuma ulmifolia* (espécie pioneira) e *Cariniana legalis* (espécie secundária tardia) foram avaliadas em casa de vegetação. O objetivo desse estudo foi verificar as respostas das trocas gasosas de ambas espécies às variações ambientais diárias em condição de casa de vegetação. Ambas espécies apresentaram decréscimos da condutância estomática (g_s) com o aumento da diferença de pressão de vapor entre folha e ar (DPV) e da temperatura do ar (T_{ar}). A assimilação de CO_2 (A) de *G. ulmifolia* não foi afetada pelos menores valores de g_s, enquanto que *C. legalis* apresentou redução de A causada por baixa g_s. O efeito do aumento de T_{ar} foi maior sobre g_s do que sobre A em ambas espécies. *G. ulmifolia* apresentou tendência de redução da eficiência do uso da água (EUA) durante o dia, enquanto *C. legalis* manteve EUA relativamente estável mesmo em altos valores de DPV. Enquanto *G. ulmifolia* aumentou a transpiração (E) em resposta ao aumento de DPV, *C. legalis* demonstrou uma tendência de redução de E. A melhor performance fotossintética de *G. ulmifolia* foi associada a maiores valores de g_s e E, suportando que características fisiológicas podem ser usadas para diferenciar classes sucessionais em condição de casa de vegetação.

PALAVRAS-CHAVE: *Cariniana legalis*, Classes sucessionais, Ecofisiologia, Fotossíntese, *Guazuma ulmifolia*

INTRODUCTION

Plant species of different successional status are present in a forest formation process, showing metabolic and physiological characteristics that are unique (Bazzaz, 1996; Strauss-Debenedetti and Bazzaz, 1996). These features allow different plant responses to the same environmental stimuli, such as large changes in daily light intensity, air temperature, and relative air humidity (Strauss-Debenedetti and Bazzaz, 1996). The intensity of these environmental changes occurs according to the microclimate conditions and it could be an important factor to survival, establishment and growth of plant species (Chazdon and Fetcher, 1984; Smith et al., 1992).

It is known that depending on the successional status, species may show physiological mechanisms, which allow plant tolerance to seasonal and daily environmental changes (Bazzaz, 1996). In this context, high photosynthetic and transpiration rates found in early successional species associated with stomatal control of water loss could be considered as characteristics that improve the efficiency of light use, plant cooling, and avoidance of plant dehydration (Bazzaz, 1996). In the other hand, late successional species show lower values of photosynthetic and transpiration rates, being less affected by environmental changes, such as water deficit (Souza et al., 2004).

Leaf gas exchange studies have been widely used as an index of plant response to specific experimental treatments or environmental conditions (Vu et al., 1986). Ecological-based studies involving gas exchange responses of different successional tree species to surrounding environment are few if compared with crops (Chazdon et al., 1996). When it is available, the information about the susceptibility degree and/or plant physiological responses to environmental factors, such as high light and atmospheric demand, greatly enhances the potential utilization of many tropical tree species in specific programs of reforestation of degraded area and forest management (Chazdon et al., 1996). In addition, the knowledge of how plants respond to microclimatic changes under nursery or greenhouse conditions may be helpful when it is considered that seedlings may grow and reach the commercial pattern faster under specific environmental condition.

The main goal of this study was to verify the response of leaf gas exchanges of *Guazuma ulmifolia* and *Cariniana legalis* (an early and a late successional species, respectively) to daily changes in greenhouse climatic condition.

MATERIAL AND METHODS

Nine-month-old seedlings of *Guazuma ulmifolia* Lam. (Sterculiaceae) and *Cariniana legalis* (Mart.) Kuntze (Lecythidaceae) were grown in 8 L pots with 10 kg of a soil mixture (one-half soil, one-quarter sand, one-quarter cow manure, and nitrogen-phosphate-potassium fertilizer). Seedlings were kept in a greenhouse (with plastic film cover) at ESALQ/USP, Piracicaba, SP, Brazil (22°42'S, 47°30'W, 576 m of altitude). Plants were irrigated daily until soil saturation. *Guazuma ulmifolia* and *Cariniana legalis* are semi deciduous trees of early (pioneer) and late (late secondary) successional status respectively (Lorenzi, 1992). Three plants of each species were used for leaf gas exchange measurements.

CO_2 assimilation (A), stomatal conductance (g_s), transpiration (E), and intercellular CO_2 concentration (Ci) were evaluated using a portable infra-red gas analyzer (Model LI-6400, LICOR, Lincoln NE USA). Leaf gas exchange values were recorded when the total CV% was smaller than 0.5. The air entering the leaf cuvette was drawn of 2.5 m aboveground and passed through 10 L mixing volume before reaching the leaf chamber (Franco and Lüttge, 2002). Water use efficiency [WUE] was calculated as the relation between CO_2 assimilation and transpiration (A/E) (Nobel, 1999). Daily leaf gas exchange was measured in intervals of 2 h between 700 and 1700 h on 15 January 2003 (Summer at South hemisphere). Gas exchange measurements were taken in fully expanded and mature leaves exposed to light.

Daily courses of air temperature (T_{air}), photosynthetic photon flux density (PPFD), and leaf to air vapor pressure difference (VPD) were measured with the LI-6400.

Data were submitted to analysis of variance procedures (ANOVA) and means were compared by Tukey's test ($p<0.01$). Mean values were composed of six replications, with two leaves sampled per plant.

RESULTS AND DISCUSSION

A rapid increase in VPD, PPFD, and T_{air} was registered in early morning (Figure 1). The highest VPD, PPFD, and T_{air} values were observed at 1100 h, when they reached around 5.0 kPa, 1,300 μmol m^{-2} s^{-1}, and 42 °C respectively. After 1100 h, PPFD values showed a quite drop reaching around 200 μmol m^{-2} s^{-1} at 1700 h (Figure 1), being the factor that showed the highest daily fluctuation.

Plant response to light intensity is an important feature to growth, affecting directly the forest succession process. According to Chazdon et al. (1996), species range from the early successional light demanding species (pioneer) to the very shade tolerant understory ones. The prior represented by *G. ulmifolia* and the late by *C. legalis*.

G. ulmifolia showed higher photosynthesis than *C. legalis* during all day (Figure 2), supporting its classification as a pioneer species (Lorenzi, 1992). However, the higher photosynthetic performance of a pioneer species could be constrained under specific environmental conditions, such as soil water deficit (Souza et al., 2004) and low light conditions (Vincent, 2001).

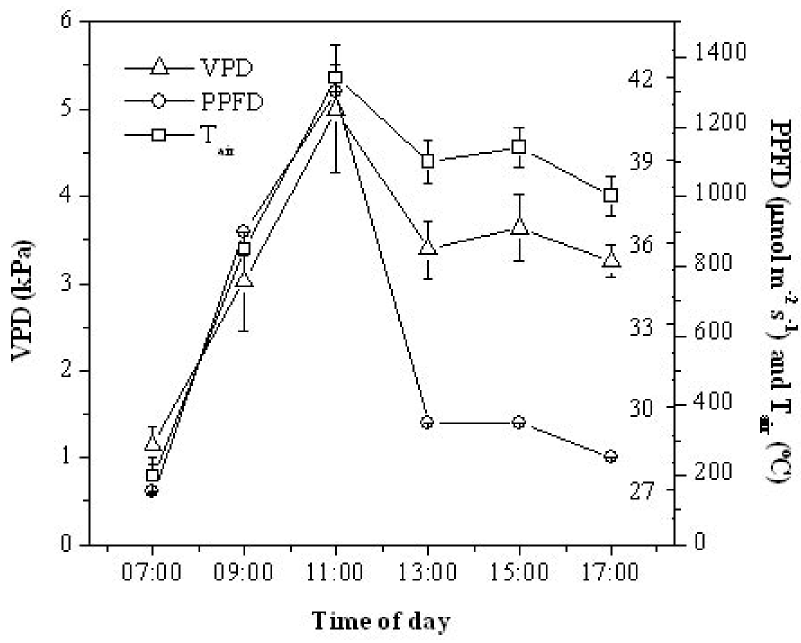

Figure 1
Daily course of leaf-to-air vapor pressure difference (VPD), air temperature (T_{air}), and photosynthetic photon flux density (PPFD). Symbols are mean values (n=6). Vertical lines are ± SD.
(Curso diário da diferença de pressão de vapor folha-ar (VPD), temperatura do ar (T_{air}) e densidade de fluxo de fótons fotossintéticos (PPFD). Símbolos são valores médios (n=6). Linhas verticais são ± DP)

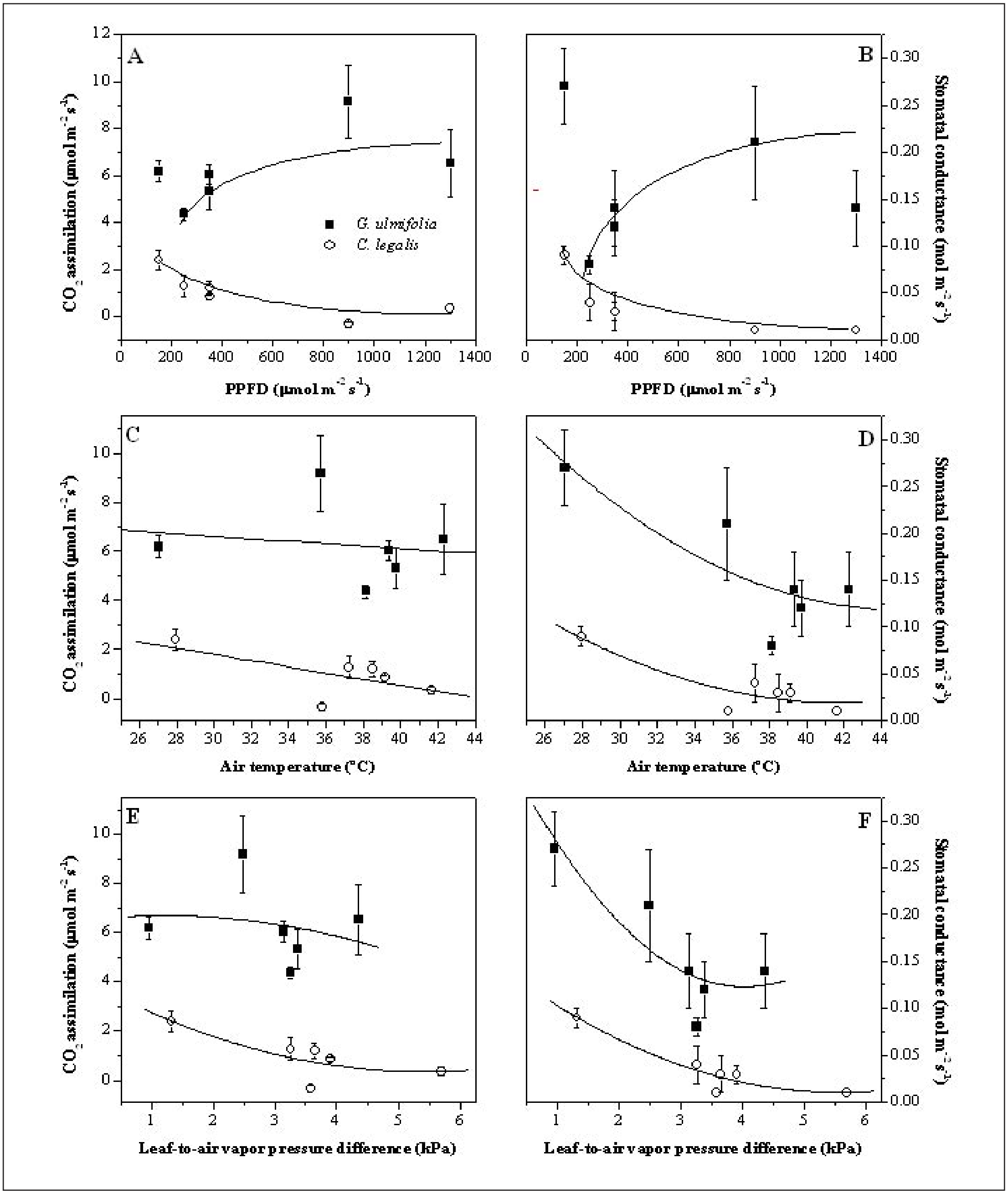

Figure 2
CO_2 assimilation (A, C, and E) and stomatal conductance (B, D, and F) as function of photosynthetic photon flux density, PPFD (A and B), air temperature (C and D), and leaf-to-air vapor pressure difference (E and F) in *G. ulmifolia* (closed square) and *C. legalis* (open circles) under greenhouse condition. Symbols are mean values (n=6) of measurements done during the daylight period. Vertical lines are ± SD.
(Assimilação de CO_2 (A, C e E) e condutância estomática (B, D e F) em função da densidade de fluxo de fótons fotossintéticos, PPFD (A e B), temperatura do ar (C e D), e diferença de pressão de vapor folha-ar (E e F) em *G. ulmifolia* (quadrados escuros) e *C. legalis* (círculos claros) sob condição de casa-de-vegetação. Símbolos são valores médios (n=6) de medições feitas durante o período diurno. Linhas verticais são ± D)

Concerning the plant physiological parameters, there were significant differences between *G. ulmifolia* and *C. legalis* in response to the changing environment. Increasing PPFD caused a tendency of higher A values of *G. ulmifolia* which was not observed in *C. legalis* (Figure 2A). The highest A values in *C. legalis* were observed at low PPFD levels found at early morning (700 h) and afternoon (1300-1700 h), contrary to what was observed in *G. ulmifolia*. This kind of response may indicate the occurrence of photoinhibition of photosynthesis in *C. legalis* as a consequence of excessive light (Long et al., 1994; Osmond, 1994).

The stomatal mechanism was also affected by increasing PPFD (Figure 2B). *C. legalis* showed decreases in g_s values with increasing PPFD during daylight period (Figure 2B), while *G. ulmifolia* showed increased g_s values with increasing PPFD. The g_s patterns observed in both species supported the A values, indicating that the smaller photosynthetic rate of *C. legalis* was due to low g_s and probable impairments in photochemical reactions (Long et al., 1994; Osmond, 1994).

In tropical regions, plant species often experience substantial daily and seasonal changes in light availability (Chazdon et al., 1996). For some species, high light availability works as a stress factor rather than as a resource that can be utilized by leaves (Chazdon et al., 1996). Moreover, plastic or acclimatory responses of species within these two extreme categories (early and late successional) are asymmetrical (Strauss-Debenedetti et al., 1996), even when they are grown under the same high-light conditions, shade-adapted species never attain photosynthetic capacities exhibited by light-demanding species.

Increasing T_{air} caused more accentuated decline in A of *C. legalis*, where the smallest values were observed around 42 °C (1100 h) (Figure 2C). At this temperature, *G. ulmifolia* showed A values around 6.5 μmol m^{-2} s^{-1}, while *C. legalis* reached about 0.5 μmol m^{-2} s^{-1} (Figure 2C). Thus, the CO_2 assimilation of *G. ulmifolia* was about thirteen times higher than *C. legalis* at same air temperature.

The effects of increasing temperature in g_s were more effective than in A (Figure 2C-F). Increasing T_{air} from 28 to 42 °C caused decreases in g_s from 0.275 to 0.145 mol m^{-2} s^{-1} in *G. ulmifolia* and from 0.095 to 0.010 mol m^{-2} s^{-1} in *C. legalis* (Figure 2D). Therefore, the natural increase of 14 °C caused reductions in g_s around 48% and 90% for *G. ulmifolia* and *C. legalis* respectively, indicating that daily changes of T_{air} (Figure 1) were more constrained to *C. legalis* (Figure 2C).

As high temperatures are a characteristic of high atmospheric demand (Nobel, 1999), decreases in g_s are expected at this condition (Khairi and Hall, 1976). Low g_s promotes decrease in E, reducing the plant body cooling capacity (Nobel, 1999). Then, heating of leaves will reduce plant photosynthetic capacity, one of the first physiological mechanisms affected by high temperature (Laisk et al., 1998; Ribeiro, 2002). The reduction of g_s due to increased leaf temperature and VPD (Figure 2D and F) is also related to the strategy of minimizing water loss relative to carbon gain (Ball et al., 1988; Nobel, 1999).

As expected, increasing VPD induced a sharp reduction in g_s, mainly in *C. legalis* (Figure 2F). The decreased g_s of *G. ulmifolia* did not cause significant changes in A, as observed in Figure 2E. *G. ulmifolia* showed g_s values around 0.15 mol m^{-2} s^{-1} at a VPD higher than 4.0 kPa which were more than sufficient to support A rates around 7.0 μmol m^{-2} s^{-1}. This was not observed in *C. legalis*, which showed decreases in A concomitant to decreases in g_s (Figure 2E and F). In fact, CO_2 assimilation decrease caused by VPD increase was also described for other tree species, such as *Eucalyptus*, citrus, and cashew (Khairi and Hall, 1976; Prior et al. 1997; Souza et al., 2002), as an indirect consequence of smaller g_s causing low CO_2 available to carboxylation reaction (Morison, 1987; Cornic, 2000).

The relation between A and g_s was similar for both species, but a slight difference was observed concerning the absolute values (Figure 3A). While g_s values around 0.10 mol m^{-2} s^{-1} in *C. legalis* was almost sufficient to permit A saturation (Figure 3A), maximum A rates of *G. ulmifolia* were reached with g_s around 0.20 mol m^{-2} s^{-1}. Decreasing g_s caused low Ci values in both species (Figure 3B). At g_s values smaller than 0.10 and 0.20 mol m^{-2} s^{-1} for *G. ulmifolia* and *C. legalis* respectively, Ci was reduced and then A was decreased as function of smaller CO_2 availability to photosynthetic activity (Morison, 1987; Cornic, 2000). The curvilinear relations between A and g_s (Figure 3A) observed for both species showed that daily greenhouse environmental changes affected g_s more than A, as proposed by Schulze and Hall (1982) and observed in Figures 2C-F.

Higher values of E were supported by higher g_s (Figure 3C), since there was evaporative demand, as indicated by VPD values (Figure 1). *G. ulmifolia* showed higher E responses to increasing g_s than *C. legalis*, with an increase from 2.5 to 6.0 mmol m^{-2} s^{-1} for changes in g_s from 0.08 to 0.15 mol m^{-2} s^{-1} (Figure 3C). *C. legalis* showed a decrease trend of E and A in response to increasing VPD (Figures 2E and 4) while *G. ulmifolia* showed a increase trend of E (Figure 4) and relative stable values of A (Figure 2E) in response to increasing VPD. Thus, WUE values of *G. ulmifolia* showed a constant tendency of reduction, while *C. legalis* maintained WUE around 1.0 μmol CO_2 (mmol $H_2O)^{-1}$ at VPD values between 3.2 and 5.5 kPa (Figure 5A).

Increasing VPD caused reductions in g_s of both species (Figure 2F), but these reductions did not decrease E in *G. ulmifolia* (Figure 4). Stomatal closing in response to increasing VPD and T_{air} is believed to be an adaptation to preserve the plant water status (Quick et al., 1992). According to Khairi and Hall (1976), in hot and dry climates, high WUE may be a greater adaptive advantage than high photosynthetic and growth rates for evergreen species. In fact, *G. ulmifolia* showed higher values of WUE than *C. legalis* during all daylight period, supporting one more time its classification as a pioneer species and indicating a possible physiological advantage under high atmospheric demand.

There was a common linear relationship between A and E for both species (Figure 5B), as observed by Franco and Lüttge (2002) in savanna tree species. Because g_s controls CO_2 and H_2O vapor exchange between leaf and environment, it is expected a positive relationship between A and E (Bazzaz, 1996).

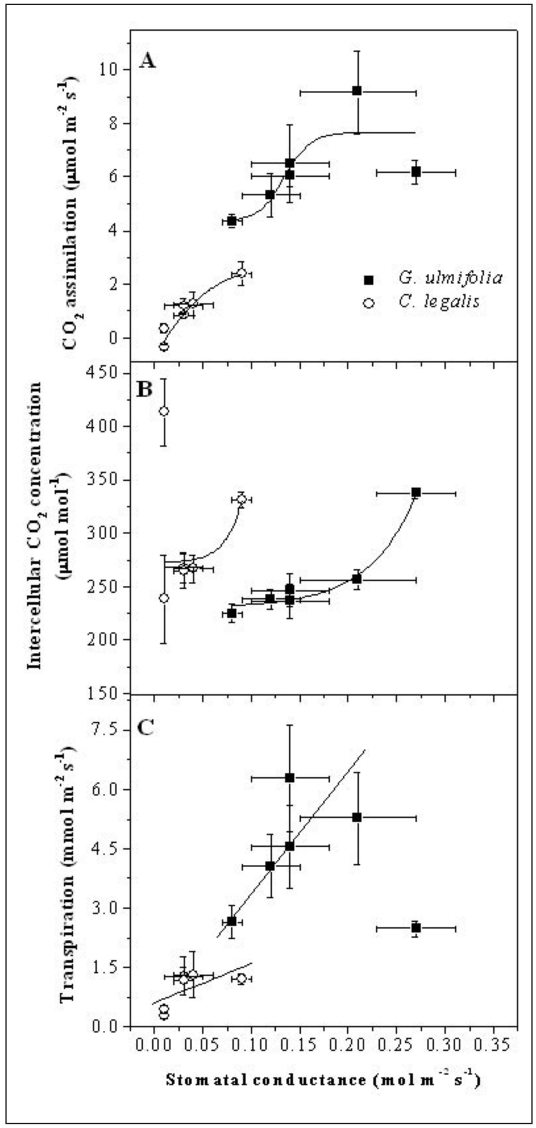

Figure 3
CO_2 assimilation (A), intercellular CO_2 concentration (B), and transpiration (C) as function of stomatal conductance in *G. ulmifolia* (closed square) and *C. legalis* (open circles) under greenhouse condition. Symbols are mean values (n=6) of measurements done during the daylight period. Vertical and horizontal lines are ± SD.
(Assimilação de CO_2 (A), concentração intercelular de CO_2 (B) e transpiração (C) em função da condutância estomática em *G. ulmifolia* (quadrados escuros) e *C. legalis* (círculos claros) sob condição de casa-de-vegetação. Símbolos são valores médios (n=6) de medições feitas durante o período diurno. Linhas verticais e horizontais são ± D)

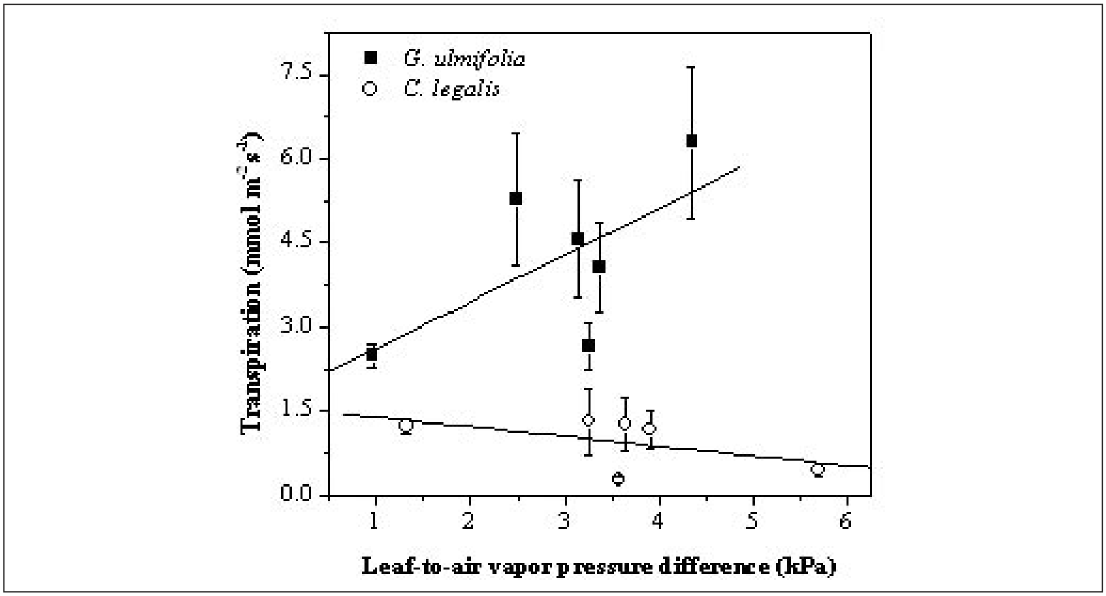

Figure 4
Transpiration as function of leaf-to-air vapor pressure difference in *G. ulmifolia* (closed square) and *C. legalis* (open circles) under greenhouse condition. Symbols are mean values (n=6) of measurements done during the daylight period. Vertical lines are ± SD.
(Transpiração em função da diferença de pressão de vapor folha-ar em *G. ulmifolia* (quadrados escuros) e *C. legalis* (círculos claros) sob condição de casa-de-vegetação. Símbolos são valores médios (n=6) de medições feitas durante o período diurno. Linhas verticais são ± DP)

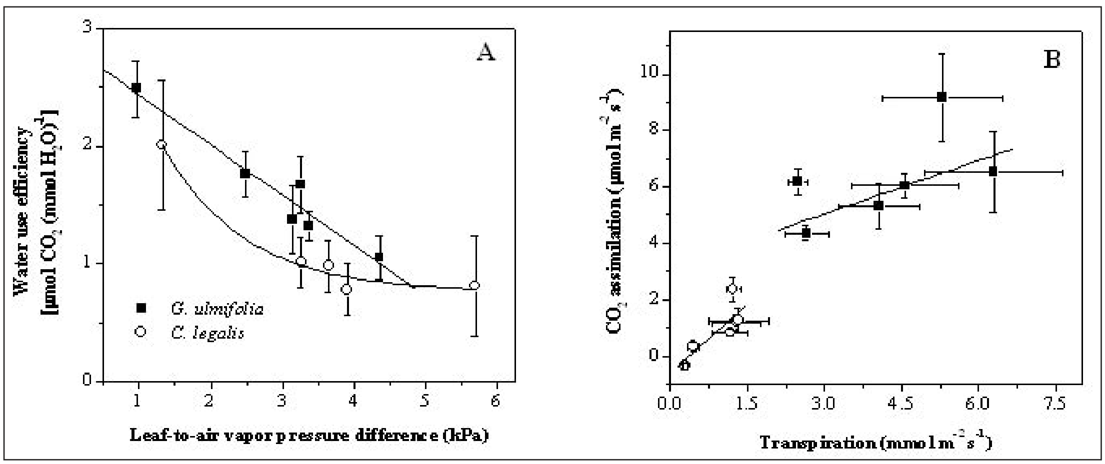

Figure 5
Water use efficiency as function of leaf-to-air vapor pressure deficit (A), and relationship between CO_2 assimilation and transpiration (B) of *G. ulmifolia* (closed square) and *C. legalis* (open circles) under greenhouse condition. Symbols are mean values (n=6) of measurements done during the daylight period. Vertical and horizontal lines are ± SD.
(Eficiência do uso da água em função da diferença de pressão de vapor folha-ar (A) e relação entre assimilação de CO_2 e transpiração (B) de *G. ulmifolia* (quadrados escuros) e *C. legalis* (círculos claros) sob condição de casa-de-vegetação. Símbolos são valores médios (n=6) de medições feitas durante o período diurno. Linhas verticais e horizontais são ± DP)

Concomitant increases in A and E permit the maintenance of photosynthetic activity, because higher E promotes plant cooling (Nobel, 1999) being a benefit to photosynthetic apparatus. In spite of the linear relationship between A and E, increasing VPD caused different E responses between the studied species (Figure 4). While *G. ulmifolia* increased E values in response to higher VPD, *C. legalis* showed a decrease trend of E. It could be a consequence of a higher stomatal control of water loss in *C. legalis* than in *G. ulmifolia*. In the other hand, plant cooling could be more efficient in the pioneer than in the secondary species, since E is the main process of heat dissipation (Nobel, 1999). These two characteristics may be more or less important, depending on ambient condition. The stomatal control of water loss may help under soil water deficiency or low water availability, but under full sunlight and without water deprivation the cooling promoted by a high transpiration may protect the photosynthetic apparatus. It may lead to increases or maintenance of high photosynthetic rates that will have as a consequence a faster plant growth.

In this context, *G. ulmifolia* shows higher growth (unpublished paper), photosynthesis, and WUE than *C. legalis*. According to Anderson and Osmond (1987), the low photosynthetic capacity of shade plants (late secondary species) result from low concentrations of synthetic enzymes and electron transport carriers. These features lead to a reduced cost of construction and maintenance respiration (Sims and Pearcy, 1991; Williams et al., 1989), an ecological advantage under resource shortage.

Leaves exposed to PPFD in excess of the photosynthesis requirements could also show reductions of the quantum yield of photosynthesis and possible photodamage, particularly in photosystem II complex (Long et al., 1994; Chazdon et al., 1996; Krause et al., 2001). According to previous studies, *C. legalis* have showed a chronic photoinhibition of photosynthesis caused by excessive light energy under field conditions (Ribeiro et al., unpublished paper). This injury has more effects in tree species because their light saturation is obtained at low light levels, mainly in species found in understory environment (Strauss-Debenedetti e Bazzaz, 1996; Krause et al., 2001).

It has been suggested that high values of CO_2 assimilation and transpiration rates of pioneer species may contribute to reduced photoinhibition (Krause et al., 2001). Higher A rates determine less excessive light energy, and higher E values reduce leaf temperature when there are high radiation loads (Nobel, 1999). Ball et al. (1988) reported that changes in gas exchanges of tropical forest trees indicated a decline in the biochemical capacity of the mesophyll to fix carbon with increase in leaf temperature.

Pioneer species generally exhibit a high flexibility of response for the photosynthetic capacity compared to species from later stages of forest succession (Chazdon et al., 1996). We suggest that the higher growth performance of early successional species could be attributed to high g_s and E values (Figures 2-5). High g_s permits more CO_2 incoming to mesophyll and then high A, while high E determines appropriate leaf temperatures to photosynthetic activity (Nobel, 1999). Bazzaz (1996) has also predicted that higher photosynthetic performance of pioneer species is also due to a high Rubisco content and low resistance to water transport through the vascular system.

Summarizing, *G. ulmifolia* and *C. legalis* showed differential gas exchange responses to T_{air}, VPD and PPFD under greenhouse condition. The higher photosynthetic performance of *G. ulmifolia* was associated to higher values of g_s and E, supporting that physiological traits can be used to differentiate successional classes under greenhouse condition.

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REFERENCES

ANDERSON, J.M.; OSMOND, C.B. Shade-sun responses: compromises between acclimation and photoinhibition. In: KULE D.J.; OSMOND C.B.; ARNTZEN C.J. **Topics in photosynthesis**. Amsterdam: Elsevier, 1987. p.1-38.

BALL, M.C.; COWAN, I.R.; FARQUHAR, G.D. Maintenance of leaf temperature and the optimization of carbon gain in relation to water loss in a tropical mangrove forest. **Australian journal of plant physiology**, v.15, p.263-276, 1988.

BAZZAZ, F.A. Physiological trends of successional plants. In: BAZZAZ, F.A. **Plants in changing environments**. Cambridge: Cambridge University Press, 1996. p.206-222.

CHAZDON, R.L.; FETCHER, N. Photosynthetic light environments in a lowland tropical forest in Costa Rica. **Journal of ecology**, v.72, p.553-564, 1984.

CHAZDON, R.L.; PEARCY, R.W.; LEE, D.W.; FETCHER, N. Photosynthetic responses of tropical forest plants to contrasting light environment. In: MULKEY S.S.; CHAZDON R.L.; SMITH A.P. **Tropical forest plant ecophysiology**. London: Chapman & Hall, 1996. p.5-55

CORNIC, G. Drought stress inhibits photosynthesis by decreasing stomatal aperture - not by affecting ATP synthesis. **Trends in plant science**, v.5, p.187-188, 2000.

FRANCO, A.C.; LÜTTGE, U. Midday depression in savanna trees: coordinated adjustments in photochemical efficiency, photorespiration, CO_2 assimilation and water use efficiency. **Oecologia**, v.131, p.356-365, 2002.

KHAIRI, M.M.A.; HALL, A.E. Temperature and humidity effects on net photosynthesis and transpiration of citrus. **Physiologia plantarum**, v.36, p.29-34, 1976.

KRAUSE, G.H.; KOROLEVA, O.Y.; DALLING, J.W.; WINTER, K. Acclimation of tropical tree seedlings to excessive light in simulated tree-fall gaps. **Plant, cell and environment**, v.24, p.1345-1352, 2001.

LAISK, A.; RASULOV, B.H.; LORETO, F. Thermoinhibition of photosynthesis as analyzed by gas exchange and chlorophyll fluorescence. **Russian journal of plant physiology**, v.45, p.412-421, 1998.

LONG, S.P.; HUMPHRIES, S.; FALKOWSKI, P.G. Photoinhibition of photosynthesis in nature. **Annual review of plant physiology and plant molecular biology**, v.45, p.633-662, 1994.

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

MORISON, J.I.L. Intercellular CO_2 concentration and stomatal response to CO_2. In: ZEIGER E.; FARQUHAR G.D.; COWAN I.R. **Stomatal function**. Stanford: Stanford University Press, 1987. p.229-251.

NOBEL, P.S. **Physicochemical and environmental plant physiology**. San Diego: Academic Press, 1999. 474p.

OSMOND, C.B. What is photoinhibition? Some insights from comparisons of shade and sun plants. In: BAKER N.R.; BOWYER, J.R. **Photoinhibition of photosynthesis: from molecular mechanisms to the field**. Oxford: BIOS Scientific, 1994. p.1-24

PRIOR, L.D.; EAMUS, D.; DUFF, G.A. Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetrodonta* samplings in a wet-dry savanna in northern Australia. **Australian journal of botany**, v.45, p.241-258, 1997.

QUICK, W.P.; CHAVES, M.M.; WENDLER, R.; DAVID, M.; RODRIGUES, M.L.; PASSAHARINHO, J.A.; PEREIRA, J.S.; ADCOCK, M.D.; LEEGOOD, R.C.; STITT, M. The effect of water stress on photosynthetic carbon metabolism in four species grown under field conditions. **Plant, cell and environment**, v.15, p.25-45, 1992.

RIBEIRO, R.V. **Influência da temperatura na fotossíntese de laranjeira ‘pera’ com clorose variegada dos citros**. Piracicaba, 2002. 58p. (Dissertação – Mestrado) - Escola Superior de Agricultura Luiz de Queiroz. Universidade de São Paulo

SCHULZE, E.D.; HALL, A.E. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. In: LANGE, O.L.; NOBEL, P.S.; OSMOND, C.B.; ZIEGLER, H. **Physiological plant ecology: 2- water relations and carbon assimilation**. Berlin: Springer-Verlag, 1982. p.181-229.

SIMS, D.A.; PEARCY, R.W. Photosynthesis and respiration in Alocasia macrorrhiza following transfers to high and low light. **Oecologia**, v.86, p.447-453, 1991.

SMITH, A.P.; HOGAN, K.P.; IDOL, J.R. Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. **Biotropica**, v.24, p.503-511, 1992.

SOUZA, G.M.; RIBEIRO, R.V.; SANTOS, M.G.; RIBEIRO, H.L.; OLIVEIRA, R.F. Functional groups of forest succession as dissipative structures: an applied study. **Brazilian journal of Biology**, v.64, 2004. (in press).

SOUZA, R.P.; MACHADO, E.C.; RIBEIRO, R.V.; OLIVEIRA, R.F.; SILVEIRA, J.A.G. Respostas da fotossíntese em plantas jovens de cajueiro (*Anacardium occidentale* L.) frente à variação das condições ambientais. In: CONGRESSO DA SOCIEDADE BOTÂNICA DE SÃO PAULO, 14, Rio Claro, 2002. **Anais**. Rio Claro: SBSP, 2002. (CD-ROM).

STRAUSS-DEBENEDETTI, S.; BAZZAZ, F.A. Photosynthetic responses of tropical forest plants to contrasting light environments. In: MULKEY, S.S.; CHAZDON, R.L.; SMITH, A.P. **Tropical forest plant ecophysiology**. London: Chapman & Hall, 1996. p.162-185.

VINCENT, G. Leaf photosynthetic capacity and nitrogen content adjustment to canopy openness in tropical forest tree seedlings. **Journal of tropical ecology**, v.17, p.495-509, 2001.

VU, J.C.V.; YELENOSKY, G.; BAUSHER, M.G. CO_2 exchange rate, stomatal conductance, and transpiration in attached leaves of 'Valencia' orange. **HortScience**, v.21, p.143-144, 1986.

WILLIAMS, K.; FIELD, C.B.; MOONEY, H.A. Relationships among leaf construction cost, leaf longevity, and light environments in rainforest plants of the genus Piper. **American naturalist**, v.133, p.198-211, 1989.