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Photosynthesis and water use efficiency in twenty tropical tree species of differing succession status in a Brazilian reforestation

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Abstract

Leaf gas exchange characteristics were measured in twenty woody species that differ in succession status ranging from pioneer species (PS) to late succession species (LS) in a Brazilian rain-reforestation ecosystem. Photon-saturated photosynthetic rate, calculated per either a leaf area (P_{NA}) or a dry mass (P_{NM}) basis, differed among species. P_{NA} and P_{NM} were highest in PS and lowest in LS. Variation among species was 3-fold (from 7 to 23 μmol m^{-2} s^{-1}) for $P_{NA,}$ and 5-fold (from 50 to 275 μmol kg^{-2} s^{-1}) for P_{NM}. The highest P_{NA} (23 μmol m^{-2} s^{-1}) and P_{NM} (275 μmol kg^{-2} s^{-1}) values were recorded in PS *Croton urucurana,* while the lowest P_{NA} (7 μmol m^{-2} s^{-1}) and P_{NM} (50 μmol kg^{-2} s^{-1}) values were recorded in LS *Aspidosperma cylindrocarpon.* A considerable overlap was recorded between PS and LS in values of stomatal conductance (g_s), transpiration rate (E), and leaf mass to area ratio (ALM). However, *C. urucurana* also showed highest g_s and *E*. P_{NM} was highly correlated with ALM in both PS and LS (r = –0.75 and –0.90, respectively). The high values of instantaneous transpiration efficiency (ITE) and intrinsic water use efficiency (WUE$_i$) were also observed in the PS when compared with the LS.

Additional key words: instantaneous transpiration efficiency; intrinsic water use efficiency; leaf gas exchange; stomatal conductance.

Introduction

Variation in the photosynthetic capacity of tree species occurring during different stages of secondary succession may reflect variation in their intrinsic traits (Bazzaz 1979). Despite the common occurrence of secondary succession in the tropics, there is scarce information available about photosynthesis and related physiological features among tropical species of differing succession status. Relatively few data are available on eco-physiological responses in the field. Recently, indications that tropical pioneer tree species (PS) have higher maximum photosynthetic capacity that the late-succession (LS) trees have been verified (Reich *et al.* 1995, Vera *et al.* 1999, Krause *et al.* 2001).

Differences among species occurring during different stages of secondary succession in physiological characteristics may reflect variation in environmental resources availability. Compared to LS, PS tend to have long-dispersal, low-density wood, which leads to rapid growth in height, short longevity, early maturation, short-lived leaves, high ALM (ratio of leaf mass to surface area), and high rates of mortality under resource deprivation. In the absence of disturbance, LS eventually exclude early-succession species competitively, because they reduce resources beneath the levels required by the PS. The PS persist as a result of two processes. High fecundity and long dispersal allow these species to colonize recently disturbed sites before the dominant competitors arrive. In addition, rapid growth under resource-rich conditions allows them temporarily to outperform LS, even if both arrive simultaneously in a recently disturbed site (Rees *et al.* 2001).

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Abbreviations: ALM – leaf mass to area ratio (area leaf mass); E – transpiration rate; g_s – stomatal conductance; ITE – instantaneous transpiration efficiency; LS – late succession species; P_{max} – maximum net photosynthetic rate; P_N – net photosynthetic rate; P_{NA} – photosynthetic rate per leaf area basis; P_{NM} – photosynthetic rate per dry mass basis; PS – pioneer species; WUE$_i$ – intrinsic water use efficiency.

It is possible to find greater leaf nutrient concentration and photosynthetic capacity at succession stages showing higher resources availability. Conversely, in low resource environments, extent leaf duration and high nutrient retranslocation capacity may be important adaptations (Reich *et al.* 1991). However, this is not universally true. Reich *et al.* (1995) found that net photosynthetic rate (P_N), maximum leaf diffusive conductance (g_s), ALM, and foliar calcium and magnesium contents were higher in the PS and lower in species common to each LS stage. These patterns were consistent with observed decreases in light and nutrient availability during secondary succession. However, these authors pointed out that leaf N and P contents did not differ among mid- and late-succession species, despite the continuing decline in P_N, g_s, ALM, and leaf Ca content. At similar P or N content, Raaimakers *et al.* (1995) found that tropical PS have a higher photon-saturated rate of photosynthesis (P_{max}) than climax species.

In the present study we describe the photosynthetic and water use characteristics of twenty woody species of differing succession status ranging from PS to LS in a Brazilian rain-reforestation ecosystem. Some leaf gas exchange features and leaf structure (ALM) were determined in order to highlight relationships among leaf traits and the succession status through the studied species. We also checked whether species of different succession stages show different instantaneous transpiration efficiency (ITE) and intrinsic water use efficiency (WUE_i) characteristics. Because tree species are dealing with available resources, the knowledge of leaf traits as gas exchange, ITE, and WUE_i can be useful criteria to select particular species for reforestation management.

Materials and methods

Study site and plants: The study was carried out at a reforestation area located in the Ribeirão Preto campus of the University of Sao Paulo (21°10'S, 47°48'W), at 650 m. a.s.l. According the Koeppen's climatic classification, this life zone is a tropical wet and dry (Aw) with mean annual precipitation of 1 518 mm and mean annual temperature of 22 °C. The experiment was carried out under natural conditions during the rainy season between 2002 and 2003. The rainy season includes spring and summer (October to March). The dry period coincides with autumn and winter (April to September). The soil is a red Latossolo.

Twenty tree species with different succession status growing at the reforestation area were selected for the study. The pioneer (early succession) species (PS) were *Croton urucurana* Baill, *Cecropia pachystachia* Trecul, *Croton floribundus* Spreng, *Solanum granuloso-leprosum* Dun, *Lafoensia pacari* St. Hil, *Cytharexyllum myrianthum* Cham, *Centrolobium tomentosum* Guill. *ex* Benth, *Guazuma ulmifolia* Lam, *Gallesia integrifolia* Spreng, Harms, *Schinus terebinthifolius* Raddi, *Cedrela fissilis* Vell, *Psidium guajava* L., and *Syzygium cumini* L. Skeels. The non-pioneer (late successional) species (LS) were *Copaifera langsdorffii* Desf., *Hymenaea courbaril* L. *var. stilbocarpa* Hayne, Lee *et* Lang, *Ficus guaranitica* Schodat, *Genipa americana* L., *Colubrina glandulosa* Perkins, *Tabebuia roseo-alba* Ridl. Sand., and *Aspidosperma cylindrocarpon* Muell. Arg. The simple division of tree species into two groups or guilds, PS and LS, was based on seed germination and seedling establishment according to Swaine and Whitmore (1988) and Lorenzi (1992).

Gas exchange measurements: The gas exchange was determined on 3–4-years-old plants growing in the field. All measurements were made on fully expanded leaves without signs of senescence that correspond to the age of peak leaf performance. Leaf gas exchange rates were measured using an open portable infrared gas exchange system (model *LCA-4*, *Analytical Development Co*., Hoddesdon, U.K.). Leaves were measured under ambient CO_2 concentration [360 $\mu mol(CO_2)\ mol^{-1}$]. A halogen radiation source was used to keep constant the photosynthetic photon flux density (PPFD) at 1 700 $\mu mol\ m^{-2}\ s^{-1}$. Air and leaf temperature during measurements were maintained constant at 26±1 °C using a Peltier system attached to the photosynthetic leaf chamber *PLC-4N* (*Analytical Development Co*., Hoddesdon, U.K.). Net photosynthetic rate per unit leaf area (P_{NA}), transpiration rate (E), stomatal conductance (g_s), and internal CO_2 concentration were measured between 07:00 to 11:00 under saturating irradiance. Twenty-five leaves per species were sampled (five leaves of each 5 individuals). Immediately after gas exchange measurements, each leaf was harvested, traced for subsequent leaf area determination, and oven-dried. Leaf samples were weighed to calculate ALM [$g\ m^{-2}$] according to Westoby (1998). ITE and WUE_i were calculated as the ratio P_{NA}/E and P_{NA}/g_s, respectively (Nobel 1999). Photosynthetic rate per dry mass basis (P_{NM}) was obtained by dividing the P_{NA} by the mean values of ALM (Prado and de Moraes 1997).

During gas exchange measurements, the leaf water potential (ψ) of detached leaves was measured utilizing a pressure chamber (model *3005*, *Santa Barbara Soil Moisture*, Santa Barbara, USA). Four samples for leaf water potential were made per species.

Statistical analysis: Regression analyses were used to examine relationships between ALM and mass-based photosynthesis. Species effects and relationships were considered to be significant if $p \leq 0.05$.

Results

Leaf water potential: During the gas exchange measurements, ψ in all species achieved values from –0.05 to –1.00 MPa. The higher values of ψ can be associated with the available water in the soil in the wet season.

Gas exchange characteristics: Photosynthetic characteristics varied considerably among species in a pattern related to their succesion status. P_{NA} and P_{NM} (Fig. 1) were higher for PS and lower for the LS as a group. Variation among species was 3-fold (from 7 to 23 µmol m^{-2} s^{-1}) for P_{NA} and 5-fold (from 50 to 275 µmol kg^{-2} s^{-1}) for P_{NM}. The highest P_{NA} (23 µmol m^{-2} s^{-1}) and P_{NM} (275 µmol kg^{-2} s^{-1}) values were recorded in the PS *C. urucurana,* while the lowest values of P_{NA} (7 µmol m^{-2} s^{-1}) and P_{NM} (50 µmol kg^{-2} s^{-1}) were recorded in the putative non-pioneer LS *A. cylindrocarpon.* P_{NA} average of 14 µmol m^{-2} s^{-1} and 8 µmol m^{-2} s^{-1} were determined on PS and LS, respectively. P_{NM} means of 106 and 98 µmol m^{-2} s^{-1} were determined on PS and LS, respectively.

A remarkable overlap was recorded between PS and

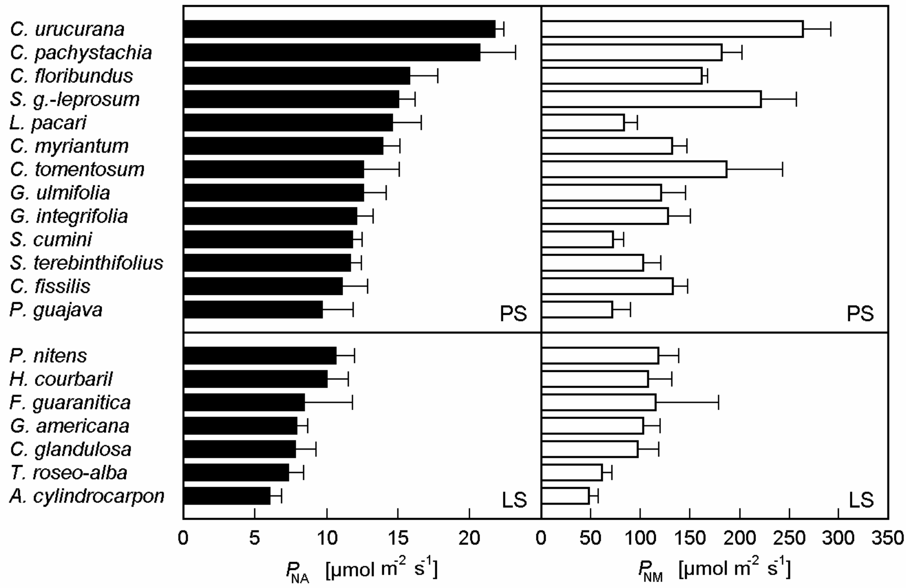

Fig. 1. Photosynthetic rate per unit leaf area (P_{NA}, *black bars*) and photosynthetic rate per unit dry mass (P_{NM}, *white bars*) for pioneer (PS) and non-pioneer (LS) Brazilian tropical forest tree species growing in a reforestation area. Means ± SE.

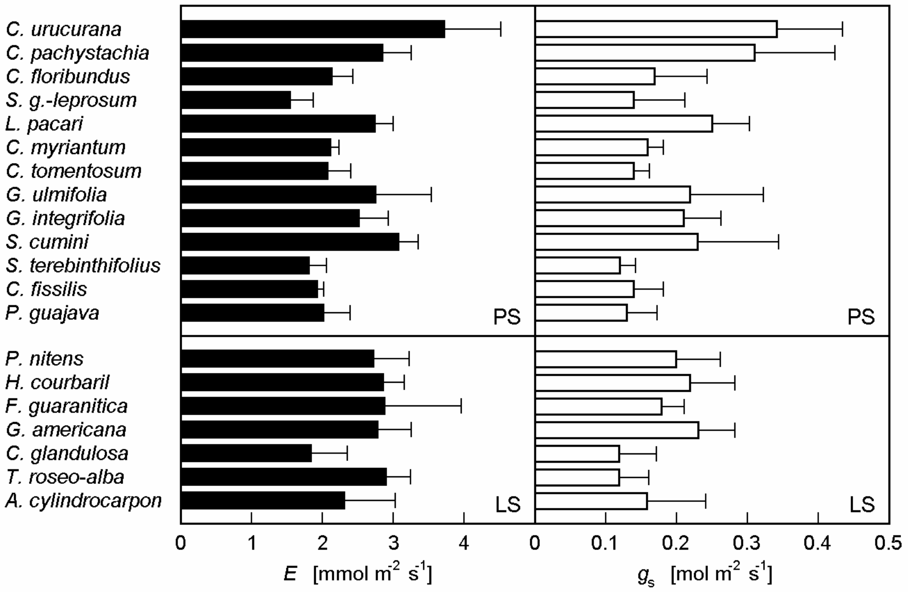

Fig. 2. Transpiration rate (E, *black bars*) and stomatal conductance (g_s, *white bars*) for pioneer (PS) and non-pioneer (LS) Brazilian tropical forest tree species growing in a reforestation area. Means ± SE.

LS in values of E and g_s (Fig. 2) and ALM (Fig. 3). However, the PS *C. urucurana* showed, besides greatest P_{NA} and P_{NM}, also highest E and g_s. The highest and the lowest ALM were observed in the PS *L. pecari* and *C. tomentosum*, respectively. Since $P_{NM} = P_{NA}/\text{ALM}$, higher ALM values observed in some PS and LS offsets higher P_{NA} such that P_{NM} decreases in some PS and increase in some LS (Fig. 1).

The highest values of WUE_i and ITE (Fig. 4) were also observed in the PS when compared with the LS. The highest WUE_i (127 μmol mol^{-1}) and ITE (11 μmol mmol^{-1}) were observed in the PS *S. granuloso-leprosum,* while the lowest mean values of WUE_i (37 μmol mol^{-1}) and ITE (2.5 μmol mmol^{-1}) were observed in the LS *G. americana*. P_{NM} was highly correlated with ALM (Fig. 5) in both PS and LS ($r = -0.75$ and -0.90, respectively).

Discussion

The present study shows strong differences in species photosynthetic characteristics corresponding to the succession status, which may imply selection for their traits through succesion replacement. Most of the variability in physiological characteristics may be explained by species identity. P_{NA} was highest in earlier succession species (pioneers) and lower in species common to each LS stage (non-pioneers). Two *Euphorbiaceae* species, *C. urucurana* and *C. floribundus* and one *Cecropiaceae* species, *C. pachystachia* (well known PS, Lorenzi 1992) showed the highest P_{NA}. On the other hand, an *Apocynaceae* species, *A. cylindrocarpon*, typical LS, showed the lowest P_{NA} (6 μmol m^{-2} s^{-1}). According to Bazzaz (1979), under optimal environmental conditions, the rate of photosynthesis of early succession species may be as high as 30 μmol m^{-2} s^{-1}. In our experiment, under 1 700 μmol m^{-2} s^{-1} PPFD and 26 °C, the P_{NA} exhibited by the PS *C. urucurana* and *C. floribundus* were 23 and 22 μmol m^{-2} s^{-1}, respectively.

Classification of tree species of tropical forests into succession groups has often been the result of subjective experience rather than of scrupulous quantitative studies (Vera *et al.* 1999). In this study we used a simple division of tree species into two groups or guilds, PS and LS according to Swaine and Whitmore (1988) and Lorenzi (1992). To classify species into groups or guilds imposes a degree of simplification, which reduces information content, but reveals general patterns and facilities prediction about forest processes. The subjective classification is commonly used for practical forest management (Hutchinson 1988). However, some research was carried out to define guilds on the basis of quantitative studies on the growth and eco-physiology of tree species (Reich *et al.* 1995, Thomas and Bazzaz 1999, Vera *et al.* 1999).

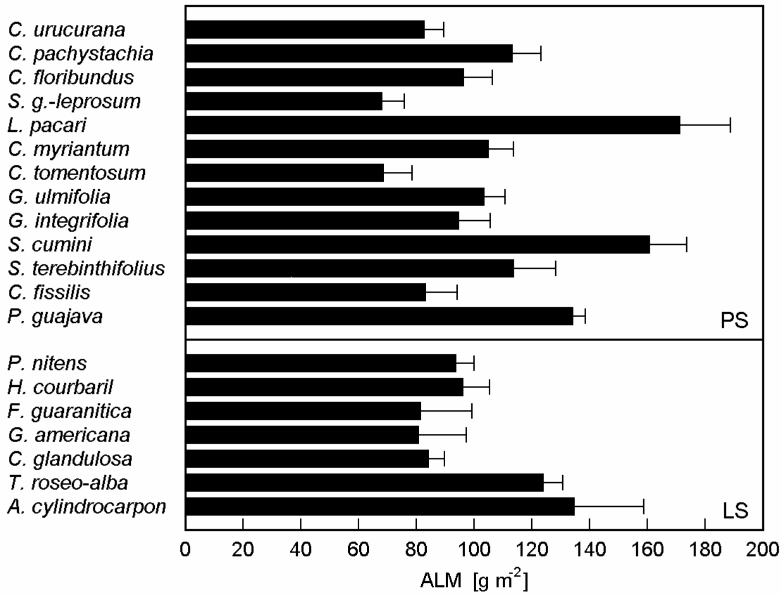

Fig. 3. Area leaf mass (ALM*)* for pioneer (PS) and non-pioneer (LS) Brazilian tropical forest tree species growing in a reforestation area. Means ± SE.

In physiological terms, variations in photosynthetic characteristics are one of the most important parameters associated with the separation of guilds of tree species. Indications that tree PS have higher P_{max} and greater photosynthetic plasticity than LS, which dominate old growth forests, have been verified by Chazdon *et al.* (1996), Reich *et al.* (1995), and Vera *et al.* (1999). According to Medina and Klinge (1983), high P_N

exhibited by PS are probably associated with their high growth rates. Dominance of the PS in recently disturbed sites depends on rapid growth (Rees *et al.* 2001).

In this experiment, the LS plants do tend to have lower P_{NA} and P_{NM} than the PS ones, even though the leaves are all sun-adapted. In contrast, although there is a wide range in ALM among species (67–170 g m^{-2}), there is no clear pattern of ALM between PS and LS. A similar lack of pattern for leaf mass per area between PS and LS was found in a mixed deciduous forest (Bassow and Bazzaz 1997).

Sometimes different results have been reported when comparisons were made of PNM vs. PNA. Thus, Reich *et al.* (1998) found that the faster-growing nine boreal species had higher P_{NM}, but similar P_{NA} than slow growers. However, in other data sets, as we found in this field work, even P_{NA} was higher in fast growing PS plants. For instance, on tropical trees (Reich *et al.* 1995) similar patterns of inter-specific differences in P_N were observed on both area and mass bases. It appears that inter-specific differences in ALM, which is highly plastic within species as a function of plant age and microenvironment, may reduce the differences among species in a large group contrasting when comparisons of P_N are made on area rather than mass bases (Reich *et al.* 1998).

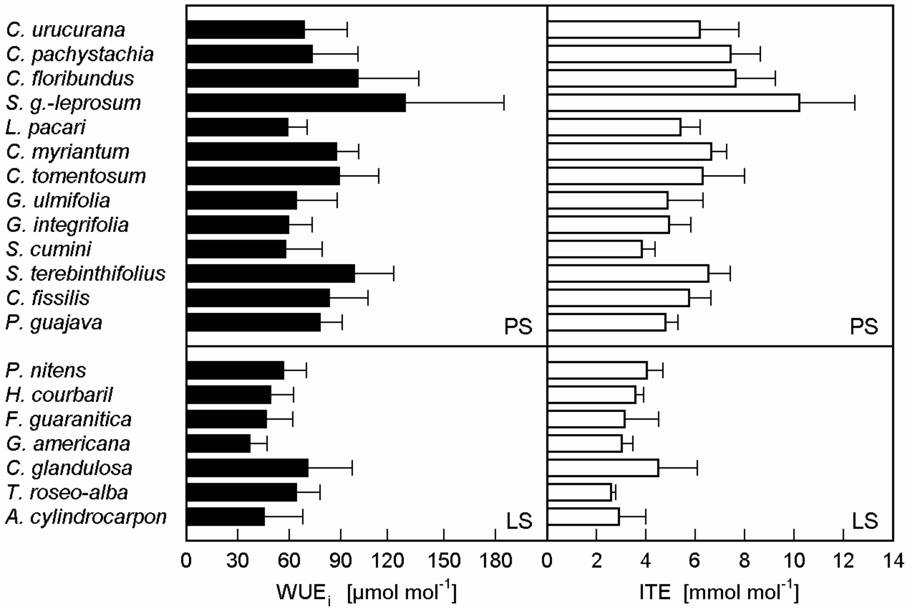

Fig. 4. Intrinsic water use efficiency (WUE_i, *black bars*) and instantaneous transpiration efficiency (ITE, *white bars*) for pioneer (PS) and non-pioneer (LS) Brazilian tropical forest tree species growing in a reforestation area. Means ± SE.

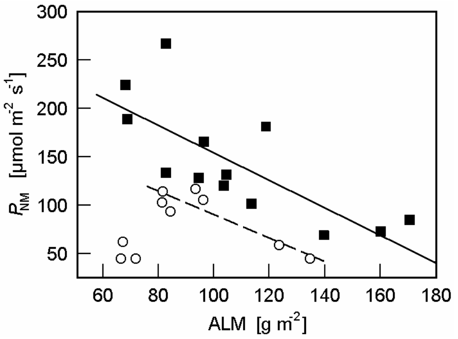

Fig. 5. Relationships between mass-based photosynthetic rate (P_{NM}) *vs.* area leaf mass (ALM) for pioneer (■) and non-pioneer (○) Brazilian tropical forest tree species growing in a reforestation area. Correlations and *p* values as follows: Pioneer P_{NM} = 293.4 – 1.395 ALM; $p<0.005$, $r = -0.75$. Non-pioneer P_{NM} = 207.6 – 1.169 ALM; $p<0.005$, $r = -0.90$.

In spite of the remarkable overlap between PS and LS in values of g_s and *E*, two out of the thirteen PS studied, *C. urucurana* and *C. pachystachia*, showed the highest g_s. The former also showed the highest *E*. In contrast, *S. granuloso-leprosum*, another PS, showed the lowest g_s and *E*. The lowest g_s and *E* associated with the higher P_{NA} of *S. granuloso-leprosum* resulted in the highest values of ITE and WUE_i showed by this PS. The results suggest that tropical PS have greater ITE and WUE_i than LS which is associated with their higher photosynthetic capacity. These eco-physiological differences may have an important impact on the performance of species occupying contrasting environments. Open habitats for PS show relatively high variability in the environmental conditions (irradiance, water availability, and soil and air temperatures). In LS forest trees, conversely, the physical environment tends to be relatively less variable. In these conditions, P_{max} and growth rates of PS trees are greater compared to LS trees because the behaviour of PS is typically opportunistic using the resources in accordance with their availability in the environment (Zangler and Bazzaz 1983). Similarly, water loss rates (Becker *et al.* 2000) as well as whole plant hydraulic conductance are larger in PS as compared to LS tree species (Becker *et al.* 1999). Thus, for maintaining efficient conducting system the PS would require an appropriate stomatal regulation as evaporative demand increases in order to prevent xylem embolism (Jones and Sutherland 1991). Recently, Sobrado (2003) found that two tropical PS tree species, *Oyeda verbesinoides* and *Clethra lannata,* were more efficient in conducting water to their leaves but had low control over water use compared to two succession forest tree species, *Croton xantochloros* and *Ficus mathewsii*. Thus, a trade-off between water transport and leaf water use efficiency was suggested.

Reich *et al*. (1995) determined that woody species of the Amazonian Venezuela showed variations in $P_{\max}$ regarding differences between guilds, with highest values of $P_{\max}$ and g_s in PS and lowest in LS trees. However, in such studies, the extent to which the eco-physiological characteristics exhibited are intrinsic or environmentally determined remains unclear.

In our experiment, because the gas exchange measurements were made under constant PPFD and temperature, the differences in $P_{\max}$ observed between PS and LS reflect the intrinsic photosynthetic capacity of each evaluated species. Only through quantifying and understanding the magnitude of variation in leaf-level photosynthesis in a forest canopy are we able to predict carbon flux consequences to environmental changes such as succession and global change (Bassow and Bazzaz 1997).

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