Photosynthetic traits and water use of tree species growing on abandoned pasture in different periods of precipitation in Amazonia

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Abstract

Pasture soils in the Amazon become unsustainable after a short period of use, typically being replaced by emergent secondary vegetation (capoeira). The aim of this research was to investigate the photosynthetic capacity and water use in the most common tree species (*Vismia japurensis*, *Vismia cayennensis*, *Bellucia grossularioides*, *Laetia procera*, and *Goupia glabra*) in successional chronosequence. This study was carried out in secondary vegetation area with ages that vary between 1 and 19 years. Responses of gas exchange were determined during different periods of precipitation. The gas exchange decreased with advancing age of the vegetation (1–19 years), except for *G. glabra*. Negative relationships of P_{Nmax} as a function of aging observed for *V. japurensis*, *V. cayennensis*, *B. grossularioides*, and *L. procera* exhibited r^2 equal to 0.59, 0.42, 0.33, and 0.58, respectively. The species of *Vismia* showed higher values for photosynthetic parameters in relation to other species across the chronosequence. Overall, there were differences in gas exchange only for some species between the different periods of precipitation. Therefore, our results suggest a distinct pattern of photosynthetic responses to species in early succession. Light decrease can exert a decisive role to reduce the photosynthetic rates in secondary succession species. On the other hand, the results of WUE showed weak evidence of changes for the species during dry and rainy periods in the abandoned pasture in central Amazonia.

Additional key words: chronosequence; light-response curve; photosynthesis, secondary succession; stomatal conductance.

Introduction

The annual deforestation in the Amazon, which currently amounts to 7,464 km^2 (period of 2008–2009), typically followed by conversion to pasture or agriculture has been considered the most common form of land use in the Amazon forest. More worrying is that such areas are often abandoned due to declining productivity after a short period of use (Veiga *et al*. 2004, Araújo *et al*. 2009, INPE 2010).

During the succession process, the abandoned pasture areas gradually change the landscape physiognomy. During initial periods, low vegetation cover is exhibited resulting from the presence of grass and a few trees of early successional species followed by dense woody vegetation dominated mainly by species of the genera *Vismia, Bellucia, Laetia*, and *Goupia* (Bentos *et al*. 2008). Due to the recovery of the vegetation and high rates of tree growth during early succession, areas of abandoned pastures (capoeiras) have been proposed as important carbon sinks to mitigate the rising levels of atmospheric carbon. Therefore, it is believed this potential sink of CO_2 has considerable involvement in the role of carbon and nutrient cycling at the regional scale (Silver *et al*. 2000, Feldpausch *et al*. 2004). However, the magnitude of this carbon sink is imprecisely known due to scarcity of information about the *in situ* photosynthetic characteristics of most species that compose different successional stages (Ellsworth and Reich 1996). This is because the carbon storage and the exchange of carbon between forest and atmosphere are also influenced by plant physiological differences, which are associated to the vegetation age, the functional group and, in the case of abandoned pasture areas, the effects of disturbances caused by animal trampling and resulting soil compaction, in addition to the damage caused by a combination of stressors that are common in these areas (Silva *et al*. 2008).

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Abbreviations: *E* – transpiration rate; g_s – stomatal conductance; I – irradiance; P_N – net photosynthetic rate; P_{Nmax} – light-saturated P_N; PPFD – photosynthetic photon flux density; R_D – dark respiration; SLA – specific leaf area; WUE – water-use efficiency.
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Given that with the abandonment of pastures, the appearance of species adapted to the new conditions of water availability, nutrient limitation and excess of irradiance, and that the availability of these resources changes with advancing age of the vegetation by forming new microclimatic conditions (Feldpausch *et al*. 2004, Silva *et al*. 2006, Letcher and Chazdon 2009), we investigate the hypothesis that gas exchange responses for species of secondary succession also show changes with time. Therefore, this study was made with an objective to quantify the carbon assimilation (CO_2) and other photosynthetic characteristics of emergent secondary vegetation trees, and determines gas exchange and water-use efficiency of the most common early succession species growing on abandoned pasture areas in a successional chronosequence during different periods of precipitation in central Amazon.

Materials and methods

Study site: The experiment was realized in the areas that compose a chronosequence of secondary vegetation growing on abandoned pasture areas (site of the Project Biological Dynamics of Forest Fragments – PBDFF), located at 63 km and 72 km of highway BR-174, north of Manaus-AM (02º34'S, 60º05'W and 02°42'S, 59°88'W). The climate is type *Afi* with average temperatures of 26 and 28°C (rainy and dry seasons, respectively). The average annual precipitation is 2,300 mm, the wetter months are from March to May (mean 300 mm) and the drier months from August to October (mean 100 mm) (PDBFF 2008). The soil of the region is classified as typic dystrophic and low in nutrients (Chauvel 1982). Although the N, P and K concentrations are low, these increased in the chronosequence, while Ca and Mg decreased with age rising of pasture abandonment (Table 1).

The chronosequence of secondary vegetation was identified and classified using the abandonment age of the area as a criterion, according to the supervised classification of satellite images performed by Moreira (2003). The ages ranged between 1 and 19 years of abandonment and were grouped into the following age classes: 1–3, 5–8, 10–13 and 15–19 years. The species selected for study were: *Vismia japurensis* Reich. (Hypericaceae), early successional; *Vismia cayennensis* (Jacq.) Pers. (Hypericaceae), early successional; *Bellucia grossularioides* Triana. (Melastomataceae), intermediate successional; *Laetia procera* (Poepp.) Eichler. (Salicaceae), intermediate successional; and *Goupia glabra* Aubl. (Goupiaceae), late successional (Finegan 1996).

CO_2 and water vapour exchange: The determination of the response curve of photosynthesis to irradiance (P_N-I), as well as stomatal conductance (g_s), transpiration (E) and dark respiration (R_D) was performed for healthy leaves, fully expanded and located in the upper third of the canopy. Measurements were realized between 8:00 and 12:00 h during April–May/2008 (high precipitation) and September–October/2008 (low precipitation), using a infrared gas analyzer (*IRGA, LI-6400, LI-COR Inc*., Lincoln, NE, USA). The water-use efficiency (WUE) was determined by the ratio between photosynthesis and transpiration (WUE = P_N/E). The curves P_N-I were calculated using software *OPEN 3.4*, modified to record gas-exchange data in 11 increasing levels of irradiance [0, 25, 50, 75, 100, 250, 500, 750, 1,000; 1,500; and 2,000 μmol(quantum) m^{-2} s^{-1}]. The equipment (*IRGA*) was adjusted to work with a flow rate of 400 μmol s^{-1}, block temperature and CO_2 and H_2O concentrations, in the leaf chamber around 30 ± 1ºC, 380 ± 3 μmol mol^{-1} and 21 ± 1 mmol mol^{-1}, respectively (Silva *et al.* 2008, Ferreira *et al.* 2009). Measurements to determine the P_N-I curve in plants located in secondary vegetation with abandonment age above five years were performed using structures of metal scaffolding to reach the plant crowns with height estimated above 2 m. The exponential model was used to adjust the curve P_N-I for each plant (Iqbal *et al*. 1997): $P_N = (P_{Nmax} + R_D)\{1 - \exp[-\alpha I/(P_{Nmax} + R_D)]\} - R_D$, where I is irradiance (PPFD – photosynthetic photon flux density); P_N is rate of net photosynthesis; P_{Nmax} is the light-saturated P_N (estimated by model); R_D is dark respiration corresponding to the value of P_N where I = 0; and α is the apparent quantum yield of photosynthesis (estimated by model). Each curve was fitted using the Levemberg-Marquardt algorithm *Statistica 6* (*StatSoft Inc*., 2003).

Table 1. Concentration of nutrients in the soil (0–10 cm of depth) in a chronosequence of abandoned pastures in a central Amazon. N – nitrogen; P – phosphorus; K – potassium; Ca – calcium; Mg – magnesium; Fe – iron; Zn – zinc; Mn – manganese. Values are averages (± SD). Averages, followed by the same letter vertically, do not show significant difference by *Tukey's* test (p<0.05), (n = 10).

Age class	N [g kg^{-1}]	P [mg kg^{-1}]	K	Ca [$cmol_c$ kg^{-1}]	Mg	Fe [mg kg^{-1}]	Zn	Mn
1–3	0.86 ± 0.17[c]	2.78 ± 0.64[b]	22.3 ± 8.67[c]	0.44 ± 0.21[a]	0.32 ± 0.13[a]	265 ± 18[a]	0.86 ± 0.39[c]	2.38 ± 1.24[bc]
5–8	1.27 ± 0.23[b]	2.75 ± 0.30[b]	34.2 ± 5.90[ab]	0.33 ± 0.19[b]	0.21 ± 0.07[b]	274 ± 20[a]	1.11 ± 0.47[b]	3.51 ± 1.15[a]
10–13	1.68 ± 0.23[a]	3.56 ± 0.99[a]	39.3 ± 9.80[a]	0.12 ± 0.05[c]	0.14 ± 0.07[bc]	257 ± 18[a]	1.48 ± 0.75[a]	2.72 ± 0.85[b]
15–19	1.83 ± 0.22[a]	3.31 ± 0.62[a]	33.2 ± 6.50[b]	0.07 ± 0.03[c]	0.09 ± 0.04[c]	270 ± 13[a]	0.78 ± 0.17[c]	2.05 ± 0.59[c]

Experimental design and statistical analysis: In the selected areas plots (20 × 40 m) in different ages of abandonment (ranging from 1 to 19 years) were demarcated in which 100 trees were identified and marked. The data obtained from quantitative experiments were submitted to the *D'Agostino-Pearson* normality test. Then regression analysis was applied to determine the effects of the dependent variables over the age of abandonment of the area, as well as for P_N-I curves. In qualitative experiments, the completely randomized design was used obeying a factoral frame (5 species × 4 age classes of secondary vegetation), then the data were subjected to analysis of variance (*ANOVA*). In some cases, the precipitation period was also taken into account. Finally, the means were compared by *Tukey's* test ($p<0.05$). The statistical software used was *Statistica 6.0* (*StatSoft Inc*., 2003).

Results

P_N-I curves showed an asymptotic pattern of slope for the five species analyzed in different age classes and in different periods of precipitation (Figs. 1, 2). The greatest responses were provided by species of genus *Vismia* followed for *B. grossularioides* species in most age classes analyzed. *G. glabra* had the lowest response to changing irradiance, except in the ages 15–19 years. Regardless of species, the larger responses were observed in the age classes between 1–3 and 5–8 years with light intensity above 500 µmol m^{-2} s^{-1}. Moreover, the photosynthetic rate decreased in periods of low precipitation.

The species exhibited a decrease in the gas-exchange responses depending on the secondary vegetation age, except for *G. glabra* (for P_N and g_s) and *V. cayennensis* (for g_s and *E*) and *V. japurensis* (for *E*) (Table 2). Moreover, there was no relationship among WUE for the species analyzed. In general, there was a negative effect of P_{Nmax} with increasing age of secondary vegetation in both periods, high precipitation (r^2 = 0.57; $p<0.01$) and low precipitation (r^2 = 0.61; $p<0.01$) (Fig. 3). The species studied exhibited positive effect of P_{Nmax} with increasing g_s (r^2 = 0.55; $p<0.001$) (Fig. 4). *G. glabra* and *L. procera* showed the best relationships (r^2 = 0.60; $p<0.001$ and r^2 = 0.52; $p<0.001$; respectively) following by *V. cayennensis* (r^2 = 0.40; $p<0.001$) and *V. japurensis* (r^2 = 0.43; $p<0.001$). *B. grossularioides* showed weak relationship of P_{Nmax} with increasing g_s (r^2 = 0.36; $p<0.001$). In the comparison between the two periods of precipitation (relative diference), *V. cayennensis* and *L. procera* exhibited significant positive values for P_{Nmax} in the ages ranged 1–3 years, indicating that higher values of P_{Nmax} were observed in the high precipitation period, whereas only *L. procera* exhibited significant values in the secondary vegetation areas with ages between 15–19 years (Fig. 5). For the variable R_D, only *V. cayennensis* differed between periods of high and low precipitation in the ages ranged 1–3 years, *B. grossularioides* and *G. glabra* differed in the ages ranged 5–8 years. *L. procera* had higher values for the responses of g_s and *E* in the high precipitation period in the secondary vegetation areas with ages between 15–19 years. *G. glabra* showed higher values for WUE in the high precipitation period in the ages ranged 1–3 years.

Discussion

The difference in the responses of photosynthetic rates in relation to successional groups (early and late) is broadly supported in the literature (Bazzaz and Carlson 1982, Reich *et al*. 1995, Ellsworth and Reich 1996). Additionally, it was found in this experiment that the difference between species decreased with increasing age of secondary vegetation, which was proposed by Ellsworth and Reich (1996). The species of the genus *Vismia*, typical of early succession on abandoned pasture area, exhibited better performance on carbon assimilation than *G. glabra,* belonging to the late successional period, which is generally consistent with the theory about carbon assimilation in different successional groups (Huc *et al*. 1994). There was a significant effect in decreasing of P_{Nmax} in the low precipitation period for some species (*V. caynnensis* and *L. procera)*, although the reduction in P_{Nmax} has been observed in the low precipitation period for most of the species of different ages in the chronosequence. These results suggest that the mechanism of stomatal regulation of the species may have been effective in maintaining high levels of photosynthetic efficiency in time of reduced water availability. When the effect of secondary vegetation age on the gas exchange was evaluated, it was observed that in most species, except *G. glabra*, P_{Nmax} decreased over time during succession. Rijkers *et al*. (2000) also observed low values of P_{Nmax} for *G. glabra* in environments with high light incidence. Probably, the constant maintenance of carbon assimilation rate with increasing secondary vegetation age is a characteristic of the *G. glabra*, since its g_s values were not affected by secondary vegetation age. The R_D also decreased with successional chronosequence, which may indicate a slowdown in the efficient conversion of carbohydrates in biomass (Newell *et al*. 2002). The high values of P_{Nmax} for pioneer species in the first years after abandonment of pastures may be associated with high values of *E*, because, as verified in another research that as higher rates of photosynthesis are associated with increased transpiration, lower leaf temperature might have contributed to reduced photoinhibition in early

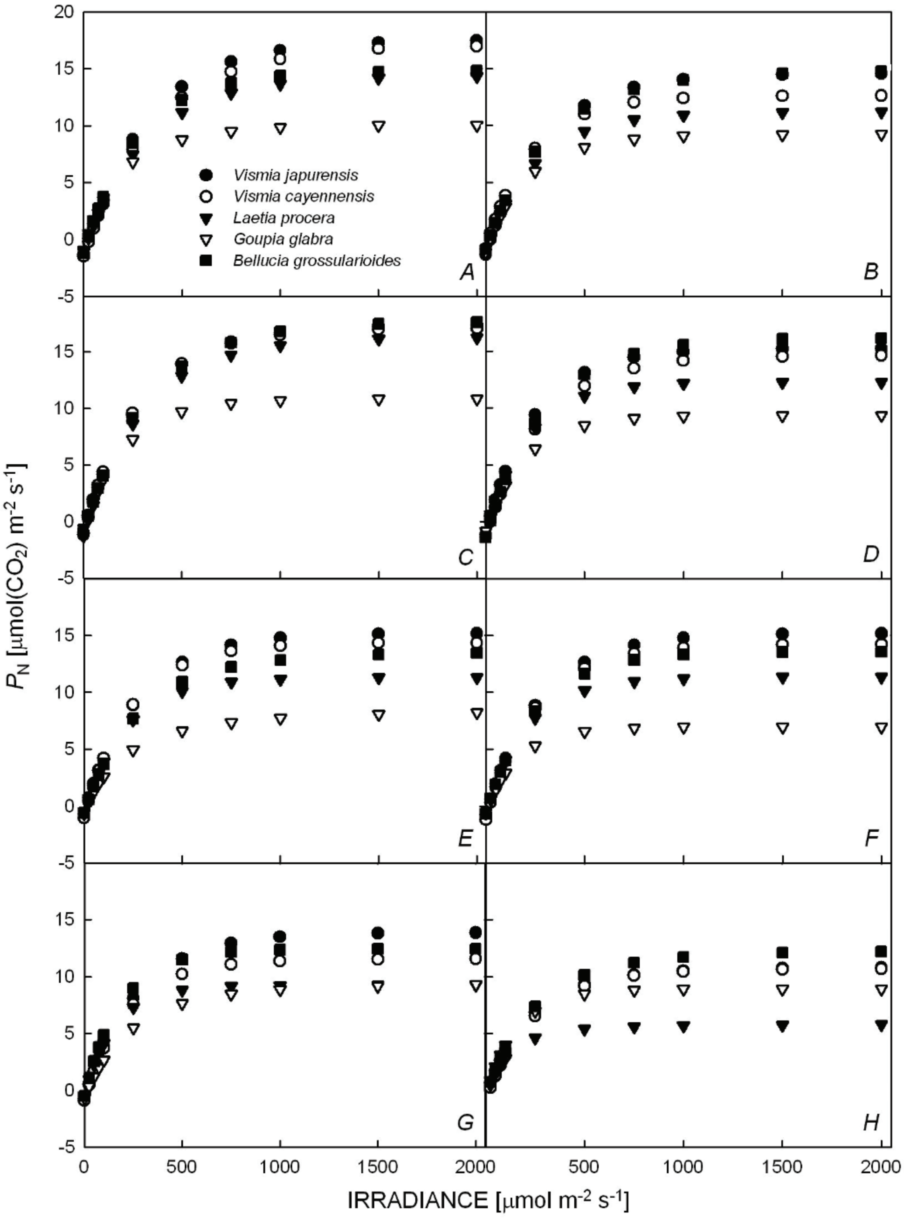

Fig. 1. Photosynthetic light-response (P_N) curve for each secondary sucession species (n = 5) in different ages of abandonment of the area in two periods of precipitation. Age class from 1–3 years, higher and low precipitation (*A* and *B*, respectively); age class 5–8 years, higher and low precipitation (*C* and *D*, respectively); age class 10–13 years, higher and low precipitation (*E* and *F*, respectively); age class 15–19 years, higher and low precipitation (*G* and *H*, respectively). Data obtained in April–May/2008 (high precipitation) and September–October/2008 (low precipitation).

successional species (Krause *et al.* 2001). It was verified that apart from the apparent intrinsic difference between species in different successional groups, an important factor that must be taken into consideration is the irradiance availability for plants with the advancement of the chronosequence, which probably more strongly affects photosynthetic responses of early successional species than soil nutrients availability, such as nitrogen (N) and phosphorus (P) (Silva *et al.* 2006). These nutrients are considered scarce for abandoned pasture areas in Amazon, but over time show an increase, mainly in the superficial layers (Feldpausch *et al.* 2004). According to Hikosaka (2005), although the photosynthetic rate increased with increasing amount of leaf N, factors such as low availability of irradiance contribute significantly to the reduction in photosynthetic efficiency. Rijkers *et al.* (2000) showed that tree height and crown density have considerable effects on the structural and physiological characteristics of early successional species shaded, for example, specific leaf area (SLA), because changes in this parameter contribute to the reduction of photosynthetic responses (Reich *et al.* 1998). Ross

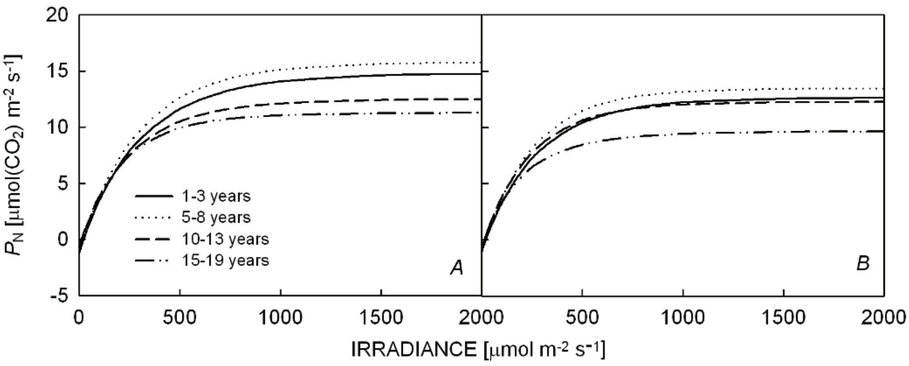

Fig. 2. Photosynthetic light-response (P_N) curve of secondary vegetation by age of abandonment in two periods of precipitation (n = 25). Periods of higher and low precipitation (*A* and *B*, respectively). Data obtained in April–May/2008 (high precipitation) and September–October/2008 (low precipitation).

Table 2. Relationship between gas exchange of the species and age of the secondary vegetation (1 to 19 years old) after abandonment. P_{Nmax} – light-saturated photosynthesis; R_D – dark respiration; g_s – stomatal conductance; E – transpiration; WUE – water-use efficiency; r^2 – coefficient of determination; p – probability; a – slope; ns – nonsignificant. WUE = P_N/E.

Species	Parameter	P_{Nmax}	R_D	g_s	E	WUE
Bellucia grossularioides	r^2	0.328	0.532	0.664	0.649	ns
	p	<0.05	<0.05	<0.01	<0.01	
	a	–0.185	–0.037	–17.50	–0.113	
Goupia glabra	r^2	ns	0.398	ns	0.449	ns
	p		<0.05		<0.05	
	a		–0.028		–0.092	
Laetia procera	r^2	0.575	0.565	0.644	0.923	ns
	p	<0.01	<0.01	<0.01	<0.001	
	a	–0.354	–0.031	–19.52	–0.158	
Vismia cayennensis	r^2	0.417	0.344	ns	ns	ns
	P	<0.05	<0.05			
	a	–0.240	–0.016			
Vismia japurensis	r^2	0.592	0.773	0.537	ns	ns
	P	<0.01	<0.001	<0.01		
	a	–0.234	–0.045	–11.30		

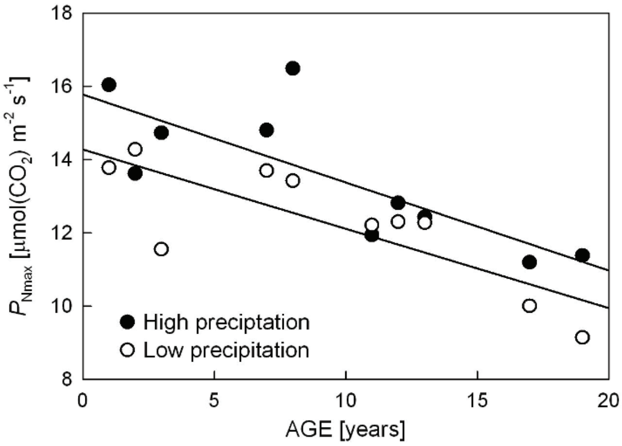

Fig. 3. Relationship between light-saturated photosynthesis (P_{Nmax}) of the species and secondary vegetation age (1 to 19 years old) after abandonment of pasture during periods of high and low precipitation.

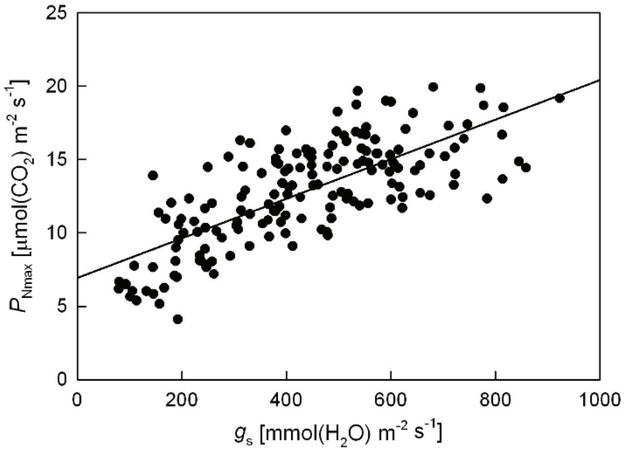

Fig. 4. Relationship between light-saturated photosynthesis (P_{Nmax}) and stomatal conductance (g_s) of species of secondary vegetation.

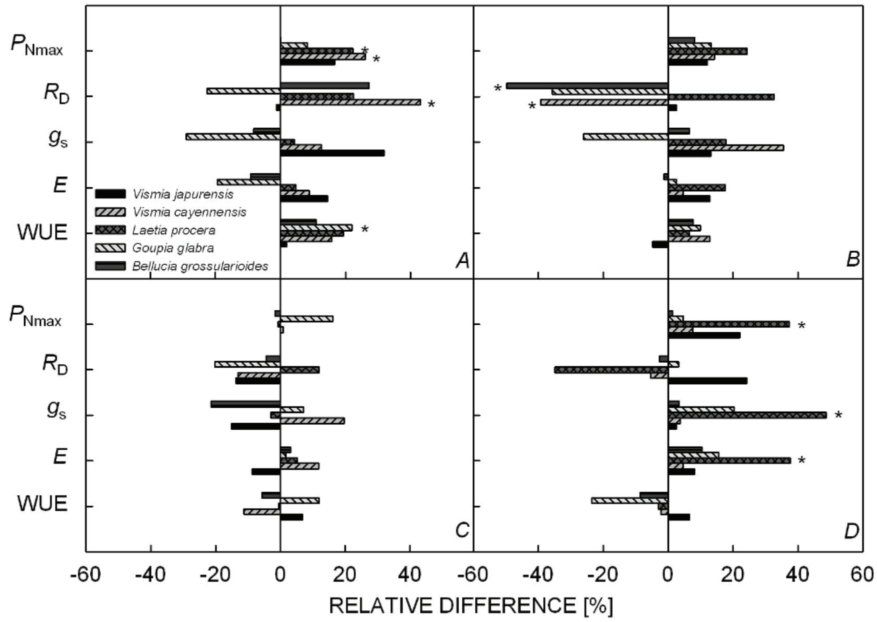

Fig. 5. Relative difference between periods of high and low precipitation for gas exchange of five early succession trees in a successional chronosequence of abandoned pastures. Age class from 1–3, 5–8, 10–13 and 15–19 years (*A, B, C* and *D*, respectively); P_{Nmax} – light-saturated photosynthesis; R_D – dark respiration; g_s – stomatal conductance; E – transpiration; WUE – water-use efficiency. The asterisk represents significant difference (p<0.05).

(1954) observed that *Trema guianensis*, an early successional species, formed a dense vegetation of 90 cm in height in just two months after deforestation, rising to about 10 m tall in five years. *Musanga cecropioides,* the dominant species, formed a canopy of approximately 23 m of height and the irradiance below canopy decreased to a levels close to that of primary forest in 14 years. Reich *et al*. (1995) found that P_{Nmax}, g_s, SLA, and leaf concentrations of calcium (Ca) and magnesium (Mg) showed variations in different successional groups with higher responses to early successional species, and these parameters were consistent with the decrease in light and increase in nutrient availability during secondary succession, although leaf N and P did not differ between species (Pooter and Evans 1998, Hikosaka 2005). Thus, in the successional chronosequence, plants acclimate to the new conditions of irradiance with direct impacts on photosynthetic rates. Therefore, the gas-exchange responses of the different species as observed in this research seem to confirm the results that, generally, are seen for plants according to position in the successional group (Bazzaz and Carlson 1982, Reich *et al*. 1995, Ellsworth and Reich 1996). That is, species in early succession have higher photosynthetic rates. Additionally, even considering the changes in soil conditions and microclimate, which might lead to benefits for plants due to expansion of the vegetation cover on abandoned pasture, there was a reduction of photosynthetic responses with the advancement of age of secondary vegetation. Given this, it is suggested that the decrease of the photosynthetic rates from early to late successional species is directly related to reduced availability of irradiance for plants in late successional chronosequence, rather than other abiotic factors such as nutrients. Furthermore, results of WUE showed weak evidence of changes for the species during dry and rainy season, indicating that photosynthesis was not limited by water availability in the abandoned pasture in central Amazonia.

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