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Phenotypic plasticity and ecophysiological strategies in a tropical dry forest chronosequence: A study case with *Poincianella pyramidalis*

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ABSTRACT

The plasticity of functional attributes is an important strategy for the acclimation and establishment of plants in areas that undergo natural regeneration. The irregular rainfall of the Brazilian tropical dry forest is an important environmental filter for the determination of the set of species that can successfully establish in different stages of the regeneration process and influences the plant acclimation responses to the environmental conditions at each stage of ecological succession. In order to test the hypothesis that pioneer plants which can establish themselves, at the same time, in areas at different stages of regeneration have high phenotypic plasticity, we investigated the endemic tree species *Poincianella pyramidalis* Tull., which can be found in all stages of the regeneration process in the Brazilian tropical dry forest. Three areas were selected at different successional stages (early, intermediate and late), and the functional attributes of water status, gas exchange, leaf nutrients, specific leaf area, leaf construction costs and payback time were assessed. In the three successional stages all individuals had similar age. Measurements were taken in April, for two consecutive years, a dry and a wet. The evaluated parameters in this study showed changes according to successional stage. The highest leaf water potential was found in the late stage in the rainy year and lowest in the dry year. This behavior may be related, in addition to soil water availability, to a stronger competition for resources in these areas. Gas exchange and nutrient use efficiency were higher in 2013 and in the late successional stage, which exhibited higher soil moisture, a lower vapor pressure deficit and higher nutrient mobilization. There were no differences in the construction cost per unit mass between the stages, but differences in specific leaf area led to changes in cost per area. The payback time was shorter in the wettest year. For the driest year, the late stage showed greater energy use efficiency. The results show that the *P. pyramidalis'* attributes varies according to the successional stage, showing phenotypic plasticity. However, the strongest differences are observed between years, demonstrating that water is the main factor that coordinates the functional changes that confers its ability to acclimatize.

1. Introduction

Functional traits are important proxies of plant response to environmental conditions (Violle et al., 2007). These conditions impose different selection forces in plants and controls, to some extent, intra-specific differences in functional traits (Poorter, 2009). The ability to adjust the expression of various phenotypes according to environmental conditions is known as phenotypic plasticity (Nicotra et al., 2010). In previously and currently disturbed environmental succession areas, plasticity can lead to partially adapted phenotypes, thereby accelerating the adaptive and evolutionary processes of the plant species (Lande, 2009).

Environmental succession, which is caused by changes in the environment, results in mosaics of areas at different stages of natural regeneration. These areas are becoming more common in tropical dry forests, which are mainly located in South America,

Abbreviations: IWUE, intrinsic water use efficiency; CC_{mass}, leaf construction cost per unit mass; CC_{area}, leaf construction cost per unit area; ψ_l, leaf water potential; A_{max}, maximum net CO_2 assimilation; SLA, specific leaf areas; g_s, stomatal conductance; SM, soil moisture; *E*, transpiration rate; TDF, tropical dry forest.

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mainly due to the strong anthropization (Quesada et al., 2009; Santos et al., 2011, 2014; Lopes et al., 2012). According to Cabral et al. (2013), 80% of Brazilian tropical dry forests are successional, and 40% are maintained in initial stage of regeneration.

Generally, a structural perspective is used to study the process of natural regeneration, like the species composition of each successional stage. However, from a functional standpoint, the ecosystem recovers its functionality even before full floristic restoration to preconditions (Guariguata and Ostertag, 2001). Thus, the study of the functional attributes of key plant species involved in regeneration processes in these ecosystems is of fundamental importance (Griscom et al., 2009).

Because the conditions of successional forest habitats are not constant in time and space, the assessment of ecophysiological processes (particularly those related to carbon investment) is important to the understanding of how plants are able to adapt and establish themselves. The acquisition of carbon by plants is determined by multiple functional attributes, such as net photosynthesis, leaf nitrogen concentrations and specific leaf area (Shipley and Almeida-Cortez, 2003; Poorter et al., 2006). Plants invest photoassimilates in the construction of leaves and other parts, in nutrient acquisition and metabolism maintenance (Wright et al., 2004). The relationship between the acquisition and use of acquired resources is known as the leaf economics spectrum, and it directly influences plant growth rates (Marino et al., 2010; Edwards et al., 2014).

The leaf construction cost is defined as the amount of glucose necessary to construct carbon skeletons, reducing power in the form of NADPH and energy for organic compound synthesis and it is indirectly related to plant growth rates (Williams et al., 1987). For plants with low leaf construction costs, energy investment in building a new leaf, rather than in strategies to maintain the old leaves, is more biochemically and structurally economical (Poorter and Bongers, 2006; Zhu et al., 2013). On the other hand, plants with high leaf construction costs can invest their resources in defense metabolites, which are costly in terms of energy (Westoby et al., 2002). Thus, the construction cost, associated with payback time (i.e., the time required by the plant to offset the expenses of leaf construction through the photosynthetic process), provides us with an important measure of the energy use efficiency (Poorter et al., 2006).

Studies to date have not reached a consensus regarding which attribute, or set of attributes, are able to provide plants with significant phenotypic plasticity. The plasticity of traits in relation to phenology, flowering time, seed longevity, is well documented (Clair and Howe, 2007; Morin et al., 2009; Kochanek et al., 2010). However, some studies point higher indexes of phenotypic plasticity in physiological traits such as maximum CO_2 assimilation, dark respiration and maximum quantum efficiency of photosystem II, in detriment of structural traits (Valladares et al., 2000; Koehn et al., 2010). It is clear that variations in functional attributes depend on the plant species, the choice of the attributes to be analyzed and the environment to which the plants are subjected. Furthermore, most studies on plasticity and succession involve the assessment of pioneer plants compared with later-stage plants, since plant species exhibit different ecophysiological responses when they are analyzed during different successional stages (Navas et al., 2003, 2010; Zhu et al., 2013). However, some pioneer plants are able to establish, at the same time, in areas in different stages of succession.

Thus, this study attempts to elucidate the functional traits that allow plants to maintain their performances throughout the succession process by evaluating the ecophysiological and functional attributes of a pioneer and endemic tree species in a tropical dry forest, in areas that are under different periods of regeneration.

2. Material and methods

2.1. Study area and plant material

The study was conducted in the month of April during the years 2012 and 2013, in a chronosequence of three successional stages of a seasonally tropical dry forest (TDF), Caatinga, in Tamanduá Farm (06°59′13″ to 07°00′14″ S and 37°18′08″ to 37°20′38″ W), located in the Santa Terezinha municipality, Paraíba, Brazil. The study area is at an average altitude of 240 meters and contains the shallow and low-fertility soil type Leptosols (EMBRAPA, 1997). The mean temperature and annual rainfall of the city are 32.8 °C and 600 mm (Fig. 1). In 2012 and 2013, the cumulative rainfall levels up to April were 257 mm and 338 mm, respectively. Rainfall was recorded monthly at a meteorological station that was installed in the study area. In April, the rainfall levels totaled 35 mm in 2012 and 84 mm in 2013, which amounted to a difference of 140% between the years. The environmental data from 2012 and 2013 are presented in Table 1.

Each successional stage was represented by an area. The area in early succession is in natural regeneration for 21 years, and the intermediate area is in succession for 43 years. The early successional area was submitted to clearcutting in 1965 for cotton planting, and in 1970 the cotton plantation was replaced for *Cenchrus ciliaris* L. (buffel grass) and used by cattle for pasture before being abandoned in 1992. The intermediate successional area was also submitted to a clearcutting in 1965 for cotton planting, however was abandoned in 1970. There is no registry of clearcutting in late successional area or major disturbances since 1950 (Freitas et al., 2012; Silva et al., 2012).

Fertilizer was not applied to any of the areas, and in 2007, they were all surrounded with barbed wire to prevent the entry of cattle, goats and sheep. In each area, a 50 × 20 m plot was delimited with a 5 m edge on all four sides. The chemical and physical properties of the soil surface layers were presented in Freitas et al. (2012).

In a phytosociological survey of tree species made in the study area, Cabral et al. (2013) have identified 6 species and 3 families in the early stage of regeneration, 15 species and 10 families in the intermediate stage, and 21 species and 12 families in the late stage, with predominance of the Fabaceae family in the three areas. The average density was 0.083 individuals m^{-2} in the early stage, 0.113 individuals m^{-2} in the intermediate stage, and 0.093

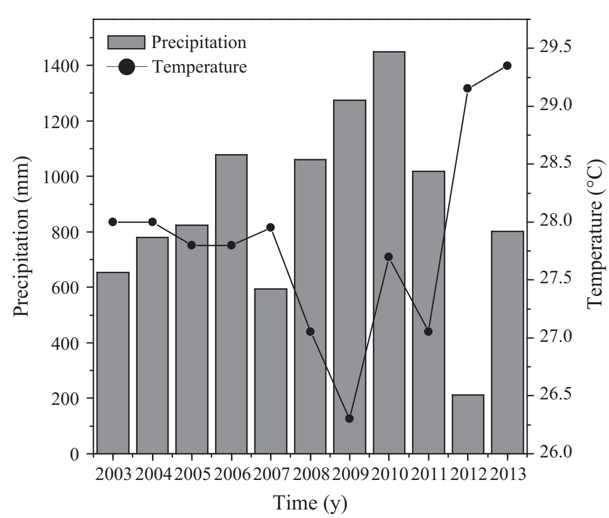

Fig. 1. Time series of annual rainfall (mm) and mean annual temperature (°C) over the past ten years in the Santa Terezinha municipality, Paraíba, Brazil.

Table 1
Rainfall, average temperature, soil moisture and vapor pressure deficit in April of 2012 and 2013 in three different successional stages. Santa Terezinha, Paraíba, Brazil.

Stage	Year	Precipitation (mm)	Temperature (°C)	Soil Moisture (%)	Vapor Pressure Deficit (kPa)
Early	2012	35	32.6	2.15	1.50
	2013	84	32.1	11.07	1.69
Intermediate	2012	35	32	1.86	2.38
	2013	84	30.6	11.88	1.15
Late	2012	35	29.2	1.25	1.63
	2013	84	28.5	12.80	0.70

individuals m^{-2} in the late successional stage. The shoot biomass was 29.9 Mg ha^{-1} in the early stage of succession, 37.5 Mg ha^{-1} in the intermediate stage and 49.4 Mg ha^{-1} in late stage.

The plant species that was used in this study was *Poincianella pyramidalis* Tull. (Fabaceae), which is a native pioneer and endemic tree species that is highly representative of the Brazilian TDF. According to Valladares et al. (2007), to avoid conclusions concerning to an age-dependent phenotypic variation in leaf traits, we selected plants with the same age in all successional stages. To determine the age of the plants, the diameters moving method described by Scolforo et al. (2008) was used, through linear regressions as a function of diameter at breast height (DBH). The results showed that all individuals, in the three successional stages, had an average age of 21 years. Despite being a pioneer species, *P. pyramidalis* can also be found colonizing intermediate and late areas during the natural regeneration process.

2.2. Leaf water potential and soil moisture

The leaf water potential (ψ_l) was determined according to Scholander et al. (1964) using a Scholandeŕs pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). The measurements were performed during the predawn (05:00) on fully expanded and undamaged leaves off our individuals from the three successional stages. Soil moisture (SM) was obtained at a depth of 30 cm at five sites from each area using a soil moisture meter (HFM 2030, Falker, Porto Alegre, BR).

2.3. Gas exchange

Gas exchange measurements were performed using an infrared gas analyzer (LCi, ADC Bioscientific, Hoddeston, UK). All evaluations were performed on fully expanded and undamaged leaves from four individuals on sunny and cloudless days in the morning (07:30). This measurement time was determined following the construction of a gas exchange daily curve in the field (data not shown), for which the saturating photosynthetic radiation that was experienced by *P. pyramidalis* in its natural conditions in the study areas (1500 μmol m^{-2} s^{-1}) was observed. Stomatal conductance (g_s), maximum net CO_2 assimilation (A_{max}) and transpiration rates (E) were measured at each of the successional stages. The intrinsic water use efficiency (IWUE) was determined by the ratio between net CO_2 assimilation and stomatal conductance.

2.4. Leaf contents and nutrient use efficiency

For the quantification of nutrients (nitrogen, phosphorus and potassium), approximately 30 *P. pyramidalis* leaves from four individuals were collected, dried in a forced air oven at 60 °C for 72 h and ground in an industrial blender. They were then digested in an acid solution (H_2SO_4) in a digester block at 350 °C to obtain plant extracts, and the total N content was determined from an extract titration with HCl after the addition of boric acid and a colored indicator (Thomas et al., 1967). The phosphorus content was determined spectrophotometrically (Spectrophotometer 600S, FEMTO, São Paulo, BR) according to Murphy and Riley (1962) using a concentration curve for phosphorus. The K content was determined by flame photometry (DM-62, Digimed, São Paulo, BR) using a solution of 5 ppm K as a standard (Silva, 2009). Photosynthetic nutrient use efficiency was determined by the ratio of maximum CO_2 assimilation (A_{max}) and the leaf content of each nutrient.

2.5. Leaf construction costs and payback time

Thirty healthy and fully expanded leaves from four individuals were collected in the three successional stages. The leaves were scanned, and their areas were determined using the program Image – Pro Plus 4.5 (Media Cybernetics, Inc., Rockville, US). After determining the leaves areas, the leaves were dried in a forced air oven at 60 °C for 72 h and weighed on a precision balance (HR-200, AND, Tokyo, JP). Specific leaf areas (SLA) were determined by the ratios between leaf areas and dry masses (cm^2 g^{-1}).

To obtain the ash contents (g kg^{-1}), 1 g of dry matter was weighed on a precision balance and then placed in a muffle, where it remained at 500 °C for 6 h. The ash contents were determined by the pre- and post-muffle weight differences (Li et al., 2011).

The calorific values (ΔHc kJ g^{-1}) were obtained by the combustion of 500 mg of dry matter in a calorimeter (C200, IKA, Heitersheim, DE) according to Villar and Merino (2001). The results were determined by the formula: ΔHc = calories/(1 − ash). The leaf construction cost per unit mass (g glucoseg^{-1}) was calculated using the results of the ash, nitrogen concentration and ΔHc according to Williams et al. (1987): $CC_{mass} = [(0.06968\ \Delta Hc - 0.065)(1 - ash) + 7.5\ (kN/14.0067)]/GE$, where k is the state of the oxidation of nitrogen (+5 to −3 for nitrate and ammonium), and GE is the growth efficiency that is estimated to be 0.87 (Penning de Vries et al., 1974). The leaf construction cost per unit area (g glucose m^{-2}) was calculated as the ratio between CC_{mass} and SLA.

The payback time was calculated from the ratio between the leaf construction cost (CC_{mass}) and the maximum CO_2 assimilation value, which were both expressed per unit mass (Navas et al., 2003). The results were expressed in days, considering a 12-h period to be a day, relative to the photoperiod.

2.6. Statistical analysis

The criterion for selection of plants to be analyzed was the same age. The selected plants were marked to make sure that the measurements were performed in the same individuals in the two consecutive years. Data were subjected to factorial ANOVA, with two independent factors: the successional stage and the year. Significant differences were compared by the Student Newmna-Keuĺs test at a 5% probability. The statistical software used was the STATISTICA 8.0 (Statsoft Inc., Tulsa, USA).

3. Results

3.1. Water potential

The higher leaf water potential was observed in the plants located in the late area in 2013, the most wet year ($P < 0.05$), and the lower in the same area in 2012, the most dry year (Fig. 2). The difference was about 13-fold between the years in the late area. The leaf water potential was higher in all areas in 2013 when compared with 2012. However the greatest differences in water potential were observed in 2012, with the initial area showing values 93% higher than the late area ($P < 0.05$), an opposite pattern to that found in the wettest year.

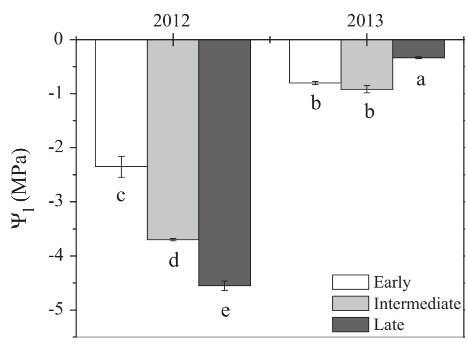

Fig. 2. Leaf water potential of *P. pyramidalis* in three different successional stages over two consecutive years. Bars ± SE with the same letter are not significantly different by Student Newman–Keuls test (5%), $n = 4$.

3.2. Photosynthetic capacity

The stomatal conductance was higher in the plants of the late area in 2013, and the lower value was found in the initial and intermediate areas in 2012 ($P < 0.05$), a 4.5-fold difference (Fig. 03A). When we observe the years separately, 2013 showed the greatest values for all successional stages when compared to the driest year ($P < 0.05$).

The maximum net CO_2 assimilation rate followed the decrease or increase in stomatal conductance (Fig. 3B). The plants in the late area in 2013 showed the greatest A_{max}, with values 3.5-fold higher, in average, than those observed in all areas in 2012, which showed the lower values and did not differed significantly between them ($P > 0.05$).

There were no differences in transpiration rates among successional stages in 2012 and 2013 ($P > 0.05$) (Fig. 3C). The transpiration rate was higher in 2013 than in 2012 ($P < 0.05$). The largest increase over the years was observed at the intermediate stage, with rates that were 17-fold higher compared with those that were measured in 2012 ($P < 0.05$).

The intrinsic water use efficiency (IWUE) was greater in the plants located in the initial area in 2012 ($P < 0.05$), a value 63% higher, in average, than those found in all areas in 2013 (Fig. 3D). It is important to note that the greatest difference was observed between the initial and the late areas in 2012, the driest year, with a difference of 137% ($P < 0.05$).

3.3. Changes in contents and nutrient use efficiencies

The greatest values of leaf *N* concentration were observed in all successional stages in 2013, when compared to 2012 ($P < 0.05$). The lower N content was observed in the late area in 2012, with

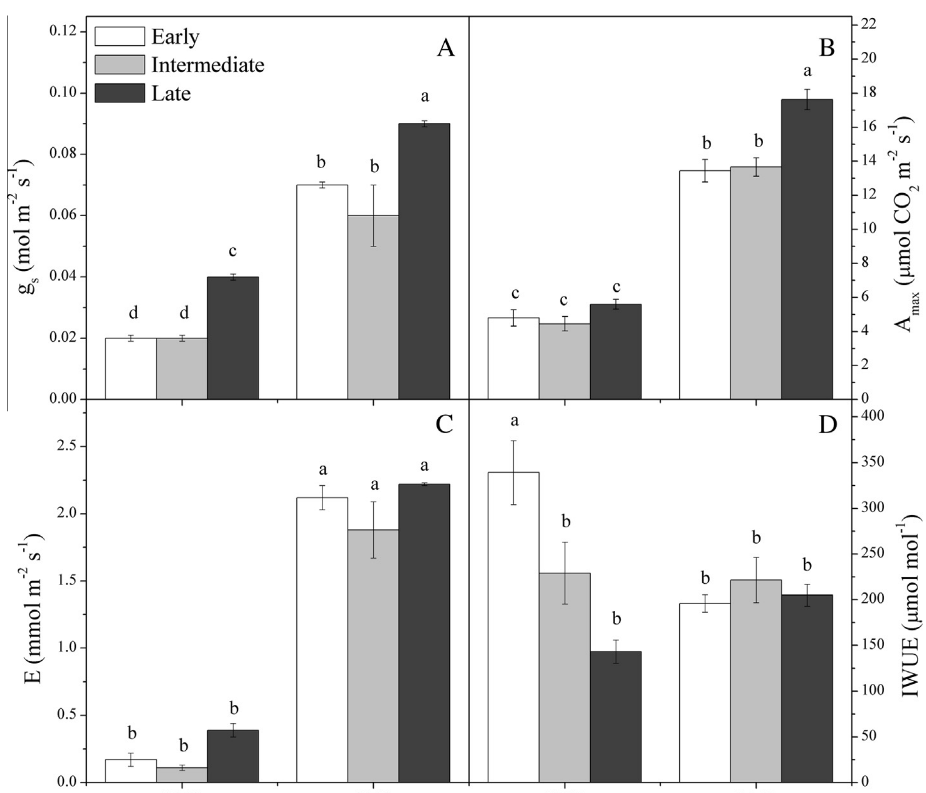

Fig. 3. Gas exchange of *P. pyramidalis* in three different successional stages over two consecutive years. (A) stomatal conductance; (B) maximum net CO_2 assimilation; (C) transpiration; (D) intrinsic water use efficiency. Bars ± SE with the same letter are not significantly different by Student Newman–Keuls test (5%), $n = 4$.

Table 2
Leaf content and nitrogen, phosphorous and potassium photosynthetic use efficiency, and N:P ratio of *P. pyramidalis* in three different successional stages in two consecutive years. Averages ± SE followed by the same letter are not significantly different by Student Newman–Keul's test (5%), $n = 4$.

Stage	Year	N		P		K		N:P
		[N] g kg^{-1}	PNUE (μmol C mmol N)	[P] g kg^{-1}	PPUE (μmol C mmol P)	[K] g kg^{-1}	PKUE (μmol C mmol kg)	Ratio
Early	2012	20.3 ± 0.3bc	69.8 ± 2.7c	3.9 ± 0.5a	863.6 ± 168.7c	8.9 ± 0.7a	447.5 ± 29.7c	6.4 ± 0.9b
	2013	26.2 ± 1.3a	118.9 ± 1.9b	1.6 ± 0.1b	4280.9 ± 366.1b	1.9 ± 0.07b	4926.5 ± 448.2b	16.2 ± 1.5a
Intermediate	2012	23.0 ± 0.8b	40.4 ± 2.6c	4.0 ± 0.2a	513.5 ± 37.8a	10.8 ± 1.2a	251.2 ± 39.0c	5.7 ± 0.1b
	2013	26.3 ± 1.0a	129.2 ± 3.5b	1.6 ± 0.04b	4700.1 ± 353.2b	2.4 ± 0.2b	3922.8 ± 369.5b	16.4 ± 1.1a
Late	2012	19,4 ± 1.3c	57.7 ± 4.3c	3.1 ± 0.5a	798.9 ± 139.2c	7.2 ± 1.5a	446.7 ± 89.6c	6.2 ± 0.9b
	2013	25.3 ± 0.5a	189.5 ± 3.7a	1.8 ± 0.1b	5783.7 ± 485.6a	1.9 ± 0.2b	7795.7 ± 828.4a	13.8 ± 1.3a

a difference of 31%, in average, between the successional stages in 2013 (Table 2). The photosynthetic nitrogen use efficiencies were significantly higher in the late stage in 2013, when compared to all other areas in the two years ($P < 0.05$).

The leaf *P* concentration did not differ between the stages in 2012 or 2013 ($P > 0.05$). In 2012, the leaves contained, in average, 2-fold more phosphorus than in 2013 ($P < 0.05$). The plants in the late stage showed a photosynthetic P use efficiency7-fold higher than all successional stages in 2012 ($P < 0.05$), which showed the lower P use efficiency.

The leaf *K* concentration was, in average, 4-fold higher in all successional stages in 2012 when compared to 2013 ($P < 0.05$). The photosynthetic potassium use efficiency was greater in the plants of the late stage in 2013, and was always higher than 2012 for all successional stages ($P < 0.05$).

The N:P ratio was higher in 2013 in all successional stages when compared to 2012, with a difference of 152%, in average ($P < 0.05$).

3.4. Specific leaf area and energy costs

The SLA was higher in 2013 than in 2012 ($P < 0.05$) with the exception of the initial stage. In 2013, the specific leaf area (SLA) was higher in the initial and late stage in 2013 ($P < 0.05$), and lower in the late stage in 2012, a difference of 84% (Fig. 4).

No differences were observed in leaf construction costs per unit dry mass among successional stages in either 2012 or 2013 ($P > 0.05$) (Fig. 5A). However the values were, in average, 9% higher in all successional stages in 2013 when compared to 2012 ($P < 0.05$). As construction costs per mass, the leaf construction cost per unit area did not differ between successional stages in 2012 or 2013 ($P > 0.05$) (Fig. 5B) but, contrary to what occurred in construction costs per mass, the values were 32% higher in all stages in 2012 ($P < 0.05$).

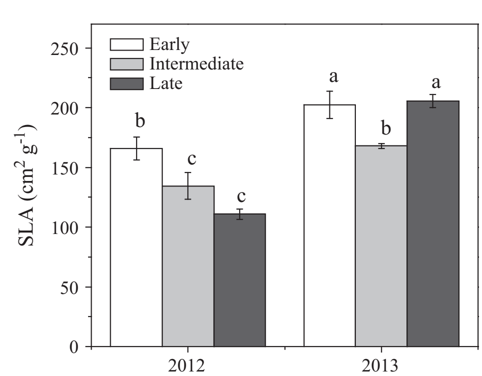

Fig. 4. Specific leaf area of *P. pyramidalis* in three different successional stages over two consecutive years. Bars ± SE with the same letter are not significantly different by Student Newman–Keuĺs test (5%), $n = 4$.

The higher payback times were observed in the initial and intermediate areas in 2012, and the lower in initial and late areas in 2013, a difference of 50% ($P < 0.05$).

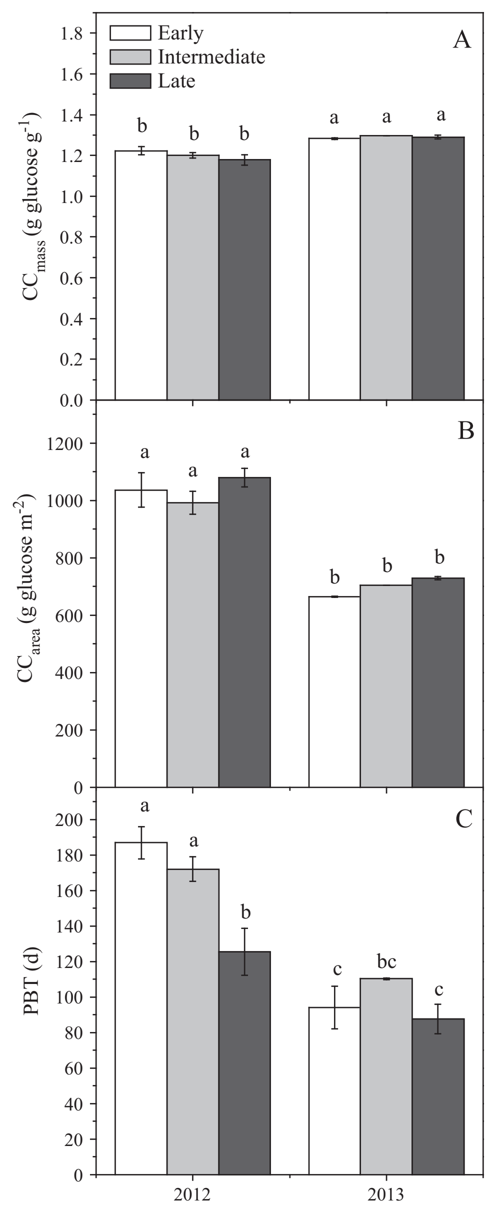

Fig. 5. Leaf construction cost of *P. pyramidalis* in three different successional stages over two consecutive years. (A) construction cost per unit of dry mass; (B) construction cost per unit of leaf area; (C) payback time. Bars ± SE with the same letter are not significantly different by Student Newman–Keuĺs test (5%), $n = 4$.

4. Discussion

4.1. Water status and gas exchange: alterations in response to successional stage and water availability

Our dataset shows that *P. pyramidalis* responds quickly to small changes in the environment, such as variations in annual rainfall and VPD, and the differences between micro-habitats that are formed at each successional stage, showing great plasticity in response to changing environmental conditions in time and space. The most striking differences, however, were found among the dry (2012) and wet (2013) years, confirming that the main environmental filter limiting the photosynthetic performance and growth of this species was water availability.

The leaf water potential was higher in all areas during the rainy year compared with the dry year. Furthermore, we expected the water potential of *P. pyramidalis* in the late stage to be greater than those in other stages in the two years of the study. There is a gradient of desiccation risk along the successional process, with late areas having greater soil water availability and lower temperatures and VPD, which would lead to higher water potentials of the plants in conserved areas (Lebrija-Trejos et al., 2011; Pineda-García et al., 2013). Such behavior was observed in the wet year but not in the dry year, with the late-stage plants exhibiting low water potentials compared with of the intermediate and initial stages. It is possible that not only the environmental conditions but the floristic compositions of the plant community of the area itself played an important role in the water status of *P. pyramidalis*. In the studied area, the late stage of regeneration had the highest species richness and plants with greater heights, circumferences at breast height and shoot biomasses (Cabral et al., 2013). Higher and more developed plants are more efficient competitors for resources, such as water and nutrients (Falster and Westoby, 2005). Thus, plants from the late stage of regeneration show more developed root systems that were able to deeply penetrate soil layers in search of water. In the driest year of 2012, the late-stage plants most likely quickly exhausted the available water supply from the soil compared with those of the intermediate and initial stages, leading to a more negative water potential.

The good hydration status of the plants in 2013 allowed them to much more efficiently photosynthesize compared with those from 2012, and they also exhibited higher rates of gas exchange, mainly in the late stage at which the soil moisture levels were higher and VPD was lower. When *P. pyramidalis* reaches a water potential of between −2 and −5 MPa in the dry year, gas exchange rates are altered, leading to reductions in g_s, and consequently, in CO_2 assimilation. The plants maintained low water potentials during this period and a low and similar assimilation rates between successional stages, indicating that even after reaching extremely negative predawn values, the plants did not reach the wilting point, which would be expected in plants with high drought tolerance (Bartlett et al., 2012). Apparently, the reduced water potential was the main strategy that was used by the plant to decrease desiccation and maintain basal rates of photosynthesis. Because the shoot:root ratio is high in trees, a reduction in transpiration via greater stomatal closure prevents excessive water loss in cases of low water availability and protects the hydraulic architecture of the plant, even under conditions of low leaf water potential (Brodribb and Holbrook, 2003; Rivas et al., 2013). The maintenance of photosynthesis even under a very restrictive water regime is a common characteristic of native deciduous plants in TDF, that need to accumulate energy during the short periods of the year when they possess leaves, while concurrently conserving as much water as possible (Souza et al., 2010; Santos et al., 2014).

Aside from the higher stomatal conductance that was observed in the late successional stage, the gas exchange rates in 2012 did not differ between the different successional stages because the plants maintained only basal rates of photosynthesis due to the severe water restrictions. The IWUE, however, showed contrasting patterns, being highest at the early stage and lowest at the late stage, possibly due the g_s values that were presented by plants in this area in association with the lower leaf water potential and low soil moisture levels.

An opposite pattern of higher IWUE in late stages has often been reported in works studies that have been performed in humid tropical or subtropical forests, which is where ecological succession research is most frequently performed (Quesada et al., 2009; Pineda-García et al., 2013; Zhu et al., 2013). The patterns and processes governing ecological interactions in addition to the establishment and performance of the species along the successional process differ between wet and dry forests, which are particularly due to the environmental filters that confer the strongest affects, including light in rainforests and water in dry areas (Vieira and Scariot, 2006; Hennenberg et al., 2008; Lebrija-Trejos et al., 2011).

4.2. Mobilization and photosynthetic nutrient limitation

Plants that colonize tropical forests in early secondary succession show low foliar nutrient contents, which increase due to their accumulation in the soil over time (Boeger et al., 2005; Davidson et al., 2007). The foliar concentrations of N, P and K, in general, did not differ between the stages in the same year in this work despite the analysis of soil from areas presenting trends of increases in some nutrients, particularly *P* and organic carbon, along the successional process (Freitas et al., 2012). In addition to availability in the soil, the water status of the plant is a key factor in the mobilization of nutrients from the soil to the leaves (Durand et al., 2010). Drought adversely affects the acquisition, assimilation and allocation of nutrients among plant organs (Gonzalez-Dugo et al., 2012). Thus, when the P. pyramidalis plants presented lower water potentials and leaf nutrient contents in 2012, detrimental effects on metabolic processes were observed.

Because basal rates of photosynthesis were observed in *P. pyramidalis* in 2012, the lowest leaf *N* concentration was associated with low *N* use efficiency, indicating that little nitrogen was being mobilized to the photosynthetic process in the form of proteins, especially Rubisco (Zhu et al., 2012). In addition, the accumulation of *P* and *K* in the leaf, and low use efficiency by the plants, demonstrated that molecules, such as ATP and NADPH, were produced or consumed in small quantities, and key enzymes for photosynthesis ceased to function (Soleimanzadeh et al., 2010). These data are corroborated by the N:P ratios, which indicated that photosynthesis was limited in the driest year by the amount of nitrogen in the leaves (Koerselman and Meuleman, 1996). In 2013, the greatest water potentials and high photosynthetic rates of *P. pyramidalis* in association to the increased availability of *N* caused the *N* use efficiency to be higher compared with that of 2012, especially in the late stage, and photosynthesis was limited due to phosphorus leaf concentrations.

4.3. Leaf construction costs and leaf energy use efficiency

Specific leaf area is a key functional trait that may allow for the understanding of the ecophysiological behaviors of plants because it directly influences the photosynthetic capacity and resources use efficiency, such as light, water and nutrients (Shipley et al., 2005; Nouvellon et al., 2010). In general, specific leaf area tend to be higher in plants that colonize areas that are at the early successional stage, where the investment in growth is more important than the investment in attributes that allow for the long-term persistence of plants, such as the production of defense compounds (Zhu et al., 2013). This behavior was observed by P. *pyramidalis* in 2012, which was the driest year. It is interesting to note that although there were differences in specific leaf area, leaf photosynthetic rates were similar in all successional stages. The intraspecific variation in several functional attributes, including specific leaf area and photosynthesis, has been demonstrated to occur along gradients of water availability (Martínez-Vilalta et al., 2009). This can be observed mainly in the initial stage of succession, which had a higher specific leaf area compared with those of the other stages, especially in 2012. Because the photosynthetic rates of *P. pyramidalis* were much higher in 2013, it is possible that the water was the determining factor in controlling this attribute because the initial stage in 2012 was associated with higher leaf water potential and increased IWUE.

During the process of natural regeneration, pioneer species, such as *P. pyramidalis,* have high rates of growth and survival, and these characteristics may be associated with low leaf construction costs; i.e., these plants require less energy and use it more efficiently for the production of biomass than those of the late successional stages (Liu et al., 2013; Martínez-Garza et al., 2013). Our results did not indicate any differences in the investment of carbon per unit mass among the three successional stages. However, in the wettest year, the plants spent more energy on biomass production. This greater amount of energy expenditure in the wettest year was likely directed toward the production of larger amounts of structural carbohydrates, such as cellulose, hemicellulose and pectin, as can be observed in association with higher specific leaf area, which are cheaper to the plants from an energy perspective (Poorter et al., 2006).

The major differences in leaf construction costs were observed when this parameter was expressed per unit area. This is due to differences in specific leaf area. Plants that have high specific leaf areas have higher leaf *N* contents, suggesting that most of the energy is used for protein synthesis, mainly in the form of Rubisco, which contributes to higher photosynthetic rates (Villar and Merino, 2001) as was observed in P. *pyramidalis* in 2013 to occur mainly in the late stage, when water availability was higher. Not only the leaf construction costs but also the benefits of the investment must be determined (Karagatzides and Ellison, 2009). Thus, payback time can be used as a measure of energy use efficiency, reflecting the energetic benefits for the plant (Poorter et al., 2006). The payback time, and consequently leaf turnover, was, in general, lower in all three stages in 2013 compared with 2012, possibly due to the high rates of photosynthesis and low leaf construction costs per unit area that were observed. According to Kikuzawa (1991), leaf longevity decreases with increased photosynthetic rates, and increases with increased leaf construction costs (Shipley et al., 2006), which was supported by this work. It should be noted that in 2012, the late-stage plants showed the lowest payback time despite their low rates of photosynthesis. It is possible that these plants produced smaller leaves as a strategy to decrease the time that was required to recoup the costs of leaf construction (Poorter et al., 2006) as can be observed by the alterations in specific leaf area. These results show the importance of the preserved areas conservation in the Brazilian TDF because the plants of the late stage demonstrated to use energy that was acquired from photosynthesis more efficiently, even with the basal rates of photosynthesis and lower water potential that occurred in the dry year.

From the results that are presented here, we conclude that *P. pyramidalis* has a high plasticity of its functional attributes, and consequently, a high capacity for acclimation to environmental changes by altering its physiological mechanisms to survive, even at the expense of productivity and biomass generation. It is also clear that the main limiting factor that shaped the ecophysiological response of this species was water restriction, and attributes that were related to the uptake of water and the maintenance of water status were the main contributors to this high capacity for acclimation. Our results suggest that in studies of TDF leaf water potential, gas exchange and payback time must be maintained among the attributes that are evaluated. Future studies should also include hydraulic conductivity to better characterize the ability of the plant to transport water. Due to its ability to adapt, without major damage, to very contrasting environmental conditions, which is demonstrated by its successful establishment indifferent stages of succession, the *P. pyramidalis* can be considered to be important species in the management and reforestation of degraded areas.

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