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Growth and ecophysiological response in juvenile clones of *Guadua* (Guaduinae: Bambusoideae) cultivated in an altered lowland tropical region

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Abstract

Guadua amplexifolia and *Guadua angustifolia* are the most promising timber substitutes amongst American bamboos due to their outstanding dimensions and structural properties. Despite the commercial potential of these species, there are few studies on the survival and adaptability of juveniles in plantations. The present study dealt with survival, growth, and ecophysiological response of juvenile clonal plants of these species, cultivated in abandoned pastures in Mérida, Venezuela. Survivorship, growth (height and culm diameter), and ecophysiological parameters were monitored the first year during wet and dry seasons. Survival rates were high in both species (95% in *G. amplexifolia* and 89% in *G. angustifolia*). Midday leaf water potentials decreased in both species during dry months (–1.28 to –2.72 MPa in *G. amplexifolia* and –1.67 to –2.37 MPa in *G. angustifolia*, respectively). Net photosynthetic rates measured during wet [16.57 ± 1.40 and 13.68 ± 2.40 μmol(CO_2) m^{-2} s^{-1}, respectively] and dry seasons [12.19 ± 2.82 and 8.12 ± 1.81 μmol(CO_2) m^{-2} s^{-1}, respectively], demonstrated that *G. amplexifolia* maintained consistently higher photosynthetic rates compared to *G. angustifolia*, which could explain the higher growth rates of the former. Similar trends were observed for stomatal conductance, transpiration, water-use efficiency, electron transport rate, and photochemical quenching of PSII. *G. angustifolia* maintained higher nonphotochemical quenching as well as a higher consumption of electrons per molecule of CO_2 fixed, indicating a lower photosynthetic efficiency. The maximal photochemical efficiency of PSII (0.73–0.76) suggested that neither of these species suffered from photoinhibition, despite persistently high radiation and air temperatures at the study site.

Additional key words: bamboo; chlorophyll *a* fluorescence; leaf water potentials; photosynthesis; Venezuela.

Introduction

Guadua amplexifolia and *G. angustifolia* are the two American bamboos of the largest dimensions; therefore they are becoming increasingly popular as a low-cost timber substitute (Londoño 1998, Londoño *et al*. 1999, Riaño *et al*. 2002, Poppens and Morán-Ubidia 2005, Cruz-Ríos 2009). Despite the commercial potential of these bamboos, there are few studies on the ecophysiological response of juvenile plants to drought and high

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Abbreviations: Chl – chlorophyll; DBC – diameter at the base of the culm; *E* – transpiration rate; ETR – electron transport rate; ETR/P_N – number of electrons used during electron transport per molecule of CO_2 fixed during net photosynthesis; F_v/F_m – maximum quantum yield of PSII photochemistry; g_s – stomatal conductance; MAT – months after transplantation; MSWC – minimum soil water content; P_N – net photosynthetic rate; q_N – nonphotochemical quenching coefficient; q_P – photochemical quenching coefficient; RH – relative air humidity; RuBP – ribulose-1,5-bisphosphate; T_A – air temperature; TH – total height; T_L – leaf temperature; VPD – leaf-to-air vapor pressure deficit; WUE – instantaneous water-use efficiency; Φ_{PSII} – effective quantum yield of PSII photochemistry; Ψ_W – leaf water potential; Ψ_{Wmax} – maximum leaf water potential; Ψ_{Wmin} – minimum leaf water potential.

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temperatures in lowland tropical and subtropical climates. These climates are characterized by elevated radiation, daily high air and soil temperatures, and oligotrophic soils (Kijeweski *et al.* 1981, Andressen 2008). Until now, no studies are available on leaf gas exchange in *G. angustifolia.* The only ecophysiological study for this species focuses on daily fluctuations in chlorophyll (Chl) *a* fluorescence variables at a commercial stand in India (Kumar *et al.* 2002).

A preliminary ecophysiological study was carried out in *G. amplexifolia*, dealing with limited aspects of the photosynthetic response of a mature plantation in China during different seasons (Ma and Chen 2013). In South America, studies on the genus *Guadua* have focused mainly on *Guadua angustifolia* and deal with growth (Londoño 1998, Cruz-Ríos 2009), carbon sequestration (Riaño *et al.* 2002), and management of natural *Guadua* forests in Colombia (Giraldo-Herrera and Sabogal 1999, Londoño *et al.* 1999, Stern *et. al.* 1999, Cruz-Ríos 2009) and Ecuador (Stern *et al.* 1999, Poppens and Morán-Ubidia 2005).

Bamboos are C_3 grasses, with net CO_2 assimilation rates ranging between 5–23 μmol(CO_2) m^{-2} s^{-1}, regardless of whether they are temperate, tropical or subtropical species (Koyama and Uchimura 1995, Lei and Koike 1998, Ishizuka and Puangchit 2000, Gratani *et al.* 2008, Motomura *et al.* 2008, Cirtain *et al.* 2009, Ely *et al.* 2011, Wen *et al.* 2011, Cao *et al.* 2012, Ma and Chen 2013, Van Goethem *et al.* 2014). Like typical C_3 grasses, photosynthetic rates in bamboos are generally saturated at radiation levels between 700 and 1,200 μmol(photon) m^{-2} s^{-1} (Koyama and Uchimura 1995, Cirtain *et al.* 2009, Ely *et al.* 2011, Ma and Chen 2013, Van Goethem *et al.* 2013), with photosynthetic rates diminishing at air temperatures above 30°C (Ishizuka and Puangchit 2000, Cirtain *et al.* 2009).

These limitations must be taken into account when growing large-scale bamboo crops in lowland tropical climates, where high temperature increases evaporative demands. Preference should be given to crops that tolerate high temperatures and seasonal droughts, without suffering damages of the photosynthetic complex or growth retardation. Thus, it is fundamental to assay specific developmental and ecophysiological responses at plantations for bamboo species, with emphasis on drought and high temperature tolerance, because their response may differ outside of their natural habitats along riverbanks and streams (Stern *et al.* 1999, Clark and Ely 2011, Ely *et al.* 2011).

A plant's response to drought, excessive radiation, and high temperature varies in different species and cultivars (Sage and Kubien 2007, Hu *et al.* 2010). Drought, excessive radiation, and high temperatures can easily compromise an overall development and productivity of plants (Flexas and Medrano 2002, Lawlor 2002, Lawlor and Tezara 2009, Hu *et al.* 2010, Ashraf and Harris 2013). Under moderate drought stress conditions, photosynthesis can be impaired by stomatal closure (Chaves *et al.* 2002, Flexas and Medrano 2002). As drought stress increases, photosynthetic constraints become determined mainly by metabolic limitations, such as low carbon carboxylation efficiency (CE), diminished regeneration of ribulose-1,5-bisphosphate (RuBP) due to diminished electron transport rate (ETR), or limitations in ATP synthesis (Tezara *et al.* 1999, Lawlor 2002, Lawlor and Cornic 2002, Flexas *et al.* 2004, Lawlor and Tezara 2009, Hu *et al.* 2010, Ashraf and Harris 2013).

Chl *a* fluorescence parameters, specifically maximum quantum yield of PSII photochemistry (F_v/F_m), effective quantum yield of PSII photochemistry (F_v'/F_m'), photochemical quenching (q_P), and nonphotochemical quenching (q_N) may also show early stages of stress induced by drought and extreme temperatures, revealing changes in the photosynthetic status (Chaves *et al.* 2002, Baker and Rosenqvist 2004, Hu *et al.* 2010). Chl *a* fluorescence studies in tropical and temperate bamboos are relatively limited; so far, available results suggest that bamboos are not particularly susceptible to suffer from chronic photoinhibition when exposed to high radiation levels under open-field conditions (Kumar *et al.* 2002, Ely *et al.* 2011, Van Goethem *et al.* 2013). Nevertheless, F_v/F_m values can diminish due to low temperatures in temperate climates (Van Goethem *et al.* 2013), or high temperatures in tropical climates during midday hours (Kumar *et al.* 2002).

The aim of this study was to assay survival, ecophysiological response, and development of juvenile clones of *G. amplexifolia* and *G. angustifolia* planted in abandoned pastures of a lowland tropical ecosystem, characterized by biannual seasonal droughts and elevated radiation levels, which are conditions for high air and soil temperatures. Considering that the establishment phase constitutes the most vulnerable stage of a crop, it is important to evaluate these early responses of bamboo in plantations, where environmental conditions differ from those of their natural habitat, with the purpose of exploring their potential as a sustainable commercial crop.

Materials and methods

Plant material and characteristics: *G. amplexifolia* and *G. angustifolia* share a close resemblance in size and morphological features. These species, however, differ in their distribution and habitat preferences. *G. amplexifolia* has a broad distribution range, from southern Mexico to northern Colombia and Venezuela, where it grows in low-elevation tropical ecosystems (0–600 m a.s.l.), such as seasonally dry forests of Central and South America. In contrast, *G. angustifolia* presents a more limited distribution, restricted to Venezuela, Colombia, and Ecuador, where it occupies a broader altitudinal distribution (0–1,800 m a.s.l.), with optimum development between 1,000–1,300 m a.s.l. *G. angustifolia* is typically associated with more humid ecosystems, mainly low-elevation montane forests, including inter-Andean valleys, and less commonly with tropical rain forests of the Amazon basin (Londoño 1998, Clark and Judziewicz 1999, Montiel and Sánchez 2006, Clark and Ely 2011).

Study site and meteorological conditions: The study was carried out at the farm Judibana, property of the Universidad de Los Andes (University of The Andes) located in the southern region of the Lake Maracaibo basin, in the state of Mérida, Municipality Alberto Adriani, Venezuela (8°37'26"N, 71°42'22"W). Originally covered by humid tropical lowland forests, the region now mostly consists of vast extensions of abandoned pastures, due to extensive timber extraction and cattle grazing during the past 50 years (Romero and Monasterio 1996, Plonczak 1998). The climate in this region is characterized by high radiation and air humidity. Average air temperature in the region is 28.5°C (Andressen 2008). Precipitation is generally distributed in a bimodal pattern. The first rainy season goes from April to June, while the second (more abundant), October through December and even sometimes to January of the following year. The first dry season is typically from February to March, the second from July to September. Recent total annual precipitation in the region was 1,890 mm. Total precipitation during the dry periods ranged between 300–543 mm, whereas total precipitation during the wet seasons reached 1,400–1,600 mm (data for the period 2010–2012 provided by the Venezuelan Air Force airport, located approximately 4 km from the study site). Previous soil studies conducted at the study site by Jaimez *et al.* (2013) revealed acidic (pH of 5.2–6.3) suboptimal soils, ranging from sandy-loams to coarse sands, with N contents between 0.03 and 0.1%, 2–8 mg(P) kg^{-1}, and 25–118 mg(K) kg^{-1}.

Experimental plantation design: The plantation was established with 3-month-old clonal plantlets of *G. amplexifolia* and *G. angustifolia*, propagated asexually from plantlets that originated directly from the rhizomes of harvested genets. A total of 160 plantlets were transplanted to bags containing an enriched substrate (30% sand, 65% loose soil, and 5% organic compost) and acclimated at the plantation site during two months prior to planting. The assay consisted of four alternating plots for *G. amplexifolia* and *G. angustifolia*, each containing 40 plantlets/species, planted in plots of five (columns) by eight (rows), with a regular spacing of 7 m between plants and 12 m between plots. Weed control and pruning were carried out in quarterly intervals. Previous soil analysis at the study site indicated that the soil types differed significantly from the optimal soil types recommended for bamboo cultivation in general (Kleinhenz and Midmore 2001, Cirtain *et al.* 2009). *Guadua* requires loamy soils with a high content of organic matter, therefore high contents of N and P (Cruz-Ríos 2009). To compensate for soil quality and improve survivorship as well as growth, regular fertilizations were carried out during the first year, in quarterly intervals after the fourth month from transplantation, and always during wet months. Commercial formulas of N:P:K (12:12:17 and 10:20:20) were applied. Initial dosage of 20 g was progressively increased every three months, until reaching a dosage of 100 g per plant by 14 months.

Survival and growth measurements: Survival rates were monitored during the first 12 months after transplantation (MAT). Growth measurements were also performed during the first 12 MAT; they were initiated at 4 MAT and continued every other month to compare growth during both wet and dry seasons. All measurements were carried out with 20 plants per species, marked at the beginning of the assay, choosing ten randomly in each plot. Growth measurements involved only the aerial portion of these species. Growth variables considered were the diameter at the base of the culm (DBC in mm, below the first node) and total height per plant (TH in cm). Measurements were always carried out in the two largest culms per plant (Londoño 1998, Riaño *et al.* 2002).

Soil measurements: Minimum soil water content (MSWC) was determined for the driest and wettest months of the year; in three samples per season, for a total 6 soil samples of 500 g. All samples were extracted at a depth of 10 cm from the surface, around 13:00–14:00 h, assuming that maximum daily evaporation had occurred. Samples were collected during the first week of September, which corresponded to the end of the second dry season, and therefore the longest dry period of the year in the Lake Maracaibo basin, and also during the last week of October, which was the peak of the second rainy period. Soil texture, pH, organic matter content, and nutrient concentrations (N, P, K, Ca, and Mg) were determined before planting, in 8 samples of 500 g, taken at depths of 0–20 and 20–40 cm from the study plots where the assay was established. All samples were processed in Mérida, at the Facultad de Ciencias Forestales y Ambientales (Faculty of Forest and Environmental Sciences) of the Universidad de Los Andes.

Microclimate and ecophysiological measurements were initiated in January (4 MAT), and were generally conducted every other month during the first year to monitor species response during both wet and dry seasons. Air and leaf temperatures (T_A, T_L) were determined using three sets of copper-constantan thermocouples in each case. Relative humidity (RH) was measured with a digital hygrometer (*RH-200F*, *OMEGA*, Stanford, USA). Measurements were done between 7:30–13:00 h, every 1.5 h. These variables were used to determine the leaf-to-air vapor pressure deficit (VPD) of each species.

Leaf water potential and gas-exchange measurements: Leaf water potential (Ψ_W [MPa]) was measured in a total of 5–6 leaves per plant using a Scholander pressure chamber (*SKPM 1400*, *Skye Instuments Ltd.*, Powys, UK). Maximum leaf water potential (Ψ_{Wmax}) was measured at 6:30 h (predawn) and the minimum one (Ψ_{Wmin} [MPa]) at 13:00 h (midday).

Leaf gas-exchange measurements were performed with a portable infrared gas analyzer (*LCA-4*, *ADC*, Hoddesdon, UK). PPFD measurements were obtained directly from the built-in quantum sensor of the leaf chamber. Leaf gas-exchange variables were measured in daily courses from 8:30 to 13:00 h, in 1.5-h intervals. At each interval, measurements were performed in three fully expanded leaves per plant, in five plants per species positioned at the mid region of the culm, between nodes 4–6 from the apex, during the first four MAT, then nodes 8–12. Average values were determined for wet and dry months, in daily courses, from which average maximum values were determined for wet and dry seasons. The following ecophysiological parameters were measured: net CO_2 assimilation, measured as net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), and instantaneous water-use efficiency (WUE).

Chl *a* fluorescence parameters: Measurements were performed with a portable Chl fluorometer (*PAM 2100*, *Heinz Walz GmbH*, Germany) and carried out simultaneously with leaf gas-exchange measurements in 5–7 leaves per plant (positioned on different culms of the same plant), in five different plants per species. Prior to all measurements, in order to maintain all photosystems in the oxidized state, leaves were covered overnight with aluminum foil. Chl *a* fluorescence parameters measured with the equipment were: maximum quantum yield of PSII photochemistry (F_v/F_m), effective quantum yield of PSII photochemistry (Φ_{PSII}), photochemical quenching (q_P), nonphotochemical quenching (q_N), and electron transport rate (ETR). Φ_{PSII} was estimated as $\Phi_{PSII} = (F_m' - F_s)/F_m'$; photochemical ($q_P$) and nonphotochemical quenching (q_N) were calculated as $q_P = (F_m' - F_s)/(F_m - F_0)$ and $q_N = F_v - (F_v'/F_v)$, respectively. ETR was calculated as ETR = $\Phi_{PSII} \times \text{PPFD} \times 0.84 \times f$, where f = 0.5, which corresponds to the fraction of electrons transported by PSII divided by the total transport of PSI and PSII, assuming an equal linear electron transport in both photosystems (Genty *et al.* 1989, Maxwell and Johnson 2000). Photosynthetic quantum efficiency was also estimated, expressed as the number of electrons used per molecule of CO_2 fixed, expressed as ETR/P_N. F_v/F_m and Φ_{PSII} were always measured at 06:30 h. Remaining Chl *a* fluorescence parameters were measured in daily courses, starting at 08:30 h and ending at 13:00 h, in 1.5-h intervals.

Statistical analysis: Average values and standard errors are presented for maximum and minimum values of all variables measured for both species. All graphs were represented using *Sigma Plot* ver. *10.0*. Statistically significant differences for all variables were determined with an analysis of variance (*ANOVA*), with a level of significance of $p<0.05$. A *Duncan*'s test was used to determine differences between means, using *SPSS* software *v. 10.0*.

Results

Survival and growth measurements: Plantlets survival rates were high for both species, 95% for *G. amplexifolia* and 89% for *G. angustifolia*. Growth rates differed between these species during the first 12 months of establishment (Fig. 1). TH values were initially higher in *G. amplexifolia*; but from 6 MAT until 10 MAT, TH values were higher in *G. angustifolia.* This tendency, however, was reversed by 12 MAT (Fig. 1*A*). In contrast, DBC values differed between these species by 6 MAT and remained consistently higher in *G. amplexifolia* during the following months (Fig. 1*B*).

Soil nutrient and water content: Soils of the study site were mostly coarse sands or sandy loams, oligotrophic and predominantly acid (pH of 4.20–4.78). Concentrations of N, Ca, Mg, Na, and K determined at the beginning of the assay were 0.04, 2.31, 0.02, 0.88, and 2.38 mg kg^{-1}(soil), respectively. P content was 0.08 mg kg^{-1}(soil). Minimum soil water content (MSWC) measured towards end of the second dry season increased from 12.0 to 41.3% during the peak of the second wet season.

Microclimate and leaf temperature: During the study, precipitation occurred in a bimodal pattern. Microclimate measurements were initiated in January (4 MAT), during the last month of the previous year second rainy season and ended in October (12 MAT). The first dry season lasted only five weeks; from the last week of February through March, while the second season lasted 12 weeks, from July to September. The first wet season registered during the measurement period included April, May, and June; the second, October, November, and December.

PPFD and air temperature (T_A) remained consistently high during the entire experiment (Fig. 2*A*,*B*). Minimum and maximum T_A were measured in daily courses, and corresponded to 6:00 h and 13:00 h, respectively (Fig. 2*B*). During the interval from 13:00–14:00 h, however, T_A frequently diminished 2–3°C due to temporary cloud formation (Fig. 2*A*,*B*). Differences between T_A and T_L ranged between 0.5 and 2°C in both species. *G. amplexifolia* maintained slightly higher temperatures (0.5–1.2°C) than that of *G. angustifolia*, except during January (the coolest month) and September (the warmest one)

(Fig. 2*B*). Predawn RH values were typically high (86–96%) during wet and dry seasons and diminished abruptly between 10:00–13:00 h, regardless of the season, reaching minimum values always by 13:00 h (Fig. 2*C*,*D*). The decline of RH was more abrupt during the second dry season, decreasing to 46%, which corresponded to the lowest value measured during the assay (Fig. 2*C*,*D*). VPD values followed a similar trend in both species; predawn values (7:00 h) remained high during wet and dry months, due to the high RH during predawn hours (Fig. 2*C*,*D*). VPD values increased after 09:00 h, reaching maximum values at 12:00 h, coinciding with the increase in T_A and T_L and the drop in RH. *G. angustifolia* had the highest VPD values during both wet and dry seasons (Fig. 2*C*,*D*).

Water relations and leaf gas exchange: Ψ_{Wmax} (predawn) varied in both species between wet and dry months; with exception of January, no statistically significant differences were observed between species for the same month (Fig. 3). Ψ_{Wmin} (midday) decreased significantly in both species on a daily as well as seasonal basis. Daily differences between Ψ_{Wmax} and Ψ_{Wmin} observed in both species during the entire experiment followed the same trend observed for VPD. During the wet months, average differences between Ψ_{Wmax} and Ψ_{Wmin} were 1.10 MPa in *G. amplexifolia* and 1.70 MPa in *G. angustifolia*; whereas during the dry months of 1.95 MPa in *G. amplexifolia* and 1.75 MPa in *G. angustifolia*. Ψ_{Wmin} varied between *G. amplexifolia* and *G. angustifolia* during both wet and dry months (Fig. 3). During dry months, Ψ_{Wmin} values dropped from –1.28 to –2.72 MPa in *G. amplexifolia*, and from –1.67 to –2.37 MPa in *G. angustifolia*. Ψ_{Wmin} values were more negative in *G. amplexifolia* compared to *G. angustifolia*, except those measured during the month of June (Fig. 3).

In the measurements taken during January, which corresponded to the 4 MAT, no significant differences were observed for P_N, g_s, E or WUE (Fig. 4). However, by 6 MAT, *G. amplexifolia* maintained higher P_N, g_s, and E compared to *G. angustifolia* on a daily and seasonal basis (Figs. 4*A*–*C*, 5*A*–*C*, respectively). Differences regarding P_N and g_s between these species diminished after 10 MAT (Fig. 4*A*,*B*). Maximum mean P_N and g_s occurred between 9–10:00 h in both species during wet and dry seasons (Fig. 5*A*,*B*) and tended to diminish after 10:30 h (Fig. 5*A*–*C*), coinciding with a marked increase in PPFD, T_A, and T_L and the progressive decline of RH (Figs. 2, 5*A*–*C*). The drop in P_N and g_s observed in *G. angustifolia* after the first dry period suggests a higher susceptibility to high temperatures and drought stress compared to *G. amplexifolia* during the first months after transplantation (Fig. 4*A*). P_N declined in both species during the dry periods (Fig. 4*A*), diminishing by 28% in *G. amplexifolia* and 42% in *G. angustifolia* during the driest month (Fig. 5*A*), when MSWC was reduced to 12%. E followed a similar trend, with a marked decline during the dry months (Figs. 4*C*, 5*C*), particularly after 10:00 h. The drop in P_N, g_s, and E after 10:30 h suggests an increase in stomatal control in both species after 10:00 h (Fig. 5*C*). Average E during the dry months declined by 15% in *G. amplexifolia* and 22% in *G. angustifolia* (Figs. 4*C*, 5*C*). WUE values remained consistently higher in *G. amplexifolia* during the wet seasons and the first short dry period (Figs. 4*D*, 5*D*). Once these species reached 10 MAT, differences in P_N rates decreased after the second dry season (which lasted for 12 weeks, Fig. 5*D*).

Chl *a* fluorescence: During the assay, maximum quantum yield of PSII (F_v/F_m) did not vary significantly in either of the species in wet or dry seasons (Table 1). Although Φ_{PSII} declined in both species during dry months, no significant differences in Φ_{PSII} values were observed between species for the same season (Table 1). q_P varied between species during wet and dry months, remaining consistently higher in *G. amplexifolia* (Fig. 6*A*), particularly at the hours of maximum P_N (Fig. 6*A*). In contrast, q_N remained slightly higher in *G. angustifolia*, regardless of the measurement

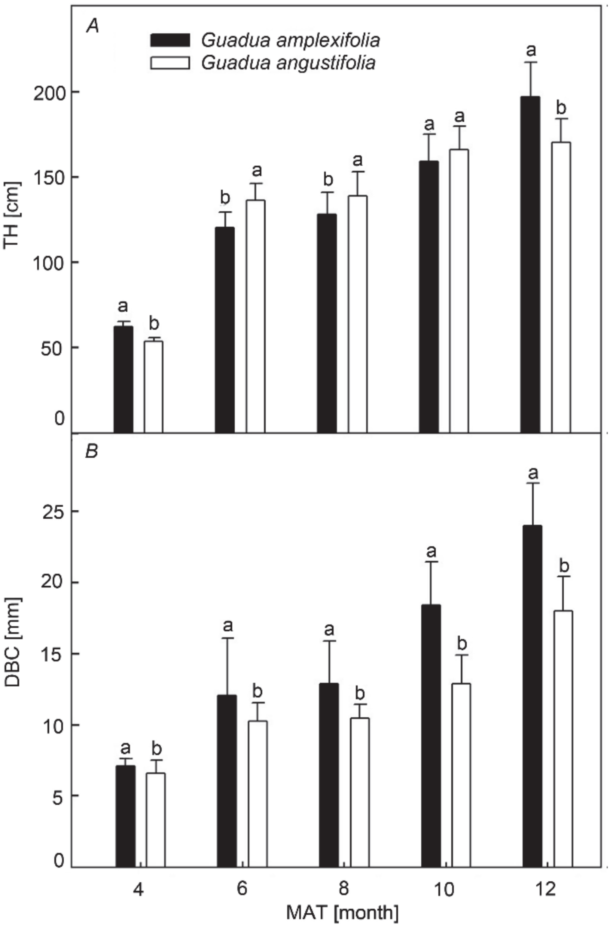

Fig. 1. Monthly growth rates in juvenile clones of *Guadua amplexifolia* and *G. angustifolia.* Total height (TH) (*A*) and diameter at the base of the culm (DBC) (*B*). Measurements were initiated the fourth month after transplantation (MAT). *Different lowercase letters* represent significant differences ($p<0.05$) between species during the same month.

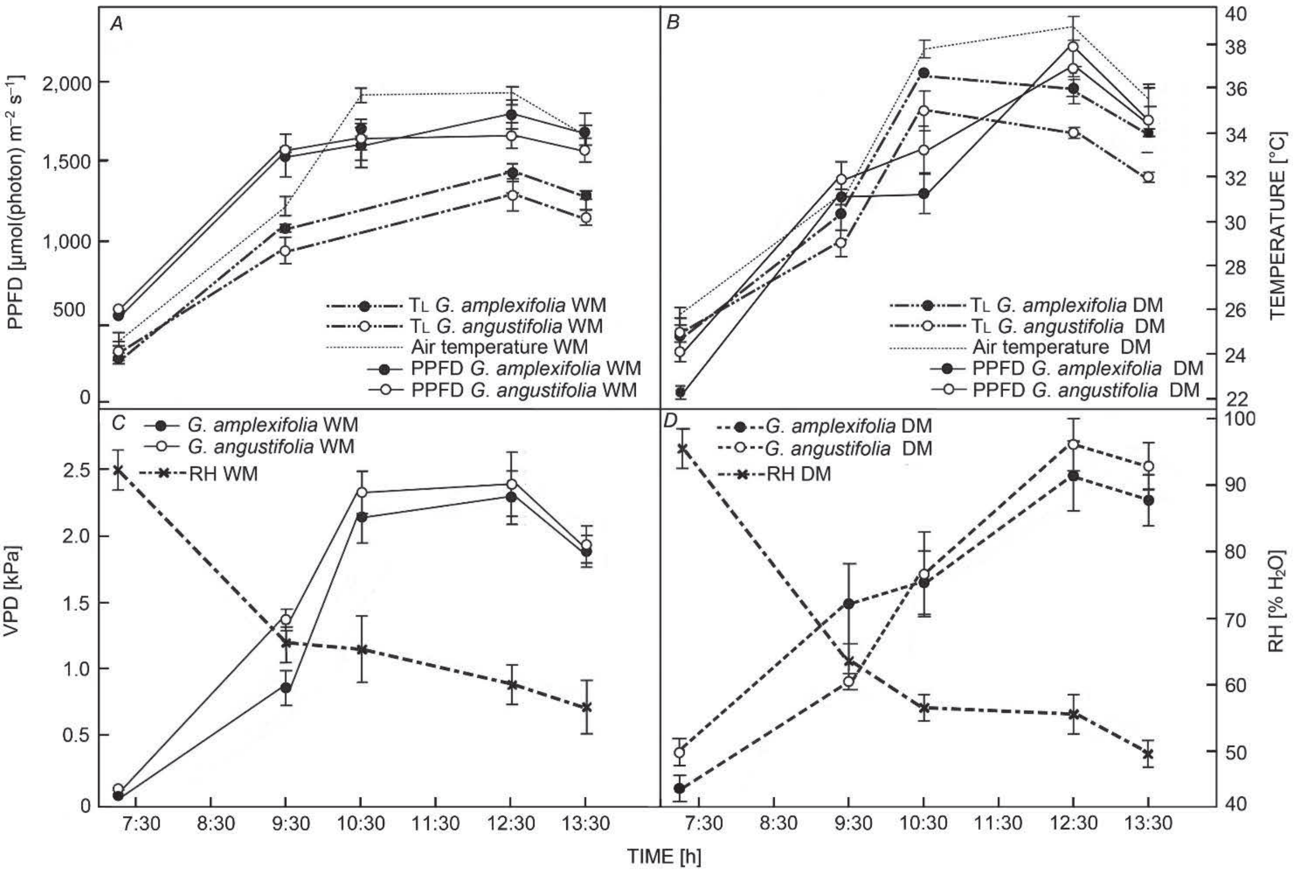

Fig. 2. Mean photosynthetic photon flux density (PPFD), air temperature (T_A), leaf temperature (T_L), relative humidity (RH), and leaf-to-air vapor pressure deficit (VPD), measured in daily courses during wet and dry months (WM and DM, respectively). Mean PPFD, T_A, and T_L measured during WM (*A*) and DM (*B*). Mean VPD and RH humidity measured during WM (*C*) and DM (*D*).

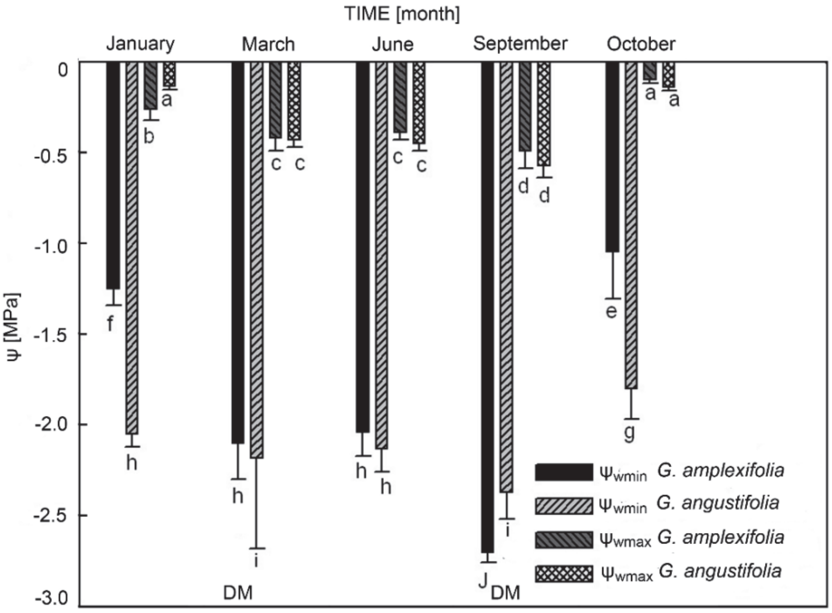

Fig. 3. Mean leaf water potentials measured in daily courses in juvenile clones of *Guadua amplexifolia* and *G. angustifolia* during wet and dry months. Predawn leaf water potentials (maximum values, 6:30 h) (Ψ_{Wmax}) and midday leaf water potentials (minimum values, 13:00 h) (Ψ_{Wmin}). *Different lowercase letters* represent significant differences (p<0.05) between species during the same month and between months.

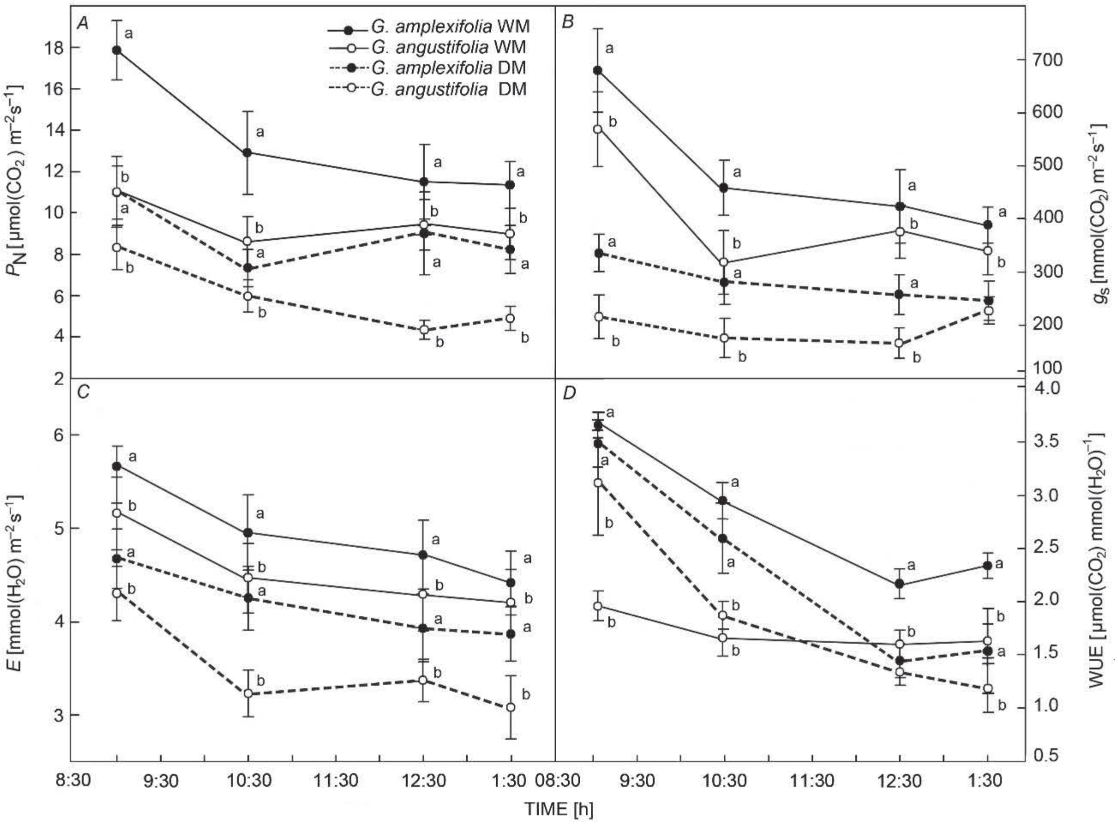

Fig. 4. Leaf gas-exchange variables measured in daily courses in juvenile clones of *Guadua amplexifolia* and *G. angustifolia* during wet and dry months (WM and DM, respectively). Mean net photosynthetic rates (P_{N}) (*A*), mean stomatal conductance (g_{s}) (*B*), mean transpiration (*E*) (*C*), and instantaneous water-use efficiency (WUE) (*D*). *Different lowercase letters* represent significant differences (p<0.05) between species during the same month.

season, reaching maximum values between 10:00–12:00 h (Fig. 6*B*). However, by 13:00 h, q_{N} values were the same for both species. ETR and ETR/P_{N} values also revealed differences in PSII photochemistry, on a daily as well as a seasonal pattern (Figs. 6*C*,*D*, 7, respectively). *G. amplexifolia* maintained higher ETR during the entire assay (Fig. 7*A*). Maximum ETR in both species during wet months were observed by 10:30 h, with a drop around 12:00 h and a slight recovery around 13:30 h (Fig. 6*C*). During dry periods, ETR diminished considerably in both species (Figs. 6*C*, 7*A*). The lowest ETR occurred at 10:30 h, with a slight recovery between 12:00–13:30 h (Fig. 6*C*).

The opposite trend was observed for ETR/P_{N}; *G. angustifolia* presented the highest electron consumption during wet and dry months (Figs. 6*D*, 7*B*). Daily measurements revealed that during wet months, ETR/P_{N} increased in both species generally between 10:00–12:30 h, reaching the highest values in *G. angustifolia* around 12:00 h (Fig. 6*D*). During dry months, ETR/P_{N} values decreased in both species around 10:00 h (Fig. 6*D*), due to the decline in ETR observed at this hour (Fig. 6*C*). ETR/P_{N} reached maximum values after midday, with a slight drop around 13:30 h in *G. amplexifolia* (Fig. 6*D*). Maximum ETR/P_{N} values in both species were observed during September, which as mentioned previously, was the driest month of the year (Fig. 7*B*).

Discussion

The study proved that juvenile clones of *G. amplexifolia* and *G. angustifolia* maintained relatively high CO_2 assimilation rates during their first year of establishment, during both wet and dry seasons, enduring environmental stress conditions, such as high PPFD, high air temperature, and seasonal droughts of limited duration. Positive growth rates observed during the first 12 months support these findings. It should be remembered, however, that both species were planted three weeks before a wet season and were fertilized and weeded at regular intervals, under conditions that most likely favored survival and ameliorated transplantation stress. The photosynthetic response and growth rates observed in these species during their first year in a plantation, devoid of irrigation, suggest that *G. amplexifolia* endured better high PPFD, T_{A}, and seasonal water deficits, compared to *G. angustifolia*, in terms of growth and CO_2 assimilation rates.

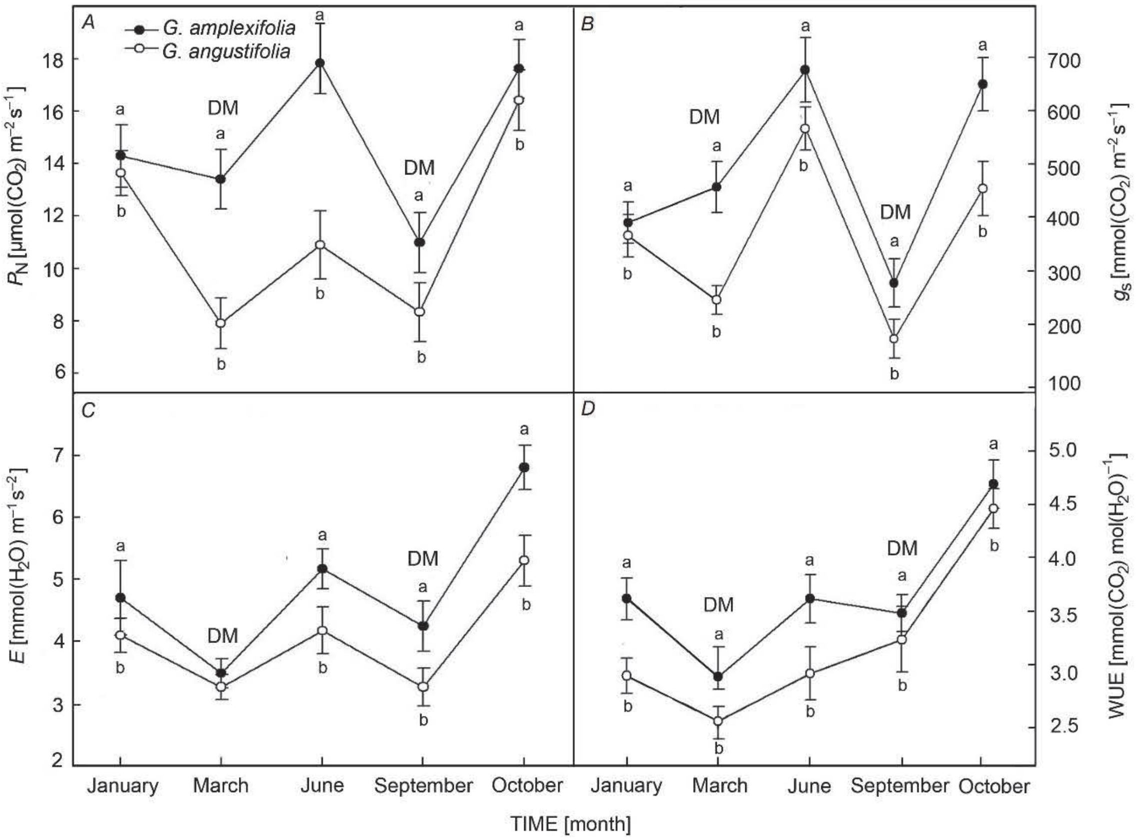

Fig. 5. Mean maximum leaf gas-exchange variables measured in daily courses (09:15 h) in juvenile clones of *Guadua amplexifolia* and *G. angustifolia* during wet and dry months (WM and DM, respectively). Mean maximum photosynthetic rates (P_N) (*A*), mean maximum stomatal conductance (g_s) (*B*), mean maximum transpiration (E) (*C*), and mean instantaneous water-use efficiency (WUE) (*D*). *Different lowercase letters* represent significant differences ($p<0.05$) between species during the same month.

Table 1. Mean maximum quantum yield of PSII photochemistry (F_v/F_m) and effective quantum yield of PSII electron transport (Φ_{PSII}) determined in juvenile clones of *Guadua amplexifolia* and *G. angustifolia* during wet and dry seasons. *Different lowercase letters* for each parameter indicate significant differences ($p<0.05$) between seasons for the same species.

Season	Species	F_v/F_m	Φ_{PSII}
Wet	*G. amplexifolia*	0.76^a	0.36^a
	G. angustifolia	0.75^a	0.34^a
Dry	*G. amplexifolia*	0.73^a	0.30^b
	G. angustifolia	0.74^a	0.28^b

Survival and growth rates: The low mortality of clonal plantlets in both species (5% in *G. amplexifolia* and 11% in *G. angustifolia*) in an open field plantation, after only two months of acclimation at the study site, indicated that with adequate management involving periodic weeding and fertilization during the first year, losses were minimal. In terms of soil quality and environmental conditions, it should be noted that the conditions that prevailed at the plantation site greatly differed from the optimum growth conditions reported for *Guadua angustifolia.* So far, no studies regarding optimum site conditions for *G. amplexifolia* are available. Optimal growth conditions for *G. angustifolia* include well drained soils with high N/C contents, precipitation above 2,000 mm, and average air temperature (T_A) of 26°C (Londoño 1998, Cruz-Ríos 2009). Such conditions differ vastly from those of our study site, which as mentioned previously, is characterized by coarse, oligotrophic soils, annual precipitation generally inferior to 2,000 mm, and high PPFD levels, which increase air temperature 9–13°C above optimum values between 10:00–14:00 h.

Additionally, natural bamboo stands are typically associated with riverbanks (Stern *et al.* 1999, Cruz-Ríos 2009, Clark and Ely 2011, Ely *et al.* 2011), which provide the plantlets with richer soils as well as a humid, shady environment. The biannual droughts, noted during the year of our study, may last as long as 12 weeks, and are an important stress factor that should be taken in account when planting bamboos in this region.

Despite these limitations, overall development of *G. amplexifolia* and *G. angustifolia*, in terms of DBC and TH, revealed positive growth rates during the early

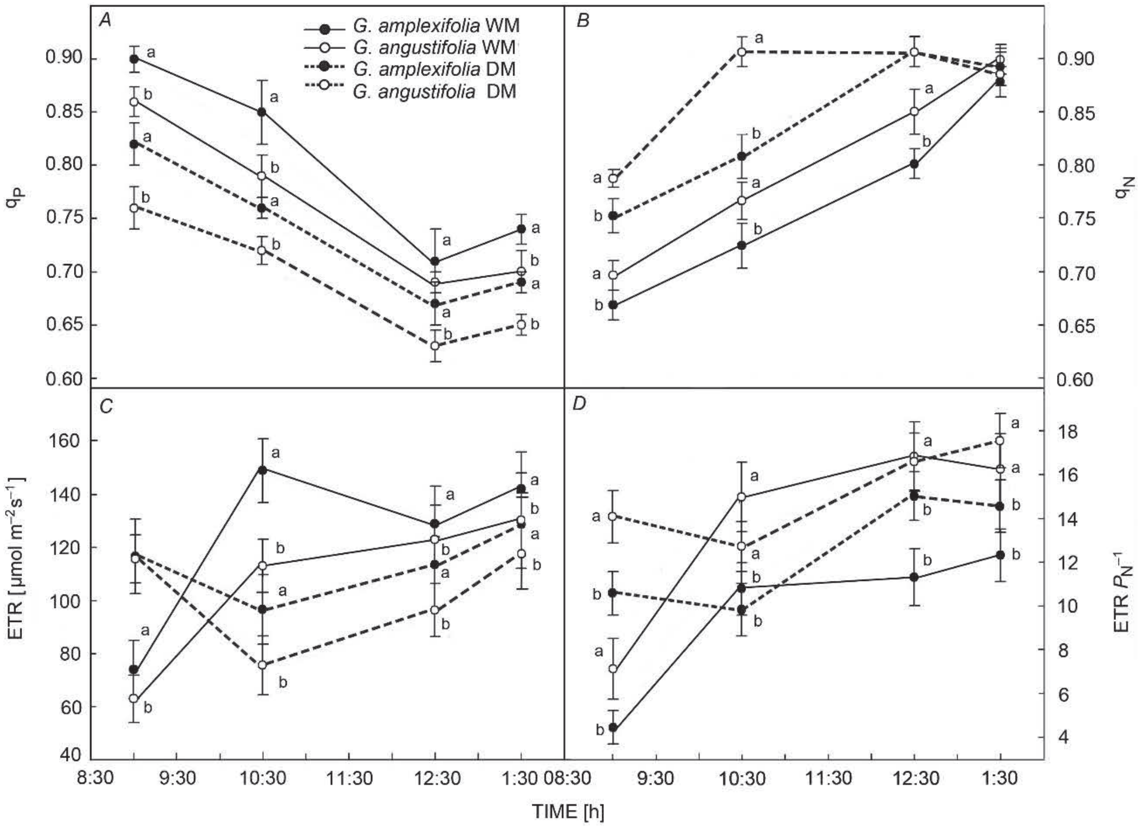

Fig. 6. Mean chlorophyll *a* fluorescence parameters measured in *Guadua amplexifolia* and *G. angustifolia* in daily courses during wet and dry months (WM and DM, respectively). Photochemical quenching (q_P) (*A*), nonphotochemical quenching (q_N) (*B*), electron transport rate (ETR) (*C*), photosynthetic quantum efficiency expressed as number of electrons consumed per molecule of CO_2 fixed (ETR/P_N) (*D*). *Different lowercase letters* represent significant differences ($p<0.05$) between species during the same month.

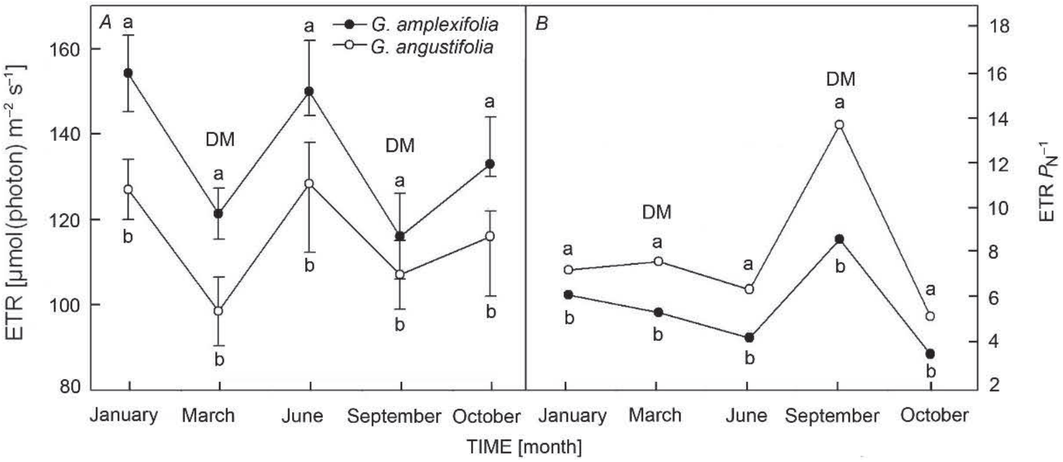

Fig. 7. Mean maximum electron transport rate (ETR) and number of electrons consumed per molecule of CO_2 fixed (ETR/P_N) in *Guadua amplexifolia* and *G. angustifolia* during wet and dry months. The mean highest ETR measured in daily courses (*A*). The mean highest ETR/P_N values were determined at 09:15 h, when P_N reached maximum values (*B*). *Different lowercase letters* represent significant differences ($p<0.05$).

establishment phase. Average TH (2.65 ± 0.4 m *vs.* 2.43 ± 0.13 m, respectively) and DBC (2.34 ± 0.22 cm *vs.* 1.85 ± 0.16 cm, respectively) values measured in *Guadua amplexifolia* and *Guadua angustifolia* during the first year are comparable to first-year growth rate values reported by Londoño (1998) for plantations of *G. angustifolia* adjacent to natural *Guadua* stands in Colombia (TH 2.5 m and DBC 0.5 cm) and are also in the range of first-year values reported by Cruz-Ríos (2009) for commercial plantations of *G. angustifolia* in Mexico (DBC 1.8 cm and TH 3.4 m). Given the lack of data regarding first-year growth rates for *G. amplexifolia*, this study may serve as a reference for future studies in this species.

Water relations and leaf gas exchange: Consistently high PPFD increased T_A and evaporative demands during midday, which in turn decreased RH and content of soil water, causing a pronounced drop in Ψ_W in both *G. amplexifolia* and *G. angustifolia*, particularly during dry months (–2.7 and –2.4 MPa, respectively). Significant daily and seasonal drops in Ψ_W have been described in American bamboos growing in seasonally dry lowland tropical forests, such as *Rhipidocladum racemiflorum* (–4.5 MPa, Cochard *et al.* 1994), *Chusquea ramossisima* and *Merostachys claussenii* (–1.9 and –2.2 MPa, respectively, Saha *et al.* 2009), as well as in tropical Asian bamboos such as *Bambusa vulgaris* and *B. multiplex* (–3.0 and –2.4 MPa, respectively, Cao *et al.* 2012). Daily and seasonal variations of Ψ_W values in woody bamboos indicate that they are strongly affected by the availability of soil water during the year (Cochard *et al.* 1994, Saha *et al.* 2009).

Woody bamboos undergo a loss in hydraulic conductivity on a daily basis caused by cavitation induced by high *E*. Predawn positive hydraulic pressures generated by the roots rapidly dissolve emboli and restore xylem conductivity in bamboos (Cochard *et al.* 1994, Saha *et al.* 2009, Cao *et al.* 2012). In *Guadua chacoensis* and *Dendrocalamus giganteus*, daily cavitation processes induced by high *E* during the morning hours may limit photosynthetic activity as much as 80% during the remaining hours of irradiance (Cao *et al.* 2012).

Both *Guadua amplexifolia* and *G. angustifolia* maintained higher mean P_N during their first year in open field plantations [7–18 μmol(CO_2) $m^{-2}s^{-1}$] compared to other native Venezuelan bamboos, such as *Chusquea* growing in its natural habitat [4.5–8.7 μmol(CO_2) m^{-2} s^{-1}, Ely *et al.* 2011]. Higher P_N in *G. amplexifolia* compared to *G. angustifolia* in the first year during wet seasons [16.57 ± 1.40 and 13.68 ± 2.40 μmol(CO_2) m^{-2} s^{-1}, respectively] and dry ones [12.19 ± 2.82 and 8.12 ± 1.81 μmol(CO_2) m^{-2} s^{-1}, respectively], suggest a higher photosynthetic efficiency in *G. amplexifolia* under conditions of environmental stress. P_N measured during this study in *G. amplexifolia* and *G. angustifolia* were in the range of values reported for commercial Asian bamboos cultivated in temperate climates, such as *Phyllostachys* and *Bambusa* (Gratani *et al.* 2008, Cao *et al.* 2012, Van Goethem *et al.* 2014) and for mature stands of *G. amplexifolia* cultivated in China (Ma and Chen 2013).

In both temperate and tropical bamboos, the highest *E* occurs usually during hours of maximum P_N (8:00–11:00 h) (Cao *et al.* 2012, Ma and Chen 2013, Van Goethem *et al.* 2013) and a similar tendency was observed during this study in *G. amplexifolia* and *G. angustifolia*. Diurnal midday decreases in P_N and g_s observed in these species have also been observed in Asian bamboos growing tropical and subtropical climates, such as *Bambusa*, *Dendrocalamus*, *Gigantochloa*, and *Phyllostachys* (Qiu *et al.* 1992, Koyama and Uchimura 1995, Ishizuka and Puangchit 2000), and more recently in stands of *G. amplexifolia* cultivated in China (Ma and Chen 2013). The midday decrease in P_N and *E* due to stomatal closure in bamboos appears to be more common in bamboos of tropical and subtropical climates, since it has not yet been reported in species of Asian bamboos of the genera *Bambusa* and *Phyllostachys* cultivated in temperate climates, where seasonal variations in P_N and g_s are more related to their susceptibility to low temperatures (Gratani *et al.* 2008, Wen *et al.* 2011, Van Goethem *et al.* 2013). The recovery of P_N, g_s, and *E* observed in *G. amplexifolia* and *G. angustifolia* after the second dry period (12 weeks), contrasted with the slow response of both species after the first dry period (5 weeks), particularly in the case of *G. angustifolia.* It is possible that the marked recovery in P_N observed in both species after the second dry season could be related to the progressive development of culms and rhizomes, which in both cases, serve as water storing organs. As a result of its capacity of maintaining higher P_N, *G. amplexifolia* also presented higher WUE compared to *G. angustifolia* during the wet seasons and the first dry period. *G amplexifolia* exhibited a more efficient WUE mechanism, which allowed to be potentially more successful than that of *G. angustifolia* in the region where the study was carried out.

Although this study did not include a comparative ecophysiological response to varying dosages of fertilizers, the addition of commercial fertilizers with a high content of N during the beginning of the wet seasons could have contributed to ameliorate stress induced by high temperature and water deficit, favoring P_N (Xu *et al.* 2008, Hu *et al.* 2010, Wu *et al.* 2013). Future studies involving comparative fertilization dosages are advisable in order to determine optimum dosages for *Guadua* plantations in regions with conditions such as the ones described in the study.

Chl *a* fluorescence: F_v/F_m values recorded for *G. amplexifolia* and *G. angustifolia* in their first year during wet and dry seasons suggest that neither high temperature nor seasonal droughts induced chronic photoinhibition. This premise is supported by the fact that throughout wet and dry seasons, F_v/F_m did not vary significantly in these species. F_v/F_m and Φ_{PSII} values measured in *G. amplexifolia* and *G. angustifolia* in this study were in the same range of values reported by Kumar *et al.* (2002) for *G. angustifolia* cultivated in India. Nevertheless, it is important to recall that both F_V/F_m and Φ_{PSII} may remain stable under conditions of moderate drought and high temperatures (Baker and Rosenquivst 2004, Hu *et al.* 2010), unlike other Chl *a* fluorescence parameters, such as q_P, q_N, and ETR. In combination with leaf gas-exchange parameters, q_P, q_N, and ETR reveal early changes in PSII photochemistry due to environmental stress (Ashraf and Harris 2013). This was corroborated by a decrease of ETR during dry periods, accompanied by an increase in the relation of ETR/P_N and lower P_N.

The decrease in q_P, which coincided with the increase of q_N observed in both species during hours of maximum PPFD, suggest photoprotective mechanisms of thermal dissipation, particularly in *G. angustifolia.* Photorespiration and generation of reactive oxygen species (ROS) are also likely providing alternative sinks for the high rate of electrons produced under conditions of elevated PPFD, high air temperature, and water deficiency (Wahid *et al.* 2007, Lawlor and Tezara 2009, Ashraf and Harris 2013). Under conditions of moderate to severe water deficit and low internal CO_2 concentrations, the flow of electrons through PSII diminishes due to downregulation in the electron transport between PSII and PSI. Parallel to this downregulation, nonphotochemical quenching increases, reducing pressure on PSII (Golding and Johnson 2003). During this study, ETR/P_N reached the highest values in *G. amplexifolia* and *G. angustifolia* during the dry months, especially by the end of the second dry period, suggesting that as stress-induced metabolic and stomatal limitations increased, nonphotochemical processes, including thermal dissipation increased (Tezara *et al.* 1999, Chaves *et al.* 2002, Flexas *et al.* 2004, Lawlor and Tezara 2009, Hu *et al.* 2010). The differences observed in PSII photochemistry during both wet and dry months indicate a higher photosynthetic efficiency in *G. amplexifolia* compared to *G. angustifolia*.

The CO_2 assimilation rates and photochemistry of PSII observed during this study in juvenile clones of *G. amplexifolia* and *G. angustifolia* suggest that in both cases they could be adequate candidates for commercial plantations as timber substitutes in lowland tropical ecosystems with similar environmental conditions. Both species seemed to tolerate seasonal droughts as long as 12 weeks during their juvenile phase, without suffering from damages of the photosynthetic complex, since they maintained positive CO_2 assimilation rates during dry months and regained maximum rates during the wet seasons. We also concluded that *G. amplexifolia* responded better to environmental stresses, such as high daily radiation, elevated air temperature, and seasonal droughts, which could explain its broader distribution in tropical and subtropical environments compared to *G. angustifolia* (Londoño 1998, Montiel and Sánchez 2006, Clark and Ely 2011). The results of this study suggest that both *G. amplexifolia* and *G. angustifolia* can be used in commercial plantations, with an adequate management involving periodic fertilizations and weed control. *G. angustifolia* may also be cultivated in regions with air temperatures superior to the optimal temperatures of natural *G. angustifolia* forests in Colombia (Londoño 1998, Londoño *et al.* 1999).

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