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Survival, growth and photosynthesis analysis of native forest species established in the tropical dry forest in Antioquia, Colombia

Análisis de supervivencia, crecimiento y fotosíntesis de especies forestales nativas en el bosque seco tropical en Antioquia, Colombia

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ABSTRACT

Keywords:
Cedrella odorata L
Efficient light use
Efficient water use
Ochroma pyramidale (Cav. Ex Lam.)
Pachira quinata Jacq

The tropical dry forest (TDF) is one of the most affected ecosystems by anthropic activities in the world; so, it is necessary to study the dynamics of its ecosystem in order to restore it. With the aim of determining the survival, development, and photosynthetic behaviors of forest species at a young age, a field study was performed using three species *Cedrela odorata* L. (Spanish cedar), *Pachira quinata* (Jacq.) W.S. Alverson (red ceiba) and *Ochroma pyramidale* (Cav. ex Lam.) Urb. (balsa) species. Field data were collected in different periods whose climatic conditions were: dry period (S.0), first rainy period (Ll.1), first dry period (S.1), second rainy period (Ll. 2), and second dry period (S.2). The total height (H) and the root collar diameter (RCD) were measured repeatedly, and two harvests were made to measure dry weight. Besides, photosynthetic performance and its effect on the species development species during three contrasting rainfall periods was evaluated by measuring photosynthetically active radiation (PAR), stomatal conductance (g_s), intercellular carbon (C_{int}), net photosynthesis (NP), transpiration (t_{rans}), efficient water use (EWU) and efficient light use (ELU) from 8:00 and 17:00 h during the day. Analysis of variance was performed obtaining significant differences ($P<0.05$) in the interaction time×species regarding variables H and RCD, and the photosynthetic variable NP. The g_s and t_{rans} variables showed statistical significance with the species and rainfall periods; C_{int} was significant only for the rainfall periods. The species *O. pyramidale* presented the best survival and tolerance to weather by adapting physiological mechanisms, while *C. odorata* was the most affected species by climatic conditions concerning overall survival.

RESUMEN

Palabras clave:
Cedrella odorata L
Uso eficiente de la luz
Uso eficiente del agua
Ochroma pyramidale (Cav. Ex Lam.)
Pachira quinata Jacq

El Bosque seco tropical es uno de los ecosistemas más afectados en el mundo por el desarrollo de actividades antrópicas, por lo que es necesario estudiar las dinámicas de su ecosistema con el fin de restaurarlo. Con el objetivo de determinar la supervivencia, desarrollo y comportamiento fotosintético de las especies forestales en edades tempranas, se realizó un estudio de campo con tres especies: *Cedrela odorata* L. (cedro rojo), *Pachira quinata* (Jacq.) W.S. Alverson (ceiba tolúa) y *Ochroma pyramidale* (Cav. ex Lam.) Urb. (balso). Los datos de campo fueron recolectados en diferentes períodos, cuyas condiciones climáticas fueron: período seco (S.0), primer período lluvioso (Ll.1), primer período seco (S.1), segundo período lluvioso (Ll.2) y segundo período seco (S.2). Se midió la altura total (H) y el diámetro en la base (RCD), y se realizó dos cosechas para medir el peso seco. Además, se evaluó el funcionamiento fotosintético y su efecto en el desarrollo de las especies en tres periodos pluviométricos contrastantes midiendo la radiación fotosintéticamente activa (PAR), conductancia estomática (g_s), carbono intercelular (C_{int}), fotosíntesis neta (PN), transpiración (t_{rans}), uso eficiente del agua (EWU) y uso eficiente de la luz (ELU) entre las 8:00 y 17:00 h del día. Así mismo, se realizaron dos cosechas, para la medición del peso seco. Se realizó un análisis de varianza, encontrando diferencias significativas ($P<0.05$) en la interacción en H y RCD, y en la variable fotosintética PN. Las variables g_s y t_{rans} mostraron significancia estadística con las especies y los periodos pluviométricos; C_{int} fue significativa sólo en los periodos pluviométricos. *O. pyramidale* fue la especies que mayor supervivencia presentó y toleró las condiciones climáticas desarrollando mecanismos fisiológicos, mientras que *C. odorata* fue la especies más afectada en términos de supervivencia por las condiciones climáticas.

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The dry tropical forest (TDF) consists of continuous forest cover and is found in regions with an average annual temperature higher than 27 °C and average annual precipitation of 1058 mm (Stoner and Sánchez-Azofeifa, 2009). The dry tropical forest is one of the ecosystems most threatened by anthropic activities because its soils are fertile and well-suited for agriculture (Calvo-Alvarado *et al*., 2009; Quesada *et al*., 2009). It is estimated that 48.5% of the world's TDF have been used for different purposes than its conservation (Portillo-Quintero and Sánchez-Azofeifa, 2010). These disturbances have given rise to plant distinct covers from those naturally found in TDF because natural regeneration processes do not ensure a return to the original state (Griscom and Ashtom, 2011). Nearly 1,000,000 km^2 of the world's remaining TDF is threatened by the expansion of human populations, habitat fragmentation, and climate change, and just 30% of TDFs are protected under conservation regimes (Fajardo *et al*., 2013). Besides, 350 million ha have been deforested, and another 500 million ha of primary and secondary forest has been degraded (Lamb *et al*., 2005). Restoration and replanting native species are strategies that can guarantee the continued provision of environmental goods and services, in addition to protecting and recovering native flora (Bastien-Henri *et al.*, 2010). These strategies have produced positive results, including the recovery of soils and nutrients and the establishment of plant cover and water balance in degraded areas (dos Santos *et al*., 2006).

Nevertheless, one of the metrics governing whether a plantation or reforestation program is successful is the survival of plants species and its growth and development time because these characteristics depend mainly on the source of seeds, the environmental requirements, and microclimatic conditions (Allen *et al*., 2010). The establishment of species and provenance trials has become a forestry tool that enables the development of programs aimed at genetic improvement for the propagation of species at determined sites, ensuring the quality of the conservation effort. At the same time, these trials provide information about species potential for use in the plant recovery of degraded areas.

Various experiments involving native species in tropical countries have been performed, and interest in this subject has grown due to the lack of information about which species will contribute most to the success of reforestation and restoration programs (Niinemets and Valladares, 2006). Despite the wide diversity of species found in tropical forests, commercial reforestation programs most commonly utilize exotic species. The most frequently used genera in the tropical Americas are *Tectona*, *Eucalyptus*, *Pinus*, and *Acacia* (Bastien-Henri *et al*., 2010; van Breugel *et al*., 2011). This common practice is because there is a risk to utilize new species when little is known about its management or its growth and survival rate under natural conditions (dos Santos *et al*., 2006).

Species such as *Cedrela odorata, Pachira quinata*, and *Ochroma pyramidale*, which are native to the tropical Americas, are known for their high commercial value. However, little information is available regarding their development and adaptation to the climatic conditions of TDF, where seasonal variations are marked by intense dry periods alternated with rainy periods, the latter of which is decisive for the growth, phenology and photosynthetic response of the plants in TDF (Eamus, 1999).

Microclimatic factors such as temperature, water availability, and relative humidity can generate stress for plants that directly impacts their physiological and photosynthetic development (Marenco *et al*., 2003; Briceño, 2017). For this reason, plants have developed diverse adaptation strategies; the results of which are manifested in growth, reproduction, survival, abundance, and geographical distribution (Cai *et al*., 2009; Araque *et al*., 2009; Esmail and Oelbermann, 2011).

With the progressive disappearance of TDF at a global level, it is necessary to obtain a better understanding of the effects of extreme climatic factors on the early establishment of native forest species and to identify the ecological requirements of these plants (Stoner and Sánchez-Azofeifa, 2009). The objective of the study was to advance the monitoring of three species in their survival, dasometric parameters, and gaseous exchange of foliage in TDF conditions in contrasting rainfall periods.

MATERIALS AND METHODS

Study area

This research was performed as part of the forest species test carried out in the project "*Study of the recovery of degraded areas in the dry tropical forest, Olaya municipality.*" Founded by the Inter-administrative

Agreement 8787 of 2010, which included the Universidad Nacional de Colombia-Sede Medellín and the Corporación Autónoma Regional de Antioquia (Corantioquia). The study was developed at the Tribio Mamey ranch located in the Sucre township, Olaya municipality, Antioquia department (6°35´33.72”N, 75°47´33.70”W) (Colombian Andean region), between 540 and 680 m of altitude. The Sucre township registers an average annual rainfall of 1058 mm and an average temperature of 27.1 °C (registering minimum temperatures of 21 °C and maximum temperatures of 40.5 °C) which places it in the dry tropical forest life zone.

During the first half of the year, rainfall occurs in April and May, with the highest amount registered in April, and temperatures reaching 37 °C. The second rainy period occurs in September and October, with the highest levels of precipitation in October. The periods with dry tendencies in the first half of the year occur during January and February, which register the highest temperatures of the year (38 °C); in the second half of the year, the dry periods occur in June and July, with temperatures between 37 and 38 °C. In December, rainfall decreases, and the temperature begins to rise (IDEAM, 2013).

Species, characteristics of the plots and evaluated variables

Between March 2011 and February 2013, the inter-administrative study was carried out with 11 native species of the TDF (Table 1), in an area of 23.66 ha. From this species, *P. quinata, C. odorata*, and *O. pyramidale* were selected because they have a high potential to be used in reforestation and restoration processes, which were followed up on their gas exchange and dasometric characteristics**.** Each species was planted over an area of one hectare distributed randomly in four complete blocks of 2,500 m^2 at a planting density of 3×3 m (i.e., 1,100 tree ha^{-1}). At the beginning of the study, the land was cleared manually with a machete, and the trees and shrubs growing as a part of natural regeneration processes were left intact. A maintenance procedure consisting of clearing one-meter radius around each plant with a machete was performed every six months. A circular plot of 250 m^2 was established in the center of each block with an average of 28 specimens per plot; each specimen was identified and labeled. *C. odorata* seeds were provided by Corantioquia and were originally obtained in the Andean region of Colombia, while Balsur and Monterrey Forestal Ltda. companies provided the *O. pyramidale* and *P. quinata* seeds, respectively. Both came from Colombia’s Atlantic region. Seed handling and the chosen pretreatments for optimal germination were based on standard recommendations for these species.

Table 1. Species used in the study Inter-Administrative Agreement 8787 of 2010[1].

Species		Family
Common name	**Scientific name**	
Yellow cedar	*Albizia guachapele*	Mimosaceae
Sandbox tree	*Hura crepitans*	Euphorbiaceae
Elephant-ear tree	*Enterolobium cyclocarpum*	Mimosaceae
Locust tree	*Hymenaea courbaril*	Caesalpiniaceae
Balsa	*Ochroma pyramidale*	Bombacaceae
Red ceiba	*Pachira quinata/Bombacopsis quinata*	Bombacaceae
Golden trumpet tree	*Tabebuia chrysantha*	Bignoniaceae
Spanish cedar	*Cedrela odorata*	Meliaceae
Coffeewood	*Caesalpinia ebano*	Caesalpiniaceae
Flamboyant	*Delonix regia*	Caesalpiniaceae
Gumbo limbo	*Bursera simaruba*	Burseraceae

[1] Technical report from the study project for the recovery of degraded areas in the dry tropical forest, Olaya municipality. Universidad Nacional de Colombia Sede Medellín and Autonomous Regional Corporation of Antioquia (2012).

Data were collected in the following periods, whose climatic conditions were: dry period S.0 (Marzo 2011), rainy period Ll.1 (Apri-May 2012), dry period S.1 (June-September 2012), rainy period Ll.2 (October-November 2012) and dry period S.2 (January-February 2013). The last period was not considered in the analysis of photosynthesis data due to the defoliation of the *C. odorata* and *P. quinata* species. During each of these periods, the species was 13 (Ll.1), 17 (S.1), 21 (Ll.2) and 23 (S.2) months old; where the total height (H) and the root collar diameter (RCD) were measured, repeatedly. A count of standing specimens was taken during each round of data collection to perform a survival analysis, and the percentage of survival for each rainfall period was determined (Ll.1, S.1, Ll.2, and S.2).

The following photosynthetic variables: photosynthetically active radiation, PAR (µmol m^{-2} s^{-1}), stomatal conductance, g_s (mmol m^{-2} s^{-1}), intercellular carbon, C_{int}, net photosynthesis, NP (µmol m^{-2} s^{-1}), and transpiration, t_{rans} (mmol m^{-2} s^{-1}), were measured simultaneously between 8:00 and 17:00 h (Ellis *et al*., 2000; Krause *et al*., 2001; Marenco *et al*., 2003; Juhrbandt *et al*., 2004; Araque *et al*., 2009). A healthy mature leaf in the upper third of the canopy was selected for each using an infrared gas analyzer (IRGA, TPS – 2 PPSYSTEMS). Efficient water use (EWU) and efficient light use (ELU) (Larcher, 1995; Lambers *et al*., 2008) were calculated using the equations:

$$EWU=\frac{NP}{trans}\left(\mu molCO_2m^{-2}s^{-1}/mmolH_2Om^{-2}s^{-1}\right) \qquad (1)$$

$$ELU=\frac{NP}{PAR}\left(\mu molCO_2m^{-2}s^{-1}/\mu molphotonsm^{-2}s^{-1}\right) \qquad (2)$$

The total height (H) of each specimen was measured with a tape, measuring from the base of the tree to the terminal bud (in the cases for which this was not possible, height was measured up to the highest leaf) and the root collar diameter (RCD) was measured at the height of 5 cm from the ground.

For the collection of biomass data, two specimens were harvested manually from each plot: one at the beginning of data collection (April-May 2012) and the other at the end (January-February 2013). In the field, the specimens were divided into the stem, leaves, and roots (primary and secondary). The samples were incubated at 60 °C until they reached a constant weight to determine their dry weight (g) in the Ecology Laboratory - Biogeochemical Area of the Faculty of Agricultural Sciences of the Universidad Nacional de Colombia - Sede Medellín.

Statistical design

To determine the behavior of the dasometric and photosynthetic variables between rainfall periods (Ll.1, S.1, and Ll.2) and species, an analysis of variance was performed, adjusting the first-order autoregressive covariance structure (type=arh(1)) through the use of mixed models. In the factorial structure (Time×Treatment). Time represents each of the stages of the bimodal regime in which the measurements were taken, and Treatment represents each of the three species. Significant differences ($P<0.05$) were determined using the Fisher test (Least Significant Difference). The assumption of normality was confirmed using the Kolmogorov-Smirnov test (Pr>D). The statistical program SAS® 9.2 (SAS Institute Inc. 2004) was used.

RESULTS AND DISCUSSION

Survival and growth of the species in TDF climate conditions

During the first rainy period (Ll.1, 13 months old), the three species presented similar averages of survival (94 and 99%), *C. odorata* species registered the lowest values. During the final period, *C. odorata* registered the lowest survival rate (15%), *P. quinata* registered 42%, and *O. pyramidale* registered 55% (Figure 1). After thirteen months, the three species showed similar behaviors in Ll.1 with high levels of survival. *O. pyramidale* was the species that shows the highest percentage of survival during periods S.1 and Ll.2, identical to the findings of Craven *et al.* (2007) with the same species in a dry tropical forest. These results also confirm that *O. pyramidale* is species that easily acclimate to weather variation (Oberbauer and Strain, 1984; Kitajima, 1994; Krause *et al*., 2001). Besides, many perennial species growing in dry climates avoid the effects of drought conditions by developing a deep root system that allows them to capture water in soil zones that are sometimes close to the phreatic stratum (Castellanos and Newton, 2015*)*. Moreover, water deficiency is an important environmental limit that is related to the physiological processes involved in the growth and development of plants. It influences a set of responses to the sequence

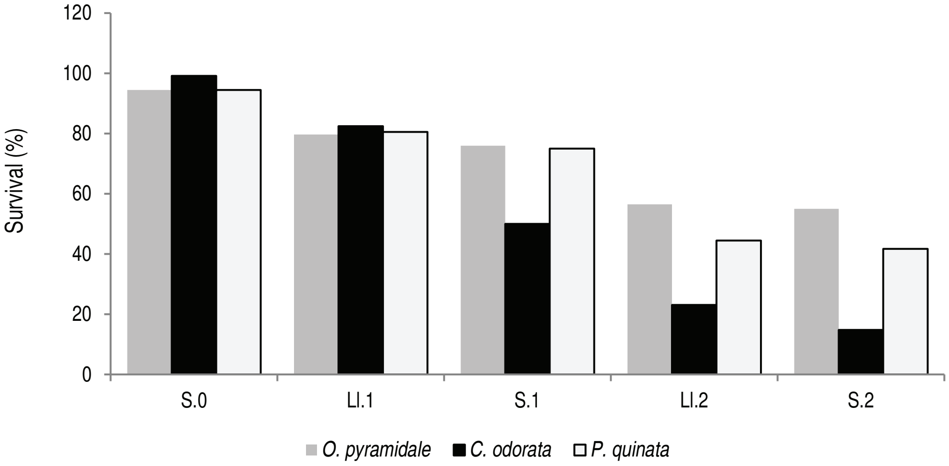

Figure 1. Survival (%) for three species during rainy period (Ll.1, April-May 2012), dry period (S.1, June-September 2012), rainy period (Ll.2, October-November 2012) and dry period (S.2, January-February 2013).

that mainly affects the mechanism of gas exchange (Centritto *et al.*, 2009).

There were significant differences in the interaction time×species in height ($P<0.0002$) and diameter ($P<0.0003$). The species that registered the greatest height was *O. pyramidale*, which reached 180 cm during the final period (S.2), followed by *P. quinata* at 68.55 cm and *C. odorata* at 50.74 cm. Regarding diameter, at 23 months after planting (S.2), *O. pyramidale* had the greatest diameter of 3.43 cm, while *P. quinata* registered a diameter of 1.43 cm and *C. odorata* of 1.01 cm.

The accumulation of total biomass of the species under study was 1,787.87 g in *O. pyramidale*, 795.61 g for *P. quinata*, while *C. odorata* had a biomass of 222.60 g (Table 2).

O. pyramidale also presented greater growth both in diameter and in height, supporting the findings of Wishnie *et al.* (2007) in the dry zones of Panama, where they reported higher annual growth in height and diameter for *O. pyramidale* than for *C. odorata* and *P. quinata*. Similarly, during the Ll.1 rainy period, this species registered greater leaf production, which agrees with the findings of dos Santos *et al.* (2006), who reported that in conditions of high solar radiation, some species make optimal use of light energy, transforming it into ATP to increase their biomass.

Site conditions had a greater influence on the survival of *C. odorata*, and confirm the reported by Gerhardt (1998) because, under dry conditions with a controlled supply of water, this species increases its survival in the field. *C. odorata* also displayed low levels of survival in plantation trials performed on Ecuadorian pastureland, Davidson *et al.* (1998) reported low survival rates for *C. odorata* (less than 50%) in the dry zones; however, with water supply, the death of the species notably decreased. Similarly, Esmail and Oelberman (2011) reported that *C. odorata* seedlings that were constantly irrigated when exposed to high-temperature conditions (34 °C) exhibited an improvement in growth response regarding height and biomass.

Between the three species, it was observed that *C. odorata* showed total defoliation during the dry periods, in addition to low foliar mass production during the rainy periods. As a result, their accumulated total biomass was low during the study period. This behavior happens because the decrease in the foliar area is one of the strategies employed by plants to counteract the stress caused by a lack of water (Lambers *et al.*, 2008). Along these lines, in Panama, Craven *et al.* (2007) found that species such as *C. odorata* maintained low leaf area and growth levels, leading to the conclusion that these plants invested more energy into withstanding stressful conditions than into accumulating biomass.

Table 2. Height, diameter and biomass of the three species during S.0 dry period (March 2011), rainy period (Ll.1, April-May 2012), dry period (S.1, June-September 2012), rainy period (Ll.2, October-November 2012) and dry period (S.2, January-February 2013).

Species	**Rainfall period**	**H (cm)**	**RCD (cm)**	**Growth rate**		**Biomass (g)**		
				H (cm month^{-1})	**RCD (cm month^{-1})**	**Root**	**Stem**	**Leaves**
	S.0	45.25 a	1.02 a	-	-	-	-	-
	Ll.1	91.66 b	2.23 b	11.60	0.30	123.22	150.58	246.99
O. pyramidale	S.1	136.75 c	3.01 c	11.27	0.20	-	-	-
	Ll.2	175.08 d	3.47 d	9.58	0.12	-	-	-
	S.2	180.00 e	3.43 d	1.23	-0.01	495.61	579.50	191.97
	S.0	43.16 a	0.64 a	-	-	-	-	-
	Ll.1	46.66 a	1.05 a	0.88	0.10	21.95	22.00	9.67
C. odorata	S.1	49.60 a	1.06 a	0.74	0.00	-	-	-
	Ll.2	50.66 a	0.98 a	0.26	-0.02	-	-	-
	S.2	50.74 a	1.01 a	0.02	0.01	73.10	95.44	0.44
	S.0	38.66 a	0.94 a	-	-	-	-	-
	Ll.1	53.66 a	1.21 a	3.75	0.07	128.93	43.04	35.82
P. quinata	S.1	63.66 a	1.27 ab	2.50	0.02	-	-	-
	Ll.2	60.00 a	1.47 ac	-0.91	0.05	-	-	-
	S.2	68.55 a	1.43 a	2.14	-0.01	268.42	319.40	0

The rows with identical letters indicate no significant differences registered between rainfall periods.
H: total height, RCD: root collar diameter.

P. quinata species has been adapted to weather conditions, and it is resistant to low rainfall rates, which facilitated its establishment in this degraded area. In the dry regions, low mortality values have been reported for *P. quinata* (Hall *et al.*, 2011). At the same time, Kane *et al.* (1993) noted that this species maintains considerable reserves of starch in its root system, which allow it to have a rapid initial growth at the beginning of the rainy season. Consistently, an increase in growth rate was observed during the Ll.1 period. The strategy employed by the plant was the reduction of its leaf biomass during the dry periods to combat hydric stress. According to Eamus (1999), stomatal sensibility in caducipholic plants increases with soil dryness, and a result attributed to the decrease in elasticity of their cell walls that in turn results in a high propensity to the loss of turgidity. *P. quinata* specimens exhibited the greatest diameter, coinciding with the findings of Wishnie *et al.* (2007) in a study of 24 species with restoration potential and commercial value. *P. quinata* is a species that acclimate to conditions of high solar radiation and low humidity (Kane *et al.*, 1993). Although soil fertility was not evaluated in the present research, it could be a factor that impacts its growth (Hall *et al.*, 2011). *O. pyramidale* performed the best in terms of height due to the ease with which it acclimates (Krause *et al.*, 2001). The results obtained are consistent with the findings of Wishnie *et al.* (2007) in Panama in a study of TDF species that also included *C. odorata* and *P. quinata*. These findings also confirm that *O. pyramidale* is a fast-growing species that acclimate well to dry areas.

Photosynthetic behavior of the species studied

It must be considered the importance of the leaves does not exclusively lie in carrying out the photosynthetic process. They are involved in nutrient storage and photoassimilate process, and as sources of nutrients in the processes of metabolic remodeling during organ senescence (Severino and Auld, 2013). In their early stages, the seedlings developed physiological mechanisms that allowed them to increase CO_2 assimilation during the dry period. Water deficiency is an important environmental limitation that affects all the physiological processes involved in the growth and development of plants. It influences a set of responses to the drought that mainly affects the mechanism of gas exchange (Centritto *et al.*, 2009). The stomatal regulation of transpiration and intercellular carbon concentration during dry periods did not decrease the CO_2 assimilation rate; for optimal control of stomata to manage hydraulic risk is likely to have significant consequences for ecosystem fluxes during drought, which is critical given projected intensification of the global hydrological cycle (Anderegg *et al.*, 2018).

The foliage response of these three species had a relationship with the climate. In such a way that stomatal regulation was identified as the rainfall was presented with stomata partially open until almost closed depending on the species. Thus, during the rainy periods, *O. pyramidale* and *C.odorata* showed partially open stomata, regardless of whether they were, although in a different degree of openness. On the contrary, *P.quinata* remained with the stomata partly or almost closed in the two climatic seasons (Table 3).

Table 3. Foliage response to the gaseous exchange of the three species during dry period (S.0, March 2011), rainy period (Ll.1, April-May 2012), dry period (S.1, June-September 2012), rainy period (Ll.2, October-November 2012) and dry period (S.2, January-February 2013).

Rainfall period	Species	Age (month)	PAR (μmol Phot m^{-2} s^{-1})	g_s (mmol H_2O m^{-2} s^{-1})	NP (μmol CO_2 m^{-2} s^{-1})	C_{int}	t_{rans} (mmol H_2O m^{-2} s$^{-1)}$	EWU (μmol CO_2 mmol^{-1} H_2O)
Ll.1		13	1,150.90 a	281.89 b	11.95 a	304.17	2.38	5.25
S.1	*O. pyramidale*	17	2,168.83 b	54.50 ab	24.34 b	0.10	0.94	14.93
Ll.2		21	682.25 a	25.83 a	7.68 a	71.00	0.29	4.06
Ll.1		13	1,997.33 a	569.58 a	16.83 a	244.00	3.68	4.62
S.1	*C. odorata*	17	1,466.24 ba	35.29 b	11.02 a	34.00	0.98	14.66
Ll.2		21	835.60 b	342.19 a	16.09 a	107.00	2.25	3.29
Ll.1		13	2,401.17 a	59.16 a	12.90 a	147.17	1.99	8.60
S.1	*P. quinata*	17	1,799.25 a	2.16 a	9.96 a	3.60	0.09	10.94
Ll.2		21	580.42 b	1.50 a	11.24 a	31.00	0.068	29.34

The rows with identical letters indicate no significant differences registered between rainfall periods.
PAR: Photosynthetically active radiation, g_s: stomatal conductance, NP: net photosynthesis, C_{int}: intercellular carbon, t_{rans}: transpiration, EWU: efficient water use, ELU: efficient light use.

According to Berry *et al.* (2010), plants with better control of stomatal function are more efficient in the use of water and have more tolerance to the drought. It is indicative that stomatal control is an important adaptive mechanism of tolerance to the drought in this species (dos Santos *et al.*, 2017). The partial closure of the stomata is a known strategy of plant tolerance to water stress since it decreases the rate of transpiration, conserves the water content of the leaves, and reduces the risk of dehydration avoiding death by desiccation (Peak *et al.*, 2004).

The vapor pressure deficit (VPD) is one of the most important environmental factors of stomatal regulation since plants from semi-arid regions showed an inverse correlation between leaf with stomatal conductance, transpiration, and photosynthesis (dos Santos *et al.*, 2017). Likewise, the castor has a high stomatal regulation under field conditions, which can reduce the loss of water by transpiration and maintain the hydric state of the plant (Pinheiro and Chaves, 2011).

The previous response of the species under study represented that *O. pyramidale* exhibited the highest NP in the dry period (24.31 μmol CO_2 m^{-2} s^{-1}), with the lowest average NP in the rainy period (9.81 μmol CO_2 m^{-2} s^{-1}). *C. odorata* expressed the highest average photosynthetic rate (16.43 μmol CO_2 m^{-2} s^{-1}) in rainy periods and intermediate in dry periods (11.02 μmol CO_2 m^{-2} s^{-1}), and *P. quinata* the lowest NP in the two climatic conditions. It can be affirmed that these species are from the group of C_3 plants by considering the photosynthetic rates. According to Ocheltree *et al.* (2014), C_3 plants reduce stomatal conductance to minimize water loss; however, the rate of CO_2 diffusion also decreases, which reduces the internal concentration of CO_2 and the efficiency in carbon fixation by plants (Table 3).

Stomatal regulation of the transpiratory process was observed in these species that are adapted to arid and semi-arid regions, with average rates of 2.96 mmol m^{-2} s^{-1} in the rainy period and 0.98 mmol m^{-2} s^{-1} in the dry period for *C. odorata*; 1.33 and 0.94 mmol m^{-2} s^{-1} in *O. pyramidale* and in *P. quinata* 1.03 and 0.09 mmol m^{-2} s^{-1} during the same climatic periods. It led to divergences between the species studied since *P. quinata* expressed average EWU values of 12.64 μmol CO_2 $mmol^{-1}$ H_2O in the rainy season, but in the dry period, it was 10.94 μmol CO_2 $mmol^{-1}$ H_2O. On the other hand, both *O. pyramidale* and *C. odorata* were around 3.00 and 14.00 μmol CO_2 $mmol^{-1}$ H_2O in the rainy and dry periods respectively.

In different species, including soybean, it has been found that the reduction in g_s increases the intrinsic efficiency of water use, especially with little availability of water in the soil (Gilbert *et al.*, 2011). Barros Junior *et al.* (2008) found that the castor, under drought stress, showed a high efficiency in the use of water, which helped maintain the production of biomass.

The reduction in stomatal conductance has been correlated with an increase in the intrinsic efficiency of water use, which indicates that the closure of stomata contributes to optimizing the efficiency of water use in plants under stress. It allows plants to absorb carbon by decreasing the loss of water in the hottest part of the day, contributing to the maintenance of photosynthesis (Broeckx *et al*., 2014). It can be considered that EWU is a preventive mechanism, as an immediate effect of water deficiency. Besides, from the physiological point of view, the high value of EWU is traditionally considered as a mechanism that provides greater productivity and survival in dry environments (Centritto *et al*., 2009; Gilbert *et al*., 2011).

Under conditions of water stress, the castor plant maintains an effective stomatal regulation with a high net CO_2 fixation (Severino *et al*., 2012); with a decrease in perspiration due to rapid stomatal closure, without damage to the photosynthetic apparatus because the deficiencies in the fixation and capture of C are due to the diffusive resistances (Sausen and Rosa, 2010). For this property, they can partially recover the functioning of the photosynthetic apparatus, while remaining in stress; but, when this is eliminated, the plants recover their photosynthetic function in 24 h (Severino *et al*., 2012). Consequently, they tolerate drought stress quite well; they become a viable crop for arid and semi-arid regions where there are few effective agricultural alternatives (Sausen and Rosa, 2010).

However, this research information is scarce in field conditions to better understand the physiological mechanisms and their interactions with climatic factors under drought (dos Santos *et al*., 2017). Finally, Anderegg *et al.* (2018) found that the stomatal response to environmental conditions forms the backbone of all ecosystem models and carbon cycles; but relies heavily on empirical relationships. Evolutionary theories of stomatal behavior are critical to protecting against prediction errors of empirical models in future climates. A longstanding theory holds that stomata maximize the ability to maintain a constant marginal efficient water use over a given time horizon. However, a recent evolutionary theory proposes that stomata instead of maximizing carbon gain reduce carbon costs/risk of hydraulic damage. Anderegg's *et al.* (2018) findings focus on the constant known as “marginal efficiency of water use” when it is not the quantity of water that governs the evolution of stomatal regulation, but the stomatal regulation is maximized with the carbon gain while maintaining the hydraulic function.

CONCLUSIONS

There were significant differences in the interaction time×species regarding height (*P*<0.0002) and diameter (*P*<0.0003), the highest was *O. pyramidale,* followed by *P. quinata* and *C. odorata*. In regard to diameter, *O. pyramidale* had the greatest diameter after 23 months (S.2) and biomass accumulation, followed by *P. quinata* and *C. odorata*.

Foliage response of these three species had a relationship with weather conditions, during the rainy periods *O. pyramidale* and *C.odorata* showed partially open stomata regardless of whether they were. Besides, *P.quinata* remained with the stomata partly or almost closed in the two climatic seasons.

The behavior of the stomatal regulation was detected in species adapted to arid and semi-arid conditions, in such a way, the intensity of the photosynthetic and transpiratory rates and the efficient water use were expressed according to the genotype×environment interaction. However, it would be interesting to auscultate and use the EWU to identify the stomatal regulation with the carbon cost/risk of hydraulic damage.

REFERENCES

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A and Cobb N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259(4): 660–684. doi: 10.1016/j.foreco.2009.09.001

Anderegg WRL, Wolf A, Arango A, Choat B, Chmura DJ, Jansen S, Kolb T, Li S, Meinzer FC, Pita P, Resco de Dios V, Sperry JS, Wolfe BT and Palaca S. 2018. Woody plants optimise stomatal behaviour relative tohydraulic risk. Ecology Letters 21(7): 968–977. doi: 10.1111/ele.12962

Araque O, Jaimez RE, Azócar C, Espinoza W and Tezara W. 2009. Relaciones entre anatomía foliar, intercambio de gases y crecimiento en juveniles de cuatro especies forestales. Interciencia 34(10): 725-729

Barros Junior G, Guerra HOC, Cavalcanti MLF and de Lacerda RD. 2008. Consumo de água e eficiência do uso para duas cultivares de mamona submetidas a estresse hídrico. Revista Brasileira de Engenharia Agrícola e Ambiental 12(4) 350-355. doi: 10.1590/S1415-43662008000400003

Bastien-Henri S, Park A, Ashton M and Messier C. 2010. Biomass distribution among tropical tree species grown under differing regional climates. Forest Ecology and Management 260(3): 403-410. doi: 10.1016/j.foreco.2010.04.035

Berry JA, Beerling DJ and Franks PJ. 2010. Stomata: key players in the earth system, past and present. Current Opinion in Plant Biology 13(3): 232-239. doi: 10.1016/j.pbi.2010.04.013

Briceño A. 2017. Dinámica del crecimiento y relación con el clima de especies arbóreas de los bosques de la región Caribe, Colombia. Ph.D's Thesis in Science. Biology. Sciences Faculty. Universidad Nacional de Colombia. Bogotá. 157 p.

Broeckx LS, Fichot R, Verlinden MS and Ceulemans R. 2014. Seasonal variations in photosynthesis, intrinsic water-use efficiency and stable isotope composition of poplar leaves in a short-rotation plantation. Tree Physiology 34 (7): 701-715. doi: 10.1093/treephys/tpu057

Cai ZQ, Wang WH, Yang J and Cai CT. 2009. Growth, photosynthesis and root reserpine concentrations of two *Rauvolfia* species in response to a light gradient. Industrial Crops and Productos. 30(2): 220-226. doi: 10.1016/j.indcrop.2009.03.010

Calvo J, McLennan B, Sanchez A and Garvin T. 2009. Deforestation and forest restoration in Guanacaste, Costa Rica: Putting conservation policies in context. Forest Ecology and Management 258 (6): 931-940. doi: 10.1016/j.foreco.2008.10.035

Castellanos C and Newton AC. 2015. Grupos funcionales y variación en rasgos foliares y de tallo de 113 especies leñosas en un bosque seco tropical species . Colombia Forestal 18(1): 117-138. doi: 10.14483/udistrital.jour.colomb.for.2015.1.a07

Centritto M, Lauteri MC, Monteverdi MC and Serraj R. 2009. Leaf gas exchange, carbon isotope discrimination, and grain yield in contrasting rice genotypes subjected to water deficits during the reproductive stage. Journal of Experimental Botany 60(8): 2325-2339. doi: 10.1093/jxb/erp123

Craven D, Braden D, Ashton MS, Berlyn GP, Wishnie M and Dent D. 2007. Between and within-site comparisons of structural and physiological characteristics and foliar nutrient content of 14 tree species at a wet, fertile site and a dry, infertile site in Panama. Forest Ecology and Management 238(1-3): 335-346. doi: 10.1016/j.foreco.2006.10.030

Davidson R, Gagnon D, Mauffette Y and Hernandez H. 1998. Early survival, growth and foliar nutrients in native Ecuadorian trees planted on degraded volcanic soil. Forest Ecology and Management. 105(1-3): 1-19. doi: 10.1016/S0378-1127(97)00295-8.

dos Santos UM, de Carvalho JF and Feldpausch TR. 2006. Growth, leaf nutrient concentration and photosynthetic nutrient use efficiency in tropical tree species planted in degraded areas in central Amazonia. Forest Ecology and Management 226(1-3): 299-309. doi: 10.1016/j.foreco.2006.01.042

dos Santos CM, Endres L, Ferreira VM, Silva JV, Rolim EV and Wanderley HCL. 2017. Photosynthetic capacity and water use efficiency *in Ricinus communis* (L.) under drought stress in semi-humid and semi-arid areas. Anais da Academia Brasileira de Ciências 89(4) 3015-3029. doi: 10.1590/0001-3765201720160729.

Eamus D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. Trends in Ecology & Evolution 14 (1): 11-16. doi: 10.1016/S0169-5347(98)01532-8

Ellis A, Hubbell S and Potvin C. 2000. *In situ* field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. Canadian Journal of Botany 78 (10): 1336-1347. doi: 10.1139/b00-095

Esmail S and Oelbermann M. 2011. The impact of climate change on the growth of tropical agroforestry tree seedlings. Agroforest Systems 83(2): 235-244. doi: 10.1007/s10457-011-9424-1

Fajardo L, Rodríguez JP, González V and Briceño JM. 2013. Restoration of a degraded tropical dry forest in Macanao, Venezuela. Journal of Arid Environments (88): 236-243. doi: 10.1016/j.jaridenv.2012.08.009.

Gerhardt K. 1998. Leaf defoliation of tropical dry forest tree seedlings – implications for survival and growth. Trees 13(2): 88-95. doi: 10.1007/PL00009741

Gilbert ME, Zwieniecki MA and Holbrook NM. 2011. Independent variation in photosynthetic capacity and stomatal conductance leads to differences in intrinsic water use efficiency in 11 soybean genotypes before and during mild drought. Journal of Experimental Botany 62(8): 2875-2887. doi: 10.1093/jxb/erq461.

Griscom HP and Ashton MS. 2011. Restoration of dry tropical forests in Central America: A review of pattern and process. Forest Ecology and Management 261(10): 1564-1579. doi: 10.1016/j.foreco.2010.08.027

Hall JS, Ashton MS, Garen EJ and Shibu J. 2011. The ecology and ecosystem services of native trees: Implications for reforestation and land restoration in Mesoamerica. Forest Ecology and Management 261(10): 1553-1557. doi: 10.1016/j.foreco.2010.12.011

IDEAM. 2013. Boletín informativo sobre el monitoreo de los fenómenos de “el niño” y “la niña” 2013. In: Instituto de Hidrología, Meteorología y Estudios Ambientales, p.; accessed: May, 2013.

Juhrbandt J, Leuschner C and Hölscher D. 2004. The relationship between maximal stomatal conductance and leaf traits in eight Southeast Asian early successional tree species. Forest Ecology and Management 202(1-3): 245-256. doi: 10.1016/j.foreco.2004.07.021

Kane M, Urueña H, Dvorak W and Atehortua C. 1993. The potential of *Bombacopsis quinata* as a commercial plantation species. Forest Ecology and Management 56(1-4): 99-112. doi: 10.1016/0378-1127(93)90106-W

Kitajima K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98(3): 419-428. doi: 10.1007/BF00324232

Krause GH, Koroleva OY, Dalling JW and Winter K. 2001. Acclimation of tropical tree seedlings to excessive light in simulated tree-fall gaps. Plant, Cell & Environment 24(12): 1345-1352. doi: 10.1046/j.0016-8025.2001.00786.x

Lamb D, Erskine PD and Parrotta JA. 2005. Restoration of degraded tropical forest landscapes. Science 310(5754): 1628-1632. doi: 10.1126/science.1111773

Lambers H, Chapin III FS and Pons TL. 2008. Plant Physiological Ecology. Second Edition. Springer Science+Business Media, New York. 604 p.

Larcher W. 1995. Physiological Plant Ecology: Ecophysiology and stress physiology of functional groups. Third Edition. Springer Science+Business Media, New York. 514 p.

Marenco RA, Vieira G and de Goncalves JF. 2003. Leaf micronutrient concentrations and potential photosynthesis in *Ochroma pyramidale* established in a degraded land. Acta Amazonica, 33(1):23-31. doi: 10.1590/1809-4392200331031.

Niinemets U and Valladares F. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecological Monographs 76(4): 521-547 doi: 10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

Oberbauer SF and Strain BR. 1984. Photosynthesis and successional status of Costa Rican rain forest trees. Photosynthesis Research 5(3): 227-232. doi: 10.1007/BF00030022.

Ocheltree TW, Nippert JB and Prasad PVV. 2014. Stomatal responses to changes in vapor pressure deficit reflect tissue-specific differences in hydraulic conductance. Plant, Cell & Environment 37(1): 132–139. doi: 10.1111/pce.12137

Peak D, West JD, Messinger SM and Mott KA. 2004. Evidence for complex, collective dynamics and emergent, distributed computation in plants. Proceedings of the National Academy of Sciences of the United States of America 101(4) 918-922. doi: 10.1073/pnas.0307811100

Pinheiro C and Chaves MM. 2011. Photosynthesis and drought: can we make metabolic connections from available data. Journal of Experimental Botany 62(3): 869-862. doi: 10.1093/jxb/erq340

Portillo CA and Sánchez GA. 2010. Extent and conservation of tropical dry forests in the Americas. Biological Conservation 143(1): 144-155. doi: 10.1016/j.biocon.2009.09.020

Quesada M, Sanchez A, Alvarez M, Stoner KE, Avila L, Calvo J, Casitllo A, Espíritu MM, Fagundes M, Fernades GW, Gamon J, Lopezaraiza M, Lawrence D, Cerdeira LP, Powers JS, Neves FS, Rosas V, Sayago R and Sanchez G. 2009. Succession and management of tropical dry forests in the Americas: Review and new perspectives. Forest Ecology and Management 258(6): 1014-1024. doi: 10.1016/j.foreco.2009.06.023

Sausen TL and Rosa LMG. 2010. Growth and carbon assimilation limitations in *Ricinus communis* (Euphorbiaceae) under soil water stress conditions. Acta Botánica Brasilica 24(3): 648-654. doi: 10.1590/S0102-33062010000300008

Severino LS, Auld DL, Baldanzi M, Cândido MJD, Chen G, Crosby W, He X, Lakshmamma P, Lavanya C, Machado OL, Mielke T, Milani M, Miller TD, Morris JB, Morse SA, Navas AA, Soares DJ, Sofiatti V, Wang ML, Zanotto MD and Zieler H. 2012. A Review on the Challenges for Increased Production of Castor. Agronomy journal 104(4): 853–880. doi: 10.2134/agronj2011.0210

Severino LS and Auld DL. 2013. A framework for the study of the growth and development of castor plan. Industrial Crops & Products 46: 25-38. doi: 10.1016/j.indcrop.2013.01.006.

Stoner KE and Sánchez GA. 2009. Ecology and regeneration of tropical dry forests in the Americas: Implications for management. Forest Ecology and Management (258): 903-906. doi: 10.1016/j.foreco.2009.05.019

van Breugel M, Hall JS, Craven DJ, Gregoire TG, Park A, Dent DH, Wishnie MH, Mariscal E, Deago J, Ibarra D, Cedeño N and Ashton MS. 2011. Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. Forest Ecology and Management 261(10): 1580-1589. doi: 10.1016/j.foreco.2010.08.019

Wishnie MH, Dent DH, Mariscal E, Deago J, Cedeno N, Ibarra D and Ashton S. 2007. Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the republic of Panama. Forest Ecology and Management 243(1): 39-49. doi: 10.1016/j.foreco.2007.02.001.