Seasonal effects on basal growth and its relationship with wood density in tropical tree species of the Yucatan peninsula, Mexico †

[Efectos estacionales en el crecimiento basal y su relación con la densidad de la madera en especies arbóreas tropicales de la península de Yucatán, México]

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SUMMARY

Background. In seasonally dry tropical forests, water availability determines the growth of plants. Diameter growth rate has a direct relationship with the density and relative water content in the wood and this relationship can be strengthened according to environmental seasonality. **Objective.** To determine the effect of seasonality in diameter growth and its relationship with wood density. **Methods**. The study was conducted at site Forest Reserve El Colegio de la Frontera Sur in Chetumal, Quintana Roo March 2010- March 2011. Diameter growth (DG), wood density (WD) and relative water content in wood (RWC) were determined during one year at two-week intervals. 16 tree species were studied. **Results.** The seasonality in rainfall directly influences the DG, this is corroborated by the high growth rate in the rainy season, plus WD is a determining factor in the growth rate, as it is directly related to RWC and the DG. In the dry season four functional groups were identified. A) soft wood trees with low WD, high RWC and high DG; B) WD trees with high, intermediate RWC and moderate DG; C) trees with high WD, intermediate RWC and slow DG; D) trees with high WD, under RWC without DG. **Implication.** The water availability significantly influences the growth rate and wood density. **Conclusions.** The growth rate is directly related to the WD and the RWC, this in turn is influenced by water availability. This relationship identifies a seasonal response and allows distinguishing functional groups.
Key words: Functional groups; functional traits; water stress; Yucatan Peninsula; dry tropical forests.

RESUMEN

Antecedentes. En los bosques tropicales estacionalmente secos, la disponibilidad de agua determina el crecimiento de las plantas. La tasa de crecimiento del diámetro tiene una relación directa con la densidad y el contenido relativo de agua en la madera y esta relación puede fortalecerse de acuerdo a la estacionalidad. **Objetivo.** Determinar el efecto de la estacionalidad en el crecimiento del diámetro y su relación con la densidad de la madera. **Métodología.** Este estudio se realizó en la Reserva Forestal El Colegio de la Frontera Sur en Chetumal, Quintana Roo marzo 2010- marzo 2011. Se determinó el crecimiento diamétrico (DG), densidad de la madera (WD) y contenido relativo de agua en la madera (RWC) durante un año en intervalos de dos semanas, en 16 especies arbóreas. **Resultados.** La estacionalidad de las precipitaciones influye directamente en el DG, esto se corrobora por la alta tasa de crecimiento en la estación lluviosa, además WD es un factor determinante en la tasa de crecimiento, ya que está directamente relacionada con el RWA y

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el DG. En la estación seca se identificaron cuatro grupos funcionales. A) árboles de madera blanda con baja DW, alta RWC y alto GD; B) árboles con alta WD, intermedia RWC y moderada GD; C) árboles con alta WD, intermedia RWC y lento GD; D) árboles con alta WD, bajo RWC sin GD. **Implicaciones.** La disponibilidad de agua inlfuencia de manera significative la tasa de crecimiento y la densidad de la madera. **Conclusiones.** La tasa de crecimiento está directamente relacionada con la densidad de madera y el contenido relative de agua en la madera, ésta a su vez está influenciada por la disponibilidad de agua. Esta relación identifica una respuesta estacional y permite distinguir grupos funcionales.
Palabras clave: Grupos funcionales; rasgos funcionales; estrés hídrico; Península de Yucatán; Selva tropical seca.

INTRODUCTION

Knowledge of the patterns of diameter growth in trees is necessary for proper forest management. Only with this information is it possible to select species for logging, to estimate cutting cycles, to prescribe silvicultural treatments and to select species for protection (da Silva *et al.* 2002, Grossman *et al.* 2018, García-Cervigón *et al*. 2021, Rosell *et al*. 2022). Particularly in seasonally dry tropical forests, plants undergo the problem of high seasonality in the precipitation (García-Cervigón *et al*. 2020). So that the availability of water in the soil and the loss by transpiration are the main determinants of the water balance in the plants (Stratton *et al.* 2000, Landsberg *et al.* 2017). The increase of the water deficit favors the closure of stomata and decreases the photosynthetic rate causing a reduction in growth (Chaturvedi *et al.* 2011). To survive in these environments, species have generated changes in their morphology and/or physiology (Landsberg *et al.* 2017). One of the main changes is the modification of the structure and composition of the xylem (Hacke *et al*. 2001, Romero *et al.* 2019, García-Cervigón *et al*. 2020, García-Cervigón *et al*. 2021), given its influence on the storage of water in the stem (Borchert and Pockman 2005, Romero *et al.* 2019). It has been found that sapwood contributes up to 50% to stored water (Waring and Running, 1978). The wood density is inversely related with the capacity of the stem to store water (Borchert, 1994), and the wood density determines water content in the xylem, transportation characteristics and plant water relations (Stratton *et al.* 2000, Borchert and Pockman 2005, Wright *et al*. 2021).

The changes of wood density in trees (within the individual) are directly linked to structural variations at a molecular, cell and organ level (Henry *et al.* 2010). Therefore, it influences the response of numerous physiological variables: saturated water content, leaf hydraulic conductivity, leaf water potential, photosynthetic capacity, rates of carbon dioxide interchange and rates of growth (Roderick 2000, Ishida *et al.* 2008, Bucci *et al.* 2009, Valdez-Hernández *et al.* 2010, Wright *et al*. 2021, Rosell *et al*. 2022). In a dry forest of Hawaii, seasonal variations in leaf water balance have been detected, species with higher wood-saturated water content are more efficient in terms of water transport at larger distance (Leaf-specific conductivity) and present less daily variation in leaf water potential and higher rates of photosynthesis (Stratton *et al.* 2000). The photosynthetic rate mainly influences in growth, considering the relationship with functional traits of the leaf like the assimilation rate of CO_2, specific leaf area and stomatal conductance (Chaturvedi *et al.* 2011).

The diameter growth rate shows an integral response of the wood density effect, and this relationship can intensify according to environmental seasonality. Studies carried out in tropical forests have shown that the existence of a positive relation between tree growth and rainy season (Brienen and Zuidema 2005, García-Cervigón *et al*. 2020, García-Cervigón *et al*. 2021), and this relationship intensifies as precipitation and diameter increases (da Silva *et al.* 2002). In addition, growth rates vary at inter- and intra-species levels spatially and seasonally (George *et al.* 2019). In general, species are classified into two large groups according to their growth rate: fast-growing pioneer species or shadow intolerant and slow-growing species or shade tolerant (Baker *et al.* 2003). This behavior is also associated with allocation to tissue density, species that allocate less biomass to stem have lower wood density; so, the increase of basal diameter is faster than in species that allocate more biomass to stem (Enquist *et al.* 1999). In addition, due to the high intra and inter-specific variability in wood density (Zobel and Van Buijtenen 1989, Rosell *et al*. 2022), it is necessary to determine growth patterns in different density groups to understand growth strategies and to manage forests properly.

Trees present a strong relationship between wood density, water content in the stem, the mechanical structure and growth (Enquist *et al.* 1999, Hacke *et al.* 2001, García-Cervigón *et al*. 2020, García-Cervigón *et al*. 2021). Therefore, wood density has been used as a key factor to identify functional groups showing characteristic physiological and phenological patterns (Reich and Borchert 1984, Rivera *et al.* 2002; Borchert and Pockman 2005; Singh and Kushwaha, 2005; Valdez-Hernández *et al.* 2010, Rosell *et al*. 2022). Those functional groups help to predict possible changes in plant communities due to climate change (Box, 1996, Rosell *et al*. 2022). This reduces the need to generate specific information for each taxon, facilitating its study and allowing the prediction of its development (Esquivel-Muelbert *et al.* 2019).

In this study, we aimed at determining the effect of seasonality in diameter growth and its relationship with wood density. Also, we explored the use of wood density as main trait, to identify functional groups in 16 tropical tree species.

MATERIALS AND METHODS

Study area

The study was carried out in the forest reserve of El Colegio de la Frontera Sur (Ecosur), Chetumal (18˚32' N, 88˚15' W). This site has a sub humid warm climate with average temperature of 26.5°C and a mean annual precipitation of 1244 mm. We recorded three seasons: dry (March-May), rainy (June-October) and "nortes" (November-February) which has low temperatures and occasional rainfall (Carrillo *et al.* 2009). Characteristic soils are vertisols, with a high degree of clays, high hydrophily and plasticity in humid state, and very hard in dry state (Tello, 2011). The characteristic vegetation is secondary semi-evergreen tropical forest, and representative species are: *Brosimum alicastrum*, *Bursera simaruba*, *Manilkara zapota*, *Vitex gaumeri*, among others (Ek 2011).

Selected species and individuals

To select the species, we considered their foliar phenological pattern (deciduous and evergreen) and which present a wood density gradient. The 16 tree species were: *Bauhinia divaricata* L., *Diospyros salicifolia* Humb. and Bonpl. ex Willd., *Piscidia piscipula* (L.) Sarg., *Chrysophyllum mexicanum* Brandagee ex Standl, *Cordia dodecandra* DC., *Metopium brownei* Urb., *Guazuma ulmifolia* Lam., *Senna racemosa* (Mill.) H.S. Irwin and Barneby, *Coccoloba spicata* Lundell, *Ehretia tinifolia* L., *Leucaena leucocephala* (Lam.) de Wit, *Bursera simaruba* (L.) Sarg., *Simarouba glauca* DC., *Cecropia peltata* L., *Brosimum alicastrum* Sw., *Talisia oliviformis* Randlk; hereinafter we refer to those species on a genus level. A short description is given in table 1; selected individuals were visibly healthy, without damage at the trunk and canopy and at reproductive age.

Table 1. Description the 16 studied tree species monitored in the ECOSUR forest reserve, Chetumal, in each species the four individuals selected have similar diameter.

	Species	Key	DBH (cm)	Description Flower	Description Fruit	Description leaf
Deciduous species						
Leguminosae	*Bauhinia divaricata*[6,8]	Bd	11	Racemose inflorescence, flowers all year	Flattened pods, fruits all year	Alternate, Bilobed
Burseraceae	*Bursera simaruba*[3,6]	Bs	19	Axillary panicles, monoecious or dioecious, flowers (February-August)	Drupe, mature (May-November)	Compound
Boraginaceae	*Cordia dodecandra*[4]	Cd	11	Axillary panicles, flowers (October-January)	Drupe, flowers (November-March)	Simple, alternate
Sterculiaceae	*Guazuma ulmifolia*[3,5]	Gu	15	Axillary panicles, flowers (April-October)	Capsule	Simple, alternate
Leguminosae	*Leucaena leucocephala*[5,6,8]	Ll	12	In axillary heads, flowers all year	Flattened pods, fruits all year	Alternate, bipinnate
Anacardiaceae	*Metopium brownei*[38]	Mb	19	Inflorescence axillary panicles, flowers almost all year	Drupe, fruits almost all year	Alternate, compound
Leguminosae	*Piscidia piscipula*[4]	Pp	20	Axillary inflorescence, flowers (April-May)	Pods, mature (June-July)	Alternate, compound
Leguminosae	*Senna racemosa*[7,8]	Sr	12	Inflorescence, axillary racemes, flowers almost all year	Pods, fruits almost all year	Compound
Simaroubaceae	*Simarouba glauca*[4]	Sg	22	Inflorescence terminal, dioecious, flowers (February-April)	Drupe, mature (July-August)	Alternate, compound, pinnate
Moraceae	*Cecropia peltata*[5,6]	Cp	22	Spike, dioecious, flowers all year	Achenes	Simple, alternate, peltate
Evergreen species						
Moraceae	*Brosimum alicastrum*[3,5]	Ba	35	In axillary heads, monoecious or dioecious,	Drupe, mature (March-May)	Simple, alternate

	Species	Key	DBH (cm)	Description Flower	Description Fruit	Description leaf
				flowers (November-February)		
Sapotaceae	*Chrysophyllum mexicanum*[5,8]	Cm	11	Clustered in leaf axils, flowers almost all year	Drupe, fruits almost all year	Simple, arranged in a spiral
Polygonaceae	*Coccoloba spicata*[1,8]	Cs	14	Spikes simple, densely flowered, often recurved, flower almost all year	Globose-ovoid or subglobose, fruits almost all year	Simple, coriaceous
Ebenaceae	*Diospyros salicifolia*[6,8]	Ds	11	Axillary inflorescence, dioecious, flower almost all year	Drupe, fruits almost all year	Simple, membranous
Boraginaceae	*Ehretia tinifolia*[2,8]	Et	17	Inflorescence terminal, flowers (February-May)	Small subglobose, fruits (May-July)	Simple, alternate
Sapindaceae	*Talisia oliviformis*[3,6,8]	To	38	Axillary inflorescence, dioecious, flower almost all year	Drupe, fruits almost all year	Paripinnate, alternate

[1]Standley and Steyermark, 1946, [2]Standley and Steyermark, 1970, [3]Ochoa-Gaona *et al.* 2012, [4]Vester and Navarro, 2007, [5]Pennington and Sarukhán, 2005, [6]Peña-Chocarro and Knapp, 2011, [7]Barreto, 1998, [8]Valdez-Hernández 2015.

Wood density (WD)

We sampled every two weeks using four individuals per species with similar diameter classes (due to the possible physical damage to the individual at constant wood extraction, individuals were not the same at each sampling) during the dry, wet and nortes season. Samples were collected with a core borer (Haglof, inner diameter of 0.5 mm). Once a sample was obtained it was placed in plastic bags with a hermetic closure and deposited in ice to avoid dehydration. In the laboratory, the bark was removed, and the length of the cylinder measured with a digital caliper, to obtain the volume of the sample. To obtain the dry weight, samples were dried in an oven at 80°C for 48 hours (Koide *et al.* 1991).

Wood density was determined with an empirical method (Valencia and Vargas, 1997; Valdez-Hernández *et al.* 2010). With the values of sample length and the diameter of the bore (5 mm) the green volume of the wood sample was obtained by the following formula:

$Gv=3.1416\ D^2 X\ L/4$

where:
Gv= estimated volume of the wooden cylinder
D= core borer diameter (5mm)
L=length of sample

With dry weight data (po) and green volume (Gv), the value of wood density was obtained.

$D=po/Gv$ (g cm^{-3})

Relative water content (RWC)

The RWC was determined with same wood cores used for wood density. Fresh wood cores were weighed on an analytical balance (PA214C, OHAUS; Parsippany, NJ USA). Later they were placed in distilled water for 72 hours to get their weight to saturation. Finally, they were dehydrated in a drying oven at 80°C for 48 hours until constant weight is obtained (Koide *et al.* 1991). RWC was obtained with the following formula:

RWC= (fresh weight-dry weight) / (saturated weight-dry weight)

Diameter growth (DG)

To determine the growth rate, every individual was marked painting a band at a height of 1.3 m. Diameter at breast height (DBH) was measured using a diameter band. The initial DBH for each species is presented in table 1. Subsequently, the DBH was measured every eight days, between 7:00 a.m. - 9:00 a.m. for one year (March 2010-March 2011) to determine the variation between the seasons.

Statistical analysis

A two-way analysis of variance (ANOVA) was used, to observe the differences between seasons and species. Then to determine the differences between levels of significant factors, the post-hoc Tukey HSD test was used. Analyses were carried out with Statistica v. 12.0.

To identify functional groups, detrended correspondence analysis (DCA) was performed, which is an analysis of indirect ordination based on an average of reciprocity. This technique helps to integrate the similarity between species, provides interpretable ordering of species, as well as sample management. In addition, the axes are staggered into standard deviation units, which facilitates more realistic graphical representations than in other sorting techniques (Hill and Gauch 1980). To compute the ordination, seasonal averages were obtained for each species of the three variables considered: wood density, relative water content, and diameter growth.

According to the season two ordinations were performed, one for the dry season and one for the rainy season and nortes.

RESULTS

Wood density

For the classification of wood density criteria, Echenique-Manrique and Plumptre (1994) were used. A modification was made considering the groups of low to medium density wood as a single group, as according to the ANOVA only three groups are distinguished (F= 222.489; P= 0.001). The groups found were low-medium density, high density, very high density (Figure 1).

In the group of low-medium density (WD= 0.42 ± 0.0202 ES; Figure 1) we found: *Cecropia* (WD= 0.38 g cm^{-3} ± 0.058 ES), *Bursera* (WD= 0.45 g cm^{-3} ± 0.004 ES) and *Simarouba* (WD= 0.45 g cm^{-3} ± 0.050 ES). In the high density (WD= 0.68 ± 0.021 ES; Figure 1) are the species: *Bauhinia* (WD= 0.69 g cm^{-3} ± 0.001 ES), *Diospyros* (WD= 0.68 g cm^{-3} ± 0.009 ES), *Piscidia* (WD= 0.71 g cm^{-3} ± 0.006 ES), *Chrysophyllum* (WD= 0.75 g cm^{-3} ± 0.003 ES), *Cordia* (WD= 0.66 g cm^{-3} ± 0.004 ES), *Metopium* (WD= 0.61 g cm^{-3} ± 0.006 ES), *Guazuma* (WD= 0.63 g cm^{-3} ± 0.004 ES), *Senna* (WD= 0.68 g cm^{-3} ± 0.007 ES), *Coccoloba* (WD= 0.75 g cm^{-3} ± 0.008 ES), *Ehretia* (WD= 0.68 g cm^{-3} ± 0.004 ES), *Leucaena* (WD= 0.69 g cm^{-3} ± 0.004 ES).

Finally, in the very high-density group (WD= 0.83 cm^{-3} ± 0.007 ES; Figure 1) are the species: *Brosimum* (WD= 0.82 g cm^{-3} ± 0.002 ES), *Talisia* (WD= 0.84 g cm^{-3} ± 0.002 ES). Regarding the effect of environmental seasonality in wood density, no significant differences in any species (Table 2) were found.

Relative water content

According to the RWC we identified three groups: low-medium density with high RWC, high density with intermediate values in RWC, very high density low RWC, which present significant differences (F= 55.259; P= 0.001).

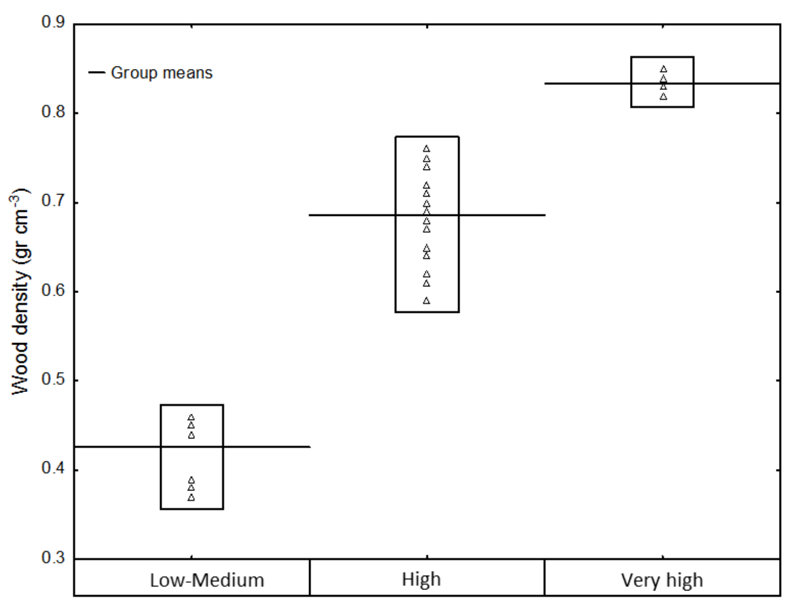

Figure 1. Integrated groups according in wood density (WD) variability for 16 tree species monitored in the ECOSUR forest reserve, Chetumal.

Table 2. Wood density (WD), relative water content (RWC) and diameter growth (DG) obtained by species, for the three seasons (dry, rainy, nortes) for 16 tree species monitored in the ECOSUR forest reserve, Chetumal.

Species	Parameters	Dry season	Rainy season	Nortes season	ANOVA (N= 96)
Bursera simaruba	WD (g cm^{-3})	0.45±0.007	0.44±0.010	0.45±0.007	F=2.56, P=0.19
	RWC (%)	63±0.022	74±0.012	66±0.013	F=27.72, P=0.0003
	DG (cm)	0.25±0.25	2.75±0.25	1.5±0.288	F=22.50, P=0.0003
Simarouba glauca	WD (g cm^{-3})	0.45±0.009	0.44±0.011	0.46±0.009	F=2.16, P=0.133
	RWC (%)	58±0.018	65±016	60±01	F=11.68, P=0.002
	DG (cm)	0.33±0.033	2.66±0.033	1.66±0.033	F=12.33, P=0.007
Cecropia peltata	WD (g cm^{-3})	0.39±0.011	0.37±0.007	0.38±0.015	F=1.70, P=0.13
	RWC (%)	60±0.013	67±0.016	62±0.007	F=15.07, P=0.0009
	DG (cm)	0.25±0.025	3±0	1.75±0.25	F=45.50, P=0.0002
Bauhinia divaricata	WD (g cm^{-3})	0.69±0.018	0.68±0.013	0.69±0.006	F=0.18, P=0.76
	RWC (%)	40±0.005	47±0.015	41±0.009	F=18.28, P=0.002
	DG (cm)	0.5±0.289	1±0	1±0	F=3.00, P=0.10
Diospyros salicifolia	WD (g cm^{-3})	0.70±0.008	0.69±0.013	0.67±0.014	F=3.35, P=0.04
	RWC (%)	43±0.015	50±0.013	45±0.017	F=13.27, P=0.001
	DG (cm)	0.5±0.288	1.25±0.25	1±0	F=3.00, P=0.10
Piscidia piscipula	WD (g cm^{-3})	0.70±0.009	0.72±0.013	0.71±0.011	F=1.93, P=0.20
	RWC (%)	47±0.014	55±0.013	51±0.004	F=18.45, P=0.0004
	DG (cm)	0.25±0.25	1.75±0.478	1.5±0.288	F=5.16, P=0.03
Cordia dodecandra	WD (g cm^{-3})	0.67±0.017	0.65±0.007	0.67±0.01	F=1.26, P=0.25
	RWC (%)	50±0.021	57±0.011	50±0.032	F=5.69, P=0.003
	DG (cm)	0.25±0.25	1.75±0.25	1.5±0.288	F=9.30, P=0.006
Metopium brownei	WD (g cm^{-3})	0.62±0.015	0.59±0.01	0.61±0.009	F=2.81, P=0.08
	RWC (%)	38±0.009	46±0.013	41±0.004	F=28.89, P=0.0003
	DG (cm)	0.5±0.288	1.5±0.288	1.5±0.288	F=4.00, P=0.05
Guazuma ulmifolia	WD (g cm^{-3})	0.64±0.023	0.62±0.011	0.62±0.012	F=0.67, P=0.93
	RWC (%)	41±0.014	47±0.014	42±0.011	F=12.69, P=0.003
	DG (cm)	0	1.5±0.289	1.25±0.25	F=13.28, P=0.002
Senna racemosa	WD (g cm^{-3})	0.67±0.014	0.69±0.015	0.69±0.007	F=1.81, P=0.18
	RWC (%)	43±0.019	49±0.012	46±0.004	F=12.00, P=0.003
	DG (cm)	0.66±0.333	1.33±0.333	1±0	F=1.50, P=0.29
Coccoloba spicata	WD (g cm^{-3})	0.76±0.009	0.76±0.017	0.74±0.01	F=2.91, P=0.07
	RWC (%)	42±0.027	51±0.016	43±0.015	F=13.26, P=0.001
	DG (cm)	0.25±0.25	1±0	1±0	F=9.00, P=0.007
Ehretia tinifolia	WD (g cm^{-3})	0.68±0.014	0.69±0.011	0.67±0.011	F=1.4, P=0.21
	RWC (%)	50±0.015	55±0.013	51±0.006	F=12.21, P=0.002
	DG (cm)	0	1.25±0.25	1±0	F=21.00, P=0.0004
Leucaena leucocephala	WD (g cm^{-3})	0.70±0.01	0.69±0.015	0.69±0.006	F=0.77, P=0.47
	RWC (%)	47±0.015	54±0.013	50±0.01	F=15.09, P=0.0001
	DG (cm)	0.5±0.289	1.75±0.25	1.5±0.289	F=5.72, P=0.24
Brosimum alicastrum	WD (g cm^{-3})	0.82±0.008	0.83±0.011	0.82±0.004	F=0.48, P=0.71
	RWC (%)	36±0.011	42±0.023	39±0.008	F=5.08, P=0.006
	DG (cm)	0	0.25±0.25	0.75±0.25	F=3.50, P=0.07
Talisia oliviformis	WD (g cm^{-3})	0.84±0.016	0.84±0.016	0.85±0.011	F=0.25, P=0.78
	RWC (%)	35±0.009	42±0.009	39±0.009	F=23.05, P=0.0008
	DG (cm)	0	0.5±0.289	0.5±0.289	F=1.50, P=0.27
Chrysophyllum mexicanum	WD (g cm^{-3})	0.75±0.007	0.76±0.008	0.75±0.009	F=1.39, P=0.39
	RWC (%)	51±0.021	57±0.019	52±0.005	F=6.78, P=0.005
	DG (cm)	0.33±0.333	1.66±0.333	1±0	F=6.00, P=0.03

The group that had the lowest RWC: *Brosimum* (RWC= 36-42 % ± 0.015 ES), *Talisia* (RWC= 35-42 % ± 0.017 ES) (Figure 2). In the RWC intermediate group we found: *Bauhinia* (RWC= 40-47 % ± 0.017 ES), *Diospyros* (RWC= 43-50 % ± 0.019 ES), *Piscidia* (RWC= 47-55 % ± 0.018 ES), *Chrysophyllum* (RWC= 51-57 % ± 0.015 ES), *Cordia* (RWC= 50-57 % ± 0.018 ES), *Metopium* (RWC= 38-46 % ± 0.02 ES), *Guazuma*

(RWC= 41-47 % ± 0.016 ES), *Senna* (RWC= 43-49 % ± 0.016 ES), *Coccoloba* (RWC= 42-51 % ± 0.023 ES), *Ehretia* (RWC= 50-55 % ± 0.014 ES), *Leucaena* (RWC= 46-54 % ± 0.018 ES) (Figure 2).

Finally, in the group with the highest RWC we found: *Bursera* (RWC= 63-74% ± 0.029 ES), *Cecropia* (RWC= 60-67% ± 0.018 ES), *Simarouba* (RWC= 58-65% ± 0.018 ES) (Figure 2).

Regarding the effect of environmental seasonality in the RWC in wood, it was found that in the rainy season the highest values were recorded in all cases (Table 2). In relation to groups, softwood species had a higher amount of water stored in the stem, on the other hand the hardwood species had lower RWC.

Diameter growth

According to the obtained values of diameter growth, it is possible to identify three clearly defined groups which were classified by their growth rate: slow, intermediate, and fast (F= 6.538; P= 0.0032).
In the group that had the values of low diameter growth (Figure 3), we found: *Brosimum* (DG= 1 cm ± 0 ES) and *Talisia* (DG= 1 cm ± 0 ES), the species did not differ significantly between seasons (Table 2).

In the group that have intermediate values of diameter growth (Figure 3), we found: *Bauhinia* (DG= 2.5 cm ± 0.288 ES), *Diospyros* (DG= 2.75 cm ± 0.25 ES), *Piscidia* (DG= 3.75 cm ± 0.478 ES), *Chrysophyllum* (DG= 2.5 cm ± 0.5 ES), *Cordia* (DG= 3.75 cm ± 0.478 ES), *Metopium* (DG= 3.25 cm ± 0.25 ES), *Guazuma* (DG= 3 cm ± 0 ES), *Senna* (DG= 3 cm ± 0 ES), *Coccoloba* (DG= 2.25 cm ± 0.25 ES), *Ehretia* (DG= 2.75 cm ± 0.25 ES), *Leucaena* (DG= 3.25 cm ± 0.25 ES).

In the high growing group (Figure 3) we found: Bursera (DG= 4.5 cm ± 0.288 ES), Cecropia (DG= 4.75 cm ± 0.25 ES), Simarouba (DG= 4.33 cm ± 0.288 ES) which showed significant differences between seasons, with the highest growth in the rainy season (Table 2).

Identified functional groups

To identify functional groups detrended correspondence DCA were performed, where the seasonal behavior recorded of the three variables were analyzed: wood density, relative water content in the wood and diameter growth. Two ordinations, one for the response of the variables in the dry season and one for the rainy season and nortes, are presented because by performing the respective ordinations, physiological parameters in the rainy season and nortes season behaved similarly.

In the dry season clearly four groups (Figure 4) are identified even though the total variance explained is low (11.5 %). Axis 1 (eigenvalue 0.094) is determined by the diameter growth, presenting a gradient of high to low (left to right); whereas the axis 2 (eigenvalue 0.025) is determined by the wood density, presenting a gradient of high to low (bottom-up).

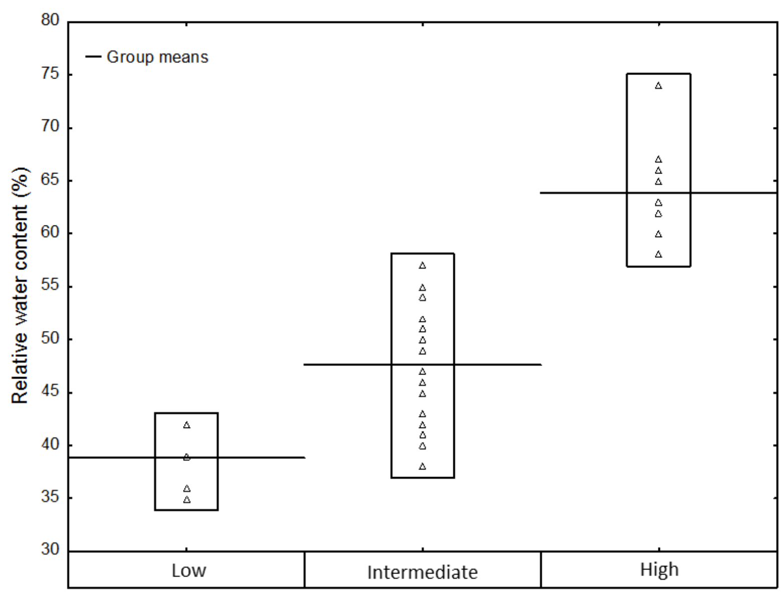

Figure 2. Integrated groups according in relative water content (RWC) in the wood variability for 16 tree species monitored in the ECOSUR forest reserve, Chetumal.

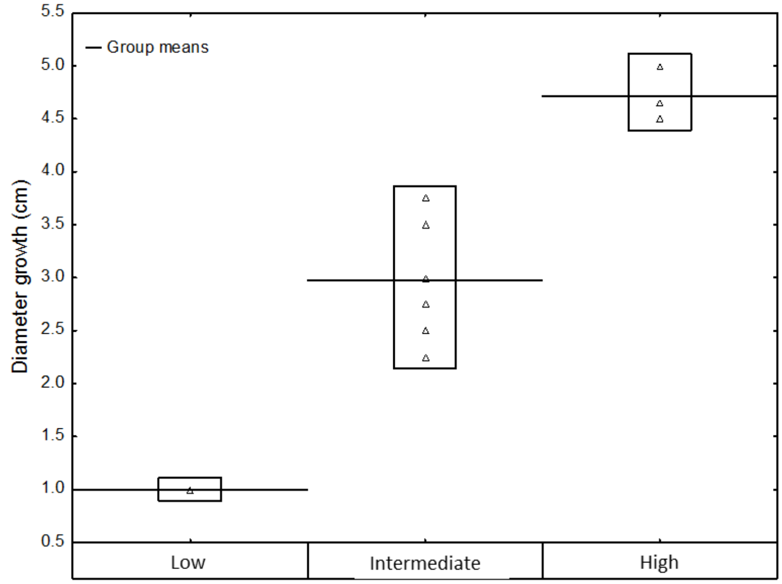

Figure 3. Integrated groups according in annual diameter growth (DG) variability for 16 tree species monitored in the ECOSUR forest reserve, Chetumal.

In group A, are the low to medium wood density species (0.43 g cm-³ ± 0.017 ES), higher relative water content (60 % ± 1.3 ES) and rate of intermediate growth (0.28 cm ± 0.024 ES). In group B, are species with intermediate values of wood density (0.68 g cm-³ ± 0.036 ES), relative water content (42 % ± 1.7 ES) and moderate growth rate (0.53 cm ± 0.037 ES).

In group C, are the intermediate wood density species (0.69 g cm-³ ± 0.019 ES), relative content of intermediate water (47 % ± 2.04 ES) and very slow growth rate (0.16 cm ± 0.077 ES). In group D, are species with very high wood density (0.83 g cm-³ ± 0.005), relative low water content (35 % ± 0.3 ES), no growth in the dry season.

In Figure 5, the ordination for the rainy season is given, the value of total variance explained is very low (6.7 %), the species align in the first axis according to their wood density (eigenvalue 0.062), as the wood density shows no seasonal differences (Table 2) and does not clearly distinguish the formation of groups. Furthermore, not having a limited availability of water, the species behave indistinctly in the use of water.

DISCUSSION

Functional groups identified

It has been documented that there are ecophysiological traits that are correlated promoting the formation of functional groups of species responding similarly to drought (Valladares *et al.* 2004, Rosell *et al*. 2022). The density of the wood is considered an important parameter to identify functional groups, because wood density is related to the ability to store water in the stem (Borchert, 1994; Valdez-Hernández *et al.* 2010, Wright *et al*. 2021, Rosell *et al*. 2022). Similarly, wood density can define the growth rate in tree diameter (King *et al.* 2005, García-Cervigón et al. 2020, García-Cervigón et al. 2021). In addition, wood density has been reported as a key endogenous factor, since it is linked to plant hydraulics in these water-limited ecosystems, so the effect of environmental variability is strongly interrelated (Luna-Nieves *et al*. 2022). The species studied allow us to identify three groups according to their wood density, relative water content and diameter growth. Classification criteria of Borchert (1994) were used. Light-wood species. - In the first group are: *Bursera simaruba*, *Cecropia peltata* and *Simarouba glauca*. These species have low to medium density, high water storage in the stem and the highest annual growth. The values obtained in wood density of *Bursera simaruba* (Figure 2) are like those observed in a dry Yucatan forest, by Reyes-García *et al.* (2012) who reported a density of 0.43 g cm-³. This group agrees with that reported by Valdez-Hernandez *et al.* (2010) in their group of light-wood species, which is characterized by a low wood density, succulent stems and high RWC stored in the stem and high leaf water potential throughout the year. High rates of annual growth of this group are characteristic of softwood species (López-Ayala *et al.* 2006). Although in the dry forests of the Yucatan Peninsula the rate of growth has not been considered as a variable for forming functional groups.

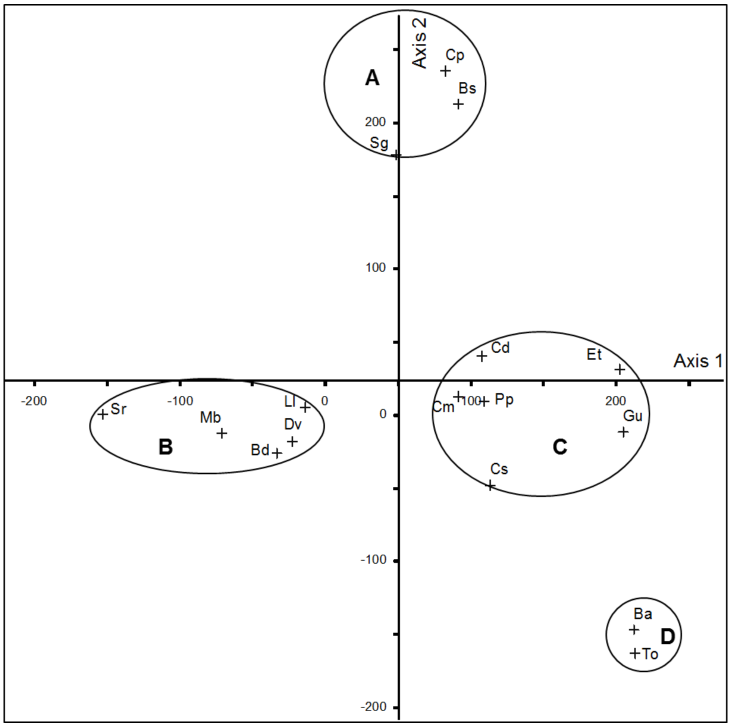

Figure 4. Detrended correspondence analysis (DCA) for 16 tree species in the dry season (March-May), considering the parameters wood density (WD), relative water content (RWC) and diameter growth (DG) for 16 tree species monitored in the ECOSUR forest reserve, Chetumal. Functional groups: A Light-wood and intermediate-growth species group. - *Bursera simaruba* (bs), *Cecropia peltata* (cp) and *Simarouba glauca* (sg). B Soft-wood and high-growth species group. - *Bauhinia divaricata* (Bd), *Diospyros salicifolia* (Ds), *Metopium brownei* (Mb), *Senna racemosa* (Sr), *Leucaena leucocephala* (Ll). C Soft-wood and low-growth species group. - *Ehretia tinifolia* (Et), *Guazuma ulmifolia* (Gu), *Cordia dodecandra* (Cd), *Chrysophyllum mexicanum* (Cm), *Piscidia piscipula* (Pp), *Coccoloba spicata* (Cs). D High-wood and low-growth species group. - *Brosimum alicastrum* (Ba) and *Talisia oliviformis* (To).

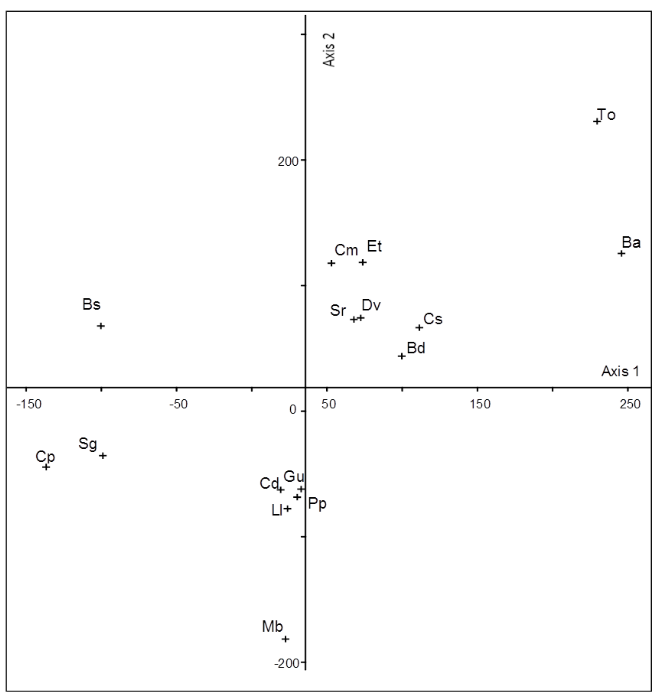

Figure 5. Detrended correspondence analysis (DCA) for 16 tree species in the rainy season (June-October) and nortes (November-February), considering the parameters wood density (WD), relative water content (RWC) and diameter growth (DG) for 16 tree species monitored in the ECOSUR forest reserve, Chetumal.

Similar results were obtained by Enquist *et al.* (1999) who found a ratio of the growth rate in species having a light wood density, and grow faster than the species with higher density (hardwood), possibly by having a large amount of water stored in the stem and a high water potential, allowing the leaves to open their stomata freely without causing a water shortage, resulting in carbon capture for photosynthesis and thus contribute to their growth. As the succulent stems have high water potentials and high water stored in the stem, they can continue to perform their metabolic and physiological processes throughout the year, also they can withstand long periods of drought (Valdez-Hernández *et al.* 2010, Wright *et al*. 2021).

Soft-wood species. - In the second group are the species: *Bauhinia divaricata*, *Diospyros salicifolia*, *Metopium brownei*, *Senna racemosa*, *Leucaena leucocephala*, *Ehretia tinifolia*, *Guazuma ulmifolia*, *Cordia dodecandra*, *Chrysophyllum mexicanum*, *Piscidia piscipula*, *Coccoloba spicata*, which exhibit high wood density, relative water content and intermediate diameter growth. The variation of growth may be determined by several factors such as the amount of precipitation (Brienen and Zuidema 2005, García-Cervigón *et al*. 2020, García-Cervigón *et al*. 2021), by fluctuation patterns in photosynthetic radiation (Clark and Clark 1994), the quality of the tree and diameter size (Interián-Ku *et al.* 2014) and the anatomical and physical characteristics of wood (Interián-Ku *et al.* 2011, García-Cervigón et al. 2021). The formation of this group confirms that wood density is a good predictor of the storage capacity of water in the stem (Borchert, 1994).

The values obtained in wood density for *Senna racemosa* (Figure 1) and *Diospyros salicifolia* (Figure 2), are like those observed by Reyes-García *et al.* (2012) in the dry forest of Dzibilchaltún, Yucatán, Mexico, where *Senna racemosa* (WD= 0.62 g cm^{-3}) and *Diospyros cuneata* (WD= 0.66 g cm^{-3}) have similar values. However, the values obtained for *Leucaena leucocephala* (Figure 2) are higher than those obtained by Reyes-García *et al.* (2012; WD= 0.56 g cm^{-3}).

This group also coincide with those reported by other authors regarding wood density and relative water content (Valdez-Hernández *et al.* 2010; Reyes-García *et al.* 2012). However, the values obtained for *Piscidia piscipula* (WD= 0.71 g cm^{-3}), are greater than those obtained by Reyes-García *et al.* (2012) in Dzibilchaltún, Yucatán (WD= 0.59 g cm^{-3}), which could indicate the influence of microenvironmental differences (ECOSUR precipitation= 1200 mm yr^{-1}, Dzibilchaltún precipitation= 750 mm yr^{-1}). This, considering the effect of the microenvironment on the rate of photosynthetic assimilation and parameters regulating water relations in tree species in dry forests (Stratton *et al.* 2000; Borchert and Pockman 2005).

Hard-wood species. - In the third group are the species *Brosimum alicastrum* and *Talisia oliviformis*. This group has high wood density, lower relative water content in the wood, and slow annual diameter growth (1 cm). This behavior is similar reported by Valdez-Hernández *et al.* (2010) in the group of hard-wood species, which have high wood density and low RWC in the stem, in addition tolerance to low water potentials. The slow diameter growth of this group is characteristic of tropical hardwood species (0.56 cm yr^{-1}, López-Ayala *et al.* 2006; 0.68 cm yr^{-1}, Interián-Ku *et al.* 2014). Specifically, for *Brosimum alicastrum* in young trees of Yucatan, an annual growth of up to 2 cm yr^{-1} has been reported (Hernández-González *et al.* 2015). However, in adult trees growth rates of 0.25 cm yr^{-1} have been reported (Peters and Pardo-Tejeda. 1982). Low growth that characterizes this group may, in addition to the high demand for biomass to increase wood density, due to the high energy requirement involving the production of fruits rich in nutrients that in both species occur. Resources can be increased in the production of the fruits instead of diametrical increase, as they are species that are dispersed by zoochory and sustain fauna (Ochoa-Gaona *et al.* 2012, Lander and Monro 2015).

Seasonal effects in the functional groups

According to the response observed in the dry season we found that the species studied can be divided into four groups according to their wood density, RWC and diameter growth (Figure 4).

The classification of Borchert (1994), was used adding a brief description of their growth.

Light-wood and intermediate-growth species group. - *Bursera simaruba*, *Cecropia peltata* and *Simarouba glauca* (group A, Figure 4). These species have low to medium density, high water storage in the stem and intermediate diameter growth in the dry season. The results indicate that the diameter of *Bursera simaruba* does not decrease in the dry season and are like the results of López-Ayala *et al.* (2006), who reported that *Bursera simaruba* does not show diametric reduction during drought. This also coincides with results of Reich and Borchert (1984) for the same species in a dry tropical forest of Costa Rica.

However, the growth rate decreased in *Bursera*, *Cecropia* and *Simarouba*. This reduction in growth rate can be explained by the reproductive phenology because in the three species, the phenophases flowering and fruiting occurred in the dry season (Zalamea *et al.* 2008; Valdez-Hernández *et al.* 2010). So, there is a change in allocation of resources by limiting the resources for growth. This observation is supported by Borchert (1994) who found that in *Bursera simaruba*, leaf buds growth occurs at the end of the dry season before the first rains, but the growth of stem and leaf growth occur only after saturation of the soil by the first rains.

Soft-wood and high-growth species group. - *Bauhinia divaricata*, *Diospyros salicifolia*, *Metopium brownei*, *Senna racemosa*, *Leucaena leucocephala* (group B, Figure 4), which have high wood density, intermediate water content, high diameter growth in the dry season. This group despite being composed of trees with high wood density may present growth in the dry season, but do not have high amount of water stored in the stem as in the low-medium group. Therefore, they use different strategies to fix carbon even under limiting conditions. *Diospyros salicifolia* and *Metopium brownei* are evergreen species, which do not have a limited season growth. In the case of *Diospyros cuneata* it has been found that it tolerates low water potentials at predawn, which could facilitate obtaining water in deeper soil layers (Valdez-Hernández *et al.* 2010). It has also been observed that in seasonally dry forests, there are tree species that can use small rainfall events during the dry season to contribute to its diameter growth (Worbes, 1999). Also, the legumes *Bauhinia*, *Senna* and *Leucaena*, can be present a wood anatomy like to *Mimosa tenuiflora*; in which it has been found a great amount of parenchyma and high hydraulic conductivity. The combination of both traits allows a fast production of biomass and growth accelerate (Romero *et al.* 2019).

Soft-wood and low-growth species group. - *Ehretia tinifolia*, *Guazuma ulmifolia*, *Cordia dodecandra*, *Chrysophyllum mexicanum*, *Piscidia piscipula*, *Coccoloba spicata* (group C, Figure 4). This group is characterized by high wood density, intermediate water content and low diameter growth in the dry season. It has been found that hardwood species growth is slower, but also more constant along the seasons indicating that precipitation plays an important role in the growth of trees (Enquist and Leffler 2001, Brienen and Zuidema 2005, López-Ayala *et al.* 2006).

The slow diameter growth in *Cordia dodecandra* may be influenced by a strong reduction in its photosynthetic capacity. Since it has been determined that in the dry season, the high air temperatures and low humidity cause a midday stomatal, closure reducing carbon fixation (Benjamin *et al.* 2001). It is remarkable that *Piscidia piscipula*, despite being a legume, is in a different group than the other leguminous plants (*Senna racemosa*, *Leucaena leucocephala*). Romero *et al.* (2019) found that some leguminous plants that dominate in different successional stages, such as *Lysiloma divaricatum*, present two types of wood. Early wood is characterized by low vessel density, low hydraulic conductivity, and high vulnerability index. Late wood is characterized by high hydraulic safety. Since *Piscidia piscipula* dominates all the successional stages of the seasonally dry forest of Yucatan, it is possible that they have a highly plastic wood anatomy that allows them to adapt to the hydraulic stress. *Guazuma ulmifolia* can be caused by an energy demand for fruiting during the dry season. Borchert (1996) in a dry forest of Costa Rica, found that in *Guazuma ulmifolia* the development of green fruits stopped during the wet season, development and maturity of the fruits resumed in the dry season. So, the start of drought could be the trigger for fruit growth. Therefore, resources could be used in fruit ripening and not in the diametric growth. *Cordia* and *Piscidia* appear to exhibit similar behavior as observed in *Guazuma*, since many of the species with flowering and fruiting during the dry season, invest more resources in the production of fruits (Valdez-Hernández 2015).

Leaves fall with increased water stress and evapotranspiration in the dry season, such behavior helps prevent excessive transpiration, however the CO_2 assimilation rate decreases (Borchert, 1996). On the other hand, evergreen species like *Ehretia tinifolia*, *Coccoloba spicata* and *Chrysophyllum mexicanum* do not show high values of growth rate. Although in the Yucatan Peninsula it has been documented that species with an evergreen habit can access deeper layers of soil for water extraction (Querejeta *et al.* 2006), this could be attributed to the allocation of more resources in the production of fruits, since the flowering and fruiting occurs in dry season (Valdez-Hernández 2015).

High-wood and low-growth species group. - *Brosimum alicastrum* and *Talisia oliviformis* (group D, Figure 4). This group has high wood density, lower relative water content in the stem, without diametric growth in the dry season.

As observed in *Brosimum alicastrum* in a tropical deciduous forest, where it presented low growth in the dry season compared to the rainy season, in young trees growth can be reduced by up to 70%, due to the lack of precipitation in the dry season, causing low water availability in the soil and high transpiration in plants (Hernández-González *et al.* 2015). In addition, *Talisia oliviformis* flowers and fruits during the dry season (Ochoa-Gaona *et al.* 2012), so the allocation of resources could focus on fruit production and not on diameter growth. Meanwhile *Brosimum alicastrum* can allocate more resources to produce biomass in the roots, and thus ensure access to the deeper layers of the soil during the dry season, this allows keeping the leaf cover. Also, it has been found that the distribution of roots in the soil layers varies seasonally (Estrada-Medina *et al.* 2013), and flowers and fruits all year, generating an increase in energy expenditure (Borchert 1996, Valdez-Hernández 2015).

CONCLUSIONS

The studied species allow us to identify four groups according to the interaction of wood density and seasonal diameter growth.

1) Light-wood and intermediate-growth species group: *Bursera simaruba*, *Simarouba glauca*, *Cecropia peltata.* With high RWC, storing large amounts of water in the rainy season allowing them to maintain a proper balance even in the dry season.

2) Soft-wood and high-growth species group: *Bauhinia divaricata*, *Diospyros salicifolia*, *Metopium brownei*, *Senna racemosa*, *Leucaena leucocephala.* Lower RWC compared to light-wood species, and moderate growth in the dry season.

3) Soft-wood and low-growth species group: *Ehretia tinifolia*, *Guazuma ulmifolia*, *Cordia dodecandra*, *Chrysophyllum mexicanum*, *Piscidia piscipula*, *Coccoloba spicata*. Intermediate RWC and low diameter growth in the dry season.

4) High-wood and low-growth species group: *Brosimum alicastrum* and *Talisia oliviformis*. Lower RWC, without diameter growth in the dry season.

The effect of seasonality in wood density for each group was not significant, but in the relative water content in wood and the diameter growth such effect was observed, with the rainy season presenting the highest values. Wood density varies among species, being an important functional group identification parameter, as it is related to the ability to store water in the stem and growth rate. However, the diameter growth can separate more finely groups, given that integrating this parameter allowed us to better understand the physiological behavior of the studied species. It is especially important in the Fabaceae, the most dominant family in the seasonal dry forests (Gillespie *et al.* 2000). In our study *Senna racemosa* and *Leucaena leucocephala* belong to the Soft-wood and high-growth species group, while *Piscidia piscipula* is found in the Soft-wood and low-growth species group. This proves a wide plasticity of the Fabaceae to adapt to stressful conditions. So, generating information to pinpoint functional groups which respond like water availability, can facilitate future modeling of responses of tree species to climate change.

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Conflict of interest. The authors declare that there was no conflict of interest in the development of this research.

Compliance with ethical standards. there are no bioethical implications in the development of this research.

Data availability (for meta-analysis). 1) Data are available with Mirna Valdez-Hernández, mavaldez@ecosur upon reasonable request.

Author contribution statement (CRediT). M. Valdez-Hernández – Conceptualization, Methodology, Formal Analysis, Funding acquisition, Supervision, Writing – original draft. **J. Palomo-Kumul** – Investigation, Data curation, Writing – original draft. **E. Osorio-de-la-Rosa** – Formal Analysis, writing - review & editing. **G.A. Islebe** – Writing – original draft. **G. Cruz-Piñón** – Writing – review & editing.

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