BOSQUE 41(3): 345-352, 2020 DOI: 10.4067/S0717-92002020000300345

Relationship between shoot and root of woody species of phenological functional groups of dry forest

Relación entre brote y raíz de especies leñosas de grupos funcionales fenológicos de bosque seco

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SUMMARY

Water availability in arid and semi-arid environments is the most limiting environmental factor for the development of plants, which use different mechanisms to capture the water from the soil. The objective of this work was to evaluate if there is differential allocation of resources between root and shoot of woody species of Brazilian dry forest and its relationship with the phenological functional groups of known adult woody: evergreen (EG), deciduous high density woody species (DHDW) and deciduous low density woody species (DLDW). The experiment was carried out in a greenhouse with a duration of six months, with plans submitted to two treatments: controlled irrigation (CI) and abundant irrigation (AI). Results showed that there was no interaction between phenological groups and applied treatments. However, the treatment with AI presented values of total biomass higher than those presented by CI. Fine root biomass was the only variable that did not differ between abundant irrigation and controlled irrigation. DLDW plants had higher root: shoot ratio compared to DHDW and EG. DLDW presented a differentiated strategy, being an indicative factor of these groups high thick root biomass, followed by low fine root biomass, with lower proportion of leaf biomass, and higher total biomass. These results show that CI reduces the development of seedlings in the groups and hence they invest in fine-root biomass. DLDW species presented higher investment in root biomass than in shoot, in addition to higher values of total biomass and specific leaf area.

Key words: water availability, Brazilian dry forest, phenological functional groups, aerial part, root of seedlings.

RESUMEN

La disponibilidad de agua en ambientes áridos y semiáridos es el factor ambiental más limitante para el desarrollo de las plantas, las que utilizan diferentes mecanismos para captar agua del suelo. El objetivo de este trabajo fue evaluar si existe una asignación diferencial de recursos entre raíz y brote de especies leñosas del bosque seco brasileño y su relación con los grupos funcionales fenológicos de leñosas adultas conocidas: perennifolias (EG), especies leñosas caducas de alta densidad (DHDW) y especies leñosas caducifolias de baja densidad (DLDW). El experimento se realizó en invernadero durante seis meses, con dos tratamientos: riego controlado (IC) y riego abundante (IA). Los resultados mostraron que no hubo interacción entre los grupos fenológicos y los tratamientos aplicados. Sin embargo, IA presentó valores de biomasa total superiores a IC. La biomasa de raíces finas fue la única variable que no difirió entre IA e IC. Las plantas DLDW tuvieron una relación raíz: brote mayor em comparación con DHDW y EG. El DLDW presentó una estrategia diferenciada, siendo un factor indicativo de estos grupos la biomasa radical alta gruesa, seguida de la biomasa radical fina baja, con menor proporción de biomasa foliar, y mayor biomasa total. Los resultados muestran que CI reduce el desarrollo de plántulas en los grupos y luego invierten en biomasa de raíces finas. La especie DLDW presentó mayor inversión en biomasa radical que brote, además de mayores valores de biomasa total y área foliar específica.

Palabras clave: disponibilidad de agua, bosque seco brasileño, grupos funcionales fenológicos, parte aérea, raíz de plántula.

INTRODUCTION

Nutrients and water present in soil are not uniformly distributed in space and time. Such heterogeneity in the distribution of these resources can affect individual plants in terms of survival, growth and biotic interactions (Pugnaire *et al.* 2019) and, therefore, change population dynamics. It is well known that availability of water in arid environments is the most limiting environmental factor and occurs according to rainfall events interspersed with different periods of drought, and this behavior is important for water supplying of plants. Vegetation not only responds to the amount of rainfall, but also to its variations in time (Reynolds *et al.* 2004). Therefore, relatively small changes in rainfall frequency may have strong effects on some species, especially on young individuals of annual plants (Sher *et al.* 2004).

Plants use some mechanisms to capture the water present in the soil. As an example, it is mentioned in literature that the investment in fine roots in plants subjected to severe water stress is one of these mechanisms, and can be interpreted as a strategy to maximize root absorption from the most superficial parts of the soil (Pereira Junior *et al.* 2016) The root is the specialized organ for the fixation of the plant in the soil and also for the absorption of water and mineral salts in solution, being able to still perform the functions of reserve of substances, among others. However, there is important lack of information regarding research on root evaluation, especially due to difficulties of collecting and processing this material (Jackson *et al.* 2007). Attempts to elaborate functional classifications of organisms have been defining the functional diversity of communities and as well as assessing the behavior of species in the ecosystems (Eviner and Chapin 2003). The approach is justified since plants tend to respond in different ways to environmental factors such as availability of resources and disturbances.

A list of characteristics that should be observed for the determination of functional groups is proposed by Weiher *et al.* (1999), as well as a standardized methodology for the collection of information. Cornelissen *et al.* (2003) cite that, when studying these groups, the interesting is a set of characteristics that are easily measured and are low cost for collection. Determination of functional groups must be based on characteristics related to the specific objectives of the research work (Weiher *et al.* 1999), and points related to plant phenology, physiology and structure are the most prominent in literature (Weiher *et al.* 1999). Structural characteristics such as wood density, stem water storage capacity, root system depth, water potential, leaf longevity, budding and flowering time, and leafless periods are particularly important for the determination of phenological functional groups (Singh and Kushwaha 2005). According to Reich *et al.* (2003), the use of functional groups can be useful to understand vegetation responses to environmental historical variability and predict vegetation responses to environmental changes without the need to know detailed information of each species, thus facilitating the comparison of the influence of global climate change on the world's diverse vegetation types.

Ecophysiological studies of woody plants of tropical forests with seasonal climate have received special attention, considering the importance of understanding the use of water by plants in these forests. In the case of the dry forest from Northeastern Brazil, the existence of three phenological functional groups of adult woody species related to the use and conservation of water is well known: evergreen, deciduous high density wood and deciduous low density wood. As commented previously, it is expected that in such environment, plants will present root biomass larger than that from the aerial part, regardless of their strategy. Regarding the functional groups of dry forest, Perennial species are expected to have deep roots, while deciduous, more superficial roots. These are common strategies developed by species located in regions of low rainfall to ensure their survival in the most critical periods (Collins *et al.* 2015, Smith-Martin *et al.* 2020). Among deciduous species, it is expected that high wood density species will have a denser main root, thus serving as a way to avoid cavitation, and to support the plant, while low wood density ones have as main function to capture and store resources. In terms of the relation of fine roots (< 2 mm) to leaf area, a larger root area is expected in deciduous species, considering the need to promptly use the first rains that occur in dry forest, which is quite irregular (Pereira Junior *et al.* 2016, Werden*et al.* 2017).

The present work has as a general goal to verify if there is a differential allocation of resources between root and shoot of woody species from Brazilian dry forest and their relationship with functional phenological groups already known in that ecosystem. More specifically, this work aimed at characterizing the morphological structure of roots, determine root surface area, length and biomass, estimate the biomass of the aerial part of the plant and evaluate growth parameters as diameter and height.

METHODS

In a research work carried out by Lima and Rodal (2010), the phenological groups here described were determined. Thus, having this informationas basis, nine wood species were selected for the present experiment forming three functional groups, each group encompassing three woody species, as showed in table 1.

Seed collection of the three functional groups started in November 2010 in an area belonging to Tamanduá Farm (coordinates 07º 00 'S and 37º 23' W), located in the municipality of Santa Terezinha (PB), about 18 km from the city of Patos-PB, in a Private Natural Heritage Reserve, RPPN. The area of the reserve is 325 hectares and for about the last thirty-five years it has not suffered any anthropic action. After seeds were collected, they were stored in properly sealed and identified plastic containers in a cold room. Some of the seeds underwent a process of improvement to increase their germination power. Seeds of *Amburana cearensis*, *Aspidosperma pyrifolium* and *Combretum leprosum* had their wings removed. Seeds of *Bauhinia cheilantha* and *Erythrina velutina* underwent mechanical scarification with nº 100 sandpaper, where part of the tegument was removed for better water absorption.

Table 1. Phenological functional groups from Brazilian dry forest and their respective woody species.

Grupos funcionales fenológicos del bosque ecobrasileño y sus respectivas especies leñosas.

Functional groups	Scientific name
DHDW, deciduous high-density wood species	*Combretum leprosum* Mart. *Bauhinia cheilantha* (Bong.) Steud. *Aspidosperma pyrifolium* Mart.
DLDW, deciduous low-density wood species	*Erythrina velutina* Willd. *Amburana cearensis* (Allemao.) A. C. Sm. *Pseudobombax marginatum* (A. St.-Hil., A. Juss. *et* Cambess.) A. Robyns
EG, evergreen	*Cynophalla flexuosa* (L.) J. Presl *Licania rigida* Benth. *Ziziphus joazeiro*Mart.

For the *Ziziphus joazeiro*, the outer layer was removed by using a hammer taking the proper care to not damage the inner parts of the seeds. Seeds of *Licania rigida* had part of fruit removed to prevent delay in germination. After these procedures, the seeds were separated by species and put to germinate in plastic bags.

To simulate the environmental characteristics of the Brazilian dry forest biome in a greenhouse, the municipality chosen to represent it was Serra Talhada - PE. The soil used in the experiment was collected at the Experimental Station LauroBezerra (7º59'00'S, 38º19'16''W), belonging to the Agronomic Institute of Pernambuco (IPA). The soil for the experiment was collected in December 2011. The soil was conditioned in 60 kg bags and taken to the experiment area located at Paudalho - PE.

The experiment was carried out according an entirely randomized design, in factorial scheme 3 x 2 (phenological groups x type of irrigation), with five replicates for each treatment, encompassing 90 experimental plots. The experiment was conducted in a greenhouse during a six-month period (February to July/2012). After emergence of the first leaves, which ranged from two to six days for all species, seedlings were transplanted to 60 kg bags. After transplantation, daily irrigation was performed for a period of 15 consecutive days to adapt the seedlings, minimizing the risk of mortality.

The species were submitted to two types of treatments, one with abundant irrigation (AI) and the other with controlled irrigation (CI), based on pulses and interpulse. The first treatment was watered daily, three times throughout the day (8 a.m., 12 a.m. and 5 p.m.), until reaching field capacity, noting if there was a need for more watering per day, it depended on the relative humidity of the air. In the second treatment, there was a simulation based on pulses (consecutive periods of rain $\geq$ 10 mm) and interpulse (dry interval or precipitation events < 10 mm), based on the historic rainfall data of the local of the experiment. To obtain these volumes, data were collected from the National Institute of Space Research (INPE) for information on the daily precipitation volume of the last 10 years, excluding years considered as atypical. Daily average was next estimated and the volume of water was calculated for the bag area. In this analysis, the years with a lot of rain were excluded because they were atypical, and based on the average distribution of normal years, the periods of pulses and interpulse were established as described above. After six months, each plant was completely removed from the substrate to take the following measurements: root morphological structure, root biomass (thin and coarse), stem and leaf, root system depth, specific leaf area, fine root surface area, root length.

Roots were stored, still moist, in plastic bags and placed in a refrigerator at 5 ± 2 °C, for up to one week. They were, afterwards, placed in a fine mesh sieve (0.2 mm) and washed in running water until cleared from the soil, which was removed as much as possible using a soft brush or fine tweezer from the root surface and between root hairs, and later were weighed. The depth of the root system was determined as the vertical root length from the soil surface to where roots penetrate the soil.

For the morphological description of the root, the organization of the primary, secondary and tertiary structure and the presence of tubers were considered. Plants were collected and separated in leaves, stems, biomass of fine roots (< 2 mm) and of thick roots (> 2 mm). Aerial and underground parts were oven dried at 65 °C under forced ventilation until reaching constant weight, and subsequently, dry biomass was determined. Root length was estimated by the grid intersection method. For this, roots were randomly arranged in a transparent tray to count the number of intersections, these being represented by the crossing points between a root and the lines that form the meshes (1.0 cm x 1.0 cm). The value was applied in the formula [1]:

$$R = N \times S \times 11/14 \quad [1]$$

Where: R = root length (cm); N = number of intersections; S = side of the grid.

Fine roots (< 2 mm length) were considered to determine the root area. Based on root diameter and root length the root surface area was calculated by the formula [2]:

$$RA = 2\pi r \times RL \quad [2]$$

Where: RA = root area (cm^2); r = radius (cm); RL = root length (cm).

The specific leaf area (SLA), which is the ratio of its area to the leaf dry weight, was analyzed in ten mature leaves in five individuals per species. The dry mass of leaves was determined after they were dried in an oven at 60 °C. The leaf area was estimated using the LAFORE program (Lehsen 2002), after leaves were scanned and image acquired. This analysis means the availability of leaf area in each leaf grass (leaf thickness indicator) as showed in the formula [3].

$$SLA = L_a/L_w \quad [3]$$

Where: SLA = specific leaf area (cm^2 g^{-1}); L_a = leaf area (cm^2); L_w = leaf weight (g).

Experimental data analysis. Initially, the collected data were processed in an electronic spreadsheet, describing in the first columns the independent variables (irrigation, functional groups and species) followed by the dependent variables (wet biomass weight and dry biomass weight, root depth, specific leaf area, root length and root area), and in the lines their respective repetitions, thus forming a database with the variables to be analyzed. Afterwards, a Normality Test was performed to observe if the variables had a normal distribution and thus to carry out the analysis of variance and, in the significant variables, to carry out the tests between averages. Once the normality of the variables was confirmed, the PROC ANOVA of SAS (Statistical Analysis System) was performed or, when a lost plot was detected, the PROC GLM (general linear model procedure) of SAS was used. As the effect of the main factors was independent, i.e., there was no interaction effect, a mean test was applied to the main factors using the program. After the analysis of variance of the experiment, it was verified that there was no interaction between independent factors (phenological groups and type of irrigation). For this reason, factors were analyzed separately.

RESULTS

In the experiment, two species were lost in the evergreen (EG) group when submitted to controlled irrigation (CI) treatment, respectively, *Licania rigida* and *Cynophalla flexuosa*, remaining only *Ziziphus joazeiro*. This high mortality when controlled irrigation was applied shows the sensitivity of these species to water deficiency. This fact was confirmed since there was no mortality of these species in the treatment with abundant irrigation (AI).

The values of leaf biomass (LB), stem biomass (SB), coarse root biomass (CRB), coarse root length (CRL), fine root length (FRL) and total biomass (TB) were significantly lower in the treatment with controlled irrigation, as showed in table 2. This indicates that the species, regardless of the groups, present the same pattern of response for the variables mentioned above.

It is important to note in table 2 that although total biomass of treatment of abundant irrigation is higher than in treatment of controlled irrigation, the proportion of root biomass overshoot is maintained independent of treatment. In this way, trade-off is maintained with or without water for the evaluated species. The fine root biomass was the only variable that did not differ between irrigation types (table 2). However, when the relationship between fine root biomass and total biomass was analyzed by treatment, it was observed that there is a higher proportion of fine root biomass in the treatment of controlled irrigation (8.43 %) than in the treatment IA (2.32 %).

Figure 1 shows the comparison for shoot height and diameter values in the evergreen species, deciduous high-density wood and deciduous low wood density species for

Table 2. Means statistical comparison, including all species by irrigation type, for leaf biomass (LB), stem biomass (STB), coarse root biomass (CRB), coarse root length (CRL), fine root biomass (FRB), fine root length (FRL), total root biomass (TRB), shoot biomass (SB) and total biomass (TB) as a function of controlled irrigation (CI) and abundant irrigation (AI) treatments.

Comparación estadística de medias, incluidas todas las especies por tipo de riego, para biomasa de hoja (LB), biomasa de tallo (SB), biomasa de raíz gruesa (CRB), longitud de raíz gruesa (CRL), biomasa de raíz fina (FRB), longitud de raíz fina (FRL)), la biomasa radical total (TRB), la biomasa de brotes (SB) y la biomasa total (TB) en función de los tratamientos de riego controlado (CI) y el riego abundante (AI).

Treat	LB	STB	CRB	CRL	FRB	FRL	TRB	SB	TB
CI	16.5 b	26.2 b	30.0 b	0.62 b	6.5 a	2.9 b	36.5 b	42.7 b	79.2 b
AI	44.4 a	131.6 a	139.2 a	0.92 a	7.5 a	5.2 a	146.7 a	175.1 a	321.8 a

Means followed by same letters in columns are statistically equal by Tukey test at 5 % of significance.

30, 60, 90, 120, 150 and 180 days of experiment. The development of plants was increasing in all groups, both in height and in diameter of the seedling for both treatments (controlled irrigation and AI). Group of evergreen species (figure 1 – A and B) presented approximate values for the treatments, unlike deciduous high density wood species (figure 1 – C and D) and deciduous low wood density group (figure 1 – E and F) that had a larger development when submitted to treatment of abundant irrigation.

In table 3, relationship between root biomass and shoot biomass analyzed for the phenological groups is shown. The highest root x shoot ratio was found in deciduous low wood density species (1.07), which almost doubled the other group, deciduous high-density wood species (0.53) and evergreen species (0.48). It is interesting to note that the behavior pattern of plants was not modified by controlled irrigation or AI, meaning that each group had a characteristic of its proportion (leaf, stem, root), which were

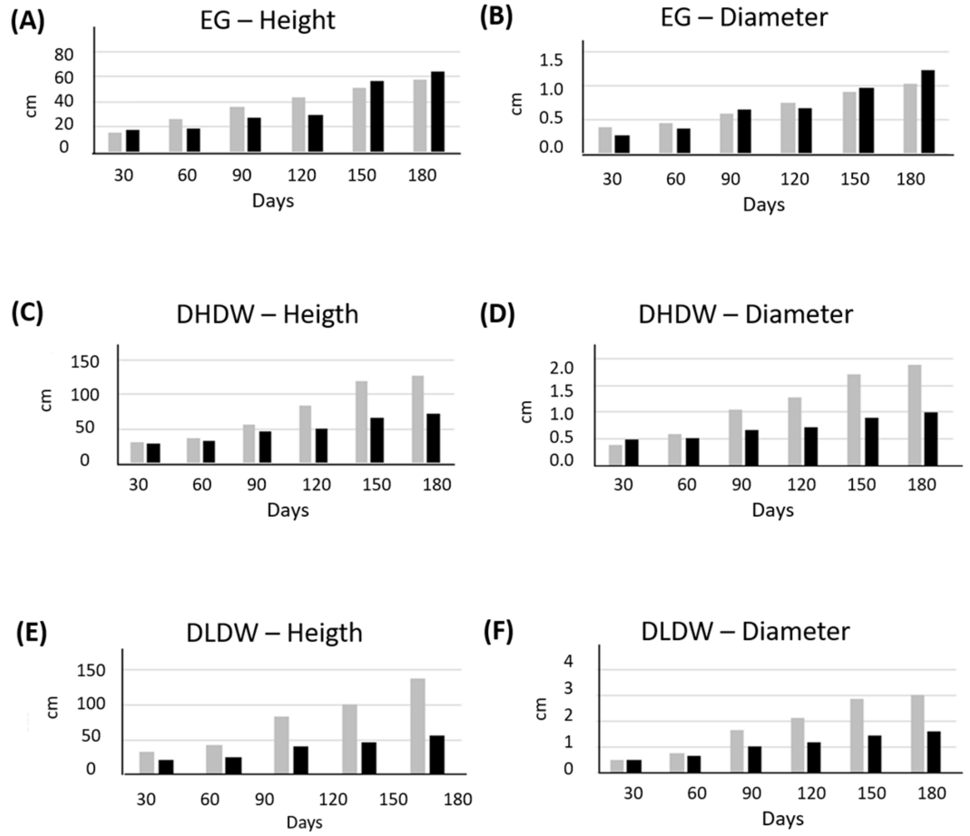

Figure 1. Shoot height and diameter for evergreen species (EG), deciduous high wood density (DHDW) and deciduous low wood density (DLDW) groups species CI (black bar) and AI (grey bar) treatments.

Altura y diámetro para EG, DHDW y DLDW bajo los tratamientos AI (barra gris) y CI (barra negra).

Table 3. Mean data for coarse root biomass (CRB), fine root biomass (FRB), total root biomass (TRB), leaves biomass (LB), stem biomass (STB), shoot biomass (SB), total biomass (TB) and specific leaf area (SLA) for phenological groups deciduous high density wood species (DHDW), deciduous low density wood species (DLDW) and evergreen species (EG).

Datos medios de biomasa de raíces gruesas (CRB), biomasa de raíces finas (FRB), biomasa total de raíces (TRB), biomasa de hojas (LB), biomasa de tallos (STB), biomasa de brotes (SB), biomasa total (TB) y área específica de hojas (SLA) para los grupos fenológicos DHDW, DLDW y EG.

Groups	CRB	FRB	TRB	LB	STB	SB	TB	SLA
DHDW	36.11 b	7.79 a	43.90 b	30.20 a	51.81 a	82.01 a	125.93 b	2.60 b
DLDW	198.79 a	5,77 b	204.56 a	33.77 a	157.52 a	191.29 a	393.75 a	8.66 a
EG	18.94 b	7,32 a	26.26 b	27.38 a	27.39 a	54.77 a	77.794 b	4.91 b

Means followed by same letters in columns are statistically equal by Tukey test at 5 % of significance.

similar for both treatments. Groups deciduous high-density wood species and evergreen species presented statistically superior FRB values when compared to deciduous low wood density species as showed in table 3. For leaf biomass, it was observed that the values did not differ among groups. However, the deciduous low wood density group had only 8.57 % of BF related to TB, a much lower value when compared to the other groups, respectively, deciduous high-density wood species (23.98 %) and evergreen species (35.19 %).

Regarding shoot biomass (SB), although there was no significant difference among groups, it is interesting to note that the deciduous low wood density group presented a value three to four times higher than those from the other groups. When coarse root biomass (CRB) was evaluated, there was a significant difference, where evergreen species and deciduous high-density wood species differed from the deciduous low wood density group, which presented a higher value. This latter group had a higher percentage of coarse root biomass than the percentage of stem biomass (39 %), which was different from the other groups that presented coarse root biomass (28.67 and 23.37 %) lower than stem biomass (41.14 and 33.80 %), when compared to deciduous high-density wood species and evergreen species, respectively. For the deciduous low wood density species group, specific leaf area (SLA) differed statistically from the other groups, presenting a higher value as showed in table 3.

DISCUSSION

According to literature (Larcher 2004), water is a fundamental resource for various metabolic processes (photosynthesis, growth, etc.). Thus, several authors have reported that the deficiency of this resource results, in a first moment, in the partial or total closure of stomata, reduction in CO_2 fixation and, consequently, plant growth (Zanine and Santos 2004). Confirming the previous assertion, studies of tree seedlings underscored the decrease of the biomass of the seedling with water restriction (Nascimento *et al.* 2011).

The higher investment in fine roots in the control irrigation (CI) treatment might be highly important for the survival of plants. As available in literature and commented previously, the investment in fine roots of plants subjected to severe water stress is a mechanism to capture water available in the soil, and can be interpreted as a strategy to maximize the root absorption of the most superficial parts of the soil (Pereira Junior *et al.* 2016).

Under severe drought or in environments with low resource availability, plants usually are limited in growth and photosynthetic capacity. Pizarro and Bisigato (2010), testing different water regimes in young plants, also observed that there was a reduction of total biomass with significant differences when submitted to water deficit. In the same study, regarding biomass partition, the authors concluded that water stress exerts a significant effect on the accumulation of biomass and dry matter partition in most species of the study, being the higher values of biomass for root and with reduction of leaf biomass. They also reported that the stem was not significantly affected when submitted to water stress. The fact that the artificially imposed drought reduces the total biomass of the plant in four of the six species studied by them is a result that shows a negative effect of water stress on plant species of Patagonia, as found in the present work. Furthermore, in an experiment performed by Brenes-Arguida *et al.* (2013), higher survival during dry season was observed, which corresponded to lower plants growth. This result is similar to that found for the group evergreen (EG), where higher mortality occurred in the control irrigation (CI) treatment at 180 days, which presented similar or even higher growth than that presented by the abundant irrigation (AI) treatment (figure 1 – A and B).

The fact that deciduous high density wood and evergreen groups had higher fine-root biomass than that presented by deciduous low wood density species can be explained by the fact that they keep their leaves for a longer period of time than does deciduous low wood density group, as pointed out by Reich; Borchert (1984), thus producing more photo-assimilates for the maintenance and growth of fine root biomass.

In the case of the deciduous low wood density group, whose strategy is the rapid loss of leaves to maintain water inside the stem and root, the non-development of fine roots may be related to the maintenance of the water column, avoiding a negative pressure within plants (Taiz and Zeiger 2010). This behavior, known as resistance to cavitation, is one of the main mechanisms presented by woody plants from environments subjected to water stress, since the strong negative pressure to remove water from the soil can rupture vessels and cause embolism (Sobrado 1993). Additionally, low-density wood plants tend to store water in their tissues (stem and root), according Reich *et al.* (2003). Such condition prevents large variations in water potential, as occurs in high-density wood plants, because their cell walls would not withstand strong negative pressures. These plants with low wood density present wide and narrow-walled vessels of xylem conducting cells (Reich *et al.* 2003).

Some authors, such as Jackson *et al.* (2007), state that one of the strategies observed in plants as a response to seasonality is the storage of water, nutrients and organic compounds in the root, even higher than in the stem as found in the group of deciduous low wood density. However, it is important to highlight that the deciduous low wood density group has a minority representation in the number of species and individuals in the Brazilian dry forest, where deciduous high-density wood predominates as shown by the works of Lima and Rodal (2010) and Oliveira (2013). The deciduous low wood density group shows a different strategy from the other groups regarding the morphofunctional characteristics of roots, and investment in biomass of coarse (tuberous) roots, with capacity to store resources, what may be an indicative factor of this functional group. Regarding this issue, Pregitzer (2003) commented that a large amount of these reserves is used during the period of dormancy of the plant for root respiration and to initiate the phase of growth, production of shoots and roots, just before or shortly after the beginning of the rainy season.

Some authors report that, unlike deciduous low wood density species, species with a high wood density, such as deciduous high-density wood and evergreen groups, tend to have lower specific leaf area, lower photosynthetic rate and to conserve the nutrient in leaves (Ishida *et al.* 2008). Generally, they present scleromorphic and longer lasting leaves (Wright *et al.* 2002), and in addition, they are more resistant to herbivorous attack and other physical damage (Reich *et al.* 1997).

CONCLUSIONS

Water stress reduces the development of plants, thus when submitted to the water stress treatment, plants from Brazilian dry forest invest their resources in fine root biomass. When considering different phenological functional groups, deciduous low wood density group (DLDW) uses a strategy different from that used by deciduous high-density wood (DHDW) and evergreen groups (EG), presenting a higher investment in root biomass (RB) rather than in shoot biomass (SB), besides larger values of total biomass (TB) and specific leaf area (SLA). Phenological functional groups presented different behaviors regarding leaf biomass x root biomass; evergreen groups showed higher leaf biomass, different from the deciduous groups that presented highest portion of root biomass. These results are important for a better understanding of plant behavior in different environmental situations, especially in the Caatinga biome, a dry forest, possessing few studies with the region endemic species. In addition, it serves as a subsidy for studies and practices of forest restoration.

ACKNOWLEDGMENTS

This work was supported by Federal Rural University of Pernambuco (UFRPE), the Postgraduate Program in Forest Sciences (PPGCF) and Foundation for the Support of Science and Technology of the State of Pernambuco (Process nº IBPG-0672- 5.02 / 09).

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Recibido: 17/04/20
Aceptado: 08/09/20