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Phenology and wood density of plants growing in the semi-arid region of northeastern Brazil

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A B S T R A C T

Nineteen woody species growing in the semi-arid region of northeastern Brazil were examined to evaluate the relationship between wood density and their vegetative and reproductive phenophases. Wood density varied between 0.29 g/cm^3 and 0.83 g/cm^3, and these values were inversely related to the quantity of water stored at saturation. The six species that initiated vegetative and/or reproductive phenophases during the dry season had low wood densities (<0.55 g/cm^3) and were able to store large quantities of water (110–271% of the dry weight of the wood). Leaf fall in these species occurred during the transition period between the rainy and the dry season, and it occurred earlier than in species with denser wood. Leaf flush among low wood density species was positively related to the photoperiod. Species with high wood densities, on the other hand, were strongly dependent on rainfall for leaf flush, flowering, and fruiting, as they are able to store only limited quantities of water in their trunks; leaf fall in these species occurred during the dry season. These results point to a strong correlation between wood density and phenology among the species studied.

1. Introduction

Many diverse and complex factors control the phenological behavior of tropical dry forest plants (Holbrook et al., 1995). Numerous authors have pointed out that the phenology of tree species growing in these forests appear to be primarily determined by rainfall (Bach, 2002; Bullock and Solís-Magallanes, 1990; Justiniano and Fredericksen, 2000; Machado et al., 1997). Other studies, however, suggest that the phenologies of some dry forest species are not determined simply by rainfall, but rather by the water status of the plants themselves (e.g. Borchert, 1994, 1999; Borchert and Rivera, 2001; Daubernmire, 1972; Reich and Borchert, 1982, 1984). These authors pointed out that plants with deep roots and/or stems capable of storing significant quantities of water will frequently demonstrate phenological patterns that are independent of actual rainfall patterns. The works of Pratt et al. (2007) and Jackson et al. (2007) likewise stressed the importance of roots in storing water and nutrients to be used during periods of scarcity or high demand, and the leaves of woody plants are known to have an important role in water absorption, representing an additional strategy for facing situations of water stress (Burgess and Dawson, 2004; Breshears et al., 2008; Munné-Bosch, 2009) that can influence phenological patterns.

According to Borchert (1994), wood density is inversely proportional to water storage capacity. As such, plants with light wood are able to store large quantities of water and can exhibit leaf flush, flowering and/or fruiting during the dry season, and will lose their leaves before species with high-density wood; high-density wood species will only demonstrate those same phenophases when ground water is available, and they delay leaf fall (Borchert, 1994; Borchert and Rivera, 2001; Borchert et al., 2002; Chapotin et al., 2006; Holbrook et al., 1995).

The positive relationship observed between wood density and leaf longevity (Chave et al., 2009; Ishida et al., 2008; Wright et al., 2004, 2007) is a consequence of factors such as resistance to cavitation and the mechanical support of the plant (Chave et al., 2009; Hacke et al., 2001; Reich et al., 2003; Swenson and Enquist, 2007). According to these authors, having high-density wood allows plants to resist strong water stress conditions without undergoing cavitation, and the same hard wood provides mechanical support to the plant against adverse physical conditions such as strong winds – allowing the plants to grow taller and compete successfully with neighboring plants for sunlight.

Plants with low-density wood can store large quantities of water, and their budding and flowering during the dry season can be triggered by photoperiod changes even in regions near the

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equator (Borchert and Rivera, 2001; Borchert et al., 2005; Rivera and Borchert, 2001; Rivera et al., 2002). These authors reported a number of observations that support the concept of photoperiodic control over budding and flowering: high intra-specific synchrony of these phenophasic events; low variability of phenophase events from year to year; and leaf flush initiated in response to an increase in the photoperiod, but not to rainfall.

Parts of NE Brazil experience six to nine-month dry seasons, and this semiarid region is dominated by a shrub–arboreal vegetation known as *Caatinga* (Sampaio, 1995). Although little is currently known about the phenology of the woody species in this area, many authors have pointed to rainfall as the principal factor regulating leaf flush and flowering (Barbosa et al., 1989; Griz and Machado, 2001; Machado et al., 1997; Pereira et al., 1989) – even though these phenophases can be observed during the dry season in some species. Species that demonstrate leaf flush and flowering during the dry season must have access to water, and moisture stored in low-density woody tissue is one probable source. As such, we hypothesize that *Caatinga* species with high-density wood will demonstrate leaf flush and flowering only when there is soil water available, while species with low-density wood can demonstrate these same phenophases in the dry season by utilizing water stored in their soft tissues. As there are currently no published works that address the relationship between wood density and phenology, the present study sought to answer the following questions: are there any relationships between wood density and phenology among woody *Caatinga* species? Which abiotic factor (either rainfall or photoperiod) is most related to a given phenophase?

2. Materials and methods

2.1. Study area

The present work was undertaken in the Maurício Dantas Private Nature Reserve, located within the municipalities of Betânia and Floresta in Pernambuco State, Brazil (8°18′43″S; 38°11′45″W). This reserve occupies 1485 ha at approximately 500 m above sea level (IBAMA, 2002). The local climate is classified as BSh'w (hot and dry) by the Köppen system, with an average rainfall of 511 mm/yr and average monthly temperatures ranging from 22.8 to 26.5 °C (CONDEPE, 2002). Rainfall in the semi-arid region of NE Brazil is extremely irregular, in both its temporal and geographical distribution; usually more than 75% of the total annual rainfall occurs within just three months (Sampaio, 1995).

Rainfall distribution differed significantly during the three field study years. In the first year, 75% of rainfall was concentrated in January and February; in the second year most of the rainfall occurred from February to May (Fig. 1); and in the third year there was significant rainfall during December, close to zero precipitation in January, followed by heavy rains in February (Fig. 1).

The study area was located in a depression zone between two higher plains (a typical landscape in the semi-arid region of northeastern Brazil) (see Andrade-Lima, 1981). The soils there are generally rich in nutrients but thin, and therefore have reduced water-retention capacities (see Rodal et al., 2008 for more information concerning the physical and chemical characteristics of the soil). These soils tend to show little geological variation over wide areas. The Brazilian semi-arid region generally receives between 400 and 800 mm of rainfall per year, so the study area represents a climatically average site (Sampaio, 1995).

Although the vegetation in the Caatinga region has only begun to be studied in depth, the research site (undertaken in an area that had previously been examined by Rodal et al., 2008) had structural characteristics similar to other areas with similar topographies, soils and rainfall levels (Griz and Machado, 2001; Nascimento et al., 2003), as well as many representatives of the families Leguminosae and Euphorbiaceae and species such as *Caesalpinia gardneriana* and *Croton blachetianus* that are commonly encountered in plant surveys in the Caatinga (Sampaio, 1995).

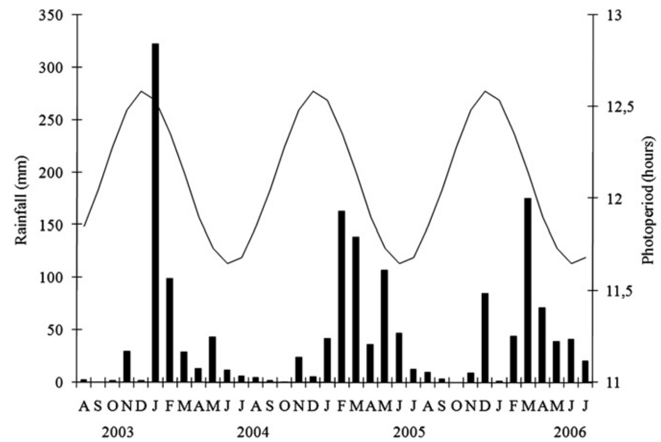

Fig. 1. Average monthly rainfall and photoperiod lengths in the municipality of Floresta, Pernambuco State, Brazil, during the period from August 2003 to July 2006.

The *Caatinga* vegetation in the study area was dominated by high densities of thin-stemmed plants (3–6 cm diameter at ground level). Rodal et al. (2008) reported 3140 individuals in 1 ha, with average heights and diameters of 2.37 m (±0.92 m) and 7.3 cm (±4.655) respectively, with only a few specimens reaching 12 m.

2.2. Collection and analysis of the phenological data

Data was collected during 36 months, between August/2003 and July/2006, in a 100 × 100 m area of *Caatinga* vegetation. Nineteen species cited in the phytosociological study of Rodal et al. (2008) were selected for observation (Table 1). From one to twenty individuals of each species (with stem perimeters ≥9 cm at soil level) were selected, for a total of 196 plants (with an average of 10.3 individuals per species, and therefore within the range recommended by Frankie et al., 1974 and Fournier and Charpantier, 1975).

The presence or absence of the phenophases of leaf flush, leaf fall, flowering and fruiting was noted on a monthly basis. Flowering was considered to include all phases from the formation of the floral bud until anthesis, while fruiting included all phases from the formation of visible fruits through their complete maturation (Bullock and Solís-Magallanes, 1990; Machado et al., 1997). The duration of flowering or fruiting for a given species corresponded to the entire period when any of the individuals of that species in the study plot demonstrated the characteristics of that phenophase (Silberbauer-Gottsberger, 2001).

Flowering and fruiting patterns were determined according to the classification system proposed by Newstrom et al. (1994). A phenophase was classified as annual if it demonstrated a yearly cycle, and supra-annual if a given cycle lasted longer than one year.

The relationships of the phenophases with rainfall (INPE, 2006) and photoperiod (Lammi, 2005) were statistically analyzed using Spearman's coefficient (Zar, 1996). Statistical analyses were performed with species having at least two individuals in the study plot. Graphs are presented for species with more than five individuals.

The quantity of leaves present on any given individual was estimated using the methodology proposed by Borchert et al. (2002) and employing a 0–3 scale, where 0 = absence of leaves, 1 = few leaves (<33%), 2 = many leaves (33–66%), and