Forest Ecology and Management 340 (2015) 62–69

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Phenotypic plasticity and ecophysiological strategies in a tropical dry forest chronosequence: A study case with *Poincianella pyramidalis*

Hiram M. Falcão [a], Camila D. Medeiros [a], Bárbara L.R. Silva [b], Everardo V.S.B. Sampaio [b], Jarcilene S. Almeida-Cortez [a], Mauro G. Santos [a,*]

[a] Departamento de Botânica, Universidade Federal de Pernambuco, CEP: 50670-901 Recife, Brazil
[b] Departamento de Energia Nuclear, Universidade Federal de Pernambuco, CEP: 50740-540 Recife, Brazil

ARTICLE INFO

Article history:
Received 9 August 2014
Received in revised form 23 December 2014
Accepted 26 December 2014
Available online 12 January 2015

Keywords:
Leaf construction cost
Natural regeneration
Pioneer species
Photosynthesis
Semiarid

ABSTRACT

The plasticity of functional attributes is an important strategy for the acclimation and establishment of plants in areas that undergo natural regeneration. The irregular rainfall of the Brazilian tropical dry forest is an important environmental filter for the determination of the set of species that can successfully establish in different stages of the regeneration process and influences the plant acclimation responses to the environmental conditions at each stage of ecological succession. In order to test the hypothesis that pioneer plants which can establish themselves, at the same time, in areas at different stages of regeneration have high phenotypic plasticity, we investigated the endemic tree species *Poincianella pyramidalis* Tull., which can be found in all stages of the regeneration process in the Brazilian tropical dry forest. Three areas were selected at different successional stages (early, intermediate and late), and the functional attributes of water status, gas exchange, leaf nutrients, specific leaf area, leaf construction costs and payback time were assessed. In the three successional stages all individuals had similar age. Measurements were taken in April, for two consecutive years, a dry and a wet. The evaluated parameters in this study showed changes according to successional stage. The highest leaf water potential was found in the late stage in the rainy year and lowest in the dry year. This behavior may be related, in addition to soil water availability, to a stronger competition for resources in these areas. Gas exchange and nutrient use efficiency were higher in 2013 and in the late successional stage, which exhibited higher soil moisture, a lower vapor pressure deficit and higher nutrient mobilization. There were no differences in the construction cost per unit mass between the stages, but differences in specific leaf area led to changes in cost per area. The payback time was shorter in the wettest year. For the driest year, the late stage showed greater energy use efficiency. The results show that the *P. pyramidalis'* attributes varies according to the successional stage, showing phenotypic plasticity. However, the strongest differences are observed between years, demonstrating that water is the main factor that coordinates the functional changes that confers its ability to acclimatize.

1. Introduction

Functional traits are important proxies of plant response to environmental conditions (Violle et al., 2007). These conditions impose different selection forces in plants and controls, to some extent, intra-specific differences in functional traits (Poorter, 2009). The ability to adjust the expression of various phenotypes according to environmental conditions is known as phenotypic plasticity (Nicotra et al., 2010). In previously and currently disturbed environmental succession areas, plasticity can lead to partially adapted phenotypes, thereby accelerating the adaptive and evolutionary processes of the plant species (Lande, 2009).

Environmental succession, which is caused by changes in the environment, results in mosaics of areas at different stages of natural regeneration. These areas are becoming more common in tropical dry forests, which are mainly located in South America,

Abbreviations: IWUE, intrinsic water use efficiency; CC_{mass}, leaf construction cost per unit mass; CC_{area}, leaf construction cost per unit area; ψ_l, leaf water potential; A_{max}, maximum net CO_2 assimilation; SLA, specific leaf areas; g_s, stomatal conductance; SM, soil moisture; *E*, transpiration rate; TDF, tropical dry forest.

* Corresponding author. Tel.: +55 81 21268844; fax: +55 81 21267803.
E-mail address: mauro.gsantos@ufpe.br (M.G. Santos).

http://dx.doi.org/10.1016/j.foreco.2014.12.029
0378-1127/

mainly due to the strong anthropization (Quesada et al., 2009; Santos et al., 2011, 2014; Lopes et al., 2012). According to Cabral et al. (2013), 80% of Brazilian tropical dry forests are successional, and 40% are maintained in initial stage of regeneration.

Generally, a structural perspective is used to study the process of natural regeneration, like the species composition of each successional stage. However, from a functional standpoint, the ecosystem recovers its functionality even before full floristic restoration to preconditions (Guariguata and Ostertag, 2001). Thus, the study of the functional attributes of key plant species involved in regeneration processes in these ecosystems is of fundamental importance (Griscom et al., 2009).

Because the conditions of successional forest habitats are not constant in time and space, the assessment of ecophysiological processes (particularly those related to carbon investment) is important to the understanding of how plants are able to adapt and establish themselves. The acquisition of carbon by plants is determined by multiple functional attributes, such as net photosynthesis, leaf nitrogen concentrations and specific leaf area (Shipley and Almeida-Cortez, 2003; Poorter et al., 2006). Plants invest photoassimilates in the construction of leaves and other parts, in nutrient acquisition and metabolism maintenance (Wright et al., 2004). The relationship between the acquisition and use of acquired resources is known as the leaf economics spectrum, and it directly influences plant growth rates (Marino et al., 2010; Edwards et al., 2014).

The leaf construction cost is defined as the amount of glucose necessary to construct carbon skeletons, reducing power in the form of NADPH and energy for organic compound synthesis and it is indirectly related to plant growth rates (Williams et al., 1987). For plants with low leaf construction costs, energy investment in building a new leaf, rather than in strategies to maintain the old leaves, is more biochemically and structurally economical (Poorter and Bongers, 2006; Zhu et al., 2013). On the other hand, plants with high leaf construction costs can invest their resources in defense metabolites, which are costly in terms of energy (Westoby et al., 2002). Thus, the construction cost, associated with payback time (i.e., the time required by the plant to offset the expenses of leaf construction through the photosynthetic process), provides us with an important measure of the energy use efficiency (Poorter et al., 2006).

Studies to date have not reached a consensus regarding which attribute, or set of attributes, are able to provide plants with significant phenotypic plasticity. The plasticity of traits in relation to phenology, flowering time, seed longevity, is well documented (Clair and Howe, 2007; Morin et al., 2009; Kochanek et al., 2010). However, some studies point higher indexes of phenotypic plasticity in physiological traits such as maximum CO_2 assimilation, dark respiration and maximum quantum efficiency of photosystem II, in detriment of structural traits (Valladares et al., 2000; Koehn et al., 2010). It is clear that variations in functional attributes depend on the plant species, the choice of the attributes to be analyzed and the environment to which the plants are subjected. Furthermore, most studies on plasticity and succession involve the assessment of pioneer plants compared with later-stage plants, since plant species exhibit different ecophysiological responses when they are analyzed during different successional stages (Navas et al., 2003, 2010; Zhu et al., 2013). However, some pioneer plants are able to establish, at the same time, in areas in different stages of succession.

Thus, this study attempts to elucidate the functional traits that allow plants to maintain their performances throughout the succession process by evaluating the ecophysiological and functional attributes of a pioneer and endemic tree species in a tropical dry forest, in areas that are under different periods of regeneration.

2. Material and methods

2.1. Study area and plant material

The study was conducted in the month of April during the years 2012 and 2013, in a chronosequence of three successional stages of a seasonally tropical dry forest (TDF), Caatinga, in Tamanduá Farm (06°59′13″ to 07°00′14″ S and 37°18′08″ to 37°20′38″ W), located in the Santa Terezinha municipality, Paraíba, Brazil. The study area is at an average altitude of 240 meters and contains the shallow and low-fertility soil type Leptosols (EMBRAPA, 1997). The mean temperature and annual rainfall of the city are 32.8 °C and 600 mm (Fig. 1). In 2012 and 2013, the cumulative rainfall levels up to April were 257 mm and 338 mm, respectively. Rainfall was recorded monthly at a meteorological station that was installed in the study area. In April, the rainfall levels totaled 35 mm in 2012 and 84 mm in 2013, which amounted to a difference of 140% between the years. The environmental data from 2012 and 2013 are presented in Table 1.

Each successional stage was represented by an area. The area in early succession is in natural regeneration for 21 years, and the intermediate area is in succession for 43 years. The early successional area was submitted to clearcutting in 1965 for cotton planting, and in 1970 the cotton plantation was replaced for *Cenchrus ciliaris* L. (buffel grass) and used by cattle for pasture before being abandoned in 1992. The intermediate successional area was also submitted to a clearcutting in 1965 for cotton planting, however was abandoned in 1970. There is no registry of clearcutting in late successional area or major disturbances since 1950 (Freitas et al., 2012; Silva et al., 2012).

Fertilizer was not applied to any of the areas, and in 2007, they were all surrounded with barbed wire to prevent the entry of cattle, goats and sheep. In each area, a 50 × 20 m plot was delimited with a 5 m edge on all four sides. The chemical and physical properties of the soil surface layers were presented in Freitas et al. (2012).

In a phytosociological survey of tree species made in the study area, Cabral et al. (2013) have identified 6 species and 3 families in the early stage of regeneration, 15 species and 10 families in the intermediate stage, and 21 species and 12 families in the late stage, with predominance of the Fabaceae family in the three areas. The average density was 0.083 individuals m^{-2} in the early stage, 0.113 individuals m^{-2} in the intermediate stage, and 0.093

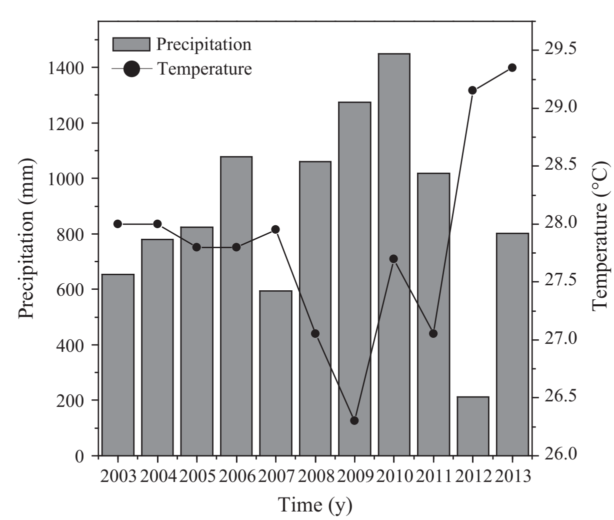

Fig. 1. Time series of annual rainfall (mm) and mean annual temperature (°C) over the past ten years in the Santa Terezinha municipality, Paraíba, Brazil.