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Forum

Spatio-temporal variation in a seed bank of a semi-arid region in northeastern Brazil

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ABSTRACT

This study aimed to evaluate variations in the seed bank within a 3-year temporal series in order to answer the following questions: 1) Does the seed bank's species richness and seed density differ among climatic seasons and between years? 2) Are there differences in the richness and density of seed banks between the litter and mineral soil? 3) Can the seed bank's species richness and seed density be explained by characteristics such as the previous year's precipitation and soil depth (litter or mineral soil)? The samples were collected from litter and mineral soil (0–5 cm), in 210 sub-plots, during the dry and rainy seasons of each year (August 2005 through February 2008). Overall, 79 species were recorded. On average, 1 168, 304 and 302 seeds.m^{-2} were recorded in the seed bank during years I, II and III, respectively. This study showed that the Caatinga's seed bank is rich in herbaceous species, yet species' density and richness are low in the litter. Furthermore, about 43% of the variation in species richness and density was explained by soil depth (litter and mineral soil) and previous years' rainfall.

1. Introduction

Dry tropical forests occur in large areas of the Americas, Africa, Asia and Australia (Khurana and Singh, 2001). In Brazil, dry forests occupy a great part of the north-eastern semi-arid region, and are mainly represented by the shrub-arboreal, deciduous, thorny and xerophytic vegetation known as caatinga (Tosi et al., 1983; Alcoforado-Filho et al., 2003; Araújo et al., 2007). This type of vegetation is marked by a clear distinction between climatic seasons: a rainy season (lasting 3–6 months and known as the growing season) and a dry season (lasting from 6 to 9 months). The rainy season is responsible for 80–90% of total rainfall, which is irregularly distributed (Araújo et al., 2007).

Temporal variations in the distribution of total rainfall influence the rhythm of seed rain in dry tropical forests (Borchert, 1994; Holbrook et al., 1995; Jolly and Running, 2004). In the case of caatinga vegetation, there are at least three patterns of seed rain: 1) species that flourish and disperse seeds within a single rainy season; 2) species that flourish at the end of the rainy season and disperse seeds during the dry season of the same year; and 3) species that flourish in the dry season and disperse seeds during the rainy season of the subsequent year (Barbosa et al., 1989; Machado et al., 1997; Barbosa et al., 2003; Lima et al., 2007; Amorim et al., 2009; Lima and Rodal, 2010). Such patterns also occur in other dry forests around the world (Shackleton, 1999; Selwyn and Parthasarathy, 2006; Valdez-Hernández et al., 2010). However, the few studies that have quantified seed rain in the caatinga have showed that the species richness and density of seeds that reach the soil vary between seasons (Lima et al., 2008; Souza, 2010). Additionally, although precipitation is unevenly distributed throughout the year, it also varies considerably between years; thus, extremely dry or extremely wet years can occur (Reis et al., 2006). These differences in the amount of rainfall per year and/or per climatic season promote variation in the production of fruit and seeds (Shackleton, 1999; Selwyn and Parthasarathy, 2006; Valdez-Hernández et al., 2010), which increases the variation in the number of seeds that reach the soil bank.

Furthermore, changes in seasonal climate can disturb populations' natural regeneration processes, thus influencing the seed bank's dynamics. For example: occasional or erratic rainfall may occur during the dry season, as well as sporadic droughts in the rainy season. Moreover, the length of the climatic seasons (rainy

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and dry) may increase or decrease between years (Araújo, 2005). For caatinga communities with high frequencies of terophytic life (species that pass to the dry season within the seed bank, in the form of seeds – Raunkiaer, 1934), erratic rainfall events during the dry season (or dry events in the rainy season) promote germination followed by death (Araújo et al., 2005a; Lima et al., 2007; Silva et al., 2008); this, in turn, leads to a reduction in the number of seeds stored in the bank, regardless of the seed rain pattern.

Thus, the distinct patterns of seed rain, in addition to the influence of seasonal climatic variation, leads us to the hypothesis that part of the variation in seed banks of dry environments (in terms of density and richness) can be explained by rainfall characteristics of both current and previous years.

Undoubtedly, there are other factors that affect seed bank dynamics, such as seed longevity following dispersal, period of germination, dormancy occurrence, predation, pathogen attacks, and depth of seed deposition. Some seeds have short lives and are not necessarily recorded by studies that evaluate seed banks based on a single annual sampling effort (Mayer and Poljakoff-Mayber, 1963; Costa and Araújo, 2003). Additionally, the period of germination varies among species; some have secondary dormancy mechanisms and need more time to germinate (Bewley and Black, 1982, 1994; Borghetti, 2004; De Villiers et al., 2004). Many seeds are rich in oils and proteins and serve as a resource for fauna, which increases chances of predation or pathogen attacks (Hulme, 1998; Ness and Morin, 2008). This, in turn, may reduce the amount of viable seeds in the soil or litter and influence seed bank dynamics.

In relation to the depth of seed deposition following dispersal, a portion of the seeds are often retained in the litter, while the remaining seeds reach different depths within the soil. In fact, some researchers have recorded an inverse relationship between soil depth and the density of the seed bank (Guo et al., 1998; Costa and Araújo, 2003; Ning et al., 2007). There is no uniform pattern of seed deposition in the litter: density may be low in some areas (Guo et al., 1998; Mamede and Araújo, 2008) and high in others (Costa and Araújo, 2003), when compared to the seed density found in the soil. In the caatinga, with higher production of deciduous litter during the dry season, the litter layer generally tends to be thick and irregularly distributed over time (Alves et al., 2006; Andrade et al., 2008).

Among the different abovementioned factors, this study only questioned the influence of temporal rainfall variation and of vertical seed depth deposition on seed bank dynamics. In short, seasonal and interannual variations in total rainfall (Coffin and Lauenroth, 1989; Mayor et al., 1999; Pugnaire and Lazaro, 2000; Lopez, 2003; Facelli et al., 2005; Williams et al., 2005), and the depth where seeds are deposited (Costa and Araújo, 2003; Lobo, 2008; Mamede and Araújo, 2008; Santos et al., 2010), influence the richness and amount of seeds stored in the soil. However, it is worth highlighting that few studies concerning seed banks have analyzed samples from consecutive years (Cabin and Marshael, 2000; Facelli et al., 2005; Williams et al., 2005), and there are no studies of this nature for the caatinga vegetation. Hence, the impact of rainfall variability on the soil seed bank density is largely unknown.

Thus, this study aimed to answer the following questions: 1) Does the seed bank's species richness and seed density differ among climatic seasons and between years? 2) Are there differences in the richness and density of seed banks between the litter and mineral soil? 3) Can the seed bank's species richness and seed density be explained by characteristics such as the previous year's precipitation and soil depth (litter or mineral soil)?

2. Materials and methods

2.1. Study area

This study was conducted in a dry forest fragment of a vegetation type known as caatinga, at the Experimental Station of the Pernambuco Company of Agricultural Research (Empresa Pernambucana de Pesquisa Agropecuária – IPA) (8°14′18″S and 35°55′20″W, 535 m altitude) in Caruaru, Pernambuco – Brazil. The area includes native vegetation where human activities and animal grazing are not allowed, and is thus considered to be preserved. The area covered by preserved vegetation is approximately 20 ha (Alcoforado-Filho et al., 2003). The climate is seasonal, with a mean annual precipitation of 680 mm and minimum and maximum absolute temperatures of 11 °C and 38 °C, respectively. The soil is Eutrophic Yellow Podzolic, and the area is drained by the Olaria Stream, a tributary of the Ipojuca River (Reis et al., 2006; Silva et al., 2008). The vegetation is arboreal, deciduous, thorny and hypoxerophytic (Alcoforado-Filho et al., 2003). The perennial woody component of the area is rich in Fabaceae and Euphorbiaceae (Lucena et al., 2008), while the herbaceous component is rich in Malvaceae, Poaceae, Asteraceae, Convolvulaceae and Euphorbiaceae (Reis et al., 2006).

Monthly precipitation data (Fig. 1) was collected from the Experimental Station. A 30-yr historical series showed that the rainy season usually occurs between March and August (Araújo et al., 2005a). However, there is significant variation in total yearly rainfall, and the rainy season can begin in February and/or extend until September. Moreover, there may be droughts during the rainy season and erratic rainfall during the dry season (Araújo et al., 2005a). The seasonality of the water regime determines the deciduousness of woody flora during the dry season and the appearance of most herbs only during the rainy season.

2.2. Sampling and data analysis

Within the native vegetation of the IPA Experimental Station there is a 1-ha sampling area with 105 1 m × 1 m fixed plots where the herbaceous vegetation has been extensively studied (Araújo et al., 2005b; Reis et al., 2006; Silva et al., 2008). In order to study the seed bank, six samplings took place in each plot (one per season): three at the end of the rainy seasons (August 30, 2005; August 30, 2006; September 28, 2007) and three at the end of the dry seasons (January 30, 2006; January 30, 2007; February 28, 2008). Sampling was carried out during the transition between

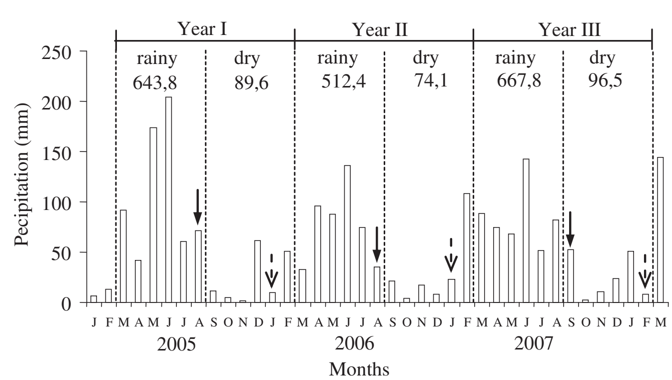

Fig. 1. Monthly precipitation and total precipitation during the rainy and dry season for three years. Arrows with solid lines indicate the samples collected at the end of the rainy seasons and arrows with dashed lines indicate samples collected at the end of the dry season. Data provided by the meteorological station of Empresa Pernambucana de Pesquisa Agropecuária (IPA) – Caruaru, Pernambuco, Brazil.