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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

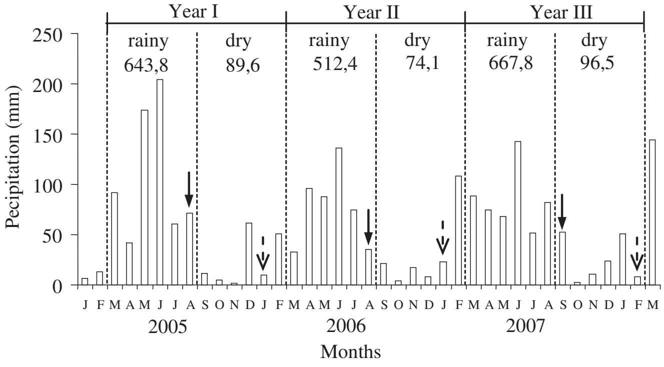

Fig. 1. Monthly precipitation and total precipitation during the rainy and dry season for three years. Arrows with solid lines indicate the samples collected at the end of the rainy seasons and arrows with dashed lines indicate samples collected at the end of the dry season. Data provided by the meteorological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

climatic seasons in order to consider the types of seed bank (persistent and transient) found in the area.

During each season (in distinct sites for the rainy and dry seasons and always around the 1 m × 1 m fixed plots), 105 samples were collected from two depths in the soil (the organic litter layer and the mineral soil from 0 to 5 cm below the litter, and henceforth these will be described as "soil depths"). We collected the top 5 cm because the topsoil has a greater contribution in terms of species richness and seed density (Dalling et al., 1995; Luzuriaga et al., 2005). The samples were collected in plots of 20 cm × 20 cm (Fig. 2). The number and size of the seed bank plots followed the method proposed by Thompson (1986).

The samples were transferred to styrofoam trays (20 cm × 38 cm × 3 cm) and distributed onto six benches in the greenhouse of the Federal Rural University of Pernambuco (UFRPE), Recife. The trays were watered daily and kept at an average temperature of 25 °C, and received no photoperiod treatment. Since the layer of mineral soil in the trays was very thin (3 cm), it was never mixed during the entire period of germination. Richness and density were determined using the emergence method (Brown, 1992; Warr et al., 1993) with daily monitoring for six months. After emergence, identified seedlings were removed from the trays. Unidentified seedlings were transplanted to plastic bags (five per morphospecies) and monitored to obtain reproductive material (herbs) for identification. Ten control trays containing washed and sterilized (autoclaved) sand were randomly placed on each bench of the greenhouse. These control trays were used to ensure that the seeds that germinated in the bank were collected from the area of origin and were not present due to potential contamination.

Seed density is expressed as seeds per square meter (Baskin and Baskin, 1998); the mean arithmetic density of seeds for the dry and rainy seasons of each year (seeds m^{-2}) was calculated to express the annual average of seed density and the arithmetic mean of the six sampling efforts to express the average value of the three years.

A floristic list of the taxa that germinated in the seed bank was generated according to the Angiosperm Phylogeny Group II botanical classification system. Species were identified by consulting the literature, through comparisons with exsiccates from the Professor Vasconcelos Sobrinho (PEUFR) and the Dárdano de Andrade Lima (IPA) herbaria and with the aid of specialists.

The explanatory power of total rainfall variation (year of sampling and preceding year), soil depth (litter and mineral soil) and their interactions on species richness and seed bank densities was evaluated using the General Linear Model (GLM). The species richness and density of seeds followed the Poisson distribution (Zar, 1996). The explained variance (pseudo R^2) was calculated as the ratio between the deviance of the model when a variable is included and the residual deviance of the null model (Dobson, 2002). E.g., for the first variable included, variable A: $R^2 =$ deviance of the model using variable A divided by the total residual deviance. For the second variable included, variable B: $R^2 =$ deviance of the model using variables $A + B$, divided by the residual deviance of the model including only variable A. We used the same procedure for all variables included and also for interactions among variables. For the year of sampling, species richness and seed bank densities estimated from the annual samples (and separately for each season) were linked to the total rainfall recorded during the corresponding sampling period.

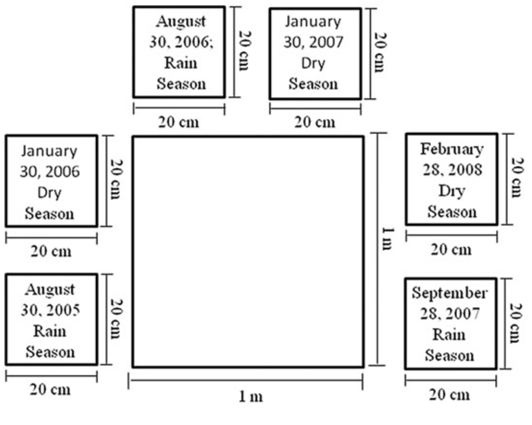

Fig. 2. Schematic view of sampling design – one 20 × 20 cm plot collected each season from around the 1 × 1 m fixed plots in a semi-arid area in northeastern Brazil.

To examine the effect of past rainfall, only the total rainfall from each preceding season or year was considered (i.e., the total precipitation of the corresponding sampling periods was disregarded); the total rainfall of the year preceding the study (2004) was considered time zero. The explanatory power of total rainfall for the past was subdivided by considering immediate (previous years and seasons) and distant ecological pasts. For the immediate past, the species richness and density of each seed bank sample was linked to total rainfall of previous years and seasons. In the case of the distant past, the seed bank's species richness and densities were linked to the average total rainfall for all seasons prior to the sampling period.

The floristic similarity between the rainy and dry seasons and between years was calculated using the Sorensen index (Krebs, 1989). To detect differences in species composition between soil depth (litter and mineral soil), between rainy and dry seasons and between years, a non-metric multidimensional scaling (NMDS) analysis and the exchange test ANOSIM (Analysis of similarities) were performed using the Primer-E software program version 6. For ANOSIM, the Bray–Curtis similarity index was used. Species abundance data were square root-transformed and standardized in order to avoid any bias resulting from highly abundant species (Clarke and Gorley, 2005). Differences in mean species richness and mean seed density between the soil and litter, among seasons and among years were verified by the Kruskal–Wallis (H) variance test (Zar, 1996). All of the tests were performed using BioEstat 2.0 software.

3. Results

3.1. Richness

A total of 79 taxa, distributed among 32 families and 50 genera (see Appendix 1), were identified from the seed bank (litter and mineral soil); 30 taxa only occurred in the mineral soil and eight only in the litter. Of the 79 taxa (henceforth referred to as "species") observed, eight were identified only as morphospecies, 14 at the family level, one at the subfamily level and five at the genus level, due to the early death of seedlings. The seedlings that were not identified to species level accounted for 5% of the total seedlings recruited in the three years. Only one seedless species (the fern *Selaginella sucata*, presumably from spores) with four individuals occurred in the seed bank, in the last year of the study. Excluding morphospecies, 80% of the species were herbs, 10% were shrubs and 6% were trees. The richest families in both the litter and mineral soil were Euphorbiaceae, Poaceae, Fabaceae and Malvaceae (see Appendix 1).

Average taxon richness (henceforth referred to as "species richness") (litter + mineral soil) decreased significantly from the first to the third year and was significantly higher during the rainy season in the first and second years (Table 1). Additionally, average species richness was significantly higher in the mineral soil than in the litter over the three years (Table 1). Only in the first year was the

Table 1
Average species richness and standard deviations, total richness (in brackets), average seed density (seeds m^{-2}) and standard deviations in the litter and soil from each season (rainy and dry) and overall during three years in a semi-arid area in northeastern Brazil. The same lowercase letters in the same line (between litter and soil at each station and between rainy and dry seasons of each year) and the same capital letters in the same column (between years) indicate no significant differences ($P < 0.05$) according to the Kruskal–Wallis analysis of variance.

Years	Rainy		Dry		Rainy	Dry	Mean annual	Total
	Litter	Soil	Litter	Soil				
Richness								
I	2.4 ± 1.9b (24)	5.5 ± 3.2a (46)	2.1 ± 1.2b (14)	4 ± 1.6a (28)	8±4aA (52)	6.2 ± 2.3bA (28)	14 ± 4.8A	58
II	1.1 ± 1b (17)	3.2 ± 1.4a (31)	0.8 ± 0.7b (12)	1.8 ± 1.2a (20)	4.3 ± 1.8aB (33)	2.6 ± 1.5bB (22)	7 ± 2.2B	40
III	0.6 ± 0.9b (19)	1.8 ± 1.4a (24)	0.7 ± 0.9b (10)	1.9 ± 1.5a (22)	2.5 ± 1.8aC (31)	2.5 ± 1.9aB (24)	5 ± 2.7C	41
Density								
I	165 ± 281b	867 ± 940a	218 ± 345b	1087 ± 1726a	1032 ± 1017aA	1305 ± 1981aA	1168 ± 1268A	–
II	50 ± 88b	309 ± 288a	59 ± 96b	189 ± 219a	360 ± 304aB	248 ± 274bC	304 ± 204B	–
III	25 ± 44b	81 ± 104a	108 ± 335b	392 ± 558a	105 ± 119bC	500 ± 789aB	302 ± 400B	–

litter's composition during the dry season equal to the species composition found for the mineral soil (see Appendix 1).

Overall, the seed bank (litter or soil) showed differences in species composition among the years monitored. Thirty-two species occurred only during the rainy season, and eleven were found only during the dry season. Fifty-nine species presented a discontinuous interannual occurrence in the seed bank. Only *Delilia biflora*, *Callisia repens*, *Cyperus uncinulatus*, *Phaseolus peduncularis*, *Panicum trichoides*, *Tallinum triangulari* and *Pilea hyalina* were present during the dry and rainy seasons for the three years studied (see Appendix 1). The floristic similarity between the rainy and dry seasons was of 37%, 37% and 34% in years I, II and III, respectively. The interannual floristic similarity was of 34% (year I *versus* year III), 41% (year II *versus* year III) and 46% (year I *versus* year II).

The ordination analysis (NMDS) detected differences in floristic composition between years, between rainy and dry seasons and between soil depths, which estimated a bi-dimensional stress of 0.21, 0,23 and 0,22, respectively (Fig. 3). The ANOSIM detected significant correlation between degree of floristic similarity between plots and year ($R = 0.269$; $p = 0.001$), and rainy and dry seasons ($R = 0.262$; $p = 0.001$) and soil depth ($R = 0.184$; $p = 0.001$).

The variation in the seed bank's species richness was significantly related to the soil depth and to both present and past (immediate and distant) rainfall – this explained 44% of the seed bank's richness. However, only two significant interactions between variables (soil depth and precipitation) were recorded, but the explanatory power of such joint action was very low. When considered separately, soil depth and previous years' rainfall explained 19 and 21% of the soil bank's species richness, respectively (Table 2).

3.2. Density

On average (rain and dry), 4907, 1276 and 1271 seedlings (98% herbaceous) emerged from the seed banks of years I, II and III, respectively – an average temporal density (three rainy seasons and three dry seasons) of 591 seeds m^{-2} (Table 1). Over the three years studied, density was significantly higher in the mineral soil than in the litter. However, considering the total seed density of the seed bank (litter + soil), only the first year presented no significant seasonal variation in density. In the second year, density was higher during the rainy season, and the opposite was true during the third year (Table 1). The species with the greatest number of individuals were *P. hyalina*, *D. biflora* and *P. trichoides*. Few individuals occurred for most species (see Appendix 1).

As recorded for richness, seed density was also significantly related to soil depth and precipitation (both present and immediate

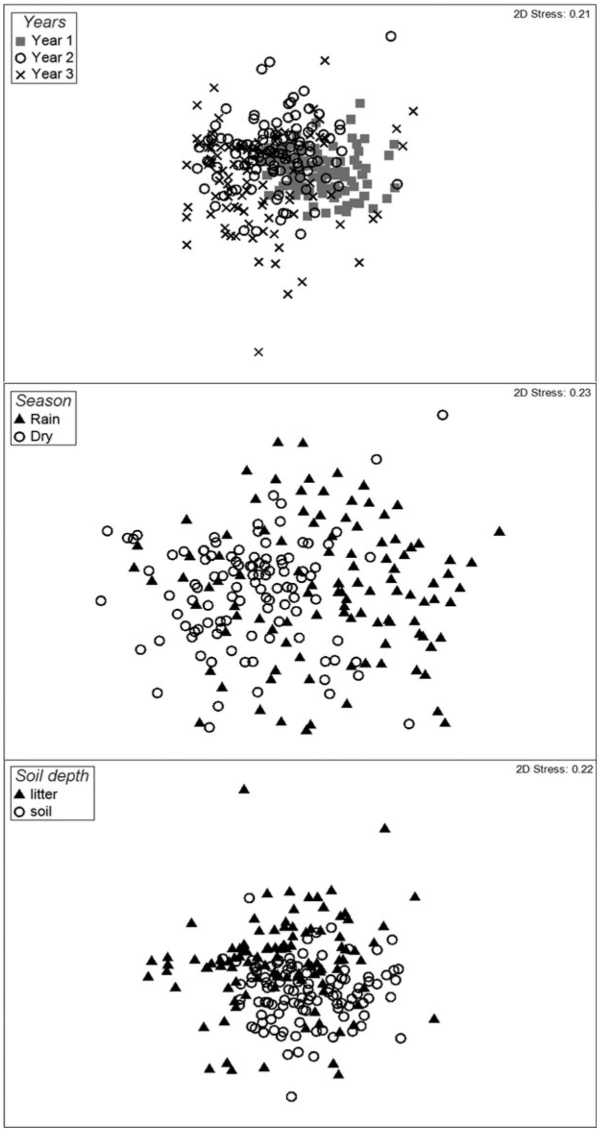

Fig. 3. Non-metric multidimensional scaling based on Bray–Curtis species similarity coefficients (between years, seasons and soil depth) in a semi-arid area in northeastern Brazil.

Table 2
Results of GLM: Explained variance (R^2) in species richness by precipitation of present and past, soil depth (litter and soil) and their interactions.

Variables	*df*	Deviance	Residual *df*	Residual deviance	*P* (chi-square)	R^2
NULL			1259	2467.1		
Soil depth	1	464.1	1258	2003.0	0.00000	0.1881
Precipitation of year	1	16.9	1257	1986.1	0.00004	0.0069
Precipitation of season	1	40.1	1256	1946.0	0.00000	0.0162
Precipitation of year previous	1	513.0	1255	1433.0	0.00000	0.2079
Precipitation of season previous	1	10.5	1254	1422.5	0.00118	0.0043
Precipitation from the distant past	1	17.1	1253	1405.4	0.00004	0.0069
Soil depth*Precipitation of season	1	4.6	1252	1400.8	0.03215	0.0019
Soil depth*Precipitation of year previous	1	10.0	1251	1390.8	0.00159	0.0040

and distant past), which explained 43% of the seed bank's density. Three significant interactions between variables (soil depth and precipitation) were recorded, but the explanatory power of these interactions was also very low. Separately, soil depth and the previous year's rainfall explained 20% and 16% of seedlings' density, respectively (Table 3).

4. Discussion

4.1. Variations in the pattern of species richness of the seed bank

Richness varied from 10 to 58 species (Table 1), which is within the range of variation for arid and semi-arid environments worldwide – 9 to 117 species (Kemp, 1989; Wagner et al., 2006; Traba et al., 2006; Ning et al., 2007; Kellerman and Van Rooyen, 2007). However, it is worth highlighting that the number of species found depends on the number of samples, the size of the samples and whether sampling occurred only in one year or across many seasons. Among the factors that generate such variation, soil depth and seasonal climate has often been investigated. Our study encompassed a three-year time series during which we recorded that soil depth, rainfall of previous years, and climatic seasons are significant variables in determining the richness of the seed bank. The interaction among these variables was also significant, despite its low explanatory power (R^2). When considered jointly, the total explanatory power of these variables and their interactions can be considered high (44%, Table 2). We acknowledge that other variables not measured by this study, such as microhabitat differentiation and seed predation, can also influence species richness of seed banks in dry environments.

The predictability of wet and dry seasons determines temporal variations in water availability. There are areas where greater water availability favors increases in diversity and areas where the opposite occurs. For example: for semi-arid vegetation in southeastern Spain, Pugnaire and Lazaro (2000) found that the number of species in the seed bank was more closely related to precipitation, since richness was highest in years with most rainfall. Similarly, Pessoa (2007) and Santos et al. (2010) found greater seed bank richness during the rainy season in areas of caatinga in northeastern Brazil. Williams et al. (2005), however, found the opposite relationship in the seed bank of a semi-arid region in northeastern Australia: these authors found most richness during the dry season, and such richness decreased significantly during the rainy season.

The contradictory behavior of seed banks' species richness responses to seasonality leads us to the question: what is the determining power of this environmental factor? This study showed that interannual variations in the seed bank's average species richness are also significant within the same area. Variations in average species richness occur between seasons (rainy and dry), but significant seasonal differences are not necessarily maintained along a 3-year temporal series such as the one studied here. The significant reduction in average species richness from the first to the third year, as recorded by our study, shows that decreases in total rainfall between years can reduce the seed bank's species richness. However, the effect of such a reduction can only be seen in the subsequent year, as precipitation of the previous year (1064.3 mm in 2004; 733.4 mm in 2005; 586.5 mm in 2006) explains 21% of the variation of average species richness (14 in 2005; 7 in 2006; 5 in 2007) (see Table 2). The fact that soil depth (19%) explained a similar amount of variance to the preceding year's rainfall (21%) shows that these two variables have great influence on the seed bank and can be considered predictors of species richness.

Overall, the floristic similarity between the rainy and dry seasons was less than 40% over the three years, and between years it was less than 50%; this value is within the range of variation for floristic similarities (22%–53% between seasons) of seed banks in dry environments (Ghermandi, 1997; López, 2003; Caballero et al., 2005). The variation in floristic similarity during the three years indicates that species composition is significantly affected by

Table 3
Results of GLM: Explained variance (R^2) in seed density by precipitation of present and past, soil depth (litter and soil) and their interactions.

Variables	*df*	Deviance	Residual *df*	Residual deviance	*P* (chi-square)	R^2
NULL			1259	34158.6		
Soil depth	1	6805.0	1258	27353.7	0.00000	0.1992
Precipitation of year	1	932.1	1257	26421.6	0.00000	0.0273
Precipitation of season	1	440.9	1256	25980.7	0.00000	0.0129
Precipitation of year previous	1	5611.4	1255	20369.2	0.00000	0.1643
Precipitation of season previous	1	674.3	1254	19694.9	0.00000	0.0197
Precipitation from the distant past	1	277.8	1253	19417.1	0.00000	0.0081
Soil depth*Precipitation of year	1	0.5	1252	19416.5	0.46723	0.0000
Soil depth*Precipitation of season	1	14.8	1251	19401.8	0.00012	0.0004
Soil depth*Precipitation of year previous	1	32.1	1250	19369.7	0.00000	0.0009
Soil depth*Precipitation from the distant past	1	33.1	1249	19336.6	0.00000	0.0010

variations in total rainfall, which creates randomness within the community's floristic composition (see Appendix 1). Moreover, seasonal floristic heterogeneity shows that there are groups of species in the seed bank that respond differently in terms of population dynamics. The difference in species composition indicated by the ANOSIM and NMDS analyses confirms the formation of groups in response to seasonal and annual variations in precipitation. These responses could be placed within two groups: 1) species that are present in all seasons and years, and 2) seasonal or annual occurring species, which reinforces the hypothesis by Araújo et al. (2005b) and Reis et al. (2006) regarding species that are permanent or that fluctuate over time within the caatinga's herbaceous flora.

Twenty-four species with a low density of seeds during the rainy season of year I disappeared during the dry season (see Appendix 1). This suggests that the significant seasonal reduction in richness can be explained by low seed densities. According to the literature, species differ in terms of germination requirements (such as light and temperature, for example) (Mayer and Poljakoff-Mayber, 1963; Bewley and Black, 1982, 1994; Araújo et al., 2006), or need some post-dispersal time to complete their maturation process (Bewley and Black, 1982; Borghetti, 2004; De Villiers et al., 2004). Thus, inadequate germination conditions (as this study was carried out in a greenhouse) and/or secondary dormancy may explain the seasonal disappearance of species with low seed densities. However, some species with low seed densities during the rainy season of year I (such as the herbaceous species *P. hyalina*, *D. biflora* and *P. trichoides*) presented significant increases in seed density during the dry season. This implies that their seeds can be dispersed during a drought or have dormancy mechanisms that prevent high seasonal recruitment; however, this was not considered in this study.

4.2. Variations in the pattern of density of the seed bank

The average seed densities were within the range of variation (50–42,000 seeds m^2) recorded in other dry tropical and subtropical environments worldwide (Kemp, 1989; López, 2003; Wagner et al., 2006; Kellerman and Van Rooyen, 2007; Zhao et al., 2007), and was lower in the litter than in the soil. In desert areas of North America (with arid climate), the litter holds few seeds, and most are stored in the superficial layers of soil (Guo et al., 1998); however, in savannah areas of the caatinga type (with semi-arid climate, according to Köppen's classification (Peel et al., 2007)), the differences in seed density between the litter and soil varies. For example, Costa and Araújo (2003) found higher seed densities in the litter than in the soil, while the opposite was found by Mamede and Araújo (2008), Lobo (2008) and Santos et al. (2010).

In dry seasonal environments, the time of the year when sampling takes place may lead to variations in seed density due to the type of seed bank sampled (persistent or transitory). Nevertheless, this study shows that differences in the number of seeds may occur even when the two types of seed bank are sampled. Despite the differences reported for seed banks of other areas of caatinga (Costa and Araújo, 2003; Mamede and Araújo, 2008; Lobo, 2008; Santos et al., 2010), the results of this study showed that soil depth accounts for 20% of the variation in the density of the seed bank (Table 3).

Additionally, the number of seeds in the seed bank varies seasonally and between years (Table 1). Such variations might be related to the periods of seed dispersal and seedling emergence, since in arid and semi-arid environments seed density may be higher after dispersal and lower after seedling emergence (Ghermandi, 1997; Caballero et al., 2005; Wang et al., 2005; Ning et al., 2007).

Specifically for the caatinga, seedling emergence occurs during the rainy season (Araújo et al., 2005a; Andrade et al., 2007; Araújo et al., 2007; Lima et al., 2007; Santos et al., 2007; Silva et al., 2008). However, as mentioned before, occasional rainfall during the dry season can also induce germination, which influences seed bank dynamics. Nevertheless, there is little chances of survival for seedlings recruited during the dry season – death generally occurs before the reproductive phase (Araújo et al., 2005a, 2007; Lima et al., 2007), which jeopardizes the production of seeds necessary to replenish the seed bank.

Erratic rainfall occurred in December 2005 and January 2008 while the seed bank was being monitored (Fig. 1). This inevitably occurs in caatinga vegetation, thus increasing the total rainfall during the dry season (Araújo et al., 2005a; Lima et al., 2007). However, the rainfall input of the dry periods of 2005 and 2008 only resulted in a difference in the estimated seed density between the rainy and dry seasons in 2008 (Table 1). The population densities of most species present in the seed bank decreased by about 50% between seasons in the second and third years (see Appendix 1), which indicates susceptibility to seasonal variations.

Evidence for arid and semi-arid environments also shows divergence in the relationship between total precipitation and increased seed density, with the following possibilities: 1) a higher number of seeds during periods with most rain, as recorded in southern Australia by Facelli et al. (2005) and in northeastern Brazil by Pessoa (2007) and Santos et al. (2010); 2) a higher number of seeds during the dry season, as recorded by Coffin and Lauenroth (1989) in northern Colorado and by Williams et al. (2005) in northeastern Australia; and 3) no difference in the number of seeds between the rainy and dry seasons, as recorded by López (2003) for the semi-arid region of Bolivia and by Mayor et al. (1999) in Argentina. These three trends were recorded in this study for the same area of caatinga, which indicates stochasticity in the seed bank's density, although the precipitation of previous years explained considerable variation in density (16% – Table 3).

Annual and seasonal differences (Table 1), and the distinct response scenarios that the seed banks of semi-arid environments present with respect to total rainfall (Coffin and Lauenroth, 1989; Mayor et al., 1999; López, 2003; Facelli et al., 2005; Williams et al., 2005; Lobo, 2008; Santos et al., 2010), led us to question the predictive role of total rainfall in the seed dynamics of caatinga soil.

On one hand it might be too early to discuss here the effects of total annual rainfall (past and present) on total seed density, since three years might be insufficient for a robust analysis. Additionally, this study was conducted in a greenhouse and did not consider the possibility of dormant seeds in the soil, despite having sampled both the persistent and the transitory seed banks. However, the annual rainfall recorded for the year before the start of this study (2004) was of 1064.3 mm, which could explain the high total density during the first year analyzed (Table 1). This trend was maintained in 2005, when precipitation decreased 30% (733.4 mm) and there was significant reduction in the total seed density in 2006. Nevertheless, the amount of rainfall was 586.5 mm in 2006, and the total seed density in the third year was similar to that of the second, which indicates a weak relationship between prior annual precipitation and total seed density.

In addition, the lack of associations between the total rainfall during the sampling period (present time) and the variation of seed density estimated within each sample is an important indication that rainfall in the current year does not allow for a full understanding of seed bank dynamics. The precipitation in the current year might mainly influence plant reproduction (fruit and seed production) and only later the density of the seed bank. The relationship between reduced rainfall and seed density found in 2004 and 2005 suggests that a series of consecutive years with high values of total precipitation are necessary to maintain the stock of seeds of the seed bank.

Overall, this study showed that the seed bank is rich in herbaceous species, yet the density and richness of species are low in the litter. Furthermore, about 43% of the variation in species richness and density of soil seed bank was explained by the influence of soil depth and the rainfall of previous years, which indicates a delay in the influence of climatic variations on the dynamics of the seed bank. In addition to precipitation and soil depth, factors that are intrinsic (such as period of germination and dormancy and longevity mechanisms) and extrinsic to the species (predation, pathogen attacks) may affect species richness and the amount of seeds in the seed bank. These factors, although not measured by this study, were present in the three years of our study and might account for the 57% of variation that was not explained by precipitation and soil depth.

4.3. Implications for conservation

The fragmentation and degradation of habitats in arid and semiarid environments has received much attention due to their threat to biodiversity. Studies on these problems have allowed for the construction of different regeneration models for wet and dry forests. These models consider the ecological roles of the species used for forest regeneration, which may help establishment (Uhl, 1987; Baider et al., 1999) or compete with other plants (Knoop and Walker, 1985; Peters, 2002), and thus affect the ecosystem's resilience.

Nevertheless, the characteristics of seed banks are also extremely important in regeneration processes, and the effects of past rainfall on the richness and density of such seed banks are not generally considered in regeneration models. The predictive power of previous rainfall on the dynamics of future seed bank in semiarid ecosystems can be considered high, which indicates that past climate characteristics may strongly influence the regeneration dynamics of disturbed areas. It is thus necessary to incorporate this factor into such regeneration models.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2012.10.008.

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