Effects of slash and burn practices on a soil seed bank of caatinga vegetation in Northeastern Brazil

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Abstract

The semiarid tropical zone covers 20% of Brazil and is dominated by caatinga, a thorny deciduous savanna well adapted to seasonal water shortage and periodic drought years. This study was focused on effects of slash and burn agriculture on the soil seed bank in a Caatinga area, in Sobral, CE, Brazil. Caatinga is rich in species, called therophytes, which remain as seeds in the soil during unfavorable seasons and rely on regeneration from the soil seed bank for persistence in the environment. Although slash and burn agriculture has been intensified in the region for the past three centuries, its effects on the soil seed bank are not well known. A seedling emergence greenhouse experiment was conducted to evaluate differences in seed bank density and diversity among soil samples collected before and after an experimental burning. Soil samples were previously submitted to sequential sieving to assess fire effects on different-sized seeds. Fire significantly reduced overall seed bank density, with smaller sieving fractions being most strongly affected. Shanon′s diversity index was also lowered by fire. Combined, these results show that agricultural practices represent a serious threat to plant biodiversity conservation in the Caatinga biome.

1. Introduction

The Brazilian semiarid tropical zone (SAT) occupies aproximately 20% of the country (Reddy, 1983). This author revised SAT climatic classification and proposed a modified Thornthwaite′s approach (Thornthwaite, 1933) as more appropriate to define SAT′s boundaries. The SAT is characterized by low mean annual rainfall, representing between 25% and 75% of mean annual potential evapotranspiration, which results in an important hydric deficit. Also, rainfall is erratic and concentred in a short rainy season (Reddy, 1983).

The drier portion of the Brazilian SAT zone, which periodically experiences drought years, has long been known as the Drought Polygon (Markham, 1967). The Drought Polygon has been the object of special federal legislation since 1936, due to the magnitude of the impact on human population of periodic droughts

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occurring in the region. It includes over a thousand municipalities located in 8 of 9 states of the Northeastern region and the Northern region of Minas Gerais state.

Ab'Saber (1974) described morfo-climatic characteristics of the Brazilian semiarid zone, defining as the typical landscape of the region the lowland areas over crystalline basement dated from the pre-Cambrian. Soils on the crystalline basement tend to be shallow, clayey and rocky, usually classified as Leptosols (Lithosols), Regosols and Luvisols (non-calcic brown) (see Sampaio, 1995). The dominant vegetation type, locally known as *caatinga* (Andrade-Lima, 1981), is a thorny deciduous savanna well adapted to seasonal hydric shortage (Cole, 1960).

According to Raunkiaer (1934) system of plant life form classification, one important feature reflecting the dependence of plants upon climate is their adaptation to survive the unfavorable season. The caatinga vegetation is rich in therophyte species, which remain as seeds in the soil during the unfavorable season (Costa et al., 2007), vegetating only in the rainy period. This life form represents an avoidance strategy for coping with seasonal drought. The woody species, classified as phanerophytes and chamaephytes, typically shed their leaves during the dry season (Andrade-Lima, 1981; Araújo et al., 2005; Costa et al., 2007).

The caatinga vegetation has a high spatial variability, both floristically and physiognomically (Andrade-Lima, 1981). However, it is hard to know to what extent the variation is due to differences in local physical conditions—for example, soil type—or to human interference (Sampaio, 1995). The available data about environmental characteristics and land use history are scarce (Barbosa et al., 2005). The semiarid zone of Brazil has been inhabited for more than 10,000 years (Sampaio, 1995), but population remained low until the 18th century, when Europeans initiated colonization of the inner and drier areas of the country. Nowadays, the population inhabiting the semiarid zone of Brazil is over 18 millions (Melo, 2004).

Livestock soon became the main economic activity of the Brazilian SAT zone. Historical records reveal that the activity was prosperous in the beginning (Brasil, 1863). Since the late 19th century, cattle raising has declined and social conditions have deteriorated with an ever increasing population pressure. Only recently, concerns about the sustainability of human activities in the Brazilian semiarid domain have arisen.

One important aspect to be considered is the loss of plant species biodiversity. Traditional agricultural practices involve slash-and-burn and shifting cultivation, and few studies have dealt with the environmental effects of cutting and burning of caatinga vegetation (Kauffman et al., 1993; Sampaio et al., 1993; Pereira et al., 2003).

In caatinga vegetation, the soil seed bank plays a crucial role in the maintenance of the herbaceous species populations (therophytes, cryptophytes and hemicryptophytes). As most of the herbaceous species of the caatinga are therophytes (Costa et al., 2007), they depend exclusively on the soil seed bank and must complete their life cycles within the short rainy season to maintain viable populations.

Considering that the annual herbaceous species account for the greatest part of caatinga's floristic richness (Araújo et al., 2005; Costa et al., 2007; Rodal et al., 2005), the potential impact of fire on the soil seed bank may represent a serious threat to native plant species conservation. We do not know of any previous studies dealing with effects of burning practices on the soil seed bank of caatinga vegetation.

In this study, we hypothesized that slash and burn practices may cause a significant reduction on caatinga soil seed bank density and diversity. Additionally, we searched for differential fire effects on different-sized seeds. We hypothesized that small-seeded species, which have fewer protective tissues around the embryo, would be more susceptible to damage by fire.

2. Materials and methods

2.1. Study area

The fieldwork was conducted in an experimental area of the *Centro Nacional de Pesquisa em Caprinos* (EMBRAPA-CNPC), in Sobral municipality, Ceará state, Brazil. The study area, *Fazenda Crioula*, is located at 3°44′56′ S and 38°34′27′ W and 145 m above sea level. Mean annual precipitation is 822 mm, with 82% of it occurring between February and May. Estimated mean temperature is 27.5 °C, oscillating between 26.3 °C in the coldest and 28.4 °C in the hottest month. Climatic data—rainfall and temperature—were obtained from the Ceará Foundation of Meteorology and Water Resources (FUNCEME).

A one-hectare rectangular area, left fallow for at least 20 years, with a previous history of use by domestic herbivores, was submitted to an experimental simulation of traditional agricultural management, as follows. Vegetation was slashed in the middle of the dry season. The bigger pieces of wood (which are traditionally used as firewood, fences and charcoal) were collected, and the fine wood debris were left to dry on the terrain surface.

Burning of the vegetation occurred by the end of the dry season, when the wood debris had lost most of their humidity. At this period of the year, after 151 days without rain, most species had finished dispersing their seeds and germination had not yet begun. The seed bank density was supposed to be near its annual maximum, cumulating both persistent and transient components.

The soil was classified as Non-Calcic Brown according to the Brazilian System, which corresponds to the Luvisol class in the FAO/UNESCO Soil Map of the World (www.fao.org/landandwater/agll/key2soil.stm). It was very rocky and moderately drained (Pinto, V.P.V.; personal communication).

2.2. Soil sampling

A total of 50 cylindrical soil samples (25 cm in diameter and 5 cm deep) were collected in the first week of November 2001, after slashing and previous to burning of the vegetation. Sample location in the study area was defined in a completely random design. Experimental burning occurred in November 27th, and a new sample collection was performed in the first week of December.

The unit sampling area was $5 \times 10^2 \, cm^2$, with total area sampled for each treatment comprising $2.5 \times 10^4 \, cm^2$. Before the fire, the litter layer was collected separately from the soil. Burning reduced it to ashes that were discarded in the second sampling. Both sample collections—pre- and post-fire—were kept in plastic bags in the laboratory for about two months until use in a seedling emergence experiment. Samples were then previously sieved and used in a greenhouse experiment were seedling emergence was recorded.

2.3. Experimental burning and soil temperatures

All vegetation around the burning site was previously removed, providing the area with fire protection borders 2 m wide. The experimental burning took place in the morning. Fire was set at the four corners of the area and allowed to spread by wind. Soil temperature was recorded at three depths: 1, 2 and 5 cm, with high-temperature resistant thermocouples (chrome–alumel) coupled to dataloggers and placed at two experimental points in the middle of the study area. Temperature data were collected every 25 s for 30 min, starting half an hour before and continuing until the extinction of the fire front.

2.4. Seedling emergence

As we intended to search for differential fire effects in seeds of different sizes, soil samples were previously submitted to sequential sieving. Each soil sample was subdivided in four sieving fractions, with distinct size exclusion limits (SELs). Sieving was performed without previous wetting. As soil structure was preserved, SELs presented in Tables 1, 2 and 4 are rather conservative, with many small-sized seeds enclosed in soil clumps remaining in fractions with SEL superior to its size. The litter layer was not submitted to sieving and was considered as an isolated fraction.

After sieving treatment, soil samples were placed on plastic trays over vermiculite substract in thin layers (up to 10 mm, as recommended by Dalling et al., 1994) and followed in a greenhouse experiment. We assumed that seeds of herbaceous species in the caatinga have positive photoblastism, as they prevail in an open vegetational formation.

The greenhouse was covered with clear corrugated (translucid) fiberglass panels, protected with nylon mesh 1 mm size, and kept in ambient temperature. Climatic data were registered at the climatic station located on campus (about 200 m far from the greenhouse). Average air temperature was 27.2 °C, ranging from 23.4 to 31.4 °C. Average air relative humidity was 74%, ranging from 54% to 100%. Average number of daylight hours was 9.8, ranging from 3.7 to 11.9.

Table 1
Mean number of seeds per sample (m) $\pm$ standard deviation (sd), density (seeds m^{-2}) and percentage of seed bank per sieving fraction, with size exclusion limits shown in the first column

Sieving fraction	m $\pm$ sd	seeds m^{-2}	%
Any	3.36 ± 3.83^c	67.2	4.7
$\geqslant 4.5$ mm	8.88 ± 9.92^b	177.2	12.3
4.5–1.5 mm	12.7 ± 10.5^b	254	17.7
1.5–0.6 mm	44.2 ± 36.1^a	884.4	61.6
$\leqslant 0.6$ mm	2.64 ± 8.98^c	52.8	3.7
All combined	–	1,436	100

Values with different superscript letters belong to different groups according to Nemenyi test, at 5% confidence level.

Table 2
Chi-square values (χ^2) for non-parametric multiple comparisons of seed density among soil sieving fractions (Nemenyi test)

Comparisons	Chi-square (χ^2)
1.5–0.6 $\times$ $\leqslant 0.6$	14.49^*
1.5–0.6 $\times$ litter	12.21^*
4.5–1.5 $\times$ $\leqslant 0.6$	8.94^*
1.5–0.6 $\times$ $\geqslant 4.5$	7.74^*
$\geqslant 4.5$ $\times$ $\leqslant 0.6$	6.75^*
4.5–1.5 $\times$ litter	6.58^*
1.5–0.6 $\times$ 4.5–1.5	5.63^*
$\geqslant 4.5$ $\times$ litter	4.47^*
Litter $\times$ / $\leqslant 0.6$	2.28
4.5–1.5 / $\geqslant 4.5$	2.11

Size exclusion limits of compared sieving fractions are shown in the first column. Values with asterisks are significant. $\chi^2_{0.05, \infty, 5} = 3.858$.

Samples were irrigated once a day for a 6-week period and emergent seedlings were transferred to individual cells, after classification into monocotyledoneous or dicotyledoneous. Growth and development of seedlings were followed until taxonomic identification was possible.

2.5. Soil seed bank analysis

Seed bank analysis was conducted after recording emergent seedlings (see Brown, 1992). This method allows to assess the pool of readily germinable seeds. Dormant seeds were not observed in this experiment. A floristic survey was realized through monthly random walks during the rainy period in a contiguous control plot, for comparisons between seed bank and standing vegetation. Sorensen's similarity index was calculated for the standing vegetation and seed bank (both before and after fire) communities (Ecological Methodology version 6.1, Exeter Software).

Density of the soil seed bank was determined for soil samples collected before and after fire, by counting the number of emergent seedlings, and expressed as seeds m^{-2}, as recommended by Baskin and Baskin (1998). Species richness was determined by observing the number of morphospecies, although not all have been taxonomically identified to species level. Values of species evenness and Shannon–Wiener Diversity index were also calculated for the two sampling groups (pre- and post-fire) according to Zar (1984).

Population densities of emergent seedlings were determined as well. Dominant species were defined as those whose populations accounted for at least 5% of total seed bank community. Germination curves were plotted for the seed bank as well as for the dominant species.

2.6. Fire effect

Pre-fire seed densities were determined for each sieving fraction and the litter layer and submitted to a non-parametric multiple comparison test, the Nemenyi test (Zar, 1984), to assess size distribution of the seeds in the bank. Fire effects were evaluated by comparing pre- and post-fire seed densities for the total seed bank and for each individual sieving fraction, using Kruskal–Wallis non-parametric ANOVA (Zar, 1984). Nemenyi test was also used to compare density distributions along post-fire sieving fractions. Finally, to test for differences in diversity related to fire effect, we used an adapted t-test as proposed by Hutcheson (1970) to compare sampling groups collected before and after fire.

3. Results

3.1. Seed bank

3.1.1. Seed density
A total of 3590 emergent seedlings were counted, which represents a total seed bank density of 1436 seeds m^{-2}. Seed distribution per sieving fraction are shown in Table 1. The sieving fraction which contained the seeds with diameter ranging from 1.5 to 0.6 mm; accounted for more than 60% of the emerging seedlings. Nemenyi test for differences between densities of different sieving fractions revealed three different groups, chi-square values for multiple comparisons are shown in Table 2.

Litter layer density (67.2 seeds m^{-2}) was low compared to total density. The sieving fraction containing seeds with diameters from 1.5 to 0.6 mm was the densest one. Fractions containing seeds with diameters greater than 4.5 mm or between 1.5 and 4.5 mm had intermediate densities, while the litter layer and the sieving fraction containing the seeds with diameter smaller than 0.6 mm represented the least dense group of soil fractions. The results show that a high percentage (more than 80%) of the seeds in this caatinga bank are below the size exclusion limit of 4.5 mm, and more than 65% of seeds are below 1.5 mm (Table 1).

3.1.2. Composition
Dicotyledons accounted for 60% and monocotyledons accounted for 40% of seed bank density. Taxonomic identification was possible for 70% of germinating seedlings and revealed a species richness of 56. Not all morphospecies were taxonomically identified to species level (Table 3). Herbaceous species (therophytes, hemicryptophytes and cryptophytes) accounted for 72%, and woody species (phanerophytes and chamaephytes) accounted for 28% of the bank density.

Euphorbiaceae was the richest family ($n = 8$ spp), followed by Convolvulaceae, Poaceae ($n = 7$ spp) and Asteraceae ($n = 4$ spp). In number of individuals, Borraginaceae was the most abundant family, followed by Poaceae, Cyperaceae, Asteraceae and Euphorbiaceae. The evenness value for the seed bank species composition was 0.587959. The Shannon–Wiener diversity index calculated for the emergent seedlings community was 3.414.

Standing vegetation as revealed by the floristic survey contained 77 species in 32 families. Asteraceae was the richest family, with 11 species. About a quarter of the species belonging to the local flora did not occur in the sampled seed bank, and 36% of the species identified in the seed bank did not appear in the standing vegetation floristic list. Sorensen similarity index for seed bank and local flora communities was 0.52; indicating a moderate similarity (Krebs, 1989).

Four species had populations that exceeded 5% of total seed bank community, being considered as dominant species. Together they accounted for 49% of the seed bank density. Three were herbaceous monocotyledons, and one was a woody dicotyledon. In order of population sizes: *Heliotropum* sp. (Borraginaceae, $n = 663$); *Rhyncospora contracta* (Cyperaceae, $n = 482$); *Brachiaria fasciculata* (Poaceae, $n = 416$) and *Panicum trichoides* (Poaceae, $n = 214$). See Table 3.

3.1.3. Germination kinetics
Seed germination initiated on the second day of irrigation. Germination rate rapidly attained a plateau and remained high for the first two weeks (see Fig. S1, electronic version). After a month of irrigation, germination

Table 3
List of species present in the soil seed bank (SB) and standing vegetation (SV), life-forms and population densities before (D_{BF}) and after fire (D_{AF}) in seeds m^{-2}

Families		Species	SV	SB	D_{BF}	D_{AF}	Habit	Life form
Acanthaceae	1	*Ruellia* cf. *paniculata* L.	X				Shrub	Ch
	2	*Dicliptera ciliaris* Juss.	X	X	3.6	0	Sub-shrub	Ch
	3	*Elytraria* sp.	X				Herb	Hm
Amaranthaceae	4	*Alternathera brasiliana* (L.) Kuntze	X	X	1.2	0	Herb	Th
	5	*Alternathera tenella* Colla	X				Herb	Th
Apocynaceae	6	*Rauwolfia ternifolia* Kunth	X				Sub-shrub	Ch
Araceae	7	*Taccarum peregrinum* (Schott.) Engl.	X				Herb	Cg
Asteraceae	8	*Baltimora recta* L.	X				Herb	Th
	9	*Bidens bipinnata* L.	X				Herb	Th
	10	*Blainvillea rhomboidea* Cass.	X	X	2.8	0.4	Sub-shrub	Ch
	11	*Centratherum punctatum* Cass.	X				Herb	Th
	12	*Delilia biflora* (L.) Kuntze	X	X	0.8	0	Herb	Th
	13	*Emilia sagittata* D.C.	X	X	55.6	18.8	Herb	Th
	14	*Melanthera latifolia* (Gardner) Cabrera	X	X	34.4	8.0	Herb	Th
	15	*Trichogonia salviifolia* Gardner	X				Herb	Th
	16	*Tridax procumbens* L.	X				Herb	Th
	17	*Pectis elongata* Kunth	X				Herb	Th
	18	*Stilpnopappus pratensis* Mart. ex D.C.	X				Sub-shrub	Ch
Boraginaceae	19	*Auxemma oncocalyx* (Allemão) Baill	X	X	1.6	0	Tree	Ph
	20	*Heliotropium* sp. 1	X	X	265.2	96.6	Sub-shrub	Ch
	21	*Heliotropium* sp. 2	X				Sub-shrub	Ch
Caesalpiniaceae	22	*Bauhinia cheilantha* (Bong.) Steud.		X	0.4	0	Tree	Ph
	23	*Caesalpinia bracteosa* Tul.	X				Tree	Ph
	24	*Senna obtusifolia* (L.) H.S. Irwin and Barneby	X	X	2.4	2.4	Sub-shrub	Ph
Combretaceae	25	*Combretum leprosum* Mart	X				Shrub "escandente"	Ph
Commelinaceae	26	*Commelina benghalensis* L.	X	X	22.0	0	Herb	Th
Convolvulaceae	27	*Evolvulus* cf. *filipes* Mart	X				Herb	Th
	28	*Ipomoea bahiensis* Willd ex.Roem. and Schult	X	X	0.4	1.2	Vine	Ch
	29	*Ipomoea* cf. *incarnata* (vahl) Choisy	X	X	2.4	0.4	Vine	Ch
	30	*Ipomoea hederifolia* L.	X	X	0.4	0.4	Vine	Ch
	31	*Ipomoea horrida* Huber	X	X	3.6	1.2	Vine	Ch
	32	*Ipomoea nil* (L.) Roth.	X				Vine	Ch
	33	*Merremia aegyptia* (L.) Urb.	X	X	4.8	8.4	Vine	Th
Cyperaceae	34	*Rhynchospora contracta* (Ness) Raynal	X	X	192.8	3.6	Herb	Th
	35	*Cyperus ligularis* L.	X	X	0.4	0	Herb	Th
Euphorbiaceae	36	*Acalypha multicaulis* Mull.Arg.		X	64.0	13.2	Sub-shrub	Ch
	37	*Bernardia sidoides* (Klotzsch) Müll. Arg.		X	9.2	0	Herb	Th
	38	*Chamaesyce hirta* (L.) Millsp.	X	X	0.4	0	Herb	Th
	39	*Chamaesyce hussopifolia* (L.) Small		X	0.4	0	Herb	Th
	40	*Croton glandulosus* L.		X	0.4	0	Sub-shrub	Ch
	41	*Croton blancheitanus* Baill	X				Shrub	Ph

Table 3 (continued)

Families		Species	SV	SB	D_{BF}	D_{AF}	Habit	Life form
	42	Dalechampia pernambucensis Baill.		X	0.8	0	Vine	Ch
	43	Euphorbia insulana Vell.	X				Herb	Th
	44	Phyllanthus tenellus Boxb		X	0.8	0	Herb	Th
	45	Phyllanthus niruri L.		X	1.2	0	Herb	Th
	46	Sebastiana brasiliensis Spreng.	X				Shrub	Ph
Fabaceae	47	Amburana cearensis (Allemão) A.C.Smith	X				Tree	Ph
	48	Arachis dardani Krapov and W. C. Gregory	X				Herb	Th
	49	Canavalia brasiliensis Mart. ex. Benth.	X	X	0.8	0.4	Vine	Ch
	50	Centrosema brasilianum (L.) Benth.	X				Sub-shrub	Ch
	51	Desmodium glabrum (Mill) D.C.		X	0.4	0	Sub-shrub	Ch
	52	Indigofera blanchetiana Benth.	X				Sub-shrub	Ch
	53	Macroptilium lathyroides (L.) Urb.		X	0.8	0.8	Vine	Ch
Labiateae	54	Hyptis suaveolens (L.) Poit.	X	X	25.2	0	Herb	Th
	55	Marsypianthes chamaedrys (Vahl) Kuntze	X	X	1.6	0.4	Sub-shrub	Ch
Loasaceae	56	Mentzelia fragilis Hub	X				Sub-shrub	Ch
Loganiaceae	57	Spigelia anthelmia L.	X	X	12.4	4.0	Herb	Th
Lythraceae	58	Cuphea circaeoides Sm. ex Sims	X				Sub-shrub	Ch
Malvaceae	59	Pavonia cancellata (L.) Cav.	X				Sub-shrub	Ch
	60	Pseudoabutilon spicatum (H.B.K.) R.E. Fries	X	X	6.0	4.8	Sub-shrub	Ch
	61	Sida abutifolia Mill.	X				Sub-shrub	Ch
	62	Sida jussieuana DC.	X	X	5.2	2.4	Sub-shrub	Ch
Mimosaceae	63	Mimosa caesalpiniifolia Benth.	X	X	3.2	1.2	Tree	Ph
	64	Mimosa cf. camporum Benth.	X	X	0.4	0.4	Sub-shrub	Ch
Onagraceae	65	Ludwigia sp.	X	X	2.0	0.4	Sub-shrub	Ch
Oxalidaceae	66	Oxalis cratensis Hook	X	X	4.8	2.0	Sub-shrub	Ch
	67	Oxalis glaucescens Norlind	X	X	0.8	0.4	Sub-shrub	Ch
	68	Oxalis oxyptera Progel	X				Sub-shrub	Ch
Passifloraceae	69	Passiflora foetida L.	X				Vine	Ch
Poaceae	70	Brachiaria fasciculata (Swartz) Parodi	X	X	166.4	10.4	Herb	Th
	71	Brachiaria mollis (Sw.) Parodi		X	0	0.4	Herb	Th
	72	Chloris inflata Link	X				Herb	Th
	73	Dactyloctenium aegyptium (L.) Willd	X	X	0.4	0	Herb	Th
	74	Digitaria bicornis (Lam.) Roem. and Schult.	X				Herb	Th
	75	Enteropogon mollis (Ness) Clayton		X	0.4	0	Herb	Th
	76	Eragrostis ciliaris (L.) R. Brown	X	X	1.2	0	Herb	Th
	77	Eragrostis glomerata (Walter) L.H. Dewey	X				Herb	Th
	78	Eragrostis tenella (L.) P. Beauv. ex. Roem. and Schult.	X				Herb	Th
	79	Panicum trichoides Swartz	X	X	85.6	1.6	Herb	Th
	80	Pennisetum polystachion (L.) Schult.	X				Herb	Th
	81	Setaria geniculata P. Beauv.	X	X	3.6	2.4	Herb	Th
Portulacaceae	82	Talinum triangulare (Jacq.) Willd	X	X	11.2	0	Herb	Th
Rubiaceae	83	Borreria laetis (Lam.) Griseb	X				Sub-shrub	Ch

Family	#	Species					Habit	
Scrophulariaceae	84	*Diodia* cf. *teres* Walter	X	X	4.8	0	Sub-shrub	Ch
	85	*Scoparia dulcis* L.	X	X	1.6	2.0	Sub-shrub	Ch
	86	*Angelonia pubescens* Benth.	X				Herb	Th
Solanaceae	87	*Physalis angulata* L.	X	X	0.4	0	Herb	Th
	88	*Solanum rhytidoandrum* Sendtn	X				Shrub	Ph
Sterculiaceae	89	*Melochia pyramidata* L.	X	X	0.8	0	Sub-shrub	Ch
	90	*Melochia longidentata* A. Goldberg	X				Sub-shrub	Ch
Tiliaceae	91	*Corchorus hirtus* L.	X	X	0.4	1.2	Herb	Th
Turneraceae	92	*Turnera* cf. *subulata* Sm	X				Sub-shrub	Ch
Urticaceae	93	*Laportea* cf. *aestuans* (L.) Chew		X	1.2	0	Herb	Th
Verbenaceae	94	*Lantana camara* L.	X				Shrub	Ph
Violaceae	95	*Hybanthus communis* (A.St.-Hil.)Taub	X	X	0.4	0	Herb	Hm
Unknown	96	Unknown	X		0.4	0.8	Vine	Hm

Species are presented in alphabetical order of families. Ph = phanerophytes, Ch = Chamaephytes, Hm = Hemicryptophytes, Cg = Cryptophytes geophytes, Th = Therophytes.

Table 4
Differences in seed bank densities among sieving fractions collected before and after fire

Sieving fraction (mm)	chi-square (χ^2)	P ($\chi^2_{0.05, \infty, 1}$)
$\geqslant 4.5$	317.681	<0.0001
4.5–1.5	387.122	<0.0001
1.5–0.6	57.927	<0.0001
$\leqslant 0.6$	42.507	0.0392

Size exclusion limits of sieving fractions are presented in the first column. Chi-square values for density comparisons are shown for each sieving fraction considered.

rate declined significantly, remaining almost null. The dominant species exhibited similar germination kinetics (Fig. S1).

The rapid germinative response of the seed bank is also illustrated by the fact that several herbaceous species flowered in the greenhouse before their cotyledons fell off. One species in particular, *Bernardia sidoides* (Euphorbiaceae), had flowers on the axil of the cotyledons by the 15th day of irrigation.

3.2. Fire effects

3.2.1. Fire characteristics

Fire consumed available biomass very slowly, in a patchy manner. Maximum soil temperature was reached at one of the two experimental points at 1 cm depth, remaining between 144 and 145 °C for at least 10 min (see Fig. S2, electronic version). Air temperature varied from 36 to 38 °C and air relative humidity was 70% at the moment of the burning. Wind speed varied from 1.6 to 2.5 m s^{-1} and the fire front speed was 1.83×10^{-2} m s^{-1}.

3.2.2. Seed density

A total of 661 seedlings emerged from soil samples collected after fire, which representsa seed bank density of 264 seeds m^{-2}. Fire reduced the overall seed density by about 80% ($\chi^2 = 83.3062$, $P < 0.0001$). Dicotyledons accounted for 91.2% and monocotyledons for 8.2% of the post-fire seed bank density. Seeds of monocotyledons appear to be more sensitive to high temperature impact than those of dicotyledoneous. The monocot/dicot ratio changed from 2/3 before fire to 1/10 after fire, considering all sieving fractions together. In the sieving fraction containing the seeds with diameter smaller than 0.6 mm, we observed complete fire mortality for monocotyledon seeds, which represented 70% of all seeds contained in this sieving fraction before fire. Fire effects in reducing seed density were significant for all sieving fractions, being greatest for the fraction which contained the seeds with diameter ranging from 0.6 to 1.5 mm (Table 5).

3.2.3. Composition and diversity

Burning reduced species richness in 44%. A total of 32 seedling morphospecies emerged from soil samples collected after fire, two of them died before possible taxonomic identification (see Table 4). Evenness value in the after-fire seed bank was 0.639814.

Shannon's Diversity Index calculated for the post-fire community was 3.226. The test performed for difference between Diversity Indexes was significant, ($t_{0.05(2),500} = 1.971320717$), showing that burning effectively reduced seed bank diversity.

4. Discussion

4.1. Seed density

The calculated density is high compared to values obtained for other seasonally dry Brazilian ecosystems, but low compared to other semiarid and desert environments (Table 5). This result indicates that caatinga vegetation exhibits the typical trend of high seed bank density common among arid and semiarid ecosystems.

Table 5
Seed bank density values from the literature, in seeds m^{-2}

Authors	Vegetation type	Local	Density (seeds m^{-2})	Method
This study	Tropical deciduous thorny savanna (*Caatinga*)	Sobral, CE-Brazil	1436	Seedling emergence
Costa and Araújo (2003)	Tropical deciduous thorny savanna (*Caatinga*)	Quixadá, CE-Brazil	807	Seedling emergence
Sassaki et al. (1999)	Tropical semi-deciduous savanna (*Cerrado*)	lItirapina, SP-Brazil	1006	Seed extracion and seedling emergence
Sassaki et al. (1999)	Tropical semi-deciduous woodland (*Cerradão*)	Itirapina, SP-Brazil	76.8	Seed extracion and seedling emergence
Grombone-Guaratini and Rodrigues (2002)	Tropical semi-deciduous forest	Campinas, SP-Brazil	32.3–49.6	Seedling emergence
Kemp (1989)	Hot deserts	USA	8000–30 000	Various
Caballero et al. (2003)	Shrub gypsum community	South Madrid, Spain	16 214	Seedling emergence
Gutierrez and Meserve (2003)	Arid thorny scrub	Fray Jorge, North Central Chile	4014.3–41 840.6	Seed extraction
López (2003)	Thorny woodland scrub	Prepuna, Bolivia	1157–1651	Seed extraction

The method employed for seed density determination is shown in the last column.

Moreover, the high standard deviation determined for density values indicates a high spatial variability of the seed bank, which is also a characteristic of arid ecosystems (Kemp, 1989).

However, it is difficult to establish comparisons due to methodological differences between studies. Some applied the seed extraction procedure (Gutierrez and Meserve, 2003; López, 2003), others adopted the seedling emergence procedure (this study, Caballero et al., 2003; Grombone-Guaratini and Rodrigues, 2002), and one combined the two techniques (Sassaki et al., 1999). It is also important to state that results are greatly affected by the season of sampling collection considering different dispersal phenologies among different vegetal communities.

4.2. Seed size

The high proportion of small-sized seeds (80% < 0.5 and 65% < 0.15 cm) in the seed bank indicates that it is mostly composed of therophytic or R-strategistic species (according to Crawley, 1997), which produce a large number of small propagules readily buried in the soil. Indeed, Thompson and Grime (1979) already noticed that small seeds were abundant in large and persistent seed banks, concluding that the selection for possession of a persistent seed bank included the selection for a small seed size.

4.3. Similarity between seed bank and flora

Moderate similarity between seed bank and local flora may be explained by a series of ecological issues such as primary and secondary dispersal (see Leal, 2003), microslope and specific physiological requirements for germination. Caballero et al. (2003), in a study of the seed bank structure of a semiarid environment in Central Spain, pointed out the importance of physical aspects of secondary dispersal, observing that microslope was a reliable predictor of seed density. Regarding germination requirements, there is little information available about dormancy among caatinga species.

4.4. Germination

Barbosa (2003) reviewed germination strategies of 8 caatinga woody species whose seeds lack dormancy, and observed that recently collected seeds of these species attained between 80% and 100% germination after 5 days of watering, similar to the results of this study. This indicates a rapid recruitment of new individuals at the beginning of the rainy season, experimentally reproduced by artificial irrigation in this study. The early

germinative boom assures an optimal use of the short rainy season. For herbaceous species, a short life cycle is another requirement for permanence in this environment.

Moreover, greenhouse observations indicate that dominant species show distinct germination peaks, indicating a temporal regulation of seedling emergence of different species in the community (see Fig. S2). Dominant species must present different germination physiologies, including amount of watering needed to trigger germination. This could lead to a temporal succession in germination peaks among many of the species in the community.

Rainfall is very erratic in the Caatinga biome (see Barbosa et al., 2006), a single rainfall event can account for a considerable proportion of the total annual rainfall and be followed by several days without rain. Therefore, the difference in germination requirements means that each species can explore a different opportunity window during the rainy period. This pattern would favor the maintenance of high diversity among annual species.

Morphological diversification in desert plants (Cody, 1989) contribute to species coexistence and diversity maintenance in arid and semiarid environments with resource pulse variability (see Chesson et al., 2004). Plants whose seeds germinate rapidly after the first rains may benefit from short rainy seasons, whereas plants with higher germination requirements may benefit from longer rainy seasons.

4.5. Fire effects

Soil temperature values registered in this study were similar to those obtained from other slash and burn experiments in Amazonia (Brinkmann and Vieira, 1971; Uhl et al., 1981); but low compared to the only available data for a Caatinga slash and burn experiment, where a maximum temperature of 300 °C at 1 cm below soil surface was recorded with pyronometers-plates with a spectrum of temperature-sensitive paints (Kauffman et al., 1993). In the present study, a sensitive and reliable method of temperature recording was employed. Yet, the use of only two temperature sampling points reduced the generality of the information.

Soil parameters measured indicate a low-propagating fire. According to fire ecology studies, fire severity increases with residence time (Whelan, 1995). Slashing of the vegetation increased fuel load availability, resulting in low propagating fire. Fire severity also varies with wind speed, air relative humidity and other physical aspects such as soil structure. Further studies on fire behavior are needed to precisely estimate soil temperatures during caatinga slash and burns. Nevertheless, the high temperatures and low fire speed recorded in caatinga slash and burn events predict a high severity and potential impact of this practice to the ecosystem, accordingly to our results.

The present study detected an 80% reduction of seed bank density and a significant reduction of diversity following fire. Thus, traditional agricultural practices do have a great impact over the soil seed bank, representing a serious threat to Caatinga plant species conservation. Herbaceous vegetation in particular, mainly composed by therophytic small-seeded species, displays little resilience to slash and burn practices.

It is also important to note that among herbaceous native communities many species are used as forage by traditional livestock populations. Those plant species have been submitted to stressful life conditions for over three centuries, due to human agricultural practices. We strongly suggest that successive slash and burn events with short fallow intervals may have contributed to diminishing livestock carrying capacity, by reducing native forrageous therophytic species diversity.

Acknowledgments

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2007.07.014.

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