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Structure of herbaceous communities in areas with different natural regeneration periods in the Brazlian semi-arid

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A B S T R A C T

The species composition and forest structure may change due to human disturbance. Changes in the arboreal component in regenerating forests has frequently been determined, but data on the herbaceous component are less available, especially those of tropical dry forests, despite their ecological and economic importance. Thus, in regenerating dry forests in the Brazilian semi-arid area, we tested the hypotheses that: (1) richness and diversity of herbaceous species are higher, but biomasses are lower in areas with longer regeneration periods; and (2) the aboveground herbaceous component is restricted to the rainy season, and species diversity, plant density and biomass vary with different patterns along this season. Four regeneration periods were analyzed: 2 (R2), 17 (R17), 39 (R39) and more than 60 years (mature caatinga) after grazed planted pasture was discontinued. The herbaceous component began growing after the onset of the rainy season (January) and disappeared in July after the rains ceased. Richness and plant density were highest in March, whereas biomass was highest in April and May. Mature caatinga and R39 had the highest herbaceous species richness (61 species), but the lowest biomasses (167 and 98 g m^{-2}), with the opposite occurring in R2 (48 and 381 g m^{-2}). Alpha diversity was highest in the mature caatinga, but beta diversity in R17. As a result, the herbaceous diversity increased while the plant density and biomass decreased as the regeneration period increased.

Keywords: Dry forests, Plant Community, Forest Regeneration, Biomass, Species Diversity.

Estrutura de comunidades herbáceas em áreas com diferentes períodos de regeneração natural no semi-árido brasileiro

R E S U M O

A composição de espécies e a estrutura da floresta podem mudar devido à perturbação humana. Mudanças no componente arbóreo em florestas em regeneração têm sido frequentemente determinadas, mas os dados sobre o componente herbáceo são menos disponíveis, especialmente os de florestas tropicais secas, apesar de sua importância ecológica e econômica. Assim, testamos as seguintes hipóteses: (1) a riqueza e diversidade de espécies herbáceas são maiores, mas as biomassas são menores em áreas com períodos de regeneração mais longos; e (2) o componente herbáceo acima do solo é restrito à estação chuvosa, e a diversidade de espécies, densidade de plantas e biomassa variam com diferentes padrões ao longo desta estação. Quatro períodos de regeneração foram analisados: 2 anos (R2), 17 anos (R17), 39 anos (R39) e mais de 60 anos (caatinga madura) após a descontinuação do pasto plantado. O componente herbáceo começou a crescer após o início da estação chuvosa (janeiro) e desapareceu em julho após o período de chuvas. A riqueza e a densidade de plantas foram maiores em março, enquanto a biomassa foi maior em abril e maio. A caatinga madura e R39 apresentaram a maior riqueza de espécies herbáceas (61 espécies), mas as menores biomassas (167 e 98 g m-2), ocorrendo o contrário em R2 (48 e 381 g m-2). A diversidade alfa foi maior na caatinga madura, mas a diversidade beta foi maior em R17. Como

resultado, a diversidade herbácea aumentou enquanto a densidade de plantas e a biomassa diminuíram com o aumento do período de regeneração.

Palavras-chave: Florestas Secas, Comunidade Vegetal, Regeneração Florestal, Biomassa, Diversidade de Espécies.

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Introduction

The herbaceous stratum of forest formations in semi-arid regions may harbor high species diversity (Araújo et al., 2007) and act to facilitate necessary ecological processes for maintaining ecosystems and local biodiversity, mainly in secondary stage successional vegetation (Feitoza et al., 2008; Graaf and Roberts, 2009; Jia et al., 2011). Its plants help maintain soil moisture, retain seeds by interweaving their roots, which are often superficial, and shade seeds of species which cannot germinate under direct sunlight (Araújo et al., 2005). As a group, herbaceous plants constitute the largest part of native pastures (Clement 2001; Giulietti et al., 2004), including legume species that can symbiotically fix atmospheric nitrogen (Freitas et al., 2012). They are also an important component of net primary productivity, carbon dynamics, energy flow, and nutrient cycling (Mureithi et al., 2014). Despite this importance, the herbaceous component of forest formations is still poorly studied, especially in regenerating dry forests of semi-arid regions. The level of human disturbance and environmental conditions in these areas can influence both the diversity and biomass of herbaceous species (Antongiovanni et al., 2020; Leßmeister et al., 2019).

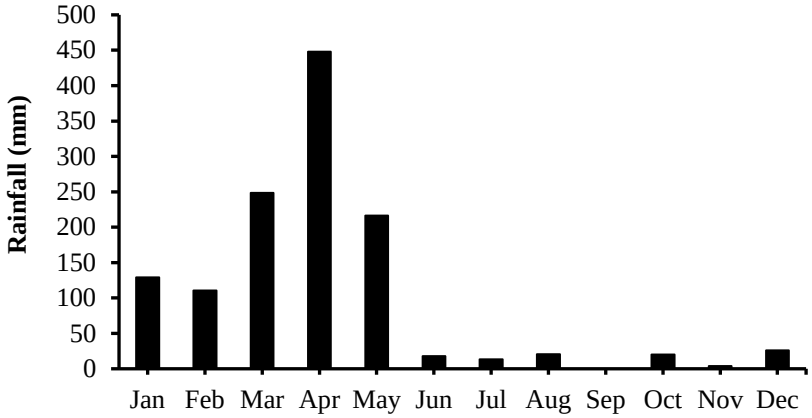
Hundreds of thousands of hectares of the native dry forest (caatinga) in the large semi-arid area in Northeast Brazil are slashed every year to produce firewood and to open land for the itinerant agricultural system (Sampaio et al., 1998). Furthermore, these activities are temporarily abandoned in an almost equivalent area and the caatinga regenerates until the next cycle. Above 80% of the caatinga is already in a successional stage (Drumond, 2000), and approximately 45% is held in a pioneering state of secondary succession (Perez-Marin et al., 2012). Detailed studies of floristic composition and secondary succession of old-growth vegetation types are necessary to subsidize establishing adequate management practices (Pereira Júnior, 2012; Dias et al., 2018).

Few studies have compared areas with different regeneration periods in semi-arid regions (Elmqvist et al., 2007; Franklin et al., 2016). Diversity is usually greater in areas with longer regeneration periods (Santos et al., 2006), but in some areas diversity is greater in the early stages (Santos, 2010), declining thereafter due to increasing shrub and tree coverage (Cheung et al., 2009; Mendes and Oliveira, 2011).

Due to the importance of regenerating anthropogenic environments and the limited knowledge on the herbaceous community structure in forest formations of semi-arid regions, this study aimed to analyze the herbaceous community structure in caatinga areas with different regeneration periods to provide data which could subsidize proper conservation strategies. Thus, the following hypotheses were tested: (1) richness and diversity indices of herbaceous species are higher, but biomasses are lower in areas with longer regeneration periods; and (2) the aboveground herbaceous component is restricted to the rainy season, and species diversity, plant density and biomass vary with different patterns along this season.

Materials and methods

The study was conducted from February to June 2009 in four successional stages in the caatinga of Tamanduá farm (06°59'13" - 07°00'14" S and 037°18'08" - 037°20'38" W), Santa Teresinha municipality, Paraíba state, Brazil. The farm is at an average altitude of 240 m with soils predominantly belonging to the Lithic Leptosol classification (WRB/FAO, 2014). The area has a Bsh (semi-arid) climate according to the Köppen classification (1948), with an average annual temperature of 32.8°C and an average annual rainfall of 600 mm, with large variation along the years, but usually concentrated from February to May (Figure 1).



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2 Fig. 1 Monthly rainfall in 2009 in Santa Teresinha municipality, Paraíba state, Brazil

3

Areas in four successional stages were selected: 1) native caatinga areas which were cleared in 1965 and planted with perennial cotton until 1970, at which time they were planted with buffel grass (*Cenchrus ciliaris* L.) and used as pasture until 2007. They were then fenced in to prevent cattle entry and left to naturally regenerate. These areas were covered by herbaceous vegetation and were called R2; 2) areas which were deforested, planted with perennial cotton and *C. ciliaris* on the same dates as the previous ones, but left to naturally regenerate since 1992. These areas (called R17) were dominated by a single species of tree-legume (*Mimosa tenuiflora* (Willd.) Poir), and the coverage area of the shrub and tree canopy was 6045 m^2 ha^{-1}; 3) areas which were planted with cotton from 1965 to 1970 and had been naturally regenerating for 39 years until 2009. These areas were covered by shrubs and trees with a canopy cover of 6278 m^2 ha^{-1} and were called R39; and 4) mature Caatinga vegetation areas which had not been clear cut or seriously disturbed since at least 1950. These areas were covered with various shrub and tree species with a canopy cover of 8458 m^2 ha^{-1} and were considered as mature caatinga (MC).

The monthly rainfall was recorded during 2009 by a weather station installed at the farm (Fig. 1). The physical and chemical analyses of the topsoil from all areas (Table 1) were described in a previous article (Freitas et al., 2012).

Next, three plots of 60 m x 30 m in each of the four regeneration stages were delimited in 2007. Then five subplots of 1.5 m x 2.5 m were randomly distributed within these plots. Each subplot was divided into 15 subsubplots of 0.5 m x 0.5 m, organized in three rows of five subsubplots. All herbaceous plants were cut at ground level in the subsubplot in the center row and two on the left and right rows so that no subsubplot was harvested adjacent to one where the plants had been previously cut. Harvests were performed monthly from March (early rainy season) to June (end of the rainy season). All plants were separated by morphospecies, counted, dried for 72 hours at 60°C and weighed. The plant was considered an herbaceous plant if it possessed a green stem with a low level of lignification.

Reproductive material of species found in the subplots were collected within the plots and herborized according to the usual herbarium techniques. The species were identified by comparison with material deposited in the Dárdano de Andrade Lima (IPA) and UFP-Geraldo Mariz (UFPE) herbariums using taxonomic keys and specialized literature. Those with a dubious identification were sent to specialists in the specific taxa. The APG III (2009) classification system was adopted. The spelling of the species names was verified using the Kewensis Index (http://www.ipni.org/ipni/plantnamesearchpage.do).

Table 1 Soil chemical and physical properties in caatinga areas regenerating for 2, 17, 39 and >60 years (R2, R17, R39, and MC, respectively) in Santa Teresinha municipality, Paraíba state, Brazil.

Area	pH	Extractable					Organic	Granulometry		
		P	K	Na	Ca	Mg	carbon	sand	silt	clay
		mg kg^{-1}	-------- $cmol_c$ kg^{-1} ---------				---------- g kg^{-1} ----------			
R2	5.61	2.72	0.25	0.12	4.31	1.37	8.37	638	269	93
R17	5.94	1.55	0.29	0.11	5.02	1.66	8.61	645	239	117
R39	5.79	1.65	0.31	0.13	3.91	1.29	14.10	668	239	93
MC	6.41	2.62	0.29	0.11	5.22	1.36	11.62	648	229	123

Source: Freitas et al., (2012)

Total plant density and herbaceous species richness were calculated from the shoot biomass that was harvested in relation to the areas and harvest months. The species richness of the five sub-subplots (1.25 m^2) was transformed into 1 m^2 using the rarefaction index of Sanders (1968). The normality and the homogeneity of the data were assessed with the Shapiro-Wilk and Levene tests, respectively. The data were subjected to analysis of variance (ANOVA), and the means were compared by the Tukey test at the 0.5 probability level. Alpha diversity was determined using the Shannon-Wiener index, beta diversity using the Whittaker index and evenness using the Pielou index (J'). Species' abundances were transformed to log (X+1) to determine the similarity of the areas with respect to the species, and the Bray-Curtis coefficient was used to generate a multidimensional scaling (MDS) graph. The observed differences in the multivariate analysis were tested by PERMANOVA.

Results

The herbaceous flora in the areas of all regeneration stages consisted of 78 species, belonging to 52 genera and 26 families (Table 2). The highest number of species occurred in the mature Caatinga (MC) and R39 (61 species each), followed by R17 (56 species) and R2 (48 species). Of the 78 species, 29 were present in all stages, and 11 were identified in only one of any of the stages. The stages with the most unique species were MC and R17, each with four species, followed by R2 with two species and R39 with only one unique species.

Table 2 Total number of herbaceous plants (15 m^2) present along the four months of growth in the rainy season, in caatinga areas regenerating for 2, 17, 39 and >60 years (R2, R17, R39, and MC, respectively) in Santa Teresinha municipality, Paraíba state, Brazil

Family	Specie	R2	R17	R39	MC
Acanthaceae	*Dicliptera ciliaris* Juss.	0	0	9	15
Aizoaceae	*Trianthema portulacastrum* L.	109	21	4	0
Amaranthaceae	*Alternanthera brasiliana* (L.) Kuntze	0	5	11	54
	Froelichia humboldtiana Seub.	20	0	0	0
	Gomphrena demissa Mart.	1	6	0	1
Asteraceae	*Bidens pilosa* L.	31	27	19	20
	Centratherum punctatum Cass.	0	1	65	22
	Stilpnopappus pratensis Mart. ex DC	0	0	28	0
	Tridax procumbens L.	7	1	44	0
Boraginaceae	*Heliotropium elongatum* (Lehm.) Willd.	3	0	3	0
	Heliotropium procumbens Mill.	0	23	72	10
	Heliotropium ternatum Vahl	0	4	0	0
Capparaceae	*Cleome guianensis* Aubl.	0	11	8	11
Convolvulaceae	*Evolvulus filipes* Mart.	2	4	6	66
	Evolvulus frankenioides Moric.	93	18	100	44
	Ipomoea bahiensis Willd. ex Roem. & Schult	0	1	14	3
	Jacquemontia confusa Meisn.	0	1	0	10
	Jacquemontia evolvuloides Meisn.	131	33	7	85
	Jacquemontia densiflora Rusby	0	1	0	0
	Merremia aegyptia (L.) Urb.	1	0	1	0
	Not identified 1	11	0	1	0
	Not identified 2	0	0	0	7
Cyperaceae	*Cyperus* sp.	41	341	15	18
Euphorbiaceae	*Croton hirtus* L' Hér.	81	4	1	0
	Not identified	118	8	101	160
Leguminosae Caesalpinaceae	*Chamaecrista nictitans* Moench	4	4	11	70
	Chamaecrista serpens Greene	0	0	26	17
	Senna obtusifolia (L.) H.S. Irwin & Barneby	1	0	7	44
	Not identified 1	0	0	1	40
	Not identified 2	11	9	7	76
Leguminosae Papilionoideae	*Arachis pusilla* Benth.	0	0	2	41
	Centrosema brasilianum Benth.	0	1	5	53
	Centrosema pascuorum Mart. ex Benth.	31	6	5	2
	Macroptilium gracile (Poepp. ex Benth.) Urb.	38	1	2	8
	Stylosanthes humilis Kunth	84	101	44	452
Lamiaceae	*Hyptis suaveolens* (L.) Poit.*	1860	1429	1124	490
Lytraceae	*Cuphea campestris* Mart. ex Koehne	116	5	142	119
Malvaceae	*Herissantia* sp.	20	4	0	4

	Pseudomalachra plumosa (Cav.) H. Monteiro	17	48	11	17
	Sida galheirensis Ulbr.*	98	76	12	9
	Waltheria indica L.	12	0	4	4
	Waltheria macropoda Turcz.	0	0	9	35
	Waltheria rotundifolia Schrank	390	24	0	7
	Not identified	4	0	0	0
Molluginaceae	*Mollugo verticillata* L.	0	7	0	21
Onagraceae	*Ludwigia octovalvis* (Jacq.) P. H. Raven	12	1	18	4
Oxalidaceae	*Oxalis divaricata* Zucc.	0	11	30	102
Poaceae	*Aristida setifolia* Kunth	4	28	31	88
	Bouteloua americana (Desv.) Pilg.	43	48	132	173
	Cenchrus ciliaris L.	129	14	3	0
	Chloris virgata Sw.	20	66	80	13
	Dactyloctenium aegyptium (L.) K. Richt.	0	5	4	0
	Eragrostis ciliaris (L.) R. Br. In Tuckey	0	1	54	34
	Paspalum faveolatum Steud.	44	0	4	35
	Tragus berteronianus Schult.	168	9	417	175
	Urochloa trichopus (Hochst.) Stapf	54	128	277	177
Polygalaceae	*Polygala brizoides* A. St.0Hil.	27	9	11	41
Rhamnaceae	*Crumenaria decumbens* Mart.	27	71	250	324
Rubiaceae	*Diodia radula* (Willd. ex Roem. & Schult.) Cham. & Schltdl.	891	7	78	170
	Diodia teres Walt.	0	0	0	9
	Borreria scabiosoides Cham. & Schltdl.	3	0	0	24
Scrophulariaceae	*Scoparia dulcis* L.	6	20	221	161
Tiliaceae	*Corchorus argutus* Kunth	8	8	111	152
Turneraceae	*Piriqueta guianensis* N.E.Br. Subsp. *elongata* (Rolfe & Urb.) Arbo	5	1	0	28
	Turnera pumilea Poir.	4	17	1	8
	Turnera subulata Sm.	0	0	0	2
	Not identified	0	0	0	9
Verbenaceae	*Stachytarpheta sanguinea* Mart.	8	14	111	227
Zygophyllaceae	*Tribulus terrestris* L.	5	27	16	18
Not identified	1	0	5	0	0
	2	0	1	3	24
	3	0	2	8	0
	4	3	0	23	28
	5	2	0	7	4
	6	0	1	2	23
	7	0	0	3	20
	8	0	3	5	0
	9	0	3	0	0

(*sub-shrub speciess)

The number of species was already high in March in all stages and decreased in June, with the mature caatinga maintaining the highest and the most recent regeneration area (R2) the lowest numbers (Figure 2). All plants had dried in July and a high proportion had fallen, and many others were fragmented, making their identification a difficult and meaningless task.

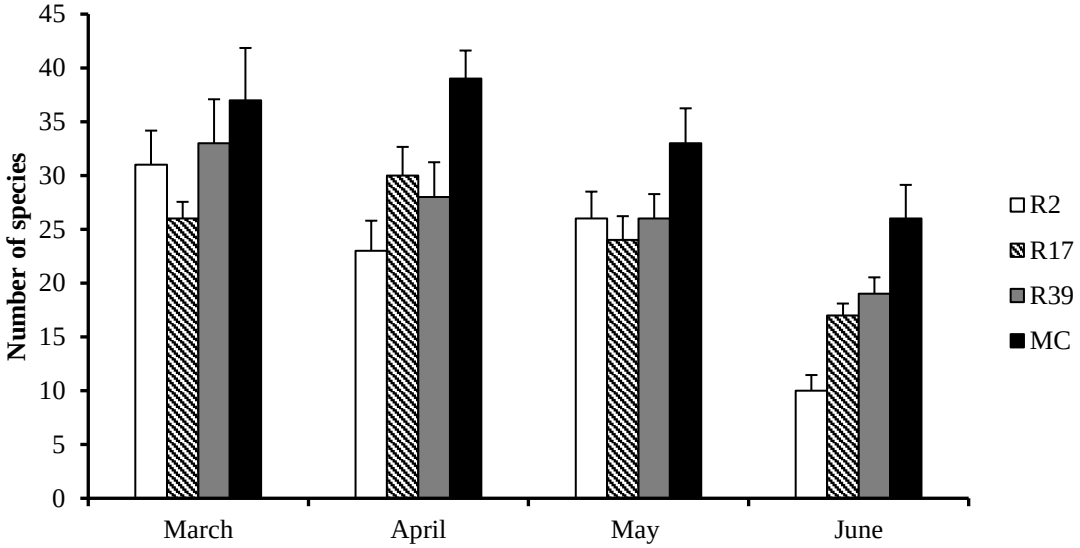

Fig. 2 Number of herbaceous species (3.75 m²) along the rainy season in caatinga areas regenerating for 2, 17, 39 and >60 years (R2, R17, R39, and MC, respectively) in Santa Teresinha municipality, Paraíba state, Brazil.

Plant density (Figure 3) generally decreased gradually from March to June in all regeneration stages and the decrease was most pronounced in the more recent stage (R2), which started with a significantly higher density than in the other stages (718 plant m^{-2} versus < 500 plant m^{-2}). The densities in all stages did not differ from April on, and by June were less than 120 plant m^{-2}.

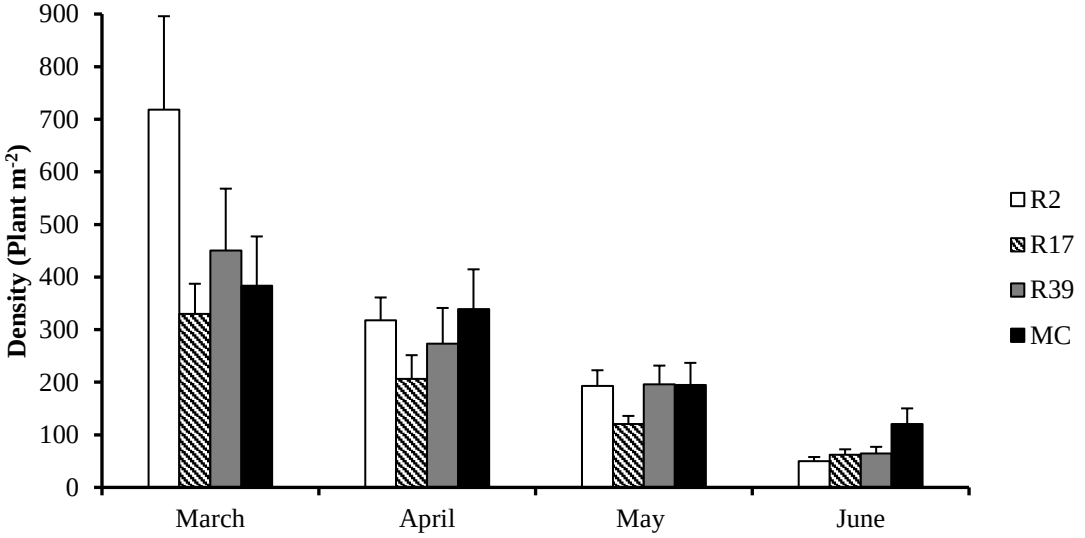

Fig. 3 Mean (± confidence interval of 95%) density of herbaceous plants (1 m²) (*P*=0.0228) along the rainy season in caatinga areas regenerating for 2, 17, 39 and >60 years (R2, R17, R39, and MC, respectively) in Santa Teresinha municipality, Paraíba state, Brazil.

Biomass progressed in a different pattern (Figure 4). It was also higher in R2 than in the other stages in March, but it peaked in R2 (381 g m^{-2}) and MC (167 g m^{-2}) in April, and in R17 (280 g m^{-2}) and R39 (98 g m^{-2}) in May. All biomasses were lower than 130 g m^{-2} by June, and still slightly higher in the two youngest regeneration stages. The increase in biomass in April with a concomitant decrease in plant density indicates that the plants were expanding, and some were outcompeted and died.

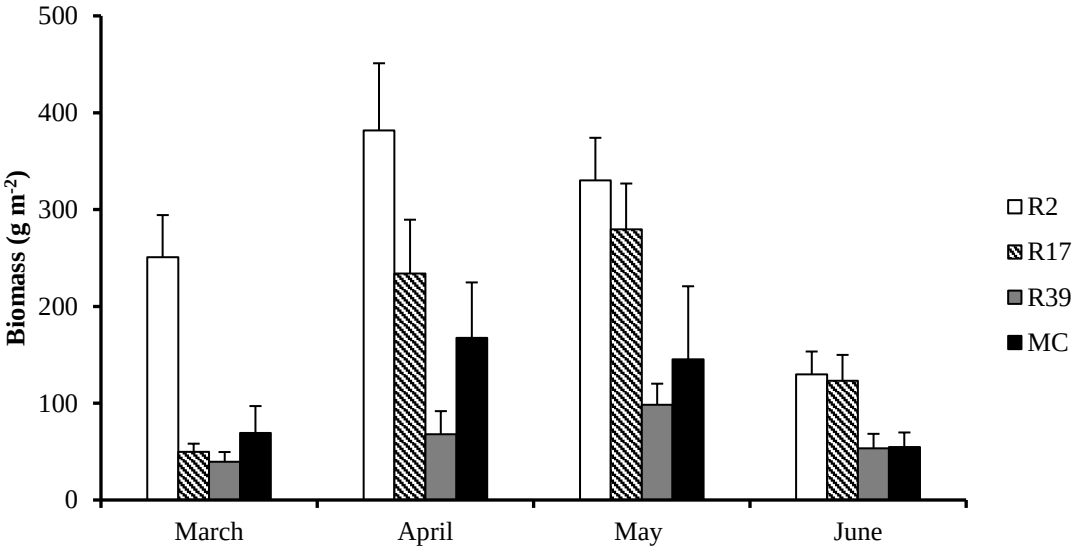

Fig. 4 Mean (± confidence interval of 95%) biomass of herbaceous plants (1 m²) (*P*=0.1678) along the rainy season in caatinga areas regenerating for 2, 17, 39 and >60 years (R2, R17, R39, and MC, respectively) in Santa Teresinha municipality, Paraíba state, Brazil.

Beta diversity was higher in the two intermediate regeneration periods (R17 = 2.74 and R39 = 2.73) than in the mature caatinga (1.88) and the more recent regeneration (R2 = 1.83). On the other hand, alpha diversity (*H'*) and richness per sample (*S*) were highest in the mature caatinga, with little differences among the other regeneration stages (Figure 5).

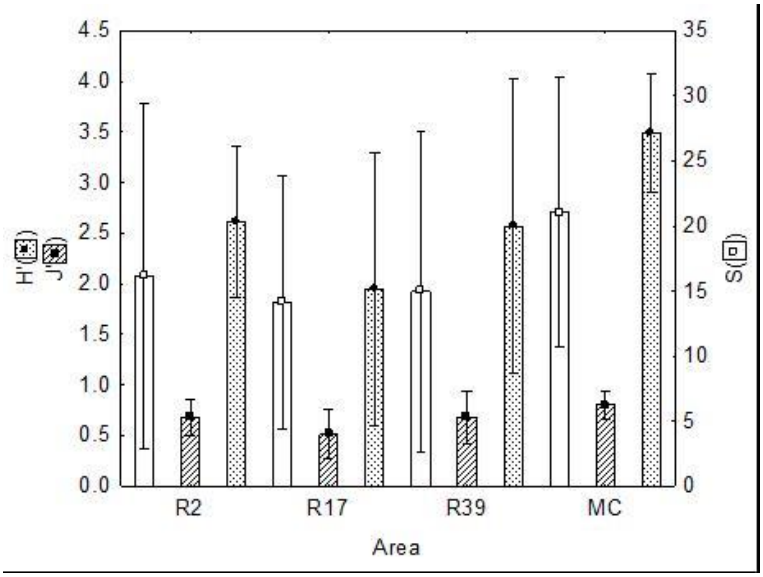

Fig. 5 Mean (± 2 *SD*) in 1 m² areas of diversity (*H'*), equitability (*J'*) and richness (*S*) of herbaceous species in caatinga areas regenerating for 2, 17, 39 and >60 years (R2, R17, R39, and MC, respectively) in Santa Teresinha municipality, Paraíba state, Brazil.

Evenness (*J'*) was similar in all stages. Multidimensional scaling (Figure 6) revealed a clear separation of the months (along the horizontal axis) and a less clear separation of the successional

stages (along the vertical axis), indicating that the flora is distinct and dynamic. The multivariate PERMANOVA analysis confirmed that the months and the successional stages differed significantly.

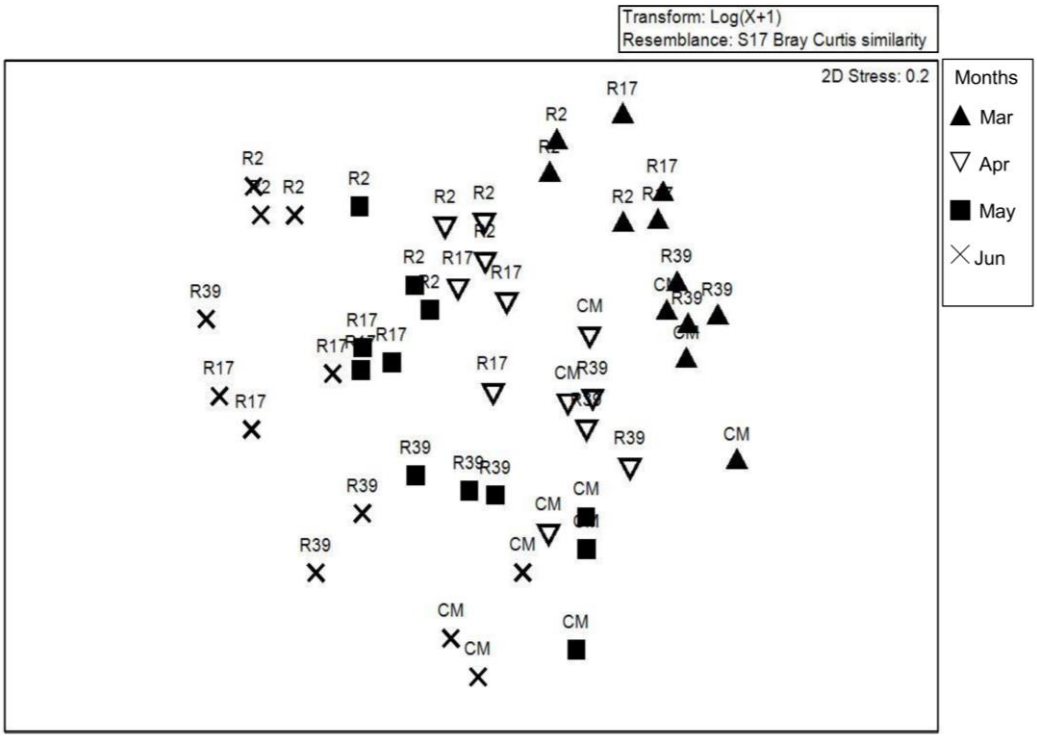

Fig. 6 Multidimensional scaling (MDS) of herbaceous species abundance present in different months of the rainy season, in caatinga areas regenerating for 2, 17, 39 and >60 years (R2, R17, R39, and MC, respectively) in Santa Teresinha municipality, Paraíba state, Brazil.

Discussion

Similar to the vegetation of other semi-arid regions, caatinga still harbors a large diversity of herbaceous species, notwithstanding its large anthropic changes (Giulietti et al., 2004). The number of herbaceous species (78) in the experimental area is near the center of the range of values observed in other caatinga areas: 62 species were identified in different microhabitats in Caruaru, Pernambuco state (Araújo et al., 2005); 70 species in areas with soils developed from the crystalline shield and 83 species in areas derived from sedimentary material in Iguatu, Ceará state (Lima et al., 2012); and 69 and 78 species in areas derived from these same parent materials in Petrolândia, Pernambuco state (Silva et al., 2009). The number of species is also within the range of those identified in other semi-arid regions: 46 species in the Mediterranean area within the north Jordan Basalt Plateau (Alhamad et al., 2010); 65 species in shrubland and grassland ecosystems in the northern Loess Plateau of China (Jia et al., 2011); 96 species in a savanna of Argentina (Arias et al., 2003); and 117 species in a savanna of Uganda (Okullo and Moe, 2012).

The two areas with the longest regeneration time (MC and R39) had a higher number of herbaceous species than the areas with less regeneration time, despite having the largest numbers of shrub and tree species and largest canopy covers, thus increasing the likelihood of competition between trees and herbs. This was probably due to a higher probability of random arrival and seedling establishment from other areas along the longer regeneration time. One study in another caatinga area (Santos et al., 2006) reported similar results, but larger numbers of herbaceous species were found in disturbed areas in other areas (Santos 2010; Zerbo et al., 2016; Leßmeister et al., 2019). The disturbances may provide microhabitats for short-lived annuals (therophytes) with high growth and reproductive rates (Grime 1979). The discrepancy in results indicates that there is no clear tendency of the effect of regeneration periods on the number of herbaceous species, which is also

influenced by the edaphoclimatic conditions, the previous usage-history of the area, the proximity and composition of vicinal vegetation and the random arrival of seeds (Bakker, 1998; Grace, 1999; Anitha et al., 2008).

The environmental factor which most influenced richness, density and biomass of the herbs throughout the year was the uneven distribution of rainfall, as has been reported in other semi-arid areas (Briggs and Knapp, 1995; O'Connor et al., 2001; Haddad et al., 2002; Santos et al., 2009). The concentrated and poorly distributed rains limited the recruitment and growth cycle of the herbaceous species to the rainy season (Fernandes and Queiroz, 2018; Silva et al., 2016), so that no alive aboveground biomass of any herbaceous species was present during the several months of the dry season. *Cactaceae* and *Bromeliaceae* species that occupy the herbaceous stratum remain alive during the dry season in other Caatinga areas (Albuquerque, 1999), but they are absent in the area where this study was conducted.

The largest initial density and highest biomass of the herbaceous stratum in the area regenerating for only 2 years most likely occurred because of the lower competition from shrubs and trees, whose plants were recently established and still in their initial growth stage. Lower light availability in the more advanced regeneration stages (MC and R39) may have been a limiting factor for the growth of the herbaceous species (Borges 2002; Pereira et al., 2005; Wayne and Auken 2010; Giladi et al., 2012). The deciduous shrub and trees have a fast response to the first rains, breaking dormancy and regenerating their leaves in the wood structure already present. The herbaceous species have to regenerate the aboveground structures from seeds or belowground organs, taking longer to respond to the increased water availability than the deciduous shrubs and trees. The diversity of herbaceous species generally increases and the biomass decreases with increasing regeneration period (Foley et al., 2005; Buscardo et al., 2008).

The biomass peaks in R17 and R39 one month later than in the other stages do not mean that all the species present in these areas had lag periods in their growth cycles. In fact, separating the plants of all species revealed that the species had biomass peaks in different months and that some species even had growth cycles limited to one single month (Freitas et al., 2012). A consequence of this separation is that considering biomass production in each area as the sum of the biomass peak of each species over the rainy cycle results in increases from 40 to 126 % in relation to the biomass of the month with the highest stand biomass. The highest increase occurred in the mature caatinga (167 to 378 g m^{-2}), probably due to the higher species richness with biomass peaks of the different species distributed along the rainy seasons. The lowest increase in R17 (280 to 393 g m^{-2}) was probably due to its lower species richness and more uniform tree cover (almost all *Mimosa tenuiflora* (Willd.) Poir trees). This indicates that measuring the biomass stock at any date underestimates biomass production along the rainy season.

No evaluation of herbaceous biomass was found for caatinga areas without grazing or manipulation of the vegetation. Grazing in areas used as pasture reduced (as expected), while cutting part of the trees and shrubs increases the herbaceous biomass stock (Santos et al., 2006; Ydoyaga-Santana et al., 2011). Comparisons of herbaceous biomass undergoing different tropical dry forest regeneration stages are also scarce in other semi-arid regions of the world. The herbaceous biomass under the tropical dry forest in a Mexican area with 924 mm annual rainfall was 73 g m^{-2}, while it increased to 472 g m^{-2} in the planted pasture without trees (López-Santiago et al., 2019). The lower biomass under this forest than under caatinga (73 g m^{-2}, versus MC, 167 g m^{-2}) may result from a more closed canopy, while the higher biomass in the pasture than in the 2-year regeneration of caatinga (381 g m^{-2}) may come from several factors, including higher rainfall and higher size, as well as better management of the planted grass.

In addition to the effect of trees and shrubs, water availability is considered the main influence on the herbaceous biomass stocks. This availability is usually evaluated based on annual rainfall. Examples of herbaceous biomass and rainfall relations in semi-arid regions of the world area can be cited: the biomass with annual rainfall of 239, 350 and 430 mm in Kenya was 73, 101 and 171 g m^{-2}, respectively (Augustine 2003); the biomass with 547 mm in South Africa varied from 110 to 230 g m^{-2} (Jacobs et al., 2008); the biomass in Mexico with 680 mm was 340 g m^{-2} (Jaramillo et al., 2008); and finally, the biomass in Burkina-Faso with 857 mm varied from 347 to 401 g m^{-2} (Sawadogo et al., 2005). These examples establish a general range of herbaceous biomass stocks, but comparisons among areas would have to consider that many other environmental factors influence plant growth. Even water availability is influenced by factors other than rainfall, particularly

temperature reflected in different potential evapotranspiration. Most caatinga sites, like Santa Teresinha, have higher potential evapotranspiration than any other large semi-arid area in the world, because of their position closer to the equator and therefore have less available water than semi-arid areas in Africa and Mexico with similar rainfall.

Contrary to biomass, the density of herbaceous plants has been determined in several undisturbed caatinga areas, usually varying from 10 to 100 plant m^{-2} (Araújo et al., 2005; Reis et al., 2006), but reaching up to 1000 plant m^{-2} in more open areas (Santos et al., 1992). The density of herbaceous plants has not usually been determined in other semi-arid areas, and no data was found for densities under different forest regeneration stages.

The number of species and biomass in other regions are related so that the highest richness is attained at a certain range of accumulated biomass. The optimal biomass range to maximize the number of species in South African savannas maintained without fire and animal grazing is 260 to 270 g m^{-2} (Van Coller and Siebert, 2015). Higher biomass, which accumulates in the absence of grazing, results in tall grass species growing and in turn shading the lower forbs and reducing the overall diversity (Jacobs and Naiman, 2008). There was an inverse quadratic response above this threshold in fully fenced areas because of larger plant size and higher biomass as a result of herbivore exclusion, implying that fewer species and individuals can coexist (Oksanen 1996). There is no data relating herbaceous biomass and species diversity in caatinga areas, but trees and shrubs in the native vegetation form denser stands than in savanna areas, and grasses are not the dominant species in most of the area. In fact, pastures are usually planted with African grasses, such as *Cenchrus ciliaris* which had been previously planted in the experimental area.

Herb biomass in R2, R39 and MC seems to have been more influenced by plant density, while that in R17 by the size of the plants. R17 had a more open tree and shrub canopy than R39 and MC, allowing greater light passage, influencing the size and development of the herbaceous plants. Herbaceous plants in R2 plots with no large trees and shrubs were subjected to stronger light intensity and higher temperatures, which may result in smaller plants than those from other areas as a survival strategy (Saynes et al., 2005; Romero-Duque et al., 2007).

The mature caatinga had the highest gamma and alpha diversity and the lowest beta diversity. The alpha richness was not significantly different among the other three areas, but R17 and R39 had the highest turnover rate (β diversity), indicating that the landscape where the replicated plots of these two regeneration periods were located may be more variable than those of the oldest regeneration area. The R2 area had low gamma and beta diversities, suggesting that the sites where grazing was recently discontinued have the lowest turnover and landscape variation. Therefore, the set of species occupying different sites are more diverse in the initial succession stages than in later succession stages. The random incoming seeds from neighboring areas in the initial stages and the progressive selection of those more apt to compete may explain the higher initial variation and the tendency to a more uniform distribution in the different sites as the regeneration proceeds. However, selecting areas for different uses may also be part of farmers' management practices. They may select areas with higher growth potential for crops and pastures and maintain the caatinga vegetation where potential is lower. Therefore, the establishment of spatial replicates may not be completely random, but conditioned by this previous farmer selection.

Richness is more sensitive to human disturbance than abundance (Gibson et al., 2011). Thus, a slashed area undergoing natural regeneration can have high diversity. Although the herbaceous diversity increased with increasing regeneration time, represented by increasing values of β diversity, and biomass and density had a similar structure between R39 and MC, it cannot be concluded that all regenerating areas, including R39, will display identical or similar profiles to MC, as both the climatic conditions and the species composition may vary. Differences in biomass and even in species composition may occur due to rainfall variation. The species composition can also vary for other reasons, such as the arrival of seeds of new species. A plant community structure which is still regenerating may vary with a new species composition and may be entirely different from the original forest because different species can cause different contexts, which can in turn influence the local density and diversity. Winter et al., (2017) stated that beta diversity of plants seems to be largely determined by specific abiotic site conditions than by stage-specific conditions.

Conclusion

Herbaceous plants appeared soon after the first rains (January) and their diversity, density and biomass peaked about two months later, while biomass peaked three to four months later. All herbaceous plants were dry in July and most had fallen to the ground, one month after the rains had almost ceased. Therefore, their growth cycle is restricted to the short rainy season, and biodiversity and biomass have different temporal progress patterns.

The herbaceous species diversity increased and plant density and biomass stock decreased with the increasing regeneration period of the caatinga vegetation. The highest density (718 plant m^{-2}) and biomass (329 g m^{-2}) in the recent regenerating stage (2 years) was within the range of those in other caatinga areas opened to be used as pastures, as well as in herbaceous formation of semi-arid areas elsewhere. The lower biomass in the mature caatinga (167 g m^{-2}) and R39 (98 g m^{-2}) than in the 2-year regenerating area (329 g m^{-2}) is compatible with its higher shrub and tree canopy cover.

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