THE ROLE OF CLONAL AND SEXUAL SPREAD IN CACTI SPECIES DOMINANCE AT THE BRAZILIAN CAATINGA

ELÂINE M.S. RIBEIRO[1*]; MARCOS V. MEIADO[2] & INARA R. LEAL[3]

[1] Programa de Pós-Graduação em Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brasil. *E-mail: **nanigesbio@yahoo.com.br**.
[2] Departamento de Biociências, Universidade Federal de Sergipe, Itabaiana, Sergipe, Brasil.
[3] Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brasil.

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ABSTRACT – A large part of flowering plants have sexual and asexual propagation. The occurrence of these reproductive modes is probably related to adaptive responses to environmental conditions, species distribution, genetic variation and the maintenance of multiple biological interactions. Here we examined populations of eight cacti species from Brazilian Caatinga (*Arrojadoa rhodantha*, *Cereus jamacaru* ssp. *jamacaru*, *Harrisia adscendens*, *Pilosocereus gounellei* ssp. *gounellei*, *Pilosocereus pachycladus* ssp. *pernambucoensis*, *Melocactus zehntneri*, *Tacinga inamoena* and *Tacinga palmadora*) and verified how clonal and sexual spread contribute to these species' dominance. We surveyed populations of these species in 30 plots of 50x20m in natural areas of Caatinga at Parnamirim municipality, in these plots adults and seedlings/saplings via sexual and asexual reproduction were recorded. We registered a total 2692 individuals from the eight studied species. The most abundant species were *A. rhodantha*, *P. gounellei* ssp. *gounellei*, *M. zehntneri*, *T. inamoena* and *T. palmadora* (> 200 individuals registered), while *C. jamacaru* ssp. *jamacaru*, *H. adscendens* and *P. pachycladus* ssp. *pernambucoensis* (< 100 individuals registered). We verified that the high investment in sexual, or in both propagation modes (clonal and sexual) explained the dominance of the cacti species. These results illustrate the vulnerability of some species with small populations, moreover the importance of both reproductive modes to understand the dominance of some cacti species. Cacti species with high investment in sexual reproduction or in both propagation modes (*e.g.*, *P. gounellei* ssp. *gounellei*) could be considered less endangered because are able to keep locally and regionally their populations.

KEYWORDS: *vegetative and sexual propagation, Cactaceae, species dominance, population's size, semi-arid vegetation.*

O PAPEL DA PROPAGAÇÃO CLONAL E SEXUAL NA DOMINÂNCIA DE ESPÉCIES DE CACTOS NA CAATINGA BRASILEIRA

RESUMO – Uma grande parte das plantas com flores possuem propagação sexual e assexual. A ocorrência desses modos de reprodução está provavelmente relacionada às respostas adaptativas às condições ambientais, distribuição das espécies, variação genética e com a manutenção de múltiplas interações biológicas. Neste estudo examinamos as populações de oito espécies de cactos ocorrentes na Caatinga brasileira (*Arrojadoa rhodantha*, *Cereus jamacaru* ssp. *jamacaru*, *Harrisia adscendens*, *Pilosocereus gounellei* ssp. *gounellei*, *Pilosocereus pachycladus* ssp. *pernambucoensis*, *Melocactus zehntneri*, *Tacinga inamoena* e *Tacinga palmadora*) e investigamos como a propagação clonal e sexual contribuem para a dominância dessas espécies. Nós amostramos as populações dessas espécies em 30 parcelas de 50x20m em áreas naturais de Caatinga do município de Parnamirim-PE, nestas parcelas os indivíduos adultos e plântulas/jovens foram registrados e identificados como clones ou indivíduos originados de reprodução sexual. Foi registrado um total de 2692 indivíduos pertencentes às oito espécies estudadas. As espécies mais abundantes foram *A. rhodantha*, *P. gounellei* ssp. *gounellei*, *M. zehntneri*, *T. inamoena* e *T. palmadora* (> 200 indivíduos registrados), enquanto que as espécies *C. jamacaru* ssp. *jamacaru*, *H. adscendens* e *P. pachycladus* ssp. *pernambucoensis* apresentaram menor abundancia (<100 indivíduos registrados). Verificamos que o alto investimento em propagação sexual, ou em ambos modos de propagação (clonal e sexual) explica a dominância das espécies de cacto estudadas. Estes resultados ilustram a vulnerabilidade de algumas espécies que possuem populações pequenas, além da importância de ambos os modos de propagação para o entendimento da dominância de algumas espécies. Espécies de cacto com alto investimento em reprodução sexual ou em ambos os modos de propagação (*e.g.*, *P. gounellei* ssp. *gounellei*) podem ser consideradas menos ameaçadas porque conseguem manter localmente e regionalmente suas populações.

PALAVRAS-CHAVE: *propagação vegetativa e sexual, Cactaceae, dominância das espécies, tamamho da população, vegetação semiárida.*

EL PAPEL DE LA PROPAGACIÓN CLONAL Y SEXUAL EN LA DOMINANCIA DE ESPECIES DE CACTUS EN LA CAATINGA BRASILEÑA

RESUMEN – Una gran parte de las plantas con flores tienen propagación sexual y asexual. La aparición de estos modos reproductivos está probablemente relacionada con las respuestas adaptativas a las condiciones ambientales, la distribución de las especies, la variación genética y el mantenimiento de múltiples interacciones biológicas. En esto estudio examinamos las poblaciones de ocho especies de cactus de Caatinga brasileña (*Arrojadoa rhodantha*, *Cereus jamacaru* ssp. *jamacaru*, *Harrisia adscendens*, *Pilosocereus gounellei* ssp. *gounellei*, *Pilosocereus pachycladus* ssp. *pernambucoensis*, *Melocactus zehntneri*, *Tacinga inamoena* y *Tacinga palmadora*) y investigamos cómo la propagación clonal y sexual contribuyen para la dominancia de estas especies. Nosotros muestreamos las poblaciones de estas especies en 30 parcelas de 50x20m en áreas naturales de Caatinga en el municipio Parnamirim-PE, en estas parcelas los individuos adultos y plántulas/jóvenes fueran registrados e identificados como clones o individuos originados de reproducción sexual. Se registraron un total de 2692 individuos de las ocho especies estudiadas. Las especies más abundantes fueron *A. rhodantha*, *P. gounellei* ssp. *gounellei*, *M. zehntneri*, *T. inamoena* y *T. palmadora* (> 200 individuos registrados), mientras que *C. jamacaru* ssp. *jamacaru*, *H. adscendens* y *P. pachycladus* ssp. *pernambucoensis* (<100 individuos registrados). Verificamos que el alto investimento en propagación sexual, o en ambos modos de propagación (clonal y sexual) explica la dominancia de las especies de cactus. Estos resultados ilustran la vulnerabilidad de algunas especies con poblaciones pequeñas, por otra parte la importancia de ambos modos reproductivos para entender la dominancia de algunas especies de cactus. Especies de cactus con alta inversión en reproducción sexual o en ambos modos de propagación (*e.g.*, *P. gounellei* ssp. *gounellei*) podrían considerarse menos peligro porque son capaces de mantener a nivel local y regional a sus poblaciones.

PALABRAS CLAVE: *propagación vegetativa y sexual, Cactaceae, dominancia das especies, tamaño de la población, vegetación semiárida.*

INTRODUCTION

Understanding the factors that explain the species abundances in natural communities is an old challenge in ecology (Margurran and Henderson, 2003; Comita *et al.*, 2007). Factors related to species life story strategies as the reproductive mode, resources acquisition, dispersal capacity (DeFalco *et al.*, 2003; Adler *et al.*, 2013; Herben *et al.*, 2014), niche conditions as resources availability and natural enemies (Laliberté *et al.*, 2012; Bachelot and Kobe, 2013) are cited as important drivers of species abundances in natural communities.

In particular, the reproduction mode may affect local and regional abundances of species and can be considered as an adaptive response (Bonser, 2013; Herben *et al.*, 2014). For instance, clonal spread is cited as an important predictor of local species abundance and also contributes to regional abundance; on the other hand, the sexual propagation seems to be more important to determine species abundance at regional scales (Meiado, 2012; Herben *et al.*, 2014). Besides affect the local and regional abundances, reproductive modes are linked to some adaptive strategies. For example, clonal reproduction has lower energetic costs and the vegetative propagules carry reserves of water and energy, allowing them to withstand prolonged drought in stressful habitats (Mandujano *et al.*, 1998; Pimienta-Barrios and Castillo, 2002). However, high investment in clonal propagation can bring negative consequences as short dispersal and low genetic variability (Zhang and Zhang, 2007; Pinheiro *et al.*, 2012; Meiado, 2012). The sexual propagation, on the other hand, is considered as more costly as it involves the outcrossing, whereas it is advantageous because contributes to keep genetic diversity and multiple biological interactions (Faegri and Pijl, 1979; Holsinger, 2000).

Between plants, clonal and reproductive spread are cited as frequent (Zhang and Zhang, 2007). The Cactaceae family, particularly, has subfamilies as Opuntioideae and Cactoideae which representatives present both reproductive modes (Mandujano *et al.*, 2010), however, the relative importance of the clonal and sexual spread in the maintenance of populations from Cactaceae species is considered as poorly understood (Godínez-Álvarez *et al.*, 2003). At the Brazilian Caatinga, the Cactaceae is the sixth family with more species (Giulietti *et al.*, 2006), and in this same region is located the third diversity center of the family (Taylor and Zappi, 2004; Ortega-Baes *et al.*, 2010). Thus, this region offers an ideal scenario to understand how the clonal and sexual spread contributes to population's maintenance because we can observe species with distinct habits, abundances and investments in both reproductive modes.

In this study, our aim was to answer how sexual and clonal reproduction can explain cacti species dominance at the Brazilian Caatinga. We consider as species dominance a measure that take in account species abundance and its coverage within the studied landscape (Tiner, 2002). To answer our question we surveyed populations of eight cacti species from Cactoideae and Opuntioideae subfamilies. Our hypothesis was that species with high investment is sexual spread or in both reproduction modes are the dominant ones, because these alternatives allows the long distance and local colonization, while just a high clonal spread investment contribute more to local species abundance (Herben *et al.*, 2014).

MATERIAL AND METHODS

Study site

We conducted this study in natural areas of Caatinga located at Pernambuco state, at Parnamirim municipality, Northeast of Brazil (8°5'26''S and 39°34'41''W; **Figure 1**). The average rainfall and temperature are 431 mm and 26°C, respectively, and the local climate is classified as tropical semi-arid BSh'w by the Köppen system (CPRM, 2005). Parnamirin municipality is inserted in a region of depression, the relief is soft wavy and the predominant soils are brown non-calcic, regosol, podzolic soils and planosol (CPRM, 2005). The Caatinga vegetation in this region is hiper xerofitic composed by a mosaic of tropical dry forests and shrubby vegetation.

Studied species

We studied the eight cacti species that occur at Parnamirim municipality, they are: *Arrojadoa rhodantha* (Gürke) Britton & Rose, *Cereus jamacaru* DC. ssp. *jamacaru, Harrisia adscendens* (Gürke) Britton & Rose, *Pilosocereus gounellei* (F.A.C. Weber) Byles & G.D. Rowley ssp. *gounellei*, *Pilosocereus pachycladus* F. Ritter ssp. *pernambucoensis* (F. Ritter) Zappi, *Melocactus zehntneri* (Britton & Rose) Luetzelb., *Tacinga inamoena* (K. Schum.) N.P. Taylor & Stuppy and *Tacinga palmadora* (Britton & Rose) N.P. Taylor & Stuppy (Meiado *et al.*, 2008). These species are distributed in other areas of Caatinga from Brazilian Northeastern (Taylor and Zappi, 2004; Meiado *et al.*, 2012), have different life story attributes and are involved in diverse biotic interactions, including their use by humans (Andrade, 2008).

Cacti survey

We performed the cacti survey at the end of 2009 rainy season. We searched for these species populations on field and try obtain the larger number of different cacti species in 30 plots of 50 x 20 m distributed in a polygon of 90 Km², with a minimum distance of 300 m between plots. All cacti individuals present in these plots were recorded, we considered as total population all cacti individuals from clonal and sexual reproduction in all life stages. The mean of total individuals multiplied by the number of plots that the cacti species occurred was the species' dominance measure utilized, because it reflects both species abundance and also take in account its coverage within the studied landscape (Tiner, 2002).

As the studied species have different habits and sizes, we classified them as seedlings/juveniles and adults in distinct ways, considering the beginning of reproductive events

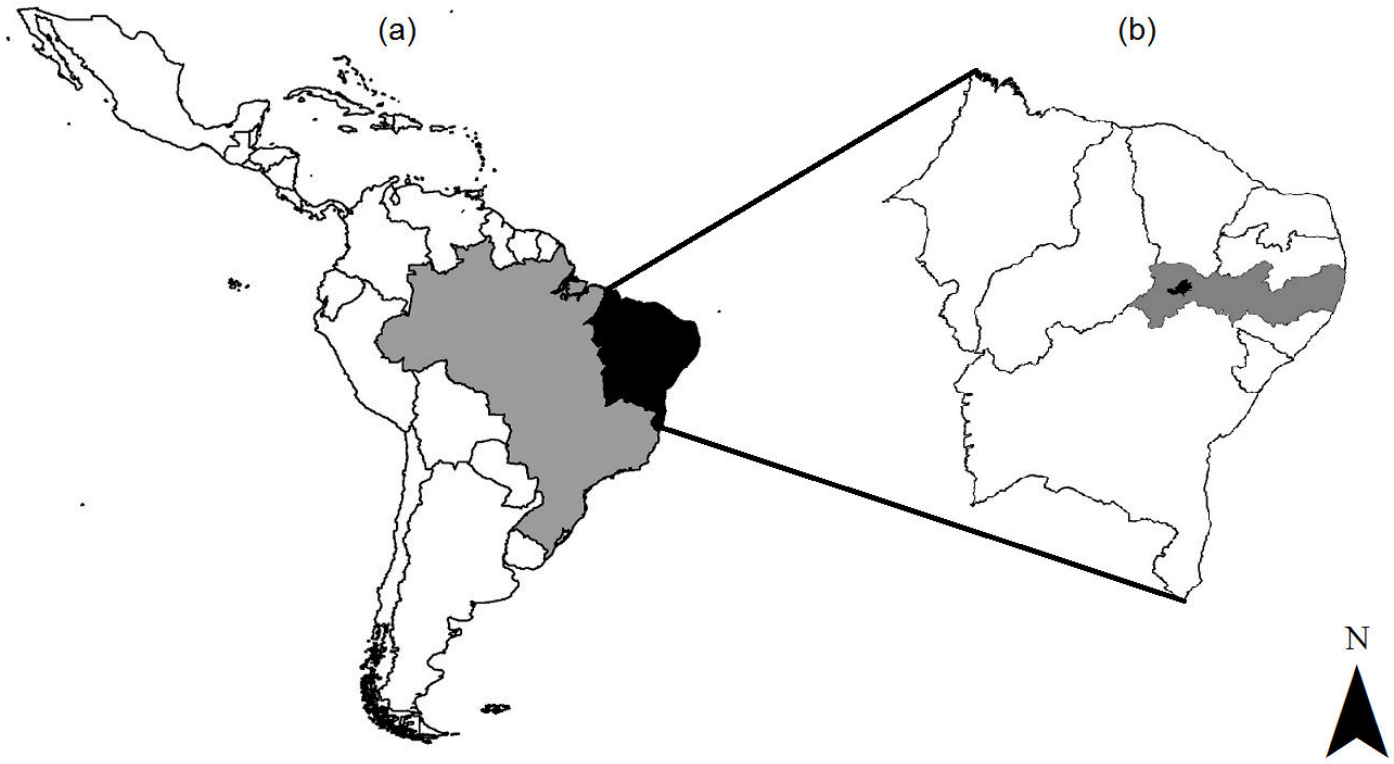

FIGURE 1. (a) Study area in north-eastern Brazil (in black), and (b) the Brazilian north-eastern region highlighted with Pernambuco state (in gray) and Parnamirim municipality (in black).

observed in the field. For the columnar species *C. jamacaru* ssp. *jamacaru* and *P. pachycladus* ssp. *pernambucoensis* we classified as seedlings/juveniles the individuals with height up to 2 m, and adults individuals with height upper to 2 m. Individuals of *P. gounellei* ssp. *gounellei* with height up to 1 m were described as seedlings/ juveniles and upper to 1 m as adults. The individuals of *A. rhodantha* with size up to 0.3 m were seedlings/juveniles and upper to 0.3 m were classified as adults. For the globose species *M. zehntneri* adult individuals were that ones with basal area larger than 0.3 cm and seedlings/juveniles with basal area less than 0.3 m.

The *T. inamoena* and *T. palmadora* were classified according the number of cladodes, seedlings/ juveniles that one's up to 25 cladodes and adults with more than 25 cladodes. As the studied species have different habits and sizes, we classified them as clones and sexual individuals in different ways. For *T. inamoena*, which an individual normally forms a clump, we considered from the center of the larger individual a radius of 2 m, and all individuals in this radius were considered as a clone. In case of the other seven species we search for vestiges of parental cladode and/or fruit (*i.e.*, *T. palmadora*) that formed these clonal individuals. For these seven species we consider seedlings/saplings without parental vestiges as representatives of the population generated by sexual spread and with parental vestiges as clones, because for adult individuals its difficult judge if their came from clonal or sexual reproduction.

Data analyses

We compared the mean number of total, sexual and clonal individuals per plot for each species, to evaluate their abundance in the studied community, and also the contribution of their sexual and clonal spread. To do these comparisons, we used Kruskal-Wallis nonparametric variance analyses. In order to verify the contribution of sexual and clonal spread on species dominance, we used a generalized linear model – GLM, where the number of sexual and clonal individuals were the fixed factors (Dominance = Sexual+ Clonal + Sexual*Clonal). To avoid collinearity problems between the fixed factors, we previously check the correlation between the number of sexual and clonal individuals which results ($r = 0.15$; $p = 0.71$) allowed include both variables in GLM (Dormann *et al.*, 2013). We check the GLM adequacy testing normal distribution of the studentized residuals using Shapiro–Wilk test. These analyses were performed using JMP version 8 (SAS Institute Inc., 2008).

RESULTS

We found a total of 2692 individuals from the eight studied species in the plots surveyed. *Pilosocereus gounellei* ssp. *gounellei* was the species with larger abundance and occurred in 29 plots, other species as *T. inamoena*, *T. palmadora*, *M. zehntneri* and *A. rhodantha* had also high total abundances, when compared with species as *P. pachycladus* ssp. *pernambucoensis, C. jamacaru* ssp. *jamacaru* and *H. adscendens* ($\chi^2 = 41.742$; df = 7; $p < 0.01$) **(Table 1, Figure 2a)**.

TABLE 1. Number of surveyed populations by cacti species. Total individuals registered per population, individuals from clonal and sexual spread (mean and error). Data registered from cacti populations at natural Caatinga areas of Parnamirim municipality, PE, Brasil.

Cacti species	Number of surveyed populations	Total individuals	Individuals from clonal population	Individuals from sexual population
Arrojadoa rhodantha	12	228 (19±5.56)	48 (4±1.69)	31 (2.58±0.82)
Cereus jamacaru ssp.*jamacaru*	20	94 (4.7±0.75)	4 (0.2±0.09)	36 (1.8±0.37)
Pilosocereus gounellei ssp. *gounellei*	29	780 (26±4.85)	136 (4.53±1.56)	363 (12.1 ±2.92)
Pilosocereus pachycladus ssp. *pernambucoencis*	21	69 (3.28±0.60)	0	11 (0.52±0.19)
Harrisia adsendens	4	13 (3.25±1.23)	0	1 (0.25±0.25)
Melocactus zehntneri	26	501(19,26±7,7)	21 (0,80±0,29)	96(3.69±1.81)
Tacinga inamoena	21	601 (25.04±5.37)	518 (21.58±4.75)	65 (2.70±0.6)
Tacinga palmadora	23	406 (17.75±7.5)	157 (6.82±2.83)	77 (3.34±0.67)

TABLE 2. Results from the generalized linear model used to test the contribution of sexual and clonal spread to cacti species dominance in Caatinga plant communities from Parnamirim municipality, PE, Brasil.

Whole model	R^2	DF	SS	F	P
	0.97	3	490474.75	76.624	0.0005
Parameter estimates of predictor variables		**Estimate**	**SE**	**t Ratio**	**P**
Sexual spread		2.024	0.160	12.63	0.0002
Clonal spread		-0.207	0.177	-1.17	0.3070
Sexual spread * Clonal spread		-0.301	0.005	-5.72	0.0046

In relation to sexual spread, we verify that the mean of sexual individuals was similar for most of studied species, with exception to *P. gounellei* spp. *gounellei* which presented a larger number of sexual individuals (χ^2 = 44.211; df = 7; $p < 0.01$) **(Table 1, Figure 2b)**. Among studied species, *T. inamoena* had the larger number of clonal individuals, followed by *T. palmadora*, *P. gounellei* spp. *gounellei, A. rhodantha, M. zehntneri* and *C. jamacaru* ssp. *jamacaru*, for *P. pachycladus* ssp. *pernambucoensis* and *Harrisia adscendens* we did not find clonal individuals on field. (χ^2 = 70.102, df = 7, $p < 0.01$; **Table 1, Figure 2c**).

In respect to the sexual and clonal spread our model showed that both reproduction modes are important predictors of species dominance (r^2 = 0.97, F = 76.624, $p < 0.01$; **Table 2**). However, just a high investment in clonal spread does not explain the dominance of studied species, but a high investment in sexual spread or in both reproduction modes explains the dominance of cacti species in Caatinga plant communities **(Table 2; Figure 3 a, b and c)**.

DISCUSSION

Besides understand how sexual and clonal reproduction can explain cacti species dominance at Brazilian Caatinga, this study provide fundamental information about cacti populations size, which is rarely effectively measured in this ecosystem (but see Meiado *et al.*, 2012). Population's size is a basic measure of species vulnerability, and large populations are able to keep populations' relative stability (Gibson, 2015). According the local populations size observed, cacti species as *C. jamacaru* ssp. *jamacaru*, *H. adscendens* and *P. pachycladus* ssp. *pernambucoensis* presented small local populations suggesting a higher vulnerability of these species, even though they were described as widespread species at the Caatinga region (Taylor and Zappy, 2004).

On field we verified that 6 of the 8 cacti species studied presented both sexual and clonal propagation, the occurrence of both spread modes is cited frequent between plant species and can vary widely between and within species (Zhang and Zhang, 2007). For cacti especially, the investment in both reproduction modes reflect their versatility to face stressful environments, keep genetic diversity and multiple biological interactions. In arid ecosystems as the Caatinga, vegetative spread is particularly important, because this reproduction mode has lower energetic costs, the vegetative propagules carry reserves of water and energy, allowing them to withstand prolonged drought (Mandujano *et al.*, 1998; Pimienta-Barrios and Castillo, 2002). However the high clonal propagation can bring negative consequences to population as short distance dispersal, the reduction in genetic diversity and increase of species vulnerability to environmental changes (Zhang and Zhang, 2007; Pinheiro *et al.*, 2012; Meiado, 2012). Like this, the occurrence of both propagation modes for the most of studied cacti species shows that they are able to keep in their populations the benefits of both reproductive modes.

As previously described for species from Opuntioideae subfamily which has high contribution or nearly

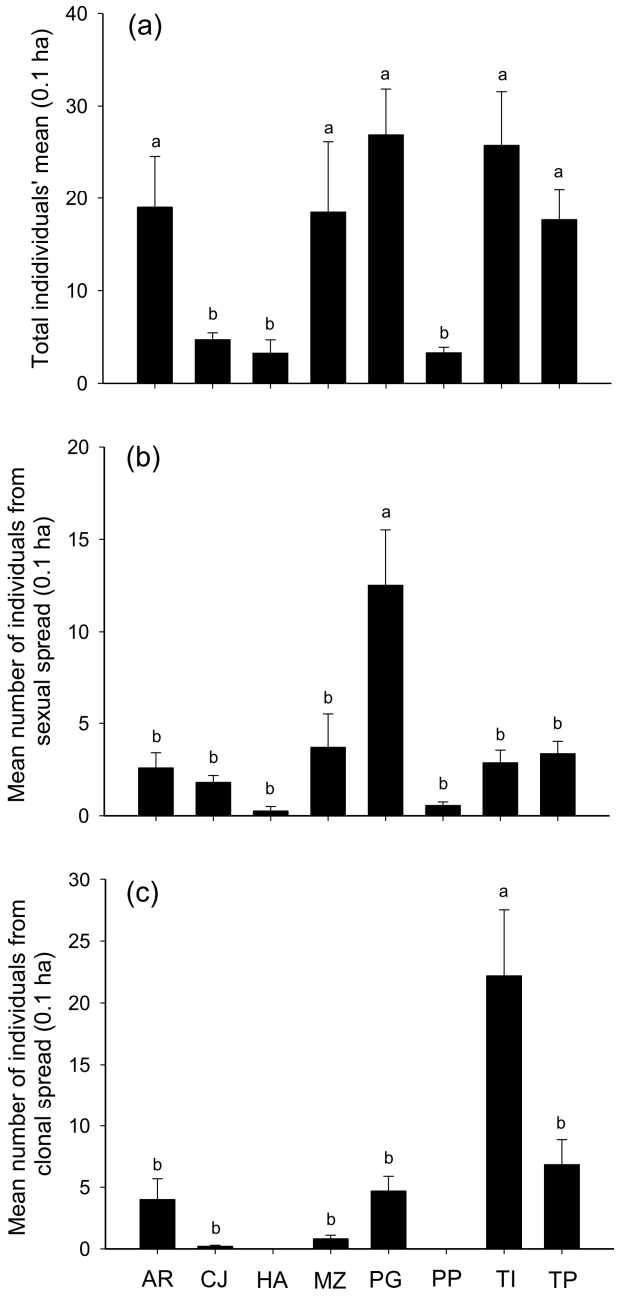

FIGURE 2. Mean of total (a), sexual (b) and clonal (c) individuals of the eight cacti species populations, data from natural areas of Caatinga at Parnamirim municipality, Pernambuco, Brazil. Black bars represent the means and standard errors. Codes: **AR** - *Arrojadoa rhodantha* (Gürke) Britton & Rose, **CJ** - *Cereus jamacaru* DC. ssp. *jamacaru*, **HA** - *Harrisia adscendens* (Gürke) Britton & Rose, **MZ** - *Melocactus zehntneri* (Britton & Rose) Luetzelb., **PG** - *Pilosocereus gounellei* (F.A.C. Weber) Byles & G.D. Rowley ssp. *gounellei*, **PP** - *Pilosocereus pachycladus* F. Ritter ssp. *pernambucoensis* (F. Ritter) Zappi, **TI** – *Tacinga inamoena* (K. Schum.) N.P. Taylor & Stuppy and **TP** – *Tacinga palmadora* (Britton & Rose) N.P. Taylor & Stuppy (Cactaceae).

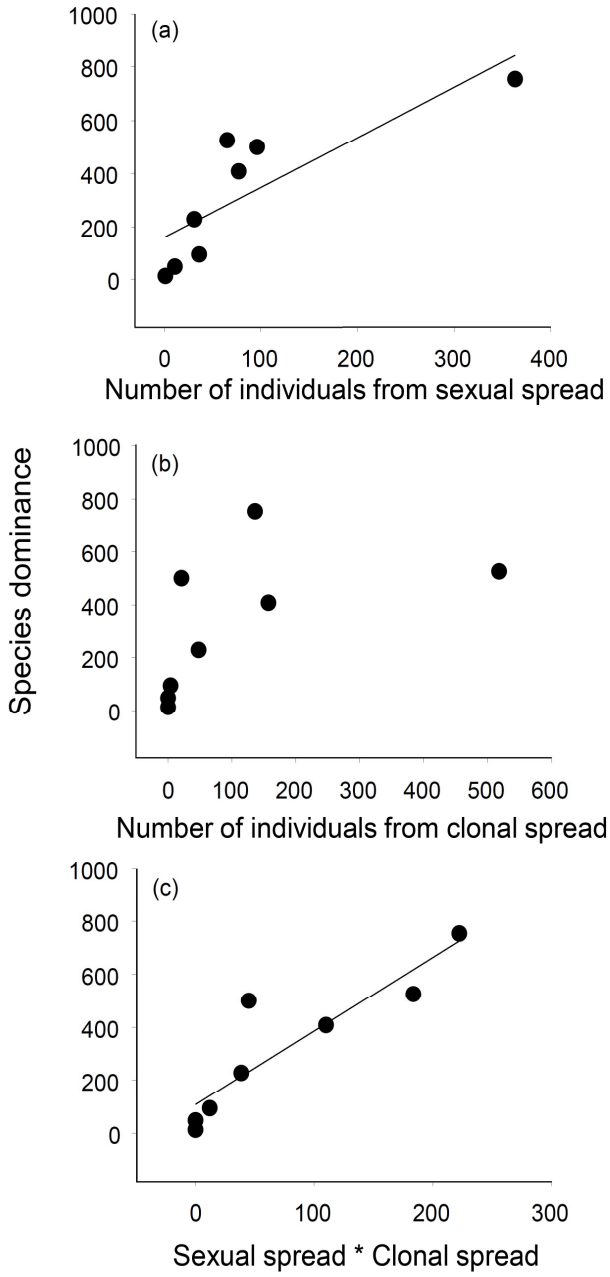

FIGURE 3. Relationships between cacti species dominance and their number of individuals from sexual (a) and clonal spread (b), and also the interaction of these predictor variables (c) in natural areas of Caatinga in Parnamirim, Pernambuco, Brazil.

exclusively clonal spread (Mandujano *et al.*, 1996; 2007; Pimienta-Barrios and Castillo, 2002; Meiado, 2012), we also registered that *T. inamoena* and *T. palmadora* presented more clonal than sexual individuals (c.a. 85% and 70%, respectively; **Table 1;** **Figure 2**), and also had a higher number of clonal individuals when compared with the other studied species. According to Meiado (2012), *T. palmadora* produces clones by

tissue (pericarpel) that covers the fruit during the reproductive phase. These clones are responsible for maintaining the population in areas where the species occurs while the seedlings from sexual propagation are established in new environments and extend the geographical distribution of the species (Meiado, 2012).

The cacti species with more individuals from sexual reproduction were *A. rhodantha*, *P. gounellei* ssp. *gounellei*, *M. zehntneri* and *C. jamacaru* ssp. *jamacaru*, for these species clonal spread accounted just with around 39%, 30%, 20% and 10% of their individuals, respectively **(Table 1; Figure 2)**. For Catoideae subfamily, which represent these four last cacti species clonal spread is also described as able to generate new offspring (Mandujano *et al.*, 2010), whereas here we observed that it occurs in lower rates when compared to species from Opuntioideae subfamily. For *P. pachycladus* ssp. *pernambucoensis* and *H. adscendens* which are also from Catoideae subfamily were not registered clonal individuals on field, suggesting that vegetative propagation is rare or absent for these species.

We verified that both sexual and the interaction of sexual and clonal spread are key factors in explaining the dominance of cacti species at Brazilian Caatinga. Besides clonal spread is cited as important to face natural stressing environments as the Brazilian Caatinga (Mandujano *et al.*, 1998; Pimienta-Barrios and Castillo, 2002), in this study just a high investment in clonal propagation not explain cacti species dominance confirming our hypothesis. This results is probably related to the limited dispersal observed in plants with high clonal spread, which contributes to individuals aggregation (Carrillo Angeles *et al.*, 2011), and consequently reduces its representativeness at regional scales. On the other hand, the more successful strategies (*i.e.*, that allowed species dominance) involved a high investment the sexual propagation or in both spread modes **(Figure 3)**. These results reflects the role of the sexual propagation by seed dispersal that enables the species colonization of most distant sites, and like this allows a larger species coverage in distinct sites (Erickson, 1993; Nathan and Muller-Landau, 2000). Besides this, the combination of high clonal and sexual reproduction (*i.e.*, *P. gounellei* spp. *gounellei*), ensure that the species is locally and regionally well represented as observed here, moreover it keeps genetic diversity and reduces extinction risk (Pinheiro *et al.*, 2012; Rabbani *et al.*, 2012; Meiado, 2012).

With this study we provide essential information about cacti populations size from Brazilian Caatinga, that indicate the vulnerability of some species as *C. jamacaru* ssp. *jamacaru*, *H. adscendens* and *P. pachycladus* ssp. *pernambucoensis* which have small local populations. These results should be considered when evaluating the risks of cacti species extinction at the Brazilian Caatinga, moreover other populations of distinct regions may be censored to confirm the populations-size patterns observed in the studied region. We also corroborate our hypothesis, both a higher investment in sexual and in both spread modes are factors that determine dominance of cacti species, and species with these features could be considered less endangered because are able to keep locally and regionally their populations. Finally, we suggest further investigations of cacti populations to evaluate the consequences of the high clonal of species as *T. inamoena* and *T. palmadora* on genetic diversity, the seasonality and habitat effects on the frequency of clonal and sexual spread, to elucidate better the propagation strategies adopted by these species in distinct contexts.

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