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CACTI SPECIES FROM THE BRAZILIAN CHACO: FLORAL AND FRUIT TRAITS

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ABSTRACT – Cacti species are recognized for providing various resources for pollinators and seed dispersers in many ecosystems, being these interactions well documented in some of them. However, for the Brazilian Chaco, these interactions remain unknown. In this study we characterize flower and fruit traits, as well as the resources offered by six species of Cactaceae (*Cleistocactus baumannii, Echinopsis rhodotricha, Harrisia balansae, Harrisia tortuosa, Opuntia retrorsa* and *Stetsonia coryne*) in order to suggest their potential pollinators and seed dispersers. In an area of Chaco vegetation, located in the southwest of Mato Grosso do Sul, we collected flowers and fruits from November 2014 to January 2015 and performed morphometric analysis in the laboratory. The cacti species showed a great diversity of forms, with flowers presenting different periods of anthesis, colors, sizes and resources offered. According to predominant flower characteristics, such as white flowers opening at night, the potential pollinators of most species are probably nocturnal, such as moths and bats. All the recorded fruits are berries, with attractive colors (red or bright lilac), suggesting birds as potential seed dispersers. This study represents a starting point for better understanding interactions between cacti species and their mutualists in the Brazilian Chaco. However, detailed field studies are still required to confirm such interactions in this threatened ecosystem.
KEYWORDS: *Cactaceae, pollination, seed dispersal.*

ESPÉCIES DE CACTOS DO CHACO BRASILEIRO: CARACTERÍSTICAS MORFOLÓGICAS DE FLORES E FRUTOS

RESUMO – Espécies de cactos são reconhecidas por fornecerem diferentes recursos para polinizadores e dispersores de sementes em diversos ecossistemas, sendo tais interações bem estudadas em alguns locais. No entanto, para o Chaco brasileiro, estas interações permanecem desconhecidas. Neste estudo caracterizamos a morfologia de flores e frutos e os recursos oferecidos por seis espécies de Cactaceae (*Cleistocactus baumannii*, *Echinopsis rhodotricha*, *Harrisia balansae*, *Harrisia tortuosa*, *Opuntia retrorsa* e *Stetsonia coryne*) e, com base em tais características, sugerimos seus potenciais polinizadores e dispersores de sementes. Em uma área do Chaco brasileiro, localizado no sudoeste de Mato Grosso do Sul, coletamos flores e frutos de novembro de 2014 a janeiro de 2015 em diferentes indivíduos e realizamos análises morfométricas em laboratório. As espécies avaliadas apresentaram grande diversidade de formas, com flores apresentando diferentes períodos de antese, coloração, tamanho e recompensas para diferentes grupos de animais. De acordo com as características florais predominantes, como coloração branca de antese noturna, os potenciais polinizadores da maioria das espécies são, provavelmente, noturnos, tais como mariposas e morcegos. Os frutos foram todos do tipo baga e de coloração atrativa (vermelho e rosa), sugerindo aves como potenciais dispersores de sementes. Este estudo representa o ponto de partida para a compreensão das interações entre os cactos e seus mutualistas no Chaco brasileiro. No entanto, estudos de campo detalhados ainda são necessários para comprovar tais interações neste ecossistema ameaçado.
PALAVRAS-CHAVE: *Cactaceae, polinização, dispersão de sementes.*

ESPECIES DE CACTUS DEL CHACO BRASILEÑO: RASGOS FLORALES Y FRUTALES

RESUMEN – Las especies de cactus son reconocidas por proporcionar diferentes recursos para los polinizadores y dispersores de semillas en diversos ecosistemas y han sido investigadas para algunas zonas. Sin embargo, en el Chaco brasileño las interacciones de polinización y dispersión de semillas son aún desconocidas. En este trabajo, se caracterizó la morfología de las flores, los frutos y las recompensas ofrecidas por seis especies de cactáceas (*Cleistocactus baumannii, Echinopsis rhodotricha, Harrisia balansae, Harrisia tortuosa, Opuntia retrorsa* y *Stetsonia coryne*) y con base en estos rasgos se sugieren sus potenciales polinizadores y dispersores de semillas. En una zona del Chaco brasileño, situada al suroeste del estado de Mato Grosso do Sul se colectaron flores y frutos en diferentes individuos entre noviembre de 2014 a enero de 2015 para realizar análisis morfométricos en laboratorio. Los resultados muestran que estas especies tienen una amplia variedad de formas, antesis, color, tamaño, dehiscencia y recompensas para los diferentes grupos de visitantes. Entre los potenciales visitantes florales se incluyen principalmente la participación de los polinizadores nocturnos como polillas y murciélagos, porque las especies dominantes producen flores blancas con antesis nocturna. Los frutos son baya de colores llamativos (rojo y rosado), lo que sugiere que las aves actuarían como potenciales dispersores de semillas. Este estudio representa el punto de partida para la comprensión de las interacciones entre los cactus y sus mutualistas en el Chaco brasileño. Sin embargo, se necesitan estudios de campo detallados para confirmar tales interacciones en este ecosistema amenazado.
PALABRAS CLAVE: *Cactaceae, polinización, dispersión de semillas.*

INTRODUCTION

Cactaceae, with more than 1600 recognized species, is one of the most diverse families in the Neotropics (Anderson, 2001), and Brazil is considered the third largest diversity center for this group (Taylor and Zappi, 2004). Currently, there are 260 cacti species described for Brazil, distributed in 39 genera and three subfamilies (Cactoideae, Opuntioideae and Pereskioideae), with specimens in all phytogeographic domains of the country: Amazon, Caatinga, Cerrado, Atlantic Forest, Pampa and Pantanal (Taylor *et al.*, 2015).

In a recent checklist for the Mato Grosso do Sul state, Zappi *et al.* (in press) reported the occurrence of 31 cacti species, belonging to 18 genera [*Brasiliopuntia* (K. Schum.) A. Berger, *Cereus* Mill., *Cleistocactus* Lem., *Discocactus* Pfeiff., *Echinopsis* Zucc., *Epiphyllum* Haw., *Frailea* Britton & Rose,

Gymnocalycium Pfeiff. ex Mittler, *Harrisia* Britton, *Hylocereus* (A. Berger) Britton & Rose, *Lepismium* Pfeiff., *Nopalea* Salm-Dyck (introduced), *Opuntia* Mill., *Pereskia* Mill., *Pilosocereus* Byles & Rowley, *Praecereus* Buxb., *Rhipsalis* Gaertn. and *Stetsonia* Britton & Rose], with a greater diversity of species occurring in the Chaco region.

The Brazilian Chaco is located in the southwest of Mato Grosso do Sul, Porto Murtinho municipality, and presents physiognomy and floristic composition similar to the Chaco *sensu stricto* of Paraguay and Argentina (Prado *et al.*, 1992). Chaco vegetation is usually associated with saline soils, and includes a great diversity of Leguminosae, Bromeliaceae and Cactaceae species (Pennington *et al.*, 2000; Silva *et al.*, 2000). According to floristic surveys conducted in Mato Grosso do Sul (Eggli, 2002; Freitas *et al.*, 2013; Zappi *et al.*, in press), and information from the Species List of Brazilian Flora (Taylor *et al.*, 2015), ca. twelve species, including globose, epiphytes and columnar cacti were reported in the Brazilian Chaco.

The majority of cacti species are pollinated and dispersed by biotic agents, bearing flowers and fruits with a great variety of morphological traits, that provide important resources (*i.e.*, pollen, nectar and fleshy fruits), which are consumed by different animals, such as birds, bats, insects and lizards (Taylor and Zappi, 2004).

The floral morphology, such as shape, size, color, presence of odour and period of anthesis as well as size, weight, color, type of dehiscence and number of seeds in the fruits are parameters that contribute to the assessment of important aspects about the interactions between flowers and pollinators, and between fruits and seed dispersers (Lenzi *et al.*, 2004). Pollination and seed dispersal are two key processes in the reproductive ecology of most plants (Hansen and Muller, 2009) that, in many cases, are highly dependent on different animal groups for performing them. Thus, knowledge about the mechanisms involved in these interactions is important, because their rupture can cause the loss of several species (Bascompte and Jordano, 2007).

Studies involving floristic, physiological, taxonomic and ecological aspects of cacti in the Brazilian Chaco are scarce. Until now, only two studies were conducted on reproductive phenology in this region, which included seven cacti species (Freitas *et al.*, 2013; Arakaki, 2014). Freitas *et al.* (2013) found that flowering and fruiting of these species occurred predominantly in the rainy season, and that all species are zoochorous. Arakaki (2014) correlated the flowering and fruiting periods with climatic variables, and found that these phenophases were not correlated with precipitation. However, temperature and photoperiod were the variables that most influenced the reproductive phenophases.

According to the National Plan for Cactaceae Conservation (PAN Cactáceas, 2011), knowledge about the total diversity of species, as well as details on their geographical distribution and conservation status are urgent, since basic information about the occurrence of cacti species in the Pantanal and its subregions are insufficient. Authors highlight that the lack of basic information cause problems on the development of protection actions for the Cactaceae in the Brazilian Midwest (Zappi *et al.*, 2011).

Considering that: i) cacti species are recognized for providing important resources for pollinators and seed dispersers in many ecosystems (Taylor and Zappi, 2004); ii) pollination and seed dispersal are key processes in the reproductive ecology of most plants (Hansen and Muller, 2009) and iii) in the Brazilian Chaco these interactions remain unknown; studies that provide insight for understanding the interactions between Cactaceae and their pollinators and seed dispersers are urgent. In this way, this study aims to characterize flower and fruit morphology, as well as the resources provided by six species of Cactaceae occurring in the Brazilian Chaco, relating these characteristics with their potential pollinators and seed dispersers. These data will contribute to the understanding of ecological aspects about cacti and support further studies on ecological interactions and conservation actions in this threatened ecosystem.

MATERIAL AND METHODS

Study site

The study was carried out in São Fernando farm, located in the municipality of Porto Murtinho (21°37′51.0″ S, 57°49′29.4″ W), Mato Grosso do Sul state (MS), Brazil **(Figure 1)**.

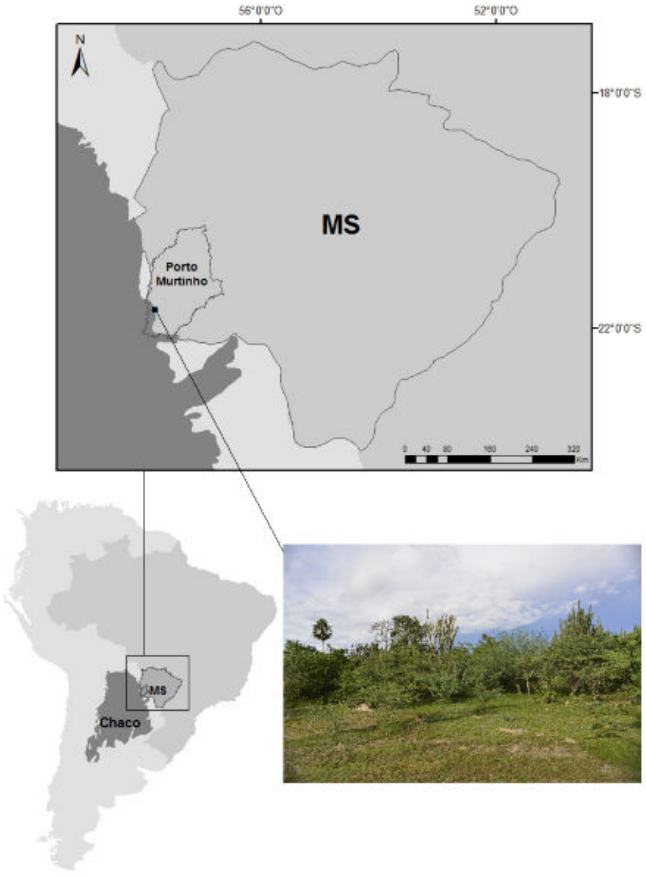

FIGURE 1. Study site in a Chaco remnant, located in Porto Murtinho municipality, Mato Grosso do Sul state (MS), Brazil. The point represents São Fernando farm (Image provided by PR Souza).

The study site is a Chaco remnant characterized by the presence of a discontinuous canopy, mostly containing thorny and microphyllous species (UNESCO, 1973). The climate of the region is characterized by a pronounced seasonality, with a hot and wet summer and a dry winter with occasional frosts (Pennington *et al.*, 2000). The dry season occurs from April to September, and the rainy season from November to February. The average annual rainfall is 970.3 mm and the average annual temperature is 25°C (Carvalho *et al.*, 2014).

Data collection

Data collection was performed from November 2014 to January 2015. We selected a total of six cacti species at reproductive stage, with enough individual bearing flowers and fruits (minimum = 15) for the development of this study. According to these criteria the selected species were: *Cleistocactus baumannii* (Lem.) Lem., *Echinopsis rhodotricha* K. Schum., *Harrisia balansae* (K. Schum.) N.P. Taylor & Zappi, *Harrisia tortuosa* (J. Forbes ex Otto & A. Dietr.) Britton & Rose, *Opuntia retrorsa* Speg. and *Stetsonia coryne* (Salm-Dyck) Britton & Rose, which represents 50% of the Cactaceae flora recorded for the Brazilian Chaco (Taylor *et al.*, 2015; Zappi *et al.*, in press). To describe flower and fruit morphology, we collected one flower and one fruit from 30 different plants and preserved them in ethanol 70% for further morphometric analysis in the laboratory. For *S. coryne*, we collected only 15 flowers and 15 fruits, due to the reduced availability of individuals in reproductive stage.

Morphological characteristics here analyzed are usually used to identify pollination and seed dispersal syndromes of plant species (*sensu* Faegri and Pijl, 1979 and Pijl, 1982) respectively. For each flower, we recorded the following variables: external corolla length (distance from corolla apex to the base of ovary); internal corolla length (distance from corolla apex to the base of the floral tube); corolla diameter (width of corolla opening); anther height (distance from the base to the top of the stamen of the uppermost anther); stigma height (pistil length), length and ovary diameter, number of stamens and ovules per flower (*sensu* Rojas-Sandoval and Meléndez-Ackerman, 2009a). All these measurements were made with the aid of a stereomicroscope and a digital caliper. Additionally, period of anthesis, color, shape and floral rewards were also recorded. To characterize fruits, we recorded color, type of dehiscence and number of seeds produced per fruit. Also, using a digital caliper and a precision scale, fruit and seed sizes, as well as fruit and seed weights were respectively recorded. All measurements were performed in the Laboratório de Ecologia from Universidade Federal de Mato Grosso do Sul (UFMS).

RESULTS AND DISCUSSION

Species evaluated in this study show characteristics that reflect different pollination and seed dispersal syndromes, offering resources for different animal groups, such as hummingbirds, bees, bats and moths. The majority of species have white and nocturnal anthesis flowers. The diurnal species have smaller flowers with yellow or red colors **(Table 1)**. All the recorded fruits are berries, with attractive colors, mostly red and bright lilac, with total length of 12.5-45.1mm **(Table 2)**. Hereafter, we present a description of those characteristics for each of the six species studied in the Brazilian Chaco, relating them to the possible pollination and seed dispersal syndromes.

Cleistocactus baumannii is a shrubby cactus that occurs in the Chaco from Argentina, Paraguay and Bolivia (Anderson, 2001), and also occurs in the Brazilian Midwest, with a restricted distribution to Mato Grosso and Mato Grosso do Sul states (Taylor *et al.*, 2015). The flowers are red, odorless, tubular, slightly curved in their base **(Figure 2)**. The individuals can reach up to 80 cm, and produce an average of 6 ± 4 flowers per branch. The flowers possess diurnal anthesis, with 44.1 ± 4.2 mm in length and 9.1 ± 0.6 mm in diameter, presenting 149 ± 8 stamens, 678 ± 117 ovules and provides pollen and nectar as rewards **(Table 1)**. This set of characteristics indicates that *C. baumannii* flowers are hummingbird pollinated (Anderson, 2001; Gorostiague and Ortega-Baes, 2015).

Ornithophilous flowers have been described for various cacti species belonging to different genera, such as *Oreocereus* (A. Berger) Riccob., *Cleistocactus* Lem., *Melocactus* Link & Otto, *Matucana* Britton & Rose and *Denmoza* Britton & Rose (Anderson, 2001; Taylor and Zappi, 2004; Hunt, 2006). In a recent publication in which bird pollination was evaluated in Cactaceae, authors reported ornithophily for 27 cacti species (Gorostiague and Ortega-Baes, 2015), and suggested that all of them, except *C. baumannii* (visited only by hummingbird), despite presenting ornithophilous attributes, actually exhibited generalized pollination systems, being also visited and/or pollinated by bees, bats or moths in addition to hummingbirds.

Fruits of *C. baumannii* are berries, bright lilac in color, dehiscent, with 12.5 ± 2.1 mm in length, 10.6 ± 1.4 mm in diameter, weight 0.6 ± 0.1 g and have 98 ± 64 black seeds embedded in a white pulp (**Table 2** and **Figure 3**). Fruit morphology, such as size, dehiscence, color and fleshy consistency make them attractive and accessible to lizards and frugivore birds, as recorded for other cacti genera with similar fruit characteristics (Figueira *et al.*, 1994; Romão *et al.*, 2007; Gomes *et al.*, 2014a).

Echinopsis rhodotricha is a short-columnar cactus distributed in northern Argentina, Bolivia, Paraguay, Uruguay and Brazil (Oakley *et al.*, 2013). In Brazil occurs only in Porto Murtinho municipality (Taylor *et al.*, 2015) with seedlings commonly associated with *Prosopis* L. genus (Leguminosae), which are recognized as nurse-species (Larrea-Alcázar *et al.*, 2005). *Echinopsis rhodotricha* have funnel-shaped white flowers that open at night and provides pollen and nectar as floral rewards. Corolla presents 167.7 ± 12.4 mm in external length, 151.6 ± 12.2 mm in internal length and 112.5 ± 17.8 mm in diameter. In each flower it was recorded 677 ± 127.7 stamens and 2648 ± 395 ovules.

White flowers with nocturnal anthesis and nectar production may associate *E. rhodotricha* primarily with bat or moth pollination. Indeed, studies on species of this genus recorded moths as their nocturnal pollinators (Schlumpberger *et*

TABLE 1. Floral traits of *Cleistocactus baumannii* (Lem.) Lem. (n = 30), *Echinopsis rhodotricha* K. Schum. (n = 30), *Harrisia balansae* (K. Schum.) N.P. Taylor & Zappi (n = 30), *Harrisia tortuosa* (J. Forbes ex Otto & A. Dietr.) Britton & Rose (n = 30), *Opuntia retrorsa* Speg. (n = 30) and *Stetsonia coryne* (Salm-Dyck) Britton & Rose (n = 15). ECL (external corolla length), ICL (internal corolla length), CD (corolla diameter), AL (anther height), SH (stigma height), OL (ovary length) and OD (ovary diameter). All measurements are presented in milimiters (mm).

	C. baumannii	*E. rhodotricha*	*H. balansae*	*H. tortuosa*	*O. retrorsa*	*S. coryne*
Color	red	white	white	White	yellow	White
Anthesis	diurnal	nocturnal	nocturnal	Nocturnal	diurnal	Nocturnal
ECL	44.1 ± 4.2	167. 7 ± 12.4	213.0 ± 8.5	131.5 ±14.8	49.4 ± 5.1	140.3 ± 9.8
ICL	38.7 ± 5.7	151.6 ± 12.2	183.0 ± 7.5	115.5± 13.4	24.1 ± 3.6	119.0 ± 8.9
CD	9.1± 0.6	112.5 ± 17.8	160.3 ± 5.8	112.0 ± 4.2	39.6 ± 4.6	87.6 ± 6.6
AH	41.7 ± 4.5	132.3 ± 9.2	169.0 ± 4.0	119.5± 30.4	11.5 ± 3.5	106.5 ± 6.3
SH	44.1± 2.3	103.3 ± 12.4	163.0± 8.30	112.0± 15.5	18.14 ± 3.3	104.0 ± 14.1
OL	6.7 ± 1.2	14.4 ± 1.7	24.9 ± 1.5	12.5 ± 0.1	23.9 ± 3.1	15.3 ± 2.4
OD	5.5 ± 0.4	12.4 ± 2.0	21.0 ± 0.5	12.6 ± 0.5	10.2 ± 4.1	12.6 ± 1.1
Stamen number	149 ± 9.8	677 ± 127.7	293 ± 22.3	219.5± 30.5	212 ± 54.2	948.5 ± 47.3
Ovule number*	678 ± 117	2648 ± 395	4247 ± 590	2081 ± 217	81 ± 13	4890 ± 565

*Ovule numbers were estimated from 10 ovaries per species.

TABLE 2. Fruit traits of *Cleistocactus baumannii* (Lem.) Lem. (n = 30), *Echinopsis rhodotricha* K. Schum. (n = 30), *Harrisia balansae* (K. Schum.) N.P. Taylor & Zappi (n = 30), *Harrisia tortuosa* (J. Forbes ex Otto & A. Dietr.) Britton & Rose (n = 30), *Opuntia retrorsa* Speg. (n = 30) and *Stetsonia coryne* (Salm-Dyck) Britton & Rose (n = 15).

	C. baumannii	*E. rhodotricha*	*H. balansae*	*H. tortuosa*	*O. retrorsa*	*S. coryne*
Fruit						
Color fruit	bright lilac	red	red	Red	red	Yellow
Color pulp	white	white	white	White	white	White
Lenght (mm)	12.5 ± 2.1	31.5 ± 5.1	45.1± 5.0	28.5 ± 1.7	34.2 ± 8.1	36.7 ± 7.3
Diameter (mm)	10.6 ± 1.4	22.4 ± 2.1	42.5 ± 3.1	30.7 ± 1.5	16.8 ± 4.3	27.4 ± 3.5
Weight (g)	0.6 ± 0.1	6.9 ± 2.4	30.5 ± 7.7	14.8 ± 3.2	4.3 ± 2.2	12.5 ± 4.9
Seed Set	98 ± 64	1114 ± 366	749 ± 110	510 ± 158	35 ± 27	1212 ± 412
Seeds						
Color	black	black	black	Black	brown	Black
Lenght (mm)	1.4 ± 0.1	1.5 ± 0.2	2.2 ± 0.3	2.3 ± 0.1	3.7 ± 0.2	1.7 ± 0.1
Diameter (mm)	1.1 ± 0.1	1.3 ± 0.2	1.8 ± 0.1	1.7 ± 0.3	1.8 ± 0.2	1.1 ± 0.1
Weight (mg)	0.5 ± 0.1	1.1 ± 0.3	2.0 ± 0.7	2.0 ± 0.3	99.2 ± 7.1	0.6 ± 0.1

al., 2005 - *Echinopsis atacamensis* (Phil.) H. Friedrich & G.D. Rowley; Ossa and Medel, 2011 - *Echinopsis chiloensis* (Colla) H. Friedrich & G.D. Rowley; Ortega-Baes *et al.*, 2011 - *Echinopsis terscheckii* (Britton & Rose) H. Friedrich & G.D. Rowley).

Although *E. rhodotricha* flowers open at night, they remain open until the next morning, characterizing this as a species with prolonged anthesis, which favors the participation of diurnal and nocturnal pollinators and suggests a generalized pollination system. Similar results were recorded to *Echinopsis schickendantzii* F.A.C. Weber (Alonso-Pedano and Ortega-Baes, 2012) that is pollinated by bees and moths, and *E. terscheckii* for which moths, bees and birds were identified as floral visitors. Fleming *et al.* (2001) suggested that this floral trait (prolonged anthesis) is a strategy to ensure sexual reproduction when the main pollinator (nocturnal pollinator) is unpredictable. The fruits are berries, red, dehiscent, weighting 6.9 ± 2.4 g and

FIGURE 2. Flowers of cacti species occurring in São Fernando farm, Porto Murtinho municipality, MS, Brazil. A) *Cleistocactus baumannii* (Lem.) Lem., B) *Stetsonia coryne* (Salm-Dyck) Britton & Rose, C) *Harrisia tortuosa* (J. Forbes ex Otto & A. Dietr.) Britton & Rose, D) *Harrisia balansae* (K. Schum.) N.P. Taylor & Zappi, E) *Echinopsis rhodotricha* K. Schum. and F) *Opuntia retrorsa* Speg. Images provided by PR Souza.

presenting 31.5 ± 5.1 mm in length and 22.4 ± 2.1 mm in diameter **(Figure 3)**. Each one presents, on average, 1114 ± 366 black seeds embedded in a white pulp. The seeds have 1.5 ± 0.2 mm in length, 1.3 ± 0.2 mm in diameter and may be dispersed by birds, lizards and ants. Those dispersers were already recorded in other cacti genera, which show characteristics like morphology/color of fruits and habits (individuals growing close to the ground) similar to the reported here to *E. rhodotricha* (Vasconcellos-Neto *et al.*, 2000, Gomes *et al.*, 2014a).

Harrisia balansae is a scandent shrubby species distributed in Argentina, Bolivia, Brazil (Mato Grosso do Sul state) and Paraguay (Hunt, 2006). Flowers are white, solitary, funnel-shaped, covered with numerous scales and present 293 ± 22.3 stamens and 4247 ± 590 ovules. Corolla is 213.0 ± 8.5 mm in length and 160.3 ± 5.8 mm in diameter (**Table 1** and **Figure 2**). Flowers open at night and provide pollen and nectar as rewards to visitors. Floral characteristics, as well rewards offered, suggest chiropterophilly as the pollination syndrome for this species, as already recorded for other members of this genus (González-Oliva and Urquiola, 2005). The fruits are globose, red, dehiscent, covered with scales, and have 45.1 ± 5.0 mm in length, 42.5 ± 3.1 mm in diameter and weight 30.5 g **(Figure 3)**. The fruits have an average 749 ± 110 seeds, embedded in a white pulp. The seeds have 2.2 ± 0.3 mm in length, 1.8 ± 0.1 mm in diameter and weight 2.0 ± 0.7 mg.

Harrisia tortuosa is a scandent shrubby occurring in Argentina, Paraguay, Bolivia and Uruguay (Hunt, 2006). However, according with Taylor *et al.* (2015), its distribution was expanded to Mato Grosso do Sul, Brazil. Flowers are white, funnel-shaped, with 131.5 ± 14.8 mm in external corolla length and 115.5 ± 13.4 mm in internal corolla length **(Figure 2)**. Corolla diameter ranges 109.0 to 115.1 mm. Flowers have 219.5 ± 30.5 stamens and 2081 ± 217 ovules. Flowers present nocturnal anthesis and offer pollen and nectar as resources to floral visitors. This set of characteristics suggests bat pollination for *H. tortuosa*, as already proposed to *H. balansae*. *Harrisia* flowers are typically described as hermaphrodite, presenting nocturnal white flowers, which produce a strong odor and provide pollen and nectar to visitors (Liogier, 1994). Based on these floral characters, a chiropterophilous syndrome is suggested to the genus (González-Oliva and Urquiola, 2005). However, despite floral traits of *Harrisia portoricensis* Britton are consistent with the bat pollination syndrome (*i.e.*, night flowering, nectar production,

FIGURE 3. Fruits of cacti species occurring in São Fernando farm, Porto Murtinho municipality, MS, Brazil. A) *Harrisia tortuosa* (J. Forbes ex Otto & A. Dietr.) Britton & Rose, B) *Echinopsis rhodotricha* K. Schum., C) *Harrisia balansae* (K. Schum.) N.P. Taylor & Zappi, D) *Cleistocactus baumannii* (Lem.) Lem., E) *Stetsonia coryne* (Salm-Dyck) Britton & Rose, and F) *Opuntia retrorsa* Speg. Images provided by PR Souza.

whitish corollas, strong odor, and large quantities of pollen), the few visits recorded for this species in the Caribbean were performed by hawkmoths (Rojas-Sandoval and Meléndez-Ackerman, 2009a).

Harrisia tortuosa fruits are globose, red, dehiscent, covered with thorns, with 28.5 ± 1.7 mm in length, 30.7 ± 1.5 mm in diameter and an average of 510 ± 158 seeds per fruit (**Table 2** and **Figure 3**). Based on these characteristics, we suggest that birds can act as potential dispersers for *H. balansae* and *H. tortuousa*, as observed in *H. portoricensis*, whose fruits are mainly consumed by birds, but also by rodents and lizards (Rojas-Sandoval and Meléndez-Ackerman, 2009b).

Opuntia retrorsa is a shrubby cactus occurring in Paraguay, southern lowland Bolivia and northern Argentina (Hunt, 2006) and Mato Grosso do Sul state (Taylor *et al.*, 2015). The flowers are diurnal, yellow, solitary, open and shallow, not displaying a floral tube, but presenting a globose pericarpel **(Figure 2)**. Flowers have 49.4 ± 5.1 mm in length and 39.6 ± 4.6 mm in diameter, and contain 212 ± 54.2 stamens and 81 ± 13 ovules **(Table 1)**. Floral morphology suggests melittophily as the pollination syndrome for *O. retrorsa*, as already reported in other species of the genus (Reyes-Aguero *et al.*, 2006, Lenzi *et al.*, 2011). In a review on the reproductive biology of *Opuntia*, Reyes-Agüero *et al.* (2006) classified this genus as presenting extended flowering period, attractive flower color, sweet fragrance, numerous anthers and pollen grains, and stigma lobes that facilitate landing of insects, therefore indicating melittophily as the floral syndrome for the genus.

The fruits are red, globose, indehiscent, covered with glochideos and present 34.2 ± 8.1 mm in length, weight 4.3 ± 2.2g and have 35 ± 2.2 seeds **(Figure 3)**. The seeds are brown, embedded in a transparent pulp, and have, on average 3.7 ± 0.2 mm in length, 1.8 ± 0.2 mm in diameter and weight 99.2 ± 7.1 mg. According with these set of characteristics small mammals can act as potential dispersers of this cactus. For another species bearing similar traits (*Opuntia monacantha* Haw.), Lenzi *et al.* (2012) reported only one marsupial (*Didelphis* sp.) acting on the dispersal of seeds.

Stetsonia coryne is a columnar arboreous cactus occurring in the Chaco region of Argentina, Paraguay and Bolivia (Hunt, 2006). Recent records extended its distribution to Brazil, where it occurs in Porto Murtinho municipality (Taylor *et al.*, 2015), with individuals that can reach up to 10 meters. The flowers are white, solitary, funnel-shaped, laterally distributed along its ramifications and have 948.5 ± 47.3

stamens and 4890 ± 565 ovules. The flowers have 140.3 ± 9.8 mm in external corolla length and 119.0 ± 8.9 mm in internal corolla length, and corolla diameter varies from 82.5 to 95.0 mm (**Table 1** and **Figure 2**).

Flowers open at night, as already recorded for *E. rhodotricha*, often remain open in the following day and may be visited by both diurnal and nocturnal pollinators (Alonso-Pedano and Ortega-Baes, 2012). Fruits are yellow berries, covered with scales, and weight 12.5 ± 4.9 g. They present 1212 ± 412 black seeds per fruit **(Figure 3)** that have 1.7 ± 0.1 mm in length, 1.1 ± 0.1 mm in diameter and weight 0.6 ± 0.1 mg **(Table 2)**. The characteristics of *S. coryne* fruits make them attractive and accessible to frugivore birds, suggesting ornithochory as the seed dispersal syndrome, as usually recorded for other columnar cacti (*Cereus hildmannianus* K. Schum – Silva, 1988; *Stenocereus griseus* (Haw.) Buxb. – Silvius, 1995; *S. griseus* e *Cereus repandus* (L.) Mill. - Soriano *et al.*, 1999; *Cereus jamacaru* DC. subsp. *jamacaru* - Gomes *et al.*, 2014b).

In this study, species with large flowers (external corolla length >10 cm), nocturnal anthesis and white color (*E. rhodotricha*, *H. balansae*, *H. tortuosa* and *S. coryne*), which are probably visited by bats or moths, were predominant. *Cleistocactus baumannii* and *O. retrorsa* have diurnal anthesis, being *C. baumannii* an ornithophilous and *O. retrorsa* a mellitophylous species. Regarding fruits, all species showed fleshy fruits with attractive color (red or bright lilac) and elevated number of seeds, suggesting ornithochory as the predominant seed dispersal syndrome.

Flowers and fruits of cacti species are recognized by their great variety of shapes, sizes, colors, period and duration of anthesis. Also, they're known for being used by various animals (Pimienta-Barrios and del Castillo, 2002). Despite all these characteristics can predict potential pollinators and dispersers of plant species, detailed fields studies, including focal observations and capture of pollinators and dispersers are crucial to understand how such interactions are occurring in fact, and which groups of animals act as effective pollinators and seed dispersers.

The majority of studies focusing on reproductive ecology of cacti in Brazil are concentrated in the semi-arid Northeast, due to the great diversity of cacti in the Caatinga (Taylor and Zappi, 2004). These studies highlight the ecological role exerted by cacti species in that ecosystem due to the consumption of its flowers and fruits by birds, bats, lizards and insects (Locatelli *et al.,* 1997; Leal *et al.*, 2007; Rocha *et al.*, 2007; Brito-Kateivas *et al.*, 2012; Gomes *et al.*, 2014a; Gomes *et al.*, 2014b).

CONCLUSION

Our results demonstrate that, in the Brazilian Chaco, the cacti species offer flowers and fruits that can be visited by a diverse range of animal species, suggesting an important ecological role of this family in this ecosystem. We emphasize that all cactus species occurring in this environment remain completely unknown from their ecological interaction's point of view. Thereby, since these interactions are important for the maintenance and functioning of ecosystems, further studies on cacti and its mutualists are required in this threatened ecosystem (Silva *et al.*, 2008).

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