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DISPERSAL OF PALM SEEDS (*BACTRIS GLAUCESCENS* DRUDE) BY THE FISH *PIARACTUS MESOPOTAMICUS* IN THE BRAZILIAN PANTANAL

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Abstract. The flowering and fruiting phenology of *Bactris glaucescens* (tucum), its fruit consumption by *Piaractus mesopotamicus* (pacu), and the possible dispersal of its diaspores were observed in riparian forests and nearby areas of a secondary channel of the Rio Paraguai. Between February and October 1998, 136 individuals of *P. mesopotamicus* were collected, and their gut contents were analyzed to verify the presence of *B. glaucescens* diaspores. The seeds found were tested in tetrazolium solution to verify their viability. The feeding indices of the diet components were calculated. Phenological observations were made for 40 palm trees. A total of 127 diaspores of *B. glaucescens* were found in the guts of the fish. Eighty of the diaspores were tested, and 67.5% of those were viable seeds. The feeding index of *B. glaucescens* varied through the year, reaching more elevated values at the time of the fruiting phenology peak, which occurs at the same time that the water level increases. *P. mesopotamicus* can be considered a potential dispersal agent of *B. glaucescens*.

Key words: flooding, riparian forest, phenology, palm, ichthyochory.

INTRODUCTION

Vertebrates are the main seed vectors of fleshy-fruit angiosperms in tropical environments (Howe & Smallwood 1982). In tropical forests, 50–90% of tree species depend on birds or mammals for dispersal (Howe & Smallwood 1982, Fleming *et al.*1987, McConkey *et al.* 2012), but other vertebrate groups have also been described as seed vectors, including turtles, lizards, and tree frogs (Silva et al. 1989, Moll & Jansen 1995). Until recently, the role played by riverine fish in dispersal was poorly known, but dispersal by fish has been considered important for several riverine tree species (Gottsberger 1978, Goulding 1980, Kubitzki & Ziburski 1994, Souza-Stevaux *et al.* 1994, Horn 1997, Chick *et al.* 2003, Mannheimer *et al.* 2003, Pollux *et al.* 2006, Galetti *et al.* 2008, Horn *et al.* 2011, Parolin *et al.* 2013).

On the Amazon floodplain, some authors, including Goulding (1980) and Anderson *et al.* (2009, 2011), have studied the relationship between seasonally flooded forests and fruit-eating riverine fish. These fish invade the inundated forests and eat fruits at the time they fall into the water. Many tree species have their diaspores dispersed through fish guts. According to Kubitzki & Ziburski (1994), synchronization exists between the flooding season and the fruiting phenology of many species, which creates a favorable situation for dispersal. In the Atlantic Forest rivers, Villela *et al.* (2002) suggest that some species of *Astyanax* can act as dispersal agents of macrophytes.

In the Pantanal, the Rio Paraguai floodplain can reach thousands of km^2 during the flooding period (Hamilton *et al.* 1996). Although some work has been done to understand the feeding habits of the local fish (Sazima & Caramaschi 1989, Almeida *et al.*

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1993, Catella *et al.* 1996, Resende *et al.* 1998, Resende & Pereira 2000), only Sabino & Sazima (1999), Reys *et al.* (2009), and Galetti *et al.* (2008) discussed the role of fish in seed dispersal. Sabino & Sazima (1999) and Reys *et al.* (2009) reported on the frugivory of *Brycon microleps*, the possibility of the dispersal of many plant species by that fish in riparian forests, and the association of *B. microleps* with monkeys (*Cebus apela*) in consuming fruits.

One common fish, *Piaractus mesopotamicus* (Teleostei, Characiformes, Myleinae), locally named "pacu" (Britski *et al.* 2007), has omnivorous feeding habits but often eats more vegetable than animal components (Silva 1985). Some authors who studied the feeding habits (Silva 1985, Paula *et al.* 1989) and seed-dispersal aspects (Galetti *et al.* 2008) of *P. mesopotamicus* found seeds in its gut, including those of *B. glaucescens Drude*, locally named "tucum", a spiny palm with multiple stems that can reach 3 m in height and an underground rhizome. Its fruits are black when ripe. This palm is commonly found in the riparian forests of the Rio Paraguai, where fishermen often use it as bait for catching pacu (Pott & Pott 1994, Lorenzi *et al.* 1996, Damasceno-Junior *et al.* 2005). Galetti *et al.* (2008) found intact seeds of *B. glaucescens* in the gut of *P. mesopotamicus* and showed that the larger the fish the greater the proportion of intact seeds in their intestines, increasing the probability of seed dispersal for the palm. However, they did not mention if the seeds were viable after being consumed by the fish, and there is no information about the relationship between the phenology of the plant and inundation, or how the variation in the feeding habits of the fish is related to this relationship.

In the present survey, we determined whether the seeds of *B. glaucescens* encountered in the digestive tracts of *P. mesopotamicus* remained viable, and we analyzed the role of the pacu as a potential palm disperser. We also studied the relationships between the hydrological variation of the river, fish diet, and palm phenology.

MATERIAL AND METHODS

Study area. The study was carried out in the Pantanal of the Rio Paraguai (Silva & Abdon 1998). The total inundation area of the Rio Paraguai varied from nearly 4000 to 16 000 km2 between the low-water and high-water seasons over the last 95 years (Hamilton *et al.* 1996). This area is around 5.87% of the total floodplain area of the Pantanal (Silva & Abdon 1998). Here, the Rio Paraguai has secondary water channels, locally named "corixos", that receive water during the flooding period, and most of them remain active even in the low-water season. The data were collected at Corixo Preza, located 50 km from Corumba, in the state of Mato Grosso do Sul (MS; 18°56'S, 57°24'W; Fig. 1). This area has large, seasonally flooded fields and riparian forests on the riverbanks. At the study site, there are several stands of *B. glaucescens* on the riverbanks.

Sampling. A total of 136 individuals of *P. mesopotamicus* was sampled between February and October 1998. The fish were caught on fish hooks attached to hand lines. On the hooks, we put small balls of boiled cassava with artificial flavors of fruit.

Immediately after being captured, each fish had its length measured and its intestine and stomach removed and opened to verify the presence of *B. glaucescens* fruits and seeds. All diaspores found were enveloped in moist cotton and put in labeled plastic bags.

Seed viability was tested in the laboratory. The seeds were opened to find the embryos and immersed in a 0.1% aqueous solution of 2,3,5-triphenyltetrazolium-chloride (tetrazolium) for 24 h. The seeds in which the embryo turned red were considered viable. Only the intact and semi-intact seeds found in the digestive tracts were tested. The tetrazolium test was chosen because it is less dependent than other methods on environmental conditions such as temperature, light, fungi, and other variables (Grabe 1976).

After the seeds had been removed, the stomachs were frozen and other items in the diet verified. The importance of each item in the diet was estimated using the feeding index (Hynes 1950, modified by Kawakami & Vazzoler 1980).

Items were classified into seven categories: preserved diaspores of *B. glaucescens*, destroyed diaspores of B. glaucescens, other preserved seeds, other destroyed seeds, vegetal tissues, animal tissues, and unidentified items.

The feeding index assesses the frequency and volume of each consumed item in the whole sample diet. To calculate the feeding index for each item, the following formula was used for non-empty stomachs:

$$IF_i = (F_i \times V_i) / \sum_{i=1}^{n} (F_i \times V_i)$$

where IF_i = feeding index,
i = 1, 2,...n food item,
F_i = frequency of occurrence of item i in all fish (%), and
V_i = volume of item i in relation to the total volume in all fish.

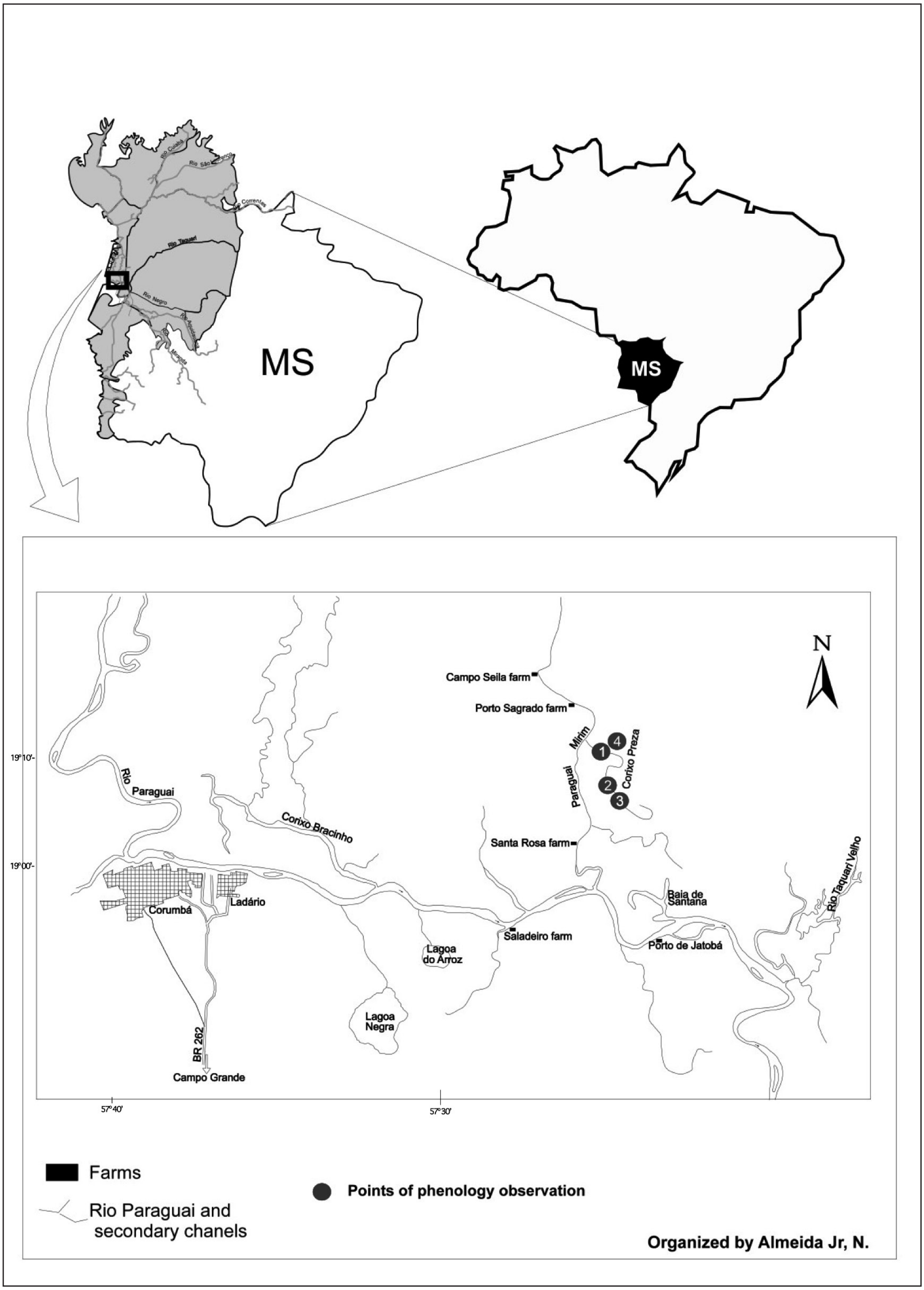

FIG. 1. Localization of the studied area in the Rio Paraguai sub-region and the points of phenological sampling.

Only the stomach contents encountered from February to October were considered. The different periods of inundation of the Rio Paraguai were divided into three trimesters: February to April, when the water levels begin to increase; May to July, when the water levels reach the highest point; and August to October, when the water levels begin to decrease.

The flowering and fruiting phenology of *B. glaucescens* were recorded monthly from March 1998 to February 1999. Forty palms were marked at four points (Fig. 1) with numbered aluminum labels and were visited monthly. For each marked plant we observed whether the flowering and fruiting were influenced by the presence of floodwater. To perform this, the level of inundation on each plant from the base of the stem was measured monthly.

The hydrological data were obtained from the Ladario staff gauge, located 30 km from Corixo Preza. The climatic data were obtained from the Meteorological Station at Corumbá Airport.

RESULTS

Piaractus mesopotamicus diet was mainly composed of vegetable matter, and had the highest proportion (64.82%) of seeds and fruits during the season when the water level was high (second trimester). In the first and third trimesters the diet was composed mainly of other vegetal items, resulting in a feeding index of 85.2 and 87.1%, respectively (Fig. 2). The proportion of animal items was very low.

The diet-index value found for tucum diaspores was also low, reaching 0.99% in the first trimester and 0.29% in the second trimester. Destroyed tucum seeds were found in only one fish in the first trimester (Fig. 2).

A total of 127 tucum diaspores was found in the digestive parts of the fish, mainly the intestine. Only 26 seeds (20.47%) were found in the stomach and included in the *IFi* calculation. Of the 136 fish collected, 30 (22.05%) had diaspores of tucum in their gut. Of the 127 seeds found, 67.5% were found to be viable by the tetrazolium test (Fig. 3).

We observed in the field that when palm fruits fall into the water, they do not submerge. After the fleshy parts of the pericarp are removed, the diaspores sink. The exocarp and mesocarp of the palm are very thin, about 5 mm thick.

The flowering period peaked in the rainy season. Fruits were present throughout the flooded season,

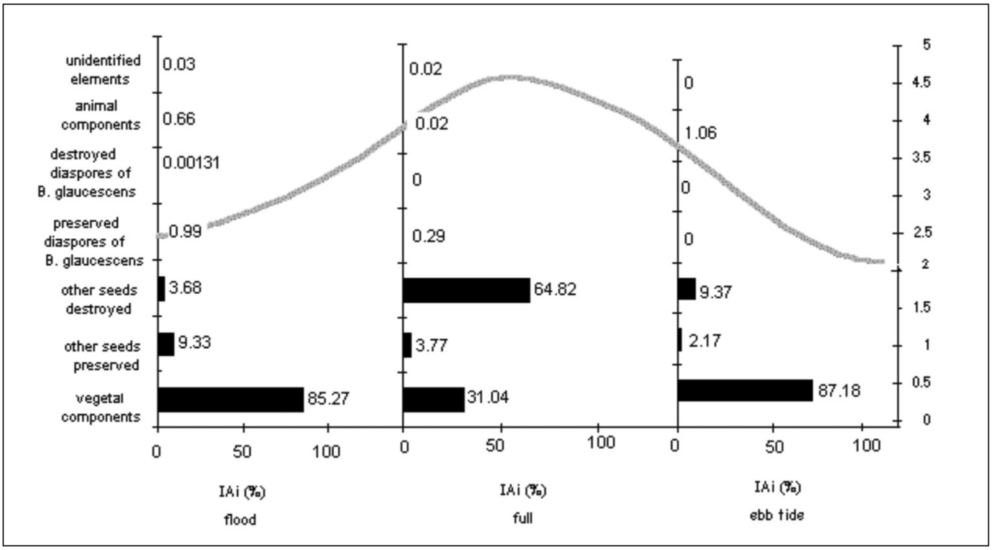

FIG. 2. Feeding index (FI) obtained for *P. mesopotamicus* in the Pantanal sub-region of the Rio Paraguai in February, March, April 1998 (rising waters); May, June, July 1998 (flood period); and August, September, October 1998 (period of low inundation). N = 62, N = 35, and N = 39, respectively (number of *P. mesopotamicus* individuals captured). Change in water levels of the Rio Paraguai in Ladario, MS (in meters) during 1998, showing the three periods considered. Data provided by the Brazilian Navy.

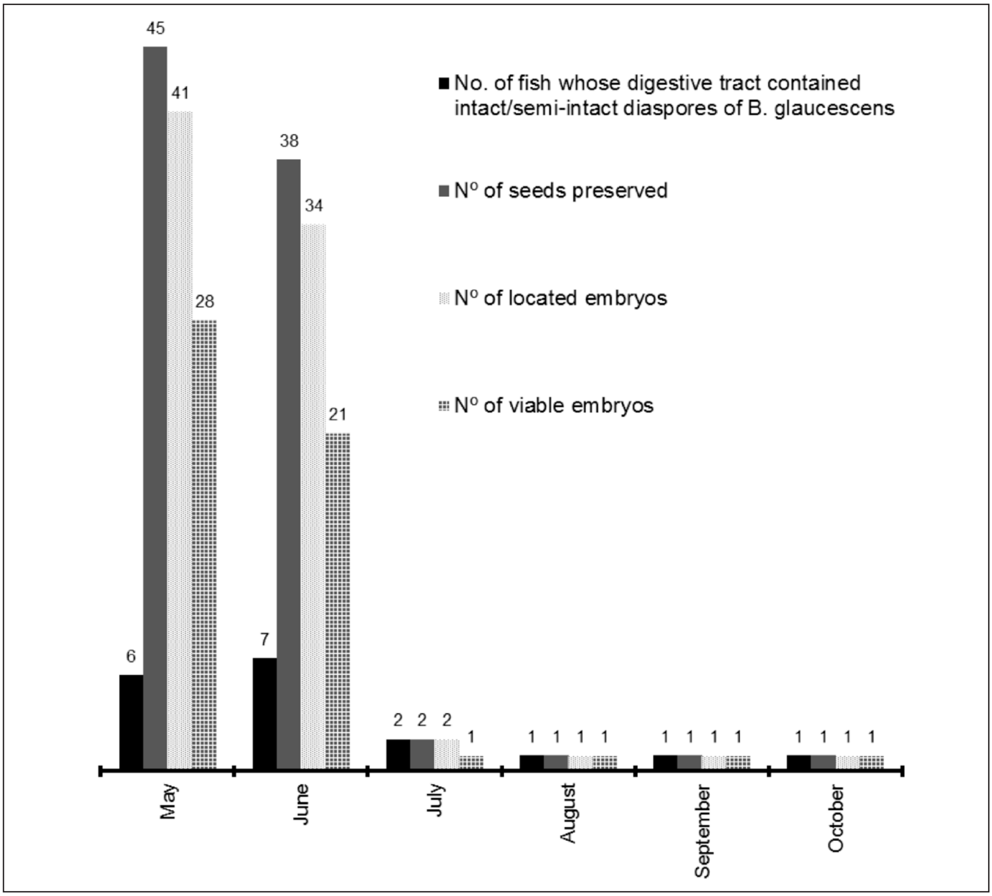

FIG. 3. Viability of the *B. glaucescens* seeds found intact or semi-intact in the digestive tracts of *P. mesopotamicus* using the tetrazolium test, and the number of fish with viable seeds inside their gut.

which is congruent with the non-rainy period (Fig. 4). The presence of flowers and fruits dropped when the river was at the highest level and increased again when the water level decreased (Fig. 4).

The plants on the lower parts of the flood gradient, which consequently are flooded first, had more fruits than those on the higher levels.

DISCUSSION

According to these data, *P. mesopotamicus* can be considered an efficient primary dispersal agent for *B. glaucescens*, as Galetti *et al.* (2008) suggested. Although the feeding index of *B. glaucescens* found in the stomachs of the pacu was low, most of the seeds were found in the intestine, and the majority of the tetrazolium tests were positive. Thus even if few seeds were consumed, the few diaspores eaten have a high probability of dispersal. Another aspect that we can consider is that we do not have data on the speed at which the seeds move through the fish digestive tract. Depending on the speed, the real contribution of this palm to its diet could be greater, taking into account that the adopted index only considers stomach volume at the moment of capture. The highest tucum feeding index was obtained when the water level of the Rio Paraguai was increasing. At that time, *B. glaucescens* was in full fruiting (Fig. 2 and 4), and *P. mesopotamicus* consumed mainly leaves and other vegetable parts (Fig. 2). *B. glaucescens* was probably the main fruit available on the river bank when the river level was increasing, because when the river was

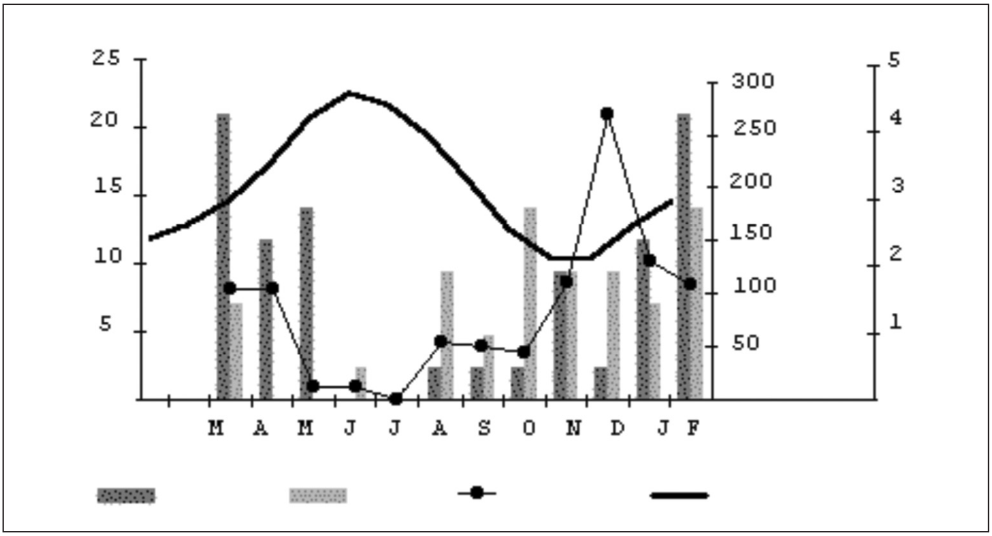

FIG. 4. Flowering and fruiting phenology of *B. glaucescens* in the riparian forest of the Rio Paraguai between March 1998 and February 1999 in relation to water levels of the river and the monthly precipitation measured in the city of Corumbá, MS. Data provided by the Brazilian Navy and Aeronautics.

full the number of other seeds in the diet increased, and the number of tucum diaspores decreased. This situation is quite favorable for *B. glauscescens* seed dispersal. When the river is full, the water flows above the grasslands and the fish has a greater availability of food. At that time, the fish can choose more vulnerable seeds, increasing the energy gain in less time (Fig. 2). This is important, because the fish reproduce when the water level decreases (Silva 1985), and it is important to accumulate energy for that process. Since the ability of fish to disperse *B. glaucescens* is related to the weight and size (Galetti *et al.* 2008) of the fish, the larger, more fully grown individuals in the river have to accumulate more energy for reproduction and hence must perform more dispersal services.

The observed fruiting peak during increasing water levels makes sense, because the *B. glaucescens* individuals are located on the lower parts of the riverbank (Damasceno-Junior 1997). During such periods fish are restricted to that area, maximizing the consumption of palm fruits.

It is probable that precipitation and flooding regulate the reproductive periodicity of *B. glauscescens*, as shown previously for *Bactris bidentula* Spruce (Moraes & Sarmiento 1992). The flowering phenology of *B. glaucescens* seems to be triggered by rain, and the fruiting periodicity seems to be regulated by flooding (Fig. 4). The flooding period in the Rio Paraguai begins nearly three months after the end of the rainy season, and the interval between the flowering and fruiting peaks is the same. Some species studied by Kubitzki & Ziburski (1994) on the Amazon floodplain showed the same behavior, indicating a strategy by which the diaspores are released when the water level is increasing, which improves the probability of dispersal by fish (Goulding 1980, Anderson *et al.* 2009).

B. glaucescens is also water-dispersed. The sinking after the removal of the fleshy parts prevents the seed from being eaten again by other fish and consequently having its embryo and endosperm destroyed. The exocarp and mesocarp of the palm are very thin, which Goulding (1980) found to be a universal characteristic of fleshy fruits on the Amazon floodplains. Sorio (unpublished data) observed that the seeds of *B. glaucescens* could remain viable for a year in submerged and non-submerged conditions. This kind of resistance can be very useful for finding the best conditions to germinate. Fruits are released, carried by water, and then deposited on the riverbanks or eaten by fish, such as *P. mesopotamicus*, which defecate the diaspores near the river bottom (where the diaspores are probably lost), on a deeper part of the flooded riverbank, or on the floodplain. This may help to explain the distribution of *B. glaucescens* in the riparian forest of the Rio Paraguai. Damasceno-Junior (1997) points out that this palm commonly occurs on low sites in the understory. Individuals were mainly found in places that remain flooded 25-35% of the year, and these are probably dispersed by fish. They can also be found in higher places that remain inundated less than 10% of the time, from which they are probably dispersed exclusively by water during the peak of inundation once the fruit with the pericarp can float. If the phenological pattern observed in this survey is the rule, it is very probable that dispersal by fish is an important strategy due to the number of individuals that can be observed on low sites on the flood gradient.

P. mesopotamicus has a great ability to move along the water channels of the Rio Paraguai, allowing *B. glaucescens* to avoid density-dependent mortality (see Howe & Smallwood 1982). These patterns were also observed in studies on the Amazon floodplain of fish like *Colossoma macropomum* (Goulding, 1980, Kubitski & Ziburski 1994, Anderson *et al.* 2011). Fish dispersal on floodplains plays a fundamental role in the life history of plants, affecting their biology, ecology, genetics, and evolution (Pollux 2011). In the Pantanal, ichthyochory plays an important role, and our study is a contribution to a better understanding of the distributional patterns of one species, the palm *B. glaucescens*, and of floodplain trees in general. This relationship is very dependent on the flood pulse (Junk *et al.* 1989), and if the pulse is altered by a changing climate (McConkey *et al.* 2012) or by the construction of dams to produce electricity, the distribution of *B. glaucescens* in riparian forests, and of other species that can be dispersed by *Piaractus mesopotamicus*, will likely also be changed.

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