Evidence for herbaceous seed dispersal by small-bodied fishes in a Pantanal seasonal wetland

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(With 2 figures)

Abstract

We analysed the germination of seeds after their passage through the digestive tract of small floodplain fishes. Samples were collected in five open flooded fields of the northern Pantanal in March 2011. All fishes were sacrificed and their intestinal contents were removed. The fecal material was weighed and stored at 4 °C in a GF/C filter wrapped in aluminum foil. The material was then transferred to a receptacle containing sterilised soil from the sampling area. The fecal samples were kept in a germination chamber for 68 days and then transferred to a greenhouse for another 67 days. We collected a total of 45 fish species and 1014 individuals which produced a total amount of 32g of fresh fecal mass and 11 seedlings. We were able to identify six seedlings: two *Banara arguta*, two *Steinchisma laxa*, one *Hymenachne amplexicaulis* and one *Luziola* sp.. The fish species that produced samples with seedlings were *Astyanax assuncionensis, Metynnis mola, Plesiolebias glaucopterus, Acestrorhyncus pantaneiro* and *Anadoras wendelli*. With the exception of *B.* arguta the remaining plant species and all fish species were not known to be associated with the seed dispersal process of these plants. We found a ratio of 0.435 seedlings.g^{-1} of fresh fecal material, which is100 times higher than the amount of seedlings encountered in fresh soil mass (92,974 grams) in seed bank studies conducted in the same study area. In particular, *Astyanax assuncionensis* and *Metynnis mola* were among the most frequent and most abundant fish taxa in the area. Together with the high seed concentration in the fish fecal material, this evidence allows us to conclude that such fish species may play an important role in seed dispersal in the herbaceous plants of the Pantanal.

Keywords: wetlands, seed bank, ichtyochory.

Evidência de dispersão de sementes de herbáceas por peixes de pequeno porte num campo inundável do Pantanal

Resumo

Nós analisamos a germinação de sementes após a passagem pelo trato digestivo de peixes de pequeno porte da planície de inundação do Pantanal de Mato Grosso. As amostras foram retiradas de cinco campos inundáveis em março de 2011. Todos os peixes foram sacrificados e seus conteúdos intestinais removidos. O material fecal foi pesado e armazenado a 4 °C em filtros GF/C envolvidos em papel alumínio. O material foi transferido para um recipiente contendo solo da região previamente esterilizado e regado diariamente. As amostras de fezes foram mantidas por 68 dias numa câmara de germinação e então mantidas por mais 67 dias na casa de vegetação. Coletamos 1014 indivíduos de peixes distribuídos em 45 espécies que produziram um total de 32g. de fezes e 11 plântulas das quais seis foram identificadas como *Banara arguta* (n=2), *Steinchisma laxa* (n=2), *Hymenachne amplexicaulis* (n=1) e *Luziola* sp. (n=1). As espécies de peixes que produziram amostras com germinações foram *Astyanax assuncionensis, Metynnis mola, Plesiolebias glaucopterus, Acestrorhyncus pantaneiro* e *Anadoras wendelli*. Esse é o primeiro relato que associa essas espécies de plantas e de peixes no processo de dispersão de sementes com exceção de *B. arguta*. Encontramos uma razão de 0,435 germinações.g^{-1} por massa úmida fecal, o que representa 100 vezes mais germinações do que o registrado por massa úmida de solo num estudo de banco de sementes de solo da mesma região. Em particular, *Astyanax assuncionensis* e *Metynnis mola* estão entre as espécies mais frequentes e abundantes da área de estudo. Considerando a alta concentração de germinações por massa de material fecal essa evidência nos permite sugerir que os peixes de pequeno porte da planície de inundação do Pantanal podem ter um efeito determinante na dispersão de herbáceas do Pantanal.

Palavras-chave: áreas úmidas, banco de sementes, ictiocoria.

1. Introduction

Life history traits determine the relationship between the number and competitive ability of offspring. However, tradeoffs in plant reproductive strategies are not simply limited to quantitative vs. qualitative aspects of seed production. The limited extent of movement in plants makes access to sites for seedling development a crucial aspect of reproductive effort.

Seed dispersal may be advantageous if it allows the seedling to escape a highly competitive environment, avoid predation associated with seed-rich sites, transport the seed to the right microhabitat (Davidson and Morton, 1981) or allow the establishment of new populations that might persist if the site of the parent population disappears (Van der Valk and Davis, 1978; Howe and Smallwood, 1982; Schneider and Sharitz, 1988; Nathan and Muller-Landau, 2000; Howe and Miriti, 2004).

Fruit and seed consumption are among the most common seed dispersal strategies. Vertebrates play an important role as dispersal vectors. Seed dispersal by vertebrates may occur due to non-intentional seed collection (adhesive seeds) or by the excretion of viable seeds (Buide et al., 1998; Herrera, 2002). The passage through the digestive trait may exert a positive or a negative effect on seed viability and on the timing of seed germination. For most plants with small seeds, the time spent in the vector's gut tends to be longer. This longer passage of time may cause more damage to soft-skinned seeds, but the seeds may also be transported farther (Traveset, 1998). Typically, the passage through the digestive tract in birds and bats increases the seed germination rate by 55% and 58%, respectively. For reptiles, no effect on the germination rate was found in 56% of the cases examined. If an effect was found, however, it was always positive (Traveset, 1998). Studies of seed dispersal by fishes are scarce. Nevertheless, most authors are aware of the substantial potential of fishes as seed dispersers, particularly in the tropics (Gottsberger, 1978; Goulding, 1980, 1983; Kubitzki and Ziburski, 1994; Waldhoff et al., 1996; Horn, 1997; Pilati et al., 1999; Banack et al., 2002; Mannheimer et. al., 2003; Gomiero and Braga, 2003; Maia et al., 2007; Lucas, 2008; Galetti et al., 2008; Anderson et al., 2009; Pollux, 2011; Anderson et al., 2011; Horn et al., 2011).

Among tropical environments, wetland vegetation may be especially sensitive to fish-mediated seed dispersal (Anderson et al., 2011). Most plant species in wetlands are herbaceous with small-sized seeds that are likely to disperse further than large-sized seeds. However, most studies of fishes as seed dispersers address relatively large fish species and woody plant species. Large fishes are usually not present in wetland floodplains with the exception of the Amazonian igapó forests floodplain (Goulding, 1980), mostly because the waters are shallow and are far from large river beds. It is important to stress that wetland floodplains such as the South American Pantanal are rich in small-seeded plants (mostly herbaceous) and have a highly dynamic patchy vegetation distribution (Junk and Piedade, 1993; Zeilhofer and Schessl, 2000). Another important aspect of the seed dispersal process that is rarely addressed in fish studies is the *in situ* quantitative effect of fishes in the seedling production. Hereby we considered all fish species as potential dispersers instead of focusing only on the frugivores. We also make a quantitative assessment of small-bodied fish contribution to the seedling production using fishes collected directly from their natural environment.

Our objective is to determine whether the small fishes inhabiting Pantanal wetlands are able to excrete viable seeds. We also address the relative contributions of seed dispersal by fish (ichthyochory) and by water (hydrochory), comparing the amount of seedlings produced by fish feces with the amount of seedlings produced in a nearby soil seed bank study. For this we assume that most seedlings produced from the soil seed bank came from hydrochoric events. Most likely, the seedlings produced from fish fecal material will belong to the herbaceous plant group due to the small size of the seeds.

2. Material and Methods

2.1. Study area

The Pantanal wetlands occupy an area of 140,000 km^2 in the central portion of South America. The area has little relief. Its elevation ranges from 100 to 180 m, and its regional hydraulic gradient does not exceed 15 cm.km^{-1}. The complex hydrography of the Pantanal is associated with a variety of soil types. These physical factors produce a landscape that tends to be organised in patches (Rio de Janeiro, 1974; Girard et al., 2010).

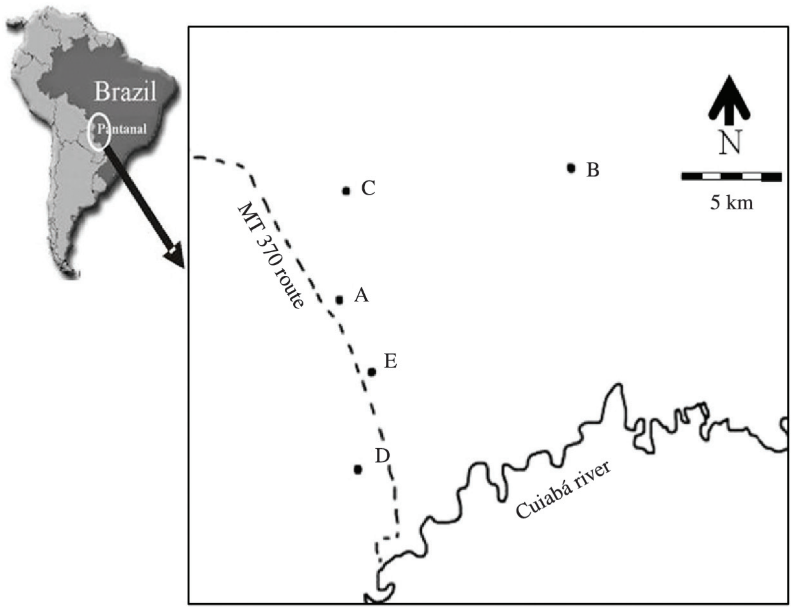
The regional climate is the Köppen AW type, hot and humid with rainy summers and dry winters (Köppen, 1948). The rainfall ranges from 800 to 1400 mm.year^{-1}, occurring primarily between November and March. The average regional temperature varies between 17° and 32 °C (Brasil, 1997; Fantin-Cruz et al.,2011).

The area sampled in this study is located near Nossa Senhora do Livramento Municipality, in the Cuiabá River drainage. All sampling sites were positioned in flooded fields away from the Cuiabá River overflow zone. The vegetation consisted primarily of *Brachiaria humidicola* pasture bordered by small bushes with little canopy cover.

2.2. Data sampling

We sampled five sites to a depth of 1 m. The sites were located at least 1 km apart (Figure 1). Fishes were collected using a 1 m^2 screen constructed of 2 mm mesh. To collect a sample, the screen was swept close to the ground and then lifted under the floating macrophytes that formed the vegetation.

Fishes were identified by species *in situ*, washed with clean water and released in a plastic bag filled with clean water. All individuals were kept alive in containers and separated by species until they were processed in the field laboratory.



Site	Coordinates
A	16° 25' 23.84" S, 56° 25' 20.58" W
B	16° 22' 1.39" S, 56° 18' 17.07" W
C	16° 22' 34.41" S, 56° 25' 3.40" W
D	16° 29' 56.64" S, 56° 24' 47.75" W
E	16° 27' 22.97" S, 56° 24' 17.54" W

Figure 1. Sampling site distribution and geographical position.

In the laboratory, the fishes were sacrificed by exposure to a low temperature, and their intestinal contents were removed. The intestinal contents were combined with the sample resulting from the filtration of the water from the plastic bag that had contained the fish. This fecal material sample (FMS) was weighed and stored at 4°C in C in Whatman® GF/C 47 mm filter wrapped in aluminum foil. Fish fecal material was grouped by fish species at each sampling site. If a determined fish species was already collected in a sampling site, it was collected nevertheless in the next site based on the premise that the possible species-specific diet variation could produce fecal samples with or without seeds. Each fish species collected was considered a subsample for a sampling site and the fecal material of all individuals was put together in the same germination sampling unit. According to that sampling design any fish species could have up to five replicates if it was collected in all five sampling sites. The material was then transferred to a receptacle containing sterilised soil from the sampling area.

These receptacles were kept in a germination chamber for 68 days and then transferred to a greenhouse for another 67 days. The soil was sterilised by treating it for 90 minutes inside a steam sterilizer under 1 atm pressure. The germination chamber was programmed to simulate a 12 hour day followed by a 12 hour night, with constant temperatures of 28°C for the diurnal period and 26 °C for the nocturnal period.

We investigated the quantitative effect of fishes on the seed dispersal process by analyzing the number of seedlings produced by the total mass of substrate at each sampling site. This number was obtained by dividing the number of seedlings produced for a sampling site by the total amount of substrate mass collected at the site. The fish fecal mass that did not produced seedlings was summed with the mass that produced seedlings to reach the total amount of fish fecal material for site. In order to evaluate the importance of ichthyochory and hydrochory in the seed dispersal process we compared the number of seedlings produced between the FMS and a soil seedbank study performed in the a neighboring area (Pagotto et al., 2011). Because the data were not normally distributed, we evaluated the difference between these values with a Mann-Whitney test. Pagotto and colleagues (2011) work was performed in a nearby area less than 10 km from the sampling sites of our study.

3. Results

We captured 1014 specimens of 45 species and collected 32 g of feces. Most of the specimens belonged to small-bodied species or were young of the year (Table 1). *Astyanax assuncionensis* (Gery, 1972)*, Plesiolebias glaucopterus* (Costa and Lacerda, 1988) and *Aphyocharax anistsi* (Eigenmann and Kennedy,1903) were found at all sampling sites, and 18 other species were found in at least three of the five sampling sites (Figure 2). *Plesiolebias glaucopterus, Moenkhausia dicroura* (Kner, 1858), *Metynns mola* (Eigenmann & Kennedy, 1903)*, Trigonectes balzani* (Perugia, 1891) and *Serrapinus* sp. (Boulenger, 1900) were the most abundant species, representing more than 50% of the total number of fishes collected (Table 1).

Table 1. Fish species presented by sampling site, total species abundance and mean body size.

Order	Family	Species	Sampling site	N	Body length (mm)
Characiformes	Characidae	*Triportheus sp.* (Cope, 1972)	B,D,E	3	98.11
		Tetragonopterus argenteus (Cuvier, 1816)	C,D	39	48.76
		Markiana nigripinis (Perugia, 1891)	A,C,D,E	20	77.63
		Gymnocorymbus ternetezii (Boulenger, 1895)	A,B,D,E	67	34.86
		Moenkhausia dichoroura (Kner, 1858)	A,B,C,E	118	24.58
		Moenkhausia santacfilomenae (Steindachner, 1907)	A,B,D	28	29.48
		Astyanax assuncionensis (Gery, 1972)	A,B,C,D,E	34	72.36
		Hyphessobrycon eques (Steindachner, 1882)	E	1	19.1
		Psellogrammus kennedyi (Eigenmann, 1903)	B	28	28.31
		Aphyocharax paraguayensis (Eigenmann & Kennedy, 1903)	D	20	20.01
		Aphyocharax anisitsi (Eigenmann & Kennedy, 1903)	A,B,C,D,E	52	19.78
		Serrapinus sp. (Boulenger, 1900)	A,B,C,E	75	15.5
		Charax leticiae (Lucena, 1987)	B,E	18	79.25
		Acestrorhynchus pantaneiro (Menezes, 1992)	A,B,C,E	30	105.04
		Poptella paraguayensis (Eigenmann, 1907)	A,B,C	10	40.01
		Metynnis mola (Eigenmann & Kennedy, 1903)	A,B,C,E	113	52.79
		Piaractus mesopotamicus (Holmberg, 1887)	A	3	49.35
		Serrasalmus maculatus (Kner, 1858)	A,B	11	54.2
		Serrasalmus marginatus (Valenciennes, 1837)	C	2	49.18
	Crenuchidae	*Characidium* aff. *zebra* (Eigenmann, 1909)	C,E	6	18.95
	Curimatidae	*Potamorhina squamoralevis* (Braga & Azpelicueta, 1983)	D	2	29.84
		Cyphocharax guillii (Eigenmann & Kennedy, 1903)	C	4	27.78
		Steindachnerina nigrotaenia (Eigenmann & Eigenmann, 1889)	A,E	2	16.21
	Anostomidae	*Leporinus frederici* (Bloch, 1794)	A,B,E	11	45.68
		Abramites hypselonotus (Günther, 1868)	E	1	18.02
	Lesbiasinidae	*Pyrrhulina australis* (Eigenmann & Kennedy, 1903)	A,B,C,D	7	22.74
	Erythrinidae	*Hoplias malabaricus* (Bloch, 1794)	A,B,D,E	12	77.54
		Hoplerytrinus unitaeniatus (Agassiz, 1892)	C,D	4	68.24
Gymnotiformes		*Gymnotus inaequilabiatus* (Valenciennes, 1839)	D	1	29.78
		Brachyhypopomus sp. (Mago leccia, 1994)	E	2	95.23
Siluriformes	Pimelodidae	*Rhandia quelen* (Quoy & Gaimar, 1824)	E	3	33.98
	Auchenipteridae	*Entomocorus benjamini (*Eigenmann, 1917)	A	1	45.33

Table 1. Continued...

Order	Family	Species	Sampling site	N	Body length (mm)
		Tatia neivai (Ihering, 1930)	C,E	2	30.12
		Trachelyopterus coriaceus (Valenciennes, 1840)	B,E	6	75.69
	Doradidae	*Anadoras wendelli* (Castelnau, 1855)	B,C	11	52.04
	Calichthyidae	*Callichthys callichthys* (Linnaeus, 1758)	E	34	28.39
		Corydoras hastatus (Eigenmann & Eigenmann, 1888)	B,C,E	11	14.78
		Brochis britskii (Nijssen & Isbrücker, 1983)	A	1	15.36
	Loricariidae	*Liposarcus anisitsi* (Eigenmann & Kennedy, 1903)	A,D	3	12.35
Cyprinodontiformes	Rivulidae	*Plesiolebias glaucopterus* (Costa & Lacerda, 1988)	A,B,C,D,E	121	26.23
		Trigonectes balzanii (Perugia, 1891)	A,C,D,E	81	58.06
		Stenolebias damascenoi (Costa, 1991)	C,D,E	10	24.97
	Cichlidae	*Aequedis plagiozonatus (*Kullander, 1984)	A,B,D,E	32	42.21
		Astronotus crassipinis (Heckel, 1840)	E	2	22.65

After 135 days of the germination experiment, the FMS from five fish species had produced a total of 11 seedlings (Table 2). All sampling sites except site B (Figure 1) had fishes that excreted viable seeds. We were able to identify six seedlings: two *Banara arguta* Briq. from, two *Steinchisma laxa* (Sw.) Zuloaga and one *Hymenachne amplexicaulis* from *Astyanax assuncionensis* FMS, and one *Luziola* sp. from *Plesiolebias glaucopterus*. All the other seedlings were monocotyledonous but failed to grow to an age that allowed them to be identified.

The soil seedbank experiment (Pagotto et al., 2011) produced fewer seedlings per gram of substrate than the FMS (Mann-Whitney U=56, p=0.05). Pagotto et al. (2011) reported a ratio of 0.004 seedlings.g^{-1} of moist soil substrate, whereas our results showed a ratio of 0.435 seedlings.g^{-1} of moist fecal substrate (Table 3).

4. Discussion

Our results have shown that certain small-bodied Pantanal fish species are able to excrete viable seeds. Although fishes have been considered key seed dispersers for certain plants (Goulding, 1980, 1983; Waldhoff et al., 1996; Horn, 1997; Banack et al., 2002; Mannheimer et. al, 2003; Lucas, 2008; Galetti et al., 2008; Anderson et al. 2011), most previous papers on the topic focus on fishes that inhabit rivers, small tributaries and Amazonian igapó forests (Goulding, 1980; Horn, 1997; Lucas, 2008; Galetti et al., 2008; Anderson et al., 2011). A small number of previous studies have focused mainly at small-bodied fishes as potential seed dispersers (Gomiero and Braga 2003; Mannheimer et al., 2003; Maia et al., 2007). Thus, published scientific information on this topic is generally lacking (Horn et al.,2011).

We obtained seedlings from fishes belonging to many different functional groups, including the piscivore *Acestrorhyncus pantaneiro,* the invertivores *Plesiolebias glaucopterus* and *Astyanax assuncionensis,* the herbivore *Metynnis mola* and the planktivore/detritivore *Anadoras wendelli.* None of the cited species were known to take part in plant seed dispersion processes. In the case of certain small-bodied species with a limited range of movement across the floodplain (e.g., *P. glaucopterus* and *A. wendelli*) seed dispersal from their feces over a distance is relatively unimportant. However, the plants may still benefit from the passage of their seeds through the fish's digestive tract. Considering the high abundance and frequent presence of *P. glaucopterus* in the region, it is possible that the passage of seeds through the digestive tract of this fish may act as a germination trigger. Although few previous studies have analysed the effect of passage through the digestive tract of fishes on seed germination, the results of these studies indicate that no effect can be demonstrated or that the observed effects are mostly positive (Traveset, 1998).

It is possible that the seedling produced by the piscivorous *A. pantaneiro* might be the result of accidental ingestion or might represent a seed that was previously ingested by one of the fish's prey. Although this species is widely distributed in the study area, its role as a disperser may be minor due to its sit-and-wait predatory strategy. In contrast, *A. assuncionensis* and *M. mola* may play significant roles as seed dispersers, and the former species may be particularly important. *A. assuncionensis* was found at all sampling sites. Its FAS produced almost one-half of the seedlings and three of the four species or morphospecies among the identified seedlings. In addition, it is a highly mobile fish and may travel throughout the study area.

Most of the seedlings that we obtained were monocotyledonous, with the exception of two *Banara*

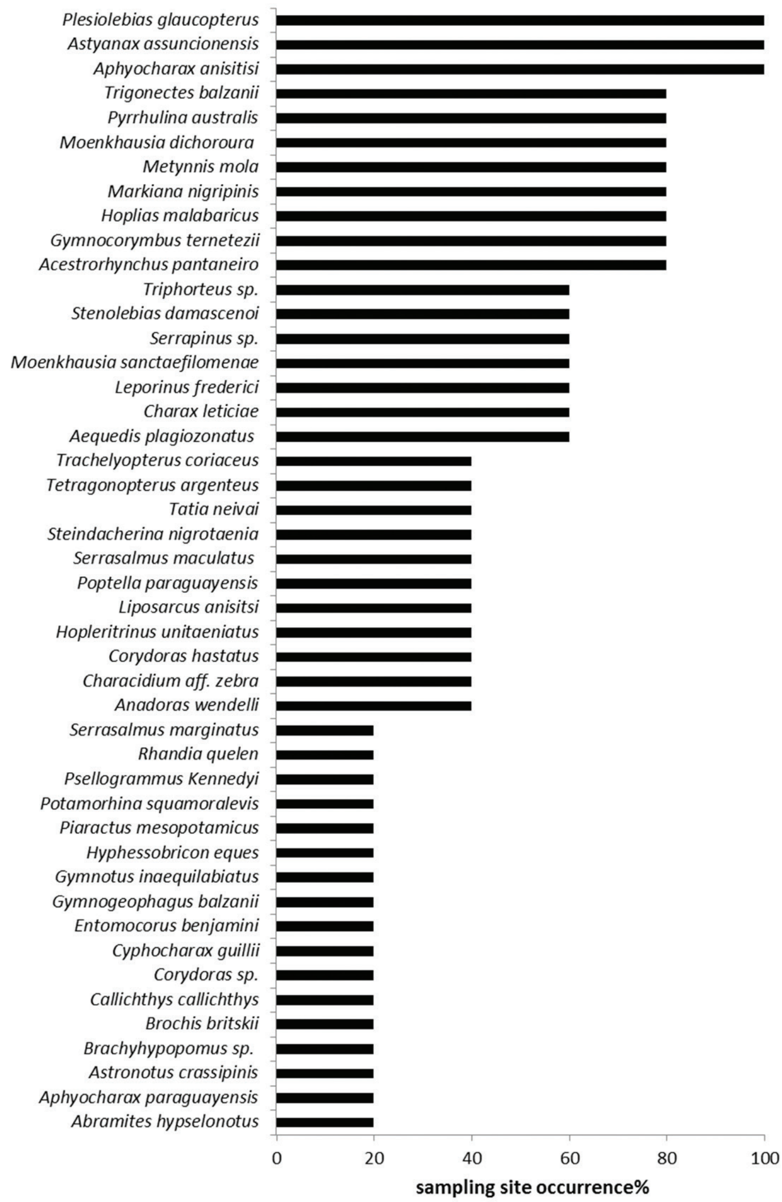


Figure 2. Occurrence frequency of fishes among sampling sites.

arguta plants. This species was expected to be dispersed by fishes due to its well-known association with aquatic environments and fruit consumption by fishes (Morais and Silva, 2010; Costa-Pereira et. al., 2011). *Steinchisma laxa* is a common herbaceous plant used as pasture in the area and associated with activities relevant to the economy of the Pantanal. Both *Hymenachne amplexicaulis* and *Luziola* sp. are aquatic plant species that occur mainly during the flooding season. With the exception of *B. arguta* these plant species were not known to interact with fishes in their seed dispersal processes.

Most herbaceous species have small seeds, which may remain in the digestive tracts of the dispersers for longer periods than bigger seeds (Garber, 1986; Levey and Grajal, 1991; Gardener et al., 1993). This prolonged passage time can increase the distance between the source plant and its seedlings, reinforcing the importance of small-bodied fishes as dispersers. Given that most of the Pantanal vegetation produces fruits and seeds during the flooding season and that small-sized seeds are also dispersed by the wind and the water, it is probable that waterborne dispersal are the primary forces responsible for soil seed bank formation. Nevertheless, this study shows that the seedling germination rate, expressed on a substrate-mass basis, is 100 times higher in fishes than in soil seed bank material.

Fish floodplain density in the area is approximately 290,000 fishes per hectare (Fernandes, 2007). Considering that a fish may retain a seed in its guts for two days it would

Table 2. Fish species that excreted viable seeds, number of fishes that contributed to a FMS for the seedlings, time elapsed for seedling germination, FMS mass.

Species	Nº of seedlings	Nº of fishes that contributed to FMS	Time elapsed until germination (days)	FMS mass (g)
Astyanax asuncionensis	5	17	7, 16, 26, 40 and 56	1.53
Metynnis mola	3	87	18, 30 e 113	7.32
Plesiolebias glaucopterus	1	30	19	0.01
Acestrorhyncus pantaneiro	1	18	81	0.27
Anadoras wendelli	1	9	94	0.73

Table 3. Basic statistics of the comparison between ichthyochory (seeds in fish feces) and hydrochory (soil seebank) seedling per substrate mass production.

Experiment	Number of replicates (sampling sites)	Minimum value Seedlings/ substrate mass (g)	Maximum value Seedlings/ substrate mass (g)	Mean value Seedlings/ substrate mass (g)	Variance	Total of substrate mass collected in all sampling sites (g)
Soil seed bank (Pagotto et al., 2011)	14	0.001	0.013	0.004	0.0001	92,974.1g
Fish fecal sampling	5	0	1.124	0.421	0.181	32.0g

excrete seeds 45 times during a 90 days typical flooding season. Our results suggest that nearly one percent of the floodplain fishes may excrete seeds. Also most of the viable seeds will produce seedlings in the last two weeks of the flooding season where the water table is already shallow or withdrawing. Considering the number of seed-carrying fishes and the last two weeks of the flooding season the number of seedlings produced by fishes could reach more than 20,000 seedlings per hectare.

Seed dispersal by fishes is particularly important in seasonally flooded environments (Galetti et al., 2008), and we have found evidence of this significance in the Pantanal. In the Pantanal, the terrestrial vegetation is closely linked to the dynamics of the aquatic environment (Girard et al., 2010), and this linkage influences the patchiness of the Pantanal landscape. It is possible that seed dispersal processes usually associated with the water itself might be enhanced by the complementary contributions made by the fishes, particularly in view of the high seed concentration found in the fish fecal material.

5. Conclusions

We conclude that small-bodied fishes of the Pantanal flooded fields are able to excrete viable seeds which associated with their elevated numbers make them potentially important seed dispersers.

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