Acta Scientiarum. Biological Sciences
ISSN: 1679-9283
eduem@uem.br
Universidade Estadual de Maringá
Brasil

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Acta Scientiarum. Biological Sciences, vol. 38, núm. 4, octubre-diciembre, 2016, pp. 419-427
Universidade Estadual de Maringá
Maringá, Brasil

Acta Scientiarum

http://www.uem.br/acta
ISSN printed: 1679-9283
ISSN on-line: 1807-863X
Doi: 10.4025/actascibiolsci.v38i4.30802

Diaspore bank of aquatic macrophytes maintaining species diversity in a Neotropical pond

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ABSTRACT. The diaspore bank is an important component of biological diversity acting mainly as storage and source of diaspores, which also indicate dynamics and patterns of maintenance of plant diversity. We tested the hypothesis that the diaspore bank would be the responsible factor for the maintenance of the aquatic plant species, used two techniques to evaluate the diaspore bank: seedling emergence and direct counting of field samples. Density and richness of the diaspore bank were correlated with plant cover of the aquatic macrophyte communities and also with the euphotic zone radiation in different phases of the hydrological cycle. The diaspore bank is a key factor in maintenance of aquatic macrophyte assemblages in this pond. *Nymphaea amazonum* was one of the dominant species in the pond and presented temporally peaks of plant cover. Furthermore, depth allowed induction of germination of stored diaspores. Therefore, the diaspore bank may predict which species colonizes a site when environmental characteristics are favorable and allows inferring which processes are linked to changes in structure of aquatic macrophyte assemblages. These mechanisms are the means for recovery of macrophyte species under natural disturbances, represented by water level oscillations in floodplains.

Keywords: aquatic plant, plant ecology, seed bank, wetland.

Banco de diásporos de macrófitas aquáticas para a manutenção da diversidade das espécies em uma lagoa Neotropical

RESUMO. O banco de diásporos é um componente importante da diversidade biológica atuando principalmente como armazenamento e fonte de diásporos, que também indicam a dinâmica e os padrões de manutenção da diversidade vegetal. Testamos a hipótese de que o banco de diásporos seria o fator responsável pela manutenção das espécies de plantas aquáticas, utilizando duas técnicas para avaliar o banco diásporo: emergência das plântulas e contagem direta de amostras de campo. Densidade e riqueza do banco de diásporos foram correlacionadas com cobertura vegetal das comunidades de macrófitas aquáticas e também com a radiação da zona eufótica em diferentes fases do ciclo hidrológico. O banco de diásporos é um fator chave na manutenção das assembleias de macrófitas aquáticas nesta lagoa. *Nymphaea amazonum* foi uma das espécies dominantes na lagoa temporalmente, apresentou picos de cobertura vegetal. Além disso, a profundidade permitiu a indução da germinação de diásporos armazenados. Portanto, o banco de diásporo é um preditor de quais espécies colonizarão um local quando as características ambientais são favoráveis e permite inferir que os processos estão ligados a mudanças na estrutura das assembleias de macrófitas aquáticas. Estes mecanismos são os meios para a recuperação de espécies de macrófitas sob as perturbações naturais, representados por oscilações do nível de água nas planícies aluviais.

Palavras-chave: planta aquática, ecologia vegetal, banco de sementes, pantanal.

Introduction

Holling (1973, p. 17) defined resilience as "[…] the persistence of relations in a system, a measure of the ability of systems to absorb changes of its state variables, the determining variables and their parameters, continuing to persist in time". Several authors have since defined resilience, with an emphasis on a system's ability to recover successfully to situations of disturbance, stress or adversity (Elmqvist et al., 2003; Gunderson, 1999; Harris, Carr, & Dash, 2014; Tilman & Downing, 1994). In freshwater wetlands, knowing seedling dynamics (e.g., input and exit) are important to assess the potential for self-restoration of ecosystems subjected to natural and anthropogenic disturbance.

In wetlands, propagules can arrive from outside the system or be already present in the water or sediment. In this sense, one of the most important structural components of wetland ecosystems is the diaspore bank, defined as an aggregation of non germinated seeds, potentially capable of replacing adult plants (Bakker, 1989). It is also a fundamental component in succession and development of plant communities in wetlands (Valk, 1981).

The diaspore bank reflects the historical process of the life cycle of plants, since their establishment in the habitat until their distribution in space and time (Christoffoleti & Caetano, 1998). In the secondary succession, which involves replacement of vegetation after a disturbance, the composition and density of species of the diaspore bank helps determine the structure of the plant community (Orlóci, 1993). The diaspore bank can also indicate what species will colonize after a disturbance or when environmental conditions become adequate for germination (Valk, 2006). In general, the number and density of species represented in the diaspore bank reflect the diversity of the established community (Leck & Brock, 2000).

The size and composition of the diaspore bank are in part determinants of its longevity. But factors which affects longevity seem to be related to morphology, especially size and thickness of seed tegument, and processes of dispersion are also related to seed morphology (DeVlaming & Proctor, 1968; Moore, 1982). Renewal of the diaspore bank depends on established dynamics of the own diaspore bank as well as on the vegetation, which in turn depends on the form of diaspore bank recruitment, for afterward reproduction, dispersal, predation and viability (Fenner, 1985; Leck, 1989). The seed banks play a critical role in the initial formation and maintenance of the zonation patterns in wetlands, as flooding may influence the seed survivorship in the seed bank (Poiani & Johnson, 1989) and recruitment from the seed bank (Keddy & Ellis, 1985; Seabloom, Valk, & Moloney, 1998).

Several studies have described the pattern of seed banks and the relationship between the standing vegetations and the seed banks in wetlands along an unmeasured water depth gradient (Yuan, Liu, Li, & Li, 2007). Some have found that the seed banks of specific zones reflect the dominant vegetation of those zones at some wetlands (Parker & Leck, 1985; Nicholson & Keddy, 1983). Density and composition are essential attributes of a diaspore bank that shall be approached first (Simpson, Leck, & Parker, 1989), hence, the understanding of species composition of these soil can help us improve the conservation and restoration efforts.

Seed bank studies usually focus on the composition and dispersion of species and not considering the effect of this bank in the floristic composition established in the ponds. Native species in wetlands commonly forming large seed banks in intermittent wetlands to permit survival during unfavorable periods (Brock, Nielsen, Shiel, Green, & Langley, 2003). In this study, we evaluated the relation between the macrophyte diaspore bank in the sediment and the plant cover of aquatic macrophytes in a temporary floodplain lake that remains mostly unconnected with the river Paraná. We tested the hypothesis that the diaspore bank would be the responsible factor for the maintenance of the aquatic plant species, and their success could be related to the depth of the euphotic zone.

Material and methods

Study area

The Upper Paraná River floodplain is a complex mosaic mostly made up of wetlands, including seasonal semideciduous alluvial forest, fragments, riparian marshy forests, shrubby vegetation and grasslands (Campos & Souza, 1997). Aside from large river beds, the floodplain contains secondary channels, shallow permanent lakes and temporary ponds (Mendonça, Lopes, & Anjos, 2009). High water levels predominate between November and March (rainy season), while low waters occur between April and October. The climate, by Köppen' (1948) system, is type Cfa – tropical-subtropical, with warm Summer (annual mean of 22ºC), and mean annual rainfall of 1500 mm, but in some years the climate seems Cwa, with dry Winter (Maack, 2002). Altitude is *c.* 230 m (Campos & Costa-Filho, 1994).

Osmar Pond (22º46'27.53''S and 53º19'57.95''W; Figure 1) is a small marginal pond (0.09 ha), isolated by the river dike, located *c.* 120 m off the Paraná River main channel (Figure 1). It is 60 m long and 15 m wide on average during the low water phase, with depths from 0.6 m to 4.5 m during the study period. During floods the pond usually connects with the river. The overbank river-pond connection occurs when the water level reaches ca. 3 m, however, flow exchanges between the river and the pond through the hyporheic corridor may also occur when the river level is < 3 m. For sediment sampling were demarcated three parallel transects to the major axis of the pond, distant 10 m from each other (Figure 1). In each transect were collected 3 samples (M1 = margin 1; M2 = margin 2 and center), totaling nine sediment samples.

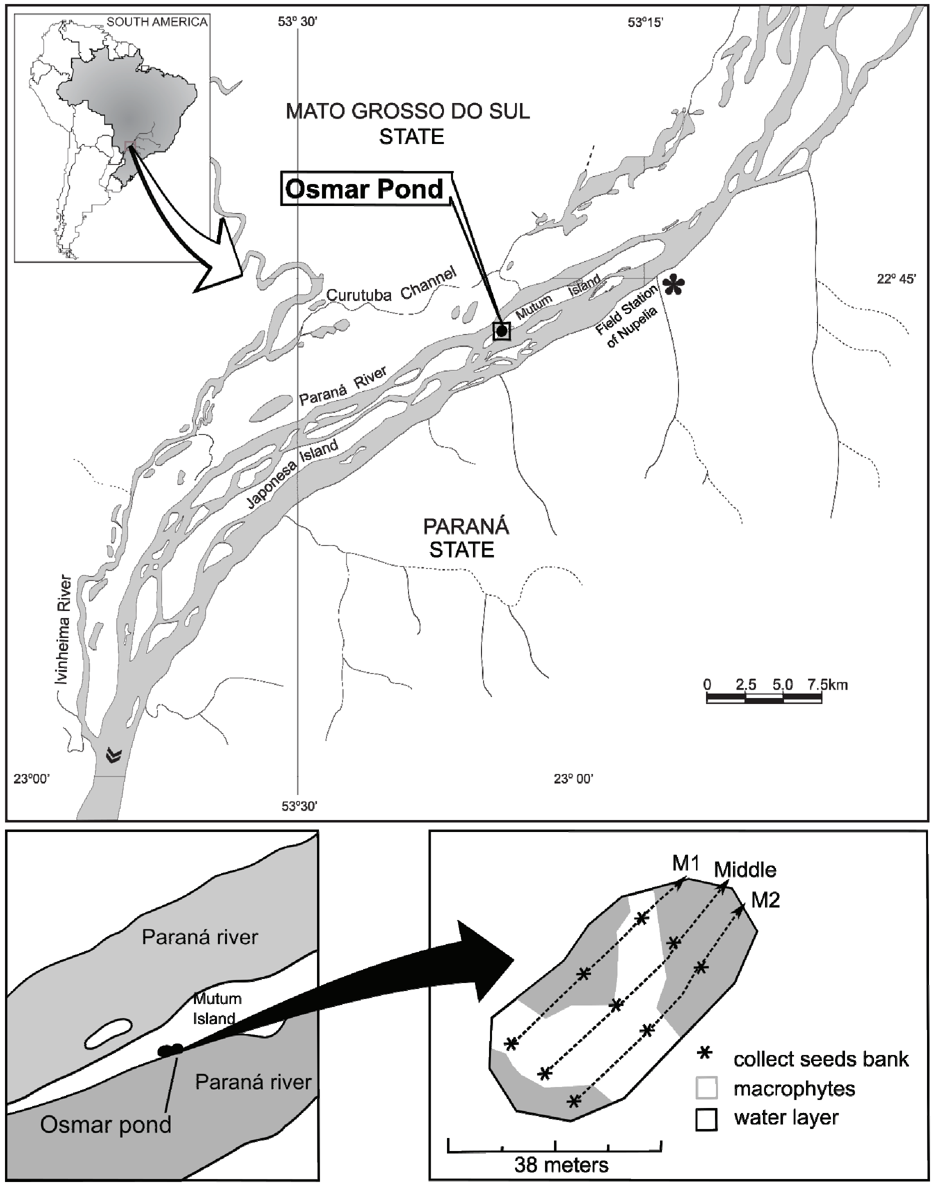

Figure 1. Map of the stretch of the Upper Paraná River floodplain showing the Osmar Pond and sampling at the sediment.

Sampling

Direct count of propagules in sediment: To estimate availability of propagules in the sediment we used a modified Pettersen grab (0.0345 m^2). Samples were collected once at the onset of the rainy season (November 2008), in six random points in the pond (80 cm depth), totalizing an area of 0.207 m^2. The quali-quantitative analysis of the diaspore bank was performed by direct count. The sediment was washed and sorted through a set of three sieves of meshes 0.2, 1 and 2 mm.

The propagules retained in the first two meshes were immediately fixed and all the sediment retained in the last sieve was fixed and preserved in alcohol 70%. The propagules captured in the three sieves were counted, identified and recorded under a stereoscopic microscope. Species identification was assured by diaspores collected from known macrophytes and by cultivation until fruit set.

We discarded injured seeds and counted only the intact ones. This technique determines number of seeds, but not their viability (Simpson et al., 1989). Viability of the diaspore bank was not tested with tetrazolium chloride because the diaspores are tiny and tender and also enclose dry and hard fruits. We estimated absolute density (m^{-2}) (Mueller-Dombois & Ellenberg, 1974).

Seedlings emergence (germination): To sample sediment for seedling viability, we marked three transects parallel (two in margin (2 m both) and one in the middle (3 m) with 30 m between rows) to the larger diameter of the pond. In each transect we collected three samples (n= 9), in November 2008, with the same Pettersen grab described above. The sediment samples were put into identified plastic bags and taken to the greenhouse at the Universidade Estadual de Maringá, screened for 30% shade, and covered with colorless plastic to prevent contamination by outside propagules and rain.

For quantification of seeds we used the emergence or germination method, counting seedlings (Brown, 1992). Seedlings were weekly identified, counted and recorded. Some seedlings were transplanted until flowering to be identified. Identification of species was achieved consulting taxonomical literature (Kissmann & Groth, 1995, 1999), comparing plants in the reference collection kept in our Laboratory of Aquatic Macrophytes, and also asking specialists.

Samples were spread in plastic trays 30 cm long, 9 cm wide, and 6 cm height (area of 0.027 m^{-2}). The trays first received a 2 cm layer of sterilized washed sand, topped with 1 cm layer of sediment. The trays were randomly placed on benches in the greenhouse. Three additional trays containing just sand were added as control of contamination by local seed rain. Individual sediment samples represent the replicates, being three replicates from margin 1 (M1), three from margin 2 (M2) and three samples from the middle of the pond (Figure 1). These sampling sites were selected to check for interference effect of the pond morphometry on the spatial distribution of diaspore bank.

Trays were watered twice a day, in the morning and afternoon, keeping a water depth c. 1 cm. We allowed seeds to germinate for a period of 15 weeks, between April and August 2009.

Floristic and plant cover measurements: Samplings for floristic survey and cover of the macrophyte species in the pond were made every three months from February 2008 to December 2009, covering two hydrological cycles. Vegetation cover was estimated separately for each species. We marked and georeferenced two permanent patches of macrophytes, in which we established transects cited above perpendicular to the margin and sampled a quadrat with 0.25 m^2 at every 2 m (Figure 1).

We estimated plant cover with the Braun-Blanquet method (1979): (1) 0% ≤ cover ≤ 5%; (2) 5% ≤ cover ≤ 25%; (3) 25% ≤ cover ≤ 50%; (4) 50% ≤ cover ≤ 75%; (5) cover ≥ 75%. Each value of the scale was transformed into mean cover (1 = 2.5%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%). To improve evaluation, we calculated the mean of visual estimates of all quadrats sampled in the pond. Additionally, to check the presence of submersed species we utilized a fork attached on an aluminum pipe. Life forms were considered according to Irgang, Pedralli, & Waecheter (1984), excluding epiphytes (Pedralli, 1990).

Evaluation of water transparency and depth: Evaluations of water transparency and depth for the pond were made from February 2008 to December 2009, using the Secchi disc, while pond level was taken from a fluviometric gauge 12 km away. The level of the Paraná River and pond depth indicate approximately the level whereby the river connects with the pond. Therefore, Secchi disc depth was used to evaluate the euphotic zone, according to Padial and Thomaz (2008).

Statistical analysis

To verify if abundances differed among sampling points (pond center and margins), we used analyses of variance for repeated measures (Zar, 1999). This analysis was chosen owing to the effect of time, as we considered the 15 weeks of sampling as repeated measures. The means were compared by the test of least significant difference (LSD) (Zar, 1999) using Statistica for Windows (Statsoft, 2005).

Results

Direct count of diaspores in the sediment

Considering only intact diaspores, the total density was 20,754 m^{-2}, belonging to 10 species, distributed in 7 genera and 7 families (Table 1). *Nymphaea amazonum* Mart. & Zucc. was the most abundant (density = 14,942 diaspores m^{-2} , 61.8% of total seeds), indicating that it dominates the diaspore bank of the studied pond. Other abundant seeds in the bank belonged to *Polygonum punctatum* Elliott (19.3%) and *Polygonum hydropiperoides* Michx. (9.17%). These three main species represented 90.27% of diaspores in the sediment.

We found diaspores of different life forms (sensu Pedralli, 1990), with predominance of emergent macrophytes (57.1%), followed by amphibious (21.4%), rooted with floating leaves and free floating (7.18%) and free-submersed (7.14%).

Seedling emergence (germination)

We found no contamination by seed rain in the control treatment. The first seeds started to germinate in the 2nd week, and during the 15 weeks period we counted 3,222 seedlings, resulting a total density of 13,260 seedlings m^{-2}. We identified 15 species of 12 genera included in 9 families. In regard to floristic richness of the diaspore bank, the most representative families were Cyperaceae and Poaceae, with three species each, followed by Polygonaceae and Pontederiaceae with two species each. The diaspore bank was dominated by *N. amazonum* (n= 2613; 81% of emerged seedlings). Other species such as *Rhynchospora corymbosa* (L.) Britton and *P. punctatum* contributed 5.1% (n= 165) and 3.4% (n= 111), respectively, of the total germinated seeds (Table 1). By virtue of the dominance, the seeds of *N. amazonum* showed good viability. After germination, transplanted to other tanks, *R. corymbosa*, *Oxycaryum cubense* (Poepp. & Kunth) Palla and *Ludwigia leptocarpa* (Nutt.) H. Hara flowered and fructified at the end of the 13rd week. We point out that *Utricularia foliosa* L., showed the fastest germination which occurred in the 2nd week with emission of the first leaf (a relevant datum, since this submerse macrophyte does not present development of radicle), and we recorded full seedling development on the 10th day.

Table 1. Composition and density of the diaspore bank and plant cover of the aquatic macrophyte species in Osmar pond, Upper Paraná River floodplain. SE= seedling emergence; DC = direct count; PC = Mean plant cover.

Family	Specie	SE (m^2)	DC (m^2)	PC (%)
Cyperaceae	*Rhynchospora corymbosa* (L.) Britton	165	72	0
	Eleocharis sp.	66	681	0
	Oxycaryum cubense (Poepp. & Kunth) Palla	49	0	0
Fabaceae	*Aeschynomene sensitiva* Sw.	4	0	0
Hydrocharitaceae	*Egeria densa* Planch.	0	0	16
Lentibulariaceae	*Utricularia foliosa* L.	8	174	0
Nymphaeaceae	*Nymphaea amazonum* Mart. & Zucc.	2613	14942	66
Onagraceae	*Ludwigia leptocarpa* (Nutt.) H. Hara	4	87	0
Poaceae	*Echinochloa polystachya* (Kunth) Hitchc.	4	0	0
	Eragrotis hypnoides (Lam.) Britton, Sterns & Poggenb.	37	0	0
	Paspalum repens P.J. Bergius	0	0	47
	Unidentified	4	14	0
Polygonaceae	*Polygonum punctatum* Elliot	111	4667	73
	Polygonum ferrugineum Wedd.	21	87	4
Pontederiaceae	*Eichhornia azurea* (Sw.) Kunth	41	14	0
	Eichhornia crassipes (Mart.) Solms	21	14	0
	Pontederia cordata L.	0	0	40
Ricciaceae	*Riccia* sp.	74	0	0

The germination peak in all treatments was between the 8th and the 10th week, but between the 3rd and the 5th weeks the samples from M1 increased seedling densities. However, samples of the middle of the pond showed the highest densities in the experiment. In addition, there was a significant difference in seedling density over time, within each sampling area (middle - F= 3.14, p < 0.01; M1- F= 2.69, p < 0.01 and M2- F= 2.38, p < 0.01) (Figure 2A). However, considering mainly the time, the middle of the pond significantly differed from both margins (M1 and M2), presenting the highest seedling densities (Figure 2B).

Although we did not observe an interaction among various factors of the analysis, it was possible to perceive by the LSD test that germination was higher in the last weeks the experiment (t8, t9, t10 and t15), of the diaspores from the middle in relation to the margins (Figure 2A).

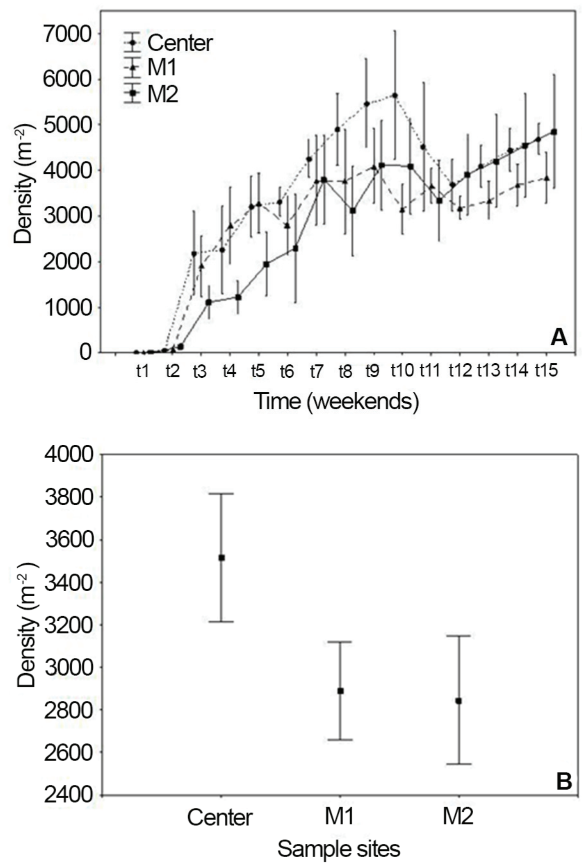

Figure 2. Mean (± standard error) seedling density at three sites of Osmar pond (middle of pond, margins M1 and M2) over the germination period (A); mean values (± standard error) of density in different sampling sites (B). [density, time (weeks), middle, margins M1, M2, sampling sites]

Floristic and plant cover measurements

During eight field surveys carried out in Osmar pond, we found 19 species belonging to 16 genera and 12 families. The family with the highest species richness was Polygonaceae (four species), followed by Poaceae and Cyperaceae (three species each). Regarding life forms, we obtained the following percentages: emergent (57.8%); amphibious (21.0%), rooted with floating leaves, rooted submerse, free submerse and epiphyte (5.2%).

However, only six species were present in the sampling quadrats used to estimate percentage cover. The estimated percentage of plant cover reflected differences among species during the evaluated period (Figure 3). *Egeria densa* Planch. (16%) and *Polygonum ferrugineum* Wedd. (4%) obtained the lowest values of cover percentage in all samplings. However, the species which contributed the most to macrophyte cover were *P. punctatum* (73%), *N. amazonum* (66%), *Paspalum repens* P.J. Bergius (47%) and *Pontederia cordata* L. (40%). We observed a significant increase in *N. amazonum* cover, from 9% in February 2008 to 49% in March 2009, yet was absent in June 2009. Meanwhile, *P. punctatum* had 65% of cover in February 2008 and reached highest values in November 2008 (50% of total area), gradually reducing it in cover beyond November sampling. Other species, such as *P. cordata*, increased in cover after November 2008, from 0% to 31%, while *P. repens* showed highest cover in September and December 2009 (15 and 20%, respectively). However, *P. ferrugineum* and *E. densa* only appeared in September 2009, the latter showing a peak in December 2009, when water showed high transparency.

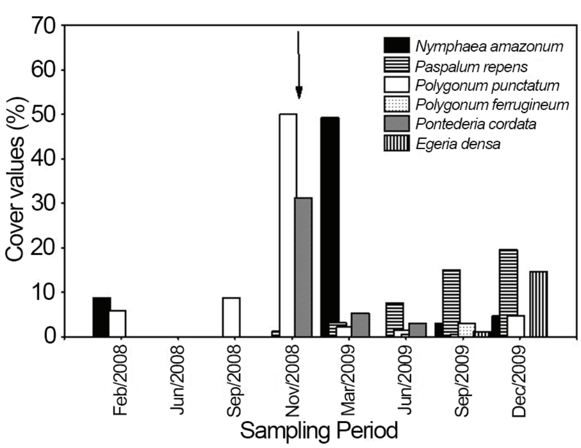

Figure 3. Change in plant cover observed in the Osmar pond, between February 2008 and December 2009. Vertical bars correspond to cover values, evaluated according to Braun-Blanquet (1979). The arrow shows the sampling moment of the diaspore bank. [macrophyte cover; Feb, Sep, Sep, Dec]

Considering both sampling techniques for diaspore bank together with phytosociology, we recorded 18 species (Table 1). Two of them were identified at the genus level and one just as sterile grass. Poaceae and Cyperaceae were the richest families (four and three species, respectively). Furthermore, five species only appeared in the method of seedling emergence: *O. cubense*, *Aeschynomene sensitive* Sw., *Echinochloa polystachya* (Kunth) Hitchc., *Eragrotis hypnoides* (Lam.) Britton, Sterns, & Poggenb and *Riccia* sp. On the other hand, *E. densa*, *P. repens* and *P. cordata* were only recorded in the established vegetation. No species occurred only in the direct count of diaspores and three species occurred in three life phases (seedling, diaspore and established vegetation: *N. amazonum, P. punctatum* and *P. ferrugineum*).

Evaluation of water transparency and depth

During the study period, three flood pulse events occurred in the Paraná River. As a result, pond depth varied, maximum depth (2.7 m), minimal depth (0.5 m), mean (1.3 m). However, during the whole sampling period the Secchi disc depth measured was high, indicating that the euphotic zone always reached the sediment, favoring the germination of seeds in the diaspore bank.

Discussion

Density of the diaspore bank, evaluated by both methods, clearly showed the reserve accumulated potential of the species present, having important function in maintenance of the communities and populations of aquatic macrophytes in the pond. This occurs because the success of the diaspore bank depends on density of diaspores ready to germinate when environmental conditions for establishment are favorable (Carvalho & Favoretto, 1995). The evidence that the store of diaspores was able to replace the adult plants was sustained mainly by *P. punctatum* and *N. amazonum*, which showed the highest density values of diaspores and seedlings, as well as the highest increments in plant cover.

The increase of plant cover of some species in the pond was certainly possible, as they showed a combination of characteristics regarding diaspore longevity. Species with long-lived diaspores, which were in the bank and developed when environmental conditions were satisfactory, as well as species with short-lived diaspores, which only can establish under favorable conditions, otherwise they lose viability (Valk, 1981).

Some species (e.g., *P. repens*, *P. cordata* and *E. densa)* were only found in the vegetation survey, and did not occur in the diaspore bank. Possibly their propagules arrived when still viable, succeeding in increasing plant cover, mechanism also observed by Riss (2008). In addition, these three species, mainly *E. densa,* have strong vegetative propagation which may account for their persistence in the pond. For *N. amazonum*, it seems that its maximum cover in March 2009, was dependent on the diaspore bank built from seed set in previous years. This species concentrates seeds close to the parent plants. The difference in germination from margins compared to the middle of the pond was likely due to the large quantity of *N. amazonum* seeds deposited in the middle, where most individuals grew.

The euphotic zone, which always reached the pond bottom, as well as the shift to dry periods with subsequent reduced water level, probably favored rupture of the seed tegument or of the pericarp of *N. amazonum* for water absorption and germination. The conditions observed allowed colonization by seed bank, according to Gomes, Goes, and Saino (2000). Our experiment in the greenhouse in fact combined characteristics similar to the natural habitat, probably the expressive light and the conditions of water level resulted in high germination rates of macrophytes.

Also, some habitat features were likely important for the reproductive success of *N. amazonum*. We observed absence of this water lily in water column months before the peak of its plant cover, so there was no physical barrier to radiation, which is an inductor of positive germination for photoblastic seeds (Sculthorpe, 1967). The plant may hinder its own germination, then a congeneric species, *Nymphaea ampla* (Salisb.) DC., with the same life form, intercepted up to 96% of the incident radiation (Esteves, 1998). However, the reproductive strategy of *N. amazonum*, through build up of a diaspore bank in this habitat can influence the plant distribution on the floodplain. According to Neiff (2003), the floodplain receives diaspores and other materials mainly during the potamophase (high waters) and the river transports and redistributes diaspores generated upstream. The expressive number of seeds of *N. amazonum*, added to its capacity of germination and to hydrological pulses, explain why this species occurs among the most frequent ones in other habitats of this stretch of the Paraná River (Ferreira, Mormul, Thomaz, Pott, & Pott, 2011).

Both sampling techniques we used to assess the diaspore bank showed to be complementary, because some species that germinated were not recorded in direct counts of diaspores. Some studies (Brown, 1992) suggest that the method of direct count, though not giving information on viability of diaspores, is more precise to detect the total number of diaspores stored in the sediments. However, since only viable seeds are generally considered to contribute with the diaspore bank, viability must be tested in germination experiments as a complementary test (Brown, 1992). The choice of method should take into consideration the research objectives. Under the same point of view, Palazzo, Bonecker, and Fernandes (2008), working in the same pond with cladoceran resting eggs, showed the efficiency and importance of the stock of diversity in the sediments of this water body.

Conclusion

We conclude that the obtained data and the applied methods demonstrate that the diaspore bank allows inferring which processes are linked to changes in structure of aquatic macrophyte assemblages. Nevertheless, little has been discussed about synchrony of biotic and abiotic factors together with the adaptive selection of species in building diaspore banks, and probably these yet unknown mechanisms are the means for recovery of macrophyte species under natural disturbances, represented by water level oscillations in floodplains. In complement, the knowledge on the diaspore bank helps to predict which species could colonize a habitat when it becomes favorable. A combined method of analysis of the diaspore bank can overcome underestimates of total number and composition of diaspores, and so we recommend them as a tool in studies on biodiversity and for conservation ex-situ, mainly in floodplain habitats. Works with a monitoring diaspores bank in ponds should be conducted to understand the dynamics of spatial and temporal variation of the macrophyte community.

Acknowledgements

We thank to the Brazilian governmental agencie CNPq (*Conselho Nacional de Desenvolvimento Científico e Tecnológico*) for the scholarship to Fernando Alves Ferreira, and Dr. Sidinei Magela Thomaz by orientation in the Ph.D. project.

References

Bakker, J. P. (1989). *Nature management by grazing and cutting*. Dordrecht, NL: Kluwer.

Braun-Blanquet, J. (1979). *Fitosociologia: bases para el estudio de las comunidades vegetales*. Madrid, ES: H. Blume Ediciones.

Brock, M. A., Nielsen, D. L., Shiel, R. J., Green, J. D., & Langley, J. D. (2003). Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. *Freshwater Biology, 48*(7), 1207-1218.

Brown, D. (1992). Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. *Canadian Journal of Botany, 70*(8), 1603-1612.

Campos, J. B., & Costa-Filho, L. V. (1994). *Proposta técnica de implantação da área de proteção ambiental do Arquipélago de ilha Grande.* Curitiba, PR: SEMA/IAP.

Campos, J. B., & Souza, M. C. (1997). Vegetação. In A. E. M. Vazzoler, A. A. Agostinho, & N. S. Hahn (Ed.), *A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos* (p. 331-342). Maringá: Eduem.

Carvalho, P. C. F., & Favoretto, V. (1995). Impacto das reservas de sementes no solo sobre a dinâmica populacional das pastagens. *Informativo Abrates, 5*(1), 87-108.

Christoffoleti, P. J., & Caetano, R. S. X. (1998). Soil seed banks. *Scientia Agricola, 55*(spe), 74-78.

DeVlaming, V., & Proctor, V. W. (1968). Dispersal of aquatic organisms: Viability of seeds recovered from the droppings of captive killdeer and mallard ducks. *American Journal of Botany, 55*(1), 20-26.

Elmqvist, T., Folke, C., Nystrom, M., Peterso, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment, 1*(9), 488-494.

Esteves, F. A. (1998). *Fundamentos de limnologia*. Rio de Janeiro, RJ: Interciência/FINEP.

Fenner, M. (1985). *Seed ecology.* London, U.K.: Chapman and Hall.

Ferreira, F. A., Mormul, R. P., Thomaz, S. M., Pott, A., & Pott, V. J. (2011). Macrophytes in the upper Paraná river floodplain: checklist and comparison with other large South American wetlands. *Revista de Biologia Tropical, 59*(2), 541-556.

Gomes, H. R., Goes, J. I., & Saino, T. (2000). Influence of physical processes and freshwater discharge on the seasonality of phytoplankton regime in the Bay of Bengal. *Continental Shelf Research, 20*(3), 313-330.

Gunderson, L. (1999). Resilience, flexibility and adaptive management - antidotes for spurious certitude? *Conservation Ecology, 3*(1), 1-10.

Harris, A., Carr, A. S., & Dash, J. (2014). Remote sensing of vegetation cover dynamics and resilience across southern Africa. *International Journal of Applied Earth Observation and Geoinformation, 28*, 131-139.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics, 4*(1), 1-23.

Irgang, B. E., Pedralli, G., & Waecheter, J. I. (1984). Macrófitos aquáticos da Estação Ecológica do Taim, Rio Grande do Sul, Brasil. *Roessleria, 6*(1), 395-404.

Keddy, P. A., & Ellis, T. H. (1985). Seedling recruitment of 11 wetland plant species along a water level gradient: shared or distinct responses? *Canadian Journal of Botany, 63*(10), 1876-1879.

Kissmann, K. G., & Groth, D. (1995). *Plantas infestantes e nocivas* (Tomo III). São Paulo, SP: BASF.

Kissmann, K. G., & Groth, D. (1999). *Plantas infestantes e nocivas* (Tomo II). São Paulo, SP: BASF.

Köppen, W. (1948). *Climatología*. Buenos Aires, AR: Fondo de Cultura.

Leck, M. A. (1989). Wetland seed banks. In M. A. Leck, V. T. Parker, R. L. Simpson (Ed.), *Ecology of Soil Seed Banks* (p. 283-305). New York, NY: Academic Press.

Leck, M. A., & Brock, M. A. (2000). Ecological and evolutionary trends in wetlands: evidence from seeds and seed banks in New South Wales, Australia and New Jersey, USA. *Plant Species Biology, 15*(2), 97-112.

Maack, R. (2002). *Geografia física do Estado do Paraná* (3a ed.). Curitiba, PR: Imprensa Oficial do Paraná.

Mendonça, L. B., Lopes, E. V., & Anjos, L. (2009). On the possible extinction of birds species in the Upper Paraná River floodplain, Brazil. *Brazilian Journal of Biology, 69*(2), 747-755.

Moore, P. (1982). How to reproduce in bogs and fens. *New Science, 95*, 369-371.

Mueller-Dombois, D., & Ellenberg, H. (1974). *Aims and methods of vegetation ecology.* New York, NY: Wiley.

Neiff, J. (2003). Planícies de inundação são ecótonos? In R. Henry (Ed.), *Ecótonos nas interfaces dos ecossistemas aquáticos* (p. 29-45). São Carlos: Rima.

Nicholson, A., & Keddy, P. A. (1983). The depth profile of a shoreline seed bank in Matchedash Lake, Ontario. *Canadian Journal of Botany, 61*(12), 3293-3296.

Orlóci, L. (1993). Conjectures and scenarios in recovery study. *Coenoses, 8*(3), 141-148.

Padial, A. A., & Thomaz, S. M. (2008). Prediction of the light attenuation coefficient through the Secchi disk depth: empirical modeling in two large Neotropical ecosystems. *Limnology, 9*(2), 143-151.

Palazzo, F., Bonecker, C. C., & Fernandes, A. P. C. (2008). Resting cladoceran eggs and their contribution to zooplankton diversity in a lagoon of the Upper Paraná River floodplain. *Lakes & Reservoirs: Research & Management, 13*(3), 207-214.

Parker, V. T., & Leck, M. A. (1985). Relationships of seed banks to plant distribution patterns in a freshwater tidal wetland. *American Journal of Botany, 72*(2), 161-174.

Pedralli, G. (1990). Macrófitos aquáticos: técnicas e métodos de estudos. *Estudos de Biologia, 26*, 5-24.

Poiani, K. A., & Johnson, W. C. (1989). Effect of hydroperiod on seed-bank composition in semipermanent prairie wetlands. *Canadian Journal of Botany, 67*(3), 856-864.

Riss, T. (2008). Dispersal and colonization of plants in lowland streams: success rates and bottlenecks. *Hydrobiologia, 596*(1), 341-351.

Schulthorpe, C. D. (1967). *The biology of aquatic vascular plants*. Konigstein, WG: Koeltz Scientific Books.

Seabloom, E. W., Valk, A. G. van der, & Moloney, K. A. (1998). The role of water depth and soil temperature in determining initial composition of prairie wetland coenoclines. *Plant Ecology, 138*(2), 203-216.

Simpson, R. L., Leck, M. A., & Parker, V. T. (1989). Seed banks: general concepts and methodological issues. In M. A. Leck, V. T. Parker, & R. L. Simpson (Ed.), *Ecology of soil seed banks* (p. 3-9). San Diego, CA: Academic Press.

Statsoft Inc. (2005). *Statistica for Windows v.6.0: computer program manual*. Tulsa, OK. Retrieved from http://www.statsoft.com/textbook/stathome.html

Tilman, D., & Downing, J. A. (1994). Biodiversity and stability in grasslands. *Nature, 367*(6461), 363-365.

Valk, A. G. van der. (1981). Succession in Wetlands: a Gleasonian approach. *Ecology, 62*(3), 688-696.

Valk, A. G. van der. (2006). *The biology of freshwater wetlands*. Oxford, UK: Oxford University Press.

Yuan, L. Y., Liu, G. H., Li, W., & Li, E. H. (2007). Seed bank variation along a water depth gradient in a subtropical lakeshore marsh, Longgan Lake, China. *Plant Ecology, 189*(1), 127-137.

Zar, J. H. (1999). *Biostatistical analysis* (4ª ed.). New Jersey, NJ: Prentice Hall.

Received on February 29, 2016.
Accepted on September 29, 2016.