



Factors driving seed dispersal in a Neotropical river-floodplain system

Florencia Facelli Fernández^{1,2} , Berenice Schneider^{2*}  and Florencia Zilli² 

Received: February 28, 2019

Accepted: April 23, 2019

ABSTRACT

Dispersal is a key process affecting the diversity of natural communities. We addressed hydrochory of wetland plant seeds in the Middle Paraná River floodplain. We first studied seed dispersal by drifting macrophytes in the Paraná River main channel (MC), in a high discharge secondary channel (HD) and in two low discharge channels (LD) during an extraordinary flood. We then experimentally analyzed the effect of standing (SW) and moving water (MW) on seed buoyancy of different plant communities. We recorded seeds of 27 taxa distributed in 12 families. Taxa richness ranged from 17 in LD to 25 in MC, and included seeds of terrestrial, palustrine and aquatic plants. River discharge did not affect seed richness and density, which was probably associated with a homogenization process caused by the flood. Seed buoyancy significantly differed between water movement treatments independently of the source community, lasting longer in SW than in MW. Our results suggest that drifting macrophytes contribute to seed dispersal of several communities in the Middle Paraná River, and probably over long distances. Furthermore, seed buoyancy might be more important for surficial dispersal in low-energy systems, where subaqueous dispersal may be difficult due to the lack of current.

Keywords: dispersal, drifting macrophytes, hydrochory, Middle Paraná River, propagules, river discharge, water movement

Introduction

Dispersal is regarded as one of the key processes affecting the richness and composition of natural communities (Levine & Murrell 2003). Hydrochory, i.e. seed dispersal by water, is important for the transportation and deposit of freshly produced seeds (Boedeltje *et al.* 2003; Levine & Murrell 2003; Sarneel 2013), structuring wetland plant communities (Nilsson *et al.* 1991; Andersson *et al.* 2000; Groves *et al.* 2009) and maintaining high landscape diversity (Junk *et al.* 1989; Thomaz *et al.* 2007). By dispersing seeds at some distance from their source community, hydrochory may extend the species dispersal period into seasons different from the vegetative ones (Boedeltje *et al.* 2004) and may be important for ecological and

genetic continuity among disjunct populations (Andersson *et al.* 2000). This may be particularly important in floodplain systems, where aquatic habitats can remain isolated during long drought periods, and where the dependence on seed banks for recolonization and plant communities structuring may be high (Junk *et al.* 1989; Neiff 1990).

Seed buoyancy may be influenced by the hydrological features of the habitats where they are released (Hyslop & Trowsdale 2012). For instance, some seeds that are able to float for long periods in standing water may be drowned by waves in a fast-flowing river and sunk immediately (Sculthorpe 1967). Nevertheless, most studies addressing seed buoyancy, evaluated this response variable only under standing water (Coops & Velde 1995; Danvind & Nilsson 1997), which may be not representative of what may happen

¹ Facultad de Humanidades y Ciencias, Universidad Nacional del Litoral, 3000, Santa Fe, Argentina

² Instituto Nacional de Limnología, Universidad Nacional del Litoral, 3000, Santa Fe, Argentina

* Corresponding author: bereschneider@gmail.com



in nature, where climatic, morphologic and hydrographic conditions make the hydrology of each waterbody unique (Lampert & Sommer 1997).

Several studies have looked at the effects of seed buoyancy on species distribution, with varying results (Hyslop & Trowsdale 2012). Studies in temperate regions found a relation between the seeds floating ability and the position of the parental plants communities (hereafter *source community*) along the hydrological gradient, suggesting that seed buoyancy probably plays a role in directing seeds towards suitable sites for germination and establishment (Coops & Velde 1995; Ozinga *et al.* 2004; Broek *et al.* 2005). Nevertheless, other studies have suggested that seed floating ability is not related to source community and, therefore, it is not important for plant distribution patterns (Danvind & Nilsson 1997).

In river-floodplains, drifting macrophytes may represent an alternative means of transport for seed dispersal (Tur 1972; Lallana 1990). This special form of hydrochory (hereafter *phytohydrochory*, *sensu* Lallana 1990), where drifting plants disperse seeds, may be particularly important in river-floodplain systems (Lallana 1990) where floods commonly produce the detachment and displacements of macrophyte stands that drift from the floodplain towards the main channel (Tur 1972; Neiff 1990; Junk & Piedade 1997; Sabattini & Lallana 2007).

Seed dispersal by drifting macrophytes is likely to be related to channel discharge. At low discharge, when velocity and turbulence is lower, roughness factors such as drifting vegetation, are likely to be very important in trapping seeds. Nevertheless, at higher discharge levels, it is more likely that turbulence and waves prevent seeds adherence to vegetation forcing them onto riverbanks (Andersson *et al.* 2000).

Dispersal by drifting plants might be important in river-floodplain systems. Although several studies have addressed phytohydrochory by animals (*e.g.*, Neiff & Zozaya 1989; Schiesari *et al.* 2003; Bulla *et al.* 2011), the role macrophytes play as seed dispersers in a Neotropical river-floodplain has received little attention (Lallana 1990).

Aquatic macrophytes play important roles in floodplain ecosystems in terms of biomass production, habitat structuring and provision of habitat, refuge, and food for other organisms (Jeppesen *et al.* 1998; Chambers *et al.* 2008; Wood *et al.* 2017). Regardless of their value, freshwater macrophytes are globally threatened, what represents a risk to the conservation of both aquatic plants and the ecosystems where they are found (Chambers *et al.* 2008; O'Hare *et al.* 2017; Zhang *et al.* 2017). Increasing knowledge about the patterns of seed dispersal by drifting macrophytes in river-floodplain systems can improve the understanding on how these landscapes are colonized by plants and how plant communities are organized (Nilsson *et al.* 2010).

We aimed to understand the potential role of drifting macrophytes as dispersal agents of plant seeds along rivers with different discharge in the Middle Paraná River

floodplain and to experimentally examine seed buoyancy from plants of different communities under different water movement conditions. We predicted that (1) the richness and density of seeds dispersed by drifting macrophytes is negatively related to river order, and that, (2) seed buoyancy of plants of different source communities differs among water movement conditions.

Materials and methods

To achieve the first objective (evaluate the phytohydrochory along rivers with different discharge in the Middle Paraná River floodplain) we performed a field study, and to achieve the second objective (analyze seed buoyancy from different source communities in different water movement conditions) we performed a microcosm experiment.

Field sampling and seed processing

Phytohydrochory

To evaluate the dispersal of seeds by phytohydrochory in channels with different flow conditions, samples of drifting stands of macrophytes were manually collected in rivers with three different discharge levels: in the main channel of the Paraná River (MC, *n* = five), in a high discharge secondary channel named Colastiné River (HD, *n* = six) and in two low discharge channels named Tiradero and Miní rivers (LD, *n* = 3, including both rivers) (31°41'48.45"S 60°37'37.79"W and 31°38'20.14"S 60°30'12.63"W). Mean annual discharges were 17.000 m³ s⁻¹ in MC, 2.200 m³ s⁻¹ in HD and 500 m³ s⁻¹ in LD (Paira & Drago 2007). During the sampling period, the hydrometric level of the Paraná River reached 14.20 m a.s.l. (Paraná Harbor staff gauge, August 2014), corresponding to an extraordinary flooding level. Field samples of macrophytes were randomly collected from a boat with nets of 0.07 m² area and 200 µm mesh size. Due to differences in plant size and stand composition, some samples consisted in a group of plants (*e.g.*, several individuals of *Salvinia* spp, and *Pistia stratiotes* L.), and other samples were composed by only one plant [*e.g.*, adult individual of *Eichhornia crassipes* (Mart.) Solms]. Nevertheless, all samples covered the same surface area (~ 0.07 m²).

In the laboratory, each sample was washed with tap water to detach all the seeds and detritus. Plant biomass was oven dried at 60 °C up to constant weight for 72 h and weighed. Seeds were separated and counted under stereoscopic microscope (C-W 10X A/22, Nikon), and identified to the lowest taxonomic level possible following Lima *et al.* (2018) and others (List S1 in supplementary material) and the collection of seeds available at the Instituto Nacional de Limnología (INALI-CONICET-UNL). The species nomenclature followed the standards of The International Plant Names Index (www.ipni.org).

Although the dispersal unit of several plants is a seed covered by adhering fruit structures (*e.g.*, Polygonaceae,



Cyperaceae, Poaceae), for the sake of simplicity, whenever we use the term *seed* is to represent all reproductive dispersal units.

Experimental design

Seed buoyancy

Seeds of 19 taxa were randomly collected from macrophyte stands before natural dispersal occurred (Tab. 1). The collection was conducted during March and April 2015 in wild populations of the Middle Paraná River floodplain.

The experiment was carried out in plastic cubic containers with sides of 15.5 cm and 9 cm in height. Each container was filled with 1.5 L of dechlorinated tap water. The experimental design consisted of two treatments: i) *moving water* (MW), containers with an aerator placed on a corner (Coops & Velde 1995) to generate water movement and simulate lotic environment with high discharge conditions; and ii) *standing water* (SW), containers with quiet water all along the experiment, except when water was carefully added to keep the level constant (see below) simulating water movement of lentic environments. All along the experiment, dechlorinated tap water was regularly added to containers to maintain water quality and to keep the water level constant at 10 cm above the bottom.

Prior to the experiment, empty or damaged seeds were removed, and uniform seeds of each taxon were selected. Seeds of each taxon were randomly assigned to the treatments (MW or SW), each with 30 seeds. For *Polygonum punctatum* (Elliott) Small, only 28 seeds were used, due to its availability in the field. Each seed group was simultaneously released into the water within the containers of both treatments resulting in a total of 38 containers [19 of each treatment, each container containing 30 (28 for *P. punctatum*) seeds of only one taxon].

The number of sunken seeds was counted 1 h and 7 h after starting the experience; at the 24th h from days two to four, every 48 h for the following four weeks and finally, weekly until the end of the experience. With this experimental setup, the floating behaviour of each individual seed could be tracked. The whole experiment lasted for 90 days and was performed indoor, under natural photoperiod conditions (allowed by the presence of transparent surfaces connected with the external environment) and at constant environmental temperature of ~ 25 °C.

Data analyses

All the seeds used (in the field study and in the microcosm experiment) were classified according to their source community into terrestrial, palustrine and aquatic (Tab. 1). Additionally, they were classified as fruits or seeds and when possible, according to their main dispersal mechanism. For this purpose, we conducted a broad bibliographic revision (List S1 in supplementary material).

To compare richness and density of seeds dispersed by drifting macrophytes among rivers we used a one-way analysis of variance (global Kruskal-Wallis tests and Post-hoc pairwise Mann-Whitney's tests, $p \leq 0.05$). Samples were tested for significant linear correlations between seed density and richness; and between seed richness and density with river order (Pearson linear correlations, $p \leq 0.05$). Data were log₁₀ transformed.

To evaluate differences among seed buoyancy between treatments (MW and SW), the number of sunken seeds was compared for each taxon after the whole experiment was completed with a Friedman test ($p < 0.01$). Additionally, the relation between seed buoyancy, source community, and water movement condition was explored by a two factor ANOVA ($p < 0.05$). All the statistical analyses were run in Past Version 2.17c (Hammer *et al.* 2001).

Results

Phytohydrochory

Although extraordinary flooding occurred, no large macrophyte stands were recorded in our study (~ 0.07 m²). The drifting macrophyte stands had different species composition but were mainly constituted by *Eichhornia azurea* and *E. crassipes* (Fig. 1). The total biomass of the sampled macrophytes was 394 g (dry weight). In terms of biomass, *E. azurea* was dominant in the MC, whereas *E. crassipes* was dominant in both types of secondary channels (HD and LD). Other species such as *Salvinia biloba*, *Limnobium laevigatum*, *Ludwigia* sp. and Poaceae were recorded in lower proportions.

The mean density of the seeds found in the drifting macrophyte stands was 168 ± 566 seeds/g (seeds per gram of plant biomass), and ranged from 5.7 ± 4.4 seeds/g in the MC and 11.7 ± 12.9 seeds/g in HD to 749.6 ± 1199.5 seeds/g in LD. We recorded a total of 27 taxa of seeds distributed in 12 botanical families (Tab. 1). Taxa richness ranged from 25 in MC and 22 in HD, to 17 in LD. The most abundant families were Poaceae and Cyperaceae (i.e. *Cyperus* spp.) which accounted for more than 50% of the seed abundance (Fig. 2). Seeds of *Ludwigia leptocarpa* and *Eclipta prostrata* were also common in all the drifting stands. According to the source community, the high proportion of seeds corresponded to terrestrial plants (78%) followed in decreasing order by palustrine (15%) and aquatic plants (7%). These taxa are also dispersed by other mechanisms such as hydrochory, anemochory and zoochory (Tab. 1).

Neither the density nor the richness of plant seeds had significant differences among rivers (global Kruskal-Wallis and partial Post-hoc pairwise comparisons Mann-Whitney tests, mostly > 0.01), and no significant correlations were found between these variables and with the river order (Pearson correlation, $p > 0.05$).



Table 1. List of the seed taxa registered in the drifting macrophytes and used in the buoyancy experience. Source community, propagule type and main dispersal mechanisms are indicated. Abbreviations refer to phytohydrochory (P), buoyancy experience (B), anemochory (A), hydrochory (H), endozoochory (EN), epizoochory (EP) and vegetative propagation (V).

Family	Taxa	Source community	Propagule type	Main dispersal mechanism	This study		Bibliography used to assign the main dispersal mechanism
					P	B	
Araceae	<i>Pistia stratiotes</i> L.	Aquatic	Seed	V/H	X		Pijl 1982; Neuenschwander <i>et al.</i> 2009
Asteraceae	<i>Chromolaena squarrosoramosa</i> (Hieron.) R.M.King & H. Rob	Terrestrial	Seed	A		X	Muniappan <i>et al.</i> 2005
	Asteraceae sp.		Seed	A/EN/EP	X		Pijl 1982; Arbo <i>et al.</i> 2001
	<i>Bidens subalternans</i> DC.	Terrestrial	Seed	H/EP		X	Pijl 1982; Calderón <i>et al.</i> 2000
	<i>Bidens laevis</i> (L.) Britton, Stern and Poggenb.	Terrestrial	Seed	H/EP	X	X	Pijl 1982; Calderón <i>et al.</i> 2000
	<i>Soliva anthemifolia</i> (Juss.) Sweet	Terrestrial	Fruit			X	
	<i>Eclipta prostrata</i> (L.) L	Terrestrial	Fruit			X	
	<i>Gymnocoronis spilanthoides</i> (D. Don en Hook. Y Arn.)	Terrestrial	Fruit			X	
	<i>Enydra anagallis</i> Gardner	Palustrine	Fruit			X	
	<i>Melanthera latifolia</i> (Gardner) Cabrera	Terrestrial	Fruit			X	
	<i>Aspilia silphioides</i> (Hook. & Arn.) Benth. ex Beker	Terrestrial	Fruit			X	
Cyperaceae	<i>Ambrosia elatior</i> L.	Terrestrial	Fruit			X	
	Cyperaceae 1		Fruit			X	
	<i>Cyperus</i> sp.	Terrestrial	Fruit	H/A	X		Arbo <i>et al.</i> 2001
	<i>Schoenoplectus californicus</i> (C.A.Mey.) Soják.	Palustrine	Fruit	H/A/EP		X	Macía & Balslev 2000
Fabaceae	<i>Cyperus virens</i> Michx. <i>virens</i>	Palustrine	Fruit	H		X	Arbo <i>et al.</i> 2001
	<i>Mimosa pigra</i> L. <i>pigra</i>	Terrestrial	Seed	H		X	Hurrell 2002
Iridaceae	<i>Sesbania virgata</i> (Cav.) Pers.	Terrestrial	Seed	H	X	X	Hurrell 2002
	<i>Sisyrinchium</i> sp.	Terrestrial	Seed			X	
Lentibulariaceae	<i>Utricularia foliosa</i> L.	Aquatic	Fruit	V		X	Pijl 1982
Onagraceae	<i>Ludwigia leptocarpa</i> (Nutt.) H. Hara	Palustrine	Seed	H/A	X	X	Calderón <i>et al.</i> 2000
Poaceae	Poaceae sp.		Fruit			X	
	<i>Setaria parviflora</i> (Poir.) Kerguélen	Terrestrial	Fruit		X	X	
	<i>Eriochloa punctata</i> (L.) Desv. ex Ham.	Terrestrial	Fruit			X	
Polygonaceae	<i>Polygonum acuminatum</i> Kunth	Palustrine	Fruit	H			Pijl 1982
	<i>Polygonum punctatum</i> Elliott	Palustrine	Fruit	H	X	X	Pijl 1982
	<i>Polygonum</i> sp.	Palustrine	Fruit	H	X		Pijl 1982
	<i>Polygonum hydropiperoides</i> Michx.	Palustrine	Fruit	H	X	X	Pijl 1982
Pontederiaceae	<i>Rumex</i> sp.	Terrestrial	Fruit	H	X		Pijl 1982; Arbo <i>et al.</i> 2001
	<i>Eichhornia azurea</i> (Sw.) Kunth	Aquatic	Seed	H/V		X	Sculthorpe 1967; Cronk & Fennessy 2001
Salicaceae	<i>Eichhornia crassipes</i> (Mart.) Solms	Aquatic	Seed	H/V		X	Sculthorpe 1967; Pijl 1982; Cronk & Fennessy 2001
	<i>Salix humboldtiana</i> Willd.	Terrestrial	Fruit	H/A	X		Neiff <i>et al.</i> 1985; Niiyama 1990; Budke <i>et al.</i> 2005
Smilacaceae	<i>Smilax campestris</i> Griseb.	Terrestrial	Seed	EN		X	Hurrell 2000
Solanaceae	<i>Solanum glaucophyllum</i> Desf.	Terrestrial	Seed			X	
Malvaceae	<i>Sida</i> sp.	Terrestrial	Seed	EP	X		Calderón <i>et al.</i> 2000
	<i>Sida rhombifolia</i> L.	Terrestrial	Seed	EP	X		Calderón <i>et al.</i> 2000
Menyanthaceae	<i>Nymphoides indica</i> (L.) Kuntze	Aquatic	Seed			X	
Verbenaceae	<i>Lippia alba</i> (Mill.) N.E. Br. ex Britton & P. Wilson	Terrestrial	Seed		X	X	
Undetermined	Morphospecie 1		Seed			X	
	Morphospecie 2		Seed			X	



Seed buoyancy

Most taxa showed significant differences in seed buoyancy between SW and MW treatments (Friedman’s test, $p < 0.01$, Tab. 2, Fig. S1 in supplementary material).

The number of total sunken seeds at the end of the experiment was 443 (78 % of the initial amount of seeds) in MW and 213 (37.5 %) in SW. Seeds sank faster in the MW treatment than in the SW one (Fig. 3). In MW, 50 % of seeds sank during the first week of the experience, while in SW the 50 % of seeds sank along the first month of the experience.

The interaction between source community (terrestrial, palustrine and aquatic) and water movement condition (SW and MW) had no significant effect on buoyancy (two ways ANOVA, $F = 0.32$; $p = 0.73$). Partial factor analysis resulted significant for water movement ($F = 8.1$; $p = 0.01$) but not for source community ($F = 2.5$; $p = 0.10$).

Discussion

Data from our field study indicated that, contrary to our expectation, richness and density of seeds dispersed by phytohydrochory were not related to river order and thus, we could not accept our first prediction. From our experimental study, seed buoyancy was significantly related to water movement condition. Therefore, our second prediction was validated.

Phytohydrochory

Rivers could act as dispersal agents transferring organisms among waterbodies and potentially across long distances (Lallana 1990; Nilsson *et al.* 1991; Moggridge *et al.* 2009; Nilsson *et al.* 2010; Sarneel 2013). In our study, we found that relatively small macrophyte stands (~ 0.07 m²) transported a large amount and diversity of seeds. Most of the dominant drifting plants collected in our study were perennials, and this could favour dispersal at long distances. Indeed, the average current velocities in the Middle Paraná River, range from 0.7 to 1.6 m s⁻¹ (Orfeo & Stevaux 2002), and under such conditions a drifting macrophyte stand could travel 60.5 – 138.25 km per day, or in other words, could cover the entire length of the Paraná River (2570 km) in 18.6 days.

Seed dispersal by water is well recognized for plants from different ecosystems (Boedeltje *et al.* 2003; Kaproth & McGraw 2008; Kowarik & Säumel 2008; Sarneel 2010). Our findings broaden the knowledge regarding seed dispersal by waterpaths, demonstrating that the dispersal involving drifting plants (or by phytohydrochory), is also effective for a great diversity of seeds and from different plant communities, such as aquatic, riparian and terrestrial. Furthermore, many of the seeds we found in the drifting macrophytes are commonly dispersed by other mechanisms

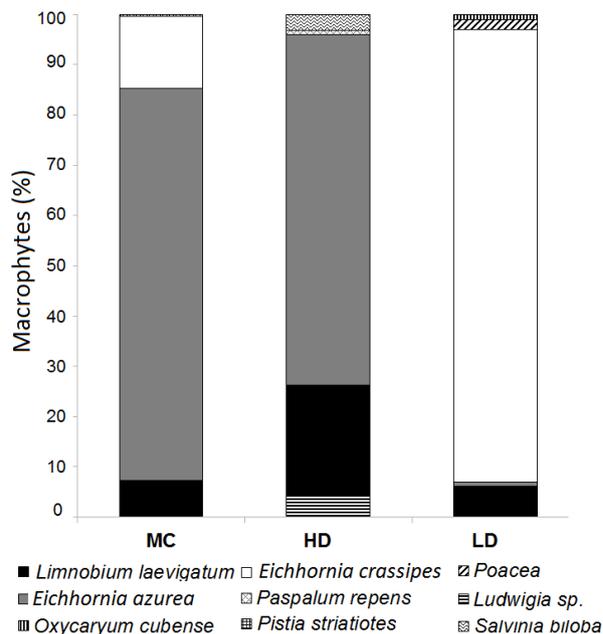


Figure 1. Composition of the total number of drifting macrophyte stands sampled at the main channel, high discharge and low discharge secondary channels (MC, HD and LD respectively) collected in the Paraná River floodplain during an extraordinary flooding (year 2014).

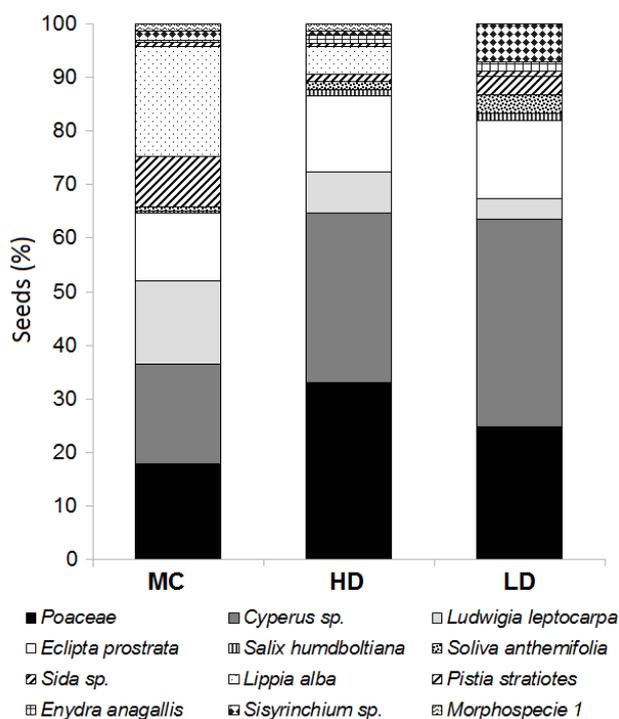


Figure 2. Taxonomic composition of drifting seeds at the main channel, high and low discharge secondary channels (MC, HD and LD respectively) collected in the Paraná River during an extraordinary flooding (year 2014).



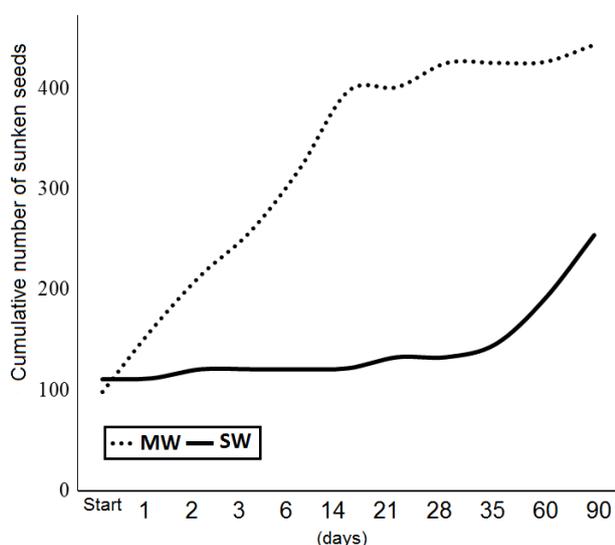


Figure 3. Cumulative number of sunken seeds along the buoyancy experience in the moving water (MW) standing water (SW) treatments.

Table 2. Results of Friedman’s comparisons performed to assess significant differences of seed buoyancy between moving water (MW) and standing water (ST) treatments. The Friedman test was performed whenever differences between tests could be explored.

Source community	Taxa	p-values
aquatic	<i>Eichhornia azurea</i>	0.001
aquatic	<i>Utricularia foliosa</i>	0.002
aquatic	<i>Eichhornia crassipes</i>	0.007
palustrine	<i>Cyperus virens</i>	0.060
palustrine	<i>Ludwigia leptocarpa</i>	0.003
palustrine	<i>Polygonum acuminatum</i>	0.001
palustrine	<i>Polygonum punctatum</i>	0.001
palustrine	<i>Schoenoplectus californicus</i>	0.001
terrestrial	<i>Bidens laevis</i>	All propagules floated along the whole experiment in SW and MW
terrestrial	<i>Lippia alba</i>	
terrestrial	<i>Mimosa pigra</i>	All propagules sank at the 1 h of the experiment in ST and MW
terrestrial	<i>Smilax campestris</i>	
terrestrial	<i>Sesbania virgata</i>	0.001
terrestrial	<i>Bidens subalternans</i>	
terrestrial	Cyperaceae sp.	0.002
terrestrial	<i>Echinochloa punctata</i>	0.002
terrestrial	<i>Chromolaena squarrosoramosa</i>	0.002
terrestrial	<i>Solanum glaucophyllum</i>	0.003
terrestrial	<i>Setaria parviflora</i>	0.011

different from phytohydrochory. For instance, several Asteraceae seeds found are typically anemochorous and *Sida rhombifolia* seeds are mainly zoochorous. This large number of potential dispersal vectors does not necessarily mean that dispersal is more effective; but it does, at least, indicate that on average these species have more opportunities for long-distance dispersal and are thus less dependent on the availability of a single dispersal vector (Ozinga *et al.* 2004).

This may represent a selective advantage for those species that succeed in spreading their propagules across large parts of the landscape (Levin *et al.* 1984), especially in ecosystems with frequent disturbances such as river-floodplains (Junk *et al.* 1989; Neiff 1990).

A significant correlation between seed richness and density was not found. This could be related to the distinct strategies of species to produce offspring. While some species invest in quality and produce seeds that can persist in the soil for long periods, other species invest in quantity and produce large numbers of seeds to increase dispersal probability (Grime 1977). In our study the higher densities of seeds corresponded only to two taxa (Poaceae and Cyperaceae), while the seeds of the remaining taxa showed much lower densities (e.g. *P. stratiotes*, *Enydra anagallis* Gardner, *Soliva anthemifolia*). This could explain the lack of correlation between seed richness and density.

In contrast to results found in other wetlands where the number of seed species was affected by river order and discharge (Nilsson *et al.* 1994; Boedeltje *et al.* 2004), our findings indicated that there was no difference in the richness nor in the density of seeds dispersed by phytohydrochory with respect to the river order. Therefore our results do not support our first prediction (seed richness and density are negatively related to river order). Our study was conducted during an extraordinary flooding, and this could have generated a homogenization of the seeds attached to plants in the different rivers, regardless of their discharge. Indeed, floods tend to connect water bodies with distinct hydrological characteristics and, as a result, biological communities tend to be more similar among the distinct habitats within a floodplain. This is in agreement with the generalized hypothesis that floods increase similarity among habitats in river-floodplain systems (Thomaz *et al.* 2007).

Seed buoyancy

Knowledge about seed buoyancy ability is critical for a better understanding of dispersal patterns and species distribution in river-floodplain systems (Kubitzki & Ziburski 1994; Coops & Velde 1995). In our study, seed buoyancy of most taxa significantly differed between SW and MW conditions. Indeed, the movement of water was a strong factor in determining seed buoyancy independently of their source community.

The fast sink of *E. crassipes*, *E. azurea* and *Utricularia foliosa* seeds in MW conditions, could be related to the fact that the survival of aquatic plant seedlings would be successful only if germination occurs in a flooded site. Thus, many aquatic species produce seeds that sink and are transported by water as bed load towards inundated sites (Soons *et al.* 2017). Furthermore, in many aquatic and several palustrine plant species, vegetative regeneration and dispersal dominate over generative regeneration and

dispersal (e.g., Sculthorpe 1967; Barrat-Segretain 1996). Therefore, considering the great buoyancy ability of vegetative propagules, their flotation time might be more critical than seed buoyancy for dispersal.

Seeds of terrestrial species varied in relation to buoyancy time. Indeed, several palustrine and terrestrial species subjected to frequent floods, produce seeds that float for long time (like *Cyperus virens* and *Lippia alba* in our study), so that many will have been stranded in favorable marginal or higher sites (Sculthorpe 1967; Soons *et al.* 2017). For instance, seeds of *Bidens laevis* and *L. alba* remained floating along the whole experiment in both treatments, whereas seeds of *Smilax campestris*, *Mimosa pigra* and *Sesbania virgata* sank at the first hour of the experiment in both treatments. The sudden sinking of *S. campestris*, *M. pigra* and *S. virgata* seeds may have been due to the fact that *S. campestris* is a climbing plant common in riverbank forests, but its fleshy fruits are dispersed by animals. *M. pigra* and *S. virgata* fruits are buoyant and indehiscent, and therefore the fruit is responsible for seed dispersal to suitable sites. Seeds of other terrestrial taxa presented intermediate buoyancy duration. These different species abilities to float on the water surface suggest that hydrochory might be an important process underlying patterns of aquatic and riparian plant zonation (Poiani & Johnson 1989; Grelsson & Nilsson 1991).

Seeds used in this study had different forms, sizes and possibly weights, all metrics that can affect buoyancy ability (Sculthorpe 1967). For instance, seed form varied from oblong (e.g. *E. crassipes*), to flattened (e.g. *B. laevis*) and to circular (e.g. *U. foliosa*) among many others. Although we did not measure seed form and weight, one might expect these characteristics to be related to the different buoyancy abilities found among taxa.

Source community had no significant effect on seed buoyancy. The reason for this may be that most wetland plants have other means of dispersal (Sculthorpe 1967; Danvind & Nilsson 1997). Multiple means of dispersal will certainly complicate the interpretation of patterns resulting from dispersal by water. For instance, anemochores seeds like those of *Schoenoplectus californicus* (or *Chromolaena squarrosoramosa*) are also able to float well. Conversely, water movement was a significant factor in determining seed buoyancy and seeds of most species floated more time in standing than in moving water. These results suggest that, in the floodplain studied, seed buoyancy may be more important for surficial seed dispersal in low-energy systems, such as lakes or slow-flowing streams, where sub-aqueous dispersal is difficult due to lack of current (Soons *et al.* 2017). In such waterbodies, the period of buoyancy, from a few hours to a day or more, may be enough to allow the propagules to be carried well away from the competitive source community (Sculthorpe 1967). In rivers, where flow speed and turbulence are higher, non-buoyant or sunken seeds may be transported in suspension by water flow, or

be re-suspended during floods, and deposited onto more suitable areas providing an opportunity to germinate and establish (Markwith & Leight 2008; Hyslop & Trowsdale 2012). Indeed, non-buoyant seeds can also be transported by drifting macrophytes as we demonstrate.

Despite some limitations in the extrapolation for our experimental results to natural conditions, our experimental study highlights the importance of using different water movement conditions to evaluate time of seed buoyancy, since in field the hydrologic features of waterbodies vary from standing waters in disconnected lakes, to flowing waters with different speed in channels.

In conclusion, in the Middle Paraná floodplain, drifting macrophytes contribute to seed dispersal of aquatic, palustrine and several terrestrial plants, and probably within large distances. Seed richness and density were not affected by river order, probably related to a homogenization of communities caused by the occurrence of an extraordinary flooding event. We evaluated seed buoyancy simulating the natural water movement conditions of lakes and rivers. However, in natural systems water movement is more complex and may vary spatially and temporally and it is probable that a different situation from the one discussed in this study may arise. Nevertheless, from our experimental study, we can state that the seed buoyancy of wetland plants can differ between habitats with different lotic and lentic conditions. This suggests that seed buoyancy may be more important for seed surficial dispersal in low-energy systems, where subaqueous dispersal may be difficult due to the lack of current.

Acknowledgements

We thank the Associate Editor and two anonymous reviewers whose constructive comments greatly improved the manuscript. This research was financially supported by Prest. BID PICT 2012 N° 2791, FONCyT, ANPCyT and PIP 318-CONICET, MinCyT, Argentina.

References

- Andersson E, Nilsson C, Johansson M. 2000. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. *Journal of Biogeography* 27: 1095-1106.
- Arbo MM, López MG, Schinini A, Pieszko G. 2001. Las plantas hidrófilas. In: Arbo MM, Tressens SG. (eds.) *Flora del Iberá*. Eudene, Corrientes. p. 9-110.
- Barrat-Segretain MH. 1996. Strategies of reproduction, dispersion, and competition in river plants: A review. *Vegetatio* 123: 13-37.
- Boedeltje G, Bakker JP, Heerdt GNJ. 2003. Potential role of propagule banks in the development of aquatic vegetation in backwaters along navigation canals. *Aquatic Botany* 77: 53-69.
- Boedeltje GER, Bakker JP, Brinke A, Groenendaal JM, Soesbergen M. 2004. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. *Journal of Ecology* 92: 786-796.
- Broek T, Diggelen R, Bobbink R. 2005. Variation in seed buoyancy of species in wetland ecosystems with different flooding dynamics. *Journal of Vegetation Science* 16: 579-586.



- Budke JC, Athayde EA, Giehl ELH, Záchia RA, Eisinger SM. 2005. Composição florística e estratégias de dispersão de espécies lenhosas em uma floresta ribeirinha, arroio Passo das Tropas, Santa Maria, RS, Brasil. *Iheringia, Série Botânica* 60: 17-24.
- Bulla CK, Gomes LC, Miranda LE, Agostinho AA. 2011. The ichthyofauna of drifting macrophyte mats in the Ivinhema River, upper Paraná River basin, Brazil. *Neotropical Ichthyology* 9: 403-409.
- Calderón J, Alán E, Barrantes U. 2000. Estructura, dimensiones y producción de semillas de malezas del trópico húmedo. *Agronomía Mesoamericana* 11: 31-30.
- Chambers PA, Lacoul P, Murphy KJ, Thomaz SM. 2008. Global diversity of aquatic macrophytes in freshwater. *Hydrobiologia* 595: 9-26.
- Coops H, Velde G. 1995. Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. *Freshwater Biology* 34: 13-20.
- Cronk JK, Fennessy SM. 2001. *Wetland plants: biology and ecology*. New York, Lewis.
- Danvind M, Nilsson C. 1997. Seed floating ability and distribution of alpine plants along a northern Swedish river. *Journal of Vegetation Science* 8: 271-276.
- Grelsson G, Nilsson C. 1991. Vegetation and seed-bank relationships on a lakeshore. *Freshwater Biology* 26: 199-207.
- Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169-1194.
- Groves JH, Williams DG, Caley P, Norris RH, Caitcheon G. 2009. Modelling of floating seed dispersal in a fluvial environment. *River Research and Applications* 25: 582-592.
- Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 1-9.
- Hurrell JA. 2000. Biota Rioplatense V. Plantas trepadoras, nativas y exóticas. Buenos Aires, LOLA.
- Hurrell JA. 2002. Biota Rioplatense VII. Leguminosas nativas y exóticas. Buenos Aires, LOLA.
- Hyslop J, Trowsdale S. 2012. A review of hydrochory (seed dispersal by water) with implications for riparian rehabilitation. *Journal of Hydrology* 51: 137-152.
- Jeppesen E, Søndergaard M, Christoffersen K. 1998. The structuring role of submerged macrophytes in lakes. *Ecological Studies* 131: 1-423.
- Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* 106: 110-127.
- Junk WJ, Piedade MTF. 1997. Plant life in the floodplain with special reference to herbaceous plants. In: Junk WJ. (ed.) *The Central Amazon floodplain: ecological studies*. Berlin, Springer. p. 147-185.
- Kaproth MA, McGraw JB. 2008. Seed viability and dispersal of the wind-dispersed invasive *Ailanthus altissima* in aqueous environments. *Forest Science* 54: 490-496.
- Kowarik I, Säumel I. 2008. Water dispersal as an additional pathway to invasions by the primarily wind-dispersed tree *Ailanthus altissima*. *Plant Ecology* 198: 241-252.
- Kubitzki K, Ziburski A. 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica* 26: 30-43.
- Lallana VH. 1990. Dispersal units in aquatic environments of the middle Parana River and its tributary, the Saladillo River. In: *Proceedings of the 8th International Symposium on Aquatic Weeds*. Uppsala, European Weed Research Society. p. 151-159.
- Lampert W, Somner U. 1997. *Limnoecology: the ecology of lakes and streams*. New York, Oxford University Press.
- Levin SA, Cohen D, Hastings A. 1984. Dispersal strategies in patchy environments. *Theoretical Population Biology* 26: 165-191.
- Levine JM, Murrell DJ. 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution and Systematics* 34: 549-574.
- Lima GT, Catian G, Luz GP, Gonçalves VM, Scremin-Dias E. 2018. Plântulas e sementes de macrófitas aquáticas de lagoas do Pantanal Sul-Mato-Grossense. *Iheringia, Série Botânica* 73: 1-87.
- Macía MJ, Balslev H. 2000. Use and management of totora (*Schoenoplectus californicus*, Cyperaceae) in Ecuador. *Economic Botany* 54: 82-89.
- Markwith SH, Leigh DS. 2008. Subaqueous hydrochory: open-channel hydraulic modelling of non-buoyant seed movement. *Freshwater Biology* 53: 2274-2286.
- Moggridge HL, Gurnell AM, Mountford JO. 2009. Propagule input, transport and deposition in riparian environments: The importance of connectivity for diversity. *Journal of Vegetation Science* 20: 465-474.
- Muniappan R, Reddy GVP, Po-Yung L. 2005. Distribution and biological control of *Chromolaena odorata*. In: Inderjit S. (ed.) *Invasive plants: ecological and agricultural aspects*. Berlin, Birkhauser Verlag. p. 223-234.
- Neiff ASG, Zozaya IYB. 1989. Efectos de las crecidas sobre las poblaciones de invertebrados que habitan macrófitas emergentes en el río Paraná. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 22: 13-20.
- Neiff JJ. 1990. Ideas para la interpretación ecológica Del Paraná. *Interciencia* 15: 424-441.
- Neiff JJ, Reboratti HJ, Gorleri MC, Basualdo M. 1985. Impacto de las crecientes extraordinarias sobre los bosques fluviales del Bajo Paraguay. *Boletín de la Comisión Especial Río Bermejo. Cámara de Diputados de la Nación (Buenos Aires)* 4: 13-30.
- Neuenschwander P, Julien MH, Center TD, Hill MP. 2009. *Pistia stratiotes* L. (Araceae). In: Rangaswamy M, Gadi VR, Anantanarayanan R. (eds.) *Biological control of tropical weeds using arthropods*. New York, Cambridge University Press. p. 332-352.
- Niiyama K. 1990. The role of seed dispersal and seedling traits in colonization and coexistence of *Salix* species in a seasonally flooded habitat. *Ecological Research* 5: 317-331.
- Nilsson C, Brown RL, Jansson R, Merritt DM. 2010. The role of hydrochory in structuring riparian and wetland vegetation. *Biological Reviews* 85: 837-858.
- Nilsson C, Ekblad A, Dynesius M, et al. 1994. A comparison of species richness and traits of riparian plants between a main river and its tributaries. *Journal of Ecology* 82: 281-295.
- Nilsson C, Gardfjell M, Grelsson G. 1991. Importance of hydrochory in structuring plant communities along rivers. *Canadian Journal of Botany* 69: 2631-2633.
- O'Hare M, Aguiar F, Asaeda T, et al. 2017. Plants in aquatic ecosystems: current trends and future directions. *Hydrobiologia* 812: 1-11.
- Orfeo O, Stevaux J. 2002. Hydraulic and morphological characteristics of middle and upper reaches of the Paraná River (Argentina and Brazil). *Geomorphology* 44: 309-322.
- Ozinga WA, Bekker RM, Schaminee JH, Groenendaal JM. 2004. Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* 92: 767-777.
- Paira AR, Drago EC. 2007. Origin, evolution, and types of floodplain water bodies. In: Iriondo MH, Paggi JC, Parma MJ. (eds.) *The middle Paraná river: Limnology of a subtropical wetland*. Berlin, Springer. p. 53-81.
- Pijl L. 1982. *Principles of dispersal in higher plants*. 3rd. edn. Berlin, Springer-Verlag.
- Poiani KA, Johnson WC. 1989. Effect of hydroperiod on seed bank composition in semipermanent prairie wetlands. *Canadian Journal of Botany* 67: 856-864.
- Sabattini RA, Lallana VH. 2007. Aquatic macrophytes. In: Iriondo MH, Paggi JC, Parma MJ. (eds.) *The middle Paraná river: Limnology of a subtropical wetland*. Berlin, Springer. p. 205-226.
- Sarneel JM. 2010. Colonisation processes in riparian fen vegetation. MSc Thesis, Utrecht University, Utrecht.
- Sarneel JM. 2013. The dispersal capacity of vegetative propagules of riparian fen species. *Hydrobiologia* 710: 219-225.
- Schiesari L, Zuanon J, Azevedo-Ramos C, et al. 2003. Macrophyte rafts as dispersal vectors for fishes and amphibians in the Lower Solimões River, Central Amazon. *Journal of Tropical Ecology* 19: 333-336.
- Sculthorpe CD. 1967. *The biology of aquatic vascular plants*. London, Edward Arnold.
- Soons MB, Groot AG, Ramirez MT, Fraijee RG, Verhoeven TA, Jager M. 2017. Directed dispersal by an abiotic vector: wetland plants disperse



Factors driving seed dispersal in a Neotropical river-floodplain system

- their seeds selectively to suitable sites along the hydrological gradient via water. *Functional Ecology* 31: 499-508.
- Thomaz SM, Bini LM, Bozelli RL. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579: 1-13.
- Tur NM. 1972. Embalsados y camalotales del Paraná Medio. *Darwiniana* 17: 397-407.
- Wood KA, O'Hare MT, McDonald C, Searle KR, Stillman F, Daunt RA. 2017. Herbivore regulation of plant abundance in aquatic ecosystems. *Biological Reviews* 92: 1128-1141.
- Zhang Y, Jeppesen E, Liu X, *et al.* 2017. Global loss of aquatic vegetation in lakes. *Earth- Science Reviews* 173: 259-265.

