Ann. Limnol. - Int. J. Lim. 50 (2014) 163–171

DOI: 10.1051/limn/2014009

Available online at:
www.limnology-journal.org

Morphometric and biotic variables as potential predictors of *Ludwigia sedoides* (Humb. & Bonpl.) Hara in a large Amazonian reservoir

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Received 14 September 2013; Accepted 3 March 2014

Abstract – Reservoirs cause hydrological changes (*i.e.*, water level stabilization) that favor the colonization of aquatic macrophytes. Knowing the ecological factors that determine the occurrence of these plants is critical for water management (*e.g.*, plant control) and biodiversity conservation. In this sense, the present study investigated colonization patterns of *Ludwigia sedoides* in Lajeado reservoir (Tocantins River, Amazon Basin), in order to identify variables that influence colonization at habitat scale. We investigated the relationship between colonization (coverage area and occurrence) and morphometric (fetch, slope, depth and distance from shoreline) and biotic variables (local diversity of macrophytes and co-occurrence patterns). Stepwise regression selected fetch, depth and slope as the best variables to explain the variation in *L. sedoides* coverage, which together explained 46% of data variability. Fetch and slope were negatively correlated with coverage, whereas depth showed a positive correlation. No biotic variable was included in the model ($P > 0.05$). However, the investigation of the geometric shape of bivariate correlations (null models) showed positive relationships with local species richness and richness of life forms (*i.e.*, submerged, emergent, floating and epiphytic). In addition, an analysis of species co-occurrence (*C*-score) revealed that *L. sedoides* is negatively associated with some macrophyte species. We believe, however, that these results may be associated with species preferences for particular environmental conditions. In conclusion, the present study indicated that morphometric variables are potential predictors of the colonization of *L. sedoides* in Lajeado reservoir. Sheltered sites with low slope and moderate depths represent favorable environment for colonization and growth.

Key words: co-occurrence / depth / fetch / slope / spatial distribution

Introduction

Reservoirs are constructed for different purposes, including water storage, energy production, navigation, recreation, irrigation and flood control (Tundisi and Matsumura-Tundisi, 2003). Impoundments change the natural flow regime (Poff *et al.*, 1997), which cause the reduction in water flow, the stabilization of water levels, the incorporation of terrestrial biomass and nutrients from surrounding areas and the alteration of limnological attributes (Agostinho *et al.*, 2008). As a consequence, eutrophication is common during the first years of the impoundment, with changes in organic matter production, nutrient availability and water transparency (*i.e.*, increases). These conditions, together with morphometric aspects of the reservoir (*e.g.*, low fetch, gentle slopes and shallow shores), tend to favor the occurrence of algae blooms or the proliferation of aquatic macrophytes (Straskraba and Tundisi, 1999; Tundisi and Matsumura-Tundisi, 2008).

The excessive growth of aquatic macrophytes has attracted the interest of the scientific community and society, basically because excessive cover may compromise the use of some freshwater resources (Coops *et al.*, 2002; van Nes *et al.*, 2002; Mjelde *et al.*, 2012). However, macrophytes also play important ecological functions (Madsen *et al.*, 2001; Engelhardt and Ritchie, 2002) as they provide habitat and resources for invertebrates,

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fish and other organisms (Pelicice *et al.*, 2005; Agostinho *et al.*, 2007a; Gualdoni *et al.*, 2009; Thomaz and Cunha, 2010). In addition, aquatic plants show high rates of primary production (Boyd, 1971; Nõges *et al.*, 2010) and participate in nutrient cycling (Carpenter and Lodge, 1986; Cronin *et al.*, 2006; Bini *et al.*, 2010). When reservoirs are formed, therefore, society must be prepared to deal with potential tradeoffs between control, eradication and conservation of aquatic macrophytes. In this sense, studies that investigate the distribution of macrophytes (*e.g.*, Neiff *et al.*, 2000; Murphy *et al.*, 2003; Bini and Thomaz, 2005; Pierini and Thomaz, 2009; Sousa *et al.*, 2009) are crucial to provide management programs with information about the factors affecting colonization; a first step to build predictive models.

Most of the large rivers in South America are now regulated by dams (Agostinho *et al.*, 2008), and colonization by aquatic plants is common in Brazilian reservoirs (*e.g.*, Walker *et al.*, 1999; Marcondes *et al.*, 2003; Thomaz *et al.*, 2003; Lolis and Thomaz, 2011). This is the case of *Ludwigia sedoides* (Humb. & Bonpl.) Hara (Onagraceae, Myrtales). This macrophyte is a rooted plant that develops submersed stems with circular floating leaves (rosettes with 5–20 cm diameter), able to form large mono-specific beds. According to Pott and Pott (2000), *L. sedoides* is evergreen and produces flowers over the year, naturally found in floodplains and lagoons with permanent shallow waters and silt/clay soils. In fact, field observations indicate that *L. sedoides* prefer shallow environments protected from wind exposure, where large mats are found. Although this species has a broad natural distribution (ranging from Mexico and Central America to Brazil) and is commonly found in Neotropical reservoirs, information about its ecology is scarce in the scientific literature. We found no quantitative assessment about the ecological factors that structure populations of *L. sedoides* in reservoirs, and little is known about patterns of colonization and distribution.

In this context, the present study investigated the occurrence and colonization of *L. sedoides* in Lajeado reservoir, Tocantins River (Amazon Basin). To identify the variables that influence the spatial distribution of this species, at habitat scale, we investigated the relationship between colonization (*i.e.*, coverage area and occurrence) and morphometric (*i.e.*, fetch, slope, depth and distance from shoreline) and biotic variables (*i.e.*, diversity of resident flora and co-occurrence patterns). As far as we know, our results are the first to indicate potential predictors of the coverage and distribution of *L. sedoides* in Neotropical reservoirs.

Material and methods

Study area

The Tocantins River, together with the Araguaia River, forms the Tocantins River Basin, draining approximately 760 000 km^2 of Central/North Brazil. This river extends through 2500 km, discharging in the right margin of the lower Amazon River. The present study was carried out in the Upper Tocantins River Basin, in the area under the influence of Lajeado Dam (Luis Eduardo Magalhães Hydroelectric Plant). Constructed in 2002, the dam formed a large reservoir with 630 km^2, 150 km long, 8.8 m mean depth (35 m near the dam), with a water residence time of 24 days and surface flow of 0.083 $m.s^{-1}$ (Agostinho *et al.*, 2007b).

The formation of the reservoir expanded the littoral zone, creating many islands and bays. These habitats within the reservoir favored the colonization of aquatic plants, since they are shallow, sheltered from wind action, with high water transparency and sediment rich in inorganic matter (personal observation). In fact, the littoral zone is heavily occupied by mono-specific and mixed beds of different species, particularly *Najas microcarpa*, *Salvinia auriculata*, *L. sedoides*, among others. A total of 50 species of macrophytes have been recorded in Lajeado reservoir (Lolis and Thomaz, 2011).

Data sampling

The study was carried out in the upper portion of the reservoir, in the municipality of Porto Nacional (Tocantins State, Brazil), between May and October 2011. We sampled seven sites in this area, distributed over approximately 8 km, located in both margins of the reservoir (Fig. 1). These sites were chosen to cover a range of environmental conditions (exposed/sheltered, different slopes and depths; Table 1) and different levels of *L. sedoides* abundance. In these sites, a total of 88 plots (5×5 m, independent sampling units) were set along the littoral zone. The first plot was randomly placed within each site, and the next ones were placed at 50 m intervals.

At each plot we obtained the area covered by *L. sedoides*, the composition of the local plant assemblage and some morphometric variables. The surface area covered (%) by *L. sedoides* was estimated visually by three independent observers, obtaining a single consensual value for each plot. Subsequently, a rake was used to remove and collect all plants in the plot. Macrophyte species were then identified according to Pott and Pott (2000); when necessary, plants were sent to the Laboratory of Plant Taxonomy (Neamb, UFT) to confirm identification. Species were grouped into life forms (submerged, emergent, floating and epiphytic), following Sculthorpe (1967) and Pott and Pott (2000). Species are deposited in the Herbário HTO, Neamb, Universidade Federal do Tocantins, Brazil.

Four morphometric variables were calculated for each plot: fetch, slope, mean depth and distance from shoreline. The fetch was calculated to evaluate the exposure to wind action, not corrected for wind direction. The calculation was based on Azza *et al.* (2007), but the first vertical line was defined perpendicular to the shore (90°), since the wind direction is variable in Lajeado reservoir. The slope

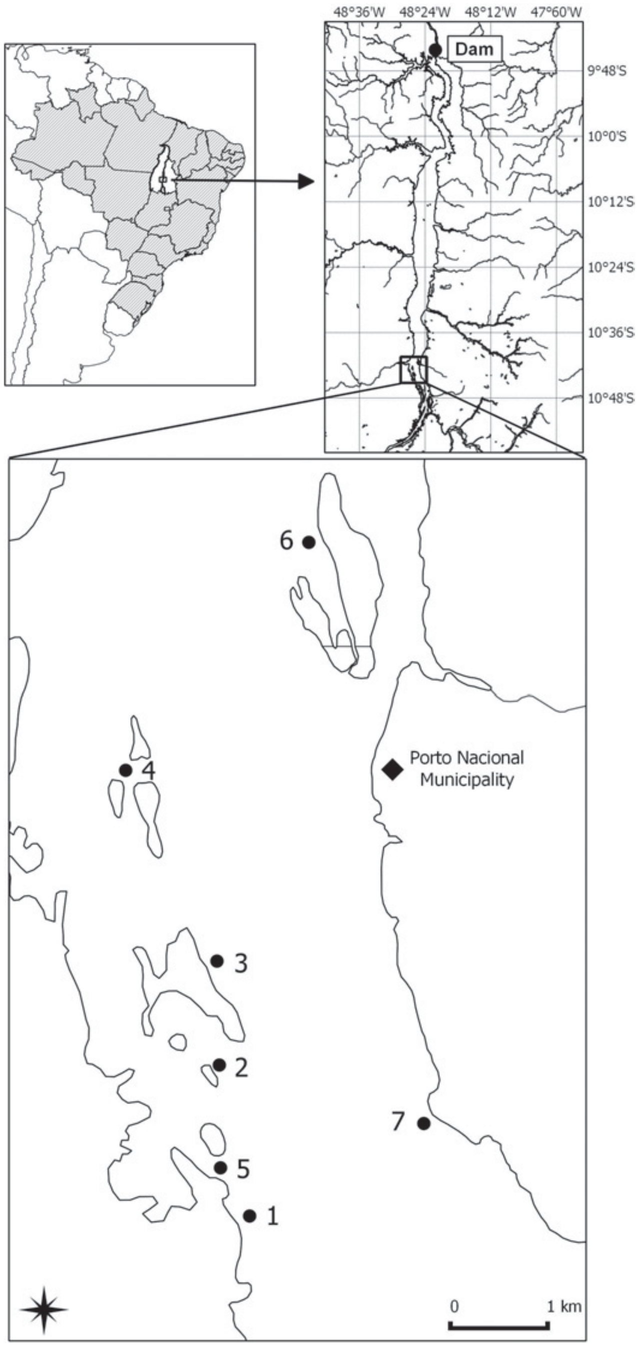

Fig. 1. Distribution of sampling sites (1–6) in the upper portion of the Lajeado reservoir, Tocantins River, Brazil.

was calculated using three equidistant (2.5 m intervals) measures of depth, taken in each side of the plot (perpendicular to the shore, 6 values in total). A ruler was used to measure each depth sample (cm). The slope of each plot (cm.m^{-1}) was then obtained through linear regression between depth (m) and distance (m), fitting a linear equation to obtain the β-coefficient (slope). We also used these six depth measures to calculate the mean depth of each plot. Finally, the distance between the plot and the nearest shoreline was estimated visually (m).

Data analysis

The relationship between the coverage of *L. sedoides* and biotic (local species richness, richness of life forms, richness of submerged and emergent species) and morphometric variables was investigated through multiple regression. To select the set of variables that best explain the coverage of *L. sedoides* in the study area, we used a stepwise regression based on the backward selection method. All of the independent variables were included in the model, and the best fit (least squares) was reached after the successive removal of variables showing a lower contribution. The importance of the predictors selected was evaluated using: (i) the semi-partial correlation coefficient (*r*, or the variance explained by the predictor, controlling for the effect of other variables) and (ii) the standardized slope (B, or the slope of the linear relationship between $x \times y$, standardized to a mean of 0 and a standard deviation of 1). All variables were $\log + 1$ transformed to meet parametric assumptions. This analysis was conducted in Statistica 7.1 (Statsoft, 2005).

Considering the non-linearity (*i.e.*, uneven variability) in the relationship between macrophyte distribution and some environmental variables (*e.g.*, Thomaz *et al.*, 2003; Bini and Thomaz, 2005; Pierini and Thomaz, 2009), we explored the geometric shape of bivariate correlations (*L. sedoides* coverage versus biotic and morphometric variables; untransformed data). Using a null model, we tested if the observed geometric shape of each relationship could be produced by chance, comparing the observed pattern with simulations generated after 1000 randomizations of the original matrix. In this case, the number of points within a specific geometric shape (left triangle, right triangle and pyramid) was compared between observed and simulated relationships, calculating the probability of finding a simulated value equal to or greater than the observed value. This analysis was conducted in the Macroecology module of the software EcoSim v. 7.0 (Gotelli and Entsminger, 2001).

Finally, the co-occurrence patterns between *L. sedoides* and other macrophyte species were investigated. The existence of segregation patterns, for example, may indicate strong biotic interactions among aquatic plants. Co-occurrence was evaluated by calculating the percentage of plots in which *L. sedoides* occurred with other macrophytes. In addition, co-occurrence patterns were evaluated using the *C*-score metric (Stone and Roberts, 1990), which calculates the average number of checkerboard units for each species combination (pairwise). A checkerboard unit is the number of plots in which species A is present and species B is absent, and *vice versa* (Stone and Roberts, 1990); a high number of checkerboards indicate that species distribution is segregated. We first calculated the number of checkerboard units for all species combinations. The *C*-score was calculated from the original matrix of species occurrence (presence/absence), and a null model was used to statistically determine if observed co-occurrence patterns could also be obtained by chance. Using the software EcoSim v.7.0 (Gotelli and

Table 1. Colonization of *Ludwigia sedoides* (occurrence and coverage area), macrophyte assemblages (*S* total and *S* local) and morphometric aspects of sites sampled in Lajeado reservoir. Occurrence, number (%) of plots in which *L. sedoides* was present; coverage area, mean plot area covered, estimated visually; *S* total, total richness/site; *S* local, mean richness/plot. Mean values are accompanied by standard error. *n*, number of plots.

		L. sedoides		Macrophyte assemblage		Morphometric variables			
Sites	*n*	Occurrence (%)	Coverage (%)	*S* total	*S* local	Slope (cm)	Distance from shore (m)	Mean depth (cm)	Fetch (km)
1	10	30	01.10 ± (0.99)	11	3.70 ± (0.52)	19.45 ± (5.78)	1.45 ± (0.53)	66.87 ± (13.69)	0.86 ± (0.22)
2	8	87.5	34.36 ± (8.89)	13	6.38 ± (0.71)	1.74 ± (0.26)	8.38 ± (1.80)	48.27 ± (03.19)	0.74 ± (0.17)
3	20	55	12.25 ± (4.11)	12	5.10 ± (0.54)	2.50 ± (0.33)	8.00 ± (1.55)	40.90 ± (02.69)	1.21 ± (0.12)
4	7	42.9	31.43 ± (9.86)	12	6.86 ± (0.51)	2.40 ± (0.41)	9.29 ± (2.29)	36.59 ± (04.97)	0.46 ± (0.16)
5	4	100	36.50 ± (12.9)	12	6.50 ± (0.96)	1.43 ± (1.03)	20.00 ± (4.08)	48.50 ± (12.44)	0.38 ± (0.06)
6	26	26.9	01.54 ± (1.16)	14	5.42 ± (0.39)	5.82 ± (1.01)	7.52 ± (1.09)	42.14 ± (03.92)	1.44 ± (0.16)
7	13	30.8	00.31 ± (0.13)	11	5.00 ± (0.59)	4.25 ± (0.36)	2.77 ± (0.30)	28.01 ± (01.73)	1.71 ± (0.12)

Entsminger, 2001), observed *C*-scores were compared with a distribution frequency of simulated *C*-scores, calculated after 10 000 randomizations of the original data matrix. Then, to investigate the patterns of segregation specifically for *L. sedoides*, we analyzed all pairwise combinations between *L. sedoides* and other macrophytes. We considered significant those combinations with number of checkerboards units within the 95th percentile, analyzing the distribution of all possible pairwise combinations in the assemblage. For all analysis, the level of statistical significance was set at $\alpha < 0.05$.

Results

Ludwigia sedoides was recorded at all sampling sites and in 44% of the plots, although plant coverage varied considerably across sites and plots (Table 1). Higher occurrence and plant coverage was recorded in sites 2, 4 and 5, but a few plots (8%) showed coverage higher than 50% of the plot area. A total of 19 aquatic macrophyte taxa were recorded in the sampling area, belonging to 11 families. Four life forms were identified among these taxa: emergent and submerged (each with eight species), free-floating (two species) and epiphytic (one species) (Table 2). We observed little variation in total species richness/site (11–14 species); mean richness/plot also showed similar values among sites, with values ranging between 3.7 and 6.8 species/25 m^2. In contrast, morphometric variables showed the relevant variation across sites and plots (Table 1).

Stepwise regression selected fetch, depth and slope as the best variables to explain the variation in *L. sedoides* coverage (Table 3), which together explained 46% of data variability ($r = 0.68$; $F3{,}84 = 24.11$, $P = < 0.00001$). Fetch and slope were negatively correlated with coverage, whereas the depth showed a positive correlation with coverage (Table 3). Individually, slope showed the highest correlation with *L. sedoides* coverage ($r = -0.39$), followed by fetch ($r = -0.30$) and depth ($r = 0.27$). No biotic variable (local species richness, richness of life forms, richness of submerged and emergent species) was included in the final model.

The geometric shape of bivariate correlations showed significant relationships between *L. sedoides* coverage and some morphometric and biotic variables. In this case, relationships with local species richness (Fig. 2A), richness of life forms (Fig. 2B) and fetch (Fig. 3A) showed a significant triangular shape (left triangle; Table 4); distance from shoreline (Fig. 3C) and richness of life forms (Fig. 2B) showed a significant pyramidal shape (Table 4). Other correlations were not significant (Table 4).

We detected a significant co-occurrence pattern among macrophyte species (observed *C*-score = 143.18; simulated mean *C*-score = 136.06; $P < 0.00001$), indicating that, in general, species present segregated spatial distribution. Some species showed high *C*-score with *L. sedoides*, with values higher than the overall mean and above the 95th

Table 2. Aquatic macrophytes recorded in Lajeado reservoir, and their respective life forms. Co-occurrence, percentage of plots in which the species co-occurred with *Ludwigia sedoides*; *C*-score, average number of checkerboard units between *L. sedoides* and other macrophyes.

Species	Life form	Co-occurrence (%)	*C*-score
ALISMATACEAE			
Echinodorus paniculatus Micheli	Emergent	5.1	222
Echinodorus tenellus (Mart.) Buch.	Submerged	46.2	567
Sagittaria guayanensis H.B.K.	Emergent	10.3	210
CABOMBACEAE			
Cabomba furcata Schult. & Schult.	Submerged	2.6	0
CHARACEAE			
Chara sp.	Submerged	48.7	800
CYPERACEAE			
Eleocharis sp.	Emergent	0.0	39
Oxycaryum cubense (Poepp. & Kunth) Lye	Epiphytic	74.4	180
Bulbostylis capillaris (L.) C.B. Clarke	Submerged	23.1	240
LENTIBULARIACEAE			
Utricularia foliosa L.	Submerged	10.3	70
Utricularia gibba L.	Submerged	43.6	154
MARSILEACEAE			
Marsilea crotophora D.M. Johnston	Emergent	0.0	39
MENYANTHACEAE			
Nymphoides indica (L.) Kuntze	Emergent	5.1	0
NAJADACEAE			
Najas guadalupensis (Spreng.) Magnus	Submerged	20.5	744
Najas microcarpa K. Schum.	Submerged	84.6	216
ONAGRACEAE			
L. sedoides (H.B.K.) Hara	Emergent	–	–
PONTEDERIACEAE			
Eichhornia azurea (Sw.) Kunth.	Emergent	10.2	105
Eichhornia crassipes (Sw.) Kunth	Floating	7.7	216
Pontederia parviflora Alexander	Emergent	53.9	216
SALVINIACEAE			
Salvinia auriculata Aubl.	Floating	94.8	46

Table 3. Stepwise regression (backward method) testing the influence of biotic and morphometric variables on the coverage of *Ludwigia sedoides*. *B*, standardized slope; *r*, semi-partial correlation coefficient; *t*, *t*-test statistic.

Variables	*B*	*r*	*t*	*P*-value
Fetch	− 0.3484	− 0.3040	− 3.8025	0.00027
Depth	0.3307	0.2682	3.3550	0.00119
Slope	− 0.4699	− 0.3929	− 4.9144	0.00001

percentile (565.5). Such species were negatively associated with *L. sedoides* and included *Chara* sp., *Echinodorus tenellus* and *Najas guadalupensis* (Table 2).

Discussion

The present results indicate some potential variables to predict the coverage and distribution of *L. sedoides* in shallow littoral areas of Lajeado reservoir, Tocantins River. Morphometric variables (fetch, slope and depth) explained a significant portion of variation in the coverage of *L. sedoides*, indicating that sheltered localities, with low slope (<5 cm.m^{-1}) and moderate depths ($\sim$30–80 cm), are suitable for colonization and growth. In addition, colonization was related to attributes of the local flora (*e.g.*, species richness, life forms and co-occurrence patterns), suggesting that resident macrophytes also affect the distribution of *L. sedoides*.

The positive relationship between depth and *L. sedoides* coverage apparently differs from the pattern found in the literature, since rooted macrophytes do not colonize deep areas (>3 m; Bini and Thomaz, 2005; Pierini and Thomaz, 2009), and emergent life forms usually colonize transitional shallow areas (Andersson, 2001). Indeed, Pott and Pott (2000) report that *L. sedoides* prefer shallow waters in natural lagoons. However, the present study investigated depths ranging from 10 to 140 cm, and deeper sites that could restrict colonization were not sampled. Moreover, extensive coverage occurred between 20 and 80 cm, characterizing a shallow littoral environment. The absence of *L. sedoides* in shallower areas

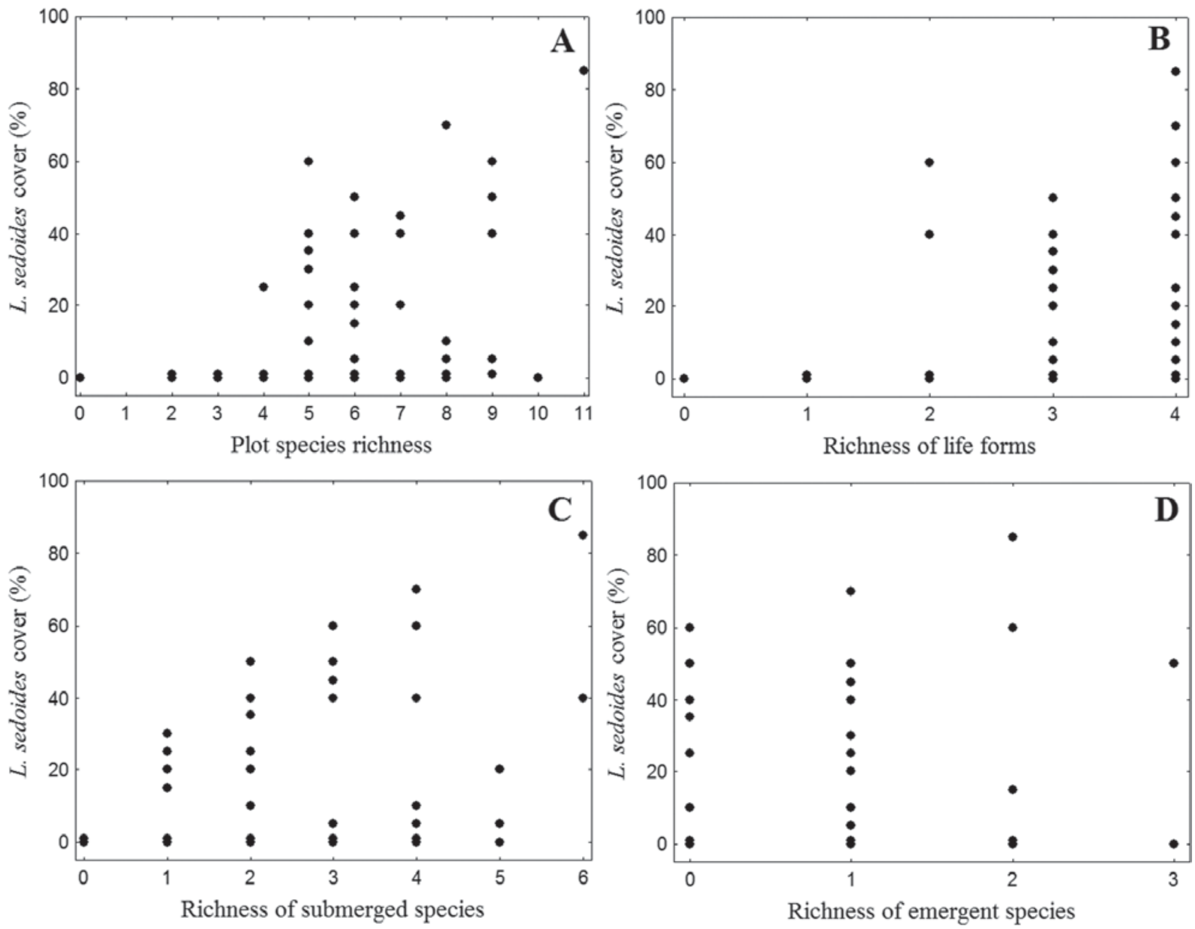

Fig. 2. Bivariate correlations between the coverage of *Ludwigia sedoides* and biotic variables (untransformed data), Lajeado reservoir, Tocantins River.

(<20 cm) is probably related to the disturbance caused by wave action. In fact, the pyramidal relationship with distance from shore indicates that localities close to the margin are unfavorable. At deeper sites, on the other hand, light attenuation may restrict initial colonization, together with morphological constraints (*i.e.*, *L. sedoides* has floating leaves, supported by long stems rooted in the sediment).

We observed a negative relationship between the coverage of *L. sedoides* and slope. This negative relationship has been reported for other aquatic plants (Duarte and Kalff, 1986; Andersson, 2001), probably associated with physical and chemical conditions of the sediment. For example, declivity affects granulometry, composition and stability of the sediment; the deposition of fine particulate matter (nutrient rich) is low in steep littoral areas (Léonard *et al.*, 2008). *Ludwigia sedoides* seemed to be very sensitive to steep margins, as it occurred in localities with slope <5 cm.m^{-1}. Therefore, extensive colonization of *L. sedoides* is expected to occur in littoral areas that are stable and shallow, with low declivity.

Fetch (*i.e.*, wind–wave exposure; Azza *et al.*, 2007) was another important variable in explaining the distribution of *L. sedoides* in Lajeado reservoir. Negative relationships between fetch and macrophyte distribution have been commonly reported, including several species of different life forms (Strand and Weisner, 1996; Rea *et al.*, 1998; Riis and Hawes, 2003; Schutten *et al.*, 2004; Bini and Thomaz, 2005; Azza *et al.*, 2007). Disturbance is mainly mechanical, damaging plants and impairing colonization and development (Schutten *et al.*, 2004; Pierini and Thomaz, 2009). This is typical in reservoirs, as these environments are large and extensive, with sites exposed to severe wave action. Thus, exposed sites in the Lajeado reservoir, such as those located in the central canal, are unsuitable for *L. sedoides*, especially when fetch >1 km. However, the relationship between colonization and fetch showed a triangular distribution of data, *i.e.*, high variability at one end of the gradient (envelope shape; Thomaz *et al.*, 2003; Pierini and Thomaz, 2009). This high variability in plant distribution indicates that other variables contribute to minimize the probability of plant colonization when fetch is low, reducing the predictive power of the relationship. In fact, regression analysis showed that the combined effect of slope, depth and fetch explained almost half of the variation in *L. sedoides* coverage. Other variables, not considered here, must explain the remaining variation. For example, the influence of nutrients, sediment grain size, water quality and presence of herbivores should be considered in future research (Mukhopadhyay and

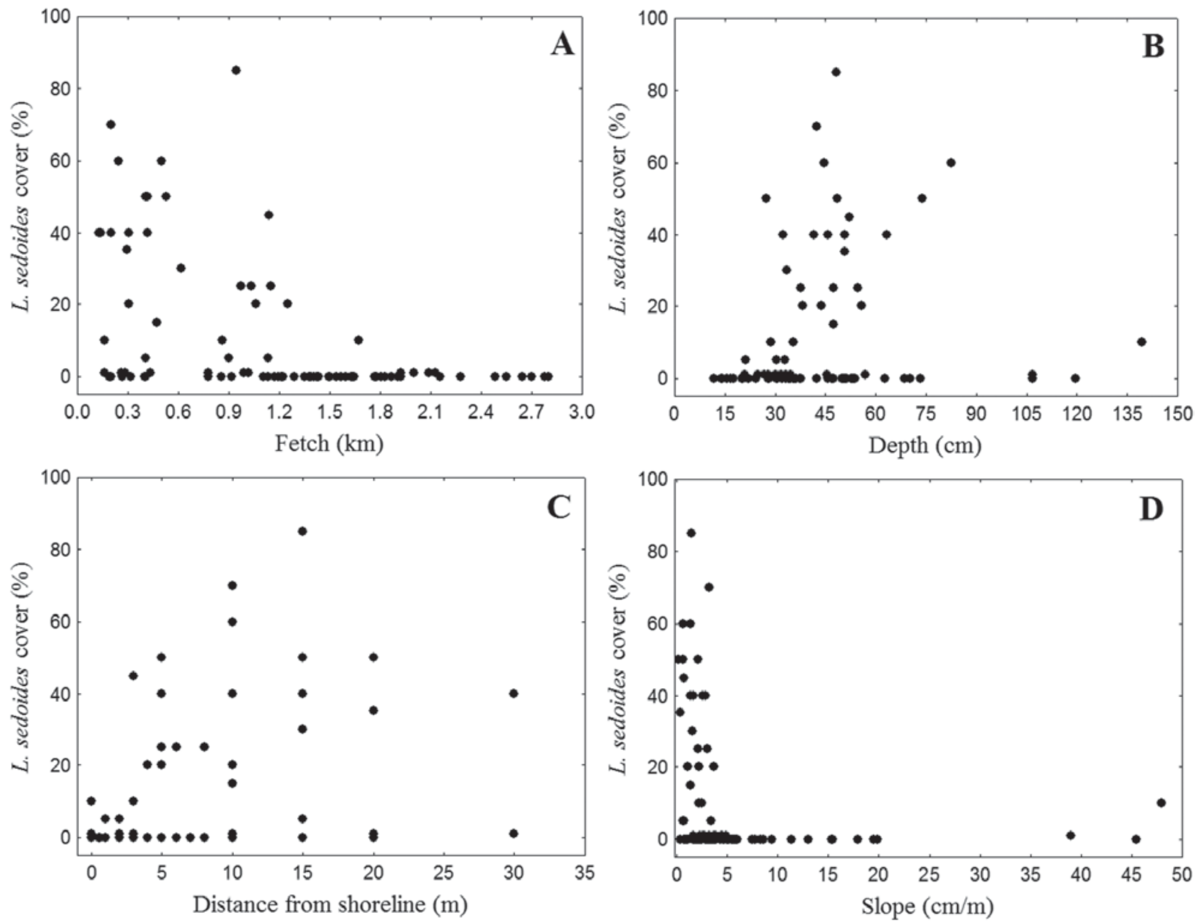

Fig. 3. Bivariate correlations between the coverage of *Ludwigia sedoides* and morphometric variables (untransformed data), Lajeado reservoir, Tocantins River.

Table 4. Geometric shape of bivariate correlations between the coverage of *Ludwigia sedoides* and biotic and morphometric variables, tested by null model analysis. O.I., Observed Index (number of points within the geometric shape); S.I., Simulated Index (mean number of points within the geometric shape after 1000 randomizations of the original matrix).

	Left triangle			Right triangle			Pyramid		
Variables	O.I.	S.I.	*P*-value	O.I.	S.I.	*P*-value	O.I.	S.I.	*P*-value
Local species richness	77	77.82	0.778	80	76.68	0.048	82	81.59	0.522
Richness of life forms	50	50.63	0.747	85	81.04	0.013	55	52.16	0.037
Richness of submerged species	78	77.82	0.588	70	75.86	1.000	80	79.94	0.626
Richness of emergent species	83	82.36	0.481	40	41.23	0.835	44	45.02	0.895
Fetch	86	79.67	< 0.00001	69	72.74	0.977	72	75.77	0.979
Depth	83	84.04	0.928	69	68.17	0.426	78	74.82	0.082
Distance from shore	79	83.05	0.999	64	64.36	0.658	72	67.84	0.032
Slope	86	85.25	0.426	62	61.64	0.519	61	64.76	0.996

Dewanji, 2005; Lacoul and Freedman, 2006), as a means of improving prediction and explanation of the distribution of *L. sedoides* in reservoirs.

In addition to the correlation with morphometric variables, we found non-linear relationships with attributes of the resident flora. In this case, a positive relationship (left triangle) with local species richness and richness of life forms (left triangle, with uneven distribution of variability) was observed, indicating that high colonization of *L. sedoides* is coincident with high diversity of macrophytes. Although these results suggest a biological mechanism (*i.e.*, facilitation), the affinity for the specific environmental settings may explain this correlation. Environmental conditions that favor *L. sedoides* must also favor other species, mainly submerged and emergent species. In fact, some macrophytes co-occurred consistently with *L. sedoides* (Table 2), and extensive colonization of aquatic plants was restricted to sheltered localities. However, the negative co-occurrence pattern also points to significant biotic interactions: high *C*-scores were observed between *L. sedoides* and some macrophyte species. Segregated distribution has been interpreted as the result of strong competitive interactions (Gotelli and McCabe, 2002), but this pattern may result from other mechanisms. In this case, *L. sedoides* presented high *C*-scores with species that were rare (*Chara* sp.), that were restricted to shallow localities (*E. tenellus*) or that occurred in exposed sites (*N. guadalupensis*). Thus, it is unlikely that co-occurrence patterns emerged from strong competitive interactions; again, it seems to be related to specific habitat affinities (Boschilia *et al*., 2008). Fernandes *et al*. (2009), studying the temporal organization of fish assemblages in floodplain lagoons, also evoked the presence of rare species and/or geographical segregation as potential explanations for patterns of segregation. We hypothesized, therefore, that the distribution of *L. sedoides* in reservoirs is significantly influenced by certain environmental conditions (*i.e*., local habitat morphometry), and that local plant assemblages co-vary positively or negatively with these conditions. Experimental studies may clarify if strong biotic interactions are important during early stages of colonization.

In conclusion, this study indicated some environmental factors that are correlated with the coverage of *L. sedoides* in Lajeado reservoir; these factors are potential predictors and must be considered in future modeling. We highlight that *L. sedoides* was present in all sites sampled in this study (distributed over a length of 8 km), indicating a wide distribution in the upper-intermediate zone of the reservoir. In fact, Lolis and Thomaz (2011) showed that *L. sedoides* is among the most frequent species in the upper reach of Lajeado reservoir. This plant is usually sparse; however, large beds are found in sheltered localities – a situation that may cause conflict with some services and resources provided by the reservoir (*e.g*., recreation, navigation, accessibility and fishing). We must consider, however, that this species may play important ecosystem functions, including habitat for the aquatic biota, nutrient cycling and biomass production – aspects to be addressed in future research on food webs and plant–animal interactions. This tradeoff (control versus preservation) must be considered in management plans that aim at controlling the colonization of *L. sedoides* in Neotropical reservoirs.

Acknowledgements. We thank Leandro Amorim, Marco Aurélio Alves Santos and Solange Fátima Lolis (Universidade Federal do Tocantins) for their assistance in field or laboratory work, and the Programa de Pós-Gradução em Ecologia de Ecótonos (PPGEE) and the Núcleo de Estudos Ambientais (Neamb) for providing infrastructure and logistical support. We also thank Rodrigo Fernandes (UFERSA) and Paula Benevides (UFT) for their suggestions and comments, and Mônica Pacheco de Araújo (PPGEE, UFT) for drawing the map. Comments provided by three anonymous reviewers improved considerably the manuscript. CNPq provided a scholarship for M.V.M.B. and a research grant for F.M.P.

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