

THE EFFECT OF HABITAT AND SEDIMENT TYPE ON THE OCCURRENCE OF NON-NATIVE AND NATIVE SPECIES OF AQUATIC MACROPHYTE IN SUBTROPICAL REGIONS

EFEITO DO HABITAT E DO TIPO DE SEDIMENTO NA OCORRÊNCIA DE UMA ESPÉCIE NÃO-NATIVA E UMA ESPÉCIE NATIVA DE MACRÓFITA AQUÁTICA NA REGIÃO SUBTROPICAL

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ABSTRACT: Non-native species of aquatic plants may become invasive and affect native communities, reducing the diversity of plants and other organisms. In general, the successful colonization of new habitats by macrophytes depends first on their dispersion ability and second on the existence of favorable abiotic conditions. In this investigation, we used a transplant experiment to test the effects of habitat water (main river channel *versus* lake) and habitat sediment (river sediment *versus* lake sediment) on the growth of two species, the non-native *Hydrilla verticillata* and the native macrophyte *Egeria najas*. We tested the hypothesis that the non-native species is more successful when it grows in the river channel with river sediment as substrate, whereas the native *E. najas* is more successful when it grows in the lake with lake sediment as substrate. Fragments of both species were planted in river and lake sediment and transported to the main river channel and a lake for the growing period. The field experiment results demonstrated that *H. verticillata* did not grow in either river or lake sediment when planted in the lake. However, this species developed higher root biomass than *E. najas* in the main river channel, which explains its predominance in this type of habitat. The results support the view that habitat characteristics are determinants of the successful or unsuccessful growth of *H. verticillata* in our study sites. Finally, *H. verticillata* invasiveness may improve after certain lag times in response to alterations in habitat, as observed for several other non-native species. Thus, future invasions of floodplain lakes by this species cannot be discarded.

KEYWORDS: Floodplain. Experimental. *Hydrilla verticillata*. *Egeria najas*.

INTRODUCTION

Non-native invasive species have attracted considerable attention due to their potential impacts on natural ecosystems (MACK et al., 2000) and their relevance for testing ecological theories (TILMAN, 1997; SAX et al., 2007).

In general, the successful colonization of new habitats by organisms (including macrophytes) depends primarily on the dispersion ability of species (SAX et al., 2007; VAN DER VALK et al., 2009). For some species of macrophytes, such as those belonging to the family Hydrocharitaceae, vegetative propagules are an important strategy for dispersion and colonization of novel sites (SCULTHORPE, 1967). Abiotic filters (e.g., transparency of water, nutrients of water and sediment, organic matter of sediment) are also important determinants of native and non-native species success; for example, the existence of favorable environmental conditions related to nutrients, underwater light and sediment properties can determine the success or failure of macrophytes in various environments (VAN DEN BERG et al., 2003; SOUSA et al., 2009).

The species *Hydrilla verticillata* (L.f.) Royle (hereafter *Hydrilla*) is native to Asia and Australia (COOK; LUOND, 1982). In Brazil, this species is found in reservoirs (THOMAZ et al., 2009) and recently invaded the Upper Parana River (SOUSA et al., 2009), a strategic ecosystem for biodiversity conservation in Brazil. Since then, it has rapidly spread along the Upper Parana River, infesting large areas with high biomass production and causing problems related to navigation, fishing and recreation activities. Although *Hydrilla* demonstrates a high amplitude of occurrence in several environmental conditions (SOUSA, 2011), in Brazil it succeeds only in the main river and lateral channels and has rarely been recorded in lakes (SOUSA et al., 2009). However, *Egeria najas* Planch. (hereafter *Egeria*), the dominant native submerged macrophyte in the Upper Parana River, is found predominantly in lakes and exhibits low occurrence in the main river channel (SOUSA et al., 2009). Although the species above (both belonging to the family Hydrocharitaceae) occur predominantly in different locations, these two species

have similar morphological characteristics (BECKER et al., 2007).

The different distribution of these two species of macrophytes may be associated with abiotic conditions (transparency of water and type of sediment), which differ between main river channels and lakes. For example, the main river channel and its lateral channels have a higher current flow and a lower concentration of organic matter in sediment lakes than floodplain lakes (SOUSA et al., 2009). In addition to the potential limitations caused by abiotic factors, dispersion may also explain the different patterns of distribution in the Upper Parana habitats.

Thus, the purpose of this paper was to investigate which factor can be responsible for the colonization of *Hydrilla verticillata* in different habitats of subtropical regions. In this investigation, we used a transplant experiment to test the effects of habitat water (main river channel *versus* lake) and habitat sediment (river sediment *versus* lake sediment) on the growth of *Hydrilla* and the native macrophyte *Egeria*. We predicted that *Hydrilla* would be more successful when grown in the river channel with river sediment as substrate, whereas the native *Egeria* would be more successful when grown in the lake with lake sediment as substrate. This prediction was based on several papers that demonstrated that *Hydrilla* does not grow in sites with high concentrations of organic matter in the sediment (BARKO et al., 1986; SOUSA et al., 2009).

MATERIAL AND METHODS

The experiment was conducted *in situ* in November 2009 during the period of low waters in two habitats: one in the main river channel (S 22°45'.887" latitude and W 053°15'.462" longitude) and the second in a lake ("Leopoldo") connected to the river (S 22°43'23.7" latitude and W 053°16'08.6" longitude), both in the Upper Paraná River.

Both habitats demonstrated differences in the sediment characteristics; the river had a more sandy sediment, and the lake had a more muddy sediment (SOUSA et al., 2009).

Apical fragments (10 cm) of the two species (*Hydrilla* and *Egeria*) were planted separately in 0.5 L plastic cups in both river and lake sediments. For each habitat (river and lake), we transplanted 10 fragments of each species; five fragments were planted in river sediment, and 5 fragments were planted in lake sediment. Each species had five replicates of each treatment combination (sediment

and habitat). In total, 40 cups were used in the experiment.

The cups containing the plants with the different sediment type were located outside the existing stands of macrophytes in the main river channel and lake to minimize the influence of these stands on plant growth. Then the cups remained in place for 30 days at a depth of ca. 1 m.

Water and sediment features

We measured the following water abiotic parameters at the beginning and end of the experiment: temperature, oxygen, pH, conductivity, alkalinity and underwater radiation (PAR). The underwater radiation was measured at 0.2 m and 0.6 m, and the coefficient of light attenuation (k) was estimated as $[\log(I_0) - \log(I_z)]/z$, where I_0 and I_z are the radiation measurements at 0.2 m and 0.6 m, respectively, and z is the difference in depth (0.4). The Kjeldahl nitrogen (N) (MACKERETH et al., 1978) and total phosphorus (P) (GOLTERMAN et al., 1978) in the water were also measured.

At the end of the experiment, we also measured the nutrient concentrations of N, P and organic matter in the sediment of all cups. The available N and P were extracted with solutions of KCl (1 hour) and NaOH-NaCl (16 hours), and the concentrations were determined in a spectrophotometer as NH_4^+ e PO_4^{3-} , following the methodology of BREMNER (1965), and expressed as $\mu\text{g gDW}^{-1}$. The organic matter content of the sediment was calculated after drying ca. 1.0 g in an oven at 550 °C for 4 hours and is expressed as % OMsed g DW^{-1} (SOUSA et al., 2009).

In addition, at the end of the experiment (time; 30 days), the cups were removed and the following attributes were measured for each plant: plant dry weight, (stems, branches, roots), root dry weight, number of lateral branches and plant length (cm). Dry weight (DW) was obtained after drying at ca. 80 °C until a constant weight was reached and is expressed as g DW^{-1} .

Statistical Analyses

Hydrilla did not grow in the lake (all values zero; Figures 1 and 2); the lake was therefore not considered a habitat type (main river channel *versus* lake) for analyses with this species. We applied two-way ANOVA to assess differences between species and sediment (river sediment and lake sediment) for all attributes where both species increased in the main river channel.

For *Egeria*, which grew in both the river and lake environments, we also applied two-way

ANOVA to analyze differences between habitat and sediment types.

We also applied one-way ANOVA to assess differences between river and lake N, P and OM in sediment. The normality of the data was tested using a Shapiro-Wilk test and homoscedasticity was tested using a Levene test.

RESULTS

The main river channel water had higher values of k and lower values of water N and P than the lake water, but all other parameters were similar between both habitats (Table 1). The assumptions of normality and homoscedasticity were met for all attributes measured in both species. The results also demonstrated that the river sediment had significantly lower N, P and OM concentrations than the lake sediment (Table 2).

Table 1. Mean (\pm SD) of the abiotic parameters registered during the *in situ* study in both environments at the beginning and end of the experiment.

Abiotic parameters	Main River Channel	Lake
Temperature ($^{\circ}\text{C}$)	30.3 \pm 0.8	29.7 \pm 0.6
OD (mg/l)	7.37 \pm 0.07	6.61 \pm 0.28
OD (%)	88.3 \pm 0.21	83.4 \pm 0.70
pH	7.15 \pm 0.07	6.83 \pm 0.02
Conductivity ($\mu\text{S cm}^{-1}$)	64 \pm 0.1	70 \pm 0.1
Alkalinity ($\mu\text{Eq l}^{-1}$)	362 \pm 12	385 \pm 14
k (m^{-1})	0.96 \pm 0.06	0.41 \pm 0.002
Kjeldahl N ($\mu\text{g l}^{-1}$)	993 \pm 108	1390 \pm 432
Total P ($\mu\text{g l}^{-1}$)	14 \pm 0.7	81 \pm 2

Table 2. Mean (\pm SD) of available N, P and organic matter measured in river sediment and lake sediment. The results of the one-way ANOVA are also shown.

Abiotic parameters	River sediment	Lake sediment	F	p
N($\mu\text{g gDW}^{-1}$)	4.9 \pm 0.57	16.6 \pm 2.58	327.18	<0.05
P($\mu\text{g gDW}^{-1}$)	7.9 \pm 0.09	14.2 \pm 3.5	61.25	<0.01
OM (% gDW $^{-1}$)	0.17 \pm 0.07	14.9 \pm 3.26	469.03	<0.05

The *Egeria* individuals grew in the river and lake independent of the type of sediment (Figures 1 and 2). However, *Hydrilla* individuals grew in the river; none of the individuals grew in the lake, regardless of the type of sediment, and thus, all attributes (plant DW and root DW, number of lateral branches and plant length) for this treatment were zero (Figures 1 and 2).

The results demonstrated that for the biomass (plant DW) of *Egeria*, the effects of sediment, habitat and the sediment and habitat interaction were not significant.

The effects of river and lake sediment and habitat on root DW were significant, and an interaction was found between these two factors ($F_{1,16}=14.20$; $p<0.001$). *Egeria* had a higher root DW when growing in lake sediment in the river

(Figure 1b), but the effects of sediment and habitat when analyzed individually were not significant.

As shown in Figure 2a, the results demonstrate that the number of lateral branches were not significant when this attribute was analyzed separately for the treatments of sediment and habitat, but the sediment x habitat interaction was significant ($F_{1,16}=37.03$; $p<0.001$). *Egeria* growing in the main river channel had more branches than those growing in the lake.

Plant length differed between habitat ($F_{1,16}=4.86$; $p<0.05$), and the sediment x habitat interaction was also significant ($F_{1,16}=12.23$; $p<0.005$); however, this interaction was not significant for sediment. In both sediment types, *Egeria* reached a greater length in the lake compared with the river (Figure 2b).

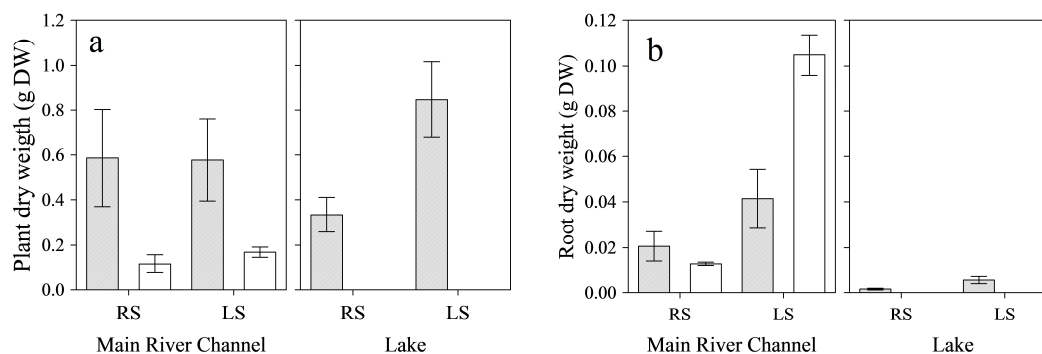


Figure 1. Mean values (\pm SD) of total plant dry weight (a) and root dry weight (b) obtained in the river sediment (RS) and in the lake sediment (LS) for plants growing in the main river channel and in the lake. *Egeria*: grey bars; *Hydrilla*: empty bars. Note that *Hydrilla* did not grow in either type of sediment in the lake.

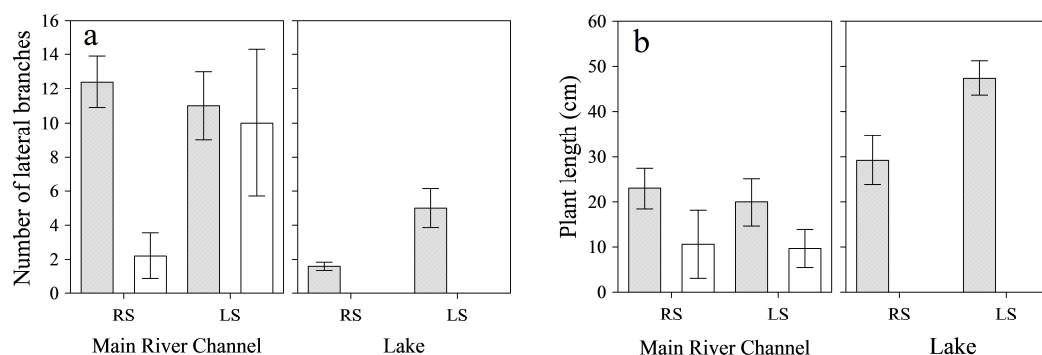


Figure 2. Mean values (\pm SD) of the number of branches (a) and plant length (b) obtained in the river sediment (RS) and in the lake sediment (LS) for plants growing in the main river channel and in the lake. *Egeria*: grey bars; *Hydrilla*: empty bars. Note that *Hydrilla* did not grow in either type of sediment in the lake.

When *Egeria* and *Hydrilla* were analyzed in the different sediment (river sediment and lake sediment) types in the river, the plant length and plant DW were not significantly different. However, root DW and the number of lateral branches demonstrated significantly different values for sediment ($F_{1,16}=18.68$; $p<0.001$ and $F=5.30$; $p<0.05$, respectively); for both attributes, root DW and the number of lateral branches also demonstrated interactions between sediment \times species ($F_{1,16}=7.85$; $p<0.01$ and $F_{1,16}=8.78$; $p<0.01$, respectively). *Egeria* had a lower root DW than *Hydrilla* in both sediment types, but the difference was greater in lake sediment (Figure 1b); by contrast, in both sediment types, *Egeria* had a higher number of branches compared with *Hydrilla* (Figure 2a).

DISCUSSION

The results indicate that *Egeria* performs better than *Hydrilla* in lentic, shallow and turbid

habitats, thus corroborating our hypothesis. These experimental findings are consistent with observational studies conducted in the Paraná River and its floodplain, which have found *Egeria* in main river channel but its success of colonization is mainly in lakes, whereas *Hydrilla* almost exclusively colonizes the river channel (SOUSA et al., 2009). However, although *Hydrilla* fragments are found in the lakes (SOUSA et al. 2009), our experiment strongly supports the idea that they are not adapted to grow in this type of habitat.

The results support the view that both lake water and sediment possibly determine the unsuccessful colonization of the Paraná floodplain lakes by *Hydrilla*. Although it is difficult to determine the main factors that influence the differential response of these two species in lake and river habitats, lower light availability and high sediment organic matter in the lake may help to explain our findings. In fact, the optimum light requirement for *Hydrilla* varies from 500-700 μ M

$\text{m}^{-2} \text{s}^{-1}$ (SOUSA, 2011), whereas it is $80\text{--}100 \mu\text{M m}^{-2} \text{s}^{-1}$ for *Egeria* (TAVECHIO; THOMAZ, 2002). These results indicate that *Egeria* is more adapted to light limitations (typical of lake habitats) than the former. Regarding sediment, a high organic matter content (typical of lake sediment) is considered limiting for *Hydrilla* growth because toxic gases such as H_2S (to which *Hydrilla* is highly sensitive) may be produced in sediments under these conditions (WANG et al., 2007; SOUSA et al., 2009).

Although this explanation has received experimental confirmation (WANG et al., 2007), it leads to an apparent contradiction because *Hydrilla* grew in cups containing lake sediment in the river habitat but did not grow in cups containing river sediment in the lake habitat (see Figures 1 and 2). However, this finding can be explained by the fact that the well-oxygenated water in the river reduces anoxic conditions in sediment and contributes to the exchange of gases between the water and the leaves, alleviating the noxious effects observed in lake sediments. In addition, water characteristics (e.g., turbidity) may also be the main factor affecting its unsuccessful colonization in lakes because *Hydrilla* did not grow in river sediment in the lake.

According to long-term data obtained from the Paraná River and its floodplain, lakes that are connected to the main river channel differ from the latter mainly by having higher turbidity and sediment organic matter (ROBERTO et al., 2009; SOUSA et al., 2009). The physicochemical data confirmed these differences, which may be one of the reasons for the predominance of *Hydrilla* in the main river channel and its unsuccessful colonization of lakes.

Because *Hydrilla* did not grow in the lake, the strategies employed in different habitats can only be analyzed for *Egeria*. An interesting finding was that this species grew in the cups maintained in the river, demonstrating that this habitat is also suitable for its development, in addition to lakes, as demonstrated by SOUSA et al., 2009. This species also developed more lateral branches in the river than in the lake (see Figure 2a). The velocity of water can be considered a stress for submerged plants, and strategies to reduce the specific leaf area may be a response of this species in sites with high velocities of water (BOEGER; POULSON, 2003; SCULTHORPE, 1967).

The difference between habitats regarding *Egeria* root development, which was higher in the

river compared with the lake, was possibly due to the need to anchor the plant against the current velocity in the river, but this result could also be a response to the low nutrient availability in this river. In fact, root:branches ratios usually increase when nutrients limit macrophyte growth (e.g., MONY et al., 2007; HUSSNER, 2009). In addition, although submerged plants absorb nutrients predominantly from their roots, they can also absorb nutrients from leaves in more eutrophic conditions (CARIGNAN; KALFF, 1980). Thus, nutrients can be supplied more through these organs in the lake (richer in nutrients), and as a consequence, the plants direct less biomass to the roots in this habitat. Investment in shoot elongation in the lake (see Figure 2b) as a response to low light availability may also explain the lower root development in this habitat.

In summary, the results indicated that habitat characteristics may be the determinant of the unsuccessful colonization of lakes by *Hydrilla* in the Upper Paraná floodplain. In addition, the rapid growth of *Egeria* in the lake observed in this study, together with the formation of a canopy, may provide some advantage to this species and may partially explain why *Hydrilla* has not been found in the Upper Paraná River lakes. However, other factors not addressed in this experiment, such as the rapid regeneration of *Hydrilla* from tubers and the influence of water velocity, might be important to explain the success of *Hydrilla* in the main channel of the Paraná River. Finally, *Hydrilla* invasiveness may improve after a certain time lag in response to alterations in habitat, as observed for several other non-native species (e.g., SIMBERLOFF, 2009). Thus, the invasion of floodplain lakes by this species cannot be discarded. Future studies on *Hydrilla* and native species in which these additional factors are considered may contribute to understanding their distribution in the Paraná River basin and to predicting which sites are the most prone to invasion.

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RESUMO: Espécies não-nativas de plantas aquáticas podem se tornar invasoras e afetar as comunidades nativas, reduzindo a diversidade de plantas e de outros organismos. Em geral, a colonização por macrófitas em novos habitats depende em primeiro lugar de sua capacidade de dispersão e à existência de condições abióticas favoráveis. Nesta investigação foi utilizado um experimento de transplante para testar os efeitos da água do habitat (calha principal do rio *versus* lago) e sedimentos do habitat (sedimento do rio *versus* sedimento do lago) sobre o crescimento de duas espécies de macrófitas aquáticas a não-nativa *Hydrilla verticillata* e nativa *Egeria najas*. Foi testada a hipótese de que a espécie não-nativa é mais bem sucedida quando cresce no canal do rio com sedimento do rio como substrato, enquanto a nativa *E. najas* é mais bem sucedida quando cresce no lago com sedimento do lago como substrato. Fragmentos de ambas as espécies foram plantadas em sedimentos do rio e do lago e transportadas para o Rio e um lago para o cultivo. Resultados em campo mostraram que *H. verticillata* não cresceu no lago, em ambos os sedimentos (rio e lago). No entanto, esta espécie desenvolveu maior biomassa da raiz no rio, comparada a *E. najas*, o que explica sua predominância neste tipo de habitat. Os resultados apóiam a visão de que as características do habitat são determinantes para o sucesso ou insucesso de *H. verticillata* nos locais em que foram estudados. Finalmente, a invasão *H. verticillata* pode melhorar após um determinado intervalo de tempo em resposta a alterações no habitat, como observado para várias outras espécies não-nativas e, portanto, a futura invasão de lagos de várzea por esta espécie não pode ser descartada.

PALAVRAS-CHAVE: Planície de inundação. Experimento de transplante. *Hydrilla verticillata*, *Egeria najas*

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