**RESEARCH ARTICLE**

# Evidence of rapid evolution of an invasive poaceae in response to salinity

Leticia Siman Bora[1,2] · Sidinei Magela Thomaz[1] · André Andrian Padial[1,2,3]

## Abstract

Understanding how environmental factors and short-term evolution affect the growth of invasive plants is a central issue in Invasion Biology. For macrophytes, salinity is one of the main factors determining distribution along estuarine environments. *Urochola arrecta* is a Poaceae with high invasive potential in several freshwater and estuarine ecosystems. In South Brazilian estuaries, this species is found sparsely in mangroves, and invades successfully freshwaters and areas with low salinity. We experimentally described the *U. arrecta* tolerance to salt. Furthermore, we tested if the response to the saline gradient depends on the population origin, through an experiment with populations inhabiting estuarine and freshwater ecosystems. We designed the experiment with three populations of this species, expecting that estuarine populations were more resistant to salinity. Plants grew in a salinity gradient and after 40 days we measured macrophytes biomass and length. Salinity was highly stressful for *U. arrecta* independently of its origin. Even so, plant growth differed significantly among populations. Despite higher growth, the population originated from freshwater habitats presented the fastest decrease in performance indicators with increasing salinity. This result indicates short-term evolutionary changes because all populations grew common-garden conditions in our experiment. Furthermore, salinity did not prevent the full establishment of this plant, since almost all propagules developed roots even in the saline treatments. Differences among populations suggest that invasion potential of this species can be higher than predicted by the environmental conditions of current invaded sites. Constant monitoring in estuarine invaded ecosystems is central to manage invasions in critical ecosystems, such as mangroves areas.

**Keywords** Aquatic plants · Salinity · Plant physiology · Environmental filters · Estuaries · Biological invasion

✉ André Andrian Padial
aapadial@gmail.com

Leticia Siman Bora
leticia.siman@gmail.com

Sidinei Magela Thomaz
smthomaz@nupelia.uem.br

[1] Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura (Nupelia), Universidade Estadual de Maringá, Maringá, PR, Brazil

[2] Laboratório de Análise e Síntese em Biodiversidade, Departamento de Botânica, Programa de Pós-graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, Curitiba, PR, Brazil

[3] Programa de Pós-graduação em Botânica, Departamento de Botânica, Setor de Ciências Biológicas, Universidade Federal do Paraná, Curitiba, PR, Brazil

## Introduction

Macrophytes play important ecological roles, but some species become invasive and threat aquatic environments. The invasion process generally occurs after the introduction of exotic species in environments with high levels of anthropogenic impacts (Elton 1958). Invasive species can be superior competitors and reduce the growth of native species, with potential to drive local extinctions (Wilcove et al. 1998; Byers 2002). Consequently, biological invasions can cause directional loss of endemic and rare species in detriment of generalist species, a process known as biotic homogenization (McKinney and Lockwood 1999). Apart from that, the excessive growth of invasive macrophytes can also affect ecosystem functions and services in several fashions (Flood et al. 2020), decreasing oxygen levels (Madsen et al. 1991; Madsen 2005), damaging water supplies (Ndimele et al. 2011), and affecting aesthetics or recreation activities in rivers (Monterroso et al. 2010). In view of the problems

caused by invasive macrophytes, the comprehension of environmental factors that restrict their occurrence is of great importance for predictions and management.

Invasive macrophytes may face a myriad of environmental filters in the invaded ranges, including stressful conditions present in sediment and water features (e.g., underwater light and low nutrient concentrations), lake morphometry (e.g., long fetches), competition with natives and predation (e.g., Thomaz et al. 2015; Gufu et al. 2019). In estuarine habitats, salinity is a key factor determining macrophyte distributions (Nunes and Camargo 2016) and interacting with invasive macrophytes colonization. For example, the stressful conditions of high salt concentrations may impact negatively the expansion of freshwater macrophytes (Thouvenot and Thiebaut 2018) but it can increase the likelihood of invasion by species adapted to saline habitats (Xue et al. 2018).

Environmental filtering is a result of evolutionary processes, making possible that short-term evolutionary changes explain the colonization history and physiological tolerance of potentially invasive organisms in environments with apparent adverse conditions (Thomas et al. 2001; Phillips et al. 2006; Lee et al. 2007). Evolutionary changes can occur in short periods of time, particularly in anthropogenic changed environments (Carrol et al. 2007). Selective pressures in relatively short periods of time can result in substantial changes among populations of a same species, allowing certain populations to colonize unfavorable areas (Filchak et al. 2000; Hendry et al. 2000; Schwarz et al. 2005; Hendry et al. 2007). In this sense, common garden experiments help to understand whether variation in performances of populations from the same species are explained by selection of plant traits to the new environment as a consequence of short-term evolutionary processes (Strauss et al. 2006; Carrol et al. 2007). This approach has been applied to a myriad of invasive terrestrial and aquatic organisms, but it is far less studied for macrophytes.

Macrophytes invasions occur both in freshwater (Fernandes et al. 2013; Amorim et al. 2015) and estuarine (Araújo 2017) environments in tropical regions, where they are of special concern in view of the high biodiversity of these ecosystems. For example, the Poaceae *Urochloa arrecta* (Hack. ex T.Durand and Schinz) Morrone and Zuloaga invades successfully and cause serious damages in aquatic Neotropical ecosystems (Pott et al. 2011; Fernandes et al. 2013; Amorim et al. 2015), having a particularly negative effect on native macrophyte biodiversity (Michelan et al. 2010a; Amorim et al. 2015). This macrophyte is native to Africa and was introduced in South America probably as a forage crop, however its accurate global invasion history is still uncertain (Wipff and Thompson 2003). *U. arrecta* is adapted to wet soils and flooded regions, intensively colonizing artificial and natural aquatic environments in Brazil

(Pott et al. 2011; Carniatto et al. 2013; Fernandes et al. 2013; Araújo 2017). Once established, the macrophyte roots in the shores and develop floating steams that extend toward the limnetic regions, accumulating higher biomass than similar natives, what enhances its impacts on native fauna and flora (e.g., Carniatto et al. 2013; Amorim et al. 2015). Interestingly, although *U. arrecta* apparently prefers freshwaters, it also colonizes estuarine ecosystems of Brazilian regions, such as the Guaraguaçu River (Araújo 2017) and other estuarine habitats in South Brazil (Bornschein et al. 2017). However, its presence along the Guaraguaçu River course is uneven: large beds develop in low-salinity and freshwater stretches of this river, whereas only few small beds occur in saline mangroves (Araújo 2017). Therefore, one of the possible causes for this heterogeneous distribution can be related to the wide saline gradient of the river (Araújo 2017). Indeed, salinity is considered one of the main factors influencing vegetation distribution along estuarine environments in aquatic systems (Burgos-Léon et al. 2013; Ribeiro et al. 2015; Rodríguez-Gallego et al. 2015; Nunes and Camargo 2016). Even so, physiological tolerance of this species seems to be high, given the variety of aquatic ecosystems invaded (Carniatto et al. 2013; Fernandes et al. 2013; Amorim et al. 2015). Particularly for salinity tolerance, we did not find information for this species, but it has already been shown high tolerance to salinity in four grasses phylogenetic similar to *U. arrecta* (Kopittke et al. 2009). According to Kopittke et al. (2009), metabolic activity was severely affected by increase in salinity concentration, although a threshold for survival could not be established, and neither a linear decrease in performance of these macrophytes with increasing salinity. Given the different responses of macrophytes similar to *U. arrecta* to salt stress, this could indicate that different populations of *U. arrecta* may respond differently to environmental gradients, including salinity. However, whether the different responses have a genetic basis, resulting from selective pressures over short-term scales, is an open question.

In this work we tested the physiological tolerance of *U. arrecta* to salinity. For that, we experimentally compared the responses of populations that invaded freshwater-only ecosystems in South Brazil with populations of the estuarine Guaraguaçu River. Therefore, we verified if there were possible adaptive differences in relation to salinity. Using both an ecological and an evolutionary view, we expected that the physiological response of *U. arrecta* to variations in salinity depends on how long the populations of this species are exposed to salinity. If this is the case, higher colonization in saline areas can be a matter of time. The following hypotheses were tested: (1) salinity limits *U. arrecta* growth and colonization, and (2) populations of estuarine regions are more resistant to high salinity than populations originated from freshwaters.

## Methods

### Study sites and samplings

*Urochloa arrecta* populations were sampled in two areas of the State of Paraná, South Brazil: the estuarine Guaraguaçu River, and the freshwater hydropower Reservoir 'Rosana', in the Parapanema River, South Brazil (Fig. 1). The Guaraguaçu River springs are located in Serra da Prata, one of the most important mountain sets of "Serra do Mar", and its outfall is in Paranaguá bay, a major bay in South Brazil. It is approximately 60 km long, it is navigable and used for fishery, water supply and tourism. Along its course there are some well-preserved forest areas including one conservation unit (see www.iap.pr.gov.br). However, the river suffers with anthropogenic

impacts, resulting in exotic species introductions (Vitule et al. 2006).

The Rosana Reservoir is located in the Paranapanema River, South Brazil (Fig. 1). The dam was closed in 1987 and it has an area of 220 km² and 116 km of extension. There are two conservation units along its perimeter; however, the region is submitted to high anthropogenic impacts, such as pasture implementations and agriculture activities (Nogueira et al. 2001). The Reservoir has a well developed littoral zone (Júlio Júnior et al. 2005) where *Urochlos arrecta* grows among other native and non-native macrophytes.

Three different populations of *U. arrecta* were collected. Two of them were originated from the Guaraguaçu River, but at two distinct locations (25° 40′ 25.8″ S 48° 30′ 47.9″ W—on day 06/04/2018; and 25°36′01.8″ S 48°29′42.4″ W—days 18/05/2018 and 17/09/2018). The first population (GN) was sampled in a freshwater sampling station (undetected levels of salinity, according to measurements



**Fig. 1** Guaraguaçu River and Rosana Reservoir with the sampling sites (green dots). RO – site where samples were obtained in the Rosana Reservoir; GS – site near the estuary, with constant high salinity, where GS population was sampled; GN – site far from the estuary with predominance of frehwhater (undetected levels of salinity). The linear distance between sampling points in the Rosana Reservoir and the Guaraguaçu River is of ca. 556 km
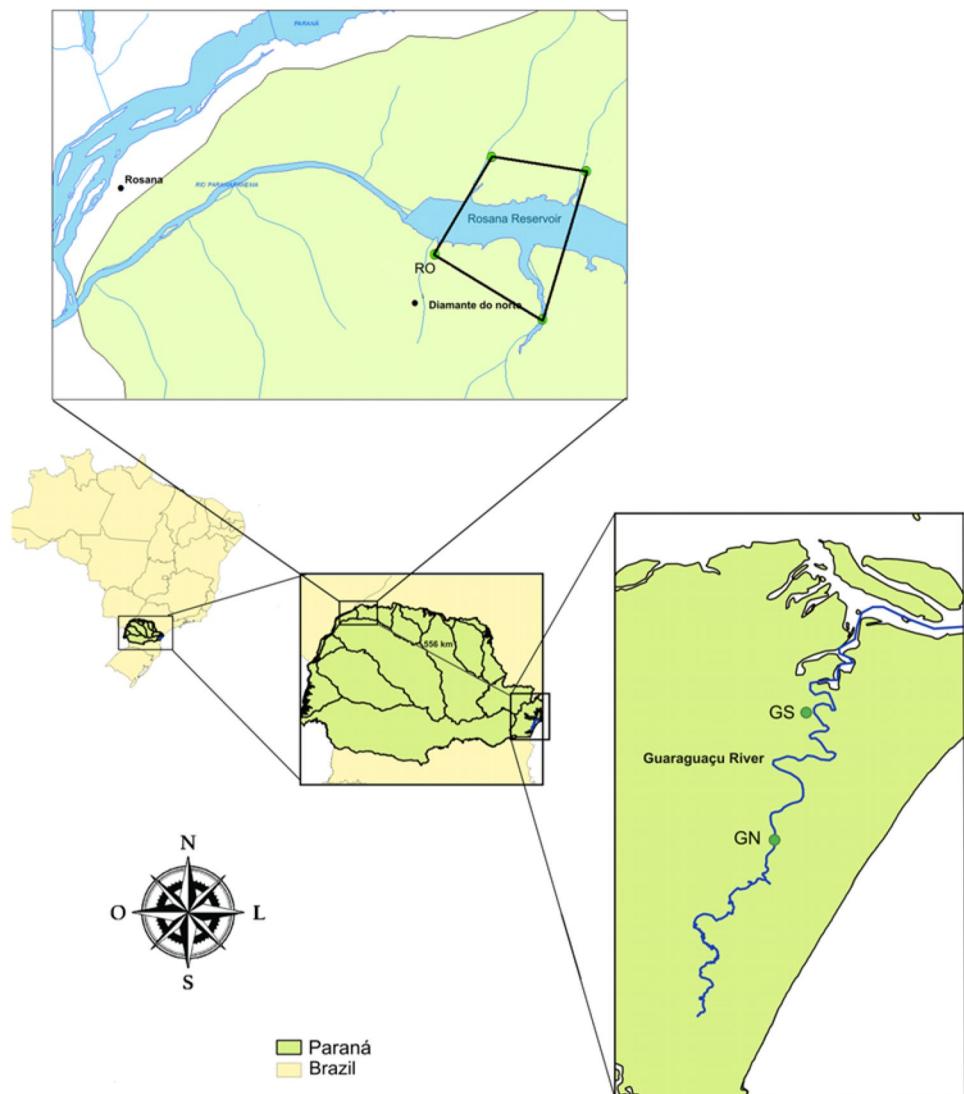
in several dates of 2018). According to information obtained with locals, it is possible that salinity levels of that location increase in extreme tides events. The second population (GS) was sampled in a mangrove region, with constantly high salinity—around 5mS/cm (measurements from several dates of 2018) (Fig. 1). The third population (RO) was sampled in the Rosana Reservoir, located ca. 550 km from the estuarine regions and with no record of any salt water, at the coordinates between 2° 33′ 37.94" S 52° 48′ 48.09" W–22° 34′ 11.63" S 52° 45′ 2.07" W and 22° 37′ 29.07" S 52° 51′ 3.00" W–22°40′ 5.37" S 52°46′ 46.46" W (Fig. 1), on April 17th, 2017. After sampling stems of all populations, they were taken to the greenhouse at the 'Universidade Estadual de Maringá' (Maringá, Paraná, Brazil) and cultivated under no salinity and standard sediment conditions until the beginning of the experiment (September/2018).

## The experiment

An average minimum temperature of 22 °C, an average maximum temperature of 28 °C and an average light intensity of 254.9 lx were estimated along all experimental days at the greenhouse. The experiment started in September of 2018 and each population was planted in 1 L plastic pots. We used in each pot 400 g of soil obtained near the greenhouse, which is considered adequate for the development of *U. arrecta* as demonstrated in previous experiments (e.g., Bando et al. 2016). Initially, we added 300 ml of tap water to each pot. All units were watered daily aiming to keep the sediment always moist and ca. 1–3 cm water layer in the pots.

A pilot test was conducted to reassure the sediment choice. Since each population was collected in a different location, we aimed to ensure that no populations would have their growth influenced by the sediment origin. In this first test, all three populations were planted in standard sediment from the greenhouse, and sediment provided from the Guaraguaçu River (sampled together with plants). During approximately 1 month the plant growth was observed. All populations developed in both types of sediment, and thus the standard sediment from the greenhouse was selected for the common garden experiment.

Two propagules with two nodes each were taken from intermediate portions of the *U. arrecta* individuals and planted in each pot. Four salinity levels were adopted, adding NaCl to the water and mixing with the sediment. The amount of NaCl added was done to control conductivity in the interstitial sediment water (i.e., pore-water conductivity), since *U. arrecta* is a rooted emergent species that consequently is affected by sediment features (Fasoli et al., 2015). Conductivity values were: near 0 (i.e. the control, without salt addition); 2.5; 5 and 7.5 mS/cm. The choice for these values was made based on the fact that the GS population was present in a region with maximum pore-water conductivity of 5 mS/cm. Therefore, we aimed to analyze the population growth in lower and higher salt concentrations than the maximum one found in the field. To achieve the above salinity levels we added 0.84 g, 1.27 and 2.00 g of pure NaCl, respectively, to the pots. To estimate the pore-water conductivity measurements, the damped sediment was passed through a cloth filter and then the conductivity of this filtered water was measured with a portable conductivity meter. All conductivities were set and measured before the experiment. There was no plant or sediment replacement during the experiment. Ten replicates of each treatment were performed, totalizing 120 units (4 salinity levels × 3 populations × 10 replicates).

The experiment set up occurred in two blocks due to logistic and space restrictions inside the greenhouse. The first block was initiated in 10/09/2018 and consisted in 4 replicates of each treatment (16 units per population, total of 48 units). The second block was initiated in 23/09/2018 and consisted on 6 replicates of each treatment (24 units per population, total of 72 units) ("Appendix 1"). The effects of blocks was assessed in our statistical analyses (see "Data analysis" below).

We finished the experiment after 40 days because we noticed signs of plant death in some experimental units. The plants were removed and we measured the maximum length (cm) of roots and aboveground tissues (stems and leaves) of every unit. We also estimated aboveground biomass (g) and root dry biomass (g), as well as the number of shoots per unit. Dry biomass was obtained after drying plant tissues at ca. 60 °C to constant weight.

Colonization capacity of *U. arrecta* was inferred mostly by root biomass and development, given these are traits necessary for successful environmental colonization by most macrophytes (Barrat-Segretain and Bornette 2000; Michelan et al. 2010b; Vari 2013). We thus interpreted number of shoots, dry biomass (g, root and aerial aboveground tissues) and macrophyte length (cm) as measures of *U. arrecta* establishment capacity. Because plants were submitted to the designed salinity treatments since the beginning of the experiment, the ability of root and shoot development would reveal the ability of species colonization and establishment in environments with high salinity. The lateral stems development were also interpreted as a parameter for species dispersion ability, because small fragments of *U. arrecta* (e.g., lateral stems) have high capacity to develop new plants (Michelan et al. 2010b).

We also calculated the ratio between aboveground dry biomass (g) and root dry biomass (g), aiming to explore if

there was a greater investment in roots or aboveground tissues development (see also Pereto et al. 2016).

Although RO populations were cultivated since 2017 in the greenhouse, and Guaraguaçu River populations were planted in May 2018, we believe that the acclimatization period was enough to validate comparisons. Firstly, it is important to note that the experimentation of all treatments was performed at the same time, starting in September of 2018, as described above. With the exception of some plants from GS populations, all other populations remained in the greenhouse for at least 3 months before the experiment (RO for c. 15 months), re-planting whenever necessary. In GS populations, we have made two samplings: the plants from the first sampling acclimatized for c. 3 months, and the plants from the second sampling GS remained only for c. two weeks before the experiment. Two samplings were necessary given our number of replicates. However, we used information from these two samplings to test for differences in acclimatization. If the difference in acclimatization periods represents an important source of variation, GS populations from the two sampling would have different values of performance indicators, suggesting that results were affected by acclimatization period. To investigate for that, we performed a Mann–Whitney–Wilcoxon Test between performance indicator variables of GS population from first (acclimatization of c. 3 months) and second block (acclimatization of c. 2 weeks). The results are in "Appendix 2", and indicated no difference between plants acclimatized for c. 3 months and c. 2 nweeks, so we believe that acclimatization periods had small influence in results.

## Data analysis

A two-way ANOVA with permutations was used to analyze the salinity concentration and population origin effects on *U. arrecta* performance indicators, excluding variation due to experimental blocks and the initial propagule dry weight (g). For that, the initial fresh weights (g) of experimental propagules were measured and the correspondent dry weight was estimated using an established regression between fresh and dry weight for this species. We included the initial propagule dry weight in our model because plant growth depends on propagules size (see Bando et al. 2016 for one example with *U. arrecta* propagules).

The performance indicators of *U. arrecta* were: (1) maximum root length (cm), (2) maximum aboveground length (cm), (3) above-ground biomass (g), (4) root biomass (g), (5) number of shoots per unit (g), (6) above-ground biomass:root biomass. Data analysis was performed through R software version 3.5.0 (R core team 2019), and the graphs were made in STATISTICA version 8.0 (Stat-Soft 2007).

## Results

Salinity was statistically relevant for all response variables, but aboveground biomass:root biomass ratio (Table 1). Similarly, population origin was also important for most variables (Table 1). For above-ground biomass and root biomass, there was an interaction between salinity effect and population origin (Table 1; Fig. 2). Above-ground biomass:root biomass was not influenced by salinity, population origin, experimental block or propagule initial weight (Table 1).

Initial propagule weight was statistically significant only for maximum aboveground length and maximum root length variables, and not for any of the biomass indicators.

Salt addition resulted in a drastic decrease in all measured variables already in the lowest salinity treatment (2.5 mS/cm). The majority of variables presented values near or equal zero in the treatment with highest salinity (7.5 mS/cm) (Fig. 2). However, even in such condition it was possible to notice a large proportion of propagules that developed roots (Table 2).

Results also evidenced that distinct populations responded differently to salinity levels. The highest values of all response variables (but above-ground biomass:root biomass ratio) on populations originated in freshwater with no history of salinity (RO); intermediate values on populations sampled in an area with occasional salinity (GN); and lower values with frequent high salinity (GS) (Fig. 2). Despite the fact that individuals from RO population attained the highest values of all response variables, it is important to note that these individuals were the ones that experienced the steepest declines in response variables along the salinity gradient (Fig. 2; "Appendix 4").

## Discussion

As expected, salinity was a highly stressful factor for *U. arrecta*, explaining its uneven distribution in estuarine rivers such as the Guaraguaçu River. We can thus assert that *U. arrecta* grows to a lesser extent in mangrove areas with high salinity. This result also agrees with previous studies, when comparing grass growth along salinity gradients (Howes et al. 1986; Kopittke et al. 2009; Xiao et al. 2011; Alldred et al. 2017; Li et al. 2018).

Even so, it is important to note that plants grew in intermediate levels of salinity and that they developed roots and shoots even in higher salinity levels (Table 2), indicating that at least in the experimental conditions and time length of our study, *U. arrecta* is able to survive in moderate to high salinity, what is confirmed by the occurrence of this plant in the mangrove of Guaraguaçu River. The presence of *U. arrecta* in new regions with conditions not usually explored
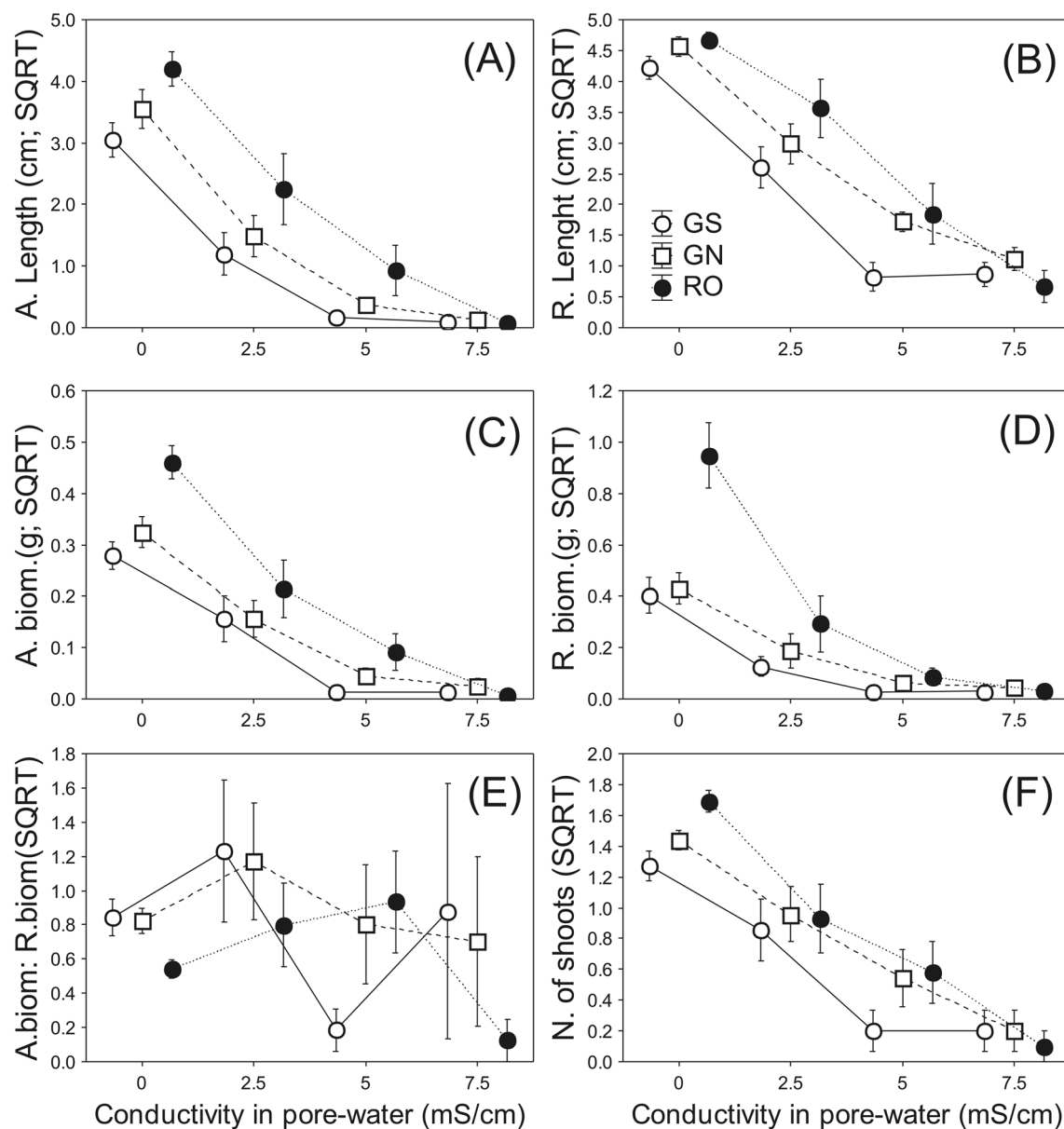
**Fig. 2** Mean ± standard error of **a** maximum aerial length (cm), **b** maximum root length (cm), **c** dry aerial biomass (g), **d** dry root biomass (g), **e** aerial biomass: root biomass ratio (g) and **f** number of shoots of *Urochloa arrecta* submitted to different levels of salinity and different population origin. Population origin treatment (see "Methods"): Rosana Reservoir (RO, filled circles); Guaraguaçu River- salinity region (GS, unfilled circles); Guaraguaçu River— region without salinity (GN, unfilled squares). Subtitles: A. Length- Maximum aerial Length; R. Length- Maximum root length; A. biom.- Aerial biomass; R. biom.- Root biomass; A.biom:R.biom- aerial biomass: root biomass; N. of shoots- number of shoots. Salinity treatment (see "Methods") is represented by pore-water conductivities (mS/cm)

by this species (i.e. high salinity in GS) could represent an indication of fundamental niche expansion; or the fundamental niche is broader than expected by the locations where it is present. However, although seen in higher frequency in freshwaters (Carniatto et al. 2013; Fernandes et al. 2013; Amorim et al. 2015) and in lower frequency in estuarine environments (Bornschein et al. 2017; Araújo 2017), we have not found any register of salinity tolerance information of this species in scientific studies to accurate make any of these assumptions. Even so, a threshold for survival to salinity was not fully established for grasses phylogenetically similar to *U. arrecta* (Kopittke et al. 2009). Our study

**Table 1** Output of the two-way ANOVAs with blocks

| Response variable | Groups | G.L | *P* |
|---|---|---|---|
| Maximum above-ground length (cm) | Salt | 3 | **≤0.001** |
| | Origin | 2 | **≤0.001** |
| | Salt*Origin | 6 | 0.099 |
| | Blocks | 1 | **≤0.001** |
| | Initial dry weight | 1 | **0.044** |
| Maximum root length (cm) | Salt | 3 | **≤0.001** |
| | Origin | 2 | **≤0.001** |
| | Salt*origin | 6 | 0.378 |
| | Blocks | 1 | **≤0.001** |
| | Initial dry weight | 1 | **≤0.001** |
| Above-ground biomass (g) | Salt | 3 | **≤0.001** |
| | Origin | 2 | **≤0.001** |
| | Salt*Origin | 6 | **≤0.001** |
| | Blocks | 1 | 0.073 |
| | Initial dry weight | 1 | 0.248 |
| Root biomass (g) | Salt | 3 | **≤0.001** |
| | Origin | 2 | **≤0.001** |
| | Salt*Origin | 6 | **≤0.001** |
| | Blocks | 1 | **≤0.001** |
| | Initial dry weight | 1 | 0.07 |
| Number of shoots | Salt | 3 | **≤0.001** |
| | Origin | 2 | **≤0.001** |
| | Salt*Origin | 6 | 0.141 |
| | Blocks | 1 | 1.000 |
| | Initial dry weight | 1 | 0.2 |
| Above-ground biomass: root biomass (cm) | Salt | 3 | 0.453 |
| | Origin | 2 | 1.000 |
| | Salt*Origin | 6 | 0.834 |
| | Blocks | 1 | 0.902 |
| | Initial dry weight | 1 | 1.000 |

*Salt* different salinity treatments (see "Methods"), *Origin* different origins/macrophyte populations (see "Methods"), *Salt*origin* interaction between Salt and Origin, *Blocks* different experimental blocks (see "Methods")

Bold values are referent to significant values (P≤0.05)

is a new step in this direction; we highlight the need for more basic studies involving this species, what would be useful in further ecological studies.

Previous studies have already demonstrated that salinity effects interact with exposition time affecting plants (Howard and Mendelssohn 2000), and survival to saline stress is common among aquatic macrophytes (Goodman et al. 2010). Therefore, invasion in apparent harsh environments (such as mangroves) for freshwater invasive plants (such as *U. arrecta*) may be possible over time, also due to the fact that such habitats have lower macrophyte diversity (Smith et al. 2009), which may decrease

biotic resistance of the native community. We also claim that concern on *U. arrecta* invasion in mangroves is even greater due to the fact that populations differed highly considering their tolerance to salinity, which proves that species plasticity is high enough to cope with adverse saline environments.

In a first moment, the faster growth of RO population on salinity treatments might seem unexpected, since it would indicate that a population from freshwaters seems to have higher resistance to salt. All measured variables had considerably higher values on RO population. In contrast, the population collected in an environment with constantly

**Table 2** Proportion of *Urochloa arrecta* roots and shoots development in propagules provided from different populations (GS, GN and RO; see description in "Methods" section), and submitted to different salinity treatments (represented by pore-water conductivities in mS/cm)

| Population | Pore-water conductivity (mS/cm) | Root presence (%) | Shoot presence (%) |
|---|---|---|---|
| GS | 0.0 | 100 | 100 |
|    | 2.5 | 100 | 70 |
|    | 5.0 | 80 | 20 |
|    | 7.5 | 80 | 20 |
| GN | 0.0 | 100 | 100 |
|    | 2.5 | 100 | 80 |
|    | 5.0 | 100 | 50 |
|    | 7.5 | 100 | 20 |
| RO | 0.0 | 100 | 100 |
|    | 2.5 | 90 | 70 |
|    | 5.0 | 80 | 50 |
|    | 7.5 | 80 | 10 |

high salinity (GS) presented always the lowest values. A possible explanation for our results can be seen in a latter experiment, which was conducted further with our data ("Appendix 3") showing that populations from the Guaraguaçu River produced more salt glands since the control treatment, which makes sense since this population was collected in a location with high salinity. Salt increases may cause toxic effects in plants and hinder water absorption (Dolatabadian et al. 2011; Rahneshan et al. 2018) and photosynthesis (Flexas et al. 2004). Therefore, to cope with salt some group of plants, such as some species of the Poaceae family, developed salt glands – specialized epidermal structures that store and exclude salt through plant leaves (Flowers and Colmer 2015; Santos et al. 2016). In this sense, estuarine stressful salinity conditions could lead to a selection of individuals with higher salt gland production, with the cost of reduced plant growth, given that salt glands production demands energy (Dschida et al. 1992; Balsamo et al. 1995). Indeed, salt gland production was lower in RO populations which may indicate that population adapted to freshwater only probably invested more energy towards growth, explaining the patterns found in our results. In view of the small number of salt glands produced by RO plants, it is possible that they would experiment higher mortality rates in high salinity over longer time lengths, although this speculation needs to be confirmed with experiments of longer duration than ours.

Furthermore, another ecological point of view that could help to explain our results is that when a population is exposed to a new form of stress (i.e. salinity in RO population), the increased growth could be the survival strategy adopted. Indeed, constant stress can develop physiological tolerance of plants through acclimatization responses that increase plant growth, as a means of reducing the exposition to the stress factor (Potters et al. 2007). Thus, GS and GN populations must be in less selective pressure, since they could have probably evolved adaptations in locations with high or occasional high salinity (i.e. salt glands). In contrast, RO population must be in great selective pressure, responding with faster growth and propagule production. Even so, we reinforce that the different responses between the three populations can be seen as evolutionary consequences (Keeley 1998; De Wild et al. 2014). This may indicate that colonization in even more saline areas may be a matter of time.

Despite the highest values of performance indicators for RO population even in saline treatments, it is also possible to notice that this was the population with faster decrease in performance indicators as salinity increased (see Fig. 2; "Appendix 4"). The fact that RO population had the highest performance in the control treatment can be explained by the fact that its origins is in regions without salinity, thus likely more adapted to those conditions. However, RO population had the highest loss proportion between the salt treatments (see "Appendix 4"), and such pattern can be interpreted as another indication of less resistance to salinity, in addition to the small number of salt glands of this population. In other words, RO population presents a higher loss in performance with increasing salinity than the other populations. The contrary seems to occur with GS and GN populations, which can be seen as more resistant to salinity changes. The lower loss in performance indicators, in addition to higher salt gland production in GS population ("Appendix 3") highlights the distinct growth form of this population. We argue that this "slow but steady" development could be interpreted as a strategy to cope with salt in mangrove regions. Again, such results emphasize the differences among populations, and suggest that the higher development in RO population can be explained by differences in growth strategies. If resistance to salt is evolutionary, as indicated in our experiment, then *U. arrecta* expansion over mangroves is possible, reinforcing the need for constant monitoring in the region.

In spite of the significant step decrease in all plant performances, *U. arrecta* was still able to keep alive in high salinity levels, producing roots in all treatments (Table 2). Oxygen diffusion through plant roots can occur in swamp

and mangrove regions (Keeley 1979; Boto and Wellington 1984). Also, previous studies have shown that the negative effects of salt stress can be minimized by soil aeration (Li et al. 2019). Therefore, the root development in our saline treatments could be related to sediment aeration and also could be a means to cope with salinity. In our experiment there was not an allocation of biomass towards the root development with increasing salinity; however, plants did present a root elongation, with comparison to above-ground length (Table 2). This could be due to the fact that, despite high root development in all saline treatments, in the two treatments with highest salinities (5 and 7.5 mS/cm), root weigh (not length) was very low. Thus, in high salinity treatments there was a larger root elongation, what could still assist the sediment aeration. Indeed, previous studies revealed greater root growth in *Spartina alterniflora* under saline treatments (Howes et al. 2010; Alldred et al. 2017). Relatively, roots may be less affected than above-ground tissues to salt stress (Stofberg et al. 2015), suggesting that investment in roots may be a strategy to cope with salt.

We evaluated *U. arrecta* responses considering establishment, or vegetative growth (biomass and length, see Tejera et al. 2006 and Teixeira et al. 2017) as well as formation of dispersal and colonization propagules (number of roots and lateral branches, *sensu* Barrat-Segretain and Bornette 2000) indicators. It is interesting to note that, overall, indicators had similar responses. Such pattern reinforces the reliability of our conclusions on the response of the invasive *U. arrecta* to salt and the difference among populations.

In summary, our work shows how salinity acts as an important environmental filter for *U. arrecta*, which may explain its heterogeneous distribution in estuarine ecosystems such as the Guaraguaçu River. In spite of our emphasis in the responses of *U. arrecta* along a salt gradient, we go beyond explaining species physiological responses and the effects in its colonization: we demonstrated that this grass presents establishment and propagation strategies when facing environmental stresses. It is noticeable the distinct responses between the different populations analyzed, despite all of them had grown in the same garden conditions, which can be the consequence of selective responses to a stress factor. Thus, we infer that the populations of *U. arrecta* colonizing the estuarine region have already developed an ecotype different from the populations colonizing freshwaters where they were never subjected to high salinity. In view of our results, it is possible to believe that this species is able to grow and establish in locations with high salinity not yet inhabited, reinforcing the need of continuous monitoring and possible management in critical areas for conservation.

**Data availability** Not applicable, datasheets are freely available, and meta-data is available at https://lasbufprbio.wixsite.com/home.

## Compliance with ethical standards

## Appendix 1: Experimental representative scheme

See Fig. 3.

**Fig. 3** Experiment representative scheme. Subtitle: *RO* Rosana Reservoir population, *GS* Guaraguaçu River population (high salinity region); *GN* Guaraguaçu River population (no salinity region). The salinity treatments are represented in the smaller squares, in mS/cm units (conductivity). Unfilled squares correspond to first experimental block, and filled squares correspond to second experimental block. Representative scheme only, on the experiment the units were randomly distributed along the greenhouse
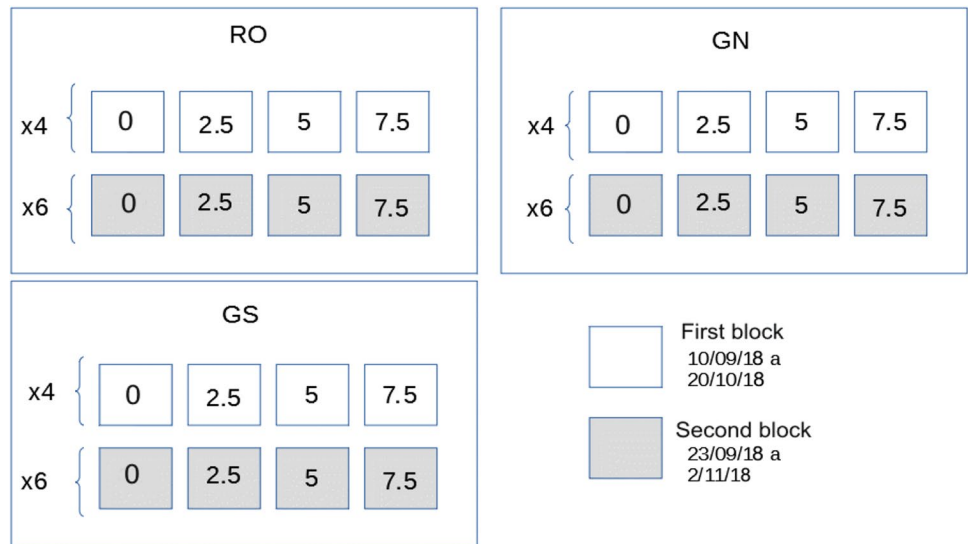


## Appendix 2: Output of the Mann–Whitney–Wilcoxon Test

See Table 3.

**Table 3** Output of the Mann–Whitney–Wilcoxon test testing for differences in performance indicators of *U. arrecta* between the two samplings of salt water (GS) population

| Performance indicators | W | P-value |
|---|---|---|
| Root length (cm) | 145.5 | 0.20 |
| Aerial biomass (g) | 136 | 0.12 |
| Aerial length (cm) | 141 | 0.14 |
| Root biomass (g) | 151.5 | 0.27 |
| Number of shoots | 135 | 0.91 |

GS populations of the first sampling had an acclimatization period of c. 3 months, and that GS populations of the second sampling had an acclimatization period of c. 2 weeks

## Appendix 3: Number of salt glands present in the leaves of *U. arrecta* populations

See Table 4

**Table 4** Average number and standard deviation (SD) of salt glands of all populations (Guaraguaçu, saline region—GS; Guaraguaçu, region with occasional salinity—GN; and Rosana, freshwater population—RO), on leafs and modified leafs on *U. arrecta* stem

| Salt gland measured on: | Populations | | |
| | GS | GN | RO |
|---|---|---|---|
| Leafs | 2.61 (SD = 1.09) | 1.38 (SD = 0.98) | 1.33 (SD = 1.05) |
| Modified leafs on stems | 2.76 (SD = 2.97) | 13 (SD = 10.18) | 1.89 (SD = 2.56) |

## Appendix 4: Proportional loss of *Urochola arrecta* performance indicators along the experiment

See Table 5

**Table 5** Proportional loss of *Urochloa arrecta* performance indicators between paired levels of salt treatments. Salt treatment 0 is the control and all the treatments are in mS/cm unit. Subtitle: GS: population originated from the Guaraguaçu River, saline region; GN: population originated from the Guaraguaçu River at the freshwater or occasionally saline site; RO: population originated from the Rosana Reservoir

| Variable | Population | Paired comparions of salt treatments (mS/cm) (treatment 1 – treatment 2) | Proportional loss (Mean value treatment2 - Mean value treatment 2) |
|---|---|---|---|
| Maximum root length | GS | 0–2.5 | 10.28 |
| | | 0–5 | 16.96 |
| | | 0–7.5 | 16.98 |
| | | 2.5–5 | 6.68 |
| | | 2.5–7.5 | 6.70 |
| | | 5–7.5 | 0.02 |
| | GN | 0–2.5 | 11.24 |
| | | 0–5 | 17.87 |
| | | 0–7.5 | 19.51 |
| | | 2.5–5 | 6.63 |
| | | 2.5–7.5 | 8.27 |
| | | 5–7.5 | 1.64 |
| | RO | 0–2.5 | 7.29 |
| | | 0–5 | 16.44 |
| | | 0–7.5 | 20.98 |
| | | 2.5–5 | 9.15 |
| | | 2.5–7.5 | 13.69 |
| | | 5–7.5 | 4.54 |
| Maximum aboveground length | GS | 0–2.5 | 7.53 |
| | | 0–5 | 9.90 |
| | | 0–7.5 | 9.98 |
| | | 2.5–5 | 2.37 |
| | | 2.5–7.5 | 2.45 |
| | | 5–7.5 | 0.08 |
| | GN | 0–2.5 | 10.25 |
| | | 0–5 | 13.20 |
| | | 0–7.5 | 13.38 |
| | | 2.5–5 | 2.95 |
| | | 2.5–7.5 | 3.13 |
| | | 5–7.5 | 0.18 |
| | RO | 0–2.5 | 10.26 |
| | | 0–5 | 15.88 |
| | | 0–7.5 | 18.25 |
| | | 2.5–5 | 5.62 |
| | | 2.5–7.5 | 7.99 |
| | | 5–7.5 | 2.37 |

**Table 5** (continued)

| Variable | Population | Paired comparions of salt treatments (mS/cm) (treatment 1 – treatment 2) | Proportional loss (Mean value treatment2 - Mean value treatment 2) |
|---|---|---|---|
| Aboveground biomass | GS | 0–2.5 | 0.04 |
| | | 0–5 | 0.08 |
| | | 0–7.5 | 0.08 |
| | | 2.5–5 | 0.04 |
| | | 2.5–7.5 | 0.04 |
| | | 5–7.5 | 0.00 |
| | GN | 0–2.5 | 0.07 |
| | | 0–5 | 0.10 |
| | | 0–7.5 | 0.11 |
| | | 2.5–5 | 0.03 |
| | | 2.5–7.5 | 0.03 |
| | | 5–7.5 | 0.001 |
| | RO | 0–2.5 | 0.14 |
| | | 0–5 | 0.20 |
| | | 0–7.5 | 0.22 |
| | | 2.5–5 | 0.05 |
| | | 2.5–7.5 | 0.07 |
| | | 5–7.5 | 0.01 |
| Root biomass | GS | 0–2.5 | 0.17 |
| | | 0–5 | 0.20 |
| | | 0–7.5 | 0.20 |
| | | 2.5–5 | 0.02 |
| | | 2.5–7.5 | 0.02 |
| | | 5–7.5 | 0.0002 |
| | GN | 0–2.5 | 0.14 |
| | | 0–5 | 0.21 |
| | | 0–7.5 | 0.21 |
| | | 2.5–5 | 0.07 |
| | | 2.5–7.5 | 0.07 |
| | | 5–7.5 | 0.002 |
| | RO | 0–2.5 | 0.84 |
| | | 0–5 | 1.02 |
| | | 0–7.5 | 1.03 |
| | | 2.5–5 | 0.17 |
| | | 2.5–7.5 | 0.19 |
| | | 5–7.5 | 0.01 |

**Table 5** (continued)

| Variable | Population | Paired comparions of salt treatments (mS/cm) (treatment 1 – treatment 2) | Proportional loss (Mean value treatment2 - Mean value treatment 2) |
|---|---|---|---|
| Number of shoots | GS | 0–2.5 | 0.60 |
| | | 0–5 | 1.50 |
| | | 0–7.5 | 1.50 |
| | | 2.5–5 | 0.90 |
| | | 2.5–7.5 | 0.90 |
| | | 5–7.5 | 0.00 |
| | GN | 0–2.5 | 0.90 |
| | | 0–5 | 1.50 |
| | | 0–7.5 | 1.90 |
| | | 2.5–5 | 0.60 |
| | | 2.5–7.5 | 1.00 |
| | | 5–7.5 | 0.40 |
| | RO | 0–2.5 | 1.60 |
| | | 0–5 | 2.20 |
| | | 0–7.5 | 2.80 |
| | | 2.5–5 | 0.60 |
| | | 2.5–7.5 | 1.20 |
| | | 5–7.5 | 0.60 |
| Aboveground length : root length | GS | 0–2.5 | 0.33 |
| | | 0–5 | 0.42 |
| | | 0–7.5 | 0.46 |
| | | 2.5–5 | 0.09 |
| | | 2.5–7.5 | 0.13 |
| | | 5–7.5 | 0.04 |
| | GN | 0–2.5 | 0.37 |
| | | 0–5 | 0.56 |
| | | 0–7.5 | 0.60 |
| | | 2.5–5 | 0.18 |
| | | 2.5–7.5 | 0.23 |
| | | 5–7.5 | 0.04 |
| | RO | 0–2.5 | 0.43 |
| | | 0–5 | 0.64 |
| | | 0–7.5 | 0.81 |
| | | 2.5–5 | 0.20 |
| | | 2.5–7.5 | 0.38 |
| | | 5–7.5 | 0.17 |

**Table 5** (continued)

| Variable | Population | Paired comparions of salt treatments (mS/cm) (treatment 1 – treatment 2) | Proportional loss (Mean value treatment2 - Mean value treatment 2) |
|---|---|---|---|
| Aboveground biomass : root biomass | GS | 0–2.5 | − 2.23 |
| | | 0–5 | 0.63 |
| | | 0–7.5 | − 4.96 |
| | | 2.5–5 | 2.87 |
| | | 2.5–7.5 | − 2.72 |
| | | 5–7.5 | − 5.60 |
| | GN | 0–2.5 | − 1.67 |
| | | 0–5 | − 0.99 |
| | | 0–7.5 | − 1.98 |
| | | 2.5–5 | 0.68 |
| | | 2.5–7.5 | − 0.30 |
| | | 5–7.5 | − 0.98 |
| | RO | 0–2.5 | − 0.85 |
| | | 0–5 | − 1.17 |
| | | 0–7.5 | 0.17 |
| | | 2.5–5 | − 0.32 |
| | | 2.5–7.5 | 1.03 |
| | | 5–7.5 | 1.35 |

# References

Alldred M, Liberti A. Baines SB (2017) Impact of salinity and nutrients on salt marsh stability. Ecosphere 8(11):e02010. https://doi.org/10.1002/ecs2.2010

Amorim SR, Umetsu CA, Toledo D, Monteiro Camargo AFM (2015) Effects of a nonnative species of Poaceae on aquatic macrophyte community composition: a comparison with a native species. J Aquat Plant Manag 53:191–196

Araújo EDS (2017) Padrões ecológicos e prováveis determinantes da comunidade de macrófitas aquáticas em um rio subtropical de maré. Master Dissertation, Universidade Federal do Paraná, p 225. Available at https://hdl.handle.net/1884/55691

Balsamo RA, Adams ME, Thomson WW (1995) Electrophysiology of the salt glands of Avicennia germinans. Int J Plant Sci 156:658–667

Bando FM, Michelan TS, Thomaz SM (2016) Propagule success of an invasive Poaceae depends on size of parental plants. Acta Limnol Bras 28:e23

Barrat-Segretain MH, Bornette G (2000) Regeneration and colonization abilities of aquatic plant fragments: effect of disturbance seasonality. Hydrobiologia 421:31. https://doi.org/10.1023/A:1003980927853

Bornschein M, Reinert B, Machado-de-Souza T, Golec C, Whitney B, Favretto M (2017) Abundance, occurrence, and seasonality of the Subtropical Doradito (*Pseudocolopteryx acutipennis*) on the coast of Brazil. Wilson J Ornithol 129:199–206

Boto KG, Wellington JT (1984) Soil characteristics and nutrient status in a Northern Australian mangrove forest. Estuaries 7:61–69. https://doi.org/10.2307/1351957

Burgos-León AM, Valdés D, Vega-Cendejas MA, Defeo O (2013) Spatial structuring of submerged aquatic vegetation in an estuarine habitat of the Gulf of Mexico. J Mar Biol *Assoc U K* 93:855–866

Byers JE (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97:449–458

Carniatto N, Thomaz SM, Cunha ER, Fugi R, Ota RR (2013) Effects of an invasive alien poaceae on aquatic macrophytes and fish communities in a neotropical reservoir. Biotropica 45:747–754

Carrol SP, Hendry AP, Reznick DN, Fox CW (2007) Evolution on ecological time-scales. Funct Ecol 21:387–393

Dolatabadian A, Modarres SAM, Ghanati F (2011) Effect of salinity on growth, xylem structure and anatomical characteristics of soybean. Not Sci Biol 3:41–45

Dschida WJ, Platt-Aloia KA, Thomson WW (1992) Epidermal peels of *Vicennia germinans* (L.) Stearn: a useful system to study the function of salt glands. Ann Bot Lond 70:501–509

Elton CS (1958) The ecology of invasions by animals and plants. The University of Chicago Press, Chicago

Fasoli JVB, Michelan TS, Thomaz SM (2015) Sediment composition mediates the invasibility of aquatic ecosystems by a non-native Poaceae species. Acta Limnol Bras 27(2):165–170. https://doi.org/10.1590/S2179-975X5214

Fernandes LFG, Teixeira MC, Thomaz SM (2013) Diversity and biomass of native macrophytes are negatively related to dominance

of an invasive Poaceae in Brazilian sub-tropical streams. Acta Limnol Bras 25:202–209

Filchak KE, Roethele JB, Feder JL (2000) Natural selection and sympatric divergence in the apple maggot, *Rhagoletis pomonella*. Nature 407:739–742

Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD (2004) Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. Plant Biol 6:269–279. https://doi.org/10.1055/s-2004-820867

Flood PJ, Duran A, Barton M, Mercado-Molina AE, Trexler JC (2020) Invasion impacts on functions and services of aquatic ecosystems. Hydrobiologia 847: 1571–1586. https://doi.org/10.1007/s10750-020-04211-3

Flowers TJ, Colmer TD (2015) Plant salt tolerance: adaptations in halophytes. Ann Bot 115(3):327–331. https://doi.org/10.1093/aob/mcu267

Goodman AM, Ganf GG, Dandy GC, Maier HR, Gibbs MS (2010) The response of freshwater plants to salinity pulses. Aquat Bot 93(2):59–67

Gufu GD, Manea A, Lishman MR (2019) Experimental evidence that CO2 and nutrient enrichment do not mediate interactions between a native and an exotic free-floating macrophyte. Hydrobiologia 846:75–85. https://doi.org/10.1007/s10750-019-04053-8

Hendry AP, Wenburg JK, Bentzen P, Volk EC, Quinn TP (2000) Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science 290:516–518

Hendry AP, Nosil P, Rieseberg LH (2007) The speed of ecological speciation. Funct Ecol 21:455–464

Howard RJ, Mendelssohn IA (2000) Structure and composition of oligohaline marsh plant communities exposed to salinity pulses. Aquat Bot 68(2):143–164

Howes BL, Dacey JWH, Goehringer DD (1986) Factors controlling the growth form of spartina alterniflora: feedbacks between aboveground production, sediment oxidation, nitrogen and salinity. J Ecol 74(3):881–898. https://doi.org/10.2307/2260404

Howes NC, Fitzgerald DM, Hughes ZJ, Georgiou IY, Kulp MA, Miner MD, Smith JM, Barras JA (2010) Hurricane-induced failure of low salinity wetlands. Proc Natl Acad Sci 107(32):14014–14019

Júlio HF Jr, Thomaz SM, Agostinho AA, Latini JD (2005) Distribuição e caracterização dos Reservatórios. In: Rodrigues L, Thomaz SM, Agostinho AA, Gomes LC (eds) Biocenoses em Reservatórios: padrões espaciais e temporais. Rima Publisher, São Carlos, pp 01–16

Keeley JE (1979) Population differentiation along a flood frequency gradient: physiological adaptations to flooding in Nyssa sylvatica. Ecol Monographs 49:89–108

Keeley JE (1998) C4 photosynthetic modifications in the evolutionary transition from land to water in aquatic grasses. Oecologia 116:85–97

Kopittke PM, Kopittke RA, Menzies NW (2009) Measurement and interpretation of salinity tolerance in four perennial grasses. J Plant Nut 32(1):30–43

Lee CE, Remfert JL, Chang Y-M (2007) Response to selection and evolvability of invasive populations. Genetica 129:179–192

Li S, Ge Z, Xie L, Chen W, Yuan L, Wang D, Li X, Zhang L (2018) Ecophysiological response of native and exotic salt marsh vegetation to waterlogging and salinity: implications for the effects of sea-level rise. Sci Rep 8:2441

Li Y, Niu W, Cao X. Wang J, Zhang M, Duan X, Zhang Z (2019) Effect of soil aeration on root morphology and photosynthetic characteristics of potted tomato plants (*Solanum lycopersicum*) at different NaCl salinity levels. BMC Plant Biol 19:331

Madsen JD (2005) Eurasian watermilfoil invasions and management across the United States. Curr J Mar Educ 21(2):21–26

Madsen JD, Sutherland JW, Bloomfield JA, Eichler LW, Boylen CW (1991) The decline of native vegetation under dense Eurasian watermilfoil canopies. J Aquat Plant Manag 29:94–99

Mckinney M, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Michelan TS, Thomaz SM, Mormul RP, Carvalho P (2010)a Effects of an exotic invasive macrophyte (tropical signalgrass) on native plant community composition, species richness and functional diversity. Freshw Biol 55:1315–1326

Michelan TS, Thomaz SM, Carvalho P, Rodrigues RB, Silveira MJ (2010)b Regeneration and colonization of an invasive macrophyte grass in response to desiccation. Nat Conserv 8:133–139

Monterroso I, Binimelis R, Rodríguez-Labajos B (2010) New methods for the analysis of invasion processes: multi-criteria evaluation of the invasion of *Hydrilla verticillata* in Guatemala. J Environ Manag 92:494–507

Ndimele PE, Kumolu-Joh CA, Anetekhai MA (2011) The invasive aquatic macrophyte, water hyacinth {{*Eichhornia crassipes* (Mart.) Solm-Laubach: Pontedericeae}}: problems and prospects. Res J Environ Sci 5(6):509–520. https://doi.org/10.3923/rjes.2011.509.520

Nogueira MG, Viana NC, Jorcin A, Britto YT (2001) Limnologia comparada de 8 reservatórios em cascata no rio Paranapanema (SP-PR), Brasil. In: Seminário Internacional Gestión Ambiental e Hidroelectricidad. Available in CD-Rom. Salto, Argentina-Uruguay, CACIER-CTMSG, pp 1–20

Nunes LSC, Camargo AFM (2016) Do interspecific competition and salinity explain plant zonation in a tropical estuary? Hydrobiologia 812:67. https://doi.org/10.1007/s10750-016-2821-8

Pereto SCAS, Ribas LGS, Wojciechowski J, Ceschin F, Dittrich J, Bezerra LAV, Padial AA (2016) Trade-off in leaf and root investment of an abundant aquatic macrophyte in a Neotropical floodplain. Fund App Limnol 188(4):309

Phillips BL, Brown GP, Webb JK, Shine R (2006) Invasion and the evolution of speed in toads. Nature 439:803–803

Pott VJ, Pott A, Lima LCP, Oliveira AKM (2011) Aquatic macrophyte diversity of the Pantanal wetland and upper basin. Braz J Biol 71:255–263

Potters G, Pasternak TP, Guisez Y, Palme KJ, Jansen MAK (2007) Stress-induced morphogenic responses: growing out of trouble? Trends Plant Sci 12:98–105

R Core Team (2019) R: a language and environment for statistical computing, version 3.5.0. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rahneshan Z, Nasibi F, Moghadam AA (2018) Effects of salinity stress on some growth, physiological, biochemical parameters and nutrients in two pistachio (*Pistacia vera* L.) rootstocks. J Plant Interact 13:73–82

Ribeiro JPN, Matsumoto RS, Takao LK, Lima MIS (2015) Plant zonation in a tropical irregular estuary: can large occurrence zones be explained by a tradeoff model? . Braz J Biol 75:511–516

Rodríguez-Gallego L, Sabaj V, Masciadri S, Kruk C, Arocena R, Conde D (2015) Salinity as a major driver for submerged aquatic vegetation in coastal lagoons: a multiyear analysis in the subtropical Laguna de Rocha. Estuar Coast 38:451–465

Santos J, Al-Azzawi M, Aronson J, Flowers TJ (2016) eHALOPH a database of salt-tolerant plants: helping put halophytes to work. Plant Cell Physiol 57(1):e10. https://doi.org/10.1093/pcp/pcv155

Schwarz D, Matta BM, Shakir-Botteri NL, McPheron BA (2005) Host shift to an invasive plant triggers rapid animal hybrid speciation. Nature 436:546–549

Smith MJ, Ough KM, Scroggie MP, Schreiber ESG, Kohout M (2009) Assessing changes in macrophyte assemblages with

salinity in non-riverine wetlands: a Bayesian approach. Aquat Bot 90(2):137–142

Stofberg SF, Klimkowska A, Paulissen MPCP, Witte JPM, Van der Zee SEATM (2015) Effects of salinity on growth of plant species from terrestrializing fens. Aquat Bot 121:83–90

Strauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecol Lett 9:357–374. https://doi.org/10.1111/j.1461-0248.2005.00874.x

Teixeira MC, Bini LM, Thomaz SM (2017) Biotic resistance buffers the effects of nutrient enrichment on the success of a highly invasive aquatic plant. Freshw Biol 62:65–71

Tejera NA, Soussi M, Lluch C (2006) Physiological and nutritional indicators of tolerance to salinity in chickpea plants growing under symbiotic conditions. Environ Exp Bot 58:17–24

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L (2001) Ecological and evolutionary processes at expanding range margins. Nature 411:577–581. https://doi.org/10.1038/35079066

Thomaz SM, Kovalenko KE, Havel JE, Kats LB (2015) Aquatic invasive species: general trends in the literature and introduction to the special issue. Hydrobiologia 746:1–12

Thouvenot L, Thiébaut G (2018) Regeneration and colonization abilities of the invasive species *Elodea canadensis* and *Elodea nuttallii* under a salt gradient: implications for freshwater invasibility. Hydrobiologia 817:193–203

Vari A (2013) Colonization by fragments in six common aquatic macrophyte species. Fund Appl Limnol 183:15–26

Vitule JRS, Umbria SC, Aranha JMR (2006) Introduction of the African catfish *Clarias gariepinus* (Burchell, 1822) into Southern Brazil. Biol Invasions 8:677–681

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615

Wipff JK, Thompson RA (2003) Urochloa. In: Barkworth ME, Capels KM, Long S, Piep MB (eds) Flora of North America North of Mexico, vol 25. Oxford University Press, Oxford, pp 492–507

Xiao Y, Tang J, Qing H, Zhou C, An S (2011) Effects of salinity and clonal integration on growth and sexual reproduction of the invasive grass *Spartina alterniflora*. Fuel Energ Abstr 206(8):736–741

Xue L, Li X, Yan Z, Zhang Q, Ding W, Huang X, Tian B, Ge Z, Yin Q (2018) Native and non-native halophytes resiliency against sea-level rise and saltwater intrusion. Hydrobiologia 806:47–65. https://doi.org/10.1007/s10750-017-3333-x