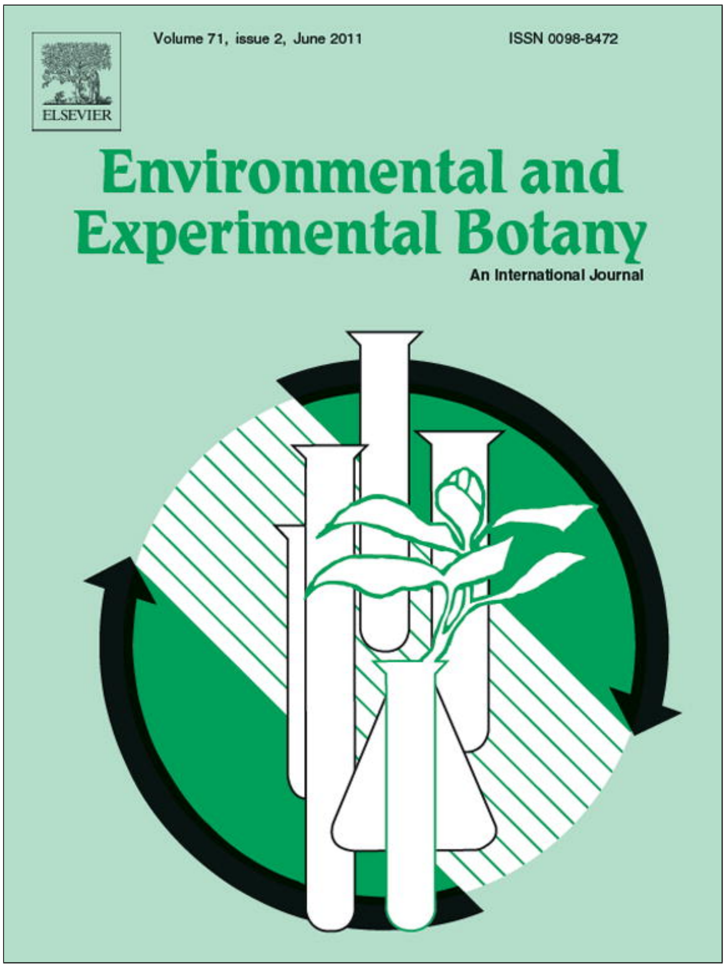
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Spatial distribution of *Crinum americanum* L. in tropical blind estuary: Hydrologic, edaphic and biotic drivers

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ABSTRACT

The competitive abilities of a given species are inversely proportional to its tolerance to environmental stress. Thus, in estuaries, vegetation is generally controlled by salinity and flooding in their lower limits, and by biotic drivers in their upper limits. *Crinum americanum* L. is vastly distributed over flooded regions of American seacoast, frequently associated with stressful habitats. We aimed to explain the role of hydrologic, edaphic, and biotic drivers in the distribution of this species on the Massaguaçu River estuary, Southeastern Brazil (23°37′20″S and 54°21′25″W). We sampled randomly 400 plots in the estuary, and registered covering of all species, the height of the *C. americanum* individuals, and the relative height of the plots. We collected soil samples from every five plots. We measured the estuary level daily for two years. We used Correspondence Analysis, Simple and Canonical, and graphic analysis. The salinity has explained the major part of the observed pattern, and the *C. americanum* population was positively related to it. The estuary level was also important. *C. americanum* has presented higher densities in intermediary flooding classes than in the extremes of the gradient. Species reduction in regions of low salinity or its absence has probably been due to the highly competitive environment, and not to the lack of salt *per* se.

1. Introduction

In estuaries, the distribution and abundance of species are directly related to their capacity of bearing environmental conditions and to their competitive abilities (Crain et al., 2004; Greenwood and MacFarlane, 2008). In these environments, the major determinant factors for the plant assemblage are salinity and flooding cycles (Bockelmann et al., 2002; Costa et al., 2003; Silvestri et al., 2005). Generally, species' competitive abilities are inversely proportional to their tolerance towards environmental stresses (Pennings et al., 2005). Thus, along with the salinity gradient of an estuary, the competitive dominant species would occupy the physically benign habitats and displace subordinate ones to physically harsh habitats (Crain et al., 2004). This way, species distribution in an estuary is usually controlled by salinity and exposure to flooding in its lower limits, and biologically controlled in its upper limits (Ungar, 1998; Castillo et al., 2000; Pennings et al., 2005).

Most experimental studies on species zonation, along with salt marshes environmental gradients, have been conducted in estuaries with permanent connection with the ocean, at middle and high latitudes of Northern Hemisphere (Costa et al., 2003). In tropical estuaries of the Southern Hemisphere, pluviosity has a relatively higher importance, and salinity gradients are expected to be more abrupt. In blind estuaries, where the connection with the ocean is sporadic (see Hume et al., 2007), the relative importance of the rain is even bigger, and both salinity and flooding cycles are less predictable. Thus, it is not clear to what extent the information about regular Northern salt marshes can be extrapolated to tropical blind estuaries (Costa et al., 2003). Plant zonation along with salinity gradients represent a major gap in the knowledge of tidal environments, and understanding this is crucial for both conservation and restoration of costal marsh systems (Crain et al., 2004).

Crinum americanum L. (Amaryllidaceae) is widely distributed throughout flooded regions, swamps and rivers of the America seacoast, frequently associated with ecologically stressful areas (Meerow et al., 2003). This is a fast growing species, which is salt and flooding resistant, with large and salt-resistant floating seeds, and strong allelopathic potential (Ribeiro et al., 2009). *C. americanum* seems to be highly aggressive, occupying several large areas (Mayer et al., 1998).

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In a blind tropical estuary, with no biologically dry season, we noticed that although *C. americanum* is evident all along the estuary, it seems to be highly abundant in areas next to the sandbar. Its vertical zonation also seems to present a pattern, with lower densities in the superior and inferior extremes in the estuary. We expect the *C. americanum* distribution pattern to arise mainly from salinity in the horizontal gradient and mainly from the flooding exposure in the vertical gradient, and both gradients to be important to determine the interspecific interactions patterns. Thus, to test this hypothesis, our objective were twofold: to better characterize the distribution of *C. americanum* along the estuary and to determine how this distribution can be explained by (1) estuary edaphic characteristics, (2) flooding cycles and, (3) inter-specific interactions.

2. Materials and methods

Study site. The estuary of the Massaguaçu River (23°37′20″S and 54°21′25″W) is a blind estuary. The sandbar which separates it from the ocean opens a few times *per* year, and on these occasions, the level of the water may result in more than a 2-m decrease. The frequency and duration of these events are irregular, and expose the flora to sudden and unpredictable changes in the environmental conditions. Although the opening cycles of the bar are natural events, the opening by antrophic action has been on the increase. We accomplished this experiment in five large banks of macrophytes belonging to the estuary. Four of them are linked to the estuary margin, and one is an island. These banks are distributed longitudinally in the estuary, and offer a propitious condition for studies of zonation in environmental gradients (supplementary data 1).

Floristic. The use of cover values to quantify populations has been largely used for species when it is not possible to count individuals (Mueller-Dombois and Ellenberg, 1974). Generally, the density in which the species occurs is not taken into account, and same-sized areas with either sparse or dense emergencies get the same cover value. The method described as follows is an adaptation of the standard procedures to include the values of different densities into the cover value. To determine the distribution and abundance of species in the estuary, we sampled randomly 80 plots (5 × 5 m) on each bank (400 plots total), and transferred the coordinates of these plots to a GPS for future field localization. We registered the cover areas (m^2) of the species which occurred in each one of the plots. We classified the densities of these areas into three categories: I – low (1–33% of the plot area covered by the species), II – medium (34–66%) and III – high (67–100%). As a species may occur in more than one spot within a single plot, and as these spots may have different densities, we calculated intermediate values for each density category (low – 16%, medium – 50% and high – 83%) and multiplied them by the cover area values from each one of these spots. By doing so, the cover value of each spot incorporated the density of the species occurring in it. The sum of the covers of each spot generated a single cover value per species per plot (supplementary data 2). To *C. americanum* the high, medium and low densities corresponded to 50, 30 and 10 individuals per m^2. Thus, depending on the analysis we could use the density (e.g. comparison with the cover area of other species) or the number of individuals (e.g. determination of the size of the population). In each plot we measured the height of six individuals of *C. americanum*, chosen at random. For the analysis, we used only the more abundant species, selected through the curve species-abundance ("Whittaker plots").

Edaphic relationships. To determine the edaphic characteristics of the estuary, we collected soil samples for every five plots (16 per bank, 80 total) and determined the pH values, organic material, the micro and macro nutrient contents, sodium, electric conductivity, and flooding. For the analyses, we created a salinity index, from the multiplication of the sodium and electric conductivity.

Table 1
Flooding classes of the Massaguaçu river estuary, with the minimum and maximum depths (cm) and the flooding time (percent) of each class.

Flooding classes	Minimum depth	Maximum depth	Flooding time (%)
C100	−50	0	100.00
C90	1	40	89.97
C80	41	66	79.94
C70	67	90	68.71
C60	91	110	57.63
C50	111	120	47.31
C40	121	138	37.87
C30	139	151	26.65
C20	152	168	14.82
C10	169	220	6.29

Hydrologic relationships. To determine the variation of the estuary level, from July 2007 to July 2009, we made daily readings of the relative level of the water (we established zero as the lowest level that the estuary reaches, which occurs in the low tide with the sand bar opened). We measured relative height of each plot as well. The lower the level of the estuary is, the faster it rises. Thus, the difference of the flooding time is smaller between the lowest plots, and bigger between the highest ones. To analyze the data more precisely in the biological sense, we grouped the levels of the estuary in flooding classes (Table 1).

Data analyses. We determined the relation between the density and height of the *C. americanum* population, and the estuary soil characteristics through Canonical Correspondence Analysis. We used the Monte Carlo with 1000 permutations to test its significance. We used Correspondence Analysis to relate the density with the flooding class. To compare the distribution of *C. americanum* along the estuary concerning the distribution of determined species, we calculated the occupation of each one of them in all banks, plotting its densities concerning the flooding classes. To perform a graphic analysis of the *C. americanum* distribution along the estuary, we made a contour map, using its densities as z values.

3. Results

3.1. Description of C. americanum distribution

C. americanum is the most abundant species of the estuary. Its density was higher nearby the bar, but it was present in all of its extension (supplementary data 3). This species presented high dominance in the more saline portion of the estuary, where on several occasions was the only species of the plot. By its density and cover, we estimated its population in around 3430 thousand individuals. In the Massaguaçu River estuary, the reproduction of *C. americanum* can happen sexually, through the production of a high number of seeds, and non sexually, through rhizomes. For this reason is not possible to know in the field if it is a genetic unit or a clone. Thus, we call individual any emergency. In bank D, and especially in bank E, where *C. americanum* occurred in lower densities, its population was estimated in more than 1.7 million individuals. The height of the individuals along the estuary did not vary much, and the total average was 1.07 m (Table 2).

3.2. Edaphic relationships

Salinity was the most important edaphic factor for the distribution and density of *C. americanum*, and the higher its values, the higher its densities. The other elements analyzed seemed to have little or no influence over the density of *C. americanum*. The analysis did not highlight any edaphic factor as determinant for the height

Table 2
Area (m^2), number of individual, density (individual/m^2) and average height of the *C. americanum* population in the macrophytes bank in the Massaguaçu river estuary.

	Area	Individuals	Density	Height
A	52434.97	985.643	18.8	1.05
B	20931.72	351.759	16.8	1.14
C	23759.31	354.042	14.9	1.06
D	95027.43	1086.816	11.4	1.03
E	86546.28	652.056	7.5	1.09
Total	278699.7	3430.316	13.9	1.07

of the individuals of this species in the Massaguaçu River estuary (supplementary data 4).

3.3. Exposure to flooding

The distribution and density of *C. americanum* in the Massaguaçu River estuary were significantly related to the exposure to flooding. Mean and high densities occurred preferably in the flooding classes C70 and C80. The lowest density occurred in the more flooded (C90) and less flooded (C60) classes. The absence of this species was related to the extreme class (C100 and C50 and lower class) (supplementary data 5).

3.4. Biotic relationships

The estuary had 51 species of aquatic or amphibian plants. We classified 12 species as abundant (Table 3). These species represented altogether near 93% of the total plant coverage of the estuary. *C. americanum* L., *Bacopa monnieri* (L.) Wettst., *Eleocharis flavescens* (Poir.) Urb., and *Acrostichum danaeifolium* Langsd. & Fisch. presented a preference for the more saline portion, being more abundant if closer to the bar. *Eleocharis interstincta* (Vahl) Roem. & Schult., *Typha dominguensis* Pers., *Scleria mitis* P. J. Berge, and *Rhynchospora corymbosa* (L.) Britton were more abundant in the less saline ones. *Acroceras zizianioides* (HBK) Dandy, *Echinochloa polystachya* (Kunth) Hitchc, *Paspalum* sp. and *Brachiaria mutica* (Forssk) Stapf did not present a clear distribution pattern along the saline gradient.

Table 3
The principal species of Massaguaçu river estuary.

Specie	Family
Crinum americanum L.	Amaryllidaceae
Eleocharis interstincta (Vahl) Roem. & Schul	Cyperaceae
Bacopa monnieri (L.) Wettst.	Plantaginaceae
Acroceras zizanioides (Kunth) Dandy	Poaceae
Eleocharis flavescens (Poir.) Urb.	Cyperaceae
Rhynchospora corymbosa (L.) Britton	Cyperaceae
Acrostichum danaeifolium Langsd & Fisch	Pteridaceae
Typha domingensis Pers.	Typhaceae
Paspalum sp.	Poaceae
Echinochloa polystachya (Kunth) Hitchc.	Poaceae
Brachiaria mutica (Forssk.) Stapf	Poaceae
Scleria mitis P.J. Bergius	Cyperaceae

The relationship between richness and diversity, and the saline gradient was not clear, and extremity banks (A and E) presented similar values for these index. On the other hand, the reduction of the *C. americanum* population in the less saline portions was accompanied by an increase of density of determined species (Fig. 1). These species were morphologically similar to *C. americanum*, and occupied similar flooding classes. The density of the species *per* flooding class *per* bank showed the decline in the *C. americanum* population and the subsequent increase in the other ones (Fig. 2).

4. Discussion

Salinity and flooding are determinant factors to the zonation of *C. americanum* in the Massaguaçu River estuary. The density of this species follows the saline gradient of the estuary, being higher in the portions with more salt. The flooding restricts *C. americanum* to specific heights of the estuary, and this species is almost absent in the extreme flooding classes. As it is maintained in non flooding conditions as an ornamental plant, the absence of this species from lower flooding class might not be related to the lack of flooding

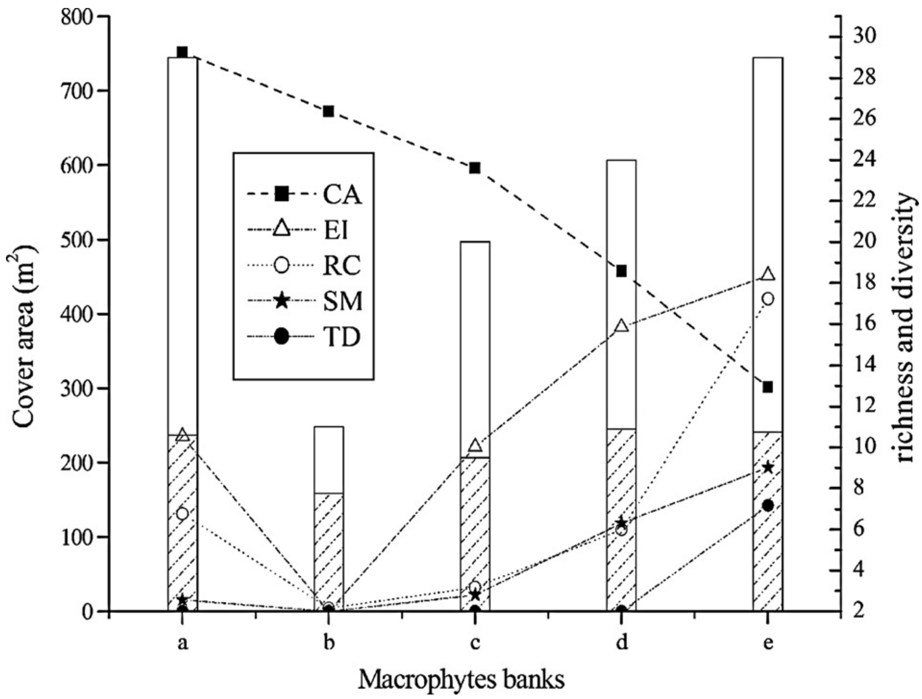

Fig. 1. Distribution (in m^2 in the 80 plots) of *Crinum americanum* (CA), *Eleocharis interstincta* (EI), *Rhynchospora corymbosa* (RC), *Scleria mitis* (SM) and *Typha dominguensis* (TD) in the five macrophytes banks of the Massaguaçu River estuary. The full bar represents the richness and the bar with hashed lines represents the diversity (Shannon × 5).

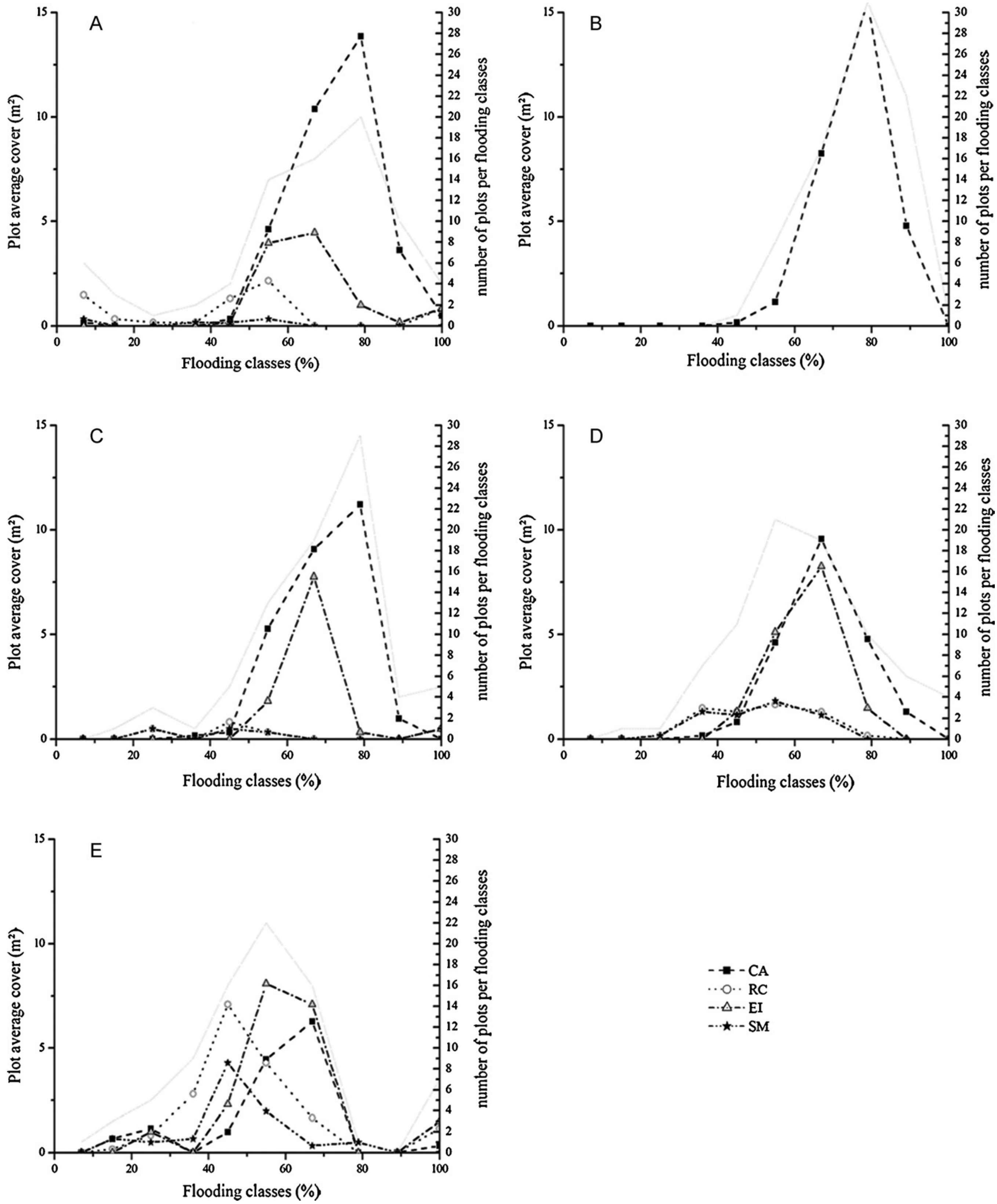

Fig. 2. Occupation of the flooding classes in each macrophytes banks (A, B, C, D and E). The line with symbols represents *Crinum americanum* (CA), *Eleocharis interstincta* (EI), *Rhyncospora corymbosa* (RC) and *Scleria mitis* (SM). The single line represents the number classes in each flooding classes.

itself. We believe that this occurs due to the arboreal component and its consequent shadowing, as this is the major limiting factor for aquatic plants (Phillips et al., 1978). However, to the best of our knowledge, no work has been done to determine the cause of this phenomenon. The absence in the very flooded class may be related to difficulties in colonization, since the floating seeds of *C. americanum* have less chances of getting fixed in a substract which is exposed for less time. This lacks investigation as well.

There is little information on ecology of *C. americanum*, and most information that is available on its biology comes from its cultivation. It is a rustic species, tolerant to salinity and little demanding about the soil characteristics (Gilman, 1999; Ribeiro et al., 2009). In the Massaguaçu River estuary, pH, macro and micro nutrients have little influence over the distribution or size of *C. americanum*. As it happens with most estuarine plants, the main edaphic factor to the distribution of this species is the salinity (Touchette, 2006; Greenwood and MacFarlane, 2008).

It is unknown how the salt interferes physiologically in *C. americanum* development. It is unlikely that low quantities of salt should be a limiting factor, though. The high number of records of its cultivation in fresh water and the size of its population in banks D and E itself support this idea. Thus, the presence of salt would bring competitive advantages to the *C. americanum* (see Ungar, 1998). Several authors have demonstrated how variations in salinity influence the interspecific competition in a saline gradient (Peyre et al., 2001; Crain et al., 2004; Silvestri et al., 2005; Touchette, 2006; Greenwood and MacFarlane, 2008), and frequently most tolerances to environmental factors are related to smaller competitive abilities. In this context, the presence of salt provides competitive advantages to *C. americanum*, increasing its dominance in the saline portions. As salinity decreases, other species become more efficient and the competitive interactions reduce the density of *C. americanum*.

For some species this relation is quite clear. *E. interstincta*, *T. dominguensis, S. mitis* and *R. corymbosa* were more abundant in the less saline portions, and the increase of its populations was followed by the reduction of population of *C. americanum*. These species are structurally alike, and occupy similar flooding classes. This relation was best noticed in the distribution of bank E (Fig. 2E), where the population of *C. americanum* presented a valley in the flooding classes where *R. corymbosa* and *S. mitis* presented maximum densities. To other species this relation is not so clear. *B. monnieri, E. flavecens*, and *A. danaeifolium*, for instance, also prefer the more saline portions, and their distributions present patterns similar to *C. americanum*, suggesting that they respond in a similar fashion to changes in the environment. *A. zizianioides* and *E. polystachya* do not seem to follow a salinity pattern, and thus it is not possible to establish its role along the salinity gradient.

The reduction of *C. americanum* in the less saline portions would not be related to the changes in number or in the species composition, but with the increase of population of some species. In that sense, the higher diversity values in the less saline portions (especially D and E) would be consequence and not cause of the reduction of the population of *C. americanum*. The hypothesis that reduction of population of *C. americanum* could be related to the increase of population of determined species seems to be quite plausible. *C. americanum* is a predominantly coastal species (Meerow et al., 2003) and *E. interstincta*, *R. corymbosa*, *S. mitis* and *T. dominguensis* are widely distributed in flooding regions in general, often occurring in environments with no salinity (Pott and Pott, 2000).

Competition seems to influence the vertical occupation of the estuary as well. *C. americanum* is dominant in two flooding classes C70 and C80 (Supplementary data 4). Its density is smaller in the portions where competition is higher, but it occupies more flooding classes, suggesting that the presence of other species detours this species from its optimum flooding classes.

Even in the less saline portions, where it appears as a subordinate form, *C. americanum* is still a highly representative species. This suggests that the trade of tolerance to stresses *versus* competitive abilities is not always true, and that one environmentally tolerant species may also be an efficient competitor (Emery et al., 2001; Costa et al., 2003).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.envexpbot.2010.12.011.

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