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Primary production and mortality of *Eleocharis interstincta* in response to water level fluctuations

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Abstract

This study evaluated the net aboveground primary production (NAPP) of *Eleocharis interstincta* in response to water level fluctuations. Sampling was carried out every 2 weeks from June 1997 to June 1998 in the littoral region of the Jurubatiba (coastal) lagoon (Rio de Janeiro), where three $0.0625\,\mathrm{m}^2$ study plots were selected for cohort observation. Three quadrats from the same area were also harvested. In the laboratory, stems were oven-dried at $70\,^{\circ}\mathrm{C}$ for 3 days to reach constant weight, their heights measured and their weights taken to determine biomass. The water level fluctuated seasonally, with two periods when the water failed to cover the macrophyte stand—the end of winter (natural dry out) and in summer (artificial breaching of the sandbar). Cohort average height and mean water level in the stand were positively correlated (r=0.91, P<0.01). The relative growth rate of *E. interstincta* was not influenced by water level fluctuations, since different growth rates were observed even when the water level was stable (P<0.05). Stem mortality and herbivory occurred throughout the year and accounted for 14.8 and 1.8% of net annual aboveground primary production (NAAPP), respectively. NAPP varied from 0.5 to 1.8 g dry weight m^{-2} per day, and there was a significant correlation with average water level (P<0.05), indicating that water level has an important role in *E. interstincta* dynamics.

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1. Introduction

Coastal lagoons are characterized by their great vulnerability to wind action and climate fluctuations (Panosso et al., 1998), especially changes in water level. Several investigations have demonstrated the influence of changes in water level on the biomass, growth, production and distribution of aquatic macrophytes in temperate (Linthurst and Reimold, 1978; Rea and Ganf, 1994; Froend and McComb, 1994) and tropical regions (Junk and Piedade, 1993a,b; Villar et al., 1996; Palma-Silva et al. (in press)). However, most investigations focusing on changes in water level and its influence on primary production of emergent aquatic macrophytes have not considered losses from mortality and herbivory. Therefore, the accuracy of the estimates of primary production of aquatic macrophytes in coastal lagoons may be seriously underestimated, unless the effects of mortality, herbivory, or other factors influencing losses in biomass are corrected for.

Eleocharis interstincta, an emergent macrophyte, is widely distributed in tropical America. It colonizes the littoral zones of rivers and shallow lakes with above water stems, enabling photosynthetic activity and gaseous exchanges (Kissmann, 1997).

The goal of the present investigation was to estimate the net aboveground primary production (NAPP) of the aquatic macrophyte *Eleocharis interstincta* in response to changes in water level in the Jurubatiba (coastal) lagoon, as well as to gain a better understanding of its population biology.

2. Study area

The Jurubatiba (Cabiúnas) lagoon has an area of 0.35 km², with a high perimeter/volume ratio and a maximum depth of 3.50 m. It is located on the northern coast of the state of Rio de Janeiro, between the municipalities of Macaé and Carapebus (22° to 22°30' S and 41°30′ to 42° W). Its origin is associated with the formation of sandbars in the last oceanic regression (Esteves, 1998). Occasionally, the sandbar that separates the coastal lagoon from the ocean is opened, usually artificially with the aim of controlling the effect of floods by lowering the water level and/or allowing the entry of economically important fishes (Faria et al., 1994; Albertoni et al., 1999). The sandbar is about 20 m wide and is occasionally run over by the waves, which bring salt water into the lagoon. However, salinity in the lagoon is usually very low since the water level in the lagoon is above mean sea level. The climate of the region is subhumid/humid, with little or no water deficit, and mesothermal with the heat well-distributed throughout the year. Mean annual relative humidity is 83%. Mean annual temperature is about 22 °C, with the January (summer) mean being 25 °C, and the July (winter) mean being 19 °C. Mean annual precipitation is 1300 mm, concentrated in the spring and summer. The period with the lowest rainfall is the winter, but there is no pronounced drought. Winds are predominantly northeasterly throughout the year and to a lesser degree easterly, southeasterly, and southwesterly (Fideri, 1977).

Some Jurubatiba lagoon littoral zone areas support dense stands of *Typha domingensis* and *E. interstincta*. In the deeper parts of the littoral zone, there are some aquatic macrophytes with floating leaves, such as *Nymphaea ampla* and *Nymphoides humboldtiana* (Henriques et al., 1988).

3. Methodology

Sampling was carried out biweekly from June 1997 to June 1998 in one of the branches of the Jurubatiba lagoon. In the littoral zone, three 0.0625 m² study plots were positioned in the center of the stand, parallel to the shoreline where *E. interstincta* was the only species. In each plot, all stems were tagged with numbered plastic labels and the height of each stem (measured from the sediment–water interface to the most distal portion of the stem) was measured. Dead stems were those with less than 50% of their height constituted by chlorophyllous tissue. In each examination, every newly emerged stem in the study plots was also tagged, constituting a new cohort, which was followed until the death of all stems. Water level was measured at the same point of the study plots.

Three $0.0625 \, \mathrm{m}^2$ quadrats were harvested in the same area of the study plots during each visit to the sampling station. In the laboratory, the samples were washed with running water and separated into stems (more than 50% of the length was chlorophyllous tissue) and detritus (less than 50% of the length was chlorophyllous tissue). The stems were measured, dried one by one in ovens at $70\,^{\circ}\mathrm{C}$ over 3 days until reaching constant weight to obtain their individual biomass, expressed in grams of dry weight per square meter (g dry weight m^{-2}). With the known stem height and its respective biomass, regression equations between the natural logarithm of the biomass and the natural logarithm of the stem height for each sample date were obtained. Thus, it was possible to estimate the increase in biomass in the cohort study plots.

3.1. Calculation of NAPP

The NAPP of *E. interstincta* was calculated with the cohort data and is a modification of the summed shoot maximum (SSM) method (Dickerman et al., 1986). In each cohort, maximum biomass registered for each stem was followed, independent of the time that the maximum biomass was reached. The stem with maximum individual biomass was chosen as "maximum potential biomass", which was multiplied by the initial density of the cohort, regardless of stem mortality, since this process is continuous in tropical environments. This procedure allowed the estimate of the maximum potential biomass incorporated into each cohort, since all the stems of the cohort would potentially have the same incorporation capacity. This method assumes that there is no difference in stem genotype, i.e. individuals would be clones (ramets). Thus, the factors that could regulate the biomass incorporated into each stem (competition, mortality and herbivory) during its lifetime, would be eliminated. To calculate net annual aboveground primary productivity, the NAPP of each cohort was summed.

3.2. Herbivory

In the harvested samples, we also verified whether the stems of *E. interstincta* showed any kind of damage. Observed damage was always in the apical part of the stems, above the water line, near the inflorescence, and just half (longitudinal section) of the stem was consumed. Damage was measured, and from regression equations, it was possible to evaluate the amount of *E. interstincta* biomass lost through grazing.

3.3. Growth

The relative growth rates (RGRs) of the stems in the cohorts were obtained using the formula described by Hunt (1982):

$$RGR = \frac{\ln W_i - \ln W_{i-1}}{T_i - T_{i-1}}$$

where W_i is the mass of the stem at T_i . To verify whether there was any significant difference in the relationship between dry weight and stem height during the sampling period, the samples were compared using covariance analysis (ANCOVA). The relative growth rate (RGR) means of the cohorts were compared using one-way variance analysis (ANOVA) and the density means of the stems were compared using the non-pastemric Friedman test, at the 5% significance level.

4. Results

The water level in the Jurubatiba lagoon varied seasonally, and the water twice failed to cover the macrophyte stand during the study. The first decrease in the water level occurred naturally in September 1997 (late winter—early spring), when rainfall is lowest. The water level gradually decreased until the water failed to cover the macrophyte stand in October 1997. The second event occurred in February 1998 (summer), the normal period of peak rainfall, when an uncommon increase in regional precipitation was recorded (398.8 mm). As a consequence of the flood, which inundated streets and houses surrounding the lagoon, the sandbar separating the lagoon from the sea was artificially opened by people, without the knowledge of the local government.

Before the artificial breaching, the water level at the stand was 1.35 m, the maximum value recorded in this study. The breaching resulted in a sudden decrease in water level (as opposed to the gradual one in September 1997), again uncovering the stand. Two weeks later, the sandbar naturally re-formed and the water level began to rise gradually.

Twenty *E. interstincta* cohorts were followed from July 1997 to July 1998. In the summer, three cohorts were not followed, since it was impossible to label the stems when the water level in the stand was higher than 1 m. Significant differences between stem dry weight and stem height were detected throughout the sampling period (ANCOVA; P < 0.01). Therefore, the biomass estimates for the data sampled from the study plots were obtained with discrete equations for each sample date (Fig. 1).

The average height of the cohorts (Fig. 2) varied from 23.8 to 97.2 cm, with the shortest cohort developing at the mean lowest water level (9 cm) and the tallest cohort at the mean highest water level (76.5 cm). Stem density (Table 1) varied from 85 to 240 individuals m⁻². The highest density recorded was obtained in the cohort that grew immediately after the sandbar breaching. The mortality rate of the cohorts (Table 1) varied from 0.6 to 1.2 stems m⁻² per day. The cohort with the highest mortality rate was that selected immediately before the sandbar breaching, since this event, by reducing the water level, resulted in the mass mortality of emergent aquatic macrophytes (Palma-Silva, 1998). The mean mortality rate was 0.8 individuals m⁻² per day. The longevity of the cohorts (Table 1) varied from

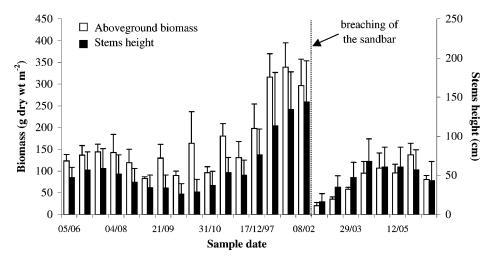


Fig. 1. Relation between stem aboveground biomass and stems height of *Eleocharis interstincta* during sampling periods (ANCOVA; P < 0.01). The bar indicates standard deviation.

112 to 163 days, disregarding those cohorts affected by the sandbar breaching, i.e. early mortality induced by reduction in water level. The cohorts with the greatest longevity were those labeled at a lower water level, following the natural reduction in water level.

The relative growth rates of the cohort stems were always higher in the first 2 weeks of life (Table 1). The peak of the aboveground biomass produced by the cohorts varied from 10.5 to 70 g dry weight m^{-2} (Table 1). The daily primary productivity values of the *E. interstincta* cohorts also showed great variability, with a minimum of 0.5 and a maximum

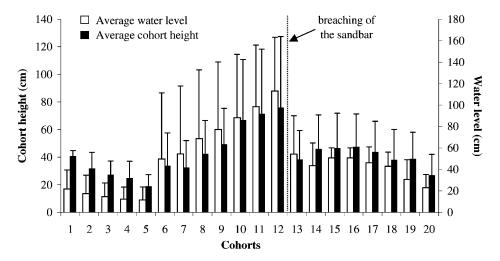


Fig. 2. Average water level and average cohorts height of *Eleocharis interstincta* during sampling periods. The bar indicates standard deviation.

Table 1 Density, longevity, maximum biomass, net aboveground primary production (NAPP), mortality and relative growth rate of *E. interstincta* cohorts in Jurubatiba coastal lagoon

Cohorts numbers	Date	Density (stems m ⁻²)	Longevity (days)	Maximum biomass (g dry wt m ⁻²)	NAPP (g dry wt m $^{-2}$ d $^{-1}$)	Mortality (% stems d ⁻¹)	$RGR (d^{-1})$
1	2 July 1997	139	120	50.2	1.4	0.9	0.13
2	18 July 1997	144	138	27.1	1.4	0.8	0.22
3	4 August 1997	155	138	25.7	1.2	0.7	0.20
4	16 August 1997	85	121	10.5	0.8	0.9	0.28
5	29 August 1997	107	106	13.1	0.7	0.9	0.23
6	21 September 1997	181	163	32.2	0.6	0.8	0.13
7	3 October 1997	149	140	62.4	1.8	0.8	0.24
8	16 October 1997	155	146	34.5	1.4	0.7	0.20
9	31 October 1997	107	123	23.3	1.1	1.0	0.24
10	17 November 1997	171	108	70.0	1.3	0.8	0.20
11	4 December 1997	149	91	65.6	1.8	1.0	0.22
12	17 December 1997	91	74	48.3	1.7	1.2	0.30
	16 February 1998	Artificial breaching of the sandbar					
13	4 March 1998	240	142	43.8	1.4	0.8	0.17
14	18 March 1998	107	126	15.9	0.5	0.9	0.26
15	29 March 1998	133	112	18.3	1.1	0.9	0.26
16	16 April 1998	91	115	16.9	0.8	0.9	0.19
17	25 April 1998	85	130	18.0	1.3	0.8	0.37
18	12 May 1998	101	120	22.8	0.8	0.8	0.18
19	9 June 1998	128	132	29.5	0.9	0.7	0.14
20	4 July 1998	112	128	22.4	0.7	0.6	0.15

The sandbar was artificially breached on 16 February 1998.

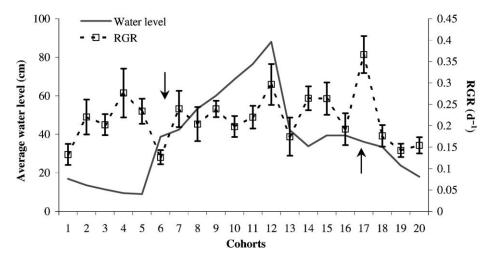


Fig. 3. Average water level and relative growth rates (RGRs) of *Eleocharis interstincta* cohorts during sampling periods. Arrows shows difference between RGRs of cohorts (numbers 6 and 17), ANOVA P < 0.001, despite the same water level. The bar indicates standard deviation.

of $1.8 \,\mathrm{g}$ dry weight m⁻² per day (Table 1). The RGRs of the *E. interstincta* cohorts did not seem to be influenced by the changes in the water level of the stand, since there was a difference in the growth rates of some cohorts, such as cohort numbers 6 and 17, when the water level was almost the same. (Fig. 3).

The amount of *E. interstincta* aboveground biomass consumed by herbivores during the sampling period was relatively low (Fig. 4). The only herbivore species observed grazing on the stems was the insect *Stenacris megacephala* (Orthoptera: Acrididae). This insect used

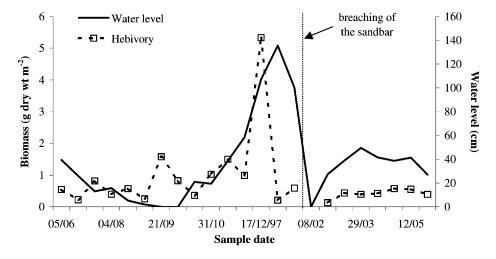


Fig. 4. Water level fluctuation and aboveground biomass of *Eleocharis interstincta* grazed by *Stenacris megacephala* during sampling periods.

E. interstincta as a feed save practically throughout the sampling period, with the exception of the period of new stem growth after the sandbar recomposition (16 February 1998).

Net annual aboveground primary production (NAAPP) of *E. interstincta* was $1012 \,\mathrm{g}$ dry weight m⁻² per year. The biomass losses from stem mortality and herbivory were 150 and $18 \,\mathrm{g}$ dry weight m⁻² per year, respectively.

5. Discussion

Santos (1999) showed that water level plays a major role in the determination of the height and therefore, of the biomass of the stems of E. interstincta. In this study, a positive correlation between cohorts average height and the mean water level was found (r=0.91, P<0.01). The seasonal variation in the water level, corresponding to a variation in the height and biomass of the stems, explains the significant difference found in the dry weight and stem height relationship throughout the sampling period. In studies involving the temporal variation of the biometric features of aquatic macrophytes, the height–dry weight relationship of the stems is often neglected, since this relationship, in most studies, is obtained with only one sampling or with a long interval between samplings which leads an unaccurated estimates of biomass. Hopkinson et al. (1980) suggested the need for different regression equations for estimating the biomass of Spartina alterniflora in length classes larger and smaller than 75 cm because the height–dry weight relationship between these two size classes was different.

After the sandbar breaching, the number of stems emerging in the study plots was the highest recorded (P < 0.05). This attests to the capacity for rapid recovery of the stand of *E. interstincta* by vegetative reproduction after a disturbance (sandbar breach). Vegetative reproduction is an important strategy in the maintenance of aquatic macrophytes species in extremely dynamic environments, such as coastal lagoons. The same phenomenon of a high stem production by vegetative reproduction after a disturbance was reported by Palma-Silva (1998), studying *Typha domingensis* in the Imboassica coastal lagoon, Rio de Janeiro.

Estimates of growth rate obtained by study plots sampling allow for a better statistical treatment (Causton, 1991), making it possible to compare results obtained in different situations. There was a significant difference between the relative growth rates of the cohorts throughout the sampling period (ANOVA, P < 0.001). The differences found in the aboveground biomass of the cohorts of E. interstincta throughout the study period indicate the variability in the responses of this species to environmental changes, especially fluctuations in water level. E. rostellata also showed differences in biomass values among three different sampling sites in the same swamp, evidence of its great adaptability (Seischab et al., 1985). Despite the methodological differences in data collection, the aboveground biomass of the cohorts of E. interstincta was relatively low compared to other species of emergent aquatic macrophytes, even within the same genus.

The NAPP of *E. interstincta* is close to that reported by Carmo and Lacerda (1984), who found a value of primary productivity of 1.7 g dry weight m⁻² per day for the aboveground portion of *E. subarticulata*. However, Palma-Silva et al. (in press) reported that the primary productivity of *E. mutata* may reach up to 18.9 g dry weight m⁻² per day, a level similar to

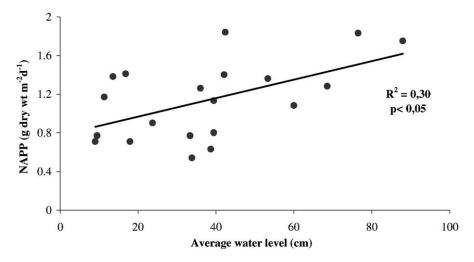


Fig. 5. Average water level and average cohorts net aboveground primary production (NAPP).

that found by Boyd and Vickers (1971) for *E. quadrangulata* (18.5 g dry weight m⁻² per day), a rate that is quite high.

Although the RGR was not influenced by water level in this study, there was a significant correlation (P < 0.05) between NAPP and mean water level (Fig. 5). This suggests that the NAPP of *E. interstincta* is determined by water level. The RGR indicates the efficiency of the plant in the production of organic matter, and *E. interstincta* was more efficient in the first 2 weeks of life. However, the RGR is not a suitable parameter for evaluating the response of the plant to environmental changes. Since, the stems must remain above the water level to obtain resources, especially light (Kissmann, 1997), the plant must invest energy in growth every time the water rises, and this investment does not necessarily occur in the first 2 weeks.

For decades, it was thought that the aquatic macrophytes were not intensively grazed because of their structure, difficult for herbivores to use, and of low nutritional quality (Lodge, 1991). Nonetheless, a recent survey by Lodge et al. (1997) showed that herbivores may reduce the abundance of freshwater plants by more than 30%, and of marine plants by more than 60%. *S. megacephala* was the only animal observed grazing on the stems of *E. interstincta*, and the grazing pressure that it causes (1.8% of the yearly biomass), does not compromise the survival of the stems, since it only grazes their tips. Coutinho (1989) observed that the leaves of *Eichhornia azurea* were also used by insects as food, especially by hymenopterans and orthopterans, which grazed up to 15% of the leaves.

6. Conclusion

The seasonal variation of the water level in Jurubatiba lagoon illustrates the statement of Panosso et al. (1998), that coastal lagoons are highly vulnerable to oscillations in environmental features. The differences found in the dry weight and stem height relationship

throughout the sampling period evidence the great adaptive ability of *E. interstincta* in the occupation of this kind of environment. The same kind of adaptation was reported in *E. rostellata* (Seischab et al., 1985). The quickly production of stems (vegetative reproduction) of *E. interstincta* that took place after the disturbance (sandbar breaching) is also an example of the adaptation of this species, ensuring its survival.

The success of *E. interstincta* in the occupation of habitats subjected to fluctuations in water level seems to be especially linked to the efficiency of the mechanisms regulating the growth of the stems, since they must remain above the water level to obtain the resources necessary for their survival, mainly gaseous exchange and light (Kissmann, 1997). The results of this study allow us to conclude that *E. interstincta* contributes to the entry and transfer of energy in the system mainly through the detritus chain (14.8% annual aboveground biomass), since only 1.8% of its annual aboveground biomass is consumed by herbivores and this entire process is water level dependent.

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