Short-term and seasonal effects of water level variations on Eleocharis interstincta (VAHL) nutrient content in a tropical coastal lagoon.

AMADO¹, A.M., ESTEVES¹, F.A., FIGUEIREDO-BARROS¹, M.P. & SANTOS¹, A.M.

¹ Universidade Federal do Rio de Janeiro, Instituto de Biologia, Departamento de Ecologia, Laboratório de Limnologia, Ilha do Fundão, Rio de Janeiro, RJ Zip Code: 21941-540; P.O.BOX: 68020, Brazil.

ABSTRACT: Short-term and seasonal effects of water level variations on Eleocharis interstincta (VAHL) nutrient content in a tropical coastal lagoon. We evaluated the influence of water level variation of a tropical coastal lagoon on the carbon, nitrogen, phosphorus and cell wall fraction contents in different structures of the aquatic macrophyte Eleocharis interstincta, in Cabiúnas lagoon (Parque Nacional da Restinga de Jurubatiba, State of Rio de Janeiro, Brazil). During the annual study, the water level decreased up to expose the sediment in the dry period and the maximum depth (141.0 cm) was registered in the rainy period. The sandbar, which separates the lagoon from the sea, was artificially breached, resulting in a sharp and rapid decrease in water level in the lagoon. After the breaching of the sandbar and the consequent water level lowering, the stems of E. interstincta died. This event strongly affected the nutrients contents, in almost all the structures of the macrophyte. In the E. interstincta studied stand all the stems died and later re-sprouted. Nitrogen and phosphorus stems contents increased significantly post-breaching (from 0.9 to 2.1 % D.W. and from 0.2 to 0.7 % D.W., respectively), while in the rhizomes accumulated nitrogen, but carbon and phosphorus did not. The N contents on detritus post-breaching increased indicating lack of leaching in the water abscence. We conclude that events capable of defining states of growth and death of stems of E. interstincta can regulate the N and P contents in the stems. The absence of water may reduce the process of leaching decreasing the C:N ratio, altering the nutritional quality of the detritus of E. interstincta and the decomposition processes. The rhizome was shown to be capable of supplying the large demand for N and P, after a stress event, reconstituting the population even in an oligotrophic, phosphorus-poor environment.

Key-Words: Aquatic Macrophytes, Water Level Changes, Nutrients Stoichiometry, Coastal Lagoon, Human Impacts.

RESUMO: Efeitos de variações rápidas e variações sazonais do nível d'água no conteúdo de nutrientes de Eleocharis interstincta (VAHL) em uma lagoa costeira. Foram avaliados os efeitos da variação do nível d'água sobre o conteúdo de carbono, nitrogênio, fósforo e fração de parede celular em diferentes estruturas da macrófita aquática Eleocharis interstincta, na lagoa Cabiúnas (localizada no Parque Nacional da Restinga de Jurubatiba, no estado do Rio de Janeiro, Brasil). Durante o estudo anual, o nível d'água diminuiu até expor o sedimento no período de estiagem e a profundidade máxima (141,0 cm) foi atingida no período chuvoso. A barra de areia, que separa a lagoa do oceano, foi artificialmente aberta e esse episódio causou uma rápida redução no nível d'água da lagoa. Essa brusca alteração ocasionou a morte e rebrotamento de todos os indivíduos de E. interstincta, promovendo o incremento da concentração de nitrogênio e fósforo nos caules (de 0,9 para 2,1 % PS. e 0,2 para 0,7 % PS., respectivamente) e apenas nitrogênio nos rizomas. O conteúdo de nitrogênio também sofreu incremento no detrito sugerindo que a ausência de coluna d'água reduziu o processo de lixiviação. Podemos concluir que eventos, como a abertura de barra, capazes de regular os estágios de crescimento e morte de uma população de E. interstincta afetam as concentrações de nitrogênio e fósforo. A exposição do sedimento (ausência de água) pode reduzir

o processo de lixiviação do detrito da macrófita promovendo o decréscimo da razão C:N, alterando a qualidade nutricional dos mesmos e o processo de decomposição. O rizoma mostrou-se capaz de suprir grande demanda de nitrogênio e fósforo após um evento de estresse, reconstituindo a população mesmo em um ambiente oligotrófico e pobre em fósforo.

Palavras-chave: Macrófitas aquáticas, variações de nível d'água, estequiometria de nutrientes, lagoas costeiras, impactos antrópicos.

Introduction

Aquatic macrophytes play an important role in nutrient cycling and productivity in coastal lagoons (Knoopers, 1994). These shallow environments have broad littoral zones, an ideal habitat for macrophytes. Besides their high productivity, these organisms participate in nutrient recycling, working as a link between the ecosystem compartments (sediment **@** water column), via herbivory or detritus food chain (Wetzel, 1969).

Many studies have shown that aquatic macrophytes developed anatomical, physiological and chemical adaptations to abrupt changes in water level (Froend & MacComb 1994). Menezes et al. (1993) concluded that the change in water depth determines an increase in productivity as well as changes in biomass of the aquatic macrophytes Nymphoides indica and Pontenderia cordata. These changes were observed during a superficial breaching at the dam zone of a reservoir, which caused a rapid change in water depth. Camargo & Esteves (1996) showed the influence of nutrient availability and changes in water level on the morphology and nitrogen and phosphorus contents in the floating aquatic macrophyte Eichhornia azurea in an oxbow lake. Enrich-Prast et al. (2002) suggested that the aquatic macrophyte Oryza glumaepatula presents different contents of carbon, nitrogen and phosphorous in the distinct hydrological phases of the flood pulse in Lake Batata (Amazon basin). Studies focusing on the nutrient contents of different organs of aquatic plants are, then, important for better understanding in the nutrients cycle through aquatic ecosystems.

Coastal lagoons are vulnerable to changes in climatic factors, and undergo changes in water level according to local precipitation regime (Panosso, 1998). Abrupt changes in the water level by human interference are usually common. People can artificially breach the sandbar of the coastal lagoons, draining most of the water to the ocean. In a one year study period, we evaluated the total carbon (C), total nitrogen (N), total phosphorous (P) and the cell wall fraction (CWF) contents in the aquatic macrophyte Eleocharis interstincta (VAHL) after short term and seasonal changes of water level, in a tropical coastal lagoon.

Study Area

This study was carried out in Cabiúnas Lagoon, located in Parque Nacional da Restinga de Jurubatiba (50'S, 44°42'W), 190 km north of the city of Rio de Janeiro, in the municipality of Macaé (Fig. 1). The regional climate is warm-humid, and the annual mean temperature varies between 18.7 °C and 27.4 °C. Mean annual relative humidity is 83%, and annual rainfall is 1,300 mm with well-defined dry (from April to August) and rainy (from September to March) seasons (Fiderj, 1977). The seasonal water level variation is mainly influenced by the local rainfall and the lagoon presents the highest depths from November to March. Cabiúnas Lagoon was formed by the damming of Cabiúnas River by a layer of marine and riverine sediments after the ocean retreated. That damming is occasionally opened to the ocean by natural causes or local residents in case of flooding. Those events cause short term reduction of water level (a rapid depth decrease according to Santos & Esteves 2002). The surface area is about 0.35 km² and its maximum depth 3.5 m, with a high perimeter/surface ratio (Esteves, 1998). The littoral zone of the lagoon is densely colonized by aquatic macrophytes, mainly Typha domingensis, E. interstincta and Potamogeton stenostachys.



AMADO, A.M. et al. Short-term and seasonal effects of water level variations...

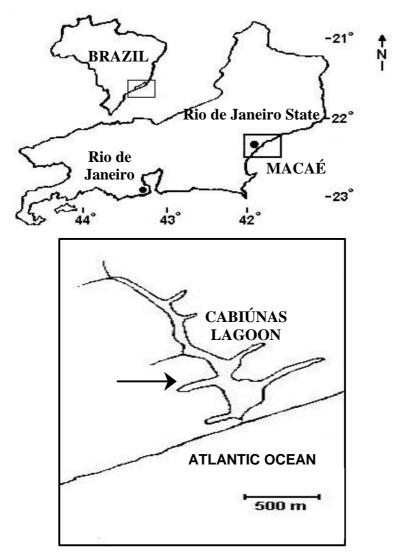


Figure 1: Geographical Location of Cabiúnas Lagoon. The arrow indicates the sampling area.

Material and methods

Samplings were made in a monospecific stand of E. interstincta, between July 1997 and June 1998 (with the periodicity of 15 days). Three quadrats (0.0625 m^2) were harvested into the macrophyte stand. The water depth in each quadrat was also measured. The samples were separated into living stems, detritus (<50% green) and rhizomes (till 20 cm deep in sediment). Plant materials were oven-dried at 70 °C for 3 days and then, triturated for chemical analysis. Total Carbon was measured with a carbon analyzer (TOC 5000-Shimadzu); Total nitrogen by the Kjeldahl method (Allen et al., 1974) and Total phosphorus by the acid-digestion method (Fassbender, 1973) and percent of cell wall fraction (CWF) in the stems by solubilizing the protoplasmic compounds (Van Soest & Wine, 1967). The results are reported as percent dry weight (% D.W.) for all samples. The C:N and C:P molecular ratios were computed for the three studied structures of the aquatic macrophyte in each phase. We compared the means between phases by ANOVA (p < 0.05), that was separated by a Tuckey post-hoc test.

93

Results

94

The water level in Cabiúnas Lagoon varied seasonally according to Fig. 2 (also described by Santos & Esteves, 2002). In this paper, according to the water level variation regime, we considered, for the analysis, three different periods: (1) a dry period (including three samplings in August and October/1997), (2) a flood period (including three samplings between January and February/1998) and (3) the drained event (two samplings in March/1998). The two first periods are natural and seasonal events while the last is an artificial short-term episode. During the dry period no standing water occurred in the sampling site and in the flood period (398.8 mm total precipitation) the column depth attained a maximum depth (141.0 cm depth). Those natural variations occurred seasonally during months. As a result of the floods, the lagoon expanded the surface area. To alleviate flooding, local residents connected the lagoon to the sea (February, 16th, see Fig. 2), excavating the sand bar that separates both. This action drained the lagoon causing a rapid decrease of the water column (the drained period). Different from the first dry period, the water level decreased to zero in about 1 or 2 days. After two weeks, the sandbar re-formed naturally and the lagoon gradually filled.

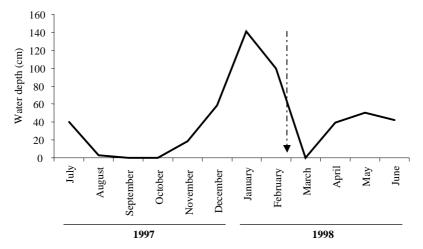


Figure 2: Water depth variation in Cabiúnas Lagoon during the sampling period. The arrow indicates the location of the sandbar breach.

The C content varied between 41.0 and 42.0 % DW (Fig. 3a) and the N content between 0.9 and 2.1 % DW (Fig. 3d), while P varied between 0.2 and 0.7 % DW in the stems (Fig. 3g). The C, N and P content of the stems was considered similar comparing the natural dry and the flooded periods. However, comparing the data of these two periods with the draining episode, after the sandbar breach, N, P and CWF contents in the stems increased significantly (p < 0.05; from 0.9 to 2.1 % D.W. and 0.2 to 0.7 % D.W. respectively; Fig. 3d, 3g and Fig. 4) while the carbon contents in the same structure were not significantly different (Fig. 3a).

In rhizomes the C content varied between 42.0 and 44.5 % DW (Fig. 3b) while N and P varied between 0.6 and 0.9 % DW and 0.15 and 0.25 % DW (Figs. 3e and 3h, respectively). No significant difference on the total carbon and total phosphorous contents was detected in the rhizomes sampled in the three periods (Fig. 3b and 3g) while total nitrogen presented higher values (p < 0.05) only in the drained phase (Fig. 3e). Similar pattern can be observed for the dead stems (detritus). But, total N showed higher values (p < 0.05) for the drained period (Fig. 3c, 3f and 3i). The carbon content in the detritus varied between 41.0 and 44.0 % DW (Fig. 3c) while N and P varied between 0.6 and 0.8 % DW (Fig. 3f) and 0.1 % DW respectively (Fig. 3i).

AMADO, A.M. et al. Short-term and seasonal effects of water level variations...

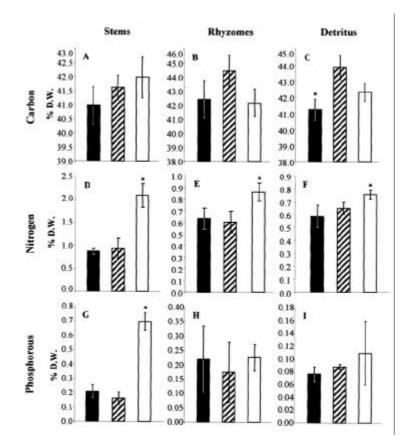


Figure 3: Carbon contents at the stems (A), rhizomes (B) and detritus (C); Nitrogen contents at the stems (D), rhizomes (E) and detritus (F) and Phosphorous contents at stems (G), rhizomes (H) and detritus (I) of E. interstincta in the dry (■), flood (□) and drained periods (□) (The asterisk indicate the statistical differences (p < 0.05) according to Tuckey post hoc test; the errors bars indicate the standard deviation, note differences in scales).</p>

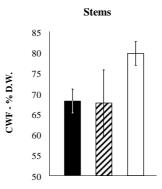


Figure 4: Cell wall fraction contents in the stems of E. interstincta in the dry period (), flood period () and drained period (). (The asterisk indicate the statistical differences, p < 0.05; according to Tuckey post hoc test; the errors bars indicate the standard deviation).

In the three morphological structures of the plant, the molecular C:N ratio was lower at the drained period when comparing the dry and flood periods (Tab. I). In the stems, the ratio in dry and flood periods was about two fold of the drained period. In the rhizomes the ratio reduced to about 46 % from dry and flood periods to the drained one. Finally,

Acta Limnol. Bras., 17(1):91-99, 2005

95

the C:N ratio recorded for detritus at the dry and flood periods was about 24 % higher than in drained period (Tab. I). As the C:N ratio, the molecular C:P ratio in the stems was also considered lower in the drained period (Tab. I). These values fell about five fold from flooded period to the drained one. The C:P ratios in the other organs did not change between periods (Tab. I).

Table I: C:N and C:P molecular ratios (mean values; in parenthesis the standard deviation) in the different structures of the aquatic macrophyte E. interstincta in three different periods: Dry (August-October/ 1997), Flood (January-February/1998) and Drained (March/1998 – after the breaching of the sandbar) periods.

Plant structures	Ratios	Periods		
		Dry	Flood	Drained
Stems	C:N	55:1 (4.12)	54:1 (13,57)	24:1* (2.75)
	C:P	545:1 (84.66)	710:1 (184.17)	157:1* (16.25)
Rhizome	C:N	77:1 (5.12)	88:1 (13.23)	56:1* (3.41)
	C:P	531:1 (177.64)	939:1 (634.20)	501:1 (130.00)
Detritus	C:N	83:1 (13.03)	79:1 (6.74)	65:1* (2.25)
	C:P	1547:1 (247.13)	1301:1 (71.97)	1227:1 (744.68

* (p<0.05)

Discussion

In dry and flooded periods no clear pattern was evidenced for carbon, nitrogen and phosphorous concentrations at all structures of E. interstincta (Fig. 3). For the aquatic macrophyte Oryza glumaepatula of an Amazonian oxbow lake in Brazil, Enrich-Prast et al. (2002) observed that with a 7 meters variation, the C, N and P contents decreased. In contrast, the abrupt draining of the coastal lagoon caused an increase of ca. 100% and 200% in total N and total P of E. interstrincta stems (Figs. 3d and 3g). This event resulted in the death of most of the plant population and was followed by an extensive resprouting of the stems resulting in an extremely high density of stems/m². At the drained period, the stems were in beginning stages of development, which differed from the preceding samples. According to Enrich-Prast et al. (2002), emergent macrophytes usually increase the carbon content as investment in supporting structures. Despite the fact that the total carbon did not change in the drained period, the CWF increase (Fig. 4) at this time was an evidence of the investment in supporting tissues during the episode of sediment exposition (terrestrial conditions).

The increase in total N and total P in the stems after draining can be explained by the fact that the tissues of re-sprouted plants will have fatally higher concentrations of N and P compared to the old plants sampled in October and February. Similarly, Furtado & Esteves (1996) showed that young plants of T. domingensis and E. fistulosa presented higher total N and total P contents when compared to older plants. Mason & Bryant (1975) recorded the highest concentrations of total N in Phragmites communis and T. angustifolia early in the growing season. Boyd & Vickers (1971) also reported for E. quadrangulata tissue, that concentrations of nitrogen, phosphorus, potassium, sodium, zinc, boron and copper declined as plants aged.

The lowest C:N ratio value in the drained period results from that highest nitrogen value. According to Carneiro et al. (1994), the lowest C:N ratio values are related to the initial development stages of the plant, in agreement with the findings of the present study (Tab. I). The lower C:P ratio in the stems of E. interstincta was consistent with this pattern (Tab. I). According to the growth rate hypothesis (Elser et al., 2000; 2003), the growing phases of organisms contain higher amounts of N and P, due to large amounts of ribossomal RNA (rRNA; P-rich) in the cells for protein transcription and also to the large protein (N-rich) contents (proteins being generated). Apparently, besides the large variation



AMADO, A.M. et al. Short-term and seasonal effects of water level variations...

in the C, N and P composition of vascular plants, this hypothesis may also be confirmed for E. interstincta. At the drained period, all live stems were in a young stage (the oldest stems of at least 2 weeks) and the C:N and C:P were higher than the other two periods (when the material was composed by organisms of different ages). This pattern was observed in temperate lakes (wide temperature variation) and ecosystems subjected to great water level variation (Westlake, 1966; Enrich-Prast et al., 2002). Those variations can define seasons of growth and death of macrophytes, synchronizing the age of all shoots.

Total N in rhizomes presented similar contents in both natural periods (dry and flood). On the other hand the N content was higher in drained period (Fig. 3e). This may be related to the death of all the stems caused by this event. In this case, the rhizome, as a storage organ, may have been stocking nitrogen for subsequent recolonization. Harrison & Mann (1975) suggested that aquatic macrophytes may translocate (from dead leaves and/or dead stems) and stock some nutrients in rhizomes, as investment for the growing season. This evidence is clear when comparing the C:N ratio in rhizomes in drained period with the other two periods, when these values are higher (Tab. I). Furtado & Esteves (1996) described that the rhizomes of E. fistulosa and T. domingensis are storage organs for nutrients. Boyd & Vickers (1971) reported that the rate of absorption of some nutrients, especially nitrogen, phosphorus and potassium by emergent aquatic macrophytes, is higher during the growing season, and that these nutrients are those which may limit the growth of the plants. However, the total P content was not similar to nitrogen and did not increase in rhizomes in drained period. Since phosphorous is not readily available in the sediment of Cabiunas lagoon (Petrucio & Faria, 1998), rhizomes could not rapidly stock it, taking into account the stems demand.

Studies on emergent aquatic macrophytes in the temperate zone have shown that large quantities of nutrients in the tissues of senescent plants are rapidly released to the environment through leaching (Mason & Bryant, 1975). According to Godshalk & Wetzel (1978), leaching of aquatic macrophytes releases large quantities of soluble carbohydrates and compounds of nitrogen and phosphorus. In this study we can note that the total C, N and P are slightly lower in detritus than in live stems in the dry and flood periods. However, in the drained period we observed a higher value of total N in dead stems, which is comparable to total N in the live stems in both dry and flood periods (Figs. 3d and 3f). Thus, leaching was less effective during the drained period. As described above, phosphorous is not so abundant in Cabiúnas lagoon. Thus, it may suggests that phosphorus was not abundantly available for the detritus chain because of translocation to living parts. As a result of the low leaching, the C:N ratio of detritus in the drained period is lower than in the others (Tab. I). Therefore, the nutritional quality of the dead stems remained relatively high (Enriquez et al., 1993).

Conclusion

We conclude that the range of natural and seasonal variations in the water level of Cabiúnas Lagoon produced no significant differences on the concentrations of carbon, nitrogen, and phosphorus in the three studied structures of E. interstincta. However, the wide variation in water level, changing the sampling site from aquatic to terrestrial condition, may change the fraction of the cell wall contents of E. interstincta.

The breaching of the sandbar of a coastal lagoon can regulate the growth and death seasons of the stems of E. interstincta, with changes in the concentrations of nitrogen and phosphorus in stems and, on the nutritional quality of the detritus. The rhizomes supplied the high demand for nitrogen and phosphorus necessary to restore the stand following the disturbance, even in an oligotrophic, phosphorus-poor environment.

Acknowledgements

The authors are grateful to PETROBRAS, CNPq, FINEP for the financial support. Dr. Vinicius Farjalla, Dr. João Leal, Dr. Sidnei M. Thomaz, Dr. Alex E. Prast, Dra. Janet Reid, Dr.

David Biesboer, Valéria M. Amado, Dr. Raoul Henry and two anonymous reviewers made invaluable contributions to the improvement of the this paper.

References

- Allen, S.E., Grimshaw, H.M., Parkinson, J.A. & Quarmby, C. 1974. Chemical analysis of ecological materials. Blackwell Scientific Publications, Oxford. 565p.
- Boyd, C.E. & Vickers, D.H. 1971. Relationships between production, nutrient accumulation, and chlorophyll synthesis in an Eleocharis quadrangulata population. Can. J. Bot., 49:883-888.
- Camargo, A.E.M. & Esteves, F.A. 1996. Influence of water level variation on biomass and chemical composition of the aquatic macrophyte Eichhornia azurea (Kunth) in an oxbow lake of the Rio Mogi-Guaçu (São Paulo, Brazil). Arch. Hydrobiol., 135:423-432.
- Carneiro, E.R.M., Azevedo, C., Ramalho, N.M. & Knoopers, B. 1994. A biomoassa de Chara hornemannii em relação ao comportamento físico químico da lagoa de Piratininga (RJ). An. Acad. Brás. Cienc., 66:213-222.
- Elser, J.J.K., Acharya, M., Kyle, J., Cotner, W., Makino, T., Markow, T., Watts, S., Hobbie, W., Fagan, J., Schade, J. & Sterner, R.W. 2003. Growth rate-stoichiometry couplings in diverse biota. Ecol. Lett., 6:936-943.
- Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., Harrison, J.F., Hobbie, S.E., Odell, G.M. & Weider, L.J. 2000. Biological stoichiometry from genes to ecosystems. Ecol. Lett., 3:540-550.
- Enrich-Prast, A., Esteves, F.A., & Breves, A.B. 2002. Variation of biometric parameters and C, N and P concentrations of Oryza glumaepatula at different depths of an Amazonial lake impacted by bauxite tailings (Lake Batata, Pará Brazil). Braz. J. Biol., 62:85-92.
- Enriquez, S., Duarte, C.M. & Sand-Jensen, K. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P Content. Oecologia, 94:457-471.
- Esteves, F.A. 1998. Lagoas Costeiras: origem, funcionamento e possibilidades de manejo. In: Esteves, F. A. (ed.) Ecologia das Lagoas Costeiras do Parque Nacional da Restinga de Jurubatiba e do Município de Macaé (RJ). NUPEM-UFRJ, Rio de Janeiro. p.63-87.
- Fassbender, H.W. 1973. Simultane P-Bestimmung in N-Kjeldahl-aufschluß von Bodenprobrn. Die Phosphorsaure, 30:44-53.
- FIDERJ. 1977. Estudos para o planejamento ambiental. Fundação Instituto de Desenvolvimento Econômico e Social do Rio de Janeiro, Rio de Janeiro. 67p.
- Froend, R.H. & McComb, A.J. 1994. Distribution, productivity and reproductive phenology of emergent macrophytes in relation to water regimes at wetlands of south-western Australia. Aust. J. Mar. Freshwater Res., 45:1491-1508.
- Furtado, A.L.S. & Esteves, F.A. 1996. Organic Compounds, Nutrients and Energy of Two Tropical Aquatic Macrophytes. Braz. Arq. Biol. Tecnol., 39:923-931.
- Godshalk, G.L. & Wetzel, R.G. 1978. Decomposition of aquatic angiosperms. I. Dissolved Components. Aquat. Bot., 5:281-300.
- Harrison, P.G. & Mann, K.H. 1975. Detritus formation from eelgrass (Zostera marina L.): The relative effects of fragmentation, leaching and decay. Limnol. Oceanogr., 20:924-934.
- Knoopers, B. 1994. Aquatic primary production in coastal lagoons. In: Kjerfve, B. (ed.) Coastal lagoon process. Elsevier, Amsterdam. p.243-286. (Elsevier oceanography series, 60).
- Mason, C.F. & Bryant, R.J. 1975. Production, nutrient content and decomposition of Phragmites communis Trin. and Typha angustifolia L. Aust. J. Ecol., 63:71-95.
- Menezes, C.F.S., Esteves, F.A. & Anesio, A.M. 1993. Influência da variação artificial do nível d'água da represa do Lobo (SP) sobre a biomassa e produtividade de Nymphoides indica (L.) O. Kuntze e Pontederia cordata L. Acta Limnol. Bras., 4:163-172.
- Panosso, R.F., Attayde, J.L. & Muehe, D. 1998. Morfometria das lagoas Imboacica, Cabiúnas, Comprida e Carapebus: implicações para seu funcionamento e manejo. In: Esteves, E.A. (ed.) Ecologia das Lagoas Costeiras do Parque Nacional da Restinga de Jurubatiba e do Município de Macaé (RJ). NUPEM-UFRJ, Rio de Janeiro. p.91-108.
- **98** AMADO, A.M. et al. Short-term and seasonal effects of water level variations...

- Petrucio, M.M. & Faria, B.M. 1998. Concentrações de carbono orgânico, nitrogênio total e fósforo disponível no sedimento das lagoas Cabiúnas e Comprida. In: Esteves, F.A. (ed.) Ecologia das Lagoas Costeiras do Parque Nacional da Restinga de Jurubatiba e do Município de Macaé (RJ). NUPEM-UFRJ, Rio de Janeiro. p.135-144.
- Santos, A.M. & Esteves, F.E. 2002. Primary production and mortality of Eleocharis interstincta in response to water level fluctuations. Aquat. Bot., 74:189-199.
- Van Soest, P.J. & Wine, R.H. 1967. Use of Detergents in the analysis of fibrous feeds. IV. Determination of plant cell-wall constituents. J. AOAC, 50:50-55.
- Westlake, D.F. 1966. The biomass and productivity of Glyceria maxima. I. Seasonal changes in biomass. J. Ecol., 54:745-753.
- Wetzel, R.G. 1969. Excretion of dissolved organic compounds by aquatic macrophytes. Bioscience, 19:539-540.

Received: 28 May 2004 Accepted: 12 January 2005