The aerobic and anaerobic decomposition of Typha domingensis Pers.

CUNHA-SANTINO[1], M.B. & BIANCHINI JR.[2], I.

[1] Programa de Pós-Graduação em Ecologia e Recursos Naturais

[2] Departamento de Hidrobiologia e PPG. Ecologia e Recursos Naturais, Universidade Federal de São Carlos. Via Washington Luiz, km 235. Cx. Postal 676. 13565-905. São Carlos, SP, Brasil. e-mail: pmbc@iris.ufscar.br; irineu@power.ufscar.br

ABSTRACT: The aerobic and anaerobic decomposition of Typha domingensis Pers. The aim of this study is to compare the kinetics of decomposition of Typha domingensis Pers. The samples of aquatic macrophyte and water were collected in the Paranapanema River (22° 56' 36.3" S and 50° 27' 57.3" W); São Paulo State, Brazil. The plant material was oven-dried and triturated and for each experimental condition (aerobic and anaerobic); 10 mineralization chambers were prepared with plant fragments and river water. On sampling days the particulate (POM) and dissolved organic matter (DOM) were quantified. Additionally, two chambers were prepared to monitor the volume of produced gases in anaerobic mineralization; two others were prepared to register the oxygen consumption in the aerobic mineralization. The results indicate that the decomposition of Typha domingensis is more efficient with regard to aerobic conditions. In this context, according to decay coefficient (k_T) the aerobic processes were 2-fold faster than anaerobic. It is assumed that the fractions responsible for the high k_D (deoxygenation rate constant) have reduced periods of half-time, and therefore do not accumulate in the ecosystems. The aerobic decay of T. domingensis can promote moderate depletion in the dissolved oxygen budget within aquatic environments. Due to k_T magnitude (half-time ($t_{1/2}$) = 141 to 238 days), the fibrous debris of this plant (i.e. refractory fractions) associated with the appropriate values of pH and oxi-reduction potential, can contributed to the gas production and storage of particulate organic matter in sediment.
Key words: decomposition, aquatic macrophytes, oxygen consumption, kinetic model, mineralization.

RESUMO: Decomposição aeróbia e anaeróbia de Typha domingensis Pers. Este estudo visou comparar as cinéticas de mineralização de Typha domingensis Pers. Foram coletadas amostras de macrófita aquática e água do Rio Paranapanema (22° 56' 36,3"S e 50° 27 ' 57,3" W); Estado de São Paulo, Brasil. O material vegetal foi seco e triturado; para cada condição experimental (aeróbia e anaeróbia), 10 câmaras de mineralização foram preparadas com fragmentos de plantas e água do rio. Nos dias de amostragem, os teores de matéria orgânica particulada (MOP) e dissolvida (MOD) foram quantificados. Adicionalmente, duas câmaras foram preparadas para monitorar o volume de gases produzidos na mineralização anaeróbia; dois outros frascos foram preparados para registrar o consumo de oxigênio durante a mineralização aeróbia. Os resultados indicaram que a decomposição de Typha domingensis foi mais eficiente sob condições aeróbias; com base no coeficiente de perda de massa (k_T), os processos aeróbios foram cerca de duas vezes mais rápidos que os anaeróbios. As frações responsáveis pelos coeficientes de desoxigenação elevados apresentam reduzido tempo de meia-vida, e assim não se acumulam nos ecossistemas. A mineralização aeróbia de T. domingensis tende a promover uma moderada depleção no balanço das concentrações de oxigênio dissolvido e da adução de gases dos ambientes aquáticos. Devido à magnitude de k_T (tempo de meia-vida ($t_{1/2}$) = 141 a 238 dias), os detritos fibrosos dessa planta (i.e. frações refratárias), associados com o pH e o potencial de oxi-redução, podem contribuir efetivamente para a produção de gases e armazenamento de MOP nos sedimentos.
Palavras-chave: decomposição, macrófitas aquáticas, consumo de oxigênio, modelo cinético, mineralização.

Introduction

The growth of aquatic macrophytes in tropical aquatic systems is favored by high temperatures and intense solar radiation (Junk & Piedade, 1993); under such conditions, the higher rates of primary

production of macrophytes maintained the cycling and the energy flow of several aquatic ecosystems (Schlickeisen et al., 2003). When primary production overcomes herbivory the exceeding photosynthetic biomass is channeled through the detritus food web (Kuehn et al., 1999).

Essentially, the dynamics of the detritus is due to decomposition, which is an intricate process that is regulated by external factors, such as nutrient concentration (López et al., 1998), pH variation (López-Archilla et al., 2001), temperature (Mendelssohn et al., 1999), electron acceptor (Cunha-Santino & Bianchini Jr., 2002). The decomposition of macrophyte detritus is also dependent on the molecular composition of tissues that are constituted by lignocellulosic compounds (i.e. particulate organic matter, POM), soluble organic (dissolved organic matter, DOM) and inorganic compounds (Little, 1979; Henry-Silva et al., 2001) and on microbial metabolism. The POM and DOM enters the pool of detritus after senescence and death of macrophyte. Metabolism associated with POM and DOM provides essential energy for the operation and metabolic stability of the entire ecosystem (Wetzel 1995). During degradation, the POM is processed at different rates; in general, the detritus that accumulate in the sediments basically are constituted by lignocellulosic compounds. As POM and DOM detritus undergoes degradation, liberation of nutrients and organic matter occurs increasing the oxygen demand due to metabolic process. Microorganisms mediate decomposition by utilizing a wide variety of organic compounds under diverse environmental conditions, extracting energy from organic compounds by fermentation, anaerobic and aerobic respiration. Overall, the decomposition is an important process to aquatic systems once it affects the release rate of nutrients, the accumulation rate of litter in sediments and the state or quality of detritus.

Considering the importance of decomposition process to cycling in aquatic ecosystems, the aim of this work is to describe and discussing the kinetics of decomposition of an emergent aquatic macrophyte, Typha domingensis, under laboratory conditions in respect to oxygen availability. The processes were modeled mathematically with an iterative procedure that associates aspects of forcing functions of the natural systems (i.e. aerobic and anaerobic condition) and the dominant specie (T. domingensis) found in the studied area with kinetics equations. The adopted decay model evaluates the rates which nutrients and carbon from T. domingensis are cycled.

Material and methods

Sampling procedures and experimental design

Samples of entire plant parts (leaves, culms and roots) were collected on April, 1998 from the floodplain of Paranapanema River, municipal district of Cândido Mota (22° 56' 36.3" S and 50° 27' 57.3" W), São Paulo State, Brazil (Fig. 1). In the laboratory, the plants were washed with tap water and distilled water to remove the coarse material (e.g. periphyton, sediment particles), and then oven-dried (45 °C), fragmented (size ca. 1.5 cm) and homogenized according to proportional parts of each morphological structure. The carbon contents of plant material were quantified using a Carlo Erba CHN elemental analyzer (model EA1110). The water samples used in the assays were collected on June, 1998 and brought immediately to the laboratory to set up the incubations. Decomposition chambers (n = 20) were prepared in the laboratory; 10 were maintained under aerobic conditions (with continuous filtered air bubbling) and 10 under anaerobic conditions. In each chamber 4.0 g (on dry weight basis; DW) of plant fragments were added to 400.0 ml of river water that had been previously filtered in glass wool. The flasks were maintained in the dark and at room temperature (23.3 ± 1.8°C). Based on the kinetics of oxygen consumption described for T. domingensis (Brum et al., 1999) and on the maximum amount of available dissolved oxygen in each chamber (ca. 3.40 mg = $(OD)_{sat}$ X, 0.4 L; where $(OD)_{sat}$ at 23.3 °C ca. 8.50 mg L^{-1}), the mixtures were considered to become anaerobic 4 h after adding the plant fragments to river water. The flasks used for evaluation of anaerobic decay were maintained closed and were opened on the sampling days.

Periodically, during 120 days, the material of a flask for each condition (aerobic and anaerobic) was fractionated into particulate (POM) and dissolved (DOM) organic matter by pre-filtration and

centrifugation (1 h; 978 g). POM samples were oven-dried at 45 °C until reaching constant weight, and their final masses were determined by gravimetric method. Aliquots of 250 ml of DOM were dehydrated at 45 °C and their final masses were also determined by gravimetric analysis (Wetzel & Likens, 1991). The total inorganic material (TIN) derived

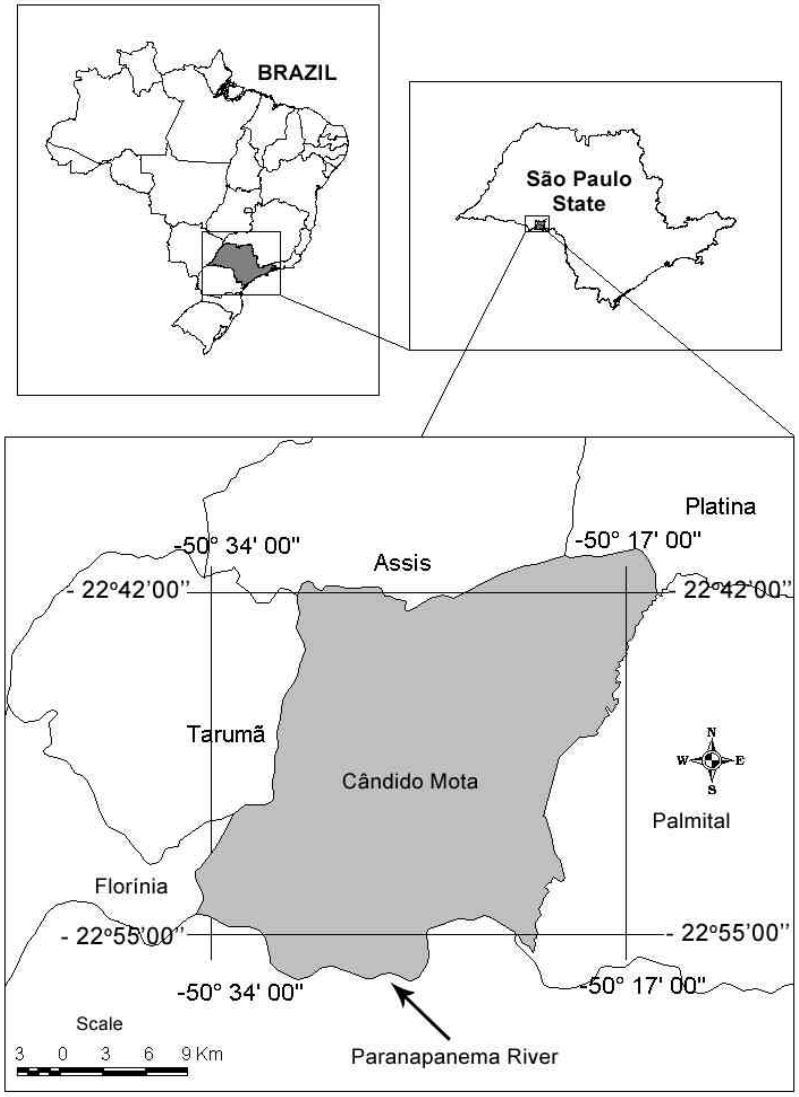

Figure 1: Paranapanema River in the district of Cândido Mota.

from organic matter mineralization was calculated by the difference between the initial contents of the plant fragments (TOM = total organic material ca. 4.0 g DW) and the remaining organic matter determined on the sampling days (POM + DOM). The optical density was measured as absorbance (optical path length: 1 cm, wavelength: 450 nm) using a spectrophotometer (Pharmacia LKB, model Novaspec II). The pH values were determined with the potentiometric method (Digimed model DMPH2) and the electrical conductivity (EC) was measured with a conductivity meter (Digimed, model DM 3).

In parallel, two chambers were prepared to monitor the formation of gases inherent in the anaerobic decomposition processes, according to the manometric method proposed by Sorokin & Kadota (1972). These incubations were prepared by the addition of 5.0 g (DW) of plant fragment in 1 L of river water. The chambers were maintained for 167 days at 23.7 ± 1.4 °C, in the dark and under anaerobic conditions. In these chambers, the temperature and the volumes of gases were recorded daily, with a mercury thermometer and a low pressure manometer (connected to the flasks). After each measurement the flasks were depressurized.

In order to measure the oxygen uptake in aerobic mineralization, 200 mg (DW) of plant fragments (size of ca. 1 cm) were

placed in duplicate in acid-washed 1-L flasks with river water, according to the experimental procedures proposed by Bianchini Jr. et al. (2003). The incubations were maintained under aerobic conditions in the dark at a 20.4 ± 1.0 °C. To establish the aerobic condition, in the beginning of the experiment the incubations were oxygenated (1 h), to keep dissolved O_2 near saturation. After oxygenation, the dissolved oxygen (DO) was measured with an ODmeter (Yellow Spring Instruments; model 58; precision 0.03 mg L^{-1}). During sampling days whenever the DO concentrations reached 2.0 mg L^{-1}, the chambers were oxygenated again, in a procedure that was adopted to ensure the aerobic condition. The oxygen consumption was estimated during 60 days. On the samples days, the pH (Digimed; model DMPH2) and electrical conductivity were also measured (Digimed; model DM3). In these incubations the total concentration of dissolved inorganic compounds (DIN) was estimated from standard curves made with electrical conductivity and NaCl solution. To remove the background DO consumption and of DIN concentration, two blank flasks (only with river water) were also incubated.

Decomposition kinetics of the detritus

A single exponential decay was used to describe the decomposition processes (Equation 1) as used by Kuehn & Suberkropp (1998) and Gamage & Asaeda (2005). The fittings were performed using nonlinear regressions (iterative algorithm of Levenberg-Marquardt), following Press et al. (1993).

$$POM = POM_i \times e^{-k_T t} \qquad (1),$$

where: POM = amount of particulate organic matter in time (%); POM_i = initial amount of particulate organic matter; k_T = global decay rate of POM (day^{-1}); t = time (day).

The kinetics of oxygen consumption during mineralization

The experimental procedures used to measure the oxygen consumption from mineralization of T. domingenses were similar to those adopted in BOD tests (Cunha-Santino & Bianchini Jr., 2003). Using a nonlinear method (Levenberg-Marquardt iterative algorithm; Press et al., 1993) the results were fitted to 1st order kinetics model (Equation 2), where the deoxygenation coefficient (k_D) and the total amount of consumed oxygen were estimated (OC_{max}).

$$OC = OC_{\max} \times (1 - e^{-k_D t}) \qquad (2),$$

where: OC = accumulated consumed oxygen (mg.g^{-1} detritus (DW)); OCmax = total amount of consumed oxygen (mg g^{-1} detritus DW); k_D = deoxygenation rate constant (day^{-1}); t = time (day).

The temporal variations of the O/C stoichiometry (ratio of consumed oxygen and oxidized carbon) were calculated by the ratio between the daily rates of consumed oxygen (dOC/dt) and the oxidized organic matter (on carbon basis). The variations of DIN concentration were fitted to 1st order kinetic model (Equation 3) that considers two phases: the formation (e.g. leaching of inorganic elements and mineralization) and consumption (e.g. biological uptake) processes. The fittings were performed using nonlinear regressions (iterative algorithm of Levenberg-Marquardt), following Press et al. (1993).

$$DIN = LSPOM \times \frac{k_F}{k_C - k_F}(e^{-k_F t} - e^{-k_C t}) \qquad (3),$$

where: LSPOM = labile compounds (easily mineralized) and/or soluble inorganic compounds of the detritus, (mg L^{-1}); k_F = DIN formation (leaching + mineralization) rate constant (day^{-1}) and k_C = DIN consumption rate constant (day^{-1}).

Results

The elemental analysis showed that carbon and ash contents of T. domingensis tissues were respectively, 50.2% and 9.4%. The values of k_T calculated by the proposed model (Equation 1; Fig. 2A and 3A) were 0.0049 ± 0.0005 day^{-1} for the aerobic process and 0.0029 ± 0.0006 day^{-1} for the anaerobic process, presenting a half-time ($t_{1/2}$) of 141 and 238 days, respectively (Tab. I). Regardless to the experimental condition (aerobic or anaerobic), it was observed an intense POM losses (ca. 10%) within first day of decomposition, as consequence an increasing in the DOM contents was registered (Fig. 2). After this initial phase, the mineralization of POM was relatively slow (Fig. 2A and 3A).

Under aerobic conditions, water color increased in the first 24 h of decomposition, after this period the optical density presented oscillations and tended to decrease, mainly after the 30th day (Fig. 2B). The pH values of incubations with high detritus content (Fig. 2B) tended to increase since the beginning. In contrast, Figure 2E indicates that the pH varied considerably in the beginning for the incubation with low detritus content, and then tended to decrease up to the 35th day. After, the pH increased until the end of process. The range within the pH varied was narrow for this incubation (from 6.43 to 7.19). Comparing the control experiments, it was observed that the detritus adduction led to a slight acid medium. Up to the 4th day an intense leaching of inorganic compounds from particulate detritus ($t_{1/2}$ = 0.7 day) was verified; in sequence, a slow consumption of inorganic compounds predominated ($t_{1/2}$ = 162 days; Fig. 2D).

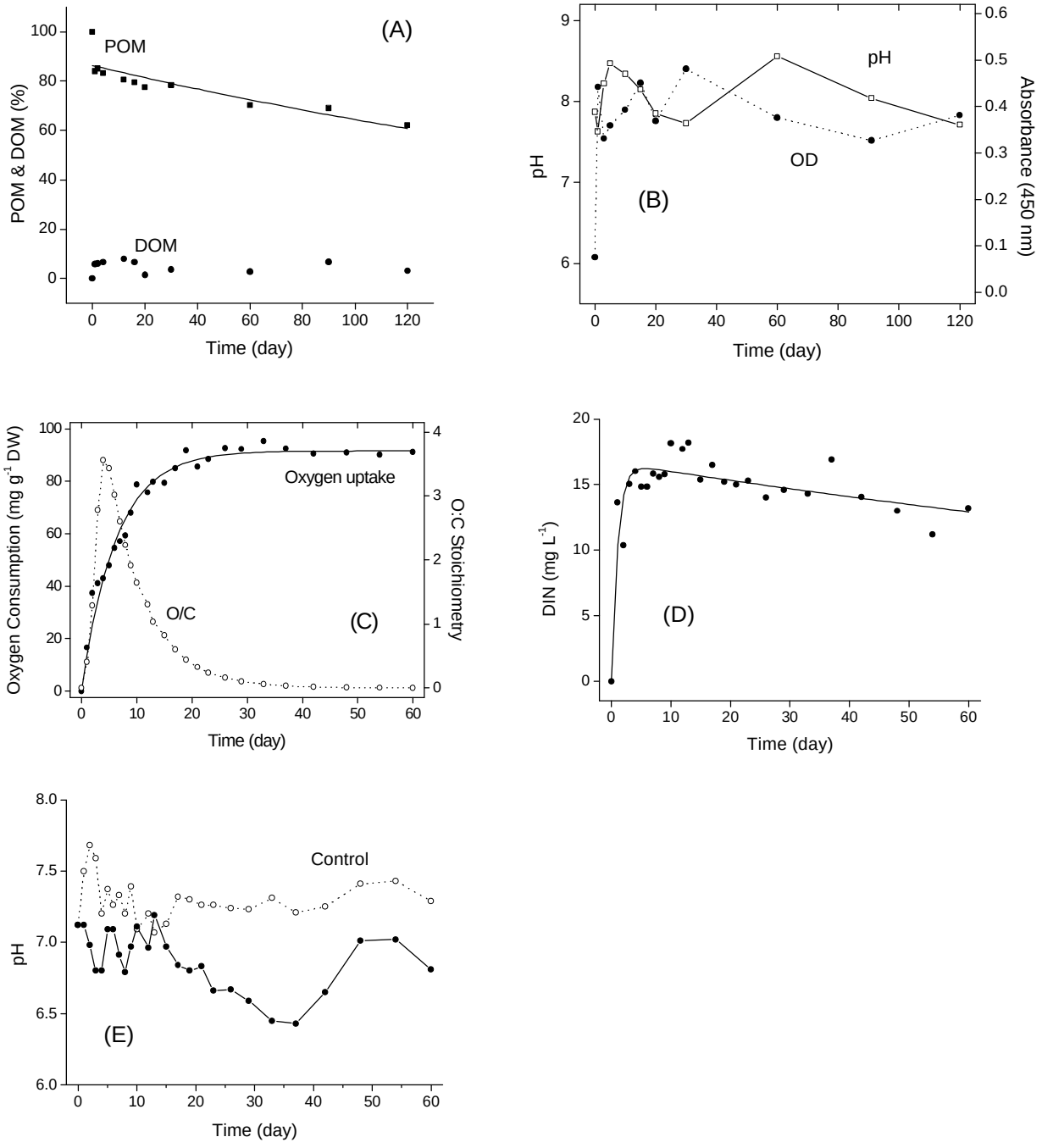

Figure 2: Aerobic decomposition of Typha domingensis: (A) variations of POM and DOM; (B) pH and optical density (OD) variations (incubations with high concentration of organic matter); (C) oxygen consumption and time changes of O/C stoichiometry; (D) kinetic of DIN (simulated and actual); (E) pH of the incubations with low concentration of organic matter.

The oxygen uptake was fast ($t_{1/2}$ = 4 days; Tab. I) until the 20th day, subsequently the consumption rates tended to decrease (Fig. 2C). The changes in stoichiometric relation reflected the tendency also observed for the oxygen consumption. The variation suggests higher demand for oxygen during the initial phase of T.domingensis decomposition, in sequence, the oxygen demand decreased. Referring to the O/C stoichiometry an increase until the 4th day (maximum value was 3.56) was observed (Fig. 2C). In sequence, the O/C values tended to decrease continually, being 0.10 and 0.01 at the 29th and 42nd days, respectively.

Table I: Kinetic parameters obtained from aerobic and anaerobic decomposition of Typha domingensis.

Parameter	**Anaerobic**			**Aerobic**		
		Error	$t_{1/2}$ (d)		Error	$t_{1/2}$ (d)
k_T (day^{-1})	0.0029	0.0006	238	0.0049	0.0005	141
r^2	0.92	-	-	0.76	-	-
CO_{max} (mg g^{-1} DW)	-	-	-	91.63	1.30	-
k_D (day^{-1})	-	-	-	0.159	0.008	4
r^2	-	-	-	0.98	-	-
DIN (%)	-	-	-	16.63	0.61	-
k_F (day^{-1})	-	-	-	0.97	0.21	1
k_C (day^{-1})	-	-	-	0.0043	0.0015	162
r^2	-	-	-	0.81	-	-

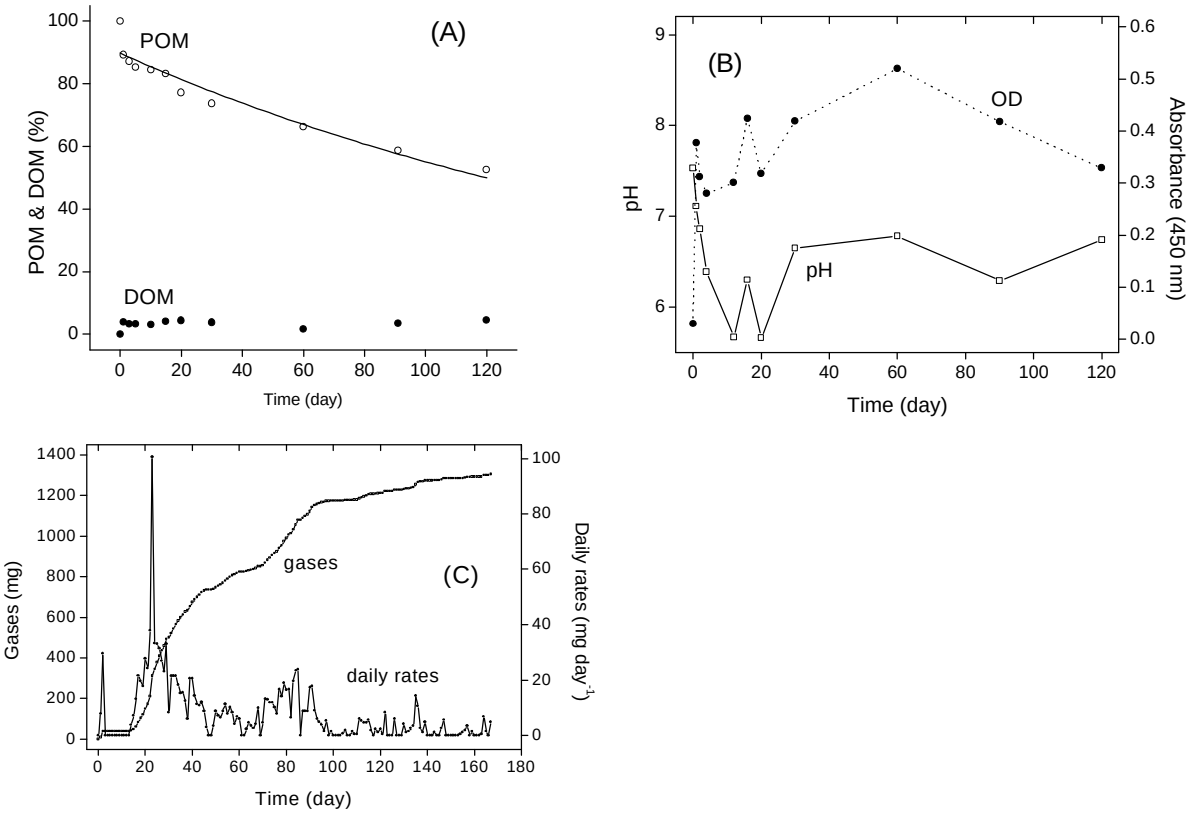

Figure 3: Anaerobic decomposition of Typha domingensis: (A) variations of POM and DOM; (B) pH and optical density (OD) variations (incubations with high concentration of organic matter); (C) Gas formation: daily rates and yield.

The changes in values of optical density in the anaerobic incubations were similar to those for the aerobic decomposition. However, the bleaching was more intense after the 60th day (Fig. 3B). Different from for aerobic decay (Fig. 2B), under anaerobic conditions the pH decreased until the 20th day (from 7.53 to 5.66), after it increased and the medium remained acid (from 6.29 and 6.78). The evolved gases presented three well-defined stages. The 1st peak of daily rates occurred on the 2nd day (29.6 mg day^{-1}), while the second (higher) peak, appeared on the 23rd day (100.5 mg day^{-1}) and lasted from up to 60th day. The last well-defined stage for gases formation (maximum: 23.89 mg day^{-1} at 85th day) started at the 61th day, lasting up to the 100th; at this stage, the gases were produced as an intermittent process with low daily rates.

Discussion

The simple exponential model has been useful to describe the decomposition of aquatic macrophytes (Nelson et al., 1990; Corstanje et al., 2006), although this kinetic approach considered the subtract as homogeneous resource, disregarding the leaching phase of decomposition, the leaching prevailed in the first stages of decomposition, being responsible for the intense mass loss (Fig. 2 A) and, consequently, for the chemical alterations of the detritus. These processes of mass loss are associated with the release of cytoplasm fractions and hydrosoluble structural compounds (Moorhead et al., 1996; Canhoto & Grace, 1996). Several events drive the leaching rates such as experimental procedures (e.g. oven-dry, mesh size of litter bag), abrasion, and chemical composition of detritus (Park & Cho, 2003). The period of leaching varies from the first 24 h up to 15 days (Brum & Esteves, 2001; Albariño & Balseiro, 2002; Schlickeisen et al., 2003; Cunha-Santino, 2003). Nelson et al. (1990) considered that the effect of leaching on Typha glauca lasted for 48 h and that green litter presented a mean mass loss of ca. 14% and senesced litter of ca. 7%. Howard-Williams & Howard-Williams (1978) reported that 26% of sodium, 7.5% of potassium, 9.2% of calcium, 11.5% of magnesium, 1.5% of phosphorous and 0.3% of nitrogen were released by leaching from Typha domingensis detritus in Lake Chilwa during flooding. For leaves, roots and steam of Typha domingensis, the mean values obtained were 4.6% DW of proteins, 65% of cell wall fraction, 6.2% of carbohydrates, 12.2% of lipids, 13.1% of ashes and 0.03% of starch (Thomaz & Esteves, 1984). The elemental composition of T. dominguensis suggests the high potential of organic matter cycling in the biomass of this specie.

The release of dissolved compounds is extremely important in aquatic ecosystems, since in these environments the senescent macrophyte biomass is permanently in contact with water (Polunin, 1984). Therefore, these compounds are rapidly incorporated in the DOM pool (Howard-Williams & Howard-Williams, 1978). Due to the large nutrient content and reactive nature of DOM, the leached compounds from decomposing macrophytes tended to be reactive, presenting labile fractions that are readily available to bacteria and phytoplankton metabolism (Sala & Güde, 1999; Faria & Esteves, 2001). These compounds have great potential of incorporation by heterotrophic organisms (Wetzel, 1995). In this context, the increase of DIN concentrations (Fig. 2D) can be related to inorganic ions released by leaching, as observed by Mun (2000) in the decomposition of mushrooms, where Mg, Ca, N, P, K were intensively released. For the present study the DIN formation (until 4th day) was related to leaching and, in sequence, the DIN content decreased probably by heterotrophic uptake.

The simple exponential model focuses basically on the refractory fraction, with the k_T expressing the mass loss of these compounds (e.g. fibers). The composition and number of microorganisms has influence on the mineralization rates of refractory fractions. The values determined for k_T suggest that, in relation to oxygen availability, the heterotrophic microbiota involved in the aerobic decomposition of lignocellulosic detritus were more efficient that in the anaerobic process. This result was similar to the organic matter cycling (Lillebf et al., 1999), in which the aerobic process was usually fast. Breakdown rates reported for different species of Typha (Tab. II) fall within the range of 0.0008 to 0.0450 days^{-1} ($t_{1/2}$ = 15 to 865 days^{-1}), presenting a mean value of 0.0067 ± 0.0089 (SD) day^{-1} (n = 26). These mean values for k_T in Table II are relatively low compared to

Table II: Decay coefficients (using simple exponential model), $t_{1/2}$ and duration of experiment, reported in the literature for Typha spp.

Species	k (day^{-1})	$t_{1/2}$ (day)	Duration (day)	Reference
Typha latifolia	0.0039	177	180	Boyd (1970)
Typha angustifolia	0.0019	363	626	Mason & Bryant (1975)
T. latifolia	0.0104	66	300	Webster & Simmons (1978)
Typha glauca	0.0012	575	525	Davis & van der Valk (1978)
Typha domingensis	0.0070	99	144	Howard-Williams & Howard-Williams (1978)
T. latifolia	0.0019	363	348	Puriveth (1980)
T. latifolia	0.0070	99	56	Hill & Webster (1982)
T. angustifolia	0.0047	147	154	Hill (1985)
T. glauca	0.0110	63	138	Nelson et al. (1990)
T. domingensis	0.0011	627	720	Davis (1991)
T. domingensis	0.0079	87	150	Delitti (1993)
T. angustifolia				
steam	0.0024	288	365	Cho & Kong (1998)
leaf	0.0008	865	365	
T. latifolia				Schnitzer & Neely (2000)
fine mesh	0.0070	99	137	
coarse mesh	0.0080	86	137	
with invertebrate colonization	0.0065	106	137	
Typha sp				Ruppel et al. (2004)
petland	0.0100	69	27	
marsh	0.0200	35	27	
stream	0.0450	15	27	
T. domingensis	0.0017	406	560	Gonçalves Jr. et al. (2004)
T. latifolia				Corstanje et al. (2006)
mineral soil	0.0021	329	362	
organic-enriched soil	0.0028	246	362	
organic soil	0.0023	300	362	
T. domingensis				This study
refractory (anaerobic)	0.0024	288	120	
refractory (aerobic)	0.0044	157	120	

other decay rates of aquatic macrophyte: 0.0350 day^{-1} for Nelubo lutea (Godshalk & Wetzel, 1978); 0.0370 day^{-1} for Eichhornia crassipes (Gamage & Asaeda, 2005); 0.0260 day^{-1} for Elodea canadensis (Hill & Webster, 1982); 0.0537 day^{-1} for Potamogetum perfoliatus (Hill & Webster, 1982); 0.0820 day^{-1} for Potamogeton pectinatus (Carpenter, 1980) and 0.0277 day^{-1} for Salvinia auriculata (Howard-Williams & Junk, 1976). Possible reasons for the lower rates could be the influence of external variables or experimental conditions such as moisture, hydrologic regime, temperature and oxygen availability. Other factors such as the season during which the study was performed,

stage of maturity of plants at collection, plant parts included in the sample and degree of sample burial must also be considered (Nelson et al., 1990). When considering in situ experiments, the colonization of macroinvertebrates on detritus could represent an additional factor that influences the decomposition, especially in temperate ecosystems (Ribas et al., 2006).

The change of pH values in the aerobic incubations (Fig. 2B) showed the same pattern for decomposing experiments with barks, leaves and litter (Cunha-Santino & Bianchini Jr., 2002). Upon decomposition, pH increased probably due to release of anions. This process was also reported in decomposition of Egeria najas (Carvalho et al., 2005) and for T. domingensis (Howard-Williams & Howard-Williams, 1978). McKinley & Vestal (1982) reported that in microcosm experiment with Carex litter, reductions below pH 5.0 of lake water increased dramatically the effect on the microbial colonization and decomposition of Carex litter. During degradation of T. domingensis the prevalence of a neutral to alkaline environment suggests that a buffer system due to humification was established. As the degradation proceed it is also proposed that a second buffer system, the carbonate system (CO_2 - HCO_3^- - CO_3^{2-}), coming from the CO_2 released by the mineralization, is also important. The relative proportions of CO_2, HCO_3^- and CO_3^{2-} are pH-dependent, and HCO_3^- predominated with pH between 7 and 8 in the aerobic incubations. According to Figure 3B, pH decreased in the beginning for the anaerobic incubations, being overall characteristic of an acid media, with intermediate compounds being formed. Fermentation of seeds extract showed pH values varying between 4 and 6.5 (Schaffner & Beuchat, 1986). During cellulose and cellobiose fermentation, acetic acid was the mainly volatile organic acid formed (Weimer & Zeikus, 1977).

The optical density (OD) from aerobic and anaerobic incubations (Fig. 2B) increased with time, presenting great variations in color in the beginning of the experiment. The greatest change in the first day indicated a fast leaching of colored organic compounds. According to Howard-Williams & Howard-Williams (1978) an increase in color is due to the release of organic humic type substances during leaching. The melanoidin solubility is pH-dependent and less soluble in acidic (Migo et al., 1993). Therefore, in the aerobic condition, the increase in pH due to the buffer system established humic substance and carbonate system generates an increase in optical density (Cunha-Santino & Bianchini Jr., 2004). This tendency is less evident for anaerobic conditions.

The total amount of CO_{max}, obtained in the dark, is usually employed as a measure of total heterotrophic activity in samples of lake water and sediments, and it is therefore reasonable to use CO_{max} to follow the process of a microbial respiration in aerobic environments (Esslemont et al., 2001). The kinetic of oxygen consumption was similar to that observed by Borsuk & Stow (2000). There was a strong increase in oxygen demand at the beginning, followed by a decrease in oxidation, tending to stabilization (Fig. 2C). Considering that aquatic macrophyte detritus is a heterogeneous source of organic matter with labile and refractory compounds, the oxygen uptake was probably related to the labile fractions. On the other hand, the reduction of oxygen uptake was associated with the mineralization of refractory fractions (e.g. cellulose, lignin and hemicellulose).

With regard to the CO_{max} found in the present study (91.63 mg g^{-1} DW; Tab. III), when compared with studies developed with the same specie, Farjalla et al. (1999) found an CO_{max} of 32.5 mg g^{-1} DW and Brum et al. (1999) a CO_{max} of 139.0 mg g^{-1} DW. Data from experiments of oxygen uptake (CO_{max} and k_D) from several macrophyte species (Tab. III) showed great variation among the species. The minimum value for CO_{max} was 32.5 mg g^{-1} DW (T. domingensis) and the maximum value was 700.0 mg g^{-1} DW (Egeria najas). The mean (SD) value of CO_{max} verified during decomposition of aquatic macrophytes (n = 26; Tab. III) was 284.2 ± 158.9 mg g^{-1} DW. The value of deoxygenation coefficient (k_D = 0.159 day^{-1}) determined for the aerobic T. domingensis was higher than the mean value (0.077 ± 0.061 day^{-1}) summarized in Table III for different species of macrophytes. It is supposed that besides the effect from the chemical structure of the detritus, the diversity and number of the microorganisms may also be responsible for the great variation of CO_{max} and k_D values.

Regarding the stoichiometry O/C, the increment in the beginning of experiment and a decrease tending to zero was also

Table III: Parameters derived from oxygen uptake model during aerobic decomposition of aquatic macrophytes.

Resource	CO_{max} (mg g^{-1})	k_D (day^{-1})	Reference
Cabomba sp	342.0	0.093	Bitar & Bianchini Jr. (2002)
Cabomba furcata	339.0	0.097	Cunha & Bianchini Jr. (1998)
Cabomba furcata	384.0	0.045	Bianchini Jr. et al. (2006)
Cyperus giganteus	317.0	0.025	Bianchini Jr. et al. (2006)
Egeria najas	700.0	0.014	Bianchini Jr. et al. (2006)
Eichhornia azurea	140.0	0.199	Bitar & Bianchini Jr. (2002)
E. azurea	279.0	0.027	Bianchini Jr. et al. (2006)
Eleocharis fistulosa	60.0	0.040	Farjalla et al. (1999)
Lemna sp	230.0	0.230	Bitar & Bianchini Jr. (2002)
Ludwigia inclinata	393.6	0.022	Romeiro (2005)
Montrichardia arborescens	235.2	0.044	Cunha-Santino et al. (2004)
Nymphaea ampla	258.0	0.136	Brum et al. (1999)
N. ampla	450.0	0.112	Farjalla et al. (1999)
Oxycaryum cubense	144.0	0.166	Bitar & Bianchini Jr. (2002)
O. cubense	160.9	0.011	Lemos & Bianchini Jr. (1998)
O. cubense	275.0	0.038	Bianchini Jr. et al. (2006)
Potamogeton stenostachys	377.0	0.054	Brum et al. (1999)
P. stenostachys	360.0	0.070	Farjalla et al. (1999)
Salvinia sp	185.0	0.079	Bitar & Bianchini Jr. (2002)
Salvinia auriculata	165.0	0.041	Bianchini Jr. et al. (2006)
Typha domingensis	139.0	0.147	Brum et al. (1999)
T. domingensis	32.5	0.014	Farjalla et al. (1999)
T. domingensis	91.6	0.159	This study
Utricularia breviscapa	260.0	0.045	Cunha-Santino (2003)
U. breviscapa	497.0	0.023	Bianchini Jr. et al. (2006)
Wolffia sp	573.5	0.079	Bitar & Bianchini Jr., 2002
Mean (all experiments)	284.2	0.077	
Standard deviation	158.9	0.061	

verified by Cunha-Santino & Bianchini Jr., (2002) and Cunha-Santino (2003). The results indicate that O/C varied with time, with higher values in the early phase. Experiments of aerobic mineralization of barks, branches, leaves and litter presented the same pattern of temporal O/C variation. In these cases, O/C relation reached the maximum value at the 3rd day, with respective values of 6.73; 1.05; 2.45 and 3.88 (Cunha-Santino & Bianchini Jr., 2002). During decomposition of aquatic macrophytes, the maximum values measured for O/C were: 5.03 (Montrichardia arborescens, maximum value at 17th day; Cunha-Santino et al., 2004), 11.88 (Eichhornia azurea, maximum value at 6th day Cunha-Santino et al., in press) and 11.05 (Salvinia auriculata, maximum value at 3rd day; Cunha-Santino & Bianchini Jr., 2001). The maximum O/C, obtained in the first stages of decomposition, was probably due to

oxidation (chemical and biochemical) of leached dissolved organic carbon; this fraction, as already discussed, is characterized by a diversity of reactive organic compounds. In a second stage, O/C may vary due to biochemical oxidation (i.e. processes associated with microbial metabolic routes) and with the microorganism diversity. Thus, the changes in the stoichiometric values can be attributed: (i) to the chemical oxidation of different organic compounds; (ii) to reactions mediated by enzymes; (iii) to the alterations of predominant metabolic routes; (iv) to variations of the quantity and species of microorganisms; (v) to the variations of the amount and quality (fibrous content) of the available organic compound and to the intrinsic content of oxygen in the molecule of compounds that integrated the detritus. In addition, other oxidations not related with organic carbon (e.g. nitrification) could interfere increasing the O/C values (Cunha-Santino & Bianchini Jr., 2002).

The accumulated gases generated during the anaerobic decay of Typha domingensis (Fig. 3C) result from fermentation and methanogenesis (Bitar, 2003). The anaerobic decay of T. domingensis presented three stages, according to Figure 3C. The first (from 2nd to the 12th day) referred to the consumption processes; there were a negative rate, which means that the assimilation (microbial uptake) of the gas produced via mineralization prevailed over its release. The second stage (until 60th day) occurred when the gases probably reached their saturation concentrations and their formation supplanted the creation of dissolved inorganic compounds (e.g. carbonate ions); this stage was characterized by intense release of gases, with strong increase in daily rates. These higher rates are probably due to the possible biochemical processes that may occur under anaerobic conditions (e.g. mineralization of labile dissolved compounds, CH_4 generation, denitrification, H_2S formation). The third stage began after two months of the experiment and suggested that labile fractions are exhausted and the mineralization rates decrease in comparison with 2nd stage; this phase is characterized by containing predominantly refractory organic matter (lignocellulosic compounds and humic substances). A possible alteration in the microbial community occurred and a smaller availability of the intermediary products, causing the rates of consumption of organic matter to decrease. In this context, from a similar experiment in that Eichhornia azurea and Egeria najas were used, the production of gases from E. azurea (44.9 ml) after 120 days was smaller than E. najas (199.2 ml). According to Bitar (2003), this difference was probably related to the structural composition of the plants (cellulose contents and labile fraction of carbon). After 213 days, the anaerobic decomposition assay performed with Eichhornia azurea and a eutrophic water sample produced 94.18 ml of gases (Cunha-Santino & Bianchini Jr., in press). In the anaerobic decomposition of Cabomba piahuyensis and Oxycaryum cubense, the volume of evolved gases (during 120 days) was, respectively, 213.1 and 36.0 ml (Cunha & Bianchini Jr., 1999). The aerobic mineralization of M. arborescens presented a gaseous yield of 236.9 ml (127 days; Cunha-Santino et al., 2004).

Overall, the results obtained in the present study point out that the aerobic cycling T. domingensis was more efficient under aerobic conditions, according to k_T, the aerobic processes were 2-fold faster than anaerobic. The effect of microbial degradation in the regulation of organic matter cycling is related with k_D. It is assumed that the fractions responsible for the high k_D have reduced periods of half-time, and therefore do not accumulate in the ecosystems. The aerobic decay of T. domingensis promoted moderate depletion in the dissolved oxygen budget within the aquatic environments. Owing to the time scale of k_T ($t_{1/2}$ = 141 to 238 days), the POM (i.e. refractory fractions), associated with the adequate conditions of pH and oxi-reduction potential contributed to the dynamics of gas production and storage of POM in sediment.

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References

Albariño, R.J. & Balseiro E.G. 2002. Leaf litter breakdown in Patagonian streams: native vs. exotic trees and the effect of

invertebrate size. Aquat. Conserv., 12:181-192.

Bianchini Jr., I. 2003. Modelos de crescimento e decomposição de macrófitas aquáticas. In: Thomaz, S.M. & Bini, L.M. (eds.) Ecologia e manejo de macrófitas aquáticas. Eduem, Maringá. p.85-126.

Bianchini Jr., I., Bitar, A.L., Verani, J.R. & Peret A.C. 2003. Experimento de mineralização aeróbia para ambientes aquáticos: determinação do número de réplicas. Acta Sci., 25:245-252.

Bianchini Jr., I., Peret, A.M. & Cunha-Santino, M.B. 2006. A mesocosm study of aerobic mineralization of seven aquatic macrophytes. Aquat. Bot., 85:163-167.

Bitar, A.L. 2003. Mineralização e formação de gases da degradação de Eichhornia azurea Kunth e Egeria najas Planch. São Carlos, UFSCar, 118p (PhD Thesis).

Bitar, A.L. & Bianchini Jr., I. 2002. Mineralization assays of some organic resources of aquatic systems. Braz. J. Biol., 62:557-564.

Borsuk, M.E. & Stow, C.A. 2000. Bayesian parameter estimation in a mixed-order model of BOD decay. Water Res., 34:1830-1836.

Boyd, C.E. 1970. Losses of mineral nutrients during decomposition of Typha latifolia. Arch. Hydrobiol., 66:511-517.

Brum, P.R. & Esteves, F.A. 2001. Dry weight loss and chemical changes in the detritus of three tropical aquatic macrophyte species (Eleocharis interstincta, Nymphaea ampla and Potamogeton stenostachys) during decompositon. Acta Limnol. Bras., 13:61-73.

Brum, P.R., Farjalla, V.F., Gonçalves Jr., J.F., Santos, A.M., Pôrto, M.T., Vieira, E.D.R., Ferreira, F.M. & Bianchini Jr., I. 1999. Aspects of the uptake of dissolved oxygen in Cabiúnas and Imboassica Lagoons (Macaé, RJ). Braz. Arch. Biol. Technol., 42:433-440.

Canhoto, C. & Graça, M.A.S. 1996. Decomposition of Eucalyptus globulus leaves and three native leaf species (Alnus glutinosa, Castanea sativa and Querus faginea) in a Portuguese low order stream. Hydrobiologia, 333:79-85.

Carpenter, S.R. 1980. Enrichment of Lake Wingra, Wisconsin by submersed macrophyte decay. Ecology, 61:1145-1155.

Carvalho, P., Thomaz, S.M. & Bini L.M. 2005. Effects of temperature on decomposition of a potential nuisance species: the submerged aquatic macrophyte Egeria najas Planchon (Hydrocharitaceae). Braz. J. Biol., 65:767-777.

Cho, K.H. & Kong, H.Y. 1998. A comparative study on litter decomposition of emergent macrophytes in the littoral zone of reservoir. Korean J. Biol. Sci., 2:333-339.

Corstanje, R., Reddy, K.R. & Portier, K.M. 2006. Typha latifolia and Cladium jamaicense litter decay in response to exogenous nutrient enrichment. Aquat. Bot., 84:70-78.

Cunha, M.B. & Bianchini Jr., I. 1998. Mineralização aeróbia de Cabomba piauhyensis e Scirpus cubensis. Acta Limnol. Bras., 10:81-91

Cunha, M.B. & Bianchini Jr., I. 1999. Degradação anaeróbia de Cabomba piauhyensis e Scirpus cubensis: cinéticas de formação de gases. Acta Limnol. Bras., 11:5-26.

Cunha-Santino, M.B. 2003. Atividade enzimática, cinética e modelagem matemática da decomposição de Utricularia breviscapa da lagoa do Óleo (Estação Ecológica de Jataí, Luiz Antonio, SP). São Carlos, UFSCar, 140p (PhD Thesis).

Cunha-Santino, M.B. & Bianchini Jr., I. 2001. Consumo de oxigênio durante a mineralização aeróbia de Utricularia gibba e Salvinia auriculata. In: VIII Congresso Brasileiro de Limnologia. UFP, João Pessoa, 1 CD-ROM.

Cunha-Santino, M.B. & Bianchini Jr, I. 2002. Estequiometria da decomposição aeróbia de galhos, cascas serapilheira e folhas. In: Espíndola, E.L.G., Mauad, F.F., Schalch, W., Rocha, O., Felicidade, N. & Rietzler, A.C. (eds.) Recursos hidroenergéticos: usos, impactos e planejamento integrado. RiMa, São Carlos. p.43-56.

Cunha-Santino, M.B. & Bianchini Jr., I. 2003. Determination of the aeration coefficient for long-term BOD experiments. Acta Sci., 25:253-256.

Cunha-Santino, M.B. & Bianchini Jr., I. 2004. Humic substances mineralization: the variation of pH, electrical conductivity and optical density. Acta Limnol. Bras., 16:63-75.

Cunha-Santino, M.B., Pacobahyba, L.D. & Biancchini Jr., I. 2004. O/C Stoichiometry from mineralization: of Montrichardia arborescens (L.) Schott. Acta Limnol. Bras., 16:351-357.

Cunha-Santino, M.B. & Bianchini Jr., I. 2006. Variação temporal da relação

estequiométrica O/C na decomposição aeróbia de Eichhornia azurea (Sw.) Kunth. (In press).

Davis, C.B. & van der Valk, A.G. 1978. The decomposition of standing and fallen litter of Typha glauca and Scirpus fluviatilis. Can. J. Bot., 56:662-675.

Davis, S.M. 1991. Growth, decomposition, and nutrient retention of Cladium jamaicense Crantz and Typha domingensis Pers. Florida Everglades. Aquat. Bot., 40:203-224.

Delitti, W.B.C. 1993. Decomposição de materiais biológicos em ambiente aquático. THEMAG Engenharia, São Paulo. (Relatório Técnico).

Esslemont, G., Maher, W.A. & Ford, P. 2001. A comparison of manometric and membrane-electrode procedures for measuring rates of leaf decay. Environ. Technol., 22:223-227.

Faria, B.M. & Esteves, F.A. 2001. Dissolved organic carbon in two Brazilian coastal lagoons: sources and utilization for heterotrophic bacteria. Oecol. Bras., 9:57-64.

Farjalla, V.F., Marinho, C.C. & Esteves F.A. 1999. Uptake of oxygen in the initial stages of decomposition of aquatic macrophytes and detritus from terrestrial vegetation in a tropical coastal lagoon. Acta Limnol. Bras., 11:185-193.

Gamage, N.P.D. & Asaeda, T. 2005. Decomposition and mineralization of Eichhornia crassipes litter under aerobic conditions with and without bacteria. Hydrobiologia, 541:13-27.

Godshalk, G.L. & Wetzel, R.G. 1978. Decomposition of aquatic angiosperms. III Zoltera MN Rina H. and a conceptual model of decomposition. Aquat. Bot., 5:329-354.

Gonçalves Jr., F.J., Santos, A.M. & Esteves, F.A. 2004. The influence of chemical composition of Typha domingensis and Nymphaea ampla detritus on invertebrate colonization during decomposition in a Brazilian coastal lagoon. Hydrobiologia, 527:125-137.

Henry-Silva, G.G., Pezzato, M.M., Benassi, R.F. & Camargo, A.F.M. 2001. Chemical composition of five species of aquatic macrophytes from lotic ecosystems of southem coast of the state of São Paulo (Brazil). Acta Limnol. Bras., 13:11-17.

Hill, B.H. 1985. The breakdown of macrophytes in a reservoir wetland. Aquat. Bot., 21:23-31.

Hill, B.H. & Webster, J.R. 1982. Aquatic macrophyte breakdown in an Appalachian river. Hydrobiologia, 89:53-59.

Howard-Williams, C. & Howard-Williams, W. 1978. Nutrient leaching from the swamp vegetation of Lake Chilwa, a shallow African lake. Aquat. Bot., 4:257-267.

Howard-Williams, C. & Junk, W.J. 1976. The decomposition of aquatic macrophytes in the floating meadows of a central Amazonian varzea lake. Biogeographica, 115-123.

Junk, W.J. & Piedade, M.T.F. 1993. Biomass and primary production of herbaceous plant communities in the Amazon floodplain. Hydrobiologia, 263:155-162.

Kuehn, K.A., Gessner, M.O., Wetzel, R.G. & Suberkropp, K. 1999. Decomposition and CO_2 evolution from standing litter of the emergent macrophyte Erianthus giganteus. Microb. Ecol., 38:50-57.

Kuehn, K.A. & Suberkropp, K. 1998. Diel fluctuations in microbial activity associated with standing-dead litter of the freshwater emergent macrophyte Juncus effusus L. Aquat. Microb. Ecol., 14:171-182.

Lemos, R.M.A. & Bianchini Jr., I. 1998. Decomposição de Scirpus cubensis Poepp & Kunth da lagoa do Infernão (SP): I Efeito do teor de nitrogênio e da quantidade de matéria orgânica. In: Anais do VIII Seminário Regional de Ecologia. UFSCar, São Carlos, p.1271-1287.

Lillebo, A.I., Flindt, M., Pardal, M.A. & Marques, J.C. 1999. The effect of macrofauna, meiofauna and microfauna on the degradation of Spartina maritima detritus from a salt marsh area. Acta Oecol., 20:249-258.

Little, E.C.S. 1979. Handbook of utilization of aquatic plants. Food and Agriculture Organization of the United Nations, Rome. (FAO Fisheries Technical Paper, 187).

López, N.I., Duarte, C.M., Vallespinós, F., Romero, J. & Alcoverro, T. 1998. The effect of nutrients additions on bacterial activity in seagrass (Posidonia oceanica) sediments. J. Exp. Mar. Biol. Ecol., 224:155-166.

López-Archilla, A.I., Marin, I. & Amils, R. 2001. Microbial community composition and ecology of an acidic aquatic environment: the Tinto River, Spain. Microb. Ecol., 41:20-35.

Mendelssohn, I.A., Sorrell, B.K., Brix, H., Schierup, H.H., Lorenzen, B. & Maltby, E. 1999. Controls on soil cellulose

decomposition along a salinity gradient in a Phragmites australis wetland in Denmark. Aquat. Bot., 64:381-398.

Manson, C.F. & Bryant, R.J. 1975. Production, nutrient content and decomposition of Phragmites communis Trin. and Typha angustifolia L. J. Ecol., 63:71-95.

McKinley, V.L. & Vestal, J.R. 1982. Effects of acid on plant litter decomposition in an arctic lake. Appl. Environ. Microbiol., 43:1188-1195.

Migo, V.P., Matsumura, M., Rosario E.J. & Kataoka, H. 1993. The effect of pH and calcium ions on the destabilization of melanoidin. J. Ferment. Bioeng., 76:29-32.

Moorhead, D.L., Sinsabaugh, R.L., Likens, A.E. & Reynolds, J.F. 1996. Decomposition processes: modeling approaches and applications. Sci. Total Environ., 183:137-149.

Mun, H.T. 2000. Mass loss and changes of mineral nutrients during decomposition of mushrooms, Russula alboaerolata and Lactarius violascens. Korean J. Biol. Sci., 4:51-55.

Nelson, W.J., Kadlec, J.A. & Murkin, H.R. 1990. Seasonal comparison of weight for two types of Typha glauca Godr. leaf litter. Aquat. Bot., 37:299-314.

Park, S. & Cho, K.H. 2003. Nutrient leaching from leaf litter of emergent macrophyte (Zizania latifolia) and the effects of water temperature on the leaching process. Korean J. Biol. Sci., 7:289-294.

Puriveth, P. 1980. Decomposition of emergent macrophytes in a Wisconsin marsh. Hydrobiologia, 72:231-242.

Press, W.H., Teukolsky, S.A., Vetterling, W.T. & Flannery, B.P. 1993. Numerical recipes in C: the art of scientific computing. Cambridge University Press, New York. 994p.

Polunin, N.V.C. 1984. The decomposition of emergent macrophyte in freshwater. Adv. Ecol. Res., 14:115-166.

Ribas, A.C.A., Tanaka, M.O. & Souza, A.L.T. 2006. An evaluation of macrofaunal effects on leaf litter breakdown rates in aquatic and terrestrial habitats: a case study in the tropics. Austral Ecol., 31:783-790.

Romero, F. Bioensaios de decomposição anaeróbia macrófitas aquáticas da lagoa do Óleo (Estação Ecológica de Jataí, Luiz Antônio SP). São Carlos, UFSCar, 90p (Marter Thesis).

Ruppel, R.E., Setty, K.E. & Wu, M. 2004. Decomposition rates of Typha spp. in northern freshwater wetlands over a stream-marsh-peatland gradient. Discip. Sci., 1:26-37.

Sala, M.M. & Güde, H. 1999. Role of protozoans on the microbial ectoenzymatic activity during the degradation of macrophytes. Aquat. Microb. Ecol., 20:75-82.

Schlickeisen, E., Tietjen, T.E., Arsuffi, T.L. & Groeger, A.W. 2003. Detritus processing and microbial dynamics of an aquatic macrophyte and terrestrial leaf in a thermally constant, spring-fed stream. Microb. Ecol., 45:411-418.

Schaffner, D.W. & Beuchat, L.R. 1986. Fermentation of aqueous plant seed extracts by lactic acid bacteria. Appl. Environ. Microbiol., 51:1072-1076.

Schnitzer, S.A. & Neely, R.K. 2000. Criticism of the litterbag technique for the study of aquatic plant decay: suppression of epiphytic algal biomass. Arch. Hydrobiol., 148:433-440.

Sorokin, Y.I. & Kadota, H. 1972. Tecniques for the assessment of microbial production and decomposition in freshwater. Blackwell, Oxford. 112p. (IBP, 23).

Thomaz, S.M. & Esteves, F.A. 1984. Estudos da biomassa de algumas espécies de macrófitas aquáticas quanto ao seu valor nutritivo. In: Anais do IV Seminário Regional de Ecologia. UFSCar, São Carlos, p.439-467.

Webster, J.R. & Simmons, Jr., G.M. 1978. Leaf breakdown and invertebrate. colonization on a reservoir bottom. Verh. Int. Verein. Limnol., 20:1587-1596.

Weimer, P.J. & Zeikus, J.G. 1977. Fermentation of cellulose and cellobiose by Clostridium thermocellum in the absence of Methanobacterium thermoautotrophicum. Appl. Environ. Microbiol., 33:289-297.

Wetzel, R.G. 1995. Death, detritus and energy flow in aquatic ecosystems. Freshwater Biol., 33:83-89.

Wetzel, R.G. & Likens, G.E. 1991. Limnological analyses. Springer-Verlag, New York. 391p.

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