VERSITA

Biologia **63**/6: 1104—1110, 2008
Section Botany
DOI: 10.2478/s11756-008-0154-4

Decomposition of *Typha angustifolia* and *Phragmites australis* in the littoral zone of a shallow lake

Edit Ágoston-Szabó* & Mária Dinka

Institute of Ecology and Botany, Hungarian Danube Research Station of the Hungarian Academy of Sciences, H-2163 Vácrátót, Hungary; e-mail: edit@botanika.hu

Abstract: Decomposition of air-dried live *Typha angustifolia* (L) stems and leaves and *Phragmites australis* (Cav. Trin ex Steud.) leaves and culms were studied in a shallow freshwater lake (Lake Fehér, Fertő-Hanság National Park, Hungary) using the litter bag technique. Samples were analyzed for dry mass, fiber (cellulose, hemicelluloses, lignin) and nutrient (C, N, P, S) contents, litter-associated fungal biomass (ergosterol concentration), potential microbial respiration (electron transport activity: ETS) and cellulolytic bacteria. In terms of mesh size, there were no significant differences in the examined parameters of *P. australis* leaves and culms and *T. angustifolia* stems with leaves. *P. australis* leaves had the highest rate of decomposition and *P. australis* culms the lowest. Hemicellulose degraded more rapidly than the other fibers, while the lignin had the slowest rate of decomposition.
The ETS activity of the examined plant litter types increased from day 91st to 237th while decomposition processes were most active, ergosterol contents were high, and there were few cellulolytic bacteria. The counts of cellulolytic bacteria fluctuated during the decomposition period, they were high at the beginning then they decreased. In each case bacteria were found to be the first colonizers of plant detritus, and were followed by fungal growth.

Key words: decomposition; nutrients; fibers; ETS-activity; fungal biomass; cellulolytic bacteria

Introduction

In wetland ecosystems, a considerable part of primary production is formed by emergent macrophytes which are the most significant 'environment forming' factors (Westlake 1982). They play an important part in the detritus food chain (Wetzel 2001), contributing considerably to ecosystem metabolism (Best et al. 1982; Gessner 2000). Being an important component of the nutrient cycling process, reed litter decay has been widely studied in aquatic environments (Polunin 1984; Webster & Benfield 1986; Hietz 1992; Newel 1993; Pieczyńska 1993).

Leaves of emergent macrophytes are normally shed some time following their senescence; dead culms can remain in a standing position for several years in the air or are broken down into the water by wind (Gessner 2001). Decomposition of aboveground plant parts begins in the air and is completed in the water, where decomposing plant material enters the detritus-based food chain (Pieczyńska 1993; Kuehn & Suberkropp 1998; Gessner 2001).

In order to understand the fate of organic matter in wetlands it is necessary to know the amounts and quality of the substrates undergoing decomposition (Pieczyńska 1986). Immediately after senescence, soluble materials are leached out and the contents of both energy and protein decline (Day et al. 1998). The remaining detrital material of emergent macrophytes consists predominantly of structural polymers such as lignin, cellulose and hemicellulose, which are decomposed more slowly than soluble substances (Berg et al. 1984). Biofilms (fungi, bacteria, protozoa, algae, etc.) and their associated meiofauna play an important role in decomposition processes, which have been only little investigated in this context (Leichtfried 1999). Two types of litter bags of 1 mm mesh size (permitting the entry of meiofauna), and 0.05 mm mesh size (excluding meiofauna, Fleeger et al. 2006), respectively were used to test if the meiofauna can play a significant role in the decomposition of *Typha angustifolia* (L) and *Phragmites australis* (Cav Trin ex Steud) litter.

The aim of this study was to compare the decomposition dynamics of *Typha angustifolia (L)* and *Phragmites australis* (Cav Trin ex Steud) litter and to elucidate the relationship between the decomposition rate, chemical composition and microbial parameters of different plant litter types. For this purpose, we investigated the changes in remaining dry mass, amounts of nutrients (C, N, P, S) and fibers (hemicellulose, cellulose, lignin), microbial activity (based on the electron transport activity: ETS), number of cellulolytic bacteria, fungal biomass (ergosterol concentrations) during the decomposition of these plants.

* Corresponding author

Material and methods

Study site

Lake Fehér (47°41′ N, 17°21′ E, altitude: 115 m) is small (area: 2.69 km^2, open water: 0.25 km^2), shallow (mean depth: 50 cm, maximum depth: 110 cm), alkaline (pH 7.0–8.3, electrical conductivity: 489–657 μS/cm), moderately eutrophic lake, situated in the Fertő-Hanság National Park, northwestern Hungary. The lake had been intensively used for fish breeding and thus heavily eutrophicated until 1987, when it was placed under legal protection, mainly because of its valuable bird fauna. The shoreline of the lake is covered with dense homogeneous stands of *Typha angustifolia* and *Phragmites australis*.

Field studies

Standing shoots of *T. angustifolia* and *P. australis* were collected from Lake Fehér (on 30.10.2000) and air-dried. *P. australis* leaves (100 g fresh weight), *T. angustifolia* stems with leaves (altogether 100 g) were put in two types of 25 × 50 cm litter bags of (a) 1 mm mesh size to prevent the loss of shoot fragments and allow microbial activity and the entry of micro- and meiofauna (Fleeger et al. 2006), and (b) 0.05 mm mesh size to permit only the entry of microfauna, bacteria and fungi, excluding benthic meiofauna (Fleeger et al. 2006).

P. australis culms (100 g) were put only in 25 × 50 cm litter bags of 1 mm mesh size.

All litter bags were exposed in the water 30 cm above the sediment on 06.12.2000 (the bags were strung together by strings and fixed to previously stuck piles). After the 152nd (02.05.2001) day of decomposition they were sunk to the sediment surface. Two bags from each type of litter: *P. australis* leaves and *T. angustifolia* litter with two mesh sizes and *P. australis* culms with one mesh size, altogether 10 bags, were periodically retrieved between 07.03.2001 and 26.08.2002.

Microbial and breakdown rate investigations

Subsamples taken for microbial investigation were stored at 0 to 4 °C during their transport to the laboratory. Freshly weighed and immediately analyzed. For wet to dry weight conversion subsamples of wet decomposing plant material (2–4 g) were dried at 105 °C to determine the dry mass. For microbial investigations, *T. angustifolia* leaves and stems were separated from each other after the sampling and analyzed separately.

Fungal biomass on plant litter was estimated by measuring the concentrations of ergosterol, a reliable indicator of living fungal biomass (Gessner & Newel 2002). 2–4 g fresh subsamples (were lyophilized, weighed, and ergosterol extracted in an alcoholic base (0.8% KOH in 95% methanol, extraction volume 10 mL) for 30 min at 80 °C. The resultant extract was partitioned into n-pentane and evaporated to dryness under a stream of N_2 gas, and ergosterol was redissolved in 2 mL of methanol using an ultra sonic bath (10 min.), filtered and quantified by liquid chromatography (HPLC Thermo Separation UV150, P200 high pressure). The system was run with HPLC-grade methanol at a flow rate of 1.5 mL min^{-1}. Ergosterol eluted after 9 min and was detected at 282 nm; peak identity was checked on the basis of retention times of commercial ergosterol (Fluka; >98% purity) (Gessner & Newel 2002).

The electron transport system (ETS) assay described by Kenner & Ahmed (1975) was used to determine the potential microbial respiratory activity, after adaptation of the method to decomposing plant material (Szabó 2003). 20–40 mg subsamples of fresh plant litter were homogenized in ice-cold buffer consisting of $MgSO_4$ (75 μM), Triton-X-100 0.5% (v/v), polyvinyl pyrolidone (PVP) 1.5% w/v, in 0.1 M phosphate buffer (pH 8.4) for 5 minutes at 0–4 °C, by using a potter homogenizer (5 000 rpm, 0–4 °C, B. Braun Biotech. International). Homogenate (0.5 mL, in triplicate) was incubated with 1.5 mL substrate solution (NADPH: 0.25 mM, NADH: 1.7 mM) and 0.5 mL reagent solution (INT: 0.8 mM) for 30 min. at a standard (20 °C) temperature. The reaction was stopped by adding 0.5 mL stopping solution (1:1 mixture of concentrated phosphoric acid and formalin). Blanks (1.5 mL substrate solution and 0.5 mL reagent solution) were incubated and stopped similarly to the test samples, and 0.5 mL of homogenate was then added. The absorbance of the formazan produced during the reaction was determined against the blind probe at a wavelength of 490 nm (Spektronom 195 D photometer). ETS-activity was measured as the rate of tetrazolium dye reduction, which was converted to equivalent oxygen utilized per organic mass in a given time interval.

Bacterial colonization was determined by counting numbers of living bacteria. The most probable number of cellulolytic bacteria was determined from the 0.3–0.4 g mechanically homogenized plant litter solution by using Rodina's (Winogardski) method (Rodina 1972). This procedure separately enumerates cellulose degrading bacteria and provides reliable estimates of the abundance and composition of cellulose-degrading microbial populations.

The data are reported as means of microbial determinations of the four replicate bags taken on each sampling date.

Chemical measurements

The remaining plant material was dried and ground with a motor mill and used for determination of nutrient and fiber contents. C, N, S concentrations were evaluated from 4–10 mg dry subsamples using a NCS analyzer (FISONS NA-1500), the P concentration from 2–4 g dry subsamples by spectrophotometry employing the molybdenum blue method, after digestion with concentrated sulfuric acid (Ruzicka & Hansen 1975).

Fiber concentrations in plant material were determined by the detergent fiber method (Van Soest 1963) with a TECATOR Fibretec M6 analyzer. 5–6 g dried plant material was successively treated with a neutral detergent solution which separates NDS (Neutral Detergent Solubles containing proteins, carbohydrates and lipids) from the NDF (Neutral Detergent Fiber) cell wall constituents, then with an acid detergent solution and 72% sulfuric acid to evaluate NDF constituent hemicellulose, cellulose and ADL (Acid Detergent Lignin) contents.

The data are reported as means of analytical determinations of the four replicate bags taken on each sampling date. C, N, P, S and fiber fraction concentrations (g g^{-1}), coupled with remaining plant mass (g dry weight), were ultimately used to determine the percentage contents of C, N, P, S, NDF, hemicellulose, cellulose and lignin mass remaining in the litter. The amounts recorded at the start of the decomposition experiment were considered as original values (100%).

Mathematical and statistical evaluation of the data

Two types of models were fitted to the data: (a) the single exponential model: $W_t = W_0 \exp(-kt)$, where W_t is the amount of detritus at time t, W_0 is the initial amount of detritus and k is the exponential breakdown rate (Olson 1963); and (b) the decaying coefficient model $W_t =$

Table 1. Results of the single exponential and the decaying coefficient model

	k	SE	w_0	SE	r^2	k_1	SE	k_2	SE	w_0	SE	r^2
T. angustifolia	−0.0025	0.0002	104.70	3.3053	0.989	−0.0022	0.0004	0.0006	0.0006	102.17	4.0352	0.990
P. australis leaf	−0.0030	0.0002	102.96	4.5614	0.981	−0.0038	0.0006	−0.0009	0.0007	108.32	6.2009	0.983
P. australis culm	−0.0014	0.0001	103.69	3.1543	1.000	−0.0015	0.0004	−0.0002	0.0009	104.32	4.6028	0.996

W_0 – the initial amount of detritus, k – the exponential daily breakdown coefficient, k_1 – the initial decay coefficient, k_2 – the relative decrease of the decay coefficient (relative decay rate), SE - standard error, r^2 – analogue of the coefficient of determination.

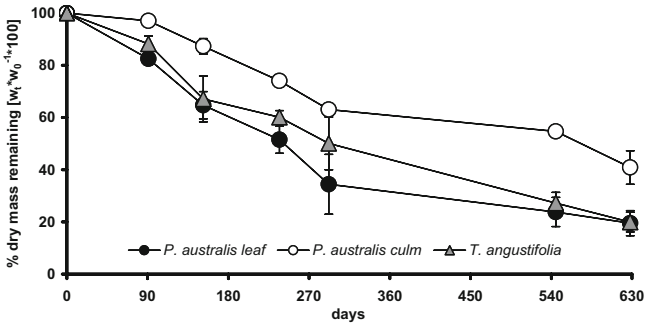

Fig. 1. Changes in the amount of dry mass remaining (mean ± SE, $n = 4$) during the decomposition of *P. australis* and *T. angustifolia* litter (day 0: 06. 12. 2000).

$W_0 \exp((k_1/k_2) * (\exp(k_2 t) - 1))$, where k_1 is the initial decay coefficient, k_2 is the relative decrease of the decay coefficient (the relative decay rate) (Godshalk & Wetzel 1978). The non-linear regression method of the SPSS 7.5 Windows programme package was used for the function fitting.

An analysis of variance (ANOVA, Statgraf 1.0 for Windows) was used for the statistical evaluation of the individual data ($P < 0.05$). The non-linear regression method of the Statistica 6 programme package was used for function fitting by the approximation method of Levenberg-Marquardt.

Results

There were no significant differences in the measured parameters of *P. australis* leaves and culms and *T. angustifolia* in litter bags of different mesh sizes. Therefore the averages of the data obtained on each sampling date are presented.

Mass loss

T. angustifolia reached the 50% breakdown level by 292, *P. australis* leaves by day 242 and *P. australis* culms by day 574 (Fig. 1). Altogther 80% of *T. angustifolia*, 80% of *P. australis* leaf and 59% of the *P. australis* culm dry mass had decomposed by the end of the experiment. *P. australis* leaves decomposed at the fastest rate ($k = -0.0030$; Table 1).

Microbial data

Cellulolytic bacteria: The counts of cellulolytic bacteria were high on the first sampling date (91st day), then they decreased for some 100 days and increased again after 300 days (Fig. 2). Higher bacterial numbers were recorded in the leaves of both macrophytes than in the culms at the start of the study while lower bacterial numbers were observed in the leaves than in the culms later during decomposition. The number of cellulolytic bacteria showed a strong positive correlation ($r^2 > 0.50$) with dry mass, C, NDF, cellulose, hemicellulose content in *T. angustifolia* leaves and stems and in *P. australis* leaves.

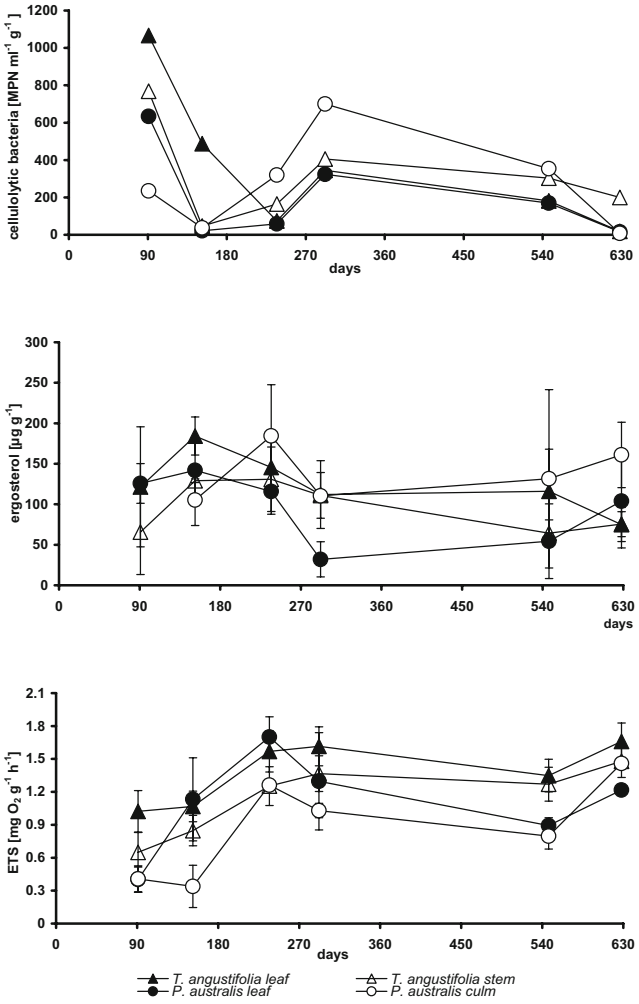

Fig. 2. Microbiological changes (number of cellulolytic bacteria, expressed as most probable number-MPN; fungal biomass expressed as ergosterol concentrations and Electron Transport System: ETS activity) associated with the decomposition of *P. australis* and *T. angustifolia* litter (mean ± SE, $n = 4$).

Fungal biomass: Living fungal biomass (as ergosterol) of *T. angustifolia* ranged from 64 to 184 μg g^{-1} and that of *P. australis* from 32 to 184 μg g^{-1}. Higher ergosterol concentrations were recorded in the leaves of *T. angustifolia* than in the stems, whereas the opposite was observed in *P. australis* (Fig. 2). Ergosterol concentrations

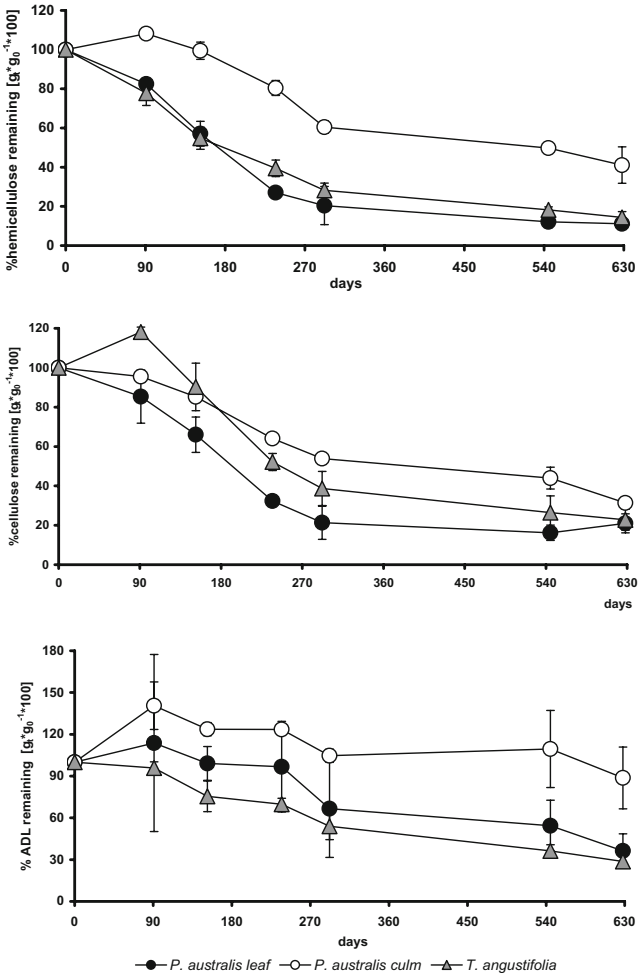

Fig. 3. Changes in the amount of fibers: hemicellulose, cellulose and acid detergent lignin: ADL [g/g $\text{fibre}_t * g_t$) * (g/g $\text{fibre}_o * g_o)^{-1} * 100$] in *P. australis* and *T. angustifolia* litter during the decomposition period (mean ± SE, $n = 4$).

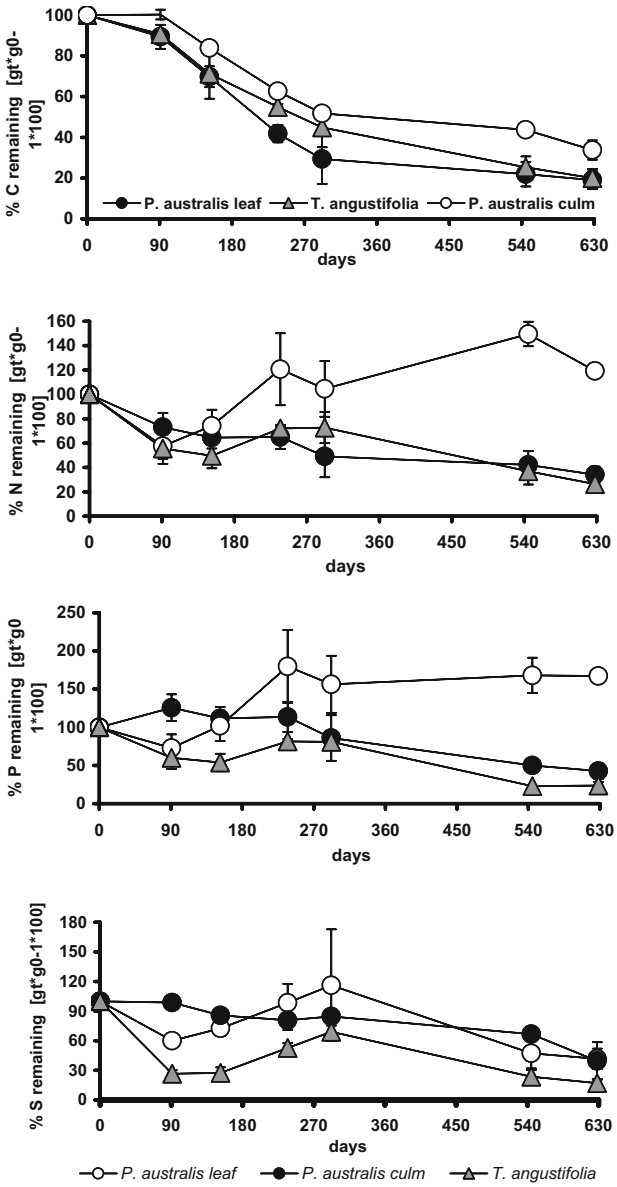

Fig. 4. Changes in the remaining amount of nutrients: C [g/g $C_t * g_t$) * (g/g $C_o * g_o)^{-1} * 100$], N [g/g $N_t * g_t$) * (g/g $N_o * g_o)^{-1} * 100$] P [g/g $P_t * g_t$) * (g/g $P_o * g_o)^{-1} * 100$], S [(g/g $S_t * g_t$) * (g/g $S_o * g_o)^{-1} * 100$] during decomposition of *P. australis* and *T. angustifolia* litter (mean ± SE, $n = 4$).

increased during the first 90 days, then decreased after 250 days and remained low until the end of the study (Fig. 2). The Pearson product moment correlation coefficients (r^2) between the most probable number of the cellulolytic bacteria and ergosterol concentrations were negative for each litter type ($r^2_{\text{P. australis leaf}} = -0.39$, $r^2_{\text{P. australis culm}} = -0.51$, $r^2_{\text{T. angustifolia leaf}} = -0.34$ and $r^2_{\text{T. angustifolia stem}} = -0.60$, $P < 0.05$).

ETS-activity: The ETS activity of *T. angustifola* ranged from 1.02 to 1.66 mg O_2 g^{-1} h^{-1} in leaves and from 0.65 to 1.48 mg O_2 g^{-1} h^{-1} in stems (Fig. 2). The ETS activity of *P. australis* leaves varied between 0.40 and 1.70 mg O_2 g^{-1} h^{-1} and that of the culms between 0.34 and 1.46 mg O_2 g^{-1} h^{-1}. The lowest ETS activity values were recorded in *P. australis* culms. The ETS activity increased from day 91st to 237th while decomposition processes were most active, ergosterol contents were high, and there were few cellulolytic bacteria.

Nutrients and fiber

Changes in fiber content: Hemicellulose content of the *P. australis* leaves and *T. angustifolia* litter decomposed with higher rates than that of the *P. australis* culms (Fig. 3). Cellulose also decomposed with similar pattern and in the following order: *P. australis* leaves, *T. angustifolia* litter, *P. australis* culms (Fig. 3). *P. australis* culms had the highest *acid detergent lignin* (ADL) content. Among the fiber components hemicellulose decomposed fastest, cellulose came next, except for the *P. australis* culms in which both components decomposed at similar rates. In all cases the ADL, the most recalcitrant plant constituent, decomposed slowest, its contents decreased by 71% in *T. angustifolia* litter, by 64% in *P. australis* leaves, and only by 11% in the culms after nearly two years (Fig. 3).

Changes in nutrient content: The C content (Fig. 4) of *P. australis* leaves decreased faster than that of *P.*

Table 2. Changes in C:N ratio of the decomposing *P. australis* and *T. angustifolia* litter (mean ± SE, $n = 4$).

days		0	91	152	237	292	545	628
T. angustifolia	leaf	54.3 ± 0.1	56.0 ± 4.3	52.3 ± 0.1	31.3 ± 27.8	28.6 ± 13.7	20.8 ± 0.0	23.1 ± 1.6
	stem	154.4 ± 8.1	196.5 ± 1.4	201.8 ± 10.6	99.6 ± 8.3	85.8 ± 3.6	72.4 ± 16.2	79.4 ± 18.0
P. australis	leaf	36.6 ± 12.4	44.8 ± 22.4	39.7 ± 12.2	23.6 ± 4.4	21.2 ± 0.1	19.1 ± 0.8	20.2 ± 5.2
	culm	203.9 ± 10.0	355.1 ± 50.9	231.3 ± 18.4	105.7 ± 4.14	101.3 ± 10.1	59.6 ± 12.4	57.2 ± 7.6

australis culms and *T. angustifolia* litter. The *N* content of *P. australis* culms increased while that of the other types of litter decreased (Fig. 4). During the first 91 days of decomposition the P content (Fig. 4) of *P. australis* leaves increased, while the P content of the *P. australis* culms and *T. angustifolia* litter decreased. Later the P content of the *P. australis* culms increased while the contents of *P. australis* leaves and *T. angustifolia* litter decreased. The S content (Fig. 4) of the *T. angustifolia* litter and *P. australis* culms decreased following a similar pattern during the decomposition period. The variation in the S content of *P. australis* leaves was different, it presented a high peak on the 292nd day and after that also decreased.

During the exposure, 81% of the C, 66% of the N, 57% of the P, and 58% of the S contents of the *P. australis* leaves were lost, and *T. angustifolia* litter had lost 80% C, 74% N, 76% P and 83% S. The C and S contents of the *P. australis* culm litter decreased by 66% and 61%, respectively, its N and P contents increased by 19% and 67% respectively by the end of the decomposition experiment. In *P. australis* and *T. angustifolia* leaf litter the C:N ratios (Table 2) were high before exposure, during the decomposition these values decreased until the 292nd day and did not change significantly afterwards. *P. australis* culms had the highest C:N ratio before exposure and this ratio increased during the first three months, then decreased, mainly until the end of decomposition period (Table 2).

Discussion

The lack of significant differences between the examined parameters of *P. australis* leaves and culms and *T. angustifolia* stems with leaves exposed in litter bags of different mesh sizes suggest that the role of the meiofauna in their decomposition dynamics was not appreciable.

Dry mass

The times required for the 50% breakdown of the *P. australis* and *T. angustifolia* in Mason & Bryant (1975) were estimated, respectively, at 426 days and 233 days for *T. angustifolia* stem with leaves and *P. australis* culm with leaves. *T. angustifolia* litter reached 50% breakdown in a similar, but *P. australis* culms in a longer period (Fig. 1). Chergui & Pattee (1990) also obtained similar values for the 50% decomposition time of *P. australis* leaves (233 days). The single exponential model fitted all data sets as well as the decaying coefficient model (Table 1). Hence it may be used for comparison with other publications.

The exponential breakdown rates of *P. australis* leaves at Lake Fertő/Neusiedler See evaluated by Dinka et al. (2004) ($k = -0.0030$ and -0.0025 d^{-1}) were similar to those found here, while the breakdown rates of *P. australis* culms ($k = -0.005$ d^{-1}) were 3.5 times higher. This difference may be due to the differences in physical and chemical conditions of the sampling sites (Lake Fertő is a soda lake with a conductivity of 2000–4000 μS cm^{-1}, Lake Fehér is an alkaline lake with a conductivity of 489–657 μS cm^{-1}. Another reason may have been the structural differences between the reeds from different habitats). The exponential breakdown rates of *P. australis* leaves and culms were similar in our experiments and those reported by Gessner (2000) ($k = -0.0033$–0.0051 and -0.0014 d^{-1}, respectively) who had placed the litter in bags with 4 mm mesh size, which enabled invertebrates to penetrate into the bags. The decay coefficient k of *T. angustifolia* litter from this study ($k = -0.0025$) was lower than the decay coefficient obtained by Jaques & Pinto (1997) for *T. angustifolia* leaf litter ($k = -0.0031$–0.0098) placed in litter bags with 5 mm^2 mesh size which did not stop invertebrates.

The similarities between our and other authors' results suggest that microorganisms play a predominant role in the control of decomposition of aquatic macrophytes; the role of invertebrates is less obvious. The numbers and composition of macroinvertebrates colonizing decomposing plant litter are influenced by the morphology (e.g. different mass and surface ratio, for some species hollow plant litter culms offer a shelter) rather than the chemical composition of the detritus, (Varga unpublished data).

Microbiological parameters

At the beginning of the experiment, cellulolytic bacteria were the main decomposer organisms, and then their numbers decreased with the increase in fungal biomass, which can be explained by competition between the bacteria and fungi. (Maamri et al. 1998; Mille-Lindblom & Tranvik 2003). Probably the increasing fungal biomass had an inhibitory effect on bacterial growth. Some previous studies on microbial colonization of plant detritus in aquatic environments have shown that fungi are primary colonizers whereas bacteria are secondary colonizers (Suberkropp et al. 1976; Lee et al. 1980), although in other studies, bacteria were the first colonizers, as in the present study (Newell 1981; Szabó et al. 2003; Ágoston-Szabó & Dinka 2005).

The increase in the ETS activity from days 92 to 152 (except for *P. australis* culms) and days from 547

to 630 appears to be related to an increase in ergosterol concentration. The further increase in the ETS-activity (from days 152 to 237) was due to both higher fungal biomass and increase in the number of cellulolytic bacteria. From days 237–292, when the ergosterol concentration decreased, increase in cellulolytic bacteria enhanced the ETS-activity of *T. angustifolia* leaves and shoots. The ETS-activity of *P. australis* leaf and culm litter decreased during this period, which may be the result of the decreasing fungal biomass. From days 292–547 all of the examined microbiological parameters decreased. The variation of the ETS activity during decomposition showed similar trends as in other studies (Maamri et al. 1998; Szabó 2003).

The slower degradation of *P. australis* culms than that of *P. australis* leaves and *T. angustifolia* litter may be explained by the chemical composition, e.g. high ADL contents, of these plant tissues, which limited the activity of microbial decomposers. Substantially lower microbial activity was also observed in decomposing *P. australis* culms than in its decomposing leaves by Andersen (1978) and Komínková et al. (2000).

Fibers and Nutrients

Fibers: Different fiber compounds decomposed at different rates over the study period. In the *P. australis* leaves and *T. angustifolia* litter, hemicelluloses was the least resistant to decay followed by cellulose. In *P. australis* culms, which had the highest ADL content, the cellulose unexpectedly decomposed faster than the hemicellulose; in all cases, the ADL decomposed at the slowest rate. ADL retards litter decomposition by several mechanisms (Berg et al. 1984). The close physical and chemical association between ADL, hemicellulose and cellulose probably prevents each substance from being degraded completely independently of the others (Nilsson 1973; Berg et al. 1984). The percentage content of such substances affects the overall decomposition (Fioretto et al. 2005). Probably the strong linkages between the hemicellulose and lignin found in *P. australis* culms are the reason why hemicellulose decomposed slower than the cellulose. Benner et al. (1986) and Dinka et al. (2004) also found that the polysaccharide components of *Carex walteriana* and of *P. australis* decomposed faster than lignin.

Nutrients: Chemical differences in the initial quality of the litter types influenced the rate of decomposition. *P. australis* and *T. angustifolia* leaf litter with a lower initial C:N ratio (Table 2) decomposed faster than the culm litter with a higher initial C:N ratio. As decomposition progressed, the carbon content of the decomposing plant material decreased, the N content per unit material was stable or increased, which resulted in a decrease of the C:N ratio.

The nitrogen content in *P. australis* culms increased after its initial decrease; higher N content was observed here than in *P. australis* leaves and *T. angustifolia* litter because of the higher lignocellulose content of the culms (Dinka et al. 2004). Increased nitrogen content in decaying plant material has also been observed in aquatic ecosystems (Kaushik & Hynes 1971; Polunin 1982; Hietz 1992; Suberkropp 1998; Casas & Gessner 1999). The accumulation of nitrogen and phosphorus during the growing season can be attributed to the uptake of these elements from the surrounding water by microorganisms associated with the decomposing plant material (Gosselink & Kirby 1974; Mason & Bryant 1975; Davis & Van der Valk 1977; Webster & Benfield 1986; Mann 1988; Dinka & Szabó 2002; Dinka et al. 2004). The decrease in the C:N ratio in the remaining litter (Table 2) also shows that nitrogen was immobilized during the decomposition. The S content of *P. australis* leaves and *T. angustifolia* litter increased after an initial decrease; greater increases were observed in *P. australis* leaves. The S content of *P. australis* culms decreased continuously. This suggests that the microbial communities developing on the different substrate types had different demands for sulfur, which must have been supplied from the surrounding water.

We can conclude that compounds of different fibers decomposed at different rates: in the *P. australis* leaves and *T. angustifolia* litter, the hemicelluloses were the least resistant to decay followed by cellulose; the ADL decomposed at the slowest rate. The nutrient content in litter (mainly N) appears to influence the early stages of decomposition (first 237 days) whereas later stages appear to be influenced by the percentage of lignin. At the beginning of decomposition, cellulolytic bacteria were the main decomposer organisms; the number of cellulolytic bacteria decreased with increases in fungal biomass. Since the decomposition took place under similar conditions, the slower degradation of *P. australis* culm litter presumably was due to the different chemical composition of these plant organs, and, consequently, different activity of microbial decomposers.

Acknowledgements

The authors express their cordial thanks to Drs W. Armstrong and J. Armstrong for reviewing the English of this manuscript and to J. Květ for providing constructive suggestions. This work was supported by the NKFP 3B/0014/2002 project.

References

Ágoston-Szabó E. & Dinka M. 2005. Decomposition of *Typha angustifolia* (L) litter at a shallow lake in Hungary. Verh. Internat. Verein. Limnol. **29:** 971–974.

Andersen F.O. 1978. Effects of nutrient level on the decomposition of *Phragmites communis* Trin. Arch. Hydrobiol. **84:** 42–54.

Benner R., Moran A.M. & Hodson R.E. 1986. Biogeochemical cycling of lignocellulosic carbon in marine and freshwater ecosystems: relative contributions of prokaryotes and eukaryotes. Limnol. Oceanogr. **31:** 89–100.

Berg B., Ekbohm G. & McClaughterty C. 1984. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long-term decomposition in a Scots pine forest. IV. Can. J. Bot. **62:** 2540–2550.

Best E.P.H., Zippin M. & Dassen J.H.A. 1982. Studies on decomposition of *Phragmites australis* under laboratory conditions. Hydrobiol. Bull. **16:** 21–33.

Casas J.J. & Gessner M.O. 1999. Leaf litter breakdown in a Mediterranean stream characterized by travertine precipitation. Freshwat. Biol. **41:** 781–793.

Chergui H. & Pattee E. 1990. The processing of leaves of trees and aquatic macrophytes in the network of river Rhone. Int. Revue ges. Hydrobiol. **75:** 281–302.

Davis C.B. & Van der Valk A.G. 1977. The decomposition of standing fallen litter of *Typha glauca* and *Scirpus fluviatilis*. Can. J. Bot. **56:** 662–675.

Day Jr. J.W., Pieczińska E. & Úlehlová B. 1998. Further fate of organic matter in wetlands. pp. 187–188. In: Westlake D.F., Květ J. & Szczepański A. (eds), The production ecology of wetlands. Cambridge University Press.

Dinka M., Ágoston-Szabó E. & Tóth I. 2004. Changes in nutrient and fibre content of decomposing *Phragmites australis* litter. Internat. Rev. Hydrobiol. **89(5–6):** 519–535.

Dinka M. & Szabó E. 2002. A nád különböző szerveinek dekompozíciója. (Decomposition of reed organs at Lake Fertő/Neusiedler See. In Hungarian with an English abstract). Hidrol. Közl. **82:** 24–27.

Fioretto A., Nardo C. Di, Papa S. & Fuggi A. 2005. Lignin and cellulose degradation and nitrogen dynamics during decomposition of three leaf litter species in a Mediterranean ecosystem. Soil Biol. & Biochem. **37:** 1083–1091.

Fleeger J.W., Tita G., Carman K.R., Millword R.N., Moser E.B., Portier R.J. & Gambrell R.P. 2006. Does bioturbation by benthic fish modify the effects of sediment contamination on saltmarsh benthic microalgae and meiofauna? J. Exp. Mar. Biol. and Ecol. **330:** 180–194.

Gessner M.O. 2000. Breakdown and nutrient dynamics of submerged *Phragmites* shoots in the littoral zone of a temperate hardwater lake. Aquatic Bot. **66:** 9–20.

Gessner M.O. 2001. Mass loss, fungal colonization and nutrient dynamics of *Phragmites australis* leaves during senescence and early aerial decay. Aquatic Bot. **69:** 325–339.

Gessner M.O. & Newell S.Y. 2002. Biomass, growth rate, and production of filamentous fungi in plant litter, pp. 390–408. In: Hurst C.J., Crawford R.L., Knudsen G.R., McInerney M.J. & Stetzenbach L.D. (eds), Manual of Environmental Microbiology, 2nd ed., ASM Press, Washington, DC, USA.

Godshalk G.L. & Wetzel R.G. 1978. Decomposition of aquatic angiosperms. II. Particulate components. Aquatic Bot. **5:** 301–327.

Gosselink J.G. & Kirby C.J. 1974. Decomposition of salt marsh grass *Spartina alterniflora* Loisel. Limnol. Oceanogr. **19:** 825–832.

Hietz P. 1992. Decomposition and nutrient dynamics of reed *(Phragmites australis* (Cav.) Trin ex. Steud) litter in Lake Neusiedl, Austria. Aquatic Bot. **43:** 211–230.

Jaques N. & Pinto P. 1997. Seasonal differences in the decomposition of *Typha angustifolia* leaves in a Mediterranean river. Limnetica. **13 (2):** 19–23.

Kaushik N.K. & Hynes H.B.N. 1971. The fate of the dead leaves that fall into streams. Arch. Hydrobiol. **68**: 465–515.

Kenner R.A. & Ahmed S.I. 1975. Measurement of electron transport system activities in marine phytoplankton. Mar. Biol. **33:**119–127.

Komínková D., Kuehn K.A., Büsing D., Steiner D. & Gessner M.O. 2000. Microbial biomass, growth, and respiration associated with submerged litter of *Phragmites australis* decomposing in a littoral reed stand of a large lake. Aquat. Microb. Ecol. **22:** 271–282.

Kuehn K.A. & Suberkropp K. 1998. Decomposition of standing litter of the freshwater emergent macrophyte *Juncus effusus*. Freshwat. Biol. **40:** 717–727.

Lee C., Howarth R.W. & Howes B.L. 1980. Sterols in decomposing *Spartina alterniflora* and the use of ergosterol in estimating the contribution of fungi to detrital nitrogen. Limnol. Oceanogr. **25:** 290–303.

Leichtfried M. 1999. Biofilme in Oberflächengewässern. Schriftenreihed. österr. Wasser- und Abfallwirtschaftsverband. **127:** 101–112.

Maamri A., Chauvet E., Chergui H., Gourbiere F. & Pattee E. 1998. Microbial dynamics on decaying leaves in a temporary Moroccan river. I. Fungi. Arch. Hydrobiol. **144 (1):** 41–59.

Mann K.H. 1988. Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Oceanogr. **17:** 58–67.

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

Mille-Lindblom L.J. & Tranvik L.J. 2003. Antagonism between bacteria and fungi on decomposing aquatic plant litter. Microb. Ecol. **45:** 173–182.

Newell S.Y. 1981. Fungi and bacteria in or on leaves of eelgrass (*Zostera marina*) from Chesapeake Bay. Appl. Environ. Microbiol. **41:** 1219–1224.

Newel S.Y. 1993. Decomposition of shoots of a salt-marsh grass. Adv. Microb. Ecol. **13:** 301–326.

Nilsson T. 1973. Studies on wood degradation and cellulolytic activity of microfungi. Stud. For. Suec. **104:** 4–40.

Olson J.S. 1963. Energy storage and the balance of producers and decomposition in ecological systems. Ecology **44:** 322–330.

Pieczyńska E. 1986. Sources and fate of detritus in the shore zones of lakes. Aquatic Bot. **25:** 153–166.

Pieczyńska E. 1993. Detritus and nutrient dynamics in the shore zone of lakes: a review. Hydrobiol. **251:** 49–58.

Polunin N.C.V. 1982. Processes contributing to the decay of reed (*Phragmites australis*) litter in fresh water. Arch. Hydrobiol. **94:** 182–209.

Polunin N.C.V. 1984. The decomposition of emergent macrophytes in fresh water. Adv. Ecol. Res. **14:** 115–166.

Rodina A.G. 1972. Methods in aquatic microbiology. University Park Press, Baltimore.

Ruzicka J. & Hansen E.H. 1975. Flow Injection Analysis. Part II. Ultrafast determination of phosphorus in plant material by continuous flow spectrophotometry. Anal. Chim. Acta. **79:** 9–91.

Suberkropp K. 1998. Microorganisms and organic matter processing, pp. 120–143. In: Naiman R.J. & Bilby R.E. (eds), River Ecology and Management: Lessons from the Pacific Coastal Ecoregion, Springer Verlag, New York.

Suberkropp K., Godshalk G.L. & Klug M.J. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology **57:** 720–727.

Szabó E. 2003. The use of the tetrazolium reduction test for the detection of the terminal electron transport system (ETS) activity in decomposing reed (*Phragmites australis* /Cav./ Trin. ex Steud.) rhizome. Ann. Limnol.-Int. J. Lim. **39 (1):** 63–70.

Szabó E., Dinka M. & Némedi L. 2003. A dekomponálódó nádrizóma kémiai összetételének és mikrobiális aktivitásának változása egy sekély tóban. Hidrol. Közl. **83 (1):** 143–146.

Van Soest P.J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for determination of fiber and lignin. JAOAC **46:** 829–835.

Webster J.R. & Benfield E.F. 1986. Vascular plant breakdown in freshwater ecosystems. Ann. Rev. Ecol. Syst. **17:** 567–594.

Westlake D.F. 1982. Primary productivity of water plants, pp. 165–180. In: Symoens J.J., Hooper S.S. & Compere P. (eds), Studies on Aquatic Vascular Plants. Handbook of Vegetation Science. Royal Botanical Society of Belgium, Brussels.

Wetzel R.G. 2001. Limnology, lake and river ecosystems. San Diego, Academic Press, 1006 pp.

Received September 20, 2007
Accepted March 17, 2008