Microbial dynamics associated with decomposing *Typha angustifolia* litter in two contrasting Lake Erie coastal wetlands

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ABSTRACT: We compared the decomposition of sediment-associated litter of *Typha angustifolia* in 2 Lake Erie coastal wetlands, examining the effects of sedimentation on microbial biomass, production and litter decay dynamics. Experimental manipulations of sediment had no statistically significant effect (p > 0.05) on microbial biomass or metabolism. However, unforeseen differences between wetland sites (i.e. permanently inundated vs. exposed) had a major influence on microbial colonization and growth, litter mass loss, and nutrient dynamics. Litter-associated bacterial biomass and production were greater at the inundated site vs. the exposed wetland site (e.g. 487 vs. 158 µg C g^{-1} detrital C after 146 d, respectively). In contrast, fungal biomass and production were greater at the exposed site (e.g. 125 vs. 56 mg C g^{-1} detrital C after 146 d, respectively). Microbial degradative enzymes involved in the acquisition of phosphorus, nitrogen and carbon followed similar patterns as observed for fungal biomass and production, with higher activities associated with decaying litter at the exposed site. Microbial respiration rates were initially similar at both sites, but increased at the inundated site towards the end of the study period. Despite greater litter-associated microbial biomass, production and enzyme activities at the exposed wetland site, rates of litter mass loss were similar, suggesting that the greater metabolic potential of microbiota at the exposed site may have been offset by environmental conditions (e.g. fluctuations in water availability). Although mass loss rates were similar, significant differences in nutrient dynamics were observed, with higher N and P associated with higher litter-associated microbial biomass. These results illustrate how microbial decay dynamics can potentially interact with environmental variables (e.g. water availability) to modulate the carbon and nutrient dynamics of a litter resource that dominates many wetlands.

KEY WORDS: Wetlands · Sedimentation · Litter · Decomposition · Fungi · Bacteria · Nitrogen · Phosphorus

INTRODUCTION

The Great Lakes region contains approximately 1209 km^2 of wetland surface area distributed across 1370 distinct coastal wetlands along the United States shorelines alone (Herdendorf et al. 1981). Emergent vascular plants, such as the genera *Typha*, *Carex* and *Scirpus*, frequently dominate annual net primary production (NPP, >2 kg m^{-2} yr^{-1}) within these coastal wetlands and serve as important reservoirs of nutrients (Mitsch & Gosselink 2000). As a consequence, these emergent plant communities can influence nearly all the structural and functional aspects of these wetlands, as well as the nutrient and metabolic characteristics of adjacent lake ecosystems (Wetzel 1990, 1992).

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In many freshwater wetlands, most of the annual plant production is not consumed during the growing season (e.g. Wetzel & Howe 1999), but eventually enters the detritus pool where it is broken down and mineralized by microorganisms. These processes mediate the retention and release of nutrients sequestered in plant tissues and control the flow of carbon and nutrients to higher trophic levels (Mann 1988, Hopkinson 1992). One factor affecting plant litter decomposition is sedimentation. Sediment retention is often cited as a beneficial function of wetlands (Mitsch & Gosselink 2000); however, elevated sediment accumulation may represent a disturbance with potentially negative consequences for important detrital processes. Vargo et al. (1998) reported significant decreases in both the mass loss rate and N concentration of sediment-associated *Typha latifolia* litter exposed to experimental increases in sediment deposition. Additional research by Martin & Neely (2000) also demonstrated significant declines in total benthic macroinvertebrate density and richness in response to sediment additions to a *T. angustifolia* marsh, further pointing to a potential sediment-induced impact on detrital-based food-webs.

Despite an abundance of quantitative data on plant litter decay and nutrient cycling in wetlands (e.g. Brinson et al. 1981, Polunin 1984, Webster & Benfield 1986, Bayley & Mewhort 2004), the effects of sedimentation on wetland litter decay processes have not been related to the composition and dynamics of the microbial decomposer communities that control nutrient retention/release and the fate of carbon. We evaluated these connections by comparing microbial community metabolism (i.e. biomass, production and respiration of bacteria and fungi) and extracellular enzyme activities associated with the decomposition of *Typha angustifolia* leaf litter in 2 Lake Erie coastal wetlands under varied sedimentation regimes. Microbial dynamics were compared to litter mass loss rate and immobilization of N and P. These data provide an integrated 'bottom-up' view of microbial decomposition for a resource that dominates the carbon and energy dynamics of many freshwater wetlands.

MATERIALS AND METHODS

Study site. This study was conducted from June 2001 through September 2002 in 2 Lake Erie coastal wetlands: Winous Point (WP) and Lake Erie Metro Park (LEMP). The WP wetland is located in the Winous Point Conservation Area on the SW shore of Lake Erie near Port Clinton, Ohio (41° 28′ N, 82° 59′ W). The study site was situated in a western portion of the marsh in a zone dominated by the emergent macro-

phyte *Typha angustifolia* and *Nulumbo lutea*. The site is isolated from nearby Sandusky Bay by earthen dike impoundments. LEMP is located on the NW shore of Lake Erie at the mouth of the Detroit River, near Brownstone, Michigan (42° 04′ N, 83° 14′ W). This site is a more hydrologically open system, containing a variety of habitats that freely interact with Lake Erie. The site is dominated by the emergent macrophytes *Phragmites australis* and *T. angustifolia*.

Experimental design. A randomized block design was used to investigate the effects of sediment size and loading rates on microbial decay of *Typha angustifolia* litter within these 2 wetland sites; 15 enclosures were randomly established at each site. Enclosures were 1.5 m long × 1.5 m wide × 1.0 m high and constructed using 1 mm fiberglass mesh and PVC tubing supports. Three enclosures were randomly assigned to 1 of 5 sediment treatments: control (no added sediment), single fine sediment (clay) application, multiple fine applications, single coarse sediment application, and multiple coarse applications. Goldart clay (Rovin Ceramics) with an average particle size of 5.8 ± 1.6 µm was used for fine sediment applications. Coarse sediment applications used natural sediment collected from the corresponding wetland sites. Collected sediment was air dried and passed through a 2.5 mm^2 standard sifting screen before application in the enclosures. Previous studies using this technique for wetland sediments in SE Michigan reported that sediment particle sizes averaged 201 ± 17 µm (Vargo et al. 1998). Each sediment application resulted in a deposition of 1633 g of sediment, which was equivalent to 725 g m^{-2} or a sediment layer of 0.8 mm. This amount reflects natural sediment inputs of 1 to 2 cm yr^{-1}, which generally arrive episodically throughout the year.

Field procedures. Over-wintered standing-dead leaf litter of *Typha angustifolia* (upper $\frac{1}{3}$ of leaf blade) was collected at LEMP and WP in March and May 2001, respectively. Collected litter was returned to the laboratory, air-dried, cut into ca. five 10 cm pieces; ca. 3 g of litter was enclosed in 20 × 15 cm plastic coarse (5 mm) mesh litter bags. Additional litter samples were dried (60°C), weighed, and ashed (≥4 h at 500°C) for determination of air-dried mass to ash-free dry mass (AFDM) ratios. Twenty litter bags containing corresponding *T. angustifolia* litter from each wetland site were either submerged (WP) or placed in a single layer on the sediment surface (LEMP) within each enclosure in May 2001. Single sediment applications (fine or coarse) to the treatment enclosures were conducted on the first sampling date only. Multiple sediment applications were performed monthly. Sediment additions were applied to the treatment enclosures in the form of slurry, which was sprinkled from a common perforated watering can.

Three litter bags from each enclosure were retrieved periodically on 5 occasions from June 2001 to September 2002, placed on ice in a cooler, and returned to the laboratory. One litter bag from each enclosure was used for the determination of litter mass loss rates and nutrient concentrations. The remaining litter bags were used for determination of microbial biomass and production (bacteria and fungi), rates of microbial respiration, microbial enzyme activities, and dissolved organic carbon (DOC) release.

Mass loss and nutrient contents. Intact plant material was removed from litter bags, washed gently to free adhering macroinvertebrates, and dried at 60°C to a constant weight. Dried plant material was ground to a 425 μm particle size (40 mesh) using a Wiley mill, and subsamples combusted (≥4 h at 500°C) to determine the AFDM remaining. Litter decay rates (–k) were calculated using a nonlinear ($M_t = M_0 \times e^{-kt}$) regression model and a linear regression model after log transformation (ln (M_t/M_0) = $-kt$ + b), where M_t is the AFDM at Time t (d) and M_0 is the initial % AFDM in the litter bags. Nitrogen and phosphorus concentrations (%) were determined spectrophotometrically using a Bran-Lubbe Autoanalyzer II System (Bran-Lubbe Methods: 696-82W and 455-762/A) after high temperature (390°C) digestion of ground litter subsamples (ca. 300 mg dry wt) in $CuSO_4$/sulphuric acid (see Kuehn & Suberkropp 1998a) using a Bran-Lubbe block digester.

Bacterial productivity and biomass. Bacterial productivity associated with *Typha angustifolia* litter was estimated from rates of [3H]-thymidine (TdR) incorporation into bacterial deoxyribonucleic acid (DNA) (see Sinsabaugh & Findlay 1995). Subsamples (ca. 50 mg dry wt) of leaf litter from litter bags were placed in sterile 15 ml centrifuge tubes containing 5 ml of membrane-filtered (0.22 μm) wetland water and 1.48 MBq [3H]-thymidine (specific activity = 3 TBq mmol^{-1}, Amersham Biosciences), vortexed, and incubated for 1 h at 23°C; 4 replicates and 2 formalin-killed controls were run for each litter bag sample. After incubation, 5 ml of 10% buffered formalin were added to the sample tubes and vortexed. Extraction and quantification of radiolabeled DNA from incubated samples followed procedures described in Sinsabaugh & Findlay (1995). Results were calculated as μg of bacterial C produced g^{-1} detrital C d^{-1} using conversion factors of 2×10^9 bacterial cells produced nmol^{-1} TdR incorporated and the mean bacterial C content based on bacterial biovolume estimates from epifluorescence direct count microscopy (see below).

Bacterial biomass associated with litter was determined by epifluorescence microscopy after staining with SYBR Green I (Molecular Probes) (see Noble & Fuhrman 1998). Subsamples of leaf litter (ca. 100 mg dry wt) were placed in 20 ml glass scintillation vials containing 10 ml of 2% (v/v) filtered (0.2 μm), phosphate-buffered formalin (sodium pyrophosphate, 0.1% w/v). Bacterial cells attached to litter samples were detached by ultrasonic probe sonication (Cole-Parmer, power output 50 W) for 1 min on ice (see Buesing & Gessner 2002). After sonication, samples were mixed and sample aliquots (30 to 200 μl) were vacuum filtered (20 kPa) through 25 mm supported Anodisc filters (0.2 μm pore size, Whatman), with a 0.8 μm mixed-ester membrane backing filter (Fisher Scientific).

Filters were removed, placed sample side up on separate drops of 2.5% (v/v diluted from stock) SYBR Green I in clean plastic Petri dishes, and stained for 15 min in the dark. Filters were then mounted on glass slides with 30 μl antifade mounting solution containing 50% glycerol, 50% PBS (120 mM NaCl, 10 mM NaH_2PO_4 at pH 7.5) and 0.1% p-phenylenediamine. A 25 mm circular glass cover slip was then placed on the filter surface and a drop of immersion oil applied (Cargille, Type DF, Formula 1261). Bacterial cells were assigned into 6 categories according to size and shape, and cells were enumerated (1000× magnification) in a minimum of 10 fields (≥350 cells) using a Leica DMRB epifluorescence microscope. Video capture photographs were taken for biovolume estimates using a DEI-470 video camera system (Optronics Engineering); 50 photographs of bacteria samples from each wetland site were examined and bacterial size classes measured using Scion Image analysis software (see Gulis & Suberkropp 2003). Biovolume (V) estimates (μm^{-3}) for each size class were calculated from length (l) and width (w) measurements using the formula $V = w^2/4 \times (l-w) \times \pi + w^3/6 \times \pi$. Biovolume estimates were converted to bacterial carbon (fg C) using a formula (C = $89.5 \times V^{0.59}$), which accounts for size-dependent differences in carbon density of bacterial cells (Simon & Azam 1989).

Fungal productivity and biomass. Instantaneous growth rates of fungi were estimated from rates of [1-14C]acetate incorporation into ergosterol (see Gessner & Newell 2002). Subsamples (ca. 0.05 g AFDM) of leaf litter from litter bags were incubated in sterile 20 ml glass scintillation vials containing 4 ml of filtered (0.7 μm, Whatman GF/F) wetland water and 5 mM Na[1-14C]acetate (specific activity = 48 MBq mmol^{-1}, MP Biomedicals) for 4 to 5 h at 23°C. Incorporation of [1-14C]-acetate label was stopped by placing vials on ice and immediately filtering (0.7 μm, Whatman GF/F) the contents. Filters and litter pieces were washed twice with 4 ml of filtered wetland water, placed in scintillation vials, and stored frozen at –20°C until analyzed. Frozen samples were lyophilized, weighed, and ergosterol extracted in alcoholic KOH (0.8% KOH in HPLC grade methanol, total extraction volume 10 ml) for 30 min at 80°C in tightly capped digestion tubes

with constant stirring. The resultant crude litter extract was cleaned by solid phase extraction (Gessner & Schmitt 1996), and ergosterol was purified and quantified by high pressure liquid chromatography (HPLC). A LichroSpher 100 RP-18 column (0.46×25 cm, Merck) maintained in a Shimadzu column oven (CTO-10AS) at 40°C and connected to a Shimadzu autosampler (SIL-10AD) and Shimadzu liquid chromatograph system (Pumps LC-10AT, Controller SCL-10A) was used for separation and analysis. The mobile phase was HPLC grade methanol at a flow rate of 1.5 ml min^{-1}. Ergosterol was detected at 282 nm using a Shimadzu (SPD-10A) UV/VIS detector (retention time = ca. 8 min), and was identified and quantified based on comparison with ergosterol standards (Fluka Chemical).

Ergosterol fractions eluting from the HPLC column were collected in 20 ml scintillation vials using an automated Advantec (SF-3120) fraction collector system, mixed with 10 ml of scintillation fluid (Ecolume, MP Biomedicals), and radioactivity assayed by using a Beckman LS 6500 scintillation counter, corrected for quenching. For determination of litter-associated fungal biomass, litter ergosterol concentrations were converted to fungal carbon assuming a conversion factor of 10 μg ergosterol mg^{-1} fungal C, and 50 % C in fungal dry mass (Gessner & Newell 2002). For determination of fungal production, rates of acetate incorporation were converted to fungal growth rates, assuming 12.6 μg fungal biomass nmol^{-1} acetate incorporated (Gessner & Newell 2002).

Microbial respiration. Rates of microbial respiration associated with decomposing *Typha angustifolia* litter were estimated from measurements of dissolved oxygen consumption (see Carter & Suberkropp 2004). Subsamples (ca. 0.1 g AFDM) of leaf litter were placed into small custom-made glass incubation chambers containing ca. 25 ml of filtered (0.7 μm GF/F Whatman) wetland water. Changes in dissolved oxygen concentration within chambers were monitored every 15 s for 30 min using a YSI 5010L BOD probe connected to a YSI 5100 dissolved oxygen meter (Yellow Springs Instrument). All measurements were conducted in darkness at 23°C. Additional chambers (ca. 2 to 4) containing only filtered wetland water were also monitored as controls. Respiration rates were calculated as the slope of regression lines from samples minus the mean slope of the controls. Rates of oxygen consumption were converted to rates of CO_2 evolution, assuming a respiratory quotient of 0.8.

DOC release. Subsamples of collected litter (ca. 100 mg dry wt) were placed into 50 ml Erlenmeyer flasks containing 25 ml of filtered (0.7 μm GF/F Whatman) wetland water for determining the amount of extractable DOC released from decomposing litter (see Komínková et al. 2000). Samples were incubated at 23°C for 24 h on a platform orbital shaker (50 rpm) in darkness. After incubation, samples were filtered through pre-ashed 0.7 μm GF/F filters (Whatman). The resultant filtrates were collected in 20×125 mm Teflon-lined screw cap tubes and the volume measured. Samples were preserved with 250 μl concentrated phosphoric acid and stored at 4°C until analyzed for DOC using a Shimadzu TOC-500 analyzer. After incubation, litter samples were frozen (–20°C), lyophilized, weighed and ashed (as above) to determine sample AFDM. All values were corrected for DOC concentrations measured in non-litter containing wetland water controls.

Enzyme assays. Microbial extracellular enzyme activity (EEA) was quantified in 96-well microplates using established fluorometric assays (see Sinsabaugh et al. 2002). Briefly, subsamples (corresponding to ca. 50 mg dry wt) of *Typha angustifolia* from collected litter bags were placed into 125 ml Nalgene bottles containing 125 ml of 50 mM, pH 5, acetate buffer. Samples were homogenized using a Brinkman polytron and activity assayed for 5 extracellular enzymes. Cellulolytic activity was measured by using assays for β1,4-glucosidase (EC.3.2.1.21), cellobiohydrolase (EC.3.2.1.91) and β1,4-xylosidase (EC.3.2.1.37). Corresponding fluorometric (methylumbelliferyl, MUB) substrates were 4-MUB-β-D-glucoside, 4-MUB-β-D-cellobioside, and 4-MUB-β-D-xyloside, respectively. Assays for acid phosphatase (EC.3.1.3.2) and β-n-acetyl-b-glucosaminidase (EC.3.2.1.30), enzymes involved in organic phosphorus and nitrogen acquisition, were assayed using 4-MUB-phosphate and 4-MUB-n-acetyl-β-glucosaminide, respectively. All assays were conducted at 23°C using procedures previously described by Sinsabaugh et al. (1994). Enzyme activities are expressed in units of μmol of substrate converted g^{-1} detrital C h^{-1}.

Data analyses. All statistical analyses were performed using SYSTAT (Wilkinson et al. 1992), with differences considered significant at the $p < 0.05$ level. Data were analyzed using repeated-measures ANOVA with site and treatment as grouping factors. All data, if needed (e.g. enzyme activities), were log-transformed prior to analysis in order to achieve a normal distribution and reduce heteroscedasticity. Plant litter decomposition rates ($-k$) between wetland sites were compared with analysis of covariance (ANCOVA).

RESULTS

Sedimentation

Experimental additions of sediment (fine or coarse) to *Typha angustifolia* litter enclosures did not have a statistically significant effect ($p > 0.05$) on litter mass

loss, nutrient concentrations, or microbial parameters. However, unforeseen environmental conditions, possibly resulting from hydrologic differences between the 2 study sites (i.e. permanently inundated vs. exposed), may have obscured our ability to experimentally test the effects of increased sedimentation on litter mass loss, nutrient patterns (N and P), and decay dynamics of litter-inhabiting microbiota. At the LEMP site, surface sediments were always water saturated, but overlying standing water was never present during the study period. As a consequence, experimental sediment additions were applied directly to the exposed litter surface. This applied sediment would dry to the litter surface, but was subject to removal by random precipitation events. Thus, large differences existed between treatment replicates in their duration and exposure to sediment accumulation. In addition, at the permanently inundated WP site, the standing water was naturally turbid and additional sediment applications may not have added significantly to the natural accumulation at this site. Statistically significant differences ($p < 0.05$) in litter mass loss, nutrient patterns (N and P), and decay dynamics of litter-inhabiting microbiota were noted between the 2 wetland sites. Consequently, data were pooled across sediment treatments within each site.

Litter mass loss and nutrient dynamics

Statistically significant differences in mass loss patterns of *Typha angustifolia* were observed between the 2 wetland sites ($p < 0.001$), with 68% mass loss at the permanently inundated wetland site by 400 d, compared to 55% mass loss at the exposed site (Fig. 1). The
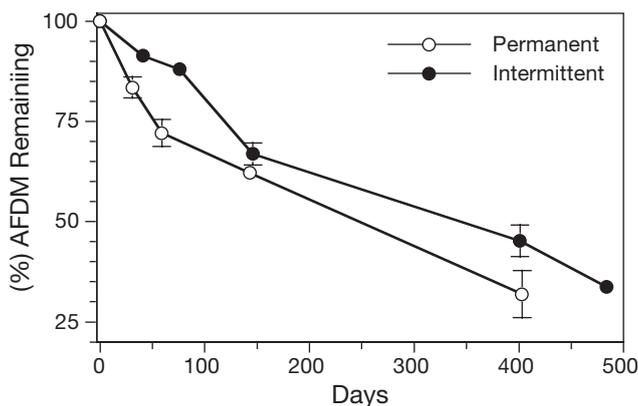
respective decay rate coefficients ($-k$) were $0.0245 \pm 0.0003 \text{ d}^{-1}$ (mean ± asymptotic standard error, ASE, $r^2 = 0.64$) and $0.00215 \pm 0.00001 \text{ d}^{-1}$ ($r^2 = 0.87$), and were statistically significantly different ($p < 0.05$, ANCOVA). Data on litter mass loss and nutrient concentrations from the permanently inundated (WP) site were not possible for the last sampling date, because insufficient amounts of litter remained in the litter bags; however, the small amount of material that did remain was used for microbial-related analyses.

Statistically significant differences in leaf litter nitrogen (N) and phosphorus (P) concentrations were also observed between the 2 sites ($p < 0.01$). Litter P concentrations increased during decomposition at both study sites (Figs. 2A & 3A), with higher concentrations of P accumulating in *Typha angustifolia* litter at the permanently inundated site vs. the exposed site (0.17% vs. 0.12% after 400 d). Litter N concentrations also increased at both sites during the first 400 d of decay (Figs. 2B & 3B). However, in contrast to P concentrations, higher litter N concentrations were observed at the exposed site (1.5% vs. 1.2%) than at the permanently inundated site. After 400 d, however, N concentrations decreased significantly (Fig. 3B).

Total amounts of immobilized P (mg) followed a similar trend to P concentrations (Figs. 2A & 3A). In con-
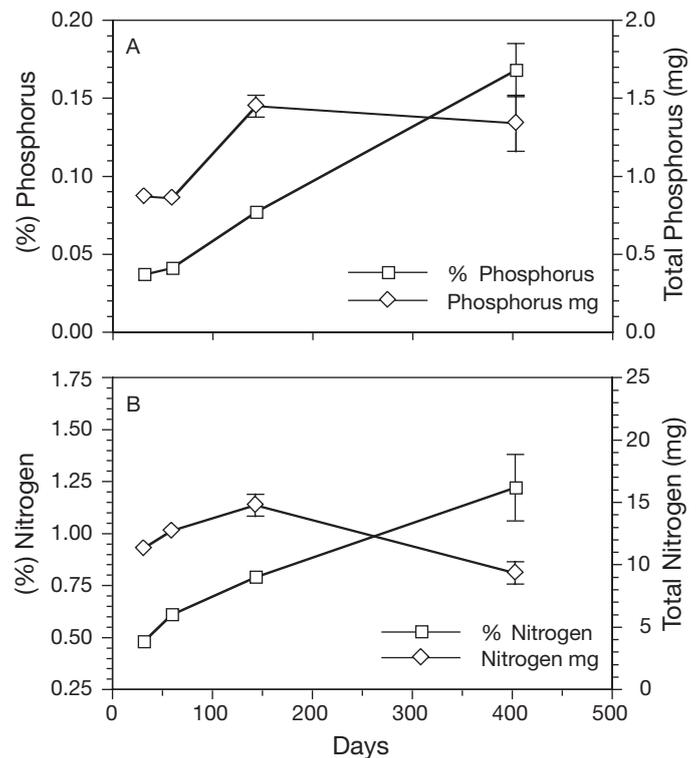

Fig. 1. *Typha angustifolia*. Mean ± SE (n = 5) percent ash-free dry mass (AFDM) of leaf litter remaining in coarse-mesh litter bags at wetland study sites. Permanent, Intermittent: permanently and intermittently inundated sites, respectively. Here and in Figs 2 & 3, lack of error bars indicates SEs smaller than data points

Fig. 2. *Typha angustifolia*. Mean ± SE (n = 5) changes in concentration (%) and total content (mg) of (A) phosphorus and (B) nitrogen of leaf litter in litter bags at the permanently inundated wetland site (Winous Point)
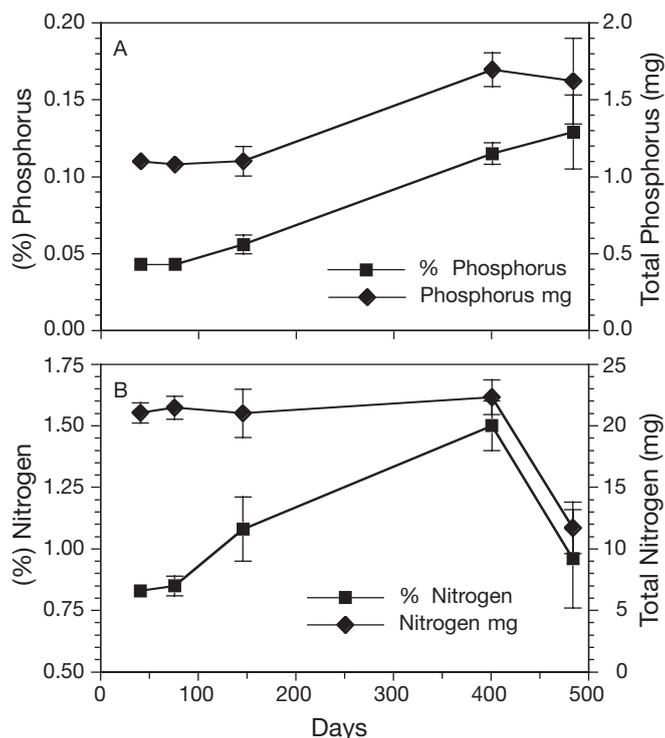
Fig. 3. *Typha angustifolia*. Mean ± SE (n = 5) changes in concentration (%) and content (mg) of (A) phosphorus and (B) nitrogen of leaf litter in litter bags at the intermittently inundated wetland site (Lake Erie Metro Park)

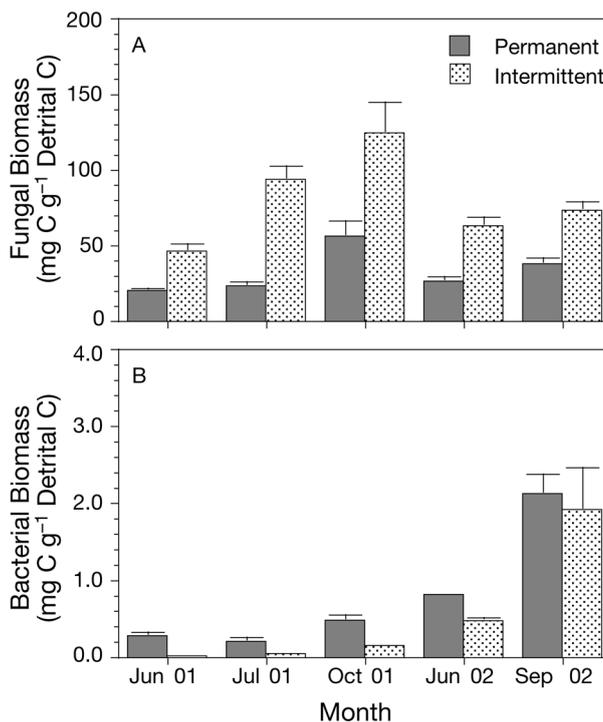Fig. 4. *Typha angustifolia*. Mean + SE (n = 5) (A) fungal and (B) bacterial biomass associated with decomposing leaf litter at the 2 wetland study sites

trast to P, total amounts of immobilized N (mg) either remained stable (exposed site) or increased slightly (inundated site) during the initial phases of litter decay, followed by a statistically significant decrease (p < 0.05) in total N at both sites by the end of the study period (Figs. 2B & 3B). Statistically significant differences in total N were observed between the study sites (p < 0.001), with litter at the permanently flooded site having markedly lower total N (20 to 58%) throughout the study period.

Microbial biomass and production

Throughout the study period there were statistically significant differences in litter-associated microbial biomass (fungi) and production (bacteria and fungi) between the 2 sites (p < 0.001). Fungal biomass concentrations on decaying *Typha angustifolia* leaf litter were 2 to 4 times higher at the exposed site than the permanently inundated site (Fig. 4A). At the exposed site, litter-associated fungal biomass increased to a maximum of 125 ± 20 mg C g^{-1} detrital C (October, 146 d), then decreased to 74 mg C g^{-1} detrital C by the last sampling date (484 d). Fungal biomass associated with submerged litter at the permanently in-

undated site followed a similar seasonal trend, but values reached a maximum of only 57 ± 10 mg C g^{-1} detrital C.

Bacterial biomass associated with decaying *Typha angustifolia* leaves showed a statistically significant increase (p < 0.001) during litter decay at both sites (Fig. 4B). In contrast to fungal biomass patterns, bacterial biomass was higher (2 to 13 times) at the permanently inundated site during most of the study period, but this difference was not statistically significant (p > 0.05). Despite the apparent differences between study sites (e.g. hydrologic), fungal decomposers accounted for ≥94% of total microbial biomass associated with decaying *T. angustifolia* litter (Table 1).

Fungal growth rates (μ_f, P:B) associated with *Typha angustifolia* were higher on average at the permanently inundated site ($4.2 \pm 3.3\%$ d^{-1}) than the exposed site ($2.7 \pm 0.7\%$ d^{-1}), despite the potential for oxygen limitation (Table 1). Consequently, a higher overall biomass turnover time was observed for fungi colonizing litter at the exposed site (37 d) relative to the permanently inundated site (24 d). Similarly, bacterial growth rates (μ_b, P:B) associated with decaying *T. angustifolia* litter were also higher on average at the permanently inundated site ($0.84 \pm 0.89\%$ d^{-1}) than the exposed site ($0.53 \pm 0.4\%$ d^{-1}). However, these μ_b were

Table 1. Mean ± SE (n = 5) biomass and growth characteristics of fungal and bacterial assemblages associated with decomposing *Typha angustifolia* leaf litter at 2 contrasting wetland sites. Microbial growth efficiencies = fungal + bacterial production/fungal + bacterial production + respiration × 100. LEMP: Lake Erie Metro Park; WP: Winous Point

Parameter	Jun 01	Jul 01	Oct 01	Jun 02	Sep 02
Intermittent exposure site (LEMP)					
Fungal:microbial biomass (%)	99.9 ± 0.01	99.9 ± 0.02	99.9 ± 0.02	99.2 ± 0.08	97.6 ± 0.53
Fungal:microbial production (%)	99.9 ± 0.01	99.9 ± 0.01	99.9 ± 0.01	99.9 ± 0.02	99.9 ± 0.03
Fungal growth rates (% d^{-1})	2.11 ± 0.35	5.27 ± 0.10	2.07 ± 0.21	2.15 ± 0.16	2.97 ± 0.43
Bacterial growth rates (% d^{-1})	0.51 ± 0.17	1.27 ± 0.33	0.41 ± 0.11	0.30 ± 0.04	0.18 ± 0.10
Microbial growth efficiency (%)	18 ± 3	54 ± 3	33 ± 3	19 ± 1	29 ± 6
Permanently flooded site (WP)					
Fungal:microbial biomass (%)	98.6 ± 0.27	99.1 ± 0.24	99.1 ± 0.16	96.9 ± 0.33	94.5 ± 0.84
Fungal:microbial production (%)	99.4 ± 0.28	99.6 ± 0.04	99.7 ± 0.10	99.8 ± 0.07	99.8 ± 0.09
Fungal growth rates (% d^{-1})	3.34 ± 0.42	4.36 ± 0.25	1.75 ± 0.64	9.84 ± 2.06	1.80 ± 0.73
Bacterial growth rates (% d^{-1})	1.16 ± 0.20	2.24 ± 0.46	0.24 ± 0.05	0.56 ± 0.16	0.02 ± 0.002
Microbial growth efficiency (%)	12 ± 2	21 ± 4	9 ± 2	25 ± 5	4 ± 1

ca. 5 times lower than corresponding μ_f (Table 1), indicating bacterial turnover times of 118 and 185 d for bacterial assemblages at the exposed and permanently inundated sites, respectively.

Rates of fungal and bacterial production followed a similar pattern to that of fungal and bacterial biomass. Production rates for fungi were consistently higher on leaf litter at the exposed wetland site (Fig. 5A), with the exception of June 2002 (Fig. 5B). Likewise, rates of bacterial production were consistently higher at the permanently inundated site, except on the last sampling date (September 2002) when higher productivities were observed at the exposed site. Estimated microbial production rates associated with decaying *Typha angustifolia* litter at both wetland sites were largely dominated by fungi, which accounted for ≥99% of the total microbial production during each sampling period (Table 1).

Microbial respiration

Rates of microbial respiration from *Typha angustifolia* leaves were similar at both wetland sites during the initial stages of litter decomposition, with a mean rate of 191 ± 49 and 170 ± 7 µg C g^{-1} detrital C h^{-1} recorded at the permanent and intermittent site during July 2001 (59 and 76 d), respectively (Fig. 6). Rates of microbial respiration associated with litter at the intermittent wetland site increased only slightly (p = 0.08) during the study period, with an average rate of 245 ± 39 µg C g^{-1} detrital C h^{-1} on the last sampling date
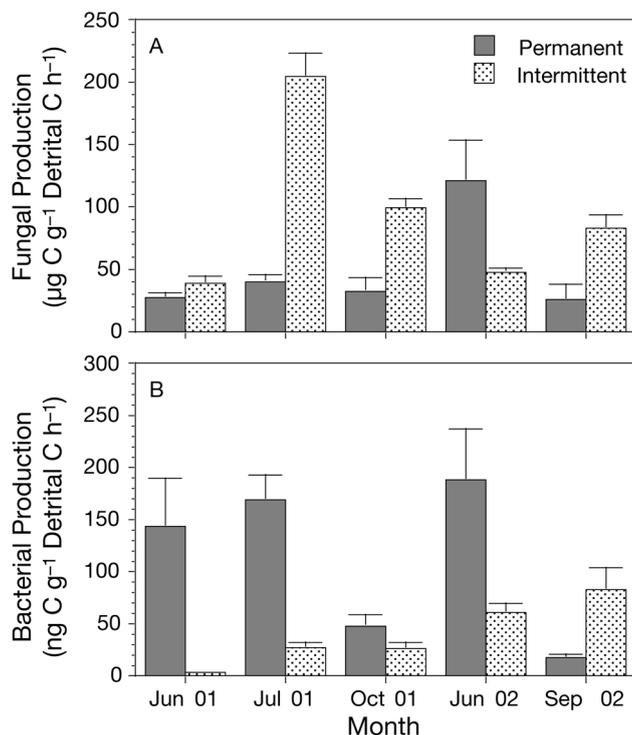

Fig. 5. *Typha angustifolia*. Mean + SE (n = 5) (A) fungal and (B) bacterial production rates associated with decomposing leaf litter at the 2 wetland study sites
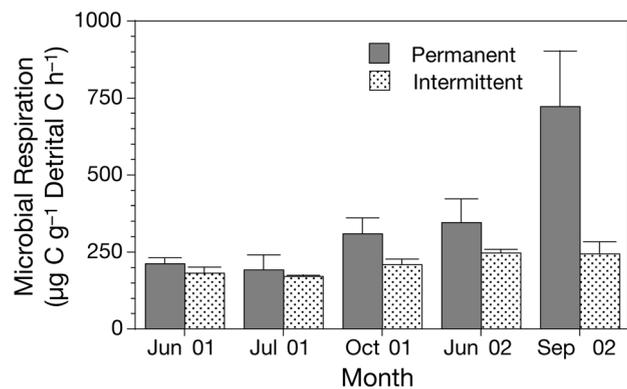

Fig. 6. *Typha angustifolia*. Mean + SE (n = 5) rates of microbial respiration from leaf litter at the 2 wetland study sites

(Fig. 6). In contrast, microbial respiration rates at the permanently inundated site showed a statistically significant increase (p < 0.001) throughout litter decay, with a final value approximately 3.4 times higher than that observed at the beginning of the study period (720 ± 180 μg C g^{-1} detrital C h^{-1}).

DOC release

The release of extractable DOC from *Typha angustifolia* litter was statistically significantly different between sites (p < 0.001), with up to 55 times greater release rates from decaying litter at the exposed wetland site than at the permanently inundated site (Fig. 7). At the exposed site, maximum release of DOC from decaying leaf litter (6.51 ± 0.88 mg C g^{-1} detrital C d^{-1}) was observed on the first sampling date, with subsequent rates declining over the study period. In contrast, maximum release of DOC from litter at the permanently inundated site (2.25 ± 0.25 mg C g^{-1} detrital C d^{-1}) occurred near the end of the study period (Fig. 7), coinciding with increases in rates of bacterial and fungal production (Fig. 5A).

Enzyme activities

Activities of microbial degradative enzymes involved in the acquisition of P (acid phosphatase), N (β-n-acetyl-glucosaminidase) and C (β-glucosidase, cellobiohydrolase, β-xylosidase) from decaying plant litter (Figs. 8 & 9) followed patterns similar to those described previously for fungal biomass (Fig. 4A). In general, potential enzyme activities per g detrital C were consistently higher at the exposed wetland site throughout the duration of the study. Differences in the distribution of EEA between the 2 decomposer communities are more apparent when
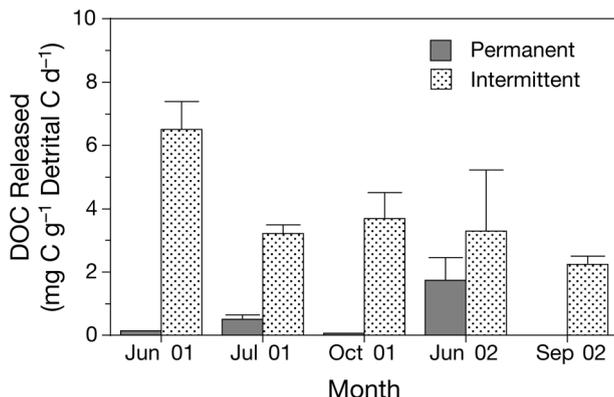

Fig. 8. *Typha angustifolia*. Mean + SE (n = 5) (A) acid phosphatase and (B) β-n-acetyl-β-glucosaminidase enzyme activity associated with decomposing leaf litter at the 2 wetland study sites

activities are compared per mg microbial biomass C (MBC). Phosphatase showed the largest differences in biomass-specific activity, averaging 330 ± 250 nmol mg MBC^{-1} h^{-1} at the exposed LEMP site, but only 86 ± 81 nmol mg MBC^{-1} h^{-1} at the inundated WP site, suggesting that cycling of P within the community was more extensive at the exposed site. Specific cellulolytic activities were also higher at the exposed site, by about 2-fold (910 vs. 440 nmol mg MBC^{-1} h^{-1} for β-glucosidase, 300 vs. 110 nmol mg MBC^{-1} h^{-1} for cellobiohydrolase, 180 vs. 140 nmol mg MBC^{-1} h^{-1} for β-xylosidase). β-n-acetylglucosaminidase was the exception to this trend in that biomass-specific activities were similar at both sites, averaging 200 nmol mg MBC^{-1} h^{-1} for the intermittent LEMP site and 220 nmol mg MBC^{-1} h^{-1} for the flooded WP site.

DISCUSSION

In contrast to previous studies (e.g. Vargo et al. 1998), we did not observe any statistically significant effects of sedimentation (size or loading rates) on *Typha angustifolia* mass loss patterns or litter nutrient concentrations. Furthermore, we observed no statistically significant effects of sedimentation on the biomass and activities of fungi and bacteria associated with decomposing *T. angustifolia* litter. However, as

Fig. 7. *Typha angustifolia*. Mean + SE (n = 5) release rates of extractable dissolved organic carbon (DOC) from decomposing leaf litter at the 2 wetland study sites
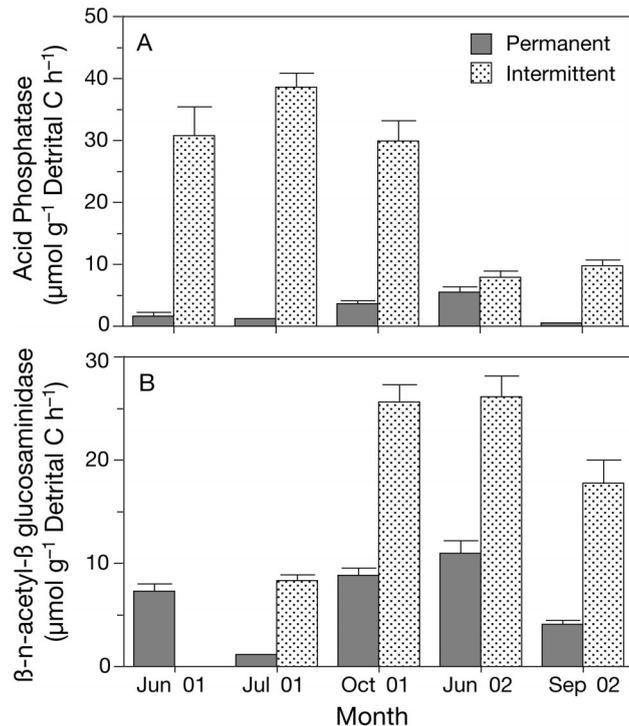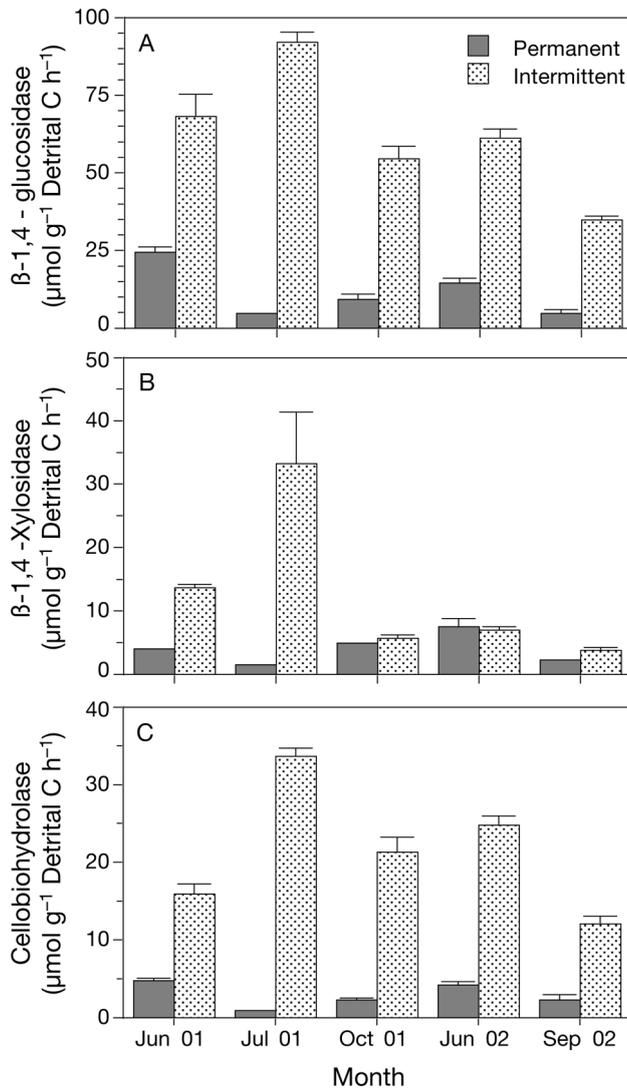
Fig. 9. *Typha angustifolia*. Mean + SE (n = 5) (A) β-1,4-glucosidase, (B) β-1,4-xylosidase, and (C) cellobiohydrolase enzyme activity associated with decomposing leaf litter at the 2 wetland study sites

Table 2. *Typha angustifolia*. Mass loss rates of at wetland study sites. k: litter decay rate; M_0: initial ash-free dry mass in litter bags; ASE: asymptotic standard error

Period (d)	$k \pm$ ASE (d^{-1})	$M_0 \pm$ ASE (%)	r^2 (corrected)
Intermittent exposure site (LEMP)			
0–484	−0.0022 ± 0.00008	99.7 ± 1.3	0.90
41–484	−0.0022 ± 0.00010	99.5 ± 1.9	0.87
76–484	−0.0021 ± 0.00013	99.1 ± 3.0	0.81
Permanently flooded site (WP)			
0–403	−0.0029 ± 0.00025	93.4 ± 3.1	0.73
31–403	−0.0025 ± 0.00027	87.3 ± 3.2	0.63
59–403	−0.0023 ± 0.00030	83.7 ± 4.6	0.90

(Table 2), indicating that differences in mass loss rates between the 2 systems were largely the result of initial processes (including leaching).

The higher mass loss rates at the permanently inundated site were consistent with some reports of litter processing under flooded vs. exposed conditions (Gurtz & Tate 1988, Neckles & Neill 1994, Glazebrook & Robertson 1999, Kelley & Jack 2002). Kelley & Jack (2002) suggested that submergence promoted faster litter decay through greater leaching losses, higher microbial metabolism, and feeding by aquatic detritivores. However, other studies have found faster rates of mass loss for litter experiencing intermittent cycles of inundation and exposure (Ryder & Horwitz 1995, Lockaby et al. 1996, Battle & Golladay 2001).

Battle & Golladay (2001) examined the effects of differing hydroperiods on litter decomposition of pond cypress *Taxodium ascendens* and swamp black gum *Nyssa sylvatica* var. *biflora* in 3 depressional wetlands of the Gulf Coast plain. They reported faster decomposition rates in wetlands experiencing multiple flooding and exposure events relative to single flooding events or continuously submerged habitats. Because microbial biomass associated with decaying litter was similar across sites, the authors hypothesized that cycles of flooding and drying accelerated litter decomposition by increasing aeration, leading to greater microbial activity. Ryder & Horwitz (1995) reported similar findings for the decomposition of 2 emergent macrophytes, *Baumea articulata* and *Typha orientalis*, in seasonal and permanent wetlands of the Swan coastal plain of western Australia. Leaf litter in seasonally inundated sites had higher rates of mass loss and greater microbial biomass (total phospholipids).

In the present study, statistically significant differences in litter nutrient dynamics were also observed between wetland sites. Both N and P concentrations increased during litter decomposition at both sites. Total N either remained stable (exposed site) or increased slightly (permanent site) during early litter decay, followed by a de-

suggested previously, unforeseen environmental conditions, possibly resulting from hydrologic differences between the 2 study sites, may have obscured our ability to test the effects of sedimentation on microbial decay processes.

We did observe statistically significant differences in overall mass loss patterns and microbial decay processes between the 2 hydrologically distinct wetland sites. Over the 400 d study period, *Typha angustifolia* litter at the permanently inundated site lost 13% more of its initial mass than litter at the exposed site and had a statistically significantly higher rate constant. However, most of this difference appeared in the first sampling interval; thereafter decay rates between the 2 sites were roughly similar

crease at the end of the study period. However, total N was considerably lower (e.g. 20 to 58%) at the permanently flooded site throughout the study period, suggesting that there was substantial N exchange (i.e. leaching) within the water column. At the exposed site, there was less N loss from leaching and greater retention of immobilized N. The pattern was similar for total P, which was about 20% lower on average at the permanently inundated wetland site.

Similar patterns in litter nutrient dynamics have been reported for other wetland habitats (Neckles & Neill 1994, Lockaby et al. 1996, Glazebrook & Robertson 1999, Battle & Golladay 2001). Neckles & Neill (1994) reported that the percentage of original N remaining in aboveground litter of the emergent plant *Scolochloa festucacea* declined in treatment sites experiencing longer periods of inundation. However, total N in *S. festucacea* litter subsequently increased in sites exposed to longer flooding regimes, suggesting that litter submergence accelerated the initial leaching losses of N and probaly promoted decomposer-mediated uptake and immobilization of dissolved N during later stages of litter decay (Neckles & Neill 1994).

Submergence of plant litter permits continual exchanges of C, N, P and mineral nutrients between the microbial decomposer community and the surrounding ecosystem. For litter exposed to an aerial environment (e.g. exposed sediments or standing-dead), the exchange of organic compounds and essential nutrients may be restricted to periods of inundation and throughfall. During the intervals between these events, the decomposition process is more restricted. As a result, substrate depletion and metabolite accumulation may limit microbial activity and increase competition for available nutrients. One metric of limited hydrologic exchange is the accumulation of soluble organic compounds in aerial litter. Throughout the study period, the extractable DOC concentration in litter exposed at the LEMP site was 2 to 55 times greater than that of submerged litter at the WP site. In the absence of leaching, this DOC may be metabolized *in situ*, rather than entering the water column for consumption in the microbial loop.

Comparisons of enzyme activity patterns for emergent and submersed litter also show the effects of limited hydrologic exchange. When calculated mg^{-1} MBC phosphatase activity associated with emergent litter was, on average, 4 times greater than activity associated with the flooded litter. If activity is calculated per unit of microbial production, then the litters differ by a factor of 11, indicating that a large portion of microbial P demand within emergent litter was met through internal cycling, rather than uptake from the environment. For cellulolytic activities, average potentials per unit MBC were twice as large for the exposed litter (6

times greater if activities are compared per unit of production) than those associated with submerged litter, suggesting that microbial communities in exposed litter were more dependent on cellulose for carbon. NAGase was the interesting exception. Activities per unit microbial biomass and production were similar for aerial and submerged litter, suggesting that activity of this chitin-degrading enzyme was more directly linked to microbial biomass and productivity than to litter degradation.

The microbial community associated with exposed litter at the LEMP site was characterized by high biomass, high rates of production, high specific extracellular enzyme activity, and high growth efficiencies compared to submerged litter at WP. As a consequence, we would have expected litter mass loss rates to be significantly higher at LEMP. However, it is likely that the high metabolic potentials associated with exposed litter were realized during relatively narrow temporal periods, similar to those observed in standing-dead decay systems (see Kuehn & Suberkropp 1998b, Kuehn et al. 2004). The more aerobic conditions at the exposed site promoted the growth of fungal decomposers, which can often metabolize at water potentials below those of bacteria. Nonetheless, it is likely that most of the decomposition activity occurred during periods of inundation, precipitation or dew formation. For LEMP, restricted windows for microbial activity were offset by the higher activity potentials. As a result, after initial leaching losses, mass loss rates were similar to those for submerged litter at WP.

At WP, submergence of litter buffered the decomposer community from environmental fluctuations, but may also have limited metabolic activity through lower oxygen availability, which averaged <2 $mg\ l^{-1}$. Submerged *Typha angustifolia* litter had higher bacterial biomass and production, and lower fungal biomass and production, than exposed litter. Previous studies have reported decreases in litter-associated fungal biomass and production rates in response to submergence (Komínková et al. 2000, Kuehn et al. 2000), supporting the idea that bacteria may assume an increased role in litter decay after collapse of litter to the overlying surface waters (Newell et al. 1995). Although bacteria biomass and production were greater for submerged than for exposed litter, the net effect of litter submergence was a decrease in total microbial biomass and production (Figs. 4 & 5), accompanied by lower specific extracellular enzyme activities (Figs. 8 & 9) and growth efficiencies (Table 1). Hence, in contrast to LEMP, *T. angustifolia* litter mass loss at WP was characterized by lower, but more sustained, metabolic activity, that was equally effective in transforming litter carbon.

Rates of fungal growth on *Typha angustifolia* litter at LEMP (2.36 mg C g^{-1} detrital C d^{-1}) and WP (1.18 mg C g^{-1} detrital C d^{-1}) were comparable to those reported

for other freshwater habitats (Table 3). In contrast, estimates for litter-associated bacteria were substantially lower in comparison to those in other published studies (Table 3). Average turnover times yielded estimates that were abnormally high, suggesting problems in our ability to accurately quantify production rates of bacterial communities attached to decaying litter (e.g. isotope dilution). Rates of microbial respiration were more similar between sites than production rates, averaging 5.1 mg C g^{-1} detrital C d^{-1} at LEMP and 8.6 mg C g^{-1} detrital C d^{-1} at WP. As a result, the mean microbial growth efficiencies of 30 and 14 % for LEMP and WP, respectively, were within the range reported in

other decomposition studies (Table 3). The greater efficiency at LEMP is consistent with the higher specific enzyme activities, higher DOC concentration, and higher N and P content of exposed litter.

Vascular plant litter is an important structural component in all wetlands. However, its specific contributions to ecosystem trophic structure and nutrient dynamics reflect the metabolism of the associated decomposer communities. This study has resolved some of the mechanisms by which edaphic and hydrologic variables may control microbial decay dynamics and mediate carbon and nutrient exchange between litter and the water column.

Table 3. Range of microbial fungal and bacterial production (ash-free dry mass, AFDM) and growth rate estimates associated with decaying litter under submerged or sediment-surface conditions in freshwater habitats. Corresponding microbial growth efficiencies are also noted. Sch: Schulz; PC: Payne Creek; WB: Walker Branch; HWC: High White Creek; BS: Basin Creek; HM: Hendrick Mill; LSB: Lindsey Spring Branch; LEMP: Lake Erie Metro Park; WP: Winous Point; –: no data

Species	Production (μg C g^{-1} AFDM d^{-1})		Growth rates (% d^{-1})		Growth efficiency (%)	Source
	Fungi	Bacteria	Fungi	Bacteria		
Juncus effusus	–	10–810[a]	–	–	–	Moran et al. (1989)
Panicum hemitomen	–	20–88[a]	–	–	–	Moran et al. (1989)
Typha latifolia	–	280–420[a]	–	–	–	Moran et al. (1989)
Trapa natans	–	0–77	–	2.8–10.0	–	Findlay et al. (1990)
Carex walteriana	–	0.5–31	–	–	–	Moran & Hodson (1992)
Juncus effusus	–	11–760[a,b]	–	6.6–20.7[b]	–	Thomaz & Wetzel (1995)
Mixed hydrophytes	19–2500[b]	8–35[b]	4.2–11.1[b]	2.7–50.0[b]	3–31	Sinsabaugh & Findlay (1995)
Carex walteriana	115–403[b]	1–22[b]	0.4–4.5[b]	0.4–2.6[b]	–	Newell et al. (1995)
Liriodendron tulipifera (Sch)	33–3258[c]	18–107[c]	0.7–15.6	–	–	Weyers & Suberkropp (1996)
Liriodendron tulipifera (PC)	6–266[c]	6–19[c]	0.1–16.0	–	–	Weyers & Suberkropp (1996)
Alnus glutinosa	50–500	25–625	0.1–40.0	3.0–8300	2–12	Baldy & Gessner (1997)
Mixed deciduous	315–1358[b,c]	–	0.9–7.0[b]	–	–	Suberkropp (1997)
Juncus effusus	73–2836	4–32	0.7–16.9	4.0–14.6	–	Kuehn et al. (2000)
Phragmites australis						Komínková et al. (2000)
Leaves	185–614[d]	–	0.5–1.9	–	13–50[e]	
Sheaths/culm	41–103	–	0.7–1.8	–	7–49[e]	
Liriodendron tulipifera (WB)	23–2624[c]	–	0.1–9.4	–	–	Suberkropp (2001)
Quercus alba (WB)	113–1386	–	0.2–5.6	–	–	Suberkropp (2001)
Liriodendron tulipifera (HWC)	131–491	–	0.4–2.3	–	–	Suberkropp (2001)
Quercus alba (HWC)	36–392	–	0.3–1.4	–	–	Suberkropp (2001)
Populus gr. *Nigra*	50–700[d]	1–210[d]	0.4–10.2	6.0–150	–	Baldy et al. (2002)
Typha angustifolia	40–715[a]	0.2–1.6[a]	0.1–3.7	7.1–12.5	–	Findlay et al. (2002)
Phragmites australis	30–211	0.3–0.5	0.1–0.3	–	–	Findlay et al. (2002)
Mixed deciduous (BS)	441–2687[b,c]	–	1.7–16.5[b]	–	–	Methvin & Suberkropp (2003)
Mixed deciduous (HM)	608–2947[b,c]	–	1.5–11.6[b]	–	–	Methvin & Suberkropp (2003)
Mixed deciduous (LSB)	207–3596[b,c]	–	1.0–10.4[b]	–	7–65[e]	Carter & Suberkropp (2004)
Mixed deciduous (PC)	279–4392[b,c]	–	0.2–4.2[b]	–	14–50[e]	Carter & Suberkropp (2004)
Alnus glutinosa	700–3600[d]	13–138[d]	2.8–47.9	–	–	Pascoal & Cássio (2004)
Phragmites australis	100–1200[b,d]	1300–9400[b,d]	1.0–6.0[b]	200–800[b]	30–66	Buesing & Gessner (2006)
Typha angustifolia (LEMP)	473–2477[d]	0.04–1.0[d]	2.1–5.3	0.2–1.3	16–54	Present study
Typha angustifolia (WP)	337–1378[d]	0.2–2.3[d]	1.8–9.8	0.02–2.2	4–26	Present study

[a]Production values are in μg C g^{-1} dry wt d^{-1}
[b]Production and growth rates determined on naturally occurring plant litter (unknown age); in all other cases determined on decaying plant matter as part of a timed litter mass loss experiment
[c]Production values converted to μg C g^{-1} AFDM d^{-1}, assuming 45 % C as fungal dry mass
[d]Production values converted to μg C g^{-1} AFDM d^{-1}, assuming 50 % C as AFDM
[e]Reported as fungal growth efficiencies based on the assumption that respiration was entirely fungal (i.e. FGE = fungal production/fungal production + respiration × 100)

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