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COMPARISON OF DETRITUS DYNAMICS IN TWO TIDAL FRESHWATER WETLANDS[1]

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Abstract. We have examined the generation and persistence of detritus in two contrasting tidal freshwater wetlands on the Hudson River. These wetlands offer a difference in vegetation, with Tivoli South Bay dominated by a floating-leafed macrophyte (water-chestnut, *Trapa natans*) and North Bay a typical *Typha* marsh. In South Bay, there was a large amount of water-chestnut dry biomass (400 g/m^2) available to enter the detritus pool, but there was no increase in the standing stock of benthic organic matter following senescence of water-chestnut. Our estimates show that mineralization plus leaching of dissolved material are sufficient to remove much of this detritus. In the *Typha* marsh, there is a large amount of detritus generated (≈25% of annual primary production) and this material persists as a thick litter layer. Decomposition of this litter is very slow (0.3/yr). A portion of the litter may be exported because decomposition alone cannot account for the observed rate of disappearance from the marsh surface.

Microbial abundance was used to estimate the amount of heterotrophic biomass supported by these different types of detritus. Bacterial growth on water-chestnut detritus is relatively slow (10^6 cells·mg^{-1}·d^{-1}), resulting in a turnover of bacterial biomass in 10–36 d. Bacterial and fungal biomass associated with *Typha* were low, and could not account for the observed increase in nitrogen content.

Key words: bacteria; decomposition; detritus; fungi; Nuphar; *tidal freshwater wetlands;* Trapa; Typha.

INTRODUCTION

One of the fundamental questions about any ecosystem is: What are the organic carbon sources that support heterotrophic production in that system? There have been relatively few studies documenting food sources in tidal freshwater wetlands (e.g., Smock and Harlowe 1983). The general consensus is that tidal freshwater wetlands are detritus-based systems where most of the annual primary production is not consumed during the growing season but serves as a food source after death of the plant (Odum et al. 1984). Although quite a bit of information exists on rates of primary production, biomass distribution, and decomposition in various wetlands (Whigham et al. 1978, Whigham and Simpson 1978, Brinson et al. 1981, Cahoon and Stevenson 1986, Hackney 1987), there has been relatively little comparative work done on the characteristics of the detritus food web in different types of tidal freshwater wetlands. Due to the wide variety of vegetation types and habitats, tidal freshwater wetlands offer an opportunity to consider how the amount of detritus generated and the persistence of this detritus varies across plant communities. Only with a comparative approach will it be possible to understand how much variability is possible in the dynamics of the detritus component.

The contribution of any food source to secondary production in a system may be described by: (1) the rate of supply of the particular food source, (2) the retention of this organic matter, and (3) the actual use by consumers. In this study, we have compared the first two components, i.e., the supply and retention of macrophyte detritus in two contrasting tidal freshwater wetlands in the Hudson Estuary. We have examined the microbial biomass associated with decomposing detritus in order to estimate one component of the detritus-consuming community.

METHODS

This study was conducted in the Tivoli Bays National Estuarine Research Reserve. The Tivoli Bays are two of the larger wetlands in the Hudson Estuary with a total area of ≈200 ha. The bays are on the eastern bank of the Hudson just north of Kingston, New York. The average tidal range is 1.1 m and exchange of water with the Hudson occurs through channels in the railroad dike.

The vegetation and topography of the two bays is strikingly different. Tivoli South Bay is almost completely subtidal with mudflats only exposed at extreme low tides. The predominant sediment type in South Bay is a moderately organic (≈10% ash-free dry mass [AFDM]) fine silt.

During mid- to late summer, South Bay is covered

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by the floating-leafed macrophyte *Trapa natans* (water-chestnut). The growth form is a long submerged stem reaching from the sediment to a floating rosette of leaves. These leaves are continually produced throughout the growing season. Large barbed seeds are produced late in the summer and overwinter in the sediment to germinate the following spring.

North Bay is a typical emergent marsh, with most of the area being intertidal. *Typha, Lythrum,* and *Phragmites* are the predominant plants in the high intertidal, with *Nuphar, Pontederia,* and *Peltandra* in the low intertidal.

For this study, we needed estimates of the seasonal changes in standing stock of living plants and amounts of nonliving plant material remaining after senescence. From these data, we estimated the amount of detritus potentially available. The amount of detritus that appears as litter or benthic organic matter represents the amount of detritus actually available.

The standing stock of water-chestnut was estimated by clipping rosettes in five replicate 0.15-m^2 quadrats. Stems and roots were not included but in general these components make up <35% of the total biomass (E. Kiviat, Hudsonia, Limited, *personal communication*). Samples were dried at 70°C for 48 h to determine the dry mass, and subsamples were combusted (500°, 4 h) to determine the ash-free dry mass (AFDM). Ground subsamples were analyzed for carbon and nitrogen content in a Perkin-Elmer 240C CHN Analyzer.

To determine benthic organic matter, sediment was collected with five replicate 30-cm^2 cores and the top 1 cm analyzed for AFDM as above. A subset of the total number of sediment cores was also analyzed for organic carbon with the CHN Analyzer. Five quadrats and five cores were collected every 2 wk from June through November 1986 and May through December 1987. Routine sampling was done at a central station in South Bay. On five occasions, five stations on an east-west transect were sampled to detect any possible gradients in sediment organic matter.

The rate of water-chestnut decomposition in the field was measured as loss of AFDM from individually tagged preweighed leaves. Leaves were collected from plants in September 1985 and dried at 70°. Leaves were put in a 1-cm mesh cage in late October 1985 and five leaves were collected every 5–7 d for 6 wk.

Laboratory studies were used to examine in more detail the processes occurring during decomposition of water-chestnut. Tagged, preweighed leaves (n = 100) were placed in a 10-L tub of aerated Hudson River water. The tub was kept at 10° (average field temperature for October–November) in the dark. Water was changed daily for the 1st wk and then 3 times per week. Mass loss, bacterial biomass and production, and oxygen consumption were measured every few days for 5 wk.

Bacterial production on individual leaves was estimated from ^{3}H-thymidine (abbreviated ^{3}H-TdR) incorporation (Findlay et al. 1984). Briefly, leaves were incubated in 10 mL of filtered Tivoli Bay water with 1.5 MBq of ^{3}H-TdR (specific activity = 3.0 MBq/nmol, final concentration of ^{3}H-TdR = 50 nmol/L). DNA was extracted, purified, and radioassayed as described in Findlay et al. (1984). Numbers of cells were determined after sonicating the leaves to release surface-attached cells. Cells were stained with acridine orange and collected on a 0.2-μm Nucleopore filter (Hobbie et al. 1977). Biovolumes of bacterial cells were measured on photographs of the epifluorescent slides. Biovolume was converted to carbon mass using 200 fg/μm^3 (cf. Bratbak 1985).

To determine oxygen consumption, five leaves were placed in a flask with 500 mL of air-saturated Hudson River water. The flasks were sealed and a magnetic stirrer was used to keep the water mixed. A YSI Model 57 oxygen meter continuously monitored the concentration of O_2. Three flasks with leaves and one blank were run at each sampling point. Linear regression was used to calculate the O_2 uptake rate.

In North Bay, we sampled the high marsh for *Typha* biomass and litter, and the low intertidal for *Nuphar*. For the *Typha* habitat, a 100-m transect was marked out perpendicular to one of the larger tidal creeks. Five stations 25 m apart were sampled every 2 wk from May through December 1987. At each station, two 0.15-m^2 quadrats were randomly selected and all vegetation clipped near the sediment surface. Live and dead material was separated and dried as above. Litter was collected from the same quadrats and two sediment cores were collected from each quadrat. All samples were analyzed for AFDM by mass loss after combustion at 500° for 4 h.

On one occasion, three other sites, each 50 m back from a creek bank, were sampled in the same way to get some indication of whether or not the routine transect was representative of other areas of the marsh.

Typha decomposition was estimated with litter bags containing 10 g of litter that had been collected in May 1987. Litter was dried at 70° for 48 h. This litter was of unknown age but must have been from the previous fall or earlier. Bags were placed on the sediment surface (August 1987) at the 50-m station of the *Typha* transect and tethered to bricks. Five bags were collected every 2 wk. Dry mass and ash-free dry mass remaining were determined as above.

Bacterial abundance and biomass on *Typha* litter were determined as described for water-chestnut detritus. Fungal biomass was estimated using epifluorescent direct counts to measure the length of hyphae (Newell and Hicks 1982). The diameters of hyphae were measured on photographs from the epifluorescent slides and the resulting biovolume of fungus converted to carbon mass assuming 250 fg/μm^3 (cf. Newell and Statzell-Tallman 1982).

The *Nuphar* habitat required nondestructive sampling because of the relatively small area of any given

site. A rope grid, 6 m by 6 m with crosspieces every metre, was suspended over the *Nuphar* site. This grid delimited 36 sample quadrats, each 1 m^2. Every 2 wk from May to November 1987, 10 grids were selected, using random numbers, and all *Nuphar* leaves in each grid were counted by two observers. Ten *Nuphar* plants from an adjacent area were collected, the number of leaves on these plants was counted, and the entire plant dried and weighed to estimate the average biomass per leaf. *Nuphar* ash-free dry biomass per square metre was calculated as the product of the number of leaves per square metre and grams AFDM per leaf. Cores for sediment organic matter were collected and analyzed as described above.

Nuphar decomposition was estimated by placing five freshly collected leaves in each of six litter bags. Leaves for this study were collected from an adjacent *Nuphar* bed and a subsample ($n = 13$) of leaves was kept for determination of the initial ash-free dry mass. One bag was collected after 7, 13, and 27 d in the field, beginning 13 October. On days 7 and 13, individual leaves were separated, rinsed, dried, and weighed. On day 27, individual leaves were no longer recognizable so the mass remaining per leaf was calculated as the total mass in the bag divided by five.

Results

In South Bay, water-chestnut plants were first seen at the water surface in mid-June and ash-free dry biomass rapidly increased to a maximum of ≈400 g/m^2 by early July (Fig. 1). For both years, biomass began to decline in mid- to late August and the rate of decrease of water-chestnut biomass after peak ash-free dry biomass was equivalent to ≈5 $g \cdot m^{-2} \cdot d^{-1}$ (Fig. 1). Despite this potentially large supply of organic matter to the sediments, there was no change in the standing stock of benthic organic matter in either year (Fig. 1). The slope of the regression of benthic organic matter on time was not significantly different from zero in either year ($P > .05$).

Mass loss from water-chestnut leaves in both the field and laboratory study was linear after an initial leaching period (Fig. 2). Mass loss in the field (1.37%/d) was faster than in the laboratory (0.86%/d).

Bacterial abundance on decomposing water-chestnut leaves increased rapidly over the first 2 wk, reaching a peak at ≈1.4×10^7 cells/mg (Fig. 3), and remained fairly constant thereafter. The average bacterial biovolume was 0.35 μm^3 per cell which corresponds to a carbon mass of 7×10^{-8} μg per cell. Production showed a more gradual increase to its maximum value (1.1×10^6 cells$\cdot mg^{-1} \cdot d^{-1}$) on day 24 and had decreased by the last sampling point (Fig. 3). The resulting turnover times for the bacterial community ranged from 10 to 36 d.

Oxygen consumption by decomposing water-chestnut leaves increased steadily over the entire interval. In the first week, oxygen consumption was ≈2 $\mu g \cdot mg^{-1} \cdot d^{-1}$ and had increased to 17 $\mu g \cdot mg^{-1} \cdot d^{-1}$ by day 34 (data not shown).

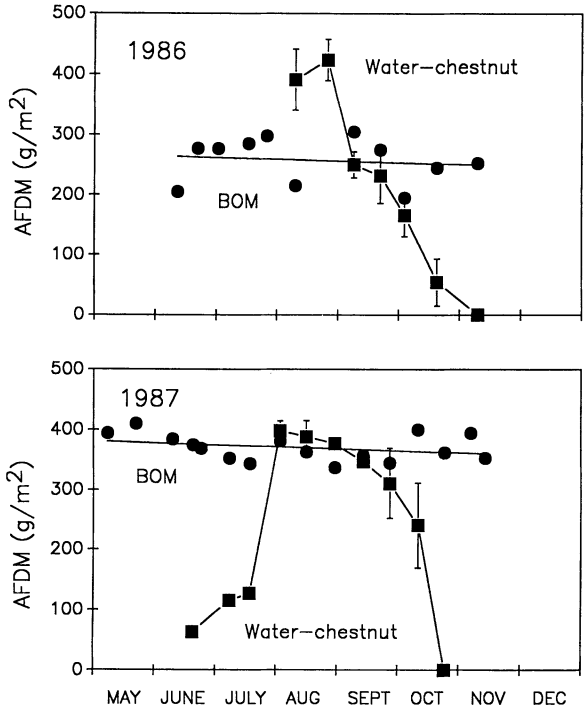

FIG. 1. Ash-free dry biomass (AFDM) of *Trapa natans* (water-chestnut, ■——■) and benthic organic matter (BOM, ●) in Tivoli South Bay in 1986 and 1987. *Trapa* biomass is the mean (±1 SE) of five quadrats. Benthic organic matter is the mean of five cores; line is best-fit regression.

There were no consistent differences in *Typha* biomass and litter among sites along the 100-m transect (ANOVA, $P > .05$) so data from all sites were combined. The seasonal pattern in abundance of live, standing dead, and down *Typha* was predictable (cf. Mason and Bryant 1975), with a peak in live biomass (as AFDM) of nearly 1.8 kg/m^2 in mid-July (Fig. 4). Down litter was always a significant component of total plant material, with maximum amounts seen in early May and in December (Fig. 4). The amount of litter declined from May to September and then increased until December.

On 3 August 1987, when we sampled three other sites in North Bay, the amounts of living *Typha* and standing dead were not significantly different from our routine transect (ANOVA, $P > .4$ and $P > .8$, respectively). Litter ash-free dry mass was significantly lower in one site (134 ± 22 g/m^2 [$\bar{X}$ ± SE]) than in the other two sites (average = 513 ± 125, 770 ± 73) or our usual site (484 ± 86).

The total amount of *Typha* biomass (live + standing dead + litter) at the time of peak standing crop of live *Typha* was 2.6 kg/m^2 in July which had declined to 1.8 kg/m^2 by the last sampling date in December indicating a net loss of *Typha* biomass from the marsh.

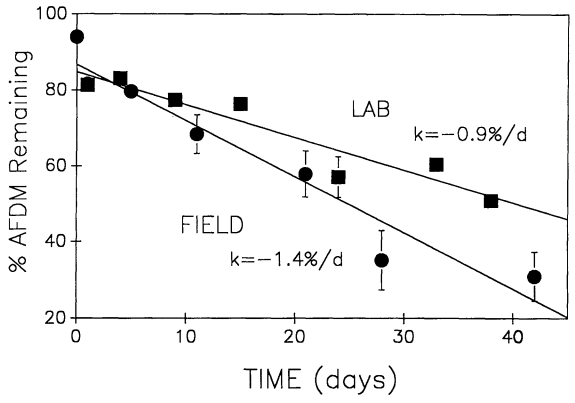

FIG. 2. Decomposition of water-chestnut leaves in the laboratory (■) and field (●). Each point is the mean (±1 SE) of five individual leaves. Some error bars were smaller than the symbols.

Sediment organic matter declined over this interval so the decrease in *Typha* biomass was not due to loss of fine particles from the litter.

Loss of AFDM from *Typha* litter was slow and the exponential decay constant was −0.31/yr (Fig. 5). This rate of decomposition is within the range of previously reported values for *Typha* mass loss (Brinson et al. 1981).

Bacterial biomass carbon on decomposing *Typha* averaged 155 μg/g and was fairly constant over time (Fig. 6A). Fungal biomass was generally 10-fold higher than bacterial biomass and showed an increase over the course of the study (Fig. 6A). These estimates are comparable to values for bacterial and fungal biovolumes for standing dead *Spartina* (Newell et al. 1985). There was a gradual but significant ($P < .004$) increase in the nitrogen content of *Typha* litter over the first 4 mo of decomposition (Fig. 6B).

Nuphar ash-free dry biomass increased rapidly beginning in early May, reaching a peak of 150 g/m² (Fig. 7). Senescence was rapid after late July and no living *Nuphar* remained by mid-November. As was seen in South Bay during senescence of water-chestnut, there was no increase in sediment organic matter during the senescence of *Nuphar* biomass (Fig. 7).

Nuphar decomposition was extremely fast with a calculated loss of 1.9%/d (data not shown), as has been reported previously by Odum and Heywood (1978).

Discussion

Our intent in this study was to document the supply and retention of detritus in these two wetlands and determine the role of microbial metabolism in detritus dynamics. There were clear differences in detritus supply and retention between these systems.

In South Bay, the potentially large input of water-chestnut detritus following plant senescence was not manifest as an increase in benthic organic matter (Fig. 1). The input of the amount of organic matter represented by the peak standing crop of water-chestnut (>400 g/m²) should have resulted in a significant increase in the benthic organic matter pool. The amount of water-chestnut available as detritus was actually higher than indicated by peak standing crop because we did not include stems or account for turnover of leaf tissue due to senescence and grazing. Consumer-generated frass is known to be important for other macrophytes (Wallace and O'Hop 1985) and turnover of water-chestnut leaves can be a significant fraction of standing stock (Tsuchiya and Iwaki 1983).

There are several possible explanations for the lack of increase in benthic organic matter following plant senescence. First is the possibility that water-chestnut detritus was buried below the top 1 cm that we routinely sampled. Four long cores (20–30 cm) taken at station 3 in 1986 and sectioned vertically showed no change in percent organic matter with depth, thus ruling out burial in a discrete layer. It seems unlikely that water movement or bioturbation would be sufficient

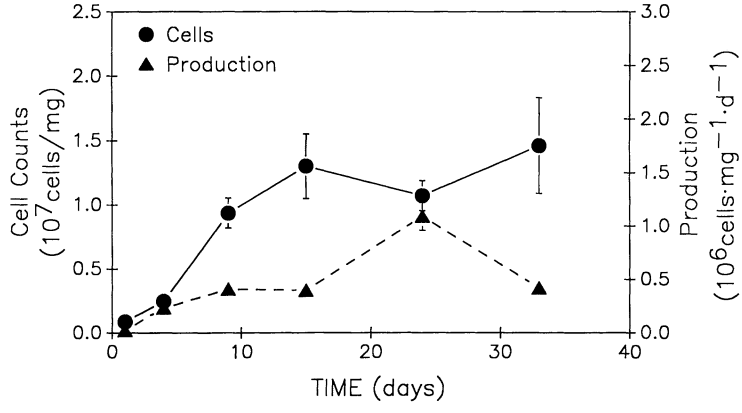

FIG. 3. Abundance and production of bacteria on decomposing water-chestnut leaves in the laboratory. Each value is the mean (±1 SE) of five individual leaves.

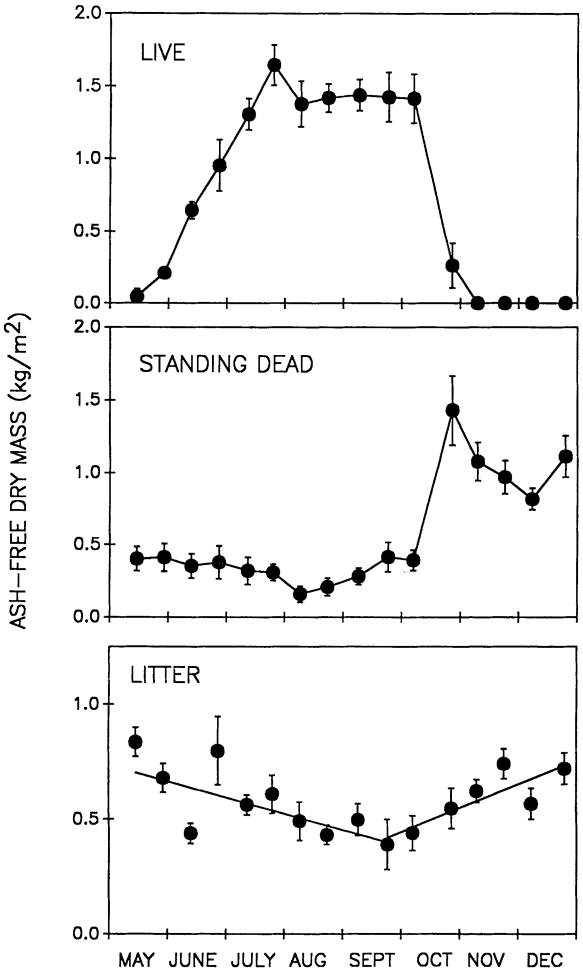

FIG. 4. Standing stocks of live *Typha,* standing dead *Typha,* and litter. Each value is the mean (±1 SE) of all 10 quadrats taken along a 100-m transect. For litter, lines shown are best-fit regressions from first sampling date to the late-summer minimum, then from this time to the last sampling date.

to spread the signal over >20 cm. For these reasons, we feel that burial within the bay was not the reason for lack of a signal.

Another possibility is that deposition of water-chestnut detritus was extremely localized and therefore not detected by our routine sampling. There was a gradient in organic matter content of sediments in South Bay ranging from ≈12% at the interior of the bay to ≈6% at the river side of the bay (data not shown). There was no increase in benthic organic matter over time at any station along this gradient (ANOVA, $P > .05$), indicating that there was no localized deposition of water-chestnut detritus.

We must also consider the possibility that water-chestnut detritus was exported from the bay, thus explaining the lack of an input to the sediments. Seston exchange was measured for eight separate tidal cycles during June–November 1987, using a tidal prism approach to estimate water exchange (Goldhammer and Findlay 1987). On only one date (24 July 1987) was there any indication of organic matter export, while on the other seven dates there was either a net import of organic matter or no net flux. It is possible that, despite the apparent net inward flux of organic matter, water-chestnut detritus was actually exported from the bay but was masked by a greater import of riverine organic matter. Also, our exchange estimates do not include the export of floating clumps of water-chestnut. At this point, we cannot rule out export as an explanation for the lack of an increase in benthic organic matter, but, as we show later, in situ decomposition is rapid enough to remove a large proportion of the potentially available water-chestnut detritus. The supply and retention of detritus in Tivoli North Bay was strikingly different from that of Tivoli South Bay. High rates of primary production, large amounts of litter, and slow decomposition seem to be general characteristics of tidal freshwater cattail marshes. North Bay certainly fits this pattern and we can construct a budget for the fate of *Typha* production as we did for water-chestnut in South Bay. Of the annual net aboveground AFDM production (≈1.7 kg/m²), ≈20% remains as litter at the end of the growing season (Fig. 4) and there was an increase in litter abundance following *Typha* senescence (Fig. 4). Thus, in contrast to South Bay, there was a clear signal of an input to the detritus pool after *Typha* senescence. The amount of litter at the end of the 1987 growing season was roughly equal to the amount in May 1987 (Fig. 4), indicating that there was no net accumulation of litter.

As for South Bay, we must consider burial, decomposition, and export as possible fates of annual litter production. Burial or deposition of fine particles does not seem to be important because there was no increase in sediment organic matter over the duration of this study (data not shown). Decomposition (0.3/yr) was too slow to account for disappearance of the annual litter production. If in situ decomposition were the only

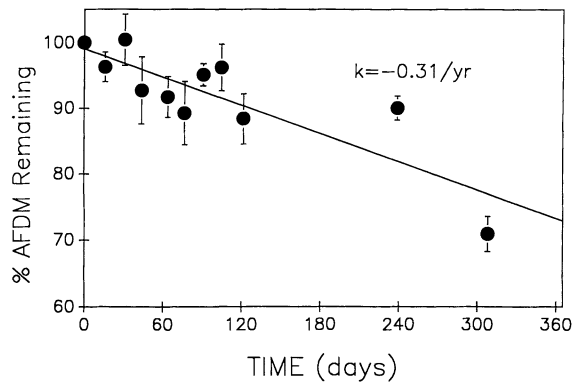

FIG. 5. Decomposition of *Typha.* Each point is the mean (±1 SE) of five litter bags. k is the exponential rate constant for loss of ash-free dry mass over the course of a year.

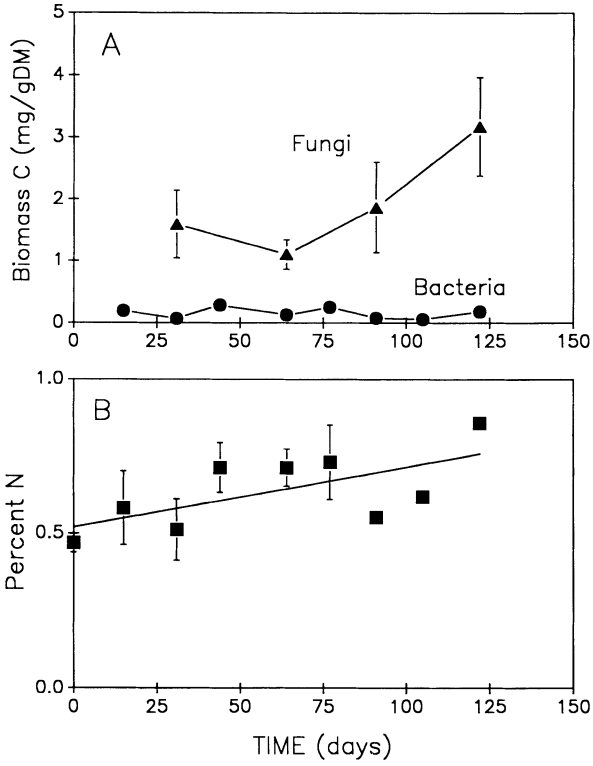

FIG. 6. Bacterial and fungal abundance on decomposing *Typha* litter (as carbon mass per unit litter dry mass, A) and concurrent changes in nitrogen content (B). Each bacterial and fungal value is the mean of three subsamples taken one from each of three litter bags. Nitrogen was determined on subsamples ($N \geq 3$) of a homogenized composite sample from three litter bags. Error bars are ±1 SE.

process removing litter, ≈70% of annual *Typha* litter production would accumulate in North Bay.

Also, the decline in litter observed from May to September (Fig. 4) was greater than could be accounted for just by decomposition. Applying our decomposition rate to the amount of litter present in May, showed that the standing stock of litter AFDM should have decreased from 700 to 626 ± 26 g/m² ($\bar{X}$ and 95% CI) by September. The actual amount of litter AFDM present in September was 400 ± 125 g/m². From these observations, it is clear that other processes must be responsible for removing this litter from the marsh.

Although we have no specific data for export from North Bay, tidal removal of litter would be a reasonable explanation for the disappearance of macrodetritus in excess of what can be accounted for by decomposition. Similar patterns and interpretations have been reported for salt marshes (Valiela et al. 1975). Export of detritus from coastal and inland tidal wetlands has long been presumed to be an important component of material budgets for these systems, but the validity of this generalization has been questioned (Nixon 1980).

Nuphar detritus in North Bay may be subject to the same processes as water-chestnut detritus in South Bay. The potential supply of *Nuphar* detritus AFDM (≈150 g/m²) would have been detectable as an increase in sediment organic matter if the material had simply been deposited (Fig. 7). *Nuphar* decomposition was extremely rapid and although we do not have specific information on processes of decomposition, it may be that leaching of DOC and carbon mineralization were responsible for removing much of the *Nuphar* detritus from the system. Odum et al. (1984) suggested that, in general, low intertidal sediments had low organic matter due to rapid decomposition and export. Our data confirm this pattern for Tivoli North Bay.

Microbial metabolism (growth and degradative activity) is considered to be a key process in models of detritus dynamics (Morris and Bowden 1986). Our results show that microbial metabolism has very different influences on detritus dynamics in these two wetlands. In Tivoli South Bay, microbial mineralization of organic carbon was responsible for a major loss of organic matter from the ecosystem. We estimated the amount of water-chestnut detritus that could be removed from the system due to leaching of dissolved matter or carbon mineralization. The AFDM loss in the first 24 h was 18.4% in the field and 18.7% in the laboratory (Fig. 2), and these losses probably represent leaching of dissolved compounds. We can also calculate the proportion of total mass loss due to release of CO_2. The total loss of AFDM over days 1–33 (i.e., ignoring the leaching period) was 30.4%. For water-chestnut, carbon = 52% of AFDM, so this was equivalent to carbon loss of 158 μg/mg. Using our laboratory estimates of O_2 consumption, and assuming an RQ of 1, we estimate a total CO_2-C release over the interval to have been 134 μg/mg. Therefore, in the laboratory, mineralization would have been responsible for 85% of the total loss of AFDM. Decomposition in the field was 1.6 times as fast as that in the laboratory, so we would estimate that CO_2 loss would be responsible for 53% of the total loss of organic carbon from leaves decomposing in the field. The sum of leaching and mineralization would be 71% of the AFDM loss observed in the field, leaving 29% for fragmentation, consumption, other loss terms, and uncertainty. These calculations suggest that carbon leaching and mineralization were responsible for the majority of carbon loss, and thus in large part they explain why we did not see a record of water-chestnut detritus input to the sediments.

In the case of *Typha* detritus in North Bay, microbial growth during decomposition is expected to lead to increases in the nitrogen content, and therefore food quality (e.g., Gosselink and Kirby 1974). Our data show an increase in fungal biomass over the first few months of decomposition and a concurrent increase in nitrogen content (Fig. 6A, B). Several other studies have reported an increase in N content of *Typha* detritus with time (Bowden 1986, Morris and Bowden 1986, Morris and Lajtha 1986), and three different mechanisms have

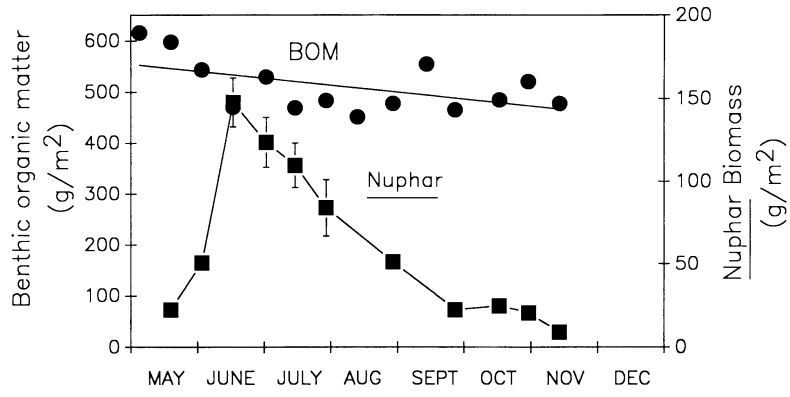

FIG. 7. Ash-free dry biomass of *Nuphar* and sediment organic matter. *Nuphar* biomass was estimated in 10 quadrats as described in Methods. Each benthic organic matter value is the mean of five determinations. Error bars are ±1 SE.

been proposed: microbial growth, rapid carbon mineralization, or abiotic N adsorption. Previous studies have not included the microbial biomass measures necessary to test each of these three possibilities. In our case, microbial growth was not sufficient to explain the observed increase in nitrogen content of decomposing *Typha*. Our observed increase in percent N over this period was from 0.47 to 0.86% which represents an N accumulation of 3.9 mg/g. Assuming a C:N ratio of 5 for fungal tissue, the peak fungal biomass N represents ≈0.6 mg/g so fungal nitrogen represents only 15% of the total nitrogen increase. Similarly, Marinucci et al. (1983) found that fungal nitrogen was 12–22% of the total N in *Spartina* detritus. The second alternative, rapid carbon mineralization, was not sufficient to explain the enrichment in nitrogen we observed. AFDM loss over this 4-mo interval was <10% so the relative increase in nitrogen due solely to loss of carbon would have been very small. Our results suggest that the N increase observed was not simply due to immobilization of nitrogen in microbial tissue or carbon mineralization, but most likely was due to abiotic adsorption as previously postulated by Odum et al. (1979), Lee et al. (1982), and Rice (1982).

Our present understanding of the functioning of the detritus food web in the Tivoli Bays shows that there can be tremendous variation in the importance and dynamics of the detritus food web in tidal freshwater wetlands. In North Bay, detritus is an abundant and persistent component of available organic matter. Also, it is conceivable that detritus export is important as a subsidy for consumers in the main-stem Hudson. In Tivoli South Bay, on the other hand, water-chestnut was not an obvious component of benthic organic matter. Rapid decomposition precludes the long-term importance of water-chestnut detritus as an organic matter source either in the bay or in the Hudson.

This study has documented large differences in detritus dynamics in two detritus-based ecosystems. These differences were a function of differences in rates of decomposition and the specific processes responsible for decomposition. Our models of detritus-based ecosystems are largely based on headwater streams (e.g., Cummins and Klug 1979) and salt marshes (e.g., Pomeroy and Wiegert 1981), two systems dominated by inputs of slowly decomposing detritus. Only by considering systems spanning a broad range in types of detritus inputs will we ever arrive at a general picture of the functioning of detritus-based ecosystems.

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