Decomposition Rates of *Typha* Spp. in Northern Freshwater Wetlands over a Stream-Marsh-Peatland Gradient

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ABSTRACT

Decomposition rates in wetlands vary with the composition of the biotic community and the physical and chemical environment. Variations in the process of decomposition in turn affect the overall rate of nutrient cycling within the wetland, affecting both primary productivity and general wetland health. This short-term study took place in northern New York within the Little Chazy River watershed. The effects of wetland factors including nutrient status, dissolved oxygen, and pH value on decay rate were measured over a freshwater stream-marsh-peatland gradient. Litterbags were utilized and collected weekly from three separate sites within or near the Altona Flat Rock ecosystem. Soil and water parameters, as well as colonization by macroinvertebrates, were studied in order to link decay rates with specific wetland characteristics. Decomposition rates for *Typha* spp. were evaluated using the change in dry biomass, and percent nitrogen content of the plant litter. Dry biomass reduction took place most rapidly in the stream site and least rapidly in the peatland site, while fluctuations of percent nitrogen content did not show a distinct trend. A high level of dissolved oxygen corresponded to a higher decay rate, while a low pH value corresponded to a lower decay rate.

Keywords: ***decomposition; Typha sp.; freshwater wetlands; stream-marsh-peatland***

INTRODUCTION

The rate of nutrient cycling in wetlands is related to both primary productivity (the rate at which plants remove nutrients from the surrounding environment and sequester those nutrients in living tissues), and decomposition (the rate at which tissues break down and release nutrients back into the surrounding environment). Plants in a nutrient rich environment exhibit high primary productivity, resulting in high available nutrient concentration in detritus. Invertebrates readily process nutrient-rich detritus, releasing nutrients into the soil and water, and thereby cycling them back into growing plants. As a part of this cycle, decomposition plays a significant role in the productivity and health of a wetland ecosystem.

The decomposition process generally takes place in three phases (Wrubleski *et al.*, 1997). First, organic particles and ions are leached from the plant matter into the surrounding water. The greatest reduction in biomass occurs over the first few days of decomposition due to leaching. In the second phase, more gradual loss occurs as microbes actively degrade plant matter over a longer time period, suggested to be more than 100 days. The final phase of decomposition takes place over an extended time period due to very slow degradation of the remaining materials, which are more resistant to decay. In addition to these steps, invertebrates that feed on detritus assist plant decomposition through mechanical fragmentation of plant material, consumption for growth and respiratory work, and production of feces (Brinson *et al.*, 1981).

Greater availability of inorganic nutrients such as nitrates and phosphates to microbial decomposers is known to accelerate loss of plant biomass (Brinson *et al.*, 1981; Mitsch and Gosselink, 2000). Therefore, decomposition of plant litter in nutrient-poor ecosystems is generally slower than in nutrient-rich ones (Webster and Benfield, 1986). This could also be a result of the adaptation by plants living in nutrient-poor ecosystems to conserve nutrients, resulting in nutrient-poor litter that decomposes slowly (Hobbie, 1992).

Type of plant material, water temperature, and hydrology can also affect decomposition rates in freshwater wetlands (Mitsch and Gosselink, 2002). Green litter decomposes more quickly than senesced litter, because it contains more components that are easily degraded (Nelson *et al.*, 1990). Different plant species also have different rates of decay depending on their composition. In addition, decay rates rise with increases in water temperature (Webster and Benfield, 1986). Hydrologically, precipitation-fed wetlands are often assumed to be more nutrient-poor than surface-water-fed wetlands, but this assumption has not been universally supported by the literature (Bridgham *et al.*, 1998). A high flow velocity increases leaching and mechanical abrasion, which causes a higher decay rate (Webster and Benfield, 1986).

Our study observed variations in decomposition rate of a standard litter across a peatland-marsh-stream gradient. A multitude of studies have focused on decomposition and decomposition rates in specific types of wetlands, but few studies have compared decomposition over an environmental gradient of various wetland types (Thormann and Bayley, 1997; Webster and Benfield, 1986). As chemical and physical properties change, decomposition rates can be expected to vary. Cattail (*Typha* spp.) was chosen as the standard litter because it grows in abundance in northern New York and many prior decomposition studies using *Typha* spp. are available for comparison of findings.

The objective of this study was to examine the effects of the physical and chemical wetland environment on the decomposition rate. We hypothesized that the decomposition rate would be highest in a wetland with high dissolved oxygen and close to neutral pH, and lowest in a wetland with low dissolved oxygen and low pH. Decomposition was evaluated by measurements of dry biomass remaining and percent nitrogen content of plant litter. Simple exponential decay rates were calculated from dry biomass data. Soil, water, and macroinvertebrate community data were collected in order to support our findings.

METHODS AND MATERIALS

Site Descriptions.

Three wetland ecosystems with distinct physical and chemical characteristics were selected for our study: a peatland, marsh, and stream. The peatland and marsh study sites (44°50' N, 73°34' W) were located within the boundaries of the Altona Flat Rock ecosystem in the Champlain Valley of northern New York. The stream study site (44°52' N, 73°29' W) was located about 7.5 kilometers from the Altona Flat Rock sites. The stream site was along Tracy Brook immediately below the dam at Lake Alice Wildlife Management Area. All three sites are part of the upper Little Chazy River watershed (Figure 1). Water temperatures among the sites remained fairly constant, with temperature data being collected every half-hour at the peatland and marsh sites for the duration of the study, and every hour at the stream site for the second half of the study (Figure 2).

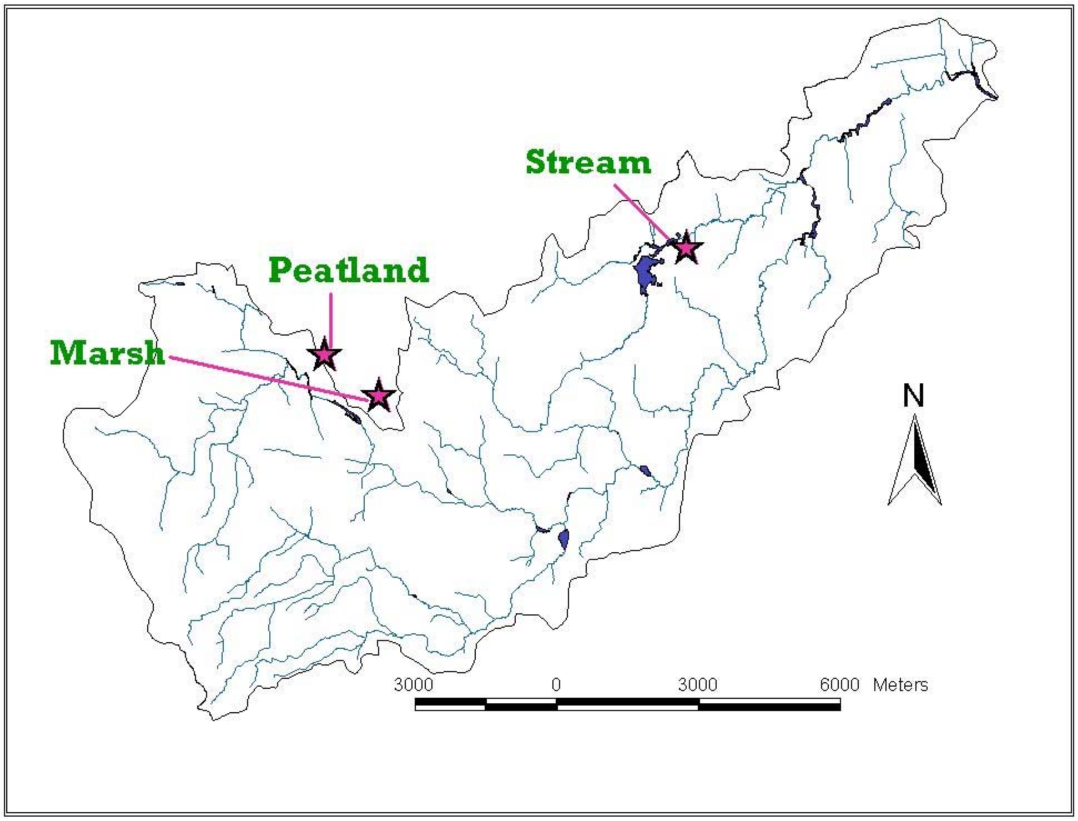

Figure 1. Map of wetland study sites in the Little Chazy River watershed in northern New York, June-July 2003.

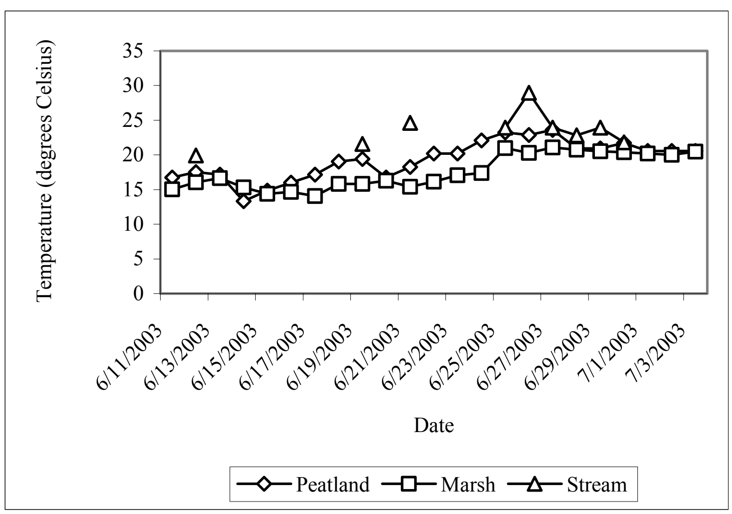

Figure 2. Comparison of water temperature for the three study sites within the Little Chazy River watershed in northern New York from 11 June to 3 July, 2003.

The peatland site was dominated by *Sphagnum* spp. and leatherleaf (*Chamaedaphne calyculata*), and had red maple (*Acer rubrum*) on the edges of the water. It was classified under the United States Classification of Wetlands and Deepwater Habitats as a palustrine wetland with persistent emergent vegetation. The wetland was mostly fed by precipitation, with some exchange of groundwater. Disturbance to the area occurred between 1910 and 1916 due to construction of a road and retaining wall adjacent to the site (*Contributions*, date unknown). This caused the soil substrate to become laden with rocks and gravel.

The marsh site was a freshwater marsh dominated by *Typha* spp. and yellow lily (*Nuphar* spp.). It was fed by surface water and located upstream of the Miner Dam in a large side pocket with negligible flow. This marsh was classified as a palustrine wetland with persistent emergent vegetation. Construction of the Miner Dam took place in 1911, which restricted water flow and increased wetland area (*Contributions*). At the same time, cement layered over a large portion of the hillside adjacent to our site caused alteration to the landscape.

Lastly, the stream site is classified as a palustrine wetland, and has a generally rocky unconsolidated substrate and an aquatic bed of Eurasian watermilfoil (*Myriophyllum spicatum*). Algae and periphyton also grow in abundance. Lake Alice was created following the 1907 construction of a dam at Tracy Brook (*Contributions*). During the dry season, usually August to November, there is often no flow over the dam, allowing material to settle at the bottom of the streambed and decompose.

Plant Decomposition.

Plant materials were harvested from another wetland, separate from the study sites and along Tracy Brook (the outlet of Lake Alice). Only *Typha* species were taken and only the stems and leaves of green new growth were used. Plant material was then cut into pieces of approximately 8 cm in length and randomly mixed. Rectangular fiberglass-mesh litterbags were constructed, with dimensions 30-cm high x 15-cm wide, and a mesh size of 1.8 mm. Each received 100 g of green, non-dried plant material. The bags were then sealed, leaving two small openings about 2 cm wide along the top, in order to allow macroinvertebrates to access plant materials and aid decomposition. The litterbags were securely attached clothesline-style to a length of nylon cord, which was suspended level with the surface of the wetland so that bags were floating in the water column. All samples were placed in an area of the site with pooled water. Rocks were also placed within the bags, in order to completely submerge the plant material. In total, 72 bags were placed in the water, allowing for three replicates of two treatments at three sites over four collection dates.

Six litterbags from each wetland were removed weekly (on days 7, 14, 21, and 27) beginning on 6 June 2003 and finishing on 3 July 2003. The litterbags were immediately placed in polyethylene bags for transport after removal from the wetland. Once in the lab, three bags from each site were randomly chosen to have macroinvertebrates removed. Macroinvertebrates were stored in vials filled with 85% ethanol until they were identified down to family and enumerated. Numbers from the three replicates were added together for a sum total of individuals per family for each site for each week. A subset of the families that eat decaying plant matter (detritivores) was created from the original set of data (Pennak, 1989). Totals of all macroinvertebrates and the detritivore subset were processed to produce the richness (number of families present), density of individuals per litterbag, and diversity index at the family level.

Following macroinvertebrate removal, litter was rinsed of debris and dried at 60ºC for 48 hrs. Dried plant material was weighed and ground into a powder using a Wiley Mill (1-mm), and then analyzed for percent nitrogen content on a LECO nitrogen/protein analyzer, model FP-428. The other three samples were rinsed of debris and dried at 105 ºC for 48 hrs prior to measurement of dry biomass on a mass balance. Our initial samples, taken on 6 June 2003, were analyzed for the same parameters immediately following plant collection.

Single-factor analysis of variance (ANOVA) tests ($\alpha = 0.05$) assessed differences due to study site on mean dry biomass remaining and mean percent nitrogen content for each week of the study. If the p-value was less than 0.05, the null hypothesis (H_o: $\mu_{peatland} = \mu_{marsh} = \mu_{stream}$) was rejected, and therefore, at least two sample means were significantly different. To determine which sample means were statistically different, Tukey's procedure was performed. Dry biomass remaining was also used to determine decay rate according to the single exponential decay model, $\ln(W_t/W_o)=-kt$, where W_t is the dry biomass remaining at time t, W_o is the initial dry biomass, k is the decay coefficient, and t is the time in days (Wrubleski *et al.*, 1997).

Water and Soil Properties.

Supplementary tests were performed to characterize water qualities at the three sites. Water pH value and dissolved oxygen concentration were measured before litterbag collection each week using pH-Electrode SenTix 41-3 and CellOx 325 probes, and a Multiline P4 Universal Meter. These measurements were taken directly adjacent to the location of the litterbags. Water samples were additionally collected near all three sites and analyzed for nitrate, ammonium, and phosphate concentrations (Pers.Comm. with Shirk and Zuidema).

Soil cores were taken from sites where soil and organic deposits existed, and soil depth of each distinct layer was recorded. The stream site had no procurable soil for sampling. Out of three samples taken, only one sample from the peatland site had sufficient soil content for analysis. The other samples were composed of living plants, organic litter, and rock material. Three replicates were obtained at the marsh site.

In the lab, soil samples were then analyzed for total nitrogen, available nitrogen, pH, and percent organic matter. Each of the soil layers was separately dried at 60°C for 48 hr. For the soil available nitrogen test, 1-g subsamples were extracted with 10-mL 2N KCl, and shaken for 1 hr. These samples were then diluted several times and combined with EDTA, salicylate-nitroprusside, and buffered hypochlorite reagents, and allowed to develop for 30 min (Mulvaney, 1996). Samples were colorimetrically analyzed for available nitrogen at 667 nm. Soil pH was determined by agitation of 1-g of soil in 10-mL of milli-q water for 1 min, followed by evaluation with a Corning pH/ion meter 150. In addition, soil subsamples were first oven-dried at 105ºC, and then placed in a 500ºC oven for 2 hr to combust organic matter (Clesceri *et al.*, 1998). The organic matter content in each soil layer was taken as the difference between the two weights.

RESULTS

Decomposition Rates.

Dry biomass decreased incrementally at all three sites over the 27 days of the study. For the first collection date (day 7), mean remaining dry biomass was similar for all three sites: 89.3% remaining in the peatland, 84.4% remaining in the marsh, and 88.0% remaining in the stream. Therefore, as much as 11-16% of mass lost may be attributed to leaching. After the first week, trends in dry biomass remaining developed, and were sustained for the duration of the study (Figure 3). The greatest retention of dry biomass, 76.5% remaining after 27 days, occurred at the peatland site, while only 30.2% of original dry biomass remained after the same period of time at the stream site. In comparison, intermediate retention of dry biomass (59.3% remaining) was recorded at the marsh site. The stream samples were statistically different from the peatland samples and the marsh samples on Day 14 ($p = 0.012$). All three sites had significantly different biomass retention on Days 21 and 27 ($p=0.000$; $p = 0.000$).

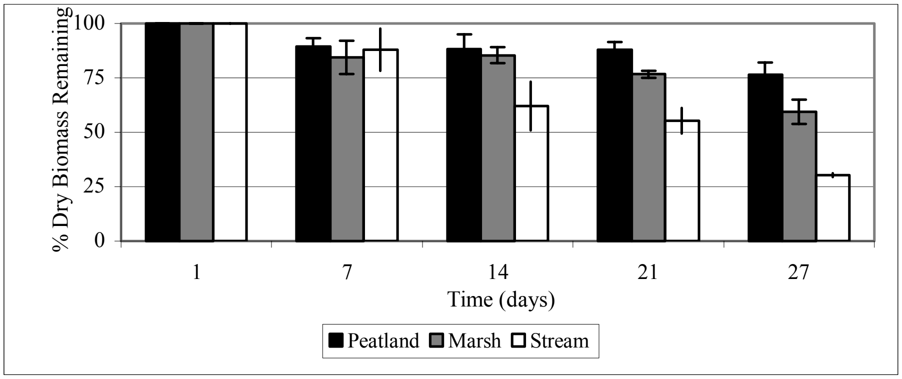

Figure 3. Mean percent dry biomass remaining of *Typha* spp. litter from three study sites in Little Chazy River Watershed of northern New York between 6 June and 2 July 2003 (n=3, except stream day 21, n=2) ± 1 standard deviation.

The lowest average decay coefficient over the study period was calculated for the peatland samples ($k=0.010\ d^{-1}$). The marsh samples had an intermediate decay coefficient (k=0.020), while the stream samples had the highest decay coefficient ($k=0.045d^{-1}$) (Figure 4).

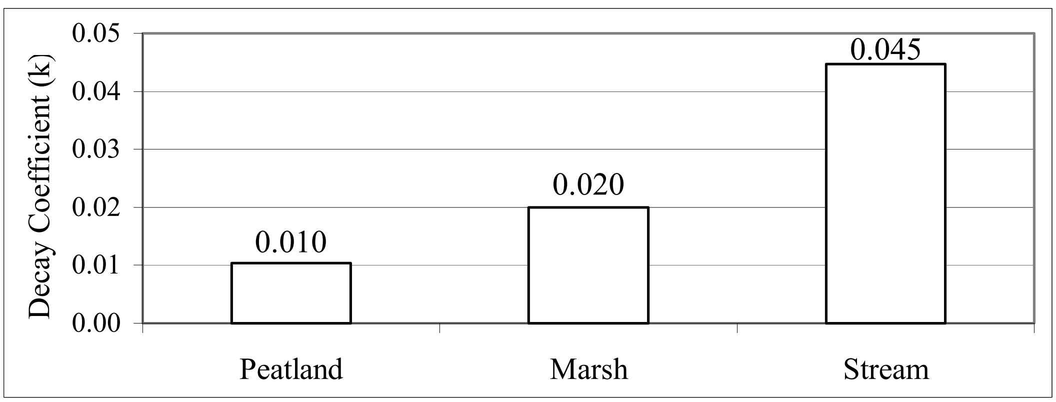

Figure 4. Decay coefficients for dry biomass loss of *Typha* spp. litter from three study sites in the Little Chazy River watershed of northern New York between 6 June and 2 July 2003.

Nitrogen.

Percent nitrogen content varied over the collection dates (Figure 5). Differences in nitrogen content were not statistically significant among sites at the end of the study ($p = 0.292$), but were statistically significant on Days 14 and 21 ($p = 0.000$; $p = 0.017$).

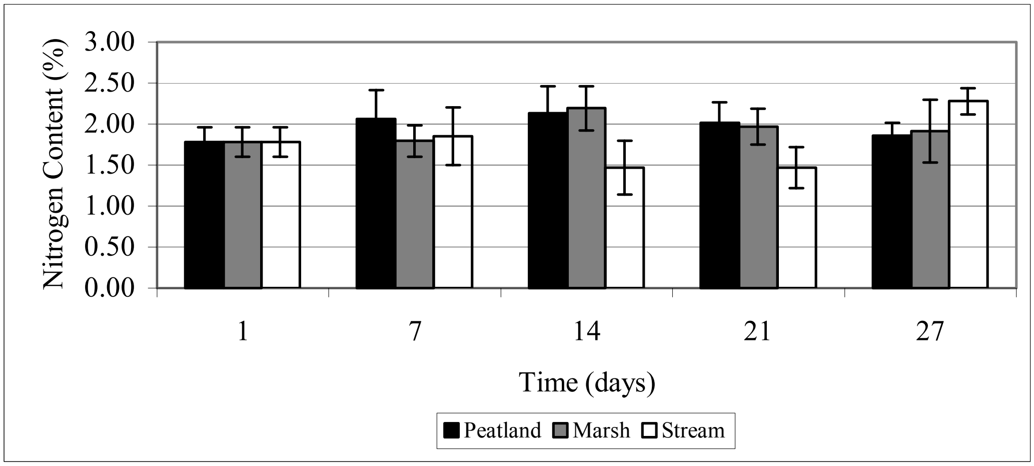

Figure 5. Mean total nitrogen content of *Typha* spp. litter as a percentage of dry biomass from three study sites in Little Chazy River Watershed of northern New York between 6 June and 2 July, 2003 (n = 3, except Stream day 27, n = 2) ± 1standard deviation.

Macroinvertebrates.

The macroinvertebrate communities within the litterbags were composed mainly of detritivores, accounting for 65-97% of the entire community with an increasing percentage over time. The stream site showed the greatest macroinvertebrate density (number of individuals per litterbag = 167-480). The peatland site tended to have the next greatest density (17-147), and the marsh site tended to have the lowest density (32-47) (Figure 6).

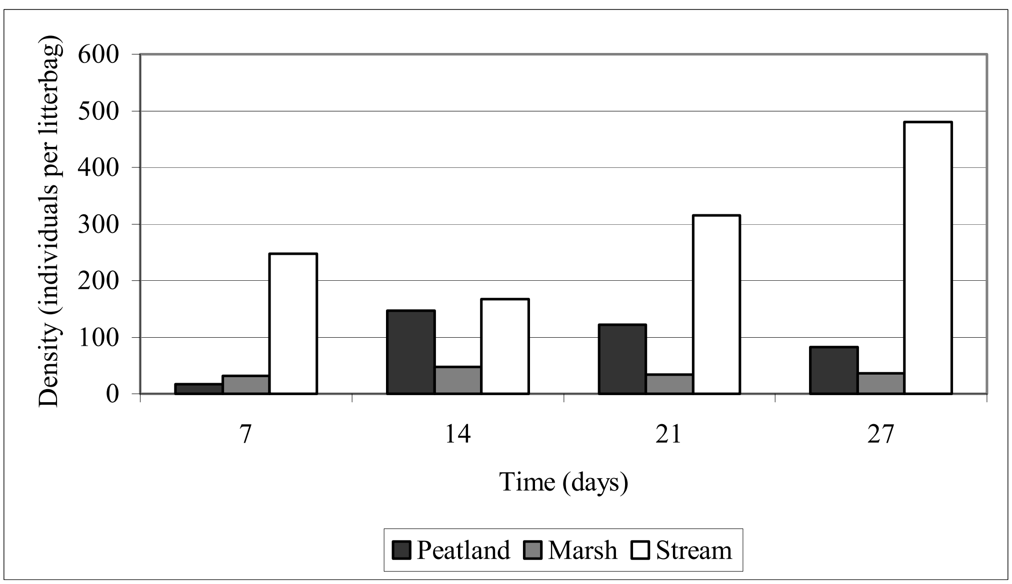

Figure 6. Density of macroinvertebrates in litterbags filled with *Typha* spp. from each collection date for three study sites in the Little Chazy River watershed of northern New York from 6 June to 2 July 2003.

Richness at the family level was highest for the stream site (8-12 families), intermediate for the marsh site (6-8), and lowest for the peatland site (3-6). The diversity index values tended to be the highest for the marsh site (1.7-3.6), intermediate for the stream site (1.4-2.4), and lowest for the peatland site (1.2-2.4). The two most dominant families per site were Chironomidae (61-93%) and Oligochaeta (14-25%) at the peatland site, Chironomidae (44-77%) and Gastropoda (10-28%) at the marsh site, and Amphipoda (44-86%) and Isopoda (4-20%) at the stream site (Figure 7).

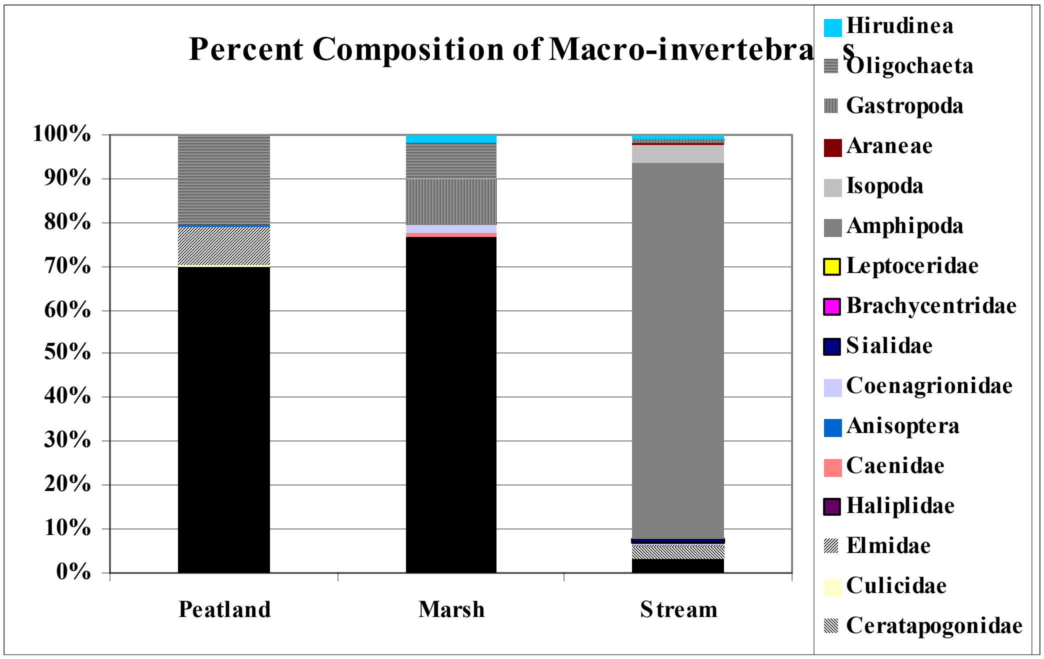

Figure 7. Macroinvertebrate families on *Typha* spp. litter from three study sites in the Little Chazy River watershed of northern New York between 6 June and 2 July 2003.

Water and Soil Properties.

Of the three sites, the peatland maintained the lowest pH and dissolved oxygen values (Table 1). Water depth was similar to that of the marsh site, and there was no flow velocity. The marsh possessed low dissolved oxygen, a similar water depth to the peatland site, and a circumneutral pH value. The stream site had a circumneutral pH and measurable flow velocity. It also had the greatest water depth and highest dissolved oxygen concentration of the three sites.

Nitrogen and phosphate levels in the water were low in the peatland as compared to the other two sites (Table 1). The stream and marsh had similar levels of nitrogen, but the dominant form in the marsh was nitrate, while the stream showed a combination of ammonium and nitrate. Phosphate levels were highest at the marsh site.

Table 1. Summary of physical and chemical parameters of water at three study sites in the Little Chazy River watershed in northern New York between 12 June and 2 July, 2003. Nutrient concentrations were sampled on 10-11 June (peatland and marsh) and 2 July (stream).

Site	**Peatland**	**Marsh**	**Stream**
pH	4.64-4.74	6.15-6.29	7.39-8.72
Dissolved Oxygen (mg/L)	1.38-3.85	2.32-4.30	9.19-10.26
Average Temperature (ºC)	19.10	17.87	25.99
Water Depth (m)	0.685	0.640	1.047
Flow Velocity (m/s)	--	--	0.033528
NO_3^- (μg/L)	18.601	93.005	0.000
NH_4^+ (μg/L)	23.288	0.000	2.786
PO_4^{3-} (μg/L)	0.000	30.846	0.633

The peatland sample had lower soil pH than the average value for the marsh samples (Table 2). Concentrations of total and available nitrogen, as well as percent organic matter, were higher in the peatland soil than in the marsh soil. However, the ratio of available nitrogen to total nitrogen was higher in the marsh than in the peatland.

Table 2. Chemical and physical data for the top soil layer from three study sites in Little Chazy River Watershed of northern New York sampled 24 June, 2003.

Site	Sample Size	pH	Total Nitrogen (μg/g soil)	Available Nitrogen (μg/g soil)	Organic Matter (%)
Peatland	1	4.494	24900	278	64.220
Marsh	3	5.474	2580	100	16.543
Stream	0	---	---	---	---

DISCUSSION

Decomposition Rates.

As an indicator of decomposition, rates of loss of dry biomass signified that decay occurred most quickly at the stream site. This suggests that decomposition is most rapid in a nutrient-rich site with high dissolved oxygen, circumneutral pH, and moving water. The correlation of decay rate with study site supported our hypotheses of faster decomposition in a wetland with high dissolved oxygen and circumneutral pH, and slower decomposition in an oxygen-limited acidic wetland. In comparison to published values, decay coefficients for plant material can range from $k = 0.0001 - 4.0\ d^{-1}$, but wetland ecosystems generally display values at the lower end of the scale (Chamie and Richardson, 1978). Our calculated decay rate for the marsh site ($k = 0.020\ d^{-1}$) were similar to those found by Nelson and his co-authors in their 1990 study of *Typha glauca* in marshes ($k = 0.022\text{-}0.0245\ d^{-1}$), but decay coefficients from other studies in marshes ($k = 0.00057\text{-}0.0024\ d^{-1}$) tended to be lower than our values (Wrubleski et al., 1997; Emery and Perry, 1996; Mitsch and Gosselink, 2000).

Our relatively high decay rates may be explained by the short duration of our study, time of year, and the type of litter used. The first two stages of decomposition, leaching and breakdown of labile materials, occur quickly, while the breakdown of recalcitrant materials occurs over a longer period of time. The 27 days of our study allowed us to capture only the decay rates during the initial rapid stages, and not the slow third stage. Completing this study during the summer months may have also resulted in higher decomposition rates, as warmer temperatures increase rates. Finally, decay rates may also have been higher than in other reports due to our use of green, rather than senesced *Typha* spp. leaves and stems. Green litter tends to lose a greater amount of dry biomass due to leaching than naturally senesced litter loses to leaching (Nelson *et al*., 1990).

Nitrogen.

Percent nitrogen content of plant litter did not show statistically significant differences among sites, and no overall trend was found throughout the study period at any of the three sites. During decomposition, percent nitrogen content has been documented in the literature to both rise and drop. From one perspective, nitrogen content might be expected to decrease during decomposition, as nitrogen would be lost during leaching and mass loss. In agreement with this, some studies of wetland decomposition rate have documented decreases in nitrogen content over the first 30 days (Nelson *et al*., 1990; Wrubleski *et al*., 1997). Yet in other studies, increases in nitrogen content have been observed over the same time period (Thormann and Bayley, 1997; Davis and Van der Valk, 1982).

The increase in nitrogen content could be a result of immobilization. The phenomenon of immobilization results when the uptake of inorganic nutrients, including nitrogen, from the surrounding water (by microbes growing at the surface of the plant litter) counteracts and exceeds losses due to leaching (Brinson *et al*., 1981). In addition, minerals containing nitrogen may be deposited into small fissures in the plant matter as water flows through the litterbags (Thormann and Bayley, 1997). Another possible explanation for an increase in percent nitrogen content would lie in the relative amounts of nitrogen and carbon in *Typha* spp. leaves and stems (Thormann and Bayley, 1997). In terms of total biomass, carbon is a dominant constituent of plants (there is 15 times the amount of carbon than nitrogen in *Typha latifolia*). During decomposition, carbon might be lost at a more rapid rate than nitrogen, which would skew values of the percentage consisting of nitrogen for the total dry biomass upward.

Macroinvertebrates.

The highest density of detritivore macroinvertebrates occurred at the site with the highest decomposition rate (the stream site). However, this correlation cannot fully attribute enhanced decomposition to increased presence of detritivore macroinvertebrates, since the peatland site exhibited higher detritivore density than the marsh site, but had a lower decomposition rate. Species richness was higher at the marsh site than the peatland site, which may have affected the differences in decomposition rates due to differential feeding rates of chironomids, gastropods, and elmids. These findings are consistent with the general proposition that macroinvertebrates assist decomposition, but do not primarily determine the decomposition rates (Brinson *et al.*, 1981). Another factor in reducing decomposition for the peatland site may have been the inhibition of macroinvertebrate colonization due to the relatively harsh chemical environment.

Water and Soil Properties.

The low pH in the peatland water may have lowered its decomposition rate by inhibiting the bacterial activity that would assist decomposition (Mitsch and Gosselink, 2000). Over our three sites, decay rate was highest in a wetland with high dissolved oxygen, measurable velocity, relatively warm temperatures, and circumneutral pH. Decay rate was lowest in the peatland, which had the lowest dissolved oxygen and pH.

Our findings are consistent with published data documenting reduced decomposition in anoxic conditions (Nelson *et al.* 1990). The low levels of nitrate and high levels of ammonium in the peatland waters reflected oxygen-limited conditions. Such conditions would slow nitrification, the aerobic conversion of ammonium to nitrite and then nitrate, but not denitrification, the anaerobic conversion of nitrate to nitrogen gas and nitrous oxide. Nitrates in the water would therefore be converted at a faster rate than ammonium, allowing for a build-up of ammonium. The water chemistry of the peatland also showed lower nitrate and phosphate levels than the marsh and stream waters, affirming the concept of a nutrient-poor site having a slower decomposition rate (Table 3).

Soil data further supported the rates of loss of dry biomass for the marsh and peatland sites. From the values for soil pH, organic content, and available nitrogen concentration, the soils from the marsh site can be classified as mineral soils, and those from the peatland can be classified as organic soils (Mitsch and Gosselink, 2000). Marsh soils had organic compositions of less than 20-35 percent, while peatland soils had high organic content (64%). The high level of total nitrogen found in the peatland soils corresponded with a large amount of organic litter sequestered in the soil. Soil pH, displaying the same trend as water pH, was lower in the peatland and higher in the marsh. Although the mass concentration of available nitrogen was higher in the peatland soils than in the marsh soils, available nitrogen per volume was lower in the peatland. This is because the density of organic soil is much less than that of mineral soil. Organic soils develop through accumulation of partially decomposed organic material, in conjunction with low decomposition rates. A higher organic content in the peatland soil indicates a lower decomposition rate, consistent with our findings.

CONCLUSIONS

Decomposition rate decreased over a stream-marsh-peatland gradient. Of those factors not held constant over the three sites, pH and DO appeared to be the most significant factors affecting the rate of decomposition, while macroinvertebrate density as well as soil and water chemistry supported the differences in decomposition rate among the wetlands. The nutrient-rich stream site exhibiting the fastest rate of decomposition was characterized by slightly alkaline water with high dissolved oxygen, high invertebrate density and richness, high flow velocity, and low peat accumulation. A nutrient-poor peatland had the lowest decomposition rate, and had many characteristics that would indicate slow decomposition: acidic water with low dissolved oxygen, negligible flow, soils with accumulated peat and nitrogen, and low invertebrate richness. The marsh had a decomposition rate between the nutrient-rich stream and nutrient-poor peatland sites. Accordingly, its water, soil, and macroinvertebrate community characteristics were not as extreme as the other two sites. Over our three sites, decay rate was highest in a wetland with high dissolved oxygen and close to neutral pH, while the lowest decay rate occurred in a wetland with low dissolved oxygen and low pH.

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LITERATURE CITED

Bridgham, S.D., Updegraff, K., Pastor, J. 1998. *Carbon, nitrogen, and phosphorus mineralization in northern wetlands*. Ecology 79:1545-1561.

Brinson, M. M., Lugo, A. E., and Brown, S. 1981. *Primary productivity, decomposition and consumer activity in freshwater wetlands*. Annual Review of Ecology and Systematics 12:123-161.

Chamie, J. P. M. and Richardson, C. J. 1978. *Decomposition in northern wetlands.* In Good, R. E., Whigham, D. F., and Simpson, R. L., eds. Freshwater Wetlands: Ecological Processes and Management Potential. New York: Academic Press. pp. 115-130.

Clesceri, L.S., Greenberg, A.E., and Eaton, A.D., eds. 1998. Standard Methods for the Examination of Water and Wastewater. 20th ed. Washington, D.C.: American Public Health Association.

Contributions to the North Country: William Henry Miner. Chazy, NY: Miner Institute.

Davis, C. B. and van der Valk, A.G. 1983. *Uptake and release of nutrients by living and decomposing* Typha Glauca *Godr. tissues at Eagle Lake, Iowa*. Aquatic Botany 16: 75-89.

Emery, S. L. and Perry, J. A. 1996. *Decomposition rates and phosphorus concentrations of purple loosestrife (*Lythrum salicaria*) and cattail (*Typha *spp.) in fourteen Minnesota wetlands*. Hydrobiologia 323: 129-138.

Hobbie, S.E. 1992. *Effects of plant species on nutrient cycling*. Trends in Ecology and Evolution 7:336-339.

Merritt, R.W. and Cummins, K.W., eds. 1984. An Introduction to the Aquatic Insects of North America. 2nd ed. Dubuque, IA: Kendall/Hunt Publishing Co.

Mitsch, W. J. and Gosselink, J.G. 2000. Wetlands. 3rd ed. New York: John Wiley and Sons.

Mulvaney, R.L. 1996. *Nitrogen -- inorganic forms. In* Bigham, J.M., ed. Methods of soil analysis part 3: chemical methods. Madison, WI: Soil Science Society of America, Inc. pp. 1123-1184.

Nelson, J.W., Kadlec, J.A., and Murkin, H.R. 1990. *Seasonal comparisons of weight loss for two types of* Typha glauca *Godr. leaf litter*. Aquatic Botany 37:299-314.

Pennak, R.W. 1989. Fresh-water Invertebrates of the United States: Protozoa to Mollusca. 3rd ed. New York: John Wiley & Sons, Inc.

Thormann, M. N. and Bayley, S.E. 1997. *Decomposition along a moderate-rich fen-marsh peatland gradient in boreal Alberta, Canada.* Wetlands 17:123-137.

Webster, J.R. and Benfield, E.F. 1986. *Vascular plant breakdown in freshwater ecosystems*. Annual Review of Ecology and Systematics 17: 567-594.

Wrubleski, D. A., Murkin, H. R., van der Valk, A. G., and Nelson, J. W. 1997. *Decomposition of emergent macrophyte roots and rhizomes in a northern prairie marsh*. Aquatic Botany 58:121-134.