



ELSEVIER

Aquatic Botany 74 (2002) 273–285

**Aquatic
botany**

www.elsevier.com/locate/aquabot

Surface water nutrient concentrations and litter decomposition rates in wetlands impacted by agriculture and mining activities

A.A. Lee¹, P.A. Bukaveckas*

Department of Biology, Center for Watershed Research, University of Louisville, Louisville, KY 40292, USA

Received 28 March 2001; received in revised form 3 June 2002; accepted 12 July 2002

Abstract

Decomposition rates of a site-specific dominant litter, a standard litter (*Typha latifolia*), and cellulose were quantified in 10 western Kentucky wetlands using the litterbag technique. Short-term (60 and 42 days) incubations were conducted during fall 1998 and spring 1999. The effect of variable tissue nitrogen content on decomposition rates was evaluated by comparing mass loss among site-specific dominant species from each wetland. Effects of variable surface water and sediment nutrient concentrations on decomposition were assessed by measuring mass loss of standard litter materials (*Typha latifolia* and cellulose) of uniform C:N ratio. Decomposition of the site-specific dominant litter was significantly correlated with tissue C:N ratios and phosphorus concentrations in wetland waters and sediments. Water column and sediment phosphorus were also significant predictors of decomposition rates for the standard litter types. Nitrogen concentrations in surface waters were not significant predictors of decomposition for any of the substrates in either season. Wetlands impacted by mine drainage exhibited slower decomposition rates and lower nutrient levels in comparison to wetlands occurring in predominantly agricultural areas.

© 2002 Elsevier Science B.V. All rights reserved.

Keywords: Wetlands; Decomposition; Nitrogen; Phosphorus; Agriculture; Mining

1. Introduction

Decomposition plays a central role in ecosystem nutrient cycling (Richardson, 1994). The cleaving of organic macromolecules into their constituent components releases bound

* Corresponding author. Tel.: +1-502-852-3726; fax: +1-502-852-0725.

E-mail address: pabuka01@athena.louisville.edu (P.A. Bukaveckas).

¹ Present address: US Army Corps of Engineers, Waterways Experiment Station, 3909 Halls Ferry Road, Vicksburg, MS 39180, USA.

elements for utilization by detritivores as well as plants. Biological processing of litter follows the general sequence of microbial colonization and conditioning followed by invertebrate feeding (Short et al., 1980; Benfield and Webster, 1985; Magonigal et al., 1996). Decomposition rates have been shown to vary greatly among wetlands in diverse physiographic settings. For example, the half-life of litter (the amount of time required for one half of the original mass to decompose) within a fringe mangrove swamp can be as little as 30 days whereas, in a boreal peatland, a half-life of 8.4 years has been reported (Mitsch and Gosselink, 1993). Decomposition rates depend on physical and chemical conditions in wetlands as well as the biochemical properties of litter. Physical and chemical factors that regulate decomposer activity include temperature, hydrologic regime (period of inundation), and various water quality attributes including pH and redox conditions (Godshalk and Wetzel, 1978; Day, 1984; Short and Smith, 1988; Hobbie, 1996; Murphy et al., 1998). Low pH and high conductivity inhibit microbial activity thereby slowing down decomposition (Kok et al., 1990; Kittle et al., 1995; Kok and Van der Velde, 1994).

Various biochemical properties of litter have been shown to influence decomposition rates. Principal among these is the relative nitrogen content of plant matter, typically expressed as a C:N ratio, which has been shown to be positively correlated with decomposition rates in a variety of aquatic ecosystems (Day, 1982; Valiela et al., 1984; Enríquez et al., 1993). Heterotrophs have a high nitrogen and phosphorus content relative to litter and as a result, nutrient demands associated with decomposer activity often exceed nutrient supply from litter (Enríquez et al., 1993). Under these conditions, dissolved inorganic nutrients may be an important determinant of decomposition rates (Aerts et al., 1992; Verhoeven et al., 1996). Investigations of Canadian peatlands by Szumigalski and Bayley (1996) and Thormann and Bayley (1997) showed that decomposition rates of standard litter types were positively correlated with surface water concentrations of ammonium and soluble reactive phosphorus (SRP). Whole-ecosystem experiments have also demonstrated increases in decomposition rates following additions of N and P (Peterson et al., 1993).

An understanding of the role of dissolved nutrients in regulating decomposition rates is important since wetlands are increasingly affected by both point and non-point sources of anthropogenic nutrients. Previous work relating decomposition rates to litter nutrient content and water column nutrient availability have largely been carried out in boreal or estuarine settings. In this study, we measured decomposition rates in 10 wetlands of the Midwestern United States that were subject to runoff from agricultural or mining (coal field) areas. We compared decomposition rates of a standard litter material (constant C:N) and a site-specific plant dominant (variable C:N) among wetlands in relation to tissue, sediment and surface water nutrient concentrations. These data were used to determine whether surface water N and P concentrations were a significant predictor of inter-site variation in litter decomposition rates.

2. Methods

2.1. Site description

The study sites were located in western Kentucky within an area approximating 37–38°N longitude and 87–89°W latitude. This region experiences a humid and continental climate

with a mean annual temperature of 14 °C and a mean annual precipitation of 122 cm. Land use in the region is characterized by agricultural development as well as bituminous coal production, predominantly by surface mining methods (McGrain, 1983). The watersheds of sites 1, 2, 3, 4, 8, 9 and 10 contained extensive agricultural development including croplands, dairy operations and confined animal farm operations. Additionally, sites 3 and 4 were adjacent to a water body that received effluent from a wastewater treatment plant. Three sites occurred in proximity to coal fields (nos. 5, 6 and 7). The study sites were palustrine wetlands dominated by trees, shrubs, persistent emergents or mosses (Cowardin et al., 1979). The wetlands were characterized by semi-permanent flooding (nos. 1, 2, 3, 4, 5 and 10), permanent flooding (nos. 6, 7 and 9) or seasonal flooding (no. 8).

2.2. Decomposition experiments

We conducted short-term incubation experiments in order to assess seasonal variation in decomposition rates that might arise from seasonal changes in anthropogenic nutrient loading. Litterbags were incubated from September to December 1998 and April to June 1999 (hereafter, fall and spring experiments, respectively). Bags containing three litter types were placed in each of the 10 wetlands. The three litter types were cellulose (Fischerbrand P8 filterpaper, diameter 9.0 cm), *Typha latifolia* and a site-specific dominant species. For the fall experiment, *Typha latifolia* was collected at each site and returned to the same site for the decomposition study. In spring, *Typha latifolia* was collected at a site that was not affiliated with any of the study areas. Twelve (fall) or 18 (spring) replicate litterbags were used for each of the three litter types (total of 36–54 bags per site). In preparation for the decomposition experiments, senesced portions of the dominant vascular plant species were collected from each site. The collected specimens were: *Salix nigra* Marsh (black willow; site 1), *Cephalanthus occidentalis* L. (button bush; site 2), *Phragmites australis* (common reed; sites 3, 7), *Rumex crispus* (dock; site 4), *Scirpus cyperinus* (bulrush; site 5), *Typha latifolia* L. (cattail; site 6), *Acer rubrum* L. (red maple; site 8), *Sagittaria brevisrostra* (arrowhead; site 9), and *Carex* sp. (sedge; site 10). All plant material was oven-dried at 60 °C until constant weight was achieved. Samples ranging in weight from 0.120 to 2.213 g were placed in fiberglass screen bags. Decomposition bags were 19 cm × 22 cm with mesh size of 1.3 mm. For cellulose only, two bag types were used: one allowed access by macroinvertebrates (mesh size 1.3 mm) and the other excluded macroinvertebrates (mesh size 0.4 mm). Subsequent statistical analyses indicated no significant difference between the two bag types (ANOVA; $P = 0.75$) and hereafter cellulose decomposition rates are reported for the 1.3 mm bags only.

2.3. Sample processing

Litterbags were incubated for 60 days (fall) or 42 days (spring) and collected at 1-month (fall) or 1-week (spring) intervals. On each date, a minimum of three replicate bags were collected for each litter type. Upon collection, sediment and debris were removed from the bags. Each bag was further cleaned by gently rinsing in two 50 ml double deionized water baths. Litter was removed to a pre-weighed filter (Gelman GF/C) and gently rinsed with 25 ml of double deionized water. The filters and litter material were dried at 60 °C to a

uniform mass and weighed to the nearest 0.001 g. For determination of carbon and nitrogen content, 150–250 µg of litter was placed in tin capsules and analyzed in a Perkin-Elmer Series II CHNS/O Analyzer 2400. Initial and final values for each litter type were obtained.

At the onset of the experiment and at each litterbag collection date, water and sediment samples were collected for analysis. Water samples were placed in a cooler immediately upon collection and refrigerated until analyses were performed. Water samples were analyzed using standard methods (APHA, 1992) for determinations of total nitrogen (TN; persulfate digestion), ammonium (modified berthiolate process), nitrate (cadmium reduction), total phosphorus (TP; persulfate digestion) and soluble reactive phosphorus (SRP; ascorbic acid two reagent method). Total nitrogen, ammonia and nitrate were analyzed on a Skalar San Plus Analyzer. Temperature and conductivity were measured in the field using an YSI 3000 T-L-C Meter. An Orion Model 410A meter was used to determine sample pH upon return in the lab. Alkalinity was determined using the potentiometric titration method (APHA, 1992). Sediment samples were obtained by collecting four 5-cm cores in proximity to the decomposition bags. The cores were composited, air-dried and pulverized to a talcum-like consistency using a mortar and pestle. Subsamples of 0.1 g were analyzed for total phosphorus using the rapid perchloric acid digestion method (Sommers and Nelson, 1972).

2.4. Data analysis

A review of the literature revealed a variety of metrics for quantifying rates of decomposition including the percent mass remaining, the decomposition constant k and the slope of the regression line relating mass remaining over time (Aerts and De Caluwe, 1997; Brinson et al., 1981; Enríquez et al., 1993). We compared various metrics and transformation procedures and found that the slope of a linear regression relating percent mass remaining over time was the best descriptor of decomposition rate. These mass change estimates (% per day) were analyzed using three-way ANOVA to determine season, litter type and site effects. To compare decomposition rates from this study to those of other investigators, we also derived the logarithmic decay constant (k) using the formula

$$X = e^{-kt}$$

where t is time in days, k the litter specific constant and X is the ratio of original material remaining. Univariate regressions were performed to assess the utility of litter and surface water nutrient concentrations in predicting variation in decomposition rates. Statistical analyses were performed using SAS (SAS Institute Inc., 1998) and Sigma Plot (SPSS Inc., 1999).

3. Results

3.1. Wetland physical–chemical conditions

Surface water and sediment chemistry data were averaged across sampling dates to characterize the physical–chemical conditions within each wetland during the litterbag incubation. Site-specific averages were aggregated by land use (coal fields versus agricultural) and measurements obtained during the two incubation periods were analyzed separately

Table 1
Physical–chemical characteristics of 10 wetlands located in western Kentucky, USA

| Physical–chemical parameters | Agriculture | | Coal fields | |
|--|-------------|--------|-------------|--------|
| | Fall | Spring | Fall | Spring |
| pH | 7.9 | 7.5 | 7.7 | 7.1 |
| Alkalinity (mg l^{-1}) | 96 | 90 | 112 | 184 |
| Conductance ($\mu\text{S cm}^{-1}$) | 592 | 254 | 2622 | 2445 |
| TN ($\mu\text{g l}^{-1}$) | 1031 | 999 | 674 | 482 |
| N-NO ₃ ($\mu\text{g l}^{-1}$) | 21 | 169 | 67 | 25 |
| N-NH ₃ ($\mu\text{g l}^{-1}$) | 103 | 84 | 241 | 140 |
| TP ($\mu\text{g l}^{-1}$) | 98 | 178 | 21 | 38 |
| P-SRP ($\mu\text{g l}^{-1}$) | 51 | 47 | 17 | 7 |
| Sediment TP (mg g^{-1}) | 0.079 | 0.076 | 0.044 | 0.036 |
| Temperature ($^{\circ}\text{C}$) | 16.9 | 20.9 | 19.5 | 23.2 |

Data shown are average values for seven sites occurring in predominantly agricultural settings and three sites located in a coal field area. Fall data were collected during September–December 1998 and spring data were collected during April–June 1999.

(Table 1). Surface waters of all the wetlands were circumneutral (pH 6.5–8.4) and had moderate to high alkalinity ($23\text{--}364 \text{ mg CaCO}_3 \text{ l}^{-1}$). Mine drainage influences on wetland water quality were most apparent in comparisons of specific conductance which were substantially higher among sites located in the coal field relative to sites in agricultural settings. Nutrient concentrations also differed with land use type and tended to be higher among wetlands in agricultural areas. Surface water concentrations of TN were approximately two-fold higher among wetlands in agricultural areas while TP concentrations were four-fold higher in comparison to the coal field sites. Similar differences were observed in SRP but not DIN which exhibited comparable concentrations in both groups. Total nitrogen concentrations tended to be higher in fall than spring whereas the opposite was true for TP. Among the seven wetlands located in agricultural settings there was considerable variation in surface water nutrient concentrations with TP values ranging from 18 to $266 \mu\text{g l}^{-1}$ and TN values ranging from 317 to $2063 \mu\text{g l}^{-1}$. Total nitrogen was not significantly correlated with TP in either season ($P = 0.31$). Sediment TP concentrations were approximately two-fold higher among the agricultural wetlands than in the coal field sites. Average water temperatures were cooler among forested sites than in wetlands dominated by emergent vegetation. In all wetlands, temperatures were higher during the spring experiment.

3.2. Decomposition rates

Statistical analyses (three-factor ANOVA) revealed that litter type, site location and season were significant predictors of variation in daily mass change (Table 2). These three factors explained 50% of the variation in decomposition rates with Site Location accounting for the largest proportion of the explained variation. Subsequent analyses (Tukey pairwise comparisons) revealed that site-specific differences were due to low decomposition rates among the three wetlands located in proximity of coal fields. For all three substrate types and in both seasons, decomposition rates were higher among the seven agricultural wetlands

Table 2
Statistical analyses (ANOVA) of decomposition rates measured in 10 Kentucky wetlands

| Source of variation | d.f. | %SS | P |
|---------------------|------|-----|--------|
| Season | 1 | 4 | 0.021 |
| Litter type | 2 | 10 | 0.003 |
| Site location | 9 | 36 | <0.001 |
| Residual | 18 | 11 | |
| Total | 59 | | |

Model parameters were: season (fall, spring), litter type (cellulose, a site-specific dominant species and a standard *Typha latifolia*) and site location (10 wetlands in western Kentucky, USA). Interaction terms were not found to be statistically significant. %SS is the percentage of the total sums of squares attributed to a factor.

(Table 3). Differences in decomposition rates between agricultural and coal field wetlands were greatest for the N-deficient cellulose and ranged from four-fold (fall) to almost 10-fold (spring). Natural litter materials (site dominant and standard *Typha*) also decomposed faster in the agricultural wetlands but differences in group averages were smaller than those observed for cellulose. In wetlands located in agricultural areas, cellulose exhibited the fastest decomposition with mass loss rates ranging from 0.9 to 2.6% per day. The *Typha* standard exhibited the slowest decomposition (<1% per day) and site-specific dominants exhibited variable (0.3–2.2% per day) and intermediate rates of decomposition. In agricultural wetlands, decomposition rates of all three substrate types were greater in the spring than in the fall. In wetlands located in the coal fields, decomposition rates were relatively uniform among substrate types and between seasons (average values <0.6% per day).

3.3. Nutrients as predictors of decomposition

For the substrate type exhibiting variable N content (site-specific dominant), we compared the utility of surface water, sediment and tissue nutrient concentrations as predictors of inter-wetland variation in decomposition rates. We found that the initial C:N ratio of the litter correlated significantly to mass change in the fall ($P = 0.019$, $r^2 = 0.52$) but not in spring (Fig. 1). During fall, decomposition rates decreased with decreasing litter N content over a range of C:N from 15 to 50. In spring, a similar pattern was observed for C:N values ranging from 10 to 30 but the regression was not significant because of two outlier points. The

Table 3
Decomposition rates of cellulose, a site-specific dominant species and a standard *Typha latifolia* incubated in 10 wetlands in western Kentucky, USA

| Substrate type | Agriculture | | Coal fields | |
|------------------------------------|-------------|-------------|-------------|-------------|
| | Fall | Spring | Fall | Spring |
| Cellulose (% per day) | 1.28 ± 0.09 | 1.91 ± 0.25 | 0.28 ± 0.14 | 0.20 ± 0.10 |
| Site-specific dominant (% per day) | 0.91 ± 0.14 | 1.28 ± 0.39 | 0.58 ± 0.14 | 0.54 ± 0.06 |
| <i>Typha latifolia</i> (% per day) | 0.64 ± 0.07 | 0.80 ± 0.05 | 0.49 ± 0.08 | 0.58 ± 0.20 |

Data shown are averages (±S.E.) among seven sites occurring in predominantly agricultural settings and three sites located in a coal field area. Decomposition rates were estimated as the slope of a linear regression relating mass loss over time (% per day) based on three replicate bags for each litter type.

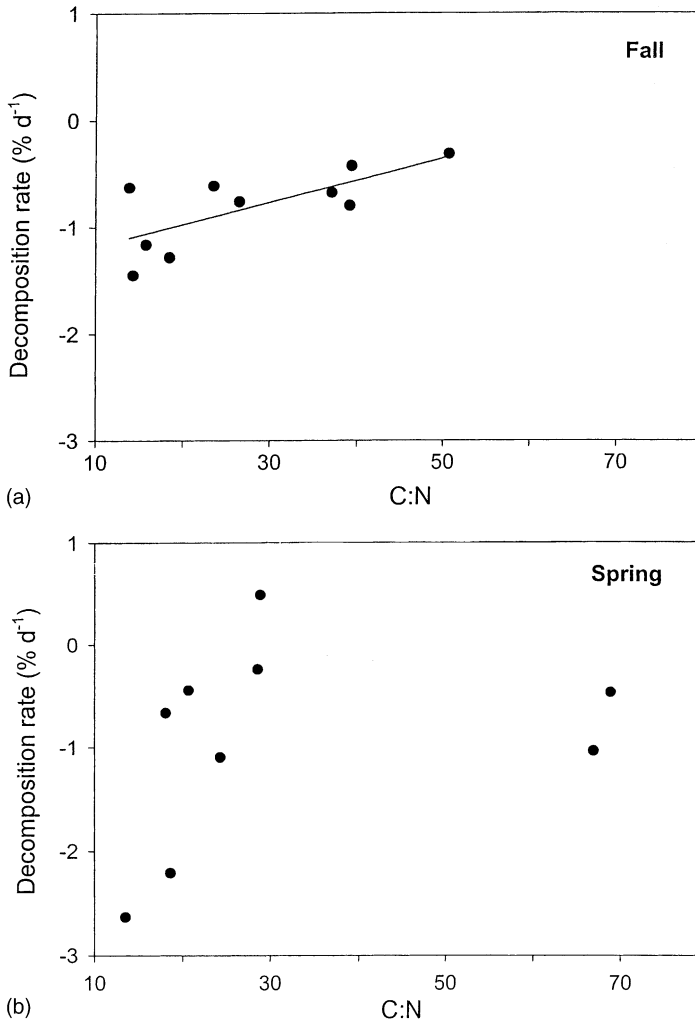


Fig. 1. Decomposition rates (as percentage of mass change per day) of site-specific dominant species as a function of their initial nitrogen content (C:N). Plant samples were collected from 10 wetlands in western Kentucky and incubated in situ during fall 1998 (a) and spring 1999 (b).

two site dominants of highest C:N (*Scirpus* and *Carex*; C:N = 70) exhibited decomposition rates comparable to materials of lower C:N (20–30). Surface water concentrations of SRP were found to be a significant predictor of decomposition rates for the site-specific dominant in both seasons (Fig. 2). Soluble Reactive Phosphorus concentrations accounted for 57% of the variation in decomposition rates during fall ($P = 0.012$) and 48% of variation in spring ($P = 0.039$). Total phosphorus concentrations in wetland sediments were also a significant predictor of decomposition rates for the site-specific dominant (spring only; $P = 0.036$, $r^2 = 0.49$; Fig. 3). For the standard litter material with uniform N content (cellulose) total

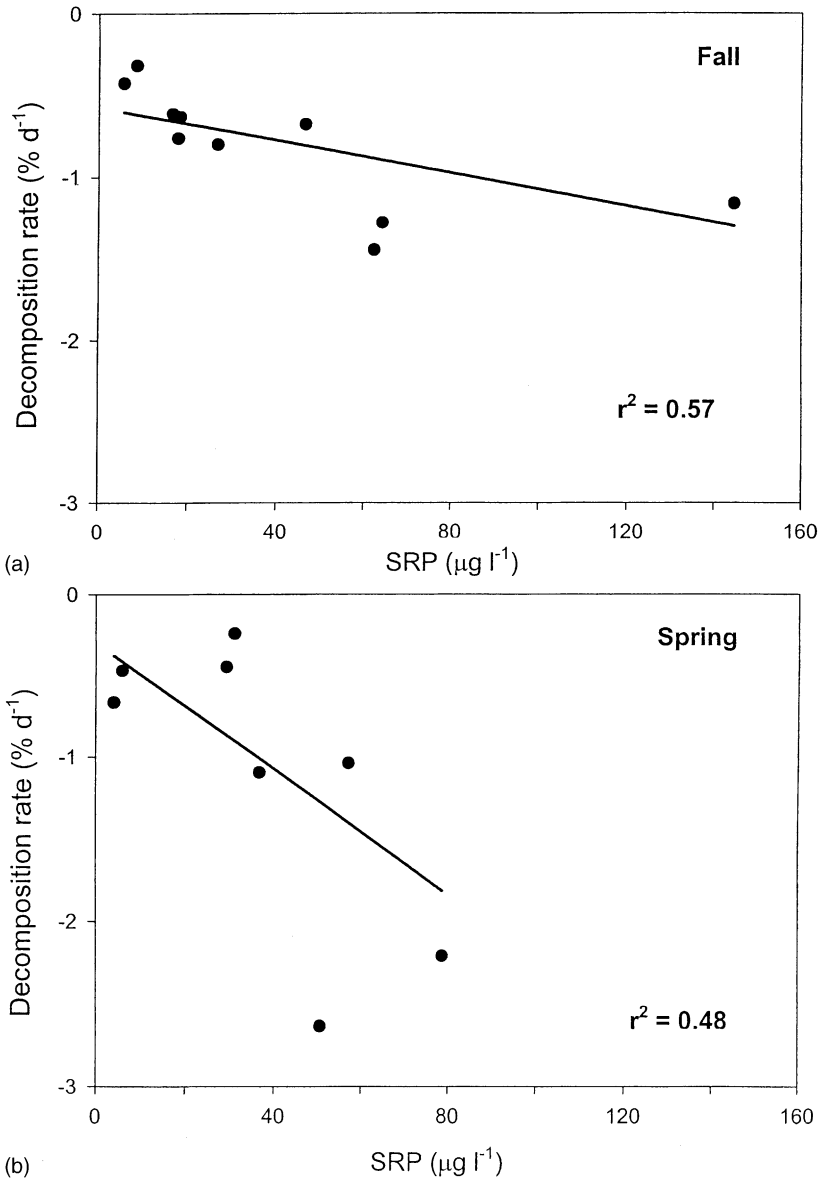


Fig. 2. Decomposition rates (as percentage of mass change per day) of site-specific dominant species as a function of surface water SRP concentrations in 10 western Kentucky wetlands during fall 1998 (a) and spring 1999 (b).

phosphorus in surface water and in sediments ($P = 0.022$, $r^2 = 0.50$) was a significant predictor of decomposition rates (Fig. 3). Nitrogen concentrations in surface water (TN, NH_3 and NO_3^-) did not correlate with decomposition rates for any of the three substrates in either season.

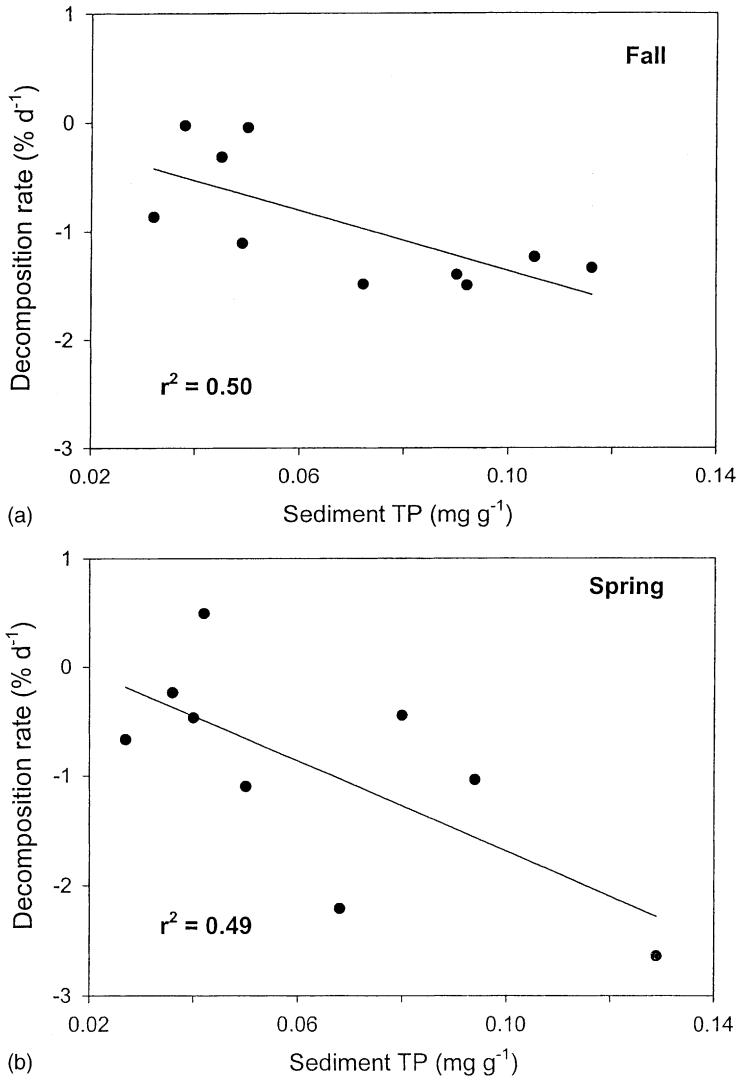


Fig. 3. Decomposition rates (as percentage of mass change per day) of a standard litter material (cellulose, a) and site-specific dominant plant taxa (b) as a function of sediment TP concentrations in 10 western Kentucky wetlands. Litterbags were incubated in situ during fall 1998 and spring 1999.

4. Discussion

Decomposition rates measured in this study were similar to previously published values for in situ litterbag incubations in wetlands from various geographic settings. Observed decomposition rates for the diverse group of litter materials represented by our site-specific plant dominants ($k = 0.010$ – 0.075 per day) corresponded to a range of litter half-life from

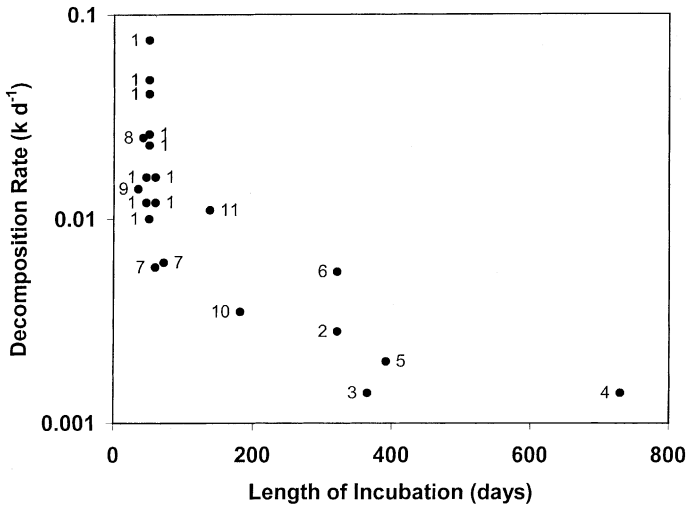


Fig. 4. Litter decomposition rates in wetlands as a function of the length of litter incubation. Data are for in situ incubations taken from the following sources: (1) this study, (2) Conner and Day (1991), (3) Day (1982), (4) Arp et al. (1999), (5) Brinson (1977), (6) Kemp et al. (1985), (7) Kittle et al. (1995), (8) Findlay et al. (1990), (9) Riley and DeRoia (1989), (10) Brinson et al. (1981), and (11) Nelson et al. (1990).

9 to 69 days. Published estimates based on incubations of comparable duration ranged from 28 to 120 days (Fig. 4). Long-term incubations (>100 day) yielded slower estimates of decomposition ($k < 0.011$ per day) and longer estimates of litter half-life (mean = 282 days). The consumption and leaching of labile fractions during the initial phase of decomposition results in rapid mass loss. Our incubation periods were of short duration (60 and 42 days) and therefore reflective of this early stage of decomposition. Recalcitrant compounds remaining in litter result in higher estimates of k during longer periods of incubation. Thus, short-term incubations such as ours likely overestimate average mass loss over longer (annual) time scales since decomposition proceeds at a greatly reduced rate in its latter stages. However, they provide a useful means for quantifying seasonal and inter-wetland variation during the initial stage of decomposition when mass loss is greatest.

It has been shown that litter materials with a low nitrogen content decompose at a slower rate and this has led some to contend that the C:N ratio of litter is a primary determinant of variation in decomposition rates (Day, 1982; Valiela et al., 1984; Enríquez et al., 1993). This contention is partially supported by our study in that the initial C:N ratio was found to be a significant predictor of variation in decomposition rates for litter materials of variable nitrogen content (site-specific dominant species). However, we found that nutrient concentrations in wetland water and sediments were also significant predictors of decomposition rates. Univariate models relating decomposition rates to tissue, surface water and sediment nutrient concentrations all yielded similar measures of reliability (ca. 50% of variance explained). Therefore, we cannot discount the possibility that nutrient levels in the environment play as important a role in determining decomposition rates as the nutrient content of the litter itself. Although nitrogen content of litter has been shown in this and

previous studies to be correlated with decomposition, we did not find that surface water concentrations of total or inorganic nitrogen were useful predictors of decomposition. Rather, inter-wetland differences in decomposition were best explained by measures of phosphorus availability. Total phosphorus concentrations in surface waters and sediments were found to be significant predictors of variation in decomposition rates for litter of variable nitrogen content (site-specific dominant) as well as standard litter of uniform C:N (cellulose and *Typha latifolia*). These findings are consistent with those of Aerts and De Caluwe (1997) who suggested that high levels of atmospheric nitrogen deposition in some parts of Europe (30–40 kg ha⁻¹) resulted in a relative shortage of phosphorus for wetland microbial communities. Although nitrogen deposition in western Kentucky is comparatively low (ca. 5 kg ha⁻¹; NADP, 2001), nitrogen inputs from agricultural sources may account for the apparent phosphorus deficiency in our wetlands. Three of our study sites were impacted by mine drainage and these exhibited lower nutrient concentrations and slower decomposition rates. Although their pH was circumneutral, high conductivity readings suggest elevated metal concentrations at these sites. Suppressed decomposition rates in wetlands receiving mine drainage have been reported elsewhere (Arp et al., 1999; Kittle et al., 1995).

5. Conclusions

Our results show that short-term decomposition rates in western Kentucky wetlands were correlated with plant tissue nitrogen levels and phosphorus availability in wetland waters and sediments. Decomposition rates were unaffected by surface water nitrogen concentrations which may be a consequence of high inputs from agricultural sources. Localized effects from mining activities were found to suppress decomposition rates.

Acknowledgements

This research was supported in part by the University of Louisville's Institute for the Environment and Sustainable Development and a Fellowship from the Graduate School. We are grateful to Rich Schultz for analyses of nutrient samples and to Gary Cobbs, Clara Leuthart, and James Wakeley for helpful comments on the manuscript. This paper is a contribution to the University of Louisville's Center for Watershed Research.

References

- Aerts, R., De Caluwe, H., 1997. Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. *Ecology* 78, 244–260.
- Aerts, R., Wallen, B., Malmer, N., 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *J. Ecol.* 80, 131–140.
- American Public Health Association (APHA), 1992. Standard Methods for the Examination of Water and Wastewater, 18th ed. American Water Works Association, Washington, DC, USA.
- Arp, C.D., Cooper, D.J., Stednick, J.D., 1999. The effects of acid rock drainage on *Carex aquatilis* leaf litter decomposition in Rocky Mountain fens. *Wetlands* 19, 665–674.

- Benfield, E.F., Webster, J.R., 1985. Shredder abundance and leaf breakdown in an Appalachian mountain stream. *Freshwater Biol.* 15, 113–120.
- Brinson, M.M., 1977. Decomposition and nutrient exchange of litter in an alluvial swamp forest. *Ecology* 58, 601–609.
- Brinson, M.M., Lugo, A.E., Brown, S., 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Ann. Rev. Ecol. Syst.* 12, 123–161.
- Conner, W.H., Day Jr., J.W., 1991. Leaf litter decomposition in three Louisiana freshwater forested wetland areas with different flooding regimes. *Wetlands* 11, 303–312.
- Cowardin, L.M., Carter, V., Golet, F.C., LaRoe, E.T., 1979. Classification of wetlands and deepwater habitats of the United States. FWS/OBS-79/31. US Fish and Wildlife Service, Washington, DC, USA.
- Day Jr., F.P., 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. *Ecology* 63, 670–678.
- Day Jr., F.P., 1984. Biomass and litter accumulation in the Great Dismal Swamp. In: Ewell, J.C., Odum, H.T. (Eds.), *Cypress Swamps*. University Presses of Florida, Gainesville, FL, USA, pp. 386–392.
- Enríquez, S., Duarte, C.M., Sand-Jensen, K., 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia* 94, 457–471.
- Findlay, S., Howe, K., Austin, H.K., 1990. Comparison of detritus dynamics in two tidal freshwater wetlands. *Ecology* 71, 288–295.
- Godshalk, G.L., Wetzel, R.G., 1978. Decomposition of aquatic angiosperms. II. Particulate components. *Aquat. Bot.* 5, 301–327.
- Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* 66, 503–522.
- Kemp, G.P., Conner, W.H., Day Jr., J.W., 1985. Effects of flooding on decomposition and nutrient cycling in a Louisiana swamp forest. *Wetlands* 5, 35–51.
- Kittle, D.L., McGraw, J.B., Garbutt, K., 1995. Plant litter decomposition in wetlands receiving acid mine drainage. *J. Environ. Qual.* 24, 301–306.
- Kok, C.J., Van der Velde, G., 1994. Decomposition and macroinvertebrate colonization of aquatic and terrestrial leaf material in alkaline and acid still water. *Freshwater Biol.* 31, 65–75.
- Kok, C.J., Van Der Velde, G., Landsbergen, K.M., 1990. Production, nutrient dynamics and initial decomposition of floating leaves of *Nymphaea alba* L. and *Nuphar lutea* (L.) SM. (Nymphaeaceae) in alkaline and acid waters. *Biogeochemistry* 11, 235–250.
- McGrain, P., 1983. The Geologic Story of Kentucky, Series XI, Special Publication 8. University of Kentucky, Kentucky Geological Survey, Lexington, KY, USA.
- Megonigal, J.P., Faulkner, S.P., Patrick, W.H., 1996. The microbial activity season in southeastern hydric soils. *Soil Sci. Am. J.* 60, 1263–1266.
- Mitsch, W.J., Gosselink, J.G., 1993. *Wetlands*, 2nd ed. Van Nostrand Reinhold, New York, NY, USA.
- Murphy, K.L., Klopatek, J.M., Klopatek, C.C., 1998. The effects of litter quality and climate on decomposition along an elevational gradient. *Ecol. Applic.* 8, 1061–1071.
- National Atmospheric Deposition Program (NADP), 2001. National Atmospheric Deposition Program 2000 Annual Summary. NADP Data Report 2001-01. NADP Program Office, Champaign, IL, 16 pp.
- Nelson, J.W., Kadlec, J.A., Murkin, H.R., 1990. Seasonal comparisons of weight loss of two types of *Typha glauca* Godr. leaf litter. *Aquat. Bot.* 37, 299–314.
- Peterson, B.J., Deegan, L., Helfrich, J., Hobbie, J.E., Hullar, M., Moller, B., Ford, T.E., Hershey, A., Hiltner, G., Kipphut, M.A., Lock, D.M., Fiebig, V., McKinely, M.C., Miller, J.R., Ventullo, R., Volk, G., 1993. Biological responses of a tundra river to fertilization. *Ecology* 74, 653–672.
- Richardson, C.J., 1994. Ecological functions and human values in wetlands: a framework for assessing forestry impacts. *Wetlands* 14, 1–9.
- Riley, T.Z., DeRoia, D.M., 1989. Early decomposition and invertebrate colonization of nodding smartweed leaves. *Wetlands* 9, 219–225.
- SAS Institute Inc., 1998. Selected SAS Documentation: Biostatistics II (spring 1998). SAS Institute Inc., Cary, NC, USA.
- Short, R.A., Smith, S.L., 1988. Seasonal comparison of leaf processing in a Texas stream. *Am. Mid. Nat.* 121, 219–224.

- Short, R.A., Canton, S.P., Ward, J.V., 1980. Detrital processing and associated macroinvertebrates in a Colorado mountain stream. *Ecology* 61, 727–732.
- SPSS Inc., 1999. SigmaPlot for Windows, Version 5.0. Exact Graphics for Exact Science. SPSS Inc., Chicago, IL, USA.
- Sommers, L.E., Nelson, D.W., 1972. Determination of total phosphorus in soils: a rapid perchloric acid digestion procedure. *Soil Sci. Soc. Am. Proc.* 36, 902–904.
- Szumigalski, A.R., Bayley, S.E., 1996. Decomposition along a bog to rich fen gradient in central Alberta, Canada. *Can. J. Bot.* 74, 573–581.
- Thormann, M.N., Bayley, S.E., 1997. Decomposition along a moderate-rich fen-marsh peatland gradient in boreal Alberta, Canada. *Wetlands* 17, 123–137.
- Valiela, I., Wilson, J., Buchsbaum, R., Rietsma, C., Bryant, D., Foreman, K., Teal, J., 1984. Importance of chemical composition of salt marsh litter on decay rates and feeding by detritivores. *Bull. Mar. Sci.* 35, 261–269.
- Verhoeven, J.T.A., Keuter, A., Van Logtestijn, R., Van Kerkhoven, M.B., Wassen, M., 1996. Control of local nutrient dynamics in mires by regional and climatic factors: a comparison of Dutch and Polish sites. *J. Ecol.* 84, 647–656.