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DIFFERENTIAL NITROGEN AND PHOSPHORUS RETENTION BY FIVE WETLAND PLANT SPECIES

Jenny T. Kao[1,2], John E. Titus[1], and Wei-Xing Zhu[1]
[1] *Department of Biological Sciences,*
State University of New York at Binghamton
Binghamton, New York, USA 13902-6000

[2] *Present address:*
Department of Soil Science
263 Soils Building
1525 Observatory Drive
University of Wisconsin-Madison
Madison, Wisconsin, USA 53706-1299

Abstract: Riparian wetlands have a demonstrated ability to filter and control nitrogen (N) and phosphorus (P) movement into streams and other bodies of water; few studies, however, have examined the roles that individual plant species serve in sequestering N and P pollutants. We evaluated the potential for growth and consequent N and P accumulation by five species of wetland perennials. We planted blocks consisting of 900-cm^2 plots of each species at 11 sites within a riparian wetland that receives large inputs of agricultural runoff. Plant shoots and roots were collected at the time of peak standing crop to determine net accumulation of biomass, N, and P for one growing season. A portion of the plant shoots was placed in decomposition litterbags in the field to determine biomass, N, and P losses for 60, 120, and 150 days. Of the five species, bur reed (*Sparganium americanum*) had the greatest aboveground accumulation of N and P but had the lowest belowground accumulation values. In contrast, woolgrass (*Scirpus cyperinus*) had the lowest aboveground values for N and P accumulation but had the highest belowground value for P. Soft rush (*Juncus effusus*) and reed canary grass (*Phalaris arundinacea*) showed high values for both aboveground and belowground N and P accumulation, while blue joint grass (*Calamagrostis canadensis*) showed low values for aboveground N and P. The five species also showed wide variations in the retention of N and P in decomposing shoots. *Juncus effusus* had the highest percentages of N and P remaining in litter after five months (87% N and 69% P), while *P. arundinacea* retained only 28% N and 18% P. *Sparganium americanum* had high retention rate for N in litter (74% N) but showed low P retention values (35%). *Scirpus cyperinus* and *C. canadensis* also showed high retention rates of litter N but lower values for P retention. Our study suggests that species show differential accumulation and release of N and P and may influence the overall potential of a wetland to retain agricultural nutrients.

Key Words: nitrogen, phosphorus, wetland perennials, retention, eutrophication, non-point source pollution, water quality, reed canary grass, *Phalaris arundinacea*, *Juncus effusus*, *Sparganium americanum*, *Scirpus cyperinus*, *Calamagrostis canadensis*

INTRODUCTION

Wetland plants play an important role in reducing the eutrophication of waterways, as plants take up and accumulate nutrients for growth, maintenance, and reproduction during the growing season. For example, wetland plants have been reported to remove 16 to 75% of nitrogen (N) inputs (Reddy and DeBusk 1987, Peterson and Teal 1996). A net release of nutrients often occurs in the fall and early spring as a result of decomposition and nutrient leaching of plant litter (Mitsch et al. 1989). Since most problems associated with eutrophication occur during the growing season, the contribution of plants to seasonal N and phosphorus (P) retention can be significant.

The importance of species differences in nutrient retention is often overlooked in input-output studies of wetlands as nutrient sinks. Plant species can have distinctly different effects on ecosystem nutrient cycling due to differential uptake and losses (Hobbie 1992, Knops et al. 2002). For example, five grass species showed significant differences in their abilities to reduce the soil solution concentration of ammonium and nitrate (Tilman and Wedin 1991). McJannet et al. (1995) reported strong interspecific variation in tissue N and P concentrations among 41 wetland plant species, with mean tissue N concentrations ranging from 0.25 to 2.1% and mean P concentrations from 0.13 to 1.1%. A separate study showed that plant species richness had an effect on P dynamics in experimental wetland mesocosms, with greater species richness resulting in lower P losses (Engelhardt and Ritchie 2001).

Another important aspect of N and P retention studies is the loss of nutrients from decaying plant litter. Depending on the rate of decomposition of senesced plant parts, the plant litter can retain a significant portion of its nutrients and release them over several years (Kadlec 1989, Davis 1991). Davis and van der Valk (1978) found interspecific variations in mass and nutrient retention within their litterbag studies of emergent macrophyte decomposition. They attributed some of the variations to species differences in tissue structure and initial tissue nutrient concentrations. Morris and Lajitha (1986) also observed differences in the decomposition of four macrophyte species and their release of N and P. They found that, although *Zizania aquatica* litter had the highest initial concentrations of N and P, by the end of 30 months, it had the lowest values of remaining N and P.

The composition of plant species in wetlands is often dominated by one or a few species such as cattail, reed canary grass, common reed, and purple loosestrife (Galatowitsch et al. 1999). These species can form large, monospecific stands that can cover several hectares of land. With the exception of reed canary grass, much attention has been given to examining the effects of these species on nutrient dynamics in wetland systems (Emery and Perry 1996, Templer et al 1998, Meyerson et al. 1999, Findlay et al 2002). Because of their abilities to accumulate N and P, many of these exotic invasive species are deliberately planted for use in wastewater and stormwater treatment (Wolverton et al. 1983, Ansola et al. 1995, Bernard and Lauve 1995). However, the aggressive growth habit and nutrient requirements of these species may have significant impacts on the cycling of N and P. Additionally, the phenology of nutrient accumulation and release in monospecific stands of the invasive species may influence the eutrophication of aquatic systems.

This paper focuses on the differential N and P retention for five herbaceous wetland perennials (one exotic invasive species and four native species) grown within a riparian wetland that receives large inputs of agricultural runoff. Our objective was to characterize species differences in N and P tissue accumulation for one growing season, and in N and P losses over a five-month decomposition period. In our study, seasonal retention refers to the accumulation of N and P in plant tissues, and longer-term retention is described as the amount of N and P remaining in decomposing litter. We estimated the total N and P retention for each species in an effort to understand the differential roles species perform in reducing non-point-source pollution.

MATERIALS AND METHODS

Study Site

Our research was conducted on a riparian wetland that borders a dairy farm on the east branch of Nanticoke Creek in southern New York, USA (42° 18′ N, 76° 00′ W). The wetland receives large inputs of N and P from activities associated with animal and crop production. Water-column concentrations of nitrogen ranged from 0.03 to 3.3 mg/L NH_4^+-N and from 0.01 to 0.72 mg/L NO_3^--N. The wetland was recently placed under the New York State Conservation Reserve Program in an effort to control non-point-source pollution from agricultural projects.

Study Species

We selected five morphologically contrasting species of wetland perennials common in the northeastern U.S: *Juncus effusus* L. (soft rush), *Phalaris arundinacea* L. (reed canary grass), *Calamagrostis canadensis* (Michx.) Beauv. (blue joint grass), *Sparganium americanum* Nutt. (bur reed), and *Scirpus cyperinus* (L.) Kunth (woolgrass) (nomenclature according to Crow and Hellquist 2000). The growth habit of *J. effusus* (a reed) consists of erect, smooth cylindrical stems that grow in dense clumps. *Scirpus cyperinus* also has a growth habit that consists of stems located in dense clumps, but it is characterized as a tussock species along with *C. canadensis* (Boutin and Keddy 1993). *Sparganium americanum* and *P. arundinacea* stems grow in a sod-like pattern, with the latter belonging to the clonal dominant grouping. *Phalaris arundinacea* occurs naturally throughout the study site.

Experimental Methods and Design

The plants used in our study were obtained from Southern Tier Consulting, Inc., located nearby in West Clarkesville, New York. To control for heterogeneity among replicates, plant propagules of each species were separated into four size categories distinguished visually, and equal numbers per size class were placed into each plot. A set of these plants was also set aside to estimate initial dry mass, tissue N, and tissue P. The plants were grown in monoculture within blocks consisting of five 900-cm^2 plots, so that each block contained all five species. The blocks were fenced off with chicken wire to prevent herbivory by geese and other animals. Existing vegetation (root and shoots) was removed while soil was being returned to the plots. The positions of the species were randomized within each block. Eleven replicate blocks were placed adjacent to the stream within the existing wetland in late April 2001. The plants were harvested during peak standing crop (early August 2001) using flat blade spades and shovels to collect all plant material within the 900-cm^2 plots. The depth of collection varied for each species, depending on the length of the rooting zone.

The aboveground and belowground biomass were separated in the laboratory and washed on a 1-mm sieve. The belowground biomass for *C. canadensis* was not included in this study due to the difficulty of separating the roots from the soil substrate. The plants were subsequently dried at 80° C to constant weight and weighed, except that a portion of the aboveground biomass was air-dried for use in the decomposition study. The biomass gained during the study (biomass accumulation) was determined by subtracting the initial biomass (initial dry mass of the propagules) from the final biomass (dry mass of the harvested biomass).

Estimates of biomass, tissue N, and tissue P lost from the decomposition of plant shoots were determined through a litterbag experiment. In late September 2001, a total of 75 litterbags consisting of 15 replicates of each species were placed in a cattail marsh within the SUNY-Binghamton Nature Preserve (42° 05′ N, 76° 57′ W). This location was used in order to compare biomass and nutrient loss rates during decomposition in a uniform setting. The location was also chosen for security of the litterbags (vandalism at the CRP site became a concern as the season progressed). The litterbags were made of fiberglass mesh fabric with dimensions 30cm × 15cm, with each bag containing 5 g of air-dried shoot material. The litterbags were positioned vertically within the marsh, held by string and wooden stakes, to simulate the standing litter habit of these emergent wetland plants. Initial dry weight of litterbag material was estimated by oven-drying parallel samples at 80°C to determine an oven-dry: air-dry biomass ratio. Five replicates of each species were collected on three separate dates: at 60, 120, and 150 days. The shoots were washed on a 1-mm sieve and dried at 80° C to constant weight.

The percentage of biomass remaining after decomposition was calculated as the ratio of the final dry mass to the initial dry mass × 100. The percentage of N and P in the remaining litter was calculated as the ratio of the final N and P content (final tissue N and P concentration × final mass) to the initial N and P content (initial tissue N and P concentration × initial mass) × 100.

Tissue Analyses

Plant tissue samples were ground to powder using a stainless steel Wiley mill with a #40 mesh screen (0.43-mm). Subsamples were digested within a Technicon BD-40 block digester using the sulphuric acid-hydrogen peroxide method, with powdered selenium and lithium sulfate added to boost digestion efficiency (Allen 1989). Total Kjeldahl nitrogen and phosphorus concentrations in plant tissue digests were analyzed using a Lachat QuikChem flow-injection autoanalyzer 8000 Series (TKN Method: 10-107-04-3-P and TKP Method: 13-115-01-1-B).

Statistical Analyses

Data were log-transformed as necessary for cases of highly non-normal (according to the Shapiro-Wilks statistic) or heteroscedastic data. One-way analysis of variance (ANOVA) of a randomized complete block design was used with the General Linear Models Procedure (SAS 1999–2000) to evaluate the effects of species on the following dependent variables: biomass accumulation, tissue nutrient concentrations, N and P accumulation, and percent mass and percent of total nutrients remaining after decomposition. Tukey's post hoc means comparisons test was performed on data with significant probability values of $p < 0.05$.

RESULTS

Biomass Accumulation

There were no significant differences in total biomass accumulation among the four species for which both aboveground and belowground data were available (Figure 1, Table 1), but differences in the aboveground: belowground biomass ratio, which ranged from 0.6 for *Scirpus cyperinus* to 2.2 for *Sparganium americanum*, resulted in several interspecific contrasts. Both *P. arundinacea* and *S. americanum* accumulated significantly more aboveground biomass than *S. cyperinus* (Figure 1, Table 1). Aboveground biomass accumulations for *P. arundinacea* and *S. americanum* were 704 and 625 $g \cdot m^{-2}$, respectively, whereas that for *S. cyperinus* was only 293 $g \cdot m^{-2}$. Mean biomass values for *J. effusus* and *C. canadensis* were intermediate and did not differ significantly from the other three species.

For belowground biomass, *S. americanum* gained significantly less biomass than *P. arundinacea* and *J. effusus* (Figure 1, Table 1). *Sparganium americanum* allocated proportionally more resources to the growth of shoots, resulting in the lowest belowground biomass value of 284 $g \cdot m^{-2}$. *Phalaris arundinacea*, *S. cyperinus*, and *J. effusus* accumulated large biomass values ranging from 528 to 630 $g \cdot m^{-2}$.

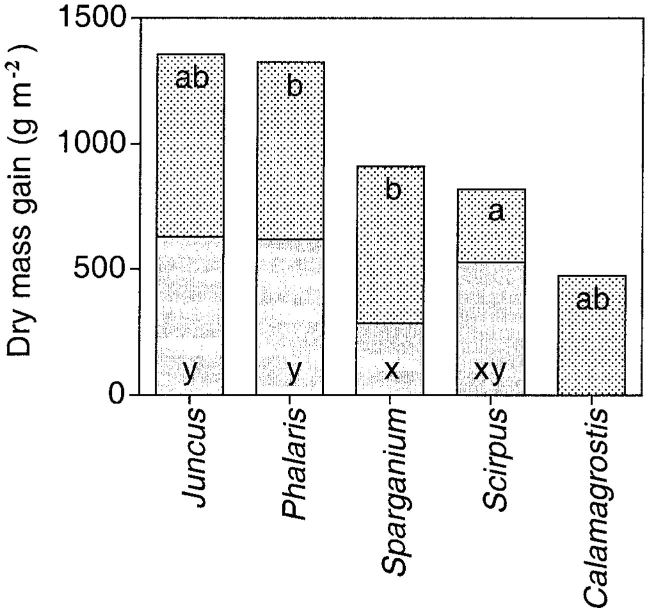

Figure 1. Dry mass accumulated aboveground (light stippling) and belowground (dark) for the five perennial species as of early August. Means shown for 11 replicates. Means not sharing the same lowercase letter (a,b for aboveground and x,y for belowground) differ significantly ($p<0.05$) according to Tukey's post hoc means comparisons test. Belowground biomass is not included for *Calamagrostis*.

Tissue N and P Concentrations

Sparganium americanum had the highest aboveground tissue concentration of N (21 mg $N \cdot g^{-1}$ tissue) and P (3.8 mg $P \cdot g^{-1}$ tissue), significantly higher than the tissue N and P concentrations for the other four species, which ranged from 14 to 15 mg $N \cdot g^{-1}$ and from 1.8 to 2.3 mg $P \cdot g^{-1}$ (Figure 2, Table 1).

For belowground tissues, tissue N levels differed significantly according to one-way ANOVA (Table 1), although no two means differed according to Tukey's means comparisons test (Figure 2a). The tissue P concentration in *S. cyperinus* was 65% greater (4.3 mg $P \cdot g^{-1}$) than in *J. effusus* (2.6 mg $P \cdot g^{-1}$, $P < 0.05$; Figure 2b, Table 1), while *P. arundinacea* and *S. americanum* had intermediate values.

N and P Accumulation

Sparganium americanum accumulated significantly more aboveground N and P than both *S. cyperinus* and *C. canadensis* (Figure 3, Table 1). Nitrogen accumulation in *Sparganium* shoots (13 g $N \cdot m^{-2}$) was 2.6-fold greater than in *S. cyperinus* and 1.9-fold greater than in *C. canadensis*, while P accumulation (2.5 g $P \cdot m^{-2}$) was 3.2-fold and 2.6-fold greater, respectively. Nitrogen accumulations for *J. effusus* and *P. arundinacea* were 10.7g $N \cdot m^{-2}$ and 11.8 g $N \cdot m^{-2}$, while P values were 1.9 g $P \cdot m^{-2}$ and 1.3 g $P \cdot m^{-2}$, respectively.

The belowground N accumulated by *S. americanum* was significantly lower than that of *J. effusus* (Figure 3a, Table 1). *Juncus effusus* yielded over a 2.5-fold greater accumulation of N (6.3 g $N \cdot m^{-2}$) when compared to *S. americanum*. *Sparganium americanum* also accumulated less P belowground than *S. cyperinus*, with respective values of 0.89 g $P \cdot m^{-2}$ and 2.4 g $P \cdot m^{-2}$.

Decomposition: Percent Mass Remaining

After 60 days of decomposition, there were no significant differences in the percentage of litter remaining, but differences among species appeared after 150 days (Figure 4, Table 1). Of the five species, *S. cy-*

Table 1. Summary of F values for one-way ANOVA to test the effects of species differences on biomass accumulation, tissue N and P concentrations, N and P accumulation, percent biomass remaining, and percent N and P retained. Decomposition data were based on sampling at day 150.

Parameters	F	df	p <
Total Biomass Accumulation	0.87	3,28	0.50 ns
Aboveground Biomass Accumulation	4.28	4,37	0.01
Belowground Biomass Accumulation	4.72	3,28	0.01
Aboveground Tissue N Concentration	15.17	4,37	0.0001
Belowground Tissue N Concentration	3.35	3,28	0.04
Aboveground Tissue P Concentration	18.07	4,37	0.0001
Belowground Tissue P Concentration	4.17	3,28	0.02
Aboveground N Accumulation	5.97	4,37	0.001
Belowground N Accumulation	2.99	3,28	0.05
Aboveground P Accumulation	4.78	4,37	0.01
Belowground P Accumulation	4.75	3,28	0.01
Decomposition: % Mass Remaining	26.5	4,20	0.0001
Decomposition: % N Remaining	55.3	4,20	0.0001
Decomposition: % P Remaining	3.32	4,20	0.05

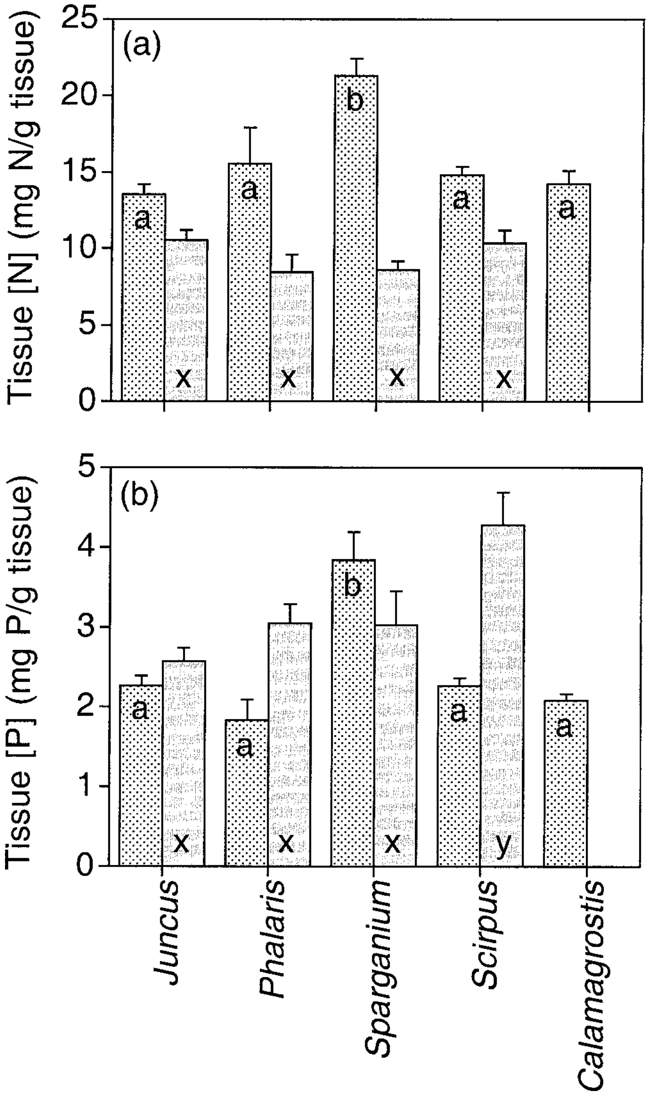

Figure 2. Tissue nutrient concentrations for aboveground (light stippling) and belowground biomass (dark): a) Tissue N concentrations and b) Tissue P concentrations. Means shown with standard errors for 11 replicates. Means not sharing the same lowercase letter (a,b for aboveground and x,y for belowground) differ significantly ($p<0.05$) according to Tukey's post hoc means comparisons test, based on log-transformed data.

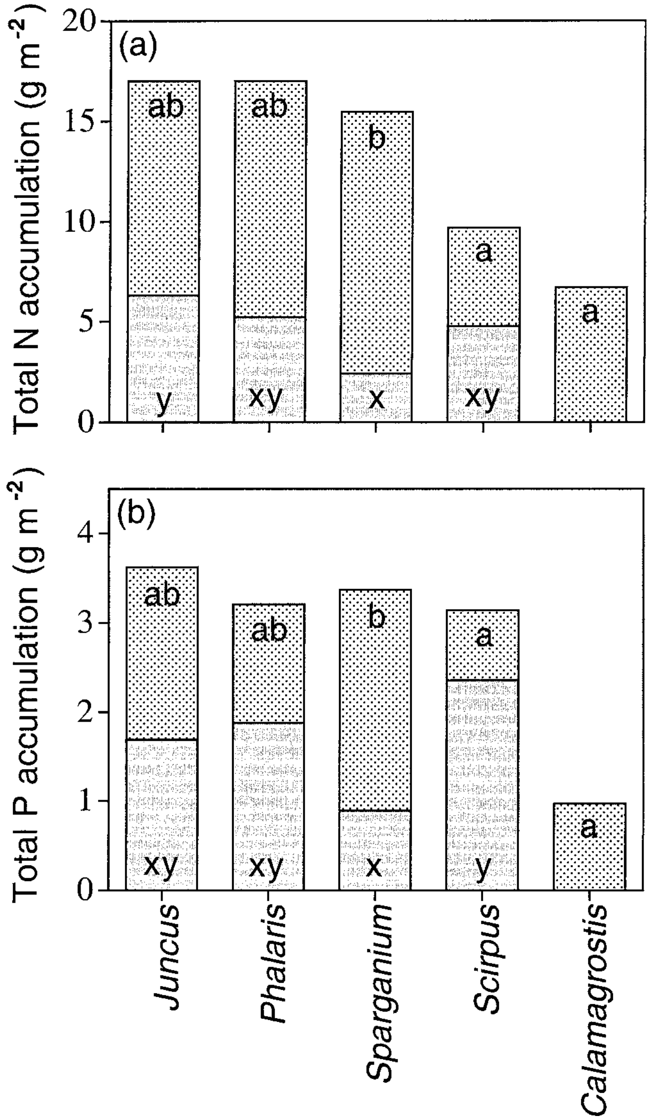

Figure 3. Total accumulation of (a) N and (b) P for aboveground (light stippling) and belowground (dark) biomass. Means shown for 11 replicates. Means not sharing the same lowercase letter (a,b for aboveground and x,y for belowground) differ significantly ($p<0.05$) according to Tukey's post hoc means comparisons test.

perinus retained the highest percentage of biomass after a 150-day decay period. The percentage of mass remaining for *S. cyperinus* was 78%, and for all other species, the mass ranged between 65–68%.

Decomposition: Percentage of N and P Retained

For both N and P, temporal patterns of retention in litterbags varied widely among species over the first 120 days (Figure 5). We focus on the data for 150 days, because it is most relevant to longer-term retention. Strong differences existed among species for the percentage of N retained in aboveground litter after five months of decay (Figure 5a, Table 1). *Phalaris arundinacea* retained the lowest percentage (28%) of N of all five species, and *S. cyperinus* retained the highest percentage of N. The percentages of N retained by both species were significantly different from all other species. The high values of N retained in the decaying shoots of *S. cyperinus* (>100%) suggest that the litter was colonized by microbes that took up additional N from the surrounding environment. For all other species, the percent N retained ranged from 70 to 87%.

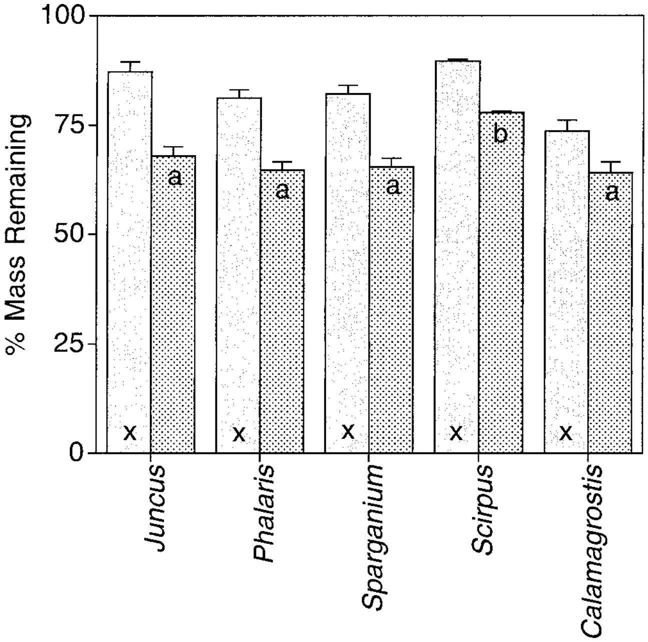

Figure 4. Percentages of shoot biomass remaining after 60 (dark) and 150 (light stippling) days of decomposition. Means shown with standard errors for five replicates. Means not sharing the same lowercase letter (a,b for 150 days and x for 60 days) differ significantly ($p<0.05$) according to Tukey's post hoc means comparisons test. No significant differences existed at 60 days.

For the percentage of P retained after five months of decay, both *S. cyperinus* and *J. effusus* had a significantly higher percentage remaining than did *P. arundinacea* (Figure 5b, Table 1). *Phalaris arundinacea* retained only 18% of P, whereas *S. cyperinus* and *J. effusus* retained 60 and 70% of P, respectively. The P retained in *C. canadensis* litter was 51%, and for *S. americanum* was 36%.

Net N and P Retention

Table 2 presents the five species in rank order of their net shoot retention of N and P, estimated as net accumulation during the growing season (Figure 3) less losses during 150 days of decomposition (Figure 5). There was approximately a three-fold range in N retention, from 3.3 g N m^{-2} for *P. arundinacea* to 9.7 g N m^{-2} for *Sparganium americanum*. Phosphorus retention varied even more, in relative terms, from 0.2 g P m^{-2} for *P. arundinacea* to 1.3 g P m^{-2} for *J. effusus*.

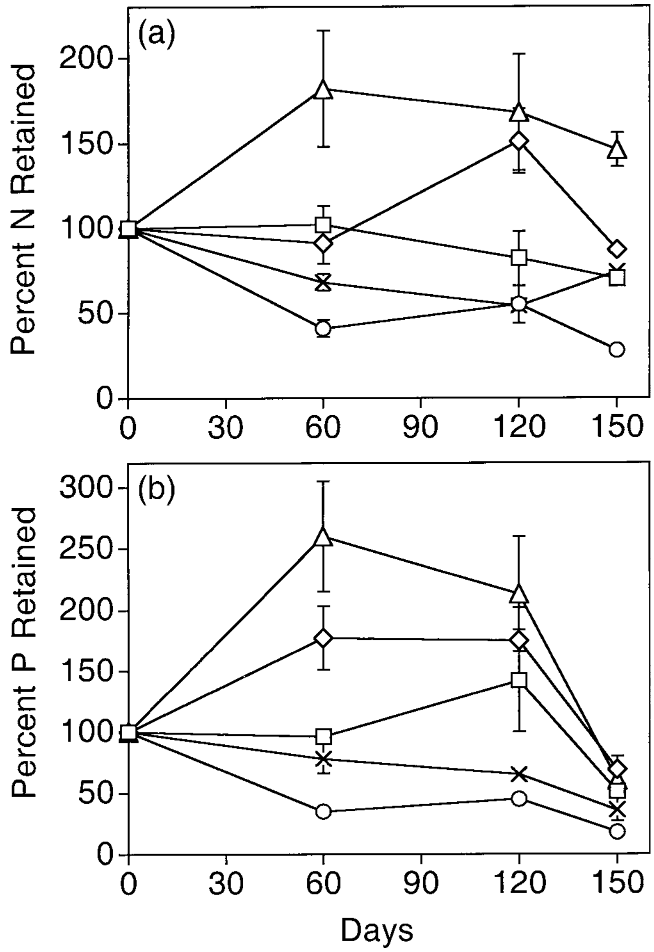

Figure 5. Percentages of a) nitrogen and b) phosphorus retained in shoot litter after 60, 120, and 150 days of decomposition. Means for *Scirpus* (triangle), *Juncus* (diamond), *Calamagrostis* (square), *Sparganium* (X) and *Phalaris* (circle) are shown with standard errors for 5 replicates. There were no significant results for 60 and 120 days.

DISCUSSION

Wide variations in nutrient accumulation and release existed among the five species used in this study. Although *S. americanum* had the greatest aboveground accumulation of N and P (Figure 3), enough P was lost during decomposition (Figure 5b) to drop it below *J. effusus* for net retention (Table 2). Its ability to retain N in litter, however, was high (74%) after 150 days of decomposition (Figure 5a, Table 2). *Phalaris arundinacea* also had exhibited a strong capacity for N and P accumulation but a low capacity for retention of the nutrients in aboveground litter. Less than half of the tissue N and P remained in the decomposing litter after only 60 days (Figure 5), indicating that N and P may be released soon after seasonal growth ends for *P. arundinacea*—consistent with its lowest rankings for net retention (Table 2). In contrast, both high accumulation and retention was found in *J. effusus*, with over three-fourths of the litter N and over two-thirds of litter P remaining after 150 days of decomposition. *Scirpus cyperinus* had the lowest aboveground values for N and P accumulation but showed

Table 2. Net shoot retention of N and P estimated for the five species in rank order.

Rank	Species	N Retention (g N m^{-2})	Species	P Retention (g P m^{-2})
1	*S. americanum*	9.7	*J. effusus*	1.3
2	*J. effusus*	9.3	*S. americanum*	0.9
3	*S. cyperinus*	7.1	*C. canadensis*	0.49
4	*C. canadensis*	4.7	*S. cyperinus*	0.46
5	*P. arundinacea*	3.3	*P. arundinacea*	0.2

high retention of P in litter. Similarly, *C. canadensis* showed low values for aboveground N and P accumulation, but its ability to retain N and P after 150 days of decomposition was high (70% N and 51% P). *Calamagrostis canadensis* and *S. cyperinus* thus shared the third and fourth rankings for net retention (Table 2).

In the short run, greater net retention such as seen for *S. americanum* and *J. effusus* seems to be beneficial for reducing nutrient inputs from agricultural runoff into streams. There may be advantages, however, to the pattern displayed by *P. arundinacea*: relatively high rates of accumulation during the growing season followed by relatively high loss rates later when the impact of nutrient losses may be less. Bernard and Lauve (1995) reported three times the amount of N in shoots of *P. arundinacea* than what was found in our study. In any case, our study species varied widely in N and P accumulation during the growing season (Figure 3), in N and P loss rates from shoots during decomposition (Figure 5), and in net shoot retention of N and P (Table 2). The percentages of tissue N in aboveground biomass for *J. effusus*, *S. cyperinus*, and *P. arundinacea* were comparable to reported values, while the reported percentages of tissue P were slightly higher than the values observed in our study (McJannet et al. 1995, Behrends et al. 1999).

Our study species also showed differences in the aboveground versus belowground accumulation of N and P. Although *S. americanum* had among the highest aboveground N and P accumulation values, it had the lowest belowground N and P values in our study (Figure 3). In contrast, aboveground N and P accumulation values were low for *S. cyperinus*, while its belowground total P value was the highest of all the species. In studies of freshwater marshes, the aboveground N stock ranged from 3 to 29 g·m^{-2} (Mitsch and Gosselink 2000). Studies of Wisconsin perennials showed belowground P stock values of 4 g·m^{-2} in *Typha* and 2.0 g·m^{-2} for *Scirpus fluviatilis* (Klopatek et al. 1978, Prentki et al. 1978). In our study, however, belowground P stock values ranged from as low as 0.9 g·m^{-2} (*S. americanum*) to as high as 2.4 g·m^{-2} (*S. cyperinus*).

The division of aboveground versus belowground biomass is of particular interest because it can describe how N and P are partitioned seasonally. In temperate climates, the aboveground biomass of most wetland perennials senesces and decomposes, releasing nutrients to the surrounding environment. Therefore, the belowground biomass of perennials is seen as a more important component to the long-term (beyond one growing season) retention of nutrients (Mitsch and Gosselink 2000, Cronk and Fennessy 2001). For some species, the belowground biomass accounts for most of the N and P found in plants (Hoagland et al. 2001). The lifespan of some wetland perennials can be several years, which can prolong the retention of nutrients within a wetland. Lifespans of 6–8 years were found for *Carex aquatilis* Wahlenb. and 5 years for *Nymphaea tetragona* Georgi. (Shaver and Billings 1975, Kunii 1993). Belowground structures consisting of rhizomes and shoot bases serve as important winter storage organs of nutrients but may undergo senescence during early summer after a significant portion of the nutrients are translocated to growing shoots (Prentki et al. 1978). Therefore, the type of belowground storage organ and lifespan of the perennial species can provide some indication of its potential for long-term N and P retention (Chapin 1990).

Although N and P retention in the aboveground biomass of herbaceous perennials is considered short-term (seasonal), the pattern of N and P release from litter can vary dramatically for different species. Litter from different plants can decompose at varying rates and thus may also release N and P at different rates (Atkinson and Cairns 2001). Although *S. americanum* accumulated the largest aboveground stock of P, much of the total P was lost during decomposition (Figure 5b). Likewise, the release of N and P was large for *P. arundinacea* litter. *Juncus effusus* had high N and P retention in our study after 150 days, as observed in another study that found that total N and P in decaying litter remained stable (Kuehn and Suberkropp 1998). The varying losses of N and P from the litter of the different species in our study suggest that the aboveground tissue structure or composition may play an important role in determining the degree of nutrient release or retention. The decomposition rate of *S. cy-*

perinus was lowest of all the species, indicating that its shoot structure or chemical composition may have slowed the decay process. After five months of decomposition, *S. cyperinus* litter appeared to gain N, while the other species showed decreases (Figure 5). Nitrogen may be bound in a form that is not readily leached from plant tissues, or it can be immobilized in microbial biomass (Kuehn and Suberkropp 1998). In the initial stages of decomposition, the nutrient content of litter may appear to increase due to the ability of microorganisms to take up nutrients from the surrounding environment (Schlesinger 1997). Thus, differences in the litter quality (e.g., C:N, C:P, tissue structure) and decay stage of plants are important in determining the mobilization of N and P in litter.

CONCLUSION

The nature of nutrient accumulation and decomposition of the species seem to be important determinants of their differences in performance as nutrient retainers. The net effect of vegetation on N and P retention is dependent on these processes (Prentki et al. 1978, Behrends et al. 1999, Reddy et al. 1999). Some species can accumulate high concentrations of nutrients and large biomass within one growing season but may lose much of the nutrients during the following fall or spring as tissues senesce and decay. In our study, *Phalaris arundinacea* had considerable N and P accumulation during the growing season, but this was followed by relatively rapid loss after the season ends. In contrast, *Juncus effusus* showed both high accumulation in the growing season and effective retention of N and P into the following spring. Such differences in the functional behavior of plants can influence the overall uptake and retention of nutrients within a wetland. Additionally, the effects of species on seasonal patterns of nutrient uptake and release can contribute to whether a wetland functions as a nutrient sink (for inorganic N or P) or source (for organic N and P) at different times of the year. The role of species should be taken into account in mass balance studies of wetlands as nutrient sinks and sources.

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