THE ROLE OF LITTER IN NUTRIENT CYCLING IN A
BRACKISH TIDAL MARSH[1]

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Abstract. The role of litter in nutrient cycling in a *Typha angustifolia* dominated brackish tidal marsh was studied with a field experiment. In replicated plots, litter was either removed, replaced with plastic strips (pseudolitter), increased threefold, or left unaltered. One set of plots received fortnightly surface applications of ammonium phosphate solution at an annual rate of 65 g/m² of N and 72 g/m² of P. The nutrient additions increased the concentrations of dissolved and extractable ammonium and phosphate, but decreased the concentration of dissolved nitrate plus nitrite in the sediment. The effects of the litter manipulations were mostly attributable to the physical structure of the litter layer rather than the decomposition process. Plots with no litter or pseudolitter developed higher concentrations of total NH_4 in the sediment than other plots. Also, when litter and pseudolitter were absent, the nutrient additions caused greater increases in PO_4 in the sediment.

We measured decomposition and changes in nutrient content of *Typha* litter in mesh bags placed in the plots containing litter. In plots with increased litter, litter placed on the top of the litter layer decomposed faster than litter placed on the sediment surface. The experimentally manipulated litter took up nutrients during the experiment. The litter in plots with extra litter took up more N and P than was in total NH_4 and dissolved PO_4 in the sediment. However, litter decomposition did not affect inorganic N and P pools in the sediment, possibly because large pools of organic N and P in the sediment buffer the supply of inorganic nutrients against short-term changes in litter.

Key words: brackish tidal marsh; decomposition; interstitial nutrients; litter; nutrient cycling; Typha angustifolia; *wetland.*

INTRODUCTION

Decomposition of plant litter is an important component of nutrient cycling in wetlands. Vascular plant litter alternately takes up and releases nutrients as it decomposes (e.g., Melillo et al. 1984). Initially, it releases soluble nutrients by leaching. Then, if the litter is relatively rich in carbon and poor in nutrients, it takes up or "immobilizes" exogenous nutrients. As decomposition proceeds further, mineralization predominates over immobilization and the litter gradually releases nutrients. By immobilizing nutrients, litter may be a significant sink for nutrients in wetlands (Davis and van der Valk 1978, Rice and Tenore 1981, Webster and Benfield 1986) and could compete for nutrients with plants (Correll et al. 1975, Barko and Smart 1983). On the other hand, if litter takes up nutrients from surface waters, becomes buried, and then releases nutrients into the sediment, it could enrich the sediment with nutrients (Bowden 1986). Nutrients released by decomposing litter may also be taken up by roots which invade the litter layer (Morris and Lajtha 1986). Thus, litter decomposition may provide a mechanism of nutrient uptake and retention in wetlands.

Besides affecting nutrient availability, decomposition processes may respond to nutrient availability. Increasing exogenous nutrient supply can increase de-

composition rates and/or increase immobilization of nutrients by litter (Hynes and Kaushik 1969, Kaushik and Hynes 1971, Howarth and Fisher 1976, Almazan and Boyd 1978, Jensen et al. 1978, Haines and Hanson 1979, Elwood et al. 1981, Melillo et al. 1984, Neely and Davis 1985, Valiela et al. 1985). Also, increasing nutrient availability to plants can result in litter with higher nutrient content, which decomposes faster and immobilizes less nutrients (Marinucci et al. 1983, Neely and Davis 1985, Valiela et al. 1985, Webster and Benfield 1986).

We conducted a field experiment to determine whether litter enriches or depletes inorganic nutrients in the sediment of a brackish tidal marsh dominated by the narrow leaved cattail, *Typha angustifolia*. In replicated plots, litter was either removed, replaced with plastic strips (pseudolitter), increased threefold, or left unaltered. One set of plots also received additions of nutrients. To assess nutrient exchanges by the decomposing litter, we measured decomposition and changes in nutrient content of *Typha* litter in mesh bags placed in the plots containing litter. We reasoned that, if litter was a source of nutrients, then the sediment in plots with more litter would develop higher nutrient concentrations. If, on the other hand, litter was a sink for nutrients, then the sediment in plots with more litter would become depleted in nutrients and, furthermore, experimentally added nutrients would be taken up in the litter layer. If litter trapped nutrients

from surface waters and released nutrients below ground, then the presence of litter would enhance the delivery of experimentally added nutrients to the sediment. Finally, if the physical structure of the litter rather than the decomposition process affected the nutrient content of the sediment, then plots with pseudolitter should resemble those with litter.

METHODS

Study site

The marsh we studied is on the Rhode River, a subestuary on the western shore of the Chesapeake Bay (38°51' N, 76°32' W). The marsh surface is 30 cm above mean low water, is flooded by 46% of high tides, and is submerged ≈7 h/d on the average (Jordan et al. 1986). Mean tidal amplitude is 30 cm. Salinity ranges from 0 g/kg in spring to as high as 18 g/kg in fall. *Typha angustifolia* is the dominant plant in the marsh, but *Scirpus olneyii* and *Spartina cynosuroides* are also common.

Experimental design

Using a factorial design, we altered the abundance of litter and nutrients in 16 2 × 2 m plots, with two plots representing each combination of litter and nutrient treatment. The four litter treatments were renewed each October after the *Typha* had senesced. In the 1st yr, we cut the standing dead shoots near the sediment surface and removed them along with the surface litter from each plot where litter was to be removed. Later, we learned that dead *Typha* shoots are important in providing oxygen to rhizomes during winter (Jordan and Whigham 1988). Therefore, in subsequent years we cut the dead shoots ≈20 cm above the sediment surface where they would rarely be submerged and, for consistency, we cut the shoots in all the plots, regardless of litter treatment.

Plots receiving artificial litter were covered by a loose 3 cm deep layer of pseudolitter (polyethylene strips, 50 × 1 × 0.1 cm) after the natural litter was removed. The pseudolitter was held in place by a covering of galvanized wire mesh (chicken wire). Litter removed from pseudolitter or no litter treatments was added to plots receiving extra litter. All of the plots were enclosed with 50 cm high chicken-wire fences and surrounded by 15 cm wide wooden catwalks.

Two plots from each category of litter treatment were sprinkled with a nutrient solution at low tide once every other week from April through October (12–13 times per year). The solution consisted of 23.6 g/L diammonium phosphate [$(NH_4)_2HPO_4$] dissolved in tidal water. For each application, 1 L of nutrient solution per square metre was sprinkled on the plots. A total of 65 g N and 72 g P were added per square metre per year.

The treatments were systematically dispersed among the plots to avoid accidental clustering which may arise with random assignment of treatments (Hurlburt 1984). Systematic dispersion of treatments results in more conservative tests of statistical significance than randomization (Hurlburt 1984). Treatment effects were tested by analysis of variance (ANOVA). To enhance detection of nutrient effects in the presence of spatial variation, plots with similar litter treatments were arranged in close pairs with one of each pair receiving added nutrients. For the ANOVA such pairs were considered to occupy the same "site" and site was treated as a random factor nested in the litter treatment factor. In cases where replicate measurements were made within each plot or when plots were sampled repeatedly through time, plot was treated as a random factor nested within site, litter treatment, and nutrient treatment. When main effects were significant ($P < .05$) but interactions were not, a posteriori multiple comparisons of means were made by the Tukey honestly significant difference (hsd) method ($P < .05$, Sokal and Rohlf 1981). When interactions were significant, comparisons among levels of a factor were made by adjusted hsd ($P < .05$, Cicchetti 1972). Prior to analysis, data expressed as percents were arcsine square-root transformed, and data on soil nutrients were log transformed (Sokal and Rohlf 1981).

Soil nutrients

Sediments were sampled at least 1 wk after the most recent nutrient application in January, May, July, and October in the 1st yr, and in October of the 2nd yr. Core samples were taken with 6 cm diameter plastic tubes with sharpened, serrated edges. The holes created by sampling were refilled with cores taken from elsewhere in the marsh and marked with a wooden stake. Samples were taken at least 20 cm from the edges of the plots and 20 cm from previously sampled locations. The samples were returned to the laboratory, placed in a glove bag filled with nitrogen gas, extruded from the tubes, and sectioned. One portion of each section was loaded into a centrifuge tube and another was reserved for analysis of total and extractable nutrients. In the 1st yr, cores were sectioned at 0–5, 5–10, and 15–20 cm, and two cores were taken per plot. In the 2nd yr, the number of replicate cores was increased to six per plot, but only the 0–5 cm depth was sampled. Total C, N, and P were only analyzed in samples taken in October from plots with unaltered litter.

To separate interstitial water from most of the solids, samples were centrifuged for 10 min at ≈98 000 m/s² at 10°C. Immediately after centrifugation, the interstitial water was filtered through 0.45-μm pore size Millipore filters. The filtrate was preserved by adding 1 μL of 18 mol/L sulfuric acid per millilitre of sample and kept refrigerated until analyzed for phosphate, ammonium, nitrate, and nitrite.

Five cm³ subsamples of core sections were suspended in 50 mL of 2 mol/L KCl solution to extract ammonium (Keeney and Nelson 1982), and in 100 mL
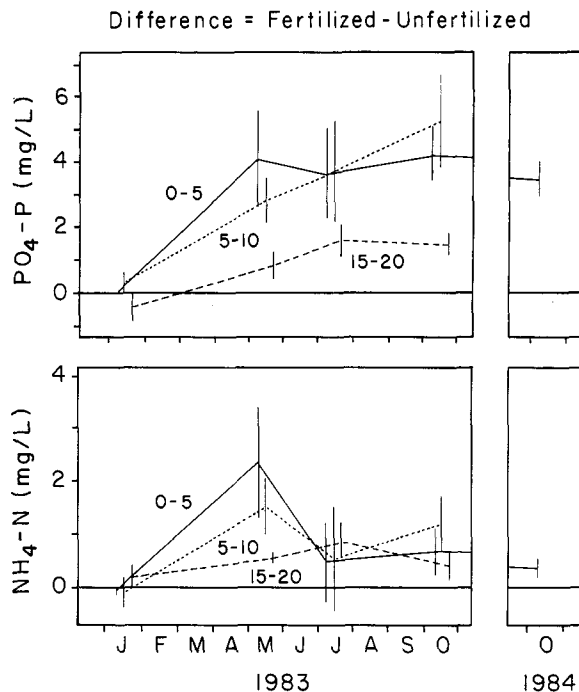
Difference = Fertilized - Unfertilized

FIG. 1. Difference between the concentrations in fertilized and unfertilized plots for dissolved interstitial ammonium and phosphate at 0–5, 5–10, and 15–20 cm depths. All litter treatments are combined. Vertical bars are ±SE. Fertilizing began in March of 1983.

of 0.25 mol/L sulfuric acid to extract phosphate. The suspensions were stirred every 10 min for 30 min. The extractants were then filtered through 0.45-μm pore size Millipore filters and refrigerated until analysis. The phosphate extraction is similar to that of Chang and Jackson (1957) which uses 0.125 mol/L sulfuric acid and extracts about half of the iron- and aluminum-bound phosphates.

Total C and N were analyzed with a Perkin Elmer CHN analyzer in the laboratory of Gordon Thayer (National Marine Fisheries Service, Beaufort, North Carolina). Total P was analyzed by perchloric acid digestion followed by reaction with ammonium molybdate and aminonaptholsulfonic acid, and extraction of color with isobutyl alcohol (Correll and Miklas 1975). Orthophosphate was analyzed by reaction with stannous chloride and ammonium molybdate (APHA 1976). Nitrate was reduced to nitrite with cadmium amalgam (APHA 1976) and ammonium was oxidized to nitrite by alkaline hypochlorite (Strickland and Parsons 1972). Nitrite was analyzed by reaction with sulfanilamide (APHA 1976). Ammonium and phosphate concentrations were high enough that the interstitial water and extract samples had to be diluted prior to analysis. This alleviated the problem of substances interfering with the analysis, but, as an additional precaution, we added an internal standard to each sample to check recovery. Each analysis was corrected if re-

covery was <100%. Analysis of dissolved ammonium and extractable ammonium and phosphate averaged ≈90% recovery of internal standards. Recovery of dissolved nitrate varied between 50 and 100%.

Litter decomposition

We studied decomposition of litter placed in mesh bags in the plots. Decomposition of the bases of leaves, which overlap to form the rigid portion of each shoot, was studied separately from decomposition of the upper blades of the leaves, which diverge. Leaf blades and bases were collected from outside the plots just after senescence and air dried for a few days. Then ≈15 g of blades and ≈20 g of bases were weighed and placed in each 1-cm mesh nylon bag. Initial C, N, and P content of the litter was determined in several weighed samples of air-dried material that were further dried at 60°, reweighed, and ground in a Wiley mill. In November of the 2nd yr of the study, litter bags were placed on the sediment surface in plots with unaltered and extra litter, and on top of the litter layer in plots with extra litter. Bags were recovered at various times. The litter inside was rinsed in tap water to remove adhering sediment. Roots and large invertebrates were removed by hand. The litter was then dried at 60°, weighed, ground, and analyzed for C, N, and P.

RESULTS

Soil nutrients

Regardless of litter treatment, fertilized plots had higher concentrations of dissolved interstitial phosphate and ammonium than unfertilized plots. The difference in ammonium concentrations was greatest in May, the first sampling after fertilizing began (Fig. 1). The difference in phosphate concentrations rose to about a constant level by May or July. The effect of fertilizing was greatest in the top 10 cm. Continued fertilizing did not cause further increases in either nutrient in the 2nd yr. There was no significant effect of fertilizing on total N and P (measured only in plots with unaltered litter in October). In unfertilized plots, the concentration of dissolved phosphate in the top 5 cm of sediment was lowest in January, ≈100–300 μg/L, compared to other months when it was ≈900–1500 μg/L. In contrast, the concentration of dissolved ammonium in unfertilized plots showed no clear seasonal trend and was ≈700–1300 μg/L.

We measured dissolved interstitial nitrate (plus nitrite) in the top 5 cm in the 2nd yr only. Fertilized plots had significantly lower concentrations of nitrate than unfertilized plots ($P = .028$). Nitrate averaged 56 ± 6 μg/L ($\bar{X} ± SE$) in fertilized plots and 79 ± 8 μg/L in unfertilized plots. There were no significant effects of the litter manipulations on nitrate concentrations.

On most sampling dates there was a significant ($P < .05$) correlation between concentrations of extractable and dissolved nutrients, suggesting that they were
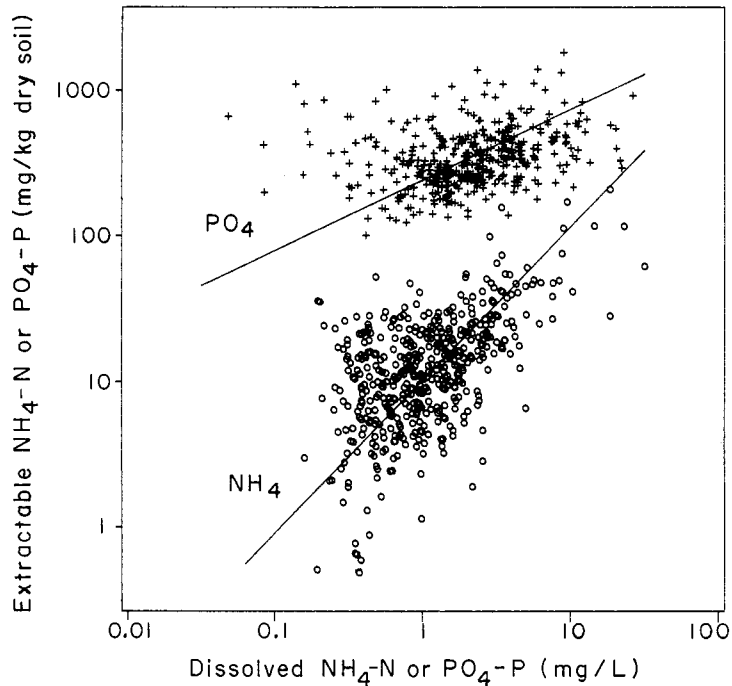
FIG. 2. Concentrations of extractable vs. dissolved phosphate and ammonium. Data are from all treatments and all samplings except for January phosphate data, which did not show a correlation between extracted and dissolved forms (see Soil Nutrients). Lines fit by geometric mean regression (Ricker 1984): phosphate, $r^2 = 0.065$; ammonium, $r^2 = 0.31$. Slopes were highly significant ($P < .001$).

readily exchangeable in situ (Fig. 2). However, in January, when dissolved phosphate concentrations were low, the extractable phosphate was not correlated with dissolved phosphate, suggesting that a portion of the extractable-phosphate pool was not readily exchangeable with the dissolved pool. The ratio of extractable to dissolved fractions was higher for phosphate than ammonium (Fig. 2). The relationships of the logarithms of the concentrations of dissolved and extractable nutrients, sometimes called Freundlich isotherms (Carritt and Goodgal 1954), were not affected by the treatments or depth. The overall relationship for phosphate was weak and possibly not linear (Fig. 2).

In October at the end of the 2nd yr, effects of the litter treatments on soil nutrients became evident, but these effects seemed to be consequences of the physical structure of the litter layer rather than decomposition. Fertilized plots with no litter had significantly higher concentrations of dissolved interstitial phosphate than other fertilized plots (Fig. 3) suggesting that the presence of either litter or pseudolitter reduced delivery of the added nutrients. In contrast, litter treatments did not significantly affect extractable phosphate (Fig. 3), dissolved ammonium, or extractable ammonium (Fig. 4). However, concentrations of total ammonium, the sum of the dissolved and extractable fractions, were higher in plots with no litter than in plots of identical nutrient treatment with either litter or pseudolitter present (Fig. 4). The main effects of litter and fertilizer
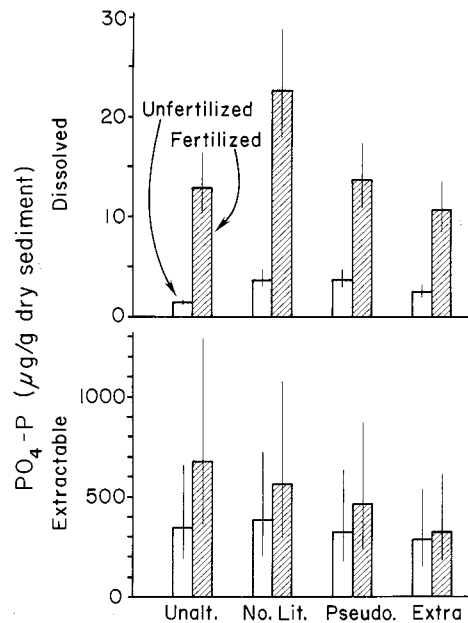

FIG. 3. Mean concentrations of dissolved and extractable phosphate in the top 5 cm of sediment in fertilized and unfertilized plots with unaltered litter, no litter, pseudolitter, and extra litter in October of the 2nd yr of the study. Conversion of dissolved phosphate concentrations to mass per unit dry sediment mass assumes an average of 4 mL of interstitial water per gram dry sediment based on wet and dry masses of core sections of known volume. Error bars are 95% confidence intervals calculated by Tukey's honestly significant difference (hsd) method for pairwise comparisons of means adjusted according to Cicchetti (1972).
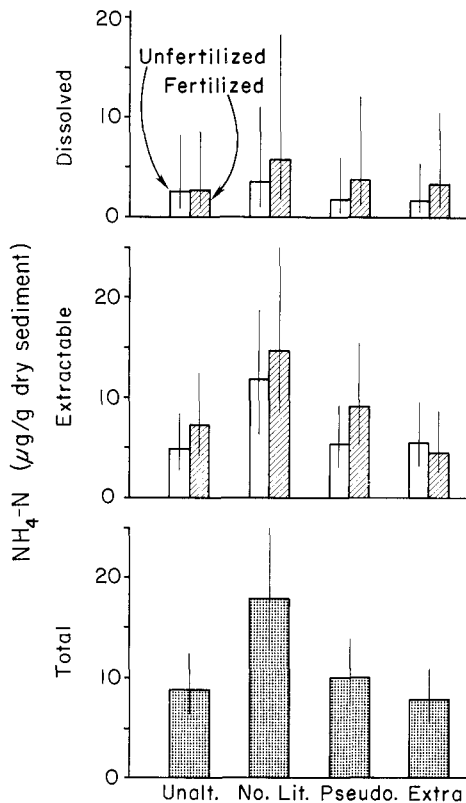
FIG. 4. Mean concentrations of dissolved, extractable, and total ammonium in the top 5 cm of sediment. Labels and symbols as in Fig. 3. Total ammonium for fertilized and unfertilized treatments is averaged to illustrate the main effect of litter treatments, with 95% confidence intervals calculated by Tukey's hsd based on ANOVA with nonsignificant interactions pooled.

on total ammonium were statistically significant ($P <$ .05), when the interaction of nutrient × litter ($P = .76$) and the effect of site nested in litter ($P = .35$) were pooled because of their lack of significance (Underwood 1981). The main effect of fertilizer (but not litter) on dissolved ammonium was also significant in the sampling of the 2nd yr if nonsignificant effects were pooled.

Litter decomposition

Nutrient applications did not affect decomposition rates, but position in the litter layer did. Litter on top of the litter layer in plots with extra litter decomposed faster than litter on the sediment surface, but the differences in mass loss were statistically significant only for leaf blade litter after 300 d in the field (Fig. 5). Leaf blades decomposed faster than bases. After 860 d in the field leaf blades lost 60–85% of their original mass, while leaf bases lost 40–60%. Decomposition did not follow a simple exponential function. Mass loss was relatively slow during the first 130 d probably because this coincided with winter. Also, mass loss after 300 d was slower than would be expected from extrapolating

an exponential function describing loss in the first 300 d. This suggests that as decomposition proceeded the material left over became increasingly refractory.

Percent N and P in litter increased linearly as the percent mass remaining declined (Fig. 6). The slopes of these linear relationships (Fig. 6) were determined by geometric mean regression (Ricker 1984) since there was variance associated with both nutrient content and percent mass remaining. The slopes were about the same for leaf blades or bases, but the intercepts for the relationships to N were different, due to lower N concentrations in leaf bases at the start of decomposition. There were no apparent treatment effects on these linear functions.

The litter mostly immobilized nutrients during the experiment. The absolute amount of N and P in decomposing leaf bases steadily increased, with N rising to 230% of its original amount and P rising to 330% of its original amount after 860 d (Fig. 7). The amount of N in leaf blades increased for about the first 200 d and then decreased to ≈80% of its original amount at 860 d. The amount of P in leaf blades increased to ≈180% of the original amount at 240 d, decreased to 130% at 300 d, and remained about constant to 860 d. We calculated the maximum amounts of N and P immobilized in the litter by using the regressions of Fig. 6 according to Melillo et al. (1984). These calculated amounts corresponded roughly to the maximum amounts we observed during our experiment (Fig. 7). There were no significant differences in the time course of N and P content among treatments despite the effect of position in the litter layer on the rate of mass loss.

DISCUSSION

The effects of the litter treatments on nutrients in the sediment seem to be primarily due to the physical structure of the litter layer rather than uptake and release of nutrients by decomposing litter. For example, plots with neither litter nor pseudolitter had elevated concentrations of total ammonium (Fig. 4). Removal of litter from prairie soils can elevate total ammonium concentrations by allowing increased solar heating of the soil which increases rates of mineralization of belowground organic matter (Ojima et al. 1985). Our marsh sediments may have behaved similarly. On one occasion in spring, we measured temperatures 10 cm deep in the sediment that were ≈3°C higher in plots with no litter than in plots with either litter or pseudolitter.

Increases in nutrient pools in the sediment due to experimental additions of nutrients totaled 0.38 g/m² N and 3.5 g/m² P (Table 1). This accounted for 0.5% of the N and 5% of the P added annually. Greater amounts of the added nutrients, especially phosphate, were taken up into the pools of extractable nutrients than into the pools of dissolved nutrients (Table 1). The extractable phosphate we measured included phosphate bound to iron and aluminum oxyhydrox-
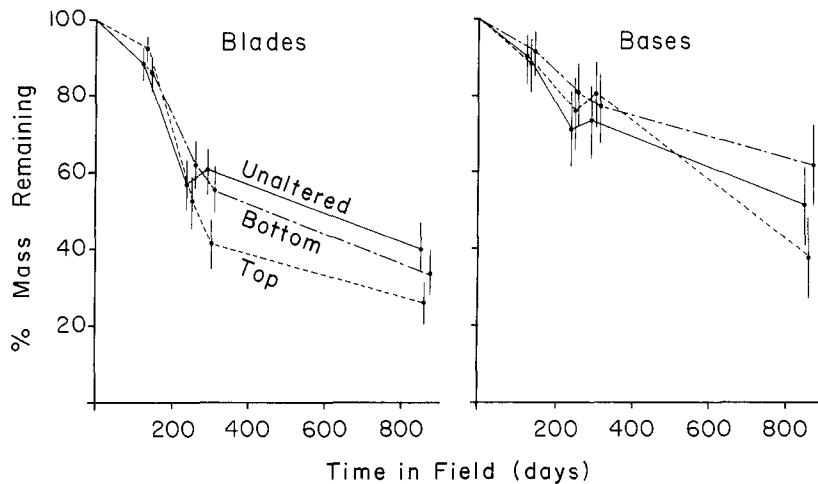
FIG. 5. Percent of original mass remaining vs. time in field for leaf blade litter and leaf base litter, comparing litter placed on the top and bottom of the litter layer in plots with extra litter, and litter placed on the sediment surface in plots with unaltered litter abundance. Error bars are 95% confidence intervals (adjusted hsd, Cicchetti 1972) for comparisons within leaf blades or bases.

ides. In many wetlands, the abundance of such oxy-hydroxides determines the capacity to retain P (Richardson 1985). Extractable ammonium comprised the majority of the total ammonium pool, but Bowden (1984) found even greater proportions of extractable ammonium in a *Typha latifolia* marsh.

Some of the added N may have also been lost via denitrification, an important sink for N in many wetlands (e.g., Bartlett et al. 1979, Kaplan et al. 1979, Brinson et al. 1984). Nitrification evidently occurs in the sediments of our marsh because the concentration of nitrate in interstitial water, 79 μg/L in unfertilized plots, exceeded the concentration in surface water, which was <10 μg/L (T. E. Jordan et al., *personal observation*), as is typical for the fall (Jordan et al. 1983). Bowden (1986) measured nitrification in a *Typha latifolia* marsh, despite the predominately anaerobic sediments. He found that the concentration of nitrate in interstitial water was controlled by the balance between nitrification and denitrification. Alteration of this balance may account for our fertilized plots having lower concentrations of nitrate than our unfertilized plots. Influx of upland groundwater to the marsh could deliver nitrate as Valiela et al. (1978) found in a salt marsh, but this is probably not the case in our marsh where ebb and flood waters have the same salinity suggesting little influx of fresh groundwater (Jordan et al. 1983).

Some of the nutrients we added became incorporated in aboveground plant tissues, but at most this accounted for only 9.6% of the N and 2.2% of the P added annually (Jordan et al., *in press*). The fact that the plants took up a larger proportion of the added N than P may account for the fact that more of the added P than N accumulated in the soil (Table 1).

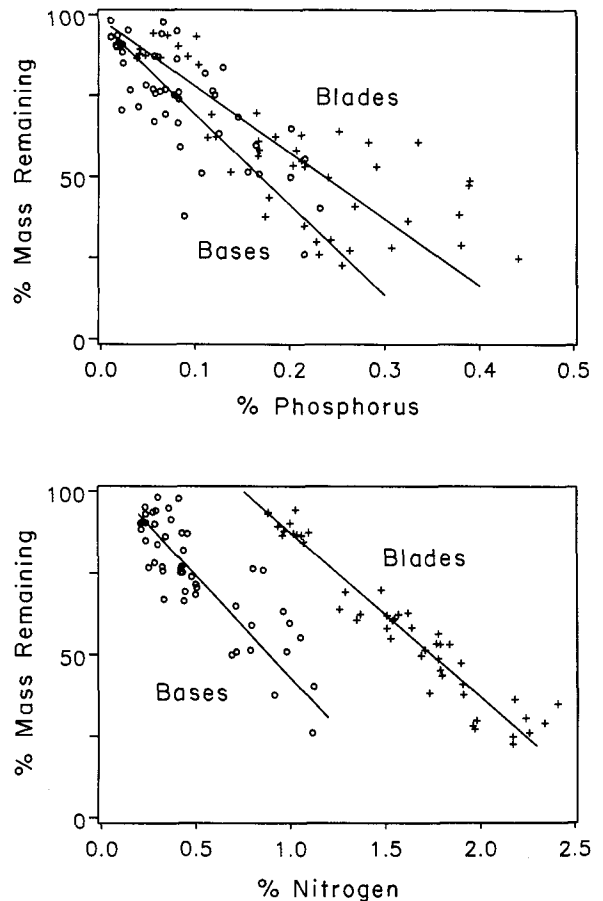Most of the nutrient pools we measured increased

FIG. 6. Percent of original mass remaining vs. initial %N and %P for leaf blade litter (+) and leaf base litter (O). Data from all treatments were combined since the effects of treatments were not significant. Lines fit by geometric mean regression (Ricker 1984): blades %P, $r^2 = 0.62$; bases %P, $r^2 = 0.58$; blades %N, $r^2 = 0.92$; bases %N, $r^2 = 0.70$. All slopes were highly significant ($P < .001$).
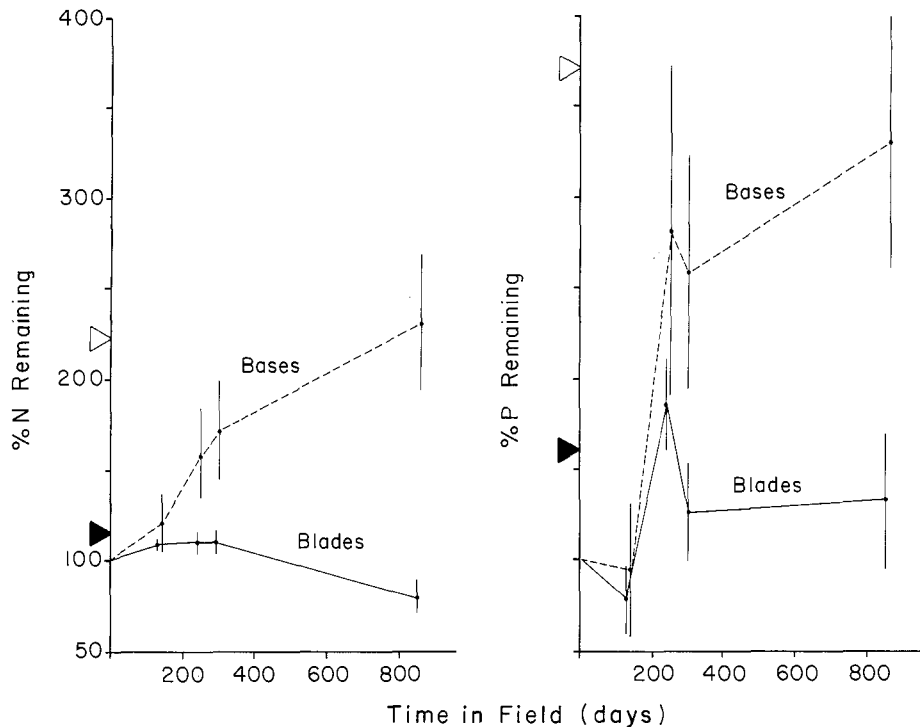
FIG. 7. Percent of original N and P remaining vs. time in the field for leaf blade litter and leaf base litter. Data from all treatments were combined since the effects of treatments were not significant. Error bars are 95% confidence intervals of the means (n = 12). Triangles on vertical axis (▶ leaf blades, ▷ leaf bases) mark the predicted maximum percent of N or P remaining, calculated from the regressions in Fig. 6 by the method of Melillo et al. (1984).

by 20–70% of their original size in response to nutrient additions, but only $\approx \frac{1}{10}$ of the nutrients we added were taken up (Table 1). However, we added nutrients at rates much higher than the natural inputs. For example, studies with radiolabeled P suggest that the natural P input to our marsh is 30 mg·m^{-2}·d^{-1} in spring (Correll et al. 1975), which is $<\frac{1}{10}$ of our experimental loading rate. In previous experiments, when P was added at double the natural loading rate, essentially all of the added P was taken up by the marsh (Correll et al. 1975).

Our nutrient additions did not affect the rate of litter decomposition or the immobilization of nutrients by the litter. However, several studies have shown that increase in available nutrients can lead to increase in the rate of decomposition and/or the amount of immobilization (Hynes and Kaushik 1969, Kaushik and Hynes 1971, Howarth and Fisher 1976, Almazan and Boyd 1978, Jensen et al. 1978, Haines and Hanson 1979, Elwood et al. 1981, Melillo et al. 1984). Valiela et al. (1985) found that adding nutrients to a salt marsh increased both the N content and decomposition rate of litter. Neely and Davis (1985) found that adding nutrients to a *Typha glauca* stand increased nutrient immobilization but did not increase decomposition rates. Other studies have found, as we did, that adding nutrients did not affect decomposition or immobilization (Triska and Sedell 1976, Webster and Benfield

1986). Evidently, nutrient supply is not always a limiting factor for decomposition and immobilization.

Litter decomposition rates were affected by the thickness of the litter layer because rates were higher on the top of the thick litter layer in plots with extra litter than on the sediment surface (Fig. 5). The relative dryness of litter on the top of the litter layer might be expected to slow decomposition as with standing dead material (Gallagher et al. 1984, Newell et al. 1985). However, microbes in standing dead material respond quickly to periodic wetting from tides or rain and, thus, standing dead material can decompose at rates approaching those of fallen litter (Newell et al. 1985). Furthermore, waterlogged litter on the sediment surface may be partly anaerobic and lack of oxygen usually slows decomposition of wetland macrophyte litter (Chamie and Richardson 1978, Godshalk and Wetzel 1978, Haines and Hanson 1979, Melillo et al. 1984, Webster and Benfield 1986).

The lack of effects of the litter manipulations on nutrient pools in sediment is surprising considering the potential importance of litter in nutrient cycling in wetlands (e.g., Neely and Davis 1985, Bowden 1986, Morris and Lajtha 1986, Richardson and Marshall 1986, Whigham et al., *in press*). Maybe the duration of the experiment was not long enough to see such effects. The litter which we manipulated was mostly taking up nutrients during the course of the experiment (Fig. 7).

TABLE 1. Comparison of pools of N and P in fertilized and unfertilized plots with unaltered litter.*

Nutrient pool	Fertilized†	−	Unfertilized	=	Difference
		Nitrogen (g/m²)			
Total in sediment	410		410		NS
Aboveground biomass	15.6		9.4		6.2
Leaf blade litter‡	5.9–6.9		4.8–5.6		1.1–1.3
Leaf base litter‡	0.40–0.91		0.33–0.74		0.07–0.17
Extractable NH_4	0.87		0.59		0.28
Dissolved NH_4	0.32		0.22		0.10
Dissolved $NO_3 + NO_2$	0.0087		0.012		−0.0033
		Phosphorus (g/m²)			
Total in sediment	85		85		NS
Aboveground biomass	4.5		2.9		1.6
Leaf blade litter‡	0.52–0.85		0.43–0.70		0.09–0.15
Leaf base litter‡	0.047–0.17		0.038–0.14		0.009–0.03
Extractable PO_4	14		11		3.0
Dissolved PO_4	0.71		0.22		0.49

* Pools in the sediment include total nutrients, nutrients dissolved in interstitial water, and extractable nutrients in the top 20 cm of sediment based on concentrations measured in October of the 1st yr, interpolating for the 10–15 cm depth. Nitrate plus nitrite is based on measurements in October of the 2nd yr, extrapolating the 0–5 cm depth to 0–20 cm. The water content of the sediment was 80% (T.E. Jordan et al., *personal observation*) and the sediment bulk density (dry mass) was 0.2 g/cm³ (Jordan et al. 1986). N and P in aboveground biomass is the maximum amount from the 2nd yr (Jordan et al., *in press*). The estimates of N and P in the annual litter crop use the aboveground biomass as the initial mass of litter consisting of 22% leaf bases and 78% leaf blades. Both the initial and maximum nutrient content of litter are shown. The initial nutrient content is based on measurements of litter collected from areas outside of the plots and used in the litter bags. The maximum nutrient content was calculated from the slopes of the relationships in Fig. 6 according to Melillo et al. (1984).

† Addition rate to fertilized plots: N, 65 g·m⁻²·yr⁻¹; P, 72 g·m⁻²·yr⁻¹.

‡ Data are shown as initial value–maximum value.

In the unfertilized plots with unaltered litter, the litter produced in the 2nd yr would have immobilized N in amounts of 1.2 g/m² and P in amounts of 0.37 g/m² (Table 1). Fertilized plots had ≈20% higher aboveground production that year than unfertilized plots (Jordan et al., *in press*), so their litter crop would have immobilized proportionally more. Plots with extra litter received three times the normal annual input of litter and, thus, their annual litter supply would have immobilized N in amounts of ≈4 g/m² and P in amounts of ≈1 g/m². Compared to other nutrient pools (Table 1) this represents a substantial nutrient sink that would not be present in plots with pseudolitter, yet plots with pseudolitter did not differ significantly from plots with extra litter in content of soil nutrients.

Release of nutrients from litter did not begin until after ≥1 yr had passed (Fig. 7) when more than half of the litter had decomposed (Fig. 5). At this stage of decomposition the litter had become very fragmented and was being invaded by roots. Invasion by roots may indicate that the litter is a source of nutrients for the plants (Aber and Melillo 1980, Morris and Lajtha 1986). As roots invade the litter and as sediment accumulates, the litter may become buried. Once buried, the litter could become an important source of nutrients in the sediment as Bowden (1986) suggests. However, the presence of a large pool of slowly decomposing organic matter below ground may be a source of gradual nutrient replenishment and could buffer the belowground nutrient supply against short-term changes in litter input.

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