

Effects of Nutrient and Litter Manipulations on the Narrow-Leaved Cattail, *Typha angustifolia* L.

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ABSTRACT

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The effects of altering litter and nutrient loading on above-ground production, nutrient content and borer infestation of *Typha angustifolia* L. were studied with a 3-year field experiment. In replicated plots, litter was either removed, replaced with plastic strips (pseudolitter), increased 3-fold or left unaltered. One set of plots received fortnightly surface applications of ammonium phosphate solution at a rate totaling 65 g N m⁻² and 72 g P m⁻² annually. Peak above-ground biomass was increased by nutrient addition, except in the third year of the experiment when peak biomass in all plots was low, possibly due to high salinity that year. The nutrient additions also decreased the rate of flowering, increased concentrations of N and P in plant tissues, and increased the frequency of shoot infestation by boring noctuid larvae. The effects of the litter manipulations seem to be attributable to the physical structure of the litter layer rather than the decomposition process. Plots with neither litter nor pseudolitter showed enhanced incorporation of added N and P in fruits, and were colonized by the herbaceous dicotyledons *Lilaeopsis chinensis* (L.) Kuntze and *Pluchea purpurascens* (Swartz) DC. Plots receiving extra litter developed a litter layer thick enough to suppress the growth of *Typha* in the third year.

INTRODUCTION

The production of tidal marshes is often limited by nutrients, particularly nitrogen (Sullivan and Daiber, 1974; Valiela and Teal, 1974; Broome et al., 1975, 1983; Gallagher, 1975; Patrick and DeLaune, 1976; Haines, 1979; Mendelssohn, 1979). Marsh macrophytes can respond to added nutrients with increases in both production and the nutrient content of their tissues. This contributes to the ability of marshes to take up added nutrients, a property often cited as evidence of their potential in reducing eutrophication and even in treating sewage effluent (Valiela et al., 1976, 1985; Whigham and Simpson, 1976; Verry and Timmons, 1982). Increases in the nutrient content of macrophyte tissues can also increase herbivory in marshes (Vince et al., 1981).

Macrophyte litter plays an important role in nutrient cycling in marshes.

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, immobilization ceases and the litter gradually releases nutrients. By immobilizing nutrients, litter may be a significant sink for nutrients in marshes (Davis and van der Valk, 1978) and could compete for nutrients with plants (Barko and Smart, 1983; DeJong and Klinkhamer, 1985). 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 marshes. Besides affecting nutrient availability, litter can affect plant production and competition through shading and allelopathy (McNaughton, 1968; Grace, 1983; van der Valk, 1986). In this paper, we report the results of a 3-year field experiment in which we manipulated nutrients and the litter layer in a brackish tidal marsh, and measured the effects on above-ground production, herbivore infestation and the nutrient content of shoots and fruits of the dominant macrophyte, *Typha angustifolia* L.

METHODS

Study site

The marsh we studied is on the Rhode River, a sub-estuary on the western shore of 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 day⁻¹ on the average (Jordan et al., 1986). Mean tidal amplitude is 30 cm. Salinity ranges from 0‰ in spring to as high as 18‰ in autumn. *T. angustifolia* L. is the dominant plant in the marsh, but *Scirpus olneyi* Gray and *Spartina cynosuroides* (L.) Roth are also common (nomenclature follows Radford et al., 1968). Live above-ground *Typha* biomass is present from mid-April to mid-October.

Experimental design

Using a factorial design, we altered the abundance of litter and nutrients in 16 2×2-m plots in the marsh, with two plots representing each combination of litter and nutrient treatment. The litter treatments included: (1) removing litter; (2) replacing litter with plastic strips (pseudolitter) to create an artificial litter layer; (3) tripling the amount of litter; (4) leaving the amount of litter unaltered. The litter treatments were repeated each October after the

Typha had senesced. In the first year, 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). The pseudolitter was held in place by a covering of galvanized wire mesh (chicken-wire). Litter removed from plots receiving pseudolitter or no litter 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⁻¹ diammonium phosphate ((NH₄)₂HPO₄) dissolved in tidal water. For each application, 1 l of nutrient solution per m² was sprinkled on the plots from a cart on an elevated track. A total of 65 g N and 72 g P were added per m² 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 the 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 ($P < 0.05$), but interactions were not, a posteriori multiple comparisons of means were made by the Tukey honestly significant difference (HSD) method ($P < 0.05$; Sokal and Rohlf, 1981). When interactions were significant, comparisons of levels of a factor were made by adjusted HSD ($P < 0.05$; Cicchetti, 1972). Prior to analysis, data expressed as percents were arcsine square-root transformed (Sokal and Rohlf, 1981).

Above-ground production and herbivory

In each plot, when the above-ground biomass was at its peak, we measured the heights of the 12 tallest *Typha* plants, the numbers of *Typha* shoots and infructescences, and the number of stems bored by larvae of the noctuid *Ar-*

chanara oblonga Grote (= *Nonagria oblonga*; Hodges, 1983). Each plot was subdivided into four 1 × 1-m quadrats, and the heights of the three tallest plants and the numbers of shoots in each quadrat were measured. We estimated biomass from a regression relating biomass in 1 × 1-m plots to the numbers of shoots per m² and the average height of the three tallest plants ($\ln[\text{g dry weight m}^{-2}] = -8.905 + 2.335[\ln(\text{cm height})] + 0.7023[\ln(\text{shoots m}^{-2})]$, $r^2 = 0.85$, $n = 22$).

Nutrients in plant tissues

We sampled four randomly selected divergent leaf blades from each plot periodically throughout the growing season for N and P analysis. In July of the second year, we sampled four randomly selected whole shoots from each plot and separated leaf bases (the rigid overlapping portion of the shoot) from leaf blades for analysis. In August of the second year, four randomly selected mature infructescences were sampled from each plot and the fruits were separated from the stalks for analysis. All samples were rinsed in tap water, dried at 60°C, ground in a Wiley mill and analyzed for total N and P. Total N was analyzed either with a Perkin Elmer CHN analyzer in the laboratory of G. Thayer (National Marine Fisheries Service, Beaufort, NC) or by Kjeldahl digestion (Martin, 1972), followed by distillation of resulting ammonia and analysis by Nesslerization (American Public Health Association, 1976). Our own checks confirmed that the two techniques yield identical results. Total P was analyzed by perchloric acid digestion followed by reaction with ammonium molybdate and aminonaphtholsulfonic acid, and extraction of color with isobutyl alcohol (Correll and Miklas, 1975).

RESULTS

Above-ground production and herbivory

Nutrient applications increased maximum above-ground biomass by 13% in the first year and by 22% in the second year (Fig. 1). In the third year, nutrient applications did not affect biomass and biomass was much lower than in previous years, possibly because salinity was high (Whigham et al., 1989).

Litter manipulations also affected above-ground biomass, shoot height and shoot density. In the second year, shoot heights were significantly increased in fertilized plots with no litter, but not in plots with either litter or pseudolitter (Fig 2). By the third year, the litter layer in plots with extra litter had apparently become thick enough (~50 cm) to reduce the number of shoots and the maximum above-ground biomass significantly. That year, plots with extra litter had only 13–21 shoots m⁻² and 79–143 g m⁻² above-ground biomass, while other plots had 33–79 shoots m⁻² and 247–564 g m⁻² above-ground biomass.

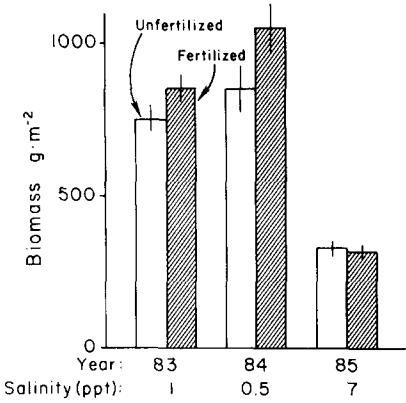


Fig. 1. Peak above-ground biomass comparing nutrient treatments. Litter treatments are combined since there were no significant effects of litter. Error bars are 95% confidence limits for comparisons within years. Shaded bars represent fertilized treatments. Salinity values are averages of weekly measurements of tidal waters during the period of rapid growth from late April to early July (Whigham et al., 1989).

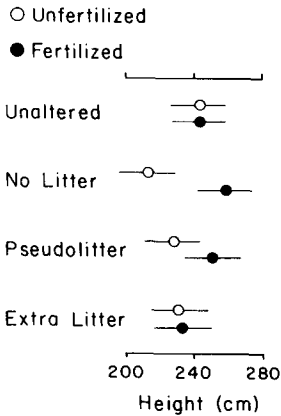


Fig. 2. Comparison of maximum plant heights among treatments in the second year of study. Filled circles are fertilized treatments; open circles are unfertilized treatments. Error bars are 95% confidence limits (adjusted HSD; Cicchetti, 1972).

Nutrient applications decreased the number of flowering shoots, except in the first year when < 1% of the shoots flowered. In the second year, ~ 10% of the shoots in unfertilized plots and 6% of the shoots in fertilized plots flowered. This difference was close to the cutoff for significance ($P=0.062$, ANOVA). In the third year, ~ 4% of the shoots in unfertilized plots and 1% of the shoots in fertilized plots flowered. We could not use parametric statistics on the third-year data because several of the plots had no flowering shoots. However, Wilcoxon's signed ranks test (Sokal and Rohlf, 1981) indicated that the effect of

nutrients was significant ($P=0.023$). There were no significant effects of litter manipulations on flowering in any year.

Removal of the litter layer allowed two herbaceous dicotyledons to invade. In plots with no litter, *Lilaeopsis chinensis* (L.) Kuntze formed an understory a few centimeters high attaining up to 75% cover and *Pluchea purpurascens* (Swartz) DC. grew under gaps in the *Typha* canopy. Neither species colonized plots with either litter or pseudolitter.

In the second year, we noted an infestation by larvae of a noctuid moth, *A. oblonga*, which bores into the bases of shoots and eats the inner leaves causing the shoots to collapse. Plants in fertilized plots were more frequently bored than plants in unfertilized plots ($P=0.0054$, ANOVA). About 20% of the shoots in fertilized plots and 8.4% in the unfertilized plots were bored. In the third year, ~4.9% of the shoots in fertilized plots and 3.6% in unfertilized plots were bored, but the difference was not significant. The litter manipulations did not affect the frequency of boring.

Nutrients in shoots and fruits

Leaf blades from fertilized plots had significantly higher concentrations of N and P than blades from unfertilized plots (Fig. 3). The concentrations of N

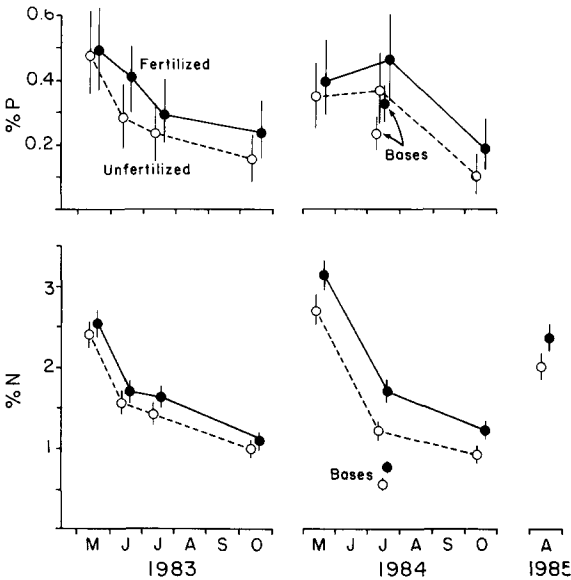


Fig. 3. N and P in leaf blades and bases (labeled) versus time in fertilized and unfertilized plots. Litter treatments are combined since there were no significant effects of litter. Filled circles and solid lines represent fertilized plots. Open circles and dashed lines represent unfertilized plots. Error bars are 95% confidence limits (adjusted HSD; Cicchetti, 1972) for comparisons within leaf blades or bases.

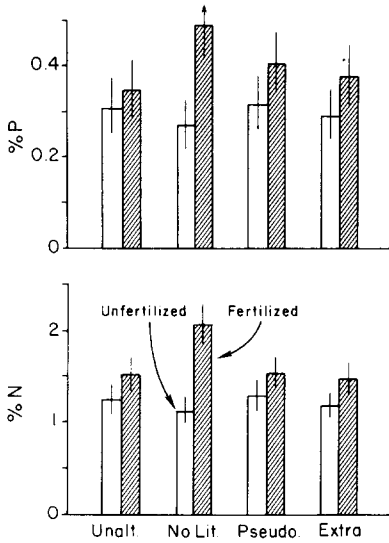


Fig. 4. N and P in fruits. Shaded bars represent fertilized treatments. Error bars are 95% confidence limits (adjusted HSD; Cicchetti, 1972).

and P in leaf blades declined throughout the growing season. The interaction between the effects of time and fertilization was significant for N in leaf blades, but only the main effects were significant for P. Leaf bases, which had lower N and P concentrations than leaf blades, had significantly higher N in fertilized plots than in unfertilized plots. In the third year, when biomass was low and salinity was high (Fig. 1), leaf blades had a higher N content in the summer than in the previous summers (Fig. 3). Litter manipulations did not affect the N and P content of leaves, but evidently did affect the N and P content of fruits since the effect of nutrient applications on fruits was more pronounced in plots with no litter than in plots with either pseudolitter or litter (Fig. 4).

DISCUSSION

Increased plant growth in response to nutrient additions probably reflects nitrogen limitation, as observed in many marshes (e.g., Valiela and Teal, 1974; Buresh et al., 1980; Broome et al., 1983; Grace, 1988), rather than phosphorus limitation. The N:P mass ratio of dissolved interstitial ammonium and phosphate and in the nutrient solution we applied was ~ 1 (Jordan et al., 1989), while the N:P mass ratio in plant tissues ranged from 2 to 6 (Fig. 3). However, salinity may be a more important control of production than nutrient supply. Yearly variations in salinity can lead to significant variations in productivity in estuarine wetlands (Zedler et al., 1986). Growth of *Typha* species is reduced by moderately high salinities (McMillan, 1959; Hocking, 1981). In our marsh,

years of low production correlate with years of high salinity (Whigham et al., 1989) and, when salinity was high, nutrient addition did not increase plant biomass (Fig. 1). Similarly, Haines and Dunn (1976) found that the effect of nutrient addition on the salt marsh grass *Spartina alterniflora* Loisel was negated when high salinities reduced growth.

During the year of high salinity, the N content of leaf tissue was also high (Fig. 3). Similarly, Hocking (1981) found that elevated salinities raised the N content of roots and rhizomes of *Typha domingensis* Persoon, but he did not observe increases in leaf N as we did. High N content might reflect accumulation of N-containing osmoregulatory substances, as in *S. alterniflora* which may invest 19–30% of its N in osmoregulation when salinity is high (Cavaliere and Huang, 1981). Alternatively, high N content may reflect the lack of ability to assimilate C relative to N, or high concentrations of available N in the soil during the year with high salinity. Soil N may have been high during the year with high salinity because the stunted plants took up less N.

Increased herbivory by boring insects, (*A. oblonga* larvae), in response to nutrient addition is consistent with findings in fertilized agricultural fields (reviewed by Scriber, 1984; White, 1984). Increased insect herbivory in response to added nutrients may reflect increased food value of the plants owing to elevated protein content, as suggested by elevated tissue N (Fig. 3). However, many studies have also shown that an increase in nutrient availability can result in a decrease in insect herbivory because increased food value means less of the plant is consumed to meet the requirements of the insect, or because the plant is better able to produce secondary substances to ward off insects if supplied with more nutrients (Scriber, 1984; White, 1984). Vince et al. (1981) found increased insect herbivory in a salt marsh due to nutrient addition, and they attributed the response mainly to enhanced survivorship and fecundity. In our study, the increase in borer damage probably does not reflect fecundity because the borer life-cycle (described by Claasen, 1921, as *N. oblonga*) is 1 year long. Adults may select enriched sites to deposit eggs, but it seems more likely that larvae select the plants they bore. Normally, there is little obvious impact of insects on the *Typha* community we studied, but during the year of high infestation as many as 30% of the shoots in fertilized plots were destroyed by borers. Chronic elevation of nutrients, combined with periodic outbreaks of borers, could have a seriously detrimental effect on net production in *Typha* stands. Although there is usually little insect herbivory in marshes, Foote et al. (1988) observed an outbreak of leaf-chewing caterpillars that removed almost half of the above-ground biomass in a *Typha* stand.

Decreased flowering in response to added nutrients may indicate a reproductive strategy favoring vegetative reproduction over sexual reproduction in times of high nutrient availability. In contrast, high light availability favors flowering in *Typha latifolia* L., suggesting that flowering is a low priority for the allocation of resources and will only occur if extra resources are available

(Grace and Wetzel, 1981). Apparently, flowering in *Typha* responds differently to the supplies of different resources. Given the effect of nutrients on flowering, it seems odd that there was no effect of litter removal on flowering since fruits in fertilized plots with no litter had a higher nutrient content than those in other plots. The annual variation in flowering exceeded the effect of adding nutrients and was not related to the yearly peak in above-ground biomass since the year with lowest production had an intermediate frequency of flowering. One factor affecting annual variation in *Typha* flowering may be the amount of energy storage from the previous growing season (Linde et al., 1976). More research is needed to determine what controls flowering in *Typha*.

The effects of the litter treatments were probably due to the physical structure of the litter layer rather than chemical exchanges during decomposition. For example, shading probably caused the reduction in shoot densities in plots with extra litter in the third year when the litter layer had become over 50 cm deep. Lack of shading in plots with no litter probably accounts for their colonization by the herbaceous dicotyledons *L. chinensis* and *P. purpurascens*. Colonization of *Typha* marshes by other species in response to the removal of litter has also been observed by van der Valk (1986). *Typha* litter can exhibit allelopathy (McNaughton, 1968; Grace, 1983), but this does not explain our results since neither species invaded plots with pseudolitter. The litter layer also seems to have acted as a barrier to the nutrients that we sprinkled on the fertilized plots because nutrient applications caused larger increases in plant heights (Fig. 2), and fruit N and P (Fig. 4) in plots with no litter than in plots with either litter or pseudolitter. Some of the nutrient solution sprinkled from above at low tide may have adhered to the litter and been washed away at high tide instead of soaking into the sediment.

Although only a small proportion of the added nutrients were taken up into above-ground biomass, the total pool of nutrients in above-ground biomass increased substantially in response to the nutrient additions. The maximum amount of N and P in above-ground plant tissues and the change in the amounts due to nutrient addition varied yearly (Table 1). In the year when nutrient additions affected plant growth the most, there was a total increase of 6.2 g N m⁻² and 1.6 g P m⁻² in above-ground plant tissues due to nutrient addition. This amounts to only 10% of the N and 2.2% of the P added annually, but it represents a 66% increase in N and a 55% increase in P in above-ground biomass. Despite the higher nutrient content of fruits from fertilized plots (Fig. 4), there was less N and P in fruits in fertilized plots than in unfertilized plots because fertilized plots produced fewer fruits.

Considering the potential importance of litter in nutrient cycling in wetlands (e.g., Neely and Davis, 1985; Bowden, 1986; Morris and Lajtha, 1986), one might expect that nutrient exchanges from decomposing litter would affect *Typha* production and lead to differences between plots with litter and plots with pseudolitter. For example, Barko and Smart (1983) and DeJong and

TABLE 1

Comparison of the maximum N and P in the above-ground biomass in fertilized and unfertilized plots based on summer concentrations and peak biomass. Distribution of tissue mass based on an average weight of fruiting stalk of 14 g, and leaves consisting of 22% bases and 78% blades

		N (g m^{-2})		P (g m^{-2})		
		Fertilized – unfertilized = difference		Fertilized – unfertilized = difference		
1983						
Leaf blades	11	8.4	2.6	1.9	1.4	0.5
1984						
Leaf blades	13	7.2	5.8	3.6	2.2	1.4
Leaf bases	1.7	0.95	0.75	0.70	0.39	0.31
Fruits	0.88	1.2	-0.32	0.20	0.30	-0.10
1985						
Leaf blades	5.8	4.7	1.1	-	-	-

Klinkhammer (1985) buried fresh litter in sediment and observed a resulting decrease in plant growth which they attributed partly to uptake of nutrients by the decomposing litter. In our experiment, litter was on the sediment surface where it may have taken up nutrients from both the tidal waters and the sediment. The litter which we manipulated was mostly taking up nutrients during the course of the experiment. In plots with extra litter, $\sim 4 \text{ g N m}^{-2}$ and 1 g P m^{-2} were immobilized by the annual load of litter (Jordan et al., 1989). This amounts to about one-third of the maximum amount of N and P in above-ground biomass. However, none of the effects of the litter treatments could be attributed to nutrient immobilization. In the short term, the physical structure of the litter layer was more important than its uptake or release of nutrients.

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