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ABSTRACT.—Loss of plant species diversity in wetlands has been linked to high nutrient conditions. In particular, *Typha* spp. are known to form monotypic stands in fertile wetland systems. In this study marsh mesocosms were used to study the effect of nitrogen (N), phosphorus (P) and nitrogen and phosphorus (N and P) additions on density, biomass and nutrient dynamics of *Typha latifolia* L. and the sedge *Schoenoplectus tabernaemontani* (C.C. Gmel) Palla (a.k.a. *Scirpus validus* Vahl.) grown in size- and density-symmetric and in size- and density-asymmetric mixtures. Dynamics of *Typha* and *Schoenoplectus* mixtures were also estimated along a nutrient gradient in a created wetland. *Typha* responded with increased growth to higher nutrient conditions more than *Schoenoplectus* in the first year, but *Schoenoplectus* responded more than *Typha* in the second year when nutrient additions were stopped. *Typha* grew better compared to the control with the addition of nitrogen and phosphorus in both the asymmetric and symmetric mixtures. Nitrogen or phosphorus, when added alone, did not increase the growth of *Typha* when it was grown with *Schoenoplectus*. The presence of a one-year-old stand of *Schoenoplectus* reduced aboveground growth of introduced *Typha* in both high- and low-nutrient conditions. In a created marsh *Typha* biomass decreased and *Schoenoplectus* biomass increased along a gradient of decreasing nutrient concentrations. N:P ratios in aboveground tissues of both plant species were less than 14:1 (by weight) suggesting N limitation. Plant tissue ratios, however, were close to the Redfield ratio of 7.2:1, suggesting no nutrient limitation.

INTRODUCTION

Changes in plant community composition and loss of species diversity in numerous wetlands around the world have been linked to nutrient additions. Among these affected wetlands are habitats of national and international importance including the New Jersey Pine Barrens, European reed-beds, Eastern Canada wetlands, Dutch dune slacks, peat lakes in England and marshes in the Florida Everglades (Phillip *et al.*, 1978; Ehrenfeld, 1983; Meltzer and Van Dijk, 1986; Day *et al.*, 1988; Moore *et al.*, 1989; Wisheu and Keddy, 1989; Hough *et al.*, 1989; Ostendorp, 1989; Van Dijk, 1989; Gunderson and Loftus, 1993; Verhoeven *et al.*, 1993; Keddy *et al.*, 1994; Ostendorp *et al.*, 1995; Newman *et al.*, 1996; Wu *et al.*, 1997). Several theories on the mechanisms of resource competition (Grime, 1979; Vermeer and Berendse, 1983; Tilman, 1987, 1994; Wisheu and Keddy, 1989; Moore *et al.*, 1989; Keddy *et al.*, 1994) have been used to explain competition in plant communities, especially in changing nutrient conditions.

Nutrient limitation has generally been recognized by increased growth in response to an addition of the limiting nutrient (Chapin *et al.*, 1986; Binkley and Vitousek, 1989), but fertilization experiments can be time consuming, costly and may cause undesirable long-term effects, particularly in freshwater wetlands. Thus an alternative metric, N:P ratios in plant tissues, has been proposed to predict nutrient limitation on a plant community in

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freshwater wetlands (Koerselman and Meuleman, 1996). A N:P ratio > 16 indicates P limitation, whereas an N:P ratio < 14 indicates N limitation.

The goal of this study is to examine the effects of nutrient enrichment on mixture dynamics between two herbaceous plant species common in midwestern USA freshwater wetlands: *Typha latifolia* L. (hereafter *Typha*) and *Schoenoplectus tabernaemontani* (C.C. Gmel) Palla (hereafter *Schoenoplectus*). *Typha* is an example of an aggressive, fast-growing, clonal perennial known to form monotypic stands (Grace and Wetzel, 1981; Grace, 1988). Its dominance is often associated with high-nutrient conditions (Hutchinson, 1975; Lieffers, 1984) and is generally considered undesirable in created and restored wetlands where diverse plant communities are often desired (Mitsch and Gosselink, 2000). *Schoenoplectus tabernaemontani* (formerly *Scirpus validus* Vahl.) is also a fast-growing clonal dominant (Boutin and Keddy, 1993) and is often found in association with *Typha* (Sculthorpe, 1967; Mitsch and Gosselink, 2000). Despite similarities, *Schoenoplectus* is not considered to be invasive and differences in growth rate and competitive ability between the two species have been observed. Growth rates were shown to be 20% higher for *Typha* than *Schoenoplectus* (Shipley and Peters, 1990) and *Typha*'s competitive performance was ranked 27% higher than *Schoenoplectus* when measured against a common phytometer (Gaudet and Keddy, 1995).

Mesocosms were used to determine the following: (1) Which of the two species is more responsive to nutrient additions and to which nutrients when the species are in competition? (2) Does the prior establishment of *Schoenoplectus* alter the growth response of *Typha* to nutrient amendments? (3) Is growth of these common wetland plants limited by N, P or N and P in combination? and (4) Do various N:P ratios provide useful indicators of growth limitation in such experiments? Finally, *Typha* and *Schoenoplectus* biomass patterns were investigated along a nutrient gradient in a naturally colonizing, created freshwater marsh to determine if the mesocosm results could be used to explain patterns observed in a large-scale system.

METHODS

This research was conducted in mesocosms at the 12-ha Olentangy River Wetland Research Park (ORWRP) at the Ohio State University, Columbus, Ohio (Mitsch and Wilson, 1996; Mitsch, 1998; Mitsch *et al.*, 1998). Two mesocosm experiments were conducted to determine the effect of nutrient additions on the responses of *Typha* and *Schoenoplectus*. One experiment simulated early successional conditions with *Typha* and *Schoenoplectus* introduced at the same time (symmetric) and a separate experiment simulated *Typha* invasion of a one-year old stand of *Schoenoplectus* (asymmetric).

Soils both in the experimental wetlands and the experimental mesocosms (hearafter referred to as "site soils") were a Ross silt loam, a fine-loamy, mixed mesic Cumulic Hapludoll, characterized as well-drained and moderately permeable, with slow runoff characteristics. Ross soils in alluvial sites such as the site are here were historically subjected to frequent flooding in winter and spring; nevertheless these soils were not classified as hydric.

EXPERIMENTAL MESOCOSMS

Two sets of plastic mesocosm tubs (area = 0.9 m^2, volume = 540 liters) were sunk into the ground to avoid winter root kill and extreme soil temperatures in the summer. The tubs were equipped with a drainage system that allowed water level manipulation with stand pipes (Fig. 1). They were filled with about 8–10 cm of pea gravel followed by about 30–35 cm of site soil. To minimize the development of algae in the water column and to ensure that all available nutrients were in the soil solution, water levels were adjusted daily to

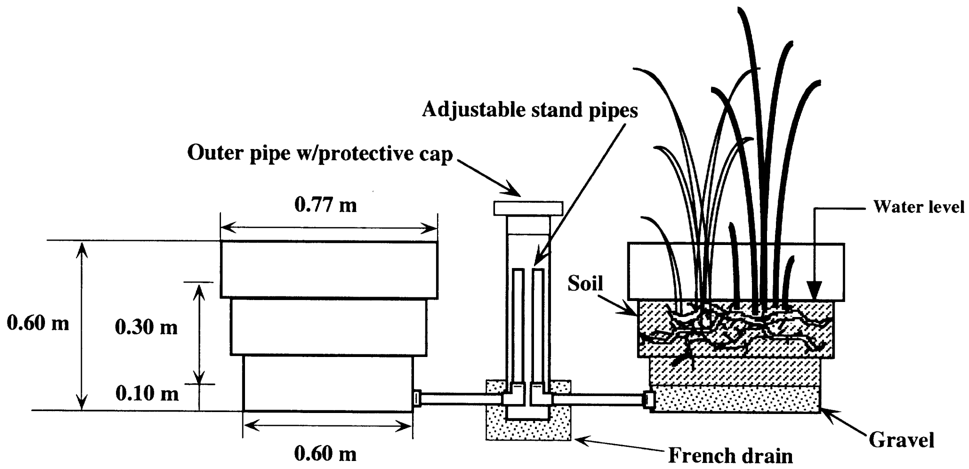


FIG. 1.—Schematic diagram of the drainage system and design of a pair of mesocosms at the ORWRP. Twenty such tubs were used in the density symmetric experiment while 10 were used in the density asymmetric experiment

maintain saturated soil conditions but little standing water. Water level was maintained by adding water pumped from an adjacent shallow groundwater well. One set of 20 mesocosms was used for the size and density symmetric study. A set of 10 mesocosms was used for the asymmetric study.

Symmetric study.—To address the question of the effects of nutrients on plant mixtures, two equal-sized rhizomes, (about 25 ± 5 g) of *Typha latifolia* and *Schoenoplectus tabernaemontani* obtained from nearby wetlands, were planted in each of 20 mesocosms in May 1996. In a completely randomized experimental design, mesocosms were selected to receive one of four treatments: nitrogen (N), phosphorus (P), nitrogen and phosphorus (N and P), or control (groundwater only). Each treatment/control was replicated five times.

Asymmetric study.—In this experiment we used 10 mesocosms that had been planted with *Schoenoplectus* rhizomes the previous year and therefore had 1 y of growth before we introduced *Typha*. Aboveground biomass of *Schoenoplectus* had been harvested at the end of the previous growing season in these 10 mesocosms and belowground parts were allowed to regenerate, leaving an extensive network of roots and rhizomes of *Schoenoplectus*. We removed two cores from the center of each of the ten *Schoenoplectus* mesocosms with a post hole digger. *Typha latifolia* rhizomes with some aboveground growth from adjacent wetlands and accompanying soil were transplanted into each hole at the beginning of the growing season to simulate vegetative invasion of *Typha* into a *Schoenoplectus* community. Five of the ten mesocosms were randomly selected to receive a daily combined N and P fertilizer solution. The remaining five mesocosms were designated as controls with no nutrient additions.

Fertilizer preparation and application.—Plants were fertilized with solutions of KNO_3 and KH_2PO_4 to ensure that potassium would not be colimiting. A loading of 0.535 g N d^{-1} and 0.180 g P d^{-1} was used to achieve an N:P ratio of 3:1 to simulate the N:P ratio of treated wastewater. Relatively high loadings of nutrients were used for two reasons: (1) to ensure that plants would not have to compete for required nutrients with microbial and chemical processes which might deplete resources (Chapin *et al.*, 1986) and (2) to simulate conditions that would be typical of a wastewater wetland. The potential effects of toxicity were considered to be minimal because both plants can withstand high concentrations of nutrients and are recommended for nutrient removal in wastewater treatment wetlands (Busnardo *et al.*, 1992; Kadlec and Knight, 1996). Fertilizer was applied daily from 9 July through 30 August 1996. Fifty-two applications were made during the experiment resulting in a total of 27.8 g N and 9.4 g P added for each N and P treatment (N:P ratio = 3:1). Control plots received only groundwater to maintain moist soil.

FIELD AND LABORATORY TECHNIQUES

Biomass of both sets of mesocosms was measured in September 1996. All aboveground stems were cut at the soil surface and sorted by species for biomass determinations. Six core samples (30 cm depth × 7.62 cm diameter) were collected from each of the symmetric mesocosms with a custom designed plant corer (description in Svengsouk, 1998). A total of 0.027 m^2 was sampled per mesocosm, only 3% of the total area. These symmetric mesocosms were then allowed to regenerate for second year measurements. Cores were rinsed with groundwater over a mesh screen to remove soil and obtain belowground biomass only. The entire belowground biomass in the 10 asymmetric mesocosms was removed and rinsed with groundwater over a mesh screen after the first growing season.

Because only a small subsample of root biomass was harvested from the symmetric mesocosms in the first year, these mesocosms were maintained for an additional growing season, but without additional fertilization, to simulate the return to natural flooding without nutrient loading. Aboveground and belowground biomass were harvested in late August of the second growing season.

Belowground and aboveground material harvested was air-dried at room temperature in paper bags and weighed. Subsamples were dried in an oven until constant mass was achieved (approximately 2 d at 80 C for aboveground material and approximately 4 d at 105 C for belowground material) to determine oven-dried/air-dried ratios. Plant nutrient analyses were performed at the Research Extension Analytical Laboratory (REAL), Ohio Agricultural Research and Development Center, Wooster, Ohio. One randomly selected representative aboveground sample for *Typha* and *Schoenoplectus* tissue was analyzed for total P and total N for each mesocosm. To ensure greater homogeneity of samples, an excess amount of plant tissue was ground with a small food processor to pass through a 2 mm sieve and a subsample of this material was placed in low-nitrogen paper and transported to REAL. Total N analysis for plant tissues used the DUMAS method (Weaver, 1994). Analysis of total P, Ca, K and Mg followed Association of Official Analytical Chemists (1990).

FULL-SCALE WETLAND STUDY

Similar measurements (aboveground biomass; nutrient analyses) of *Typha* and *Schoenoplectus* were made in an adjacent 1-ha created wetland (*see* Mitsch *et al.*, 1998) to validate mesocosm results at full scale and to determine relative success of these two species in nutrient gradients (high nutrients near inflow; low nutrients near outflow). Average decreases in nutrient water chemistry in this wetland from inflow to outflow were 64% for total phosphorus, 89% for soluble reactive phosphorus and 33% for nitrate + nitrite-nitrogen during this study (Mitsch *et al.*, 1998), illustrating a strong nutrient gradient.

Two criteria were used to select vegetation sampling locations within this wetland that had been allowed to colonize naturally since it was constructed in early 1994. The areas contained both *Typha* and *Schoenoplectus* growing adjacent and in direct contact to one another, thus ensuring the potential for competition; and water depth among all sites was similar (<2.0 cm difference). Five sampling locations from inflow to outflow were selected and distance from the inflow was measured. A 0.5 m^2 quadrat was sampled at each location. Within each sampling area, five mature shoots of *Typha* and 50 stems of *Schoenoplectus* were randomly selected for harvesting. This method was used to avoid a sampling bias for either *Typha* or *Schoenoplectus* that might occur by random placement of sampling quadrats. All stems were cut at the soil surface.

STASTICAL ANALYSES

Multiple comparisons between means were made using unpaired, independent *t*-tests, assuming unequal variances. Significant differences were determined at $\alpha = 0.05$, unless otherwise noted. Regression analyses were used for plant material to correlate oven-dry weight to air-dry weight. All statistical analyses were performed using Minitab 9.0.

RESULTS

SYMMETRIC STUDY

Biomass.—After one growing season, fertilizer additions to the symmetric mesocosms had a significant effect on production of aboveground biomass of *Typha,* but not *Schoenoplectus* (Fig. 2). Relative to the control (102 ± 20 g/m^2), mean aboveground *Typha* biomass was not different with the addition of N or P separately but was 84% higher ($P = 0.047$) with the addition of both N and P. Average belowground biomass production of *Typha* was marginally lower in the control (75 ± 24 g/m^2) than all other nutrient treatments but the differences were not significant ($P > 0.09$). *Schoenoplectus* did not show any aboveground or belowground response to any nutrient treatment.

At the end of the second growing season, during which the symmetric mesocosms did not receive any additional nutrients, the aboveground biomass of *Typha* continued to be significantly higher ($P = 0.043$) in the N and P treatment than in the control and the belowground biomass became significantly higher ($P = 0.025$) than the control (Fig. 2). A delayed response to nutrients occurred for *Schoenoplectus* with greater growth than the control for all treatments except belowground biomass in the N and P treatment.

Typha : Schoenoplectus ratios.—The ratio of *Typha*: *Schoenoplectus* (T:S) biomass was used as another measure of relative growth within given nutrient regimes. *Typha* comprised a marginally lower proportion (by weight) of the aboveground biomass than did *Schoenoplectus* in the control and in the separate N and P treatments after 1 growing season (T:S < 1; Fig. 3a). After 2 growing seasons, the ratio was even lower where *Typha* biomass was 20–40% of the *Schoenoplectus* biomass in the control and 2 separate nutrient treatments. A higher ratio of *Typha* to *Schoenoplectus* biomass was found only in the combined N and P treatment for the first growing season.

Mean T:S ratios in belowground samples were variable for both years (Fig. 3b). On average, the control and N and P mesocosms belowground cores contained *Typha* biomass that was 40–80% that of *Schoenoplectus.* The highest belowground T:S ratio (N:P = 1.09:1) resulted from fertilization with P only. During the second year, the T:S ratio was significantly greater than the control in the combined N and P treatment.

ASYMMETRIC STUDY

Biomass.—The asymmetric study involved only a control and combined N and P treatment (hereafter called the nutrient treatment) in mesocosms that had 1-y-old *Schoenoplectus. Typha,* introduced to these mesocosms, had biomass of less than 15% of the total biomass in all ten asymmetric mesocosms after one growing season (Fig. 4). Mean aboveground biomass of *Typha* was nonetheless significantly higher in the nutrient (N and P) treatment

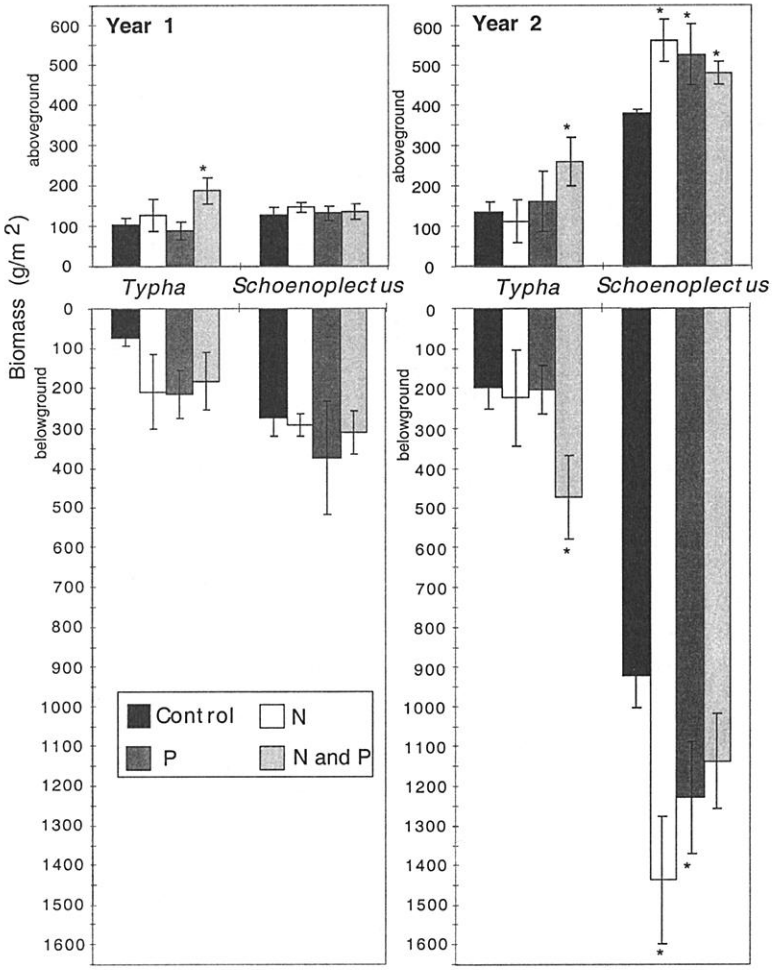
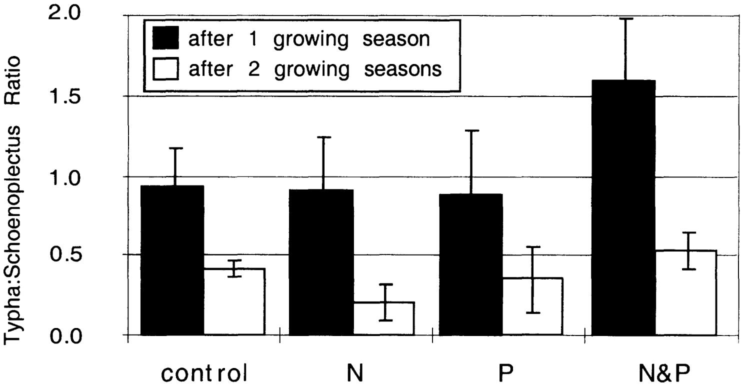


FIG. 2.—Biomass of *Typha* and *Schoenoplectus* in response to fertilization with nitrogen (N), phosphorus (P) and nitrogen + phosphours together (N and P) after one and two growing seasons in the symmetric mesocosms (mean ± SE; n = 5). * = significantly different from control ($P \leq 0.05$)

(56 ± 6.3 g/m^2) compared to the control (29.0 ± 7.7 g/m^2). Aboveground biomass of *Schoenoplectus* did not differ between nutrient treatment and control.

Despite the relatively large size of *Typha* transplants in the asymmetric mesocosms (larger rhizomes with some aboveground growth compared to leafless rhizomes in the symmetric mesocosm study) growth was greatly reduced in the more established *Schoenoplectus* stands (asymmetric study) than when both plants started equally (symmetric study). *See* Figure 2 (Year 1) compared to Figure 4. The established *Schoenoplectus* reduced *Typha* aboveground growth in low-nutrient (control) conditions by 72% (102 ± 20 g/m^2 in the symmetric study compared to 29 ± 7.7 g/m^2 in this asymmetric study). It reduced aboveground *Typha* biomass in high-nutrient mesocosms (N and P treatment) by 70% (188 ± 30 g/m^2 to 56.5 ± 6.3 g/m^2 in symmetric and asymmetric studies, respectively). The presence of mature

a) aboveground ratios



b) belowground ratios

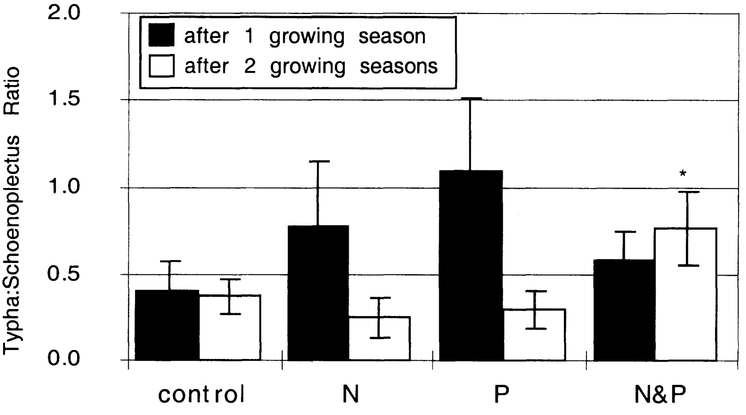


FIG. 3.—Ratio of *Typha* to *Schoenoplectus* in (a) aboveground biomass and (b) belowground biomass cores in response to fertilizer treatments in density symmetric mesocosms (mean ± SE, n = 5). * = significantly different from control ($P \leq 0.05$)

Schoenoplectus reduced the growth of *Typha* similarly in both low and high-nutrient conditions. Fertilization with nitrogen and phosphorus resulted in 17 and 10% decreases in belowground biomass for *Typha* and *Schoenoplectus*, respectively, although differences were not significant.

TISSUE NUTRIENTS AS LIMITING FACTOR INDICATORS

Tissue N:P ratios for each treatment and the control were compared to Koerselman and Meuleman's (1996) and Redfield's (1958) N:P ratios (Fig. 5). According to Koerselman and Meuleman (1996), ratios ≤14:1 indicate nitrogen limitation and ratios ≥16:1 indicate phosphorus limitation. The Redfield (1958) ratio for N:P is 7.2:1 by weight. All mean N:P ratios in the mesocosm studies were below 14:1 suggesting nitrogen limitation in all mesocosms

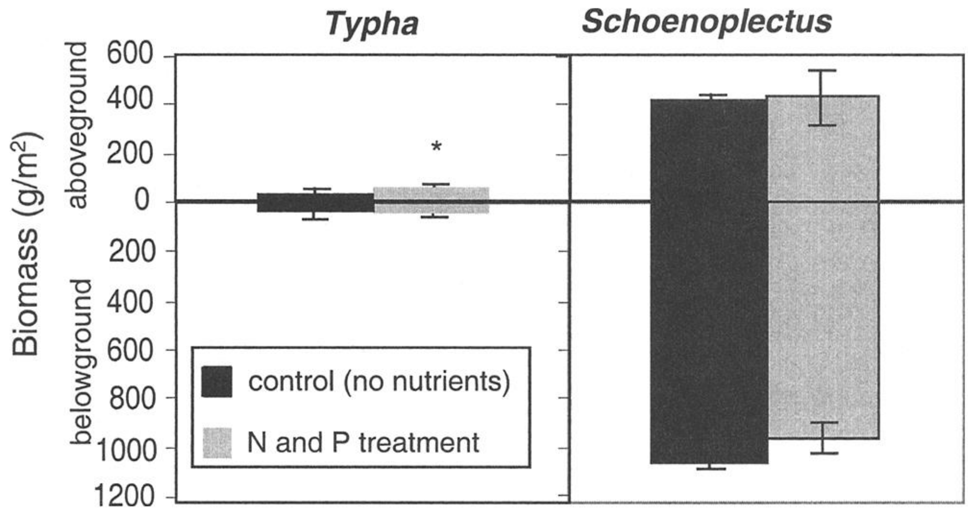


FIG. 4.—Aboveground biomass of *Typha* and *Schoenoplectus* in response to fertilization (N and P combined only) after one growing season in asymmetric mesocosms (mean ± SE; n = 4 for control, n = 5 for N and P). * = significantly different from control ($P \leq 0.05$)

according to the Koerselman and Meuleman (1996) index, even in the N and N and P treatments. In the symmetric study, N:P ratios for all *Typha* (Fig. 5a) and *Schoenoplectus* (Fig. 5b) treatments were not significantly different from Redfield's N:P ratio of 7.2:1 with the exception of the *Schoenoplectus* N and P treatment ($P < 0.01$).

Mean N:P ratio for *Typha* in the asymmetric study was lower in combined N and P treatment (5.3:1) than in the control (6.9:1) (Fig. 5c). With a N:P ratio of 5.3:1 *Typha* appeared to be limited by nitrogen using either index. Both species had N:P ratios less than 14:1 suggesting nitrogen limitation according to the Koerselman and Meuleman index (Fig. 5c, d). *Schoenoplectus* was phosphorus limited according to the Redfield ratio (Fig. 5d).

FULL-SCALE WETLAND COMPARISON

Biomass of *Typha* and *Schoenoplectus* from the naturally colonized wetland showed inverse trends along the nutrient gradient from inflow to outflow of the 1-ha naturally colonizing wetland (Fig. 6). *Typha* shoot biomass decreased with increasing distance from the inflow (and decreasing nutrients). Conversely, *Schoenoplectus* stem biomass increased with increasing distance from inflow.

N:P ratios for all locations and for both species in the wetland basin were comparable, with values ranging from 4.0:1 to 9.5:1. All values were below N:P of 14:1 (suggesting N limitation) but most were clustered around the Redfield ratio of 7.2:1. Using the Redfield ratio, plants near to the inflow (stations A and B) were nitrogen-limited (N:P < 7.2:1) while plants near the outflow (stations D and E) were phosphorus-limited (N:P > 7.2:1); but differences were slight.

DISCUSSION

PLANT DYNAMICS IN DIFFERENT NUTRIENT CONDITIONS

Results of both mesocosm studies showed that *Typha* responded to increased nutrients more than *Schoenoplectus* when both nitrogen and phosphorus were in plentiful supply.

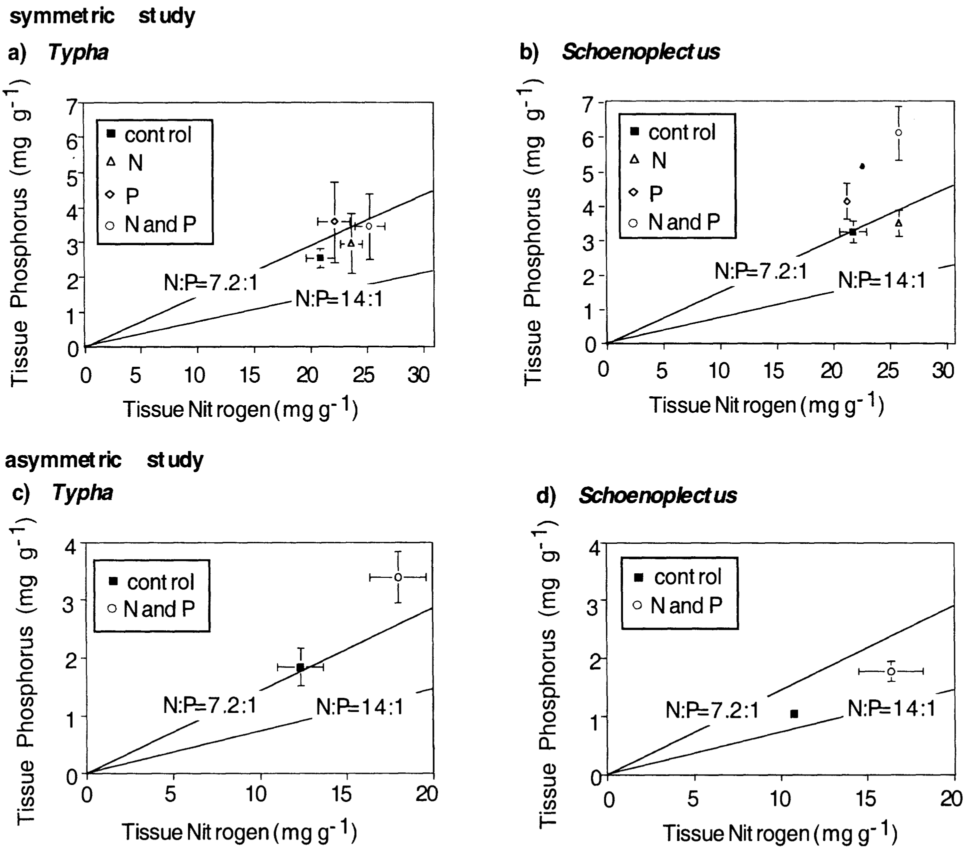


FIG. 5.—Total phosphorus concentrations versus total nitrogen concentrations in aboveground tissues of (a) *Typha* and (b) *Schoenoplectus* from symmetric mesocosm study and (c) *Typha* and (d) *Schoenoplectus* from asymmetric mesocosm study. N:P ratios of 14:1 (Koerselman and Meuleman, 1996) and 7.2:1 (Redfield, 1958) are shown for comparison and to suggest possible limitation

Schoenoplectus responded to the nutrient additions by the second year in the symmetric study when nutrient additions were relaxed, but the data clearly illustrate that this response is dampened when *Typha* growth is high. The presence of mature *Schoenoplectus* before *Typha* introduction significantly reduced growth of *Typha*, due to shading and competition for nutrients caused by the more mature *Schoenoplectus*. Sensitivity to low light levels has been reported for *Typha* (Sifton, 1959; Sharma and Gopal, 1978; Stewart *et al.*, 1997). This same effect occurred in both low- and high-nutrient conditions. This suggests that the establishment of a well-developed plant community will effectively reduce *Typha* invasion in newly created wetlands, at least for a year or two.

The ability of *Schoenoplectus* to effectively compete with *Typha* may be also a result of its root morphology. The belowground structure of *Schoenoplectus* is characterized by thick fibrous roots and a vast network of root hairs, even more dense than that of *Typha*. This type of structure is likely to facilitate nutrient uptake and storage (Berendse and Elberse, 1990; Caldwell, 1994). The increase of tissue nutrients in response to fertilization also sug-

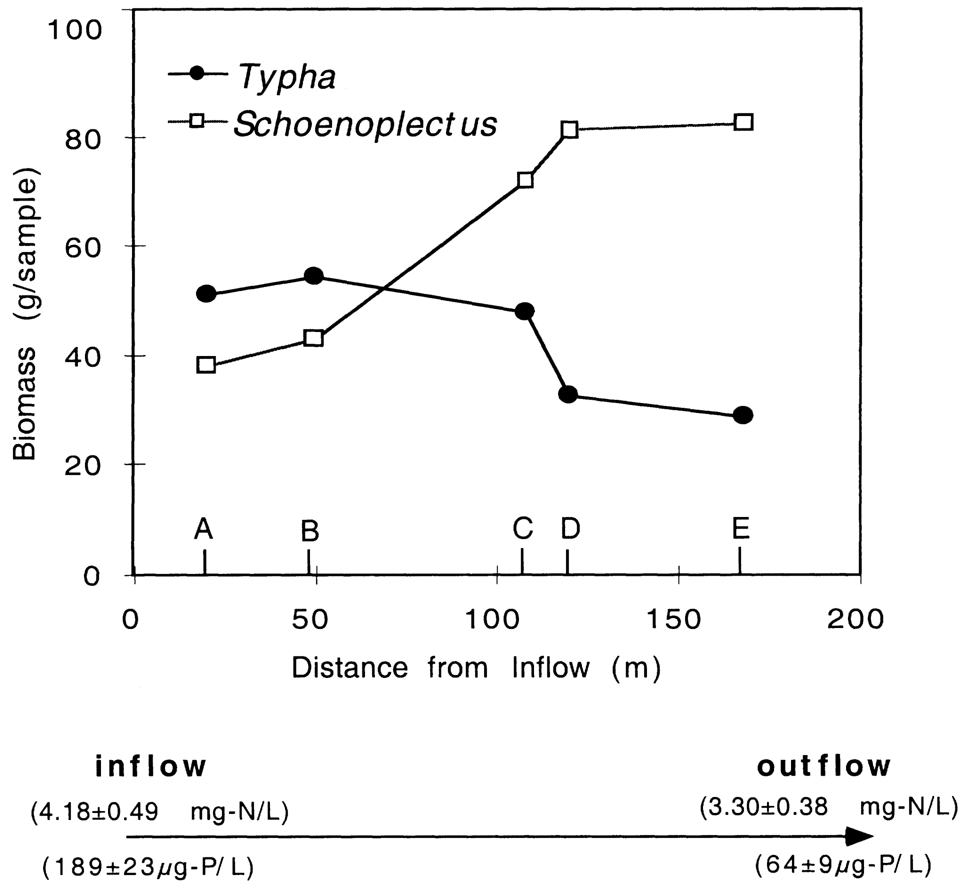


FIG. 6.—Aboveground biomass of *Typha* and *Schoenoplectus* harvested along a decreasing nutrient gradient (A–E) in ORWRP Wetland 2 (naturally colonized freshwater wetland), September 1996. Samples consisted of five mature shoots of *Typha* and 50 stems of *Schoenoplectus* randomly selected from within an area of 0.5 m^2 where the two plants were growing in proximity. Nutrient concentrations of NO_3-N and total phosphorus in water for that year shown for comparison

gests high root absorption capacity and nutrient storage. This conservative strategy may account for *Schoenoplectus'* better growth compared to *Typha,* especially in nutrient-poor conditions.

Tanner (1996) reported two distinct types of response in wetland plants treated with high concentrations of nutrients. Plants tend to either immediately increase growth to maximize productivity or, alternatively, have slower growth with nutrient accumulation. In the first case, nutrients are efficiently converted to biomass as they are available, as with *Typha.* In the latter scenario, nutrients may be stored and used to maintain growth during times of nutrient stress, as with *Schoenoplectus.*

The smaller increase in belowground biomass of *Schoenoplectus* when both nutrients were available in abundance is presumably a result of competition from *Typha.* Out study found that belowground competition did not have a large effect in the first year but that it did have an effect the second year. Early development of root systems in unvegetated soils may reflect low or no belowground competition during the establishment phase. Whigham *et al.* (1978) found an overall increase in belowground production in response to nutrient-treated plots in a freshwater wetland macrophyte community. He attributed this to an initial establishment phase in bare soils when competition for space was probably not very high.

NUTRIENT LIMITATION

The greater response of *Typha* to nitrogen and phosphorus in combination but not separately suggests that the aggressive invasion and takeover of wetlands by *Typha* require multiple nutrients. *Schoenoplectus* did better than *Typha* in all single nutrient treatments for two reasons: (1) the effects of the nutrients themselves, and (2) the lack of competition from *Typha.* Only when both nutrients were added in combination did *Schoenoplectus* decrease in productivity, not for lack of nutrients but because of competition from *Typha.* Koerselman and Meuleman's N:P ratios, on the other hand, suggested that all mesocosms were nitrogen-limited. This discrepancy may be the result of: (1) luxury uptake of phosphorus, (2) significant losses of nitrogen due to denitrification and (3) translocation of nutrients.

Nutrient concentrations of both *Typha* and *Schoenoplectus* indicate luxury uptake of phosphorus rather than nitrogen. Phosphorus concentrations in plant tissues in the P and N and P treatments increased by 28–90% relative to the control, whereas plant tissue nitrogen in the N and N and P treatments increased by only 12–18%. Low N:P ratios in plant tissues are another indication of luxury uptake of phosphorus. Koerselman and Meuleman (1996) determined that N:P ratios in plant tissues are strongly correlated with N:P supply ratio. The low ratio of N:P used in this study (N:P = 3:1) would cause low N:P ratios of plant tissues. However, luxury uptake of phosphorus may falsely suggest nitrogen limitation when another resource such as light may be limiting growth.

Denitrification is a significant pathway of nitrate-nitrogen loss in wetlands (Mitsch and Gosselink, 2000) and, thus, nitrogen may be more limiting than phosphorus for that reason alone. The rate of development of anoxic conditions in the mesocosms is unknown; however, the lack of sufficient carbon in the soil and the relatively short duration of the experiment were probably insufficient to result in significant depletion of nitrogen.

Translocation of nutrients is the most plausible explanation of low N:P ratios. Chapin and Van Cleve (1989) reported reabsorption of up to 50% of nitrogen and phosphorus from leaves before abscission. Time of harvest significantly affects aboveground nutrient concentrations. Seasonal changes are common in aboveground nutrient concentrations, where summer tissues often serve as storage organs and autumn tissues tend to have lower concentrations as a result of reabsorption to roots. Regardless of the cause of low N:P ratios, evidence of nitrogen limitation is strong because nitrogen promoted aboveground production and phosphorus alone did not.

Redfield's (1958) N:P ratio of 7.2:1 (by weight) found for most living material can be used in a similar manner as Koerselman and Meuleman's (1996) critical N:P ratios. An N:P ratio <7.2:1 implies nitrogen limitation; a ratio >7.2:1 implies phosphorus limitation. In the symmetric mesocosms none of the *Typha* N:P ratios were significantly different from 7.2:1. Only the *Schoenoplectus* N:P ratios for P ($P < 0.05$) and N and P ($P < 0.01$) treatments were less than 7.2:1. In the asymmetric mesocosms introduced *Typha* N:P ratios were either close to Redfield's ratio (control) or lower that the ratio (nutrient treatment). N:P ratios of mature *Schoenoplectus* were substantially greater than N:P of 7.2:1 (both $P < 0.05$), indicating phosphorus limitation.

These results contradict the nitrogen limitation predicted by Koerselman and Meuleman's (1996) critical N:P ratios. Based on Redfield's ratio, mature *Schoenoplectus* was nutrient-limited and higher ratios indicate phosphorus limitation. Significant response was seen with phosphorus addition in the second year of the symmetric mesocosm experiment. Interpretation based on Redfield's ratio does suggest that an important relationship exists between N:P tissue ratio and age or size of the plant community. During colonization biomass is low and relative nutrient requirements of the plant community is also low. N:P ratios are more likely to reflect luxury uptake than limitation. Established communities with substantial biomass have a greater nutritional need; thus, growth may be limited by nutrients. In this case, N:P ratios are more likely to reflect nutrient limitation since available nutrients are in short supply. This explanation would not contradict the study of Koerselman and Meuleman (1996) since they looked at mature growth in natural field conditions where N:P ratios would reflect nutrient limitation on a community level.

FULL-SCALE WETLAND PATTERNS

The trends of *Typha* biomass decreasing along the decreasing nutrients gradient and *Schoenoplectus* biomass increasing along the decreasing nutrients gradient in the full-scale wetland study suggest that *Typha* is not reaching its maximum growth potential near the outflow where nutrient availability is lower. This trend is consistent with results from the mesocosms. Larger *Typha* near the inflow may be a result of ample supply of both nitrogen and phosphorus. The larger individuals of *Schoenoplectus* near the outflow are due to less competition from the smaller *Typha* there since both phosphorus and nitrogen, particularly phosphorus, are lower there.

Typha and *Schoenoplectus* sampled from the wetland had similar N:P ratios but *Typha* consistently showed greater concentrations of nutrients in aboveground tissues. Based on Koerselman and Meuleman (1996), all N:P ratios seen here indicate nitrogen limitation (N:P < 14). However, the Redfield ratio shows that plants near the inflow are more nitrogen limited whereas plants near the middle and outflow are phosphorus limited. This is consistent with the water quality data at the site which showed an overall decrease in total phosphorus of 56–66% from inflow to outflow in the wetland while nitrate + nitrite-nitrogen decreased by only 33–49% (Mitsch *et al.*, 1998). The wetland shifts from a phosphorus- and nitrogen-rich wetland near the inflow to a phosphorus-poor wetland near the outflow. This gradient favors *Typha* near the inflow and *Schoenoplectus* near the outflow.

PREDICTING PLANT DOMINANCE

We propose a general hypothesis of the effect of nutrients and successional stage on *Typha* and *Schoenoplectus* dynamics (Fig. 7). During first-year establishment under low-nutrient conditions, even-aged *Typha* and *Schoenoplectus* are approximately equal in aboveground production (Fig. 7a). Growth is symmetrical. Development of *Typha* and *Schoenoplectus* in the low-nutrient symmetric mesocosms (controls) more closely resembled this development. The development of the macrophyte community in the full-scale river-fed wetland is also similar to this situation. *Typha* was first observed in this wetland during the first growing season before establishment of *Schoenoplectus.* By the second growing season Schoenoplectus individuals outnumbered *Typha* individuals in this naturally colonizing wetland (Weihe and Mitsch, 1996). *Typha* and *Schoenoplectus* were in a tenuous balance by the third year (same year of this field study; Liptak *et al.*, 1997), with *Typha* dominating where both phosphorus and nitrogen are adequate but deferring to *Schoenoplectus* where there is less phosphorus.

When nutrients are added to wetlands, such as wastewater wetlands used for tertiary treatment, *Typha* is able to reach its maximum growth potential and outproduce most

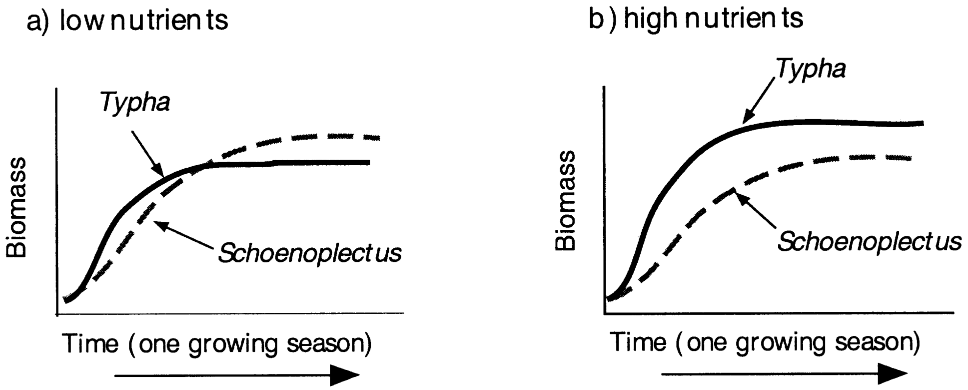


FIG. 7.—Hypotheses of *Typha* and *Schoenoplectus* growth dynamics during early colonization for a) low-nutrient and b) high-nutrient conditions in one growing season

competitors quickly (Fig. 7b). Wastewater wetlands receiving high concentrations of nutrients are usually dominated by *Typha* and similar clonal dominants, despite efforts my managers to establish diverse macrophyte communities (Kadlec and Knight, 1996; Mitsch and Gosselink, 2000). These diversification efforts generally fail and *Typha* invariably dominates after several years. More moderate conditions near wastewater wetland outflows are sometimes more acceptable for other species, and these areas are where a high planting density of good competitors such as *Schoenoplectus* may reduce complete dominance by *Typha.*

TYPHA INVASION IN NATURAL WETLANDS

Patterns of *Typha* invasion in more mature stands of *Schoenoplectus* or similar "more desirable" species is complicated, depending on the level of nutrients. Newly colonizing *Typha* is inhibited by previously existing dominants in low-nutrient conditions. Competition for resources is keen and *Typha* invasion is checked as it is unable to reach its maximum potential growth. In high-nutrient conditions, the advantage held by established plant communities over colonizing *Typha* is lost.

Wetland vegetation is rarely isolated from major changes, whether the changes are due to water level changes, grazing or other impacts. Muskrat (*Ondatra zibethicus*) "eat-outs" are a common feature of freshwater marshes as is overgrazing by geese (*e.g., Branta canadensis* or *Chen caerulescens*). Muskrats preferentially graze on *Typha* and *Schoenoplectus* for food and housing material and can defoliate large areas of these macrophytes in a relatively short time. In effect, this kind of grazing results in a wetland version of gap formation. Where plants such as *Schoenoplectus* dominate, *Typha* can come in and compete with other plants for space and light. Gap formation has the effect of reverting to an earlier stage of successional development. *Typha* and *Schoenoplectus* then compete on symmetrical terms and patterns similar to the conditions and *Schoenoplectus* can make a rapid recovery because of its ability to regenerate from an existing, large, belowground, root-mass in low-nutrient wetlands where *Typha* is still limited by nutrients. In a high-nutrient system with a gap formation, relative growth rates allow *Typha* to quickly outproduce *Schoenoplectus.* This pattern of *Typha* domination in high-nutrient wetlands is common, even with initial planting of other species. Herbivores, as gap developers, are major contributors to the successional processes.

MANAGEMENT IMPLICATIONS

Wetland managers with an interest in creating or maintaining a diverse plant community use planting as a technique to achieve rapid and dense vegetative growth. For wetlands that receive low concentrations of nutrients, this may be an effective strategy to slow the invasion of *Typha*. Areas that are known to receive high nutrients could also be planted in hopes of delaying *Typha* invasion but even slight disturbances will open niches for *Typha* to take over. Muskrats or geese, invariably attracted to the wetland because of the vegetation, will create gaps in early vegetation that lead to an increase of *Typha* in subsequent growing seasons. The idea of planting in newly created wetlands to prevent invasive species from "taking over" is consistent with the concept of "self-design" (Mitsch and Wilson, 1996; Mitsch *et al.*, 1988). Maximizing the number of taxa and the amount of propagules through natural and human means to these created ecosystems will give selection processes more choices and will, in principle, lead to a more stable wetland ecosystem. However, high nutrient conditions reduce the competitiveness of most species relative to a clonal dominant like *Typha*.

Another practical application of our findings relates to the major efforts currently underway to control the spread of *Typha* in the Florida Everglades (Gunderson and Loftus, 1993; Newman *et al.*, 1996; Wu *et al.*, 1997). Major efforts are being made to control phosphorus with the expected outcome that control of only this nutrient will control the spread of *Typha*. Our results generally support this contention that reducing phosphorus will reduce the spread of *Typha*. However, our results also suggest that control of nitrogen as well might also be necessary to reduce invasive *Typha*. Using buffer wetlands that remove both nutrients is therefore a solution to the Everglades *Typha* invasion that makes ecological sense. Using chemical and physical treatment approaches designed to remove only phosphorus, as are now being discussed, would be less effective.

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