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Effects of nutrient and soil moisture on competition between *Carex stricta, Phalaris arundinacea,* and *Typha latifolia*

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Abstract

We investigated the importance of nutrients, soil moisture, arbuscular mycorrhizal fungi (AMF), and interspecific competition levels on the biomass allocation patterns of three wetland perennial plant species, *Carex stricta* Lam., *Phalaris arundinacea* L., and *Typha latifolia* L. A factorial experiment was conducted with high-low nutrient levels, high-low soil moisture levels, and with and without AMF inoculation. Under the experimental conditions, plant inoculation by AMF was too low to create a treatment and the AMF treatment was dropped from the total analysis. *P. arundinacea* and *T. latifolia* biomass were 73% and 77% higher, respectively, in the high nutrient treatment compared to the low nutrient treatment. Biomass allocation between shoots and roots remained relatively constant between environmental treatments, although shoot:root ratios of *P. arundinacea* declined in the low nutrient treatment. For *C. stricta*, the high nutrient and soil moisture treatments resulted in an increase in biomass of 50% and 15%, respectively. Shoot:root ratios were nearly constant among all environmental conditions. Biomass of *T. latifolia* and *C. stricta* was greatly decreased when grown with *P. arundinacea*. The rapid, initial height growth of *P. arundinacea* produced a spreading, horizontal canopy that overshadowed the vertical leaves of *T. latifolia* and *C. stricta* throughout the study. This pattern was repeated in both high and low nutrient and soil moisture treatments. When grown with *P. arundinacea*, *C. stricta* and *T. latifolia* significantly increased their mean shoot height, regardless of the nutrient or soil moisture level. The results of this experiment suggest that *C. stricta* and *T. latifolia* were light limited when growing with *P. arundinacea* and that canopy architecture is more important for biomass allocation than the other environmental conditions tested. The results also suggest that *Phalaris arundinacea* is an inherently better competitor (*sensu* Grime 1979) than *C. stricta* or *T. latifolia*.

Introduction

Individual plant resources are often limited, forcing a tradeoff of resources that can be allocated to growth, reproduction, and maintenance (Harper 1977; Wilson 1988). Among plant species, growth and biomass allocation patterns are influenced by environmental factors, different life-history strategies, and the presence of competitors, or a combination of these factors (Carter and Grace 1990; Wilson and Keddy 1986). For example, the shoot:root ratio was higher for an annual forb, particularly when grown at a high nutrient level, when compared to that of a perennial grass, but the greater investment in shoot biomass reduced the annual's ability to survive inundation (Figiel et al. 1995). Plants growing along hydrologic gradients have also been found to adjust their biomass allocation and distribution in response to interspecific competition (Carter and Grace 1990; Grace and Wetzel 1982).

Within native and restored sedge meadow wetland communities in the American Midwest, severe competition from *Phalaris arundinacea* L. and *Typha* spp. can result in the displacement of characteristic wet meadow species such as *Carex stricta* Lam. (Reinartz & Warne 1993; Galatowitsch & van der Valk 1995). Both *P. arundinacea* and *Typha latifolia* L. have growth forms that maximize the capture of available resources in productive environments and

are considered to be exploiters (Grace 1989) or competitively selected (C-selected) species, *sensu* Grime (1979). *C. stricta* is moderately productive and can tolerate low intensity stress and would be classified as a stress tolerant competitor (Grime 1979).

Arbuscular mycorrhizal fungal (AMF) colonization has been observed in the field for all the plants used in this study. AMF colonization of *P. arundinacea* averaged 34% (SEM = 8%) and *T. latifolia* averaged 18% (SEM = 8%) (Wetzel and van der Valk, unpublished data). Stenlund and Charvat (1994) also report an average colonization of 13% on *T. latifolia* floating mats growing in Minnesota. Although members of the Cyperaceae generally have been considered non-mycorrhizal or rarely mycorrhizal (Gerdemann 1968; Powell 1975; Anderson et al. 1984), *Carex stricta* had 6–22% AMF colonization in natural prairie wetlands (Wetzel & van der Valk 1996). An AMF treatment was included in this experiment to be sure that the absence of AMF would not invalidate the results of the nutrient treatment, especially the low nutrient treatment.

Ultimately, biomass allocation patterns of all species found along an environmental gradient determines the distribution and abundance of individual species along these gradients; in other words, the composition of the plant community found at any point along the gradient. The objective of the experiment was to investigate the importance of nutrient, soil moisture, arbuscular mycorrhizal fungi (AMF), and interspecific competition levels on the biomass allocation patterns of three wetland perennial plant species, *C. stricta*, *P. arundinacea*, and *T. latifolia*. Specifically, we were interested if it was possible to significantly change the composition of the vegetation under different environmental conditions. This experiment is a test of Grime's (1979) hypothesis that a competitive species will produce more biomass than a less competitive species, regardless of environmental conditions.

Plant descriptions

The wetland species *C. stricta*, *P. arundinacea*, and *T. latifolia* grow together and have similar life histories. *Carex stricta* Lam. is a perennial, with culms ranging from 5–8 mm wide and 40–60 cm tall. It produces both long and short lateral rhizomes (15–25 cm in length), causing formation of a tiller clump (Bernard 1990). Vertical growth in the tiller clump can be rapid, forming tussocks. Tiller clumps are an important functional unit, preventing colonization of a site from other species and providing an extended root system for the tiller clump and colonizing shoots (Bernard 1990).

Phalaris arundinacea L., reed canary grass, is a perennial grass originating from creeping rhizomes, with culms ranging from 60–150 cm tall. *P. arundinacea* tolerates short periods of flooding, growing in the low prairie and wet meadow zones of wetlands, along streambanks, and in lowland areas. This aggressive, cool season grass grows throughout the northern hemisphere and is commonly planted for hay and erosion control (Hitchcock 1950).

Typha latifolia L., common cattail, is a rhizomatous perennial, ranging in height from 120–230 cm, and produces extensive lateral rhizomes, up to 70 cm in length. *T. latifolia* grows in wet or saturated soils in wet meadows, shallow emergent zones, along lakeshores, and in roadside ditches throughout North America, from central Alaska to Mexico (Grace and Harrison 1986). Although native to North America, the rapid clonal growth of *T. latifolia*, particularly in disturbed, high nutrient environments, has transformed entire wetlands into monotypic cattail stands, classifying *T. latifolia* as a serious aquatic weed (Grace and Harrison 1986).

Methods

Experimental design

A common sedge meadow plant, *C. stricta*, and two invasive sedge meadow species, *P. arundinacea* and *T. latifolia*, were grown in a factorial experiment with four treatments: high-low nutrient levels, high-low soil moisture, with-without arbuscular mycorrhizal fungal (AMF) inoculation, and inter- or intraspecific competition. A randomized block design was used with each treatment replicated three times. The overall experimental design involved two nutrient treatments (40:60 and 90:10 sand:wetland soil) × two water treatments (0.5 l and 1.0 l every two days) × two mycorrhizal treatments (+/− AMF) × six competition treatments (*C. stricta* with *P. arundinacea*, *C. stricta* with *T. latifolia*, *P. arundinacea* with *T. latifolia* and only *C. stricta*, *P. arundinacea*, or *T. latifolia*) × three replicates for a total of 144 trays.

The high nutrient treatment consisted of a 40:60 mixture of sand:wetland soil, organic matter, 2.9%; available phosphorus, 20 mg/g; potassium, 120 mg/g; nitrate, 7 mg/g (Iowa State University Soil Testing

Laboratory). The low nutrient treatment was a 90:10 mixture of sand:wetland soil with an organic matter, 0.5%; available phosphorus, 5 mg/g; potassium, 30 mg/g; nitrate, 2 mg/g. The wetland soil used in this study, Webster clay loam, was obtained from a prairie pothole wetland in Story County, Iowa. The soil mixtures were steamed for 2 hours to sterilize them.

Seeds of all three species were washed with a 0.5% NaOCl solution and rinsed three times with distilled water. *C. stricta* and *P. arundinacea* seeds were spread into petri dishes containing a filter paper disk on the bottom, stratified at 4 °C for 48 hours, and then placed in a greenhouse to germinate. Seedlings were transplanted to community trays filled with sterilized potting soil (peat moss and perlite) when they were 2 cm tall. *T. latifolia* seeds were mixed directly with sterilized potting soil, stratified at 4 °C for 48 hours and placed in the greenhouse to germinate.

After two weeks, seedlings were transplanted to deep trays (32 × 28.5 × 17.8 cm) filled with approximately 0.012 m^3 of steamed soil (19.4 kg dry soil of the 90:10 mixture and 13.6 kg dry soil of the 40:60 mixture). Drainage holes in the bottom of the trays were covered with fiberglass mesh (1 mm) to prevent soil loss. Six plants were planted in two rows of three in each tray. The same arrangement was used in the competition treatments, where three individuals of each species were planted in positions alternating with each other. The few seedlings that died were replaced with same age seedlings only during the first four weeks after the initial planting. The greenhouse temperature ranged from 18 to 30 °C, and plants were grown under high intensity lights (average sunny day photosynthetically active radiation, 420 mmol m^{-2} s^{-1}) with a 14-hour photoperiod.

All plants were grown for six weeks in trays before the soil moisture treatments were begun. The low soil moisture trays received 0.5 l of water every four days for the first two weeks then 0.5 l every two days for the remainder of the experiment. Trays in the high soil moisture treatment received 1.0 l of water every two days. The experiment ran eight weeks from the start of water treatments.

Treatments with arbuscular mycorrhizal fungi (AMF) were inoculated with spores of *Glomus intraradices* (Schenck & Smith) and *Glomus claroideum* (Schenck & Smith) (courtesy of B. Hetrick, University of Northern Iowa), two species found in prairie pothole wetlands in Iowa (Wetzel & van der Valk 1996). Spores of each fungal species were suspended in water, and approximately 40 spores of both species were pipetted into a small depression in the soil immediately prior to planting a seedling. A total of approximately 480 fungal spores was added to each tray in the plus AMF treatments.

Data collection

After seedlings were transplanted to trays, height of the longest green leaf and the total number of leaves for the experimental plants were measured each week for six weeks and then biweekly until the end of the experiment. Above and below-ground biomass was harvested, oven dried for 3–5 days at 65 °C to minimize nitrogen loss (Chapin & Van Cleve 1989), and weighed. Above-ground biomass of each species in the entire tray was ground with a Wiley mill to a 0.5-mm (#40) mesh size. Percent foliar total nitrogen and carbon were determined on each treatment replicate with a Carlo-Erba NA 1500 Carbon-Nitrogen-Sulphur analyzer. Total foliar phosphorus was measured with a sodium hypobromite oxidation extraction and colorimetric determination using a heteropoly blue method (Dick & Tabatabai 1982).

Percent AMF colonization was measured to establish the extent of colonization in each treatment. After drying, an arbitrary sample of secondary roots with attached tertiary roots from each tray was stained to detect AMF, following the procedure of Koske and Gemma (1989). The roots were autoclaved in a 2.5% KOH solution for 3 minutes and then bleached by soaking 10–30 min in a 1% hydrogen peroxide solution. After rinsing with water, the roots were autoclaved in 0.05% acid fuchsin in acidic glycerol solution for 3 min and then destained at room temperature. Percent AMF colonization was determined with the magnified intersections method described by McGonigle et al. (1990). Root segments were placed on a glass slide and viewed at 200× magnification. The presence or absence of mycelium, vesicles, arbuscules, or spores was recorded for 100 root-microscope cross hair intersections, providing percentage of roots colonized with AMF for each tray.

The relative growth rate (RGR) of each plant species in each treatment was calculated as:

$$\mathrm{RGR} = [\ln(M_2/M_1)]/t_2 - t_1,$$

where M_1 is initial biomass, M_2 is final biomass, and $t_2 - t_1$ is the length of the growth period in days (Harper 1977). The RGR was calculated for the

last twelve weeks (87 days) of the experiment. Regression relationships between plant height and dry above-ground biomass of control plants were used to determine the initial biomass of the plants of each species. Control plants of each species were grown under the same light and temperature conditions in the greenhouse as the experimental plants. These plants were grown in trays containing a 40:60 sand:soil mixture, with six individuals per tray, and were watered to saturation regularly. Plant height and biomass were measured biweekly by harvesting one tray of each species. The regression equation for each species was:

Carex stricta

$$\ln(\text{ABIO} = \ln(\text{HT}) * 2.607 - 10.863,$$

$$r^2 = 0.74,$$

Phalaris arundinacea

$$\text{ABIO} = \text{HT} * 0.0896 - 2.964,$$

$$r^2 = 0.52,$$

Typha latifolia

$$\ln(\text{ABIO}) = \ln(\text{HT}) * 2.514 - 10.233,$$

$$r^2 = 0.87,$$

where ABIO = above-ground biomass and HT = length of longest leaf.

The competitive effects of *T. latifolia* and *P. arundinacea* were examined by calculating the relative yield of individuals of a species when grown with another species (interspecific competition) compared to the relative yield of the species grown alone (intraspecific competition) while maintaining the same overall density. Relative Yield (RY) was calculated as

$$\text{RY} = Y_{ij}/Y_i,$$

where Y_{ij} is the mean biomass yield of individuals of species i grown with individuals of species j and Y_i is the mean biomass yield of individuals of species i grown alone (Harper 1977). A RY value less than one indicated that interspecific competition exerted a greater influence on plant biomass than intraspecific competition.

Statistical analysis

Analysis of variance was performed on total root, mycelium, vesicle, and spore AMF colonization and the relative yield for each plant species. Only the main treatment effects (block, nutrient level, water level, AMF inoculation, and competition) and the first order interactions were included in the analysis of variance models. All proportional data were arcsine square root transformed to reduce heteroscedasticity and improve normality.

To determine the relative importance of competition to each species in different environmental conditions, a principal components analysis was conducted on six measured variables: above- and below-ground biomass, relative growth rate, percent total foliar nitrogen, percent foliar carbon, and total foliar phosphorus for each plant species. The object of principal components analysis is to find linear combinations of the variables that explain the largest amount of variance. The combinations or principal components are by definition independent (orthogonal) of each other (Manly 1994). The sum of the variances of the principal components is equal to the sum of the variances of the original variables. To prevent one variable from unduly influencing the principal components, the data were normalized to have means of zero and variances of one (Manly 1994). Because the normalized data began with a variance of one, a principal component with an eigenvalue less than one explains less variance than the original data and was not used in further analyses. Analysis of variance by the same models described above was performed on the principal components with an eigenvalue of one or greater. The proportion of variance described by the model was calculated and plotted for all statistically significant main treatment effects and first order interactions.

Results

Total AMF colonization ranged from 0–25% in *C. stricta*, 0–15% in *P. arundinacea*, and 0–14% for *T. latifolia* across all treatments. However, 44% of the plus AMF treated trays had 1% AMF colonization or less. AMF colonization was not different between mycorrhizal and non-mycorrhizal treatments for *C. stricta* and *T. latifolia* ($p = 0.56$ and $p = 0.61$, respectively), but was significant for *P. arundinacea* ($p = 0.05$). Successful plant inoculation by AMF was too low to be meaningful and the AMF treatment was dropped from further analysis.

Principal components analysis

The first principal component of each plant species accounted for variation (loadings) from above-ground,

below-ground, and relative growth rate factors, all representing a measure of plant productivity (Table 1). The productivity component explained 38% of the experimental variation of the *C. stricta* data, 49% for *P. arundinacea*, and 41% for *T. latifolia* (Table 1). As expected, the above-ground, below-ground, and relative growth rate factors within each plant species were positively correlated with each other.

The second principal component of each plant species contained high loadings of two macronutrients, total foliar nitrogen, and phosphorus (Table 1). The macronutrient component of *C. stricta* also included a total carbon loading and explained 29% of the experimental variation. The macronutrient component of *P. arundinacea* explained 18% of the variation. For *T. latifolia*, the macronutrient component explained 26% of the variation (Table 1). Total foliar nitrogen and phosphorus were positively correlated with each other in all plant species.

Treatment effects on plant productivity and macronutrient concentration

The proportion of the variance attributable to each treatment was calculated to estimate the effect that a treatment or treatment interaction had on each plant species (Figure 1). Nutrient level, soil moisture level, interspecific competition, and the nutrient $\times$ competition interaction all had statistically significant effects on the productivity of *C. stricta* (Table 2, Figure 1). For *C. stricta*, interspecific competition explained the largest amount of variation (21%) on the productivity and macronutrient uptake (Figure 1). When interspecific competition was present, productivity of *C. stricta* declined as nutrient levels increased. Nutrient level and the nutrient $\times$ interspecific competition interaction also had statistically significant effects on macronutrient uptake (Table 2). Macronutrient uptake increased as nutrients increased when interspecific competition was present. Conversely, macronutrient uptake was higher at the low nutrient level without interspecific competition. *C. stricta* had greater nutrient concentration under stressful conditions (low nutrient or interspecific competition).

Nutrient level had the most impact on *P. arundinacea* (46% of the variation). This accounted for more than twice the amount of variation in its productivity and macronutrient concentration when compared to *T. latifolia* and three times that when compared to *C. stricta* (Figure 1). Biomass in the low nutrient treatment was 73% lower than in the high nutrient treatment (Figure 2). Except for a small impact of soil moisture on macronutrient concentration (Table 2), none of the other experimental treatments or main interactions had an impact on the productivity or macronutrient concentration of *P. arundinacea*.

Nearly 23% of the variation in productivity and nutrient acquisition of *T. latifolia* was attributable to interspecific competition, followed by nutrient level (18%) and a nutrient x competition interaction (13%) (Figure 1). Productivity and macronutrient uptake increased as nutrients increased when interspecific competition was present. The soil moisture treatment and interactions with nutrient level had a significant effect on productivity. The soil moisture $\times$ interspecific competition interaction had a significant effect on nutrient acquisition (Table 2).

P. arundinacea culms were taller than *C. stricta* or *T. latifolia* culms in all treatments, although *T. latifolia* was $\leq$ 10 cm shorter than *P. arundinacea* by the end of the experiment (Figure 3). Nutrient, soil moisture, or interspecific competition did not affect the height of *P. arundinacea*. Low nutrient levels reduced the height of *C. stricta* growing with *P. arundinacea*, but height was not affected in the soil moisture treatment. Plant heights of all species were nearly equal until week four, after which *P. arundinacea* grew faster than *C. stricta* or *T. latifolia* (Figure 3).

Leaf production patterns followed height patterns, except that the low nutrient level reduced *P. arundinacea* leaf production by 50%. Nutrient and soil moisture levels had little effect on leaf production of *C. stricta* or *T. latifolia* (Figure 3). After week five, *P. arundinacea* began producing many more leaves than *C. stricta* or *T. latifolia* in all treatment conditions.

Treatment effects on shoot:root ratios

In general, the pattern of biomass allocation was similar between environmental treatments for all plant species (Figure 2). *C. stricta* allocated greater biomass to root than shoot production, but the proportion of shoot:root allocation was the same with different competitors and over all environmental treatments, even though biomass yield was greatly affected by the treatments (Figure 2). Shoot production increased when growing with *P. arundinacea*, and resources were nearly equally allocated between shoots and roots in the high soil moisture treatment.

P. arundinacea shoot:root ratios were constant between competition treatments under all environmental conditions (Figure 2). Biomass resources were allo-

Table 1. Loading factors contributing to the principal components of *C. stricta*, *P. arundinacea*, and *T. latifolia*. The first principal component consisted of two productivity variables, biomass and relative growth rate. The second principal component consisted of two macronutrient variables, nitrogen and phosphorus.

	Variables	Principal component I (productivity)	Principal component II (macronutrients)
Carex stricta	Above-ground biomass	0.63	0.05
	Below-ground biomass	0.62	0.00
	Relative growth rate	0.45	0.08
	Total nitrogen	−0.03	0.57
	Total carbon	−0.14	0.52
	Total phosphorus	0.02	0.63
Eigenvalue		2.30	1.73
% eigenvalues		0.38	0.29
Cumulative % eigenvalues		0.38	0.67
Phalaris arundinacea	Above-ground biomass	0.55	−0.14
	Below-ground biomass	0.52	−0.21
	Relative growth rate	0.51	−0.11
	Total nitrogen	0.20	0.57
	Total carbon	0.34	0.20
	Total phosphorus	0.08	0.75
Eigenvalue		2.91	1.10
% eigenvalues		0.49	0.18
Cumulative % eigenvalues		0.49	0.67
Typha latifolia	Above-ground biomass	0.57	0.34
	Below-ground biomass	0.56	0.31
	Relative growth rate	0.47	−0.25
	Total nitrogen	−0.17	0.56
	Total carbon	0.28	−0.10
	Total phosphorus	−0.20	0.64
Eigenvalue		2.44	1.54
% eigenvalues		0.41	0.26
Cumulative % eigenvalues		0.41	0.67

cated equally between shoots and roots in the high nutrient treatment, even with a 73% increase in biomass production (Figure 2). Root production increased in the low nutrient treatment and remained constant between the soil moisture treatments.

T. latifolia consistently allocated equal or greater biomass resources to shoot production in all treatments (Figure 2). This allocation was greatest when competing with *P. arundinacea*, despite the fact that very little biomass per plant was produced (Figure 2). When growing with *C. stricta* or by themselves, biomass allocation to the shoots was greater in the low nutrient than the high nutrient treatments.

Treatment effects on interspecific competition

Competition with *P. arundinacea* had a greater influence on above- and below-ground relative yield (RY) of *C. stricta* than competition with *T. latifolia*. The above- and below-ground RY values were less than one, which indicated that interspecific competition was greater than intraspecific competition (Figure 4). This pattern was true in all the experimental treatments, but there were no statistically significant differences in RY among treatments (Figure 4). When *C. stricta* and *T. latifolia* were grown together, above- and below-ground RY values were near or slightly below one. Relative yield values were not statisti-

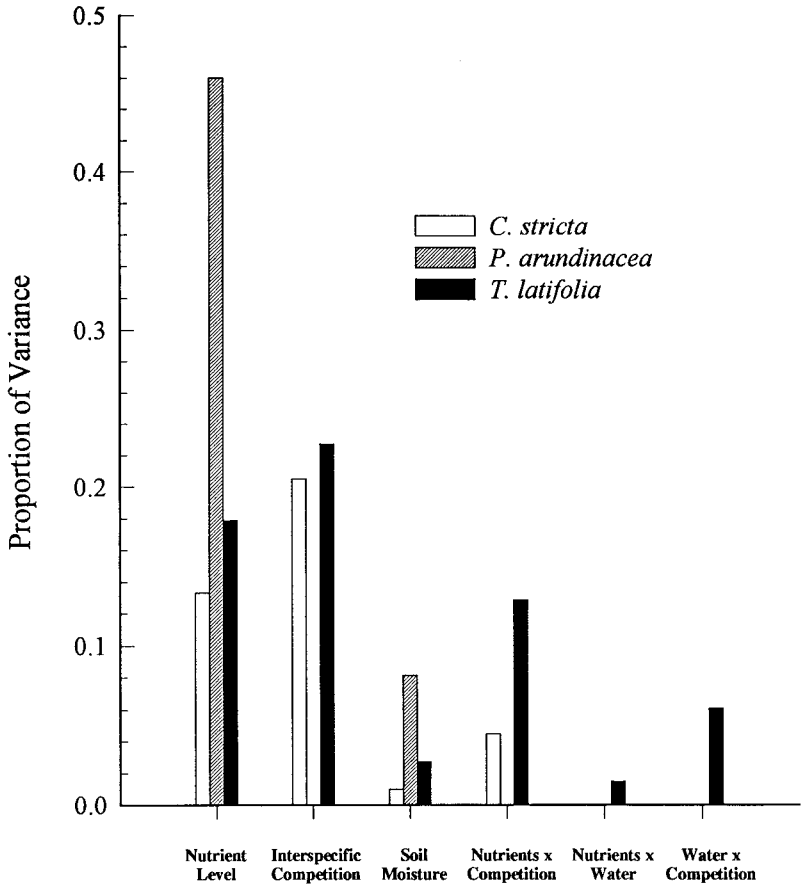

Figure 1. Proportion of variation explained by the productivity and foliar macronutrient concentration principal components for all three experimental plants, *C. stricta*, *P. arundinacea*, and *T. latifolia*. All factors and interactions plotted are statistically significant ($p \leq 0.05$).

cally different for any of the treatment combinations (Figure 4).

Discussion

The abundance of species in plant communities is a function of both environmental factors and interspecific competition. Nutrient levels and interspecific competition were the most important factors affecting biomass allocation patterns of the three wetland species, *C. stricta*, *P. arundinacea*, and *T. latifolia* in this study. AMF and soil moisture levels were the least important factors tested. The results of our test of the hypothesis that species with competitor characteristics (*sensu* Grime, 1979) produce more biomass than less competitive species regardless of environmental conditions was true for *P. arundinacea*, but not for *T. latifolia*.

Nutrient level was the environmental factor with the greatest impact on biomass for all three species tested. The biomass of the competitor species in this study, *P. arundinacea* and *T. latifolia*, increased 73% and 77% respectively in the high nutrient treatment compared to the low nutrient treatment. The increase in *P. arundinacea* biomass in high nutrient environments agrees with Figiel et al. (1995), in which *P. arundinacea* biomass increased 71–83% in the high nutrient compared to the low nutrient environment across four different soil moisture levels. High nutrient levels increased *C. stricta* biomass by 50%, but *C. stricta* consistently invested greater biomass resources into root production, regardless of the nutrient level. Aerts et al. (1992) also measured greater root investment at high and low nutrient levels in four *Carex* spp.

In this experiment, the biomass of *T. latifolia* and *C. stricta* was greatly decreased by competition with

Table 2. Analysis of variance of the principal components productivity (Principal Component I) and foliar macronutrients (Principal Component II) for *Carex stricta*, *Phalaris arundinacea*, and *Typha latifolia*. Nut. = nutrient level.

	Source of pariation		Productivity (principal component I)	Macronutrients (principal component II)
Carex stricta	Block	2	0.208	0.000
	Nutrient	1	0.000	0.033
	Soil moisture	1	0.005	0.814
	Competition	2	0.000	0.947
	Nut. × Soil moisture	1	0.375	0.163
	Nut. × Competition	2	0.000	0.030
	Soil moisture × competition	2	0.495	0.065
	Error	57		
Phalaris arundinacea	Block	2	0.003	0.096
	Nutrient	1	0.000	0.753
	Soil moisture	1	0.077	0.004
	Competition	2	0.928	0.429
	Nut. × water	1	0.811	0.641
	Nut. × competition	2	0.285	0.801
	Soil moisture × competition	2	0.094	0.692
	Error	55		
Typha latifolia	Block	2	0.100	0.056
	Nutrient	1	0.000	0.000
	Soil moisture	1	0.000	0.342
	Competition	2	0.000	0.021
	Nut. × water	1	0.005	0.103
	Nut. × competition	2	0.000	0.001
	Soil moisture × competition	2	0.431	0.000
	Error	55		

P. arundinacea. The initial and persistent height advantage of *P. arundinacea* resulted in the other two species growing in its shade in all nutrient and soil moisture treatments. A similar temporal competitive advantage has been observed in other wetland perennials. For example, *Glyceria* was competitively superior to *Phragmites* because of rapid early growth and the creation of a thick vegetative cover before the appearance of *Phragmites* shoots (Buttery and Lambert 1965).

However, rapid growth was not the only factor that allowed *P. arundinacea* to outcompete *T. latifolia* and *C. stricta*. Our results suggest that plant architecture played a significant role. Grime and Hodgson (1987) listed characteristics of species with high competitive ability: (1) a robust perennial life form with a strong capacity to ramify vegetatively, (2) the rapid commitment of captured resources to the construction of new leaves and roots, (3) high morphological plasticity during the differentiation of leaves and roots, and (4) short life spans of individual leaves and roots. Both *P. arundinacea* and *T. latifolia* are robust perennials, that rapidly produce ramets, have a tall stature, and high growth rates. In addition, *T. latifolia* produces large storage rhizomes and high growth rates have been measured (McNaughton and Fullem 1970). Leaf biomass is plastic and may be allocated to improve the efficiency of light utilization over a range of intensities (Grace and Wetzel 1981). Therefore, it was surprising that *T. latifolia* competed so poorly when growing with *P. arundinacea*. However, the leaves of *T. latifolia*, as well as those of *C. stricta*, are vertically oriented, compared to the horizontally oriented leaves of *P. arundinacea*. The response of both *C. stricta* and

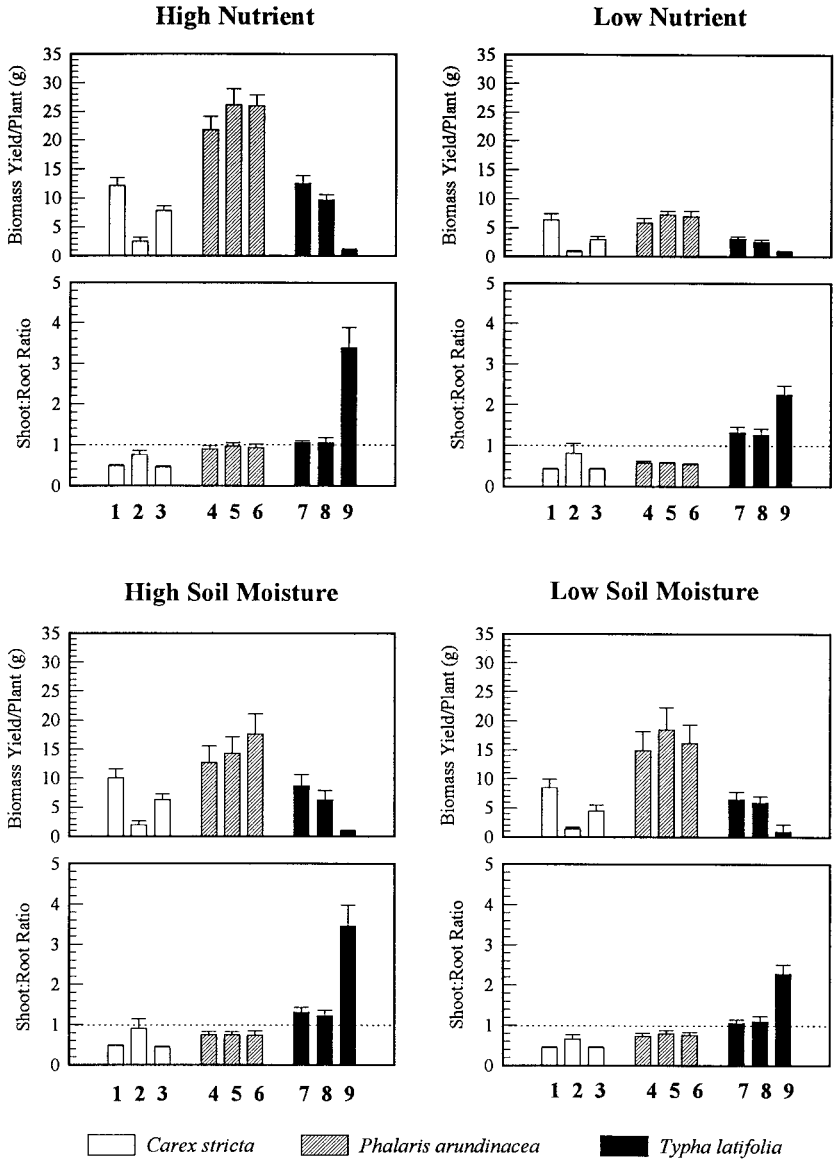

Figure 2. Effects of competition and environmental conditions on mean biomass yield per plant and shoot:root ratios (± standard error of the mean) for *Carex stricta*, *Phalaris arundinacea*, and *Typha latifolia*. 1 = *C. stricta* only, 2 = *C. stricta* with *P. arundinacea*, 3 = *C. stricta* with *T. latifolia*, 4 = *P. arundinacea* only, 5 = *P. arundinacea* with *C. stricta*, 6 = *P. arundinacea* with *T. latifolia*, 7 = *T. latifolia* only, 8 = *T. latifolia* with *C. stricta*, and 9 = *T. latifolia* with *P. arundinacea*.

T. latifolia to competition with *P. arundinacea* was to increase shoot height, regardless of the nutrient or soil moisture level. Resources were allocated to shoots at the expense of roots, even though the total biomass per plant was extremely small (Figure 2). That is, even though *T. latifolia* and *C. stricta* were light limited when growing with *P. arundinacea*, their genetically programmed architecture and growth response to low light conditions was not adequate for them to be able to successfully compete with *P. arundinacea* for light reception.

Morphological characteristics of a plant affect competition for light in agricultural environments (Loomis et al. 1971; McLachlan et al. 1993; Webster et al. 1994) and in woody plant hedges and forest gaps (Kohyama 1993; Küppers 1985; Sipe and Bazzaz 1994). Tremmel and Bazzaz (1993) found that leaf deployment of target plants and light intercep-

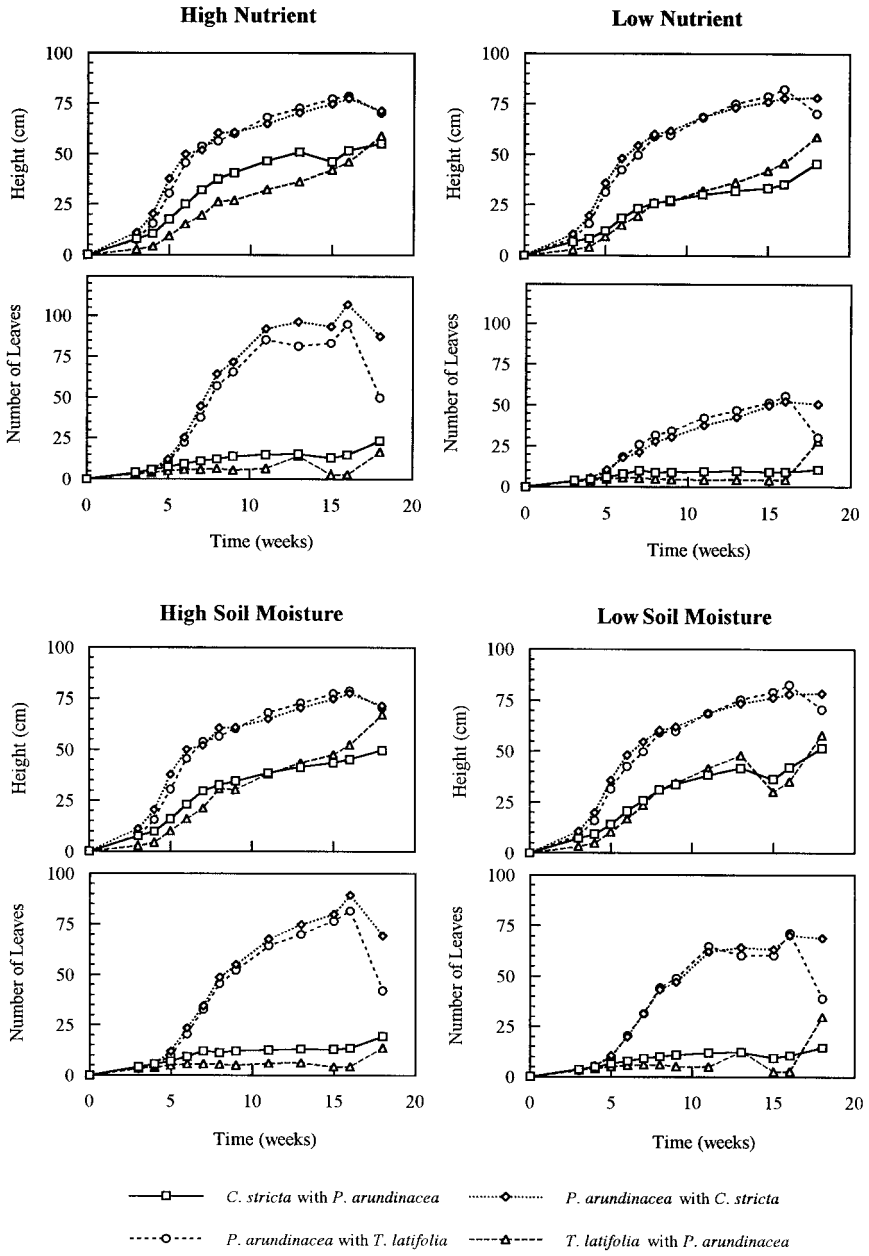

Figure 3. Tallest leaf height and leaf production patterns for *C. stricta*, *P. arundinacea*, and *T. latifolia* in nutrient, soil moisture, and interspecific competition treatments.

tion by neighbor plants were correlated with target plant biomass. A grass, having a more open canopy, was consistently a weak competitor when grown with forbs. Under a single set of environmental conditions, Gaudet and Keddy (1988) found that tall shoots, leaf shape (length:width ratio), and large canopy diameter were morphological characteristics that were significantly correlated with increased competitive ability in wetland plants. In our study *P. arundinacea* maximized the capture of light and nutrient resources by maximizing vegetative growth, even under low nutrient or soil moisture conditions (Figures 2 and 3). This study indicates that *P. arundinacea* is a superior competitor, regardless of the environmental conditions, as predicted by Grime (1979). Other studies of competitive interactions involving perennial grasses grown

at different nutrient levels have reported similar results, e.g., Mahmoud and Grime (1976), but a study of emergent macrophyte seedlings across nutrient gradients found that relative growth rates were affected by nutrient level (Shipley and Keddy 1988).

The resource allocation patterns observed in this experiment may also reflect the short length of the experiment. Resource allocation is known to change during the growing season for most plant species, including those species used in this experiment or species that are closely related (Aerts et al. 1992; Bernard and Hankinson 1979; Dickerman and Wetzel 1985). For example, competition between *C. stricta* and *T. latifolia* was much less intense over all experimental conditions (Figures 2 and 3) during this study than that between *C. stricta* and *P. arundinacea*. *T. latifolia* grows three to four times taller than *C. stricta* and eventually produces dense monotypic stands due to clonal growth. We suspect that competition between *T. latifolia* and *C. stricta* would have intensified if the experiment had extended over a longer time period. Nevertheless, the general competitive outcomes seen in this experiment would remain the same regardless of the length of time that the study lasted.

In a natural wetland plant community, species abundance's are affected by environmental conditions and competitive interactions, among other factors. A wetland plant community containing *P. arundinacea* or *T. latifolia* will be greatly influenced by nutrient inputs from agricultural land use activities because both grow much better in high nutrient regimes. High nutrient inputs will favor these species in landscapes such as the intensely agricultural Midwest in the United States, where nutrient inputs into wetlands have increased due to the application of crop fertilizer (Neely and Baker 1989). The results of this study suggest that wetland restorations on an agricultural landscape must consider an area greater than the delineated wetland boundary and that nutrient inputs must be minimized to maintain a diverse plant community.

In summary, the results of this experiment indicated that soil nutrients and interspecific competition have the greatest influence on productivity and nutrient acquisition of the three plants tested. The morphological characteristics of *P. arundinacea*, including its rapid growth rate, tall leafy shoots, and extensive lateral spread of the canopy and ramets, enabled it to maximize the capture of light and nutrient resources even under low nutrient or soil moisture conditions. The results of this experiment also indicated that plant architecture, as it relates to the capture of light resources, is as important as other environmental conditions for determining the outcome of competition among plant species.

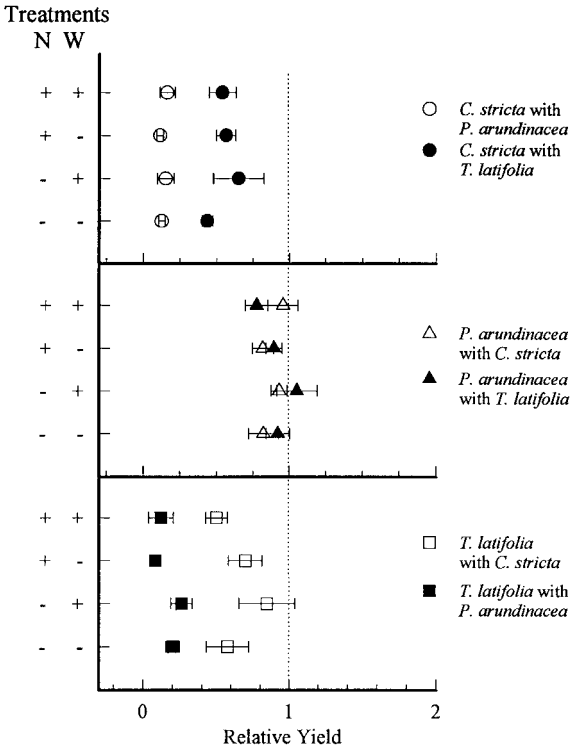

Figure 4. Total biomass relative competitive yield (± standard error of the mean) by treatment for *C. stricta*, *P. arundinacea*, and *T. latifolia*. A value greater than one indicates that interspecific competition < intraspecific competition; a value less than one indicates that interspecific competition > intraspecific competition; and a value of one indicates that inter- and intraspecific competitive effects were similar. N = nutrient level and W = soil moisture level.

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