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Nitrogen and phosphorus effect on *Typha domingensis* Presl. rhizome growth in a matrix of *Schoenoplectus americanus* (Pers.) Volkart ex Schinz and Keller

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ABSTRACT

In an outdoor mesocosm experiment of 80 weeks, the effect of nitrogen and phosphorus addition was tested on growth of *Typha domingensis* Presl. rhizomes in a matrix of *Schoenoplectus americanus* (Pers.) Volkart ex Schinz and Keller, under loading rates of 0.23 $gm^{-2}\,d^{-1}$ of nitrogen, 0.17 $gm^{-2}\,d^{-1}$ of P, both nutrient together and control conditions, to assess the potential expansion of *T. domingensis* in response to nutrient inputs.

T. domingensis responded to nitrogen addition but not to phosphorus addition. When nitrogen was added, the number of rhizomes and their weight increased. Mesocosms with nitrogen had an average of 8 rhizomes, control mesocosms 5, the differences being significant ($P < 0.05$). Fresh rhizome biomass per mesocosm (0.58 m^2) differed among treatments ($P < 0.05$): with nitrogen addition it was 110 ($\pm$31) g, with phosphorus addition 71 ($\pm$39) g, nitrogen and phosphorus 137 ($\pm$57) g, control mesocosms 67 ($\pm$30) g. The number and weight of rhizomes were highly correlated (Pearson's correlation = 0.84). Because *T. domingensis* responds to nitrogen additions by increasing the number and biomass of its rhizomes, it might be able to out-compete *S. americanus* when nitrogen concentrations increase.

1. Introduction

Nutrients that drain down from the watershed tend to converge in wetlands (Prepas et al., 2001) and although wetlands have the capability of removing nutrients from the system, high nutrient inputs can alter their function and composition (Khan and Ansari, 2005). High nutrient inputs favor establishment of fast growing species and the replacement of native vegetation (Zedler and Kercher, 2004).

Species of the genus *Typha* are native to many wetland types worldwide (Cronk and Fennessy, 2001). Some species have expanded greatly either because of changes in disturbance regimes or nutrient shifts (Woo and Zedler, 2002; Zedler and Kercher, 2004) or because they form aggressive hybrids (Levin et al., 2006; Gaskin and Schaal, 2002; Galatowitsch et al., 1999).

Competition has been shown to be an important factor in the patterning zonation along water depth gradients for coexisting *Typha* species (Grace, 1987, 1988; Grace and Wetzel, 1981), but competitive outcomes can be altered by changes in nutrient availability (Newman et al., 1996, 1998).

Typha domingensis Presl. is a characteristic species of many freshwater and brackish wetlands in western Mexico, forming dense mono-specific stands in disturbed areas (Rojas Moreno and Novelo Retana, 1995; Ramos Ventura and Novelo Retana, 1993). In many well-preserved wetlands, the vegetation shows a zonation where *S. americanus* (Pers.) Volkart ex Schinz and Keller is dominant close to the upland edge of the wetland and *T. domingensis* is dominant close to the water edge, because of the tolerance of the first species to drier conditions. If nutrient inputs increase, we hypothesize that *Typha* can expand to areas dominated by *S. americanus*. As a consequence, *T. domingensis* could become dominant across the whole gradient, as has been the case in other regions (Craft, 1995). A mesocosm experiment was conducted for assessing the effect of increased nitrogen and phosphorus inputs on the growth responses of *T. domingensis* in a matrix of *Schoenoplectus americanus*.

2. Materials and methods

Our study system, the Mintzita wetland complex (101°17′47″W, 19°38′43″N) is located to the south of the city of Morelia, the capital

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Table 1
Experimental results of the mesocoms experiment

Treatment	*n*	*Schoenoplectus americanus*		*Typha domingensis*					
		Initial number of stems	Stems grown during the season	Number of new rhizomes	New rhizomes fresh weight (g)	New rhizomes dry weight (g)	Aerial Biomass dry weight (g)	% Starch in new rhizomes	% Starch of total plant dry biomass
Control	5	93 ± 4	328 ± 40	5.4 ± 1.4	67.3 ± 29.6	39.5 ± 11.4	158.4 ± 56.5	34.5 ± 3.1	8.8 ± 2.1
Nitrogen	5	94 ± 17	293 ± 18	7.2 ± 1.3	110.5 ± 31.4	54.5 ± 13.2	148.0 ± 39.7	35.7 ± 2.3	10.2 ± 1.3
Phophorus	5	87 ± 4	342 ± 24	4.6 ± 0.8	71.1 ± 38.8	41.1 ± 9.5	122.8 ± 41.8	33.6 ± 2.9	9.7 ± 2.2
N + P	5	93 ± 7	510 ± 33	7.8 ± 1.5	137.4 ± 57.4	56.2 ± 12.9	270.1 ± 77.0	32.5 ± 2.3	6.4 ± 1.5

Schoenoplectus americanus data are the initial number of stems and the stems that grew during the length of the experiment (one growing season). *Typha domingensis* data correspond to rhizomes that grew during the growing season. Data are means and standard errors.

of the state of Michoacán, Mexico. The dominant species are *T. domingensis* and *S. americanus*. Two major impacts on the wetlands are nitrogen inputs from the watershed and phosphorus release from wetland fires (Escutia Lara, 2008).

We set up 30 mesocosms in May 2005, in an outdoor facility at the Universidad Michoacana de San Nicolás de Hidalgo. Each mesocosm consisted of a 210-L (100 cm × 68 cm × 40 cm) tub with a surface area of 0.58 m^2, filled with a 1:1 mix of locally collected soil and commercial peat moss. The mesocosms were leveled and connected with PVC pipes to a water tank with a float valve that maintained water levels at soil surface (±2 cm) in all mesocosms. The mesocoms were planted with 10 *S. americanus* rhizomes in June 2005. During March 2006, *S. americanus* stems were counted in each mesocosm, 20 mesocosms were selected for the experiment because they contained close to 100 stems each, the density observed in the natural wetland. Five replicates of any one of four treatments were randomly assigned to the mesocosms: nitrogen addition (N treatment), phosphorus addition (P treatment), nitrogen plus phosphorus addition (N + P treatment) and control (C treatment). During the first week of June 2006, two previously weighed rhizomes of *T. domingensis* were planted in the center of each mesocosm at a distance of 30 cm from each other. Five monthly nutrient additions that started the last week in June 2006 were applied. Each N mesocosm was fertilized with 28.6 g of KNO_3 (equivalent to a loading rate of 0.23 $g m^{-2} d^{-1}$ of N); P mesocosms were fertilized with 13 g of KH_2PO_4 (equivalent to a loading rate of 0.17 $g m^{-2} d^{-1}$ of P) and N + P mesocosms with 28.6 g of KNO_3 and 13 g of KH_2PO_4. These loadings are equivalent to the concentrations of these nutrients detected in the areas of the natural wetlands subject to agricultural run-off (Gómez, 2003; Escutia Lara, 2008). In terms of concentrations, considering that each mesocosm had a volume of 190 l of water-saturated soil, the fertilization treatments correspond to a pulse of 21 μg/l for N and 16 μg/l for P.

During the month of December, the number of stems of *S. americanus* was recorded. From each mesocosm, *T. domingensis* rhizomes were harvested. Before fresh weight was recorded roots from each rhizome were carefully removed. Rhizomes were dried until constant weight in a drying oven at 60 °C. *T. domingensis* aerial biomass (shoots and leaves) was harvested and dried following the same procedure. Starch content was analyzed colorimetrically (Hassid and Neufeld, 1964).

Data were analyzed with ANOVA, ANCOVA and multiple regression techniques using Helmert contrasts (Crawley, 2007), residuals were checked for compliance with analyses assumptions. All analyses were carried out using R (R Development Core Team, 2007). Data shown are means and standard errors.

3. Results

3.1. Responses of the matrix species to nutrients

The *S. americanus* canopy continued to increase during the experiment and differed among fertilization treatments (Table 1). The largest increase in number of stems was obtained in N + P mesocosms that had an average increment of 510 (±33) stems/mesocosm (879 stems/m^2), followed by P mesocosms, 342 (±24) stems/mesocosm (590 stems/m^2), control mesocosms 328 (± 40) stems/mesocosm (566 stems/m^2), and finally, *N* mesocosms, with the lowest increment, 293 (±18) stems/mesocosm (505 stems/m^2). The ANOVA results indicate that nitrogen ($F_{(1,16)} = 4.78$, $P = 0.044$) and phosphorus ($F_{(1,16)} = 14.43$, $P = 0.001$) additions, as well as their interaction ($F_{(1,16)} = 11.09$, $P = 0.004$) were significant. Since the number of stems of *S. americanus* changed differentially among treatments, the increment in the number of stems of this species was used as a covariable for the analyses of *T. domingensis* rhizome responses.

3.2. Responses of *T. domingensis* rhizomes to nutrients and the matrix species

T. domingensis rhizomes showed highly variable responses to experimental treatments (Table 1). The increment in the number of *T. domingensis* rhizomes in each mesocosm responded to nutrient additions. The highest number of new rhizomes was found in N + P mesocoms with an average of 7.8 (±1.5) rhizomes/mesocosm; close to this value was that for N mesocosms with an average of 7.2 (±1.3) rhizomes/mesocosm. P mesocosms had a significantly lower average number of rhizomes (4.6 ± 0.8) than control mesocosms, (5.4 ± 1.4) rhizomes/mesocosm, as indicated by ANCOVA (Table 2a). Under control conditions, mesocosms that grew more *S. americanus* stems developed less *T. domingensis* rhizomes. In contrast, when nitrogen was added, although *S. americanus* developed more stems in some mesocosms, *T. domingensis* was able to grow more rhizomes independently of the number of stems of *S. americanus*. The increase in rhizome fresh biomass responded to nitrogen addition in a similar way as the number of rhizomes (Tables 1 and 2b), because these variables were, as expected, highly correlated as shown by Pearson's

Table 2
Analyses of covariance, with the ^{10}log transformed increment in the number of *Schoenoplectus americanus* stems as covariable, for the ^{10}log transformed number of *Typha domingensis* rhizomes that grew during the length of the experiment (a) and the ^{10}log transformed increase in fresh rhizome biomass (b)

	Sum of sq.	d.f.	*F*	*P*
a				
Covariable	0.76	1	3.98	0.06
Nitrogen	1.36	1	7.09	<0.05
Phosphorus	0.13	1	0.70	0.41
Nitrogen + phosphorus	0.37	1	1.95	0.18
Error	2.87	15		
b				
Covariable	1.77	1	1.69	0.21
Nitrogen	4.86	1	4.62	<0.05
Phosphorus	0.61	1	0.58	0.46
Nitrogen + phosphorus	0.43	1	0.42	0.52
Error	15.77	15		

Table 3
Linear regression analysis for the percentage of rhizome starch of total plant dry weight in response to nitrogen addition and the increase in *Schoenoplectus americanus* stems (ISaS) in mesocosms with phosphorus fertilization

	Value	Std. error	*T*	*P*
Intercept	1.74	5.14	0.34	0.74
^{10}log(ISaS)	0.11	0.85	0.13	0.90
nitrogen	12.79	5.14	2.49	$<$0.05
^{10}log(ISaS): nitrogen	−2.16	0.85	−2.54	$<$0.05

test (0.84). The starch accumulated in the rhizomes did not show a simple trend in response to nutrient addition or the number of stems of *S. americanus*. The percent rhizome-starch was similar across treatments the differences not statistically significant. Significant differences were found for the percentage of rhizome starch of total plant dry weight, in response to nitrogen addition and the increase in *S. americanus* stems, but only for mesocosms with phosphorus fertilization. The statistical model (Table 3) indicates a significant effect of nitrogen ($P < 0.05$), and for the interaction between nitrogen and the number of stems of *S. americanus*. When phosphorus was present, *Typha* plants accumulated more starch ($9.7 \pm 4.9\%$), but when nitrogen was added starch accumulation was reduced ($6.4 \pm 3.5\%$) and *S. americanus* produced more stems (Table 1). All other variables that where evaluated did not show statistical differences among means.

4. Discussion

In our study wetland, plant species diversity depends on the presence of both *S. americanus* and *T. domingensis,* species that form a complex matrix that follows the water-depth gradient from the edge to the center of the wetlands. Areas where both species coexist have between 5 and 6 species/meter^2 and areas dominated by either species have less than 4 species/meter^2 (Escutia Lara, 2008). Our results are useful for understanding the dynamics of complex systems where a native species, in our case *T. domingensis*, can out-compete other natives after human disturbance reducing diversity. In other wetlands in the area that show higher disturbance and nutrient loads than those occurring currently at our study area, *T. domingensis* forms monospecific stands covering large areas all the way to the upland edge of the wetlands (Rojas Moreno and Novelo Retana, 1995; Ramos Ventura and Novelo Retana, 1993).

Responses to nutrient addition were different for *S. americanus* and *T. domingensis*. *S. americanus* responded to phosphorus and nitrogen combined, since both nutrients added together had the most noticeable effect, causing a considerable increase in the density of stems; in contrast, nitrogen by itself did not have a positive effect on *S. americanus* stem growth.

T. domingensis responded to nitrogen addition by increasing the number of rhizomes and their biomass as fresh weight. The effect of this nutrient was statistically significant after accounting for the effect of the increment in the number of stems of *S. americanus* during the growing season. Data show that under low nutrient conditions (control mesocosms), the number of *T. domingensis* rhizomes decreased. This relationship no longer occurred when nitrogen was added; *T. domingensis* produced more rhizomes. This suggests that under high nitrogen inputs, at least some *T. domingensis* plants are able to "escape" from the effect of *S. americanus* and develop large numbers of rhizomes, a potential displacement mechanism if high nitrogen conditions remain for long periods of time or for more than a growing season. Phosphorus caused more starch to accumulate as a function of total plant dry biomass, however, this required the presence of nitrogen; *S. americanus* growth was higher and seemed to prevent *T. domingensis* from accumulating starch through competition. Nitrogen and phosphorus additions had differential effects on *T. domingensis* tissue growth; more rhizomes with increased nitrogen, but more starch with increased phosphorus. Differential responses similar to these have been found for *T. angustifolia* (Steinbachova-Vojtiskova et al., 2006).

Nitrogen concentration of the water and sediments has increased in the Mintzita wetlands mostly because of changes in the watershed (Gómez, 2003; Ledesma, 2001); at the same time fires are common occurrences because of agricultural fires that propagate into the wetlands (Escutia Lara, 2008). In the last four years, three such fires have occurred during the dry season in the month of February. Our results suggest that *S. americanus* has some resilience because it responds to both nitrogen and phosphorus additions, and responds particularly well to the combination of both. Both nutrients have increased in response to different human disturbances. *T. domingensis* responds mostly to nitrogen additions and if concentrations of this nutrient continue to increase it might be able to out-compete *S. americanus*.

Our results contrast with other studies that have shown that *T. domingensis* responds to phosphorus releases after fires (Smith et al., 2001) and when transplanted to phosphorus enriched sites (Miao et al., 2000), but in these studies *Typha* was the dominant species and also high nitrogen levels occurred. Macek and Rejmmánková (2007) and Lorenzen et al. (2001) found positive responses of *T. domingensis* to phosphorus additions in monotypic plantings. In both studies, *Typha* plants were grown by themselves, and not in a matrix of another competing species as in our experiment.f

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