



Polibotánica

ISSN: 1405-2768

polibotanica@gmail.com

Departamento de Botánica

México

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Polibotánica, núm. 40, agosto, 2015, pp. 153-161

Departamento de Botánica

Distrito Federal, México

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INTERACTIONS BETWEEN DOMINANT HYDROPHYTIC SPECIES OF THE WETLANDS OF WESTERN MEXICO MEDIATED BY FIRE AND NITRATE CONCENTRATION

INTERACCIONES ENTRE ESPECIES HIDRÓFITAS DOMINANTES DE HUMEDALES DEL OCCIDENTE DE MÉXICO MEDIADAS POR EL FUEGO Y LA CONCENTRACIÓN DE NITRATOS

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SUMMARY

Wetland plant community dynamics are strongly driven by abiotic factors such as nutrient levels and fire. In wetlands where invasive species are present assessing the role of abiotic factors in plant-plant interactions is fundamental for both understanding community dynamics and management. In this study the interaction between pairs of species was quantified between one non-invasive (*Schoenoplectus americanus*), one that can become overdominant after human disturbances (*Typha domingensis*) and one that has an invasive lineage present in North America (*Phragmites australis*), growing under different nitrate concentrations and subjected to fire. All species responded by increasing growth to nitrate addition, but depending on the species, the response was significant for different variables. *Phragmites* for height and root biomass, *Typha* for aerial and root biomass and *Schoenoplectus* for all variables. Interactions between species were

complex and differed between sampling years. For the first year, only the effect of *Typha* on itself was significant. For the second year, the effect of *Typha* was negative on *Phragmites*, the effect of *Schoenoplectus* was negative on itself and, the effect of *Typha* and *Phragmites* was negative on *Typha*. The effect of fire was significant for *Phragmites* and *Schoenoplectus*, not burned plant were taller. Interactions between plants were altered by fire, the presence of *Schoenoplectus* benefited the performance of *Typha*, and the opposite was also true. For early stages of these species growth, the strongest competition occurs between the native species, allowing the invasive to mostly respond to nitrate levels, and fire have a strong effect also on the interactions between the natives and not with the invasive.

Key words: wetland, negative interactions, management, nutrients, ecological restoration.

RESUMEN

La dinámica de comunidades vegetales de humedales está influenciada por factores abióticos, como los nutrientes y el fuego. En humedales en donde hay especies invasoras, determinar el papel de factores abióticos en las interacciones planta-planta es fundamental para entender la dinámica de la comunidad y para su manejo. En este estudio, la interacción entre pares de especies fue cuantificada entre una no invasora (*Schoenoplectus americanus*), una que puede volverse sobredominante como consecuencia de disturbios humanos (*Typha domingensis*) y una que posee un linaje que es invasor en norteamérica (*Phragmites australis*), las cuales crecieron bajo diferentes concentraciones de nitrato y fueron sometidas al efecto del fuego. Todas las especies respondieron a la adición de nitratos incrementando su crecimiento. *Phragmites* respondió en altura y biomasa de raíces, *Typha* en biomasa aérea y de raíces y *Schoenoplectus* para todas las variables. Las interacciones entre especies fueron complejas y variaron entre años. Durante el primer año, sólo el efecto de *Typha* en sí misma fue significativo. Para el segundo año, el efecto de *Typha* fue negativo en *Phragmites*, el efecto de *Schoenoplectus* fue negativo en sí mismo y el efecto de *Typha* y *Phragmites* fue negativo en *Typha*. El fuego fue significativo para *Phragmites* y *Schoenoplectus*, las plantas no quemadas fueron más altas. Se detectaron efectos del fuego en las interacciones, la presencia de *Schoenoplectus* benefició el desempeño de *Typha*, y viceversa. En etapas tempranas, las interacciones más fuertes ocurrieron entre las especies no invasoras, permitiendo a la invasora responder a la concentración de nitratos, y el fuego tuvo su mayor efecto

en la interacción entre nativas y no con la invasora.

Palabras clave: humedal, interacciones negativas, manejo, nutrientes, restauración ecológica

INTRODUCTION AND METHODS

Wetland plant communities are complex systems in which abiotic factors can significantly alter its floristic composition (Zedler and Kercher, 2004). Among the most important of these factors are hydroperiod, salinity, and nutrient concentration, especially that of nitrogen and phosphorus (Cronk and Fennessy, 2001). It has been suggested that when wetlands are subjected to changes in the chemical composition of their water supply, particularly in the form of increases in nitrogen concentration, changes can occur in the richness and/or composition of species that can facilitate the domination of the system by invasive species (Cronk, 1995), whether native or exotic (Zedler and Kercher, 2004). Among the native species that present invasive behavior in wetlands many belong to the genus *Typha* which, in response to increases in nutrient concentration and other human disturbances, can form dense monospecific patches and thus displace other native species (Galatowitsch *et al.*, 1999; Smith *et al.*, 2001; Woo and Zedler, 2002; Levin *et al.*, 2006). Others, such as certain lineages of *Phragmites australis* (Swearingen and Saltonall, 2010) are particularly aggressive invasives (Rickey and Anderson, 2004; Laeue *et al.*, 2006; Saltonstall and Stevenson, 2007). *Phragmites australis* is a species considered to be native to Eurasia by some authors without recognizing subspecies (Lot *et al.*, 2013), others (Saltonal *et al.*, 2004) recognize one subspecies that they consi-

der to be native to Canada and the United States of America, *Phragmites australis* subsp. *americanus*, and a lineage present from the Southern United States to Central America with uncertain origin, although this last lineage has been proposed as a new species, *Phragmites karka* (Ward, 2010). Despite the taxonomical discrepancies, an invasive form is recognized, characterized by morphological and population dynamics characteristics, in particular that forms dense clumps that exclude all other plant species (Swearingen and Saltonall, 2010).

To understand the dynamics of the displacement of native species by invasive species in wetlands, it is necessary to quantify the effects of factors, such as nutrient contents or fire, that can modify the interactions between species. The present study is based on observations of the vegetation structure and dynamics in a model system, the spring wetlands of the Mintzita (101°17'47" W, 19°38'43" N: 1930 masl) in the municipality of Morelia, in Michoacán, México (Escutia-Lara *et al.*, 2009a). These wetlands are characterized by a natural zonation consisting of an area dominated by *Schoenoplectus americanus* close to the edge of the wetland, and a zone dominated by *Typha domingensis* that conforms to changes in the water level. Between both of these areas, there is a zone in which the two species coexist and where the distributions respond partially to the water level throughout the wetland; however, other factors, such as nutrient concentration and fire also seem to play an important role. *Phragmites australis* forms dense clumps consistent with those reported for the invasive lineage (Swearingen and Saltonall, 2010) in the wetlands irrespective of the dominant native species. In a previous study, it was found that individuals of *T. domingensis* in

the wetland respond mainly to the addition of nitrogen; *S. americanus* also responds to increased nitrogen, but also to phosphorus in terms of the accumulation of aerial biomass (Escutia-Lara *et al.*, 2010). The responses of *P. australis* have not been evaluated in this system but, in other wetlands, it has been reported that this species responds to increases in the concentrations of both nitrogen and phosphorus and also to the interaction of these two nutrients (Boar, 1996; Ennabili *et al.*, 1998; Ehrenfeld, 2003). From field observations in the model wetland (Escutia-Lara *et al.*, 2009a) and from controlled experiments (Escutia-Lara *et al.*, 2009b; Escutia-Lara *et al.*, 2010), it can be suggested that the competitive capacity of *P. australis* is greater or equal to that of *T. domingensis* and, in turn, greater than that of *S. americanus*; however, the magnitude and exact nature of the interactions between these species remains unknown. The objectives of the present study were to quantify the response of these species to different concentrations of nitrate, as this is the macronutrient to which all three species respond most markedly (Escutia-Lara *et al.*, 2010) and to fire, in order to relate this recurring disturbance factor to patterns of species growth.

Rhizomes of the three species were collected at the study site; these were selected to be of similar size at the start of the experiment and were assigned at random to each of the replicates of the experiments described below. Experiments were conducted to quantify the effect of interactions between pairs of species: *Typha domingensis*, *Phragmites australis* and *Schoenoplectus americanus*. Each experimental unit consisted of two plants, either of the same species or of each possible pairing between them. Rhizomes

were planted in five liter pots (25 cm high x 16 cm wide) filled with commercial peat. Thirty pots were planted with each one of the six possible species combinations (three with interspecific and three with intraspecific pairs) giving a total of 180 experimental units. In addition, for each species-interaction treatment, the effect of five treatments of fertilization with potassium nitrate (KNO_3) was tested: 0, 0.08, 0.16, 0.24 and 0.32 g/l of cultivation medium. In this way, six replicates were produced for each treatment of the combination of competition x fertilization. Addition of KNO_3 was carried out every 15 days for a period of six months (May to October). During the dry season (February of the following year), 15 pots were chosen at random from each interaction treatment (three for each fertilization X interaction combination of treatments) in order to burn the aerial biomass, while the other 15 were left as a control. In June, all remaining plants were harvested and aerial and root biomass recorded. In order to assess the importance of the interaction between the different species, three response variables were analyzed: plant height, and aerial and root biomass. In the case of same species interactions, the response variable considered was the average value from both plants in each pot. For different species interactions, the variable was measured in the individual of the species on which the effect of the interaction was to be determined. Analysis was conducted with general linear models, considering fertilization as a continuous variable, and the interaction and aerial biomass burning as categorical variables. Tests of hypothesis were carried out to generate ANOVA tables (Crawley, 2007) and to determine the effect of each of the variables and their interactions. All analyses

were conducted with the statistical program R (R Development Core Team, 2011).

RESULTS

Following burning of the aerial parts of the plants in the second growing season, all species responded to the addition of nitrate and, in some cases, to the interaction treatments and burning. For *P. australis*, there was a significant response in plant height to the added fertilizer (fig. 1a; $F(1,78) = 71.2$, $P < 0.000001$). The effect of the interactions (fig. 1b) was significant ($F(2,78) = 6.6$, $P = 0.002$): the intraspecific interaction produced the greatest average plant height (138 cm), followed by the interaction with *S. americanus* (120 cm) and with *T. domingensis* (115 cm). Burning of the aerial parts did not affect height in *P. australis*. In the case of aerial biomass (fig. 1b), significant differences were observed due to the addition of nitrate ($F(1,78) = 118.3$, $P < 0.000001$) and to the effect of the interaction ($F(2,78) = 6.9$, $P = 0.002$). These followed the same pattern observed in plant height (41 g for intraspecific interaction, 32 g for the interaction with *S. americanus* and 26 g for the interaction with *T. domingensis*). Significant differences ($F(1,78) = 8.32$, $P = 0.005$) were found with the burning treatment, since greater quantities of aerial biomass accumulated in those plants that had not been burned (36 g), relative to those that had (30 g). Root biomass (fig. 1c) only increased with increased nitrate addition ($F(1,78) = 18.4$, $P < 0.0001$).

Schoenoplectus americanus presented a more complex set of responses than *P. australis*. In terms of height (fig. 1d), this species responded to both nitrate addition

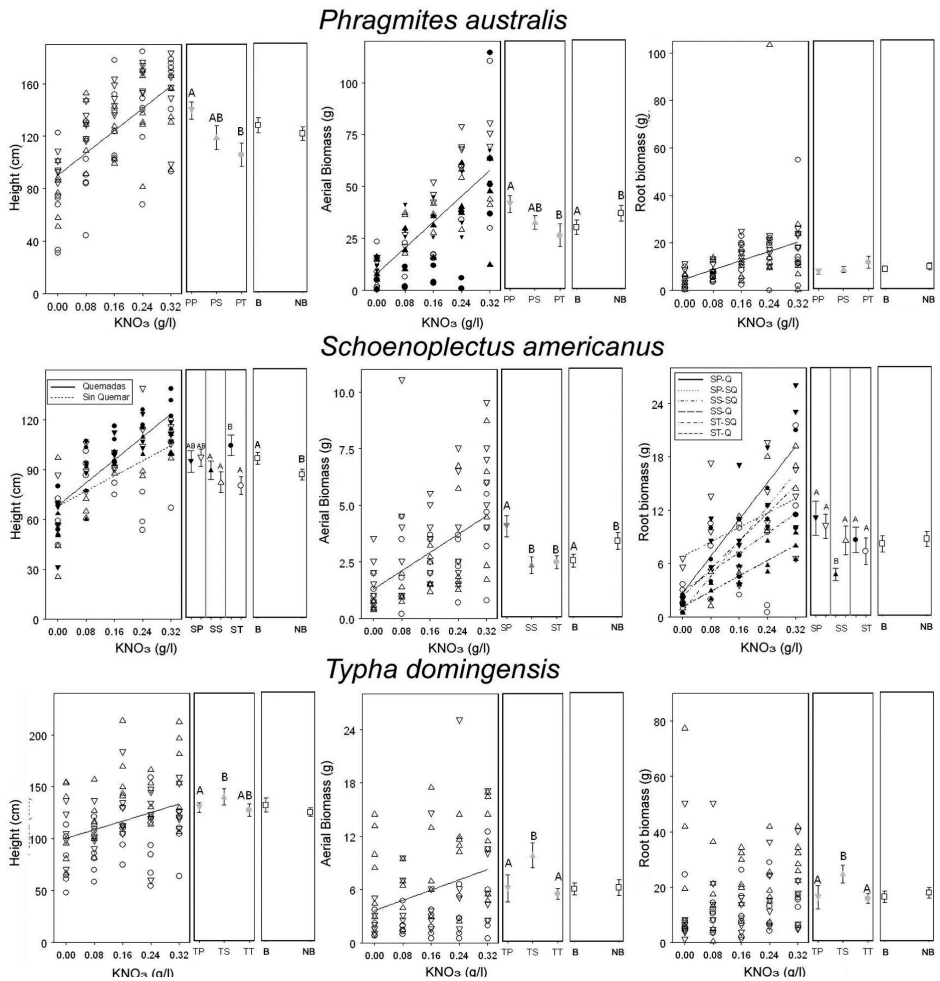


Fig. 1. Response of *Phragmites australis*, *Schoenoplectus americanus* and *Typha domingensis* to the treatments of nitrate addition, competition and burning at the end of the experiment. Each panel (a to h) shows the relationship between the response variable and the concentration of added nitrate, and the means and standard errors for the response variable as a function of the competition interaction or the burning treatments. Slope curves are shown only when the effect of the nitrate addition was significant. In cases where some of the interactions between factors were significant, adjustment curves are shown for each combination of levels. Different letters denote significant differences in means according to the Tukey test.

($F(1,78) = 99.1$, $P < 0.000001$) and to the interaction with other individuals ($F(2,78) = 3.24$, $P = 0.045$), since the plants reached the tallest average height (95 cm) in the presence of *P. australis*, followed by those grown with *T. domingensis* (92 cm) and finally by those grown in the intraspecific treatment (86 cm). They also responded to the burning treatment ($F(1,78) = 9.1$, $P = 0.003$), with plants that had been burned reaching an average height of 96 cm, while non-burned plants only reached 86 cm. There were also significant effects of the interaction between nitrate addition and burning treatment ($F(1,78) = 4.15$, $P = 0.045$), since non-burned plants presented lower rates of height increase than burned plants, with increasing concentrations of nitrates, as reflected in the slopes of the curves. The interaction between competition and burning treatment was also significant ($F(2,78) = 5.73$, $P < 0.004$) because the burned plants from the treatment of competition with *T. domingensis* reached a greater height (104 cm) than any other combination of levels of the two factors while non-burned plants of the same competition treatment were the shortest (80 cm).

Regarding aerial biomass (fig. 1e), *S. americanus* responded to the addition of nitrate ($F(1,78) = 43.1$, $P < 0.000001$) and to competition ($F(2,78) = 56.2$, $P < 0.001$), accumulating more biomass in the interspecific treatment with *P. australis* (4.0g) relative to the other two treatments (2.4 g with *T. domingensis* and 2.3 g in intraspecific competition). In the burning treatment, more aerial biomass was accumulated in the non-burned plants (3.35 g) than in burned plants (2.5 g). Regarding root biomass (fig. 2f), *S. americanus* presented the most com-

plex pattern of responses to treatments: there were significant effects of nitrate addition ($F(1,78) = 91.0$, $P < 0.000001$), plant-plant interactions ($F(2,78) = 8.0$, $P = 0.0006$) and of the combination of factors ($F(2,78) = 4.1$, $P = 0.02$), since the intraspecific interaction treatment with fire produced a lower root biomass (4.6 g). Finally, the interaction between the three factors; addition of nitrate, plant-plant interactions and burning was also significant ($F(2,78) = 5.5$, $P = 0.005$), as reflected in the slopes of the curves of root biomass as a function of nitrate addition for each combination of the levels of experimental factors.

Typha domingensis responded to fewer factors than the other two species, since for no variable was there a response to the burning treatment. For plant height (fig. 1g), this species responded to the addition of nitrate ($F(1,78) = 17.0$, $P < 0.0001$) and to plant-plant interactions ($F(2,78) = 18.3$, $P < 0.000001$) since the plants reached greatest height on interaction with *S. americanus* (137 cm) and presented the shortest height with *P. australis* (118 cm). Accumulation of aerial biomass (fig. 1h) also responded to nitrate addition ($F(1,78) = 12.0$, $P < 0.0008$), and to plant-plant interactions ($F(2,78) = 14.5$, $P < 0.0001$), since the plants in intraspecific treatments accumulated the least biomass on average (3 g), followed by plants grown with *P. australis* (5.8 g) and finally those grown with *S. americanus* (9.0 g); the accumulation of root biomass only responded to plant-plant interactions ($F(2,78) = 7.5$, $P = 0.001$), and followed the same pattern observed in the aerial biomass; 11.8 g in intraspecific competition, 14.1 g with *P. australis* and 23.9 g with *S. americanus*).

DISCUSSION

The results show, as expected, that all the study species responded positively to the addition of nitrate; however, in the presence of other individuals, performance variables differed depending on species. Interspecific interactions are not important for *Phragmites australis* and *Schoenoplectus americanus* since they present the same rates of growth as when they are growing alongside individuals of their own species. For *Typha domingensis*, the situation is different since intraspecific interactions were more detrimental than interspecific ones. Given that *P. australis* is invading the wetland, it was expected that *P. australis* would be a superior competitor to both *T. domingensis* and *S. americanus* and would suppress their performance, but this did not in fact occur. The addition of nutrients alone cannot explain the increase in abundance of *P. australis* in the Mintzita wetland, as nutrients do for other invasive species in other wetlands (Woo and Zedler, 2002). In the case of other species that present invasive behavior, it has been documented that they require anthropogenic disturbances in order to increase their numbers (Jesson *et al.*, 2000; Fireswyck and Zedler, 2007).

In this experiment, the added disturbance is related to the burning of vegetation, a practice that currently takes place in Mintzita (Escutia-Lara *et al.*, 2009a). With this disturbance, the plant response to nutrients remained surprisingly unchanged; the three species grew in line with the increases in nitrate concentration. However, the interrelations associated with plant-plant interactions did change. For burned *P. australis* plants, interspecific interactions caused

diminished growth, since taller and more robust plants were produced when grown in the presence of individuals of the same species. For *T. domingensis*, the contrary was true as the presence of *S. americanus* benefited its performance after burning and for *S. americanus*, the plants most favored were those grown with *T. domingensis*. The positive effects of ash from *S. americanus* in the growth of *T. domingensis* seedlings have been reported (Lopez-Arcos *et al.*, 2012). It therefore appears that competition between these two species is less when growing together and there is a likelihood of fire. The modification of these competitive interrelations by anthropogenic disturbance, reported in previous studies for other wetland species (Woo and Zedler, 2002) as being of benefit to those species with invasive attributes, was not reflected in this experiment. It is worth noting that *P. australis* is always taller and of greater biomass than the other two species, making it likely in the long term that competition for light becomes a determining factor in its invasion of the site, and therefore this is a factor that must be fully taken into account in any future studies to predict the behavior of this invasive species.

CONCLUSIONS

The series of experiments indicate that nitrate availability altered the intensity of plant-plant interactions but that fire was more instrumental in altering these, in particular that presence of *Schoenoplectus* benefited *Typha*. Since several species of the later genus have shown invasive behavior, this study suggests an additional mechanism that deserves more attention under natural conditions, since the controlled conditions of the experiments undertaken limits its realism.

Finally, fire was a significant factor altering growth for *Phragmites* and *Schoenoplectus*, benefiting more the former than the later, therefore, strongest competition occurred between natives, leaving *Phragmites*, the invasive, free to respond to increased nitrate availability by growing more.

ACKNOWLEDGEMENTS

This work was funded by the Universidad Nacional Autónoma de México through the project PAPIIT IN203608 and CONACYT (SEP-CONACYT-2008-101335).

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Recibido: 17 octubre 2013. Aceptado: 23 enero 2015.