



Interspecific Competition for Space Between Wetland Plants with Clonal Growth

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Received: 22 September 2013 / Accepted: 4 July 2014 / Published online: 23 July 2014
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Abstract Several plant species of wetland habitats expand through clonal growth, often forming dense, nearly monospecific stands. Adjoining interspecific colonies represent an ideal model for testing hypotheses about competitive interactions between clonal species and developing predictive theories on plant competition for space. In this study, we evaluated the outcome of competition between colonies of *Phragmites* and *Typha*. First, we compared the progression and density of colonies in roadside ditches 1) at the zone of contact of two well-established monospecific colonies, and 2) in zones where the progression fronts are free from competition. Second, we used an experimental mesocosm approach to simulate competition for space between two plant colonies. The experiment was done under three salinity levels in order to better understand how deicing salt may influence interspecific competition. In roadside ditches, *Typha* did not slow down *Phragmites* progression. In the mesocosm experiment, both species showed optimal growth in low salinity, but *Phragmites* was superior at all salinity levels. In opposition to previous classical pair-wise experiments, the results of our experiments on *Phragmites* – *Typha* interactions concur with field evidence of dynamics between neighboring colonies. Our experiment approach succeeds in better simulating competitive interactions for space between plants with clonal growth.

Keywords Competition · Wetland · Clonal growth · Salinity · *Phragmites* · *Typha*

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Introduction

Plant competition theory and approaches have contributed significantly to understanding the competitiveness of exotic plant invaders. Classical garden or greenhouse competition experiments using seedlings or transplants, with various combinations of mixed and pure populations depending on design (simple pair-wise, additive or replacement series), represent the most common approach for evaluating competitive interaction between two plant species (Gibson et al. 1999). Such types of experiments on the competitive ability of native vs alien species (Vilà and Weiner 2004; Callaway et al. 2008) or between introduced vs native populations of the same species (Vilà et al. 2003; McKenney et al. 2007) are thus currently performed to test hypotheses related to plant invasion.

Wetland habitats are particularly vulnerable to exotic plant invasion. Several invasive wetland species significantly decrease native plant diversity by developing nearly monospecific stands (Zedler and Kercher 2004), thus suggesting high competitive ability. One such plant is *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), a tall perennial grass considered invasive in many parts of the world, but particularly in eastern North America. Over the past few decades, *Phragmites* has spread dramatically in freshwater wetlands (Lavoie et al. 2003; Tulbure and Johnston 2010), coastal salt marshes (Chambers et al. 1999; Bart et al. 2006) and roadside ditches receiving runoff of deicing salt (Maheu-Giroux and de Blois 2007; Jodoin et al. 2008; Brisson et al. 2010). *Phragmites* dispersion in new habitats was believed to occur mainly through spread of rhizome fragments, especially in the northern part of its distribution, but new observations suggest that establishment of new colonies by sexual dispersion is now a common phenomenon (Brisson et al. 2008; Belzile et al. 2010). Whatever the mode of establishment, lateral expansion of new colonies always occurs through strong vegetative spreading of a dense front of roots, rhizomes and

aboveground stems. Physiological integration of ramets may contribute to the competitive success of *Phragmites* by allowing expansion in more stressful habitats (Amsberry et al. 2000) and by suppressing other wetland species.

In roadside ditches, *Phragmites* stands are frequently found in alternation with mixed stands of *Typha* (*Typha angustifolia* L. [narrow-leaved cattail], *Typha latifolia* L. [broad-leaved cattail], and their hybrid, *Typha x glauca* Godr.) (Bellavance and Brisson 2010). *Phragmites* and *Typha* are colonial macrophytes that share several morphological traits, such as tall unbranched shoots and both rhizomes and roots as underground structures. They also share similar habitats and a large range of site conditions, including a resistance to saline conditions (Whigham et al. 1989; Miklovic and Galatowitsch 2005). Like *Phragmites*, *Typha* often form dense stands due to their strong vegetative propagation, and both *Typha* species and their hybrid display invasive tendencies in disturbed wetlands of North America (Farnsworth and Meyerson 2003; Shih and Finkelstein 2008). Consequently, the contact zone between *Phragmites* and *Typha* stands is probably characterized by intense competition for space, and competitive outcome is best revealed by the spatial dynamics at that contact zone over time as one species progresses to the detriment of the other. Thus, adjoining colonies of *Phragmites* and *Typha* represent an ideal model for testing hypotheses about competitive interactions between clonal species and developing predictive theories on plant invasion and competition for space.

There are numerous well-documented accounts of *Phragmites* invasion at the expense of *Typha*, under various site conditions, suggesting that *Phragmites* has a competitive advantage (Clevering and van der Toorn 2000; Meyerson et al. 2000; Choi and Bury 2003; Chun and Choi 2009; Bellavance and Brisson 2010). However, the findings of competition experiments are not always consistent with these field observations. For example, in a pot experiment by Szczepanska and Szczepanski (1982), a total of 10 seeds of *Typha latifolia* and *Phragmites* were germinated, either in monoculture or mixed culture. At the end of the growing season, *Typha latifolia* had a higher average biomass in mixed culture with *Phragmites* than in monoculture, while the opposite was true for *Phragmites*. The authors thus attributed a net competitive advantage to *Typha* over *Phragmites* (Szczepanska and Szczepanski 1982).

Environmental gradients may influence the intensity and outcome of competition (Jung et al. 2009, Coates et al. 2013). Yet, in a phytometer experiment to determine the competitive performance of 26 wetland plant species by measuring their relative ability to suppress the growth of a common indicator (*Penthorum sedoides* L.), competitive performance of *T. x glauca* ranked higher than *Phragmites* under both low and high nutrient levels (Keddy et al. 2000). Salinity has also been shown to interact with competition to determine species

abundance and growth (Barbour 1978, Greiner La Peyre et al. 2001, Greenwood and MacFarlane 2009). Still, the same outcome of *Typha* competitive advantage over *Phragmites* was found across a gradient of salinity in a garden-type competitive experiment comparing 6 species (Konisky and Burdick 2004). Plant shoots were transplanted in a tidal marsh across a gradient of three flooding and three salinity regimes and arranged into pair-wise competitive combinations. Competitive trends were examined by comparing the relative growth of the plants in the presence of one species with growth in the presence of each of the others. With salinity and flooding as stressors, it was found that competition with *Typha* reduced the relative aboveground growth (RABG) of *Phragmites*, while RABG of *Typha angustifolia* growing with *Phragmites* was enhanced (Konisky and Burdick 2004).

Experimental conditions may explain the apparent contradictions between field observations and experiments. For example, in classical greenhouse or garden experiments, the initial size of the individuals is critical and may determine, unwittingly, the outcome of competition (Kikvidze et al. 2006). More importantly, classical pair-wise competition experiments may not adequately emulate competitive interaction for space between colonies of plant species with strong clonal growth. In these species, competition (both intra and interspecific) often occurs at the contact zone between colonies that are spatially expanding, rather than between intermixed monopodial individuals (Amsberry et al. 2000, Koppitz and Kühl 2000, Woo and Zedler 2002).

The goal of our study was to evaluate the outcome of competition for space between *Phragmites* and *Typha*, both in terms of population structure and morphological changes, at the zone of contact between well-established colonies. First, we compared their progression and density 1) at the contact zone of colonies located in roadside ditches (with competition) and 2) in zones where the progression fronts are free from interference due to experimental removal (no competition). Second, we designed and tested an experimental mesocosm approach to simulate competition for space between two plant colonies. Each species was allowed to grow to maturity in two halves of mesocosms separated by a panel. Then, the panel was removed to allow lateral expansion from each side into the other, and after an adequate time delay, progression and population attributes were compared with those of control mesocosms with free expansion (no competitor in the opposing half of the mesocosm). Since salinity may play an important role in determining the outcome of competition between wetland species (Medeiros et al. 2013), we tested our mesocosm approach under three salinity regimes.

Materials and Methods

Roadside Ditch Experiment

This experiment took advantage of the linear nature of the colonies and the homogeneous conditions in the roadside ditches under study. Twelve sites of contact zones between *Phragmites* and *Typha* stands located in roadside ditches were selected along a 4 km stretch of highway 640 (Quebec, Canada) between exit 2 (St-Joseph-du-Lac; latitude: 45°31' 45.85" N; longitude: 73°58'21.23" W) and exit 8 (Deux-Montagnes; latitude: 45°32'38.69" N; longitude: 73°55' 37.49" W). This highway receives deicing salt in winter, most of which eventually runs off in the ditches. This stretch of road is homogeneous, with no apparent change in soil type or topography. A contact zone between two stands consisted of a narrow zone (generally less than 2 m) intermixed with both species, and where competitive interaction is assumed to be maximal. For each species, the stands always extended at least 10 m from the contact zone. While most of the *Typha* were *Typha angustifolia*, they were occasionally mixed with *Typha latifolia*, and several individuals showed intermediate characters, suggesting hybridization. Identification to species (or hybrid) level without genetic analysis is virtually impossible for some intermediate plants with flowers or fruits, and even more so for non-flowering individuals (Kuehn and White 1999). While ecological differences in water level preferences have been documented (Grace and Wetzel 1981), a recent study in southern Ontario found no evidence of water level segregation between the two species and their hybrid where they co-occur (McKenzie-Gopsill et al. 2012). For the purposes of this experiment, we simply considered all *Typha* irrespective of species.

Of the 12 sites, six were left intact (competition sites) and vegetation was removed and excavated to a depth of about 60 cm from a portion of the other six to allow free progression (unvegetated sites). In June 2005, at the competition sites, temporary markers (pigtailed and flags) were used to identify the last *Phragmites* shoot in the *Typha* stand. From this point, the progression of *Phragmites* in the *Typha* stands was measured at the end of the following growing seasons. The endpoint of *Typha* colonies was more diffuse and a few non-flowering shoots of *Typha* were occasionally present inside *Phragmites* stands, away from the contact zone. Because of this, we could not indisputably determine the endpoint of the colony, so annual progression of the endpoint of *Typha* stands could not be monitored as it was for *Phragmites*. Also in June 2005, vegetation was removed to create six unvegetated sites along a 5 m strip centered at the contact zone between the *Phragmites* and *Typha* stands. The soil was excavated using a mechanical shovel, cleansed of all rhizomes, and replaced. While *Phragmites* rhizomes may reach and even exceed 1 m in depth, depending on soil type (Moore et al. 2013), most

rhizomes in our site were in the first 20 cm. We excavated down until no rhizomes were visible, a depth of approximately 60 cm. The excavation created an unvegetated zone, with *Phragmites* on one side and *Typha* on the other. From their respective sides, the species could thus freely invade the unvegetated zone by vegetative expansion without negative effects of competition. For the rest of the first growing season, plants were left to form new buds and shoots and recover from the procedure: as expected, progression in the unvegetated zone was minimal for both species during this period. Thus, progression of *Typha* and *Phragmites* colonies was determined for 2006, based on plant positions measured at the end of 2005 and 2006. We did not remove seedlings naturally establishing in the unvegetated zone (some of which that were *Phragmites* and *Typha*, easily distinguishable from sprouts), because of their low impact on the emergence of sprouts.

In addition to linear progression, density of shoots was measured in two 1-m circular quadrats with the center located in the unvegetated zone, at 1 m from the limit of the respective monospecific zone. Density was also measured in the center of the contact zone of competition sites for comparison purposes. Finally, 12 randomly chosen flowering shoots of *Phragmites* and *Typha* were collected in their respective unvegetated zones (unvegetated sites) as well as in contact zones (competition sites) in order to compare morphology and biomass allocation of shoots growing in these two types of conditions. Measures included shoot height, shoot diameter, number of leaves, leaf biomass, number of nodes (*Phragmites* only), inflorescence biomass and stem biomass.

Mesocosm Experiment

The mesocosm experiment took place on the site of the Montréal Botanical Garden, and was designed to mimic competition for space between two mature stands (Fig. 1). Twenty-four mesocosms (140 cm long × 100 cm wide × 39 cm deep), divided into two equal compartments by a removable PVC separator panel, were filled with gravel (5 to 10 mm in diameter) up to 5 cm from the top. The separator is permeable to water yet prevents plants from growing into the adjoining compartment. Each mesocosm was individually connected to a secondary reservoir where water level, nutrient solution and salinity could be regulated. Fertilization was performed using a 20:20:20 fertilizer solution, adjusted weekly to maintain constant electrical conductivity between flushing operations, depending on the salinity treatment (see below). Because water and nutrients were maintained constant at optimal levels throughout the experiment, belowground competition between plants was for growing space alone. Solution pH was stabilized between 5.5 and 6.5 using nitric acid to maintain the nutrients in their optimal range of bioavailability. Water level was adjusted to gravel surface on a daily basis. Each mesocosm was assigned to one of three plant competition



Fig. 1 Competition mesocosm experiment at the Montréal Botanical Garden

treatments: competition (*Typha* in one compartment and *Phragmites* in the other), *Typha* control (*Typha* in one compartment, no plants in the other), and *Phragmites* control (*Phragmites* in one compartment, no plants in the other) (Fig. 2). Note that in competition mesocosms, the original compartment of *Typha* is also the opposite compartment of *Phragmites*, and vice versa. There were 12 control mesocosms (6 for each species) and 12 competition mesocosms. The mesocosms were arranged in two rows of 12 oriented north–south, with 6 competition and 6 control mesocosms (3 per species) randomly positioned in each row. In May 2006, the *Phragmites* and *Typha* compartments were respectively planted with 6 rhizome clumps of comparable biomass collected from a nearby wetland site. For this experiment, we harvested the *Typha* rhizome clumps in a marsh dominated by *Typha* with narrow leaves (most likely *T. angustifolia* but possibly *T. x glauca*).

Each mesocosm was randomly assigned to one of three salinity levels, with an equal number of salinity treatments for each plant treatment (full factorial design) within each row. Sodium chloride (NaCl) was added to the nutrient solution to obtain the predetermined salinity levels: Low salinity (control): no salt added, salinity depending only on nutrients; Medium salinity: 5.85 g NaCl L⁻¹ (0.1 M, 6 ppm); High

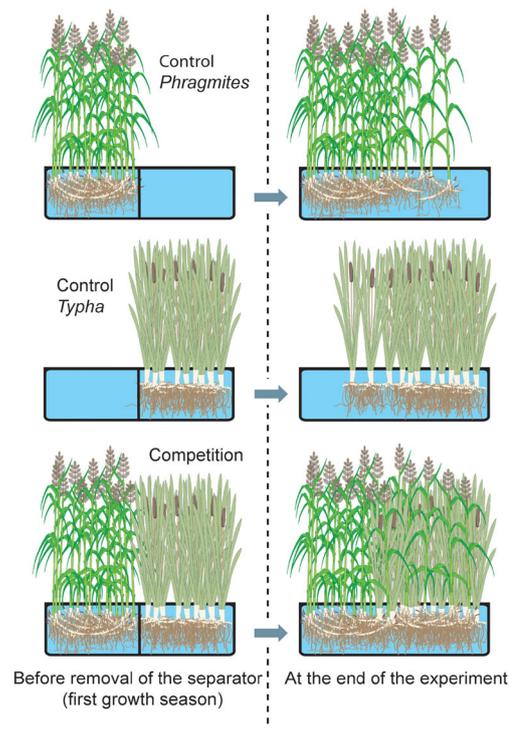


Fig. 2 Representation of the three types of mesocosm used to study the effects of competition

salinity: 11.7 g NaCl L⁻¹ (0.2 M, 12 ppm). In 2006, salinity treatments were applied gradually to allow plant establishment: no salt during the first two weeks after plantation, half the intended salinity levels the following two weeks, full treatment thereafter. The solution was flushed and restored to the original salinity conditions every two weeks at the beginning of the growing season, and every 3–4 weeks at the end of the growing season, to ensure maximal constancy in experimental conditions. Edge effects are considered a drawback in pot and mesocosm experiments. For example, shoots at edge of the mesocosms receive higher light and are more susceptible to bend out or break by wind because they are unsupported by other vegetation. To reduce this effect, we installed a white cloth around the base of the basin up to 1.25 m in early July of each year. The light level passing through this cloth better simulated sideways light level in the interior of a colony, and the cloth offered a physical resistance to bending. To control occasional aphid outbreaks, an insecticide treatment (Pirliss™, Plant Products Co. Ltd., Canada) was used when needed, following the manufacturer's instructions. At the end of each growing season, the shoots were cut and the basins were protected from frost damage by a mulch cover and a plastic sheet.

The separator panels were removed on 13-Jun-2007, to allow the stands from the original compartment to begin their progression into the opposite compartment: they could either colonize the empty compartment, free of vegetation (control mesocosms), or progress (if at all) and compete for space in a

compartment already occupied by the competitor (competition mesocosms). In the fall of 2008, the number of shoots, length of the longest shoot and average shoot length were measured for each species in each compartment (original and opposite) of each mesocosm. The number of shoots in the opposite compartment was counted according to 3 equal sections progressively more distant from the separator in order to evaluate spatial progression. The aboveground portion was harvested and the belowground portion was excavated in each compartment, by species, then dried for biomass determination. The negative effect of competition was estimated as the reduction in growth parameters (density, biomass) in the opposite compartment due to the presence of the competitor compared to the same parameters in opposite compartment of control mesocosms (see the next section).

Data Analysis

The effect of competition (both experiments) and salinity (mesocosm experiment) on stand and plant parameters was tested using *t*-test and ANOVA. For the ditch experiment, differences in morphological characters between treatments (unvegetated vs competition) were analyzed using a nested ANOVA, with sites nested within treatment. This design allows us to look at the factors of interest (competition treatment) after removing the unwanted variation due to possible differences in environmental conditions between sites.

For the mesocosm experiment, each of the two rows was considered as a block for statistical purposes. First, we tested the effect of competition on plant growth parameters (shoot height, number of shoots, biomass and root shoot ratio) in the opposite compartment of competition mesocosms and control mesocosms. We used ANOVA, with block, salinity and competition as explanatory variables, and growth parameters as response variables. Block and the interactions block*salinity and block*competition were noted as random factors. Second, to compare *Typha* and *Phragmites*, a competitive effect was calculated as the percentage of reduction of a plant growth parameter (shoot height, number of shoots, biomass) in the opposite compartment of competition mesocosms compared to control mesocosms of the same species, same salinity level and located in the same block:

$$\left(\frac{X_{\text{control}} - X_{\text{competition}}}{X_{\text{control}}} \right) \cdot 100$$

where X is a growth parameter. This simple competition index, often coined the “Relative Neighbourhood Effect index” (RNE), is quite commonly used to study the interaction between species (Weigelt and Jolliffe 2003). The use of RNE makes it possible to account for the inherent differences in biomass and density when comparing different species such as *Phragmites* and *Typha*. We tested the difference of RNE between the two species using ANOVA with block, species

and salinity as explanatory variables, and competition indices as response variables.

Finally, we compared spatial progression in the opposite compartment of competition and control, within each species, using shoot density in each of three equal sections progressively more distant from the separator. For this test, we used ANOVA, with salinity, competition treatment and section as explanatory variables and density as response variable.

Data were submitted to Box–Cox transformation when model assumptions of normality and/or homoscedasticity of variance were not met. We report all effects with $p < 0.1$. All statistical tests were performed using JMP IN 5.1 (SAS Institute Inc.) and R (R Development Core Team 2005).

Results

Roadside Ditches Experiment

In unvegetated zones, *Phragmites* progression was significantly greater than *Typha* ($p < 0.001$), with an average progression of 3.9 m yr^{-1} compared to 1.4 m yr^{-1} for *Typha*. The presence of *Typha* did not appear to slow down *Phragmites* progression: with an average of 3.3 m yr^{-1} , progression in competition sites was not significantly different from that in unvegetated sites (Table 1). There was no difference in *Phragmites* shoot density between unvegetated and competition sites, and this was also the case for *Typha*. For *Phragmites*, shoots were taller, and had more leaves and higher stem and aboveground biomass in competition than in unvegetated zones. *Typha* stems were taller in competition zones than in unvegetated zones (Table 1).

Mesocosm Experiment

Both species survived on their original side and partly colonized the opposite side of the mesocosms at all salinity levels and under all competition treatments. *Phragmites* flowered and set seeds in all treatments. *Typha* flowered and set seeds on the opposite side only in low and medium salinity. Both species showed optimal growth in low salinity. Salinity stress reduced shoot height and biomass in both species, and number of shoots in *Typha* (Fig. 3).

The effect of competition expressed in terms of RNE was significantly more severe on *Typha* than on *Phragmites* for all growth parameters (Fig. 3). For *Typha*, the reductions in number of shoots and biomass were always higher than 92 %, irrespective of salinity level. The reduction in shoot height for *Typha* was also significant and ranged between 20 and 77 %, depending on salinity level. For *Phragmites*, the number of shoots was reduced by competition, with 34 to

Table 1 Mean values (± 1 SD), and p-value of statistical differences for various growth parameters between *Phragmites* and *Typha*, according to the treatment (unvegetated vs competition sites), in the roadside ditch experiment

	Unvegetated sites	Competition sites	P value ¹
<i>Phragmites</i>			
Progression (m)	3.9 \pm 0.3	3.3 \pm 1.6	0.437
Density (shoots m ⁻²)	21.0 \pm 4.4	17.5 \pm 9.5	0.471
Biomass per shoot			
Leaf (g)*	5.9 \pm 3.0	7.4 \pm 3.6	< 0.001
Inflorescences (g)	1.5 \pm 1.2	1.4 \pm 0.9	0.568
Stem (g)*	15.2 \pm 7.8	18.8 \pm 7.5	0.002
Total aboveground biomass (g)*	22.5 \pm 11.3	27.2 \pm 10.7	0.005
Morphological characteristics			
Height (cm)	234.6 \pm 41.8	268.1 \pm 31.9	< 0.001
Diameter (cm)	0.7 \pm 0.1	0.7 \pm 0.1	0.143
Number of leaves	13.2 \pm 1.7	14.1 \pm 2.2	< 0.001
Number of nodes*	16.5 \pm 2.3	16.7 \pm 2.8	0.445
Biomass allocation per shoot			
Leaf (%)	26.3 \pm 6.0	27.7 \pm 10.0	0.994
Inflorescence (%)	6.7 \pm 3.2	5.2 \pm 2.6	< 0.001
Stem (%)*	67.6 \pm 5.4	67.6 \pm 6.9	0.115
<i>Typha</i>			
Progression (m)	1.4 \pm 0.4	n. a.	n. a.
Density (shoots m ⁻²)	19.8 \pm 7.5	13.0 \pm 8.4	0.204
Biomass per shoot			
Total aboveground biomass (g)*	24.3 \pm 16.9	25.4 \pm 14.0	0.117
Morphological characteristics			
Height (cm)	194.5 \pm 36.7	222.4 \pm 29.2	< 0.001
Diameter (cm)	1.4 \pm 0.4	1.5 \pm 0.3	0.743
Number of leaves	6.4 \pm 1.4	6.3 \pm 1.1	0.327

1: Progression and density were compared using a *t*-test. Differences in biomass, morphological characteristics, and biomass allocation were tested using a nested ANOVA. Site effects were significant for most characters (results not shown). Box-Cox transformation of data is indicated by an asterisk. For each species, $N=144$, (12 plants \times 6 sites \times 2 settings). *P* values <0.05 are in bold

64 % reduction depending on salinity level, although these reductions were not statistically significant (Fig. 3).

For *Typha*, there was an interaction effect between salinity and competition on root-shoot ratio, suggesting that at high salinity, *Typha* invests relatively more energy belowground. There was no interaction effect of competition and salinity on any trait for *Phragmites* (Fig. 3).

The effects of salinity and competition on spatial progression of shoots differed between *Typha* and *Phragmites* (Fig. 4). For *Typha*, both salinity and competition significantly slowed progression inside the opposite compartment. In low salinity, *Typha* colonized up to the opposite wall of the control mesocosms, while it only penetrated to 2/3 of the competition mesocosm. In high salinity, *Typha* reached the 2/3 mark of the mesocosms in the absence of *Phragmites*, and only to the first 1/3 in competition mesocosms. For *Phragmites*, there was no significant effect of salinity on the distribution of shoots. Indeed, at all salinity levels, in both control and competition

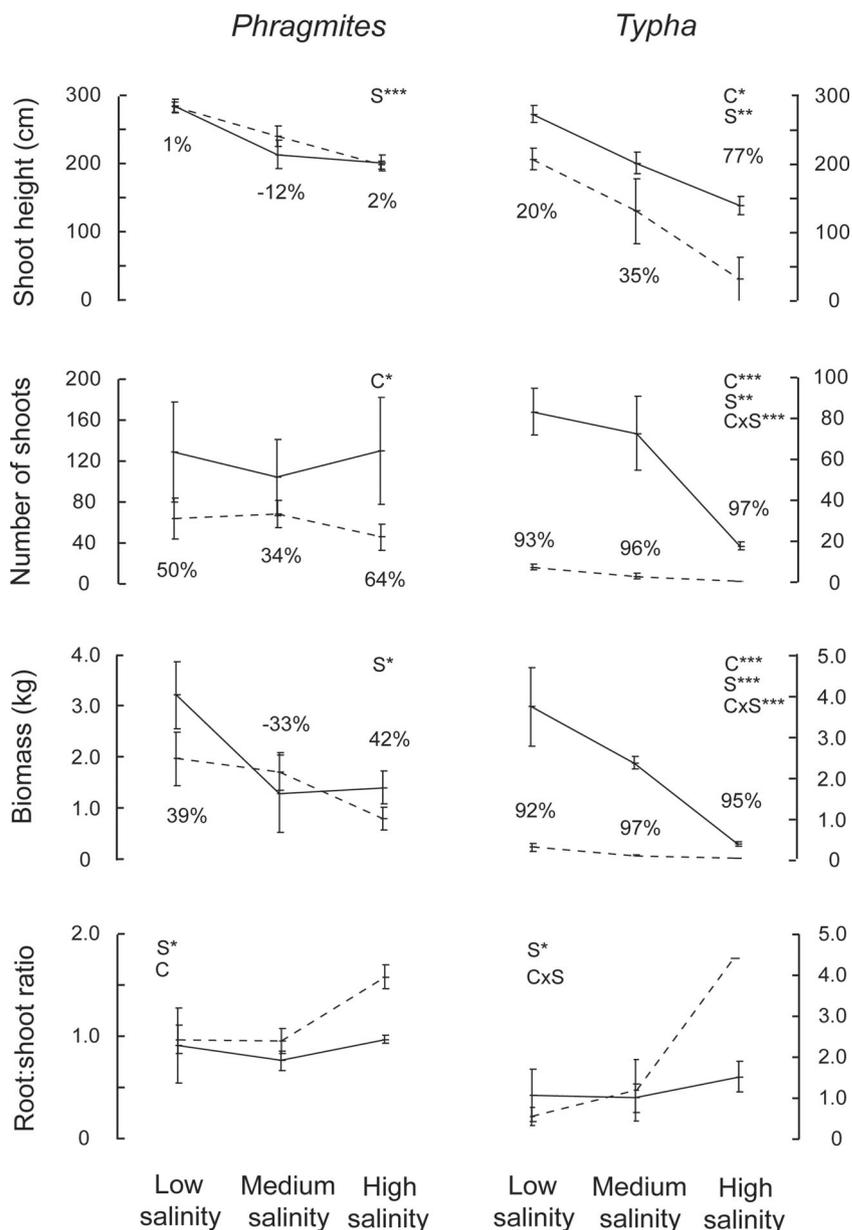
mesocosms, *Phragmites* colonized the opposite half up and at least some shoots reached the far edge. At low and medium salinity levels, the response was very similar: an apparent reduction in number of shoots due to competition was mainly restricted to the area near the central panel (first 1/3 of the opposite half).

Discussion

Outcome of Competition

Results from the roadside ditch experiment showed that *Phragmites* is able to colonize unvegetated sites faster than *Typha*, and linear progression of *Phragmites* was not slowed much by competition with *Typha*. In the mesocosm experiment, because of the very high density attained in the sections

Fig. 3 Growth parameters of *Phragmites* and *Typha* measured in the opposite compartment of competition mesocosms (dashed line) and control mesocosms (complete line) at the three salinity levels. Bars indicate standard error. Letters and asterisks in the right upper corner of each graph indicate significant effect of treatments from the ANOVA (C: competition; S: salinity; C×S: interaction competition×salinity; no asterisk: $0.05 < P < 0.10$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$) Percentages on the graph indicate Relative Neighborhood Effect (reduction in growth) at each salinity level. The RNE is significantly higher in *Typha* for shoot height ($p=0.002$), shoot number ($p=0.001$) and biomass ($p=0.005$)



planted prior to removal of the panel separating each species, competition was artificially maximized, leading to greater measurable competitive effects. Not surprisingly, both *Phragmites* and *Typha* progression were slowed down by interspecific competition. Yet, *Typha* was negatively affected by competition to a greater extent than *Phragmites*.

While both species have been cited as showing some tolerance to moderate salinity levels, the comparison of the competition index shows that *Phragmites* is globally more competitive than *Typha* at all salinity levels tested. According to Gorai et al. (2011), the high salinity tolerance of *Phragmites* seems to be due to its ability to lower its osmotic potential and adjust the osmotically active solutes in its leaves. In inland

North America, roadsides represent the most important pathway of invasion for *Phragmites*. It has been hypothesized that the increased salinity in roadside ditches caused by runoff of deicing salt may favor *Phragmites* over other less tolerant species (Maheu-Giroux and de Blois 2007; Jodoin et al. 2008). Our findings, which demonstrate a competitive advantage of *Phragmites* over *Typha* in clonal expansion under medium and high salinity levels, are consistent with this hypothesis. Interestingly, in a competition experiment between *Phragmites australis* and *Spartina alterniflora*, a higher salinity benefited *S. alterniflora* under higher salinity (Medeiros et al. 2013), showing that the salinity tolerance of *Phragmites* is still limited and may not provide a strong

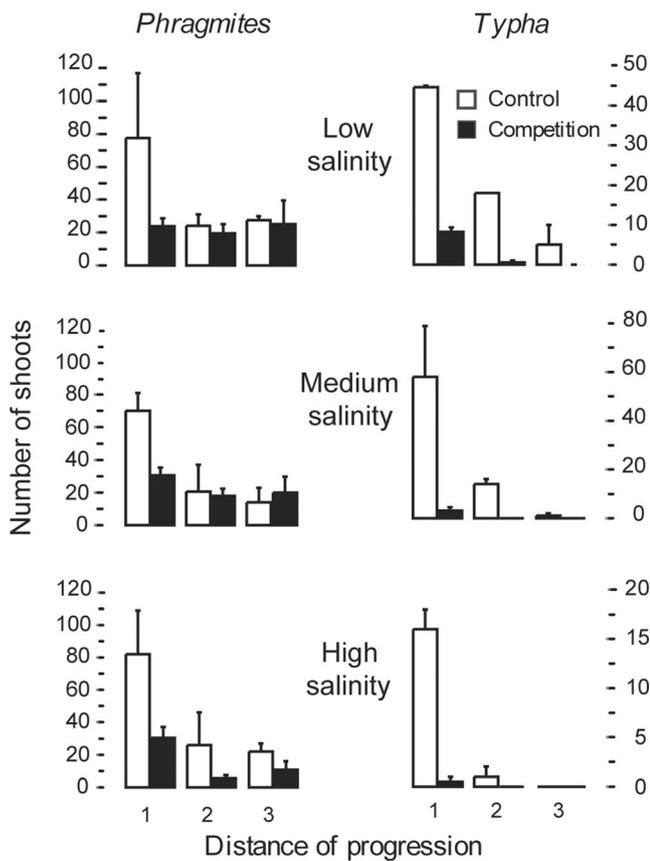


Fig. 4 Spatial distribution of the stems of *Phragmites* and *Typha* in the opposite compartment of control and competition mesocosms. Numbers represent distance of progression from the separator (1 : 0–23 cm; 2: 23–47 cm; 3: 47–70 cm). Competition and salinity have a significant effect on progression on *Typha* ($p=0.098$ and 0.076 respectively) but not on *Phragmites*

competitive advantage against halophytes in brackish tidal marshes.

One important environmental factor that may influence competitive outcome but that was not investigated in the current study is water level. At the establishment phase, *Phragmites* seedlings are less tolerant of submerged conditions than *Typha* (Coops et al. 1996). Also, on average, mature colonies of *Phragmites* can be found on drier parts of wetlands than *Typha*, although there is a wide range of overlap between the conditions favorable to both species. Water level in the experimental ditches and in our mesocosm experiment fell within the ideal range for *Typha* and *Phragmites*, so no conclusions can be drawn. We suspect that drier conditions may provide further advantage to *Phragmites* over *Typha*, with the inverse situation being the case in deeper water. The advantage of *Phragmites* under drier soil conditions could be due to its deeper rooting depth (Chun and Choi 2009).

A second important factor that may influence competitive outcome is morphological plasticity. Both the roadside ditch and the mesocosm experiments reveal insights about

morphological plasticity and resource allocation in relation to clonal growth. In the roadside ditch experiment, both species showed a stem-elongation response to interspecific competition. This density-dependent response is frequently exhibited by plants competing for light (Callaway et al. 2003; Kurashige and Agrawal 2005). For *Typha*, this response did not result in a significant increase in shoot biomass. In contrast, for *Phragmites*, the stem-elongation response, combined with an increase in number of leaves, resulted in a significant increase in shoot biomass. These results suggest that a higher morphological plasticity in the shoots of *Phragmites* might be an important advantage contributing to the high intrinsic competitive ability. We found no shoot-elongation response in our mesocosm experiment. We believe that in this latter context, competition was primarily for belowground space and minimally for light because of an edge effect allowing higher light intensity at the margins of the mesocosms.

Competition Experiments and Clonal Growth

There are widespread reports of the invasion of *Phragmites* within *Typha* stands in North America (Clevering and van der Toorn 2000; Meyerson et al. 2000; Chun and Choi 2009; Bellavance and Brisson 2010). Yet, in phytometer and pairwise competition experiments, *Typha* outperformed *Phragmites* (Szczepanska and Szczepanski 1982; Konisky and Burdick 2004; Keddy et al. 2000). We believe that this apparent contradiction is due to the different stages of plant development at which competition was studied. *Phragmites* seedlings are known to be intolerant to competition, and seedling establishment only takes place on bare ground, free of vegetation cover. It is thus not surprising that in competition experiments using seedlings, *Phragmites* does not fare particularly well. However, once well established, a *Phragmites* colony may show an exponential expansion through strong and rapid clonal growth, producing belowground an advancing dense front of rhizomes and roots. One commonly cited advantage of clonal growth is the physiological integration of ramets within the clone, allowing support of peripheral ramets invading more stressful habitats or expansion into neighboring vegetated zones (Ostrowski and Kenkel 2008). In transplantation and rhizome-severing experiments in saltmarshes in New England, Amsberry et al. (2000) showed that *Phragmites* first establishes in the high marsh and then expands clonally into the less favorable low marsh zone, using clonal integration.

For several invading wetland species, competition is mostly for space at the edge of well-established clones, and the outcome of competition may only be modeled by considering clonal growth. Competition patterns and processes differ, and spatial pattern becomes as or more important than density (Silvertown et al. 1992). While clonal integration may partly explain the success of expanding colonies of *Typha* and its

invasive status in several areas, both our experiments and field evidence show that *Phragmites* is superior at the expansion stage. The different processes underlying competition in seedling stages and between colonies, and the different potential outcome, show that an absolute competitive hierarchy between species with clonal growth only makes sense when the appropriate developmental stage is specified.

The experimental design we developed succeeded in better simulating competitive interactions for space between plants with clonal growth: our experimental results are more consistent with the general trend of a competitive advantage on the part of *Phragmites*, observed in our roadside ditch experiment and previous field studies, than with classical pair-wise competitive experiments. Yet, our mesocosm approach shares some of the same advantages (replication, control over treatments, etc.) and limitations (unrealistic soil conditions, edge effect, short-term, etc.) of pot competition experiments (Passioura 2006; Freckleton et al. 2009). As in conventional experimental approaches, it allows to determine which species is superior, or to determine a ranking (if more than two species are studied) that would probably still hold in comparable field conditions. However, exact quantitative reduction in plant performance can not simply be extrapolated from pot/mesocosm experiments to real field conditions. Some spatial processes important for plant interaction may be altered under the tight belowground confinement of the mesocosms. Yet, our approach may be useful in contributing to a better understanding of competition between clonal plants, especially if it is supplemented with other approaches, such as long-term field experiments under natural conditions.

Acknowledgments The authors thank Jean-François Dallaire, Noémie Boulanger-Lapointe and Vincent Gagnon for field assistance, Stéphane Daigle for his comments on experimental design and statistical analyses, and Sylvie de Blois and Karen Grislis for comments on a previous version of the manuscript. This research received financial support from the Natural Sciences and Engineering Research Council of Canada.

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