Spatial dynamics and morphological plasticity of common reed (*Phragmites australis*) and cattails (*Typha* sp.) in freshwater marshes and roadside ditches

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ABSTRACT

Over the last decades, the abundance of common reed has significantly increased in freshwater wetlands of eastern North America, and stands of this species are now commonly alternating with stands of cattails. Since these species share many characteristics, the contact zone between common reed and cattail stands may witness strong interspecific interactions. We surveyed stand dynamics in roadside ditches and freshwater marshes at these contact zones over three years, and we examined the morphological plasticity in response to neighbors. Results indicate that common reed is clearly gaining ground over time, while cattails stands are retreating. We also found annual variability in the spatial dynamics, suggesting that other factors, such as the effect of weather conditions on water level, may affect population processes. Interspecific interactions had a detrimental effect on both common reed and cattail biomass. However, common reed showed morphological plasticity in shoot height, number of nodes, and internodes length, while cattails did not. Our observations suggest that common reed has a net competitive advantage over cattails in roadside ditches and freshwater marshes.

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1. Introduction

Plant species composition has greatly changed over the last decades in North American wetlands, due to human activities and the invasion of exotic species (Farnsworth and Meyerson, 2003; Minchinton et al., 2006), such as the common reed (*Phragmites australis* (Cav.) Trin. ex Steud.). In the 1950s, common reed was found at a few scattered sites in the northeastern part of its distribution (Gervais et al., 1993). Since then, it has significantly increased in abundance in natural (Lavoie et al., 2003) and artificial wetlands (Delisle et al., 2003; Maheu-Giroux and de Blois, 2005), especially in roadside ditches (Brisson et al., 2010; Jodoin et al., 2008; Lelong et al., 2007). Common reed stands, alternating with pure or mixed stands of cattails (*Typha angustifolia* L., *Typha latifolia* L. and their hybrid *Typha × glauca* Godr.), are now very common in marshes and roadside ditches (Chun and Choi, 2009; Marburger et al., 2006). Common reed and cattails are clonal emergents that share many morphological traits, such as tall, unbranched shoots and a network of rhizomes, usually forming dense monospecific stands. These species can also thrive in a wide range of abiotic conditions (Grace and Harrison, 1986; Marks et al., 1994; Mal and Narine, 2004), and are considered invasive in many areas (Shih and Finkelstein, 2008). Given their similarity in habitat preferences and traits, the contact zone between common reed and cattail stands is probably characterized by intense interspecific interactions.

A pair-wise competition experiment showed that broad-leaved cattail is a better competitor than common reed (Szczepanska and Szczepanski, 1982). Broad-leaved cattail produced more biomass in competition with common reed than in monoculture. In contrast, common reed biomass was lower when planted with cattail than when grown alone. A field experiment including salinity and flooding as stressors found a small competitive advantage to cattail (this time *T. angustifolia*) over common reed (Konisky and Burdick, 2004). On the other hand, observational studies in freshwater habitats in North America have shown that common reed is increasing its dominance over time and is displacing native wetland species, including cattails (Choi and Bury, 2003; Chun and Choi, 2009; Lavoie et al., 2003; Meyerson et al., 2000). Chun and Choi (2009) attributed the expansion of common reed into cattail wetlands to its efficient shoot development and the adaptability of its roots and rhizomes to fluctuating water tables.

Phenotypic plasticity, a property that increases fitness, can alter the balance of competition in a plant community (Bradshaw, 1965; Callaway et al., 2003; Trewavas, 2003). This plasticity can be defined as the changes in the phenotype of an organism induced by different environmental conditions (Alpert and Simms, 2002; Callaway et al., 2003; Kurashige and Agrawal, 2005). These conditions are numerous and include the presence or absence, and identity of neighbors (Umeki, 1995; Callaway et al., 2003). Thus, plasticity in response to neighbors may influence the dynamic relationship

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between competing species. Higher phenotypic plasticity is frequently cited as a trait that can enhance the ability to invade and gain dominance in a community (Claridge and Franklin, 2002; Funk, 2008). Clevering (1999) showed that clones of common reed originating from infertile habitats were less plastic than those from fertile and eutrophicated habitats. Vretare et al. (2001) found that common reed exhibits phenotypic plasticity in biomass allocation and morphology when exposed to different water depths. Wetzel and van der Valk (1998) found that broad-leaved cattail seedlings allocated more biomass to stem when in competition with *Phalaris arundinacea* L.

We examined spatial dynamics in common reed and cattails, and the morphological plasticity in response to interspecific interaction, in natural and artificial wetlands. Our specific objectives were: (1) to determine the spatial and temporal dynamics of common reed and cattails at their contact zone, in freshwater marshes and in roadside ditches and (2) to determine the effect of interspecific interaction at the contact zone in roadside ditches on common reed and cattails morphology.

We monitored, over the course of three years, the progression of common reed and cattails in two freshwater marshes and at eight contact zones in roadside ditches. We also measured several morphological characteristics of common reed and cattails collected in roadside ditches, in mixed and monospecific stands.

2. Methods

2.1. Freshwater marsh surveys

Two protected inland freshwater marshes located in the Hochelaga (Montreal) Archipelago (Québec, Canada) were surveyed. The first marsh is located in the Parc national des Iles-de-Boucherville (PNIB; latitude: 45°35′52.98″N; longitude: 73°28′02.24″W). The 8 km^2 park is composed of a few low-lying islands and channels in the middle of the Saint-Lawrence river. PNIP is dominated by open fields and wet meadows on the islands, and wide marshes around the edges and in the channels, with a few forests and inland marshes. Shallow marshes and wet meadows are dominated by emergent macrophytes, with a high degree of invasion by common reed and reed canarygrass (*P. arundinacea* L.; Hudon, 2004). The study site is a small (0.2 ha), elongated, inland wetland located on Sainte-Marguerite Island. Maximum water depth is approximately 50 cm in spring and the wetland occasionally dries out completely by late summer. Common reed and cattails, mostly represented as two large adjoining stands, largely dominate the wetland. The surveyed area consisted of a 22.8 m linear contact zone between the common reed and cattail stands.

The second marsh is located in Parc-nature de la Pointe-aux-Prairie (PNPP), at the Eastern tip of Montreal Island (latitude: 45°41′13.33″N; longitude: 73°31′27.67″W), some 10.5 km North-West of PNIP. PNPP (2.6 km^2) is dominated by open fields, forests and a network of marshlands in depressions. The surveyed area consisted of a 27.6 m long contact zone between nearly pure common reed and cattail stands in a shallow part of the wetland (water depth < 30 cm).

Surveys were conducted at the end of summer (late August, early September) in three consecutive years (2003–2005). A permanent linear transect approximately following the contact zone of 2003 was established in each wetland. Every 30 cm, the perpendicular distance between the transect and the cattail closest to the common reed zone was measured, and reciprocally for common reed (Fig. 1). There were 76 measuring points along the transect in PNIB and 92 in PNPP. The difference in distance from the stand to the transect at a specific point between two consecutive years is an estimate of the progression (or regression) of the stand at this location. Using
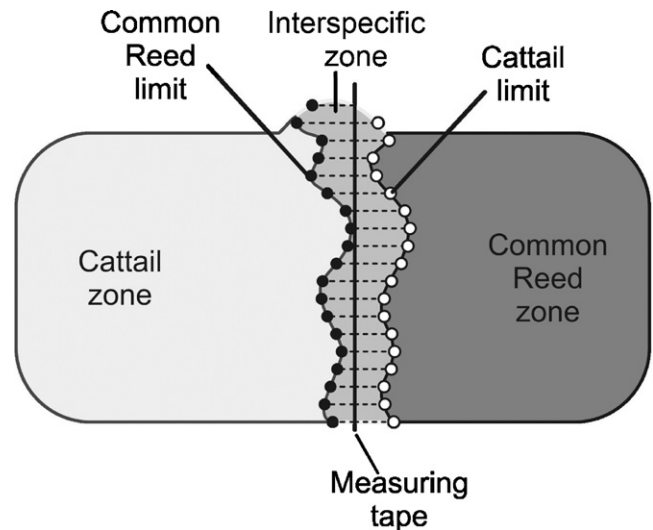

Fig. 1. Field measurement for the annual survey of the front location at the contact zone between common reed and cattails in the marshes. The black vertical line represents the transect (marked on the field by a measuring tape). The horizontal dotted lines at the right side represent the distance from the transect to the cattail nearest to the common reed zone. The horizontal line at the left represents the distance from the transect to the common reed shoot nearest to the cattail zone. Nearest cattail to the common reed zone and nearest common reed to the cattail zone are respectively represented by white and black dots.

2003 as the reference year, we calculated for each species the mean annual progression and the annual percentage of advances in 2004 and 2005 (annual percentage of points where the species advances in the direction of the opposite species).

2.2. Roadside ditch survey

Study sites in roadside ditches were located in a 3 km segment of highway 640 between exit 8 (Deux-Montagnes; latitude: 45°32′38.69″N; longitude: 73°55′37.49″W) and exit 2 (St-Joseph-du-Lac; latitude: 45°31′45.85″N; longitude: 73°58′21.23″W), Quebec, Canada. Within the segment of highway under study, the landscape is flat and growth conditions (water level, soil type, orientation) are homogeneous. The roadside ditches are 2–4 m wide in their lowest portion. They are mostly colonized by nearly pure colonies of cattails and common reed, presumably favored by road disturbances such as occasional ditch cleaning and de-icing salt (Brisson et al., 2010). Except in spring or during strong rainfall event, water level is always low, with little or no standing water in summer. The survey took place during the same periods as for the natural wetlands.

Eight contact zones between common reed and cattail stands in roadside ditches were selected as study sites. There was never less than 100 m between each site. The main selection criterion was that stands had to be at least 10 m long for each species. We did not differentiate between narrow-leaved and broad-leaved cattails due to a large number of individuals with intermediate characters, suggesting hybridization (*Typha* × *glauca*). At the 8 contact zones, permanent markers were planted in 2003 at the location of the last common reed shoot in a cattail stand, in order to monitor the annual progression of this species over the years. The progression of common reed in the cattail stand from this reference point was measured at the end of each growing season in 2004 and 2005. However, progression of cattails could not be measured in the same way: since a few cattail shoots were occasionally present among some of the common reed stands, we could not identify the definite ending point of cattail stands. Rather, we developed a simple measure of spatial dynamics based on spatial changes in densities.
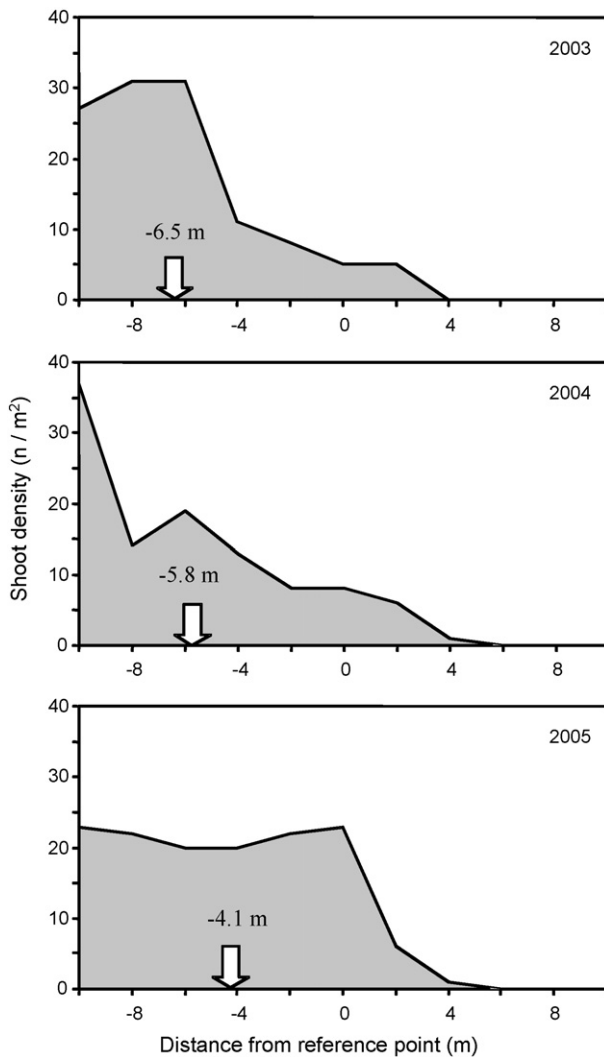
Fig. 2. Example of graphs used to calculate the position of the centroid of density of common reed at one particular site. Arrows indicate the position of the centroid of density for each year.

From the reference point, shoot density was measured at the end of each growing season in 2003–2005: every 2 m on a total of 20 m (10 m on each side of the reference point), we counted the number of shoots included within a 1 m² circular quadrat. For a given site and a given year, cattail densities were represented in a graph according to the location along the sampled transect, resulting in a "polygon of density". The area of the polygon was calculated and the position of its centroid along the distance (*x*-axis) was determined (Fig. 2). The centroid is an estimate of the center of the stand along the transect based on the distribution of shoots, and its location corresponds to the distance from the reference point to where the surface of the polygon is divided in two halves. Thus, as an alternative to measuring progression of a "front", the relative position of the centroid of density from one year to the next provides an integrated measure of progression of the whole colony of cattails along a ditch, within the limit of the transect. For comparison purposes, we also used the same approach of changes in centroid location to estimate common reed progression as a complementary measure to the one based on the last shoot. It must be noted that the absolute measure of progression of the centroid depends on the length of the transects surveyed: for example, the method becomes less sensitive to progression rates as the centroid approaches one of the edges of the transect (centroids were never less than 3 m from

the edges in our case). As a result, while this approach provides an appropriate relative measure of spatial dynamics between years or between species within a site, interpretation of the absolute values and comparison with progression rates obtained with other methods should be done with care.

In September 2005, aboveground parts of common reed and cattails were harvested and dried to test for morphological differences between plants in mixed stands and monospecific stands. In each of the 8 sites, twelve mature common reed shoots with panicles were randomly selected and cut at ground level in the monospecific common reed stands and twelve more in mixed stands. The same was done for cattails. However, since the number of mature cattails with spikes was occasionally insufficient in mixed stands, we also sampled large shoots with no spikes, in both mixed and monospecific stands, and treated them separately in the analysis. The measures taken were shoot height, shoot diameter, number of leaves, leaf dry weight, and spike or panicle dry weight. In addition, number of nodes, the length of the first 9 internodes, and stem biomass were taken for common reed. From these measures, total aboveground dry weight was calculated as well as biomass allocation to leaves and to reproduction, and for common reed only, biomass allocation to stems (leaves mostly basal in cattails).

2.3. Statistical analysis

T-tests were used to test for differences in annual mean progression between common reed and cattails in each of the two freshwater marshes, and in the roadside ditches. Pearson correlation was used to test for correlation of progression between species for a given year. Differences in morphological characters between settings (mixed vs. monospecific stands) were analyzed using a nested ANOVA, with sites nested within settings and individual plants nested within sites. Data were submitted to Box–Cox transformation when model assumptions of normality and/or homoscedasticity of variance were not met

3. Results

3.1. Freshwater marshes surveys

In freshwater marshes, the dynamics of common reed and cattails is complex along the contact zone, with advances and retreats for both species. However, there is a net overall advantage in favor of the common reed. In the PNIB marsh, common reed had a greater mean progression ($p < 0.001$ for both years) and a higher percentage of advances than cattail (Fig. 3). However, common reed and cattail progression at each location was not correlated, neither in 2004 nor in 2005. In 2005, common reed mean progression ($p < 0.001$) and percentage of advance were greater than in 2004. For cattail, the trend was opposite, with lower mean progression ($p < 0.001$) and lower percentage of advances in 2005. While cattail made little progression in 2004, the stands clearly retreated in 2005. In the PNPP marsh, both species progressed in the opposite stands in 2004, with no significant difference between species. In 2005, reed still progressed in the reed stand at a similar rate, while cattails showed no progression or regression, with a significant difference between the two species in mean progression ($p < 0.005$), and a significant difference between cattail in 2004 and 2005 ($p < 0.001$).
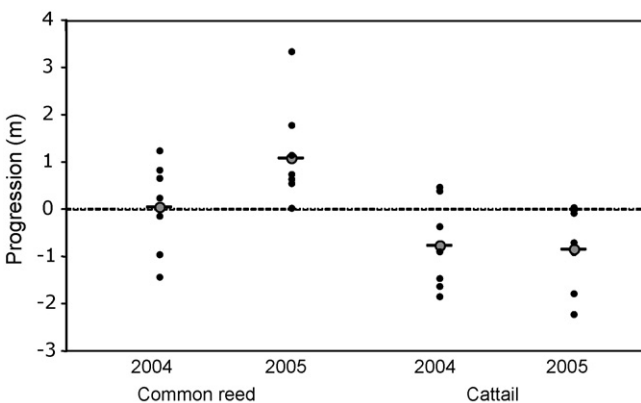
3.2. Roadside ditches survey

In roadside ditches, common reed showed a strong overall progression at the expense of cattail (Fig. 4). In 2004 at the 8 sites studied, common reed mean progression from point 0 based on the location of the last shoot was 1.7 ± 0.6 m, with a minimum of 1 m and a maximum of 2.9 m. In 2005, mean progression was
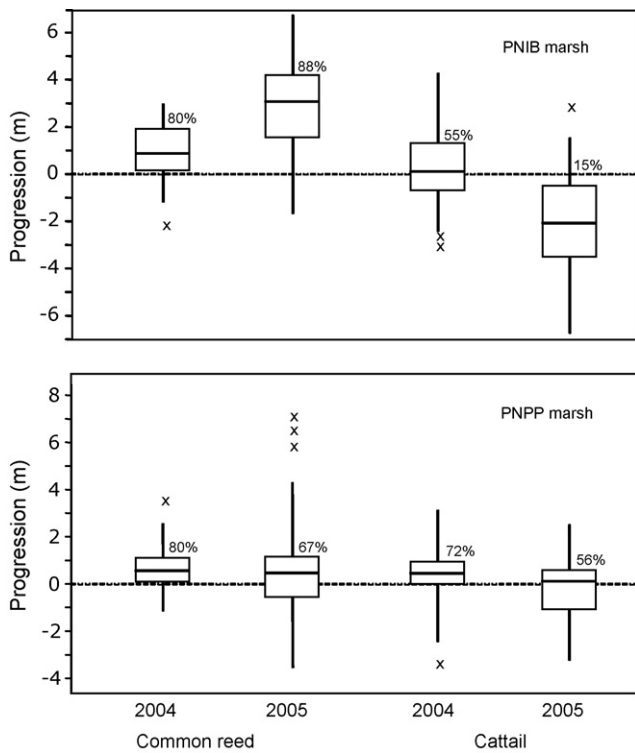
Fig. 3. Box-plots of progression of common reed and cattail, in 2004 and 2005, in the Parc national des Iles-de-Boucherville (PNIB) and in the Parc-nature de la Pointe-aux-Prairies (PNPP) freshwater marshes. Percentage of points with positive progression is presented along each Box-plot.

3.7 ± 1.5 m, with a minimum of 2 m and a maximum of 5.6 m. For both years, common reed progressed in the cattail zone at the 8 sites. When considering the progression of the centroids of density over both years (from 2003 to 2005), common reed mean centroid advanced in 7 of the 8 sites and cattails mean centroid regressed in 7 of the 8 sites. However, there appeared to be a difference between years for common reed, with a lower mean progression of the centroid density in 2004 compared to 2005 ($p = 0.06$) and even a regression in 3 sites in 2004 (Fig. 4). For cattail, the regression was steady, with no differences between years ($p = 0.91$). There appeared to be a strong negative correlation between common reed and cattail progression in a particular site in 2005 (Pearson = −0.65)

Fig. 4. Progression of centroid of density for common reed and cattail, in 2004 (i.e., from 2003 to 2004) and 2005 (i.e., from 2004 to 2005), in 8 sites located in roadside ditches along highway 640 between Deux-Montagnes and St-Joseph-du-Lac. Not all sites are apparent because of overlap. Grey circles are averages. Because of a sampling error, density data for common reed in 2004 for one site were not considered.

Table 1
Mean values (±S.D.) and results of nested ANOVA (*p*-value) for setting effect (monospecific stands or mixed with cattail) for biomass, morphological characteristics, and biomass allocation for shoots of common reed. Site effects were significant for all characters (results not shown). Box–Cox transformation of data is indicated by an asterisk (*). $N = 188$, (12 plants × 8 sites × 2 settings). *p*-Values < 0.05 are in bold.

Common reed	Mixed stands	Monospecific stands	*p*-Value
Biomass per shoot			
Leaf (g)	6.7 ± 3.0	8.8 ± 3.3	**<0.001**
Inflorescence (g)	4.3 ± 2.6	4.5 ± 3.1	0.571
Stem (g)	25.8 ± 12.5	32.5 ± 15.0	**<0.001**
Total aboveground biomass (g)	36.8 ± 17.1	45.8 ± 20.4	**<0.001**
Morphological characteristics			
Height (cm)	257.7 ± 35.7	303.6 ± 37.5	**<0.001**
Diameter (cm)	0.79 ± 0.18	0.84 ± 0.18	**0.030**
Number of leaves	11.3 ± 1.6	11.9 ± 2.1	**0.006**
Number of nodes	19.8 ± 2.4	22.4 ± 2.5	**<0.001**
Length of internode 1 (cm)	10.5 ± 5.4	10.7 ± 5.4	0.782
Length of internode 2 (cm)	15.6 ± 6.3	16.1 ± 6.5	0.581
Length of internode 3 (cm)	18.8 ± 5.9	20.8 ± 6.3	**0.010**
Length of internode 4 (cm)	21.4 ± 6.1	23.4 ± 5.4	**0.011**
Length of internode 5 (cm)	20.8 ± 4.9	23.9 ± 4.7	**<0.001**
Length of internode 6 (cm)	19.6 ± 4.3	22.5 ± 4.3	**<0.001**
Length of internode 7 (cm)	17.5 ± 4.3	20.2 ± 4.6	**<0.001**
Length of internode 8 (cm)	15.7 ± 4.0	17.6 ± 4.5	**<0.001**
Length of internode 9 (cm)	14.4 ± 3.4	15.9 ± 3.9	**<0.001**
Biomass allocation			
Leaf (%)	19.0 ± 5.4	20.0 ± 4.1	0.114
Inflorescence (%)	11.3 ± 3.9	9.3 ± 4.1	**<0.001**
Stem (%)*	69.6 ± 6.6	70.7 ± 3.9	0.250

although this relation was not significant (*p*-value = 0.11), most likely due to our low replication. There was no such discernable pattern of relation between cattail and common reed in 2004.

3.3. Morphological plasticity

Common reed showed more plasticity than cattails for the morphological traits we measured. In common reed, shoots from monospecific stands were taller and larger, had more nodes, and the lengths of internodes 3–9 were greater when grown in monospecific than in mixed stands (Table 1). Also, leaf biomass, stem biomass and total aboveground biomass were larger in monospecific stands, but a smaller percentage of biomass was allocated to the inflorescence (Table 1). For cattail, both with or without inflorescence, total aboveground biomass was higher in monocultures (Table 2). Leaf–stem and spike biomass was also higher for cattail with inflorescence in monoculture. There were no significant differences in height, diameter, number of leaves, and biomass allocation between leaf–stem and inflorescence was not significantly different between plants in monocultures and plants in mixed stands.

4. Discussion

Results from the spatial dynamics surveys indicate that common reed was clearly gaining ground in the cattail colony during the period of the surveys, both in natural wetlands and in roadside ditches.

Comparison of common reed rates of expansion measured in different studies has shown that this rate varies among marshes (Farnsworth and Meyerson, 2003). In the two natural wetland sites we surveyed, there were both differences in progression between the two years and between sites. Common reed advance in PNIB was twice as important in 2005 compared to 2004, but there was little interannual difference in PNPP. Cattail lost more ground in 2005 in both marshes. In freshwater marshes, water level may influence the spatial dynamics of these species (Grace and Wetzel, 1981;

Table 2
Mean values (±S.D.) and results of ANOVA (p-value) for biomass, morphological characteristics, and biomass allocation for shoots of cattail with or without inflorescence, in monospecific stands or mixed with common reed. Cattail with inflorescence: total N = 164 (from 14 to 26 depending on site); without inflorescence: total N = 64 (from 0 to 19 depending on site). Site effects were significant for all characters (results not shown). p-Values < 0.05 are in bold.

Cattails with inflorescence	Mixed stands	Monospecific stands	p-Value
Biomass per shoot			
Leaf–stem (g)	16.7 ± 6.0	23.4 ± 7.8	**<0.001**
Spike (g)	6.1 ± 2.5	7.3 ± 2.2	**0.004**
Total aboveground biomass (g)	22.8 ± 7.7	30.7 ± 9.1	**<0.001**
Morphological characteristics			
Height (cm)	194.4 ± 17.7	192.6 ± 18.0	0.648
Diameter (cm)	1.2 ± 0.3	1.3 ± 0.3	0.707
Number of leaves	6.4 ± 1.1	6.8 ± 1.0	0.602
Biomass allocation			
Leaf–stem (%)	72.9 ± 6.3	75.5 ± 5.7	0.886
Inflorescence (%)	27.0 ± 6.3	24.5 ± 5.7	0.886
Cattails without inflorescence			
Biomass per shoot			
Total aboveground biomass (g)	16.5 ± 7.0	18.3 ± 9.2	**0.043**
Morphological characteristics			
Height (cm)	218.7 ± 27.0	211.1 ± 30.3	0.324
Diameter (cm)	1.5 ± 0.4	1.7 ± 0.6	0.156
Number of leaves	6.3 ± 1.3	6.2 ± 1.2	0.140

Marks et al., 1994). Although there is a very large overlap in terms of their tolerance to water depth, common reed occupies drier portions of the gradient compared to cattail (Asaeda et al., 2005). Moreover, common reed can retreat when summer water level is higher than 50 cm (Hudon et al., 2005). Windham (1999) found that, within a marsh, there are variations in the rate of expansion of common reed that are related to micro-site variations in water level. Chun and Choi (2009) documented progression of common reed in cattail wetlands in Indiana and attributed the competitive advantage of common reed to a greater vegetative expansion of its rhizomes under varying water levels. In our study sites, water level was well within the tolerance limits of both species, but there was some spatial heterogeneity that might have played a role in the competitive outcome at the contact zone. The largest gain in common reed at PNIB may be explained by the fact that this site has a lower summer water level than PNPP. The interannual difference in progression could be due to climatic conditions such as temperature and precipitation, which also influence water level. Hudon et al. (2005) found annual variability in vegetative gains of common reed, with maximal progressions measured the year following a fall in water level. The same pattern may explain the largest retreat of cattail at both sites in 2005 and the largest gain in common reed in PNIB, total precipitation at our study sites being lower in 2004 (899 mm) than in 2003 (1122 mm; Environment Canada, 2010).

In roadside ditches, we found a strong pattern of advance of common reed over cattail, consistent with the recent expansion of common reed along roadsides reported by others (Delisle et al., 2003; Maheu-Giroux and de Blois, 2007). Yet, cattail is known to grow well in the conditions found in roadside ditches such as frequent disturbances, higher salinity due to de-icing salt and higher nutrient level due to leaching from nearby agricultural fields (Galatowitsch et al., 1999; Grace and Harrison, 1986; Woo and Zedler, 2002). Not surprisingly, it is highly invasive in these habitats (Grace and Harrison, 1986; Olson et al., 2009). Cattails are considered to have strong competitive abilities and it is even suspected that they secrete allelochemicals into the rhizosphere (Jarchow and Cook, 2009). However, our study shows that in roadside ditches, as in natural wetlands, common reed displaces well-established cattail stands. There was little variation in cattail and common reed

progression between sites, probably because of the lack of differences in water level along the roadside ditches under study. The largest advance of common reed in 2005 compared to 2004 suggests a similar climatic influence on spatial dynamics as the one observed in natural wetlands.

While common reed has an advantage in spatial expansion over cattail, we observed a negative effect of interspecific competition on both common reed and cattail biomass. For common reed, this result is in accordance with Chun and Choi (2009) who found that biomass per shoot of either species was lower in mixed stands compared to monospecific stands. We found that competition not only affected the biomass of common reed but also its morphology and biomass allocation. With its longer shoots, higher number of nodes and longer internodes in monospecific stands, common reed seems to exhibit a shade-induced stem elongation response. This response may be due to a decrease of the red to far-red light ratio, which allows plants to adjust their morphology to improve light interception in dense stands (Harley and Bertness, 1996; Jarzyna, 2002; Kurashige and Agrawal, 2005). The fact that this response occurs in monospecific stands suggests that intraspecific competition for light between common reed shoots is more intense than when mixed with cattail, which have shorter shoots that are less likely to shade common reed.

Contrary to common reed, cattail showed no plasticity in morphology or biomass allocation in this study. Cattail biomass was reduced in mixed stand, with both vegetative structures (stem and leaves) and spikes apparently contributing to this reduction. Thus, the effect of interspecific competition appeared to be a simple reduction in size with no apparent reallocation of resources or changes in morphology. In the mixed stands, we found fewer cattails with spikes than in monospecific stands, further suggesting a negative effect of common reed on cattails. Our study suggest that common reed is a more plastic species than cattail, and this characteristic may contribute to its advantage in the balance of competition.

Acknowledgements

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