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ORIGINAL RESEARCH

Expansion of *Phragmites australis* (Cav.) Trin. ex Steud. (Common Reed) into *Typha* spp. (Cattail) Wetlands in Northwestern Indiana, USA

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Abstract Expansion of *Phragmites australis* (Cav.) Trin. ex Steud. (common reed) into stands of *Typha* spp. (cattail; *Typha australis* L. and *T.* x *glauca*) is common in the wetlands of northwestern Indiana (USA). To understand this phenomenon better, we investigated the production of shoot sprouts and proportional allocation of biomass as well as a potential role for the water table in the relative dominance of each species. The reduction in sprouts from rhizomes upon vegetative expansion of *Phragmites* appeared to be the most likely process causing the decline of *Typha*. The latter had a shoot density of 39/m^2 in plots without *Phragmites*, but this dropped to 13 shoots m^{-2} in plots that had been invaded by *Phramites*. Such a decline was likely caused by reduced reserves; e.g., the belowground biomass of *Typha* decreased from 11.3 g m^{-2} without *Phragmites* to 8.1 g m^{-2} with *Phragmites*. The latter also reduced its belowground biomass but not its shoot density in the presence of *Typha*. The mean weight of *Phragmites* shoots was 2.9 g, and nearly all produced inflorescences. Meanwhile, *Typha* failed to develop spadices despite its shoots having a greater biomass (7 g). This suggests that *Phragmites* is more efficient than *Typha* in shoot growth. Springtime flooding appeared to promote the sprout of *Typha* shoots from shallow rhizomes (≈18 cm below the soil surface), whereas the shoot density of *Phragmites* showed no correlation with water level in that season. Deep-rooted *Phragmites* (≈39 cm) occurred on both high and low water-table sites, whereas the shallow-rooted *Typha* was limited to only the former. *Phragmites* will likely continue its expansion, by vegetative sprouts from rhizomes, into *Typha* wetlands.

Keywords Biomass · Expansion · *Phragmites australis* · *Typha* · Water table

Introduction

The spread of invasive species, both native and nonnative, is common in disturbed freshwater wetlands in North America (Wilcox et al. 1985, 1986; Ellison and Bedford 1995; Galatowitsch et al. 1999; Choi 1999/2000; Lougheed et al. 2001; Choi and Bury 2003). Choi (1999/2000) has reported that over 97% of the wetlands in the Grand Calumet River watershed in northwestern Indiana comprise more than 120 such invasive species, including *Typha* spp. and *Phragmites australis* (Cav.) Trin. ex Steud. (common reed).

Two species of *Typha* and their hybrid occur in the Great Lakes region: *Typha latifolia* L. (broad-leaved cattail), native to North America (Gleason and Cronquist 1991); and *Typha angustifolia* L. (narrow-leaved cattail), introduced from Europe (Stuckey and Salamon 1987). The latter is considered invasive and problematic because of its ability to spread rapidly and establish monospecific stands in the freshwater wetlands of the northeastern and Great Lakes regions (Galatowitsch et al. 1999; Selbo and Snow 2004). *T. angustifolia* often hybridizes with *T. latifolia* L. to form *Typha* x *glauca* (Smith 1987; Gleason and Cronquist 1991; Eggers and Reed 1997). The occurrence and aggressive expansion of this hybrid have also been noted throughout the Great Lakes states (Galatowitsch et al. 1999).

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P. australis (hereafter *Phragmites*) is another undesirable species that shares a similar geographical and ecological range with *Typha* spp. (McNabb and Batterson 1991; Marks et al. 1994; Galatowitsch et al. 1999; Choi 1999/2000; Ailstock et al. 2001; Saltonstall 2002; Choi and Bury 2003; Pagter et al. 2005; White et al. 2007; Carlson et al., in press). In all, 27 haplotypes occur in North America; the spread of the Eurasian haplotype (type M) is the most aggressive (Saltonstall 2002).

Although *Typha* species (hereafter *Typha*) and *Phragmites* share many characteristics of "weedy" invasive species (McNaughton 1966; Bjork 1967; Haslam 1971; Baker 1974; Smith 1987; Gleason and Cronquist 1991), *Phragmites* often exhibits dominance when they occur together. Wilcox et al. (1986) have observed that the expansion of *Typha* is followed by invasions of *Phragmites* in northwestern Indiana wetlands. Choi and Bury (2003) have found that dominance of the invading *Phragmites* then increases in pre-existing *Typha* stands.

Phragmites usually occurs on the upper fringes or elevated areas of wetland basins (Haslam 1970, 1971; Marks et al. 1994; Bart and Hartman 2000; Rice et al. 2000; Ailstock et al. 2001; Hudon 2004) where water tables are likely low. In contrast, *Typha* normally occurs in depressions where those tables are relatively high (Wilcox et al. 1986; Eggers and Reed 1997). Both Wilcox et al. (1986) and Choi and Bury (2003) note that the colonization of *Phragmites* usually begins in raised mounds and then expands to *Typha*-dominated depressions. This may suggest that the former can grow on sites with either low or high water tables, whereas the latter prefers an elevated table. *Phragmites* usually is also taller (Haslam 1970, 1971; Smith 1987; Gleason and Cronquist 1991; Eggers and Reed 1997), suggesting its more efficient shoot growth.

The purpose of this study was to investigate how dominance by *Typha* declines upon the expansion of *Phragmites*. We tested three hypotheses: (1) the concurrence of *Typha* and *Phragmites* diminishes the above- and belowground biomass production of both species; (2) reductions in belowground biomass suppress shoot production by *Typha* but not necessarily by *Phragmites*, and (3) the absence of springtime flooding discourages shoot formation by *Typha* but not necessarily by *Phragmites*. Therefore, we compared the above- and belowground biomasses and shoot densities of *Phragmites* and *Typha* in the absence and presence of each other, as well as their rooting depths. We also evaluated water tables within individually populated plots and examined correlations between shoot densities and water levels for each species.

Materials and Methods

Study Sites

Our study sites were located along the southern coast of Lake Michigan in northwestern Indiana, USA (Fig. 1). For 1965 through 1994, the mean annual precipitation was 96 cm, and mean January and July temperatures were approximately −5°C and 23°C, respectively (Garwood 1996). Geomorphology in that region is best described as a "lake plain," a landscape with repeated patterns of sand dune ridges and swales formed by the retreating and fluctuating shoreline of Lake Michigan during the past 14,000 years since the Wisconsin glaciation (Reshkin 1981; Thompson 1992; Chrzastowski et al. 1994; Labus et al. 1999).

We selected three wetland sites that were infested by *Typha*, *Phragmites*, or both (Fig. 1). All *Phragmites* individuals that occurred in our study area appeared to be of the European haplotype M, based on our field identification (Blossey 2004) and RFLP (restriction fragment length polymorphism) DNA analysis (Saltonstall 2003). The occurrence of *Typha* x *glauca* has been reported in the Indiana Dunes National Lakeshore (Marburger et al. 2005). However, because *T. angustifolia* and *T.* x *glauca* are morphologically and ecologically similar, it is hard to distinguish them in the field (Gleason and Cronquist 1991; Eggers and Reed 1997). Although RAPD (randomly amplified polymorphic DNA) markers have been used to examine these species (Kuehn and White 1999; Selbo and Snow 2004; Marburger et al. 2005), this molecular technique is often time-consuming and expensive. Due to this difficulty in field identification, we combined *T. angustifolia* and *T.* x *glauca* into a single taxon of *Typha* for this project. No *T. latifolia* occurred in our study area.

Our first site was on a floodplain along the Grand Calumet River (41°36′ N, 87°28′ W). Its soil is best described as Carlisle and Tawas muck mixed with Oakville sand (USDA Soil Conservation Service 1992). Little or no *Phragmites* existed there in 1972, according to an aerial photo from that year (USDA Soil Conservation Service 1992). However, a photo from 1990 (available at Northwestern Indiana Regional Planning Commission, www.nirpc.org) showed an extensive occurrence of that species. Therefore, we could assume that this invasion on that site began between 1970 and 1990. The second site was a floodplain of the Little Calumet River (41°34′ N, 87°28′ W), adjacent to the US Interstate Highway 80/94. The major soil type is Pewamo Series (poorly drained, silty clay loam; USDA Soil Conservation Service 1992). Like the first site, our aerial photo interpretation suggested a major invasion of *Phragmites* prior to 1990. The third site was a depression that was impounded by a railroad in the Oak Ridge Prairie Nature Preserve (41°30′ N, 87°24′ W). Maumee series (wet fine sand) is its major soil type (USDA Soil Conservation Service 1992). Unlike with the two rivers, *Typha* dominated this prairie site, according to the 1990 aerial photo, and *Phragmites* began to invade in the mid-1990s (personal observation).

Sample Plots

A total of 39 plots (2×2 m) were established on these three sites in March, 2004 (Fig. 1). According to our aerial photos and preliminary field survey, approximately two thirds of the Grand Calumet River site was composed exclusively of *Phragmites*, and the remaining one third included both *Phragmites* and *Typha*. Following this proportion, we randomly chose ten plots that contained only *Phragmites* (hereafter *Phragmites* plot) and five that were mixed *Phragmites* and *Typha* (hereafter mixed plot) within a 20×100 m transect belt perpendicular to the river channel.

Both species occurred together on approximately two thirds of the Little Calumet River site, and the remaining one third was exclusively *Typha*. This site had 14 plots: two *Phragmites*, eight mixed, and four covered solely by *Typha* (hereafter *Typha* plots) within a 20 m (east–west)×100 m (north–south) rectangular section. About half of the Oak Ridge Prairie site included both species, while the other half was occupied by *Typha*. A total of ten plots, five each of mixed and *Typha* plots, were randomly established in a 20×50 m transect belt parallel to the railroad.

Field Data Collection and Plant Harvest

All pre-existing shoots were removed to ground level in each plot in March, 2004. During that growing season, we counted the new shoots from each species per plot once every 2 weeks, from May 1 until the cessation of sprouting.

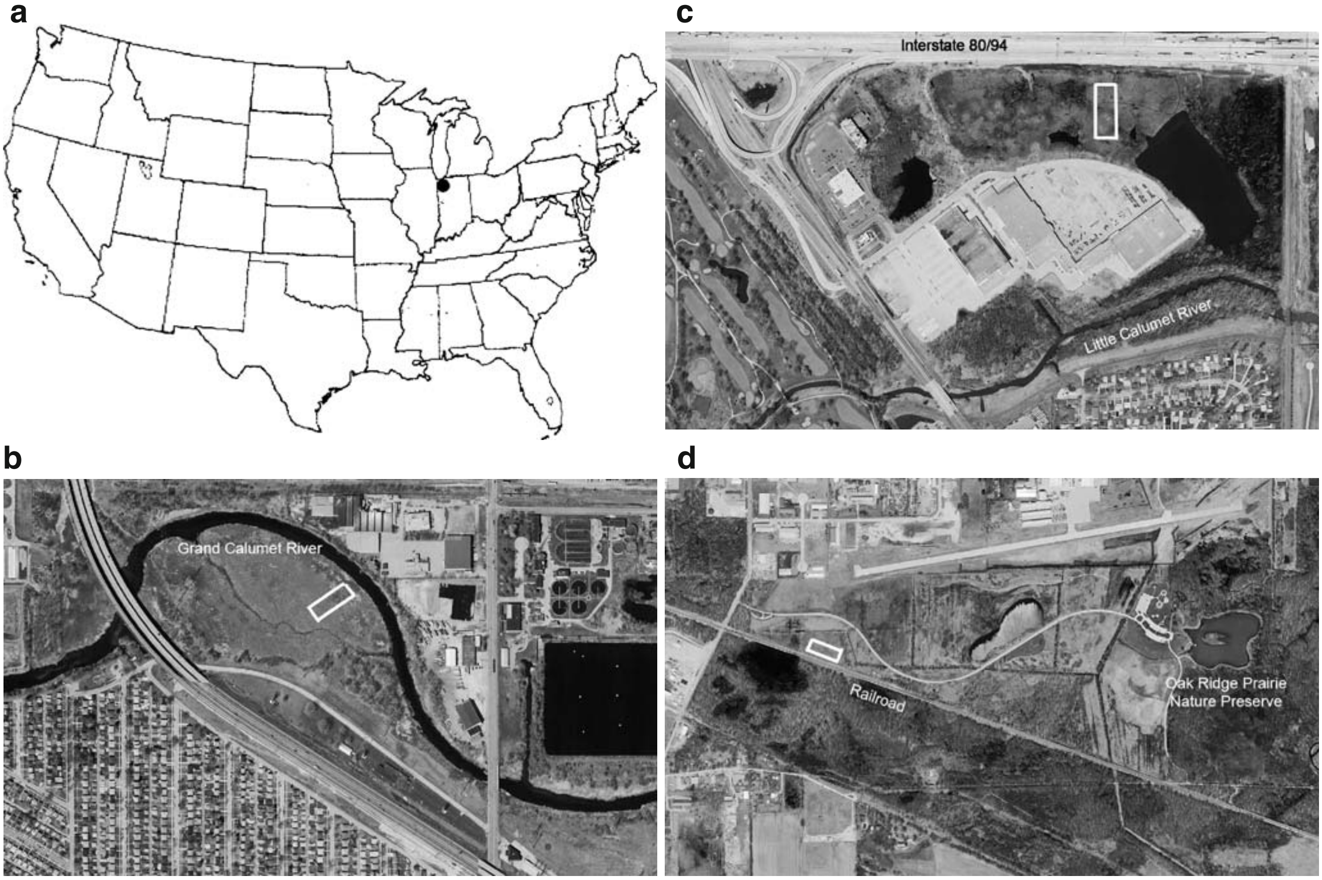

Fig. 1 Geographical location of northwestern Indiana (**a**), and aerial photos, taken in 2005, of sample sites (*in rectangles*) for Grand Calumet River floodplain (**b**), Little Calumet River floodplain (**c**), and Oak Ridge Prairie depression along railroad track (**d**). Photo courtesy: Northwestern Indiana Regional Planning Commission

The cumulative number of shoots was taken as the density for each plot (shoots m^{-2}). The presence or absence of inflorescences was also checked for both species in all plots in October, 2004. Aboveground biomass was harvested by clipping the shoots to ground level in a randomly chosen subplot (1×1 m) in each plot in November, 2004. To harvest belowground biomass, each subplot was excavated to the maximum rooting depth (≈80 cm), and the entire block of sediment, rhizomes, and roots was taken from the pit. Blocks were loosened by hand, sieved through a 2-mm mesh, and rinsed with tap water to remove sediments. The harvested plant material was sorted by species and parts (stem, blade, inflorescence, rhizome, and root) and dried at 60°C to a constant weight (approximately 2 weeks for shoots and 4 weeks for rhizomes).

The aboveground biomass included shoots (stems, blades, and inflorescences), and the belowground biomass comprised rhizomes and roots. Per-shoot total biomass, per-shoot aboveground biomass, and per-shoot belowground biomass were calculated by dividing the per-plot total biomass, per-plot aboveground biomass, and per-plot belowground biomass by shoot density in each plot.

A Student's *t* test (Rosner 1995) was used to compare the per-plot total biomass, per-plot aboveground biomass, per-plot belowground biomass, shoot density, per-shoot total biomass, per-shoot aboveground biomass, and per-shoot belowground biomass between species in 12 *Phragmites*, 18 mixed, and nine *Typha* plots.

Rooting Depth, Water Table, and Correlations with Shoot Densities

We monitored the depth of the water table at wells (PVC pipe 5 cm in diameter and 1.5 m deep) installed at plot centers. Average values in 2004 were calculated from measurements taken in spring (May 1, May 15, and May 30), early summer (June 15, June 30, and July 14), late summer (July 30, August 14, and August 30), and fall (September 14, September 29, and October 15). Rooting depth was measured in the excavated pit of each plot in November, 2004. We used a Wilcoxon rank-sum test, followed by a display with box-and-whisker plots, to compare these parameters between the 30 plots with *Phragmites* (12 *Phragmites* plots and 18 mixed plots) and the 27 plots with *Typha* (nine *Typha* plots and 18 mixed plots). Correlations between water levels and shoot densities of both species were determined by linear regression (Rosner 1995).

Results

Shoot Density and Biomass

The shoot density of *Typha* decreased significantly in the presence of *Phragmites*, whereas the latter showed no such response (Table 1). Both species had lower biomass values when they occurred together (mixed plots) than when alone (i.e., *Phragmites* or *Typha* plots). However, the reduction in *Phragmites* biomass (33%, 34%, and 34% for aboveground, belowground, and total, respectively) was much less significant than for *Typha* (86%, 80%, and 82% for aboveground, belowground, and total, respectively). *Phragmites* dominated the mixed plots, constituting 82%, 86%, and 80% of the total, aboveground, and belowground biomass, and had >6 times greater shoot density than *Typha* (Table 1). Overall, both rhizomes and shoots (stems and blades) comprised >95% of the total belowground and the total aboveground biomass for each species.

Per-shoot total biomass also decreased in the *Phragmites* and *Typha* plots compared with the mixed plots (Table 2). This aboveground decline (*Phragmites* 52%, *Typha* 61%) was approximately 1.6 and 2.1 times greater than the belowground reduction (*Phragmites* 33%, *Typha* 29%). No difference was found in the proportional above/belowground biomass of *Phragmites* between mixed and *Phrag-*

Table 1 Means (±standard error) for biomass (g m^{-2}) and shoot density (shoots m^{-2}) of *P. australis* and *Typha* spp. in exclusively *Phragmites* plots ($n=12$), exclusively *Typha* plots ($n=9$), and mixed plots ($n=18$)

Species/parameter	*Phragmites* plots	Mixed plots	*Typha* plots	p^a
Phragmites australis				
Aboveground biomass	357±48	234±34	–	<0.01
Belowground biomass	620±55	415±55	–	<0.01
Total biomass	977±85	649±71	–	<0.01
Shoot density	72±7	78±9	–	0.67
Typha spp				
Aboveground biomass	–	38±38	283±48	<0.01
Belowground biomass	–	105±21	45±47	<0.01
Total biomass	–	143±28	728±89	<0.01
Shoot density	–	15±2	39±3	<0.01

[a] Probability of type I error (reject H_0) in Student's *t* test

Table 2 Means (± standard error) for per-shoot total, aboveground, and belowground biomasses (g) of *P. australis* and *Typha* spp. in exclusively *Phragmites* plots (n=12), exclusively *Typha* plots (n=9), and mixed plots (n=18)

Species/Parameter	*Phragmites* plots	Mixed plots	*Typha* plots	p^a
Phragmites australis				
Aboveground biomass	6.2±0.5	2.9±0.3	–	0.02
Belowground biomass	7.9±1.1	5.3±0.4	–	0.02
Total biomass	14.1±1.1	8.2±0.5	–	<0.01
Typha spp				
Aboveground biomass	–	2.7±0.3	7.0±0.8	<0.01
Belowground biomass	–	8.1±0.9	11.3±0.6	<0.01
Total biomass	–	10.9±1.0	18.3±1.1	<0.01

Per-shoot biomass was calculated by dividing per-plot total, aboveground, or belowground biomass by density for each species

[a] Probability of type I error (reject H_0) in Student's t test

mites plots. However, the belowground proportion of *Typha* biomass in the *Typha* plots increased significantly compared with the mixed plots (Table 3). This pattern was consistent at both Little Calumet River (from 56±2% to 68±3%; n=12, t=2.38, p=0.02) and Oak Ridge Prairie (from 68±2% to 80±2% at n=10, t=4.10, p<0.01). Although the per-shoot masses for that species were similar to those of *Phragmites* (Table 2), *Typha* shoots failed to produce spadix in >94% of the mixed plots and >56% of the *Typha* plots. In contrast, the *Phragmites* shoots produced inflorescences and seed in all plots, even in the presence of *Typha* (100% in both mixed and *Phragmites* plots).

Rooting Depth, Water Table, and Correlations to Shoot Density

Pragmatism roots and rhizomes penetrated deeper than those of *Typha* (Fig. 2). Of the four monitoring periods, only in spring did the water level differ significantly between the plots with *Phragmites* (*Phragmites* and mixed plots) and those with *Typha* (*Typha* and mixed plots). Plots with *Phragmites* had a lower water table during the springtime recordings (Fig. 3), and this difference was magnified when the 18 mixed plots were excluded (*Phragmites* plots 2.4±2.6 cm belowground and *Typha* plots 8.7±1.4 cm aboveground; n=21, Wilcoxon rank-sum t=2.74, p<0.01). Although the density of *Typha* shoots was strongly correlated with the springtime water level, *Phragmites* showed no such correlation (Fig. 4).

Discussion

Shoot Production

The dominance of *Phragmites* over *Typha* has been documented previously (Wilcox et al. 1986; Levine et al. 1998; Meyerson et al. 2000; Choi and Bury 2003). One plausible hypothesis for this is stature, i.e., shading by the relatively taller *Phragmites* (Haslam 1970, 1971; Smith 1987; Gleason and Cronquist 1991; Eggers and Reed 1997) could inhibit the growth of *Typha* shoots. The drastic reduction in shoot biomass from *Typha* (Table 2) and its failure to produce spadices in the presence of *Phragmites* may support this argument. However, our results do not provide conclusive evidence for whether suppression of *Typha* is caused by *Phragmites* shading.

The decline in *Typha* more likely resulted from a reduction in shoot density rather than growth suppression. Its less dense pattern could have left space for encroach-

Table 3 Comparison of above- and belowground biomass proportions (%) between *P. australis* and *Typha* spp. in exclusively *Phragmites* plots (n=12), exclusively *Typha* plots (n=9), and mixed plots (n=18)

Species	Portion	*Phragmites* plots	Mixed plots	*Typha* plots	p^a
Phragmites	Aboveground	35.8±2.6	34.9±2.4	–	0.81
	Belowground	64.2±9.1	65.1±10.1	–	
	Above/below ratio	0.56	0.54	–	
Typha	Aboveground	–	21.3±5.3	37.6±10.2	0.02
	Belowground	–	72.3±10.2	62.4±7.8	
	Above/below ratio	–	0.29	0.60	

[a] Probability of type I error (reject H_0) in Student's t test

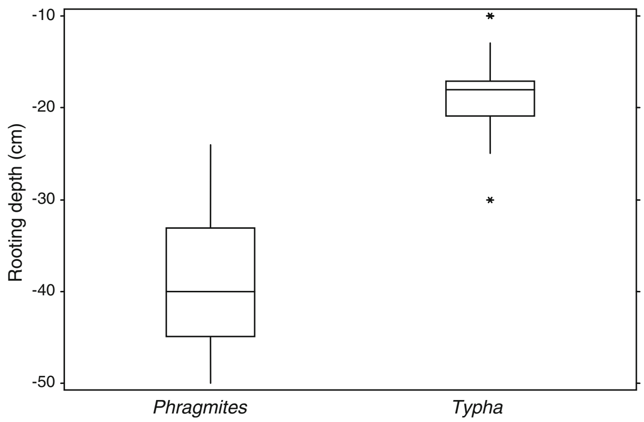

Fig. 2 Comparison of rooting depths between *P. australis* (n=30) and *Typha* spp. (n=27, Wilcoxon rank-sum t=6.36, p<0.01). *Upper and lower boxes* represent brackets of inter-quartile range, *whiskers* indicate limits of upper and lower fences, and *asterisks* are outliers

ment by *Phragmites*, whose shoot formation was not affected by the presence of *Typha* (Table 1). The drastic reduction in aboveground production could have led to a decline in carbohydrate reserves in the rhizomes, with such a reduction then inhibiting *Typha*. Meanwhile, the decrease in belowground biomass of *Phragmites* seemed not to deter its shoot production or maturation (formation of inflorescences; Tables 1 and 2).

Potential Rhizome Competition

Although we could identify the larger reduction in shoot numbers rather than root/rhizome biomass as the main reason for the increased proportion of *Typha* belowground biomass (Table 3), we cannot exclude the possibility of rhizome competition between species as an explanation for the lower density of *Typha* shoots. This shift of *Typha* biomass to the belowground region could also be a

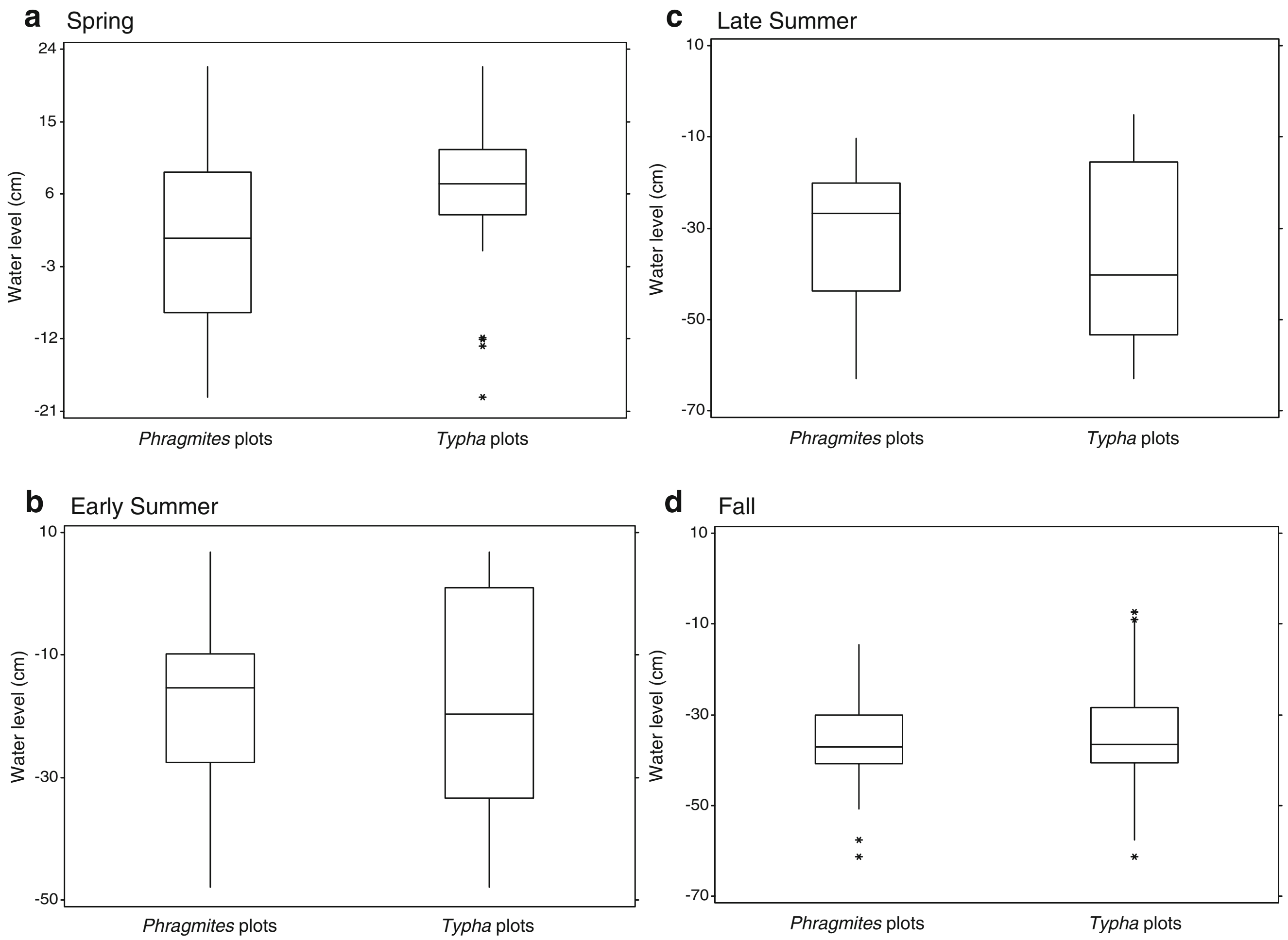

Fig. 3 Comparison of water levels between plots with *P. australis* (n=30) and those with *Typha* spp. (n=27) in **a** spring (Wilcoxon rank-sum t=1.64, p=0.10), **b** early summer (t=0.38, p>0.70), **c** late summer (t=0.39, p>0.69), and **d** fall (t=0.42, p>0.67). *Positive and negative values on vertical axis* represent above- and belowground levels, respectively. *Upper and lower boxes* represent brackets' inter-quartile range, *whiskers* indicate limits of upper and lower fences, and *asterisks* are outliers

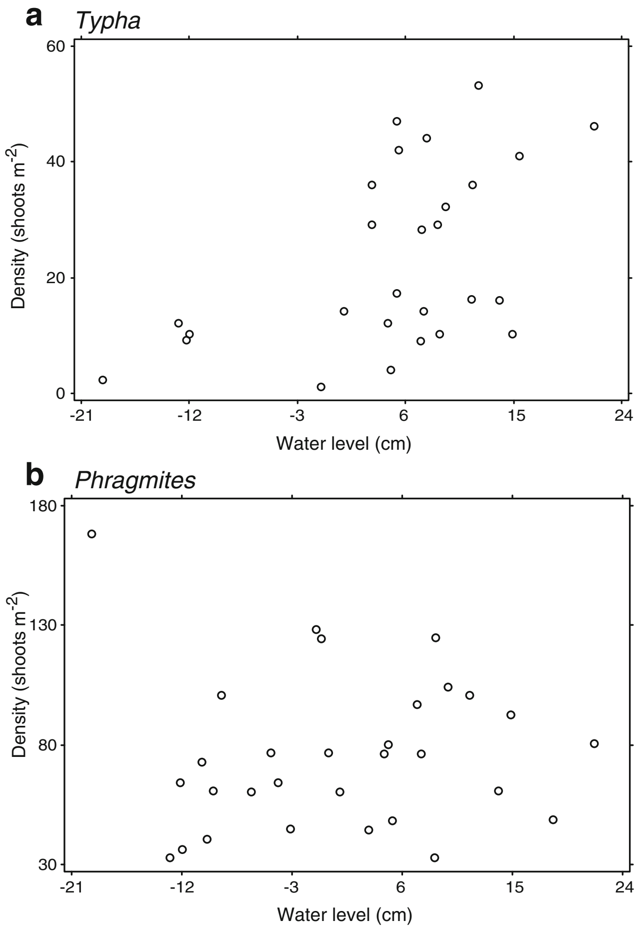

Fig. 4 Scatterplots for linear regression between springtime water level and shoot density of **a** *Typha* spp. (n=30, r^2=0.27, p<0.01) and **b** *P. australis* (n=30, r^2<0.01, p>0.99). *Positive and negative values on horizontal axis* represent above- and belowground levels, respectively

response to the encroaching *Phragmites*. The investment of energy in rhizome production over that of shoots can be advantageous for clonal species, such as *Typha* and *Phragmites*, by decreasing the risk of mortality, promoting vegetative expansion, and enhancing the ability to claim space (Waller 1988; Grace 1993; Wilson and Tilman 1995). However, our study was not designed to investigate whether such competition occurs or to determine how much this might contribute to biomass allocation by *Typha*. Thus, separate experiments are needed to test this hypothesis.

Rooting Depth, Shoot Sprouts, and Spring Flooding

The limited occurrence of *Typha* in sites with a high water table (Fig. 3) and the positive correlation between shoot density and water table (Fig. 4) suggest that springtime flooding can facilitate its sprouting from shallow rhizomes (Fig. 2). Meanwhile, the deeper roots and rhizomes of *Phragmites* (Fig. 2) appear to be more adaptive to both low- and high-water sites (Figs. 3 and 4). *Phragmites* is known to favor less waterlogged soil for sprouting (Hellings and Gallagher 1992; Weisner et al. 1993), and its dominance in low water table locations has been well reported (Haslam 1970, 1971; Marks et al. 1994; Bart and Hartman 2000; Rice et al. 2000; Ailstock et al. 2001; Hudon 2004; Asaeda et al. 2005). However, this species, with its rhizomes adapted to fluctuating water levels (Fig. 2; Chambers et al. 2003; Pagter et al. 2005; White et al. 2007) and its efficient shoot growth (Table 2), may become established first on sites with a lower water table, then expand to higher water levels through vegetative expansion of the rhizomes (Cross and Fleming 1989; Amsberry et al. 2000). Meanwhile, *Typha* has a shallower rooting depth (Fig. 2), and its potential for shoot production and growth requires a larger amount of biomass than does *Phragmites* (Table 2). Therefore, *Typha* expansion from high to low water levels, particularly in the presence of *Phragmites*, is less likely.

Summary and Management Implications

With its efficient shoot development and an adaptability by roots and rhizomes to fluctuating water tables, *Phragmites* will likely continue to expand into *Typha* stands. Such activity has already been observed by Wilcox et al. (1985, 1986) and Choi and Bury (2003) in the wetlands of northwestern Indiana. As *Typha* shoots diminish, *Phragmites* plants grow larger (Tables 1 and 2) and taller (heights >3 m in *Phragmites* plots versus ≈2 m in the mixed plots; unpublished data), and produce more viable seeds (unpublished data). This may give *Phragmites* an opportunity for further expansion through seed dispersal (Levine et al. 1998; Meyerson et al. 2000; Choi and Bury 2003). That species also might directly invade wetlands with high conservation value (Phillips 1987; Marks et al. 1994; Chambers et al. 1999). Recently, P. Labus (The Nature Conservancy, internal data file) observed *Phragmites* invasions in relatively undisturbed wetlands in the Indiana Dunes National Lakeshore. A similar strategy (rhizomes adapted to varying water levels) might also be utilized by that species when it invades wetlands that are occupied by native rhizome-building species (e.g., sedges and rushes).

The detection and removal of rhizomes during their early stage of intrusion is critically important to curbing the establishment of *Typha* and *Phragmites* because most rhizomatous species tend to invest more energy in rhizomes then (Grace 1993; Kowalski and Wilcox 1999; Wilcox and Whillans 1999; Saltonstall and Stevenson 2007). Although it favors drained soil above a low water table (Hellings and Gallagher 1992; Weisner et al. 1993; Armstrong et al. 1999; Welch et al. 2006), *Phragmites* can expand to sites with higher water tables through vegetative growth by its rhizomes (Table 3 and Fig. 2; Cross and Fleming 1989; Amsberry et al. 2000; Chambers et al. 2003; Pagter et al. 2005; White et al. 2007). Therefore, flooding would not likely discourage the spread of this species. In addition, such inundations may pose another threat, i.e., the expansion of *Typha* that is more tolerant than *Phragmites* to anoxic conditions (Wilcox et al. 1985, 1986; Choi and Bury 2003). Burning and mowing outside of the growing season removes shoots but not rhizomes so is not effective against either species unless performed many times over multiple years. However, repeated application of a rhizome-killing herbicide, followed by physical extraction of the plants, seems to provide more control (Carlson et al., in press).

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