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## STABILIZED WATER LEVELS AND *TYPHA* INVASIVENESS

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**Abstract:** Because *Typha* × *glauca* often dominates wetlands where humans have stabilized the natural hydrologic regime, we 1) compared its expansion rates where water levels were stabilized vs. fluctuating and 2) explored the potential for stabilized water levels to allow plants to accumulate more phosphorus (P) and increase growth. In three Wisconsin marshes, the area dominated by *Typha* expanded linearly over time, but rates were higher where water levels were stabilized than where they fluctuated naturally (based on nine aerial photos from 1963 to 2000). In a large wetland (412 ha) behind a dam, *Typha* × *glauca* expanded 81,152 m<sup>2</sup>/year, and clone diameters extended 3.9 ± 0.61 m/year. In contrast, a mixed stand (mostly *T. angustifolia*) in an upstream wetland with fluctuating water levels expanded only 2,327 m<sup>2</sup>/year, and clones extended only 2.5 ± 0.75 m/year. While various factors could have caused these differences, a separate two-factor experiment in outdoor microcosms supported the hypothesis that stabilized water levels alone can enhance *T. × glauca* spread. The experiment indicated that both stabilized water levels and P additions increased P accumulation and growth of *T. × glauca*. Constant inundation (5–10 cm deep) allowed *T. × glauca* to produce 56% more biomass (61.6 ± 4.0 g) than a regime with two drawdowns (39.4 ± 1.9 g;  $p < 0.001$ ). Plants under constant inundation accumulated 0.15 ± 0.007 g P, which was 36% more than with one drawdown (0.12 ± 0.004 g;  $p < 0.001$ ) and 67% more than with two drawdowns (0.09 ± 0.005 g;  $p < 0.001$ ). Also as expected, the addition of 2 g P/m<sup>2</sup> increased biomass 23% more than the control (57.8 ± 3.0 vs. 46.9 ± 3.0 g/plant;  $p = 0.02$ ). Our microcosm results suggest that unavailable P can shift to a form that *T. × glauca* can use. Thus, internal eutrophication can augment rates of *T. × glauca* invasion.

**Key Words:** hydroperiod, internal eutrophication, invasive species, P release, phosphorus, *Typha* × *glauca*, water control structures, wetland

### INTRODUCTION

Water-control structures (dams, levees, and dikes) can reduce or eliminate water-level fluctuations in wetlands (Hill et al. 1998). Control structures in Lake Ontario reduce amplitudes of high and low water levels, and many dikes impound water in the southern Great Lakes (Wilcox et al. 2007). Drawdowns are now shorter or less frequent than naturally (Albert and Minc 2004). Changes from variable to stabilized water levels likely affect the availability of nutrients in wetland soil (Pant and Reddy 2001, Venterink et al. 2002, Aldous et al. 2005). For example, Koerselman et al. (1993) demonstrated that nitrogen (N), phosphorus (P), and potassium (K) could be released from wetland soils by varying water levels. They measured “release” as the increased amounts of each nutrient that percolated through a 10-cm column of various soils subjected to varied environmental conditions. They termed the process “internal eutrophication,” meaning that unavailable nutrients became available

for uptake by plants. Phosphorus, in particular, moves into the soil solution during anoxic conditions due to reduction of iron oxides and solubilization of sorbed P (Young and Ross 2001; also called P release or P flux, Aldous et al. 2005). In addition, some mineralization might contribute to P release (Young and Ross 2001).

The release of P could favor the spread of aggressive invasive species that are P-limited. An example is *Typha* × *glauca* (Godr.) (hybrid cattail), which responds to P-rich nutrient additions (Woo and Zedler 2002). *Typha* × *glauca* is a hybrid of the native *T. latifolia* (L.) (broad-leaved cattail) and the introduced *T. angustifolia* (L.) (narrow-leaved cattail) (Smith 1967). *Typha* × *glauca* spreads vegetatively, produces large, dense stands (Galatowitsch et al. 1999), dominates prairie potholes (Mulhouse and Galatowitsch 2003), and is a consistent dominant of wetlands along the U.S. shores of the Great Lakes (Frieswyk et al. in press).

*Typha* × *glauca* is especially abundant where water levels are regulated (Wilcox et al. 2007). In the

Indiana Dunes National Lakeshore, rates of *Typha* spp. spread increased where water levels were stabilized (Wilcox et al. 1985). Likewise, in six lacustrine wetlands in Manitoba, Canada, *Typha* nearly doubled in area of dominance (from 33% to 60%) within 20 years of water-level stabilization (Shay et al. 1999). Others agree that flooding and/or high nutrient levels favor dominance by *Typha* spp. (Day et al. 1988, Newman et al. 1996, Svengsouk and Mitsch 2001). *Typha*  $\times$  *glauca* displaces native species as it becomes dominant (Galatowitsch et al. 1999). In 10 constructed wetlands in Manitoba, five years of sustained inundation allowed *T. \times glauca* to increase in above-ground biomass from 7 to 160 g/m<sup>2</sup>, while the above-ground biomass of all other macrophytes declined from 295 to 140 g/m<sup>2</sup> (van der Valk 2000). And in experimental wetlands in Illinois, *T. \times glauca* cover was 80% where the water table was stable, and species richness was one-third that of higher elevations with infrequent inundation and 10% cover of *T. \times glauca* (Boers et al. 2007).

A mechanism that might contribute to such pattern is that stabilized water levels increase the release of P, which then increases P uptake and growth of *T. \times glauca*. We hypothesized that *T. \times glauca* would increase its biomass in response to stabilized water levels and P availability (added experimentally or released under anoxic conditions). We conducted an outdoor, two-factor microcosm experiment, with three levels of P addition and three hydroperiods (stabilized high water and with one and two drawdowns), and we assessed the P accumulation and growth of *T. \times glauca* in all nine treatments. In addition, we compared rates of *Typha* expansion in three wetlands that differ in the degree of water level fluctuation, asking if results corroborate those of the microcosm experiment (Petersen et al. 2003). We quantified the spread of *Typha* in three wetlands along the headwaters of the Mukwonago River using aerial photos taken over a period of 33 years. We predicted greater expansion in the two sites behind the Eagle Spring Dam, where water levels had been stabilized for more than 100 years, than in the upstream reference wetland with fluctuating water levels.

## METHODS

### Field Expansion Rates

We compared *Typha* clone area and spread rate in two wetlands with stabilized water levels (behind a dam) and in a reference wetland with variable water level. All three were within The Nature Conservancy's (TNC) Mukwonago River Watershed (Wal-

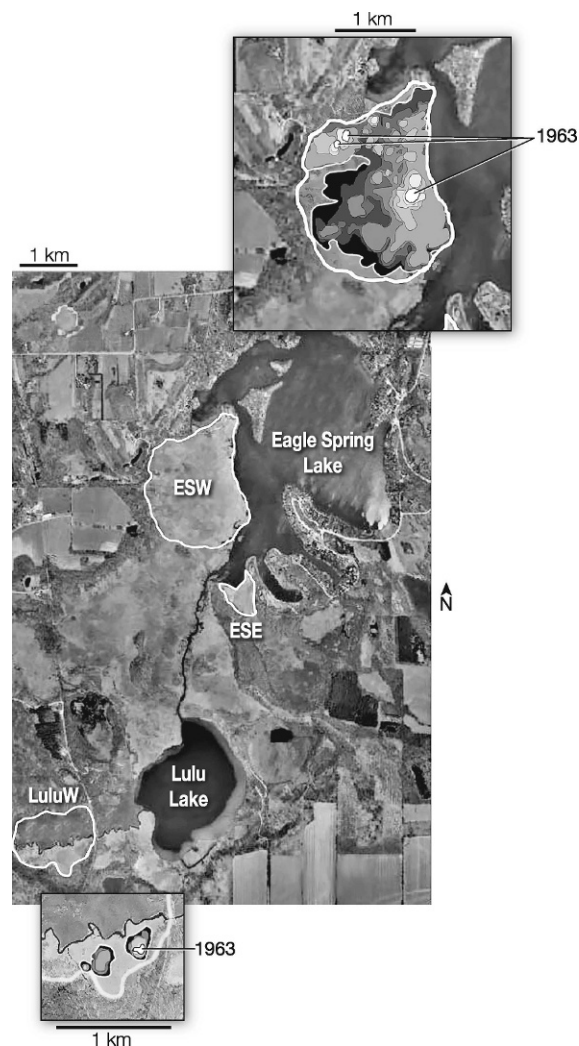


Figure 1. Aerial photo from 2000, showing Lulu Lake and Eagle Spring Lake. The reference wetland (LuluW) has fluctuating water levels, while two wetlands upstream of the Eagle Spring dam (ESE, and ESW) have stabilized water levels. The Mukwonago River flows from west to east through LuluW, into Lulu Lake, then north into Eagle Spring Lake, and out over a dam to the northeast. Enlargements of ESW (above the site map) and LuluW (below) show areas dominated by *Typha*. The small polygons labeled 1963 were the earliest clones documented. Increasingly darker polygons indicate areas dominated by *Typha* in 1967, 1970, 1975, 1980, 1985, 1990, 1995, and 2000.

worth and Waukesha counties, Wisconsin, USA; 42°50' N, 88°27' W; Figure 1). All were on the same river, in close proximity, and with low nutrient inputs due to their spring-fed, headwater positions in the watershed. Large tracts within the headwaters of the Mukwonago River and upstream of Lulu and Eagle Spring Lake were acquired by TNC (2005) and WDNR to reduce human impact. In choosing wetlands within a single river basin in a watershed

with minimal agricultural and urban conversion, we aimed to reduce the number of confounding variables that might explain *Typha* invasions.

Lulu Lake is a natural lake with a maximum depth of 12 m and a surface area of 38 ha (WDNR 2005). Water levels fluctuate, with maximum and minimum levels differing by 35 cm between September 2002 and September 2004 (Gittings 2005). Eagle Spring Lake is about 2.5 km downstream. It was damned more than 100 years ago and has an average depth of approximately 1.1 m, maximum depth near 3 m, and total surface area of 126 ha (Shoemaker 2002). The reference wetland (LuluW) is unaffected by the dam on Eagle Spring Lake (Gittings 2005).

The wetlands with stabilized water levels (ESE and ESW) border Eagle Spring Lake. The outflow of the lake is strictly regulated to keep water levels constant for lakeside residents and boaters. From June 2001 to April 2002, minimum and maximum water levels differed by only 12 cm, whereas a hydrologic model predicted a 46-cm difference without water-level regulation (Shoemaker 2002). Based on April–August water quality monitoring from 1991 to 2001 (79 samples, mean total P of  $0.017 \pm 0.0008$  mg/L; USGS 2005), Eagle Spring Lake is mesotrophic (Carlson 1977). The Eagle Spring wetlands have less groundwater input, more nearby homes, and more recreational activity than LuluW (Gittings 2005).

All three wetlands have emergent marsh vegetation near open water, grading into sedge meadow toward the upland. LuluW covers 163 ha, ESW covers 412 ha; and ESE covers 31 ha. Control burning was used to discourage invasive plants in LuluW in 1991, 1992, 1997, 1999, and 2003 north of the river; and in 2001 and 2003 south of the river, but neither ESE nor ESW has been burned (H. Spaul, Wisconsin Chapter, TNC, pers. comm.).

We obtained aerial photographs of LuluW, ESE, and ESW from the Southeastern Wisconsin Regional Planning Commission. We analyzed all available photos, which were taken in March, April, or May of 1963, 1967, and every five years from 1970 to 2000. Photos taken before 1995 were black and white prints at a scale of  $1'' = 400'$ , images from 1995 and 2000 were black and white digital orthophotographs with 1-m resolution. To manipulate the prints digitally, we scanned the pre-1995 photos with a Microtek Scanmaker 9800 XL scanner in 8-bit grayscale at 1,000 pixels per inch resolution. We then orthographically rectified the images using OrthoMapper software (Image Processing Software, Inc.). The orthorectification process removes distortion from the images caused by relief displacement and orientation of the camera,

allowing accurate comparisons of images across time. OrthoMapper uses a digital elevation model and a set of user-defined control points that match features on an existing orthophotograph (we used the 2000 image) to an unrectified image to produce a new orthophotograph. The root mean square error of the resulting orthophotographs was near 1, meaning that on average the images have a positional error of approximately 1.7 pixels, or in this case 1.7 m.

*Typha* clones appear as dark circular features in the images, and their texture differs from that of other herbaceous vegetation. In all images we delineated the areas dominated by *Typha* using ArcMap (ESRI 2004) software. We also visited the wetlands and noted the current locations of *Typha* clones and flew over the site at low altitude to take color photos and help classify the most recent image. We first analyzed the 2000 image and then tracked clones back in time. Boers classified all images, and Christin Frieswyk, another professional with *Typha*-delineating experience (Frieswyk and Zedler 2007), duplicated classifications of the 1985 and 1995 images to assess consistency. Our quality assurance exercise found strong agreement in the area dominated by *Typha*. In the 1985 image, Boers classified 1,596,850 m<sup>2</sup> as *Typha*; Frieswyk classified 1,568,346 m<sup>2</sup> as *Typha*, with 1,380,849 m<sup>2</sup> (86% of our total) of the image classified as *Typha* by both. In the 1995 image, Boers classified 2,577,076 m<sup>2</sup> as *Typha*; Frieswyk classified 2,625,787 m<sup>2</sup> as *Typha* with 2,488,219 m<sup>2</sup> (95% of our total) of the image classified as *Typha* by both. The interpreters agreed on what was a *Typha* clone; the differences were in the exact boundary of the *Typha*-dominated area. The 1995 image had a lower edge:volume ratio of *Typha*-dominated areas than the 1985 image, which is a likely reason for the greater percentage of agreement between interpreters.

The *Typha* stand in ESE was a single patch, so we could not measure the linear spread of individual clones. In LuluW and ESW, however, we followed the expansion of individual clones using the same orthophotos. We first located the center of the clone in the earliest image in which it was distinguishable. We then measured the distance that the clone spread along north–south and east–west diameters in each subsequent image. We calculated linear expansion rate by dividing the distance spread by the number of years between images. For LuluW, we measured the linear expansion of two *Typha* clones; one in three images, the other in seven images ( $n = 40$  measures); for ESW, we measured two clones; one in five images, the other in eight images ( $n = 52$ ).



To determine the identity of the *Typha* (*T. latifolia*, *T. angustifolia*, or their hybrid *T. × glauca*), we collected specimens from several locations in each wetland and used morphological traits following Tompkins and Taylor (1983) and Kuehn and White (1999). Although the literature is inconsistent about hybridization between *T. latifolia* and *T. angustifolia* (Fassett and Calhoun 1952, Sharitz et al. 1980, Selbo and Snow 2004, Tsyusko et al. 2005), it is generally accepted that *T. × glauca* is a widespread hybrid (Smith 1967, 1987, Lee 1975, Kuehn et al. 1999). Recent studies suggest that Great Lakes populations comprise a swarm of advanced generation hybrids following backcrossing (Windels et al. 2005).

### Microcosm Experiment

We grew *T. × glauca* plants in individual outdoor microcosms in a 2-factor, fully crossed experiment comparing the effects of three hydroperiods and three levels of P addition ( $3 \times 3 \times 8$  replicates = 72 microcosms). On June 13, 2004, we collected 72 *T. × glauca* ramets from Gardner Marsh in the University of Wisconsin-Madison Arboretum. We collected field grown ramets from a continuous *Typha* stand approximately 20 m<sup>2</sup> in area. Because this hybrid rarely produces seed (Smith 1967), it is likely that the ramets came from one clone. We pruned the leaves to 35 cm and rhizomes to approximately 10 cm and washed them to remove soil and debris. The average wet weight of ramets was  $39.7 \pm 1.91$  g. We then transplanted the ramets into 30-cm-diameter buckets (microcosms) that were 37 cm tall. We added 15 cm of screened pulverized loamy topsoil, which had pH = 6.8, organic matter = 3%, soil nitrogen =  $8820 \pm 56$  ppm, and total soil P =  $510 \pm 13$  ppm, for an average N:P ratio of 17.3. We planted one *T. × glauca* ramet in each microcosm and set the microcosms outdoors under a plastic canopy that transmitted 95% of sunlight. The canopy excluded rainfall and allowed us to control water levels.

We began water-level treatments after allowing the plants to establish in moist conditions for 2 weeks. Three plants died prior to the start of the treatment and were excluded, leaving 69 microcosms with one *T. × glauca* plant in each. On July 1, 2004, we randomly assigned the microcosms to one of three water-level treatments. The stabilized high water treatment (hereafter, HHH) had water levels at 5–10 cm above the soil surface until October 1, 2004. The treatment with one drawdown had high water (5–10 cm) early and later and low water in between (moist but no standing water) (HLH), similar to fluctuations of inland wetlands in the

Great Lakes region (Hill et al. 1998). The two-drawdown treatment had low water early and late, with high in between (LHL), similar to fluctuations in Great Lakes wetlands (Keough et al. 1999). In the latter two treatments, water levels changed on July 21 and Sept. 7. The number of days inundated was held constant, so that the drawdown conditions differed only in timing, not duration. We then randomly assigned microcosms in each water level treatment to three P-addition treatments ( $n = 8$ ). Treatments were 2 g P/m<sup>2</sup> of soil surface area (hereafter LP), 6 g P/m<sup>2</sup> (HP), and no addition (-P), by adding triple super phosphate (0% N, 45% P, 0% K; P in P<sub>2</sub>O<sub>5</sub>) on July 20 and August 15, 2004.

We continued the experiment for three months, because a pilot experiment in 2003 demonstrated that young *T. × glauca* would not overwinter in shallow containers due to freezing and thawing. During the outdoor experiment, weather conditions were typical of Madison Wisconsin's temperate climate. Ambient temperature averaged 20.8°C in July (1.2°C below average), 18.6°C in August (2.1°C below average), and 18.4°C in September (2.4°C above average; NOAA 2005). Average daytime cloud cover was 40% in July and August, and 20% in September (ibid).

On October 1, 2004, after plants had begun to senesce, we assessed *T. × glauca* growth by recording the number of leaves and total leaf length and collecting the above- and below-ground tissue. After thoroughly washing soil from below-ground tissues, we dried all biomass in a 60°C oven until constant weight (3 days). We sent tissue samples from each microcosm to the University of Wisconsin-Madison Soil and Plant Analysis Lab for grinding and determination of P concentrations (using Inductively Coupled Plasma Optical Emission Spectrometry) in above- and below-ground tissues. We calculated the accumulated P per plant as P concentrations times biomass for below- plus above-ground tissues. We also collected soil samples from the top 3 cm of soil, and the same Lab determined levels of minerals in each microcosm.

We used R (version 2.2.0; R Development Core Team 2005) for all analyses of experimental data. Treatments had either seven or eight replicates, so we randomly selected seven replicates to create equal  $n$ . The distributions of the response variables (biomass, leaf length, etc.) in the experiment fit normal distributions, the variances among treatments were approximately equal, and the observations were independent, so we used two-way ANOVAs to test for significant differences in response to water-level treatments and P additions. When ANOVAs indicated a significant difference

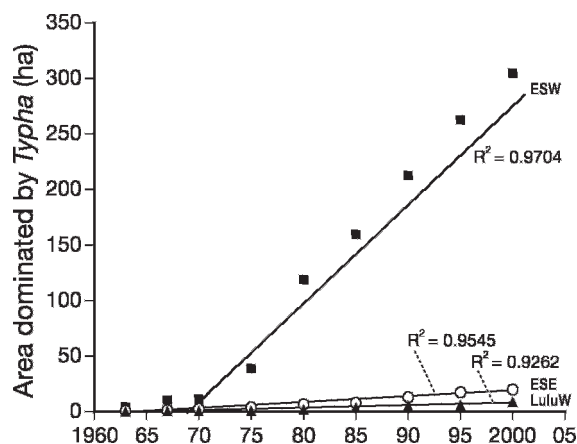


Figure 2. Increase in area dominated by *Typha* in wetlands west of Eagle Spring Lake (ESW), east of Eagle Spring Lake (ESE) and west of Lulu Lake (LuluW). Lines represent best fit linear rate of spread.

among treatments, we used Tukey's method to test for significant differences among the three pairs of means. Alpha = 0.05 for all statistical tests.

## RESULTS

### *Typha* Expansion Rates Were Greater Where Water Levels Were Stabilized

In the LuluW reference site, *T. angustifolia* formed the clones we delineated. *Typha latifolia* was also present, but at a density too low to be detected in the aerial photos. Despite the presence of both parent species, we did not find any areas dominated by the hybrid, *T. × glauca*, where water levels fluctuated. With stabilized water levels, however, the hybrid was more common than either parent (in both ESE and ESW).

On the 2000 aerial photo, *Typha* was dominant in 8.6 ha (5.3% of the area) of LuluW, 19.7 ha (62.5% of the area) of ESE, and 304.5 ha (73.8% of the area) of ESW. *Typha* spread an average of 2,327.3 m<sup>2</sup>/year from 1963–2000 in LuluW. With stabilized water levels, *Typha* spread 5,115.4 m<sup>2</sup>/year in ESE and 81,152.7 m<sup>2</sup>/year in ESW (Figure 2).

Between 1967 and 2000, *Typha* invaded only 0.14% of the area of LuluW per year, whereas it invaded an average of 1.63% and 1.97% of the areas of ESE and ESW per year, respectively (Table 1, Figure 2).

In LuluW, the clones extended their boundaries an average of  $2.5 \pm 0.75$  m/year (Figure 2). We delineated only three discrete clones (Figure 3), with no new clones appearing after the 1985 image. In ESW, however, new clones appeared in each image, and they extended an average of  $3.9 \pm 0.61$  m/year. Clonal extension rates could not be measured in ESE, because the *Typha* clones merged by 2000. Rates were highly variable in both LuluW and ESW, ranging from no change to up to 14 m/year, but histograms were significantly different (Kolmogorov-Smirnov two-sample test;  $p < 0.01$ ) and consistent with area expansion rates (Figure 2, 3; Table 1).

### *Typha × glauca* Accumulated More P and Produced More Biomass with Stabilized Water Levels

The positive effects of inundation and P addition on *T. × glauca* growth were significant, with no interactions on any response variable (total biomass [Table 2], above-ground biomass, below-ground biomass, leaf length, or P incorporated into biomass) (2-way ANOVA interaction term  $p = 0.60, 0.81, 0.74, 0.21, 0.56$ , respectively; Figure 4) and no effect of initial ramet weight on final biomass or total leaf length (regression analysis for each treatment, all  $p > 0.05$ ). *Typha × glauca* in the stable (HHH) and one-drawdown (HLH) water level treatments did not differ in above-ground, below-ground, or total biomass, but both produced more above- and below-ground biomass, and 56% more total biomass than the two-drawdown treatment (LHL; Figure 4a). Consistent with increased above-ground biomass, we found 23%–28% more total leaf length in HHH ( $14.4 \pm 0.5$  m) and HLH ( $15.0 \pm 0.5$  m) treatments than in LHL ( $11.7 \pm 0.6$  m;  $p < 0.05$  for both comparisons). Average leaf length in HHH ( $78.4 \pm 1.5$  cm) was greater than that of HLH

Table 1. Rates of *Typha* spread in wetlands west of Lulu Lake (LuluW), east of Eagle Spring Lake (ESE), and west of Eagle Spring Lake (ESW). See aerial photo in Figure 1.

	LuluW	ESE	ESW
Total wetland area (ha)	163	31	412
Area dominated by <i>Typha</i> in 2000 (ha)	8.7	19.7	304.5
% of wetland dominated by <i>Typha</i> in 2000	5%	62%	74%
Average rate of <i>Typha</i> spread (m <sup>2</sup> /year)	2,327	5,115	81,152
Maximum rate of <i>Typha</i> spread (m <sup>2</sup> /year)	5,641	10,147	160,100
Average percentage of wetland invaded by <i>Typha</i> per year	0.14%	1.63%	1.97%

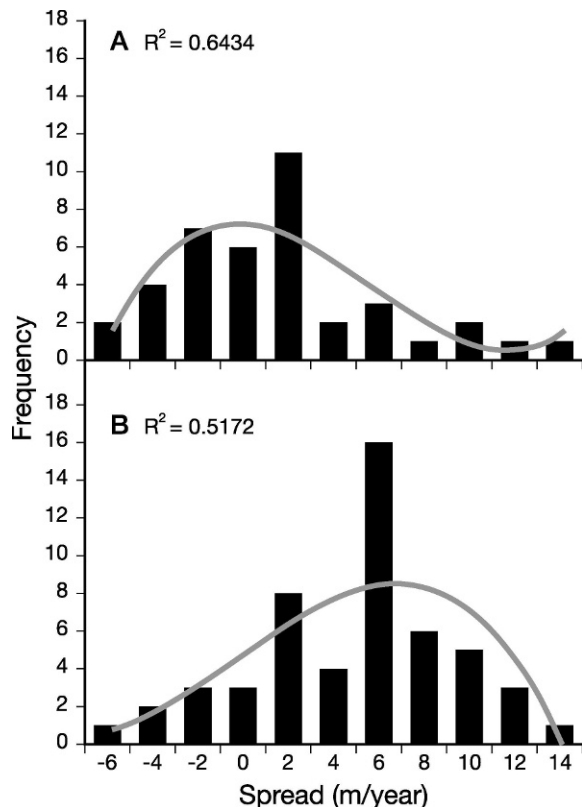


Figure 3. Histogram of north-south and east-west extension rates of *Typha* clones in A) the naturally-fluctuating water levels of Lulu Lake's west side (LuluW) and B) stabilized water levels of Eagle Spring Lake (ESW). Data are from aerial photos from 1963–2000.  $R^2$  values are for a 3<sup>rd</sup> order polynomial trendline. Distributions differ according to the Kolmogorov-Smirnov two-sample test ( $D_{\max} = 0.35$ ;  $p < 0.01$ ).

( $70.5 \pm 1.8$  cm;  $p < 0.05$ ), which was greater than for LHL ( $62.1 \pm 2.0$  cm;  $p < 0.05$ ).

Accumulation of P mirrored the biomass response (Figure 4b). *Typha*  $\times$  *glauca* accumulated the most P ( $0.15 \pm 0.007$  g) in the HHH treatment; plants in the HLH treatment were intermediate ( $0.12 \pm 0.004$  g); and those in the LHL treatment accumulated the least P ( $0.09 \pm 0.005$  g;  $p < 0.0005$  in each comparison; Figure 4b). Likewise, the total P in plants was greater with the addition of 2 g P/m<sup>2</sup> (LP)

( $0.12 \pm 0.006$  g) than with no P addition (-P) ( $0.10 \pm 0.007$  g;  $p = 0.03$ ); but P content under 6 g/m<sup>2</sup> of P (HP) ( $0.12 \pm 0.007$  g) did not differ significantly from LP or -P (Figure 4b). Biomass and P uptake had a strong linear correlation ( $R^2 = 0.585$ ;  $p < 0.001$ ), with no indication of luxury uptake of P.

The addition of 2 g P/m<sup>2</sup> (LP) increased the total biomass of *T.  $\times$  glauca* by 23% over the -P control ( $57.8 \pm 3.0$  g vs.  $46.9 \pm 3.0$  g;  $p = 0.02$ ; Figure 4b). The differences in total biomass were similar for below-ground biomass, with 28% more in LP than the -P control ( $45.8 \pm 3.0$  g vs.  $35.8 \pm 2.7$  g;  $p = 0.02$ ). However, the average total biomass with the addition of 6 g/m<sup>2</sup> (HP) was intermediate ( $51.4 \pm 3.9$  g). The same was true for P content, with HP intermediate ( $0.116 \pm 0.005$  g/plant). Neither biomass nor P content was significantly different from LP or -P. Above-ground biomass, total leaf length, and average leaf length showed no response to P fertilization in this 3-month experiment.

The experimental soil initially had  $510 \pm 13$  mg/L total P. At the end of the experiment, average available P and total P in microcosm soils were highest in the HP microcosms ( $77.7 \pm 3.6$  mg/L and  $610 \pm 11$  mg/L, respectively), intermediate in LP ( $57.9 \pm 1.2$  mg/L and  $570 \pm 5.0$  mg/L), and lowest in -P ( $52.4 \pm 1.2$  mg/L and  $530 \pm 5.0$  mg/L;  $p < 0.05$  for each comparison). Available P in the soil did not differ significantly among the hydroperiod treatments; however, total P remaining in the soil was 7% lower in HHH and HLH ( $560 \pm 8$  mg/L and  $560 \pm 7$  mg/L, respectively) than in the LHL treatment ( $600 \pm 10$  mg/L;  $p = 0.01$ ), consistent with greater uptake by plants.

## DISCUSSION

Plants are likely to expand most rapidly where field conditions (invasibility) match the species' abilities (invasiveness). For example, coastal wetlands receive nutrient-rich runoff whether or not water-control structures are present, allowing eutrophication to drive invasions of *Typha*  $\times$  *glauca*, an aggressive hybrid that takes up available nutrients and expands vegetatively (Frieswyk and Zedler

Table 2. Total biomass of *T.  $\times$  glauca* plants grown in microcosms in response to P additions (6 g P/m<sup>2</sup> "HP", 2 g P/m<sup>2</sup> "LP", or no P addition "-P") and hydrologic regimes (constant flooding to 5 cm "HHH", high-low-high water "HLH", or low-high-low water "LHL"),  $\pm$  S.E.,  $n = 13$ .

	-P	LP	HP	Mean
LHL	$31.4 \pm 1.7$	$45.9 \pm 3.8$	$40.9 \pm 1.9$	$39.4 \pm 1.9$
HLH	$51.9 \pm 3.8$	$63.7 \pm 6.0$	$51.7 \pm 2.1$	$55.9 \pm 2.7$
HHH	$57.5 \pm 4.6$	$64.7 \pm 5.3$	$63.1 \pm 10.7$	$61.6 \pm 4.0$
Mean	$46.9 \pm 3.0$	$57.8 \pm 3.0$	$51.4 \pm 3.9$	$52.0 \pm 2.0$



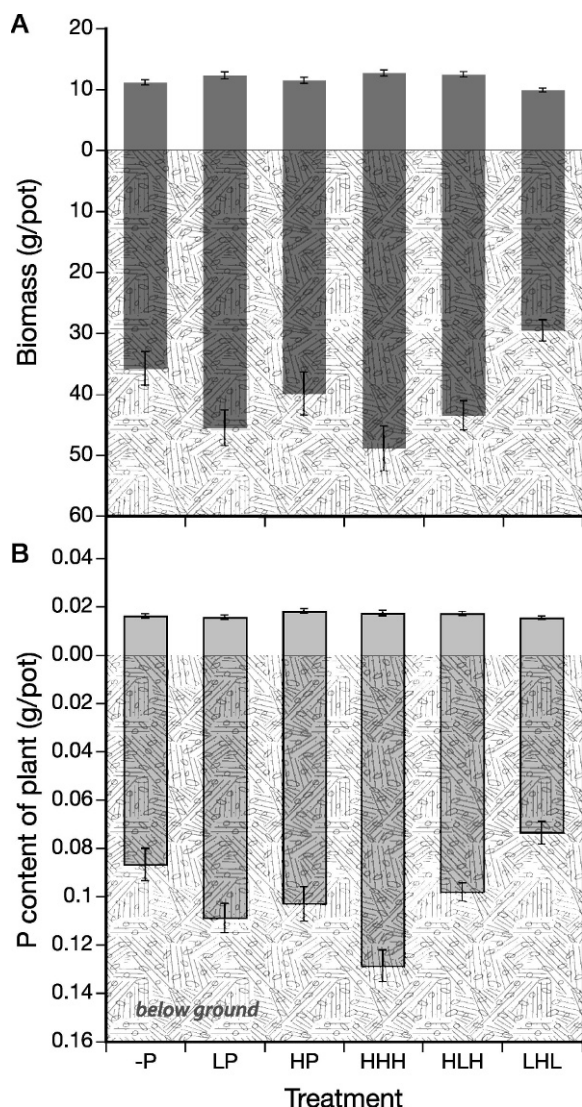


Figure 4. Biomass and phosphorus (P) content of *Typha*  $\times$  *glauca* plants grown in microcosms. There were no interactions in this fully crossed, two-factor experiment. A) Biomass above and below ground with three P treatments (6 g P/m<sup>2</sup> "HP", 2 g P/m<sup>2</sup> "LP", or no P addition "-P") and three water level treatments (constant inundation, "HHH", high-low-high water "HLH", and low-high-low water, "LHL"). B) Calculated amount of P accumulated by *T. x glauca* plants grown in the same P and water level treatments. Error bars are S.E.; n = 21.

2007). Wetlands that are altered hydrologically could become more invisable if waterlogged soils undergo internal eutrophication, i.e., a change in soil chemistry that makes nutrients more available for plant uptake. Here we show that *T. x glauca* expanded rapidly behind a dam, which stabilized water levels, and that *T. x glauca* took up more P when water levels were experimentally stabilized.

Lacking ideal field conditions (same *Typha* strain, no confounding variables), we evaluated a realistic

situation, wherein a fluctuating-water wetland (LuluW) had the native and exotic parents, but was not yet dominated by the hybrid, while sites behind a dam were dominated by *T. x glauca*. Differences among taxa could contribute to the field pattern, as *T. x glauca* is considered to be more invasive than either of its parent species (Smith 1987, Waters and Shay 1991). Nevertheless, stabilized water levels are a potential cause.

Under LuluW's fluctuating water levels, *Typha* (mostly the invasive *T. angustifolia*) also expanded linearly over time, but one-fifteenth as fast as *T. x glauca* expanded at ESW and < 1/2 as fast as at ESE (comparing % of wetland dominated; Table 1). The low rate occurred despite the large size of LuluW (163 ha). Our spatial comparisons corroborate a temporal shift in *Typha* expansion rates found by Wilcox et al. (1985) before and after water-level stabilization, when rates increased 7.5-fold, from ~2,400 to ~18,000 m<sup>2</sup>/year. Future dominance by *Typha* can be predicted as a linear increase, since linear correlations were high ( $R^2 = 0.97$  for ESW, 0.95 for ESE, and 0.93 for LuluW). If rates remain constant, ESW will be completely dominated by *T. x glauca* by 2014 and ESE by 2025, but LuluW would not be completely dominated by *Typha* until the year 2684.

The effect of water-level stabilization on *Typha* expansion is not new to wetland ecology (Wilcox et al. 1985, Day et al. 1988, Wilcox 1993, Shay et al. 1999, Albert and Minc 2004). What our study contributes is experimental support for the hypothesis that such invasions can be influenced by internal eutrophication (the process whereby nutrients already in the soil become available for plant uptake; Koerselman et al. 1993). Given that anaerobic conditions can release P from an otherwise insoluble Fe complex (Patrick and Khalid 1974, Richardson 1999), P flux is a plausible form of internal eutrophication.

For stabilized water levels to enhance *Typha* growth via P flux, the soil must release P and *Typha* must take it up and produce more biomass. Even though the microcosm soil differed from that of the Eagle Spring and Lulu Lakes wetlands (in having higher K, Al, and Mn, and lower P, Ca, Na, B, and S), all soils exhibited measurable P flux under 5 weeks of inundation in a pilot lab experiment (Boers 2006). The pore water had four times as much P when inundated with 3 cm of water than when soil was moist but not inundated. Other studies have found similar P release from incubated soil cores with standing water (Patrick and Khalid 1974, Phillips 1998, Pant and Reddy 2001, Aldous et al. 2005).



Others have tested the effects of nutrients on *Typha* species (DeLaune et al. 1999, Miao et al. 2000, Lorenzen et al. 2001, Svengsouk and Mitsch 2001, Woo and Zedler 2002, Miao 2004), and Newman et al. (1996) combined a test of the effects of N and P on *T. domingensis* with flooding (60 cm depth), but they did not vary hydroperiod. *Typha* is known to expand with P enrichment, especially *T. domingensis* in the oligotrophic Florida Everglades (Childers et al. 2003, King et al. 2004); however, in some cases *Typha* growth might be limited by N or co-limited by N and P (Neill 1990, Svengsouk and Mitsch 2001). *Typha* can even be limited by P and N in different parts of the same wetland (Drexler and Bedford 2002).

In our experiment, prolonged high water allowed *T. × glauca* to take up additional P and to increase its growth rate. We calculated that plants in the high treatment took up the most P, one-drawdown an intermediate amount, and two-drawdowns the least. Growth enhancement by P is indicated by our finding that *T. × glauca* produced substantially (25%) more total biomass after adding 2 g/m<sup>2</sup> of P. Also, the N:P = 17.3 ratio of the experimental soil suggests P limitation (Bedford et al. 1999). The high-P treatment did not increase *T. × glauca* growth in the microcosms, and we speculate that algae took up the excess nutrients, since we observed algal growth in several HP microcosms, but in only one LP microcosm. Richardson and Marshall (1986) showed that more available P in fens is taken up by algae or microorganisms than by higher plants.

In comparison with the one-drawdown treatment, the no-drawdown and two-drawdown treatments produced more total leaf length and more total biomass regardless of P addition level. The differences in biomass production between each of the drawdown treatments occurred even though both had six weeks of inundation. Either more P was liberated with two inundations or the first high water in the one-drawdown treatment increased P availability at a critical early-season time, resulting in greater uptake and total biomass. *Typha × glauca* responded more strongly below than above ground to both P addition and water level treatments. Given more P, plants first developed their root and rhizome system. Above-ground biomass might also respond as plants age and shift allocation from roots to shoots.

In future research, we recommend testing the release of P from a range of wetland soils subjected to stabilized vs. variable hydroperiods, as well as tracking P concentrations in the pore water over time. We suggest measuring P uptake rates (mass accumulated per time per root biomass) for com-

parison with other studies (e.g., Lorenzen et al. 2001). We further recommend tests to explain the lack of interaction between hydroperiod and P addition, since Newman et al. (1996) saw interactions between nutrient additions, water depth and species (not including *T. × glauca*). Also, we would like to know the source of P released during inundation, since both inorganic and organic sources of P could add to P flux. More work on nitrogen dynamics and other essential elements would also further understanding of internal eutrophication. Future field studies should follow clonal expansion of known *Typha* genotypes in areas where hydroperiods are measured.

## CONCLUSIONS

High rates of clonal expansion of *T. × glauca* behind a dam were consistent with our finding of high growth rates under an experimentally stabilized water level. In addition, P release was implicated by the greater ability of *T. × glauca* to take up more P and produce more biomass with P addition. Our experiment thus offered support for the hypothesis that water level stabilization can increase P uptake and growth of *T. × glauca*.

Wetlands that occur upstream of water-control structures and have stabilized water levels have high potential for internal eutrophication (especially P release). *Typha × glauca* is an opportunistic invader capable of utilizing an influx of P to increase its growth rate. The potential for internal eutrophication to facilitate *T. × glauca* invasions deserves more attention.

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