



# Response of *Typha* to phosphorus, hydrology, and land use in Lake Ontario coastal wetlands and a companion greenhouse study

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**Abstract** Loss of Great Lakes wetlands due to changes in land use, hydrology, nutrient inputs, and invasive species led to the need for studies involving physical factors that influence growth of invasive cattails (*Typha*). Thus, in 18 Lake Ontario coastal wetlands, we sampled vegetation along stratified random transects and collected water samples for total phosphorus (TP) analyses. We used GIS to determine watershed area, percent land use as croplands, and length of lotic surface waters entering wetlands. A greenhouse growth experiment with a full factorial random block design was used to investigate the effects of variable hydroperiod and phosphorus concentrations on *T. × glauca* biomass changes. Correlation analyses of wetland data revealed that TP in field studies was related to percent croplands but not lotic length; mean percent *Typha* was not related to TP. In the growth experiment, above- and below-ground biomass increased significantly for simple main effects of hydroperiod and phosphorus concentrations. Multiple pairwise interaction comparisons between hydrology

and nutrient treatments showed that effects of phosphorus concentration were present only at longer hydroperiods. Lack of correlation between *Typha* and phosphorus concentrations in the field was likely due to the overwhelming effect of water-level regulation on Lake Ontario. The greenhouse study demonstrated that increasing concentrations of phosphorus positively influenced cattail growth in a controlled setting. Although phosphorus positively influenced growth, hydrologic regime had the greatest influence on cattail growth, with increased biomass as hydroperiod increased. More natural hydrology and management of phosphorus inputs may help limit spread of *Typha*.

**Keywords** Cattail invasion · Wetland vegetation · Greenhouse growth experiment · Hydroperiod · Nutrients · Croplands

## Introduction

Since European settlement of the Great Lakes region in the early 1800s, 50 to 90 percent of Great Lakes coastal wetlands have been lost due to anthropogenic land-use changes, hydrological alterations, climate change, nutrient inputs, and invasive species (Moser et al. 1996; SOLEC 2005). Loss of Great Lakes wetlands has continued to occur despite regulations, and their value in aquatic processes such as sediment and nutrient filtration and habitat for plants, mammals, fish, invertebrates, and birds has

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decreased (Maynard and Wilcox 1997; Environment Canada 2002). The historical and current loss and alteration of wetlands reinforces the importance of preserving and restoring these systems, including studying the interactions between such factors as nutrient inputs and invasive species.

One of the most common invasive plants found in emergent zones of Lake Ontario coastal wetlands is the cattail (hybrid cattail *Typha* × *glauca* Godr. and narrowleaf cattail *Typha angustifolia* L.) (Galatowitsch et al. 1999; Wilcox et al. 2005, 2008; Vaccaro et al. 2009; Bansal et al. 2019; Smith et al. 2021). Several traits allow *Typha* to proliferate in Lake Ontario wetlands. Clonal expansion via rhizomes allows it to spread rapidly, and aerenchyma tissue enables it to tolerate high water conditions. *Typha* also has a great capacity for biomass production (Grace and Wetzel 1981). The large amount of above-ground biomass of *Typha* allows it to shade out competitors, while rapid rates of nutrient uptake enable it to out-compete native species (Galatowitsch et al. 1999; Bansal et al. 2019).

Water availability to *Typha* rhizomes is critical for survival, and hydrologic alterations can influence cattail invasion. When operation of the St. Lawrence Seaway began in about 1960 following construction of the Moses-Saunders hydroelectric dam, regulation of Lake Ontario water levels under Plan 1958DD reduced annual fluctuations from 1.5 to 0.7 m, approximately half the pre-regulation amplitude (Wilcox and Xie 2007). Wilcox et al. (2008) showed that these regulated lake levels enabled *Typha* × *glauca* invasion in the sedge/grass meadow marsh zone, as native sedge and grass species lost the competitive advantage they held over *Typha* during low lake-level periods, which no longer occurred. *Typha angustifolia* invasion was generally in the emergent zone, often as floating mats (Wilcox et al. 2005, 2008). In January 2017, a new water-level-regulation plan was enacted (Plan 2014) that “strives to return the Lake Ontario-St. Lawrence River system to a more natural hydrologic regime, while limiting impacts to other interests” (IJC 2014). However, extreme water flows from the upper Great Lakes resulted in high water levels in Lake Ontario in 2017 and 2019, so invasion of *Typha* × *glauca* into sedge/grass meadow has likely continued, and floating mats of *T. angustifolia* likely survived.

If high water conditions also carry nutrients, the competitive advantage of high nutrient uptake rates may allow *Typha* to maintain and expand its dominance (Miao and Sklar 1997; Bansal et al. 2019). Due to its relatively fast growth rates and ability to take up nutrients rapidly, *Typha* thrives in areas of high nutrient input (i.e., nitrogen and phosphorous) (Newman et al. 1996; Miao and Sklar 1997; Mack et al. 2000). Woo and Zedler (2002) conducted nitrogen- and phosphorous-addition experiments with *T. × glauca* and native sedge-meadow species to determine if these additions accelerated the expansion of *T. × glauca* into wet meadow zones. They found that *T. × glauca* increased above-ground biomass, stem density, and height with nutrient additions, while native sedge species showed no significant response. In addition, phosphorus binds to oxidized Fe<sup>3+</sup> in dewatered soil during low water conditions but is released under flooded conditions when redox reactions convert the iron to Fe<sup>2+</sup>. Boers and Zedler (2008) determined that this reaction caused “internal eutrophication,” which increased cattail growth. Thus, on regulated Lake Ontario, lack of periodic years with low water levels likely kept phosphorus available, even in the higher elevation sedge/grass meadow.

Nutrient loading to Lake Ontario wetlands likely comes from non-point sources that include but are not limited to agriculture, urban runoff, and atmospheric deposition of nitrogen (Makarewicz 2009; DeBues et al. 2019). Modeling by Hamlin et al. (2020) showed agricultural fertilizer to be a major nutrient source along the southern shore of Lake Ontario. Agricultural and urban land use in wetland catchments of the Great Lakes has been shown to affect nutrient enrichment, water clarity, and sediment quality (Crosbie and Chow-Fraser 1999; Trebitz et al. 2007; Morrice et al. 2008; Robertson and Saad 2011; Harrison et al. 2020). In a basin-wide study, Lougheed et al. (2001) concluded that the proportion of agricultural and urban land in wetland watersheds was a statistically significant predictor of water quality.

Experiments with nutrient additions involving *Typha* have involved either a mesocosm approach (Woo and Zedler 2002; Boers and Zedler 2008) or cattail species other than *T. × glauca*, which we chose to study (Farmer et al. 2005; Macek and Rejmánková 2007). Lishawa et al. (2014) combined field and mesocosm approaches to assess effects of *T. × glauca* populations on wetland functions along

Lake Michigan. There has been relatively little or no research performed with *T. × glauca* from Lake Ontario coastal wetlands involving phosphorus and altered hydroperiods, leaving much to be learned from further studies.

Studies have found spatio-temporal correlations between a watershed's agricultural land use and phosphorus loading in streams and their outputs (Makarewicz and Lewis 2002, 2009; Makarewicz 2009). In this study, we hypothesized that as the proportion of agriculture (croplands) increases in a wetland's watershed, the concentration of total phosphorus (TP) within wetland waters would also increase. Concentrations of TP might also be predicted by the total length of lotic surface waters. We expected that in watersheds with greater total lengths of lotic surface waters, wetland waters would have decreased concentrations of TP and vice versa based on the adage, "dilution is the solution to pollution." Previous studies also demonstrated a positive relationship between the biomass of aquatic micro- and macrophytes and TP at stream mouths in littoral systems of Lake Ontario (Makarewicz and Lampman 1994; Makarewicz 2009). Ultimately, we predicted that increases in TP would increase the density (as percent cover) of *Typha* in Lake Ontario wetlands.

To assess relationships between land use, phosphorus concentrations, and *Typha* invasion, data were collected on mean wetland water phosphorus concentrations and densities of the cattail in 18 Lake Ontario wetlands over a 2-year span during the growing seasons of 2011 and 2012. We also assessed percent cropland in wetland watersheds and length of lotic waters flowing into wetlands. To augment field observations, we conducted a greenhouse growth experiment on cattail (selecting *T. × glauca*) using several combinations of hydroperiods and phosphorus concentrations. We hypothesized that the cattail would amass greater amounts of above- and below-ground biomass as the duration of hydroperiods increased. We also hypothesized that the cattail would respond to the interaction of hydroperiod and increasing phosphorus concentrations by increasing total biomass; this interaction would be increasingly pronounced with simultaneous increases in hydroperiod and phosphorus additions.

## Methods

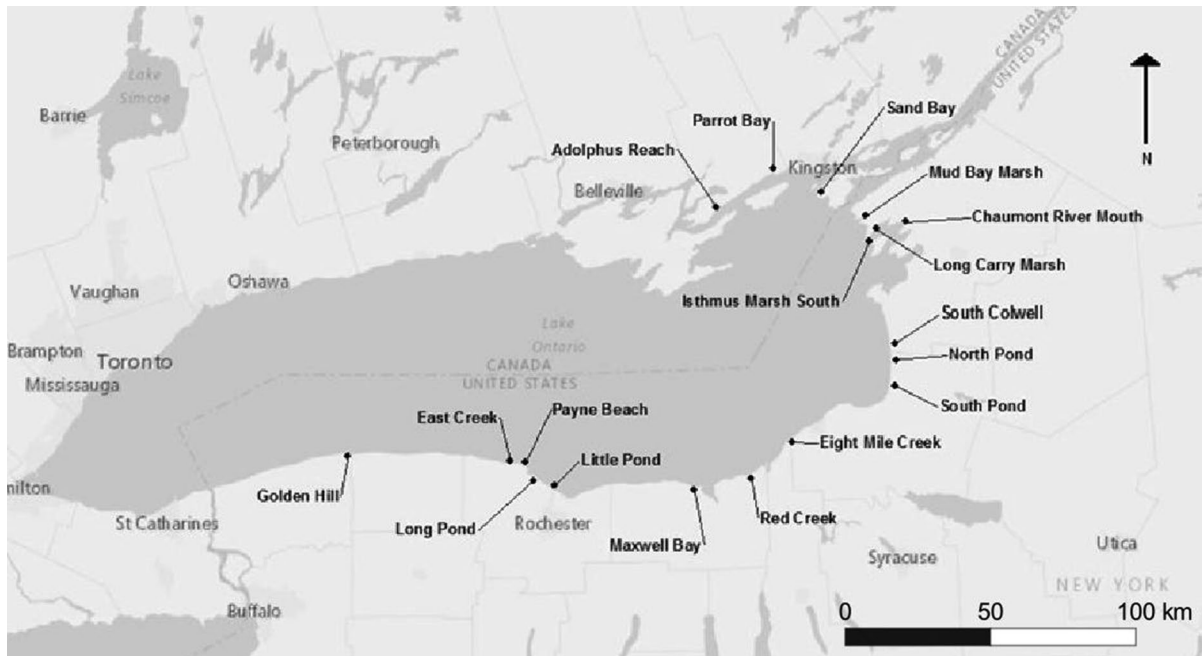
### Field studies

#### *Study sites*

Eighteen Lake Ontario coastal wetlands were sampled from May to August in 2011 and 2012 (Fig. 1). The sites were selected randomly as part of the U.S. Environmental Protection Agency, Great Lakes Restoration Initiative, Coastal Wetland Monitoring Program (Uzarski et al. 2017). Lacustrine, riverine, and barrier-protected wetlands (Albert et al. 2005) sampled were all connected to Lake Ontario. Submergent and emergent vegetation zones were present at all sites, but due to anthropogenic influences, including lake-level regulation and land use, some wetlands sampled did not contain a wet meadow zone. Where present, wet meadow was often restricted to a narrow fringe (<12 m) between the emergent zone and upland edge, and cattail invasion was largely by *T. × glauca*. Emergent zones were dominated by cattails, *T. × glauca* and *T. angustifolia*, and associated standing dead material. Substrate in all emergent zones often was composed of floating mats of organic material, in many cases >250 cm thick. Relative water quality in sampled sites ranged from hypereutrophic and turbid to mesotrophic with low turbidity. All sampled wetlands met the following criteria: (1) 4 ha or larger, (2) a direct, obvious surface-water connection to Lake Ontario, (3) close enough to the lake to be influenced by it, and (4) herbaceous or standing-water wetland zones present (Uzarski et al. 2017).

#### *Transect sampling*

Data collection at each site focused on identification and quantification of all wetland plant species occurring in 1-m<sup>2</sup> quadrats on three transects that ran perpendicular to depth contours and therefore crossed submergent, emergent, and wet meadow vegetation zones (if present). The starting point of each transect was randomly located along the upland or swamp forest edge or the outer wetland edge. The width of each vegetation zone on a transect was established using a 100-m measuring tape, and that width was divided by six to establish where five equidistant quadrats would be placed in each zone. Forty-five quadrats were sampled per wetland (15 quadrats/zone) if all zones were



**Fig. 1** Location of Lake Ontario coastal wetlands sampled in 2011 and 2012

present. Within each quadrat, all macrophyte species were identified to lowest possible taxonomic unit, generally to species level. Visual estimates were made for percent cover of each plant species, total vegetation cover, standing dead cover, and detritus cover to the nearest one percent up to ten percent, then by five percent increments. Only percent cover of *Typha* was used for analysis here. Starting and ending locations for each transect and associated quadrats were recorded using a Garmin Rino model 530HCx global positioning system.

#### *Water quality: macronutrient quantification*

Water quality sample collection and analyses also followed protocols set by the Coastal Wetland Monitoring Program (Uzarski et al. 2017). In summary, in situ samples were collected in clean containers at mid-depth at each of three locations where fish sampling was conducted by fyke net as part of the overall sampling program (Uzarski et al. 2017), with special care that substrates were not disturbed before or during sample collection. Our samples were all taken from the SAV zone adjacent to the emergent (cat-tail) zone. Water samples were immediately placed in

coolers and then frozen for shipment to the Natural Resource Research Institute at University of Minnesota-Duluth for analysis. Laboratory and field measurement parameter objectives, precision, accuracy, and method detection limits are found in Uzarski et al. (2017). Lab results were averaged for TP (mg/L) across three fyke net sampling locations in each wetland for ease of analysis.

#### *Wetland watershed land use and surface waters*

ESRI ArcGIS v10.1 was used to determine size of sampled wetlands (ha), size of wetland watersheds (ha), length of lotic surface waters (km), and size (ha) and extent (percent) of croplands at each of the 18 wetland watersheds. The National Hydrography Dataset (NHD), which provides an ArcGIS base layer for lotic surface waters, was accessed to aid in determining the area of each wetland's watershed. However, the available GIS-layer datasets for agricultural land use were out-of-date for the years of 2011 and 2012. Therefore, the current size and extent of croplands within watersheds were revised by manually digitizing each cropland and creating maps using ArcGIS orthoimagery basemaps, which are updated on a more

frequent basis than land-use GIS layers. After digitization, cropland areas were converted to percentage of the wetland's total watershed area to represent the proportion of influence that agriculture may have on other site variables. Lacustrine wetlands were assigned zero values for the variables total watershed area, percentage of agriculture in wetland watershed, and total length of lotic surface waters in the wetland watershed.

### Growth experiment

An 8-week hydroponic greenhouse growth experiment initiated on 1 June 2012 was used to assess the potential interaction and discrete effects of variable hydrology and phosphorus concentrations on cattail growth and biomass allocation. Eighty individual *T. × glauca* plants were collected randomly at distance from each other, to avoid sampling the same individual, from Brush Creek, a Lake Ontario coastal wetland, on 31 May 2012. Leaves were trimmed to a standard length of  $20 \pm 1$  cm from the base of the plant where the leaf sheaths meet the rhizomes. Rhizomes were trimmed to  $10 \pm 1$  cm in length measured from the start of the rhizome below the leaf sheaths. Roots on all rhizomes were trimmed to  $1 \pm 0.2$  cm. Trimmed plants were then cleaned of residual soil with deionized water and placed in deionized water for 12 h to clean remaining wetland soil from the samples and to help flush nutrients from the rhizomes.

Rhizomes with attached 20-cm leaves were weighed prior to the growth experiment to provide the initial weight for measuring rhizome growth. At the end of the experiment, the leaves were trimmed to a same length of  $20 \pm 1$  cm from the base of the plant where the leaf sheaths meet the rhizomes, and the remaining rhizome plus leaves were used for post-experiment weighing, with roots on all rhizomes again trimmed to  $1 \pm 0.2$  cm. The trimmed leaves from above the 20-cm mark were used for measuring leaf growth. Leaves, rhizomes, and roots were then dried and weighed.

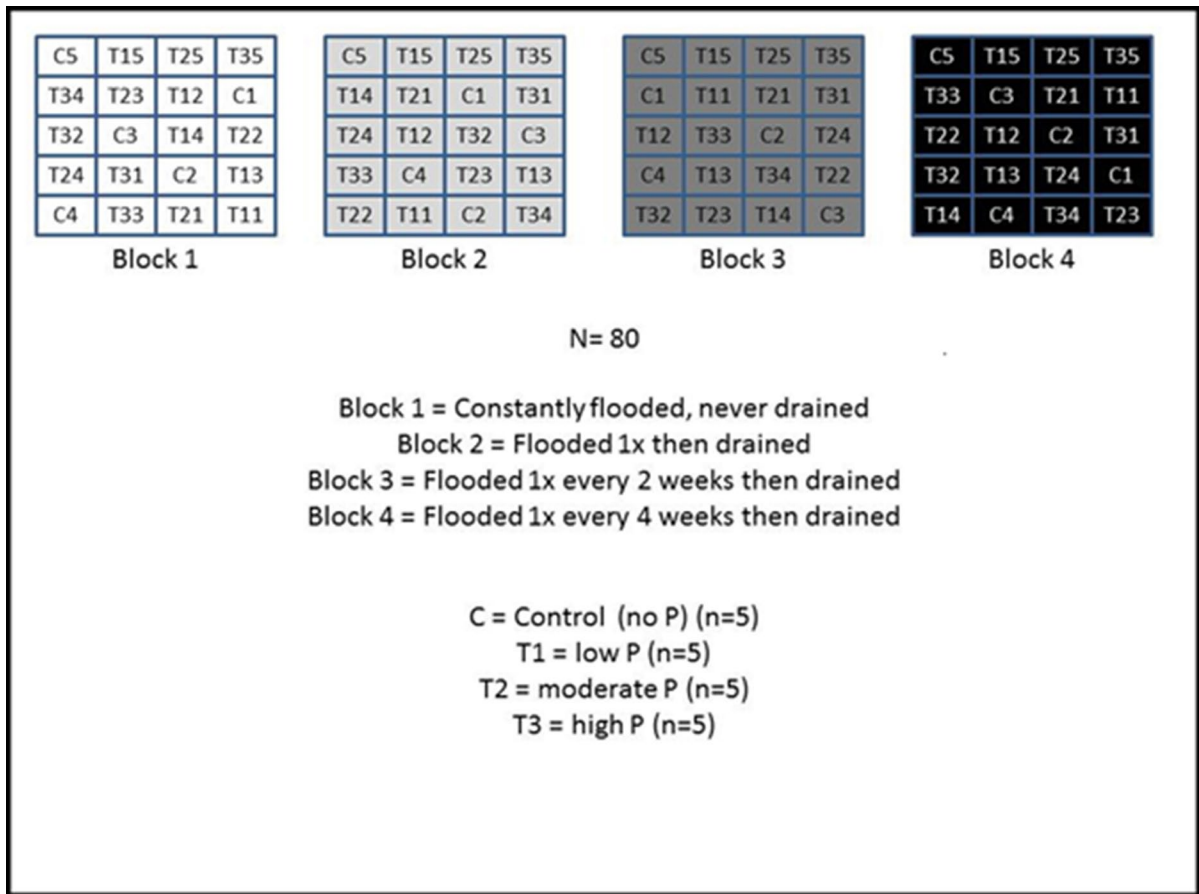
A two-factor balanced and complete random block design was used for the growth experiment (Fig. 2), which was blocked by hydroperiod (hydro-block) to limit variation among units within blocks rather than between blocks. The experiment was designed with the intent of using MANOVA, as it assesses two (or more) related dependent variables (leaf and

rhizome biomass) while controlling for the correlation between the dependent variables.

Twenty trimmed cattails were randomly assigned to each of four hydro-blocks: static standing, pulsed every two weeks then drained, pulsed every four weeks then drained, and pulsed just one time then drained. For pulsed treatments, nutrient solutions were applied for 15 min to allow for complete media saturation and then gravity-drained. Nutrient treatments varied only by phosphorus concentrations: control group with no phosphorus (C), low concentrations as treatment one (T1), moderate concentrations as treatment two (T2), and high concentrations as treatment three (T3) (Fig. 2). Each of the nutrient treatments was assigned to cattail samples randomly, with five replicates each in the four hydro-blocks for a total  $N = 80$ .

Nutrient additions were performed with modified Hoagland's nutrient solutions (with ammonium to lower pH) mixed with deionized water (Table 1) (Hoagland and Arnon 1950; Epstein 1972). Higher plants are able to assimilate nitrogen as  $\text{NH}_4^+$  and  $\text{NO}_3^-$ . In aerated soils with a pH above 4,  $\text{NO}_3^-$  is the prevailing nitrogen compound, and  $\text{NH}_4^+$  is found in low concentrations, but in waterlogged soils, this ratio is reversed as a consequence of depressed bacterial nitrification activity and denitrification of  $\text{NO}_3^-$  (Brix et al. 2002). Ammonium was included in the micronutrient solution (Table 2), which was applied similarly in all treatments, in this experiment in the form  $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$ ; nitrate was included in the macronutrient solution in the forms of  $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$  and  $\text{KNO}_3$ . Phosphorus was added in the form of  $\text{KH}_2\text{PO}_4$ , a form commonly used in cattail growth experiments (Shipley and Keddy 1988; Woo and Zedler 2002; Macek and Rejmánková 2007; Escutia-Lara et al. 2009). All stock solutions were prepared with deionized water and stored in a refrigerator at 3 °C for the duration of the experiment. Stock solutions were not combined into macro- and micro-mixes until the day of application to avoid chemical reactions that would alter availability. Once solutions were mixed, pH was adjusted to 6 with 1 M HCl or 1 M NaOH and set aside until ambient air temperature was reached before application.

The cultivation medium was a 50:50 mix of silica sand and granulated absorbent rockwool in individual 5 mm 4.7 L hydroponic polyethylene film containers, which were then placed in 5 L HDPE containers for



**Fig. 2** Random block design of eight-week greenhouse experiment on *Typha x glauca* with varying phosphorus treatments and hydroperiods. Individual cells are hydrologically isolated

**Table 1** Macronutrients and concentrations of modified Hoagland's solution used in 8-week *Typha x glauca* greenhouse growth experiment

Macronutrients	Control		T1 (low)		T2 (moderate)		T3 (high)				
	Form	g L <sup>-1</sup>	Stock (M)	mL stock L <sup>-1</sup>	μM	mL stock L <sup>-1</sup>	μM	mL stock L <sup>-1</sup>	μM		
KH <sub>2</sub> PO <sub>4</sub>		136.09	1	0	0	0.50	500	2.00	2000	6.00	6000
KNO <sub>3</sub>		101.11	1	5.10	5100	5.10	5100	5.10	5100	5.10	5100
Ca(NO <sub>3</sub> ) <sub>2</sub> * 4H <sub>2</sub> O		236.15	1	2.02	2020	2.02	2020	2.02	2020	2.02	2020
MgSO <sub>4</sub> * 7H <sub>2</sub> O		246.48	1	1.00	1000	1.00	1000	1.00	1000	1.00	1000

stability and isolation. There was no artificial aeration of hydroponic solutions in any block. Before application of new nutrient solutions in pulsed and constant block treatments, the growth media were drained and containers flushed with deionized water to avoid toxic salt accumulation.

Daily records for ambient air temperature and relative humidity inside the greenhouse were recorded with General Tools© HT50 RH/Temp Data Loggers (Appendix Table 5). Weekly measurements of volumetric water content (percent) were recorded using a Vegetronix™ VG-METER-200

**Table 2** Micronutrients and concentrations of modified Hoagland's solutions used in eight-week *Typha × glauca* greenhouse growth experiment

Micronutrients				Final concentration (μM)	
	Form	G L <sup>-1</sup>	Stock solution (M)		mL stock L <sup>-1</sup> of DI water
MnCl <sub>2</sub> ·4H <sub>2</sub> O		1.979	0.010	0.406	4.06
ZnSO <sub>4</sub> ·7H <sub>2</sub> O		0.288	0.001	0.618	6.18
CuSO <sub>4</sub> ·5H <sub>2</sub> O		0.250	0.001	0.420	4.20
(NH <sub>4</sub> ) <sub>6</sub> Mo <sub>7</sub> O <sub>24</sub> ·4H <sub>2</sub> O		1.236	0.001	0.278	2.78
H <sub>3</sub> BO <sub>3</sub>		0.618	0.010	1.936	19.36
NaFe-DTPA (10% Fe)		33.240	0.071	1.000	71.00

soil moisture meter before solution renewals to ensure consistency.

During the course of the experiment, a leaf or genet was considered dead if more than two-thirds of its length was brown and dry; its mortality then was noted and final length recorded. Any cattail not surviving past week three was not included in analyses as it was most likely using stored starches for growth until mortality and was not responding to treatment. At test termination on 28 July 2012, leaves were cut above the 20-cm starting point and all plants were rinsed in deionized water before being fractionated into leaves, rhizomes, and roots and placed in labeled paper bags. Bagged samples were then placed in a drying oven at 60 °C to dry for biomass determination. After 24 h, each bag was weighed hourly until weight changes were less than 0.01 g, which was achieved at 29 h.

#### Statistical analyses

##### Field studies

Mean percent cover of combined *T. angustifolia* and *T. × glauca* was calculated based on total number of quadrats in the emergent and wet meadow zones, including those with no *Typha*. As some parameters quantified were not normally distributed, Spearman's rank correlation in Minitab V. 18 was used to assess the relations among field data—mean concentration of TP vs. percent of watershed in cropland, mean TP vs. length of surface lotic waters, and mean percent cover *Typha* vs. mean TP. Significance was determined at  $p \leq 0.05$ .

##### Growth experiment

Two-way MANOVA with the General Linear Models multivariate procedure in SPSS was used, with the independent variables (IV) hydro-block and nutrient treatments alone, as well as with interactions, to determine possible effects on the dependent variables (DV), dried leaf weight (g), dried root weight (g), and dried rhizome weight (g). Significance was determined at  $p \leq 0.05$ . Data were tested for normality using the Descriptive Statistics function of SPSS. For testing normality with a two-way MANOVA, the file was split to organize the output based on groups—in this case, the hydro-block and phosphorus treatment. Skewness, normality plots, histograms, and Shapiro-Wilks outputs were examined for the assumption of normality. Assessments of Q-Q plots were used to check the assumption of linearity, and boxplots were checked for outliers. Heteroscedasticity was assessed by Levene's Test of Equality of Error Variances. Box's Test of Equality of Covariance Matrices was produced and assessed for violation of the assumption of equal covariance matrices. Since sample sizes were equal, if data failed Box's test of equality of covariance matrices, this result can be ignored, as MANOVA test statistics are robust to violations of this assumption (Field 2009). Pearson's Correlation analysis was used to determine if the dependent variables were significantly correlated to determine if multicollinearity was present. If data did not meet the assumptions, they were transformed and assumptions were re-investigated. Pearson's Correlation was also run for dried rhizome and dried root weights, as these two variables are likely correlated.

A full factorial two-way multivariate linear model with main effects of the independent variables, as well as interactions using Type III sum of squares, was then performed with Tukey's Post Hoc test to identify if significant interactions occurred once the data met required assumptions. The six combinations produced for each pairwise comparison among hydro-blocks, nutrient treatments, and their interactions allowed determination of whether there were any significant differences on their effects on leaf and rhizome biomass.

Mortality after Week 3 occurred in three of the four hydro-blocks. There was no mortality in the static standing hydroperiod. When pulsed every two weeks, average mortality occurred in week 7, in week 6 when pulsed every four weeks, and in 5.9 weeks when pulsed just once. To maintain a balanced design and account for this systematic loss, a randomly chosen replicate of each treatment in each

block was selected to be removed from the dataset. The removal of a replicate using the random function in SPSS resulted in four replicates per treatment remaining, for a total population of  $N = 64$ .

## Results

### Field studies

The mean concentration of TP by site ranged from 0.015 to 0.214 mg/L and increased with percent of watershed in cropland (Spearman's  $\rho = 0.717$ ,  $p = 0.001$ ); however, there was no increase in mean TP with increased lotic length ( $\rho = 0.402$ ,  $p = 0.098$ ) (Table 3). Percent cover of *Typha* showed no relation to mean concentration of TP ( $\rho = 0.124$ ,  $p = 0.624$ ) (Table 3).

**Table 3** Lake Ontario wetland field sites showing geomorphic type, wetland area, watershed area, percent cropland in watershed, length of lotic surface waters, mean total phosphorus, and mean percent cover of *Typha* from sampling in wetlands

Wetland site	Geomorphic Type	Wetland Area (ha)	Watershed Area (ha)	Percent Cropland	Lotic Length (km)	Mean total P (mg/L)	Mean percent Cover <i>Typha</i>
Adolphus Reach	Lacustrine	20.3	0	0	0	0.015	0
Chaumont R. mouth	Lacustrine	11.3	0	0	0	0.038	18.1
East Creek	Riverine	14.2	863	55.3	14.5	0.214	38.1
Eight Mile Creek	Riverine	6.3	2638	7.9	22.9	0.086	0.9
Golden Hill	Riverine	3	5506	36.9	91	0.173	0
Isthmus South	Lacustrine	6.5	0	0	0	0.034	19
Little Pond	Riverine	16.3	1423	0	12.2	0.085	22.3
Long Carry	Lacustrine	7.7	0	0	0	0.094	27.9
Long Pond	Barrier Beach	233.9	6400	17.6	78.6	0.122	33.2
Maxwell Bay	Barrier Beach	19.2	11,829	17.2	136.8	0.201	10.5
Mud Bay	Riverine	113.6	5898	15.7	99.6	0.201	18.9
North Pond	Barrier Beach	1020.8	21,720	7.7	311.8	0.023	11.1
Parrot Bay	Lacustrine	31.4	0	0	0	0.042	25.2
Payne Beach	Barrier Beach	77	443	24.9	5.8	0.115	0
Red Creek	Riverine	154.3	6843	19	85	0.054	30.6
Sand Bay	Lacustrine	9.8	0	0	0	0.016	27.6
South Colwell	Barrier Beach	85.4	26,177	7.5	435.6	0.072	9.3
South Pond	Barrier Beach	143.6	7209	11.7	99	0.053	0.1

Spearman's rank correlation showed mean concentration of TP to increase with percent of watershed in cropland ( $\rho = 0.717$ ,  $p = 0.001$ ) but not with increase in lotic length ( $\rho = 0.402$ ,  $p = 0.098$ ). Mean percent cover of *Typha* was not related to mean concentration of TP ( $\rho = 0.124$ ,  $p = 0.624$ )



## Growth experiment

*Cattail biomass, hydroperiod, and phosphorus treatments*

As expected, rhizome weights and root weights were significantly correlated ( $r=0.933$ ,  $p \leq 0.001$ ), so root

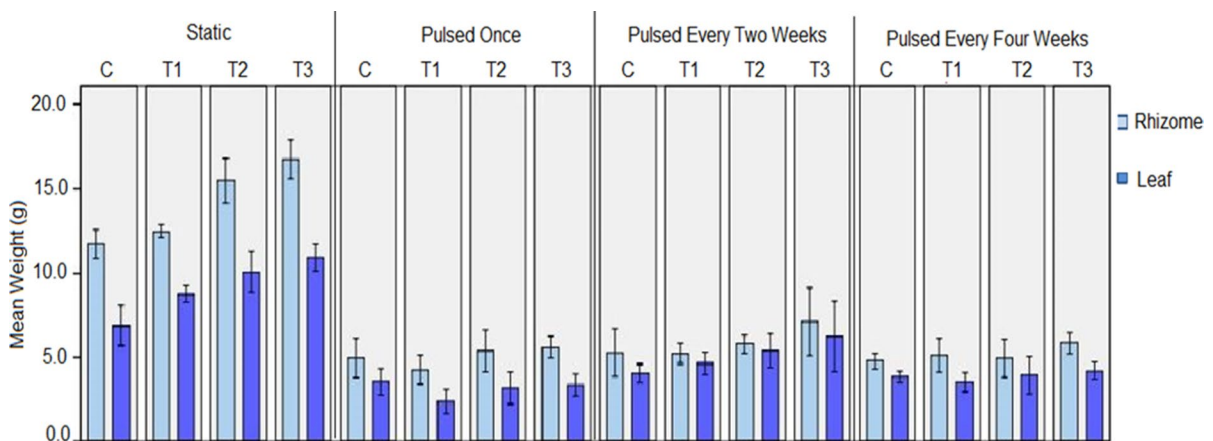
**Table 4** MANOVA Tukey's HSD post-hoc multiple comparisons of the interaction effects within hydro-blocks (static standing, pulsed and drained every two weeks, every four weeks, and once) among control (C), 500  $\mu\text{M}$  (T1), 2000  $\mu\text{M}$  (T2), and 6000  $\mu\text{M}$  (T3) phosphorus treatments after an eight-week *Typha \times glauca* growth experiment

	C	T1	T2	T3
<b>Rhizome</b>				
Static	11.74 <sup>ab</sup>	12.46	15.48 <sup>a</sup>	16.75 <sup>b</sup>
2-Week	5.30 <sup>c</sup>	5.24 <sup>d</sup>	5.80 <sup>e</sup>	7.12 <sup>c,d,e</sup>
4-Week	4.80	5.14	4.95	5.85
Once	4.97	4.28 <sup>f</sup>	5.41	5.61 <sup>f</sup>
<b>Leaf</b>				
Static	6.88 <sup>g</sup>	8.76 <sup>g,h,i</sup>	10.08 <sup>g,h</sup>	10.94 <sup>g,i</sup>
2-Week	4.05 <sup>j,k</sup>	4.66 <sup>l</sup>	5.24 <sup>j</sup>	6.24 <sup>k,l</sup>
4-Week	3.86	3.54	3.95	4.20
Once	3.58 <sup>m</sup>	2.39 <sup>m</sup>	3.20	3.37

Increases in rhizome and leaf weights (g) over eight weeks are presented. Paired superscripts indicate significant differences ( $p \leq 0.05$ )

weights were removed before MANOVA was initiated. Roots consistently measured only 3 to 5% of the weight of the individual rhizomes from which they came. The main effects of hydroperiod, phosphorus treatments, and their interaction all had significant effects on cattail, generally increasing all biomass measurements as duration of hydroperiod and phosphorus concentrations increased. Although all the main effects were significant, rhizome weights were a better fit of the corrected model ( $F=153.657$ ,  $df=15$ ,  $p \leq 0.001$ ) than leaf weights ( $F=75.710$ ,  $df=15$ ,  $p \leq 0.001$ ).

Cattail grown in the static standing hydroperiod accumulated a greater amount of below-ground ( $F=703.657$ ,  $df=3$ ,  $p \leq 0.001$ ) and above-ground ( $F=328.823$ ,  $df=3$ ,  $p \leq 0.001$ ) biomass than in all other hydro-blocks. On average, cattails also responded to increasing phosphorus concentrations by increasing both below-ground ( $F=37.742$ ,  $df=3$ ,  $p \leq 0.001$ ) and above-ground ( $F=24.850$ ,  $df=3$ ,  $p \leq 0.001$ ) biomass. In the static standing hydroperiod, increases in mean dried rhizome weight was 11.74 g in the control and increased across low phosphorus treatment T1 to moderate phosphorus treatment T2 to 16.75 g in high phosphorus treatment T3 (Table 4, Fig. 3). When pulsed and drained every two weeks, the range from control to T3 was from 5.30 to 7.12 g; when pulsed and drained every four weeks,



**Fig. 3** Means and 95% confidence intervals (error bars) of dried rhizome weights (g) and dried leaf weights (g) within hydro-blocks between nutrient treatments in an eight-week *Typha \times glauca* greenhouse growth experiment. The hydroperiod of Block 1 was static, Block 2 was pulsed once, Block 3 pulsed every 2 weeks, and Block 4 pulsed every 4 weeks.

Treatments consisted of a control (C) with no phosphorus additions, treatment T1 with low phosphorus concentrations (500  $\mu\text{M}$ ), T2 with moderate phosphorus concentrations (2000  $\mu\text{M}$ ), and T3 with high phosphorus concentrations (6000  $\mu\text{M}$ )

it was from 4.80 to 5.85 g; and for pulsed only once, it was 4.97 to 5.61 g. Increases in mean dried leaf weight in the static standing hydroperiod ranged from 6.88 g in the control to 10.94 g in high phosphorus treatment T3 (Table 4, Fig. 3). That range was from 4.05 to 6.24 g when pulsed and drained every two weeks, from 3.86 to 4.20 g when pulsed and drained every four weeks, and from 3.58 to 3.37 g when pulsed only once.

#### *Cattail biomass response to hydroperiod and phosphorus interactions*

Since independent variables of duration of hydroperiod and phosphorus concentrations generally showed increases in cattail rhizome and leaf weights (Table 4), interaction of these two variables was expected to produce similar results. However, such was not the case. For rhizome biomass ( $F=8.962$ ,  $df=9$ ,  $p\leq 0.001$ ), Tukey's Post-Hoc (Table 4) revealed there were four significant differences in the interactions by cattails grown in the static hydro-block (C vs. T2 and T3, T1 vs. T2 and T3; all  $p\leq 0.001$ ). There were three significant differences within the hydro-block pulsed every two weeks (C vs. T3,  $p=0.002$ ; T1 vs. T3,  $p=0.001$ ; T2 vs. T3,  $p=0.040$ ). However, there were none within the hydro-block pulsed every four weeks and one within the hydro-block pulsed just once (T1 vs. T3,  $p=0.039$ ).

For leaf biomass ( $F=8.292$ ,  $df=9$ ,  $p\leq 0.001$ ), Tukey's Post-Hoc assessment showed five significant differences in the interactions by those cattail grown in the static hydro-regime (C vs. T1, T2, and T3, all  $p\leq 0.001$ ; T1 vs. T2,  $p=0.018$ ; T1 vs. T3,  $p\leq 0.001$ ). There were three differences in the hydro-block pulsed every two weeks (C vs. T2,  $p=0.012$ ; C vs. T3,  $p\leq 0.001$ ; T1 vs. T3,  $p=0.003$ ). There were none in the hydro-block pulsed every four weeks and one in the hydro-block pulsed only once (C vs. T1,  $p=0.039$ ).

With little interaction between hydroperiod and phosphorus concentration when pulsed only every four weeks or just once, it seems that the effect of phosphorus on rhizome and leaf biomass mostly depended on hydroperiod. Phosphorus had significant impacts in the static hydroperiod and the

every-2-week hydroperiod but was rarely important in the other hydroperiods that remained drier.

## Discussion

### Field studies

Percent of croplands, but not lotic length, was a significant influence on TP concentrations. With more croplands in a watershed relative to watershed area, there could be more sources for nutrient inputs into individual wetlands. Similar conclusions have been drawn in other studies of land use and nutrient input into waterbodies (e.g., Johnes and Heathwaite 1997; Johnson and Rejmankova 2005). However, Debues et al. (2019) found that total phosphorus concentrations were typically greater in urban Lake Ontario stream watersheds in Canada than in agricultural watersheds. Lack of significance for lotic length into wetlands on TP concentration is likely because stream size differs and the volume or rate of water flowing into a wetland would not affect phosphorus inputs by itself. Large volumes and seasonality of inflowing water could have differing dilution effects in downstream wetlands. Riparian buffers and concentration/frequency of nutrient applications to lands along inflowing streams could also influence the amount of phosphorus transported from terrestrial sources to wetlands (Dillaha et al. 1989; Keddy 2010).

All but one of the riverine wetlands/two of the barrier beach wetlands were along the south shore of the lake, where agriculture is generally more prevalent than on the eastern or northern shores. However, those wetlands did not have uniformly greater lotic lengths or phosphorus concentrations (Fig. 1, Table 3). Lacustrine wetlands with no inflowing streams mostly had lower phosphorus concentrations, likely due to dilution from lake waters.

In the field studies, mean percent cover of *Typha* did not increase with mean TP concentration. Although water samples for TP were taken in the adjacent SAV zone, most of the cattail stands consisted of floating mats where water was derived from lake waters. Cattails in the wetlands may respond to increased concentrations of phosphorus and limited variability in inundation by increasing biomass

(which was not measured), especially below-ground biomass, which is the main method by which cattails propagate (Grace and Harrison 1986; Bansal et al. 2019). Cover of *Typha* varied broadly with wetland geomorphic type and shore of the lake (Table 3). This was unexpected because lacustrine wetlands are generally subjected to greater erosive forces and short-term hydrologic variability than barrier beach and riverine systems (Minc 1997; Keough et al. 1999; Lishawa et al. 2010). However, the lacustrine wetlands sampled in this study were mostly in bays that were oriented away from prevailing winds. One lacustrine wetland (Parrot Bay) was located behind a road bridge that narrowed the hydrologic connection point to Lake Ontario and served as a buffer from waves.

The emergent zones in Lake Ontario coastal wetlands have expanded since lake-level regulation began in about 1960, in large part influenced by the altered hydrologic regime (Wilcox and Xie 2007). Lack of periodic years with low lake levels allowed moisture-requiring *T. × glauca* to invade into sedge/grass wet meadow at upper elevations of wetlands, where sedges and grasses that can tolerate low soil moisture once held a competitive advantage (Wilcox et al. 2008). *Typha angustifolia* expanded broadly offshore, largely as floating mats that were not affected by higher waters (Wilcox et al. 2008; Wilcox and Bateman 2018). Much of the cover of *Typha* as measured in this study was similarly in response to lake-level history.

### Growth experiment

The cattail response of increased growth in above- and below-ground biomass to increasing durations of hydroperiod and increasing phosphorus concentrations was consistent with other growth experiments with cattails involving nutrient additions and variable water regimes (Farmer et al. 2005; Boers and Zedler 2008). This pattern of growth was especially pronounced in the constantly flooded conditions of hydro-block 1. Cattails grown in all hydro-blocks were greater in below-ground than above-ground biomass allocation (Table 4, Fig. 3), which was the pattern shown by Boers and Zedler (2008), especially with greater hydroperiod. This result may be due to

the season in which cattails for this experiment were collected. Commencing in late spring, they had begun metabolizing starch reserves that were stored during the winter months to grow leaves (Sojda and Solberg 1993). By the time the cattails were collected in late May, they had used some of their starch reserves for above-ground biomass growth. In future experiments, the cattails could be collected for a similar experiment in late fall, when starch reserves in the rhizomes are greatest, to test if they would respond similarly.

Decreasing water availability in hydro-blocks impacted the growth of the cattails, resulting in earlier weekly mean mortality as the duration between pulses of water increased. Constant flooding may result in anaerobic conditions, and cattails are adapted to saturated, anaerobic conditions (Bendix et al. 1994; Tornberg et al. 1994). A growth experiment involving the parent species, *Typha latifolia*, reported similar results in biomass allocation with increasing water depths (Grace 1989). With extended anoxic conditions in another experiment, *T. latifolia* responded with increased shoot elongation (Braendle and Crawford 1987). Constantly flooded conditions in the block with a static hydroperiod over the eight-week experiment may also have created conditions under which phosphorus that was bound to  $\text{Fe}^{3+}$  was released when the iron was reduced to  $\text{Fe}^{2+}$ . This would be consistent with results from similar studies (Farmer et al. 2005; Boers and Zedler 2008). Cronk and Fennessey (2001) hypothesized that rapid leaf and rhizome growth enables such a plant to have greater access to light,  $\text{O}_2$ , and  $\text{CO}_2$ .

### Conclusions

Lake Ontario coastal wetlands have been degraded by unnaturally managed hydrologic regimes, nutrient inputs, and other cultural factors that negatively influence natural processes. Anthropogenically induced stressors increase susceptibility of wetland systems to invasion by *Typha*, which often outcompetes and displaces native species in emergent and wet meadow zones.

In our growth experiment, as hydroperiod and phosphorus concentrations increased, so did cattail biomass. However, the effect of increased phosphorus

concentration was diminished as water availability decreased from hydro-blocks with static to two-week to four-week to single pulsing, suggesting that hydroperiod, as on Lake Ontario, had an over-riding influence. In the Lake Ontario wetland field studies, although TP concentration in wetland waters increased with greater percent land use as croplands, mean percent cover of *Typha* did not increase correspondingly. Cover of *Typha* as measured in this study showed the response to lake-level regulation that was seen in other studies (Wilcox and Xie 2007; Wilcox et al. 2008; Wilcox and Bateman 2018). These responses of *Typha* to hydrology in the field and variable hydrology and nutrient inputs in the greenhouse study may provide insight into effective methods of cattail control and restoration in many wetlands. In managed wetlands or waterbodies, control methods could include mimicking natural hydrologic regimes that favor wet meadow species and decrease habitat availability for cattails. While it is not possible to eliminate nutrient inputs into wetlands and waterbodies, increasing the width of vegetative buffers around riparian areas and abutting uplands could reduce transport of nutrients into these systems through reduced erosion and nutrient uptake by the vegetation in the buffers. Landowners, soil and water conservation districts, scientists, and the agricultural industry could use the results of this study to aid in making informed decisions regarding nutrient applications and their effects on the spread of the cattail.

Specific to Lake Ontario, implementation of a new lake-level regulation plan (Plan 2014) in 2017 that seeks to return the Lake Ontario-St. Lawrence River system to a more natural hydrologic regime (IJC 2014) could reduce cattail invasion of wet meadows. However, periods of low water supply from the upper Great Lakes and the surrounding Lake Ontario watershed will be necessary for the new plan to provide lower water levels during the growing season that can restore the competitive advantage of sedges and grasses. In the interim, active restoration via excavation and herbicide treatments seeks to reduce existing stands of cattail and increase wet meadow (Wilcox et al. 2018; Neveldine et al. 2019; Massa and Farrell

2020; Graham et al. 2021; Silva et al. 2021; Polzer and Wilcox 2022).

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#### Declarations

**Competing interests** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix

See Table 5.

**Table 5** Monthly mean maximum and minimum temperatures (°C) and relative percent humidity inside greenhouse during eight week *Typha* × *glauca* growth experiment

Month	Mean maximum temperature (°C)	Mean minimum temperature (°C)	Mean maximum relative humidity (%)	Mean minimum relative humidity (%)
June	32.02	16.70	98.20	78.93
July	35.04	19.50	99.03	76.32

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