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Synergistic impact of water level fluctuation and invasion of *Glyceria* on *Typha* in a freshwater marsh of Lake Ontario

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Abstract

The effects of multiple stressors on the native *Typha* marsh community (mainly *Typha latifolia*) were examined using historical records of water levels, human census population, and field vegetation maps. Percent cover of the major plant species was estimated in a GIS, and the percent cover of *Typha* was related to changes in water level, human population growth, and percent cover of exotic *Glyceria maxima* and invasive *Phragmites australis*. Water level fluctuation was the major natural disturbance and it alone accounted for 88% of the variation in *Typha*. After partitioning out the effect of water level, both human population growth and the presence of exotic species were still significantly related to the decline of native *Typha*. We suggest that multiple stressors interact with each other to influence changes in native *Typha* community and cause greater detrimental impact. An important implication of our results is that projected water level decline due to climate change may not necessarily favor the restoration of a desirable native marsh because of the presence of other disturbances such as exotic and invasive species and altered nutrient regime.

Keywords: Multiple stressors; Disturbance; Climate change; Water level; Exotic species; Urbanization; *Typha*; *Glyceria*; Wetland

1. Introduction

Coastal wetlands of large lakes are characterized by simultaneous variations in many environmental attributes, including interannual water level fluctuations (Chow-Fraser, 2005; Hudon, 1997; Keddy and Reznicek, 1986), eutrophication (Chow-Fraser et al., 1998; Wei and Chow-Fraser, 2005) and the presence of invasive and exotic plant species (Wilcox et al., 2003). Of these, water level fluctuation is considered a natural disturbance, and the cyclical expansion and contraction of emergent marshes in response to Great Lakes water level fluctuations have been well documented (e.g. Chow-Fraser et al., 1998; Gottgens et al., 1998; Hudon, 1997; Lyon et al., 1986; Williams and Lyon, 1997). Effects of the other two factors, however, are considered anthropogenic, since both degraded water quality and invasion of exotic species have been directly related to urbanization (e.g., Baldwin, 2004; Chow-Fraser, 2006; Crosbie and Chow-Fraser, 1999; Davis and Froend, 1999; Eyles et al., 2003).

Although water level fluctuations is likely the largest single disturbance affecting the response of coastal marsh communities, it is necessary to study the effects of multiple factors simultaneously, since the response of ecosystems to one factor may be significantly influenced by others (Nilsen and Orcutt, 1996). Recent declines in lake levels of the Laurentian Great Lakes, especially in Lakes Huron and Michigan, have significantly affected the availability and diversity of coastal habitats for plants, fish, and wildlife. This situation is likely to worsen in the next several decades because climate change models predict a further drop in lake levels by 0.23–2.48 m for all five Great Lakes (Mortsch and Quinn, 1996). There is therefore a critical need for development of multi-stressor models that can predict the response of these coastal communities to the simultaneous effects of lower water level, increased eutrophication and invasion by exotic species since many of these coastal marshes are located in areas that are already stressed by these factors due to increased urban and recreational development (Green Bay, Lake Michigan; Brazner and Beals, 1997; Georgian Bay, Lake Huron; Chow-Fraser, 2006).

There are currently several models that can be used to predict the response of wetland communities to climate change. Keddy and Reznicek (1986) proposed a simple model relating the type of wetland vegetation (i.e. emergent, wet meadow) to water level fluctuations alone, while van der Valk (1981)

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proposed a model based on water level fluctuations and life-history traits of different plant species under consideration (from seekbank/propagule information). However, as van der Valk pointed out, his model only predicted which species would be present, but not the relative abundance of species and their potential interactions. The predictability of the model will likely improve if other abiotic factors such as topography of the site and water quality, as well as the magnitude and type of biotic factors (e.g. abundance of invasive exotic species) are included.

The purpose of this study is to examine the simultaneous effects of multiple stressors (i.e. water level, human population growth, and invasion of exotic species) on the distribution of the native cattail population in a Great Lake coastal marsh. Historical records show that there were extended periods during the late 1800s when water levels were relatively high in Lake Ontario (see Chow-Fraser, 2005), and yet, there was no evidence of permanent damage to the marsh vegetation in the ensuing decades. This implies that factors other than water level can contribute to the long-term reduction of the emergent vegetation. Wei and Chow-Fraser (2005) have already demonstrated that increased urbanization in the Hamilton region contributed to loss of the emergent community as a whole in Cootes Paradise Marsh, independently of sustained high water levels. In this paper, we have expanded our investigation to examine these simultaneous impacts at the species level. Our hypothesis is that both the total percent cover of all wetland vegetation as well as that of a single species will be negatively correlated with water level fluctuations. We further hypothesize that increased nutrient availability and increased organic content of sediments due to urbanization should favor the growth of exotic species (e.g. *Glyceria maxima*) over that of the native species (e.g. *Typha*) and that the synergistic effect of multiple stressors will be greater than that of any stressor alone.

2. Methods

2.1. Study site

Cootes Paradise is a 250 ha coastal wetland (43°16′N, −79°55′W), located at the extreme west end of Lake Ontario (see Fig. 1 in Wei and Chow-Fraser, 2005). It is a drowned river-mouth marsh that drains into the west end of Hamilton Harbour, and has three main tributaries: Spencer Creek, Borer's Creek and Chedok Creek. The marsh receives runoff from adjacent agricultural, residential, industrial, commercial, and recreational lands, as well as effluent from the Dundas Sewage Treatment Plant. It is surrounded by the city of Hamilton to the south, and the towns of Ancaster, Dundas and Flamborough to the north and west.

During the 1920s and early 1930s, the most abundant emergent plant was *Typha* sp. (mostly *T. latifolia* with some *T. angustifolia*) and it was associated with many other common native wetland species such as *Sparganium* sp. and *Polygonum punctatum*. Like many other marshes in eastern N. America, Cootes Paradise has been invaded by Eurasian species that

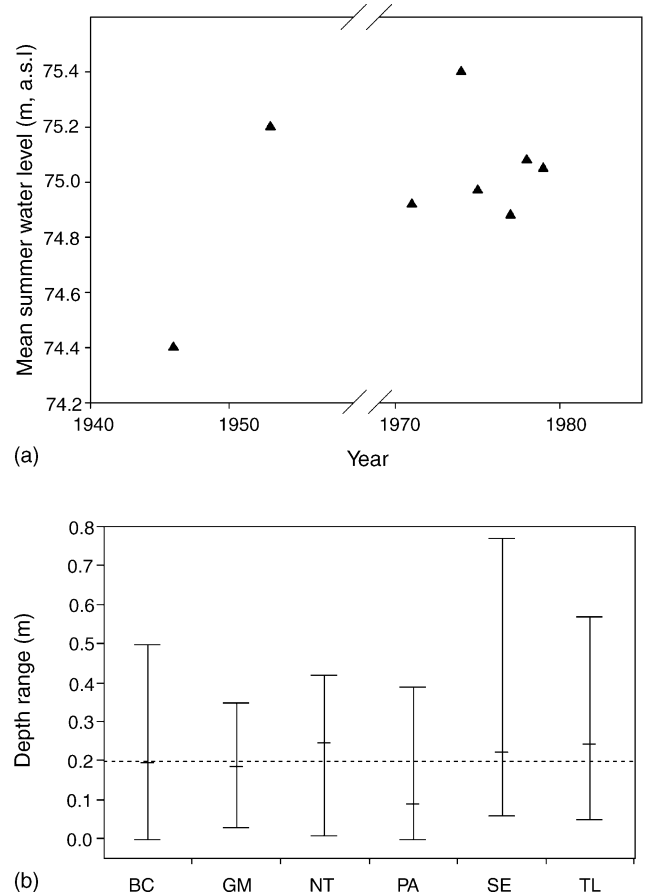

Fig. 1. Summer mean water level and water depth range for the major species of emergent plants in Cootes Paradise marsh: (a) water level, (b) water depth range. The dashed line indicates the grand mean water depth.

became established following European settlement. The first record of *Glyceria maxima* (manna grass) a Eurasian invasive species, was first collected from Cootes Paradise in the 1940s (Mills et al., 1993). By the early 1950s, it overtook *Typha* as the dominant emergent plant. Over the next 30 years, its distribution expanded quickly. Currently, marsh restoration efforts that are being implemented as part of the Remedial Action Plan for Hamilton Harbour (see Lougheed et al., 2004) are being severely challenged by the invasive species, including *Lythrum salicaria* (purple loosestrife), *Phragmites australis* (common reed), as well as *Glyceria*.

2.2. Data

Percent cover of the major emergent vegetation between 1946 and 1979 was taken from Chow-Fraser et al. (1998). These data were available in a GIS format and assembled from field vegetation maps that had been archived by the Royal Botanical Gardens (Burlington, Ontario, Canada). The percent cover of six major taxa was calculated in ArcView GIS and is shown in Table 1. Water level (WL) data for Cootes Paradise were obtained from Chow-Fraser et al. (1998). The percent cover of open water was calculated from the same digitized historical vegetation maps of Cootes Paradise. Mean water depths (Fig. 1) for the major species during the years of

Table 1
Long-term changes in the percent cover of the major species of emergent plants in Cootes Paradise Marsh during the years of observation

Major species	1946	1953	1971	1974	1975	1977	1978	1979
Typha latifolia	24.0	4.0	3.6	0.3	0.4	0.6	1.7	1.2
Glyceria maxima	14.7	4.3	15.4	5.2	8.9	6.8	9.1	10.7
Sparganium eurycarpum	0.3	0.3	0.0	0.0	0.2	0.0	0.5	1.0
Nymphaea tuberosa	0.2	1.6	0.1	0.1	0.0	0.0	0.0	0.1
Bidens cernua	0.0	1.7	0.2	0.3	3.4	6.4	1.4	0.3
Phragmites australis	0.0	0.0	1.0	0.2	0.2	0.1	0.1	0.1

observation were estimated from the digital elevation model of the marsh. Detailed information on the digital elevation model was documented in Wei and Chow-Fraser (2005).

Open water area in a marsh is usually positively correlated with changes in water level. However, linear changes in water levels may not correspond linearly with changes in open water areas due to spatial variation in marsh bathymetry (Table 2; Wei and Chow-Fraser, 2005). Since changes in water level will not reflect spatial variability in marsh topography, the percentage of open water (OP) was used as a surrogate to reflect both changes in water levels and site-to-site differences in marsh depth. We used historical census population data (POP) as a surrogate of potential cultural eutrophication (Wei and Chow-Fraser, 2005; Fig. 2) because water quality data were not available prior to 1975 (see Chow-Fraser et al., 1998). Data for the Hamilton–Wentworth region (including Hamilton, Dundas, Ancaster, and Flamborough) were obtained from Statistics Canada and Ontario Ministry of Revenue. Detailed description of data processing is documented in Wei and Chow-Fraser(2005).

2.3. Statistical analysis

Correlation and regression analyses were performed to assess the relationships among water level (WL), census population (POP), and percent cover for *Typha sp* (TL), *Glyceria maxima* (GM), and *Phragmites australis* (PA). To assess the relationships among native species, exotic species, and POP, we partitioned out the effect of water level fluctuation by regressing percent cover of the major species and POP against OP, and used the residuals of these in corresponding regression models: e.g. to estimate the effect of GM on TL using residuals regression, we regress the residuals of the regression on TL on OP on the residuals of the regression of GM on OP (see Freckleton, 2002). The statistical analyses were performed in SAS JMP 4.0.

The spatial displacement of major species between 1946 and 1979 was performed through the Union process in ArcView GIS. The 1979 vegetation map was used as the input theme and the 1946 map as the overlay theme to produce a union theme that indicated the total replacements of a species by any other species in space.

Table 2
Summary of correlation analyses for this study

Variables	*r*	*P*
Glyceria maxima vs. *Typha latifolia*	0.554 (−0.8768)	0.154 (0.051)
Glyceria maxima vs. human population	−0.188 (0.827)	0.656 (0.042)
Glyceria maxima vs. water level	−0.724	0.042
Glyceria maxima vs. open water	−0.772	0.025
Typha latifolia vs. human population	−0.842	0.009
Typha latifolia vs. water level	−0.809	0.015
Typha latifolia vs. open water	−0.935	0.001
Water level vs. open water	0.942	<0.001
Water level vs. human population	0.514	0.192
Open water vs. human population	0.672	0.068

Values in brackets are partial correlation controlling for water level, open water, and human population.

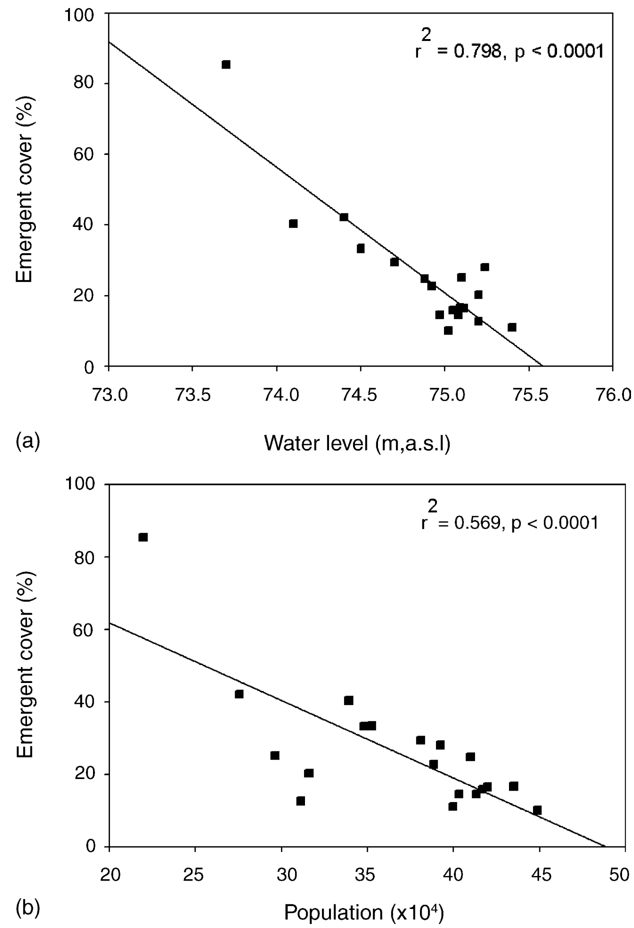

Fig. 2. Relationship between percent total emergent cover vs. (a) water levels in Cootes Paradise Marsh and (b) human population census for the Hamilton-Wentworth Region from the 1930s to 1990s.

3. Results

3.1. Long-term change of emergent plants

Percent cover of the major species of emergent plants in Cootes Paradise Marsh for 1946, 1953, 1971, 1974, 1975, 1977, 1978, and 1979 is given in Table 1. In 1946, *Typha latifolia* and *Glyceria maxima* were the two dominant emergent taxa, accounting for 24.0 and 14.7% of the total area of the marsh, respectively. By 1979, 95% of the *Typha,* and 27% of the *Glyceria* had been eliminated. Although there had been a consistent overall decline in the cover of all emergent taxa, the loss was disproportionately higher for cattails than for manna grass. In 1953, *Glyceria* overtook *Typha latifolia* as the dominant species, and thereafter retained this dominance. Distribution of the other major species fluctuated over the years of observation, and did not reveal any trends.

3.2. Effects of multiple stressors on Cootes Paradise marsh

Relatively high water levels in Cootes Paradise Marsh have adversely affected the wetland since the 1930s (Chow-Fraser, 2005; Chow-Fraser et al., 1998). During 1946, average depths for the major emergent taxa (*Typha*, *Glyceria* and *Sparganium*) ranged from 3 to 6 cm, while that for the floating water lily, *Nyphaea tuberosa*, was 24 cm. In all subsequent years, water depths were uniformly higher for all species, with plants occurring in water as deep as 77 cm deep during the historic high water levels experienced in 1974 (Fig. 1). In general, *Typha* appeared to tolerate deeper water than did *Glyceria*, and both appeared to be more tolerant of inundation than *Phragmites*, which were found in water depths ranging from mudflat to 39 cm in 1974. *Typha* and *Glyceria* both responded negatively to high water levels (Table 2). Up to 66 and 79% of the variation in percent cover of *Typha* and *Glyceria*, respectively, could be explained by the percent of open water (OP) in the marsh(Fig. 3).

We found that apart from the effect of high water levels, human population growth correlated negatively with *Typha* ($r^2 = 0.644$, $P = 0.0165$), but positively with *Glyceria* ($r^2 = 0.507$, $P = 0.0477$) (Fig. 4a and b, respectively).

In addition to the effects of high water levels and urbanization, we further investigated the possibility that distribution of native marsh species such as *Typha* could be displaced by invasive species such as *Glyceria* and *Phragmites*. Mixed patches of these species often occurred side-by-side within the marsh, and in shallow areas, *Typha* appeared to have been outcompeted by *Glyceria*. This observation is supported by the significant relationship between *Typha* and *Glyceria* after the effect of water levels has been partitioned out (Fig. 5a; $r^2 = 0.55$, $P = 0.0354$). By excluding the 1977 data point, we obtained a stronger negative relationship between *Typha* and *Glyceria* ($r^2 = 0.88$, $P = 0.0020$); therefore, high water levels and invasion of *Glyceria* had a synergistic impact on *Typha*: the combination of these two factors caused greater detrimental impact than either factor alone (Table 3). By comparison,

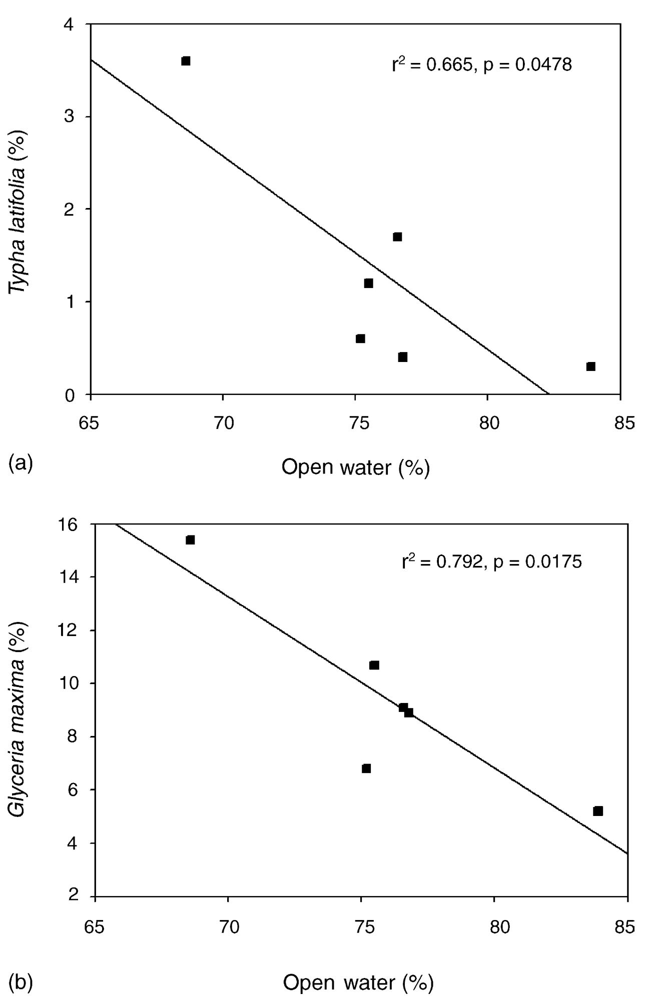

Fig. 3. Relationship between (a) *Typha* and (b) *Glyceria* with percent open water for 1971–1979 ($n = 6$).

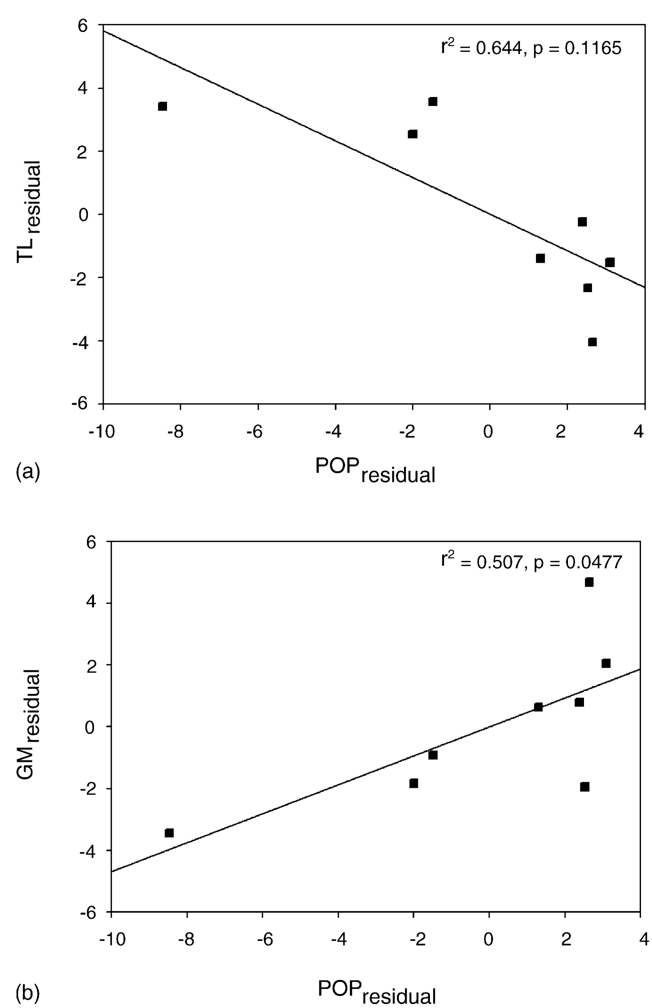

Fig. 4. Relationship between residual of (a) *Typha* and (b) *Glyceria* with human population census ($n = 8$).

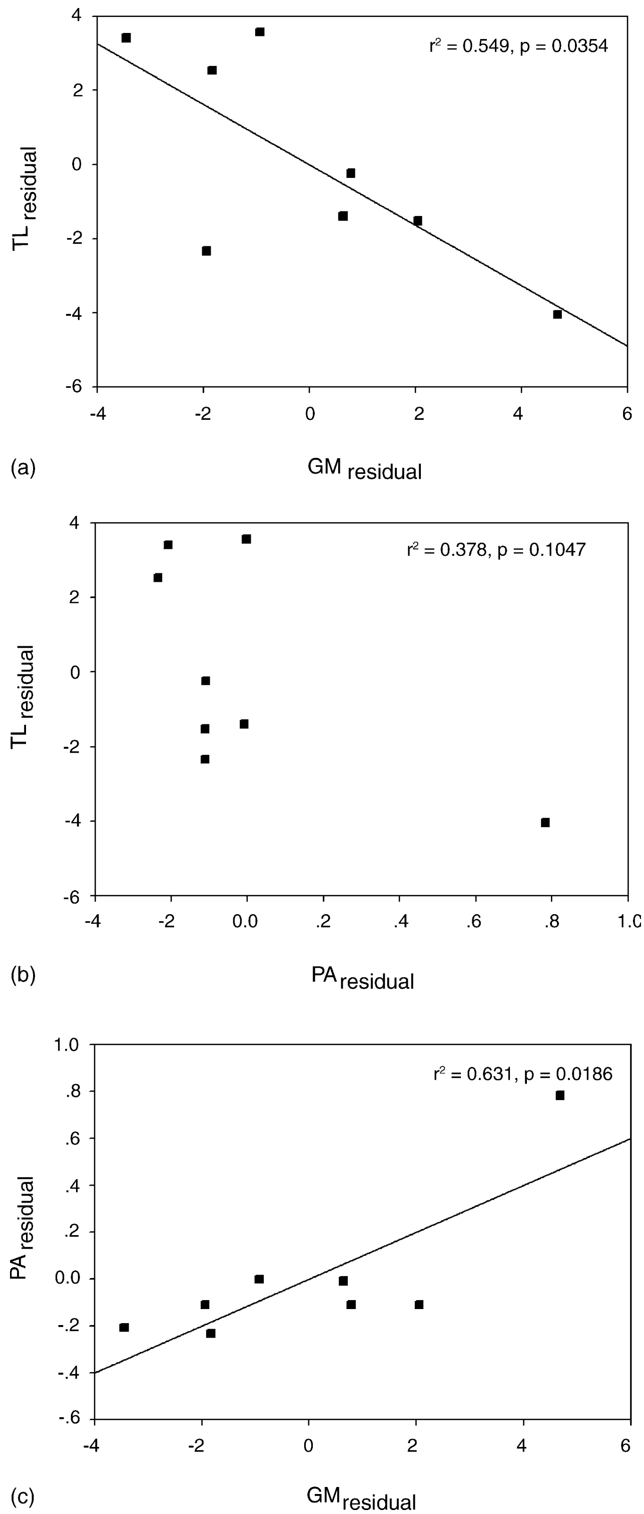

Fig. 5. Relationship between (a) residual of *Typha* and residual of *Glyceria maxima*, (b) residual of *Typha* and residual of *Phragmites*, and (c) *Phragmites* and residual of *Glyceria* ($n = 8$).

there was a weak but not significant effect of *Phragmites* on the recovery of *Typha* (Fig. 5b; $r^2 = 0.38$, $P = 0.1047$), perhaps because *Phragmites* had only been a minor component in the marsh (Table 1). Nevertheless, *Glyceria* and *Phragmites* were positively correlated and both may have contributed to the overall reduction in *Typha* (Fig. 5c).

Table 3
Summary of multiple regression ($n = 7$; 1977 data excluded)

Dependent variable	Term	Estimate	SE	t	P
TL ($R^2 = 0.996$)	Intercept	40.875	4.168	9.81	0.0023
	GM	−0.706	0.143	−4.93	0.0160
	OP	−0.797	0.076	−10.51	0.0018
	(GM-9.388) × (OP-73.038)	−0.043	0.013	−3.21	0.0490
TL ($R^2 = 0.996$)	Intercept	41.482	4.108	10.10	0.0005
	OP	−0.250	0.054	−4.64	0.0098
	POP	−0.532	0.066	−8.03	0.0013
	(OP-73.038) × (POP-37.725)	0.039	0.006	6.26	0.0033

TL: *Typha latifolia*; GM: *Glyceria maxima*; OP: open water; POP: human population census data.

3.3. Spatial displacement of *Typha* and *Glyceria*

A change detection analysis clearly demonstrated that the invasive *Glyceria* had spatially displaced the native *Typha* between 1946 and 1979 (Table 4). Over this period, almost 60% of the *Typha* had been damaged by high water levels (14.1/24); 24% had been replaced by *Glyceria* (5.8/24), 13.7% by other species, while only 1.6% (0.8/24) remained in their original habitat. Throughout the period of observation, *Typha* only accounted for 2% (0.4/24) of newly colonized area. By comparison, 67% of the *Glyceria* present in 1946 had been damaged by higher water levels, only 3.4% (0.5/14.7) of this had been replaced by other species (of which only 1.4% was *Typha*), and close to 30% of the original growth remained in the same location. Overall, 44.2% (6.5/14.7) *Glyceria* invaded new habitat, primarily areas that had previously been occupied by *Typha* (41.4%). This high rate of replacement of *Typha* by *Glyceria* was supported by the partial correlation (Table 2): a negative correlation was found between *Typha* and *Glyceria* after having controlled for the effects of water level and human population growth.

Table 4
Spatial displacement of major species from 1946 to 1979

Displacement from 1946 to 1979
48.1% open water was occupied by open water
14.1% *Typha latifolia* was occupied by open water
9.8% *Glyceria maxima* was occupied by open water
8.2% other species was occupied by other species
5.8% *Typha latifolia* was occupied by *Glyceria maxima*
4.2% *Glyceria maxima* was occupied by *Glyceria maxima*
3.6% other species was occupied by open water
3.2% *Typha latifolia* was occupied by other species
0.8% *Typha latifolia* was occupied by *Typha latifolia*
0.5% open water was occupied by other species
0.5% *Glyceria maxima* was occupied by other species
0.5% open water was occupied by *Glyceria maxima*
0.2% other species was occupied by *Glyceria maxima*
0.2% *Glyceria maxima* was occupied by *Typha latifolia*
0.2% open water was occupied by *Typha latifolia*
0.0% other species was occupied by *Typha latifolia*

Values in bold correspond to percentage area that had been replaced by *Glyceria maxima* in 1979.

Table 5
Summary of correlation analyses between percent cover of major taxa and exposed habitats during the 1971–1979 surveys

	Typha	*Glyceria*	*Phragmites*	Exposed
Typha	1.00	0.91	0.85	0.26
Glyceria		1.00	0.80	0.35
Phragmites			1.00	0.24
Exposed				1.00

3.4. Correlations between exposed habitats and response of emergent cover for 1971–1979

Typha in Cootes Paradise Marsh was mainly distributed in the west end of the marsh. The year-to-year regrowth of emergent plants could have been attributed to either vegetative structures or propagules in the seed bank or both, but unpublished field notes from the Royal Botanical Gardens archives reveal that most of the growth had been through rhizome production. This is consistent with results of a 1999 survey conducted by the Royal Botanical Gardens that confirmed the paucity of viable *Typha* seed in the seed bank at the west end of the marsh. In this study, the realized habitats were estimated from field vegetation maps that did not distinguish between growth by rhizome or seedlings, and any exposed habitats were estimated from the digital elevation model in combination with the historical water level information. Although all three species were positively correlated with the increase in exposed habitats (Table 5), *Glyceria maxima* appeared to have benefited most from exposed mudflat during 1970s.

4. Discussion

In Cootes Paradise, emergent cover was found to correlate negatively with water depth, and increased water levels during the past six decades was reflected in the steady decline in the emergent marsh (Fig. 2a), a pattern that has been well documented for many other coastal marshes of the Great Lakes (Hudon, 1997; Lyon et al., 1986; Wilcox et al., 2003; Williams and Lyon, 1997). Recently, we showed that both increased urbanization (indicated by human population census data in the Hamilton region) and water level had independent and negative effects on the community of emergent plants in Cootes Paradise Marsh (Wei and Chow-Fraser, 2005).

Sustained high water level is the major factor that contributed to the decline of the emergent marsh in Cootes Paradise. Water level alone explained 88% of the variation in the distribution of *Typha*. Addition of human population growth as a variable to the regression equation further accounted for 11.3% (99.6–88.3%) of the remaining variation (Table 3). There is a positive correlation between water level and human population census data (Table 2), and we therefore partitioned out the effect of water level and found that *Typha* was still negatively related to the increased human population. This is consistent with the view that both urban and agricultural development in the watershed contributes to wetland degradation by increasing the loading of nutrients, road salts, pesticides and heavy metals, and by altering the hydrologic regime (Crosbie and Chow-Fraser, 1999; Davis and Froend, 1999). In contrast to *Typha*, *Glyceria* was positively related to human population growth, once water level effects had been partitioned out (Fig. 4b). This observation is consistent with Lambert (1947) that soil samples associated with *Glyceria* have relatively high concentrations of iron, phosphorus and nitrogen and stands of *Glyceria* in Britain were favored by application of manure. We therefore suggest that part of the reason for the successful introduction of *Glyceria* in Cootes Paradise is the increased nutrient availability resulting from urbanization. We also suggest that *Glyceria* and *Typha* have a similar niche (Mountford and Chapman, 1993), and will compete for any habitat that is released by reduced water levels.

High water levels limited the distribution of both *Typha* and *Glyceria* (Fig. 3); however, once water levels receded, *Glyceria* appeared to be the more successful colonizer, as indicated by its rapid replacement rate (Table 4) and correlations between exposed habitats and response of major emergent plants (Table 5). The replacement of *Typha* by *Glyceria* especially in the shallow areas could have been due to (1) increased nutrient availability in the sediments and (2) differences in life-history traits. Increased nutrient availability in the sediments favoring *Glyceria maxia* over *Typha* is consistent with results from Lambert (1947) and Weiher et al. (1996). Weiher at al. found that *Typha* were unable to become established in enriched sediments. *Glyceria* appears to favor shallow water and begins growth earlier in the year (Buttery and Lambert, 1965a,b), thus making it superior to *Typha* when competing for newly released habitat. *Typha* and *Glyceria* were often segregated according to water depths, with *Typha* in deeper water and *Glyceria* in shallower water (Fig. 1). Another invasive species, *Phragmites australis*, has also colonized the marsh, and may further impact *Typha*, a scenario that is consistent with Wilcox et al. (2003) observation that *Phragmites* frequently displaced *Typha* in a Lake Erie marsh during periods of high water level.

It is important to note that it has been 25 years since the last complete vegetation survey has been conducted in Cootes Paradise Marsh. Even though the marsh had been surveyed in 1993 and 1999, different sampling protocols and classification schemes precluded their inclusion in this study. The major problem with the 1993 survey was that many of the plant taxa had been lumped together during the survey, while the major problem with the 1999 survey was that only the west end of the marsh had been mapped. Therefore, we recommend that a future survey be undertaken of the entire marsh, following the protocol and classification scheme used in the historic surveys to validate the results of this study.

An important implication of our results is that projected water level decline due to climate change may not necessarily favor the restoration of a desirable native marsh because of the presence of other disturbances such as exotic and invasive species and altered nutrient regime. Based on the synergistic effect of multiple stressors, we predict that native marsh restoration will be difficult due to the present availability of more efficient colonizer species such as *Glyceria* and possibly *Phragmites*.

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