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# Mechanisms of dominance by the invasive hybrid cattail *Typha × glauca*

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**Abstract** The mechanisms by which invasive plants displace native species are often not well elucidated, limiting knowledge of invasion dynamics and the scientific basis for management responses. *Typha × glauca* Godr. invades wetlands throughout much of North America. Like other problematic wetland invaders, *Typha* is large, grows densely, and leaves behind copious litter. It thus has the potential to impact wetlands both in life and after death. We assessed patterns in field settings and used simulated wetland-plant communities to experimentally test abiotic and community responses to live *Typha*, *Typha* litter, and water-level differences (confounded in the field) using a full-factorial design. In general, litter was a stronger driver of change than live *Typha*. The greatest impacts were seen where, as in nature, live and dead *Typha* co-occurred. Live-*Typha* treatments did not differ from controls in light or temperature conditions but did reduce community biomass and alter community composition. Litter strongly affected light, temperature and its variability, community and species-level plant biomass, and community composition. Interactions between live *Typha* and litter affected aspects of plant-community composition. Advantageously for *Typha*, interspecific litter effects were not mirrored by intraspecific suppression of live *Typha*. These findings clarify how *Typha* is such an effective invader. Similar mechanisms are likely involved in invasions by other plant species, particularly in wetlands. Managers should respond quickly to new *Typha* invasions and, when dealing with established stands, remove litter in addition to eradicating live plants.

**Keywords** Competition · Invasive species · Litter · *Typha × glauca* · Wetland

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## Introduction

The mechanisms by which aggressive invasive plant species displace native species are often unknown and are rarely tested (Levine et al. 2003; Minchinton et al. 2006). Elucidation of dominance mechanisms is a critical step toward understanding and mitigating the impacts of invasive species (Byers et al. 2002).

Many of the world's most problematic wetland invasive species share key traits. They often form

dense, nearly monotypic stands; spread by clonal growth; are taller than the species they displace; and leave behind abundant litter following senescence (Galatowitsch et al. 1999; Zedler and Kercher 2004). In the Great Lakes region, this trait syndrome is shared by the invasive graminoids *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), *Phalaris arundinacea* L. (reed canarygrass), and *Typha × glauca* Godr. (hybrid cattail), which greatly alter wetland structure and function (Galatowitsch et al. 1999; Zedler and Kercher 2004).

We chose *T. × glauca* as a focal species for investigation of dominance mechanisms because of its aggressiveness and the magnitude of its ecological impacts. *Typha* is an invasive hybrid species derived from a native parent species, *T. latifolia* L. (broad-leaved cattail), and *T. angustifolia* L. (narrow-leaved cattail), considered introduced in the Great Lakes region (Smith 1987; Stuckey and Salamon 1987). *Typha × glauca* (hereafter *Typha*) rapidly spreads, achieves high dominance, and reduces plant diversity (Frieswyk et al. 2007; Tuchman et al. 2009). It is known to benefit from anthropogenic disturbance and is associated with changes in soil properties and biogeochemistry (Angeloni et al. 2006; Craft et al. 2007; Woo and Zedler 2002). A notable feature of *Typha*-dominated areas is high litter biomass. *Typha* is highly productive, subjected to relatively little herbivory, and slow to decompose (Christensen et al. 2009; Freyman 2008; Penko and Pratt 1987).

Superior competition for resources, allelopathy, and habitat modification are some of the means by which invasive plant species can become dominant (Levine et al. 2003). Dominance is enhanced when the *inter*-specific effects of invasion on co-occurring plant species are high relative to *intra*-specific effects on other individuals of the same species (Holly and Ervin 2006; Perry et al. 2005).

The functional traits shared by *Typha* and other invasive wetland plants (large stature, dense growth, abundant litter) could promote dominance through two pathways: (1) litter modifying habitat conditions (e.g., reduced light, soil temperature, and space availability), and (2) live plants altering habitat conditions and/or outcompeting other species for resources such as space, light, and nutrients. The relative importance of these pathways has important implications for understanding *Typha* invasion and developing sound management responses.

There is support for both pathways as mechanisms for *Typha* dominance (Brown and Bedford 1997; Farrer and Goldberg 2009; Hager 2004; Vaccaro et al. 2009; Weiher and Keddy 1995; Woo and Zedler 2002). In addition, confounding factors such as water levels that co-vary with *Typha* abundance can influence invasion outcomes (Farrell et al. 2008; Wilcox et al. 2008). Here, we report the results of a 6-year study designed to untangle the effects of live *Typha*, *Typha* litter, and water-level variability. This was done through a mesocosm experiment with treatments of ±live *Typha*, ±*Typha* litter, and high versus low water levels in a fully crossed factorial design.

In earlier and parallel studies, we found strong correlations in the field between *Typha* abundance and plant-community and environmental variables (Angeloni et al. 2006; Lishawa et al. 2010; Tuchman et al. 2009) (Table 1). In the present study, we used field data and a mesocosm experiment to determine the relative effects of live *Typha*, its litter, and both in combination, and to look for evidence of intraspecific competition in *Typha*. In general, we expected live *Typha* and *Typha* litter to influence environmental and plant-community variables, with strongest responses where, as in nature, they occurred in combination. We expected *Typha* treatments to lower light penetration and temperature at the soil surface (Angeloni et al. 2006; Hager 2004) and to decrease native plant

**Table 1** Comparison of plots with and without *Typha* spp. in 14 northern Lake Huron and Lake Michigan coastal wetlands (adapted from Lishawa et al. 2010)

| Variable | *Typha* present Mean (S.D.) | *Typha* absent Mean (S.D.) | P value |
|---|---|---|---|
| Water depth (cm) | 12.0 (12.1) | 13.9 (16.71) | 0.37 |
| Litter depth (cm) | 9.3 (7.0) | 5.2 (6.06) | <0.001 |
| Organic substrate depth (cm) | 16.0 (18.7) | 3.4 (3.85) | <0.001 |
| Soil organic matter (%) | 14 (20) | 4.7 (6.5) | 0.004 |
| Distance to open water (m) | 136.2 (107.0) | 74.4 (72.2) | <0.001 |
| NH$_4$ (µg g$^{-1}$ dry soil) | 24.3 (53.3) | 3.4 (8.3) | 0.011 |
| FQI (floristic quality index) | 7.4 (4.7) | 11.0 (3.3) | <0.001 |
| Species richness | 6.1 (4.2) | 7.3 (3.9) | 0.086 |

FQI calculations based on Herman et al. (2001) and P values calculated using two-tailed t tests

species' abundances (Frieswyk et al. 2007; Tuchman et al. 2009; Zedler and Kercher 2004). We anticipated negative, intraspecific effects of *Typha* density and *Typha* litter on the biomass of individual *Typha* plants and overall *Typha* biomass (Gurevitch et al. 1992; Holly and Ervin 2006) and hypothesized that water-level treatments would have species-specific effects on native plant biomass (Fraser and Miletti 2008; Weiher and Keddy 1995).

## Materials and methods

### Field site

We based the identity and densities of plant species in our mesocosm experiment on plant-community sampling of Cheboygan Marsh (located at 45° 39′ 29″ N, 84° 28′ 47″ E; Cheboygan Co., MI, USA). We also collected data from Cheboygan Marsh to test for intraspecific effects of *Typha* density on *Typha* performance. Cheboygan Marsh is a ∼150-ha lacustrine, open-embayment coastal wetland along the northern lower Michigan shoreline of Lake Huron (Albert et al. 2005). This site is heavily invaded by *Typha* spp., with abundant *T. × glauca* and *T. angustifolia* and smaller amounts of *T. latifolia*. *Typha × glauca* is particularly abundant in higher-elevation, lower-water-level portions of the site. The wetter, lakeward margin of Cheboygan Marsh is largely uninvaded and characterized by native sedge-rush vegetation, such as *Carex*, *Eleocharis*, *Juncus*, and *Schoenoplectus* spp. For detailed site descriptions, see Angeloni et al. (2006) and Tuchman et al. (2009).

### Mesocosm experimental design

We conducted our mesocosm experiment at the University of Michigan Biological Station (UMBS; Pellston, Cheboygan Co., MI, USA), ∼19 km from Cheboygan Marsh. In 2002, 40 mesocosms were constructed using open-topped, bottomless plywood box frames that were 2-m long, 1-m wide, and 1-m deep. The plywood frames were lined with 1.0-mm thick rubber pond liner and counter-sunk into the ground, with the top 20 cm of each mesocosm exposed above the soil surface. All mesocosms were filled with identical soil blends consisting of hydric soils from a nearby wetland (excavated for road construction by the Michigan Dept. of Transportation) mixed with 20% Rubicon sand. The sand was added to approximate nutrient and organic-matter concentrations found in areas of Cheboygan Marsh at an early stage of *Typha* invasion. The 11 most-abundant native plant species found in Cheboygan Marsh (accounting for ∼95% of non-*Typha* plant biomass) were transplanted into the mesocosms in 2003. Each species was planted at the mean density at which it was found in Cheboygan Marsh (N. Tuchman, *unpub. data*; values in parentheses are stems m$^{-2}$): *Carex aquatilis* Wahl. (2), *C. hystericina* Willd. (1), *C. viridula* Michaux (4), *Eleocharis* spp. R. Brown (87), *Juncus alpinoarticulatus* Chaix (9), *J. balticus* Willd. (142), *J. nodosus* L. (208), *Schoenoplectus acutus* Muhlenberg ex Bigelow (7), *S. pungens* Vahl (7), and *S. tabernaemontani* C. C. Gmelin (34) (taxonomy after Flora of North America Editorial Committee 2002; Hametahti 1980; Voss 1972).

Beginning in 2004, we applied experimental treatments to the mesocosms using a fully crossed multi-factorial design: (1) ±live *Typha*, (2) ±*Typha* litter, and (3) high versus low water levels. There was fivefold replication of each of the eight unique *Typha* × litter × water-level combinations. Into each of the 20 mesocosms that contained live *Typha*, we transplanted 16 individual *Typha* plants (standardized to 12-cm long rhizomes with 20 cm of senesced stem attached) from Cheboygan Marsh. To create litter treatments, we harvested the previous season's *Typha* litter from 20 2-m$^2$ plots in Cheboygan Marsh, homogenized the litter, and allocated it evenly among 20 mesocosms (mean addition: 400 ± 20 g m$^{-2}$ in 2004 and 2006–2009). Water-level treatments were maintained by controlling the duration of watering. Low water-level treatments received ∼50 l of water each week during the growing season, an amount that kept soils saturated but without standing water. High water-level treatments received ∼150 l of water per week, which maintained ∼5 cm of standing water.

### Field sampling

We used a field survey to investigate whether the performance of *Typha* plants was related to the density of *Typha* neighbors. In summer 2005, we

established a 64-m long transect in Cheboygan Marsh across an area varying in *Typha* density. Nine 0.5-m$^2$ plots were positioned at regular intervals along this transect. *Typha* density in plots ranged from 6 to 34 stems m$^{-2}$ (mean ± s.e.: 19.3 ± 3.1). We counted and measured the shoot height of each *Typha* individual within plots weekly on seven occasions from mid-June through late-July 2005. As a proxy for plant productivity, we converted heights of *Typha* individuals to biomass using site-specific height to dry-mass regressions. While this approach allowed us to test for correlations between neighbor density and biomass, we could not control for potentially confounding environmental factors (e.g., water depth or nutrient availability) or for the possibility that multiple stems in a plot represented shoots from the same individual. Thus, we also tested for intraspecific effects in mesocosms, where environmental factors were controlled and *Typha* was added as discrete individuals (see above).

Mesocosm sampling

We measured light intensity just above the soil–water surface on seven occasions from early June through early November 2005. In each low-water mesocosm ($n = 5$ for each *Typha* × litter combination), three light readings were taken from horizontally randomized locations using a Li-Cor® LI-189 quantum radiometer sensor (Lincoln, NE, USA). Readings were always taken between 1300 and 1400 h and under sunny conditions. We measured soil temperature at 5-cm depths in low-water mesocosms (two randomly selected replicates for each *Typha* × litter treatment combination) using digital temperature loggers (Maxim Integrated Products, Inc.; Sunnyvale, CA, USA). Temperature loggers recorded data hourly from early June through late August 2005.

Plant censuses were performed in all mesocosms in mid-July 2004, late-June and early-August 2005, mid-July 2007, early-August 2008, and late-July 2009. Each mesocosm was divided into four 10-cm wide × 180-cm long transects, with 10-cm buffers on all sides to minimize edge effects. Within each transect, all stems were identified to species and their heights were recorded. Heights were converted to biomass using species-specific height to dry-mass regressions.

Data analyses

Field and mesocosm data were used to test for intraspecific effects of *Typha* abundance on plant performance. We used linear regression to test whether the biomass of individual *Typha* plants in Cheboygan Marsh (summer 2005) or in the mesocosm experiment (summer 2009) were correlated with density of surrounding *Typha* plants. These and all subsequent statistical analyses were performed in R 2.10.1 (R Development Core Team 2009), except as noted.

We tested whether live-*Typha* and litter-addition treatments affected light transmittance, daily mean soil temperatures, and diurnal soil-temperature variability in the mesocosms using linear mixed-effects (LME) models. LME models were used because measurements were repeated over time within mesocosms (Demidenko 2004). These and all subsequent mixed-effects models were fitted by restricted log-likelihood using the 'nlme' package in R (Pinheiro et al. 2009) and pairwise comparisons between unique litter × *Typha* treatment combinations were performed using fitted contrasts.

LME models were employed to test for effects of treatments on native plant biomass. Log-transformed non-*Typha* biomasses (total of all species, and separate analyses for each species) were the dependent variables; with ±live *Typha*, ±*Typha* litter, low versus high water levels, and interaction terms as independent variables. Interaction terms were selected using maximum-likelihood-based Akaike Information Criterion (AIC) scores, which quantify the goodness of fit of multiple alternative models (Burnham and Anderson 2002). AIC scores were calculated using the 'MASS' package in R (Venables and Ripley 2002). Pairwise comparisons among unique treatment combinations within years were performed using Tukey's HSD post hoc tests. We also used an LME model to test for effects of litter and water-level treatments on log-transformed *Typha* biomass.

Effects of mesocosm treatments on overall plant-community composition were tested by permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) using the computer program PERMANOVA (Anderson 2005). PERMANOVA is a multivariate analog of ANOVA that can handle complex experimental designs, such as the factorial

crosses and repeated measurements over years found in our study. The dependent variables included biomass of all non-*Typha* species (log-transformed to better meet model assumptions), with sampling years and treatments as independent variables. The analysis was based on Bray-Curtis dissimilarities with 999 permutations and *P*-values were calculated using a Monte-Carlo procedure (Anderson 2005).

Multivariate plant-community responses were also analyzed using principal response curves (PRC) (Van den Brink and Ter Braak 1998). PRC is a technique derived from redundancy analysis (RDA) that can be used to evaluate the community-level effects of experimental treatments when there is a control treatment and effects are evaluated over time. PRCs are generated by measuring the multivariate distance (differences in community composition) between treated experimental units and matched controls at each point in time. The results are plotted as curves with time as the *x*-axis and a multivariate distance measure, the canonical coefficient ($C_{dt}$), as the *y*-axis. A second plot shows species' weights, i.e., the relative contribution of each individual species to the overall community response. A high weight indicates a strong contribution of that species to the $C_{dt}$, while weights near zero and negative weights indicate lack of a relationship and an inverse relationship, respectively. Differences between the treatments and control are assessed with Monte-Carlo permutation tests (Shaw 2003). PRC analysis was performed using the 'vegan' package in R (Oksanen et al. 2010). Dependent variables were log-transformed biomass of each non-*Typha* species measured over time. Independent variables were *Typha* and litter treatments, with no-*Typha*/no-litter mesocosms as controls. Monte-Carlo results were based on 199 permutations.

## Results

### *Typha* invasion and environmental conditions

The amount of light reaching the soil surface in mesocosms was significantly affected by sampling date ($F_{6, 114} = 3.1$, $P = 0.008$) and litter treatment ($F_{1, 16} = 10.0$, $P = 0.006$) but not by *Typha* treatment ($F_{1, 16} = 0.6$, $P = 0.45$) or *Typha* × litter interaction ($F_{1, 16} = 0.002$, $P = 0.96$) (Fig. 1). Overall, light
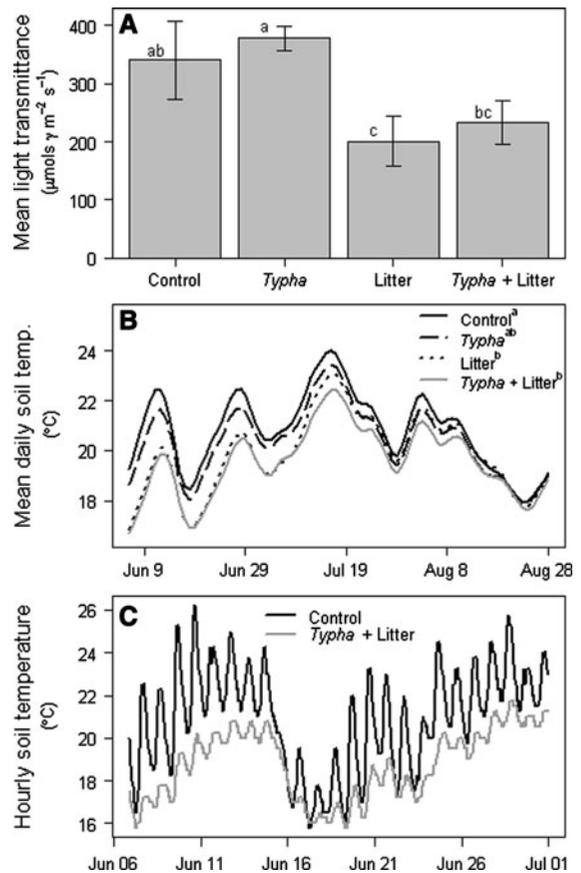


**Fig. 1** Effects of *Typha* and litter treatments in mesocosms on light transmittance to the soil surface (**a**) and soil temperature 5-cm below the surface (**b** and **c**) in 2005. **a** Treatment type had a significant effect on light transmittance ($F_{3, 16} = 3.5$, $P = 0.039$). *Error bars* are ± 1 s.e. *Different letters* denote statistically significant differences between treatments based on fitted contrasts of a mixed-effects model. **b** Mean daily *soil temperature* was significantly related to treatment type ($F_{3, 4} = 7.0$, $P = 0.046$). Lines were fitted using a LOWESS smoothing function. Pairwise comparisons as in (**a**, **c**). Diurnal variability in *soil temperature* was significantly related to treatment type ($F_{3, 4} = 8.7$, $P = 0.032$). Variability was highest in the control treatment and lowest in the +*Typha*/ + litter treatment, which significantly differed from each other in pairwise comparisons ($P = 0.008$). The live-*Typha*-only and litter-only treatments and July–August data are excluded for ease of interpretation

transmission in +litter mesocosms was reduced by 40% relative to −litter treatments.

The pattern for soil temperature was similar to that for light transmittance. Mean daily soil temperatures differed by sampling date ($F_{83, 581} = 78.0$, $P < 0.0001$) and litter treatment ($F_{1, 4} = 17.1$, $P = 0.014$) but not *Typha*

treatment ($F_{1, 4} = 3.7$, $P = 0.13$) or $Typha \times$ litter interaction ($F_{1, 4} = 0.05$, $P = 0.84$) (Fig. 1). On average, soil temperatures in +litter mesocosms were 0.9°C cooler than those in −litter mesocosms. Diurnal variability in soil temperature (daily temperature range) was affected by date ($F_{83, 581} = 7.4$, $P < 0.0001$) and litter treatment ($F_{1, 4} = 18.5$, $P = 0.013$) and was marginally affected by $Typha$ treatment ($F_{1, 4} = 7.2$, $P = 0.056$), but there was no significant interaction between $Typha$ and litter treatments ($F_{1, 4} = 0.5$, $P = 0.53$) (Fig. 1). Variability in mesocosms without live $Typha$ or litter was more than twofold that in mesocosms with both treatments (mean diurnal range $\pm$ s.e. = $3.34 \pm 0.14$ and $1.54 \pm 0.08$, respectively).

## $Typha$ invasion and intraspecific competition

There was no evidence that the growth of individual $Typha$ plants was affected by intraspecific competition with live $Typha$ or impeded by the presence of $Typha$ litter. There were no significant relationships between the biomass of individual $Typha$ plants and overall $Typha$ density in the field or in the mesocosm experiment (Fig. 2). There were also no effects of litter on live-$Typha$ biomass in mesocosms (Table 2).

## Native plant community response to $Typha$ invasion

The aggregate aboveground biomass of all 11 native plant species was significantly reduced by the presence of $Typha$ and its litter but there was not a significant $Typha \times$ litter interaction (Table 2). At the beginning of the mesocosm experiment (2004), none of the $Typha \times$ litter treatment combinations differed in pairwise comparisons from −$Typha$/− litter controls but all except for +$Typha$/− litter did at the end of the experiment (Fig. 3). There was a strong temporal pattern in the effects of $Typha$ invasion, with sampling year a highly significant factor ($F_{1, 147} = 15.0$, $P = 0.0002$) and all treatments except controls significantly declining in biomass between 2004 and 2009 (Fig. 3).

There were no species that showed significant positive responses to the presence of $Typha$ or $Typha$ litter. While the trend for 10 of the 11 species was greater decline over time in +$Typha$ treatments than in −$Typha$ treatments, this trend was only significant
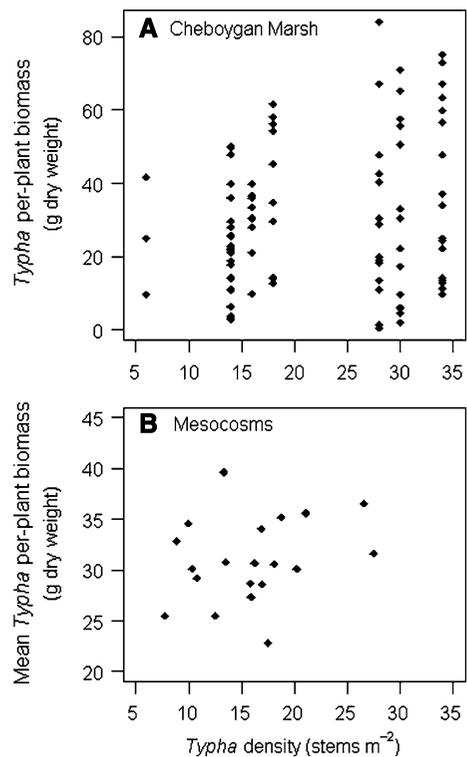


**Fig. 2** Correlations between neighborhood $Typha$ density and performance of individual $Typha$ plants in **a** Cheboygan Marsh in summer 2005 and **b** mesocosms in summer 2009. Points represent individuals in (**a**) and means for individuals in each +$Typha$ mesocosm in (**b**). The data were analyzed by linear regression and showed no significant relationships. **a** $F_{1, 85} = 2.7$, $P = 0.10$, $R^2 = 0.03$; **b** $F_{1, 18} = 1.2$, $P = 0.28$, $R^2 = 0.06$

for *Juncus nodosus* (Table 2). Seven species significantly declined with litter addition. Two species, *Carex aquatilis* and *Eleocharis erythropoda*, were significantly reduced by $Typha \times$ litter interaction (Table 2).

Multivariate analyses revealed differences between treatments in overall plant-community composition. PERMANOVA showed significant effects of sampling year ($F_3 = 56.5$, Monte Carlo $P = 0.001$) and litter ($F_1 = 11.1$, $P_{MC} = 0.005$) and significant year × litter ($F_3 = 2.6$, $P_{MC} = 0.014$) and litter × $Typha$ ($F_1 = 5.4$, $P_{MC}$ $P = 0.022$) interactions, but not effects of $Typha$ alone ($F_1 = 1.8$, $P_{MC}$ $P = 0.21$). Principal response curves showed significant plant-community differences between treatment and control mesocosms ($F_1 = 21.9$, $P = 0.005$) with successively greater effects from $Typha$ to litter to combined $Typha$ and litter treatments (Fig. 4).

**Table 2** Effects of experimental treatments on plant biomass in wetland mesocosms (2004–2009)

| Species | +*Typha* | | | +Litter | | | +*Typha* +Litter | | | High water | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Relative change[a] | $F$ | $P$[b] | Relative change[c] | $F$ | $P$[b] | Relative change[d] | $F$ | $P$[b] | Relative change[e] | $F$ | $P$[b] |
| All native species combined | **−3.41** | **4.05** | **0.052** | **−2.77** | **27.01** | **<0.0001** | −2.92 | 1.99 | 0.17 | −1.75 | 1.92 | 0.17 |
| *Carex aquatilis* | −0.23 | 1.65 | 0.21 | −0.18 | 0.04 | 0.84 | **−0.41** | **3.73** | **0.062** | 0.26 | 1.79 | 0.19 |
| *C. hystericina* | 0.65 | 0.38 | 0.54 | 0.04 | 0.42 | 0.52 | −0.12 | 0.03 | 0.87 | 0.39 | 1.06 | 0.31 |
| *C. viridula* | −2.77 | 0.04 | 0.85 | −2.06 | 0.56 | 0.46 | −11.66 | 1.53 | 0.23 | **−6.49** | **8.30** | **0.007** |
| *Eleocharis erythropoda* | −1.24 | 2.23 | 0.14 | **−2.60** | **8.49** | **0.0063** | **−2.66** | **4.11** | **0.050** | 0.34 | 0.17 | 0.68 |
| *E. smallii* | −2.44 | 0.00 | 0.99 | **−2.97** | **16.22** | **0.0003** | −2.61 | 0.07 | 0.80 | −1.60 | 2.83 | 0.10 |
| *Juncus alpinoarticulatus* | −2.08 | 0.00 | 0.99 | **−2.08** | **22.41** | **<0.0001** | −2.06 | 0.44 | 0.51 | −2.05 | 0.00 | 0.95 |
| *J. balticus* | −1.41 | 1.11 | 0.30 | **−1.87** | **32.07** | **<0.0001** | −3.09 | 2.13 | 0.15 | −0.73 | 0.08 | 0.78 |
| *J. nodosus* | **−2.00** | **6.15** | **0.018** | **−2.00** | **46.42** | **<0.0001** | −2.00 | 1.24 | 0.27 | −2.00 | 0.13 | 0.72 |
| *Schoenoplectus acutus* | −2.24 | 1.09 | 0.30 | −2.12 | 0.10 | 0.75 | −2.22 | 1.19 | 0.28 | **−1.70** | **3.19** | **0.08** |
| *S. pungens* | −2.14 | 0.19 | 0.66 | **−14.78** | **5.08** | **0.031** | −4.87 | 0.14 | 0.71 | −4.50 | 0.79 | 0.38 |
| *S. tabernaemontani* | −2.00 | 0.03 | 0.86 | **−2.00** | **4.03** | **0.053** | −2.00 | 0.87 | 0.36 | −2.00 | 0.51 | 0.48 |
| *Typha* spp. | – | – | – | 0.97 | 0.56 | 0.47 | – | – | – | 1.16 | 0.31 | 0.59 |

For each treatment, changes in biomass from 2004 to 2009 were relativized to controls (2005–2009 for *Typha* response). Positive and negative values indicate that the treatment increased and decreased biomass, respectively. *Bold* text denotes statistically significant effects ($\alpha < 0.10$)

Relative change = $([\Delta_{treatment} - \Delta_{control}] \div |\Delta_{control}|) - 1$

$\Delta = (Biomass_{2009} - Biomass_{2004}) \div Biomass_{2004}$, except *Typha*: 2009 versus 2005

Numerator degrees of freedom = 1 for all comparisons. Denominator df = 16 for *Typha* response and 34 for all other analyses

[a] *vs.* −*Typha* mesocosms

[b] *P*-values calculated from linear mixed-effects models testing the effects of year, *Typha* (for non-*Typha* spp. only), litter, and water-level treatments, and AIC-selected interaction terms on log-transformed biomass

[c] *vs.* −Litter mesocosms

[d] *vs.* −*Typha* −Litter mesocosms

[e] *vs.* Low-water mesocosms

## Effects of water-level manipulations

Overall, there was a trend toward lower biomass in high-water relative to low-water treatments but this trend was only significant for *Carex viridula* and *Schoenoplectus acutus* and was not significant for native species as a whole (Table 2). There were also no effects of water level on changes in *Typha* biomass ($F_{1, 16} = 0.3$, $P = 0.59$). PERMANOVA showed weak effects of water level ($F_1 = 2.9$, $P_{MC} = 0.099$) and water × *Typha* interaction ($F_1 = 2.8$, $P_{MC} = 0.095$) and moderate to strong effects of litter × water ($F_1 = 6.0$, $P_{MC} = 0.018$) and litter × water × *Typha* ($F_1 = 10.1$, $P_{MC} = 0.007$) interactions.

## Discussion

In field settings, *Typha* invasion was associated with environmental and plant community changes, notably greater plant litter, soil nitrogen, and soil organic matter and lower plant-species richness and floristic quality (Table 1) (Lishawa et al. 2010; Tuchman
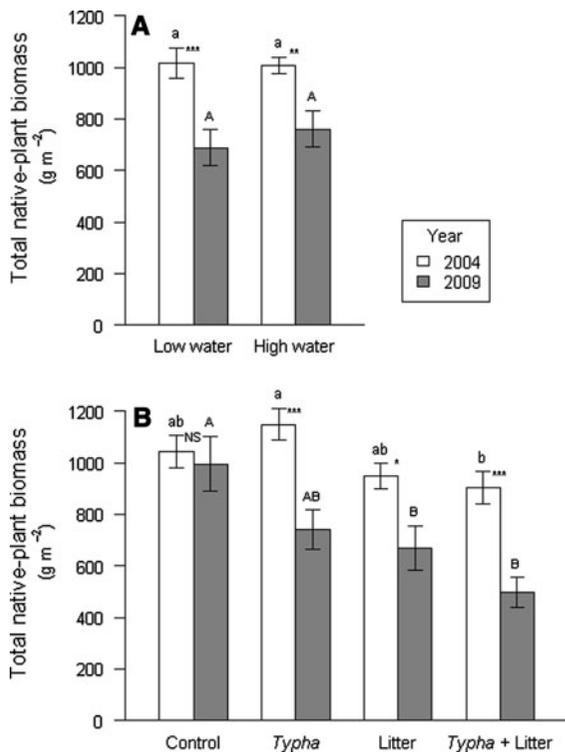
Fig. 3 Effects of water-level (a) and *Typha* and litter treatments (b) on native-plant biomass at the beginning and end of the mesocosm experiment. Tukey's HSD comparisons across treatments within years are shown with *lowercase* (2004) and *uppercase* (2009) letters. Differences within treatments between years are depicted as: $P > 0.10$ 'NS', $P < 0.05$ '*', $P < 0.01$ '**', $P < 0.001$ '***'



Fig. 4 Principal response curves showing plant-community responses over time to experimental *Typha* and litter treatments versus no-*Typha*/no-litter controls and species weights (the relative contribution of each species to the overall community response). Monte-Carlo test: $F = 21.9$, $P = 0.005$

Final *Typha* densities in mesocosms ($15.9 \pm 1.2$ stems m$^{-2}$) were somewhat lower than those in the field ($19.3 \pm 3.1$). Effects of live *Typha* might have been much greater were densities as high as has been observed at advanced stages of *Typha* invasion (30+ stems m$^{-2}$, Tuchman et al. 2009). Litter treatments had strong effects on light, temperature, plant biomass, and community composition. Interactions between live *Typha* and litter significantly affected some aspects of plant-community composition. Water-level treatments had some species-specific effects on plant biomass. The low and high water treatments in this study were both within the range of where *Typha* is found in field settings (Table 1). A higher high-water treatment (e.g., 15-cm standing water) would likely have impaired the performance of *Typha* and other species.

Our results are consistent with recent work demonstrating that it is litter production in particular that drives the strong environmental and plant-community changes associated with *Typha* invasion (Farrer and Goldberg 2009; Vaccaro et al. 2009). This collection of studies had some notable methodological differences: ours was performed as a mesocosm experiment and the others as field experiments, we added litter as smaller annual increments rather than larger one-time additions, and two of the studies reflected conditions in northern Michigan coastal wetlands (ours and Farrer and Goldberg 2009) while the third

et al. 2009). A 6-year mesocosm study enabled us to experimentally test *Typha*'s dominance mechanisms and untangle the effects of live *Typha*, *Typha* litter, and water depth, which were confounded in the field. It also enabled us to directly test the impact of *Typha* invasion on a native wetland plant community, as it is possible that native-species declines in the field covary with *Typha* due to additional factors such as disturbance history or soil conditions, rather than the invasion itself.

In general, the environmental and biotic impacts of *Typha* litter were stronger than those of live *Typha*. For several response variables, relative responses increased in the order: Control $\leq$ *Typha* < litter $\leq$ *Typha* + litter. Live-*Typha* treatments did not differ from controls in terms of light penetration or soil temperature but did reduce overall native-plant biomass and alter community composition.

focused on Lake Ontario wetlands (Vaccaro et al. 2009). Despite these differences, the overall patterns observed were quite similar. In all cases, *Typha* litter caused loss of plant diversity. Litter appeared to drive this loss by affecting seed germination and establishment (Vaccaro et al. 2009) and altered the growth environment for native species (the present study and Farrer and Goldberg 2009). In the studies that separately manipulated *Typha* litter and stem density, litter either did not impair the performance of live *Typha* (our study) or even enhanced it (Farrer and Goldberg 2009).

The findings from these *Typha* studies may have parallels in the invasion dynamics of other problematic invasive wetland species. Species that are highly invasive in North America and elsewhere share key traits with *Typha*, such as rapid clonal growth, large size relative to displaced species, formation of dense monotypes, and copious litter production (Galatowitsch et al. 1999; Zedler and Kercher 2004).

That *Typha* litter had strong effects on environmental and community characteristics is consistent with the central role that litter plays in plant-community dynamics (Bergelson 1990; Facelli and Pickett 1991). Litter has a particularly strong influence on the assembly and functioning of wetland ecosystems (Aerts et al. 1999; Weiher and Keddy 1995). Since northern lower Michigan and much of the Great Lakes region has a relatively short growing season (Cathey 1990), delays in soil thaw, reduced light availability, and altered plant productivity associated with copious litter are likely to influence wetland species' performance.

Seed germination is strongly influenced by both temperature and variability in temperature (Baskin and Baskin 2001). Litter-driven reduction of mean soil temperatures and dampening of temperature fluctuations is likely to reduce seed germination in many wetland species (Schutz and Rave 1999; Seabloom et al. 1998). Litter can also spatially and mechanically interfere with the emergence of other species' seedlings (Bergelson 1990). Overlying litter a decimeter or more deep (Table 1) is a substantial barrier to the emergence of many wetland species. Frieswyk and Zedler (2006) found that seed-bank species richness often exceeded the richness of extant vegetation in Great Lakes wetlands. Keddy and Reznicek (1986) noted that high water periods in coastal wetlands can kill dominant species, such as

*Typha*, allowing for germination from persistent, species-rich seed banks. These findings, together with the litter impacts we observed, suggest that *Typha* and its litter act as "filters" (Weiher and Keddy 1995) that differentiate realized from potential plant communities.

The effects of *Typha* litter on native plant communities are of particular concern given how long *Typha* litter can persist (Davis and van der Valk 1978). Penko and Pratt (1987) found little insect herbivory on non-native *Typha* spp., though muskrats can substantially reduce cattail biomass (Connors et al. 2000). The majority of *Typha* biomass enters detrital pools, with a long standing-dead phase that slows decay (Christensen et al. 2009; Kuehn and Suberkropp 1998). Even after standing-dead *Typha* collapses to the marsh surface, its morphology and tissue chemistry, as well as environmental conditions in invaded habitats, result in very slow decomposition (Freyman 2008), leading to *Typha* litter biomass on the order of 2.5 kg m$^{-2}$ (Angeloni et al. 2006; Christensen et al. 2009). In this regard, *Typha* invasion differs from general patterns found in terrestrial invaders, which often have faster rates of decomposition than co-occurring natives (Ehrenfeld 2003). Similar reductions in decomposition rates have been found in *P. australis* (Warren et al. 2001; Windham 2001).

The effects of live *Typha* alone were modest relative to those of litter. While live *Typha* has the capacity to outcompete native species for resources such as light and nutrients, it does not occupy as great a horizontal footprint as a comparable quantity of collapsed litter. Thus live *Typha* may be less "efficient" than litter at modifying environmental conditions and reducing the growth and reproductive fitness of co-occurring species. Consistent with this idea, Vaccaro et al. (2009) found that fallen litter had stronger effects than standing litter. The greater impacts of litter relative to live *Typha* add to a growing literature demonstrating the importance of mechanisms other than direct resource competition in biological invasions (Callaway and Ridenour 2004; Crooks 2002; Suding et al. 2004).

It is also possible that the duration of the mesocosm experiment was not sufficient for the emergence of potential time- or density-dependent effects of live *Typha*, e.g., buildup of allelochemicals or more complete appropriation of space (Carlsen et al. 2000;

Gallardo et al. 1998; McNaughton 1968). Community effects of *Typha* invasion on nutrient-cycling pathways or other plant-soil feedbacks might emerge over time frames longer than the course of this study. For example, studies of restored wetlands indicate that development of soil properties can be incomplete even after several decades (Ballantine and Schneider 2009; Craft et al. 2003). The edaphic effects of invasive species might follow similarly long trajectories.

Our study's small species pool ($n = 11$) makes interpretations of how species with different functional traits may respond to *Typha* invasion tenuous. Still, it is interesting that "losers" and "non-losers" tended to have different growth forms. We found negative associations with *Typha* for the following species: *Carex aquatilis*, *Eleocharis erythropoda*, *E. smallii*, *Juncus alpinoarticulatus*, *J. balticus*, *J. nodosus*, *Schoenoplectus acutus*, *S. pungens*, and *S. tabernaemontani*. All of these species with the exception of *C. aquatilis* are rhizomatous "interstitial reeds" or "matrix clonal dominants" (the latter category includes *Typha*) with many erect, mostly leafless shoots or stem-like leaves (Boutin and Keddy 1993; Keddy et al. 1994). Vegetative reproduction of these plants involves belowground spread via rhizomes followed by vertical growth (Bouzille et al. 1997; van Groenendael et al. 1996). This type of spread requires substantial investment of resources (Mony et al. 2010), which may be disadvantageous to clones in the presence of an overlying obstacle like *Typha* litter.

In contrast, the two species that were not significantly affected by *Typha* invasion, *C. hystericina* and *C. viridula*, and *C. aquatilis*, which was only weakly affected by the interaction of both *Typha* and litter, are cespitose sedges that grow in clumps with thin but numerous leaves. New stems emerge aboveground at the base of existing stems (van Groenendael et al. 1996). This clump-forming morphology may confer better resistance to the physical effects of *Typha* and its litter. And asexual reproduction in these species does not require potentially costly investment in belowground spread (Bouzille et al. 1997; Mony et al. 2010).

In addition to our relatively small species pool, there are other caveats regarding functional-trait interpretations. One is that the resistant species in our study were congeners. We are thus unable to control for the possibility of phylogenetic, rather than trait-based, explanations for their relative success in

this experiment (Webb et al. 2002). In addition, field-based and correlative studies of *Typha* invasion have found declines in a wide range of forb and graminoid species representing numerous functional traits (e.g., Tuchman et al. 2009; Vaccaro et al. 2009). Interestingly, the field-based litter treatments of Farrer and Goldberg (2009) led to slight increases in the relative abundance of *S. americanus* (*S. pungens*) and *J. balticus* and decreases in *C. viridula* and *C. hystericina*, among other species; results opposite of ours. These conflicting outcomes may stem from differences in study design. Farrer and Goldberg (2009) applied litter treatments to extant vegetation that may have been part of larger clones. In contrast, our plants were added as individuals and subjected to treatments 1 year after planting. They thus faced perturbation by litter without the advantages conferred from being part of an extensive, well-established clone (van Groenendael et al. 1996).

While *Typha* invasion affected a majority of the native species in our study, there was no evidence that *Typha* or its litter limited *Typha* production (Table 2; Fig. 2). The lack of a significant relationship between neighbor density and individual biomass in the field may have been confounded by covarying environmental factors or the possibility that different stems represented the same clone. However, the same pattern occurred in the mesocosm experiment, with abiotic factors controlled and *Typha* added as 16 distinct individuals. The ability to displace other species while not self-inhibiting (or even self-facilitating, Farrer and Goldberg 2009) should help an invader achieve high stem densities and rates of spread. This may be a key factor underlying the ability of *Typha* to aggressively expand and create near monotypes.

In reality, wetlands invaded by *Typha* face not just live *Typha* or *Typha* litter but a combination of both through a sustained, multigenerational attack. The year's new *Typha* can compete directly with native species for resources while more than a year of standing-dead *Typha* intercepts light and occupies space and the collapsed litter of many years past modifies the environment and smothers new growth. Similar dynamics occur in invasions by other wetland species, such as *P. australis* and *P. arundinacea* (Foster and Wetzel 2005; Zedler and Kercher 2004).

Attempts to restore invaded wetlands need to address this multigenerational dynamic. It is not

enough to control live *Typha* using herbicide. The robust "life after death" (*sensu* Bergelson 1990) that *Typha* achieves through its dead cohorts creates a legacy that must be considered in restoration efforts. Removal of senesced material following treatment of live plants should be experimentally implemented in efforts to restore previously invaded wetlands. Prescribed fire is a commonly used approach but comes with the caveat that treatment at the wrong time or of the wrong intensity may be ineffective or counterproductive (Thompson and Shay 1985). Harvesting of litter can be done where fire is not feasible but is likely to be prohibitively costly and time-consuming on large scales. The strong effects of *Typha* litter and challenges associated with its removal are arguments in favor of rapidly responding to new invasions. By eradicating *Typha* as it first appears in a site, i.e., before there has been substantial litter accumulation, managers can avert the ecological consequences and practical difficulties associated with its litter.

A novel approach being tested is to forgo herbicide application and burning and instead harvest biomass of *Typha* and other invasive species for use in controlled anaerobic digestion that generates renewable energy in the form of methane (ongoing research, investigators NC Tuchman, SC Lishawa, and DA Albert). The energy produced could be utilized to offset the substantial costs associated with ecological restoration activities in invaded wetlands.

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