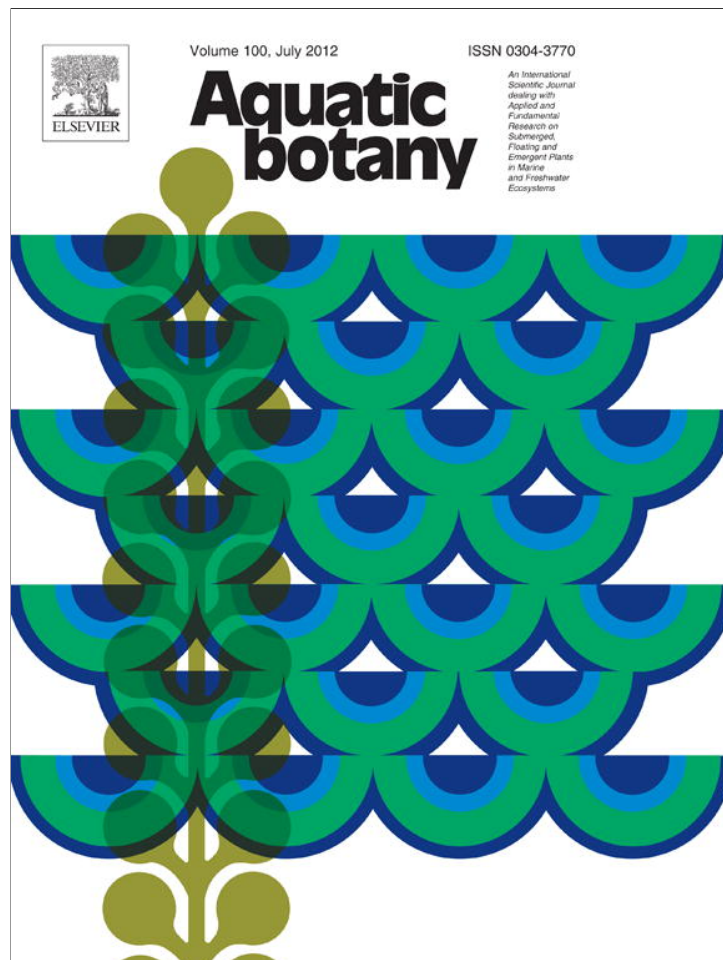


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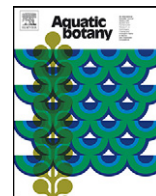


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## Short communication

Appropriation of nitrogen by the invasive cattail *Typha* × *glauca*Daniel J. Larkin<sup>a,\*</sup>, Shane C. Lishawa<sup>b,c</sup>, Nancy C. Tuchman<sup>b,c</sup><sup>a</sup> Plant Science and Conservation, Chicago Botanic Garden, Glencoe, IL 60022, USA<sup>b</sup> Center for Urban Environmental Research & Policy and Department of Biology, Loyola University Chicago, Chicago, IL 60626, USA<sup>c</sup> University of Michigan Biological Station, Pellston, MI 49769, USA

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## ABSTRACT

A <sup>15</sup>N-addition mesocosm experiment was used to study competition for nitrogen (N) between the aggressive cattail species *Typha* × *glauca* (*T. latifolia* × *T. angustifolia*) Godr. (hybrid cattail) and a suite of native plant species often found in marshes *Typha* invades. Plant uptake of <sup>15</sup>N released from labeled *Typha* and native-species litter was then measured in a pot experiment with new cohorts of two native plant species (*Juncus balticus* Willd. and *Schoenoplectus acutus* Muhlenberg ex Bigelow) grown with and without *Typha*. In both experiments, species differed in their above- and belowground uptake of <sup>15</sup>N, with *Typha* outperforming the other species (1.7–5.0-times greater mean uptake,  $P < 0.0001$ – $0.007$ ). *Typha* then held on more strongly to the N it acquired: newly grown native plants in the pot experiment acquired more <sup>15</sup>N from native litter than from *Typha* litter (1.4–12.0-times greater mean uptake,  $P = 0.0006$ – $0.017$ ). In contrast, *Typha* showed no differences in N uptake by litter type ( $P = 0.16$ – $0.54$ ). There were no main effects of live *Typha* on native-plant N uptake ( $P = 0.64$ – $0.86$ ), but there were modest interactions between *Typha* presence and litter type ( $P = 0.030$ – $0.091$ ). Where native plants and *Typha* co-occurred, native species matched *Typha* in recovering <sup>15</sup>N from native litter ( $P = 0.17$ – $0.33$ ) but recovered 90–96% less <sup>15</sup>N from *Typha* litter ( $P = 0.020$ – $0.021$ ). *Typha*'s higher overall N recovery was due to both greater biomass production and uptake efficiency (<sup>15</sup>N per unit dry weight). *Typha*'s greater N uptake and retention, repeated over multiple cycles of senescence and new growth, should lead to an increasing appropriation of N away from native species and into living and dead *Typha* biomass.

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## 1. Introduction

Wetland vegetation is typically limited by either nitrogen (N) or phosphorus (P) (Verhoeven et al., 1996). In North American wetlands, marshes are generally N- rather than P-limited and their defining vegetation, herbaceous vascular plants, are the most N-limited of plant types (Bedford et al., 1999). Thus, for North American marshes, N availability is a critical determinant of plant-community dynamics. Plant uptake and release of N, in turn, are major biogeochemical pathways that drive functioning of wetland ecosystems and resource availability for other biota (White and Howes, 1994; Findlay et al., 2002).

N uptake in co-occurring wetland species can vary greatly. Kao et al. (2003) found that N uptake differed among five wetland perennials and differed within plants as well, e.g., the species with the greatest aboveground N accumulation had the lowest belowground accumulation. Species able to perform “luxury uptake” of nutrients (accumulation in excess of their immediate

requirements) are at an advantage when nutrient levels increase (Chapin, 1980; Cronk and Fennessy, 2001).

There is evidence that increased nutrient availability in wetlands disproportionately favors invasive or rapidly expanding, vigorous species (Weiher and Keddy, 1995; Zedler and Kercher, 2004). For example, with nutrient enrichment, uptake and/or growth responses have been shown to be greater in *Phalaris arundinacea* L., *Phragmites australis* (Cav.) Trin. ex Steud., *Typha domingensis* Pers., and *T. × glauca* (*T. latifolia* × *T. angustifolia*) Godr. than in native species of invaded communities (Davis, 1991; Green and Galatowitsch, 2001; Lorenzen et al., 2001; Woo and Zedler, 2002; Windham and Ehrenfeld, 2003; Kercher and Zedler, 2004). Such invasive wetland plants can be seen as “opportunists” well-suited to exploit the condition of sudden pulses of nutrient availability created by eutrophication and other disturbances (Zedler and Kercher, 2004).

*Typha × glauca* (hybrid cattail) is a tall, highly productive emergent macrophyte. Though one of its parent species is native to the area (*T. latifolia*), *T. × glauca* (hereafter *Typha*) is considered one of the most problematic invaders of wetlands in the upper Midwest/Great Lakes region (Galatowitsch et al., 1999). *Typha* responds strongly to increased nutrient availability (Woo and Zedler, 2002; Lishawa et al., 2010); can assimilate, retain, and

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internally cycle high concentrations of N (Davis and van der Valk, 1983); and produces abundant, persistent litter (Mitchell et al., 2011). These traits suggest that *Typha* might keep N away from co-occurring plants by sequestering it in living and dead biomass.

We used a  $^{15}\text{N}$  stable-isotope addition experiment to study competition for N between *Typha* and species characteristic of marshes it invades, and then tracked subsequent uptake by a new cohort of plants of  $^{15}\text{N}$  released from labeled litter. We hypothesized that (1) the presence of *Typha* would reduce co-occurring species'  $^{15}\text{N}$  uptake through direct competitive effects, (2) *Typha* would outperform native species in acquiring  $^{15}\text{N}$ , and (3)  $^{15}\text{N}$  in labeled *Typha* litter would be less accessible to plant uptake than  $^{15}\text{N}$  in labeled native-species litter.

## 2. Methods

### 2.1. Experiment 1: $^{15}\text{N}$ addition

In 2007, we used an existing mesocosm experiment at the University of Michigan Biological Station (UMBS) to contrast N uptake by *Typha* vs. an assemblage of native species characteristic of northern Great Lakes coastal wetlands. Details of mesocosm construction and design are described in an earlier study on the effects of *Typha* and its litter on plant-community dynamics (Larkin et al., 2011). Briefly, mesocosms were planted in 2003 at mean densities found in a nearby marsh (numbers in parentheses are stems  $\text{m}^{-2}$ ): *Juncus nodosus* L. (208), *Juncus balticus* Willd. (142), *Eleocharis* spp. R. Brown (87), *Schoenoplectus Tabernaemontani* C. C. Gmelin (34), *Juncus alpinoarticulatus* Chaix (9), *Schoenoplectus acutus* Muhlenberg ex Bigelow (7), *Schoenoplectus pungens* Vahl (7), *Carex viridula* Michaux (4), *Carex aquatilis* Wahl. (2), *Carex hystericina* Willd. (1). In 2004, we added *Typha* to half of the mesocosms at a density of 8 stems  $\text{m}^{-2}$ . We did not include mesocosms subjected to *Typha*-litter or high-water treatments in the present study.

Our experimental design consisted of 10 mesocosms with native-species only and 10 with native species plus *Typha*. Half of the 10 mesocosms with and without *Typha* were randomly assigned to receive 3.3  $\text{g N m}^{-2}$  as 99%  $^{15}\text{N}$ -enriched  $\text{NH}_4\text{Cl}$  ( $^{15}\text{N}$ ) while the other half received the same amount of N as standard  $\text{NH}_4\text{Cl}$  (control) ( $N=5$  for each combination). N was added in June and above and belowground plant material was harvested from subplots of each mesocosm after 2 d, 30 d, and 4 months and dried and weighed. We differentiated aboveground material by species, focusing on *J. balticus* and *S. acutus* because of their relatively high biomass and presence in all mesocosms. We differentiated belowground material into three categories: native species (from mesocosms lacking *Typha*), *Typha* (distinguishable rhizomes), and a mixture of native species and *Typha* (other root material from mesocosms containing *Typha*). Subsamples were ground and analyzed for N-isotopic composition at the UMBS analytical lab using a coupled Costech CHN elemental analyzer/Finnigan Delta Plus XL IR mass spectrometer.

### 2.2. Experiment 2: $^{15}\text{N}$ -labeled litter addition

Standing-dead plant material was harvested from mesocosms in spring 2008, hand-cut into ~5-cm lengths, and homogenized by litter type (control-native, control-*Typha*,  $^{15}\text{N}$ -native, and  $^{15}\text{N}$ -*Typha*). In spring 2009, an outdoor pot experiment was set up using 28-cm diameter, plastic-lined pots filled with a 10:1 sand and peat mix. Pots were either planted with one individual each of two native species (again using *J. balticus* and *S. acutus*) or with this same planting design plus one *Typha* plant. Plants were added as 10-cm sections of rhizome with

attached clipped stems. Each pot was randomly assigned a litter type ( $N=4$  for each of the eight *Typha*-treatment  $\times$  litter-type combinations). At the end of the summer, all plant material was harvested from each pot and divided into the following fractions: aboveground-native, aboveground-*Typha*, belowground-native, and belowground-*Typha*. Plant material was dried, weighed, and analyzed as described above.

### 2.3. Data analysis

For both experiments,  $^{15}\text{N}$  enrichment of plant material was calculated as atom-percent  $^{15}\text{N}$  ( $^{15}\text{NAP}$ ). Excess  $^{15}\text{N}$  enrichment of plant material from mesocosms or pots receiving  $^{15}\text{N}$  was corrected by subtraction of the mean  $^{15}\text{NAP}$  found in equivalent control samples, i.e., samples that were subjected to the same treatment combinations but received control  $\text{NH}_4\text{Cl}$  or control litter. Experiment 1 was analyzed using excess  $^{15}\text{N}$  by unit dry weight ( $\mu\text{mol excess } ^{15}\text{N g}^{-1}$ ). Experiment 2 was analyzed using total excess  $^{15}\text{N}$  ( $\mu\text{mol excess } ^{15}\text{N g}^{-1} \times \text{g dry weight}$ ), since biomass production in pots was de novo from a common starting condition.

Experiment 1 involved repeated sampling of plant material from the same mesocosms over time. To account for non-independence among these measurements, we analyzed experiment 1 using linear-mixed effects (LME) models with mesocosm identity as a source of random effects. Experiment 2 data did not include repeated measures and were analyzed by ANOVA. For both experiments, we constructed separate models to test: (1) the effects of live *Typha* on native-plant N uptake (using *Typha* presence/absence as an independent variable and excluding *Typha*  $^{15}\text{N}$ -uptake data), and (2) differences in N uptake between *Typha* and native species (excluding data from experimental units without *Typha* if there was a significant *Typha* main effect or interaction). In experiment 2, we also tested the effects of litter type (native vs. *Typha* litter as a  $^{15}\text{N}$  source) on  $^{15}\text{N}$  uptake. Experiment 2 data were log-transformed to better meet model assumptions. Interaction terms were included where appropriate. All analyses were performed in R 2.13.1, with the nlme package used for LME models (Pinheiro et al., 2009; R Development Core Team, 2011).

## 3. Results

In experiment 1, plant  $^{15}\text{N}$  concentrations varied significantly over time (Table 1, Fig. 1A and B). Species differences were more pronounced early-on and had dissipated by day 30 for belowground tissue. There were no effects of *Typha* on native-plant above- or belowground  $^{15}\text{N}$  uptake (Table 1, Fig. 1A and B). However, *Typha* outperformed native species in efficiency of  $^{15}\text{N}$ -uptake (excess  $^{15}\text{N}$  per unit dry weight) to above- and belowground tissues (Table 1, Fig. 1A and B; a priori contrasts of *Typha* vs. other composition categories:  $P=0.005$  [aboveground],  $P=0.002$  [belowground]).

In experiment 2, there were no significant main effects of *Typha* presence on native-plant  $^{15}\text{N}$  uptake but there were moderately and weakly significant effects of *Typha*  $\times$  litter-type interactions above- and belowground, respectively (Table 1, Fig. 1C and D). Native litter and *Typha* litter added to pots did not differ in  $^{15}\text{N}$  enrichment ( $F_{1,13}=0.20$ ,  $P=0.66$ ). Despite this, litter type did significantly influence above- and belowground  $^{15}\text{N}$ -uptake (Table 1, Fig. 1C and D). Native plants acquired more  $^{15}\text{N}$  from native litter than from *Typha* litter (aboveground:  $F_{1,14}=7.28$ ,  $P=0.017$ ; belowground:  $F_{1,14}=19.62$ ,  $P=0.0006$ ), while *Typha* showed no differences in uptake by litter type (aboveground:  $F_{1,4}=0.45$ ,  $P=0.54$ ; belowground:  $F_{1,5}=2.66$ ,  $P=0.16$ ). Where native plants and *Typha* co-occurred, native species did not differ from *Typha* in recovery of  $^{15}\text{N}$  from native litter (aboveground:  $F_{1,4}=2.81$ ,  $P=0.17$ ; belowground:  $F_{1,5}=1.14$ ,  $P=0.33$ ) but recovered less N

**Table 1**  
Results of statistical tests for experiment 1 (LME models) and experiment 2 (ANOVA).

| Experiment   | Source      | Factor                 | df    | F     | P          |
|--|-------------|------------------------|-------|-------|------------|
| 1. <sup>15</sup> N addition<br>Effects of <i>Typha</i> on N uptake <sup>a</sup>                                | Aboveground | <i>Typha</i> treatment | 1, 8  | 0.04  | 0.8560     |
|  |             | Plant species          | 1, 27 | 14.84 | 0.0007***  |
|  |             | Sampling date          | 2, 27 | 6.17  | 0.0062**   |
|  |             | Species × date         | 2, 27 | 0.42  | 0.6583     |
|  |             | <i>Typha</i> treatment | 1, 8  | 0.24  | 0.6379     |
|  |             | Sampling date          | 2, 23 | 7.12  | 0.0039**   |
|  | Belowground | Plant species          | 2, 38 | 13.81 | <0.0001*** |
|  |             | Sampling date          | 2, 38 | 9.24  | 0.0005***  |
|  |             | Species × date         | 4, 38 | 2.41  | 0.0662*    |
|  |             | Root composition       | 2, 32 | 7.84  | 0.0017**   |
|  |             | Sampling date          | 2, 32 | 17.71 | <0.0001*** |
|  |             | Composition × date     | 4, 32 | 6.34  | 0.0007***  |
| 2. <sup>15</sup> N-labeled litter addition<br>Effects of <i>Typha</i> and litter type on N uptake <sup>a</sup> | Aboveground | Litter type            | 1, 12 | 7.74  | 0.0166*    |
|  |             | <i>Typha</i> treatment | 1, 12 | 0.01  | 0.9299     |
|  |             | <i>Typha</i> × litter  | 1, 12 | 6.04  | 0.0302*    |
|  |             | Litter type            | 1, 12 | 14.88 | 0.0023**   |
|  |             | <i>Typha</i> treatment | 1, 12 | 0.99  | 0.3397     |
|  |             | <i>Typha</i> × litter  | 1, 12 | 3.38  | 0.0910*    |
|  | Belowground | Plant composition      | 1, 10 | 26.45 | 0.0004***  |
|  |             | Litter type            | 1, 10 | 50.20 | <0.0001*** |
|  |             | Composition × litter   | 1, 10 | 19.57 | 0.0013**   |
|  |             | Plant composition      | 1, 11 | 10.95 | 0.0070**   |
|  |             | Litter type            | 1, 11 | 7.56  | 0.0189*    |
|  |             | Composition × litter   | 1, 11 | 1.96  | 0.1890     |

<sup>a</sup> *Typha* <sup>15</sup>N-uptake data excluded from analysis.

<sup>b</sup> Analysis restricted to pots containing *Typha* due to *Typha* × litter interaction.

\*  $P < 0.10$ .

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

from *Typha* litter (aboveground:  $F_{1,6} = 9.79$ ,  $P = 0.02$ ; belowground:  $F_{1,6} = 9.69$ ,  $P = 0.02$ ). Greater <sup>15</sup>N acquisition by *Typha* was due to both higher biomass production—*Typha* final dry weight exceeded the combined weight of both co-occurring native plants—and uptake efficiency in aboveground tissues ( $F_{1,19} = 78.03$ ,  $P < 0.0001$ ;  $F_{1,19} = 4.77$ ,  $P = 0.042$ ; respectively). Belowground, *Typha* had greater biomass production but not uptake efficiency ( $F_{1,19} = 34.67$ ,  $P < 0.0001$ ;  $F_{1,19} = 0.63$ ,  $P = 0.44$ ; respectively).

#### 4. Discussion

There was not compelling evidence to support our hypothesis that the presence of *Typha* would reduce uptake of <sup>15</sup>N by other species. *Typha* treatments had no significant above- or belowground main effects in either experiment. However, there were modest *Typha* × litter-type interactions in experiment 2, with native plants acquiring more <sup>15</sup>N from *Typha* litter where live *Typha* was absent. Our second hypothesis, that *Typha* would acquire more <sup>15</sup>N than co-occurring species, was supported. This pattern held true for both above- and belowground measurements in both experiments, although the effect was short-lived for belowground tissue in experiment 1. The results also supported our third hypothesis of <sup>15</sup>N in native litter being more available to plant uptake than <sup>15</sup>N in *Typha* litter—at least for native plants, which showed greater sensitivity to litter differences.

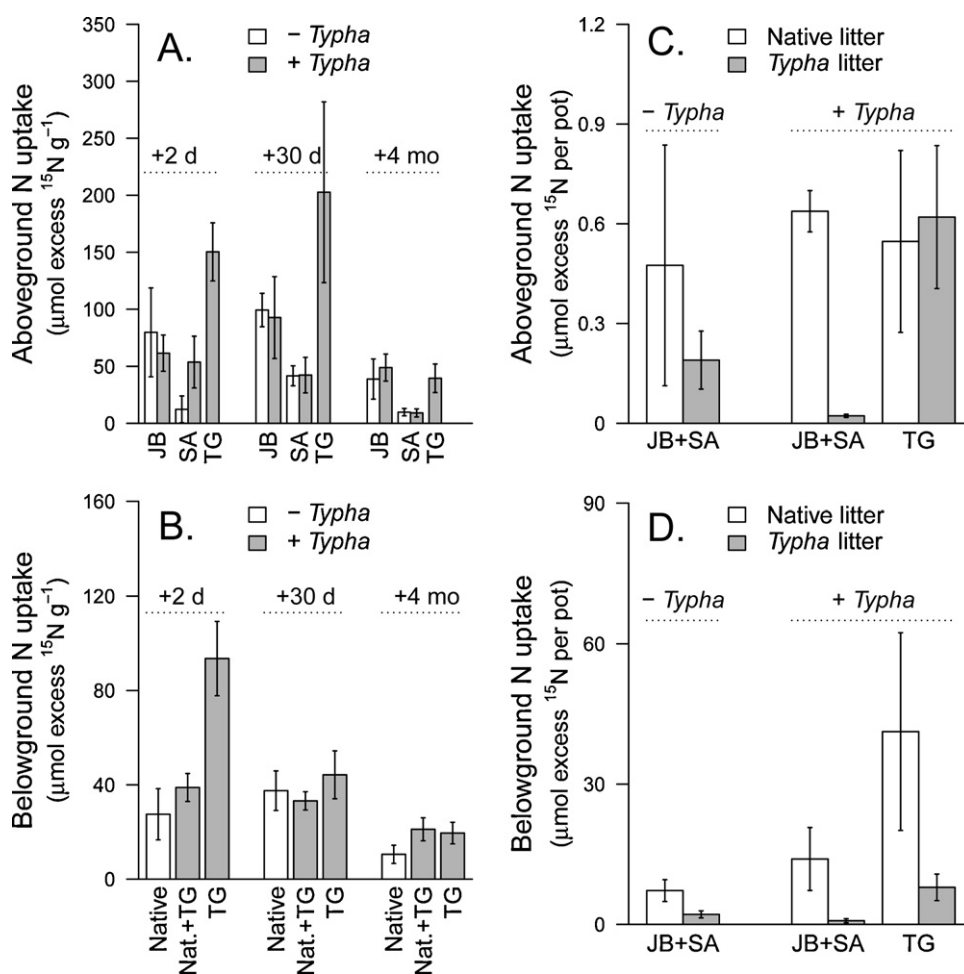
Based on our experiments, we conclude that *Typha* × *glauca* had advantages over our other study species in acquiring N. Initially, *Typha* took up labile N at a higher rate than an assemblage of *J. balticus*, *S. acutus*, and nine other species. It then held on to the N it acquired: newly grown native plants could acquire more N from their own litter than from *Typha* litter, while *Typha* took up N equally from both litter types. Where native plants and *Typha* co-occurred, native species matched *Typha* in recovering N from native litter but recovered less N from *Typha* litter. *Typha*'s higher

overall N recovery was due to both greater uptake efficiency and greater biomass production.

The net effect of *Typha*'s superior N uptake and retention, repeated over multiple cycles of senescence and new growth, would be an increasing appropriation of N away from native species and into living and dead *Typha* biomass. Together with other means by which *Typha* and its litter can alter environmental conditions and displace native species (Farrer and Goldberg, 2009; Larkin et al., 2011), appropriation of N may be a mechanism of its dominance. Similar dynamics may occur with P, which can be taken up at high rates by *Typha* and increase its biomass production (Davis and van der Valk, 1983; Woo and Zedler, 2002).

Plant species adapted to low-N conditions are vulnerable to displacement by nitrophiles under elevated N (Pennings et al., 2005; Fréville et al., 2007). And wetlands are particularly susceptible to eutrophication due to their typically low positions in watersheds and hydrological connectivity to nutrient sources. As previously N-limited wetlands receive large pulses of N, robust growth of opportunistic plant species can occur to the detriment of less-responsive species (Zedler and Kercher, 2004). Pennings et al. (2005) synthesized the effects of increased N on 20 herbaceous species across multiple experiments. Our plant assemblage did not overlap with theirs at the species level. However, of the 5 out of 20 species that consistently decreased in abundance with increasing nitrogen in their study, two were *Juncus* species congeneric to our study species *J. balticus*, *J. alpinoarticulatus*, and *J. nodosus*.

With *Typha*, robust growth following eutrophication leads to strong post-senescence (litter) effects on invaded wetlands. *Typha* litter appears to alter environmental conditions and plant communities more than live *Typha* (Farrer and Goldberg, 2009; Vaccaro et al., 2009; Larkin et al., 2011). Our findings indicate that these litter effects intersect with nutrient-uptake mechanisms: mineralized N from *Typha* litter was more likely to end up in new biomass of *Typha* than that of co-occurring species. *Typha* dominance should



**Fig. 1.** Mean plant <sup>15</sup>N-uptake for: (A) experiment 1, aboveground; (B) experiment 1, belowground; (C) experiment 2, aboveground; and (D) experiment 2, belowground. Dotted lines in (A) and (B) indicate data collected 2 d, 30 d, and 4 months after <sup>15</sup>N addition. Dotted lines in (C) and (D) indicate treatments with and without live *Typha*. Abbreviations: JB = *Juncus balticus*, SA = *Schoenoplectus acutus*, TG = *Typha × glauca*. Error bars are ±1S.E.

be facilitated by this stronger retention of N within the species over multiple generations, along with a lack of suppression of new *Typha* growth by *Typha* litter (Larkin et al., 2011).

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