

Does clonal resource translocation relate to invasiveness of *Typha* taxa? Results from a common garden experiment

Kenneth J. Elgersma^{a,*}, Radka Wildová^{a,b}, Jason P. Martina^{a,c,d}, William S. Currie^c, Deborah E. Goldberg^a

^a Department of Ecology & Evolutionary Biology, University of Michigan, 830 N. University Ave, Ann Arbor, MI 48109, USA

^b Ecological Research Institute, 676 Lapla Rd., Kingston, NY 12401, USA

^c School of Natural Resources & Environment, University of Michigan, 440 Church St., Ann Arbor, MI 48109, USA

^d Department of Mathematics and Sciences, Our Lady of the Lake University, San Antonio, TX 78207, USA

ARTICLE INFO

Article history:

Received 3 September 2014

Received in revised form 13 June 2015

Accepted 24 June 2015

Available online 29 June 2015

Keywords:

Cattails

Clonal integration

Plant invasion

Traits

Translocation

Community assembly

ABSTRACT

Plant species traits such as leaf and seed characteristics are increasingly used to understand drivers of species dominance and invasiveness. Because many plants are clonal, traits that influence the connectivity of clonal ramets might also be important in community assembly, species dominance, and invasion. We investigated the resource translocation (both amount of translocation and translocation distance) in three different native and non-native cattail (*Typha*) taxa that differ in their invasiveness by varying the initial amount of maternal resources available to clonal fragments and measuring their growth response in a field experiment. We found the non-native invasive taxa *Typha angustifolia* and *Typha x glauca* responded most strongly to increased maternal resource availability, and grew significantly more than the native *Typha latifolia*. *T. angustifolia* translocated resources to the largest number of daughter ramets, while *T. latifolia* translocated resources to the fewest and their hybrid (*T. x glauca*) was intermediate. These results are consistent with the hypothesis that resource translocation confers advantages for invasion and that the invasiveness of *Typha* taxa is related to clonal traits. Future studies and meta-analyses relating invasiveness to plant traits should consider clonal traits in addition to leaf and seed traits.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Clonal species dominate most herbaceous plant communities and many common invaders are clonal. Therefore clonal traits likely play an important role in community assembly and invasion; indeed several studies have demonstrated a link between clonality and invasion success (Ostrowski and Kenkel, 2008; Okada et al., 2009; Roiloa et al., 2010; Li and Wang, 2011; Dong et al., 2012). Though the importance of clonal traits is well-established, data on clonal traits in invasive plants are not as widely available as more commonly-measured leaf and seed characteristics (van Kleunen et al., 2010; but see Klimešová and de Bello, 2009).

The degree of clonal integration likely influences invasiveness because integration among ramets allows a single genetic individual (i.e., genet) to mitigate the negative consequences of spatial and temporal resource heterogeneity in highly variable environ-

ments. We define the degree of clonal integration as the extent to which stored or recently-obtained resources are shared between ramets. We consider two distinct traits that contribute to clonal integration; first, the amount of stored resources that are mobilized and translocated to other ramets, and second, the distance (measured in number of ramets) over which those resources are moved. Do only adjacent ramets transfer resources or does translocation extend to more distant ramets? Together, these traits enable ramets growing in unfavorable microsites to persist through resource subsidies from ramets in high-resource microsites (Schmid and Bazzaz, 1987; Poor et al., 2005; He et al., 2011; Eilts et al., 2011; Li and Wang, 2011; Gao et al., 2012). The benefit of translocation in heterogeneous environments is largely confirmed by population-level process models of clonal growth (Oborny et al., 2001; Herben, 2004; Oborny and Englert, 2012) and in experimental isotope tracer studies (Noble and Marshall, 1983; Callaghan, 1984; De Kroon et al., 1998; D'hertefeldt and Jónsdóttir, 1999; Santos, 2002). Thus, species that can translocate more resources to new ramet growth over greater distances are expected to be more successful in habitats with heterogeneous resources. Wetlands are highly heterogeneous habitats both spatially and temporally (Reddy and Delaune, 2008; Courtwright and Findlay, 2011). Clonal plants usu-

* Corresponding author. Present address: Department of Biology, University of Northern Iowa, 144 McCollum Science Hall, Cedar Falls, IA 50614, USA. Fax: +1 319 273 7125.

E-mail address: kenneth.elgersma@uni.edu (K.J. Elgersma).

ally dominate wetland vegetation, which may be partly due to the advantage clonality confers through resource translocation in these heterogeneous habitats (Santamaría, 2002; Song and Dong, 2002). Thus, interspecific variability in clonal traits such as clonal integration may especially affect dominance or invasiveness in heterogeneous wetlands (Sosnová et al., 2011).

Many wetlands in the Laurentian Great Lakes region of North America are highly dominated by cattails (*Typha* spp.), all of which grow through extensive clonal networks of underground rhizomes (Larkin et al., 2012; Farrer and Goldberg, 2014). *Typha latifolia* L. (broadleaf cattail) is a common clonal wetland plant native to North America that can dominate wetland plant communities in the region, especially in nutrient-rich areas (Kercher and Zedler, 2004). *Typha angustifolia* L. (narrowleaf cattail) is a cryptogenic wetland species that has recently invaded many wetlands from the Atlantic coast to the Laurentian Great Lakes region (Shih and Finkelstein, 2008). Though there is some uncertainty regarding this species' origins, molecular markers indicate it was most likely introduced to North America after European settlement (Ciotir et al., 2013), and expanded into the Laurentian Great Lakes region in the late 19th and early 20th centuries (Grace and Harrison, 1986). The hybrid between *T. latifolia* and *T. angustifolia*, *T. x glauca* Godr., is a highly competitive wetland invader in the Great Lakes region (Travis et al., 2010). It reduces species richness and increases litter mass, soil organic matter, and nutrient concentrations where it invades (Angeloni et al., 2006; Tuchman et al., 2009; Larkin et al., 2012; Farrer and Goldberg, 2014). While all three *Typha* taxa are clonal, the degree of clonal integration (as defined above) for these taxa is unknown. Furthermore, it is unknown whether taxon-specific differences in clonal attributes are correlated to differences in their dominance or their invasiveness in the region.

Based on our own and others' observations in the Laurentian Great Lakes region, we rank these from most prevalent and dominant to least prevalent as the following: *T. x glauca*, *T. angustifolia*, *T. latifolia* (Shih and Finkelstein, 2008). We hypothesize (1) more regionally-dominant *Typha* taxa translocate more resources to new ramets than less successful invaders, (2) in more dominant *Typha* taxa, a greater number of parent ramets contribute to each daughter ramet's growth, and (3) *Typha* taxa that translocate a greater amount of resources to a large number of daughter ramets have higher productivity. Thus, we expect *T. x glauca* to be the most productive and have the greatest amount of translocation from the largest number of parent ramets. We tested these hypotheses in the field by varying the mass of rhizomes (and thus the amount of maternal resources) available to individual genets of all three taxa, and measuring their growth responses. We measured growth of daughter ramets in the absence of interspecific competition in a low-nutrient environment to determine the potential for translocation.

2. Methods

2.1. Field experiment

Clonal fragments of the three *Typha* taxa were collected from a relatively nutrient-rich area of Cheboygan Marsh in northern lower Michigan, USA (see Tuchman et al., 2009 for site details). Fragments were collected in August 2004 by uprooting 15 rhizomes 15–30 cm long with associated stems (typically 1–2 stems per fragment) from each of 3 locations per taxon, for a total of 45 rhizome fragments for each of the three taxa. Species identification was later verified by microsatellite analysis (Snow et al., 2010). Rhizome fragments collected within one location were all located within 2 m of one another. To minimize maternal effects due to location differences, rhizomes were grown under identical conditions for two

years before the start of the field experiment. Rhizomes were initially grown in peat in a greenhouse at the University of Michigan Matthaei Botanical Gardens, Ann Arbor, MI, USA. At the start of the 2006 growing season, all plants were transferred into an experimental garden and grown in a common soil (Rubicon series sand with 10% commercial reed-sedge peat added) at the University of Michigan Biological Station (Pellston, MI) during the 2006 growing season. In May 2007, plants were removed from the common garden, and carefully washed to remove soil from rhizomes and roots. We removed lateral buds from the washed plants to obtain unbranched linear rhizome fragments of varying sizes (see below).

To study the influence of clonal integration on subsequent expansion, we measured all linear rhizome fragments and sorted them by the number and size of rhizome segments, where 'segments' are defined as a piece of rhizome between existing (live or dead) stems (Fig. 1). Note that segments are not synonymous with rhizome internodes because each segment typically contained several internodes (Fig. 1). The length of rhizome fragments ranged from 1 to 68 cm (Mean = 15.5 cm, S.D. = 11.2 cm) and 1–5 rhizome segments. This experimental treatment resulted in differences in both the total amount of resources available for clonal growth and the potential distance over which resources could be translocated.

The youngest end of each linear rhizome fragment (hereafter 'genet') ended with a young stem and a new bud (Fig. 1) and was then designated as the expanding end. All other rhizome buds along the length of the rhizome were removed with a razor blade to ensure the initial expansion of the genet branched out from a single point of expansion. Before planting, the height and diameter of each young stem was recorded, as well as the diameter and length of each rhizome segment. All other stems along the rhizome were senescent from the previous growing season and were cut at 50 cm before planting. All genets were planted on 5 June 2007 in a recently-exposed, completely unvegetated sandy area at Pointe La Barbe Marsh, MI, USA (45° 50' 36" N, 84° 44' 54" W), an oligotrophic Lacustrine Protected Embayment (sensu Albert et al., 2005). Because little photosynthetic tissue was present at the time of planting and nutrients were extremely scarce in this sandy oligotrophic soil, most growth immediately after planting was necessarily due to resource translocation. Three genets per taxon were planted into each of 15 blocks, for a total of 135 planted genets. Within each 6 m × 6 m block, we established a grid of 2 m × 2 m plots and planted one genet into each plot. We used a Latin square design within each block to ensure each taxon occurred in exactly one row and one column of the 3 × 3 grid, and selected genets to ensure a relatively even distribution of rhizome sizes across the blocks. Rhizomes were planted 5 cm below the soil surface. We characterized the soil before planting by collecting and compositing 3 randomly-placed soil samples (5 cm depth) from each block. Compositing soil samples were analyzed for total C and N, soil organic matter (measured as loss on ignition after 4 h at 500 °C), and soil texture (Buchanan et al., 1993). The soil at this site was sandy and very nutrient poor, containing on average only 4.7% (±0.7% standard deviation) silt and 2.3% (±0.4%) clay content, very low organic matter (0.4% ± 0.2%), low total nitrogen (0.03% ± 0.01%), and a high C/N ratio (79 ± 23).

After planting, the above- and below-ground biomass of each genet was non-destructively estimated throughout two growing seasons by surveying the number and size of aboveground stems of each genet. Stem heights were measured six times (27 June 2007, 17 July 2007, 28 July 2007, 29 August 2007, 25 May 2008, and 14 August 2008) and stem diameters were also measured during the last four surveys. On each survey date, individual stems were mapped, and new stems were tagged. Live stems present at the time of planting were tagged during the planting process. These numbered tags enabled us to track the growth and survival of individual ramets, as well as growth and survival of whole genets,

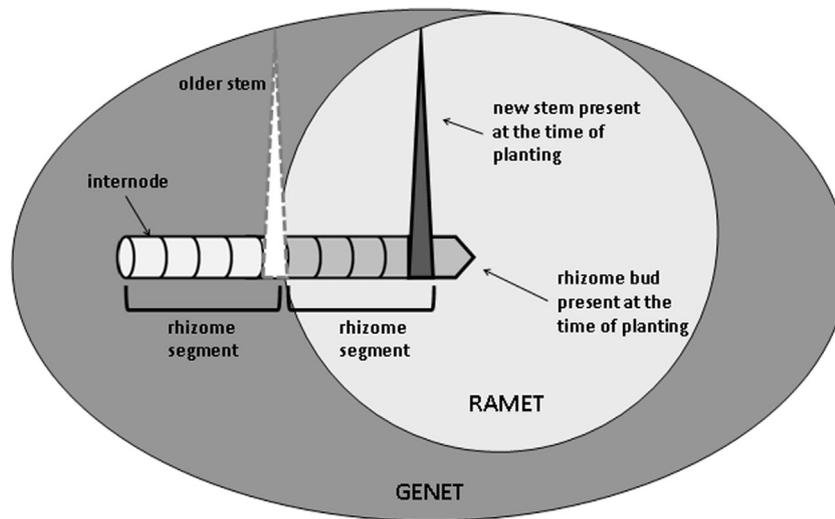


Fig. 1. Schematic diagram of terminology used for different components of an individual *Typha* fragment. Rhizome segments are defined as the length of rhizome between two consecutive stems (live or dead). Rhizome segments are usually comprised of multiple nodes and internodes. Ramets are defined as the aboveground stem (live or dead) plus the rhizome segment which produced that aboveground stem. The genet is defined simply as all physically connected ramets.

through the two growing seasons. Immediately after the last survey date (14 August 2008), all aboveground ramets and belowground rhizomes were harvested completely, washed, dried at 60 °C to constant mass, and weighed. Roots below 20 cm were not excavated because it would be impractical in this large field experiment and rhizome biomass is a large portion of the total belowground biomass for these taxa (Asaeda et al., 2008). For a subset of the genets harvested at the last survey, the length and diameter of each individual stem and rhizome segment between each stem was measured before drying, and then individual stems and rhizome segments were weighed separately to determine allometric relationships for each taxon so that biomass could be non-destructively estimated at census dates before the final harvest.

2.2. Data analysis

To estimate ramet biomass from stem measurements, we developed allometric relationships for each taxon between non-destructive stem measurements (height and diameter) and biomass measured by destructive harvest. Individual stem heights and diameters from 159 ramets (at least 44 ramets per taxon) were related to total biomass of the ramet (biomass of stem + rhizome that produced that stem; hereafter 'total biomass'). We used these regressions to estimate total biomass at each survey date. These estimates of total biomass were highly correlated to the actual total biomass of the genets harvested in the last survey (overall $R^2_{\text{prediction}} = 0.96$, $r > 0.95$ for all taxa). Production of new biomass on each survey date was determined using these regression equations to estimate the biomass of all new stems that were measured. We used the estimated initial biomass and estimated biomass production to calculate growth rates for subsequent analyses.

Because lateral buds were removed from the rhizome before planting, all genets initially expanded uni-directionally outward from the single meristem at the youngest end of the genet. To estimate the amount of translocation during this expansion, we regressed the growth rate of new ramets against the genet's initial biomass, and used the slope of the regression line as an index of translocation, where a greater slope indicates more translocation. It is important to note that because plants initially had little or no photosynthetic biomass at the time of planting, initial growth most likely arose from translocation. Furthermore, this slope is a good index of translocation during the very initial stages of growth when little or no photosynthesis is occurring, but as the genet grew

and accumulated photosynthetic tissue that contributed to growth, we expect the index to become less tightly linked to translocation. In addition, we expected the signal-to-noise ratio of translocation to be highest initially, but diminished as other ecological processes (e.g., herbivory, disturbance) became relatively more influential. Thus, we used analysis of variance (ANOVA) only on data from the first field survey to test for differences between taxa in estimated translocation. We also used repeated-measures ANOVA to test for the expected decline over time in the relationship between initial biomass and new growth.

To determine if resources were translocated only from the rhizome segment immediately adjacent to the expanding meristem or if additional resources also came from more distant rhizome segments, we fit 5 candidate regression models using initial biomass of a portion of each genet to predict new growth during the first growing season. The first candidate model used only the biomass of the rhizome segment immediately adjacent to the expanding meristem to predict clonal growth. The second candidate model used the sum of the biomass of the two segments nearest the expanding meristem to explain the growth of the genet. Similarly, the third, fourth, and fifth models used the sum of the biomass of the three, four, or five closest segments, respectively, to explain clonal growth rates. These 5 candidate models were ranked using Akaike's Information Criterion (AIC). Because all 5 candidate models had the same number of parameters, the model with the lowest AIC score corresponded to the model with the greatest likelihood (Burnham and Anderson, 2002), and we selected this model as the 'best' model. We also used model averaging to combine predictions for the top-ranking models with $\Delta\text{AIC} < 2$. We repeated this process independently for each of the three *Typha* taxa. This statistical model selection process therefore determines the most likely number of ramets contributing to new growth for each taxon, an estimate of resource translocation distance.

All analyses were conducted in R version 3.0.1 (R Core Team, 2013), and Box-Cox transformations were used when needed to fit assumptions of the models.

3. Results

3.1. Overall plant growth and survival

Despite the low-nutrient conditions in the field, genet survival was high and unaffected by the initial genet size at the time of

Table 1

Mean (standard deviation) initial and final biomass of the rhizome fragments after two growing seasons, and the number of ramets and distance between ramets within individuals. Means are total (aboveground + rhizome) biomass, but do not include root mass, which was relatively small. Different superscript letters within a column indicate significant post-hoc comparisons between species using Tukey's HSD. Sample size (*N*) at the start of the experiment was 45 for each taxon, but mortality reduced *N* by the end of the experiment to the numbers reported.

Taxon	<i>N</i>	Initial mass (g)	Final mass (g)	Final # of ramets per individual	Distance between connected ramets (cm)
<i>T. angustifolia</i>	42	3.67 (1.38) ^A	28.19 (19.00) ^M	5.06 (2.82) ^Q	5.23 (3.21) ^Y
<i>T. x glauca</i>	43	3.55 (1.37) ^A	30.14 (20.98) ^M	5.57 (3.33) ^Q	8.65 (4.94) ^Z
<i>T. latifolia</i>	42	4.13 (2.68) ^A	18.44 (10.90) ^N	4.19 (1.80) ^Q	10.27 (5.40) ^Z

Table 2

ANOVA of the effect of initial biomass and *Typha* taxa on new biomass production during the first three weeks after planting. Initial biomass of each genet was estimated based on stem and rhizome length and diameter measured at the time of planting. New biomass production was estimated based on the height and diameter of all new stems surveyed on 27 June 2007.

Source	Df	<i>R</i> ² _{partial}	<i>F</i>	<i>P</i>
Initial biomass	1	0.034	5.648	0.019
Taxon	2	0.178	14.76	<0.0001
Initial biomass × Taxon	2	0.036	2.980	0.054
Error	125	0.752		

planting. Overall, 127 of 135 genets (94%) survived through the end of the experiment. Neither survival nor initial biomass differed among the taxa ($p > 0.10$), but biomass production did ($p = 0.004$), with *T. angustifolia* and *T. x glauca* producing 72% and 80% more biomass, respectively, compared to *T. latifolia* after two growing seasons (Table 1).

3.2. Amount of translocation

The initial biomass of the whole genet at the time of planting was a strong predictor of the amount of biomass accrued initially ($p = 0.019$, Table 2, Fig. 2), confirming that initial growth was fueled by translocation. As expected, the strength of this relationship declined significantly over time ($p = 0.005$, Table 3) and was not significant in the second (2008) growing season for any species (Fig. 2). The strength of the relationship differed initially among the three taxa ($p = 0.054$, Table 2), largely due to the consistently stronger responses of *T. angustifolia* and *T. x glauca* (Fig. 2). The three taxa also differed in the timing of response to initial biomass ($p = 0.005$, Table 3). Both *T. x glauca* and *T. angustifolia* responded rapidly, showing the largest effect sizes on the first survey date. *T. x glauca*'s response was strongest and most consistent, while *T. angustifolia*'s initial response was strong but highly variable and first became significant on the second survey date. In contrast, the native *T. latifolia* showed a consistently small and usually insignificant response to initial biomass, indicating little translocation to daughter ramets on any date. This ranking confirmed our hypothesis based on prior observations of dominance in the Great Lakes region (*T. x glauca* > *T. angustifolia* > *T. latifolia*).

Table 3

Repeated measures ANOVA of the effect of initial biomass on new biomass production during the first growing season. Initial biomass of each genet was estimated based on stem and rhizome length and diameter measured at the time of planting. New biomass production was estimated based on the height and diameter of all new stems surveyed on 27 June, 17 July, 28 July, and 29 August 2007.

	Df	Wilks'λ	<i>F</i>	<i>p</i>
Between-date factors				
Initial biomass	1, 125	0.834	24.88	<0.0001
Taxon	2, 125	0.854	10.70	<0.0001
Initial biomass × Taxon	2, 125	0.935	4.341	0.0150
Within-date factors				
Initial biomass × time	3, 123	0.902	4.450	0.0053
Taxon × time	6, 246	0.873	2.882	0.0099
Initial biomass × Taxon × Time	6, 246	0.951	1.050	0.3937

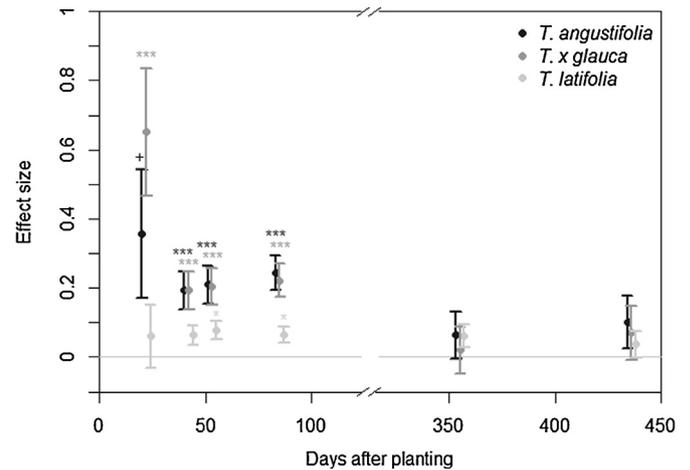


Fig. 2. The regression coefficients (± 1 SE) for the effect of initial biomass on subsequent clonal biomass production. Plants were measured at 22, 42, 53, 85, 355, and 436 days after planting (27 June 2007, 17 July 2007, 28 July 2007, 29 August 2007, 25 May 2008, and 14 August 2008, respectively), but x-axis values are jittered for clarity. Large effect sizes (regression coefficients) indicate strong responses to initial biomass, evidence for translocation of parental resources to new growth. Effect sizes significantly greater than zero are indicated by asterisks (+ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

3.3. Distance of translocation

AIC model selection indicated that the most likely number of rhizome segments (parent ramets) contributing to translocation to growth over the season differed among the three *Typha* taxa. With the best-fit model for each taxon, rhizome biomass (estimated by regression from rhizome length and diameter) explained 35–46% of the variance in new growth. For the native *T. latifolia*, the best predictor of new growth rate (lowest AIC score and greatest likelihood) was the initial biomass of the two rhizome segments closest to the growing ramets; models which used only the closest rhizome segment or the closest three rhizome segments to predict growth performed nearly as well ($\Delta AIC < 2$, Table 4). Model averaging of these three top-ranked candidate models resulted in a model that accounted for the initial biomass of the closest 1.9 rhizome segments. In contrast, for *T. angustifolia* and *T. x glauca*, factoring in the biomass of rhizome segments further away from the growing

Table 4

Δ AIC model scores of 5 candidate regression models to explain the production of new biomass during the first (2007) growing season. 1st rhizome segment refers to the segment closest to the growing stem, while the 5th is furthest away. Lower scores indicate better fit to the data. Models were assessed separately for each of the three taxa. The top-ranked models for *T. angustifolia*, *T. x glauca*, and *T. latifolia* explained 37%, 46%, and 35% of the data, respectively.

Candidate model	Δ AIC		
	<i>T. angustifolia</i>	<i>T. x glauca</i>	<i>T. latifolia</i>
1st rhizome segment	14.04	13.35	0.54
1st + 2nd rhizome segments	11.91	11.73	0
1st through 3rd rhizome segments	9.64	0	1.64
1st through 4th rhizome segments	2.92	1.91	5.88
1st through 5th rhizome segments	0	1.91	5.88

ramet increased the amount of variance explained and improved model fit. *T. angustifolia* new ramet growth was best explained by the cumulative biomass of all five segments of the initial rhizome, while the growth of new *T. x glauca* ramets was best predicted by the cumulative biomass of the three closest rhizome segments. Model averaging of the top-ranked candidate models for *T. x glauca* resulted in a model that accounted for the initial biomass of the first 3.7 rhizome segments.

4. Discussion

T. angustifolia and *T. x glauca* exhibited the fastest overall growth rates and the strongest effect of initial biomass during the first few weeks of growth. We interpret this rapid initial growth as evidence for higher translocation of maternal resources, especially in *T. x glauca*. Only the native *T. latifolia* had a significantly lower overall growth response to its initial genet biomass. Sullivan et al. (2010) also found that in the control treatment of an experiment, *T. angustifolia* and *T. x glauca* produced twice as much stem biomass per unit rhizome biomass than *T. latifolia* did, although their study integrated growth over the entire growing season and did not isolate effects of initial translocation. Nevertheless, results from both that study and the present are consistent with the hypothesis that *T. x glauca* and *T. angustifolia* either mobilize a greater amount of resources per unit biomass to subsidize new growth, or they use mobilized resources more efficiently, thereby producing more biomass per unit resource than *T. latifolia*. In either case, these results show that maternal subsidies drive more rapid growth in *T. x glauca* and *T. angustifolia* than in *T. latifolia*.

More efficient use of maternal resources in *T. x glauca* and *T. angustifolia* could result if these two taxa have higher rates of nutrient resorption during senescence of aboveground tissues, freeing these remobilized nutrients to subsidize new ramet growth (Rejmánková, 2005). However, since there was little live aboveground biomass in our study at the time of planting, differential nutrient resorption likely did not play a large role. Another possible mechanism is that the non-native taxa may have a greater proportion of non-structural carbon in their rhizomes (Asaeda et al., 2008; Tursun et al., 2011). While our experiment did not separate these two mechanisms, tracer studies could be used to determine the balance between them and whether that balance differs among taxa.

In addition to these possible differences in efficiency, *Typha* taxa may also differ in the absolute amount of resources translocated, either due to more resources coming from the parent ramet or due to more parent ramets (rhizome segments) contributing to daughter ramet growth. We found evidence for the latter; new growth in *T. angustifolia* was related to the biomass of the entire rhizome fragment planted (up to 5 rhizome segments), but growth of *T. latifolia* was only related to the biomass of the two closest segments. *T.*

x glauca, which is primarily an F1 hybrid between *T. latifolia* and *T. angustifolia* (Snow et al., 2010), was intermediate between its two parent species.

We expected the taxa that could translocate resources further would also translocate more resources because a greater number of segments contributing resources might increase the total amount of resources contributed to new growth. While this expectation was partially supported (*T. latifolia* had both the smallest number of contributing ramets and lowest total amount of translocation), the largest number of contributing ramets was found in *T. angustifolia* (Table 4), while *T. x glauca* exhibited the highest amount of translocation (Fig. 2). It is interesting that *T. x glauca* invests a greater amount in translocation of maternal subsidies than either parent taxa, but its translocation distance is intermediate between its two parent taxa.

Because *T. angustifolia* and *T. x glauca* showed evidence of translocation over a greater number of rhizome segments than *T. latifolia*, these two taxa should have a relatively greater competitive advantage in patchy environments (Hartnett and Bazzaz, 1983; Alpert et al., 2003; Herben et al., 2004; He et al., 2011; Song et al., 2013). However, maintenance of clonal connections does incur a cost under some environmental conditions (Friedman and Alpert, 1991; Hay and Kelly, 2007), so *T. latifolia* may have responded to adaptive pressures by reducing resource translocation. The evidently lower reliance on maternal subsidies in *T. latifolia* might be a factor related to its lower current abundance and lower dominance in Great Lakes coastal wetlands, where disturbances and fluctuating lake levels can result in unvegetated ground that is open to invasion (Lishawa et al., 2010; Larkin et al., 2012). Wisgerhof (2009) found that *T. angustifolia* tolerated fluctuations in water levels better than *T. latifolia*. If greater use of maternal subsidies allows a more rapid expansion into newly-exposed unvegetated ground, then the clonal trait differences revealed in our study may help explain *T. angustifolia*'s higher tolerance to water level fluctuations.

Measuring clonal subsidies in field studies in a realistic way poses difficult logistical challenges. The majority of studies measure subsidies by comparing the growth of genets with severed versus unsevered rhizomes, but severing rhizomes can itself induce physiological changes and introduce pathways for pathogens (Hay and Kelly, 2007). While our field study used severed rhizomes, all rhizomes experienced the same amount of manipulation, so we do not expect this affected our conclusions.

The findings in this study provide evidence that the two non-native *Typha* taxa in the Great Lakes region exhibit a higher investment in clonal subsidies, with a greater number of parent ramets subsidizing daughter ramet growth than the native *Typha latifolia* which is currently less dominant. A recent meta-analysis showed equivocal support for the theory that high investment in clonal subsidies contributes globally to invasiveness, though investment in clonal subsidies did increase plant biomass (Song et al., 2013), and investment in clonal subsidies has been linked to invasiveness of several other invasive herbaceous species (Yu et al., 2009; Aguilera et al., 2010). While our field study, which is correlational in nature, cannot mechanistically establish the causality underlying the observed results, our results are nevertheless consistent with the hypothesis that greater translocation in *T. angustifolia* and *T. x glauca* contributes to invasiveness in Great Lakes wetlands.

Acknowledgments

We thank Emily Farrer, Nicolás Cabrera-Schneider, Lauren Sullivan, and Laurel Billings for their help in the field and laboratory. Comments from two anonymous reviewers greatly improved the manuscript. This work was supported through funding from

the University of Michigan and NASA ROSES program grant NNX11AC72G. The authors declare no conflicts of interest.

References

- Angeloni, N.L., Jankowski, K.J., Tuchman, N.C., Kelly, J.J., 2006. Effects of an invasive cattail species (*Typha x glauca*) on sediment nitrogen and microbial community composition in a freshwater wetland. *FEMS Microbiol. Lett.* 263, 86–92.
- Aguilera, A.G., Alpert, P., Duker, J.S., Harrington, R., 2010. Impacts of the invasive plant *Fallopia japonica* (Houtt.) on plant communities and ecosystem processes. *Biol. Invasions* 12, 1243–1252.
- Albert, D.A., Wilcox, D.A., Ingram, J.W., Thompson, T.A., 2005. Hydrogeomorphic classification for Great Lakes coastal wetlands. *J. Great Lakes Res.* 31, 129–146.
- Alpert, P., Holzapfel, C., Slominski, C., 2003. Differences in performance between genotypes of *Fragaria chiloensis* with different degrees of resource sharing. *J. Ecol.* 91, 27–35.
- Asaeda, T., Sharma, P., Rajapakse, L., 2008. Seasonal patterns of carbohydrate translocation and synthesis of structural carbon components in *Typha angustifolia*. *Hydrobiologia* 607, 87–101.
- Buchanan, B., Khresat, S., Lindemann, W., Pelletier-Hunyadi, M., Purves, P., Shelton, P., Vinson, J., Williams, B., Jones, T., McCaslin, B., 1993. Introduction to Soils: A Laboratory Manual, 7th edn. New Mexico State University, Las Cruces, NM, USA.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multi-Model Inference*, 2nd ed. Springer, New York.
- Callaghan, T., 1984. Growth and translocation in a clonal southern hemisphere sedge, *Uncinia meridensis*. *J. Ecol.* 72, 529–546.
- Ciotir, C., Kirk, H., Row, J.R., Freeland, J.R., 2013. Intercontinental dispersal of *Typha angustifolia* and *T. latifolia* between Europe and North America has implications for *Typha* invasions. *Biol. Invasions* 15, 1377–1390.
- Courtwright, J., Findlay, S.E.G., 2011. Effects of microtopography on hydrology, physicochemistry, and vegetation in a tidal swamp of the Hudson River. *Wetlands* 31, 239–249.
- De Kroon, H., Van der Zalm, E., Van Rheenen, J., Van Dijk, A., Freulen, R., 1998. The interaction between water and nitrogen translocation in a rhizomatous sedge (*Carex flacca*). *Oecologia* 116, 38–49.
- D'hertefeldt, T., Jónsdóttir, I., 1999. Extensive physiological integration in intact clonal systems of *Carex arenaria*. *J. Ecol.* 87, 258–264.
- Dong, B.C., Alpert, P., Guo, W., Yu, F.H., 2012. Effects of fragmentation on the survival and growth of the invasive, clonal plant *Alternanthera philoxeroides*. *Biol. Invasions* 14, 1101–1110.
- Eilts, J.A., Mittelbach, G.G., Reynolds, H.L., Gross, K.L., 2011. Resource heterogeneity, soil fertility, and species diversity: effects of clonal species on plant communities. *Am. Nat.* 177, 574–588.
- Farrer, E., Goldberg, D.E., 2014. Mechanisms and reversibility of the effects of hybrid cattail on a Great Lakes marsh. *Aquat. Bot.* 116, 35–43.
- Friedman, D., Alpert, P., 1991. Reciprocal transport between ramets increases growth of *Fragaria chiloensis* when light and nitrogen occur in separate patches but only if patches are rich. *Oecologia* 86, 76–80.
- Gao, Y., Xing, F., Jin, Y., Nie, D., Wang, Y., 2012. Foraging responses of clonal plants to multi-patch environmental heterogeneity: spatial preference and temporal reversibility. *Plant Soil* 359, 137–147.
- Grace, J.B., Harrison, J.S., 1986. The Biology of Canadian Weeds. 73. *Typha latifolia* L., *Typha angustifolia* L. and *Typha x glauca* Godr. *Can. J. Plant Sci.* 66, 361–379.
- Hartnett, D.C., Bazzaz, F.A., 1983. Physiological integration among intracolonial ramets in *Solidago canadensis*. *Ecology* 64, 779–788.
- Hay, M.J.M., Kelly, C.K., 2007. Have clonal plant biologists got it wrong? The case for changing the emphasis to disintegration. *Evol. Ecol.* 22, 461–465.
- He, W.-M., Alpert, P., Yu, F.-H., Zhang, L.-L., Dong, M., 2011. Reciprocal and coincident patchiness of multiple resources differentially affect benefits of clonal integration in two perennial plants. *J. Ecol.* 99, 1202–1210.
- Herben, T., 2004. Physiological integration affects growth form and competitive ability in clonal plants. *Evol. Ecol.* 18, 493–520.
- Herben, T., Mandák, B., Bímová, K., Münzbergová, Z., 2004. Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology* 85, 3223–3233.
- Kercher, S., Zedler, J., 2004. Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species. *Aquat. Bot.* 80, 89–102.
- Klimešová, J., de Bello, F., 2009. CLO-PLA: the database of clonal and bud bank traits of Central European flora. *J. Veg. Sci.* 20, 511–516.
- Larkin, D.J., Freyman, M.J., Lishawa, S.C., Geddes, P., Tuchman, N.C., 2012. Mechanisms of dominance by the invasive hybrid cattail *Typha x glauca*. *Biol. Invasions* 14, 65–77.
- Li, W., Wang, J., 2011. Influence of light and nitrate assimilation on the growth strategy in clonal weed *Eichhornia crassipes*. *Aquat. Ecol.* 45, 1–9.
- Lishawa, S.C., Albert, D.A., Tuchman, N.C., 2010. Water level decline promotes *Typha x glauca* establishment and vegetation change in Great Lakes coastal wetlands. *Wetlands* 30, 1085–1096.
- Noble, J., Marshall, C., 1983. The population biology of plants with clonal growth II. The nutrient strategy and modular physiology of *Carex arenaria*. *J. Ecol.* 71, 865–877.
- Oborny, B., Englert, P., 2012. Plant growth and foraging for a patchy resource: a credit model. *Ecol. Model.* 234, 20–30.
- Oborny, B., Czárán, T., Kun, Á., 2001. Exploration and exploitation of resource patches by clonal growth: a spatial model on the effect of transport between modules. *Ecol. Model.* 141, 151–169.
- Okada, M., Grewell, B.J., Jasieniuk, M., 2009. Clonal spread of invasive *Ludwigia hexapetala* and *L. grandiflora* in freshwater wetlands of California. *Aquat. Bot.* 91, 123–129.
- Otfinowski, R., Kenkel, N.C., 2008. Clonal integration facilitates the proliferation of smooth brome clones invading northern fescue prairies. *Plant Ecol.* 199, 235–242.
- Poor, A., Hershock, C., Rosella, K., Goldberg, D.E., 2005. Do physiological integration and soil heterogeneity influence the clonal growth and foraging of *Schoenoplectus pungens*. *Plant Ecol.* 181, 45–56.
- R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org/>
- Reddy, K.R., Delaune, R.D., 2008. *Biogeochemistry of Wetlands*. CRC Press, Boca Raton.
- Rejmánková, E., 2005. Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. *New Phytol.* 167, 471–482.
- Roiloa, S.R., Rodríguez-Echeverría, S., Peña, E., Freitas, H., 2009. Physiological integration increases the survival and growth of the clonal invader *Carpobrotus edulis*. *Biol. Invasions* 12, 1815–1823, 2010.
- Santamaría, L., 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecol.* 23, 137–154.
- Santos, P.M., 2002. Nitrogen dynamics in the intact grasses *Poa trivialis* and *Panicum maximum* receiving contrasting supplies of nitrogen. *J. Exp. Bot.* 53, 2167–2176.
- Schmid, B., Bazzaz, F.A., 1987. Clonal integration and population structure in perennials: effects of severing rhizome connections. *Ecology* 68, 2016–2022.
- Shih, J.G., Finkelstein, S.A., 2008. Range dynamics and invasive tendencies in *Typha latifolia* and *Typha angustifolia* in Eastern North America derived from herbarium and pollen records. *Wetlands* 28, 1–16.
- Snow, A.A., Travis, S.E., Wildová, R., Fér, T., Sweeney, P.M., Marburger, J.E., Windels, S., Kubátová, B., Goldberg, D.E., Mutegi, E., 2010. Species-specific SSR alleles for studies of hybrid cattails (*Typha latifolia* x *T. angustifolia*; Typhaceae) in North America. *Am. J. Bot.* 97, 2061–2067.
- Song, Y.-B., Yu, F.-H., Keser, L.H., Dawson, W., Fischer, M., Dong, M., Van Kleunen, M., 2013. United we stand, divided we fall: a meta-analysis of experiments on clonal integration and its relationship to invasiveness. *Oecologia* 171, 317–327.
- Song, M., Dong, M., 2002. Clonal plants and plant species diversity in wetland ecosystems in China. *J. Veg. Sci.* 13, 237–244.
- Sosnová, M., Van Diggelen, R., Macek, P., Klimešová, J., 2011. Distribution of clonal growth traits among wetland habitats. *Aquat. Bot.* 95, 88–93.
- Sullivan, L., Wildová, R., Goldberg, D., Vogel, C., 2010. Growth of three cattail (*Typha*) taxa in response to elevated CO₂. *Plant Ecol.* 207, 121–129.
- Travis, S.E., Marburger, J.E., Windels, S., Kubátová, B., 2010. Hybridization dynamics of invasive cattail (Typhaceae) stands in the Western Great Lakes Region of North America: a molecular analysis. *J. Ecol.* 98, 7–16.
- Tuchman, N.C., Geddes, P., Larkin, D., Wildová, R., Jankowski, K.J., Goldberg, D.E., 2009. Patterns of environmental change associated with *Typha x glauca* invasion in a Great Lakes coastal wetland. *Wetlands* 29, 964–975.
- Tursun, N., Seyithanoglu, M., Uygun, F.N., Elibuyuk, I.O., Elibuyuk, E.A., 2011. Seasonal dynamics of soluble carbohydrates in rhizomes of *Phragmites australis* and *Typha latifolia*. *Flora* 206, 731–735.
- van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* 13, 235–245.
- Wisgerhof, V.J., 2009. *Helophyte Zonation in Tidal Freshwater Wetlands*. MS thesis, Utrecht University.
- Yu, F.-H., Wang, N., Alpert, P., He, W.-M., Dong, M., 2009. Physiological integration in an introduced, invasive plant increases its spread into experimental communities and modifies their structure. *Am. J. Bot.* 96, 1983–1989.