The invasiveness of the cattail hybrid *Typha x glauca*: a study of seedling growth rates

Stephanie Levy
stephlev@umich.edu
Mentor: Allison Snow
Aug 17, 2007

Abstract

Hybridization may play an important role in the formation of invasive species (Ellstrand and Schierenbeck 2000). Throughout North American wetlands the native cattail species *Typha latifolia* is hybridizing with the introduced species *Typha angustifolia*. It has been suggested that the hybrid cattail species *Typha x glauca* is experiencing hybrid vigor and is therefore more invasive than its parent taxa. The objective of this study was to examine whether *Typha x glauca* is in fact more invasive than its parent taxa by studying the growth patterns of *Typha* seedlings. The seedlings used in this experiment fit into five different species groups: *T. angustifolia*, *T. latifolia*, hybrids produced by pollinating T. *angustifolia* with *T. latifolia*, hybrids produced by pollinating *T. latifolia* with *T. angustifolia*, and backcrosses produced by pollinating *T. x glauca* with *T. angustifolia*. This study consisted of a factorial design experiment that manipulated the environmental conditions of soil moisture and soil nutrients. Data from a previous study examining variation in percent germination between *T. latifolia*, *T. angustifolia* and *T. x glauca* was analyzed. The data from the seedling experiment did not suggest that the F1 *T. x glauca* seedlings were experiencing hybrid vigor. Instead, the T. x glauca backcross seedlings were the most successful. Further research should be conducted examining the success of advanced hybrids.

Introduction

Since species are continuously introduced to new environments due to anthropogenic interference, it has become increasingly important to understand how hybridization between previously separated organisms will affect populations, communities, and ecosystems. Additionally, the movement of organisms' distribution ranges caused by recent global warming will also lead to new opportunities for hybridization. It has been proposed that hybridization may possibly serve as a stimulus for the evolution of invasiveness, at least in some cases. Hybrids may exhibit higher fitness than their parent taxa through mechanisms such as evolutionary novelty, greater genetic variation, fixed heterosis, and dumping of genetic load (Ellstrand and Schierenbeck 2000). For example, studies suggest that the hybrid between introduced *Carpobrotus edulis* and native *C. chilensis* found along the coast of California exhibits hybrid vigor for vegetative growth and greater resistance to mammalian herbivory than its parent taxa, and therefore is highly invasive (Vilà and D'Antonio 1998).

Similarly, in wetlands across North America, hybridization is occurring between the native cattail *Typha latifolia* and the introduced European species *T. angustifolia* (Kuehn *et al*. 1999). It has been reported that the cattail hybrid, *T. x glauca* may be more invasive than its parent species (Galatowitsch *et al*. 1999), however very little research has been done to investigate this possibility. *T. x glauca* often exists in semi-sterile F1 hybrid stands with very few advanced hybrids (Smith 1967, Kuehn *et al*. 1999). Previous research suggests that *T. latifolia* can out-compete *T. angustifolia* in shallow water due to their higher leaf surface area, while *T. angustifolia* is more tolerant of deeper water due to their larger rhizome size and taller leaves (Grace and Wetzel 1981). It has been suggested that *T. x glauca* is very successful in areas of high nutrients, such as urban wetlands (Woo and Zedler 2002). No studies have been conducted to examine whether *T. x glauca* is exhibiting a form of hybrid vigor.

The objective of this study was to help determine whether hybrid cattail progeny grow faster and tolerate stress better than parent taxa by examining average plant size of seedlings that were subjected to various environmental conditions. Variation in the proportion of germinating seeds between taxa was also studied. By examining differences between *T. latifolia, T. angustifolia* and *T. x glauca*, we were able further inspect the role of hybridization in producing invasive species.

Materials and Methods

In this study, potted *Typha* seedlings were used in a factorial design experiment (See Table 1). Five different species groups were tested: *T. angustifolia, T. latifolia*, hybrids produced by pollinating

T. *angustifolia* with *T. latifolia*, hybrids produced by pollinating *T. latifolia* with *T. angustifolia*, and backcrosses produced by pollinating *T. x glauca* with *T. angustifolia*. The seeds of the hybrids and the backcross were the result of hand pollinations of cattails that were identified by RAPD markers, while the *T. latifolia* and *T. angustifolia* seeds were the products of open pollinations. The female spikes used in the hand pollinations were pollinated by one paternal plant for each species. The number of maternal families for each species group was as follows: *T. angustifolia* seeds consisted of a single maternal parent, *T. angustifolia* hybrid seeds consisted of three maternal families, *T. glauca* backcross seeds consisted of one maternal parent, *T. latifolia* seeds consisted of three maternal parents, and *T. latifolia* hybrid seeds consisted of two maternal families (See Table 2). The parent cattails occurred in Columbus, Ohio. On June 29, 2007 the seeds were planted in trays of moist Hyponex Potting Soil® and stored in a greenhouse, and three days later the seeds germinated. The seedlings were then transplanted into individual 16 oz. polystyrene cups from July 13, 2007 to July 19, 2007 and their initial heights were measured on July 23, 2007.

Table 1. Setup of the factorial design experiment and sample sizes. Maternal species is listed for the hybrids.

Low nutrients + Flooded		**High nutrients + Flooded**	
Species group	Number of pots	Species group	Number of pots
T. angustifolia	28	*T. angustifolia*	22
T. angustifolia hybrid	21	*T. angustifolia* hybrid	21
T. glauca backcross	22	*T. glauca* backcross	26
T. latifolia	23	*T. latifolia*	22
T. latifolia hybrid	25	*T. latifolia* hybrid	26
Low nutrients + Fluctuating		**High nutrients + Fluctuating**	
Species group	Number of pots	Species group	Number of pots
T. angustifolia	23	*T. angustifolia*	21
T. angustifolia hybrid	20	*T. angustifolia* hybrid	24
T. glauca backcross	22	*T. glauca* backcross	26
T. latifolia	17	*T. latifolia*	22
T. latifolia hybrid	24	*T. latifolia* hybrid	25

Table 2. Number of maternal families for each species group.

Species Group	**Number of Maternal Families**
T. angustifolia	1
T. angustifolia hybrid	3
T. glauca backcross	1
T. latifolia	3
T. latifolia hybrid	2

Two environmental conditions were manipulated – soil fertility and soil moisture. The soil fertility condition consisted of two treatments: higher soil nutrients and lower soil nutrients. All seedlings were potted with topsoil mixed with peat in a 3:1 ratio. Miracle Grow Pour and Feed Plant Food® was diluted with water in a 3:1 ratio, and 60 mL was added to each of the seedlings undergoing the higher soil nutrients treatment on July 24, 2007. The soil moisture condition consisted of a flooded treatment and a fluctuating water treatment. Pots undergoing the fluctuating water treatment contained 11 small holes to drain them. The seedlings were grown outside starting July 26, 2007. The heights of the seedlings were measured Aug 2, 2007 and Aug 12, 2007. In order to analyze the data from the potted plant experiment, an Analysis of Variance (ANOVA) was used to test the main effects of Group, Nutrients, Water and interactions among these variables. Means of species groups in the same

environmental conditions were compared using a Tukey test. Further analyses were carried out to test for differences among maternal plants.

I also analyzed data from a study examining percent germination of *T. latifolia*, *T. angustifolia* and *T. x glauca* (data from Deborah Goldberg, Radka Wildora and Jessica Hyde, a former REU student). Seeds were collected from 10 *T. latifolia* plants and 7 *T. angustifolia* plants, from Alanson, Ohio in 2006. At Cheboygan Marsh, Michigan seeds were collected from 10 *T. latifolia* plants, 10 *T. angustifolia* plants, and 10 *T. x glauca* plants. The seeds were planted May 15, 2006 at the University of Michigan, Ann Arbor. For each plant there were 6 pots with 10 seeds each, for a total of 60 seeds per plant. The number of newly germinated seeds was recorded on May 20, May 21, May 24, and May 25, 2006 in order to determine the percent germination for each plant. A one-way ANOVA was used to analyze the data, followed by Tukey tests to compare means.

Results

After analyzing the means of the initial heights of each of the five species groups, it became apparent that the *T. x glauca* backcross seedlings, with a mean of height of 1.522 cm, were larger than the other species groups (see Fig.1). This value was significantly larger than the other mean heights ($p < .005$).

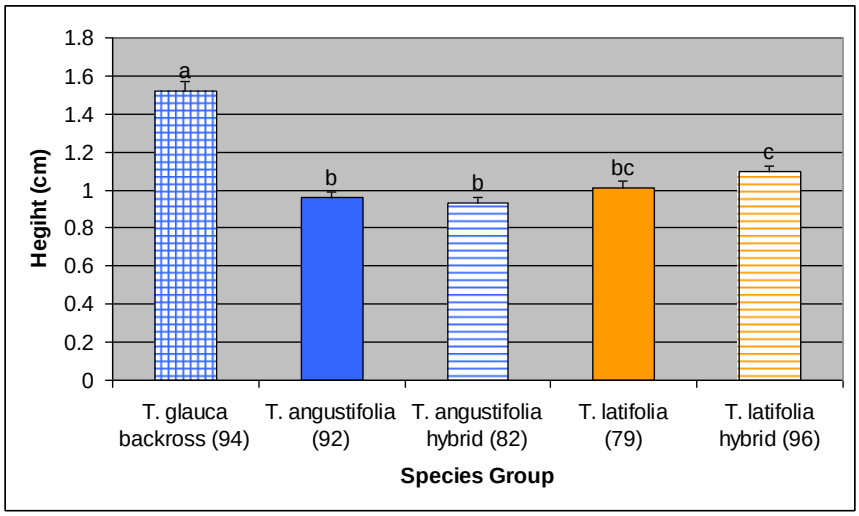

Figure 1. Means of the initial heights for each species group.

At the end of the experiment, the effect of each treatment on the growth of the seedlings depended on the species group. Overall, only the moisture treatment had a significant effect on the final seedling heights ($p < .001$), while the effect of the nutrients treatment and any interactions between the two treatments was insignificant (see Table 3); however, within a species group the effects varied (see Table 4). Within the *T. angustifolia*, *T. latifolia*, and the *T. latifolia* hybrid species groups, only the moisture treatment had a significant effect on the final seedling heights. For the *T. angustifolia* hybrid seedlings, the moisture treatment having a significant effect ($p < .001$), and there also was a significant interaction between the moisture and the nutrients treatments ($p = .014$).

Table 3. The overall effect of the treatments on the final seedling heights.

Source	Significance
Species	.000
Moisture	.000
Nutrients	.058
Species * Moisture	.117
Species * Nutrients	.273
Moisture * Nutrients	.194

Species * Moisture * Nutrients	.238

Table 4. The effect of the treatments on the final seedling heights for each species group.

Species Group	Source	Significance
T. angustifolia	Moisture	.000
	Nutrients	.506
	Moisture * Nutrients	.806
T. angustifolia hybrid	Moisture	.000
	Nutrients	.123
	Moisture * Nutrients	.014
T. x glauca backcross	Moisture	.000
	Nutrients	.048
	Moisture * Nutrients	.590
T. latifolia	Moisture	.036
	Nutrients	.676
	Moisture * Nutrients	.179
T. latifolia hybrid	Moisture	.007
	Nutrients	.977
	Moisture * Nutrients	.866

When performing the ANOVA tests on the final heights data, the square roots of the heights were taken in order to make more of the data normally distributed. It was found that throughout all four treatments, the mean heights of the *T. x glauca* backcross seedlings were the largest of the five species groups. Within the flooded and high nutrients treatment, the *T. x glauca* backcross was significantly larger than the other species groups ($p < .001$); however, the difference between the other four species groups was not statistically significant (see Fig. 2). Under the flooded and low nutrients treatment the *T. x glauca* backcross was again significantly larger than the other species groups ($p < .001$) (see Fig. 3). It is also interesting to point out that within this treatment the *T. angustifolia* hybrid seedlings were significantly smaller than the *T. angustifolia* seedlings ($p = .002$). Within the drained and high nutrients treatment the *T. x glauca* backcross seedlings, with a mean final height of 7.867 cm, were significantly larger than the seedlings of the other species groups ($p < .005$), (see Fig. 4). Only within the drained and low nutrients treatment is the difference in mean final height between the *T. x glauca* backcross and the other species groups not significant (see Fig. 5). Overall there is much less variation between the species groups within this treatment and none of the differences in mean heights are statistically significant.

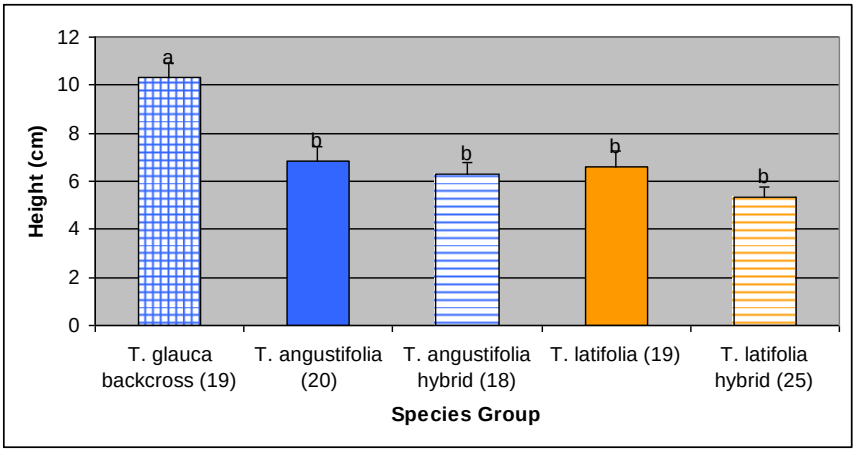

Figure 2. Means of final heights under flooded and high nutrients treatment

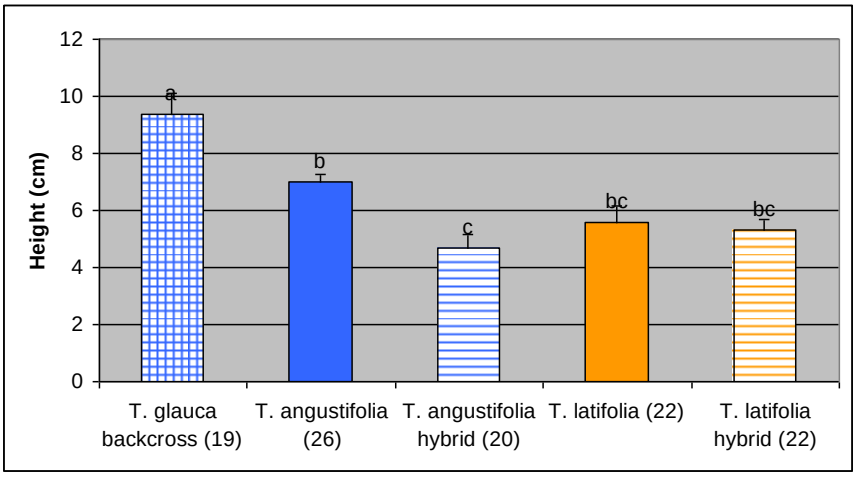

Figure 3. Means of final heights under flooded and low nutrients treatment.

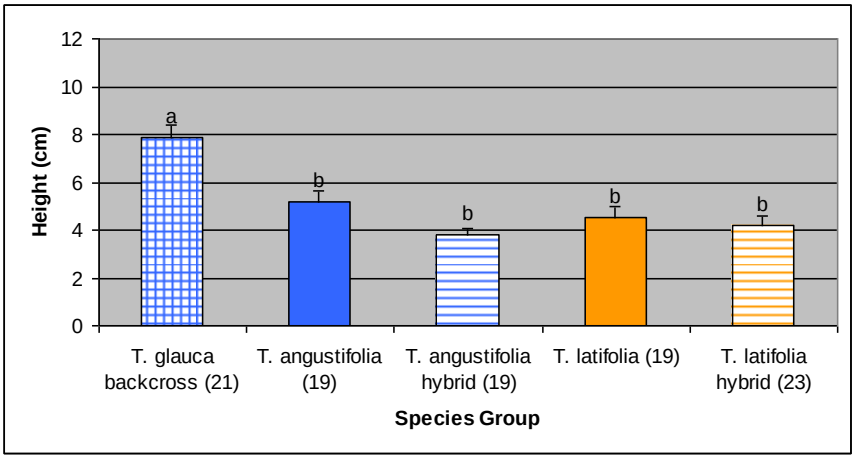

Figure 4. Means of final heights under drained and high nutrients treatment.

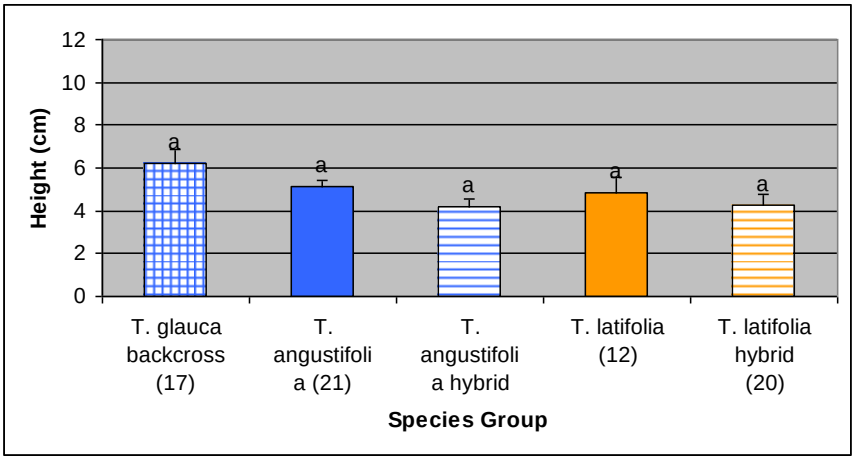

Figure 5. Means of final heights under drained and low nutrients treatment.

There were no statistically significant differences in height between the three *T. angustifolia* hybrid maternal families in neither the initial measurements (Height0) nor the final measurements (Height2) (see Fig. 6). Within the first set of measurements taken after the commencement of the experiment (Height1), one of the maternal families was significantly different from the other two ($p <$

.03). None of the average heights of *T. latifolia* maternal families were ever significantly different from each other (see Fig. 7). The mean heights of the *T. latifolia* hybrid maternal families began significantly different from each other (p = .047), however these differences decreased and became insignificant in next to set of measurements (see Fig. 8).

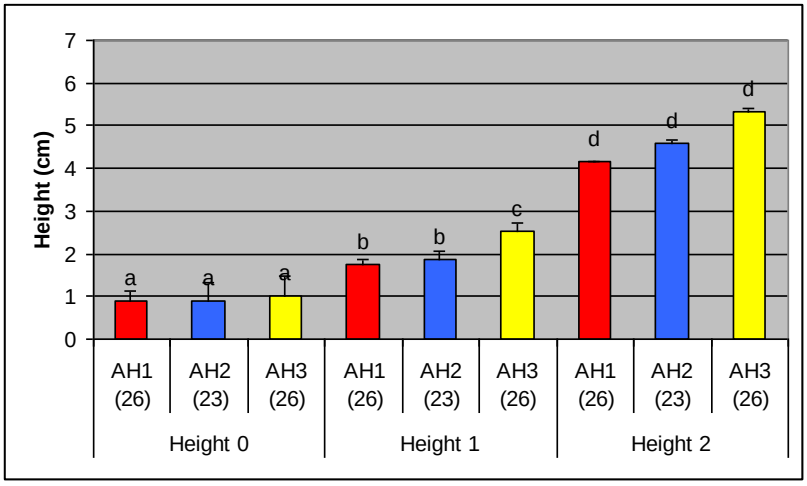

Figure 6. Means of final heights of *T. angustifolia* hybrid maternal families.

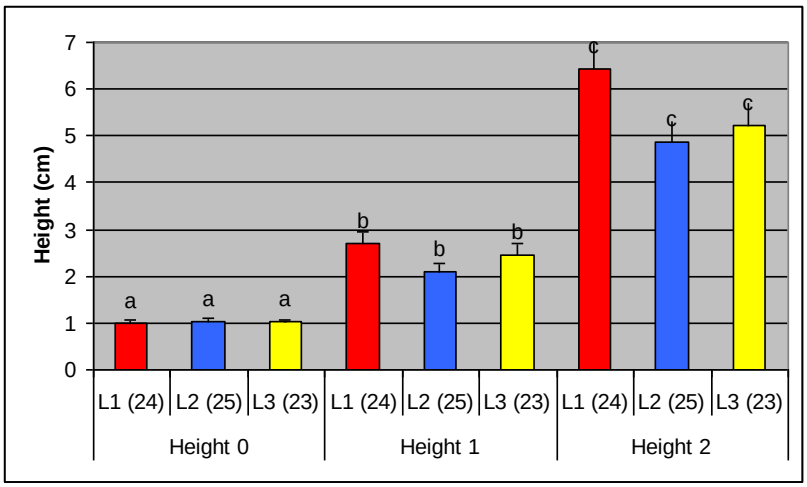

Figure 7. Means of final heights of *T. latifolia* maternal families.

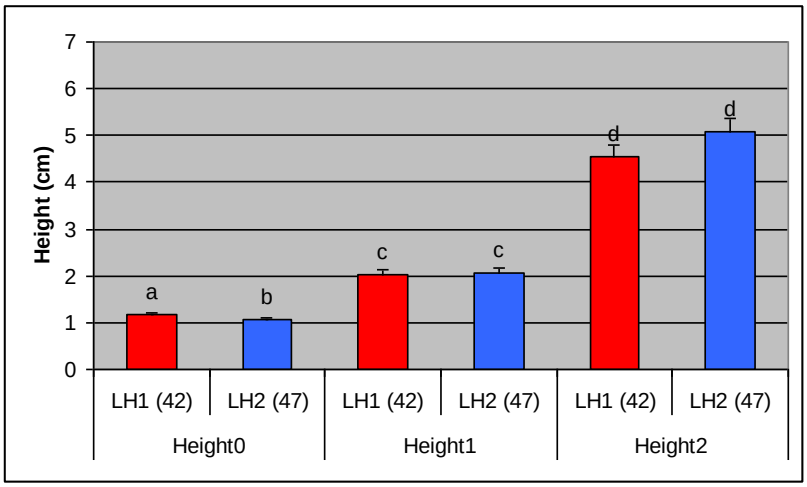

Figure 8. Means of final heights of *T. latifolia* hybrid maternal families.

The percent growth between Height0 and Height1 varies between the five species groups (see Fig. 9). The *T. angustifolia* seedlings, at 179%, had the highest percent growth, while *T. latifolia* hybrid seedlings, at 87%, had the lowest percent growth. The percent growth between Height1 and Height2 was less variable and none of the differences in percentages were statistically significant (see Fig. 10). There were no statistically significant differences in percent survival between the five species groups (p = .9935) (see Fig. 11).

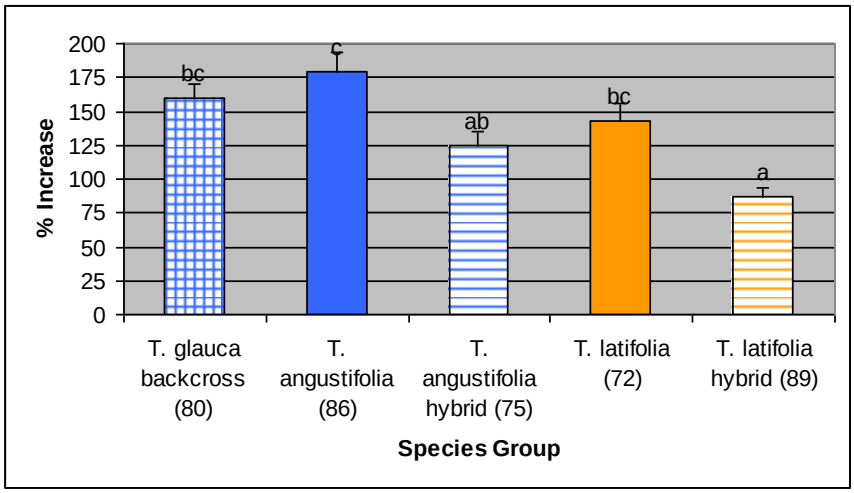

Figure 9. The percent growth from Height0 to Height1 for each species group.

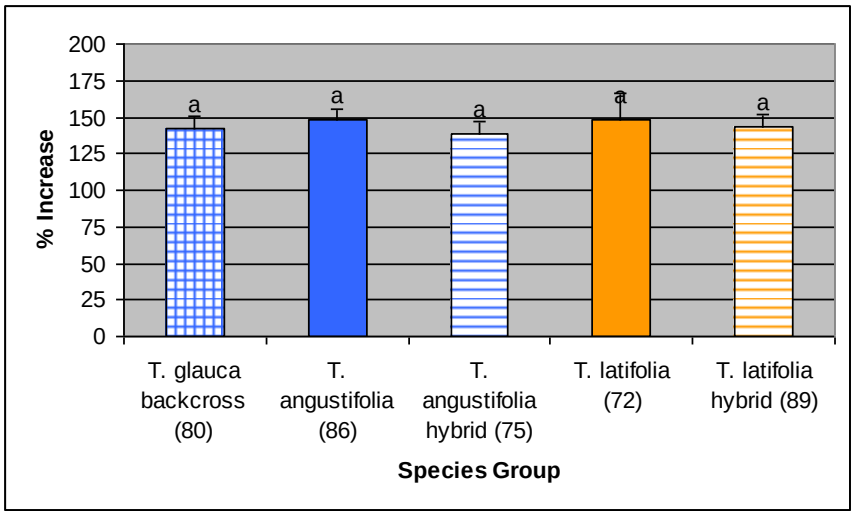

Figure 10. The percent growth from Height1 to Height2 for each species group.

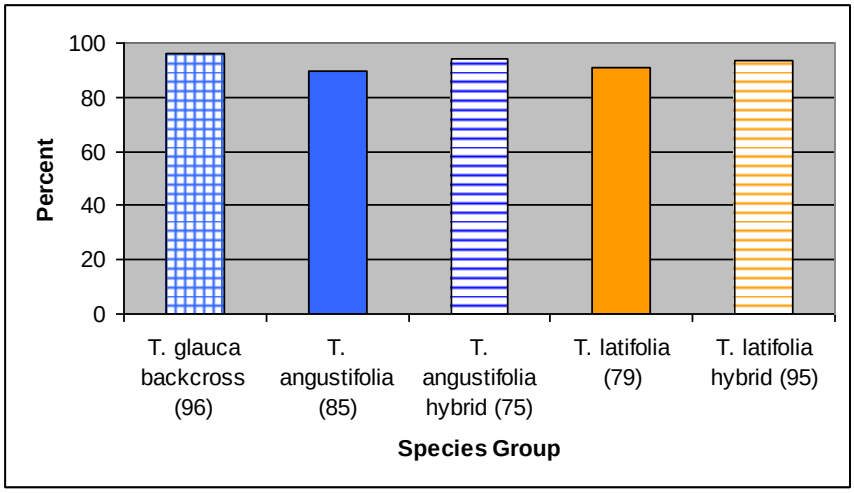

Figure 11. The percent survival by species group.

There was a statistically significant difference in percent germination between T. *latifolia*, which had a percent germination of 25%, and *T. angustifolia* and *T. x glauca*, which both had a percent germination of 10% ($p < .001$) (see Fig. 12). The site from which the seeds came also had a statistically significant effect ($p = .003$).

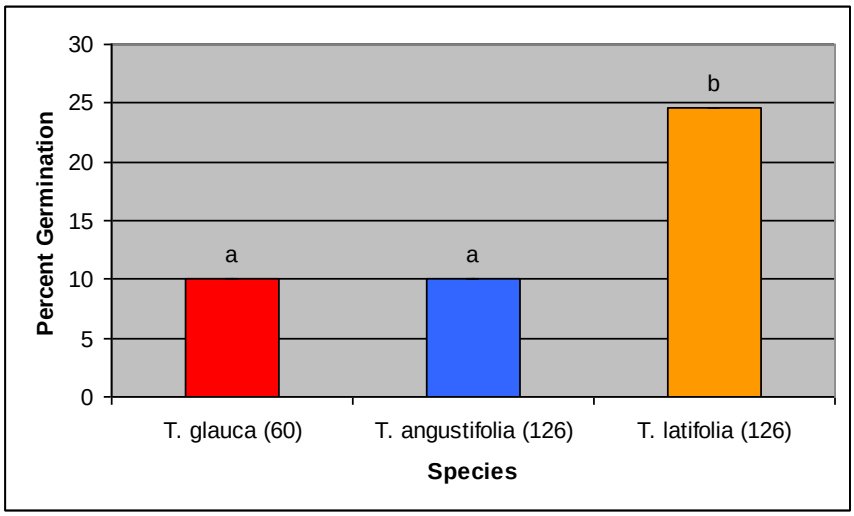

Figure 12. The percent germination by species.

Discussion

The results of this study suggest that the F1 *T. x glauca* hybrids are not experiencing hybrid vigor as seedlings. The mean heights of the *T. angustifolia* and *T. latifolia* hybrid seedlings were never significantly larger than the parent species seedlings. Along with genetic mechanisms that may lead to hybrid vigor, such as evolutionary novelty, greater genetic variation, fixed heterosis, and dumping of genetic load, there are also genetic mechanisms that can lead hybrids to have lower fitness than their parents, such as outbreeding depression (Ellstrand and Schierenbeck 2006, Kuehn *et al* 1999). It is possible that some *T. x glauca* plants are experiencing hybrid vigor while others are experiencing outbreeding depression. Also, seedling success is just one component of the total fitness of an individual plant. It is possible that the F1 *T. x glauca* are exhibiting hybrid vigor as adults through increased clonal growth, more efficient nutrients uptake, or through many other systems.

It seems as though, however, that the *T. x glauca* backcross seedlings are exhibiting a form of hybrid vigor. From early on in their life cycle these seedlings are larger than their parent taxa, and this advantage seems to continue as they grow older. This trend does seem to be dependent on the environmental conditions because the *T. x glauca* backcross seedlings were not significantly larger than the other species groups in the drained and low nutrients condition, which was most stressful to the plants. As the only species group that had statistically significant reaction to the two nutrients treatments, it is possible that the *T. x glauca* backcross seedlings are more efficient at taking advantage of high nutrients environments, as it is suggested by Woo and Zedler (2002).

The statistically significant differences in average height between maternal families of the F1 *T. x glauca* hybrids suggests that it may be important to use plants from several different maternal families when examining trends in *T. x glauca*. Considering the phenotypic variation among *T. x glauca* that is observed in the field, it is not very surprising that there would be a significant difference in heights among maternal families of the same species. Along with the statistically significant difference in mean heights of the two T. latifolia hybrid maternal families, it was also observed that seeds from a third maternal family did not germinate. It has been suggested that F1 hybrids may be less successful when *T. latifolia* is providing the egg and *T. angustifolia* is providing the pollen, and this observed decrease in germination may be due to maternal effects (Kuehn *et al* 2002). Since significant differences between maternal families were found, it very important that further research on the success of *T. x glauca* backcross seedlings have plants that represent various maternal families because the observed success could be due to the random pairing of two plants with very strong fitness.

There was very little variation in the percent growth between the Height1 and the Height2 measurements compared to the variation in percent growth between Height0 and Height1. However, despite a decrease in variation in growth rate as time went on, variation in average plant height persisted. This might suggest that the very beginning of the cattails lifecycle is a very critical time, and more studies should be done to quantify the growth rates of seedlings at a younger age. Although there was not a statistically significant trend in percent survival, it is still very early in the seedlings lifecycle, and therefore it would be interesting to continue recording the percent survival to see if a trend appears as the seedlings grow older.

After analyzing the data from the percent germination experiment it appears as though *T. latifolia* may have a significantly larger percent germination than *T. angustifolia* and *T. x glauca*. However, since the site from which the seeds were collected also had a statistically significant effect on percent germination, it may be important for further studies examining percent germination to collect seeds from several locations.

In conclusion, the F1 *T. x glauca* seedlings did not appear to be undergoing hybrid vigor, but instead the *T. x glauca* backcross seedlings seemed to be experiencing their own form of hybrid vigor. Therefore, it would be very valuable to repeat this experiment using seeds from more maternal families, especially for the *T. x glauca* backcross species group. Also, when repeating this experiment it may prove useful to begin measuring the heights of the seedlings at an earlier date in order to gain a better understand of the growth patterns of the seedlings starting at an earlier stage. If the topsoil used in the pots was already very rich in nutrients, then adding the diluted Miracle Grow Pour and Feed® would not have a significant effect on seedling growth. Therefore, I would repeat this experiment using a different soil. In the seed germination experiment, since the site from which the seeds were produced had a significant effect on the percent germination, it would be beneficial to use seeds from multiple sites. It would be very interesting for a future study to examine the mass of the seeds produced from the five different crosses to see whether the *T. x glauca* backcross seeds are larger.

Works Cited

Ellstrand, N.C. and K.A. Schierenbeck. 2006. Hybridization as a stimulus for the evolution of invasiveness in plants? Euphytica 148: 35-46.

Galatowitsch, S. M., N.O. Anderson and P.D. Ascher. 1999. Invasiveness in wetland

plants in temperate north America. Wetlands 19: 733-755.
Grace, J.B. and R.G. Wetzel. 1981. Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. Can. J. Bot. 60: 46-57.
Kuehn, M.M., J.E. Minor and B.N. White. 1999. An examination of hybridization between the cattail species *Typha latifolia* and *Typha angustifolia* using random amplified polymorphic DNA and chloroplast DNA markers. Mol. Ecol. 8: 1981-1990.
Smith, S.G. 1967. Experimental and natural hybrids in North American *Typha* (Typhaceae). The American Midland Naturalist 78: 257-287.
Vilà, M. and C.M. D'Antonio. 1998. Hybrid vigor for clonal growth in *Carpobrotus* (Aizoaceae) in coastal California. Ecol. Appl. 8: 1196-1205.
Woo, I. and J.B. Zedler. 2002. Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha x glauca*? Wetlands. 22: 509-521.
Citing Jessica's data?