Understanding morphological responses of *Typha* (cattail) species to nutrient pollution

Anna Marie Shapiro
Understanding Morphological Responses of *Typha* (Cattail) Species to Nutrient Pollution

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science

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University of Northern Iowa
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Abstract

In the Midwestern United States, *Typha x glauca* is a hybrid of the native *Typha latifolia* and the non-native *Typha angustifolia*. *Typha x glauca* is considered invasive, and it is dominating *Typha latifolia* when they co-occur. Wetlands in the Midwest face nutrient pollution, due to fertilization used within the agricultural industry. Wetlands are nutrient sinks, which store the increased levels of nitrogen and phosphorus. These nutrients are known to increase *Typha* growth. Within this thesis, it was hypothesized that an increase of nitrogen in the wetland may increase the width of *Typha* leaves, making it difficult to distinguish the native *Typha latifolia* from the invasive *Typha angustifolia* and *Typha x glauca*. Other factors that may affect leaf width, such as the length of the leaf and whether or not the ramet was flowering were also analyzed. It was found that leaf length, nitrogen levels, flowering status, and taxa significantly impacted the leaf width of *Typha* taxa, making leaf width alone an unreliable identifier in the field.

A secondary potential cause of *Typha* invasion was examined through a simulation using the wetland modeling program MONDRIAN. Through MONDRIAN, the effects of differing nitrogen levels and rhizome branching probability in both monocultures of *Typha* and in a scenario with five different theoretical *Typha* taxa in competition with one another were analyzed. *Typha* taxa with a low rhizome branching probability had a higher growing season stem density and net primary productivity under high nutrient conditions than taxa with a high rhizome branching probability, regardless of whether taxa are grown in monoculture or in competition with one another.
This Study by: Anna M. Shapiro

Entitled: Understanding Morphological Responses of *Typha* (Cattail) Species to Nutrient Pollution

has been approved as meeting the thesis requirements for the

Degree of Master of Science

Date Dr. Kenneth Elgersma, Chair, Thesis Committee

Date Dr. Laura Jackson, Thesis Committee Member

Date Dr. Mark Myers, Thesis Committee Member

Date Dr. Gabriela Olivares, Interim Dean, Graduate College
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I am also thankful for the guidance of my first mentor, Dr. Paul Weihe at Central College, who introduced me to Ecology and sparked my interest in wetlands and cattails, and who allowed me to assist him in his research for two summers outside of undergraduate research established by the college.

I am especially thankful for my advisor and chair of my thesis committee at the University of Northern Iowa, Dr. Kenneth Elgersma, for accepting me as a graduate student, for his guidance in statistical analyses, and his support throughout the entirety of my time at the University of Northern Iowa. I appreciate all of his guidance in programming, statistical analysis, and the writing process. I am grateful for his patience and instruction, and I don’t know how I could have come this far without his help. I thank you from the bottom of my heart.
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Chapter 1: Introduction

Background

The plants in the genus *Typha*, commonly known as cattails, are perennial flowering monocots commonly found within wetlands, near the edges of ponds, or within ditches. They grow in wet conditions, often within or near standing water. *Typha* grow 1-3 m tall, and they form dense, tightly packed stands. Their inflorescence is a pistillate spike with a staminate spike above it. They also reproduce asexually using rhizomes (Crow et al. 2000). In the Midwestern United States, three taxa of cattail (*Typha*) are present. The Broadleaf cattail (*Typha latifolia*) is native to the Midwest. The Narrowleaf cattail (*Typha angustifolia*) is non-native and invasive. Together, these species hybridize to form *Typha x glauca*, which is also considered invasive (Bansal et al. 2019).

*Typha latifolia* is distinguished by its broad leaves and wide inflorescence. The pistillate part of the spike is notably thicker in *Typha latifolia* than *Typha angustifolia*. *Typha latifolia* does not have a gap between the staminate and pistillate parts of the inflorescence, while *Typha angustifolia* has narrow leaves and a narrow inflorescence, with a distinct gap between the staminate and the pistillate parts of the inflorescence (Bansal et al. 2019). The morphological traits of the inflorescence aid in the identification of these cattail species, but not all individual ramets produce an inflorescence for sexual reproduction. The ramets without an inflorescence in all three taxa reproduce asexually through rapid growth of vegetative rhizomes.

*Typha x glauca* has intermediate morphological traits of both of its parents, with varying combinations of leaf width, inflorescence width, and the size of the gap between the staminate and pistillate parts of the inflorescence. This hybrid creates a gradient
between the morphological traits of these three *Typha* taxa, complicating identification (Bansal et al. 2019; Freeland et al. 2013). Backcrosses between the hybrid and its parent taxa further blurs the distinction in morphological traits between taxa (Freeland et al. 2013).

**Invasion Methods**

*Typha x glauca* and to a lesser extent *Typha angustifolia* are highly invasive and alter wetland conditions and ecosystem functions (Bansal et al. 2019). It would be beneficial to determine why *Typha x glauca* is so invasive and capable of outcompeting many native wetland plants. One hypothesis is that the live plants may alter their habitat and outcompete other species for resources present (Larkin et al. 2012). Another hypothesis is that *Typha x glauca*’s leaf litter modifies habitat conditions by decreasing light and soil temperature (Farrer & Goldberg 2009; Larkin et al. 2012).

**Leaf Litter Production**

All three of these taxa of *Typha* easily dominate wetlands due to their advantage in height over native graminoids and their ability to reproduce both sexually and asexually (Galatowitsch et al. 1999; Geddes et al. 2021). They also produce copious amounts of leaf litter, which takes up much of the space on the surface and crowds out other plants. The leaf litter is slow to decompose and creates a light barrier that prevents sunlight from reaching shorter plants. *Typha* is tolerant of the high amounts of litter that it produces, due to its capacity to reproduce asexually and gain support from the other individuals within the stand through its rhizomes, while other wetland plants are not (Larkin et al. 2012).
It is hypothesized that *Typha x glauca* is capable of growing taller than *Typha latifolia* and *Typha angustifolia* as a result of hybrid vigor, which may help it to dominate wetlands over both species (Bansal et al. 2019). By growing taller, *Typha x glauca’s* leaf litter is denser than *Typha latifolia* and *Typha angustifolia*, which reduces the sunlight available to these and to other, shorter native plants.

**Nutrient Addition**

Many North American wetlands face disturbances such as the addition of nutrients, filling, and excavation (Galatowitsch et al. 1999). Invasive species seem to do well in these disturbed wetlands, and once they are established it can be quite difficult to remove them and restore the wetland to its natural state (Bansal et al. 2019; Elgersma et al. 2017; Graham et al. 2022). The addition of nutrients increases the growth of *Typha* but it has little effect on native graminoids (Woo & Zedler 2002).

It has been hypothesized that one of the factors that makes *Typha x glauca* so invasive is its ability to grow well, compared to native species, in agricultural regions altered by nutrient pollution. Regions invaded by *Typha x glauca* have higher concentrations of nutrients, as well as decreased plant diversity, increased above ground biomass, and an increased concentration of nutrients (Angeloni et al. 2006; Bansal et al. 2019; Currie et al. 2014). Wetlands act as nutrient sinks, accumulating sediments and nutrients and preventing them from reaching the open water (Zedler & Kercher 2004). These nutrients help opportunistic plant species, such as *Typha x glauca*, to grow (Zedler & Kercher 2004). With additional nutrients entering wetlands through nutrient runoff, these nutrients may help the invasive *Typha* to dominate the wetland.
*Typha* responds well to an increase in nutrients in wetlands, and the addition of nutrients commonly used in fertilizer, such as nitrogen and phosphorus, have been found to increase the height of *Typha x glauca* (Woo & Zedler 2002). It may be that *Typha x glauca* impacts the removal of nutrients from the wetland (Angeloni et al. 2006). However, at this time not much is known about whether the higher nitrogen levels observed in these regions are a cause of *Typha x glauca* invasion or an effect. High nutrients might be a cause of invasion if they increase *Typha*’s competitive ability, but they also may be a consequence because of the role wetlands play in retaining nutrients. Wetlands retain nutrients and prevent them from reaching bodies of water (Currie et al. 2014). Higher nutrient levels increase *Typha*’s net primary productivity and carbon accretion. This causes more nutrient cycling to occur and more nutrients to be retained (Currie et al. 2014; Martina et al. 2016), potentially creating a positive feedback that makes high nutrients more of an effect of invasion than a cause.

Martina et al. (2016) found evidence of such a feedback effect in a study of the effects of nitrogen on wetland carbon accretion. The study used a wetland model simulating the effects of nitrogen loading and how both native plants and non-native invasive plants affected carbon accretion. Plants in conditions with more nitrogen had higher rates of carbon accretion and increased net primary productivity (Martina et al. 2016). Greenhouse studies have also demonstrated that elevated nitrogen levels relative to the amount of phosphorus present help *Typha x glauca* to invade wetlands and decrease wetland plant diversity (Woo & Zedler 2002).

Additional evidence for interactions between *Typha* and nutrients comes from another species of cattail, *Typha domingensis*, which is native to the Florida Everglades.
though it is not historically dominant. The effects of phosphorus on other taxa of *Typha* have not yet been studied as closely as nitrogen, but phosphorus and nitrogen are often both present in regions susceptible to nutrient runoff. Work has been done with this species due to the sensitivity of the region and observing the effects of phosphorus on this species may be useful in understanding *Typha latifolia* and *Typha angustifolia*. *Typha domingensis* grows well in phosphorus-rich areas, which may be helping it to dominate these areas (Brix et al. 2010; Li et al. 2010). *Typha domingensis*’s phosphorus uptake is twice as high as sawgrass (*Cladium mariscus*), and two to three times as high in plants that were not acclimated to high levels of phosphorus (Brix et al. 2010). In areas that have been enriched with phosphorus, *Typha domingensis* may be capable of outcompeting the historically dominant *Cladium mariscus*. In a similar way, elevated phosphorus levels caused by nutrient pollution may benefit *Typha x glauca* more than native graminoids in the Midwest. The leaf length of *Typha x glauca* increases when there is a higher concentration of phosphorus than nitrogen, but this effect has not been observed in native graminoids (Woo & Zedler 2002).

The complexity of nutrient wetland dynamics—particularly for phosphorus—also introduces the possibility of more complex interactions between nutrients and invasion. The center of a *Typha* stand typically has a lower dissolved oxygen concentration while there is a higher concentration of dissolved oxygen near the open water (Grace et al. 2008). The cattail stand shades the water, limiting the growth of algae and further contributing to low levels of oxygen within the water (Grace et al. 2008). As phosphorus levels increase in a wetland, the density of the stand and litter increase. As a result of the lack of oxygen, microbes in the water take in less phosphorus, decreasing the cycling of
phosphorus and resulting in higher levels of phosphorus accumulating within the wetland (Grace et al. 2008). Shade-induced inhibition of algal growth likely also affects nitrogen cycling, potentially increasing nitrogen availability to plants (Quinn et al. 1997).

**Nutrient Effects on *Typha* Morphology**

In addition to changing the dominance of plant species, nutrient additions can change plant morphology as well. As nitrogen and phosphorus levels increase, *Typha* leaf length increases (Woo & Zedler 2002). As *Typha* leaf length increases, leaf width also increases (Snow et al. 2010). I hypothesize that due to an increase in nitrogen levels, the leaf width will also increase.

Morphological responses to nutrient additions may make it more difficult to distinguish between native *Typha latifolia* and the invasive *Typha angustifolia* and *Typha x glauca*, because leaf width is a commonly used morphological trait in species identification. In the field, the only practical means to identify *Typha* without an inflorescence is using leaf width. Reducing our ability to accurately distinguish the native taxa from the non-native taxa makes it more difficult to manage wetlands facing invasion.

In clonal plants, ecological theory also predicts nutrient availability can influence another aspect of plant morphology, such as clonal structure. Specifically, rhizome branching rate (the probability that a given node branches into two rhizomes) increases as a plastic response to increasing nutrients (de Kroons & Hutchings 1995). These theoretical predictions have been verified both through empirical studies (Li et al. 2010; Larkin et al. 2012; Batzer et al. 2017) and modeling efforts (Cain 1994; Oborny et al. 2012).
Clonal Structure

When studying wetland ecology, questions regarding the response to nutrients of Typha belowground growth, such as rhizome branching probability, are difficult to study experimentally due to constraints in time, effort, or desired sample size. As an alternative, nutrient dynamics in wetland ecosystems are commonly studied using models (Currie et al. 2014; Elgersma et al. 2017; Goldberg et al. 2017; Martina et al. 2016). To further examine what makes Typha x glauca so invasive, the belowground rhizome branching patterns of Typha was manipulated using a simulation model under differing levels of nutrients in the environment.

MONDRIAN (Modes of Nonlinear Dynamics, Resource Interactions, and Nutrient Cycling, Currie et al. 2021) has been used to simulate plant invasion, management techniques, and nutrient cycling (Currie et al. 2014; Elgersma et al. 2017; Goldberg et al. 2017). Using MONDRIAN, several variables can be examined, including nutrient levels, rhizome branching, flooding mortality, the amount time passed, and the behavior of each simulated species. MONDRIAN has been used to study the nitrogen inputs into wetlands and the influence of plant size on invasion success (Currie et al. 2014). Further work has been done relative to plant size and nutrient gradients in herbaceous, clonal wetland plants, where invader net primary productivity was found to be a unimodal function of plant size, and the maximum potential mass of an individual ramet increased with increased nitrogen availability and increased competition for nutrients (Goldberg et al. 2017). It also has been used to study management techniques (Elgersma et al. 2017) and carbon accretion (Martina et al. 2016).
In asexual reproduction, *Typha* produce rhizomes belowground. These rhizomes may either branch from one node into two or continue to grow straight. If the genet has the resources needed, a node will form another ramet. The biomass of the new ramet will come from the rhizome, connecting belowground morphological traits to aboveground morphological traits of the genet (Sullivan et al. 2010). Because rhizome branching rate affects the spatial arrangement of ramets, it therefore influences the genet’s exploration and utilization of space and nutrients. Because MONDRIAN is a spatially-explicit individual-based model, the effects of rhizome branching rate on resource and space utilization can be explored through simulation. Gaining a better understanding of how *Typha* morphological traits are influenced by nutrient pollution will assist in conservation efforts to remove the invasive taxa from Midwestern wetlands. In this thesis, Chapter 2 presents the results of an experiment on the effect of nitrogen levels on the leaf morphology of these three *Typha* taxa and Chapter 3 will present the results of a simulation study using MONDRIAN to explore how rhizome branching probability impact *Typha* invasion success under differing nutrient levels.
Chapter 2: Genetic and Environmental Correlates of Leaf Allometry

Methods

Sample Selection

Typha samples were collected from the Edwin S. George Reserve (ESGR) and the University of Michigan Biological Station (UMBS) in Summer 2016. The Edwin S. George Reserve is located near Pickney, Michigan (42.4580506, -84.0117986) and is managed by the University of Michigan. The University of Michigan Biological Station (45.558653, -84.6797864) is located near Pellston, Michigan. Several constructed wetlands were established in Fall 2011 in 400-L livestock tanks where nitrogen levels and species present were controlled. The tanks were filled with sand with a 1.5cm layer of reed-sedge peat on the surface. An irrigation system established a constant flow of water, mimicking the natural flow of groundwater. At each site, 48 tanks were randomly assigned a nutrient level (0, 1.5, 3, 6, 9, 12, 15, 21, 27, 33, 39, or 45 gN m$^{-2}$ yr$^{-1}$), representing the full range of nitrogen inputs reported in the literature for Midwestern wetlands (Neely & Baker 1989; Davis et al. 1981; Green & Galatowitsch 2002). Nitrogen was administered as slow-release urea pellets, aerially scattered on the soil surface in the first year and through a fertigation system in subsequent years. The tanks underwent one of two randomly-assigned vegetation treatments. Half of the tanks at each site lacked vegetation before invasion with Typha and the other half contained native competitors established in spring 2012, one year prior to planting Typha rhizomes. One rhizome each of Typha angustifolia, Typha latifolia, and Typha x glauca was planted in each tank. For more information on the establishment of the tanks at these sites, see Ruiz 2018.
Harvested *Typha* samples were randomly selected from each constructed wetland, identified using morphological traits (leaf width & height, and inflorescence measurements when available), dried, and stored in paper bags. A subset of these samples was haphazardly selected for analysis. Due to some uncertainty when identifying these samples using their morphological traits at the time of collection, it was hypothesized that several samples identified as *Typha latifolia* or *Typha angustifolia* may actually be *Typha x glauca*. A random number generator was used to select samples from this pool of potential samples for genetic identification. This yielded about a 2:3 ratio of *Typha latifolia* to *Typha angustifolia*. Samples from the same tank were selected pseudo-randomly to achieve a split closer to 1:1, so there was a more balanced sample size of each taxa within the dataset.

**Genetic Identification**

In May 2021, 20 mg of dried leaf tissue was finely cut using alcohol-sterilized scissors and weighed. Tissue was placed into a 2mL tube with three 5.5mm zinc pellets and two 2.3mm steel pellets. The samples were placed in a MM400 mixer mill for 45 seconds at 20 hertz for two separate runs, for a total of 90 seconds. Between runs, 350 µL of Fisher plant GeneJet kit lysis buffer was added to the samples. The Plant Genomic DNA Purification Main Protocol included within the Fisher GeneJet kit was followed beginning with step 2 to extract and purify the DNA using purification columns. Samples underwent PCR using M13 6-FAM florescent dye, TA 5 forward and reverse primers, TA 20 forward and reverse primers, and TA 3 forward and reverse primers (Snow et al. 2010). Samples were sent to the Iowa State University DNA Facility for microsatellite analysis. Peaks were observed at TA 20, TA 3, and TA 5 to identify the samples as *Typha*
latifolia, Typha angustifolia, or Typha x glauca. Once samples were genetically identified, the relationships between leaf length and leaf width, nutrient levels and leaf width, and flowering status and leaf width of all three taxa were analyzed in R version 4.0.3 using linear regression tests and ANOVA.

Results

Relationships Between Morphological Traits

Leaf length was found to have a significant positive correlation with leaf width in Typha angustifolia but there were no significant effects of nitrogen levels or reproductive status (flowering or vegetative) on leaf width, nor were there any interactions between nutrients, reproductive status, or leaf length. (Table 1). Similar results were observed in Typha latifolia (Table 2) with one important difference: in addition to the significant correlation with leaf length (p < 0.0001), nutrients also directly increased leaf width (p = 0.053) and there was a marginally significant interaction between these two as well (p = 0.079). In Typha x glauca, leaf length (p < 0.0001), nitrogen level (p = 0.016), and reproductive status (p = 0.003) all had significant effects on leaf width, however there were no significant interactions between any of these factors (Table 3). When comparing the impact of these factors across all taxa simultaneously, taxon had a significant effect on leaf width (p < 0.0001), as did its interaction with leaf width (p < 0.0001, Table 4).
Table 1: ANOVA for the effect of leaf length, nitrogen, reproductive status on *Typha angustifolia* leaf width. “Length” signifies the length of the leaf, “N” signifies soil nitrogen level, and “Flowering” signifies reproductive status in *Typha angustifolia*

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Table 2: ANOVA for the effect of leaf length, nitrogen, reproductive status on *Typha latifolia* leaf width. “Length” signifies the length of the leaf, “N” signifies soil nitrogen level, and “Flowering” signifies reproductive status in *Typha latifolia*

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Table 3: ANOVA for the effect of leaf length, nitrogen, reproductive status on *Typha x glauca* leaf width. “Length” signifies the length of the leaf, “N” signifies soil nitrogen level, and “Flowering” signifies reproductive status in *Typha x glauca*.

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<td>Length:Flowering</td>
<td>1</td>
<td>0.841</td>
<td>0.841</td>
<td>0.258</td>
<td>0.613</td>
</tr>
<tr>
<td>N:Flowering</td>
<td>1</td>
<td>0.507</td>
<td>0.507</td>
<td>0.156</td>
<td>0.694</td>
</tr>
<tr>
<td>Length:N:Flowering</td>
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<td>0.198</td>
<td>0.198</td>
<td>0.061</td>
<td>0.806</td>
</tr>
<tr>
<td>Residuals</td>
<td>68</td>
<td>221.476</td>
<td>3.257</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4: ANOVA for the effect of leaf length, nitrogen, reproductive status, and taxa on leaf width of all *Typha* taxa. “Length” signifies the length of the leaf, “N” signifies soil nitrogen level, “Flowering” signifies reproductive status.

<table>
<thead>
<tr>
<th></th>
<th>df</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
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<th>P</th>
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<td>793.520</td>
<td>199.401</td>
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</tr>
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<td>112.270</td>
<td>28.213</td>
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</tr>
<tr>
<td>Flowering</td>
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<td>99.110</td>
<td>24.906</td>
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</tr>
<tr>
<td>Taxa</td>
<td>2</td>
<td>1268.480</td>
<td>634.240</td>
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<tr>
<td>Length:N</td>
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<td>5.520</td>
<td>1.386</td>
<td>0.241</td>
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<tr>
<td>Length:Flowering</td>
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<td>31.110</td>
<td>7.817</td>
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<tr>
<td>N:Flowering</td>
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<td>1.320</td>
<td>0.333</td>
<td>0.565</td>
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<tr>
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</tr>
<tr>
<td>N:Taxa</td>
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<td>13.690</td>
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</tr>
<tr>
<td>Flowering:Taxa</td>
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<td>1.630</td>
<td>0.810</td>
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</tr>
<tr>
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<td>0.020</td>
<td>0.005</td>
<td>0.947</td>
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<tr>
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<td>2.550</td>
<td>0.640</td>
<td>0.529</td>
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<tr>
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<td>2.780</td>
<td>0.698</td>
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<tr>
<td>N:Flowering:Taxa</td>
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<td>0.710</td>
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<td>0.089</td>
<td>0.915</td>
</tr>
<tr>
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<td>0.490</td>
<td>0.124</td>
<td>0.883</td>
</tr>
<tr>
<td>Residuals</td>
<td>159</td>
<td>632.740</td>
<td>3.980</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Averaged across all taxa, the relationship between leaf length and leaf width differs in high nitrogen and low nitrogen conditions (Figure 1). In high nitrogen conditions, leaves are generally wider at any given leaf length than leaves in low nitrogen conditions. Comparing taxa, *Typha latifolia* had the widest leaves, *Typha angustifolia* had the narrowest leaves, and *Typha x glauca* was intermediate between *Typha latifolia* and *Typha angustifolia* (Figure 2). However, due to the wide range of leaf length variation in all taxa, there was a broad range of overlap in leaf widths between taxa. When comparing the leaf width of each taxa (Figure 3) to the ratio of the leaf length and leaf width of each taxa (Figure 4), *Typha x glauca* has a greater ratio than *Typha latifolia*, rather than forming an intermediary between *Typha angustifolia* and *Typha latifolia*. There is little difference in the relationship between leaf length and width in high and low nutrient conditions among both flowering and nonflowering *Typha angustifolia* (Figure 5); however, in nonflowering *Typha x glauca* and flowering *Typha latifolia* there is a greater difference between high and low nutrient conditions. On average, the leaves of a flowering ramet were found to be almost 35% wider than a non-flowering ramet.
Figure 1: Linear regression of leaf length and leaf width of all genetically identified samples, with subsets of high nitrogen and low nitrogen conditions.
Figure 2: Linear regression of leaf length and leaf width. TYAN is *Typha angustifolia*, TYGL is *Typha x glauca*, TYLA is *Typha latifolia*
Figure 3: Box-and-whiskerplot of the average leaf width of each taxon. TYAN is *Typha angustifolia*, TYGL is *Typha x glauca*, TYLA is *Typha latifolia*
Figure 4: Box-and-whiskerplot of the leaf height to leaf width ratio of each taxon. TYAN is *Typha angustifolia*, TYGL is *Typha x glauca*, TYLA is *Typha latifolia*
Figure 5: Linear Regression for nitrogen level in Flowering and Non-flowering states of *Typha angustifolia, Typha latifolia,* and *Typha x glauca.* The top row, “F”, signifies those with the reproductive status of “Flowering” and the bottom row, “V”, signifies those with the reproductive status of “Vegetative” (Nonflowering).
Discussion

*The Relationship Between Leaf Length and Leaf Width*

In all three taxa, leaf length has a significant relationship to leaf width. In *Typha angustifolia, Typha latifolia,* and *Typha x glauca,* as the leaf grows longer it also grows wider. Likewise, the inverse is true; as the leaf grows wider, it grows longer. This finding is important because it implies that field identification based on leaf morphology, which typically uses leaf width alone, is insufficient and instead it is the ratio of leaf width to leaf length, not leaf width alone, that morphologically distinguishes these taxa from one another. Furthermore, a large degree of overlap between taxa was observed, not only in individual leaf widths, but in the average leaf width. *Typha x glauca* is a good example to demonstrate this because of its intermediate leaf morphology. According to linear regressions, a 25-cm long *Typha x glauca* leaf is predicted to be approximately 6.3 mm wide on average. While *Typha x glauca* has wider leaves on average than *Typha angustifolia,* a very long (175 cm) *Typha angustifolia* leaf is predicted to be slightly wider on average than a 25-cm long *Typha x glauca* leaf. Similarly, a very long (225 cm) *Typha x glauca* leaf is predicted to be wider than a short (e.g. 50 cm) *Typha latifolia* leaf, even though *Typha latifolia* leaves are generally wider than *Typha x glauca.* Thus, even in the absence of random individual-level variation, the results show a large degree of overlap in leaf width between these three taxa. Individual-level variation adds to the degree of overlap, making leaf width alone a relatively unreliable tool for taxonomic identification. However, accounting for both leaf width and leaf length allows much better—though still limited—prediction of genetic identity (Snow et al. 2010).
**The Relationship Between Nitrogen and Leaf Width**

Nitrogen significantly impacts the leaf width of *Typha x glauca*, and this finding further complicates the use of leaf width as a tool for field species identification. Nitrogen had a moderate effect on the leaf width of *Typha latifolia*, but no effect was seen in *Typha angustifolia*. *Typha x glauca* is again useful for understanding the implications of these results due to its intermediate morphology. *Typha x glauca* growing in high nutrient conditions is expected to have wider leaves on average for any given leaf length, pushing its predicted leaf width closer to the predicted width of *Typha latifolia*. Grown under low nutrient conditions on the other hand, *Typha x glauca*'s predicted width decreases and becomes closer to that of *Typha angustifolia*. Despite this, the nutrient environment in which a plant is growing in the field is typically not known, adding a significant degree of uncertainty to the use of leaf width for taxonomic identification.

**The Relationship Between Reproductive Status and Leaf Width**

Whether the individual is flowering or in a vegetative state had a significant effect on the leaf width of *Typha x glauca* (*p < 0.0001*), but less of an effect was observed in *Typha latifolia* (*p = 0.2272*) and *Typha angustifolia* (*p = 0.1153*). When *Typha x glauca* is flowering, its leaf length and leaf width have a similar slope in high and low nutrient conditions. *Typha x glauca* tends to be shorter and has narrower leaves when it is not flowering and in low nitrogen conditions. It could be that in low nitrogen conditions, non-flowering *Typha x glauca* allocates more energy to rhizome branching for asexual reproduction rather than leaf width. *Typha x glauca*'s leaf width under these conditions remains relatively constant despite the wide variation in leaf length observed.
These results demonstrate that multiple factors influence leaf width outside of taxonomic identity, making it difficult to use to identify the taxon of an individual in the field. Leaf length, nutrients, flowering status, and a few of the interactions between these and taxonomic identity can influence leaf width, making identification by leaf width alone unreliable. Accounting for more of these factors when conducting identification in the field might improve taxa predictability using leaf width, but genetic confirmation of field identification remains vital when taxonomic identity must be certain.
Chapter 3: Clonal Structure

Methods

MONDRIAN is a wetland ecosystem model for ecological research designed to simulate interactions between plants within the community under various ecological conditions (Currie et al. 2021). Two sets of simulations were run using MONDRIAN version 5.1 to investigate the effects of nutrient levels on the probability of a belowground rhizome branching. One set was used to investigate how the probability of rhizome branching affects net primary productivity of individual plants, across a range of soil fertility levels. The second set placed individual plants with different rhizome branching probabilities in competition with one another.

In this individual-based model, at each node individual aboveground stems (ramets) are connected to other ramets within a clone (genet) through a belowground rhizome. Ramets are modeled as “individuals” that grow and acquire resources (light and nutrients) until they accumulate enough resources to produce a new belowground rhizome and aboveground stem. Nutrient resources (nitrogen and phosphorus) are supplied to grid cells in the model area on a daily basis, and ramets within a grid cell compete for these nutrients daily through size-symmetric competition (Currie et al. 2014). Ramets within a grid cell also compete with one another for light in a daily timestep via user-parameterized light response curves (Martina et al. 2016). Thus, each node along a rhizome can acquire resources and produce an aboveground stem and a belowground rhizome. This rhizome can branch into two rhizomes at the node in order to utilize more of the model area, but the ramet needs to gain enough nutrients before it can try to branch. After the rhizome node has enough nutrients, it performs a check to
determine whether or not it has the ability to branch. If it does, it will branch at that node into two rhizomes at a user-defined rate, ranging from 0 (never branching) to 1 (always branching). Nodes that do not branch continue growing linearly as a single rhizome. The rhizome also separately performs a check to determine whether or not it is going to form a new ramet. A new ramet need not be created every time the rhizome branches (Figure 6, Meyer & Currie unpublished data).

Figure 6: Ramets in the model space. Individual ramets represented by dots, their connecting rhizomes are represented by lines, and branching is represented by bifurcating lines.
The first set of simulations, hereafter referred to as the monoculture simulations, used parameters representative of a generic *Typha* species monoculture under differing levels of nitrogen and phosphorus coinciding with the range of nitrogen inputs found within Midwestern wetlands (Neely & Baker 1989; Davis et al. 1981; Green & Galatowitsch 2002) using the same levels of nitrogen input as the mesocosm experiment described in the previous chapter (0, 1.5, 3, 6, 9, 12, 15, 21, 27, 33, 39, or 45 gN m\(^{-2}\) yr\(^{-1}\)). The values of 0 through 12 are classified as “low” nitrogen levels, and the values from 15 through 45 are classified as “high” nitrogen levels. Parameter values for generic *Typha* were taken from Elgersma et al. 2017. A fixed N:P ratio of 24:1 was used, based on data collected from 188 sites in the Great Lakes basin from 2008-2012 (Wan, unpublished data). The probability of rhizome branching (0.1, 0.3, 0.5, 0.7, 0.9) was altered between simulations to test whether branching more or less under each nutrient condition increases the genet’s net primary productivity. In each simulation, 15 rhizomes were planted each year in years 1-4, for a total of 60 *Typha* rhizomes planted. Since the intention was to see the long-term effects of *Typha* growth in the wetland after 40 years, only the average of the last 5 years was analyzed.

The second set of simulations, hereafter referred to as the competition simulations, represented five different hypothetical *Typha* grown simultaneously, with the only difference between them being their probability of rhizome branching, with values of 0.1, 0.3, 0.5, 0.7, and 0.9. These hypothetical *Typha* taxa were grown in competition with each other under differing nutrient levels (0, 1.5, 3, 6, 9, 12, 15, 21, 27, 33, 39, or 45 gN m\(^{-2}\) yr\(^{-1}\)) over a 40 year timespan. Similar to the first set of simulations, 15 rhizomes were planted in years 1-4 for each of the 5 hypothetical taxa observed,
equaling 60 rhizomes per taxon planted, or a total of 300 rhizomes. Taxon success was measured using growing season stem density and aboveground net primary productivity. As in the monoculture simulations, only the average of the last 5 years was analyzed, and the first 35 years were discarded.

In both sets of simulations, the water level stayed at a consistent 0.02 m deep and daily mean temperature followed a sinusoidal annual fluctuation with annual minimum of -3.4°C and maximum of 26.4°C. Nutrient inputs were supplied to the wetland at a constant daily rate throughout the year, and the flushing rate of water in the simulated wetland was similarly held constant at 10% per day throughout each simulation. The hypothetical wetland was divided into 100 10-cm X 10-cm cells, with rhizomes randomly distributed between cells at the beginning of the simulation. The 1 m² model area had toroidal boundaries, so that rhizomes growing off the edge of the model area simply wrapped around to the opposite edge. Each simulation scenario was replicated 10 times to simulate stochastic variation in plant growth patterns.

Results

Monoculture Simulations

Nutrient levels, branching probability, and the interactions between the two were found to have significant effects on both the growing season stem density (Table 5) and total aboveground net primary productivity (Table 6). Under high nutrient conditions, individuals with a lower rhizome branching probability had a higher growing season stem density (Figure 7) and higher aboveground net primary productivity rate (Figure 8), suggesting low branching probability is favored at high nutrient levels.
Table 5: ANOVA for the effect of nitrogen and branching probability on the growing season stem density. “N” signifies soil nitrogen level, “Branching” signifies the probability of a rhizome branching at any given node.

<table>
<thead>
<tr>
<th></th>
<th>df</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
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<th>p</th>
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<td>N</td>
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<td>13145312</td>
<td>13145312</td>
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<td>2169</td>
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<td>N:Branching</td>
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<td>15053</td>
<td>32.433</td>
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<tr>
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<td>596</td>
<td>276610</td>
<td>464</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 6: ANOVA for the effect of nitrogen and branching probability on the above ground net primary productivity. “N” signifies soil nitrogen level, “Branching” signifies the probability of a rhizome branching at any given node.

<table>
<thead>
<tr>
<th></th>
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<th>Mean Sq</th>
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<td>15152541</td>
<td>25424</td>
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</table>
Figure 7: Plot of growing season stem density and nitrogen levels of a single hypothetical *Typha* species with differing rhizome branching probabilities
Figure 8: Plot of total aboveground net primary productivity and nitrogen levels of a single hypothetical *Typha* species under differing rhizome branching probabilities

**Competition Simulations**

Nutrient levels, branching probability, and their interaction had significant effects on the growing season stem density (Table 7) and the above ground net primary productivity (Table 8). Under low nutrient conditions, individuals with a higher branching probability tended to have a higher growing season stem density and aboveground net primary productivity, but under high nutrient conditions individuals with a low branching probability had a much greater growing season stem density (Figure 9) and aboveground net primary productivity (Figure 10) than those with a higher branching probability. These results demonstrate a strong competitive advantage of having low branching probability at high nutrients, but a slight competitive advantage of
having high branching probability at low nutrients. The competitive effect of branching appears to intensify as nutrient inputs increase, resulting in competitive exclusion at high nutrient levels but apparent stable co-existence at low to medium nutrient levels.

Table 7: ANOVA for the effect of nitrogen and branching probability on the growing season stem density. “N” signifies soil nitrogen level, “Branching” signifies the probability of a rhizome branching

<table>
<thead>
<tr>
<th></th>
<th>df</th>
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<th>Mean Sq</th>
<th>F value</th>
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<td></td>
</tr>
</tbody>
</table>

Table 8: ANOVA for the effect of nitrogen and branching probability on the above ground net primary productivity. “N” signifies soil nitrogen level, “Branching” signifies the probability of a rhizome branching.

<table>
<thead>
<tr>
<th></th>
<th>df</th>
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<td>105028555</td>
<td>176222</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 9: Plot of growing season stem density and nitrogen levels under differing rhizome branching probabilities.
Figure 10: Plot of total aboveground net primary productivity and nitrogen levels under differing rhizome branching probabilities.
Discussion

Monoculture

Without competition in high nutrient conditions, individuals with a low branching probability are more productive than frequently-branching individuals. As nitrogen availability decreases (e.g., lower than 25 gN m\(^{-2}\) yr\(^{-1}\)), those with a lower branching probability produce fewer ramets than individuals with a higher branching probability. However, between 25 and 35 gN m\(^{-2}\) yr\(^{-1}\), the relationship flips and those with a low branching probability produce more ramets than those with higher branching probabilities. This is interesting, given that high branch probability typically corresponds to higher ramet density, while low branch probability leads to lower ramet density (Sutherland & Stillman 1988). At high nitrogen levels, individuals with a low branching probability also have higher above ground net primary productivity; however, this advantage disappears at low nitrogen levels. This suggests that individuals that are less likely to branch belowground focus more of their energy in their growth aboveground, given that their net primary productivity is higher.

Competition

In a situation where multiple hypothetical *Typha* taxa with differing branching probabilities are competing with each other in high nutrient conditions, individuals with a low branching probability are able to outcompete those taxa with a high branching probability. These results are concordant with the results of the monoculture simulations, which suggest a competitive advantage to low branching probability only in high-nutrient conditions. This difference is most notably observed when nitrogen levels are greater than 25 gN m\(^{-2}\) yr\(^{-1}\). When nitrogen levels are greater than 40 gN m\(^{-2}\) yr\(^{-1}\), individuals
with higher branching probabilities have a growing season stem density and above
ground net primary productivity near 0, indicating they have been largely excluded
through competition. However, is it interesting to note that at low nitrogen levels, the
taxon with the lowest branching probability had a lower growing season stem density and
net primary productivity, while the taxon with the highest branching probability had the
highest growing season stem density and net primary productivity. In these simulations,
only the species with a low branching probability had any above ground net primary
productivity or growing season stem density. If this trend were to continue for several
more years in our model, it is likely that only this species would continue to grow, while
the rest would face eradication from this wetland. This indicates a potential mechanism
for competitive exclusion among *Typha* taxa, as is often observed in the field with *Typha*
x *glauca* outcompeting other *Typha* taxa. However, the model works by establishing the
growing environment as a taurus. When a rhizome reaches the edge of the wetland it
begins to grow on the other side of the wetland in the same direction, as close to the
previously established rhizomes as possible. In this way, it is not necessary for rhizomes
to branch in the model for ramets to be placed close together. It is likely that the high net
primary productivity and growing season stem density observed in the taxon with the
lowest branching probability in Figure 7 and Figure 8 at high nutrient levels is impacted
by this looping behavior. Whether this potential mechanism actually contributes to the
phenomenon observed in the field requires future field validation and testing.
Chapter 4: Conclusion

The most important findings of this thesis are that leaf width alone is not a reliable way to identify *Typha* taxa. Instead, the ratio of leaf length to leaf width is important to increasing accuracy of identification in the field. There is a high degree of overlap between *Typha angustifolia*, *Typha latifolia*, and *Typha x glauca*, which makes identification using morphological traits complex. *Typha x glauca* growing in nutrient rich environments has wider leaves (similar to *Typha latifolia*) further complicating identification. In low nutrient conditions, *Typha x glauca* is narrower, like *Typha angustifolia*. Whether or not the individual is flowering or not also has an effect on the leaf width of *Typha x glauca*.

In both a simulated monoculture of a single *Typha* species and in a scenario where multiple species of *Typha* with different probabilities of rhizome branching were simulated, those with a lower branching probability had a higher above ground net primary productivity in high nitrogen environments. It seems that ramets with rhizomes that are not branching may not spend as much energy producing another ramet, and therefore more energy goes towards the production of its own biomass. The optimal branching probability responds to nutrient availability, suggesting that evolutionary pressure on branching probability depends on the amount of nutrients in the environment.

These key findings provide insights into the biology of *Typha* taxa that may contribute to a better understanding of their competitive ability and invasiveness in disturbed wetlands.
References


