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The effects of nutrient resorption, photosynthetic rate, and leaf longevity on the success of *Typha × glauca*

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THE EFFECTS OF NUTRIENT RESORPTION, PHOTOSYNTHETIC RATE, AND
LEAF LONGEVITY ON THE SUCCESS OF *TYPHA* × *GLAUCA*

An Abstract of a Thesis
Submitted
in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Clarissa Marie Ruiz
University of Northern Iowa
July 2018

ABSTRACT

The hybrid cattail *Typha × glauca* is invasive in the Midwestern United States, and outcompetes wetland natives and its parent species, *Typha angustifolia* and *Typha latifolia* under high nutrient conditions. *Typha × glauca*'s large size and copious litter production are the main factors known to contribute to its success, although research is lacking on physiological processes that contribute to its nitrogen use efficiency.

Nitrogen resorption was investigated as a mechanism of dominance in *Typha × glauca*. Due to nitrogen resorption being a nutrient conservation strategy, nitrogen resorption should be high in areas of low nitrogen availability. Since nitrogen resorption is an energetically-costly process, we hypothesized that *Typha × glauca* would exhibit lower nitrogen resorption than either parent species, thereby not wasting energy on unnecessary nutrient conservation in the nutrient-rich environments where it is dominant. Nitrogen resorption was evaluated in *Typha × glauca* and its parent species across a nutrient gradient. Our results showed significant differences in resorption across the nutrient gradient; in areas of high nutrients nitrogen resorption was lower. However, resorption did not differ significantly between taxa. This suggests that nitrogen resorption is not a primary factor in *Typha × glauca*'s success.

Producing longer-lived leaves also conserves nutrients but decreases photosynthetic capacity. Because of this, we hypothesized that *Typha × glauca* would have a shorter leaf lifespan and a higher photosynthetic rate than its parents because in high nutrient areas competition is mainly for light and nutrient conservation is less advantageous. Leaf longevity and photosynthetic rate were measured in *Typha × glauca*

and its parent species across a nutrient gradient. Our results showed that leaf longevity did not differ between the three taxa or across a nutrient gradient. Photosynthetic rate differed between taxa; *T. angustifolia* exhibited the highest rates followed by *Typha* × *glauca* and *T. latifolia*. These results show that photosynthetic rate may be playing a role in *Typha* × *glauca*'s dominance over *T. latifolia*, but not *T. angustifolia*. There were significant differences in photosynthesis across a nutrient gradient with high soil nitrogen levels having the highest rates.

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This Study by: Clarissa M Ruiz

Entitled: THE EFFECTS OF NUTRIENT RESORPTION, PHOTOSYNTHETIC RATE,
AND LEAF LONGEVITY ON THE SUCCESS OF *TYPHA* × *GLAUCA*

has been approved as meeting the thesis requirement for
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TABLE OF CONTENTS

	PAGE
LIST OF TABLES	v
LIST OF FIGURES	vi
INTRODUCTION	1
CHAPTER 1. NITROGEN RESORPTION	11
CHAPTER 2. LEAF LONGEVITY AND PHOTOSYNTHETIC RATE.....	30
REFERENCES	51
APPENDIX: SUPPLEMENTAL DATA	60

LIST OF TABLES

TABLE	PAGE
1 AIC scores for Michaelis-Menten models to model the effect of fertilizer on live tissue nitrogen	19
2 ANOVA for the effect of fertilizer on live tissue nitrogen	19
3 The effect of reproductive status on live tissue nitrogen content	20
4 ANOVA for the effect of fertilizer on NRP.....	21
5 The effect of reproductive status on NRP.....	22
6 ANOVA for the effect of fertilizer on NRE	24
7 Quantity of slow-release fertilizer used for each soil nutrient level	34
8 ANOVA for the effect of fertilizer on leaf longevity for leaves assessed individually	38
9 ANOVA for the effect of fertilizer on leaf longevity for leaves assessed by their respective plant	39
10 Repeated-measures Analysis of Variance for the effects of fertilizer and taxa on photosynthetic rate in three different <i>Typha</i> taxa over the 10-week experiment.....	41
11 Tukey's Post-Hoc for the effect of fertilizer on the photosynthetic rate by taxa for weeks 4, 6, and 8.	41
12 ANOVA for the effect of fertilizer on photosynthetic rate.....	42
13 Average leaf longevity for each <i>Typha angustifolia</i> individual.....	60
14 Average leaf longevity for each <i>Typha</i> \times <i>glauca</i> individual	61
15 Average leaf longevity for each <i>Typha latifolia</i> individual	61

LIST OF FIGURES

FIGURE	PAGE
1 Michaelis-Menten model for live tissue nitrogen	20
2 NRP across a nutrient gradient	22
3 Differences in NRP between flowering and vegetative individuals across a nutrient gradient	23
4 NRE across a nutrient gradient	25
5 NRE by taxa across nutrient gradient	25
6 Leaf longevity assessed as individual leaves	38
7 Leaf longevity averaged by respective plant	39
8 Average photosynthesis for each taxon for each week of measurements	40
9 Average photosynthetic rate across a nutrient gradient with a linear fit	42
10 Changes in photosynthesis across a nutrient gradient over 10 weeks	43

INTRODUCTION

Background

The genus *Typha* in the family *Typhaceae* is a group of flowering plants commonly known as cattails. These perennial plants are herbaceous monocots that grow approximately 1 – 3 meters tall. *Typha* are semi-aquatic and found in areas with saturated soils, such as ponds, marshes, and ditches (Hellquist and Crow 2006). They propagate primarily asexually by rhizomes. Due to the nature of their reproduction, *Typha* form dense stands of vegetation with low biodiversity (Chadde 1998).

Two species within the genus *Typha*, *Typha latifolia* L. and *Typha angustifolia* L., grow and hybridize in the Midwestern and Great Lakes regions of the United States. *T. latifolia* is native to North America, but the native status of *T. angustifolia* is less clear. Previously the species was thought to have been introduced from Eurasia in the 1800's (Stuckey and Salamon 1987), but pollen from stratified soil samples (Carmichael 1980; Pederson et al. 2005), and herbarium records (Shih and Finkelstein 2008) show possible establishment of *T. angustifolia* in New England prior to European colonization. From New England, *T. angustifolia* spread to the Midwest. It has been documented as an invader in the Great Lakes region but has also been known to coexist with *T. latifolia* (Grace and Wetzel 1998). Environmental factors such as salinity (McMillan 1959) and water depth (Grace and Wetzel 1982) were found as partitioning factors that allowed the species to coexist. However, more recent studies did not find evidence of water depth causing niche partitioning in *Typha* taxa (McKenzie-Gopsill et al. 2012; Zapfe and Freeland 2015).

Although to some extent *T. angustifolia* and *T. latifolia* differ in their habitat, their flowering times overlap and the two readily hybridize (Ball and Freeland 2013). Their hybrid, *Typha* \times *glauc*a Godr., has become a problematic invader. This naturally occurring hybrid is mostly sterile and therefore spreads mainly asexually, although backcrosses have been documented (Travis et al. 2010). *T* \times *glauc*a displays high morphological plasticity (Bellavance and Brisson 2010), in part because of the occurrence of backcrossing (Snow et al. 2010). Consequently, identification of *T* \times *glauc*a can be difficult since characters such as leaf width and spike length vary widely across individuals (Snow et al. 2010). Nevertheless, *T* \times *glauc*a exhibits hybrid vigor, resulting in individuals typically being larger than either parent (Chadde 2013; Zapfe and Freeland 2015). *T* \times *glauc*a's success at outcompeting its parents is generally attributed to its size (Goldberg et al. 2017).

T \times *glauc*a is an opportunistic invader; its presence (Lawrence et al. 2016) and dominance (Elgersma et al. 2017) are correlated with areas of high nutrients and empirical research supports this phenomenon. In field experiments, Woo and Zedler found that in high nutrient treatments, *T* \times *glauc*a's aboveground biomass was more than double that of control plots (Woo and Zedler 2002). Additionally, modelling research using a computer simulation program called MONDRIAN showed that large invaders, such as *T* \times *glauc*a, are not successful under all nutrient conditions. In a community of established native vegetation, a large introduced invader like *Typha* could only dominate if there were sufficient nutrients. Under low nutrient conditions, the native vegetation persisted and the invader could not dominate (Currie et al. 2014).

Effects of Cattail Invasions

When *T. × glauca* invades a wetland, it forms dense monocultures that decrease biodiversity and change community dynamics (Tuchman et al. 2009). *T. × glauca*'s large quantity of litter reduces species diversity and the total stem density of native species of the neighboring plant community by significantly reducing light at the soil surface (Farrer and Goldberg 2009). Additionally, this litter increases extractable soil NH_4^+ , N-mineralization rates (Farrer and Goldberg 2009), soil NO_3 , and PO_4 (Tuchman et al. 2009).

A study performed at the Cheboygan Marsh in Michigan also found that *T. × glauca* caused changes in soil chemistry and composition. The researchers found that zones invaded by *T. × glauca* had higher soil organic matter and higher levels of nitrate and phosphate than uninvaded zones. This, coupled with their findings that bacterial and denitrifier communities were altered in invaded zones, led researchers to hypothesize that invasion by *T. × glauca* impacts wetlands' ability to remove nutrients (Angeloni et al. 2006). This is a noteworthy effect, since one of wetlands' most valuable ecological services is removing nitrogen from the environment (Zedler and Kercher 2005).

Research by McKee et al. (1989) supported that *T. × glauca* may interfere with wetlands' ecological services. McKee et al. showed that due to its aerenchyma, *T. × glauca* has significantly larger cross-sectional air spaces than the sampled native wetland species *Scolochloa festuacea* (Willd.) Link., *Phragmites australis* (Cav.) Trin. ex. Steud., *Scirpus acutus* Muhl., and *Scirpus validus* Vahl. (McKee et al. 1989). Large aerenchyma in wetland plants have been found to change redox potential in the soil

(Dacey and Howes 1984). Shifting the soil redox potential can significantly impact many biogeochemical processes such as methanogenesis (Jespersen et al. 1998). Changes in redox potential may consequently alter wetland functions and services.

In addition to impacting plant communities and soil chemistry, *T. × glauca*'s far-reaching effects can impact animal communities. A study in the Rainwater Basin of Nebraska found that migrating ducks prefer to rest in wetlands with intermediate emergent vegetation coverage (Webb et al. 2010). Their data show that a 50:50 ratio of vegetation to open water is most appealing to migrating ducks. Ducks are likely to avoid wetlands invaded by *T. × glauca* due to an insufficient amount of open water. Additionally, researchers in northeastern North Dakota found the diversity and abundance of ducks in invaded wetlands to be altered. For instance, wetlands sprayed by glyphosate herbicide (commonly used to reduce *T. × glauca* abundance) harbored significantly more Mallard (*Anas platyrhynchos*) and Northern Pintail (*Anas acuta*) ducks than unsprayed wetlands (Linz et al. 1996).

While the consequences of *T. × glauca* invasion are generally assessed in terms of environmental effects, there is evidence that *T. × glauca* invasions may have economic effects as well. Since *T. × glauca* has the potential to change waterfowl patterns, conservation funds can be impacted due to the alteration of revenue generated by duck license sales. Additionally, *Typha* spp. have been hypothesized to indirectly affect sunflower crop fields. This is due to *Typha* stands creating habitats for red-winged blackbirds, a predator of sunflower seeds. By reducing the abundance of cattails,

blackbird populations would likely decline and sunflower seed yields subsequently increase (Leitch et al. 1997).

Control of Cattail Invasions

To preserve functional wetlands, conservation and land management organizations have been working to manage *T. × glauca*. Spraying invaded areas with herbicide is one of the most frequently used treatments, although it may not be the best management option. Research shows that while herbicides kill aboveground plant matter, that organic matter remains where it is and decomposes. As it decomposes, nutrients are returned to the soil, further facilitating *T. × glauca* growth. Other treatment options such as burning and mowing were found to be ineffective for the same reason, although burning does volatilize some nitrogen if high enough temperatures are achieved. Data show that harvesting and removing *T. × glauca* is the most effective control strategy, since it removes the nutrient-rich biomass from the site (Lawrence et al. 2016). Unfortunately, this solution is rarely employed due to its cost and logistic concerns, and the need for continual treatment because *Typha* quickly regrows after cutting.

A study by Wilcox et al. (2017) corroborates that herbicide spraying may not be the best management option. Their research evaluated the following management options: cutting cattail ramets, hand-spraying cut stems with herbicide, tilling rhizomes by hand, and applying herbicide to re-sprouting cattail stems by hand-wicking. Researchers found that mixed method treatments were more effective at reducing *Typha* than any single management strategy. In particular, mixed method treatments that included either wicking or cutting performed the best. Time was also assessed as a

variable; treatments were either performed only in year one or in years one and two. Researchers found that in general, effectiveness of treatments such as cutting and spraying increased when applied in consecutive years. Similarly to Lawrence et al. (2016), Wilcox and associates recommended that to reduce *Typha*, cattail litter needs to be removed. In addition, Wilcox et al. recommended that ramets should be cut, and wicking or spraying treatments should be subsequently applied, both of which should be done for at least two years (2017).

Modelling research using the computer simulation program MONDRIAN further complicates the management issue by showing that the effectiveness of *Typha* management strategies are dependent on the level of nutrients in that wetland (Elgersma et al. 2017). Researchers found that in eutrophic wetlands, herbicide was the most effective singly-applied treatment, and repeated applications of herbicide resulted in more effective management. Combined methods treatments, especially herbicide and burning, were generally more effective than single method treatments. However, different effects were observed in oligotrophic wetlands. The results showed that in lower-nutrient wetlands, aggressive management techniques had relatively greater effects on natives than on *Typha*, making combination treatments less effective than single method treatments.

Causes of Cattail Invasions

T. × glauca invasions are likely caused by multiple, non-exclusive methods. There are at least three major potential mechanisms for *T. × glauca*'s success that have been studied, all of which are related to *T. × glauca*'s large size. The first is that live *T. ×*

glauca individuals outcompete neighboring plants for light (Woo and Zedler 2002; Larkin et al. 2012). *T. × glauca*'s height leads to a direct effect on the surrounding community. This mechanism aligns with the theory that in productive, nutrient-abundant areas, light should be more limiting than soil resources (Wilson and Tilman 1991; Tilman 1987; 1988).

The second mechanism is that *T. × glauca*'s dominance is caused by its large production of litter. This mechanism has been hypothesized to be more influential in the taxon's dominance than the presence of live individuals (Farrer and Goldberg 2009; Larkin et al. 2012). For example, Hager found that the shading caused by *T. × glauca* litter is more influential than light competition from live plants (Hager 2004). This is because live leaves, which are vertically oriented, cast little shade, but horizontally-oriented dead leaf litter casts a larger shadow. This significant reduction of light at the soil surface has been shown to reduce species diversity and the total stem density of native species of the neighboring plant community (Farrer and Goldberg 2009). *T. × glauca*'s litter also changes soil properties, such as levels of extractable soil NH_4^+ , N-mineralization rates (Farrer and Goldberg 2009), and soil NO_3^- and PO_4^{3-} (Tuchman et al. 2009). This can create a positive feedback effect which raises soil nutrients, further facilitating invasion (Farrer and Goldberg 2009; Tuchman 2012).

The third mechanism, described in Goldberg et al. 2017, is related to a plant's reproductive cost. When larger clonal plants have higher reproductive requirements, these large clonal plants expend more energy and resources in order to reproduce than do smaller plants. Historically, wetlands in the Midwestern Great Lakes region tended to be

oligotrophic systems, therefore plants that were adapted to those conditions would have a small size and consequently a lower reproductive cost. However, in recent years many of these once oligotrophic wetlands have been enriched by agricultural run-off, creating a mismatch between the environment that these small plants evolved in and the environment that they are currently in. In such a situation, a large invader with a high reproductive cost would be adequately adapted to these enriched wetlands and have a competitive advantage (Goldberg et al. 2017).

While *Typha × glauca*'s size can explain its dominance by means of the above mechanisms, little is known about the taxon's physiology. None of the aforementioned mechanisms are exclusive, therefore it is possible that physiological processes and traits are influential as well. It is likely that multiple mechanisms, including those described above and those yet to be described, are acting in concert to promote *T. × glauca*'s dominance. Previous research has defined a number of traits associated with faster growth and greater litter production, such as higher photosynthesis (Wright et al. 2004), higher surface leaf area, and high nitrogen concentration (Poorter and Bongers 2006).

Of these physiological traits, nitrogen use efficiency stands out as a being a possible key influence in systems with altered nitrogen inputs. Nitrogen use efficiency (NUE) is a measure of how efficient a plant is with the nitrogen that it takes up from the soil. NUE is the product of the mean residence time of a unit of nitrogen and the nutrient productivity (the rate of carbon fixation per unit nitrogen) within a plant (Aerts 1990). Having a higher NUE can lead to competitive success; numerous studies have found that

invasive species have higher NUE's than the native species that they outcompete (Matzek 2001; Feng et al. 2008; Feng and Fu 2008; Osunkoya et al. 2010).

While in general having a high NUE may tend toward competitive success, it is also possible that optimal NUE's exist under certain nutrient conditions. For instance, it seems intuitive that species characteristic of nutrient-limited conditions would exhibit higher NUE's in order to conserve nutrients. However, having a high NUE under high nutrient conditions may not be advantageous, as a trade-off may exist between nutrient conservation and other traits influential for fitness under high nutrient conditions, such as growth rate (Aerts 1999; Wright et al. 2004). This idea is supported by a number of studies of forest ecosystems that found that under low nutrient conditions, plants had higher NUE's (Vitousek 1982, 1984; Pastor et al. 1984). These studies suggest that soil fertility has helped shape the evolution of NUE.

However, a paper by Birk and Vitousek proposes that it is difficult to determine whether or not NUE is plastic in response to soil nutrient status (Birk and Vitousek 1986). These researchers sought to disentangle this problem with a study on loblolly pines (*Pinus taeda* L.) across a nutrient gradient. They concluded that within a species, changes in NUE occurred across a nutrient gradient, meaning that at least in loblolly pines, NUE is a plastic trait. Expanding on their findings, some species may exhibit more NUE plasticity than others, thereby responding more effectively to nutrient gradients. Studies such as Davidson et al. (2011) found that in general, invasive species exhibit more phenotypic plasticity in traits that affect fitness; one of which was NUE.

While the above studies are from forests (Vitousek 1982, 1984; Pastor et al. 1984; Birk and Vitousek 1986) and metanalyses of invasive and native plant species (Davidson et al. 2011), their principles can be hypothesized for other invaders, such as *T. × glauca*. The current literature on the NUE of *T. × glauca* across a nutrient gradient is lacking. Understanding this taxon's NUE can help give researchers a multi-faceted explanation of *T. × glauca*'s dominance and potentially allow for more effective management. In order to quantify the NUE of a species, both the mean residence time and nutrient productivity must be well understood. In this thesis, mean residence time will be explored both theoretically and experimentally in Chapters 1 and 2, and nutrient productivity will be similarly explored in Chapter 2.

CHAPTER 1

NITROGEN RESORPTION

Introduction

One of the two main physiological processes that influences the mean residence time of a unit of nitrogen in a plant is nitrogen resorption. Nitrogen resorption is a nutrient conservation strategy that recycles a portion of the nutrients that were invested into a leaf (Lambers et al. 2006), thereby increasing the residence time of those nutrients. This process occurs before leaf abscission and allows plants to withdraw nitrogen from the senescing leaf and translocate it to storage tissues.

Since nitrogen resorption is characterized as a nutrient conservation strategy, it is logical to assume that plants adapted to nutrient-poor environments would exhibit higher rates of nutrient resorption than those adapted to nutrient-rich environments. Many studies have shown that mean residence time of nitrogen is longer in plants that grow in nitrogen-limited environments (Aerts and de Caluwe 1995; Eckstein and Karlsson 1997; Vásquez de Aldana and Berendse 1997), and high nitrogen resorption may be a driving mechanism. However, trends from experimental data do not clearly support this theory. Some studies have found that nitrogen resorption is negatively correlated with soil nutrient status (Pugnaire and Chapin 1993; Enoki and Kawaguchi 1999), while other studies found no such relationship (Del Arco et al. 1991; Aerts 1996; Cartaxana and Catarino 2002).

There are multiple hypotheses for why this disconnect exists, one of which is the variation of nitrogen resorption. There are two methods used in the literature to quantify

nitrogen resorption, both of which illustrate the wide range in resorption values. The first of these methods, nitrogen resorption efficiency (NRE), is defined as “the amount of nutrients resorbed during senescence and is expressed as a percentage of the amount present in the leaves prior to senescence” (Aerts 1996). The second is nitrogen resorption proficiency (NRP), which is defined as “the levels to which nutrients have been reduced in senesced leaves” (Killingbeck 1996). Both methods are frequently utilized in the literature. NRE and NRP are negatively correlated in graminoids (Lawniczak 2011), as these methods measure the inverse of each other.

Across taxa, NRE varies from 0-80% (Killingbeck, 1996), and a metanalysis found NRE to average around 62% globally (Vergutz et al. 2012). The NRE of graminoids (such as *Typha*) was found to be about 59% (Aerts 1996). Although NRE data for *T. angustifolia*, *T. latifolia*, and *T. × glauca* is absent from the literature, researchers found the NRE of *Typha domingensis*, a cattail species in the southern United States, to be approximately 45% in experimentally enriched sites and 33% in unenriched sites (Miao 2004). Sampling of *T. domingensis* from Belize, California, and New Caledonia found an average NRE of 50.8% (Rejmánková 2005), meaning approximately half of the nitrogen in *Typha* leaves was resorbed.

As for nitrogen resorption proficiency, a paper found that in a lake in Poland, NRP in *T. angustifolia* was approximately 1.1% (Lawniczak 2011), meaning that nitrogen comprised 1.1% of leaf mass after senescence. Gürsoy et al. (2013) found slightly higher NRP in *T. latifolia* in two lakes differing in nutrient availability; NRP was 2.24% in one lake with lower nutrients and 1.23% in a higher nutrient lake.

Due to the evident variation in both NRE and NRP and conflicting data on the influence of a nutrient gradient on resorption, extrapolating a trend for all plant species may not be very predictive or biologically meaningful. However, determining a trend for the influence of a nutrient gradient on nitrogen resorption in *Typha* is more attainable, and has the potential to be beneficial for management of invasive taxa within the genus. One of the reasons for this is that nitrogen resorption directly affects the quantity of nitrogen that remains in leaf litter. Since high-nutrient litter exhibits faster rates of decomposition, this high-nutrient litter increases nutrient availability in the soil (Shaver and Melillo 1984). This mechanism provides the framework for the positive feedback loop identified by Lawrence et al. (2016) and Wilcox et al (2017) and their findings that effective management of *Typha* requires removing nutrient-rich litter.

Similarly to NUE, it is intuitive that resorption in species would vary across a nutrient gradient, due to within-species plasticity or between-species adaptations across the gradient. Resorption is an energetically-costly process (Lambers et al. 2006), which means that species that are well-adapted to nutrient-rich environments would be expected to have lower resorption values. In low-nutrient environments where nutrient uptake is more energetically expensive, resorption is expected to be higher. Also, similarly to NUE, certain species may exhibit more plasticity in their resorption—therefore, certain species may be able to modify physiological processes such as resorption under varying environmental conditions. While not directly addressed in this project, studies such as Funk (2008) and Davidson et al. (2011) support Baker's (1965) long-standing hypothesis that in general, invasive species are more plastic in their traits. However, other studies

have found results that do not support this theory (Drenovsky et al. 2012; Scharfy et al. 2011).

Based on *T. × glauca*'s dominance being correlated with areas of high nutrients, I hypothesize that *T. × glauca* will resorb less nitrogen than its parent species, thereby using less energy on nutrient conservation when nutrients are abundant. Additionally, this experiment seeks answers to the following three questions about nitrogen resorption in *Typha*. First, does nitrogen resorption in each taxon differ significantly across a soil nutrient gradient? Second, does nitrogen resorption differ significantly across taxa? And third, does variation in nitrogen resorption across a soil nutrient gradient differ between *Typha* taxa? The answers to these questions will improve our understanding of the mechanisms that make *T. × glauca* a successful invader.

Methods

Leaf tissue samples were collected from two research sites in Michigan as part of a large wetland mesocosm experiment. The first site, the Edwin S. George Reserve (42.4580506, -84.0117986), near Pickney, Michigan is owned and managed by the University of Michigan. The average annual temperature in the area is 8.89 °C and the average annual precipitation is 811.28 mm (NOAA 2010). The second site, the University of Michigan Biological Station (45.558653, -84.6797864), is at the northern tip of Michigan's Lower Peninsula near Pellston, Michigan. The average annual temperature there is 5.5 °C and the average annual precipitation is 766.32 mm (NOAA 2010).

Each site contained 50 mesocosms, two of which were unvegetated controls and therefore not included in this experiment. The remaining 48 tanks at each site were randomly assigned to one of 12 nutrient levels (0, 1.5, 3, 6, 9, 12, 15, 21, 27, 33, 39, or 45 gN m⁻² yr⁻¹). These nutrient levels were chosen to represent the full range of nitrogen inputs reported in the literature for Midwestern wetlands, with an emphasis (more levels) on the low end of the range where it was hypothesized that added nutrients would have greater effects on plant community composition. Nitrogen levels were factorially crossed with two vegetation treatments (*Typha* invading bare ground and *Typha* invading established vegetation), resulting in two sites with two vegetation treatments, each with 12 nitrogen levels and two replicates of each to compose a total of 96 experimental mesocosms.

The mesocosms were constructed in fall 2011. Mesocosms were composed of 1135-liter galvanized steel livestock tanks approximately 1.8 m across and 61 cm deep. These livestock tanks were lined with plastic to prevent leaching of heavy metals and filled almost entirely with sand. A thin (1.5 cm) layer of reed-sedge peat was added to the surface. Tanks were sunk flush with the ground to prevent overheating, and a buried irrigation system was installed to provide constant water flow into and out of the tanks to mimic groundwater flows through a wetland. Water was delivered to the bottom of the tank at an average rate of 2.5 L/min; water filtered up through the soil profile to mimic groundwater influx, and any water in excess of evapotranspiration exited an outflow at the soil surface to maintain constant saturated but unflooded conditions.

Native plant species were initially established in a greenhouse by planting seed obtained from commercial seed suppliers into soil plugs in 2011. The native species were *Juncus balticus* Willd., *Juncus nodosus* L., *Schoenoplectus acutus* (Muhl.) Á. & D. Löve, and *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller, the last of which was found to be contaminated with *Bulboscoenus maritimus* (L.) Palla. These species were chosen because they are very common in surveys of Michigan wetlands (DE Goldberg, unpublished data) and readily available from seed suppliers. Established plugs of these plants were subsequently transported to the mesocosms in May 2012.

Native vegetation plugs were planted in May 2012 by randomly assigning plugs to a gridded pattern within each mesocosm. Plugs were spaced 15 cm apart, and plants rapidly expanded into the bare spaces between plugs during the 2012 growing season. Mesocosms were invaded with cattails in May 2013. Cattail rhizomes were collected in and around Ann Arbor, MI in spring 2013 and each individual was measured upon collection. One rhizome of *T. angustifolia*, *T. × glauca*, and *T. latifolia* were planted into each tank, but survivorship varied among taxa. Plants that did not survive were replaced with new rhizomes in July 2013.

Fences were put up in summer 2013 at each location to prevent deer herbivory. Fertilizer was applied by hand-broadcasting twice in 2012. At the beginning of 2013 fertilizer was applied through a slow-release fertigation system that was replenished six times during the growing season, creating an even release of nutrients throughout the growing season (KJ Elgersma, unpublished data). Two slow-release fertilizers were mixed to create an N:P ratio of 30, which is the median N:P ratio of an extensive survey

of surface water nutrient concentrations throughout Michigan (Luszcz et al. 2015).

Periodic mowing around the tanks was done to prevent shading or invasion by weeds.

Samples of live leaf tissue were collected in August and early September 2015, and senesced tissue samples were collected in November 2015. Leaf tissue was taken by clipping one haphazardly-selected leaf from each taxon present in each tank. Because many of the cattails planted did not survive, not every taxon was present in every tank, resulting in an unbalanced design. The 359 total tissue samples were air dried and ground using a Wiley Mini Mill (Thomas Scientific, Swedesboro, NJ, USA) and 3 – 5 mg of sample were packed into tin capsules. Samples were processed by a Flash 2000 elemental analyzer (CE Elantech, Lakewood, NJ, USA).

For the resorption calculations, a mass correction factor was not used. Live tissue nitrogen data was calculated from 184 leaf tissue samples. NRP data was calculated by using senesced leaf tissue nitrogen from 174 leaf tissue samples. NRE was calculated by using live and senesced leaf tissue samples from 127 individuals in which both live and senesced samples were available. For each of these 127 individuals, NRE was calculated using the formula below:

$$\text{NRE} = \frac{N_{\text{live}} - N_{\text{senesced}}}{N_{\text{live}}} \times 100$$

Data were analyzed using R version 3.3.1. Three outliers with negative resorption efficiency values were excluded from the analysis. Residuals were checked for normality and heteroscedasticity. No transformations were needed to satisfy the assumptions of normality and homoscedasticity.

Results

Nitrogen Concentration in Live Leaves

All plants exhibited an increase in leaf N concentration in response to the fertilizer gradient (Figure 1). However, this increase was not linear but asymptotic, meaning increases at low levels of nitrogen result in a larger response of nitrogen concentration in live leaves than increases at high levels of nitrogen. Due to this nonlinear response, the quantity of nitrogen in the live tissue was analyzed using a Michaelis-Menten model:

$$N_{\text{leaf}} = \text{Int} + \frac{[V_{\text{max}} * N]}{[K_m + N]}$$

where N_{leaf} is the concentration of nitrogen in leaf tissue, Int is an intercept term, V_{max} is the asymptotic maximum leaf nitrogen concentration, N is the amount of nitrogen in each fertilizer treatment, and K_m is a half-constant. There are multiple versions of this model that differ in the way the intercept, V_{max} , and K_m parameters are considered. The most complex model is the Michaelis-Menten Full model, which allows the intercept, V_{max} , and K_m parameters to vary by taxon. The K_m , V_{max} , and Int models restrict each of these respective parameters so it cannot vary by taxon. The Reduced model restricts all three of the parameters (K_m , V_{max} , and intercept) from varying by taxon. Akaike information theory criteria (AIC) was utilized to select the most appropriate Michaelis-Menten model. Based on the results of each model's AIC scores, the reduced model was selected as the best model (Table 1), meaning none of the parameters in the final model varied by taxon.

Table 1: AIC scores for Michaelis-Menten models to model the effect of fertilizer on live tissue nitrogen.

Model	Df	AIC
Michaelis-Menten Reduced	4	311.6774
Michaelis-Menten K_m	8	318.2876
Michaelis-Menten V_{max}	8	318.3145
Michaelis-Menten Int	8	318.6091
Michaelis-Menten Full	10	324.8883

Significant differences in live leaf nitrogen were found across the nutrient gradient (Table 2) and live tissue nitrogen content increased as soil nutrient status increased (Figure 1). Significant differences in nitrogen content in green leaves were not found between taxa and there was no significant taxon*nutrient interaction (Table 2).

Significant differences were found between flowering and vegetative (nonflowering) individuals (Table 2); however this difference varied between taxa. *T. angustifolia* and *T. x glauca* had higher live leaf nitrogen in vegetative individuals, whereas *T. latifolia* had higher levels of nitrogen in reproductive individuals (Table 3).

Table 2: ANOVA for the effect of fertilizer on live tissue nitrogen. “Flower” signifies reproductive status and “Nlevel” signifies soil nitrogen level.

	Df	SS	MS	Fvalue	Pr(>F)
Flower	1	2.174	2.1737	7.0672	0.00857
Taxa	2	0.403	0.2013	0.6544	0.52103
Nlevel	1	17.366	17.366	56.4594	2.74E-12
Taxa:Nlevel	2	0.068	0.0338	0.1098	0.89607
Residuals	177	54.442	0.3076		

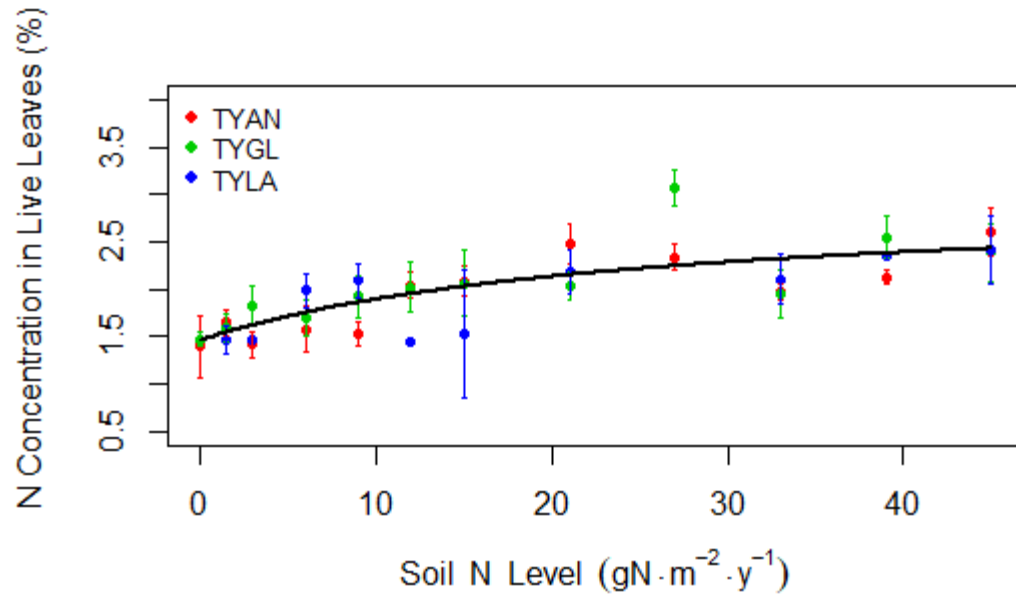


Figure 1: Michaelis-Menten model for live tissue nitrogen. TYAN refers to *T. angustifolia*, TYGL to *T. × glauca*, and TYLA to *T. latifolia*.

Table 3: The effect of reproductive status on live tissue nitrogen content. Reproductive status is designated as flowering (F) or vegetative (V).

Taxon	Average Live Tissue N (%)	
	F	V
<i>T. angustifolia</i>	1.87 (0.10)	2.02 (0.10)
<i>T. × glauca</i>	1.86 (0.09)	2.24 (0.12)
<i>T. latifolia</i>	2.03 (0.10)	1.79 (0.30)
All taxa	1.92 (0.006)	2.02 (0.008)

Nitrogen resorption proficiency

The average NRP for all taxa was 0.82, meaning senesced leaves contained on average 0.82% nitrogen by mass. There were significant differences in NRP across the nutrient gradient, varying from an average of 0.54 at the low end of the nutrient gradient to an average of 1.01 at the high end of the gradient. This represents a doubling of NRP across the gradient, with consistent linear increases along the gradient (Figure 2). No significant differences were found for nitrogen resorption proficiency between the three taxa (Table 4). There was not a significant flower:Nlevel interaction, so this term was dropped from the model.

Table 4: ANOVA for the effect of fertilizer on NRP.

	Df	SS	MS	F value	Pr(>F)
Flower	1	0.516	0.516	12.0804	0.000649
Species	2	0.1655	0.08273	1.9367	0.147398
Nlevel	1	2.5584	2.55841	59.8963	9.07E-13
Species:Nlevel	2	0.0869	0.04344	1.0171	0.363883
Residuals	167	7.1332	0.04271		

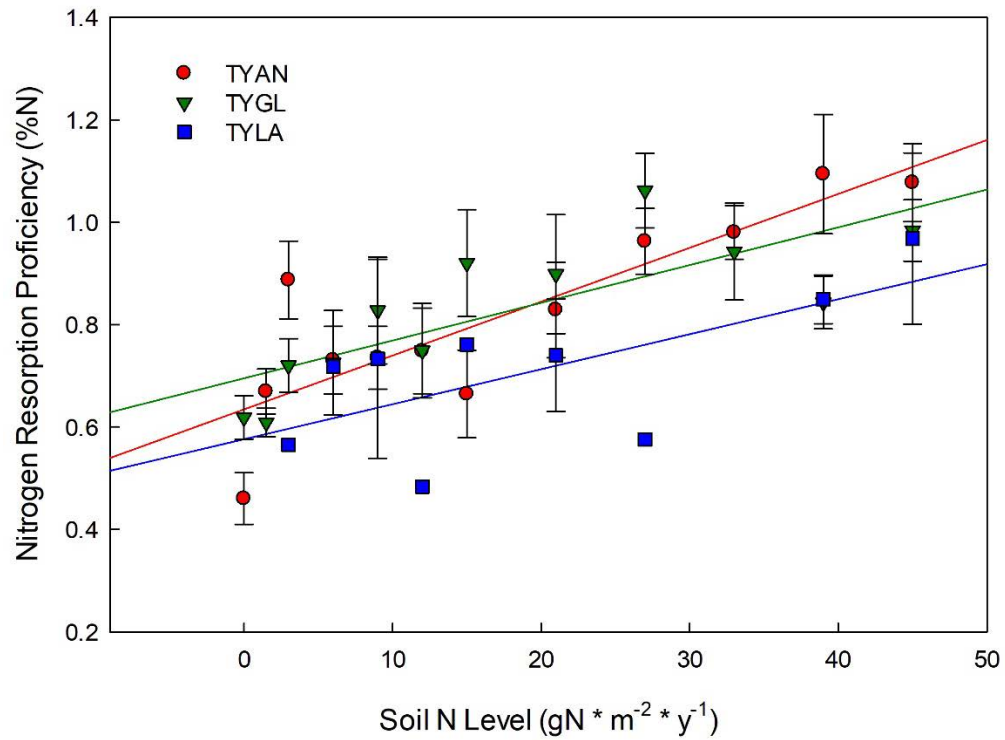


Figure 2: NRP across a nutrient gradient. Absence of error bars in some TYLA samples are due to there only being a single replicate.

There were also significant differences in NRP between vegetative and flowering individuals. Flowering individuals exhibited higher NRP than vegetative on average across taxa (Table 5) and across the nutrient gradient (Figure 3).

Table 5: The effect of reproductive status on NRP.

Taxon	Average NRP	
	F	V
<i>T. angustifolia</i>	0.89 (0.008)	0.77 (0.006)
<i>T. × glauca</i>	0.90 (0.005)	0.78 (0.006)
<i>T. latifolia</i>	0.78 (0.019)	0.66 (0.031)
All taxa	0.88 (0.003)	0.77(0.003)

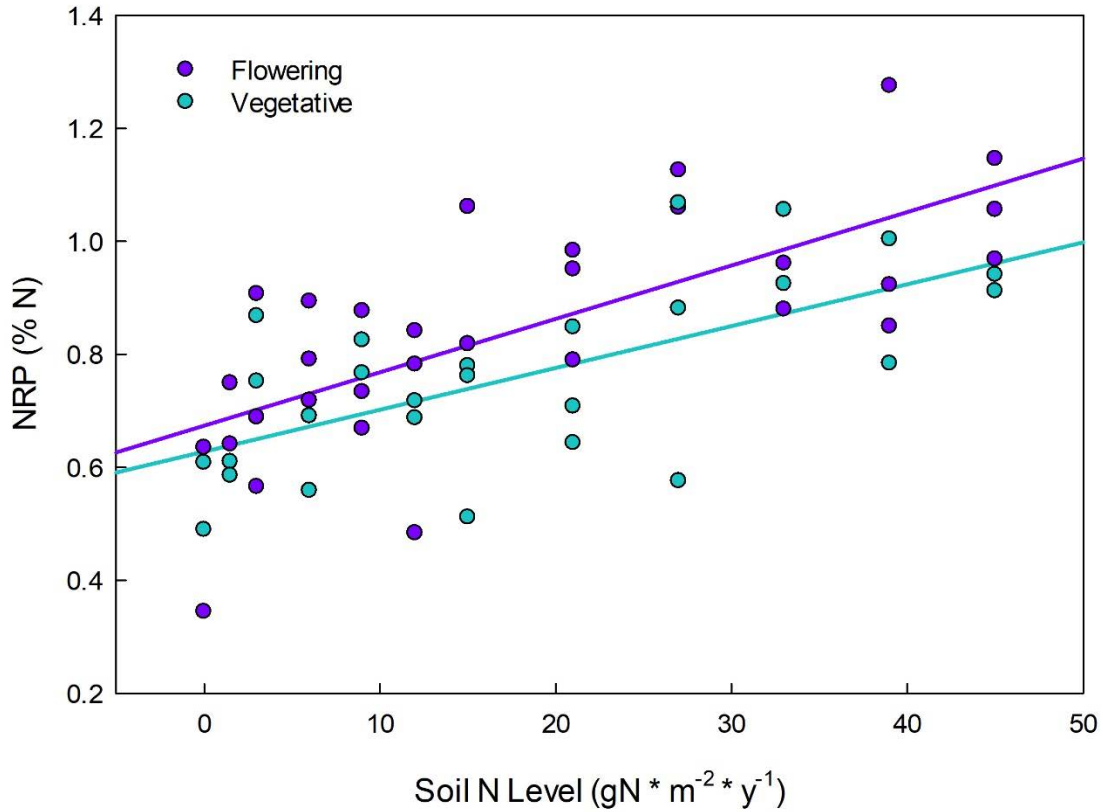


Figure 3: Differences in NRP between flowering and vegetative individuals across a nutrient gradient.

Nitrogen Resorption Efficiency

NRE calculated for the 127 samples in which both green and senesced tissue was available averaged 56% across all taxa and soil nitrogen levels, and averaged 55% for *T. angustifolia*, 60% for *T. × glauca*, and 58% for *T. latifolia*. No significant differences in NRE were found between the three taxa or between flowering and vegetative individuals (Table 6). When evaluating all taxa together, a slight, nonsignificant decrease in NRE was observed as soil nitrogen status increased (Figure 4). When individual taxa were examined, this trend was observed in *T. angustifolia* and *T. × glauca* (Figure 5). This

trend was not observed in *T. latifolia*, likely due to its sample size being much smaller than that of *T. angustifolia* and *T. × glauca* ($n = 12$ compared to $n = 54$ and $n = 61$, respectively). Variability was lower when resorption was expressed as NRE (st. dev. = 0.15) than when it was expressed as NRP (st. dev. = 0.25).

Table 6: ANOVA for the effect of fertilizer on NRE.

	Df	SS	MS	F value	Pr(>F)
Flower	1	0.03592	0.035924	1.6432	0.2024
Taxa	2	0.01988	0.009939	0.4546	0.6358
Nlevel	1	0.03144	0.031439	1.4381	0.2328
Taxa:Nlevel	2	0.00782	0.003909	0.1788	0.8365
Residuals	120	2.62341	0.021862		

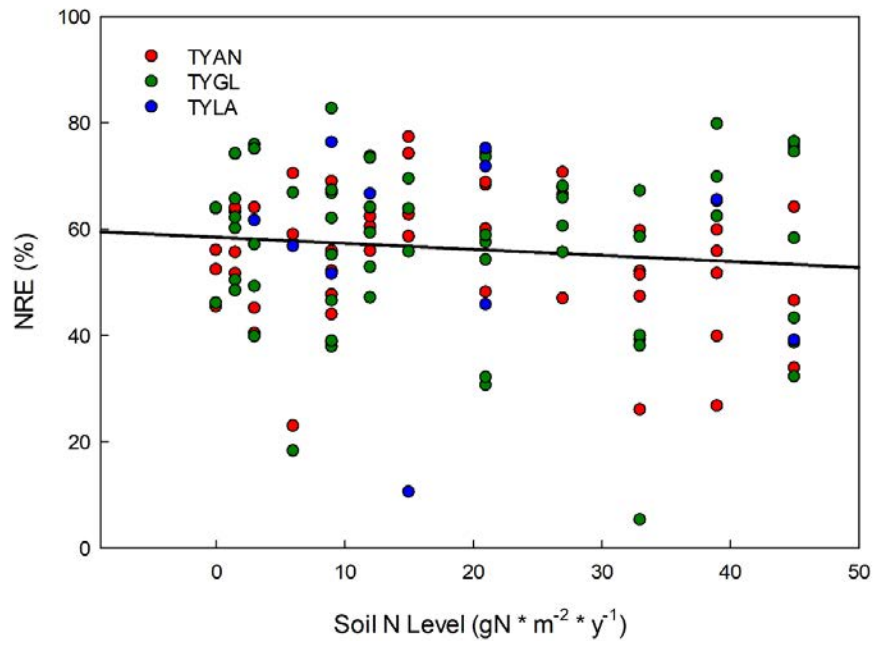


Figure 4: NRE across a nutrient gradient. TYAN refers to *T. angustifolia*, TYGL to *T. × glauca*, and TYLA to *T. latifolia*.

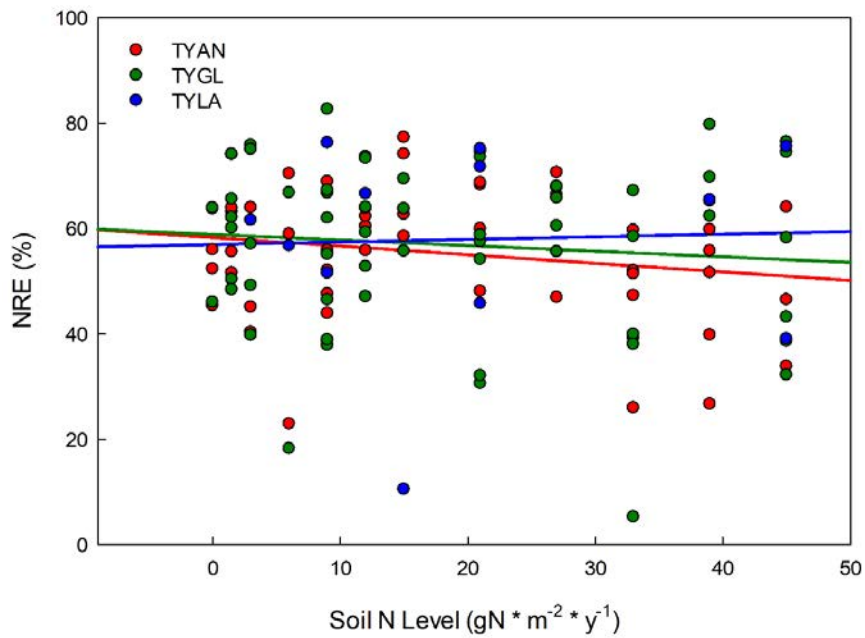


Figure 5: NRE by taxa across nutrient gradient. TYAN refers to *T. angustifolia*, TYGL to *T. × glauca*, and TYLA to *T. latifolia*.

Discussion

Nitrogen Concentration in Live Leaves

The live tissue results indicate that the quantity of nitrogen in a plant's live tissues is highly dependent on the nutrient status of the surrounding soil. As seen in Figure 1, an increase in soil nitrogen corresponds to an increase in live tissue nitrogen. However, this trend is not linear; at high nitrogen levels, live tissue nitrogen values level off. Either leaf nitrogen in *Typha* is maximized or uptake is saturated.

Nitrogen resorption proficiency

Nitrogen resorption proficiency was significantly different across a nutrient gradient; NRP was highest at high soil nitrogen levels and lowest at low soil nitrogen levels. This means that terminal nutrient content in senesced tissue was higher under high nutrient conditions. It appears that at least for *Typha*, NRP is strongly influenced by soil nutrient gradients.

A limitation to NRP is that its calculation does not include live tissue nitrogen. Because of this, it is possible that similar amounts of nitrogen were resorbed across all nutrient levels, yet the plants at high nutrient levels had more nitrogen in their tissues to start with (higher live tissue nitrogen), resulting in higher terminal nitrogen levels. The live tissue data support this possibility, since at high nutrient levels, the plants had higher live tissue nitrogen levels (Figure 1).

Across taxa, NRP was not found to be significantly different. This lack of significance may have been caused by multiple reasons. The first reason is that due to asexual reproduction, each *T. × glauca* individual is the clone of a single F1 hybrid that was likely formed de novo in its specific environment. Also, in the rare instances that F2

or advanced hybrids persist, these hybrids are very recently formed (typically <50 years in the Midwest) and selection has not yet had time to act (Lishawa et al. 2013). A second potential explanation is that the possible phenotypes of NRP generated from *T. × glauca*'s parent species do not differ from those of its parents.

Nitrogen Resorption Efficiency

Similarly to NRP, NRE did not differ between species, likely for the same reasons stated above. In contrast to NRP, NRE did not differ across a nutrient gradient. This may be attributed to a smaller sample size in NRE, as there were only 127 individuals from which both live and senesced tissue samples were taken (compared 184 live tissue samples and 174 senesced samples). Additionally, calculating NRE inherently introduces greater variance than calculating NRP. This is because NRP only includes variance from the senesced data, rather than the variance of both the live and the senesced data (which is included in the NRE calculation).

Aside from the above limitations in the data and calculations, the conflicting NRE and NRP results do align with the literature. For instance, a study on Australian sclerophyll species examined NRE and NRP in multiple species at nutrient-rich and nutrient-poor sites. The researchers found that NRE did not differ between low and high nutrient soils, however NRP did differ significantly. They found that in nutrient-poor habitats, NRP was lower than in nutrient-rich habitats (Wright and Westoby 2003). They correlate their findings with Killingbeck's ideas in his 1996 paper, which proposes that selection has acted on terminal nutrient content in senesced leaves (NRP) rather than the proportion of resorbed nitrogen (NRE).

Conclusions

Nitrogen resorption measured as NRP yielded clear results, however there are multiple explanations for these results. It is possible that NRP was higher at high nutrient levels because resorption was lower. It is also possible that resorption was similar across nutrient levels, however at higher nutrient levels, plants had higher live tissue nitrogen. This would lead to plants at high nutrient levels having higher terminal nitrogen and the appearance of lower rates of resorption. To disentangle these explanations, NRP should be used in conjunction with NRE, as was done in this study. However, our NRE results did not show differences in NRE across a nutrient gradient. This, along with the trends from the live tissue data, leads me to believe that resorption was similar across a nutrient gradient and that the apparent effect on NRP is caused by live tissue nitrogen. However, in order to reach a concrete conclusion more information is needed. Increasing the sample size for NRE would provide greater resolution to the relationship between live tissue nitrogen, NRP, and NRE.

While nitrogen resorption does not appear to be related to the dominance of *T. × glauca* over its parents, mean residence time still be may playing a role in fitness. Leaf longevity or other physiological factors may have a stronger impact on mean residence time than nitrogen resorption. For example, studies on evergreen and deciduous woody species in Central Spain by Escudero et al. (1992) showed that leaf longevity was far more important as a nutrient conservation mechanism than high resorption efficiency. Reich et al. (1995) arrived at a similar conclusion in a study with evergreen and deciduous woody species of an oligotrophic Amazonian forest. Their findings make sense

because variation usually observed in leaf life span is much larger than that in resorption efficiency, leading to a greater potential for impact on mean residence time. While a larger sample size for NRE may improve resolution of results, it is also possible that other physiological processes, like leaf longevity, are contributing more strongly to $T. \times glauca$'s dominance.

CHAPTER 2

LEAF LONGEVITY AND PHOTOSYNTHETIC RATE

Introduction

Mean residence time is a measure of how long a unit of a given nutrient remains within a plant (Small 1972; Berendse and Aerts 1987; Kazakou et al. 2007). Mean residence time strongly affects a plant's nitrogen use efficiency (NUE), since NUE is equal to the product of mean residence time and nutrient productivity (the rate of carbon fixation per unit nitrogen) within a plant (Aerts 1990). Mean residence time is highly influenced by leaf longevity, because leaf senescence and litter production result in a loss of nutrients due to incomplete nutrient resorption. In this way, having long-lived leaves can increase a plant's nutrient use efficiency.

Since leaf longevity has the potential to increase a plant's NUE, having longer living leaves could give a plant a competitive advantage due to nutrient conservation. Long leaf lifespan is a common attribute of nutrient-conserving species (Reich et al. 1997), which in turn have been found to dominate nutrient-poor habitats (Grime 1977; Chapin 1980). This suggests that under low nutrient conditions, having a long leaf life may be advantageous.

However, increasing leaf lifespan has been found to have a negative effect on nutrient productivity, as photosynthesis generally decreases as a leaf ages past maturity (Reich et al. 1991, 1992). Therefore, having a long-lived leaf can negatively impact a plant's fitness because the leaf may become energetically negative (taking in more energy for respiration than it is producing from photosynthesis). Also, in more productive ecosystems, where competition is mainly for light (Tilman 1987, 1988), it may be

disadvantageous to have long-lived leaves because it is reducing the plant's ability to capture and utilize light.

Because of leaf longevity's contrasting effects on fitness, many researchers have proposed and found evidence for a trade-off effect in which increasing leaf longevity corresponds to a decrease in nutrient productivity (Eckstein and Karlsson 1997; Yasumura et al. 2002; Silla and Escudero 2004; Yuan and Li 2007, Yuan, Chen and Li 2008). Due to this trade-off, an optimal balance may exist between leaf longevity and nutrient productivity, which may lead to a competitive advantage. Hence, a plant at this optimal balance would have leaves that senesce and are replaced by new, photosynthetically effective leaves before a leaf becomes energetically negative.

It is likely that the location of this balance point in which leaf longevity and nutrient productivity are optimized would be strongly influenced by soil nutrient status. In lower-nutrient areas, it may be advantageous to fall higher on the range for leaf longevity, and lower on the range for nutrient productivity. In higher-nutrient areas, the reverse would likely be true, and plants that are adapted to high-nutrient environments should have shorter leaf lifespans because the energetic cost of nutrient uptake to replace nutrients lost in leaf litter will be lower in high-nutrient soil.

Since *Typha × glauca* often dominates in high-nutrient environments (Lawrence et al. 2016; Elgersma et al. 2017), I am hypothesizing that *T. × glauca* would exhibit shorter living leaves in relation to its parent species. This is because in high nutrient areas where *T. × glauca* dominates, nutrients are abundant so plants with long-lived leaves will

be unnecessarily conserving nutrients, thereby losing out on potential photosynthetic capacity.

To understand leaf longevity in *Typha* taxa, this study seeks to answer the following research questions: First, does leaf longevity differ across taxa? Second, does leaf longevity differ across a soil nutrient gradient? And third, does variation in leaf longevity across a soil nutrient gradient differ between *Typha* taxa?

In conjunction with these questions, answers to the following three questions will be sought: First, does photosynthetic capacity differ across taxa? Second, does photosynthetic capacity differ across a soil nutrient gradient? And third, does variation in photosynthetic rate across a soil nutrient gradient differ between *Typha* taxa?

The answers to these research questions will improve our understanding of the mechanisms that make *T. × glauca* a successful invader and increase our understanding of the potential existence and consequences of a trade-off between leaf longevity and photosynthetic capacity.

Methods

T. × glauca, *T. angustifolia*, and *T. latifolia* individuals were collected from wetlands in Iowa. Since *Typha* species reproduce clonally, individuals at each site were collected at least five meters from any other collected individual. Collecting ramets from several meters away greatly increases the likelihood of genetic diversity (Travis et al. 2011). Each individual's collection location was recorded using a Garmin GPS device. *T. × glauca* was collected from Sweet Marsh Wildlife Management Area in Bremer County (42.8263917,-92.2271329) and *T. angustifolia* was collected from a marsh in Cedar Falls,

on the Cedar Valley Trail just northeast of the pedestrian bridge that crosses Highway 58 (42.491962, -92.454070). *T. latifolia* was collected from Engeldinger Marsh in Polk County (41.7764722, -93.3513255), which is an area with high *T. latifolia* abundance. However, since collection occurred when leaves were not yet fully expanded, identification in the field was difficult. Genetic analysis revealed that of the 21 individuals originally identified in the field as *T. latifolia*, only four proved to be *T. latifolia*.

Once collected, the individuals were placed in 25 cm diameter × 23 cm deep pots. The pots had drainage holes and were placed into 6-cm deep trays containing water, with two pots per tray. This arrangement maintained saturated soil conditions in the pots. Each pot contained 50% peat moss and 50% sand as a layered mix, with the sand as the bottom layer to facilitate drainage. Additionally, each pot contained a fertilizer treatment mixed into the peat moss layer. The fertilizer was Alaska brand slow-release pellets with a 6-4-6 NPK. There were seven nutrient treatment levels, shown in Table 1. Initially, four replicates of each species were established for each treatment level, although transplant mortality and genetic identification results produced an unbalanced experimental design with reduced replication (Table 7).

Table 7: Quantity of slow-release fertilizer used for each soil nutrient level

Taxon	Treatment (gN/m²/yr)	Area of pot (m²)	Quantity of fertilizer (gN)	Sample size
<i>T. angustifolia</i>	0	0.048	0	6
	3	0.048	2.4	6
	9	0.048	7.2	5
	15	0.048	12	5
	27	0.048	21.6	4
	39	0.048	31.2	2
	45	0.048	36	3
<i>T. × glauca</i>	0	0.048	0	3
	3	0.048	2.4	3
	9	0.048	7.2	3
	15	0.048	12	4
	27	0.048	21.6	5
	39	0.048	31.2	4
	45	0.048	36	2
<i>T. latifolia</i>	0	0.048	0	1
	3	0.048	2.4	0
	9	0.048	7.2	0
	15	0.048	12	1
	27	0.048	21.6	1
	39	0.048	31.2	0
	45	0.048	36	1

The trays were set up outdoors at the University of Northern Iowa Tallgrass Prairie Center on level ground in full sunlight and fenced to deter mammalian herbivory. The pots were assigned to trays and arranged in rows using a modified random approach: to prevent nutrient contamination between treatment levels, both pots in each tray had the same nutrient treatment, but otherwise pots were arranged randomly. Pots were re-randomized on an approximately monthly basis. Water levels in the trays were checked regularly to maintain soil moisture and the pots were watered as needed to maintain soil

moisture. Pots were weeded and new *Typha* propagules were clipped as necessary to maintain a single ramet in each pot.

The individuals were allowed to acclimate for approximately two weeks, and on May 28 all aboveground growth was cut back. Starting on June 11, the length and width of each leaf on each plant were recorded every other week until October 25, when all leaves on all plants had senesced. Leaf longevity was determined by subtracting the birth and death date of each individual. The death date was determined as when the leaf was 100% brown.

Throughout the growing season (June 29, 2017 to September 14, 2017), light-saturated photosynthesis (A_{sat}) on one leaf from each plant was measured using an open path gas-exchange system (LI-6400, Li-Cor Inc., Lincoln, NE). For the first measurement, the youngest fully expanded leaf was selected and all subsequent measurements were made on that same leaf for the remainder of the season. Measurements were made once per week, between 1000 and 1300 CST, at a controlled cuvette temperature of 29°C, a reference CO₂ concentration of 410 $\mu\text{mol}\cdot\text{mol}^{-1}$, a vapor pressure deficit of 1.4-1.6 kPa, and a saturating irradiance of 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Plants were measured in random order each day. Leaf area was measured in the field using a digital caliper. Plants were measured until the time at which the focal leaf senesced (i.e., photosynthetic rate $\approx 0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The photosynthetic rates of plants with a senesced leaf were assigned a value of 0 from that point forward. Any photosynthetic rates that were measured as negative were replaced with zeros.

On September 27th, green leaf tissue samples were collected from each individual to use for genetic confirmation of taxonomic identity using previously-published microsatellite markers. All of the collected samples were from vegetative individuals, as no plant produced a stem with a spike. The tissue samples were frozen immediately after collection, and the leaf collected for genetics was excluded from other analyses. DNA was extracted using a Thermo Scientific GeneJET Plant Genomic DNA Purification Mini Kit (#K0791, #K0792). A 3-primer PCR method was used (Schuelke 2000) with a FAM labeled M13 primer 5'-/56-FAM/CGAGTTTCCCAGTCACGAC. Primers for locus TA 3, TA 5, and TA 20 were used (Tsyusko-Omelchenko et al. 2003) with an M13 tag (5'CGAGTTTCCCAGTCACGAC) added to the 5' end of each forward primer (Schuelke 2000) and a short tag (5'GTTTCTT) on the 5' end of each reverse primer to reduce stutter (Brownstein et al. 1996). Our primer mix was made with 30 μ L of M13 FAM; 30 μ L of TA 5 R, TA 20R, and TA 3 R; 3 μ L of TA 5 F, TA 20 F, and TA 3 F; and 171 μ L of H₂O. GoTaq G2 Hot Start Colorless Master Mix was utilized. PCR was performed in a T gradient machine. Cycling parameters were 95 °C for 2 min; 28 cycles of 94 °C for 40 sec, 53 °C for 40 s, and 72 °C for 40 s; 72 °C for 45 min; then 15 °C until ready to be frozen. The samples were then sent to Iowa State University DNA Facility to be genotyped. Results were analyzed using SoftGenetics GeneMarker V2.6.4 software. Our samples were compared to three samples of extracted DNA from genetically confirmed *T. angustifolia*, and four genetically confirmed *T. latifolia* from Snow et al. 2010, which were prepared as above. For all individuals, the alleles at the

three microsatellite loci (TA 5, TA 20, and TA 3) were in agreement, meaning that species designations were clear and further analysis was not needed.

Results

Leaf Longevity Results

Differences in leaf longevity were calculated by assessing all leaves individually (Figure 6) using a mixed model to account for non-independence of leaves from the same plant, and by calculating an average leaf longevity for each plant (Figure 7). This was based on our hypothesis that all leaves would not exhibit similar longevity. For example, the first leaf on a plant may have a different longevity than the last leaf produced on a plant. By averaging leaf longevity for each plant, both early and late leaves and their respective longevity are included. However, neither method of analysis resulted in significant differences between taxa (Tables 8 and 9) and leaf longevity was highly similar between taxa. Leaf longevity increased slightly as soil nitrogen increased, however this increase was not significant.

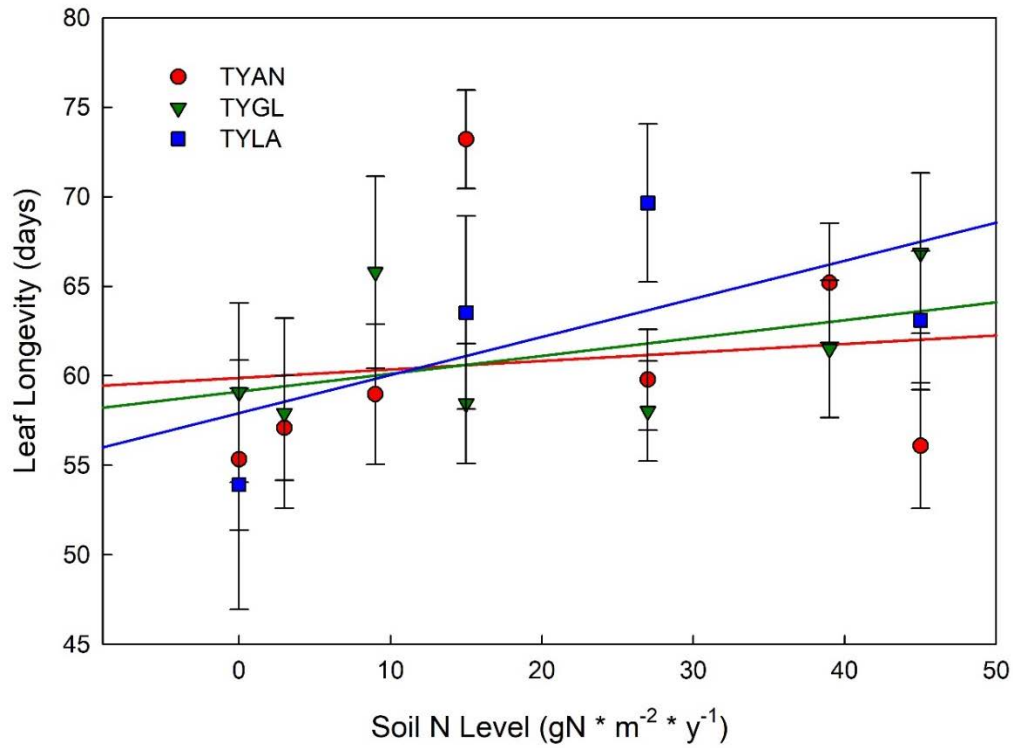


Figure 6: Leaf longevity assessed as individual leaves. Data points are means for each taxon at each nitrogen level, and regression lines are determined by ordinary least squares. TYAN refers to *T. angustifolia*, TYGL to *T. × glauca*, and TYLA to *T. latifolia*.

Table 8: ANOVA for the effect of fertilizer on leaf longevity for leaves assessed individually. Nlevel signifies soil nitrogen level.

	numDF	denDF	F-value	p-value
(Intercept)	1	696	1654.955	<.0001
Taxa	2	53	0.0866	0.9172
Nlevel	1	53	0.7883	0.3786
Taxa:Nlevel	2	53	0.0615	0.9404

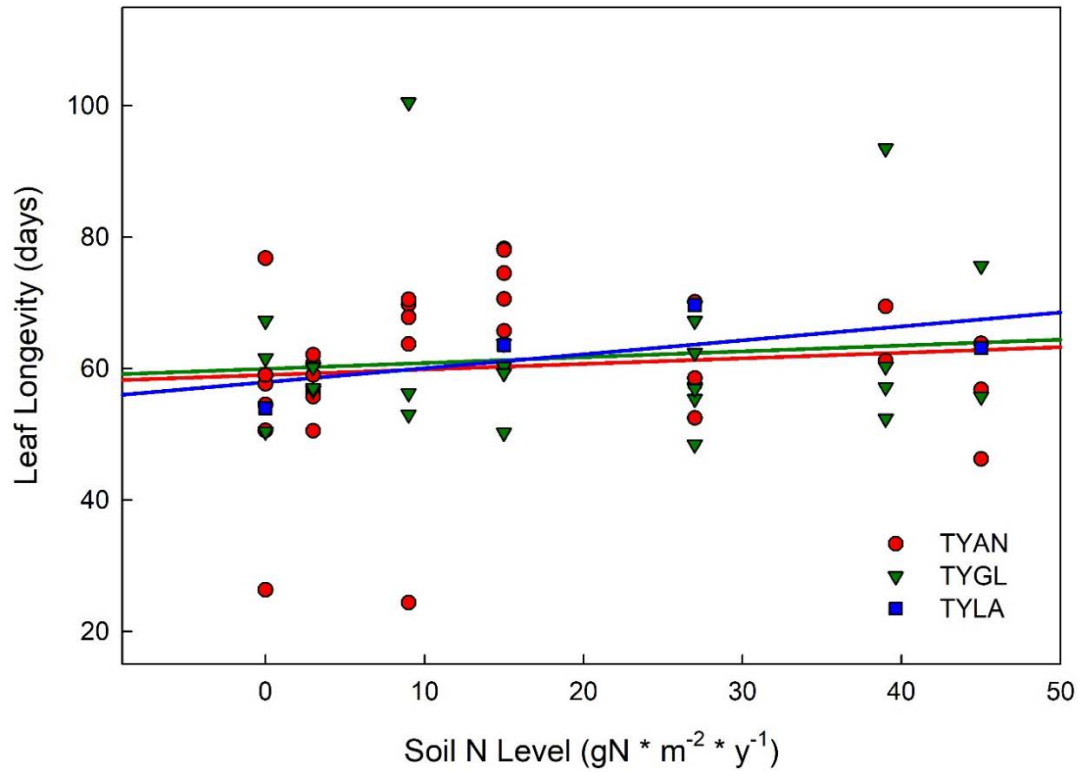


Figure 7: Leaf longevity averaged by respective plant. Regression lines are determined by ordinary least squares. TYAN refers to *T. angustifolia*, TYGL to *T. × glauca*, and TYLA to *T. latifolia*.

Table 9: ANOVA for the effect of fertilizer on leaf longevity for leaves assessed by their respective plant.

	Df	SS	MS	F-value	Pr(>F)
Species	2	38.2	19.086	0.1223	0.8851
Nlevel	1	126.7	126.728	0.8122	0.3716
Species:Nlevel	2	15.8	7.892	0.0506	0.9507
Residuals	53	8269.8	156.034		

Photosynthesis Results

Photosynthesis was analyzed using a repeated measures analysis. From week 1 to week three, photosynthesis generally increased across taxa. From week 3 to week 10, photosynthesis decreased in all taxa (Figure 8). Our results showed that there were significant differences in photosynthesis between taxa (Table 10). Since week was also found to be a significant factor in photosynthetic rate (Table 10), Tukey post-hoc tests were used to determine which species were different from each other and in which weeks they were different (Table 11). Photosynthesis measurements with a value of 0 were included in all analyses.

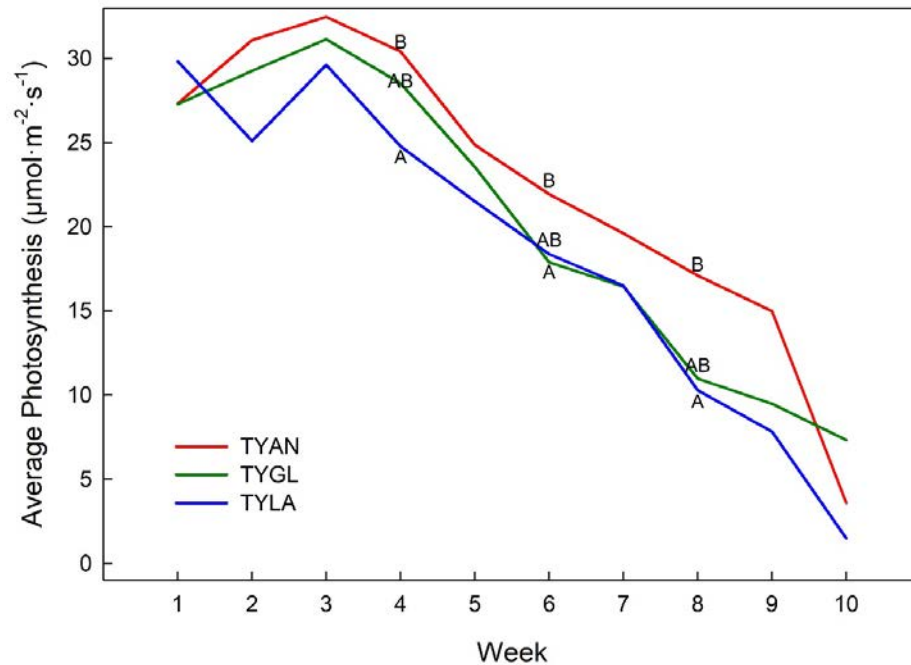


Figure 8: Average photosynthesis for each taxon for each week of measurements. TYAN refers to *T. angustifolia*, TYGL to *T. × glauca*, and TYLA to *T. latifolia*. Significantly different values between taxa for weeks 4, 6, and 10 are notated by letters. For week 8, TYAN was considered to be significantly different from TYLA although its p-value was 0.0526 (Table 11).

Table 10: Repeated-measures Analysis of Variance for the effects of fertilizer and taxa on photosynthetic rate in three different *Typha* taxa over the 10-week experiment.

	numDF	denDF	F-value	p-value
Between subjects				
(Intercept)	1	517	1919.909	<.0001
Taxa	2	53	3.8124	0.0284
fertilizer	1	53	12.8425	0.0007
Taxa: fertilizer	2	53	1.763	0.1814
Within subjects				
Week	9	576	9.147128	7.280153e-52

Table 11: Tukey's Post-Hoc for the effect of fertilizer on the photosynthetic rate by taxa for weeks 4, 6, and 8. TYAN refers to *T. angustifolia*, TYGL to *T. × glauca*, and TYLA to *T. latifolia*.

		diff	lwr	upr	p adj
Week 4	TYGL-TYAN	-1.89341	-4.369502	0.582674	0.165399
	TYLA-TYAN	-5.64758	-10.4859	-0.80926	0.018463
	TYLA-TYGL	-3.75417	-8.672462	1.164129	0.166428
Week 6	TYGL-TYLA	-4.04083	-7.555877	-0.52579	0.020644
	TYLA-TYAN	-3.56333	-10.3954	3.2686836	0.424924
	TYLA-TYGL	0.477500	-6.454260	7.40926	0.984893
Week 8	TYGL-TYAN	-6.12492	-12.3068	0.05692922	0.052641
	TYLA-TYAN	-6.82001	-18.8354	5.19535496	0.364210
	TYLA-TYGL	-0.69508	-12.8859	11.49569	0.989624

Photosynthesis differed significantly across the soil nutrient gradient (Table 10). Photosynthetic rate increased linearly as soil nitrogen increased (Figure 9). As expected, over the ten-week period, photosynthetic rates of individuals at all nutrient levels declined over time after the initial increase in the first 3 weeks (Figure 10).

Figure 9: Average photosynthetic rate across a nutrient gradient with a linear fit. Colors indicate which week each data point is from.

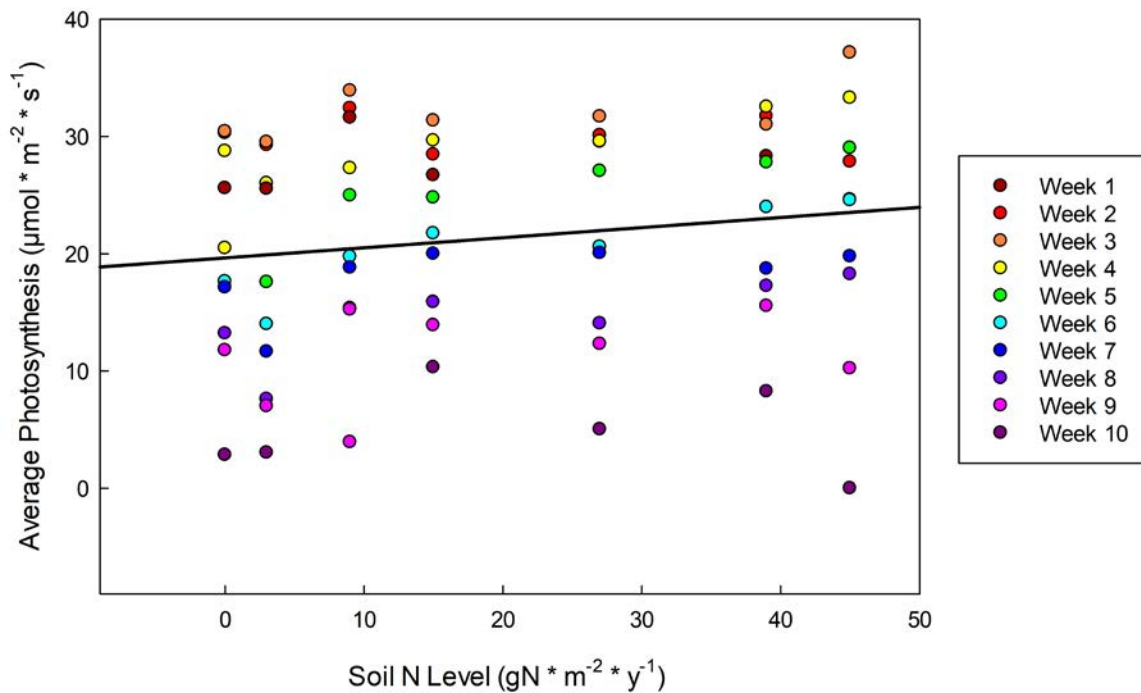


Table 12: ANOVA for the effect of fertilizer on photosynthetic rate

	numDF	denDF	F-value	p-value
(Intercept)	1	517	1959.371	<.0001
Taxa	2	52	3.8926	0.0266
Nlevel	1	52	13.0878	0.0007
Taxa:Nlevel	2	52	1.6411	0.2036

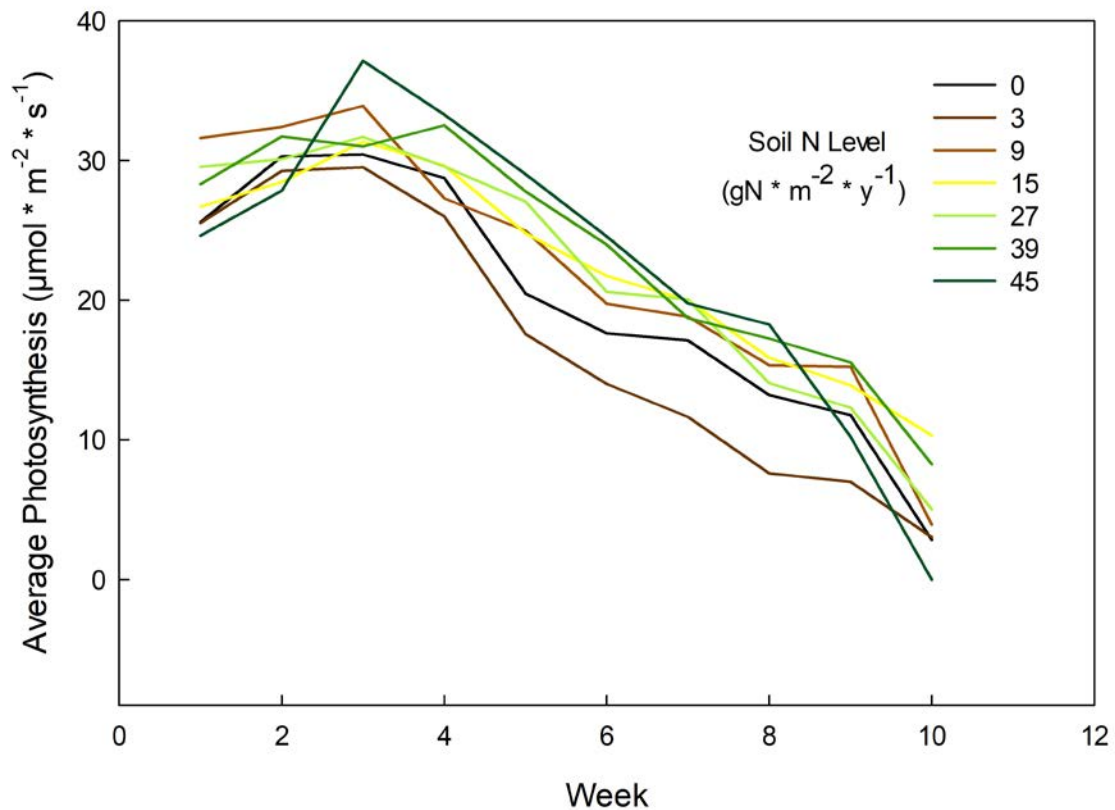


Figure 10: Changes in photosynthesis across a nutrient gradient over 10 weeks.

Discussion

Leaf Longevity

Assessing leaf longevity as individual leaves and by calculating an average leaf longevity for each plant yielded similar results. The lack of differences in leaf longevity between taxa and that leaf longevity was highly similar between these *Typha* is likely due to the three taxa being so closely related. These findings align with Williamson and Fitter (1996), who found that there was not a significant difference in leaf longevity between

invasive and native species of British flora. In the case of these *Typha* taxa, leaf longevity appears to not play a role in dominance between the three.

Ecological theory proposes that since leaf longevity is a nutrient conservation strategy, as nutrients in the soil are more available leaf longevity should decrease. This is due to the cost of constructing new, photosynthetically efficient leaves being lower since nutrients are abundant for uptake. This theory is supported by studies on an Alaskan evergreen shrub, *Ledum palustre* (Shaver 1981, 1983), and a study in Central Spain which included evergreen and deciduous woody species (Escudero et al. 1992). Both studies found an inverse relationship between soil nutrients and leaf lifespan. However, a study of bog species in southern Ontario found mixed results on the effects of nutrients on leaf longevity. One of the three study species exhibited increased longevity with fertilization, whereas the other species had decreased leaf longevity (Reader 1980). In our study, neither method of assessing leaf longevity resulted in significant differences in leaf longevity across a nutrient gradient, however, counter intuitively, leaf longevity increased slightly as soil nutrients increased.

Because the literature on fertilization's effects on leaf longevity is sparse and mainly focused on evergreen species, it is difficult to determine how our findings relate to their findings. Two of the above studies focus exclusively on an evergreen tree species (Shaver 1981, 1983), one focuses on deciduous and evergreen trees (Escudero et al. 1992), and one focuses on evergreen bog species that retain their leaves for two years (Reader 1980). However, in general, our findings do not support their overall conclusions that increased soil nutrients led to decreased leaf longevity.

This inconsistency could be due to vastly different genetics and life strategies among the groups – perhaps evergreen species utilize increased leaf longevity as a nutrient conservation strategy, whereas *Typha* do not. Clonality in *Typha* taxa may also impact their nutrient conservation strategies. Additionally, it is possible that there is an element of publication bias as well. For instance, if leaf longevity is not significantly influenced by a nutrient gradient in many species, these nonsignificant findings may not have been published because they do not have the appeal of significant results.

Overall, there are many reasons why these findings on *Typha* taxa do not align with ecological theory or other studies. Using different methodology such as a metaanalysis would allow the inclusion of taxa closely related to these *Typha* and also individuals from distantly related taxonomic groups. A metaanalysis would help to reveal if these *Typha* respond differently than other taxa to a nutrient gradient in terms of their leaf longevity.

Photosynthesis

A significant difference in photosynthetic rate was predicted between taxa, and the data supported that prediction. Interestingly, *T. × glauca* did not exhibit the highest rates of photosynthesis. Overall, *T. angustifolia* exhibited the highest rates of photosynthesis, *T. latifolia* exhibited the lowest, and *T. × glauca* was intermediate between its two parents. In the case of photosynthetic rate, *T. × glauca* appears to have a phenotype intermediate of its parents. However, determining the genetics that produced that phenotype are complex, as there are many genes (both nuclear and organellar) involved in the function and regulation of photosynthesis (Wang et al. 2014).

Another interesting component of *T. angustifolia* exhibiting the highest photosynthetic rate is that *T. angustifolia* can be invasive and outcompete *T. latifolia* (Grace and Wetzel 1998). Its invasive tendencies have been attributed to the findings that *T. angustifolia* can outcompete *T. latifolia* in deeper water (Grace and Wetzel 1981, 1982, Weisner 1993, Chow-Fraser et al. 1998, Chow-Fraser 2005) and that *T. angustifolia* is more tolerant of salinity and acidity (Hotchkiss and Dozier 1949, Brix et al. 2002). While published literature on photosynthesis in *T. angustifolia* is sparse, it is possible that photosynthetic rate is playing a role in *T. angustifolia*'s invasiveness. Other invasive species, such as *Pennisetum setaceum* (Forssk.) Chiov. in Hawaii, have higher photosynthetic rates than their native analogs (Williams and Black 1994). If *T. angustifolia* is more effective at capturing and utilizing light, this mechanism could be contributing to its invasiveness.

Even though *T. × glauca* did not exhibit higher photosynthetic rates than both of its parents, it still had higher rates than *T. latifolia*. This raises the question of whether *T. × glauca* outcompetes both of its parents with the same mechanisms. It is possible that photosynthetic rate plays a role in competition between *T. latifolia* and *T. × glauca*, but not between *T. angustifolia* and *T. × glauca*. Additionally, the leaf longevity results showed that all three taxa have very similar leaf longevities. However, since *T. angustifolia* and *T. × glauca* have higher photosynthetic rates, they will have higher NUE's than *T. latifolia* overall.

All three taxa showed a linear relationship between soil nutrients and photosynthetic rate. The increase in photosynthesis along a nutrient gradient was

expected based on the physiological requirements for photosynthesis, as plants require nitrogen to produce enzymes such as rubisco. However, at very high nitrogen levels, nitrogen toxicity is possible. Nitrogen toxicity is a well-documented phenomenon that results in a decreased yield of the desired plant above a certain level of a given nutrient (Goyal and Huffaker 1984; Taiz and Zeiger 2010). The effects of nitrogen toxicity are typically assessed by decreases in growth and yield, however it is intuitive that photosynthetic rate would be impacted as well. While the cellular processes responsible for the effects of nitrogen toxicity are not well understood (Britto et al. 2001), studies have shown that increased nitrogen in the form of NH_4^+ can disrupt pH, and disruptions in pH have been shown to impact photosynthetic rate (Enser and Heber 1980).

The point at which nitrogen toxicity occurs varies by species, as some plants are more sensitive to nitrogen toxicity than others (Britto and Kronzucke 2002). A study on three bioenergy crops that modelled A_{max} across a nutrient gradient showed an asymptotic relationship across all three species; initially, increases in soils nitrogen caused large increases in photosynthetic rate, however around $3.2 \text{ gN} \cdot \text{m}^{-2}$, A_{max} leveled off. (Archontoulis et al. 2012). It is likely that further increase of soil nitrogen would push these plants into the toxic zone. However, in my experiment, soil nitrogen levels were more than ten times that of their study, and photosynthesis was still increasing linearly. Compared to these productive bioenergy crops, *Typha* seem to be well-tolerant of nitrogen toxicity.

Conclusions

Assessing leaf longevity both as individual leaves and as leaves on individual plants resulted in a lack of differences between *T. angustifolia*, *T. × glauca*, and *T. latifolia*. This is likely due to the three taxa being so closely related. In the case of these *Typha* taxa, leaf longevity appears not to play a role in dominance between the three.

Leaf longevity also did not vary significantly across a soil nutrient gradient, which is in contrast to what was expected based on ecological theory. Ecological theory hypothesizes that leaf longevity would increase as soil nutrients decrease in order to conserve nutrients. This theory is supported by a few studies (Reader 1980; Shaver 1981, 1983; Escudero et al. 1992), however they include or exclusively contain evergreen species. In order to determine how our results align with or contrast with the above studies, more research is needed on groups or taxa with more similar genetics and life strategies to *Typha*.

My live leaf nitrogen findings from Chapter 1 show that plants do not or cannot take up nitrogen from the soil beyond a certain saturation point. Interestingly, my findings from Chapter 2 show that at soil nitrogen levels above this saturation point, photosynthetic rate is still increasing linearly.

This conclusion about cattail's nitrogen uptake saturation point has interesting implications for the uses of cattails. One of these uses is for phytoremediation, which is the use of plants to remove contaminants from the soil (Galatowitsch 2012). Constructed wetlands are a popular form of phytoremediation to remove nitrates from water and emergent vegetation such as cattails frequently used in these systems (Herath and

Vithanage 2015). Constructed wetlands are often installed between agricultural fields and streams to intercept nutrient-rich agricultural runoff. However, their efficacy values vary. Studies by Vymazal (2005, 2007) found the removal of total nitrogen from the observed constructed wetland to be between 40-50%.

Vymazal's findings on the efficacy of constructed wetlands in conjunction with our live leaf nitrogen data paint the picture that while constructed wetlands are beneficial and provide many ecological services, they are not a perfect system. Our live tissue data show that nitrogen uptake is saturated at a certain point in these *Typha* taxa. Around 20-25 gN m⁻² yr⁻¹, the cattails either cannot or will not uptake much more nitrogen. In some areas, constructed wetlands may not be enough to remediate nitrate levels that extend into above that range. In these areas, constructed wetlands consisting mainly of *Typha* may not be effective and other solutions should be explored. One of these solutions is to construct diverse wetlands, as a study by Bachand and Horne (1999) showed that constructed wetlands that included multiple types of vegetation were most effective at removing nitrates. The inclusion of other plant species along with *Typha* in constructed wetlands along with strategies to reduce nitrogen loading are the most desirable solutions to reduce nitrogen in our water systems.

On the other hand, *Typha*'s high photosynthetic rates and large biomass may make it a good candidate as a biofuel crop. My photosynthesis results showed that *Typha* has high photosynthetic rates at very high soil nitrogen, whereas other popular bioenergy crops' photosynthesis rates leveled out. Because of this, *Typha* may be able to be utilized

as a non-grain bioenergy crop, especially in countries with limited farmland which cannot dedicate cropland to bioenergy crops (Zhuang et al. 2010).

While *T. × glauca*, may have negative consequences for the surrounding environment and vegetation, it is also possible that it and its parent species can be used strategically to benefit the environment overall. Further research on traits such as surface leaf area, leaf thickness, and aerenchyma structure could help to better understand and manage this invader. Further research could also enhance the way *Typha* is currently implemented in technology like phytoremediation and possibly open doors for these taxa to be used in new ways, such as bioenergy crops.

REFERENCES

- Aerts R. 1990. Nutrient use efficiency in evergreen and deciduous species from heathlands. *Oecologia*. 84:391-397.
- Aerts R. 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? *J of Ecol*. 84:597-608.
- Aerts R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant–soil feedbacks. *J of Exp Bot*. 50(330):29–37.
- Aerts R, de Caluwe H. 1995. Interspecific and intraspecific differences in shoot and leaf lifespan of four *Carex* species which differ in maximum dry matter production. *Oecologia*. 102:467-477.
- Angeloni NL, Jankowski KJ, Tuchman NC, Kelly JJ. 2006. Effects of an invasive cattail species (*Typha×glauca*) on sediment nitrogen and microbial community composition in a freshwater wetland. *FEMS*. 263(1):86-92.
- Archontoulis SV, Yin X, Vos J, Danalatos NG, Struik PC. 2012. Leaf photosynthesis and respiration of three bioenergy crops in relation to temperature and leaf nitrogen: how conserved are biochemical model parameters among crop species? *J Exp Bot*. 63(2):895-911.
- Bachand PAM, Horne AJ. 1999. Denitrification in constructed free-water surface wetlands: II. Effects of vegetation and temperature. *Ecol Eng* 14:17–32.
- Baker H. 1965. Characteristics and modes of origin of weeds. In H. G. Baker and G. L. Stebbins. *Genetics of colonizing species*. New York (NY): Academic Press. p. 147-168.
- Ball D, Freeland, JR. 2013. Synchronous flowering times and asymmetrical hybridization in *Typha latifolia* and *T. angustifolia* in northeastern North America. *Aquat Bot*. 104:224-227.
- Bellavance M, Brisson J. 2010. Spatial dynamics and morphological plasticity of common reed (*Phragmites australis*) and cattails (*Typha* sp.) in freshwater marshes and roadside ditches. *Aquat Bot*. 93:129–134.
- Berendse F, Aerts R. 1987. Nitrogen use efficiency: a biologically meaningful definition? *Funct Ecol*. 1:293-296.
- Birk EM, Vitousek PM. 1986. Nitrogen availability and nitrogen use efficiency in loblolly pine stands. *Ecology*. 67(1):69-79.
- Britto DT, Kronzucke HJ. 2002. NH_4^+ toxicity in higher plants: a critical review. *J Plant Physiol*. 159:567 –584

- Britto DT, Siddiqi MY, Glass ADM, Kronzucker HJ. 2001. Futile transmembrane NH_4^+ cycling: A cellular hypothesis to explain ammonium toxicity in plants. *Proc Natl Acad Sci USA*. 98(7): 4255-4258.
- Brix H, Dyhr-Jensen K, Lorenzen B. 2002. Root-zone acidity and nitrogen source affects *Typha latifolia* L. growth and uptake kinetics of ammonium and nitrate. *Journal of Experimental Botany*. 53:2441–50.
- Brownstein MJ, Carpten JD, Smith JR. 1996. Modulation of non-templated nucleotide addition by Taq DNA polymerase: primer modifications that facilitate genotyping. *BioTechniques*. 20:1004-1010.
- Carmichael DP. 1980. A record of environmental change during recent millennia in the Hackensack tidal marsh, New Jersey. *Bull Torrey Bot Club*. 107(4):514-524.
- Cartaxana P, Catarino F. 2002. Nitrogen resorption from senescing leaves of three salt marsh plant species. *Plant Ecology*. 159:95-102.
- Chadde SW. 1998. *A Great Lakes Wetland Flora: A Complete, Illustrated Guide to the Aquatic and Wetland Plants of the Upper Midwest*. University of Michigan: PocketFlora Press.
- Chadde SW. 2013. *Minnesota Flora: An Illustrated Guide to the Vascular Plants of Minnesota*. United States of America: CreateSpace Independent Publishing Platform.
- Chapin FS. 1980. The mineral nutrition of wild plants. *Annu Rev Ecol Evol Syst*. 11:233–260.
- Chow-Fraser P. 2005. Ecosystem response to changes in water level of Lake Ontario marshes: lessons from the restoration of Cootes Paradise Marsh. *Hydrobiologia* 539:189–204.
- Chow-Fraser P, Loughheed V, Thiec L, Crosbie B, Simser L, Lord J. 1998. Long-term responses of the biotic community to fluctuating water levels and changes in water quality in Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario. *Wetl Ecol Manag* 6:19–42.
- Currie WS, Goldberg DE, Martina J, Wildova R, Farrer E, Elgersma KJ. 2014. Emergence of nutrient-cycling feedbacks related to plant size and invasion success in a wetland community–ecosystem model. *Ecol Modell*. 282: 69-82.
- Dacey JWH, Howes BL. 1984. Water Uptake by Roots Controls Water Table Movement and Sediment Oxidation in Short *Spartina* Marsh. *Science*. 224(4648): 487-489.

- Davidson AM, Jennions M, Nicotra AB. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecol Lett.* 14:419-431.
- Del Arco JM, Escudero A, Garrido MV. 1991. Effects of site characteristics on nitrogen retranslocation from senescing leaves. *Ecology.* 72(2):701-708.
- Drenovsky RE, Khasanova A, James JJ. 2012. Trait convergence and plasticity among native and invasive species in resource-poor environments. *Am J Bot.* 99(4):629-639.
- Eckstein RL, Karlsson PS. 1997. Above-Ground Growth and Nutrient Use by Plants in a Subarctic Environment: Effects of Habitat, Life-Form and Species. *Oikos.* 79(2):311-324.
- Elgersma KJ, Martina JP, Goldberg DE, Currie, WS. 2017. Effectiveness of cattail (*Typha* spp.) management techniques depends on exogenous nitrogen inputs. *Elementa.* 5(19).
- Enoki T, Kawaguchi H. 1999. Nitrogen resorption from needles of *Pinus thunbergii* Parl. growing along a topographic gradient of soil nutrient availability. *Ecol Res.* 14(1):1-8.
- Enser U, Heber U. 1980. Metabolic regulation by pH gradients. Inhibition of photosynthesis by indirect proton transfer across the chloroplast envelope. *Biochimica et Biophysica Acta (BBA)-Bioenergetics.* 592(3): 577-591.
- Escudero A, del Arco JM, Sanz IC, Ayala J. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia.* 90(1):80-87.
- Farrer EC, Goldberg DE. 2009. Litter drives ecosystem and plant community changes in cattail invasion. *Ecol Appl.* 19(2):398-412.
- Feng Y, Fu G. 2008. Nitrogen allocation, partitioning and use efficiency in three invasive plant species in comparison with their native congeners. *Biol Invasions.* 10(6):891-902.
- Feng Y, Fu G, Zheng Y. 2008. Specific leaf area relates to the differences in leaf construction cost, photosynthesis, nitrogen allocation, and use efficiencies between invasive and noninvasive alien congeners. *Planta.* 228(3):383-390.
- Funk JL. 2008. Differences in plasticity between invasive and native plants from a low resource environment. *J Ecol.* 96:1162-1173.
- Galatowitsch SM. 2012. Ecological Restoration. Sunderland (MA): Sinauer Associates.

- Goldberg DE, Martina JP, Elgersma KJ, Currie WS. 2017. Plant Size and Competitive Dynamics along Nutrient Gradients. *Am Nat.* 190(2):229-243.
- Goyal SS, Huffaker RC 1984. Nitrogen toxicity in plants. Nitrogen in crop production. Madison (WI): ASA. 97-118.
- Grace JB, Wetzel RG. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *Am Nat* 118:463–74.
- Grace JB, Wetzel RG. 1982. Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Can J of Bot.* 60(1):46-57.
- Grace JB, Wetzel RG. 1998. Long-term dynamics of *Typha* populations. *Aquat Bot.* 61(2):137-146.
- Grime JP. 1977 Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat.* 111:1169-1194.
- Gürsoy S, Kutbay HG, Kilic DD, Huseyinova R, Bilgin A, Yilmaz H. 2013. Nitrogen and phosphorus resorption in two wetland macrophytes. *Pak J Bot.* 45(5):1707-1714.
- Hager HA. 2004. Differential effects of *Typha* litter and plants on invasive *Lythrum salicaria* seedling survival and growth. *Biol Invasions* 6:433–444.
- Hellquist CB, Crow GE. 2006. Aquatic and Wetland Plants of Northeastern North America (Volume 2) University of Wisconsin Press.
- Herath I and Vithanage M. 2015. Phytoremediation in Constructed Wetlands. *Phytoremediation: Management of Environmental Contaminants Volume-2.* Springer International Publishing. p. 243-263.
- Hotchkiss N, Dozier HL. 1949. Taxonomy and distribution of N. American Cat-tails. *The American Midland Naturalist* 41:237–54.
- Jespersen DN, Sorrell BK, Brix H. 1998. Growth and root oxygen release by *Typha latifolia* and its effects on sediment methanogenesis. *Aquat Botany.* 61:165-180.
- Kazakou E, Garnier E, Navas M-L, Roumet C, Collin C, Laurent G. 2007. Components of nutrient residence time and the leaf economics spectrum in species from Mediterranean old-fields differing in successional status. *Ecology.* 21:235-245.
- Killingbeck KT. 1996. Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology.* 77(6):1716-1727.
- Lambers H, Chapin SF III, Pon TL. 2006. *Plant Physiological Ecology.* New York: Springer.

- Larkin DJ, Freyman MJ, Lishawa SC, Geddes P, Tuchman NC. 2012. Mechanisms of dominance by the invasive hybrid cattail *Typha x glauca*. *Biol Invasions*. 14:65-77.
- Lawniczak A. 2011. Nitrogen, Phosphorus, and Potassium Resorption Efficiency and Proficiency of Four Emergence Macrophytes from Nutrient-Rich Wetlands. *Pol J Environ Stud*. 20(5):1227-1234.
- Lawrence BA, Lishawa SC, Rodriguez Y, Tuchman NC. 2016. Herbicide management of invasive cattail (*Typha x glauca*) increases porewater nutrient concentrations. *Wetl Ecol Manag*. 24(4):457-467.
- Leitch JA, Linz GM, Baltezo JF. 1997. Economics of cattail (*Typha* spp.) control to reduce blackbird damage to sunflower. *Agric Ecosyst Environ*. 65:141–149.
- Linz GM, Blixt DC, Bergman DL, Bleier WJ. 1996. Response of ducks to glyphosate-induced habitat alterations in wetlands. *Wetlands*. 16(1):38-44.
- Lishawa SC, Treering DJ, Vail LM, McKenna O, Grimm EC, Tuchman NC. 2013. Reconstructing plant invasions using historical aerial imagery and pollen core analysis: *Typha* in the Laurentian Great Lakes. *Divers Distrib*. 19(1):14-28.
- Luszcz EC, Kendall AD, Hyndman DW. 2015. High resolution spatially explicit nutrient source models for the Lower Peninsula of Michigan. *J Great Lakes Res*. 41(2):618-629.
- Matzek V. 2001. Superior performance and nutrient-use efficiency of invasive plants over non-invasive congeners in a resource-limited environment. *Biol Invasions*. 13:3005-3014.
- McKee KL, Mendeissohn IA, Burdic DM. 1989. Effect of long-term flooding on root metabolic response in five freshwater marsh plant species. *Can J Bot*. 67(12):3446-3452.
- McKenzie-Gopsill A, Kirk H, Van Drunen W, Freeland JR, Dorken, ME. 2012. No evidence for niche segregation in a North American Cattail (*Typha*) species complex. *Ecol Evol*. 2:952–961.
- McMillan C. 1959. Salt Tolerance within a *Typha* Population. *Am J Bot*. 46(7):521-526.
- Miao S. 2004. Rhizome growth and nutrient resorption: mechanisms underlying the replacement of two clonal species in Florida Everglades. *Aquat Bot*. 78:55-66.
- NOAA (National Oceanic and Atmospheric Administration). 2010. Data Tools: 1981-2010 Normals [Internet]. National Centers for Environmental Information [cited 2018 April 4]. Available from <https://www.ncdc.noaa.gov/cdo-web/datatools/normals>

- Osunkoya OO, Bayliss D, Panetta FD, Vivian-Smith G. 2010. Leaf trait co-ordination in relation to construction cost, carbon gain and resource-use efficiency in exotic invasive and native woody vine species. *Ann Bot.* 106(2):371–380.
- Pastor J, Aber JD, McClaugherty, CA, Melillo JM. 1984. Aboveground Production and N and P Cycling Along a Nitrogen Mineralization Gradient on Blackhawk Island, Wisconsin. *Ecology.* 65(1):256-268.
- Pederson DC, Peteet DM, Kurdyla D, Guilderson T. 2005. Medieval Warming, Little Ice Age, and European impact on the environment during the last millennium in the lower Hudson Valley, New York, USA. *Quat Res.* 63:238-249.
- Poorter L, Bongers F. 2006. Leaf Traits Are Good Predictors of Plant Performance across 53 Rain Forest Species. *Ecology.* 87(7):1733-1743.
- Pugnaire FI, Chapin FS III. 1993. Controls over Nutrient Resorption from Leaves of Evergreen Mediterranean Species. *Ecology.* 74(1):124-129.
- Reader RJ. 1980. Effects of nitrogen fertilizer, shade, and the removal of new growth on longevity of overwintering bog ericad leaves. *Can J Bot.* 58(16):1737-1743.
- Reich PB, Ellsworth DS, Uhl C. 1995. Leaf Carbon and Nutrient Assimilation and Conservation in Species of Differing Successional Status in an Oligotrophic Amazonian Forest. *Funct Ecol.* 9(1):65-76.
- Reich PB, Uhl C, Walters MB, Ellsworth DS. 1991. Leaf Lifespan as a Determinant of Leaf Structure and Function among 23 Amazonian Tree Species. *Oecologia.* 86(1):16-24.
- Reich PB, Uhl C, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol monogr.* 62(3):365-392.
- Reich PB, Uhl C, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proc Natl Acad Sci.* 94:13730–13734.
- Rejmánková E. 2005. Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. *New Phytol.* 167(2):471-482.
- Scharfy D, Funk A, Venterink HO, Gusewell S. 2011. Invasive forbs differ functionally from native graminoids, but are similar to native forbs. *New Phytol.* 189(81):818-828.
- Schuelke M. 2000. An economic method for the fluorescent labeling of PCR fragments. *Nature Biotechnol.* 18:233-234.

- Shaver GR, Melillo JM. 1984. Budgets of Marsh Plants: Efficiency Concepts and Relation to Availability. *Ecology*. 65(5):1491-1510.
- Shaver, GR. 1981. Mineral Nutrition and Leaf Longevity in an Evergreen Shrub, *Ledum palustre* ssp. *Decumbens*. *Oecologia*. 49(3):362-365.
- Shaver, GR. 1983. Mineral Nutrition and Leaf Longevity in *Ledum palustre*: the Role of Individual Nutrients and the Timing of Leaf Mortality. *Oecologia*. 56:160-165.
- Shih JG, Finkelstein SA. 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):1-16.
- Silla F, Escudero A. 2004. Nitrogen-use efficiency: trade-offs between N productivity and mean residence time at organ, plant and population levels. *Funct Ecol*. 18:511–521.
- Small E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Can J Bot*. 50:2227–2233.
- Snow AA, Travis SE, Wildová R, Fér T, Sweeney PM, Marburger JE, Windels S, Kubátová B, Goldberg DE, Mutegi E. 2010. Species-specific SSR alleles for studies of hybrid cattails (*Typha latifolia* × *T. angustifolia*; Typhaceae) in North America. *Am J Bot*. 97(12):2061-2067.
- Stuckey RL, Salamon DP. 1987. *Typha-Angustifolia* in North-America-a foreigner masquerading as a native. *Am J Bot*. 74:757-757.
- Taiz L, Zeiger E. 2010. *Plant Physiology*, Fifth Edition. Sunderland (MA): Sinauer Associates, Inc.
- Tilman D. 1987. On the meaning of competition and the mechanisms of competitive superiority. *Funct Ecol*. 1:304-315.
- Tilman D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton, New Jersey: Princeton University Press.
- Travis SE, Marburger JE, 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.
- Travis SE, Marburger JE, Windels S, Kubátová, B. 2011. Clonal structure of invasive cattail (Typhaceae) stands in the Upper Midwest Region of the US. *Wetlands*. 31(2):221-228.

- Tsyusko-Omeltchenko OV, Schable NA, Smith MH, Glenn TC. 2003. Microsatellite loci isolated from narrow-leaved cattail *Typha angustifolia*. *Mol Ecol Notes*. 3:535–538.
- Tuchman NC, Larkin DJ, Geddes P, Wildova R, Jankowski K, Goldberg DE. 2009. Patterns of environmental change associated with *Typha x glauca* invasion in a Great Lakes coastal wetland. *Wetlands*. 29(3):964-975.
- Vázquez de Aldana BR, Berendse F. 1997. Nitrogen-use efficiency in six perennial grasses from contrasting habitats. *Funct Ecol*. 11:619-626.
- Vergutz L, Manzoni S, Porporato A, Novais NF, Jackson RB. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecol Monograph*. 82(2):205-220.
- Vitousek P. 1982. Nutrient Cycling and Nutrient Use Efficiency. *Am Nat*. 119(4):553-572.
- Vitousek PM. 1984. Litterfall, Nutrient Cycling, and Nutrient Limitation in Tropical Forests. *Ecology*. 65(1):285-298.
- Vymazal J. 2005. Horizontal sub-surface flow and hybrid constructed wetlands systems for wastewater treatment. *Ecol Eng*. 25:478–490.
- Vymazal J. 2007. Removal of nutrients in various types of constructed wetlands. *Sci Total Environ*. 380:48–65.
- Wang B, Du Q, Yang X, Zhang D. 2014. Identification and characterization of nuclear genes involved in photosynthesis in *Populus*. *BMC Plant Biol*. 14(81).
- Webb EB, Smith LM, Vrtiska MP, Lagrange TG. 2010. Effects of Local and Landscape Variables on Wetland Bird Habitat Use during Migration through the Rainwater Basin. *J Wildl Manage*. 74(1):109-119.
- Weisner SEB. 1993. Long-term competitive displacement of *Typha latifolia* by *Typha angustifolia* in a eutrophic lake. *Oecologia* 94:451–56.
- Wilcox DA, Buckler K, Czayka A. 2017. Controlling Cattail Invasion in Sedge/Grass Meadows. *Wetlands*. 1-11.
- Williams DG, Black RA. 1994. Drought response of a native and introduced Hawaiian grass. *Oecologia*. 97:512-519.
- Williamson MH, Fitter A. 1996. The Characters of Successful Invaders. *Biol Conserv*. 78:163-170.

- Wilson SD, Tilman D. 1991. Component of Plant Competition Along an Experimental Gradient of Nitrogen Availability. *Ecology*. 72(3):1050-1065.
- Woo I, Zedler JB. 2002. Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha* × *glauca*? *Wetlands*. 22(3):509-521.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, et al. 2004. The worldwide leaf economics spectrum. *Nature*. 428:821-827.
- Wright IJ, Westoby M. 2003. Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Funct Ecol*. 17:10-19.
- Yasumura Y, Hikosaka K, Matsui K, Hirose T. 2002. Leaf-level nitrogen-use efficiency of canopy and understorey species in a beech forest. *Funct Ecol*. 16:826–834.
- Yuan ZY, Chen HYH, Ling HL. 2008. Nitrogen use efficiency: does a trade-off exist between the N productivity and the mean residence time within species? *Aust J Bot*. 56:272–277.
- Yuan ZY, Li LH. 2007. Soil water status influences plant nitrogen use: a case study. *Plant Soil*. 301:303–313.
- Zapfe L, Freeland JR. 2015. Heterosis in invasive F1 cattail hybrids (*Typha* × *glauca*). *Aquat Bot*. 125:44-47.
- Zedler JB, Kercher S. 2005. WETLAND RESOURCES: Status, Trends, Ecosystem Services, and Restorability. 30:39-74.
- Zhuang J, Gentry RW, Yu GR, Sayler GS, Bickham JW. 2010. Bioenergy Sustainability in China: Potential and Impacts. *J Environ Manage*. 46(4):525-530.

APPENDIX
SUPPLEMENTAL DATA

Table 13. Average leaf longevity for each *Typha angustifolia* individual

Species	Soil Nitrogen level	Replicate	Plant ID	Average Leaf Longevity
TYAN	0	A	TA0A	57.64
TYAN	0	B	TA0B	54.50
TYAN	0	C	TA0C	76.78
TYAN	0	D	TA0D	59.00
TYAN	0	E	TA0E	26.29
TYAN	0	F	TA0F	50.56
TYAN	3	C	TA3C	50.50
TYAN	3	D	TA3D	56.58
TYAN	3	L	TA3L	60.80
TYAN	3	M	TA3M	59.00
TYAN	3	N	TA3N	62.11
TYAN	3	O	TA3O	55.70
TYAN	9	A	TA9A	69.75
TYAN	9	D	TA9D	24.36
TYAN	9	S	TA9S	70.50
TYAN	9	T	TA9T	67.80
TYAN	9	U	TA9U	63.70
TYAN	15	B	TA15B	78.25
TYAN	15	C	TA15C	78.00
TYAN	15	D	TA15D	70.60
TYAN	15	G	TA15G	65.69
TYAN	15	H	TA15H	74.50
TYAN	27	A	TA27A	57.60
TYAN	27	B	TA27B	52.47
TYAN	27	D	TA27D	58.50
TYAN	27	J	TA27J	70.13
TYAN	39	C	TA39C	61.18
TYAN	39	K	TA39K	69.44
TYAN	45	P	TA45P	46.25
TYAN	45	Q	TA45Q	56.80
TYAN	45	R	TA45R	63.79

Table 14. Average leaf longevity for each *Typha* × *glauca* individual

Species	Soil Nitrogen level	Replicate	Plant ID	Average Leaf Longevity
TYGL	0	A	TG0A	67.27
TYGL	0	B	TG0B	50.38
TYGL	0	C	TG0C	61.56
TYGL	3	A	TG3A	56.67
TYGL	3	C	TG3C	57.00
TYGL	3	D	TG3D	60.20
TYGL	9	A	TG9A	100.50
TYGL	9	B	TG9B	56.23
TYGL	9	C	TG9C	53.00
TYGL	15	A	TG15A	50.21
TYGL	15	B	TG15B	63.79
TYGL	15	C	TG15C	60.27
TYGL	15	D	TG15D	59.31
TYGL	27	A	TG27A	67.25
TYGL	27	B	TG27B	55.40
TYGL	27	C	TG27C	48.43
TYGL	27	D	TG27D	62.39
TYGL	27	I	TG27I	56.93
TYGL	39	A	TG39A	52.35
TYGL	39	B	TG39B	60.27
TYGL	39	C	TG39C	93.50
TYGL	39	D	TG39D	57.16
TYGL	45	A	TG45A	55.73
TYGL	45	B	TG45B	75.63

Table 15. Average leaf longevity for each *Typha latifolia* individual

Species	Soil Nitrogen level	Replicate	Plant ID	Average Leaf Longevity
TYLA	0	B	TL0B	53.92
TYLA	15	A	TL15A	63.53
TYLA	27	C	TL27C	69.65
TYLA	45	C	TL45C	63.10