5-12-2014

Effect of Herbivory on the Growth and Competitive Ability of Reed Canary Grass (Phalaris arundinacea)

Lisa A. Kratzer

Recommended Citation

Kratzer, Lisa A., "Effect of Herbivory on the Growth and Competitive Ability of Reed Canary Grass (Phalaris arundinacea)" (2014). Thesis. Rochester Institute of Technology. Accessed from

Effect of Herbivory on the Growth and Competitive Ability of Reed Canary Grass (*Phalaris arundinacea*)

By

Lisa A. Kratzer

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

Thomas H. Gosnell School of Life Sciences

College of Science

Rochester Institute of Technology

Rochester, NY

May 12, 2014

Anna Christina Tyler, Ph.D. Date

Thesis Advisor

Elizabeth N. Hane, Ph.D. Date
Committee Member

Susan Smith Pagano, Ph.D. Date
Committee Member

Table of Contents

Tables and Figures

Acknowledgements

I would like to thank my advisor Christy Tyler for her continuous support and guidance throughout the development, execution, and analysis of this project. Thank you for the constant encouragement and pushing me to set higher goals. I am grateful to my committee members Elizabeth Hane and Susan Smith Pagano for their valuable feedback and guidance in my project.

I am appreciative of the funding received from the Thomas H. Gosnell School of Life Sciences and Waste Management throughout the course of this project. Thank you to the Seneca Park Zoo for their assistance in completing this project, especially for Robin English's coordination and Tina Fey's experience and assistance with the geese logistics.

The feedback and suggestions of the many members of the Tyler Aquatic Ecology Lab group past and present were incredibly helpful. Thank you to Kristin Berger, Morgan Bida, Kathryn Boa, Michael Burkett, Nicole Dutcher, Nicole Kinlock, Kerry Kuntz, and Taylor Williams. This project would not have been possible without the help of the many hands in the field including Elizabeth Bruen, Brenna DeAngelis, Samantha Gonzalez, and Gabe Pendleton. Kaitlyn Moranz was a tremendous help, especially with her eye for finding snails. Thank you especially to Melissa Maurer for her help through the field season and into the analysis and writing stages for this project.

A special thank you goes to Bruce and Mary Ann Cady for all of the time and passion they have poured into the High Acres Nature Area. When I first started working at HANA, I was told that they hoped it would become a place that I loved as much as they do, and I can truly say that HANA is one of my favorite places.

Finally, I would especially like to thank my parents, sister, and friends for their constant support throughout my undergraduate and graduate career at RIT.

Abstract

Herbivory plays an important role in plant community structure in many ecosystems through preferential selection, plant regrowth, and seed transport. *Phalaris arundinacea*, reed canary grass, is a prevalent wetland invasive species consumed by geese, muskrats, and snails. We lack a clear understanding of how herbivory impacts *P. arundinacea*'s invasion potential. Therefore, I sought to understand the effect of herbivory by generalist macrograzers and micrograzers on the competitive dominance of *P. arundinacea* in created wetlands, especially the degree to which herbivory alters the competitive relationship between *P. arundinacea* and *Typha latifolia* (broadleaf cattail). To address this enclosure/exclosure cages were constructed in June 2013. Half of the plots contained only *P. arundinacea* and half were placed along the edge between *P. arundinacea* and *T. latifolia.* In caged treatments, amber snails (*Succinea putris*) were either included or removed. Control plots without cages assessed the effect of larger grazers. I predicted that herbivory would negatively impact the growth of *P. arundinacea*, and mixed plots would allow *T. latifolia* to spread into the *P. arundinacea* zone. Choice experiments were conducted with *Branta canadensis*, Canada geese, and *S. putris* to evaluate their preference for *P. arundinacea* or *T. latifolia*. I did not find any significant differences in *P. arundinacea* growth due to grazing but competition with *T. latifolia* did impact *P. arundinacea*. Edge plots at RIT had a significantly reduced growth rate compared to stems from plots containing *P. arundinacea* only. In choice experiments, geese showed a preference for *P. arundinacea* over *Typha*, whereas snails showed no preference. Despite the observed preference, I was unable to demonstrate effects of herbivory in the field. Herbivory appears to play a minor role in *P. arundinacea*'s success as an invasive plant in created wetlands, with other factors, such as competition for light and nutrients of potentially greater importance.

Introduction

Herbivores can play a significant role in determining plant community dynamics, increasing or decreasing diversity and dominance by selectively removing plants, and affecting regeneration opportunities and the transport of seeds (Clay et al. 1993; Huntly 1991; Olff and Ritchie 1998). While run-away grazing may lead to extreme effects on plant communities (e.g. Silliman et al., 2005; Silliman, 2001), most examples of the influence of herbivores on plant communities are more subtle. Herbivores can mediate positive feedbacks in plants, thus influencing nutrient cycling; for instance depending on the limiting factor of the system, nitrogen cycling can be either accelerated or decelerated (Ritchie et al., 1998). Additionally by prohibiting the dominance of tall plant species and opening the canopy, grazing may affect plant succession by removing dominant late-successional species and effectively resetting the successional clock (Oene et al. 1999). Likewise, by preferentially grazing on select species, herbivores may promote dominance by unpalatable or invasive species (Grosholz, 2009; Srivastava & Jefferies, 1996). The balance between herbivore selectivity, plant resistance to herbivory, and environmental heterogeneity leads to an array of outcomes in natural plant communities.

Food selection and consumption is a time-consuming process that must be balanced against an organism's ability to consume sufficient calories in the time it has available. Decisions that an animal must make as it grazes include where to search, when to feed, what types of food to consume, and when to move on (Owen-Smith et al., 2010). Some factors of optimal foraging theory include abundance of the food type, if the animal is satiated or starved, and presence of predators (Emlen, 1966). Geese, for instance, are selective grazers, feeding on high quality foods for extended periods in order to fulfill their nutritional and energetic requirements (Cadieux et al. 2005; Gawlik & Slack 1996; Wink et al. 1993)**.** In a large, diverse patch an animal will be more selective of the foods chosen than if the patch is small with limited selection of food available (Emlen, 1966; Macarthur & Pianka, 1966).

Many characteristics of plants impact the susceptibility to herbivory and influence the rate of food intake, including toughness, secondary metabolites, nitrogen, protein, and energy content, the presence of spines/thorns, life-history variation, gross morphology, and other physical traits of the plant (Carmona et al., 2011; Pennings et al., 1998; Provenza et al., 2007; Villalba & Provenza, 2007). Nitrogen content is of vital importance to consumers because nitrogen is central to metabolic processes, cell structure, genetic coding as well as organism health, growth and reproduction (Mattson, 1980). A plant's nitrogen content is influenced by a variety of factors, including but not limited to seasonal cycles, temperature and moisture stresses, tissue damage, and human interventions such as fertilization (Mattson, 1980).

Secondary compounds such as alkaloids or cardiac glycosides are unpalatable compounds produced by some plants to deter herbivory (Joshi & Vrieling, 2005; Wink et al., 1993). While they are thought to be toxic, at lower doses these compounds could be medicinal to herbivores (Provenza et al., 2007). A plant may defend itself from herbivory with the use of secondary metabolites at all times, known as constitutive resistance, or synthesize these compounds as a result of damage by herbivores, providing induced resistance. It is thought that induced resistance is beneficial to a plant because it limits the amount of resources a plant uses to create the defense compounds and this energy can be allocated elsewhere (Karban et al. 1997; Wittstock & Gershenzon, 2002). The gain from eating a particular food must be greater than the time lost, including the time for search, pursuit, capture, and consumption (Macarthur & Pianka, 1966). Plant structure directly affects consumption rate by dictating bite rate and bite mass, and indirectly by dictating grazing time (Hodgson et al. 1996; Provenza et al., 2007).

The external factors of the field environment, such as temperature, desiccation, natural enemies, plant abundance, and architecture (height, branching, and flexibility) can also play a role in preferences made by herbivores (Pennings et al., 1998). Gastropods are severely constrained by abiotic (heat, desiccation) and biotic (predators) factors which limit the time they can spend foraging (Garrity, 1984). The presence of predators reduces the feeding time of an herbivore, due to evasive measures, which also lowers the herbivory risk for plants (Schmitz et al., 1997; Schmitz et al., 2004). For instance geese alter foraging locations since they are wary of predators and will avoid ponds that are surrounded by tall vegetation (Cadieux et al., 2005; Owen, 1972).

Not all plants suffer reduced fitness as a result of herbivore damage. Rather, some have evolved tolerance of herbivore damage, leading to compensatory growth (Oesterheld & McNaughton, 1991). Species receiving the least damage inflicted by herbivores have an advantage because of a reduced biomass and growth potential of species receiving more damage (Clay et al. 1993). For example under rotational grazing, the proportion of the invasive *Phalaris arundinacea* in a riparian zone was reduced, which allowed for the greatest native species diversity (Paine & Ribic, 2002). This selectivity by herbivores leads to alterations in plant community structure, as shown by Bazely and Jeffries (1986) in a salt marsh, where exclusion of the lesser snow goose (*Anser cauerulescens caerulescens*) resulted in increased abundance of certain species, that were then less susceptible to grazing once the exclosures were removed, suggesting that grazing provides a positive feedback, increasing both the quantity and quality of forage.

The preference of generalist herbivores can be crucial to the community dynamics and biodiversity of an ecosystem. The ability of herbivores to modify their environment and select for particular plants has been used in a variety of attempts to explain what allows a species to become invasive (Keane & Crawley, 2002; Schaffner et al., 2011). Analysis of eighteen studies over a twelve year period showed that herbivory by generalist herbivores on invasive plants resulted in a one-third reduction in the plants' performance during the early life history stages and reduced the size of adult plants by half (Maron & Vila, 2001). Some invasive plants such as *Lonicera japonica*, have greater compensatory growth ability than native con-specifics (Maron & Vila, 2001), suggesting that invaders may have greater resistance to herbivory. The ability of herbivores to regulate species invasions has also been demonstrated in some wetland systems. For example Canada geese (*Branta canadensis*) preferentially consumed the softer native *Spartina foliosa* over an invasive *Spartina* hybrid, allowing the invasive hybrid to expand into the *S. foliosa* zone (Grosholz, 2009). Not every plant that enters into a new range grows excessively and becomes a pest, and the biological attributes of the new species, environmental characteristics of the introduced ecosystem, and the biotic interactions within the novel community determine invasion potential (Vila & Weiner 2004). There are a number of theories to predict invasion success, but no one unified theory has been developed.

One such hypothesis, the Evolution of Increased Competitive Ability (EICA) hypothesis, developed with the invasive wetland plant *Lythrum salicaria* (Purple Loosestrife), predicts first that when grown under identical conditions, individuals of species taken from an introduced region will produce more biomass than individuals taken from a species' native range, and second that specialized herbivores from the native range will demonstrate an improved performance on plant individuals originating from the introduced region (Blossey & Notzold, 1995). This hypothesis was expanded by Keane and Crawley (2002) with the Enemy Release Hypothesis (ERH), which posits that decreased herbivory in the novel environment will lead to an increase in distribution and abundance because of reduced herbivory on the invasive relative to native species that suffer from losses due to native specialized herbivores (including disease causing bacteria or viruses, fungi, and vertebrate or invertebrate herbivores (Keane and Crawley 2002)). Support for this hypothesis has been met with varying success; in a meta-analysis of studies only 60% of the cases supported the ERH (Colautti et al., 2004).

The role of herbivory in the outcome of plant invasions in wetlands is not well understood. Wetland communities are highly susceptible to invasion, particularly by monotype-forming plants (Zedler and Kercher 2004). Wetlands are landscape sinks, accumulating debris, excess water, nutrients, salts, sediments, *et cetera* from both terrestrial inputs and wetland disturbances, which can open ecological niches and allow for invasion (Galatowitsch et al., 1999; Zedler & Kercher, 2004). Common wetland invaders, such as *Typha* spp., *Phragmites australis*, *L. salicaria*, and *P. arundinacea*, are all good colonizers and good competitors (Zedler and Kercher 2004, Galatowitsch et al., 1999). These plants can grow and spread through seeds that are typically dispersed through water, the dispersal of plants and/or plant fragments through flotation, and a rapid uptake of nutrients (Zedler & Kercher, 2004). *P. arundinacea*, *P. australis*, and *Typha* spp. are capable of forming monotypic stands that crowd out native species and reduce biodiversity. Because wetlands provide important ecosystem functions and services (Zedler, 2000), but unfortunately have declined in size and number both within New York State and nationally (Dahl & Johnson, 1991; Dahl, 2000; Galatowitsch et al., 1999), it is important to understand the processes leading to invasion and the subsequent loss of important functions.

Phalaris arundinacea L. (reed canary grass) appears to have been repeatedly introduced from Europe since the mid-1800s for a variety of purposes including pasture cover, forage, shoreline stabilization, wastewater treatment, and bioenergy production (Galatowitsch et al., 1999; Lavergne and Molofsky 2004). Following introduction, its early season growth, rapid spread, rhizomatous growth, and ability to compete in a range of ecological conditions such as intermittent flooding, and nutrient enrichment have helped *P. arundinacea* to spread widely, becoming particularly problematic in emergent wetlands (Lavergne & Molofsky, 2004; Spyreas et al., 2009). Because the seeds go dormant, they are a major component of seed banks (Lavergne & Molofsky, 2004) making *P. arundinacea* a ubiquitous and widespread invader. Once established, *P. arundinacea* lowers the diversity of native plants, herbivores and predators (Lavergne & Molofsky, 2004; Spyreas et al., 2009). The monotypic stands also clog waterways and alter hydrologic regimes, with enhanced sediment deposition in invaded areas further altering the hydrologic regime (Lavergne & Molofsky, 2004).

Phalaris arundinacea has multiple genotypes in North America including a native genotype, a Eurasian genotype, and cultivars that were bred for forage. Despite selective breeding, the Eurasian genotype is the pernicious invader (Jakubowski et al., 2014; Lavergne & Molofsky, 2004). The use of *P. arundinacea* for livestock forage has been investigated for centuries, with mid-1700s studies suggesting that *P. arundinacea* is one of the most palatable forage grasses to all livestock except swine (Alway, 1931). Even today, cattle herbivory on *P. arundinacea* is enough to reduce abundance of the grass when utilized under rotational or continuous land management regimes (Lavergne & Molofsky, 2004; Paine & Ribic, 2002). Domestic animals are not alone in consuming *P. arundinacea.* Researchers investigating a *P. arundinacea*-dominated wetland in Illinois frequently observed grazing by muskrats (Ahlers et al., 2010). In an experiment testing the palatability of forage plants for greater snow geese, *P. arundinacea* was a preferred plant (Gauthier & Bedard, 1991). In wetlands in New York State, I observed that *P. arundinacea* had been clipped close to the ground, presumably by geese or muskrats, but that there was no similar evidence of grazing on nearby *Typha latifolia*, an aggressive native invader (pers. obs.). Additionally I observed snails and the associated grazing-induced radulations on *P. arundinacea*.

With altered environmental conditions, such as unusual rainfall or temperature, nutrient inputs, or other disturbance, native plants may exhibit invasive characteristics, forming dense colonies and outcompeting less aggressive plants (Alpert et al. 2000; Cretaz & Kelty 1999). However, the use of the term “invasive species” is not consistent throughout the ecological literature (Richardson et al. 2000). Some refer to invasive species as an alien species in a novel environment; whereas others use invasive to refer to species that spread in time and space resulting in negative environmental consequences (Richardson et al. 2000; Zedler & Kercher, 2004). Here I use the latter definition, as my study concerns two invasive wetland plants, one native and one alien.

The overall aim of this study was to investigate the role of herbivores in controlling the spread and competitive ability of invasive *P. arundinacea* in created emergent wetlands where it co-occurs with *Typha* spp. By performing choice experiments with snails and geese I was able to determine if these generalist herbivores have a preference for native plants over an alien invasive. I hypothesized that both of these generalist grazers would prefer the native *A. subcordatum* to the native invasive *T. latifolia* and that *P. arundinacea* would be the least consumed. The use of field exclosure experiments allowed me to investigate the effect of herbivory on *P. arundinacea* growth and competitive dominance in created wetlands in Rochester, NY. I hypothesized that grazing would reduce *P. arundinacea* growth and promote the spread of *Typha* spp. into the *P. arundinacea* zone. Together this information will help to understand the role generalist herbivores play in the spread of *P. arundinacea*, a pernicious wetland invader.

Methods

Goose grazing on native and non-native plants

I conducted a choice experiment at the Seneca Park Zoo in Rochester, NY with two captive Canada geese (*Branta canadensis*) based on the methods of Grosholz (2009). One goose has been with the zoo since 1990, the other since 2009. The geese, part of the Genesee Trail exhibit, are fed a diet of grains, lettuce, and kale. On the days I visited, grains were made available at all times, but the lettuce and kale were withheld from the geese until after the day's trial(s) were over.

Between September 9, 2013 and October 8, 2013 there were 1-2 trials per day, for a total of 12 trials. On days that there were multiple trials, there was at least 2.5 hours between the end of the first trial and the start of the second. The geese were offered intact turfs of *P. arundinacea, Typha latifolia,* and *Alisma subcordatum* a native wetland species, in fully-crossed pairs during separate trials. I obtained the turfs either the night before the trial or shortly before the trials began for that particular day. I placed the turfs directly in a shallow part of the exhibit's pond, spacing them in a line 0.5 m apart, alternating the species so that there were two turfs of each species for a total of four turfs.

Prior to placement in the exhibit the number of leaves were counted and recorded. The geese had access to the plants for a two-hour period, during which I recorded the location of each goose every minute. At the end of the two hours, I re-counted the number of leaves per turf. Consumption was calculated as the remaining percentage of leaves (Grosholz, 2009) additionally the proportion of leaves consumed was determined based on the number of leaves eaten relative to the initial number of leaves. The data for each pair was analyzed using paired t-tests (Grosholz, 2009), where each of the individual timed trials represented a pairing. The time each of the two geese was at a plant species was kept separate however the number of leaves eaten by each goose could not be separated out so the leaf counts are representative of the consumption by both geese.

Gastropod grazing on native and non-native plants

Using the same plant pairings as the geese at the Seneca Park Zoo, I set up a choice experiment with *Succinea putris* snails in the lab. I collected *S. putris* snails in early August and placed them in groups of three in small vented containers, on the 12 hr light/dark cycle. I offered them the same plant pairings as in the Goose grazing on native and non-native plants (*P. arundinacea* and *T. latifolia* (n=18), *T. latifolia* and *A. subcordatum* (n=18), *P. arundinacea* and *A. subcordatum* (n=18)), there were six replicates of each pairing during each of the three rounds of trials. I placed fresh plant clippings of approximately the same area in the containers every two days. After three rounds I was no longer able to find healthy *A. subcordatum*. The plants that were removed from the containers were examined for radulations. The number and length of these radulations was recorded. To keep water available to the snails, I placed a dampened paper towel at the bottom of each container.

Paired t-tests were used as described above to analyze the preferences for each of the pairs based on the length of radulations on each species per species per container.

The effect of grazers in the field

Two created wetlands near Rochester, NY were selected for this experiment. The first site, High Acres Nature Area (HANA) in Monroe, County, New York, USA (N 43^o 5’35.73’’, W 77^o 23’9.59’’) is owned and managed by Waste Management, LLC. Originally wetlands, the land was drained in the 1820s and was used for agricultural purposes and later by a sand and gravel company. Waste Management acquired the land in 1986 and since then the area has been used for recreational purposes with trails that are open to the public. The site now contains forested upland, forested wetland, emergent wetlands and open water ponds (Mary Ann Cady pers. comm.). Wetlands were created to mitigate wetland destruction as a result of a 2009 expansion of the High Acres Landfill. A summer 2011 vegetation survey of the created wetlands found *P. arundinacea* in 11.9% of the plots and *Typha* spp. in 18.1% of the plots, with co-occurrence in numerous plots (Boa, 2013).

In the 1960s, the Rochester Institute of Technology (RIT), the second site, began to build its campus in Monroe, County, New York, USA (N 43^o 4’47.24’’, W 77^o 40’0.74’’). Prior to that time, much of the land was used for row crop agriculture. The natural areas of the campus are primarily secondary growth forests and wetlands. There are two created wetlands on the RIT campus, my plots are in the more recent wetland which was created in 2007 and contains a mix of different communities, including meadow, open water, persistent emergent, and herbaceous emergent plant communities in which *T. latifolia* and *P. arundinacea* co-occur (Scheiner, 2011; Tyler unpub data).

To experimentally examine the effect of grazers on the growth and competitive ability of *P. arundinacea*, I established 24 - 1 m^2 experimental plots at each site. Plots were assigned one of three grazing treatments (Table 1) and were established in two zones. The control treatment, with no cage, evaluated the effects of both micro- and macrograzers at ambient densities. I attached quarter inch galvanized hardware cloth to PVC pipe that marked the corners of the remaining plots, surrounding all four sides and placed flush with the ground. Half of the plots enclosed in cages contained added snails (“Cage + Snail” treatment), or had all snails removed (“No Snail” treatment). These treatments (n=4) were replicated in two zones, the *P. arundinacea* dominant zone (minimum cover 50% *P. arundinacea*) and at the border of *P. arundinacea* and *T. latifolia*, in the wetlands at both HANA and RIT. Plots were randomized in each zone to account for environmental heterogeneity within the site.

The field density of snails at each site was determined in June 2012 by haphazardly throwing a ¼ m^2 quadrat 60 times and counting all snails within the quadrat. At HANA, this yielded a maximum field density of 296 snails m^{-2} and 44 snails m^{-2} at RIT. The measurements at HANA were conducted earlier in the season when the cooler weather made the snails easier to locate relative to the survey at RIT which was conducted in late June when the temperatures were unseasonably warm and snails were more difficult to locate. Because it is likely that the later measurements substantially underestimated the true field densities, I chose to increase the density of snails used in cages at RIT to 148 snails m^{-2}, half the density used at HANA. Snail densities in each plot were monitored regularly, removing extra snails and adding missing ones.

Fifteen *P. arundinacea* stems per plot were individually marked using plastic poultry bands to identify individual plants (Silliman, 2001). In plots along the *Typha* border, if there were fewer than fifteen *T. latifolia* stems, all were tagged. The initial height of all tagged plants was recorded, along with number radulations per plant, and whole plot number of stems. Plots were established at HANA between June 4 and June 14, 2013, and RIT between May 30 and June 3, 2013. The plots were re-measured for the above characteristics as well as whole plot inflorescences at HANA between July 17 and July 19, 2013 and at RIT between July 24 and July 30, 2013. This mid-season data was used to determine the percent flowering stems based on the whole plot's number of flowering stems and total stems were counted to calculate the percent flowering stems. The aforementioned data was collected for each plot at the end of the growing season at HANA between September 9 and October 3, 2013 and RIT between September 16 and October 4, 2013. After taking the measurements the aboveground biomass of the tagged stems of both species was measured destructively by clipping all plants to ground level and drying at 65 °C for 48 h prior to weighing (Kellogg & Bridgham, 2004).

I multiplied the biomass per stem by the number of stems in the plot at the end of the growing season to determine the biomass of the plot. I calculated the relative growth rate using the equation: [log(final height) – log(initial height)]/time in order to evaluate growth for both species. I normalized the stem density by using [(final stem density – initial stem density) / initial stem density].

The data collected was checked for normalcy and heterogeneity of variance. Because there were large differences in plant characteristics between the two sites, I evaluated the influence of treatment and zone for each site separately using a two way analysis of variance (ANOVA) with treatment (grazing level) and monotypic vs edge as fixed factors for each site. Since we would expect to find more *P. arundinacea* stems in monotypic plots than in edge plots I ran one-way ANOVAs to analyze the plot biomass, which was calculated at average stem biomass x number of stems in the plot. In the one-ways ANOVAs the sites were separate as well as the edge and monotypic plots being kept separate. For *T. latifolia* in edge plots a one way ANOVA was conducted for each site separately.

Results

Goose grazing on native and non-native plants

When observing the geese at the Seneca Park Zoo during the timed trials, the geese spent the most time at *Phalaris arundinacea*, followed by *Typha latifolia*, and the least amount of time at *Alisma subcordatum* (Figure 1a). The time spent at *P. arundinacea* was significantly greater relative to *A. subcordatum* and marginally greater than *T. latifolia* (p = 0.048), but there was no difference between *A. subcordatum* and *T. latifolia* trial (Table 2).

The geese consumed slightly more *T. latifolia* than *A. subcordatum* (p = 0.005, Figure 1b, Table 2). The number of *P. arundinacea* leaves consumed was significantly greater than *A. subcordatum* (p = 0.005) and *T. latifolia* (p = 0.017, Table 2). For the proportion of number leaves consumed to the number of leaves that were present at the start of the trial, there were no significant differences between the species due to the difference in the number of leaves among species (Figure 1c, Table 2).

Gastropod grazing on native and non-native plants

Succinea putris created marginally longer radulations on *T. latifolia* than *A. subcordatum* (p = 0.058, t = 1.658, df = 17), but the pairings of *A. subcordatum* and *P. arundinacea* (p = 0.279, t = 0.596, df = 17) and *T. latifolia* and *P. arundinacea* (p = 0.931, t = -1.557, df = 17) were not significantly different (Figure 1d).

Effect of grazers in the field

In the edge plots with *Typha* at both sites the *P. arundinacea* stems were initially taller than in the monotypic plots (RIT: df =1, 21 $F = 15.747$ $p = 0.001$, HANA df = 1, 21 $F = 9.054$ $p = 0.008$). In plots assessing the effect of grazing there were differences in the initial heights of *P. arundinacea* (RIT: df = 2,21 $F = 0.057$, $p = 0.945$; HANA: df = 2,21 $F = 0.995$ $p = 0.389$). There were no significant differences in the initial number of radulations on each stem at either RIT (treatment: df = 2,21 $F = 0.161$ $p = 0.853$, edge: df = 1,22 $F = 0.023$ $p = 0.877$) or HANA (treatment: df =2,21 $F = 1.950$ $p = 0.171$, edge: df = 1,21 $F = 0.272$ $p = 0.608$).

I recovered 84.4% of the tagged *P. arundinacea* stems at HANA and 94.2% of the *P. arundinacea* stems at RIT. At the end of the growing season, *P. arundinacea* was taller in border zone plots than in monotypic plots at RIT (Table 3), but not at HANA. In contrast, the relative growth rate of *P. arundinacea* at RIT was slower in the edge plots than monotypic plots, and slightly higher in edge zone plots than monotypic plots at HANA (Figure 2, Table 3). There were no significant differences in the biomass of *P. arundinacea* as a result of the grazing treatment in edge plots (RIT: df = 2, $F = 1.6068$, $p = 0.2531$; HANA: df = 2, $F = 0.7956$, $p = 0.4807$) or in monotypic plots (RIT: df = 2, $F = 0.0261$, $p = 0.9743$; HANA df = 2, $F = 1.5297$, $p = 0.2738$). Neither grazing treatment nor zone resulted in significant differences at either site in the percentage of *P. arundinacea* stems that produced an inflorescence (Table 3, Figure 2) or in the normalized stem densities (Table 3).

Typha latifolia

There were no differences in the heights of the *Typha latifolia* stems at HANA (df = 2, $F = 1.745$ $p = 0.229$) or RIT (df = 2 $F = 0.275$ $p = 0.766$). No differences were found in the initial radulation counts at RIT (df = 2, $F = 0.602$, $p = 0.568$) or HANA (df = 2. $F = 1.039$, $p = 0.393$). At the end of the growing season I recovered 99.0% of the *T. latifolia* stems at RIT and 87.5% of the stems at HANA. The grazing treatments did not result in any significant differences in the final number of radulations on or final heights of the *T. latifolia* stems at either site (Table 4). There was no significant difference in the relative growth rate of *T. latifolia* stems at either site (Table 4). Grazing treatment did not result in any significant differences in the percentage of stems that produced inflorescences at RIT or HANA (Table 4). At HANA none of the stems in the plots without grazers produced an inflorescence (Figure 3). I found no differences in the amount of *T. latifolia* biomass produced per plot at either RIT (df = 2, *F* = 0.409, *p* = 0.676) or HANA (df = 2, *F* = 1.278, *p* = 0.325).

Discussion

These results indicate that herbivory by these generalist grazers only plays a minor role in *Phalaris arundinacea*'s success as an invasive wetland species. *P. arundinacea's* growth during the field experiment did not support my hypothesis that herbivory would reduce *P. arundinacea* growth. I did not find substantial differences in level of grazing incurred by larger grazers, or by smaller invertebrate grazers. Based on the lack of significant differences found in the various plant traits I measured (stem height, number of stems, percent flowering, or biomass) it appears that *P. arundinacea* is either tolerant to grazing or incurs compensatory growth.

Some plants have the ability to compensate for the loss of plant tissue from herbivory or other natural physical damage (McNaughton, 1983), and while there is still a loss of photosynthetic area there is not necessarily a proportional reduction in growth, giving the plant a selective advantage (McNaughton, 1983; van Staalduinen & Anten, 2005). Despite the lack of directly measured effects of herbivory on either *P. arundinacea* or *T. latifolia,* the generalist grazers in this study did show preferences in choice experiments.

Digestion in geese is rapid and inefficient, thus a goose must spend a great deal of time feeding (often more than half of their day) and will consume nearly one quarter of its body weight daily (Owen, 1972). Both adult geese and goslings will try a variety of plant species but may discontinue the consumption of a plant species over time, in favor of selecting high quality foods despite the need to consume a large quantity (Buchsbaum et al., 1984; Cadieux et al., 2005; Owen, 1972; Wink et al., 1993). *B. canadensis* likely found some value in *P. arundinacea* over the other two species in order to have spent more time at *P. arundinacea* than *T. latifolia* or *Alisma subcordatum*.

There are a variety of factors that can influence the preferences for foods chosen by an herbivore. Geese have been shown to seek nitrogen content, extractable energy, and protein (Buchsbaum et al., 1984; Buchsbaum et al., 1981; Conover, 1991) however high nitrogen content has not been a consistent indicator in geese grazing. Avoidance of secondary metabolites has been shown to be a better predictor of preference than either digestibility or nutrient content for *B. canadensis* as well as multiple snail species, including *Helix aspersa* and *Pomacea* spp. (Buchsbaum et al., 1984; Caño et al., 2009; Morrison & Hay, 2011).

Secondary compounds, chemicals produced but not required by the plant for normal growth or reproduction, are often unique to a specific plant lineage (Howe & Jander, 2008). Common molecule families for secondary compounds include alkaloids, phenolics, steroids and terpenes (Bourgaud et al., 2001). Plant secondary compounds are typically deterrents and in some cases toxic to herbivores (Carmona et al., 2011). Recent work investigating genetic variability in plant families found no correlation between concentrations of secondary compounds and herbivore susceptibility (Carmona et al., 2011). However a study of the bulk phenolic content of invasive and non-invasive wetland species in local wetlands revealed that *A. subcordatum* had higher bulk phenolic content than *T. latifolia* or *P. arundinacea* (Maurer, 2014). It is thus conceivable that the generalist grazers of my study were avoiding unpalatable phenolic compounds in *A. subcordatum*. Populations of both captive and wild *B. canadensis* actively avoid consumption of plants with high concentrations of phenolic compounds (Buchsbaum et al., 1984).

Not every plant will produce secondary compounds all the time. By having an inducible resistance to herbivory, which waits for an herbivore "attack" to produce defenses, a plant can allocate resources toward growth and reproduction (Karban et al., 1997; Wittstock & Gershenzon, 2002). Constitutive defenses however, can also be beneficial to the plant because the plant would be able to protect those parts that are crucial to fitness and reproduction but are also vulnerable to attack by herbivores or pathogens (Wittstock & Gershenzon, 2002). *A. subcordatum*, for instance, utilizes constitutive resistance as a defense against herbivory (Prusak et al., 2005). While phenolics and other defenses may deter herbivory, sometimes the distribution of the phenolics and nitrogen within the plant may lead to the higher nitrogen content masking the herbivory deterrents.

Physical characteristics are also important to herbivore selection. Studies of crabs, gastropods, and geese have indicated that herbivores prefer softer plant tissue, suggesting that tough tissue is a deterrent to herbivory (Grosholz, 2009; Pennings et al., 1998; Pennings & Paul, 1992). *P. arundinacea* may be a softer plant and easier for *B. canadensis* to tear, and combined with the lower phenolic content may lead to *B. canadensis*'s preference for *P. arundinacea*.

A component of cell walls, fiber, is generally avoided by herbivores, but it is important to herbivorous birds (Durant, 2003; Manseau & Gauthier, 1993). Fiber represents over half the biomass of the green parts of plants and if cells walls can be digested, then digestion will be more complete because the content of the cells is more accessible (Durant, 2003). For an herbivore of their size geese, including *B. canadensis,* are able to efficiently digest cellulose and fiber (Buchsbaum et al., 1986).

Other factors besides quality go into which foraging materials are sought by animals such as geese including, age and sex of the organism, time of year, and whether the geese are brooding or preparing for migration (Cadieux et al., 2005). Greater snow geese who had been living in captivity for over one year preferred *P. arundinacea* as a forage grass (Gauthier & Bedard, 1991), indicating that while *B. canadensis* in my study have been living in captivity, thus releasing them from the need for brooding or migration, their native instincts and preferences may still be intact. Care should still be taken when extrapolating preferences in captivity to the wild because a feeding choice experiment is most valuable when the focal animals have been kept on natural foods (Prop et al., 2005).

In spite of the need to feed nearly constantly, geese can be wary animals, as such there is almost always at least one member of the flock with its head up on the watch for danger (Owen, 1972). In an observational study of three goose species, the majority of each species' time was spent either foraging or in an alert behavior (Gawlik & Slack, 1996). *B. canadensis* has also been shown to generally prefer to feed in zones closest to their roost (Coleman & Boag, 1987). They will select feeding sites that offer an abundance of their favorite foods while still providing protection from disturbance (Buchsbaum & Valiela, 1987). Geese have also been reported to avoid ponds that are surrounded by tall vegetation, possibly due to the inability to see predators and that may also explain why they spend quite a bit of time in open fields (Cadieux et al., 2005).

This wariness may have prevented them from coming up out of the water into the experimental zone, and may be the reason I saw little to no evidence of grazing by megagrazers in my plots. It is possible that despite the preference I saw at the Seneca Park Zoo, *B. canadensis* are not important grazers of *P. arundinacea* at these study wetlands, however, had the plots been closer to the water, the outcome may have differed, and I suggest that further study should be undertaken before a final conclusion on the lack of importance of herbivory is reached. Muskrats (*Ondatra zibethicus*) are another candidate vertebrate grazer that consumes and builds habitats from both *P. arundinacea* and *Typha* (Ahlers et al., 2010; Kadlec et al., 2007), and their role in wetland vegetation communities bears further investigation.

While herbivory did not have an impact in my study, herbivory by geese and other herbivores still play an important role in the competition between species in other systems. Herbivorous snails have influenced the distribution and abundance of freshwater macrophytes in lakes (Sheldon, 1987). *Littoraria irrorata,* periwinkle snail, decreased stands of *Spartina alterniflora* by over 50%, in a salt marsh (Silliman, 2001). Preferential grazing by *Branta canadensis* on the native *Spartina foliosa* in a salt marsh facilitated a higher rate of lateral expansion per year by the invasive hybrid into the zone occupied by *S. foliosa* (Grosholz, 2009). In a meadow invaded by non-native grasses, herbivory reduced the performance of focal native species at various life stages suggesting that the invasive dominance is an indirect consequence of herbivory and that herbivory is more limiting than competition (Gonzales & Arcese, 2008). Riparian plant communities under rotational grazing by ungulates had the smallest proportion of *P. arundinacea* compared to sites that had either no grazing or were continuously grazed (Paine & Ribic, 2002). While there are species, including *P. arundinacea*, that are controlled by herbivory I was unable to demonstrate this in the created wetlands studied.

Herbivores having a greater impact on native species over an invasive species is one of the predictions of the Enemy Release Hypothesis (Keane & Crawley, 2002). Despite individual case studies showing support for this hypothesis, there are still cases in which the Enemy Release Hypothesis is not the mechanism behind an invasive plant’s success (Colautti et al., 2004), and this study appears to fall into this category. Both grazers preferred an invasive species over a native species which refutes one of the premises of the Enemy Release Hypothesis, that there will be a greater impact on native species (Keane & Crawley, 2002).

There are other explanations that have been offered in order to understand invasion success that do not necessarily tie into herbivory (Alpert et al., 2000; D’Antonio & Meyerson, 2002; Davis et al., 2000; Schaffner et al., 2011). Invasive species can be the first to colonize following a disturbance, even if they were not previously present in the community (Alpert et al., 2000; D'Antonio & Meyerson, 2002; Hobbs & Huenneke, 1992). *P. arundinacea* invasion is facilitated in areas with higher disturbance from roads and trails (Marlor et al., 2014). Following a disturbance, such as wetland creation, the abiotic features of the landscape are altered; these abiotic features may be important to invasibility (Zedler & Kercher, 2004, 2005). *Typha* species can become an aggressive invaders, forming dense monocultures in disturbed aquatic systems when hydrology, nutrients, or salinity change (Baldwin & Cannon, 2007; Galatowitsch et al., 1999; Kercher & Zedler, 2004; Wilcox, 1985). It may be these abiotic factors that are facilitating the invasion of *P. arundinacea* in my study wetlands rather than biotic interactions.

Disturbance and interspecific competition are key factors determining zonation of marsh plants (Bertness & Ellison, 1987). I anticipated that grazing would alter the competition between *P. arundinacea* and *Typha* spp., promoting further expansion of *Typha*. However, the lack of a shift in the boundary between the species in any of the treatments, suggests that this boundary is stable and the zonation of the plants is controlled by other factors. These factors, which may include nutrient availability, light availability, herbivory, allelopathic chemicals, soil moisture and hydrology (Bertness & Ellison, 1987; Callaway & Walker, 1994; Emery et al., 2011; Keddy et al., 1994), also appear to be site specific given that I observed opposing results at the two sites. RIT, an old agricultural field had significantly more soil nitrogen in summer 2013 than HANA, which has a diverse history including use as a sand/gravel quarry (Maurer, 2014; Mary Ann Cady, pers. comm.; Scheiner, 2011). This difference in available nutrients could be a factor in the zonation of the two species studied in these wetlands. Levine et al. (1998) found that nutrient additions disrupted the competitive relationships of native salt marsh plants altering the zonation along a physical gradient. They thus concluded that nutrients have important consequences on the distribution of species along environmental gradients (Levine et al., 2003). While herbivory did not directly influence the competition between the two species examined here, an understanding of the competitive dynamics between these two species is necessary for maintaining the functionality of created wetlands.

Conclusion

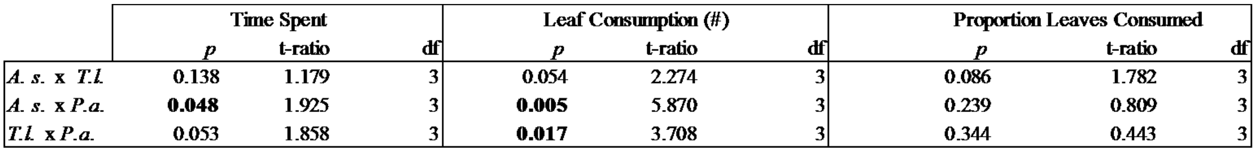
There are a variety of explanations for why a plant invaded an ecosystem, including by not limited to, herbivore influences and disturbance of the ecosystem (Alpert et al., 2000). In this ecosystem, herbivory appears to only play a minor role in the success of *P. arundinacea* as an invasive species. To some extent competition with another invasive species appears to affect the growth rate of *P. arundinacea* in created wetlands. Further understanding of the effect of herbivory on *P. arundinacea* as well as understanding the competitive dynamics between *P. arundinacea* and *T. latifolia* will be crucial to improving the overall functionality and quality of wetlands.

Tables

Table 1: Field Enclosure/Exclosure Experimental Setup

Treatment	**Set up**	**Herbivores Present?**	**Objective**
Control (No Cage)	No cage	Allows for snails and geese	Compare to “No Grazer” herbivore for effect of mega grazer on reed canary grass
Cage	Cage	All snails removed, prohibits macro grazer access	How reed canary grass grows with no herbivores present
Cage + Snail	Cage	Allows snails at field density, prohibits macro grazer access	Impact of the snails on reed canary grass growth

Table 2: Results of paired t-tests on the feeding preferences of *B. canadensis* at the Seneca Park Zoo. Values in **bold** are significant. *A.s.* is *Alisma subcordatum*, *T.l.* is *Typha latifolia*, *P.a.* is *Phalaris arundinacea*



	Time Spent			**Leaf Consumption (#)**			**Proportion Leaves Consumed**		
	p	**t-ratio**	**df**	***p***	**t-ratio**	**df**	***p***	**t-ratio**	**df**
A. s. x *T.l.*	0.138	1.179	3	0.054	2.274	3	0.086	1.782	3
A. s. x *P.a.*	**0.048**	1.925	3	**0.005**	5.870	3	0.239	0.809	3
T.l. x *P.a.*	0.053	1.858	3	**0.017**	3.708	3	0.344	0.443	3

Table 3: Results of a two-way ANOVA using Treatment (grazing level) and Edge (monotypic versus edge between *P. arundinacea* and *T. latifolia*) as the fixed factors on the *P. arundinacea* at RIT and HANA. Values in **bold** are significant

		RIT			HANA		
Measurement	Factor(s)	df	*F*	*P*	df	*F*	*P*
Inflorescence (%)							
	Treatment	2, 21	0.937	0.410	2, 21	2.001	0.164
	Edge	1, 22	0.337	0.569	1, 22	1.001	0.330
	Treatment x Edge	5, 18	1.398	0.273	5, 18	0.046	0.955
Final Height							
	Treatment	2, 21	0.665	0.526	2, 21	1.970	0.168
	Edge	1, 22	14.464	**0.001**	1, 22	0.068	0.797
	Treatment x Edge	5, 18	0.346	0.712	5, 18	1.537	0.242
Final Radulations							
	Treatment	2, 21	0.835	0.450	2, 21	1.542	0.241
	Edge	1, 22	3.116	0.094	1, 22	3.072	0.097
	Treatment x Edge	5, 18	0.037	0.963	5, 18	1.725	0.206
Relative Growth Rate							
	Treatment	2, 21	1.493	0.251	2, 21	0.990	0.392
	Edge	1, 22	5.071	**0.037**	1, 22	3.521	0.078
	Treatment x Edge	5, 18	0.303	0.743	5, 18	0.065	0.367
Normalized Stem Number							
	Treatment	2, 21	1.2123	0.3207	2, 21	3.2930	0.7242
	Edge	1, 22	2.8387	0.1093	1, 22	1.8417	0.1936
	Treatment x Edge	5, 18	3.0190	0.0740	5, 18	1.0855	0.3614

Table 4: Results of a one way ANOVA using Treatment (grazing level) on *T. latifolia* at RIT and HANA. Values in bold represent significant values

	RIT			HANA		
Measurement	df	*F*	*P*	df	*F*	*P*
Inflorescence (%)	2	0.566	0.587	2	3.400	0.080
Final Height	2	0.163	0.853	2	0.112	0.896
Final Radulations (#)	2	0.590	0.575	2	0.871	0.451
Biomass (g m^{-2})	2	0.409	0.676	2	1.278	0.325
Relative Growth Rate	2	0.015	0.985	2	1.141	0.362
Change # stems	2	0.275	0.766	2	0.584	0.578

Figures

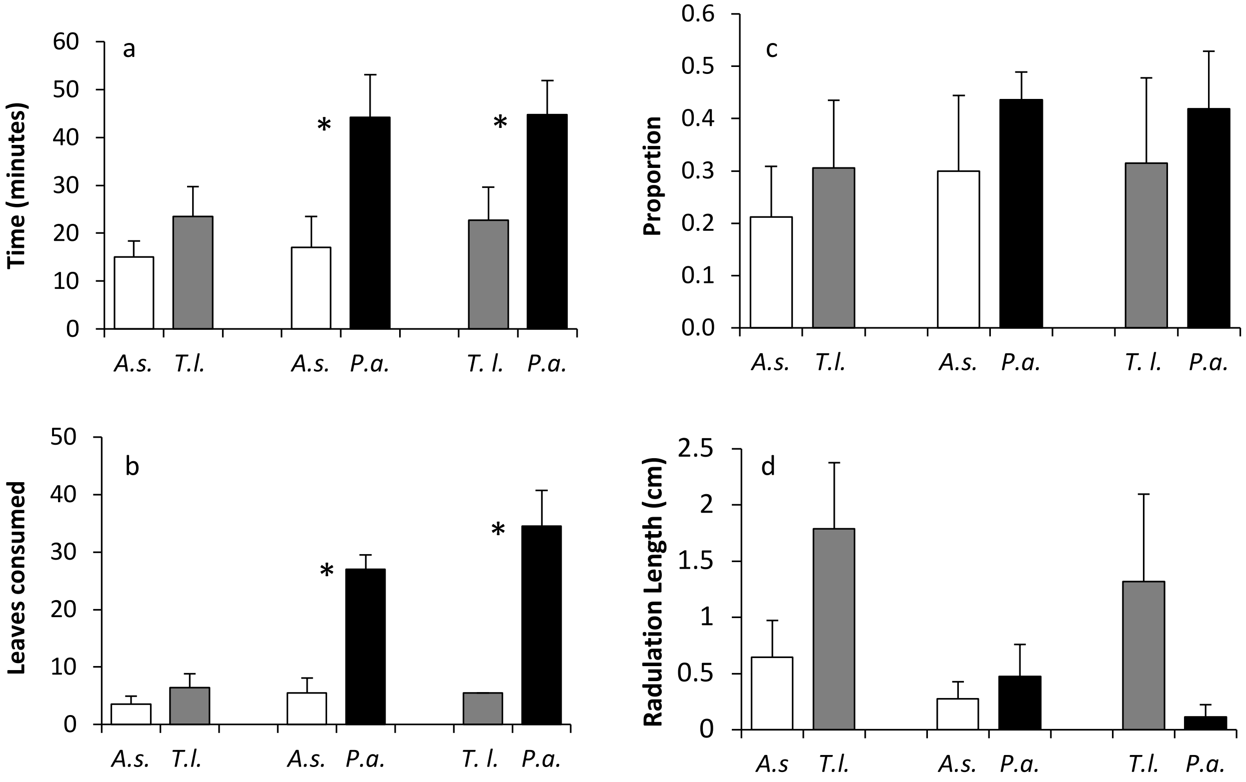


Figure 1. Feeding preferences of *Branta canadensis* at the Seneca Park Zoo and *Succinea putris*. *B. canadensis*: time spent at each species (a), number leaves consumed (b) and proportion of leaves eaten (c). *S. putris*: length of radulations made(d). *A. s.* is *Alisma subcordatum, T. l.* is *Typha latifolia*, and *P.a.* is *Phalaris arundinacea*. Error bars are standard error of the mean. A “ * ” denotes a significant difference between the species offered.

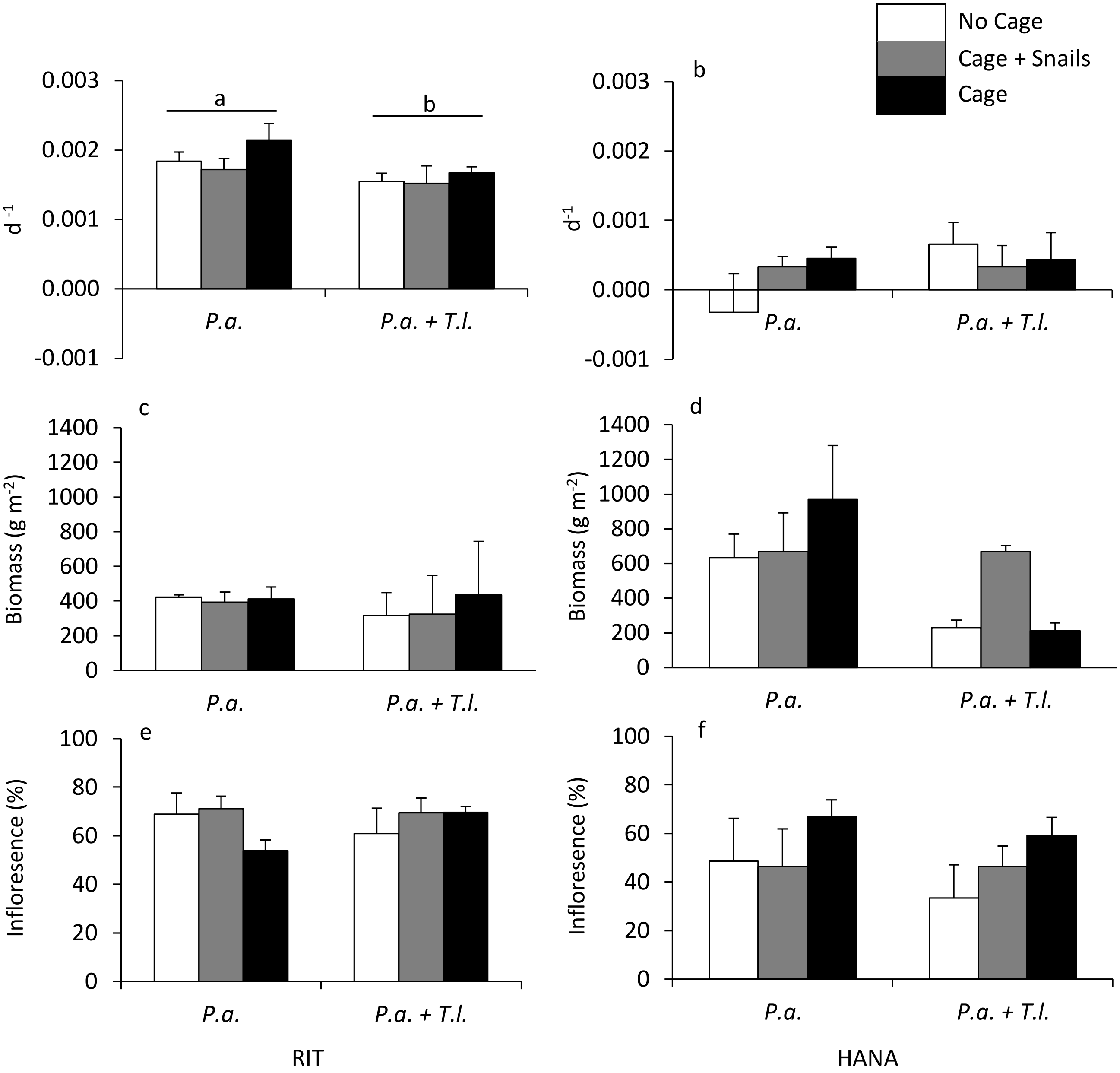


Figure 2. Phenology of *Phalaris arundinacea* from field experiments, including relative growth rate at RIT (a) and HANA (b), biomass (g m^{-2}) at RIT (c) and HANA (d) and percentage of stems with an inflorescence at RIT (e) and HANA (f). Plots from RIT on the left and HANA on the right. *P.a.* denotes plots within the *P. arundinacea* zone, while *P.a.* + *T.l.* represents *P. arundinacea* in plots that were within the zone containing both *T. latifolia* and *P. arundinacea*. Error bars signify standard error of the mean. Lower case letters indicate significant differences between *P.a.* and *P.a.* + *T. l.*

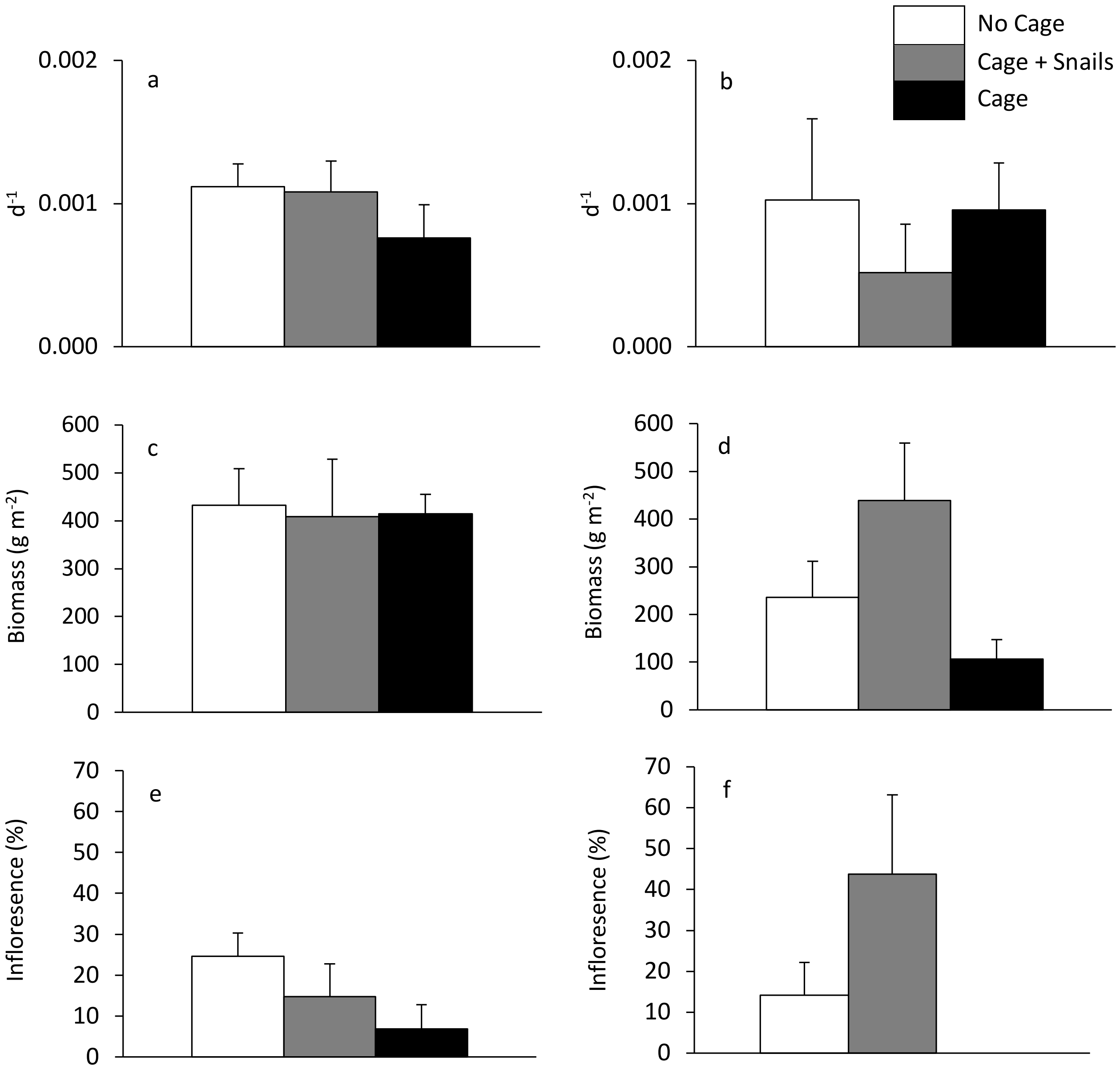


Figure 3. Phenology of *Typha latifolia* from field experiments, including relative growth rate at RIT (a) and HANA (b), biomass (g m^{-2}) at RIT (c) and HANA (d) and percentage of stems with an inflorescence at RIT (e) and HANA (f). Plots from RIT are on the left and HANA on the right. The caged plots at HANA without snails did not produce any inflorescences. Error bars signify standard error of the mean.

Literature Cited

Ahlers, A. a., Heske, E. J., Schooley, R. L., & Mitchell, M. a. (2010). Home ranges and space use of muskrats Ondatra zibethicus in restricted linear habitats. *Wildlife Biology*, *16*(4), 400–408.

Alpert, P., Bone, E., & Holzapfel, C. (2000). Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution, and Systematics*, *3*(1), 52–66.

Alway, F. J. (1931). Early trials and use of reed canary grass as a forage plant. *Agronomy Journal*, *23*(1), 64.

Baldwin, B., & Cannon, A. (2007). *Typha review*.

Bertness, M. D., & Ellison, A. M. (1987). Determinants of Pattern in a New England Salt Marsh Plant Community. *Ecological Monographs*, *57*(2), 129–147.

Blossey, B., & Notzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *The Journal of Ecology*, *83*(5), 887.

Boa, K. J. (2013). *Control of invasive Typha spp . in a restored freshwater wetland*. Rochester Institute of Technology.

Bourgaud, F., Gravot, A., Milesi, S., & Gontier, E. (2001). Production of plant secondary metabolites: a historical perspective. *Plant Science*, *161*(5), 839–851.

Buchsbaum, R., & Valiela, I. (1987). Variability in the chemistry of estuarine plants and its effect on feeding by Canada geese. *Oecologia*, *73*, 146–153.

Buchsbaum, R., Valiela, I., & Swain, T. (1984). The role of phenolic compounds other plant constituents in feeding by Canada geese in a coastal marsh, *63*(3), 343–349.

Buchsbaum, R., Valiela, I., & Teal, J. M. (1981). Grazing by Canada Geese and Related Aspects of the Chemistry of Salt Marsh Grasses. *Colonial Waterbirds*, *4*, 126–131.

Buchsbaum, R., Wilson, J., & Valiela, I. (1986). Digestibility of plant constitutents by Canada Geese and Atlantic Brant. *Ecology*, *67*(2), 386–393.

Cadieux, M.-C., Gauthier, G., & Hughes, R. J. (2005). Feeding ecology of Canada Geese (Branta canadenssi interior) in sub-arctic inland tundra during brood - rearing. *The Auk*, *122*(1), 144–157.

Callaway, R. M., & Walker, L. R. (1994). Competition and facilitation : a synthetic approach to interactions in plant communities. *Ecology*, *78*(7), 1958–1965.

Caño, L., Escarré, J., Vrieling, K., & Sans, F. X. (2009). Palatability to a generalist herbivore, defence and growth of invasive and native Senecio species: testing the evolution of increased competitive ability hypothesis. *Oecologia*, *159*(1), 95–106.

Carmona, D., Lajeunesse, M. J., & Johnson, M. T. J. (2011). Plant traits that predict resistance to herbivores. *Functional Ecology*, *25*(2), 358–367.

Clay, K., Marks, S., & Cheplick, G. P. (1993). Effects of insect herbivory and fungal endophyte infection on competitive interactions among grasses. *Ecology*, *74*(6), 1767–1777.

Colautti, R. I., Ricciardi, A., Grigorovich, I. a., & MacIsaac, H. J. (2004). Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, *7*(8), 721–733.

Coleman, T. S., & Boag, D. A. (1987). Foraging characteristics of Canada geese in the Nisultlin River delta Yukon. *Canadian Journal of Zoology*, *65*, 2358–2361.

Conover, M. R. (1991). Herbivory by Canada Geese : diet selection and effect on lawns. *Ecological Applications*, *1*(2), 231–236.

Cretaz, A. L. De, & Kelty, M. J. (1999). Establishment and control of hay-scented fern : a native invasive species. *Biological Conservation*, *1*, 223–236.

D'Antonio, C., & Meyerson, L. A. (2002). Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology*, *10*(4), 703–713.

Dahl, T. E. (2000). *Status and Trends of Wetlands in the Conterminous United States 1986 to 1997*. *Wetlands* (p. 82).

Dahl, T. E., & Johnson, C. E. (1991). *Wetlands: Status and Trends in the Conterminous United States Mid - 1970's to Mid - 1980's*. *Wetlands* (p. 28).

Davis, M. A., Grime, P., & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, *88*, 528 – 534.

Durant, D. (2003). The digestion of fibre in herbivorous Anatidae - a review, 7–24.

Emery, N. C., Ewanchuk, P. J., & Bertness, M. D. (2001). Competition and salt-marsh plant zonation : stress tolerators may be dominant competitors. *Ecology*, *82*(9), 2471–2485.

Emlen, J. M. (1966). The role of time and energy in food preference. *The American Naturalist*, *100*, 611–617.

Galatowitsch, S., Anderson, N., & Ascher, P. (1999). Invasiveness in wetland plants in temperate North America. *Wetlands*, *19*(4), 733–755.

Garrity, S. D. (1984). Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology*, *65*(2), 559–574.

Gauthier, G., & Bedard, J. (1991). Experimental tests of the palatability of forage plants in greater snow geese. *Journal of Applied Ecology*, *28*, 491–500.

Gawlik, D. E., & Slack, D. (1996). Comparative foraging behavior of sympatric Snow Geese, Greater White-fronted Geese, and Canada Geese during the non-breeding season. *The Wilson Bulletin*, *108*(I), 154–159.

Gonzales, E. K., & Arcese, P. (2008). Herbivory More Limiting than Competition on Early and Established Plants in an Invaded Meadow. *America*, *89*(12), 3282–3289.

Grosholz, E. (2009). Avoidance by grazers facilitates spread of an invasive hybrid plant. *Ecology Letters*, *13*(2), 145–53.

Hobbs, R. J., & Huenneke, L. F. (1992). Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, *6*(3), 324–337.

Hodgson, J., Cosgrove, G. P., & Woodward, S. J. R. (1996). Research on foraging behaviour: progress and priorities.

Howe, G. a, & Jander, G. (2008). Plant immunity to insect herbivores. *Annual Review of Plant Biology*, *59*, 41–66.

Huntly, N. (1991). Herbivores and the dynamics of communities and ecosystems. *Annu. Rev. Ecol. Syst.*, *22*, 477–503.

Jakubowski, A. R., Jackson, R. D., & Casler, M. D. (2014). The history of reed canarygrass in North America: persistence of natives among invading Eurasian populations. *Crop Science*, *54*(1), 210.

Joshi, J., & Vrieling, K. (2005). The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters*, *8*(7), 704–714.

Kadlec, R. H., Pries, J., & Mustard, H. (2007). Muskrats (Ondatra zibethicus) in treatment wetlands. *Ecological Engineering*, *29*(2), 143–153.

Karban, R., Agrawal, A. A., & Mangel, M. (1997). The benefits of induced defenses against herbivores. *Ecology*, *78*(5), 1351–1355.

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, *17*(4), 164–170.

Keddy, P. A., Twolan-strutt, L., & Wisheu, I. C. (1994). Competive effect and response rankings in 20 wetland plants: are they consistent across three environments? *Journal of Ecology*, *82*(3), 635–643.

Kellogg, C. H., & Bridgham, S. D. (2004). Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. *Biological Invasions*, *6*(3), 319–329.

Kercher, S. M., & Zedler, J. B. (2004). Multiple disturbances accelerate invasion of reed canary grass (Phalaris arundinaceaL.) in a mesocosm study. *Oecologia*, *138*(3), 455–64.

Lavergne, S., & Molofsky, J. (2004). Reed canary grass (Phalaris arundinacea) as a biological model in the study of plant invasions. *Critical Reviews in Plant Sciences*, *23*(5), 415–429.

Levine, J. M., Vilà, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K., & Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London: Biological Sciences*, *270*(1517), 775–781.

Macarthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*, 603–609.

Manseau, M., & Gauthier, G. (1993). Interactions between Greater Snow Geese and their rearing habitat. *Ecology*, *74*(7), 2045–2055.

Marlor, K. M., Webster, C. R., & Chimner, R. a. (2014). Disturbance and wetland type alter reed canarygrass cover in Northern Michigan. *Invasive Plant Science and Management*, *7*(1), 121–131.

Maron, J. L., & Vila, M. (2001). When do herbivores affect plant invasions? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, *95*, 361–373.

Mattson, W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, *11*, 119–161.

Maurer, M. (2014). *Phenolic compound production in wetland plant species with a focus on typha*. Rochester Institute of Technology.

McNaughton, S. J. (1983). Compensatory plant growth as a response to herbivory. *Oikos*, *40*, 329 – 336.

Morrison, W. E., & Hay, M. E. (2011). Herbivore preference for native vs. exotic plants: generalist herbivores from multiple continents prefer exotic plants that are evolutionarily naïve. *PloS One*, *6*(3), e17227.

Oene, H. Van, Deursen, E. J. M. Van, & Berendse, F. (1999). Plant-herbivore interaction and its consequences for succession in wetland ecosystems : a modeling approach. *Plant Ecology*, *2*, 122–138.

Oesterheld, M., & McNaughton, S. J. (1991). Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia*, *85*, 305–313.

Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Science*, *13*(7), 261–265.

Owen, M. (1972). Some factors affecting food intake and selection in White-fronted Geese. *Journal of Animal Ecology*, *41*(1), 79–92.

Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1550), 2267–78.

Paine, L. K., & Ribic, C. a. (2002). Comparison of riparian plant communities under four land management systems in southwestern Wisconsin. *Agriculture, Ecosystems & Environment*, *92*(1), 93–105.

Pennings, S. C., Carefoot, T. H., Siska, E. L., Chase, M. E., & Page, T. A. (1998). Crab feeding preferences rel importance of multiple plant traits. *Ecology*, *79*(6), 1968–1979.

Pennings, S. C., & Paul, V. J. (1992). Effect of plant toughness, calcification, and chemistry on herbivory by Dolabella auricularia. *Ecology*, *73*(5), 160–1619.

Prop, J., Lichtenbelt, W. D. V. M., Beekman, J. H., & Faber, J. F. (2005). Using food quality and retention time to predict digestion efficiency in geese geese. *Wildlife Biology*, *11*(1), 21–29.

Provenza, F. D., Villalba, J. J., Haskell, J., MacAdam, J. W., Griggs, T. C., & Wiedmeier, R. D. (2007). The value to herbivores of plant physical and chemical diversity in time and space. *Crop Science*, *47*, 382–398.

Prusak, A. C., Neal, J. O., & Kubanek, J. (2005). Prevalence of Chemical Defenses among freshwater plants. *Journal of Chemical Ecology*, *31*, 2005.

Richardson, D. M., Pysek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants : concepts and definitions. *Diverstiy and Distributions*, *6*, 93–107.

Ritchie, M. E., Tilman, D., & Knops, J. M. H. (1998). Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology*, *79*(1), 165–177.

Schaffner, U., Ridenour, W. M., Wolf, V. C., Bassett, T., Müller, C., Müller-Schärer, H., … Callaway, R. M. (2011). Plant invasions, generalist herbivores, and novel defense weapons. *Ecology*, *92*(4), 829–835.

Scheiner, K. R. (2011). *Comparison of geochemical and biological characteristics of natural and constructed wetlands in Western NY.* Rochester Institute of Technology.

Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, *78*(5), 1388–1399.

Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, *7*(2), 153–163.

Sheldon, S. P. (1987). The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology*, *68*(6), 1920–1931.

Silliman, B. (2001). Top-down control of Spartina alterniflora production by periwinkle grazing in a Virginia salt marsh. *Ecology*, *82*, 2830–2845.

Silliman, B., van de Koppel, J., Bertness, M. D., Stanton, L. E., & Mendelssohn, I. a. (2005). Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science (New York, N.Y.)*, *310*(5755), 1803–1806.

Spyreas, G., Wilm, B. W., Plocher, A. E., Ketzner, D. M., Matthews, J. W., Ellis, J. L., & Heske, E. J. (2009). Biological consequences of invasion by reed canary grass (Phalaris arundinacea). *Biological Invasions*, *12*(5), 1253–1267.

Srivastava, S., & Jefferies, R. L. (1996). A positive feedback: herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. *Biomass*, *84*, 31–42.

Van Staalduinen, M. a, & Anten, N. P. R. (2005). Differences in the compensatory growth of two co-occurring grass species in relation to water availability. *Oecologia*, *146*(2), 190–9.

Vila, M., & Weiner, J. (2004). Are invasive plant species better competitors than native plant species? evidence from pair-wise experiments. *Oikos*, *2*, 229 – 238.

Villalba, J. J., & Provenza, F. D. (2007). Self-medication and homeostatic behaviour in herbivores: learning about the benefits of nature's pharmacy. *Animal : An International Journal of Animal Bioscience*, *1*(9), 1360–70.

Wilcox, D. A. (1985). *Cattail invasion of sedge meadows following hydrologic disturbance in the Cowles Bog wetland comples, Indiana Dunes National Lakeshore*.

Wink, M., Hofer, A., Bilfinger, M., Englert, E., & Martin, M. (1993). Geese and dietary allelochemicals - food palatability and geophagy. *Chemoecology*, *4*, 93–107.

Wittstock, U., & Gershenzon, J. (2002). Constitutive plant toxins and their role in defense against herbivores and pathogens. *Current Opinion in Plant Biology*, *5*(4), 300–7.

Zedler, J. B. (2000). Progress in wetland restoration ecology. *Trends in Ecology & Evolution*, *15*(10), 402–407.

Zedler, J. B. (2005). Restoring wetland plant diversity: a comparison of existing and adaptive approaches. *Wetlands Ecology and Management*, *13*(1), 5–14.

Zedler, J. B., & Kercher, S. (2004). Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences*, *23*(5), 431–452.

Zedler, J. B., & Kercher, S. (2005). Wetland resources: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources*, *30*(1), 39–74.

Appendix:

The effect of experimental grazers in the field