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# The Effects of Invasive Grasses on the Survival and Germination of Native Forbs

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**THE EFFECTS OF INVASIVE GRASSES ON THE SURVIVAL AND  
GERMINATION OF NATIVE FORBS**

A THESIS PRESENTED

by

RACHEL A. KING

TO:

THE KECK SCIENCE DEPARTMENT  
OF CLAREMONT MCKENNA, PITZER, AND SCRIPPS COLLEGES

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THE DEGREE OF BACHELOR OF ARTS

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## Abstract

Invasive species are an increasingly severe conservation problem that can dramatically alter native plant communities. Although ecologists have proposed many mechanisms for the dominance of invasive species, superior competitive ability is one of the longest standing hypotheses. In winter annual plant communities, germination timing affects competition among plants. I hypothesized that grass invasion has changed the costs and benefits of early and late germination, and that species with flexible germination timing would compete better with invasives. Experiments at the Bernard Field Station in Claremont, CA and germinator trials in a controlled environment were used to examine the survivorship and germination rate of three native forbs in the presence or absence of invasive grass competition. Germinator trials revealed that most *Clarkia purpurea* seeds germinated in fall conditions, though newer seeds had higher proportions germinate under winter conditions. Older seeds had a lower germination success, indicating a potential decrease in seed viability. In the field experiment, November germinants had higher survival rates than October germinants for *Amsinckia menziesii* and *Phacelia distans*, and both species had similar numbers of new germinants at each census. Removal of invasive grasses did not significantly affect the survival of either species, though a trend towards increased survivorship was observed in removal plots of November germinants. Taken together, these results show evidence for variation in germination timing and responses to environmental cues among native annual seeds, and also support the idea that germination timing has important consequences for survivorship, and potentially competitive interactions, with invasive grasses.

## Introduction

The emergence of non-native species in new ecosystems is hardly a recent phenomenon. The dispersal of organisms to new areas is an evolutionary process, and often occurs without the aid of human forces. Previously, introductions would occur only when formerly-separated ecosystems were connected, through collisions of continents, a rise or drop in sea level, or distribution of seeds by vertebrates, to name a few possibilities (Mooney and Cleland, 2001; Mooney et al., 2005). However, the onset of accidental and intentional anthropogenic dispersal of organisms around the world has greatly increased the rate of species introductions (Levine and D'Antonio, 2003).

When a species arrives in an ecosystem to which it is not native, it may either die out (through increased competition, limited reproduction, limited genetic diversity, unsuitable habitat or environmental conditions) or become an established species in that ecosystem (Mack et al., 2000). In general, the number of species that survive an introduction into a novel habitat is very small, and even if an introduced species survives the initial transplant it will likely remain a small portion of the native plant community (Mack et al., 2000; Mooney et al., 2005). However, occasionally a translocated species will land in an ecosystem in which it thrives and becomes the leading competitor, dominating the landscape and significantly reducing the abundance of, or eliminating, native species (Mack et al., 2000; Mooney et al., 2005; Pimentel et al., 2005). The eruption of *Bromus tectorum*, commonly known as cheatgrass, in the Western United States is an example of a translocated species thriving in a new environment. Non-native species such as cheatgrass that become abundant and begin to alter the native community are often referred to as “invasive” species.

The categorization of species as “invasive” is fairly controversial. Because of differences in the severity of invasions, the difficulty in discerning whether a newly introduced species will become invasive, the lag times of many decades in the eruption of invasions, and whether the definition includes species that are simply non-native and widespread, it can be difficult to arrive at a conclusive definition of what “invasive” means (Mack et al., 2000; Mooney and Cleland, 2001; Mooney et al., 2005). In fact, there are whole papers dedicated to defining the terminology of invasive species, such as the recent work by Colautti and MacIsaac (2004), which describes the current issues in classifying invasive species and emphasizes the biogeographical nature of invasive species. A general ecological definition of invasive species refers simply to an organism that has become established outside of its native habitat (Mooney et al., 2005). For the purposes of this thesis, an “invasive species” will refer to the strictly ecological definition, as the other ways of defining an invasive species are more ambiguous or narrow.

Although biotic invasions are naturally-occurring phenomena, in recent times humans have drastically increased the number of invasions around the world. Shipping and transport of goods across oceans have allowed species access to a wide range of habitats that were previously unavailable due to geographic barriers such as mountains, oceans, and deserts (Mooney et al., 2005; Sax et al., 2005). Human activities such as construction, livestock grazing, and off-road vehicle use also disturb ecosystems, which can increase the susceptibility of a community to invasion. These disturbances open up new resources, space, or both, which is thought to increase the invasibility of a community (Grime, 2001; Gurevitch et al., 2002; Sax et al., 2005). As human activities

continue to degrade the environment, more land is opened up for possible invasion by non-native species. This is particularly problematic, because with an increase in the number of introductions, there is a greater chance that some species will survive an introduction and become a damaging invasive species in a new community.

When a non-indigenous species persists in and comes to dominate a new ecosystem, there can be drastic, detrimental changes to the original ecosystem. These effects can include changes in ecosystem structure and function (eg. fire regime, nutrient cycling, hydrology, or energy budgets), decreasing biodiversity, alteration of native plant characteristics (root growth, average plant size, etc.), and economic impacts (Mack et al., 2000; Pimentel et al., 2005; Rowe and Leger, 2010; Puliafico et al., 2011). These effects are not limited to the plant community, and may in turn affect the community's fauna and ecological processes (Mooney et al., 2005). As mentioned previously, European cheatgrass (*Bromus tectorum*) has become a problematic invasive plant in the Great Basin region of the US, and has made the region prone to much more frequent fires (Whisenant, 1990, cited in Pimentel et al., 2005). This inhibits or reduces the establishment of shrubs and other vegetation, which in turn has decreased the abundance of animals that depend on the shrubs and native vegetation for food (Pimentel et al., 2005; Mooney et al., 2005).

Invaders can also decrease the biodiversity of an ecosystem by monopolizing resources and therefore decreasing the abundance of other species. In the United States alone, it is estimated that around 400 of the 958 species listed as threatened or endangered are listed as such because of competition with or predation by invasive species (Wilcove et al., 1998, cited in Pimentel et al., 2005). Biodiversity is often used as a

measure of an ecosystem's health or stability, so a decrease in biodiversity may be detrimental to the functioning of the ecosystem (Loreau et al., 2001). Invasions also have an economic impact associated with them. Removal efforts require a considerable amount of time and money, and even then may not be completely effective. Invaders may also decrease an ecosystem's value for recreation, and have caused over \$24 billion in damages to economically-valuable crop species (Pimentel et al., 2005).

#### *Interactions between native and invasive species*

There are many factors that may contribute to the dominance of exotic species in invaded ecosystems. One of the most widespread ideas in invasion ecology is that some introduced species are able to become invasive because they are better competitors than native species (Gurevitch et al., 2002; Sax et al., 2005). This is based on the theory that all plants need water, sunlight, and nutrients to survive and that the introduction of a new species to a community will likely result in greater interspecific competition for those resources. Competition can affect a plant's ability to grow and reproduce, and, in intense competition, even its survival (Gurevitch et al., 2002). In order to survive an initial introduction, an invasive species would need to be able to obtain resources in a community containing plants with growth strategies that evolved in that environment. To do this, the successful invading species may have characteristics that give them a competitive advantage over native species. These qualities include characteristics such as faster germination, quick growth rates, early development of extensive root systems, and resistance to herbivory (Grime, 2001; Gurevitch et al., 2002; Mooney et al., 2005).



Earlier or faster germination and increased growth rates can allow a species to become large enough so that it is able to use resources necessary to other plants, effectively depriving them of essential nutrients, water, or sunlight. A study of competition between cheatgrass and desert needlegrass seedlings showed that height of the desert needlegrass shoots was significantly decreased by the presence of cheatgrass, most likely through competition for moisture (Rafferty and Young, 2002). In a similar study, the native California bunchgrass *Nassella pulchra* was planted with itself and non-native species at varying densities (Dyer and Rice, 1999). These experiments demonstrated that the interspecific competitors reduced the growth and reproduction of *N. pulchra* by limiting the amount of light available, and that the presence of the non-native species reduced the ability of *N. pulchra* to access belowground resources. The evidence of competition between native and non-native plant species makes this an important factor to consider when examining the effects of an invasive species on a new community.

Species may also interact with each other through indirect forms of competition. For example, invasive annual grasses often leave behind a dense thatch when they die, covering the ground and decreasing the amount of light that reaches the soil surface (Heady et al., 1977, cited in Levine and Rees, 2004). Increased litter cover can also alter soil moisture retention and temperature, which are important factors in seed germination (Cox and Allen, 2008). An alteration in the amount of litter at a site would result in different germination conditions, which may affect the timing or success of seeds (Gleichman, 2010). This sort of interaction has also been observed with the rhizomatous fern, *Pteridium aquilinum*. Sites with a large presence of this species have a

dense accumulation of litter from the fern, which serves to impede germination and growth of smaller or slow-growing species (Grime, 2001). The removal of litter through various means has been shown to increase the abundance of some native species, indicating that this may be another important limiting factor in invaded communities (Cox and Allen, 2008).

However, while there is evidence that invasive species can reduce the abundance of natives through competition, many studies suggest that increased competition is not necessarily the primary effect of many exotic species (Sax et al., 2005). Studies of native forbs in California and annual grasses have shown that removal of competitors through mowing and burning had no impact on seedling success, but that seeding plots significantly increased the number of native seedlings (Rees, 1997; Seabloom et al., 2003). This suggests that certain native species may be seed limited, meaning they can successfully compete with invasive plants, but remain rare in the community because of poor dispersal and low propagule availability, potentially as a result of past disturbance. In a study of native shrubs and downy brome, seeding was only partially effective when coupled with removal of the invasive downy brome (Owen et al., 2011). These studies reveal that invasive species may limit natives in different ways, depending on the community, which would require the use of different restoration techniques to help restore native populations.

An additional complicating factor is that for native species that survive in an invaded community and end up coexisting with invasive species, the direct competition that results can exert selective pressure on them (Rowe and Leger, 2010). Studies have shown that seedlings from invaded areas are more tolerant of competition from invasive

species, and can even be better at suppressing the growth of the invasives (Rowe and Leger, 2010; Leger and Espeland, 2010). For invasive species possessing a competitive advantage over native species, it is likely that the native species' abundance will decrease unless a trait in the native species evolves in response.

Many studies have examined the ability of native species to respond and adapt to competition from invasive species. Comparisons of plants from invaded and non-invaded sites have revealed that native plants from invaded sites are better competitors when grown with invasive species than the natives from non-invaded sites, suggesting that the plants from invaded sites have adapted to become more competitive with the invasive species (Callaway et al., 2006; Lau, 2006). This can be exhibited by a faster regrowth time when replanted and watered for plants from invaded communities, as well as an increased ability at suppressing the invasive species' own growth (Leger, 2008; Goergen et al., 2011). Native plants that are experienced with invaders also have shown increased resilience to novel competitors and phenotypic differences from plants from non-invaded sites (Ferrero-Serrano et al., 2009; Bergum et al., 2010). These studies have important implications for restoration efforts, as using seeds from plants that were grown with invasive species may be more effective for restoration of native habitats due to increased resilience and their ability to compete with invasive species. Therefore, understanding the interactions of invasive and native species can lead to more effective restoration techniques.

### *Seed germination and survival*

Most previous work on invasive-native plant competition and on evolutionary responses of native plants to invasion has focused on the adult stages of organisms. Since the establishment of seedlings is a critical and often limiting stage in the life cycle of plants, it is important to understand the factors that affect germination, as well as the consequences of germination-related traits for plant fitness. Rainfall, temperature, timing of rains, plant community, and amount of light all influence the success and timing of seed germination (Rees, 1997; Young et al., 2003). Seeds are generally adapted to a specific temperature regime that signals when it is time to germinate. Big and bottlebrush squirreltail seeds have been shown to have the highest germination rate at specific temperature regimes (Young et al., 2003), demonstrating the importance of temperature for germination. Precipitation is another extremely important germination cue, as it signals the availability of water for new seedlings. As young seedlings are particularly susceptible to mortality from drought stress, germinating in response to rainfall is essential to seed survival (McLaren and McDonald, 2003).

The timing of germination can also have a significant impact on the survivorship of seedlings. Seeds that germinate early may have the advantage of more access to resources, such as light and water (McGlone et al., 2010; Dyer et al., 2000). Early established seedlings may then out-compete later germinating seeds for important resources they need to grow, which may cause higher mortality rates in late-germinating seedlings (Dyer et al., 2000). The influx of invasive species into a community may cause an increase in native seedling mortality if their traditional germination timing is preserved, since many invasive species are quick germinators or

growers, relying on this head start to get established. Therefore, for native seedlings to compete, they might also need to germinate earlier. Seeds of perennial grasses planted in a highly competitive neighborhood have been shown to germinate more rapidly than seeds in a non-competitive neighborhood (Dyer et al., 2000; Leger, 2008). In locations where the timing of germination with rains is crucial to seedling survivorship, this shift could be critical. If seeds germinate too early, before the rainy season starts in full, those seeds may die before they are successfully established due to heat, temperature, or water stress (Gurevitch et al., 2002). However, the need to compete with early germinating invasive species may outweigh precipitation cues if invasive species significantly reduce the survival rate of later germinating seedlings. Therefore, timing of germination may indicate an effect of invasive species on native plant communities, and could also pose a challenge for conservation or restoration of native habitats if it affects the survivorship of native species.

Another factor to consider with seed germination is seed dormancy. If conditions are not ideal for germination, some plant species produce dormant seeds that delay growth of the seedling and reduce the rate of respiration to allow the seed to wait for ideal conditions (Murray, 1984; Rees, 1997). Depending on the plant community and life history of the species in question, seed dormancy and germination can be influenced by a wide variety of factors. Light availability, chemical environment, and temperature have all been shown to affect dormancy (Rees, 1997). If the conditions for germination are not met, dormancy allows seeds to wait for more ideal conditions rather than risk early germination and mortality. For example, certain species of forbs often remain dormant after a very productive year for invasive grasses, because the accumulation of

thatch left by the dead annual grasses reduces the light reaching the soil (Gonzales and Clements, 2010). Therefore, an alternating climate that reduces grass production allows forbs to have higher germination rates the next year, important for allowing native species to compete with invasives (Levine and Rees, 2004). If there are too many productive years for grasses in a row, or a shift in climate caused by climate change, this could influence the abundance of native forbs at the site.

#### *California grasslands and the Bernard Field Station in Claremont, CA*

Like most of the United States, California has experienced a large number of exotic plant introductions in the past century. Currently, it is estimated that about 20% of California's vascular taxa are now exotic species (Goergen et al., 2011). Southern California, which experiences a Mediterranean climate, has a wide variety of plant communities, including annual grassland (Hobbs, 1986). Southern California used to have significant areas of native annual grassland, but due to the introduction of invasive species, large portions of these grasslands are now dominated by annual grasses and forbs from the Mediterranean region (Minnich and Dezzani, 1998; Seabloom et al., 2003). In addition, some areas of coastal sage scrub have been replaced by disturbed grassland habitat with a high proportion of invasive species (Thomson et al., unpublished manuscript). The switch from native communities to exotic annual grasses has important implications for native seed germination. The shift may alter the plant community in which the seeds are used to germinating, by increasing competition in the early growth stages of seedlings, potentially decreasing the survivorship of native seedlings, or altering the timing of germination (Dyer et al., 2000). The combination of

these effects may help explain the low abundances of native plants in most southern California grasslands, and a better understanding of how they operate may aid in the restoration of these habitats.

The interactions of invasive grasses with native annual herbaceous species have been previously studied at the Bernard Field Station in Claremont, CA. This research has examined the influence of invasive species removal and native seed addition on native forb germination, abundance, and mortality (Thomson et al., unpublished manuscript). To date, these studies have shown some interesting trends, with some native forbs appearing to benefit from invasive grass removal and others from seed addition (Thomson et al., unpublished manuscript). However, the underlying reasons for these differences in response are not yet clear, in part because abundance changes could be the result of effects on the frequency or timing of germination, on seedling survivorship, or some combination of these factors. In addition, past results suggest that treatment effects vary substantially between years with different weather conditions, indicating that multiple years of data may be needed to determine the responses of seeds and seedlings under different environmental conditions.

#### *Research questions and study goals*

This study utilized both field and lab germinator experiments to explore several questions related to the interaction of native and invasive species. A continuation of past research at the BFS will examine the effects of invasive species removal and native seed addition on the timing and frequency of native species germination and seedling survivorship. I also hypothesized that the presence of early germinating invasive

grasses may change the costs and benefits of early or late germination. To address this hypothesis, I asked the following questions:

- (1) Do native species differ in their germination timing?
- (2) Does germination timing affect seedling survival?
- (3) Is seedling survival affected by the presence of invasive grasses?
- (4) Do the effects of grasses on seedling survival vary between early and late germinating native annuals?

## Materials and Methods

### *Study site*

Field experiments were carried out at the Bernard Field Station (BFS) in Claremont, CA (Fig. 1). The BFS is a 75-acre parcel of land north of the Claremont Colleges, bordered by roads, residential communities, and the Rancho Santa Ana Botanic Garden. The area experiences a Mediterranean climate, with hot dry summers and cool, wet winters. The growing season lasts from October to April with an average rainfall of 44.05 cm per year (1971 - 2000, Pomona College Station in Claremont, CA). The BFS's main vegetation type is coastal sage scrub, with patches of live oak forest and a riparian forest around a man-made lake.

**Fig. 1** - Map of the vegetation communities of the Bernard Field Station. (image from: <http://bfs.claremont.edu/overview.html>)

As in much of southern California, some areas of the BFS that were previously coastal sage scrub have transitioned to annual grasslands as a result of past disturbance (Thomson et al., unpublished manuscript). Several invasive Mediterranean grasses are common throughout these habitats. Common species include *Bromus diandrus*, *B.*



*madritensis*, *B. hordeaceous*, and *Vulpia myuros*. The introduced forb *Erodium botrys* is also common. In addition, some species of annual herbaceous plants are found patchily throughout this habitat, at least in some years. The invasive grasses tend to germinate earlier than the native species, after early fall rainstorms or even late summer thunderstorms (Thomson, unpublished manuscript). The native annuals typically germinate later in the season after the arrival of the winter rainstorms and cooler temperatures, which they may use as a germination cue (Levine et al., 2008), although some seeds germinate after early fall rainstorms in October.

Two separate fields housed the experimental plots in this study. A driveway leading into the field station separates the east field and the west field (Fig. 1). The native annuals focused on in this study are *Amsinckia menziesii* var. *intermedia* (*Amsinckia*), *Phacelia distans* (*Phacelia*), *Clarkia purpurea* var. *quadrivulnera* (*Clarkia*), and *Camissonia bistorta* (*Camissonia*). All four species have been found in annual grasslands at the BFS, though *Amsinckia* and *Phacelia* are the most common, while *Clarkia* and *Camissonia* are rare in the grasslands themselves and more common in surrounding coastal sage scrub.

### *Field Experiment*

In September 2011, eight blocks were established in random locations in fields at the BFS, four in the west field and four in the east field. Each block was 2.5 m x 2.5 m with four 0.75 m x 0.75 m plots, one in each corner, and a 1 m buffer in between plots (Fig. 2). The experiment crossed two factors—native seed addition and invasive competitor reduction—for a total of four potential treatments: control, native seed

addition, competitor reduction, and both native seed addition and competitor reduction. Each plot was randomly assigned a treatment so that one plot per block received each of the four treatments. Thatch was removed from competitor reduction plots immediately following their establishment, and grasses were clipped every 4-5 weeks thereafter, while seed addition took place in mid-November,



**Fig. 2** - Example of one of the blocks at the Bernard Field Station. Tall poles mark the corner of the block, while red flags mark the individual plots.

2011. Seed addition treatments were part of a separate experiment, and in past years did not influence the patterns I was interested in testing, so they were not included in any of the analyses.

Plant surveys to determine the number of new native and invasive germinants took place a week following each significant rainstorm ( $> 0.1$  cm), starting after the first rainstorm on October 5, 2011 (Table 1). During the surveys, all of the blocks established in 2011 were surveyed for native plant seedlings. In addition, after the first rainstorm the densities of invasive grass and forb germinants were measured as well. Each plot was divided into nine  $0.1 \text{ m} \times 0.1 \text{ m}$  subplots, and the plant species present in each subplot were recorded. Grass species in the initial census could only be distinguished by narrow- and broad-bladed species. For each species found in the subplots, the abundance was estimated and classified into the following categories: (a) 1, (b)  $> 1$  but •

5, (c) > 5 and • 10, (d) > 10 but • 25, (e) > 25 and • 50, (f) > 50. For native species that were found in fewer than three subplots, a “whole” plot estimate of abundance was recorded using the previous categories. For any *Amsinckia*, *Phacelia*, or *Clarkia* seedlings present in the subplots, up to one of each species was marked per subplot. If no seedlings of a particular species were marked in any subplot, or if there were less than five marked in the entire plot, plants outside of the subplot were marked, up to a total of five per plot. Seedlings were marked with a colored wire loop, to signify the germination month, (green – October, red – November, yellow – December) held in place by a colored plastic fork, yellow for *Amsinckia*, blue for *Phacelia* and green for *Clarkia*.

Survivorship checks were performed every 2-3 weeks following the initial survey. The eight blocks initially surveyed were again visited and all the marked plants were checked for mortality. Seedlings were recorded as alive or dead, and the markers for dead plants were removed. If possible, another native seedling was marked nearby or in a suitable location to maintain a good sample size of native seedlings if germination month could be accurately determined.

**Table 1.** Dates of the censuses for seedling abundance.

<i>Census</i>	1	2	3
Storm Date	10/05/11	11/20/11	12/15/11
Census Date	10/12/11	12/01/11	12/22/11

**Table 2.** Dates of the censuses for seedling survival and mortality.

<i>Census</i>	1	2	3	4	5	6
Date	10/21/11	11/01/11	11/30/11	01/06/12	02/01/12	03/21/12

### *Germinator Trials*

Two germinator trials were run in a controlled environment chamber (Conviron). Four 30 cm x 40 cm trays were filled with sand to a depth of 5 cm and dusted with approximately 0.2 cm of mulch. Each tray had six rows and seven columns, and each row was assigned a seed source. Seeds from the forb *Clarkia purpurea* var. *quadrivulnera* were used, with the first two sources as seeds collected from the BFS in 2011 or 2010, and the last source seeds ordered from a native seed supplier (Seedhunt: <http://www.seedhunt.com/>). Seeds from the BFS were harvested in June of the collection year, dried at 80 °C for 72 hours, and then stored at room temperature. Each row was randomly assigned a different seed type, and two rows per tray had the same source. Each row was marked with colored toothpicks to mark the seed location and the treatment type (blue – 2011, yellow – 2010, red – commercial). Two germination protocols were followed, one to approximate fall conditions and one for winter conditions. Fall conditions were set to a high temperature of 25.4 °C, a low temperature of 11.28 °C, sunrise at 6:31, sunset at 18:13, and humidity of 60%. Winter conditions were set to a high temperature of 17.72 °C, low temperature of 5.11 °C, sunrise at 6:11, sunset at 17:09, and humidity at 60%. The fall watering regime was set up to mimic a short, late summer thunderstorm. Seeds were watered 4 times over a period of 24 hours with up to 750 mL per watering. After the watering, the trays were checked daily for new germinants. When a seed germinated, the toothpick marking that seed was removed and the day of germination was recorded. After ten days, the germinator was

set to the winter protocol, and the seeds were watered 12 times over 96 hours, with up to 750 mL per watering, to simulate a winter rainstorm. Seeds were checked once per day to check for germination of the remaining seeds. In the second germination trial, all the seeds were weighed to determine the mean seed weight for each seed type. The seeds were too small to weigh individually, so 11 groups of five seeds each were weighed to determine mean seed weight for each seed type.

### *Data Analysis*

All data collected in the field and lab experiments were first entered into Microsoft Excel for organization and initial analysis, followed by exporting to SPSS (IBM SPSS Statistics, Version 19) for continued statistical analysis. For the seedling abundance data, after being entered into Excel the density of seedlings was calculated for each plot. The plot density was the sum of the abundance score from the nine subplots multiplied by 6.25 (1/ratio of subplot area to plot area). If the species was found in less than three subplots, a whole plot count was used for the abundance measure. Only the data for *Amsinckia* and *Phacelia* were analyzed in this thesis. Because of problems with normality, particularly due to the large number of plots with no native species, the abundances were scaled from 0-9, based on the number of subplots in which a species was found inside a particular plot. For plots that contained no individuals within the 9 subplots but had some within the plot as a whole, a score of 0.5 was given. To normalize the data, a square root transformation was used, and then the data were aggregated to determine a block mean. The block mean was subtracted from the plot mean to give the deviation of each plot from the block mean. These block-normalized data were analyzed using a

General Linear Model for both *Amsinckia* and *Phacelia* to determine effects of invasive grasses on germination timing.

For the germinator trials, chi-square contingency table tests were used to test for significance of the differences between the three treatments and the germination conditions with respect to germination success and the number of days to germination. Since almost all seeds germinated in five days or less, for analysis days to germination greater than five were grouped with those that came up on day 5. A one-way ANOVA with Tukey's post-hoc tests was used to test for significant differences between the mean seed weights of the different seed sources.

Effects of germination timing and competitor removal treatment on seedling survivorship were analyzed using chi-square contingency table tests. The survivorship of seedlings at each census was also used to calculate a cumulative survivorship for the entire year for early and late germinants and the control vs. competitor reduction treatment. Survivorship data were not analyzed for *Clarkia* because very few seedlings were observed.

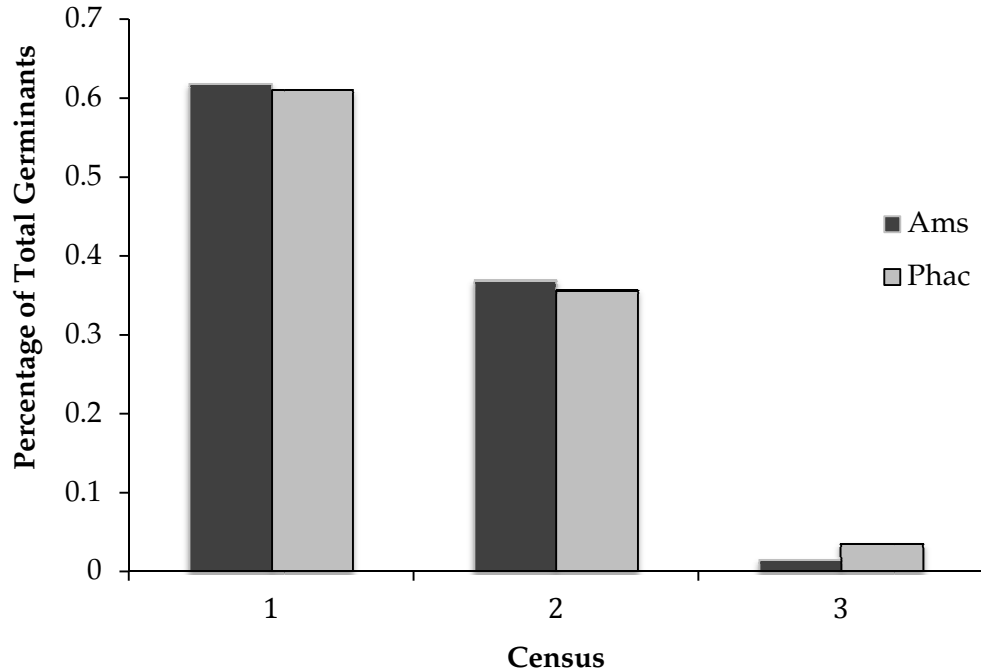
## **Results**

### *Germination Timing*

The largest number of new seedlings for both *Amsinckia* and *Phacelia* was found in census 1, following the October rainstorms. In the 32 plots, there was a total estimated density per plot of 177.3 new *Amsinckia* seedlings and 140.7 new *Phacelia* seedlings. A fair number of seedlings also emerged in census 2, with an estimated density per plot of 105.8 new *Amsinckia* seedlings and 82.1 new *Phacelia* seedlings. The last census saw very

sparse germination, with a total of only 4 *Amsinckia* and 8 *Phacelia* emerging in all of the plots combined. The number of plots with new seedlings was significantly different between the three censuses for both species ( $\chi^2 = 41.787$ ,  $df = 2$ ,  $p < 0.001$ ;  $\chi^2 = 32.015$ ,  $df = 2$ ,  $p < 0.001$ ). For both *Amsinckia* and *Phacelia*, the first and second censuses had similar numbers of plots with new germinants (27 and 23 for *Amsinckia*, 25 and 27 for *Phacelia*). However, in the third census, only 3 plots had new *Amsinckia* seedlings and only 7 plots had new *Phacelia* seedlings. This is another illustration of the decrease in the number of new germinants between the first two censuses and the third census, and shows that both species germinated almost entirely after the first two rainstorms. In addition, because of the very small number of new seedlings in the third census, it was left out of subsequent analyses to help reduce variance in the data.

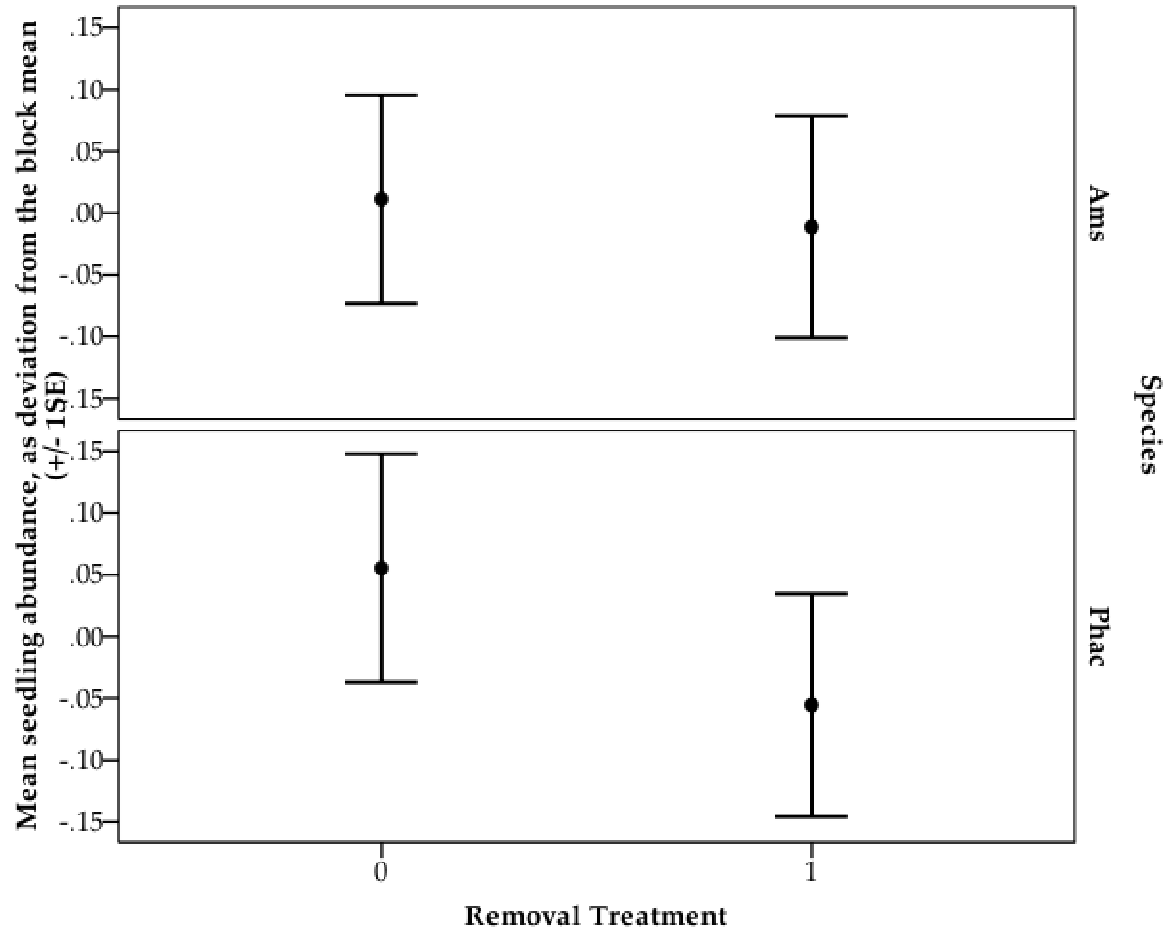
The species of the seedlings did not have an effect on the abundance of new germinants, demonstrating that both *Amsinckia* and *Phacelia* had similar numbers of new germinants at census 1 and census 2 ( $F = 1.570$ ,  $df = 3,1$ ,  $p = 0.202$ ; Fig. 3). There was a strong but non-significant trend towards higher seedling densities after the first census ( $F = 2.960$ ,  $df = 3,1$ ,  $p = 0.088$ ). There was not a significant interaction effect between species and census ( $F = 0.108$ ,  $df = 3,1$ ,  $p = 0.743$ ), which shows that the abundance of new germinants for each species followed the same temporal pattern.



**Fig. 3** – Proportion of new *Amsinckia* and *Phacelia* seedlings at each census with respect to the total number of new seedlings for all censuses.

The competitor reduction treatments did not show a significant effect on the abundance of new germinants for either *Amsinckia* or *Phacelia* ( $F = 0.313$ ,  $df = 3,1$ ,  $p = 0.577$ ; Fig. 4), indicating that both control and removal plots had similar numbers of new germinants. There was still no difference between the abundances of *Amsinckia* compared to *Phacelia* germinants ( $F = 1.610$ ,  $df = 3,1$ ,  $p = 0.207$ ), and there was also no interaction effect seen between the removal treatment and species ( $F = 0.138$ ,  $df = 1,3$ ,  $p = 0.711$ ). Therefore, neither species responded to the removal treatment in terms of germination timing or frequency.





**Fig. 4** – The effect of invasive plant removal (0–control, 1–removal) on the abundance of new seedlings, as the deviation from the block mean. Competitor removal did not have a significant effect on the number of new seedlings for either species ( $p > 0.05$ ).

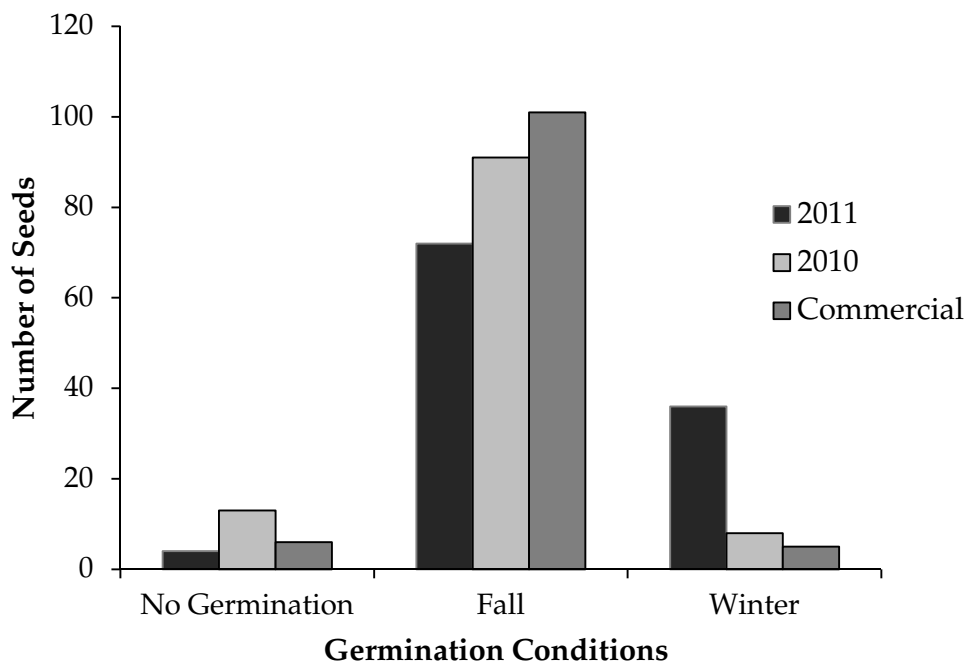
#### *Germination Trials*

Out of 336 seeds planted for the two germination trials, 313 seeds successfully germinated (93.2%). While the seeds from 2011 and the commercial seeds germinated at similar rates (96.4% and 94.6%, respectively), only 88.3% from 2010 germinated (Table 3). Seed source had a significant effect on the relative number of seeds that germinated under winter versus fall conditions ( $X^2 = 46.554$ ,  $df = 4$ ,  $p < 0.001$ ). A larger number of commercial seeds germinated under fall conditions (101 seeds, 90.2%) than of the other

two treatments, while seeds from 2011 had larger numbers germinating under winter conditions (36 seeds, 32.1%; Fig. 5). The germination success of the three different treatments also varied significantly, with seeds from 2010 having the lowest number of successful germinants ( $X^2 = 6.254$ ,  $df = 2$ ,  $p = 0.044$ ). Of the 2010 seeds that did germinate, most germinated under fall conditions (91.9% of germinating seeds). For all seed sources, fewer total seeds germinated under winter conditions than fall conditions, with 78.6% of seeds germinating under fall conditions compared to 14.6% of seeds germinating under winter conditions. 23 seeds (6.8%) did not germinate at all during the two trials.

**Table 3.** Percentage of seeds that germinated in each trial, by seed type.

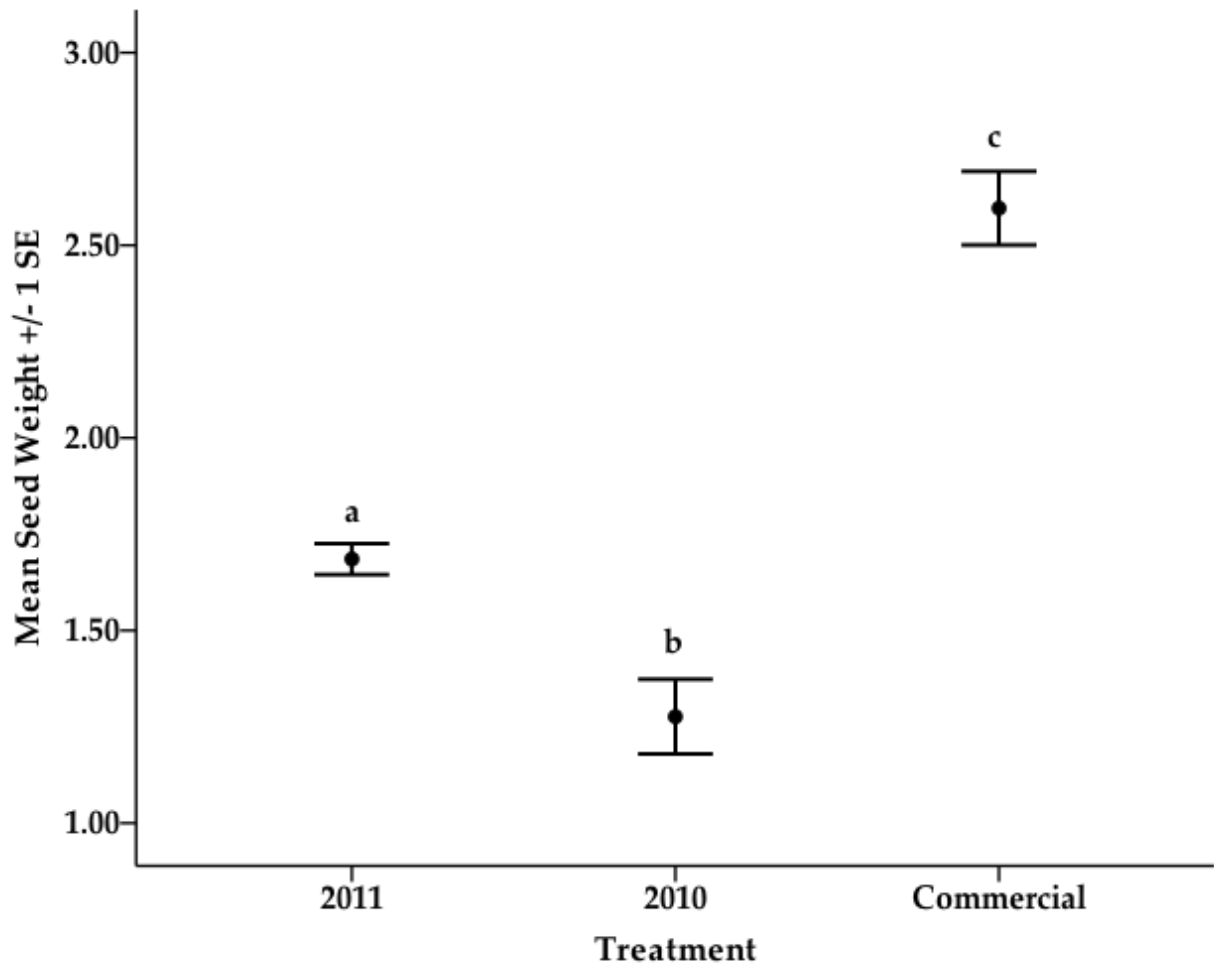
<i>Seed Type</i>	<i>2011</i>		<i>2010</i>		<i>Commercial</i>	
Germinated	Yes	No	Yes	No	Yes	No
Trial 1	96.4%	3.6%	98.2%	1.8%	94.6%	5.4%
Trial 2	96.4%	3.6%	78.6%	21.4%	94.6%	5.4%
Total	96.4%	3.6%	88.4%	11.6%	94.6%	5.4%



**Fig. 5** - Number of seeds that germinated in all trials by germination condition (Fall, winter, or no germination) and treatment (BFS seeds from 2010 or 2011 or commercial seeds).

The number of days until germination for seeds also varied by source ( $X^2 = 60.572$ ,  $df = 4$ ,  $p < 0.001$ ). Commercial seeds had the largest number of seeds germinate in three days, with 66.1% germinating in three days, compared to only 23.3% of 2011 seeds and 35.7% of 2010 seeds. Seeds from 2011 took longer to germinate, as this treatment had the highest number of seeds germinating in five or more days (26.8%). The three seed types also had significantly different weights ( $F = 67.896$ ,  $df = 2, 30$ ,  $p < 0.001$ ; Fig. 6).

Commercial seeds ( $2.60 \pm 0.10$  mg) were significantly heavier than 2010 ( $1.28 \pm 0.10$  mg;  $p < 0.001$ ) and 2011 seeds ( $1.69 \pm 0.04$  mg;  $p = 0.004$ ). Seeds from 2011 were also heavier than those from 2010 ( $p < 0.001$ ).

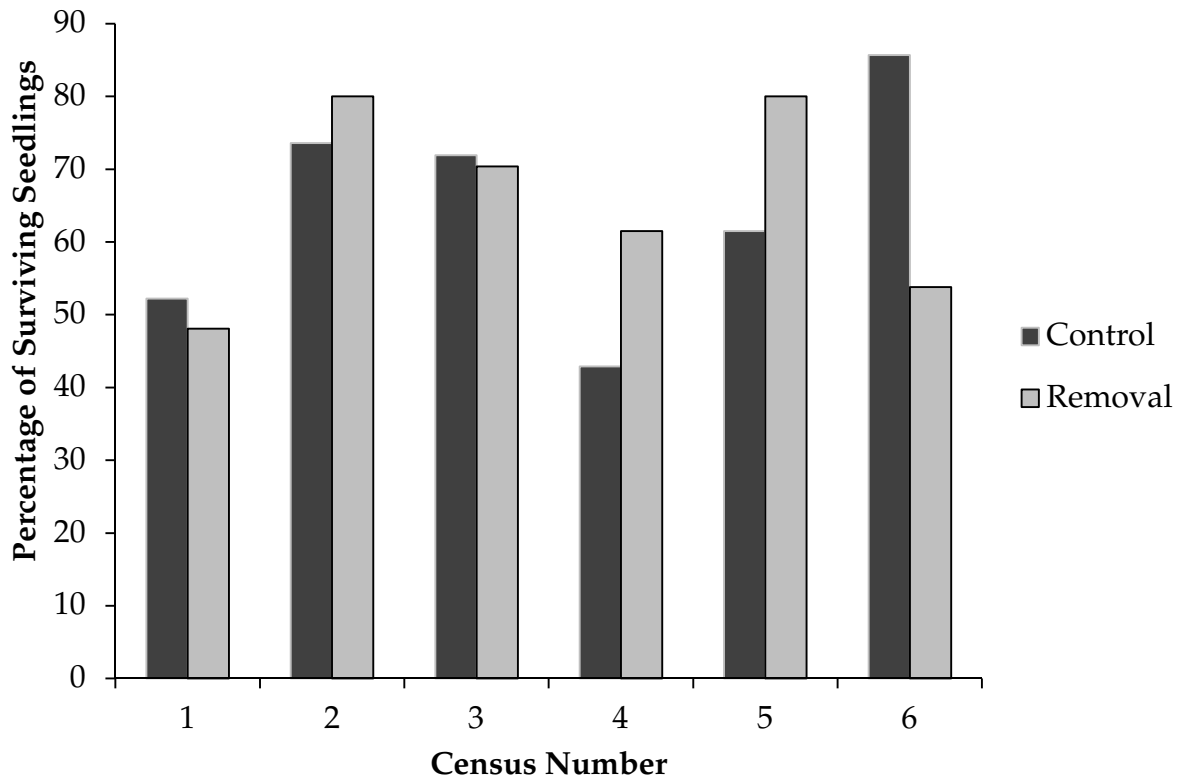


**Fig. 6** – Mean seed weights (+/- 1 SE) for each seed type from Trial 2. Seeds had significantly different weights ( $p < 0.001$ ) and different letters represent significant differences in seed weights between the seed sources.

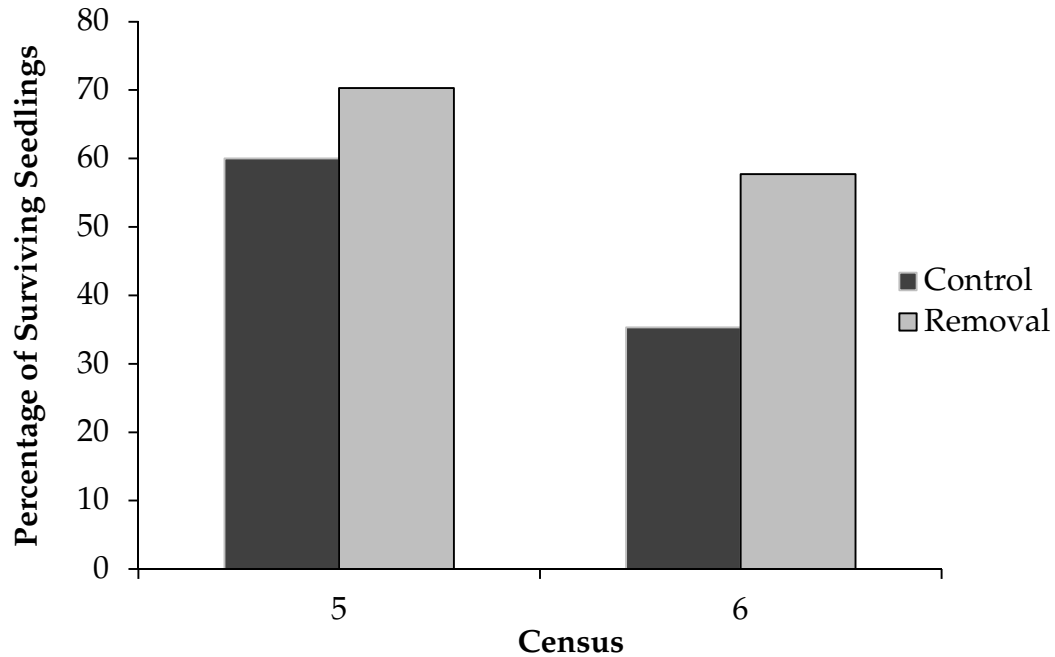
### *Seedling Survivorship*

Survival rates of October *Amsinckia* germinants varied significantly between each set of successive censuses ( $X^2 = 21.230$ ,  $df = 5$ ,  $p = 0.001$ ). The highest survivorship was observed in census 2, with 76.5% of the seedlings surviving from the previous census (Table 4). Census 1 saw the highest mortality for October germinants, with only 50.4% of marked seedlings surviving. The removal treatments did not show a clear trend in affecting the survival of early (October) germinants. In some censuses, survival was

higher in control plots, while other censuses showed higher survival in removal plots (Fig. 7). The effect was also not significant in any census ( $p > 0.05$  for all).



**Fig. 7** – *Amsinckia* survival rates at each census for October germinants, showing control and removal treatments. Competitor removal did not have a significant effect on survivorship in any of the censuses ( $p > 0.05$ ).



**Fig. 8** – *Amsinckia* survival rates at each census for November germinants, showing control and removal treatments. Competitor removal did not have a significant effect on survivorship in either census ( $p > 0.05$ ).

November germinants of *Amsinckia* had similar survival rates in the two censuses in which they were observed ( $X^2 = 3.070$ ,  $df = 1$ ,  $p = 0.080$ ). Although survivorship was higher in both census 5 and census 6 in removal plots of late (November) germinants (Fig. 8), this difference was not statistically significant in either case ( $p > 0.05$ ).

**Table 4.** *Amsinckia* survival rates for all censuses, by germination month and treatment.

Germination Month	Treatment	Census						Cumulative
		1	2	3	4	5	6	
October	Control	52.2%	73.6%	71.9%	42.9%	61.5%	85.7%	6.25%
	Removal	48.1%	80.0%	70.4%	61.5%	80.0%	53.8%	7.17%
November	Control	—	—	—	—	60.0%	35.3%	21.2%
	Removal	—	—	—	—	70.3%	57.7%	40.6%

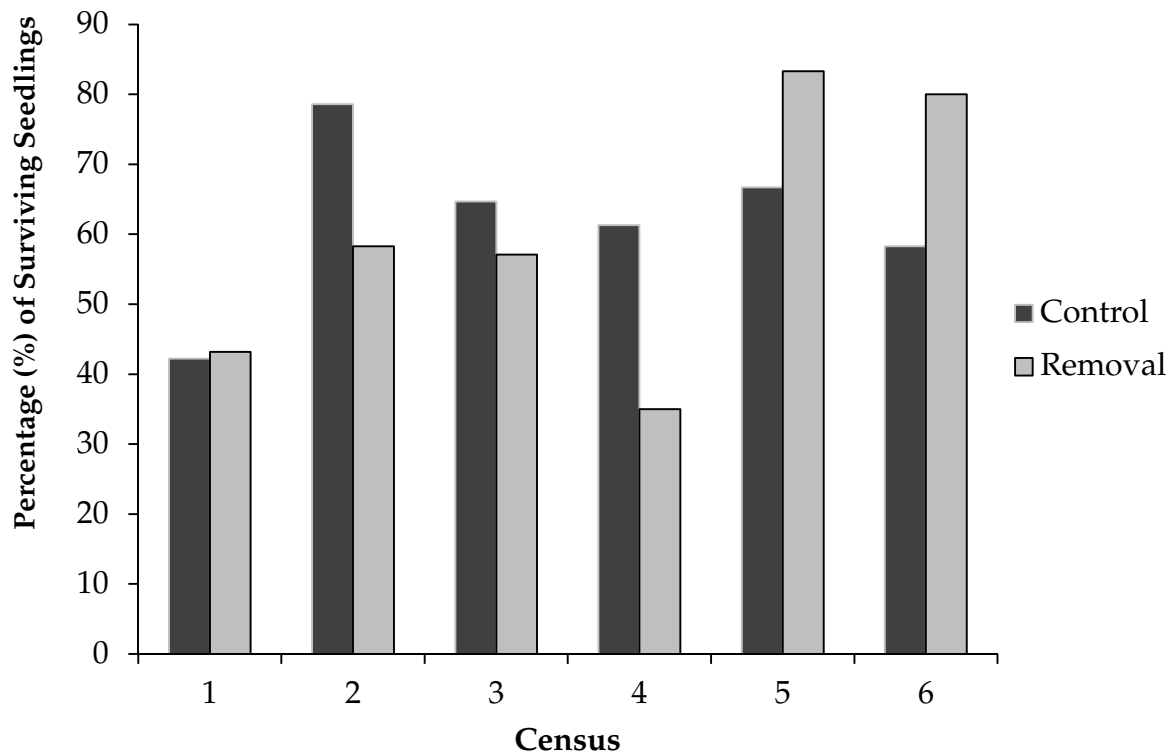
**Table 5.** *Phacelia* survival rates for all censuses, by germination month and treatment.

Germination Month	Treatment	Census						Cumulative
		1	2	3	4	5	6	
October	Control	42.2%	78.6%	64.7%	61.3%	66.7%	58.3%	5.12%
	Removal	43.2%	58.3%	57.1%	35.0%	83.3%	80.0%	3.35%
November	Control	—	—	—	—	60.0%	33.3%	20.0%
	Removal	—	—	—	—	68.2%	46.7%	31.9%

October germinants of *Phacelia* also varied significantly in their survivorship between censuses ( $X^2 = 15.766$ ,  $df = 5$ ,  $p = 0.008$ ). The highest percent survival was observed in census 4, with 70.8% of marked seeds surviving (Table 5). Census 1 also had the lowest rate of seedling survival, with only 42.7% of the marked plants alive at the first survival check. Early *Phacelia* germinants also did not display a consistent removal effect, with the survival rates of the removal plots higher in some censuses, while the control plots had higher survival rates in others (Fig. 9). The control and removal plots also had statistically similar survival rates in all censuses ( $p > 0.05$ ). November *Phacelia* germinants, like the *Amsinckia*, had similar survivorship rates in both census 5 and 6 ( $X^2 = 3.175$ ,  $df = 1$ ,  $p = 0.075$ ). Survivorship of late *Phacelia* germinants tended to be higher in removal plots, although this difference was not significant in either census ( $p > 0.05$ ; Fig. 10). Since no December *Phacelia* germinants were alive in census 6, no comparison between the two censuses could be made.

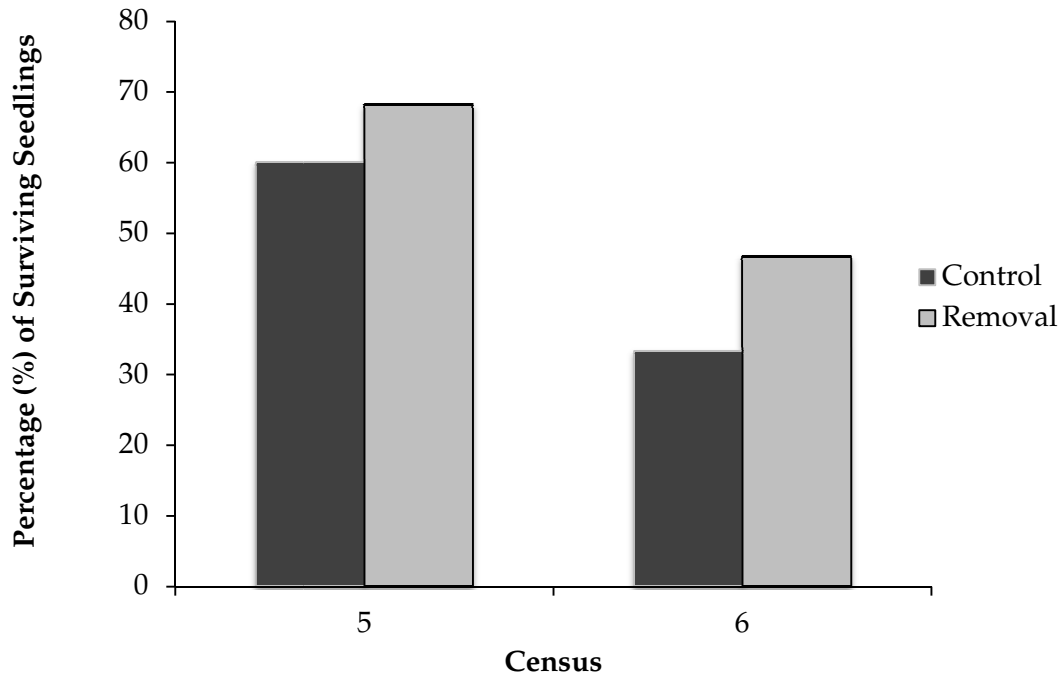
The survivorship of October and November *Phacelia* germinants in the two later censuses where both were present (5 and 6) did not differ significantly ( $X^2 = 0.235$ ,  $df = 1$ ,  $p = 0.628$ ;  $X^2 = 2.114$ ,  $df = 1$ ,  $p = 0.146$ ). However, though not significant, November germinants had a trend towards lower survival rate in both censuses, with 64.9% survival rate in census 5, compared to 70.8% for October germinants, and a 41.7% survival rate for November germinants in census 6, compared to 64.7% for October

germinants. *Amsinckia* seedlings displayed a similar trend. Although October and November germinants had statistically similar survivorships in censuses 5 and 6 ( $X^2 = 0.298$ ,  $df = 1$ ,  $p = 0.585$ ;  $X^2 = 1.435$ ,  $df = 1$ ,  $p = 0.231$ ), October *Amsinckia* germinants showed a trend towards higher survival rates than the November germinants in census 5 (71.4% versus 65.7%) and census 6 (65.0% versus 48.8%).



**Fig. 9** – Survival rates of *Phacelia* October germinants at each census, by removal treatment. Competitor removal did not have a significant effect on survivorship for any of the censuses ( $p > 0.05$ ).





**Fig. 10** – Survival rates of *Phacelia* November germinants at each census, by removal treatment. Competitor removal did not have a significant effect on survivorship in either census ( $p > 0.05$ ).

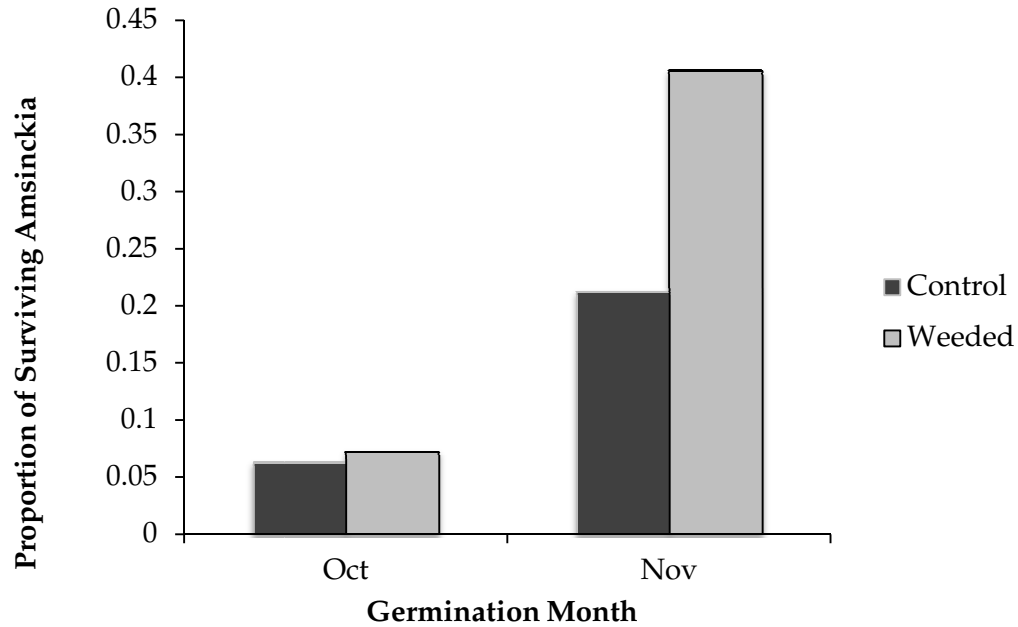
Cumulative survival rates across the entire growing season were higher for late germinants (November) in both *Amsinckia* and *Phacelia* ( $X^2 = 18.81$ ,  $df = 1$ ,  $p < 0.001$ ; Fisher's  $p = 0.0008$ , respectively) (Figs. 11, 12). For October *Amsinckia* germinants, removal of invasive grasses did not have a large or significant effect on the overall survivorship (less than a 1% difference in survivorship) ( $X^2 = 0.51$ ,  $df = 1$ ,  $p = 0.48$ ; Fig. 11). However, November germinants displayed a much larger difference in survivorship between the control and removal plots. November germinants in removal plots had a cumulative survival rate of 40.6%, compared to only 21.2% for control plots. Though this difference was large, it was not statistically significant, potentially due to a small sample size ( $X^2 = 2.95$ ,  $df = 1$ ,  $p = 0.0859$ ). A similar, though not identical, trend was observed in *Phacelia*. October germinants did not display a large treatment effect on

survivorship (5.12% versus 3.35%) (Fig. 12)( $X^2 = 0.61$ ,  $df = 1$ ,  $p = 0.435$ ). November germinants of *Phacelia* showed a similar, though smaller in magnitude, potential difference in survivorship between control and removal plots. Removal plots had a 31.9% survival rate, while control plots had only 20.0% of seedlings survive, but this difference was also not statistically significant ( $X^2 = 0.639$ ,  $df = 1$ ,  $p = 0.44$ ).

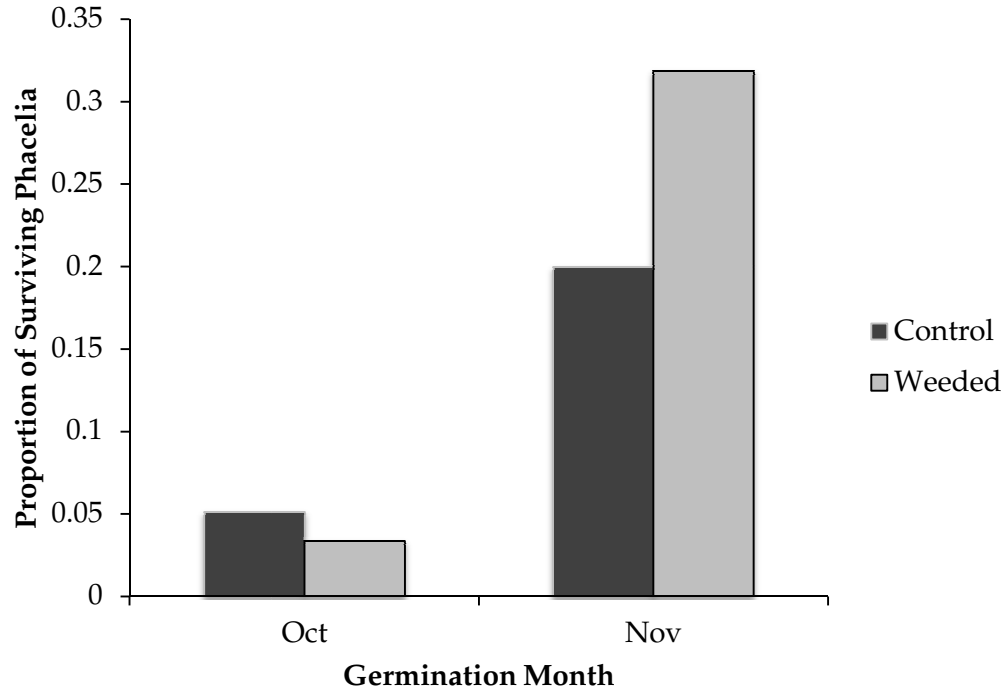
For qualitative comparison, I also looked at survivorship data for early (October) and late (December) germinants for both species from 2009-2010 (Table 6). Early *Amsinckia* germinants had an overall survival rate of 83.3% in removal plots and 69.5% in control plots, while later germinants survived at a rate of 52.8% of in removal plots, and 37.7% in control plots. For early *Phacelia* germinants, overall survival rate was 58.8% in removal plots and 40.0% in control plots, while later germinants had lower survival rates of 46.7% in removal plots and 23.8% in control plots.

**Table 6.** *Amsinckia* and *Phacelia* survival rates for early and late germinants in 2009-2010.

<i>Species</i>	<i>Amsinckia</i>		<i>Phacelia</i>	
<b>Treatment</b>	<b>Oct</b>	<b>Dec</b>	<b>Oct</b>	<b>Dec</b>
Control	0.695	0.377	0.4	0.238
Removal	0.833	0.528	0.588	0.467
Difference	0.1384	0.151	0.188	0.229



**Fig. 11** – Cumulative proportion of surviving *Amsinckia* through all six censuses. Survivorship of all November germinants was significantly higher survival than that of October germinants ( $X^2 = 18.81$ ,  $df = 1$ ,  $p < 0.001$ ).



**Fig. 12** – Cumulative proportion of surviving *Phacelia* through all six censuses. Survivorship of all November germinants was significantly higher than the survivorship of all October germinants ( $p = 0.0008$ ).

## Discussion

### *Germination Timing*

Both *Amsinckia* and *Phacelia* had large numbers of new seedlings present in the first and second censuses. The third abundance census contributed only a very small number of new seedlings relative to the total number of seedlings that emerged. Although there were larger numbers of new seedlings present in the first census compared to the second for both *Amsinckia* and *Phacelia*, the difference was not enough to be statistically significant. Both species also had almost identical proportions of their total new seedlings emerge in the first two censuses, showing that there was not a detectable difference in timing of seed germination between the two species this year. This also shows that if the presence of early germinating invasive grasses is affecting the timing of germination for these two native species, it is having a similar effect on both. Even though early germination has the potential for increased mortality of seedlings, the vast majority of seeds germinated in either the first or second census. In consideration with the survival data, this could indicate that even though earlier germination may result in increased risk of mortality, the potential benefits in terms of reproduction or surviving competition with invasive grasses may be enough to make germinating early a successful strategy, at least in some years (Kalisz, 1986).

The fairly equal spread of germination in census 1 and 2 also demonstrates that both species have what were classified as “early” and “late” germinants. Although the two species germinated at the same time this year, field observations from past years have seemed to indicate that *Phacelia* tend to germinate later than *Amsinckia* (anecdotal observation, Thomson). If this is the case, continuing to monitor germination for these

species is necessary to reveal if the germination timing of these species varies by year, if they always germinate at the same time, and whether larger numbers of natives start to germinate earlier.

The removal treatments had little impact on the number of seedlings germinating for both *Amsinckia* and *Phacelia*. The lack of a competitor reduction effect is not entirely unexpected. The presence or absence of invasive grasses may only affect the survival of natives, instead of the number of seeds germinating. If that is the case, the treatment effect would be most likely observed later on in the growth stages of the natives, as changes in seedling mortality and the abundance of established plants. Other studies on forb germination in the presence of grasses have demonstrated that the thatch left behind from grasses in productive years may inhibit forb germination in the subsequent year (Levine and Rees, 2004). The absence of an effect of invasive grasses on germination rates in these species indicates that they may not respond to that germination cue. However, the numbers of emerging seedlings would need to be compared across years to determine if this pattern is absent at the BFS.

Only two total *Clarkia* seedlings were observed in our plots, and only in the later censuses. *Clarkia* has similarly appeared later on in the season in previous years at the BFS, indicating that its germination timing may differ from *Amsinckia* and *Phacelia*. In spring 2011, *Clarkia* was abundant later in the season and produced a large number of seeds, after a mass mortality occurred in both the grasses and other native species (unpublished data, Thomson). The mortality in the other native species and grasses did not occur in 2012, and *Clarkia* was found in very low abundances, with none surviving to the final census. The small number of *Clarkia* germinants indicates that there may be

germination cues for this species that involve the abundance of other plants, or the below average rainfall of this year did not allow for germination (McGlone et al., 2010). This could also be evidence of that *Clarkia* seeds undergo dormancy if the germination conditions are not ideal, for example, due to a large abundance of invasive grasses. If the presence of invasive grasses reduces the ability of *Clarkia* to germinate, it would be essential for grasses to experience higher mortality in periodic years for *Clarkia* to persist. Levine and Rees (2004) found that variation in mortality of these grasses was critical to the persistence of rare native plants, as they would not germinate in years with lots of thatch from grasses. This may be one potential strategy for *Clarkia*, however, additional research would be necessary to make conclusions about its germination strategy.

#### *Germination of Clarkia under controlled conditions*

In both germination trials, the *Clarkia* seeds germinated with a very high success rate. Commercial seeds had both the fastest time to germination following watering, as well as the largest number of seeds germinating under fall conditions. The fast germination of the commercial seeds is expected, as the seeds were propagated under greenhouse conditions, which are likely to select for quick germination. The seeds from the BFS have to be able to respond to environmental cues that may mean the life or death of the germinant, so the slower germination time may be evidence of the effect of seed source on germination behavior. Whether seeds are commercially raised or locally collected has been shown to affect the emergence timing of seeds in field studies (Humphrey and Schupp, 2002), which agrees with the findings of our germinator trials.

In addition to having a longer time to germination than commercial seeds, seeds from 2011 also had a higher proportion germinating under winter conditions. This also supports the possibility that seeds from the BFS may require stronger germination cues than the commercial seeds due to the stronger selection effects at the field station compared to green houses or gardens, (Humphrey and Schupp, 2002). However, even though seeds from 2011 took slightly longer to germinate than seeds from the other two sources, overall *Clarkia* seeds germinated quicker than what field observations would predict. This suggests that there may be other factors influencing the germination of *Clarkia* in the field that were not present in the germinator trials. Additional experiments could explore what these factors may be and how they affect the germination of *Clarkia* seeds.

Interestingly, the seeds from 2011 and the commercial seeds had almost identical germination success for both trials. The seeds from 2010 had a similar success rate as the other two seed types in the first trial, but in the second trial they suffered a significant decrease in their germination success. Since the germination success only differed for seeds from 2010, it is unlikely that the set up of the second trial caused a difference in germination success for these seeds, in which case the seeds themselves may be the cause of the discrepancy. The seeds from 2010 were significantly smaller than the seeds from 2011 and the commercially attained seeds, which is one potential factor that could explain the difference in germination success. In some species, smaller seeds have been shown to have decreased germinating success than seeds of larger size (Weis, 1982). However, the seeds from the first trial were not weighed, so it may be that seeds from 2010 are smaller in general and seed weight was not the factor contributing to the

decreased germination success of the second trial. There is also the potential that the lack of germination resulted from the age of the seeds, and that some of the seeds from the 2010 census were simply no longer viable. Since the seeds from 2010 that did germinate, germinated primarily under the fall germinator conditions, the storage of the seeds could have caused the viable seeds from 2010 to germinate quickly.

The ability of *Clarkia* seeds from 2010 (from two generations ago) to germinate with a fairly high success rate after sitting in storage for over a year suggests that it may be able to undergo dormancy in the field if conditions are not ideal and still have successful germination in the following year. This could be an important characteristic for the survival of *Clarkia* in the face of the continued presence of invasive grasses in its habitat. If *Clarkia* seeds are able to germinate under the most ideal conditions possible, the seedlings have a higher chance of surviving to reproduce, contributing to the persistence of this species in invaded habitats.

### *Seedling Survival*

Early (October) germinants of both *Amsinckia* and *Phacelia* exhibited lower overall survival rates than those of the late (November) germinants of the same species. A higher mortality for early germinants is not entirely unexpected, as early germination exposes the seedlings to warmer temperatures and longer dry periods than emergence later on in the year. Both species suffered mortalities of around 50% or greater between being marked and the first survivorship check in mid-October. The first census followed a particularly warm October with essentially no precipitation except the storm that stimulated germination, so a fairly high mortality rate is reasonable. The overall high



mortality of the October germinants may have also reduced the ability to distinguish any effects of invasive grass removal on survivorship. With less than 8% of the early germinants surviving until March, any difference between the control and removal plots would also be very small. However, this lack of a clear effect of grass removal on *Amsinckia* early germinant survival may also indicate that competitors were a much less important influence on fall survivorship this year than the stressful abiotic conditions. In contrast, during 2009-2010, there was a larger overall survival rate for early germinants compared to late germinants, and there was also an observable difference in the survival rates of seedlings in the control and removal plots (Thomson, unpublished data; Table 6). This difference in results may indicate that in 2011-12, there was a high cost to early germination because of the particularly stressful abiotic conditions in the fall, so that treatment effects made little difference for these individuals.

The same sort of patterns are evident for October *Phacelia* germinants. The overall survivorship was less than 6% from October-March, lower than the *Amsinckia* survival rate, which again suggests little difference in survivorship between control and removal treatments. One alternative reason for the absence of an effect of removal treatment on October germinants is the process by which grasses were removed. Since the treatment consisted of clipping, only the above-ground biomass of the invasive plants was reduced. Since the plants could not be removed completely without disturbing the native species, clipping allowed for the regrowth of invasive species between treatment applications. Seabloom et al. (2003) demonstrated that mowing and burning had differing effects on the reduction in abundance of invasive grasses, and therefore different effects on the survival and abundance of the focal species. Therefore, the

partial presence of invasive species in the removal plots may have contributed to the difficulty in discerning differences between the two treatments.

Another interesting trend occurred in the survival rates in the early censuses. In the removal plots, the survival rates for *Phacelia* were actually lower than in the control plots, while in later censuses the removal plots had higher survivorship rates. Although these differences were not significant, data from previous years at the BFS showed the same trend, which suggests that this may not be a random occurrence. Though many studies have shown that removal of invasive competitors should reduce competition for resources and therefore increase the survivorship, this potential pattern could suggest that early on in the life of *Phacelia* the presence of competitors increase survivorship (Gurevitch et al., 2002). One possible explanation for this is that in the early phases of growth for early *Phacelia* germinants, grasses facilitate growth by providing partial shade and cover (Grime, 2001). The removal of grasses from the plots leaves them very exposed to the sun, and may also increase the rate at which the soil is depleted of water. Since the periods between the early censuses were also fairly hot and dry, the removal of grasses that keep the most intense sun off and retain moisture may actually negatively affect the survival of early *Phacelia* germinants.

November germinants of both *Amsinckia* and *Phacelia* not only displayed a higher overall survival rate than the October germinants, but also exhibited a trend towards higher survival in the removal treatments compared to controls. This appears to be due to the very high mortality experienced by early germinants in the first three censuses this year, because at censuses 5 and 6 there was a trend towards higher survivorship in the older and more established October germinants compared to the November ones.

Interestingly, in past years at the BFS, early germinants had higher overall survivorship (Thomson, unpublished data). A study by Miller (1987) also discovered that earlier emerging seedlings of several species had a higher biomass and a higher chance of survival than later germinants. A possible explanation for the difference in survival rates of early germinants between this year's results and others may be from the shorter length of time later germinants were exposed to stressful abiotic conditions in past years, especially the extremely warm and dry periods experienced by October germinants. This result supports the idea that germinating early may be beneficial in some years, but can greatly increase mortality risk in others. However, there is also the potential that October germinants that did survive grew larger or produced more flowers than November germinants, resulting in higher reproductive fitness, which would agree with the findings in Miller (1987). Analysis of this growth and reproduction data would be needed to determine whether this is occurring, and to fully understand the fitness differences between early and late germinants.

Although the late germinants did not have to withstand the warmer temperatures of October and early November, they emerged when the grasses were larger in control plots, since they germinated almost entirely with the early October rainstorm. Although the higher survival rate of the removal plots compared to the control plots was not quite significant for either the late *Amsinckia* or *Phacelia* germinants, the low sample size may account for that, and it is an interesting trend that should be examined in future years. If significant, it would demonstrate that later germinants might experience competition from invasive grasses, affecting the survival ability of the seedlings. This matches data from 2009-2010, removal plots displayed an overall higher survivorship than the control

for *Amsinckia* and *Phacelia*, and other studies have shown that the establishment of invasive grasses may make it more difficult for native seedlings to survive (Rafferty and Young, 2002).

Since the later November germinants exhibited an overall survival rate significantly higher than that of the October seedlings, even including control plots with grasses, the question arises why any plants would germinate in October. If invasive grasses were not present at the BFS, germinating later would be a safe strategy, as the high mortality from this year illustrates the perils of germinating early. However, the presence of invasive grasses complicates the germination dynamics of these native forbs. Data from previous years at the BFS has shown higher survival rates for October germinants than for later germinants (Thomson, unpublished data). Therefore, relative survivorship of early and late germinants could vary in different years, depending on abiotic conditions such as rainfall and temperature. Native forbs are placed in difficult circumstances with the presence of invasive grasses. While germinating early may allow them to avoid potential competition with grasses later in the year, exhibited in the data from 2009-2010, early germination also carries risks of high mortality. There is also the potential for trade-offs in different aspects of the plants' fitness. For example, though October seedlings suffered a higher mortality this year, they may gain an advantage in growth and reproduction from germinating earlier, which has been shown in studies on other plants (Marks and Prince, 1981, cited in Kalisz, 1986). At the end of both the 2009-2010 and 2011-2012 growing seasons for annuals, plant height, diameter, and the presence of inflorescences on plants were recorded. An analysis of this data could reveal

whether October germinants suffer a higher mortality initially so that surviving plants produce more offspring.

## Conclusions and Further Research

The relationships between the invasive and native species at the BFS are clearly very complex. This thesis has addressed certain factors that may contribute to the abundance and survival of different native species with the presence of invasive grasses and forbs. *Amsinckia* and *Phacelia* were found to have similar germination timing, regardless of removal treatment or census. *Clarkia* may germinate later in the year, but insufficient germination in the 2011-12 year made this impossible to test. The germinator trials revealed that seed origin plays an important role in the germination timing of *Clarkia* seeds, and that older seeds may germinate quickly unless they lose their viability. The germination of *Clarkia* may also be interesting to examine in future field experiments to look for evidence of the potential seed dormancy and the potential heritability of early or late germination. The fluctuating survival rates observed for early germinants highlight both the benefits and risks of early seedling emergence. Years with less stressful abiotic conditions are likely to see higher survival rates for early germinants, while in other years early germinants may suffer massive mortality. Therefore, germinating early is not a foolproof strategy for forbs to avoid potential competition with invasive grasses. Though the effects of competition were not significant in this study, the trends were consistent with biological expectations and data from previous years. For later germinating species, the competition from larger

invasive grasses may reduce their survival rate more than earlier germinants, sometimes making it preferable to be an early germinant.

In future studies, the trend between survivorship and removal of invasive grasses should continue to be examined. If later germinants tend to be affected more by the presence of invasive grasses, it could have significant implications for the persistence and evolution of native forbs. The continued study of this habitat at the BFS will help increase the understanding of the interactions between native and invasive species, and perhaps reveal potential strategies for mitigation of invasions.

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