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Tracking above- and below- ground seed persistence and mortality in a native tallgrass prairie restoration

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TRACKING ABOVE- AND BELOW-GROUND SEED PERSISTENCE AND MORTALITY IN A NATIVE TALLGRASS PRAIRIE RESTORATION

An Abstract of a Thesis

Submitted

in Partial Fulfillment

Of the Requirements for the Degree

Master of Science

Carmen Pellish

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ABSTRACT

The large cost of seed and low seedling establishment rates make restoring native tallgrass prairies expensive and difficult. Tallgrass prairie restorations typically achieve seedling emergence rates of only 10%. This begs the question of what happens to the remaining 90% of seeds that do not emerge as seedlings. This thesis sought to assess or quantify the importance of seed predators and death by microorganisms or to senescence on seed survival and seedling establishment within a newly planted native tallgrass prairie restoration under typical restoration conditions.

I hypothesized that small vertebrate seed predators would play be detrimental to overall seedling emergence and would shift species composition in favor of smaller seeded species in newly restored areas. A second hypothesis was that the recovery rate of seeds within the soil seed bank and the viability of recovered seeds would decrease over time due to natural decay and death. To explain these questions I used an above- and below-ground approach. The above-ground approach used sham and closed exclosures to measure the amount of seedling emergence and loss to small vertebrate granivores at three sites. The below-ground seed fates approach attempted to measure the loss of seeds and viability of four prairie species over three sampling dates.

The above-ground approach found that small vertebrate predators had a significant effect on overall seedling establishment but did not affect species composition regardless of response variable: percent emergence, seedlings emerged/g planted, and the difference in seedling emergence between the sham and closed exclosure. The below-

ground approach found that, while each species varied, the overall percent recovery declined and the viability of the recovered seeds decreased over time.

Though the fate of many seeds was unknown, my results suggest that granivores significantly reduce seedling emergence. By excluding small vertebrate granivores, my study was able to increase overall seedling emergence by four percent or 17 seedlings/m^2 which could result in fewer seeds planted and hundreds of dollars saved in future restorations. Further studies should test methods to reduce predation by small vertebrate granivores, focusing on methods that are feasible for practitioners. It is also important to investigate the causes of as yet unknown seed losses. This thesis has demonstrated that there is still more work that needs to be done and questions to be answered about seed loss to above- and below-ground sources in tallgrass prairie restorations.

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Entitled: Tracking Above- and Below-Ground Seed Persistence and Mortality in a Native Tallgrass Prairie Restoration

has been approved as meeting the thesis requirement for the

Degree of Master of Science

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DEDICATION

For Brian, Karen, Mackenzie, and Mike whose support and love helped me finish this thesis when I thought it was impossible.

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CHAPTER 1

INTRODUCTION

After European settlement of the central Midwest in the 1800s, much of the native tallgrass prairie landscape was converted to crop land. Within the last four decades, new initiatives have been implemented by government and non-governmental agencies to restore the native landscape and the services that it once provided. This undertaking has been difficult with many obstacles to overcome.

One of the largest hurdles for those who restore tallgrass prairies is the cost of seed. High costs are due to two factors: 1) lack of abundant, cheap seed (either for collection or purchased commercially), and 2) high seeding rates required to achieve desired plant density. Due to intense cultivation of land for corn and soybean production, few remnant seed sources remain and the native seed bank once found within the soil has been depleted (Smith 1998). Prairie seeds are available commercially, but the price for the seed is high. Within the state of Iowa, there are ten commercial seed suppliers that provide various mixes. Low diversity seed mixes (20-30 species) can cost between $500-1500/ha while the diverse mixes (50-70 species) can cost between $3600-5000/ha (Ion Exchange 2013; Prairie Moon Nursery 2013). For example, in 2000, The Nature Conservancy undertook a 9000 hectare prairie restoration in northwest Minnesota. Total expenditures, including land acquisitions, direct restoration costs such as exotic species management and wetland contouring, and labor, were $27 million, with 15% ($4.1 million) toward hand collection rare seeds and purchase of other commercial seeds (Gerla *et al.* 2012).

In a typical restoration, 400 to 950 pure, live seeds/m^2 (PLS) are planted to achieve 30 adult plants/m^2 (Smith *et al.* 2010). Thus, establishment rates for prairie restorations (3.1%- 7.5%) are an order of magnitude lower than modern agricultural practices which can achieve establishment rates of 83%- 92% (Lauer 2005; Smith *et al.* 2010). Williams *et al*. (2007) found that of the 350 PLS/m^2 planted in a tallgrass prairie restoration, no more than 52 seedlings/m^2 emerged (14%). This begs the question of what happened to the remaining 298 seeds/m^2 while within the seed bank.

Low adult establishment rates in prairie restorations can be explained by the numerous hazards that a seed must survive to become a mature adult plant. A seed and seedling's fate can be placed into four categories: pre-dispersal mortality while still on the mother plant, persistence in the soil, post-emergence mortality, and establishment (Chambers and MacMahon 1994; Clark and Wilson 2003). This study will focus on post-dispersal but pre-emergent seed losses and seedling recruitment in a tallgrass prairie setting (Figure 1). Many of the conditions that lead to reduced seedling establishment, such as persistence and mortality, have not been studied in detail in prairie restorations (Chambers and MacMahon 1994; Fenner and Thompson 2005).

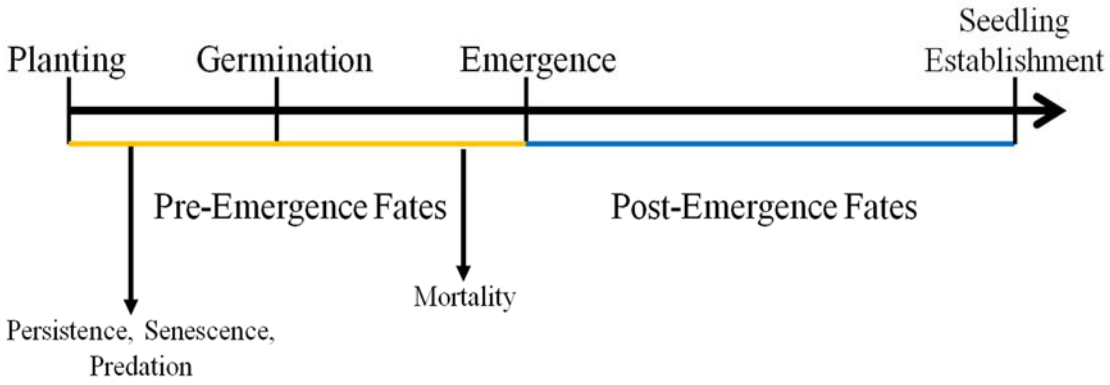

Figure 1: Timeline of seed fates after planting and up to establishment as an adult plant.

Two pre-emergence fates can befall seeds after entering the soil seed bank: persistence and death (Figure 1). Persistent seeds can remain viable in the soil for any amount of time depending on life history characteristics (Baskin and Baskin 2001; Fenner and Thompson 2005). Seed death is caused by predation by vertebrate and invertebrate granivores, attack by microorganisms, and senescence (Chambers and MacMahon 1994; Clark and Wilson 2003; Fenner and Thompson 2005). Taken together, these fates could help explain why prairie restorations have low seedling emergence rates.

The present study seeks to assess or quantify the importance of granivores, soil microorganisms, and senescence on seed survival and seedling emergence within typical, newly planted native tallgrass prairie restorations. The following literature review will focus on the effects of above-ground predation by granivores, below-ground seed fates in the seed bank, and one of the few studies to jointly address above- and below-ground seed loss within the same experiment.

Literature Review: Above-Ground Seed Mortality

It has long been recognized that vertebrate and invertebrate predators can have a large effect on plant community composition (Janzen 1971; Chambers and MacMahon 1994; Fenner and Thompson 2005). These effects and that impact may vary spatially and temporally and may also depend on which type of granivore is most abundant (Janzen 1971; Mittlebach and Gross 1984; Chambers and MacMahon 1994). This review will primarily focus on the effects of small vertebrate granivores, such as mice and birds, on the overall rate of seedling emergence and species composition but invertebrates will also be considered (Janzen 1971; Chambers and MacMahon 1994; Blaney and Kotanen 2001; Fraser and Madson 2008).

Vertebrate seed predators may greatly reduce the number of newly dispersed seeds in a matter of days and this has been consistently observed in a variety of plant communities including forests, grasslands, and agricultural fields (Archer and Pyke 1991; Schnurr *et al.* 2004; Westerman *et al.* 2003, 2006; Heggenstaller *et al*. 2006). In a 1998 study, Barnett tested the effects of multiple chemical compounds in deterring small vertebrate seed predators in long leaf pine communities. He found that small vertebrate granivores consumed 78% of the seeds in the control plot within eleven days. Similar effects of seed predation have been experienced in deciduous forest communities (Heithaus 1981; Schnurr *et al*. 2004; Orrock 2006).

Studies done on native grasslands have found that excluding vertebrate predators from seed sources can significantly increase the number of seedlings that emerge (Edwards and Crawley 1999; Orrock *et al*. 2009). Orrock *et al.* (2009) conducted a

predator exclusion study in an exotic species-dominated California grassland. They used a native grass, *Nassella pulchra*, in two densities to measure the effect of small, medium, and large vertebrate consumers on plant establishment and tested whether seed density made a difference in the amount of predation. Four different exclosures were used to exclude or allow the different levels of predators. Plots were sampled four times: the first to measure seedling recruitment, the second to estimate herbivory, and the third and fourth to measure mature plants. The researchers found that seed predators reduced seedling emergence by 30% for this native species outside the exclosures but the seeding density had no effect on the amount of predation (Orrock *et al.* 2009).

While restorationists are trying to decrease seed predation in their systems, agronomists are trying to increase seed predation in weed seed communities. Westerman *et al*. (2003) performed a study in the Netherlands on weed seed banks in organic cereal fields. Three common weed species (*Stellaria media, Chenopodium album,* and *Avena fatua*) were studied. Seeds were glued to sandpaper seed cards and 120 seed cards were placed in each of four farm fields. After four weeks, the cards had lost 32-70% of their seeds to small seed predators. Westerman *et al.* (2003) also found that the amount of seed loss varied depending on weather and location of the study area.

Seed predators affect plant communities by preferentially consuming certain types of seeds, which affects seedling species composition (Janzen 1971; Kerley and Erasmus 1991; Chambers and MacMahon 1994; Howe and Brown 1999, 2000). To understand how granivores affect species composition in plant communities, one must first understand the mechanisms that drive seed predators to make preferences. In theory,

small vertebrate granivore seed preference is thought to follow the optimal diet theory, which proposes that a predator will tend to maximize the rate of energy intake per unit of time, switching to a different prey species when the rate of energy intake of the first species drops (Sih and Christiansen 2001). Seed defenses such as thick coats and feeding deterrents may increase processing time and thus reduce the net rate of energy intake for seeds of a given size (Kerley and Erasmus 1991; Chambers and MacMahon 1994; Blaney and Kotanen 2001).

Several seed predator exclusion studies have found that unprotected plots had a greater proportional abundance of smaller-seeded species established while the protected/predator-free sites had relatively more large-seeded and presumably preferable species (Reader 1993; Howe and Brown 1999; Blaney and Kotanen 2001). In two old-field studies in Canada, researchers found that seed mass or size was directly related to the rate of seedling emergence and that protecting seeds from predation could increase certain large seeded species by 7% (Reader 1993; Blaney and Kotanen 2001).

Howe and Brown (2000) investigated how seed predation by small rodents affected the early stages of a grassland restoration. The study was conducted in a 5-year old prairie restoration in Viola, Wisconsin and looked at emergence rates of a variety of large and small seeded species commonly planted in restorations. To measure emergence in an open/sham versus closed setting, the researchers created hardware cloth fences to exclude seed predators. The study found that the large-seeded *Silphium integrifolium* had a 59% reduction in percent emergence within the sham exclosures while some small

seeded species, such as *Aster laevis* and *Ratibida pinnata*, had a large increase in their percent emergence within the sham exclosures (Howe and Brown 2000).

However, large seeds are not always preferred. Heggenstaller *et al.* (2006) conducted a study on weed seed predation in an experimental agricultural field in Iowa using two weed seeds, *Abutilon theophrasti* and *Setaria faberi*, to test the effect of cropping practices on levels of seed predation. Using the same seed card method as Westerman *et al.* (2003), Heggenstaller *et al.* (2006) found that the large, nutrient-rich species, *A. theophrasti*, was preyed upon less than the smaller seeded *S. faberi* and speculated that this was because it had a thick seed coat that contained a natural deterrent, a tannin, which increased the processing time and decreased the palatability of the seed.

Literature Review: Below-Ground Seed Fates

Compared to above-ground fates, what happens to a seed within the soil seed bank is poorly understood and few studies have tried to address this question (Chambers and MacMahon 1994). Based on lab experiments, three fates are known to await seeds within the soil seed bank: death, germination, and dormancy (Baskin and Baskin 2001; Fenner and Thompson 2005). Germination and dormancy are easy to measure and can be readily observed in lab and greenhouse experiments but they are not easily observed within a natural soil seed bank (Baskin and Baskin 2001). The causes of seed death in the soil are much harder to observe but can be primarily attributed to soil microorganisms or senescence (Fenner and Thompson 2005). The question of below-ground seed mortality is plagued by methodological issues. Fenner and Thompson (2005) point out, that once a seed has entered the soil, retrieving that seed is extremely difficult and small seeds can be

lost easily. Due to this, few studies have observed seed-soil dynamics in a natural seed bank setting. By better understanding what happens to a seed within the soil seed bank, new paths for research can be opened. This below-ground review focuses on how seed death, dormancy, and senescence influence seed loss and viability loss over time.

Dormancy and senescence are closely linked in a seed's life history requirements. While there is vast literature on dormancy and senescence in laboratory and greenhouse experiments, under natural conditions these processes are not well characterized for most seed species (Baskin and Baskin 2001; Fenner and Thompson 2005). Dormancy is thought to be a safety mechanism for a dispersed seed that prevents it from germinating in unsuitable conditions (Baskin and Baskin 2001; Fenner and Thompson 2005). Each species of plant has its own unique germination cues to break dormancy. Dormancy mechanisms can fall into four categories: physical, morphological, physiological, and morphophysiological. Each type of dormancy will dictate how a seed receives germination cues from its surroundings (Baskin and Baskin 2001; Fenner and Thompson 2005).

Dormancy can be a double-edged sword for any seed within the soil seed bank. The longer a seed is dormant in the soil without germinating, the longer it is exposed to soil pathogens, variable abiotic conditions, and the potential to be found and eaten by a seed predator. All seeds lose viability with age (senesce). The amount of time that a seed can remain viable varies depending on temperature, moisture content, and the life history characteristics of the species. The causes of senescence are not well understood, but it

appears that the seed coat simply deteriorates and exposes the embryo to unfavorable external conditions (Fenner and Thompson 2005).

Quantifying the Fates of Seeds in Natural Conditions: A Case Study

Due to the large scale and time-consuming nature of seed mortality experiments in natural settings, very few studies have attempted to combine and quantify all of the known sources of seed mortality in a field setting. Clark and Wilson (2003) tracked seven seed fates (persistence in the seed bank, seed predation, death by soil fungi, death by senescence, germination, secondary dispersal, and death or disappearance to unmeasured factors) of four species (two native, *Bromus carinatus* var. *carinatus* and *Prunella vulgaris* var. *lanceolata*, and two non-natives, *Cynosurus echinatus* and *Daucus carota*) in a Willamette Valley, Oregon grassland. All four species were dominant at the site or commonly known to invade prairie restorations. A randomized block design was created using five treatments. Seed predation was measured using closed and sham exclosures. Persistent seeds and senescence were measured by finding the seeds within the soil one year after planting and testing for viability. Germination was measured in the field as seedlings emerged. Secondary dispersal was measured using recovered beads within the plots. Death by unmeasured factors was calculated by subtracting the sum of the seeds whose fates were known, from the total number of planted seeds (Clark and Wilson 2003).

For all species, the largest source of loss was to unmeasured factors (i.e. seed were never recovered or accounted for) (Figure 2). The results for each species varied. *B. carinatus* had little germination. *C. echinatus* had higher rates of germination than *B.*

carinatus. *D. carota* had a large survival of persistent seeds in the first year. *P. vulgaris* had a substantial loss to fungal disease compared to the other three species.

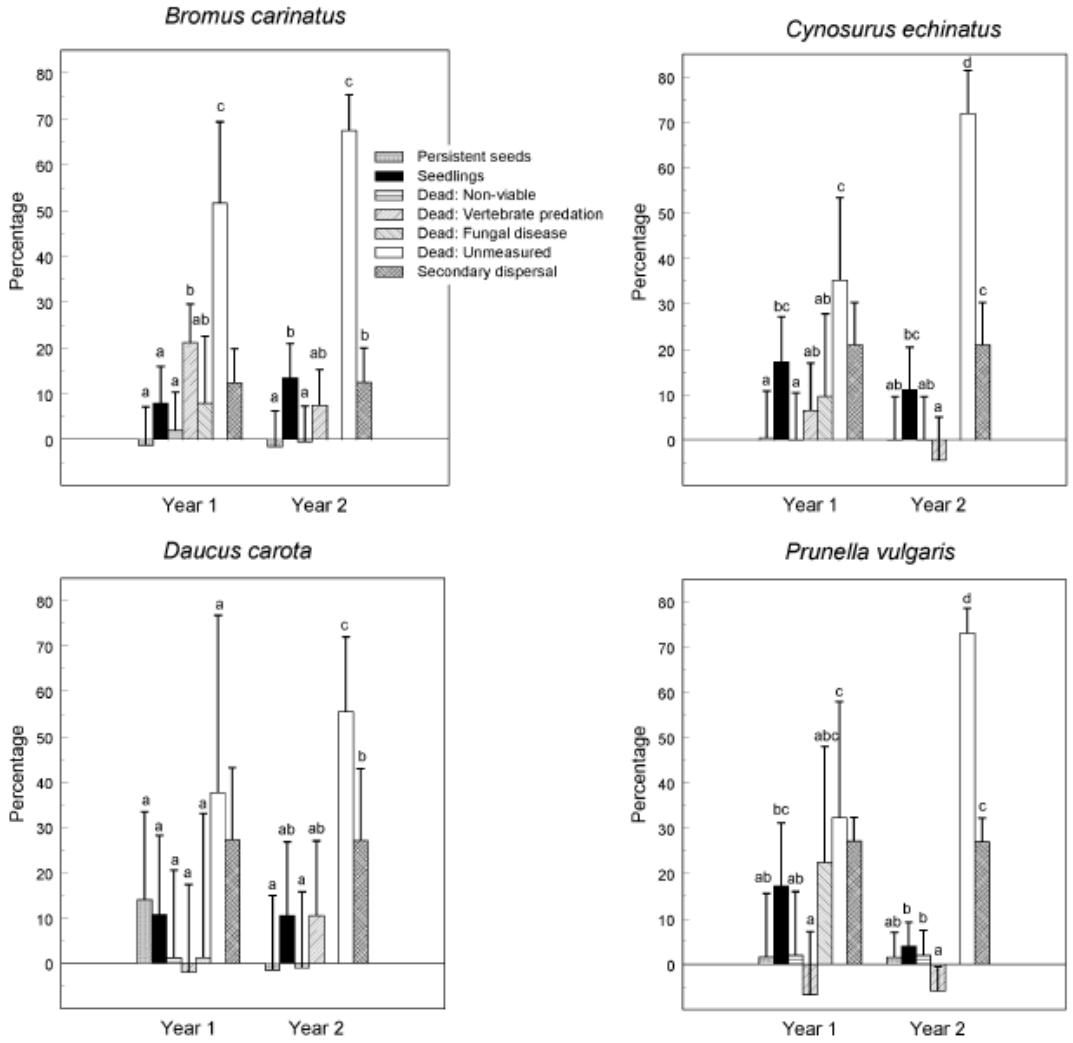

Figure 2: Figure 1 reproduced from Clark and Wilson (2003). Post-dispersal seed fates and causes of death in 1991–1992 and 1992–1993 for four plant species of western Oregon native prairies. Categories are expressed as a percentage of the total number of experimentally sowed seeds (with 95% confidence intervals). Differences between means were tested using Fisher's protected least significant difference (a 5 0.05). Means sharing letters within a single year were statistically indistinguishable. Details on calculations for each fate or mortality factor are found in the text.

The Clark and Wilson (2003) study presents four interesting findings that could be potential outcomes in my study. All four species had their greatest losses to unmeasured factors. The authors attribute these unmeasured factors to invertebrate predation, abiotic factors, and nonfungal diseases. The authors suggest that invertebrate predation was the likely cause of the large unmeasured fate for *P. vulgaris,* based on a concurrent study being done at the site that excluded invertebrates as well as vertebrates. Another significant result for this study was that the larger sized *B. carinatus* had greater losses to seed predation than the other three species (Clark and Wilson 2003). Senescence was not a significant cause of death for any species but the authors attribute this to the seeds fully decaying in the soil before retrieval leaving the seeds unrecoverable (Clark and Wilson 2003).

Experimental Approaches and Predictions

Ecological restoration that depends upon sowing seed must contend with above- and below-ground sources of seed mortality, yet this review has revealed very little research on this topic, either basic or applied. By quantifying the importance of small vertebrate seed predators in real prairie restoration settings for both seedling number and plant community composition, I may draw attention to the importance of this process and begin to devise methods of protecting seeds from the source of mortality. Furthermore, by developing methods to detect and characterize the fates of seeds below-ground over time, we may learn new ways to improve seed persistence and reduce overall seed death.

First, I investigated the effect of seed predators on overall seedling emergence and species composition. Experiments conducted at three sites tested whether exclusion of

small vertebrate predators can influence initial seedling emergence or species composition. I hypothesized that vertebrate seed predation is a significant force in prairie restorations, and predicted that: 1) the exclosures would have a greater overall seedling emergence and 2) that exclosures would favor the emergence of seeds with a higher seed mass than the open, sham exclosures.

Second, I investigated the fate of four native tallgrass prairie species within the seed bank using a seed recovery experiment. I predicted that the recovery rate of seeds and the viability of recovered seeds would decrease over time. The goal of this experiment was to develop methodology for studying seed fates in the soil and to characterize the below-ground seed losses and persistence for representatives of three major functional groups: forbs, forbs-legume, and grasses.

CHAPTER 2

METHODS

To track the above- and below-ground fates of seeds following a restoration planting, I conducted two field experiments. The first experiment (above-ground seed mortality) attempted to measure the above-ground loss of seeds attributed to small vertebrate predators. This experiment was set up as a nested factorial design using sham and closed exclosures to measure the amount of seedlings emerging. The second experiment approach attempted to measure below-ground seed mortality. Four prairie species that were easily identifiable as seeds and seedlings were chosen, coated with fluorescent dye, and planted in known amounts within 25 exclosures.

Above-Ground Seed Mortality

Site Descriptions

I conducted my research at three sites being restored to tallgrass prairie vegetation using typical restoration conditions in spring 2013. Typical restoration conditions were classified as those that used a typical restoration seeding rate and seed mix and used seeding methods that are commonly used in prairie restorations in the Midwest, U.S.A. The experiment included three sites: (1) University of Northern Iowa (UNI) and two sites in Dickinson County: (2) Kettleson-Hogsback Complex (KH) and (3) Spring Run Graff (Graff).

UNI. The University of Northern Iowa prairie restoration site (42° 30’ 30” N; 92° 27’ 27” W) was located in Cedar Falls, IA. The site was 0.61 ha located on a small alluvial bench along the University branch of Dry Run Creek. The soils are classified as a

Saude-Urban land complex with zero to two percent slopes (NRCS, 2013). Prior to May 2013, the site was next to an abandoned trailer park and dominated by *Bromus inermis* Leyss. (Smooth brome), *Agropyron repens* (L.) Gould (Quack grass), and *Poa pratensis* L. (Kentucky blue-grass). Management consisted of semiannual mowing. On May 24, 2013, the herbicide glyphosate was applied to kill all vegetation. On June 3, 2013, the site was prescribed burned and drill seeded using a Truax drill (Truax Company, Inc., 2009) with a 41 species seed mix (Table 1) by the Tallgrass Prairie Center. The mix excluded the four species used in the below-ground seed mortality experiment. The average temperature from June 23 to November 8 was 15.6°C. Temperatures were much cooler than average in March and April. The average precipitation per month was 90.1 mm (Figure 3, NOAA, 2013). The site experienced a wetter spring which continued into the summer and delayed planting into June.

Table 1: UNI site seed mix with the pure live seed (PLS)/g planted (Williams, 2013).

Grasses	**Scientific Name**	**Rate(PLS/g)**
Big Bluestem	*Andropogon gerardii* Vitman	444.6
Side-Oats Grama	*Bouteloua curtipendula* (Michx.) Torr.	514.0
Prairie Brome	*Bromus kalmii* A. Gray	555.7
Blue Joint Grass	*Calamagrostis canadensis* (Michx.) P. Beauv	26.8
Yellow Fox Sedge	*Carex annectens* (E.P. Bicknell) E.P. Bicknell	49.4
Copper-Shoulder Oval Sedge	*Carex bicknellii* Britton	130.8
Field Oval Sedge	*Carex molesta* Mack. ex Bright	46.3
Brown Fox Sedge	*Carex vulpinoidea* Boeckeler	44.5
Switchgrass	*Panicum virgatum* L.	44.5
Indian Grass	*Sorghastrum nutans* (L.) Nash	290.6

Table Continues

Grasses	Scientific Name	Rate(PLS/g)
Little Bluestem	*Schizachyrium scoparium* (Michx.) Nash	138.9
Prairie Cordgrass	*Spartina pectinata* Bosc ex Link	386.6
Forbs (Legumes)		184.0
Milk Vetch	*Astragalus canadensis* L.	130.8
White Wild Indigo	*Baptisia alba* (L.) Vent.	65.4
Purple Prairie Clover	*Dalea purpurea* Vent.	148.2
Round-Headed Bush Clover	*Lespedeza capitata* Michx.	27.8
Forbs (Non-Legumes)		
Prairie Sage	*Artemisia ludoviciana* Nutt.	8.9
Prairie Coreopsis	*Coreopsis palmate* Nutt.	22.2
Pale Purple Coneflower	*Echinacea pallida* Nutt.	104.9
Grass-Leaved Goldenrod	*Euthamia graminifolia* (L.) Nutt.	6.4
Sneezeweed	*Helenium autumnale* L.	34.2
Bigtooth Sunflower	*Helianthus grosseserratus* M. Martens	14.8
Prairie Sunflower	*Helianthus laetiflorus* Pers.	27.8
Ox-Eye Sunflower	*Heliopsis helianthoides* (L.) Sweet	176.4
Prairie Blazingstar	*Liatris pycnostachya* Michx.	50.5
Great Blue Lobelia	*Lobelia siphilitica* L.	4.4
Wild Bergamot	*Monarda fistulosa* L.	31.8
Wild Quinine	*Parthenium integrifolium* L.	31.8
Foxglove Beardtongue	*Penstemon digitalis* Nutt. ex Sims	17.1
Common Mt. Mint	*Pycnanthemum virginianum* (L.) T. Dur. & B.D. Jacks. ex B.L. Rob. & Fernald	10.1
Yellow Coneflower	*Ratibida pinnata* (Vent.) Barnhart	74.1
Sweet Coneflower	*Rudbeckia subtomentosa* Pursh	51.7
Rosinweed	*Silphium integrifolium* Michx.	18.5
Compass Plant	*Silphium laciniatum* L.	33.7
Old Field Goldenrod	*Solidago nemoralis* Aiton	7.4
Showy Goldenrod	*Solidago speciosa* Nutt.	23.4
Smooth Blue Aster	*Symphyotrichum laeve* (L.) Á. Löve & D. Löve	40.4
New England Aster	*Symphyotrichum novae-angliae* (L.) G.L. Nesom	33.7
Ohio Spiderwort	*Tradescantia ohiensis* Raf.	69.5
Culver's Root	*Veronicastrum virginicum* (L.) Farw.	2.8
Golden Alexanders	*Zizia aurea* (L.) W.D.J. Koch	202.1

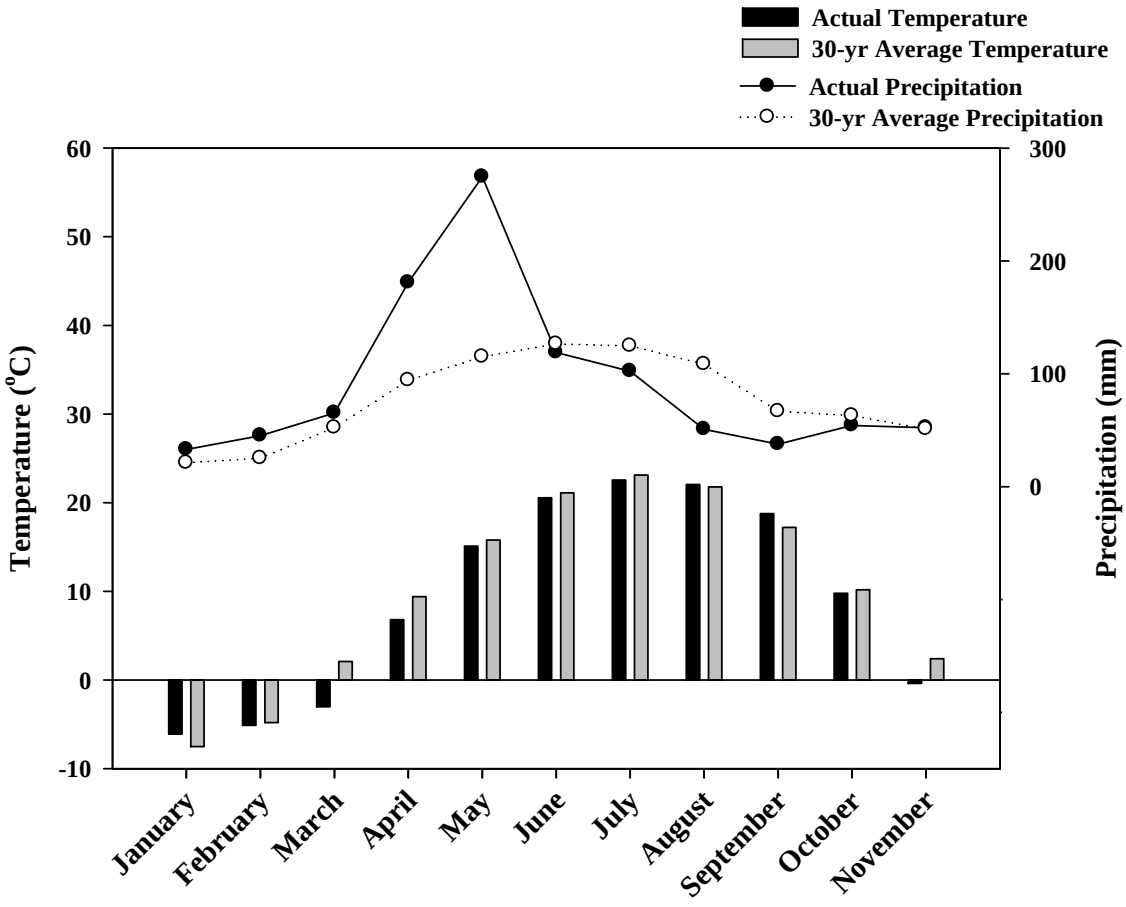

Figure 3: Mean monthly temperatures and precipitation and 30-year average for the Cedar Falls, Black Hawk County, IA UNI site from the beginning of the year to the end of the study period (NOAA, 2013).

Dickinson County Sites. The average temperature during the study, March 28 to August 20 was 13°C. The average precipitation per month was 67.4 mm (Figure 4, NOAA, 2013). The sites experienced a cooler, wetter spring and a dry summer compared to the 30-year average.

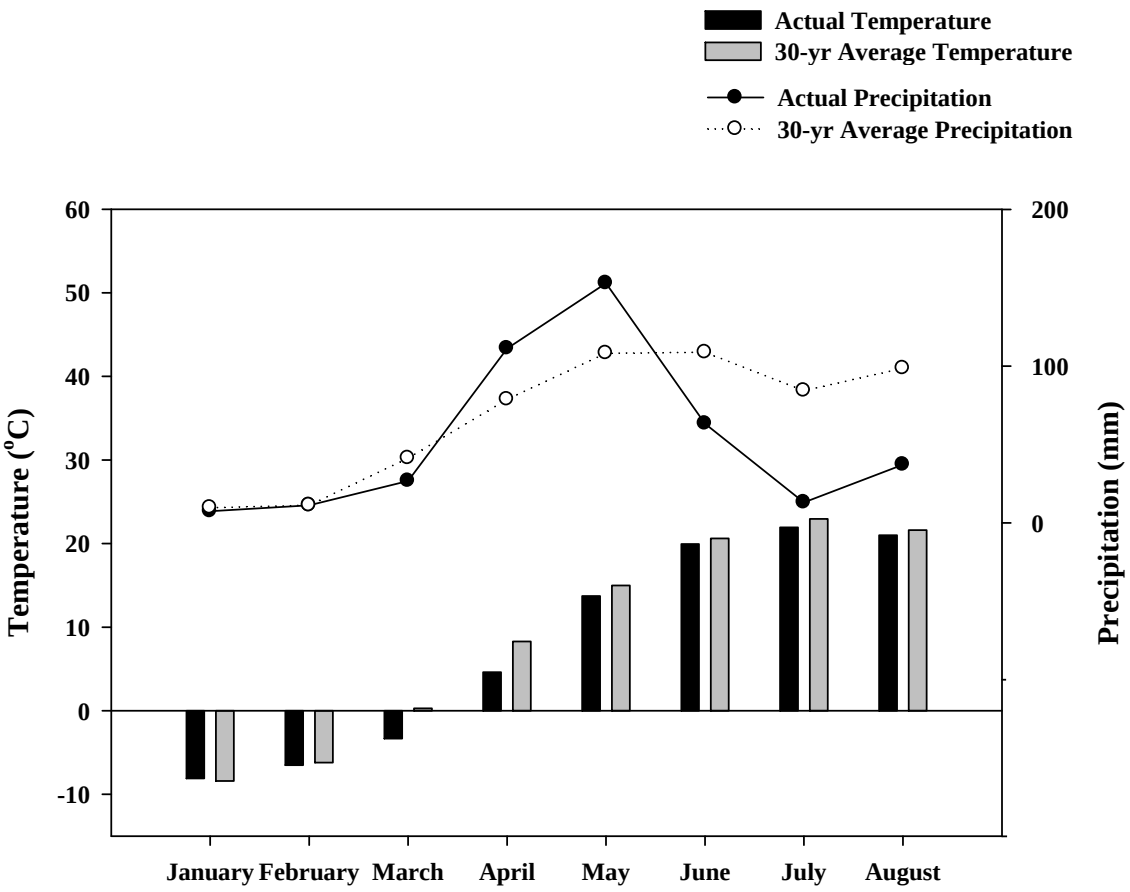

Figure 4: Mean monthly temperature and precipitation and 30-year average for the Spirit Lake, Dickinson County, IA sites from the beginning of the year to the end of the study period (NOAA, 2013).

The Kettleson-Hogsback Complex prairie restoration (43° 27’ 59” N; 95° 8’ 59” W) was located in Dickinson County, IA. The site was 12.1 ha located west of Spirit Lake in northwest Iowa. The soils in the research area are moderately eroded Clarion-Storden complex, five to nine percent slopes and Omsrud-Storden complex, nine to fourteen percent slopes (NRCS, 2013). The site was managed for soybean production in 2012. On March 28, 2013, the site was frost seeded using a broadcast seeding method with a minimum of 23 species seed mix (Table 2) by the Iowa Department of Natural

Resources (DNR) (LaRue, 2013). The broadcast seeding implement was a modified fertilizer spreader. An additional mix of local, hand-collected seed was also planted but the species composition and seeding rates were unknown (LaRue, 2013).

Table 2: Dickinson County seed mix with the pure live seed (PLS)/g planted (LaRue, 2013).

Grasses	**Scientific Name**	**Rate (PLS/g)**
Big bluestem	*Andropogon gerardii*	19.84
Side-Oats Grama	*Bouteloua curtipendula*	7976.62
Switchgrass	*Panicum virgatum*	14.17
Little Bluestem	*Schizachyrium scoparium*	7995.88
Little Bluestem	*Schizachyrium scoparium*	39.69
Indian Grass	*Sorghastrum nutans*	28.35
Rough Dropseed	*Sporobolus compositus* (Poir.) Merr.	5.67
Prairie Dropseed	*Sporobolus heterolepis* (A. Gray) A. Gray	34.02
Forbs		
Prairie Onion	*Allium stellatum* Fraser ex Ker Gawl.	8.50
Lead Plant	*Amorpha canescens* Pursh	2628.07
Aster sp.	*Aster sp.*	34.01
Prairie Coreopsis	*Coreopsis palmata*	11.34
False Sunflower	*Heliopsis helianthoides*	82.21
Western Sunflower	*Helianthus occidentalis* Riddell	53.86
Round-Headed Bush Clover	*Lespedeza capitata*	28.35
Rough Blazingstar	*Liatris aspera* Michx.	8.50
Stiff Goldenrod	*Oligoneuron rigidum* (L.) Small	1048.93
Cinquefoil	*Potentilla arguta* Pursh	2.83
Mountain Mint	*Pycnanthemum virginianum*	5.67
Yellow Coneflower	*Ratibida pinnata*	19.84
Goldenrod sp.	*Solidago sp.*	54.43
Goldenrod sp.	*Solidago sp.*	5.67
Blue Vervain	*Verbena hastata* L.	5.67
Golden Alexanders	*Zizia aurea*	14.17

The Spring Run Graff prairie restoration (43° 22’ 46” N; 95° 1’ 56” W) was located in Dickinson County, IA. The site was 3.6 ha. The soils are Nicollet loam with one to three percent slopes, Clarion loam with two to five percent slopes, and a moderately eroded Clarion-Storden complex with five to nine percent slopes (NRCS, 2013). In fall 2012, the site was taken out of soybean monoculture and on March 29, 2013, seeded using the same methods and seed mix as the Kettleson-Hogsback Site (LaRue, 2013).

Exclosure Design and Installation

Seedling emergence under typical restoration conditions was measured using a sham and closed exclosure design. Exclosures were placed within the sites no more than three hours after planting to reduce seed predation prior to cage installation. A transect line was randomly placed at each site; however, transect lines were not placed within 20 m of any plot edge to avoid potential edge effects. Five exclosures were placed at restrictively random positions (min. 10m apart) along the length of each transect line (Figure 5). The UNI site included a second transect line, adding five additional exclosures to the site.

Figure 5: An example of the transect line at the Graff site.

The exclosures were created using a maximum opening of 9.1 mm wire hardware cloth. Each exclosure measured 1 × 0.5 × 0.6-m with a 0.5 × 0.6-m divider placed at the half-meter mark within each exclosure (Figure 6). This created two, 0.5 × 0.5-m exclosures. Each side of the exclosure was randomly assigned to be the sham or closed side of the exclosure. The closed side of the exclosure had two, 0.5 × 0.3-m hardware cloth strips fastened to the exclosure and tied shut with wire, creating a closed lid that could be opened later for data collection. The sham exclosure had 0.12 × 0.15-m openings cut into the three outward-facing sides to allow small vertebrates to enter and exit.

Figure 6: Photo of a completed cage at the UNI site.

Each exclosure was placed into a 5 cm deep opening created using a flat metal blade. All the exclosures were anchored down using six wire staples. Once in place, the exclosure divider was fastened into place and the lid secured onto the closed exclosure (Figure 6).

A 0.1 × 1-m strip of duct tape was placed around the closed side of the exclosure and coated with Tree Tanglefoot™ (Contech Inc., 2014), a sticky sap that prevents insects that contact the surface from moving. The Tree Tanglefoot™ and duct tape were reapplied once and then removed after it proved to be ineffective at keeping insects out of the exclosure. To ensure exclosure safety during establishment mowing, maps were created for all three sites that detailed the exclosure locations within the field.

Seedling Emergence

Emerging seedlings were identified (based on: Royer and Dickinson 1999, NRCS 2005, and Williams 2010) at nine time points at the UNI site and seven time points at the Dickinson County sites over the growing season (Table 3). Seedlings and most of their associated root mass were removed at each sampling date to prevent reestablishment of any counted individuals. Every effort was made to minimize soil disturbance during removal. All removed seedlings were pressed and the date, site, exclosure, and treatment were recorded. Any weeds present within the exclosures were identified, removed by pulling or cutting to minimize soil disturbance, and discarded.

Table 3: 2013 sampling dates at each site.

Date	UNI	KH	Graff
6/11		X	X
6/18		X	X
6/25			X
6/26	X	X	
7/2		X	X
7/9			X
7/10	X	X	
7/16	X		
7/23	X		
7/24		X	X
7/29	X		
8/7	X		
8/20		X	X
8/23	X		
9/5	X		
9/16	X		

Field data sheets recorded the researcher, date, exclosure, treatment, total number of known and unknown seedlings found, and abundance of each seedling found to

minimize chances of misidentifying species. If the seedling was unknown, it received a letter designation until it could be correctly identified. Known weed seedlings were not recorded.

Coordinating seedling identification between the UNI site and KH/Graff sites, 320 km apart, was an instrumental part of the seed predation experiment. The Dickinson County sites were monitored by an undergraduate assistant. To ensure correct identification, all native and unknown seedlings from the Dickinson County sites were photographed, uploaded to a Powerpoint® (Microsoft Company, 2014) file, and was shared with all researchers in Google Drive® (Google, 2012). Three trips to the Dickinson County sites with all three researchers present were performed on June 12, 2013, July, 2, 2013, and August 20, 2013 and seedling identification was reviewed on May 1, 2013, July 15, 2013, and July 29, 2013, to ensure seedlings were identified the same.

Data Manipulation

Seedling data from each site were entered into Excel spreadsheets, one for UNI and one for Dickinson County. After samplings were completed at all three sites, the two individual spread sheets were combined into one which replaced sampling dates with sampling number (Appendix A).

The final compiled data sheet removed three types of seedlings, those that were not known to be planted, seedlings that remain unknown, and all *Solidago* species and *Symphyotrichum laeve* from the UNI site. The *Solidago* species and *Symphyotrichum laeve* were removed from the final set after they could not be positively distinguished

from other similar looking species in the seed bank. Prior to removing seedlings, a total of 572 seedlings were collected. After removal, a total of 277 seedlings were included in the final data from all three sites. Henceforth, the data set with only the planted species will be called “all emerged perennial, planted seedlings”.

Data Analysis

The effect of sham versus closed exclosure was tested using a mixed effects general linear model:

Seedling Emergence = Overall Mean + Site effect + Cage(site) + Type effect + Site × Type effect + Error.

In this model, site, type or exclosure type, and site × type are fixed effects. Cage(site) is a random effect. Cage(site) takes into account the spatial variation throughout the sites. The planted seedling data set did not violate any assumptions. The effect of the exclosure type did not vary between sites and the interaction term was removed from the analysis after it was found to be non-significant and I had no specific hypotheses about the interaction.

Species composition in the closed and sham exclosures were compared using a general regression analysis where the percent emergence and seedlings emerged/g of seed planted were based on the interaction of seed mass and exclosure type. The seeding rate for each species varied in this study and this approach attempts to correct for this bias, which assumes that the more seeds that are planted, the more seedlings that will emerge. The second response variable measures the amount of seedlings emerged/g of seed planted. Using this analysis corrects the bias within the amount of seed mass planted. In a typical restoration, larger-seeded species are planted in lower numbers because of their

higher mass which assumes that those with a greater mass should have increased emergence. The final response variable is the difference in abundance of emerged species between the closed and sham exclosures. This analysis will include all emerged perennial, planted seedlings from all three sites, unlike percent emergence and seedlings/g planted which only use data collected at UNI. KH and Graff are excluded from the first two analyses because the exact seed mix could not be correctly determined.

The effect of seed mass and exclosure type on percent emergence was run twice. The first run was significant but had one outlier (S*ilphium laciniatum*) that exerted heavy influence, it was removed and the test rerun. Since the linear regression assumptions were badly violated, the data were transformed using the square-root function and the following fitted model was used:

Closed cage: sqrt(% Emergence) = 0.303619 + 48.7398 Mass (g)

Open cage: sqrt(% Emergence) = 0.224628 + 48.7398 Mass (g)

The test for the number of seedlings emerged/g planted experienced the same problem (*Silphium laciniatum* was a high leverage observation and the linear regression assumptions were badly violated). *Silphium laciniatum* was removed and the cube-root transformation was applied to the data. The following fitted model was used:

Closed cage: crt(Sdlgs) = 7.26735 - 904.754 Mass (g)

Open cage: crt(Sdlgs) = 4.12988 - 159.324 Mass (g)

The amount of difference in species composition between the sham and closed exclosure was tested using a general regression analysis where the amount of difference was based on the seed mass and location of the cage within the site. This analysis included the data from all three sites. The first test found one outlier that exerted heavy influence, *Andropogon gerardii*. It was deleted from the set the analysis was rerun. The fitted models were:

G: Diff=0.384711-16.5608 Mass

KH: Diff=0.0597197-16.5608 Mass

UNI: Diff=0.615965-16.5608 Mass.

All data were analyzed using Minitab v16 (Minitab Inc., 2013). Graphs were produced using SigmaPlot v10 (Systat Software Inc. 2014).

Below-Ground Seed Fates

Experimental Design

To measure below-ground seed loss over time due to senescence and/or dormancy, a second experiment was designed to recover seeds after burial at the UNI site. The species chosen were *Desmodium canadense* (L.) DC., *Elymus canadensis* L., *Eryngium yuccifolium* Michx., and *Oligoneuron rigidum* (L.) Small. These species were chosen based on: expected ease of recovery as seeds, differences in appearance as seedlings, and as representatives of the three main functional groups, grass, forb, and forb-legume. To facilitate seed recovery each seed was coated with Glo Germ™ (Glo Germ Company, 2013), a bright florescent orange dye that can be detected with an

ultraviolet light (UV) light. Previous unpublished greenhouse experiments performed by our lab found that the dye did not inhibit seed germination (Huisman unpublished).

Three replicates of five exclosures, for a total of 15 total exclosures, were created using wire hardware cloth with 9.1 mm openings. Each exclosure was folded into 1 × 0.5 × 0.05-m exclosures and fastened together in each corner. The location of each exclosure within the UNI site was randomized with no exclosure closer than 5 m from all other exclosures. Openings that were at least 2.5 cm deep were made for each exclosure using a splitting maul and garden trowel. Prior to exclosure installation, above-ground biomass was removed. Four, 1 m × 1 cm deep grooves were created 10 cm apart using a garden trowel. Each species was randomly assigned a location within one of the four rows. One hundred seeds per species per exclosure were sown approximately one cm apart along the row and covered with soil. Exclosures were then placed in the 2.5cm deep openings and anchored using six wire staples. Exclosures and seeds were placed at the UNI site on June 11, 2013. Each exclosure was labeled and marked with a metal tag. The remaining seeds from Ion Exchange Inc. that were not used in the study were stored at 5°C.

Sampling

To measure the rate of seed loss below-ground, five sampling dates were set up with five replicates being destructively sampled on each date. To determine the fates of the planted seeds, the mesh exclosures were removed, the plot was weeded, emergence of seedlings was recorded, and the four grooves containing the buried seeds removed. One set of five randomly chosen exclosures were sampled on July 17, 2013, September 11, 2013, and November 8, 2013. Seedling emergence for the ten remaining exclosures, after

the July 17 sampling, was collected on July 31, 2013 when all hardware cloth exclosures were removed and the plots were weeded. Emergence data was collected for the remaining ten exclsoures to ensure that the seedlings did not die before future sampling dates. Any seedlings that emerged after the initial emergence collection were added into the July 31 data. Permanent metal stakes were placed next to the plots and the metal tag transferred to the marker at this same time.

On each sampling date, four 500cm^3 rows were removed using a garden trowel to recover any remaining seeds within the soil. Each row was placed into separate Ziploc® freezer bags and labeled with the exclosure and row number. Soils were stored at 5°C until the seed recovery could begin. Soil samples were examined using magnifying lenses, UV lights, and forceps in a dark room. All intact recovered, fluoresced seeds were recorded as partially germinated or as recovered seeds and placed into vials for viability testing. If a seed coat or chaff was found, it was also recorded. Seed recovery on a bag ended when all soil in a bag had been searched twice.

The viability of each recovered seed was tested using a 1 % tetrazolium chloride test (TZ) (Patil and Dadlani 2011). All seeds were soaked in deionized water for one hour to imbibe them. Seeds were then transferred to the TZ solution and soaked for thirty minutes in a 35°C oven. Each seed was then dissected in half and examined under a dissecting microscope. For a seed to be considered to be viable, the embryo had to be completely pink.

Commercial Seed Supplier

The four species were ordered from Ion Exchange Inc. in March, 2013 (Ion Exchange Inc. 2013). Viability was tested on various dates by a third party company (Table 4). To control for natural loss of viability over time, 50 seeds of each species from the stored seeds were tested for viability after five months of storage at 5°C. The seeds were all tested on August 10, 2013 using the same viability testing methods as above.

Table 4: Seed source viability versus in-lab seed viability.

Species	**Ion Exchange Viability (%) (Date Conducted)**	**In-Lab Viability (%)**
Elymus canadensis	90 (3/6/13)	54
Oligoneuron rigidum	94 (10/4/12)	0
Desmodium canadense	99 (3/23/13)	86
Eryngium yuccifolium	92 (1/9/13)	84

Data Analysis

After the completion of viability testing, all data was entered into Excel® (Microsoft Company, 2014). Seed fates included percent viable, percent non-viable, percent that partially germinated, and emergence as seedlings. The calculation for the percent viable, partially germinated, and nonviable was found using the formula Y=# Seeds per Fate/Total Seeds Accounted for per Species and averaging that number over the five replicates (Appendix C). Standard error for each of the fates was calculated in Excel. Graphs were produced using SigmaPlot v10 (Systat Software Inc. 2014).

CHAPTER 3

RESULTS-ABOVE-GROUND SEED MORTALITY

The effect of the exclosure type on all emerged perennial, planted seedling emergence was significant (p=0.035) (Table 5). The within site variation was significant (p=0.001) while the site was not significant (p=0.40). Across all sites, there were 33.8 seedlings/m^2 in the closed exclosure and 24.0 seedlings/ m^2 in the sham exclosure (Figure 7). Each site varied in amount of seedling emergence but there was no significant site × type interaction (p=0.56). The Graff site experienced the greatest overall difference in total seedling emergence with 30.4 and 14.4 seedlings/m^2 in the closed and sham exclosure, respectively, while KH had the lowest difference of only 1.6 seedlings/m^2 (Figure 7). Of the seeds/m^2 planted at the UNI site, the total percent emergence in the closed and sham exclosures were 19 and 14%, respectively.

Table 5: General linear model ANOVA results for all emerged perennial, planted seedlings for closed versus sham exclosures at all three sites.

Source	**DF**	**SS**	**Adj SS**	**Adj MS**	**F**	**p**
Site	2	99.28	99.28	49.64	0.98	0.40
Type	1	60.02	60.02	60.02	5.17	0.03
Cage (Site)	17	861.20	861.20	50.66	4.37	0.001
Error	19	220.48	220.48	11.60		
Total	39	1240.98				

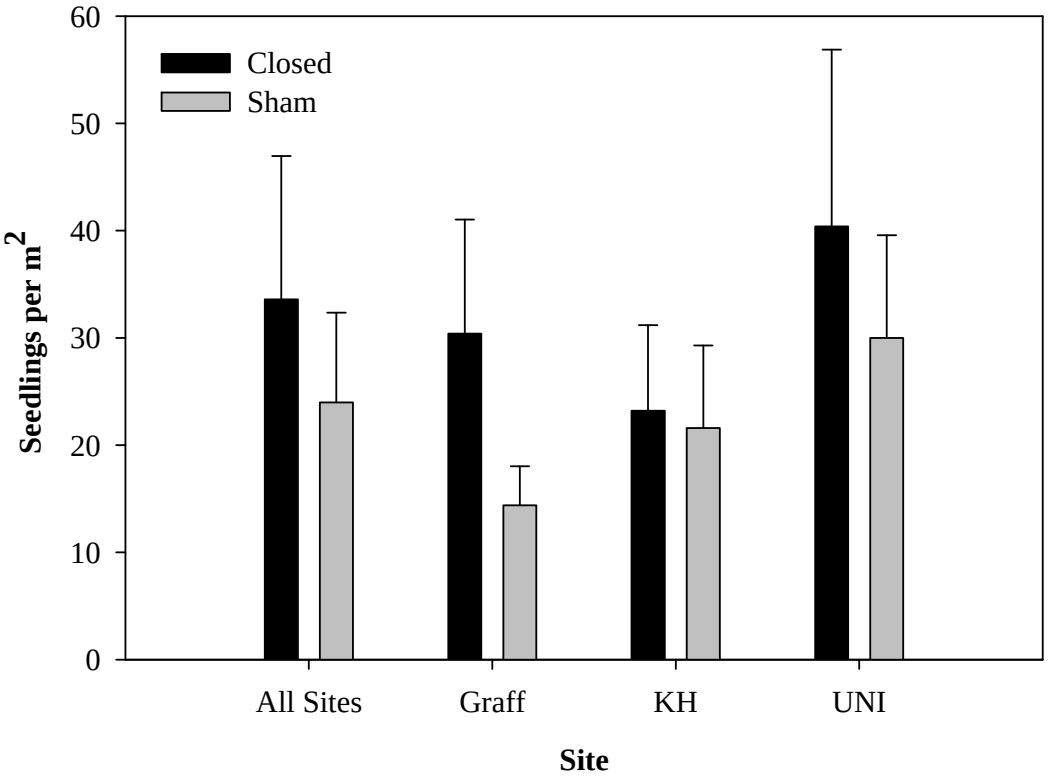

Figure 7: Average number of seedlings for all emerged perennial, planted seedlings in the sham and closed exclosures at each site.

Closed versus Sham Exclosure Effect on Species Composition

Percent Emergence

The regression analysis for percent emergence based on mass, exclosure type, and mass x exclosure type was not significant (p=0.20) (Table 6). The R^2 for this regression was 4.81%. The term being examined, seed mass × exclosure type, was not significant (p=0.70).

Table 6: General linear regression analysis ANOVA results for the UNI site after taking the cube roots of percent emergence and with the deletion of high-leverage *Silphium laciniatum*.

Source	DF	SS	Adj SS	Adj MS	F	p
Regression	3	0.34	0.34	0.11	1.62	0.20
Seed Mass (g)	1	0.28	0.28	0.28	3.95	0.06
Exclosure Type	1	0.06	0.05	0.05	0.70	0.41
Seed Mass (g) x Exclosure Type	1	0.01	0.01	0.01	0.09	0.77
Error	34	2.40	2.40	0.07		
Total	37	2.75				

Seedlings Emerged per Gram Planted

The regression analysis for seedlings emerged/g planted was marginally not significant (p= 0.06) (Table 7). The R^2 represented within the regression was 12.51%. Exclosure type was significant (p=0.04) but the interaction between seed mass planted and exclosure type was not (p=0.07).

Table 7: General regression analysis ANOVA results for the UNI site taking the cube root of the number of seedlings emerged/g planted after the deletion of high-leverage *Silphium laciniatum*.

Source	DF	SS	Adj SS	Adj MS	F	p
Regression	3	77.03	77.03	25.68	2.76	0.06
Seed Mass Planted (g)	1	33.27	33.27	33.27	3.58	0.07
Exclosure Type	1	27.44	42.45	42.45	4.57	0.04
Seed Mass Planted (g) x Exclosure Type	1	16.33	16.33	16.33	1.76	0.19
Error	34	315.91	315.91	9.29		
Total	37	392.95				

Difference in Seedling Abundance between Closed and Sham Exclosures

The regression analysis for difference in seedling abundance based on site and seed mass was not significant (p= 0.394) (Table 8). The R^2 represented within the regression was 0.01%.

Table 8: General regression analysis ANOVA results for all three sites assessing the effect of site and mass on the difference in seedling abundance between the closed and sham exclosures after the deletion of high-leverage *Andropogon gerardii*.

Source	DF	SS	Adj SS	Adj MS	F	p
Regression	3	7.92	7.92	2.64	1.00	0.39
Seed Mass (g)	1	1.93	1.81	1.81	0.69	0.41
Site	2	5.99	5.99	2.99	1.14	0.32
Error	123	323.94	323.94	2.63		
Total	126	331.86				

CHAPTER 4

RESULTS-BELOW-GROUND SEED MORTALITY

The largest loss of seeds happened between planting on June 11th and the first sampling on July 17th with only 10-30% of the original 500 planted seeds recovered (Table 9). The September 11th and November 8th samplings experienced similar recovery percentages and had smaller seed loss between the samplings. The percent recovery varied depending on species and was consistent between species with the exception of *O. rigidum*, whose recovery percentages were much lower. The percent recovery in individual exclosures ranged across the three samplings from 1%-51% (Appendix C).

Table 9: Percent of seeds recovered from each species with the standard error across the three sampling dates (N=5 replicates of 100). Standard errors for *E. canadensis* and *E. yuccifolium* on September 11th could not be calculated due to pooling of replicates during viability testing.

Species	**July 17th (%SE)**	**September 11th (%SE)**	**November 8th (%SE)**
D. canadense	26.4 (7.4)	11.4 (3.5)	18.4 (4.9)
E. canadensis	27.0 (8.1)	13.6 (-)	11.6 (4.0)
O. rigidum	10.2 (1.5)	4.0 (1.5)	3.2 (0.7)
E. yuccifolium	25.0 (8.6)	12.8 (-)	9.2 (3.0)

Seed Recovery, Germination, and Viability of Four Planted Species

D. canadense recovery rates varied among sampling periods (Table 9). July 17th recovery rates were similar to recovery rates of *E. canadensis* and *E. yuccifolium*. September 11th experienced a lower recovery rate than November 8th which was not expected. Of the four planted species, *D. canadense* had the greatest percent emergence with 100% emergence on July 17th and 88% on July 31 (Figure 8). While *D. canadense*

had the largest percent germination, it also had the lowest percent of recovered seeds fall into the partially germinated, viable, and nonviable categories. Two and a half percent of September 11th's recovered seeds were equally split into partially germinated and viable while 1% of recovered seeds on November 8th were nonviable (Figure 9a).

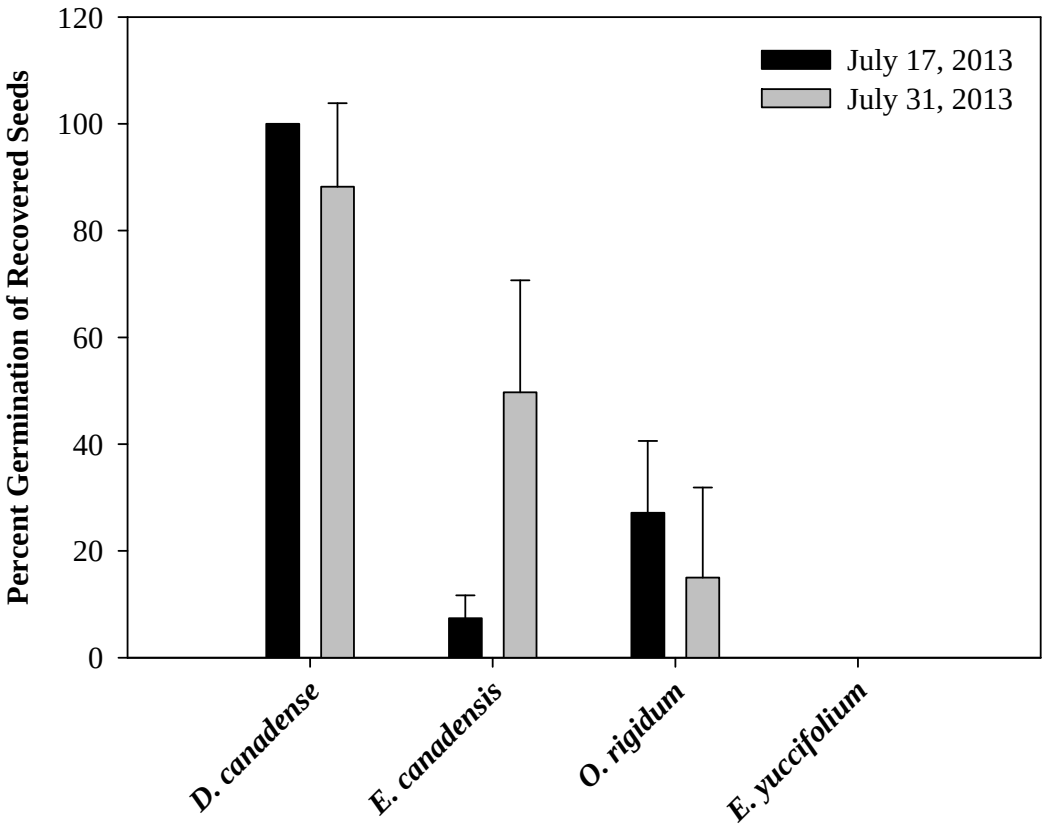

Figure 8: Percent germination of recovered seeds on July 17 (N=5) and July 31 (N=10).

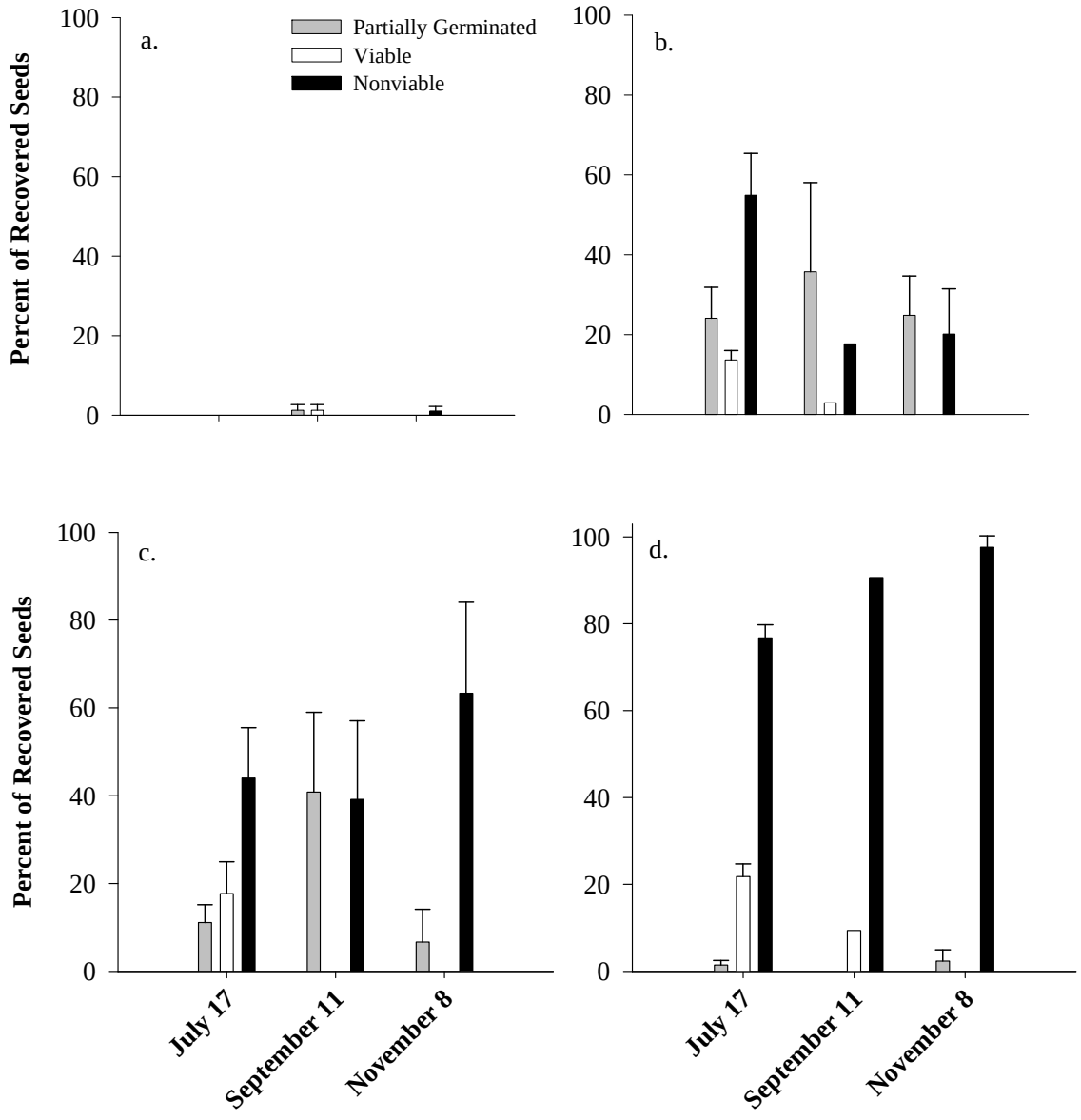

Figure 9: Percent of recovered seeds that were partially germinated, viable, or nonviable. Seed recovery occurred on July 17, September 11, and November 8. (a) *Desmodium canadense* (132, 57, 92 respectively), (b) *Elymus canadensis* (135, 68, 58 respectively), (c) *Oligoneuron rigidum* (51, 20, 16 respectively), (d) *Eryngium yuccifolium* (125, 64, 46 respectively). Standard error bars are missing from the viable and nonviable bars on September 11th in (b) and (d) due to pooling of replicates during viability testing.

Recovery rates of *E. canadensis* decreased throughout the study with the largest decrease happening between planting and the first sampling (Table 9). The greatest proportion of recovered seeds were found on July 17th which is consistent with *D. canadense* and *E. yuccifolium*. *Elymus canadensis* experienced the largest fluctuation in germination rates between the two germination sampling dates (7% to 50%) (Figure 8). The proportion of viable seeds decreased with increasing length of time in the soil (Figure 9b). Partially germinated seeds remained consistent on July 17th and November 8th but increased roughly 10% during the September 11th sampling. The percent of recovered nonviable seeds deceased after the first sampling but then remained constant for the second and third samplings. It is important to note that a larger proportion of intact seed coats with missing embryos were found on November 8th than during the previous samplings (Appendix C).

Oligoneuron rigidum had the lowest recovery rate of the four study species with only 10.2% being the largest percent recovery (Table 9). The germination rate for *O. rigidum* experienced a 10% reduction between samplings (Figure 9c). Partially germinated seeds peaked to 41% during the September 11th sampling while the July 17th and November 8th samplings remained under 15%. The proportion of viable seeds recovered was small on July17th (17.7%) and went to zero in the second and third samplings. *O. rigidum* had an overall increase in proportion of nonviable seeds throughout the study (44-63%) but had a slight decrease to 39% on September 11th.

The percent of recovered *E. yuccifolium* seeds decreased at similar rates to *D. canadense* and *E.canadensis* with the largest percent of recovered seeds occurring on the

July 17th sampling (Table 9). *E. yuccifolium* was the only species to have no germination during the study period (Figure 8). One percent and 2% of seeds partially germinated during the July 17th and November 8th samplings respectively with zero germination on September 11th (Figure 9d). *Eryngium yuccifolium* experienced its largest proportion of viable seeds on July 17th (22%) with the proportion decreasing in the September 11th and November 8th samplings (9 and 0% respectively). The proportion of nonviable seeds recovered increased by 21% throughout the study.

CHAPTER 5

DISCUSSION

The goal for this study was to explore causes of seed mortality under natural restoration conditions. The two approaches used in this study hint at new areas for further research in hopes of reducing the cost of tallgrass prairie restorations by increasing seedling emergence and eventually decreasing seeding rates. The first experiment found that protecting seeds increased seedling emergence for newly planted seeds by 18% at the UNI site. The second experiment found that the percent recovery of seeds within a natural soil seed bank decreases with time and identified specific methodological improvements needed to study seed burial and recovery in restoration conditions. The results of both experiments present a unique look into tallgrass prairie restorations and provide information for future studies.

Above-Ground Seed Mortality

For the above-ground seed mortality approach, I predicted the closed exclosure would have a greater overall seedling emergence and the seedling species composition would favor the emergence of seeds with a higher seed mass in the closed exclosure and smaller seed mass in the sham exclosure. The results support my predictions.

Closed versus Sham Exclosure Effect on Overall Seedling Emergence

The focus of this study was on the effect of vertebrate predators on recently planted seeds which is why 51.6% of the total seedlings identified were eventually excluded from the analyses. The final analyses included 277 seedlings that could be positively identified as part of the original seed mix. A statistically significant effect was

detected between the closed and sham exclosures, supporting my original hypothesis and previous research that state that protecting seeds from vertebrate granivores would increase the amount of seedling emergence (Janzen, 1971; Chambers and McMahon 1994; Howe and Brown 2000; Clark and Wilson 2003).

One alternative interpretation of the significant exclosure type that must be considered, is the temporary presence of duct tape on the closed exclosures. It is possible the seedling emergence at the Graff and KH sites was increased due to microclimate changes imposed by the duct tape. Duct tape was present on the exclosures within these two sites from planting in March to mid-June, when it was deemed ineffective at excluding invertebrates, and removed. The UNI site had duct tape present on the exclosures for only one week before removal.

Closed versus Sham Exclosure Effect on Species Composition

Small vertebrate granivores had no significant impact on species composition using any of the three response variables analyzed: percent emergence, seedlings/g planted, and difference in emerged species abundance. It is important to note that this experiment did not set out to directly measure species composition differences but only to try to detect differences after the fact. Many studies have indicated that small vertebrate predators can greatly influence species composition (Mittlebach and Gross 1984; Edwards and Crawley 1999; Howe and Brown 1999, 2000; Orrock *et al.* 2006, 2009; Fraser and Madson 2008). It is possible that this study did not have enough statistical power to detect a species-level difference between the closed and sham exclosure because the number of replicates used and the size of the sampling area was small. Another cause

could have been sparseness of the data due to low seeding and emergence rates of many species.

Implications for Future Studies

The major finding of this experiment was a significant effect of small vertebrate granivores on seedling emergence. This has many implications for future studies. My study used wire hardware cloth to exclude predators but this is not a practical application for prairie restoration practitioners. More practical methods to exclude vertebrate predators will need to be examined, such as supplemental seed additions or chemical deterrents. Other studies have found that coating seeds with chemicals such as capsaicin or thiram will decrease the number of seeds consumed (Barnett 1998).

If this seed predation study were replicated, it will need two key improvements design and increased replicates, and therefore statistical power. Our study found that only 18% of the total seeds/m^2 planted at the UNI site emerged even after protection from small vertebrate predators compared to 14% in the sham exclosures. This leaves an 82% loss of seeds to unknown sources or removal. In future studies, exclosure design must be improved to control for possible unknown sources. Clark and Wilson (2003) found similar results with a loss of 35-75% of seeds to unknown sources. The authors attributed these unknown losses to invertebrate, nonfungal disease, and abiotic requirements such as light and nutrients. Some studies have suggested using elevated petri dishes to raise seeds up off the ground and exclude invertebrates but the problem is those studies typically occur in desert communities where precipitation is not a large factor (Kelrick *et al.*, 1986).

The second improvement will be increasing the number of exclosures used. Increasing the sampling area will add more power to the study and the effects of the closed versus sham exclosure on species composition will become more apparent. Additional factors that could be considered in the future include the effect of planting time, site preparation and seeding method, crossed with exclosure type. It is possible that some seeding methods are more susceptible to seed predation than others, but we were not able to test this in our study design. The Dickinson County sites and the UNI site utilized different methodologies for each of these areas which may play a factor in seedling emergence and seed death within the soil.

Below-Ground Seed Mortality

The results from the seed recovery experiment varied by species but the overall results on seed loss and viability were expected based on germination and seed recovery experiments done in lab settings (Baskin and Baskin 2001; Fenner and Thompson 2005). These results also highlight areas where methods can be improved in future studies.

The amount of recovered seeds decreased over time (Table 9) with the greatest loss of planted seeds during the first five weeks within the soil. One possible cause for this decrease is invertebrate seed predators. My exclosure design did not exclude small invertebrate predators, only small vertebrate predators. Some studies have found that invertebrate predators can remove up to 19.5% of some seed species within one day of planting (Mittlebach and Gross 1984; Heggenstaller *et al.* 2006). I chose to use this type of exclosure over others, such as trays and mesh bags, to prevent alternation of the

microclimate but future seed recovery studies will need create a better exclosure design to fully exclude all seed predators while preserving the microclimate.

Seed Recovery, Germination, and Viability of Four Planted Species

Results for seed fates within the soil seed bank varied based on species. Overall viability of recovered seeds decreased with time with the exception of *D. canadense*. This species had an almost 100% germination rate of its recovered seeds and left few seeds to test for viability. The average percent of seed recovery for all four species was low and decreased overtime, as I predicted (Table 9). Individual cage recoveries varied but rarely exceeded 50% which creates more questions about seed fates within the seed bank (Appendix C).

Some interesting trends were found within the recovered seeds. *E. canadensis* had an increase in the number of seedlings germinated between July 17th and 31st which can be attributed to an increase in the average temperature towards the end of July (Figure 3). The optimal soil temperature for *E. canadensis* is 25.5±0.8 °C (Baskin and Baskin 2001). The average air temperatures for the UNI site prior to the first sampling were cooler than the historical averages (Figure 3) and thus probably the optimal germination temperature.

O. rigidum had the smallest percent recovery of the four species. This has two possible causes. First, in-lab seed viability tests found that *O. rigidum* had zero viability after five months of cold storage (Table 9). This represents a 94% decrease from the seed company's provided viabilities which may indicate a lower viability at planting. This possibility is not certain because the seeds were not tested upon arrival from the seed company. If the seeds were dead upon planting, they may have decayed before retrieval

and reduced percent recovery. Second, *O. rigidum* had the smallest seed size of the four species. The smaller size increased the difficulty of recovery after extended time periods.

E. yuccifolium had the lowest germination rate of the four species. A possible cause for this is the type of dormancy that this species has morphophysiological dormancy (Baskin and Baskin 2001). This form of dormancy requires the seed embryo to mature and for the seed to be imbibed with water (Baskin and Baskin 2001; Fenner and Thompson 2005). It is possible that because the seed planting happened in late June, that the *E. yuccifolium* seeds did not receive the germination cues needed to break dormancy during the spring.

Implications for Future Studies

Very few seed recovery studies have been done in natural seed banks due to the difficulty. The seed recovery experiment used in this study was a new design and much was learned about how to improve the methods. The first key improvement will be testing the viability of any seeds from a seed source upon arrival to obtain a base viability. This study did not immediately test the viability upon arrival of the seeds in March or again prior to planting in June. The cause of the observed declines during storage could not be differentiated between the seed company and my storage methods. Not knowing the actual viability of the species before planting presented challenges for this study in the interpretation of data.

A second key improvement will be in seed selection. The smaller seeds, such as *O. rigidum*, should not be used because they lead to increased human error during recovery. The fluorescent dye greatly increased the ease of finding seeds and because of

this, seeds with coats that hold on to the dye should be chosen. *D. canadense* and *O. rigidum* had smooth seed coats and the dye was easily rubbed off while *E. canadensis* and *E. yuccifolium* had rough seed coats that held the dye very well. Seed specific germination requirements, such as stratification, will need to be done prior to planting to ensure some germination.

A third improvement will be accounting for partially germinated seeds. The partial germination fate was not originally part of the below-ground approach but all four species, at some point, had seeds that were classified as this. This study was unable to distinguish partially germinated seeds as either alive and germinating or failed germination. Future studies will need to either conduct short-term experiments that search for them right away or create a way to confidently distinguish between the two fates within the partially germinated category.

A fourth improvement will be redesigning aspects of the experiment. The exclosure used in this experiment did not exclude invertebrate predation which may have been a cause of reduced seed recovery. In addition, a new exclosure will also need to reduce seed loss due to secondary dispersal such as rain and wind. Studies have found that 15-30% of seed losses can be to secondary sources (Clark and Wilson 2003). Adding a control to the system will also be necessary. Past studies have added colored beads to the soil seed bank with the seeds to help measure the accuracy of the person performing the recovery (Clark and Wilson 2003). Recovering seeds immediately after planting will also ensure more accurate recovery rates and help determine losses to retrieval methods.

Using a natural setting, like a new restoration, will be necessary if reliable results are to be gathered.

The final improvement to the below-ground approach will be accounting for seed loss to fungal decomposition. My study never directly measured the effects of fungi on seed death but adding in the effects of fungi could help account for some of the 70% of unrecovered seeds. Fungi are thought to have a greatest influence on seed death by producing chemicals that alter germination cues or degrade cell membranes and expose the embryo (Fenner and Thompson 2005; Mitschunas *et al.* 2006; Wagner and Mitschunas 2008). Lab and field studies commonly add a fungicide treatment to quantify seed losses which should be considered in future seed recovery studies (Clark and Wilson 2003; Mitschunas *et al.* 2006).

Summary

This study was one of the first to attempt to track and measure the amount of seed loss above- and below-ground in a native tallgrass prairie restoration under restoration conditions. Working under restoration conditions can be intrinsically difficult as I learned during this study. There are numerous variables that cannot be controlled including seeding rates, seed mixes, and site selection. Site selection can be limited to those sites set to undergo restoration which brings issues with size, location, and planting time. Seed mixes and seeding rates may not be exactly as stated which creates difficulties when interpreting data.

Like the Clark and Wilson (2003) experiment, my above- or below-ground experiments had their largest loss of seeds attributed to unknown causes. The above-

ground seed predation approach found that only 18% of planted seeds established at the UNI site after protection from small vertebrate granivores while the below-ground approach found that, on average, no more than 30% of planted seeds were recovered. Where 70% of seeds are disappearing to is still unanswered. The likely cause is predation by invertebrates and losses to secondary sources in the form of wind and rain.

While the largest losses in this study were to unknown sources, I was able to find that vertebrate seed predators have a significant effect on seed mortality in tallgrass prairie restorations. I was able to increase the number of emerged seedlings by 17 seedlings/m^2. If seeding rates could be lowered because of this, hundreds of dollars could be saved by practitioners. My methodology is not practical for large restorations but this study demonstrates that seed protection is a potentially valuable avenue of research.

Both of my experiments demonstrate that there is still much work that needs to be done in addressing seed loss in tallgrass prairie restorations. The results from the below-ground approach help account for some seed loss but a large percentage of the seeds were never found. Studying seeds in this environment is difficult but this study attempted to set a base line for future seed recovery studies in prairies. The results of the above-ground seed predation approach added support to the idea of granivores playing a large and detrimental role on overall seedling emergence in newly restored areas. By understanding and addressing the underlying mechanisms that drive a restoration after planting, such as unknown sources of seed loss, practitioners can alter restoration practices to enhance seedling emergence which will in turn reduce the cost of restorations.

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APPENDIX A

ABOVE-GROUND SEED MORTALITY COMPILED DATA INCLUDING ALL SAMPLED SEEDLINGS

Genus	Sp.	Site	Loc	O/C	S1	S2	S3	S4	S5	S6	S7	S8	S9	Total
An	ge	G	1	C	0	0	3	0	0	1	0	0	0	4
El	ca	G	1	C	0	0	0	0	0	0	0	0	1	1
Ph	pi	G	1	C	0	0	0	0	1	0	0	0	0	1
So	sp	G	1	C	0	0	0	0	0	2	0	0	0	2
Sy	la	G	1	C	0	0	0	0	1	0	0	0	0	1
Am	ca	G	1	O	0	0	0	0	2	0	0	0	0	2
Sc	sc	G	1	O	0	0	0	0	0	1	0	2	0	3
Bo	cu	G	2	C	0	0	0	0	0	1	0	0	0	1
Sc	sc	G	2	C	0	0	0	0	0	1	0	0	0	1
Am	ca	G	2	O	0	0	0	0	1	0	0	0	0	1
An	ge	G	2	O	0	0	1	0	0	0	0	0	0	1
Bo	cu	G	2	O	0	0	1	0	0	0	0	0	0	1
Am	ca	G	3	C	0	0	0	0	1	0	0	0	0	1
An	ge	G	3	C	0	0	2	0	0	0	0	0	0	2
As	ca	G	3	C	0	0	0	0	1	0	0	0	0	1
Bo	cu	G	3	C	0	0	1	0	0	1	0	0	2	4
Ol	ri	G	3	C	0	0	0	0	2	0	0	0	0	2
Po	ar	G	3	C	1	1	0	0	0	0	0	0	0	2
St	sp	G	3	C	0	0	1	0	0	0	0	0	0	1
Unkn	CH	G	3	C	0	0	0	0	1	0	0	0	0	1
El	vi	G	3	O	0	0	0	0	0	1	0	0	0	1
Le	ca	G	3	O	0	0	0	0	1	0	0	0	0	1
Po	ar	G	3	O	0	0	0	0	1	0	0	0	0	1
Sc	sc	G	3	O	0	0	0	0	0	2	0	0	0	2
So	sp	G	3	O	0	0	0	0	0	1	0	0	0	1
Unkn	CI	G	3	O	0	0	0	0	1	0	0	0	0	1
An	ge	G	4	C	0	0	2	0	0	0	0	0	0	2
Bo	cu	G	4	C	0	0	0	0	1	0	0	1	2	4
Da	pu	G	4	C	0	1	0	0	0	0	0	0	0	1
He	he	G	4	C	0	0	0	0	0	1	0	0	0	1
Ol	ri	G	4	C	0	0	0	0	1	0	0	0	0	1

Ph	pi	G	4	C	0	0	0	0	1	0	0	0	0	1
So	sp	G	4	C	0	0	0	0	0	0	0	0	1	1
Sy	no	G	4	C	0	0	1	0	0	0	0	0	0	1
Unkn	CJ	G	4	C	0	0	0	0	0	1	0	0	0	1
Am	ca	G	4	O	0	0	0	0	1	0	0	0	0	1
Sc	sc	G	4	O	0	0	0	0	0	1	0	0	0	1
Ko	ma	G	5	C	0	0	0	0	1	0	0	0	0	1
So	sp	G	5	C	0	0	0	0	0	0	0	0	1	1
Am	ca	G	5	O	0	0	0	0	1	0	0	0	0	1
Bo	cu	G	5	O	0	0	0	0	1	0	0	0	0	1
As	ca	KH	1	C	1	0	0	0	0	0	0	0	0	1
Bo	cu	KH	1	C	0	0	0	0	1	0	1	0	0	2
Br	ka	KH	1	C	0	0	0	0	1	0	0	0	0	1
Ol	ri	KH	1	C	0	0	0	0	0	0	1	0	0	1
Sc	sc	KH	1	C	0	0	0	0	0	0	5	0	1	6
So	sp	KH	1	C	0	0	0	0	0	0	0	1	0	1
Unkn	CD	KH	1	C	0	0	0	0	1	0	0	0	0	1
Unkn	CK	KH	1	C	0	0	0	0	0	0	1	0	0	1
Bo	cu	KH	1	O	0	0	0	0	0	0	1	0	0	1
Da	pu	KH	1	O	0	0	0	0	1	0	0	0	0	1
Ol	ri	KH	1	O	0	0	0	0	0	0	1	0	0	1
Po	ar	KH	1	O	0	1	0	0	0	0	0	0	0	1
Sc	sc	KH	1	O	0	0	0	0	0	0	4	0	2	6
So	ne	KH	1	O	0	0	0	0	0	0	1	0	0	1
Unkn	CC	KH	1	O	0	0	0	0	1	0	0	0	0	1
Unkn	CE	KH	1	O	0	0	0	0	1	0	0	0	0	1
Unkn	CG	KH	1	O	0	0	0	0	1	0	0	0	0	1
Ol	ri	KH	2	C	0	0	0	0	0	0	1	0	0	1
Sc	sc	KH	2	C	0	0	0	0	0	0	1	1	0	2
So	sp	KH	2	C	0	0	0	0	0	0	0	1	0	1
St	sp	KH	2	C	0	0	0	0	0	0	1	0	0	1
Unkn	CF	KH	2	C	0	0	0	0	1	0	0	0	0	1
Am	ca	KH	2	O	0	0	0	0	2	0	0	0	0	2
Br	ka	KH	2	O	0	0	0	0	1	0	0	0	0	1
Ol	ri	KH	2	O	0	0	0	0	0	0	1	0	0	1
Ru	hi	KH	2	O	0	0	0	0	1	0	0	0	0	1
Sc	sc	KH	2	O	0	0	0	0	0	0	0	0	1	1
St	sp	KH	2	O	0	0	0	0	0	0	1	0	0	1

Am	ca	KH	3	C	0	0	0	0	1	0	0	0	0	1
De	ca	KH	3	C	0	0	0	0	1	0	0	0	0	1
El	ca	KH	3	C	0	0	0	0	1	0	0	0	0	1
So	nu	KH	3	C	0	0	0	0	0	0	1	0	0	1
Unkn	CL	KH	3	C	0	0	0	0	0	0	1	0	0	1
Sc	sc	KH	3	O	0	0	0	0	0	0	1	0	0	1
El	vi	KH	4	C	0	0	0	1	0	0	0	0	0	1
Unkn	CM	KH	4	C	0	0	0	0	0	0	1	0	0	1
Unkn	CN	KH	4	C	0	0	0	0	0	0	1	0	0	1
El	vi	KH	4	O	0	0	0	1	0	0	3	0	0	4
Ol	ri	KH	4	O	0	0	0	0	0	0	1	0	0	1
Sc	sc	KH	4	O	0	0	0	0	0	0	2	0	0	2
El	ca	KH	5	C	0	0	0	0	1	0	0	0	0	1
Sc	sc	KH	5	C	0	0	0	0	0	0	3	1	0	4
Unkn	CG	KH	5	C	0	0	0	0	7	0	0	0	0	7
Am	ca	KH	5	O	0	0	0	0	2	0	0	0	0	2
El	ca	KH	5	O	0	0	0	1	0	0	0	0	0	1
Unkn	CG	KH	5	O	0	0	0	0	1	0	0	0	0	1
Bo	cu	UNI	1	C	0	1	0	0	1	0	0	0	0	2
Da	pu	UNI	1	C	0	2	0	0	0	0	0	0	0	2
He	he	UNI	1	C	0	0	1	0	0	0	0	0	0	1
Sp	pe	UNI	1	C	0	1	0	0	0	0	0	0	0	1
Sp	as	UNI	1	C	0	1	0	0	0	0	0	0	0	1
An	ge	UNI	1	O	0	9	0	0	0	0	0	0	0	9
As	ve	UNI	1	O	0	1	0	0	0	0	0	1	0	2
Ca	am	UNI	1	O	0	1	0	0	0	0	0	0	0	1
Ru	hi	UNI	1	O	0	0	0	0	1	0	0	0	0	1
Sy	la	UNI	1	O	0	0	0	0	1	0	0	0	0	1
Unkn	T	UNI	1	O	0	1	0	0	0	0	0	0	0	1
Unkn	U	UNI	1	O	0	1	0	0	0	0	0	0	0	1
An	ge	UNI	2	C	0	1	0	0	0	0	0	0	0	1
Ol	ri	UNI	2	C	0	2	0	0	0	0	0	0	0	2
Ra	pi	UNI	2	C	0	1	0	0	0	0	0	0	0	1
Ru	hi	UNI	2	C	0	1	0	0	0	0	0	0	0	1
So	ne	UNI	2	C	0	0	0	1	0	0	0	0	2	3
So	sp	UNI	2	C	0	0	0	0	2	0	0	0	0	2
Sy	la	UNI	2	C	0	0	0	0	1	0	0	0	0	1
Unkn	BC	UNI	2	C	0	0	3	0	0	0	0	0	0	3

Unkn	CO	UNI	2	C	0	0	0	0	0	0	0	1	0	1
Ve	st	UNI	2	C	0	0	2	0	0	0	0	0	0	2
He	he	UNI	2	O	0	1	1	0	0	0	0	0	0	2
Mo	fi	UNI	2	O	0	1	0	0	0	0	0	0	0	1
Ol	ri	UNI	2	O	0	10	0	0	0	0	0	0	0	10
Ra	pi	UNI	2	O	1	0	0	0	0	0	0	0	0	1
So	ne	UNI	2	O	0	0	0	3	0	0	0	0	0	3
So	sp	UNI	2	O	0	0	0	4	7	0	0	0	0	11
So	spp.	UNI	2	O	0	0	0	1	0	0	0	0	0	1
Sy	la	UNI	2	O	0	0	0	0	6	0	0	0	0	6
Unkn	BC	UNI	2	O	0	0	11	0	0	0	0	0	0	11
Unkn	W	UNI	2	O	0	1	0	0	0	0	0	0	0	1
Da	pu	UNI	3	C	0	1	0	2	0	0	0	0	0	3
Ec	pa	UNI	3	C	0	0	1	0	0	0	0	0	0	1
Mo	fi	UNI	3	C	0	2	0	0	0	0	0	0	0	2
Ol	ri	UNI	3	C	0	1	0	0	0	0	0	0	0	1
Ra	pi	UNI	3	C	1	1	0	0	0	0	0	0	0	2
Ru	hi	UNI	3	C	0	1	0	1	0	0	0	0	0	2
Ru	su	UNI	3	C	0	2	0	0	1	0	0	0	0	3
So	ca	UNI	3	C	0	1	0	0	0	0	0	0	0	1
So	ne	UNI	3	C	0	0	0	1	0	0	0	0	0	1
So	sp	UNI	3	C	0	2	3	6	3	0	0	0	2	16
Sy	la	UNI	3	C	0	2	0	1	1	0	0	0	0	4
Unkn	BC	UNI	3	C	0	0	1	0	0	0	0	0	0	1
Unkn	CQ	UNI	3	C	0	0	0	0	0	0	0	0	1	1
Bo	cu	UNI	3	O	0	0	0	0	1	0	0	0	0	1
Da	ca	UNI	3	O	0	0	0	0	1	0	0	0	0	1
Le	ca	UNI	3	O	0	1	0	0	0	0	0	0	0	1
Mo	fi	UNI	3	O	0	1	0	0	0	0	0	0	0	1
Po	ar	UNI	3	O	0	1	0	0	0	0	0	0	0	1
Ra	pi	UNI	3	O	0	1	0	0	0	0	0	0	0	1
Ru	hi	UNI	3	O	0	0	0	1	0	0	0	0	0	1
Ru	su	UNI	3	O	0	1	0	0	2	0	0	0	0	3
So	ne	UNI	3	O	0	1	0	4	1	0	0	0	0	6
So	sp	UNI	3	O	0	6	1	3	14	0	0	0	0	24
Sy	la	UNI	3	O	0	6	0	0	0	0	0	0	0	6
Unkn	AD	UNI	3	O	0	1	0	0	0	0	0	0	0	1
Unkn	BC	UNI	3	O	0	0	3	0	0	0	0	0	0	3

Unkn	BR	UNI	3	O	0	0	0	0	1	0	0	0	0	1
Unkn	BS	UNI	3	O	0	0	0	0	1	0	0	0	0	1
Br	ka	UNI	4	C	0	0	0	0	2	0	0	0	0	2
Ol	ri	UNI	4	C	0	2	0	0	0	0	0	0	0	2
Ra	pi	UNI	4	C	1	1	0	0	0	0	0	0	0	2
Ru	hi	UNI	4	C	0	0	0	1	0	0	0	0	0	1
Ru	su	UNI	4	C	0	1	0	0	1	0	0	0	0	2
So	ca	UNI	4	C	0	3	0	0	0	0	0	0	0	3
So	ne	UNI	4	C	0	1	0	0	0	0	0	0	1	2
So	sp	UNI	4	C	0	4	0	0	0	0	0	0	1	5
Sy	la	UNI	4	C	0	0	0	0	1	0	0	0	0	1
Unkn	BC	UNI	4	C	0	0	1	0	0	0	0	0	0	1
Da	pu	UNI	4	O	3	0	0	0	0	0	0	0	0	3
Py	pi	UNI	4	O	0	2	0	0	0	0	0	0	0	2
Ra	pi	UNI	4	O	0	0	1	0	0	0	0	0	0	1
Ru	hi	UNI	4	O	0	0	0	0	0	0	0	1	0	1
Ru	su	UNI	4	O	0	0	1	0	0	0	0	0	0	1
So	sp	UNI	4	O	0	6	0	0	0	0	0	0	0	6
Sy	la	UNI	4	O	0	0	0	0	2	0	0	0	0	2
Unkn	BC	UNI	4	O	0	0	1	0	0	0	0	0	0	1
An	ge	UNI	5	C	0	1	0	0	0	0	0	0	0	1
El	ca	UNI	5	C	0	0	0	1	3	0	0	0	0	4
He	he	UNI	5	C	0	2	0	0	0	0	0	0	0	2
Ra	pi	UNI	5	C	1	0	0	0	0	0	0	0	0	1
Ru	su	UNI	5	C	0	0	0	0	1	0	0	0	0	1
Sy	la	UNI	5	C	0	3	0	0	0	0	0	0	0	3
Unkn	AK	UNI	5	C	0	3	0	0	0	0	0	0	0	3
Unkn	BC	UNI	5	C	0	0	2	0	0	0	0	0	0	2
Unkn	CQ	UNI	5	C	0	0	0	0	0	0	0	1	0	1
Ve	st	UNI	5	C	0	0	0	1	1	0	0	0	0	2
An	ge	UNI	5	O	0	1	0	0	0	0	0	0	0	1
El	ca	UNI	5	O	0	5	0	3	2	0	0	4	0	14
He	he	UNI	5	O	0	1	0	0	0	0	0	0	0	1
Ol	ri	UNI	5	O	0	1	0	0	0	0	0	0	0	1
Ra	pi	UNI	5	O	1	0	0	0	0	0	0	0	0	1
So	ne	UNI	5	O	0	1	0	0	0	0	0	0	0	1
So	sp	UNI	5	O	0	1	0	0	0	0	0	0	0	1
Sy	la	UNI	5	O	0	0	0	0	1	0	0	0	0	1

Unkn	BC	UNI	5	O	0	0	1	0	0	0	0	0	0	1
Unkn	CP	UNI	5	O	0	0	0	0	0	0	0	1	0	1
Ve	ha	UNI	5	O	0	0	0	0	0	0	0	1	0	1
Ve	st	UNI	5	O	0	0	0	0	1	0	0	0	0	1
Ar	lu	UNI	6	C	0	2	0	0	0	0	0	0	0	2
As	ve	UNI	6	C	0	0	1	0	0	0	0	0	0	1
Bo	cu	UNI	6	C	1	0	0	0	0	0	0	0	0	1
Br	ka	UNI	6	C	0	1	3	1	0	0	0	0	0	5
Da	pu	UNI	6	C	5	2	0	0	0	0	0	0	0	7
El	ca	UNI	6	C	0	1	0	0	0	0	0	0	0	1
He	he	UNI	6	C	0	0	1	0	0	0	0	0	0	1
Le	ca	UNI	6	C	0	2	0	0	0	0	0	0	0	2
Mo	fi	UNI	6	C	0	0	1	0	0	0	0	0	0	1
Ra	pi	UNI	6	C	3	0	1	2	0	0	0	0	0	6
Ru	hi	UNI	6	C	0	0	1	0	0	0	0	0	0	1
Ru	su	UNI	6	C	0	1	0	0	0	0	0	0	0	1
Sc	sc	UNI	6	C	0	1	1	0	0	0	0	0	0	2
So	ne	UNI	6	C	0	3	0	0	0	0	0	0	0	3
So	nu	UNI	6	C	0	1	0	0	0	0	0	0	0	1
An	ge	UNI	6	O	1	1	0	0	0	0	0	0	0	2
Ar	lu	UNI	6	O	0	1	1	0	0	0	0	0	0	2
Da	pu	UNI	6	O	3	0	0	0	0	0	0	0	0	3
Ec	pa	UNI	6	O	1	1	0	0	0	0	0	0	0	2
El	ca	UNI	6	O	0	0	3	0	0	0	0	0	0	3
Le	ca	UNI	6	O	1	1	0	0	0	0	0	0	0	2
Li	spp.	UNI	6	O	1	0	0	0	0	0	0	0	0	1
Mo	fi	UNI	6	O	0	0	1	0	0	0	0	0	0	1
Ra	pi	UNI	6	O	1	0	1	0	0	0	0	0	0	2
Ru	su	UNI	6	O	0	1	0	0	0	0	0	0	0	1
Sc	sc	UNI	6	O	1	0	2	0	0	0	0	0	0	3
So	ne	UNI	6	O	0	2	1	0	0	0	0	0	0	3
Sp	as	UNI	6	O	1	0	0	0	0	0	0	0	0	1
Sy	la	UNI	6	O	0	0	1	0	0	0	0	0	0	1
Unkn	BC	UNI	6	O	0	0	1	0	0	0	0	0	0	1
Ar	lu	UNI	7	C	0	1	0	0	0	0	0	0	0	1
Ca	ca	UNI	7	C	0	0	1	0	0	0	0	0	0	1
Carex	spp.	UNI	7	C	0	0	0	0	1	0	0	0	0	1
Da	pu	UNI	7	C	3	0	0	0	0	0	0	0	0	3

Mo	fi	UNI	7	C	0	1	1	0	1	0	0	0	3
Ra	pi	UNI	7	C	0	0	1	0	0	0	0	0	1
Ru	su	UNI	7	C	0	1	0	0	0	0	0	0	1
So	ne	UNI	7	C	0	1	0	0	0	0	0	0	1
So	sp	UNI	7	C	0	1	0	0	0	0	0	0	1
Sp	pe	UNI	7	C	0	0	0	0	1	0	0	0	1
Sp	as	UNI	7	C	0	3	0	0	1	0	0	0	4
Unkn	BW	UNI	7	C	0	0	0	0	1	0	0	0	1
Unkn	CR	UNI	7	C	0	0	0	0	0	0	0	1	0	1
Da	pu	UNI	7	O	1	0	0	0	0	0	0	0	0	1
El	ca	UNI	7	O	0	0	0	0	2	0	0	0	0	2
Ru	su	UNI	7	O	0	1	0	0	1	0	0	0	0	2
So	ne	UNI	7	O	0	1	1	0	1	0	0	0	0	3
So	sp	UNI	7	O	0	0	0	0	1	0	0	0	0	1
Sp	pe	UNI	7	O	0	0	1	0	0	0	0	0	0	1
Sy	la	UNI	7	O	0	1	0	0	0	0	0	0	0	1
Unkn	BX	UNI	7	O	0	0	0	0	1	0	0	0	0	1
Unkn	BY	UNI	7	O	0	0	0	0	1	0	0	0	0	1
Ar	lu	UNI	8	C	0	1	0	0	1	0	0	0	0	2
As	ve	UNI	8	C	0	2	0	0	0	0	0	0	0	2
Br	ka	UNI	8	C	0	0	1	1	1	0	0	0	0	3
Ca	ca	UNI	8	C	0	0	0	0	1	0	0	0	0	1
Da	pu	UNI	8	C	0	1	0	0	0	0	0	0	0	1
Ec	pa	UNI	8	C	0	0	1	0	0	0	0	0	0	1
El	ca	UNI	8	C	0	1	0	0	0	0	0	0	0	1
Mo	fi	UNI	8	C	0	2	0	0	1	0	0	0	0	3
Ru	hi	UNI	8	C	0	0	1	0	0	0	0	0	0	1
Ru	su	UNI	8	C	0	3	0	0	1	0	0	0	0	4
So	nu	UNI	8	C	0	0	0	0	1	0	0	0	0	1
Unkn	BC	UNI	8	C	0	0	1	0	0	0	0	0	0	1
Unkn	N	UNI	8	C	4	0	0	0	0	0	0	0	0	4
Ve	vi	UNI	8	C	0	1	0	0	0	0	0	0	0	1
Br	ka	UNI	8	O	0	0	1	0	0	0	0	0	0	1
Da	pu	UNI	8	O	3	0	0	0	0	0	0	0	0	3
Mo	fi	UNI	8	O	0	1	0	0	0	0	0	0	0	1
Ru	hi	UNI	8	O	0	3	0	0	0	0	0	0	0	3
Ru	su	UNI	8	O	0	2	0	0	0	0	0	0	0	2
Si	la	UNI	8	O	1	0	0	0	0	0	0	0	0	1

So	ne	UNI	8	O	0	1	0	0	0	0	0	0	0	1
So	sp	UNI	8	O	0	1	0	0	0	0	0	0	0	1
Sy	la	UNI	8	O	0	1	0	0	0	0	0	0	0	1
Unkn	BC	UNI	8	O	0	0	1	0	0	0	0	0	0	1
Vi	so	UNI	9	C	0	2	0	0	0	0	0	0	0	2
Da	pu		9	C	1	2	0	0	0	0	0	0	0	3
Eu	gr	UNI	9	C	0	1	0	0	0	0	0	0	0	1
So	ne	UNI	9	C	0	2	0	0	0	0	0	0	0	2
Sy	la	UNI	9	C	0	1	0	1	0	0	0	0	0	2
Ve	st	UNI	9	C	0	0	1	0	0	0	0	0	0	1
Vi	so	UNI	9	O	0	1	0	0	0	0	0	0	0	1
Da	pu	UNI	9	O	1	0	0	0	0	0	0	0	0	1
Mo	fi	UNI	9	O	0	1	0	0	0	0	0	0	0	1
Py	vi	UNI	9	O	0	1	0	0	0	0	0	0	0	1
Sy	la	UNI	9	O	0	1	0	0	0	0	0	0	0	1
Unkn	BV	UNI	9	O	0	0	0	0	1	0	0	0	0	1
Unkn	P	UNI	9	O	1	0	0	0	0	0	0	0	0	1
El	ca	UNI	10	C	0	2	0	0	0	0	0	0	0	2
He	au	UNI	10	C	0	0	0	1	0	0	0	0	0	1
Ra	pi	UNI	10	C	0	0	0	1	0	0	0	0	0	1
Ru	su	UNI	10	C	0	2	0	0	0	0	0	0	0	2
Sp	as	UNI	10	C	0	1	0	0	0	0	0	0	0	1
Sy	la	UNI	10	C	0	1	0	0	0	0	0	0	0	1
An	ge	UNI	10	O	1	0	0	0	0	0	0	0	0	1
Bo	cu	UNI	10	O	0	1	0	0	0	0	0	0	0	1
El	ca	UNI	10	O	0	1	0	0	0	0	0	0	0	1
Mo	fi	UNI	10	O	0	3	0	0	0	0	0	0	0	3
Ol	ri	UNI	10	O	0	0	0	0	1	0	0	0	0	1
Po	ar	UNI	10	O	0	1	0	0	0	0	0	0	0	1
Ra	pi	UNI	10	O	1	0	0	0	0	0	0	0	0	1
Ru	hi	UNI	10	O	0	1	0	0	0	0	0	0	0	1
Si	la	UNI	10	O	1	0	0	0	0	0	0	0	0	1
Sy	la	UNI	10	O	0	3	0	0	0	0	0	0	0	3
Unkn	BV	UNI	10	O	0	0	0	0	1	0	0	0	0	1

	Closed Emergence	Open Emergence
All Sites	285	287
G	40	20
KH	42	31
UNI	203	236

APPENDIX B

ABOVE-GROUND SEED MORTALITY BY GRANIVORES STATISTICAL ANALYSES FOR OPEN VERSUS SHAM EXCLOSURE EFFECT

General Linear Model: Log(Total) versus Site, Type, Cage for All Native Emerged Seedlings (No Site*Type Interaction)

Factor	Type	Levels	Values
Site	Fixed	3	G, KH, UNI
Cage(Site)	Random	20	1, 2, 3, 4, 5, 1, 2, 3, 4, 5, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Type	Fixed	2	Closed, Open

Analysis of Variance for Log(Total), using Adjusted SS for Tests

Source	DF	Seq SS	Adj MS	F	p
Site	2	3.23	1.61	12.74	0.00
Type	1	0.06	0.06	0.96	0.34
Cage (Site)	17	2.15	0.13	2.14	0.056
Error	19	1.13	0.06		
Total	39	6.56			

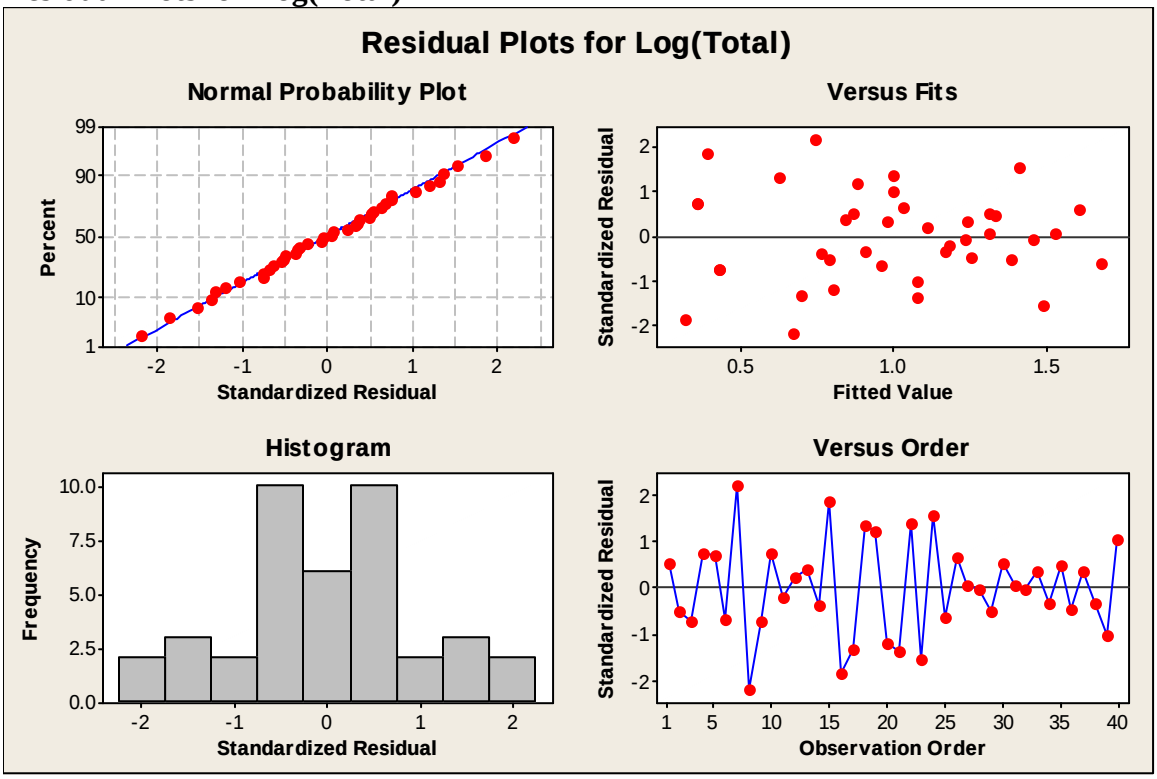
S = 0.243482 R-Sq = 82.84% R-Sq(adj) = 64.77%

Unusual Observations for Log(Total)

Obs	Log(Total)	Fit	SE Fit	Residual	St Resid
7	1.11394	0.74516	0.17642	0.36878	2.20 R
8	0.30103	0.6698	0.17642	-0.36878	-2.20 R

R denotes an observation with a large standardized residual.

Residual Plots for Log(Total)



General Linear Model: Y versus Site, Type, Cage for All Emerged Seedlings that were Planted

Factor	Type	Levels	Values
Site	Fixed	3	G, KH, UNI
Cage(Site)	Random	20	1, 2, 3, 4, 5, 1, 2, 3, 4, 5, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Type	Fixed	2	Closed, Open

Analysis of Variance for Y, using Adjusted SS for Tests

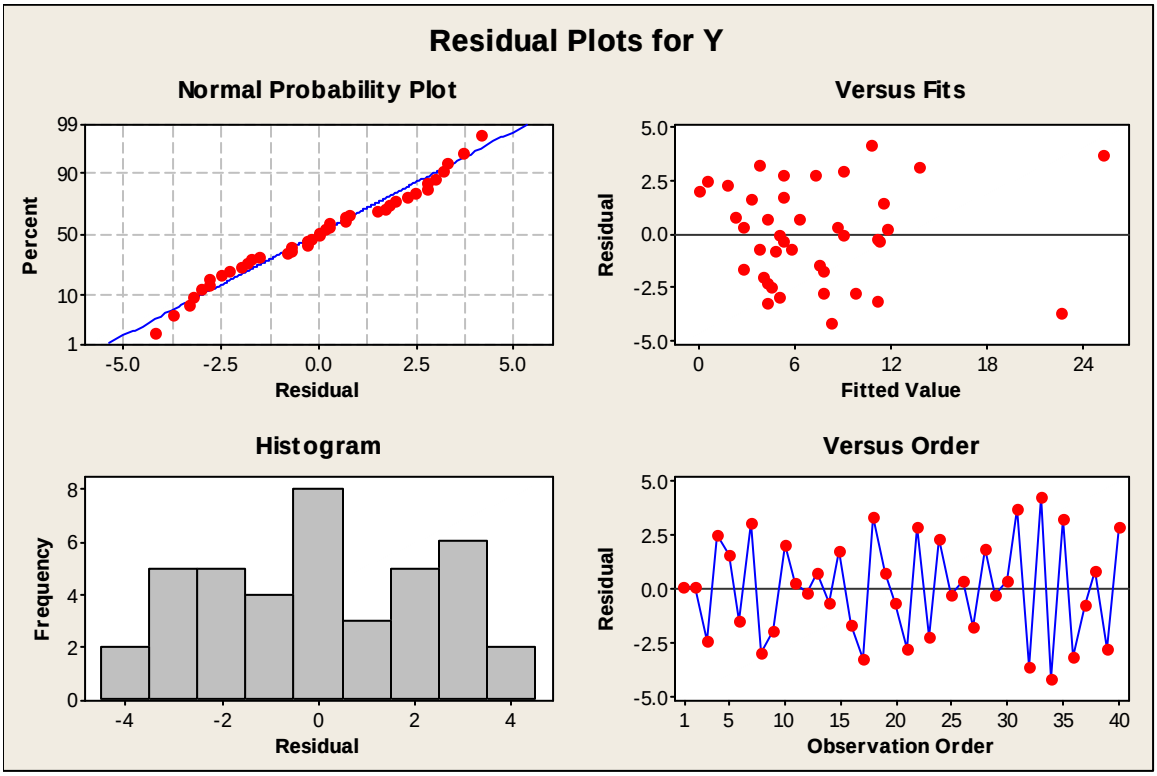
Source	DF	SS	Adj SS	Adj MS	F	p
Site	2	99.28	99.28	49.64	0.98	0.40
Type	1	60.03	51.84	51.84	4.28	0.05
Site x Type	2	14.67	14.67	7.34	0.61	0.56
Cage (Site)	17	861.20	861.20	50.66	4.18	0.003
Error	17	205.80	205.80	12.11		
Total	39	1240.97				

S = 3.47935 R-Sq = 83.42% R-Sq(adj) = 61.95%

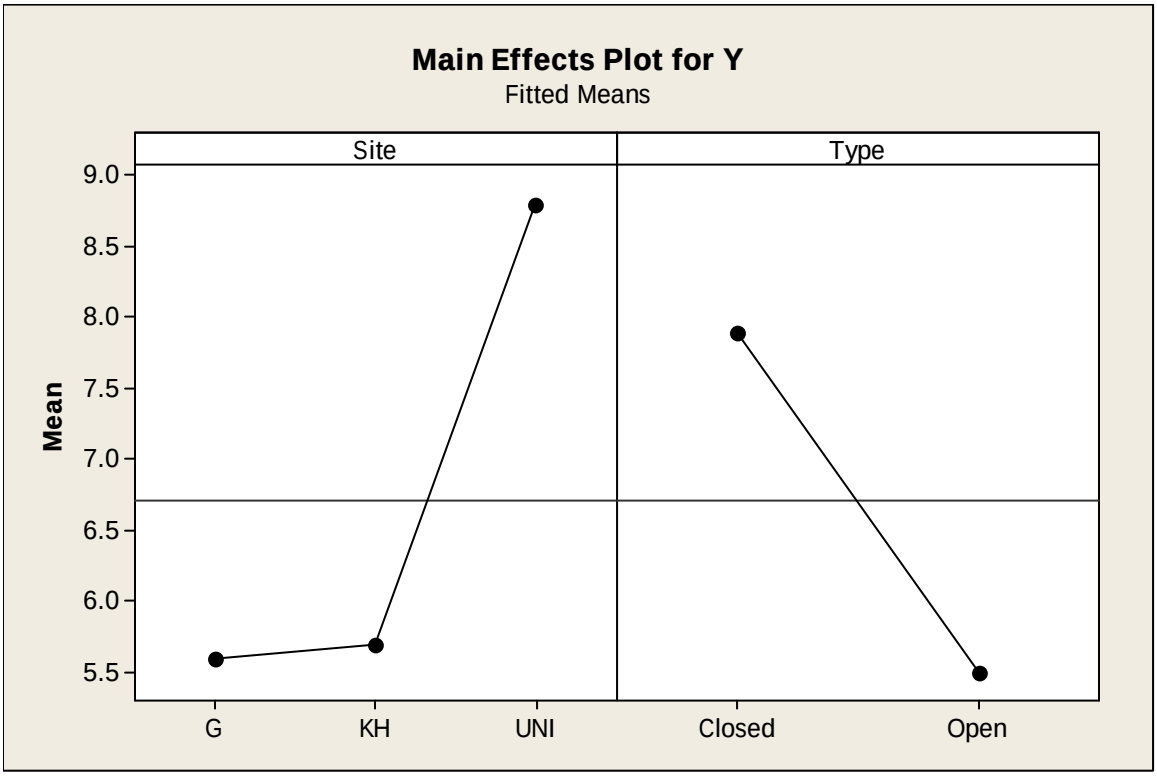
Least Squares Means for Y

Site*Type		Mean
G	Closed	7.600
G	Open	3.600
KH	Closed	6.000
KH	Open	5.400
UNI	Closed	10.100
UNI	Open	7.500

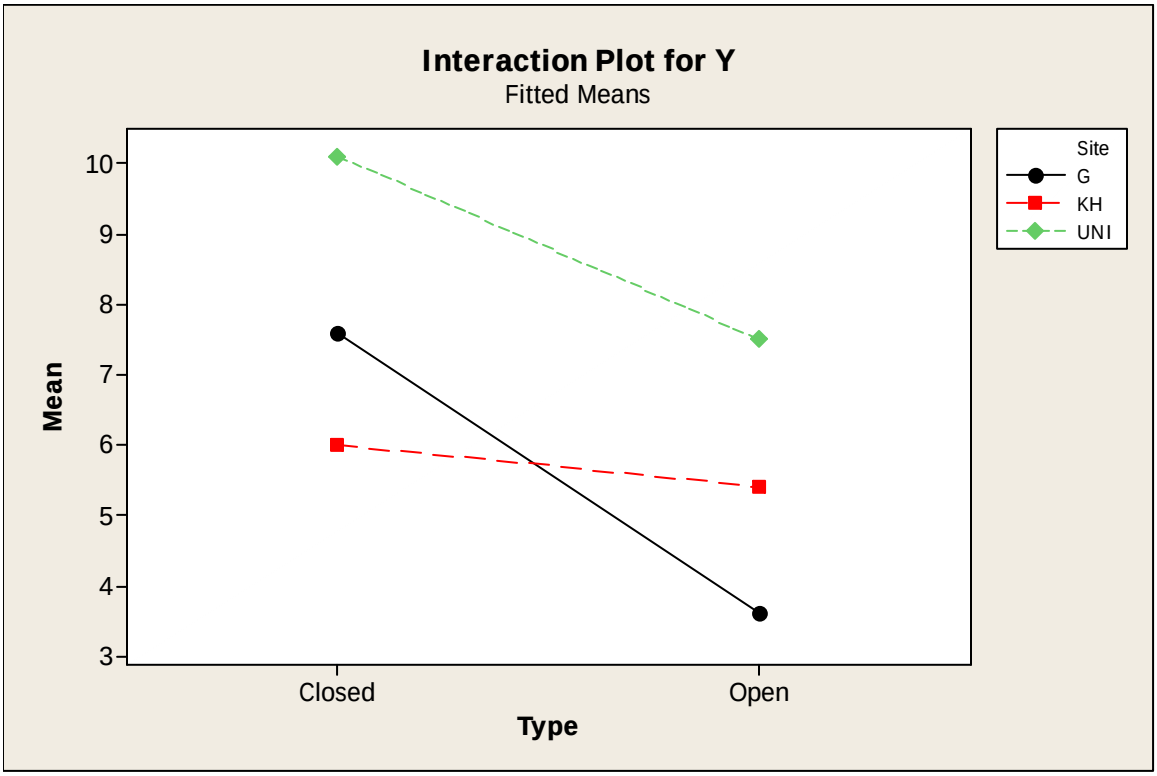
Residual Plots for Y



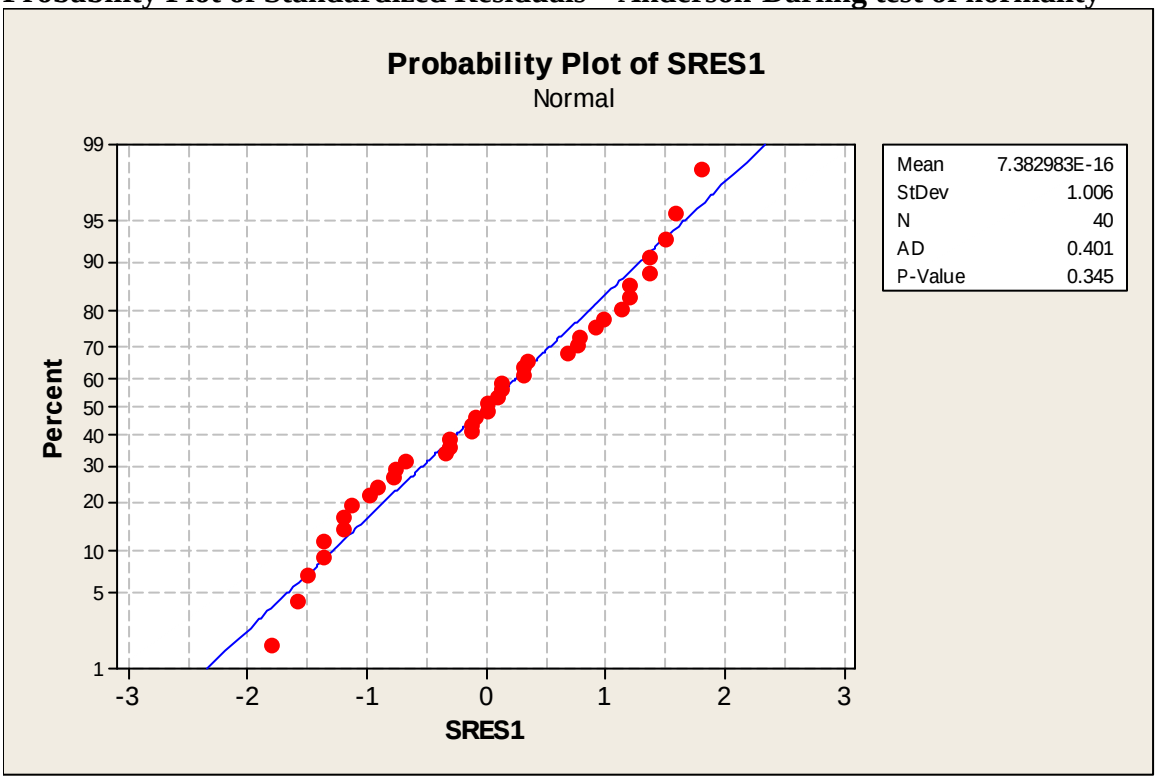
Main Effects Plot for Y



Interaction Plot for Y



Probability Plot of Standardized Residuals – Anderson-Darling test of normality



APPENDIX C

BELOW-GROUND SEED MORTALITY RESULTS

Desmodium canadense for All Three Samplings

Date	Cage	Germ	Partial Germ	Seed Coats	V	NV	Total	% Recovered	% Germ	% Partial Germ	% V	% NV
17-Jul	7	25	0	8	0	0	25	18.939394	100	0	0	0
17-Jul	11	40	0	5	0	0	40	30.30303	100	0	0	0
17-Jul	14	5	0	0	0	0	5	3.7878788	100	0	0	0
17-Jul	21	41	0	3.5	0	0	41	31.060606	100	0	0	0
17-Jul	24	21	0	4.5	0	0	21	15.909091	100	0	0	0
	AVE:	26.4	0		0	0	26.4	20	100	0	0	0
	STER:	7.44648	0		0	0	7.44648	5.6412695	0	0	0	0
	SUM:	132	0		0	0	132	26.4				
11-Sep	8	12	0	0	0	0	12	21.052632	100	0	0	0
11-Sep	13	11	0	0	0	0	11	19.298246	100	0	0	0
11-Sep	15	18	0	0	0	0	18	31.578947	100	0	0	0
11-Sep	17	0	0	0	0	0	0	0	0	0	0	0
11-Sep	23	14	1	0	1	0	16	28.070175	87.5	6.25	6.25	0
	AVE:	11	0.2		0.2	0	11.4	20	77.5	1.25	1.25	0
	STER:	3.3541	0.2236		0.2236	0	3.49285	6.1278067	21.83	1.39754	1.3975	0
	Sum:	55	1		1	0	57	11.4				
8-Nov	5	21	0	1	0	0	21	22.826087	100	0	0	0
8-Nov	10	18	0	7	0	1	19	20.652174	94.737	0	0	5.263
8-Nov	16	5	0	0	0	0	5	5.4347826	100	0	0	0
8-Nov	19	32	0	1	0	0	32	34.782609	100	0	0	0
8-Nov	25	15	0	6	0	0	15	16.304348	100	0	0	0
	AVE:	18.2	0		0	0.2	18.4	20	98.947	0	0	1.053
	STER:	4.89132	0		0	0.2236	4.89387	5.319428	1.1769	0	0	1.177
	Sum	91	0		0	1	92	18.4				

Elymus canadensis for All Three Samplings

Date	Cage	Germ	Partial Germ	Seed Coats	V	NV	Total	% Recovered	% Germ	% Partial Germ	% V	% NV
16-Jul	7	0	7	3	2	11	20	14.81481	0	35	10	55
16-Jul	11	6	16	8	8	21	51	37.77778	11.7647	31.3725	15.6863	41.1765
16-Jul	14	0	0	4	1	9	10	7.407407	0	0	10	90
16-Jul	21	7	6	2	4	18	35	25.92593	20	17.1429	11.4286	51.4286
16-Jul	24	1	7	6	4	7	19	14.07407	5.26316	36.8421	21.0526	36.8421
AVE:		2.8	7.2		3.8	13.2	27	20	7.40557	24.0715	13.6335	54.8894
STER:		1.7103	2.8592		1.342	3.008	8.07	5.977782	4.27125	7.75914	2.3786	10.4836
SUM:		14	36		19	66	135	27				
10-Sep	8	0	0	0	2	12	14		0.0000	0		
10-Sep	13	0	2	0	0	0	2		0.0000	100		
10-Sep	15	18	3	0	0	0	21		85.7143	14.2857		
10-Sep	17	17	0	2	0	0	17		100.0000	0		
10-Sep	23	5	9	0	0	0	14		35.7143	64.2857		
AVE:		8	2.8		0.4	2.4			44.2857	35.7143	2.9412	17.6471
STER:		4.4581	1.85068		0.447	2.683			23.4738	22.3036		
SUM:		40	14		2	12	68	13.6				
7-Nov	5	0	2	3	0	2	4	6.896552	0	50	0	50
7-Nov	10	2	3	1	0	3	8	13.7931	25	37.5	0	37.5
7-Nov	16	17	3	7	0	3	23	39.65517	73.913	13.0435	0	13.0435
7-Nov	19	6	0	2	0	0	6	10.34483	100	0	0	0
7-Nov	25	13	4	12	0	0	17	29.31034	76.4706	23.5294	0	0
AVE:		7.6	2.4		0	1.6	11.6	20	55.0767	24.8146	0	20.1087
STER:		3.6159	0.75829		0	0.758	4.04	6.966243	20.568	9.84632	0	11.3319
Sum		38	12		0	8	58	11.6				

Oligoneuron rigidum for All Three Samplings

Date	Cage	Germ	Partial Germ	Seed Coats	V	NV	Total	% Recovered	% Germ	% Partial Germ	% V	% NV
16-Jul	7	1	1	5	4	5	11	21.568627	9.09091	9.09091	36.364	45.455
16-Jul	11	2	2	1	3	4	11	21.568627	18.1818	18.1818	27.273	36.364
16-Jul	14	8	1	2	1	2	12	23.529412	66.6667	8.33333	8.3333	16.667
16-Jul	21	5	0	2	2	5	12	23.529412	41.6667	0	16.667	41.667
16-Jul	24	0	1	0	0	4	5	9.8039216	0	20	0	80
	AVE:	3.2	1		2	4	10.2	20	27.1212	11.1212	17.727	44.03
	STER:	1.6355	0.3536		0.791	0.6124	1.47479	2.8917414	13.4999	4.06403	7.2546	11.481
	SUM:	16	5		10	20	51	10.2				
10-Sep	8	0	2	0	0	4	6	30	0.0000	33.3333	0	66.667
10-Sep	13	0	3	0	0	0	3	15	0.0000	100	0	0
10-Sep	15	0	1	0	0	2	3	15	0.0000	33.3333	0	66.667
10-Sep	17	0	3	0	0	5	8	40	0.0000	37.5	0	62.5
10-Sep	23	0	0	0	0	0	0	0	0.0000	0	0	0
	AVE:	0	1.8		0	2.2	4	20	0.0000	40.8333	0.0000	39.1667
	STER:	0	0.6519		0	1.1402	1.5411	7.7055175	0	18.186	0	17.897
	SUM:	0	9		0	11	20	4				
7-Nov	5	0	0	2	0	4	4	25	0	0	0	100
7-Nov	10	0	1	0	0	2	3	18.75	0	33.3333	0	66.667
7-Nov	16	0	0	1	0	5	5	31.25	0	0	0	100
7-Nov	19	1	0	0	0	1	2	12.5	50	0	0	50
7-Nov	25	2	0	1	0	0	2	12.5	100	0	0	0
	AVE:	0.6	0.2		0	2.4	3.2	20	30	6.66667	0	63.333
	STER:	0.4472	0.2236		0	1.0368	0.65192	4.0745015	22.3607	7.45356	0	20.75
	Sum	3	1		0	12	16	3.2				

Eryngium yuccifolium for All Three Samplings

Date	Cage	Germ	Partial Germ	Seed Coats	V	NV	Total	% Recovered	% Germ	% Partial Germ	% V	% NV
16-Jul	7	0	0	4	3	8	11	8.8	0	0	27.2727	72.727
16-Jul	11	0	0	1	12	33	45	36	0	0	26.6667	73.333
16-Jul	14	0	0	1	1	6	7	5.6	0	0	14.2857	85.714
16-Jul	21	0	1	0	7	33	41	32.8	0	2.43902	17.0732	80.488
16-Jul	24	0	1	9	5	15	21	16.8	0	4.7619	23.8095	71.429
	AVE:	0	0.4		6	19	25	20	0	1.44019	21.8216	76.738
	STER:	0	0.27386		2.1095	6.6049	8.63134	6.9050706	0	1.06811	2.9206	3.067
	SUM:	0	2		28	95	125	25				
10-Sep	8	0	0	0	6	58			0.0000	0		
10-Sep	13	0	0	0	0	0			0.0000	0		
10-Sep	15	0	0	0	0	0			0.0000	0		
10-Sep	17	0	0	0	0	0			0.0000	0		
10-Sep	23	0	0	0	0	0			0.0000	0		
	AVE:	0	0		1.2	11.6			0.0000	0.0000	9.3750	90.6250
	STER:	0	0		1.3416	12.969			0	0		
	SUM:	0	0		6	58	64	12.8				
7-Nov	5	0	2	6	0	15	17	36.956522	0	11.7647	0	88.235
7-Nov	10	0	0	2	0	12	12	26.086957	0	0	0	100
7-Nov	16	0	0	1	0	10	10	21.73913	0	0	0	100
7-Nov	19	0	0	3	0	6	6	13.043478	0	0	0	100
7-Nov	25	0	0	3	0	1	1	2.173913	0	0	0	100
	AVE:	0	0.4		0	8.8	9.2	20	0	2.35294	0	97.647
	STER:	0	0.44721		0	2.7249	3.02903	6.5848397	0	2.63067	0	2.6307
	Sum	0	2		0	44	46	9.2				