MAXIMIZING WIREGRASS REPRODUCTION FOR RESTORATION PURPOSES

By

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Dedicated to Smoke M. Rodriguez

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Abstract of Thesis Presented to the Graduate School
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Maximizing viable seed yields of wiregrass (*Aristida stricta*) is an important goal of land managers attempting to restore this species across large landscapes. I used field trials to examine the effect of growing season burn month and seed harvest date on wiregrass seed production and viability. The experiment was replicated in two study sites in xeric sandhill longleaf pine (*Pinus palustrus*) savannas, one in north Florida and the other in central Florida. At each site, six 5 x 5 m plots were burned during each month of the May - August 2010 growing season, with six plots left unburned as a control. At two-week intervals, from mid-September through December 2010, I manually harvested seeds from a wiregrass plant in each plot and sent them to a laboratory for tetrazolium viability and germination testing. I used a two-way, split-plot ANOVA to test for main and interactive effects of burn month and harvest date on the number of culms per plant, number of seeds per culm, percent filled seed, percent viable seed, and percent germinating seed, at each site.

Overall, May and June burns resulted in the greatest seed quantity and quality, while viability and germination rates were highest from seed collected in early December. Optimal viable seed yields were obtained after June burns in north Florida

and May burns in Central Florida. At both sites, filled seed percent peaked by late October and by mid-November, most of the seed had fallen off the stalk, although viability of harvestable seed remained low at this time (2 - 15%). Late season gains in viability were modest (10 - 20%) compared to the amount of seed shed by this time (> 50%), suggesting that harvesting in early to mid-November, prior to peak seed rain, may result in greater overall gains in the amount of viable seed obtained.

In a separate greenhouse study, I examined the effects of mechanized seed cleaning and coating on germination and establishment. Wiregrass seed awns are removed through cleaning to facilitate seed movement through sowing machinery, but awns are thought to play a role in preventing seedling desiccation. Seeds were planted in a greenhouse with and without awns (uncleaned and cleaned) on flat and cultivated soil surfaces. Three to six percent more uncleaned seeds germinated on the flat surface than cleaned seeds, indicating that cleaned seeds should not be broadcast without taking additional steps to bury the seed, such as seed bed cultivation. In another set of greenhouse trials, there was no benefit to germination or seedling establishment of a super-hydrating polymer coating on cleaned seeds.

CHAPTER 1
INTRODUCTION

After a century or more of fire suppression, land conversion, and environmental degradation, efforts are now underway to restore wiregrass (*Aristida stricta*) dominated groundcover as part of large-scale longleaf pine (*Pinus palustrus*) restoration efforts. Throughout its geographic range in the Southeastern United States, wiregrass functions as a fine fuel that promotes the spread of low intensity fires (Clewell 1989). Under natural conditions with frequent fire, wiregrass is vigorous and long-lived, but seed germination rates are highly variable and typically < 50% (e.g. Seamon and Myers 1992, Outcalt 1994, Hattenbach et al. 1998, Cox et al. 2004).

Maximizing viable seed production is now an important goal of land managers attempting to restore wiregrass populations across large landscapes as efficiently as possible. Seed for restoration plantings is primarily harvested from relatively pristine donor sites, managed with growing season burns (Trusty and Ober 2009). It is well known that wiregrass flowers more abundantly after growing season fires (Parrot 1967, Clewell 1989, van Eerden 1997); but the effect of burn timing within the growing season on seed production has not been examined thoroughly, particularly across sites. Furthermore, there is some speculation that low seed viability may be a function of the collection time, which has typically occurred from mid-November to mid-December.

Once wiregrass seed is harvested, there are a number of steps involved in the practice of direct seeding, or directly sowing the seed onto the restoration site. These steps can include seed treatments such as cleaning large batches to increase the number of high quality seeds per unit weight, and coating the seeds with ingredients that improve moisture retention. There is growing interest among landowners throughout the Southeast in direct seeding of wiregrass and more information is needed to improve its efficacy. Little is understood about seed characteristics that affect establishment and there is considerable debate over the necessity of various seed treatments (Walker and Stilletti 2006). Successful cleaning and coating of wiregrass seed is expensive and difficult, but potentially results in lower broadcast seeding rates and higher yields.

CHAPTER 2
EFFECT OF GROWING SEASON BURN MONTH ON WIREGRASS SEED PRODUCTION

Introduction

Burn Timing

A host of herbaceous plant species in the longleaf pine ecosystem exhibit increased flowering in response to growing season burns (Robbins and Myers 1992). Dominant grasses in particular, such as *Andropogon* spp., *Schizachyrium scoparium*, and *Sporobolus junceus*, produce more seed when burned during the growing season (Streng et al. 1993, Shepherd et al. 2011). It is possible that the plants of the longleaf pine ecosystem became adapted to lightning ignited fires which are more common during the growing season (May – August) than during the dormant season (Robbins and Myers 1992). Even so, there remains much variation in flowering response to burn month among individual understory species and functional groups, with some species responding more favorably to dormant season burns, such as the legume *Tephrosia virginiana* (Hiers et al. 2000), and others not affected by season of burn, such as the panic grass, *Paspalum setaceum* (Streng et al. 1993).

There is much uncertainty among land managers about the best month(s) to burn wiregrass for maximum seed production. Several studies have demonstrated increased flowering and seed viability of wiregrass following growing season over dormant season burns, but few have investigated the effects of fire timing within the growing season. In one important study on this topic, Outcalt (1994) measured the effect of burn month (May – August) on wiregrass seeds harvested in December from longleaf sandhills of the Ocala National Forest in north-central Florida. Seed germination rates were highest from plants burned in August, followed by July. In contrast, Myers et al. (unpublished data) observed decreasing amounts of viable seed as burns progressed from May to August in the Florida Panhandle region.

For several perennial herbs of longleaf pine savannas, flowering induction through fire is thought to interact with seasonal cues, such as photoperiod (Platt et al. 1988, Brewer and Platt 1994). Flowering in some species, including grasses, is strongly correlated with day length and temperature (Heide 1994). Work by Parrot (1967) suggests that long days and high temperatures may be required for production of large amounts of viable wiregrass seed. Several wiregrass plants were defoliated at different times of the year and subjected to a range of temperatures and photoperiods. The only plants that did not exhibit flowering induction were those that experienced maximum daily temperatures below 32°C and a photoperiod < 12 hours.

Peak flowering in response to month of burn is expected to vary predictably across latitudes where growing season intervals, and therefore timing of seasonal cues, shift. Growing season is most commonly defined as the period when air temperature is continuously above 0°C, which occurs between the last spring and first fall freezes (Henry et al. 1994). In Florida, northern regions experience distinct growing and dormant seasons, whereas in South Florida, a wet/dry distinction between the seasons is more pronounced (Robbins and Myers 1992). Therefore, flowering should occur later in northern regions where the growing season is shorter and earlier in southern regions where the growing season is less distinct from the dormant season.

Seed Collection Timing

Historically, viable wiregrass seed has been harvested from September through December, following growing season burns (Bill Cleckley and Ann Blount, pers. comm.). Within days of burning, fresh green growth is visible and seed stalks are produced within a couple of months. The inflorescence is a panicle, 25 – 30 cm long, consisting of spikelets (the dispersal unit) subtended by paired glumes. Not all of the seeds fill, as a viable embryo may never develop within the three awned lemma and palea. Filled seeds begin to mature from the bottom of the stalk up to the terminal end, in October, and remain on the stalk for a few weeks, barring high winds (Pfaff et al. 2002). Seeds become firm and dark in color when mature and require no special treatments for breaking dormancy. Fallen seeds germinate in the field the following spring and into the fall (Mulligan and Kirkman 2002, Wenk 2009). Seed can be stripped from the stalk manually, but harvesting is more efficient with the use of machinery such as the Flail-Vac Seed Stripper (Ag-Renewal Inc., Weatherford, OK). This machine strips seed off the stalk with rotating brushes and a vacuum system and can be tractor mounted (Pfaff et al. 2002).

Study Objectives

The objectives of this study were to 1) determine an optimal month of the growing season to burn north and central Florida wiregrass, resulting in maximum viable seed yields, and 2) determine an optimal time for seed harvesting, depending on burn month and geographic location. I measured both quantity and quality (viability and germination rates) of seed produced. Optimal harvesting time of wiregrass seed occurs after the seed has matured and before it falls off the stalk (Seamon and Myers 1992), therefore the timing of wiregrass seed rain was also assessed with seed traps.

Methods

Study Sites

Two study sites were located in xeric sandhill longleaf pine - wiregrass communities. The northern site is in the Econfina Creek Water Management Area of the

Northwest Florida Water Management District at 30°25’57”.06 N, 85°36’41”.29 W. The southern site is in Annutteliga Hammock of the Southwest Florida Water Management District at 28°40’13”.00 N, 82°31’9”.46 W.

The northern site is a 12 ha stand of approximately 80-year old longleaf pine woodland, in northern Bay County, FL. The stand is notable for its open, two-storied structure, with an over story of primarily widely-spaced longleaf pine, and an intact ground story of 50 - 80% wiregrass cover. The most recent prescribed burn in the study area occurred two years before this study in May 2008 and the stand was prescribe burned during the growing season on a three year return interval several times previously (Eric Toole, pers. comm.). The ground-story consisted primarily of runner oak (*Quercus pumilia*), dwarf huckleberry (*Gaylussacia dumosa*) and forbs such as blazing star (*Liatris patens*) and gulf coast lupine (*Lupinas westianus*), in addition to wiregrass. The terrain is gently rolling hills of excessively-drained Lakeland sand (thermic, coated typic quartzipsamments) atop ancient marine terraces, with a mean depth of > 2 m to the water table (USDA 2011).

The southern site is in Hernando County, FL in two adjacent stands of approximately 60-year old longleaf pine woodlands, together comprising 18 ha. As with the northern site, the overstory consisted predominately of widely spaced longleaf pine trees, but an open mid-story consisting of turkey oak (*Quercus laevigata*) was also present. The land was grazed by cattle during the 1950s – 1970s (Mary Barnwell, pers. comm.) and had last been burned 15 years prior to my study, as estimated based on the age of invasive and serotinous-coned sand pines (*Pinus clausa*). Wiregrass cover was not as uniform or widespread as in the northern site, ranging from approximately 5

– 65% cover. Other grasses present were pineywoods dropseed (*Sporobolus junceus*), other *Aristida* species, and several species of bluestem (*Andropogon* spp.). Despite the difference in fire frequency between the two sites, fuel loads appeared similar. Topography was similar to the northern site, with gently rolling hills of excessively drained Candler fine sand (hyperthermic, uncoated lamellic quartzipsamments) atop the ancient marine terrace known as the Brooksville Ridge, with a mean depth of > 2 m to the water table (USDA 2011).

The two sites are approximately 320 km apart in straight line distance and are affected by somewhat different climates. Growing and dormant seasons in the Florida Panhandle are distinguished most from each other by temperature, whereas these seasons in peninsular Florida differ most in precipitation. The northern site receives an average of 160 cm of precipitation annually, with 46% falling June – September. In contrast, the southern site receives approximately 132 cm of precipitation annually, with 55% falling June – September (National Climate Data Center, Asheville, NC). Both areas experience spring and fall droughts but spring droughts in the Panhandle region are less severe due to higher levels of winter precipitation. Temperatures are an average of 3°C lower in the Panhandle than in central Florida, with an average frost-free period of 277 days at the northern site, compared to 324 days at the southern site (USDA 2011).

During the year of this study, the northern site experienced a summer drought, while there was a typical season of summer convective storms at the southern site (Figures 1-1 and 1-2). Rainstorms occurred at both sites throughout the collection period, particularly in November (Figure 1-3). Deviation from average precipitation and temperature patterns may influence the phenological responses to fire that are reported here (Fox 1990).

Experimental Design and Treatments

A split plot design was utilized at each site with the whole plot reflecting month of burn and the split plots reflecting time of seed collection (Figure 1-4). At each site, six randomly selected replicate 5 x 5 m plots were burned during a different month of the May – August 2010 growing season. Plots were burned with a backing fire using a drip torch and flames were extinguished at the perimeter with a water hose. Flame lengths were an average of 1 m tall, and each plot took approximately 5 minutes to burn. Burning occurred as close to the middle of each month as possible, at around mid-day, when relative humidities are around 50%, but not yet at their lowest values. Six plots were left unburned as a control treatment, for a total of 30 plots at the southern site, while three additional plots were burned in April at the northern site, for a total of 33 plots. Each plot was randomly located within an approximately 5 ha contiguous area, with the only requirement being the absence of large trees, which might have significantly lowered radiation reaching the understory. At both sites, the remaining forest stand surrounding the plots was prescribe burned in the middle of May. Eight 1 m^2 sub-plots, each corresponding to a different collection date, were randomly located within a central 3 x 3 m sample area of each 5 x 5 m burn plot, with the remaining perimeter acting as a buffer.

Data Collection

Every two weeks, from mid-September until the end of December 2010, culms (seed stalks) were destructively harvested from a single wiregrass plant nearest to the center of the designated collection sub-plot that had a minimum of 4 culms. Each culm holds approximately 50 seeds and a 200 seed minimum was judged to be needed for accurate tetrazolium viability and germination testing (AOSA 2000, AOSA 2010). Wiregrass plant size was determined by measuring the length of the longest axis of the base and its perpendicular width, and basal area was calculated using the equation for the area of an ellipse. Culms were placed in paper bags and taken to the laboratory where glume pairs from one randomly chosen culm in each collection plot were counted. Glume pairs were counted instead of seeds to obtain a measure of the total amount of seed produced, independent of seed rain.

If there were fewer than 200 seeds on a single plant, culms from additional plants in the collection plot or from a nearby buffer area were collected, but these were kept separate from the culms initially collected until after the number of seeds per culm had been counted. If there were no wiregrass plants with four culms in the designated collection plot, this was noted and culms were collected from a plant or plants in a nearby buffer area. In some cases, there were no culms or there were not 200 seeds in either the collection plot or the buffer area, resulting in missing data values for seeds per culm, percent filled seed, percent viable seed, and/or percent germinating seed.

The seed tests were conducted according to the general procedure for tetrazolium viability and germination testing as described in the AOSA Rules (AOSA 2010) and the AOSA TZ Handbook (AOSA 2000). These tests were conducted by trained personnel at the USDA Forest Service, National Seed Laboratory, in Dry Branch, GA. First, X-rays were taken to determine percentage of filled seeds per 200 seed lot. If there were > 10% filled seeds, this test was followed by tetrazolium viability and germination testing on 100 seeds each, randomly selected from the original seed lot. Viability testing involved cutting open the seed and staining it with a tetrazolium solution that is reduced to a red dye by respiring (viable) tissue. Germination tests were conducted on moist filter paper under a 16/8 hr (light/dark) photoperiod with corresponding temperatures of 30/20 ^{o}C (light/dark) over 28 days.

To assess patterns of seed rain over time, seed traps were placed in the center 1 m^2 subplot of each burn plot beginning in September (Figure 1-4). Seed traps were similar to those used in a number of other grass seed studies (Ellison 1987, Rand 2000, Kettenring 2006), made of 22.5 cm diameter circular Styrofoam plates covered with Tangle-Trap ® Sticky Coating which remains tacky after repeated submersion in water. Traps were pinned to the ground a few centimeters above the surface to exclude crawling insects and to prevent sand from being washed onto the plate by heavy rains. Maximum distance of wiregrass recruitment has been recorded at approximately 4 m from the mother plant (Mulligan et al. 2002). Seed traps in each burn plot were at least that distance from the other burn plots to minimize the collection of wiregrass seeds from outside the plot. Seeds were counted and removed from traps every two weeks at the same time culms were harvested and seed traps were replaced when their surfaces were no longer tacky.

Statistical Analyses

Analyses of variance were conducted using a two-way, split-plot ANCOVA and ANOVA to test for main and interactive effects of burn month and collection date on the number of culms per plant, number of seeds per culm, percent filled seed, percent viable seed, and percent germinating seed, at each site. All models were analyzed using the GLIMMIX procedure (v 9.2, 2008, SAS Institute Inc., Cary, NC) and square root transformed data to achieve a normal distribution and homogeneous variances. Experimental treatments and the covariate were analyzed as fixed effects, with variation within a burn month treatment treated as a random effect. Differences were assumed to be significant at $\alpha = 0.05$ and p-values were adjusted for multiple comparisons using the Tukey-Kramer method. Since the control plots did not contain any flowering wiregrass plants, only their seed trap data were analyzed.

The basal area of each sampled wiregrass plant was included as a covariate in the analyses of culms per plant and seeds per culm. This covariate was included to control for differences in pre-existing vegetative growth that may have affected reproductive capacity. Wiregrass is a bunchgrass that increases in basal area very slowly, with the center becoming hollow and reported to reach a diameter of 15 cm in 15 years (Clewell 1989). Ideally, the size measurement should have occurred prior to applying burn treatments but treatment effects on plant size were assumed to be negligible compared to pre-existing differences.

Differences between the sites were analyzed in a three-way ANCOVA and ANOVA with site added as a fixed, main effect. In order to compare data from the two sites, the April burn treatment was removed from the northern site data set, and collection dates were assigned approximate values (i.e. mid-September, late-September, etc.).

Seed trap data were analyzed for each site in a two-way ANOVA with burn month and collection date as fixed treatment effects, and whole plot (i.e. burn month treatments) as a random effect.

Results

Seed Quantity

At both sites, there was a main effect of burn month, but not collection date on number of culms per plant (Tables 1-1 and 1-2). Plots burned in August produced fewer culms per plant than those burned in May, June, and July at both sites (Figure 1-5) while at the southern site; plots burned in May produced more culms per plant than those burned in June, July, or August. An interaction between burn month and collection date at the northern site ($p = 0.0062$, Table 1-1) occurred because the August burns initially produced fewer culms, but culm number gradually reached comparable values to the other burn months by the late October harvest.

There was also an effect of burn month but not collection date on the number of seeds per culm at both sites (Tables 1-1 and 1-2). At the northern site, April, May and June burns resulted in greater seeds per culm than July and August, while at the southern site, August burns resulted in the fewest seeds per culm compared to May, June, and July burns (Figure 1-6). Plant size increased culms per plant at both sites ($p < 0.0001$), and plant size increased seeds per culm at the southern site ($p = 0.0383$), but not at the northern site ($p = 0.1922$) (Tables 1-1 and 1-2). Plants at the southern site were on average, 107 cm^2 larger than those at the northern site.

At both sites, there were a number of treatment sub-plots that lacked seed or lacked seed that was > 10% filled; thus precluding viability and germination testing. This was particularly true at the northern site, which experienced a drought during the burn months. At the northern site, 14 of the 216 treatment sub-plots plots lacked seed and 96 lacked seed that were > 10% filled. Plots that did not contain any seed were entirely from the August burn treatments that were sampled early in the harvesting season.

Plots with seed between 0 and 10% filled, while fairly evenly distributed across burn treatments, were concentrated toward the end of the harvesting season (Figure 1-7). At the southern site, 18 of 192 treatment sub-plots lacked seed, and seed that was collected from 41 plots were < 10% filled. As in the northern site, missing data were concentrated in the August burn treatment, with 17 of these plots lacking seed and 14 containing seed that was < 10% filled.

Seed Quality

Early in the harvesting season (between mid-September and mid-October) both sites exhibited peaks in the percent of filled seed collected (Figures 1-7 and 1-8). There was an interaction between burn month and collection date at both sites on percent filled seed (Tables 1-1 and 1-2). At the northern site, this interaction reflected a lack of seed in July burn plots until 9/24 and in August burn plots until 10/8 (Figure 1-7). At the southern site, there was a lack of seed in the August burn plots until 10/1 and these plots peaked in seed fill at 54% on 10/15. By comparison, May and June burn plots exhibited a peak in seed fill at roughly the same percentages as the August burn plots but these peaks occurred a month earlier, on 9/18 (Figure 1-8). Subsequent seed fill percentages followed similar trends among all burn treatments within a site; declining towards 6% by the end of the harvesting season at the northern site, and hovering around 19% for the remainder of the harvesting season at the southern site.

Seed viability differed by both main effects of burn month and collection date (Tables 1-1 and 1-2). At the northern site, there were two observable peaks in viability for seeds collected on 10/8 and 12/3. These collection dates yielded higher seed viability percentages than 9/12, 10/22 and 11/7 (Figure 1-9). At the southern site, all seeds collected from 11/11 onward had higher viability than those collected before that date. Comparisons among burn month treatments show that August burns resulted in lower viability rates than June burns at the northern site, while August burns resulted in less viable seed than both May and June burns at the southern site (Figure 1-10).

Germination rates increased as seed was collected toward the end of the harvest season at both sites, with interactions between burn month and collection date (Figures 1-11 and 1-12). In general, this interaction reflected later peaks in germination rates for plots burned later in the growing season. At the northern site, germination rates hovered around 0% through the 11/7 harvest, except for plots burned in June, which had a slightly greater percent germination at this time (2%, Figure 1-11). For the remaining six weeks, germination rates were greater for all burn months, except August. Within burn treatments, May plots peaked at 7% germination on 11/18 (different from all other collection dates except 12/3) while July plots peaked at 11% on 12/3. By 12/17, while there was no longer > 10% filled seed left on the stalk in May burn plots, June burn plots exhibit their greatest germination percentage on this date at 11% (different from all other collection dates except 12/3).

At the southern site, germination rates did not begin to increase until 10/29 from the May and June burn plots, 11/24 from the July burn plots, and 12/10 from the August burn plots (Figure 1-12). May burn plots reach their peak germination at 18% on 11/24 (different from all other dates except 11/11 and 12/10). Germination rates from June burn plots peaked at 12% on 12/10, while July and August burn plots peaked on 12/10, at approximately 12% and 6%, respectively. Comparisons among burn treatments revealed that August burns resulted in the lowest germination rates at both sites, while additionally at the southern site, July burns resulted in lower germination percentages than May burns.

Seed Traps

At both sites, there were interactive effects of burn month and collection date on seed trap counts (Tables 1-1 and 1-2). Seed traps at both sites contained the most seeds in early November, particularly from May and June burn plots (Figures 1-13 and 1-14). For plots burned in April, May, June, and July at the northern site, there was a peak in seeds trapped between 10/22 and 11/7 (Figure 1-13). During this peak, nearly half of all seeds collected in traps over six collection periods were trapped (19 out of 45 seeds/0.04m^2). At the southern site, seed trapped from the May and June burn plots increased sharply between 10/29 and 11/11 and this was much greater than the amount of seed trapped from the July and August burn plots (Figure 1-14). During this peak, roughly a quarter of all seeds collected in traps over five collection periods were trapped (10 out of 39 seeds/0.04m^2). The peak at the southern site was less pronounced compared to the northern site: peak values for the May and June burn plots at this time were, in general, not different from counts measured from these plots for the rest of the collection period.

Overall, seed traps at both sites contained less seed from August burn plots than from plots burned during the three previous months. Other differences among months included May burns resulting in greater amounts of seeds trapped compared to July plots at the northern site, while at the southern site, both May and June burn plots had more trapped seeds than July and August burn plots. As an additional comparison, counts were also taken from seed traps placed in the area adjacent to the study plots that was burned in May at both sites. These trap counts were consistent with the date effects observed from the May experimental plots.

The majority of seed traps in control plots at the northern site did not contain any wiregrass seed, while the rest contained between 1 and 4 seeds. However, control traps at the southern site contained a much larger range of seed counts. While the majority of these traps contained between 0 and 3 seeds, 8 out of the 36 sampling periods for control seed traps contained between 10 and 33 counts of what appeared to be wiregrass seeds, despite a lack of flowering wiregrass plants in these plots. These counts exhibited similar collection date effects as the rest of the plots at the southern site (data not shown).

Comparison of Sites

Overall, the degree of response from the southern site was greater than the northern site for all variables (seeds per culm, percent filled seed, percent viability, and percent germination), except culms per plant (Table 1-3). Plants in the north exhibited particularly strong responses to June burns, while at the southern site, May burn responses tended to be greater than June burn responses. At the northern site, culms per plant, seeds per culm, and seed trap counts were similar among May and June burn plots. However, June burns resulted in greater percentages of overall viability ($p = .0153$, Figure 1-10) and germination (1.3% for June burns compared to 0.6% for May, $p = .0401$). In contrast, at the southern site, May burns produced the most culms per plant, the highest percentages of viable and germinating seed, and the most trapped seed. These values were statistically different from those produced through June burns for overall culms per plant ($p = .0002$, Figure 1-5) and for May's peak germination percentage on 11/24 ($p = .0014$, Figure 1-12). June burns resulted in greater seeds per culm at the southern site, however, when comparing number of culms multiplied by number of seeds per culm, May burns produced more seeds per plant than June burns, although this difference was not significant ($p = 0.0508$, data not shown).

Discussion

Burn Timing

May and June burns resulted in the greatest numbers of high quality wiregrass seed compared to burning in April, July and August, as reflected by greater seeds per plant and higher percentages of viable and germinating seed. These findings are consistent with two out of three studies that have tested the effect of growing season burn month on wiregrass seed production (Myers et al., unpublished data, Streng et al. 1993, and Outcalt 1994). In all three studies, naturally occurring wiregrass populations in longleaf pine sandhill communities were prescribe burned. Myers et al. (unpublished data) observed that May burns resulted in the greatest numbers of culms and percent germination, followed by June burns, but these results were not conclusive. Number of culms peaked following May burns at 32/plant but was not statistically different from results of burning during the months April – August. Percent germination from May burns (33%) was statistically greater than all other months, except June and July. These values are higher than those obtained for number of culms and percent germination in this study (24 culms/plant and 18% germination), but reflect similar trends in terms of the best months to burn wiregrass for both increased quantity and quality of seed produced. In another Florida panhandle study, Streng et al. (1993) did not test the effect of June burns, however, percentage of plants flowering following May burns (90%) was greater than from July and August burns (70% for both months), and similar to April burns.

In contrast, Outcalt (1994) conducted burns from May - August in central Florida, collected seed in early December, and found increasing quantity and quality of seed produced through burning later in the growing season. Number of culms was not different among all months, but June burns produced the fewest number of seeds per culm (9 compared to 24, 27, and 15 for May, July, and August, respectively). Additionally, August burns resulted in the greatest percent germination (36%), followed by July (21%), and then May (7%) and June (5%). I observed percent germination from August burn plots to peak in early December, and the late timing of collection in this study may have played a role in favoring later growing season burns. Other unknown variables, such as weather and site history could also explain the contradictory findings between our studies.

July and August were not good months to burn wiregrass for viable seed production at either of our study sites, despite opposing rainfall patterns in which the northern site experienced a summer drought, while the southern site experienced normal rainfall (Figure 1-1). In Florida, May is when the most acreage historically burned due to lightning strikes, followed by June (Robbins and Myers 1992). During this period, lightning activity is increasing and fuel moisture is still low following the typically dry spring. This climactic pattern is thought to have been in place since the establishment of extensive longleaf pine forests in northern Florida approximately 8,000 years ago (Watts and Hansen 1988, Watts et al. 1992).

The historical frequency of May/June fires may have exerted evolutionary pressure for increased flowering on once widespread populations of wiregrass. For fire-stimulated flowering to be considered an adaptive trait subject to natural selection, genetic variation in this trait must exist among populations (Brewer 1995). Gordon and Rice (1998) demonstrated significant variation in flowering between wiregrass populations from the panhandle to central Florida, while differences in culm number within populations were observed in flatwoods, but not sandhill populations. In a more homogenous, resource limited environment like the sandhills, natural selection may have played a large role in stabilizing local adaptation of fire-induced flowering.

Fire is thought to improve conditions for reproduction through the removal of vegetation and litter and by providing a flush of available soil nutrients (Brewer 1995). Through these mechanisms, fire increases light reaching the understory and the amount of nitrogen and phosphorous in the soil, nutrients particularly important for speeding reproductive maturity (Christensen 1977). Differences in flowering with respect burn timing may reflect differences in the ability of populations to exploit resource availability (Hiers et al. 2000). Plants burned in May and June have a longer growing season in which to take advantage of favorable conditions, compared to plants burned in July and August.

The results of this study indicate that it may be more advantageous to burn sandhill wiregrass populations in June in northern Florida, and somewhat earlier in central Florida, if seed production is desired. Optimal flowering in response to earlier burns was expected at the southern site based on the earlier onset of warmer temperatures and longer days. Flowering phenology of a number of temperate perennial grasses is highly influenced by both temperature and photoperiod (Heide 1994). The average date of last frost at the southern site is approximately one month earlier than at the northern site and this may have selected for earlier flowering phenology of these southern wiregrass populations over time.

Seed Collection Timing

Timing harvests to obtain maximum amounts of viable seed is a considerable challenge in restoring wiregrass populations (Pfaff et al. 2002). This study was one of the first to examine the quantity and quality of wiregrass seed over a prolonged harvesting period. Published reports of wiregrass collection periods typically ranged from mid-November through December (Seamon 1998, Seamon and Mizell 2004). In this study, most of the seed had fallen off the stalk by mid-November. Late season gains in viability were modest (10 – 20%) compared to the amount of seed shed by this time, therefore harvesting by mid-November is recommended to ensure the greatest amount of seed, and presumably the greatest amount of viable seed, is collected.

For all burn treatments, with the exception of the early July and August collections, seeds produced per culm did not increase over the 16 week collection period. Month of burn also appeared to have little effect on the timing of maximum viability and seed shed. By contrast, filled and germinating seed percentages generally peaked earlier after May burns and latest after August burns. These results indicate that production of a filled seed with high germination potential may be particularly dependent on month of burn and possibly on resource availability.

Percent viability and germination of seed harvested from the stalk did not begin to differ from zero until seed rain began and these values peaked after peak seed rain occurred in early November. While average germination rates among all burn plots peaked at both sites in December, percentages of filled seed peaked in September and October and declined as the season progressed. A peak in seed fill, followed by a peak in seed rain, and then a peak in seed viability has previously been demonstrated for *Hordeum brevisubulatum*, a fire-dependent, perennial bunchgrass native to China (Zhou and Valentine 2006). Maximizing proportion of filled seed soon after seeds are produced may ensure the greatest number of seeds are filled by the time most of them are shed. Wind-dispersed grass seeds are often shed by gravity close to the parent plant (Fenner and Thompson 2000). If this were the case for the majority of wiregrass seeds, the heavier, filled seeds would fall off the stalk more readily than empty seeds.

As seed rain progressed, there were greater percentages of unfilled seed remaining on the stalk; however, the seed that was filled was more likely to be viable. Total amounts of viable and germinating seeds harvested from the stalk were lower than amounts of filled seeds, presumably because maintaining viability is more resource demanding than filling a seed and aborting the embryo. Increased percentages of viable and germinating seeds later in the season were likely due to higher quality seed remaining on the stalk as seed rain progressed. High quality seeds tend to have a stronger abscission zone and disperse in higher winds (van Dorp et al. 1996), making them more likely to travel long distances required for population expansion (Neubert and Caswell 2000). Also, more seeds may have been reaching maturity as time progressed. After-ripening of wiregrass seed on the stalk has been reported (Pfaff et al. 2002).

To estimate the amount of viable seed to be harvested at any one time, percent viability may be multiplied by the amount of seed available on the stalk. However, I counted glume pairs on the stalk, rather than seed number per stalk, as an estimate of seed produced per burn treatment over time. However, indirect measurements of amount of seed left on the stalk were obtained. Following the peak seed rain period, a tipping point was reached whereby the majority of plants sampled did not have more than 200 seeds. Two hundred seeds per plant are approximately 30% of the average total seeds per plant from June burns at the northern site and approximately 10% of the seed remaining on the stalk from May burned plots in the south. Based on a rough estimation of 200 seeds per plant at the time of peak seed rain, maximum values of viable seed can be estimated for each site. June burn plots in the north contained seed that was 4.5% viable on 11/7, which resulted in 28 viable seeds per plant, while May burn plots in the south contained 50 viable seeds per plant, at 25% viability on 11/11.

At the northern site, there was a significant peak in seed rain, while at the southern site, seed rain was more uniform across the latter half of the harvesting season. As indicated by the large number of *Aristida* seeds trapped in control plots, seed counts at the southern site were likely confounded by the presence of other *Aristida* species whose seeds are almost indistinguishable from wiregrass. However, similar trends were observed in counts from seed traps in all burn treatments among and within sites, including control plots in the south. The rate of seed rain peaked in early November, irrespective of days since burn, geographic location, or perhaps even species.

This may indicate that environmental factors, such as wind and precipitation are important in the timing of seed rain (McGraw and Beuselinck 1983, Garcia-Diaz and Steiner 2000). Both sites exhibit local peaks in daily rainfall (2.5cm/day at both sites) and average daily wind speeds (13 km/h and 15km/h at the northern and southern sites, respectively) during the two weeks of peak seed rain (Figure 1- 3). There is no clear link between these elevated levels and increased rate of seed shed, however, as these events were not unusual over the course of the entire season.

Increased Seed Production at the Southern Site

Compared to the northern site, the southern site produced higher values of nearly every response variable (Table 1-3). Based on anecdotal evidence, increased flowering was expected at the southern site, because it had experienced a much longer fire return interval (fifteen years) compared to the northern site (two years). Wiregrass plant size was much larger at the southern site, possibly due to this lack of fire. However, after taking plant size into account, number of seeds per culm (and to a lesser extent, number of culms) was still greater at the southern site. Pollination has not been shown to be limiting at densities as low as 5 wiregrass plants per 10 m^2 (Mulligan et al. 2002) and the increased flowering response occurred at the southern site despite a lower density of wiregrass.

Fire suppression is an environmental stress in longleaf pine – wiregrass ecosystems and limits population expansion of these keystone species (Brockway and Lewis 1977). Compared to healthy plants burned more recently, fire-suppressed wiregrass populations would have more to gain from increased flowering, seed set, and ultimately seedling recruitment. This phenomenon has not been widely documented and the physiological mechanism behind it is unknown. Interestingly, re-instatement of regular prescribe burns at the northern site was reported to have resulted in significant seed production and viability (Bill Cleckley, pers. comm.). The peak values of 44% viability and 18% germination at the southern site were within ranges normally reported for wiregrass (e.g. Hattenbach et al. 1998, Seamon and Myers 1992). Precipitation in the months following burning was much greater at the southern site compared to the northern site and differences in seed production, as well as seed rain, could also be due to local climactic conditions.

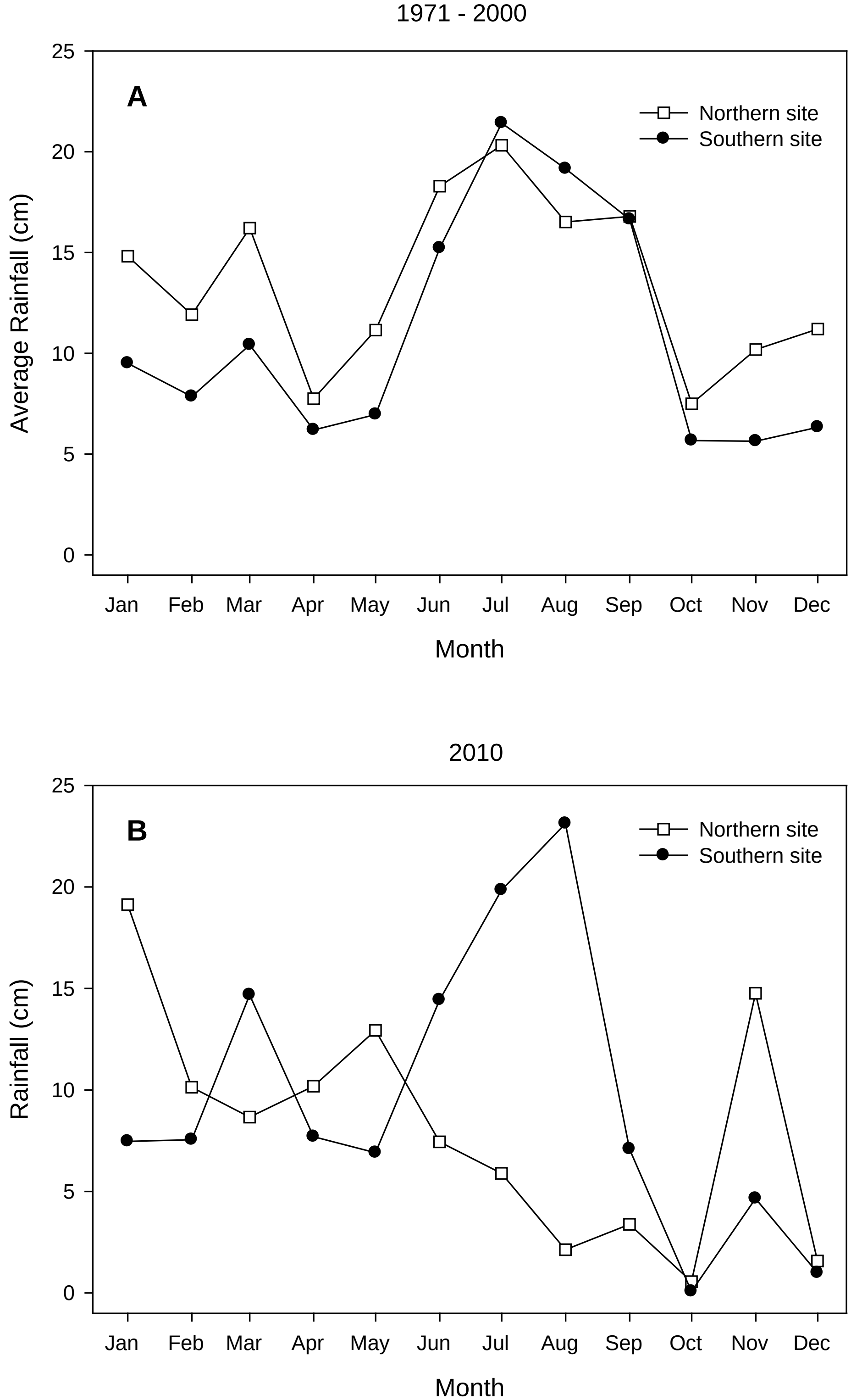

Figure 1-1. Total monthly rainfall at weather stations near each study site for A) 1971 – 2000 (National Climate Data Center, Asheville, NC) and B) 2011 (Florida Automated Weather Network, Gainesville, FL).

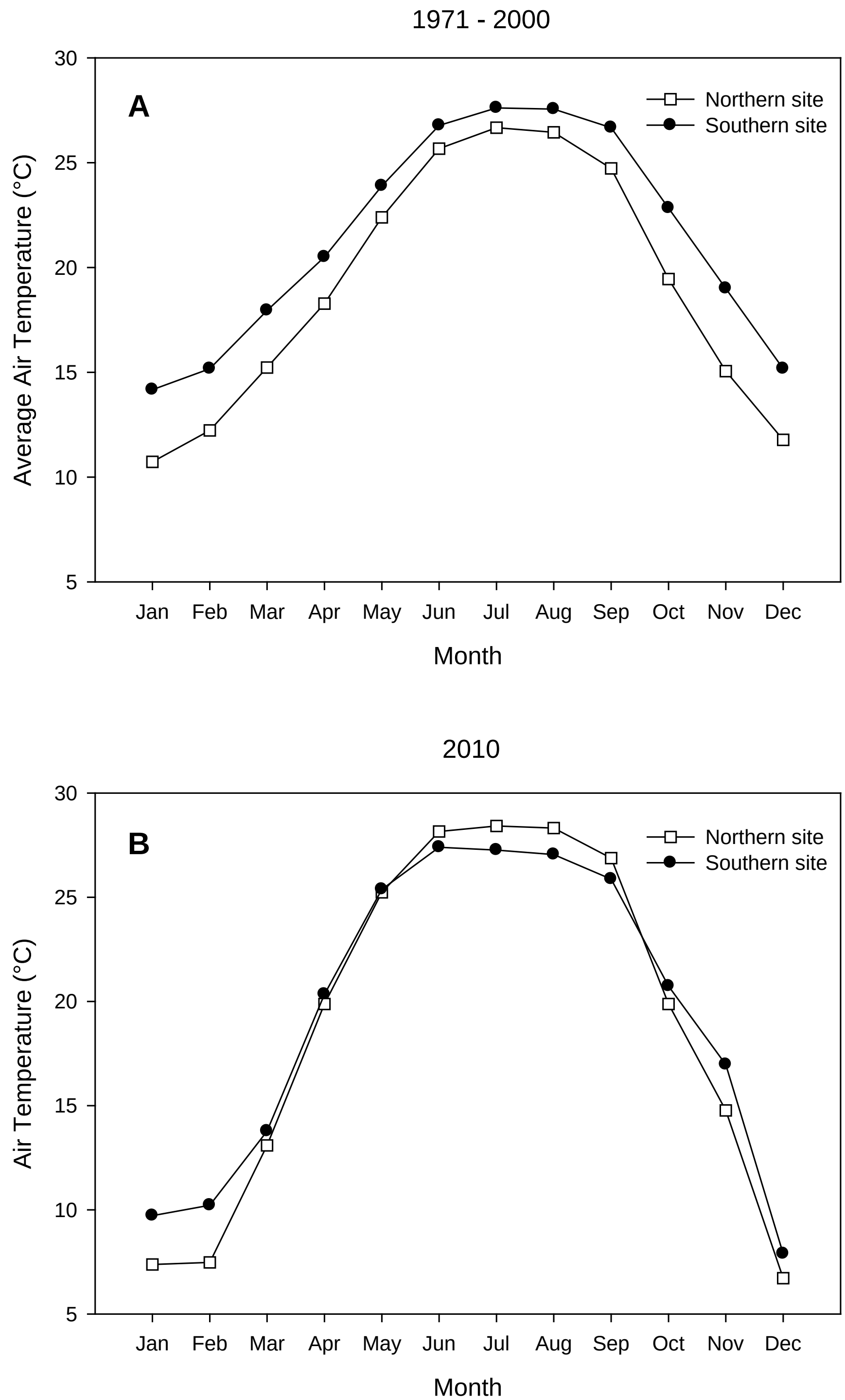

Figure 1-2. Monthly air temperatures at ground level at weather stations near each study site for A) 1971 – 2000 (National Climate Data Center, Asheville, NC) and B) 2010 (Florida Automated Weather Network, Gainesville, FL).

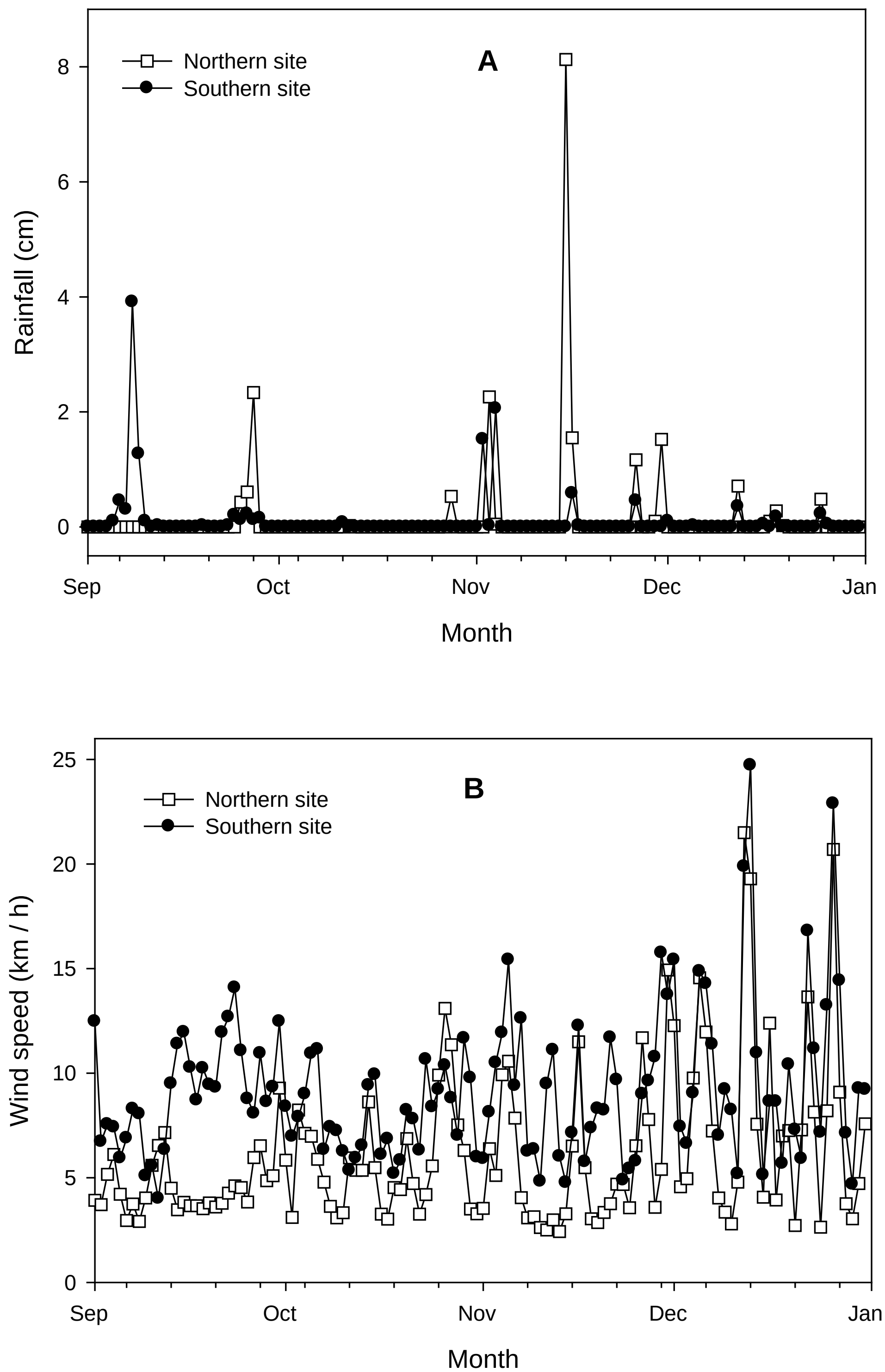

Figure 1-3. Weather conditions at weather stations near each study site during the seed collection period in 2010. A) Total daily rainfall and B) Average daily wind speed (Florida Automated Weather Network, Gainesville, FL)

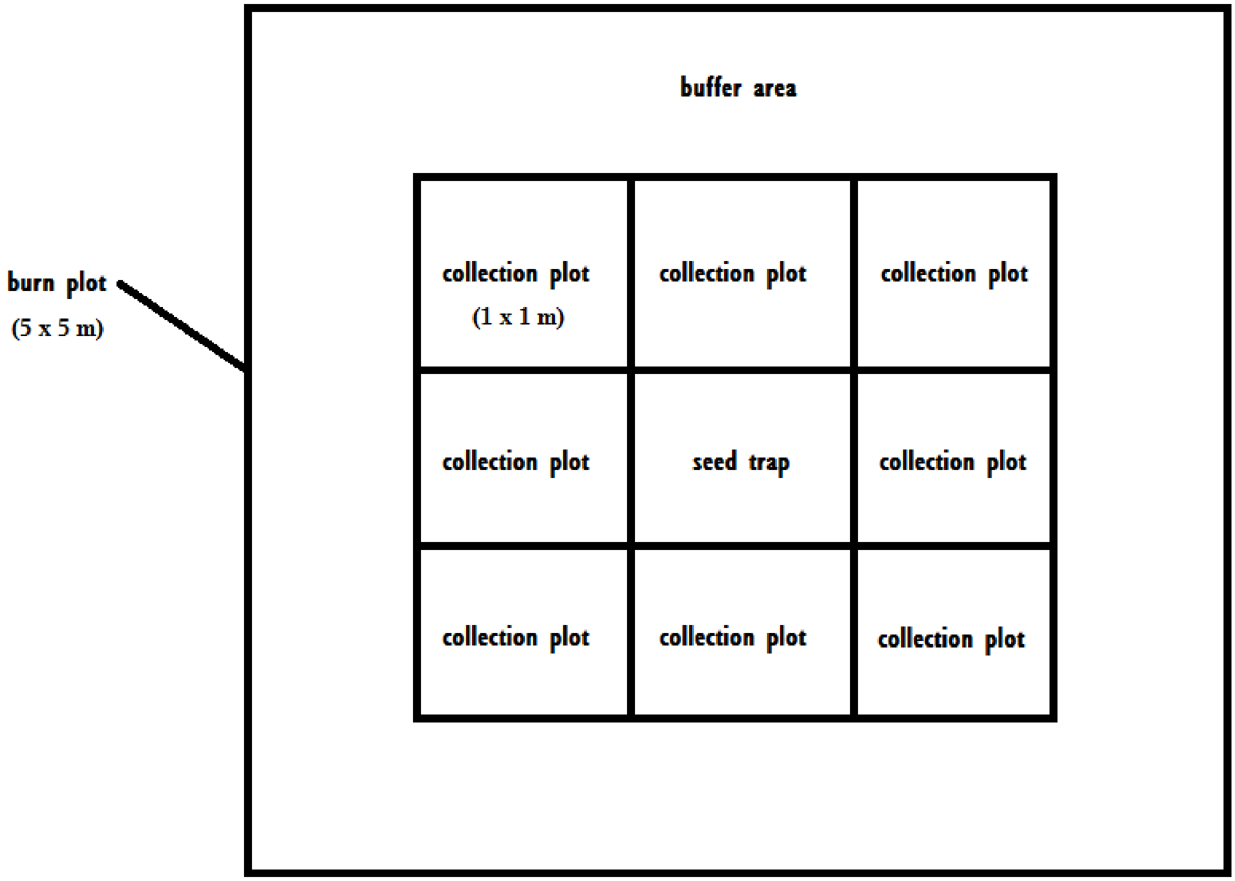

Figure 1-4. Split plot design of burn treatments and seed collection plots at both sites.

Table 1-1. ANCOVA and ANOVA results of the effects of burn month and collection date on the number of culms per plant, number of seeds per culm, percent filled seed, percent viable seed, percent germinating seed, and seed trap counts, at the northern site (*significance at α = .05)

Response Variable	Source of Variation	ndf	ddf	F	p-value	
culms per plant	plant size	1	170.1	38.61	<0.0001	*
	burn month	4	22.11	12.64	<0.0001	*
	collection date	7	153.4	1.45	0.1894	
	month*date	28	153.2	1.94	0.0062	*
seeds per culm	plant size	1	159.8	1.72	0.1922	
	burn month	4	20.35	8.32	0.0004	*
	collection date	7	138.9	1.03	0.4146	
	month*date	26	138.8	0.75	0.8021	
% filled	burn month	4	24.26	1.68	0.1877	
	collection date	7	141	26.86	<0.0001	*
	month*date	26	140.9	2.95	<0.0001	*
% viability	burn month	4	75	4.61	0.0022	*
	collection date	7	75	6.89	<0.0001	*
	month*date	19	75	0.7	0.8073	
% germination	burn month	4	27.76	15.59	<0.0001	*
	collection date	7	68.38	21.06	<0.0001	*
	month*date	19	65.91	4.25	<0.0001	*
seed trap counts	burn month	4	22	14.25	<0.0001	*
	collection date	6	132	26.56	<0.0001	*
	month*date	24	132	3.02	<0.0001	*

Table 1-2. ANCOVA and ANOVA results of the effects of burn month and collection date on the number of culms per plant, number of seeds per culm, percent filled seed, percent viable seed, percent germinating seed, and seed trap counts, at the southern site (*significance at α = .05)

Response Variable	Source of Variation	ndf	ddf	F	p-value	
culms per plant	plant size	1	159	45.74	<0.0001	*
	burn month	3	159	42.51	<0.0001	*
	collection date	7	159	0.44	0.8730	
	month*date	21	159	0.76	0.7609	
seeds per culm	plant size	1	138.6	4.37	0.0383	*
	burn month	3	20.23	12.05	<0.0001	*
	collection date	7	122.7	1.53	0.1627	
	month*date	20	122	1.3	0.1887	
% filled	burn month	3	22.41	1.81	0.1737	
	collection date	7	127	5.39	<0.0001	*
	month*date	20	125.9	2.83	0.0002	*
% viability	burn month	3	20.53	6.8	0.0023	*
	collection date	7	92.22	30.31	<0.0001	*
	month*date	18	91.77	1.37	0.1651	
% germination	burn month	3	105	16.24	<0.0001	*
	collection date	7	105	33.06	<0.0001	*
	month*date	18	105	2.77	0.0006	*
seed trap counts	burn month	3	20.1	19.4	<0.0001	*
	collection date	5	98.21	15.78	<0.0001	*
	month*date	15	98.2	2.48	0.0040	*

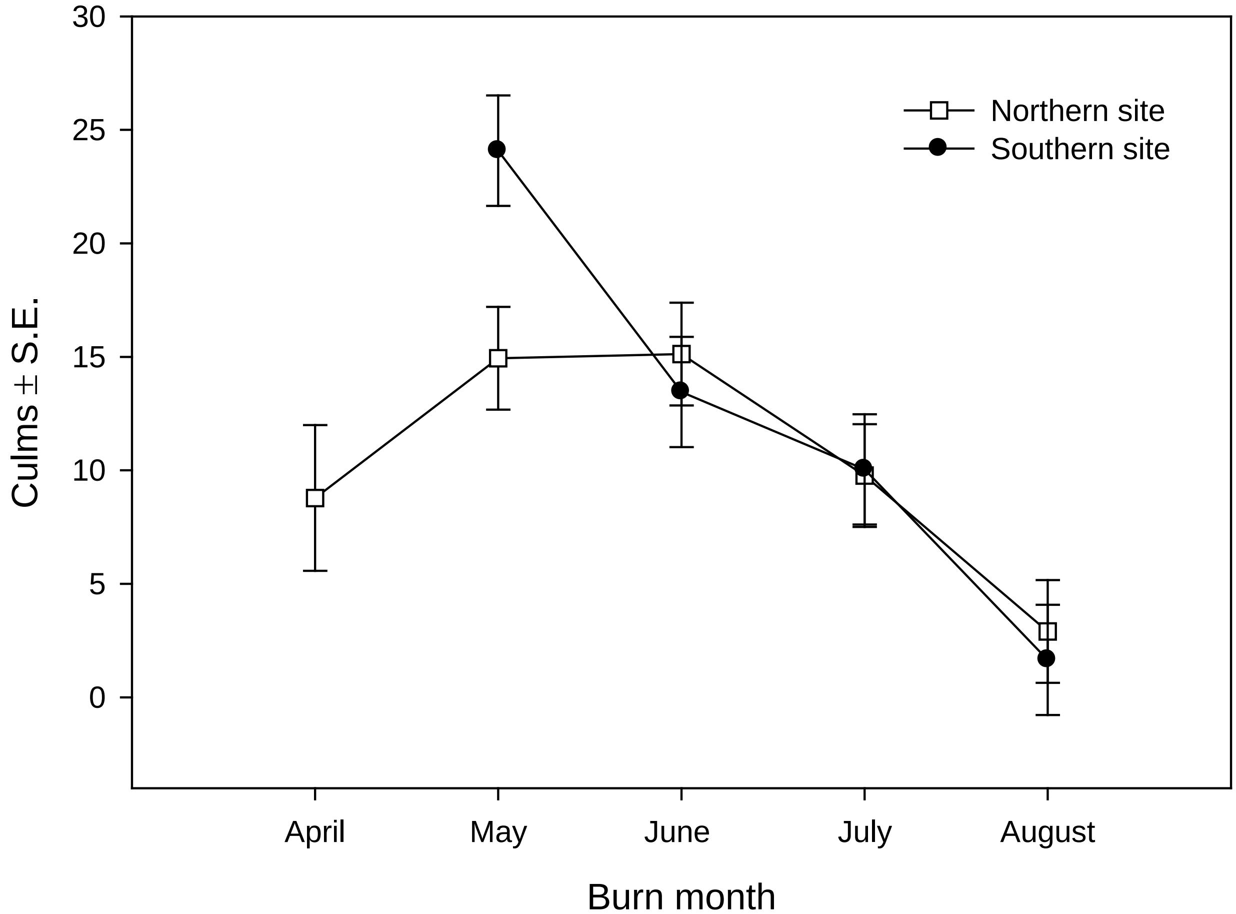

Figure 1-5. Number of culms per plant at both sites as related to burn month.

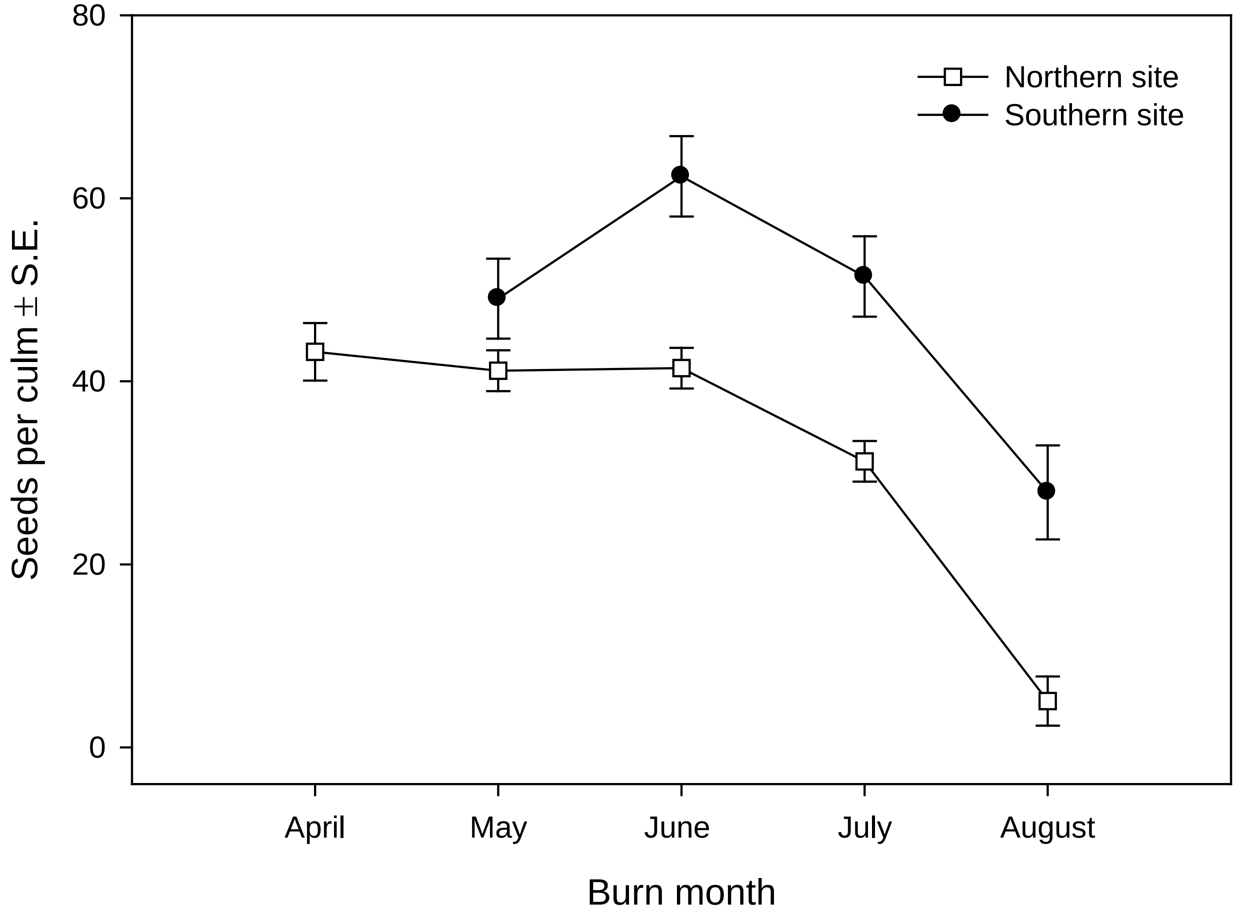

Figure 1-6. Number of seeds per culm at both sites as related to burn month.

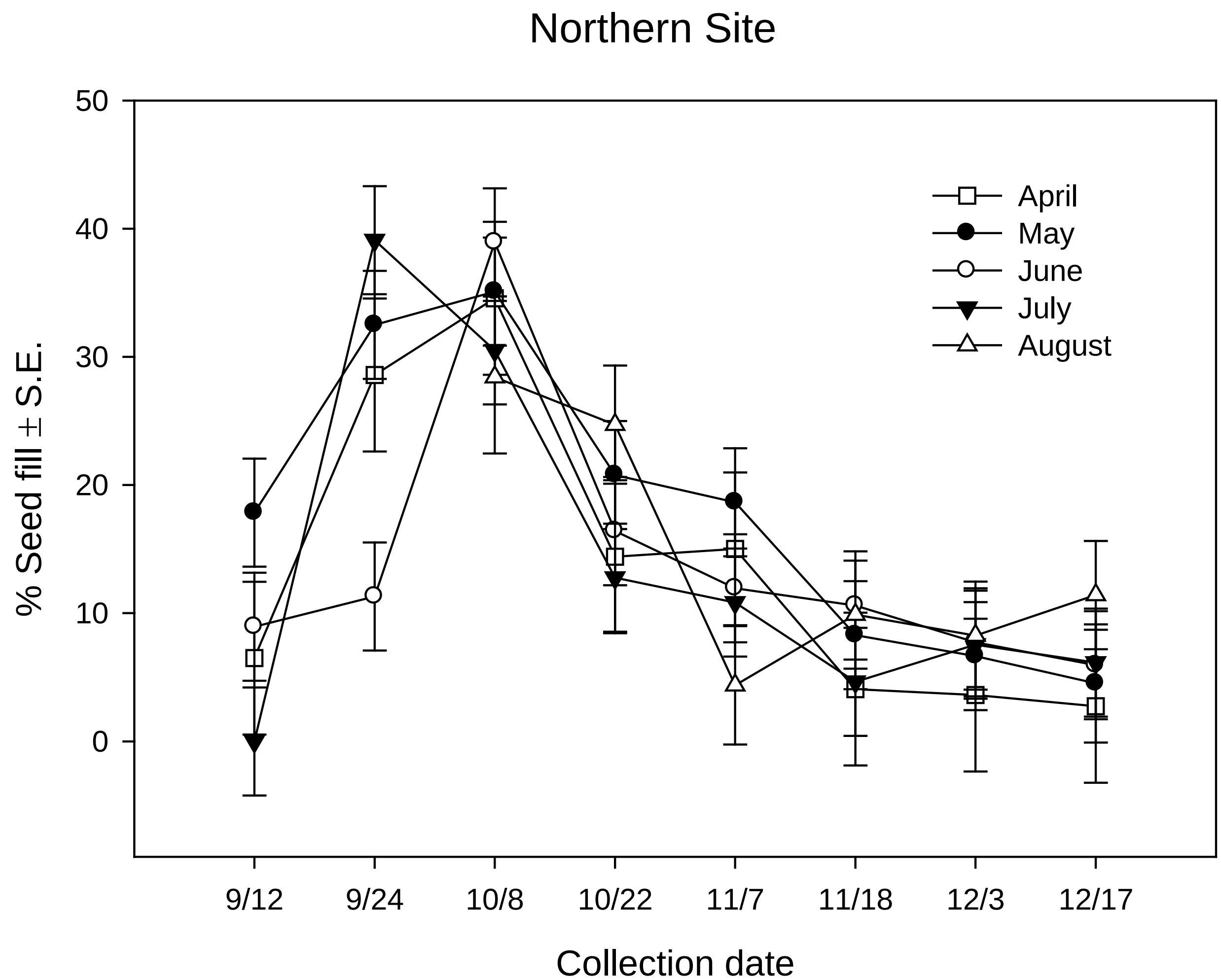

Figure 1-7. Percent seed fill of seed harvested from the stalk at the northern site as related to burn month and collection date.

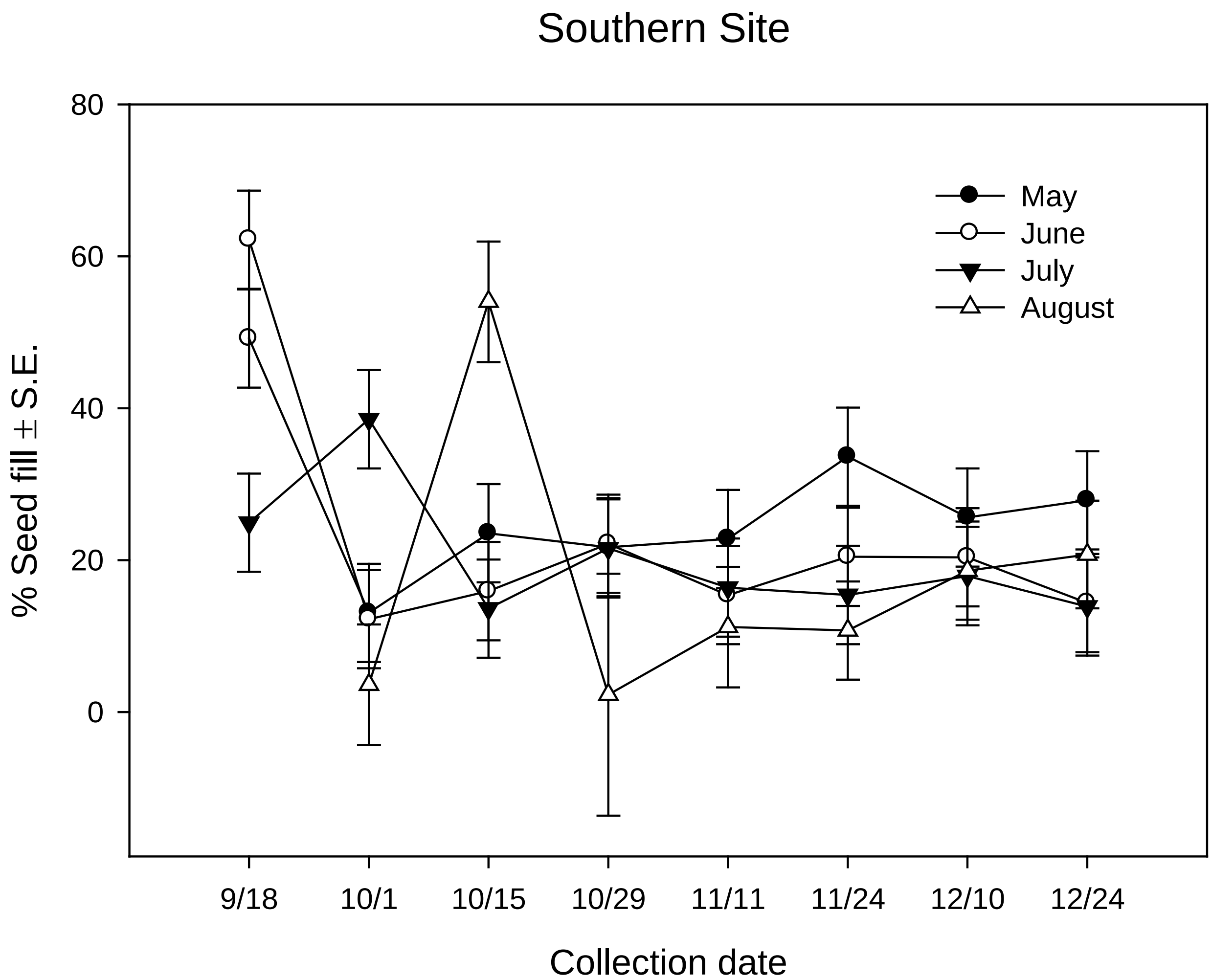

Figure 1-8. Percent seed fill of seed harvested from the stalk at the southern site as related to burn month and collection date.

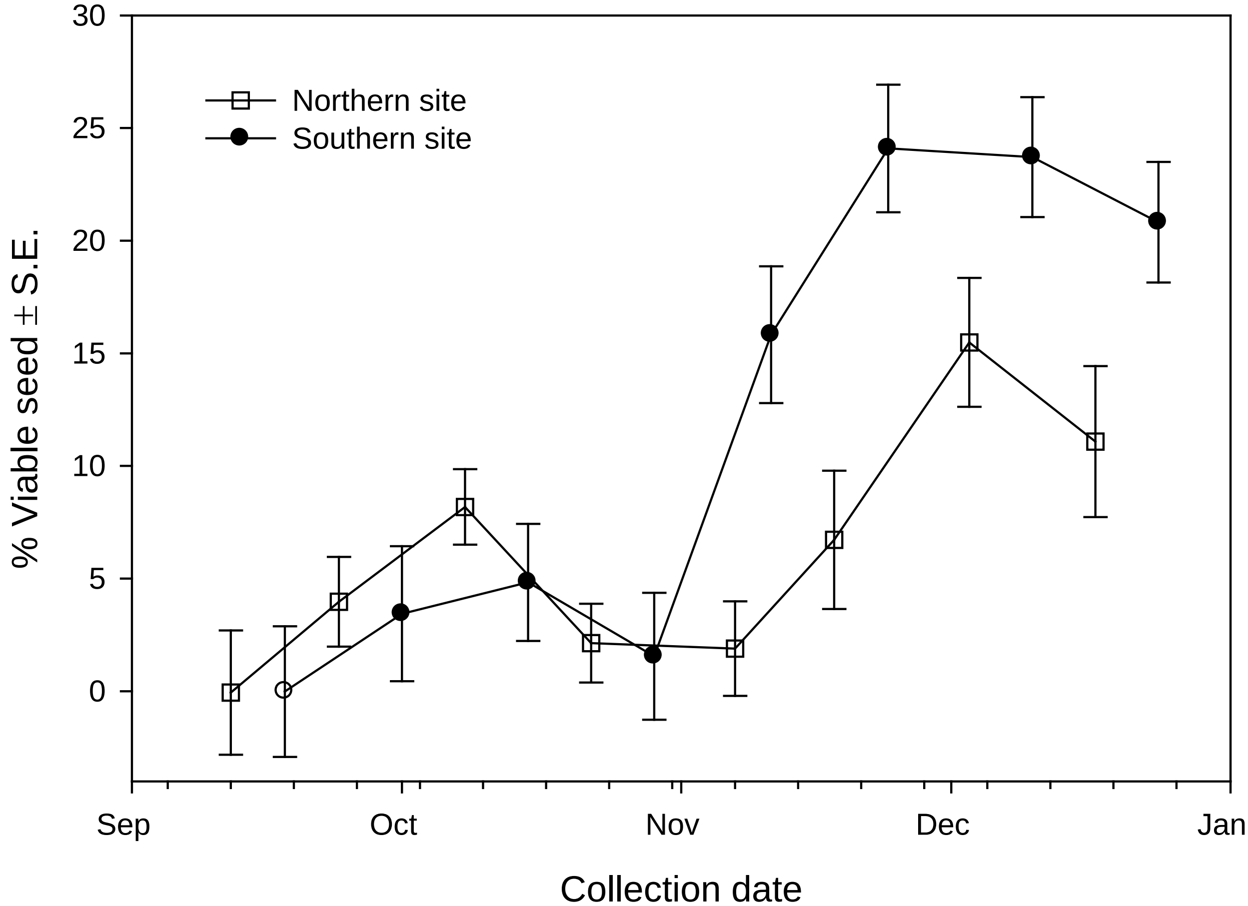

Figure 1-9. Percent viable seed of seed harvested from the stalk that was > 10% filled at both sites as related to collection date.

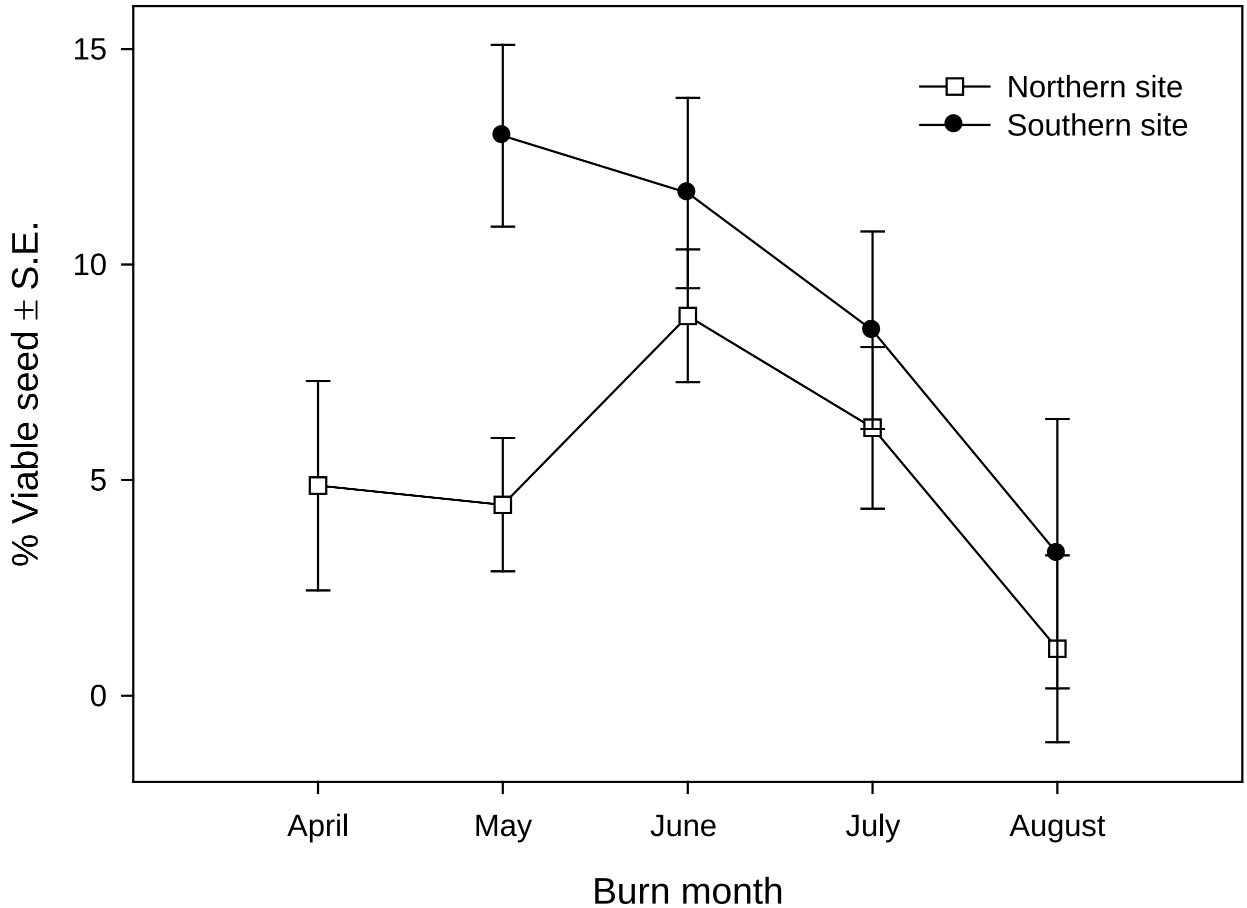

Figure 1-10. Percent viable seed of seed harvested from the stalk that was > 10% filled at both sites as related to burn month.

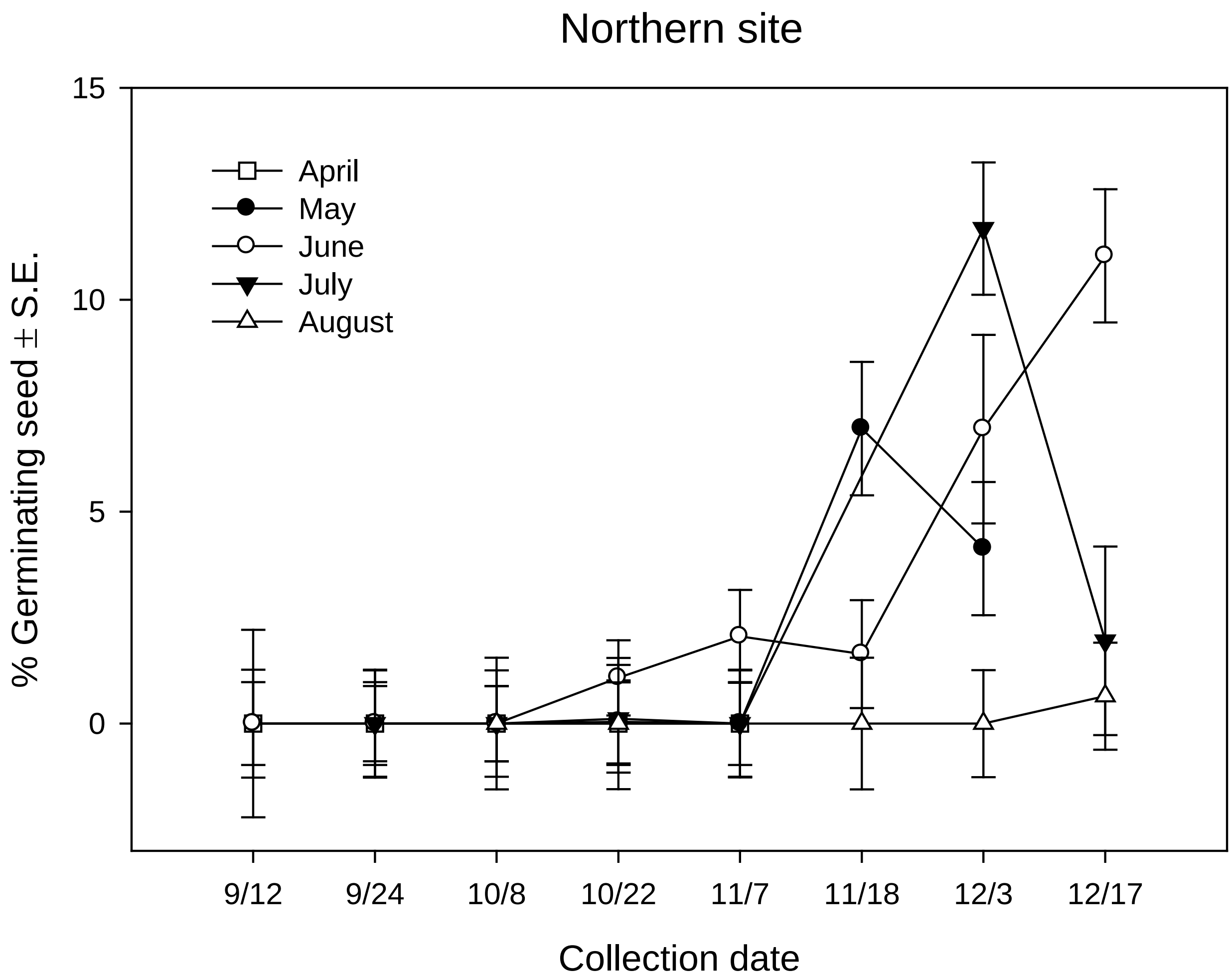

Figure 1-11. Percent germinating seed of seed harvested from the stalk that was > 10% filled at the northern site as related to burn month and collection date.

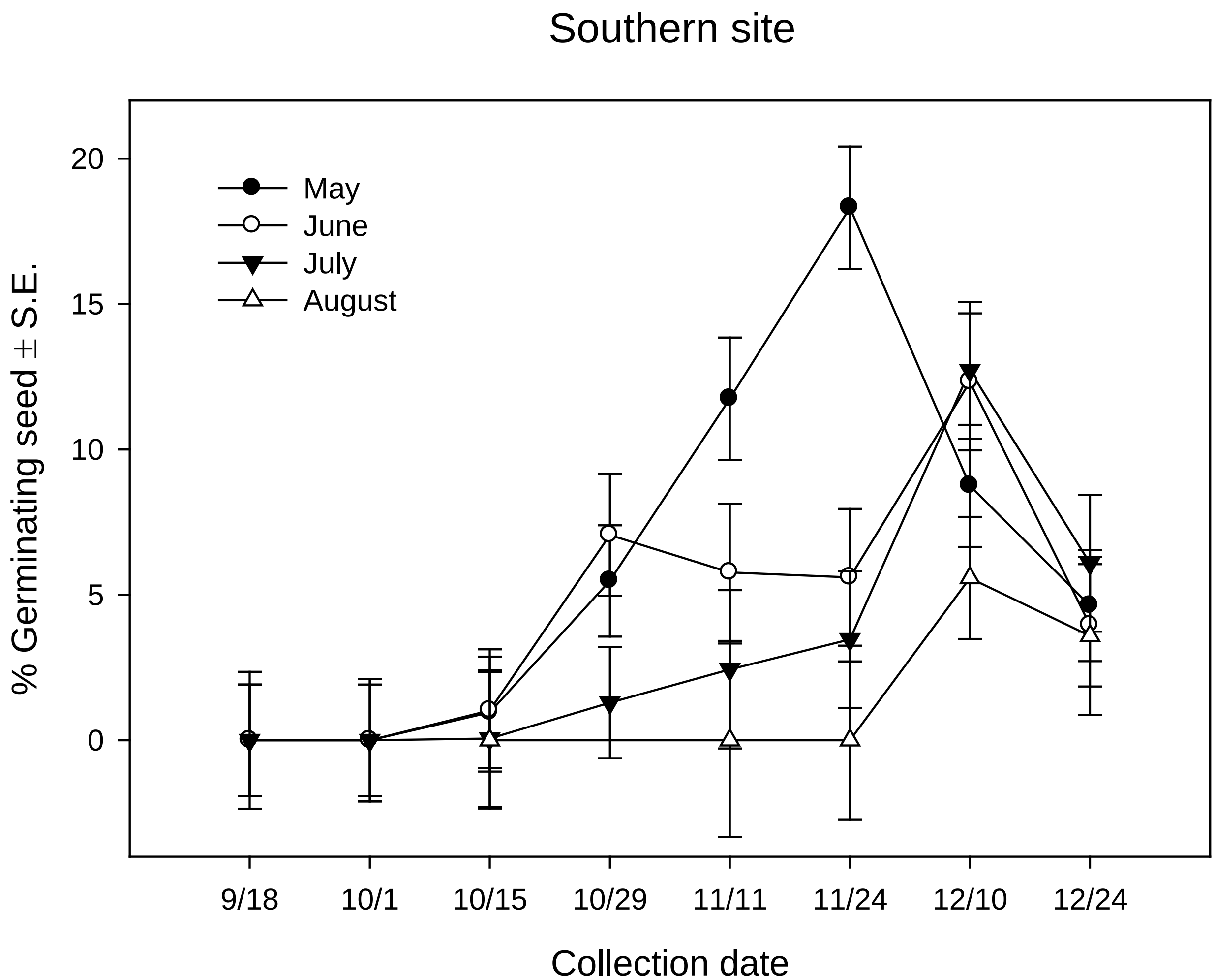

Figure 1-12. Percent germinating seed of seed harvested from the stalk that was > 10% filled at the southern site as related to burn month and collection date.

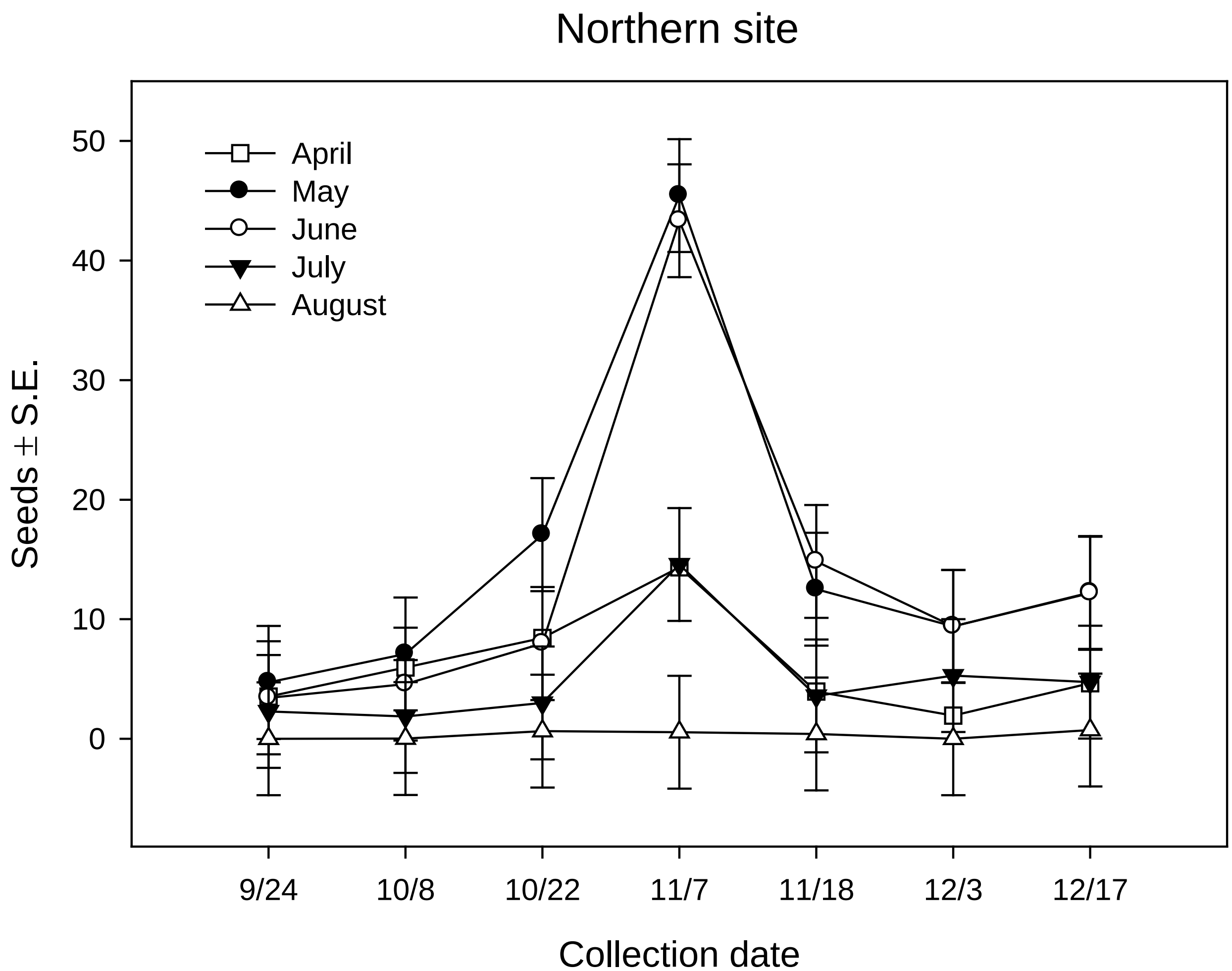

Figure 1-13. Number of seeds removed from seed traps at the northern site as related to burn month and collection date.

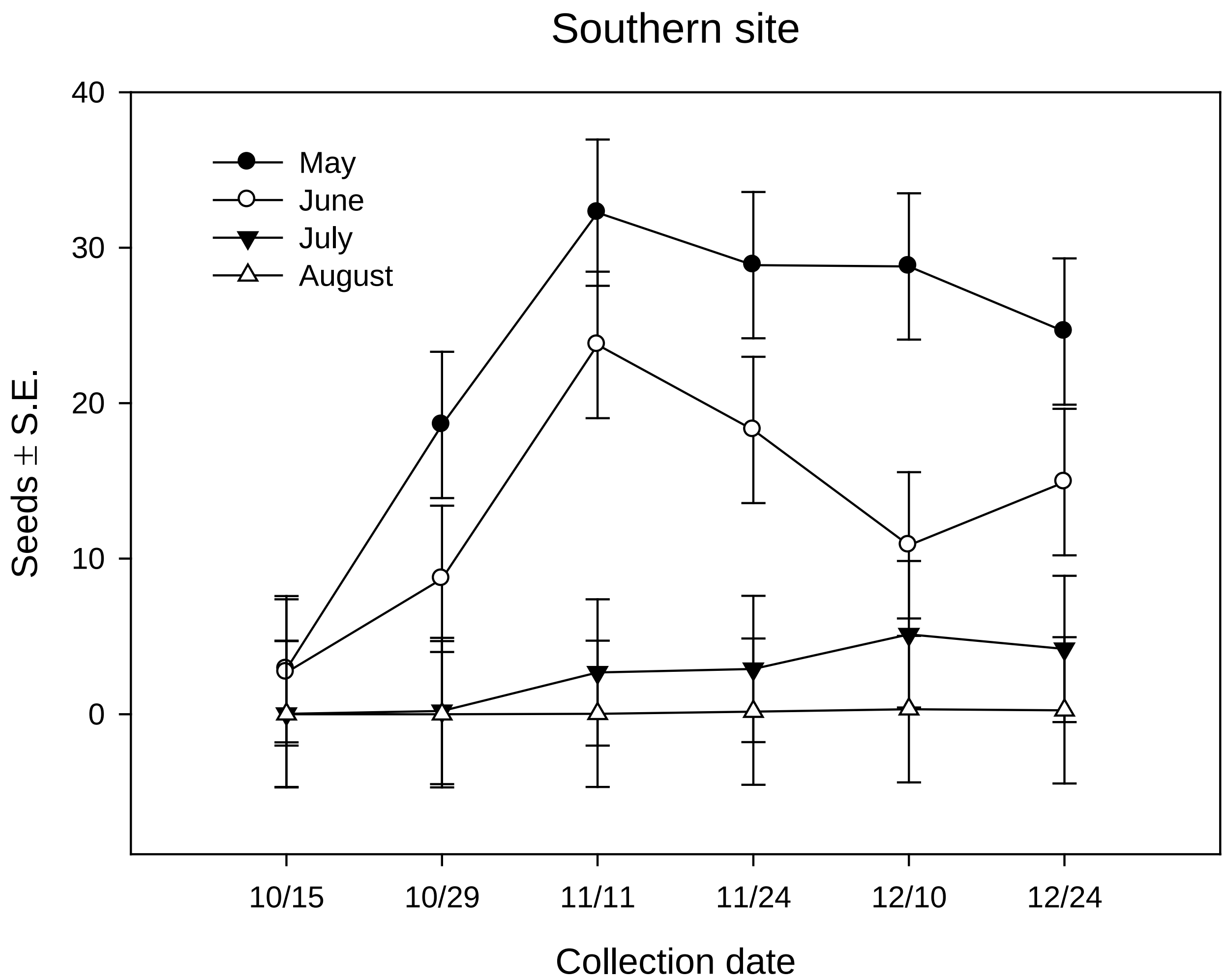

Figure 1-14. Number of seeds removed from seed traps at the southern site as related to burn month and collection date.

Table 1-3. ANCOVA and ANOVA results of the main effect of site on the number of culms per plant, number of seeds per culm, percent filled seed, percent viable seed and percent germinating seed (*significance at α = .05)

Response Variable	Source of Variation	ndf	ddf	F	p-value	
culms per plant	plant size	1	370.6	104.96	<0.0001	*
	site	1	47.42	2.84	0.0985	
	burn month	3	42.99	47.12	<0.0001	*
	collection date	7	328.4	1.1	0.3647	
seeds per culm	plant size	1	331.8	1.87	0.1720	
	site	1	44.69	22.75	<0.0001	*
	burn month	3	41.98	16.64	<0.0001	*
	collection date	7	293.7	0.83	0.5612	
% filled	site	1	42.31	22.67	<0.0001	*
	burn month	3	45.23	2.83	0.0487	*
	collection date	7	297.6	5.03	<0.0001	*
% viability	site	1	43.6	7.23	0.0101	*
	burn month	3	43.15	8.55	0.0001	*
	collection date	7	192.1	30.33	<0.0001	*
% germination	site	1	216	40.88	<0.0001	*
	burn month	3	216	17.64	<0.0001	*
	collection date	7	216	34.19	<0.0001	*

CHAPTER 3
EFFECTS OF SEED TREATMENTS ON WIREGRASS GERMINATION AND ESTABLISHMENT

Introduction

Wiregrass persists vegetatively for decades with sufficiently high light levels, only sexually reproducing when specific microsite conditions are favorable (Mulligan et al. 2002). A clearer picture of these conditions has emerged in recent years, but little is understood about seed characteristics that affect establishment. This knowledge is needed to improve direct seeding; a set of techniques that are increasingly showing potential for the restoration of wiregrass populations to thousands of hectares throughout the Southeast (Hattenbach et al. 1998). In the rapidly expanding field of groundcover restoration, there is considerable debate over the necessity of various seed treatments, and their effect on broadcast seeding rates and resulting yields (Walker and Stilletti 2006).

Environmental factors that limit natural seed germination and seedling establishment include soil moisture (Glitzenstein et al. 2001, Cox et al. 2004), light levels (Mulligan et al. 2002) and competition (Mulligan and Kirkman 2002, Asenbach et al. 2009). Under natural fire regimes, soil moisture is likely the most important environmental factor limiting seedling establishment and survival (Kirkman et al. 2001, Wenk 2009). Fires reduce competition and increase light at the ground level, thus creating conditions conducive for germination and establishment, given adequate rainfall. In addition to soil moisture, seed contact with the mineral soil surface reduces the likelihood of seedling desiccation (Fenner and Thompson 2005).

Given the importance of soil moisture for wiregrass establishment, natural mechanisms exist that minimize seedling desiccation. The presence of one or more awns on some grass seeds, including *Aristida* species, is thought to increase seed contact with the soil. Some awns are hygroscopically active, moving in response to varying levels of moisture. This movement can propel the seed both across and into the soil surface, increasing its chances of locating and becoming lodged in a microsite suitable for germination (Peart 1979). Both hygroscopically active and rigid, passive awns increase the likelihood that a seed will land in a position favorable for germination and establishment (Peart 1981). This position is standing as opposed to horizontal and results in burial of the base of the seed which facilitates rapid soil penetration of the seedling radicle. Clewell (1989) hypothesized that varying levels of moisture cause wiregrass seed awns to twist in a way that buries seeds, but this has apparently not been tested. Simpson (1952) demonstrated that 12 times as many *Danthonia penicillata* seedlings were produced when seeds were sown on a rough seed bed with hygrocopically-active awns intact compared to when awns were removed. She concluded that de-awned seed broadcast onto uncultivated soil would have lower planting success compared to broadcasting awned seed.

Wiregrass seed cleaning, in which awns are removed from the lemma, is necessary for large scale, mechanized plantings to facilitate seed movement through machinery (Pfaff et al. 2002). Cleaning large batches of wiregrass seed can be a complex, multi-step process, as it involves passing the seed through different sized screens (John Seymour, pers. comm.). Wiregrass seeds are small, brittle, and lightweight, making treatments, such as cleaning, to alter the seed difficult and costly (Bill Cleckley, pers. comm.). Nevertheless, successful seed cleaning allows for lower and less costly seeding rates per unit area because of the removal of lighter, low quality seeds or chaff (Loch 1993).

Awns may add little benefit when sowing onto well-prepared seed beds with an abundance of favorable microsites (Loch 1993). In support of this hypothesis, Peart (1981) found that the standing position afforded to *Aristida vagans* seed by the presence of rigid, passive awns, only favored establishment on a seed bed that was covered with litter, as opposed to bare mineral soil. Preparation of the seed bed is an important step in the direct seeding process designed to increase planting success and thus reduce planting rates. Depending on the initial site conditions, mechanical site preparation can include mowing, roller chopping, or disking (Trusty and Ober 2009). After sowing, rolling seed with a cultipacker, or commercial landscape roller, so it makes contact with the ground is also recommended (Seamon 1998, Cox et al. 2004). The use of these techniques when sowing cleaned seed may compensate for awn removal in large-scale direct seeding endeavors.

In addition to cleaning, seeds can be coated with a variety of materials, although this is a less common practice than cleaning. Seed coating improves metering capabilities (i.e. allowing for more controlled, uniform seed sowing) by increasing their weight and/or size and making their shape more elliptical or spherical (Loch 1993). The use of certain ingredients in the coating, such as acrylamide, a super-hydrating polymer, can impart moisture retention and/or nutrients, possibly increasing the chances of germination and establishment (Loch 1993). Previous research investigating seed coatings has not been widely applicable due to the lack of information on specific ingredients in these proprietary products (Scott 1989).

To clarify the need for seed treatments in preparation for direct seeding of wiregrass, I investigated germination of seeds that were either awned or de-awned and coated or uncoated. The objectives of this research were to 1) determine if the presence of awns increases the likelihood that wiregrass seeds will land in a position favorable for germination and establishment, and 2) demonstrate the effect of seed cleaning/coating on germination and establishment compared to cleaning alone.

Methods

Awn Experiment

To examine the role of awns in germination and establishment, a two-way (2 seed types x 2 soil preparations) factorial greenhouse experiment (18 replicates and repeated once), was conducted from March – August 2011. Seeds were cleaned in a mechanized process at Roundstone Native Seed, LLC (Upton, KY), a commercial seed cleaning company. For both seed treatments, only filled seeds were used as determined by conducting an enhanced forceps press test on every seed (Perez and Norcini 2010).

Eighteen trays were arranged in a completely randomized design on a single bench, approximately 1.2 m wide and 6 m long. All trays contained a mix of 10:1 potting soil to native soil. The native soil was moderately well drained Foxworth sand (thermic, coated typic quartzipsamments). Nine trays contained soil that was flat and compacted, while the other 9 trays contained soil that was cultivated with a hand garden trowel, creating a rough surface. Fifty cleaned seeds were dropped onto a randomly selected half of each tray, while fifty uncleaned seeds were dropped onto the other half. Seeds were dropped from 25 cm above the soil surface to mimic natural dispersal. Trays were watered from below to minimize disturbance to the soil surface and kept moist for the first three weeks, after which they were allowed to dry before being re-watered.

Seeds were monitored every day until three weeks post-planting which is when most germination occurred. For each seed that germinated, the date and its position were recorded. A seed was designated vertical if its embryonic axis was more than 22 degrees inclined from horizontal and its base was in contact with the soil. Seeds that were less than 22 degrees inclined from horizontal or that were not touching the soil with their base were designated horizontal. Newly germinated seeds were given a number and identified with a toothpick placed nearby in the soil. Seedling death was also noted. After three weeks, the point at which most germination had occurred, monitoring occurred every few days until 50 days (in the first experiment) or 40 days (in the second experiment) following the average date of germination. At this time, surviving seedlings were extracted from the soil, including the roots, and were dipped first in a solution of dish soap and water to rid them of soil and then in tap water. Each seedling was placed in a coin envelope, dried for 48 hours in an oven and then weighed.

Coating Experiment

To examine the effect of an artificial seed coating on germination and establishment, 900 cleaned seeds with a coating and 900 cleaned seeds without a coating were planted under either a relatively heavy or light watering regime. Seeds were coated in a mechanized process at Summit Seed, Inc. (Manteno, IL) with a material consisting primarily of finely ground limestone, plus acrylamide and an adhesive. Acrylamide is a water soluble, super-hydrating polymer with a crystalline structure that can absorb 400 times its weight in water (Stu Barclay, pers. comm.)

A randomized complete block design was used with 72 pots, 15 cm in diameter and 20 cm deep, arranged in three blocks in a greenhouse. Twenty-five randomly selected seeds of either the coated or uncoated treatment were sown 2 mm deep in pots containing native soil. To mimic xeric conditions under which a coating might provide more benefit, pots were watered from above to field capacity, every three days until 1 week following peak germination, and once a week thereafter. The heavy watering regime consisted of watering every other day to field capacity until one week following peak germination, and twice a week thereafter.

Pots were monitored daily for three weeks, followed by monitoring every few days, to record seedling survival. The date each seed germinated was recorded and seeds were tracked with a number on a toothpick placed nearby in the soil. Establishment was assumed at 40 days following the average date of germination and the entire biomass of the surviving seedlings was harvested, dried, and weighed according to the procedure outlined above. The experiment was repeated in the same fashion but the total number of planted seeds was reduced by half and blocking was omitted from the study design.

In both the awn and coating experiments, the same seed source and the same greenhouse were used. Seeds were harvested the previous fall, using a Flail-Vac Seed Stripper from a wet prairie site managed with growing season burns in the Florida panhandle and stored at room temperature in the dark until used. The greenhouse was located at the Gainesville campus of the University of Florida and provided shelter from wind and rain but did not regulate other environmental variables. A coating of white paint on the greenhouse and a tree canopy overhead provided moderate shade. Average evening temperature in the greenhouse was 33°C during the first replicate experiments (March – May) and 34°C during the second replicate experiments (June – August).

Statistical Analyses

A two-way ANOVA was used to test for main and interactive effects of awns and soil surface type on percent germination, days until germination, percent survival, and relative growth rate of the seedlings. In cases where awns had an effect on a response variable within the flat or cultivated soil type, the effect of position was added to the model in a separate ANOVA. All models were analyzed using the GLIMMIX procedure (v 9.2, 2008, SAS Institute), with the exception of the test of treatment effects on days until germination in the second awns experiment. To meet assumptions of normality for the ANOVA of these data, days until germination was log transformed and analyzed using the GLM procedure. Both procedures used mixed models, with awns, soil type, and seed position as fixed effects, and variation among soils types at the tray level as a random effect. For each half-tray, or experimental unit, the following response variables were included in the model: percent seeds that germinated, percent seedlings that survived, average number of days until germination, and percent germinating seeds that landed in a horizontal position. The first awn experiment had 35 experimental units, instead of 36, because one half-tray was accidentally overlooked at the time of planting.

A two-way ANOVA was used to test for main and interactive effects of seed coating and watering on percent germination, days until germination, percent survival, and relative growth rate of the seedlings. Response variables were averaged within each pot for analysis in a mixed model using the GLIMMIX procedure. The coating and watering treatments were included as fixed effects, while blocks were included as a random effect in the first experiment and only the residual errors were considered random effects in the second experiment.

In both the awn and the coating experiments, relative growth rate of each seedling was calculated as the number of days since germination divided by seedling mass in grams. Differences were assumed to be significant at $\alpha = 0.05$ and p-values were adjusted for multiple comparisons using the Tukey - Kramer adjustment method.

Results

Awn Experiment

Out of 1800 seeds planted in the first replication of the awn experiment, 375 germinated (21%). For percent germination, there was an interaction between awns and soil type (Table 2-1), with 6% more awned seeds germinating on the flat soil surface than de-awned seeds (Figure 2-1). Independent of awn or soil effects, seed position also affected percent germination ($p = .0249$). For half trays with awns, higher percentages of horizontal seeds increased germination of the seeds. There were no effects of awns or their interaction with soil type on days until germination, survival rates, or relative growth rates (Table 2-1).

Out of 1800 seeds planted in the second replication of the awn experiment, 180 germinated (10%). As in the first replicate, there was an interaction between awns and soil type for percent germination (Table 2-2). Three percent more awned seeds germinated than de-awned seeds on the flat surface and additionally, 4% fewer awned seeds germinated than de-awned seeds on the cultivated surface (Figure 2-1). Unlike in the first replicate, there was no additional effect of position on percent germination ($p = .2293$) and a much higher percent of germinating awned seeds landed in a vertical position (90% in the second replication compared to 66% in the first replication). There was also an interaction between awns and soil type for the percent of seedlings that survived, but there were no differences between awn treatments within soil types (Table 2-2). A main effect of awns on days until germination revealed that de-awned seeds germinated more quickly than awned seeds across both soil types ($p = .0402$, Table 2-2). There were no main effects of awns or their interaction with soil type for relative growth rate in the second replication (Table 2-2).

Additional tests were conducted on the seeds to explore potential causes for results obtained in the greenhouse experiment. Tetrazolium and germination tests (USDA Forest Service, National Seed Laboratory, Dry Branch, Georgia) on a random sample of 200 filled cleaned and uncleaned seeds each (identified with the press test), confirmed that the two seed types were of similar viability (68% viability and 30% germination rate). A random sampling of 50 seeds on each soil type at the time of planting revealed that roughly a third of awned seeds on both soil types landed in a horizontal position, while roughly half of the de-awned seeds landed in a horizontal position. Visual inspection of awned vs. de-awned seeds confirmed that the awns are hygroscopically active. Awned seeds lying on a paper towel that was repeatedly wetted and allowed to dry displayed considerable movement from initial positions over the course of 8 hours, while de-awned seeds displayed hardly any movement.

Coating Experiment

Out of 1800 seeds planted in the first replication of the coating experiment, 405 germinated (23%). There were no main or interactive effects of the seed coating on any of the response variables measured (percent germination, days until germination, percent survival, or relative growth rate) (Table 2-3). The heavy watering regime increased seed germination and survival (Table 2-3).

Out of 900 seeds planted in the second replication of the coating experiment, 204 germinated (23%). In contrast to the previous replication, there was a significant interactive effect of the coating and watering level on relative growth rate, with uncoated seeds having higher relative growth rate compared to coated seeds in the light watering treatment ($p = .0033$, Table 2-4). There were no other treatment effects on any other response variables in this replication (Table 2-4). Laboratory tetrazolium and germination tests on a random sample of cleaned, uncoated and cleaned, coated seeds revealed that the coated seeds had nearly twice the viability (60%) and germination rates (48%) as the uncoated seeds (33% viability and 26% germination).

Discussion

Few differences in wiregrass germination and establishment were found between cleaned and uncleaned seeds or between coated and uncoated seeds. The most notable difference was that 3 - 6% more awned seeds germinated on the flat soil surface. The higher germination rate of awned seeds on the flat surface was the only significant finding of seed treatment differences across both replications for either the awn or the coating experiments.

More awned seeds germinated than de-awned seeds in both replicate experiments, despite lower total germination in the second replication. Previous work has demonstrated that most wiregrass germination occurs during June - August, contrary to the results of this experiment (Coffey and Kirkman 2006). Germination rates in the second replication were likely suppressed by increased mold growth on the (mostly potting) soil as a result of higher ambient temperatures. Interestingly, awned seeds had a much higher likelihood of germinating under these harsh conditions in the second replication if they landed in a vertical position compared to the first replication. A smut fungus (*Sporosporium* spp.) commonly infects wiregrass seeds (Farr et a. 1989) and these results indicate that the vertical seed position afforded by the awns may aid in avoiding fungal pathogens.

There is considerable variation in the morphology and functionality of grass seed appendages. This study documented the hygroscopic nature of wiregrass seed awns. The presence of awns increases the likelihood that a seed will land in a position favorable for germination and establishment, while hygroscopically active awns are also capable of causing lateral seed movement across the soil surface as well as downward movement into the soil bed (Peart 1978, Ghermandi 1995). Indeed, in this study, awned seeds were observed to become buried in the soil over time.

These results concur with the findings of Peart (1979 and 1981) and Simpson (1952) that fewer *Poaceae* seeds germinate on a compacted surface when hygroscopic awns are removed. However, the germination differences between awned and de-awned seeds in this study were small compared to reports with other grass species. Simpson (1952) found that awn removal from *Danthonia penicillata* reduced germination by a factor of 12. In comparison, Peart (1978 and 1981) found much smaller proportional decreases in germination with removal of grass seed awns, but awn removal also resulted in lower survival rates, unlike in these experiments.

Certain characteristics of wiregrass may make removal of the awn less problematic compared to other grasses. For example, with awns removed, wiregrass seed dispersal units are smaller (< 2 mm), making them more likely to fall into tiny crevices where humidity is high and desiccation is less likely. In the absence of awns, wiregrass seeds lie flat on the soil surface and the contact:surface area ratio is larger for smaller seeds (Harper and Benton 1966). In addition, wiregrass seedlings exhibit rapid (pers. obs.) and extensive (Parrot 1967) root growth; characteristics particularly important for re-sprouting species found in fire-dependent communities (Mulligan and Kirkman 2002). Therefore wiregrass seed awns may not play as critical a role in natural recruitment of this species, compared to other grasses. Wiregrass appears particularly adapted for germination and establishment in the longleaf pine-wiregrass ecosystem, where moisture at the soil surface, not competition for space, limits recruitment (Kirkman et al. 2001, Kirkman et al. 2004).

These wiregrass seed adaptations may be one reason why coating cleaned seeds with a hydro-philic substance did not increase germination or establishment in this study. In addition, all seeds were buried 2mm in the soil, perhaps compensating for the benefit a coating might have provided to seeds lying on the soil surface. Interestingly, laboratory tests of tetrazolium viability and germination rates showed the coated seeds to be nearly twice likely to germinate as the uncoated seeds. Previous investigations of this same coating on *Poa pratensis* (Kentucky bluegrass) seeds also found a diminished effect of the coating on germination in a greenhouse, as compared to a laboratory (OSUSL 2010). It may be that benefits of this seed coating are not conferred under field conditions and more research is needed to test its efficacy before wide-spread use is encouraged. It should be noted, however, that there were problems with the coating process reported by Summit Seed, Inc. due to the small number of seeds sent for coating.

CHAPTER 4
CONCLUSION

Land managers should consider burning Florida wiregrass populations in May and June to maximize viable seed production. Burning in June may be more advantageous in north Florida, while central Florida wiregrass populations may produce more high quality seed from May burns. The results of this study favored burning wiregrass during May and June at both study sites, despite summer drought conditions at the northern site. Nevertheless, these results should be confirmed with future studies during normal weather patterns.

At both sites, filled seed percent had peaked by late October and by mid-November, most of the seed had been shed, although viability of harvestable seed remained low at this time (2 - 15%). Higher percentages of seed viability (15 -25%) later in the season were likely due to patterns of seed rain and heightened maturation of seed over time. Based on these results, wiregrass seed harvesting should be conducted around the first week in November to ensure the greatest amount of seed is collected, despite potentially modest increases in seed quality later in the season.

Wiregrass seed cleaning, in which awns are mechanically removed, is recommended prior to direct seeding; whereas application of a seed coating to increase moisture retention is not recommended at this time. This study found that awns caused a slight increase (3 – 6%) in germination of seeds on a flat soil surface, indicating that broadcasting cleaned seeds onto an uncultivated surface may result in decreased germination rates compared to broadcasting uncleaned seed. Seed cleaning is still recommended to facilitate movement of seed through broadcasting machinery; however, seed bed cultivation and drilling seed into the soil should also occur to ensure maximum planting success. While seed coating may improve metering capabilities during sowing, this study found no evidence for a benefit of a super-hydrating polymer coating in wiregrass germination and establishment. Additional coating treatments and field testing is required prior to recommending such an investment.

Table 2-1. ANOVA results of the effects of awns and soil type on % germination, days until germination, % survival, and relative growth rate (rgr) of seedlings in the first replicate experiment, which occurred from March - May 2011 (*significance at α = .05)

Response Variable	Source of Variation	ndf	ddf	F	p-value	
% germination	awns	1	15.71	0.37	0.5492	
	soil	1	16.01	2.38	0.1425	
	awns*soil	1	15.71	6.26	0.0238	*
	planned contrasts:					
	(flat soil - no awns) vs. (flat soil - yes awns)			5.07	0.0395	*
	(cult. soil - no awns) vs. (cult. soil - yes awns)			1.71	0.2089	
days until germination	awns	1	15.87	1.96	0.1804	
	soil	1	16.26	7.93	0.0123	*
	awns*soil	1	15.87	0.31	0.5866	
% surviving	awns	1	15.63	0.23	0.6387	
	soil	1	15.98	2.99	0.1032	
	awns*soil	1	15.63	1.00	0.3329	
rgr	awns	1	16.01	2.08	0.1689	
	soil	1	16.09	1.82	0.1964	
	awns*soil	1	16.01	1.82	0.1963	

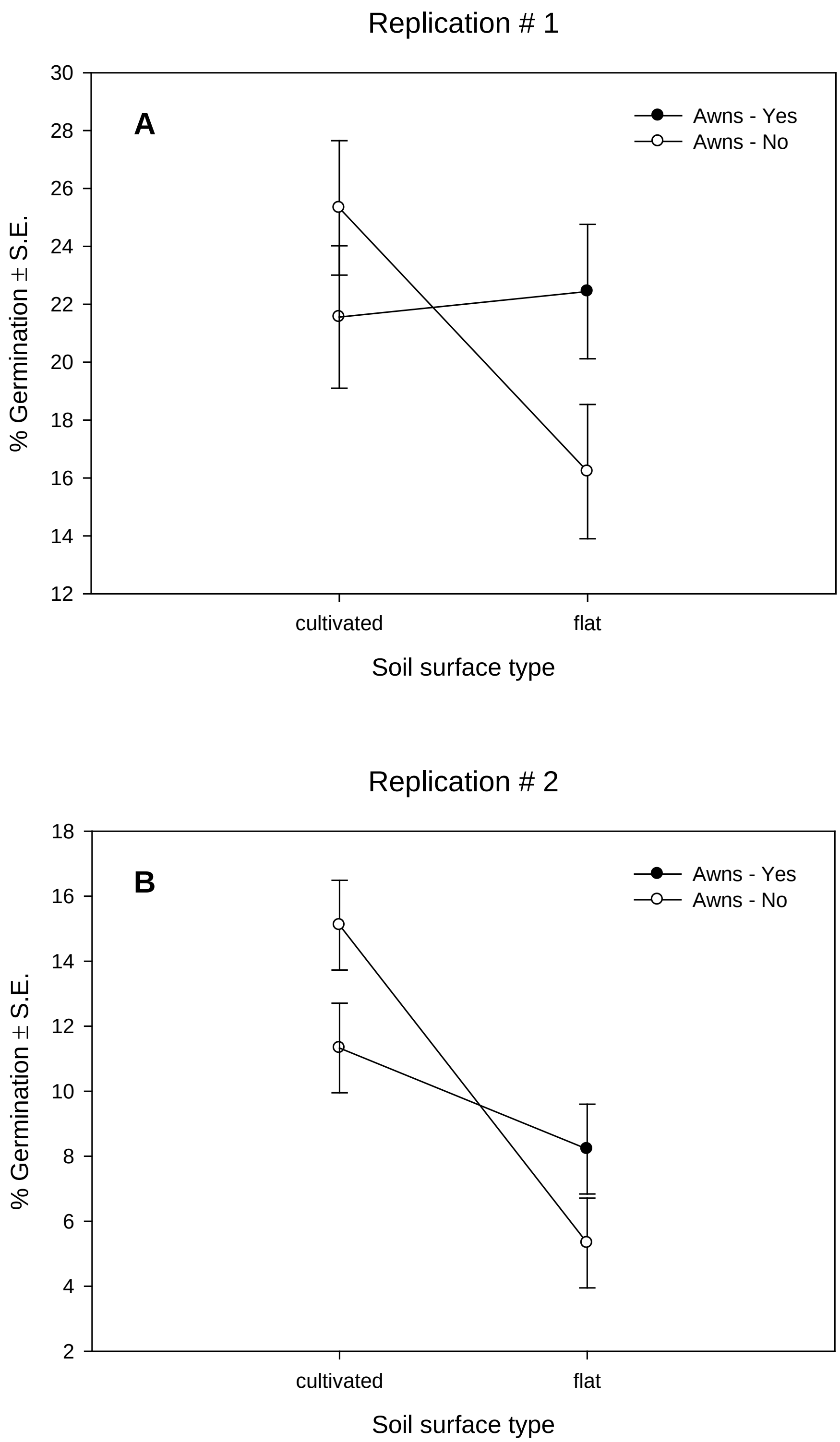

Figure 2-1. Percent germination of seeds with and without awns planted on a flat and cultivated soil surface in the A) first replicate experiment, which occurred from March – May 2011 and B) second replicate experiment, which occurred from June – August 2011.

Table 2-2. ANOVA results of the effects of awns and soil type on % germination, days until germination, % survival, and relative growth rate (rgr) of seedlings in the second replicate experiment, which occurred from June - August 2011 (*significance at α = .05)

Response Variable	Source of Variation	ndf	ddf	F	p-value	
% germination	awns	1	16	0.32	0.5822	
	soil	1	16	13.05	0.0023	*
	awns*soil	1	16	17.73	0.0007	*
	planned contrasts:					
	(flat soil - no awns) vs. (flat soil - yes awns)			6.66	0.0201	*
	(cult. soil - no awns) vs. (cult. soil - yes awns)			11.39	0.0039	*
% surviving	awns	1	16	0.02	0.9021	
	soil	1	16	10.12	0.0058	*
	awns*soil	1	16	4.52	0.0495	*
	planned contrasts:					
	(flat soil - no awns) vs. (flat soil - yes awns)			2.53	0.1312	
	(cult. soil - no awns) vs. (cult. soil - yes awns)			2.00	0.1765	
rgr	awns	1	12.94	1.56	0.2337	
	soil	1	13.86	1.01	0.3320	
	awns*soil	1	12.94	1.65	0.2211	

Response Variable	Source of Variation	df	Sums of Squares	Mean Square	F	p-value	
days until germination	awns	1	1.0314	1.0314	4.99	0.0402	*
	soil(tray)	16	2.4667	0.1542	0.75	0.7183	
	soil	1	1.6201	1.6201	7.83	0.0129	*
	awns*soil	1	0.2069	0.2069	1.00	0.3322	

Table 2-3. ANOVA results of the effects of watering and seed coating on % germination, days until germination, % survival, and relative growth rate (rgr) of seedlings in the first replicate experiment, which occurred from March - May 2011 (*significance at $\alpha = .05$)

Response Variable	Source of Variation	ndf	ddf	F	p-value	
% germination	coating	1	68.00	0.06	0.8092	
	water	1	68.00	10.62	0.0017	*
	coating*water	1	68.00	0.45	0.5054	
days until germination	coating	1	66.08	1.43	0.2354	
	water	1	66.08	3.30	0.0736	
	coating*water	1	66.00	0.99	0.3233	
	coating	1	66.09	0.26	0.6096	
% surviving	water	1	66.09	26.29	<0.0001	*
	coating*water	1	66.00	0.79	0.3775	
	coating	1	56.16	0.05	0.8203	
rgr	water	1	57.28	0.01	0.9202	
	coating*water	1	56.09	1.95	0.1686	

Table 2-4. ANOVA results of the effects of watering and seed coating on % germination, days until germination, % survival, and relative growth rate (rgr) of seedlings in the second replicate experiment, which occurred from March - May 2011 (*significance at α = .05)

Response Variable	Source of Variation	ndf	ddf	F	p-value	
% germination	coating	1	32	2.15	0.1521	
	water	1	32	0.00	1.0000	
	coating*water	1	32	0.01	0.9108	
days until germination	coating	1	32	0.35	0.5580	
	water	1	32	0.00	0.9941	
	coating*water	1	32	0.49	0.4877	
% surviving	coating	1	32	2.27	0.1419	
	water	1	32	0.14	0.7090	
	coating*water	1	32	0.02	0.9009	
rgr	coating	1	32	2.72	0.1086	
	water	1	32	3.18	0.0838	
	coating*water	1	32	8.04	0.0079	*
	planned contrasts:					
	(light water - no coating) vs. (light water - yes coating)			10.06	0.0033	*
	(heavy water - no coating) vs. (heavy water - yes coating)			0.70	0.4084	

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BIOGRAPHICAL SKETCH

Emily Rodriguez has lived all her life in Gainesville, Florida; a community with a longstanding tradition of progressive land conservation. She received a first-rate education in the International Baccalaureate program and at the University of Florida before working for five years at the Alachua County Library District Headquarters. Serving the public at the downtown branch was an eye-opening and rewarding experience that deepened her love of libraries. While working at the library, Emily began volunteering at the City of Gainesville's Nature Operations Division and at the Gainesville Clean Water Partnership where she discovered her passion for protecting the environment. This led her to pursue a graduate education, specializing in Forest Ecology and Wetland and Water Resource Management. She hopes to gain work experience as a land manager before contributing to the development of sustainable environmental policies.