

Investigating a Possible Arrested Succession in a Desert Grassland
Following Prescribed Burns: Muleshoe Ranch, Arizona

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Abstract

The Muleshoe Ranch is a cooperatively managed Nature Conservancy Preserve located in the desert grassland of southeastern Arizona. The desert grassland ecosystem is sensitive to change, as the species composition is dependent on the set of conditions particular to this region (McClaran and Van Devender 1995, Gonzales 2006). There was a prescribed burn several years ago at the Muleshoe Ranch, after which annual dicots began to grow in some habitats. It is natural for annual plants to dominate at first, while the perennials recover after a fire (McClaran and Van Devender 1995); in this case however, some patches remain dominated by annuals. The species of perennial grasses used in this study include; *Bouteloua curtipendula* (sideoats grama), *Muhlenbergia porteri* (bush muhly), *Bouteloua eriopoda* (black grama), *Bouteloua chondrosoides* (spruce-top grama) and *Aristida ternipes* (spider-grass). Differences between soils from habitats dominated by perennial grasses and annuals were examined. Germination experiments were performed in the laboratory and in the field to compare the growth of perennial grass species in soil from the different habitat types. Paired annual and grassy transects in two different locations were used to assess overall abundance of all plant species (June 2008) and biomass (August 2008). Results indicate a difference in soil electrical conductivity between sites. Germination was not significantly affected by habitat type. The frequency of perennial grasses was greater in transects in grassy habitats versus annual habitats. Biomass from the transects showed no significant patterns. It is important to understand what is happening to the plant community so that the Muleshoe Ranch can continue to be restoratively managed, and the natural desert grassland community can persist (Suding et al. 2004).

Introduction

Fires occur naturally in desert grasslands, but have been suppressed by humans (McClaran and Van Devender 1995, Bahre 1991, Humphrey 1949). Plant species composition may change substantially with changes in fire frequency (McClaran and Van Devender 1995, McAuliffe 1994). Fire suppression has changed the composition of many desert grassland plant communities often favoring woody species (McClaran and Van Devender 1995, Archer 1989, Brown 1982). Woody plants are able to survive to maturity because fires are not frequent enough to kill them when they are young, and woody growth allows them to be more tolerant of future fires (McClaran and Van Devender 1995).

In the desert grassland prescribed burns are used as a restoration technique to control the growth of woody plant species (Moyes et al. 2005). Prescribed burns encourage the growth of native perennial grasses that are tolerant of fire or have adopted reproductive strategies that allow them to increase in abundance following fire. Grasses generally recover to preburn levels within three years (McClaran and Van Devender 1995, Cable 1967, Wright and Bailey 1982). However, annual dicots are also adapted to fire and may dominate for the first few years after a burn while perennial grasses recover (Gonzales 2006, McClaran and Van Devender 1995, Bock and Bock 1990, Bock et al. 1976). For example, Drewa and Havstad (2001) found that perennial grass cover decreased by 30% while annual cover increased by 10% four years after a burn. Sometimes, however, annual dicots dominate for several years or more and perennial grasses do not increase in relative abundance, a pattern that I will hereafter refer to as arrested succession.

The term arrested succession was first used by Niering and Goodwin (1974) to describe the succession of an abandoned pastureland into shrubland and forest, but has since been used in a variety of ecological systems (Paul et al. 2004, Acácio 2007). The mechanisms behind arrested succession and other changes in plant communities are not well understood, which makes it difficult to restore the desert grassland ecosystem (Suding et al. 2004). One possible cause of arrested succession may be a positive feedback which occurs when the conditions at a site are altered by the plant community present in a way that favors the persistence of that community (Suding et al. 2004). Assuming that the soils colonized by the annual dicots and those colonized by the perennial grasses were initially the same, a positive feedback could occur if the plants present in one type of habitat change the conditions in that habitat to favor their growth over the growth of plants present in other habitats. For example, some annual dicots may produce litter that inhibits the growth of perennial grasses in areas where annual dicots are established (Hovstad and Ohlson 2007). The presence of annual dicots may change basic soil properties such as nutrient levels to favor the growth of more annual dicots. The microbial community could have been disrupted by the growth of annual dicots as well (Snyder et al. 2002). Perennial grasses also have the potential to cause a positive feedback. Established perennial grasses facilitate the growth of more perennial grasses by providing a moist microclimate for germination (Marone et al. 2000). Alternatively, initial differences could have existed between soils from habitats dominated by annual dicots versus perennial grasses.

It is important to understand how conditions at the site both past and present affect the current plant community in order to return the site to its original state in the

most effective manner. The total amount of precipitation and temperature in the years before and after the fire are very important to the regeneration of perennial grasses (Drewa et al. 2006, Geiger and McPherson 2005). Perennial grasses could be negatively affected by low precipitation or extreme temperature in the years before or after a fire. In a montane desert ecosystem germination of all plants is greater in wetter years, but while perennial grasses tend to germinate year round, annuals germinate in warmer temperatures (Marone et al. 2000). Thus, a trend towards warmer temperatures could favor the germination of annuals over perennial grasses.

Grazing by cattle and other ungulates is another important factor that destabilizes the desert grassland ecosystem (McClaran and Van Devender 1995). Grazing has been shown to cause changes in the plant community composition throughout the desert grassland (Roundy and Jordan 1988). It can affect the stability of the soil by causing erosion (Ludwing et al. 2000). In the desert grassland intense grazing reduces the abundance of perennial grasses and increases the abundance of woody dicots when compared to protected areas (Smith and Schmutz 1975). Native plants tend to do worse than non-native plants under intense grazing, and protection from grazing can reduce invasion by non-native species (Bock et al. 2007). Populations of perennial grasses in grazed sites may have lower genetic variability compared to populations in ungrazed sites (Aguado-Santacruz et al. 2004). Animals also change nutrient balances through their excrement (Willott et al. 2000, Afzal and Adams 1992, Williams and Haynes 1995, Lovell and Jarvis 1996). Intense over-grazing in combination with drought might reduce the chances that a population of perennial grasses will survive (Biondini and Manske 1996).

In this study I investigated a possible arrested succession in a desert grassland ecosystem at Muleshoe Ranch, located in southeastern Arizona's Galiuro Mountain Range. The Muleshoe Ranch is cooperatively managed by the Nature Conservancy (TNC), the Bureau of Land Management and the Coronado National Forest and includes 49,120 acres of desert grasslands between the Sonoran and Chihuahuan Deserts (www.nature.org). Although the Muleshoe Ranch is not actively grazed today, a past history of grazing exists on most of the property. A series of prescribed burns took place at different locations within the Muleshoe Ranch over the past decade. In some habitats the prevalence of perennial grasses increased after the burn, as expected. However, in other habitats the perennial grasses that commonly dominate this type of ecosystem declined after the burn, and annual dicots began to dominate these habitats instead (Bob Rogers, TNC Arizona, personal communication). This pattern of arrested succession has emerged in different locations throughout the ranch.

The purpose of this study was to compare habitats at the Muleshoe Ranch that are dominated by annuals versus perennial grasses. I compared basic soil properties including pH, electrical conductivity and texture. To test the possibility of a positive feedback mechanism germination of perennial grasses in soil from the two different habitat types was examined. Two germination studies were conducted; once in the laboratory where germination could be observed more accurately, and once in the field at Muleshoe Ranch in order to test germination under natural conditions. If the grasses responded differently to the two different soils in the laboratory or when planted in different habitats in the field, this could indicate other possible differences in the soils or the site conditions which could then be investigated further. In addition, transects were

set up in both grassy and annual habitats to characterize the plant community. Paired transects were used in annual and grassy habitats to provide a basis for comparison of the two habitat types.

Methods

Soil Collection

Two separate sets of soils were collected. The first set of eight soil samples was taken from four different locations. Three of the locations were ungrazed at the Muleshoe Ranch and one location was a nearby grazed ranch. Within each location two samples were taken; one from a habitat dominated by annuals and one from a habitat dominated by perennial grasses. A small portion of soil from the first collection was put aside in order to characterize the soils and the remaining soil was used for a germination experiment in the laboratory. A second set of sixteen soil samples was collected from three additional locations; two of these locations were at the Muleshoe Ranch and one was at a nearby, actively-grazed ranch. Six samples were taken from the locations at the Muleshoe Ranch; three from habitats dominated by perennial grasses and three dominated by annuals. Four samples were taken from the active ranch; two from habitats dominated by perennial grass and two dominated by annuals.

Soil Analyses

Soils were analyzed for pH, texture and electrical conductivity. All samples were air dried and sieved (2mm) to remove stones and organic debris. To measure pH 15g of soil was mixed with 30ml of deionized water (Donald Zak, University of Michigan, Personal Communication). This slurry was allowed to sit for 30 minutes and pH was measured using a pH meter (ThermOrion). Three replicates were measured for each soil

sample. Soil texture was measured using the hydrometer method (Donald Zak, University of Michigan, Personal Communication). 50g of soil was placed in an Erlenmeyer flask and wetted with tap water, and 100ml of a 5% sodium hexametaphosphate solution was added to the slurry. This slurry was then transferred to a metal blender cup and water was added to the slurry until the cup was 2/3 full. The slurry was blended for approximately five minutes and then transferred to a 1,000ml sedimentation cylinder. Water was added to fill the cylinder to 1,000ml. The slurry was then thoroughly mixed with a plunger and the hydrometer was inserted. Three hydrometer readings were taken in 40 second intervals after the hydrometer was initially inserted and one additional reading was taken two hours later. Temperature was recorded and the necessary corrections were made if the temperature deviated from 60°F. Electrical conductivity was measured using the soil extraction method (Donald Zak, University of Michigan, Personal Communication). Deionized water was added to 200g of soil until the slurry was fully saturated. After four hours this slurry was placed in a centrifuge and the water was extracted. One drop of a 0.1% sodium hexametaphosphate solution was added to each 25ml of extract and conductivity was measured using an electrical conductivity meter (Orion Model 122).

Laboratory Germination Experiment

A growth chamber experiment was used to test the effects of the habitat type of the soil on germination. Seeds were grown in a one inch layer of soil placed over a layer of sand in 2 ¼" pots. Sterile sand was used to increase the number of possible replicates with the soil available. The effects of the different soil treatments were tested on three different perennial grass species common in the area; *Bouteloua curtipendula* (Michx.)

Torr., *Muhlenbergia porteri* Scribn. ex Beal, and *Aristida ternipes* Cav (See species profiles below). Ten seeds from *B.curtipendula* and *A. ternipes* and approximately 40 seeds of *M. porteri* were planted in each pot. Each soil treatment and species combination was replicated 10 times for a total of 240 pots. Pots were placed in trays on shelves in the growth chamber and were bottom watered to minimize fungal growth. Watering was generous so that it was not a limiting factor of germination. The growth chamber was kept at approximately 30°C 16 hours per day with the growth lights on and 18°C 8 hours per day with the growth lights off, the most favorable temperature and light conditions for the germination of these three species according to the Fire Effects Information Systems database (www.fs.fed.us/database/feis/index.html). Fifteen days after germination seedlings were thinned to a single individual and up to five of the thinned seedlings were collected, dried, and roots and shoots were weighed for biomass. After thirty days the roots and shoots of the isolated seedlings were collected, dried, and weighed for biomass.

Field Germination Experiment

The field portion of this study took place in the summer of 2008. In June, two locations within the Muleshoe Ranch were selected based on information from a previous study (David Gori, TNC New Mexico, Personal Communication) that indicated that the number of annuals at these locations had increased after the locations were burned. Both locations had a similar slope and aspect (40-45°, SW). Six 1m by 1m germination plots were set up at both locations, for a total of twelve plots. In each location three of the plots were in annual habitat types and three were in grassy habitat types. The perennial grass species used in the germination plots were *Bouteloua curtipendula* (Michx.) Torr.,

Bouteloua chondrosoides (Kunth) Benth. ex S. Watson and *Bouteloua eriopoda* (Torr.) Torr. (See species profiles below). The 1m by 1m plot was divided into four subplots and each of the three species and a control were randomly assigned to a subplot. Fifty seeds from a species were planted in a subplot under the existing litter. A small amount of soil from the surrounding area was scattered over the seeds. Nothing was planted in the control subplot, but a thin layer of soil was scattered over it to account for effects of disturbance.

Species Profiles

All seeds were obtained from Wildlands Restoration located at 2944 N. Castro, Tucson, Arizona 85705. Their telephone number is (520)-882-0969.

Muhlenbergia porteri (Bush Muhly) has been described by Aleksoff (1999). This perennial grass regenerates mostly by seeds and does not have rhizomes. It is shade tolerant, and is often found growing under woody shrubs in the desert grassland. It is not tolerant of grazing. It germinates best when temperatures alternate between 20°C at night and 35°C during the day. Germination from seed takes place from February to April. Flowering occurs from April to May and seeds begin to appear in September.

Bouteloua curtipendula (Sideoats Grama) has been described by Chadwick (2003). This is one of the dominant perennial grass species at Muleshoe Ranch. It regenerates from seeds, rhizomes and tillering. There is often a mass flowering two to three years after a fire, however germination from seeds is minimal. Competition and grazing strongly affect its recovery after a fire. It has seed dormancy, which makes germination more variable. It germinates best with ample amounts of light when kept at 12°C at night and 31°C during the day.

Bouteloua eriopoda (Black Grama) has been described by Simonin (2000). This is a well studied perennial grass species of the desert grassland. It regenerates by tillering, layering and stolons. It needs favorable growth conditions in consecutive years in order for its stolons to spread. Its flowers are often sterile and there is little germination from seed. Seedling establishment usually occurs after the fall rains. Seedlings are vulnerable to grazing; however after establishment grazing may actually stimulate growth of this species.

Bouteloua chondrosoides (Spruce-top Grama) has been described by The Grass Manual (<http://herbarium.usu.edu/webmanual/info2.asp?name=Bouteloua&type=treatment>). This species of perennial grass grows in dense tufts and does not have rhizomes or stolons. It grows on dry rocky slopes and grassy plateaus. Information on this species is very limited.

Aristida ternipes (Spider-grass) has been described by The Fire Effects Information System (<http://www.fs.fed.us/database/feis/index.html>). This is also a native perennial grass that grows in dense tufts and does not have rhizomes or stolons. Flowering in this genus is variable, but is encouraged by disturbance such as fire or grazing. Germination from seed requires high temperatures.

Transects

Six 10 m transects were set up at both locations, for a total of twelve transects. Transects were paired so that each pair contained one transect in a habitat where perennial grasses dominated and one in a habitat where annuals dominated. In June, I recorded the presence of any species (dead or alive) rooted within 10 cm on either side of

each transect in 0.5 m intervals. In August all above ground shoots rooted within 10 cm of each transect were collected, dried, and then weighed for biomass. Specimens of species that were not easily identified in the field were collected and pressed for further reference. Identification was carried out with the aid of the herbaria of the University of Arizona and the University of Michigan.

Statistical Analyses

Data were analyzed using Excel, SPSS version 16.0, Canoco 4.5 and CanoDraw 4.13. All data were tested for normality prior to analysis and were found to be normally distributed in all cases. Soil pH, conductivity and texture were compared between annual versus grassy habitat types using ANOVAs. The soil data from both collection dates were considered together since they were both dry season collections. ANOVAs were performed on the data from the laboratory germination experiment using location, habitat type and grass species as fixed factors. Dependent variables for these analyses included; the cumulative number of germinants, days to 50% germination, days to 100% germination, mean mass of thinned seedlings after fifteen days and mass of the isolated seedlings after thirty days. To test for density dependence of germination ANCOVAs were performed on the average mass of thinned seedlings and the mass of the isolated seedlings using the total number of germinants as a covariate. For the frequency and biomass transect data each species was coded as one of four growth forms; annual dicot, annual grass, perennial dicot or perennial grass. ANOVAs were performed to determine if abundance of growth form differed between annual versus grassy habitats. Canonical correspondence analyses (CCA) on the June frequency and August biomass transect data were used to test if the variation in species composition is explained by the location

and/or habitat type (ter Braak and Šmilauer 2002). CCA is a multivariate ordination technique that investigates the dependence of a related set of response variables on external explanatory variables. In this case variation in the community of plant species was evaluated as a function of location and habitat type.

Results

Soil Analyses

Soil pH did not significantly differ between annual and grassy habitats, but conductivity was higher in annual habitats (Table 1, Figure 1). All soil samples had a sandy texture and no silt. The percentage of sand and percentage of clay did not differ significantly between annual and grassy habitat types (Table 1, Figure 1).

Laboratory Germination Experiment

The scatter plots of the five germination dependent variables do not show any constant pattern with regards to location, soil habitat type or species (Figures 2 through 6). None of the factors or interactions between factors was consistently significant for all of the dependent variables tested in the ANOVAs (Table 2). Location was significant for the majority of dependent variables, but no one location showed consistently greater germination and growth in the scatter plots. Species differed significantly for all germination dependent variables except for the mass of the isolated seedling after thirty days, but in the scatter plots no particular species showed consistently greater germination or growth. Habitat type was insignificant for most variables tested and this is reflected in the inconsistency of the scatter plots. Similarly, the interactions with habitat type were not significant and there is no consistent pattern in the scatter plots with regards to habitat type and location or species. This suggests that the habitat type did not

impact germination as was hypothesized. The location by species interaction was significant for all variables except for the mass of the isolated seedling after thirty days, but no single location and species combination showed consistently greater germination and growth. The three way interaction between location, habitat type and species was significant for all variables except for the days to 50% or 100% germination. ANCOVA tests were performed using the total number of germinants as a covariate to assess density dependence of growth, and showed similar results to the ANOVA tests (Table 2, Table 3).

Field Germination Experiment

There was no germination in the field experiment by August; therefore there are currently no data to present from this portion of the study.

Transects

The ANOVA tests of the transect data show that the only growth form which differed significantly between annual and grassy habitats was perennial grasses in the June frequency data (Table 4). The August biomass data show that there are no significant differences for any of the different plant growth forms between annual and grassy habitats (Table 4). Figure 7 shows the mean June frequency for each growth form in the Green Acres and North Pole locations. August biomass of each growth form did not differ significantly between annual and grassy habitats at either location (Figure 8). Mean total biomass for both locations was greater in the grassy habitats, although this difference was not significant.

Ordination plots were made to show the results from the CCA for both the June frequency (Figure 9) and August biomass (Figure 10) data in order to see the effects of

location and habitat type on species composition. The first CCA axis is associated with location in both data sets and explains 26% (June) and 15% (August) of the variation in species composition. The second CCA axis is associated with habitat type and explains only 10% (June) and 8% (August) of the variance in species composition.

Discussion

Overall, habitat type did not influence the plant community as expected. The results of the soil analyses indicate that electrical conductivity, but not pH or texture, differed between soils from grassy and annual habitats. This could be a result of the past grazing history at the ranch, or the presence of other animals such as rabbits and packrats. Willott et al. found that rabbit pellets had a similar nutrient content as excrement from cattle and sheep, and electrical conductivity was higher at sites with pellets (2000). The higher electrical conductivity in soils from annual habitats reflects the salinity levels of the soil. The higher salinity of annual habitats may encourage the growth of a more halophytic flora, such as annual dicots from the Chenopodiaceae. These halophytes may be able to outcompete the perennial grasses in a high salinity environment.

The laboratory germination experiment had variable results, but showed no consistent effects of soil habitat type on germination. Location and species were significant for the majority of germination dependent variables measured, but habitat type was not. Furthermore, no one location or species showed a consistent pattern with regards to the five germination dependent variables. As with any natural system, it is impossible to exactly replicate field conditions in the laboratory. At the same time that a laboratory setting presents limitations, it also allows for a higher degree of control over the experiment. By using the comparatively manageable laboratory setting, I was able to

isolate the soil as a factor in the germination of perennial grasses and showed that the success of perennial grass germination did not differ between annual and grassy habitat types. A field component was added to this study to test germination under natural conditions and to document a possible pattern of arrested succession in the plant community.

No seeds germinated in the field germination experiment. This may have been because the perennial grass seeds were planted in June during one of the driest parts of the year. The summer monsoon began in August, so the seeds may not have had sufficient moisture or time to germinate in the field when this experiment was last observed. Germination of perennial grasses occurs throughout the year, but is generally greater in wetter months (Marone et al. 2000).

A pattern of arrested succession was not reflected in the data collected to characterize the plant community. Although there was greater abundance of perennial grasses in the grassy habitat transects in June, the annuals were not necessarily more abundant in annual habitat transects. Furthermore, a pattern of arrested succession was not demonstrated from the biomass data collected in August. This indicates that although the frequency of perennial grasses may have been greater in grassy habitat transects, these transects were not more productive for perennial grasses. The site of each transect was selected by visually evaluating the vegetation present, and some level of human error can be expected in this subjective method. However, the similarity of the plant communities present between the apparent habitat types is still surprising given that experienced land managers identified the different habitats.

The spatial scales at which this study was conducted may not have been sufficient to show a pattern of arrested succession in the plant community. Transects may not have been the proper approach for characterizing the plant community. Differences in habitat type may occur on a much smaller or larger spatial scale than was evaluated here. Using smaller or larger spatial scales of measurement can reveal different patterns in the plant community (Lortie et al. 2005). Vega and Montaña (2004) use the concept of vegetation arcs to measure plant communities and within each arc different successional stages exist. Vegetation arcs typically occur on slopes with later successional species near the center of the arc and early successional species on the edges of the arc (Vega and Montaña 2004). Perhaps the transects used in this study were not properly spaced to fully identify the different successional stages present in each location.

The temporal scale used here may have been too brief to properly document a pattern of arrested succession. Populations of perennial plants in the desert can be composed of cohorts that establish in successful years with sufficient precipitation and temperature, and there can be large temporal gaps between establishments (Escudero et al. 2000). Years of severe drought in combination with grazing can lead to changes in the plant community that can last for over 50 years (Hennessy et al. 1983, Archer 1991). Although the Muleshoe Ranch is not an active ranch today, it may still be recovering from a past history of grazing. In addition, there was relatively little rainfall at the ranch in the years following the prescribed burns (Bob Rogers, TNC Arizona, personal communication). The amount of rainfall has been shown to be more important than grazing history in controlling net aboveground primary productivity and nutrient cycling

(Biodini and Manske 1996), and water could be a limiting resource for perennial grasses in this system.

The results of this study provide some insight into the plant community at the Muleshoe Ranch. Electrical conductivity of the soil may play some role in the development of annual dicot and perennial grass habitats. A combination of grazing history and recent climate patterns may explain why perennial grasses were not positively affected by the prescribed burns in some areas. The desert grassland can be a difficult ecosystem to restore because the plant community relies heavily on favorable temperature and precipitation, especially in the years following a fire. Further research incorporating different spatial scales and longer time periods is urgently needed so that the desert grassland can be restoratively managed in an effective way.

Table 1. Results of ANOVA comparing annual and grassy sites soil pH, electrical conductivity and texture. F-values shown. * indicates $p \leq 0.05$, ** indicates $p \leq 0.01$, ***indicates $p \leq 0.001$.

	Df	F
pH	1, 70	0.121
Electrical Conductivity	1, 70	7.802**
Percent Sand	1, 22	1.300
Percent Clay	1, 22	0.703

Table 2. Results of ANOVA data from laboratory germination experiment showing F-values. * indicates $p \leq 0.05$, ** indicates $p \leq 0.001$, ***indicates $p \leq 0.001$.

	Denominator df	Location	Habitat	Species	Location*Habitat	Location*Species	Habitat*Species	Location*Habitat*Species
Numerator df		3	1	2	3	6	2	6
Cumulative Germination (Day 15)	216	7.623***	3.406	108.788***	1.211	2.171*	0.349	3.764**
Days to 50% Germination	216	8.422***	3.997*	28.501***	6.148***	8.930***	3.065*	1.074
Days to 100% Germination	216	2.600	3.063	14.606***	0.260	2.789*	1.074	0.859
Average Mass of Thinned Seedlings (Day15)	216	8.054***	1.252	17.233***	2.561	7.056***	1.748	2.690*
Mass of Isolated Seedling (Day30)	216	4.070**	0.089	1.039	2.620	0.834	0.767	3.536**

Table 3. Results of ANCOVA from laboratory germination experiment with total number of germinants as the covariate. F-values shown. * indicates $p \leq 0.05$, ** indicates $p \leq 0.01$, ***indicates $p \leq 0.001$. The covariate did not have a significant effect on the average mass of thinned seedlings or the mass of the isolated individual

	Denominator df	Total Germinants (N)	Location	Habitat	Species	Location*Habitat	Location*Species	Habitat*Species	Location*Habitat*Species
Numerator df		1	3	1	2	3	6	2	6
Average Mass of Thinned Seedlings (Day15)	215	2.537	8.596***	0.838	18.537***	2.732*	7.302***	1.887	2.674*
Mass of Isolated Seedling (Day 30)	215	0.087	3.673*	0.067	.512	2.602	0.836	0.776	3.530*

Table 4. Results of ANOVA comparing annual and grassy habitats for abundance of growth form. F-values are shown. * indicates $p \leq 0.05$, ** indicates $p \leq 0.01$, ***indicates $p \leq 0.001$.

	Annual Dicots	Annual Grasses	Perennial Dicots	Perennial Grasses
June Frequency	0.442	0.429	1.660	7.469*
August Biomass	0.475	1.170	0.027	0.551

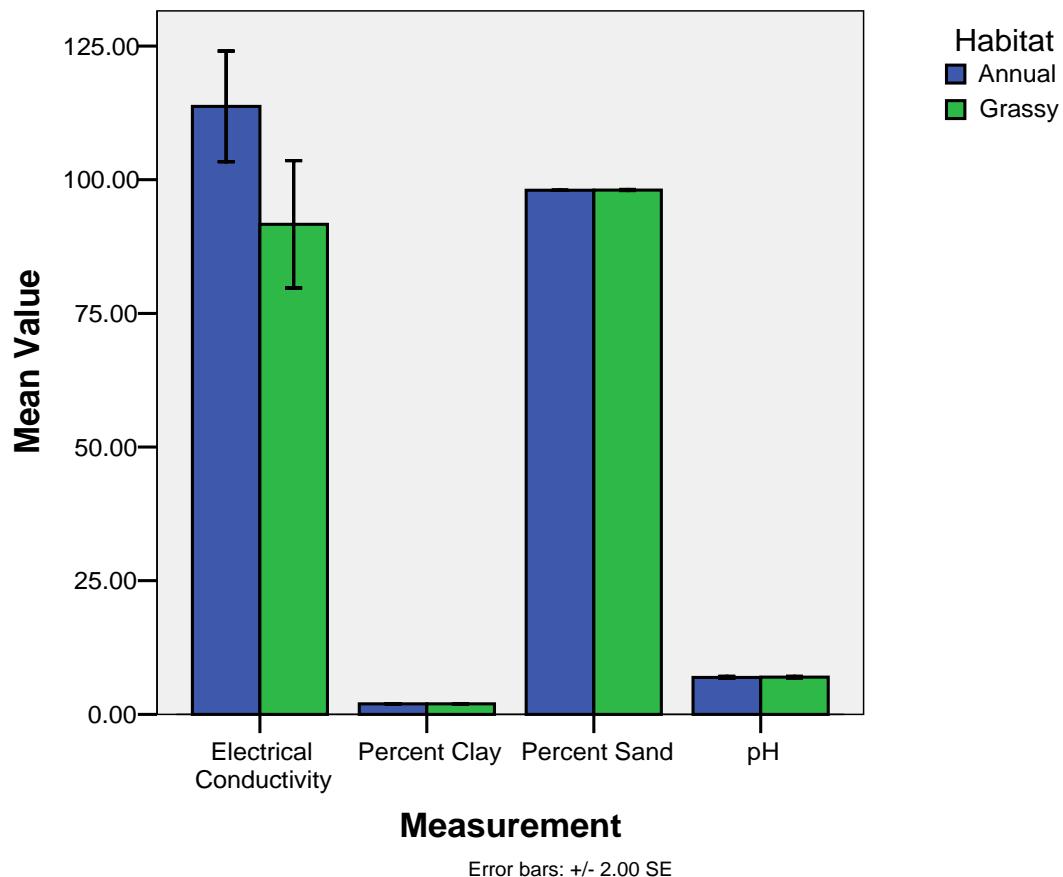


Figure 1. Mean (± 2 SE) percent sand and clay, and pH and electrical conductivity(mS/m) in annual (blue) and grassy (green) habitats.

Cumulative Number of Germinants

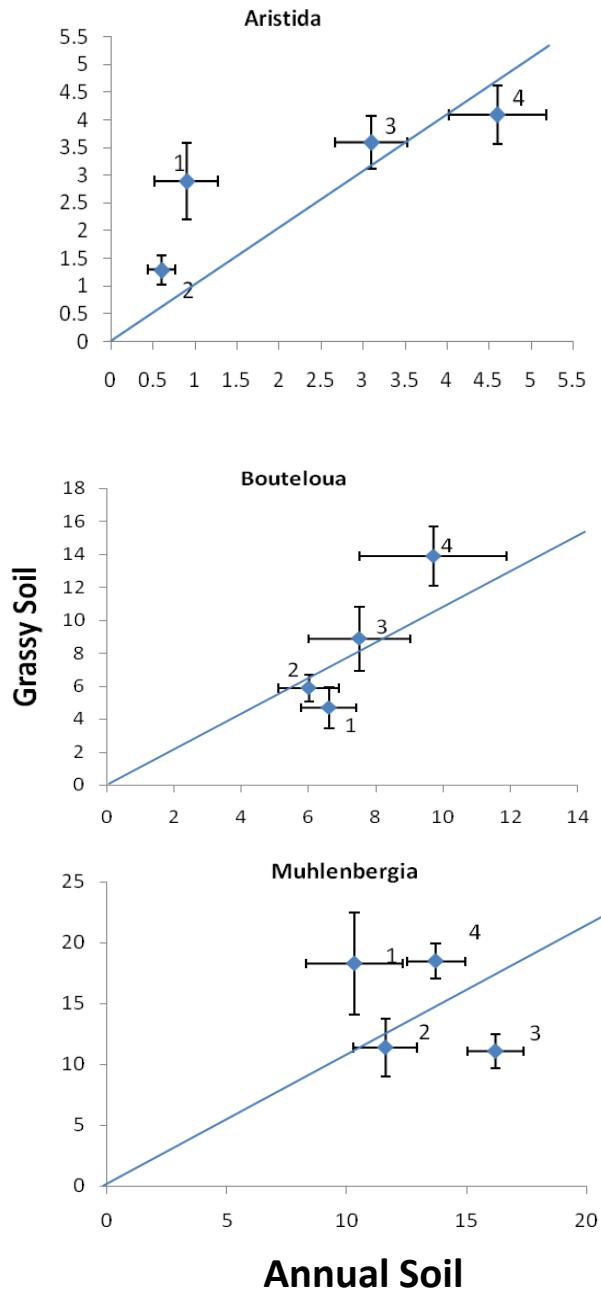


Figure 2. Mean cumulative number of germinants (± 1 SE) comparing soil in annual and grassy habitats.

Number of Days to 50% Germination

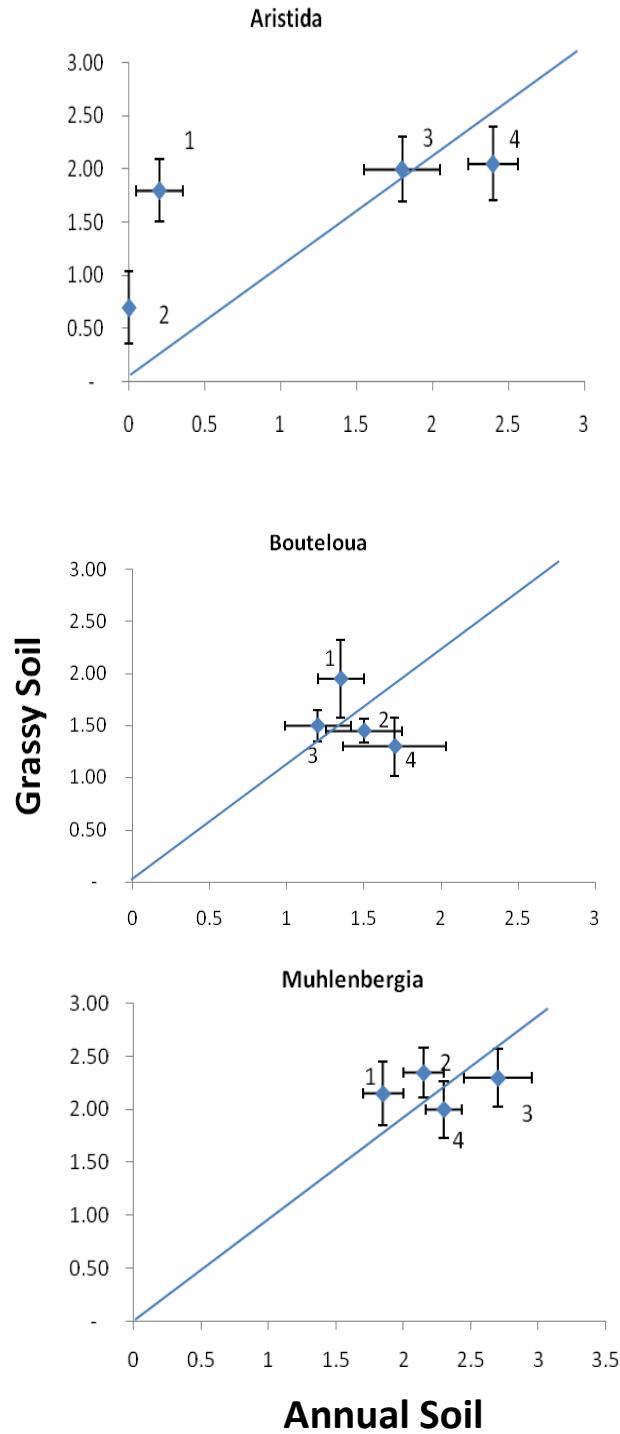
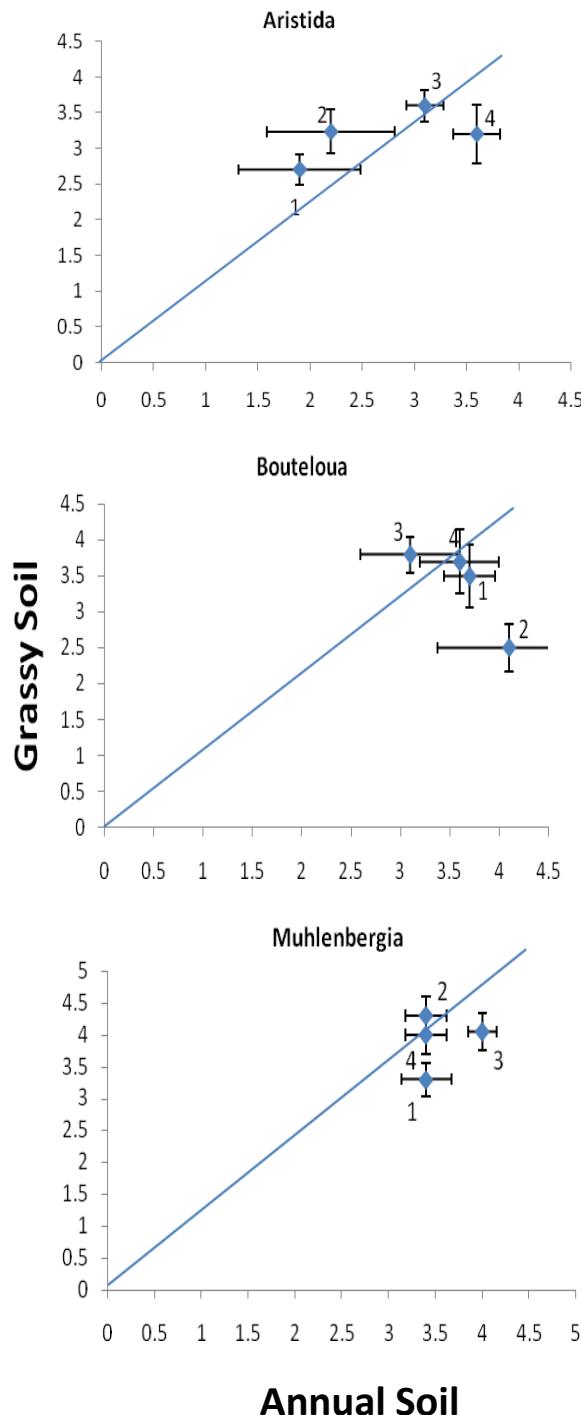


Figure 3. Mean number of days to 50% germination (± 1 SE) comparing soil in annual and grassy habitats.

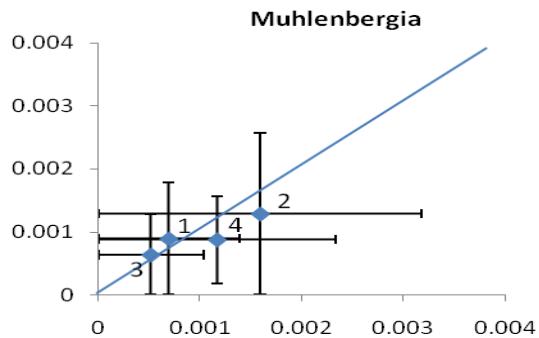
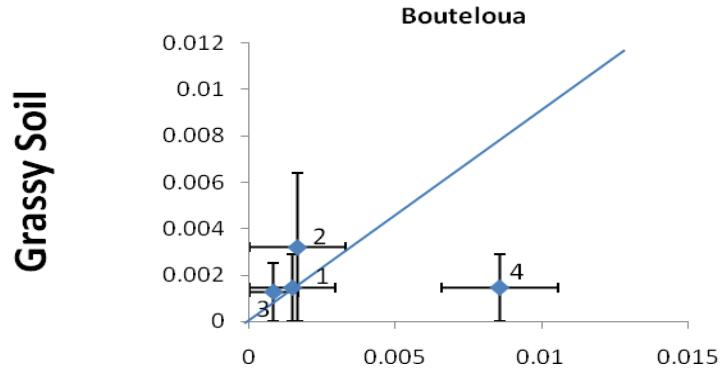
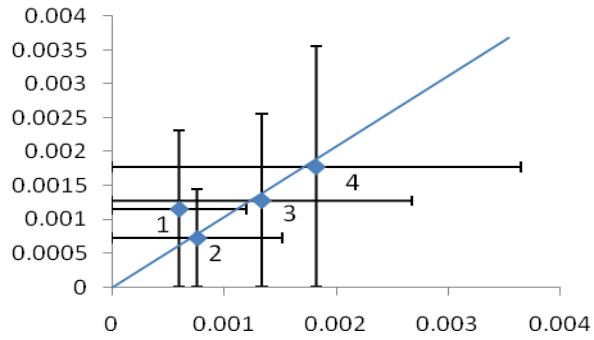
Number of Days to 100% Germination



Annual Soil

Figure 4. Mean number of days to 100% germination (± 1 SE) comparing soil in annual and grassy habitats.

Mass (g) of Thinned Seedlings Fifteen Days After Germination
Aristida



Annual Soil

Figure 5. Mean mass in grams (± 1 SE) of thinned seedlings 15 days after germination comparing soil in annual and grassy habitats.

Mass (g) of Isolated Seedling Thirty Days After Germination

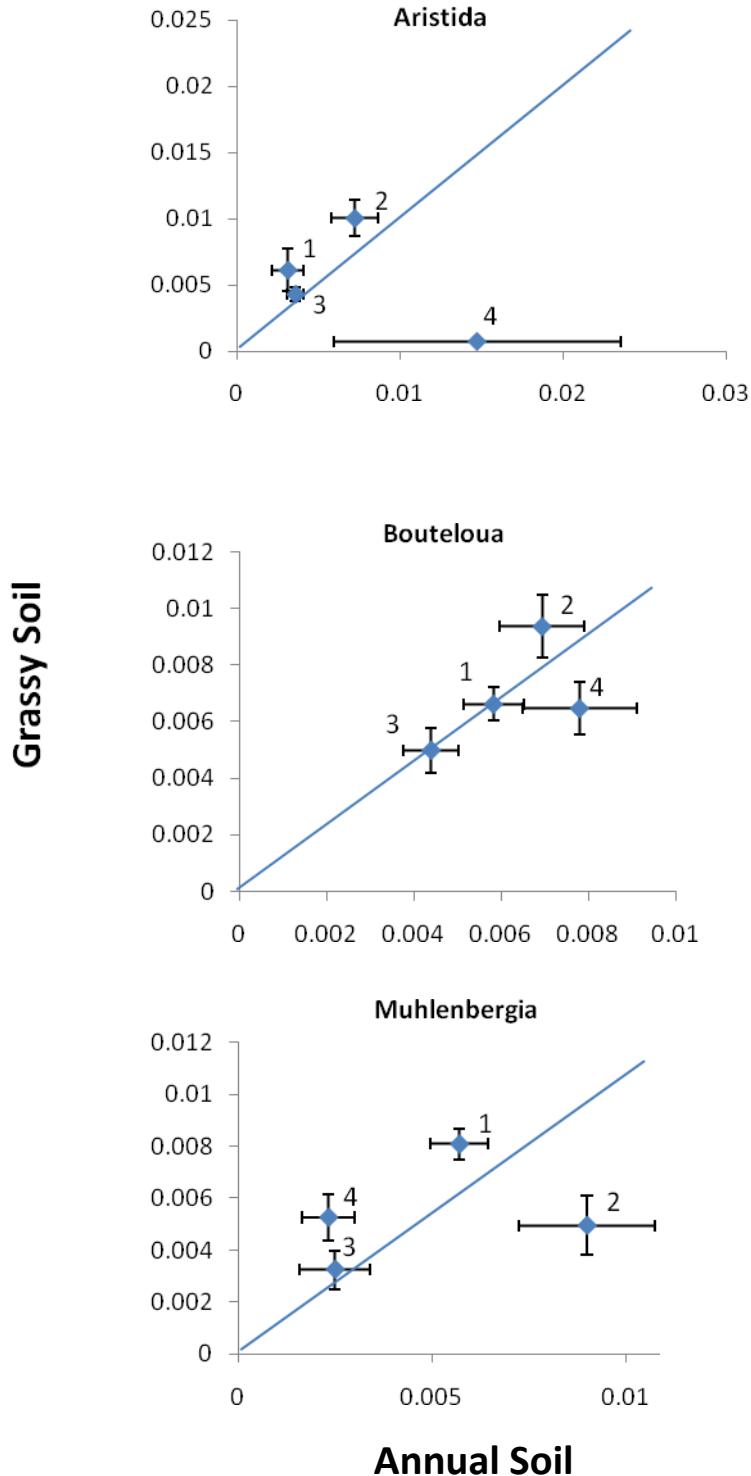


Figure 6. Mean mass in grams (± 1 SE) of isolated individual seedlings 30 days after germination comparing soil in annual and grassy habitats.

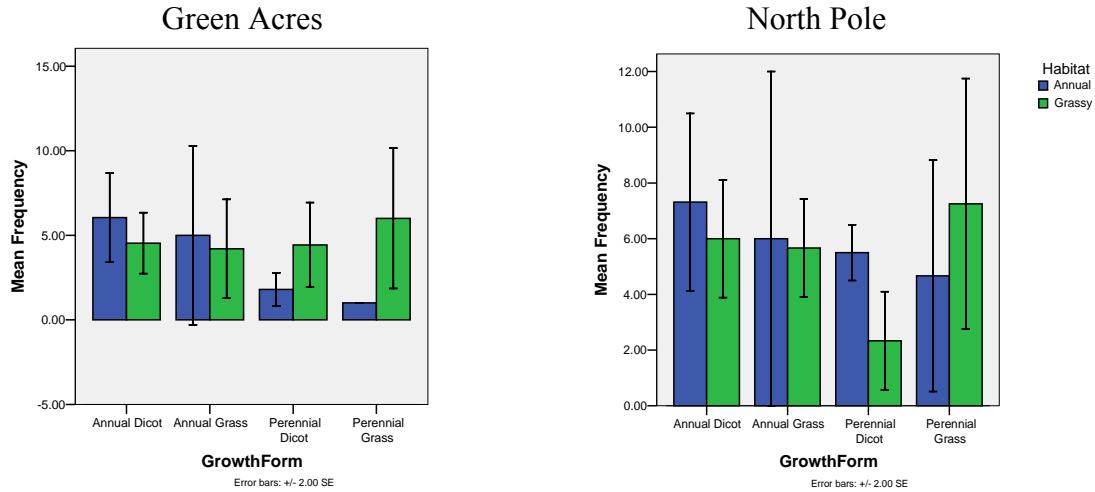


Figure 7. Mean frequency (± 2 SE) from June for each growth form in annual (blue) and grassy (green) habitats.

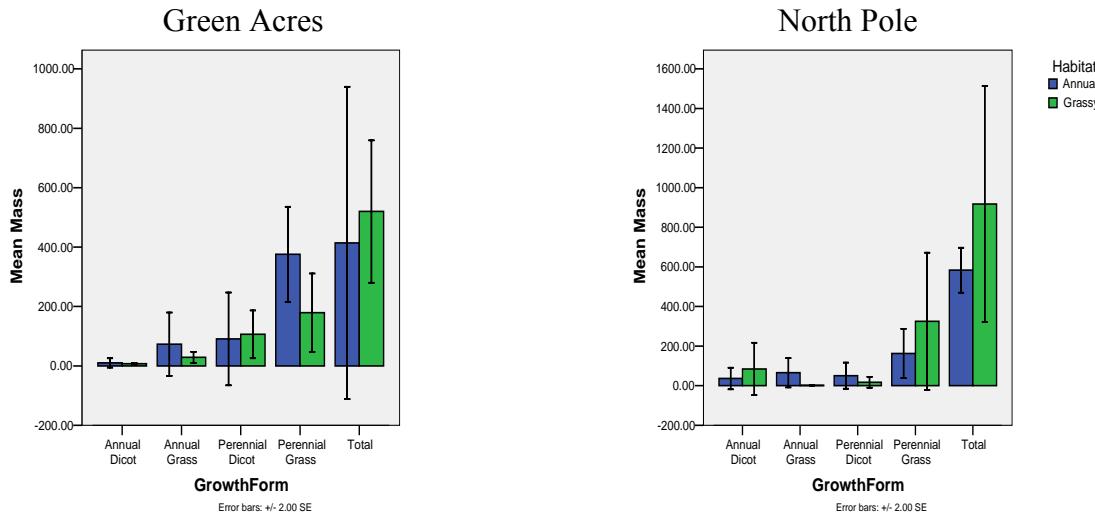


Figure 8. Mean biomass in grams (± 2 SE) from August for each growth form in annual (blue) and grassy (green) habitats.

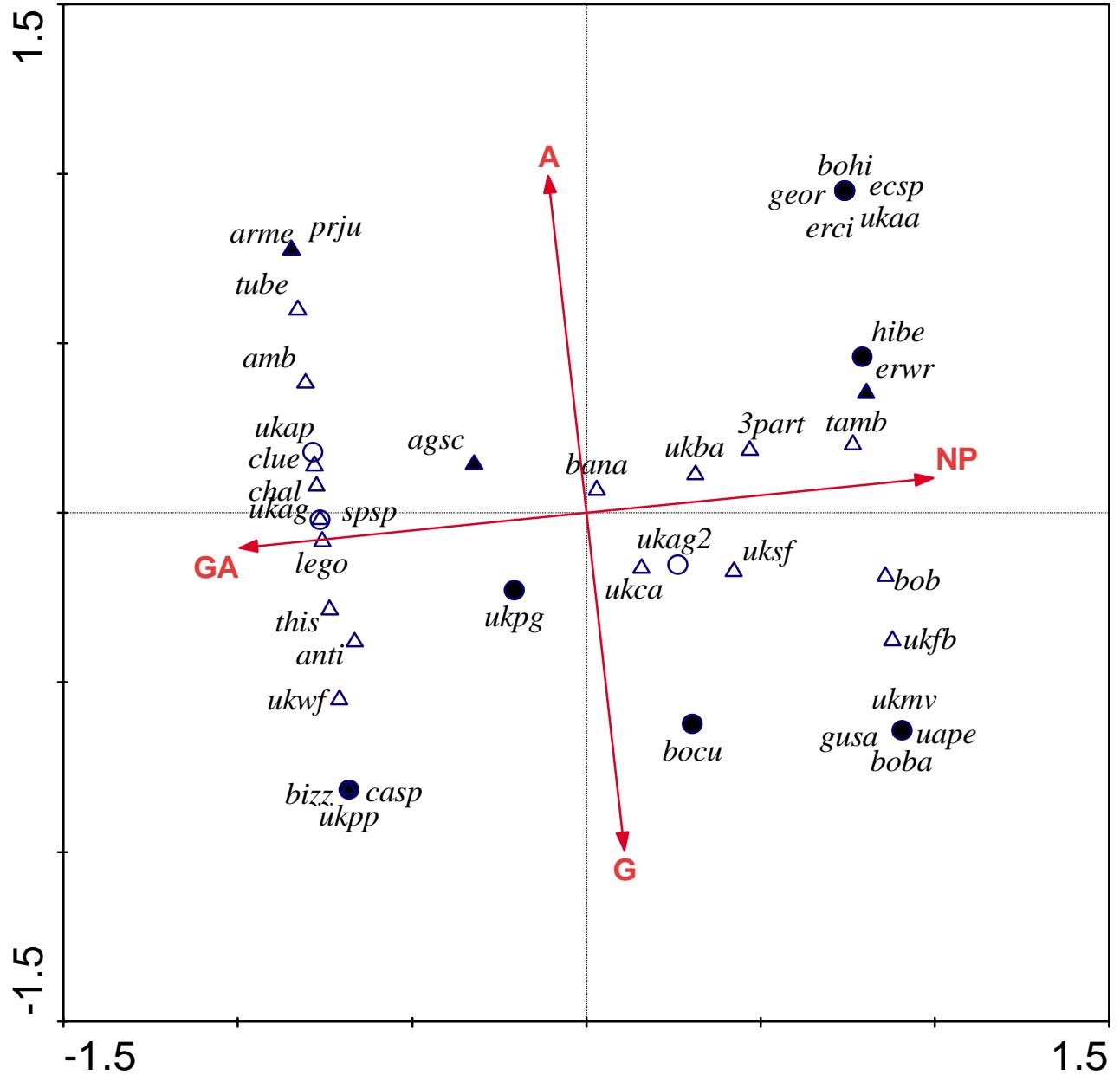


Figure 9. Ordination plot from the CCA showing June frequency data for each species. The horizontal axis represents the Green Acres (GA) and North Pole (NP) location and explains 25.86% of the variance. The vertical axis represents the grassy (G) and annual (A) habitats and explains 9.78% of the variance. Annual dicots are represented by unfilled triangles, annual grasses are represented by unfilled circles, perennial dicots are represented by filled triangles and perennial grasses are represented by filled circles. Some points have more than one label and represent more than one species or plant type. See Appendix 1 for explanation of species name abbreviations.

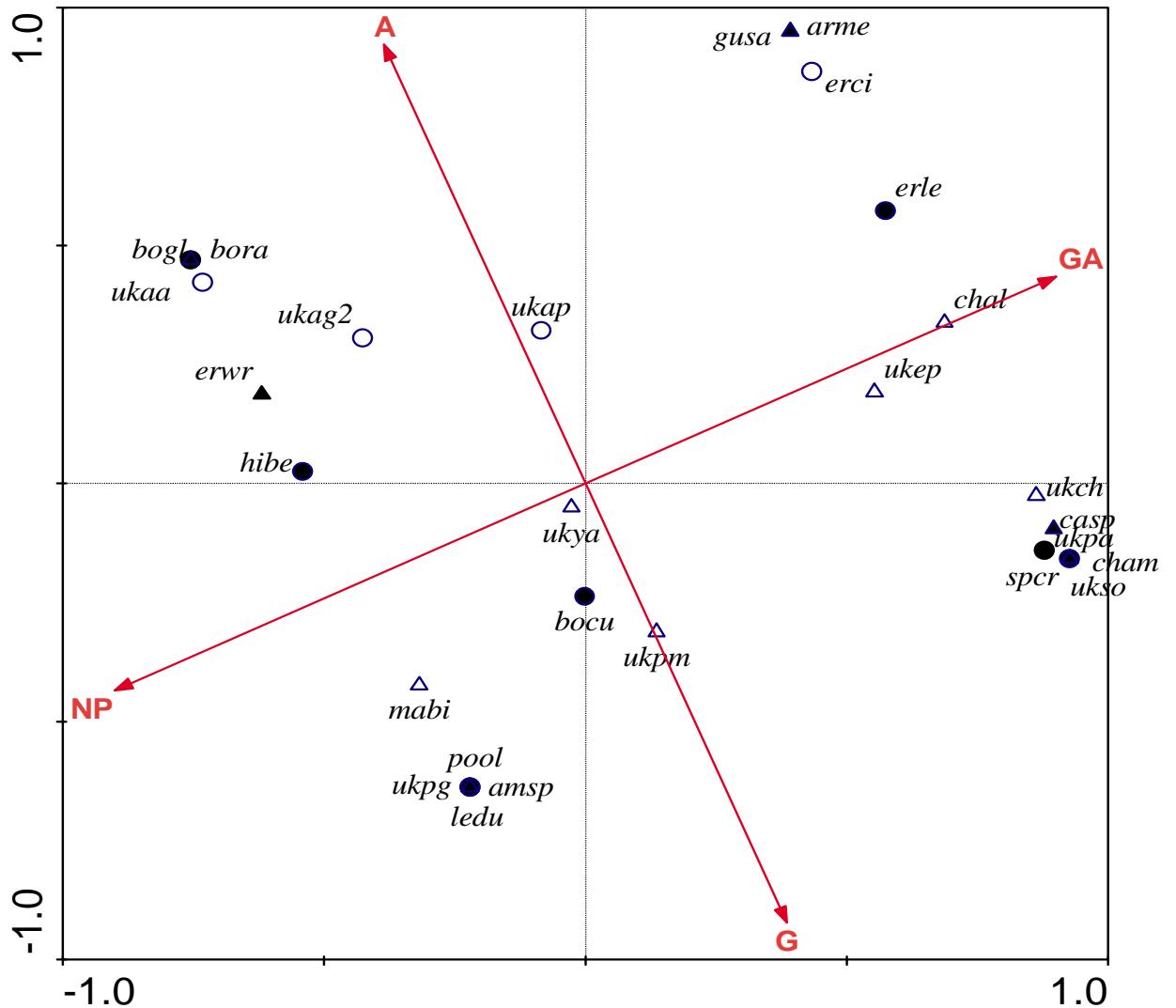


Figure 10. Ordination plot from the CCA showing August biomass data for each species. The horizontal axis represents the Green Acres (GA) and North Pole (NP) location and explains 15.04% of the variance. The vertical axis represents the grassy (G) and annual (A) habitats and explains 7.95% of the variance. Annual dicots are represented by unfilled triangles, annual grasses are represented by unfilled circles, perennial dicots are represented by filled triangles and perennial grasses are represented by filled circles. Some points have more than one label and represent more than one species or plant type. See Appendix 1 for explanation of species name abbreviations.

Appendix 1.
**Species
 names and
 abbreviations
 used for
 biplots**

Abbreviation	Species	Abbreviation	Species
3part	Unknown Forb	this	Unknown Thistle
agsc	Agave schottii	tube	Unknown Forb
amb	Unknown Ambrosia	uape	Unknown Apiaceae
amsp	Amaranthus sp.	ukaa	Unknown Annual Aristida
arme	Argemone mexicana	ukag	Unknown Annual Grass
bana	Unknown Forb	ukag2	Unknown Annual Grass 2
bizz	Unknown Forb	ukap	Unknown Annual Panicum
bob	Unknown Forb	ukba	Unknown Brassicaceae
boba	Bothriochloa barbinodis	ukca	Unknown Caryophyllaceae
bocu	Bouteloua curtipendula	ukch	Unknown Chenopodium
bogl	Bougainvillea glabra	ukep	Unknown Euphorb
bohi	Bouteloua hirsuta	ukfb	Unknown Fabaceae
bora	Bouteloua radicosa	ukmv	Unknown Malvaceae
casp	calliandra sp.	ukpa	Unknown Perennial Aristida
chal	Chenopodium albidum	ukpg	Unknown Perennial Grass
cham	Chenopodium ambrosoides	ukpm	Unknown Forb
clue	Unknown Forb	ukpp	Unknown Perennial Panicum
ecsp	Echinocereus sp.	uksf	Unknown Forb
erci	Erodium cicutarium	ukwf	Unknown Woody Shrub
erci	Eragrostis ciliaris	ukya	Unkown Yellow Aster
erle	Eragrostis lehmanniana		
erwr	Eriogonum wrightii		
geor	Unkown Forb		
gusa	Gutierrezia sarothrae		
hibe	Hilaria belangeri		
ledu	Leptochloa dubia		
lego	Lepidium		
mabi	Machaeranthera bigelovii		
pool	Portulaca oleracea		
prju	Unknown Woody Shrub		
spcr	Sporobolus cryptandrus		
spsp	Sphaeralcea sp.		
tamb	True Ambrosia		

References

- Acácio, V., Holmgren, M., Jansen, P.A. and O. Schrotter. 2007. Multiple recruitment limitation causes arrested succession in Mediterranean cork oak systems. *Ecosystems.* 10: 1220-1230.
- Afzal, M. and W.A. Adams. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. *Soil Science Society of America Journal.* 56: 1160-1166.
- Aguado-Santacruz, G.A., Leyva-López, E., Pérez-Márquez, K.I., García-Moya, E., Arredondo-Moreno, J.T. and J.P. Martínez-Soriano. 2004. Genetic variability of *Bouteloua gracilis* populations differing in forage production at the southernmost part of the North American Graminetum. *Plant Ecology.* 170: 287-299.
- Aleksoff, Keith C. 1999. *Muhlenbergia porteri*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> [2008, March 31].
- Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist.* 134: 545-561.
- Archer, S. 1991. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, USA. In *Savanna ecology and management: Australian perspectives and intercontinental comparisons*, page 109-118. Werner, P.A. (Ed.). Blackwell Scientific Publications: Oxford, UK.
- Bahre, C.J. 1991. A legacy of change: historic impact on vegetation in the Arizona borderlands. University of Arizona Press, Tucson.
- Biodini, M.E. and L. Manske. 1996. Grazing frequency and ecosystem processes in a northern mixed prairie, USA. *Ecological Applications.* 6(1): 239-256.
- Bock, C.E. and J.H. Bock. 1990. Effects of fire on wildlife in southwestern low-land habitats. Page 50-64 in Effects of fire management of southwestern natural resources. U.S. Department of Agriculture, Foest Service General Technical Report. J.S. Krammes (Technical Coordinator).
- Bock, J.H., Bock, C.E. and J.R. McKnight. 1976. A study of the effects of grassland fires at the research ranch in southeastern Arizona. *Journal of the Arizona Academy of Science.* 11: 49-57.
- Bock, C.E, J.H. Bock, L. Kennedy and Z.F. Jones. 2007. Spread of non-native grasses into grazed versus ungrazed desert grasslands. *Journal of Arid Environments.* 71(2): 229-235.

- Brown, D.E. (ed.). 1982. Biotic communities of the American Southwest-United States and Mexico. *Desert Plants*. 4: 1-342.
- Cable, D.R. 1967. Fire effects on semi-desert grasses and shrubs. *Journal of Range Management*. 20: 170-176.
- Chadwick, Amy C. 2003. *Bouteloua curtipendula*. In: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> [2008, March 31].
- Drewa, P.B. and K.M. Havstad. 2001. Effects of fire, grazing, and the presence of shrubs on Chihuahuan desert grasslands. *Journal of Arid Environments*. 48: 429-443.
- Drewa, P.B., D.P.C. Peters, K.M. Havstad. 2006. Population and clonal level responses of a perennial grass following fire in the northern Chihuahuan Desert. *Oecologia* (Berlin). 150(1): 29-39.
- Escudero, A., Iriondo, J.M., Olano, J.M., Rubio, A. and R.C. Somolinos. 2000. Factors affecting establishment of a gypsophyte: the case of *Lepidium subulatum* (Brassicaceae). *American Journal of Botany*. 87(6): 861-871.
- Fire Effects Information System. USDA Forest Service. Accessed March 17, 2008. <http://www.fs.fed.us/database/feis/index.html>. Updated March 13, 2008 by Jane Kapler Smith.
- Geiger, E. L. and G.R. McPherson. 2005. Response of semi-desert grasslands invaded by non-native grasses to altered disturbance regimes. *Journal of Biogeography*. 32(5): 895-902.
- Gonzales, F.J.G. 2006. Vegetation changes after 12 years in four private ranches under short-duration and continuous grazing systems in Chihuahua, Mexico. Texas Tech University Dissertation.
- Gori, David. Senior Ecologist. The Nature Conservancy, New Mexico.
- Grass Manual. Utah State University. Accessed October 4, 2008. <http://herbarium.usu.edu/webmanual/info2.asp?name=Bouteloua&type=treatment>. Maintained by J.K. Wipff.
- Hennessy, J.T., Gibbens, R.P., Tromble, J.M. and M. Cardenas. 1983. Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *Journal of Range Management*. 36: 370-374.

- Hovstad, K.A. and M. Ohlson. 2007. Physical and chemical effects of litter on plant establishment in semi-natural grasslands. *Plant Ecology*. 196(2): 251-260.
- Humphrey, R.R. 1949. Fire as a means of controlling velvet mesquite, burrowed, and cholla on southern Arizona ranges. *Journal of Range Management*. 2: 175-182.
- Lortie, C.J., Ellis, E., Novoplansky, A. and R. Turkington. 2004. Implications of spatial pattern and local density on community-level interactions. *OIKOS*. 109(3): 495-502.
- Lovell, R.D. and S.C. Jarvis. 1996. Effect of cattle dung on soil microbial biomass C and N in a permanent pasture soil. *Soil Biology and Biochemistry*. 28: 291-299.
- Ludwing, J.A, E. Muldavin and R.K. Blanche. 2000. Vegetation change and surface erosion in desert grasslands of Otero Mesa, Southern New Mexico: 1982 to 1995. *American Midland Naturalist*. 144(2): 273-28
- Marone, L., M.E. Horno and R.G. Lez del Solar. 2000. Post-dispersal fate of seeds in the Monte desert of Argentina: patterns of germination in successive wet and dry years. *Journal of Ecology*. 88: 940-949.
- McAuliffe, J.R. 1994. Landscape evolution, soil formation and ecological patterns and processes in Sonoran Desert bajadas. *Ecological Monographs*. 64: 111-148.
- McClaran, M.P. and T.R. Van Devender. 1995. The Desert Grassland. University of Arizona Press: Tuscon, AZ.
- Moyes, A.B., M.S. Witter, and J.A. Gamon. 2005. Restoration of native perennials in a California annual grassland after prescribed spring burning and solarization. *Restoration Ecology*. 13(4): 659–666.
- Nature Conservancy. www.nature.org. Muleshoe Ranch CMA: Cooperative Management Area. Accessed March 31, 2008.
- Niering, W.A. and R.H. Goodwin. 1974. Creation of relatively stable shrublands with herbicides: arresting “succession” on rights-of-way and pastureland. *Ecology*. 55 (4): 784-795.
- Paul, J.R., Randle, A.M., Chapman, C.A. and L.J. Chapman. 2004. Arrested succession in logging gaps: is tree seedling growth and survival limiting? *African Journal of Ecology*. 42: 245-251.
- Rogers, Bob. Muleshoe Ranch Manager. The Nature Conservancy, Arizona.
- Roundy, B.A. and G.L. Jordan. 1988. Vegetation changes in relation to livestock exclusion and root plowing in southeastern Arizona USA. *Southwestern Naturalist*. 33 (4): 425-436.

- Simonin, Kevin A. 2000. *Bouteloua eriopoda*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> [2008, March 31].
- Smith, D.A. and E.M. Schmutz. 1975. Vegetative changes on protected versus grazed desert grassland ranges in Arizona. *Journal of Range Management*. 28(6): 453-458.
- Snyder, S. R, T.O. Crist and C.F. Friese. 2002. Variability in soil chemistry and arbuscular mycorrhizal fungi in harvester ant nests: The influence of topography, grazing and region. *Biology and Fertility of Soils*. 35(6): 406-413.
- Suding, K.N, K.L. Gross and G.R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *TRENDS in Ecology and Evolution*. 19(1): 4
- ter Braak, C.J.F. and P. Šmilauer. 2002. CANOCO Refernce Manual and CanoDraw for Windows User's Guide Version 4.5. Microcomputer Power. Ithaca, New York, USA
- Vega, E. and C. Montaña. 2004. Spatio-temporal variation in the demography of a bunch grass in a patchy semiarid environment. *Plant Ecology*. 175: 107-120.
- Williams, P.H. and R.J. Haynes. 1995. Effect of sheep, deer and cattle dung on herbage production and soil nutrient content. *Grass Forage Science*. 50: 263-271.
- Willott, S.J., Miller, A.J., Incoll, L.D. and S.G. Compton. 2000. The contribution of rabbits (*Oryctolagus cuniculus* L.) to soil fertility in semi-arid Spain. *Biol Fertil Soils*. 31: 379-384.
- Wright, H.A. and A.W. Bailey. 1982. Fire ecology: United States and Southern Canada. John Wiley & Sons, New York.
- Zak, Donald. Professor. School of Natural Resources and the Environment. University of Michigan, Ann Arbor. drzak@umich.edu