THE EFFECTS OF MOWING ON TALLGRASS
PRAIRIE COMMUNITIES

By

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THE EFFECTS OF MOWING ON SPECIES RICHNESS

Introduction

Prairies have developed under the influence of numerous factors including fire, grazing and/or seasonally limited water availability (Stewart 1951, Bragg and Hulbert 1976, Anderson 1982, Axelrod 1985, Gibson 1988). Intentional or accidental, human activities have also impacted prairie communities. Native Americans' use of fire influenced prairie communities (Pyne 1986). Under modern management plans, fire has been often suppressed, or applied at seasons and frequencies different from those used historically (Hulbert 1986). These changes have altered plant communities. Large populations of bison and other indigenous herbivores have been reduced or eliminated and replaced by cattle or other livestock species which have influenced plant communities (Plumb and Dodd 1993, Damhoureyeh and Hartnett 1997, Knapp et al. 1999). Perhaps more important, managers have changed herbivore densities and the spatial and temporal patterns of grazing (Coughenour 1991, Hickman et al. 2004). Exotic plant species have also become established, further changing plant communities.

The loss or modification of factors such as fire and grazing have produced changes in the plant communities that may be reflected in changes in plant species richness and species composition. For example, in a tallgrass prairie the absence of fire

and grazing may result in the accumulation of litter. Under these conditions, forbs

become less abundant, or woody species may invade causing the loss of many prairie

species (Weaver and Rowland 1952, Rice and Parenti 1978, Facelli and Pickett 1991). In

contrast, in the presence of moderate levels of grazing, burning and/or mowing, species

richness may increase (Collins 1987, Güsewell et al. 1998, Howe 1999).

When designing and implementing management plans for prairies, it may not be

feasible to reintroduce the historical factors that shaped prairie communities. Mowing

may serve as an alternative management tool where or when fire and grazing are not

viable options (Davison and Kindscher 1999). Burning, grazing, and mowing are similar

in that they all remove some of the above-ground biomass (Gibson 1989). However, they

differ in their effects, such as:

> 1) Burning generally removes most living and nonliving herbaceous
>
> vegetation down to the soil surface (dependent on a number of conditions).
>
> Mowing and grazing leave standing stubble. Mowing removes all
>
> vegetation above a determined height, whereas grazing (except at high
>
> densities) exerts selective pressure on animal-preferred species and results
>
> in a nonuniform grazing height.
>
> 2) Burning leaves a blackened soil surface that may warm more quickly
>
> than an unburned area (Volesky and Connot 2000).
>
> 3) Mowing without removal of clippings leaves nutrients in place.
>
> Grazing results in partial removal of nutrients, and a nonuniform
>
> deposition of nutrients in feces. During burning, volatilization of some

nutrients occurs, e.g. nitrogen, whereas others are mineralized and left

behind as ash (Hulbert 1986).

Because of these differences, mowing may be considered as a complementary

management tool, rather than a replacement for burning and/or grazing.

Mowing, burning, and grazing are all disturbances in plant communities. A

disturbance is a discrete event that removes individuals, entirely or in part, or modifies

the environment (Pickett and White 1985, Collins 1987). As disturbances, mowing,

burning and grazing negatively impact some individuals, killing some and removing

accumulated biomass. Their impact varies from species to species. Factors including

plant height, location of meristems, shoot:root ratios, and life history may influence the

vulnerability of a species or individual. Grass production may increase with the initiation

of mowing (Rice and Parenti 1978, Turner et al. 1993). Similarly, fires occurring as C_4

grasses begin growth in the spring may increase production (Anderson et al. 1970).

However, frequent mowing that depletes plant reserves may decrease production (Turner

et al. 1993). Neiland and Curtis (1956), investigating the effects of haying, cut native

grasses at 28 day intervals and found *Andropogon gerardii* Vitman, and *Panicum*

virgatum L. densities decreased, whereas *Schizachyrium scoparium* (Michx.) Nash, and

Sorghastrum nutans (L.) Nash were little affected. Under this same regime, *Bouteloua*

curtipendula (Michx.) Torr. increased in density. Hutchinson (1969) found

Schizachyrium scoparium frequency and density decreased in response to annual

mowing, whereas *Sorghastrum nutans* increased. Crockett (1966) found an increase in

basal area of most species following mowing. Though not abundant, Crockett (1966)

found forbs had the greatest percent increase in basal area and frequency.

An important environmental factor influenced by mowing is light availability near the soil surface (Collins 1998). Species vary in their light compensation points and the light intensities at which photosynthetic rates reach a maximum. For example light compensation points for sun vs. shade leaves, or C_3 vs. C_4 plants, may be quite different (Taiz and Zeiger 1998). Fifteen to 30% of full sun (approximately 300-600 μmol m^{-2} s^{-1}) is within the range that photosynthetic rates for many species reach their maximum. Below that range, light may limit production and survival. As a result, species richness may decrease with decreasing light availability.

An objective of this study was to determine the effects of mowing on tallgrass prairie species richness. Mowing, grazing and fire have been found to increase richness (Howe 1995, Collins et al. 1998, Hickman et al. 2004). I investigated effects of mowing by reversing the past treatments on an annually cut hay meadow and lightly grazed pasture. If mowing was an important factor contributing to the differences in species richness at these two sites, richness at both sites should become more similar under comparable mowing treatments.

A second objective of this study was to determine the effects of season and frequency of mowing on species richness. Season of burning has been found to influence species composition in prairies (Hover and Bragg 1981, Howe 1995). I compared combinations of three different mowing seasons, March, June and September. These times correspond to different stages in the life cycles of many species and should maximize differences among the effects of mowing seasons.

Annuals, perennials, forbs and graminoids differ in life cycles and morphology. These differences may result in varying responses to mowing. Grasses, as a group, are

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more tolerant of defoliation than forbs, and therefore I expected to see stronger responses by forbs. Annuals have been found to respond positively to grazing (Collins 1987, Hickman et al. 2004), and I expected them to respond more quickly than perennials to mowing.

Light has been identified as an important factor influencing prairie communities (Hulbert 1986, Collins et al. 1998). I measured light levels near the soil surface to determine if light could be used to predict species richness. If light limited species richness there should be a positive relationship between light and species richness.

At the beginning of my study, I observed thick stands of *Bothriochloa ischaemum* (L.) Keng on my study site with low species richness. If *B. ischaemum* limited species richness, there should be a negative relationship between species richness and *B. ischaemum* cover.

Methods

Study Sites

For this study, I selected two sites with opposing past management regimes. Both were located in north-central Oklahoma, USA, 16 km west of Stillwater, at approximately $36^{o}5'$ N, $97^{o}15'$ W. The Oklahoma State University Veterinary Medicine Ranch site (VMR) was located in the SE quarter of section 36, T19N, R1W. In 1996 it was lightly grazed by horses, *Equus caballus*, and infrequently cut for hay or burned. VMR was fenced to exclude horses in 1996. The Lake Carl Blackwell site (LCB) was located in the NE quarter of section 17, T19N, R1E. It was in a hay meadow that was cut annually in late July, for more than 15 years. The soils at both sites were Grainola-

Lucien complex, clay loam soils with moderate fertility (Soil Conservation Service 1987). Small sandstone rocks were rarely encountered at the soil surface, but were present in the subsoil. Both sites were slightly sloping (<5% slope) with a westerly aspect.

In 1996, at the beginning of the study, VMR had a heavy accumulation of grass litter and low forb density. In contrast, LCB had very little litter accumulation above the annual mowing height and I observed a greater density of forbs. Based on my initial observation of the sites, I found *Schizachyrium scoparium* (Michx.) Nash and *Sorghastrum nutans* (L.) Nash were widespread at both sites. *Andropogon gerardii* Vitman, *Panicum virgatum* L. and *Bouteloua curtipendula* (Michx.) Torr. also were present at both sites. *Bothriochloa ischaemum* (L.) Keng was present at VMR, forming nearly pure stands in some areas of the site, but very uncommon at LCB. At LCB *Solidago nemoralis* Ait., *S. missouriensis* Nutt., *Erigeron strigosus* Muhl. ex Willd. and *Gaillardia aestivalis* (Walt.) Rock were common forbs, whereas *Ambrosia psilostachya* DC., *Aster ericoides* L*., A. oblongifolius* Nutt. and *Artemisia ludoviciana* Nutt. were present at VMR.

Climatic Data

I obtained weather data from the Oklahoma Mesonet, a network of automated monitoring stations (Oklahoma Climatological Survey). With the exception of long-term averages, which were not available, all data came from the Marena site, located about 3.2 km east of VMR and 6.5 km south of LCB. Long-term averages were from the Stillwater station, approximately 13 km east and 6 km north of VMR.

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<u>Mowing</u> <u>Treatments</u>

My experimental treatments reversed the prior management at each site. I established seven mowing treatments at VMR and one unmowed control (C). The mowing treatments at VMR varied in season and frequency of mowing. The mowing treatments consisted of: March only (M); June only (J); September only (S); March and June (MJ); March and September (MS); June and September (JS); and March, June and September (MJS). The three mowing seasons of March, June and September were selected because they correspond to three different stages in the life cycles of the dominant warm-season grasses, prior to initiation of growth, during vegetative growth, during flowering and seed maturation. These mowing times also allow for sampling twice per year with at minimum of 6 weeks time between the last mowing and vegetation sampling. At LCB the experimental treatment was the cessation of annual mowing. The control plots at LCB were mowed in late July, a continuation of the long-term management.

I mowed plots at both sites to a height of eight cm above the ground. The clippings were removed from the paths, buffers and plots during each mowing at both sites using a bagging attachment on the mower. Clippings from the one square meter plots were collected and dried at 60 degrees C to a constant mass and weighed to the nearest 0.1g. I made no attempt to separate or determine amounts of living versus nonliving biomass. Biomass was measured so that I could investigate relationships between biomass and species richness.

Using the data from the 1996 sample, I ranked the plots at VMR by species richness. Plots with the same species richness were arranged sequentially based on

August 1996 Shannon species diversity index scores. I then assigned the plots to 18

consecutive blocks of similar species richness, each block with eight plots. The eight

different treatments were randomly assigned within each block. The 18 blocks, each

containing eight different treatments accounted for the total of 144 plots at VMR. At

LCB, mowing treatments were assigned randomly, 18 July-mowed controls and 18

unmowed plots for a total of 36.

Plot Layout and Sampling

       I established permanent one square meter plots in a grid at each site. Eighteen

replicates were assigned to each of the mowing treatments and controls. There were 144

plots at VMR (12 rows of 12 plots each), and 36 at LCB (9 rows of 4 plots each). More

plots were necessary at VMR because eight mowing treatments were assigned whereas

only two treatments were used at LCB. A 73.5 cm wide buffer surrounded each plot and

received the same mowing treatment.   Between the plots I maintained 53 cm wide

mowed paths that provided access to the plots and aided in their location and

identification.

       Short sections of PVC pipe (1.25 cm I.D. by 20 cm long), driven into the soil,

established the opposite corners (SE and NW) of each permanent plot. The PVC pipe

facilitated accurate placement of the one square meter frame during each sampling

period. The sampling frame was constructed of aluminum channel. I attached two 30 cm

long legs made from 6.35 mm diameter (1/4 inch) all-thread rods to opposite frame

corners using short strips of galvanized flat iron. During sampling, the all-thread rods

slid into the PVC pipe and held the frame slightly above the soil surface.

I sampled each site in the late summer of 1996, prior to the initiation of mowing treatments. VMR was sampled in August and LCB in September. In the subsequent years of 1997-1999, I sampled each site twice per year, VMR in early May and early August, and LCB in late May and early September. Sampling at VMR lasted approximately two to three weeks. I usually finished sampling LCB in less than two weeks. I sampled rows of plots at both sites in a random sequence, changing the sequence for each sample period. Sampling always occurred at least one month after the most recent mowing.

Light Sampling

I used a Li-Cor LI-190SA spot quantum sensor and a Li-Cor LI-191SA 1 m line quantum sensor to simultaneously measure above- and below-canopy PAR (photosynthetically active radiation measured in $\mu mol\ s^{-1}\ m^{-2}$). I measured in 33 cm from the north and south sides of each plot and then slid the line quantum sensor, oriented east-west, along the ground under the vegetation within each plot. I sampled PAR five times at both VMR and LCB. Sampling preceded each March, June and September mowing from June 1998 through September 1999. The sensor was leveled north-south. The spot quantum sensor sat level on a tripod in a central position near the sampled plots at a height of approximately 1.5 m above the soil surface. This single standard height was used for all plots and placed the sensor above all immediately surrounding vegetation. Percent transmitted PAR was calculated by dividing the below-canopy value by the corresponding above-canopy reading and then multiplying by 100. The mean percentages for PAR were calculated for each plot. I usually completed taking

readings taken for a given site during a single day, or occasionally on two consecutive days. Readings were taken only between 1000 and 1600 hours CDST and when cloud cover was absent or minimal and not obstructing the sun.

I measured light availability near the ground level for two reasons. First, light availability is an environmental factor influenced directly by mowing that has an effect on plant growth and survival. Second, I wanted to use the percentage of light transmitted as an indirect measure of overlying biomass. Using transmitted light as an indicator of production provided an advantage over the direct harvest of biomass in that measurement of light was nondestructive. I could measure light at anytime, whereas there was no one time during the year when I could obtain biomass measurements from all my treatments at the same time.

Analyses

I used analyses of variance to test the effects of mowing treatments on the species richness data for each sampling period at VMR for the May and August data separately. I used LSD post-hoc tests to compare means. First, I investigated the changes in species richness within each treatment separately over time. I also noted changes in species richness of annual forbs, perennial forbs and perennial graminoids. I did not include woody species or annual graminoids in the comparisons because there were few species present in very low numbers and in very few plots. In a second set of analyses, I used separate factorial ANOVAs for each sampling period to compare the effects of mowing seasons within a given sampling period on total species richness. I also compared changes in the species richness of annual forbs, perennial forbs and perennial graminoids.

Similar comparisons were investigated using the LCB data. I used t-tests rather than ANOVAs in the statistical analyses of the LCB data because only two means, mowed versus unmowed, were compared within each sampling period,.

I tested the effects of mowing on photosynthetically active radition (PAR), biomass and yearly total species richness data using ANOVAs with LSD post-hoc tests on means from successive years within a treatment. Linear regressions were used to investigate the relationships among species richness and PAR, and the relationships among species richness and *Bothriochloa ischaemum* cover. Statistics were conducted using SAS and SPSS (1998).

I calculated species turnover rate using the formula: $(A + B)/(A + B + C)$. A was the number of species present only during the first sampling period. B was the number of species present only in the second sampling period. C was the number of species present during both sampling periods (Güsewell et al. 1998). I compared species turnover rates of consecutive May samples from VMR and LCB separately, also consecutive August VMR and consecutive September LCB samples.

<center>Results</center>

VMR August Sampling Period

Species Richness I observed significant changes in mean species richness in both the treatment and control plots at VMR. In the unmowed controls, mean species richness varied ($p<0.05$) during the study, ranging from a low of 10.2 spp m^{-2} in August 1996 to a high of 12.6 spp m^{-2} in 1997 (Table 1). Although there were significant differences from year to year in the control plots, there was no consistent trend of increasing or decreasing

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mean species richness. The August 1996 mean was not significantly different from 1998, and mean richness in 1997 was not different from 1999. In contrast, mean species richness in most of the mowed plots increased significantly from 1996 to 1997, many had no significant change from 1997 to 1998, and then all increased significantly ($p < 0.05$) from 1998 to 1999.

Mean August species richness in all the mowed treatments and the control increased, at least slightly, from 1996 to 1997 (Table 1). The increase in the S treatment, which had not been mowed, was not significant. In plots mowed in March 1997, species richness increased 49% (5.1 spp m^{-2}) or more from August 1996 to 1997. Means in the other plots increased by 24% (2.4 spp m^{-2}) or less. Analysis of the August 1997 data revealed a significant March main effect (Table 2). Neither the June nor September main effects were significant, nor were any of the season interactions. All of the March simple effects, which compare each treatment with a March mowing to its complementary treatment lacking the March mowing, were significant. All treatments including a March mowing produced greater mean species richness than those not mowed in March. The J, S and JS treatments were not significantly different from the control.

From August 1997 to 1998, mean species richness in treatments mowed in March and/or June did not change significantly though richness did decrease in the control plots ($p < 0.05$). All treatments that were mowed in September 1997 increased at least slightly from 1997 to 1998. The increases in species richness the S (3.1 spp m^{-2}) and JS (3.2 spp m^{-2}) treatments were statistically significant ($p < 0.05$). The increases in the MS (0.5 spp m^{-2}) and MJS (1.2 spp m^{-2}) treatments were not. Comparisons among treatments in the August 1998 data revealed that all three main effects, M, J and S were statistically

significant. None of the interactions were significant indicating that multiple mowings per year tended to increase species richness. Inclusion of a March or September mowing (e.g., MS vs. S, JS vs. J) resulted in an increase ($p<0.05$) in mean species richness. While inclusion of June mowing consistently resulted in slightly higher mean species richness and therefore a significant J main effect, none of the comparisons between individual treatments were the increases statistically significant.

Mean species richness increased significantly in all treatments, including the control, from August 1998 to 1999. The mean richness in the control, however, was not significantly different from August 1997. In contrast, mean richness in all the mowed treatments in August 1999 were at their highest observed values. Within each treatment all means were significantly greater than those from all previous August samples. The largest increase, 5.9 species, was in the J plots.

Comparing mowing treatments in August 1999, all three main effects were highly significant. However, with the exception of the M*J interaction, all of the interaction terms were significant. Investigation of the individual treatments revealed that only the comparisons with the controls were significantly different. There was little additive effect of the mowing seasons on total species richness. Comparing all the mowing treatments, the only means significantly different were: MJS > M and MJS > J. Overall, species richness increased in response to all combinations of frequency and season of mowing from August 1996 to August 1999. August mean species richness in mowed plots increased by a minimum of 75% (7.7 spp m^{-2}) for the J mowing treatment, to a maximum of 103% (10.4 spp m^{-2}) for the MJS mowing treatment over the three years of the study.

<u>Mean</u> <u>Richness</u> <u>Within</u> <u>Growth</u> <u>Forms</u> The greatest total increase in mean species richness within a group of species from August 1996 to 1999 at VMR was observed in the annual forbs (Figure 1).   Mean August annual forb species richness increased by a minimum of 4.0 spp m^{-2} in the M treatment to a maximum of 5.2 spp m^{-2} in the MJ and JS treatments during this study. During this same period, mean annual forb richness in the control plots increased only 0.9 spp m^{-2}.

Mean annual forb richness increased at least slightly from 1996 to 1997 in all treatments except JS. However, only in treatments mowed in March were the increases greater than 1 sp m^{-2}. Increases ranged from 1.6-2.3 spp m^{-2} in the March-mowed plots. The effects of the initial September mowings were evident in increased annual forb richness in 1998, ranging from 1.2 in the MJS treatment to 3.4 spp m^{-2} in the JS treatment. Means in annual forb richness were essentially unchanged in the other treatments. Finally, in 1999 annual forb richness increased in all treatments, including the control, from a minimum of 0.6 spp m^{-2} in C to a maximum of 4.1 spp m^{-2} in J. A strong positive effect of the J mowing treatment was observed on annual forb richness only in August 1999.

Mean richness of perennial forbs also increased in response to all mowing treatments (Figure 1). Mean richness in the control also varied during this period reaching a high of 4.9 spp m^{-2} in August 1997 compared to 3.9 spp m^{-2} in August 1996. However, the richness in August 1998 and 1999 were only slightly different from the 1996 mean perennial forb richness. The overall increases from 1996 to 1999 in the treatment plots were less than those observed for annual forbs, ranging from 1.1 spp m^{-2} (J) to 2.8 spp m^{-2} (S). Unlike the annual forbs, mean richness of perennial forbs

increased not only in the plots mowed in March, but also in the control and J plots from 1996 to 1997. The results from 1998 also were different from those observed for annual forbs. None of the perennial forb means increased sharply, and four of the seven (M, J, MS and C) experienced decreases. From August 1998 to 1999 mean richness increased at least slightly in all treatments and the control. Perennial forb richness was at their highest observed values in 1999 in all mowed treatments except M.

Mean perennial graminoid species richness increased in all treatment plots and the control from August 1996 to 1999 (Figure 1). The control increased the least, albeit starting with the highest mean richness, 6.1 spp m^{-2}, it ended with the lowest richness, 6.9 spp m^{-2}. Increases in mean perennial graminoid species richness were similar to those I observed for perennial forbs, ranging from 1.4 spp m^{-2} (S) to 2.3 spp m^{-2} (JS) in the mowed treatments. All means, except in the S treatment, which had not yet been mowed, increased by more than 1 spp m^{-2} from August 1996 to 1997. From 1997 to 1998 the largest increase in species richness was in the S plot, but the increase was only 0.7 spp m^{-2}. The other treatments changed little, with JS and the C decreasing slightly. From August 1998 to 1999 there was again little change in perennial graminoid species richness. The largest increase was 1.3 spp m^{-2} in the JS plots. The difference in mean species richness across all treatments was only 1.3 spp m^{-2}, MJS (8.2 spp m^{-2}) versus C (6.9 spp m^{-2}).

Throughout my study, mean August richness of perennial graminoids were higher than perennial or annual forbs. August species richness inceased in all the plots, including the control, from 1996 to 1999. However, the net increases in the controls were less than 1 spp m^{-2}. The few obvious differences between treatments involved primarily

differences in timing of the initial mowing. The MJS mowing had relatively high increases in all three groups of species and as a result slightly higher total species richness. September mowing generally produced greater increases in perennial forb richness, except for the JS treatment, compared to combinations of M and/or J mowing. The J treatment had a positive effect on annual forb richness only following the drought in 1998.

<u>VMR</u> <u>May</u> <u>Sampling</u> <u>Period</u>

   <u>Species</u> <u>Richness</u> May mean species richness in the control plots at VMR did not vary significantly during the study. In contrast, mean species richness increased significantly each year in each of the mowed treatments (Table 3). Overall changes in the mowed plots ranged from an increase of 64% (9.9 spp m^{-2}) in the M plots to 124% (14.6 spp m^{-2}) in the S plots. From May 1997 to May 1998 mean species richness increased by a minimum of 5.5 spp m^{-2} (M) to a maximum of 9.6 spp m^{-2} (JS) in the mowed treatments. These increases in mean species richness were greatest in the treatments that included a September mowing (8.5 spp m^{-2} or more). Although the increases within each treatment in mean species richness were again statistically significant from 1998 to 1999, the increases were less than the previous year in all treatments except J. Increases ranged from 2.3 spp m^{-2} for MS to 6.7 spp m^{-2} for J.

   There was a highly significant March main effect in the VMR May 1997 total species richness (Table 4). Each of the simple effect comparisons for March was also significant. The June main effect was also significant in May 1997. The June effect was an artifact of plot assignments because the June mowing treatment had not been applied

at this time. In support of this argument, none of the individual comparisons between treatments mowed in June and the corresponding treatments not mowed in June were significant in 1997, but the treatments scheduled to include a June mowing consistently had slightly higher richness than the other treatments. None of the interactions were significant.

In May 1998 all three main effects were significant, as well as the M*J and J*S interactions. All of the March-mowed versus corresponding not mowed in March comparisons were significant. Looking at similar comparisons for the June and September treatments, the only comparisons significantly different were those compared to the control. Including March with either June or September produced significant increases in richness. However, combining June and September did not increase total species richness significantly over either June or September separately, nor did the MJS treatment result in an increase in total species richness over MJ or MS.

In May 1999 all three main effects and all the interactions were significant indicating no additive effect of multiple mowings per year. Of the simple effects, only those comparisons with the control were significantly different, with the mowing treatments producing higher species richness than the control.

Mean Richness Within Growth Forms As with the August data, annual forbs at VMR experienced greater increases in May mean species richness in response to the mowing treatments than perennial forbs or graminoids (Figure 2). Overall, mean annual forb richness increased from 1997 through 1999 by a minimum of 6.1 in M to a maximum of 9.6 spp m^{-2} in J and JS. Means increased similarly each year in each mowing treatment. In contrast, mean annual forb species richness in the control plots

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changed little, from a minimum of 0.7 spp m^{-2} in 1998 to a maximum of 1.3 spp m^{-2} in 1999.

In May 1997, following the initial March mowing, all mowed treatments had annual forb richness greater than 1 spp m^{-2}. The richness in each of the unmowed treatments (C, J, S and JS) was less than 1 spp m^{-2}. By May 1998, annual forb richness had increased by more than 3 spp m^{-2} in the mowed plots whereas they had decreased slightly in the unmowed control. The greatest increases were in the plots mowed more than once per year and those that included a September mowing (MS, JS and MJS). In May 1999 mean annual forb richness increased in all plots, including the control. The increases in the mowed plots were generally not as great as observed in 1998. Whereas the M treatment had the lowest annual forb richness of the mowed treatments, it was much higher than the control. Presence of annual forbs from May to August was low during 1998 in the J plots. Whereas May annual forb richness in the J plots was similar to the other treatments in 1998 and 1999, August richness was much lower in 1998.

The mean richness of perennial forbs also increased from May 1997 to 1999 in all treatment plots (Figure 2). Mean perennial forb richness was slightly greater following the initial March mowing in the March-mowed plots compared to the as yet unmowed plots in May 1997. The largest increases tended to occur from May 1997 to 1998, with all treatments exhibiting increases ranging from 0.8 (J) to 2.0 (S) spp m^{-2} while the control decreased by 0.7 spp m^{-2}. From May 1998 to 1999 mean richness increased slightly in all mowing treatments, but only J (1.4 spp m^{-2}), S (1.0 spp m^{-2}) and JS (1.6 spp m^{-2}) resulted in increases equal to or greater than one species per square meter. The mean number of perennial forbs decreased slightly in the control plots during the study.

Mean species richness of perennial graminoids tended to increase in the mowed plots over the course of the study. However, the increases were smaller than the other groups of species (Figure 2). Only in the MJS, where both perennial forbs and graminoids increased by 1.7 spp m^{-2}, was the increase in perennial graminoids equal to that of the other groups of species. Unlike the means for annual and perennial forbs, one treatment, MJ, had an increase of less than 1 spp m^{-2} in perennial graminoid richness over the course of this study. Only in the control was the increase less.

LCB September Sampling Period

Species Richness There were very few significant differences in mean total species richness at LCB from September 1996 to 1999 when I compared means within each separate treatment. Mean September species richness at LCB increased significantly in 1997 in both the unmowed treatment plots and the controls that were mowed in July (Table 5). However, the September 1998 and 1999 means were not different ($p<0.05$) from the 1996 mean. When I compared the two treatments within each sampling season, mean species richness in the July-mowed plots was significantly lower than those in the unmowed controls beginning in September 1997 and continuing through 1999.

Mean Richness Within Growth Forms The highest mean September species richness for perennial graminoids, annual forbs and perennial forbs at LCB was observed in 1997 (Figure 3). Perennial grass richness varied less from year to year than the perennial or annual forbs richness.

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Species Richness Initially in May 1997 there was no significant difference
between the two treatments (Table 6). Mean May species richness increased from 1997
to 1998 ($p<0.05$) in the control (July-mowed) plots. The total increase in mean richness
in these plots was 6.3 spp m^{-2} from 1997 through 1999. During this same time period,
mean richness decreased in the unmowed treatment plots by a similar amount, 6.1
spp m^{-2}. There was essentially no change from 1997 to 1998, followed by a significant
decrease in 1999. Comparisons between the two treatments revealed significantly higher
mean species richness in the July-mowed plots in both 1998 and 1999 over the unmowed
plots.

Mean Richness Within Growth Forms Mean annual forb species richness
decreased in the unmowed treatment plots at LCB from May 1997 to 1999 (Figure 3).
The decrease from May 1997 to 1998 was only 0.8 spp m^{-2}. From 1998 to 1999 the
decrease was much greater, 3.6 spp m^{-2}. The opposite response occurred in the mowed
treatment plots. From May 1997 to 1998 mean annual forb richness increased sharply by
3.6 spp m^{-2}. The increase in May 1999 was only 1.1 spp m^{-2}. The May 1999 annual forb
richness was much greater in the mowed (13.4 spp m^{-2}) versus unmowed plots (5.3 spp
m^{-2}).

In contrast to annual forbs, perennial forb richness changed very little during my
study (Figure 3). There was a slight increase each year in the July-mowed plots, while in
the unmowed treatment plots the May 1999 richness was essentially identical to May
1997. Like the perennial forb mean richness, graminoid richness varied little from May
1997 to 1999 (Figure 3). In the July-mowed plots the change each year was less than one

spp m^{-2}. Mean richness declined slightly, 1.6 spp m^{-2}, in the unmowed plots. The slower

response of perennial forbs and grasses to cessation of mowing could have been due to

their reduced dependence on recruitment and reserves stored from previous growing

seasons.

<u>Yearly</u> <u>Total</u> <u>Number</u> <u>of</u> <u>Species</u>

<u>VMR</u> I determined the mean total number of species encountered during each

year for each mowing treatment at VMR (Figure 4). The 1996 totals were from only one

sampling period, the pretreatment August sample, and thus are artificially much lower

than the other years. However, based on the results from the control plots, the 1996 totals

were probably less than 5 spp m^{-2} lower than the expected yearly totals. The other means

combined both May and August samples.   Means for the control remained relatively

constant during my study whereas means increased each year in all of the mowed

treatments. In 1997 each treatment that included a March mowing tended to have higher

totals than those without a March mowing. However, the mean for M was not

significantly different from the treatments without a March mowing. Also, J was not

significantly different from the March-mowed treatments. In 1998 and 1999, the single

mowing treatments tended to produce lower means than multiple mowing treatments per

year, but only the extremes among the mowed treatments differed significantly from one

another.

<u>LCB</u> The mean yearly total number of species I found in the LCB plots are

presented in Figure 5. The 1996 means include data from only the September sample and

thus are much lower than the other totals. These totals are not representative of the actual

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1996 totals because spring ephemerals were much more abundant at LCB and were largely absent in the September samples. The treatment and control means were not significantly different in 1996 or 1997. While yearly totals increased from 1997 through 1999 in the July-mowed controls, the means declined in the unmowed plots during this same time period. In both 1998 and 1999, the means in the July-mowed plots were significantly greater than unmowed plots. By 1999, the mean in the unmowed plots (25.4 spp m^{-2}) was more than 10 spp m^{-2} less than the July-mowed plots (35.6 spp m^{-2}).

Species Turnover Rate

May species turnover rates for VMR are presented in Figure 6. Turnover rates were higher when mowing treatments were first applied (1997-1998). Turnover rates for the control were not different ($p>0.05$) the other mowing treatments, and varied less over time than the mowed treatments. The control had among the lowest turnover rates in 1997-1998 and among the highest in 1998-1999. Even though species richness in the control plots remained relatively stable over time, the turnover rates were similar to the mowed plots. The June and September mowing treatments had not been applied by May 1997. The slightly higher turnover rates resulted from comparisons of the plots not yet mowed in 1997 and mowed in 1998. The March-mowed plots, mowed in both 1997 and 1998, had the lower turnover rates. Mowing produced an increase in species richness and initially higher species turnover rates. The mowing tended to decrease May turnover rates later as new species tended to persist on the mowed sites.

August species turnover rates for VMR are presented in Figure 7. Turnover rates varied more in August than May, both in the range of rates I observed and patterns of

change. However, none of the treatment means are different from the control ($p>0.05$).

Whereas all May turnover rates decreased with time, there was no consistent trend among

treatments in August. Even the control varied considerably. In part this variability was

because most, but not all of the treatments were mowed prior to the August 1996-1997

comparison. The S treatment had not been mowed by August 1997. All of the treatments

that included mowing in March had the highest 1996-1997 species turnover rates. The

effect of the initial September mowings, including those combined with other seasons of

mowing, are seen in higher turnover rates in the 1997-1998 comparisons.

Precipitation

Precipitation varied considerably during my study. Notable periods of below

average precipitation included January through June 1996, when monthly precipitation

levels were 28.4 cm below long-term average, and May through September 1998 when

precipitation was 18.1 cm below average (Figure 8). The summers of 1996 (July-Sept.

+12.5 cm) and 1997 (June-Aug. +13.9 cm) received above average precipitation. The

greatest monthly precipitation occurred during June 1999, with 28.9 cm, making March –

June 1999, the wettest spring during my study.

Biomass Removed from Treatment Plots

Amounts of biomass (g m^{-2} oven dried) removed from the treatment plots at VMR

are presented in Table 7. Initial mowings in 1997 included considerable amounts of

accumulated litter from previous growing seasons. Less biomass was produced during

the dry 1998 growing season than during 1997 or 1999. The reduced biomasses in the M,

J and MJ treatments in 1999, which included accumulated biomass from 1998, also reflected the effects of reduced precipitation.

Little litter accumulated in the LCB plots during its management as a hay meadow. The mean amount of biomass removed increased annually, from 152.6 g m^{-2} in 1996, to 283.5 g m^{-2} in 1997, to 318.2 g m^{-2} in 1998 and 414.9 g m^{-2} in 1999. The mean biomass removed in 1997 was not significantly ($p = 0.06$) different from 1998. The other comparisons were significantly different ($p<0.05$). These changes were most likely due to changing growing conditions. The spring of 1996 was very dry and the following springs were wetter.

Photosynthetically Active Radiation

I found a negative linear relationship between biomass and the logarithm of photosynthetically active radiation (PAR). In the spring of 1999 (similar results at other times), the relationship between the log of PAR and biomass was highly significant ($p < 0.001$) and had an r^2 of 0.795.

The percentages of above canopy PAR at VMR from samples in 1998 and 1999 are shown in Figure 9. Light levels immediately after mowing are not shown in the graphs. These were approximately 90% of above canopy PAR. Except for the J treatment in June 1998 which followed abundant growth in the summer of 1997 and spring of 1998 due to above average precipitation, all mowing treatments had mean light levels significantly greater than the control on VMR. With the exceptions of J (June sample) and C (both June and September samples), the drought and resulting lower productivity in the late spring and summer of 1998 resulted in higher PAR levels in June

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and August of 1998 compared to the same samples in 1999. The higher June 1999 PAR in the J plots also reflected the 1998 drought because it was influenced by the decreased accumulated biomass from the previous growing season.

At LCB mean below canopy light levels were significantly lower in the unmowed treatment plots compared to the July-mowed controls during each sampling period (Figure 10). With the exception of higher light levels in the March 1999 sample which followed the drought in the summer of 1998, PAR levels did not change significantly in the unmowed treatment plots. The effect of increased litter depth in the unmowed plots, which I expected to decrease PAR, was apparently offset by decreased living biomass as indicated by the decreased graminoid cover (Table 8).

At each sampling time during the study, light levels in the unmowed plots at LCB were higher ($p<0.01$) than the unmowed controls at VMR. Also, during each sampling time, the mean light levels in the unmowed treatment at LCB were significantly lower ($p<0.05$) than each of the mowed treatments at VMR.

PAR and Species Richness

The different mowing seasons complicated my investigation of light as a limiting factor on species richness. Only the C and J plots were not mowed during March or the previous September. As a result, plots either had high light levels in early spring (M, S, MJ, MS, JS and MJS treatments) or were much darker from accumulated litter (J and C). There was a significant positive linear relationship between the logarithm of the March 1999 PAR and May 1999 species richness in the J plots ($r^2 = 0.6$, $p<0.0002$). There were no significant linear trends between March PAR and species richness in the other

treatments or control. All treatments except J and C were mowed in March and/or

September and therefore early spring light levels were not limiting species richness in

those treatments. Light levels in the C plots were much lower (<10% of full sun) than in

the J plots.

I also used linear regression to investigate the relationship within each treatment

for May 1999 species richness and light measured prior to mowing in June 1999 at VMR.

The results are presented as scatterplots with fitted trendlines in Figure 11. The control

plots all had both low PAR levels and low species richness, but there was no significant

linear relationship between PAR and species richness. The J plots also had PAR values

that all fell below 30% of above canopy PAR. A regression line fitted to these data had a

positive slope, but the relationship was not statistically significant. PAR values for the

remaining mowing treatments were generally greater than those in the J plots, falling

roughly in the range of 15-60% of above canopy PAR. For the March and/or September

mowed plots, the regression lines had negative slopes, but in only the S, MJ and MJS

treatments were the trends statistically significant ($p<0.05$). All plots mowed in March

and/or September had high light levels early in the spring. In early June those light levels

in the March and/or September mowed plots averaged between 29.2% (M) and 37.7% of

full sun (MS). Assuming plants were similar in size, plots with greater shading, and

therefore greater numbers of individuals, would be expected to have greater species

richness.

As I found in J plots at VMR, May 1999 species richness tended to increase with

increasing June 1999 light levels in the LCB unmowed plots (Figure 12). The unmowed

treatment plots had PAR values of approximately 13% of above canopy PAR and less. In

these plots, there was a significant positive linear relationship between species richness and light. The July-mowed controls had PAR values of approximately 12% and greater. As seen in the March and/or September mowed plots at VMR, a regression line fitted to the data had a negative slope. However, the relationship was not statistically significant (p=0.06).

Influence of *Bothriochloa ischaemum*

I found no relationship between species richness and the total graminoid cover or amount of bare soil. However, when I investigated the VMR plots with species richness markedly less than the values predicted using PAR observations, I found these plots often had relatively high cover values of *Bothriochloa ischaemum*. *B. ischaemum* was not the only plant species that influenced species richness. For example, the "outlier" in the MS plot of Figure 11 is one of the few plots with both relatively high forb cover and high cover of *Andropogon gerardii*, *Sorghastrum nutans* and *B. ischaemum*.

Because the high cover *B. ischaemum* plots appeared to have an important influence on species richness, I next investigated the relationships between species richness and *B. ischaemum* cover for each treatment at VMR (Figure 13). In seven of the eight treatments, including the control, a significant negative relationship existed between species richness and *B. ischaemum* cover. Only in the S treatment was there no significant linear relationship. PAR and *B. ischaemum* cover are not independent. Plots with high *B. ischaemum* cover had low PAR.

Discussion

Regardless of season or frequency, I found mowing tended to increase plant species richness in prairie communities. Studies on a variety of plant communities have also reported increased species richness following the initiation of mowing (Penfound 1964, Hover and Bragg 1981, Collins et al. 1998, Güsewell et al. 1998, Lepš 1999). In addition to an initial increased richness due to mowing, data from LCB and other studies (Güsewell et al. 1998, Ryser et al. 1995) support the conclusion that long-term mowing promotes higher species richness. The LCB plots, cut annually for 15+ years, had the highest May richness of any treatment on either site throughout my study. Whereas species richness of both perennial forbs and grasses increased under all mowing regimes, the greatest changes were due to annual forbs. Carson and Peterson (1990) reported the greatest impact of litter removal was on annual forb richness.

Whereas mowing causes some direct mortality, I saw little evidence that this mortality was an important factor influencing species richness from year to year. Excluding comparisons between spring and summer samples, the only multiyear trend of decreasing species richness I observed was associated with the cessation of mowing. Potentially, mowing targeted on phenological development that prevents a species from reproducing may greatly reduce a species' abundance in a community (Sheley et al. 2002). This would be most likely for annuals, species that do not reproduce vegetatively, or plants whose seeds are not available in the seed bank or through dissemination. I observed a few individual species that disappeared at least temporarily from individual plots in response to mowing. These were typically species with low abundance (low cover values). However, the more common response was the species returning to a plot

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and the appearance of new species. My analyses of short-term (3 year) effects revealed no evidence of a decline in species richness due to repeated mowing, even with three mowings per year.

In part, species richness generally remained high or increased potentially because many prairie plants, either as individuals or populations, have adaptations that allow them to capitalize on or readily recover from moderate disturbances. Characteristics utilized by annuals include early maturation, abundant seed production, effective seed dispersal mechanisms and long seed viability (Rice 1989). Location of meristems (Branson 1953), vegetative reproduction from stolons and/or rhizomes (Hartnett and Keeler 1995), survival independent of annual reproduction are probably most important in perennials. In the absence of frequent major disturbances, grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum* and *Schizachyrium scoparium* tend to dominate tallgrass prairies (Weaver and Rowland 1952). These perennials have sufficient height, the potential to produce abundant litter and their shoots have the ability to penetrate the accumulated litter (Knapp and Seastedt 1986). As a result, they are effective competitors for light.

One of the conditions necessary for increased species richness is sufficient light reaching the soil surface early in the growing season. In my experimental design, mowing in March and/or September maximized spring light levels prior to most species' resumption of growth. In these treatments, average June light levels exceeded 30% of full sun, measured near the soil surface. Further, my research indicated that a June light level equivalent to about 15% of full sun (300 μmol s^{-1} m^{-2}) generally corresponded with the highest species richness, regardless of mowing treatment. The relationship was

strongest after accumulated biomass below mowing height was reduced after two seasons of mowing. In my sites, these light levels were found in plots that had approximately 300-400 g m^{-2} oven dry biomass (above the mowing height of eight cm). Al-Mufti et al. (1977) reported similar findings in plant communities in England. They found greatest species richness in areas where biomass was in the range of 350-750 g m^{-2}. Weaver and Rowland (1954) found low species richness in prairies they characterized as big-bluestem or switchgrass types with litter amounts generally exceeding 750 g m^{-2}. Pretreatment biomass levels on VMR were similar and had low species richness.

It appears that biomass levels sufficient to reduce light levels below 300 μmol s^{-1} m^{-2} limit species richness. Light compensation and saturation levels vary among species, not only between shade and sun adapted species, but also between C_3 and C_4 species. For C_3 species, 300 to 1000 μmol s^{-1} m^{-2} (Salisbury and Ross 1992, Turner and Knapp 1996, Harvey 1979 in Taiz and Zeiger 1998) corresponds to the approximate level where photosynthetic rates are no longer limited by light. In contrast, under conditions of adequate soil moisture, *Andropogon gerardii*, a C_4 grass, does not light saturate (Turner and Knapp 1996) at light levels I observed (approximately 2000 μmol s^{-1} m^{-2}). With adequate rainfall, early June light levels in the J plots averaged less than 300 μmol s^{-1} m^{-2}. In the unmowed plots, light levels approaching light compensation points, below 20 μmol s^{-1} m^{-2}, were not uncommon. Knapp (1984) found similar light levels in undisturbed prairies.

Production, especially by the shorter species, was likely limited by these low light levels. Assuming survival is related to productivity, light-limited species should have lower survival in darker plots. These individuals likely have fewer stored reserves and

may be more susceptible to mowing-induced mortality. Knapp and Seastedt's work (1986) supports the hypothesis that light levels affect fitness. They found *Andropogon gerardii* individuals growing through mulch exhibited evidence of morphological and physiological changes that reduced fitness compared to individuals growing in full sun. Further, shaded plants may be more susceptible to drought induced stress. Working with soybeans, Fay and Knapp (1998) found shaded leaves had characteristics that made them less productive and more sensitive to drought-induced stress. These included reduced water use efficiency and lower photosynthetic carbon uptake. These factors may have been responsible for the sharp decrease in annual forb richness I observed in the plots mowed in June only during the summer of 1998 compared to the other treatments (including MJ, JS and MJS). Above average precipitation through April promoted growth, but then May through August were dry. These lower spring light levels in the J plots, in conjunction with stress induced by the June mowing, reduced August species richness. The reduced species richness was not simply the result of June mowing because treatments including June and March and/or September mowing did not result in similar reductions. Annuals may have fared better in those treatments due to the higher spring light levels. Also, I did not observe a similar reduction in August species richness when spring light levels in the June-mowed plots were higher.

The drought of 1998 had the opposite effect in 1999. Due to decreased productivity the previous growing season, June light levels were higher in 1999 than in 1998 in the June-mowed plots. Consistent with the hypothesis that improved light levels increased forb survival, I did not observe a similar decrease in annual forb richness during the summer similar to that in 1998. Instead August annual forb species richness in

the J plots was similar to those I observed in the other treatments. Turner and Knapp (1996) also observed higher forb richness following droughts that they attributed to higher light levels resulting from decreased grass production. These results suggest that higher spring light levels promote the survival of annual forbs through the summer, even with the added stress of drought and/or a June mowing.

Light alone did not explain all the variation I observed in species richness, and did not explain the lower species richness I observed at higher light levels in the March and/or September mowed plots. Another obvious factor that influenced species richness was the initial species composition. In particular the presence of the highly productive exotic, *Bothriochloa ischaemum,* seemed to have a significant impact on species richness. *Bothriochloa ischaemum* had an important impact on species richness for several reasons. First, not only did it produce abundant biomass, but the litter from *B. ischaemum* appeared to be more resistant to decomposition and therefore formed a dense litter layer that tended to persist longer below the mowing height than litter from *Andropogon gerardii* or *Schizachyrium scoparium*. The difference appeared to result from both the numerous culms produced that had more stem and less leaf material, and the taxon's tendency towards a more decumbent growth form than *A. gerardii* or *S. scoparium*. These differences were most pronounced in stands of *B. ischaemum* that had not been recently mowed. The amount of leaf material versus stem appears to increase on *B. ischaemum* with mowing. A second factor was that, unlike native tallgrass dominants, I often saw abundant reproduction by *B. ischaemum* from seed in newly open areas. Finally, once the leaf litter decomposed, few seedlings established immediately. This

was obviously different from plots dominated by *S. scoparium* where a variety of seedlings established quickly.

Perhaps the most important information from the species turnover rates was that it indicated the dynamic nature of prairie plant communities. Species turnover rates were in the range of 30-50% of the combined year species lists in both mowed and unmowed plots. Even though the turnover rates were comparable, the effect on community composition was different in that in the controls turnover occurred largely through replacement of species without an increase in species richness. In contrast, turnover rates in the mowed plots resulted from increased in species richness.

I found mowing during any season, and at any frequency, resulted in an increase in species richness. The differences between mowed and unmowed treatments were greater than differences among those with various combinations of mowing season and frequency. Higher mowing frequencies often produced higher species richness compared to single season mowing treatments, but not consistently for all mowing treatments. These results and the increased species richness I observed after a drought during a growing season suggest that higher fall and spring light levels near the soil surface are more important than mid-growing season mowing in promoting increased species richness.

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Table 1. Mean August species richness at Veterinary Medicine Ranch (VMR).
Shown are means and the results of LSD post-hoc tests within individual sampling years
comparing all treatments, and within each mowing treatment comparing different years.
Means within a column sharing the same Roman numeral in brackets are not different
($p > 0.05$). Means within a row sharing the same letter in parentheses are not different
($p > 0.05$). Symbols for mowing treatments are: M = March only; J = June only; S =
September only; MJ = March and June; MS = March and September; JS = June and
September; MJS = March, June and September; C = unmowed controls.

MOW TRT	SAMPLE TIME			
	AUGUST 1996	AUGUST 1997	AUGUST 1998	AUGUST 1999
M	10.5 [i] (c)	15.6 [i] (b)	14.3 [iii] (b)	18.4 [ii] (a)
J	10.2 [i] (c)	12.4 [ii] (b)	12.0 [iv] (b)	17.9 [ii] (a)
S	10.5 [i] (c)	11.8 [ii] (c)	14.9 [iii] (b)	19.4 [i, ii] (a)
MJ	10.3 [i] (c)	16.8 [i] (b)	16.0 [ii, iii] (b)	19.4 [i, ii] (a)
MS	10.3 [i] (c)	16.6 [i] (b)	17.1 [i, ii] (b)	19.3 [i, ii] (a)
JS	10.2 [i] (d)	11.8 [ii] (c)	15.0 [iii] (b)	19.4 [i, ii] (a)
MJS	10.1 [i] (cc)	16.9 [i] (b)	18.1 [i] (b)	20.5 [i] (a)
C	10.2 [i] (b)	12.6 [ii] (a)	10.4 [iv] (b)	12.3 [iv] (a)

Table 2. Results from ANOVAs on August Veterinary Medicine Ranch (VMR) species richness. Shown are means and *p* values from three separate factorial ANOVAs on total species richness from August sampling. Symbols for mowing treatments are: M = March only; J = June only; S = September only; MJ = March and June; MS = March and September; JS = June and September; MJS = March, June and September; C = unmowed controls.

COMPARISONS		SAMPLING TIME					
		AUGUST 1997		AUGUST 1998		AUGUST 1999	
		MEAN	*p*	MEAN	*p*	MEAN	*p*
March main effect	March	16.5	<0.0001	16.4	<0.0001	19.4	<0.0001
	No Mar.	12.2		13.1		17.2	
June main effect	June	14.5	0.3809	15.3	0.0213	19.3	0.0002
	No Jun.	14.2		14.2		17.4	
September main effect	Sept.	14.3	0.8837	16.3	<0.0001	19.6	<0.0001
	No Sept.	14.3		13.2		17.0	
M*J interaction			0.2738		0.6072		0.0986
M*S interaction			0.1264		0.1401		0.0016
J*S interaction			0.6609		0.2163		0.0096
M*J*S interaction			0.5107		0.6501		0.0052

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Table 3. Mean May species richness at Veterinary Medicine Ranch (VMR).
Also shown are the results of LSD post-hoc tests within sampling years and mowing
treatments. Means within a column sharing the same Roman numeral in brackets are not
different ($p > 0.05$). Means within a row sharing the same letter in parentheses are not
different ($p > 0.05$). Symbols for mowing treatments are: M = March only; J = June only;
S = September only; MJ = March and June; MS = March and September; JS = June and
September; MJS = March, June and September; C = unmowed controls.

MOW TRT	SAMPLE TIME		
	MAY 1997	MAY 1998	MAY 1999
M	15.6 [i] (c)	21.1 [ii] (b)	25.5 [ii] (a)
J	13.8 [ii] (c)	20.3 [ii] (b)	27.0 [i, ii] (a)
S	11.8 [iii] (c)	20.3 [ii] (b)	26.4 [ii] (a)
MJ	17.0 [i] (c)	24.0 [i] (b)	28.1 [i, ii] (a)
MS	16.1 [i] (c)	25.3 [i] (b)	27.6 [i, ii] (a)
JS	12.7 [ii, iii] (c)	22.3 [i, ii] (b)	27.8 [i, ii] (a)
MJS	17.1 [i] (c)	26.1 [i] (b)	29.4 [i] (a)
C*	13.0 [ii, iii]	11.9 [iii]	12.9 [iii]

* no significant treatment effect from May 1997 through May 1999

Table 4. Results from ANOVAs on May Veterinary Medicine Ranch species richness. Shown are means and *p* values from three separate factorial ANOVAs on May total species richness. Symbols for mowing treatments are: M = March only; J = June only; S = September only; MJ = March and June; MS = March and September; JS = June and September; MJS = March, June and September; C = unmowed controls.

COMPARISONS		SAMPLING TIME					
		MAY 1997		MAY 1998		MAY 1999	
		MEAN	*p*	MEAN	*p*	MEAN	*p*
March main effect	March	16.4	<0.0001	24.1	<0.0001	27.6	<0.0001
	No Mar.	12.8		18.7		23.5	
June main effect	June	15.2	0.0215	23.2	<0.0001	28.1	<0.0001
	No Jun.	14.1		19.6		23.1	
September main effect	Sept.	14.4	0.3337	23.5	<0.0001	27.8	<0.0001
	No Sept.	14.8		19.3		23.4	
M*J interaction			0.6514		0.0048		0.0001
M*S interaction			0.0951		0.0857		0.0002
J*S interaction			0.7962		0.0005		<0.0001
M*J*S interaction			0.7469		0.0776		<0.0001

Table 5. Mean September species richness at Lake Carl Blackwell.
Shown are the results of LSD post-hoc tests within mowing treatments. Means in a row
with the same letter in parentheses are not different ($p<0.05$), and results of independent
t-tests comparing control and mowing means within each sampling season. Means in a
column with the same Roman numeral in brackets are not different ($p<0.05$). Symbols for
mowing treatments are: no mow = unmowed treatment plots, mow = control, continued
long-term July mowing.

MOW TRT	SAMPLE TIME			
	SEPT. 1996	SEPT. 1997	SEPT. 1998	SEPT. 1999
no mow	13.3 [i] (b)	18.2 [i] (a)	13.7 [i] (b)	15.1 [i] (b)
mow	13.2 [i] (b)	16.3 [ii] (a)	11.4 [ii] (b)	13.1 [ii] (b)

Table 6. Mean May species richness at Lake Carl Blackwell.
Shown are the results of LSD post-hoc tests within mowing treatments. Means in a row
with the same letter in parentheses are not significantly different ($p<0.05$), and results of
independent t-tests comparing control and mowing means within each sampling season.
Symbols for mowing treatments are: no mow = unmowed treatment plots, mow =
control, continued long-term July mowing.

MOW TRT	SAMPLE TIME		
	MAY 1997	MAY 1998	MAY 1999
no mow	29.9 [i] (a)	29.5 [ii] (a)	23.8 [ii] (b)
mow	28.1 [i] (b)	33.4 [i] (a)	34.4 [i] (a)

Table 7. Mean oven-dried biomass (g m^{-2}) removed with mowing from treatment plots at Veterinary Medicine Ranch (VMR). Mowing treatments are: M – March only, J – June only, S – September only, MJ – March and June, MS – March and September, JS – June and September, MJS – March, June and September. s.e. = standard error

Month Mowed		M	J	S	MJ	MS	JS	MJS
March 1997	mean	659.8			733.5	721.3		720.6
	s.e.	210.9			188.1	164.0		163.6
June 1997	mean		799.9		99.8		779.1	118.3
	s.e.		143.3		30.0		230.1	35.9
Sept. 1997	mean			1036.2		407.9	327.4	329.9
	s.e.			130.7		132.5	119.5	84.1
March 1998	mean	389.7			290.7	11.7		12.0
	s.e.	177.1			102.4	4.5		6.9
June 1998	mean		578.5		148.3		148.9	136.7
	s.e.		168.2		41.3		39.8	66.8
Sept. 1998	mean			303.3		215.3	96.0	70.3
	s.e.			93.0		87.5	48.1	26.1
March 1999	mean	229.8			76.5	4.9		5.4
	s.e.	148.9			51.9	1.1		2.2
June 1999	mean		351.6		192.8		172.2	178.5
	s.e.		98.1		55.0		45.7	78.6
Sept. 1999	mean			457.3		407.2	180.3	168.6
	s.e.			141.8		130.0	66.1	41.4

Table 8. Mean total percent cover of graminoids, forbs, bare soil and litter for the unmowed (no mow) and July-mowed (mow) treatments at Lake Carl Blackwell (LCB) during three consecutive May samples. Symbols for mowing treatments are: no mow = unmowed treatment plots, mow = control, continued long-term July mowing.

	Graminoids		Forbs		Bare Soil		Litter	
Month Mowed	no mow	mow	no mow	mow	no mow	mow	no mow	mow
May 1997	36.7	35.3	21.4	14.2	1.7	2.6	86.1	83.3
May 1998	28.1	24.2	8.9	6.7	0.5	2.0	86.1	73.6
May 1999	21.9	27.8	18.6	14.7	0.3	8.3	87.5	51.4
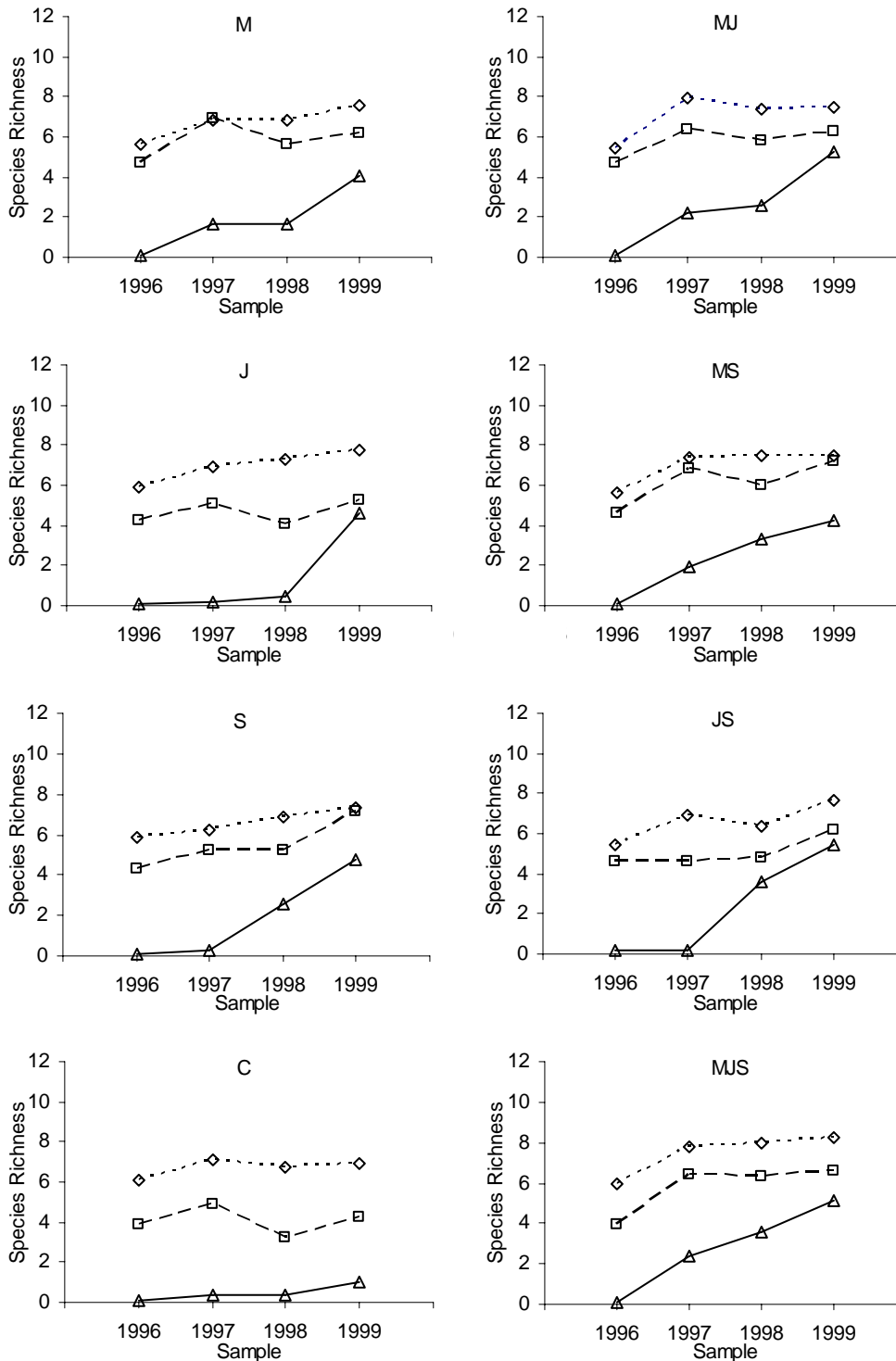
Figure 1. August Veterinary Medicine Ranch (VMR) species richness of perennial graminoids, perennial forbs and annual forbs (diamonds = perennial graminoids, squares = perennial forbs, triangles = annual forbs). Symbols for mowing treatments are: M = March only; J = June only; S = September only; MJ = March and June; MS = March and September; JS = June and September; MJS = March, June and September; C = unmowed controls.
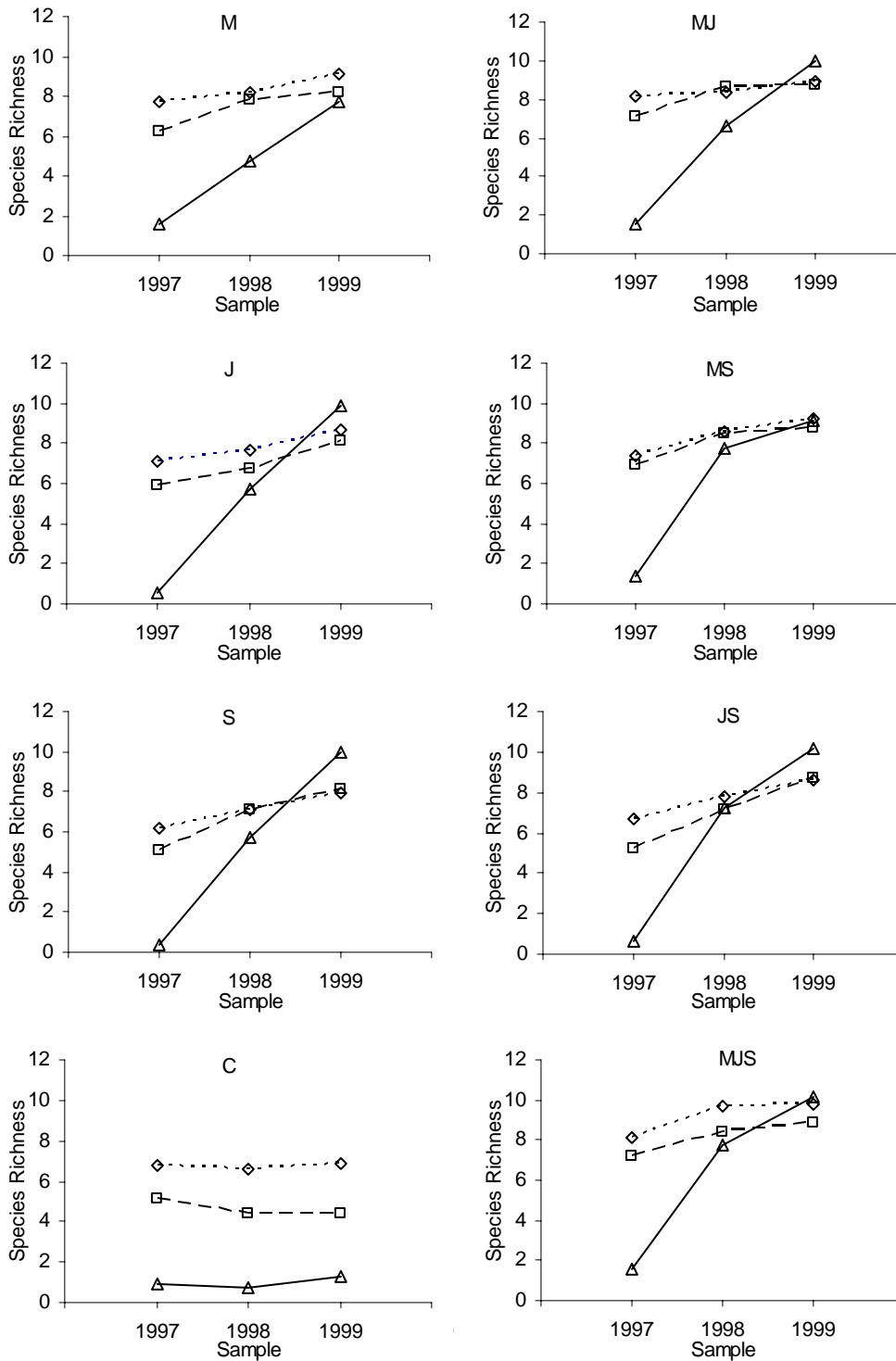
Figure 2. May Veterinary Medicine Ranch (VMR) species richness of perennial graminoids, perennial forbs and annual forbs (diamonds = perennial graminoids, squares = perennial forbs, triangles = annual forbs). Symbols for mowing treatments are: M = March only; J = June only; S = September only; MJ = March and June; MS = March and September; JS = June and September; MJS = March, June and September; C = unmowed controls.
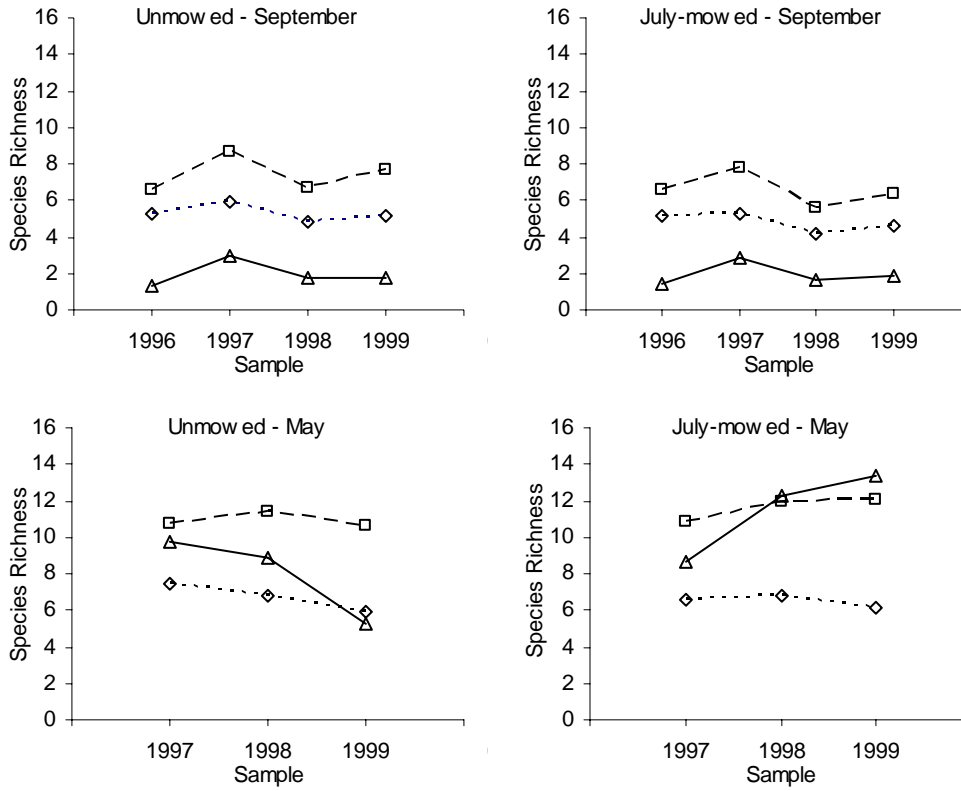
Figure 3. September and May Lake Carl Blackwell species richness of perennial graminoids, perennial forbs and annual forbs (diamonds = perennial graminoids, squares = perennial forbs, triangles = annual forbs).

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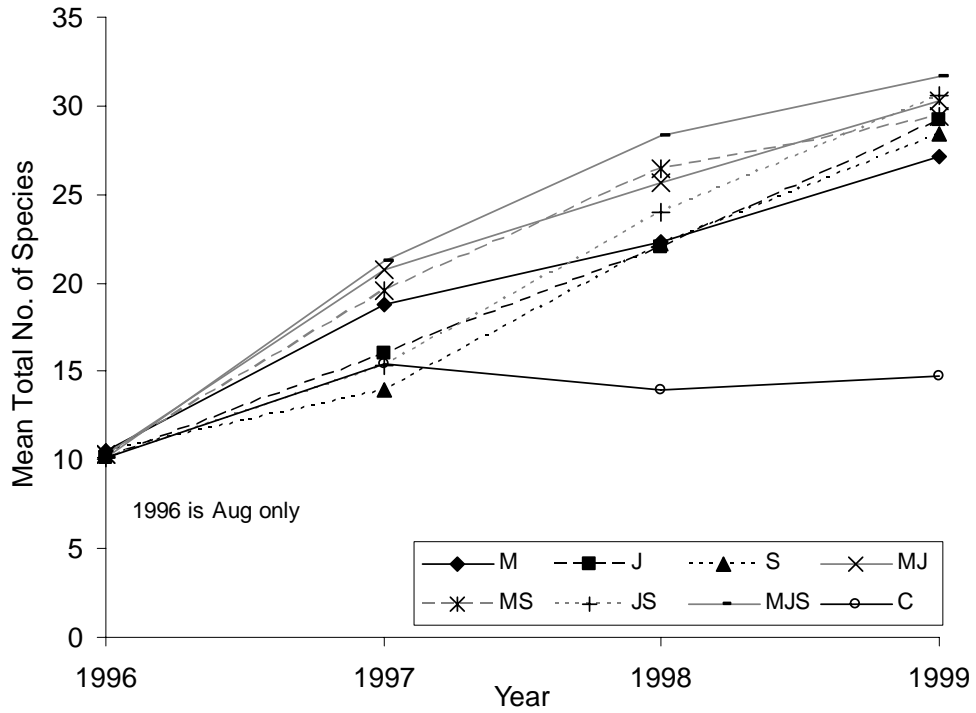
Figure 4. Veterinary Medicine Ranch (VMR) mean yearly total species richness by mowing treatment. The 1996 total is from only the August sample, all others include May and August.
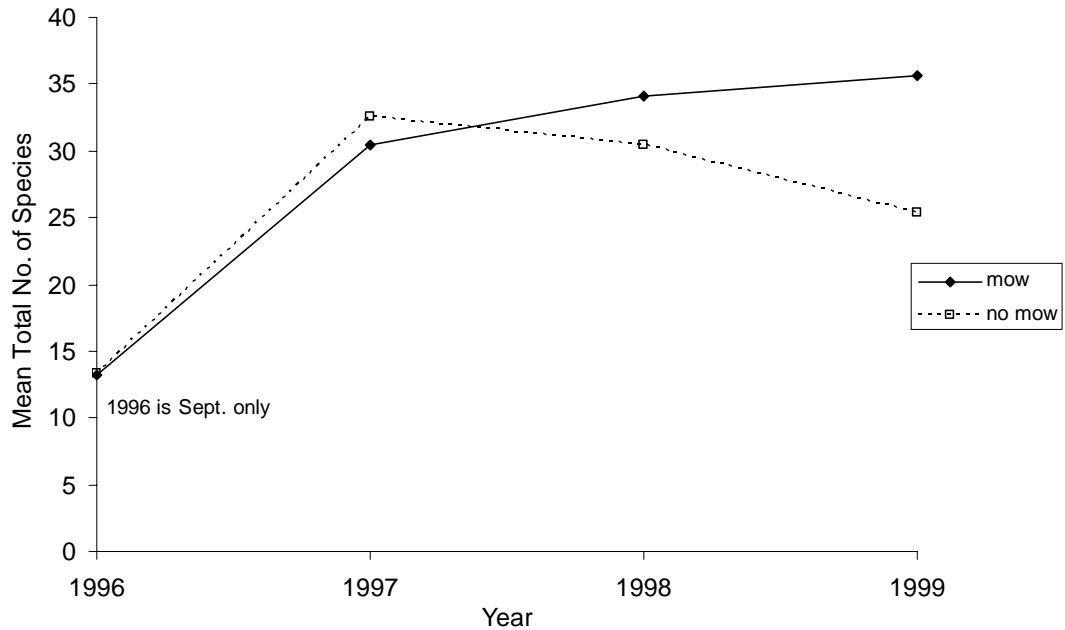
Figure 5. Lake Carl Blackwell mean yearly total species richness by mowing treatment. The 1996 total is from only the September sample, all others include May and September.
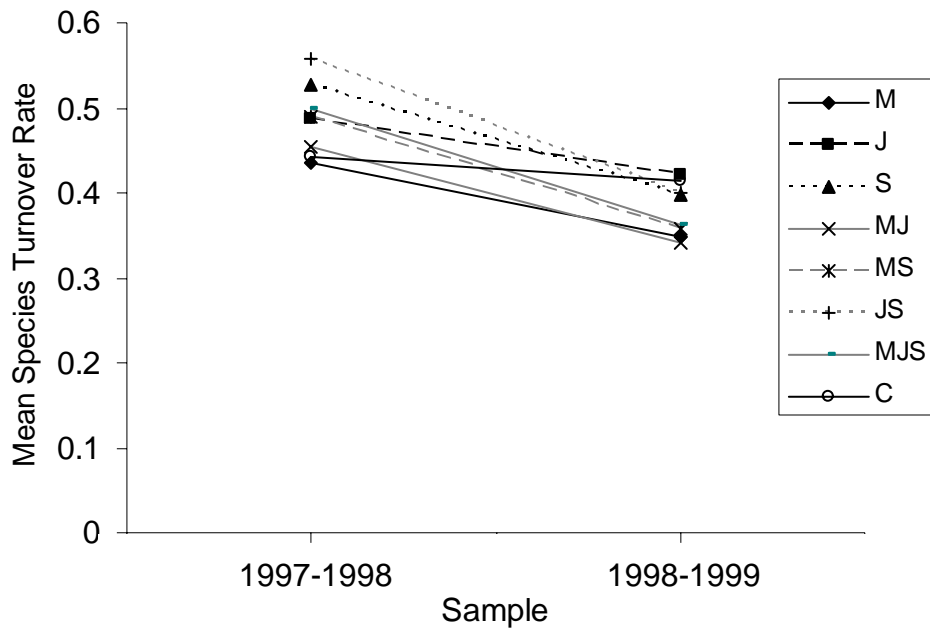
Figure 6. May Veterinary Medicine Ranch (VMR) species turnover rates by mowing treatment. All March-mowed plots were mowed once prior to May 1997. All other treatments had not been mowed prior to May 1997. None of the means are significantly different ($p>0.05$).
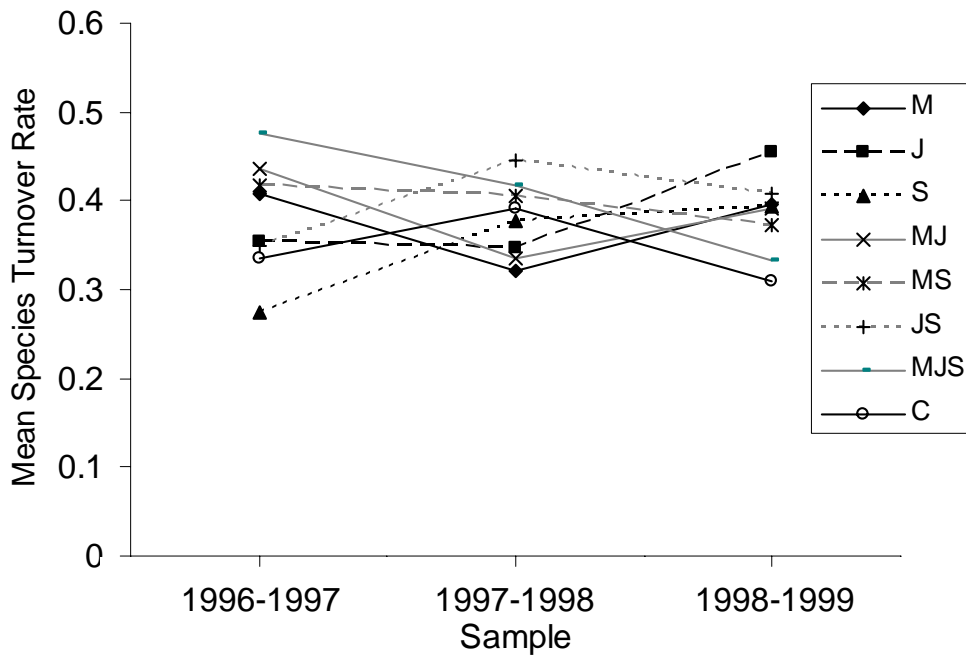
Figure 7. August Veterinary Medicine Ranch (VMR) species turnover rates by mowing treatment. All March and June-mowed treatments had been mowed prior to August 1997. The September mowing treatment had not yet been applied in 1997. None of the means are significantly different ($p>0.05$).
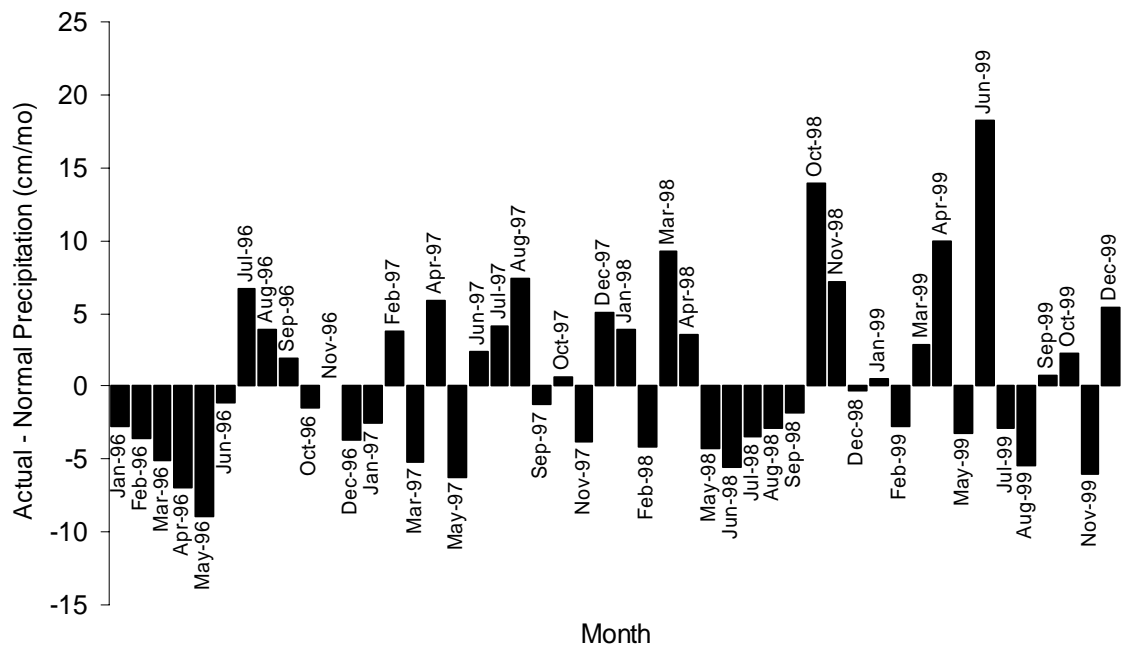
Figure 8. Deviations from long-term mean monthly precipitation at the Marena Mesonet station.
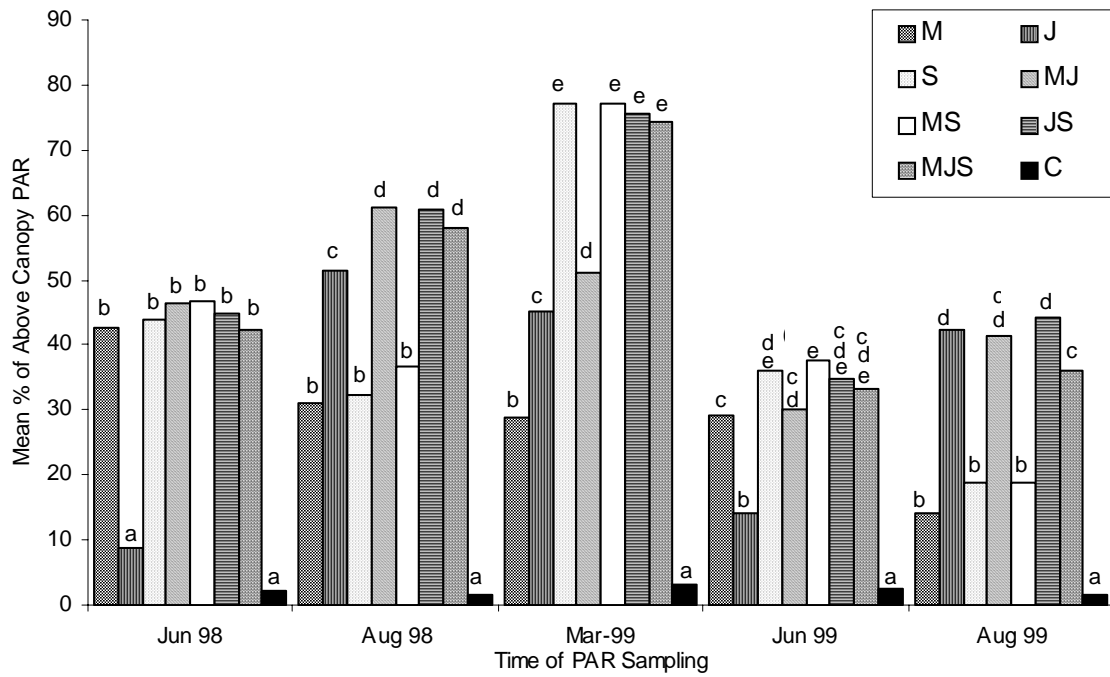
Figure 9. Mean percentage of above canopy PAR as a function of sampling period at Veterinary Medicine Ranch. Columns within each sampling time that have the same lower case letter above are not significantly different ($p < 0.05$).
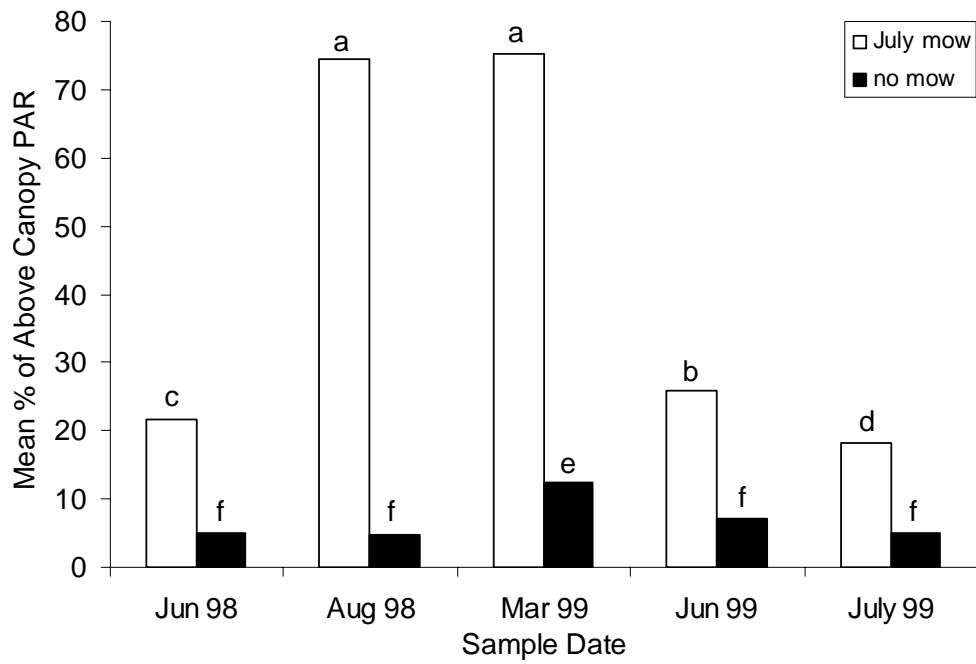
Figure 10. Mean percentage of above canopy PAR for both treatment at Lake Carl Blackwell (LCB). Columns with the same letter are not significantly different ($p < 0.05$). The two categories represent the July-mowed controls and the unmowed treatment plots.
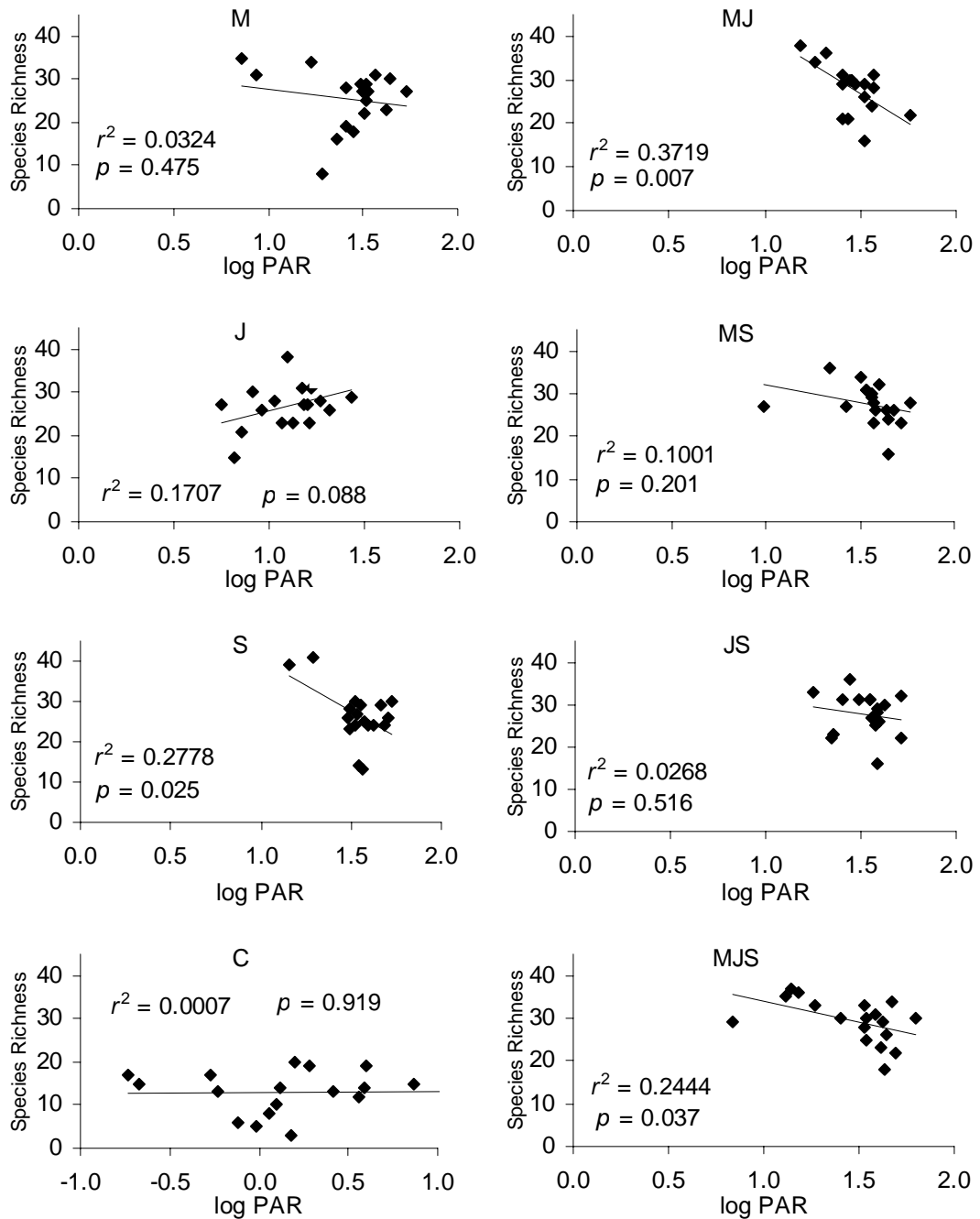
Figure 11. May 1999 Veterinary Medicine Ranch species richness as a function of the logarithm of the percentage of June 1999 above canopy photosynthetically active radiation (PAR). Symbols for mowing treatments are: M = March only; J = June only; S = September only; MJ = March and June; MS = March and September; JS = June and September; MJS = March, June and September; C = unmowed controls.
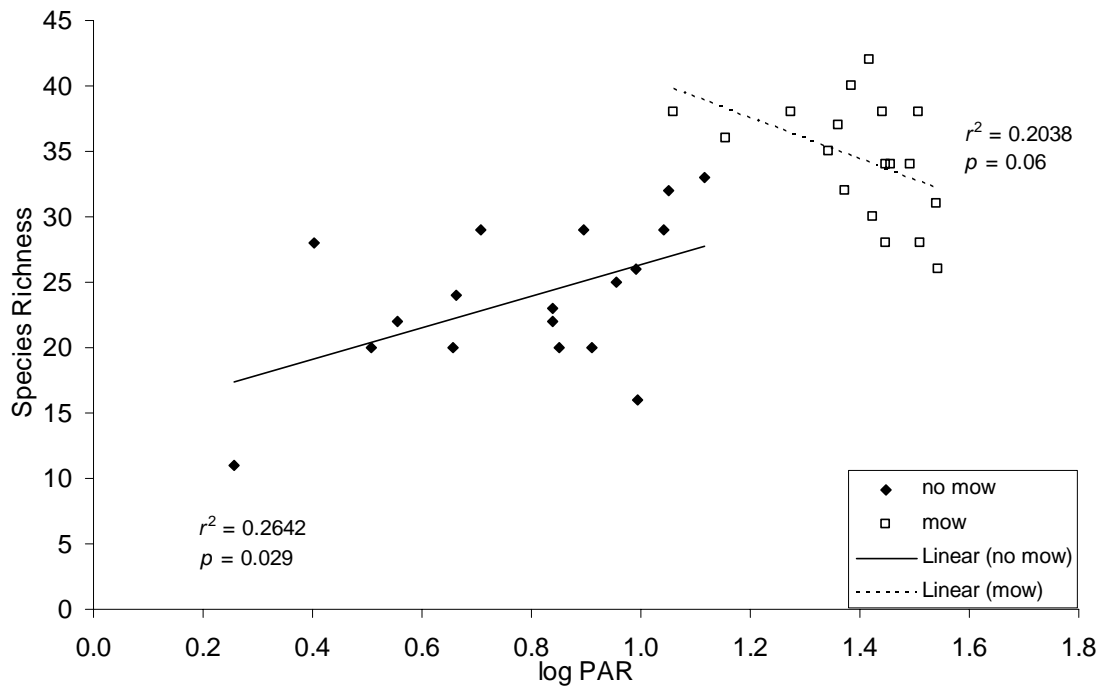
Figure 12. May Lake Carl Blackwell mean species richness versus June mean percentage of above canopy PAR during 1999.
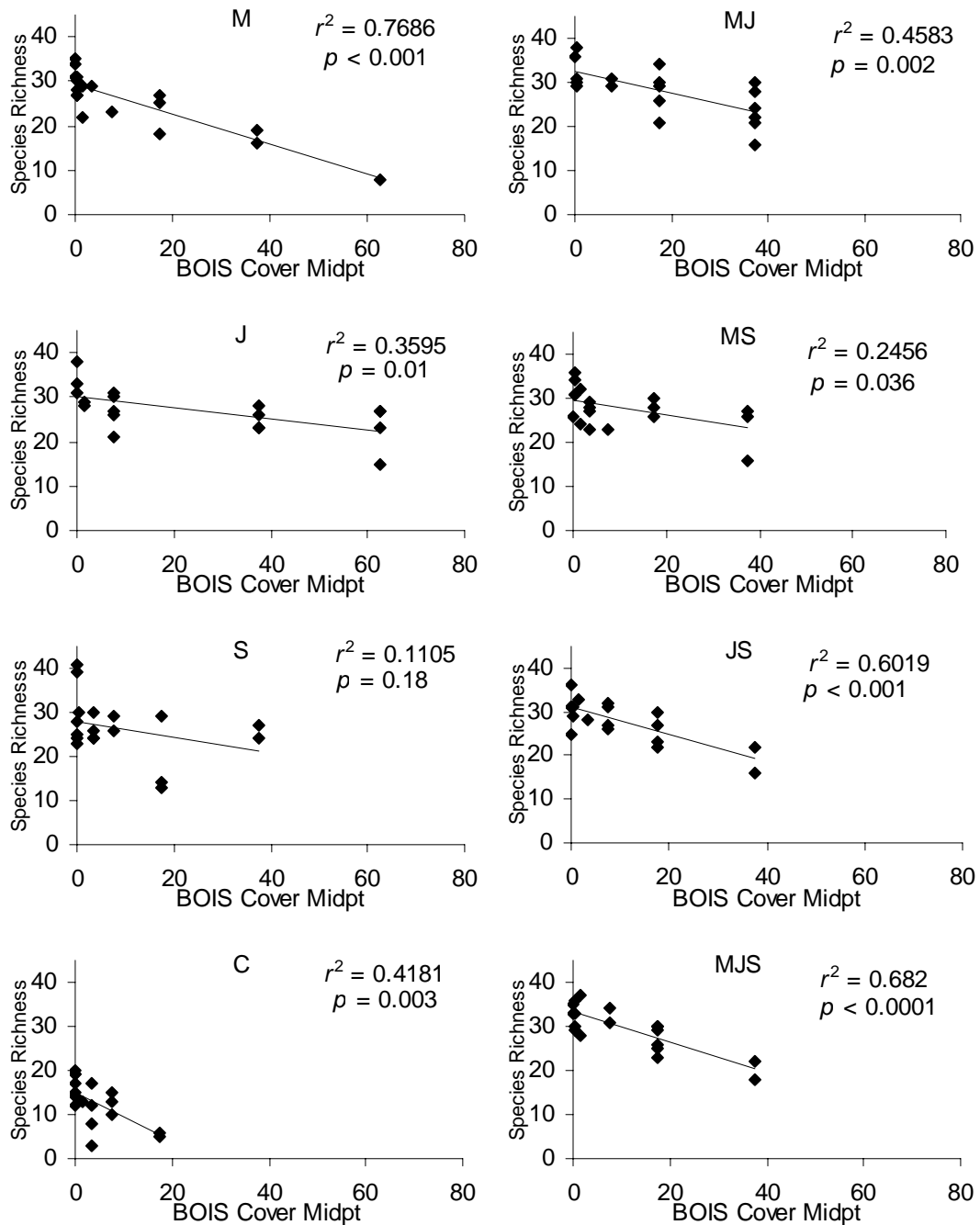
Figure 13. May 1999 Veterinary Medicine Ranch species richness as a function of
Bothriochloa ischaemum cover class midpoint for each mowing treatment. Symbols for
mowing treatments are: M = March only; J = June only; S = September only; MJ =
March and June; MS = March and September; JS = June and September;
JS = March, June and September; C = unmowed controls.

CHAPTER II

THE EFFECTS OF MOWING ON SPECIES COMPOSITION

Introduction

In chapter one, I reported the effects of mowing on species richness. In general, I found mowing increased species richness. Presence versus absence of mowing produced the greatest differences in species richness, with season and frequency of mowing of lesser importance. I also found variables such as precipitation, light availability near the soil surface and abundance of *Bothriochloa ischaemum* (L.) Keng were important factors influencing species richness. Analysis of richness alone ignores species abundance. In this chapter I report the effects of season of mowing on species composition, incorporating frequency and aerial cover as measures of abundance. Others have used above-ground cover as a measure of abundance (Hover and Bragg 1981, Gibson and Hulbert 1987, Güsewell et al. 1998).

Although mowing removes vegetation at a relatively uniform height, its effect on species may not be uniform. Plants initiate growth at differing times, and vary in growth rates and heights at maturity. Therefore, mowing at different seasons removes varying amounts of biomass from different species. Smaller stature species, if their survival or productivity is limited by light, may benefit from the removal of overlying biomass, and experience less damage from mowing (Neiland and Curtis 1956). Also, the effect of

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mowing varies among species due to differences in the position of their apical meristems. Grasses vary in their tolerance, but are generally more resistant to mowing and grazing than forbs or woody species because their meristems are located below or near the soil surface early in the growing season (Branson 1953). Tolerance to grazing varies among grasses. A cespitose habit may decrease resistance while rhizomes and stolons may provide greater grazing resistance (Mack and Thompson 1982). In contrast, dicots with apical meristems near shoot tips are more susceptible to removal by mowing or grazing (Rechenthin 1956). Also grasses often overcompensate, thus quickly replacing lost leaf area (Turner et al. 1993, Damhoureyeh and Hartnett 2002).

In both North American tallgrass prairies (Hover and Bragg 1981, Collins et al. 1998, Davison and Kindscher 1999) and European grasslands (Ryser et al. 1995, Huhta et al. 2001) mowing significantly affects species composition. Ryser et al. (1995) reported that annual or semiannual mowing promoted higher species richness in Swiss grasslands than less frequent or no mowing. They also found that October mowing increased forb richness more than July mowing. However, Güsewell et al. (1998), also in Switzerland, found similar species compositions on summer and winter cut meadows. They also reported differences between mowed and unmowed plots.

In this study I investigated the effects of season and frequency of mowing on two prairie communities in north-central Oklahoma, an annually mowed hay meadow and a lightly grazed pasture. I used multivariate statistics to test the hypothesis that composition responds to different combinations of mowing seasons. In addition to the initiation of mowing, I also compared the results of cessation of mowing on an area that had been mowed annually for several years.

Methods

<u>Study Sites</u>

I selected two sites with complementary historical management regimes for this study. Both were located in north-central Oklahoma, USA, approximately 16 km west of Stillwater. The Veterinary Medicine Ranch site (VMR) was in a pasture that was lightly grazed by horses, *Equus caballus*, and infrequently cut for hay or burned. The Lake Carl Blackwell site (LCB) was in a hay meadow that was cut annually in late July, for more than 15 years. The soils at both sites were Grainola-Lucien complex, a clay loam with moderate fertility (Soil Conservation Service 1987). I found a few small sandstone rocks on the soil surface, and in the subsoil. Both sites sloped slightly (<5% slope) with a westerly aspect.

In 1996, at the beginning of the study, VMR exhibited a heavy accumulation of grass litter and low forb density. In contrast, LCB had much less litter accumulation above the annual mowing height and supported a greater density of forbs. *Schizachyrium scoparium* (Michx.) Nash and *Sorghastrum nutans* (L.) Nash were abundant at both sites. *Andropogon gerardii* Vitman, *Panicum virgatum* L., and *Bouteloua curtipendula* (Michx.) Torr. also occurred at both sites, but were more abundant at VMR. *Bothriochloa ischaemum* (L.) Keng was abundant at VMR, forming nearly pure stands in some areas, but very uncommon at LCB. *Solidago nemoralis* Ait., *S. missouriensis* Nutt., *Erigeron strigosus* Muhl. ex Willd., and *Gaillardia aestivalis* (Walt.) Rock were abundant forbs at LCB, whereas *Ambrosia psilostachya*DC., *Aster ericoides* L., *A. oblongifolius* Nutt., and *Artemisia ludoviciana* Nutt. were more abundant at VMR.

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<u>Climatic</u> <u>Data</u>

I obtained weather data from the Oklahoma Mesonet, a network of automated monitoring stations (Oklahoma Climatological Survey). With the exception of long-term averages, which were not available, all data were from the Marena site, located about 3.2 km east of VMR and 6.5 km south of LCB. Long-term averages came from the Stillwater station, approximately 10 km east and 6 km north of Marena.

<u>Plot</u> <u>Layout</u>

I established permanent 1 m^2 plots in a grid at each site. Eighteen replicates were assigned to each of the mowing treatments and controls. The VMR site consisted of a total of 144 plots (12 rows of 12 plots each), and LCB had 36 plots (9 rows of 4 plots each). A 73.5 cm wide buffer surrounded each plot at both sites. The buffer received the same mowing treatment as the plot. Among the plots, mowed paths 53 cm wide provided access to the plots and aided in their location and identification.

I drove short sections of PVC pipe (1.25 cm I.D. by 20 cm long) into the soil at opposite corners (SE and NW) of each permanent plot. The PVC pipe facilitated accurate placement of the one square meter frame during each sampling period. I constructed the sampling frame of aluminum channel and attached two 30 cm long legs made from sections of 6.35 mm (1/4 inch) diameter all-thread rods to opposite corners using short strips of galvanized flat iron. During sampling, the all-thread rods slid into the PVC pipe and held the frame slightly above the soil surface.

I sampled each site in the late summer of 1996 prior to initiating the mowing treatments. VMR was sampled in August and LCB in September, 1996. In 1997-1999, I sampled each site twice per year. VMR was sampled in early May and early August. LCB was sampled in late May and early September. Sampling at VMR occurred over a period of two to three weeks. LCB sampling usually took less than two weeks. I sampled the north-south oriented rows at both sites in a random sequence that I changed for each sample period. Sampling always occurred at least one month after the most recent mowing.

During sampling, I listed all species present and estimated live cover for individual species and also cover for vegetation and habitat classes within each plot. Individual plants were included in a sample if any portion of the shoot was present in the plot. Vegetation/habitat cover classes consisted of graminoid, forb, woody, cryptogam, litter, bare soil, and rock. Vegetation cover for individuals and classes were assigned to one of following categories: rare (one small seedling), <1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75% or 75-100% of 1 m^2.

Mowing Treatments

Assigned treatments reversed the existing management at each site. I established seven mowing treatments at VMR and one unmowed control (C). The mowing treatments at VMR varied in season and frequency of mowing. The mowing treatments included: March only (M); June only (J); September only (S); March and June (MJ); March and September (MS); June and September (JS); and March, June and September

(MJS). At LCB the experimental treatment was cessation of annual mowing. The control plots at LCB were mowed in late July, a continuation of the long-term management. I cut all mowed plots at both sites at a height of eight cm above the ground. The clippings were removed from the plots, buffers and paths during each mowing at both sites.

Using the data from the 1996 sample, I ranked the plots at VMR by species richness. Plots with the same species richness were arranged sequentially based on Shannon species diversity index scores. I then assigned the plots to 18 consecutive blocks of similar species richness, each block with eight plots. Treatments were randomly assigned within each block. At LCB, mowing treatments were assigned randomly.

Analyses

I used Detrended Correspondence Analysis (DCA) to compare the species composition of VMR and LCB. I then used a series of partial Redundancy Analyses (pRDA) to investigate further changes in the species composition of VMR in response to the mowing treatments for individual sample times. I used pRDAs because of the short gradient length, approximately two standard deviation units (sdu), in the DCAs for VMR (ter Braak and Prentice 1988). The August 1996 species richness blocks served as covariables in the pRDAs. Assigned mowing treatments, served as environmental variables regardless of when treatments were initiated. Dividing species scores by the standard deviation reduced the influence of species with high variance in the ordination diagrams (ter Braak and Smilauer 1998). I used a square-root transformation to

normalize the data. Significance was evaluated using reduced model Monte-Carlo

permutations. Permutations were restricted to within the species richness blocks. I

repeated each pRDA, omitting the controls, to test for significant differences among only

the mowing treatments.

I performed analyses of variance on the summed cover of perennial graminoids,

perennial forbs, and annual forbs per plot. I omitted annual graminoids and woody

species because of their rarity at VMR. I used LSD post-hoc tests to compare means

among treatments, and also within treatments over time. These analyses were conducted

using SPSS (1998). I also compared mean percent cover and frequencies for selected

species, including some perennial graminoids, perennial forbs and annual forbs. I

selected species that were relatively abundant and had longer vectors in some of the

ordination diagrams. Longer vectors indicate a stronger relationship between a species

and a mowing treatment. I calculated mean percent cover using the number of plots in

which a species was present, not the total number of plots in a treatment, because I

assumed the initial presence or absence of a species from a plot was primarily due to the

influence of seed dispersal, not the mowing treatment. The often small sample sizes and

skewed data precluded using statistical tests on these.

<div align="center">Results</div>

Total Numbers of Species

In May 1997, the total number of species I encountered in plots at LCB was much

higher than in unmowed VMR plots. A total of 76 species, 31 perennial forbs, 16

perennial graminoids, 25 annual forbs, 2 annual graminoids, 1 woody species and 1

unknown occurred in the LCB mowed treatment. In contrast, the unmowed treatments at

VMR had 50-54 total species, with 26-27 perennial forbs, 15-17 perennial graminoids, 7-

12 annual forbs, 0 annual graminoids, 1-2 woody species, and few unknown plants.

Delayed regrowth or germination of forbs between the July mowing and September

sampling at LCB, resulted in smaller differences between the August VMR and

September LCB totals.

Combining all seven sampling periods, I found a total of 122 species at LCB and.

134 species at VMR. Of these totals 35% (LCB) - 37% (VMR) were perennial forbs,

33% (LCB) – 32% (VMR) were annual forbs, 25% (LCB) – 24% (VMR) were perennial

graminoids, 4% (LCB) – 1% (VMR) were annual graminoids, and 3% (LCB) - 5%

(VMR) were woody species. Comparing different mowing treatments at VMR, the total

number of annual forbs identified were very similar among the mowed treatments, 30 (M,

MJ, MS, JS) -33 species (MJS), whereas only 17 species were found in the unmowed

controls. I found the fewest number of perennial forbs, 29 species, in the C, whereas

numbers ranged from 32 (MS) – 39 species (J, JS, MJS) in the mowed treatments. The

number of different perennial graminoids was also lowest in the control, with 21 species,

and varied from 24 (M) – 27 species (J, MJ) in the mowed plots. Annual graminoids and

woody species were not abundant in either the controls or any of the mowed plots at

VMR. I found *Juniperus virginiana* L. in each of the mowing treatments after mowing

was initiated at VMR, but never in the unmowed controls. *J. virginiana* also occurred at

LCB.

Twenty-five species were unique to a mowing treatment at VMR. None of the

species found in the C were unique to that treatment. Of the 25 unique species, I

encountered 20 only once. Ten were unidentified seedlings. The five species whose

distributions were limited to single treatments which I encountered more than once

included: *Tragopogon dubius* Scop.(total of three times in two different JS plots, during

three different sampling times), *Tradescantia occidentalis* (Britt.) Smyth (three different

sampling times in the same J plot), *Phalaris caroliniana* Walt. (two different sampling

times in the same MJ plot), *Nelumbo lutea* (Willd.) Pers. (two different sampling times in

the same MJS plot), and an unidentified seedling (in two different MJS plots during the

same sampling period). Each of these species had aerial cover of less than one percent.

Comparison of VMR and LCB

I compared the 1996 species composition of VMR (August) and LCB

(September) using DCA. The resulting ordination diagram had a first axis length of

3.144 standard deviation units (sdu) and an eigenvalue of 0.479. This axis separated the

LCB plots from the VMR plots (Figure 1). Species scores from the 1996 DCA were

plotted separately (Figure 2, see Appendix A for species' abbreviations). For clarity,

only species with weights greater than five are shown. *Schizachyrium scoparium* was

found in many of the plots at both sites. However, there were some VMR plots that

shared no species with any of the LCB plots.

Bothriochloa ischaemum contributed to the separation of the VMR and LCB plots

(Figure 2). *B. ischaemum* was abundant and widely distributed at VMR, but not present

in the LCB plots in 1996. Cover values for *B. ischaemum* tended to decrease as axis 1

sample scores increased. I found the opposite relationship between *S. scoparium* cover

and axis 1 scores. Most of the highest *S. scoparium* cover values occurred in LCB plots.

The presence of several forbs also distinguished LCB from VMR. These forbs included *Solidago nemoralis, Erigeron strigosus, Achillea millefolium* L. and *Gaillardia aestivalis* which were abundant in LCB and absent, or rarely encountered, at VMR in 1996. Species abundant at VMR, but not LCB, included: *Bouteloua curtipendula, Sporobolus asper* (Michx.) Kunth*, Ambrosia psilostachya,* and *Aster ericoides*. *Schizachyrium scoparium*, *Andropogon gerardii* and *Sorghastrum nutans* were common at both sites and were located near the middle of axis 1.

DCA axis 2 had a gradient length of 2.436 sdu and an eigenvalue of 0.263 (Figure 1). I found the greatest variability in axis 2 scores among the VMR samples. Those plots with high *A. gerardii* cover values had low axis 2 scores. In the one LCB plot with a very low axis 2 score, *A. gerardii* was abundant. It was also the only LCB plot in which *S. scoparium* was absent. There were also a few VMR plots dominated by *A. gerardii* or *B. ischaemum* in which *S. scoparium* was not present. Among the more abundant grasses, *A. gerardii* had the lowest axis 2 score (Figure 2). As axis 2 scores increased, I next found *B. ischaemum*. It was followed by *S. nutans. Bouteloua curtipendula, Panicum virgatum* and *S. scoparium*, were next, all with very similar axis 2 scores. *Bouteloua hirsuta* had a high axis 2 score that was surpassed only by the less abundant *Leptoloma cognatum* (Schult.) Chase. I did not measure soil depth, but based on observations of surrounding areas, number of rocks hit during installation of the PVC pipe quadrat corners, and vegetation composition and height, DCA axis 2 appears to correspond to a gradient of soil depth, with soil depth decreasing as axis 2 scores increased. DCA axes 3 and 4 had eigenvalues of 0.159 and 0.126 respectively and gradient lengths of approximately 2.1 sdu. I could not interpret either of these axes.

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Ordination diagrams resulting from DCAs performed on other sampling times appeared similar to August 1996. In all, the VMR and LCB sample scores were separated from one another along axis 1. The ordination diagrams using May data differed in that the range of axis 1 sample scores for VMR were narrower, most within 1 sdu of each other, compared to a range of 2 sdu in the August samples. The most obvious shift in the more abundant species' scores from the May samples was an increase in *B. ischaemum* axis 2 scores, placing it near *B. hirsuta.*

In 1996, none of the mowing treatments had been applied. The plots assigned to the different treatments were intermixed with little separation between assigned treatments. By May 1999, the unmowed plot scores on both VMR (control) and LCB (unmowed treatment) were fairly distinctly separated from the mowing treatments by axis 3 scores (Figure 3). The sample scores for the various VMR mowing treatments remained intermixed. Axis 3 had a gradient length of 1.96 sdu and eigenvalue of 0.11. The DCA ordination diagram from the analysis of August-September 1999 (not shown) revealed that the VMR controls remained somewhat separated from the mowed treatments. The controls tended to have lower axis 3 scores than the mowed plots. The September 1999 LCB mowed and unmowed plots were not separated by axis 3 (or other axes) scores. The July-mowed controls and non-mowed treatment plots at LCB in September 1999 were not clearly separated because many of the annuals which distinguished the mowed from non-mowed plots in the spring had completed their life cycles or were removed by the July mowing.

Responses to Initiation of Mowing Treatments at VMR

The pRDA on the August 1996 pretreatment data with assigned mowing treatments as environmental variables revealed low eigenvalues for the axes. The axes did not explain a significant amount of the variation in species data (Table 1). The August 1997 through 1999 pRDAs revealed an increasingly important influence of mowing on species composition (Table 1). Eigenvalues for the first two axes increased from 1996 to 1999 as did the cumulative percentages of variance explained by the axes. The sums of all the canonical axes were significant ($p<0.05$) in August 1998 and 1999. The first axis alone was significant only in 1999. In a similar fashion, analyses on the May data revealed eigenvalues for the first axis and cumulative percentages of variance explained increased yearly from 1997 through 1999 (Table 2). In May 1997, the eigenvalues for the first canonical axis and the sum of all the canonical axes were greater than those from August 1996, but neither were significant. Both the first axes and sums of the axes were statistically significant in May 1998 and 1999.

The biplot of the assigned mowing treatments as environmental centroids and perennial graminoid species scores from August 1996 (Figure 4) revealed three groups of species. Listing the more abundant species, one group included *Andropogon gerardii*, *Schizachyrium scoparium* and *Sorghastrum nutans*. A second group had *Bothriochloa ischaemum*, *Panicum virgatum*, *Sporobolus asper* and *Bouteloua curtipendula*. A third group included *Bothriochloa laguroides*, *Eleocharis montevidensis* and *Bouteloua hirsuta*. Corresponding species groupings were not distinct in the biplot including perennial forbs (Figure 5). These two sets of species scores are from the same analysis. Throughout these analyses, I separated the species by the growth forms, perennial

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graminoids, annual graminoids, perennial forbs, annual forbs, and woody species to facilitate readability and recognition of any potential patterns within growth forms. Annual graminoids were absent, and annual forbs and woody species were very rare in 1996.

Although the variance in species composition explained by the first axis was not statistically significant, the environmental centroid scores in May 1997 separated the March-mowed (M, MJ, MS, and MJS) from unmowed treatments (J, S, JS, and C) along axis 1 (Figure 6). The centroids for the March-mowed treatments all had positive axis 1 scores whereas the centroids for the unmowed treatments had negative scores. Several annual forbs present in the May sample did not occur in August 1996 (Figure 6). In part, this increase in annual forbs resulted from the spring sampling time. However, rather than increasing equally among all mowing treatments, most of the annual forbs were positively correlated with one or more of the March mowing treatments. The few species positively correlated with the unmowed plots were present in very few plots per treatment. There were also more perennial forbs (Figure 7) and graminoids (Figure 8) positively correlated with the March-mowed plots than unmowed. However, for both the perennial forbs and graminoids, the extent of separation between species correlated with March-mowed versus unmowed was not as strong as I observed with the annual forbs.

In August 1997, I found most annual forb species ordinated closely together, positively correlated with the March-mowed treatments (Figure 9). The one exception was *Tragia bentonticifolia* Nutt., which was present in only two plots (one JS and one J). Although not statistically significant, axis 1 separated the March-mowed from those treatments that did not include a March mowing. The August 1997 sample followed the

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first June mowing, but the June mowing had little additional affect on annual forb species composition compared to the March mowing. The MJS and MJ centroid scores were much closer to the M and MS (only mowed in March at that time) than the J and JS (both mowed only in June at this time), or S and C (both unmowed) centroids.

Comparing the August 1996 and 1997 biplots, I found the perennial forb species scores still centered around the origin in 1997 (Figure 10). Of the more widespread species, the species score for *Psoralidium tenuiflorum* (Pursh.) Rydb. showed the most obvious change. It moved from no correlation with the C in 1996, to more strongly correlated with the C and S treatments, both unmowed in August 1997.

Perennial graminoid scores were more strongly correlated with the March-mowed treatments in August 1997 compared to 1996 (Figure 11). *Schizachyrium scoparium* and *Dichanthelium oligosanthes* (Schult.) Gould scores showed obvious changes. These species moved from being positively correlated with the C (*S. scoparium*) and the assigned J treatment (*D. oligosanthes*) to correlated with the mowing treatments that included a March mowing.

The first sample that followed the application of all the mowing treatments occurred in May 1998. It produced the first statistically significant axes (Table 2). The biplot from this analysis revealed that the C environmental centroid was separated further from the other treatments than in previous samples (Figure 12). The J centroid was also quite separate from the others. Axis 1 separated the plots that had been mowed either once (J and S) or never (C) from those that had been mowed two or more times. Several annual forbs continued to be primarily correlated with the March mowing treatments, but others now ordinated nearer the origin and were not strongly correlated with a specific

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treatment (Figure 12). Perennial forbs were generally scattered among the various

mowed treatments, most with negative axis 1 scores (Figure 13). Like the perennial

forbs, most of the perennial graminoids also had negative axis 1 scores. Among the

perennial grasses, *Andropogon gerardii* remained positively correlated with the C (Figure

14). As I observed in May 1997, *Schizachyrium scoparium* and *Sorghastrum nutans*

continued to be positively correlated with treatments including a March mowing.

In August 1998 the control environmental centroid moved further from the other

treatments compared to previous samples (Figure 15). The M centroid did not ordinate as

closely to MS and MJS as it had in August 1997. With the exceptions of *Physalis pumila*

Nutt. and *Lithospermum arvensis* L. all annual forbs had negative axis 1 scores. The

August 1996 through 1998 perennial forb scores revealed a slight trend of species more

closely correlating with mowing in general and less with the control (Figure 16). I found

these species fairly evenly distributed along axis 2 and discerned no apparent patterns

associated with flowering time or plant height. I observed a similar pattern of species

distribution for the perennial graminoids in August 1998 (Figure 17). Only *Andropogon*

gerardii and *Elymus canadensis* L. showed strong positive correlations with the Control.

Schizachyrium scoparium was positively correlated with the March mowing, whereas *S.*

nutans and *Panicum virgatum* were most strongly correlated with the September mowing.

Bothriochloa ischaemum remained correlated with June.

In both the May and August 1998 ordination diagrams, axis 1 could be interpreted

as a mowing intensity gradient. The MJS treatment was at one extreme (negative axis 1

score) and the unmowed control was at the other (positive axis 1 score). Moving from

left to right from MJS, next were located the two mowings per season treatments. These

were followed by the single mowing per season treatments with J closest to the C. The period of May through September 1998 was marked by a drought, but I do not believe the gradient was only due to reduced growth because the plants probably were not experiencing the effects of the drought in early May.

In May 1999, the C environmental centroid was further separated from the other treatments compared to the previous May samples (Figure 18). The mowing treatments including a S mowing ordinated closely together. The J and MJ centroids were positioned close to one another, but separate from the C and the other mowing treatments. The majority of the annual forbs correlated positively with the treatments that included a September mowing (Figure 18). Many of the perennial forbs were also positively correlated with the September mowings, or the J and MJ treatments (Figure 19). *Tridens flavus* (L.) Hitchc. joined *A. gerardii* and *E. canadensis* as positively correlated with the C (Figure 20). *Bothriochloa ischaemum* remained closely correlated with the June treatment. *Schizachyrium scoparium* ordinated more strongly with the September-mowed treatments.

The pRDA of the August 1999 data revealed the C and MJS environmental centroids were located directly opposite to one another (Fig. 21). The March and/or September mowing treatments centroids had negative axis 2 scores wheras all treatments including a June mowing, except MJS, had positive axis 2 scores. The annual forbs were more evenly distributed among the mowing treatments than during any of the previous sampling seasons (Figure 21). More perennial forb species were present than in any of the previous August samples. Many of these species had negative axis 1 scores, although a few species, including *Psoralidum tenuifolium, Baptisia bracteata* Muhl. ex Ell. and

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Salvia azurea Lam. were positively correlated with C (Figure 22). Most of the perennial graminoids had species scores positively correlated with the same mowing treatments as in the previous August (Figure 23). Of the more abundant species, *S. nutans*' score changed the most, moving to a positive correlation with MJS.

Ordination diagrams of the plot scores from the various samples revealed considerable overlap among the treatments. I found the greatest degree of separation among the treatments in the May 1999 sample (Figure 24). The C plots were separate from most of the treatment plots. Of the mowed treatments, J and MJ had the least overlap with the other treatments. The treatments including a September mowing were quite similar. There was quite a bit of variability in the M plot scores.

As mowing continued, the unmowed controls at VMR became more distinct from the mowed treatments. I repeated the pRDAs, omitting the control plots, to test the hypotheses that the different VMR mowing treatments had significant effects on species composition and were not simply different from the control. Similar to the results that included C, the first axes and sums of the canonical axes were significant in May 1998 and 1999 (Table 3). As expected, the eigenvalues and percentages of variance in species data were smaller with exclusion of the controls. Unlike the previous August results, none of the axes were significant when the controls were excluded from the August samples.

Cover of Growth Forms

Few consistent trends developed in August graminoid cover on VMR (Figure 25). The means appear to decrease, in most treatments the 1998 cover values are significantly

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lower than in 1997, but in most the 1999 means were not significantly different from 1996. Only J and JS are significantly lower. The M mean graminoid cover remained the most constant of any of the treatments over time. May mean total cover of perennial graminoids tended to increase each year with mowing (Figure 26). However, none increased significantly all three years. Of the mowed treatments, only M and MS did not increase significantly. Cover also did not change significantly in the control. The J treatment resulted in the greatest increase from 1997 to 1999 and the largest mean graminoid cover in May 1999 (greater than any of the other treatments, $p=0.005$). The control had the lowest mean graminoid cover in May 1999, but was not significantly different from S and JS. September mean covers in the mowed plots at LCB were consistently lower ($p<0.0005$) than the unmowed (Figure 27). The May at LCB means for perennial graminoid cover were very similar in the two treatments until May of 1999. In May 1999, the cover in the mowed plots was higher ($p=0.04$) than the unmowed (Figure 28).

I observed a pattern of increasing annual forb cover in the August samples (Figure 29). Means on all mowed treatments were greater in 1999 than 1996 ($p>0.05$) However, the J mean annual forb cover treatment was not significantly different from the control until August 1999. M was significantly lower than only JS in August 1999. None of the other mowed treatments differed significantly from each other in August 1999, whereas all the mowed treatments were significantly greater than the control.

The mean May total annual forb cover at VMR increased significantly ($p<0.05$) in each mowed treatment from 1997 through 1999 (Figure 30). In May 1997, after the initial mowing in March, the March-mowed plots yielded significantly greater mean

annual forb cover than the plots not yet mowed (J, S, JS). However, in May 1997 none of the mowed treatments were significantly different from the control. In 1998 and 1999 all the treatment plots had mean covers significantly greater than the control. The M treatment had the lowest mean cover of the treatment plots in both 1998 and 1999. In 1998, M was significantly lower than only MS and MJS. By May 1999, the mean annual forb cover in M was significantly lower than all but MS. The rest of the treatments did not differ significantly from one another in 1999. Cover in the controls changed very little during this time.

September mean annual forb cover at LCB did not vary significantly among years (Figure 31). The means between treatments were not significantly different during any September sampling period. The May mean annual forb cover decreased significantly in 1999 in the unmowed plots whereas it increased each year in the mowed controls (Figure 32).

In August at VMR, significant differences occurred among years within treatments, but the changes appeared more related to differences in precipitation than mowing treatments (Figure 33). Mean perennial forb cover in the control plots often varied as much or more than those in the mowing treatments. By 1999, I found consistently lower means in the June-mowed plots than in plots not mowed in June, but many of these were not significant. Only M showed significantly greater perennial forb cover than all the June-mowed treatments. However, the M mean did not differ significantly from the control in 1999.

Very few statistically significant differences among May mean covers of perennial forbs occurred over time, or among treatments at VMR (Figure 34). However,

mowed plots at VMR consistently had greater May perennial forb cover than unmowed. That, together with the March-mowed plots exhibiting slightly higher perennial forb cover than the June-mowed in 1997 and 1998, suggested a positive effect of March mowing.

At LCB, September mean perennial forb cover was slightly higher from 1997 through 1999 ($p<0.05$) in the unmowed plots after mowing ceased (Figure 35). May perennial forb cover remained very similar in the two treatments (Figure 36). The cover appears to be diverging, but the mean cover in the unmowed plots was not significantly greater than the mowed plots in May 1999.

Individual Species Responses to Mowing

The perennial graminoids, as a group, tended to increase or maintain their frequencies in response to mowing in general. However, graminoid cover of various species did not respond consistently to the different mowing treatments. The frequency of *A. gerardii* in VMR plots changed little over the course of the study (Appendix B). Changes were limited to one to two plots per treatment. *Andropogon gerardii* disappeared only in plots where it was initially present as single shoots. Its August mean cover was initially among the highest in the C plots and it increased each year of the study in the C (Figure 37). May mean cover in the M plots increased each spring (Figure 38), but this earlier start did not produce greatly increased August cover. August cover in the other March-mowed treatments increased with the initial mowing and higher precipitation in 1997, but then decreased in 1998. The cover in the other treatments tended to decrease over time.

Schizachyrium scoparium was the most widespread perennial grass species. Its frequency changed very little in the plots (Appendix B). With the exception of S plots, *S. scoparium* cover decreased in all treatments in August (Figure 39). May mean cover became very similar in the mowed treatments by 1999, and was consistently higher than in the C plots (Figure 40).

Sorghastrum nutans also was widespread at VMR, occurring in over 65% of the May plots (Appendix B). Only in the C plots did the frequency decrease from May 1997 to 1999. *Sorghastrum nutans'* cover generally increased with mowing, although its mean was never above 3.5% (Appendix C). Unlike *A. gerardii* or *S. scoparium*, the mean cover in M was never greater than mean cover in the C after mowing started.

Bothriochloa ischaemum initially occurred in 50% or more of each treatment's plots at VMR and its frequency increased in most treatments with the initiation of mowing (Figure 41). Only in the C did its frequency decrease slightly from 1996 to 1999. In August 1996, *B. ischaemum* was present with the greatest frequency in the J plots. By August 1999, the frequencies in all the March-mowed plots equaled or exceeded that in J. Frequencies increased only slightly in the S and JS treatments. The greatest increase in May mean cover was in the J plots (Figure 42). By August 1999, mean covers were similar for all the treatments at VMR (Figure 43). *Bothriochloa ischaemum* reproduction from seed was very obvious in some plots, producing high seedling densities.

Though never as abundant as *B. ischaemum*, I observed evidence of reproduction by *Bouteloua curtipendula* in the form of higher August frequencies. Frequencies increased in all mowed treatments while declining in the control (Figure 44). August *B.*

curtipendula mean cover fluctuated, especially with the wet growing season in 1997, but never exceeded two percent (Appendix C).

The frequencies of *Dichanthelium oligosanthes*, a smaller stature perennial grass, also varied with season, increasing in most treatments during wet years and decreasing during drier periods (Appendix B). Comparing 1996 to 1998 and 1997 to 1999, most of the variability appears related to precipitation rather than mowing treatment. However, the frequency of *D. oligosanthes* in the control was greater than the other plots in 1996. This status was reversed in 1999 when frequency in C was lower than all the mowed treatments. *Dichanthelium oligosanthes* was not abundant in any of the plots. Mean August cover was less than one percent in all the treatments (Appendix C). The slight increase in cover in C reflects *D. oligosanthes* disappearing from some plots where it had low cover values.

As a group, the perennial forbs did not respond in a consistent manner to mowing. Whereas individual frequencies of several graminoids were often fairly consistent, the frequencies of some of the perennial forb species were quite variable. For example, the August frequencies of *Ambrosia psilostachya* varied considerably, even in the controls (Figure 45). In none of the treatments did frequency consistently increase or decrease all three years. The August 1999 *A. psilostachya* frequency exceeded that of August 1996 only in the M treatment. During this time the frequency in the control decreased more than in any of the mowed treatments. In most of the treatments, May frequencies generally varied much less than the August samples, and were typically greater than those in August (Figure 46). The JS treatment produced the only consistent increase in May *A. psilostachya* frequency over all three years. August mean cover was lower in all the

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mowed treatments, except M, in 1999 compared to 1996 (Appendix C). In contrast, the August 1999 cover in C was much higher than in previous years. The 1998-1999 increase in cover accompanies an increase in frequency during that same time. *Ambrosia psilostachya* apparently capitalized on conditions following the 1998 drought.

In contrast to *A. psilostachya*, *Artemisia ludoviciana* frequencies varied very little (Appendix B). Only in the C was the net change, an increase, in May or August frequencies greater than 12%. In both the May and August samples, the mean cover of *A. ludoviciana* also increased each year in the C (Appendix C). The S (not mowed at that time) and MS (mowed only in M at that time) had much higher covers in August 1997, but they declined sharply after September mowing started. August mean covers in 1998 and 1999 were lower in the June-mowed plots than the unmowed or March and/or September mowed plots. By 1999, *A. ludoviciana* cover in the C exceeded that in the other treatments, in both the May and August samples.

In August, the frequencies of *A. ericoides* increased in the S, MS and MJS treatments (Figure 47). March and/or June only mowing resulted in a net decrease in frequency. Frequencies changed only slightly in the JS treatment. Although the August 1996 and 1999 values in the C were similar, the variability in frequencies was greater than any other treatment except J. August mean covers generally fluctuated with precipitation, though J and JS initially decreased in response to the first mowing in spite of higher precipitation in 1997 compared to 1996 (Appendix C). *Aster ericoides* cover in M changed very little during my study. The May 1999 *Aster ericoides* frequencies exceeded those in 1997 in all mowed treatments except J, which remained constant.

During this time, the C frequency consistently decreased from year-to-year in May (Figure 48).

In comparison with *A. ericoides*, the August frequencies of *Aster oblongifolius* varied much less, changing by no more than two plots per treatment (Appendix B). August mean cover varied greatly in the M treatment, increasing in wet years 1997 and 1999, and decreasing in the dry years (Appendix C). The other March and/or September-mowed treatments varied similarly, but with less amplitude. Except for a decrease from August 1997 to 1998 in the MJ treatment, cover in none of the treatments varied to the same degree as in M.

Oxalis dillenii Jacq. was never very abundant. Its mean cover never exceeded one percent. While August frequencies of *O. dillenii* varied between treatments (Figure 49), its May frequencies increased greatly with all mowing treatments (Figure 50). In wet years and after the initial mowing, August frequencies tended to increase. The S and JS did not result in increased frequencies until after the initial September mowing, and the *O. dillenii* frequency in J did not increase sharply until after the dry summer in 1998.

Psoralidium tenuiflorum August frequencies varied greatly with precipitation in all treatments, including the control, increasing in wet years and decreasing during dry periods (Figure 51). Frequencies were lowest in the June-mowed plots. May frequencies were much less variable (Figure 52). Only in the C plots did frequencies decrease each May, though they remained greater than 65%. *Psoralidium tenuiflorum* cover varied, but never exceeded 1.6%.

Annual forbs responded positively to all seasons and frequencies of mowing. In mean total cover, they became as abundant as perennial forbs by May 1999. Whereas

perennial forbs were often present with low cover in the C plots, annual forbs were much less abundant. Annual forbs generally exhibited the greatest increases in frequency in the plots mowed more than once per year. Prior to the dry growing season in 1998 annual forb frequencies were generally lowest in the J plots. After all the mowing treatments had been initiated, M plots often had among the lowest annual forb frequencies of the mowed treatments.

The frequency of *Amphiachyris dracunculoides* (DC.) Nutt. increased dramatically in all mowing treatments, but its mean cover never exceeded one percent. In 1998 and 1999, August frequencies in all treatments including a September mowing were higher than the treatments not mowed in September (Figure 53). May frequencies were similar except that the M treatment had lower *A. dracunculoides* frequencies than any of the other mowed treatments (Figure 54).

The frequency of *Conyza canadensis* (L.) Cronq. also increased sharply in the mowed treatments. However, whereas *A. dracunculoides* were highest in the September-mowed plots, *C. canadensis* frequencies were highest in the June-mowed plots. All of the June-mowed treatments had August 1999 frequencies of *C. canadensis* greater than the other treatments (Figure 55). Whereas J frequencies were also higher than the other treatments in May 1999, the other mowed treatments, with the exception of MS, were generally more similar in May (Figure 56). Like *A. dracunculoides*, mean cover of *C. canadensis* never exceeded one percent in any of the treatments.

Like the other annual forbs, the *Erigeron strigosus* frequency increased in response to all mowing treatments. In August, the *E. strigosus* frequencies were highest in plots mowed in J and at least one other mowing (Figure 57). By May 1999 it occurred

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in over 80% of all the mowed plots whereas its frequency decreased in the unmowed controls (Figure 58). Mean cover was less than one percent in all treatments during both the May and August sampling times.

The frequency of *Linum sulcatum* increased in response to mowing. The August frequency in J did not increase above 10% until 1999 (Figure 59). Frequencies in all the June-mowed treatments were less than those in the other treatments in August 1999. The frequency in the J treatment in May 1998 was similar to the other treatments (Figure 60), but August 1998 its levels were much lower. *L. sulcatum* cover was less than one percent in all the treatments.

Plantago virginica was present only during May. Its frequency increased with all mowing treatments while decreasing in the C (Figure 61). It tended to occur in higher frequencies in treatments with multiple mowings per year than in the single mowing treatments. The M and S treatments had the lowest May frequencies of *P. virginica*.

Initially, the treatments mowed in March and June produced the highest August frequencies of *Polygala verticillata* L. (Figure 62). August 1999 *P. verticillata* frequencies increased in all treatments following the 1998 drought. May frequencies of *P. verticillata* also increased in all mowed treatments from 1997 to 1998 (Figure 63). However, the May frequencies decreased slightly in M, MS, MJS and JS from May 1998 to May 1999.

Like *P. virginica, Viola rafinesquii* Greene occurred only in the May samples. As with the other annual forbs, frequency increased with mowing (Figure 64). Frequencies

in the J plots were similar to the multiple mowings per year treatment, whereas frequencies increased the least in the M treatments. I never found *Viola rafinesquii* in the C.

DISCUSSION

Mowing significantly affected the species composition of my study sites. The plant communities at VMR and LCB were initially distinct, though they shared similar physiographies. These initial differences support the hypothesis that the distinct communities resulted from opposing mowing regimes. However, these were two geographically separate sites and other factors may have also affected species composition of the communities.

Initially, VMR had a greater amount of accumulated leaf litter than LCB. Numerous investigators have identified accumulation of leaf litter due to infrequent grazing, burning or mowing as an important factor limiting species diversity in grasslands and herbaceous plant communities (Weaver and Rowland 1952, Al-Mufti et al. 1977, Knapp and Seastedt 1986, Milchunas et al. 1988, Carson and Peterson 1990, Davison and Kindscher 1999, Huhta et al. 2001). The total number of species present and the mean cover of forbs in May 1997 were lower in the unmowed VMR plots than the mowed LCB. However, by the end of my study the total numbers of species per treatment increased in the mowed VMR plots while they decreased in the unmowed LCB plots. These changes were largely due to annual forbs.

After three years of mowing, the two sites remained distinct with several species unique to each. However, I observed parallels in the two communities' responses to the

presence versus absence of mowing. Many of the new species that became established at VMR were also present at LCB. Additionally, the numbers of species within the groups of annual forbs, perennial forbs, annual graminoids, perennial graminoids and woody species became quite similar.

Annual forbs experienced the greatest changes in species richness, frequency, and the most consistent increases in cover with mowing. Annuals' short life cycles, abundant seed production, and persistence in seed banks enabled them to take advantage of the disturbance caused by mowing. Increases in forb richness and abundance have been observed following mowing (Ryser et al. 1995, Carson and Peterson 1990), grazing (Collins et al. 1998, Hickman et al. 2004) and growing season fires (Howe 1995). A few annual grasses also became established at VMR after mowing began, but they were never as abundant as at LCB. The paucity of these grasses at VMR probably reflected the absence of these species in the seed bank and little seed dispersal from adjacent areas, rather than selective pressure by the different mowing regimes.

At both sites, forb species richness and the cover of annual forbs were higher with mowing. The sites differed in that perennial forb cover did not decrease after the cessation of mowing at LCB, whereas it remained low in the unmowed plots at VMR. This suggests that whereas perennial forb recruitment may have been limited by high litter levels, established plants competed successfully with perennial graminoids, at least short term, following the cessation of mowing. From a management perspective, my results indicate that annual mowing would not be required to maintain perennial forb diversity. Similarly, Howe (1995) found burning on a three year rotation increased the cover of rhizomatous perennials. In contrast to perennial forbs, I found abundance of

annual forbs began to decrease after two years without mowing. Ryser et al. (1995) also observed that annual and biennial mowing produced similar results, whereas species richness decreased in plots mowed every five years. Annuals' short life spans make them susceptible to decreases due to unfavorable conditions for seedling survival.

Though the greatest changes occurred between mowed and unmowed treatments, there also were significant differences among mowing seasons and frequency at VMR. The species composition of plots overlapped greatly among treatments. Most species increased in frequency or cover when mowing began. The differences among mowing treatments were primarily in the strength of the species responses. Very few species were unique to a mowing treatment.

After one complete season of mowing, I consistently found that treatments mowed two or more times per season were more distinct from the control than the treatments mowed once per year. The M and J treatments were the least similar of the once per season mowed treatments. By 1999, mowing in March had little additional effect on species composition when combined with another mowing time. In August 1999 the treatment pairs, MJ and J, MS and S, JS and MJS were similar. M was also the treatment most similar to the control. The M mowing treatment had a direct negative impact on few species because it was the only treatment which removed very little living biomass.

As the only treatment without a March or September mowing, J had the lowest spring light levels of any of the mowed treatments. Though not true for all species, many annual forbs did not increase dramatically in August cover or frequency in the J treatment until after the 1998 drought. This suggests that the survival of these annuals is enhanced

by higher light levels. I suspect the differences between the June and March, or June and September treatments would have been greater if the drought had not occurred during the 1998 growing season. The timing of the 1999 increases in species abundances in the J treatment, as well as the previous increases in the March and September mowing treatments, support the hypothesis that increased light availability in the fall and early spring was a major factor promoting germination, seedling survival and ultimately frequency and cover of many species. The 1998 drought resulted in decreased cover of many species in 1998 compared to my other August samples. The reduced cover produced increased light levels near the soil level in the fall of 1998 and spring of 1999 in the J plots. Following the drought, forb cover did not increase only in the June mowing treatment. Cover of *Ambrosia psilostachya* and *Artemisia ludoviciana* also increased sharply in the control after the drought.

The J results agree with observations that species diversity is inversely related to productivity in grasslands (Collins et al. 1998, Tilman 1993). During more productive, in this case higher precipitation years, spring light levels near the soil surface were lower. Apparently the interaction of June mowing and sufficient biomass accumulation depressed August annual forb survival in the J plots. May annual forb covers and frequencies were similar in the J plots to the other mowed treatments, but were lower in August. Following the drought in 1998, August 1999 annual forb frequency and cover in the J plots were very similar to those in the other mowing treatments. I did not observe increases as large in forb covers or frequencies in the March and/or September mowed plots in 1999. Regardless of other factors influencing productivity, these treatments

always had high spring (M) or high spring and fall (S) light levels. The drought occurred a year after I initiated mowing, so short-term trends could be misleading.

There was also a short-term drought in 1996 that preceded my initial samples. However, the August 1996 and May 1997 species richness and abundances of annual forbs were the lowest I observed during my study. It seems plausible that the difference between the effects of the 1996 and 1998 droughts were that a major component of the biomass shading the plots in 1996 accumulated from previous years, and was not limited to the production since that last mowing, as in 1998. The short duration drought in 1996 had little effect on the persistent litter that kept soil light levels low. Therefore, light levels and seedling densities remained low.

Mowing had a greater effect on species richness and frequency of annual forbs than perennial forbs or graminoids. The less pronounced effect of mowing on frequency of perennial species resulted from their higher initial frequencies, perennial life history and perhaps greater abilities to tolerate disturbance. The tolerance of grasses to mowing was not surprising due to their adaptation to grazing and fire (Branson 1953, Howe 1994). I did not observe the loss of many perennial forb species in response to mowing even though forbs, due to the position of their apical meristems, are generally less tolerant of mowing and grazing than the grasses. Reduced August forb cover was a common response to June mowing. However, May cover and frequency values showed little reduction over time, and often increased. In many perennial species, August fluctuations in cover appeared to result more from differences in precipitation than mowing treatments.

Comparison of my results from mowing to results from burning observed by others reveals some differences between the two disturbances. Spring fires are often used by land managers to increase grass production and decrease forbs (Aldous 1934, Owensby and Anderson 1967, Towne and Owensby 1984). Fires that increased grass production were typically conducted near the time when the C_4 grasses initiated growth and while many C_3 plants were actively growing. I also observed an increase in mean May perennial grass cover in the mowed treatments over time compared to the control. This increase probably reflected an earlier initiation of growth in the spring. However, I did not see evidence of increased annual grass production in August. I did not measure production directly, but treatments mowed in March and/or September had August mean graminoid covers similar to, or below those of the unmowed control. August cover did not provide direct inferences for the June-mowed treatments because part of the annual production was removed with the June mowing.

A fundamental difference between mowing and burning is that early spring mowing does not cause the mortality of some species associated with fire. In my plots, there was little green biomass above the eight centimeter mowing height in March. Potentially, all species initially benefited from the increased spring light levels. I observed an increase in mean May cover of perennial graminoids, and also annual and perennial forbs. However, the increased May perennial graminoid cover was not accompanied by an increase in August cover compared to the control. The lack of an increase in August perennial graminoid cover may have resulted from increased competition with forbs.

Howe (1995) observed spring flowering species responded favorably to summer burning. I found similar, but more subtle, responses to mowing. Without the fire induced spring mortality, forbs increased in all mowing treatments. The strength of the response in my plots was related to the amount of biomass that accumulated by the end of the previous growing season and its effect on spring and fall light levels near the soil surface. Spring and/or fall germination increased with all mowing treatments. In the J treatment, the increased germination produced higher August forb cover and richness only following a season with lowered productivity following a short-term drought.

Graminoid production might also be reduced if mowing depleted the plants' reserves. Turner et al. (1993) observed a negative impact of late season harvest on grasses, if the process of replacing lost shoots, depleted the grasses' resources prior to dormancy. I observed very little regrowth after the September mowing. Repeated mowing might also deplete resources. However, only during the dry summer of 1998 were the mean graminoid covers of my multiple-mowing-per-year treatments, as a group, lower than the single mowing treatments.

The presence of *Bothriochloa ischaemum* at VMR was an important factor that distinguished VMR from LCB. It was not planted at VMR, but was suspected to have been introduced to the site in bales of hay (personal communication with VMR ranch manager). *Bothriochloa ischaemum* also was present along the roadside adjacent to the LCB site, but rarely present in the plots. Taliferro et al. (1984) found *B. ischaemum* to be tolerant of repeated mowing. I saw no evidence that any combination of mowing seasons slowed or prevented the establishment of *B. ischaemum*. To the contrary, *B. ischaemum* maintained or increased its frequency of occurrence following mowing. I suspect the

infrequent incidence of *B. ischaemum* at LCB resulted from its recent arrival at the site, not inhibition by mowing.

I saw evidence that mowing strongly favored *B. ischaemum*. Perennial grasses were reproducing, indicated by a small increase in the number of grass species in many plots. However, for tallgrass species, I rarely found seedlings in my plots. *Bothriochloa ischaemum* was a notable exception. It responded with an obvious increase in the number of seedlings germinating in some plots after mowing. During my study, continued mowing prevented a reduction in species richness that might accompany an increase in *B. ischaemum* density. However, with a decrease in mowing frequency, or its cessation, *B. ischaemum* might have a distinct advantage in dominating these areas.

My initial observations revealed dramatically lower species richness and cover of other species in plots at VMR with high *B. ischaemum* cover. Mowing during any season increased the richness, cover and frequency of other species in plots dominated by *B. ischaemum*. March and September mowings were more effective in increasing species abundances, especially during years with normal to above average precipitation probably because these treatments produced higher spring light levels than June mowing. Species richness was not only limited by *B. ischaemum* at VMR. Other plots, for example some of those with high *Andropogon gerardii* cover, also had abundant accumulated biomass and reduced species richness prior to the initiation of mowing.

After observing a drop in species richness and slow recovery following a severe drought, Tilman and Haddi (1992) concluded that grassland species richness was limited by recruitment. My results do not support this conclusion. Instead, my results suggest the initial low forb abundance, both in frequency and cover, at VMR resulted from low

light levels at the soil surface, not the result of poor seed dispersal or the lack of seeds in the soil. I base this conclusion on the rapid increase in forbs observed in the first May sample following the initiation of mowing in March or September. Though I did not observe the effect of a prolonged drought after I initiated mowing, the 1998 late spring and summer were dry. In the March and/or September mowed treatments, the drought adversely affected cover more than frequency for most species. For example, following the initial mowing in September 1997, 1998 richness in the S plots increased in spite of the drought. In agreement with Tilman's (1993) observations, I did observe apparently poor annual forb survival, indicated by decreased frequencies from May to August, during the 1998 drought in conjunction with lower light levels in the J plots. Species richness in the J plots was similar to the other treatments in the spring of 1998. However, it was lower than the other treatments three months later in August. In 1999, when precipitation increased, species richness in J in the May and August samples were similar to that of the other treatments. Survival was greater in the treatments with higher light levels, including those with June mowing combined with other mowing times. The higher richness in the MJ, MJS and JS treatments compared to J prior to 1999 indicated that it was not simply the stress induced by June mowing that decreased richness and frequencies in the J plots.

In the majority of my plots, recruitment was high when light levels were high. However, there was some evidence to the contrary. In some plots, mowing produced few seedlings in May. This occurred in some plots dominated by *B. ischaemum* with low initial species richness. In some cases I observed very low seedling densities even after repeated mowings. Either viable seeds were not present, or germination was inhibited. I

found nothing in the literature concerning allelopathy by *B. ischaemum*. Often these plots were surrounded by other plots dominated by *B. ischaemum* and seed dispersal into these plots may have been poor for several years.

Seed dispersal, or the lack thereof, may be a concern in my experimental design. Ryser et al. (1995) noted that the dispersal of seeds from adjacent plots affected species composition in small plots. Short-term, I do not think this was a problem. In general, I observed rapid, widespread establishment of new species in many plots. I attribute this sudden increase to a rich seed bank. Long-term, I believe this could be a serious problem if certain mowing treatments prevented or reduced seed production. Then species, that otherwise might be eliminated by a mowing treatment, could persist via seed dispersal from neighboring plots.

Individual species responded in various ways to mowing treatments. The different responses reflect interactions of many mowing effects. The importance of these interactions varied among species. By reducing the competitive advantage of accumulated tallgrass biomass, mowing may benefit other species by increasing germination and seedling survival through increasing light availability. Mowing may also be beneficial to shorter species by removing overlying biomass which could potentially cause direct mortality, or reduce photosynthesis and overall fitness thus reducing survival and seed production. For example the tall, late spring flowering forb *Psoralidium tenuiflorum* did not benefit from June mowing, whereas the short, annual forb *Polygala verticillata*, and the taller, later flowering forb, *Conyza canadensis*, responded positively to June mowing. Similar in stature to *P. tenuiflorum*, the late flowering annual forb, *Amphiachyris dracunculoides* had greater frequencies in the

treatments that included a September mowing. Even among plants of similar stature and life histories, I observed different responses. The August cover of *Andropogon gerardii* decreased slightly in the J, JS and MJS treatments, whereas *Sorghastrum nutans'* cover increased in these same treatments. Silletti and Knapp (2002) also observed differences in the responses of *A. gerardii* and *S. nutans* to disturbance and environmental factors.

The intermediate disturbance hypothesis (IDH) predicts higher diversities at intermediate levels of disturbance (Connell 1978). Contradictory to the IDH, Collins et al. (1995) observed species richness increased with decreasing fire frequency when they investigated the influence of April fire frequency on prairie communities. A complicating factor is that different species are not affected equally by the same disturbance (Milchunas et al. 1988). Spring fires timed close to the initiation of growth by tallgrass species might be considered a disturbance to these C_4 species because it removes accumulated biomass that may impede the growth of other plants. However, these tallgrass species are not negatively impacted in the same to the same degree as C_3 species which initiated growth prior to the fire. As a result, a relatively small number of C_4 grass species tend to increase whereas the larger potential pool of C_3 species tend to decrease with frequent spring burning.

I observed increased species richness with increased mowing frequency. In part the differing results compared to those of Collins et al. (1995) may reflect initial conditions. Grazing, which at lower intensities tends to promote species richness, was an important component on the sites investigated by Collins et al. (1995) whereas VMR was not grazed. Also important, my March mowing removed little living biomass. Richness increased with all mowing treatments compared to the control, but was generally higher

in the more frequently mowed treatments. June and September mowings directly impacted species to a greater degree than March by removing more living biomass. As a result, I observed different species composition with the various mowing treatments. The impact of mowing on species composition and cover varied, influenced by factors such as plant height and position of meristems. However, these responses appeared to be secondary to light availability in influencing the establishment of new seedlings.

When I initiated this study, I expected three mowings per year to be a rather severe disturbance that would reduce species richness, frequency and cover of many forb species. Instead, diversity increased which increasing mowing frequency. If three mowings per year is a moderate disturbance, then my results could support the IDH. A test of this hypothesis would be to mow more frequently. This test assumes that increasing frequency of mowing would increase the severity of the disturbance.

A complicating factor with this proposed test of the IDH is that at higher mowing frequencies, less biomass would be removed with each mowing. Assuming some new growth occurred above the mowing height, the intensity would change, but mowing would continue to be a disturbance at higher frequencies. The IDH predicts that diversity will reach a maximum at some mowing intensity and then decrease at higher levels. My results indicate three mowings per year do not surpass this maximum. My results suggest that the rate of change in diversity decreased as mowing frequency increased. My results do not predict where maximum diversity will be reached, or if and how it will decline.

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Table 1. Results from four separate partial Redundancy Analyses on August Veterinary Medicine Ranch data.

Sample		Axis 1 (signif.)	Axis 2	Axis 3	Sum of all canonical axes (signif.)
Aug 1996	Eigenvalues	0.018 (p=0.382)	0.006	0.004	0.034 (p=0.418)
	% var spp	3.0	3.9	4.5	
Aug 1997	Eigenvalues	0.022 (p=0.178)	0.012	0.007	0.050 (p=0.07)
	% var spp	3.3	5.1	6.1	
Aug 1998	Eigenvalues	0.028 (p=0.122)	0.012	0.006	0.058 (p=0.026)
	% var spp	4.0	5.7	6.6	
Aug 1999	Eigenvalues	0.035 (p=0.038)	0.016	0.007	0.070 (p=0.006)
	% var spp	4.8	7.0	8.0	

Table 2. Results from three partial Redundancy Analyses on May Veterinary Medicine Ranch data.

Sample		Axis 1 (signif.)	Axis 2	Axis 3	Sum of all canonical axes (signif.)
May 1997	Eigenvalues	0.022 (p=0.072)	0.011	0.005	0.051 (p=0.058)
	% var spp	3.1	4.7	5.4	
May 1998	Eigenvalues	0.041 (p=0.002)	0.019	0.008	0.082 (p=0.002)
	% var spp	5.8	8.5	9.7	
May 1999	Eigenvalues	0.062 (p=0.002)	0.018	0.005	0.100 (p=0.002)
	% var spp	8.5	10.9	11.6	

Table 3. Results from three partial Redundancy Analyses on May Veterinary Medicine Rranch data excluding the controls.

Sample		Axis 1 (signif.)	Axis 2	Axis 3	Sum of all canonical axes (signif.)
May 1997	Eigenvalues	0.021 (*p=0.148*)	0.011	0.005	0.047 (*p=0.128*)
	% var spp	2.9	4.5	5.2	
May 1998	Eigenvalues	0.035 (*p=0.006*)	0.010	0.008	0.065 (*p=0.002*)
	% var spp	5.2	6.7	7.9	
May 1999	Eigenvalues	0.030 (*p=0.028*)	0.008	0.006	0.056 (*p=0.014*)
	% var spp	4.4	5.6	6.5	
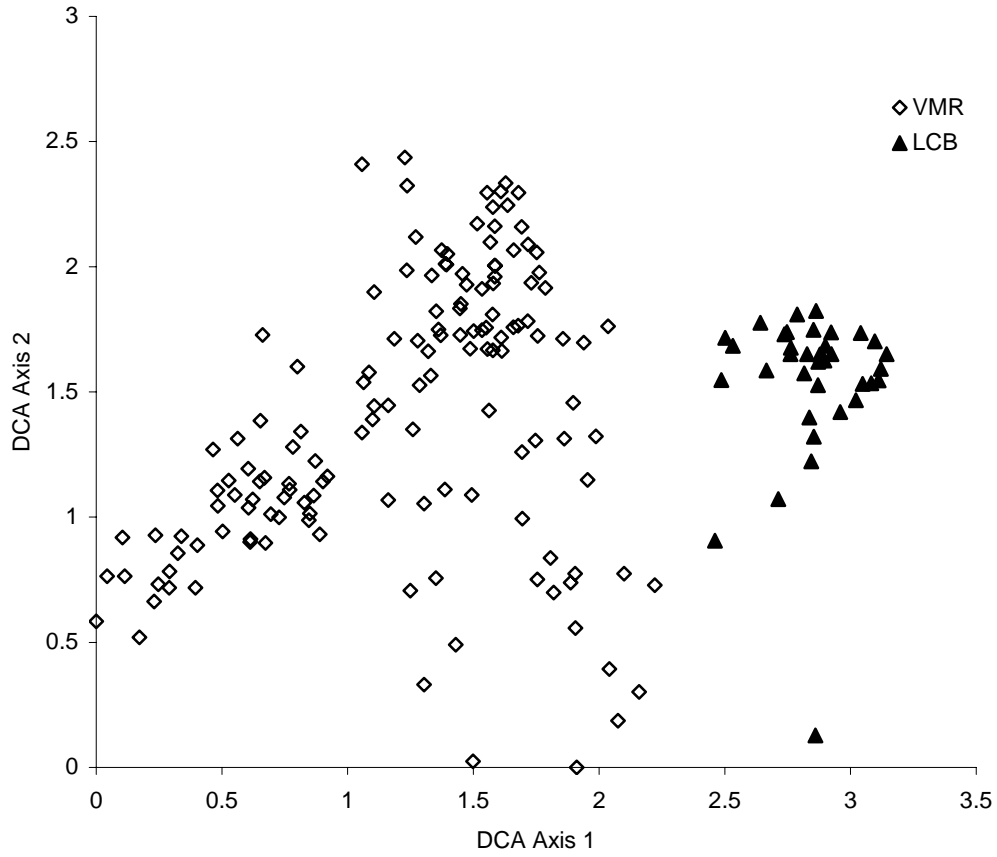
Figure 1. Ordination diagram of sample scores from a DCA using 1996 pretreatment
data from Veterinary Medicine Ranch and Lake Carl Blackwell.
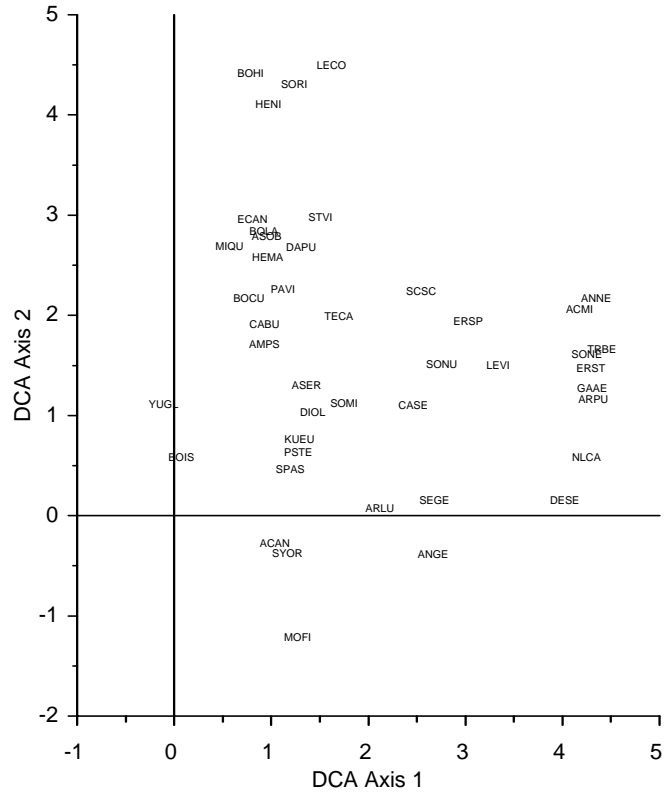
Figure 2. Ordination diagram of species scores from DCA on 1996 Veterinary Medicine Ranch and Lake Carl Blackwell pretreatment data. Only species with weights greater than 5 are displayed.
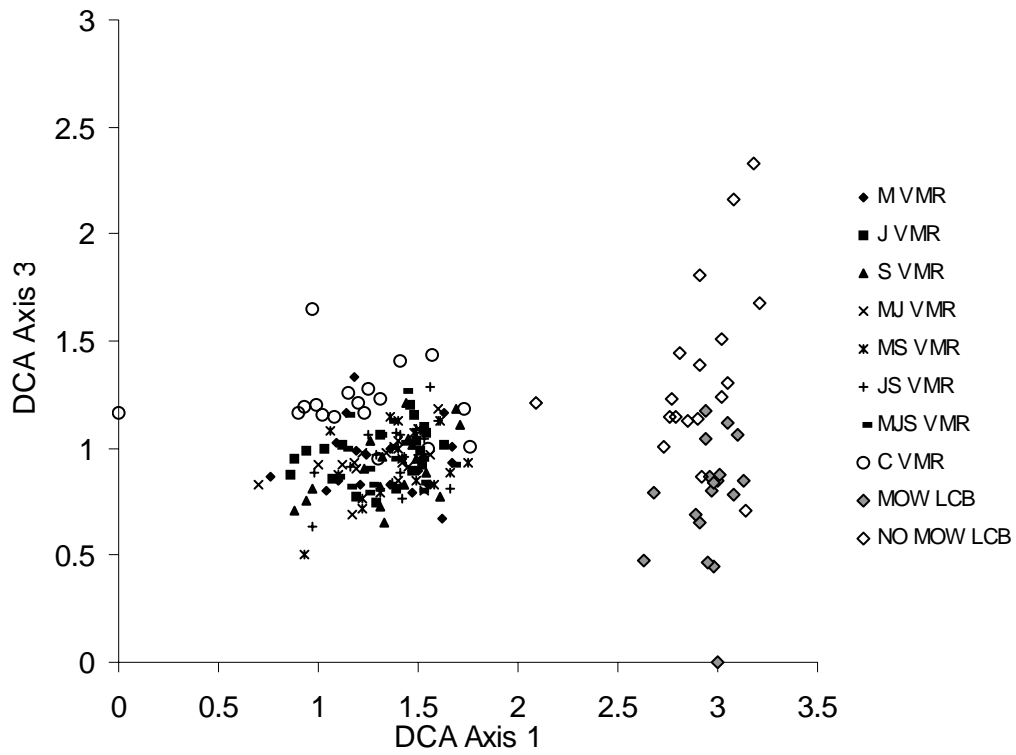
Figure 3. Ordination diagram of axes 1 and 3 sample scores from DCA on May 1999 Veterinary Medicine Ranch and Lake Carl Blackwell data.
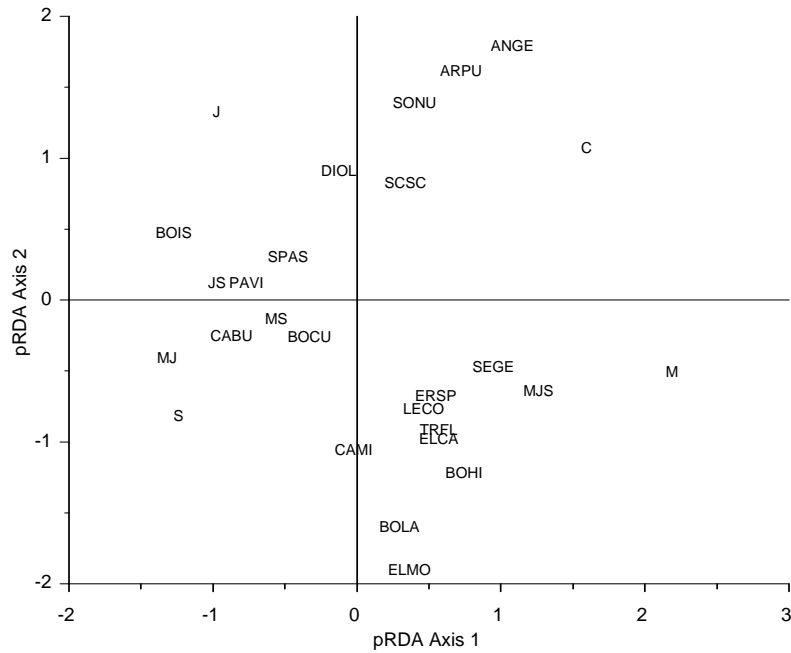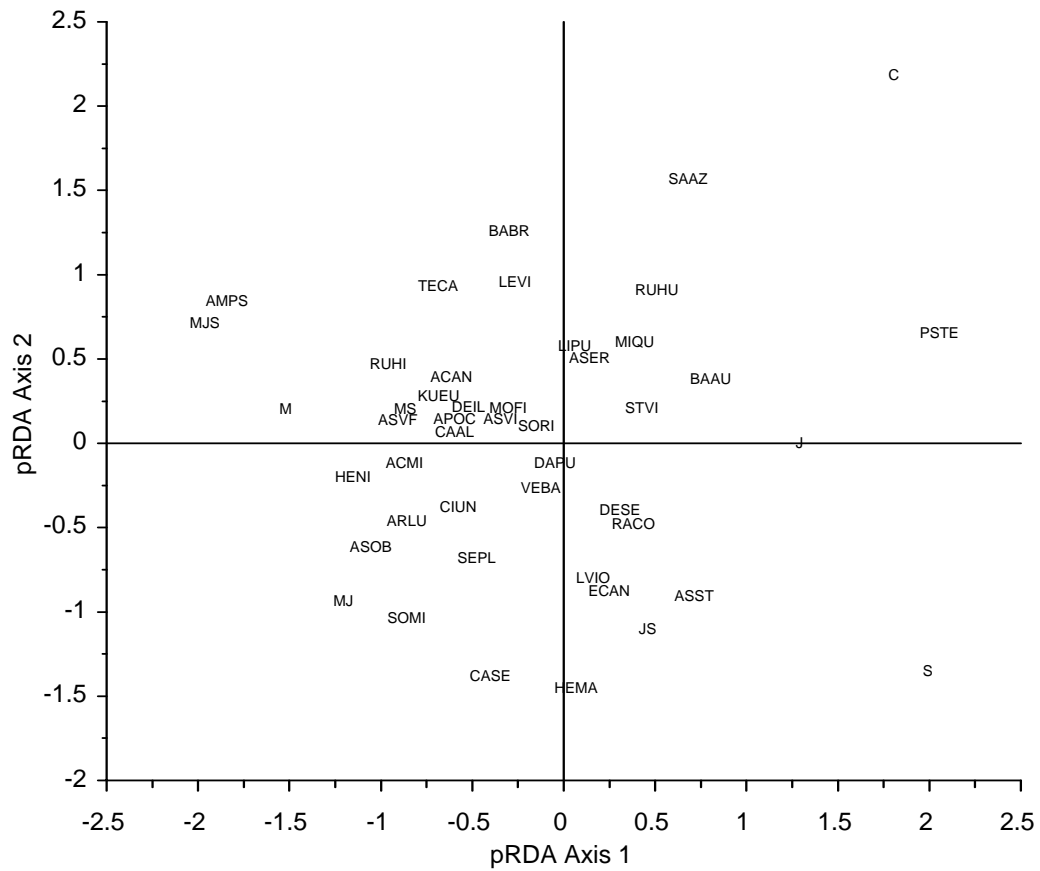
Figure 4. Biplot of environmental centroids and perennial graminoid species scores from pRDA using August 1996 Veterinary Medicine Ranch data. Lines on species vectors were omitted from pRDA biplots to facilitate readability. ELCA, PAVI and TRFL labels were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.
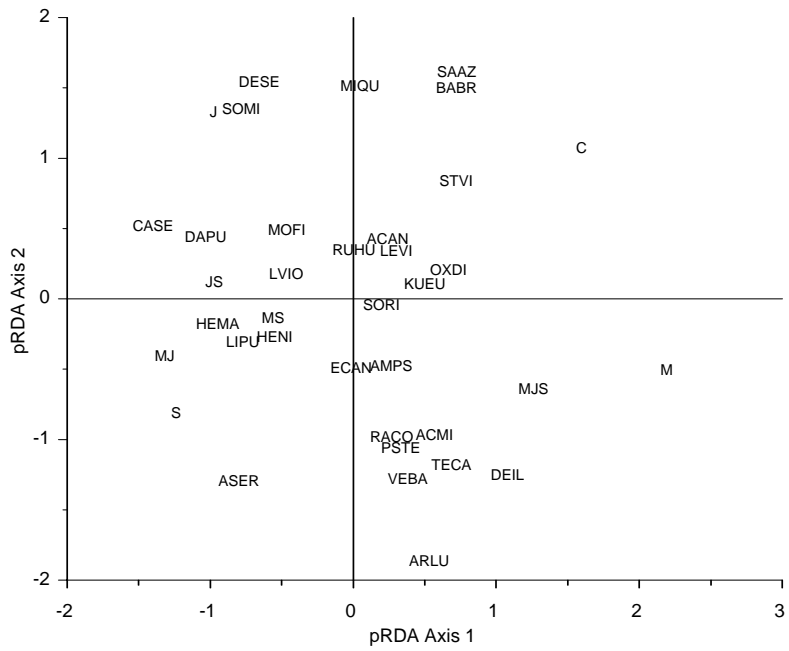
Figure 5. Biplot of environmental centroids and perennial forb species scores from
pRDA on August 1996 Veterinary Medicine Ranch data. Labels for ACAN, BABR and
OXDI were moved slightly to improve readability. Environmental centroid scores on all
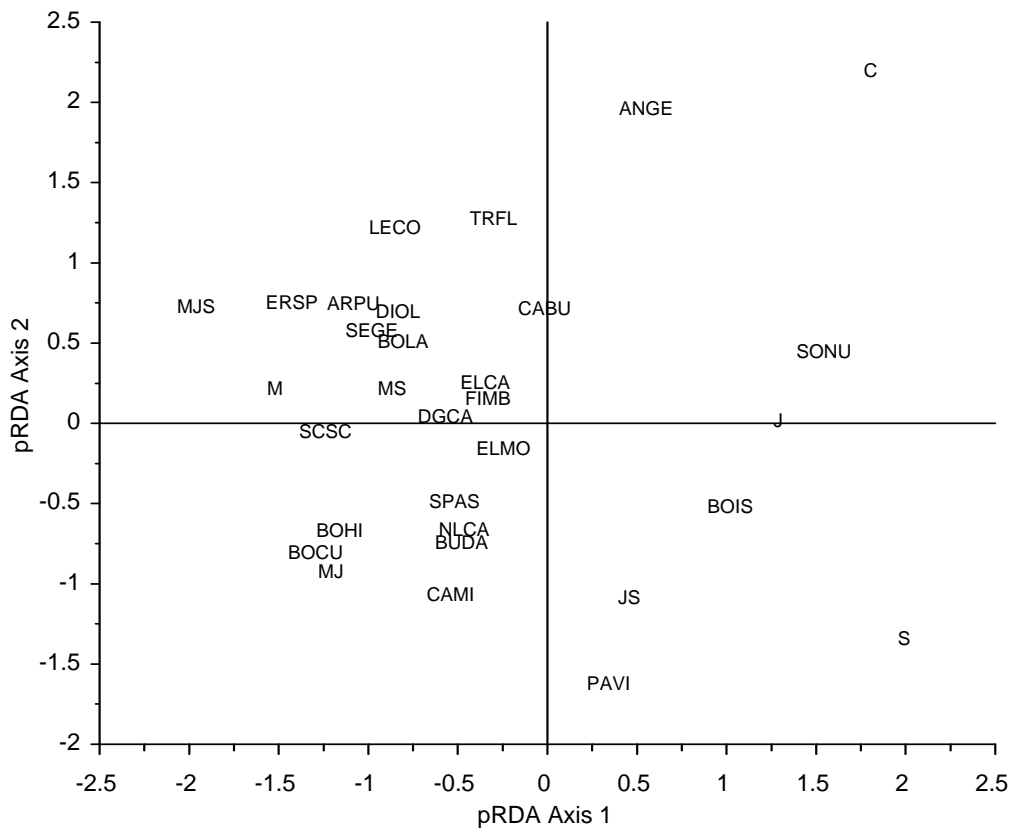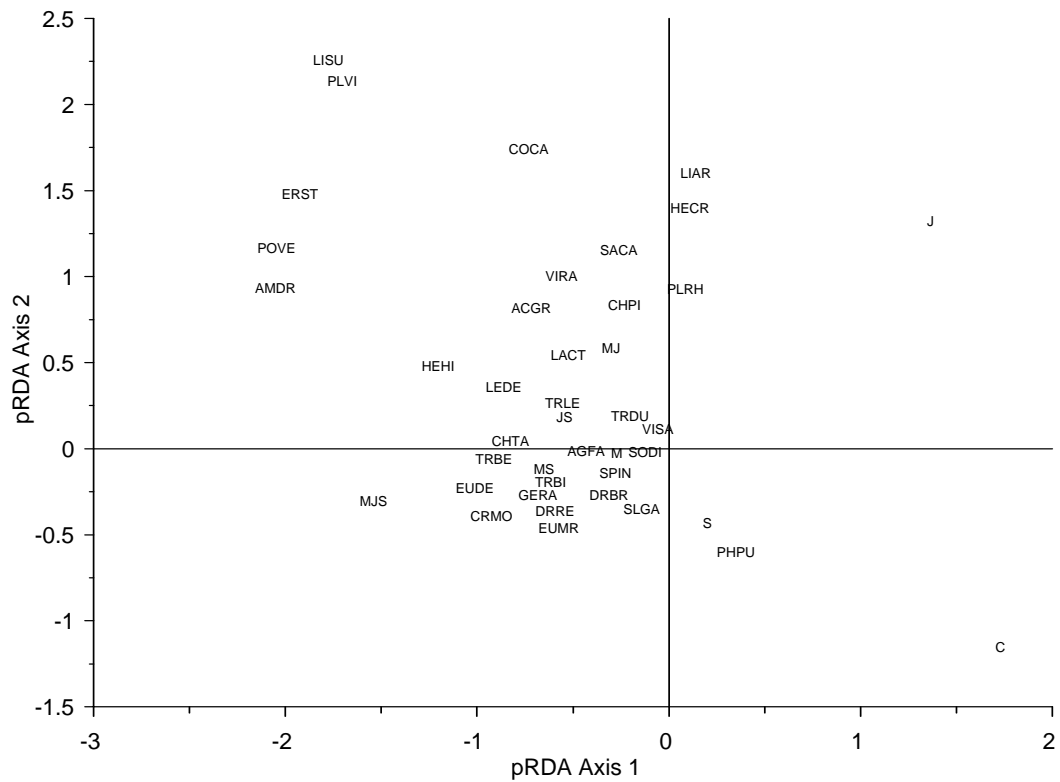August biplots were multiplied by 10.
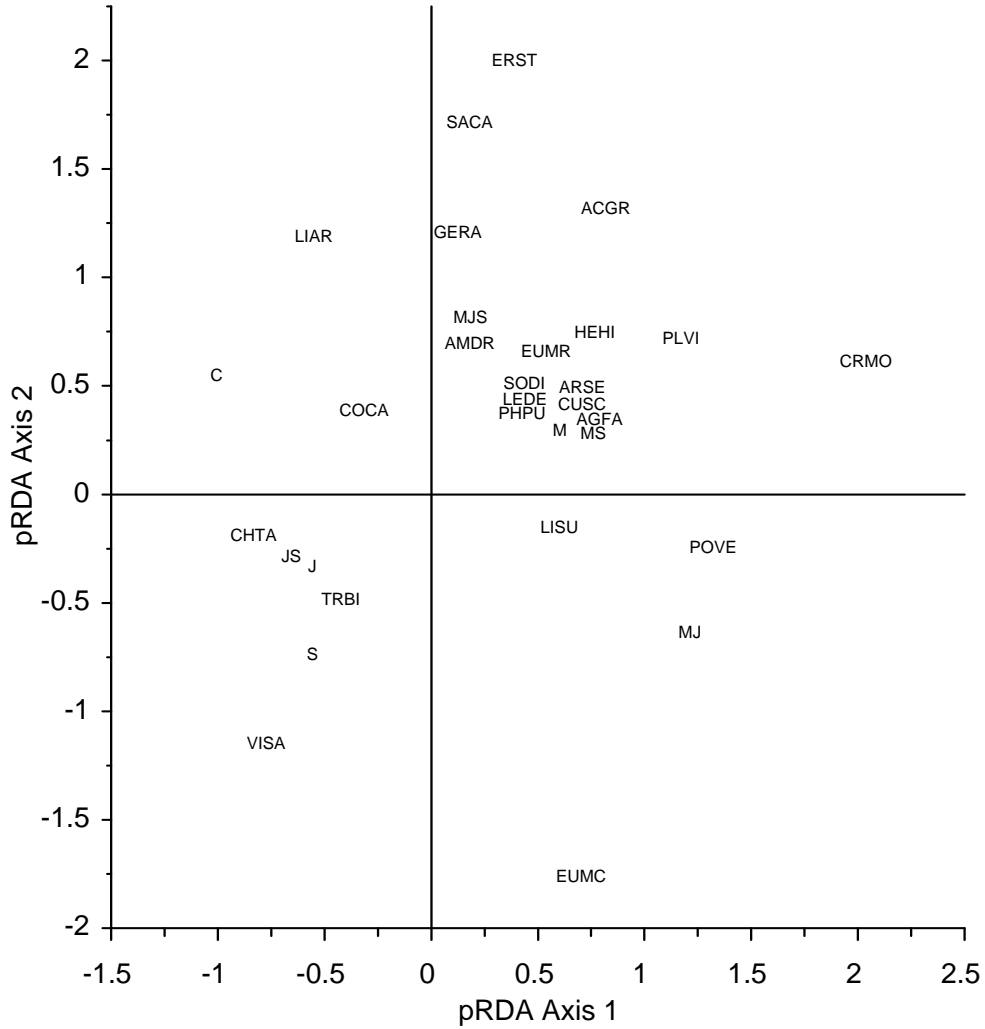
Figure 6. Biplot of environmental centroids and annual forb species scores from pRDA on May 1997 Veterinary Medicine Ranch data. Environmental centroid scores for all May biplots were multiplied by five. Labels for AGFA, ARSE, CUSC, PHPU and SODI were moved slightly to improve readability.
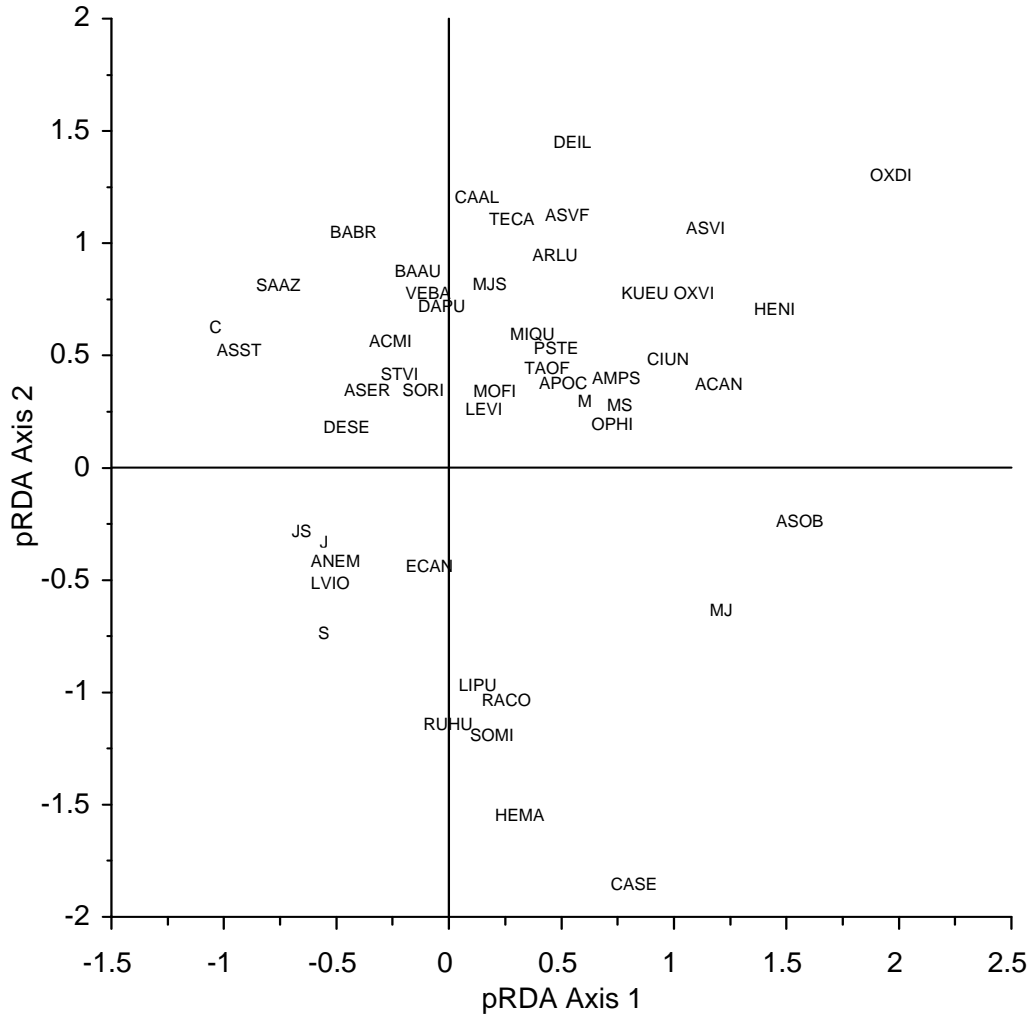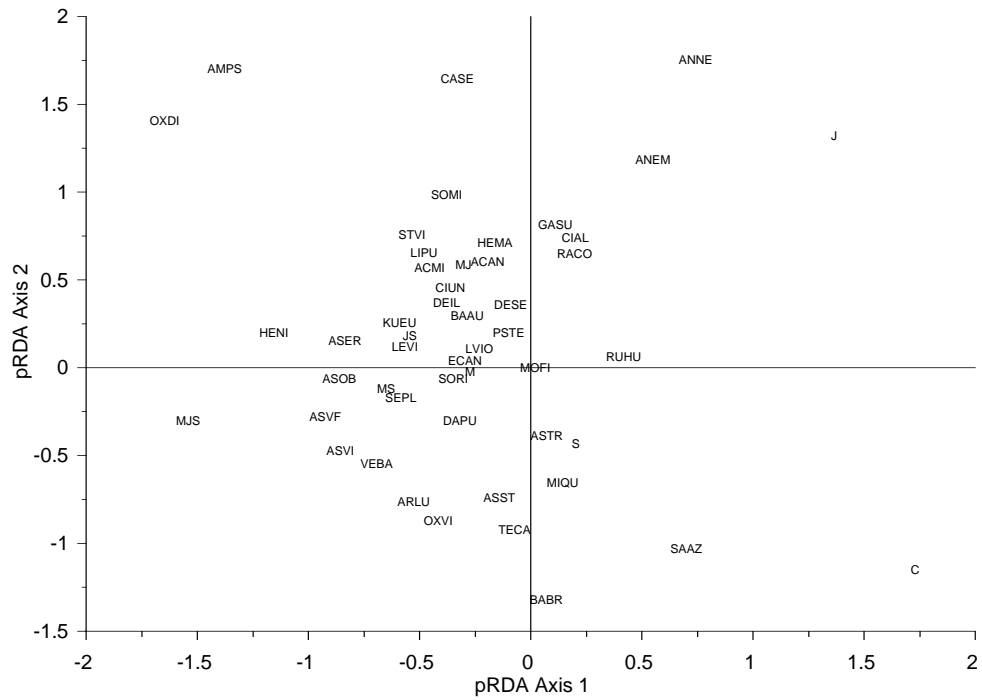
Figure 7. Biplot of environmental centroids and perennial forb species scores from pRDA on May 1997 Veterinary Medicine Ranch data. Labels for APOC, ASER, and SORI were moved slightly to improve readability. Environmental centroid scores for all May biplots were multiplied by five.
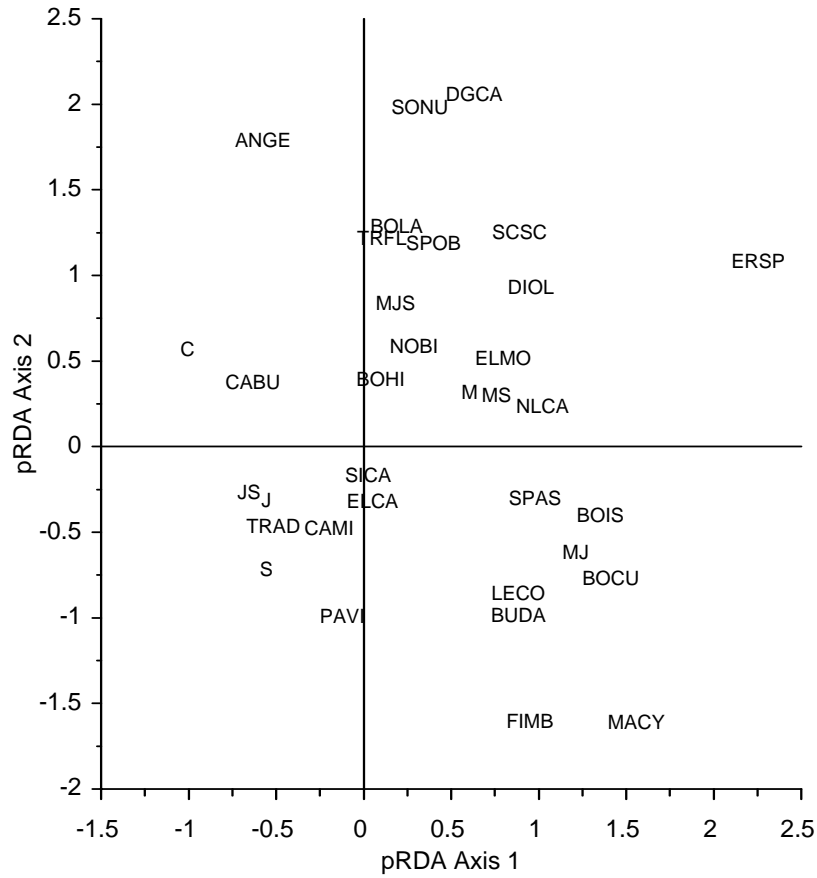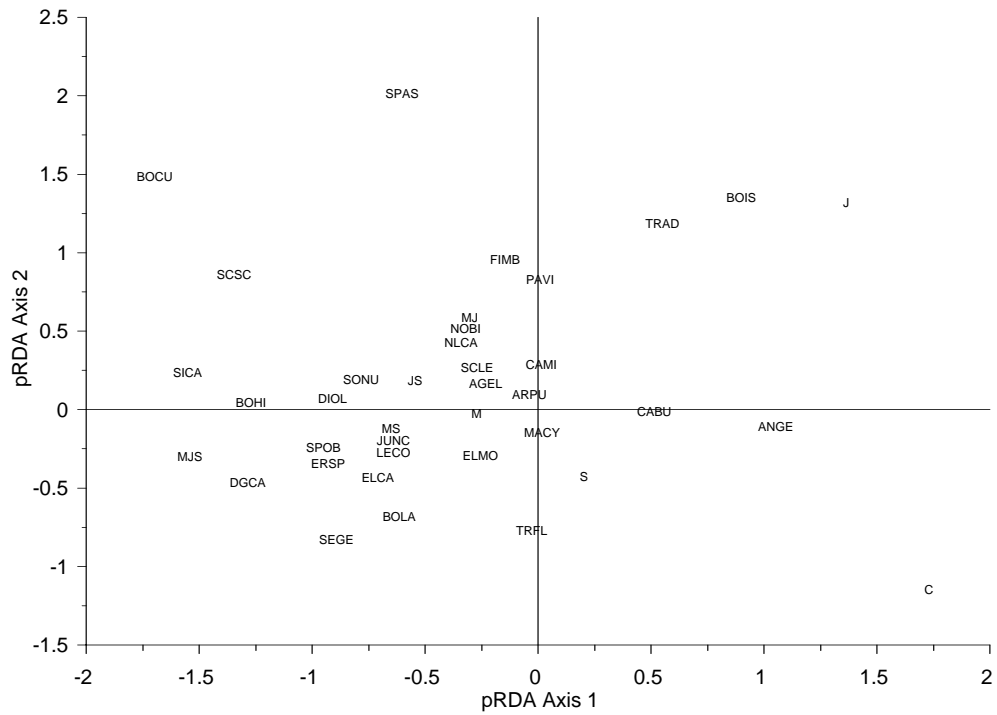
Figure 8. Biplot of environmental centroids and perennial graminoid species scores from pRDA on May 1997 Veterinary Medicine Ranch data. Labels for BUDA, CAMI, LECO, TRAD and TRFL were moved slightly to improve readability. Environmental centroid scores for all May biplots were multiplied by five.
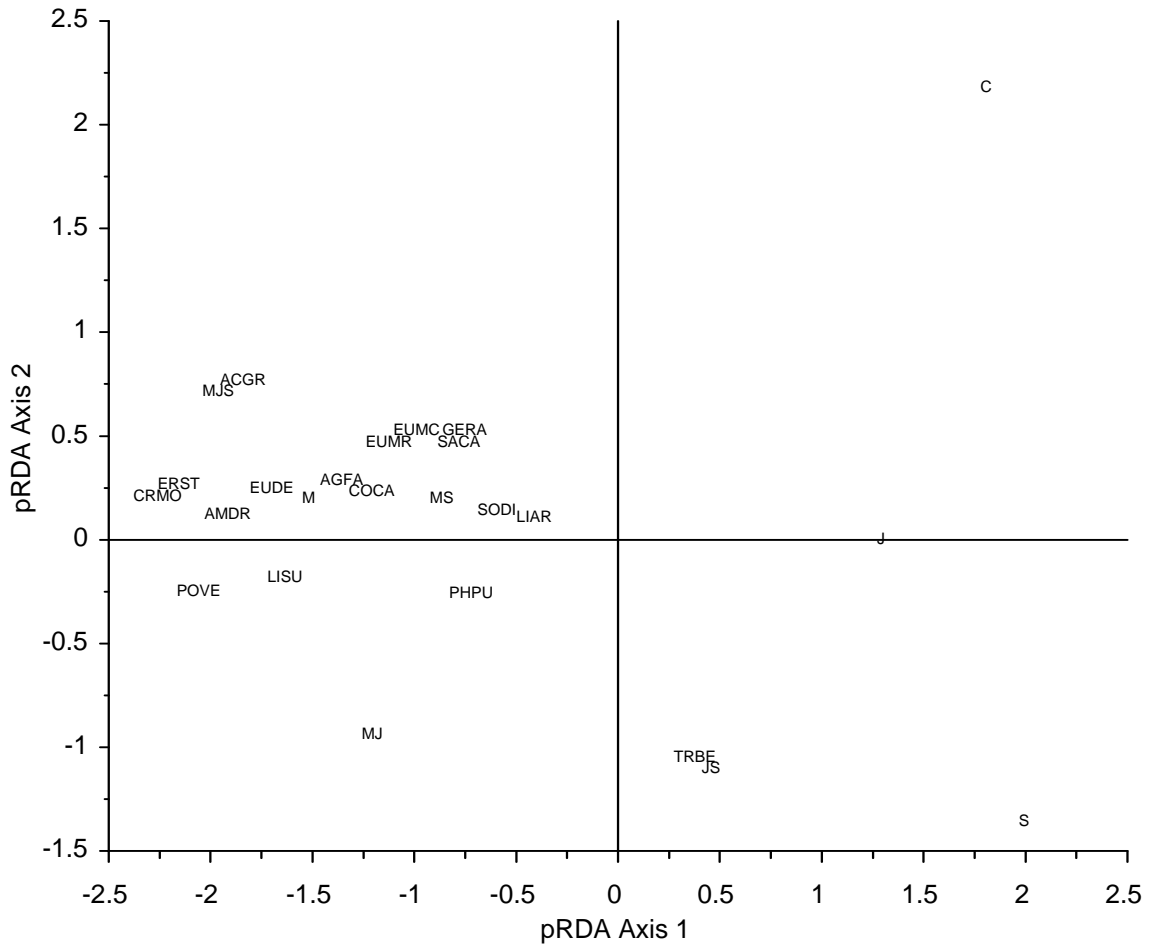
Figure 9. Biplot of environmental centroids and annual forb species scores from pRDA on August 1997 Veterinary Medicine Ranch data. Labels for ACGR, AGFA, EUMC and GERA were moved to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.
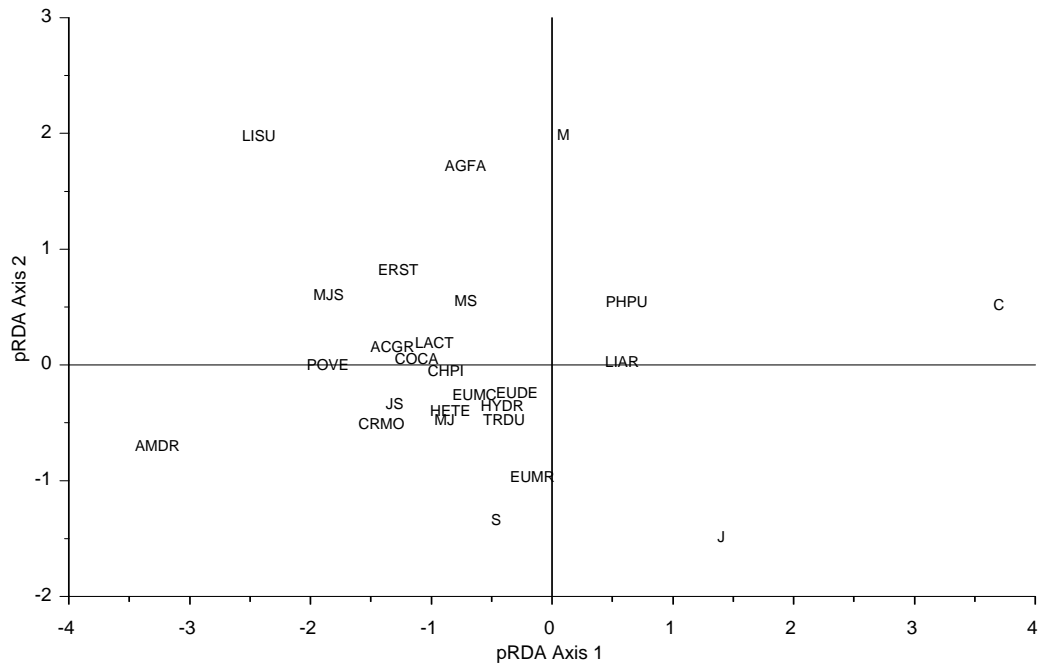
Figure 10. Biplot of environmental centroids and perennial forb species scores from pRDA on August 1997 Veterinary Medicine Ranch data. Labels for CAAL, LIPU and MOFI were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.

Figure 11. Biplot of environmental centroids and perennial graminoid species scores from August 1997 Veterinary Medicine Ranch data. Labels for BUDA and ELCA were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.

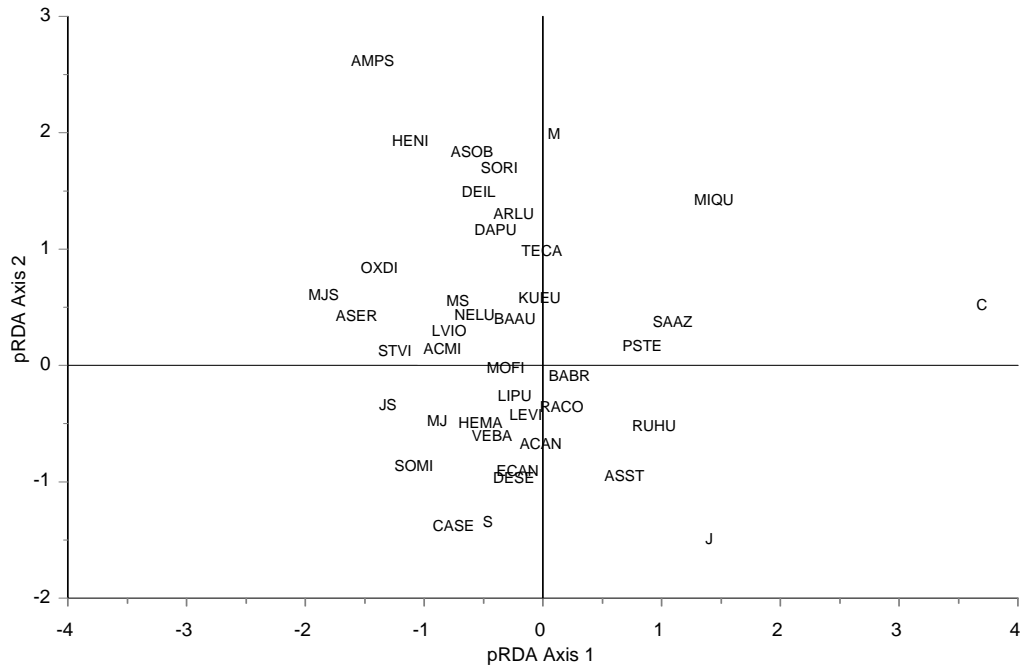Figure 12. Biplot of environmental centroids and annual forb species scores from pRDA on May 1998 Veterinary Medicine Ranch data. AGFA, CHTA, CRMO, DRBR, DRRE, EUDE, EUMR, GERA, LEDE, LISU, SPIN, TRBE, TRBI, TRDU, TRLE and VISA were moved slightly to improve readability. Environmental centroid scores for all May biplots were multiplied by five.

Figure 13. Biplot of environmental centroids and perennial forb species scores from pRDA on May 1998 Veterinary Medicine Ranch data. ACMI, DEIL, DESE, ECAN, KUEU, LEVI, LIPU, MOFI, SORI, LVIO, OXVI, CIUN, CIAL and SEPL were moved slightly and OPHI (-0.266, 0.375) was omitted to improve readability. Environmental centroid scores for all May biplots were multiplied by five.
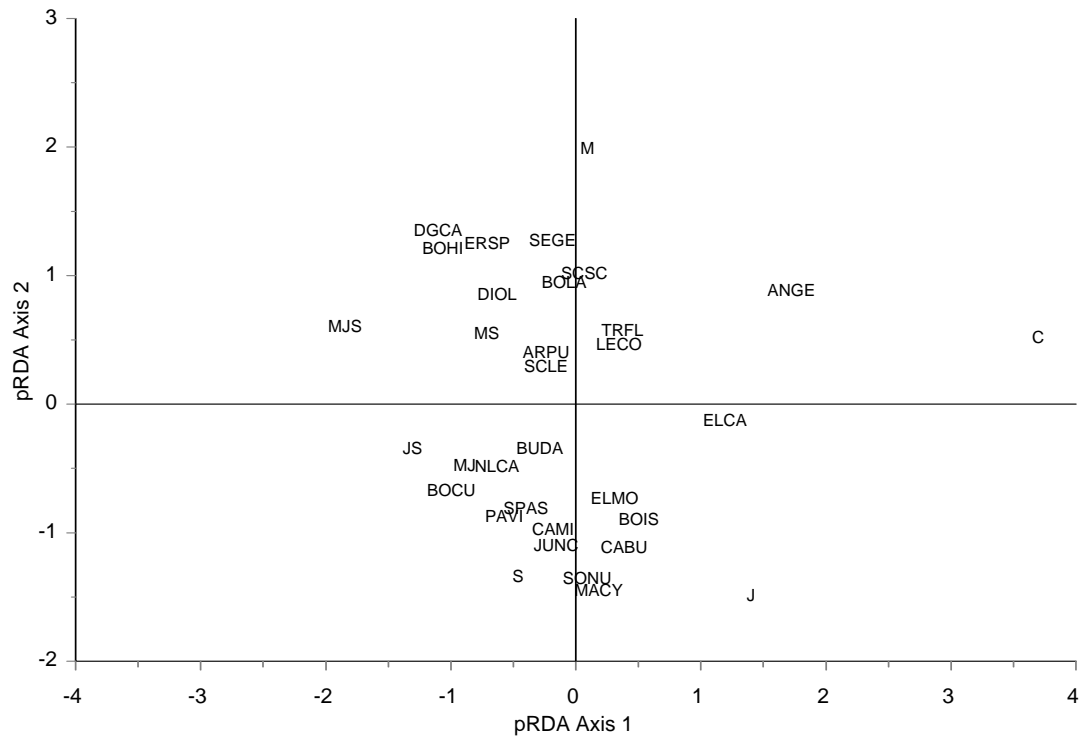
Figure 14. Biplots of environmental centroids and perennial graminoid species scores from pRDA on May 1998 Veterinary Medicine Ranch data. DIOL, FIMB, SCLE, SPOB, NLCA and JUNC were moved slightly to improve readability. Environmental centroid scores for all May biplots were multiplied by five.
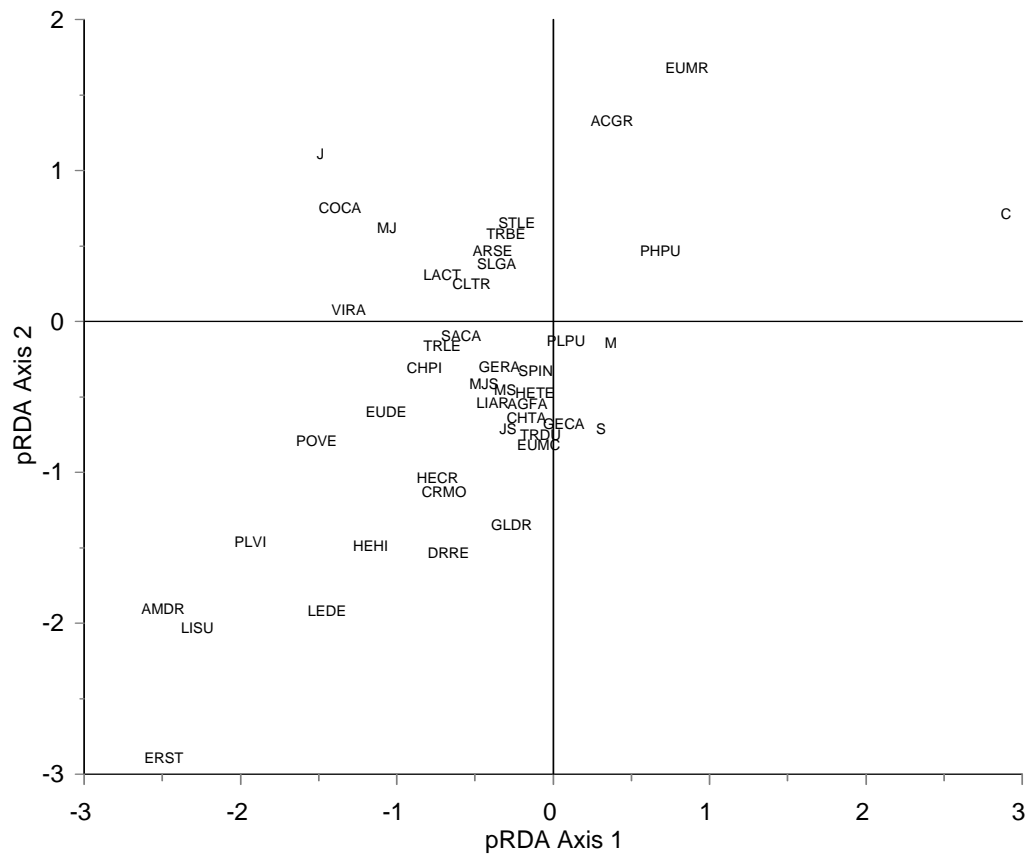
Figure 15. Biplot of environmental centroids and annual forb species scores from pRDA on August 1998 Veterinary Medicine Ranch data. Labels for ACGR, COCA, EUDE, EUMC, HETE, HYDR and TRDU were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.
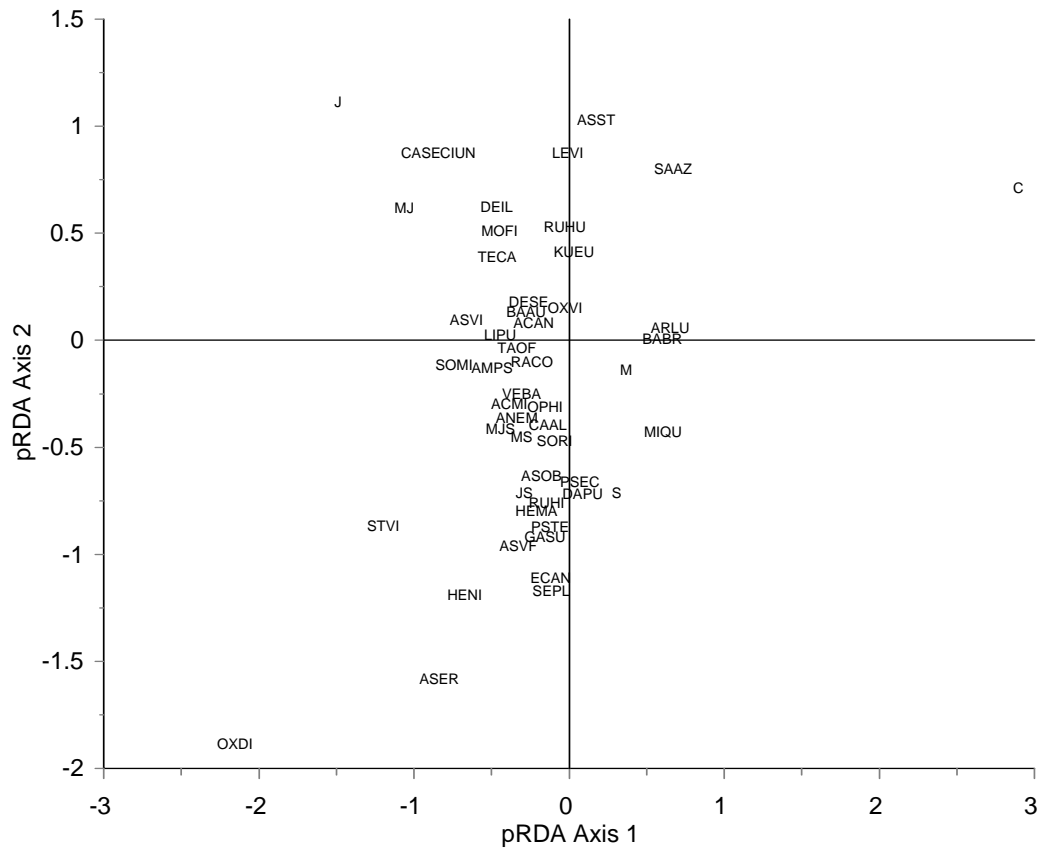
Figure 16. Biplot of environmental centroids and perennial forb species scores from pRDA on August 1998 Veterinary Medicine Ranch data. Labels for ACMI and LVIO were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.

Figure 17. Biplot of environment centroids and perennial graminoid species scores from pRDA on August 1998 Veterinary Medicine Ranch data. Labels for CAMI, DGCA, JUNC and SCLE were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.

Figure 18. Biplot of environmental centroids and annual forb species scores from pRDA on May 1999 Veterinary Medicine Ranch data. AGFA, EUMC, HETE, SLGA, TRLE, and TRDU, were moved slightly. HYDR and VISA were omitted to improve readability. Environmental centroid scores for all May biplots were multiplied by five.
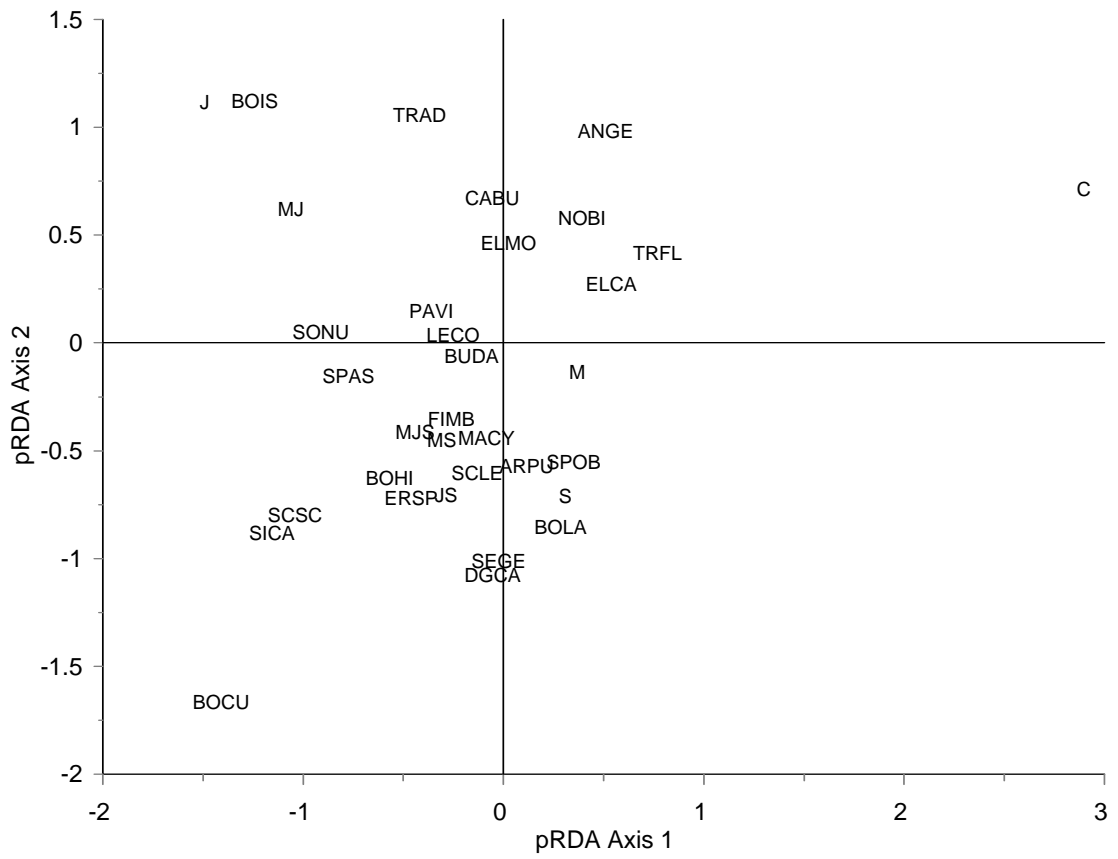
Figure 19. Biplot of environmental centroids and perennial forb species scores from pRDA on May 1999 Veterinary Medicine Ranch data. ACMI, ARLU, BAAU, CASE, CIUN, GASU, HEMA, PSEC, RUHI, TAOF, VEBA were moved slightly and LVIO was omitted to improve readability. Environmental centroid scores for all May biplots were multiplied by five.

Figure 20. Biplot of environmental centroids and perennial graminoid species scores from pRDA on May 1999 Veterinary Medicine Ranch data. Environmental centroid scores for all May biplots were multiplied by five.
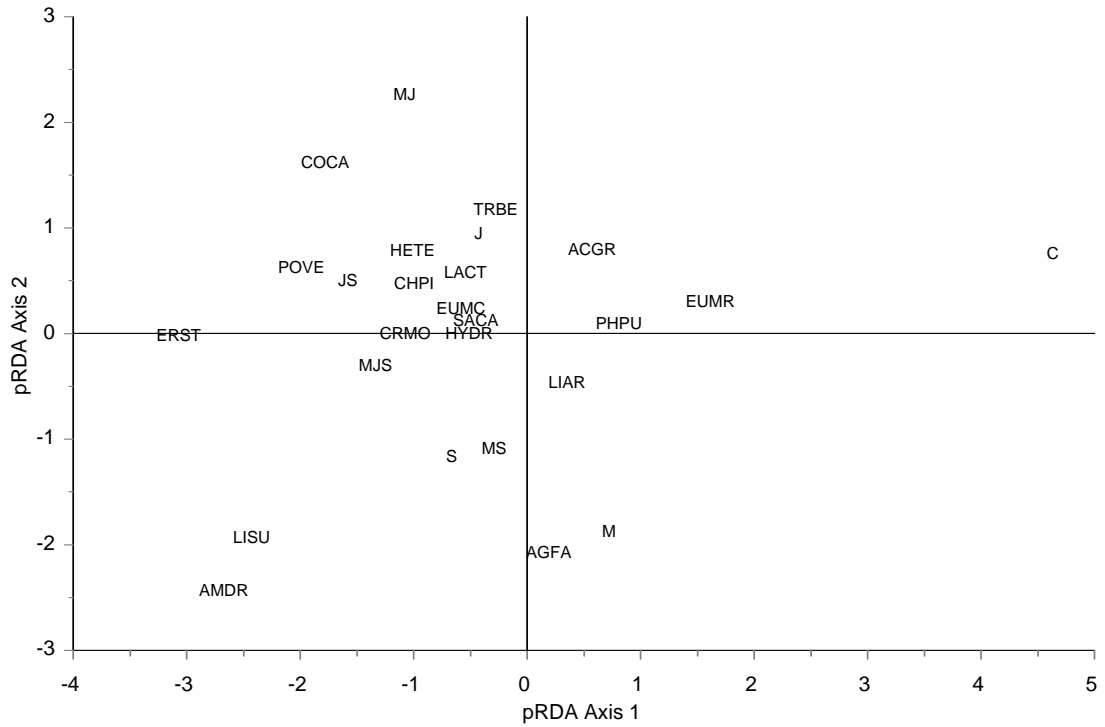
Figure 21. Biplot of environmental centroids and annual forb species scores from August 1999 Veterinary Medicine Ranch data. HYDR and SACA were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.
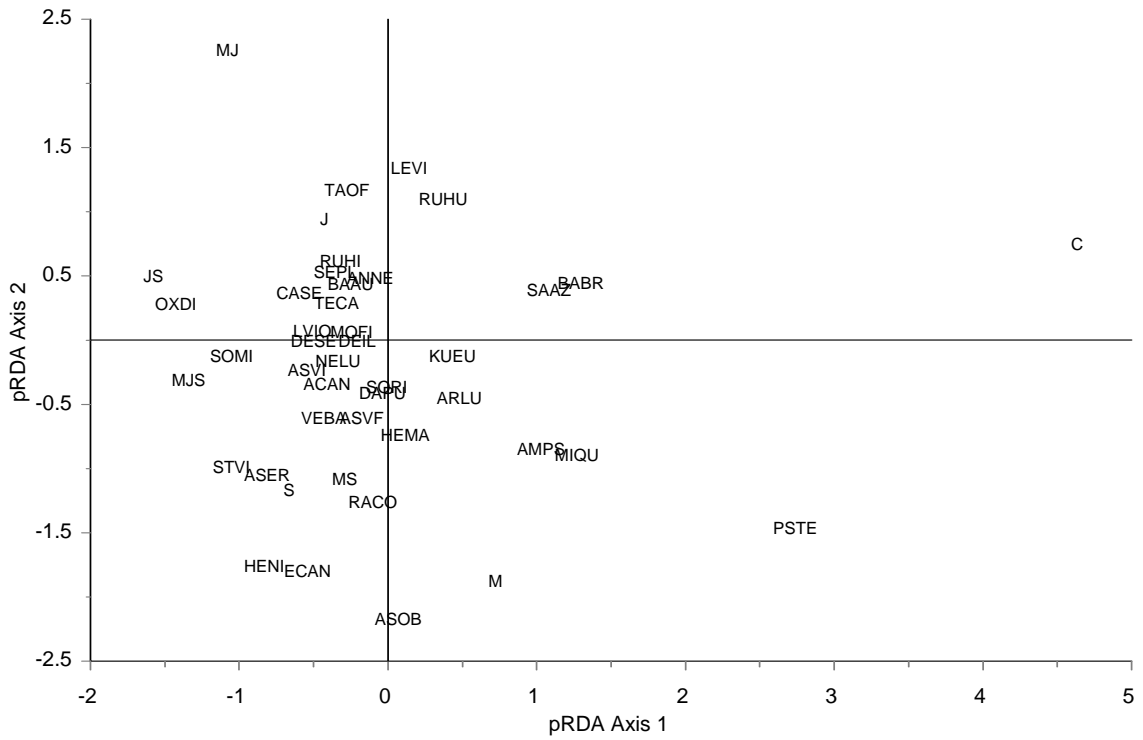
Figure 22. Biplot of environmental centroids and perennial forb species scores from pRDA on August 1999 Veterinary Medicine Ranch data. ACAN, ACMI, ASVF, ASVI, BAAU, CIUN. LIPU, LVIO, MIQU and SORI were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.
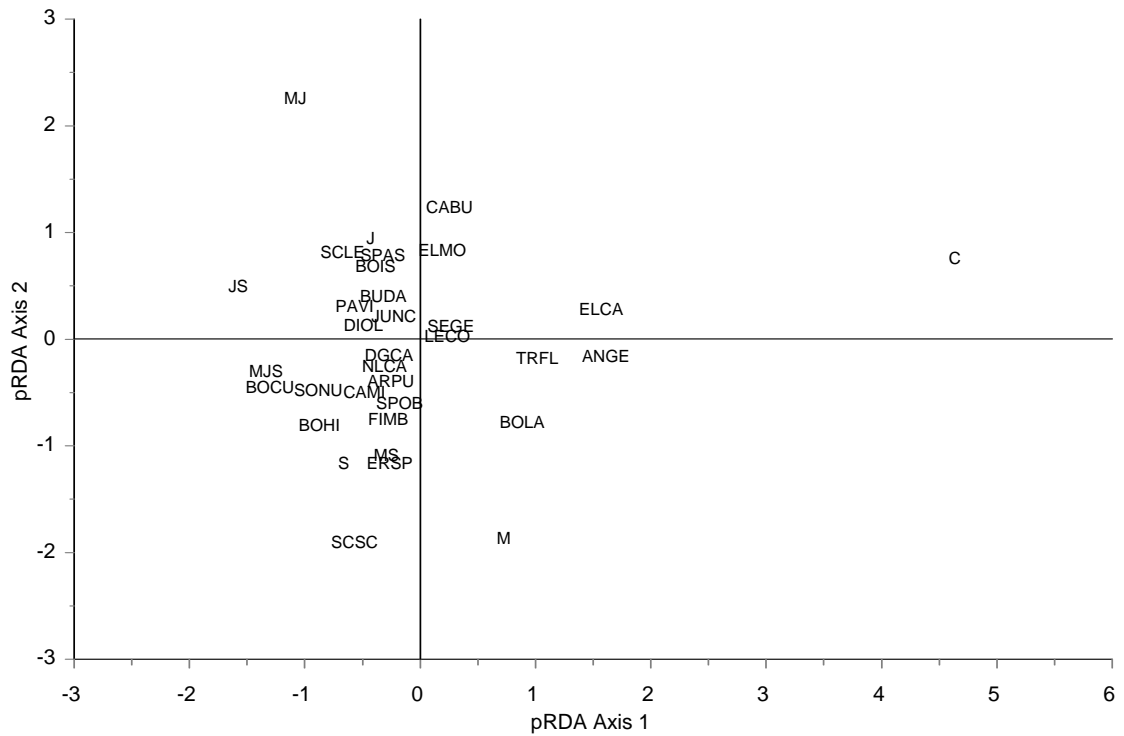
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Figure 23. Biplot of environmental centroids and perennial graminoid species scores from pRDA on August 1999 Veterinary Medicine Ranch data. ARPU, BOCU, BOIS, CAMI, DGCA, NLCA, SCLE, SEGE and SPAS were moved slightly to improve readability. Environmental centroid scores on all August biplots were multiplied by 10.
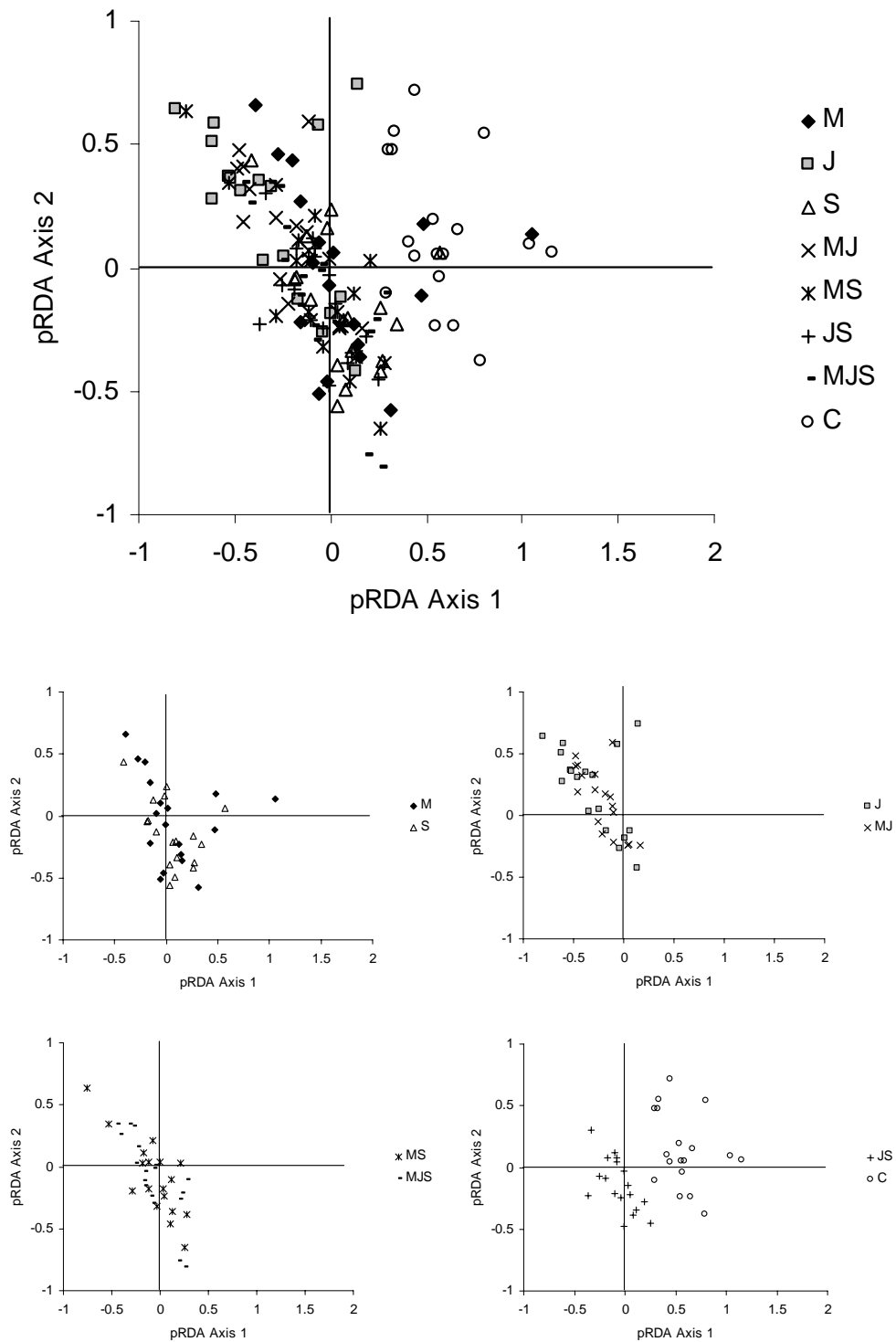
Figure 24. Scatter plots of May 1999 Veterinary Medicine Ranch pRDA sample scores. Upper and lower graphs contain the same results. The lower plots each contain only two treatments to facilitate readability. Environmental centroid scores for all May biplots were multiplied by five.
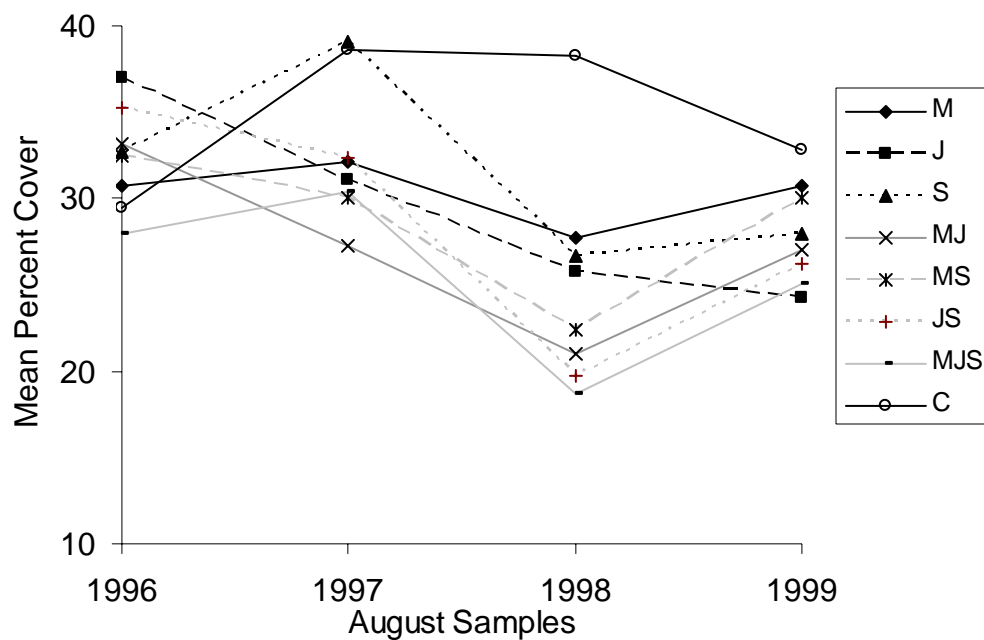
Figure 25. Veterinary Medicine Ranch August perennial graminoid mean percent live cover per mowing treatment. Only cover means for J and JS are different in 1996 compared to 1999 ($p<0.05$). None of the means are different in 1999 ($p>0.05$)
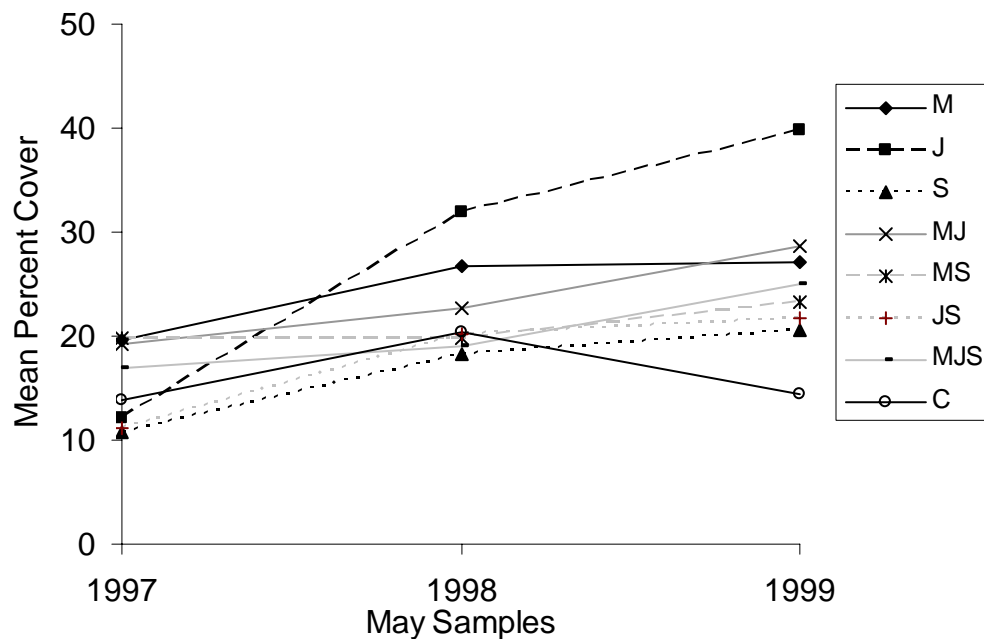

Figure 26. Veterinary Medicine Ranch May perennial graminoid mean percent live cover per mowing treatment. From 1997 to 1999, the changes in cover on M, MS and C were not significant. In 1999, J cover is greater than all other treatments ($p<0.05$). None of the other mowing treatments are different. The C cover is not different from S or JS in 1999 ($p>0.05$).
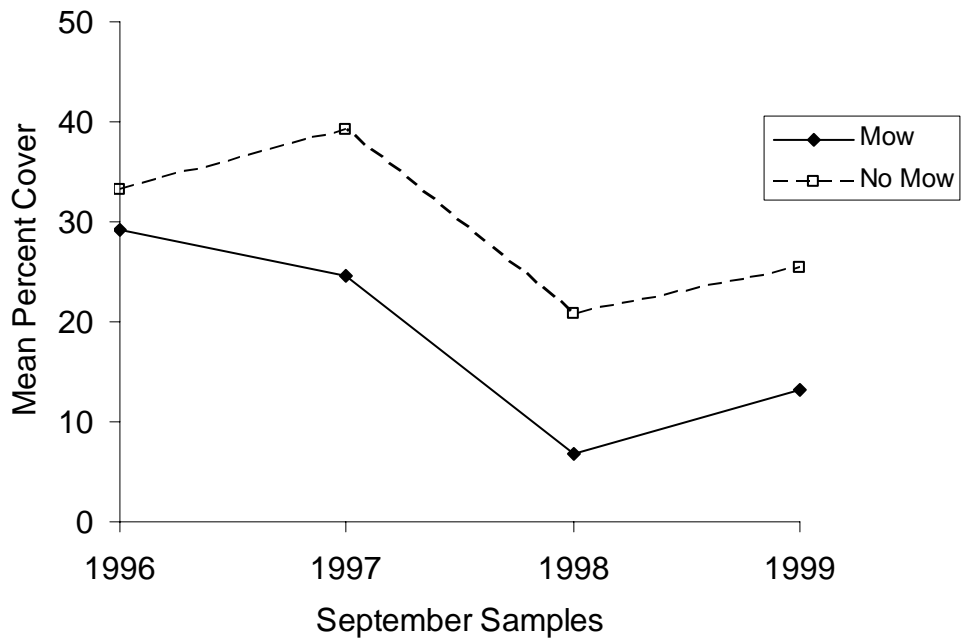
Figure 27. Lake Carl Blackwell September mean perennial graminoid percent live cover per mowing treatment. Mowed treatment means are different from the unmowed means in 1997 through 1999 ($p<0.05$).
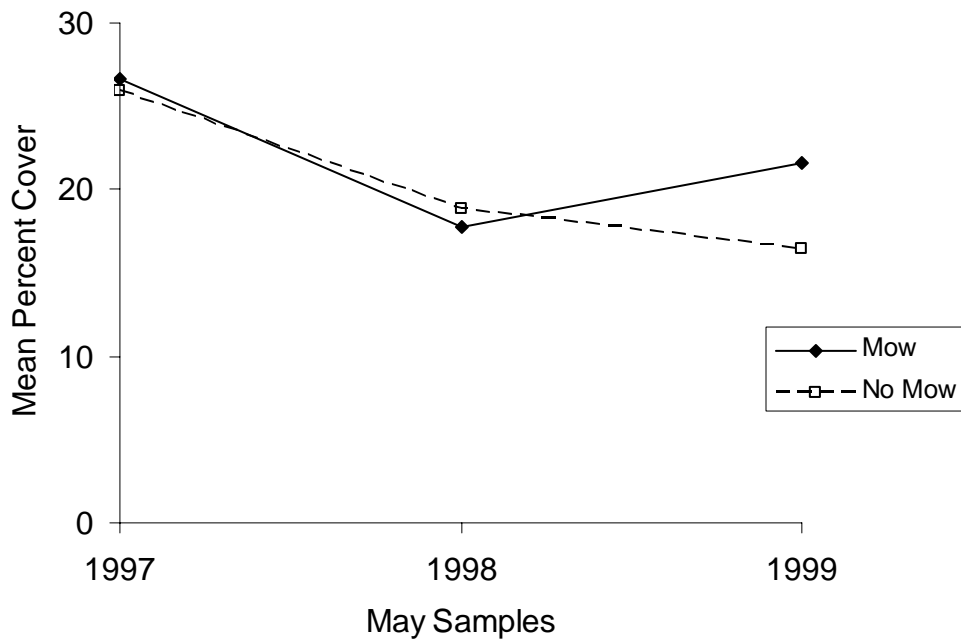

Figure 28. Lake Carl Blackwell May mean perennial graminoid percent live cover per mowing treatment. Means between treatments are not different until 1999 ($p<0.05$).
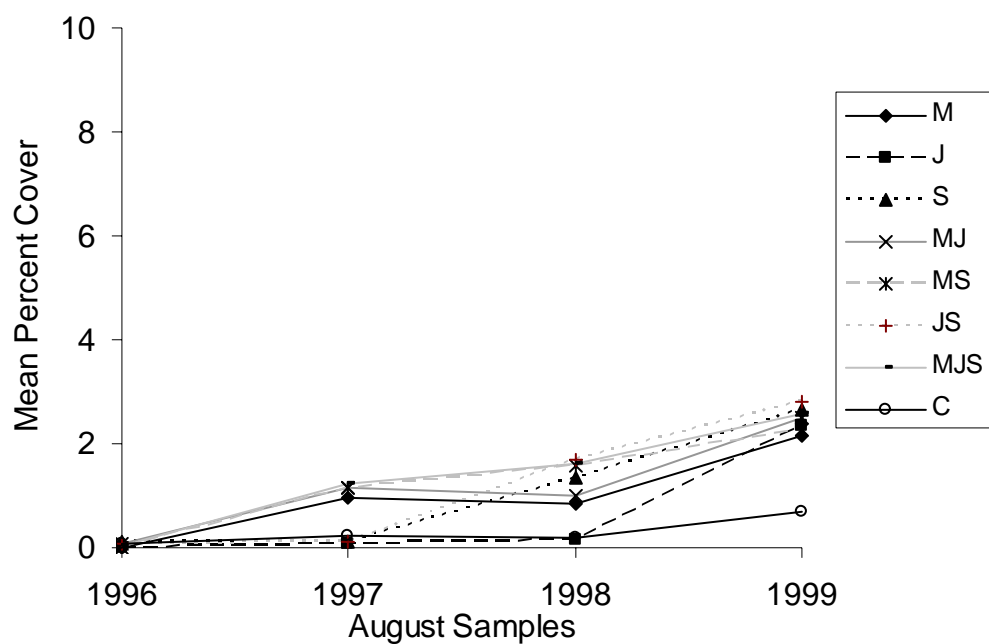
Figure 29. Veterinary Medicine Ranch August annual forb mean percent live cover per treatment. All means on mowed treatments are greater in 1999 than 1996 ($p<0.05$). All mowed means in 1999 are greater than the C ($p<0.05$).
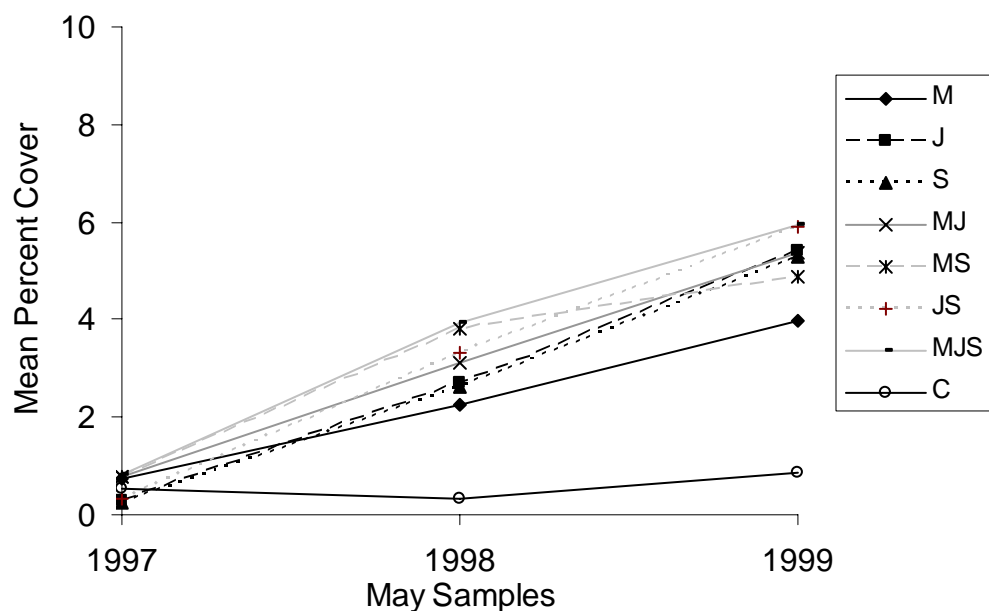

Figure 30. Veterinary Medicine Ranch May annual forb mean percent live cover per mowing treatment. Means increased each year on the mowed plots ($p<0.05$), while remaining unchanged on the C. In 1999, only MS is not different from M , and all mowed means are different from the C ($p>0.05$).
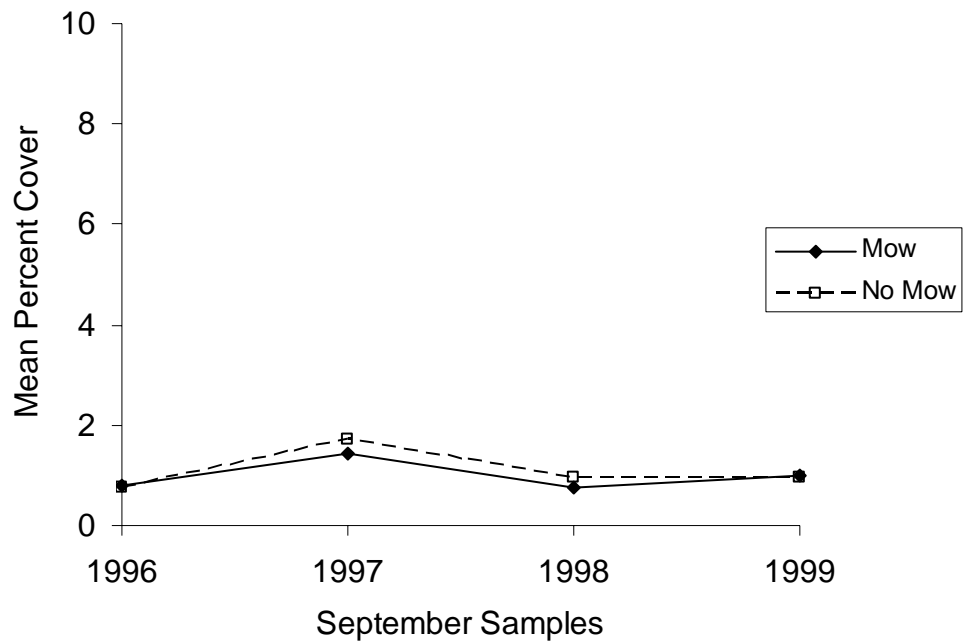
Figure 31. Lake Carl Blackwell September mean annual forb percent live cover per mowing treatment. There are no significant differences among years or between treatments (*p*>0.05).

Figure 32. Lake Carl Blackwell May mean annual forb percent live cover per mowing treatment. Means between treatments are different in 1999 (*p*<0.05).
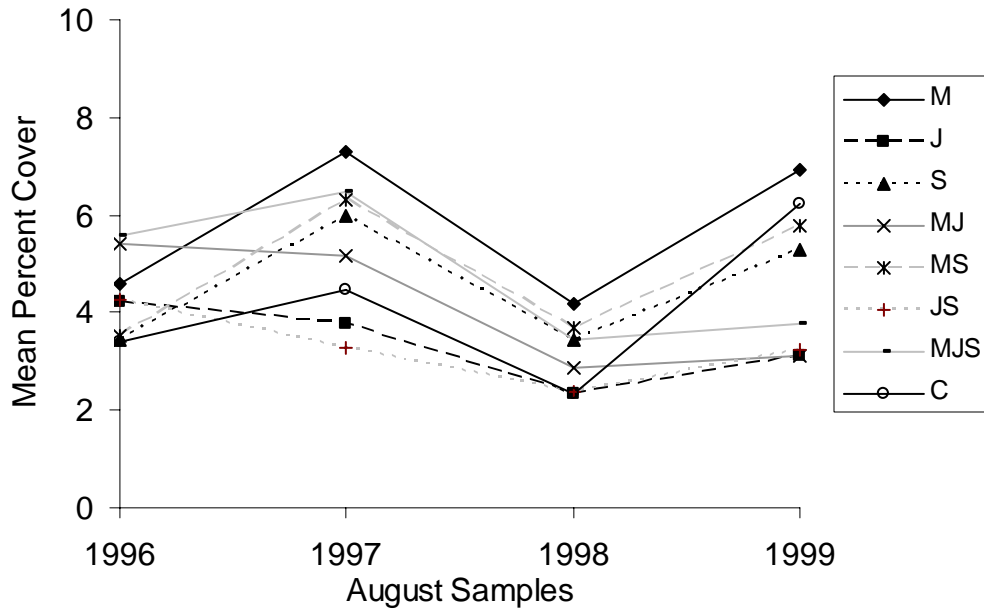
Figure 33. Veterinary Medicine Ranch August perennial forb mean percent live cover per mowing treatment. Within each year most means are not significantly different (*p*>0.05). In 1999, C was not different from M, MS or S (*p*>0.05).
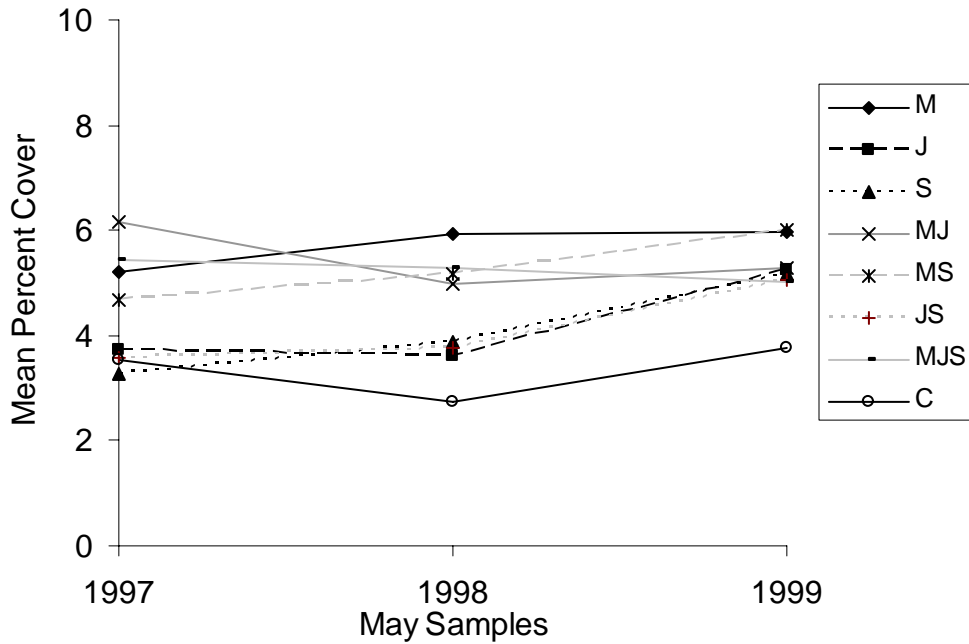
Figure 34. Veterinary Medicine Ranch May perennial forb mean percent live cover per mowing treatment. In 1999, C is different from only M and MS (*p*<0.05).
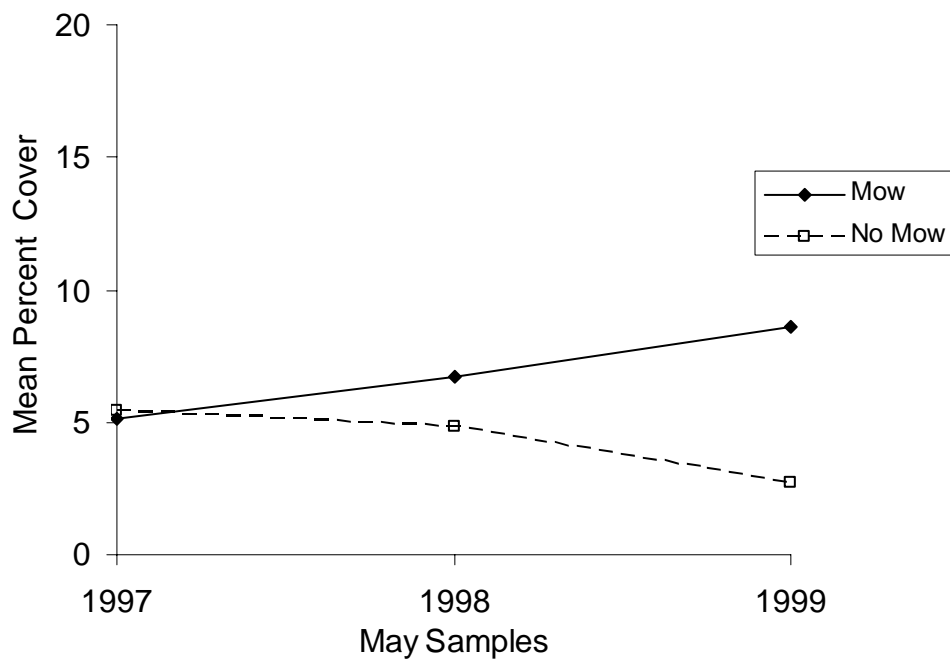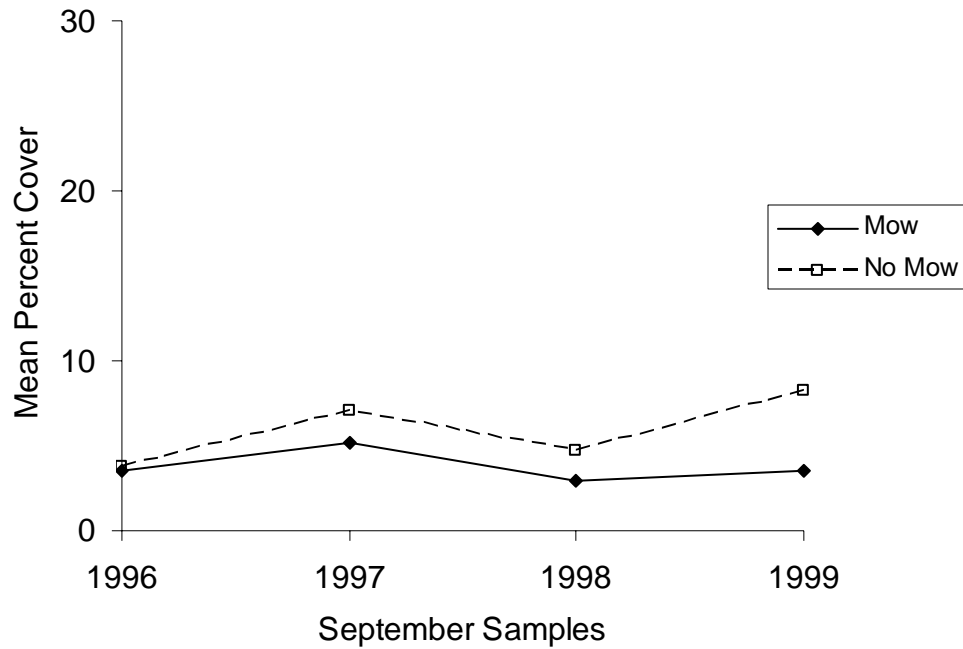
Figure 35. Lake Carl Blackwell September mean perennial forb percent live cover per mowing treatment. Means between mowing treatments are different in 1997 through 1999 ($p<0.05$).
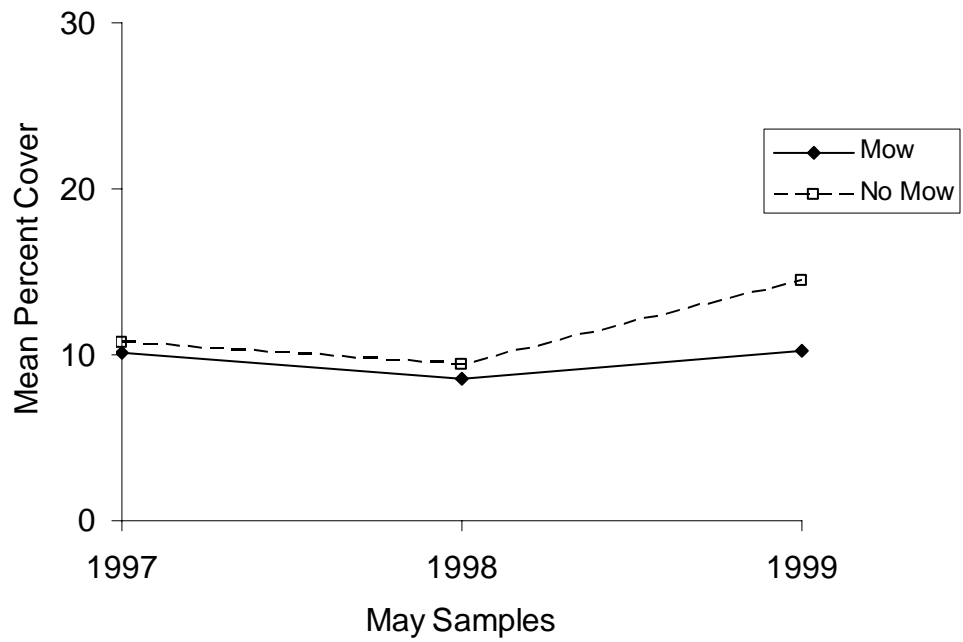
Figure 36. Lake Carl Blackwell May mean perennial forb percent live cover per mowing treatment. Means within each year are not different ($p>0.05$)

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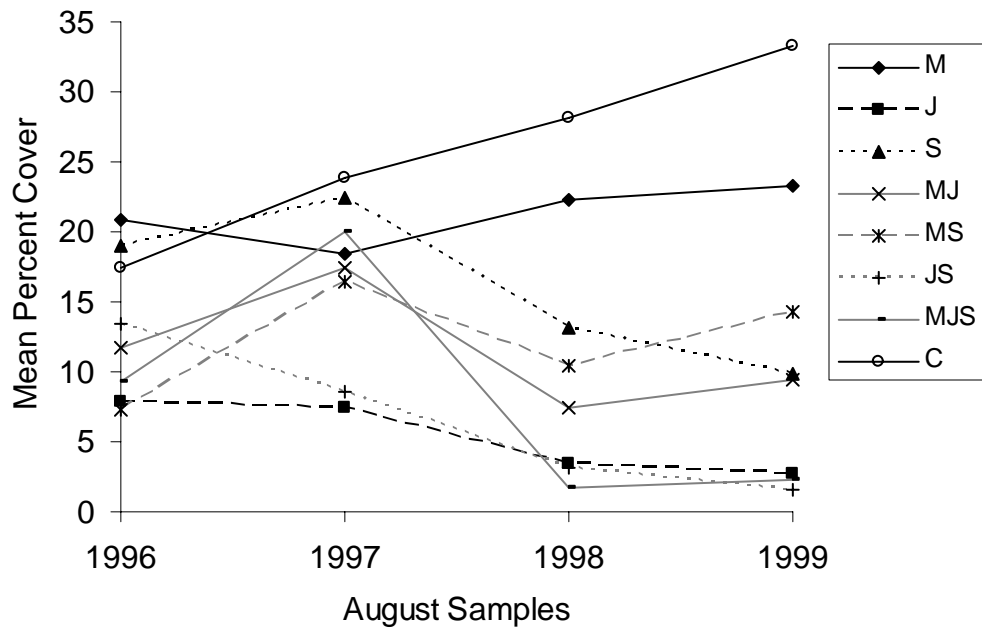
Figure 37. *Andropogon gerardii* mean August percent live cover per mowing treatment at Veterinary Medicine Ranch.
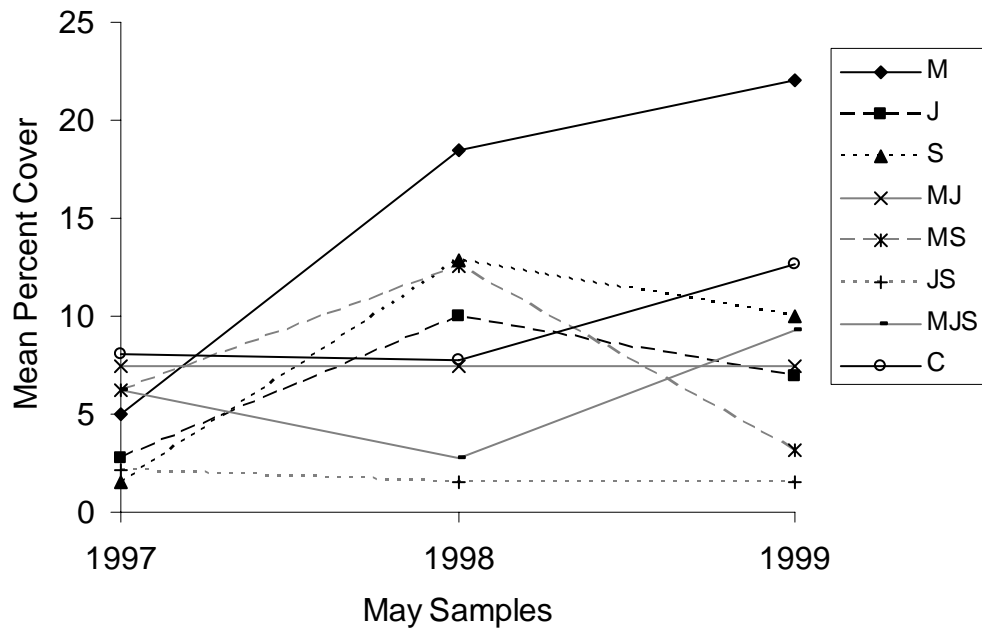
Figure 38. *Andropogon gerardii* mean May percent live cover per mowing treatment at Veterinary Medicine Ranch.
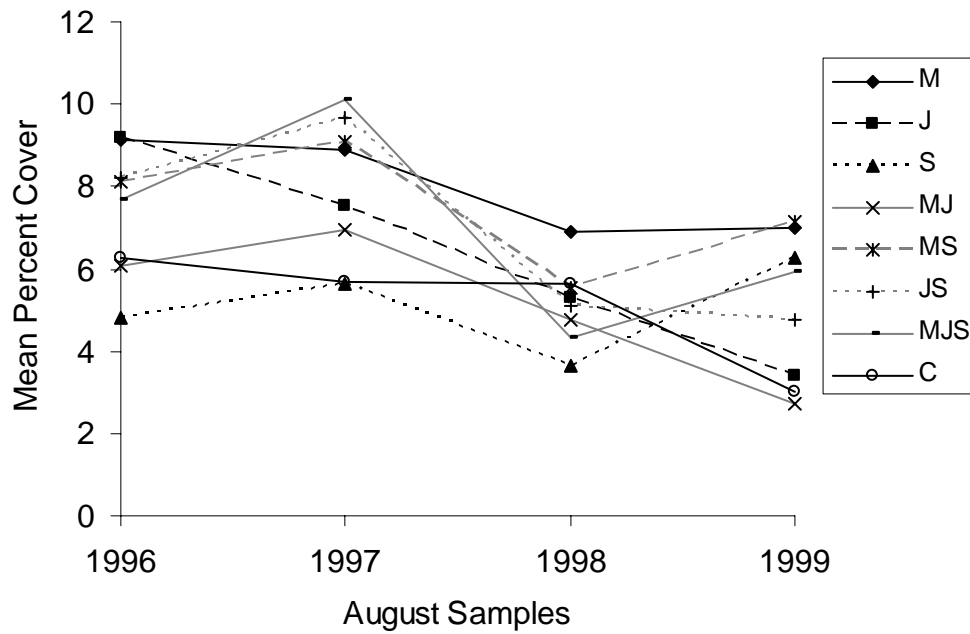
Figure 39. *Schizachyrium scoparium* August mean percent live cover per mowing treatment on Veterinary Medicine Ranch.
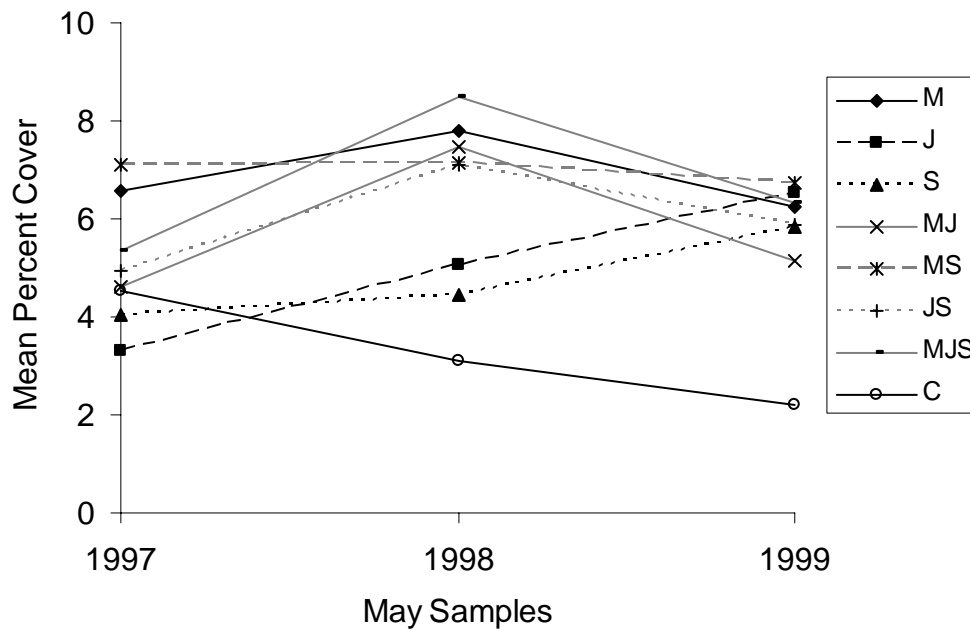
Figure 40. *Schizachyrium scoparium* May mean percent live cover per mowing treatment on Veterinary Medicine Ranch.
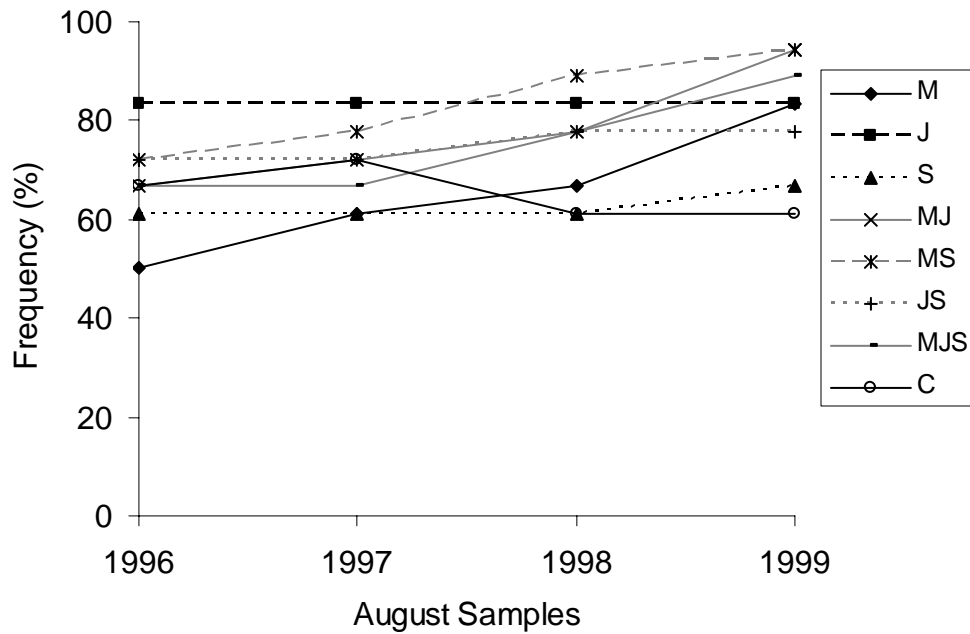
Figure 41. *Bothriochloa ischaemum* August frequencies per mowing treatment on Veterinary Medicine Ranch.
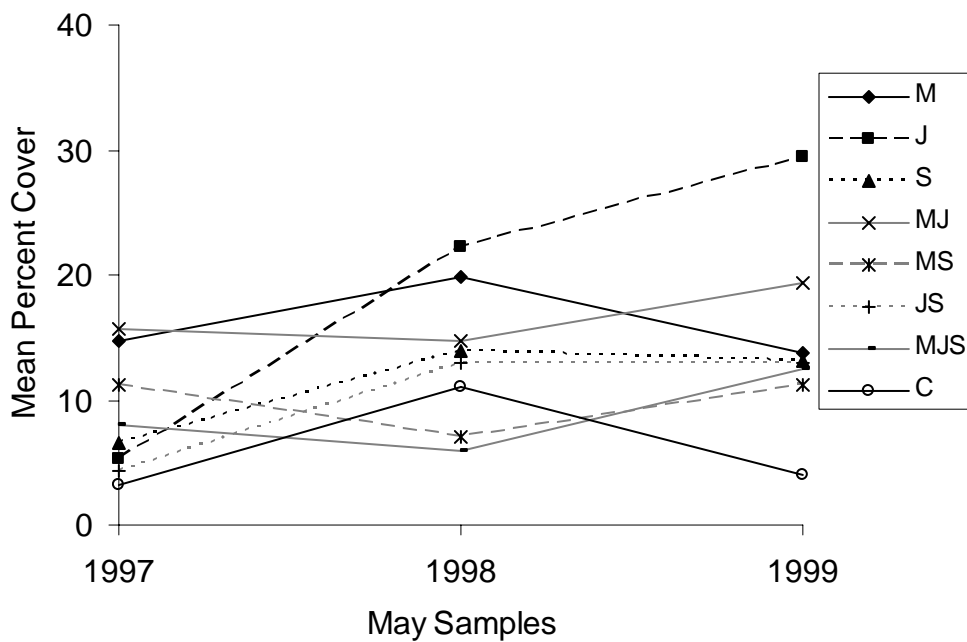
Figure 42. *Bothriochloa ischaemum* May mean percent live cover per mowing treatment on Veterinary Medicine Ranch.
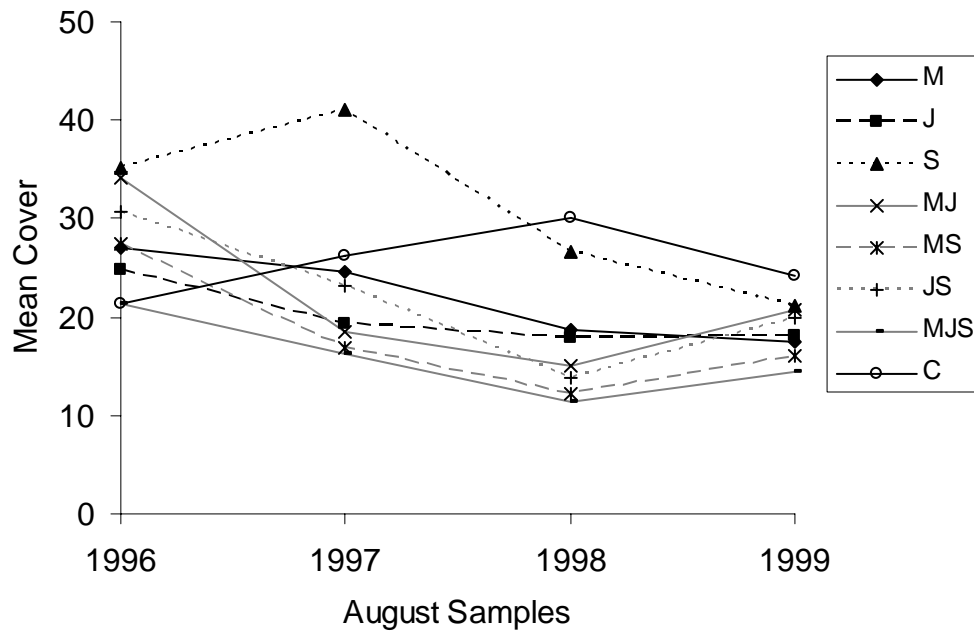
Figure 43. *Bothriochloa ischaemum* mean August percent live cover per mowing treatment on Veterinary Medicine Ranch.
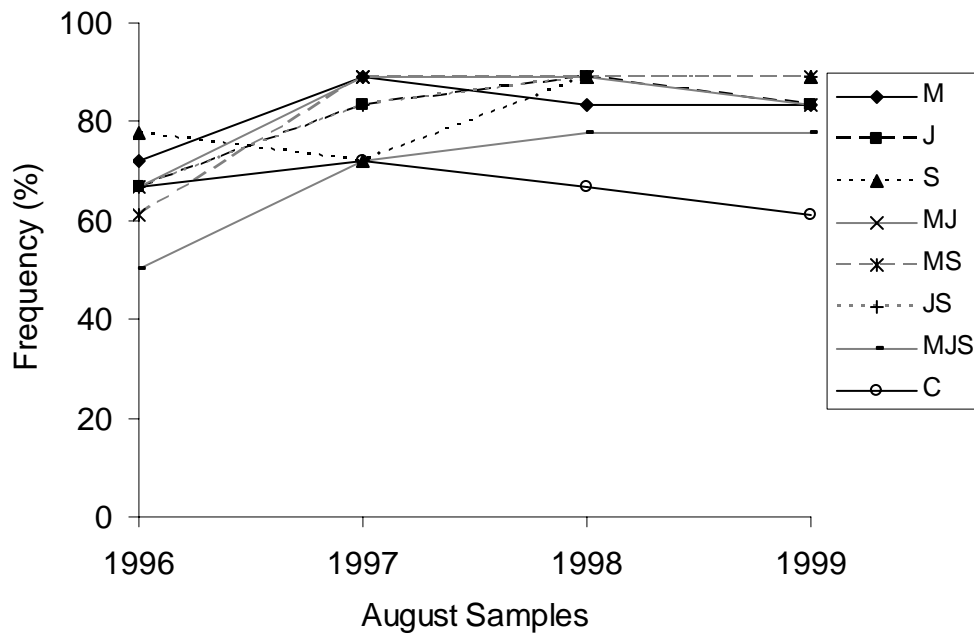
Figure 44. *Bouteloua curtipendula* August frequencies per mowing treatment on Veterinary Medicine Ranch.
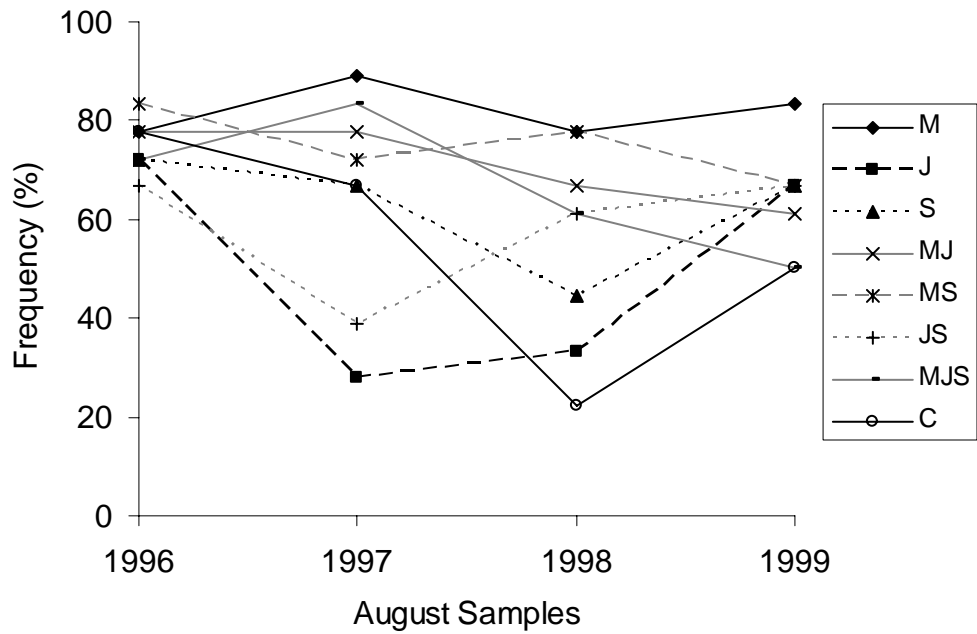
Figure 45. *Ambrosia psilostachya* August frequencies per mowing treatment on Veterinary Medicine Ranch.
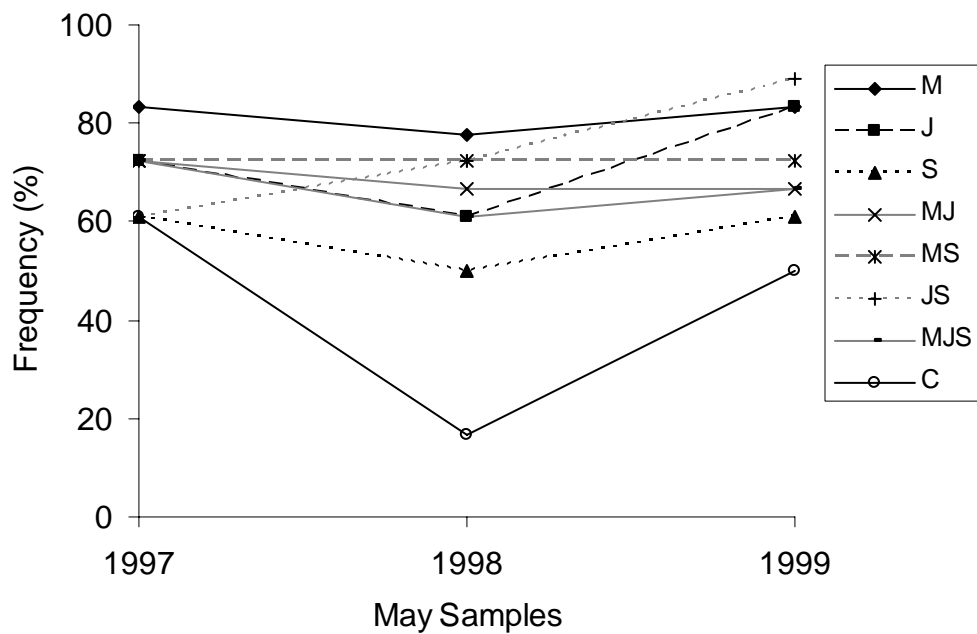
Figure 46. *Ambrosia psilostachya* May frequencies per mowing treatment on Veterinary Medicine Ranch.
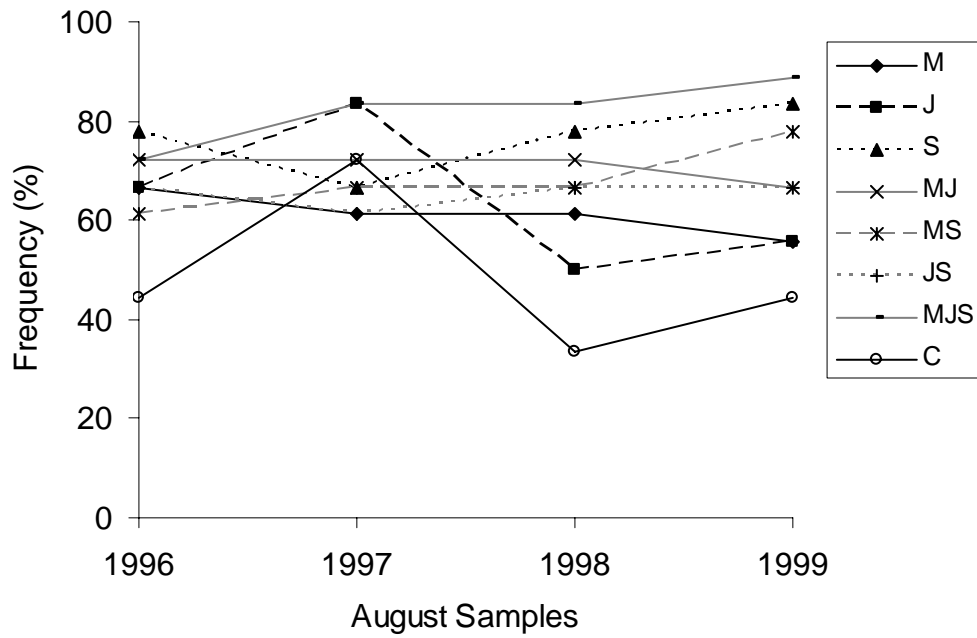
Figure 47. *Aster ericoides* August frequencies per mowing treatment on Veterinary Medicine Ranch.
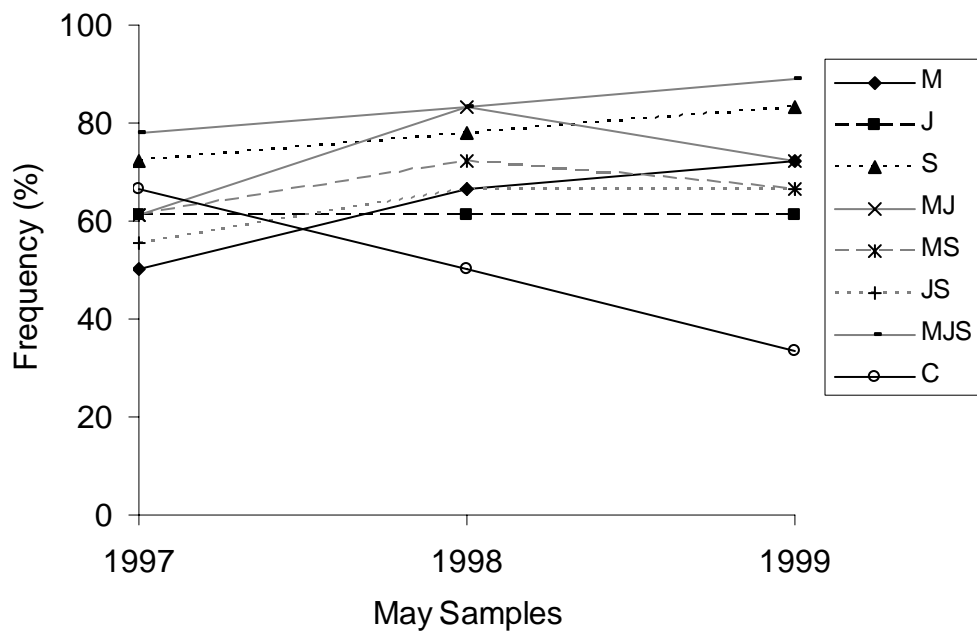
Figure 48. *Aster ericoides* May frequencies per mowing treatment on Veterinary Medicine Ranch.
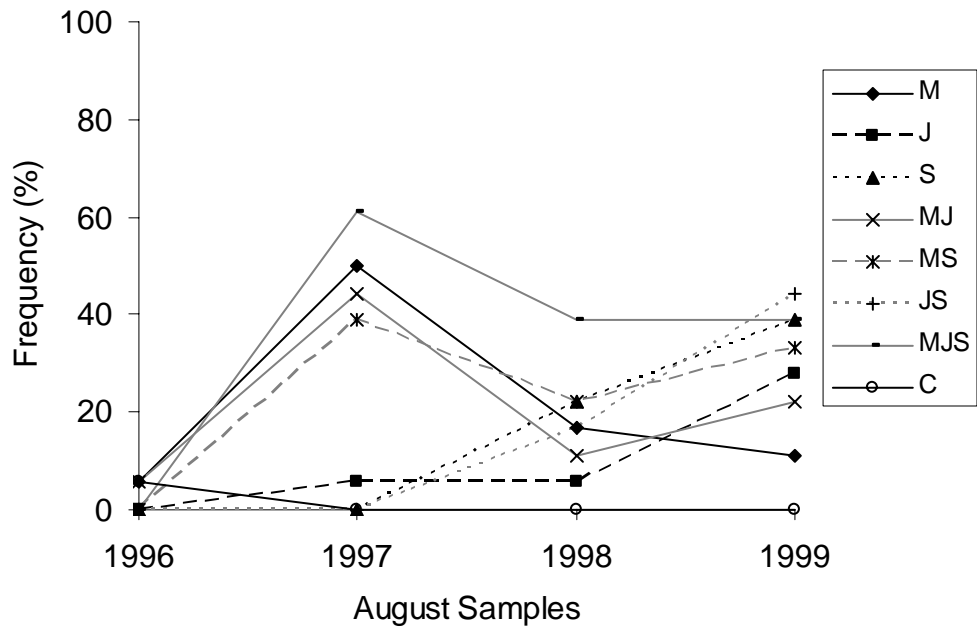
Figure 49. *Oxalis dilenii* August frequencies per mowing treatment on Veterinary Medicine Ranch.
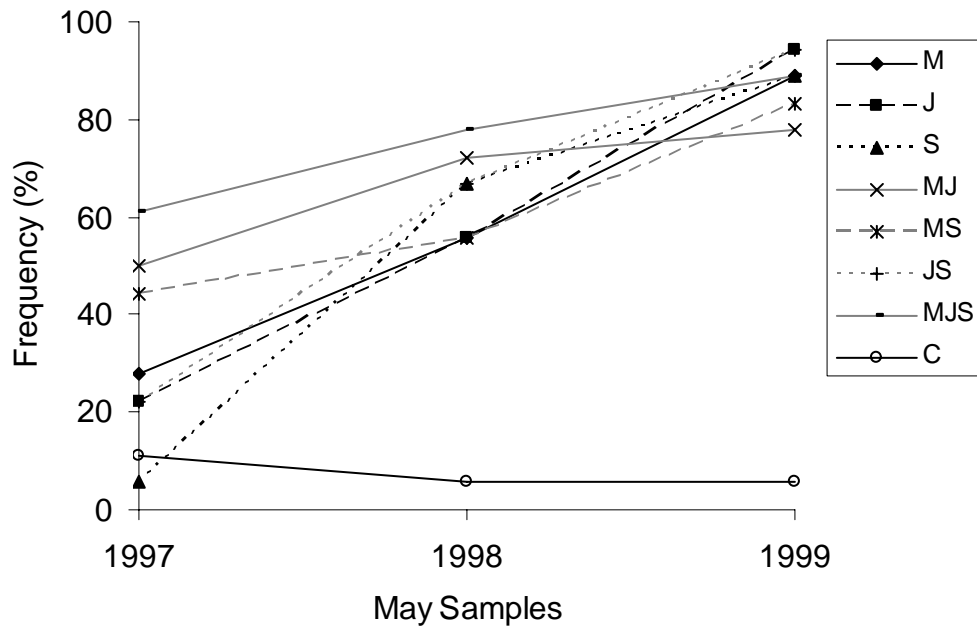
Figure 50. *Oxalis dillenii* May frequencies per mowing treatment on Veterinary Medicine Ranch.
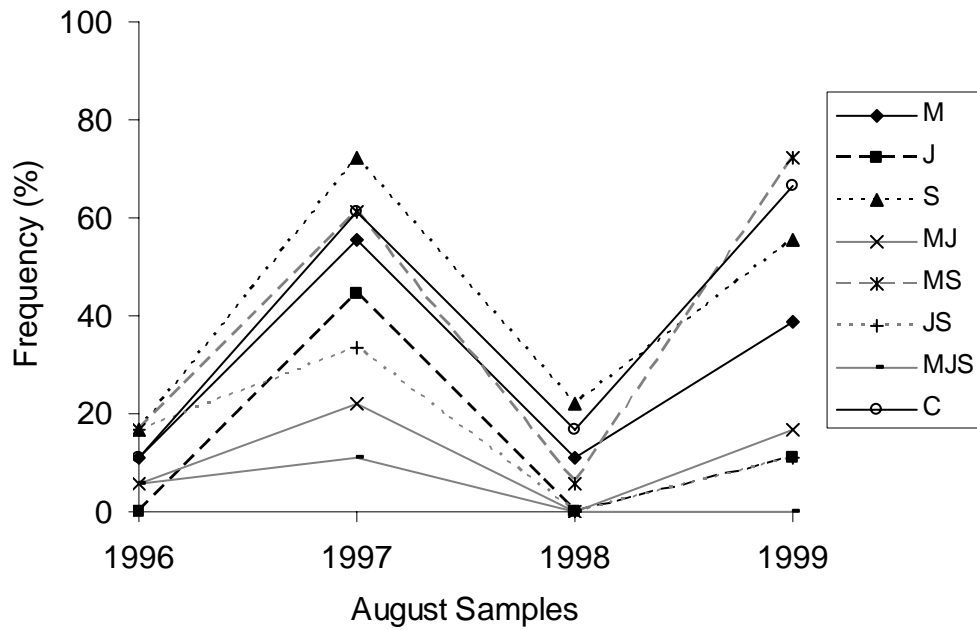
Figure 51. *Psoralidium tenuiflorum* August frequencies per mowing treatment on Veterinary Medicine Ranch.
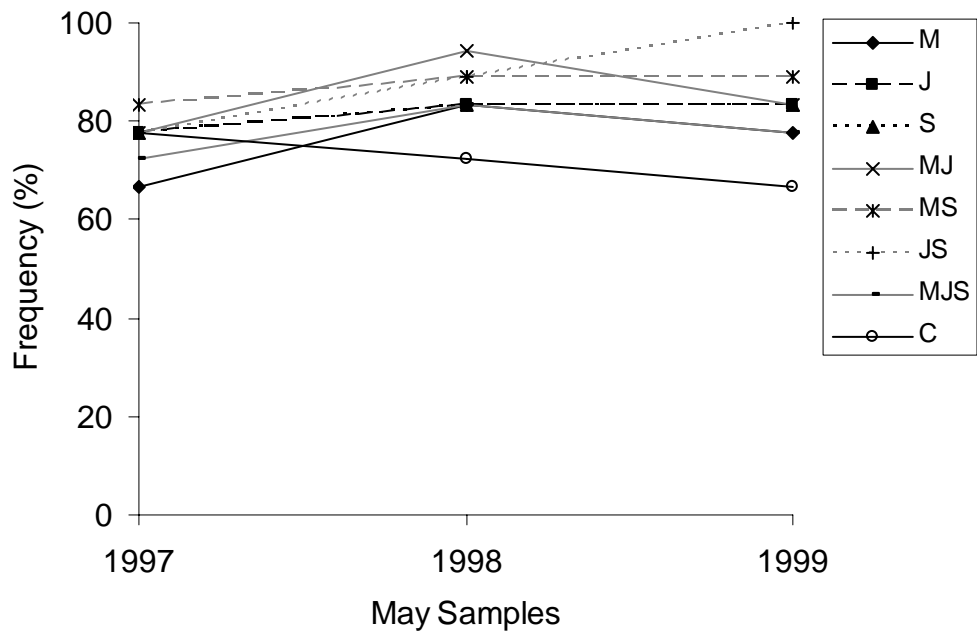
Figure 52. *Psoralidium tenuiflorum* May frequencies per mowing treatment on Veterinary Medicine Ranch.
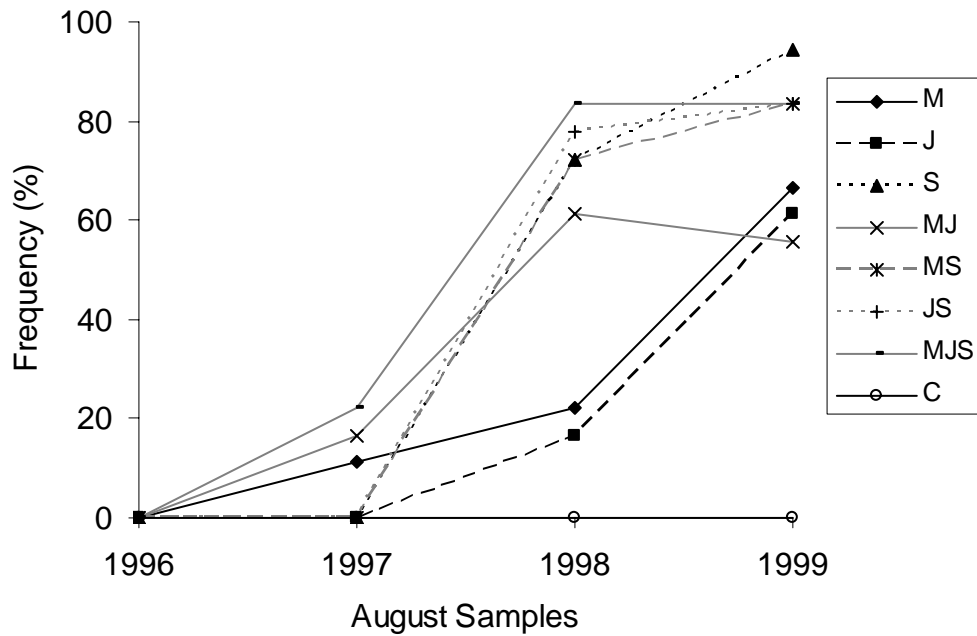
Figure 53. *Amphiachyris dracunculoides* August frequencies per mowing treatment on Veterinary Medicine Ranch.
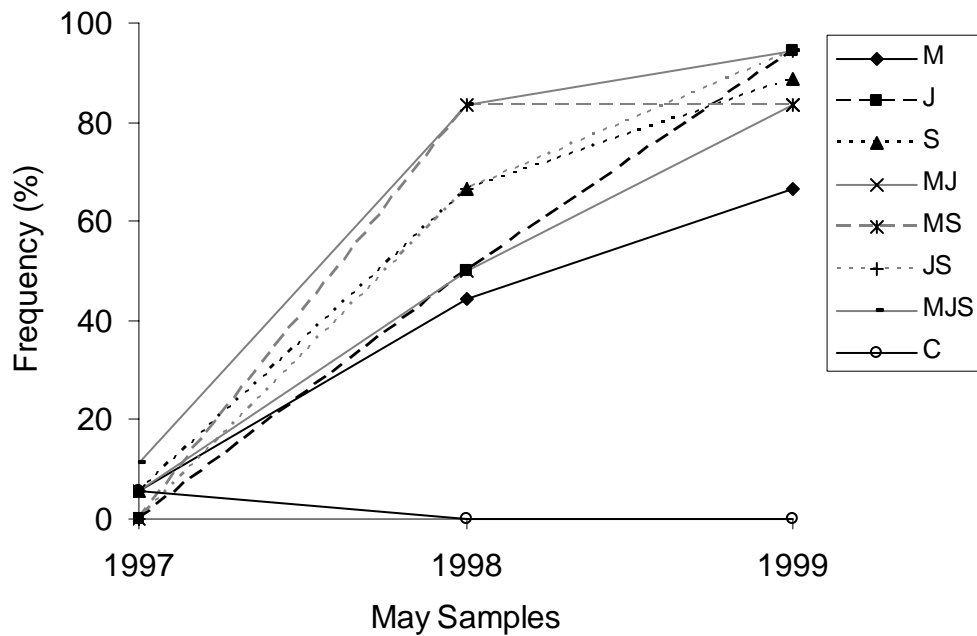
Figure 54. *Amphiachyris dracunculoides* May frequencies per mowing treatment on Veterinary Medicine Ranch.
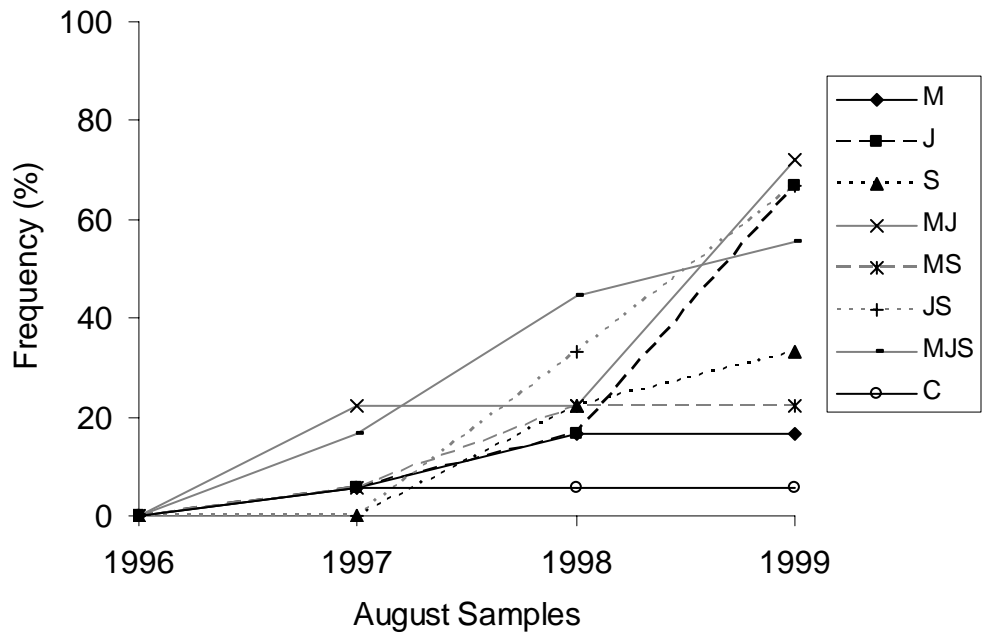
Figure 55. *Conyza canadensis* August frequencies per mowing treatment on Veterinary Medicine Ranch.
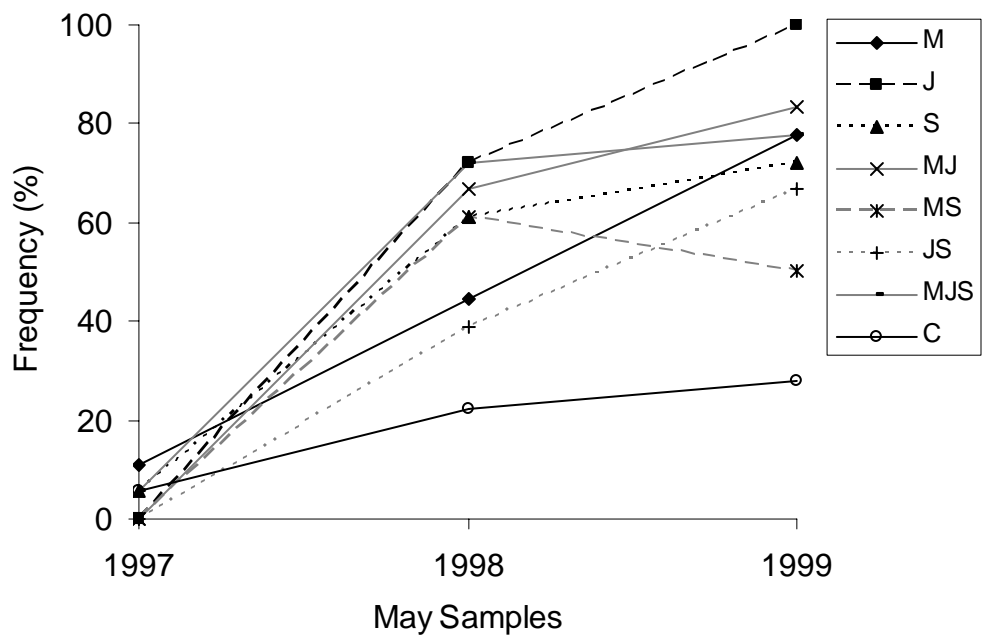
Figure 56. *Conyza canadensis* May frequencies per mowing treatment on Veterinary Medicine Ranch.
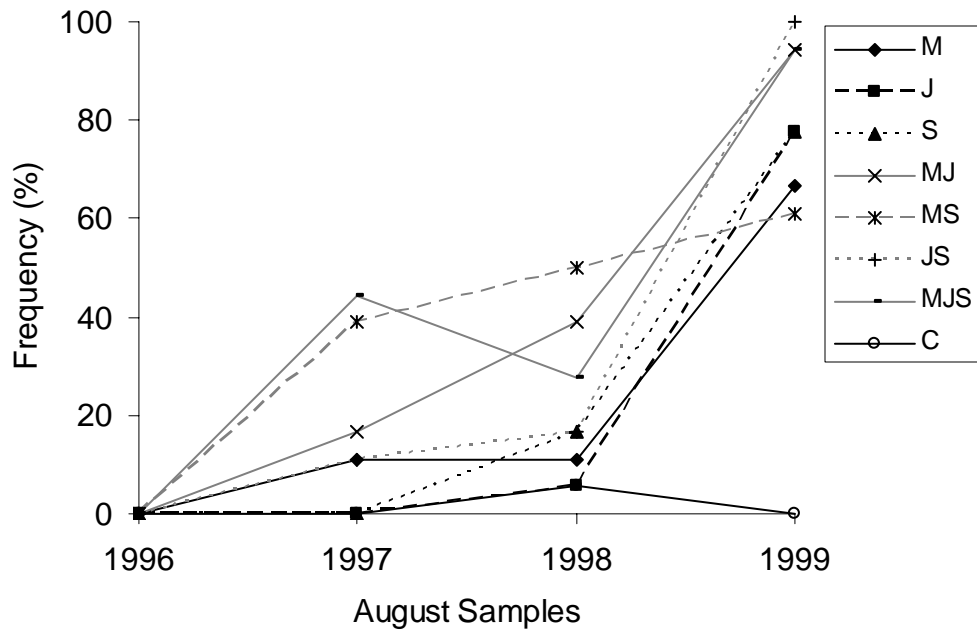
Figure 57. *Erigeron strigosus* August frequencies per mowing treatment on Veterinary Medicine Ranch.
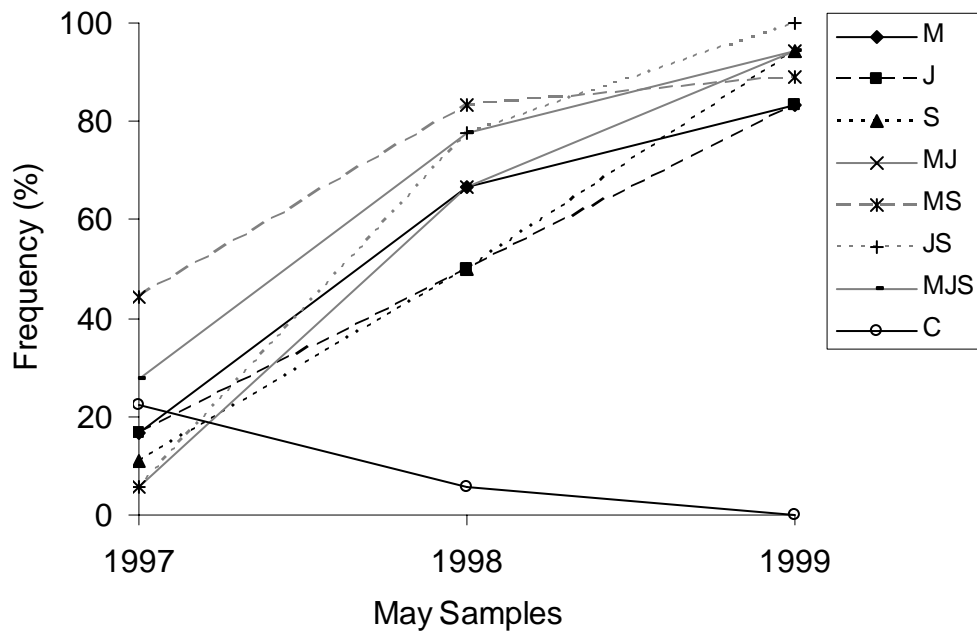
Figure 58. *Erigeron strigosus* May frequencies per mowing treatment on Veterinary Medicine Ranch.
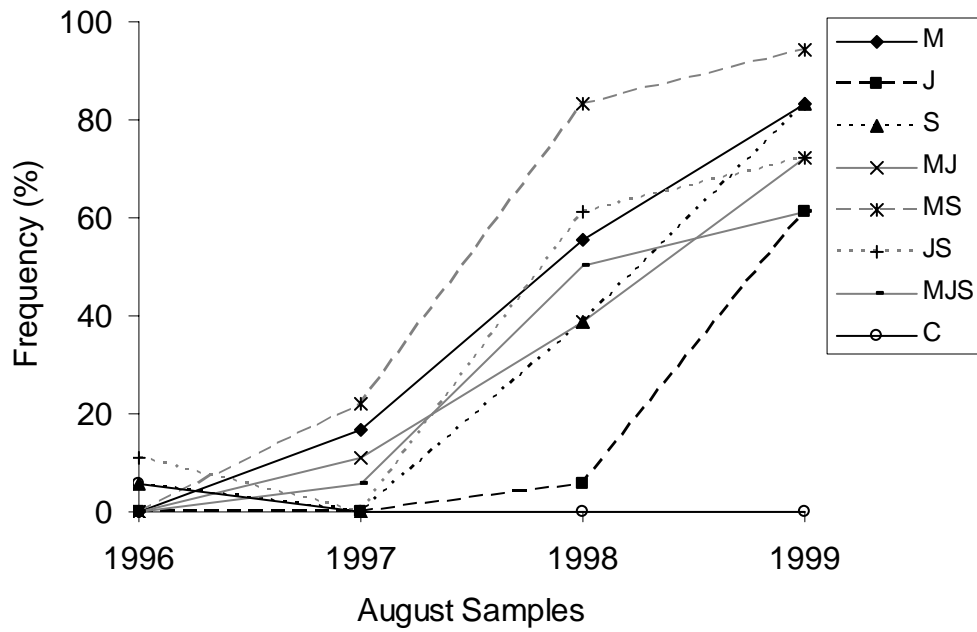
Figure 59. *Linum sulcatum* August frequencies per mowing treatment on Veterinary Medicine Ranch.
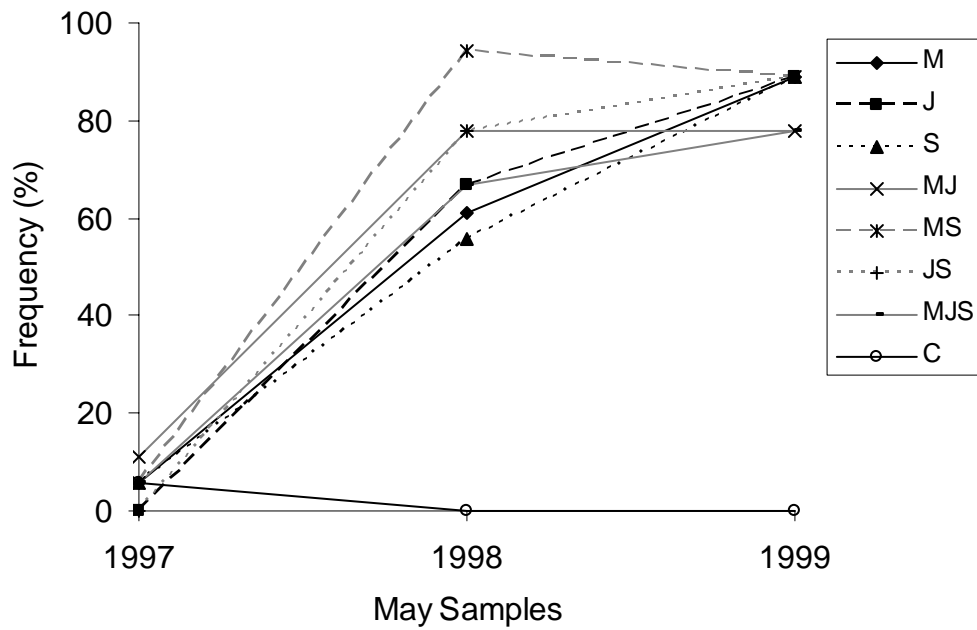
Figure 60. *Linum sulcatum* May frequencies per mowing treatment on Veterinary Medicine Ranch.
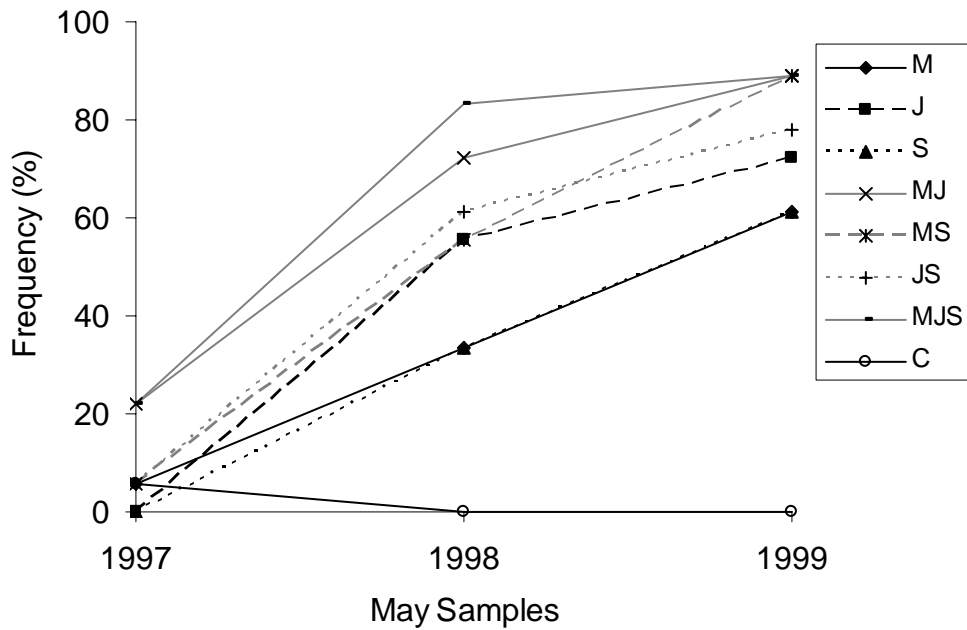
Figure 61. *Plantago virginica* May frequencies per mowing treatment on Veterinary Medicine Ranch.
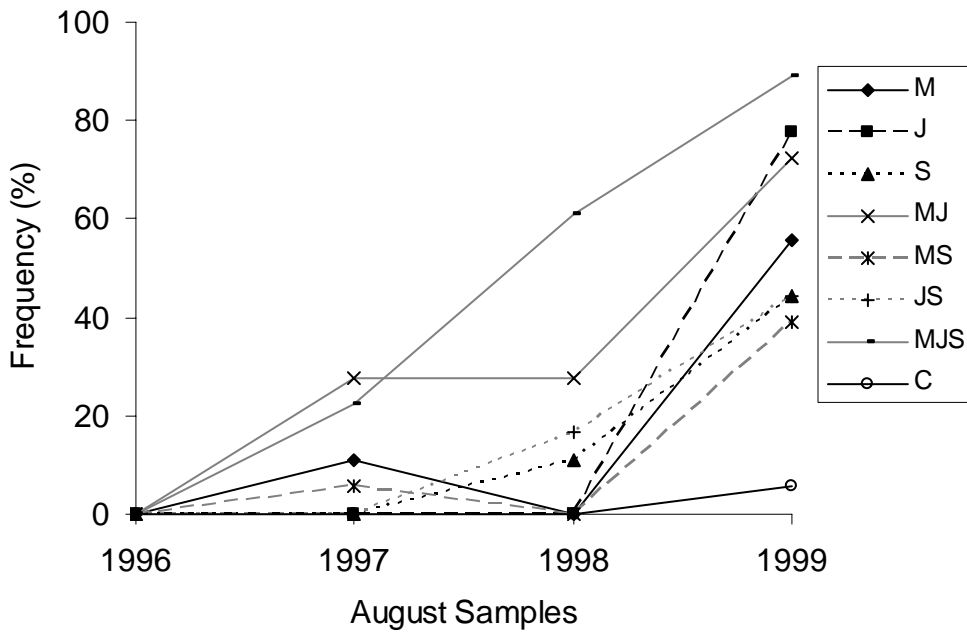
Figure 62. *Polygala verticillata* August frequencies per mowing treatment on Veterinary Medicine Ranch.
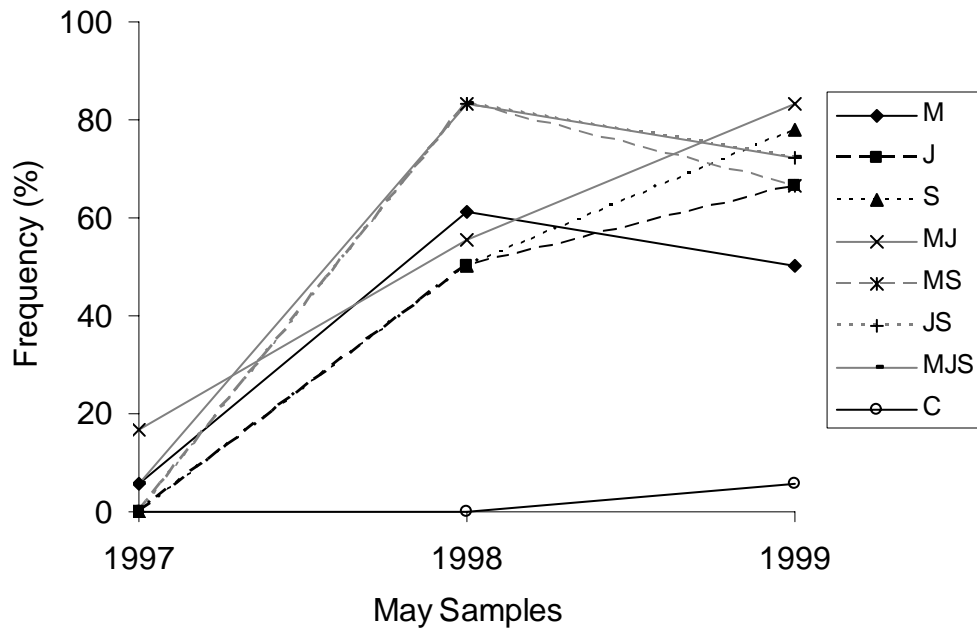
Figure 63. *Polygala verticillata* May frequencies per mowing treatment on Veterinary Medicine Ranch.
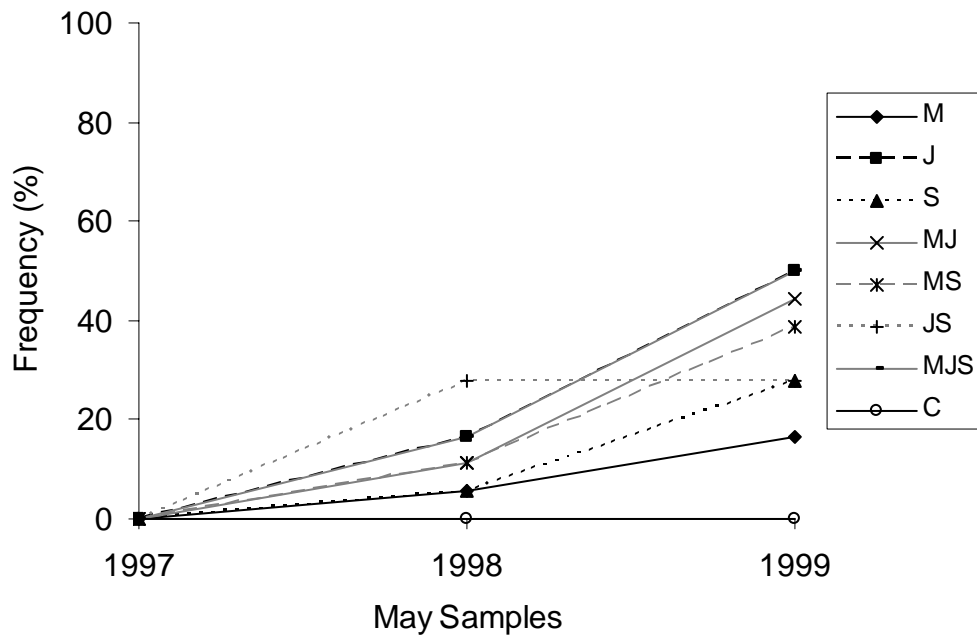
Figure 64. *Viola rafinesquii* May frequencies per mowing treatment on Veterinary Medicine Ranch. J and MJS are superimposed.

Appendix A. List of species, identifying code and life form. Nomenclature mainly follows: Great Plains Flora Association. 1986. *Flora of the Great Plains.* University Press of Kansas. Lawrence, Kansas.

<u>Code</u>	<u>Life Form</u>	<u>Species</u>
ACAN	PF	*Acacia angustissima* (P. Mill) O. Ktze.
ACGR	AF	*Acalypha gracilens* A. Gray
ACMI	PF	*Achillea millefolium* L.
AGEL	PG	*Agrostis elliottiana* Schult.
AGFA	AF	*Agalinis fasciculate* (Ell.) Raf.
AHOV	UF	
AMDR	AF	*Amphiachyris dracunculoides* (DC.) Nutt.
AMPS	PF	*Ambrosia psilostachya* DC.
ANEM	PF	*Anemone* sp. L.
ANGE	PG	*Andropogon gerardii* Vitman
ANNE	PF	*Antennaria neglecta* Greene
ANTE	PG	*Andropogon ternarius* Michx.
ANVI	PG	*Andropogon virginicus* L.
AOSA	UF	
AOSF	UF	
APOC	PF	*Solidago speciosa* Nutt.
ARLU	PF	*Artemisia ludoviciana* Nutt.
ARPU	PG	*Aristida purpurascens* Poir.
ARSE	AF	*Arenaria serpyllifolia* L.
ASER	PF	*Aster ericoides* L.
ASOB	PF	*Aster oblongifolius* Nutt.
ASSP	PF	*Asclepias* L.
ASST	PF	*Asclepias stenophylla* A. Gray
ASTR	PF	*Psoralea esculenta* Pursh.
ASVF	PF	*Asclepias viridiflora* Raf.
ASVI	PF	*Asclepias viridis* Walt.
BAAU	PF	*Baptisia australis* (L.) R. Br.
BABR	PF	*Baptisia bracteata* Muhl. ex Ell.
BG	UF	
BOCU	PG	*Bouteloua curtipendula* (Michx.) Torr.
BOHI	PG	*Bouteloua hirsuta* Lag.
BOIS	PG	*Bothriochloa ischaemum* (L.) Keng
BOLA	PG	*Bothriochloa laguroides* (DC.) Herter
BRJA	AG	*Bromus japonicus* Thunb. ex Murr.
BRTE	AG	*Bromus tectorum* L.
BUAM	PF	*Buchnera Americana* L.
BUDA	PG	*Buchloe dactyloides* (Nutt.) Engelm.
CAAL	PF	*Callirhoe alcaeoides* (Michx.) A. Gray
CABU	PG	*Carex bushii* Mack.
CAFA	AF	*Cassia fasciculata* Michx.
CAMI	PG	*Carex microdonta* Torr. & Hook
CARX	PG	*Carex* sp. L.
CASE	PF	*Calylophus serrulatus* (Nutt.) Raven
CELT	W	*Celtis* sp. L.
CHPI	AF	*Chrysopsis pilosa* Nutt.

Code	Life Form	Species
CHTA	AF	*Chaerophyllum tainturieri* Hook.
CIAL	PF	*Cirsium altissimum* (L.) Spreng.
COCA	AF	*Conyza canadensis* (L.) Cronq.
COTI	AF	*Coreopsis tinctoria* Nutt.
CRMO	AF	*Croton monanthogynus* Michx.
CUSC	AF	*Cuscuta* sp. L.
DACA	PF	*Dalea candida* Michx. ex Willd.
DAPU	PF	*Dalea purpurea* Vent.
DAUP	AF	*Daucus pusillus* Michx.
DEIL	PF	*Desmanthus illinoensis* (Michx.) MacM.
DESE	PF	*Desmodium sessilifolium* (Torr.) T. & G.
DGCA	PG	dark green carex
DIAC	PG	*Dichanthelium acuminatum* (Sw.) Gould & Clark.
DIOL	PG	*Dichanthelium oligosanthes* (Schult.) Gould
DISP	PG	*Dichanthelium* sp. (Hitchc. & Chase) Gould
DIVI	W	*Diospyros virginiana* L.
DRBR	AF	*Draba brachycarpa* Vahl.
DRRE	AF	*Draba reptans* (Lam.) Fern.
ECAN	PF	*Echinacea* angustifolia DC.
ELCA	PG	*Elymus canadensis* L.
ELMO	PG	*Eleocharis montevidensis* Kunth.
ERSP	PG	*Eragrostis spectabilis* (Pursh) Steud.
ERST	AF	*Erigeron strigosus* Muhl. ex Willd.
EUDE	AF	*Euphorbia dentata* Michx.
EUMC	AF	*Euphorbia maculata* L.
EUMR	AF	*Euphorbia marginata* Pursh
EUSP	UF	*Euphorbia* sp. L.
FEOC	AG	*Festuca octoflora* Walt.
FFCA	PG	
FIMB	PG	*Fimbristylis puberula* (Michx.) Vahl.
FZBO	UF	
GAAE	PF	*Gaillardia aestivalis* (Walt) Rock
GASU	PF	*Gaillardia suavis* (Gray & Engelm.) Britt & Rusby.
GECA	AF	*Geranium carolinianum* L.
GHMI	UF	
GLDR	AF	glabrous *Draba*?
GLPA	AF	*Ammoselinum popei* T. & G.
GOLO	UF	
GPLM	UG	
GYGC	UF	
HECR	AF	*Hedyotis crassifolia* Raf.
HEHI	AF	*Hedeoma hispidum* Pursh.
HEMA	PF	*Helianthus maximilanii* Schrad.
HENI	PF	*Hedyotis nigricans* (Lam.) Fosb.
HETE	AF	*Heliotropium tenellum* (Nutt.) Torr.
HIFR	UF	
HILO	PF	*Hieracium longipilum* Torr.
HLLF	UF	
JUNC	PG	*Juncus* L.

Code	Life Form	Species
JUTE	PG	*Juncus tenuis* Willd.
JUVI	W	*Juniperus virginiana* L.
KUEU	PF	*Kuhnia eupatorioides* L.
LACT	AF	*Lactuca scariola* L.
LECO	PG	*Leptoloma cognatum* (Schult.) Chase.
LECU	PF	*Lespedeza cuneata* (Dumont) G. Don
LEDE	AF	*Lepidium densiflorum* Schrad.
LEVI	PF	*Lespedeza virginica* (L.) Britt.
LIAR	AF	*Lithospermum arvensis* L.
LIPU	PF	*Liatris punctata* Hook.
LISU	AF	*Linum sulcatum* Ridd.
LOHL	UF	
LOL	UF	
LPPL	UF	
LSCA	PG	long sheath *Carex*
LVIO	PF	*Lespedeza violacea* (L.) Pers.
MACY	PG	*Manisuris cylindrical* (Michx.) O. Ktze.
MELU	AF	*Medicago lupulina* L.
MEOF	AF	*Melilotus officinalis* (L.) Pall.
MIQU	PF	*Mimosa quadrivalvis*
MOFI	PF	*Monarda fistulosa* L.
MORU	W	*Morus rubra* L.
NELU	PF	*Nelumbo lutea* (Willd.) Pers.
NERG	PG	*Eragrostis intermedia* Hitchc.
NGCA	PG	
NLAS	PF	
NLCA	PG	narrow leaved *Carex*
NLLA	UF	
NLRS	UF	
NOBI	PG	*Nothoscordum bivalve* (L.) Britt.
NOHO	UF	
OBOF	UF	
OEHL	UF	ovate hairy euphorb
OHEU	UF	
ONOF	UF	
OOAH	UF	opposite ovate appressed hairy forb
OOGF	UF	
OOLF	UF	
OPHI	PF	*Ophioglossum* sp. L.
OPLF	UF	
ORCH	PF	Orchid - *Spiranthes*?
OTHF	UF	
OTRU	UF	
OXDI	PF	*Oxalis dillenii* Jacq.
OXVI	PF	*Oxalis violacea* L.
PAVI	PG	*Panicum virgatum* L.
PHAL	AG	*Phalaris caroliniana* Walt
PHPU	PF	*Physalis pumila* Nutt.
PLPU	AF	*Plantago pussilla* Nutt.

Code	Life Form	Species
PLRH	AF	*Plantago rhodosperma* Dcne.
PLVI	AF	*Plantago virginica* L.
POIN	AF	*Polygala incarnata* L.
POVE	AF	*Polygala verticillata* L.
PSEC	PF	*Psoralea esculenta* Pursh.
PSTE	PF	*Psoralidium tenuiflorum* (Pursh.) Rydb.
PYSC	PF	*Pyrrhopappus grandiflorus* (Nutt.) Nutt.
RACO	PF	*Ratibida columnifera* (Nutt.) Woot. & Standl.
RHGL	W	*Rhus glabra* L.
RSTA	UF	
RTSF	UF	
RUBR	W	*Rubus* sp. Rydb.
RUHI	PF	*Rudbeckia hirta* L.
RUHU	PF	*Ruellia humilis* Nutt.
SAAZ	PF	*Salvia azurea* Lam.
SACA	AF	*Sabatia campestris* Nutt.
SCLE	PG	*Scleria ciliata* Michx.
SCSC	PG	*Schizachyrium scoparium* (Michx.) Nash
SEGE	PG	*Setaria geniculata* (Lam.) Beauv.
SEPL	PF	*Senecio plattensis* Nutt.
SIAN	AF	*Silene antirrhina* L.
SICA	PG	*Sisyrinchium campestre* Bickn.
SLGA	AF	*Galium virgatum* Nutt.
SNCA	PG	
SODI	AF	*Solanum dimidiatum* Raf.
SOMI	PF	*Solidago missouriensis* Nutt.
SONE	PF	*Solidago nemoralis* Ait.
SONU	PG	*Sorghastrum nutans* (L.) Nash
SORI	PF	*Solidago rigida* L.
SOSP	PF	*Solidago speciosa* Nutt.
SPAS	PG	*Sporobolus asper* (Michx.) Kunth
SPIN	AF	*Spermolepis inermis* (Nutt.) Math. & Konst.
SPOB	PG	*Sphenopholis obtusata* (Michx.) Scribn.
STBI	PF	*Stylosanthes biflora* (L.) B.S.P.
STLE	AF	*Strophostyles leiosperma* (T. & G.) Piper
STVI	PF	*Stenosiphon virgatus* (Nutt.) Heynh.
SYOR	W	*Symphoricarpos orbiculatus* Moench
TAG	AG	*Agrostis elliottiana* Schult.
TAOF	PF	*Taraxacum officinale* Weber
TECA	PF	*Teucrium canadense* L.
TLBC	PF	*Oenothera speciosa* Nutt.
TLGE	UF	
TOOF	UF	
TOOL	UF	
TRAD	PG	*Tradescantia occidentalis* (Britt.) Smyth.
TRBE	AF	*Tragia betonicifolia* Nutt.
TRBI	AF	*Triodanis biflora* (R. & P.) Greene
TRDU	AF	*Tragopogon dubius* Scop.

Code	Life Form	Species
TRFL	PG	*Tridens flavus* (L.) Hitchc.
TSC	AF	*Froelichia* sp. Moench
ULMU	W	*Ulmus* sp. L.
UNID	UF	
UNKA	UF	
UNKG	UG	
VARA	AF	*Valerianella radiata* (L.) Dufr.
VEAR	AF	*Veronica arvensis* L.
VEBA	PF	*Vernonia baldwinii* Torr.
VIRA	AF	*Viola rafinesquii* Greene
VISA	AF	*Vicia sativa* L.
YUGL	PF	*Yucca glauca* Nutt.

Life Form abbreviations:

AF – annual forb
AG – annual graminoid
PF – perennial forb
PG – perennial graminoid
UF – unidentified forb
UG – unidentified graminoid
W – woody species

Appendix B. Selected Veterinary Medicine Ranch August and May Species Frequencies.

Andropogon gerardii

Aug	1996	1997	1998	1999	May	1997	1998	1999
M	27.8	22.2	22.2	22.2	M	33.3	22.2	22.2
J	38.9	44.4	44.4	44.4	J	44.4	44.4	44.4
S	11.1	16.7	16.7	22.2	S	16.7	16.7	22.2
MJ	16.7	11.1	11.1	11.1	MJ	11.1	11.1	11.1
MS	22.2	22.2	22.2	22.2	MS	22.2	22.2	27.8
JS	16.7	27.8	16.7	16.7	JS	27.8	16.7	16.7
MJS	27.8	22.2	22.2	22.2	MJS	33.3	22.2	22.2
C	38.9	44.4	38.9	33.3	C	44.4	50.0	38.9

Artemisia ludoviciana

Aug	1996	1997	1998	1999	May	1997	1998	1999
M	16.7	22.2	22.2	22.2	M	22.2	22.2	22.2
J	11.1	16.7	5.6	11.1	J	16.7	11.1	5.6
S	11.1	11.1	16.7	16.7	S	11.1	16.7	16.7
MJ	16.7	22.2	22.2	22.2	MJ	22.2	22.2	27.8
MS	11.1	11.1	16.7	22.2	MS	11.1	11.1	16.7
JS	22.2	27.8	22.2	22.2	JS	27.8	22.2	22.2
MJS	38.9	44.4	44.4	44.4	MJS	38.9	44.4	27.8
C	11.1	11.1	22.2	27.8	C	11.1	27.8	27.8

Aster oblongifolius

Aug	1996	1997	1998	1999	May	1997	1998	1999
M	55.6	61.1	61.1	61.1	M	66.7	61.1	61.1
J	33.3	38.9	27.8	27.8	J	38.9	38.9	27.8
S	50.0	50.0	50.0	55.6	S	50.0	50.0	50.0
MJ	44.4	50.0	55.6	55.6	MJ	50.0	50.0	55.6
MS	50.0	55.6	55.6	55.6	MS	55.6	55.6	50.0
JS	33.3	33.3	33.3	27.8	JS	33.3	38.9	27.8
MJS	44.4	50.0	55.6	50.0	MJS	50.0	55.6	61.1
C	27.8	27.8	33.3	33.3	C	38.9	33.3	33.3

Dichanthelium oligosanthes

Aug	1996	1997	1998	1999
M	55.6	77.8	66.7	77.8
J	72.2	66.7	44.4	72.2
S	72.2	72.2	72.2	83.3
MJ	72.2	88.9	77.8	88.9
MS	66.7	77.8	66.7	77.8
JS	61.1	72.2	61.1	83.3
MJS	72.2	83.3	88.9	77.8
C	83.3	83.3	66.7	66.7

May	1997	1998	1999
M	83.3	83.3	83.3
J	72.2	66.7	83.3
S	66.7	77.8	77.8
MJ	88.9	88.9	88.9
MS	66.7	83.3	83.3
JS	55.6	72.2	72.2
MJS	88.9	88.9	88.9
C	77.8	61.1	66.7

Schizachyrium scoparium

Aug	1996	1997	1998	1999
M	88.9	100.0	100.0	100.0
J	94.4	100.0	100.0	100.0
S	88.9	94.4	94.4	88.9
MJ	94.4	100.0	94.4	94.4
MS	88.9	94.4	94.4	94.4
JS	94.4	94.4	94.4	100.0
MJS	100.0	100.0	100.0	100.0
C	94.4	94.4	94.4	94.4

May	1997	1998	1999
M	94.4	100.0	100.0
J	100.0	100.0	100.0
S	94.4	88.9	88.9
MJ	94.4	94.4	94.4
MS	94.4	94.4	94.4
JS	94.4	94.4	94.4
MJS	100.0	100.0	100.0
C	94.4	94.4	94.4

Sorghastrum nutans

Aug	1996	1997	1998	1999
M	83.3	94.4	88.9	88.9
J	94.4	100.0	100.0	100.0
S	77.8	88.9	88.9	88.9
MJ	77.8	77.8	77.8	77.8
MS	77.8	94.4	88.9	88.9
JS	72.2	83.3	77.8	88.9
MJS	83.3	83.3	88.9	88.9
C	88.9	88.9	83.3	83.3

Aug	1997	1998	1999
M	88.9	94.4	94.4
J	88.9	94.4	100.0
S	72.2	94.4	88.9
MJ	72.2	83.3	83.3
MS	94.4	94.4	94.4
JS	66.7	77.8	83.3
MJS	88.9	100.0	94.4
C	83.3	88.9	77.8

Appendix C. Mean August and May Percent Covers for Selected Species on Veterinary Medicine Ranch.

Ambrosia psilostachya

Aug	1996	1997	1998	1999	May	1997	1998	1999
M	1.31	0.61	0.76	1.27	M	0.55	0.55	0.87
J	0.92	0.55	0.22	0.51	J	0.55	0.46	0.48
S	0.92	0.55	0.49	0.55	S	0.55	0.44	0.46
MJ	1.10	0.55	0.43	0.46	MJ	0.55	0.71	0.51
MS	1.00	0.85	0.44	0.55	MS	0.55	0.51	0.40
JS	1.19	0.55	0.46	0.51	JS	0.55	0.55	0.49
MJS	1.00	0.55	0.41	0.38	MJS	0.55	0.50	0.47
C	0.93	0.55	0.66	3.31	C	0.55	0.38	0.49

Artemisia ludoviciana

Aug	1996	1997	1998	1999	May	1997	1998	1999
M	1.18	1.03	1.26	1.03	M	1.53	1.26	1.76
J	1.03	0.55	0.55	0.55	J	0.55	0.55	0.55
S	1.03	2.50	1.18	1.18	S	0.55	0.55	0.87
MJ	1.53	0.79	0.43	0.43	MJ	0.79	0.55	0.55
MS	1.03	2.03	0.70	1.16	MS	1.03	1.03	0.70
JS	0.79	0.74	0.55	0.55	JS	0.93	1.03	0.55
MJS	1.66	0.55	0.55	0.43	MJS	1.11	0.67	0.55
C	0.30	0.55	1.29	1.33	C	0.55	0.74	2.13

Aster ericoides

Aug	1996	1997	1998	1999	May	1997	1998	1999
M	0.51	0.55	0.55	0.55	M	0.55	0.55	0.55
J	0.63	0.55	0.33	0.55	J	0.55	0.55	0.55
S	0.51	0.88	0.51	1.00	S	0.55	0.55	0.68
MJ	0.55	0.58	0.51	0.55	MJ	0.55	0.48	0.62
MS	0.55	0.71	0.55	0.69	MS	0.55	0.55	0.63
JS	0.80	0.50	0.47	0.51	JS	0.50	0.47	0.63
MJS	0.62	0.61	0.48	0.55	MJS	0.55	0.55	0.55
C	0.55	0.62	0.71	0.92	C	0.55	0.55	0.55

Aster oblongifolius

Aug	1996	1997	1998	1999
M	0.96	2.10	0.99	2.43
J	0.29	0.21	0.13	0.15
S	0.71	1.15	0.60	1.01
MJ	1.23	1.21	0.33	0.46
MS	0.41	0.88	0.44	0.79
JS	0.16	0.18	0.18	0.13
MJS	0.90	0.54	0.28	0.43
C	0.26	0.42	0.24	0.40

May	1997	1998	1999
M	1.13	0.77	1.10
J	0.32	0.21	0.21
S	0.38	0.43	0.65
MJ	1.76	0.71	0.85
MS	0.36	0.52	0.60
JS	0.24	0.24	0.21
MJS	0.43	0.63	0.44
C	0.27	0.24	0.24

Bouteloua curtipendula

Aug	1996	1997	1998	1999
M	0.70	1.53	0.87	0.74
J	0.63	0.94	0.73	0.68
S	0.69	0.70	1.10	0.91
MJ	0.71	1.65	0.79	0.74
MS	0.64	0.85	0.97	0.73
JS	0.71	1.27	0.73	1.35
MJS	0.66	1.14	0.96	0.69
C	0.63	0.78	0.63	0.55

May	1997	1998	1999
M	0.68	0.69	0.68
J	0.55	0.55	0.61
S	0.55	0.55	0.79
MJ	0.55	0.81	0.68
MS	0.55	0.61	0.73
JS	0.55	0.67	0.73
MJS	0.55	0.67	0.75
C	0.55	0.55	0.55

Dichanthelium oligosanthes

Aug	1996	1997	1998	1999
M	0.65	0.62	0.55	0.55
J	0.62	0.55	0.55	0.51
S	0.58	0.55	0.55	0.55
MJ	0.55	0.55	0.55	0.55
MS	0.55	0.69	0.55	0.55
JS	0.64	0.51	0.55	0.55
MJS	0.55	0.61	0.55	0.55
C	0.52	0.55	0.63	0.63

May	1997	1998	1999
M	0.58	0.55	0.55
J	0.55	0.55	0.48
S	0.55	0.51	0.44
MJ	0.55	0.55	0.55
MS	0.71	0.55	0.52
JS	0.55	0.47	0.62
MJS	0.55	0.61	0.49
C	0.55	0.55	0.55

Sorghastrum nutans

Aug	1996	1997	1998	1999		May	1997	1998	1999
M	1.13	0.61	0.73	1.16		M	0.55	0.61	0.84
J	1.29	1.48	1.53	2.07		J	0.55	1.06	2.58
S	1.33	1.16	1.78	3.34		S	0.78	1.27	1.22
MJ	0.55	0.62	0.97	1.45		MJ	0.55	0.87	1.34
MS	1.10	0.83	0.91	2.39		MS	0.66	1.01	1.99
JS	0.92	1.00	1.53	2.39		JS	0.55	2.09	2.26
MJS	1.06	0.74	1.72	2.83		MJS	0.98	1.64	1.71
C	0.88	1.16	1.40	1.34		C	0.61	0.67	1.04

VITA

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