PRESCRIBED FIRE AND SPECIES COMPOSITION IN A RELICTUAL TALLGRASS PRAIRIE

Honors Thesis

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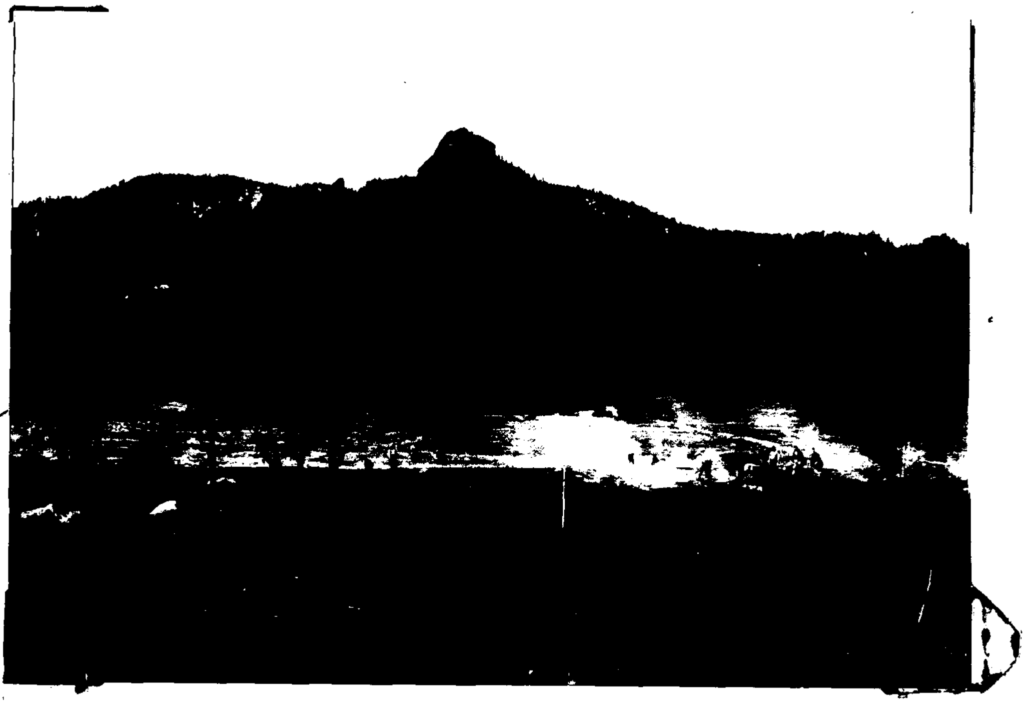

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ABSTRACT

Fire is a large-scale natural disturbance that maintains the health and species composition of grassland ecosystems. Through fire suppression, agriculture, and development, humans have upset the natural balance between grassland species and their environment. Research indicates that prescribed burning may be an effective tool for helping to restore this balance. Because prescribed fire often enhances the growth of the native grasses in undisturbed tallgrass prairie, it may be beneficial to the restoration of native species. However, the benefits of prescribed fire in a heavy-use recreational area have not been previously studied.

I evaluated changes in species composition following two prescribed burns. The study site was Chautauqua Meadow, a relictual tallgrass prairie which is subject to fire suppression and extremely heavy recreational use (approximately 200,000 visitors per year). A system of nested quadrats was utilized to allow evaluation of the changes in frequencies of native and exotic grasses and other herbaceous plants. I used the G-statistic to evaluate the changes in frequencies of each individual species, changes in native vs. exotic species, and changes in graminoids with the C3 vs. C4 photosynthetic pathway. Contrary to my hypothesis, the relative frequency of native graminoids did not increase after the prescribed burns. However, native non-grass herbaceous species (forbs) did increase their relative frequency in both plots. Only one of the study plots

had a significant shift toward more native species overall. Variables such as climatic conditions before and after the fires, percent of total burned area, and recreational use may account for these deviations from the expected patterns of change.

INTRODUCTION

The vast grasslands that once covered much of North America exist today only as patchy relicts dominated by agriculture. These agricultural uses have not only taken up large portions of land, but they also have replaced the natural patterns of disturbance to which grassland species are adapted with destructive disturbances associated with farming and ranching. Grasslands evolved with a disturbance regime that included drought, fire, grazing, and soil disturbances such as bison wallows and prairie dog towns (Collins & Barber, 1985), in addition to other small-scale animal disturbances (Gibson, 1989).

Prior to the arrival of Europeans in North America, fires were common in grassland ecosystems, generally occurring every 1-5 years (Collins & Barber, 1985). Fire was an important evolutionary force in maintaining the health and integrity of these ecosystems (Vogl, 1974). Through fire suppression, agriculture and development, humans have seriously altered the complex disturbance regime that maintained the grasslands of North America. These factors, in addition to the replacement of native grazers by domestic livestock, contributed to the introduction and spread of exotic species that threaten the health of nearly all of our Great Plains ecosystems (Bock & Bock, 1995).

The tallgrass prairie is dominated by bunch grasses, which possess several adaptations to fire. These deep-rooted species only produce lateral growth as tillers, or upright stems, that are formed near the root crown (Bock & Bock, 1995). When a prairie is burned, the fire burns back the vegetation to the soil surface. However, the ground-level shoot meristems and the underground roots remain intact (Bock et al., 1986). As a result, the bunch grasses have the ability to recover quickly from a fire (Vogl, 1974), often with enhanced growth (Anderson, et al., 1969; Bidwell et al., 1990; Hulbert, 1969; Peet et al., 1975; Svejcar & Browning, 1988; Towne & Owensby, 1984).

Tallgrass prairie is usually defined by the presence of the "Big Four" tallgrasses. These include Big Bluestem *(Andropogon gerardii)*, Little Bluestem *(Schizachrium scoparium)*, Indian Grass *(Sorghastrum nutans)*, and Switchgrass *(Panicum virgatum)* (J. Bock, personal communication). All of the "Big Four" are matrix-forming species, or bunch grasses, with the C4 photosynthetic pathway (Waller & Lewis, 1979).

The tallgrass prairie is a mosaic of bunch grasses, many of which exhibit the C4 photosynthetic pathway, and other grasses which utilize C3 photosynthesis (Waller & Lewis, 1979). Ecological theory states that there is a limit to the similarity of co-existing species (MacArthur, 1965), so C3 and C4 species must have some ecological traits that distinguish them from one another. To test this idea, Williams (1974) examined rates of photosynthesis at different temperatures in C3 and C4 species. He found that the optimum temperature for photosynthesis in *Agropyron smithii*, a C3 grass, was much cooler than that for the

C4 grass *Bouteloua curtipendula*. Williams suggests that photosynthetic adaptations to temperature allow for the co-existence of these species by reducing the interspecific competition between them. This trend is also evidenced in the phenology of these species: C3 grasses tend to initiate growth earlier in the season when temperatures are still cool, whereas C4 species do not initiate growth until the warmer portion of the growing season. Due to this observation, ecologists refer to C3 species as "cool-season" and C4 species as "warm-season."

Today, ecologists and managers frequently use prescribed burning as a tool to restore and improve grasslands (Wright, 1974). The phenology of C3 and C4 species is very important when developing the burn prescription. The responses of tallgrass species vary by species and timing of the fire (Glenn-Lewin et al., 1990), so it is important that the burn be conducted during the appropriate season to get the desired effect. For example, Towne and Owensby (1984) examined the responses of ungrazed tallgrass prairie plots to prescribed burning conducted during different seasons. They found that late-spring burning, coinciding with the emergence of the warm-season grasses, had a favorable effect and resulted in increased grass production. In contrast, prescribed burns conducted in winter, early-spring, and mid-spring reduced herbage production compared to unburned sites.

In a similar study, Seuter (1987) evaluated the productivity of C3 and C4 grasses after prescribed burning based on the season of the burn. In the lowland prairie community, spring burning shifted the production ratio towards warm-season C4 herbage relative to unburned, mid-summer burned, and fall-burned treatments. Anderson et al. (1969) also found that spring burning reduced the yield of cool-season species while enhancing the growth of warm-season species. However, some weedy species with a similar phenology were also favored. In order to write an effective burn prescription, ecologists must identify the desirable species and conduct the burn during the most beneficial season.

Disturbances such as fire are important forces in ecosystems because they maintain the composition, spatial heterogeneity, and structure of plant communities (Collins, 1987). The effects of individual disturbances may vary based on their frequency, intensity, and magnitude (Collins, 1990). In addition, the season and climatic conditions at the time of the disturbance may influence the ecosystem's response (Sousa, 1984; Vogl, 1974). In the absence of the normal disturbance regime, the natural balance between organisms and their environment is disrupted, and this inevitably causes changes in the ecosystem.

Fire suppression can have many long-term effects on both the composition and structure of prairies and may threaten their very existence (Bragg & Hulbert, 1976). An important cause of these changes is the accumulation of detritus, or dead plant material (Knapp & Seastedt, 1986). Due to the relatively dry climate of grassland ecosystems, the rate of decomposition in tallgrass prairies is quite slow (Vogl, 1974) and this can result in the rapid build-up of a thick litter layer after just a few years of fire suppression (Rice & Parenti, 1978).

The most harmful effect of a thick litter layer is a reduction in the productivity of the warm-season grasses (Knapp & Seastedt, 1986; Ode et al., 1980; Rice & Parenti, 1978). Initially, the shade produced by the litter layer and early growth of the cool-season grasses (Ode et al., 1980) results in cooler soil temperatures and delayed emergence of the warm-season species (Knapp & Seastedt, 1986). After the warm-season grasses begin to emerge, the warmer air temperature under the litter increases the water stress on young shoots, and the reduced light availability negatively affects the development of the leaves (Knapp & Seastedt, 1986). Consequently, when the tillers emerge through the litter layer, they have a reduced rate of photosynthesis, increased water stress due to a lack of convective cooling and reduced root biomass, and, ultimately, reduced productivity over the growing season (Knapp & Seastedt, 1986).

Additionally, the build-up of litter affects species composition by changing the ratio of C3 to C4 species (Ode et al., 1980). The cooler temperatures produced by litter and self-shading favor the cool-season C3 grasses while reducing the competitive ability of the C4 warm-season species (Ode et al., 1980).

Species composition is also directly changed by fire suppression which allows the invasion of woody species into areas with sufficient moisture (Axelrod, 1985; Bragg & Hulbert, 1976; Veblen & Lorenz, 1991; Vogl, 1974; Wright, 1974). Axelrod (1985) noted the importance of fire in the evolution of grasslands as a force keeping nearby wooded areas at bay. In a quantitative study, Bragg and Hulbert (1976) reported a 34% increase in tree and shrub cover in unburned bluestem prairie from 1937 to 1969, whereas the cover of woody species remained at presettlement levels on regularly burned sites. Locally, Veblen and Lorenz (1991) used photographs in a comparative study which examined the effects of fire suppression on woody species. Their study documents the encroachment of *Pinus ponderosa* into nearby grasslands on the mesas and foothills surrounding Boulder. Fire has been suppressed in this area for a century or more.

In addition to its affects on species composition, many studies demonstrate the importance of fire as factor determining productivity in grassland ecosystems. For example, Hulbert (1969) found *A. gerardii* production to be increased following burning in areas with sufficient litter buildup. Likewise, Anderson et al., (1969); Bidwell et al., (1990); and Peet et al., (1975) all found that the productivity of tallgrass prairie species is enhanced after fire. However, burning alone does not guarantee increased productivity; timing of the fire is also important in determining the community's response. Studies have shown that burning in the late-spring is most effective for increasing the productivity of tallgrass species. For example, Svejcar and Browning (1988) found that late-spring burning can nearly double tiller production and triple the aboveground biomass of the dominant tallgrass species *Andropogon gerardii*. Likewise, Towne and Owensby (1984) found that late-spring burning increased total herbage production, and that two of the "Big Four," *Andropogon gerardii* and *Sorghastrum nutans*, were especially favored.

Why is fire beneficial to the tallgrass prairie? What causes the enhanced growth observed in the bunch grasses? Studies have isolated several factors that stimulate the growth of C4 grasses. Hulbert (1988) replicated various effects of burning to isolate the beneficial aspects of fire. He reported that warming of the soil resulted in increased production and flowering of the dominant tallgrasses. Productivity was also enhanced by the removal of standing dead by clipping or burning; conversely, additional shading reduced total productivity. When Hulbert simulated the increased availability of nitrogen following fire, the addition of ammonium nitrate also resulted in increased yield and flowering of the dominant tallgrasses.

In a less comprehensive study, Rice and Parenti (1978) concluded that increased production following fire is due primarily to higher soil temperatures which stimulate the growth of warm-season grasses earlier in the spring. Also, Peet et al. (1975) attribute increased production of *Andropogon gerardii* to more favorable conditions for net photosynthesis, specifically warmer soil temperatures and increased photosynthetically active radiation (PAR) availability earlier in the growing season. These results are consistent with Knapp and Seastedt (1986) who conclude that changes in the productivity of tallgrass prairie are due to the amount of plant litter present.

Understanding the effects of fire and the mechanisms behind them provides ecologists with an invaluable tool for improving and maintaining the tallgrass prairie. The use of prescribed burning has the potential to restore productivity to normal levels through the removal of litter (Knapp & Seastedt, 1986), to help restore grassland species composition by enhancing the competitive ability of the dominant C4 grasses (Ode et al., 1980), and to stop the encroachment of woody species into mesic sites (Wright, 1974). In addition, prescribed burning during the appropriate season can help to curb the growth of C3 species (Anderson, 1969).

At Chautauqua Meadow, a relictual tallgrass prairie (J. Bock, personal communication; Weber, 1995) in Boulder, Colorado, a series of prescribed burns are being conducted as part of a new management plan. The first burn was conducted on April 7, 1995; an adjacent area was burned on April 26, 1996. Both of these were spring burns designed to stimulate the growth of the native C4 tallgrasses.

The prescribed burning at Chautauqua was proposed to aid in the control of exotic grasses because all of the exotic grasses in the study plots were cool-season C3 species (Waller & Lewis, 1979). This pattern may be explained, in part, by the region of origin of these weeds (Table 1).

Table 1: **Exotic Grasses at Chautauqua & Their Origins**

Species	Region of Origin	Notes
Agropyron repens	Eurasia	Perennial, withstands harsh summers & winters
Bromus inermis	Russia & Hungary	Perennial, drought and cold tolerant
Bromus japonicus	Asia	Annual, drought and cold tolerant
Bromus tectorum	Europe	Annual, prolific seeder, high rate of germination, early germination
Dactylis glomerata	Eurasia	Perennial, cold & shade tolerant
Phleum pratense	Eurasia	Perennial, cold & shade tolerant
Poa compressa	Europe	Perennial, adapted to poor soil
Poa pratensis	Europe	Perennial, early spring to late fall growth

Source: Grasses Introduced into the United States, U.S. Department of Agriculture, Forest Service Agriculture Handbook #58, 1954.

Because these species are likely to be found in cooler, moister regions of the world, they have retained the C3 photosynthetic pathway which is favored under these conditions.

The life-history traits and phenology of these exotic species allow them to successfully invade regions of unnaturally disturbed tallgrass prairie (Table 1). At Chautauqua, the C3 species would be more tolerant of the cooler, shadier microhabitat (Ode, et al., 1980) created by the build-up of litter from fire suppression. Because C3 grasses initiate growth early in the growing season, these exotic species could establish themselves in disturbed soil before the native C4's begin growth. The rapid growth and high seed output of many of these exotics also enhance their ability to compete with native species. Additionally, their adaptations to environmental extremes such as drought, shade, harsh summers and winters, and poor soil make them effective competitors in unnaturally disturbed prairies. This suite of characteristics allows these C3 exotics to aggressively invade and persist at Chautauqua.

However, the fact that they are all C3 grasses offers the potential for spring fires to reduce their production while simultaneously stimulating the growth of the native C4 species. The exotic C3's have not evolved in a fire-system, so prescribed burning may give the native species a competitive advantage. Over time, prescribed burning may be an effective tool for controlling non-native species at Chautauqua.

While the benefits of prescribed fire have been clearly demonstrated for tallgrass prairie subject to agricultural use and undisturbed prairie (Anderson et al., 1969; Hulbert, 1969; Towne & Owensby, 1984) the effectiveness of prescribed fire as a management tool in a heavy-use recreational area remains unknown. The objective of this study is to evaluate the changes in species composition after prescribed fires in a recreational area receiving approximately 200,000 visitors a year (Boulder Mountain

Parks preliminary study). Two tallgrass prairie plots were established at Chautauqua Meadow; each was subject to a prescribed burn during one of the years of this study. Evaluating individual species' responses tests the hypothesis that late spring burning will reduce the frequency of C3 graminoids while increasing the frequency of C4 graminoids. Also, the study evaluates the burn's efficacy in reducing the frequency of exotic species relative to the frequency of native species to determine if spring burning is an effective management tool for this area.

MATERIALS & METHODS

Study Site:

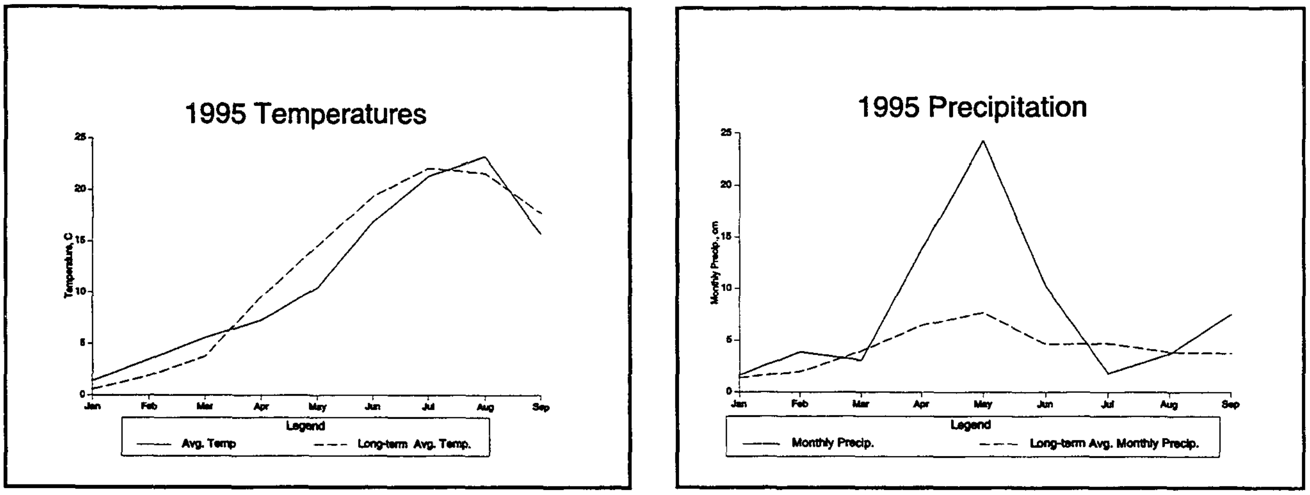
The study was conducted at Chautauqua Meadow, in Boulder, Colorado. The meadow, maintained by Boulder Mountain Parks, is located in the City of Boulder's Open Space. Several factors make Chautauqua a unique study site. This is a relictual tallgrass prairie (J. Bock, personal communication; W. Weber, 1995) seldom found in the foothills near lower montane forest. Fire has been suppressed in this area for a century or more, potentially contributing to the invasion of non-native species. Unlike many grassland study sites, this meadow has not been grazed by domestic cattle. In addition, heavy recreational use has contributed to soil erosion and compaction, as well as the introduction and spread of exotic plant species.

Climatic Conditions:

The first burn was conducted on April 7, 1995. This was an unusually rainy year for Boulder weather; it was the wettest in our history (Weather Enthusiast of Boulder, 1995). It rained for 16 days in April, 23 days in May, and 19 days in June.

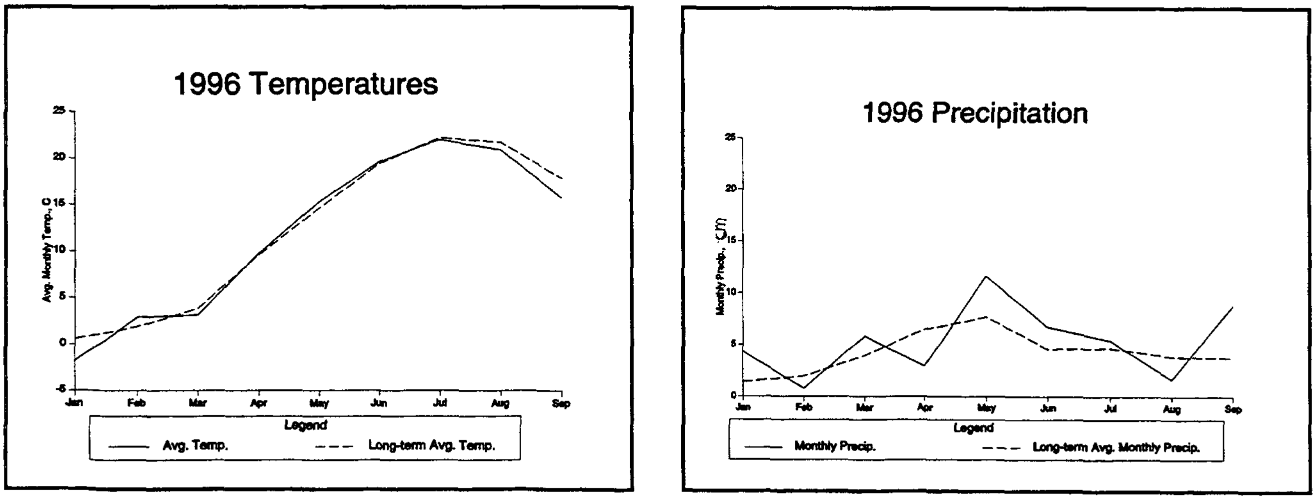
In fact, 1995 had more days with precipitation (127) than ever before in Boulder. Additionally, the overcast skies resulted in temperatures that were unseasonably cool during the spring and early summer (Figure 3).

Figure 3: 1995 Weather Data



In 1996, the weather returned to a "normal" pattern, with little variation between the observed and long-term average values for temperature and precipitation on a month-to-month basis (Figure 4).

Figure 4: 1996 Weather Data

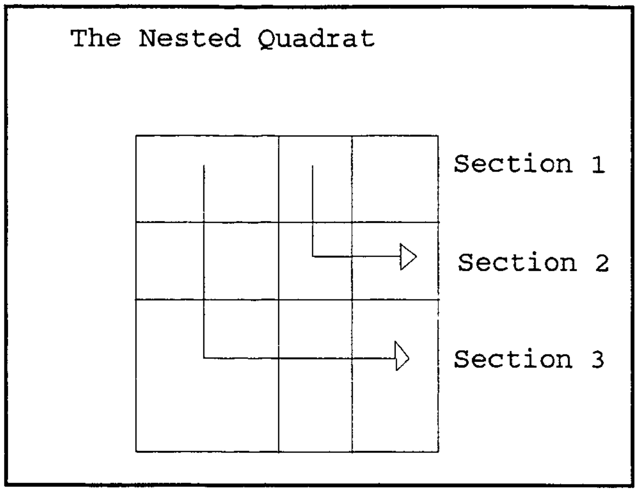


Field Methods:

Two adjacent plots were established in the meadow, one that was burned in the spring of 1995 (Plot B95), and one that was burned in the spring of 1996 (Plot B96). Plot B95 is 1 hectare and plot B96 is 2 hectares. Data were collected in both plots for both the 1995 and 1996 growing seasons. In plot B95, data were collected for two growing seasons following the prescribed burn in 1995. Plot B96 data were collected for one growing season previous to the burn and one growing season after the burn in 1996. Frequency data were collected for each species along a series of transects extending from the center of each plot. These transects totaled 308 meters in plot B95 and 300 meters in plot B96. The same transects were utilized during both seasons of data collection, to document temporal changes in the frequencies of each species.

Frequency data were collected using nested quadrats (Smith et al., 1987) placed every four meters on alternating sides of the transects, totaling 77 quadrats in plot B95 and 75 quadrats in plot B96.

Figure 5:



The quadrats consist of three sections "nested" within a 1m^2 frame. These sections are mutually exclusive, such that species found in section 1 are not counted in the other sections. Next, the frequencies of each species are tallied; species occurring in section 1 are given a frequency of 3, because they are assumed to occur in all of the sections. Likewise, those in section two are only given a frequency of 2, and those in section three are given a frequency of 1. The frequencies from all quadrats are then summed to give a total frequency for each species. This method is advantageous because it provides accurate frequency information on the dominant species, but is also sensitive to the occurrence of rare species.

Statistical Methods:

Frequencies of each species were compared between years for each plot, to determine if there was a significant change from one growing season to the next. The G-test (Sokal & Rohlf, 1981) was run for each species, and values were compared with a Chi-square table (1, .05) = 3.841.

Next, a series of G-tests were performed to determine if the frequency of native species and exotic species found on each plot was independent of the sampling year. Separate G-tests were run for the graminoids, forbs (non-grass, herbaceous), and total species for each plot. Species were also classified as native or exotic based on Weber (1995).

In addition, G-tests were run for each plot to assess if the number of C3 and C4 graminoid individuals was independent of sampling year. Grasses were classified as C3 or C4 based on Waller & Lewis (1979).

RESULTS

PLOT B95: Burned April 7, 1995

Graminoid Responses:

Plot B95 had a richness of 21 graminoid species. From 1995 to 1996, 52% of these species had a significant change in frequency. Seven graminoid species increased significantly, whereas four showed a significant decrease (Table 2).

Table 2: **Plot B95 Individual Graminoid Species' Responses**

	Natives	Exotics
Significant Increase 1995-1996 $p = 0.05$	*Agropyron smithii* *Koeleria macrantha* *Stipa spartea* *Stipa viridula*	*Dactylis glomerata* *Phleum pratense* *Poa compressa*
Significant Decrease 1995-1996 $p = 0.05$	*Bouteloua curtipendula* *Sporobolous airoides* *Sporobolous heterolepsis* *Stipa comata*	*Agropyron repens*

The species with the most significant change in frequency was *Stipa spartea*, increasing from 3 individuals recorded in 1995 to 22 individuals in 1996 ($p < 0.001$). Conversely, the greatest decrease was observed for *Stipa comata*, with 14 individuals in 1995 and 0 in 1996 ($p < 0.005$).

The relative frequency of native to exotic Graminoid species also changed significantly from 1995 to 1996 (Table 3).

Table 3: **G-test for Native vs. Exotic Graminoids, Plot B95**

	Natives Observed	Exotics Observed	Natives Expected	Exotics Expected	G_{calc}
1995	579	310	552	337	6.49
1996	581	397	608	370	p <.025

In this plot, there were fewer native individuals and more exotic individuals than expected in 1996. Expected values were calculated using row and column totals assuming independence of these factors between years. While the conditions in 1995 may have initially reduced the number of exotic species, they increased in frequency relative to the natives in the second growing season after the fire.

Similarly, there was a significant change in the relative frequencies of C3 and C4 graminoids, however, this change was not consistent with my hypothesis (Table 4). There were more C3 and fewer C4 species observed in 1996, and this change was highly significant ($p < 0.001$).

Table 4: **G-test for C3 vs. C4 Graminoids, Plot B95**

	C4 Observed	C3 Observed	C4 Expected	C3 Expected	G_{calc}
1995	263	626	228	661	13.72
1996	216	762	251	727	p< .001

These tests are not entirely independent; however, they do reveal a shift toward more exotic and native C3 graminoid species from

1995 to 1996.

Forb Responses:

Over the course of the study, 37 different forb species were recorded in plot B95. There was a significant change in the frequency of 9 forb species, or 24%, from 1995 to 1996 (Table 5). Only one species increased significantly, whereas eight forb species decreased significantly.

Table 5: **Plot B95 Individual Forb Species' Responses**

	Natives	Exotics
Significant Increase 1995-1996 $p = 0.05$	*Helianthus rigidus*	
Significant Decrease 1995-1996 $p = 0.05$	*Arnica fulgens* *Liatris punctata* *Lomatium orientale* *Nothocalais cuspidata* *Opuntia macrorhiza* *Packera pseudoaurea*	*Alyssum minus* *Taraxacum oficinale* *Tragopogon dubius*

Helianthus rigidus, a native, was the only forb to show a significant increase in frequency. This species increased 238%, from 8 to 27 individuals in 1996 ($p < 0.001$). In contrast, there was a 95% decrease observed for the native *Lomatium orientale*, dropping from 66 individuals observed in 1995 to only 3 in 1996 ($p < 0.001$). The two most abundant exotic forbs in 1995 (Appendix 1) both decreased significantly in 1996: *Tragopogon dubius* and *Alyssum minus*.

Similar to the graminoids, a significant change was observed in the composition of native to exotic forbs for plot B95 (Table 6). However, the composition shifted in the opposite direction, towards more native species relative to exotics in the second season after this plot was burned.

Table 6: **G-test for Native vs. Exotic Forbs, Plot B95**

	Natives Observed	Exotics Observed	Natives Expected	Exotics Expected	G_{calc}
1995	864	208	898	174	18.88
1996	740	102	705	136	**p< .001**

Although only one native forb increased significantly on an individual basis, the shift toward native forb species was highly significant when the forbs were tested as a whole ($p < 0.001$).

Total Species Response:

When graminoid and forb species were grouped, the composition of native vs. exotic species did not change significantly (Table 7). However, there were more natives and fewer exotics than expected in 1996.

Table 7: **G-test for Total Species, Native vs. Exotic, Plot B95**

	Observed Natives	Observed Exotics	Expected Natives	Expected Exotics	G_{calc}
1995	1443	518	1433	527	0.48
1996	1321	499	1330	490	**n.s.**

PLOT B96: Burned April 26, 1996

Graminoid Responses:

Plot B96 had a richness of 19 graminoid species; six (32%) of these changed significantly in frequency from 1995 to 1996 (Table 8).

Table 8: **Plot B96 Individual Graminoid Species' Responses**

	Natives	Exotics
Significant Increase 1995-1996 $p = 0.05$	*Bouteloua curtipendula* *Bouteloua gracilis* *Carex heliophylla*	*Poa compressa* *Poa pratensis*
Significant Decrease 1995-1996 $p = 0.05$		*Bromus japonicus*

The most significant increase was seen in the native sedge *Carex heliophylla*, from 119 to 168 individuals ($p < 0.005$), a 66% increase. In contrast, the exotic species *Bromus japonicus* decreased 33%, from 128 to 86 individuals ($p < 0.005$). This was the second most abundant exotic graminoid in 1995. Even after the 33% reduction in frequency, it was still the third most abundant exotic graminoid in 1996.

In contrast to plot B95, there was not a significant change in the composition of native and exotic graminoid species from 1995 to 1996 in this plot (Table 9).

Table 9: **G-test for Native vs. Exotic Graminoids, Plot B96**

	Natives Observed	Exotics Observed	Natives Expected	Exotics Expected	G_{calc}
1995	404	370	414	359	1.09
1996	496	410	485	421	**n.s.**

Contrary to my hypothesis, the burn in the spring of 1996 did not significantly change the relative composition of native and exotic graminoid species. However, there were more natives and fewer exotics than expected, and this shift was in the predicted direction.

A similar pattern was observed for the composition of C3 and C4 graminoids (Table 10). Again, the hypothesized shift toward more C4 species did occur, but this change was not statistically significant.

Table 10: **G-test for C3 vs. C4 Graminoids, Plot B96**

	C4 Observed	C3 Observed	C4 Expected	C3 Expected	G_{calc}
1995	129	645	138	636	1.39
1996	171	735	162	744	**n.s.**

Forb Responses:

Plot B96 had a richness of 36 forb species, and the frequencies of nine forb species (25%) changed significantly in plot B96 over the sampling period (Table 11).

Table 11: **Plot B96 Individual Forb Species' Responses**

	Natives	Exotics
Significant Increase 1995-1996 p = 0.05	*Ratibida columnifera*	*Tragopogon dubius*
Significant Decrease 1995-1996 p = 0.05	*Calochortus gunnisonii* *Lomatium orientale*	*Alyssum minus* *Carduus nutans* *Camelina microcarpa* *Galium aparine* *Lactuca serriola*

Tragopogon dubius increased most significantly, from 59 to 97 individuals ($p < 0.005$), making it the most abundant exotic forb in 1996. This was a 70% increase, whereas this species decreased by nearly 50% in plot B95 over the same sampling period. There was a large reduction in the two most abundant exotic forbs in 1995 (Appendix 1). *Lactuca serriola* dropped in frequency from 83 to only 15 individuals ($p < 0.001$). Also, *Alyssum minus* decreased from a frequency of 60 to just 9, an 85% drop ($p < 0.001$). This species decreased significantly in plot B95 as well, but only by 54%.

Unlike the graminoids in plot B96, the change in native vs. exotic forb species composition was highly significant (Table 12).

Table 12: **G-test for Native vs. Exotic Forbs, Plot B96**

	Observed Natives	Observed Exotics	Expected Natives	Expected Exotics	G_{calc}
1995	724	237	767	194	26.12
1996	721	128	678	171	p< .001

As in plot B95, the native forbs were favored. However, the forb responses were more pronounced in plot B96. The G-value for this plot was 26.12, whereas the G-value for plot B95 was only 18.88. Both of these tests had similar degrees of freedom, so these G-values are directly comparable.

Total Species Responses:

The burn in 1996 appears to have had a favorable affect for the overall native vs. exotic species composition for this plot. When the graminoids and forbs were analyzed jointly, the change in the frequency of native individuals relative to exotics was highly significant (Table 11).

Table 13: **G-test for Total Species, Native vs. Exotic, Plot B96**

	Observed Natives	Observed Exotics	Expected Natives	Expected Exotics	G_{calc}
1995	1128	607	1167	568	7.81
1996	1223	538	1184	577	**$p < .01$**

Although the shift towards more native species was not significant for the graminoids, all three G-tests revealed a greater relative frequency of native species after the burn in plot B96. In contrast to plot B95, the composition of C3 and C4 graminoids did not show a significant response from 1995 to 1996.

DISCUSSION & CONCLUSIONS:

In contrast to my hypothesis, the 1995 and 1996 prescribed fires at Chautauqua did not increase the frequency of native graminoids or C4 graminoids. However, there was a significant shift towards more native forb species for both plots, and there were more native species overall in plot B96. It appears that the major objective of these two burns, to increase the frequency of native graminoids and reduce the frequency of exotic graminoids, has not been met. The results of this study exemplify the difficulty in predicting the effects of prescribed fire on species composition, and demonstrate the importance of external factors in determining a plant community's response.

While prescribed burns in the spring have generally been shown to favor native C4 species, plant community responses to fire can vary based on a wide range of factors. Vogl (1974) noted that the regrowth of grassland vegetation after fire may be affected by precipitation before and after the fire, the air temperature and humidity at the time of the burn, the wind speed during the fire, the fire temperature, and the season of the burn. In addition, the interaction of other disturbances at Chautauqua, principally recreation, may have also affected the community's response.

The burn in 1995 was in the midst of an atypical weather year for Boulder (Figure 3). Prior to the burn, temperatures in January, February and March were 0.8 to 1.7 degrees Celsius above the long-term average temperatures for these months. Following the burn on April 6, the months of April - July were unseasonably cool and wet. The average temperatures for April, May, and June were 2.3, 4.1, and 2.5 degrees Celsius below the long-term average temperatures, respectively. In addition, precipitation was unusually high for the spring and summer of 1995. May, for example, had 24.36 centimeters of precipitation; this is 16.66 centimeters more than the long-term average precipitation for that month.

These unusual weather patterns affected the time of emergence for both the C3 and C4 species at Chautauqua. Due to the abnormally warm temperatures in January, February, and March, the C3 graminoids initiated growth earlier in the year than they normally would. When the burn was conducted on April 6, the C3 species had already begun to "green up." In contrast, the cool and wet conditions after the 1995 burn resulted in a delayed initiation of growth for the warm-season C4 species.

Both the early onset of growth and the cool, wet weather that followed in 1995 favored the spread of the exotic and C3 graminoids at the expense of the native C4 species. After the fire, the weather conditions were more favorable to the exotic C3 species, causing them to grow vigorously. The C4 species, in contrast, had a delayed emergence and did not compete with the C3 species as well as they might have in a typical weather year. This temporal separation meant that openings in the soil and the available resources were utilized by the C3 species before the C4 species were able to initiate growth.

Graminoid Responses:

This change in the competitive relationship between C3 and C4 species is evidenced by the observed graminoid species composition in plot B95. The vigorous growth of the C3 species in 1995 translated into their increased frequency observed in 1996. All of the graminoid species which increased significantly in this plot were perennials, and underground vegetative growth in 1995 may have resulted in larger bunches with more tillers in 1996. This would account for the increased frequency of these species as measured with the nested quadrat. Both native and exotic C3 species were favored by the weather in 1995; three of the four native species that increased significantly in plot B95 were C3: *Agropyron smithii, Stipa spartea,* and *Stipa viridula*. However, because all of the exotic graminoids at Chautauqua are C3, there was a significant increase in the frequency of exotic graminoids relative to native graminoids in plot B95.

The composition of graminoid species in plot B96 was also influenced by the 1995 weather, however, this effect was offset by the prescribed fire in the spring of 1996. Initially, the weather in 1995 enhanced the growth of C3 species in this plot. However, the burn in the spring of 1996 curbed the growth of the C3 species while enhancing the growth of the C4 species. When these factors are considered jointly, the composition remained approximately the same over the course of the study. There was no significant shift in the composition of native and exotic or C3 and C4 graminoid species in plot B96.

Forb Responses:

A greater response was observed in the forbs than the graminoids; there were highly significant increases in the number of native forbs relative to exotics for both plots. Again, the weather and the prescribed fire are the two principal factors influencing this pattern.

First, the weather contributed to the reduction in the frequency of early blooming forbs, many of them exotics, from 1995 to 1996. These species could have been favored by the weather conditions in 1995, and their frequencies may have been abnormally high during that year. The forbs that bloom earliest in the spring are adapted to cooler temperatures and wetter conditions, and they may have been favored in much the same way as the C3 graminoids. When the weather returned to normal in 1996, their frequencies dropped again to levels observed in a typical weather year. For example, *Alyssum minus*, an exotic early-spring bloomer, decreased significantly in both plots: 51% in plot B95 and 85% in plot B96. Because the decrease occurred in both plots, this indicates that the pattern is likely a function of the weather in addition to fire. Many of the other forbs observed to decrease were early-spring bloomers, with a phenology similar to *Alyssum minus*.

The second factor potentially influencing forb frequencies is the evolutionary history of these species as they relate to fire. The native forbs evolved in the North American prairies where fires were common, so they are likely to possess adaptations to fire. These may include adaptations to help survive fire and adaptations to take advantage of conditions such as reduced litter, changed albedo, and increased nutrient availability after the fire. In contrast, the exotic forb species, depending upon their places of origin, may not have evolved these mechanisms for responding to fire. Therefore, their frequencies would have been reduced following the fire, especially in plot B96.

Both of these factors contributed to the increased frequency of native forbs relative to exotics. In plot B95, the reduction in exotic forbs was largely due to the return to normal weather patterns. In plot B96, both the weather and the prescribed fire caused and increase in native forbs relative to exotics.

Additional Factors Influencing Species Composition:

Another important determinant of the plant community's response is the percentage of burned area within each plot. In plot B95, the fire was relatively cool and did not spread; large patches of the meadow remained unburned. In addition, the areas of the meadow with the highest concentrations of exotic species were the areas that were burned the least. For example, the vegetation adjacent to the designated trails is composed almost entirely exotics due to the heavy trampling that occurs there. However, because the trails were designated fire breaks and at the edge of the burned area, the vegetation near the trails was almost untouched by the fire in 1995 (Photos 3 & 4).

Photo 3: Trail lined with the exotic graminoids *Bromus japonicus* and *B. tectorum*.

Photo 4: Trail edge burned area, April 7, 1995.

Photo 5: Grove area dominated by the exotic graminoids *Bromus inermis* and *Dactylis glomerata*.

Photo 6: Grove area after prescribed burn, April 7, 1995.

Another patch containing mostly exotic graminoids is located beneath a small grove of trees in a slightly more mesic part of the meadow. This area was the greenest portion of the meadow on the day of the burn, and the moist conditions there prevented the fire from spreading. This area is a large seed source for *Bromus inermis* and *Dactylis glomerata*, and these species were not adequately damaged by the 1995 burn (Photos 5 & 6).

Based on my photographs, it is evident that an even smaller portion of the vegetation was burned in the 1996 fire than in 1995. This would likely cause localized patches of enhanced growth, and increased frequency of C4 species in regions where litter had been removed. In the unburned patches, the species composition would likely be unchanged (except by the weather and other external factors). When my transects were run across this mosaic, the result may have been an "averaging" of these two effects, especially in plot B96. Therefore, when I analyzed my data, changes in species composition in the burned patches would not be evident.

Because this study was conducted in a recreational area, the influence of human visitors and their pets cannot be discounted. Although there are designated trails through the meadow, a considerable amount of short-cutting did occur in this area. Also, unleashed dogs frequently ran through the study plots.

The ecological impacts of recreational use are clearly visible at Chautauqua; the high concentration of exotic colonizing species adjacent to the trail is evidence of the repercussions of trampling (Photo 3). The trail edges have become a seed source, and the effects of short-cutting are exacerbated by the spread of these exotic seeds into the interior of the meadow. After a prescribed burn, the presence of openings in the soil, created by the removal of litter, provides an additional opportunity for these species to establish.

I believe that recreational use also creates a litter layer much different than in an area not subject to trampling. The litter is much more compressed in this area, and standing dead is also flattened down by the foot traffic. Further study is needed to assess the differences in the litter layer and its affects on productivity, and how this potentially different litter layer translates into species responses to burning.

Finally, further study is needed to determine the effectiveness of prescribed fire in recreational areas as a tool for curbing the spread of exotic species. At Chautauqua, data on species composition is needed for several years before and after burning to isolate species responses to burning, weather, and other external factors. Also, quantitative data is needed to relate the percentage of burned area to changes in the plant community as a whole.

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Appendix 1

Plot B95 Graminoids

Species			1995 Freq.	1996 Freq.	G_{calc}	Family
Agropyron repens	C3	E	6	0	4.16	Poaceae
Agropyron smithii	C3	N	81	113	5.30	Poaceae
Andropogon gerardii	C4	N	69	59	0.78	Poaceae
*Bouteloua curtipendula**	C4	N	88	56	7.17	Poaceae
Bouteloua gracilis	C4	N	22	17	0.64	Poaceae
Bromus inermis	C3	E	10	18	2.32	Poaceae
Bromus japonicus	C3	E	64	68	0.12	Poaceae
Bromus tectorum	C3	E	17	18	0.03	Poaceae
Carex heliophylla	C3	N	191	174	0.79	Cyperaceae
*Dactylis glomerata**	C3	E	4	15	6.78	Poaceae
*Koeleria macrantha**	C4	N	30	59	9.62	Poaceae
*Phleum pratense**	C3	E	2	12	7.92	Poaceae
*Poa compressa**	C3	E	115	164	8.65	Poaceae
Poa pratensis	C3	E	92	102	0.52	Poaceae
Schizachrium scoparium	C4	N	17	13	0.53	Poaceae
*Sporobolous airoides**	C4	N	8	0	5.55	Poaceae
*Sporobolous heterolepsis**	C4	N	29	12	7.27	Poaceae
*Stipa comata**	C3	N	14	0	9.70	Poaceae
*Stipa spartea**	C3	N	3	22	16.31	Poaceae
*Stipa viridula**	C3	N	27	56	10.35	Poaceae

* indicates a significant change, X^2 (1,0.05) = 3.841
E = exotic species
N = native species

Plot B96 Graminoids

Species			1995 Freq.	1996 Freq.	G_{calc}	Family
Agropyron smithii	C3	N	122	132	0.39	Poaceae
Andropogon gerardii	C4	N	59	64	0.20	Poaceae
*Bouteloua curtipendula**	C4	N	30	49	4.61	Poaceae
*Bouteloua gracilis**	C4	N	7	19	5.75	Poaceae
Bromus inermis	C3	E	3	3	0.00	Poaceae
*Bromus japonicus**	C3	E	128	86	8.30	Poaceae
Bromus tectorum	C3	E	24	19	0.58	Poaceae
*Carex heliophylla**	C3	N	119	168	8.41	Cyperaceae
Dactylis glomerata	C3	E	0	3	2.08	Poaceae
Koeleria macrantha	C4	N	16	19	0.26	Poaceae
Phleum pratense	C3	E	1	2	0.34	Poaceae
*Poa compressa**	C3	E	77	111	6.18	Poaceae
*Poa pratensis**	C3	E	137	186	7.46	Poaceae
Schizachrium scoparium	C4	N	12	13	0.04	Poaceae
Sporobolous airoides	C4	N	1	0	0.69	Poaceae
Sporobolous heterolepsis	C4	N	4	7	0.83	Poaceae
Stipa comata	C3	N	10	5	1.70	Poaceae
Stipa spartea	C3	N	5	2	1.33	Poaceae
Stipa viridula	C3	N	19	18	0.03	Poaceae

* indicates a significant change, X^2 (1,0.05) = 3.841
E = exotic species
N = native species

Plot B95 Forbs

Family	Species		1995 Freq.	1996 Freq.	G_{calc}
Alliaceae	*Allium textile*	N	4	0	2.77
Apiaceae	*Lomatium orientale**	N	66	7	55.07
Asteraceae	*Achillea lanulosa*	N	48	51	0.09
	Ambrosia psilotachya	N	143	154	0.41
	Arnica fulgens	N	16	0	11.09
	Artemesia frigida	N	2	0	1.39
	Artemesia ludoviciana	N	137	133	0.06
	Aster falcatus	N	167	175	0.19
	Aster porteri	N	0	3	2.08
	Grindelia squarrosa	N	0	1	0.69
	*Helianthus rigidus**	N	8	27	10.89
	Lactuca serriola	E	11	5	2.31
	*Liatris punctata**	N	38	20	5.68
	*Nothocalais cuspidata**	N	22	3	16.31
	*Packera pseudaurea**	N	9	0	6.24
	Ratibida columnifera	N	0	1	0.69
	Solidago missouriensis	N	15	14	0.03
	*Taraxacum officinale**	E	27	10	8.11
	*Tragopogon dubius**	E	82	42	13.14
	Tragopogon porrifolius	E	2	0	1.39
Boraginaceae	*Mertensia lancceolata*	N	3	0	2.08
	Onosmodium molle	N	10	5	1.70
Brassicaceae	*Alyssum minus**	E	71	33	14.21
Cactaceae	*Opuntia macrorhiza**	N	13	3	6.74
Calochortaceae	*Calochortus gunnisonii*	N	5	0	3.47
Convolvulaceae	*Convolvulus arvensis*	E	0	1	0.69
Fabaceae	*Astragalus dasyglottis*	N	19	11	2.16

	Lathyrus latifolius	E	10	11	0.05
	Lupinus argenteus	N	13	6	2.64
	Melilotus officinale	E	2	0	1.39
	Psoralea tenuiflora	N	18	30	3.03
	Thermopsis divericarpa	N	11	8	0.48
Liliaceae	*Leucorinium montanum*	N	5	0	3.47
Rosaceae	*Drymocallis fissa*	N	0	2	1.39
	Rosa arkansa	N	92	86	0.20
Rubiaceae	*Galium aparine*	E	1	0	0.69
Verbenaceae	*Verbena bracteata*	E	2	0	1.39

* indicates a significant change, X^2 (1,0.05) = 3.841
E = exotic species
N = native species

Plot B96 Forbs

Family	Species		1995 Freq.	1996 Freq.	G_{calc}
Alliaceae	*Allium textile*	N	2	0	1.39
Anacardiaceae	*Rhus trilobata*	N	12	9	0.43
Apiaceae	*Lomatium orientale**	N	14	0	9.70
Asteraceae	*Achillea lanulosa*	N	27	29	0.07
	Ambrosia psilotachya	N	113	134	1.79
	Arnica fulgens	N	1	0	0.69
	Artemesia ludoviciana	N	144	126	1.20
	Aster falcatus	N	152	162	0.32
	Aster porteri	N	3	0	2.08
	*Carduus nutans**	E	7	0	4.85
	Erigeron divergens	N	5	0	3.47
	Grindelia squarrosa	N	0	3	2.08
	Gutierrezia sarothrae	N	2	0	1.39
	Helianthus rigidus	N	35	42	0.64
	*Lactuca serriola**	E	83	15	51.97
	Liatris punctata	N	34	21	3.10
	Nothocalais cuspidata	N	7	10	0.53
	*Ratibida columnifera**	N	0	9	6.24
	Solidago missouriensis	N	26	19	1.09
	Taraxacum officinale	E	7	7	0.00
	*Tragopogon dubius**	E	57	97	10.51
Boraginaceae	*Onosmodium molle*	N	18	27	1.81
Brassicaceae	*Alyssum minus**	E	60	9	42.22
	*Camelina microcarpa**		9	0	6.24
Cactaceae	*Opuntia macrorhiza*	N	13	20	1.50
Calochortaceae	*Calochortus gunnisonii**	N	12	0	8.32

Convolvulaceae	*Convolvulus arvensis*	E	3	0	2.08
Fabaceae	*Astragalus dasyglottis*	N	22	35	2.99
	Lupinus argenteus	N	17	17	0.00
	Psoralea tenuiflora	N	31	42	1.66
	Thermopsis divericarpa	N	5	0	3.47
Liliaceae	*Leucorinium montanum*	N	4	0	2.77
Onagraceae	*Gaura coccinea*	N	1	0	0.69
Rosaceae	*Drymocallis fissa*	N	9	6	0.60
	Rosa arkansa	N	15	10	1.01
Rubiaceae	*Galium aparine**	E	11	0	7.62

* indicates a significant change, X^2 (1,0.05) = 3.841
E = exotic species
N = native species

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