THE VEGETATION COVER, SEED BANK, SEED RAIN AND SEED REPRODUCTION OF THE RELICTUAL TALLGRASS PRAIRIE OF BOULDER COUNTY, COLORADO

BY

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A Thesis submitted to the

Faculty of the Graduate School of the

University of Colorado in Partial fulfilment

of the requirements for the degree of

Doctor of Philosophy

Department of Environmental, Population,

and Organismic Biology

1992

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Tallgrass Prairie once was common along the Front Range in eastern Colorado. As a result of overgrazing, agriculture and urban development, most of tallgrass habitats in Colorado have been destroyed. The best protected remnants of Tallgrass Prairie are scattered in the foothills near Boulder, Colorado. This site is widely separated from the principal Tallgrass area of the eastern Great Plains. I examined the ecological processes that underlie this remnant Tallgrass Prairie and also compared and contrasted it with the Tallgrass Prairie to the east.

I investigated the effect of fire on the above-ground vegetation and on the seed bank. Also, seed rain and seed bank were compared to present vegetation. In addition, the seed bank of Boulder Tallgrass Prairie was compared to that of the Konza Tallgrass Prairie. Seed production of the two dominant grasses which characterized the Tallgrass Prairie, Andropogon gerardii and Sorghastrum avenaceum were studied.

In 1988, the cover classes for each species were estimated using the Braun-Blanquet method. In 1989 and 1990, vegetation cover was estimated by percentage cover within quadrats. The Kruskal-Wallis Analysis was used to test for differences in mean cover between burned and unburned plants. Correspondence Analysis Ordination was used to examine changes in community composition due to burning. The seed bank was evaluated by both bioassay and mechanical separation. Kruskal-Wallis and Correspondence Analysis were used to test for differences in mean seed numbers and for changes in seed bank composition due to burning. The non-parametric Spearman's rank correlation coefficient, Kolmohorov-Smirnov two sample test, and the Czekanowski coefficient were used to compare seed bank and seed rain. The mean differences of florets, seeds, midge, midge parasites and seed weight were tested by using the Kruskal-Wallis analysis. Additional comparisons of percent seed set, seed parasitism and secondary parasitism were carried out as well.

Above-ground vegetation was recorded for a total of 156 species in Boulder Tallgrass Prairie. Major exotic grasses, Bromus spp. and Poa spp., were eliminated on the burned sites. Fire also caused reduction in the seed banks of these two weedy exotic grasses. Burning enhanced most native species, especially the shortgrasses, e.g., Chondrosum gracile, Bouteloua curtipendula and Buchloë dactyloides. The Tallgrass species responses to burning were not clear cut. This contrasts with previous studies done on the eastern Tallgrass Prairie.

The seed banks represent potential future vegetation. A total of 105 plant species were germinated from the Boulder soil seed bank. Of these, 35% were natives and 65% were introduced species. In contrast, the Konza soil seed bank comprised of 28 plant species, including of 65% native, 33% introduced species and 2% unknowns. The seed bank corresponded poorly to the above-ground's frequency of distribution. For Boulder, only 0.33% of the soil seed bank belonged to the dominant grasses. This implies that should current aboveground vegetation die, it would be replaced with exotic weedy vegetation, because

The bioassay method was used to identify seeds in the seed bank. Mechanical separation was used as a complementary method in order to get the most complete information about the seed bank. The seed rain showed little similarity to the seed bank. This difference is due in large part to predation, disease, and loss through germination.

Andropogon gerardii and Sorghastrum avenaceum from the Boulder Tallgrass Prairie produced more seeds than their Konza counterparts. Year to year variation existed for seed reproduction and for numbers of both midges and midge parasites. Andropogon gerardii responded positively to burning by increasing its seed numbers. The opposite was true for Sorghastrum avenaceum. The 4-year-burning regime at Konza gave higher seed production than either annual burning or 10-year-burning. Long term studies of seed reproduction are needed for a better understanding of reproductive performance.

Practical recommendations can be taken from this research. Revegetation by means of seeds collected locally should be implemented. Seeds should be grown both in the greenhouse and sown in nature. For greenhouse germinated seeds, seedlings can be transplanted to the field. Also, manual removal of weed seedlings is highly recommended because this is the most effective and safest way to control weeds. Because fire helps reduce major weed species, I recommend periodic burns to eliminate the excess litter and to discourage the invasion of exotic grasses and forbs.

Many questions in population genetics and physiology can be approched by comparing the morphology and development, genetics, and physiological resources of the Konza and Boulder populations. Understanding the Tallgrass ecosystem will not only help maintain and enhance the remnants of natural Tallgrass Prairie, but also help save the disturbed Prairie from extinction by mismanagement.

I dedicate this work to the Prairies and those who work to conserve them.

ACKNOWLEDGEMENTS

The five years of my stay in the U.S. not only have broadened my knowledge in academics but also have taught me to always see things from different angles. Thinking back, I can not believe how much I have grown, both academically and mentally during this time. I could not have learned so much and understood the world as much if I had not come here. Behind my success is the help, support, and care from the people around me. First, I am most grateful to my major advisor, Dr. Jane Bock for her patience, understanding, encouragement and above all her love of leveling women's education. I am thankful to my committee members for sharing their skills, constructive comments and invaluable advice: Dr. Michael Grant, Dr.Yan Linhart, Dr. Meridith Lane, Dr. Pamela Diggle, Dr. William Bowman and Dr. Darna Dufour. My thanks also go to other faculty members, staff, and off-campus persons who have helped me in various ways: Dr. Jeffry Mitton, Dr. Carl Bock, Mr. Dick Antonio, Mr. Steve Slavik, Dr. Thomas Swain, Dr. William Weber, Dr. Marilyn Walker, Mr. David Stirts, Mr. David Underwood, Mr. Larry Harwood, Dr. James Hanken, Mr. Michael Weissmann, Dr. Thomas Ranker, Dr. William Lewis and Dr. Arnold Larsen. I thank you the University Learning Center and the Computing Network Services of the University of Colorado for providing me the excellent learning skills and computing facilities.

As a foreigner, being in the U.S. is a challenge and an adventure; I myself could not have survived without help from friends. Friends for me are the most precious treasures. Listening, sharing, cheering and helping through all the difficult times were the major drives of my success. I am so fortunate to have you as my friends: Somchai Rattanayun, Penprawon Tranphong, Elizabeth O'Dowd, Irma Furbech, Maureen O' Shea Stone, Michele Lee, Robyn Tierney, Heidi Rodel, Blanca Léon Young, Ken Young, Claudia Peck, Shin Chang Meadows, Jorge Moreno, Diane Fisher Shin, Paul Shin, Bo Khosrovi, Hojat Khosrovi, Jason Jaeger, Nancy Auerbach, Leanne Lestak and Kieu Tran. I also want to give my special thanks to my undergraduate assistants who shared all those long hours lab work with me: Ms. Nga Dang, Mr. Jeffrey Cann, Ms. Leanne Johnson and Mr. Charles Lynch.

My dream of studying here would never have come true without the assistance from these organizations: Fulbright, Institute of International Education and especially Delta Kappa Gamma, which initially and continuously provided the World Fellow Scholarship during my study. The Research Grants were provided by University of Colorado Fund Award, Kathy Lichty Memorial Fund Award, Ramaley Fund Award and University of Colorado Museum Research Fund Award.

My deepest gratitude goes to my mother, father, sisters, sister-in-laws, brothers, nieces and nephews. Without their love, care and support, I would not have come this far.

CONTENTS

TABLES

Table

FIGURES

APPENDIX

CHAPTER I

INTRODUCTION

ORIGIN OF THE NORTH AMERICAN PRAIRIES

The origin of the North American Prairie probably dates back 25 million years to the Oligocene Epoch of the Tertiary Period (Risser, et al.,1981). Earlier in the warm, moist Eocene a temperate forest occupied the Great Plains, but as the Rocky Mountains arose, they intercepted moisture from the prevailing western winds resulting in low summer precipitation and accompanying dry winters (Weaver and Albertson, 1956). This climate change caused a rapid evolution of the grassland species during the upper Oligocene until the forerunner of the modern prairie developed by the Miocene (Clements, 1936). The formation and spread of extensive grasslands probably commenced in the Miocene-Pliocene transition about 7-5 million years ago (Axelrod, 1985).

NORTH AMERICAN GRASSLANDS

North American Grasslands stretch from the highlands of central Mexico to the Canadian provinces of Alberta, Saskatchewan and Manitoba and from eastern Indiana to California (Sims, 1988). Grasslands are the largest of North American vegetation formations, originally covering 300 million of the 770 million ha in the United States (Kuchler,1964). Today, grasslands remain the largest of natural biomes in the United States, covering more than 125 million ha (U.S. Forest Service, 1980). Most of the productive, arable lands in North America were once grasslands (Sims, 1988).

Major North America grasslands include the tall-grass, mixed-grass, and shortgrass prairies of the central plains, the desert grasslands of the southwestern United States and Mexico, the California grasslands, and the Palouse prairie in the intermountain region of the northwestern United States and British Columbia, Canada (Sims, 1988). The California grasslands and desert grasslands account for about 2% and 8% respectively of all grasslands, with the remaining 90% distributed as shortgrass (23%), mixed-grass (21%), tall-grass (22%), and Palouse prairie (24%) (Sims, 1988).

In my study, I focus on the tallgrass prairie, which is the most mesic of the grasslands of the central plains. The vegetation of tallgrass prairie is composed of bunchgrasses and sod-forming grasses. The dominant grasses are big bluestem (Andropogon gerardii), Indian grass (Sorghastrum avenasceum), little bluestem (Schizachyrium scoparium), and switch grass (Panicum virgatum). Sporobolus asper is an important intermediate-height grass, especially in grazed areas. Most of the tallgrass prairie is now in cultivation. Natural tallgrass prairie remains in the Osage and Flint Hills of Oklahoma and Kansas, in the Nebraska Sandhills, and in isolated locations through the central lowlands geographical region (Sims, 1988). Tallgrass prairies are disjunct to the west of their principal area (Risser, et al, 1985); the farthest west disjunct population of tallgrass prairie is found in the foothills near Boulder, Colorado (Vestal,1914).

GRASSLANDS AND DISTURBANCES

Grasslands evolved under a combination of the following disturbances: grazing by native herbivores, drought and periodic fire (Anderson, 1982; Bock and Bock,1989). The same adaptations that permit grassland species to endure extreme drought also provide protection during fires (Anderson, 1982). These adaptations are manifested in the herbaceous habit and the placement of perennating organs beneath the surface of the soil, which exposes only dead annual tops during droughts, or when grasses are dormant (Gleason, 1923). Grasslands can support fires whenever the vegetation is dry during droughts or periods of dormancy because the meristems of the grassland species are protected beneath the surface of the soil. Since soil is a good insulator, the heat from fires does not penetrate deeply. Soil temperatures increase little a centimeter or less below the surface (Anderson, 1972a; Vogl, 1974).

Historically, fire has played a critical role in the spread of grassland as evidenced by buried layers of charcoal, and scattered tree trunks show fire records every few years in the past (Cooper, 1960). Disturbance by fire is now recognized as essential to the perpetuation of prairie and savanna (Daubenmire, 1968; Gillion, 1983; White, 1983; Bock and Bock, 1989). Without fires, grasslands become retarded and are invaded by shurbs and trees (Wright, 1974). All natural communities are characterized by two features. First, communities are dynamic systems. The densities and age structures of populations change with time as do the relative abundances of species; local extinctions are commonplace (Connell and Sousa, 1983; Sousa, 1984). Secondly, communities are spatially heterogenous, preserve a mosaic of patches, and can be identified as spatial communities in the overlapping distributions of populations (Wiens, 1976).

Even where background physical conditions are relatively uniform across a site, opportunities for recruitment, growth, reproduction and survival vary spatially, reflecting variation in the intensity of biological interactions, resource avialability, and microclimatological conditions. It is necessary to consider both temporal and spatial variability are the essential features of population and community (Sousa, 1984).

Disturbance such as fire is a major source of temporal and spatial heterogeneity in the structure and dynamics of natural communities and also serves as an agent of natural selection in grassland. Sousa defined disturbance as a discrete, punctuated killing, displacement or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established.

THE SIGNIFICANCES OF THIS STUDY

Tallgrass prairie once was common in eastern Colorado, and early botanists described it along the length of the Front Range including the foothills near Boulder (Vestal, 1914; Branson, et al.,1965). As the result of overgrazing, cultivation, agricultural practices, and urban development, most of the tallgrass prairie habitats in Colorado have been destroyed. Today, a remnant of this prairie, acquired by City of Boulder, contains most of the vegetation necessary to restore a true tallgrass prairie.

To restore, conserve and perpetuate the native plants so as to approximate natural tallgrass prairie, one has to understand the ecological processes of that plant community. In my study, I investigated the ecological importance of the seed bank and seed rain after a fire, and monitored the aboveground vegetation cover of Boulder tallgrass prairie. Additionally, I compared the seed bank of Boulder tallgrass prairie with the seed bank of Konza tallgrass prairie, a large natural tallgrass prairie in eastern Kansas. The results from this study may lead to a better understanding of this ecosystem and help develop management guidelines to restore Colorado relictual Tallgrass Prairie.

CHAPTER II

COLORADO AND KANSAS TALLGRASS PRAIRIE AREA DESCRIPTION

COLORADO TALLGRASS PRAIRIE: HISTORICAL BACKGROUND

Moir(1972), who studied the vegetation of Colorado in the late 1960's, realized the significance of the remnants of tallgrass prairie in the Boulder area and encouraged the City of Boulder to acquire and protect this relict prairie. Since then the City of Boulder has purchased several parcels of relictual prairie and in 1984, Colorado Tallgrass Prairie was designated a Colorado Natural Area. In 1986, the city of Boulder and the Colorado Natural Areas program developed a management plan designed to maintain and enhance the tallgrass vegetation. This plan included monitored grazing and prescribed burns (Colorado Tallgrass Management Plan, 1986). Land use and manipulation patterns on the relictual

Tallgrass Prairie prior to purchase by the city of Boulder are shown in Table 1.

On April 12, 1988, prescribed burns were carried out on portions of Colorado Tallgrass parcels 3 and 7 (Figure 1). No work on the effects of fire on Colorado Tallgrass Prairie has been done. Therefore, to help understand how this remnant tallgrass prairie was affected by fire, I studied the vegetation and seed banks in the two parcels burned in 1988. The results of these findings can be compared with research in other places, especially at the Konza Tallgrass Prairie in Kansas and can be applied in management plans for Colorado Tallgrass Prairie.

Site description

The Colorado Tallgrass Prairie Natural Area is located immediately south of Boulder, Colorado in the South Boulder Creek Valley at elevation ranging between 1636 and 1727 meters. It is made up of eight parcels, totaling 1.09 km^2 (269 acres) (Figure 1).

South Boulder Creek Valley in the vicinity of the Natural Area is covered by Quaternary alluvium deposited as fans and aprons along the ancient

Table 1. Summary of Land Use and Manipulation patterns on the relictual Tallgrass Prairie of Boulder prior to purchase by the City of Boulder

Parcel numbers	Domestic stock	Land Manipulation
1,2 and part of 10	cattle	irrigated
4,6,9 and part of 10	cattle	hayed, fertilized, no chemical weed control
3,7	sheep, goats, mules and horses	hayed, irrigated and fertilized, no chemical weed control

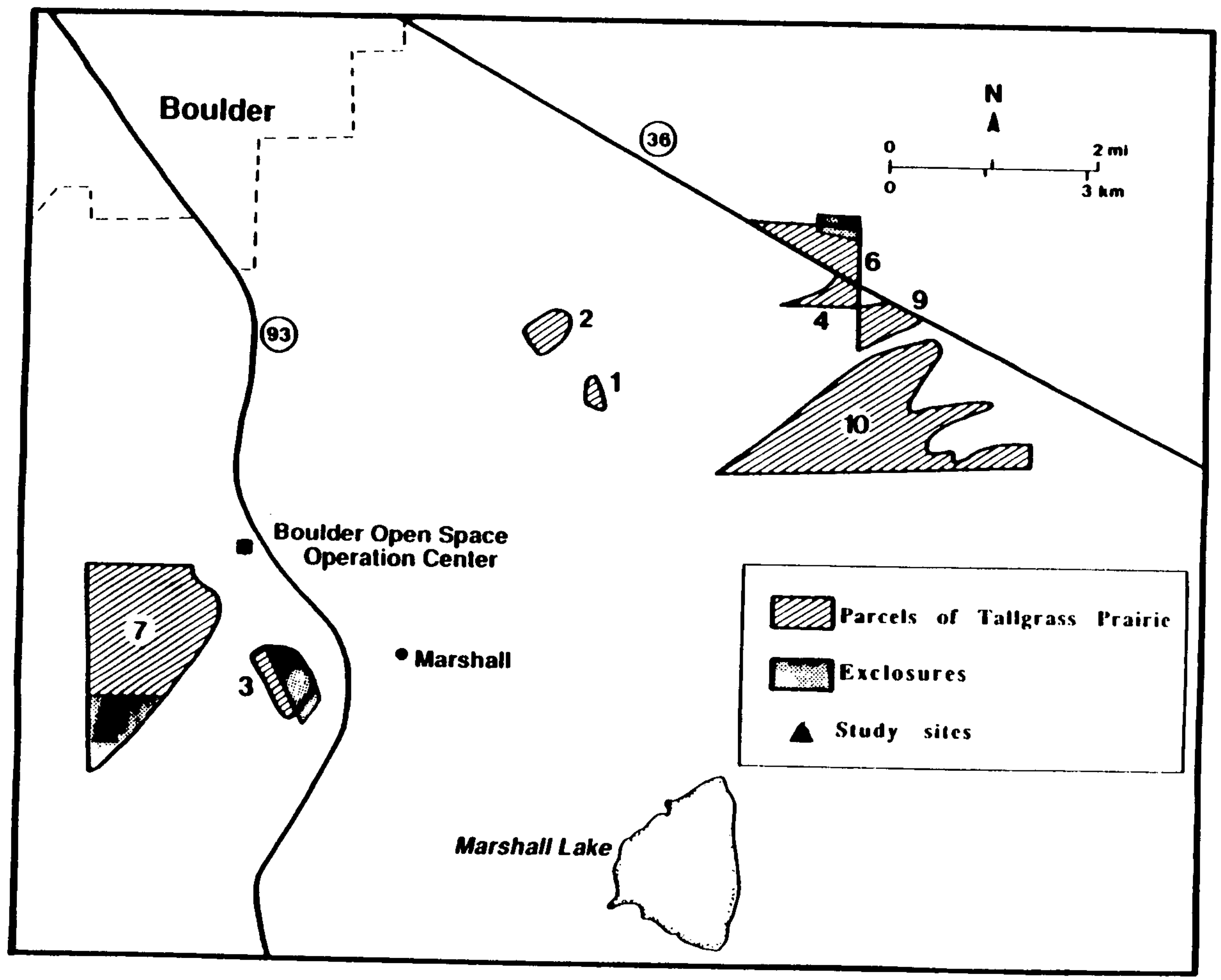

Figure 1. Map of the Boulder Tallgrass Prairie

course of the river. Parcel 10, the north face of Davidson Mesa, is part of a mountain pediment, eroded through sedimentary rocks and later covered with gravel (Chronic, 1980).

Soils of the Nederland series, classified as very cobbly sandy loam, occur in the western portion of the Natural Area and on the bottomlands along South Boulder Creek. Soils of the Valmont series, classified as cobbly clay loam, occur on the eastern edge of the outwash fans. Hargreave series soils, fine sandy loam, occur in the eastern portion of the Natural Area (Soil conservation Service, 1975).

The climate in the vicinity of the Natural Area is strongly affected by the mountains. The precipitation in the area is orographic; moist air is forced upward by the mountains, moisture condenses and precipitates. Orographic precipitation falls in the lower foothills in spring and fall, when air masses from the Gulf of Mexico back up against the mountains creating upslope conditions. Convective storms are frequent on late spring and summer afternoons. The average annual precipitation is 45 cm(18 inches) per year. The area in the vicinity of the Natural Area has a

May precipitation maximum falling as rain or heavy, wet snow and a midwinter precipitation minimum (Mutel, 1976). The average temperature in the vicinity of Boulder, Colorado is 10.5° C(51° F) with 152 frost free days (Soil Conservation Service, 1975).

Site Vegetation

Tallgrass Prairie communities in the Natural Area are assumed to be relicts from early in the Holocene Atlantic episode of glaciation, 800 years before present (Gould et al.,1979, Axelrod, 1985). These communities are restricted to the mesic conditions that exist in a narrow band along the foothills of the Rocky Mountains. The coarse gravel stones in the top layer of substrate appear to act as a mulch, preventing evaporation from the surface while at the same time allowing a rapid infiltration of water to support plant growth (Branson et al., 1965).

A continuum of Tallgrass Prairie communities occur on the Natural Area. Moist, low-lying areas (representing mesic prairie) are dominanted by big bluestem (Andropogon gerardii), little bluestem (Schizachyrium scoparium), switchgrass (Panicum virgatum) and Indiangrass (Sorghastrum avenaceum). Drier, upland sites (xeric prairie) are dominated by big bluestem, little bluestem, blue grama (Bouteloua gracilis), and side-oats grama (B.curtipendula).

Research site description

Study Plots: Parcel 3

Parcel 3 is 0.099 km^2(24.6 acres) (Figure 2) in size and includes both xeric and mesic tallgrass communities (Figure 2). Under current management by the City of Boulder, and 0.05 km^2(12.3 acres) are grazed by cattle, 0.05km^2(12.3 acres) are ungrazed exclosures Of this 0.05 km^2, 0.02 km^2(5 acres) were burned on April 12, 1988, and 0.03 km^2(7.5 acres) were being unmodified. My study plots were on burned and unburned mesic sites in the ungrazed exclosures.

Soil at this parcel is in the Niwot-Loveland-Calkins association. This association is formed from loamy alluvium and occupies narrow, nearly level areas (slopes are 0 to 3%) adjacent to major streams in the eastern part of the Natural Area. The soil is comprised of 35% Niwot soils, 15% Loveland soils, 10% Calkins soils, and others 40%.

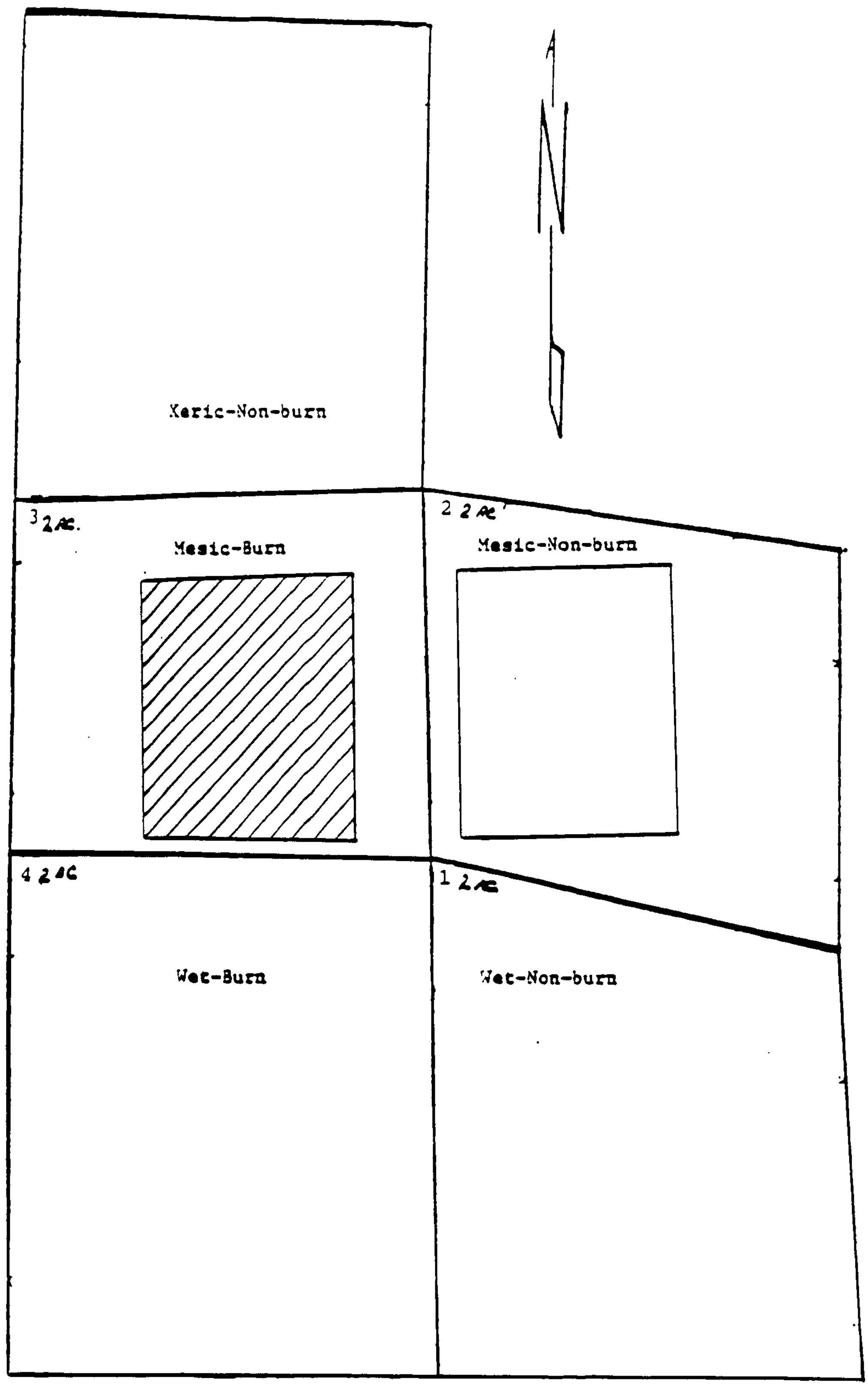

Figure 2. Parcel 3.Boulder Tallgrass Prarie

The Niwot soils have a surface layer of clay loam and loam and are underlain by gravelly sand at a depth of 25 to 50 cm(10 to 20 inches) Loveland soils have a surface layer and underlying material of clay loam. They are underlain by gravelly sand at a depth of 50 to 100 cm(20 to 40 inches). Calkins soils have a surface layer and underlying material of sandy loam.

Study Plots: Parcel 7

Parcel 7 is 0.405 km^2(100 acres) (Figure 3) and includes both xeric and mesic tallgrass communities. Also under current management by the City of Boulder, 0.275 km^2(68 acres) are grazed, and 0.129 km^2(32 acres) are ungrazed exclosures. Of these latter, 0.032 km^2 were burned on April 12, 1988. My study plots are on the xeric burned and unburned portions of the ungrazed exclosures.

Soil at this parcel is classified as the Nederland-Valmont association. It is comprised of approximately 25% Nederland soils, about 25% Valmont soils, and 50% other soils. This association is made up of nearly level to moderately steep old high terraces, benches, and alluvial fans in the west-central part of the

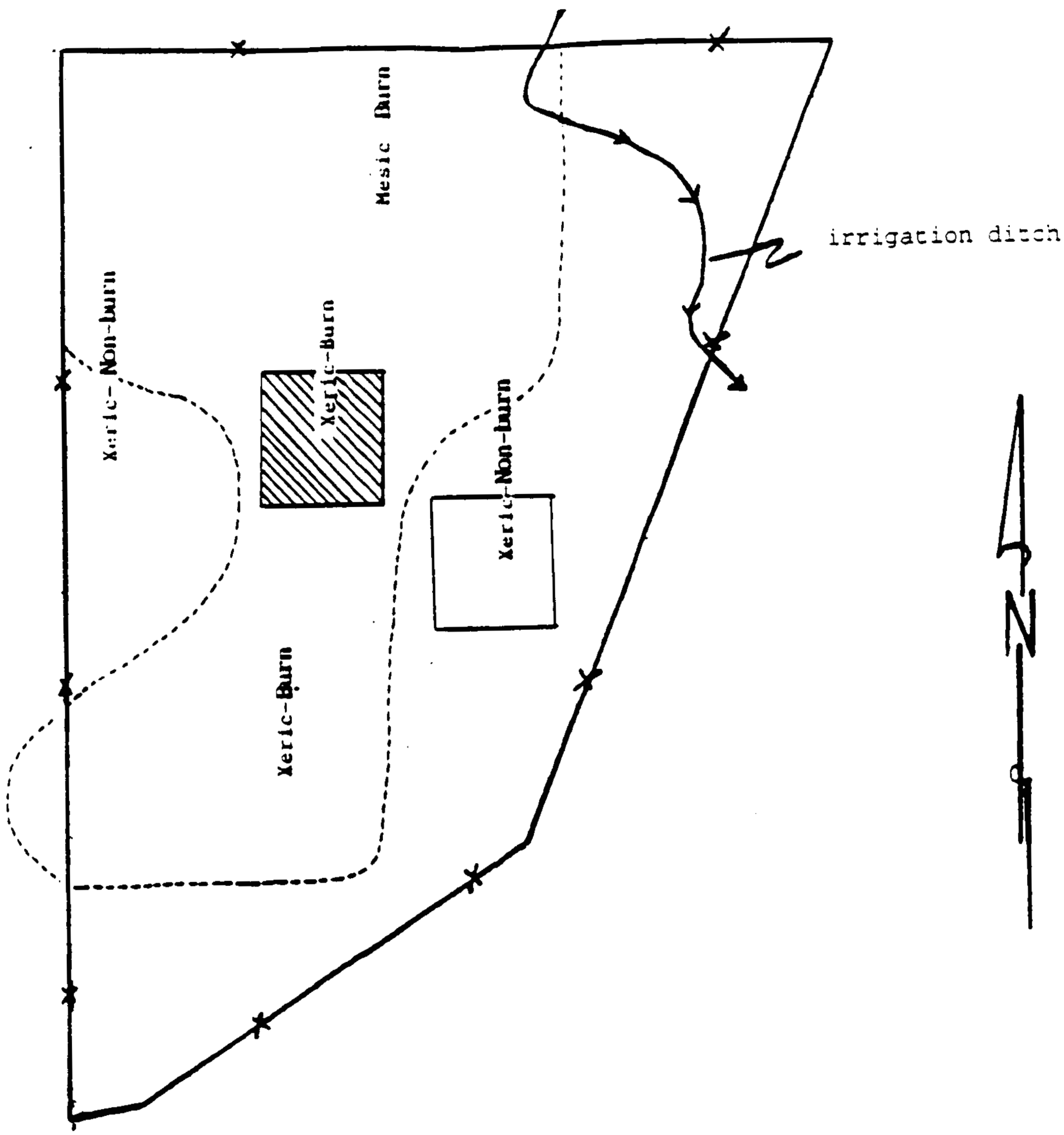

Figure 3. Parcel 7 Boulder Tallgrass Prairie

Boulder area. The soils formed in gravelly and cobbly alluvium. Slopes are 1 to 25 percent.

Nederland soils are older, higher lying terraces and alluvial fans. They have a very cobbly sandy loam surface layer and a subsoil of very cobbly sandy clay loam. Valmont soils are mainly near the eastern edge of high terraces and lower lying benches. They have a surface layer of cobbly clay loam or clay loam and a subsoil of clay and clay loam.

KONZA TALLGRASS PRAIRIE: HISTORICAL BACKGROUND

Konza Prairie Research Natural Area is located in two counties, Geary and Riley, in the Flint Hills of northeastern Kansas, near Manhattan, Kansas. Konza Prairie is the largest natural Tallgrass Prairie left in North America. It is 34.87 km^2 (8613 acres) in size and dominated by Andropogon gerardii, Schizachyrium scoparium and Sorghastrum avenaceum The Flint Hills are along the western border of the Tallgrass Prairie province and because of the steep and rocky topography include the only extensive area of unploughed Tallgrass Prairie in North America.

Most of the Konza prairie was once a part of the Dewey ranch. It has a history of grazing by cattle, and both present and past managers have used fire as a management strategy. The ecological importance of this area of Tallgrass Prairie was recognized thirty years ago by Lloyd Hulbert, a biologist at Kansas State University. The land was eventually purchased with funds from the Nature Conservancy, a foundation dedicated to preserving endangered habitats, and Mrs. Katharine Ordway, a private citizen. The area has been protected as Research Natural Area since 1971 and serves as a Long term Ecological Research Site(Reichman,1987). A fire management plan initiated in 1971(Hulbert, 1973) placed different watershed units under variety of prescribed burning regimes varying from annual, 2-,4- and 10-year intervals and unburned. Prescribed burning takes place in early April(Abrams,1988).

Site description

The climate at Konza Prairie is characteristic of the continental area with hot summers, cold winters, moderately strong surface winds and relatively low humidities. The average precipitation is 8.29 cm(32 inches).

Two majors type of soil dominate Konza Prairie, although many other minor types also occur there. The flat uplands and portions of the slopes are from the Florence soil series, which is composed of loam(a silt and clay mixture) with fairly large pieces of chert. Chert, a type of flint that gives the Flint Hills their name, which may make up 70-80 percent of the soil. The upland soil form a thin veneer, usually exhibiting a top soil less than 30 cm thick and a subsoil no more than 50 cm deep. The soils were formed in situ from weathered limestone bedrock, which still exists less than one meter below the soil surface. Florence soils are well drained and are somewhat firm when wet; when dry, they are indurate, thus exacerbating the effects of droughts.

The lowland Tully soils, which are significantly deeper, were formed by alluvial (stream) deposits and soils washed down the adjacent slopes during rainfall runoff. The Tully soils have a 25 cm topsoil, similar to the Florence soils, but they contain appreciably less chert. A lower horizon, about 30 cm thick, resembles the topsoil but contains less organic matter. Below that is a subsoil over 1.2 meters thick, composed of silty clay. The Tully soils are very productive, supporting what little farming occurs on the Flint Hills (Reichman, 1987).

Site Vegetation

Big bluestem(Andropogon gerardii) and little bluestem(Schizachyrium scoparium), the two main species of grass in Konza Prairie, compose 73 per cent of the vegetation. Next most important grasses are, in order, side-oats grama(Bouteloua curtipendula), blue grama(Chondrosum(Bouteloua) gracile), Indian grass(Sorghastrum avenaceum), switchgrass(Panicum virgatum), buffalo grass (Buchloë dactyloides) and tall dropseed(Sporobolus asper). These major grasses compose 87 to 97 percent of the cover and forbs another 2 percent (Weaver, 1954).

CHAPTER III

VEGETATION ANALYSIS

INTRODUCTION

Grassland plant community responses can be quite varied depending mainly on precipitation patterns and amounts, species composition, herbivory and fire intensity. For instance, in North American grasslands, burning generally enhances plant productivity in the eastern Tallgrass Prairies, but west of the Tallgrass Prairies, in areas with less rainfall, productivity does not always increase following burns(Wright and Bailey, 1982).

Increased dry matter production and flowering of the Tallgrass Prairies after burning have been well documented(Curtis and Partch, 1948; Knapp, 1984a, 1984b, 1985; Knapp and Hulbert, 1986; Patton et al., 1988; Svejcar and Browning, 1988). Anderson et al.(1970) reported the effects of early spring burn for 17 years on species productivity responses. There was a ten-fold increase in the flowering and production rate for the native grasses such as big bluestem, little bluestem and Indian grass; and a decrease in the exotic grasses,for instance, Bromus inermis and Poa pratensis(Anderson et al.,1970). Hulbert(1988) evaluated many possible causes for fire effects in Tallgrass Prairies, i.e. increased light intensity, ash effects, direct effects of heat of the fire, and changes in soil nitrogen. His conclusion was that the incidence of solar radiation and changes in nitrogen are the major causes of fire effects in this system.

In the Shortgrass Prairie, semi-arid northern mixed prairie, California prairie, Palouse prairie and mountain grasslands, fires do not always appear to cause major beneficial effects on productivity, but they help control invading shrubs and trees, improve livestock distribution or remove litter that retards plant growth(Wright and Bailey, 1982). The litter affects energy flow to the grasses by blocking sunlight and reducing the convective cooling air flow aboveground. By blocking the sunlight, it restricts the quantity of photosynthetically active radiation(PAR) available at soil surface, and by preventing air movement, it creates high temperature, especially to the young leaves during the early spring growth(Knapp, 1984a, 1985).

Bock and Bock(1989) reported the effects of wildfire on virgin Northern Mixed Grassland at Custer Battlefield National Monument. They documented the elimination of big sagebrush (Artemisia tridentata) and suppression of the two common exotic grasses, Japanese brome (Bromus japonicus) and Kentucky bluegrass (Poa pratensis) following fires. In contrast, the native grasses such as bluebunch wheatgrass (Agropyron spicatum), grama grasses (Bouteloua), junegrass (Koeleria macrantha), needle and thread (Stipa comata), green needlegrass (Stipa viridula) and Poa juncifolia all showed significant increases in cover during at least one post-fire growing season in comparison with unburned plots. Similarly, some native herbs for example, Alyssum, Gaura, Phacelia, Psoralea, and Sphaeralcea did better on the burned plots, while exotic herbs, for example Melilotus and Lactuca were less successful on the burned sites.

In semi-desert grassland, Bock and Bock(1986) found that fire reduced numbers of grasses, herbs, and shrubs resulting in less biomass after one post-fire season. Two invading shrub species, Mimosa biuncifera and M.dysocarpa, were reduced by burning; however, another invading shrub, Baccharis pteronioides, was unaffected. The latter species appeared to be well adapted to surviving fires. Also, numbers of Agave palmeri and Opuntia engelmannii decreased on the burned plots.

Since most of the results from the eastern Tallgrass Prairie showed increasing in vegetation percent cover of the Tallgrass species because of burning, and the contradictory results seemed to be associated with the western grassland. Also, the Boulder Tallgrass Prairie had no burning records in the past for many years, and there were no studies done on Boulder Tallgrass Prairie before. Therefore, it is important to understand the fire responses of the Boulder Tallgrass Prairie compared to the eastern Tallgrass Prairie. The following is the question posed in this study.

Does burning have any effect on vegetation cover in terms of percent covers?

METHODS

In August 1988, twenty permanent transects (each 50 m long) were established in the Boulder

Tallgrass Prairie. Ten were located on a mesic cattle exclosure(parcel 3) and ten on a xeric cattle exclosure(parcel 7). For each group of ten transects, five had been burned in 1988 and five were unburned. Transects in each burned and unburned site were set up 10 meters apart.

The burned plots were established by means of a prescription fire on April 12, 1988, carried out by the City of Boulder in cooperation with the Colorado State Forest Service. The fire conditions were consistent with those used by Kansas State University, Texas Tech University, and Colorado Division of Wildlife for similar habitats.
No pre-burn vegetation data were collected on the burned(experimental) plots. However, control (unburned) plots were established adjacent to the burned areas in sites matched for slope, aspect, and soil type with the burned plots. This approach, while not ideal, has been used in many fire ecology studies(Collins and Wallace, 1990).

Vegetation cover for each species was estimated from vertical perspective by placing twenty-five 0.5 X 1 m quadrats at 2 meter intervals along each transect. In August 1988 when the study was begun, the canopy cover of each species was estimated using Braun-Blanquet cover scale(Causton, 1988). In 1989 and 1990, the vegetation crown cover of each species was estimated in more detail in terms of percentages of total area of the quadrat(0.5 X 1m). In addition, the relative proportions of vegetation, litter, bare ground, and rock were recorded as percentages of total quadrat area. The rock cover was included in this study because it appeared to act as a mulch, preventing evaporation from the surface while at the same time allowing a rapid infiltration of water to support plant growth(Branson et al., 1965). In 1988 when the study was initiated, vegetation was monitored only on August(4 months after the fire). In the two following years, data were collected in both June and August, representing late spring and summer samples.

Kruskal-Wallis Analysis(K-W), a non-parametric test for differences in means for data sets with non-normal distribution, was applied to test the differences in mean cover between burned and unburned species. The SPSS statistical package(SPSS Inc., Chicago, Illinois) was used to calculate the K-W analyses. Canonical Correspondence Analysis ordination was used to examine changes in community composition due to burning. This analysis is available in the program CANOCO- a FORTRAN program for "Canonical community ordination by partial detrended canonical correspondence analysis"(Ter Braak,1987). Canonical ordination is a combination of ordination and multiple regression. Ordination techniques such as principal components and correspondence analysis(i.e.reciprocal averaging) are commonly used to reduce the variation in community composition to the scatter of species in an ordination diagram. Accordingly, in my study the species scores representing the response curves of species with respect to the ordination axis were presented as a scatter diagram. The CANOCO analysis provides two major advantages. Firstly, the mean cover and the frequency distribution of species are taken into account simultaneously during the analysis. Secondly, it included Monte Carlo permutations which examine the variables randomly, and calculate the probability of community changes that might happen by chance alone, rather than as a result of the treatment itself. Therefore, if the difference between burned versus unburned species is high(P-value

>0.05), then the burning treatment has probably not significantly affected the community. Any differences that occur will be interpreted as chance effects.

RESULTS

Vegetation Cover, Rock, Bareground and Litter

In August 1988, four months after the prescription burn, neither the xeric nor the mesic sites showed differences in total vegetation cover (Braun Blanquet cover rate) between the unburned and burned areas(Tables 2,3). But, there was a 75% reduction in litter on the xeric burned plot and a 90% reduction for mesic site(Tables 2,3). From June 1989 to June 1990), both xeric and mesic sites had significantly higher total vegtation cover on the burned than on unburned areas. For the two burned sites, litter accumulation increased through time after the burn, but there still was less litter($p<0.001$) on the burned plots than on the unburned plots during the study. There was more bare ground($p<0.001$) on the burned plots than on the unburned at all times of monitoring.

Table 2. Mean total vegetation cover, rock, bare ground and litter ± s.d. compared between xeric unburned and burned plots(K-W) with the statistical level of significances (n=500).

Species	burn vs non burn	Aug-88 mean± s.d.	signif level	Jun-89 mean± s.d.	signif level	Aug-89 mean± s.d.	signi level	Jun-90	signi level	Aug-90	signi level
VEGETATION	UB	22.02±5.5		19.42±5.2		20.48±6.1		20.03±4.3		23.73±7.2	
	B	21.09±3.6	ns	20.52±4.6	*	22.32±5.3	**	21.58±5.4	*	25.28±7.1	ns
ROCK	UB	12.92±13.9		12.90±13.9		13.00±13.9		12.88±13.8		13.02±13.9	
	B	12.70±10.8	ns	12.72±10.9	ns	13.27±11.0	ns	12.72±10.9	ns	12.78±10.9	ns
BARE GROUND	UB	18.26±16.2		19.82±16.6		19.30±16.5		15.88±13.9		15.93±13.7	
	B	56.01±15.3	**	45.89±14.5	**	36.26±14.0	**	34.50±15.8	**	17.76±10.2	**
LITTER	UB	47.06±22.2		48.63±21.5		48.12±21.9		51.88±20.1		50.70±20.3	
	B	10.18±13.2	**	20.86±12.9	**	31.53±38.9	**	31.70±15.5	**	46.38±15.4	*

ns=non significant, *=P-value≤0.05, **=P-value≤0.01, ***=P-value≤0.001

Table 3. Mean total vegetation cover, rock, bare ground and litter ± s.d. compared between mesic unburned and burned plots(K-W) with the statistical level of significances (n=500).

Species	burn vs non burn	Aug-88 mean± s.d.	signif level	Jun-89 mean± s.d.	signif level	Aug-89 mean± s.d.	signi level	Jun-90	signi level	Aug-90	signi level
VEGETATION	UB	17.29±3.8		17.88±4.2		16.30±4.2		19.56±5.9		25.74±5.5	
	B	17.49±4.7	ns	20.07±3.7	* *	18.14±4.6	* *	24.18±4.9	* *	25.38±4.6	ns
ROCK	UB	3.48±4.6		3.57±4.8		3.59±4.8		3.52±4.8		3.58±4.8	
	B	6.01±5.2	* *	6.04±5.2	* *	6.04±5.2	* *	6.04±5.2	* *	6.02±5.2	* *
BARE GROUND	UB	9.51±6.9		6.10±5.4		4.71±5.1		4.02±5.6		6.63±6.8	
	B	82.20±10.1	* *	84.82±6.6	* *	49.12±17.7	* *	30.34±17.3	* *	21.15±9.0	* *
LITTER	UB	86.14±9.9		88.47±10.6		89.88±9.8		90.34±11.2		89.03±11.1	
	B	7.65±4.3	* *	9.06±6.0	* *	43.06±19.1	* *	62.08±19.7	* *	72.30±12.1	* *

ns=non significant, *=P-value≤0.05, **=P-value≤0.01, ***=P-value≤0.001

Species responses after fire

Aboveground area was recorded for a total of 156 species in the study sites(Appendix A.1). Mean cover of most common species of the xeric and mesic sites, calculated by year are listed in Appendices A.2 and A.3 respectively. All of the species that occurred in at least 1% of the samples were tested for mean cover differences between the burned and unburned sites using the Kruskal-Wallis Analysis Table 4,5). About half of these common species of the Boulder Tallgrass Prairie showed significant difference in mean cover between the burned and unburned sites at least once during the study.

The Monte Carlo tests of the CANOCO ordination results indicated that the xeric burned and unburned sites were significantly different in community composition($p \leq 0.02$) due to burning from August 1988 to August 1989(Table 6). The mesic burned and unburned sites were significantly different in community changes($p \leq 0.02$) due to burning for from August 1988 to August 1990 (Table 6). Therefore, the analysis of species responses were drawn only from the date with significant P-value which is during August 1988 to

Table 4. Mean cover± s.d. comparison between xeric unburned and burned plots(K-W) with the statistical level of significances. The species listed below occurred at least in 1% of the the total species occurrences

Species	burn vs non burn	Aug-88 mean± s.d.	signi level	Jun-89 mean± s.d.	signif level	Aug-89 mean± s.d.	signif level	Jun-90	signif level	Aug-90	signif level
Stipa comata	UB	2.22±0.64		3.47±2.82		4.05±3.26		4.40±2.97		3.98±3.34	
	B	2.22±0.56	ns	3.41±2.89	ns	3.43±2.70	ns	4.83±3.18	ns	3.66±2.47	ns
Bromus spp.	UB	1.76±0.44		1.33±1.30		1.62±1.25		2.03±1.85		1.38±1.27	
	B	1.22±0.42	***	0.82±1.21	***	0.31±0.35	***	1.29±2.29	***	0.93±1.16	***
Chondrosum gracile	UB	1.84±0.56		1.03±0.81		1.90±1.85		1.70±1.35		2.50±2.24	
	B	1.97±0.39	*	1.31±1.22	ns	2.13±1.69	ns	2.18±1.60	*	2.30±2.13	ns
Andropogon gerardii	UB	2.36±0.73		5.39±4.29		6.36±4.78		5.40±4.03		7.91±6.31	
	B	2.44±0.66	ns	5.30±3.48	ns	5.77±3.80	ns	5.43±4.18	ns	8.15±6.11	ns
Artemisia frigida	UB	2.07±0.57		2.70±2.43		2.69±2.32		2.90±2.40		3.16±2.92	
	B	2.21±0.70	ns	4.19±4.63	*	4.27±4.38	**	3.97±4.09	ns	4.96±4.89	**
Echinocereus viridi-	UB	1.19±0.39		0.63±0.29		0.69±0.44		0.72±0.38		0.76±0.45	
florous	B	1.44±0.50	***	0.63±0.36	ns	0.94±0.69	***	0.98±0.73	*	1.00±0.70	*
Opuntia frigida	UB	1.48±0.61		1.21±1.22		1.36±1.62		1.41±2.45		1.29±2.42	
	B	***	ns	1.05±1.19	ns	0.97±0.94	ns	0.99±0.93	ns	1.21±1.33	ns
Oligosporus pacificu	UB	1.67±0.47		1.52±1.47		1.24±1.01		1.29±1.20		1.48±1.29	
	B	1.88±0.36	**	1.41±1.21	ns	1.62±1.31	ns	1.22±0.79	ns	1.36±0.89	ns
Carex pensylvanica	UB	1.52±0.50		0.77±0.50		0.89±0.55		1.37±1.14		1.42±1.77	
ssp. heliophila	B	1.70±0.48	*	0.89±0.74	ns	1.12±0.97	ns	1.40±1.41	ns	1.56±1.66	ns
Ambrosia artemisii-	UB	1.65±0.67		0.84±0.98		1.51±1.84		0.64±0.34		2.02±1.50	
folia	B	1.78±0.44	ns	0.68±0.45	ns	1.00±1.22	ns	0.50±0.00	ns	0.81±0.66	***
Tragopogon dubius	UB	1.38±0.49		0.58±1.80		0.62±0.23		0.62±0.28		0.52±0.10	
	B	1.67±0.47	**	0.60±0.20	ns	0.50±0.00	ns	0.54±0.16	*	0.56±0.34	ns

Table 4. cont.											
	burn	Aug-88	signi	Jun-89	signif	Aug-89	signif	Jun-90	signif	Aug-90	signif
Species	vs nor	mean± s.d.	level	mean± s.d.	level	mean± s.d.	level		level		level
	burn										
Senecio spartioides	UB	1.37±0.49		0.82±0.46		0.97±0.99		0.76±0.41		0.95±0.48	
	B	1.43±0.50	ns	0.68±0.39	ns	0.87±0.55	ns	0.81±0.40	ns	1.26±0.94	ns
Psoralidium tenuifl	UB	2.20±0.58		2.01±1.47		3.48±3.44		1.74±1.47		5.00±4.94	
rum	B	2.20±0.54	ns	2.75±4.85	ns	3.08±5.22	ns	2.18±3.84	ns	4.62±8.35	ns
Alyssum minus	UB	1.53±0.74		1.16±1.56		2.92±2.65		2.41±3.66		2.44±3.42	
	B	1.20±0.45	ns	0.55±0.25	* *	0.50±0.00	* *	0.88±1.64	* *	1.67±2.81	ns
Opuntia compressa	UB	1.72±0.57		1.14±0.85		1.03±1.16		1.23±1.01		1.21±0.98	
	B	1.64±0.63	ns	0.85±0.54	ns	1.10±1.22	ns	1.12±1.12	ns	1.61±1.63	ns
Liatris punctata	UB	1.58±0.51		0.94±0.66		1.07±0.81		1.02±0.53		1.14±0.96	
	B	1.77±0.50	ns	0.93±0.88	ns	1.10±1.13	ns	0.97±0.85	ns	1.18±0.95	ns
Heterotheca fulcrata	UB	1.56±0.51		0.69±0.40		1.09±0.92		1.00±0.74		1.35±1.37	
	B	1.74±0.45	ns	1.03±1.03	ns	1.23±1.08	ns	1.00±0.92	ns	1.01±0.88	ns
Bouteloua curtipend	UB	1.79±0.42		0.60±0.21		1.00±0.89		0.55±0.16		1023±1.03	
la	B	1.70±047	ns	0.60±0.29	ns	0.74±0.39	ns	0.52±0.11	ns	0.90±0.71	ns
Lepidium densifloru	UB	-		0.52±0.09		-		0.51±0.08		-	
	B	-	-	0.52±0.15	ns	-	-	0.57±0.29	ns	-	-
Poa spp.	UB	1.50±0.52		0.83±0.44		0.86±0.56		0.64±0.35		0.68±0.42	
	B	1.00±0.00	* *	0.75±0.38	ns	0.50±0.00	ns	0.92±1.07	ns	0.59±0.20	ns
Panicum virgatum	UB	2.07±0.61		2.50±3.46		2.62±2.59		2.00±2.86		2.90±4.00	
	B	2.33±0.49	ns	4.14±2.28	*	3.93±2.43	*	2.00±1.65	ns	3.12±2.34	ns
Camelina microcarpa	UB	-		0.90±1.29		0.96±0.65		0.65±0.33		-	
	B	-	-	0.50±0.00	*	-	-	0.50±0.00	*	-	-

Table 4. cont.											
	burn	Aug-88	signi	Jun-89	signif	Aug-89	signif	Jun-90	signif	Aug-90	signif
Species	vs non burn	mean± s.d.	level	mean± s.d.	level	mean± s.d.	level		level		level
Phacelia heterophylla	UB	2.00±0.00		0.57±0.29		0.91±1.04		1.08±0.86		1.22±1.17	
	B	-	-	0.50±0.00	ns	0.02±0.25	ns	0.64±0.38	ns	0.58±0.20	ns
Sporobolus cryptan-	UB	0.86±0.53		0.64±0.23		1.28±1.17		0.70±0.48		1.03±0.79	
drus	B	1.87±0.52	ns	0.69±0.63	ns	2.77±2.30	ns	0.78±0.51	ns	2.09±1.38	*
Chenopodium lepto-	UB	-		0.50±0.00		0.50±0.00		-		0.50±0.00	
phyllum	B	-	-	0.50±0.00	ns	0.52±0.19	ns	0.50±0.00	-	0.87±0.75	ns
Koeleria macrantha	UB	1.33±0.58		0.70±0.27		0.50±0.00		0.62±0.23		0.50±0.00	
	B	1.65±0.49	ns	0.70±0.34	ns	0.87±0.89	ns	1.13±0.84	ns	0.61±0.21	ns
Aristida purpurea	UB	1.78±0.44		1.57±1.50		02.08±1.11		0.58±0.20		1.67±1.47	
	B	1.96±0.21	ns	0.66±0.33	* *	0.95±1.00	* *	0.50±0.00	ns	0.50±0.00	* *
Erigeron flagellaris	UB	1.67±0.82		2.15±1.72		1.85±1.69		3.65±3.88		5.19±6.46	
	B	2.00±0.63	ns	2.11±2.47	ns	2.25±2.61	ns	2.67±3.28	ns	2.26±2.12	ns
Plantago patagonica	UB	-		0.50±0.00		-		0.50±0.00		0.50±0.00	
	B	1.00±0.00	-	0.50±0.00	ns	-	-	0.50±0.00	ns	-	-
Erodium cicutarium	UB	1.00±0.00		1.11±1.12		-		1.32±1.26		0.50±0.00	
	B	-	-	1.29±0.98	ns	0.50±0.00	-	1.92±1.51	ns	0.50±0.00	ns

ns=non significant, *=P-value≤0.05, **=P-value≤0.01, ***=P-value≤0.001

Table 5. Mean cover± s.d. comparison between mesic unburned and burned plots(K-W) with statistical level of significances. The species listed below occurred at least in 1% of the the total species occurrences

Species	burn vs non burn	Aug-88 mean± s.d.	signif level	Jun-89 mean± s.d.	signif level	Aug-89 mean± s.d.	signif level	Jun-90	signif level	Aug-90	signif level
Poa spp.	UB	2.15±0.50		4.05±2.11		2.84±1.95		4.46±2.18		3.03±2.13	
	B	1.82±0.52	***	2.53±1.69	***	1.85±1.49	***	2.54±1.47	***	2.07±1.41	***
Plantago lanceolata	UB	2.20±0.59		2.34±2.08		2.96±2.17		4.20±3.24		6.91±4.60	
	B	2.48±0.67	***	5.09±3.26	***	5.29±3.44	***	7.56±4.56	***	8.85±5.55	**
Sporobolus asper	UB	2.06±0.57		1.72±1.49		2.41±1.99		1.46±1.37		2.48±2.27	
	B	1.83±0.58	*	1.93±1.87	ns	2.14±1.46	ns	2.05±1.56	**	2.79±2.07	ns
Virgul s falcatus	UB	1.13±0.33		0.52±0.09		0.57±0.21		0.56±0.20		0.80±0.68	
	B	1.13±0.34	ns	0.56±0.43	ns	0.54±0.21	ns	0.56±0.26	ns	0.79±0.91	ns
	UB	1.56±0.50		2.30±2.42		1.00±0.65		4.13±3.62		2.68±2.45	
	B	1.66±0.47	ns	3.09±2.58	**	0.81±0.51	**	5.82±4.78	*	2.73±2.34	ns
Sorghastrum avena-ceum	UB	2.24±0.64		2.80±2.68		3.64±2.97		3.36±2.43		5.66±4.11	
	B	2.24±0.67	ns	2.85±2.90	ns	3.56±3.46	ns	3.29±3.00	ns	4.39±3.40	ns
Panicum virgatum	UB	1.94±0.64		1.67±1.90		2.01±2.09		2.17±2.11		3.03±3.18	
	B	1.78±0.70	ns	1.35±1.18	ns	1.59±1.63	ns	2.09±2.50	ns	2.53±3.00	ns
Buchloë dactyloides	UB	1.44±0.50		0.77±0.61		0.87±0.77		2.30±2.90		1.28±1.33	
	B	1.81±0.54	***	1.08±1.28	ns	1.19±1.96	ns	1.56±1.99	ns	1.67±2.25	ns
Chondrosum gracile	UB	1.82±0.58		0.89±1.08		1.14±1.39		3.24±4.16		3.02±3.81	
	B	2.04±0.59	*	1.93±1.74	***	2.79±2.50	***	3.78±3.17	ns	3.94±3.26	*
Ambrosia artemisii-folia	UB	1.44±0.59		0.65±0.58		1.52±1.83		1.01±1.44		2.19±2.90	
	B	1.31±1.47	ns	0.58±0.25	ns	0.75±0.49	**	0.50±0.00	***	0.72±0.47	***
Oligoneuron rigidum	UB	1.38±0.49		0.56±0.17		0.71±0.48		0.81±0.61		0.88±0.71	
	B	1.60±0.60	ns	0.56±0.17	ns	0.75±0.64	ns	0.55±0.16	ns	0.79±0.50	ns

Table 5 cont.

Species	burn vs non burn	Aug-88 mean± s.d.	signif level	Jun-89 mean± s.d.	signif level	Aug-89 mean± s.d.	signif level	Jun-90	signif level	Aug-90	signif level
Hippochaete hyemali	UB	1.03±0.18		0.56±0.17		0.53±0.12		0.59±0.29		0.52±0.09	
	B	1.00±0.00	ns	0.50±0.00	ns	0.50±0.00	ns	0.50±0.00	ns	0.50±0.00	ns
Convolvulus arvense	UB	1.24±0.43		0.66±0.38		0.63±0.36		0.85±0.66		1.37±1.43	
	B	1.67±0.56	**	0.82±0.53	ns	1.11±1.13	*	1.54±2.11	ns	1.69±1.75	ns
Psoralidium tenuiflo	UB	1.75±0.55		1.09±1.07		1.50±1.61		2.19±3.21		2.66±3.19	
rum	B	1.58±0.58	ns	0.80±0.69	ns	1.00±0.98	ns	1.14±1.18	ns	1.07±1.09	**
Andropogon gerardii	UB	2.44±0.69		2.70±2.55		4.64±3.46		5.12±5.13		9.54±7.34	
	B	2.25±0.67	ns	5.18±4.35	*	5.85±5.08	ns	4.15±3.88	ns	8.01±6.45	ns
Pascopyrum smithii	UB	1.61±0.70		1.51±2.73		1.37±2.20		1.55±1.83		2.34±3.73	
	B	1.09±0.29	**	0.73±0.83	ns	0.54±0.13	ns	0.82±0.83	*	0.63±0.37	*
Agrostis gigantea	UB	1.92±0.90		1.67±2.81		2.21±5.62		2.70±4.51		1.97±4.01	
	B	1.50±0.71	ns	0.67±0.29	ns	0.60±0.22	ns	2.25±2.47	ns	1.17±1.15	ns
Juncus arcticus	UB	1.42±0.51		0.78±0.51		0.70±0.50		0.75±0.60		0.77±0.64	
	B	1.46±0.50	ns	0.86±0.52	ns	0.86±0.56	ns	0.84±0.56	ns	0.86±0.64	ns
Eleocharis palustris	UB	1.25±0.50		0.67±0.46		0.50±0.00		2.18±2.23		2.09±1.92	
	B	-	-	0.50±0.00	ns	-	-	0.85±0.62	*	0.50±0.00	*
Taraxacum officinale	UB	-		0.53±0.11		0.56±0.17		0.62±0.27		0.67±0.24	
	B	-	-	0.57±0.19	ns	0.50±0.00	ns	0.50±0.00	ns	0.62±0.25	ns
Dianthus armeria	UB	1.45±0.51		0.50±0.00		0.50±0.00		0.50±0.00		0.50±0.00	
	B	1.32±0.47	ns	0.50±0.00	ns	0.60±0.22	ns	0.50±0.00	ns	0.52±0.10	ns
Carex praegracilis	UB	-		0.71±0.92		1.20±2.04		2.58±2.09		2.17±1.89	
	B	-	-	0.50±0.00	ns	0.50±0.00	ns	0.75±0.48	*	0.54±0.15	*
Alyssum minus	UB	1.71±0.47		0.58±0.19		-		1.23±1.59		1.32±1.55	
	B	-	-	0.50±0.00	*	-	-	0.69±0.51	ns	0.81±0.69	ns
Bromus spp.	UB	1.31±0.48		0.57±0.18		-		0.82±0.60		0.54±0.15	

	B	1.33±0.50	ns	0.50±0.00	ns	-	-	0.50±0.00	*	0.50±0.00	ns
Tragopogon dubius	UB	1.00±0.00		0.50±0.00		0.50±0.00		0.50±0.00		0.50±0.00	
	B	1.00±0.00	ns	0.50±0.00	ns	0.50±0.00	ns	0.50±0.00	ns	0.50±0.00	ns
Aster porteri	UB	1.50±0.84		1.17±1.40		1.62±2.15		2.28±3.29		2.93±3.82	
	B	1.47±0.51	ns	0.69±0.49	ns	0.82±0.73	ns	1.28±1.11	ns	1.68±1.27	ns
Phleum pratense	UB	1.10±0.32		0.58±0.20		0.50±0.00		0.83±0.82		0.50±0.00	
	B	1.17±0.39	ns	0.79±0.67	ns	0.60±0.35	ns	0.97±0.77	ns	0.50±0.00	ns
Opuntia fragilis	UB	1.00±0.00		0.50±0.00		0.50±0.00		-		0.50±0.00	
	B	1.05±0.23	ns	0.52±0.11	ns	0.50±0.00	ns	0.50±0.00	-	0.50±0.00	ns
Opuntia compressa	UB	1.17±0.41		0.87±0.75		1.00±1.12		0.58±0.20		05.0±0.00	
	B	1.36±0.67	ns	0.50±0.00	ns	0.58±1.90	ns	0.59±0.20	ns	0.68±0.37	ns
Carex pensylvanica	UB	1.54±0.52		0.72±0.51		0.50±0.00		0.62±0.25		0.87±0.75	
ssp. heliophila	B	1.23±0.44	ns	0.55±0.16	ns	0.50±0.00	ns	0.57±0.19	ns	0.50±0.00	ns

ns=non significant, *=P-value≤0.05, **=P-value≤0.01, ***=P-value≤0.001

Table 6. The significant differences in vegetation between burned and unburned sites by using Monte Carlo permutation test

	August 1988	June 1989	August 1989	June 1990	August 1990
Xeric	p= 0.02	p= 0.01	p= 0.01	p= 0.12	p= 0.19
Mesic	p= 0.01	p= 0.02	p= 0.02	p= 0.01	p= 0.01

August 1989 for the xeric site. Meanwhile, analysis of species responses for the mesic site were based on the result during August 1988 to August 1990. The schematic ordination diagrams based on CANOCO analysis are shown in Appendix B.4.

In order to analyze the vegetation changes after the burn, the results from two analyses, K-W test and CANOCO, were combined. Species were categorized as: Fire enhanced species, Fire indifferent species and Fire depressed species respectively. Fire enhanced species are the species which either have significantly higher cover(K-W) in the burned plots than in the unburned plots or tend to have higher cover or higher frequency(CANOCO) in the burned than in the unburned plots. In contrast, Fire depressed species are the species which either have lower cover(K-W) or tend to have lower cover or less frequency(CANOCO) in the burned than in the unburned plots. Fire indifferent species are the species that did not differ in either cover or frequency after the burn(Tables 7,8).

Table 7. Plant responses to fire on the xeric sites categorized as Fire enhanced species, Fire depressed species and Fire indifferent. (*) = significantly different in mean cover between unburned and burned sites($p \leq 0.05$).

Fire enhanced species

Grasses and grass-like plants

Bouteloua curtipendula
Carex pensylvanica spp. heliophila *
Chondrosum(Bouteloua) gracile *
Koeleria macrantha
Panicum virgatum *
Sporobolus cryptandrus *

Fire enhanced species

Forbs

Artemisia frigida *
Chenopodium leptophyllum
Echinocereus viridifloreus *
Erigeron flagellaris
Heterotheca fulcrata
Liatris punctata
Psoralidium tenuiflorum
Talinum parviflorum
Tragopogon dubius

Fire depressed species

Grasses and grass-like plants

Andropogon gerardii
Aristida purpurea *
Bromus spp.*
Poa spp.*
Stipa comata

Fire depressed species

Forbs

Alyssum minus *
Ambrosia artemisiifolia
Camelina microcarpa *
Oligosporus pacificus
Opuntia compressa
Opuntia fragilis

Fire indifferent species

Erodium cicutarium
Plantago lanceolata
Senecio spartioides

Table 8. Plant responses to fire on the mesic sites categorized as Fire enhanced species, Fire depressed species and Fire indifferent. (*) = significantly different in mean cover between unburned and burned sites($p \leq 0.05$).

Fire enhanced species

Grasses and grass-like plants

Andropogon gerardii *
Buchloë dactyloides *
Chondrosum(Bouteloua) gracile *
Juncus articus

Fire enhanced species

Forbs

Alyssum minus
Cichorium intybus *
Dianthus armeria
Medicago lupulina
Opuntia compressa
Opuntia fragilis
Plantago lanceolata *
Tragopogon dubius

Fire depressed species

Grasses and grass-like plants

Carex praegracilis
Eleocharis palustris
Panicum virgatum
Pascopyrum smithii
Poa spp. *
Sporobolus asper *

Fire depressed species

Forbs

Ambrosia artemisiifolia *
Hippochaete hyemalis
Medicago lupulina
Oligoneuron rigidum
Tragopogon dubius

Fire indifferent species

Aster porteri
Bromus spp.
Convolvulus arvense

DISCUSSION

Major weedy species of the mesic and the xeric site were depressed as the result of burning. The two introduced grasses: Poa spp.(Poa compressa and Poa pratensis) and Bromus spp.(Bromus japonicus and Anisantha(Bromus) tectorum) were significantly lower in mean cover on the burned areas of the mesic and xeric respectively for all three years of this study. Burning enhanced most native grasses especially the shortgrasses, for example, Chondrosum(Bouteloua) gracilis, Bouteloua curtipendula, Buchloë dactyloides, Sporobolus cryptandrus. The reduction of the cover of introduced grasses and increase the cover of native species are in agreement with previous studies (Abrams, 1988; Bock and Bock, 1989). The tallgrasses, however, did not show consistent results. For example, Andropogon gerardii on the mesic site was fire enhanced. In contrast, it tended to be fire depressed on the xeric site. Sorghastrum avenaceum and Panicum virgatum of the mesic site tended to be fire depressed. The responses of the tallgrasses to burning in this study contrast with other studies done on the eastern Tallgrass Prairies(Curtis and Partch, 1948;

Ehrenreich and Aikman, 1963; Anderson et al, 1970; Johnson, 1987 and Abrams, 1988). This might be due to the differences in environmental conditions, between the eastern Tallgrass Prairie and the western Tallgrass Prairie, including the average maximum temperature, average maximum snow depth and average annual precipitation. The Boulder Tallgrass Prairie exists at what is likely to be an unusually low precipitation regime, compared to the eastern Tallgrass Prairie such as, Kansas Tallgrass Prairie. This statement is supported by the 98 years of records of Boulder's and Kansas's Mean Annual Precipitation with the mean of 18.24 inches (44.74 cm), and 32.65 inches(80.01 cm) respectively (Figure 4.). Perhaps, Boulder's Tallgrass Prairie almost never reaches the optimal water availability in comparison with its counterpart in Kansas, Missouri and Illinois. However, the average maximum snow depth of Boulder is approximately four times higher than Kansas(Table 9). Also, the average maximun temperature of Kansas is 7 degree celsius higher than that of Boulder(Table 9), which may help counteract Boulder's lower precipitation. The two

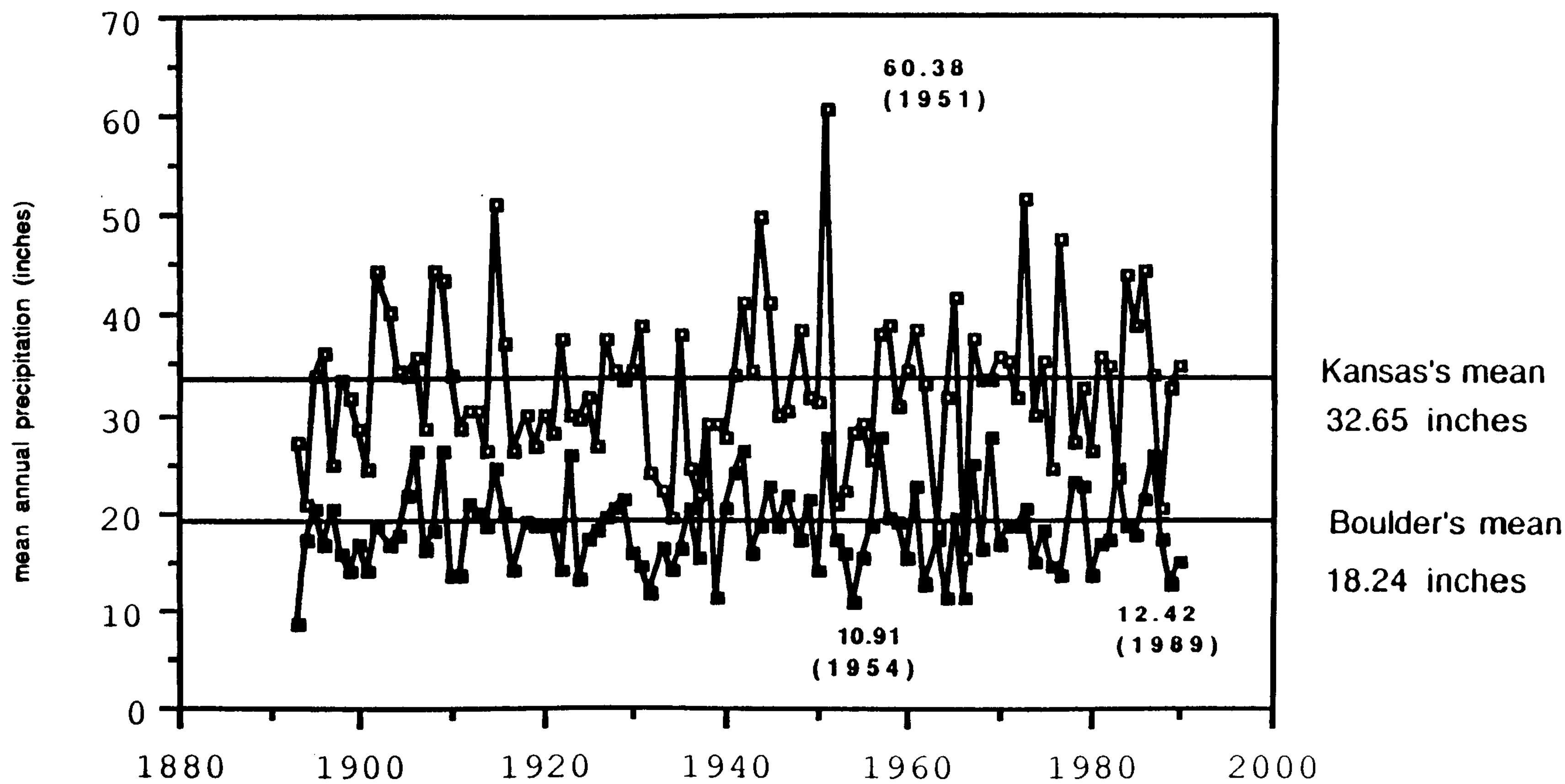

Figure 4. Mean annual precipitation of Kansas and Boulder, recorded from 1893-1990

Table 9. Average maximum snow depth and Average maximum temperature comparisons beteween Boulder(Boulder County) and Kansas(Manhattan County), recorded from 1948-1988 for Boulder and 1900-1988 for Kansas

Locations	Boulder	Kansas
Average Maximum snow depth.	15.9inch.	4.6 inch.
	(39.00cm)	(11.28 cm)
Average Maximum temperature	104°F	116°F
	(40°C)	(47°C)

growing seasons following the burning of Boulder Tallgrass Prairie were unusually dry, especially 1989 when annual precipitation was 12.42 inches(30.47 cm), which closed to record low precipitation of 1890s, 1940s and 1960s. Therefore, the climatic factors may also have been important in controlling species responses in Boulder Tallgrass Prairie in addition to the burning. Addtional evidence showing that the Tallgrass species at Boulder barely exists and does not grow well as compared to the Konza Tallgrass species is the percent cover of Andropogon gerardii. The cover of Andropogon gerardii at Konza and Boulder were 76-81%(Abrams, 1988) and 5% from this study respectively.

Most forbs tended to be enhanced by burning, i.e., Liatris puntata, Echinocereus viridiflorus, Artemisia frigida, Cichorium intybus, Plantago lanceolata, etc. However,the three major weedy forbs of the xeric site: Alyssum minus, Opuntia compressa and Opuntia fragilis, were depressed in the burned xeric site. Alyssum minus was suppressed successfully on the xeric burned site because the plants were burned before seed set.

In contrast, Alyssum minus, Opuntia compressa and Opuntia fragilis, which were not the major weedy forbs of the mesic site were enhanced on the burned mesic site. The enhancement on the mesic site might be due to the great reduction in litter thickness on the mesic site. The average height of litter of the unburned mesic site were 2.31 cm as compared to 0.31 cm of the burned mesic site (personal observation). Plants of low stature, such as Opuntia compressa and Opuntia fragilis may not compete and grow well under such thick cover. Fire also provided the opportunity for annual plants, such as Alyssum minus which exits as buried seeds in soil, to germinate and establish when the space is opened up. On the mesic site, burning also enhanced the two aggressive introduced forbs: Cichorium intybus and Plantago lanceolata. This is probably due to the large seed banks of the two species(Chapter IV). A large amount of seeds germinated and new plants began colonizing the opened space.

SUMMARY

Burning on Boulder Tallgrass Prairie eliminated two major weedy grasses: Bromus spp. and

Poa spp. Native shortgrasses such as Chondrosum(Bouteloua) gracile, Bouteloua curtipendula and Buchloë dactyloides were enhanced after the burn. The responses to burning of tallgrass species at Boulder varied depending on species and habitats. Andropogon gerardii on the xeric site, Sorghastrum avenaceum and Panicum virgatum on the mesic site were depressed by burning. In contrast, Andropogon gerardii on mesic sites and Panicum virgatum on the xeric site were enhanced in the burned plots.

Weedy forbs on the xeric site especially the annual species: Alyssum minus decreased mainly because either plants or seeds were destroyed by fire before seed set. However, on the mesic site, two aggressive species, Cichorium intybus and Plantago lanceolata were increased after the burn as the result of the large seed bank, the source of new generations when the open space was available.

CHAPTER IV

SEED BANK, SEED RAIN

INTRODUCTION

Significance of Seed Bank and Seed Rain

Seed bank by definition is the population of viable seeds in soil(Harper, 1977). Major and Pyott (1966) suggested that a complete description of a plant community must include the buried viable seeds in the soil because the plants occurring in this form are part of the flora. The ecological significance of viable seeds in the soil, lies not only in their association with the past, but also in their bearing on the plant communities likely to develop in the future (Roberts, 1970). The seed bank, is a store of "evolutionary memory", representing a pool of long-lived seeds for individual species which have been laid down by many generations of plants. If disturbance brings a mixture of seeds to the surface, germination requirements are met, the resulting plants will be the progeny of parents that existed at widely different times. The information from seed bank can be applied to solve ecological problems and to plan for proper managements such as, agricultural practice, forestry, and conservation(Chippindale and Milton, 1934; Hassan, 1983; Fenner, 1985)

The ecological significance of seed bank study in natural vegetation was first introduced by Oosting and Humphrey (1940). They found that the species of the early successional phases contribute more to the buried population than do the dominants of the more mature phases. Species vary a great deal in terms of seed lifespans. Some species have evolved the capacity to remain viable for at least decades, as documented by Beal's experiment (Brenchley, 1918 and Kivilaan and Bandurski, 1973).

A general conclusion, based on previous studies of various plant communities, for example, grasslands, pastures, wetlands, and forests, was that there is low correspondence between the composition of vegetation and of its associated seed bank (Harper, 1977; Thompson, 1978; Thompson and Grime, 1979; Fenner, 1985). As a result, Rabinowitz (1981) suggested that seed rain should be more direct and appropriate basis for comparison between the above and below ground populations.

Seed rain by definition is the dispersing seeds forming a "rain" of propagules onto the soil surface (Harper, 1977). Therefore, to understand the dynamics of any single population, it is essential to quantify seed rain and seedling recruitment for comparison with patterns of established vegetation and seed banks.

At present, there are very few records of total seed rain on grassland communities. In Missouri, Rabinowitz and Rapp (1981) found that the majority of common species in the seed rain appeared in the soil bank. In contrast, many of the common elements of the seed bank are not found in the seed rain. O'Shea Stone (1988) compared the seed rain with the seed bank and aboveground vegetation of the semidesert grassland in Arizona. and found no strong correlations among three of them. Fenner (1985) generalized that in frequently disturbed vegetation, there is a greater similarity between seed banks and seed rain than for more stable, mature vegetation. This conclusion is based on the idea that colonizing species tend to produce large seed banks, whereas plants of the later successional stages tend to produce smaller, less persistent seed banks.

There were no previous studies on the effect of burning and seed bank investigated on the Boulder Tallgrass Prairie. In addition, it is interesting to compare the seed bank of Boulder Tallgrass with the seed bank of Konza Tallgrass Prairie, as Konza Prairie represents the largest Tallgrass Prairie which located at the western most border of the principal area where the Tallgrass Prairies exist now a day. A complete understanding of seed bank dynamics must also include an investigation of seed rain. Therefore, the following questions were asked:

1. How large is Boulder seed bank size?
2. Does burning have any effect on seed bank size in terms of species number and frequency?
3. Does Boulder seed bank differ from Konza seed bank?
4. Does seed bank composition correspond to the ground vegetation?
5. Does seed rain composition correspond to the seed bank?

SEED BANK

METHODS

To answer the questions 1 to 4 the bioassay technique was performed. This purpose of this technique is to identify viable seeds in the soil by taking samples and maintaining them at a favourable temperature and stirring at intervals and counting the seedlings as they germinate.

Soil samples were taken from Boulder Tallgrass Prairie and Konza Tallgrass Prairie. Sampling included soils from:

Boulder
1) Unburned xeric site
2) Burned xeric site
3) Unburned mesic site
4) Burned mesic site

Konza
1) Non-burned site
2) Annual burned site
3) 10 year burn cycle site

Bioassay Germination Tests in Greenhouse

For Boulder, at all sites during each monitoring, soil collections were made using a stratified random sampling technique along each transect. This technique was adopted from Bigwood and Inouye (1988) because it provides an adequate degree of precision of seed bank estimation. There were five collection times: August 1988, June and August 1989 and June and August 1990).

For each collection time, 125 soil samples were collected from the burned and unburned xeric and mesic plots. Before the soil samples were taken, litter was removed in order to be certain that only the seeds in soil would be examined. Each sample was removed by using a hand shovel making a soil core of 7cm in diameter and 7cm in depth with the volume of 270ml. The soil samples were stored in paper bags. The germination trials were conducted in the Ramaley greenhouse under natural light conditions. One hundred ml of each soil sample was placed over 100ml of soil-less potting mix in a 3 inch plastic pot. Pots were put in trays filled with water to keep the soil moist. Before seedlings germinated and while the seedlings were small, soil was moistened from below by adding water to the trays. After seedlings were large enough to hold the soil, plants were watered daily by sprinkling. Unidentified seedlings were transplanted to 3 inch individual pots to grow until identifiable.

During the study, seeds and seedlings were photographed. Herbarium plant specimens as well as seed specimens were made for reference purposes. Kodachrome 35 mm slides of the seeds and the herbarium specimens are now deposited in the Herbarium of the University of Colorado at Boulder. Plant nomenclature follows Weber (1990).

For Konza, in June 1990 and November 1990, fifteen soil samples were taken along a 60m transect in the non-burned, burned annually, and 10 year burn cycle sites by means of stratified random sampling. Procedures were performed in the same manner as for Boulder soil samples.

The statistical analyses followed the same procedures described in the preceeding chapter (Chapter III)

RESULTS OF BOULDER SEED BANK BIOASSAY

From 2500 soil samples, there were a total of 105 species(Appendix B.1) comprising 26,665 seedlings: 15,728 were monocots and 10,937 were dicots(Table 10). There were approximately 40 seedlings recovered per liter of soil. Germinated seedlings classified as Native and Introduced are presented in Table 11 and 12. The burned xeric

Table 10. Monocot and Dicot seedlings germinated during 1988-1990. Different letters indicate significant differences between burned and unburned treatment (K-W analysis)

Years	Monocot/Dicot	Unburned xeric		Burned xeric		Unburned mesic		Burned mesic	
1988	Monocots	505	a	573	a	1490	c	1760	c
	Dicots	1101	b	1352	b	404	d	979	d
1989	Monocots	953	a	782	b	2371	d	2501	d
	Dicots	1420	c	1578	c	829	e	1284	f
1990	Monocots	948	a	947	a	1404	c	1494	c
	Dicots	719	b	627	b	253	d	391	d

Table 11. Comparison of germinated seedlings classified as native and introduced species from the xeric unburned and burned plots

	XERIC UNBURN	XERIC BURN	LEVEL OF SIGNIFICANCE
NATIVE SPECIES	2723	3426	$p = 0.02$
INTRODUCED SPECIES	2891	2408	$p = 0.005$

Table 12. Comparison of germinated seedlings classified as native and introduced species from the mesic unburned and burned plots

	MESIC UNBURN	MESIC BURN	LEVEL OF SIGNIFICANCE
NATIVE SPECIES	1490	1734	p=0.63
INTRODUCED SPECIES	5240	6651	p =0.02

plots contained greater seedling numbers of native species and fewer introduced species when compared to the unburned plots. The mesic burned plot showed no significant differences in numbers of native seedlings, but significantly higher in seedlings of introduced species as compared to the unburned plot(Table 11,12).

All the species had a 1% or greater occurence were tested for differences in mean seedling count on the burned and unburned sites by using the Krauskal-Wallis Analysis(Table 13,14). About half of commonly found species of Boulder Tallgrass Prairie's seedlings showed at least once difference in mean seedling counts comparing between the burned and unburned sites (Table 13,14).

The Monte Carlo tests of the CANOCO ordination results indicated that the xeric burned and unburned sites were significantly different in seedling changes($p \leq 0.02$) due to burning from June 1989 to August 1990(Table 15). The mesic burned and unburned sites were only significantly different in seedling counts ($p=0.05$) due to burning in June 1989. Meanwhile, species trends of the mesic site from CANOCO discussed in this study were based on the result of June 1989.

Table 13. Mean seedling ± s.d. comparison between xeric unburned and burned plots (K-W) with the statistical level of significances. The species listed below occurred at least 1% of the the total species occurrences

Species	burn vs no burn	Aug-88 mean± s.d.	signi level	Jun-89 mean± s.d.	signi level	Aug-89 mean± s.d.	signi level	Jun-90	signi level	Aug-90	signi level
Oligosporus pacificus	UB	2.68±2.30		1.38±0.81		1.59±1.16		1.44±0.99		2.10±3.85	
	B	3.39±3.03	*	1.27±0.53	ns	1.88±1.23	*	1.29±0.70	ns	1.58±0.87	ns
Bromus spp.	UB	3.19±2.46		1.08±0.39		03096±3.85		1.72±1.14		4.27±2.86	
	B	2.76±1.92	ns	1.00±0.00	ns	2.89±2.57	*	1.30±0.84	*	2.96±2.40	* *
Juncus bufonius+	UB	1.09±0.29		1.59±1.11		1.29±0.62		1.62±1.30		1.37±0.69	
J.dudleyi	B	1.82±1.56	* *	1.49±1.13	ns	1.58±1.10	ns	1.81±1.75	ns	2.78±2.73	* *
Artemisia frigida	UB	2.35±2.12		1.08±0.28		1.56±1.19		1.12±0.34		1.56±0.94	
	B	2.13±1.67	ns	1.21±0.65	ns	1.75±1.64	ns	1.13±0.34	ns	1.86±1.25	ns
Lepidium densiflorum	UB	1.17±0.48		1.02±0.14		1.24±0.57		1.00±0.00		1.18±0.58	
	B	1.25±0.64	ns	1.05±0.23	ns	1.46±0.91	ns	1.00±0.00	ns	1.34±0.58	ns
Silene antirrhina	UB	1.63±0.97		1.00±0.00		1.57±1.06		1.00±0.00		1.65±0.92	
	B	1.85±1.71	ns	1.14±0.48	ns	1052±1.23	ns	1.00±0.00	ns	1075±1.53	ns
Sporobolus cryptandrus	UB	2.17±1.60		1.65±1.31		1.22±0.43		1.84±1.54		-	
	B	1.00±0.00	* *	1.90±2.00	ns	1.00±0.00	ns	2.11±1.87	ns	1.00±0.00	-
Festuca rubra	UB	2.31±4.52		1.07±0.26		1.73±1.77		1.00±0.00		3.12±2.36	
	B	3.23±2.33	ns	1.37±0.95	ns	2.92±8.14	ns	1.00±0.00	ns	2.21±3.42	ns
Poa spp.	UB	1.44±1.03		1.20±0.77		0.07±0.27		1.00±0.00		3.94±5.79	
	B	1.64±1.65	ns	1.12±0.33	ns	1.44±0.77	ns	1.00±0.00	ns	2.85±2.46	ns
Talinum parviflorum	UB	1.33±0.59		1.35±0.61		1.22±0.65		1.23±0.60		1.37±0.52	
	B	1.10±0.32	ns	1.59±1.10	ns	1.11±0.32	ns	1.36±0.74	ns	1.00±0.00	ns
Camelina microcarpa	UB	1.80±1.15		1.40±0.55		1.44±0.82		-		1.00±0.00	
	B	2.80±3.10	ns	1.50±0.71	ns	2.06±2.83	ns	-	-	1.22±0.44	ns
Verbascum thapsus	UB	1.00±0.00		1.60±1.15		1.00±0.00		1.21±0.52		1.20±0.45	

	burn	Aug-88	signi	Jun-89	signi	Aug-89	signi	Jun-90	signi	Aug-90	signi
Species	vs no	mean± s.d.	level	mean± s.d.	level	mean± s.d.	level		level		level
	burn										
	B	1.00±0.00	ns	1.35±0.57	ns	1.30±0.67	ns	1.53±0.91	ns	1.33±0.50	ns
Erodium cicutarium	UB	2.44±2.00		1.00±0.00		1.61±1.37		1.50±1.00		1.00±0.00	
	B	2.54±2.37	ns	1.33±0.82	ns	2.69±2.36	*	1.00±0.00	ns	1.20±0.45	ns
Tragopogon dubius	UB	1.00±0.00		1.00±0.00		1.16±0.50		1.00±0.00		1.05±0.22	
	B	1.00±0.00	ns	1.00±0.00	ns	1.60±1.01	ns	1.00±0.00	ns	1.15±0.37	ns
Acetosella vulgaris	UB	11.00±14.97		3.53±2.10		5.17±5.87		1.33±0.58		1.86±0.90	
	B	7.00±9.16	ns	1.86±0.90	*	2.75±2.19	ns	1.25±0.50	ns	4.60±3.51	ns
Triodanis perfoliata	UB	1.46±0.83		1.14±0.83		1.54±1.03		1.00±0.00		1.83±0.98	
	B	1.38±1.16	ns	1.25±0.50	ns	1.57±0.75	ns	1.00±0.00	ns	1.00±0.00	ns
Alyssum minus	UB	1.55±0.73		1.67±0.58		4.50±4.41		-		3.30±4.79	
	B	1.40±0.70	ns	1.00±0.00	ns	1.28±0.49	*	-	-	1.10±0.32	*
Sisymbrium altissimun	UB	1.00±0.00		1.00±0.00		1.91±1.95		-		1.14±0.38	
	B	1.00±0.00	ns	1.00±0.00	ns	2.50±3.45	ns	-	-	1.25±0.50	ns
Monarda pectinata	UB	1.20±0.42		1.00±0.00		1.44±1.31		1.00±0.00		1.50±0.71	
	B	1.28±0.57	ns	1.00±0.00	ns	1.31±0.55	ns	1.00±0.00	ns	1.00±0.00	ns
Juncus marginatus	UB	-		1.00±0.00		-		1.08±0.08		1.50±0.71	
	B	-	-	1.00±0.00	ns	-	-	1.00±0.00	ns	1.00±0.00	*
Erigeron flagellaris	UB	1.17±0.41		1.37±0.74		1.00±0.00		-		1.33±0.58	
	B	1.17±0.41	ns	1.11±0.33	ns	1.55±0.89	*	1.00±0.00	-	1.10±0.32	ns
Plantago patagonica	UB	1.11±0.33		1.33±0.58		1.31±0.48		-		-	
	B	1.36±0.66	ns	1.00±0.00	ns	1.25±0.67	ns	-	-	1.22±0.44	-
Senecio spartioides	UB	1.00±0.00		-		1.00±0.00		-		1.00±0.00	
	B	1.14±0.38	ns	1.00±0.00	-	1.12±0.35	ns	-	-	-	-
Juncus arcticus	UB	-		1.67±0.58		3.00±2.00		1.00±0.00		-	
	B	-	-	1.12±0.35	ns	1.00±0.00	ns	1.08±0.28	ns	1.00±0.00	-

Table 13 cont.

Species	burn vs no burn	Aug-88 mean± s.d.	signi level	Jun-89 mean± s.d.	signi level	Aug-89 mean± s.d.	signi level	Jun-90	signi level	Aug-90	signi level
Linaria canadensis	UB	1.75±1.75		2.00±1.41		1.00±0.00		-		1.50±0.71	
	B	1.17±0.41	ns	-	-	1.48±1.08	ns	-	-	-	-

ns=non significant, *=P-value≤0.05, **=P-value≤0.01, ***=P-value≤0.

Table 14. Mean seedling±s.d. comparison between the mesic unburned and burned plots(K-W) with the statistical level of significances. The species listed below occurred at least in 1% of the total species occurrences

Species	burn vs nonburn	Aug-88 mean± s.d.	signif. level	Jun-89 mean± s.d.	signif. level	Aug-89 mean± s.d.	signif. level	Jun-90	signif. level	Aug-90	signif. level
Poa spp.	UB	5.18±4.38		3.36±2.68		4.17±4.29		4.52±3.84		5.31±7.91	
	B	7.05±7.81	ns	3.07±2.51	ns	4.57±4.03	*	4.06±2.88	ns	4.81±3.11	ns
Juncus bufonius+	UB	2.62±2.43		1.99±1.38		1.54±1.16		2.28±2.50		2.42±3.81	
J.dudleyi	B	1.79±1.21	*	2.30±2.01	ns	1.89±1.21	*	2.36±2.53	ns	2.43±3.04	ns
Dianthus armeria	UB	1.67±1.23		1.83±2.29		1.83±1.40		2.20±1.98		1.59±1.01	
	B	1.07±0.27	ns	1.64±1.24	ns	1.92±1.53	ns	1.68±1.32	ns	2010±1.67	ns
Plantago lanceolata	UB	1.06±0.34		1.36±0.86		1.35±0.63		1.19±0.40		1.09±0.30	
	B	1.59±1.16	* *	1.35±0.89	ns	1.59±1.04	ns	1.73±1.40	ns	1.36±0.68	ns
Camelina microcar-	UB	2.14±1.35		1.28±0.83		1.26±0.56		-		1.00±1.00	
pa	B	1.36±0.66	* *	1.20±0.42	ns	1.32±0.60	ns	-	-	1.25±2.50	ns
Bromus spp.	UB	3.29±3.27		1.14±0.38		2.29±1.65		1.33±0.58		1.17±0.39	
	B	2.50±1.71	ns	1.20±0.45	ns	1.54±1.03	ns	1.00±0.00	ns	1.11±0.33	ns
Sporobolus asper	UB	1.00±0.00		1.24±0.75		1.00±0.00		1.28±0.57		2.00±0.00	
	B	-	-	1.00±0.00	ns	1.67±1.15	ns	1.00±0.00	ns	1.00±0.00	ns
Veronica peregrina	UB	1.39±0.70		1.65±0.10		1.07±0.26		1.28±0.75		2.00±0.00	
	B	1.48±0.80	ns	2.74±0.81	ns	2.05±2.28	*	1.09±0.30	ns	1.43±0.79	ns
Alyssum minus	UB	1.75±0.87		1.08±0.28		1.35±0.88		-		1.17±0.41	
	B	1.33±0.58	ns	1.17±0.41	ns	1.33±0.82	ns	-	-	1.25±0.62	ns
Sorghastrum avena-	UB	1.23±0.59		1.17±0.41		1.00±0.00		-		2.50±1.73	
ceum	B	1.33±0.52	ns	1.00±0.00	ns	-	-	-	-	-	-
Silene antirrhina	UB	1.37±0.74		1.00±0.00		1.27±0.65		-		2.00±1.33	
	B	1.48±1.20	ns	1.00±0.00	ns	1.60±1.25	ns	-	-	1.44±0.73	ns
Hypericum perfora-	UB	3.48±3.43		1.00±0.00		-		-		-	
tum	B	5.01±4.50	ns	-	-	-	-	-	-	-	-
Verbascum thapsus	UB	1.00±0.00		1.50±0.97		1.00±0.00		1.20±0.45		1.00±0.00	
	B	1.00±0.00	ns	1.12±0.33	ns	1.00±0.00	ns	1.00±0.00	ns	-	-

Table 14 cont.

Species	burn vs non burn	Aug-88 mean± s.d.	signif. level	Jun-89 mean± s.d.	signif. level	Aug-89 mean± s.d.	signif. level	Jun-90	signif. level	Aug-90	signif. level
Cichorium intybus	UB	1.18±0.40		1.00±0.00		1.00±0.00		1.33±0.82		1.00±0.00	
	B	1.67±1.68	ns	1.11±0.39	ns	1.06±0.25	ns	1.17±0.41	ns	1.00±0.00	ns
Acetosella vulgaris	UB	3.50±1.91		1.67±0.87		1.37±0.52		1.00±0.00		3.00±2.83	
	B	1.64±0.81	ns	1.37±0.74	ns	1.64±0.74	ns	1.00±0.00	ns	2.67±1.15	ns
Draba reptans	UB	1.08±0.28		1.00±0.00		1.00±0.00		1.00±0.00		1.00±0.00	
	B	1.21±0.42	ns	2.00±0.00	*	1.25±0.50	ns	-	-	1.00±0.00	ns
Tragopogon dubius	UB	1.28±0.75		1.00±0.00		1.12±0.35		1.00±0.00		1.00±0.00	
	B	1.23±0.44	ns	1.00±0.00	ns	1.50±1.00	ns	-	-	2.00±0.00	ns
Festuca rubra	UB	1.57±1.13		1.00±0.00		1.50±0.53		-		1.00±0.00	
	B	1.22±0.44	ns	2.00±2.00	ns	1.00±0.00	*	1.50±0.71	-	1.00±0.00	ns
Juncus arcticus	UB	-		1.00±0.00		2.00±0.00		1.00±0.00		-	
	B	1.00±0.00	-	1.13±0.52	ns	2.60±2.51	ns	1.35±0.80	ns	1.17±0.41	-
Grindelia subalpina	UB	1.00±0.00		1.00±0.00		1.00±0.00		-		-	
	B	1.00±0.00	ns	1.11±0.33	ns	1.12±0.35	ns	1.00±0.00	-	1.00±0.00	-
Lactuca serriola	UB	1.00±0.00		1.50±1.00		1.37±0.74		-		-	
	B	1.00±0.00	ns	1.00±0.00	ns	1.24±0.51	ns	-	-	-	-
Lepidium densiflor-	UB	1.33±0.52		1.00±0.00		1.00±0.00		-		1.00±0.00	
um	B	1.00±0.00	*	1.00±0.00	ns	1.00±0.00	ns	-	-	1.00±0.00	ns
Erodium cicutarium	UB	1.00±0.00		1.00±0.00		1.00±0.00		1.00±0.00		1.00±0.00	
	B	1.50±1.20	ns	1.00±0.00	ns	1.50±0.55	ns	-	-	-	-

ns=non significant, *=P-value≤0.05, **=P-value≤0.01, ***=P-value≤0.001

Table 15. The significant differences in bioassay seed bank between burned and unburned sites by using Monte Carlo permutation test

	August 1988	June 1989	August 1989	June 1990	August 1990
Xeric	p= 0.34	p= 0.05	p= 0.01	p= 0.02	p= 0.01
Mesic	p= 0.44	p= 0.05	p= 0.84	p= 0.10	p= 0.14

In order to analyze the seed bank changes after the burn, the results from the two analyses: K-W test and CANOCO were combined. Species were categorized as: Fire enhanced species, Fire indifferent species and Fire depressed species respectively. Fire enhanced species are the species which either have significantly higher seedling count(K-W) in the burned plots than in the unburned plots or tend to have higher seedling count or higher frequency(CANOCO) of seedling found in the burned than in the unburned plots. In contrast, Fire depressed species are the species which either have lower seedling count(K-W) or tend to have lower seedling count or less frequency (CANOCO) in the burned than in the unburned plots. Fire indifferent species are the species that did not differ in either seedling count or frequency after the burn. Species lists based on the seed bank fire responses are shown in Table 16 and 17.

Schematic ordination diagrams based on Canonical Correspondence Analysis of the bioassay seedlings with respect to the burning are shown in Appendix B.5.

Table 16. Species list of seedlings germinated under Bioassay method, of the xeric site categorized as: Fire enhanced, Fire indifferent and Fire depressed species
*= p≤0.05, **= p≤0.01 (K-W analysis)

FIRE ENHANCED	FIRE INDIFFERENT	FIRE DEPRESSED
Artemisia frigida	Camelina microcarpa	Alyssum minus *
Erigeron flagellaris *	Erodium cicutarium *	Bromus spp.**
Festuca rubra	Juncus marginatus	Triodanis perfoliata
Juncus arcticus	Oligosporus pacificus	
Juncus bufonius+J.dudleyi**	Senecio spartioides	
Lepidium densiflorum *	Sisymbrium altissimum	
Monarda pectinata	Sporobolus cryptandrus	
Plantago patagonica	Talinum parviflorum	
Poa spp.	Verbascum thapsus	
Silene antirrhina		
Tragopogon dubius *		

Table 17. Species list of seedlings germinated under Bioassay method from the mesic site categorized as: Fire enhanced Fire indifferent and Fire depressed species
*= p≤0.05 (K-W analysis)

FIRE ENHANCED	FIRE INDIFFERENT	FIRE DEPRESSED
Cichorium intybus	Silene antirrhina	Alyssum minus
Dianthus deltoides		Bromus spp.
Epilobium ciliatum		Camelina microcarpa
Festuca rubra		Draba reptans
Grindelia subalpina		Juncus bufonius+J.dudley
Juncus arcticus		Medicago lupulina
Lepidium densiflorum		Poa spp.
Neolepia campestre		Sporobolus asper
Plantago lanceolata		
Verbascum thapsus		
Veronica peregrina *		

DISCUSSION

Seed bank as measure by bioassay of Bromus spp., the major weedy grass of the xeric site was depressed by burning. This was confirmed by both K-W analysis and CANOCO analysis. However, from the five study periods, seedling counts of Poa spp., the major weedy grass of the mesic site did not show significant differences(K-W analysis), except once in August 1989. At that time the seedling count was higher in the burned than in the unburned mesic site. According to CANOCO analysis, Poa spp. showed trend of decreasing representation through out the five collection times. Burning did not appear to significantly reduced the seed bank size of Poa spp. but it showed the decreasing trend detected by the CANOCO analysis through out the collection times. The native tallgrass species, Andropogon gerardii and Sorghastrum avenaceum showed no differences in mean seedling numbers on burned and unburned sites. Dominant grasses of Boulder Tallgrass Prairie have very small seed bank size. Only 0.33% of the total germinated seedlings belonged to the dominant grasses of this prairie(Table 18). This finding leads me to persue further study on seed reproduction of the two

Table 18. Seedlings of the dominant grasses of Boulder Tallgrass Prairie germinated under the Bioassay method during 1988-1990

Sites	Stipa comata	Andropogon gerardii	Sorghastrum avenaceum	Total
Xeric unburned	6	1	1	**8**
Xeric burned	15	4	0	**19**
Mesic unburned	0	3	50	**53**
Mesic burned	0	0	9	**9**
Total	**21**	**8**	**60**	**89**

The total seedling count of all species during 1988-1990= 26,665 seedlings.
Seed bank of the dominant grasses was approximately **0.33%** of the total seed bank

dominant tallgrasses: Andropogon gerardii and Sorghastrum avenaceum. This topic is discussed in Chapter V.

Seed banks of most forbs especially the ones on the xeric site tended to be enhanced by burning. About half of the most common seedlings of the xeric site showed significantly differences in seedling counts(K-W analysis) between the burned and the unburned plot at least once during the five collection times(Table 13). On the mesic site about one third of the common species showed differences in seedling counts at least once during this study(Table 14). Out of 43 of most common species, there were 22 species categorized as Fire enhanced species, 11 species categorized as Fire depressed species and 10 species categorized as Fire indifferent species(Table 16,17). The seed bank of the major weedy forbs on the xeric site, Alyssum minus, was also depressed by fire. This result corresponds with the aboveground result mentioned in Chapter III. Spring burning of Boulder Tallgrass Prairie successfully controlled the population of the annual spring blooming plants, such as Bromus spp. and Alyssum minus. Burning not only controlled the aboveground population but also caused a smaller seed bank in the burned plots.

There are two possible ways that can cause reducing in seed bank sizes. First, seeds might be lost from the seed bank by germination following the fire. In that case, the aboveground cover for that particular species should be greater than that of the unburned plot, for example, the Medicago lupulina. I noticed a lot of seedlings of Medicago lupulina(one of the Fire depressed species) in the field while I was monitoring the vegetation. Therefore, seed bank was smaller in the burned site than the unburned site because of the loss due to germination. Also, Sporobolus asper which has a small seed bank in the burned than the unburned plot has vegetation cover greater in the burned than the unburned plot. It seems likely that seeds were recruited from seed bank by post fire seed germination in the burned plot. A second possible factor causing smaller seed bank in the burned plot is that the individuals were burned before setting seeds. In this case, the aboveground cover of that species should be less in the burned than in the unburned plot. This may be the case for Bromus spp., as both vegetation and seed bank were less in the burned than in the unburned xeric site.

KONZA SEED BANK

A total of 90 soil samples were taken in June 1990 and November 1990 from non-burn, ten year burn cycle and annually burn sites. Seeds of the seed bankgermination were identified with the bioassay method in the same manner as Boulder's soil samples.

RESULTS

A total of 28 species comprising 159 seedlings were found: 126 were monocots, 30 were dicots and 3 were unidentifiable (Appendix B.2). A total of 20 native and 8 introduced species were identified. Seventy one seedlings were from native plants (65.14%), 35 from introduced species(32.11%) and 3 unknowns(2.75%). In contrast, 35% and 65% of the Boulder seed bank belonged to native and introduced species respectively.

The Boulder Tallgrass seed bank had 3451 seeds/m^2 and Konza Tallgrass seed bank had 459 seeds/m^2. My preliminary explanation for this remarkable difference is that as the undisturbed community reaches a stable stage, long lived perennial native species will maximize vegetative rather than sexual reproduction. By contrast, the Boulder Prairie contains many annuals and short lived perennial species that tend to have high seed production in comparison with the long lived perennial grasses.

Among the Konza sites, the annual-burned site had the smallest seed bank(12 seedlings/0.9 liter of soil). It was approximately one-sixth of the size of either non-burned(83 seedlings/0.9liter of soil) or ten year burn cycle(73 seedlings/0.9liter of soil). In the annual-burned site, neither _Poa_ spp. or _Bromus_ (the exotic grasses) seeds was found. The non-burned and 10-yr-burned sites are similar to each other in their species composition and total seedlings. However, the ten yr-burned site had fewer numbers of _Poa_ spp. and _Bromus_ spp.than the non-burned site. In addition, 10 yr-burned site had more _Andropogon gerardii_(7 vs 3) and _Sorghastrum avenaceum_(2 vs 0) germinated seedlings than non-burned site.

Many short-lived annuals and perennials, were represented in the Boulder seed bank and could potentially, take over the relictual prairie.

Although, Konza Prairie seed bank is 3 times smaller than the Boulder seed bank, the Konza seed bank has a higher ratio of tallgrass seeds in the seed bank as compared to Boulder seed bank. This suggests that Konza seed reservoir, even though small in size, will favor perpetuation of the Tallgrass Prairie as opposed to the situation for Boulder's Tallgrass Prairie, where the introduced species are favored in its seed bank.

Boulder's Prairie has very large seed bank, which contains approximately 3451 seedlings/m^2. However, only 0.33% belong to native grasses. According to this result, it seems less likely that Boulder Tallgrass Prairie could reproduce itself by means of sexual reproduction. If the vegetative parts of these grasses are destroyed or lost in some way such as overgrazing or ploughing, the whole community might not come back again. In order to help restore and enhance this Tallgrass Prairie, I suggest 3 management plans: 1) seeding and transplanting 2) Burning is required to eliminate the excess litter. 3) Hand-picking weeds is recommended, especially when weedy species are young or just start to establish after germination.

SUMMARY

Burning helped eliminated aboveground vegetation of major weedy species as well as seed bank reduction.

The Boulder seed bank is extremely different from the Konza seed bank especially in terms of natives vs introduced species.

TWO ALTERNATIVE METHODS OF SEED BANK ESTIMATION

Species distributions describing by vegetation analysis and seed bank study, show remarkable differences in frequency of occurrence. The 50 most frequently occurring species in each study are listed in Table 19. The dominant native grasses, for example, Chondrosum gracile, Andropogon gerardii, Stipa comata, Sorghastrum avenaceum and Panicum virgatum are ranked in the order of 1,3,4,15 and 18 respectively in the vegetation cover frequency of occurrence. In contrast, they ranked in the order of 86,70,46,35 and no rank for Panicum virgatum(no seedlings of this species germinated from the seed bank) in the seed bank. The seed bank is the source of the above ground vegetation, and conversely, the aboveground

Table 19. The top 20 species occurring during vegetation monitoring and seedling bioassay methods

SPECIES	VEGETATION	BIOASSAY
Chondrosum(Bouteloua) gracile	1	86
Poa spp.	2	2
Andropogon gerardii	3	70
Stipa comata	4	46
Bromus spp.	5	4
Plantago lanceolata	6	7
Cichorium intybus	7	20
Echinocereus viridiflorus	8	42
Artemisia frigida	9	5
Sporobolus asper	10	27
Ambrosia artemisiifolia	11	53
Aster vulgaris	12	-
Carex pensylvanica ssp. heliophila	13	-
Oligosporus pacificus	14	3
Sorghastrum avenaceum	15	35
Buchloë dactyloides	16	95
Panicum virgatum	17	-
Opuntia fragilis	18	-
Tragopogon dubius	19	13
Alyssum minus	20	15
(-) = THE SPECIES WERE NOT DETECTABLE UNDER THE BIOASSAY METHOD		

vegetation is the source of seed bank. However, the lack of close correspondence between seed bank and vegetation was detected, and therefore, led me to ask following questions:

1. Does the bioassay method represent an accurate measurement of seed bank? The actual composition of seed bank might not be revealed by the bioassay if there is seed dormancy. For dorminant seeds to germinate, particular requirements, such as the fluctuating temperature, light, scarification, and etc. must be met (Bradbeer, 1988) Those seeds unable to germinate under the conventional conditions required by most seeds, such as the conditions provided in the Bioassay method would not be detected. To provide an alternative measure of the seed bank that does not require germination investigate whether or not, the Mechanical separation method was called for. The results from this method can be compared with the results from the Bioassay method in terms of species compositions and species frequency occurrences.

2. The measurement of frequency of occurrence of standing vegetation may not be a proper descriptor of input to seed bank. Rabinowitz(1981)

suggested that the comparison of the species composition of seed bank and that of emerged adult plants are not comparable because the counting units are not equivalent. The rain of seeds onto the soil is a more direct and appropriate basis for assessment of similarity of the above ground and below ground populations because the seed rain is the most proximate source of the seed bank (Rabinowitz, 1981). In my study, the seed rain was chosen as a direct measurement of the input into seed bank. The result then is compared with the seed bank measured from both the Bioassay and the Mechanical separation methods.

METHODS

Alternative seed bank measure--Mechanical Separation Technique

For comparison with the conventional bioassay described earlier, a floating technique (Malone, 1967) for seed removal was performed. The floating technique, theoretically, allowed identification of all (or most) seeds in the soils including those that did not germinate in the bioassay.

Ten soil samples per site per collection time were randomly chosen from Boulder total soil samples. These soil samples were subsets of the soils tested under the bioassay method, therefore, they can be directly compared. For this purpose, each soil sample was split in half(100ml) and two tests were run on the halved samples. The steps for mechanical separation are as follows:

One hundred ml of a soil sample was placed in a solution of 10g sodium hexametaphosphate (Calgon), 5g sodium bicarbonate, and 25g magnesium sulphate (Epsom salts), dissolved in 200 ml of tap water. Once the soil sample was added, it was stirred vigorously with a glass rod for about two minutes, then the soil particles were allowed to settle. The debris containing the seeds floated to the top of the solution. The supernatant was then decanted on to filter paper and filtered with suction. The flotation and suction steps were repeated three times. The filter disks were scanned under a Zeiss dissecting microscope, and seeds were sorted into species when possible, or genera. Some seeds that were not identifiable by species were grouped together because of the similarity in their seed morphology as follows:

Poa compressa and *Poa pratensis*

Anisantha(Bromus) tectorum and Bromus japonicus

Oligosporus pacificus and Artemisia frigida

Juncus bufonius and Juncus dudleyi

Seeds obtained from soil samples were identified using seed manuals (Martin and Barkley, 1961; Montgomery, 1977) and the reference seed collection made at Boulder tallgrass prairie during this study. This seed collection is now deposited at the herbarium of the University of Colorado at Boulder. Seeds recovered from the soil were also dissected to determine if they contained endosperm and embryos; such seeds are referred to as viable seeds.

Because the data were not normally distributed, non-parametric tests were required, i.e. (1)the Non-parametric Spearman's Rank Correlation Coefficient(Sokal and Rohlf, 1981) for testing correlations of seed/seedling counts and (2) Kolmogorov-Smirnov two sample test for differences in species frequency distribution between the two methods. The similarity between Bioassay, Mechanical methods was calculated by using Czekanowski Coefficient (Causton, 1988). The range of the coefficient is from 0(complete dissimilarity) to 1(complete identity).

SEED RAIN AND SEED BANK

Seed Rain was sampled by trapping seeds monthly in the field from August to November in 1988, and from June to November in 1989 and 1990. The traps consisted of 10 X 10 X 1 cm wooden boxes. Hardware cloth was fastened over the top of the seed traps, allowing seeds to enter, but preventing access by vertebrate granivores. This trap was designed by Dr. Ron Pullium, University of Georgia. Traps were placed at nine points in a diagonal across each burned and unburned plot. Seed traps were emptied monthly from June to November, except in 1988 when the collections were made from August to November. Seeds were stored in coin envelopes at room temperature. Each sample was sorted by hand under a dissecting microscope. The seeds were identified by species and counted.

The Spearman's Rank Correlation Coefficient and Czekanowski coefficient were performed to test and calculated for any correlation and similarity of species representatives between the seed rain, bioassay and mechanical separation methods.

Kolmogorov-Smirnov two sample test was additionally used to test for any differences in frequency distributions between the seed rain method and the other two methods, i.e. bioassay, and mechanical methods.

RESULTS

Numbers of seeds or seedling counts per species from Bioassay, Mechanical Separation and Seed Rain are listed in Table 20. The Spearman's Rank Correlation Coefficient showed highly significant negative correlations ($p \leq 0.001$) between paired comparisions of the three methods(Figure 5). Furthermore, Czekanowski's Coefficient indicated little similarity among the three methods(Figure 5). The result from mechanical separation and seed rain comparision represented the lowest similarity. To further test if this low similarity might be caused by the frequency distribution differences, Kolmogorov-Smirnov two

sample test was performed. The species that showed significant difference in frequency distribution between each paired-comparison among the methods were listed in Tables 21-23.

Table 20. Species lists and numbers of seeds or seedlings counts from Bioassay (n=160), Mechanical separation(n=160) and Seed rain(n=144). Species in Bioassay were listed according to the frequency of occurrences from the highest to the lowest. The numbers in parenthesis means no of seeds or seedlings been found from that particular methods

Bioassay	rank	Mechanical Separation	rank	Seed Rain	rank
Poa spp.(445)	1	Poa spp. (113)	4	Poa spp. (713)	2
Juncus bufonius+J.dudleyi(246)	2	Juncus bufonius+J.dudleyi (287)	1	Juncus bufonius+J.dudleyi (3)	40
Artemisia frigida+		Artemisia frigida+		Artemisia frigida+	
Oligosporus pacificus (127)	3	Oligosporus pacificus (62)	10	Oliosporus pacificus (969)	1
Bromus spp. (117)	4	Bromus spp. (139)	3	Bromus spp. (447)	3
Lepidium densiflorum (48)	5	Lepidium densiflorum (4)	32	Lepidium densiflorum (218)	6
Silene antirrhina (41)	6	Silene antirrhina(62)	9	Silene antirrhina (9)	30
Cichorium intybus (39)	7	Cichorium intybus (25)	18	Cichorium intybus (304)	4
Dianthus armeria (39)	8	Dianthus armeria (92)	5	Dianthus armeria (28)	16
Plantago lanceolata (32)	9	Plantago lanceolata (36)	14	Plantago lanceolata (221)	5
Juncus arcticus (29)	10	Juncus arcticus (3)	37	_	_
Verbascum thapsus (26)	11	_	_	_	_
Festuca rubra (23)	12	_	_	Festuca rubra (54)	12
Linaria canadensis (23)	13	_	_		_
Tragopogon dubius (22)	14	Tragopogon dubius (4)	34	Tragopogon dubius (10)	29
Alyssum minus (19)	15	Alyssum minus (2)	47	Alyssum minus (64)	11
Sisymbrium altissimum (19)	16	_	_	Sisymbrium altissimum (1)	53
Veronica perigrina (18)	17	_	_	_	_
Camelina microcarpa (17)	18	_	_	_	_
Erigeron flagellaris (15)	19	_	_	Erigeron flagellaris (2)	43
Mollugo verticillata (12)	20	Mollugo verticillata (2)	42	_	_
Talinum parviflorum (11)	21	Talinum parviflorum (26)	17	_	_

Table 20. cont.					
Bioassay	rank	Mechanical Separation	rank	Seed Rain	rank
Sporoborus asper (11)	22	Sporobolus asper (40)	12	Sporobolus asper (170)	7
Acetosella vulgaris (10)	23	Acetosella vulgaris (44)	11	Acetosella vulgaris (22)	21
Dischanthelium oligosanthes		Dischanthelium oligosanthes		–	–
var, wilcoxianum (8)	24	var. wilcoxianum (17)	24	–	–
Plantago patagonica (8)	25	Plantago patagonica (18)	22	Plantago patagonica (12)	27
Monarda pectinata (7)	26	Monarda pectinata (34)	15	Monarda pectinata (1)	50
Agrostis gigantea (7)	27	–	–	Agrostis gigantea (75)	9
Echinocereus viridiflorus (7)	28	Echinocereus viridiflorus (69)	8	Echinocereus viridiflorus (1)	51
Erodium cicutarium (7)	29	Erodium cicutarium (75)	7	–	–
Cerastium strictum (6)	30	–	–	Cerastium strictum (19)	22
Cichorium intybus (5)	31	–	–	–	–
Juncus marginatus (5)	32	Juncus marginatus (5)	31	–	–
Grindelia subalpina (5)	33			–	–
Nasturium officinale (4)	34	–	–	–	–
Andropogon gerardii (4)	35	–	–	Andropogon gerardii (7)	33
Epilobium ciliatum (4)	36	–	–	–	–
Senecio spartioides (4)	37	–	–	Senecio spartioides (25)	17
Lappula redowskii (4)	38	Lappula redowskii (11)	25	Lappula redowskii (1)	49
Triodanis perfoliata (4)	39	–	–	–	–
Unknown dicots (4)	40	Unknown dicots (3)	39	–	–
Oreocarya virgata (3)	41	Oreocarya virgata (1)	59	–	–
Typha spp. (3)	42	–	–	–	–
Ambrosia artemisiiflora (3)	43	Ambrosia artemisiifolis (21)	21	–	–
Stipa comata (3)	44	Stipa comata (24)	20	Stipa comata (65)	10
Taraxacum officinale (3)	45	Taraxacum officinale (1)	65	–	–
Neolepia campestre (3)	46	Neolepia campestre (25)	19	–	–
Sorghastrum avenaceum (2)	47	Sorghastrum avenaceum (3)	40	Sorghastrum avenaceum (23)	19

Table 20. cont.

Bioassay	rank	Mechanical Separation	rank	Seed Rain	rank
Trisetum spicatum (2)	48				
Lomatium occidentale (2)	49				
Gnaphalium stramineum (2)	50				
Hypericum perforatum (2)	51			Hypericum perforatum (24)	18
Potentilla anglica (2)	52				
Draba reptans (2)	53	Draba reptans (2)	48		
Artemesia ludoviciana (1)	54				
Mariscus fendlerianus (1)	55				
Bouteloua gracilis (1)	56	Bouteloua gracilis (1)	51	Bouteloua gracilis (14)	25
Eleocharis palustris (1)	57	Eleocharis palustris (32)	16		
Chamaesyce serpyllifolia (1)	58				
Carex sp. (1)	59	Carex spp. (9)	26		
Unknown monocots (1)	60				
Cirsium arvense (1)	61	Cirsium arvense (4)	36	Cirsium arvense (1)	48
Died dicots (1)	62				
Androsace occidentalis (1)	63	Androsace occidentalis (1)	64		
Lactuca serriola (1)	64			Lactuca serriola (13)	26
Tradescantia occidentalis (1)	65	Tradescantia occidentalis (1)	61		
Medicago lupulina (1)	66	Medicago lupulina (8)	27	Medicago lupulina (19)	23
Critesion brachyantherum (1)	67	Critesion brachyantherum (1)	63		
Calylophus serrulata (1)	68				
Verbena bracteata (1)	69	Verbena bracteata (3)	38		
Oenothera villosa (1)	70			Oenothera villosa (8)	32
		Sporobolus cryptandrus (215)	2	Sporobolus cryptandrus (28)	15
		Chenopodium leptophyllum (81)	6	Chenopodium leptophyllum (10	8
		Camelina microcarpa (43)	13	Camilina microcarpa (42)	13
		Cyperus esculentus (18)	23		

Table 20. cont.

Bioassay	rank	Mechanical Separation	rank	Seed Rain	rank
_	_	Dalea purpurea (8)	28	_	_
_	_	Juncus torreyi (6)	29	_	_
_	_	Erysimum capitatum (5)	30	Erysimum capitatum (11)	28
_	_	Oxytropis lambertii (4)	33	_	_
_	_	Buchloë dactyloides (4)	35	_	_
_	_	Iva axillaris (2)	41	_	_
_	_	Argemone polyanthemos (2)	43	_	_
_	_	Podospermum lacinatum (2)	44	Podospermum laciniatum (2)	42
_	_	Astragalus sp. (2)	45	_	_
_	_	Carex praegracilis (2)	46	_	_
_	_	Genum sp. (1)	49	_	_
_	_	Physalis sp. (1)	50	_	_
_	_	Dalea candida (1)	52	_	_
_	_	Juncus tenius (1)	53	_	_
_	_	Lithospermum incisum (1)	54	_	_
_	_	Grindilia squarrosa (1)	55	_	_
_	_	Panicum virgatum (1)	56	Panicum virgatum (23)	20
_	_	Elymus trachycalus (1)	57	Elymus trachycalus (1)	46
_	_	Polygonum arenastrum (1)	58	_	_
_	_	Psoralidium tenuiflorum (1)	60	Psoralea tenuiflorum (6)	34
_	_	Conyza cannadensis (1)	62	Conyza cannadensis (36)	14
_	_	Rumex crispus (1)	66	_	_
_	_	_	_	Phyla cuneifolia (14)	24
_	_	_	_	Heterotheca villosa (8)	31
_	_	_	_	Aristida purpurea (4)	35

Table 20. cont.

Bioassay	rank	Mechanical Separation	rank	Seed Rain	rank
–	–	–	–	Oligoneuron rigidum (3)	36
–	–	–	–	Daucus carota (3)	37
–	–	–	–	Liatris punctata (3)	38
–	–	–	–	Solidago spp. (3)	39
–	–	–	–	Gutierrezia sarothrae (3)	41
–	–	–	–	Centauria diffussa (2)	44
–	–	–	–	Carex pensylvanica subsp.	
–	–	–	–	heliophila (2)	45
–	–	–	–	Muhlenbergia arenicola (1)	47
–	–	–	–	Lupinus argenteus (1)	52

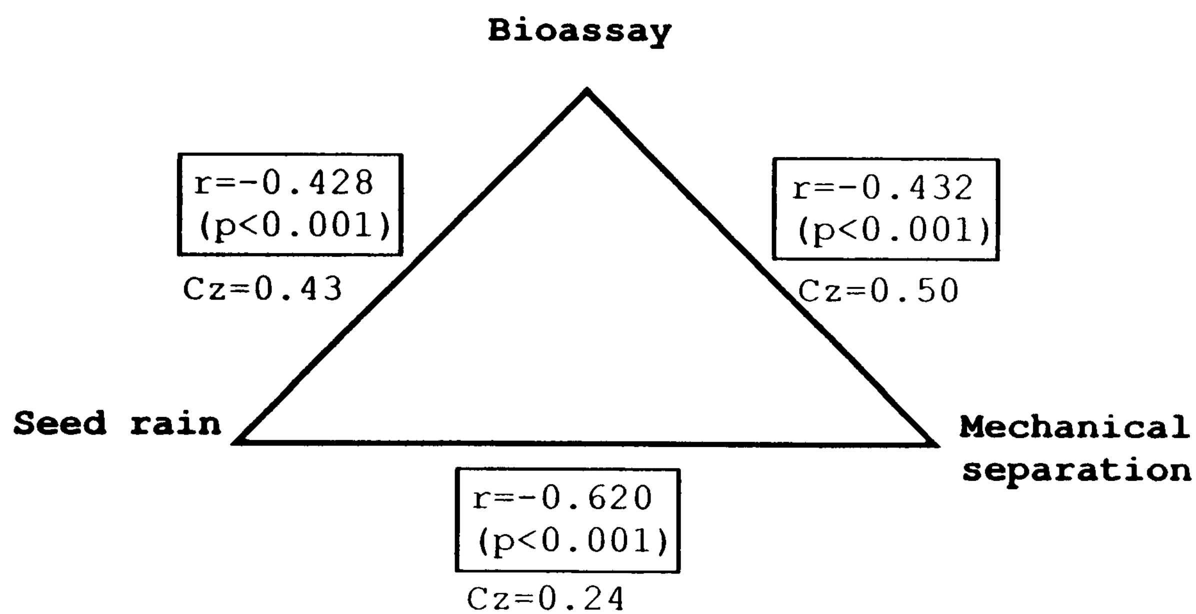

Figure 5. Diagram showing the Spearman's correlation coefficient value (r) and the Czekanowski's coefficient value (Cz) comparisons between the Bioassay, Mechanical separation and seed rain

Table 21. Frequency of seeds and seedlings comparison between Bioassay and Mechanical Separation methods and significant value of Kolmogorov- Smirnov test for differences in frequency distributions

Species	Bioassay	Mechanical	Significance
Oligosporus pacificus+			
Artemisia frigida	125	61	* * *
Monarda pectinata	7	34	* *
Tragopogon dubius	22	4	* * *
Lepidium densiflorum	48	5	* * *
Erodium cicutarium	7	75	* *
Alyssum minus	19	2	* *
Camelina microcarpa	17	43	* *
Verbascum thapsus	26	0	* * *
Erigeron flgellaris	16	0	* * *
Senecio spartioides	4	0	*
Sisymbrium altissimum	19	0	*
Linaria cannadensis	23	0	*
Sporobolus asper	17	43	* *
Grindelia squarrosa	5	0	*
Festuca rubra	23	0	* * *
Cichorium intybus	5	25	* * *
Sporobolus cryptandrus	40	228	* * *
Chenopodium leptophyllum	0	81	* * *
Neolepia campestre	3	25	* * *
Poa spp.	456	120	* * *
Medicago lupulina	1	8	*
Juncus marginatus	5	0	*
Juncus bufonius+J.dudleyi	248	287	* * *
Ambrosia artemissiifolia	5	23	* * *
Stipa comata	3	24	* * *
Veronica peregrina	18	0	* * *
Epilobium ciliatum	4	0	*
Andropogon gerardii	9	0	* *
Juncus arcticus	29	3	* * *
Allium textile	0	5	*
Echinocereus viridiflorus	3	69	* * *

Table 21 cont.

Species	Bioassay	Mechanical	Significance
Carex sp.	0	12	**
Agrostis gigantea	8	0	*
Eleocharis palustris	0	32	***

*=P-value ≤0.05, **=P-value ≤0.01, ***=P-value≤0.001

Table 22. Frequency of seeds and seedlings of Seed rain and Bioassay methods and results of Kolmogorov-Smirnov two-sample test for differences in frequency distribution

Species	Bioassay	Seed Rain	Significance
Olgosporus pacificus+	98	969	*
Artemisia frigida			
Talinum parviflorum	17	0	***
Monarda pectinata	6	1	*
Heterotheca fulcrata	0	8	***
Lepidium densiflorum	24	218	**
Erodium cicutarium	4	0	*
Camelina microcarpa	49	42	***
Verbascum thapsus	14	0	***
Triodanis perfoliata	9	0	**
Erysimum capitatum	0	11	**
Conyza canadensis	0	36	***
Silene antirrhina	44	9	***
Senecio spartioides	3	25	***
Bromus spp.	117	447	**
Sisymbrium altissimum	10	1	*
Linaria cannadensis	3	0	*
Sporobolus asper	12	170	***
Grindelia subalpina	2	0	*
Draba reptans	8	0	***
Festuca rubra	14	54	***
Cichorium intybus	11	304	***
Chenopodium leptophyllum	1	101	**
Lactuca serriola	4	13	**
Poa spp.	467	713	*
Juncus bufonius+J.dudleyi	167	3	***
Stipa comata	1	65	***
Sorghastrum avenaceum	2	23	***
Veronica peregrina	14	0	**
Plantago lanceolata	31	221	**
Typha sp.	4	0	*
Andropogon gerardii	0	7	***
Juncus arcticus	7	0	***
Aristida purpurea	0	4	*
Bouteloua curtipendula	0	14	***
Panicum virgatum	0	23	***
Oligoneuron rigidum	0	3	***
Agrostis gigantea	0	75	***

* = P-value≤ 0.05, ** = P-value≤0.01, *** = P-value ≤0.001

Table 23. Significant differences in frequency distributions of seeds and seedlings between Mechanical Separation and Seed Rain methods using Kolmogorov-Smirnov two sample test

Species	Mechanical counts	Seed Rain counts	Significance
Oligosporus pacificus +	53	969	***
Artemisia frigida			
Talinum parviflorum	24	0	***
Monarda pectinata	30	1	***
Heterotheca fulcrata	0	8	*
Lepidium densiflorum	3	218	***
Erodium cicutarium	52	0	***
Alyssum minus	2	64	***
Camelina microcarpa	42	42	***
Conyza canadensis	1	36	**
Silene antirrhina	45	9	***
Senecio spartioides	0	25	***
Bromus spp.	119	447	***
Sporobolus asper	31	170	*
Hypericum perforatum	0	24	**
Cichorium intybus	24	304	***
Sporobolus cryptandrus	75	28	***
Chenopodium leptophyllum	75	101	***
Neolepia campestre	21	0	***
Lactuca serriola	0	13	***
Poa spp.	103	713	***
Juncus bufonius+J.dudleyi	270	3	***
Ambrosia artimissifolia	18	0	***
Stipa comata	23	65	**
Sorghastrum avenaceum	3	23	**
Dianthus ameria	81	28	**
Plantago lanceolata	34	211	*
Andropogon gerardii	0	7	**
Echinocereus viridiflorus	60	1	***
Bouteloua curtipendula	1	14	*
Panicum virgatum	0	23	***
Agrostis gigantea	0	75	**
Eleocharis palustris	28	0	***

* = P-value≤ 0.05, ** = P-value≤0.01, *** = P-value ≤0.001

The total number of seeds or seedlings from each method, including the total number of shared species and species unique to one or two method is shown in Tables 24-26.

Table 27 shows 25 species of seeds/seedlings common to bioassay, mechanical and seed rain methods. Table 28 presents 80 species, unique to either one or two of these three methods, but not all three methods.

The total species found in each method were close in numbers, between 50 and 70. However, only 25 species were common to all three methods. For each comparison, approximately half of the species were common to both methods and half were uncommon. Seed Rain provided the lowest total species count, as compared to the bioassay and mechanical methods.

DISCUSSION

Bioassay and Mechanical separation

Species composition in seed bank as measured by the bioassay and mechanical separation methods were strikingly different. The Bioassay and Mechanical separation showed significantly high negative correlation, indicating that species most common in one tended to be least common in the

Table 24. Comparison between Bioassay and Mechanical separation in total number of seeds/seedlings from each method, and the total number of shared species and species unique to one method

	BIOASSAY	MECHANICAL EXTRACTION
Total species	62	62
Total seed or seedling counts	1323	1397
Common species	35	35
Unique species (only found with that particular method)	27	27

Table 25. Comparison between Bioassay and Seed Rain in total number of seeds/seedlings from each method, and the total number of shared species and species unique to one method

	BIOASSAY	SEED RAIN
Total species	62	54
Total seed or seedling counts	1323	3840
Common species	33	33
Unique species (only found with that particular method)	29	21

Table 26. Comparison between Mechanical separation and Seed Rain in total number of seeds/seedlings from each method, and the total number of shared species and species unique to one method

	MECHANICAL SEPARATION	SEED RAIN
Total species	62	54
Total seed or seedling counts	1397	3840
Common species	30	30
Unique species (only found with that particular method)	32	24

Table 27. Species list of 25 species of seeds/seedlings common to Bioassay(n=160), Mechanical Separation(n=160) and Seed Rain(n=144) methods

ACETOSELLA VULGARIS

ALYSSUM MINUS

ARTEMISIA FRIGIDA

BOUTELOUA CURTIPENDULAR

BROMUS SPP.

CAMELINA MICROCARPA

CICHORIUM INTYBUS

CIRSIUM ARVENSE

DIANTHUS AMERIA

ECHINOCEREUS VIRIDIFLORUS

JUNCUS BUFONIUS

JUNCUS DUDLEYI

LEPIDIUM DENSIFLORUM

MEDICAGO LUPULINA

MONARDA PECTINATA

OLIGOSPORUS PACIFICUS

PLANTAGO LANCEOLATA

PLANTAGO PATAGONICA

POA SPP.

SILENE ANTIRRHINA

SORGHASTRUM AVENACEUM

SPOROBOLUS ASPER

SPOROBOLUS CRYPTANDRUS

STIPA COMATA

TRAGOPOGON DUBIUS

Table 28. Species list of 80 unique species of seeds/seedlings found in either one or two of these methods:Bioassay(n=160), Extraction(n=160) and Trapping(n=144)

ACOSTA DIFFUSSA
AGROSTIS GIGANTEA
ALLIUM TEXTILE
AMBROSIA ARTIMISIIFOLIA
ANDROPOGON GERARDII
ANDROSACE OCCIDENTALIA
ARGEMONE POLYANTHEMOS
ARISTIDA PURPUREA
ASCLEPIAS SPECIOSA
ASTRAGALUS SP.
BUCHLÖE DACTYLOIDES
CALAMOVILFA LONGIFOLIA
CALYLOPHUS SERRULATUS
CAREX PENSYLVANICA
Subsp.HELIOPHILLA
CAREX PRAEGRACILIS
CAREX SPP.
CERASTIUM STRICTUM
CHAMAESYCE SERPYLLIFOLIA
CHENOPODIUM LEPTOPHYLLUM
CONYZA CANADENSIS
CRITESION BRACHYANTHERUM
CYPERUS ESCULENTUS
DALEA CANDIDA
DALEA PURPUREA
DAUCUS CAROTA
DICHANTHELIUM
OLIGOSANTHES
DRABA REPTANS
ELEOCHARIS PALUSTRIS
ELEOCHARIS SP.
ELYMUS TRACHYCALUS
EPILOBIUM CILIATUM
ERIGERON FLAGELLARIS
ERIOGONUM EFFUSUM
ERODIUM CICUTARIUM
ERYSIMUM CAPITATUM
FESTUCA RUBRA
GNAPHALIUM STRAMINEUM
GRINDELIA SQUARROSA
GRINDELIA SUBALPINA
GUTIERREZIA SAROTHRAE
HETEROTHECA FULCRATA
HYPERICUM PERFORATUM
JUNCUS ARCTICUS
JUNCUS MARGINATUS
JUNCUS TENUIS
JUNCUS TORREYI
LACTUCA SERRIOLA
LIATRIS PUNCTATA
LINARIA CANNADENSIS
LITHESPERMUN INCISUM
LOMATIUM ORIENTALE
LUPINUS ARGENTEUS
MARISCUS FENDLERIANUS
MOLLUGO VERTICILLATA
MUHLENBURGIA ARENICOLA
NASTURIUM OFFICINALE
NEOLEPIA CAMPESTRE
OENOTHERA VILLOSA
OLIGONEURON RIGIDUM
OREOCARYA VIRGATA
OREOCARYA VIRGATA
OXYTROPIS LAMBERTII

Table 28. Species list of 80 unique species of seeds/seedlings found in either one or two of these methods:Bioassay(n=160), Extraction(n=160) and Trapping(n=144)

PANICUM VIRGATUM

PHYLA CUNEIFOLIA

PHYSALIS SP.

PODOSPERMUM LACINIATUM

POLYGONUM ARENASTRUM

POTENTILLA ANGLICA

PSORALIDIUM TENUIFLORUM

RUMEX CRISPUS

SENECIO SPARTIOIDES

SISYMBRIUM ALTISSIMUM

SOLIDAGO SP.

TALINUM PARVIFLORUM

TARAXACUM OFFICINALE

TRADESCANTIA

OCCIDENTALIS

TRIODANIS PERFOLIATA

TYPHA SP.

VERBASCUM THAPSUS

VERBENA BRACTEATA

VERONICA PEREGRINA

other. The Czekanowski's Coefficient was only 0.50(50% similarity). Some species showed up more frequently in one method as compared to another method. For example, Oligosporus pacificus and Artemisia frigida were found approximately twice as frequently with bioassay as with the mechanical separation. In contrast, Erodium cicutarium was ten times more common with the mechanical separation as compared to the bioassay method (see Table 21 for other examples).

This lack of correspondence between Bioassay and Mechanical separation may arise from two sources: It is possible that small seeds are not recovered with the mechanical separation. Most species that showed lower frequency under the mechanical separation had very small seed size. Perhaps the solution concentration for extracting(floating) seeds was not right for species of all sizes or shapes, and therefore, some may have been missing during the process of separation. Malone, who proposed this technique, claimed that the method is typically 100% efficient in extracting all seeds (Malone, 1967). However, more testing on Malone's floating technique should be performed in order to see if it is indeed equally suited for all sizes and for different seed morphology.

In addition, the fact that some species were found less frequently with the bioassay method than with the mechanical separation method(Table 29) may be due to their germination requirements. These species may not germinate under conventional conditions because of dormancy which must be broken by special conditions before germination can take place. These requirements may not have been met under the bioassay method.

After conducting both methods of assessing the seed bank, I conclude that Mechanical separation is important because it helps complete the information gathered from the bioassay method alone, especially in terms of seed dormancy. Furture needs in seed morphology and seed size studies, related to contrasting results between the Mechanical separation method and the Bioassay method as well as the germination requirements of seeds are suggested to be explored in order to assess the proper method for seed bank recruitment.

Table 29. Species potentially acquire dormancy seeds

Allium textile	_Medicago lupulina_
Ambrosia artemisiifolia	_Monarda pectinata_
Chenopodium leptophyllum	_Neolepia campestre_
Dianthus armeria	_Silene antirrhina_
Echinocereus viridiflorus	_Sporobolus asper_
Erodium cicutarium	_Sporobolus cryptandrus_
Juncus bufonius	_Stipa comata_
Juncus dudleyi	

Seed rain and seed bank

There was surprisingly little correlation in species composition between seed rain and either measure of seed bank species, i.e. bioassay and mechanical separation methods. The Czekanowski Coefficient for seed rain vs. bioassay was 0.43(43%), almost twice as much agreement as between mechanical separation vs. seed rain(0.24 or 24%).

There are three possible causes for these differences in results across methods. The first is methodological:

Trapping for my study was not done year round. The monitoring was performed only during the growing seasons, spring and summer. There might be some seeds produced beyond these times that were unrecorded.

The second and third are biological: Both mechanical and bioassay methods for seed bank composition represent an actual measure of underground seed storage. They were the results of accumulation and screening processes occuring over time. Seed rain represents the input which has yet to be subjected to the screening processes before becoming part of the seed bank. Seeds must first go through the filtration processes of predators, diseases, aging, and death before they are part of the seed bank. Thus, the seed bank is dynamic with constant input from seed rain and non-random loss due to screening processes through time. Dormant long-lived seeds could cause increasing in dissimilarity between extraction and trapping. Dormant long-lived seeds will accumulate through time without loss by germination or death. The disproportion in seed bank compartment will increase the gap differences between seed rain and seed bank.

Trapping might favor more short-lived seeds that would die and decay or germinate before being detectable in a bioassay or mechanical separation method(Table 30). Interestingly, this list included most dominant grasses of Boulder Tallgrass Prairie: Andropogon gerardii, Sorghastrum avenaceum, Panicum virgatum and Agrostis gigantea. This implied that seeds of most dominant grasses in this grassland are short-lived or have little dormancy. Therefore, their seed bank is very small as compared to others. The other factor that can cause the variation in sizes of seed bank might be partly due to the seed productivity of each

Table 30. Species list of transient (short-term) seed bank

Agrostis gigantea	Lepidium densiflorum
Alyssum minus	Oligosporus pacificus
Andropogon gerardii	Panicum virgatum
Bromus spp.	Plantago lanceolata
Conyza cannadensis	Poa spp.
Festuca rubra	Senecio spartioides
Heterotheca fulcrata	Sorghastrum avenaceum
Lactuca serriola	

species. For example, the high numbers of seeds of both Poa spp.and Bromus spp were found in seed rain. This evidence implies that both species are very productive in terms of seed production, even though they are short-lived and most seeds are lost before germination. In contrast, the opposite was true for the 4 dominant grasses mentioned above, where not only are they short-lived seeds, but also they are less productive. Thus their occurrences are quite low in all methods.

SUMMARY

The seed bank did not well correspond to species distribution frequency of the aboveground vegetation. The Bioassay method alone does not represent an accurate measurement of seed bank, as some species were found less frequently with the Bioassay method than with the Mechanical separation method. On the other hand, the bioassay method was very useful for recruiting most of the seeds which normally do not require special treatments for germination. Therefore, both Bioassay and Mechanical separation methods are suggested as complementary methods in order to get the complete information on the seed bank composition.

Seed rain is a measure of initial input into seed bank but there are many other processes that determine the actual composition of the seed bank such as, predators, diseases, germination loss, aging and death. The seed bank is thus dynamic and representing an instantaneous balance between input from seed rain and loss due to seed bank dynamics. To fil the gaps between seed rain and seed bank in this study, seedling recruitments in the field as well as monitoring seed bank and seed rain all year round are suggested to be performed.

CHAPTER V

SEED PRODUCTION

INTRODUCTION

Andropogon gerardii and *Sorghastrum avenaceum* are the most abundant and most characteristic grasses of Tallgrass Prairies. Therefore, I expected to find a large seed bank of these two dominant species. However, very few seedlings germinated under the bioassay method (chapter IV). To find out what might be the reason for the presence of so few seeds of the two dominant grasses in the seed bank, I studied seed production of the inflorescences.

During my observations, I found infestations by parasitic pupae of Gall midges(Order Diptera, Family Cecidomyiidae) inside the florets of both species. As a result, seeds did not develop, and therefore the plants had reduced seed set. The mechanism of how this parasite functions is not clear at the moment, but it seems to me that the parasites compete with the developing seeds for the nutrients that normally provide seed growth. The Gall midges lay the eggs inside the florets near the ovary and only one pupa develops in a position parallel to and behind the ovary. When the pupa is fully developed, it fits well inside the floret where the seed is supposed to be. In addition, there are midge parasites(Order Hymenoptera), a secondary parasite, which infest the Gall midge larvae and may affect their population dynamics. Midge parasites feed on the hemolymph of the larvae of the Gall midge.

These observations led me to ask the following questions:

1. How large was the seed output per inflorescence for Andropogon gerardii and Sorghastrum avenaceum from Konza Prairie versus Boulder Tallgrass Prairie plants?

2. Does burning have any effect on the number of flowers, seeds, parasitic pupae and egg parasites?

3. Do different burning regimes have any effects on the number of flowers, seeds, infestations of parasitic pupae and population of midge parasites?

In addition to focusing on the effects of fire upon seed reproduction and parasitism, I was also interested in the roles of fire in terms of seed quality (seed weight). Therefore, I also asked the following questions:

1. Does burning cause changes in seed weight?

2. Do different burning regimes correlate with changes in seed weight?

METHODS

Inflorescences of *Andropogon gerardii* and *Sorghastrum avenaceum*, were randomly chosen at least two meters apart and collected from Boulder and Konza Prairie study sites in November 1989 and November 1990. In 1989, 25 inflorescences were sampled per species per site; in 1990, 10 inflorescences were sampled per species per site. Study sites where inflorescences were collected are listed in Table 31. A stereomicroscope was used for dissecting the florets where the seeds, pupae and midge parasites are located. Numbers of florets, seeds, pupae and midge parasites were counted per inflorescence. The mean differences of florets, seeds, pupae, egg parasites and seed weight were tested by using Kruskal-Wallis

Table 31. Study sites and species collected for analyses of reproduction biology

Sites	*Andropogon gerardii* 1989	*Andropogon gerardii* 1990	*Sorghastrum avenasceum* 1989	*Sorghastrum avenasceum* 1990
Konza:				
Non-burned	X	X	X	X
4-year-burned	X	X	X	X
Annual-burned	X	X	X	X
10-year-burned	-	X	-	X
Total Inflorescences	75	40	75	40
Boulder:				
Xeric unburned	X	X	-	-
Xeric burned	X	X	-	-
Mesic unburned	-	X	X	X
Mesic burned	-	X	X	X
Mesic, cattle grazed	-	X	-	X
Total Inflorescences	50	50	50	30

X means samplings

\- means no samplings

analysis. Additional comparisons of percent seed set, seed parasitism and secondary parasitism were carried out as well. The descriptions and meanings of each calculation are as follows:

1. Percent seed set

Definition:

$$= \frac{\text{mean of seeds/inflorescence X 100}}{\text{mean of florets/inflorescence}}$$

This value represents percent success in seed reproduction effort.

2. Percent seed parasitized

Definition:

$$= \frac{\text{mean of pupae/inflorescence X 100}}{\text{mean of pupae+seeds/inflorescence}}$$

This value represents the percent of potential seed infected by pupae.

3. Percent midge parasites per floret

Definition:

$$= \frac{\text{mean of midge parasites/inflorescence X 100}}{\text{mean of floret/inflorescence}}$$

This value shows the relative proportion of midge parasites per floret.

RESULTS

KONZA : *Andropogon gerardii*(Table 32)

In 1989, no significant differences in floret numbers per inflorescence were detected between the non-burned and the annual burned sites($p=0.94$). However, the floret numbers at the annual burned site were significantly higher than that of the 4-year-burned site($p=0.01$). In 1990, the annual burned site was the one that had the lowest floret numbers of all sites; comparisons of significance with other sites are as follows: non-burned ($p<0.05$), 10-year-burned($p=0.07$) and 4-year-burned($p=0.07$) sites.

In 1989, the annual burned site had significantly higher seed numbers than both non-burned and 4-year-burned sites($p<0.05$). However, in 1990, the 4-year-burned site had significantly higher seed numbers than the other sites($p\leq0.001$).

In 1989, there were significantly higher pupae numbers per inflorescence on the non-burned than on the annual burned and 4-year-burned sites($p<0.05$). However, in 1990, there were no significant differences in pupae numbers among sites. Percent seed parasitized varied during the two years of investigations.

Table 32. Mean florets, mean seeds, mean pupae , mean midge parasites, mean seed weight (mg) of 5 seeds, %seeds set, %seeds parasitized, %pupae and %midge parasites of <u>Andropogon gerardii</u> in 1989-1990 from Konza and Boulder Tallgrass Prairie (- means no records)

	YR	Konza Non burn	Konza 10yr burn	Konza 4yr burn	Konza Annual burn	Boulder Mesic grazed	Boulder Mesic unburn	Boulder Mesic burn	Boulder Xeric unburn	Boulder Xeric burn
MEAN FLORET	89	157.9±85.6	-	126.6±73.9	152.6±36.6	-	-	-	99.4±41.6	107.4±39.9
±SD	90	127.8±73.1	91.2±50.9	104.6±48.9	64.0±38.1	94.2±30.1	94.7±29.9	86.4±37.9	93±14.6	85.1±31.2
MEAN SEED	89	1.3±2.1	-	2.6±4.9	6.1±9.8	-	-	-	0.1±0.3	0.04±0.2
±SD	90	1.5±1.8	0.7±1.5	13.3±6.7	1.8±2.0	4.4±3.2	5.5±4.9	9.2±15.3	5.7±7.6	4.5±3.1
MEAN PUPAE	89	0.2±0.4	-	0.08±0.3	0	-	-	-	0.08±0.3	0.04±0.2
±SD	90	0.1±0.3	0.2±0.4	0.3±0.5	0.2±0.4	0.1±0.3	0	0.1±0.3	0.1±0.3	0.1±0.3
MEAN MIDGE	89	1.9±2.6	-	11.5±11.4	4.2±6.0	-	-	-	14.7±21.9	11.9±16.4
PARASITE±SD	90	0.7±2.2	4.6±4.7	0.3±0.9	0.4±1.3	2.7±4.3	0	0.4±0.8	0.7±1.5	0.2±0.6
MEAN SEED	89	4.3±0.6	-	5.9±0.8	4.6±1.4	-	-	-	5.0±0	3.0±0
WEIGHT	90	6.7±2.1	10.0±7.1	6.5±2.2	7.3±1.0	8.8±3.1	8.6±2.2	8.3±1.4	9.7±3.6	8.3±1.4
(5 seeds)±SD										
% SEEDS SET	89	0.81	-	2.02	4.01	-	-	-	0.12	0.04
	90	1.17	0.77	12.72	2.81	4.67	5.81	10.65	6.13	5.29
% SEEDS	89	11.11	-	3.03	0	-	-	-	40.00	50.00
PARASITIZED	90	6.25	22.22	2.26	10.00	2.22	0	1.08	1.72	2.17
% MIDGE	89	1.22	-	9.07	2.78	-	-	-	14.81	11.1
PARASITES	90	0.55	5.04	0.29	0.63	2.87	0	0.46	0.75	0.24

In 1989, midge parasites were significantly higher in the 4-year-burned than in the annual burned site($p<0.01$), and the non-burned site, while the latters showed no differences. However, in 1990, when the 10-year-burned site was first included, it was this site that showed the highest numbers of midge parasites as compared to the other sites($p\leq0.01$). Meanwhile, the non-burned, the 4-year-burned and the annual burned showed no significant differences in midge parasite numbers In general, both pupa and midge parasite populations fluctuated in size quite a lot among and within sites during the two years of study (Table 32, 33).

Seed weight from the 4-year-burned site of 1989 was significantly higher than that at all other sites($p<0.05$). However, no significant differences were found among the sites in 1990 (Table 32).

KONZA: Sorghastrum avenastrum(Table 33)

No significant differences in floret numbers were found among the Konza sites either in 1989 or 1990.

Table 33. Mean florets, mean seeds, mean pupae , mean midge parasites, mean seed weight (mg) of 5 seeds, %seeds set, %seeds parasitized, %pupae and %midge parasites of *Sorghastrum avenaceum* in 1989-1990 from Konza and Boulder Tallgrass Prairie (- means no records)

	Year	Konza Non burn	Konza 10 yr burn	Konza 4 yr burn	Konza Annual burn	Boulder Mesic grazed	Boulder Mesic unburn	Boulder Mesic burn
MEAN FLORET	1989	159.8±43.8	-	134.3±47.2	160.8±43.3	-	87.0±53.4	108.6±53.2
±SD	1990	71.0±18.0	80.1±30.2	103.5±46.4	87.9±42.7	77.4±23.0	87.1±36.1	128.6±74.0
MEAN SEED	1989	58.1±34.7	-	45.0±34.3	27.3±20.2	-	13.3±21.7	19±16.5
±SD	1990	1.1±2.0	13.0±16.7	7.7±12.5	0	11.9±15.2	46.1±29.6	51.6±54.2
MEAN PUPA	1989	0	-	0.04±0.2	0.04±0.2	-	0.44±1.6	0.12±0.3
±SD	1990	0	0	0	0	0	0	0
MEAN MIDGE	1989	0	-	0	0	-	3.08±5.4	0.6±2.1
PARASITE±SD	1990	0	0	0	0	0	0	0
MEAN SEED WEIGHT	1989	6.45±1.0	-	6.57±1.3	3.88±0.9	-	7.80±1.3	7.75±0.9
(5 seeds) ±SD	1990	11.50±5.0	9.87±1.0	10.69±2.1	0	7.43±2.0	7.72±1.7	8.41±1.4
%SEEDS SET	1989	36.36	-	33.54	16.99	-	15.27	17.45
	1990	1.55	16.23	7.44	0	15.37	52.93	40.12
%SEEDS	1989	0	-	0.09	0.15	-	3.21	0.63
PARASITIZED	1990	0	0	0	0	0	0	0
%MIDGE PARASITES	1989	0	-	0	0	-	3.54	0.55
	1990	0	0	0	0	0	0	0

In 1989, seed numbers on the annual burned site were significantly lower than on the non-burned ($p<0.01$) and the 4-year-burned ($p<0.05$) site. In 1990, there was no seed found in the inflorescences of the annual burned site. The annual burned site differed significantly from the 10-year-burned ($p<0.01$); the 4-year-burned ($p=0.005$); and the non-burned ($p=0.07$) sites. However, in the same year, the 4-year-burned site showed no significant differences in seed numbers as compared to the 10-year-burned and non-burned sites. There were significantly more seeds at the 10-year-burned site than at the non-burned site($p<0.05$).

Sorghastrum avenaceum showed tremendous reduction both in floret numbers and in percent seed set from 1989 to 1990. This pattern is probably not associated with burning regime, because if one looks at the trend of seed numbers varying between 1989 to 1990, one sees the same trend across all sites, regardless of burning regimes.

No significant differences in populations of mean pupae and midge parasites were detected among sites in either 1989 or 1990. In addition, parasitism did not seem to be the major factor controlling seed production for Konza *Sorghastrum avenaceum*, as the pupae were found only in 1989 at the 4-year-burned and annual burned sites. No midge parasites were found either in 1989 or 1990.

In 1989, seeds from the 4-year-burned site weighed significantly more than seeds from annual burn sites($p<0.001$), but not significantly more than those from the non-burned site. However, I noticed that most seeds of the 4-year-burned showed little variation in seed sizes, and appearing fuller when compared to seeds at the non-burned site. In 1990, however, there were no differences in mean seed weight in plants from any of the sites. No seeds were produced at the annual burned site in 1990.

BOULDER: Andropogon gerardii(Table 32)

In 1989 and 1990 data on floret numbers, seed counts, pupae, midge parasites and seed weights were collected from the xeric burned and unburned sites. In 1990, these data were also collected for the mesic burned, mesic unburned, and mesic grazed sites. No significant differences among sites were found in numbers of florets, seeds, or pupae in either year. However, the mesic grazed site had significantly more egg parasites than the unburned mesic($p<0.05$) and slightly more than the burned xeric site($p=0.09$).

For Boulder, percent seed set and percent seed parasitized were dramatically different in 1989 and 1990. The percent seed set increased by 51 and 132 fold for the xeric unburned and xeric burned sites respectively from 1989 to 1990. Meanwhile, the percent seed parasitized decreased by 23 fold for both xeric unburned and xeric burned sites from 1989 to 1990. Percent midge parasites per floret varied from year to year.

In 1989, seeds from the xeric unburned site seemed to be heavier than the xeric burned site. However, the mean differences in seed numbers between the two sites of 1989 could not be statistically tested by Kruskal-Wallis analysis, since there was only one replicate of seed weight data in each site. No distinctions in seed weights across sites were found in 1990.

BOULDER: Sorghastrum avenaceum(Table 33)

In 1989, the mesic burned site produced significantly higher floret numbers($p=0.01$) and seed numbers($p<0.05$) than the mesic unburned site. However, there were no significant differences in floret and seed numbers between these sites for 1990. In that year, the mesic grazed site had slightly fewer floret numbers than the mesic unburned site($p=0.09$), and significantly fewer seed numbers than both the mesic unburned($p=0.004$) and the mesic burned($p<0.05$) sites.

In 1989, percent seed set of _Sorghastrum avenaceum_ was higher in the mesic burned than in the mesic unburned site. However, in 1990, the mesic unburned site had the highest percent seed set, followed by mesic burned and mesic grazed respectively.

There were no differences in numbers of pupae per inflorescence on any mesic site in either 1989 or 1990. However, the percent seed parasitized, percent midge parasites per floret were all higher in the mesic unburned than the mesic burned site in 1989. Both pupae and midge parasites decreased in numbers from 1989 to 1990.

In 1989, significantly more midge parasites were found in plants from the mesic unburned site than from the mesic burned site. In 1990, neither pupae nor midge parasites were found in the three

Boulder sites: mesic burned, mesic unburned and mesic grazed.

In 1989, there were no differences in seed weights from mesic unburned and mesic burned plants(Table 45). However, in 1990, mesic burned seeds were significantly heavier than mesic unburned($p=0.001$) and mesic grazed($p<0.05$) sites (Table 33).

DISCUSSION

FLORET PRODUCTION

In general, floret numbers varied among different burning regimes and locations. However, many of these differences were not statistically significant. Also, floret numbers changed quite dramatically during the two years of study. In overview, floret numbers at Konza seemed to be greater than at Boulder if one takes the mean floret numbers of Konza and Boulder into account. For example, the two year mean floret numbers of <u>Sorghastrum avenaceum</u> at Konza and Boulder were 119 and 102 respectively. The two year mean florets of <u>Andropogon gerardii</u> at Konza and Boulder were 122 and 96 respectively. This result confirmed the finding of Sala et al.(1988) on the productivity of central grasslands of the United States. The conclusion of their study was that "Lowest values of aboveground net primary production were observed in the west and highest in the east. The pattern of production reflected the east-west gradient in annual precipitation". The floret production at these sites can be thought of as an indication of reproductive effort, and seemed to follow this pattern as the Konza and Boulder Prairies represented the east and the west central grassland. The mean annual precipitation is the major factor that limits the productivity of the western grassland such as Boulder Prairie.

PARASITES

Three generalizations can be drawn from my study:

1. Andropogon gerardii of both Konza and Boulder seemed not only to be more susceptible to midges, but also to have higher numbers of midge parasites than Sorghastrum avenaceum when the percent seeds parasitized were compared.

2. Boulder Andropogon gerardii and Sorghastrum avenaceum had higher percent seeds parasitized and midge parasites per floret than Konza Andropogon

gerardii and Sorghastrum avenaceum. Therefore, Boulder has higher populations of both midges and midge parasites than Konza.

3. Boulder Andropogon gerardii seem to have higher fluctuations acsoss years in the percent seeds parasitized than do Konza. For example, the percent seeds parasitized decreased by 23 fold(40 vs.1.72 and 50 vs 2.17) for both xeric unburned and xeric burned sites from 1989 to 1990. In contrast, the change between years in percent seeds parasitized among Konza sites was either not very large, or showed no clear pattern. For instance, on the Konza non-burned site, the difference was apparently only 1.78 fold between 1989-1990. And the difference across years for the annual burned site(from 0 to 10), cannot be measured in terms of ratios.

SEED PRODUCTION

In general, Sorghastrum avenaceum has higher seed numbers per inflorescence than Andropogon gerardii. Therefore, Sorghastrum avenaceum seems to be more successful in terms of seed output than Andropogon gerardii.

Frequent burns, such as those at Konza's annual burned site might cause a reduction in seeds of Sorghastrum avenaceum. This could lead to no seed production at all in some cases, as in the 1990 annual burned site at Konza. Boulder's Sorghastrum avenaceum produced more flowers and seeds on the mesic burned site, suggesting that some burning, at a frequency as yet unknown, may enhance seed production in Sorghastrum avenastrum in the Boulder Tallgrass Prairie. However, these changes might also be due more to the climatic responses than to the burning responses.

At Konza, burning was associated with an increase in seed numbers for the annual burned(1989) and 4-year-burned sites(1990) for Andropogon gerardii. Both sites showed significantly higher seed numbers than the other sites. I hypothesize that Andropogon gerardii may be more fire tolerent at Konza and more adapted to the frequent burns than is Sorghastrum avenaceum.

For Boulder, however, no general distinctions among sites were noted in seed numbers. This could be because the 1988 fire was the first burn for the Boulder Tallgrass Prairie study sites in many years, and no patterns can be detected from just one burn. Also, I speculate that there might be some other contributing environmental factors in Boulder, such as climatic extremes, for example, in the winter, when the average minimum temperature is lower and snow depth is greater in Boulder than in Konza (see chapter III). In summer, water deficiency is the major problem that plants in Boulder area have to face in order to survive (Callahan, 1986). These extreme conditions might be the key factors controlling the differences between the Konza and Boulder Tallgrass Prairies.

The mean seed weight of Boulder's Sorghastrum avenaceum was higher in the second-post burn year. However, Boulder's Andropogon gerardii did not differ in mean seed weight across sites in either 1989 or 1990. At Konza, the high quality seeds, i.e. seed weight and seed fullness(personal observation) of both Andropogon gerardii and Sorghastrum avenaceum were associated with the 4-year-burned site, suggesting that good health seeds, may be associated with the 4-year-burning cycle.

The increase in vegetative growth and flower reproduction that would normally be associated with burning applied to the eastern Tallgrass Prairies

(Curtis and Partch, 1948; Knapp, 1984a,1984b,1985; Knapp and Hulbert,1986; Patton et al.,1988; Svejcar and Browning, 1988), perhaps cannot be applied to the western Tallgrass Prairies. Plant responses in Boulder may be more influenced by climatic factors such as water supply than by burning. Therefore, the natural response due to burning that might have occurred at Boulder Tallgrass Prairie may be affected, or inhibited because of the limited water supply in Boulder. The mean annual precipitation of Boulder is only 45.61 cm as compared with 81.08 cm at Konza. This scarcity of water may have inhibited the growth that would naturally occur as a response to burning.

In general, percent seed set varied depending on species. For example, on the Konza's non burned site, this value in Andropogon gerardii increased by 1.4 fold during 1989-1990. However, Sorghastrum avenaceum on the same site decreased in percent seed set by 23 fold during the same period. This kind of variation is also revealed in Boulder. For instance, the mesic unburned and mesic burned Andropogon gerardii increased in percent seed set by 51 and 132 fold respectively from 1989 to 1990. Besides the climatic conditions and species variables that might directly influence the productivity, burning might represent an additional factor affecting seed set as well. For example, Andropogon gerardii in the 4-year-burned site increased by 6 fold after the scheduled burn in 1990. However, in 1990 Sorghastrum avenaceum at Konza showed a decreasing trend in seed set across all sites. The smallest change occurred on the 4-year-burned site. Sorghastrum avenaceum seemed to be most adversely affected on the annual-burned site, representing the most extreme decrease from 16.99 to 0 between 1989 and 1990. Also, Andropogon gerardii of the annual-burned site showed the same decreasing trend in seed set, but less extreme than that of Sorgastrum avenaceum.

BOULDER AND KONZA PRAIRIE COMPARISONS IN REPRODUCTIVE PATTERNS AND PARASITISM(Table 34,35)

In order to test the hypothesis that Boulder and Konza populations of Andropogon gerardii and Sorghastrum avenaceum are similar in their reproductive features(i.e. in numbers of florets, seed, midge, midge parasites and seed weight), I compared the Boulder mesic burned(burned in 1988)

Table 34. Mean florets, mean seeds, mean pupae, mean midge parasites, mean seed weight(mg) of 5 seeds, %seed set, %seeds parasitized, %pupae and %midge parasites of *Andropogon gerardii* and *Sorghastrum avenaceum* of Konza 10-year-burned and Boulder mesic-burned sites. K-W test was performed for testing in mean differences, others was performed by relative comparisons

	Konza 10-year-burned site	Boulder mesic burned site	significances
Andropogon gerardii			
MEAN FLORET±SD	91.2±50.9	86.4±37.9	NS
MEAN SEED±SD	0.7±1.5	9.2±15.3	p=0.08
MEAN PUPAE±SD	0.2±0.4	0.1±0.3	NS
MEAN MIDGE PARASITE±SD	4.6±4.7	0.4±0.8	p<0.01
MEAN SEED WEIGHT±SD (5seeds)	10.0±7.1	8.3±1.4	NS
% SEED SET	0.77	10.65	B>K
%SEEDS PARASITIZED	22.22	1.08	K>B
%MIDGE PARASITES	5.04	0.46	. K>B
Sorghastrum avenaceum			
MEAN FLORET±SD	80.1±30.2	128.6±74	NS
MEAN SEED±SD	13.0±16.7	51.6±54.2	p=0.07
MEAN PUPAE±SD	0	0	NS
MEAN MIDGE PARASITE±SD	0	0	NS
MEAN SEED WEIGHT±SD (5seeds)	9.87±1.0	8.41±1.4	P<0.001
%SEED SET	16.23	40.12	B>K
%SEEDS PARASITIZED	0	0	NS
%MIDGE PARASITES	0	0	NS

Table 35. Comparison in mean seed numbers, percent seed set and seed weight of *Andropogon gerardii* and *Sorghastrum avenaceum* between all site of Boulder and Konza (except the annual burned site)

Andropogon gerardii	Konza	Boulder	Differences
SEED NUMBERS	3.35	4.85	1.5
%SEED SET	3.04	5.38	2.34
SEED WEIGHT(5 seeds in mg)	6.68	7.38	0.7
Sorghastrum avenaceum			
SEED NUMBERS	22.98	25.63	2.65
%SEED SET	18.55	26.08	7.53
SEED WEIGHT(5 seeds in mg)	9.02	7.82	1.2

population with the Konza 10-year-burned population (burned in 1973 and last burned in 1986) because they are probably the closest match in terms of the years they were burned and type of habitat. This hypothesis was tested using the Kruskal-Wallis analysis to detect any mean differences in the features mentioned above between two populations.

The mean floret numbers, seed weights and pupae did not differ between Boulder's and Konza's Andropogon gerardii. Sorghastrum avenaceum showed no significant differences in florets, pupae and midge parasites between the two sites. However, the average of mean floret numbers from all sites at Konza was higher than the average of mean floret numbers at Boulder sites(see the discussion on page 123).

Boulder Andropogon gerardii had slightly higher seed numbers than did Konza($p=0.08$), and there were more egg parasites present in Konza 10-year-burned site than in Boulder mesic-burned site($p<0.01$). Sorghastrum avenaceum had higher seed numbers at the Boulder mesic-burned site than at Konza 10-year-burned ($p=0.07$), however, seeds from the Konza site weighed significantly more than Boulder seeds($p<0.001$). There were no significant differences in seed weight of *Andropogon gerardii* between the two sites.

I also compared seed output between the two locations by combining in seed output across all sites from both Boulder and all but the annual burned site at Konza. This latter site was not included because annual burning represents an unnatural situation, which historically did not occur in North American Grassland(Wright and Bailey, 1982; Hulbert, 1988). Seed output was compared in terms of mean seed numbers, percent seed set and seed weight(Table 35). This last variable was included because seed size is an important determinant of success in seedling establishment: higher seed weight has been said to correlate with successful germination (Harper,1977; Marshall,1986). Seed numbers and percent seed set of both species were higher in Boulder than they were in Konza. The seed weight of *Andropogon gerardii* was slightly higher in Boulder than it was in Konza, while the seed weight of *Sorghastrum avenaceum* was higher in Konza than it was in Boulder. This result matched that from comparison between Konza 10-year-burned and Boulder mesic-burned site. In both species, Boulder plants put more effort into reproduction in terms of seed numbers and percent seed set than did Konza plants, although Konza Sorghastrum avenaceum had slightly heavier seeds than Boulder's.

Linhart(1974) studied on the intraspecific competition of Veronica peregrina encountered seed weight correlated with moisture gradients in vernal pool. His study revealed that plants in the center of the pool(where the moisture and the competition among plants was high) had larger seeds. The peripheral plants(low moisture) favored numbers of seeds at the expense of seed weight. According to my study, Konza and Boulder represent more mesic and more xeric locations respectively, with regard to substantial differences in mean annual precipitation. Sorghastrum avenaceum in my study followed the same pattern as Linhart's study, as Sorghastrum avenaceum at Konza, where it is moister had heavier seeds and smaller seed numbers than had Boulder. Boulder Andropogon gerardii, on the other hand, produced heavier seeds as well as higher seed numbers than did Konza. The trend of heavier seeds of Andropogon gerardii associated with drier habitat seemed to match Baker's generalization on seed weight and environmental conditions(Baker,1972). In his study, he surveyed the California flora involving 2500 taxa and analyzed the correlations between seed weight and environmental gradients. His conclusion about herbaceous plants was " Seed weights are higher on the average, for the taxa whose seedlings are exposed to the risk of drought soon after establishment ". At present, no general pattern representing both Sorgastrum avenaceum and Andropogon gerardii in terms of seed weight can be made. The two year information was not enough for drawing any firm conclusions, mainly because of the high fluctuations in plant responses between the years.

SUMMARY

1. On the average, Boulder Andropogon gerardii and Sorghastrum avenaceum showed higher seed numbers per inflorescence and higher percent seed set than did Konza counterparts at all sites(the annual burned site was excluded in this comparison). As a result, I conclude that, on the average, Boulder Andropogon gerardii and Sorghastrum avenaceum had a greater reproductive effort. However, seed production of Boulder both

at xeric and mesic sites varied quite a lot during the two years of my study. This year to-year variability might be due to either the climatic variations or the population dynamics.of each species itself.

2. No particular conclusions can be drawn from either Boulder or Konza regarding the effect of burning on numbers of florets, seeds, midge and midge parasites. In general, Andropogon gerardii appeared to respond positively to burning, as reflected for example in the increased seed numbers on the annual-burned and 4-year-burned sites in 1989 and 1990 respectively. On the contrary, the opposite was true for Sorghastrum avenaceum. The responses of Andropogon gerardii and Sorghastrum avenaceum to burning seemed to depend locations and year to-year fluctuations. Populations of midge and midge parasites varied a good deal from year to-year and seemed to be fire independent.

3. Among different burning regimes at Konza, the 4-year-burned site is associated with higher numbers of flowers, higher numbers of seeds and heavier seeds as compared to the other sites. Therefore, 4-year-burning regime appears to be correlated with high seed reproduction potential.

4. At Konza, the seed weight of Andropogon gerardii was less variable across different burning regimes and between years than it was in Sorghastrum avenaceum.

5. At present, there is no explanation why Sorghastrum avenaceum has higher seed output than Andropogon gerardii. The result from seed bank also revealed this same trend by containing more seeds of Sorgastrum avenaceum than of Andropogon gerardii. Refering to the previous studies on Cytology done by Riley and Vogel(1982), Sorghastrum avenaceum is tetraploids (2n=40) and Andropogon gerardii is hexaploids (2n=60). Both species behaved meiotically as diploids with normal bivalent pairing. There might be other factors, causing this big difference in seed output of the two species. Therefore, the in depth studies in reproductive biology are suggested in order to explain this phenomenon

In order to have a better understanding of the reproductive biology of these two tallgrasses in different areas and with different burning regimes, I suggest a long term study in reproductive biology of these two dominant species. This study should consider climatic information as well as other physical environments such as soil moisture, soil pH and soil structure. With long term information and measurements of multiple variables, one may expect to find a clearer picture of how the plants respond and what factors most influence their reproductive performances.

CHAPTER VI

CONCLUSION

Tallgrass Prairie was once widespread along the Front Range in eastern Colorado. Human influences such as overgrazing, agriculture and urban development have destroyed most of the Tallgrass Prairie sites in Colorado. Only a few small patches of this relictual Tallgrass Prairie remain. The best protected ones are scattered around the foothills near Boulder, Colorado. The Colorado Tallgrass is widely separated from the principal Tallgrass area of the eastern Great Plains.

It is important to examine the ecological processes that underlie this remnant Tallgrass Prairie. It also behooves us to compare and contrast it with the Tallgrass Prairie to the east. In this way we can come to a better understanding of the structure of Tallgrass Prairie and to grasslands in general. To this end, I studied reproductive resources of the Boulder Tallgrass

Prairie, and compared them with those of the largest protected natural Tallgrass Prairie of North America: Konza Tallgrass Prairie. My goal for findings of this study can be applied to planning, management, and future research in many ways.

The Boulder Tallgrass Prairie distributes restrictly to the mesic conditions that exist in a narrow band along the foothills of the Rocky Mountains. Besides, temperature and moisture regimes of the Boulder Tallgrass Prairie are at the extremes of those factors at Konza(see chapter III page 44). By examining the parameters of plant reproduction in this Tallgrass remnant we may be able to restore disturbed or destroyed portions of this flora elsewhere along the base of the Colorado Front Range. A few decades ago this vegetation extended from Boulder to Colorado Springs, Colorado, but now it exists only in scattered unprotected patches except in Boulder.

The seed banks of both grasslands(Konza and Boulder) contain important exotic plants. This means should current aboveground vegetation die, it would be replaced with exotic weedy vegetation, because seed banks represent potential future vegetation. Konza's Tallgrass seeds, has half as many exotic seeds as that of the Boulder Prairie. This most likely reflects the tenuous nature of the relictual grassland in Colorado plus improper practices on this grassland for the past few decades.

The Boulder seed bank represents that of a disturbed grassland. Its very large seed bank is comprised mostly of non-native weedy species. This indicates that there has been improper management of this grassland. Seed bank size appears to increase relatively with disturbance in a perennial grassland. Proportionately, the Boulder seed bank is comparable in size with the seed bank of the disturbed short grasslands(Table 36).

Practical recommendations can be taken from this research. Revegetation by means of seeds collected from the local native Tallgrass plants should be implemented. Seeds should be grown in the greenhouse and sown in nature. For greenhouse germinated seeds, after germination, seedlings can be transplanted to the field. Manual removal of weedy species seedlings is highly recommended

Table 36. Comparison of densities of seeds/m2 from various studies done on Tallgrass Prairie and other grasslands.

Seed/m2	Authorities
2091	Johnson and Anderson (1986) (Weston cemetery prairie, Illinois)
5640	Rabinowitz (1981) (Missouri ramnant tallgrass prairie)
300-800	Lippert and Hopkins(1950) (undisturbed short and midgrass prairie)
3638	Lippert and Hopkins(1950) (disturbed short and midgrass prairie)
8230	Major and Pyott(1966) (California bunch grass, dominated by annual grasses)
3451	Santanachote(1991) (relictual Boulder Tallgrass Prairie)

because this is the most effective time and the safest way for weed controls. Other methods of weed removal may destroy native species as well as causing mutant plants which are resistant to that particular chemicals. The hand-removing weeds practice has never been seriously followed before in any of the public grasslands; weeds are controlled mostly either through herbicides or through grazing by exotic herbivores. However, the city of Boulder has an active volunteer corps, eager to participate in conservation and restoration activities. Therefore, this way of controlling weeds should be a successful project when it is introduced to the management planning. Fire reduced the aboveground vegetation of major weedy species and removed their seeds from the seed bank. Besides seeding native plants and hand-removing weeds, periodic burning is recommended in order to eliminate excess litter and invasion by exotic grasses and forbs.

The biological and ecological properties of the plants that comprise the relictual population can give us an insight into long term survival vs. extirpation or extinction of the vegetation through geologic and contemporary time. Many questions in population genetics and physiology can be approched by comparing the morphology and development, genetic and physiological resources of the Konza and Boulder populations.

Understanding the Tallgrass Prairie ecosystem not only helps maintain and enhance the remnants of natural Tallgrass Prairie to reach its maximum potential, but also helps save the disturbed Prairie from extinction by mismanagement.

Appendix

Appendix A.1. Species list of Boulder Tallgrass Prairie's Vegetation

AGAVACEAE
- *Yucca glauca* Nuttall

ALLIACEAE
- *Allium textile* Nelson & Macbride

ALSINACEAE
- *Cerastium strictum* L.
- *Eremogone fendleri* (Gray) Ikonnikov
- *Paronychia jamesii* Torrey & Gray

ANACARDIACEAE
- *Rhus aromatica* Aiton subsp. *trilobata* (Nuttall)Weber

APIACEAE
- *Lomatium orientale* Coulter & Rose

ASCLEPIADACEAE
- *Asclepias speciosa* Torrey

ASTERACEAE
- *Achillea lanulosa* Nuttall
- *Acosta(Centauria) diffusa* (Lamarck) Sojak
- *Ambrosia artemisiifolia* L. var. *elatior* (L.) Descourtils
- *Artemisia frigida* Willdenow
- *Artemisia ludoviciana* Nuttall
- *Aster porteri* Gray
- *Cichorium intybus* L.
- *Cirsium undulatum* (Nuttall) Sprengel
- *Conyza canadensis* (L.) Cronquist
- *Erigeron flagellaris* Gray
- *Erigeron speciosa* (Lindley) de Candolle
- *Gaillardia aristata* Pursh
- *Grindelia squarrosa* (Pursh) Dunal
- *Gutierrezia sarothrae* (Pursh) Britton & Rusby
- *Heterotheca fulcrata* (Greene) Shinners
- *Heterotheca villosa* (Pursh) Shinners
- *Lactuca serriola* L.
- *Liatris punctata* Hooker
- *Nothocalais cuspidata* (Pursh) Greene
- *Oligoneuron rigidum* (L.) Small
- *Oligosporus pacificus* (Nuttall) Poljakov
- *Podospermum laciniatum* (L.) de Candolle
- *Senecio spartioides* Torrey & Gray
- *Solidago serotinoides* Love & Love
- *Taraxacum officinale* G.H.Weber
- *Thelesperma megapotamicum* (Sprengel) Kuntze
- *Townsendia hookeri* Beaman
- *Tragopogon dubius* Scopoli subsp. major (Jacquin) Vollmann
- *Virgulus(Aster) falcatus* (Lindley) Reveal & Keener

BORAGINACEAE
- *Cryptantha crassisepala* (Torrey & Gray) Greene
- *Lappula redowskii* (Hornemann) Greene
- *Lithospermum incisum* Lehmann
- *Oreocarya virgata* (Porter) Greene

BRASSICACEAE
- *Alyssum minus* (L.) Rothmaler
- *Camelina microcarpa* Andrzejowski
- *Descurainia sophia* (L.) Weber
- *Draba reptans* (Larmarck) Fernald
- *Erysimum capitatum* (Douglas) Greene
- *Neolepia(Lepidium) campestre*
- *Sisymbrium altissimum* L.
- *Lepidium densiflorum* Schrader

Appendix A.1. Species list of Boulder Tallgrass Prairie's Vegetation

CACTACEAE
- Coryphantha missouriensis (Sweet) Britton & Rose
- Echinocereus viridiflorus Engelmann
- Opuntia compressa (Salisb) Macbr.
- Opuntia fragilis (Nuttall) Haworth

CAPPRIFOLIACEAE
- Symphoricarpos rotundifolius Gray

CARYOPHYLLACEAE
- Dianthus armeria L.
- Silene antirrhina L.

CHENOPODIACEAE
- Chenopodium leptophyllum (Nuttall) Watson

COMMELINACEAE
- Tradescantia occidentalis (Britton) Smyth

CONVOLVULACEAE
- Evolulus nuttallianus Roemer & Schultes
- Convolvulus arvensis L.

CYPERACEAE
- Carex pensylvanica Larmarck subsp. heliophila (Mackenzie) Weber
- Carex praegracilis Boott
- Carex sp.
- Cyperus esculentus L.
- Eleocharis palustris (L.) Roemer & Schultes
- Mariscus fendlerianus (Bockeler) Koyama
- Mariscus schweinitzii (Torrey) Koyama

EQUISITACEAE
- Hippochaete hyemalis (L.) Bruhin subsp. affinis (A.Braun) Weber

EUPHORBIACEAE
- Euphorbia sp.

FABACEAE
- Amorpha nana Nuttall
- Dalea candida Michaux var. oligophylla (Torrey) Shinners
- Dalea purpurea Ventenat
- Lespedeza sp.
- Lupinus argenteus Pursh
- Medicago lupulina L.
- Melilotus officinalis (L.) Pallas
- Oxytropis lambertii Pursh
- Psoralidium tenuiflorum (Pursh) Rydberg
- Thermopsis divaricarpa Nelson
- Trifolium pratense L.
- Vexibia(Sophora) nuttalliana (Turner) Weber

GERANIACEAE
- Erodium cicutarium (L.) L'Heritier
- Geranium caespitosum James

HELLEBORACEAE
- Delphinium carolinianum Walter subsp virescens (Nuttall) M.C.Johnston

HYDROPHTLLACEAE
- Phacelia heterophylla Pursh

HYPERICACEAE
- Hypericum perforatum L.

IRIDACEAE
- Sisyrinchium montanum Greene

JUNCACEAE
- Juncus arcticus Willdenow subsp. ater (Rydberg) Hulten
- Juncus bufonius L.
- Juncus dudleyi Wiegand

Appendix A.1. Species list of Boulder Tallgrass Prairie's Vegetation

Juncus nodusus L.

LAMIACEAE

Monarda pectinata Nuttall

Prunella vulgaris

MOLLUGINACEAE

Mollugo verticillata L.

NYCTAGINACEAE

Oxybaphus linearis (Pursh) B.L. Robinson

ONAGRACEAE

Calylophus serrulatus (Nuttall) Raven

Gaura coccinea Nuttall

Oenothera villosa Thunberg

OROBANCHACEAE

Orobanche fasciculata (Nutt.) Torrey & Gray

OXALIDACEAE

Oxalis dillenii Jacquin

PLANTAGINACEAE

Plantago lanceolata L.

Plantago patagonica Jacquin

POACEAE

Agrostis gigantea Roth

Andropogon gerardii Vitman

Anisantha(Bromus) tectorum (L.) Nevski

Aristida purpurea Nuttall

Bouteloua curtipendula (Michaux) Torrey

Bromopsis inermis (Leysser) Holub

Bromus japonicus Thunberg

Buchlöe dactyloides Engelmann

Calamovilfa longifolia (Hooker) Scribner

Chondrosum(Bouteloua) gracile Humboldt, Bonpland & Kunth

Critesion brachyantherum (Nevski) Weber

Dactylis glomerata L.

Dichanthelium oligosanthes (Schultes) Gould var. *scribnerianum* (Nash) Gould

Distichlis spicata (L.) subsp. stricta

Elymus longifolius (Smith) Gould

Elytrigia repens (L.) Nevski

Festuca pratensis Hudson

Festuca rubra L.

Koeleria macrantha (Ledebour) Schultes

Lycerus phleoides Humboldt, Bonpland & Kunth

Muhlenbergia richardsonis (Trinius) Rydberg

Muhlenburgia asperifolia (Nees & Meyen)

Muhlenburgia wrightii Vasey

Panicum virgatum L.

Pascopyrum smithii (Rydberg) Love

Phleum pratense L.

Poa compressa L.

Poa pratensis L.

Schizachyrium scoparium (Michaux) Nash

Sorghastrum avenaceum (Michaux) Nash Scribner

Sporobolus asper (Michaux) Kunth

Sporobolus cryptandrus (Torrey & Gray)

Sporobolus heterolepis (Gray) Gray

Appendix A.1. Species list of Boulder Tallgrass Prairie's Vegetation

Stipa comata Trinius & Ruprecht

POLEMONIACEAE

Collomia linearis Nuttall

Gilia pinnatifida Nuttall

POLYGONACEAE

Acetosella vulgaris (Koch) Fourreau

Eriogonum effusum Nuttall

Eriogonum umbellatum Torrey

Polygonum ramosissimum Michaux

Pterogonum alatum (Torrey) Gross

Rumex crispus L.

PORTULACACEAE

Talinum parviflorum Nuttall

RHAMNACEAE

Ceanothus herbaceus Rafinesque

ROSACEAE

Drymocallis fissa (Nuttall) Rydberg

Potentilla hippiana Lehmann

Rosa arkansana Porter

SANTALACEAE

Comandra umbellata (L.) Nuttall

SCROPHULARIACEAE

Linaria canadensis (L.) Dum.

Penstemon secundiflorus Bentham

Verbascum thapsus L.

TYPHACEAE

Typha sp

VERBENACEAE

Phyla cuneifolia (Torrey) Greene

VIOLACEAE

Viola nuttallii Pursh

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Appendix A.2. Vegetation cover on the Xeric unburned and burned plots. In 1988 cover was recorded, using Braun-Blanquet classes; in 1989 and 1990, it was recorded in %. Species listed had at least 0.5% of total species occurrences.

Species	Treatment	1988	1989	1990
		mean±S.D.	mean±S.D.	means±S.D.
Bromus spp.	Unburn	1.76 ± 0.5	1.44 ± 1.3	1.73 ± 1.6
	Burn	1.22 ± 0.4	0.57 ± 0.9	1.12 ± 1.8
Stipa comata	Unburn	2.22 ± 0.7	3.75 ± 3.0	4.18 ± 3.2
	Burn	2.22 ± 0.6	3.42 ± 2.8	4.23 ± 2.9
Bouteloua curtipendula	Unburn	1.84 ± 0.6	1.46 ± 1.5	2.12 ± 1.9
	Burn	1.98 ± 0.4	1.72 ± 1.5	2.24 ± 1.9
Andropogon gerardii	Unburn	2.36 ± 0.7	5.88 ± 4.6	6.73 ± 5.5
	Burn	2.44 ± 0.7	5.54 ± 3.6	6.80 ± 5.4
Artemisia frigida	Unburn	2.07 ± 0.6	5.69 ± 2.4	3.03 ± 2.7
	Burn	2.21 ± 0.7	4.23 ± 4.5	4.48 ± 4.5
Echinocereus viridiflorus	Unburn	1.19 ± 0.4	0.66 ± 0.4	0.74 ± 0.4
	Burn	1.44 ± 0.5	0.79 ± 0.6	0.99 ± 0.7
Oligosporus pacificus	Unburn	1.67 ± 0.5	1.40 ± 1.3	1.38 ± 1.2
	Burn	1.88 ± 0.4	1.51 ± 1.3	1.29 ± 0.8
Opuntia fragilis	Unburn	1.48 ± 0.6	1.29 ± 1.4	1.35 ± 2.4
	Burn	1.44 ± 0.5	1.01 ± 1.0	1.11 ± 1.2
Carex pensylvanica ssp. heliophila	Unburn	1.52 ± 0.5	0.82 ± 0.5	1.40 ± 1.5
	Burn	1.70 ± 0.5	1.01 ± 0.9	1.49 ± 1.6
Tragopogon dubius	Unburn	1.38 ± 0.5	0.59 ± 0.2	0.59 ± 0.2
	Burn	1.67 ± 0.5	0.60 ± 0.2	0.55 ± 0.2
Senecio spartioides	Unburn	1.37 ± 0.5	0.89 ± 0.8	0.87 ± 0.5
	Burn	1.43 ± 0.5	0.77 ± 0.5	1.09 ± 0.8

Appendix A.2 cont.				
Species	Treatment	1988	1989	1990
		mean±S.D.	mean±S.D.	means±S.D.
Ambrosia artemissifolia	Unburn	1.66 ± 0.7	1.16 ± 1.5	1.36 ± 1.3
	Burn	1.78 ± 0.4	0.79 ± 1.0	0.65 ± 0.5
Poralidium tenuiflorum	Unburn	2.20 ± 0.6	2.64 ± 2.6	3.22 ± 3.8
	Burn	2.21 ± 0.5	2.92 ± 5.0	3.40 ± 6.6
Chondrosum(Bouteloua) gracile	Unburn	1.79 ± 0.4	0.81 ± 0.7	0.93 ± 0.8
	Burn	1.70 ± 0.5	0.67 ± 0.4	0.76 ± 0.6
Liatris punctata	Unburn	1.58 ± 0.5	1.01 ± 0.7	1.08 ± 0.8
	Burn	1.77 ± 0.5	1.02 ± 1.0	1.07 ± 0.9
Opuntia compressa	Unburn	1.72 ± 0.6	1.08 ± 1.0	1.22 ± 1.0
	Burn	1.64 ± 0.6	0.99 ± 1.0	1.42 ± 1.5
Heterotheca fulcrata	Unburn	1.56 ± 0.5	0.92 ± 0.8	1.15 ± 1.1
	Burn	1.74 ± 0.4	1.13 ± 1.1	1.01 ± 0.9
Poa spp.	Unburn	1.50 ± 0.5	0.84 ± 0.5	0.65 ± 0.4
	Burn	1.00 ± 0.0	0.73 ± 0.4	0.81 ± 0.9
Alyssum minus	Unburn	1.53 ± 0.7	1.68 ± 2.1	2.42 ± 3.5
	Burn	1.20 ± 0.5	0.54 ± 0.2	1.07 ± 2.0
Panicum virgatum	Unburn	2.07 ± 0.6	2.55 ± 3.5	2.54 ± 4.0
	Burn	2.33 ± 0.5	4.03 ± 2.3	2.60 ± 2.1
Sporobolus cryptandrus	Unburn	1.86 ± 0.5	1.02 ± 1.0	0.90 ± 0.7
	Burn	1.87 ± 0.5	1.69 ± 1.9	1.63 ± 1.3
Comandra umbellata	Unburn	1.73 ± 0.5	1.73 ± 1.0	1.41 ± 0.9
	Burn	2.11 ± 0.3	2.36 ± 1.7	1.38 ± 0.8
Talinum parviflorum	Unburn	1.00 ± 0.0	0.50 ± 0.0	0.55 ± 0.2
	Burn	1.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
Aristida purpurea	Unburn	1.78 ± 0.4	1.81 ± 1.1	1.13 ± 1.2
	Burn	1.96 ± 0.2	0.80 ± 0.7	0.50 ± 0.0

Appendix A.2. cont				
Species	Treatment	1988	1989	1990
		mean±S.D.	mean±S.D.	means±S.D.
Rosa arkansana	Unburn	1.88 ± 0.4	2.70 ± 2.6	2.81 ± 1.9
	Burn	2.00 ± 0.0	1.00 ± 0.0	0.00 ± 0.0
Acetosella vulgaris	Unburn	1.75 ± 0.5	2.63 ± 1.5	4.78 ± 3.9
	Burn	2.00 ± 0.0	1.50 ± 0.7	2.44 ± 1.5
Yucca glauca	Unburn	2.71 ± 0.8	10.22 ± 10.7	7.45 ± 7.1
	Burn	2.13 ± 0.4	2.00 ± 1.4	5.91 ± 7.7
Thelesperma megapotamicum	Unburn	2.00 ± 0.0	0.63 ± 0.2	0.70 ± 0.3
	Burn	1.75 ± 0.5	0.75 ± 0.5	0.56 ± 0.2
Lactuca serriola	Unburn	1.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	Burn	1.25 ± 0.5	0.88 ± 0.8	0.50 ± 0.0
Geranium caespotosum	Unburn	2.33 ± 0.5	2.93 ± 1.4	3.77 ± 2.8
	Burn	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
Paronychia jamesii	Unburn	1.83 ± 0.8	0.90 ± 0.7	2.00 ± 0.0
	Burn	1.67 ± 0.6	2.13 ± 1.8	2.00 ± 1.7
Cerastium strictum	Unburn	1.83 ± 0.8	3.53 ± 2.9	4.14 ± 3.7
	Burn	1.50 ± 0.6	4.64 ± 7.5	4.17 ± 6.8
Erigeron flagellaris	Unburn	1.67 ± 0.8	1.98 ± 1.7	4.42 ± 5.3
	Burn	2.00 ± 0.6	2.18 ± 2.5	2.49 ± 2.8
Oxytropis lambertii	Unburn	1.67 ± 0.5	0.85 ± 0.5	1.40 ± 0.6
	Burn	1.73 ± 0.5	0.81 ± 0.5	1.19 ± 1.1
Gutierrezia sarothrae	Unburn	1.67 ± 0.8	1.20 ± 1.4	1.83 ± 1.5
	Burn	0.00 ± 0.0	1.22 ± 1.3	1.13 ± 1.0
Koeleria macrantha	Unburn	1.33 ± 0.6	0.63 ± 0.2	0.57 ± 0.2
	Burn	1.65 ± 0.5	0.78 ± 0.6	0.92 ± 0.7
Eriogonum effusum	Unburn	1.80 ± 0.8	4.94 ± 6.9	3.75 ± 5.6
	Burn	2.09 ± 0.3	2.62 ± 2.5	3.53 ± 3.2

Appendix A.2. cont.				
Species	Treatment	1988	1989	1990
		mean±S.D.	mean±S.D.	means±S.D.
Pascopyrum smithii	Unburn	0.00 ± 0.0	1.60 ± 1.5	1.86 ± 1.6
	Burn	1.80 ± 0.4	0.56 ± 0.2	0.52 ± 0.1
Calamovilfa longifolia	Unburn	2.00 ± 0.0	1.34 ± 1.3	2.44 ± 2.2
	Burn	2.13 ± 0.4	1.10 ± 0.8	2.10 ± 1.6
Unknown Monocots	Unburn	1.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
	Burn	1.71 ± 0.5	0.00 ± 0.0	0.00 ± 0.0
Unknown Dicots	Unburn	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
	Burn	1.43 ± 0.5	0.50 ± 0.0	0.00 ± 0.0
Dalea candida	Unburn	2.00 ± 0.0	1.35 ± 1.1	0.67 ± 0.3
	Burn	2.00 ± 0.0	0.69 ± 0.4	1.00 ± 0.9
Virgulus falcatus	Unburn	1.60 ± 0.6	0.75 ± 0.4	0.50 ± 0.0
	Burn	2.00 ± 0.0	1.00 ± 0.6	1.03 ± 1.0
Dalea purpurea	Unburn	0.00 ± 0.0	1.00 ± 0.0	0.50 ± 0.0
	Burn	1.50 ± 0.6	0.64 ± 0.2	0.69 ± 0.5
Camelina microcarpa	Unburn	0.00 ± 0.0	0.91 ± 1.1	0.65 ± 0.3
	Burn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
Phacelia heterophylla	Unburn	2.00 ± 0.0	0.67 ± 0.6	1.14 ± 1.0
	Burn	0.00 ± 0.0	0.52 ± 0.1	0.62 ± 0.3
Lepidium densiflorum	Unburn	0.00 ± 0.0	0.52 ± 0.1	0.51 ± 0.1
	Burn	0.00 ± 0.0	0.52 ± 0.2	0.57 ± 0.3
Chenopodium leptophyllum	Unburn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	Burn	0.00 ± 0.0	0.51 ± 0.1	0.80 ± 0.7
Plantago patagonica	Unburn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	Burn	1.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
Tradescantia occidentalis	Unburn	0.00 ± 0.0	0.53 ± 0.1	0.50 ± 0.0
	Burn	0.00 ± 0.0	0.50 ± 0.0	0.52 ± 0.1

Appendix A.2. cont.				
Species	Treatment	1988	1989	1990
		mean±S.D.	mean±S.D.	means±S.D.
Erodium cicutarium	Unburn	1.00 ± 0.0	1.11 ± 1.1	1.22 ± 1.2
	Burn	0.00 ± 0.0	1.21 ± 1.0	1.66 ± 1.5
Lomatium orientale	Unburn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	Burn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
Eriogonum umbellatum	Unburn	2.00 ± 0.0	2.44 ± 1.2	5.87 ± 3.1
	Burn	2.00 ± 0.0	3.75 ± 1.0	4.21 ± 5.8
Sisymbrium altissimum	Unburn	1.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	Burn	0.00 ± 0.0	0.85 ± 1.3	0.50 ± 0.0
Gaillardia aristata	Unburn	1.25 ± 0.5	0.50 ± 0.0	0.50 ± 0.0
	Burn	1.60 ± 0.6	0.50 ± 0.0	1.06 ± 1.5
Monarda pectinata	Unburn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	Burn	0.00 ± 0.0	0.50 ± 0.0	0.57 ± 0.3
Viola nuttallii	Unburn	0.00 ± 0.0	0.54 ± 0.1	0.50 ± 0.0
	Burn	0.00 ± 0.0	0.52 ± 0.1	0.50 ± 0.0
Silene antirrhina	Unburn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	Burn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
Evolvulus nuttallianus	Unburn	1.00 ± 0.0	1.75 ± 1.8	0.50 ± 0.0
	Burn	0.00 ± 0.0	1.83 ± 1.6	1.47 ± 0.9
Lupinus argenteus	Unburn	2.60 ± 0.6	2.15 ± 5.2	0.69 ± 0.3
	Burn	2.40 ± 0.9	0.50 ± 0.0	0.74 ± 0.6
Schizachyrium scoparium	Unburn	2.00 ± 0.0	1.58 ± 0.7	1.92 ± 1.0
	Burn	2.25 ± 0.5	2.64 ± 2.5	2.61 ± 2.5

Appendix A.3. Vegetation cover on the Mesic unburned and burned plots. In 1988, cover was recorded, using Braun-Blanquet classes; in 1989 and 1990, it was recorded in % .
Species listed had at least 0.5% of total species occurrences.

		1988	1989	1990
Species	Treatment	mean±S.D.	mean±S.D.	mean±S.D.
Poa spp.	unburn	2.16 ± 0.5	3.45 ± 2.1	3.75 ± 2.3
	burn	1.83 ± 0.5	2.21 ± 1.6	2.30 ± 1.5
Plantago lanceolata	unburn	2.20 ± 0.6	2.65 ± 2.1	5.58 ± 4.2
	burn	2.48 ± 0.7	5.19 ± 3.4	8.21 ± 5.1
Sporobolus asper	unburn	2.06 ± 1.8	2.07 ± 1.8	1.98 ± 1.9
	burn	1.83 ± 0.6	2.04 ± 1.7	2.43 ± 1.9
virgulus falcatus	unburn	1.13 ± 0.3	0.55 ± 0.2	0.69 ± 0.5
	burn	1.13 ± 0.3	0.55 ± 0.3	0.65 ± 0.7
Sorghastrum avenaceum	unburn	2.24 ± 0.6	3.22 ± 2.9	4.58 ± 3.6
	burn	2.24 ± 0.7	3.20 ± 3.2	3.85 ± 3.2
Cichorium intybus	unburn	1.56 ± 0.5	1.65 ± 1.9	3.40 ± 3.2
	burn	1.66 ± 0.5	1.97 ± 2.2	4.28 ± 4.1
Buchlöe dactyloides	unburn	1.44 ± 0.5	0.82 ± 0.7	1.71 ± 2.2
	burn	1.81 ± 0.5	1.14 ± 1.7	1.61 ± 2.1
Panicum virgatum	unburn	1.94 ± 0.6	1.84 ± 2.0	1.61 ± 2.4
	burn	1.78 ± 0.7	1.47 ± 1.4	2.30 ± 2.7
Bouteloua curtipendular	unburn	1.82 ± 0.6	1.01 ± 1.2	3.11 ± 3.9
	burn	2.04 ± 0.6	2.37 ± 2.2	3.86 ± 3.2
Ambrosia artimisiifolia	unburn	1.44 ± 0.6	1.07 ± 1.4	1.61 ± 2.4
	burn	1.31 ± 0.5	0.67 ± 0.4	0.62 ± 0.4
Oligosporus rigidum	unburn	1.38 ± 0.5	0.64 ± 0.4	0.84 ± 0.7
	burn	1.60 ± 0.6	0.66 ± 0.5	0.68 ± 0.4

Appendix A.3. cont.				
		1988	1989	1990
Species	Treatment	mean±S.D.	mean±S.D.	mean±S.D.
Hippochaete hyemalis	unburn	1.03 ± 0.2	0.55 ± 0.2	0.55 ± 0.2
	burn	0.00 ± 0.0	0.50 ± 0	0.50 ± 0
Convolvulus arvense	unburn	1.24 ± 0.4	0.64 ± 0.4	1.12 ± 1.1
	burn	1.67 ± 0.6	0.96 ± 0.9	1.61 ± 1.9
Andropogon gerardii	unburn	2.44 ± 0.7	3.67 ± 3.2	7.42 ± 6.9
	burn	2.25 ± 0.7	5.53 ± 4.7	6.04 ± 5.6
Psoralidium tenuiflorum	unburn	1.75 ± 0.6	1.25 ± 1.3	2.45 ± 3.2
	burn	1.58 ± 0.6	0.86 ± 0.8	1.10 ± 1.1
Dianthus ameria	unburn	1.45 ± 0.5	0.50 ± 0.0	0.50 ± 0.0
	burn	1.32 ± 0.5	0.53 ± 0.1	0.51 ± 0.1
Bromus spp.	unburn	1.32 ± 0.5	0.57 ± 0.2	0.68 ± 0.5
	burn	1.33 ± 0.5	0.50 ± 0.0	0.50 ± 0.0
Pascopyrum smithii	unburn	1.61 ± 0.7	1.46 ± 2.5	1.88 ± 2.8
	burn	1.09 ± 0.3	0.64 ± 0.6	0.74 ± 0.7
Alyssum minus	unburn	1.71 ± 0.5	0.58 ± 0.2	1.28 ± 1.5
	burn	0.00 ± 0.0	0.50 ± 0.0	0.75 ± 0.6
Agrostis gigantea	unburn	1.92 ± 0.9	1.94 ± 4.4	2.29 ± 4.2
	burn	1.50 ± 0.7	0.63 ± 0.2	1.60 ± 1.6
Juncus arcticus	unburn	1.42 ± 0.5	0.74 ± 0.5	0.76 ± 0.6
	burn	1.46 ± 0.5	0.86 ± 0.5	0.85 ± 0.6
Carex pensylvanica ssp. heliophila	unburn	1.55 ± 0.5	0.63 ± 0.4	0.75 ± 0.5
	burn	1.24 ± 0.4	0.53 ± 0.1	0.56 ± 0.2
Phleum pratense	unburn	1.10 ± 0.3	0.55 ± 0.2	0.68 ± 0.6
	burn	1.17 ± 0.4	0.70 ± 0.5	0.73 ± 0.6
Tragopogon dubius	unburn	1.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	burn	1.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0

Appendix A.3. cont.				
		1988	1989	1990
Species	Treatment	mean±S.D.	mean±S.D.	mean±S.D.
Aster porteri	unburn	1.50 ± 0.8	1.43 ± 1.8	2.56 ± 3.4
	burn	1.47 ± 0.5	0.77 ± 0.7	1.52 ± 1.2
Opuntia compressa	unburn	1.17 ± 0.4	0.94 ± 0.9	0.54 ± 0.1
	burn	1.36 ± 0.7	0.54 ± 0.1	0.64 ± 0.3
Chondrosum(Bouteloua) gracile	unburn	2.00 ± 0.0	0.50 ± 0.0	0.56 ± 0.2
	burn	1.50 ± 0.7	0.96 ± 1.0	0.91 ± 1.0
Achillea lanulosa	unburn	1.40 ± 0.6	1.11 ± 1.2	3.23 ± 4.2
	burn	1.30 ± 0.5	1.42 ± 1.1	1.88 ± 1.9
Unknown seedlings	unburn	1.20 ± 0.5	0.00 ± 0.0	0.00 ± 0.0
	burn	1.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
Opuntia fragilis	unburn	1.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	burn	1.05 ± 0.2	0.51 ± 0.1	0.50 ± 0.0
Acetosella vulgaris	unburn	0.00 ± 0.0	0.57 ± 0.2	1.17 ± 0.7
	burn	1.11 ± 0.3	1.00 ± 8.0	0.98 ± 0.8
Rosa arkansana	unburn	2.33 ± 1.5	12.50 ±13.5	17.00 ± 19.3
	burn	2.20 ± 0.4	4.88 ± 3.5	5.13 ± 3.2
Taraxacum officinale	unburn	0.00 ± 0.0	0.54 ± 0.1	0.64 ± 0.3
	burn	0.00 ± 0.0	0.53 ± 0.1	0.56 ± 0.2
Carex praegracilis	unburn	0.00 ± 0.0	0.85 ± 1.3	2.38 ± 2.0
	burn	0.00 ± 0.0	0.50 ± 0.0	0.64 ± 0.4
Eleocharis palustris	unburn	1.25 ± 0.5	0.66 ± 0.5	2.14 ± 2.1
	burn	0.00 ± 0.0	0.50 ± 0.0	0.72 ± 0.5
Unknown Monocots	unburn	0.00 ± 0.0	2.71 ± 2.8	0.50 ± 0.0
	burn	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0

Appendix A.3. cont.

Species	Treatment	1988 mean±S.D.	1989 mean±S.D.	1990 mean±S.D.
Carex sp.	unburn	2.00 ± 0.0	1.15 ± 1.2	0.00 ± 0.0
	burn	0.00 ± 0.0	1.15 ± 1.2	0.50 ± 0.0
Medicago lupulina	unburn	0.00 ± 0.0	0.50 ± 0.0	0.64 ± 0.6
	burn	1.00 ± 0.0	0.76 ± 0.8	1.81 ± 3.0
Podospermum laciniatum	unburn	0.00 ± 0.0	0.50 ± 0.0	0.75 ± 0.5
	burn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
Species	Treatment	mean±S.D.	mean±S.D.	mean±S.D.
Erodium cicutarium	unburn	0.00 ± 0.0	0.50 ± 0.0	0.50 ± 0.0
	burn	0.00 ± 0.0	0.50 ± 0.0	0.00 ± 0.0
Distichlis spicata	unburn	0.00 ± 0.0	0.50 ± 0.0	2.32 ± 2.6
	burn	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
Cristesion brachyantherum	unburn	0.00 ± 0.0	0.50 ± 0.0	0.77 ± 0.7
	burn	0.00 ± 0.0	0.50 ± 0.0	0.64 ± 0.4
Mariscus schweinitzii	unburn	0.00 ± 0.0	0.00 ± 0.0	0.63 ± 0.4
	burn	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
Heterotheca fulcrata	unburn	1.67 ± 0.6	0.75 ± 0.3	1.00 ± 0.7
	burn	1.00 ± 0.0	0.50 ± 0.0	0.58 ± 0.2
Elytrigia repens	unburn	1.00 ± 1.0	0.50 ± 0.0	0.00 ± 0.0
	burn	0.00 ± 0.0	2.75 ± 1.1	2.91 ± 5.3
Centauria diffussa	unburn	0.00 ± 0.0	1.00 ± 0.5	2.29 ± 1.9
	burn	2.00 ± 0.0	0.50 ± 0.0	1.50 ± 1.3

Appendix B.1. Species list of Boulder Tallgrass Prairie's seed banks

ALSINACEAE
- *Cerastium strictum* L.
- *Paronychia jamesii* Torrey & Gray

APIACEAE
- *Lomatium orientale* Coulter & Rose

ASTERACEAE
- *Acosta(Centauria) diffusa* (Lamarck) Sojak
- *Ambrosia artemisiifolia* L. var. *elatior* (L.) Descourtils
- *Artemisia frigida* Willdenow
- *Artemisia ludoviciana* Nuttall
- *Aster porteri* Gray
- *Cichorium intybus* L.
- *Cirsium arvense* (L.) Scopoli
- *Cirsium undulatum* (Nuttall) Sprengel
- *Cirsium vulgaris* (Savi) Tenore
- *Conyza canadensis* (L.) Cronquist
- *Erigeron flagellaris* Gray Candolle
- *Gnaphalium stramineum* Humboldt, Bonpland & Kunth
- *Grindelia subalpina* Greene Britton & Rusby
- *Heterotheca fulcrata* (Greene) Shinners
- *Lactuca serriola* L.
- *Oligosporus pacificus* (Nuttall) Poljakov
- *Podospermum laciniatum* (L.) de Candolle
- *Senecio spartioides* Torrey & Gray
- *Taraxacum officinale* G.H.Weber
- *Thelesperma megapotamicum* (Sprengel) Kuntze
- *Tragopogon dubius* Scopoli subsp. major (Jacquin) Vollmann

BORAGINACEAE
- *Cryptantha crassisepala* (Torrey & Gray) Greene
- *Lappula redowskii* (Hornemann) Greene
- *Oreocarya virgata* (Porter) Greene

BRASSICACEAE
- *Alyssum minus* (L.) Rothmaler
- *Camelina microcarpa* Andrzejowski
- *Descurainia sophia* (L.) Weber
- *Draba reptans* (Larmarck) Fernald
- *Erysimum capitatum* (Douglas) Greene
- *Nasturtium officinale* R. Brown
- *Neolepia(Lepidium) campestre*
- *Sisymbrium altissimum* L.
- *Lepidium densiflorum* Schrader

CACTACEAE
- *Echinocereus viridiflorus* Engelmann
- *Opuntia compressa* (Salisb) Macbr.

CAMPANULACEAE
- *Triodanis(Specularia) perfoliata* (L.) Nieuwland

CARYOPHYLLACEAE
- *Dianthus armeria* L.
- *Silene antirrhina* L.

CHENOPODIACEAE
- *Chenopodium leptophyllum* (Nuttall) Watson
- *Chenopodium* sp.

COMMELINACEAE

Appendix B.1. Species list of Boulder Tallgrass Prairie's seed banks

Tradescantia occidentalis (Britton) Smyth

CONVOLVULACEAE

Convolvulus arvensis L.

CYPERACEAE

Carex sp.

Eleocharis palustris (L.) Roemer & Schultes

Eleocharis sp

Hemicarpha micrantha (M.Vahl) Pax var. *aristulata* Coville

Mariscus fendlerianus (Bockeler) Koyama

EQUISITACEAE

Hippochaete hyemalis (L.) Bruhin subsp. *affinis* (A.Braun) Weber

EUPHORBIACEAE

Chamaesyce serpyllifolia (Persoon) Small

Tithymalus spathulatus (Larmack) Weber

FABACEAE

Medicago lupulina L.

Psoralidium tenuiflorum (Pursh) Rydberg

GERANIACEAE

Erodium cicutarium (L.) L'Heritier

HYPERICACEAE

Hypericum perforatum L.

IRIDACEAE

Sisyrinchium montanum Greene

JUNCACEAE

Juncus arcticus Willdenow subsp. *ater* (Rydberg) Hulten

Juncus bufonius L.

Juncus dudleyi Wiegand

Juncus marginatus Rostkov

Juncus nodusus L.

LAMIACEAE

Monarda pectinata Nuttall

MOLLUGINACEAE

Mollugo verticillata L.

ONAGRACEAE

Calylophus serrulatus (Nuttall) Raven

Epilobium ciliatum Rafinesque

Epilobium palustre L.

Gaura parviflora Douglas

Oenothera villosa Thunberg

OXALIDACEAE

Oxalis dillenii Jacquin

PAPAVERACEAE

Argemone polyanthemos Vitman

PLANTAGINACEAE

Plantago lanceolata L.

Plantago patagonica Jacquin

POACEAE

Agrostis gigantea Roth

Andropogon gerardii Vitman

Anisantha(Bromus) tectorum (L.) Nevski

Bouteloua curtipendula (Michaux) Torrey

Bromus japonicus Thunberg

Buchlöe dactyloides Engelmann

Appendix B.1. Species list of Boulder Tallgrass Prairie's seed banks

Calamovilfa longifolia (Hooker) Scribner
Chondrosum(Bouteloua) gracile Humboldt, Bonpland & Kunth
Critesion brachyantherum (Nevski) Weber
Dichanthelium oligosanthes (Schultes) Gould var. *scribnerianum* (Nash) Gould
Distichlis spicata (L.) subsp. stricta
Festuca rubra L.
Koeleria macrantha (Ledebour) Schultes
Phleum pratense L.
Poa compressa L.
Poa pratensis L.
Nash
Sorghastrum avenaceum (Michaux) Nash
Sporobolus asper (Michaux) Kunth
Sporobolus cryptandrus (Torrey & Gray)
Stipa comata Trinius & Ruprecht

POLEMONIACEAE
Gilia pinnatifida Nuttall
Microsteris gracilis (Hooker) Greene

POLYGONACEAE
Acetosella vulgaris (Koch) Fourreau
Polygonum ramosissimum Michaux
Rumex crispus L.

PORTULACACEAE
Portulaca oleracea L.
Talinum parviflorum Nuttall

PRIMULACEAE
Androsace occidentalis Pursh

ROSACEAE
Potentilla anglica Laicharding

SALICACEAE
Populus tremuloides Michaux

SCROPHULARIACEAE
Linaria canadensis (L.) Dum.
Verbascum thapsus L.
Veronica peregrina L.

TYPHACEAE
Typha sp

VERBENACEAE
Verbena bracteata Lagasca & Rodriguez

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Appendix B.2. Species list of Konza Tallgrass Prairie's seed banks

ASTERACEAE
- *Ambrosia artemissiifolia* L. var. *elatior* (L.) Descourtils
- *Artemisia ludoviciana* Nuttall
- *Aster porteri* Gray
- *Cirsium undulatum* (Nuttall) Sprengel
- *Conyza cannadensis* (L.) Cronquist
- *Erigeron flagellaris* Gray

CAMPANULACEAE
- *Triodanis(Specularia) perfoliata* (L.) Nieuwland

CARYOPHYLLACEAE
- *Silene antirrhina* L.

CYPERACEAE
- *Mariscus fendlerianus* (Bockeler) Koyama

EQUSITACEAE
- *Equisetum arvense* L.
- *Hippochaete hyemalis* (L.) Bruhin subsp. *affinis* (A.Braun) Weber

IRIDACEAE
- *Sisyrinchium montanum* Greene

JUNCACEAE
- *Juncus dudleyi* Wiegand

LAMIACEAE
- *Hedeoma hispidum* Pursh

PLANTAGINACEAE
- *Plantago virginica* L.

POACEAE
- *Agrostis gigantea* Roth
- *Andropogon gerardii* Vitman
- *Anisantha(Bromus) tectorum* (L.) Nevski
- *Bromus japonicus* Thunberg
- *Dichanthelium oligosanthes* (Schultes) Gould var. *scribnerianum* (Nash) Gould
- *Festuca rubra* L.
- *Poa compressa* L.
- *Poa pratensis* L.
- *Sorghastrum avenaceum* (Michaux) Nash
- *Sphenopholis obtusata* (Michaux) Scribner
- *Sporobolus asper* (Michaux) Kunth
- *Sporobolus cryptandrus* (Torrey & Gray)
- *Trisetum spicatum* L.

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Appendix B.3. Species abbreviations using in the ordination diagrams and their full scientific names

AGRPOL	Agremone polyanthemos
ALYMIN	Alyssum minus
AMBART	Ambrosia artemisiifolia
ANDGER	Andropogon gerardii
ARTFRI	Artemisia frigida
ARTPUR	Aristida purpurea
ASTPOR	Aster porteri
BOUCUR	Bouteloua curtipendula
BOUDAC	Buchloë dactyloides
BROSPP	Bromus spp.
CAMMIC	Camelina microcarpa
CARPEN	Carex pensylvanica ssp. heliophila
CHELEP	Chenopodium leptophyllum
CHOGRA	Chondrosum gracile
CICINT	Cichorium intybus
CIRARV	Cirsium arvense
CONARV	Convolvulus arvense
DIAAME	Dianthus armeria
DRAREP	Draba reptans
ECHVIR	Echinocereus viridifloreus
ELEPAL	Eleocharis palustris
EPICIL	Epilobium ciliatum
ERIFLA	Erigeron flagellaris
EROCIC	Erodium cicutarium
FESRUB	Festuca rubra
HETFUL	Heterotheca fulcrata
HIPHYE	Hippochaete hyemalis
HYPPER	Hypericum perforatum
JUNARC	Juncus arcticus
JUNBUF	Juncus bufonius
JUNDUD	Juncus dudleyi

Appendix B.3 cont. Species abbreviations using in the ordination diagrams and their full scientific names

JUNMAR	Juncus marginatus	PASSMI	Pascopyrum smithii
KOEMAC	Koeleria macrantha	PHAHET	Phacelia heterophylla
LACSER	Lactuca serriola	PHLPRA	Phleum pratense
LAPRED	Lepidium redowskii	PLALAN	Plantago lanceolata
LEPDEN	Lepidium densiflorum	PLAPAT	Plantago patagonica
LIAPUN	Liatris puntata	POASPP	Poa spp
LOMORI	Lomatium occidentale	PSOTEN	Psoralidium tenuiflorum
LUPARG	Lupinus argenteus	SENSPA	Senecio spartioides
MEDLUP	Medicago lupulina	SILANT	Silene antirrhina
MONPEC	Monarda pectinata	SISALT	Sisymbrium altissimum
NEOCAM	Neolepia campestre	SORAVE	Sorghastrum avenaceum
OLIPAC	Oligosporus pacificus	SPOASP	Sporobolus asper
OLIRIG	Oligoneuron rigidum	SPOCRY	Sporobolus cryptandrus
OPUCOM	Opuntia compressa	STICOM	Stipa comata
OPUFRA	Opuntia fragilis	TALPAR	Talinum parviflorum
PANVIR	Panicum virgatum	TAROFF	Taraxacum officinale

Appendix B.3 cont. Species abbreviations using in the ordination diagrams and their full scientific names

THEMEG	Thelesperma megapotamica
TRADUB	Tragopogon dubius
TRAOCC	Tradescantia occidentalis
TRIPER	Triodanis perfoliata
TYPSPP	Typha spp.
VERPER	Veronica peregrina
VERTHA	Verbascum thapsus
VIONUT	Viola nuttallii
VIRFAL	Virgulus falcatus
YUCGLA	Yucca glauca

Appendix B.4.

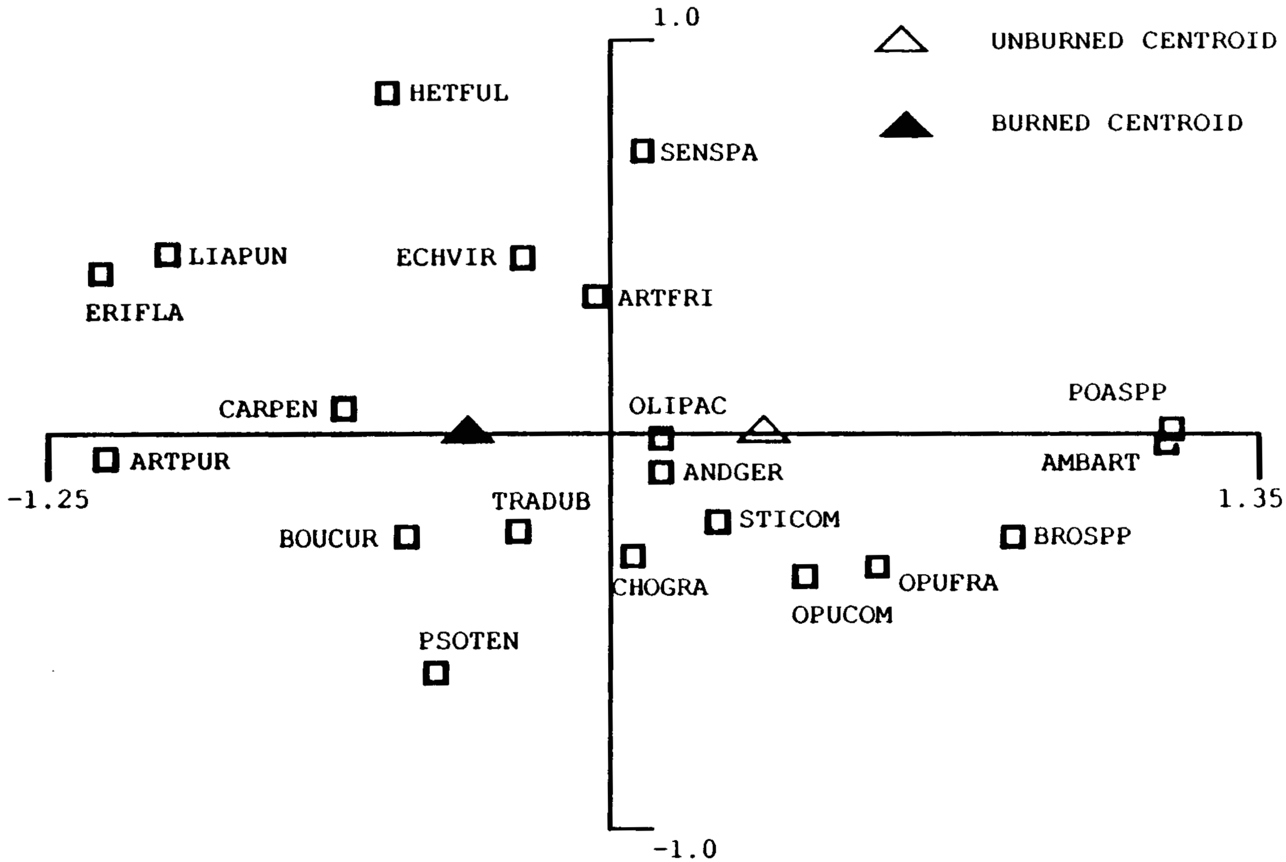

Figure 1. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Xeric site, August 1988 species abbreviations are listed in Appendix B3.

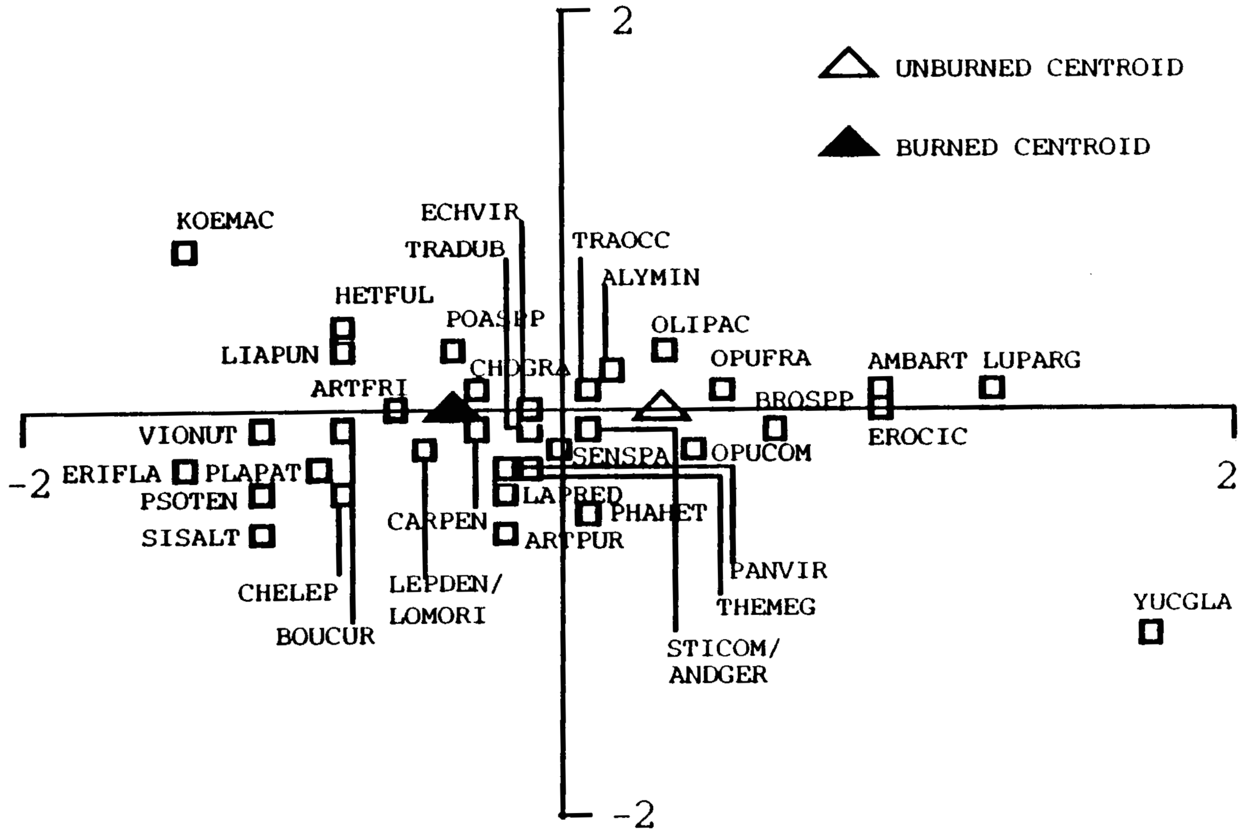

Figure 2. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Xeric site, June 1989 species abbreviations are listed in Appendix B3.

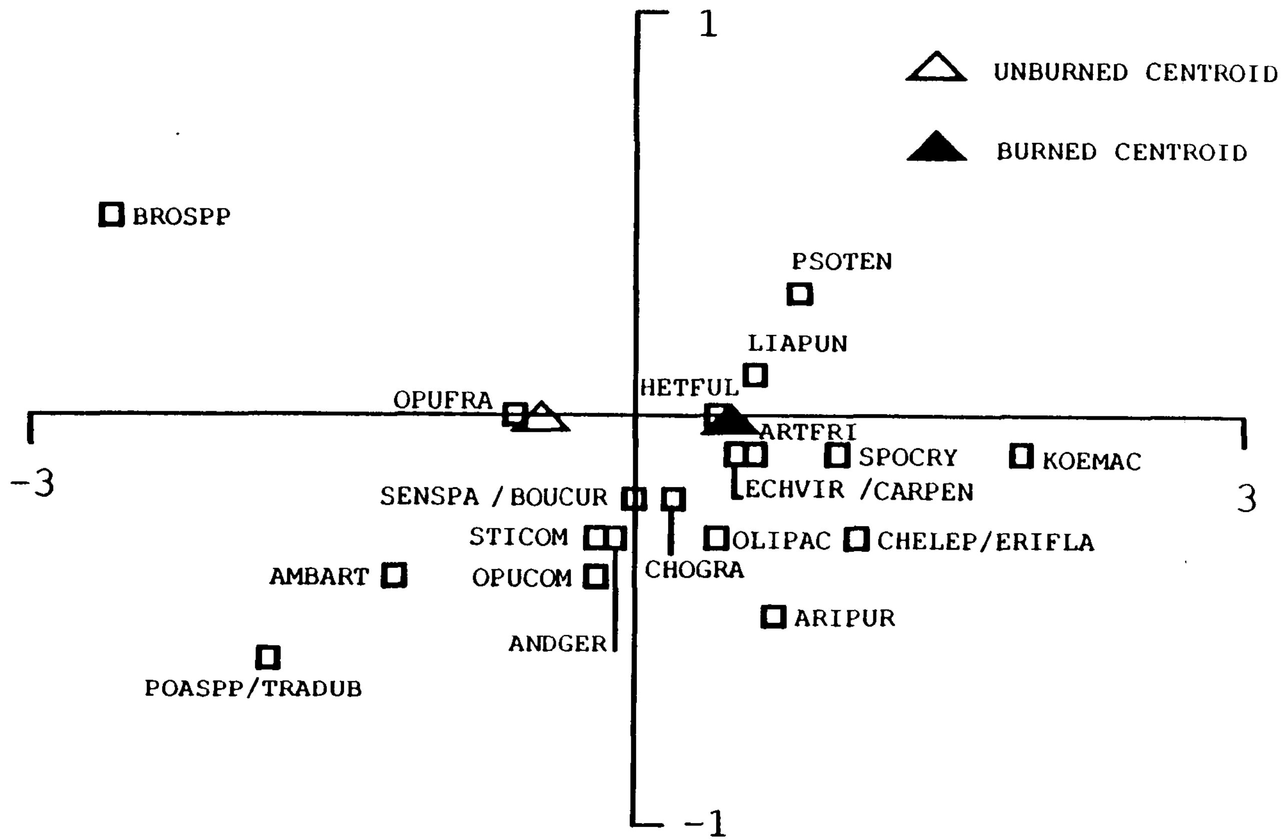

Figure 3. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Xeric site, August 1989 species abbreviations are listed in Appendix B3.

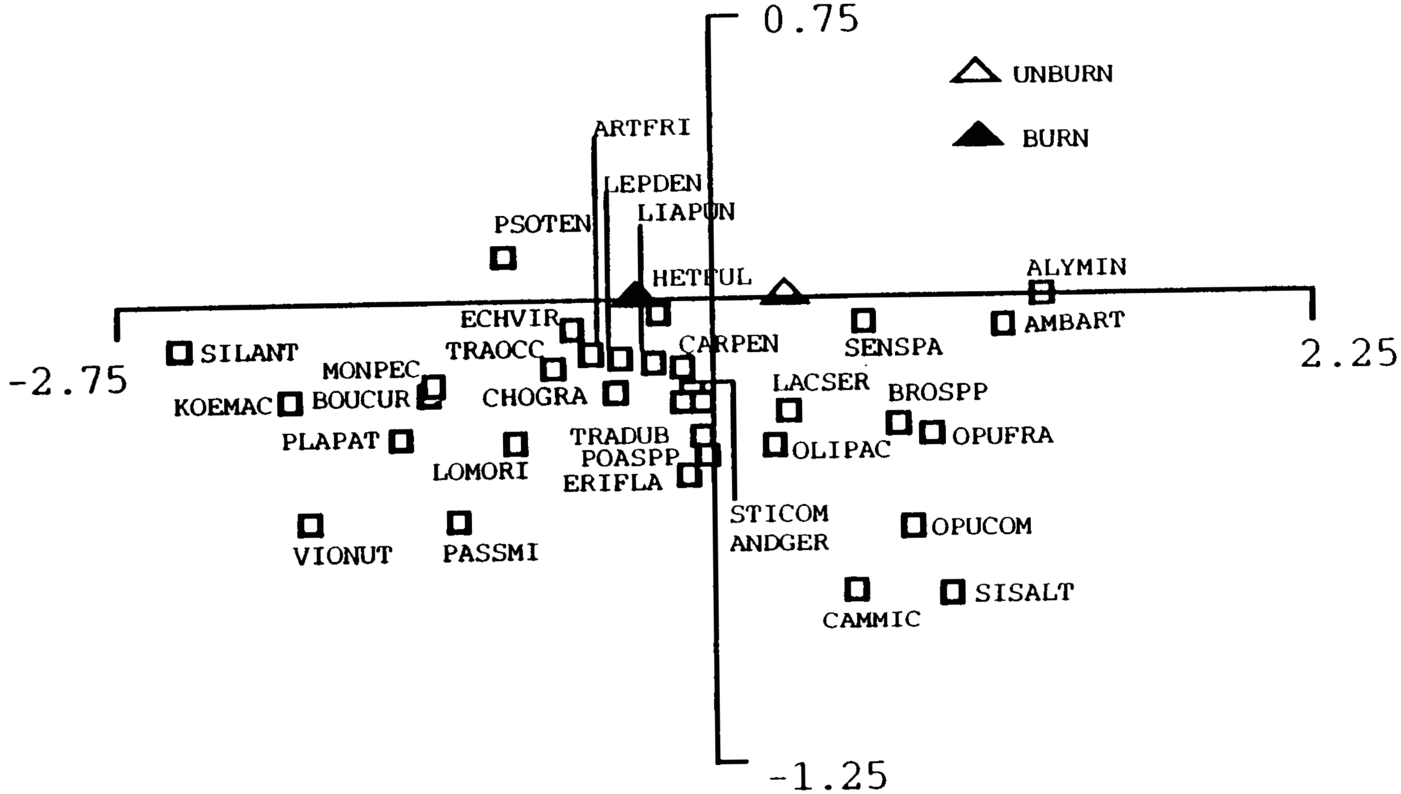

Figure 4. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Xeric site, June 1990 species abbreviations are listed in Appendix B3.

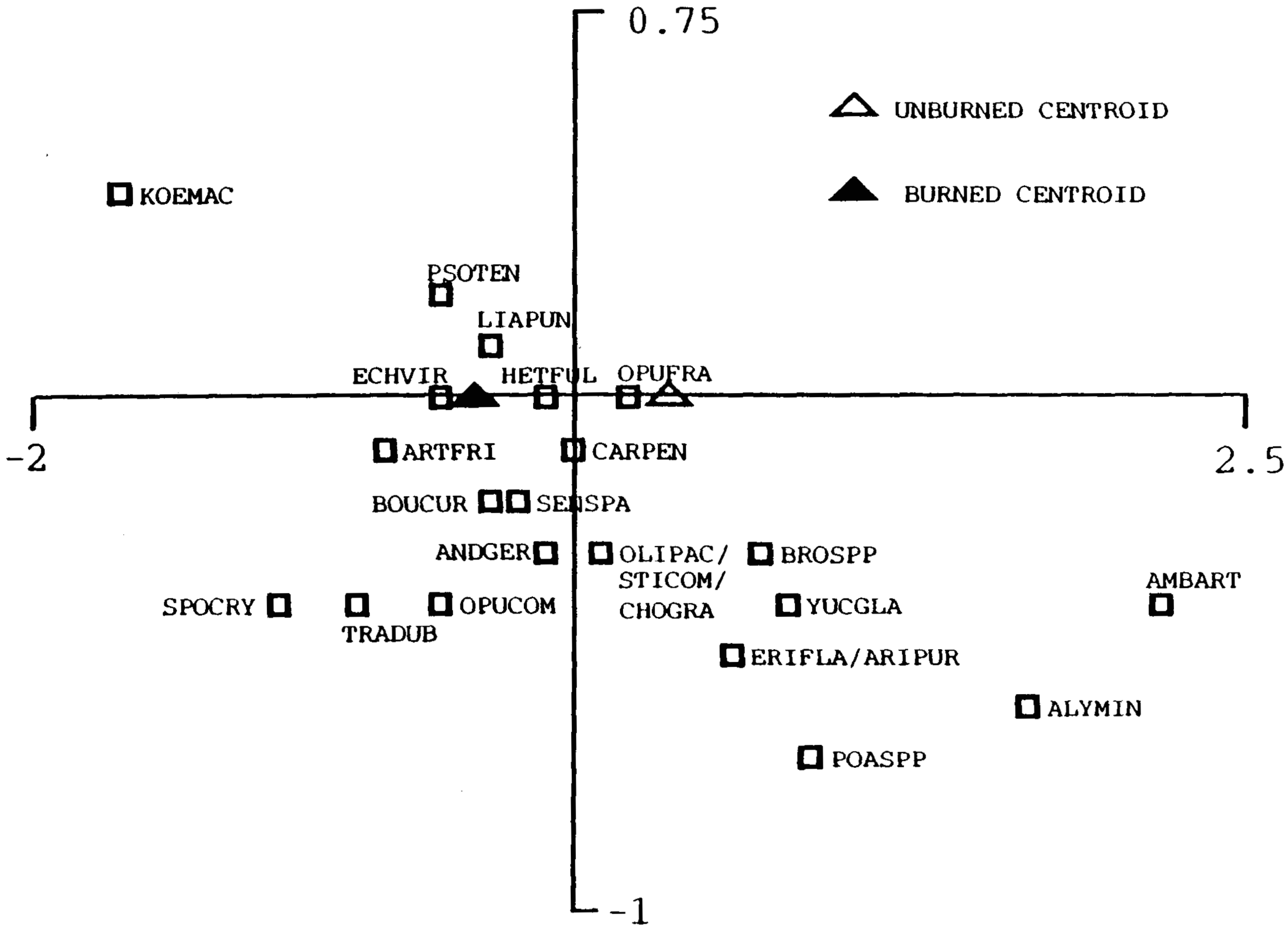

Figure 5. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Xeric site, August 1990 species abbreviations are listed in Appendix B3.

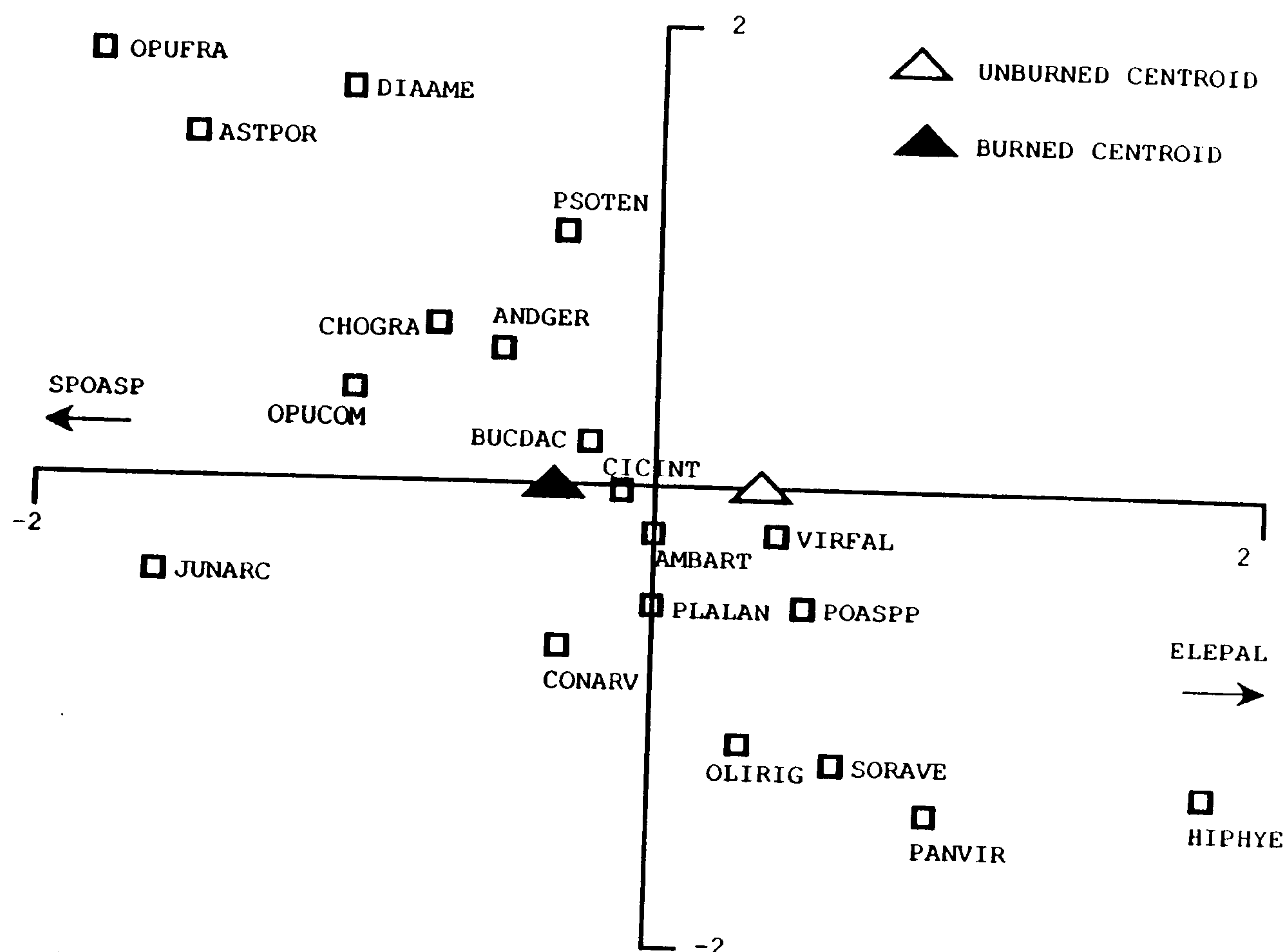

Figure 6. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Mesic site, August 1988 species abbreviations are listed in Appendix B3.

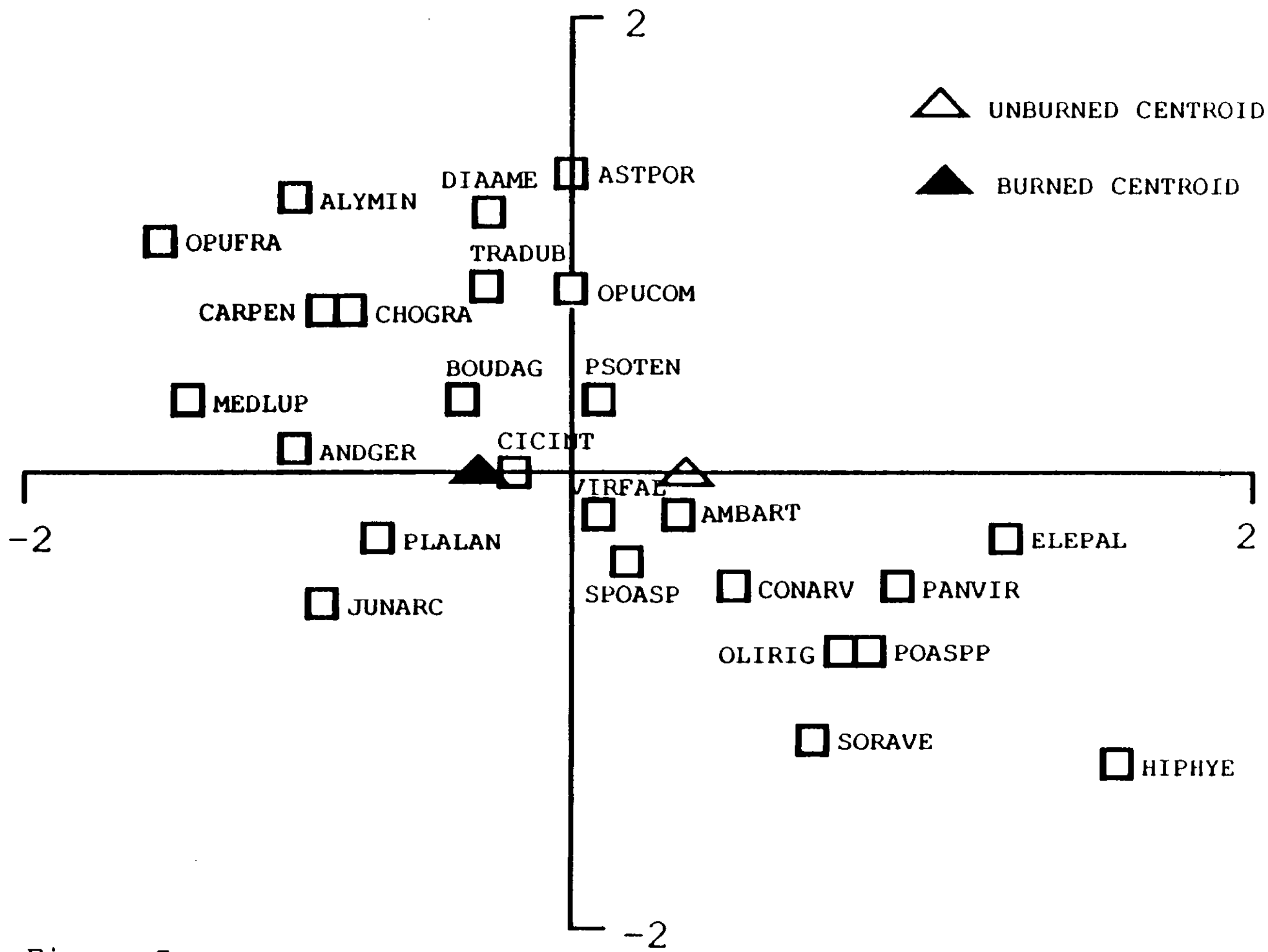

Figure 7. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Mesic site, June 1989 species abbreviations are listed in Appendix B3.

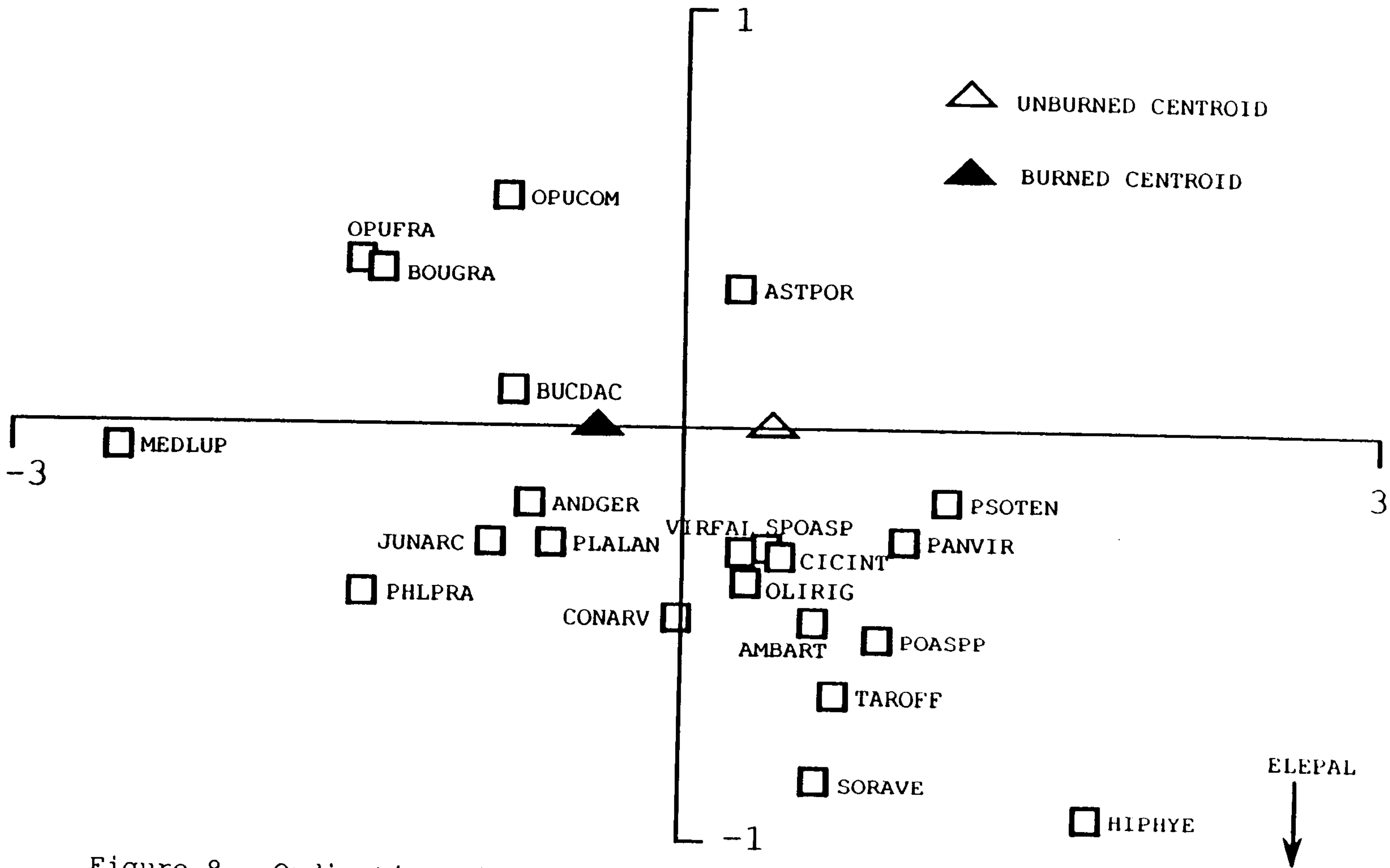

Figure 8. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Mesic site, August 1989 species abbreviations are listed in Appendix B3.

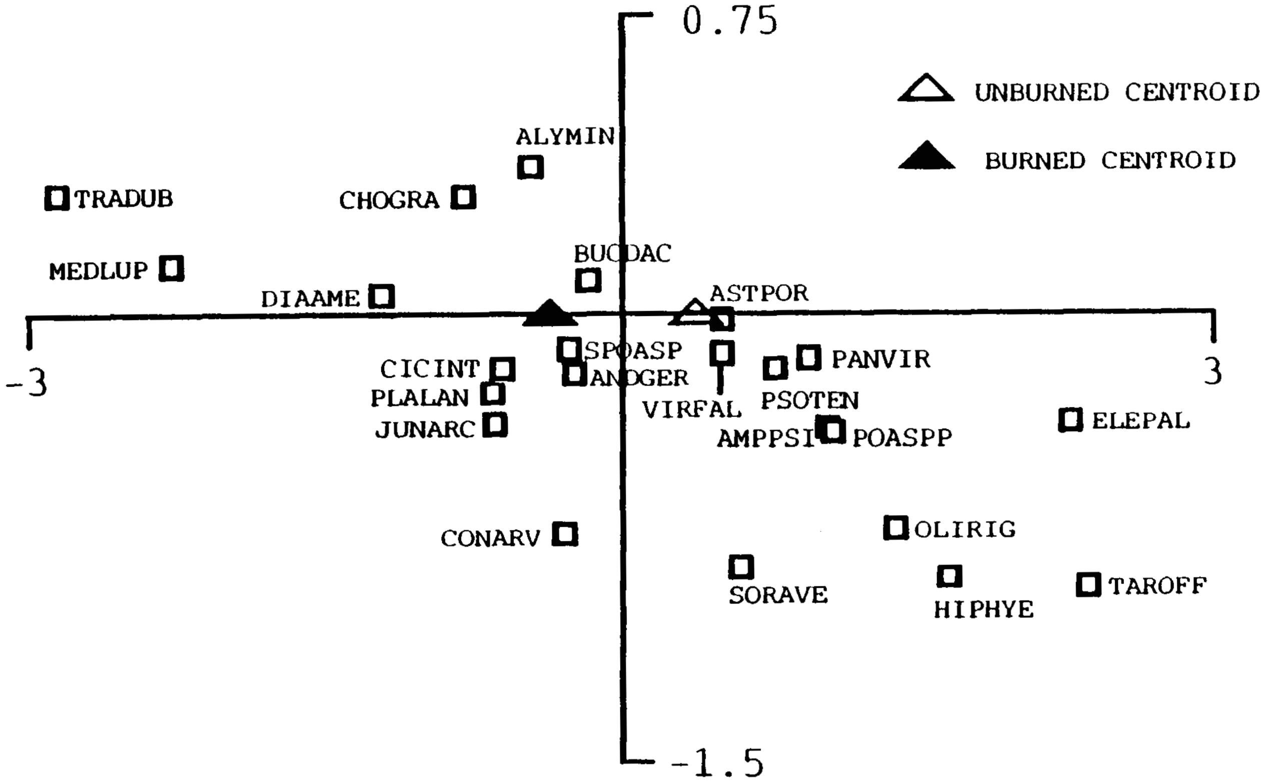

Figure 9. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Mesic site, June 1990 species abbreviations are listed in Appendix B3.

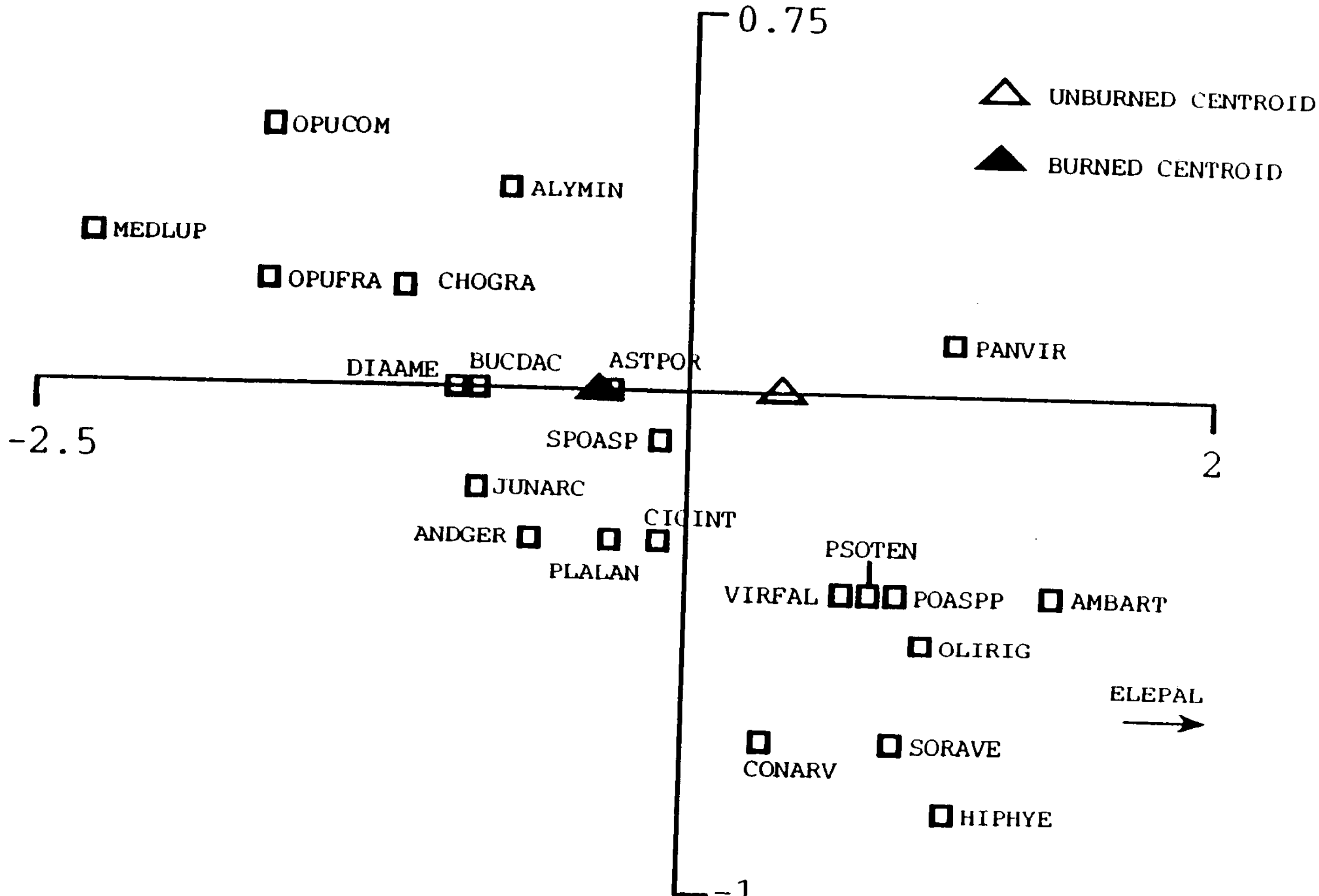

Figure 10. Ordination diagram of Boulder Tallgrass Vegetation with respect to burning: Mesic site, August 1990 species abbreviations are listed in Appendix B3.

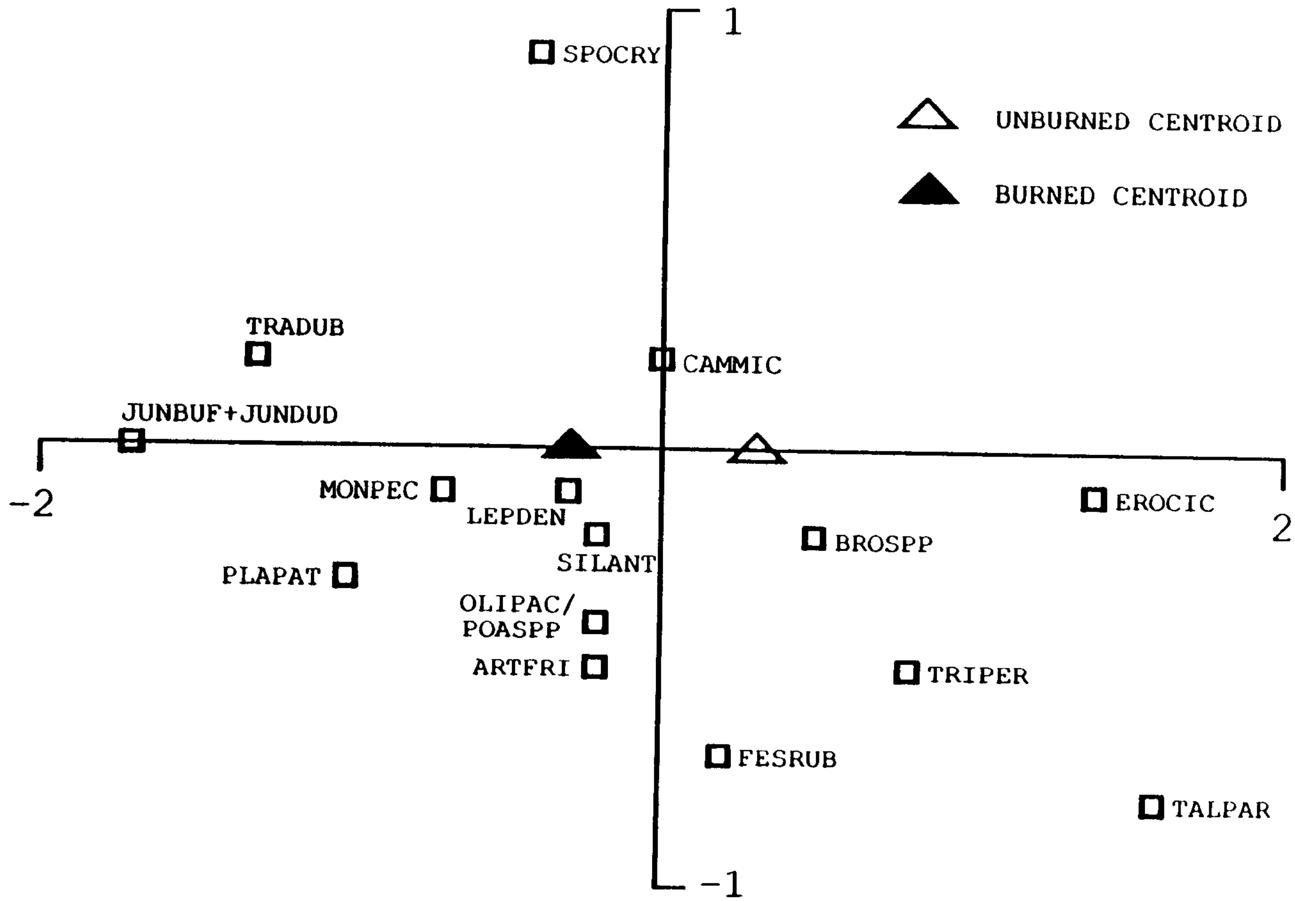

Figure 11. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Xeric site, August 1988 species abbreviations are listed in Appendix B3.

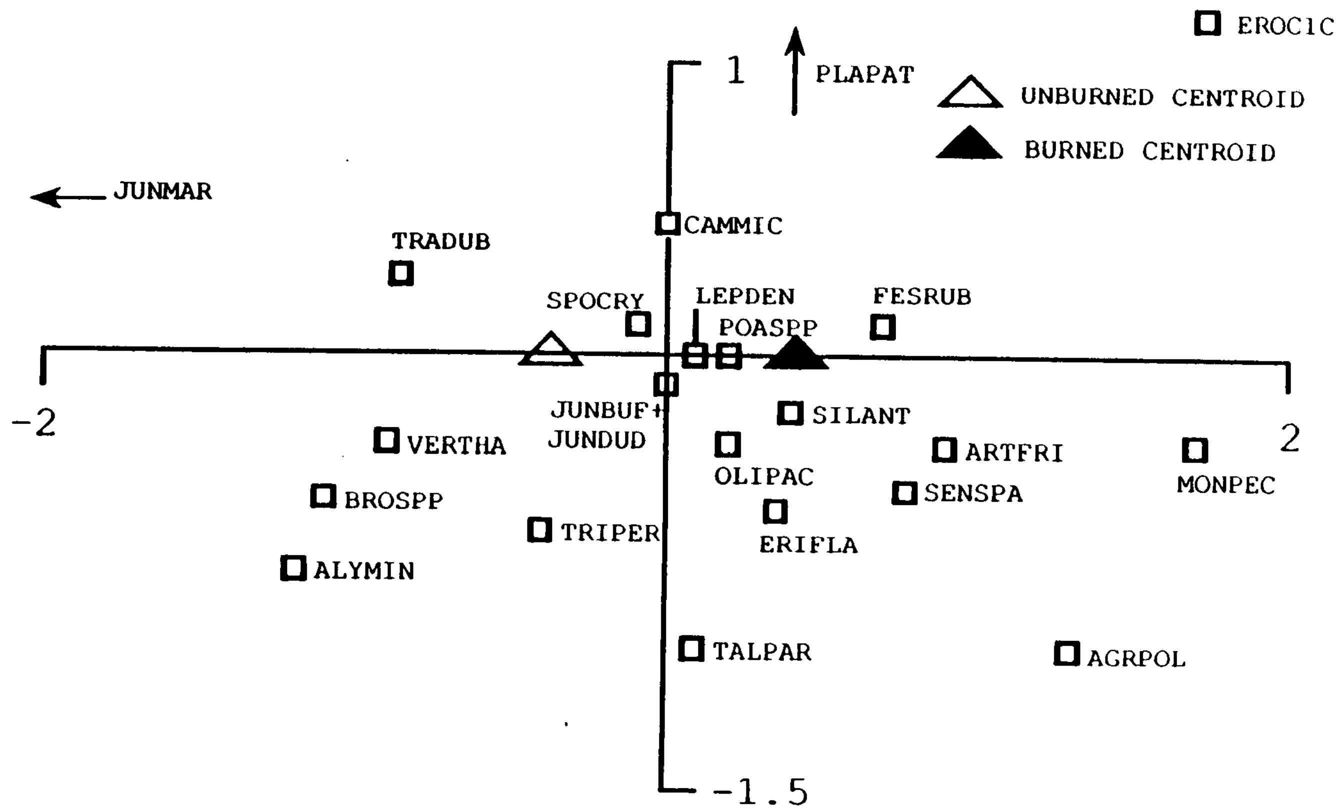

Figure 12. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Xeric site, June 1989 species abbreviations are listed in Appendix B3.

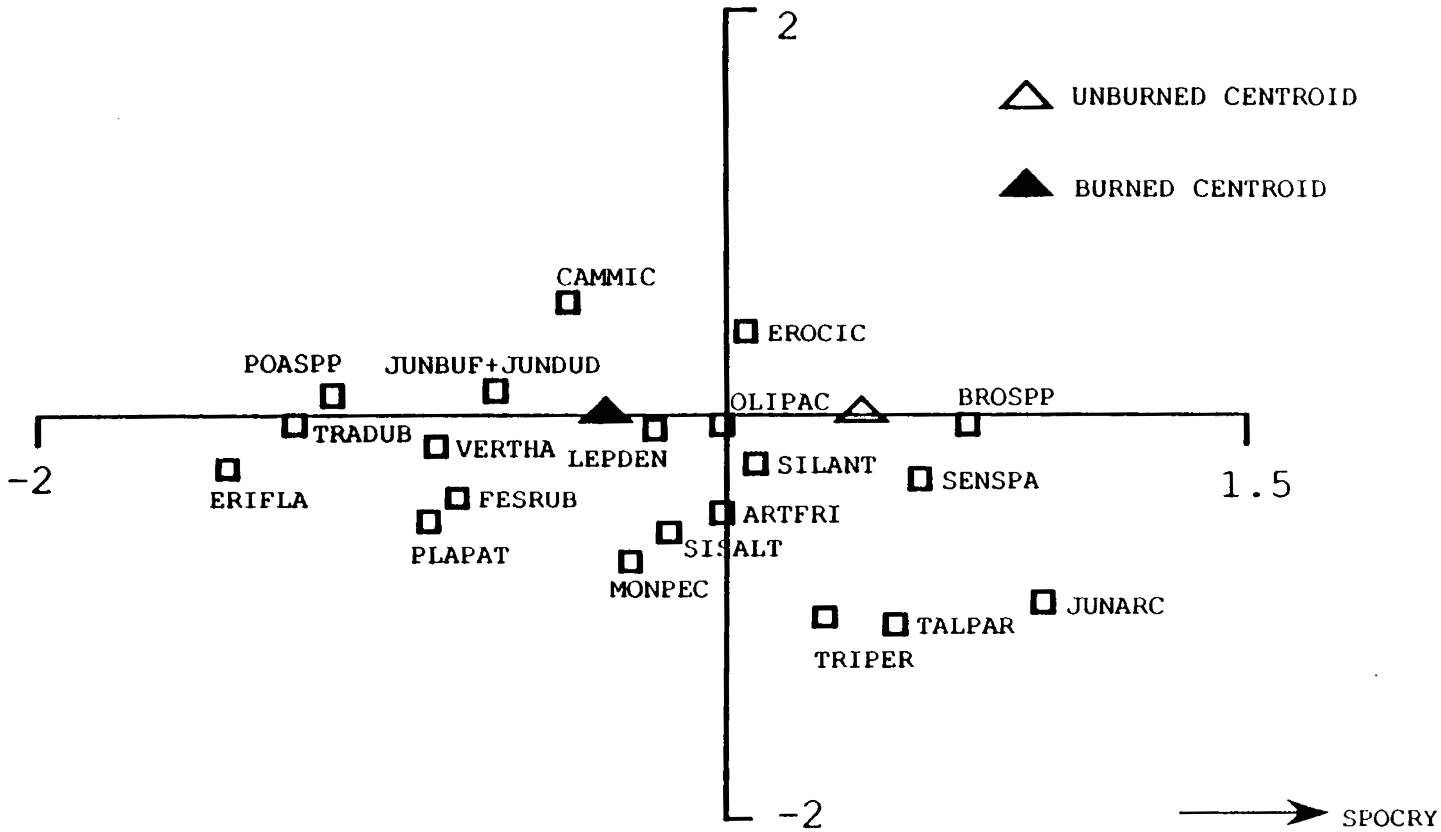

Figure 13. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Xeric site, August 1989 species abbreviations are listed in Appendix B3.

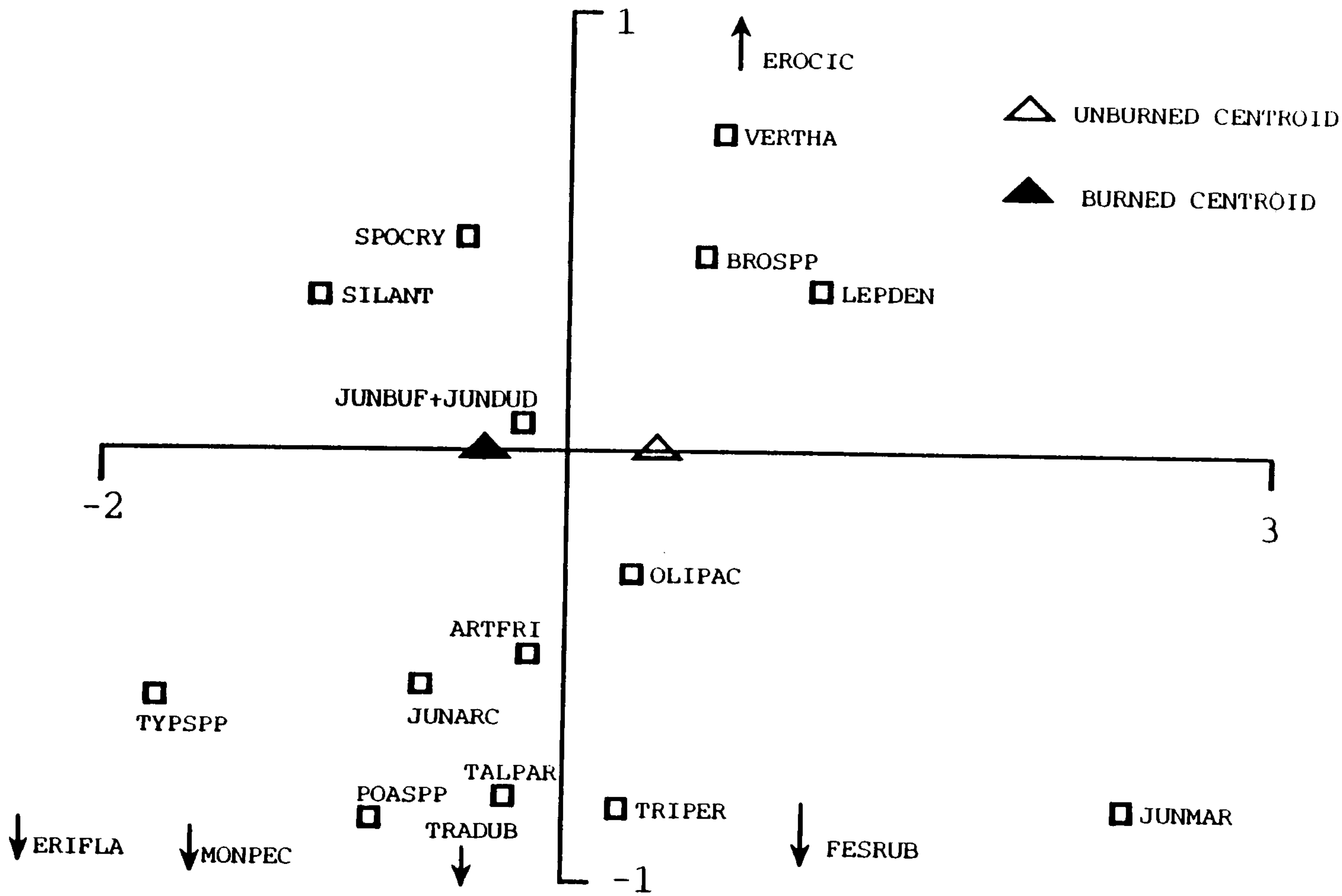

Figure 14. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Xeric site, June 1990 species abbreviations are listed in Appendix B3.

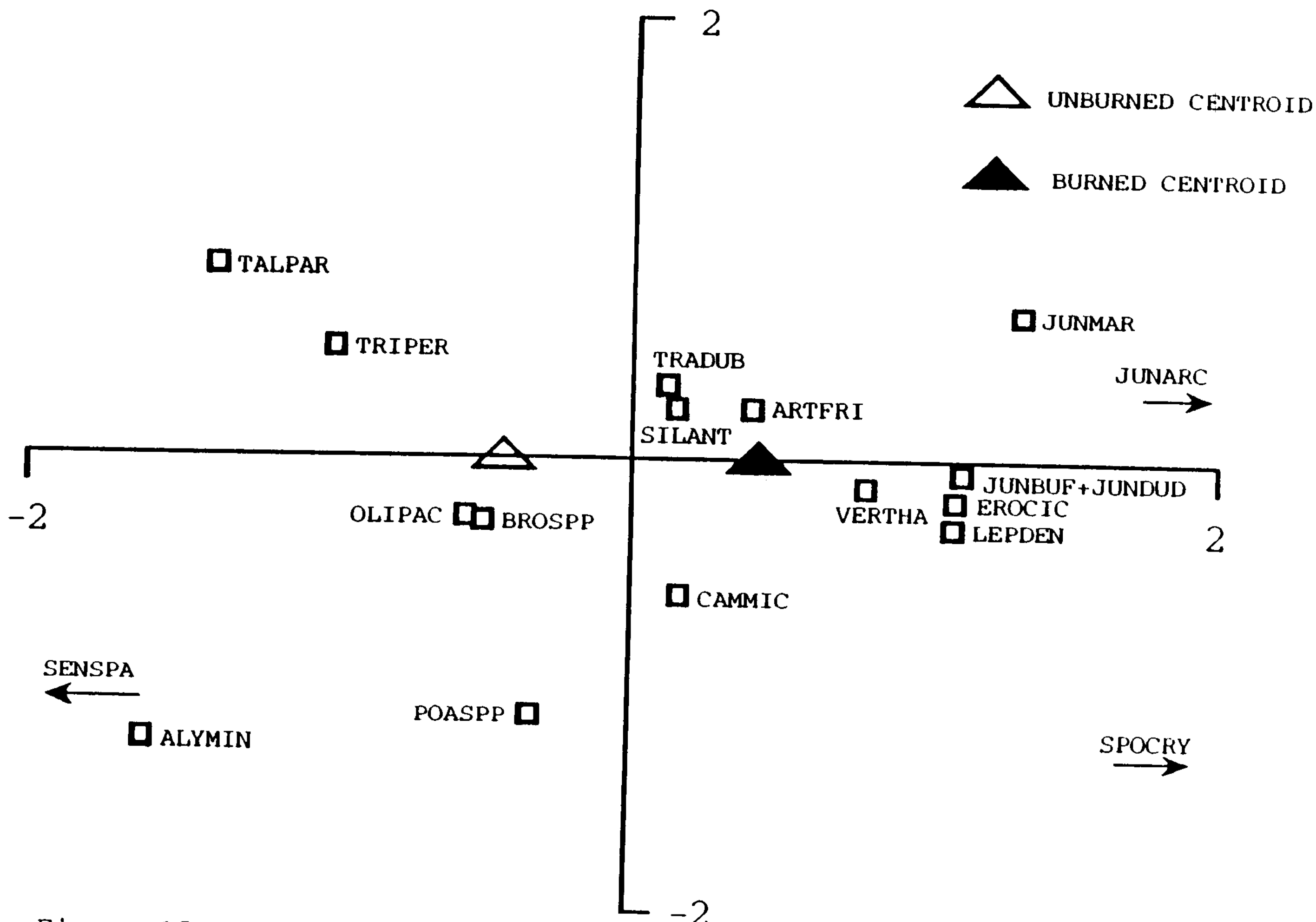

Figure 15. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Xeric site, August 1990 species abbreviations are listed in Appendix B3.

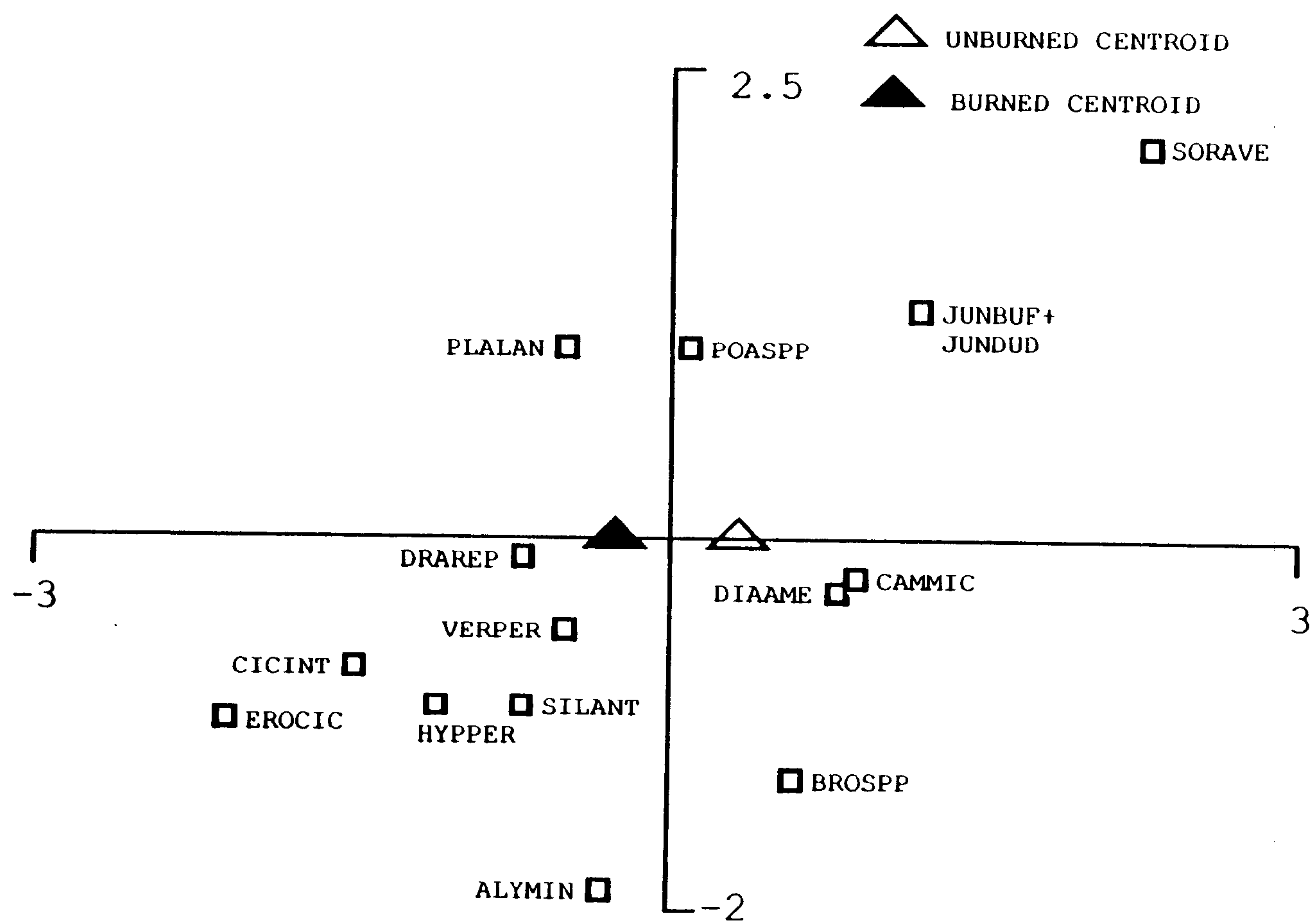

Figure 16. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Mesic site, August 1988 species abbreviations are listed in Appendix B3.

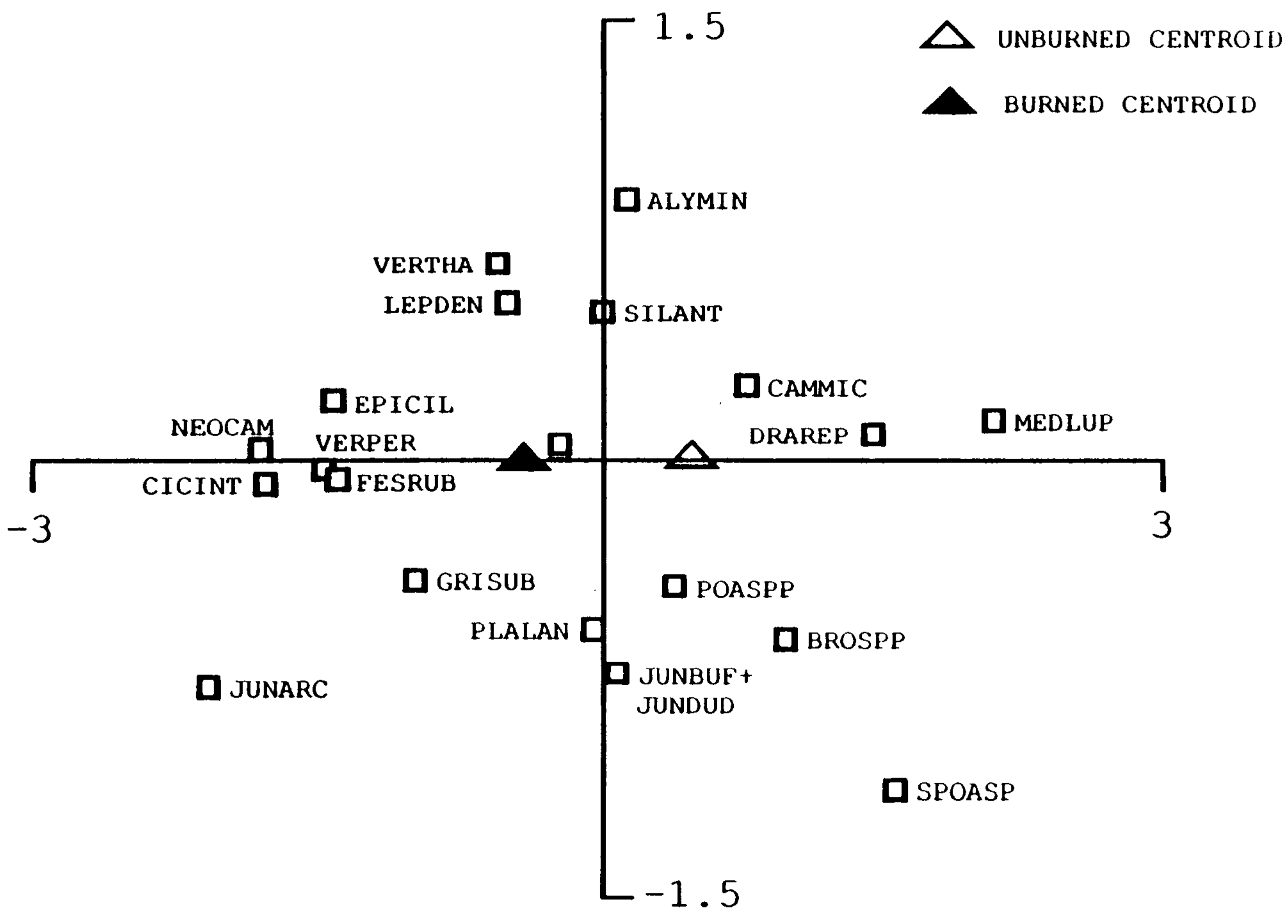

Figure 17. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Mesic site, June 1989 species abbreviations are listed in Appendix B3.

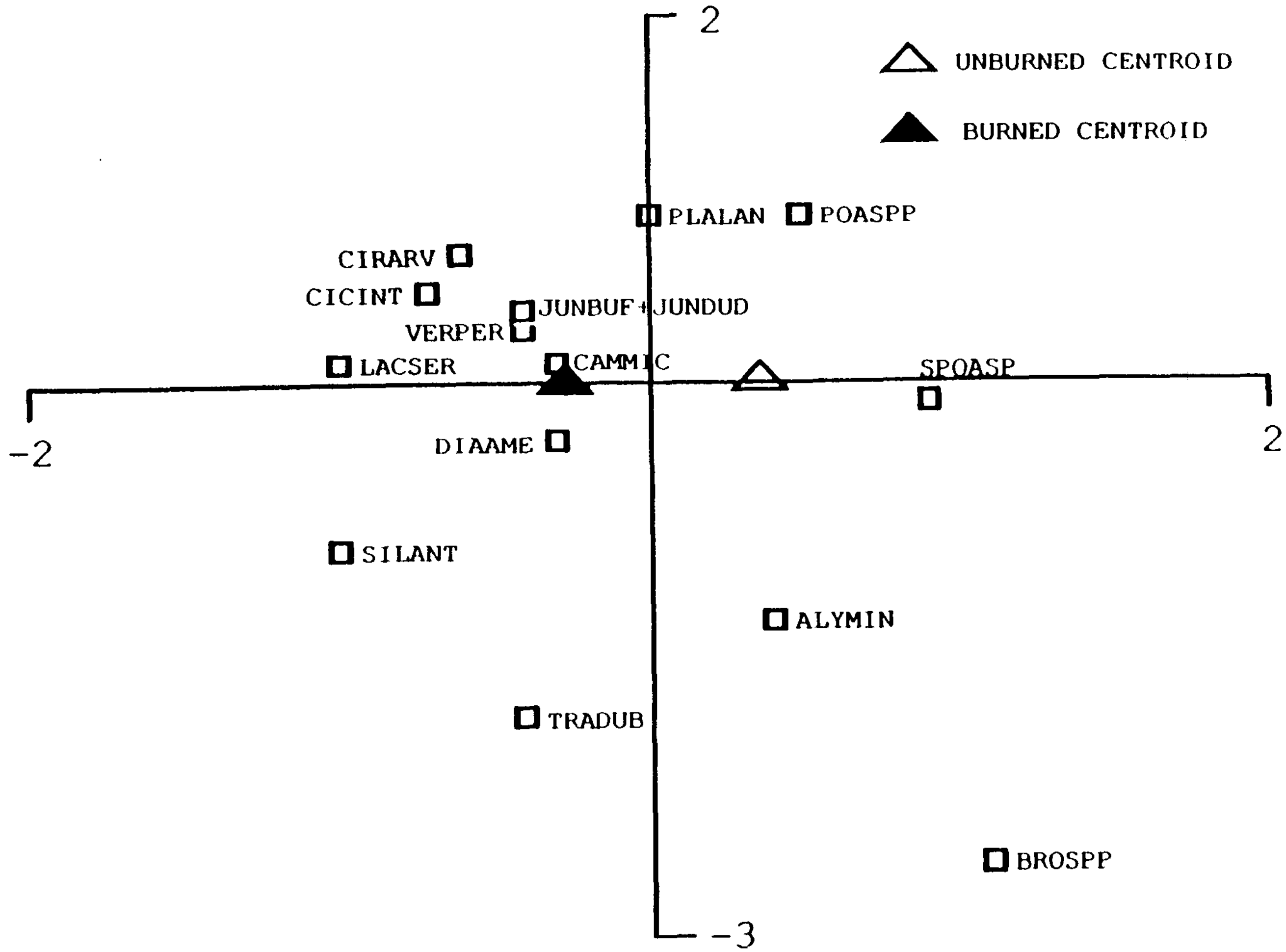

Figure 18. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Mesic site, August 1989 species abbreviations are listed in Appendix B3.

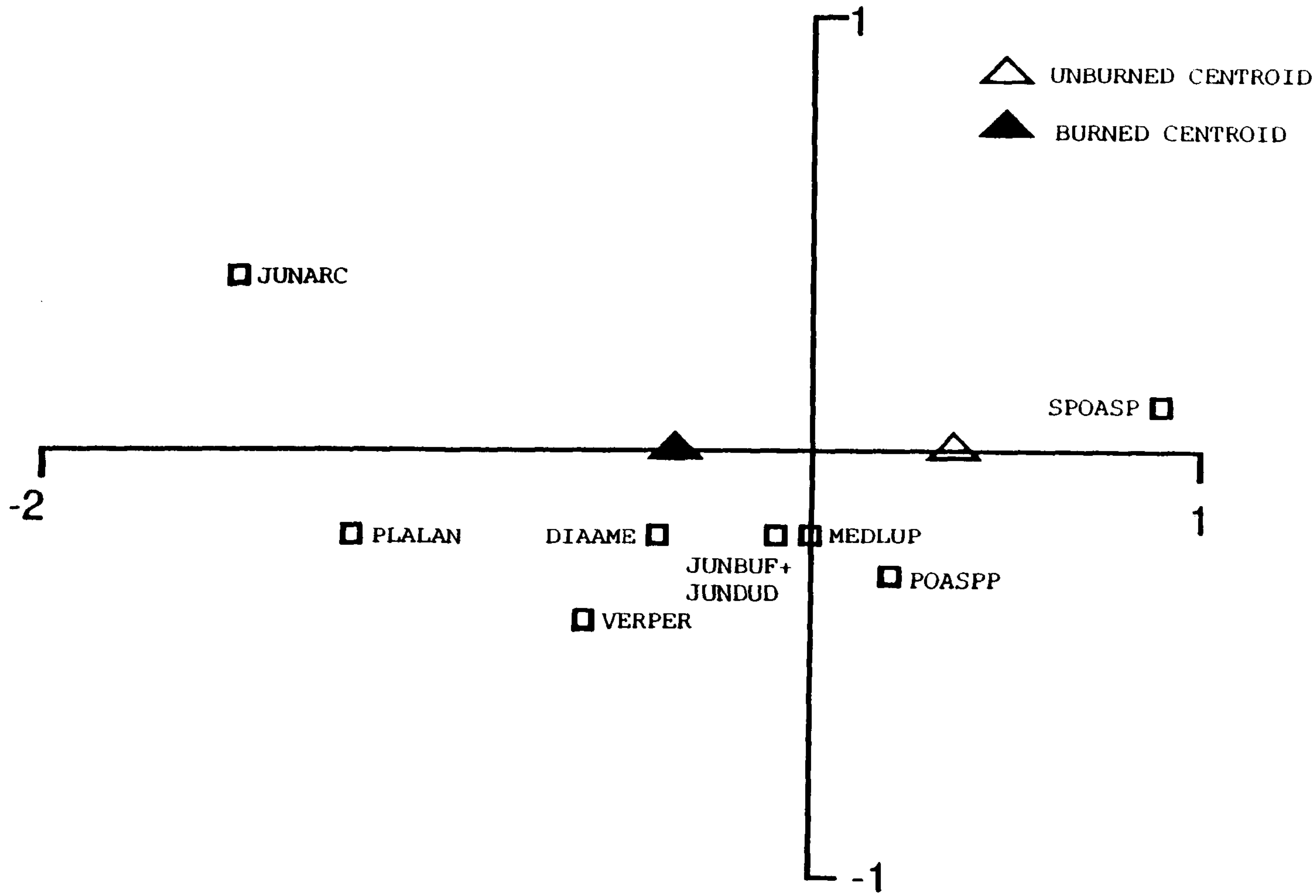

Figure 19. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Mesic site, June 1990 species abbreviations are listed in Appendix B3.

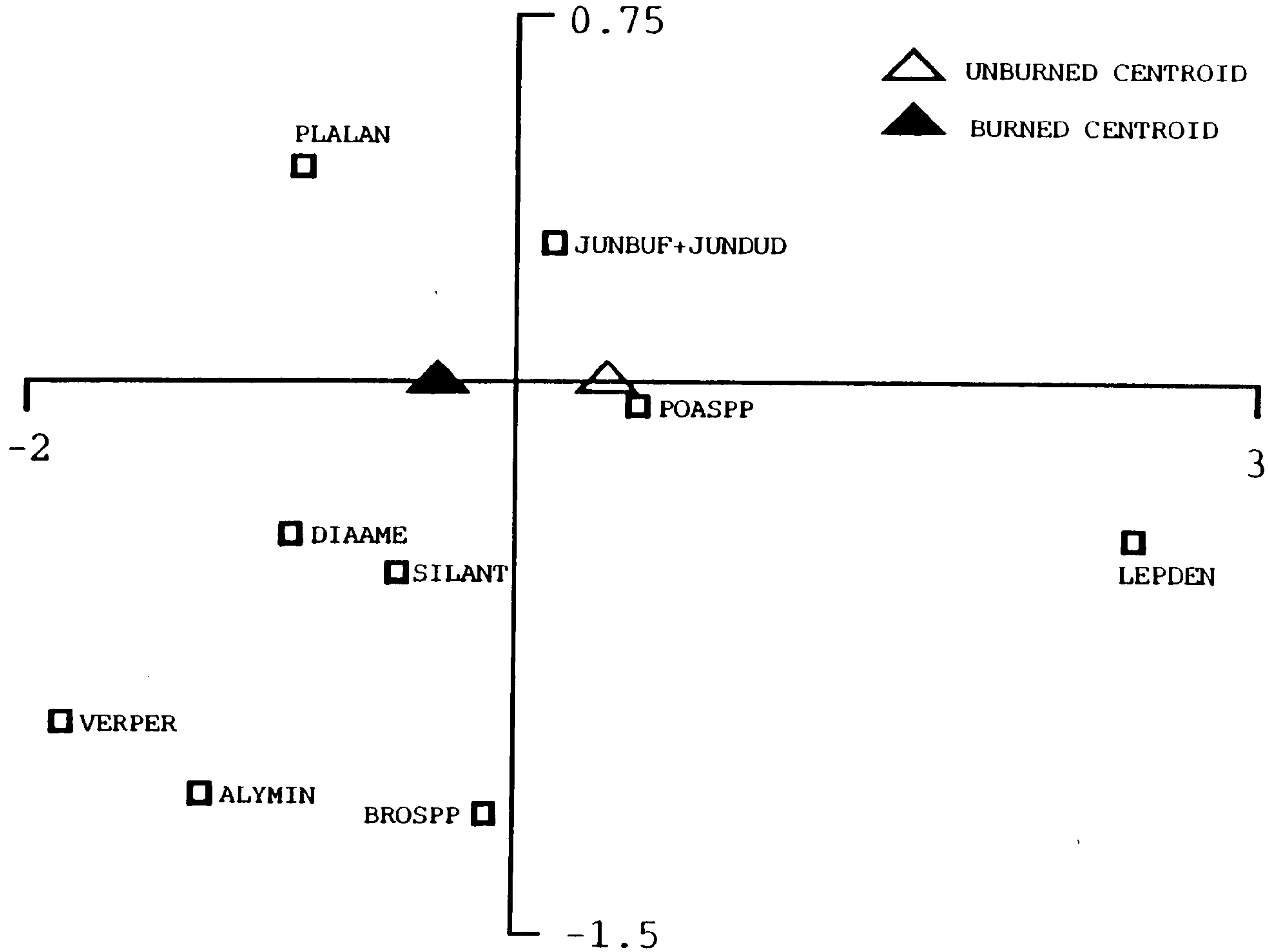

Figure 20. Ordination diagram of Boulder Tallgrass Seedling Bioassay with respect to burning: Mesic site, August 1990 species abbreviations are listed in Appendix B3.

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