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Dissertation

RESTORATION AT THE ROCKY MOUNTAIN ARSENAL NATIONAL WILDLIFE REFUGE

Submitted by
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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer, 2000

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DENISE T. ARTHUR ENTITLED RESTORATION AT THE ROCKY MOUNTAIN ARSENAL NATIONAL WILDLIFE REFUGE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Advisor

Department Head

Abstract of Dissertation

RESTORATION AT THE ROCKY MOUNTAIN ARSENAL NATIONAL WILDLIFE REFUGE

Two ecological restoration studies were implemented in 1995 and continued through 1997 on the Rocky Mountain Arsenal National Wildlife Refuge (Refuge). The Refuge is 17 square km and is located 10 km northeast of Denver, Colorado. The studies were initiated to identify restoration practices that could accelerate the establishment of late seral perennial plant communities on areas of the Refuge dominated by exotic species. The long-term goal for the site is to restore the entire Refuge to native prairie in order to provide diverse habitat for the variety of wildlife that reside on the Refuge.

A number of research objectives were developed to provide specific restoration information. The following are the objectives addressed by the research: 1) determine if supplemental water improves establishment of warm and cool season perennial species; 2) determine if supplemental water, in combination with sucrose, accelerates the establishment of native prairie species by reducing the time that weedy species dominate a revegetated site; 3) determine the effect of mulch or a cover crop on native species establishment; 4) determine the effect of seeding technique (drill vs. broadcast) on native species establishment;and 5) determine the effect of carbon (sucrose) and nitrogen additions with supplemental water on native species colonization in weed infested areas.

The Crested Wheatgrass Replacement Study and the Nitrogen Sucrose Study assessed plant community development over a three year period. Both studies assessed a number of restoration practices including: irrigation, seeding technique (drill vs. broadcast), mulch treatments, and the application of a carbon (sucrose) or a nitrogen (fertilizer) soil amendment.

Results from the Crested Wheatgrass Replacement Study showed that increased irrigation had a two-fold benefit to native restoration. Irrigation played an important role in the successful establishment of native perennial species and inhibited the growth of early-seral weedy species. Broadcast seeding doubled perennial species biomass and decreased annual species biomass by 20 % when compared to drill seeding. Mulch application improved perennial forb biomass but perennial grass biomass and biomass of annual species was the same with and without mulch. The cover crop treatment was not an effective treatment, and resulted in low perennial species biomass, and high annual forb biomass, compared to the mulch and no mulch treatments. The sucrose applications showed no clear benefit in overall perennial production or a decrease in annual or perennial production. Plant available soil nitrogen (N) decreased with addition of sucrose compared to those sites not amended, however, there was no significant plant community response to the lower plant available soil nitrogen.

The Nitrogen Sucrose Study showed that two years of irrigation in combination with three years of sucrose applications improved perennial forb and grass production. Irrigation in combination with nitrogen amendments during the same period did not increase perennial grass production but greatly increased annual forb production over plots receiving sucrose. The nitrogen plus irrigation plots shifted community structure toward one dominated by annuals while the sucrose and irrigation plots shifted community structure toward a later seral community dominated by perennial grasses.

In general the two studies demonstrate that with the use of various restoration techniques perennial community development can be enhanced and provides insight into how nutrient availability may be important in observed shifts in community structure.

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This Dissertation Is Dedicated
To My Husband

William J. Thibedeau

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Chapter One

INTRODUCTION

Background

The primary focus of this research was to provide restoration recommendations to the U. S. Fish and Wildlife Service (Service) at the Rocky Mountain Arsenal National Wildlife Refuge (Refuge) in Denver, Colorado. The refuge is seventeen square kilometers and is one of the largest urban wildlife areas in the United States. The U.S. Army acquired the land in 1942 to make weapons for World War II. The facilities were later leased to Shell Oil Company to make agricultural pesticides. Both the Army and Shell Oil generated waste during the manufacturing of chemical products. Clean up of the chemical by-products is currently under way and will take approximately 10-15 years. A large buffer zone surrounds the contaminated area where wildlife reside. The Service has been charged with managing wildlife and wildlife habitat during and following cleanup of contaminants at the Rocky Mountain Arsenal since 1986. This management includes the conversion of sites currently dominated by exotic species to native prairie, in order to provide diverse habitat for the variety of wildlife that reside on the Arsenal. Some of the wildlife species on the Refuge include bald eagles (*Haliaeetus leucocephalus*) , burrowing owls (*Athene cunicularia*), white tail and mule deer (*Odocoileus virginianus, Odocoileus hemionus*), black tail prairie dogs (*Cynomys ludovicianus*), and coyotes (*Canis latrans*). This restoration research was designed to provide specific information on restoration practices that could accelerate the ecological recovery process through the establishment of late seral species. These restoration practices could then be used by the Service to restore sites dominated by exotic species or sites disturbed during cleanup activities.

In addition to providing restoration recommendations, a second focus of this research was to investigate some of the underlying ecological processes that may affect the rate of secondary succession. One important ecological process is the cycling of nitrogen (N). In order to assess how plant available N might influence the rate of secondary succession, the soil, carbon:nitrogen (C:N) ratio was manipulated. A carbon amendment (sucrose) was added to the soil to increase N immobilization, thereby decreasing plant available soil N. Manipulation of the C:N ratio was used to test whether lower plant available soil N might increase late-seral plant production and decrease early-seral plant production. The relationship between plant available N and the rate at which early- and late-seral species replace one another could have important implications in restoration. Long-term domination of recently restored sites by early-seral plants could negatively influence plant community development and result in poor quality habitat for wildlife. Exotic weeds have been shown to change the trajectory of community development inhibiting the growth of native perennials (Allen 1988, Hobbs and Humphries 1995). Many exotic species provide poor quality forage for wildlife and may not meet nutritional requirements for growth or maintenance (Dean 1980, McCall et al. 1997, Ortega et al. 1997). Long-term dominance of sites with low quality forage could decrease wildlife survival on the Refuge.

Research objectives

Two restoration studies were implemented at the Refuge in 1995. The first was implemented to test restoration techniques to convert a non-native crested wheatgrass community to a native prairie. The second was designed to test restoration approaches to convert a cheatgrass dominated site to native prairie. The following objectives were addressed by the research: 1) determine if supplemental water improves establishment of warm and cool season perennial species; 2) determine if supplemental water, in combination with sucrose, accelerates the establishment of native prairie species by reducing the time that weedy species dominate a revegetated site; 3) determine the effect of mulch or a cover crop on native species establishment; 4) determine the effect of seeding technique (drill vs. broadcast) on native plant establishment; 5) determine the effect of sucrose and N additions on the colonization of native species in weed infested areas.

Research Hypotheses

Soil Nitrogen Availability (H1,H2)

Sucrose (H1)

Soil N availability can be manipulated with additions of amendments with high C:N ratios such as sucrose. Sucrose amendments have been shown to stimulate microbial activity and reduce plant available N through microbial immobilization (Klein et al. 1996). Previous studies also show a strong correlation between soil N availability and the rate of secondary succession (McLendon and Redente 1991, McLendon and Redente 1992a, Paschke et al. 2000, Redente et al. 1992).

H1: A reduction in plant available soil N in sucrose amended treatments at the Refuge will result in an increase in late-seral species production and a decrease in early-seral species production.

Nitrogen (H2)

An increase in soil N through fertilization will increase aboveground biomass production in systems where N is limited. Recent studies have shown that N slows the rate of succession by enhancing early-seral species and inhibiting late-seral species (McLendon and Redente 1991, McLendon and Redente 1992a, Milchunas and Lauenroth 1995, Paschke et al. 2000).

H2: Nitrogen additions will result in increased early-seral species production and decreased late-seral species production.

Irrigation and Application of Amendments (H3, H4, H5)

Irrigation (H3)

Irrigation has been used in restoration work to improve plant establishment (Munshower 1994). Many native species have very specific water requirements for germination and establishment. Providing supplemental water to native species during these critical growth periods should improve overall germination and establishment when compared to no irrigation.

H3: The use of irrigation will result in improved establishment and aboveground production by native species.

Irrigation and sucrose (H4)

Additions of supplemental water and sucrose will provide two essential components for increased microbial activity. The net result of supplemental water and sucrose amendments should be immobilization of N. Supplemental water alone may improve establishment of both early- and late-seral species. However, the combined effect of sucrose and supplemental water should increase late-seral species production and decrease early-seral species production.

H4: The application of water and sucrose will result in increased establishment by late-seral species as shown by an increase in production. Early-seral species will have decreased production when compared to late-seral species.

Irrigation and nitrogen (H5)

The addition of N and water will increase the effect of adding N alone. The combination of water and N will add two essential resources for plant growth. Both early- and late-seral species should be favored by additions of N and water. However, when both early- and late-seral species are grown together early seral will have a competitive advantage in a high soil N environment. This competitive advantage will allow early-seral species to dominate the community and slow the rate of succession.

H5: The application of water and N will result in an increase in early-seral species biomass production when compared to late-seral species.

Seeding technique (H6)

Broadcast Seeding Versus Drill Seeding (H6).

Seeding technique can influence species establishment. Broadcast seeding will result in a more diverse plant community because specific germination requirements will be satisfied for a wider variety of species than with drill seeding.

H6: Broadcast seeding will result in increased late-seral seeded species biomass production compared to drill seeding.

The Use of Mulch or Cover Crop (H7, H8)

Mulch Application (H7)

The use of mulch is a common restoration technique in the semiarid west and effectively reduces evaporation, increases infiltration, moderates soil temperature, and reduces wind and water erosion (Burgess 1978). Mulch will improve overall plant growth conditions and will have a positive effect on plant production.

H7: The use of mulch will result in an increase in aboveground production by late-seral species compared to non-mulched treatments.

Cover Crop (H8)

The use of the sorghum as a cover crop may result in a decrease in soil N through plant uptake and immobilization by the soil community. Lowering of soil N availability can lead to decreased early-seral plant production (Klein et al. 1996). Cover crops have also been used in agricultural systems to reduce weed establishment though increased competition resources. Decreased weed establishment will lead to an increase in late-seral species production.

H8: The use of a cover crop will result in increased production by late-seral species when compared to non-mulched areas.

Chapter Two

Literature Review

Successional Theory

The concept of succession is an important basic principal in ecology. However, definitions of succession still differ among ecologists and no unifying theory of succession has yet to emerge. MacMahon (1980), in his relatively comprehensive review of succession, defines ecological succession as "merely the biocoenosis of a plot of the earth's surface over a moderate time period, i.e., ten to a few hundred years". MacMahon's definition neither ascribes nor assumes an orderly process, or a defined time line (MacMahon 1980). The classical ecologist Fredrick Clements codified the process of ecological succession (Clements 1916). Clements (1916) proposed that plant communities progressed through time in an orderly and predictable fashion toward a climax community that would remain stable for long periods of time. He saw the process as a logical progression from nudation, migration, ecisis, reaction and finally stabilization or climax (Clements 1916, Clements 1936). Later, the Clemetsian climax model was applied within an ecosystem framework by a more contemporary ecologist, Eugene Odum (Odum 1969). Odum (1969) defined ecological succession in terms of three broad parameters: 1) community development proceeds in a reasonably directional and orderly fashion and therefore is predictable 2) succession is community controlled within the constraints of the physical environment. The physical environment therefore determines the pattern and rate of change, and may limit developmental patterns and, 3) successional changes lead to a stable (climax) community which is resistant to change over long time scales. Odum (1969) hypothesized that the "strategy" of succession was, homeostasis or stability, which makes climax communities resistant to change when exposed to environmental perturbations.

The climax model of succession is, and has been, under scrutiny since Clements first presented his ideas (Connell and Slatyer 1977, Gleason 1926, Grime 1977, Whittaker 1974). Gleason (1926), a contemporary of Clements, did not support the climax succession model but rather considered plant communities as developing in an individualistic manner. He proposed the individualistic model of succession which emphasized that plant community development was driven by individual interactions and migrations of species in a particular community. Within the individualistic successional framework, Gleason emphasized that no two species compositions were exactly alike, therefore vegetation did not culminate into a particular climax vegetation type.

Alex Watt's (1947) ideas lay somewhere between the diametrically opposed views of Clements and Gleason. Watt conceptualized that ecological communities were a mosaic of plant associations or in his terms "patches" (Watt 1947). These vegetation patches progressed though a series of changes over time due to cyclic environmental changes and disturbance. He termed this ecological process patch dynamics. In Watt's view, communities did move toward a dominant vegetation type late in successional time, a climax of sorts, but did not necessarily persist for long periods of time. In his hypothetical model, communities do not inexorably develop toward a single persistent vegetation composition, but rather, continually interact with both the environment, and individual plants, in a cyclic pattern. The cyclic changes in the environment accounted for plant communities with individualistic compositions.

Disagreements over successional theory continue today. However, a detailed review of the classical and more recent successional literature, reveals that many controversies that arise among proponents of either, the climax or individualistic models, are fundamentally a matter of scale. The scale at which one studies community structure, whether at a broad scale (climax), or a fine scale (individualistic), will influence what patterns emerge. Clements studied vegetation patterns at a broader scale than Gleason. Clements viewed the overall character of the climax formation as defined by the dominate plant forms. He developed a system of classification for vegetation units, which then formed various categories of the climax formation. Clements studied vegetation on the broadest of scales and states that "the visible unit of the climax is due primarily to the life-form of the dominants, which is the concrete expression of the climate" (Clements 1936). Gleason, on the other hand, examined vegetation on a finer scale and did not think fixed vegetation units could be constructed. At the scale Gleason studied vegetation, he argued that every plant association was unique and was driven by fluctuating environmental conditions in each particular time and place. Gleason states that, a "more careful examination of one of these areas, especially when conducted by some statistical method, will show that the uniformity is only a matter of degree, and that two sample quadrats with precisely the same structure can scarcely be discovered" (Gleason 1926). As can be gleaned from this short review, scale considerations are important when studying succession.

All classical ecologists bring valuable ideas to light on the subject of succession. More recent ideas on succession depend heavily on the early work of the classical ecologists. McIntosh (1981) goes so far as to propose that a re-reading of early ecologists work on succession would reveal that "current" ideas about succession, which are propounded to be "new" or "recent", have already been thought of and discussed by these early ecologists. However, some of the more recent work on succession can elucidate the processes and interactions which are the agents of change in a seral sequence. Understanding the processes which drive successional change may be paramount to the field of restoration ecology, and ecological restoration studies will aid in understanding successional change. Bradshaw (1987) proposes that restoration ecology can be used as an "acid test" for ecological understanding. He contends that by reconstructing systems through the use of sound ecological restoration practices, we can develop a better understanding of how ecological systems function.

Understanding ecosystem processes and how they contribute to successional change are important in restoration ecology because assessing how nutrients and other community dynamics influence seral stage community development can affect how restoration is conducted. Odum (1969) adds to our understanding of successional/ecosystem dynamics by suggesting that succession is an orderly and directional change toward a predictable and stable community, but changes are driven by a complex set of community and ecosystem processes. Two of these processes include nutrient cycling (e.g. mineralization), and community energetics (e.g. gross production/community respiration) (Odum 1969). By manipulating ecological processes in the restorative process we can begin to identify their role in the successional progression.

Egler (1954) introduced two models of succession which have important implications in ecological restoration research and application. They are, initial floristics and relay floristics (Egler 1954). Initial floristics suggests that successional vegetation patterns emerge as a result of residual propugales which remain after disturbance. These residual species determine future species composition. The relay floristic model suggests that only certain species can establish after disturbance and that these species modify the environment so a suite of late-seral species can become established. Both these models could have important ecological and financial implications in restoration ecology. One goal of restoration ecologists is to decrease the time revegetated sites are dominated by early-seral species and hasten the establishment of late-seral species, hence increasing the rate of secondary succession. The presence of residual species could have positive or negative effects on late-seral species establishment. Residual species may contribute to creating a suitable environment for perennial species establishment by influencing nutrient availability, adding organic matter to the soil, shading, or influencing soil community development. However, residual species may also inhibit perennial species establishment by competing for water, soil nutrients, space and light, or inhibiting soil microbial development.

Grime (1977) outlined three plant strategies important within a successional framework and important to consider in the ecological restoration process. Grime theorized that three plant strategies were recognizable with respect to the type of environmental stress they could tolerate (Grime 1977). He outlined three environmental stresses: competition, resource stress, and disturbance; and three plant strategies: ruderal, competitive, and stress tolerant. The existence of stress and disturbance in the environment and understanding what plant strategies are adapted to particular environmental conditions gives us a conceptual framework for anticipating what species may colonize a particular habitat. For instance, ruderal plant strategies do well in highly disturbed habitats because of plant characteristics such as, the ability to allocate photsynthetic resources to high seed production and rapid plant growth at the expense of root and vegetative development. Ruderal plants are also able to effectively utilize resources that are highly variable in time and space, by having an annual or short-lived perennial life cycle. In an early successional sequence, ruderal plants will likely be the first species to establish. Most restoration ecologists seek to bypass the ruderal stage and focus on enhancing late-seral species (Redente and Depuit 1988) because in many cases the ruderal plants that establish are exotic annuals. Exotic early-seral species may dominate communities for undesirable lengths of time (Allen 1988) and competition between early and late seral species can change the structural dynamics of a community (Harris 1967, Morrow and Stahlman 1984, Nasri and Doescher 1995). Vallentine (1980) reports that some revegetation failures have been attributed to intense competition for limited resources among early-seral weedy species and revegetated species. Therefore, it may be important to control or decrease the establishment of weedy early-seral species after native plant restoration.

Competitive strategy plants do well in circumstances where there are ample resources for growth. The aggressive growth of competitive species often leads to reduced diversity by the exclusion of less competitive species. For instance, fertilizer application was shown to slow the successional process by enhancing weedy competitive species (McLendon and Redente 1992a, Mclendon and Redente 1992b, Milchunas and Lauenroth 1995, Paschke et al. 2000). Therefore a reduction in resources may enhance higher species diversity. The planting of competitive species may have long term effects on a seeded community. For instance, Newman (1999) found that a competitive introduced grass species, *Festuca ovina*, was the second most dominate species twenty years after native restoration having invaded from neighboring introduced species plots. If a diverse habitat is one of the restoration goals, then a reduction in the number of competitive species in seed mixtures, or a decrease in the seeding rate for these species could allow less competitive species to become established and compete with more aggressive species.

Stress tolerant species do well in limited resource environments and are less successful in resource rich environments. This is especially true when stress tolerant species are in competition for resources with competitive plants (Redente and Depuit 1988, Richards and Redente 1995). It is important to consider how plants, with differing strategies, interact with each other and the environment in order to recreate a diverse functioning ecosystem. A common goal when restoring native communities is to achieve a balance between competitive and stress tolerant plant species in order to enhance the development of a diverse late seral community.

Rate of Secondary Succession and Plant Available Nitrogen

Studies have shown that a decrease in plant available soil N can inhibit early seral species and potentially increase the rate of secondary succession (McLendon and Redente 1991, McLendon and Redente 1992a, Paschke et al. 2000, Redente et al. 1992). Plant available N in the form of nitrate (NO_3^-) and ammonium (NH_4^+) can change during successional time (Michelsen et al. 1995, Rice 1984). Rice (1984) hypothesized that late-seral plant species produce toxins which inhibit nitrifying bacteria thereby lowering plant available N. By influencing plant available soil N communities may effectively be shifted toward late seral communities. Redente et al. (1992) found that at low N levels early-seral species had restricted growth rates of 1 to 1.5 times that of late-seral species. Their work supported the concept that early seral species may be inhibited at low soil N levels while late seral species may be enhanced. If early seral species can be inhibited, then late seral species should have a competitive advantage and increase their rate of establishment.

Research shows that plant tissue N levels differ between early- and late-seral species (Mclendon and Redente 1992b, Redente et al. 1992, Tilman 1984, Wedin and Tilman 1990). This implies that N uptake and utilization differ between early and late seral species. Therefore, N requirements may also differ among early- and late-seral species. Perennials have lower N requirements than annuals because of higher N use efficiency (Salisbury and Ross 1992). Therefore, as plant available soil N resources become limited, perennial species should have a competitive advantage over annual species (Grime 1979, McLendon and Redente 1992a, Mclendon and Redente 1992b, Redente et al. 1992).

Plant available nitrogen can also affect successional dynamics and community structure. An inverse relationship between plant available soil N, and the rate at which perennial species became established, was shown in a sagebrush ecosystem in Colorado (McLendon and Redente 1991, McLendon and Redente 1992a, Mclendon and Redente 1992b). The higher the plant available N, the slower succession proceeded. In contrast, the lower the available N, the more rapid succession progressed.

High levels of inorganic N may also affect plant community structure by decreasing species diversity (Milchunas and Lauenroth 1995, Redente and Depuit 1988). At high levels of inorganic N a few early-seral species can dominate the community and severely decrease species diversity. High species diversity is important to native fauna (Pellant 1989, Roberts 1989) and could be important to long-term ecosystem stability (McNaughton 1985, Tilman and Downing 1994).

Water Supplementation and Community Structure Development

Water availability can significantly affect successional dynamics and community structure by influencing plant germination and establishment.

Vegetation patterns and ecosystem processes are also closely tied to soil water dynamics (Dodd and Lauenroth 1997, Noy-Meir 1973, Sala et al. 1992). Noy-Meir (1973) considered water availability the most important factor influencing community structure and dynamics in arid and semi-arid ecosystems and considered it to be the major limiting factor to plant establishment and growth. Native and introduced species have various soil moisture and temperature requirements for germination and specific moisture requirements during seedling development (Frasier et al. 1984, Majerus 1975, Trlica and Biondini 1990). Highly variable precipitation patterns in arid and semi-arid regions can cause severe water stress during germination and seedling development, which could lead to decreased plant community establishment (Frasier 1989, Frasier et al. 1984, Lichthart and Weaver 1985, Petersen et al. 1986, Ries and Day 1978).

Supplemental water can enhance the establishment of species with specific germination and growth requirements that are rarely met under natural precipitation conditions (Redente and Depuit 1988). The use of irrigation as a revegetation practice has been shown to improve plant establishment and increase species diversity (DePuit et al. 1982, Kocher and Stubbendieck 1986, Vallentine 1980).

One or two years of irrigation can greatly enhance the establishment of native species by providing water during critical germination periods. DePuit et al. (1982) showed that two years of irrigation in a revegetation project increased perennial grass establishment and decreased weedy annual forb production over non-irrigated plots. Their study shows that irrigation can improve perennial species establishment and may be an important tool for inhibiting early seral species during revegetation projects. Farmer et al. (1974) showed that revegetation success on overburden material with an all native seed mixture was improved with irrigation. Newman (1999) returned to a study site twenty-one years after revegetation had been preformed on profoundly disturbed land and showed that irrigation can have long-term community effects. He found that irrigated plots, which had been seeded, to an all-native seed mixture, still had greater total biomass production compared to non-irrigated (Newman 1999).

While one or two years of irrigation can increase native revegetation success and increase the rate of plant community development, excessive or, long-term irrigation could be detrimental to restoration success. Multiple year irrigation in excess of two years could decrease long-term vegetation viability by creating plant communities dependant upon supplemental water (Munshower 1994). Excessive or high frequency irrigation can decrease rooting depth, lateral root distribution, and root mass, which are all crucial to plant survival once irrigation has been terminated (Ries and Day 1978). Deep rooting and adequate root mass are critical to plant survival in semi-arid regions during periods of drought (Ries and Day 1978, Trlica and Biondini 1990). Therefore, if irrigation is to be used in revegetation projects, then the frequency and duration of irrigation must be carefully considered.

Linking Water, Nitrogen, and Carbon Influences to Plant Community Development.

Nitrogen, carbon, and water cycles are closely linked, influencing both plant growth and microbial activity. Microbial activity can increase or decrease plant available N depending on four major factors: water, temperature, N, and carbon (Binkley and Vitousek 1993).

Burke (1989) examined how microbial mineralization is affected by both soil moisture and soil temperature in a semi-arid ecosystem. She found that 90% of annual N mineralization occurred in the spring when soil moisture and temperature are high (Burke 1989). This indicates that the addition of water in a semi-arid environment could increase N mineralization by increasing microbial activity. In addition, a soil disturbance could increase soil N mineralization as a result of the mixing of soil organic matter (Binkley and Vitousek 1993) and by increasing soil temperature.

Additions of a carbon source to the system, could further increase microbial activity by increasing the C:N ratio (Klein et al. 1996). Pashcke et. al. (2000) showed that sucrose additions to old-field successional sites of varying ages significantly decreased plant available N. The decrease in available N in the system was attributed to microbial N immobilization. Jackson et al. (1989) found that soil microbial uptake rate of both NO_3^- and NH_4^+ was faster than uptake by plants. They reported that soil microbial uptake of NH_4^+ was five times more rapid and NO_3^- uptake was two times more rapid than plant uptake. Therefore, by increasing the C:N ratio through additions of an outside carbon source (e.g. sucrose or sawdust) and adding water in arid systems, immobilization could significantly increase. Microbial N immobilization would reduce plant available N which could inhibit early-seral species and favor the establishment of late-seral species (Mclendon and Redente 1992b, Redente et al. 1992).

Additions of water and N should produce the opposite effect of adding a carbon source and water, appreciably slowing the rate of plant community development. Additions of N and water would increase mineralization, thus releasing plant available N. Experimentally adding N and water can significantly alter the seral community structure (Dodd and Lauenroth 1979). Dodd and Lauenroth (1979) found that annual weeds dominated an experimental area where N and water were added. Milchunas and Lauenroth (1995) returned to the study site eight years later and found that annual grasses still had higher production in the experimental plots which had received N and water amendments. This indicates that there is a long-term community effect to applications of N and water and that weedy species can persist for extended lengths of time.

Revegetation Techniques

Seeding Technique

The application of various revegetation techniques can influence plant community development by decreasing the amount of time communities are dominated by early seral species. For instance, providing plant propagules through seeding and transplanting can accelerate plant community development (Redente and Depuit 1988). In order for plant propagules to germinate, a favorable micro-environment must be established. Favorable micro-sites have adequate water, temperature, and provide adequate seed soil contact. Seedbed preparation and planting method can influence seed micro-environment (Kocher and Stubbendieck 1986, Vallentine 1980, Winkel et al. 1991). For instance Kocher and Stubbendieck (1986) found that broadcast seeding was more successful after discing in a sandy soil compared to broadcast seeded sites not disced. They hypothesized that surface litter on untilled plots prevented the broadcast seeds from obtaining adequate seed soil contact while the disced plots had improved micro-relief and seed soil contact by litter incorporation. Roundy and Call (1988) suggested that drill seeding was superior to broadcast seeding because seeds were generally covered to a proper depth and had good seed soil contact. However, this was on a site where the seedbed was firm and uniform in surface roughness. If the seedbed is rough or the soil texture is sandy, then maintaining a proper seeding depth can be difficult. Choosing a seeding method becomes particularly important when revegetating with native species. Many native seed mixtures combine species with a variety of seed sizes, shapes, and weights, and are often seeded at the same time. Small light seeds in a varied seed mixture could easily be planted too deep using a drill seeding method. Planting depth will influence establishment and competitive relationships among species and is directly influenced by the seeding technique used (DePuit et al. 1980, Roundy and Call 1988). Research in Montana by DePuit et al. (1980) suggested that higher species diversity can be achieved with broadcast seeding compared to drill seeding. They found that broadcast seeding was better able to satisfy specific germination requirements for difficult-to-establish species. However, broadcast seeding should be followed by some mechanical treatment like chaining so that seeds are adequately covered, insuring good seed soil contact (Roundy and Call 1988, Vallentine 1980). When choosing a seeding method, a number of factors should be considered including: soil texture, diversity of the seed mixture, and species competitive relationships.

Use of Mulch/Cover Crop

Mulching and the use of cover crops are common restoration practices in the semi-arid west. Mulches and cover crops are used to control erosion, increase moisture retention, reduce evaporation, and thus provides a more favorable environment for plant establishment.

Mulch can be especially important for increased infiltration and reduced evaporation from the soil surface, when revegetation first occurs. If mulch can retain soil moisture for extended periods of time, then germination may be significantly improved over areas not mulched. Mulch can also serve as an important carbon source for microbes by adding organic matter to the system. The added carbon source due the incorporation of senesced cover crop tissue could increase microbial activity, which could lead to either N mineralization, or N immobilization, (Doran and Smith 1991) depending on the carbon:nitrogen ratio of the mulch applied. A laboratory study showed that decomposing non-legume cover crop residues showed significant amounts of net N immobilization (Somada et al. 1991). Therefore the use of non-legume cover crops could decrease plant available N which could lead to an inhibition of weedy species establishment, and an enhancement of perennial species establishment.

In agricultural systems, cover crops are planted to decrease weed invasion, reduce soil erosion, and provide increased organic matter during crop rotation (Lal et al. 1991). Inhibition of weedy species invasion by planting a cover crop is realized through competition for resources and through allelopathy (Lal et al. 1991). However, it is unclear whether the planting of a cover crop before native plant revegetation will inhibit weed establishment.

Chapter Three

The Crested Wheatgrass Replacement Study

Introduction

The goal of restoration ecology is not only to restore native functioning ecosystems but also to understand some of the underlying processes that may decrease the time these ecological systems are dominated by early seral species. Various restoration techniques can influence plant community development and enhance or inhibit early and late seral species. The use of restoration techniques can aid in the recovery of disturbed systems to diverse, productive, and self-sustaining, plant communities. Common questions that face restoration ecologists involve revegetation practices associated with irrigation, method of seeding, mulching, and application of soil amendments. While it is accepted that these techniques help plant establishment, their effect on community development is inconsistent.

Water is a major limiting factor in the semi-arid west. Noy-Meir (1973) considered water availability to be the most important factor influencing the structure and dynamics of arid and semi-arid ecosystems. He also considered water to be the major limiting factor to plant establishment and growth. Numerous revegetation projects have failed because of low and unpredictable precipitation patterns (Packer and Aldon 1978, Power 1978, Ries and Day 1978). Precipitation patterns may only be suitable for plant reproduction and establishment one out of every ten years (Ries and Day 1978). Therefore, supplemental water in the form of irrigation can be an important tool for native revegetation on disturbed lands.

Water availability affects many processes involved in plant community development. Irrigation can improve seed germination and seedling emergence (Munshower 1994, Ries and Day 1978, Vallentine 1980). O'Keefe (1996) showed that restoration success, even in a fairly moist system, is linked to soil water availability. He found that there was a close correlation between soil water availability and level of reproduction in a prairie restoration project in Iowa over a nine year span (O'Keefe 1996). Vegetation patterns, and community structure, are also closely tied to soil water dynamics (Dodd and Lauenroth 1997, Sala et al. 1992). These studies suggest supplemental water is important not only to plant establishment, but that it also affects the composition and structure of the restored community.

Many factors need to be carefully considered when using irrigation in restoration work, however, there is limited information on how to apply irrigation in native plant community restoration. Traditional irrigation techniques are appropriate for maximizing crop production but may not be appropriate for restoring native plant communities. Prolonged irrigation or excessive supplemental water can produce plant communities that are dependent on irrigation. This would result in a failure to reach the goal of a self-sustaining native ecosystem. However, if properly applied, irrigation could be a useful tool to accelerate ecosystem recovery.

Seeding method is another important consideration in restoration projects because the planting method can influence seed germination and seedling emergence. Perennial community development can ultimately be influenced by seeding method because planting depth influences establishment and competitive relationships among species (DePuit et al. 1980, Roundy and Call 1988). Confounding information exists in the literature about the best method to use in restoration projects. Native plant mixtures typically have seeds of varying sizes and therefore would be especially sensitive to planting depth. Small seeds need to be planted at a more shallow depth than large seeds. A seeding method that accommodates a wide variety of seed sizes should be the most effective in achieving perennial plant establishment and inhibiting the growth of undesirable early-seral species.

Mulching and the use of a cover crop are common revegetation practices in arid and semi-arid regions. Mulching and cover crops are used to control erosion, increase moisture retention, reduce evaporation, and thus, provide a more favorable environment for plant establishment (Burgess 1978, Lal et al. 1991). However, studies that examine combinations of restoration techniques are uncommon, and it is unclear how successful mulch and cover crop applications in combination with other restoration techniques would effect plant community development.

Soil amendments can affect community dynamics in a restoration project and may help produce the desired community more rapidly. Plant available soil N can have a major influence on plant community development. A number of studies have shown that a decrease in plant available N can inhibit early seral species and enhance late seral species (McLendon and Redente 1991, McLendon and Redente 1992a, Paschke et al. 2000, Redente and Richards 1997, Tilman 1984).

Plant available N has experimentally been lowered in some studies through the addition of a high carbon amendment such as sucrose (Klein et al. 1996, Paschke et al. 2000). The observed decrease in plant available N has been attributed to an increase in microbial immobilization (Klein et al. 1996, Mclendon and Redente 1992b, Paschke et al. 2000). Plants and microbes both compete for soil inorganic N during plant community development. Microbes can either mineralize or immobilize soil N depending on the soil C:N ratio. Additions of a carbon source can change the C: N ratio and theoretically move the system toward microbial N immobilization (Klein et al. 1996, Paschke et al. 2000). Jackson et. al. (1989) reported that microbes are better competitors for available nitrogen than plants. The authors traced a stable isotope ^{15}N through an annual savanna grassland system in California and found that microbes were able to take-up five times as much ammonium and twice as much nitrate as plants. Therefore, when extra carbon is made available to microbes, it is possible that microbial N immobilization can occur which would lower inorganic N available to plants.

Microbial N immobilization and shifts in community structure through N manipulation has been demonstrated on a short grass steppe community in Colorado (Paschke et al. 2000). Paschke et. al. (2000) showed a decrease in plant available N on sites where sucrose was applied as a carbon source. They also found that the plant community structure was shifted toward a perennial community on plots with carbon additions and shifted toward an early seral community on plots were N was added. The use of carbon amendments in restoration, may reduce the time needed to reach a desired perennial community.

The objective of this study was to look at different revegetation techniques to determine if restoration of a native perennial community could be enhanced. The revegetation techniques tested were irrigation, seeding method, and the use of mulch. In addition, a carbon amendment was applied to the soil to determine if a high carbon amendment would accelerate the development of a native perennial community. Two questions were addressed by experimentally manipulating soil N: 1) does the addition of carbon decrease plant available N, and 2) does this decrease in N availability affect native plant community development.

Methods

Study site

The study site was located at Rocky Mountain Arsenal National Wildlife Refuge (Refuge) approximately 10 km northeast of Denver, Colorado. The soil type is an aridic argiustoll and the area receives an average of 380 mm of precipitation annually. The Refuge is 17 square km and without disturbance would be a short-midgrass prairie. Exotic perennial grasses and weedy forb species currently dominate most of the Refuge. The study site was a crested wheatgrass (*Agropyron cristatum*) community, established some forty years earlier. Crested wheatgrass is difficult to eradicate after establishment; therefore, an aggressive mechanical control was used to remove the crested wheatgrass and simultaneously prepare a seedbed. The following four phase seedbed preparation method was used to remove crested wheatgrass: the site was chisel plowed, moldboard plowed, disked, and harrowed prior to seeding a native seed mixture in the spring of 1995.

Study Design

The study design included ten treatments arranged in a 5-way randomized nested design with four replications (Appendix A Figure 1). There were five irrigation treatments. The first irrigation treatment began in May, the last irrigation treatment ended in August. The irrigation treatments were applied during the first two years of the study (1995 and 1996). The following irrigaation treatments were included in the experimental design:

1. Irrigation in May (5 cm)
2. Irrigation in May and June (5 cm/ month)
3. Irrigation in May June and July (5 cm/ month)
4. Irrigation in May June, July and August (5 cm/ month)
5. No irrigation (control)

Each treatment measured 18 m x 18 m and was separated by a 3 m buffer strip between irrigation treatments. Half of each replicate received sucrose at a rate of 1600 kg sucrose/ha/yr. The second half of the replicate was not treated with sucrose. Sucrose applications were divided into eight equal increments, applied every two weeks, beginning in May.

Six subtreatments were nested within each irrigation treatment. The subtreatments included mulch, no mulch, and cover crop (sorghum). The three mulch treatments where then either broadcast seeded, or drill seeded. Each subtreatment measured 5 m x 9 m. The seed mixture used in the study consisted of native perennial grasses, forbs and shrubs (Appendix Table 1). The mulch and no mulch treatments were seeded with a native mixture in the spring of 1995. The cover crop treatment was planted with sorghum at the same time. The following spring (1996) the cover crop was mowed, lightly harrowed, and either drill or broadcast seeded with the native mixture. Plant community development on the cover crop treatment was therefore one year behind the remaining treatments.

Data Collection

Vegetation sampling was conducted in July 1995, 1996 and 1997. Only data from the third growing season (1997) will be presented in this chapter. This is because the third growing season results should be a better indicator of the long-term community response since no supplemental water was added in that final year. Aboveground biomass was measured by clipping all vegetation within randomly placed 0.25 m^2 quadrats. Five quadrats in each subtreatment were sampled for a total of 30 quadrats per irrigation treatment. A total of 1200 quadrats were sampled for the entire study. Vegetation was clipped at ground level and separated by species. All plant samples were oven dried at 55 ° C for 48 hours and then weighed.

Plant available soil N was determined using *in situ* incubations of ion exchange resin (IER) bags (Binkely and Matson 1983). Three IER bags per subtreatment were buried 5 cm below the soil surface in all treatment combinations, except the drill treatments. The resin bags remained in the soil for forty-five days and adsorbed inorganic nitrogen from the soil solution during the incubation period. Two sets of IER bags were placed, the first in late May, and the second in late July. Results from the two sets of resin bag data were combined for the statistical analysis. The IER bags experience the same edaphic conditions as plant roots, therefore, they give an approximation during the incubation period of plant available inorganic nitrogen. Therefore, analysis of the inorganic nitrogen adsorbed by the IER bags allows a means to compare relative plant available N across treatments. The IER bags were kept on ice after removal from the soil, then refrigerated until extraction could be preformed a few days later. Extraction was executed by placing the bags in 75 ml of 1 N KCl solution and then shaken with a mechanical agitator for 1.5 hours. The extract solution was then filtered and cold stored until analysis. The extracts were then analyzed for nitrate and ammonium using a Timberline Inorganic Nitrogen Analyzer.

Statistical Analysis

Vegetation

The statistical analysis was based on a multilevel experimental design including a split-plot, a split-split-plot, and a strip-plot design. A mixed model analysis was used to include both fixed and random effects in the analysis. Statistical analysis of the production data was preformed using an Analysis of Variance (ANOVA) procedure with SAS PROC MIXED version 6.12 (SAS 1996). Analysis of variance mean separation was determined at a $p \leq 0.05$ significance level. Studentized residual plots were generated to determine if the data fit the model assumption of homogeneous variance. The biomass data were log transformed to stabilize the variance. Statistical significance was then determined from the transformed data. Aboveground biomass means are presented graphically in the original scale.

Plant available Soil Nitrogen

Statistical analysis of the resin bag data was preformed using an Analysis of Variance (ANOVA) procedure with SAS PROC GLM version 6.12 (SAS 1996). This was a randomized split-plot, strip-plot design. Residual plots were generated and the assumptions of the model were met. Differences between means were compared with the least squared means procedure at the $p < 0.01$ significance level.

Results

Aboveground Biomass Third Growing Season

Irrigation Treatments

Production by life-form group differed among irrigation treatments (Figure 3-1). Annual forb production was greatest in the control and May (M) treatments (631 g/m^2 and 585 g/m^2). The control treatment was different from all other treatments except the May (M) treatment. The May treatment was different from both the May, June, July, (MJJ) and May, June, July, August (MJJA) treatments. The MJJ and MJJA treatments had the lowest annual forb production with 464 g/m^2 and 261 g/m^2, respectively. The general trend was decreasing production by annual forbs with increasing amounts of irrigation.

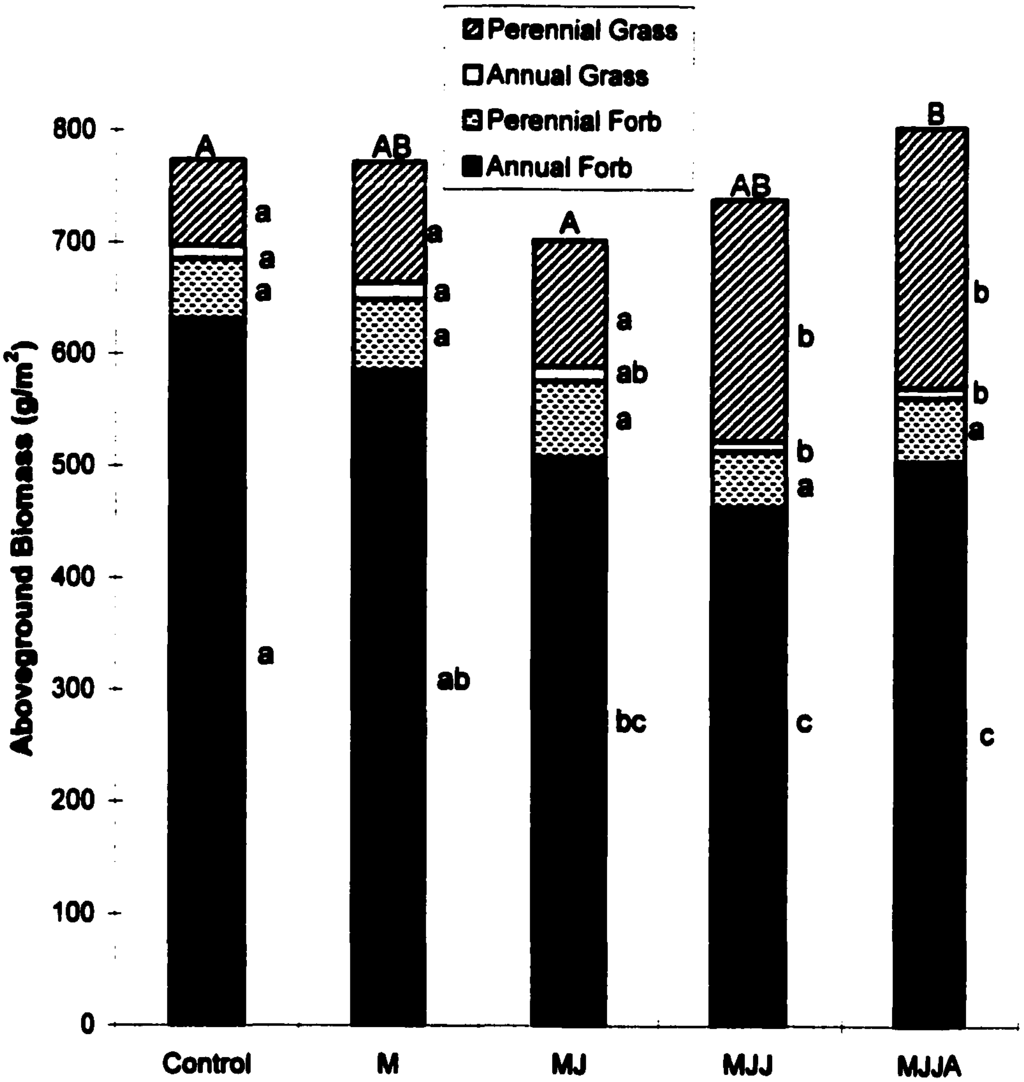

Figure 3-1. Mean aboveground biomass among irrigation treatments on the Crested Wheatgrass Replacement Study in 1997. Irrigation: Control=no irrigation, M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+August Irrigation. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different upper case letters indicate significant differences in total production across treatments ($p \leq 0.05$).

The largest contributors to annual forb production were Canada horse weed (*Conyza canadenses),* Russian thistle (*Salsola iberica*), and tumbling hedgemustard (*Sisymbrium altissimum*).

There was a trend toward increased production by perennial grasses with increased irrigation. MJJ and MJJA had the greatest perennial grass production (216 g/m^2 and 232 g/m^2, respectively) and were different from the control, M, and MJ treatments. The control, M, and MJ treatments were not different from each other. The largest contributors to perennial grass production were three seeded species including, sand bluestem *(Andropogon halli),* blue grama (*Bouteloua gracillis),* and prairie sandreed (*Calamovilfa longifolia).*

Perennial forb production was relatively uniform among irrigation treatments, ranging from 50 g/m^2 for the MJJ treatment to 69 g/m^2 for the MJ treatment. The three major contributors to perennial forb production were Louisianna sagewort (*Artemisia ludovisianna),* common gallardia *(Galardia aristida),* and golden aster *(Heterotheca villosa).*

Annual grass production was negligible for all irrigation treatments, ranging from 0.3 g/m^2 to 6 g/m^2. Total production showed no clear trend across irrigation treatments.

Seeding technique

Seeding treatment influenced production by life-form group (Figure 3-2).

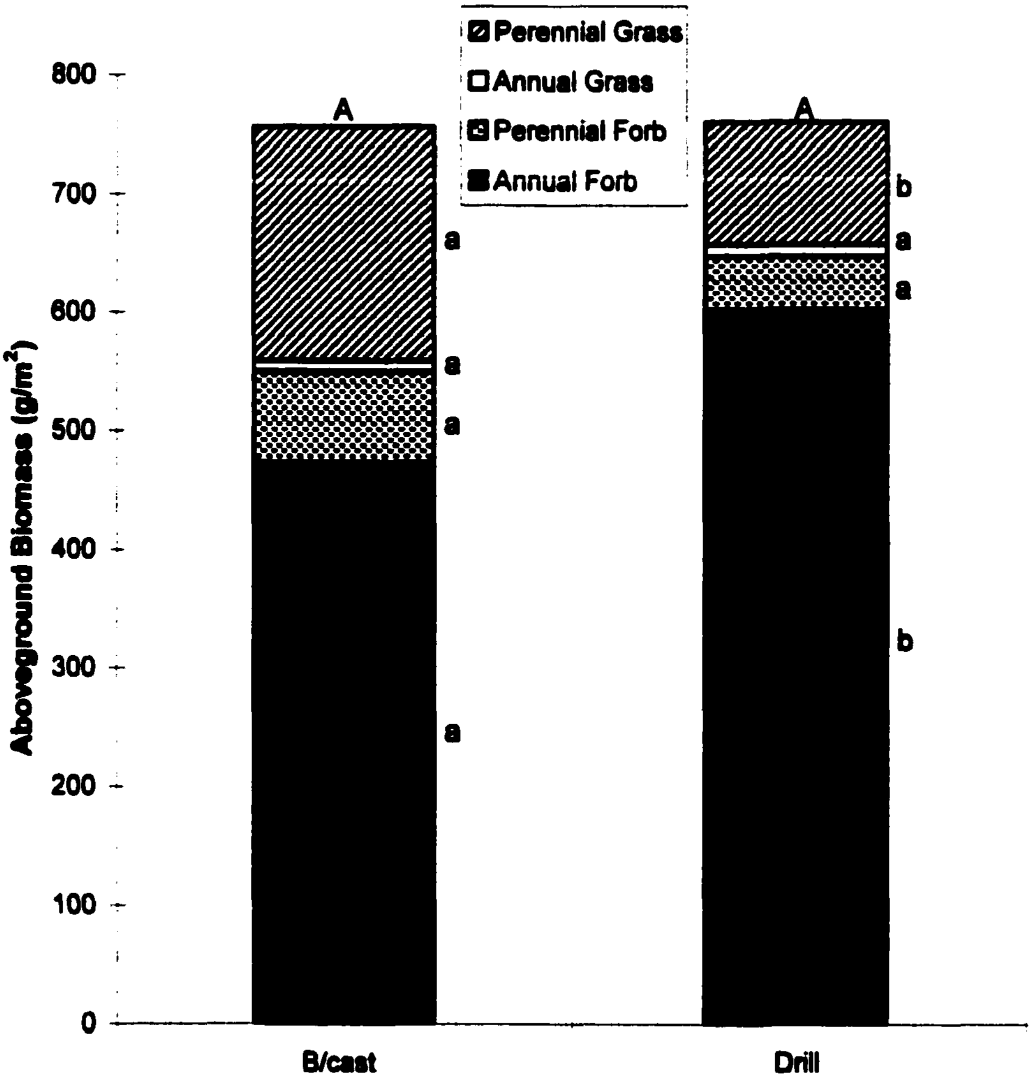

Figure 3-2. Mean aboveground biomass between seeding techniques on the Crested Wheatgrass Replacement Study in 1997. Seeding techniques, B/cast=broadcast seeding, Drill=drill seeding. Different lower case letters within lifeform groups and between treatments indicate significant differences ($p \leq 0.05$). Different upper case letters indicate significant differences in total production across treatments ($p \leq 0.05$).

Annual forb production was greater with drill seeding than broadcast seeding (602 g/m^2 and 473 g/m^2, respectively), while perennial grass production was greater with broadcast seeding than drill seeding (197 g/m^2 and 103 g/m^2, respectively). Perennial forb production was not different between treatments, however perennial forb production was 60 % greater in the broadcast treatment (77 g/m^2) compared to the drill treatment (45 g/m^2). Annual grass production was negligible in both treatments and seeding treatment had no effect on total production.

Mulch Treatments

The mulch treatment resulted in differences in production by all life-form groups except annual grasses (Figure 3-3). Perennial grass production was greatest in the mulch and no mulch treatments and both differed from the cover crop treatment (211 g/m^2, 216 g/m^2 , and 22 g/m^2, respectively). The cover crop treatment had greater annual forb production than both the mulch and no mulch treatments (735 g/m^2, 452 g/m^2, and 426 g/m^2, respectively). Perennial forb production was greatest in the mulch treatment (84 g/m^2) and was different from both the cover and no mulch treatments (44 g/m^2 and 56 g/m^2, respectively). Annual grass production was negligible, ranging from 1 to 4 g/m^2,

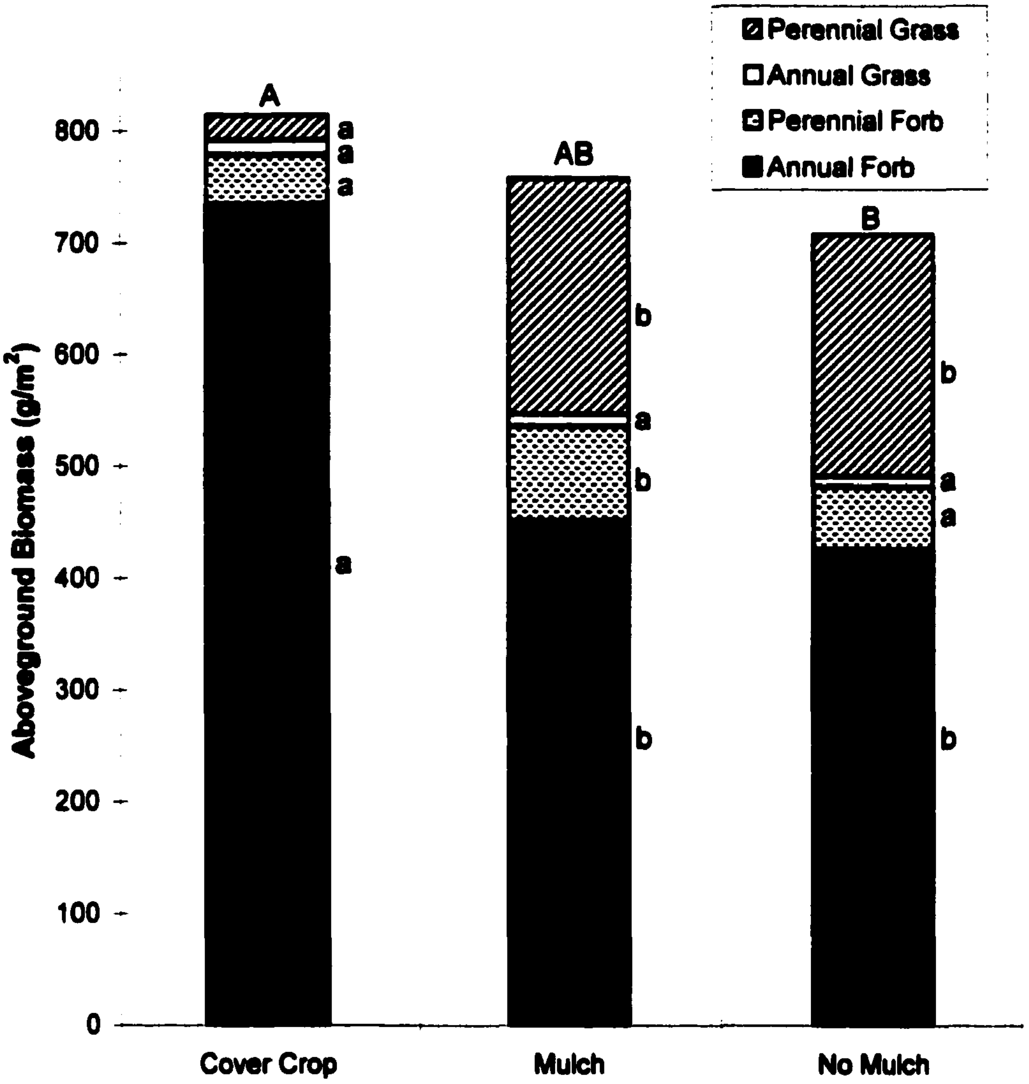

Figure 3-3. Mean aboveground biomass among mulch treatments on the Crested Wheatgrass Replacement Study in 1997. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different upper case letters indicate significant differences in total production across treatments ($p \leq 0.05$).

with no differences among treatments. Total production was greatest in the cover crop treatment and was different from the no mulch treatment (805 g/m^2 and 699 g/m^2, respectively).

Sucrose Additions

The addition of sucrose resulted in only minimal differences when comparing life-form groups (Figure 3-4). However, sucrose additions resulted in greater perennial forb production compared to the no sucrose treatment but the difference was not significant (73 g/m^2 and 50 g/m^2, respectively). Annual and perennial grasses and annual forb production showed no differences between treatments. Total production was also similar between the sucrose and non-sucrose treatments.

Comparison of Plant Available Nitrogen

The application of sucrose affected total plant available nitrogen as measured by IER bag adsorption (Figure 3-5). Sucrose application decreased total plant available nitrogen over treatments not receiving sucrose (18μg/bag/day and 24 μg/bag/day, respectively). Sucrose applications also decreased both NO_3^- and NH_4^+ individually, when compared to treatments not receiving sucrose. Ammonium differences were the largest at 10 μg/bag/day for the sucrose

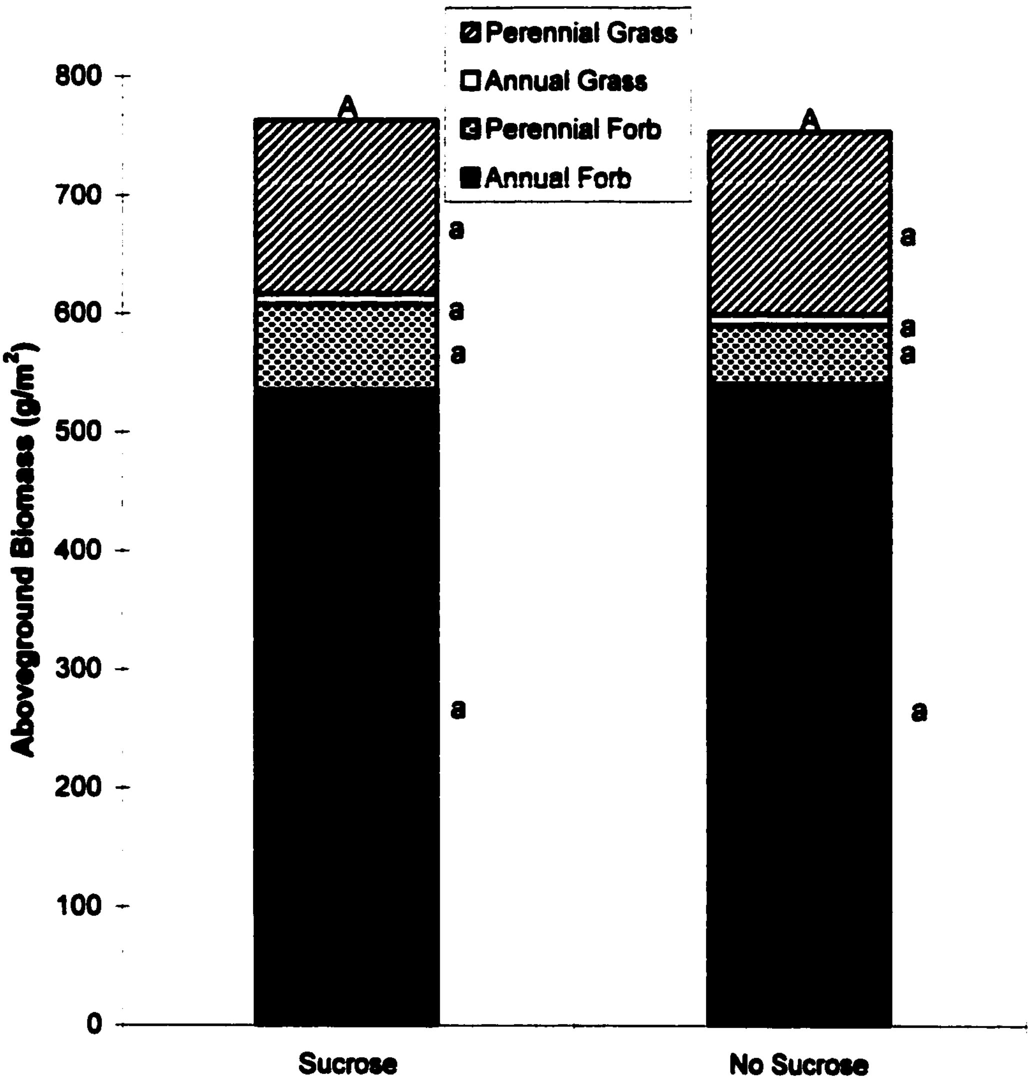

Figure 3-4. Mean aboveground biomass between sucrose treatments on the Crested Wheatgrass Replacement Study in 1997. Different lower case letters within lifeform groups and between treatments indicate significant differences ($p \leq 0.05$). Different upper case letters indicate significant differences in total production across treatments ($p \leq 0.05$).

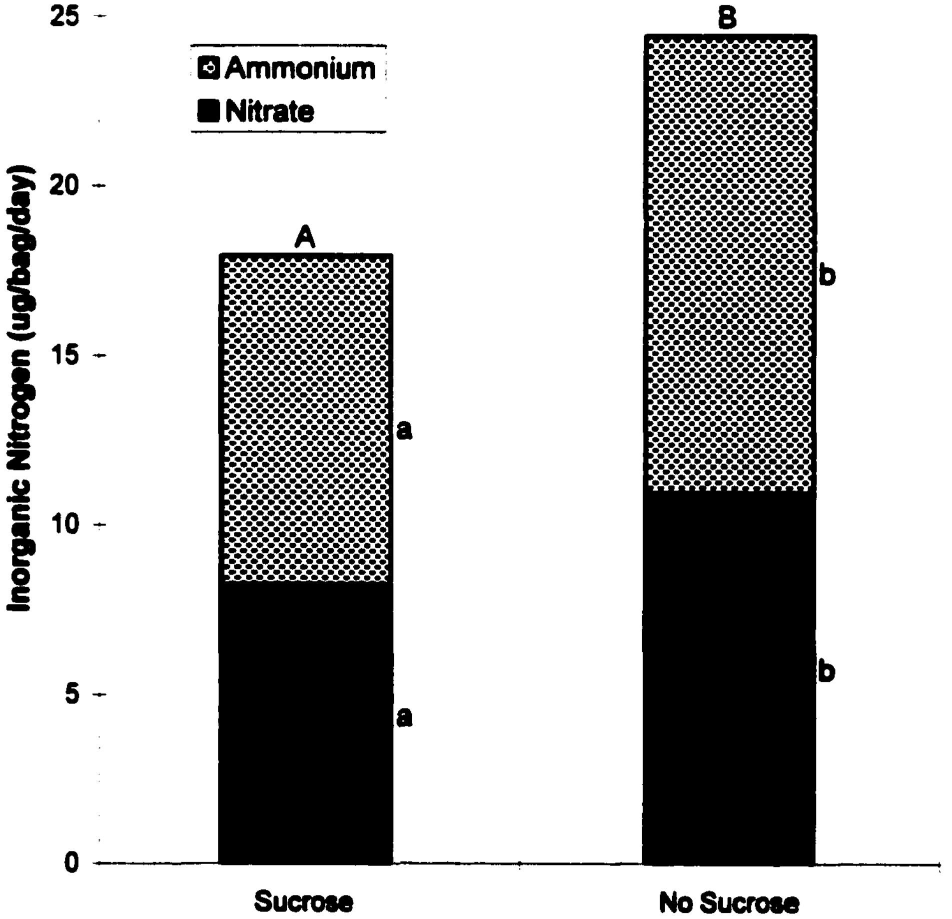

Figure 3-5. Mean plant available nitrogen between sucrose treatments on the Crested Wheatgrass Replacement Study in 1997. Different lower case letters within nitrogen type and between treatments indicate significant differences ($p < 0.006$). Different upper case letters indicate significant differences in total plant available nitrogen between treatments ($p < 0.0001$).

treatments compared to 14μg/bag/day for the non-sucrose treatments. Nitrate differences were slightly smaller at 8 μg/bag/day for the sucrose treatment and 11 μg/bag/day for the non-sucrose treatment.

Discussion

This study provides evidence that restoration techniques can influence the development of a native perennial community. The goals of restoration are usually the prompt establishment of native perennial or late seral communities and to reduce the time early seral species dominate a site. This study examined four different revegetation techniques to determine how each could be used to enhance native perennial community development. Three of the revegetation techniques, irrigation, seeding technique, and mulching influenced plant production within four-life form groups. The fourth technique, a soil carbon amendment, produced significant changes in soil chemistry, but had limited influence on plant community development within the time frame of this study.

Irrigation has been shown to increase plant establishment on disturbed land revegetation in arid and semi-arid regions (DePuit et al. 1982, Farmer et al. 1974, Munshower 1994, Newman 1999, Vallentine 1980). DePuit et al. (1982) looked at irrigated verse non-irrigated treatments with a combined native and introduced seed mixture. They showed an increase in both native and non-native cool season perennial grasses and a decrease in non-legume weedy forbs with irrigation. However, some of the seeded native species declined with irrigation in this study. Farmer et al. (1974) used an all native seed mixture and found that revegetation of overburden material was improved with irrigation over sites not irrigated. Newman (1999) returned to a study site twenty-one years after the study inception and compared a native, introduced, and a combined native and introduced seed mixture, with and without one year of irrigation. He found that the all-native irrigated plots had improved total biomass production over plots not irrigated. While these studies show that irrigation can improve native species revegetation, few irrigation studies have been conducted using an all-native seed species, and irrigation of increased duration during the growing season.

I hypothesized that two years of irrigation over four months would improve the establishment of native perennial species, compared to no irrigation or fewer months of irrigation. The results from this study show that two years of irrigation can play an important role in the successful establishment of native perennial species during restoration and that irrigating longer into the growing season results in a linear increase in native perennial plant production. Irrigating May through July, or May through August showed the largest improvement in perennial grass production when compared to shorter periods of irrigation. Water supplies, however, are costly and are often limited. Therefore, watering through July may yield the greatest benefit compared to the needed resources.

Increasing irrigation improved not only perennial plant production but also decreased weedy annual forb production during the same time frame after the cessation of irrigation. An inverse relationship between increasing irrigation and total annual forb production was observed. Irrigating from May through July decreased relative annual forb production by 18 %, compared to plots not irrigated. Therefore, supplemental water benefits restoration in two ways, it can decrease annual plant production and improve perennial plant production

This two fold response to irrigation may have stemmed from changes in competitive relationships among annual and perennial species. Perennial species typically do better than annual species when resources become increasingly limited (Grime 1977, Grime 1979, Redente et al. 1992). In this study, irrigation may have facilitated the establishment of more perennials during the first two years of irrigation and then when irrigation ceased in the third growing season, perennials species may have had a competitive advantage over annual species.

Seeding technique in this study also influenced perennial and annual species production in the third growing season. Comparing broadcast and drill seeding techniques was important because there are conflicting findings in the literature on the best seeding technique to use in revegetation (Munshower 1994, Newman 1999, Redente and Depuit 1988, Roundy and Call 1988). Native revegetation projects commonly have seed mixtures containing seeds of varying sizes, shapes and weights. Because of the diverse mix of seed architecture, determining the most appropriate and effective seeding technique can be difficult. Roundy and Call (1988) stated that drill seeding can be superior to broadcast seeding, however, greater species diversity has been achieved with broadcast seeding (DePuit et al. 1980). Newman (1999) found twenty years after revegetation, that drill and broadcast seeding were equivalent as long as the broadcast treatment was seeded at twice the drill seeding rate.

The results from this study indicate that broadcast seeding can be superior to drill seeding. Both perennial grass and forb production were greatly improved with the use of a broadcast seeding technique. Perennial grass and forb production in the broadcast treatment were approximately twice the drill treatment. Higher perennial plant production in the broadcast treatment may have occurred because seeds were spread on the surface and then lightly harrowed, which increased seed soil contact but did not bury the seeds too deep. Drill seeding may have buried some seeds too deep, inhibiting seed germination and seedling emergence. Another possible factor that influenced plant production was the difference in seeding rate between broadcast and drill seeding. As is commonly practiced, the broadcast seeding rate was twice the drill rate. As noted, perennial species production in the broadcast plots was approximately twice the perennial production in the drill seeded plots. The increased seeding rate could have contributed to the success of the perennial species in the broadcast seeded plots. However, a decrease in weedy annual forb production was observed in the broadcast plots which may not be explained by the difference in seeding rate.

Weedy annual forb production declined with broadcast seeding while perennial plant production improved. Annual forb production in the drill seeded treatments was 20 % greater than in the broadcast treatment. A reduction in annual forb production may have decreased competition with seeded perennial species and enhanced their production in the broadcast treatments. This study provides evidence that seeding technique not only influences the success of a seeded community but may also accelerate the development of a perennial community.

The third restoration technique studied was mulching. The treatments included a native hay mulch treatment, a non-mulch treatment, and a cover crop treatment that incorporated the senesced residue before seeding. The use of straw and hay mulches in semi-arid regions has been recognized as a way to improve plant community establishment by improving the seed and seedling environment (Thornburg and Fuches 1978, Vallentine 1980). This study showed an improvement in perennial forb production but no improvement in perennial grass production with hay mulch compared to the non-mulch treatment. Annual forb production was the same with and without mulch, indicating no advantage for weed control. The absence of any difference in perennial grass production with the application of mulch may be associated with the addition of supplemental water. The major advantage of mulch (i.e. reduced evaporation from soil surface) is negated, when supplemental water is applied. Without improved perennial grass production or a reduction in weedy forbs, it is unclear whether the use of hay mulch, in combination with irrigation, has any advantage as a restoration practice.

The cover crop mulch treatment was an inferior restoration practice when compared to the mulch and non-mulch treatments. Contrary to the notion that cover crop residues can act as a weed suppressant (Worsham 1991), this study showed that a sorghum cover crop did not suppress weeds in the second growing season after the senesced residue had been incorporated into the seedbed. There was greater annual forb production and less perennial plant production compared to the mulch and non-mulch treatments in the second growing season. Perennial grass production was significantly less in the cover crop treatment and was less than 3 % of the total production found in the mulch and non-much treatments. Annual forb production in the cover crop treatment was 91% of the total production compared to the mulch and non-mulch treatments of 60% and 61%, respectively. The cover crop mulch treatment was clearly an inferior restoration technique compared to the mulch and non-mulch treatments in this study.

The use of a carbon amendment to reduce soil N availability was effective in reducing both ammonium and nitrate in the soil. Total plant available soil nitrogen in the sucrose treated plots was significantly reduced over plots not receiving a carbon amendment. In addition both NH_4^+ and NO_3^- individually were reduced in the carbon amended plots compared to the non-amended plots. While there was a soil response to carbon amendments, a large plant community response was not apparent. Sucrose additions increased perennial forb production over the non-sucrose treatment, but no other life form groups showed a response. Other studies have shown that carbon additions can enhance perennials and inhibit annuals over several years (Mclendon and Redente 1992b, Paschke et al. 2000, Wilson and Gerry 1995). The lower sucrose application rate in my study compared to the previously cited work (1600 kg/ha/yr. versus 3800 kg/ha/yr.) may explain the limited plant community response. With these lower rates, it may take longer than three years to observe a response to carbon amendments.

Conclusions

This study shows that implementing different restoration techniques can influence the development of a native perennial community. Careful selection of restoration techniques can enhance perennial community development and decrease the time a system is in an early-seral phase. Accelerating the development of perennial communities is important for many reasons including, socioeconomic, aesthetic and ecological. As the amount and quality of wildlife habitat declines, the need for restoring native perennial communities becomes increasingly important.

In addition, this research provides some insights into how plant available soil N might be influenced through carbon amendments. If soil nitrogen can be decreased during the restorative process, then ecologist may be able to manipulate successional dynamics and accelerate the restorative process.

Chapter Four

The Nitrogen Sucrose Study

Introduction

The establishment of self-sustaining native communities is a primary goal for restoration ecologists. Vast hectares of land in the United States have been severely disturbed by intensive agricultural practices, and later abandoned. Many of these lands have limited value because of the abundance of early seral plant species which provide limited forage for both wildlife and domestic livestock (Clements and Young 1997, Vallentine 1980, Whisenant 1989). This study examined two restoration approaches to shift a weed infested grassland community to a community dominated by native perennial species. Also evaluated in this study were some of the underlying ecological processes that may contribute to shifts in community structure.

It is well documented that soil nutrient availability affects community structure (Dodd and Lauenroth 1979, Milchunas and Lauenroth 1995, Paschke et al. 2000, Redente et al. 1992, Tilman 1984, Vitousek et al. 1989). Changes in community structure have been tied to the natural progression of secondary succession and the subsequent decrease in resource availability (Grime 1979, Rice 1984, Tilman 1984, Tilman 1986). Experimental manipulation of soil resource availability through additions of nitrogen (N) have shifted grassland and shrubland communities toward communities dominated by early-seral species (McLendon and Redente 1992a, Milchunas and Lauenroth 1995, Redente et al. 1992). In contrast, reductions in soil N have shifted grassland and shrubland communities toward later-seral communities (Mclendon and Redente 1992b, Paschke et al. 2000).

Additions of a carbon source can lower plant available N by increasing the soil C:N ratio by moving the soil system toward microbial N immobilization. This would effectively lower inorganic N available for plant uptake. It has been shown that soil microbes are better competitors for available N than plants, capturing five times more ammonium, and two times more nitrate (Jackson et al. 1989).

Additions of inorganic N can produce a high nitrogen environment and is a common agricultural practice. However, it is relatively unknown how effective fertilizer applications will be in a non-agricultural situation. A high N environment might enhance existing perennials species within a weedy matrix, or may inhibit perennials through increased competition from annual weedy species for resources such as light and space.

Plant species of different seral stages differ in their nutrient requirements. For instance, many early-seral plants species require greater N availability while late-seral plant species require less N availability (Coyne et al. 1995, Grime 1979, Vitousek et al. 1989). A number of studies have shown that tissue nitrogen levels also differ between early and late-seral species (Mclendon and Redente 1992b, Redente et al. 1992, Tilman 1984, Wedin and Tilman 1990). This implies that N uptake and utilization may differ among early and late-seral species. Perennials typically have lower N requirements than annuals because of higher N use efficiency (Salisbury and Ross 1992). Therefore, as N become limited, perennial species should have a competitive advantage over annual species (Grime 1979, Leps et al. 1982, McLendon and Redente 1992a, Mclendon and Redente 1992b, Redente et al. 1992). However, it is not clear how a non-agricultural weed infested perennial community will respond to increased or decreased N availability. In situ perennial species may improve with augmented N availability and might become more competitive for other resources than annual species. On the other hand, increased N may enhance annual species and through competitive relationships may inhibit perennial species.

Manipulation of soil N availability may elucidate some of the processes that drive changes in community structure, and how perennial species can be enhanced with human intervention. This information could improve our ability as restorationist and land mangers to influence shifts in community structure toward a desired perennial community.

Water is considered to be a major limiting factor for plant germination and growth in arid and semi-arid regions (Noy-Meir 1973). Noy-Meir (1973) considered water availability to be the most important factor influencing the structure and dynamics in arid and semi-arid ecosystems. Many factors influence soil water dynamics including soil texture, vegetation cover by species, and precipitation patterns (Dodd and Lauenroth 1997, Paruelo and Sala 1995, Sala et al. 1992, Trlica and Biondini 1990). Water limitations can effect seed germination, seedling emergence, and plant production. In the semi-arid west, precipitation patterns are highly variable and are largely made up of small precipitation events (Sala et al. 1992). Precipitation patterns may only be suitable for plant reproduction and establishment one out of every ten years (Ries and Day 1978). Applying supplemental water could greatly improve plant germination, establishment, and recruitment into native communities. Applying irrigation to weedy perennial communities may help native perennial plants to germinate, improving overall perennial establishment.

The objectives of this study were to: 1) determine if manipulating soil N and soil water availability would alter plant species composition in a community dominated by annual weeds; and 2) identify ecological processes that might contribute to a shift in community structure.

Methods

Study Site

This study was conducted at the Rocky Mountain Arsenal National Wildlife Refuge (Refuge) which is located 10 miles northwest of Denver Colorado. The soil type is a aridic argiustoll and the area receives an average of 380 mm of precipitation annually. The study site was heavily infested with cheatgrass (*Bromus tectorum*), with some native grasses and forbs present including sand dropseed (*Sporobolus cryptandrus)*, purple three-awn (*Aristida longiseta)*, needle and threadgrass (*Stipa comata)*, and golden hairy aster (*Heterotheca villosa*). The study site was in agricultural use approximately forty years prior to conducting the study and then abandoned

Experimental Design

The study includes ten treatments arranged in a completely randomized spit-plot design with four replications (Appendix A Figure 2). There were five irrigation treatments, including a control. Irrigation was applied during the first two years of the study (1995 and 1996), the treatments are shown below. Each irrigation treatment received either a carbon amendment (sucrose) or a N amendment. Each treatment measured 10m x 10m and was separated by a 3m buffer strip between irrigation treatments and a 10m buffer strip between the nitrogen (N) and sucrose treatments. The sucrose treatments received 1600 kg sucrose/ha/yr. Sucrose applications were divided into eight equal increments, and applied every two weeks beginning in May. Nitrogen was applied as ammonium nitrate at a rate of 100 kg N/ ha/year. The application of N was divided into three equal increments and applied in May, July, and August. The following were the treatments included in this experiment.

1. Irrigate in May (5 cm) and apply sucrose (1600 kg sucrose/ha /yr)
2. Irrigate in May & June (5 cm/month) and apply sucrose (1600 kg sucrose/ha /yr)
3. Irrigate in May, June, & July (5 cm/month) and apply sucrose (1600 kg sucrose/ha /yr)
4. Irrigate in May, June, July & August (5 cm/month) and apply sucrose (1600 kg sucrose/ha/yr)
5. Apply sucrose (1600 kg sucrose/ha /yr) no irrigation (control)
6. Irrigate in May (5cm) and apply nitrogen (100 kg N/ha/yr)
7. Irrigate in May & June (5 cm/month) and apply nitrogen (100 kg N/ha/yr)
8. Irrigate in May, June, & July (5 cm/month) and apply nitrogen (100 kg N/ha/yr)
9. Irrigate in May, June, July & August (5 cm/month) and apply nitrogen (100 kg N/ha/yr)
10. Apply nitrogen (100 kg N/ha/yr) no irrigation (control)

Data Collection

Vegetation sampling was conducted in July, for three consecutive years beginning in 1995. The focus of this dissertation will be on the results from the third year data (1997). Results from the third year should be a better indicator of the community response to all treatments since supplemental water was not supplied. Aboveground biomass was measured by clipping all vegetation within 0.25 m^2 quadrats. Five randomly placed quadrats were sampled in each irrigated sucrose or N plot. Vegetation was clipped at ground level and separated by species. All plant samples were oven dried for 48 hours at 55 °C and weighed.

Plant available soil N was sampled using *in situ* incubations of ion exchange resin (IER) bags (Binkely and Matson 1983). Three IER bags per treatment were buried 5 cm below the soil surface in all treatment combinations. The resin bags remained in the soil for forty-five days and adsorbed inorganic nitrogen from the soil solution during the incubation period. Two sets of resin bags were buried, the first in late May and the second in late July. Results from the two sets of resin bag data were combined for the statistical analysis. The resin bags experienced the same edaphic conditions as plant roots, therefore, they provide a relative index of the inorganic nitrogen available during the incubation period. Analysis of the inorganic nitrogen adsorbed by the IER bags provides a means to compare relative N availability across treatments.

At the end of the incubation period the IER bags were air-dried overnight and then extracted in 75 ml of 1 N KCL for 1.5 hours. Extracts were then equilibrated, filtered, and stored at –20 °C until analysis. The extracts were analyzed for NH^{+}_{4}-N and NO3 $^{-}$ -N using a Perstorp total flow solution autoanalyzer.

Tissue analysis was conducted on one perennial species (*Sporoboluos cryptandrus*) and one annual species (*Bromus tectorum*) within each plot. The plant biomass from the five randomly placed quadrats for each treatment and species was combined into one sample and ground to pass through a 40-mesh sieve. A representative sample was then analyzed for N concentration on a LECO CHN-1000 Analyzer (LECO Corp., St. Joseph, MI).

Statistical Analysis

The statistical analysis was based on a split plot design. A mixed model analysis was used to include both fixed and random effects in the analysis. Statistical analysis of the production data was preformed using an Analysis of Variance (ANOVA) procedure with SAS PROC MIXED version 6.12 (SAS 1985). Analysis of variance mean separation was determined at a $p \leq 0.05$ significance level for the production data and for the resin bag data. Studentized residual plots were generated to verify that the data fit the model assumption of homogeneous variance. No transformations were necessary to meet the model assumptions.

Results

Aboveground Biomass in Third Year of Treatments

Soil Amendments

Aboveground biomass of all life-form groups were significantly different between the nitrogen and sucrose amended sites after three growing seasons (Figure 4-1). Annual forb production showed the largest difference between treatments, with 394 g/m^2 for the nitrogen treated plots and 121 g/m^2 for the sucrose plots. The three species that were the largest contributors to annual forb production were, *Sisymbrium altissimum*, *Salsola iberica* and *Carduus nutans*. The sucrose amended plots had greater production by perennial grasses than the nitrogen plots (297 g/m^2 and 141 g/m^2, respectively). The major contributors to perennial grass production were three native species, *Sporobolus cryptandrus*, *Aristida longiseta*, and *Stipa comata*. Perennial forb production was greater in the sucrose plots than the nitrogen treated plots (49 g/m^2 and 12 g/m^2, respectively). Annual grass production was also greater in the sucrose treated plots compared to the nitrogen plots (105 g/m^2, and 40 g/m^2, respectively). Total production of all life-form groups combined was not significantly different between the nitrogen and sucrose treatments.

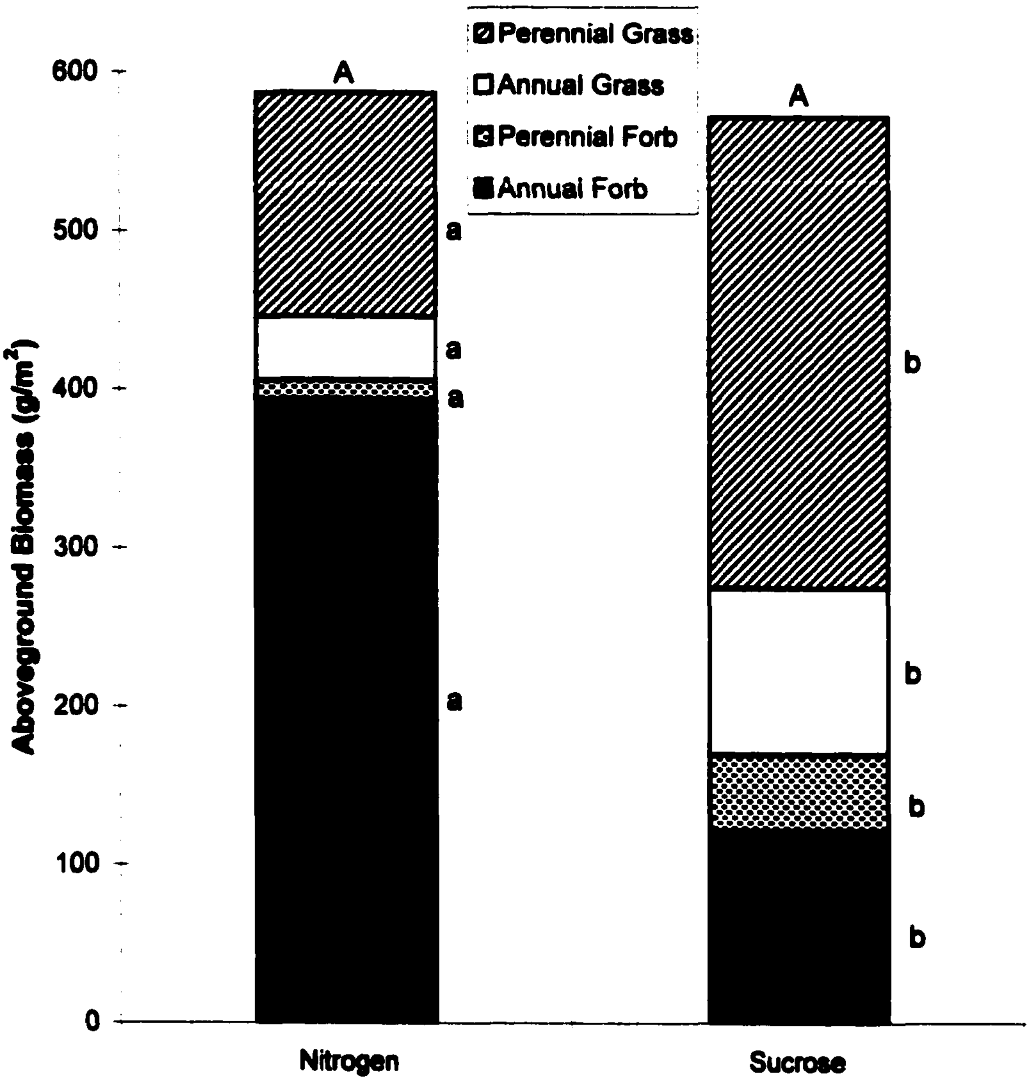

Figure 4-1. Mean aboveground biomass between nitrogen/sucrose treatments on the Nitrogen Sucrose Study in 1997. Different lower case letters within lifeform groups and between treatments indicate significant differences ($p \le 0.05$). Similar upper case letters indicate no significant differences in total production between treatments

($p \le 0.05$).

Irrigation Treatments and Soil Amendments

The irrigation treatments amended with sucrose showed differences in production by life-form group after three growing seasons, even though irrigation was not applied in the third year of the study (Figure 4-2). In general, increased irrigation resulted in increased plant production in the combined sucrose water treatments. Annual forb production in the MJJA treatment (258 g/m^2) was greater than the control, M, and MJ treatments (32 g/m^2, 92 g/m^2, and 64 g/m^2, respectively). Perennial grass production was greatest in the MJJ and MJJA treatments (361 g/m^2 and 460 g/m^2, respectively). Perennial forb production showed no differences among treatments, but the MJJA treatment had the most absolute production of perennial forbs among the treatments (89 g/m^2). Annual grass production did not follow any obvious pattern but was lower in the MJJA treatment (18 g/m^2) compared to all other treatments.

Total aboveground production in the combined irrigation and sucrose treatments was somewhat variable, with no differences among the control, M and MJ treatments (441 g/m^2, 515 g/m^2, and 416 g/m^2, respectively). However, there was a significant increase in total production on the MJJ and MJJA treatments (667 g/m^2 and 852 g/m^2, respectively) compared to the control and MJ treatments.

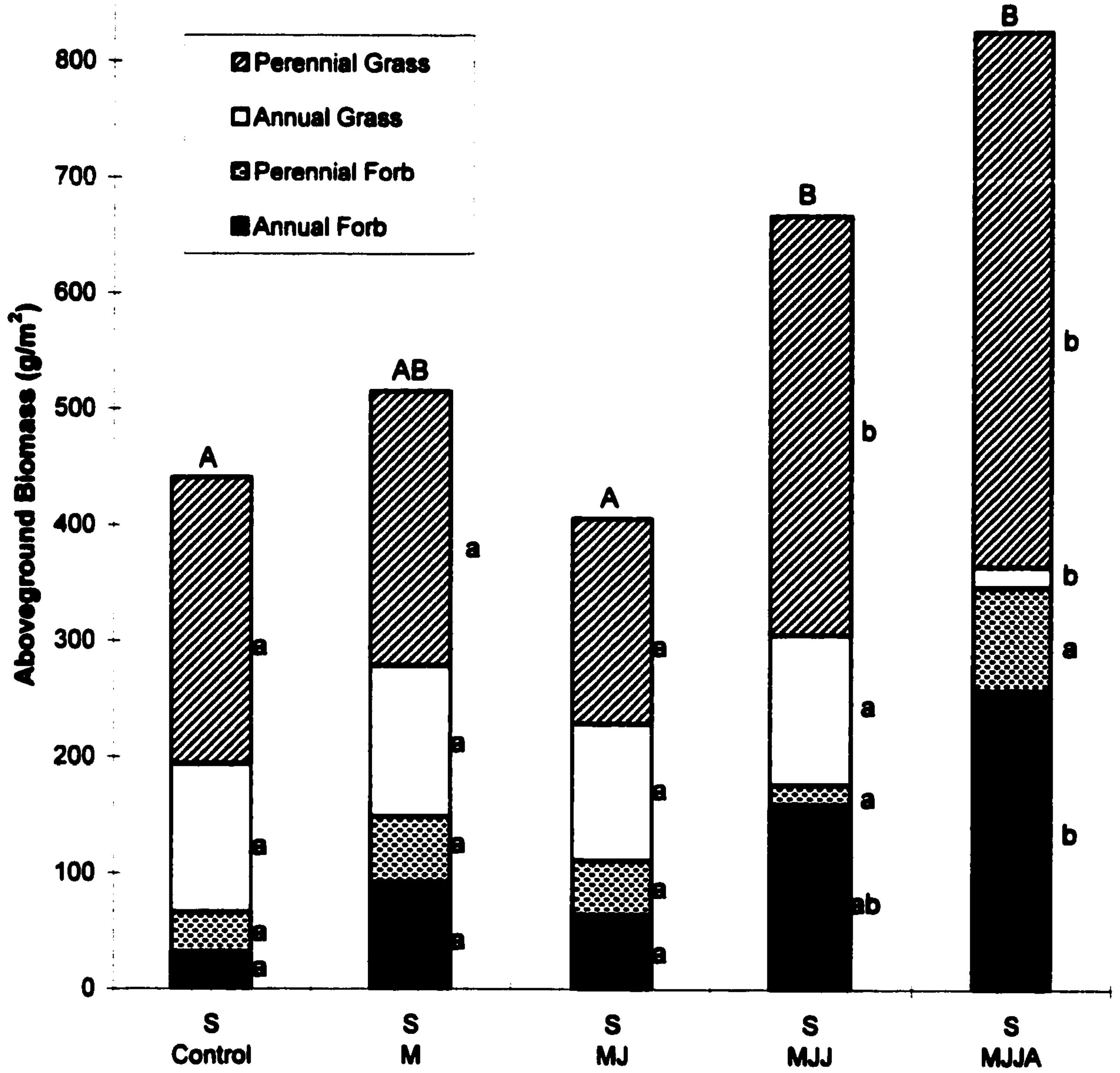

Figure 4-2. Mean aboveground biomass among irrigation treatments (with sucrose) on the Nitrogen Sucrose Study in 1997. Irrigation, Control=no irrigation, M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+August Irrigation. S=sucrose. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different upper case letters indicate significant differences in total production across treatments ($p \leq 0.05$).

The irrigation treatments amended with N showed fewer differences in production by life-form group than did the irrigation treatments amended with sucrose (Figure 4-3). Annual forb production was greatest in the MJJA treatment (671 g/m^2) and did not differ among the other four treatments. Perennial forb production was greatest in the M treatment (37 g/m^2) and no other differences were detected among the other four treatments. Annual and perennial grasses did not differ among the combined irrigation and nitrogen treatments.

Total production in the combined irrigation and nitrogen treatments was relatively uniform among the control, M, MJ, and MJJ treatments. The greatest total production was in the MJJA treatment (853 g/m^2) compared to 491 g/m^2 for the control, 512 g/m^2 for M, 539 g/m^2 for MJ, and 541 g/m^2 for MJJ.

Inorganic Soil Nitrogen

Average total inorganic nitrogen was markedly different between the N amended plots and the sucrose amended plots (Figure 4-4). The nitrogen treated plots averaged 143 μg/bag/day compared to 12 μg/bag/day in the sucrose treated plots.

Total inorganic soil nitrogen in the combined irrigation and sucrose treatments generally resulted in an inverse relationship between increasing supplemental water and decreasing inorganic nitrogen (Figure 4-5).

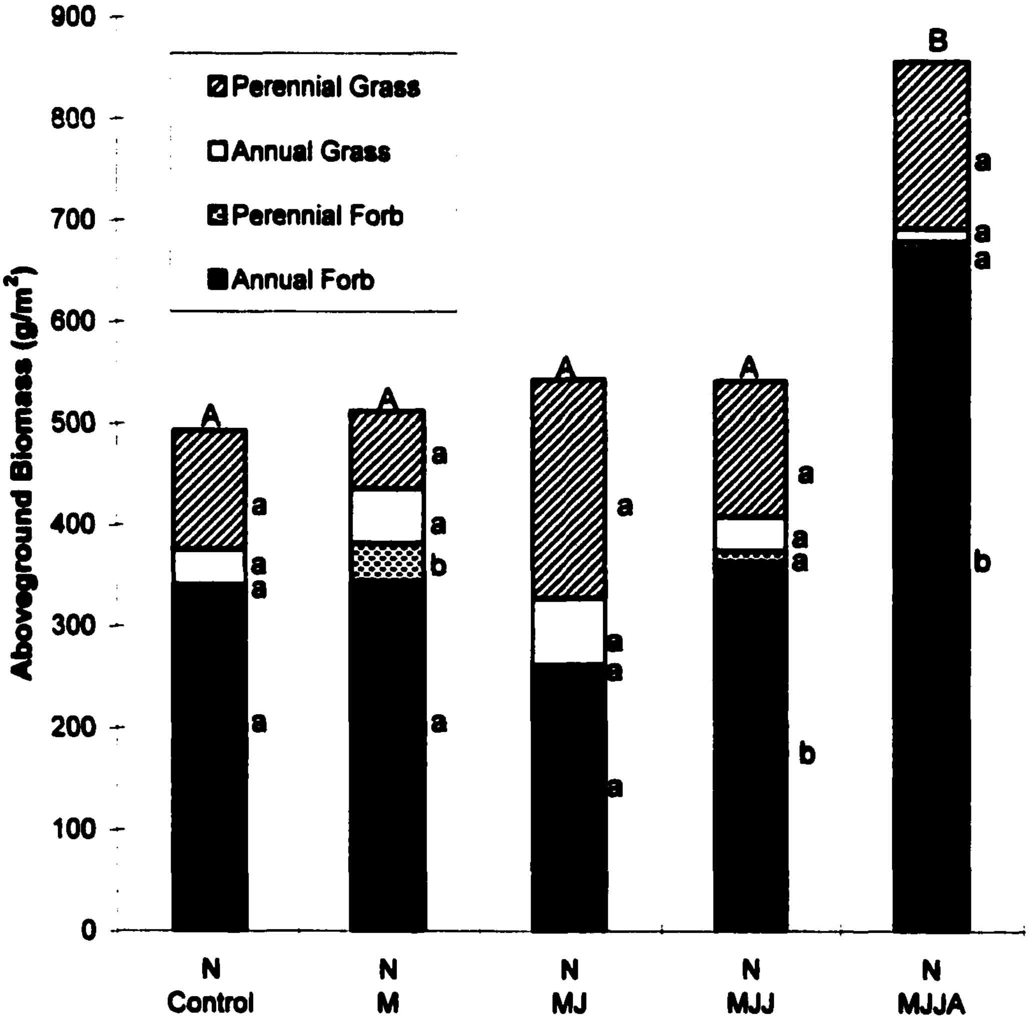

Figure 4-3. Mean aboveground biomass among irrigation treatments (with Nitrogen) on the Nitrogen Sucrose Study in 1997. Irrigation, Control=no irrigation, M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+August Irrigation. N=nitrogen. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different upper case letters indicate significant differences in total production across treatments ($p \leq 0.05$).

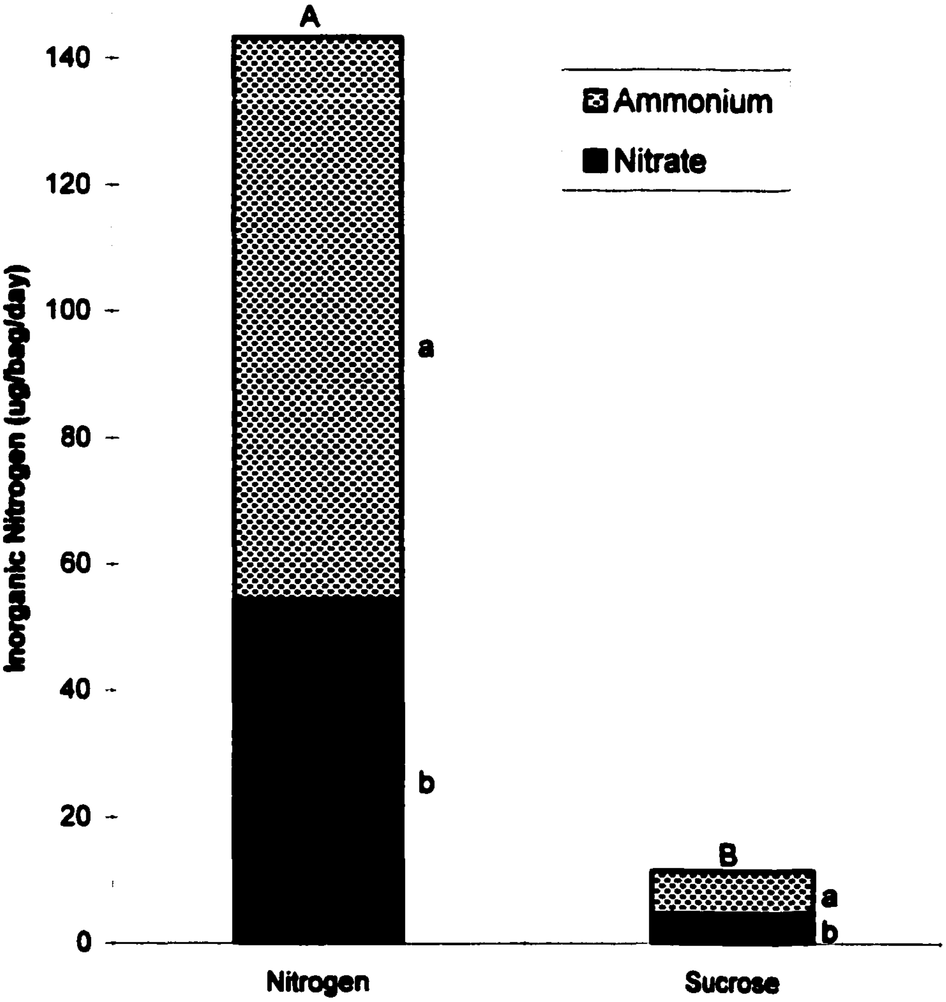

Figure 4-4. Inorganic nitrogen in micrograms per ion exchange resin bags per day between nitrogen treated plots and sucrose treated plots in the Nitrogen Sucrose Study in 1997. Different lower case letters within ammonium and nitrate groups and between treatments indicate significant differences ($p < 0.0001$). Different upper case letters indicate significant differences in total mineral nitrogen ($p < 0.0001$).

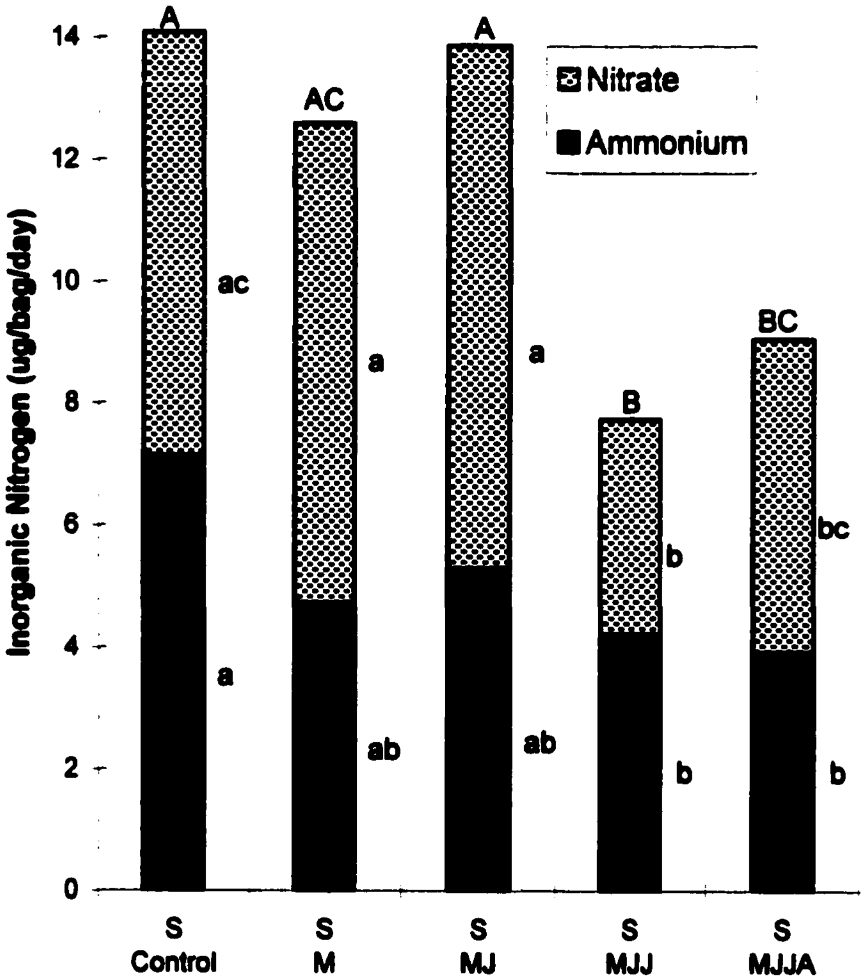

Figure 4-5. Inorganic nitrogen among irrigation plus sucrose treated plots on the Nitrogen Sucrose Study in 1997. Irrigation, Control=no irrigation, M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+August Irrigation. S=sucrose. Different lower case letters within ammonium and nitrate groups and between treatments indicate significant differences ($p < 0.05$). Different upper case letters across treatments indicate significant differences in total mineral nitrogen ($p < 0.05$).

The MJJ and MJJA treatments had the lowest total inorganic nitrogen (8 and 9 µg/bag/day, respectively). The control, M, and, MJ treatments had the greatest inorganic nitrogen (14, 13, and 14 µg/bag/day, respectively).

Ammonium in the combined irrigation sucrose treatments, decreased with increasing irrigation as did NO_3^--N (Figure 4-5). Ammonium in the control sucrose treatment (7µg/bag/day) was greater than both the MJJ and MJJA treatments (4µg/bag/day for both treatments). Nitrate was lowest in the MJJ treatment (4 µg/bag/day) compared to the control, M, and MJ treatments (7, 5, and 5µg/bag/day, respectively).

Total available inorganic N was much greater in the combined nitrogen and irrigation treatments (Figure 4-6) compared to the combined sucrose and irrigation treatments. The lowest total available N among the combined N treatments was 176 µg/bag/day (Figure 4-6), compared to the greatest among the combined sucrose treatments of 14 µg/bag/day (Figure 4-5). There was no pattern within the nitrogen and irrigation treatments. The M treatment (176 µg/bag/day) had the lowest available N when compared to the control and MJJ treatments (314 and 349µg/bag/day, respectively). Ammonium was greatest in the MJJ and control, N treatments (130 and 122 µg/bag/day, respectively) compared to the M treatment (59 µg/bag/day). Nitrate was lowest in the M, and MJJA treatments

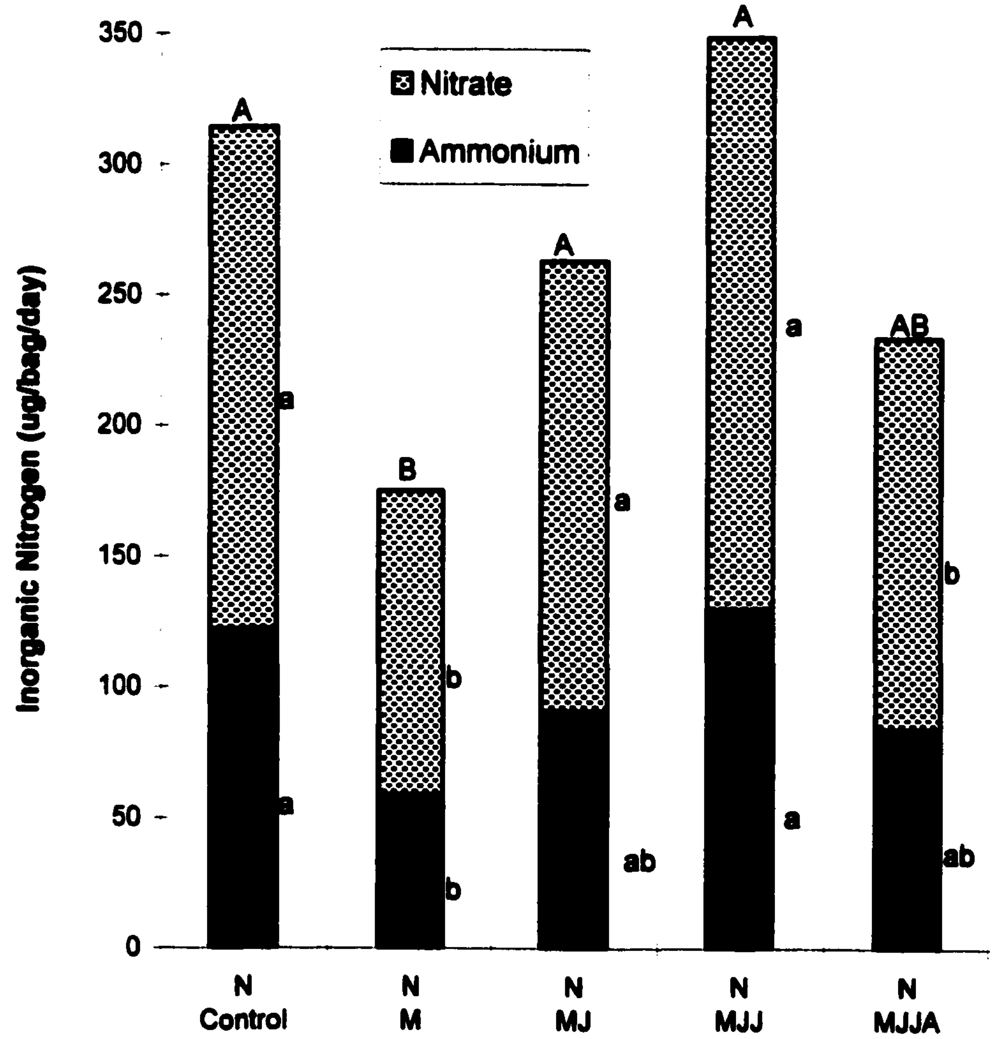

Figure 4-6. Inorganic nitrogen among irrigation plus nitorgen treated plots on the Nitrogen Sucrose Study in 1997. Irrigation, Control=no irrigation, M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+ August Irrigation. N=nitrogen. Different lower case letters within ammonium and nitrate groups and between treatments indicate significant differences ($p < 0.05$). Different upper case letters across treatments indicate significant differences in total mineral nitrogen ($p< 0.05$).

(117 and 149 μg/bag/day, respectively) and greatest in the control, MJ, and MJJ treatments (192, 172, and 219 μg/bag/day, respectively).

Percent Tissue Nitrogen

Percent tissue nitrogen was markedly different between the annual and perennial grasses tested (Figure 4-7). Regardless of treatments, the annual grass *Bromus tectorum* had significantly less tissue nitrogen as the perennial grass, *Sporobolus cryptandrus* (0.1 % and 1.9 % N, respectively). Amendment application affected accumulated tissue N within these species (Figure 4-8). *Bromus tectorum* in the sucrose treated plots had less tissue N than the *Bromus tectorum* in the nitrogen treated plots (0.6 % and 1.2 % N, respectively). The same pattern was true for the perennial grass *Sporobolus cryptandrus*, with 1.4 % tissue N in the sucrose treated plots and 2.5 % tissue nitrogen in the nitrogen treated plots.

Discussion

Manipulation of the soil C:N ratio was used to assess the influence of nutrient availability on plant community structure. In addition, irrigation was applied for increasing lengths of time to determine if supplemental water would magnify the effects of N manipulations. Furthermore, if water could be supplied

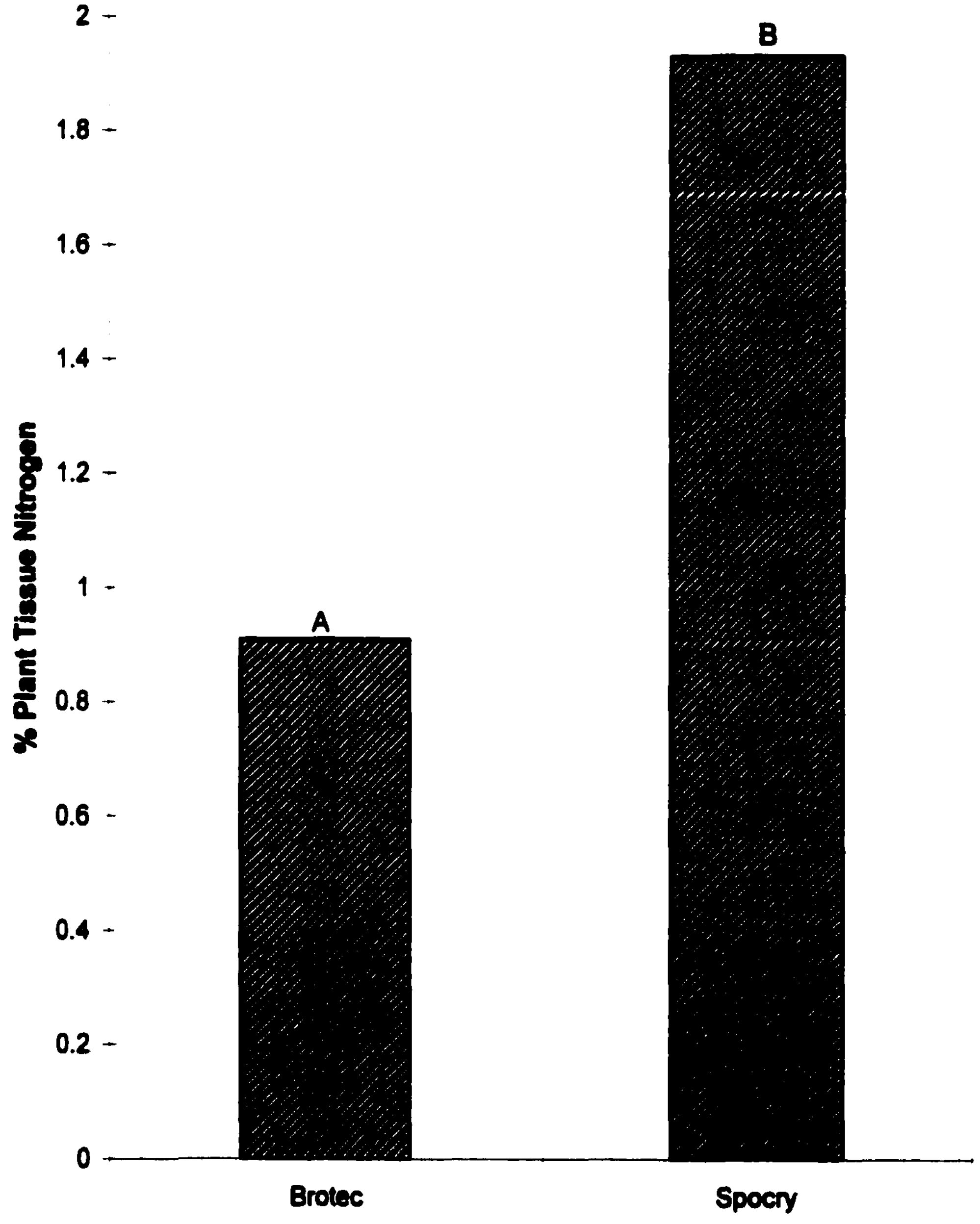

Figure 4-7. Percent plant tissue nitrogen between an annual and perennial grass in the Nitrogen sucrose Study in 1997. Values are an average of all irrigated, nitrogen and sucrose treated plots. Brotec = *Bromus tectorum*, Spocry = *Sporobolus cryptandrus*. Different letters indicate significant difference between species ($p \leq 0.0001$).

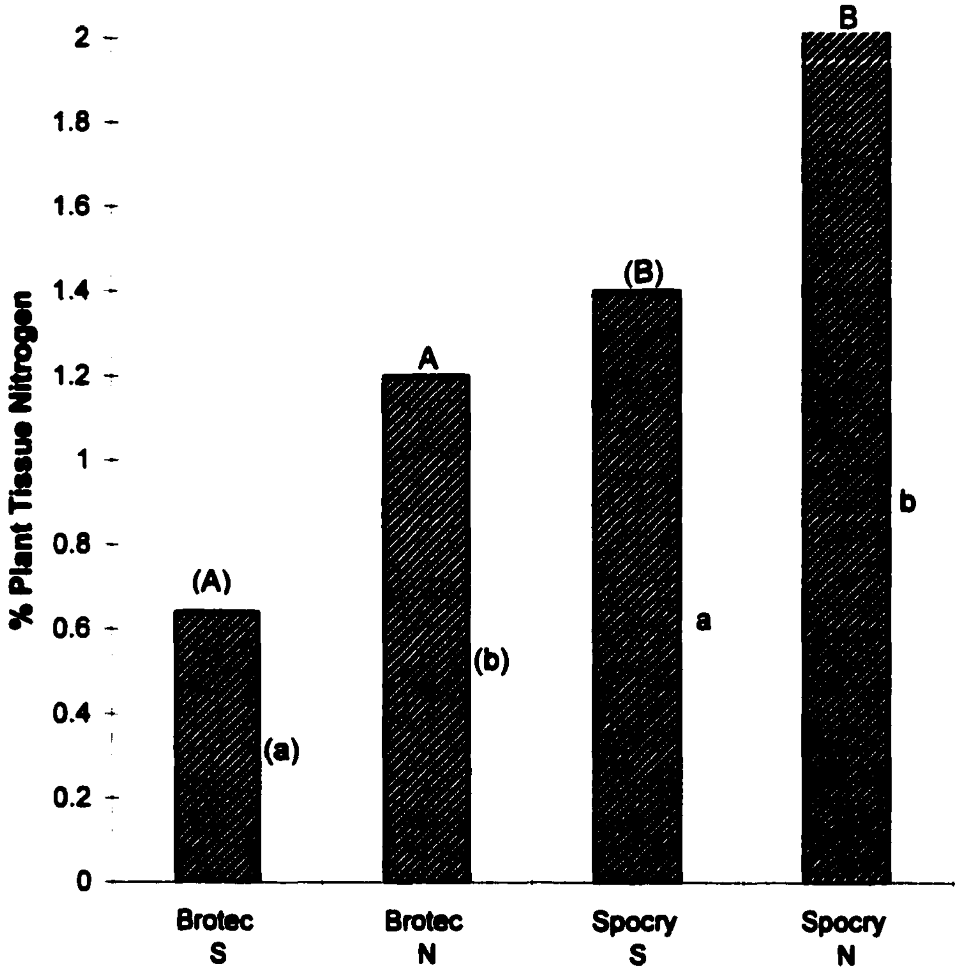

Figure 4-8. Percent plant tissue nitrogen between an annual and perennial grass within plots treated with nitrogen or sucrose, on the Nitrogen Sucrose Study in 1997. Brotec = *Bromus tectorum*, Spocry = *Sporobolus cryptandrus*. S = sucrose, N = nitrogen. Different upper case letters, in parenthesis or not, indicate significant differences within sucrose or nitrogen treated plots and between species ($p< 0.0001$). Different lower case letters, in parenthesis or not, indicate significant differences within species and between treatments ($p< 0.0001$).

to native perennial plants during critical germination periods, perennial community development may be enhanced. Five irrigation schedules were implemented to determine when, and if, there was a critical irrigation time period.

Results from this study demonstrate that soil N manipulation and supplemental water contribute to significant shifts in plant community structure.

Edaphic Response to Treatments

Results indicate that additions of both N and sucrose produced large differences in plant available soil nitrogen. Inorganic N was thirteen times greater in N amended plots compared to sucrose amended plots. Paschke et al. (2000) reported similar results on a chronosequence of four old-field successional sites on a shortgrass steppe in northeast Colorado. They found that inorganic nitrogen was significantly increased by N additions and significantly decreased by sucrose additions compared to non-amended control plots at all sites.

My study showed an inverse relationship between irrigation treatment and inorganic soil N in the sucrose treated plots. Inorganic soil N was lowest on the treatments receiving the greatest amount of supplemental water. When the amount of inorganic N was compared to biomass productions in the same plots, it was clear that as inorganic N decreased, plant production increased (Figures 4-2 and 4-5). This pattern of decreasing inorganic soil N with increasing plant production could be explained by increased N immobilization by both the plant and microbial communities. Inorganic N concentrations were followed using a mixed-bed ion exchange resin bag (IER) method (Binkely and Matson 1983), which adsorbs and retains mineral N from the soil solution. The IER bags experience the same soil conditions as plant roots, including leaching losses, and competition from microbes and plants. Therefore, as plant production increased, available N decreased in the resin bags as they experienced competition from plants and microbes. The same pattern was not observed in the combined water and N treatments. In fact no pattern emerged in this set of treatments when comparing total biomass and plant available N. This may have been due to excess available N in the system. With excessive nitrogen in the system it is not surprising that plant available N was not sensitive to increases in plant production.

Plant Tissue Nitrogen

Studies show that tissue N concentrations are affected by soil N availability (Mclendon and Redente 1992b, Redente et al. 1992, Richard and Redente 1995, Tilman 1986). My data supports this assertion. Increased N availability led to higher tissue N for both the annual and perennial species sampled. Richard and Redente (1995) also found that low and high N availability influenced tissue N in two native perennial grass species grown in a controlled greenhouse study. In their study, low N availability resulted in lower tissue N and high N availability resulted in higher tissue N. In another field study McLendon and Redente (1992) showed that high N plots resulted in high tissue N for both annuals and perennials.

Studies show that tissue N concentrations differ between early and late seral species (Mclendon and Redente 1992b, Redente et al. 1992, Tilman 1984, Wedin and Tilman 1990). My study also demonstrated differences in tissue N between annual and perennial grasses. The perennial grass species analyzed, *Sporobolus cryptandrus*, had two times more tissue N than the early seral annual grass species *Bromus tectorum*, regardless of N availability. This implies that N uptake and utilization may differ among annual and perennial species. Differences in uptake and utilization by annuals and perennials also imply that N requirements are different. Many perennials have lower N requirements than annuals because of higher N use efficiency (Trlica and Biondini 1990). Therefore, as resources become limited, perennial species should have a competitive advantage over annual species (Grime 1979, Leps et al. 1982, Mclendon and Redente 1992b, Redente et al. 1992). It was suggested by McLendon and Redente (1992) that nitrogen depletion of the upper rooting zone, could inhibit annual plant production because annual plants have higher N requirements. They also suggest this may be an important mechanism driving community change from one seral stage to the next. In my study, manipulating available N produced significant shifts in community structure.

Shifts in Community Structure

Soil amendments shifted species composition in one of two directions: either toward a perennial dominated community, or an annual dominated community. The plots supplemented with nitrogen were dominated by early-seral forb species while the sucrose amended plots were dominated by late-seral perennial grasses. Other studies have shown similar patterns on disturbed sites receiving carbon or N amendments (McLendon and Redente 1992a, Mclendon and Redente 1992b, Paschke et al. 2000, Tilman 1984).

McLendon and Redente (1992) showed that nitrogen amendments increased annual forb canopy cover while sucrose additions decreased annual forb canopy cover in a disturbed sagebrush community. Their study showed that sucrose applications following disturbance could increase the rate of perennial species establishment, when compared to N or control plots. Milchunas and Lauenroth (1995) returned to a study site sixteen years after the application of treatments. One of the study treatments applied N (100-150 kg/ha/year) and water (510-590 mm/year) over a five year period. This combined treatment showed an increase in exotic annual species 16 years after treatments had ceased, when compared to a control.

In my study, shifts in community structure appeared to be driven by N availability. Production by all life-form groups was significantly different between the N and sucrose plots. Production by annuals in sucrose plots was half that of the N plots. Production by perennials in the sucrose plots was more than twice that of the N plots. In the first year (1995) of the study, community structure was similar in both the high and low N plots. Large changes in relative annual forb production were observed between the first and third year of the study (Table B-7). In the N plots, relative annual forb production increased from 1% in the first year to 67% in the third year, while perennial grass production decreased from 31% in the first year to 24% in the third year. In the sucrose treated plots, relative total annual species production decreased from 67% in the first year to 39 % in the third year, while relative perennial grass production increased from 25% to 52 % in the third year. Therefore, in the third growing season after amendment application, perennial grass production in the sucrose treated plots was more than twice that of the N treated plots, while annual forb production in the sucrose treated plots was less than half that of the N treated plots.

While N additions did alter community structure, N amendment did not increase overall plant production as expected. There was no difference in total plant production between the N and sucrose plots in the third year of the study. It can be inferred from this response that N was not a limiting factor to total production in this grassland system. In the first and second years of the study, when supplemental water and amendments were being applied, the N plots had greater total production than the sucrose plots. However, in the third year of the study, N without supplemental water did not increase plant production, therefore it appears that water may be more limiting to production than N in this system. This provides some support for Noy-Meir's (1973) assertion that water is the major limiting resource in arid and semi-arid ecosystems.

In fact, an irrigation effect was still evident in the third year of the study even though irrigation was only applied for two growing seasons. Other studies have shown that supplemental water can have a long-term effect on plant community structure years after applications have ceased. For instance, Milchunas and Lauenroth (1995) showed that a native short-grass community watered for five years had increased numbers of native grasses seven years after cessation of supplemental water. In my study, plant production responded to irrigation treatments in a similar manner regardless of whether the sites received N or sucrose. Increased amounts of irrigation water resulted in increased plant production. In addition, there were large differences in community composition when examining irrigation in combination with N or sucrose. The combined sucrose and water treatments had up to three times more perennial grass production than the respective combined N and water treatments. Perennial forb production was also greater in the sucrose and water plots with up to 19 times more perennial forb production as the corresponding N and water plots. Perennial grasses were the dominate life-form group in the sucrose and water treatments while weedy annual forbs were the dominate life-form group in the N plus water treatments. The N and water treatment plots had up to ten times more annual forb production as the corresponding sucrose plus water plots. Overall, the N plus irrigated plots were dominated by early-seral plant species and the sucrose plus irrigated plots were dominated by native perennial species.

The results also demonstrate that longer water applications into the growing season with additions of a carbon source can increase perennial community development. Irrigating through August, in combination with sucrose, had almost twice the perennial grass production as the sucrose plots without irrigation and those irrigated in May, and May and June. Irrigation and sucrose also improved perennial forb production. The MJJA irrigation treatment with sucrose had two times the perennial forb production as the sucrose plot without irrigation. This study therefore demonstrates that reducing soil available N with sucrose and increasing amounts of supplemental water can effectively shift species composition toward a community dominated by perennial species.

The reverse was true for the plots with increased soil N and increased supplemental water; the community shifted toward a community dominated by annual species. Watering through August in combination with N fertilization resulted in approximately twice the annual forb production as the N treatments irrigated in May, May-June, or not irrigated. Dodd and Lauenroth (1979) also demonstrated that additions of supplemental water (compared to no supplemental water) and N can increase exotic species over control treatments. Paschke et. al. (2000) showed that even without supplemental water, N amendments shifted plant communities toward an earlier seral community. My study also demonstrates that without supplemental water, additions of N can shift the plant community toward an earlier seral-stage community. In the control treatments that received no irrigation, but received N or sucrose, the N treatment plots had ten times more annual plant production, implying a reversal of seral stage development.

Conclusions

Manipulation of soil N availability and providing supplemental water could be important tools for the restoration of abandoned agricultural lands and weed infested rangelands in semi-arid ecosystems. Land managers and restoration ecologists face many challenges when trying to improve degraded habitats. As the impact of human disturbances expands, sound land management practices dictate that larger tracts of land will require restoration in order to return them to functioning native communities.

The results of this study show that by lowering plant available soil N and applying supplemental water for two growing seasons, significant shifts toward a community dominated by perennials can be achieved. After three years, total perennial biomass doubled with two years of supplemental water and three years of sucrose applications, when compared to N and irrigation treatment. If an affordable source of carbon could be found, such as manufacturing by-products with a high carbon content, then a doubling of perennial species biomass could greatly improve forage availability and quality for both wildlife and domesticated stock.

The study also demonstrated that by increasing plant available soil N, perennial community development is inhibited and weedy annual species can be recruited into the site where they were not originally present, reversing perennial community development. Amending native sites with N is therefore not likely to enhance perennial species production and would not be a productive restoration technique.

In general, this study provides insight into how nutrient availability may be important in observed shifts in community structure. This may have implications in ongoing research on increasing N deposition due to anthroprogenic atmospheric changes, which may inexorably shift community structure toward communities dominated by weedy annuals. Atmospheric nitrogen deposition could lower soil C:N ratios in established native communities and shift them toward annual weedy communities or make restoration of perennial communities much more difficult.

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Appendices

Appendix A

Figures

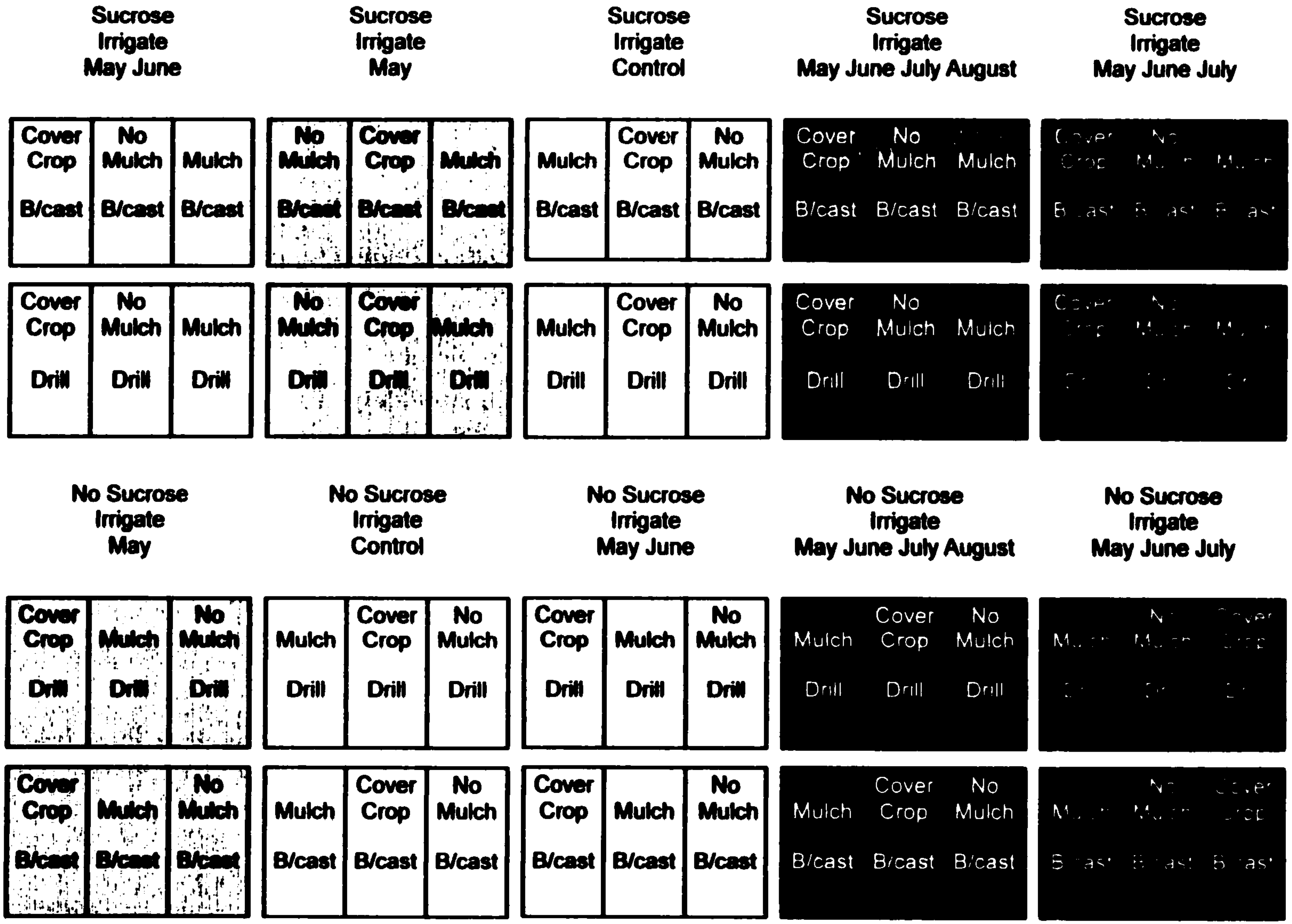
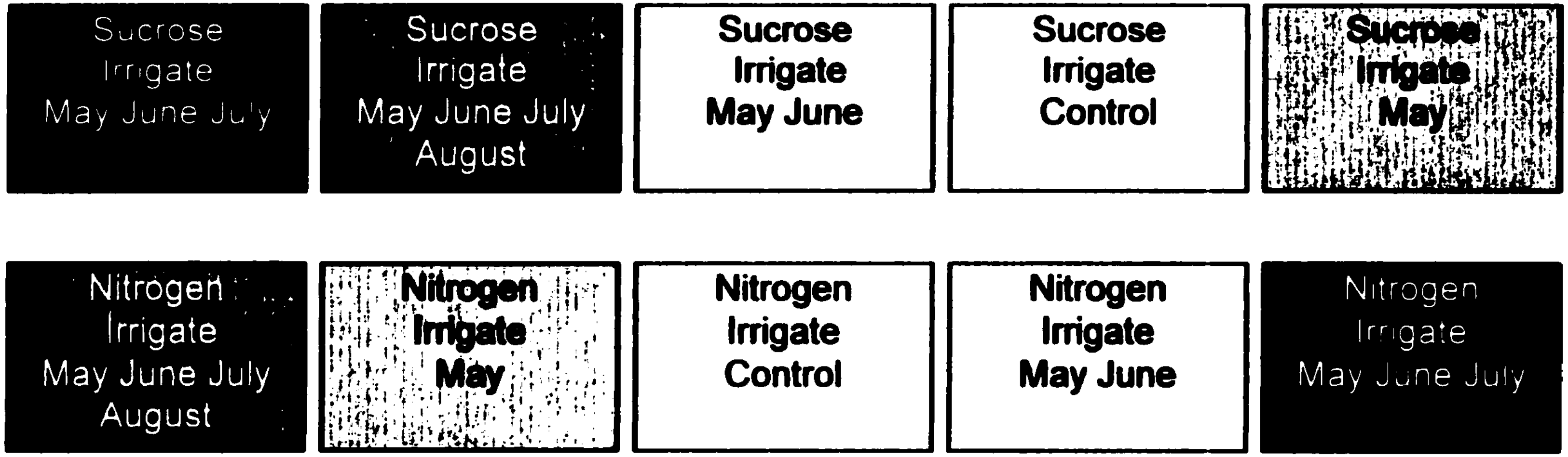


Figure A-1. Experimental design for one replicate of the Crested Wheatgrass Replacement Study.



Sucrose Irrigate May June July	Sucrose Irrigate May June July August	Sucrose Irrigate May June	Sucrose Irrigate Control	Sucrose Irrigate May
Nitrogen Irrigate May June July August	Nitrogen Irrigate May	Nitrogen Irrigate Control	Nitrogen Irrigate May June	Nitrogen Irrigate May June July

Figure A-2. Treatment arrangement design for one replicate of the Nitrogen Sucrose Study.

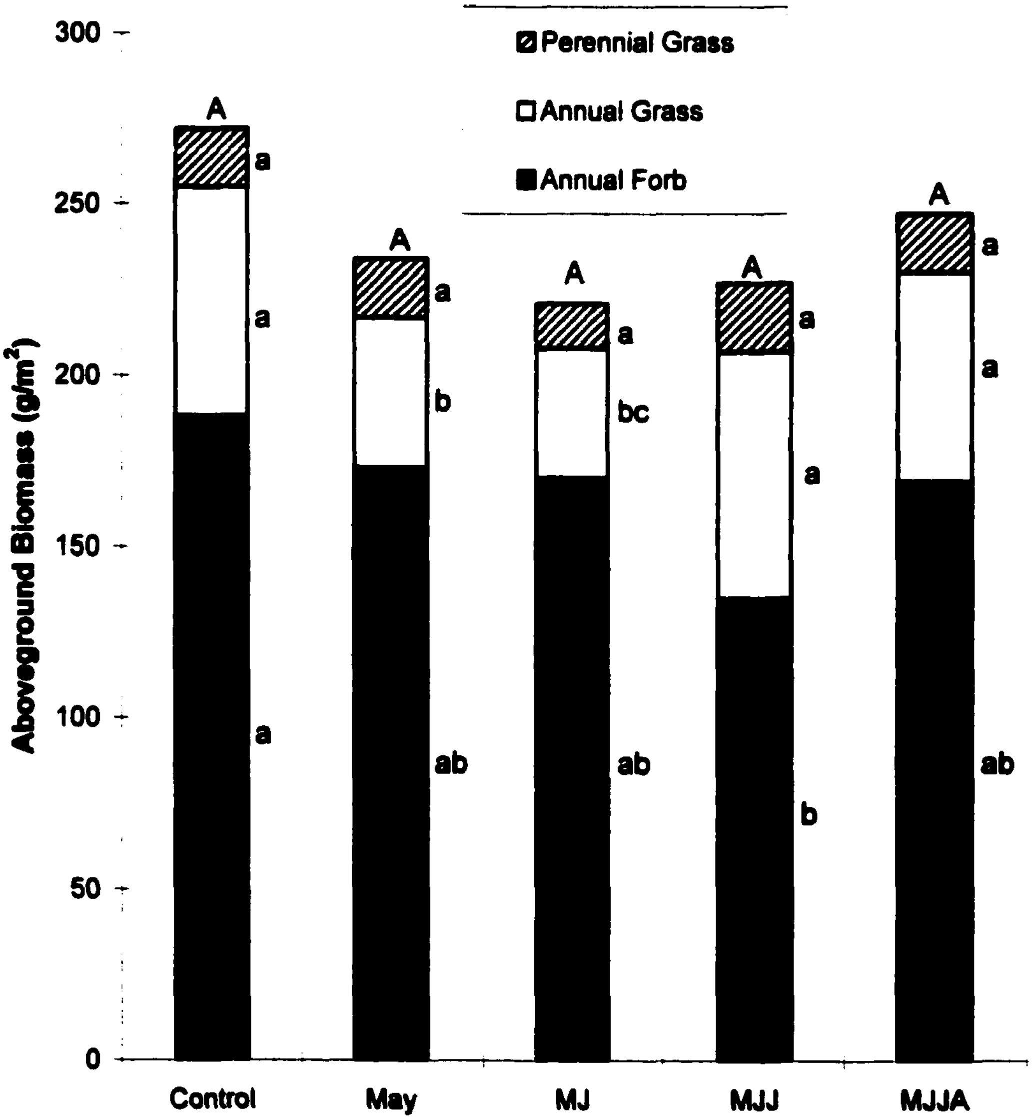


Figure A-3. Mean aboveground biomass among irrigation treatments on the Crested Wheatgrass Replacement Study in 1995. Irrigation, Control=no irrigation, M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+August Irrigation. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \leq 0.05$). {Perennial forb production, not shown, was ≤ 1g/m^2 and was not significantly different within lifeform groups and across treatments}

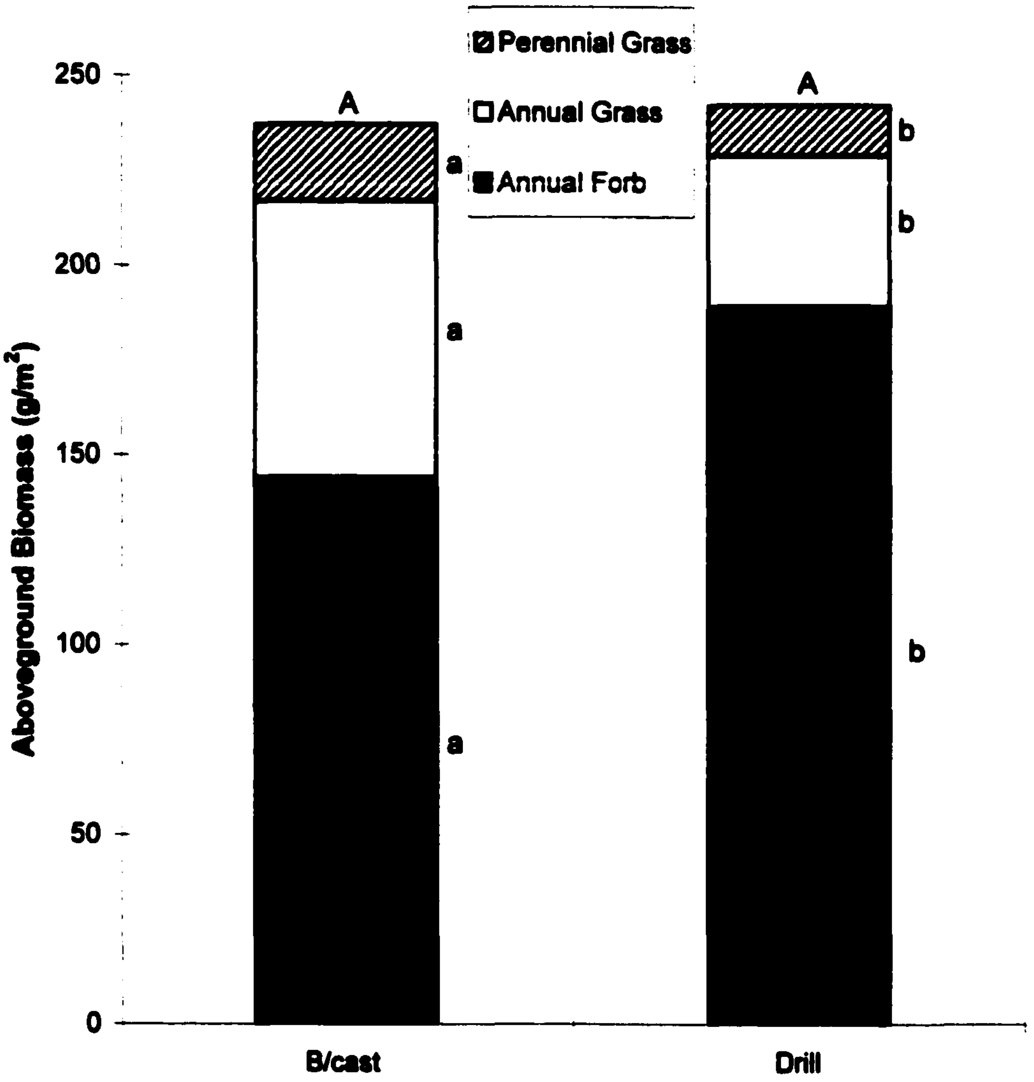


Figure A-4. Mean aboveground biomass between seeding techniques on the Crested Wheatgrass Replacement Study in 1995. Seeding techniques, B/cast=broadcast seeding Drill=drill seeding. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \le 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \le 0.05$). (Perennial forb production, not shown, was ≤ 1 g/m^2 for both treatments and was not significantly different)

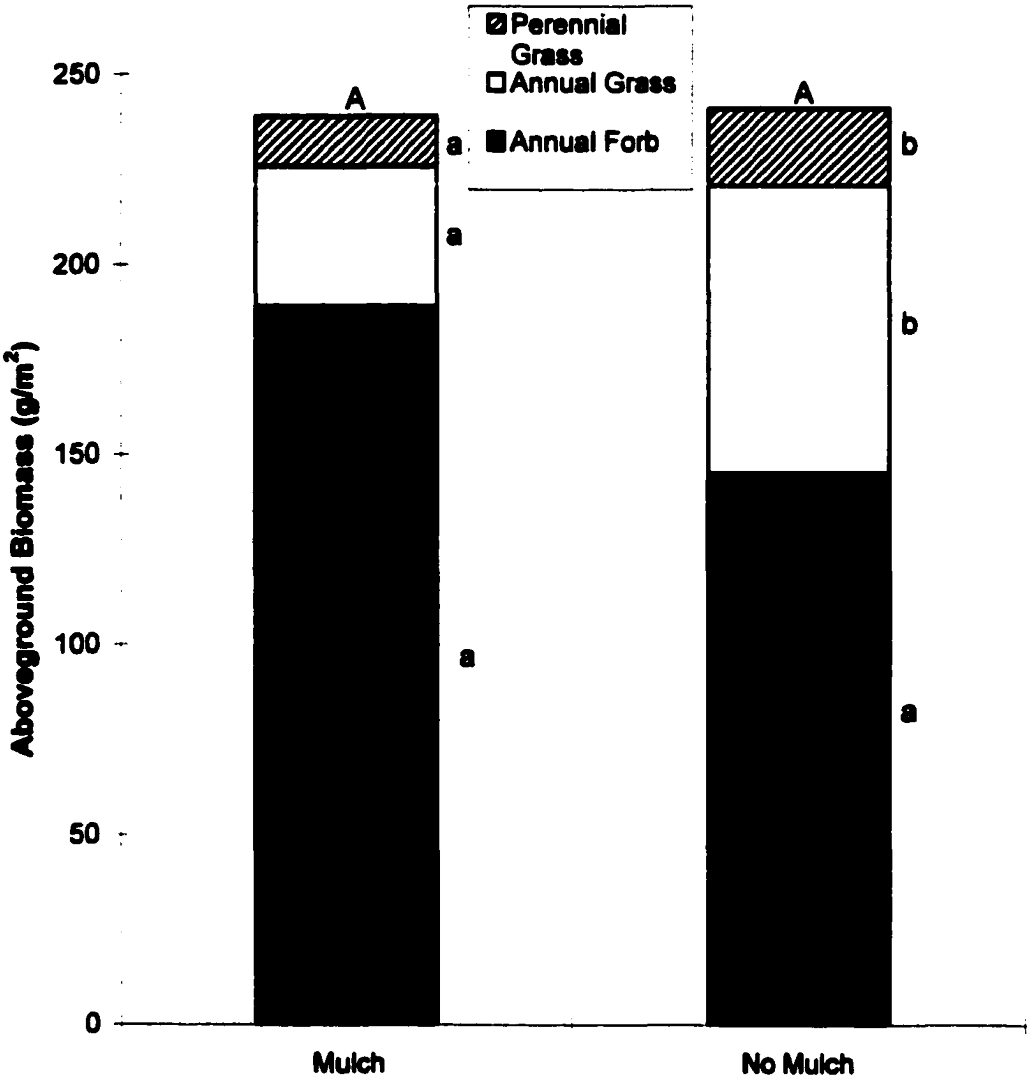


Figure A-5. Mean aboveground biomass between mulch treatments on the Crested Wheatgrass Replacement Study in 1995. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \le 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \le 0.05$). (Perennial forb production, not shown, was ≤ 1 g/m2 and was not significatnly different)

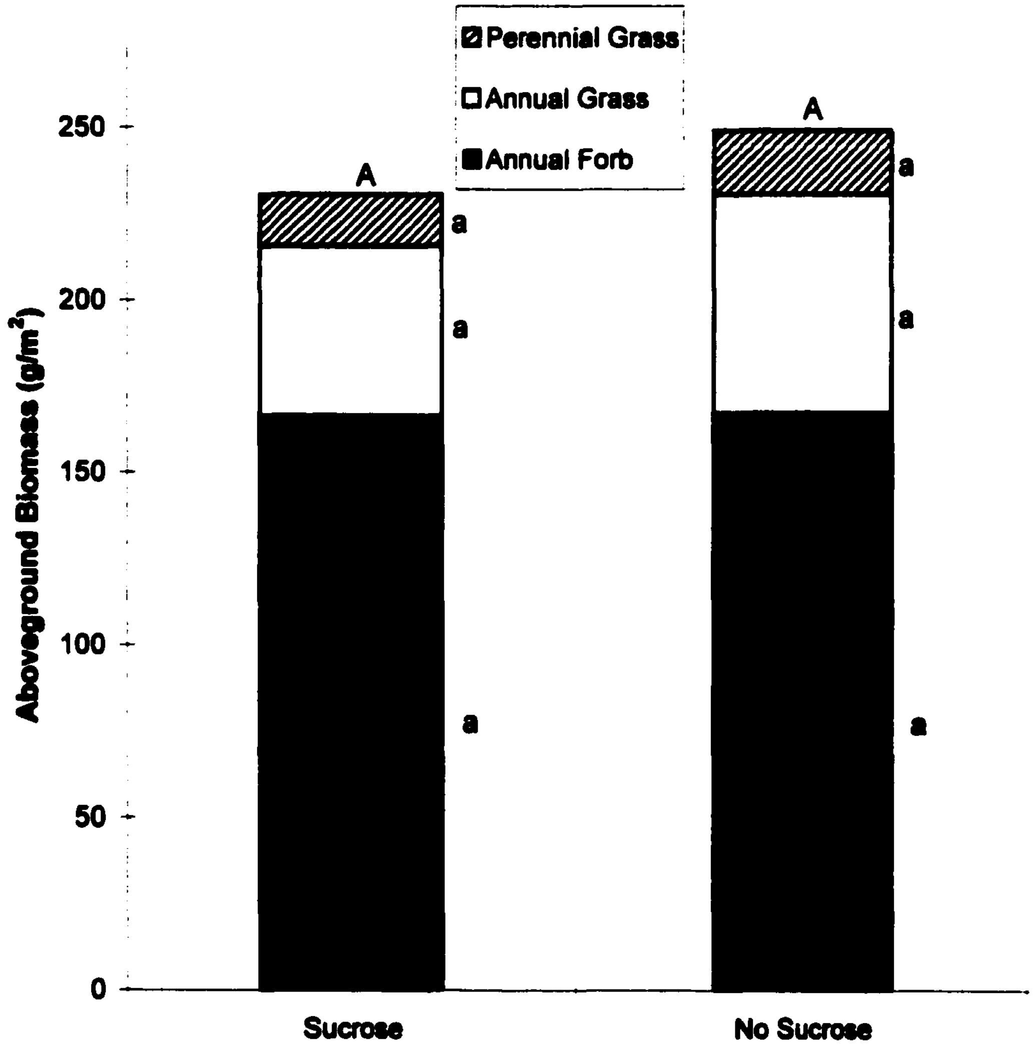


Figure A-6. Mean aboveground biomass between sucrose treatments on the Crested Wheatgrass Replacement Study in 1995. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \leq 0.05$). (Perennial forb production, not shown, was ≤ 1 g/m² and was not significantly different between treatments.)

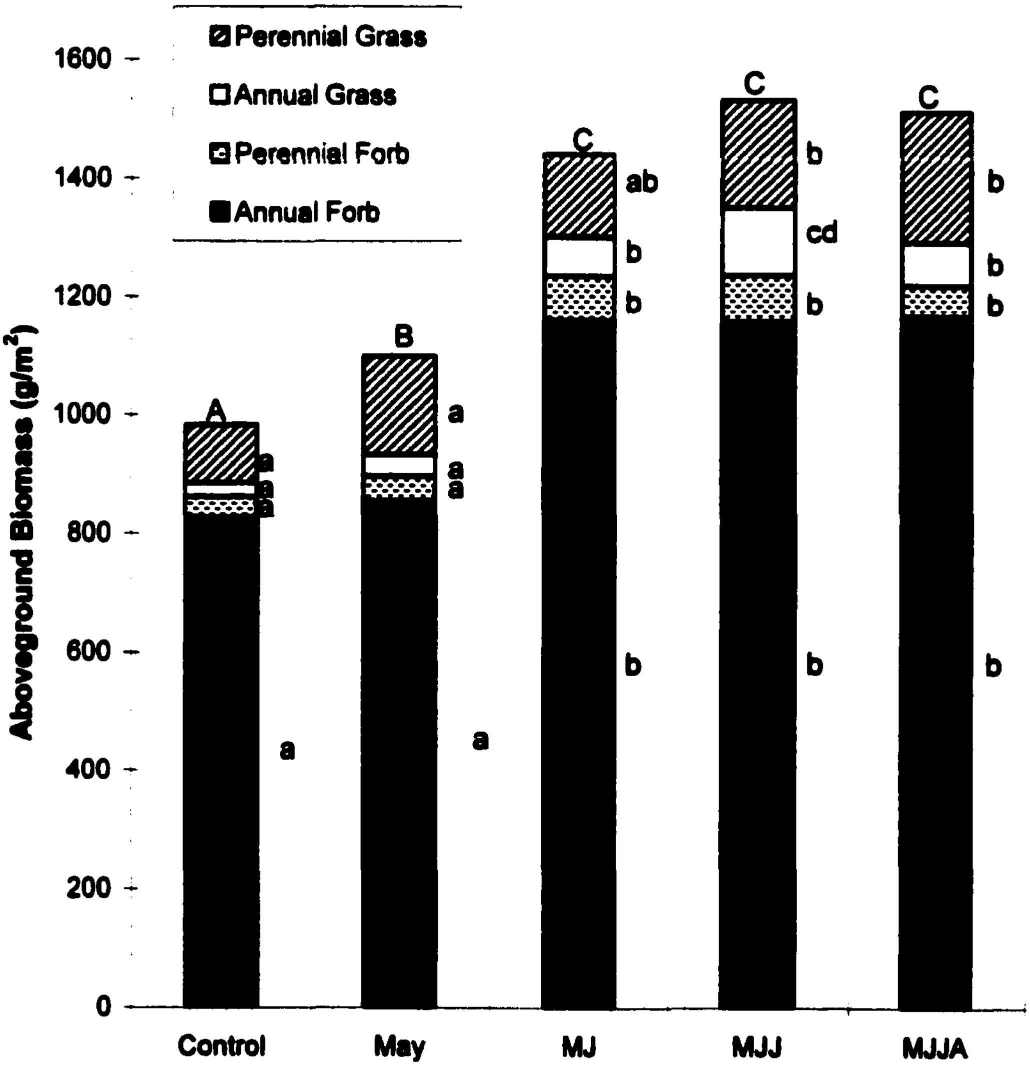


Figure A-7. Mean aboveground biomass among irrigation treatments on the Crested Wheatgrass Replacement Study in 1996. Irrigation, Control=no irrigation M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+August Irrigation. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \leq 0.05$).

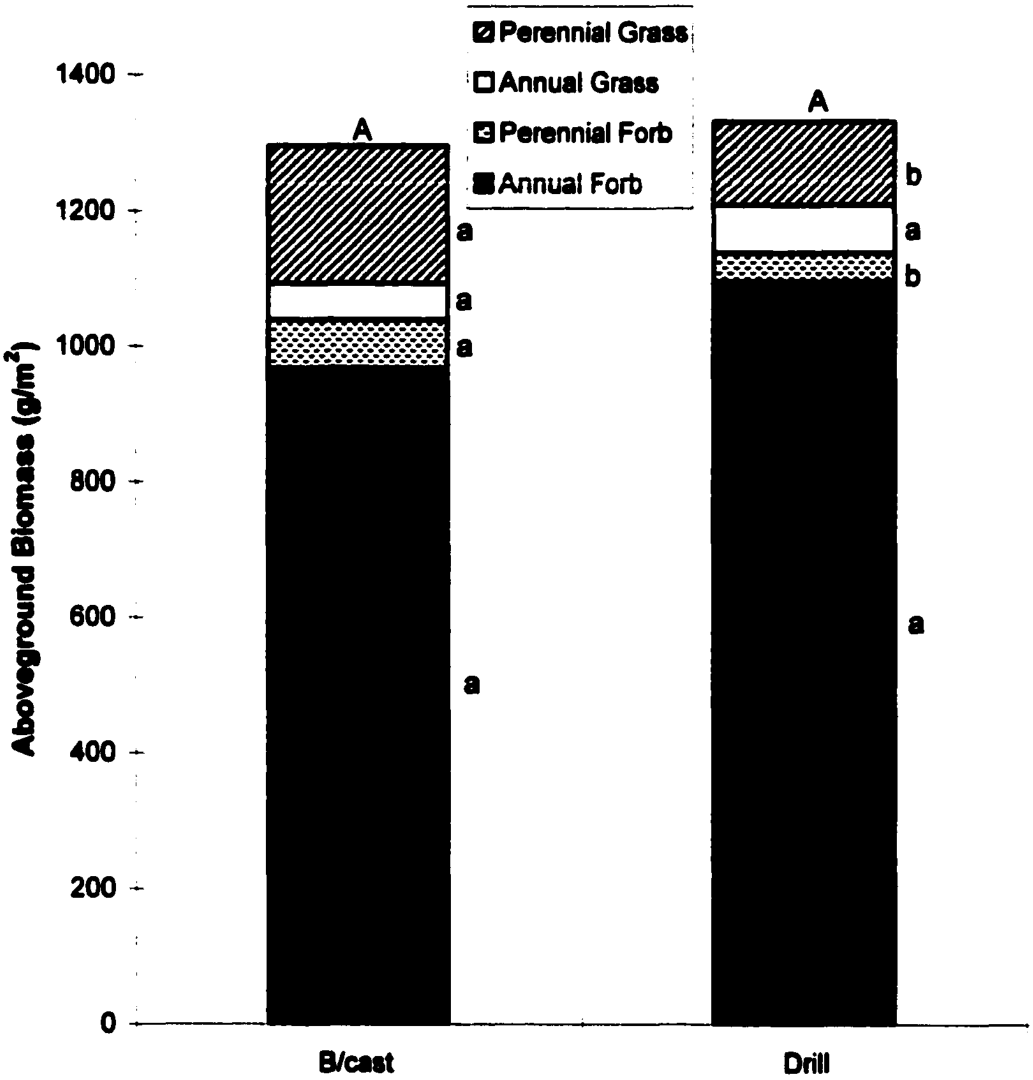


Figure A-8. Mean aboveground biomass between seeding techniques on the Crested Wheatgrass Replacement Study in 1996. Seeding techniques, B/cast=broadcast seeding Drill=drill seeding. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \leq 0.05$).

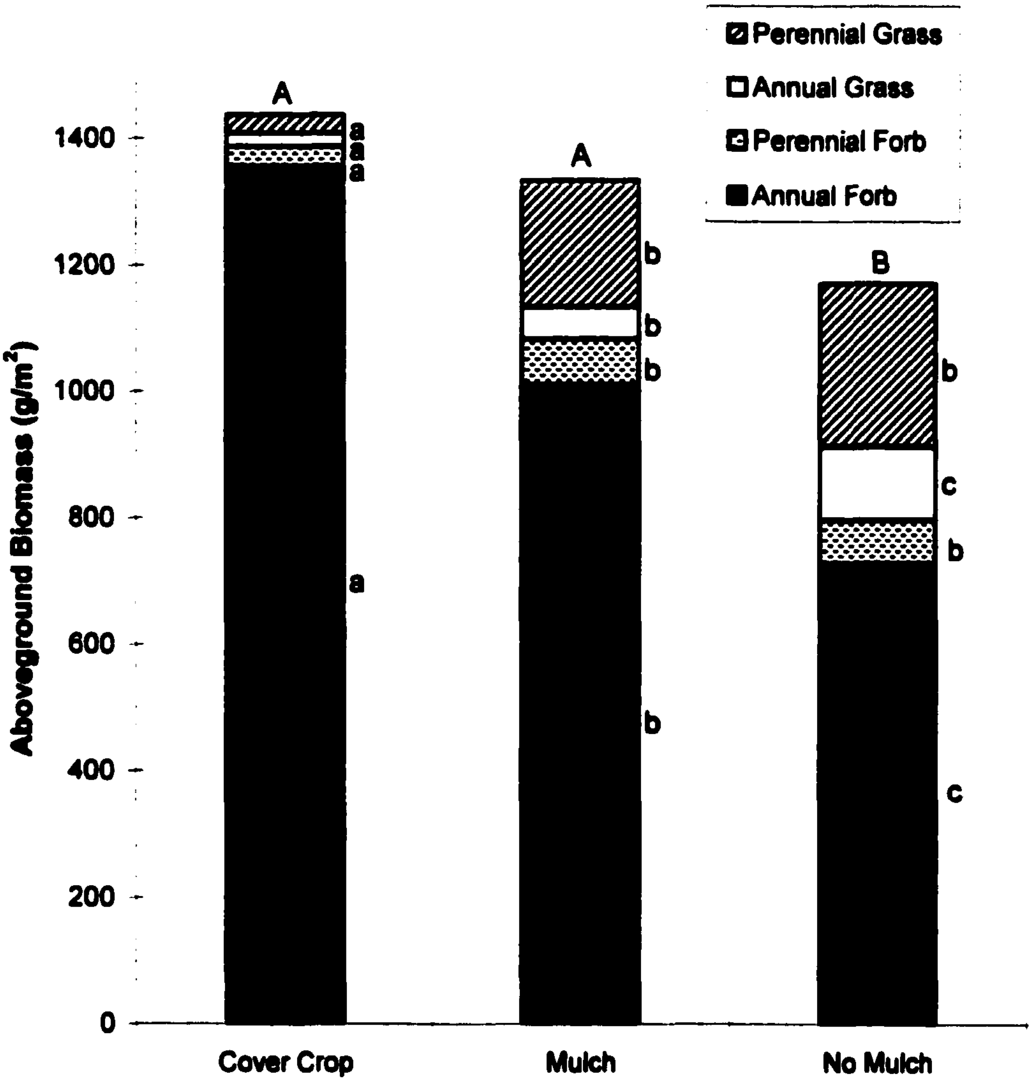


Figure A-9. Mean aboveground biomass among mulch treatments on the Crested Wheatgrass Replacement Study in 1996. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production across treatments
($p \leq 0.05$).

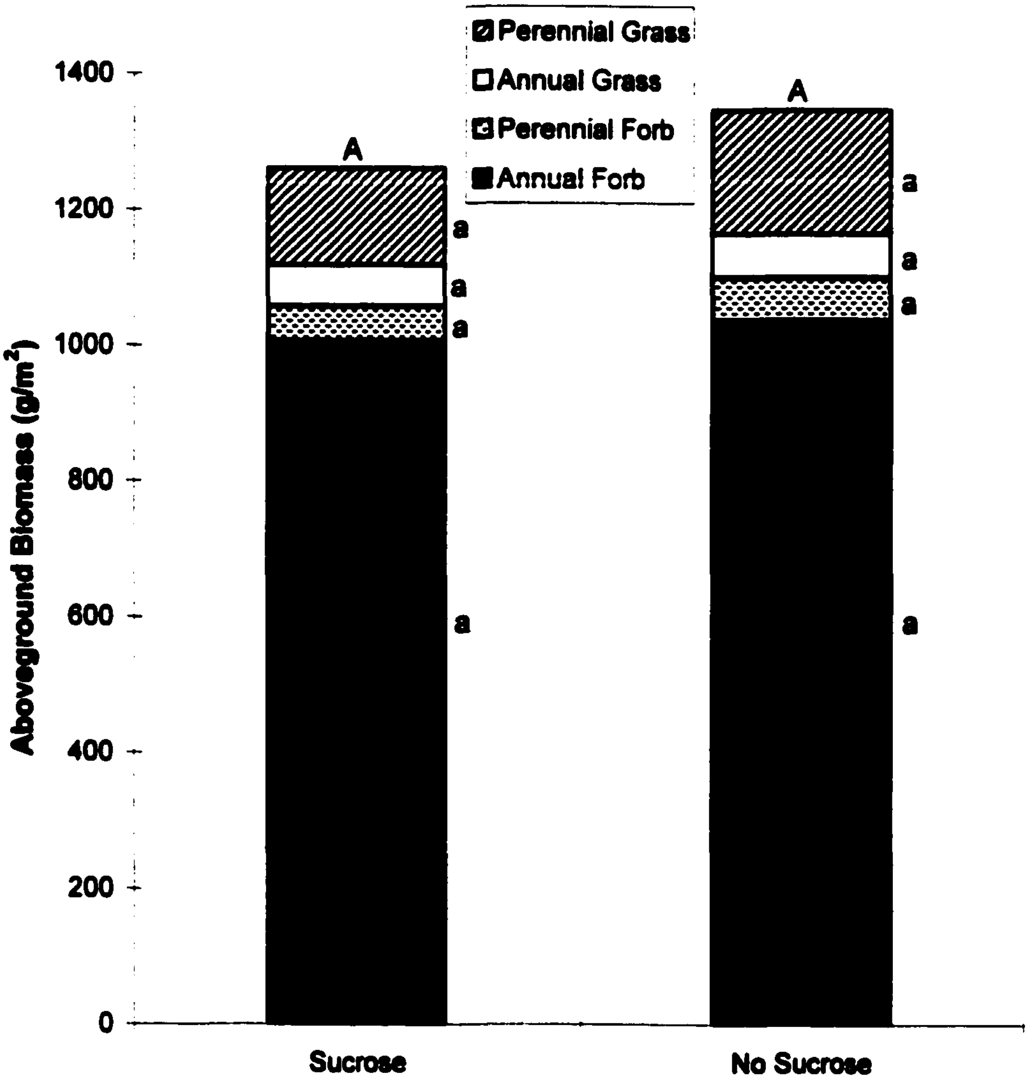


Figure A-10. Mean aboveground biomass between sucrose treatments on the Crested Wheatgrass Replacement Study in 1996. Different lower case letters within lifeform groups and between treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production between treatments ($p \leq 0.05$).

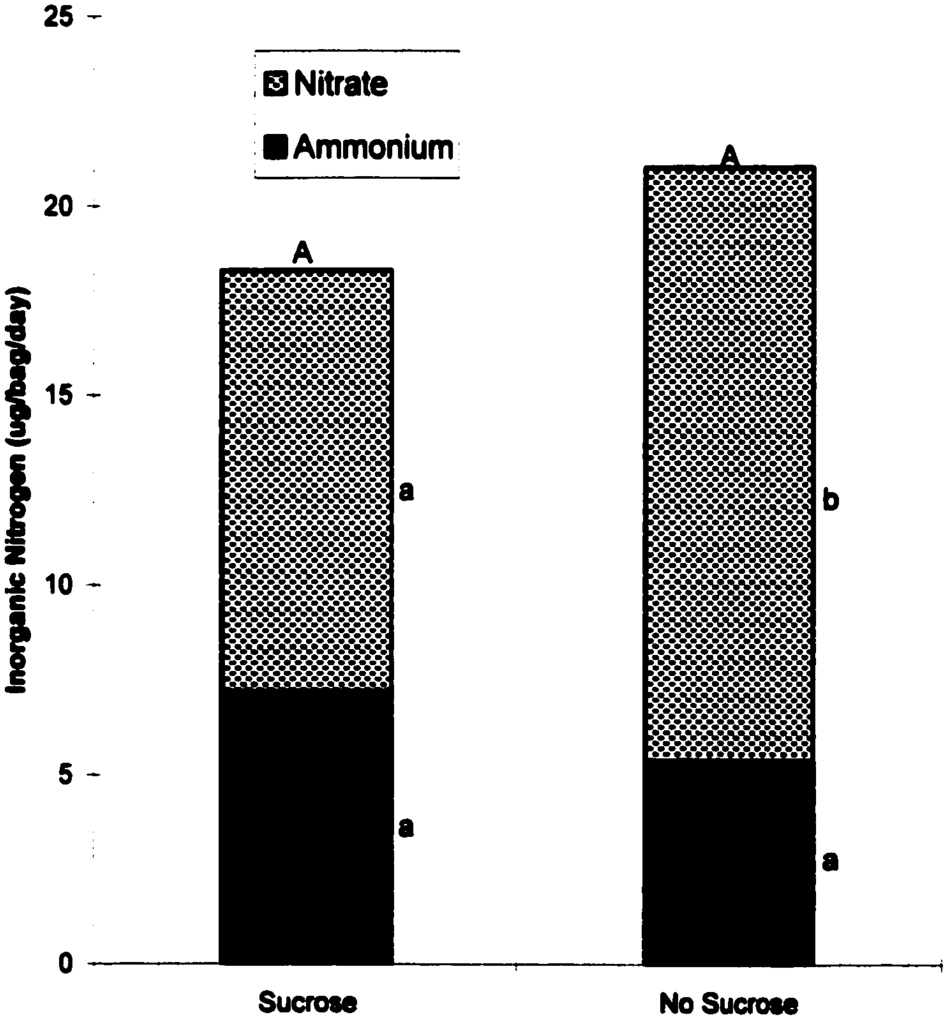


Figure A-11. Mean plant available nitrogen between sucrose treatments on the Crested Wheatgrass Replacement Study in 1996. Different lower case letters within nitrogen type and between treatments indicate significant differences ($p < 0.01$). Similar upper case letters indicate no significant differences in total plant available nitrogen between treatments.

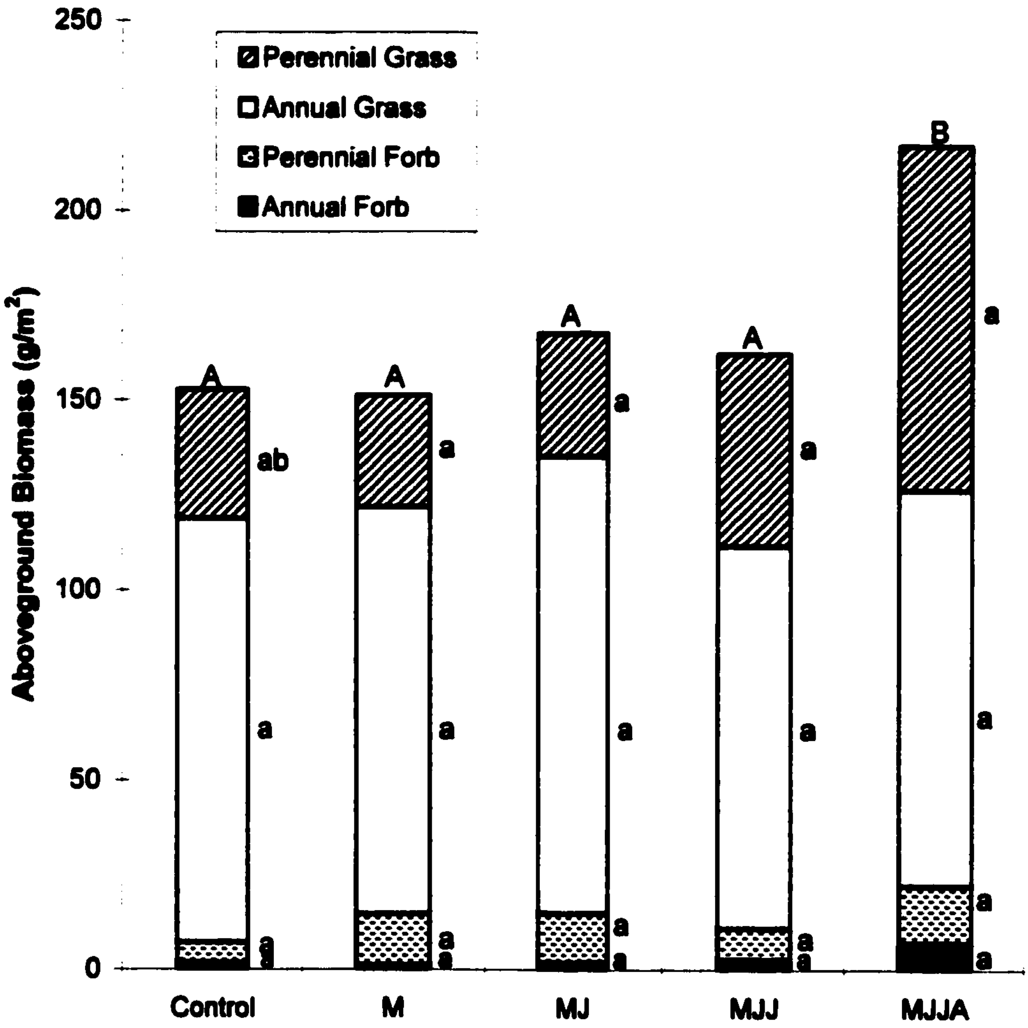


Figure A-12. Mean aboveground biomass among irrigation treatments on the Nitrogen Sucrose Study in 1995. Irrigation, Control=no irrigation, M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+August Irrigation. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \leq 0.05$).

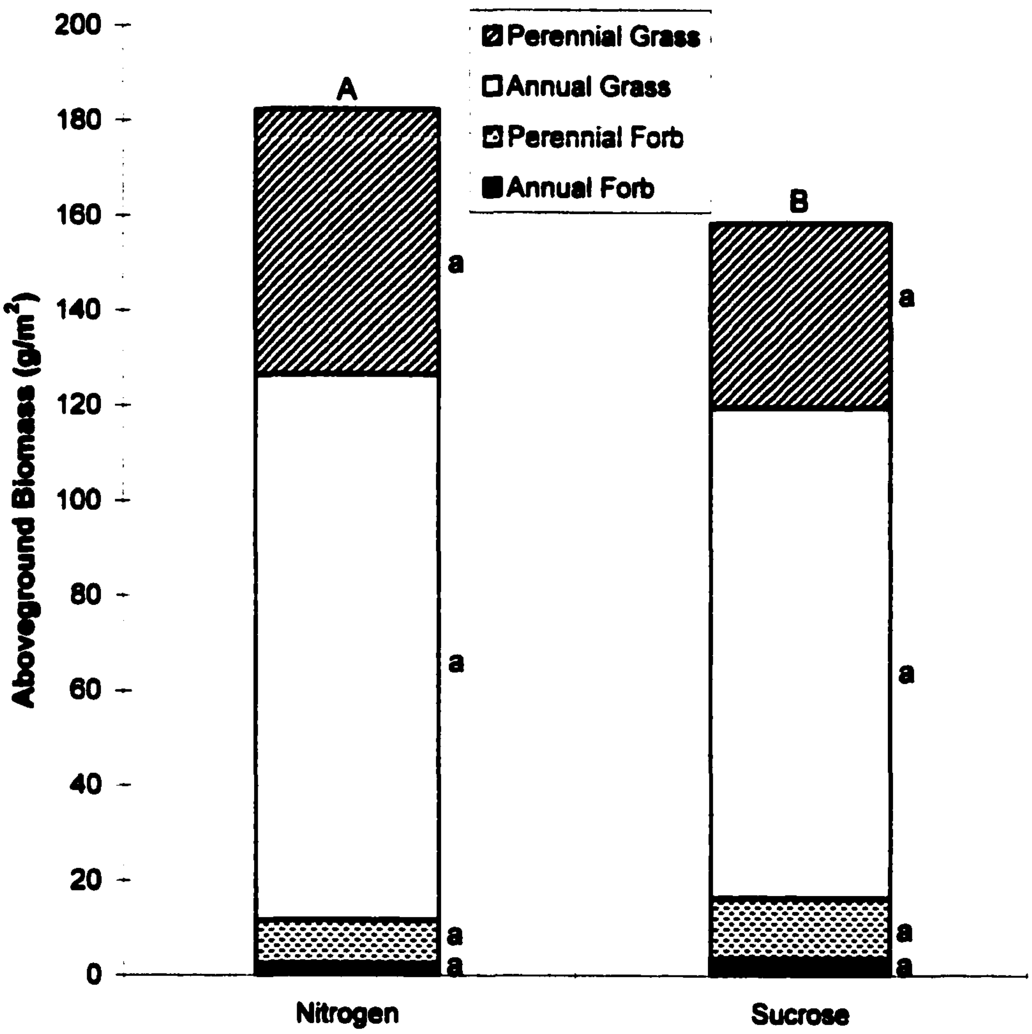


Figure A-13. Mean aboveground biomass between nitrogen/sucrose treatments on the Nitrogen Sucrose Study in 1995. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \leq 0.05$).

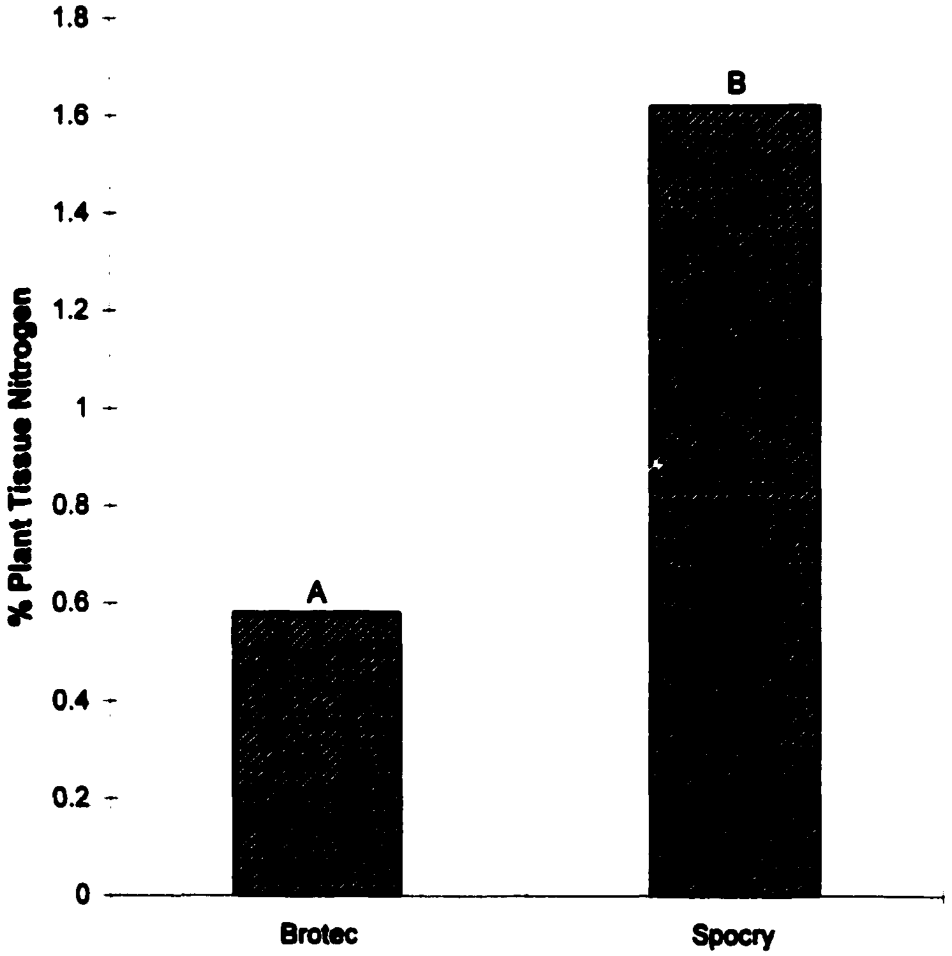


Figure A-14. Percent plant tissue nitrogen between an annual and perennial grass in the Nitrogen sucrose Study in 1995. Values are an average of all irrigated, nitrogen and sucrose treated plots. Brotec = *Bromus tectorum*, Spocry = *Sporobolus cryptandru* s. Different letters indicate significant difference between species ($p \leq 0.0001$)

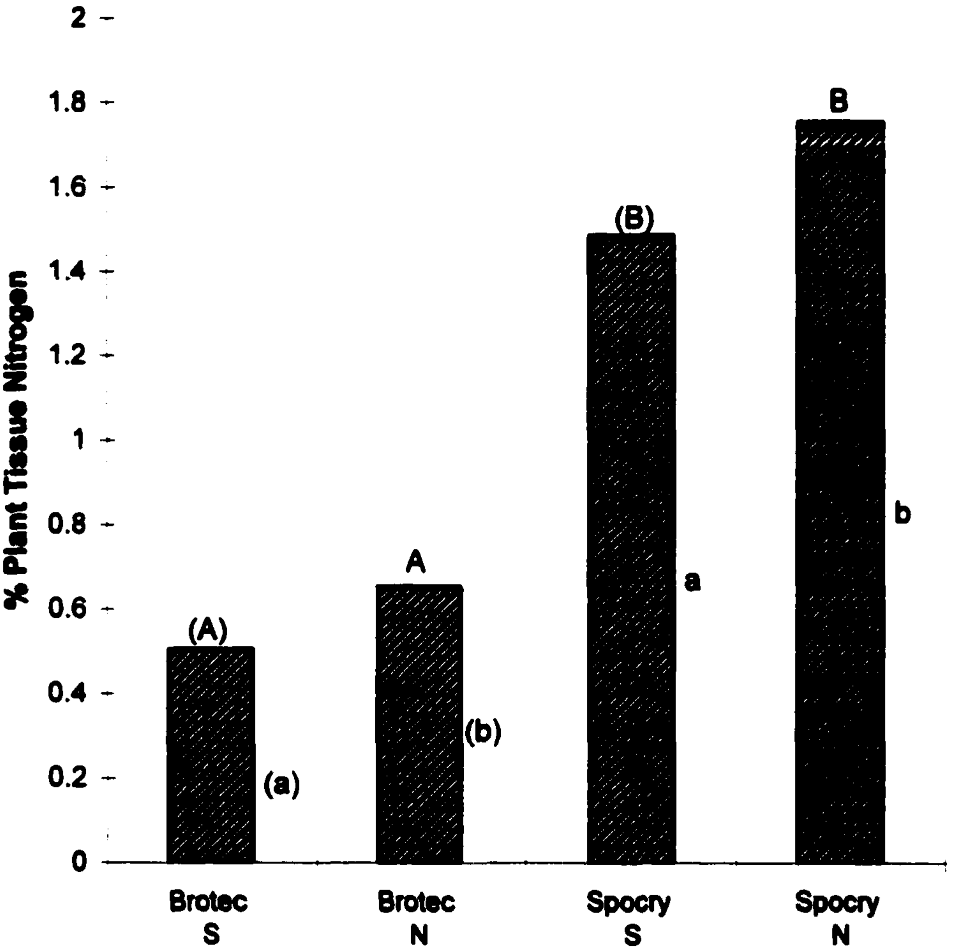


Figure A-15. Percent plant tissue nitrogen between an annual and perennial grass within plots treated with nitrogen or sucrose, on the Nitrogen Sucrose Study in 1995. Brotec = *Bromus tectorum*, Spocry = *Sporobolus cryptandrus*. S = sucrose, N = nitrogen. Different upper case letters, in parenthesis or not, indicate significant differences within sucrose or nitrogen treated plots and between species ($p < 0.0001$). Different lower case letters, in parenthesis or not, indicate significant differences within species and between treatments ($p < .0002$).

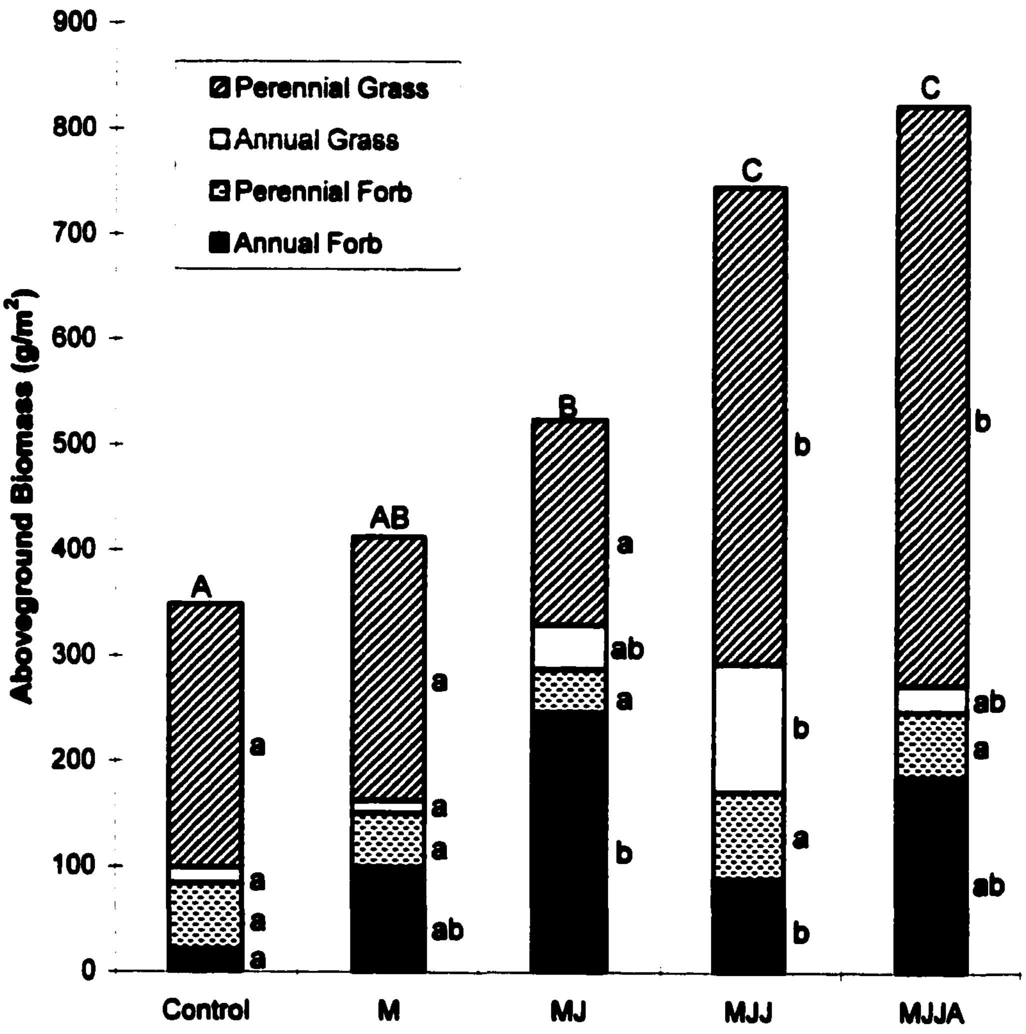


Figure A-16. Mean aboveground biomass among irrigation treatments on the Nitrogen Sucrose Study in 1996. Irrigation, Control=no irrigation, M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July +August Irrigation. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production across treatments ($p \leq 0.05$).

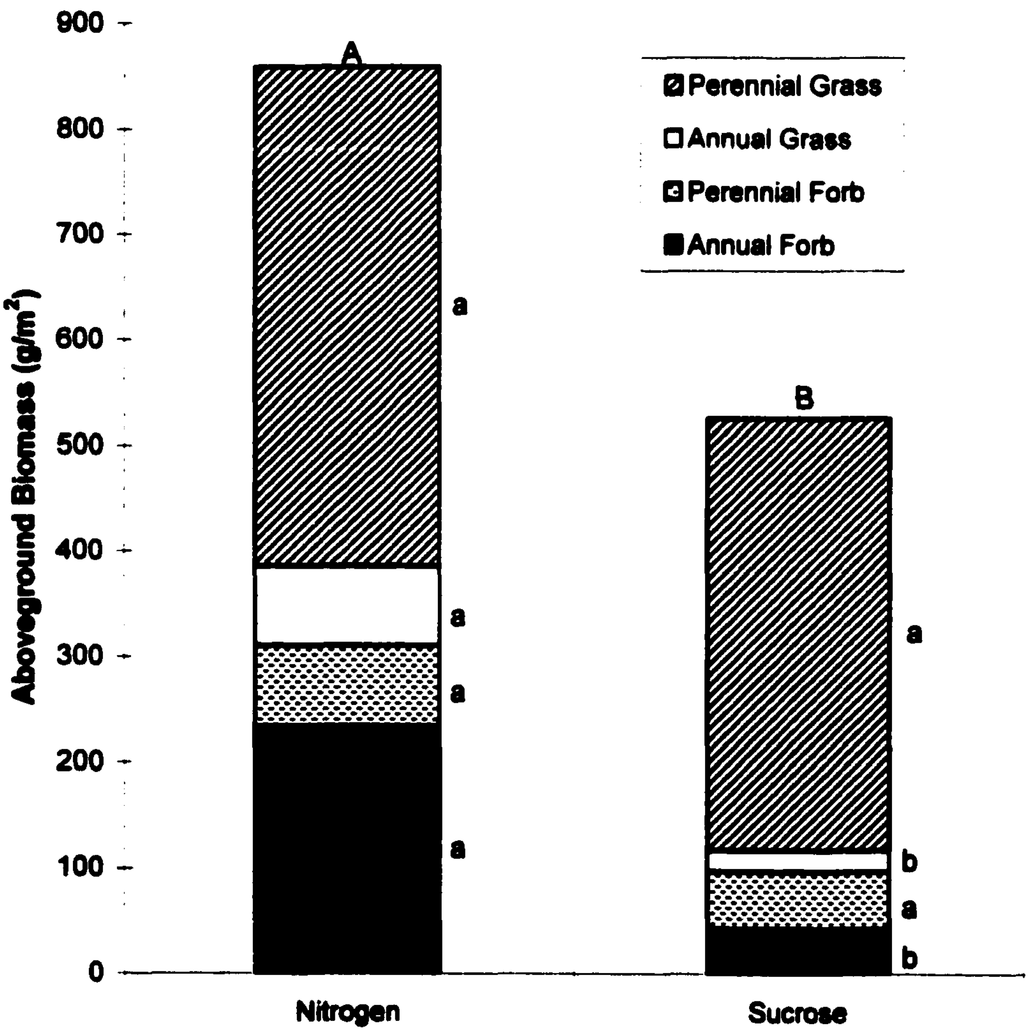


Figure A-17. Mean aboveground biomass between nitrogen/sucrose treatments on the Nitrogen Sucrose Study in 1996. Different lower case letters within lifeform groups and across treatments indicate significant differences ($p \leq 0.05$). Different capital letters indicate significant differences in total production between treatments ($p \leq 0.05$).

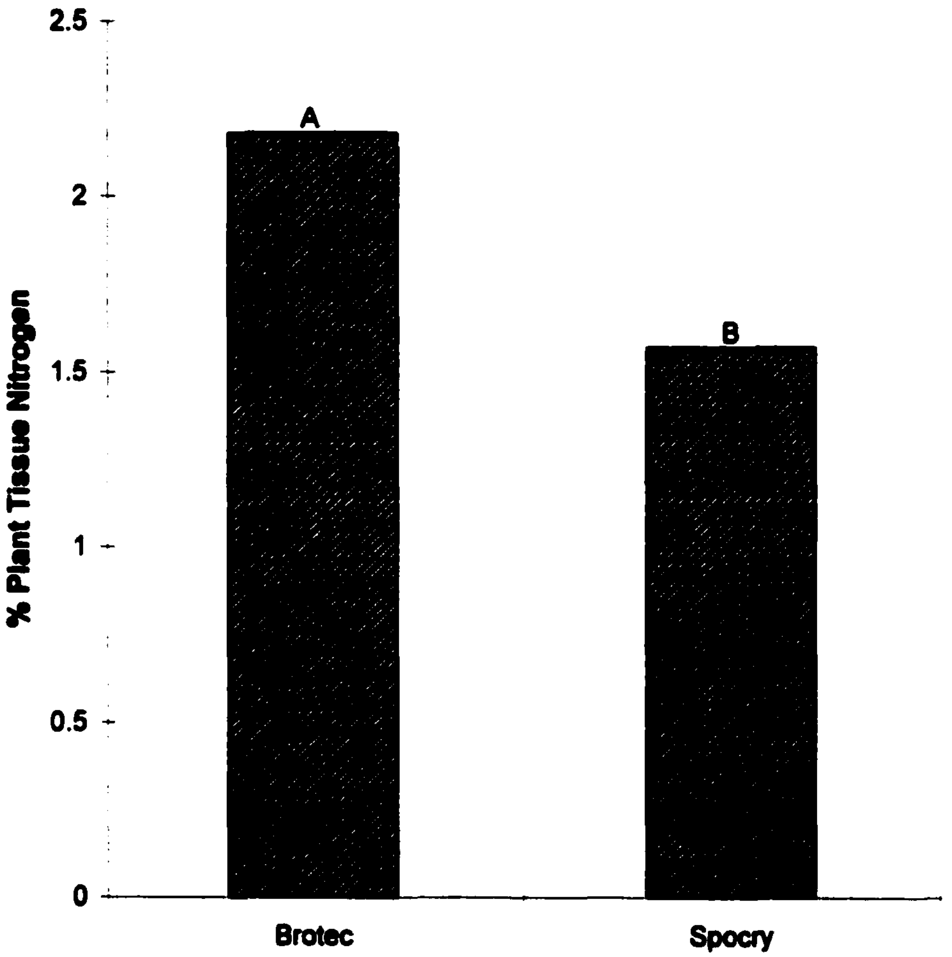


Figure A-18. Percent plant tissue nitrogen between an annual and perennial grass in the Nitrogen Sucrose Study in 1996. Values are an average of all irrigated, nitrogen and sucrose treated plots. Brotec = *Bromus tectorum*, Spocry = *Sporobolus cryptandrus*. Different letters indicate significant difference between species ($p \leq 0.0001$)

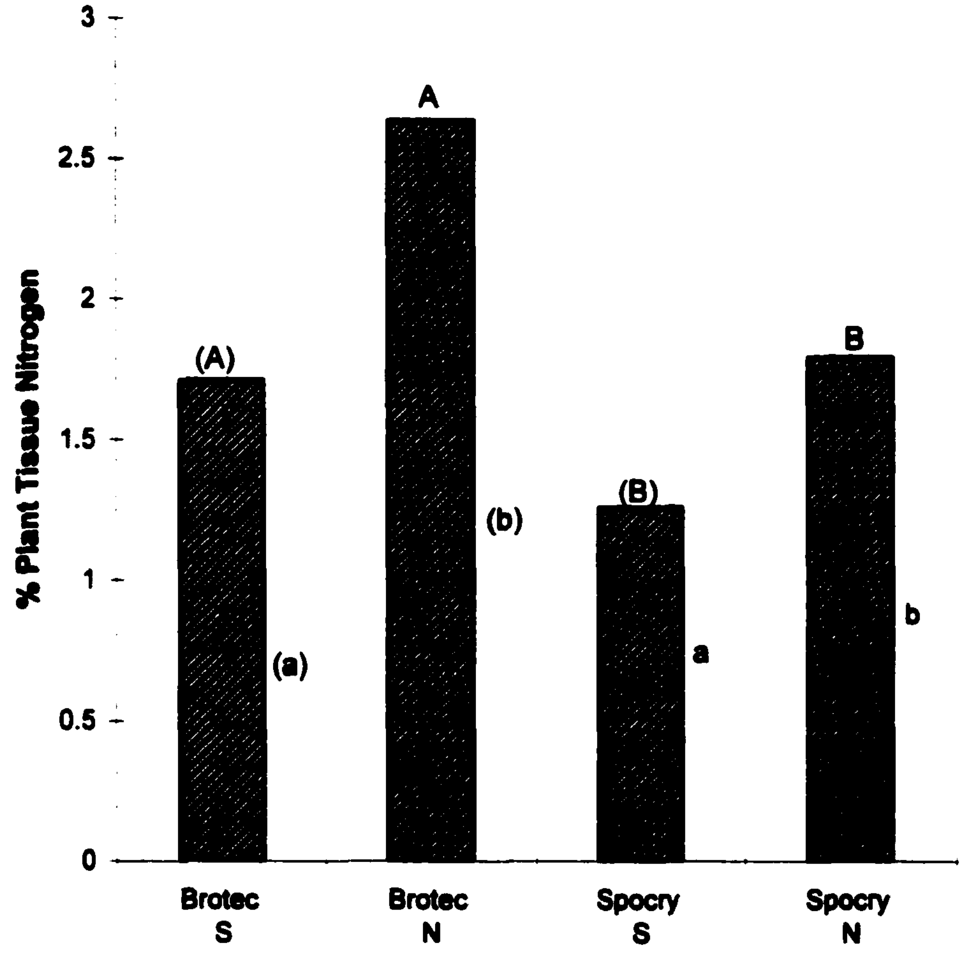


Figure A-19. Percent plant tissue nitrogen between an annual and perennial grass within plots treated with nitrogen or sucrose, on the Nitrogen Sucrose Study in 1996. Brotec = *Bromus tectorum*, Spocry = *Sporobolus cryptandrus*. S = sucrose, N = nitrogen. Different upper case letters, in parenthesis or not, indicate significant differences within sucrose or nitrogen treated plots and between species ($p< 0.0001$). Different lower case letters, in parenthesis or not, indicate significant differences within species and between treatments ($p< 0.0008$).

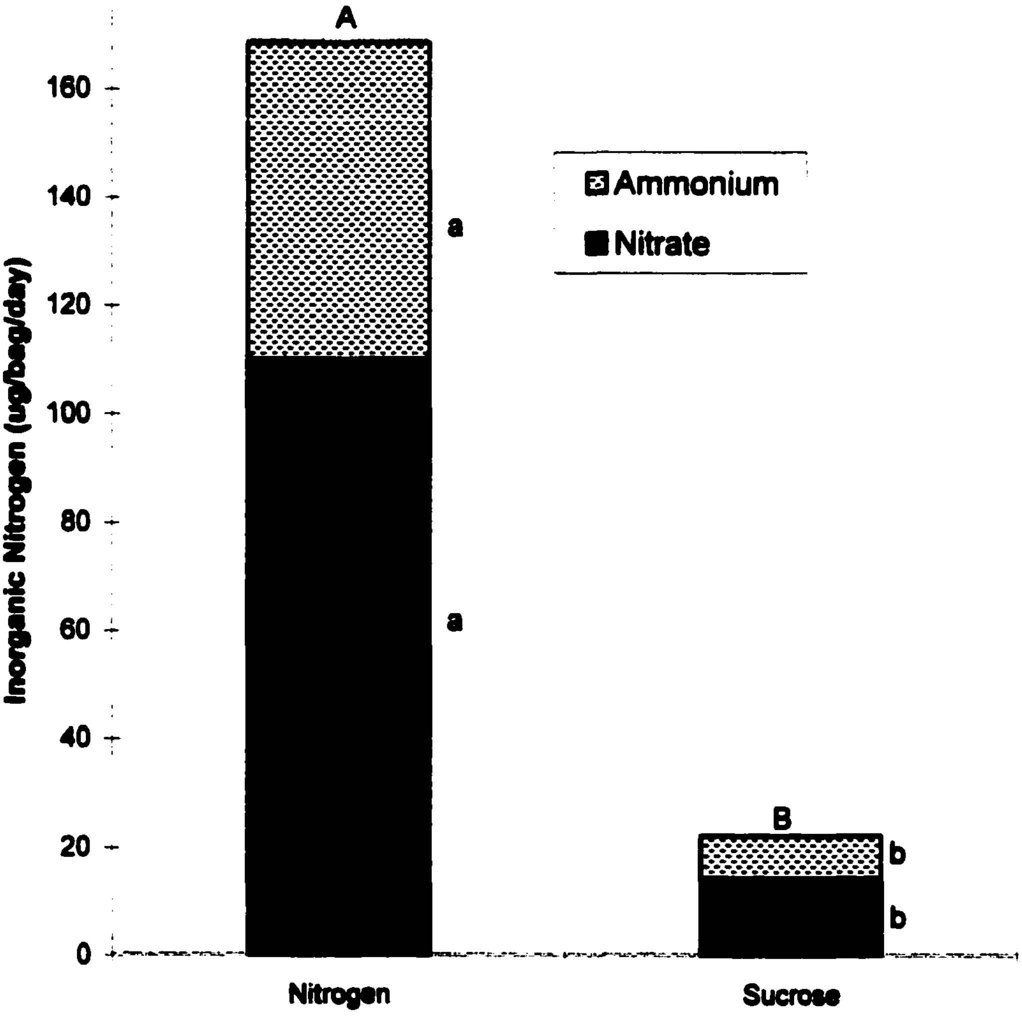


Figure A-20. Inorganic nitrogen in micrograms per ion exchange resin (IER) bags per day between nitrogen treated plots and sucrose treated plots in the Nitrogen Sucrose Study in 1996. Different lower case letters within ammonium and nitrate groups and between treatments indicate significant differences ($p < 0.0001$). Different upper case letters indicate significant differences in total mineral nitrogen ($p < 0.0001$).

Appendix B

Tables

Table B-1. Seed mixture for Crested Wheatgrass Replacement Study

Scientific Name	Common Name	Variety	lbs PLS/A
Perennial Grasses			
Bouteloua gracilis	Blue grama	Hachita	0.14
Calamovilfa longifolia	Prairie sandreed	Goshen	1.74
Bouteloua curtipendula	Side-oats grama	Vaughn	0.20
Andropogon hallii	Sand bluestem	Woodward	5.09
Pascopyron smithii	Western wheatgrass	Arriba	0.20
Panicum virgatum	Switchgrass	Nebraska 28	0.41
Oryzopsis hymenoides	Indian ricegrass	Nezpar	0.38
Perennial Forbs			
Cleome serrulata	Rocky Mountain bee plant		0.10
Gaillardia aristata	Blanket flower		0.10
Linum lewisii	Blue flax		0.10
Helianthus annuus	Annual sunflower		0.10
Achillea lanulosa	Yarrow		0.003
Artemisia ludoviciana	Louisiana sagewort		0.03
Coreopsis tinctoria	Plains coreopsis		0.09
Artemisia frigida	Fringed sage		0.02
Shrubs			
Chrysothamnus nauseosus	Rubber rabbitbrush		0.15
Atriplex canescens	Fourwing saltbush		0.88
Yucca glauca	Yucca		0.10
TOTAL			9.833

Table B-2. Mean aboveground biomass in g/m^2 among irrigation treatments on the Crested Wheatgrass Replacement Study in 1995, 1996 and 1997. Control=no irrigation, M=may irrigation, MJ=May+June irrigation, MJJ=May+June+July irrigation, MJJA=May +June +July+August irrigation.

	Control	May	MJ	MJJ	MJJA	1-SE
1995						
Annual Forb	188	173	170	135	169	19
Perennial Forb	0.6	1	0.3	1	1	0.4
Annual Grass	67	44	38	72	61	10
Perennial Grass	17	17	13	20	17	3
Total	273	235	221	228	248	19
1996						
Annual Forb	827	855	1159	1157	1166	111
Perennial Forb	35	42	76	79	52	13
Annual Grass	23	36	67	114	73	20
Perennial Grass	98	166	139	181	220	43
Total	983	1099	1441	1531	1511	123
1997						
Annual Forb	631	585	507	463	504	46
Perennial Forb	54	64	69	50	57	22
Annual Grass	3	6	3.7	0.3	0.3	2
Perennial Grass	77	108	113	216	232	31
Total	765	763	692.7	729.3	793.3	40

Table B-3. Mean aboveground biomass in g/m^2 between seeding treatments on the Crested Wheatgrass Replacement Study in 1995, 1996 and 1997. B/cast = broadcast seeding, Drill = drill seeding.

	B/cast	Drill	1-SE
1995			
Annual Forb	144	189	12
Perennial Forb	1	1	0.3
Annual Grass	73	40	7
Perennial Grass	20	13	2
Total	238	243	13
1996			
Annual Forb	967	1095	102
Perennial Forb	72	43	10
Annual Grass	54	71	19
Perennial Grass	202	122	40
Total	1,295	1,331	116
1997			
Annual Forb	473	602	39
Perennial Forb	77	45	18
Annual Grass	2	3	1
Perennial Grass	197	103	27
Total	749	753	32

Table B-4. Mean aboveground biomass in g/m^2 among mulch treatments on the Crested Wheatgrass Replacement Study in 1995, 1996 and 1997.

	Cover	Mulch	No Mulch	1-SE
<u>1995</u>				
Annual Forb		189	145	12
Perennial Forb		1	1	0.45
Annual Grass		37	76	6
Perennial Grass		13	20	2
Total		240	242	12
<u>1996</u>				
Annual Forb	1356	1010	728	104
Perennial Forb	31	72	69	11
Annual Grass	21	51	116	19
Perennial Grass	29	200	257	41
Total	1,437	1,333	1,170	118
<u>1997</u>				
Annual Forb	735	452	426	42
Perennial Forb	44	84	56	20
Annual Grass	4	2	1	2
Perennial Grass	22	211	216	29
Total	805	749	699	35

Table B-5. Mean aboveground biomass in g/m^2 between sucrose treatments on the Crested Wheatgrass Replacement Study in 1995, 1996 and 1997.

	Sucrose	No Sucrose	1-SE
1995			
Annual Forb	166	167	12
Perennial Forb	0	1	0.32
Annual Grass	49	64	8
Perennial Grass	15	18	2
Total	231	250	12
1996			
Annual Forb	1006	1037	102
Perennial Forb	51	63	11
Annual Grass	61	64	18
Perennial Grass	143	181	40
Total	1261	1346	115
1997			
Annual Forb	535	540	39
Perennial Forb	73	50	20
Annual Grass	3	3	1
Perennial Grass	146	154	29
Total	757	746	38

Table B-6. Mean inorganic nitrogen in micrograms per ion exchange resin (IER) bags per day between sucrose treated plots on the Crested Wheatgrass Replacement study in 1996 and 1997. 1996 results reflect one set of resin bags placed for 45 days while the 1997 results reflect an average of two sets of IER bags placed for 45 days each.

	Sucrose	No Sucrose
1996		
Nitrate	11	16
Ammonium	7	5
Total Inorganic Nitrogen	18	21
1997		
Nitrate	8	11
Ammonium	10	13
Total Inorganic Nitrogen	18	24

Table B-7. Mean aboveground biomass in g/m^2 among irrigation treatments on the Nitrogen Sucrose Study in 1995, 1996 and 1997. M=May Irrigation, MJ=May+June Irrigation, MJJ=May+June+July Irrigation, MJJA=May+June+July+August Irrigation.

	Control	May	MJ	MJJ	MJJA	1-SE
1995						
Annual Forb	2	1	2	3	7	3
Perennial Forb	6	14	13	8	15	7
Annual Grass	112	107	121	101	104	14
Perennial Grass	34	29	32	51	91	17
Total	153	151	168	162	217	15
1996						
Annual Forb	21	99	247	88	185	69
Perennial Forb	63	52	41	83	63	34
Annual Grass	15	12	42	122	25	20
Perennial Grass	250	250	194	452	549	122
Total	349	413	524	745	822	144
1997						
Annual Forb	183	219	160	261	464	68
Perennial Forb	19	47	25	14	47	19
Annual Grass	82	92	92	81	16	20
Perennial Grass	182	155	197	247	312	70
Total	466	513	474	603	839	118

Table B-8. Mean aboveground biomass in g/m^2 between nitrogen/sucrose treatments on the Nitrogen Sucrose Study in 1995, 1996 and 1997.

	Nitrogen	Sucrose	1-SE
1995			
Annual Forb	2	3	3
Perennial Forb	9	13	7
Annual Grass	115	103	11
Perennial Grass	56	39	18
Total	182	158	15
1996			
Annual Forb	234	43	69
Perennial Forb	77	54	34
Annual Grass	76	20	23
Perennial Grass	472	409	122
Total	859	526	114
1997			
Annual Forb	394	121	53
Perennial Forb	12	49	12
Annual Grass	40	105	16
Perennial Grass	141	297	60
Total	587	571	89

Table B-9. Percent plant tissue nitrogen between an annual and perennial grass within plots treated with nitrogen or sucrose on the Nitrogen Sucrose Study in 1995, 1996, and 1997. Brotec=*Bromus tectorum*, Spocry=*Sporobolus cryptandrus*, S=sucrose, N=nitrogen.

	Brotec S	Brotec N	Spocry S	Spocry N
1995				
% Tissue Nitrogen	0.5	0.7	1.5	1.8
1996				
% Tissue Nitrogen	1.7	2.6	1.3	1.8
1997				
% Tissue Nitrogen	0.6	1.2	1.4	2.4

Table B-10. Mean inorganic nitrogen in micrograms per ion exchange resin (IER) bags per day between sucrose or nitrogen treated plots on the Nitrogen Sucrose Study in 1996 and 1997. 1996 results reflect one set of resin bags placed for 45 days while the 1997 results reflect an average of two sets of IER bags placed for 45 days each.

	Sucrose	Nitrogen
1996		
Nitrate	14	110
Ammonium	8	58
Total Inorganic Nitrogen	22	168
1997		
Nitrate	5	54
Ammonium	7	89
Total Inorganic Nitrogen	12	143