AN ABSTRACT OF THE THESIS OF

Jianguo Wang for the degree of Master of Science in Rangeland Resources Presented on August 12, 1988.

Title: Response of Artemisia tridentata ssp. wyomingensis and Stipa thurberiana to Nitrogen Amendments

Signature redacted for privacy.

Abstract approved: ______________________________
Richard F. Miller and Paul S. Doescher

The effect of nitrogen on influencing the competitive balance between a shrub, Artemisia tridentata ssp. wyomingensis (ARTRW) and a perennial grass Stipa thurberiana (STTH) in a sagebrush steppe community was determined. Nitrogen levels were altered on 5x5 m plots by applying 4.5 g/m^2 of nitrogen in the form of ammonium or nitrate, or 45 g/m^2 of sugar. Treatments were compared with untreated control plots. Plant growth, production, leaf nitrogen content, soil water content and soil nitrogen content were measured throughout growing season of 1987. Both forms of nitrogen, ammonium and nitrate, increased shoot densities, shoot length, ephemeral leaf number per terminal bud, reproductive shoots and leaf nitrogen content in ARTRW. Additions of nitrogen significantly increased tiller density, reproductive shoots, biomass and leaf nitrogen content in STTH. Nitrate provided the greatest increase in reproductive shoots, for the two forms of nitrogen. Reproductive tiller density in STTH increased 66% for ammonium and 250% for nitrate, and 56% for ammonium and 193% for nitrate in ARTRW over control. Nitrogen form did not appear to favor either the shrub or grass. Although both species responded positively to increases in available nitrogen, leaf area, above ground net annual primary productivity and nitrogen uptake increased in ARTRW to a greater magnitude than STTH. Addition of sugar did not appear to decrease soil nitrogen availability comparing to control treatment in this research. Environmental conditions causing temporary increases in ammonium and or nitrate may drive the successional process towards a ARTRW dominated site.

Response of
Artemisia tridentata ssp. *wyomingensis*
and *Stipa thurberiana* to Nitrogen Amendments

by

Jianguo Wang

A THESIS
submitted to
Oregon State University

in partial fulfillment of
the requirements for the degree of

Master of Science

Completed August 12, 1988

Commencement June 1989

Acknowledgements

Many people gave me considerable help through the course of this project. I would like to take this opportunity to extend a sincere and heartfelt thanks to each of them.

I extend my appreciation to the staff of Squaw Butte Experiment Station for second year financial support, use of equipment and facilities, and hospitality throughout my graduate program. The author expresses his appreciation for the warmth and friendship shown by the faculty, staff, and all graduate students in the Department of Rangeland Resources. I express high appreciation to my major professors, Dr. Rick F. Miller and Dr. Paul S. Doescher, for invaluable guidance, direction, kind help, and friendship throughout my program. I want to thank all the members of my committee, Dr. Rick Miller, Dr. Paul Doescher, Dr. Steven Rodosevich, Dr. Richard Dick, and Dr. Larry Lev for their critical review of the thesis.

Dr. R.H. Waring is given special thanks for his enthusiastic support and very useful suggestions to this research.

Finally, my special gratitude and thanks are given to my parents, wife and son for their tremendous support, patience, and encouragement.

TABLE OF CONTENTS

LIST OF FIGURES

List of Figures Cont'd

LIST OF TABLES

Tables Page

Response of *Artemisia tridentata* ssp. *wyomingensis* and *Stipa thurberiana* to Nitrogen Amendments

INTRODUCTION

Artemisia tridentata Nutt. ssp. *wyomingensis* (ARTRW) is one of the most successful plants in the Great Basin of North America. During the past 100 years, its numbers have increased dramatically while the abundance of high-seral perennial grasses, such as *Stipa thurberiana* Piper. (STTH), have declined. Reasons for this change include overgrazing of perennial grasses by domestic ungulates, fire suppression, poor land management practices such as farming, and possible climatic shifts (Doescher 1983; Hironaka and Tisdale 1963; Tisdale et al. 1969; Tisdale and Hironaka 1981).

Morphological and physiological characteristics of ARTRW make it well suited to its environment. Winter persistent leaves which last approximately 1-year accompanied by large spring ephemeral leaves enhance its ability to maximize leaf area when environmental conditions are favorable (Miller and Schultz 1987; DePuit and Caldwell 1973). A deep well developed root system also allows ARTRW to capture soil moisture from a soil volume much larger than that of perennial grasses (Sturges 1977).

Most of the past research on ARTRW has examined its interaction with other species with respect to water (Moore et al. 1972; Dina and Klikoff 1973; DePuit and Caldwell 1975; Branson et al. 1976; Campbell and Harris 1977; Everett et al. 1977; Miller et al. 1985; Miller and Shultz 1987; Miller 1988). Water is a primary limiting factor to plant growth in the Great Basin. There is some evidence, however, to suggest that ARTRW also is competitive with native perennial grasses for soil nutrients (Hyder and Sneva 1958; West and Klemmedson 1978; James and Jurinak 1978; Patterson and Youngman 1960; Romney et al. 1978; Wilson 1966). Past research indicates grasses have a greater ability to absorb nitrate than shrubs (West and Skujins 1978). Big sagebrush, however, has been shown to absorb a larger proportion of phosphorous than bluebunch wheatgrass (Caldwell et al. 1985).

Limited work has been done to determine if nitrogen or forms of available nitrogen influence the competitive interactions between plant species and plant succession in the sagebrush steppe. No research to date has been published on the effect of nitrogen availability in a Artemisia tridentata ssp. wyomingensis / Stipa thurberiana habitat type on growth, physiology and the competitive interactions between shrubs and perennial grasses. Most nitrogen fertilization studies in the arid and semiarid regions have primarily focused on biomass production.

Although this qualitative approach for the analysis of nitrogen meets the immediate needs of range managers, a more quantitative method of assessing the underlying mechanisms of competition for nitrogen in sagebrush communities would provide better predictability of shrub and grass growth, and changes in plant composition.

This study was designed to determine the effects of addition or depletion of different nitrogen forms on ARTRW and STTH growth in a ARTRW/STTH community in eastern Oregon. Our hypothesis was that the availability and forms of nitrogen in the sagebrush steppe influence the competitive balance between shrubs and perennial grasses, which is reflected by both vegetative and reproductive growth. Specific objectives were: (1). To evaluate the effects of nitrate and ammonium availability on vegetative and reproductive growth for ARTRW and STTH. (2). To evaluate the competitive interactions between ARTRW and STTH.

LITERATURE REVIEW

Role of Nitrogen in Arid and Semiarid Systems

Nitrogen is one of the mineral nutrients plants require in greatest quantity, and that most frequently limits growth in both agricultural and natural systems (Chapin et al. 1987). Agricultural grain yield is highly correlated with the level of nitrogen application. Natural ecosystems respond to nitrogen fertilization with increased productivity, changes in species composition, or both (Lee et al. 1983). Productivity in desert and semiarid plant communities is generally low. Low levels of production result from limited availability of water and nitrogen. Water alone will not ensure high productivity without readily available nitrogen for growth in arid and semiarid areas because of the genetic nature of plants, especially shrubs (Noy-Meir 1973). Nitrogen plays a central role in plant productivity because it is a major component of amino acids, proteins, nucleic acids, and chlorophyll (Chapin et al. 1987).

Nitrogen, as the most abundant element in the atmosphere, becomes available to plants largely through the recycling of organic matter or through the energetically expensive reduction of dinitrogen gas (West and Skujins 1978). Most plants obtain their nitrogen entirely through root absorption of the inorganic ions ammonium and nitrate.

The nitrogen cycle in arid environments has atmospheric inputs as the major source of nitrogen, but differs from mesic systems substantially. Unlike mesic systems, nitrogen fixation by soil cryptogamic crusts, including blue-green algae associated with several genera of lichen, is a major source of nitrogen input to soils in the Great Basin Desert (West and Skujins 1978). Nitrogen fixation by heterotrophic, free-living microorganisms is generally a very minor process in deserts due to the lack of major inputs of carbon (Farnsworth et al. 1978). Rapid decomposition and oxidation of organic nitrogen to nitrite in desert ecosystems also reduces levels of available nitrogen.

A significant proportion of nitrogen necessary for plant growth is provided by mineralization of organic matter. Factors that affect quantities of mineralizable organic nitrogen, or alter the rates of nitrogen mineralization, should alter ecosystem function. There is considerable potential for nitrite and nitrate formation in arid and semiarid area (West and Skujins 1978). Nitrification is a prominent process in nitrogen turnover (Skujins and Fulgham 1978). Nitrification rates, however, varies with climate, soil types and environmental factors: pH, oxygen supply, soil moisture, temperature, organic matter content, CO_2 content and cation exchange capacity of the soil (Mahendrappa et al. 1966), and the availability of substrate (Skujins and Fulgham 1978). Soil with low carbon:nitrogen ratios has low nitrate-producing power (West and Skujins 1978).

Nitrogen losses from arid and semiarid ecosystems are primarily through denitrification and volatilization of ammonia. Denitrification is the major pathway for nitrogen loss from the system. Denitrification rates increase with increased moisture, temperature, organic carbon and nitrogen-containing amendments (West and Skujins 1978). Volatilization of ammonia apparently contributes much less to the gaseous loss of nitrogen from arid soil than denitrification. Volatilization of ammonia is more important in the case of decomposing higher plant residue under plant canopies than in interspaces, and may be important when nitrogen fertilizer is applied (West and Skujins 1978).

Acquisition of limited resources (especially water and nitrogen) by plants in desert ecosystems is a key factor determining plant community composition and succession (Harris 1977; Miller 1987, 1988). For example, Lancaster (1976) suggested nitrate uptake kinetics of annual range species has ecological consequences for their survival and distribution. The ability of uptake and assimilation of the major forms of nitrogen (nitrate and ammonium) by a plant species; and the ability of species to efficiently use low, fluctuating, and often localized supplies of nitrogen (Lee and Stewart 1978; Taylor et al. 1982) can stongly influence plant species ecological distribution and physiological characteristics.

Plant Response to the Form of Nitrogen

Plant species utilize the ammonium and nitrate forms of nitrogen differently (Barker and Mills 1980; Haynes and Goh 1978). These differences are due to pH of the nutrient medium (Weissman 1950; Wallace and Mueller 1957) and carbohydrate supply (Michael et al. 1970). The forms of nitrogen also is known to affect concentrations of other ions in plants (Barker and Mills 1980; Haynes and Goh 1978) which in turn may affect plant growth. The ability of a plant to utilize ammonium and nitrate has been found to be related to its relative soil environmental adaptations (Barker and Mills 1980; Haynes and Goh 1978).

In most arable and calcareous soils, the predominant form of mineralized nitrogen is nitrate, a major form of nitrogen used by most higher plants (West and Skujins 1978). In acid soils, nitrification is often, although not always, inhibited. Ammonium rather than nitrate is the predominant form of available nitrogen absorbed by plants. For example, in forest sites which are wet or seasonally wet and slightly acidic, ammonification is little affected but nitrification is reduced (Haynes and Goh 1978). This leads to ammonium being the predominant form of nitrogen although small quantities of nitrate would also be present. Several workers have shown forest tree species, originating from acidic soil environments, generally prefer ammonium while those from more fertile soils of higher pH tend to prefer nitrate (Krajina et al. 1973; Nelson and Selby 1974).

In desert conditions, the forms and amounts of nitrogen available on a seasonal basis have not been satisfactorily documented (Wallace at al. 1978). Soil nitrate concentrations are generally low as compared to ammonium (Nishita and Haug 1973). Because nitrogen uptake by desert plants is, in part, regulated by the concentrations of nitrate and ammonium, it might be anticipated that desert plants make greater use of exchangeable ammonium. Wallace et al. (1978) pointed out that nitrate concentrations, although obviously low in desert systems, are seasonally high enough to meet the majority of the short-term plant needs for nitrogen. If nitrate and ammonium are equally available, plants take up these two sources of nitrogen with almost equal facility (Kirkby 1970). Information concerning the quantities of available forms of nitrogen and their flux through soil is vital for the consideration of nitrogen uptake in a desert ecosystem (Wallace et al. 1978). The ionic balance in some field-grown desert plants for which cation-anion values were estimated implies that nitrate is a major form of nitrogen absorbed by desert plants (Wallace et al. 1978).

A combination of both nitrate and ammonium appears to produce the greatest growth in the majority of plant species, the optimum ratio probably varing with species and with plant age (Michael et al. 1970; Ta and Ohira 1981). Observations of higher plant growth with ammonium + nitrate or ammonium alone rather than with nitrate alone have been made on plants which occur naturally in soils where nitrification is reduced (Barker and Mills 1980; Haynes and Goh 1978). Higher yields of plants which prefer nitrate, however, have also been obtained with a ammonium + nitrate mixture than with nitrate solely (Haynes and Goh 1978). Cox and Reisenauer (1973) attributed the growth stimulation by ammonium + nitrate to a decreased energy requirement for assimilation of ammonium compared to nitrate by the plant. If this were the case, ammonium grown plants should yield higher than ammonium + nitrate plants. However, ammonium may become toxic or adversley affects plants in an indirect way by affecting cation-anion balance.

Increased nitrate uptake as opposed to ammonium uptake leads to increased uptake of cations, while anion uptake is diminished (Barker and Mills 1980; Haynes and Goh 1978). To balance the negative charges absorbed by the plant in the form of nitrate, cations are taken up along with nitrate to the top for nitrate reduction (Kirkby and Knight 1977). With increasing levels of nitrogen supply, however, they reported an increase in nitrate uptake, with no increase in cation uptake (Kirkby and Knight 1977). The site of nitrate reduction varies with species and nitrogen concentration (Barker and Mills 1980; Haynes and Goh 1978). Barker and Maynard (1972) found ammonium does not affect cation concentration relative to nitrate in pea plant translocating a higher proportion of nitrogen as organic nitrogen from root to shoot.

Cox and Reisenauer (1973) attributed the decrease in cation uptake during ammonium absorption to ionic competition with ammonium ions at the site of intake. They attributed the increase in cation uptake with nitrate nutrition to reduced competition in the absorption process. The antagonistic effect of ammonium on the uptake of cations might lead to deficiency of cations in the plant species growing under conditions where ammonium is the predominant form of nitrogen. Some species, Deschampsia flexuosa (Haynes and Goh 1978) and Vaccinium sp. (Ingested 1973), adapted to ammonium utilization, appear to have the ability to absorb cations, even in the presence of ammonium. Such an efficient ion uptake mechanism may be a significant property in species able to grow in habitats where availability of ions are low.

Plant absorbtion of different forms of nitrogen is ecologically significant in plant succession. Haines (1977), after comparing the relative uptake of applied ammonium and nitrate in a Georgia old-field with forest sere, concluded plants from early successional stages preferentially utilize nitrate while those from the later stages used ammonium. Franz and Haines (1977) examined levels of nitrate reductase in foliage in the same sere and reached the same conclusion.

Plant Response to Limited Soil Nitrogen

In many natural ecosystems the rate of nitrogen mineralization shows a distinct seasonal trend with peaks in availability generally occurring in spring and fall (Gupta and Rorison 1975; Taylor et al. 1982). Such seasonal flushes in soil nitrogen availability results in short periods of high mineral nitrogen concentrations followed by periods of comparatively low supply. Seasonal nutrient absorption by plants follows a similar pattern. Activity of nitrogen-assimilating enzymes in plants, such as nitrate reductase, shows seasonal trends similar to mineral nitrogen availability. Activity of ammonium assimilating enzymes do not change greatly with availability of ammonium or nitrate (Lee and Stewart 1978; Taylor and Havill 1981), presumably because they utilize whichever source of nitrogen is absorbed. The activity pattern of nitrogen-assimilating enzymes indicates which plant species are adapted to fluctuating nitrogen supplies. In infertile habitats it is likely a large percentage of the annual nutrient absorption occurs during nutrient flushes (Chapin et al. 1978), particularly during late winter or early spring (Chapin and Bloom 1976; Mooney and Rundel 1979), rather than steady state absorption.

Soils are known to possess both lateral and vertical spatial variability in nitrate concentrations (Biggar 1978; Greenwood 1978). Thus, when the supply of mineral nitrogen is low, plants must extract nitrate or ammonium from localized zones within the rooting zone. Root elongation and root hair formation occuring in response to low nitrogen supply is a mechanism where root systems increase their surface area. This response is important for the acquisition of nutrients delivered to the root surface by diffusion. At low nutrient availability, nutrient diffusion to the root surface limits absorption, and even a low root absorption capacity (per gram root rather than total absorption per plant) is adequate to absorb those nutrients that reach the root (Nye 1977; Nye and Tinker 1977). Plants growing in nutrient-poor soil maximize nutrient intake more through high root:shoot ratios and mycorrhizal associations than through a high root absorption capacity (Nye 1977). The most distinct characteristics of plant species in infertile habitats are leaf longevity and low relative growth rates (Chapin 1980).

Plant Response to Excess Soil Nitrogen

The tolerance of plants to an ample supply of ammonium is generally low, whereas the tolerance for nitrate is high. Toxic reactions occur when ammonium accumulates in plants, particularly when translocated to the shoots (Puritch and Barker 1967). In contrast, plants will accumulate nitrate and transport it through the plant with few toxic effects (Mills and Jones 1979).

Excess amounts of ammonium, unlike nitrate, increases root respiration (Matsumoto and Tamura 1981). This effect can be attributed to enhancement of root exudation and hence stimulation of bacterial growth (Trolldenier and Rheinbaben 1981a). It also enhance the necessity for increasing substrate flux rate in the tricarboxylic acid cycle in order to supply more carbon skeletons for ammonia assimilation.

The accumulation of nitrate in plants has received much study because high concentrations of nitrate in food can be toxic to animals ingesting it (West and Skujins 1978). Excess nitrate absorbtion by plant tends to increase the demand on the carbohydrate metabolism. When nitrate concentration increases, root hair numbers and root hair length decrease. In contrast to nitrate, ammonium leads to the formation of a dense layer of long root hairs (Bhat 1983). Accumulation of large amounts of nitrate in plant tissues would also upset the cation-anion balance of the plant. Normally, plants absorb more anions than cations when nitrate is the major form of nitrogen available. The ratio of cations to anion absorbed is usually in the range 1:2 to 7:10 (Nye 1981). Nitrate normally constitutes more than half the total equivalent anions absorbed. Nitrate anions, however are rapidly reduced to organic components within the plant. Thus, within the plant there is almost always an excess of free cations over anions, and ionic balance is maintained by the plant synthesizing organic acid anions such as malate and citrate (Raven and Smith 1976; Haynes and Goh 1978).

Plant Response to Fertilization of Nitrogen

Soil water and nitrogen availability in desert rangelands is generally low (West and Klemmedson 1978). There are significant interactions between these two factors for plant growth. It is apparent that if moisture availability is sufficient for a complete plant growth cycle, then the probability is high that plants will respond to nitrogen fertilization (James and Jurinak 1978). There are, however, many subtle effects of both nitrogen and water that must be considered in the interaction of limiting factors in determining whether or not response to either will be obtained (Romney et al. 1978). Plant response to nitrogen fertilization also depends on other environmental factors such as soil aeration and the availability of other mineral nutrients (Kramer and Kozlowski 1979).

Cook (1965) reported nitrogen fertilization increased crested wheatgrass herbage, number of reproductive heads per plant, basal area of crowns and number of roots. Protein content also increased by about one-third. His research indicated that 45 kg N/ha increased herbage up to 1,100 kg/ha. Sneva (1973a, b, c) evaluated the effects of nitrogen fertilization in conjunction with grass clipping treatments, herbicide applications, time and source of nitrogen fertilization in eastern Oregon. Over a 13 year period, 34 kg N/ha gave 83% more spring growth, 29% more regrowth after clipping and 78% more biomass at maturity. There appeared to be no interaction between nitrogen fertilization with clipping of the grass during the growing season (Sneva 1973a), or with application date (Sneva 1973b), the interaction between nitrogen and paraquat was significant in increasing yield and quality of crested wheatgrass (Sneva 1973c).

Few studies have been made on the effects of fertilization on desert shrubs. Carpenter (1972), working in the Colorado Plateau reported that 134 kg N/ha applied to sagebrush yielded an 81% increase in total leafy material compared to the nontreated control. Bayoumi (1975) found that nitrogen fertilization up to 100 kg N/ha linearly increased twig growth of both sagebrush and bitterbrush in the Bear River Mountain Range of northern Utah.

Factors Influcing Nitrogen Uptake

Uptake rate of nitrogen may be influenced by different environmental factors such as temperature, soil aeration, plant age, and concentration of competing ions.

Ambient ammonium restricts net nitrate uptake in numerous plant species (Minotti et al. 1969; Youngdahl et al. 1982). There have been some examples, however, where ammonium had little or no effect on nitrate uptake (Edwards and Barber 1976a). Uptake rates of ammonium are normally unaffected by the presence or absence of nitrate in nutrient solution (Youngdahl et al. 1982).

If uptake rate of ammonium by the plant is high, then plant growth results in a net efflux of H ions into the rhizosphere, resulting in a decrease of pH close to the root surface (Riley and Barber 1971). In contrast, when uptake rate of nitrate is high, plants absorb an excess of anions, causing a net efflux of HCO_3 or OH^- ion resulting in an increase in rhizosphere pH (Smiley 1974).

Limited absorbtion sites on the root surface creates competition between cations and between anions for uptake. For example, the more uptake of ammonium or nitrate by plant species reduced the rate of uptake of other cations (e.g. K, Ca Mg) or other anions (e.g. Cl, SO_4) at the same time. Both ammonium and nitrate uptake are active processes, requiring energy to sustain the uptake system (Pearson and Steer 1977). Uptake of these forms of nitrogen require photosynthates. Uptake of ammonium by plants shows a wide diurnal variation (Van Egmond 1978). Low light intensity greatly reduces uptake of both forms of nitrogen (Ta and Ohira 1981).

Low temperatures inhibits nitrate uptake more than ammonium uptake (Clarkson and Warner 1979). Uptake of nitrate usually becomes greater than ammonium at around 23°C increasing up to 35°C (Frota and Tucker 1972). Uptake varies, however, with plant species. In most plants, low temperatures generally increase reliance upon ammonium as a mineral nitrogen sources (Haynes and Goh 1978). For any given plant species, the uptake and utilization of ammonium is greater than that of nitrate at low temperatures (Clarkson and Warner 1979). Ammonification is less temperature sensitive than nitrification so relative availability of ammonium versus nitrate increases in cold soils (Flint and Gersper 1974). In addition, roots absorb ammonium more readily than nitrate at low temperatures (Clarkson and Warner 1979). Added ammonium delayed or completely suppressed nitrate accumulation at low temperature (Anderson and Boswell 1964).

Light is a very important factor for increasing photosynthetic capacity with increasing leaf nitrogen. At low light levels, photosynthesis increases little, if at all, with increasing leaf nitrogen (Gulmon and Chu 1981). High light permits nitrate assimilation at minimal carbon cost which should favor the use of nitrate; conversely, the low respiratory costs of ammonium assimilation should favor acquisition of this form in low light (Chapin et al. 1987).

Plant water potential is another factor affecting the relationships between nitrogen and photosynthesis. When limited water availability causes plants to operate at low stomatal conductances (thereby decreasing water use), increasing leaf nitrogen produces diminishing returns in photosynthesis and leads to a dominant limitation of photosynthesis by stomata (Mooney and Gulmon 1979).

Mycorrhizal associations enable plants to use soil nutrients more effectively through the exploration of a greater volume of soil and expanded absorbtion surface area. This is particularly important when considering the nutrition of plants for immobile nutrients such as phosphorus (Nye and Tinker 1972) and when the relatively immobile ammonium rather than the mobile nitrate is the major source of plant-available nitrogen (Bowen and Smith 1981). Additions of nitrate to the soil decrease mycorrhizal infection (Azcon et al. 1982).

The Relationship between Photosynthesis and Nitrogen

The relationship between photosynthesis and leaf nitrogen is important since photosynthesis provides energy and structural substrate necessary for reproduction, growth, or foraging for additional nutrients (Field and Mooney 1986). The proportion of total leaf nitrogen allocated to photosynthetic reactions is undoubtedly large (Field and Mooney 1986). All the biochemical and photobiological processes of photosynthesis require nitrogenous compounds. Photosynthetic rate is proportional to leaf nitrogen concentration over a broad range, because the bulk of leaf nitrogen is directly involved in photosynthesis as a component of photosynthetic enzymes and chlorophyll (Brady 1973; Murata 1969; Natr 1975). Respiration rate, being roughly proportional to tissue protein content (Penning de Vries 1975), also declines under nutrient stress (Ryle and Hesketh 1969).

Nitrogen availability regulates plant growth through its effects on leaf expansion and photosynthesis. Both activities have high requirements for nitrogen and are thus strongly influenced by the nitrogen nutritional status of the plant (Radin 1983). When nitrogen content in a plant is low, leaf expansion is reduced (Radin and Parker 1979; Radin 1983; Steer and Hocking 1983), possibly resulting from rising water deficits in the expanding leaf cells (Radin and Boyer 1982). Nitrogen nutrition possibly affects photosynthetic rate most directly through its effect on ribulose-1,5-bisphosphate carboxylase synthesis and activity (Friedrich and Huffaker 1980; Wittenbach et al. 1980; Uchida et al. 1982; Makino et al. 1984). This enzyme tends to be directly correlated with the nitrogen content of leaves (Boon-Long et al. 1983a, 1983b; Makino et al. 1984). Nitrogen influences photosynthesis also by affecting chlorophyll and protein synthesis and stomatal response. Since chlorophyll content is more or less proportional to nitrogen supply over a wide range, a deficiency of nitrogen inhibits photosynthesis (Kramer and Kozlowski 1979). Both leaf size and chlorophyll content were well correlated with nitrogen content.

If nitrogen influences photosynthesis, then the ability to acquire nitrogen may be a primary determinant of above-ground growth. Alternatively, manipulating the nitrogen-photosynthesis relationship may provide effective routes toward increasing agricultural production without increasing nitrogen fertilization (Chapin et al. 1987). Generally, nitrogen stress has a greater effect upon growth than upon photosynthesis and net assimilation rate. If nutrient absorption is not maintained at substantial rates, photosynthetic and growth rates decline.

Nitrogen Use Efficiency

A high efficiency of nutrient use could be an important adaptation to low nutrient availability or nutrient stress (Grundon 1972; Loneragan and Asher 1967; White 1972, 1973). Nitrogen use efficiency (NUE) is defined as the rate of CO_2 uptake for photosynthesis per unit of nitrogen in leaf biomass, expressed in micromoles per gram per second or as the quantity of dry matter produced per gram of nutrient. It is simply the inverse of tissue concentration (Chapin 1980). According to Chapin (1980), however, NUE as currently defined, is not an important adaptation to nutrient stress, because slow growing species from infertile habitats generally have higher tissue concentration (low efficiency) of a limiting nutrient than rapidly growing species.

A plant allocates nitrogen most efficiently when nitrogen is equally limiting to each plant process (Bloom et al. 1985). Generally, NUE is low with low leaf nitrogen content increasing with leaf nitrogen content (Field and Mooney 1986). Evans (1983), however, found within a species, NUE decreases with increasing nitrogen beyond a critical level.

Nitrogen and Water Use Efficiency of Plants

Water use efficiency of a species can be expressed either as transpiration ratio (TR) using the quotient transpiration / net photosynthesis, or as its reciprocal, the assimilation ratio. The transpiration ratio indicates how many milligrams of water are transpired while 1 mg CO_2 is assimilated. Thus a plant with a low TR appears to be better suited for dry climates. It has been suggested by Monk (1966) that nutrient efficient species are efficient in use of water, since nutrient poor sites are often dry. Nilsen et al. (1986) found increased nitrogen levels in Prosopis species leaf tissue increased individual leaf productivity as a result of increased leaf conductance rather than increased WUE on the Sonora Desert. Vankeulen (1981) found the lower nitrogen concentration in the leaves of Hordeum and Phalaris sp. hardly affected their stomatal conductance. WUE is apparently more unfavourable under nitrogen-limited conditions.

In the field, the moisture content in the soil may become so low that nutrient transport and hence uptake are restricted (Vankeulen 1981). Soil moisture can influence mineralization of nitrogen in three major ways: moisture stress inhibits microbial growth directly; as moisture content increases, aeration decreases and microbial growth is inhibited; and cycles of wetting and drying tend to increase the amount of available substrate. It is difficult to predict its influence on WUE. Basically, water use efficiency relates primary production and evapotranspiration. The primary production of a population depends on its genetic composition and the abiotic driving variables.

Factors Influencing on Accumulation of Nitrogen in Plant

Primary factors known to affect the accumulation of nitrogen in plants include nutrient supply, soil moisture level, temperature, light, soil type, herbicides, and disease (Mckee 1962), and nitrogen fertilization (Willhite et al. 1955; Rumburg 1969, 1972). Leaf nitrogen declines with increasing leaf age in essentially all plants, which causes a natural source of intraspecies variation (Field and Mooney 1986). Environmental stress upsetting the photosynthesis-respiratiory balance can cause dangerous amounts of nitrate to accumulate in plant tissues (Neinum 1971; Murata 1969).

Competition for Natural Resources

Competition was recently defined as "the induction of strain in one organism as a result of the use, defense or sequestering of resource items by another organism" (Welden and Slauson 1986). The importance of competition for resources such as light, moisture and mineral nutrients in influencing plant growth and community structure has long been recognized. Variation in the availability of resources must be considered when examining plant responses to them. This variability of resources is particularly important when considering a plant in relation to its competitors. If plant species differ seasonally in their growth or physiology, their relative abilities to compete for a resource may vary with the time of year. The relative competitive ability of a plant species may also depend on the supply of the resource in question, its relation to other resources (Tilman 1982), plant age, physiological condition, and many other physical and biological factors. Timing of resource use and release by a plant can be an additional source of variation for its competitors. Such features can affect the composition of plant communities (Fowler and Antonovics 1981; Rogers 1983).

A faster growth rate can give one species a competitive advantage of increased size (Harper 1977). Species with high competitive ability are best able to exploit a resource, to the detriment of their less competitive neighbors, under conditions of incresed resource availability. Under lower resource availability, other plant attributes, such as stress tolerance, may become more important to plant survival than competitive ability (Grime 1979). In the Pacific Northwest, fertilization with high levels of nitrogen have been shown to promote cheatgrass development at the expense of native grasses. Idaho fescue and bluebunch wheatgrass exhibit very little growth response to nitrogen fertilization and were greatly reduced by cheatgrass competition (Schmisseur and Miller 1978).

STUDY AREA

Research was conducted at the Squaw Butte Experimental Range in southeastern Oregon, 67 km west of Burns, on the northern fringe of the Great Basin. The study site was located in a ARTRW/STTH habitat type, at an elevation of 1372 m (Doescher et al. 1984; Miller et al. 1985; Winward 1970). This site has been excluded from grazing by domestic herbivores for the past 40 years. The site was chosen for this study because: (1) it is in good ecological condition; (2) management history is known; (3) the site is representative of a ARTRW/STTH habitat, which covers extensive areas throughout southeastern Oregon, northeastern California and northern Nevada, and (4) extensive measurements have been recorded on soil nutrients, plant growth, and plant water relations over the last six years. This site and plant community have been previously described in details by Doescher et al. (1984), Miller et al. (1985), and Miller and Shultz (1987).

Climate

The 40-year mean annual precipitation for the Squaw Butte Experimental Range is 300 mm. Approximately 60% of the total precipitation is received during the fall and winter months, often as snow. Almost 25% of the precipitation falls as rain during May and June. Summer drought is a distinctive characteristic of the study site.

The mean annual temperature is 7.6°C, average annual minimum temperature is 0.3°C, and average annual maximum temperature is 14.9°C. In winter the mean temperature is -0.6°C with the daily minimum averaging -4.8°C. In summer the mean temperature is 17.6°C with the daily maximum averaging 26.8°C (National Climatic Center, NOAA, 1987). This represents a seasonal change of nearly 22°C.

Soil

Parent material in this site is alluvium weathered from rhyolite and basalt rock sources. Soils are classified as Xerollic Durothids with a sandy loam texture in the surface horizon (Lentz and Simonson 1986). Soils, which vary in depth from 35 to 45 cm, are underlain by an indurated duripan 5 to 20 cm thick, which is underlain by unweathered bedrock (Miller 1988). Soil pH are 6.9 and 7.37 in soil depth (0-10 cm) and (10-20 cm), respectively (Doescher et al. 1984).

Plant Community

Overstory is dominated by ARTRW with some green rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus* (Hook.) Nutt.) and a herbaceous understory dominated by STTH (Miller 1988). Other perennial species present on the site are Sandberg's bluegrass

(_Poa secunda_ Presl.), Squrrieltail (_Sitanion hystrix_ (Nutt.) Smith), and a sparse occurrence of several native forbs.

METHODS

Experimental Design

A completely randomized plot design was used with 10 replications of each treatment. Field plots, 5m x 5m in size, were established on the research site in 1987 (Fig.1). In order to maximize homogenity, plots were selected on the basis of a vigorous ARTRW with a vigorous stand of STTH adjacent to the ARTRW canopy. Plots were layed out so a ARTRW was located in the center of each plot. All ARTRW measurements were recorded on this plant and all STTH measurements were recorded within 1.5 m of the ARTRW stem base. The remainder of the plot was used as a buffer to minimize border effects among adjacent treatments.

Treatments were applied in spring and November of 1986 to the plots. Treatments were (1) control, no amendments added; (2) granulated sugar (45 g/m^2); (3) ammonium sulfate $(NH_4)_2SO_4$ (4.5 gN/m^2); and (4) nitrate HNO_3 (4.5 gN/m^2). Sugar addition was assumed to increase the C:N ratio to decrease availability of soil nitrogen (Johnson and Edwards 1979; Waring 1982). Both ammonium and sugar were broadcast onto the plots. Nitrate was diluted in water (1 part HNO_3 to 5 parts water) and applied with a pack sprayer. All herbaceous plants were dormant at time of nitrogen and sugar application. The level of nitrate and ammonium added

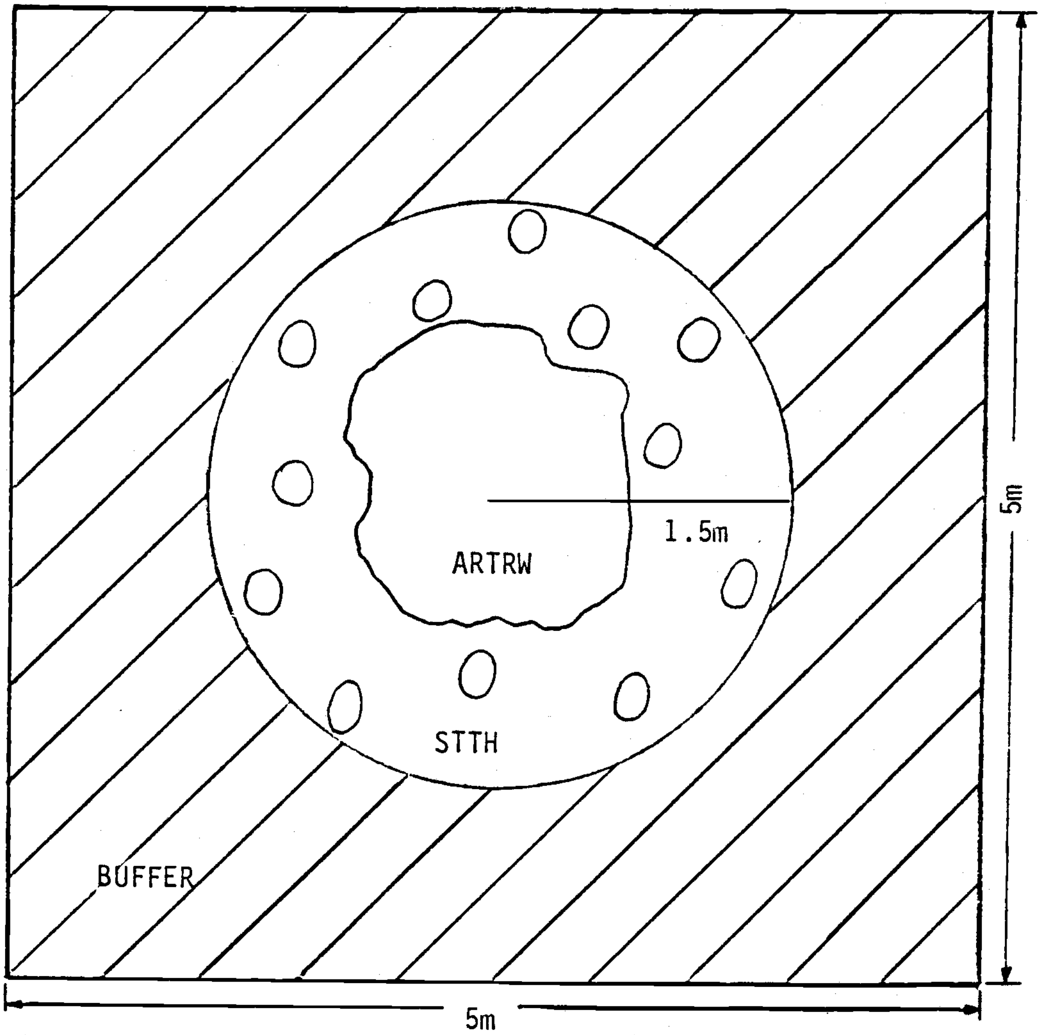

Figure 1. Plot design

was based on plant responses reported in several nitrogen fertilization experiments in the sagebrush steppe (Schmisseur and Miller 1978). Plant growth measurements were recorded during the growing season following treatment in 1987.

Soil Water

Soil water content was measured within 1.5 m from the center ARTRW plant from April 1 to September 15 biweekly at two depths, 2-20 cm (A horizon = gravelly fine sandy loam) and 20 cm to the duripan (Bt to Bct = gravelly clay loam to a gravelly silt clay loam). One soil sample was collected for each of the 2 depths within each plot for all treatments. Soil water was measured gravimetrically (Gardiner 1965) and soil water release curves were developed for each depth to define soil water potential (Miller 1988).

Total Plant Water Potential

Total water potential on a ARTRW branchlet was measured during the 1987 growing season with a pressure chamber (Scholander et al. 1965; Waring and Clary 1967). Predawn (May 19, June 3, and July 21) and midday (April 15 and June 3) measurements were made between 0430 and 0630, 1130 and 1230 hr, respectively. Five to 10 twigs were measured in each treatment. Samples were selected at random on each shrub, removed from the shrub and immediately measured in the pressure chamber.

Soil Nitrate and Ammonium Measurements

Soil samples were randomly collected from 0-20 cm and 20 cm to the duripan (40 cm) depths within 1.5 m of the center shrub, using a 2.5 cm diameter soil sampling tube. Soils were sampled during early, mid and late stages of the growing season (mid April, late May, and late July). One sample at each profile was collected in 5 plots for each treatment. Soils analysis was performed at the Oregon State University Soil Testing Laboratiry using KCL extracting solution (Horneck et al. in press).

Leaf Nitrogen Content

Leaves on current year's vegetative ARTRW stems and current year's STTH leaves were collected on April 15 and 21, June 1, and August 1, 1987 on all plots. Collections represented three growth stages (ARTRW in initial leaf elongation, rapid leaf and stem elongation and early flowering; STTH in vegetative, flowering and seed) for both species during the growing season. Leaf samples were dried at 60°C for 48 hr, then ground in a Wiley mill to pass through a 1.0 mm screen for total nitrogen analysis. Semimicro-Kjeldahl method was used to determine the total nitrogen content in the leaves of ARTRW and STTH. Analysis procedures used were those suggested by Bremner (1965) with 10 replicates per treatment.

STTH Growth Measurements

At the end of the growing season (August 5, 1987), 5 STTH plants within each plot (1.5 m from the base of the center shrub) were harvested. Before clipping STTH for aboveground biomass, vegetative and reproductive tillers were counted on each of the 5 plants in each plot. Total and reproductive tiller density measurements are in numbers per cm^2 of crown area. Crown area was determined by measuring maximum crown width (a) and perpindicular line to the width (b), and then calculating crown area from $((a+b)/4)^2 \times \pi$. Total tiller density and reproductive tiller density were determined by total tiller and reproductive tiller numbers divided by crown area. Aboveground biomass from the 5 STTH plant was collected, dried at 60°C for 48 hrs and weighted.

ARTRW Growth Measurements

During the growing season, 5 terminal branchlets were selected biweekly on each shrub for measurements of stem and leaf development within each plot. Ephemeral leaf numbers, leaf maximum length and stem length were recorded. In late summer when stem and leaf growth had ceased, a 20 x 20 cm^2 frame was placed in the center top of each

ARTRW in each plot to measure vegetative and reproductive stem density. Only current years elongated branchlets were recorded (non elongated lateral stems were not recorded). Data were converted to number of stems per m^2 of canopy. In early August 1987, we sampled current year's production per vegetative and reproductive shoot of ARTRW. For each shoot of 50 samples in each treatment we measured total leaf biomass, leaf area using a LI-COR-3100 (LI-COR Inc. Lincoln, NE) leaf area meter, shoot biomass, shoot diameter, and shoot length. All biomass measurements were put on a dry weight basis by drying samples for 48 hrs at 60°C. We estimated current year biomass within each treatment with the following formula:

(reproductive shoot weight) x (reproductive shoot density) + (vegetative shoot weight) x (vegetative shoot density).

Specific Leaf Weight

Specific leaf weight (dry weight/unit leaf area) (SLW) was obtained by measuring current year leaf area once per month of 20 samples for each treatment for both species through the growing season. SLW was calculated following each leaf area measurement, oven-drying at 60°C for 48 hrs, using 10 replicates of each species. Leaf roll was not corrected for STTH leaf area.

Uptake of Nitrogen

Nitrogen uptake rate (mg N/m^2 of leaf area) was calculated from specific leaf weight (g/m^2) x leaf tissue nitrogen content (mg N/g) for both species through the growing season (Jarrell and Beverly 1981).

Statistical Analysis

Statistically significant treatment effects on variables measured for ARTRW and STTH were identified using the analysis of variance procedure (PROC ANOVA) of Software System for Data Analysis and Report Writing (SAS) (Helwig and Council 1979). Least significant differences (LSD) ($p < 0.05$) were calculated only when the F value indicated significance using ANOVA (Steel and Torrie 1980). Only significant differences are reported in the text. When seasonal and diurnal measurements were recorded, we set time as a variable in addition to treatment. Therefore, these results included the interaction (Treatment x time) effects on the both species. If a significant treatment x time interaction was detected, means were seperated in an interaction table using the LSD approach.

RESULTS

Soil Water

Soil water content and soil water potential within each of the four treatments for the 1987 growing season are shown in (Fig.2,3). Soil water content gradually decreased as growing season progressed. There were no differences ($p<0.05$) in soil water content among treatments within each soil profile throughout the growing season. Increased soil water content on May 4 was due to precipitation on May 3.

Total Plant Water Potential

There were differences between each sample date and between treatments on June 3 for total plant water potential of ARTRW at predawn and midday (Table 1). No differences between the four treatments were detected for predawn and midday total plant water potential in the early and late growing season.

Soil Nitrate And Ammonium Availability

Application of nitrate increased soil nitrate concentration at both soil depths as compared to the remaining three treatments. No interaction was detected for nitrate analysis in the upper soil profile (0-20 cm). Nitrate concentration at this depth was initially high in April for all treatments, declined in May and then

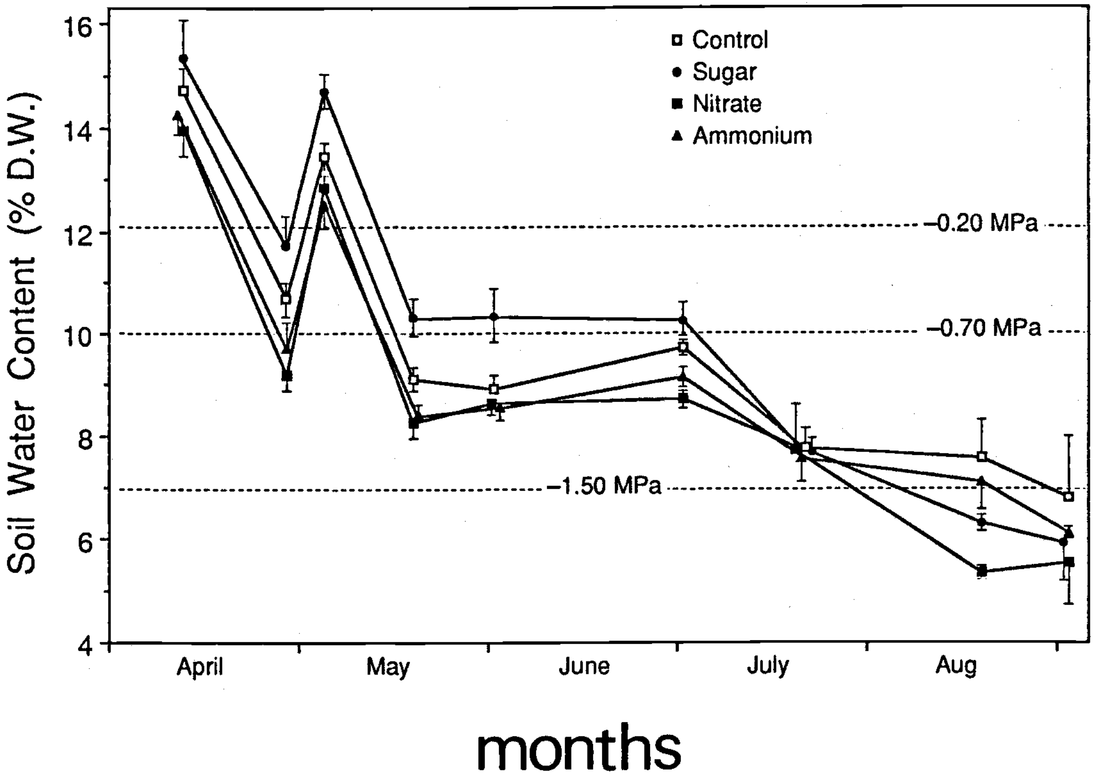

Figure 2. Seasonal pattern of soil water content in the upper soil profile (2-20 cm) for four different nitrogen treatments in 1987. Vertical bars are 95 percent confidence limits. Field capacity (-0.03 MPa) = 18% soil water content.

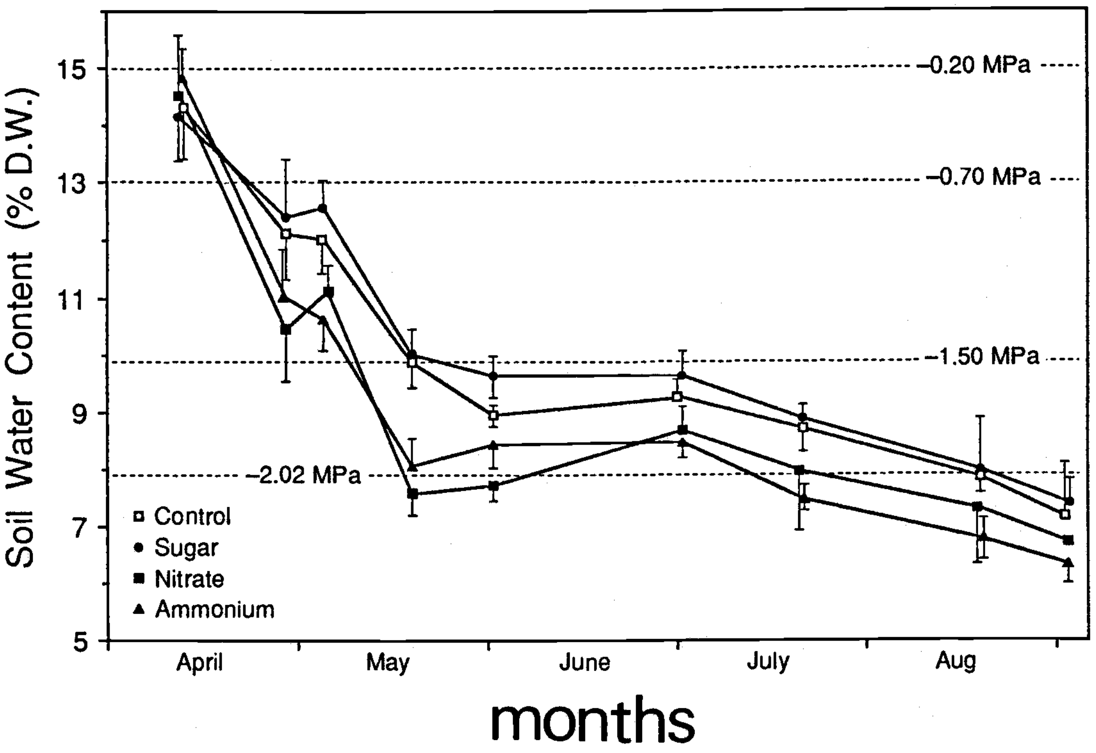

Figure 3. Seasonal pattern of soil water content in the lower soil profile (20-40 cm) for four different nitrogen treatments in 1987. Field capacity (-0.03 MPa) = 21% soil water content.

Table 1. Predawn and midday plant water potentials (MPa) in *Artemisia tridentata* ssp. *wyomingensis* through the growing season in 1987.

PREDAWN

	Treatments			
Date	Control	Sugar	Nitrate	Ammonium
May 19	-1.24±0.03aA	-1.05±0.03aA	-1.04±0.02aA	-1.21±0.04aA
June 3	-1.31±0.09aA	-1.44±0.04bA	-1.77±0.03bB	-1.72±0.09bB
July 21	-1.62±0.09bA	-1.62±0.15bA	-1.74±0.18bA	-1.77±0.13bA

MIDDAY

April 15	-1.85±0.06aA	-1.67±0.06aB	-1.65±0.08aB	-1.62±0.05aB
June 3	-2.09±0.02bA	-2.06±0.03bA	-2.24±0.02bB	-2.31±0.05bB

Predawn: LSD(time,0.05)=0.1958; LSD(treatment,0.05)=0.221;
Midday:LSD(treatmentxtime,0.05)=0.129;
Numbers followed by same lower case letters are not significantly different ($p<0.05$) between dates for each treatment;
Numbers followed by same upper case letters are not significantly different ($p<0.05$) between treatments for each date.

increased in July. Highest nitrate levels were found in plots that had nitrate applied. No differences in nitrate content were detected between ammonium, sugar and control treatments (Fig.4,5).

There was a time x treatment interaction for nitrate concentration in the second soil profile (Table 2). The same trend in nitrate concentration between treatments for the lower soil profile (20-40 cm) was found as for the upper soil profile. The nitrate plot had higher nitrate concentration than the other treatments. Nitrate concentration declined over the season only in the nitrate plots.

Soil ammonium concentration was different among four treatments only in the lower soil profile (Fig.6,7). It decreased in both profile as the growing season progressed (Fig.8).

Leaf Nitrogen Content

Application of nitrate and ammonium increased leaf nitrogen content for both species over the control and sugar treatments. Total leaf nitrogen content in ARTRW decreased in the nitrate treatment and increased in control and sugar treatments during the growing season (Table 3,4). Leaf nitrogen content in STTH decreased in the nitrate, ammonium and control treatments from April to August. Leaf nitrogen content of STTH was lowest on the sugar plots

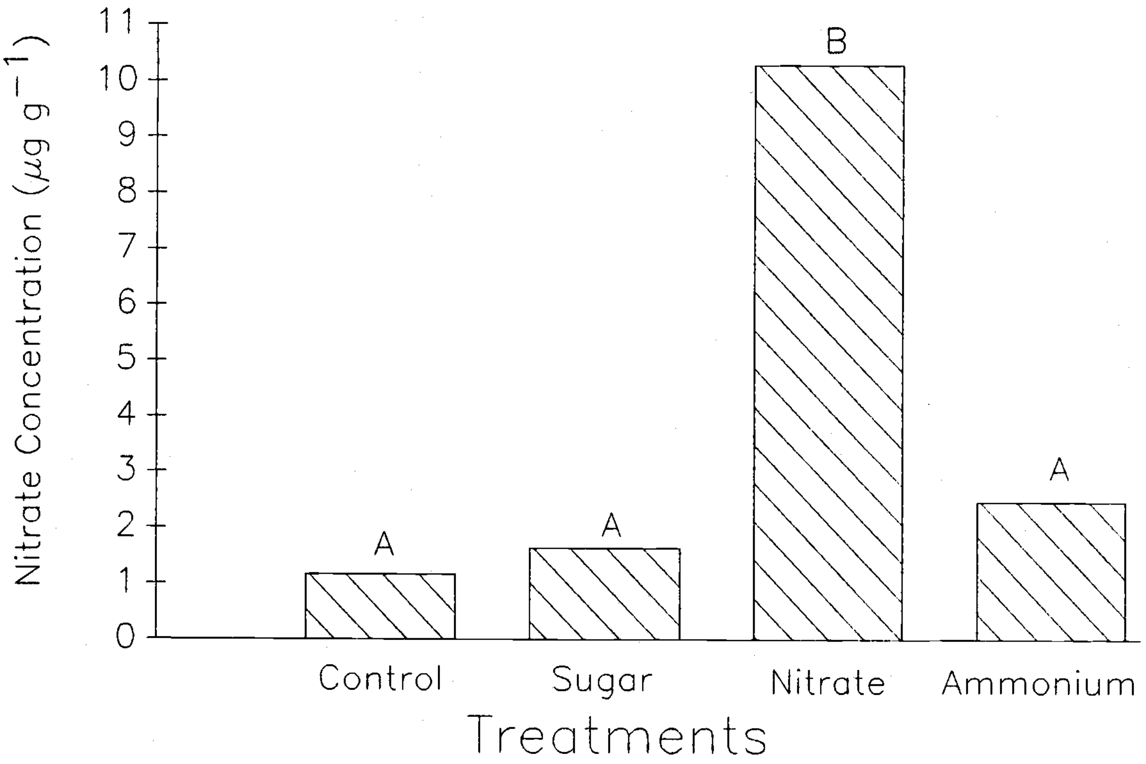

Figure 4. Soil nitrate concentration of averaged across dates in the upper soil profile (0-20 cm). Similar letters are not significantly different ($p<0.05$) between treatments. Each value is the mean of 10 samples.

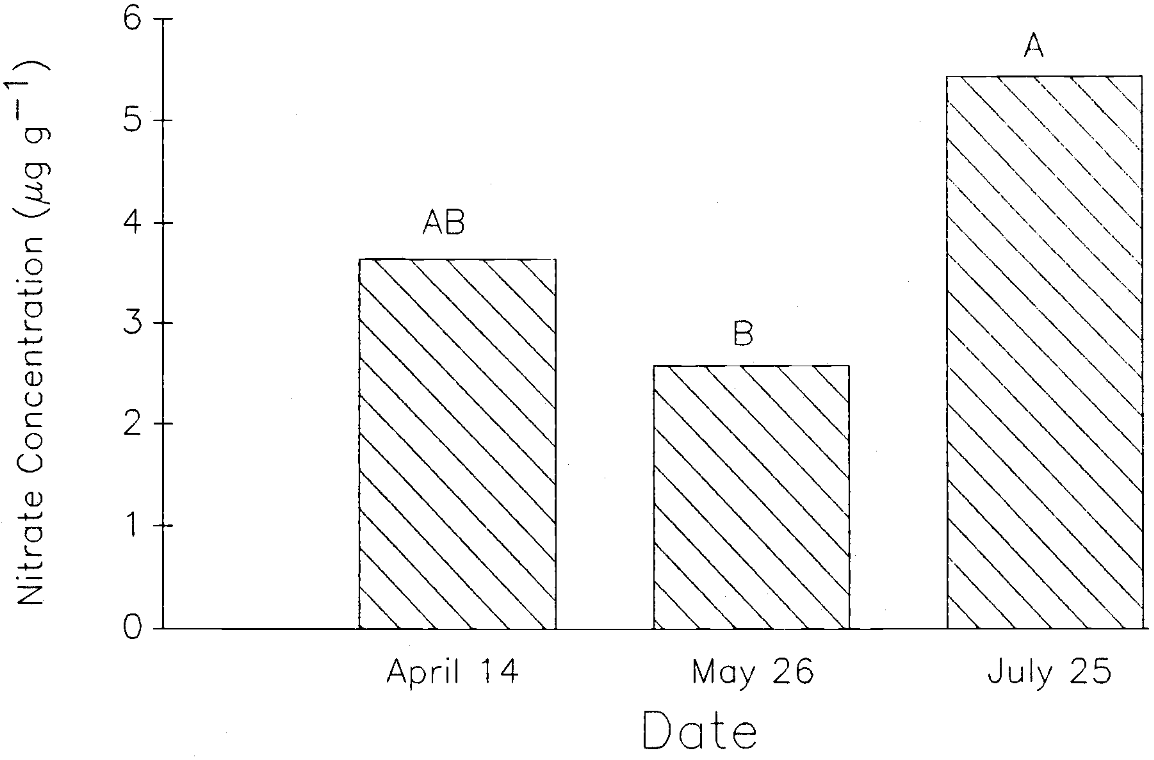

Figure 5. Soil nitrate concentration of averaged across treatments in the upper soil profile (0-20 cm). Similar letters are not significantly different ($p<0.05$) between dates. Each value is the mean of 10 samples.

Table 2. Soil nitrate concentration (ug/g) in the lower soil profile (20-40 cm) through the growing season in 1987.

		Treatments		
Date	Control	Sugar	Nitrate	Ammoniun
April 14	0.74aA	0.84aA	20.6aB	1.64aA
May 26	1.56aA	1.10aA	8.64bB	1.46aA
July 25	1.62aA	1.90aA	9.02bB	3.46aA

F (treatment x time)=21.68
Pr>F=0.0001
LSD (0.05)=2.29
Numbers followed by same lower case letters are not significantly differnt ($p<0.05$) between dates for each treatment;
Numbers follewed by same upper case letters are not significantly different ($p<0.05$) between treatments for each date.

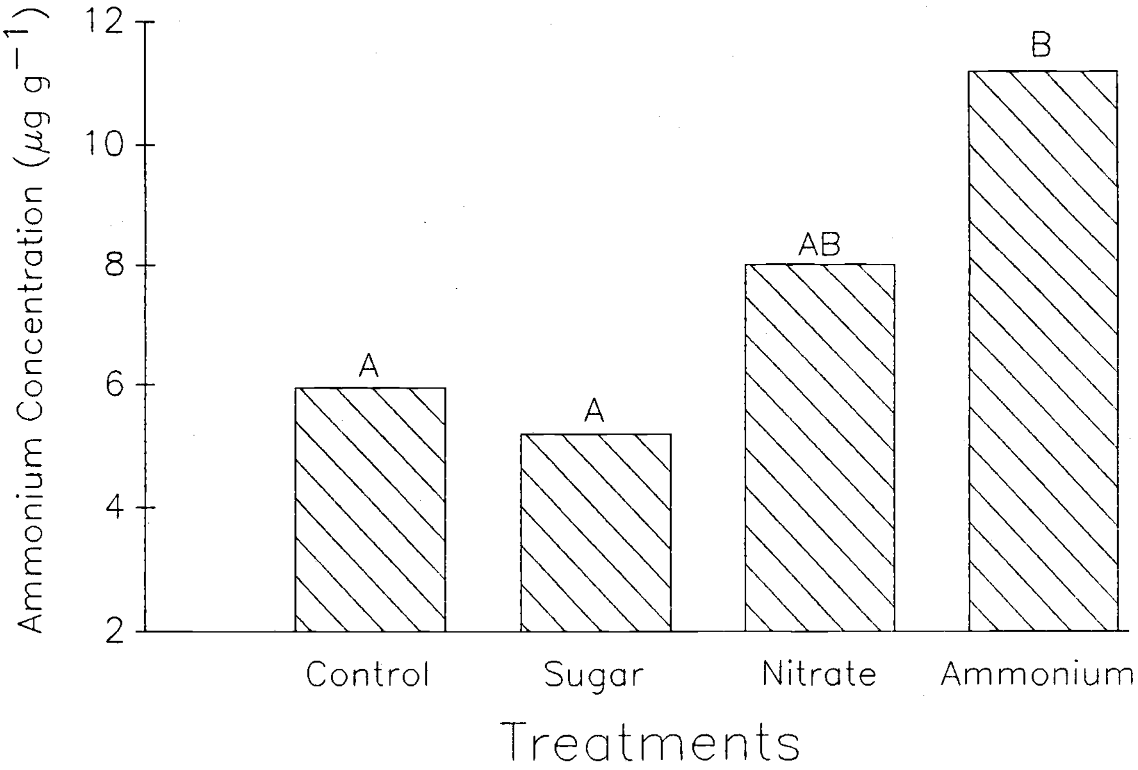

Figure 6. Soil ammonium concentration of averaged across dates in the lower soil profile (20-40 cm). Similar letters are not significantly different ($p<0.05$) between treatments. Each value is the mean of 10 samples.

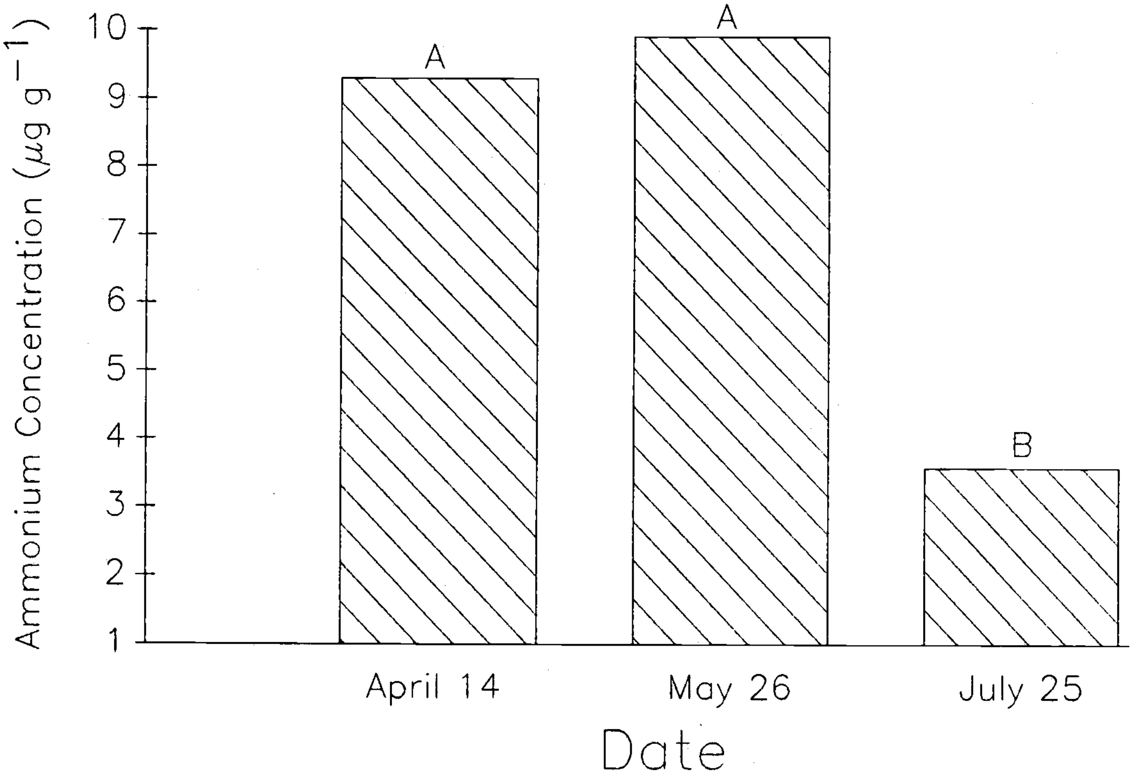

Figure 7. Soil ammonium concentration of averaged across treatments in the lower soil profile (20-40 cm). Similar letters are not significantly different ($p<0.05$) between dates. Each value is the mean of 10 samples.

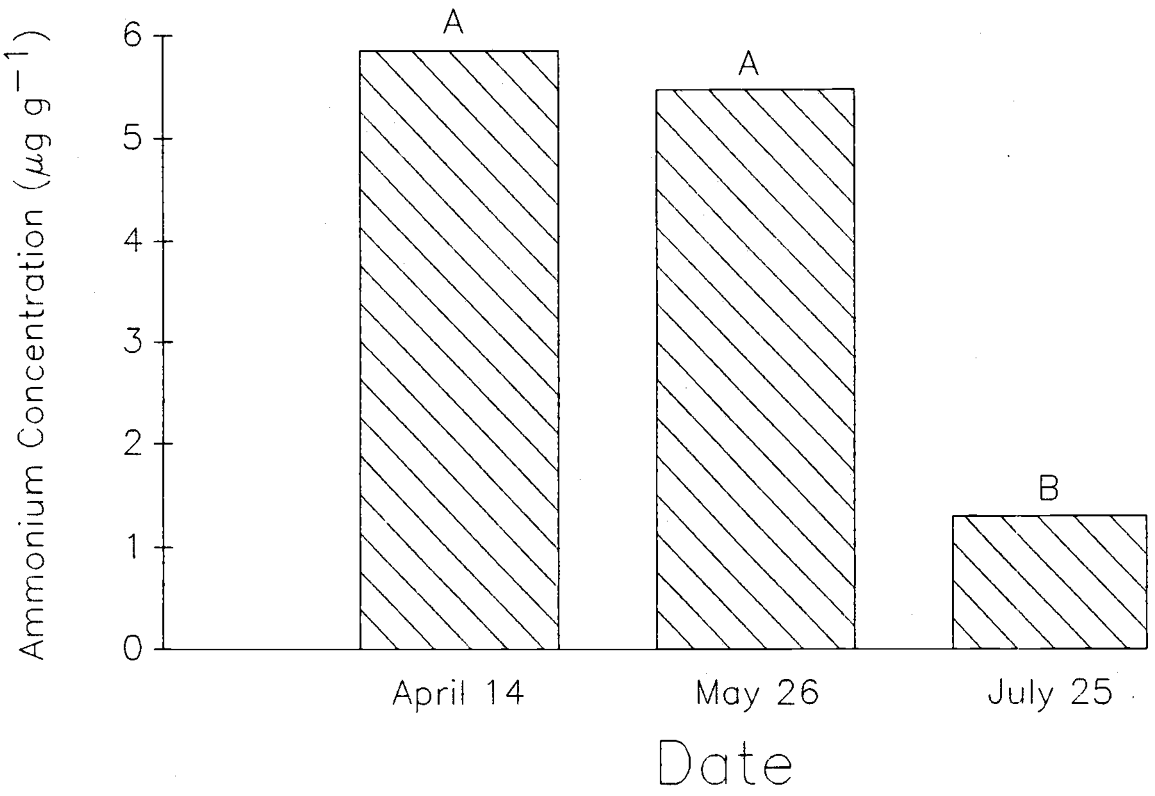

Figure 8. Soil ammonium concentration of averaged across treatments in the upper soil profile (0-20 cm). Similar letters are not significantly different ($p<0.05$) between dates. Each value is the mean of 10 samples.

Table 3. Total leaf nitrogen per unit dry weight (mg/g) in *Artemisia tridentata* ssp. *wyomingensis* through the growing season in 1987.

	Treatments			
Date	Control	Sugar	Nitrate	Ammonium
April 15	17.9±0.5aA	18.1±0.8aA	27.9±1.5aB	25.7±0.5aB
April 21	19.4±0.7aA	18.5±0.2aA	27.4±0.8abB	25.9±0.9aB
June 1	20.6±0.7bA	21.5±1.1bA	27.3±1.2abB	24.7±0.5aC
August 1	20.6±0.5bA	20.5±1.1bA	25.2±0.2bB	24.2±0.5aB

F(treatment x time)=3.08
Pr > F = 0.0077
LSD (0.05)=2.2
Numbers followed by same lower case letters are not significantly different ($P<0.05$) between dates for each treatment;
Numbers followed by same upper case letters are not significantly different ($P<0.05$) between treatments for each date.

Table 4. Toatl leaf nitrogen per unit dry weight (mg/g) in *Stipa thurberiana* Piper. through the growing season in 1987.

	Treatments			
Date	Control	Sugar	Nitrate	Ammonium
April 15	19.2±1.8aA	15.2±0.9aB	24.8±1.7aC	23.1±0.9aC
April 21	16.6±1.1abAC	14.6±0.5aAB	19.2±0.4bC	17.4±0.7bAC
June 1	13.7±0.5bA	14.5±2.0aAB	16.8±1.3bB	17.4±1.2bB
August 1	14.1±0.4bA	14.0±0.7aA	16.7±1.3bAB	19.4±0.6bB

F (treatment x time)=2.33

Pr > F =0.03

LSD (0.05)=3.05

Numbers followed by same lower case letters are not significantly different ($p<0.05$) between dates for each treatment;

Numbers followed by same upper case letters are not significantly different ($p<0.05$) between treatments for each sampling date.

early in the growing season.

In comparing the two species, ARTRW had higher leaf nitrogen content per unit dry weight than STTH within each treatment through the growing season (Fig.9,10). ARTRW exhibites an increase in leaf nitrogen through June, while STTH had highest level in April and then declined.

STTH Growth Response

In STTH, total tiller density, reproductive tiller density, and biomass were greatest in the nitrate plots and lowest in the sugar plot (Table 5). The addition of nitrate increased total tiller (70.8%) and reproductive tiller (250%) density per unit crown area, and biomass (49%) over the control treatment. There were no differences among the ammonium, sugar and control treatments for reproductive tiller density. Addition of both forms of nitrogen increased aboveground biomass. Nitrogen availability did not increase dry weight per tiller. The increase in biomass was due to an increase in tiller density and reproductive shoots.

ARTRW Growth Response

Wyoming big sagebrush initiated early spring growth during the first week of April in 1987. Addition of both forms of nitrogen increased maximum ephemeral leaf length per terminal bud in the early growing season (Fig.11).

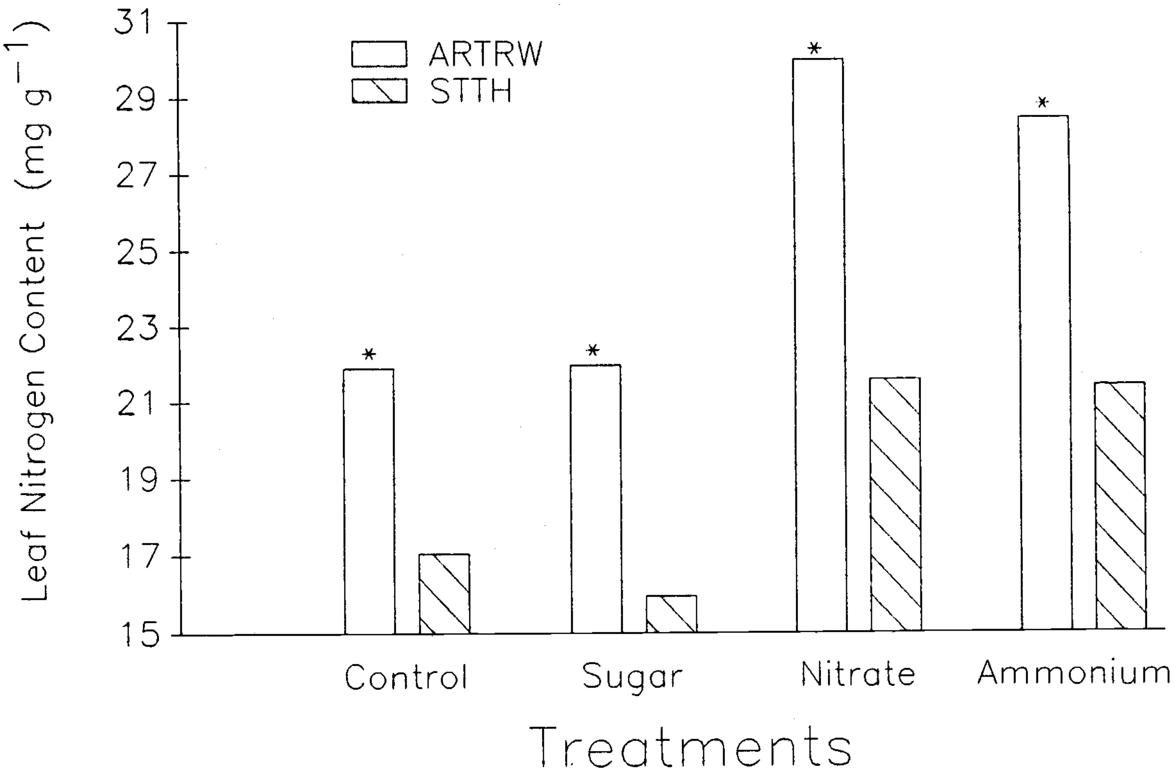

Figure 9. Main effect means of total leaf nitrogen content of Artemisia tridentata ssp. wyomingensis and Stipa thurberiana. *:significantly different ($p<0.05$) between species for each treatment. Each value is the mean of 10 samples.

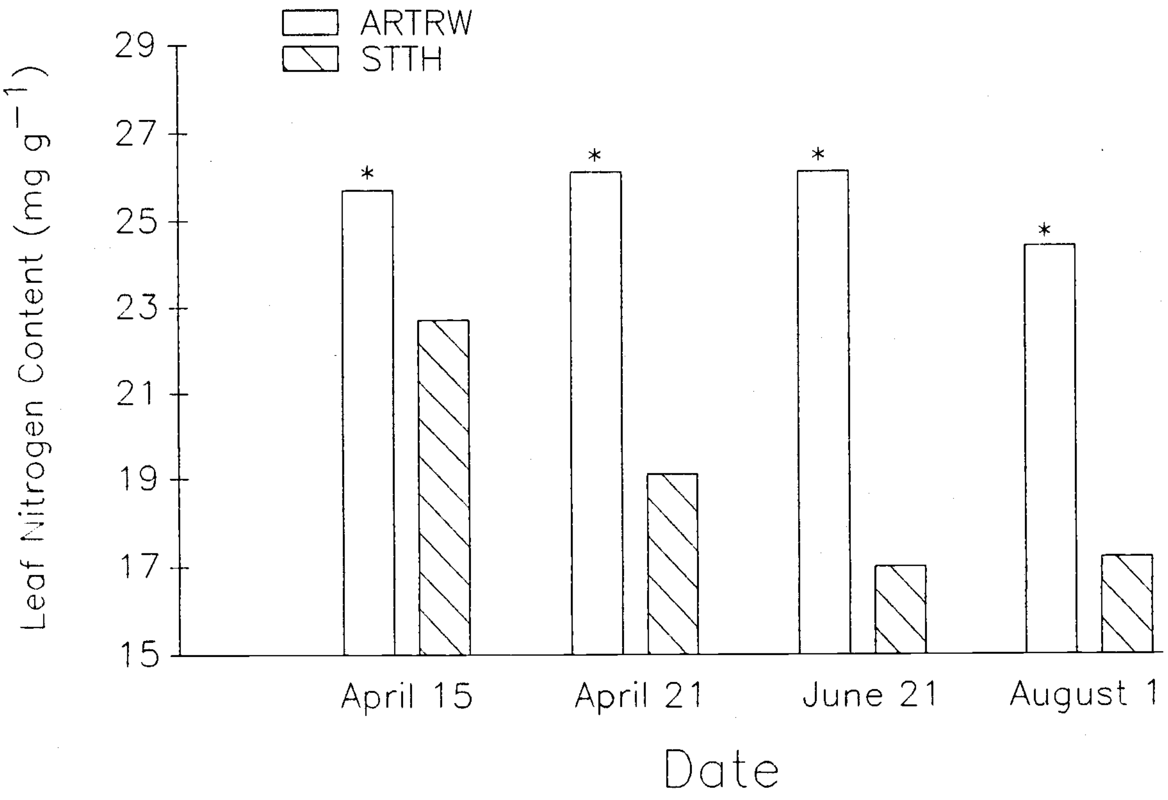

Figure 10. Main effect means of toatl leaf nitrogen content of Artemisia tridentata ssp. wyomingensis and Stipa thurberiana. *:significantly different ($p<0.05$) between species for each date. Each value is the mean of 10 samples.

Table 5. Growth performance of _Stipa_ _thurberiana_ under four nitrogen treatments on August 5, 1987.

Variables	Treatments Control	 Sugar	 Nitrate	 Ammonium	F
Biomass (g/m^2)	510a	420a	760b	710b	4.17*
Total tiller density (numbers/cm^2)	2.44ac	2.19a	4.06b	3.04c	13.46**
Reprod. tiller density (numbers/cm^2)	0.06a	0.05a	0.21b	0.10a	18.58**
Dry wt. per tiller (mg/tiller)	23.4a	24.3a	23.6a	27.3a	0.3ns

*: significantly different at $p=0.05$; **: $p=0.01$;
ns: no significantly different;
Numbers followed by same letters are not significantly different ($p<0.05$) between treatments;
Samples per treatment were 50 for each treatment.

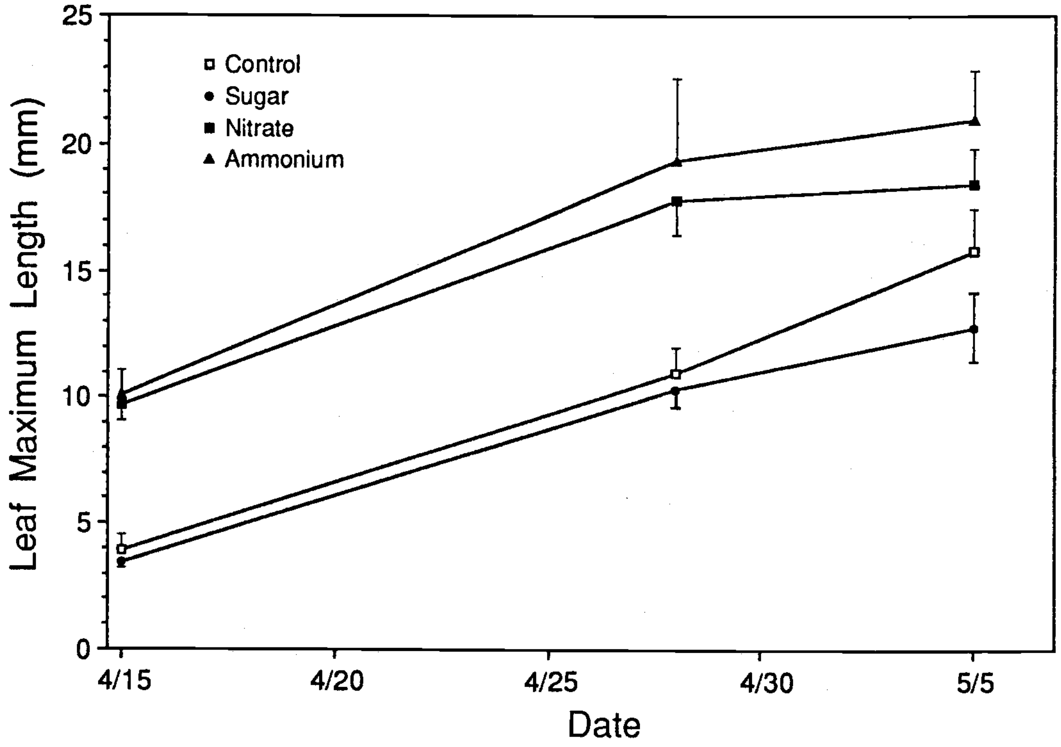

Figure 11. Ephemeral leaf maximum length of Artemisia tridentata ssp. wyomingensis during the early growing season. Each value is the mean of 25 samples for each treatment at each date.

When the older ephemeral leaves had reached full extension in early May, the smallest leaves were found in the sugar plots. Both forms of nitrogen also stimulated ARTRW ephemeral leaf numbers per terminal bud (Fig.12).

Current year's vegetative shoot length increased with the addition of both forms of nitrogen as compared to no nitrogen addition throughtout the growing season (Fig.13). Total shoot numbers per m^2 of canopy in ARTRW was increased in the nitrate and ammonium treatments as compared to sugar and control treatments on August 5, 1987. Increase in shoot density was due to many of the lateral or short shoots becoming elongated with nitrogen addition. The nitrate treatment also resulted in greatest increase in reproductive shoot numbers per m^2 of canopy as compared to the other treatments (Table 6).

Addition of ammonium increased leaf area (cm^2/shoot), leaf dry weight (g/shoot), specific leaf weight (g/m^2), shoot dry weight (g/shoot), shoot diameter (mm) and shoot length (mm) in vegetative shoots of ARTRW as compared to the sugar and control treatments. The addition of nitrate also increased leaf area, leaf dry weight, shoot dry weight, shoot diameter and shoot length in reproductive shoot comparing with other three treatments. Nitrate and ammonium increased current years production 235% and 218%, respectively as compared to the control plots. Increase in reproductive effort, based on reproductive shoot biomass

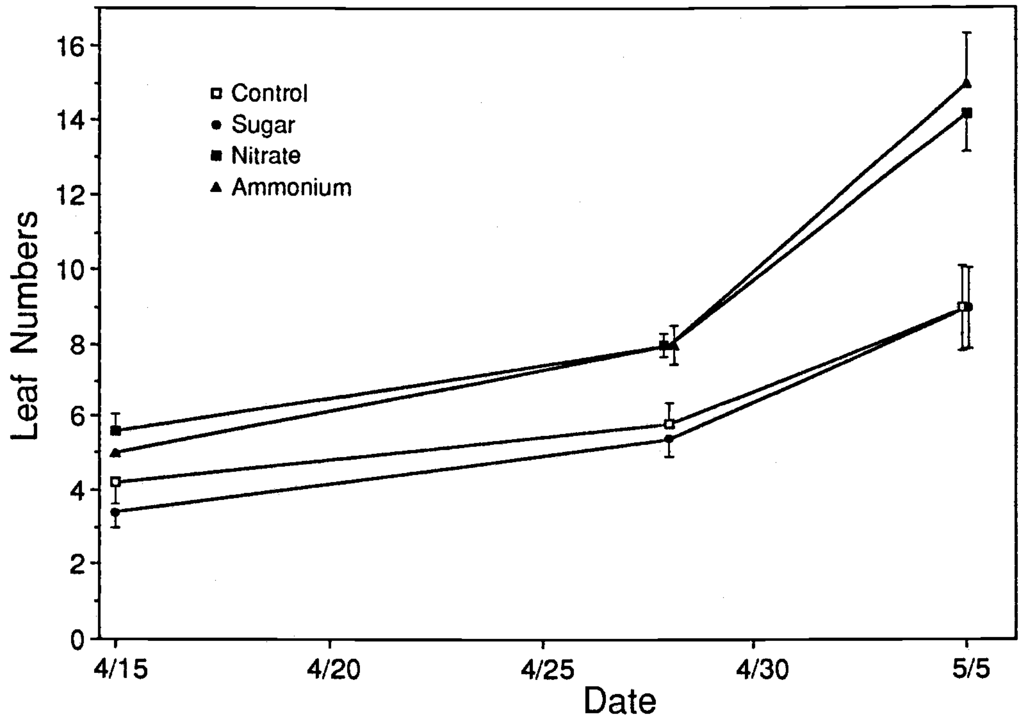

Figure 12. Ephemeral leaf numbers per terminal bud of Artemisia tridentata ssp. wyomingensis during the early growing season. Each value is the mean of 25 samples for each treatment at each date.

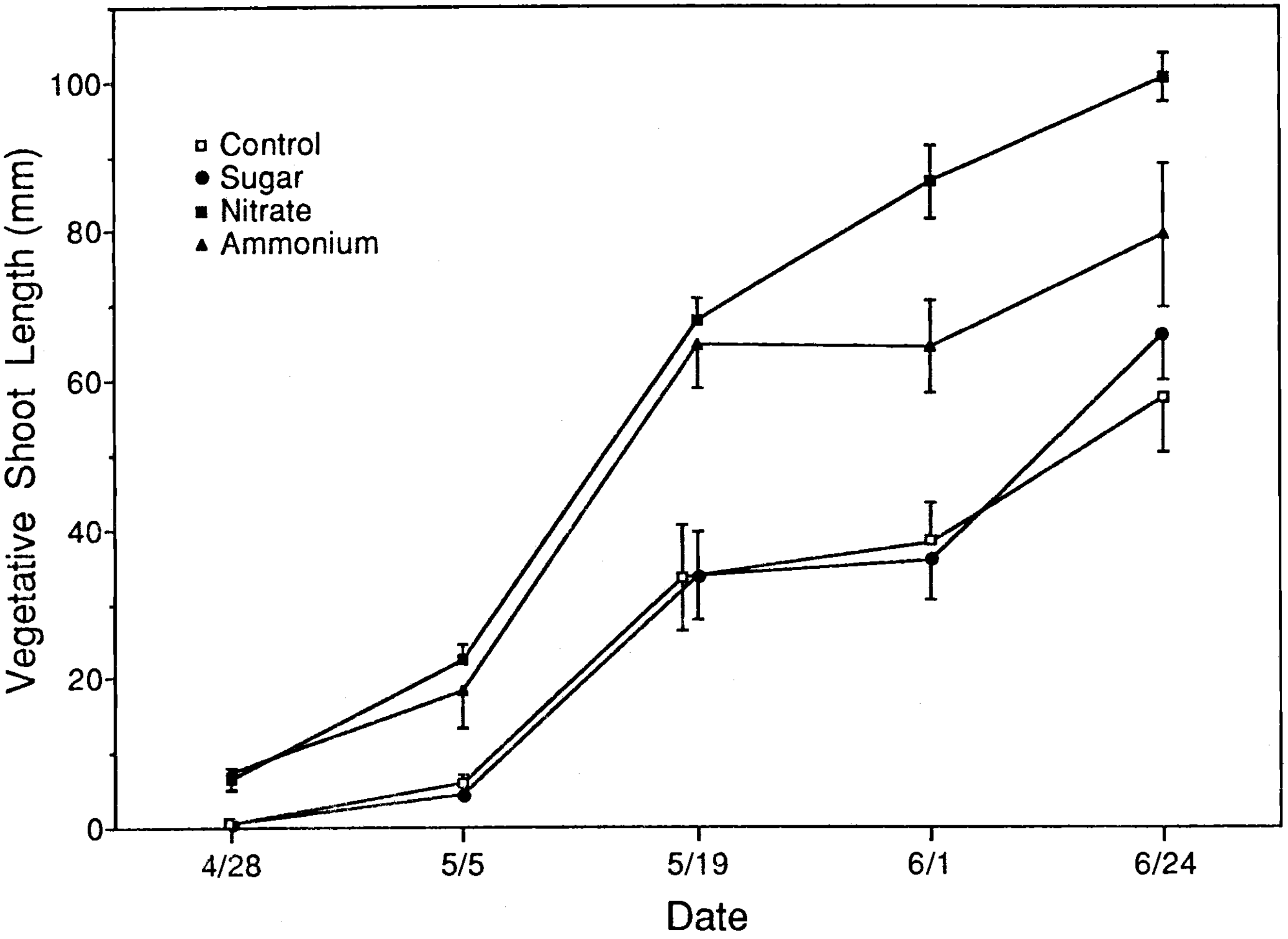

Figure 13. Effects of four different nitrogen treatments on current year vegetative shoot length of Artemisia tridentata ssp. wyomingensis. Each value is the mean of 25 samples for each treatment at each date.

Table 6. Growth performance of *Artemisia tridentata* ssp. *wyomingensis* under four nitrogen treatments on August 3, 1987.

		Treatments			
Varibles	Control	Sugar	Nitrate	Ammonium	F
Biomass (g/m^2)	199a	140a	1004b	471c	6.47**
Total shoot density ($numbers/m^2$)	870a	882a	1450b	1270b	13.1**
Reprod. shoot density ($numbers/m^2$)	387a	402a	1137b	605a	14.7**
Leaf dry wt. (g/shoot)					
Vegeta.	0.1a	0.1a	0.16ab	0.2b	5.39*
Reprod.	0.29ab	0.15a	0.7c	0.39b	8.07**
Shoot dry wt. (g/shoot)					
Vegeta.	0.04a	0.04a	0.07ab	0.1b	6.47*
Reprod.	0.05ac	0.03a	0.12b	0.06c	21.0**

*: significantly different at $p=0.05$; **: $p=0.01$;
Numbers followed by same letters are not siginificantly different ($p<0.05$) between treatments;
Samples per treatment were 50 for each treatment.

was 483% and 334% grerater in the nitrate and ammonium treatments respectively as compared to the control.

Specific Leaf Weight

Specific leaf weight (g/m^2) was different between ARTRW and STTH for each treatment through the growing season (Fig.14). Addition of nitrogen increased SLW in both species compared to the control and sugar treatments. Specific leaf weight of both species increased from the early growing season in April to late growing season in August (Fig.15). Specific leaf weights of the oldest (ARTRW in August and STTH in late July) foliage were 112 and 41% of those for the youngest (both in April) foliage for ARTRW and STTH, respectively. Therefore considerabl dry matter accumulated in the leaves as the foliage matured. Specific leaf weight sharply increased in August due to senescence of the large ephemeral leaves.

Nitrogen Uptake

Total uptake of nitrogen ($g\ N/m^2$ of leaf area) was greater in ARTRW than STTH for whole season for each treatment (Fig.16). Addition of nitrate resulted in the highest nitrogen uptake for ARTRW but not STTH which does not differ between nitrate and ammonium treatments.

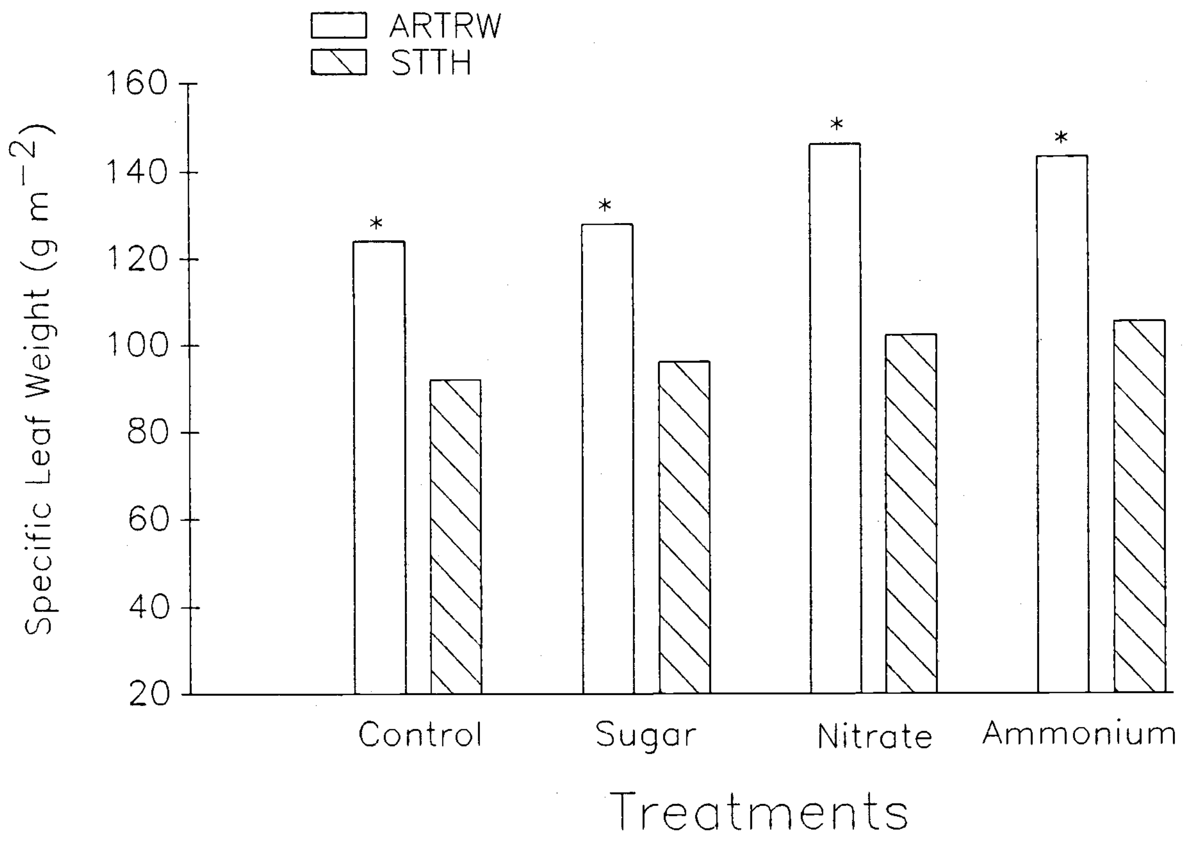

Figure 14. Specific leaf weight of Artemisia tridentata ssp. wyomingensis and Stipa thurberiana. *:significantly different ($p<0.05$) between species for each treatment. Each value is the mean of 100 samples.

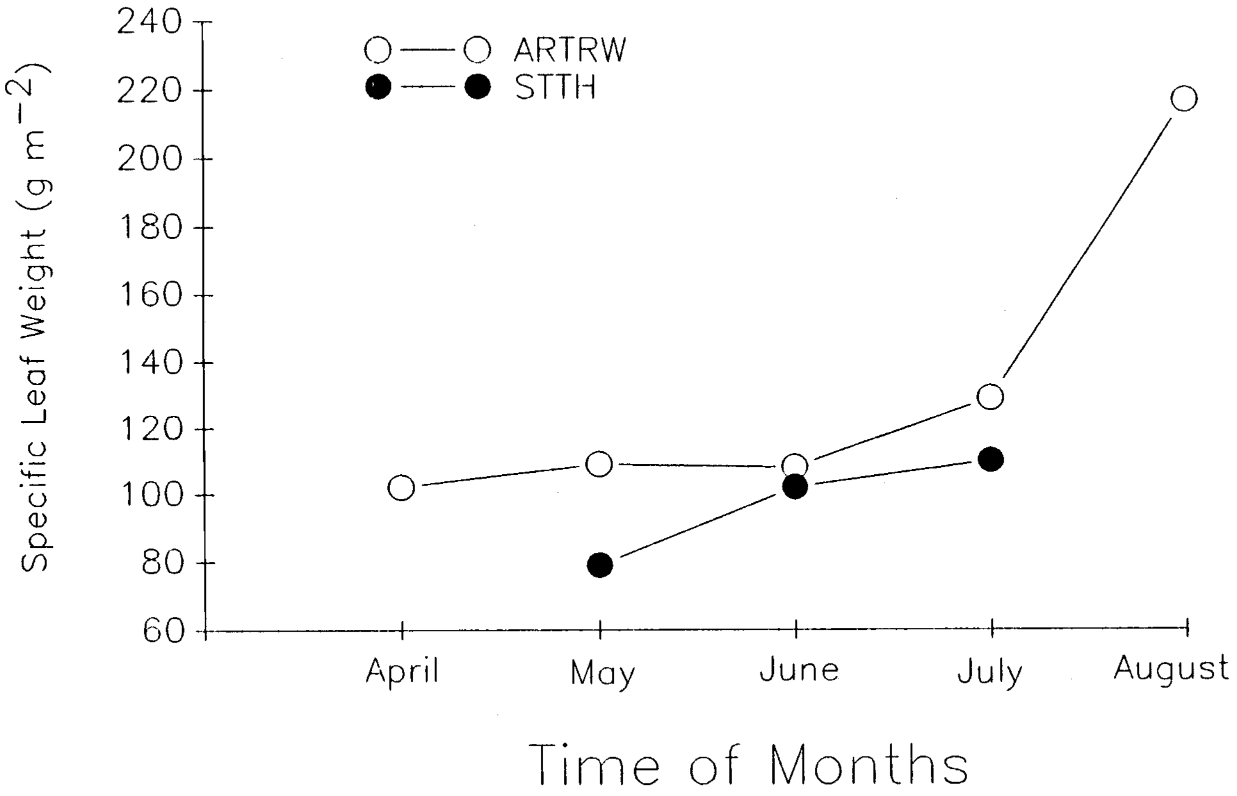

Figure 15. Seasonal specific leaf weight of *Artemisia tridentata* ssp. *wyomingensis* and *Stipa thurberiana*. Each value is the mean of 100 samples.

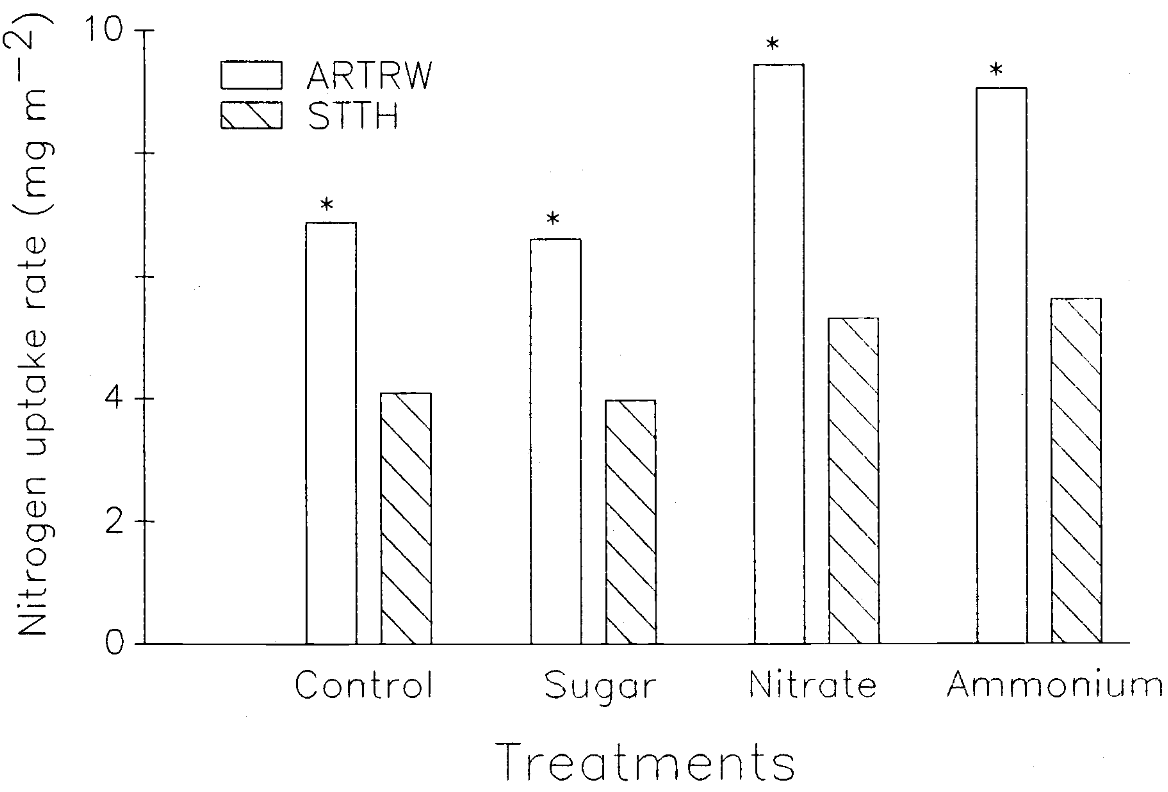

Figure 16. Total nitrogen uptake rate across date in Artemisia tridentata ssp. wyomingensis and Stipa thurberiana.

DISCUSSION AND CONCLUSIONS

Our initial hypothesis was that the availability and or forms of nitrogen in the sagebrush steppe influences the competitive balance between shrubs and perennial grasses, which is reflected by both vegetative and reproductive growth. In this study, plant species showed marked differences in growth response to the different nitrogen treatments. Both ARTRW and STTH exhibited a strong response in vegetative and reproductive growth to addition of soil nitrogen in comparison to the sugar and control treatments. If soil nitrogen was limited, increased availability should lead to increased plant productivity and aboveground biomass (Tilman 1985). Addition of both forms of nitrogen, nitrate and ammonium, stimulated growth in both ARTRW and STTH, and addition of sugar had little impact compared to control treatment on ARTRW and STTH growth. Some growth response in both species also varied with form of nitrogen applied.

Nitrate and ammonium concentrations were higher in the lower soil profile than in the upper soil profile which is probably below the primary rooting zone of STTH. STTH exhibits root systems which have been found to be fibrous in nature and extend in a vertical fashion below the crown of the plant (Doescher et al. 1984). This is in contrast to ARTRW root systems which have been shown to consist of a well-developed lateral and vertical root network (Sturges 1977). The net effect of a limited root system for STTH may be a relatively small volume of soil available for nutrient extraction. ARTRW with an extensive root system appears to be better adapted to remove soil nutrients from adjacent interspace areas and deeper in the soil profile.

In semiarid conditions, the forms and amounts of nitrogen available on a seasonal basis have not been satisfactorily documented (Wallace et al. 1978). Addition of both forms of nitrogen significantly increased nitrogen availability throughout the soil profile. Nitrate concentration especially increased at both soil profiles. Nitrate tends to be the dominant form of available nitrogen in the upper soil profile for semiarid shrublands (Charley and West 1977). I felt that application of sugar would decrease nitrogen availability in the soil by providing an increased carbon to denitrifying bacteria as an energy source (Westerman and Tucker 1978). Total nitrogen concentration of the soil would be increased while the C:N ratio decreased. Addition of sugar, however, did not appear to decrease soil nitrogen availability in our study.

Several reasons may help explain the observed response. First, simple sugar may have been oxidized quickly and utilized by microorganisms to a greater degree than less-readily decomposed plant tissues or residues. Second, if the soil had adequate native available organic carbon present, addition of sugar may have very litter effect on denitrification (McGarity 1961). Organic matter under ARTRW canopy has been shown to be high on this site (Doescher et al. 1984). This may help explain why the plant response in sugar plots was similar to control plots.

Nitrogen availability has been shown to regulate plant growth through its effects on leaf expansion. This activity has a high nitrogen requirement and is thus strongly influenced by the nitrogen content of the plant (Radin 1983). In this study addition of nitrogen significantly stimulated leaf growth and leaf numbers per terminal bud of ARTRW in the early growing season when soil water was available. Ammonium resulted in a higher response of leaf numbers and leaf growth per terminal bud than nitrate treatment in the early growing season when soil and air temperatures were low. The relative availability of ammonium may have been higher than nitrate under cold soil conditions, because ammonification is less temperature-sensitive than nitrification (Flint and Gersper

1974; Thiagalingham and Kanehiro 1973). In addition roots absorb ammonium more readily than nitrate at low temperatures (Clarkson and Warner 1979; Frota and Tucker 1972; Lycklama 1963; Sasakawa and Yamamoto 1978).

Plant competition for limited nitrogen resources play an important role in determining plant growth and plant composition (Tilman 1982, 1984). If nitrogen availability limits production, then it also may influence the outcome of competition (Tilman 1982). Based upon 1 year individual plant response, this research indicates that ARTRW may hold an advantage for nitrogen acquisition over STTH under natural conditions. Several reasons lead me to this conclusion. First, past research by Doescher et al. (1984) on the same study site and Charley and West in Utah (1975) documented an accumulation of soil nutrients including total nitrogen beneath the ARTRW canopy. Similar accumulations were not found under the canopy of STTH (Doescher et al. 1984). Under conditions of readily available soil moisture, nitrogen mineralization activity should be increased over dry soil conditions. Having soil nitrogen in close proximity to the plant would conceivably enhance the efficiency of ARTRW to capture and utilize this resource. Nutrient accumulations beneath shrub canopies may improve the competitiveness of shrubs in semiarid ecosystems (Doescher et al. 1984), by increasing plant growth rate and leaf area, especially for spring ephemeral leaves (Miller 1988; Caldwell 1978). Second, the presence of a relatively large leaf area early in the spring may be extremely important for ARTRW to take advantage of increased availability of soil water and nitrogen (Slayter 1970; Caldwell 1978; Miller 1986, 1988). These results suggested that ARTRW was more opportunistic than STTH in accumulating nitrogen. Not only did leaf nitrogen content increase in ARTRW but the pool size (leaf biomass) also increased to a greater degree than in STTH. Leaf nitrogen uptake was also enhanced to a greater extent in ARTRW than in STTH when available nitrogen was increased. For both species, the greater plant uptake of nitrogen in the fertilized treatments was probably driven by the high levels of soil nitrate that were observed in the fertilized plots.

One of the interesting results shown by both species was the difference in vegetative and reproductive response to nitrate and ammonium additions. Nitrate strongly stimulated reproductive development and ammonium increased the growth of vegetative structures. Although it has been well documented that plant species utilize nitrate and ammonium differently (Barker and Mills 1980; Haynes and Goh

1978), this difference in promoting vegetative or reproductive efforts has not been well documented. Several reasons may help to explain this observed response. First, enhanced availability and uptake of nitrate may stimulate the plant to greater production of nitrate reductase (Millard 1988). Because more carbon may be allocated to nitrate reductase synthesis, the plant may then become carbohydrate limited (Bhat 1983). A reduction in vegetative growth may then occur. Reproductive effort, however, may not be impacted by this possible mechanism. A second possible explanation fot this observation may be related to the evolutionary history of plants in the sagebrush steppe. Pertebations such as fire may cause soil nitrate content to increase. Plants may have evolved to respond to these sudden increases in nitrate by an increase in reproductive effort to ensure the survival of the species following a pertebation. The third reason is timing of nitrogen uptake may have differred between the two forms. Nitrate uptake may have been greatest in May when floral initiation was occurring.

In conclusion we suggest environmental conditions causing temporary increases in ammonium and or nitrate would drive the successional process towards an ARTRW dominated site. Although both species responded positively to increases in available nitrogen, ARTRW appeared to be more opportunistic. These results support those reported by Caldwell et al. (1985) that <u>Artemisia tridentata</u> ssp. <u>vaseyana</u> contains a greater capacity for absorbing phosphorus than adjacent native grasses. In our study leaf area, aboveground net annual primary productivity and nitrogen uptake increased in ARTRW by a greater magnitude than STTH when nitrogen availability increased. A deeper root system, ability to accumulate nutrients beneath its canopy, maintainence of winter persistent leaves for early use of soil nutrients and the development of ephemeral leaves enable the plant to capitalize on conditions causing increases in nutrient resources. Nitrogen form did not appear to favor either the shrub or grass.

LITERATURE CITED

Azcon, R., M. Gomez-Ortega, and J.M. Barea. 1982. Comparative effects of foliar-or soil-applied nitrate on vesicular-arbuscular mycorrhizal infection in maize. New Phytol. 92:553-559.

Barker, A.V. and D.N. Maynard. 1972. Cation and nitrate accumulation in pea and cucumber plants as influenced by nitrogen nutrition. J. Amer. Soc. Hort. Sci. 97:27-30.

Barker, A.V. and H.A. Mills. 1980. Ammonium and nitrate nutrition of horticultural crops. Hort. Rev. 2:395-423.

Bayoumi, M.A. 1975. Response to fertilization of big game winter range vegetation. Ph.D. Dissertation. Utah State Univ., Logan. 104pp.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. Ann. Rev. Ecol. Syst. 10:351-371.

BenZioni, A., Y. Vaaidia, and S.H. Lips. 1971. Nitrate uptake by roots as regulated by nitrase reduction products in the shoot. Physiol. Plant 24:288-290.

Bhat, K.K.S. 1983. Nutrient inflows into apple roots. Plant Soil 71:371-380.

Biggar, J.W. 1978. Spatial variability of nitrogen in soils. In:Nitrogen in the Environment. (ed.) by D.R. Nielsen and J.G. MacDonald. Vol. 1, p. 201-211. Academic Press, New York.

Binkley, D. 1985. Ion exchange resin bags: factors affecting estimates of nitrogen availability. Soil Sci. Am. J. 48:181-184.

Bloom, A.J., F.S. Chapin III, and H.A. Mooney. 1985. Resource limitation in plants-an economic analogy. Annu. Rev. Ecol. Syst. 16:363-392.

Boon-Long, P.D., D.B. Egli, and J.E. Leggett. 1983a. Effects of nitrogen stress on nitrogen redistribution and photosynthesis in soybeans. J. Sci. Soc. Thailand 9:245-256.

Boon-Long, P.D., D.B. Egli, and J.E. Leggett. 1983b. Leaf N and photosynthesis during reproductive growth in soybeans. Crop Sci. 23:617-620.

Boryslawski, Z. and B.L. Bentley. 1985. The effect of nitrogen and clipping on interference between C_3 and C_4 grasses. J. Ecol. 73:113-121.

Bowen, G.D. and S.E. Smith. 1981. The effects of mycorrhizas on nitrogen uptake by plants. In:Terrestrial Nitrogen Cycles: Processes, Ecosystem Strategies and Management Impacts. (ed.) by F.E. Clark and T. Rosswall. p.405-426. Ecological Bulletins, Stockholm.

Brady, C.J. 1973. In Chemistry and Biochemistry of Herbage, (ed.) G.W. Butler and R.W. Bailey. 2:317-351. London:Academic.

Branson, F.A., R.F. Miller, and I.S. McQueen. 1976. Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado. Ecol. 57:1104-1124.

Breteler, H. and A.L. Smit. 1974. Effect of ammonium nutrition on uptake and metabolism of nitrate in wheat. Neth. J. Agri. Sci. 22:73-81.

Caldwell, M.M. 1979. Physiology of sagebrush. pp. 74-85 in The sagebrush ecosystem: a symposium, Utah State Univ., Logan, Utah, 1978.

Caldwell, M.M., D.M. Eissenstat, J.H. Richards, and M.F. Allen. 1985. Competition for phosphorus: differential uptake from dual-isotope-labeled soil interspaces between shrub and grass. Sci. 229:384-386.

Campbell, G.S. and G.A. Harris. 1977. Water relations and water use patterns for Artemisia tridentata Nutt. in wet and dry years. Ecol. 58:652-659.

Carpenter, L.H. 1972. Middle Park deer study: range fertilization. Game Reserach Report. Part II. Colorado Div. of Wildlife, Denver.

Chapin, F.S. III, R.J. Barsdate, and D. Barel. 1978. Phosphorus cycling in Alaskan coastal tundra:A hypothesis for the regulation of nutroent cycling. Oikos 31:189-199.

Chapin, F.S., III. 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11:233-260.

Chapin, F.S., III and A.J. Bloom. 1976. Phosphate absorption: adaptation of tundra graminoids to a low temperature, low phosphorus environment. Oikos 26:111-121.

Chapin III, F.S., A.J. Bloom, C.B. Field, and R.H. Waring. 1987. Plant responses to multiple environmental factors. Biosci. 37:49-57.

Charley, J.L. and N.E. West. 1975. Plant induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Ecol. 63:945-964.

Charley, J.L. and N.E. West. 1977. Micro-patterns of nitrogen mineralizatio activity in soils of some shrub-dominated ecosystems of Utah. Soil Biol. Biochem. 9:357-366.

Clarkson, D.T. and A.J. Warner. 1979. Relationships between root temperature and the transport of ammonium and nitrate ions by Italian and perennial ryegrass *Lolium multiflorum* and *Lolium perenne*. Plant Physiol. 64:557-561.

Cook, C.W. 1965. Plant and livestock responses to fertilized rangelands. Utah Agric. Exp. Sta. Bull. 455.

Cox, D.A. and H.M. Reisenauer. 1973. Growth and ion uptake by wheat supplied nitrogen as nitrate, or ammonium, or both. Plant Soil 38:363-380.

DePuit, E.J. and M.M. Caldwell. 1973. Seasonal pattern of net photosynthesis of *Artemisia tridentata*. Amer. J. Bot. 60:426-435.

DePuit, E.J. and M.M. Caldwell. 1975. Gas exchange of three cool semi-desert species in relation to temperature and water stress. J. Ecol. 63:835-858.

Dina, S.J. and L.G. Klikoff. 1973. Effect of plant moisture stress on carbohydrates and nitrogen content of bigsagebrush. J. Range Manage. 26:207-209.

Doescher, P.S., R.F. Miller, and A.H. Winward. 1984. Soil chemical patterns under eastern Oregon plant communities dominated by big sagebrush. Soil Sci. Soc. AM. J. 48:659-663.

Edwards, J.H. and S.A. Barber. 1976a. Nitrogen uptake characteristics of corn roots at low N concentration as influenced by plant age. Agron. J. 68:17-19.

Elliott, O.M. and P.V. Nelson. 1983. Relationship among nitrogen accumulation, nitrogen assimilation and plant growth in chrysanthemums. Physiol. Plant. 57:250-259.

Ettershank, G., J.A. Ettershank, M. Bryant, and W.G. Whitford. 1978. Effects of nitrogen fertilization on primary production in a Chihuahuan Desert ecosystem. J. Arid Sci. 19:184-188.

Evans, J.R. 1983. Nitrogen and photosynthesis in the flag leaf of wheat (<u>Triticum</u> <u>aestivum</u> L.) Plant Physiol. 72:297-302.

Everett, R.L., R.O.Meewig, P.T. Tueller, and R.A. Evans. 1977. Water potential in sagebrush and shadscale communities. N.W. Sci. 51:271-281.

Farnsworth, R.B., E.M. Romney, and A. Wallace. 1978. Nitrogen fixation by microfloral-higher plant associations in arid to semiarid environments. pp. 17-19. In: West, N.E. and J. Skujins. (ed.) Nitrogen in desert ecosystems. Dowden,Hutchingson and Ross, Inc.

Field, C. and H.A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. pp. 25-55 in T.J. Givinish, (ed.) On the Economy of Plant Form and Function. Cambridge Univ. Press, Cambridge, UK.

Fischer, R.A. and N.C. Turner. 1978. Plant productivity in the arid and semiarid zones. Annu. Rev. Plant Physiol. 29:277-317.

Flint, P.S. and P.L. Gersper. 1974. Nitrogen nutrient levels inarctic tundra soils. In Holding, A.J., O.W. Heal, S.F. MacLean, Jr, P.W. Flanagan, (eds.) Soil Organisms and Decomposition in Tundra, Tundra Biome Steering Committee, Stockholm, p. 375-387.

Fowler, N. and J. Antonovices. 1981. Competition and coexistence in a North Carolina grassland. I. Patterns in undisturbed grassland. J. Ecol. 69:825-841.

Franz, E.H. and B.L. Hanies. 1977. Nitrate reductase activities of vascular plants in a terrestrial sere: relationship of nitrate to uptake and the cybernetics of biogeochemical cycles. Bulletin of the Ecological Society of America 58:62 (abstract).

Friedrich, J.W. and R.C. Hffaker. 1980. Photosynthesis, leafresistance, and ribulose-1,5-bisphosphate carboxylase degradation in senescing barly leaves. Plant Physiol. 65:1103-1107.

Frota, J.N.E. and T.C. Tucker. 1972. Temperature influence on ammonium and nitrate absorption by lettuce. Soil Sci. Soc.Am. Proc. 36:97-100.

Gardiner, W.H. 1965. Water content. p. 82-127. In: Methods of Soil Analysis, C.A. Black (ed.). Amer. Soc. Agron. Series No. 9. Madison, Wisconsin.

Goodman, G.T. and D.F. Perkins. 1968. The role of mineral nutrients in *Eriophorum* communities. III. Growth responses to added inorganic elements in two *Eriophorum vaginatum* communities. J. Ecol. 56:667-683.

Greenwood, D.J. 1978. Influence of spatial variability in soil on microbial activity, crop growth, and agronomic research. In: Nitrogen in the Environment. (ed.) by D.R. Nielsen and J.G. MacDonald. Vol. 1, p. 213-222. Academic Press, New York.

Grim, J.P. 1979. Plant Strategies and Vegetation processes. John Wiley and Sons, New York.

Grime, J.P. and R. Hunt. 1975. Relative growth rate: Its range and adaptive significance in a local flora. J. Ecol. 64:975-988.

Grundon, N.J. 1972. Mineral nutrition of some Queensland heath plants. J. Ecol. 60:171-181.

Gulmon, S.L. and C.C. Chu. 1981. The effects of light and nitrogen on photosynthesis, leaf characteristics, and dry matter allocation in the chaparral shrub, *Diplacus aurantiacus*. Oecol. 49:207-212.

Gupta, P.L. and I.H. Rorison. 1975. Seasonal differences in the availability of nutrients down a podzolic profile. J. Ecol. 63:521-534.

Haines, B.L. 1977. Nitrogen uptake: apparent pattern during old-field succession in southeastern United States. Oecol. 26:295-303.

Harper, J.L. 1977. Population Biology of Plants. Academic Press. London.

Harris, G.A. 1977. Root phenology as a factor of competition among grass seedlings. J. Range Manag. 172-177.

Haynes, R.J. and K.M. Goh. 1978. Ammonium and nitrate nutrition of plants. Biol. Rev. 53:465-510.

Helwig, J.T. and K.A. Council. 1979. (eds.). SAS User's Guide. Raleigh, NC: SAS Institute.

Hironaka, M. and E.W. Tisdale. 1963. Secondary succession in annual vegetation in southern Idhao. Ecol. 44:810-812.

Holmgren, R.C. 1956. Competition between annuals and young bitter-brush (Purshia tridentata) in Idaho. Ecol. 37:370-377.

Horneck, D.A., J.M. Hart, and K. Topper. (in press). Methods of soil analysis used in the Soil Test Lab. at Oregon State Univ.

Huffaker, R.C. and D.W. Rains. 1978. Factors influencing nitrate acquistion by plants; assimilation and fate of reduced nitrogen. p. 1-43. In: D.R. Nielsen and J.G. MacDonald (ed.) Nitrogen in the environment. Vol. 2. Academic Press, New York.

Hyder, D.N. and F.A. Sneva. 1961. Fertilization on sagebrush-bunchgrass range: a progress report. Ore. Agric. Exp. Sta. Misc. pp. 115.

Ingestad, T. 1973. Nitrogen and cation nutrition of three ecologically different plant species. Physiol. Plant. 38:29-34.

Ingestad, T. 1976. Nitrogen and cation nutrition of three ecologically different plant species. Physiol. Plant 38:29-34.

Ingestad, T. 1979. Mineral nutrient requirements of *Pinus silvestris* and *Picea abies* seedlings. Physiol. Plant 45:373-380.

Ismunadji, M. and W. Dijkshoorn. 1971. Nitrogen nutrition of rice plants measured by growth and nutrition content in pot experiments. Ionic balance and selective uptake. Neth. J. Agric. Sci. 19:223-236.

James, D.W. and J.J. Jurinak. 1978. Nitrogen fertilization of dominant plants in the northeastern great basin desert. pp. 219-231. In: West, N.E. and J. Skujins. (ed.) Nitrogen in Desert Ecosystems. Dowden, Hutchingson and Ross, Inc.

Johnson, D.W. and N.T. Edwards. 1979. The effects of stem girdling on biogeochemical cycles within a mixed deciduous forest in eastern Tennessee. II. Soil nitrogen mineralization and denitrification rates. Oecologia 40:259-271.

Kirkby, E.A. 1970. A note on the utilization of nitrate, urea, and ammonium nitrogen by *Chenopodium album*. Z. Pflanzenernaehr. Bodenkd. 117:204-209.

Kirkby, E.A. and A.H. Knight. 1977. The influence of the level of nitrate nutrition on ion uptake and assimilation, organic acid accumulation and cation-anion balance in whole tomatoplants. Plant Physiol. 60:349-353.

Klubek, B., P.J. Eberhardt, and J. Skujins. 1978. Ammonia volatilization from great basin desert soils. pp. 107-129. In: West, N.E. and J. Skujins. (ed.) Nitrogen in Desert Ecosystems. Dowden, Hutchingson and Ross, Inc.

Krajina, V.J., S. Madoc-Jones., and G. Mellor. 1973. Ammonium and nitrate in the nitrogen economy of some conifers growing inDouglas-fir communities of the Pacific northwest of America. Soil Biol. Biochem. 5:143-147.

Kramer, P.J. 1942. Species differences with respect to water absorption at low soil temperatures. Am. J. Bot. 29:828-832.

Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of Woody Plants. Academic Press.

Lancaster, D.L. 1976. Ecological significance of nitrate uptake and reduction by three annual grass species. Ph.D. Thesis. Univ. of California, Davis. (Diss. Abstr. No. 77-6347).

Lee, J.A. and G.R. Stewart. 1978. Ecological aspects of nitrogen assimilation. Adv. Bot. Res. 6:1-43.

Lee, J.A., R. Harmer, and R. Ignaciuk. 1983. Nitrogen as a limiting factor in plant communities. Nitrogen as an Ecological Factor (Ed. by J. A. Lee, S. Mcneill, and I. H. Rorison). p. 95-112. Blackwell Scientific Publications, Oxford.

Lentz, R.D. and G.H. Simonson. 1986. A detailed soils inventory and associated vegetation of Squaw Butte Range Experiment Station. Oregon State Univ. Agr. Exp. Sta. Spec. Rep. 760.

Loneragan, J.F. and C.J. Asher. 1967. Response of plants to phosphate concentration in solution culture: II. Rate of phosphate absorption and its relation to growth. Soil Sci. 103:311-318.

Lycklama, J.C. 1963. The absorption of ammonium and nitrate by perennial ryegrass. Acta Bot. Neerl 12:361-423.

Makino, A., T. Mae, and K. Ohira. 1984. Effect of nitrogen, phosphorus or potassium on the photosynthetic rate and ribulose-1,5-bisphosphate carboxylase content in rice leaves during expansion. Soil Sci. Plant Nutr. 30:63-70.

Matsumoto, H. and K. Tamura. 1981. Respiratory stress in cucumber roots treated with ammonium or nitrate nitrogen. Plant Soil 60:195-204.

McGraph, S.P. and I.H. Rorison. 1982. The influence of nitrogen source on the tolerance of _Holcus_ _lanatus_ L. and _Bromus_ _erectus_ Huds. to manganese. New Phytol. 91:443-452.

McKee, H.S. 1962. Nitrogen Metabolism in Plants. Oxford Univ. Press, London and New York. 728p.

Michael, G., P. Martin, and I. Owassia. 1970. The uptake of ammonium and nitrate from labelled ammonium nitrate in relation to the carbohydrate supply of the roots. P. 22-29. In: E.A. Kirkby. ed. Nitrogen nutrition of the plant. The university of Leeds Agric. Chem. Symp. The Univ. of Leeds, England.

Miller, R.F., P.S. Doescher, T. Svejcar, and M.R. Haferkamp. 1985. Growth and internal water status of three subspecies of Artemisia tridentata. pp. 347-352 in E.D. McArthur and B.L. Welch, eds., Symposium on the biology of Artemisia and Chrysothamnus. Gen. Tech. Rep. INT-200. Ogden, Utah.

Miller, R.F. and L.M. Shultz. 1987. Development and longevity of ephemeral and perennial leaves on Artemisia tridentata Nutt. ssp. wyomingensis. Great Basin Nat. 47:227-230.

Miller, R.F. and L.M. Shultz. 1987. Seasonal and diurnal water relations and growth of Juniperus occidentalis in the Great Basin of eastern Oregon. For. Sci. 33:690-706.

Miller, R.F. 1988. Comparison of water use by Artemisia tridentata ssp. wyomingensis and Chrysothamnus viscidiflorus ssp. viscidiflorus. J. Range. Manage. 41:58-62.

Mills, H.A. and J.B. Jones. 1979. Nutrient deficiencies and toxicities in plants:Nitrogen. J. Plant Nutr. 1:101-122.

Minotti, P.L., D.C. Williams, and W.A. Jackson. 1969. Nitrate uptake in wheat as influenced by ammonium and other cations. Crop Sci. 9:9-14.

Monk, C.D. 1966. An ecological significance of evergreenness. Ecol. 47:504-505.

Monson, R.K. and S.R. Szarek. 1979. Ecophysiological studies of Sonoran Desert plants. V. Photosynthetic adaptations of Machaeranthera gracilis, a winter annual. Oecol. (Berl.) 41:317-327.

Mooney, H.A. and S.L. Gulmon. 1979. Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. pp. 316-337 in O.T. Solbrig, S. Jain, G.B. Johnson, and P.H. Raven, eds. Topics in Plant Population Biology. Columbia Univ. Press, New York.

Moore, R.T., R.S. White, and M.M. Caldwell. 1972. Transpiration of Atriplex confertifolia and Eurotia lanata in relation to soil-plant and atmospheric moisture stress. Can. J. Bot. 50:2411-2418.

Murata, Y. 1969. Physiological response to nitrogen in plants. p. 235-259. In: J.D. Eastin, F.A. Haskins, C.Y. Sullivan, and C.H.M. Van Bavel (Eds.). Physiological Aspects of CropYield. Ame. Soc. Agron. 396p.

Natr, L. 1975. In Photosynthesis and Productivity in Different Emvironments, (ed.). J.P. Cooper, p. 537-555. Cambridge:Cambridge Univ. Press.

Nelson, L.E. and R. Selby. 1974. The effect of nitrogen sources and iron levels on the growth and composition of sitka spruce, and scots pine. Plant Soil 41:573-588.

Neter, J. and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin Inc., Illinois. 816p.

Nishita, N. and R.M. Haug. 1973. Distribution of different forms of nitrogen in some desert soils. Soil Sci. 116:51-58.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Syst. 4:25-51.

Nye, P.H. 1977. The rate-limiting step in plant nutrient absorption from soil. Soil Sci. 123:292-297.

Nye, P.H. 1981. Changes of pH across the rhizosphere induced by roots. Plant Soil 61:7-26.

Nye, P.H. and P.B. Tinker. 1977. Solute Movements in the Soil-Root system. Berkeley, Calif:Univ. California Press. 342 pp.

Pastor, J., J.D. Aber, and C.A. McClaugherty. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on blackhawk island, wisconsin. Ecol. 65:256-268.

Patterson, J.K. and V.E. Youngman. 1960. Can fertilizers increase our rangeland production. J. range Manage. 13:255-257.

Pearson, C.T. and B.T. Steer. 1977. Daily changes in nitrate uptake and metabolism in Capsicum annuum. Planta 137:107-112.

Power, J.F. 1980. Response of semiarid grassland sites to nitrogen fertilization: I. Plant growth and water use. Soil Sci. Soc. Am. J. 44:545-550.

Puritch, G.S. and A.V. Barker. 1967. Structure and function of tomato leaf chloroplasts during ammonium toxicity. Plant Physiol. 42:1229-1238.

Radin, J.W. 1981. Water relations of cotton plants under nitrogen deficiency. IV. Leaf senescence during drought and its relation to stomatal closure. Physiol. Plant 51:118-134.

Radin, J.W. 1983. Control of plant growth by nitrogen: differences between cereals and broadleaf species. Plant Cell Environ. 6:65-68.

Radin, J.W. and J.S. Boyer. 1982. Control of leaf expansion by nitrogen nutrition in sunflower plants: role of hydraulic conductivity and turgor. Plant Physiol. 69:771-775.

Radin, J.W. and L.L. Parker. 1979. Water relations of cotton plants under nitrogen deficiency. I. Dependence upon leafstructure. Plant Physiol. 64:495-498.

Raven, J.A. and Smith, F.A. 1976. Nitrogen assimilation and transport in vascular land plants in relation to intracellular pH regulation. New Phytol. 76:415-431.

Robinson, D. and I.H. Rorison. 1983. A comparison of the responses of Lolium perenne L., Holcus lanatus L., and Deschampsia flexuosa (L.) Trin. to a localized supply ofnitrogen. New Phytol. 94:263-273.

Rogers, R.S. 1983. Annual variability in community organization of forest herbs:effect of an extremely warm and dry early spring. Ecol. 64:1086-1091.

Romney, E.M., A. Wallace, and R.B. Hunter. 1978. Plant response to nitrogen fertilization in the northern mohave desert and its relationship to water manipulation. pp. 232-243. In:West, N.E. and J. Skujins. (ed.) Nitrogen in Desert Ecosystems. Dowden, Hutchingson and Ross, Inc.

Rorison, I.H. 1980. The effects of soil acidity on nutrient availability and plant response. In: Effects of Acid Precipitation on Terrestrial Ecosystems. (ed.) by T.C. Hutchinson and M. Havas. p. 283-304. Plenum, New York.

Rumburg, C.B. 1969. Yield and N concentration of meadow hay fertilized with three N sources. Agron. J. 61:824-825.

Rumburg, C.B. 1972. Yield and N accumulation of meadow forage fertilized at advancing maturity with N. Agron. J. 64:187-189.

Ryle, G.J.A. and J.D. Hesketh. 1969. Carbon dioxide uptake in nitrogen-deficient plants. Crop Sci. 9:451-454.

Sasakawa, H. and Y. Yamamoto. 1978. Comparison of the uptake of nitrate and ammonium by rice seedlings. Plant Physiol. 62:665-669.

Schmisseur, E. and R.F. Miller. 1978. Economics of range fertilization in eastern Oregon. Circular of Infor. 673. p. 1-49. Agric. Experi. Station, Oregon State Univ. Corvallis.

Scholander, P.F., H.T. Hammel., E. D. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. Sci. 148:339-346.

Skujins, J. and P. Trujillo Y. Fulgham. 1978. Nitrification in great basin desert soils. pp. 60-74. In: West, N.E. and J. Skujins. (ed.) Nitrogen in desert ecosystems. Dowden, Hutchingson and Ross, Inc.

Sneva, F.A. 1973a. Crested wheatgrass response to nitrogen and clipping. J. Range Manage. 26:47-50.

Sneva, F.A. 1973b. Wheatgrass response to seasonal applications of two nitrogen sources. J. Range Manage. 26:137-139.

Sneva, F.A. 1973c. Nitrogen and paraquat saves range forage for fallgrazing. J. Range Manage. 26:294-295.

Steel, R.D.G. and J.H. Torrie. 1980. Principles and procedures of statistics. A biometrical approach. 2nd ed. McGraw-Hill, Inc., Hightstown, NJ.

Steer, B.T. and P.J. Hocking. 1983. Leaf and floret production in sunflower (Helianthus annuus L.) as affected by nitrogen supply. Ann. Bot. 52:267-277.

Sturges, D.L. 1973. Soil moisture response to spraying big sagebrush the year of treatment. J. Range Manage. 26:444-447.

Sturges, D.L. 1977. Soil water withdrawal and root characteristics of big sagebrush. Amer. Midl. Nat. 98:257-273.

Ta, T.C. and K. Ohira. 1981. Effects of various environmental and medium conditions on the response of Indica and Japonica rice plants to ammonium and nitrate nitrogen. Soil Sci. Plant Nutr. (Tokyo) 27:347-355.

Taylor, A.A. and D.C. Havill. 1981. The effect of inorganic nitrogen on the major enzymes of ammonia assimilation in grassland plants. New Phytol. 87:53-62.

Taylor, A.A., J. De-Felice., and D.C. Havill. 1982. Seasonal variation in nitrogen availability and utilization in an acidic and calcareous soil. New Phytol. 92:141-152.

Thiagalingham, K. and Y. Kanehiro. 1973. Effect of temperature on nitrogen transformation in Hawaiian soils. Plant Soil 38:177-189.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ.

Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. Ecol. 65:1445-1453.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125:827-852.

Tisdale, E.W., Hironaka, M., and M.A. Fosberg. 1969. The sagebrush region in Idaho-problem in range resource management. Ida. Agric. Exper. Stn. Bull. 512:15pp.

Tisdale, E.W. and M. Hironaka. 1981. The sagebrush-grass region: A review of the ecological literature. Forest, Wildlife and Range Experimental Station, Univ. of Idaho. No. 209.

Trolldenier, G. and W. von Rheinbaben. 1981a. Root respiration and bacterial population of roots. I. Effect of nitrogen source, potassium nutrition and aeration of roots. Z. Pflanzenernaehr. Bodenkd. 144:366-371.

Uchida, N., Y. Wada, and Y. Murata. 1982. Studies on the changes in the photosynthetic activity of a crop leaf during its development and senescence. II. Effect of nitrogen deficiency on the changes in the senescing leaf of rice. Jpn. J. Crop Sci. 51:577-588.

Van de Dijk, S.J., L. Lanting, H. Lambers, F. Posthumus, I. Stulen, and R. Hofstra. 1982. Kinetics of nitrate uptake by different species from nutrient-rich and nutrient-poor habitats as affected by the nutrient supply. Physiol. Plant 55:103-110.

Van Egmond, F. 1978. Nitrogen nutritional aspects of the ionic balance of plants. In:Nitrogen in the Environment. (ed.) by D.R. Nielsen and J.G. MacDonald. Vol. 2, p. 171-189. Academic Press, New York.

Walker, J. M. 1969. One-degree increments in soil temperatures affect maize seedling behavior. Soil Sci. Soc. Am. Proc. 33:729-736.

Wallace, A. 1971. The competitive chelation hypothesis of lime-induced chlorosis. In: Regulation of the Micro-Nutrient Status of Plants by Chelating Agents and other Factors. (ed.) by A. Wallace. p. 230-239. Los Angeles, California.

Wallace, A. and R.T. Muller. 1957. Ammonium and nitrate nitrogen absorption from sand culture by rough lemon cuttings. Proc. Am. Soc. Hortic. Sci. 69:183-188.

Wallace, A., A.M. Abou-Zamzam, and E. Motoyama. 1971. Cation and anion balance in the xylem exudate of tobacco roots. Plant Soil 35:433-438.

Wallace, A., E.M. Romney, G.E. Kleinkopf, and S.M. Soufi. 1978. Uptake of mineral forms of nitrogen by desert plants. pp. 130-151. In: West, N.E. and J. Skujins. (ed.) Nitrogen in Desert Ecosystems. Dowden, Hutchingson and Ross, Inc.

Waring, R.H. 1982. Coupling stress physiology with ecosystem analysis. In Carbon uptake and allocation in subalpine ecosystems as a key to management. R.H. Waring (ed). Forest Research Laboratory, Oregon State Univ., Corvallis, OR. pp. 5-8.

Waring, R.H. and B.D. Cleary. 1967. Plant moisture stress: Evaluation by pressure bomb. Sci. 155:1252-1254.

Waring, R.H., A.J.S. McDonald, S. Larsson, T. Ericsson, A. Wiren, E. Arwidsson, A. Ericsson, and T. Lohammar. 1985. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. Oecol. (Berlin). 66:157-160.

Warncke, D.D. and S.A. Barber. 1973. Ammonium and nitrate uptake by corn (Zea mays L.) as influenced by nitrogen concentration and NH_4/NO_3 ratio. Agron. J. 65:950-953.

Weissman, G.S. 1950. Growth and nitrogen absorption of wheat seedling as influenced by ammonium: Nitrate ratio and the hydrogen ion concentration. Am. J. Bot. 37:725-738.

Welden, C.W. and C.W. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quart. Rev. Biol. 61:23-44.

Welkie, G.W. and M.M. Caldwell. 1970. Leaf anatomy of species in some dicotyledon families as related to the C_3 and C_4 pathways of carbon fixation. Can.J. Bot. 48:2135-46.

West, N.E. and J. Skujins. (ed.) 1978. Nitrogen in deaert ecosystems. Dowden, Hutchinson, and Ross, Stroudsburg, Pa, 307 pp.

West, N.E. and J.O. Klemmedson. 1978. Structural distribution of nitrogen in desert ecosystem. pp. 1-16. In: West, N.E. and J. Skujins (ed.). Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc.

West, N.E. and J. Skujins. 1978. Summary, conclusions and suggestions for further research. pp. 244-253. In: West, N.E. and J. Skujins (ed.). Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc.

Westerman, R.L. and T.C. Tucker. 1978. Denitrification in desert soils. pp. 75-106. In: West, N.E. and J. Skujins. (ed.) Nitrogen in Desert Ecosystems. Dowden, Hutchingson and Ross, Inc.

Willhite, F.M., H.K. Rouse, and D.E. Miller. 1955. High altitude meadows in Colorado. 3. The effect of nitrogen fertilization on crude protein production. Agron. J. 47:117-121.

Williams, D.E. and J. Vlamis. 1962. Differential cation and anion absorption as affected by climate. Plant Physiol. 37:198-202.

Williams, G.J. and J.L. Markley. 1973. The photosynthetic pathway type of north American shortgrass prairie species and some ecological implications. Photosynthetica. 7:262-70.

Wilson, A.M., G.A. Harris, and D.H. Gates. 1966. Fertilization of mixed cheatgrass-bluebunch wheatgrass stands. J. Range Manage. 19:134-134.

Winward, A.H. 1970. Taxonomic and ecological relationships of the big sagebrush complex in Idaho. Ph.D. Diss. Univ. of Idaho, Moscow. Univ. Microfilms. Ann Arbor, MI(Diss. Abstr. 31(B):3791B-3792B).

Wittenbach, V.A., R.C.Ackerson, R.T. Giaquinta, and R.R. Herbert. 1980. Changes in photosynthesis, ribulose bisphosphate carboxylase, proteolytic activity and ultrastructure of soybean leaves during senescence. Crop Sci. 20:225-231.

White, R.E. 1972. Studies on mineral ion absorption by plants. I. The absorption and utilization of phosphates by Stylosanthes humilis, Phaseolus atropurpureus and Desmodium intortum. Plant Soil 36:427-447.

White, R.E. 1973. Studies on mineral ion absorption by plants. II. The interaction between metabolic activity and the rate of phosphorus absorption. Plant Soil 38:509-523.

Youngdahl, L.J., R. Pacheco, J.J. Street, and P.L.G. Vlek. 1982. The kinetics of ammonium and nitrate uptake by young rice plants. Plant Soil 69:225-232.

APPENDICES

APPENDIX A

A-1. ANOVA of plant water potentials of *Artemisia tridentata* ssp. *wyomingensis* in predawn

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	0.41	0.14	3.58	0.056
TrtxRep+Rep	16	0.628	0.039		
Time	2	3.35	1.67	23.22	0.0005
TimexRep	8	0.58	0.07		
TrtxTime	6	0.58	0.096	2.44	0.0554
TrtxTimexRep	24	0.947	0.039		
Total	59	6.49			

d.f.: degree of freedom
S.S.: sum of squares
M.S.: mean squares
Trt: treatments
Rep: replications

A-2. ANOVA of plant water potentials of *Artemisia tridentata* ssp. *wyomingensis* in midday

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	0.07	0.024	1.20	0.1376
TrtxRep+Rep	16	0.25	0.02		
Time	1	2.28	2.28	295.39	0.0001
TimexRep	4	0.03	0.007		
TrtxTime	3	0.31	0.102	7.59	0.0042
TrtxTimexRep	12	0.16	0.013		
Total	39	3.099			

A-3. ANOVA of nitrate concentration (ug/g) in the upper soil profile (0-20 cm)

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	835.18	278.39	34.07	0.0001
TrtxRep+Rep	16	130.76	8.17		
Time	2	83.79	41.89	5.60	0.0302
Time+Rep	8	59.88	7.48		
TrtxTime	6	82.46	13.74	1.79	0.1443
TrtxTimexRep	24	184.49	7.69		
Total	59	1376.56			

A-4. ANOVA of nitrate concentration (ug/g) in the lower soil profile (20-40 cm)

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	1409.68	469.89	56.14	0.0001
TrtxRep+Rep	16	133.87	8.37		
Time	2	80.82	40.41	10.34	0.0001
TimexRep	8	31.26	3.91		
TrtxTime	6	399.03	66.50	21.68	0.0001
TrtxTimexRep	24	73.64	3.07		
Total	59	2128.29			

A-5. ANOVA of ammonium concentration (ug/g) in the upper soil profile (0-20 cm)

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	28.29	9.43	2.91	0.102
TrtxRep+Rep	16	51.91	3.24		
Time	2	255.23	127.62	21.48	0.0006
TimexRep	8	47.54	5.94		
TrtxTime	6	47.65	7.94	1.57	0.1986
TrtxTimexRep	24	121.28	5.05		
Total	59	551.91			

A-6. ANOVA of ammonium concentration (ug/g) in the lower soil profile (20-40 cm)

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	323.07	107.69	7.09	0.007
TrtxRep+Rep	16	242.90	15.18		
Time	2	489.34	244.67	18.86	0.0009
TimexRep	8	103.76	12.97		
TrtxTime	6	53.35	8.89	0.69	0.6579
TrtxTimexRep	24	308.17	12.84		
Total	59	1520.59			

A-7. ANOVA of total leaf nitrogen content (mg/g) of *Artemisia tridentata* ssp. *wyomingensis*

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	852.47	284.16	63.86	0.0001
TrtxRep+Rep	16	71.15	4.45		
Time	3	14.56	4.85	0.92	0.4607
TimexRep	12	63.31	5.28		
TrtxTime	9	81.18	9.02	3.08	0.0077
TrtxTimexRep	36	105.53	2.93		
Total	79	1188.19			

A-8. ANOVA of total leaf nitrogen content (mg/g) of *Stipa thurberiana*

Source	d.f.	S.S	M.S.	F	Pr>F
Trt	3	358.84	119.61	15.97	0.0001
TrtxRep+Rep	16	119.97	7.49		
Time	3	302.23	100.74	10.92	0.001
TimexRep	12	110.66	9.22		
TrtxTime	9	118.88	13.21	2.33	0.0348
TrtxTimexRep	36	204.06	5.67		
Total	79	1214.63			

A-9. ANOVA of biomass of <u>Stipa</u> <u>thurberiana</u>
on August 5, 1987

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	748670.02	249556.67	4.17	0.0124
Error	36	2154477.28	59846.59		
Total	39	2903147.31			

A-10. ANOVA of dry weight per tiller of *Stipa thurberiana* on August 5, 1987

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	0.000098	0.000033	0.30	0.8268
Error	36	0.0039	0.00011		
Total	39	0.0041			

A-11. ANOVA of total tiller density (numbers/cm^2) of *Stipa thurberiana* on August 5, 1987

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	103.91	34.64	13.46	0.0001
Error	196	504.53	2.57		
Total	199	608.44			

A-12. ANOVA of reproductive tiller density (numbers/cm^2) of <u>Stipa</u> <u>thurberiana</u> on August 5, 1987

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	0.811	0.27	18.58	0.0001
Error	196	2.85	0.015		
Total	199	3.66			

A-13. ANOVA of total shoot density (numbers/m^2) of
Artemisia tridentata ssp. *wyomingensis*
on August 5, 1987

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	2502921.8	834307.3	13.1	0.0001
Error	36	2293312.5	63703.1		
Total	39	4796234.3			

A-14. ANOVA of reproductive shoot density (numbers/m^2) of *Artemisia tridentata* ssp. *wyomingensis* on August 5, 1987

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	3687046.8	1229015.6	14.68	0.0001
Error	36	3014687.5	83741.3		
Total	39	6701734.4			

A-15. ANOVA of ephemeral leaf maximum length (mm) of *Artemisia tridentata* ssp. *wyomingensis*

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	664.62	221.54	14.84	0.0002
TrtxRep+Rep	16	238.91	14.93		
Time	2	1138.32	569.16	56.99	0.0001
TimexRep	8	79.89	9.98		
TrtxTime	6	32.57	5.43	0.69	0.6567
TrtxTimexRep	24	187.72	7.82		
Total	59	2342.04			

A-16. ANOVA of ephemeral leaf numbers per terminal bud of *Artemisia tridentata* ssp. *wyomingensis*

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	151.65	50.55	13.96	0.0003
TrtxRep+Rep	16	57.87	3.62		
Time	2	550.83	275.42	54.63	0.0001
TimexRep	8	40.33	5.04		
TrtxTime	6	49.70	8.28	4.54	0.0033
TrtxTimexRep	24	43.80	1.83		
Total	59	894.18			

A-17. ANOVA of current year's vegetative shoot length (mm) of *Artemisia tridentata* ssp. *wyomingensis*

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	15862.36	5287.45	27.96	0.0001
TrtxRep+Rep	16	3026.31	189.14		
Time	4	73900.82	18475.2	101.24	0.0001
TimexRep	16	2919.84	182.49		
TrtxTime	12	5076.15	423.01	5.51	0.0001
TrtxTimexRep	48	3686.24	76.79		
Total	99	104471.73			

A-18. ANOVA of leaf area (cm^2) per current year's vegetative shoot of *Artemisia tridentata* ssp. *wyomingensis* on August 3, 1987

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	169.53	56.51	3.42	0.0327
Error	25	413.43	16.54		
Total	28	582.96			

A-19. ANOVA of leaf area (cm^2) per current year's reproductive shoot of *Artemisia tridentata* ssp. *wyomingensis* on August 3, 1987

Source	d.f.	S.S.	M.S.	F	Pr>F
Trt	3	2334.42	778.14	10.00	0.0001
Error	62	4822.35	77.78		
Total	65	7156.78			

APPENDIX B

B-1. Response of vegetative shoot of *Artemisia tridentata* ssp. *wyomingensis* to four nitrogen treatments on August 3, 1987

	Treatments				
Response	Control	Sugar	Nitrate	Ammonium	F
Leaf area (cm^2/shoot)	6.5a	7.7a	10.8ab	12.4b	3.42*
Leaf dry wt. (g/shoot)	0.1a	0.1a	0.16ab	0.2b	5.39**
SLW (g/m^2)	140ab	137a	157bc	169c	4.61*
Shoot dry wt. (g/shoot)	0.04a	0.04a	0.07ab	0.1b	6.47*
Shoot diameter (mm)	0.96a	0.81a	1.1ab	1.29b	3.66*
Shoot length (mm)	43a	49ab	63bc	72c	4.77**

SLW: specific leaf weight;
*: significant difference at p=0.05; **: at p=0.01;
Samples per treatment was 25 for each response.

B-2. Response of reproductive shoot of *Artemisia tridentata* ssp. *wyomingensis* to four nitrogen treatments on August 3, 1987

Response	Treatments Control	Sugar	Nitrate	Ammonium	F
Leaf area (cm^2/shoot)	11.5ab	7.9a	24.5c	15.1b	10**
Leaf dry wt. (g/shoot)	0.29ab	0.15a	0.70c	0.39b	8.07*
SLW (g/m^2)	238a	187b	266c	245ac	5.68**
Shoot dry wt. (g/shoot)	0.05ac	0.03a	0.12b	0.06c	21**
Shoot diameter (mm)	0.84a	0.73a	1.41b	0.84a	16.5**
Shoot length (mm)	81a	60b	116c	95a	13.7**

SLW: specific leaf weight;
*: significant difference at $p=0.05$; **: at $p=0.01$;
Samples per treatment was 25 for each response.