

## EFFECTS OF NITROGEN AVAILABILITY ON GROWTH AND PHOTOSYNTHESIS OF *ARTEMISIA TRIDENTATA* SSP. *WYOMINGENSIS*

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**ABSTRACT.**—This study examined the effects of alterations in soil nitrogen on the growth of *Artemisia tridentata* ssp. *wyomingensis* Nutt. Soil nitrogen content was altered by applying sugar (45 g/m<sup>2</sup>), nitrate (4.5 g/m<sup>2</sup>), or ammonium (4.5 g/m<sup>2</sup>), and the results were compared with a control treatment (no soil amendments). Addition of either form of nitrogen significantly increased leaf nitrogen content, mean maximum length of ephemeral leaves, number of ephemeral leaves per terminal shoot, and current year's vegetative stem length over the control and sugar treatments. Both soil water and predawn xylem potentials during active growth were lower in the nitrogen-treated plots. The higher growth activity and greater leaf mass of *A. tridentata* in the nitrogen treatments may have been responsible for this result. Higher photosynthetic rates observed in the nitrogen treatments during an early June sampling period also lend support to this observation. This study suggests *A. tridentata* ssp. *wyomingensis* would opportunistically take advantage of increased availability of soil nitrogen. The ability of this species to respond positively to increased soil nitrogen may enhance its competitiveness over associated perennial species.

*Artemisia tridentata* Nutt. is a semideciduous perennial shrub occupying 44.8 million ha in the western Intermountain sagebrush-steppe. It is the most abundant shrub in this ecosystem. During the past century, increases of *A. tridentata* have been attributed to overgrazing of perennial grasses by domestic livestock, cultivation of lands too arid to produce crops, and alterations in fire frequency (Hironaka and Tisdale 1963, Tisdale et al. 1969, Tisdale and Hironaka 1981). As *A. tridentata* has increased in the Great Basin, both production and diversity of herbaceous understory species have declined. Numerous physiological and morphological characteristics of *A. tridentata* have been shown to enhance its effectiveness as a competitor with native bunchgrasses, especially for soil moisture (DePuit and Caldwell 1973, Eissenstat and Caldwell 1988, Miller and Shultz 1987, Miller 1988). Among these, the ability of *A. tridentata* to maximize leaf area early in the growing season by overwintering one-third of its leaf biomass and by developing ephemeral leaves early in the spring strongly enhances its ability to photosynthesize during favorable growth periods (DePuit and Caldwell 1973, Miller and Shultz 1987, Miller 1988). A deep, well-developed root system also allows *A. tridentata* to capture soil moisture from a soil

volume much larger than that of perennial grasses (Sturges 1977).

Relatively little research has examined the response of this species to soil nutrients such as nitrogen. Limited work, however, indicates *A. tridentata* to be an effective competitor for soil nutrients. Caldwell et al. (1985) demonstrated that this species successfully competes for soil phosphorus with the native perennial grass *Agropyron spicatum* (Pursh) Scribn. & Smith. The accumulation of nutrients and higher soil nitrogen mineralization rates in surface soils beneath *A. tridentata* canopies may also convey an ecological advantage to plants during active growth periods (Charley and West 1975, 1977, Doescher et al. 1984). Few studies, however, have evaluated the response of *A. tridentata* to increased or decreased amounts of available soil nitrogen. Carpenter (1972), working in the Colorado Plateau, reported that 134 kg N/ha applied to *A. tridentata* yielded an 81% increase in total leafy material compared with a nontreated control. However, Carpenter and West (1987) found little response to nitrogen in *A. tridentata* grown on mine spoils. The form of nitrogen, whether NH<sub>4</sub> or NO<sub>3</sub>, may also be an important factor in the mineral nutrition of aridland shrubs (Wallace et al. 1978).

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Our experiment was designed to determine how depletion or addition of different forms of nitrogen affects *A. tridentata* growth and carbon-assimilation rates. Our hypothesis was that *A. tridentata* responds favorably to increases in soil nitrogen.

#### MATERIALS AND METHODS

The study was conducted at the Squaw Butte Experimental Range in southeastern Oregon (119°43'W longitude, 43°29'N latitude), 67 km west of Burns, on the northern fringe of the Great Basin. The 37-year mean annual precipitation for this area is 284 mm. Precipitation during the 1987 crop year (September–August) was 296 mm. The Squaw Butte Experimental Range typically receives most of its moisture between October and June, generally as snow, with little precipitation received in July and August. The mean temperature in winter is  $-0.6$  C, with the daily minimum averaging  $-4.8$  C, and the mean temperature in summer is  $17.6$  C, with the daily maximum averaging  $26.8$  C. The study site is located in an *Artemisia tridentata* spp. *wyomingensis*/*Stipa thurberiana* habitat type, at an elevation of 1,372 m (Doescher et al. 1984). This site has been excluded from grazing by domestic herbivores for the past 40 years. Soil texture is gravelly fine sandy loam and classified as Xerollic Durothids (Lentz and Simonson 1986). Soils vary in depth from 35 to 45 cm and are underlain by an indurated duripan 5–20 cm thick, which is underlain by unweathered basalt. A detailed description of soil nutrient levels is provided by Doescher et al. (1984).

#### Experimental Procedures

A completely randomized plot design was used with 10 replications of each treatment. Plots  $5 \times 5$  m were laid out with an *A. tridentata* located in the center of each plot. To maximize uniformity, we selected plots that had vigorous-appearing *A. tridentata* plants of similar growth form and size. Plant measurements were recorded on the center *A. tridentata* plants, and soil measurements were collected within 1.5 m of the stem base. The remainder of the plot was used as a buffer.

Treatments were applied both in March and late November of 1986. Treatments were (1) control (no amendments added), (2) granu-

lated sugar ( $45 \text{ g/m}^2$ ), (3) ammonium— $(\text{NH}_4)_2\text{SO}_4$  (nitrogen =  $4.5 \text{ g/m}^2$ ), and (4) nitrate— $\text{HNO}_3$  (nitrogen =  $4.5 \text{ g/m}^2$ ). Sugar addition was assumed to increase the C:N ratio to decrease availability of soil nitrogen (Baath et al. 1978). Both ammonium and sugar were broadcast onto the  $5 \times 5$ -m plots. Nitrate was diluted in water (1 part  $\text{HNO}_3$  to 5 parts water) and applied with a backpack sprayer. All herbaceous plants were dormant at the time of application. Soil and plant growth measurements were recorded during the following 1987 growing season.

Soils were analyzed for ammonium and nitrate concentration in the A and B horizons in five plots per treatment on 14 April, 26 May, and 25 July. Soil analysis was performed using a KCl extracting technique (Horneck et al., in press).

Soil water content was measured from 1 April to 15 September once every two weeks in each of the A and B horizons. One soil sample was collected for each of the two depths within each plot for all treatments. Soil water was measured gravimetrically, and soil water release curves were developed for each depth to define soil water potential.

Ephemeral leaf number and maximum length, and vegetative stem elongation were measured on five randomly selected terminal branchlets of the single *Artemisia* located within each plot. Leaf measurements were recorded on three dates during initiation and expansion of ephemeral leaves (15 April to 5 May). Vegetative stem elongation was measured on five dates from initiation to termination of growth. Leaf nitrogen content was measured on current year's leaves (both ephemeral and persistent) collected from vegetative stems on 15 and 21 April, 1 June, and 1 August on all plots. Collections represented three phenological stages: initial leaf elongation, rapid leaf and stem growth, and early flowering. The Semimicro-Kjeldahl method was used to determine total leaf nitrogen content (Bremner 1965). Specific leaf weight ( $\text{g/m}^2$ ) was obtained by measuring leaf area on current year's green leaves on 12 dates during the growing season. Leaves were removed from one randomly selected terminal branch in each plot and placed in a damp cooler. Several hours later leaf area was measured on a leaf area meter, and weight was determined by oven-drying the leaves at 60 C for 48 hr.

TABLE 1. Soil nitrate and ammonium content (ppm) at soil depths of 0–20 cm and 20–40 cm.

Sampling date	Treatment			
	Control	Sugar	Nitrate	Ammonium
			<b>NO<sub>3</sub></b>	
			0–20 cm	
April 14	0.50 <sup>a</sup>	0.48 <sup>a</sup>	12.42 <sup>b</sup>	1.20 <sup>a</sup>
May 26	1.16 <sup>a</sup>	1.14 <sup>a</sup>	6.84 <sup>a</sup>	1.16 <sup>a</sup>
July 25	1.82 <sup>a</sup>	3.28 <sup>a</sup>	11.64 <sup>b</sup>	5.02 <sup>ab</sup>
			20–40 cm	
April 14	0.74 <sup>a</sup>	0.84 <sup>a</sup>	20.60 <sup>b</sup>	1.64 <sup>a</sup>
May 26	1.56 <sup>a</sup>	1.10 <sup>a</sup>	8.46 <sup>b</sup>	1.46 <sup>a</sup>
July 25	1.62 <sup>a</sup>	1.90 <sup>a</sup>	9.02 <sup>b</sup>	3.46 <sup>ab</sup>
			<b>NH<sub>4</sub></b>	
			0–20 cm	
April 14	6.32 <sup>a</sup>	4.18 <sup>a</sup>	5.14 <sup>a</sup>	7.78 <sup>a</sup>
May 26	4.92 <sup>a</sup>	4.82 <sup>a</sup>	7.22 <sup>a</sup>	4.92 <sup>a</sup>
July 25	0.80 <sup>a</sup>	0.70 <sup>a</sup>	3.00 <sup>a</sup>	0.70 <sup>a</sup>
			20–40 cm	
April 14	7.88 <sup>a</sup>	6.82 <sup>a</sup>	10.18 <sup>a</sup>	12.32 <sup>a</sup>
May 26	8.96 <sup>a</sup>	7.68 <sup>a</sup>	11.04 <sup>a</sup>	11.96 <sup>a</sup>
July 25	1.04 <sup>a</sup>	1.10 <sup>a</sup>	2.84 <sup>a</sup>	9.30 <sup>b</sup>

\*Numbers followed by the same letters are not significantly different ( $P < .05$ ) between treatments for each soil depth and date.

Xylem potentials (Scholander et al. 1965, Waring and Cleary 1967) on current year's vegetative branchlets were measured during the 1987 growing season with a pressure chamber (PMS Corporation, Corvallis, Oregon). Predawn (19 May, 3 June, and 21 July) and midday (15 April and 3 June) measurements were recorded between 0430 and 0630, 1130 and 1230 hr, respectively. Five branchlets were measured in each treatment. Samples were selected at random, removed from the shrub, and immediately measured in the pressure chamber.

Photosynthesis was measured on one randomly selected vegetative branchlet of an *Artemisia* plant in 5 of the 10 plots for each treatment on eight dates from mid-April through early August. Measurements were recorded between 1200 and 1300 hr using a LI-6000 (LI-COR, Lincoln, Nebraska) portable photosynthesis meter with a quarter-liter chamber. To attain an adequate amount of leaf area in the chamber, we recorded measurements on both previous and current season vegetative branchlets. Initial photosynthesis values were used and corrected using the formula developed by LI-COR (McDermitt 1987).

Statistically significant treatment effects for variables measured on *Artemisia* were identi-

fied using analysis of variance procedures. Time was set as a variable, in addition to treatment. Least significant differences (LSD) ( $P < .05$ ) were calculated only when the F value was significant ( $P < .05$ ) (Steel and Torrie 1980). The General Linear Model Procedure of SAS was used to evaluate treatment differences for specific leaf weight and photosynthesis (SAS 1988). This procedure permitted statistical analysis of unbalanced data sets. Both interactions and main effect means were separated using Fischer's least significant difference test. Only statistically significant results are reported in the Results and Discussion.

## RESULTS

### Soil Nitrogen

The addition of nitrate increased nitrate levels 25- and 28-fold in the upper and lower soil depths, respectively, at the beginning of the growing season (Table 1). Nitrate levels remained high compared with the other three treatments at both depths during the growing season. The shallow character of the soil probably limited nitrate losses to leaching, maximizing the amount available for plant uptake. The addition of ammonium increased ammonium 188% in the B horizon. The increase in

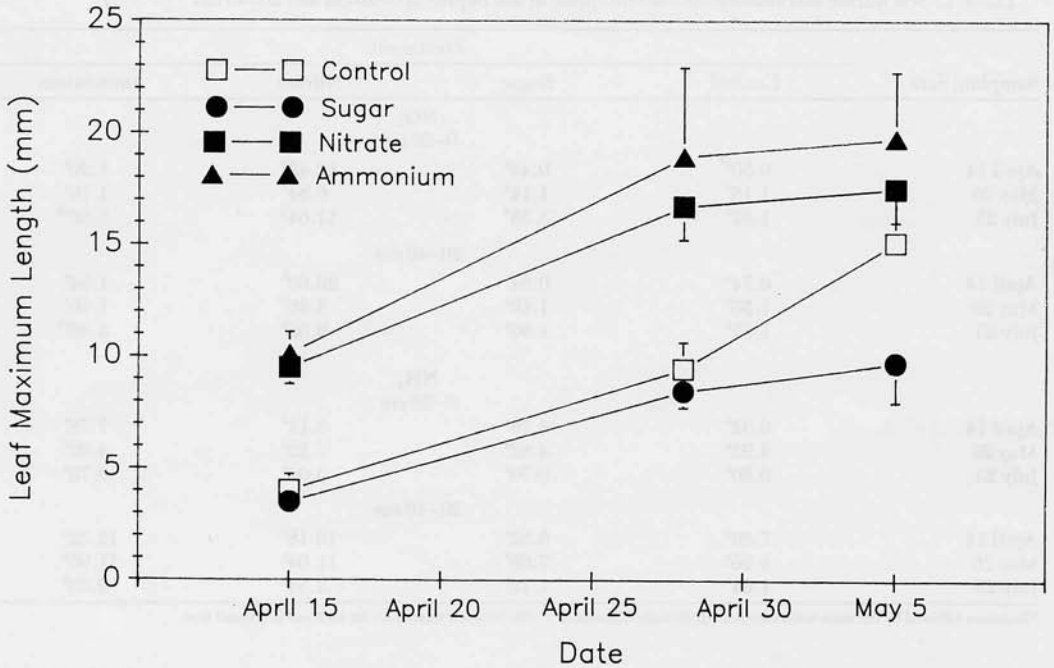


Fig. 1. Ephemeral leaf maximum length of *Artemisia tridentata* ssp. *wyomingensis* during the early growing season. Standard errors are presented for each mean.

the A horizon was not significant. The sugar treatment did not appear to change soil nitrogen levels when compared with the control, possibly indicating that carbon was not limiting decomposer microflora (McGarity 1961).

### Growth

In the early spring both mean maximum length of ephemeral leaves and number of ephemeral leaves per terminal shoot were greater in the ammonium and nitrate treatments than in the sugar and control treatments (Figs. 1, 2). Ephemeral leaf lengths during April in the nitrogen-treated plots did not differ from one another but were greater than in the nonnitrogen treated plants. Control and nitrate-treated plants did not differ from one another in leaf length for the May sampling period. Analysis of main effect means for ephemeral leaf numbers revealed that plants in nitrogen-treated plots did not differ from one another, and that their values were greater than similar values found for the control and sugar treatments. In addition, the development of new leaves on terminal shoots in both nitrate and ammonium treatments

appeared to increase at a greater rate in early May than in sugar and control plots.

The addition of nitrogen increased current year's vegetative stem length compared with no nitrogen addition throughout the growing season (Fig. 3). Stem length was similar between both nitrogen forms in April and May but continued at a more rapid rate in the nitrate treatment in June. At the termination of vegetative stem elongation, stems in the nitrate and ammonium treatments were 175 and 140% longer, respectively, than shoots in the control treatment. Stem elongation in the control and sugar treatments was similar.

The addition of either form of nitrogen did not increase specific leaf weight averaged across the growing season as compared with the control treatment (Table 2). The addition of sugar, however, reduced specific leaf weight across dates on the average by 12% compared with the control. The major difference in specific leaf weight between control and sugar treatments occurred during abscission of ephemeral leaves in late July and early August (Fig. 4). Specific leaf weight increased approximately 180 to 200% when ephemeral

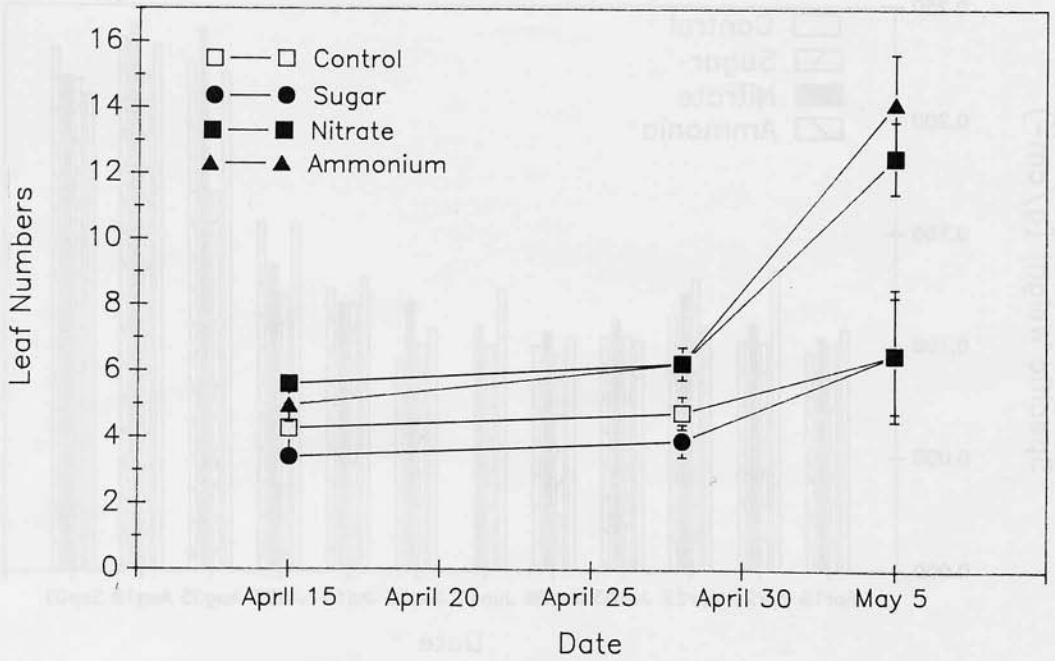


Fig. 2. Ephemeral leaf numbers per terminal bud of *Artemisia tridentata* ssp. *wyomingensis* during the early growing season. Standard errors are presented for each mean.

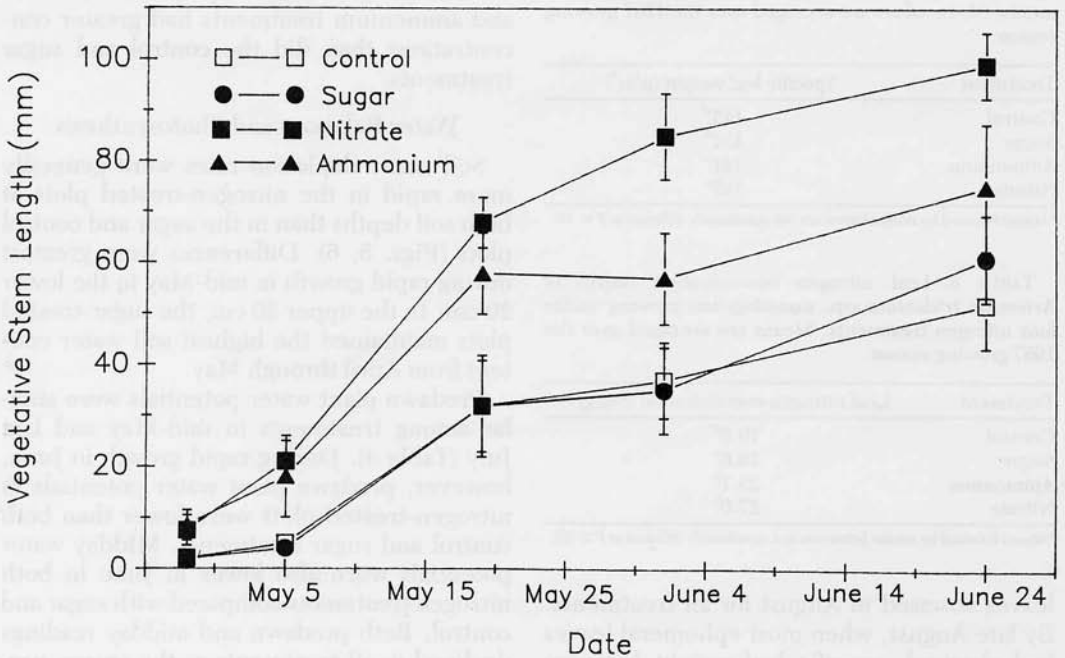


Fig. 3. Effects of four different nitrogen treatments on current year vegetative stem length of *Artemisia tridentata* ssp. *wyomingensis*. Standard errors are presented for each mean.

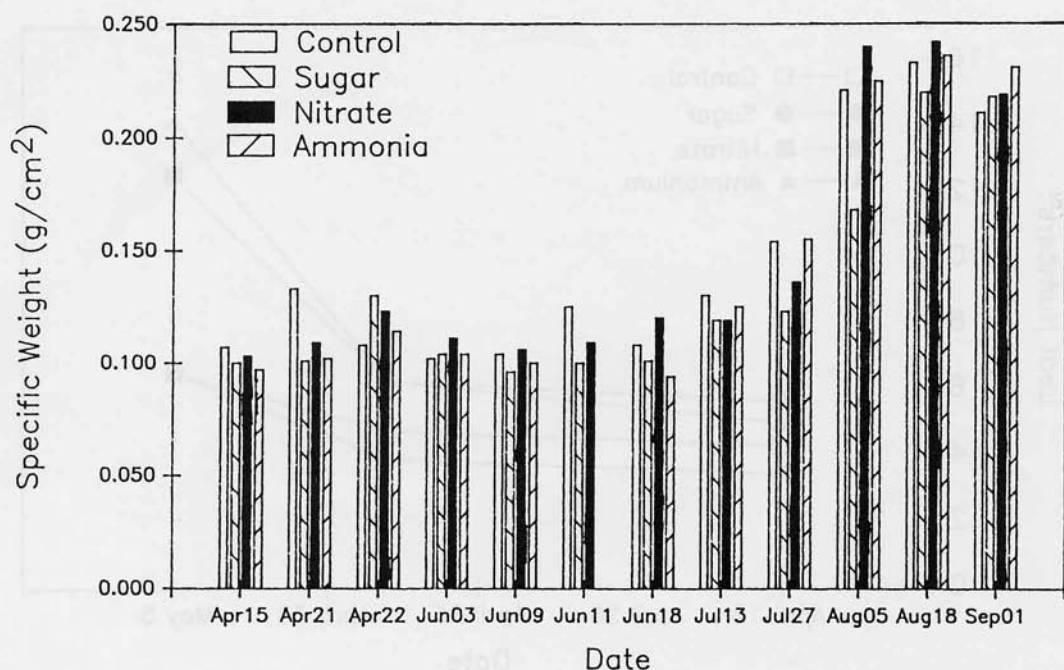


Fig. 4. Specific leaf weights of *Artemisia tridentata* ssp. *wyomingensis* during the course of the 1987 growing season.

TABLE 2. Specific leaf weights of *Artemisia tridentata* ssp. *wyomingensis* growing under four nitrogen treatments. Mean values are averaged over the 1987 growing season.

Treatment	Specific leaf weight (g/m <sup>2</sup> )
Control	145 <sup>a*</sup>
Sugar	132 <sup>b</sup>
Ammonium	141 <sup>a</sup>
Nitrate	145 <sup>a</sup>

\*Means followed by similar letters are not significantly different at  $P \leq .05$ .

TABLE 3. Leaf nitrogen concentration (mg/g) of *Artemisia tridentata* ssp. *wyomingensis* growing under four nitrogen treatments. Means are averaged over the 1987 growing season.

Treatment	Leaf nitrogen concentration (mg/g)
Control	19.6 <sup>a*</sup>
Sugar	19.6 <sup>a</sup>
Ammonium	25.1 <sup>b</sup>
Nitrate	27.0 <sup>b</sup>

\*Means followed by similar letters are not significantly different at  $P \geq .05$ .

leaves abscised in August for all treatments. By late August, when most ephemeral leaves had abscised, specific leaf weight between treatments was similar.

Application of both forms of nitrogen resulted in greater leaf nitrogen contents of

*Artemisia* plants (Table 3). Analysis of main effect means revealed that plants in the nitrate and ammonium treatments had greater concentrations than did the control and sugar treatments.

#### Water Relations and Photosynthesis

Soil water depletion rates were generally more rapid in the nitrogen-treated plots at both soil depths than in the sugar and control plots (Figs. 5, 6). Differences were greatest during rapid growth in mid-May in the lower 20 cm. In the upper 20 cm, the sugar-treated plots maintained the highest soil water content from April through May.

Predawn plant water potentials were similar among treatments in mid-May and late July (Table 4). During rapid growth in June, however, predawn plant water potentials in nitrogen-treated plots were lower than both control and sugar treatments. Midday water potentials were also lower in June in both nitrogen treatments compared with sugar and control. Both predawn and midday readings declined in all treatments as the season progressed.

Photosynthesis was significantly different between treatments on only the 15 June 1987

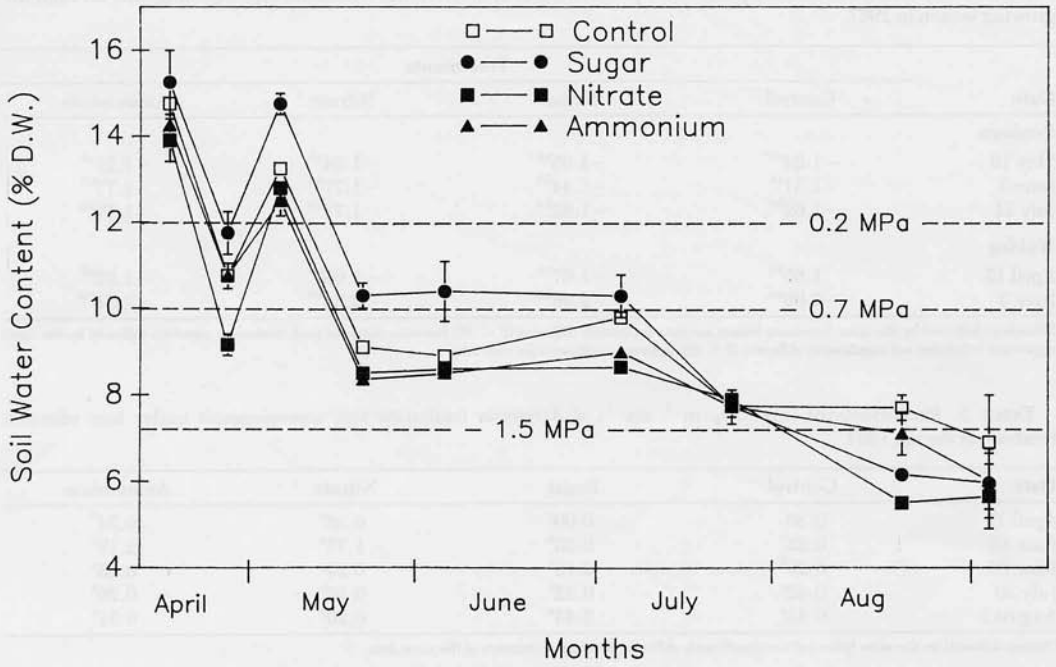


Fig. 5. Seasonal pattern of soil water content in the upper soil profile (2-20 cm) for four different nitrogen treatments in 1987. Vertical bars are 95% confidence limits. Field capacity (-0.03 MPa) = 18% soil water content.

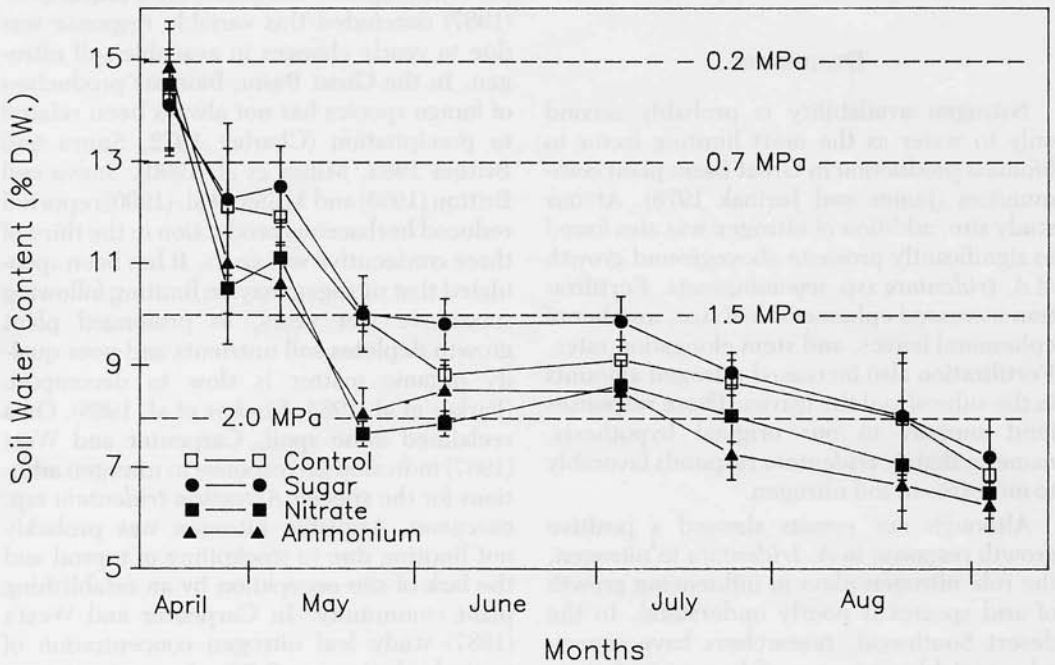


Fig. 6. Seasonal pattern of soil water content in the lower soil profile (20-40 cm) for four different nitrogen treatments in 1987. Vertical bars are 95% confidence levels.

TABLE 4. Predawn and midday plant water potentials (MPa) in *Artemisia tridentata* ssp. *wyomingensis* through the growing season in 1987.

Date	Treatments			
	Control	Sugar	Nitrate	Ammonium
<i>Predawn</i>				
May 19	-1.24 <sup>AA*</sup>	-1.05 <sup>AA</sup>	-1.04 <sup>AA</sup>	-1.21 <sup>AA</sup>
June 3	-1.31 <sup>AA</sup>	-1.44 <sup>BA</sup>	-1.77 <sup>BA</sup>	-1.77 <sup>BB</sup>
July 21	-1.62 <sup>BA</sup>	-1.62 <sup>BA</sup>	-1.74 <sup>BA</sup>	-1.77 <sup>BA</sup>
<i>Midday</i>				
April 15	1.85 <sup>AA</sup>	-1.67 <sup>AB</sup>	-1.65 <sup>AB</sup>	-1.62 <sup>AB</sup>
June 3	-2.09 <sup>BA</sup>	-2.06 <sup>BA</sup>	-2.24 <sup>BB</sup>	-2.31 <sup>BB</sup>

\*Numbers followed by the same lowercase letters are not significantly different ( $P < .05$ ) between dates for each treatment; numbers followed by the same uppercase letters are not significantly different ( $P < .05$ ) between treatments for each site.

TABLE 5. Photosynthesis ( $\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) of *Artemisia tridentata* ssp. *wyomingensis* under four nitrogen treatments during 1987.

Date	Control	Sugar	Nitrate	Ammonium
April 17	0.30 <sup>*</sup>	0.00 <sup>a</sup>	0.36 <sup>a</sup>	0.54 <sup>*</sup>
June 15	0.25 <sup>b</sup>	0.33 <sup>b</sup>	1.73 <sup>a</sup>	2.18 <sup>a</sup>
June 20	0.20 <sup>b</sup>	0.16 <sup>a</sup>	0.28 <sup>a</sup>	0.25 <sup>a</sup>
July 30	0.42 <sup>a</sup>	0.22 <sup>a</sup>	0.22 <sup>a</sup>	0.20 <sup>a</sup>
August 1	0.43 <sup>a</sup>	0.43 <sup>a</sup>	0.20 <sup>a</sup>	0.51 <sup>a</sup>

\*Means followed by the same letter are not significantly different between treatments at the same date.

date (Table 5). Increased photosynthesis on this date corresponded to the period of rapid leaf and stem growth in early June.

## DISCUSSION

Nitrogen availability is probably second only to water as the most limiting factor to biomass production in Great Basin plant communities (James and Jurinak 1978). At our study site, addition of nitrogen was also found to significantly promote aboveground growth of *A. tridentata* ssp. *wyomingensis*. Fertilization increased ephemeral leaf size, number of ephemeral leaves, and stem elongation rates. Fertilization also increased nitrogen amounts in the subsoil and the leaves. These responses lend support to our original hypothesis, namely, that *A. tridentata* responds favorably to increases in soil nitrogen.

Although our results showed a positive growth response in *A. tridentata* to nitrogen, the role nitrogen plays in influencing growth of arid species is poorly understood. In the desert Southwest, researchers have reported a variable response of *Larrea tridentata* (DC.) Cov.-dominated communities to water and nitrogen inputs (Gutierrez and Whitford 1987, Fischer et al. 1987). During certain

years, application of water and/or nitrogen resulted in enhanced growth, while in other years no response was observed. Fischer et al. (1987) concluded this variable response was due to yearly changes in available soil nitrogen. In the Great Basin, biomass production of forage species has not always been related to precipitation (Charley 1972, Sneva and Britton 1983, Miller et al. 1990). Sneva and Britton (1983) and Miller et al. (1990) reported reduced herbaceous production in the third of three consecutive wet years. It has been speculated that nitrogen may be limiting following successive wet years, as prolonged plant growth depletes soil nutrients and poor quality organic matter is slow to decompose (Parker et al. 1984, Fischer et al. 1988). On a reclaimed mine spoil, Carpenter and West (1987) indicated no response to nitrogen additions for the species *Artemisia tridentata* ssp. *vaseyana*. Available nitrogen was probably not limiting due to stockpiling of topsoil and the lack of site occupation by an establishing plant community. In Carpenter and West's (1987) study leaf nitrogen concentration of control plants was 3.2%. In contrast, our study had leaf nitrogen concentrations of 2.0, 2.7, and 2.5%, for control, nitrate, and ammonium, respectively. Site and subspecies



differences may have also contributed to the different response.

A positive growth response was shown for the ammonium plots in spite of enhanced ammonium levels being found only in the 20–40 cm soil depth. The nonsignificant concentrations of ammonium in the surface soils may have been caused by losses due to volatilization, absorption of ammonium on soil colloids, high biological activity, and/or ammonium being hydrolyzed to nitrate in the lower soil depth. Also, the growth response may have been related to the application of ammonium in the sulfate form. Whether or not *A. tridentata* responds to sulfur additions has yet to be determined. Despite the lack of enhancement in the upper soil depth of the ammonium-treated plots, the extensive root system of *A. tridentata* would allow this species to readily utilize ammonium in the lower soil depths.

Xylem potential and soil moisture readings found in this study would, at first, appear contradictory to the observed growth responses. The more negative soil moisture and plant water potentials reported for *A. tridentata* growing in the nitrogen plots suggest that these plants were more water stressed, and thus should have reduced aboveground growth. However, the opposite was found. We feel that a possible explanation for these results centers on the greater growth and physiological activity of plants in the nitrogen plots. Since specific leaf weights were similar between treatments during active leaf growth, we can assume that differences in leaf area between treatments are approximately proportional to biomass. Leaf biomass of *A. tridentata* in the nitrate and ammonium plots was found to have increased 520 and 230%, respectively, over control (Wang 1989). Greater growth and leaf area of these plants may mean that more soil water was used by plants in the nitrogen treatments. This observation is supported by the research of Svejcar and Browning (1988). They reported a greater leaf area, higher physiological activity, and a subsequently more rapid soil water depletion in burned versus unburned stands of *Andropogon gerardii* Vitman. The greater photosynthetic rates of *A. tridentata* in the nitrogen plots during early June also further support this observation. In addition, an increase in shoot-to-root ratio could have influenced plant-water relations.

Nitrogen additions have been reported to increase shoot-to-root ratios in *Larrea tridentata* (Fischer et al. 1988, Lajtha and Klein 1988).

Specific leaf weights averaged across the growing season were significantly influenced by the sugar treatment. Prior to leaf senescence, specific leaf weights were similar between treatments on seven of eight dates measured. Specific leaf weights in the sugar treatment, however, were significantly less than in the control during senescence and abscission of current year's ephemeral leaves. Once the majority of ephemeral leaves had abscised in mid-August for all treatments, specific leaf weights were again similar. The decrease in specific leaf weights in the sugar treatment was probably a function of delayed leaf senescence and abscission rather than leaves being lighter per unit of surface area. Although not indicated by the soil nitrogen data, some reduction in available soil nitrogen may have occurred on the sugar plots.

Marschner (1986) reported an increase in leaf area indices in plant populations with an increase in nutrient supply. Increased leaf development during the early part of the growing season and a larger leaf area index in the years when mineralizable nitrogen levels are relatively high may increase *Artemisia*'s competitive advantage for nutrient resources over associated species. Miller (1988) reported that *Artemisia* maintained a relatively high leaf area early in the spring compared with associated species, allowing it to capture soil water resources early in the growing season. Early increased leaf area also enhances its ability to maximize photosynthesis when environmental conditions are favorable (DePuit and Caldwell 1973). In warm desert shrubs, rate of leaf area development was the primary factor limiting whole-plant carbon gain during the early portion of the growing season (Comstock et al. 1988).

In conclusion, application of both nitrate and ammonium increased growth response of *A. tridentata* over control and sugar treatments. Apparently this species can opportunistically take advantage of increased soil nitrogen by increasing amount of leaf area available for growth. Increases in available soil nitrogen might occur following events such as several consecutive years of below-average precipitation or weakening of

perennial grasses through overgrazing. *A. tridentata* may enhance its competitiveness by responding favorably to increased levels of soil nitrogen.

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