Response of Artemisia tridentata ssp. wyomingensis and Stipa thurberiana to Nitrogen Amendments[1]

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ABSTRACT.—Artemisia tridentata has increased dramatically during the past 100 yr throughout the sagebrush steppe at the expense of late-seral perennial grasses. This study was designed to determine the effects of addition or depletion of different nitrogen forms on aboveground vegetative and reproductive growth of Artemisia tridentata ssp. wyomingensis and Stipa thurberiana, a late-seral grass. Treatments included application of sugar (45 g m^{-2}), nitrate (4.5 g N m^{-2}), ammonium (4.5 g N m^{-2}) and a control. Both nitrogen forms significantly increased Stipa aboveground biomass and tiller density. Individual tiller weight was not different among treatments. Added nitrogen also increased aboveground biomass, total shoot density and individual shoot weight in Artemisia. Biomass production, however, was greater in the nitrate plots than the ammonium plots. Reproductive shoot weight and density for Artemisia, and density for Stipa were greater in nitrate than the ammonium, sugar and control plots. Reproductive shoot density increased 350% and 294% over controls for Stipa and Artemisia, respectively. Aboveground biomass increased by a significantly greater percentage in Artemisia than Stipa in nitrogen treated plots. Based on aboveground response, data suggests that Artemisia responds more to available nitrogen than Stipa.

INTRODUCTION

Artemisia tridentata Nutt. is the most abundant shrub in the Great Basin of North America, encompassing approximately 0.63×10^6 km^2 (West, 1983). During the past 100 yr, its numbers have increased dramatically while at the same time late-seral perennial grasses, such as Stipa thurberiana Piper., have declined. Reasons for this change include overgrazing of perennial grasses by domestic ungulates, increased soil disturbance by farming, and alterations in fire frequency (Hironaka and Tisdale, 1963; Tisdale et al., 1969; Tisdale and Hironaka, 1981).

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

Water, generally believed to be the most limiting factor in the Great Basin (West and Skujins, 1978), has been the primary factor studied in evaluating plant response and interactions between Artemisia tridentata and associated species (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, 1988). These studies have shown that A. tridentata is an effective competitor for soil moisture. Although less information has been gathered on soil nutrients, nitrogen is also considered to be a primary limiting nutrient to plant growth in arid and semiarid systems (Charley, 1972; West and Skujins, 1978). Some evidence suggests

that *A. tridentata* is very competitive with native perennial grasses for soil nutrients (Hyder and Sneva, 1961; West and Klemmedson, 1978; James and Jurinak, 1978; Patterson and Youngman, 1960; Romney *et al.*, 1978; Wilson *et al.*, 1966). Caldwell *et al.* (1985), in an experiment using isotopes of phosphorus, demonstrated that *A. tridentata* adsorbed a larger proportion of phosphorus than *Agropyron spicatum* (Pursh) Scribn. and Smith, a late-seral perennial grass. Past work, however, suggests that grasses are more able to absorb nitrate than shrubs (West and Skujins, 1978). Skujins and West (1974) reported big sagebrush consistently absorbed more ammonium than nitrate, in soils supplied with both forms of nitrogen.

Few studies have been done examining the effects of nitrogen availability on in situ growth and physiology between neighboring *Artemisia tridentata* and late-seral native perennial grasses. Most nitrogen studies in semiarid regions have primarily focused on forage production response to fertilization (Schmisseur and Miller, 1978).

This study was designed to determine the effects of addition or depletion of different nitrogen forms on *Stipa thurberiana* and *Artemisia tridentata* ssp. *wyomingensis* in an *A. tridentata*-dominated community in eastern Oregon. Our hypotheses are: (1) late-seral shrubs have a greater affinity for NH_4 than late-seral grasses; (2) late-seral grasses have a greater affinity for NO_3 than late-seral shrubs, and (3) late-seral shrubs have a greater capacity to utilize increased levels of soil nitrogen than late-seral grasses.

MATERIALS AND METHODS

The study was conducted at the Squaw Butte Experimental Range in southeastern Oregon, 67 km W of Burns, on the northern fringe of the Great Basin (119°43'W lat, 43°29'N long). The climate for this area is semiarid (Fig. 1). The 37-year mean annual precipitation is 284 mm. Precipitation during the 1987 crop year (September–August) was 296 mm. The study site was located in an *Artemisia tridentata* ssp. *wyomingensis*/*Stipa thurberiana* habitat type, at an elevation of 1372 m (Doescher *et al.*, 1984). This site has not been grazed by domestic herbivores for the past 40 yr. Soils are classified as Xerollic Durothids (Lentz and Simonson, 1986) and vary in depth from 350–450 mm. They are underlain by an indurated duripan 50–200 mm thick, which is underlain by unweathered basalt.

A completely randomized plot design was used with 10 replications of each treatment. Forty, 5 × 5 m plots were laid out, each centered on an *Artemisia*. Plant growth measurements were recorded on the center *Artemisia* and five *Stipa* plants growing within 1.5 m of the *Artemisia* stem base. Soil samples were also collected within 1.5 m of the stem base. The remainder of each plot was used as a buffer.

Treatments were applied in November of 1986. Treatments were (1) control; (2) granulated sugar (45 g m^{-2}); (3) ammonium $(NH_4)_2SO_4$ (nitrogen = 4.5 g m^{-2}); and (4) nitrate HNO_3 (nitrogen = 4.5 g m^{-2}). Sugar was added presumably to increase the C:N ratio and decrease availability of soil nitrogen (Waring, 1982). Both ammonium and sugar were broadcast onto the 5 × 5 m plots. Nitrate was diluted in water (one part HNO_3 to five parts water) and applied with a pack sprayer. All herbaceous plants were dormant at time of application. Soil and plant growth measurements were recorded during the 1987 growing season.

One soil sample for ammonium and nitrate analysis was collected in each A (0–200 mm) and B (200–duripan) horizon at the canopy edge of *Artemisia* in five plots for each treatment. Soils were sampled mid-April, late May and late July. Soils analysis was performed using a KCL extracting solution (Horneck *et al.*, 1989).

A sample of current year's leaves was collected randomly on *Artemisia* vegetative stems and *Stipa* on 21 April, 1 June and 1 August 1987 on all plots. Collections represented three
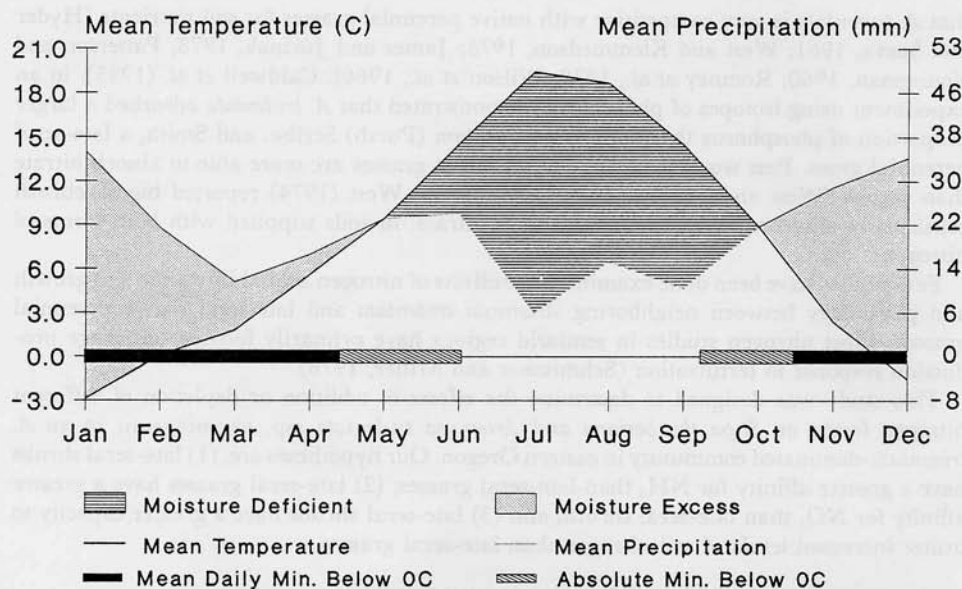
Fig. 1.—Climatic diagram, following Walter (1963), for the Squaw Butte Experiment Station, Elevation 1350 m

growth stages for both species: *Artemisia* in initial leaf elongation, rapid leaf and stem elongation, and flowering, and *Stipa* in vegetative, flowering, and seed development. Leaf samples were dried at 60 C for 48 h, ground, and analyzed for total leaf nitrogen content using the Semimicro-Kjeldahl method (Bremner, 1965).

Stipa growth was measured on five randomly selected plants in each plot on 5 August 1987. Vegetative and reproductive tillers were counted on each of the five plants. Standing crop was then harvested to a 10-mm stubble height on these same plants, dried at 60 C for 48 h and weighed. Crown area was measured on each plant following clipping. Tiller density and biomass data are presented as units per unit crown area.

Artemisia growth was also recorded in each plot on 5 August 1987. Stem and leaf growth had ceased by this time. Vegetative and reproductive stem densities were measured in a 0.2 × 0.2 m frame placed in the center top of each *Artemisia*. Only current year's elongated branchlets were recorded (nonelongated lateral stems were not recorded). Data were converted to number of stems per m^2 of canopy. Current year's leaf and stem biomass on vegetative and reproductive shoots were measured on 50 current year's branchlets randomly selected on the central *Artemisia* in each plot. All biomass measurements were put on a dry weight basis by drying samples for 48 h at 60 C. We estimated current year aboveground biomass m^{-2} of canopy for each treatment with the formula: current year's aboveground biomass (g m^{-2}) = (mean reproductive shoot weight) × (reproductive shoot density) + (mean vegetative shoot weight) × (vegetative shoot density).

Statistically significant treatment effects on variables measured for *Artemisia* and *Stipa* were identified using analysis of variance procedures. Least significant differences (LSD) were calculated only when the F value indicated significance using ANOVA (Steel and Torrie, 1980). Differences reported in the text were significant at $P < 0.05$. When seasonal measurements were recorded, we set time as a variable in addition to treatment. Therefore, these results included the interaction, treatment × time.

TABLE 1.—Soil nitrate and ammonium content (ppm) at soil depths of 0–200 mm and 200–400 mm

Sampling date	Treatment			
	Control	Sugar	Nitrate	Ammonium
			NO$_3$	
			0–200 mm	
14 April	0.50[a1]	0.48[a]	12.42[b]	1.20[a]
26 May	1.16[a]	1.14[a]	6.84[a]	1.16[a]
25 July	1.82[a]	3.28[a]	11.64[b]	5.02[ab]
			0–200 mm	
14 April	0.74[a]	0.84[a]	20.60[b]	1.64[a]
26 May	1.56[a]	1.10[a]	8.46[b]	1.46[a]
25 July	1.62[a]	1.90[a]	9.02[b]	3.46[ab]
			NH$_4$	
			0–200 mm	
14 April	6.32[a]	4.18[a]	5.14[a]	7.78[a]
26 May	4.92[a]	4.82[a]	7.22[a]	4.92[a]
25 July	0.80[a]	0.70[a]	3.00[a]	0.70[a]
			200–400 mm	
14 April	7.88[a]	6.82[a]	10.18[a]	12.32[a]
26 May	8.96[a]	7.68[a]	11.04[a]	11.96[a]
25 July	1.04[a]	1.10[a]	2.84[a]	9.30[a]

[1] Numbers followed by the same letters are not significantly different (P < 0.05) between treatments

RESULTS

Application of nitrate significantly increased soil nitrate concentration at both soil depths as compared to the remaining three treatments which did not differ (Table 1). Nitrate levels in the control plots were similar to levels reported in desert soils of the Mojave Desert (Wallace et al., 1978). No interaction was detected for nitrate analysis in the upper soil profile (0–200 mm). Nitrate concentration at this depth was initially high in April in the nitrate treatment, declined in May and then increased in July. There was a time × treatment interaction for nitrate concentration in the B horizon (200-duripan). Nitrate concentration declined early in the growing season only in the nitrate plots.

Soil ammonium concentration differed among the four treatments only in the lower soil profile in late July, possibly as the result of volatilization in the upper soil profile (Table 1). Highest ammonium content was found in plots which had received ammonium application. Ammonium decreased in both soil profiles as the growing season progressed in all treatments.

Stipa aboveground biomass was significantly larger in the ammonium and nitrate plots than sugar and control plots (Table 2). This response to nitrogen amendment was attributed to an increase in tiller density; not an increase in individual tiller weight. Nitrate plots had 166% greater total tiller density and 350% greater reproductive tiller density than the control treatment. Vegetative tiller density did not differ between ammonium and nitrate treatments; however, reproductive tiller density was greater in the nitrate plots. Control and sugar plots exhibited similar values in all *Stipa* growth measurements.

Artemisia also exhibited a significant growth response to nitrogen amendments. Both forms

TABLE 2.—Growth performance of *Stipa thurberiana* under four nitrogen treatments on 5 August 1987

	Treatments			
Variables	Control	Sugar	Nitrate	Ammonium
Aboveground biomass (g m^{-2} crown)	510[a1]	420[a]	760[b]	710[b]
Total tiller numbers·1000 m^{-2}	24.4[ab]	21.9[a]	40.6[c]	30.4[b]
Reproductive tiller number·1000 m^{-2} crown	0.6[a]	0.5[a]	02.1[b]	01.0[a]
Vegetative tiller number·1000 m^{-2} crown	23.8[a]	21.4[a]	38.5[a]	29.4[ab]
Dry weight per tiller (mg/tiller)	23.4[a]	24.3[a]	23.6[a]	27.3[a]

[1] Numbers followed by the same letters are not significantly different ($P < 0.05$) between treatments for each variable

of nitrogen increased aboveground biomass in comparison to control and sugar, although nitrate plots were higher than ammonium plots (Table 3). Total shoot density did not differ between nitrate and ammonium treatments but was greater than the other two treatments. Increased shoot density in both nitrogen treatments was due to the elongation of short lateral shoots. Reproductive shoot density increased in the nitrate treatment only. Leaf and stem weight of individual reproductive shoots was also greater in the nitrate plots than the remaining three treatments. In contrast, vegetative shoot density decreased in the nitrate treatment, compared to the ammonium treatment. Only in the ammonium treatment did leaf and stem weights of vegetative shoots increase in comparison to sugar and control. The large increase in *Artemisia* biomass in the nitrate plots was primarily a result of increased reproductive shoot size and number. In the nitrate treatment, 93% of the current year's aboveground biomass was composed of reproductive shoots, as compared to 67, 52 and 58% in the control, sugar and ammonium treatments, respectively. The addition of sugar had no impact on *Artemisia* growth compared to the control treatment.

Nitrate and ammonium treatments increased leaf nitrogen content 137 and 130%, respectively, in *Artemisia* as compared to control plants (Fig. 2). Leaf nitrogen content in *Stipa*

TABLE 3.—Growth performance of *Artemisia tridentata* ssp. *wyomingensis* under four nitrogen treatments on 3 August 1987

	Treatments			
Variables	Control	Sugar	Nitrate	Ammonium
Aboveground biomass (g m^{-2} canopy)	198[a1]	140[a]	1104[c]	472[b]
Total shoot number m^{-2} canopy	870[a]	882[a]	1450[b]	1270[b]
Reproductive shoot numbers m^{-2} canopy	387[a]	402[a]	1137[b]	605[a]
Vegetative shoot numbers m^{-2} canopy	483[ab]	480[ab]	313[a]	665[b]
Leaf dry weight (g/shoot)				
Vegetative	0.10[a]	0.10[a]	0.16[ab]	0.20[b]
Reproductive	0.29[ab]	0.15[a]	0.7[c]	0.39[b]
Stem dry weight (g/shoot)				
Vegetative	0.04[a]	0.04[a]	0.07[ab]	0.10[b]
Reproductive	0.05[ac]	0.03[a]	0.12[c]	0.06[b]

[1] Numbers followed by the same letters are not significantly different ($P < 0.05$) between treatments for each variable
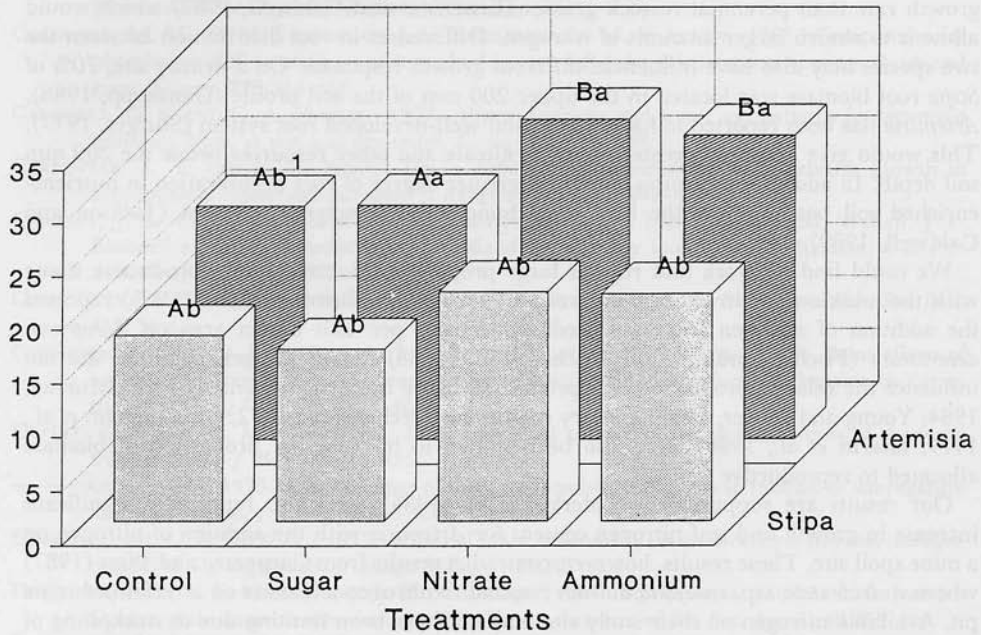
FIG. 2.—Leaf nitrogen content for *Artemisia tridentata* ssp. *wyomingensis* and *Stipa thurberiana* among four treatments. Similar upper case letters are not significantly different (P < 0.05) between treatments for each species. Similar lower case letters are not significantly different (P < 0.05) between species for each treatment

did not differ among treatments. Within treatments, *Artemisia* had higher leaf nitrogen content per unit dry weight than *Stipa*. Leaf nitrogen content remained higher in *Artemisia* throughout the growing season.

DISCUSSION

If grasses do have a greater affinity for nitrate than shrubs, we would expect *Stipa* to do better in the nitrate plots than *Artemisia*. This, however, was not the case. Compared to the control treatment, aboveground biomass increased 149% for *Stipa* as compared to 456% for *Artemisia* in the nitrate treatment. Although total shoot densities increased similarly for both species in the nitrate treatment, *Stipa* shoots did not increase in weight, whereas *Artemisia* shoot weights did. Based on these results, we reject the hypothesis that late seral grasses have a greater affinity for nitrate than late seral shrubs. However, we accept the hypothesis that late seral shrubs have a greater affinity for ammonium than late seral grasses. Aboveground biomass for *Artemisia* increased 238% in the ammonium treatments compared to 139% for *Stipa*.

Based on aboveground plant response, we accept our last hypothesis that late seral shrubs have a greater capacity to use increased levels of soil nitrogen than late seral grasses. We believe there are several mechanisms that allow this to happen. *Artemisia* displays a larger amount of leaf area than associated species early in the growing season due to a carry-over of winter-persistent leaves allowing it to be more opportunistic for absorption of soil resources

during early growth (Miller, 1988). *Artemisia* is also characterized by a greater potential growth rate than perennial tussock grasses (Eissenstat and Caldwell, 1987) which would allow it to absorb larger amounts of nitrogen. Differences in root distribution between the two species may also have influenced different growth responses. On a nearby site, 70% of *Stipa* root biomass was located in the upper 200 mm of the soil profile (Ganskopp, 1988). *Artemisia* has been reported to have a deep and well-developed root system (Sturges, 1977). This would give *Artemisia* greater access to nitrate and other resources below the 200 mm soil depth. In addition, *Artemisia* exhibits a greater degree of root proliferation in nutrient-enriched soil patches than the high seral bunchgrass *Agropyron spicatum* (Jackson and Caldwell, 1989).

We could find no work that reports large proportional increases in reproductive tissue with the addition of nitrate as compared to ammonium. However, Cook (1965) reported the addition of nitrogen increased seedhead density per unit crown area on *Agropyron desertorum* (Fisch.) Schult., while Fischer *et al.* (1988) found nitrogen additions did not influence the relative proportion of reproductive tissue in *Larrea tridentata*. Fire (Murray, 1984; Young and Miller, 1985) and dry conditions (Oechel *et al.*, 1972; Cunningham *et al.*, 1979; Sharifi *et al.*, 1988) have also been shown to increase the proportion of biomass allocated to reproductive tissue.

Our results are supported by Elderkin *et al.* (1986), who also reported a significant increase in growth and leaf nitrogen content for *Artemisia* with the addition of nitrogen on a mine spoil site. These results, however, contradict results from Carpenter and West (1987) where *A. tridentata* ssp. *vaseyana* did not respond to nitrogen additions on a reclaimed mine pit. Available nitrogen on their study site may not have been limiting due to stockpiling of top soil with plant material, and the early establishment of plants not fully occupying the site. Leaf nitrogen content in *Artemisia* for control plots in their study was 3.2% as compared to 2.2, 3.0 and 2.8%, for control, nitrate and ammonium, respectively, in our study. Elderkin *et al.* (1986) reported leaf nitrogen contents ranged from 1.9–2.5% for the control and irrigated-fertilized treatments, respectively. Different leaf nitrogen content may indicate varying levels of nitrogen availability between study sites. Both site and subspecies differences may also contribute to the different response.

In conclusion, both the late seral shrub and late seral grass responded positively to both forms of nitrogen. Although the degree in growth response between the two nitrogen treatments may have been caused by different levels of available soil nitrogen between the two treatments, nitrate stimulated a greater proportion of total biomass to reproductive tissue as compared to ammonium. Our data also showed that aboveground parts of *Artemisia* responded more to increased levels of nitrogen than *Stipa*. Future work should determine the effects of annual fluxes of available nitrogen on belowground growth of late seral shrubs and grasses and the long-term response of plant composition. If late seral shrubs are more responsive than perennial grasses to increases in nitrogen, possible annual fluctuations in available nitrogen (Fischer *et al.*, 1987; Charley, 1972; Sneva and Britton, 1983; Miller *et al.*, 1990) may play an important role in shifting composition toward a shrub-dominated community.

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