J. Range Manage.
50:536–540

Influence of nitrogen on antelope bitterbrush seedling establishment

JAMES A. YOUNG, CHARLIE D. CLEMENTS, AND ROBERT R. BLANK

Authors are range scientist, wildlife research assistant, and soil scientist, USDA, Agricultural Research Service, 920 Valley Road, Reno, Nev. 89512.

Abstract

Nitrogen enrichment, immobilization, or inhibition of nitrification were used to investigate the influence of available nitrogen on the seedling recruitment of antelope bitterbrush (*Purshia tridentata* [Pursh] DC) and annual grass competition. The influence of nitrogen enrichment on antelope bitterbrush seedling recruitment depended on the form of nitrogen applied. Ammonium sulfate applications markedly enhanced growth of herbaceous annuals resulting in the loss of all antelope bitterbrush seedlings the first growing season. Enrichment with calcium nitrate marginally enhanced growth of herbaceous annuals and enhanced the growth of antelope bitterbrush seedlings. Immobilization of nitrogen with carbon (sucrose) applications suppressed the growth of herbaceous annuals and produced large, vigorous antelope bitterbrush seedlings. Similar results were obtained by inhibiting nitrification with applications of nitrapyrin or combining nitrapyrin and carbon applications.

Key Words: nitrification, nitrogen enrichment, seedling recruitment, rodent predation, *Purshia tridentata*

Antelope bitterbrush (*Purshia tridentata* [Pursh] DC), endemic to North America, is one of the most important browse species in the western United States (Anon. 1937, Nord 1965). The general lack of seedling recruitment in certain antelope bitterbrush stands has long been a concern of wildlife and range managers (Hubbard 1957, Sanderson 1962, Nord 1965). Seedling recruitment is most often a problem at lower elevations in the big sagebrush (*Artemisia tridentata* Nutt.) zone. These stands are often critical winter habitat for mule deer (*Odocoileus hemionus*) (Hormay 1943, Smith 1950).

Seeds of antelope bitterbrush are initially dormant and require a period of moist chilling before they will germinate (Young and Evans 1976). Under controlled conditions in the laboratory, the duration of this moist chilling requirement is relatively short. Under field conditions, with fluctuating moisture and temperature, it may be prolonged (Young et al. 1993). These internal changes in the physiology of the antelope bitterbrush seeds occur while the seeds are exposed in the field to secondary predation by granivores.

Competition with annual weeds for soil moisture is usually given as a major cause of seedling mortality for antelope bitterbrush (Hubbard 1957, Ferguson 1972). Recently, nitrogen enrichment-immobilization and nitrification inhibition have been used to investigate seedling recruitment and growth of annual weeds on sagebrush rangelands (Young et al. 1996). Our purpose was to investigate the interaction of nitrogen enrichment-immobilization and nitrification inhibition on recruitment of antelope bitterbrush seedlings.

Manuscript accepted 26 Oct. 1996.

Methods

Experimental plots were located at the Wildlife Management Area near Doyle, Calif., about 72 km north of Reno, Nev. The site is an important wintering area for the Lassen-Washoe interstate mule deer herd (Dassmann and Blaisdell 1954, Leach 1956). The site, which occurs at a relatively low elevation (1,292 m) for antelope bitterbrush in the western Great Basin, supports an old growth stand of antelope bitterbrush with intermingled big sagebrush and desert peach (*Prunus andersonii* A. Gray) (Nord 1965, Clements and Young 1996). The location is within the home range of the Lassen cultivar of antelope bitterbrush (Shaw and Monsen 1995). The site has been free from domestic livestock grazing since the early 1950s, but the understory is primarily cheatgrass (*Bromus tectorum* L.) and annual forbs. Low elevation antelope bitterbrush sites are the most difficult sites for recruitment of antelope bitterbrush seedlings. Wildfires burned portions of the Wildlife Management Area in the 1950s and again in 1985. Soils on the study site are sandy, mixed, mesic, Torripsammentic Haploxerolls with inclusions of loamy, mixed, mesic Xerollic Haplargids.

The site was prepared in the fall of 1993 by disking. This tillage killed the perennial forbs (*Eriogonum nudum* Benth.), sagebrush, and rabbitbrush (*Chrysothamnus nauseosus* [Pallas] Britton), and partially dispersed in the soil the cheatgrass seedbank which is primarily located in the litter and on the soil surface (Young et al. 1969). The experimental design consisted of 4 replications of 3 by 3 m plots arranged in a completely randomized design. Nitrogen enrichment (30 kg ha^{-1} N) treatments were 1) ammonium sulfate, 2) urea, and 3) calcium nitrate. Nitrogen immobilization was obtained by adding 580 kg ha^{-1} of carbon as sucrose. Inhibition of nitrification was obtained with 2.2 kg ha^{-1} of nitrapyrin applied in an aqueous solution. Combination treatments were 1) carbon plus nitrapyrin, and 2) ammonium sulfate plus nitrapyrin. The final treatment was an untreated control. The chemical treatments were initiated in September 1993 and repeated in December 1993 and February 1994. In 1994 and 1995 all 3 treatments were repeated at the same dates on the same plots.

In October 1993, 5 caches (a cache simulates a natural rodent cache of seeds) of 25 seeds each of locally collected antelope bitterbrush were planted in each replication of each treatment. The 5 caches within each plot were arranged in an H pattern within the square plot. In February 1994, 2 caches of 25 seeds each were planted in each treatment plot. These seeds were pre-treated by soaking in a 3% aqueous solution of hydrogen peroxide (H_2O_2) to overcome moist-chilling requirements that impose dormancy (Everett and Meeuwig 1975). At the same time, 25 untreated seeds were planted as a control in each plot. The February plantings were made between the arms of the H, formed by the distribution of the caches planted in the fall.

Surface soils were collected in March and June 1994 and March and July 1995 by replication and treatment, immediately transported to the laboratory for extraction, and analyzed for nitrate (NO_{3-}) and ammonium (NH_{4+}) following approved standard procedures (AOAC 1984).

As antelope bitterbrush seedlings began emerging from the caches in March 1994, we randomly selected 2 caches from each plot to be protected from predation and placed an open-topped, wire mesh cylinder 30 cm high and 15 cm in diameter around each selected cache. During the spring emergence period the number of seedlings in each cache were counted weekly through April, and then monthly through September. Seedling heights were also measured. The cover of cheatgrass and other herbaceous species was estimated ocularly on each treatment monthly. Annually, at the maturity of cheatgrass, herbaceous vegetation was clipped, dried, and weighed on 0.1 m^2 quadrants randomly located in each plot at cheatgrass maturity.

Data were subject to analysis of variance and means of noncontinuous variables separated by Duncan's Multiple Range Test.

Results and Discussion

The long-term annual precipitation for Doyle, Calif., is 24.5 cm (Anon. 1941). Precipitation (1 July–30 June) recorded on the site for 1993–1994 was 15.5 cm, for 1994–1995 it was 73.8 cm, and for 1995 through March 1996 it was 36 cm. There was sufficient soil moisture over-winter so that the moist-chilling dormancy requirements of antelope bitterbrush seeds (Young and Evans 1976) were satisfied. We know this because of a study conducted at the same time at the location where antelope bitterbrush seeds from the same source were recovered monthly and their dormancy-germinability status determined (unpublished data). The 1993–1994 drought may have influenced subsequent seedling survival, but it should not have unduly influenced initial seedling emergence.

Initial Emergence 1994

Maximum initial seedling emergence was 44% and all treatments averaged only 20% (Table 1). Potential emergence from laboratory testing was above 90% (data not shown). The difference between potential and observed emergence is at least partially due to rodent predation. Rodent predation was verified by direct observations, immediately after seeding with night vision equipment, and evidence of rodent digging and scattering of caches in the plots.

There does not appear to be any clear-cut relationship between nitrogen status and initial emergence of antelope bitterbrush. The nitrapyrin plus ammonium sulfate treatment had significantly ($P \leq 0.05$) higher emergence than other treatments (Table 1). The carbon enrichment plots had the next highest initial emergence, with the remainder of the treatments not being significantly different from the control. The purpose of the nitrapyrin plus ammonium sulfate application was to increase NH_4+ in the seedbed and that was clearly accomplished (Table 2). The ammonium sulfate alone treatments also markedly increased NH_4+ in the surface soil with no corresponding increase in antelope bitterbrush emergence.

Seedling Survival-First Season

After initial emergence in March the number of seedlings appear to slightly increase during April (Table 1). There was some late emergence, but part of this apparent increase was due to the initial difficulty in finding emerging seedlings in caches that were widely scattered (scattered in a rough circle about 2 dm in diameter) by rodent activities. The caches were not marked because experience has shown the rodents will associate marker stakes with the caches. During the spring and summer (May–August), there was a greater than 50% decline in seedling numbers. This

Table 1. Initial emergence of antelope bitterbrush seedlings in 1994 from plots with nitrogen enrichment, immobolization, or inhibitation of nitrification.[1]

Treatment	Emergence Sampling date								
	March 18	March 29	April 11	April 28	May 13	May 26	June 7	June 20	August 30
	(%)								
Control	20c	21bc	17b	22bc	24b	21ab	7bc	10bc	10bc
Urea	10c	17c	18b	22bc	14b	12b	10c	12b	6bc
Calcium nitrate	12c	16c	27ab	21bc	22ab	21ab	20a-c	17b	15ab
Ammonium sulfate	15c	23bc	15b	14c	10b	11b	0d	0c	0c
Carbon	34b	30ab	27ab	27b	26ab	24ab	22ab	15b	11b
Nitrapyrin	12c	17c	18b	22bc	25ab	22ab	21a-c	20b	12b
Carbon + Nitrapyrin	12c	25bc	23b	30b	25ab	23ab	25ab	19b	13b
Nitrapyrin + Ammonium sulfate	44a	38a	48a	49a	36a	37a	32a	35a	25a
Mean	20w-y	23wx	24w	26w	23wx	21wx	17x-z	16yz	12z

[1]Means within columns followed by the same letter (a through d) and overall mean in rows (w through z) are not significantly different at the 0.05 level of probability as determined by Duncan's Multiple Range Test.

Table 2. Ammonium (NH_4+) and nitrate (NO_3-) nitrogen levels in the surface soils of nitrogen enrichment, immobilization, or nitrification immobilization plots in March 1994 when antelope bitterbrush seedlings were emerging and in June when competition for soil moisture occurred.[1]

Treatment	March		June	
	NO_3-	NH_4+	NO_3-	NH_4+
	----- (mg kg^{-1}) ----		----- (mg kg^{-1}) ----	
Control	3.75bc	2.95c	3.00de	2.80ef
Urea	4.75b	13.00b	6.50b	10.10c
Calcium nitrate	5.00b	6.05c	4.30c	5.60d
Ammonium sulfate	16.25a	31.00a	10.40a	25.00b
Carbon	3.85bc	5.85c	2.10ef	1.80f
Nitrapyrin	5.00b	3.75c	2.40ef	4.80de
Carbon + nitrapyrin	2.93c	2.75c	1.80f	2.00f
Nitrapyrin + ammonium sulfate	3.13c	32.25a	3.60cd	30.10a

[1]Means, within columns, followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's Multiple Range Test.

loss of seedlings is attributed to competition for moisture with herbaceous vegetation and seedling predation.

Nitrogen and Herbaceous Competition. By June 1994, all the antelope bitterbrush seedlings were dead in the ammonium sulfate nitrogen enrichment plots (Table 1). All 3 of the nitrogen enrichment treatments had significantly ($P \leq 0.05$) greater levels of NO_3- compared to the control, but the ammonium sulfate treatments were markedly higher (Table 2). Cheatgrass is usually considered the most competitive species in seedbeds in the sagebrush zone (Evans 1961). The density of this annual grass was not significantly higher in the nitrogen enrichment plots than the control, but the nitrogen immobilization and nitrification inhibition treatments had lower densities (Table 3). The nitrapyrin + ammonium sulfate treatment was very similar to the control in cheatgrass density and herbaceous cover (Table 3). The broadleafed annual tumble mustard (*Sisymbrium altissimum* L.) was much higher in density in the ammonium sulfate enriched plots. The herbaceous cover in the ammonium sulfate treated plots was more than twice that found in the control and dramatically higher than that found in the treatments with lowered NO_3-, even though the reduced nitrate levels were not statistically different from the control (Tables 2 and 3).

Table 3. Cheatgrass and tumble mustard density (per m^2) and total herbaceous vegetation cover in May 1994 for nitrogen enrichment, immobilization, or nitrification inhibition plots.[1]

Treatment	Density		Cover
	Cheatgrass	Tumble mustard	
	-------- (per m^2) ---------		(%)
Control	10a	13b	26b
Urea	10a	10b	14bc
Calcium nitrate	10a	18b	28b
Ammonium sulfate	10a	30a	63a
Carbon	8b	13b	12bc
Nitrapyrin	3b	10b	4c
Nitrapyrin + carbon	3b	10b	4c
Nitrapyrin + ammonium sulfate	10a	10b	27b

[1]Means within columns followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's Multiple Range Test.

These plots were disked in the fall before the experiment was established. The density of cheatgrass, only 10 plants per m^2, reflects partial stand reduction by disking. Tumble mustard is normally not considered as effective a competitor as cheatgrass, but in the 1994 experiment it was the most abundant species on the ammonium sulfate plots where all the antelope bitterbrush seedlings died. However, the cheatgrass plants on the ammonium sulfate treated plots were much larger, if not greater in density, than on the control plots. This is apparent in the yield of herbaceous species from the treatments at cheatgrass maturity. Ammonium sulfate treated plots had significantly ($P \leq 0.05$) higher yield (Table 4). The cheatgrass yield plots where nitrogen was immobilized or nitrification was inhibited were not significantly lower than the control.

Table 4. Herbaceous vegetation yield (g per m^2) at cheatgrass maturity (June 1994 and July 1995) in nitrogen enrichment, immobilization, or nitrification inhibition plots. Plots were harvested at peak standing crop which was considered to occur at cheatgrass maturity.[1]

Treatment	Herbaceous yield	
	June 1994	July 1995
	------- (g m^{-2}) --------	
Control	22bc	38bc
Urea	16bc	26c
Calcium nitrate	32b	46b
Ammonium sulfate	61a	82a
Carbon	4c	8d
Nitrapyrin	6c	10d
Nitrapyrin + carbon	2c	6d
Nitrapyrin + ammonium sulfate	18bc	52b

[1]Means, within columns, followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's Multiple Range Test.

Seedling Height. By the end of the initial growing season in 1994, the antelope bitterbrush seedlings were significantly ($P \leq 0.05$) taller in the plots where available nitrogen was reduced (Table 5). Part of this growth may be due to decreased competition from herbaceous species compared to the control or nitrogen enriched plots, and part may be due to the ability of antelope bitterbrush seedlings to grow satisfactorily under very low levels of available nitrogen. Antelope bitterbrush plants are known to be symbiotic nitrogen fixers when inoculated with the actinomycete *Frankia* (Dalton and Zobel 1977, Righetti et al. 1983). Klemmedson and Ferguson (1969) considered

Table 5. Antelope bitterbrush seedling height (cm) in nitrogen enrichment, immobilization or nitrification inhibitions plots 1993–1996.[1]

Treatment	Antelope bitterbrush seedling height				
	1994		1995		1996
	June	August	February	August	February
	-------------- (cm) --------------				
Control	3cd	3de	4de	8d	8c
Urea	5cd	5de	6cd	9d	13c
Calcium nitrate	8bc	8cd	26a	38a	33a
Ammonium sulfate	0d	0e	0e	0e	0d
Carbon	15a	18a	18a	24bc	22b
Nitrapyrin	12ab	12bc	11c	18c	19b
Nitrapyrin + carbon	18a	20	20ab	28b	36a
Nitrapyrin + ammonium sulfate	4cd	4de	4de	8d	13c

[1]Means within columns followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's Multiple Range Test.

antelope bitterbrush to be a true pioneering species that did not have a high demand for nitrogen.

Seedling Predation. As previously noted, about 50% of the antelope bitterbrush seedlings were lost the first summer after emergence. At emergence, protective cages were placed around 2 of the antelope bitterbrush seed caches in each plot. We did not observe seedling damage within the cages. Over all treatments, there was no significant difference in seedling survival between the open and caged seedlings (Table 6). For both the urea and calcium nitrate plots there was significantly higher survival within the cages. Seedling predation is a very significant factor at the time of seedling emergence at this site (Clements and Young 1996). After antelope bitterbrush seedlings develop their first true leaf, small rodents do not appear to be serious predators of seedlings. Based on the characteristics of the damage and tracks in the plots, most of the predation, subsequent to the development of the first true leaf was by black-tailed jackrabbits (*Lepus californicus*).

Table 6. Survival (%) of emerged antelope bitterbrush seedlings with and without protective cages during summer of 1994 in nitrogen enrichment, immobilization, or nitrification inhibition plots.[1]

Treatment	Seedling survival	
	Caged	Open
	------- (%) --------	
Control	49a	51a
Urea	82a	18b
Calcium nitrate	96a	4b
Ammonium sulfate	0	0
Carbon	36b	64a
Nitrapyrin	44a	56a
Nitrapyrin + carbon	60a	40b
Nitrapyrin + ammonium sulfate	55a	45a
Mean	60a	40a
N-enhanced	89a	11b
N-reduced	47a	53a

[1]Means, within columns, followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's Multiple Range Test.

February Seeded Antelope Bitterbrush. None of the untreated antelope bitterbrush seeds planted in February of 1994 emerged that year (data not shown). These seed caches were protected by cages, and in 1995 three seedlings appeared from separate caches, in different treatments. In 1994, one seedling emerged in a control plot from a spring seeded antelope bitterbrush seed cache where the seeds had been treated with H_2O_2. The significance of even these very low levels of subsequent emergence is that it indicates that antelope bitterbrush seeds can persist and build seedbanks.

Second Year Seedling Survival and Growth from 1994 Planting

The abundant precipitation of the winter of 1994–1995, with prolonged rainfall in the spring, produced greater growth of herbaceous vegetation compared to the previous season (Table 4). The plots enriched with ammonium sulfate had progressed to nearly complete cheatgrass dominance with 17 times the density of cheatgrass compared to the control, and over 300 times the density of cheatgrass found on the carbon plus nitrapyrin treated plots (Table 7). The surface soil levels of NO_3- nitrogen were significantly ($P \leq 0.05$) higher than the control in all the nitrogen enriched treatments in March and July 1995 (Table 8). Levels of NH_4+ nitrogen were greatly enhanced in the ammonium sulfate and ammonium sulfate plus nitrapyrin treated plots.

Table 7. Cheatgrass and tumble mustard density (per m²) and total herbaceous vegetation cover in May 1995 for nitrogen enrichment, immobilization, or nitrification inhibition plots.[1]

Treatment	Density		Cover
	Cheatgrass	Tumble mustard	
	-------- (per m^2) ---------		(%)
Control	110c	30a	35c
Urea	140c	10b	60b
Calcium nitrate	210c	8b	85a
Ammonium sulfate	1,880a	30a	100a
Carbon	10d	4b	10d
Nitrapyrin	8d	0b	12d
Nitrapyrin + carbon	6d	0b	4d
Nitrapyrin + ammonium sulfate	440b	38a	90a

[1]Means within columns followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's Multiple Range Test.

Seedling Density. The density of antelope bitterbrush seedlings remained nearly constant at the same levels as the seedling year during 1995 (Table 1), except in the ammonium sulfate plus nitrapyrin plots where they dropped dramatically (data not shown). The loss of seedlings in this treatment coincides with the elevated NO_3- nitrogen levels in this treatment and increased density of cheatgrass (Table 7 and 8).

Table 8. Ammonium (NH_4+) and nitrate (NO_3-) nitrogen levels in the surface soils of nitrogen enrichment, immobilization, or nitrification immobilization plots in March 1995 and in July when competition for soil moisture occurred.[1]

Treatment	March		June	
	NO_3-	NH_4+	NO_3-	NH_4+
	----- (mg kg^{-1}) ----		----- (mg kg^{-1}) ----	
Control	4.00d	2.05c	3.00d	2.00d
Urea	8.60c	12.80b	7.50c	9.80c
Calcium nitrate	9.89c	6.80c	8.60c	4.60d
Ammonium sulfate	22.60a	38.00a	21.80a	26.00b
Carbon	1.80e	2.16c	1.60e	1.60d
Nitrapyrin	4.20d	3.50c	2.10de	1.70d
Carbon + nitrapyrin	0.90e	1.40c	0.80e	1.10d
Nitrapyrin + ammonium sulfate	14.60b	36.25a	13.90b	38.10a

[1]Means, within columns, followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's Multiple Range Test.

Seedling Height. At the end of the 1995 growing season the antelope bitterbrush seedlings were tallest in the calcium nitrate enriched plots and in the carbon and carbon plus nitrapyrin treated plots (Table 5). These are treatments with the tallest antelope bitterbrush seedlings which reflect environments with contrasting vegetation and nitrogen regimes. The calcium nitrate treated plots were not significantly higher in cheatgrass density than the control, but supported more than 20 times as much cheatgrass density as the carbon or carbon plus nitrapyrin treated plots at the height of the 1995 growing season (Table 7). Although the density of cheatgrass in the calcium nitrate plots was lower than the ammonium sulfate treated plots, the cover of herbaceous vegetation in the calcium nitrate plots was not significantly lower (Table 7). The NO_3- nitrogen levels were much higher in the calcium nitrate treated plots than in the nitrogen immobilization or nitrification inhibition treatments in both March and July 1995.

In conclusion, immobilization of nitrogen with carbon (sucrose) applications suppressed the growth of herbaceous annuals and produced large, vigorous antelope bitterbrush seedlings. Similar results were obtained by inhibiting nitrification with applications of nitrapyrin or combining nitrapyrin and carbon applications.

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