

Soil Nitrogen Controls on Grass Seedling Tiller Recruitment

Thomas A. Monaco
Jay B. Norton
Douglas A. Johnson
Thomas A. Jones
Jeanette M. Norton

Abstract: Establishment of perennial grass seedlings is critical for repairing rangeland ecosystems in the Western United States. Mineral N in the soil may be one of the controlling factors for seedling establishment and may improve the competitive ability of perennial grasses compared to the annual grass, cheatgrass (*Bromus tectorum* L.). A greenhouse experiment was conducted to investigate the effects of immobilizing mineral soil N on tiller recruitment in grass seedlings. The perennial grasses big squirreltail (*Elymus multisetus* [J.G. Smith] M.E. Jones), "Goldar" bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), and "CD II" crested wheatgrass (*Agropyron cristatum* [L.] Gaertner x *A. desertorum* [Fisch. ex Link] Schultes) were grown alone or with cheatgrass in pots for 7 weeks. Plants were grown in soil amended with ground barley straw to produce the following four treatments designed to immobilize mineral N: (1) no straw added (control), (2) 0.25 mg straw kg⁻¹ soil, (3) 0.50 mg straw kg⁻¹ soil, and (4) 1.00 mg straw kg⁻¹ soil. Number of tillers for perennial grasses grown alone was not significantly different than perennial grasses grown with cheatgrass. Cheatgrass and crested wheatgrass plants grown alone produced significantly fewer (36 to 39 percent) new tillers per plant in the 1.00 mg kg⁻¹ treatment compared to the control. Squirreltail had significantly fewer tillers per plant in the highest straw treatment compared to the control when grown with cheatgrass. Cheatgrass produced more than twice as many tillers as the perennial grasses both in the control (high mineral N) and in the high straw treatment (low mineral N). Soil in pots containing cheatgrass had 94 percent less mineral N than soil in pots containing bluebunch wheatgrass. These results suggest that cheatgrass will likely be an effective competitor with perennial grasses even if mineral soil N is drastically reduced by microbial immobilization.

Introduction

Establishing perennial grasses in rangelands degraded by invasive annual grasses continues to be one of the

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Thomas A. Monaco, Douglas A. Johnson, and Thomas A. Jones, USDA-ARS Forage and Range Research Laboratory, Utah State University, Logan, UT 84322-6300, U.S.A. Jay B. Norton and Jeanette M. Norton, Utah State University, Plants, Soils, and Biometeorology Department, Logan, UT 84322-4820, U.S.A.

greatest challenges to repairing ecosystems in the Intermountain West. Many characteristics of the invasive annual cheatgrass (*Bromus tectorum* L.) allow it to be a superior competitor for belowground soil resources (Harris 1967). A better understanding of how changes in mineral N availability alters species competitive interactions between cheatgrass and perennial grasses (Grime and others 1987; Tilman 1984) may lead to new weed management strategies for enhancing perennial grass establishment.

Annual plants such as cheatgrass generally have a higher growth rate than longer lived perennial grasses (Arredondo and others 1998). In addition, annual grasses have higher NO₃⁻ uptake and greater N productivity (Garnier and Vancaeyzeele 1994; Poorter and others 1990), which may reduce the success of seeded perennial grasses on semiarid rangelands (Hironaka 1961). High growth rate and mineral N uptake allow cheatgrass seedlings to emerge earlier (for example, Pyke 1990) and exhibit greater early spring root growth and root proliferation in fertilized soil microsites (Caldwell and others 1991; Eissenstat and Caldwell 1988) than native perennial grasses. Recent evidence suggests that low concentrations of mineral N hinder potential shoot and root growth of both cheatgrass and native perennial grasses (Monaco and others 2003). However, it is uncertain whether reducing mineral N will improve the establishment of perennial grasses under competition with cheatgrass.

We conducted a greenhouse experiment with potted plants to evaluate the hypothesis that low mineral N would improve the competitive ability of perennial grasses when grown with cheatgrass. Specifically, we anticipated that treatments designed to reduce soil mineral N would hinder juvenile tiller recruitment of cheatgrass relatively more than that of perennial grasses. Number of tillers were evaluated because tiller numbers directly affect numerous demographic and ecological processes including plant size, competitive ability, productivity, grazing resistance, and population persistence (Briske 1991). In seedlings of perennial and annual grasses, tiller number provides an effective measure of a plant's potential growth and establishment.

Materials and Methods

The effects of low mineral N on tiller recruitment in cheatgrass, squirreltail, bluebunch wheatgrass, and crested wheatgrass were evaluated in a greenhouse experiment in Logan, UT. A coarse-loamy soil characterized as a Xeric

Torrionhent was excavated from Dugway Proving Grounds (40° 14' 23" N, 112° 50' 47" W) in Tooele County, UT, to a maximum depth of 60 cm. The top 2 cm of soil and litter were discarded to remove existing seeds in the upper soil layer. Total soil carbon (C) (13 g kg⁻¹) and total soil N (1.0 g kg⁻¹) were determined by direct combustion. The soil was passed through a 6-mm sieve to remove rocks and organic debris, and then thoroughly mixed.

Four soil treatments were established by mixing 7 kg of soil with 0, 0.25, 0.50, and 1.00 mg kg⁻¹ of ground barley straw in a 5-gallon bucket and then placing the individual soils into 8-L plastic pots. The 0 mg kg⁻¹ straw treatment served as a control. The straw treatment was designed to decrease overall mineral N (NH₄⁺, NO₂⁻, and NO₃⁻) availability by promoting microbial immobilization of mineral N with a high C:N ratio organic material. The C:N ratio of the straw was 98 as measured by direct combustion. Preliminary experiments indicated nearly all (>95 percent) extractable soil mineral N was immobilized by the 1.00 mg kg⁻¹ level within 5 days when soils were maintained at field capacity (6.9 percent soil water content). Mineral N concentrations (mg kg⁻¹) were 0.75 ± 0.01 (n = 8) in the control and 0.07 (n = 8) in the 1.00-mg-kg⁻¹ straw treatment. All pots were watered and weighed to reach field capacity for 5 consecutive days before seedlings were transplanted into pots.

Soil mineral N concentrations were analyzed according to the methods described by Hart and others (1994). A 10-g soil sample was taken, homogenized, and extracted with 2 M KCl within 4 hours. Extracts were filtered through filter paper preleached with 2 M KCl and frozen until analyzed. Concentrations of NO₂⁻ + NO₃⁻ and NH₄⁺ were analyzed colorimetrically with a flow injection autoanalyzer using standard procedures (Lachat 1989, 1990).

Seeds of each grass were germinated on blotter paper, and four seedlings were transplanted into each pot. Grasses were planted alone or in a 2:2 mixture with cheatgrass. Each grass × mixture × treatment combination was replicated four times. Pots were randomly arranged on greenhouse benches and grown for 7 weeks under 50-percent ambient solar radiation to help maintain air temperature at 70 °C during the experiment in late spring and summer (May to June 2001). Plants were watered each day with the amount of water required to reach field capacity. After 7 weeks, the number of tillers produced was counted on all plants. Many plants of each grass appeared to be N deficient in the straw treatments. As a result, all pots were fertilized at 7 weeks

with 500 ml of NPK (20-20-20) fertilizer to revive active vegetative growth. After an additional 6 weeks of growth, soil mineral N was analyzed for the control pots of grasses grown without cheatgrass competition (n = 4).

Tiller numbers were analyzed individually for each species with analysis of variance to determine the effects of straw treatment and species mixture. A Tukey's test was performed on treatment means when a significant main effect was observed. All statistical tests were performed with α = 0.05.

Results and Discussion

No significant differences in tiller numbers were observed between perennial grass plants grown alone and those grown in competition with cheatgrass (table 1). In contrast, the high straw treatment significantly reduced the number of tillers compared to the control for squirreltail when grown with cheatgrass and for crested wheatgrass when grown alone. Immobilizing mineral N with straw also significantly reduced tiller numbers of cheatgrass plants grown alone (table 2). Of the four grasses we evaluated, bluebunch wheatgrass was the only grass that did not show a significant decrease in tiller numbers under low mineral N. Our results do not support our initial hypothesis that reducing mineral N would improve the establishment of perennial grasses with cheatgrass competition.

Two alternative hypotheses may account for our results that tiller numbers of cheatgrass, squirreltail, and crested wheatgrass were negatively impacted by low soil concentrations of mineral N, while tiller numbers for bluebunch wheatgrass were not. One possible hypothesis is that high growth rates in the three responsive grasses could not be supported when mineral N was limiting (Berendse and others 1992; van der Werf and others 1993a,b). Bluebunch wheatgrass, which is known to have a lower growth rate than the other three grasses (Arredondo and others 1998), may have been the least responsive grass to the straw treatments because it is likely functioning closer to its "optimal growth and metabolic rate" when soil N is limiting (for example, Chapin and others 1987).

A second hypothesis that may partially explain the tiller number responses we observed is that fast-growing invasive annual grasses and slow-growing perennial grasses may allocate available soil N differently to shoots and roots. For

Table 1—Mean (± 1 SE, n = 4) number of tillers per plant for squirreltail, bluebunch wheatgrass, and crested wheatgrass when grown alone and in equal mixture with cheatgrass. Means within a row followed by the same letters are not significantly different.

Species		Treatment			
		Control	0.25	0.50	1.00
		----- mg barley straw kg ⁻¹ soil -----			
Squirreltail	Alone	3.8 ± 0.4	4.4 ± 0.7	3.6 ± 0.6	2.8 ± 0.6
	with cheatgrass	5.0 ± 1.0a	3.1 ± 0.3ab	2.8 ± 0.4ab	2.1 ± 0.4b
Bluebunch wheatgrass	Alone	3.8 ± 0.7	2.3 ± 0.3	2.3 ± 0.4	2.0 ± 0.6
	with cheatgrass	2.8 ± 0.6	2.8 ± 0.3	3.3 ± 0.8	3.8 ± 1.0
Crested wheatgrass	Alone	6.3 ± 0.3a	4.9 ± 0.1ab	4.3 ± 0.3b	4.0 ± 0.5b
	with cheatgrass	6.6 ± 0.6	3.9 ± 0.6	5.0 ± 0.5	4.9 ± 0.1

Table 2—Mean (± 1 SE) number of tillers for cheatgrass plants when grown alone and in equal mixture with squirreltail, bluebunch wheatgrass, and crested wheatgrass for 6 weeks. Means within a row followed by the same letters are not significantly different.

Cheatgrass	n	Treatment			
		Control	0.25	0.50	1.00
		----- mg barley straw kg ⁻¹ soil -----			
Alone	12	11.2 \pm 0.8a	9.2 \pm 0.6ab	7.5 \pm 0.6b	6.8 \pm 0.6b
With squirreltail	4	14.5 \pm 1.9	8.3 \pm 2.1	9.0 \pm 1.8	5.9 \pm 1.3
With bluebunch wheatgrass	4	12.5 \pm 1.7	11.6 \pm 2.2	7.3 \pm 0.8	9.1 \pm 1.0
With crested wheatgrass	4	12.1 \pm 2.3	8.4 \pm 0.8	9.6 \pm 1.1	7.0 \pm 0.7

example, Monaco and others (2003) found that invasive annual grasses primarily allocate N and biomass to shoots, whereas allocation was primarily to roots in the native perennial bluebunch wheatgrass. Thus, cheatgrass, squirreltail, and crested wheatgrass may have responded to reductions in soil N by altering aboveground structures (tillers), while low N conditions may have had greater impacts on root growth in bluebunch wheatgrass.

High growth rates and different shoot and root allocation patterns may have collectively enabled cheatgrass, squirreltail, and crested wheatgrass to better exploit the limiting N supply in pots and perform relatively better than or equal to bluebunch wheatgrass (fig. 1). The amount of soil N remaining in pots occupied by these grasses indicated that cheatgrass pots had the least amount of mineral N followed by crested wheatgrass, squirreltail, and bluebunch wheatgrass. Pots containing cheatgrass had 94 percent less mineral N than bluebunch wheatgrass. High consumption of mineral N by cheatgrass likely facilitated its production of more than twice as many tillers as the perennial grasses, both in the control (high mineral N) and in the high straw treatment (low mineral N). However, it remains unclear why tiller numbers for perennial grasses grown alone were not significantly different than when

grown with cheatgrass, given the ability of cheatgrass to modify mineral N availability. Additional insight into the question of whether competitive ability of perennial grasses increases relative to cheatgrass under low mineral N may become apparent with more detailed experiments (Gibson and others 1999). Our results suggest that cheatgrass will likely be an effective competitor with perennial grasses even if mineral soil N is drastically reduced by microbial immobilization.

Acknowledgments

Research was funded by USDA-ARS and USDA-CSREES Grant No. 97-38300-4892. We thank Justin Williams, Brandon Gordon, Kevin Connors, and Jacqueline Adams for assisting with plant maintenance and data collection.

References

- Arredondo, J. T.; Jones, T. A.; Johnson, D. A. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. *Journal of Range Management*. 51: 584–589.
- Berendse, F.; Elberse, W. Th.; Geerts, R. H. M. E. 1992. Competition and nitrogen loss from plants in grassland ecosystems. *Ecology*. 73: 46–53.
- Briske, D. D. 1991. Developmental morphology and physiology of grasses. In: Heitschmidt, R. K.; Stuth, J. W., eds. *Grazing management: an ecological perspective*. Portland, OR: Timber Press: 85–108.
- Caldwell, M. M.; Manwaring, J. H.; Durham, S. L. 1991. The microscale distribution of neighbouring plant roots in fertile soil microsites. *Functional Ecology*. 5: 765–772.
- Chapin, F. S., III; Bloom, A. J.; Field, C. B.; Waring, R. H. 1987. Plant responses to multiple environmental factors. *Bioscience*. 37: 49–57.
- Eissenstat, D. M.; Caldwell, M. M. 1988. Seasonal timing of root growth in favorable microsites. *Ecology*. 69: 870–873.
- Garnier E.; Vancaeyzeele, S. 1994. Carbon and nitrogen content of congeneric annual and perennial grass species: relationships with growth. *Plant, Cell and Environment*. 17: 399–407.
- Gibson, D. J.; Connolly, J.; Hartnett, D. C.; Weidenhamer, J. D. 1999. Designs for greenhouse studies of interactions between plants. *Journal of Ecology*. 87: 1–16.
- Grime J. P.; Mackey, J. M. L.; Hillier, S. H.; Read, D. J. 1987. Floristic diversity in a model system using experimental microcosms. *Nature*. 328: 420–422.
- Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs*. 37: 89–111.
- Hart, S. C.; Stark, J. M. E.; Davidson, A.; Firestone, M. K. 1994. Nitrogen mineralization, immobilization and nitrification. In: Weaver, R. W.; Angle, S.; Bottomley, P.; Bezdicek, D.; Smith, S.;

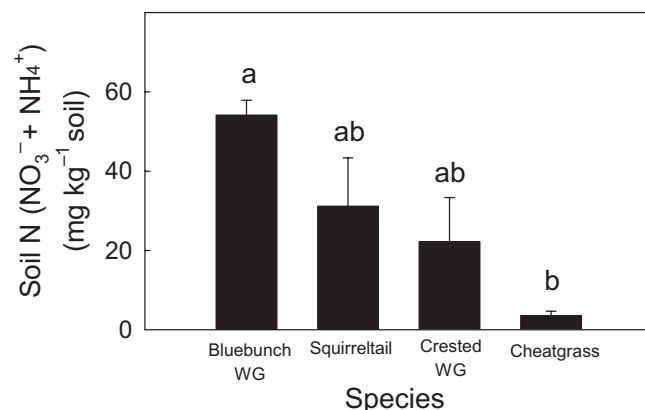


Figure 1—Mean (± 1 SE, n = 4) mineral N (NO_3^- and NH_4^+) of soils containing bluebunch wheatgrass (WG), squirreltail, crested wheatgrass (WG), and cheatgrass. Vertical bars labeled with different lowercase letters are significantly ($P < 0.05$) different.

- Tabatabai, A.; Wollum, A., eds. *Methods of soil analysis microbiological and biochemical properties*. 3d ed. Madison, WI: Soil Science Society of America: 985–1018.
- Hironaka, M. 1961. The relative rate of root development of cheatgrass and medusahead. *Journal of Range Management*. 14: 263–267.
- Lachat. 1989. Operations manual for the QuikChem automated ion analyzer. Quikchem 12-107-04-1-B (nitrate). Milwaukee, WI: Lachat.
- Lachat. 1990. Operations manual for the QuikChem automated ion analyzer. Quikchem 12-107-06-2-A (ammonium). Milwaukee, WI: Lachat.
- Monaco, T. A.; Johnson, D. A.; Norton, J. M.; Jones, T. A.; Connors, K. J.; Norton, J. B.; Redinbaugh, M. B. 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. *Journal of Range Management*. 56: 282–290.
- Poorter, H.; Remkes, C.; Lambers, H. 1990. Carbon and nitrogen ecology of 24 wild species differing in relative growth rate. *Plant Physiology*. 94: 621–627.
- Pyke, D. A. 1990. Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia*. 82: 537–543.
- Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. *Ecology*. 65: 1445–1453.
- van der Werf, A.; van Nuenen, M.; Visser, A. J.; Lambers, H. 1993a. Contribution of physiological and morphological plant traits to a species' competitive ability at high and low nitrogen supply. *Oecologia*. 94: 434–440.
- van der Werf, A.; Visser, A. J.; Schieving, F.; Lambers, H. 1993b. Evidence for optimal partitioning of biomass and nitrogen at a range of nitrogen availabilities for fast and slow-growing species. *Functional Ecology*. 7: 63–74.