Influence of Plant Functional Group Removal on Inorganic Soil Nitrogen Concentrations in Native Grasslands

Kirk W. Davies,[1] *Monica L. Pokorny,*[2] *Roger L. Sheley,*[3] *and Jeremy J. James*[4]

Authors are [1]*Rangeland Scientist,* [3]*Weed Scientist, and* [4]*Plant Physiology Scientist, Eastern Oregon Agricultural Research Center, USDA-ARS, 67826-A Highway 205, Burns, OR 97720; and* [2]*Research Associate, Montana State University, 334 Leon Johnson Hall, Bozeman, MT 59717-3120.*

Abstract

High plant functional group diversity has been hypothesized to reduce resource concentrations based on the assumption that species from one functional group acquire resources similarly to one another, while species from other functional groups acquire resources dissimilarly. To determine if functional groups use soil nutrients different from one another, we investigated the impact of removing individual functional groups on soil inorganic nitrogen (NO_3^- and NH_4^+) concentrations in the Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) habitat type in Montana. Treatments were imposed by removing 1) all plant species (total plant removal), 2) shallow-rooted (< 15 cm) forbs, 3) deep-rooted (> 15 cm) forbs, 4) all forbs (total forb removal), 5) grasses, and 6) spikemoss, compared to intact control plots. Inorganic nitrogen was measured at 2 soil depths (0–15 cm and 16–40 cm) in the spring, summer, and fall 1 year after treatment imposition. The removal of individual functional groups generally increased soil NO_3^- and NH_4^+ concentrations. Total plant removal increased NO_3^- concentrations more than removing individual functional groups. Grass removal generally increased soil NO_3^- concentrations in the 0–15-cm depth more than other functional groups removal. Whether the grass or total forb removal treatment resulted in greater soil NH_4^+ concentrations in the 0–15-cm depth depended on season. These results suggest that functional groups vary in their soil nutrient acquisition patterns and that increased functional diversity decreases soil nutrient concentrations. Therefore, maintaining or improving functional diversity may be a method to more fully utilize soil nutrients because functional groups can differ in their spatial and temporal acquisition of resources.

Resumen

La alta diversidad del grupo funcional de plantas ha sido sugerida para reducir las concentraciones de recursos, en base al supuesto de que las especies forman un grupo funcional para adquirir recursos comunes para cada uno de los miembros del grupo, mientras que las especies de otros grupos funcionales adquieren recursos diferentes. Para determinar si los grupos funcionales usan los nutrientes en forma diferente, investigamos el impacto de la remoción de grupos funcionales individuales sobre las concentraciones de nitrógeno inorgánico (NO_3^- y NH_4^+) en el suelo del hábitat "Idaho fescue" (*Festuca idahoensis* Elmer)/"Bluebunch wheatgrass" (*Pseudoroegneria spicata* [Pursh] A. Löve) en Montana. Los tratamientos se implementaron removiendo 1) todas las especies (remoción total de plantas), 2) hierbas con raíz superficial (< 15 cm), 3) hierbas con raíz profunda (> 15 cm), 4) todas las hierbas, 5) zacates, y 6) musgos, y se compararon con parcelas intactas que fueron el control. El nitrógeno inorgánico se midió a dos profundidades del suelo (0–15 cm y 16–40 cm) en primavera, verano y otoño un año después de aplicar los tratamientos. La remoción de grupos funcionales individuales generalmente incrementó las concentraciones de NO_3^- y NH_4^+ en el suelo. La remoción total de plantas incrementó las concentraciones de NO_3^- más que la remoción de grupos funcionales individuales. La remoción de zacates generalmente incrementó más las concentraciones de NO_3^- en el suelo a la profundidad de 0–15-cm que la remoción de otros grupos funcionales. La mayor concentración de NH_4^+ en la profundidad de 0–15 cm, resultado de la remoción de los zacates o la remoción total de las hierbas, dependió de la época del año. Estos resultados sugieren que los grupos funcionales difieren en sus patrones de adquisición de nutrientes del suelo y que el incremento en la diversidad funcional disminuye las concentraciones de nutrientes en el suelo. Por lo tanto, mantener o mejorar la diversidad funcional puede ser un método de utilizar más completamente los nutrientes del suelo, porque los grupos funcionales pueden diferir espacial y temporalmente en la adquisición de los recursos.

Key Words: ammonium, competition, grasslands, nitrate, removal experiment, seasonal nutrient use, soil nutrients

INTRODUCTION

Plant species are often classified into functional groups based on morphological and physiological traits (Lauenroth et al. 1978) to simplify data analysis and interpretation (Boyd and Bidwell 2002). Plant species within unique functional groups

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Correspondence: Kirk W. Davies, Eastern Oregon Agricultural Research Center, USDA-ARS, 67826-A Highway 205, Burns, OR 97720. Email: kirk.davies@oregonstate.edu

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are presumed to acquire resources from different spatial or temporal niches than species of other functional groups. However, there is little experimental evidence demonstrating that functional groups differ in resource use patterns. In addition, the importance of plant functional diversity to maintaining low resource concentrations remains largely unexplored. Previous investigations have implied that plant functional groups partition soil resources (Parrish and Bazzaz 1976; Berendse 1979; McKane et al. 1990). In contrast, Rundel et al. (2005) found that morphologically based "functional groups" did not differ physiologically in an alpine plant community. Similarly, McCarron and Knapp (2001) concluded that C_3 shrubs were not functionally similar in terms of ecophysiology to one another and that as a group they were not distinct from the dominant C_4 grass in a tallgrass prairie. Evaluation of soil nutrient concentrations following the removal of individual functional groups is needed to determine if there are differences in the utilization of soil nutrients among functional groups in rangeland ecosystems.

The importance of plant functional diversity in maintaining low soil nutrient concentrations also needs to be evaluated. Excess resources can increase the susceptibility of the plant communities to exotic plant invasions (Dukes 2001; Pokorny et al. 2004; Sheley and Carpinelli 2005). Functional groups coexisting in one plant community are probably exploiting soil nutrients from different spatial and temporal niches (Parrish and Bazzaz 1976; Berendse 1979; McKane et al. 1990). Dissimilarity in soil nutrient use patterns among functional groups would imply that functional diversity is important to utilizing soil nutrients throughout the growing season. Increased functional group diversity has been presumed to result in greater niche occupation and thus greater total resource use (Lavorel et al. 1999; Symstad 2000; Pokorny et al. 2005). If functional groups are utilizing soil nutrients from different locations or at different time periods, functional group removal would be anticipated to increase soil nutrient concentrations and potentially increase the vulnerability of the plant community to weed invasion.

The loss of functional groups has been speculated to alter soil nutrient concentrations, water cycling, and community production (Hooper and Vitousek 1997; Tilman et al. 1997; Hooper 1998). Dukes (2001) reported that increased functional diversity reduced resource concentrations in southern California; however, his functional groups included introduced species. Extrapolating his findings to native, perennial vegetation and/or different regions may not be appropriate. To increase resistance of plant communities to exotic plant invasions and improve the success of restoration projects, land managers need to know if increased functional group diversity lowers soil nutrient concentrations and the potential for community invasibility. This will provide land mangers with information to assess the potential implications of disturbances, such as selective herbivory or herbicide application, that may decrease functional group diversity.

The objectives of this study were to determine if plant functional groups acquire soil nutrients from different locations and time periods and if functional group diversity is important in maintaining low nutrient concentrations. The impact of removing functional groups on inorganic forms of soil nitrogen (NO_3^- and NH_4^+) was evaluated in the Idaho fescue (*Festuca idahoensis* Elmer)/bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) habitat type (Mueggler and Stewart 1980). Inorganic forms of nitrogen were selected for evaluation because nitrogen is often the most limiting soil nutrient to rangeland plant communities (Owensby et al. 1972; Bobbink 1991; Holechek et al. 1998; Paschke et al. 2000) and was found to be the most limiting resource to plant growth in this habitat type (Krueger-Mangold et al. 2004). Nitrate and NH_4^+ were analyzed separately because plants can prefer one form over another and partitioning a nutrient by form may be an evolutionary mechanism for coexistence in plant communities (McKane et al. 2002). We specifically hypothesized that removing individual functional groups would increase soil NO_3^- and NH_4^+ concentrations and that the pattern of increase in soil NO_3^- and NH_4^+ concentrations would depend on which functional group was removed from the plant community.

METHODS

Study Sites

This study was conducted on 2 sites about 70 km west of Bozeman, Montana (lat 45°34′N, long 111°34′W) in the Idaho fescue/bluebunch wheatgrass habitat type (Mueggler and Stewart 1980). Common forbs of this habitat type include *Artemisia ludoviciana* Nutt., *Lupinus* sp., and *Balsamorhiza sagittata* (Pursh) Nutt. (Mueggler and Stewart 1980).

Sites are approximately 1 625 m above sea level on an east–northeast aspect of a 20-degree slope. Soils at site 1 are a loamy-skeletal, mixed, frigid, active Typic Haplocryolls, and soils at site 2 are a coarse-loamy, mixed, frigid, active Typic Haplocryolls. Average precipitation is 410 mm annually. The study sites have been livestock grazed for 50–60 years, with sporadic grazing in the last 10 years prior to this study (Pokorny et al. 2005). Each site was fenced to prevent livestock and wildlife use during the study. Sites differed in their soil NO_3^-, S, and P concentrations and vegetation density and biomass (Pokorny et al. 2005). Precipitation was 73% and 84% of the long term (1892–2005) for the 1999–2000 and 2000–2001 crop years (September–September), respectively, at the weather station at Montana State University, Bozeman, Montana (National Oceanic and Atmospheric Administration 2006).

Experimental Design

Vegetation was categorized into functional groups based on morphological characteristics. Forb excavation revealed a distinct break in rooting depths at 15 cm. To more thoroughly evaluate the potential for functional group removal influences on NO_3^- and NH_4^+ soil concentrations, shallow-rooted (< 15 cm) forbs were distinguished from deep-rooted (> 15 cm) forbs. Treatments were removal of all plant materials (total removal), shallow-rooted forbs, deep-rooted forbs, all forbs, grasses, spikemoss, and intact plots served as a control. At each site, treatments were arranged in a randomized block design and replicated 4 times. Treatment replications were applied to 2 × 2 m plots.

Targeted functional groups were removed by brushing the foliage with a 6% glyphosate (N-[phosphonomethyl] glycine) solution in May 2000. Disturbance to nontarget functional groups and soil was minimized using this method. Treatments were checked biweekly to maintain desired composition, but little maintenance was required. Removal experiments are more useful than synthetically assembled plant community (additions) experiments for understanding the effects of varied functional group composition within plant communities (Díaz et al. 2003). Additional justification for functional group removals over additions is presented in Pokorny et al. (2005). A potential limitation of our study was that we could not remove belowground biomass to control for nutrient turnover from decomposing roots. However, we believe it had little influence on our results. Gill and Jackson (2000), in a summary of the literature, estimated that over half the root biomass in grasslands naturally turns over each year. Treatment-by-season interactions in our data and the lack of correlations between remaining aboveground biomass and inorganic N concentrations also suggested that root turnover had a limited influence on our results.

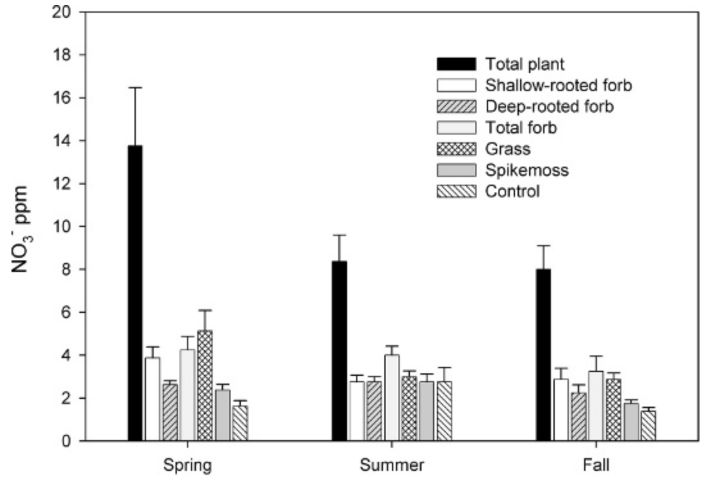

Figure 1. Soil NO_3^- concentrations (means + SE) at the 0–15-cm depth for the total plant, shallow-rooted forb, deep-rooted forb, total forb, grass, and spikemoss removal and control treatments.

Soil Sampling

The second growing season following functional group removals (2001), soils were sampled in the spring (late May), summer coinciding with peak production (mid-July), and fall when 95% of the vegetation had senescent (late August). Three 2.2-cm-diameter soil cores were randomly collected from 0–15-cm and 16–40-cm soil depths in each treatment replicate in each season. The 3 soil cores were compiled into 1 sample for each depth in each treatment replicate in each season for analysis. Nitrate and NH_4^+ concentrations were determined on a 1 M KCl extract (5 g soil, 50 ml extractant) (Mulvaney 1990). Extracted soil solutions were analyzed by MDS Harris Lab, Lincoln, Nebraska.

Statistical Analysis

Data were analyzed separately for each soil depth. Data not normally distributed were square-root transformed to stabilize variance. Results were back-transformed for reporting purposes. Because we were concerned that removing different functional groups may have affected total plot biomass and thus inorganic nitrogen concentrations, we analyzed the influence of remaining biomass on soil inorganic nitrogen concentrations. When remaining biomass was included as a covariate in the analyses of the effects of removing different functional groups, it and its interactions were not correlated with soil inorganic nitrogen concentrations ($P > 0.05$). Thus, remaining biomass was not included in the final analyses. Statistical significance of all tests was set at $P < 0.05$.

Repeated-measures analysis of variance using Proc Mixed (SAS Institute 2001) with fixed and random effects were used to determine if functional group removal treatments differed in their NO_3^- and NH_4^+ soil concentrations and to compare individual functional group removal treatments to the control and total removal treatments. Season was analyzed with a repeated statement and site and block were included as random effects. Treatments were considered a fixed effect. Interactions between random effects and other effects were considered random effects. Total forb removal was compared to removal of other functional groups by excluding shallow- and deep-rooted forbs from the model because they were not independent of one another. Shallow- and deep-rooted forb removal treatments were compared to the other functional group removal treatments without the total forb removal treatment in the model.

RESULTS

Functional Group Comparison

When forbs were divided into 2 functional groups, soil NO_3^- concentrations at both depths varied by which functional group was removed ($P < 0.01$) (Figs. 1 and 2). At the upper depth (0–15 cm), the interaction between season and which functional group was removed influenced soil NO_3^- concentrations ($P < 0.01$). Grass removal generally increased the NO_3^- concentrations in the upper soil depth more than removal of other functional groups. Soil NO_3^- concentrations where other functional groups were removed varied in relation to one another by season. At the lower soil depth (16–40 cm), shallow-rooted forb removal generally increases NO_3^- concentrations more than removing other functional groups. Soil NH_4^+ concentrations did not depend on which functional group was removed at either the upper or the lower depth ($P = 0.13$ and 0.78, respectively; Figs. 3 and 4).

When all forbs were removed as a single functional group, soil NO_3^- and NH_4^+ concentrations at the upper depth both depended on which functional group was removed ($P \leq 0.01$ and 0.04, respectively; Figs. 1 and 3). The interaction between season and which functional group was removed influenced soil NH_4^+ concentrations ($P = 0.02$). Soil NO_3^- concentrations were generally greater where grass and forbs had been removed compared to where spikemoss was removed. Whether removing all forbs or grasses produced higher soil NH_4^+ concentrations depended on season. The difference in soil NH_4^+ concentrations where spikemoss was removed compared to where other functional groups were removed varied by season. Soil NO_3^- and NH_4^+ concentrations at the lower depth

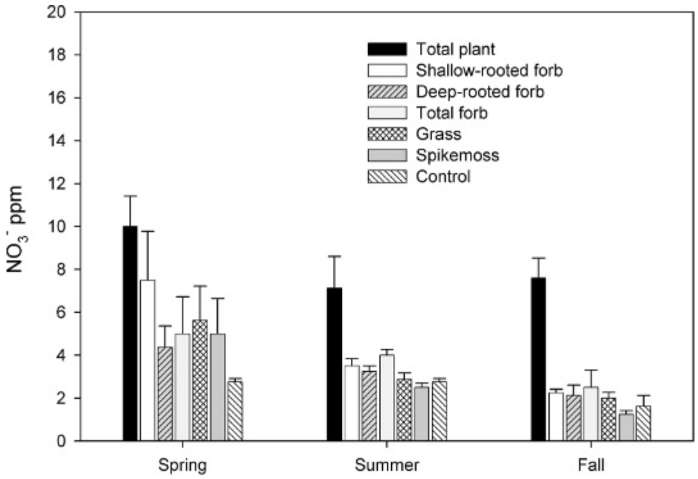

Figure 2. Soil NO_3^- concentrations (means + SE) at the 16–40-cm depth for the total plant, shallow-rooted forb, deep-rooted forb, total forb, grass, and spikemoss removal and control treatments.

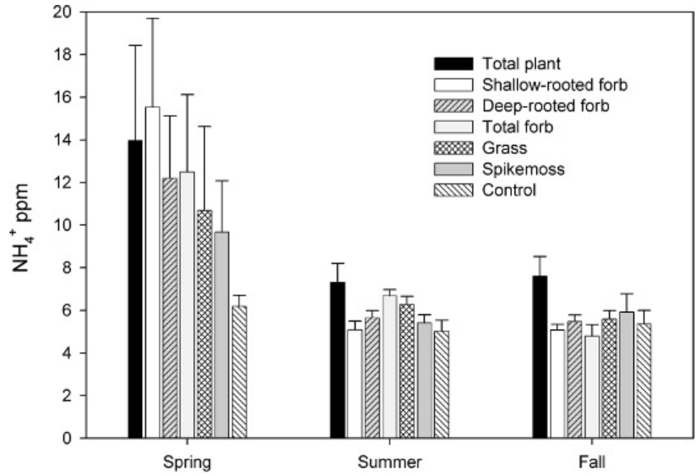

Figure 4. Soil NH_4^+ concentrations (means + SE) at the 16–40-cm depth for the total plant, shallow-rooted forb, deep-rooted forb, total forb, grass, and spikemoss removal and control treatments.

did not vary with which functional group was removed ($P = 0.54$ and 0.83, respectively; Figs. 2 and 4).

Total Plant Removal

Inorganic N concentrations in the upper soil depth were greater in the total plant removal treatment compared to the control ($P \leq 0.01$ and 0.01, respectively; Figs. 1 and 3). Total plant removal produced NH_4^+ and NO_3^- concentrations in the upper soil depth that ranged from 1.2- to 2.2-fold and 3.0- to 8.5-fold higher, respectively, than the control. Total plant removal also increased NO_3^- and NH_4^+ concentrations at the lower soil depth ($P \leq 0.01$ and 0.02, respectively; Figs. 2 and 4). The magnitude of differences in NH_4^+ and NO_3^- concentrations at the lower soil depth between the total plant removal and control treatments was similar to the upper soil depth. Soil NO_3^- and NH_4^+ concentrations in the upper depth varied by season ($P < 0.01$) but at the lower depth did not vary with season ($P = 0.12$ and 0.20, respectively).

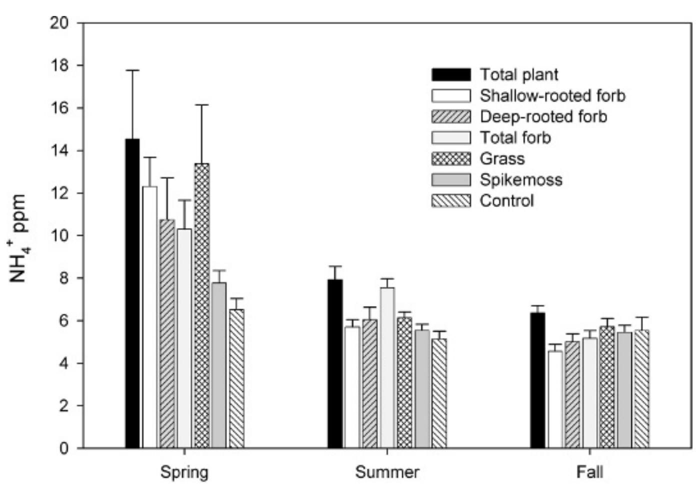

Figure 3. Soil NH_4^+ concentrations (means + SE) at the 0–15-cm depth for the total plant, shallow-rooted forb, deep-rooted forb, total forb, grass, and spikemoss removal and control treatments.

Shallow-Rooted Forb Removal

Removing shallow-rooted forbs generally produced higher NO_3^- and NH_4^+ concentrations in the upper soil depth compared to the control ($P < 0.01$; Figs. 1 and 3; Table 1). Soil NO_3^- and NH_4^+ concentrations in the upper soil depth where shallow-rooted forbs were removed were up to 2.4- and 1.9-fold higher, respectively, than the control. Shallow-rooted forb removal also generally increased NO_3^- and NH_4^+ concentrations at the lower soil depth ($P = 0.01$ and 0.04, respectively; Figs. 2 and 4). Shallow-rooted forb removal produced soil NH_4^+ and NO_3^- concentrations at the lower depth that were up to 2.5- and 2.7-fold higher, respectively, than the control. Total plant removal increased NO_3^- concentrations more than shallow-rooted forb removal at both soil depths ($P < 0.01$), but they did not differ in NH_4^+ concentrations at the upper and lower soil depths ($P = 0.12$ and 0.62, respectively). Soil NO_3^- concentrations were up to 3.4-fold higher in the total plant removal treatment than shallow-rooted forb removal treatment. Soil NO_3^- and NH_4^+ concentrations varied by season at both depths when removing shallow-rooted forbs were compared to the total plant removal and control treatments ($P < 0.05$).

Deep-Rooted Forb Removal

At both soil depths, removing deep-rooted forbs generally increased NO_3^- and NH_4^+ concentrations compared to the control with increases up to 2-fold ($P < 0.04$; Figs. 1–4; Table 1). Removing deep-rooted forbs increased NO_3^- concentrations at both soil depths less than total plant removal ($P < 0.01$). Differences in NO_3^- soil concentrations were up to 5.2-fold higher in the total plant removal treatment. Concentrations of NH_4^+ did not differ between removing deep-rooted forbs and total plant removal at the upper and lower soil depths ($P = 0.15$ and 0.28, respectively). Soil NO_3^- and NH_4^+ concentrations varied by season at both depths when comparing removing deep-rooted forbs to the control and total plant removal treatments ($P < 0.05$), except when NO_3^- concentrations at the lower soil depth were compared between removing deep-rooted forbs and total plant removal ($P = 0.10$).

Table 1. *P* values for differences in NO_3^- and NH_4^+ soil concentrations when comparing functional group removal treatments to the total plant removal and control treatments.[1]

Functional group removal	Nitrogen form	Sample depth (cm)	Total plant removal	Control
Shallow-rooted forb	NO_3^-	0–15	$P < 0.01$*	$P < 0.01$*
	NO_3^-	16–40	$P < 0.01$*	$P < 0.01$*
	NH_4^+	0–15	$P = 0.12$	$P < 0.01$*
	NH_4^+	16–40	$P = 0.62$	$P = 0.04$*
Deep-rooted forb	NO_3^-	0–15	$P < 0.01$*	$P < 0.01$*
	NO_3^-	16–40	$P < 0.01$*	$P = 0.03$*
	NH_4^+	0–15	$P = 0.15$	$P = 0.04$*
	NH_4^+	16–40	$P = 0.28$	$P = 0.04$*
Total forb	NO_3^-	0–15	$P < 0.01$*	$P < 0.01$*
	NO_3^-	16–40	$P < 0.01$*	$P < 0.01$*
	NH_4^+	0–15	$P = 0.17$	$P < 0.01$*
	NH_4^+	16–40	$P = 0.38$	$P = 0.07$
Grass	NO_3^-	0–15	$P < 0.01$*	$P < 0.01$*
	NO_3^-	16–40	$P < 0.01$*	$P = 0.02$*
	NH_4^+	0–15	$P = 0.49$	$P = 0.02$*
	NH_4^+	16–40	$P = 0.30$	$P = 0.17$
Spikemoss	NO_3^-	0–15	$P < 0.01$*	$P = 0.15$
	NO_3^-	16–40	$P < 0.01$*	$P = 0.24$
	NH_4^+	0–15	$P = 0.02$*	$P = 0.15$
	NH_4^+	16–40	$P = 0.14$	$P = 0.08$

[1]Asterisk indicates significant differences between treatments ($P < 0.05$).

Total Forb Removal

Total forb removal increased NO_3^- concentrations at both soil depths compared to the control ($P < 0.01$), with increases ranging from 1.5- to 2.6-fold (Figs. 1 and 2; Table 1). Soil NH_4^+ concentrations in the upper soil depth were generally higher where all forbs had been removed than the control ($P < 0.01$), with increase up to 1.6-fold (Fig. 3). At the lower soil depth, no difference in NH_4^+ concentrations were detected when comparing total forb removal to the control ($P = 0.07$; Fig. 4). Total forb removal did not increase NO_3^- concentrations as much as total plant removal at both soil depths ($P < 0.01$); however, no differences were detected between NH_4^+ soil concentrations at either depth ($P > 0.05$). Soil NO_3^- concentrations were 1.8–3.4-fold greater with total plant removal compared to total forb removal. Soil NO_3^- and NH_4^+ concentrations varied with season when comparing total forb removal to total plant removal and the control ($P < 0.05$), with 2 exceptions. Soil NO_3^- concentrations did not vary with season at the upper depth when comparing total forb removal to the control ($P = 0.19$) or at the lower depth when comparing total forb removal to total plant removal ($P = 0.07$).

Grass Removal

At the upper soil depth, grass removal increased NO_3^- and NH_4^+ concentrations up to 3.2- and 2.1-fold, respectively, compared to the control ($P < 0.01$ and $= 0.02$, respectively; Figs. 1 and 3; Table 1). Grass removal produced higher NO_3^- concentrations than the control at the lower soil depth ($P = 0.02$; Fig. 2), but NH_4^+ concentrations did not differ ($P = 0.17$; Fig 4). Grass removal increased soil NO_3^- concentrations up to 3.2-fold. Total plant removal increased NO_3^- concentrations more at both soil depths than grass removal ($P < 0.01$), with increases up to 3.8-fold. Soil NH_4^+ concentrations did not differ between total plant removal and grass removal at the upper and lower soil depths ($P = 0.49$ and 0.30, respectively). Soil NO_3^- and NH_4^+ concentrations varied by season at both depths when comparing grass removal to the control and total plant removal ($P < 0.05$), except when NH_4^+ concentrations in the upper soil depth grass removal were compared to total plant removal and the control ($P = 0.07$ and 0.11, respectively).

Spikemoss Removal

At both soil depths, NO_3^- and NH_4^+ concentrations did not differ between spikemoss removal and the control ($P > 0.05$; Figs. 1–4; Table 1). Total plant removal produced higher NO_3^- concentration at both soil depths compared to spikemoss removal ($P < 0.01$). Total plant removal also produced higher NH_4^+ concentration at the upper soil depth than spikemoss removal ($P = 0.02$), but they did not differ at the lower soil depth ($P = 0.14$). Soil NO_3^- and NH_4^+ concentrations varied with season when comparing spikemoss removal to the control and total plant removal ($P < 0.05$).

DISCUSSION

The importance of plant functional group diversity to maintaining low resource concentrations has profound implications to community stability (Hooper and Vitousek 1997; Tilman et al. 1997; Hooper 1998; Dukes 2001; Pokorny et al. 2004; Sheley and Carpinelli 2005). Management actions that results in the selective removal of a functional group or groups can potentially decrease the stability and increase community invasibility. The general increase in soil NO_3^- and NH_4^+ concentrations with the removal of a functional group demonstrated that functional group diversity is important to maintaining low soil inorganic N concentrations. Similar to our results, Dukes (2001) reported that high functional group diversity reduced resource concentrations in grassland microcosms. These results supported our hypothesis that removing individual functional groups would increase soil NO_3^- and NH_4^+ concentrations.

Soil NO_3^- concentrations were dependent on which functional group was removed, which implies that functional groups have different roles within the plant community. Interactions between season and functional group removal suggest that soil nutrient acquisition of individual functional groups vary throughout the growing season. Similarly, Booth et al. (2003) reported that seasonal patterns of water and N uptake varied among an annual grass, perennial grass, and shrub species. These results supported our hypothesis that soil NO_3^- concentrations depended on which functional group was removed. Results were not conclusive enough to accept the hypothesis that soil NH_4^+ concentrations would also vary with which functional group was removed. However, when the total forb removal treatment was included in the model, soil NH_4^+ concentration at the upper depth depended on the interaction between season and functional group removal and was, thereby, consistent with our hypothesis. Similar to our results, Golluscio and Sala (1993) reported that functional groups varied in the portion of the water resource they used. Dukes (2001) results also suggested that soil resource use varied among functional groups.

The general trend of soil NO_3^- concentrations being more affected by removal treatments than soil NH_4^+ concentrations may suggest that plant species in this system prefer NO_3^- over NH_4^+. McKane et al. (2002) demonstrated that plants can prefer one form of nitrogen over another.

The increase in soil NO_3^- and NH_4^+ concentrations with individual functional group removals, combined with the magnitude of these increases often depending on which functional group was removed and/or varying with the interaction between season and functional group removal, suggests that functional groups acquire soil nutrients from different locations and at different time periods. Our results support previous research that has implied functional groups occupy different niches (Parrish and Bazzaz 1976; Berendse 1979; McKane et al. 1990). Inconsistent with our findings, Symstad (2000), McCarron and Knapp (2001), and Rundel et al. (2005) suggested that functional groups do not necessarily differ in function, but these inconsistencies could be due to inadequate separation of functional groups (Symstad 2000).

The results of this study reveal the importance of proper separation of functional groups. We assumed that categorizing forbs into 2 functional groups would be insightful, but there was little difference in inorganic soil nitrogen concentrations between deep- and shallow-rooted functional group removal treatments. This suggests that separating forbs into functional groups based on rooting depths in this system is not justified. Symstad (2000) suggested that when functional groups do not necessarily differ in function, the underling problem may be inadequate separation of functional groups. Proper separating of plant communities into functional groups is needed for functional group classifications to be useful to management.

Our results demonstrate the importance of managing for a greater diversity of functional groups on rangelands. Grass removal generally increased inorganic nitrogen more in the spring than total forb removal (Fig. 2). However, in the summer, total forb removal generally had higher inorganic nitrogen concentrations compared to grass removal. This may be a function of differing phenology between grasses and forbs because grasses in this system generally mature earlier in the growing season than forbs. However, this investigation does not enable us to sort out the various morphological, physiology, and environmental variables or test the causal mechanisms. These results also imply that during some times of the year, forbs are as critical as or more critical than grasses in maintaining low soil nutrient concentrations. However, functional groups, other than grasses, have not been the primary focus of most land management practices (Fuhlendorf and Engle 2001). Results from this study and Pokorny et al. (2004, 2005) suggest that land managers should focus on more than just the grass functional group. We suggest that functional group classification systems can assist land managers in accomplishing this goal and that they are an important and practical tool to simplify revegetation and rangeland management.

Our results imply that functional group diversity is important to community stability, community invasibility, and ecosystem function. Tilman et al. (1997) also suggested that alterations to functional diversity would likely have significant impacts on ecosystems. The removal of a functional group likely increases the susceptibility of plant communities to invasive species by decreasing niche occupation and increasing resource concentrations. In support of this supposition, previous research concluded that increasing functional group diversity reduced the success of invasions (Symstad 2000; Dukes 2001). Pokorny et al. (2005) also suggested that functional group diversity was an important factor contributing to plant community resistance to invasions. Our results demonstrated reduced functional group diversity increased soil inorganic N concentrations, which could increase the potential of invasive plant establishment. Resource increases, even transient pulses, can increase invasibility (Huenneke et al. 1990; Burke and Grime 1996; Davis et al. 2000). Thus, rangeland communities are more stable with a diversity of functional groups.

MANAGEMENT IMPLICATIONS

Plant functional groups are an important and useful classification system for land managers. Functional groups may be a more valuable classification than species for management and revegetation efforts because this classification can simplify management by creating species groups that acquire soil nutrients from different locations and at different time periods within plant communities. Management based on functional group classification may also be more effective because high species diversity doesn't always translate to high functional diversity within a plant community. Caution should be exercised, however, when delineating plant functional groups because the appropriate separation of functional groups may be community dependent. Promoting and maintaining high functional group diversity should be a primary objective of land managers to maintain low resource concentrations and decrease the invasibility of plant communities. The response of functional groups to management actions should be monitored and adjusted if they are disproportionately impacting specific functional groups. Management should also limit disturbances that selectively reduce or eliminate functional groups. Of particular concern is to minimize nontarget plant mortality induced by herbicide applications and undesirable selective herbivory. Revegetation efforts should focus on establishing functionally diverse plant communities to increase the likelihood of target plant dominance and to more fully utilize resources.

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