# Different Root and Shoot Responses to Mowing and Fertility in Native and Invaded Grassland

Vasiliki G. Balogianni,[1] Scott D. Wilson,[2] Brenda M. Vaness,[3] Andrew S. MacDougall,[4] and Bradley D. Pinno[5]

Authors are [1]PhD Student and [2]Professor, Biology Department, University of Regina, Regina, SK S4S0A2, Canada; [3]Research and Development Co-ordinator, Western Ag Innovations, Sherwood, ND 58782, USA; [4]Associate Professor, Department of Integrative Biology, University of Guelph, Guelph, ON N1G2W1, Canada; and [5]Research Scientist, Northern Forestry Centre, Natural Resources Canada, Canadian Forest Service, Edmonton, AB T6H3S5, Canada.

## Abstract

Grassland root responses to mowing and fertility are less well known than shoot responses, even though as much as 90% of productivity in semiarid grasslands occurs belowground. Thus, understanding root responses may aid the management of invasive grassland species such as *Agropyron cristatum* (L.) Gaerth (crested wheatgrass). We asked whether root responses reflect shoot responses to mowing and fertility in native grassland with and without a major component of crested wheatgrass. We subjected grasslands in northern Montana to 5 yr of mowing at two nitrogen (N) levels and followed root responses with minirhizotrons. Surprisingly, the roots of both native and invaded grasslands were unaffected by mowing and N addition, despite significant changes in shoot mass across both vegetation types. Root length was significantly greater beneath areas heavily occupied by crested wheatgrass ($363$ m $\cdot$ m$^{-2}$ image $\pm 200$, mean $\pm$ standard deviation [SD]) than areas comprising largely native grassland ($168$ m $\cdot$ m$^{-2}$ image $\pm 128$ SD). Also, no interactions occurred between year and any other factor, indicating that there were no changes in belowground responses over the 5 yr examined. In contrast, shoot mass was significantly reduced by mowing (not mowed, $612$ g $\cdot$ m$^{-2}$ $\pm 235$ SD; mowed, $239$ g $\cdot$ m$^{-2}$ $\pm 81$ SD) and was significantly increased by N addition (no added N, $380$ g $\cdot$ m$^{-2}$ $\pm 215$ SD; added N, $488$ g $\cdot$ m$^{-2}$ $\pm 287$ SD). In conclusion, 5 yr of mowing decreased shoot mass, but not root mass. On the other hand, 5 yr of N addition increased shoot mass, but not root mass. Given that most production and competition in grasslands occurs belowground, this suggests that mowing may not be a successful tool for reducing crested wheatgrass root length, regardless of soil fertility.

Key Words: belowground, crested wheatgrass, invasion, management, minirhizotron, nitrogen

## INTRODUCTION

Management of invasive species in the semiarid grasslands of North America is often required because widely seeded exotic plants have subsequently invaded native grasslands (Foster et al. 2003; Henderson and Naeth 2005; Otfinowski and Kenkel 2010). *Agropyron cristatum* (L.) Gaerth (crested wheatgrass) is one of the most widespread invasive species in the northern Great Plains and is difficult to control (Vaness and Wilson 2007). Root traits may give crested wheatgrass an advantage over native species. Crested wheatgrass has greater root length (MacDougall and Wilson 2011) and density (Caldwell et al. 1996) than native grasses and can invade disturbed soil more rapidly (Eissenstat and Caldwell 1989).

Grazing and mowing are common grassland management practices (Bork et al. 2008) that have been suggested to both facilitate (Sinkins and Otfinowski 2012) and inhibit (McKenzie 1997) the invasion of native communities by exotic species. Shoot responses to grazing in grasslands vary with grazing intensity (Van der Maarel and Titlyanova 1989). Heavy grazing and simulation of grazing by clipping reduces crested wheatgrass shoot mass (Wilson and Pärtel 2003; Bleak and Plummer 2006; Hansen and Wilson 2006). However, according to the Herbivore Optimization Hypothesis, moderate grazing should maintain net primary production or stimulate it (Leriche et al. 2003). This hypothesis was supported by experiments with crested wheatgrass where lower intensity grazing and clipping had no effect (Roundy et al. 1985) or even increased crested wheatgrass shoot mass (Frank et al. 2002).

Although aboveground effects of grazing on grasslands are well studied, belowground effects are less studied. Belowground interactions are relatively important in semiarid grasslands: net primary productivity (NPP) is controlled by belowground resources such as water and nitrogen (Coffin and Laurenroth 1992), and 90% of NPP (Steinaker and Wilson 2005) and most plant competition occurs belowground (Cahill 2003). Therefore, understanding the impact of grazing or mowing on roots may be crucial in understanding grassland invasions (Bork et al. 2008).

Root responses to grazing measured in laboratory experiments, as well as core-harvesting studies from field trials, suggest that heavy grazing or clipping reduces (Frank et al. 2002; Gao et al. 2008; Bagchi and Richie 2010) or has no effect (Loeser et al. 2004) on grass root productivity. Results from continuous, nondestructive minirhizotron observations at greater depths in natural grassland also produce mixed results

(Ziter and MacDougall 2013), depending on whether biomass removal is applied by grazing or mowing. Grazing can reduce root length in some grass species (Becker et al. 1997), but mowing can increase it (Hubbard 2003). The few studies that deal with crested wheatgrass root response to grazing or mowing also report contradictory results, such as reduced root productivity after clipping (Roundy et al. 1985) and mowing (Richards 1984), increased root productivity after grazing from native mammals (Frank et al. 2002), or no effect (Miller and Rose 1992).

Another major factor promoting grassland invasion by exotics is elevated soil fertility (Foster et al. 2009). In particular, raised nitrogen (N) levels increase invasion in N-limited ecosystems such as semiarid grasslands (Brooks 2003). Crested wheatgrass shows higher root growth than native grasses in nutrient-rich soil patches (Jackson and Caldwell 1989). Therefore, to increase generality of our results, we conducted our field experiment at two N levels.

Our main research question was whether the decrease in shoot mass caused by mowing is accompanied by a decrease in root length and mass. We examined both crested wheatgrass and native grasses, at two N levels and over 5 yr.

## METHODS

### Study Area

We worked in Medicine Lake National Wildlife Refuge, Montana (48°28′16″N, 104°22′16″W). Native grassland was dominated by the $C_4$ grass *Bouteloua gracilis* (Wild. ex Kunth.) Lag. ex Griffiths, the $C_3$ grass *Pascopyrum smithii* (Rydb.) Á. Löve, and *Selaginella densa* Rydb. Average annual precipitation is 34 cm, the average July temperature is 20.8°C, and the average January temperature is –13.1°C (NOAA 2012). Soils are Mollisol Ustolls (ftp://ftp-fc.sc.egov.usda.gov/NSSC/Soil_Taxonomy/maps.pdf) well-drained loam (A-horizon, 0–15 cm) over clay-loam (B-horizon, 15–100 cm), $> 200$ cm above the water table (USDA-NRCS 2012).

We sampled 40 plots (5 m diameter, $> 10$ m apart) scattered across 6 ha. Half the plots were randomly located in grassland dominated by native species, and half in grassland dominated by crested wheatgrass (67% cover of crested wheatgrass in 2011; V. Balogianni, unpublished data), and all plots were c. 200 m from fireguards that had been sown with crested wheatgrass during 1940–1960 (J. Rodriguez, unpublished data). Native grassland sites had $\approx 17\%$ cover of crested wheatgrass in 2011 (V. Balogianni, unpublished data). The two vegetation types had similar topography and soils. Previous management included occasional moderate grazing and prescribed burning every 5–7 yr (M. Borgreen, unpublished data).

In each vegetation type, we randomly assigned five plots to each of the following treatments: 1) no treatment (controls), 2) mowing, 3) N addition, 4) mowing, and N addition. Mowed plots were mowed at $\approx 2$ cm above the ground. Mowing was applied every May during 2006–2011. In late June, plots were mowed again at $\approx 5$ cm above the ground. N was added twice a year, at the same time as mowing. Plots received $2.7 \text{ g} \cdot \text{m}^{-2}$ of urea (46-0-0) annually. N application rates mimicked the highest deposition rates of N in the northern Great Plains (22 $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) (Köchy and Wilson 2001). Two years after the

beginning of the experiment, it was found that N addition had no effect on biomass, so N addition rates were increased to 44 $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ during 2008–2011.

### Root and Shoot Measurements

We measured root length during five growing seasons (2007–2011) using minirhizotrons (Bartz Technology Corporation, Santa Barbara, CA). Although minirhizotrons may underestimate root production due to its small sampling area (Taylor et al. 2013), they detect more root length than do harvest methods (Hendricks et al. 2006) and allow repeated nondestructive sampling of identical locations without continuing soil disturbance. In each plot, one transparent rhizotron tube (180 cm long, 5 cm internal diameter) was installed at a 45° angle to the soil surface in spring 2006. Tube length within the soil varied (40–160 cm) according to the presence of rocks, which prevented deeper installation, but even the shortest length sampled the top layer of grassland soil that contains the bulk of roots (Steinaker and Wilson 2005) and organic carbon (Jobbagy and Jackson 2000). Five images (each $18 \times 14$ mm) per tube were collected in late July or early August annually, at 4, 8, 15, 21, and 27 cm vertically down from the soil surface. Root length and diameter were measured in the images.

Root mass was calculated from root length by determining specific root length (SRL; $\text{m} \cdot \text{g}^{-1}$ root) for three diameter classes ($< 0.2$ mm, 0.2–0.3 mm, 0.3–2.0 mm). Diameter classes were selected based on the diameter of roots we encountered in sampled root cores. Roots for determining SRL were collected in May 2011 at a depth of 10–20 cm (with 5.5 cm diameter cores) within 2 m of 16 rhizotron tubes (2 vegetation types $\times$ 4 treatments $\times$ 2 replicates). After sieving to remove loose soil, roots were washed and dried to constant mass. Roots from each diameter class were taken from all samples, measured for length, and weighed. It is possible that roots shrank during drying, but this should not affect comparisons between vegetation types and treatments because the relative differences remain robust. SRL was determined (roots $> 0.3$ mm in diameter: $10 \text{ m} \cdot \text{g} \pm 3.6$, mean $\pm$ standard deviation [SD]; 0.2–0.3 mm: $24 \text{ m} \cdot \text{g} \pm 9$ SD; $< 0.2$ mm: $73 \text{ m} \cdot \text{g} \pm 51$ SD) and used to calculate the mass of each root in each image. Total mass of roots in each image was expressed as g root $\cdot \text{ m}^{-2}$ image. Shoot mass was collected from a quadrat ($8 \times 100$ cm) in each plot, after the application of the treatments, in late July 2008, 2009, and 2011, dried to constant mass, and weighed.

### Statistical Analyses

Root length, root mass, and shoot mass were analyzed using repeated measures multivariate analysis of variance (rmMANOVA) with vegetation type, mowing, and nitrogen as main effects. Statistical analyses were conducted using JMP 10.0 (SAS Institute, Cary, NC). To help stabilize the variance, all data were fourth-root transformed. Fourth-root transformations are an effective and widely used method for normalizing skewed data (Quinn and Keough 2002).

The analyses of root data were also conducted for the same 3 yr (2008, 2009, and 2011) for which shoot data were available. This allowed us to examine below- and aboveground responses from the same years. These 3-yr analyses produced identical rmMANOVA results to the analysis that included all 5 yr and
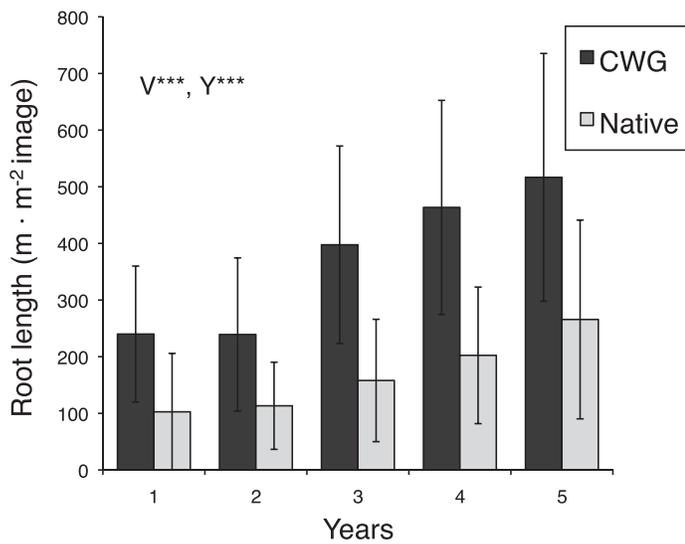
**Figure 1.** Total root length (mean ± standard deviation [SD]), per m² of minirhizotron image beneath crested wheatgrass (CWG)–dominated areas and native grassland over 5 yr and averaged across mowing and nitrogen treatments. V indicates vegetation type; Y, year; and ***$P < 0.0001$. Length was significantly greater beneath crested wheatgrass and with year.
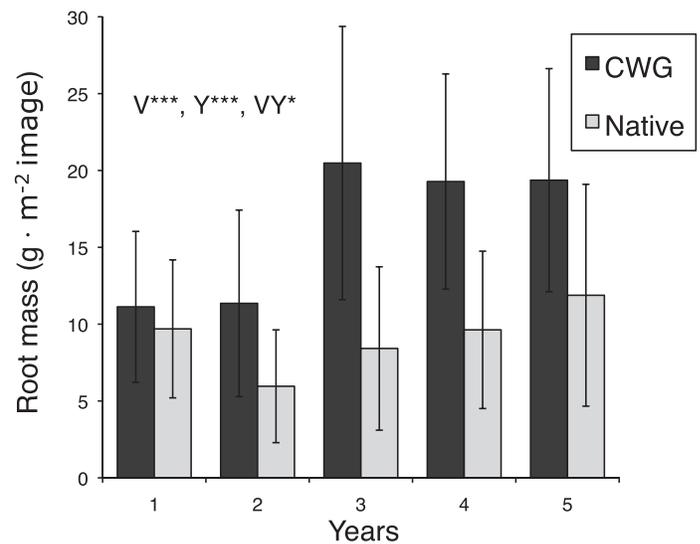


**Figure 2.** Total root mass (mean ± SD), per m² of minirhizotron image beneath crested wheatgrass–dominated areas and native grassland over 5 yr and averaged across mowing and nitrogen treatments. V indicates vegetation type; Y, year; VY, interaction; ***$P < 0.0001$; and *$0.01 < P < 0.05$. Mass was significantly greater beneath crested wheatgrass and with year. The interaction of vegetation type×year was also significant.

are presented in the Supplemental Files (Tables S1 and S2; available online at http://dx.doi.org/10.2111/ REM-D-13-00080.s1 and http://dx.doi.org/10.2111/ REM-D-13-00080.s2).

## RESULTS

Root length was significantly (about twofold) greater beneath native grassland with a major component of crested wheat-

grass, as compared to areas with little crested wheatgrass (Fig. 1; Table 1). Root length varied significantly among years, increasing over time (Fig. 1; Table 1). There was no significant interaction between vegetation type and year because root length increased in both vegetation types (Tables S3 and S4; available online at http://dx.doi.org/10.2111/ REM-D-13-00080.s3 and http://dx.doi.org/10.2111/ REM-D-13-00080.s4). Root length did not vary significantly

**Table 1.** Repeated measures ANOVA results for root length with all the factors and their interactions.

| Source of variation | NumDf[1] | DenDF[2] | F value | P value |
|---|---|---|---|---|
| Between subjects | | | | |
| Vegetation type | 1 | 28 | 28.4456 | < 0.0001[3] |
| Mowing | 1 | 28 | 0.2958 | 0.5908 |
| Vegetation type × mowing | 1 | 28 | 0.0003 | 0.9857 |
| Nitrogen | 1 | 28 | 0.0624 | 0.8046 |
| Vegetation type × nitrogen | 1 | 28 | 2.1716 | 0.1517 |
| Mowing × nitrogen | 1 | 28 | 0.7027 | 0.4090 |
| Vegetation type × mowing × nitrogen | 1 | 28 | 0.2879 | 0.5958 |
| Within subjects | | | | |
| Year | 4 | 25 | 33.6569 | < 0.0001[3] |
| Year × vegetation type | 4 | 25 | 1.3185 | 0.2904 |
| Year × mowing | 4 | 25 | 1.6960 | 0.1824 |
| Year × vegetation type × mowing | 4 | 25 | 0.2331 | 0.9171 |
| Year × nitrogen | 4 | 25 | 0.4899 | 0.7431 |
| Year × vegetation type × nitrogen | 4 | 25 | 0.5521 | 0.6993 |
| Year × mowing × nitrogen | 4 | 25 | 0.5478 | 0.7023 |
| Year × vegetation type × mowing × nitrogen | 4 | 25 | 0.1319 | 0.9692 |

[1]NumDF indicates degrees of freedom in the numerator.
[2]DenDF, denominator.
[3]Statistically significant difference $P < 0.05$.

**Table 2.** Repeated measures ANOVA results for root mass with all the factors and their interactions.

| Source of variation | NumDf | DenDF | F value | P value |
|---|---|---|---|---|
| Between subjects | | | | |
| Vegetation type | 1 | 28 | 27.7936 | < 0.0001[1] |
| Mowing | 1 | 28 | 0.0541 | 0.8178 |
| Vegetation type × mowing | 1 | 28 | 0.0013 | 0.9712 |
| Nitrogen | 1 | 28 | 0.0901 | 0.7663 |
| Vegetation type × nitrogen | 1 | 28 | 2.9785 | 0.0954 |
| Mowing × nitrogen | 1 | 28 | 2.2424 | 0.1455 |
| Vegetation type × mowing × nitrogen | 1 | 28 | 0.01859 | 0.4947 |
| Within subjects | | | | |
| Year | 4 | 25 | 21.4305 | < 0.0001[1] |
| Year × vegetation type | 4 | 25 | 3.1836 | 0.0304[1] |
| Year × mowing | 4 | 25 | 0.7659 | 0.5574 |
| Year × vegetation type × mowing | 4 | 25 | 0.2932 | 0.8796 |
| Year × nitrogen | 4 | 25 | 0.6144 | 0.6562 |
| Year × vegetation type × nitrogen | 4 | 25 | 0.8311 | 0.5181 |
| Year × mowing × nitrogen | 4 | 25 | 0.0628 | 0.9923 |
| Year × vegetation type × mowing × nitrogen | 4 | 25 | 0.1903 | 0.9412 |

[1]Statistically significant difference $P < 0.05$.

**Table 3.** Repeated measurements ANOVA results for shoot mass with all the factors and their interactions.

| Source of variation | NumDf | DenDF | F value | P value |
|---|---|---|---|---|
| Between subjects | | | | |
| Vegetation type | 1 | 28 | 4.6015 | 0.0408[1] |
| Mowing | 1 | 28 | 166.1001 | < 0.0001[1] |
| Vegetation type × mowing | 1 | 28 | 8.7019 | 0.0064[1] |
| Nitrogen | 1 | 28 | 6.2286 | 0.0187[1] |
| Vegetation type × nitrogen | 1 | 28 | 0.0091 | 0.2260 |
| Mowing × nitrogen | 1 | 28 | 0.00623 | 0.9245 |
| Vegetation type × mowing × nitrogen | 1 | 28 | 0.1537 | 0.6980 |
| Within subjects | | | | |
| Year | 2 | 27 | 3.9656 | 0.0309[1] |
| Year × vegetation type | 2 | 27 | 4.5722 | 0.0195[1] |
| Year × mowing | 2 | 27 | 0.5882 | 0.5623 |
| Year × vegetation type × mowing | 2 | 27 | 0.0409 | 0.9712 |
| Year × nitrogen | 2 | 27 | 12.9263 | 0.0001[1] |
| Year × vegetation type × nitrogen | 2 | 27 | 1.2277 | 0.3088 |
| Year × mowing × nitrogen | 2 | 27 | 2.7485 | 0.0819 |
| Year × vegetation type × mowing × nitrogen | 2 | 27 | 0.0632 | 0.9389 |

[1]Statistically significant difference $P < 0.05$.

with either mowing or nitrogen addition, or with the interaction between these treatments (Table 1).

Root mass was also significantly greater beneath crested wheatgrass–dominated areas than native grassland (Fig. 2; Table 2 vegetation type effect) and increased significantly with time. Further, there was a significant vegetation type × year interaction because root mass was more similar between vegetation types in the first year of the experiment than in the later years (Fig. 2). Root mass did not vary significantly with either mowing or nitrogen addition, or the interaction between these treatments (Table 2).
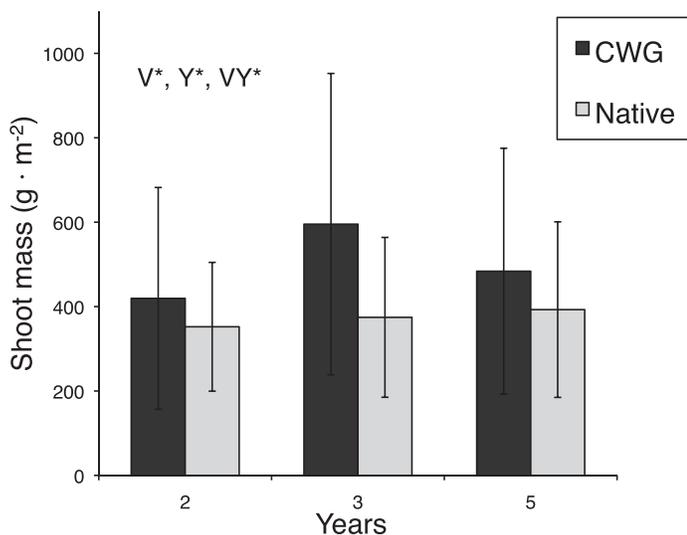


**Figure 3.** Shoot mass (mean ± SD) per m² of crested wheatgrass–dominated areas and native grassland, measured 3 yr, and averaged across mowing and nitrogen treatments. V indicates vegetation type; Y, year; VY, interaction; and *$0.01 < P < 0.05$. Mass was significantly greater for crested wheatgrass and with year. The interaction of vegetation type × year was also significant.
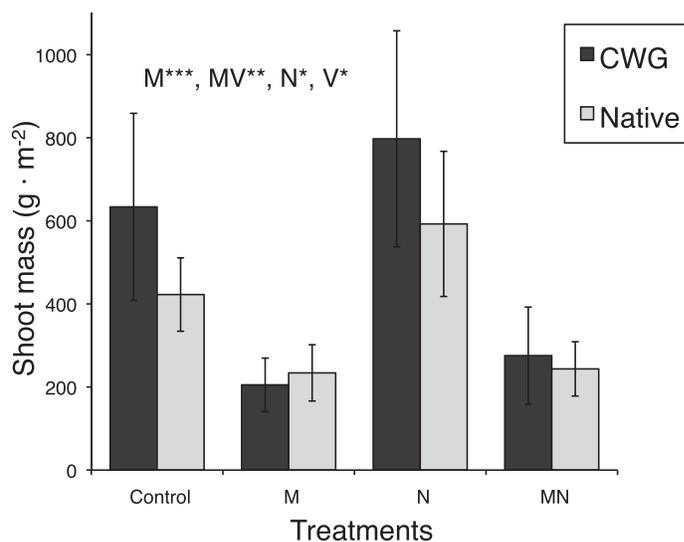


**Figure 4.** Shoot mass (mean ± SD) per m² of crested wheatgrass–dominated areas and native grassland plots for four mowing and nitrogen treatments and averaged across years. M indicates mowing; N, nitrogen; MN, mowing and nitrogen; V, vegetation type; MV, interaction of vegetation with mowing; ***$P < 0.0001$; **$0.001 \leq P \leq 0.01$; and *$0.01 < P < 0.05$.

Shoot mass was significantly greater (25%) for crested wheatgrass than native grassland (Table 3: vegetation type effect, Fig. 3). Shoot mass varied significantly among years (Table 3: year effect; Fig. 3). A significant vegetation type × year interaction occurred because the difference in shoot mass between vegetation types in yr 3 was larger than in the other years (Fig. 3). Mowing significantly reduced shoot mass to ~ 61% of than in controls (Fig. 4; Table 3). The lack of a significant mowing × year interaction suggests that mowing reduced shoot mass to about the same extent every year. A significant vegetation type × mowing interaction occurred because mowing reduced crested wheatgrass shoot mass more
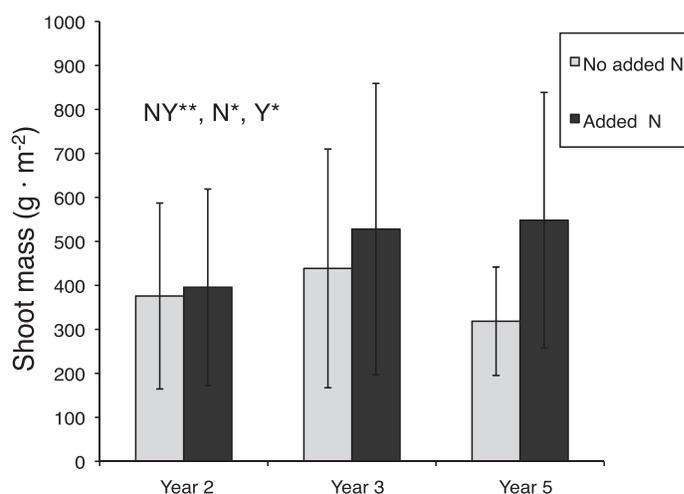


**Figure 5.** Shoot mass (mean ± SD) per m² through year averaged across vegetation types and mowing treatments. N indicates nitrogen; Y, year; NY, interaction of nitrogen with year; **$0.001 \leq P \leq 0.01$; and *$0.01 < P < 0.05$.

than it did native shoot mass (Fig. 4). Nitrogen addition significantly increased shoot mass. Additionally, a significant nitrogen×year interaction occurred because shoot mass increased over time in plots receiving N (Table 3; Fig. 5).

## DISCUSSION

We tested for long-term impacts of mowing and fertilization on root dynamics in grassland dominated by crested wheatgrass and native species. Based on relatively strong aboveground responses to mowing, we anticipated the potential for belowground differences between crested wheatgrass and native grassland. In contrast, belowground dynamics were mostly insensitive to 5 yr of treatments.

Root length varied most strongly between vegetation type, being ≈1.7 times greater beneath crested wheatgrass–dominated areas than native grasses. This observation corresponds with previous findings for this species based on rhizotron images from the field (Eissenstat and Caldwell 1989; MacDougall and Wilson 2011). In contrast, studies using soil coring report more soil mass under native prairie than crested wheatgrass (Dormaar and Smoliak 1985; Dormaar et al. 1995; Christian and Wilson 1999). Minirhizotrons produce greater estimates of root mass than do soil cores (Milchunas 2009). In addition, soil cores are typically limited to 15 cm or less in depth, while we sampled to 27 cm soil depth, and crested wheatgrass has more mass at depth than does native grassland (MacDougall and Wilson 2011).

Surprisingly, 5 yr of mowing did not reduce the root length of either crested wheatgrass–dominated areas or native grassland. Field studies of mowing responses in crested wheatgrass are rare and varied. Some studies agreed with our results, showing that root growth beneath crested wheatgrass was not affected by severe mowing (Caldwell et al. 1981; Miller and Rose 1992), especially at greater depths (Hild et al. 2001). In contrast, experiments that employ light grazing report increased root growth (Frank et al. 2002). Taken together, these results and ours suggest that low-intensity grazing may promote root growth but repeated intense mowing does not.

We found no effect of N addition on roots, in agreement with previous studies that report no response of crested wheatgrass roots to our levels of increased N availability (Bilbrough and Caldwell 1995; Verburg et al. 2013). In contrast, experiments that applied higher N levels ($225 \: kg \cdot ha^{-1}$) have shown as much as a 100% increase in root mass of crested wheatgrass (Power 1985).

Year had a large and significant effect on root dynamics. Root length doubled by the end of the experiment for both vegetation types because root colonization of the surface of the minirhizotron tube was ongoing throughout the experiment. Thus, the significant effect of year in root length might represent roots returning to their predisturbance condition. Despite among-year variation in root length, differences between the two vegetation types remained relatively similar throughout the experiment. Since no significant year×vegetation type interaction occurred for root length (Fig. 1) but only a weak significant year×vegetation type interaction ($0.01 < P < 0.05$) was detected for root mass (Fig. 2), the colonization effect on differences between vegetation types may be minor. The interaction between year and

vegetation type for root mass indicates that the vegetation types differed in their responses over time, either because of intrinsic differences, or possibly due to differences in among-year variation in environment or differences in time lags to their responses to among-year variations.

The greater root length of crested wheatgrass–dominated areas (Fig. 1) might contribute to the successful establishment of crested wheatgrass. Greater root length might allow crested wheatgrass to occupy a larger soil volume, or occupy a similar volume more densely, than can native grasses. In turn, this may limit the belowground space available for roots of native species. Additionally, greater root length enables crested wheatgrass to access a larger area for nutrient uptake, which is a crucial function in semiarid grasslands due to limited water and nutrient availability. Moreover, the fact that the greater root length of crested wheatgrass relative to native grassland was not affected by time (no year×vegetation type interaction observed; Fig. 1) may account for the long-term dominance of crested wheatgrass over native grasses.

Similar to root mass, our findings regarding the significantly greater shoot mass of crested wheatgrass–dominated areas than the native species are in agreement with previous studies (Christian and Wilson 1999; Bakker and Wilson 2001). Additionally, the significant vegetation type×year interaction observed for root mass but not for root length, was also observed for shoot mass. Specifically, the largest difference in shoot mass between the vegetation types occurred in yr 3, the same year when the largest difference in shoot mass occurred. During that year, crested wheatgrass showed an abrupt increase in root and shoot mass, whereas the native species did not have the same increase. This implies that annual variation has a significant effect on the difference between vegetation types in shoot and root mass, whereas differences between vegetation types in root length are more stable.

Field studies of shoot responses of crested wheatgrass to mowing are more common than those of root responses. In general, previous grazing studies agree with our results related to crested wheatgrass shoot reduction under mowing (Lodge 1960; Caldwell et al. 1981; Bleak and Plummer 2006; Schönbach et al. 2011). The reduction in shoot mass after mowing is expected in our experiment, since the shoot mass collected from the mowed plots is essentially regrowth in plots mowed earlier in May. However, some studies found increased shoot mass of crested wheatgrass following light grazing (Frank et al. 2002), and other studies report no effect of mowing in crested wheatgrass aboveground biomass (Miller and Rose 1992; Fanselow et al. 2011). Finally, studies that use low levels of N fertilization, similar to our experiment, also report no change in shoot biomass of crested wheatgrass (Bilbrough and Caldwell 1995; Pan et al. 2011).

Vegetation types differed in their shoot responses to mowing (vegetation type×mowing interaction) because shoot mass in crested wheatgrass–dominated areas was reduced more than native shoot mass (Fig. 4). This effect was perhaps a result of the direct shoot mass removal via mowing. Since crested wheatgrass has greater shoot mass than native prairie and it has more initial growth early in the season (Pyke 1990), mowing removed more biomass, and that led to the significant vegetation type×mowing interaction.

Nitrogen addition demonstrated a cumulative positive effect on shoot mass (Fig. 5). In contrast, shoot mass from plots with no added nitrogen followed an annual variation similar to the root mass, peaking in the third year of the experiment. Consequently the difference in shoot mass between non-fertilized and fertilized plots increased among years. This suggests that a longer-term fertilization may increase the difference in shoot mass between the two vegetation types.

Overall, root length was insensitive to mowing and N addition, and it varied most strongly between vegetation types. In contrast, shoot mass was most strongly controlled by mowing. These results differ substantially from other studies employing similar methods (Ziter and MacDougall 2013). These differences may be dependent on environmental context, with roots tending to be unaffected by mowing in semiarid environments.

Our results suggest that the much greater root length and mass of crested wheatgrass–dominated areas may allow it to dominate belowground space and associated soil resources, relative to native grassland vegetation. Although our sampling was restricted to the top 27 cm of soil, crested wheatgrass root length exceeds that beneath native prairie in the top 90 cm of soil (MacDougall and Wilson 2011).

Additionally, roots had different responses to mowing and nitrogen addition than did shoots, since roots did not respond at all to treatments but shoot mass was halved by mowing and doubled by N addition. Thus, the belowground advantage afforded to crested wheatgrass by greater root length and mass was not altered by 5 yr of mowing and N addition. Since most competition for resources in semiarid grasslands occurs belowground (Martens et al. 1997), mowing may not be an effective management tool for reducing crested wheatgrass. Overall, our results suggest that mowing and N manipulation have little effect on the belowground component of crested wheatgrass stands, and may partly explain why eradication of this species from native grassland remains a challenge.

## IMPLICATIONS

Crested wheatgrass is widely spread in the northern Great Plains, currently occupying over 10 million ha (Lesica and DeLuca 1996). Results from our long-term field experiment suggest that lack of response of roots to mowing and fertility contributes to the stability of crested wheatgrass stands. However, the findings regarding the greater root length of crested wheatgrass might be related to its greater ability to recover after disturbance. Hence, continuing studies are needed to describe the trajectory of recovery from the disturbance of tube installation and long-term monitoring is clearly essential to understanding the long-term differences between vegetation types.

A good deal of effort has gone into controlling crested wheatgrass in native grassland. Our results indicate that mowing is unlikely to reverse the profound belowground advantage of crested wheatgrass over native species, since it did not reduce the root length of crested wheatgrass at either nitrogen level. Thus, our results highlight the need for research toward alternative management techniques for crested wheat-grass elimination and toward invasion prevention programs.

## LITERATURE CITED

Bagchi, S., and M. E. Ritchie. 2010. Herbivore effects on above-and belowground plant production and soil nitrogen availability in the Trans-Himalayan shrub-steppes. *Oecologia* 164:1075–1082.

Bakker, J., and S. Wilson. 2001. Competitive abilities of introduced and native grasses. *Plant Ecology* 157:119–127.

Becker, G. F., C. A. Busso, T. Montani, M. A. Burgos, A. C. Flemmer, and M. B. Toribio. 1997. Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: root growth. *Journal of Arid Environments* 35:269–283.

Bilbrough, C. J., and M. M. Caldwell. 1995. The effects of shading and N status on root proliferation in nutrient patches by the perennial grass *Agropyron desertorum* in the field. *Oecologia* 103:10–16.

Bleak, A. T., and A. P. Plummer. 2006. Grazing crested wheatgrass. *Journal of Range Management* 7:63–68.

Bork, E. W., J. F. Cahill, S. X. Chang, E. S. Deutsch, B. Attaeian, P. Wang, B. Shore, and S. White. 2008. Rangeland responses to climate change. Edmonton, AB, Canada: Dept. of Agricultural, Food & Nutritional Science, Agriculture/Forestry Centre, University of Alberta. 106 pp.

Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40:344–353.

Cahill, J. F. 2003. Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. *Journal of Ecology* 91:532–540.

Caldwell, M. M., J. H. Manwaring, and S. L. Durham. 1996. Species interactions at the level of fine roots in the field: influence of soil nutrient heterogeneity and plant size. *Oecologia* 106:440–447.

Caldwell, M. M., J. H. Richards, D. A. Johnson, R. S. Nowak, and R. S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14–24.

Christian, J. M., and S. D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology* 80:2397–2407.

Coffin, D. P., and W. K. Lauenroth. 1992. Spatial variability in seed production of the perennial bunchgrass *Bouteloua gracilis* (*Gramineae*). *American Journal of Botany* 79:347–353.

Dormaar, J. F., M. A. Naeth, W. D. Willms, and D. S. Chanasyk. 1995. Effect of native prairie, crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and Russian wildrye (*Elymus junceus* Fisch.) on soil chemical properties. *Journal of Range Management* 48:258–263.

Dormaar, J. F., and S. Smoliak. 1985. Recovery of vegetative cover and soil organic matter during revegetation of abandoned farmland in a semiarid climate. *Journal of Range Management* 38:487–491.

Eissenstat, D. M., and M. M. Caldwell. 1989. Invasive root growth into disturbed soil of two tussock grasses that differ in competitive effectiveness. *Functional Ecology* 3:345–353.

Fanselow, N., P. Schönbach, X. Y. Gong, S. Lin, F. Taube, R. Loges, P. Qingmin, and K. Dittert. 2011. Short-term regrowth responses of four steppe grassland species to grazing intensity, water and nitrogen in Inner Mongolia. *Plant and Soil* 340:279–289.

Foster, B. L., K. Kindscher, G. R. Houseman, and C. A. Murphy. 2009. Effects of hay management and native species sowing on grassland community structure, biomass, and restoration. *Ecological Applications* 19:1884–1896.

Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53:77–88.

Frank, D. A., M. M. Kuns, and D. R. Guido. 2002. Consumer control of grassland plant production. *Ecology* 83:602–606.

Gao, Y. Z., M. Giese, S. Lin, B. Sattelmacher, Y. Zhao, and H. Brueck. 2008. Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. *Plant and Soil* 307:41–50.

Hansen, M. J., and S. D. Wilson. 2006. Is management of an invasive grass *Agropyron cristatum* contingent on environmental variation? *Journal of Applied Ecology* 43:269–280.

Henderson, D. C., and M. A. Naeth. 2005. Multi-scale impacts of crested wheatgrass invasion in mixed-grass prairie. *Biological Invasions* 7:639–650.

Hendricks, J. J., R. L. Hendrick, C. A. Wilson, R. J. Mithell, S. D. Pecot, and D. Guo. 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology* 94:40–57.

Hild, A. L., M. G. Karl, M. R. Haferkamp, and R. K. Heitschmidt. 2001. Drought and grazing III: Root dynamics and germinable seed bank. *Journal of Range Management* 54:292–298.

Hubbard, J. A. 2003. Fire-grazing interactions in a mixed grass prairie [dissertation]. College Station, TX, USA: A&M University. 63 p.

Jackson, R. B., and M. M. Caldwell. 1989. The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. *Oecologia* 81:149–153.

Jobbagy, E. G., and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* 10:423–436.

Köchy, M., and S. D. Wilson. 2001. Nitrogen deposition and forest expansion in the northern Great Plains. *Journal of Ecology* 89:807–817.

Leriche, H., X. Le Roux, F. Desnoyers, D. Benest, G. Simioni, and L. Abbadie. 2003. Grass response to clipping in an African savanna: testing the grazing optimization hypothesis. *Ecological Applications* 13:1346–1354.

Lesica, P., and T. H. DeLuca. 1996. Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. *Journal of Soil and Water Conservation* 51:408–409.

Lodge, R. W. 1960. Effects of burning, cultivating, and mowing on the yield and consumption of crested wheatgrass. *Journal of Range Management* 13:318–321.

Loeser, M. R., T. E. Crews, and T. D. Sisk. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. *Journal of Range Management* 57:442–447.

Macdougall, A. S., and S. D. Wilson. 2011. The invasive grass *Agropyron cristatum* doubles belowground productivity but not soil carbon. *Ecology* 92:657–664.

Martens, S. N., D. D. Breshears, C. W. Meyer, and F. J. Barnes. 1997. Scales of aboveground and below-ground competition in a semi-arid woodland detected from spatial pattern. *Journal of Vegetation Science* 8:655–664.

McKenzie, E. 1997. The influence of grazing management on weed invasion of *Lolium perenne* pastures under subtropical conditions. *Tropical Grasslands* 31:24–30.

Milchunas, D. G. 2009. Estimating root production: comparison of 11 methods in shortgrass steppe and review of biases. *Ecosystems* 12:1381–1402.

Miller, R. F., and J. A. Rose. 1992. Growth and carbon allocation of *Agropyron desertorum* following autumn defoliation. *Oecologia* 89:482–486.

[NOAA] Western Regional Climate Center. 2012. Available at: http://www.wrcc.dri.edu/. Accessed 25 September 2012.

Otfinowski, R., and N. C. Kenkel. 2010. Covariance between disturbance and soil resources dictates the invasibility of northern fescue prairies. *Biological Invasions* 12:1349–1361.

Pan, Q., Y. Bai, J. Wu, and X. Han. 2011. Hierarchical plant responses and diversity loss after nitrogen addition: testing three functionally-based hypotheses in the Inner Mongolia grassland. *PloS ONE* 6:e20078.

Power, J. F. 1985. Nitrogen-and water-use efficiency of several cool-season grasses receiving ammonium nitrate for 9 years. *Agronomy Journal* 77:189–192.

Pyke, D. A. 1990. Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia* 82:537–543.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge, UK: Cambridge University Press. 537 p.

Richards, J. H. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia* 64:21–25.

Roundy, B. A., G. J. Cluff, J. K. McAdoo, and R. A. Evans. 1985. Effects of jackrabbit grazing, clipping, and drought on crested wheatgrass seedlings. *Journal of Range Management* 38:551–555.

Schönbach, P., H. Wan, M. Gierus, Y. Bai, K. Müller, L. Lin, A. Susenbeth, and F. Taube. 2011. Grassland responses to grazing: effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. *Plant and Soil* 340:103–115.

Sinkins, P. A., and R. Otfinowski. 2012. Invasion or retreat? The fate of exotic invaders on the northern prairies, 40 years after cattle grazing. *Plant Ecology* 213:1251–1262.

Steinaker, D. F., and S. D. Wilson. 2005. Belowground litter contributions to nitrogen cycling at a northern grassland-forest boundary. *Ecology* 86:2825–2833.

Taylor, B. N., K. V. Beidler, E. R. Cooper, A. E. Strand, and S. G. Pritchard. 2013. Sampling volume in root studies: the pitfalls of under-sampling exposed using accumulation curves. *Ecology Letters* 16:862–869.

USDA-NRCS. 2012. Web Soil Survey. Available at: http://websoilsurvey.nrcs.usda.gov. Accessed 10 October 2012.

Van der Maarel, E., and A. Titlyanova. 1989. Above-ground and below-ground biomass relations in steppes under different grazing conditions. *Oikos* 56:364–370.

Vaness, B. M., and S. D. Wilson. 2007. Impact and management of crested wheatgrass (*Agropyron cristatum*) in the northern Great Plains. *Canadian Journal of Plant Science* 87:1023–1028.

Verburg, P. S., A. C. Young, B. A. Stevenson, I. Glanzmann, J. A. Arnone, G. M. Marion, H. Holmes, and R. S. Nowak. 2013. Do increased summer precipitation and N deposition alter fine root dynamics in a Mojave Desert ecosystem? *Global Change Biology* 19:948–956.

Wilson, S. D., and M. Pärtel. 2003. Extirpation or coexistence? Management of a persistent introduced grass in a prairie restoration. *Restoration Ecology* 11:410–416.

Ziter, C., and A. S. MacDougall. 2013. Nutrients and defoliation increase soil carbon inputs in grassland. *Ecology* 94:106–116.