

Research Article

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Effects of *Ventenata dubia* removal on rangelands of northeast Wyoming

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Abstract

Ventenata [*Ventenata dubia* (Leers) Coss.] is one of several annual grass invaders of the western United States. *Ventenata dubia* is documented reducing the forage availability for livestock and wildlife as well as lowering biodiversity in the Great Basin. This species has recently spread to the Great Plains, where it could bring these impacts with it. We attempt to answer questions on whether or not conservation practices, in this case removal of *V. dubia* with herbicide, result in recovery of forage resources and biodiversity. We answer these questions by measuring biomass, cover, and nutrient content 1-yr posttreatment at 9 sites in Sheridan County, WY, conducted in two years. Perennial grasses have higher crude protein and total digestible nutrients than *V. dubia*, and removal of *V. dubia* resulted in a positive perennial grass response both years. Further, the differences in pattern of growth between perennial and annual species, with annual grasses quickly senescing early in the year, make perennial grasses a more dependable forage base with higher available nutrients. Interestingly, total biomass and nutrient mass did not change after *V. dubia* removal due to equal replacement with perennial grasses. Species richness and diversity were unaffected by removal of *V. dubia*. Our results suggest that managing invasive annual grasses, particularly *V. dubia*, in the Northern Great Plains can improve forage resources for livestock and wildlife while maintaining species diversity. Therefore, proactive monitoring and management efforts to prevent spread should be prioritized in this region.

Introduction

Western North American rangelands have been invaded by nonnative species that have caused considerable damage to ecosystem services (DiTomaso et al. 2017), such as providing forage for cattle and wildlife. Several of these invasive species are cool-season annual grasses such as the well-known European species cheatgrass [*Bromus tectorum* L.]. Other cool-season annual grass invaders like ventenata [*Ventenata dubia* (Leers) Coss.] and medusahead [*Taeniatherum caput-medusae* (L.) Nevski] have also become problematic in rangelands of the western United States, particularly in the Great Basin and grasslands of the Pacific Northwest (Hironaka 1992; Scheinost et al. 2008a, 2008b; Wallace et al. 2015; Wallace and Prather 2016; Washington State Noxious Weed Control Board 2016; Young 1992). In high densities, these grasses tend to displace native species and desirable introduced grasses, due in part to their life histories (D'Antonio and Vitousek 1992). In some cases, substantive ecological changes occur, such as conversion to an annual grass-dominated system.

Ventenata dubia was introduced into North America no later than 1952 in Spokane County, WA (Barkworth et al. 1993). Since that time, it has spread to other western states and Canada (Fryer 2017). In the Pacific Northwest, *V. dubia* was spreading at an estimated rate of 1.2 million ha yr⁻¹ in 2001 (Fryer 2017). Although the first documentation of *V. dubia* in Wyoming was in 1997, this documentation went unnoticed until *V. dubia* was confirmed in northeastern Wyoming with self-sustaining populations in 2016 before control efforts began (Garner and Lakes 2019). This recently invaded area is within the Great Plains ecoregion, where *V. dubia* threatens to spread rapidly as it has done farther west.

Winter annual grasses such as *V. dubia* usually germinate in the fall and take advantage of early spring moisture, although some annual grasses are able to produce seed early in the summer even if they fail to germinate until spring (Young 1992). This early use of spring moisture by annual grasses depletes soil moisture that would normally be available to desirable perennial grasses, causing water stress for perennials earlier in the summer than would be expected without invasive grasses (D'Antonio and Vitousek 1992; Evans et al. 1970). This depletion of resources, in addition to disturbances, such as fire, that reduce the abundance of perennial species (Anderson and Inouye 2001; Melgoza et al. 1990), is a possible mechanism that has allowed cool-season annual species to undermine the dominance of perennial grasses.

Management Implications

Ventennata dubia (*ventennata*) is a nonnative species that is quickly spreading into the Great Plains ecoregion. Along with it, negative impacts such as lower forage availability for cattle and wildlife and reduced biodiversity can be expected. These negative effects have been documented in the Great Basin and Pacific Northwest. This research was conducted to answer several questions surrounding conservation efficacy. We concluded that removal of *V. dubia* results in a positive response from perennial grasses and that this perennial forage base is of higher quality. Further, whereas annual grasses such as *V. dubia* grow quickly and senesce early in the growing season, perennial grasses continue growing later into the growing season before senescing. This provides a longer green grazable forage window, giving landowners and land managers greater control and reliability of their forage resources. Additionally, *V. dubia* is unpalatable to livestock and therefore has little forage value. Both studies presented here took place 1 yr after control of *V. dubia*. In that time, species richness and biodiversity did not change as a result of *V. dubia* removal. Whether this is due to failure of native species to reestablish or that they were simply not reduced in the first place is not clear. We also found that total biomass and nutrient mass did not increase, even with increases in more nutritious perennial grasses. This is likely due to replacement of annual grass biomass with an equal amount of perennial grass biomass because of limited resources. However, available forage and nutrient mass from palatable perennial grasses increased. Therefore, preventing invasion by *V. dubia* is preferable. With this in mind, removal of *V. dubia* resulted in many benefits to ecosystem goods and services and is worth pursuing where invasion occurs.

Reductions in perennial forage grasses cause other issues as well. *Ventennata dubia* has little value as a forage species early in the growing season (Pavek et al. 2011). Any small value is short-lived, as *V. dubia* becomes unpalatable once it becomes dry (Fryer 2017; but see work by McCurdy et al. [2017] on pelletizing *V. dubia*). Although this invasive annual grass has been present in North America for nearly 70 yr, it has only recently been documented in the Great Plains, where its impacts on ecosystem goods and services, such as forage production and biodiversity, are still being discovered. Reduced forage production has been observed in areas infested by annual grasses such as *V. dubia* (Jones et al. 2018). The forage quality of cool-season perennial grasses, often used to improve forage resources on former cropland, have been tracked through a growing season in a planted, weed-free setting (Jenson et al. 2016). However, to our knowledge, no studies have documented how forage quality and quantity of an invaded rangeland change through a growing season.

Ventennata dubia can reduce biodiversity of areas it invades (Jones et al. 2018, 2020) and has negative impacts on wildlife and its habitat, namely birds, through trophic cascades (Mackey 2014). Similar to other invasive species, species richness and diversity were negatively correlated with increasing *V. dubia* cover (Jones et al. 2018, 2020). In some areas, this species has been observed replacing *B. tectorum* and *T. caput-medusae*—two infamously difficult species to control over the long term—as dominants (Barkworth et al. 1993).

Details on the effects of conservation and restoration on rangelands affected by invasive species are lacking (Sheley et al. 2011). Historically, restoration efforts have often attempted to return

ecosystems to a previous condition (Choi 2007; Choi et al. 2008; Hobbs 2007). Large restoration projects with goals such as this have raised concerns about whether such a goal is feasible. Critics argue such goals are too idealistic to apply in real-world situations with economic, social, and political interests in addition to the large ecological changes that have occurred, which prevent a return to previous ecological states (Choi et al. 2008; Hobbs 2007).

With these concerns and research needs in mind, we studied two conditions: a Northern Great Plains rangeland invaded by *V. dubia* and a rangeland previously invaded by *V. dubia* that was subsequently controlled using herbicides. By comparing these two conditions, we evaluate whether chemical control of *V. dubia* improves attributes of rangeland condition. This overarching goal can be broken down into two questions: (1) Does *V. dubia* control improve forage quality and quantity? (2) Does *V. dubia* control increase plant species richness and diversity? Understanding the effects of *V. dubia* control on forage and plant community characteristics is a critical step in making informed recommendations to weed managers and restoration practitioners in this new region of spread.

Materials and Methods

Study Area

We conducted two single-year studies separated in space and time in conjunction with a cooperative, landscape-scale program focused on managing invasive annual grasses. Both studies took place in a region that represents a transition between northern mixed prairie and sagebrush grasslands. As part of an early detection–rapid response program for *T. caput-medusae* and *V. dubia*, the Northeast Wyoming Invasive Grasses Working Group (NEWIGWG) applied herbicide aerially to multiple sites in 2017 and 2018 to control annual grasses on sites where *V. dubia* was the dominant invasive grass (Supplementary Table S1). NEWIGWG treated approximately 1,200 ha in 2017, in numerous patches ranging from 20 to 400 ha per patch, which resulted in multiple instances of treated/nontreated paired sites across the landscape. Herbicide treatments consisted of fall treatments of 123 g ae ha⁻¹ of aminopyralid plus 123 g ai ha⁻¹ of imazapic in 2017. In 2018, NEWIGWG treated another 2,800 ha in the same vicinity as before using 73 g ai ha⁻¹ of indaziflam in a total solution of 46.8 L ha⁻¹. Sites for both years varied in slope, aspect, and plant community and accounted for a wide range of environmental conditions within the locale (Table 1). Mean annual precipitation ranges from 254 to 482 mm and topsoils are clay, loam, clay-loam, or very fine sandy loam (USDA-NRCS 2019).

Data Collection

We collected vegetation data from four sites in 2018 and five sites in 2019 for treatments that occurred in 2017 and 2018, respectively, using slightly different approaches in each year (Figure 1). For our 2018 data collection, we sampled canopy cover by species along three 15.24-m transects placed in treated and nontreated portions of each site. Transects within a treatment area were separated by 30 to 60 m and between areas (treated/nontreated) were separated by at least 15 m. We sampled three 0.25-m² quadrats spaced evenly along each transect (Figure 1). In each quadrat, we recorded canopy cover by species as a cover class: trace = 0% to 1%; class 1 = 1% to 5%; class 2 = 5% to 25%; class 3 = 25% to 50%; class 4 = 50% to 75%; class 5 = 75% to 95%; class 6 = 95% to 100%. We then clipped all aboveground herbaceous biomass near ground level, sorted it

Table 1. Site information for the 2018 and 2019 studies of *Venttenata dubia* removal in Sheridan County, WY.^a

Site	Year	Soil type, slope, and topsoil texture	Aspect	Three most abundant perennial species	Annual precipitation
Berry	2018	Jonpol-Platmak association (fine, smectitic, mesic Aridic Paleustolls), 9%–25% slope, loam	Southwest facing	<i>Pascopyrum smithii</i> <i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex Griffiths <i>Sphaeralcea coccinea</i> (Nutt.) Rydb.	381–482 mm
Halfway	2018	Shingle-Samday clay loam (loamy, mixed, superactive, calcareous, mesic, shallow Ustic Torriorthents), 3%–55% slope, clay loam	South facing	<i>Pascopyrum smithii</i> <i>Lithospermum incisum</i> Lehm. <i>Taraxacum officinale</i> F.H. Wigg.	381–482 mm
Amsden Creek	2018	Norbert-Doney Rock outcrop complex (clayey, smectitic, calcareous, frigid, shallow), 8%–45% slope, clay	South facing to nearly skyward	<i>Pascopyrum smithii</i> <i>Danthonia unispicata</i> (Thurb.) Munro ex Macoun <i>Symphyotrichum ericoides</i> (L.) G.L. Nesom	381–482 mm
6 Mile Reservoir	2018	Shingle-Worfka-Samday complex (loamy, mixed, superactive, calcareous, mesic, shallow Ustic Torriorthents), 6%–30% slope, clay-loam	Southwest facing to nearly skyward	<i>Pascopyrum smithii</i> <i>Artemisia tridentata</i> Nutt. <i>Plantago patagonica</i> Jacq.	254–356 mm
Little Wolf Ranch	2019	Jonpol-Platmak complex (fine, smectitic, mesic Aridic Paleustolls), 0%–9% slope, loam	Skyward	<i>Pascopyrum smithii</i> <i>Symphyotrichum ericoides</i> <i>Sphaeralcea coccinea</i>	381–432 mm
Master's Ranch North	2019	Shingle-Worfka-Samday complex (loamy, mixed, superactive, calcareous, mesic, shallow Ustic Torriorthents), 6%–30% slope, clay-loam	North and Northwest facing	<i>Pascopyrum smithii</i> <i>Danthonia unispicata</i> <i>Artemisia tridentata</i>	254–356 mm
Master's Ranch South	2019	Samday-Hilight clay loam (clayey, smectitic, calcareous, mesic, shallow Ustic Torriorthents), 2%–45% slope, clay-loam	South facing	<i>Pascopyrum smithii</i> <i>Artemisia tridentata</i> <i>Opuntia polyacantha</i> Haw.	254–356 mm
JC Ranch	2019	Platmak loam (fine, smectitic, mesic Aridic Paleustolls), 3%–6% slope, loam	East-Northeast facing	<i>Pascopyrum smithii</i> <i>Poa pratensis</i> L. <i>Symphyotrichum ericoides</i>	381–482 mm
Wolf Creek	2019	Jonpol-Platmak association (fine, smectitic, mesic Aridic Paleustolls), 9%–25% slope, loam	North facing	<i>Pascopyrum smithii</i> <i>Tragopogon dubius</i> Scop. <i>Pediomelum argophyllum</i> (Pursh) J. Grimes	381–482 mm

^aTreatment was 123 g ai ha⁻¹ of imazapic and 123 g ae ha⁻¹ of aminopyralid for the 2018 study and 73 g ai ha⁻¹ of indaziflam for the 2019 study.

into functional groups (perennial grasses, perennial forbs, annual forbs, and annual grasses), dried the samples at 60 C for 48 h, and weighed them.

Sampling in 2019 was adjusted from the 2018 study. Instead of sampling once in July, as in the 2018 study, we sampled monthly from May to October, excluding September, at all five locations. At each site, we sampled four paired 30-m² treated and nontreated plots along a treatment boundary (Figure 1). The size of treated and nontreated areas varied (see above), but all plots for each site were placed within 100 m of one another. We haphazardly placed two 0.25-m² quadrats in each plot at each biomass collection date—avoiding previously clipped quadrats to prevent sampling of regrowth. We collected all aboveground herbaceous biomass in these quadrats, separated it into the same functional groups described earlier, and pooled each functional group for each plot

before drying and weighing. In July, we collected additional data on species richness and canopy cover by species in each quadrat before clipping biomass. We collected these data using the same method as in 2018, but with adjusted cover classes for increased resolution of data as follows: trace = 1% to 3%, class 1 = 3% to 10%, class 2 = 11% to 20% class 3 = 21% to 30%, class 4 = 31% to 40%, class 5 = 41% to 50%, class 6 = 51% to 60%, class 7 = 61% to 70%, class 8 = 71% to 80%, class 9 = 81% to 90%, and class 10 = 91% to 100%.

Forage Quality

For the 2018 study, after we recorded the weight for each functional group, we pooled the biomass from a subset of sites into perennial and annual grasses for further nutritional content analysis. We

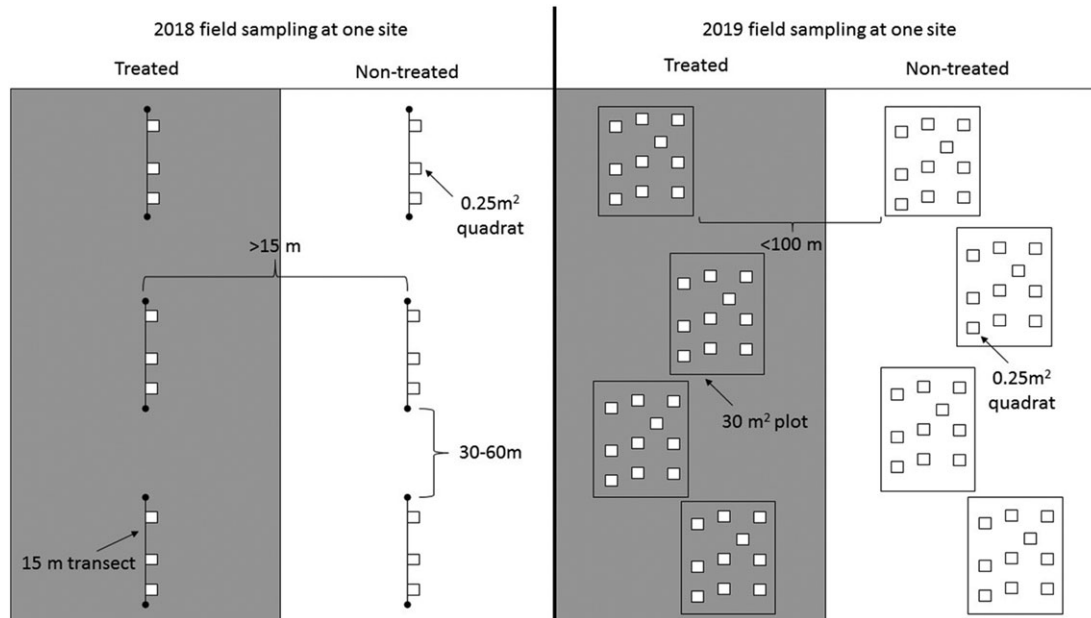


Figure 1. Field vegetation sampling scheme for *Ventenata dubia* treatment sites in 2018 and 2019 in northeast Wyoming. Plant cover and biomass data were collected in July from three 0.25-m² quadrats along three transects per treatment per site at four sites in 2018. Plant biomass data were collected each month from two separate 0.25-m² quadrats randomly placed within four 30-m² sampling “plots” per treatment per site at five sites in 2019. Plant species cover data were collected only in July 2019. Vegetation data were pooled to the treatment × site level for statistical analysis (each site was treated as a replicate).

ground this pooled biomass and analyzed the samples for crude protein and total digestible nutrients (TDN) using the combustion method (Padmore 1990) and acid detergent fiber method (ANKOM Technology 2017). Crude protein and TDN are used because these are available and commonly used measures of nutrition.

For 2019 forage analysis, after biomass collection, we randomly selected plots from each site to provide separate samples: annual grass, perennial grass, and composite samples including all functional groups to provide a measure of total nutrients on the site. Randomization was done once and applied to both treatments and all sites for consistency of the samples. As previously, the primary metrics of forage quality were crude protein and TDN.

Data Analysis

For each sampling year, we pooled data among transects (2018) or plots (2019) by treatment (treated, nontreated) within a site and considered each site a replicate (Figure 1). In 2018, we used paired *t*-tests to compare biomass, cover, species richness, species diversity, crude protein, and TDN between herbicide treatments for the single sampling time in July. For the 2019 data, we used lack-of-fit tests and the Akaike information criterion to sequentially compare full and reduced regression models to evaluate effects of sampling time (month), herbicide treatment, and model shape (linear vs. curvilinear). We evaluated total biomass, biomass of separate functional groups, nutrient composition (%), and nutrient mass (kg ha⁻¹). We calculated the Shannon-Wiener diversity index (Shannon 1948) using the midpoints of each canopy cover class as a measure of abundance for native and all species at each site. We analyzed species richness and diversity at the site level in treated and nontreated areas using paired *t*-tests, as we did in 2018. We analyzed and visualized all data using R v. 3.6.3 (R Core Team 2016) using base R and the GGPlot2 and DPLYR packages.

Results and Discussion

2018 Study

The imazapic and aminopyralid herbicide mix reduced total annual grass biomass, the most dominant of which was *V. dubia* ($P = 0.002$) and cover of *V. dubia* ($P < 0.001$; Table 2; Supplementary Table S1) effectively in 2018, 1 yr after treatment. However, we did not see an increase in perennial grass biomass with treatment. Canopy cover of western wheatgrass [*Pascopyrum smithii* (Rydb.) Á. Löve], a species either dominant or codominant at all sites, increased ($P = 0.04$; Table 2). Because perennial grass cover appeared to respond positively to *V. dubia* removal, the lack of a statistically significant biomass response was likely high variability in biomass production across sites.

Annual grasses had lower crude protein and TDN than perennial grasses ($P < 0.001$; Table 3) in 2018. This is likely because annual grasses had senesced by July, when the samples were taken. Regardless, it is an indication of the loss of forage value due to *V. dubia* invasion. Loss of perennial grasses and replacement with annual grasses that become unpalatable early in the growing season result in a loss of nutrients available to cattle and wildlife (Fryer 2017; McCurdy et al. 2017).

Control of *V. dubia* did not affect species richness 1 yr after treatment in 2018 (Table 4). Nontreated sites had 29.5 (± 4.1) total species present, 17.3 (± 2.29) of which were native. Treated sites had 27 (± 5.7) total species with an average of 16.8 (± 4.17) being native. Shannon diversity of total species and native species was similar between treatments (Table 4).

2019 Study

NEWIGWG used indaziflam in 2018 under a Section 18 registration for Wyoming. Indaziflam is a PRE root growth-inhibiting herbicide (Sebastian et al. 2016a, 2017) thought to remain close

Table 2. Mean biomass, crude protein (CP), total digestible nutrients (TDN), and cover of *Venttenata dubia* and *Pascopyrum smithii* before and after treatment with 123 g ai ha⁻¹ of imazapic and 123 g ae ha⁻¹ of aminopyralid in northeast Wyoming, 2018.

Treatment	Total biomass	CP	TDN	<i>V. dubia</i> cover	<i>P. smithii</i> cover
	kg ha ⁻¹			% ^a	
Nontreated	1,682.30	103.85	925.93	37.5	17.5
Standard error	377.78	23.87	210.82	7.9	5.1
Treated	1,776.94	121.76	1,002.73	1.6	40.2
Standard error	862.81	47.78	494.41	1.2	4.8

^aBold values are statistically significant ($P < 0.05$).

Table 3. Crude protein (CP) and total digestible nutrients (TDN) of nontreated samples of perennial and annual grasses collected in July 2018 from four sites in Sheridan County, WY.^a

Functional group	CP	TDN
	% ^a	
Perennial	6.8 (0.2)	59.3 (0.6)
Annual	5.2 (0.3)	50.7 (1.0)

^aStandard error is in parentheses. Means between annual and perennial grasses differed for both crude protein and TDN ($P < 0.001$). All findings are significant ($P < 0.001$).

Table 4. Total and native species richness and Shannon diversity for 2018 and 2019 with associated P-values of treated and nontreated plots in Sheridan County, WY.^a

		Treated	Nontreated	P-value
2018 Total	Species richness	28.0	29.3	$P = 0.69$
	Shannon diversity	2.7	2.6	$P = 0.71$
2018 Native	Species richness	16.8	16.0	$P = 0.74$
	Shannon diversity	2.1	2.1	$P = 0.96$
2019 Total	Species richness	18.6	17.2	$P = 0.52$
	Shannon diversity	2.0	1.7	$P = 0.35$
2019 Native	Species richness	11.8	9.8	$P = 0.19$
	Shannon diversity	1.5	1.6	$P = 0.84$

^aTreatment was 123 g ai ha⁻¹ of imazapic and 123 g ae ha⁻¹ of aminopyralid for the 2018 study and 73 g ai ha⁻¹ of indaziflam for the 2019 study. Species richness and Shannon diversity did not change as a result of *Venttenata dubia* control.

to the soil surface for several years, thus targeting annual species, which must reproduce by seed each year. Indaziflam is an effective herbicide for several winter annual species, including *V. dubia* (Sebastian et al. 2016a). Similar to the herbicides used in the 2018 study, indaziflam reduced annual grass biomass to nearly zero the year after treatment (2019), which was sustained through the growing season ($P < 0.001$; Figure 2).

Because *V. dubia* was controlled effectively in both studies despite using different herbicides, we can be confident similar results between the two studies are due to removal of *V. dubia* and not simply direct effects of the herbicides themselves. Annual and perennial biomass curves differed between treatments ($P < 0.001$; Figure 2). In nontreated plots, annual grass biomass had a linear downward trend through the growing season as annual grasses quickly senesced and began to deteriorate after reproducing. In contrast, perennial grass biomass increased from the start of the growing season to peak biomass in August before senescing. This trend was true whether treated or nontreated; however, *V. dubia* control resulted in an overall increase in perennial grass biomass the season after treatment ($P < 0.001$; Figure 2). This difference in patterns between annual and perennial biomass is important, because it affects when forage is palatable and nutritious to cattle and wildlife. Biomass data indicate that perennial grasses have a longer, more stable, and more

predictable green, grazable forage window than annual grasses. In this way, *V. dubia* control has given the land manager more grazing flexibility and reliability of the forage resource.

Regression of annual and perennial grass nutrient content in 2019 corroborated results from 2018. Perennial grasses had higher content of crude protein and TDN overall ($P < 0.001$; Figure 3). However, early in the growing season, when *V. dubia* is still green and growing, perennial and annual grasses had similar crude protein content. It would be tempting to view this as a positive. In this way, *V. dubia* is similar to *B. tectorum*, in that it could be valuable as an early forage (Young and Allen 1997) if it were palatable. However, this small benefit would need to be weighed properly against the many negatives.

Given our findings that perennial grasses are higher in nutrient content and more abundant 1 yr after treatment, one would expect to see more nutrients available on the landscape. Treatment resulted in a higher percentage of crude protein and TDN ($P < 0.001$) of composite samples. However, even though perennial grasses and composite samples have higher nutritive content, converting to mass (kg ha⁻¹) of crude protein or TDN did not reflect this. Total crude protein ($P = 0.79$) and TDN mass ($P = 0.28$) did not differ between treated and nontreated areas. This is likely due to the loss of *V. dubia* biomass confounding with the mass of these nutrients. In other words, the mass of crude protein and TDN lost from annual grass biomass removal was replaced by that gained from increases in perennial grasses, but not exceeded. Here it is important to keep in mind that even though *V. dubia* does have comparable nutrient mass, it is reportedly unpalatable to cattle unless it has been processed by pelletizing (McCurdy et al. 2017). Nutrients are not available to cattle or wildlife if they are not ingested. For this reason, we also analyzed nutrition in 2019 using only perennial grass biomass. Treatment increased mass of available crude protein and TDN ($P < 0.001$; Figure 4). Because perennial grass biomass increased as a result of *V. dubia* removal, we saw a corresponding increase in the mass of crude protein and TDN available to livestock and wildlife. This increase of available nutrients via annual grass control and restored perennial grasses on the landscape has direct benefits to grazing animals (Haferkamp et al. 2001) and is one of the main benefits of *V. dubia* removal.

Because *V. dubia* invasion has been documented lowering species diversity (Jones et al. 2018, 2020; Novak et al. 2015), we hypothesized some increase of species diversity with *V. dubia* control. Although removal of *V. dubia* resulted in large changes in cover for some species, such as *P. smithii*, we did not find a change in species richness 1 yr after treatment as a result of *V. dubia* removal in either study ($P > 0.18$; Table 4). In 2019, nontreated plots had 17.2 (± 2.94) total species and 9.8 (± 1.83) native species per site, while treated plots had 18.6 (± 0.98) total species and 11.8 (± 0.86) native species per site. Species diversity was also unaffected by treatment. This was true whether analyzing diversity for total species ($P = 0.35$) or native species only ($P = 0.84$). Shannon

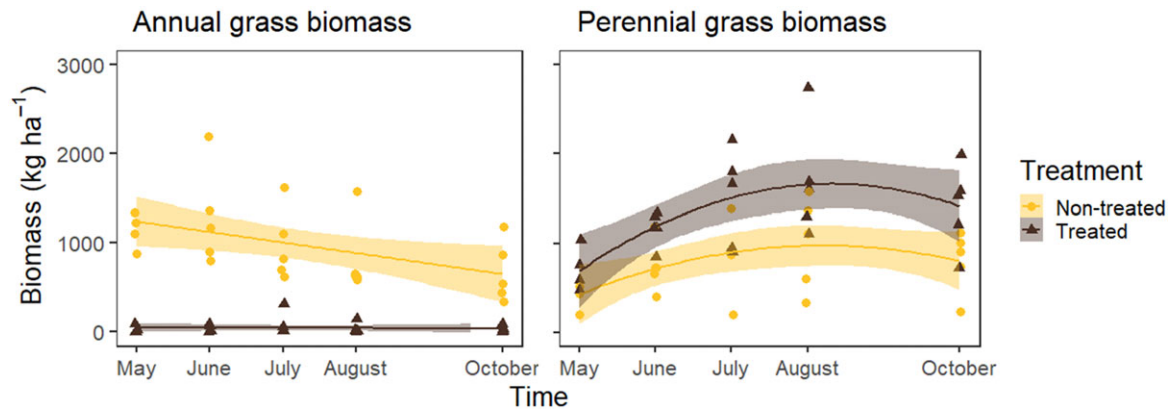


Figure 2. Annual and perennial grass biomass through the 2019 growing season with and without treatment with 73 g ai ha⁻¹ indaziflam in Sheridan County, WY. Annual grass biomass was reduced to nearly zero after treatment ($P < 0.001$), while perennial grass biomass increased ($P < 0.001$). Differences in life histories are also apparent. Equations are as follows: nontreated annual grass biomass: $y = 1239.12 - 117.62x$ [1]; treated annual grass biomass: $y = 49.58 - 2.16x$ [2]; nontreated perennial grass biomass: $y = 433 + 337.94x - 52.72x^2$ [3]; treated perennial grass biomass: $y = 693.75 + 582x - 87.58x^2$ [4].

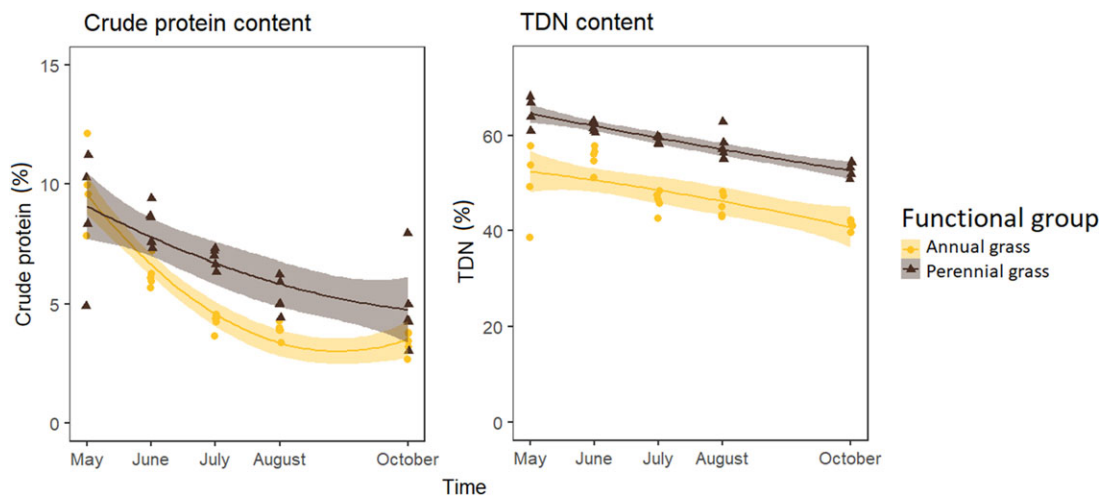


Figure 3. Crude protein and total digestible nutrients (%) of perennial and annual grasses through the 2019 growing season in Sheridan County, WY. Perennial grasses were higher in both crude protein and TDN ($P < 0.001$). Equations are as follows: perennial grass crude protein (%): $y = 9.08 - 1.40x + 0.11x^2$ [5]; annual grass crude protein (%): $y = 9.55 - 3.34x + 0.43x^2$ [6]; perennial grass TDN (%): $y = 64.42 - 2.44x$ [7]; annual grass TDN (%): $y = 55.91 - 2.99x$ [8].

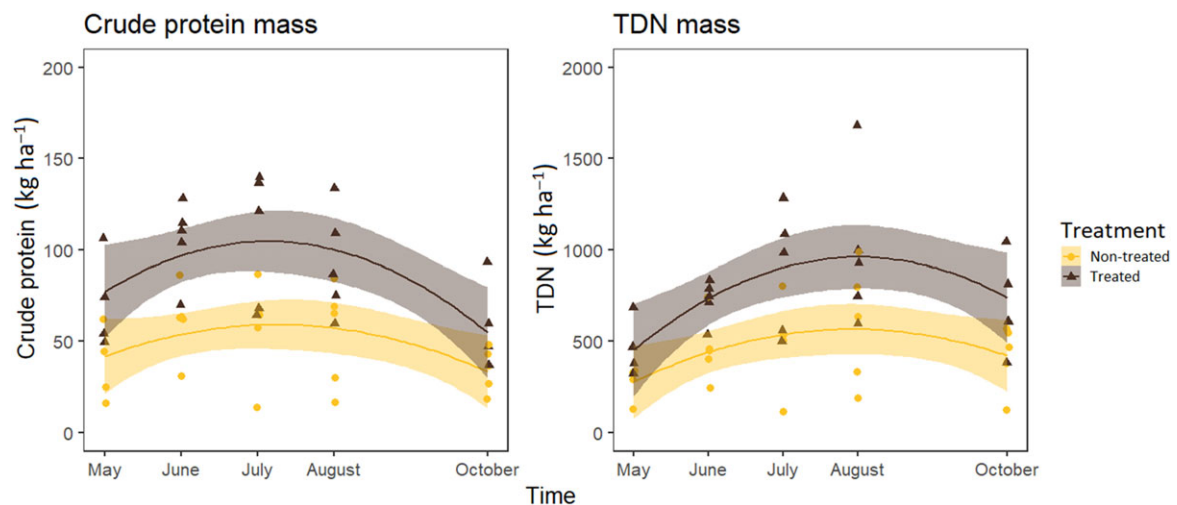


Figure 4. Mass of available crude protein and total digestible nutrients (TDN) found in perennial grasses through the growing season of 2019 for treated (73 g ai ha⁻¹ indaziflam) and nontreated sites in Sheridan County, WY. Crude protein and TDN mass ($P < 0.001$) both increased as a result of treatment. Equations are as follows: nontreated available crude protein mass: $y = 41.93 + 15.37x - 3.41x^2$ [9]; treated available crude protein mass: $y = 77.27 + 25.72x - 6.04x^2$ [10]; nontreated available TDN mass: $y = 278.51 + 197.06x - 33.66x^2$ [11]; treated available TDN mass: $y = 454.15 + 337.19x - 56.02x^2$ [12].

diversity was 1.69 (± 0.27) and 1.58 (± 0.15) for total and native species diversity, respectively, on nontreated plots. Treated plots had Shannon diversity indexes of 2.04 (± 0.15) and 1.51 (± 0.23) for total and native species, respectively.

Other than the possibility that species richness is unaffected by *V. dubia* on our study sites, which could be because they may already be negatively impacted by other nonnative species, the lack of species richness response could be due to a lack of recovery time after treatment. It may be that *V. dubia* has not been present at the sites long enough to extirpate any species as it has done farther west, where it has been present for longer. Indaziflam can remain in the soil for three or more years (Sebastian et al. 2016b, 2017) while these sites were sampled 1 yr posttreatment. Previous work indicates that indaziflam does not negatively impact species richness or abundance 1 yr after treatment and may increase richness in the second year after treatment in rangelands of Colorado (Clark et al. 2019; Sebastian et al. 2016b, 2017). Species richness and diversity data from 2020, the second year after indaziflam application (data not presented), did not display an increase in species richness or diversity in this transitional ecoregion of northeast Wyoming. However, our data clearly support that species richness is not further negatively impacted by indaziflam in this ecosystem. Indaziflam is therefore a potential tool for weed control where decreasing species richness is a concern. However, it should be noted that confident conclusions could not be made for annual forbs, as they constituted a very small ($< 1 \text{ g m}^{-2}$) proportion of biomass on these sites, making trends difficult to measure effectively.

Species diversity is perhaps a more mathematical issue. The lack of response here is surprising, because we observed apparent visual differences between treated and nontreated areas. Our observations show that the reduction in *V. dubia* was replaced with a similarly dominant abundance of *P. smithii*, making the calculated diversity similar (Table 2; Supplementary Table S1). *Pascopyrum smithii* is a rhizomatous perennial grass and was the dominant native grass species at all sites. In this case, additional management may be required to affect richness and diversity.

These results are important and powerful when taken together in context. *Venttenata dubia* removal was a successful restoration effort that improved aspects of rangeland condition. The benefits of *V. dubia* control are not limited to simply increasing perennial forage biomass and available nutrition, often an explicitly stated goal of conservation, but having a more predictable, steady forage base through the growing season due to the demonstrated differences in biomass production between annual and perennial grasses. Our nutrition analyses would suggest that *V. dubia* could serve as an early forage, as its crude protein content is similar to that of perennial grasses early in the season and treatment did not result in higher total nutrient mass. It may be tempting to consider this high nutrition from annual grasses a benefit if more palatable annual grasses such as *B. tectorum* were dominant. Although *B. tectorum* was at one point thought of as beneficial in some ways (Young and Allen 1997), we believe this would be unwise. From our regression analyses, we demonstrated that the benefits would only be realized for a short period early in the year and would not offset the many negatives of annual grass invasion.

This study shows the impacts of annual grass control on sites where *V. dubia* was the dominant invader rather than the direct impacts of *V. dubia* itself on northern mixed prairie plant communities, because we did not include noninvaded sites in the analysis. However, this research documents improved forage quality and quantity where *V. dubia* and other, less-dominant, annual grasses

were controlled—particularly with indaziflam. Landowners and managers in the Northern Great Plains concerned with maintaining grazing productivity and flexibility may benefit from proactive monitoring and management of this species in the region where it is rapidly expanding.

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