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Ventenata (*Ventenata dubia*) Response to Grazing and Prescribed Fire on the Pacific Northwest Bunchgrass Prairie☆

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ABSTRACT

The exotic annual grass ventenata (*Ventenata dubia* L.) is raising concern as it rapidly invades multiple ecosystem types within the United States, including sagebrush steppe, ponderosa pine forests, woodlands, and much of the Palouse and Pacific Northwest Bunchgrass Prairie (PNB). Despite increasing attention, little is known about the invasion dynamics of ventenata, especially its response to disturbances such as grazing and fire. In this study, we examined how cattle grazing and prescribed fire affect the abundance (standing crop, cover, frequency, and density) of ventenata and other plant groups on the PNB over time using two separate long-term studies established in 2004. The first study (Cattle Grazing) looked at the 14-yr effect of cattle grazing exclusion on ventenata aboveground biomass and cover. Our second study (Grazing and Prescribed Fire) examined main and interactive effects of cattle exclusion and prescribed fire on ventenata over three sampling periods (2008, 2016, and 2018). We documented a 30% increase in ventenata cover and 55% increase in frequency on the PNB over the past 15 yr, including areas that were not disturbed by fire or cattle grazing. We found only weak evidence that cattle grazing increased ventenata standing crop when compared with cattle-excluded paddocks, something that could be related to timing of use. There was no evidence that prescribed burning impacted the response of ventenata on its own. However, we found some evidence of interactions between cattle grazing and prescribed fire that suggests prescribed burning could help reduce the abundance of ventenata in areas grazed by livestock. These studies reinforce the important differences between ventenata and other invasive winter annuals in grasslands and clarify a need for research that focuses primarily on the dynamics between this relatively new exotic species in grasslands and the many ecosystems it now inhabits.

Introduction

Temperate grasslands across the globe have been highly modified by human activity for centuries, and the few remaining natural state ecosystems continue to be threatened due to anthropogenic stressors such as cultivation, settlement, land-use abandonment, overgrazing by livestock, and the introduction of invasive species (Henwood 2010). Exotic and invasive annual grasses pose a particularly serious threat to the temperate grasslands of North America (Ogle et al. 2003; McGranahan et al. 2012; Endress et al. 2020) as these species can effectively alter many local, regional, and global aspects of ecosystem function (D'Antonio and Vitousek 1992). Ventenata (*Ventenata dubia* L.) is a relatively new exotic annual grass rapidly spreading across much of the Palouse and Pacific Northwest Bunchgrass Prairie (PNB) in the northwestern United States (Nyamai et al. 2011; Averett et al. 2020). First recorded in the United States in 1952 in the state of Washington, the species has been documented in at least 10 states, as well as several provinces of southern Canada (Scheinost et al. 2008). It is now well established in pasturelands, croplands, and a variety of ecosystems including grasslands, sagebrush steppe, ponderosa pine forests, and woodlands (Averett et al. 2016; Bernards and Morris 2016; Fryer 2017; Jones et al. 2018; Tortorelli et al. 2020). Despite this wide ecological distribution, the basic ecology and dynamics of this annual grass, including the species response to disturbances

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such as grazing and fire, are just beginning to be studied (Wallace et al. 2015; Jones et al. 2018).

While grazing is used to control some invasive species in grasslands (Menke 1992; Porensky et al. 2020), studies have also demonstrated a connection between overgrazing by livestock and the invasion of exotic grasses such as cheatgrass (*Bromus tectorum* L.) (Young 1943; Reisner et al. 2013). Grazing by large ungulates such as cattle *(Bos taurus)* and elk *(Cervus canadensis)* can contribute to invasion by spreading seeds via endozoochary (passage through digestive track) and epizoochary (attachment to body) (Janzen 1984). Large ungulates also disturb soil and biological crusts, increase soil compaction and bare ground, and reduce the cover and density of native grasses, which can all facilitate the establishment and germination of invasive plants (Schulz and Leininger 1990; Sheley and Petroff 1999; Slate et al. 2019; Root et al. 2020). Invasive species response to grazing also depends on species palatability (Augustine and McNaughton 1998). We are aware of numerous anecdotal reports that cattle, elk, and horses avoid eating ventenata or bite off seed heads and spit the rest of the plant out. The only reported ventenata silica content (~2.7%) has been implicated as an important factor in palatability (Pavek et al. 2011), although this content is well within the range of common rangeland grasses (Johnston et al. 1966; McNaughton et al. 1985). Limited empirical studies demonstrate little consensus regarding livestock grazing and ventenata invasion dynamics. Pekin et al. (2016) found no increase in cover of ventenata in plots grazed by elk and cattle in semiarid conifer forests. In contrast, others have reported ventenata can increase in areas that are heavily used by elk populations and excluded from cattle (Pavek et al. 2011; Johnson et al. 2013). Finally, grazing and invasion dynamics can interact with soil parent material. Bryant et al. (2013) found that ventenata was an indicator of the interaction of grazed alluvial Mima Mounds compared with ungrazed mounds in eastern Washington.

Natural and prescribed fire can also play an important role in the invasion success and management of a wide variety of exotic plant species (Menke 1992; D'Antonio 2000; DiTomaso et al. 2006; Alba et al. 2015). Fire can promote or inhibit invasion depending on the traits of the exotic species and adaptations of the native plant community to fire (DiTomaso et al. 2006; Leffler et al. 2013; Jauni et al. 2015; Porensky and Blumenthal 2016). For example, the fire-invasion feedback cycle is well known for promoting and maintaining dominance of exotic annual grass invasions in arid and semiarid ecosystems (D'Antonio and Vitousek 1992; D'Antonio 2000; Balch et al. 2013; Bradley et al. 2018). Fire can promote the establishment and spread of exotic plant species by removing or reducing competition from native plant species and provide a nutrient-rich environment for fast-growing ruderal species, especially annual grasses (D'Antonio 2000; Alba et al. 2015). In the western United States, plant-community dominance of cheatgrass has resulted in a significant increased fire frequency, which favors its own lifecycle (D'Antonio and Vitousek 1992) and can result in the native shrub communities' inability to recover (Whisenant 1990).

Knowledge regarding the response of ventenata to natural and prescribed fire is only beginning to emerge. Landowner survey respondents suggest fire is an ineffective management tool to control ventenata and describe dominance of ventenata following fire (Pavek et al. 2011). Some have reported an increase in ventenata density after summer fires in Washington and Oregon (Haferkamp et al. 1984). However, Mackey (2014) found a reduction in ventenata density on Conservation Reserve Program (CRP) reseeded fields the year after a fall burn. Variability in species response to fire may be linked to burn timing, as spring fires are thought to be more damaging to vulnerable young plant tissues (Bond and van Wilgen 1996), whereas later-season fires can be less harmful to cool season bunchgrass species (Wright and Klemmedson 1965). Youngblood et al. (2006) found ventenata established in trace amounts (< 3%) following thinning and prescribed fire treatments in the forested ecosystems of Oregon's Blue Mountains. In another northwestern forest study, Tortorelli (2020) found that ventenata was similarly abundant in both open unburned and wildfire burned areas, but with stronger negative relationships between ventenata cover and community diversity where burned. In the only study to date to examine ventenata's response to historical fires on the PNB, ventenata increased regardless of burning (Ridder et al. 2021).

Although it is widely accepted that many grasslands evolved with both ungulate grazing and fire (Risser et al. 1981; Collins 1987; Knapp et al. 1999), most research focuses on their main effects and less on their interactions (Fuhlendorf and Engle 2004). More attention is now given to understanding the interactions between fire and grazing in numerous ecosystem types including the tallgrass prairie (Collins 1987; Hobbs et al. 1991; Fuhlendorf and Engle 2004; Collins and Smith 2006), annual grasslands in California (Harrison et al. 2003), ponderosa pine forests (Kerns et al. 2011), savannas (Van Langevelde et al. 2003; Staver et al. 2009), and the Great Basin (Diamond et al. 2009; Diamond et al. 2012). In many grasslands, large herbivores may preferentially use high-quality forage in recently burned areas over unburned areas (Fulehndorf and Engle 2004; Clark et al. 2017). Fire and grazing are thought to mediate factors important for the dominance of cheatgrass in the shrub-steppe ecosystems of the Great Basin, (Pyke et al. 2016; Condon and Pyke 2018), although they are seldom examined concurrently (but see Davies et al. 2016). While interactions between fire and grazing are variable by ecosystem type, their contribution to the development of grasslands makes them important tools for management of invasive species (Collins 1987; Fuhlendorf and Engle 2004). However, the evolutionary history of these two disturbance processes may influence the interaction between fire and grazing (Milchunas et al. 1988). Like the Great Basin shrublands, the Pacific Northwest Bunchgrass Prairie did not evolve with strong large ungulate grazing pressure as was found in the Great Plains (Mancuso and Mosley 1994). Conversely, fire is an important evolutionary process in all temperate grasslands. Before modern fire suppression efforts, reportedly low to moderate severity fires occurred every 10−20 yr based on climate and fuel conditions in the PNB (Hall 1976; Black et al. 1998; Bartuszevige et al. 2012). There is no research examining the role of grazing, prescribed fire, and the interactions of these disturbances on ventenata invasion in the PNB.

We explore how cattle grazing and prescribed fire affect the abundance (biomass, cover, frequency, and density) of ventenata and other plant groups on the PNB over time. This grassland system, now mostly converted to agriculture, once encompassed 8 million ha, including several states in the United States and portions of British Columbia in Canada (Tisdale 1982). We describe outcomes from two separate long-term studies from the Zumwalt Prairie Preserve that were established in 2004. The first study (Cattle Grazing) allowed us to explore the 14-yr effect of cattle-grazing exclusion on ventenata aboveground biomass and cover. Our second study (Grazing and Prescribed Fire) examines main and interactive effects of cattle exclusion and prescribed fire through time. For both studies, extant elk herbivory was not controlled. Given the documented spread of this new annual grass across the PNB and other systems, we expected to find increases in all measures of ventenata abundance over time. Because large ungulate herbivory can reduce the abundance and vigor of native bunchgrasses and ventenata is reportedly unpalatable, we expected that long-term cattle grazing would result in higher ventenata abundance compared with sites with cattle exclusion. On the basis of prior retrospective work in the area (Ridder et al. 2021) we expected that ventenata abundance would not increase in response to fall prescribed fire and grazing. We anticipated interactions between prescribed fire and grazing that would favor ventenata abundance.

Methods

Study site

We conducted this study on the Zumwalt Prairie Preserve (ZPP), owned and managed by The Nature Conservancy. The ZPP, located in northeastern Oregon (45°34′N, 116°58′W), is a 13 300-ha remnant of the PNB. Approximately 90% of the historical extent of the PNB has been converted to agriculture (Tisdale 1982), making the ZPP the largest remaining remnant of this grassland type under conservation. The Nez Perce people (Nimiipuu) inhabited the Zumwalt Prairie seasonally for many thousands of years until the US Government forced them off their land in 1877. The Nez Perce hunted game and gathered food plants on the prairie. In the early 18th century and mid-19th century, when the Nez Perce acquired horses and cattle, the Zumwalt Prairie became important for grazing (Reid 1985; Bartuszevige et al. 2012). Through the Homestead Acts of 1862 and 1909, Euro-American settlers acquired land on what is now the ZPP (Bartuszevige et al. 2012). The large herds of livestock that accompanied settlement likely consumed much of the fine fuels for fire (Bartuszevige et al. 2012). Large herds of ungulates are a relatively recent addition to the PNB; therefore the plant associations on the prairie have not evolved with strong grazing pressure (Mancuso and Mosley 1994). However, elk herds on the ZPP have been increasing over recent decades from approximately 586 individuals in 1990 with 20% being counted on the Zumwalt to approximately 2 577 individuals in 2017 with 66% being counted on the Zumwalt, where they use this prairie as a winter range (TNC, unpublished data). Although there is no complete fire history for the ZPP, it is believed to have low- to moderate-severity fires every 10–20 yr due to the climate and fuel conditions (Black et al. 1998; Bartuszevige et al. 2012). Before 2005, when The Nature Conservancy initiated a prescribed burning program, fires on the ZPP and surrounding grasslands were infrequent (Morgan et al. 1996; The Nature Conservancy, unpublished data).

The ZPP plant community is dominated by native perennial bunchgrass species including bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), Idaho fescue (*Festuca idahoensis* Elmer), Sandberg bluegrass (*Poa secunda* J. Presl), and prairie junegrass (*Koeleria macrantha* [Ledeb.] Schult.) (Kennedy et al. 2009). The ZPP also hosts a high diversity of native forbs. The soils are categorized as Xerolls, consisting of colluvium and loess over Basalt (Schmalz et al. 2013). The Zumwalt Weather Station located on site (elevation of 1 335 m) recorded average winter (December–February) temperature at −2.7°C over the 2006–2015 period, and average summer (July–August) temperature was 15°C (Taylor 2016). This system is categorized by cold, moist winters and warm, dry summers. Total annual precipitation in the same 2006–2015 timeframe averaged 34.9 cm with 14.7 cm falling between April 1 and July 31, which is considered the primary growing season (Taylor 2016).

Study design

Cattle grazing

For the first long-term study (Cattle Grazing), we resurveyed a subset of monitoring plots established in 2004 that were originally part of a larger, multidisciplinary study examining the effects of cattle stocking rates on grassland food webs (Damirian et al. 2007; Darambazar et al. 2007; Johnson et al. 2011; Johnson et al. 2013; Schmalz et al. 2013). The original 2004 study used a randomized complete block design with four blocks (A, B, C, D) and four stocking rate treatment levels (**Fig. 1**). We used only two treatment levels: "grazed" (1.3–1.6 ha/animal unit months [AUM]; considered moderate for the region) and "excluded" (fenced to exclude cattle, but open to elk). The experimental units (treatment paddocks) under the excluded treatment have maintained this treatment since 2004, and the grazed experimental units have had inconsistent grazing history. Therefore, we selected two of the experimental units where a moderate grazing intensity (Wyfells 2009) was maintained since 2009 (**Table S1**, available online at doi:10.1016/j.rama.2021.09.003). Each paddock is 40 ha in size. To guard against confounding conditions based on the legacy of stocking rates, we conducted preliminary analysis on the standing crop of ventenata on the dataset from the original study and found no treatment effect. In fact, ventenata represented only a fraction of the biomass of annual grasses (data not shown), and all exotic annual grasses made up only 4% of total production in the paddocks in 2006 (Darambazar et al. 2007). Within each paddock we resurveyed 18 equally spaced (180 m apart) sampling plots (for a total of 144 for the entire study; also see Schmalz et al. 2013 and Ridder 2018).

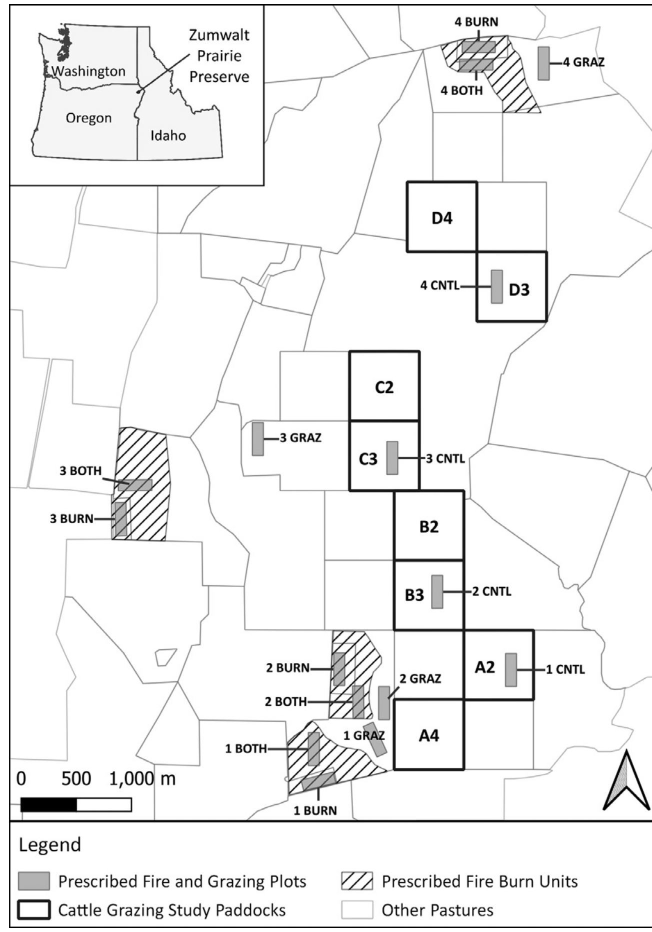

Figure 1. Map illustrating the design of both studies. The eight paddocks of the Cattle Grazing study are labeled as A2, B3, C3, and D3 (excluded) and A4, B2, C2 and D4 (moderately grazed). Prescribed Fire and Grazing study treatments included four replicates of BURN (burn, excluded), GRAZ (unburned, grazed), BOTH (burn, grazed), and CNTL (unburned, excluded). Gray lines represent pasture fences. Areas with hashed lines indicate areas burned in fall prescribed fires in 2006 and 2016 (map provided by Heidi Schmalz, The Nature Conservancy).

Grazing and prescribed fire

The second long-term study (Grazing and Prescribed Fire) was also established in 2004 on the ZPP with the intention of studying the effects of prescribed fire, grazing, and their interaction (see Fig. 1). The study is a randomized complete block two-way factorial design with two levels of grazing (grazed and excluded) and two levels of prescribed burn (burned every 10 yr and unburned) (Taylor and Schmalz 2012). Each block was split into four experimental units and randomly assigned to one of two grazing levels and one of two prescribed fire treatment levels. Thus, each treatment combination was replicated four times, once in each block ($N = 4$). Each experimental unit is 100×300 m. The experimental units that were randomly assigned to control for the grazing treatment were fenced to exclude cattle. The grazed experimental units have been grazed by cattle every year from late July through August with a stocking rate ranging from 1.3 to 1.6 ha AUM^{-1} depending on available forage (The Nature Conservancy [TNC] personal communication, Heidi Schmalz). Livestock were removed after no more than 7 d. Experimental units assigned the prescribed-fire treatment were burned in the fall of 2006 and 2016 (TNC personal communication, Heidi Schmalz) by US Forest Service personnel in accordance with their prescribed burning procedure.

Sampling

We collected data on the Cattle Grazing plots between June 12 and July 9, 2018 before any cattle utilization. We relocated the monitoring plots using a handheld Global Positioning System. Following previous methods (Damiran et al. 2007), we placed a rectangular frame (0.5×1 m) lengthwise on the east side of the sampling plot. We collected cover data to the nearest 1% using ocular estimation by functional group: ventenata, forb, annual grasses (other nonnative annual grass), and perennial grass (Damiran et al. 2007). We collected standing crop (aboveground biomass) for ventenata by clipping all vegetation within the 0.5×1 m rectangular frame to ground level, removing dead plant material, and then separating out and bagging ventenata and all other vegetation. All the samples were oven dried at 60°C for at least 24 h before weighing to the nearest 100th of a gram.

The original data from the Grazing and Prescribed Fire plots were collected 2 yr after the first burns (2006) in 2008 within each 100×300 m experimental unit using six 100-m transects that ran parallel to the 100-m side of the unit and were spaced 50 m apart. Foliar cover data for ventenata was collected using the line-point intercept (LPI) method with hits recorded every 3 m along each transect (Taylor and Schmalz 2012). These points were then converted to percent cover. Ventenata nested frequency data were collected every 6 m on the same six transects using frame sizes of 10×10 cm. In 2016 the monitoring protocol was adjusted, and foliar cover data were collected using LPI every meter along nine, 50-m transects that were 30 m apart within each experimental unit. Nested frequency data were collected every 2 m along six of the nine transects (150 measurements per experimental unit). In addition, density of ventenata was collected from 10×10 cm quadrats every 2 m along the same six nested frequency transects. We collected data in 2018 two yr after the second burn following the protocol for cover, frequency, and density as in 2016. Each year's data were collected before utilization by cattle.

Data analysis

Cattle grazing

Plot data were averaged at the experimental unit level (paddock). Response variables included ventenata cover and standing crop (g m^{-1}), cover of annual grass (A-GRASS), perennial grass (P-GRASS), and forbs (FORB). We used a mixed linear model analysis of variance (ANOVA) and Proc MIXED in SAS 9.4 (SAS Institute 2013) to test for treatment effects (grazed or excluded). Treatment was fixed, and block was the random effect. Residuals were examined to ensure assumptions were met and none were violated; therefore, no transformations were needed. We report actual P values and interpret these as a continuous measure of the strength of evidence, with small values ($P < 0.05$) indicating stronger evidence of a treatment effect and larger values indicating weaker evidence ($P > 0.10-0.15$), assuming the effect size is biologically relevant (Ramsey and Schafer 2002; Murtaugh 2014; Wasserstein and Lazar 2016). We also explored variability in treatment responses among the experimental blocks to assist with interpretation.

Grazing and prescribed fire

To account for the repeated measures and blocked design of the Grazing and Prescribed Fire study, we used a randomized block repeat measures mixed linear model ANOVA using Proc MIXED in SAS 9.4 (SAS Institute 2013). Year, burn, graze, and their interactions were treated as fixed effects. Block and the nested burn by grazing within block were treated as random effects. Year was the repeated measure with nested burn by grazing within block as the subject effect and the Kenward-Rogers degree of freedom method. Several covariance structures were examined: compound symmetry, heterogeneous compound symmetry, antedependence, unstructured, and spatial power for the analysis. The antedependence covariance structure was selected on the basis of Akaike information criterion. We ran pairwise comparisons to examine the differences within years and among treatment combinations, as well as possible interactions irrespective of overall P values as we had an a priori interest in comparisons between combinations of both levels of grazing and burning within each sampling year, along with comparisons between treatment combinations across years. Residuals were examined to ensure the assumptions of the mixed linear model were met. None were violated; therefore, no transformations were necessary. The P values from all comparisons are reported and interpreted as noted earlier, and graphical interpretations display P values < 0.05.

Results

Cattle grazing

Ventenata accounted for 16% and 19% of the standing crop in excluded and grazed paddocks, respectively, in 2018 (calculated from **Table 1**). There was some weak evidence that ventenata was more abundant in grazed paddocks. Most notably, standing crop in grazed paddocks was about 14 g m^{-1} higher as compared with cattle-excluded paddocks ($P = 0.14$; see Table 1). We undertook a descriptive block scale examination of treatments even though we did not have replication for analysis ($N = 2$ per block) to better understand this result. We found higher values in standing crop and cover of ventenata in grazed paddocks than in those paddocks where cattle grazing was excluded in three of the four blocks (**Table 2**). Block A had nearly $26\times$ more standing crop and almost $8\times$ more ventenata cover in the grazed paddock compared with excluded blocks. Blocks C and D had almost $2\times$ and 1½ × more standing crop, respectively, and about twice the ventenata cover in grazed paddocks than in excluded ones. Block B had a contrasting pattern, more standing crop and cover of ventenata in paddocks with grazing excluded, but the difference between the two paddocks was less than 1¼ × the amount of standing crop and only about 3% more cover in the excluded paddocks.

Grazing and prescribed fire

Results for overall fixed main effects by response variable are shown in **Table 3.** Unsurprisingly, there was strong evidence for all the response variables that treatment effects differed based on the sampling year (all $P < 0.01$; see Table 3). We found no evidence that the main effect of burning was important for any of the response variables or that burning interacted with year or grazing. There was some evidence that the global main effect of grazing

Table 1
Mean standing crop and cover of ventenata and other plant groups in 2018, 14 yr after cattle grazing exclusion (Cattle Grazing study). Difference is calculated between excluded and grazed.

Response	Excluded	Grazed	Difference	*P*	Lower CI	Upper CI
Ventenata standing crop (g/m^2)	25.15	39.19	−14.05	0.143	−36.66	8.57
Other vegetation standing crop (g/m^2)	194.23	199.15	N/A	N/A	N/A	N/A
Ventenata (%)	5.91	10.19	−4.28	0.177	−12.017	3.462
Annual grass (%)	3.45	4.83	−1.38	0.509	−7.009	4.342
Perennial grass (%)	28.84	28.05	0.79	0.765	−6.857	8.427
Forb (%)	26.38	24.19	2.19	0.502	−6.989	11.378

CI indicates confidence interval.

Table 2
Mean cover and standing crop of ventenata by block and treatment (Cattle Grazing study).

	Cover (%)		Standing crop (g/m$^{2)}$	
Block	Excluded	Grazed	Excluded	Grazed
A	1.36	9.00	0.98	26.38
B	7.94	4.63	31.86	25.92
C	7.76	16.33	17.76	31.66
D	9.57	18.18	49.97	72.81

was important for ventenata frequency ($P = 0.11$), but this varied by year (graze ⁎ year, $P = 0.03$). Results for ventenata cover and density demonstrated weak evidence of a grazing by year interaction ($P = 0.15$).

Pairwise comparisons within sampling year suggest that ventenata cover remained low and there was no evidence of a difference among treatments in 2008 (**Fig. 2**). In 2016 there is weak evidence that the excluded and burned treatment had about 17% lower cover compared with the grazed and unburned treatments ($P = 0.15$; Table S2, available online at doi:10.1016/j.rama.2021.09.003). By 2018, there was no evidence of a difference ($P = 0.45$). There was some evidence that ventenata was less frequent on the excluded and burned paddocks as compared with grazed and unburned areas in 2008 ($P = 0.08$), although the effect size was small (about 7%; **Fig. 3**; Table S3, available online at doi:10.1016/j.rama.2021.09.003). By 2016, there was strong evidence that ventenata was much more frequent on the grazed and unburned treatment plots (65% vs. 25%; $P = 0.02$; see Fig. 3 and Table S3). For the grazed treatment, there was weak evidence that ventenata was 25% less frequent in areas that were burned ($P = 0.13$; see Fig. 3 and Table S3). Similar to the results for cover, there was no evidence of a difference in frequency among the treatments in 2018. Density was only recorded in 2016 and 2018. There was no evidence that ventenata density differed among the treatments in 2016 (**Fig. 4; Table S4**, available online at doi:10.1016/j.rama.2021.09.003). But there was some evidence that the grazed and unburned treatments had more than twice as many (over 800 plants/m^2) ventenata plants as compared with excluded treatments regardless of burning ($P = 0.12$ for both comparisons; see Fig. 4 and Table S4).

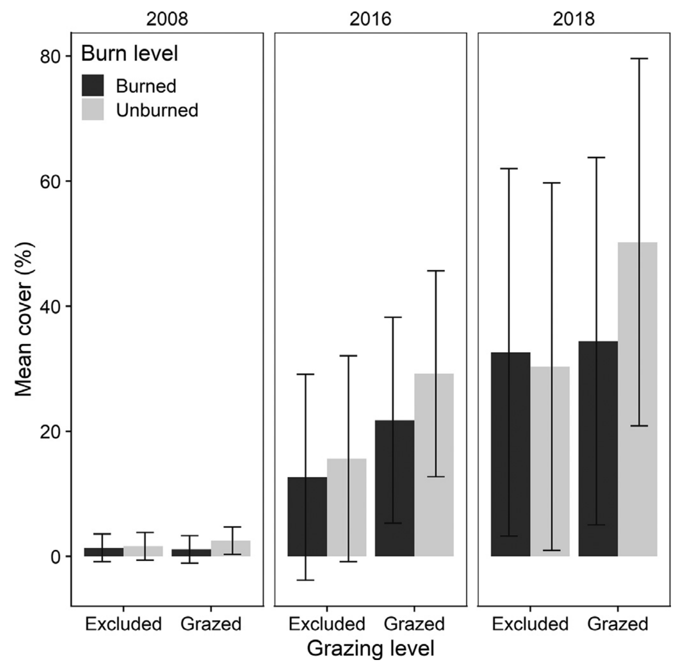

Figure 2. Ventenata cover (with 95% confidence interval) in response to cattle grazing exclusion and two fall prescribed fires (2006, 2016) by sampling year. There was no evidence ($P > 0.20$, Table S2, available online at doi:10.1016/j.rama.2021.09.003) for most treatment differences within years, but there was weak evidence that cover in the excluded and burned treatment was lower when compared to the grazed unburned treatment in 2016 ($P = 0.15$; Table S2).

Discussion

Our study documents the rapid spread and increase of ventenata in the PNB over the past 15 yr, including areas that were not disturbed by fire or cattle grazing. Our findings are consistent with a number of other studies documenting the increase in ventenata through time in this region, including forested systems (Averett et al. 2016) and canyon grasslands near the Zumwalt Prairie preserve (Johnson et al. 2013; Bernards and Morris 2016). This invasive species was too rare to analyze in our Cattle Grazing study in

Table 3
Results from repeat measures mixed linear model by response variable (ventenata cover, frequency, density) for main effects and interactive effects (Grazing and Prescribed Fire study).

	Cover			Frequency			Density		
Effect	DF	*F* value	*P*	DF	*F* value	*P*	DF	*F* value	*P*
Yr	11.2	13.19	0.0011	11.2	26.81	< .0001	21.6	15.63	0.0007
Burn	12	0.37	0.5558	12	0.65	0.4346	24	0.18	0.6744
Graze	12	1.14	0.3066	12	2.93	0.1128	24	1.41	0.2468
Burn ⁎ Graze	12	0.32	0.5849	12	1.14	0.3065	24	0.29	0.5925
Graze ⁎ Yr	11.2	2.25	0.1512	11.2	5.01	0.0279	21.6	2.17	0.1553
Burn ⁎ Yr	11.2	0.21	0.8165	11.2	0.93	0.4217	21.6	0.78	0.3871
Burn ⁎ Graze ⁎ Yr	11.2	0.61	0.5584	11.2	0.59	0.5689	21.6	0.48	0.4958

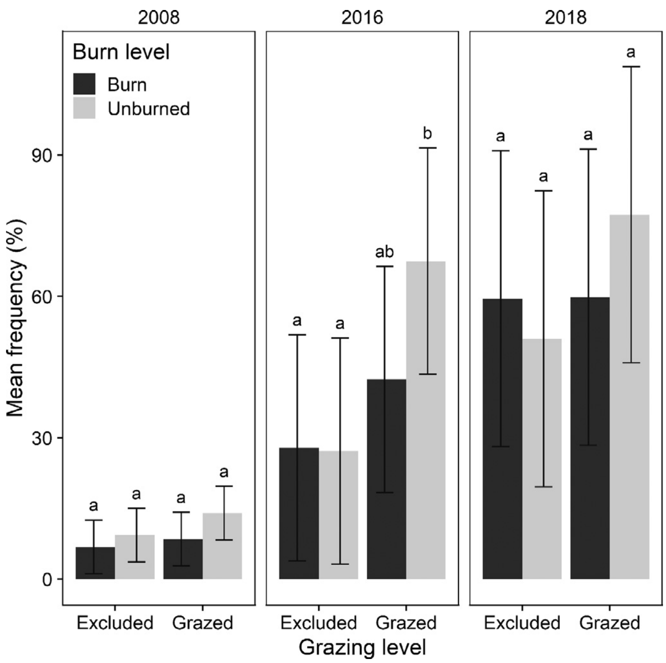

Figure 3. Ventenata frequency (with 95% CI) in response to cattle grazing exclusion and two fall prescribed fires (2006, 2016) by sampling year. Different letters denote strong evidence for differences ($P < 0.05$) within sampling year. There was weaker evidence that frequency in the excluded and burned treatment was lower when compared to the grazed unburned treatment in 2008 ($P = 0.08$; Table S3, available online at doi:10.1016/j.rama.2021.09.003).

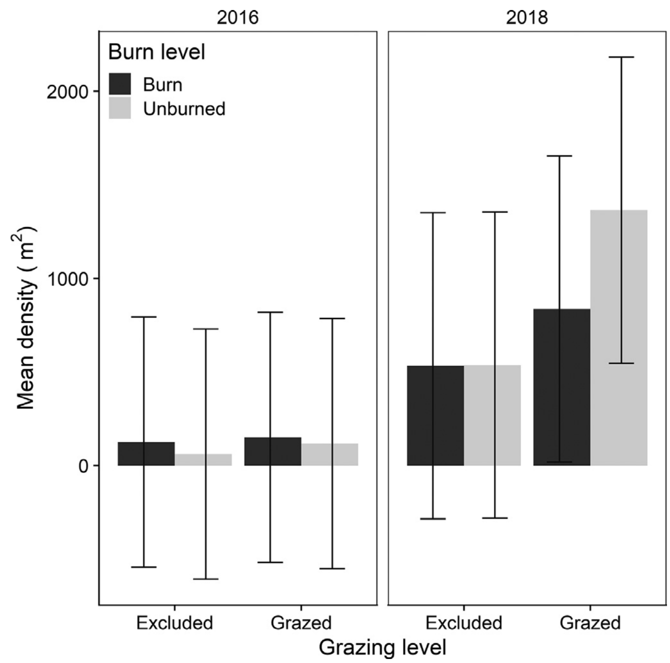

Figure 4. Ventenata density (with 95% CI) in response to cattle grazing exclusion and two fall prescribed fires (2006, 2016) by sampling year. Evidence for treatment differences within years was not strong ($P > 0.05$; Table S4, available online at doi:10.1016/j.rama.2021.09.003), but there was some evidence that ventenata density was higher in the unburned and grazed treatments when compared with both excluded treatments in 2018 ($P = 0.12$ for both comparisons; Table S4).

2006 but, by 2018, made up 16−19% of the standing crop in both excluded and grazed paddocks. Likewise, ventenata cover and frequency were both under 20% in 2008 and by 2018 both measures exceeded 50−75%, respectively. In addition, we document that ventenata density doubled from 2016 to 2018, regardless of treatment. The patterns we report here are all too familiar within invasion ecology, a rapid expansion phase following a lag time during the introductory phase (Radosevich et al. 2003; Morris et al. 2013). While it is still unknown where the invasion curve will plateau for ventenata in the PNB, the results of our two studies are useful for understanding how grazing and fire, individually and together, contribute to this invasion.

Our findings also raise concerns that fire regimes could be altered by the rising abundance of ventenata in the PNB, especially in unburned areas. The differences in standing crop between our grazed and excluded paddocks were not strong, and the aboveground biomass of ventenata was characteristically small (James 2008; McKay et al. 2017). On average, standing crop was only about 32 g m^{-1}. However, these values may be biologically relevant in a management context since they translate to a 138-kg ha^{-1} (125-lb $acre^{-1}$) difference between grazed and excluded paddocks with highly flammable infilling of fuels in late season (Kerns et al. 2020). In the forested systems of the Blue Mountains in northeastern Oregon, for example, there is also concern that infilling of ventenata will provide more fine fuels that alter fire dynamics in open sites where native species ground cover is typically low (Oliver 2016; Fryer 2017). It is still unknown if ventenata will influence fine fuels in a way that initiates a positive feedback cycle promoting its own invasion, like the annual cheatgrass (Balch et al. 2013; Kerns et al. 2020).

Cattle grazing

Our Cattle Grazing study did not strongly support our expectation that paddocks with both cattle (and elk) herbivory would have higher cover and standing crop of ventenata than those excluded from cattle. A lack of strong evidence is consistent with another study that found no differences in cover of annual grasses (including ventenata) with herbivory by cattle and elk (Pekin et al. 2016). However, we did find some evidence for an increase in ventenata standing crop in the cattle-grazed areas as compared with areas where cattle were excluded, especially when finer-scale block-related patterns were noted. For three out of the four experimental blocks, the patterns for ventenata standing crop and cover suggest that cattle grazing may be exacerbating the ventenata invasion. It is likely that the variability between blocks and our relatively small replication contributed to the limited evidence that we found. This could suggest the possibility that combined herbivory by cattle and elk may lead to increased invasion in the future. This was a retrospective study, and we did not employ different experimental stocking rates, which can often reveal significant responses owing to soils (Schmalz et al. 2013) and vegetation structure (Fuhlendorf et al. 2001; Johnson et al. 2011). It is possible that our findings are related to the overall moderate level of grazing on the Zumwalt Prairie Preserve, a characteristic of management that makes it a model system for positive interactions (Wyffels 2009). Different stocking rates could result in different ventenata cover and standing crop in the future or in other locations.

Despite our limited number of replicates (blocks), the variability we found among blocks raised interesting questions regarding timing of grazing and the increase in ventenata over time. Timing of grazing affects grass palatability and potentially offers a control method for undesirable species (Daubenmire 1940; O'Connor and Pickett 1992). However, ventenata is considered unpalatable (Pavek et al. 2011) and its late phenological development is suggested to contribute to its increase with spring grazing pressure because it is simply too short to be consumed by cattle while native species are much taller (Wallace and Prather 2015). The timing of use could contribute to the contrasting pattern in block B because it was most often grazed in June (Table S1), when ventenata is still green and possibly tall enough to be eaten by cattle. The other blocks are most often grazed in July or later, when the annual grass has senesced and is likely least palatable. Future research on grazing interactions should include variation in timing of use to fully understand this dynamic.

Grazing and prescribed fire

As expected, we found no evidence that prescribed burning impacted the response of ventenata on its own. These results are also consistent with other findings regarding prescribed fire in the PNB grasslands, as well as annual grasses in other grassland systems. For example, Taylor and Schmalz (2012) reported that ventenata frequency increased on the Zumwalt Prairie Preserve regardless of prescribed fire, and a retrospective study showed historical prescribed fire did not appear to affect ventenata cover or frequency (Ridder et al. 2021). Inland forest mosaic communities surrounding the ZPP are also heavily invaded by ventenata following wildfire in both unburned and burned areas (Tortorelli et al. 2020). Conversely, our findings differ from other research in the region and in other grasslands in several ways. For example, Haferkamp et al. (1984) reported an increase in ventenata density after summer fire. Other studies found ventenata established in trace amounts following forest thinning and prescribed fire treatments in Oregon's Blue Mountain forest systems (Youngblood et al. 2006). Prescribed burns are hypothesized to reduce the thatch layer created by ventenata, which may promote its own seedling survival (Wallace et al. 2015), although we did not see any evidence to support this dynamic.

We did not find interactions between prescribed fire and grazing that would favor ventenata abundance. However, we did find some evidence that prescribed burning might make a difference in areas grazed by livestock. A pattern of lower ventenata when grazed and burned in all three response variables suggests prescribed fire could be an important control factor. For example, we found weak evidence that without prescribed fire, livestock grazing alone produced higher ventenata frequency starting in 2008, a pattern that was more strongly supported in 2016. By 2018, ventenata abundance was so extensive and pervasive that it seemed to overwhelm all treatment effects, indicating the invasion may have reached a plateau phase in invasion (Radosevich et al. 2003; Morris et al. 2013). Further, although density more than doubled by 2018, we were only able to detect weaker evidence of higher density in grazed but not burned paddocks in 2018, suggesting density levels may detect more significant differences in the future. Our findings are consistent with those in a tallgrass prairie system, where *Bromus tectorum* cover was significantly lower in burned and grazed plots than in plots that were just grazed (Collins 1987).

Alternatively, the significant increase in ventenata frequency in grazed-only experimental units in the yr 2016 could be related to other factors. One possibility is precipitation differences. Our study was not designed to account for precipitation; however, the yr 2015 represented the warmest year on record and total precipitation received was 31.9 cm, ≈3 cm lower than the 2005–2008 average (Taylor 2016). Spring and early fall precipitation patterns in 2018 were above the 13-yr average for the ZPP (2006–2018). April and May precipitation totals in 2018 also exceeded 145% of the 13-yr average for those months, followed by a drier than normal July–September. Rainfall in October was close to double the 13-yr average (Thomas and Rossman 2018). Therefore, it is possible the differences we found in 2016 were not detectable in 2018, when abundance and production ventenata may have been higher overall.

Another possible reason for the patterns we found could relate to the differences in timing since burns between sampling years. Both 2008 and 2018 were 2 yr after the last fall prescribed fire. The sampling done in 2016 was 10 yr after the last fire, which could influence results because time since fire can affect temporal patterns of plant species abundance, structure, and composition (Bond and Wilgen 1996). Unfortunately, there were no data before 2006 for comparison. Still, our findings seem consistent enough across response variables to suggest that livestock grazing without the use of prescribed fire may have undesirable impacts in terms of ventenata abundance in the PNB.

We caution that there are several limitations to the inferences for both studies. As described earlier, we did not experimentally manipulate cattle stocking rates or exclude elk herbivory. In addition, fine-scale spatial analysis of grazing behavior within burned patches was beyond the scope of this study. Therefore, further research is necessary to fully understand time of use, stocking rates, exclusion of native herbivory, and patch-burn grazing impacts. It is also possible that differences in site conditions, soils, and plant community play a confounding role in our results. For example, Endress et al. (2020) found that ventenata distribution and abundance can be related to location in either xeric, mesic, or reseeded old fields. Interactions between livestock grazing, soil parent material, and topography may have influenced the abundance of ventenata as they did in Bryant et al. (2013). Likewise, the findings in our fire and grazing study only relate to fall prescribed fire in this grassland type. Ventenata may have different fire dynamics across different ecosystems (Ridder et al. 2021). In addition, we did not experimentally manipulate fire intensity, timing of burn, or pretreatments that reduce the fuel load and can also impact fire severity (D'Antonio et al. 2003). Burn severity indices on our experimental units never reached a heavily burned category for substrate, the only class that may have affected ventenata seeds at this time of year (Movich and Schmalz 2016). Season of burn could impact fire severity, but even more so, a spring or summer burn could have more impact on ventenata seed before seed shattering. Further research should be done to determine the effect of timing of prescribed fire on ventenata abundance.

Management Implications

Our study illustrates an overall trend showing the rapid spread and increase of ventenata in the PNB over the past 15 yr regardless of fall prescribed fire or cattle grazing. Taken together, the findings from our two studies suggest that livestock grazing with extant elk herbivory could be related to increasing ventenata abundance in the PNB, though more research is needed to understand how different grazing systems can influence that outcome. Moreover, our findings highlight the management implications of prescribed fire as a necessary disturbance for mitigating invasion in grazed grasslands. Fall prescribed fire does not appear to effectively contain the spread of ventenata. However, the overall pattern of higher ventenata cover, frequency, and density where livestock are grazed without prescribed fire suggests prescribed fire could be a factor contributing to reduced abundance when grazed and burned. If so, prescribed fire could be an effective management tool to reduce ventenata where livestock grazing occurs.

Finally, as a winter annual grass, ventenata control and management considerations are often grouped with cheatgrass and other invasive winter annuals (Nyamai et al. 2011). Ventenata differs enough from other invasive winter annual grasses in both phenology and plant traits that it requires a closer study of the dynamics that influence its invasion success, particularly the role fire plays in facilitating or controlling its spread (James 2008; Bansal et al. 2014; Rinella et al. 2014; Fryer 2017; McKay et al. 2017). We did not find evidence that fall prescribed fire exacerbates ventenata invasion by increasing its cover, frequency, and density like has been found with cheatgrass in the Great Basin (Young and Evans 1978). These findings add support to previous studies suggesting that managers may be able to reintroduce prescribed fire to this system without high risk of conversion to ventenata and where the native system is still intact (Taylor and Schmalz 2012; Mackey 2014; Ridder et al. 2021). These studies further illustrate the important differences between ventenata and other invasive winter annuals in grasslands, highlighting a need for research that focuses primarily on the dynamics between this relatively new exotic species in grasslands and the many ecosystems it now inhabits.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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