Tortorelli *et al. Fire Ecology* (2026) 22:54
https://doi.org/10.1186/s42408-026-00468-6

Fire Ecology

Association for Fire Ecology

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Prescribed fire drives divergent invasive annual grass responses in a dry forest-mosaic landscape

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Abstract

Background The reintroduction of fire, with the goal of reducing fuels and restoring forest resilience, is a critical management practice in dry conifer forests of the western United States. In dry forest landscapes, invasion by non-native annual grasses could complicate restoration goals if fire exacerbates invasion and associated impacts, particularly in areas with low tree cover and in adjacent open areas. Although annual grasses are becoming increasingly pervasive across the West, little is known about how species differ in their response to burning, especially in historically invasion-resistant forest-mosaic ecosystems. We use field data collected before and after a prescribed burn in eastern Oregon, USA, to uncover how prescribed fire impacts three problematic invasive annual grass species, cheatgrass (*Bromus tectorum*), ventenata (*Ventenata dubia*), and field brome (*B. arvensis*) and understory plant communities for 3 years after burning in a dry forest-mosaic landscape.

Results Plant communities shifted towards invasive dominance over time regardless of burning. All three invasive annual grass species recovered within 2 years of burning to at or above pre-treatment levels and continued to increase in cover over time. Ventenata increased at the fastest rate across both burned and unburned areas, averaging less than 10% in 2016 to nearly 20% in 2020. This increase was slightly slower in burned areas than in unburned areas.

Conclusions Our study demonstrates that invasive annual grasses are rapidly spreading across the study area regardless of prescribed fire. Low severity prescribed fire may not exacerbate the invasion of some annual grasses in forested areas and sagebrush patches where the canopy cover is already open. However, burning in sagebrush patches may have negative effects on important non-forest ecosystems when burning results in the loss of fire-sensitive species. This information can help aid decision making and improve species-specific management and treatment effectiveness in dry forest landscapes.

Keywords Cheatgrass, Field brome, Ponderosa pine, Prescribed burn, Ventenata

Resumen

Antecedentes La reintroducción del fuego, con el objetivo de reducir la carga de combustibles y restaurar la resiliencia del bosque, es una práctica de manejo crítica en bosques secos de coníferas del oeste de los EEUU. En paisajes de bosques secos, la invasión de pastos anuales no nativos puede complicar los objetivos de restauración, si el fuego exacerba la invasión de gramíneas y sus impactos asociados, particularmente en áreas con bajas coberturas de

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árboles y más abiertas en sus adyacencias. Aunque las gramíneas se están incrementando de manera dominante en el oeste de los EEUU, es muy poco conocido el cómo estas especies difieren en su respuesta a las quemas, especialmente en ecosistemas de mosaicos forestales históricamente resistentes a las invasiones de exóticas. Usamos datos de campo colectados antes y después de una quema prescripta en el oeste de Oregón, EEUU, para descubrir como estas quemas impactan sobre tres especies problemáticas de pastos anuales: cheatgrass o bromo caído (*Bromus tectorum*), ventenata (*Ventenata dubia*), y bromo de campo (*B. arvensis*), y otras comunidades de plantas del sotobosque tres años después de una quema prescripta en un mosaico de paisaje forestal seco.

Resultados Las comunidades cambiaron hacia una dominancia de plantas invasoras de manera independientemente de la quema. Las tres anuales invasoras se recuperaron dentro de los dos años luego de la quema a, o por encima de los niveles que tenían previo a la misma, y con el tiempo continuaron aumentando su cobertura. Ventenata se incrementó a una tasa más alta tanto en áreas quemadas como no quemadas, promediando menos de un 10% en 2016 y cerca de un 20% en 2020. Este incremento fue un poco más lento en áreas quemadas que en no quemadas.

Conclusiones Nuestroestudio demostró que las plantas anuales invasoras se propagan rápidamente a través del área de estudios independientemente de las quemas prescriptas. Las quemas prescriptas de baja severidad pueden no exacerbar la invasión de algunos pastos en áreas de bosques y parches de arbustos de artemisia donde el dosel es muy abierto. Sin embargo, la quema de parches de arbustales de artemisia puede tener efectos negativos en ecosistemas no forestales cuando la quema resulta en la pérdida de especies sensibles al fuego. Esta información puede ayudar en el proceso de decisión y mejorar el manejo específico de especies y la efectividad de los tratamientos en paisajes de bosques secos.

Background

The reintroduction of fire into dry conifer forests of the western United States is often considered essential for promoting long-term ecosystem health and biodiversity (Agee 1994; Kerns et al. 2006; Stephens et al. 2019; Moreira et al. 2020; USDA Forest Service 2022). Invasive species, namely non-native grasses, may complicate restorative burning efforts by altering fire behavior and post-fire plant community composition and forest recovery. Despite increasing concern regarding annual grass invasions into western US forests, especially in open canopy forests and along non-forest ecotones (Harrod and Reichard 2002, Kerns et al. 2020, Krosby et al. 2020, Gray et al. 2021), relatively little is known about how these species influence and respond to prescribed fire over time in forests and forest-mosaic ecosystems. This is especially true for the newer invasive grasses, including ventenata (*Ventenata dubia*), which is rapidly spreading throughout dry forests of the American West (Nietupski et al. 2024; Tortorelli et al. 2020; Downing et al. 2020). Understanding how prescribed fire impacts invasion and understory vegetation is critical for planning efficient and effective post-fire treatments to control non-native species and promote desired ecosystem functions.

The reintroduction of fire into western dry forest landscapes is a common management practice designed to decrease woody fuels and wildfire risk and restore resilient structure and composition (Allen et al. 2002; Sexton 2006; Hessburg et al. 2015; Vaillant and Reinhardt 2017). Prescribed burning and mechanical thinning fuel treatments have accelerated over the last decade, incentivized by recent federal policies, initiatives, and funding (e.g., the USDA Forest Service Wildfire Crisis Strategy; USDA Forest Service 2022). The Forest Service reported over 768,000 ha treated with prescribed fire across the nation in 2023 alone, with goals of reducing the risk of severe wildfire, improving wildlife habitat and biodiversity, and promoting overall forest health and future resilience (USDA Forest Service 2023). The Wildfire Crisis Strategy calls for over 8 million ha of fuel reduction treatments on National Forest lands and an additional 12 million ha on other federal, state, tribal, and private lands over the next 10 years using both mechanical thinning and prescribed fire (USDA Forest Service 2022).

Prescribed fire is often successful at reducing wildfire hazard through the reduction of woody fuels, but the extent to which treatments meet ecological objectives is more variable and may depend on pre-fire understory composition and prescribed fire season, frequency, and intensity and post-fire management (Abella and Springer 2015; Kerns and Day 2017). Prescribed burning can have unexpected and undesirable effects on forest health, biodiversity, and future resistance if fire exacerbates invasive species, including altering surface fuels and community composition in an undesirable way (Abella and Springer 2015; Jang et al. 2021). Additionally, invasive species can influence fuel characteristics and fire behavior, complicating management actions (Poulos and Roy 2015; Tortorelli et al. 2023; Harrison et al. 2024; Brooks et al. 2004). Studies evaluating understory response to prescribed burning in dry western forest landscapes often have mixed results and generally occur in forests with low initial levels of invasion by annual grasses (Abella and Springer 2015, Jang et al. 2021). Given that the influence of forest disturbance on invasion has been found to depend on invasion stage and propagule supply (Kerns and Day 2017; Eschtruth and Battles 2009), there is a need for additional studies that evaluate understory response to prescribed burning in areas with different levels of initial invasion.

Annual grasses are a dominant invader in many dry forest ecosystems (Gray et al. 2021, Kerns et al. 2020). Much of our understanding about how fire influences invasive annual grasses has been developed around the widespread and problematic invader, cheatgrass (*Bromus tectorum*), which generally increases in the first few years following fire (Shinneman and Baker 2009; Chambers et al. 2024). However, many invasive annual grass species can invade forested sites (Kerns et al. 2020). Although they are often lumped into a single category, annual grass species can vary in their response to fire, influence community dynamics differently, and may require individualized and context-dependent management strategies (Tortorelli et al. 2020; Berleman et al. 2016; Applestein and Germino 2022). With limited post-fire invasion treatment budgets and personnel, it is critical that control efforts are applied during times when they can have the greatest effect on the target species, highlighting the importance of understanding how different species influence and respond to prescribed burning.

A large, 1540 ha prescribed burn within the Ochoco National Forest of central Oregon, USA (Fig. 1), provided an ideal opportunity to examine how different invasive annual grass species influence and respond to burning in an invaded forest-mosaic landscape. The primary goals of the treatment included reintroducing fire into a dry conifer forest ecosystem, reducing hazardous fuels and the potential for future high-intensity wildfires, and promoting palatable grasses and forbs to improve forage for livestock and wildlife (USDA Forest Service 2010). Here, we use a Before-After-Control-Impact study design to

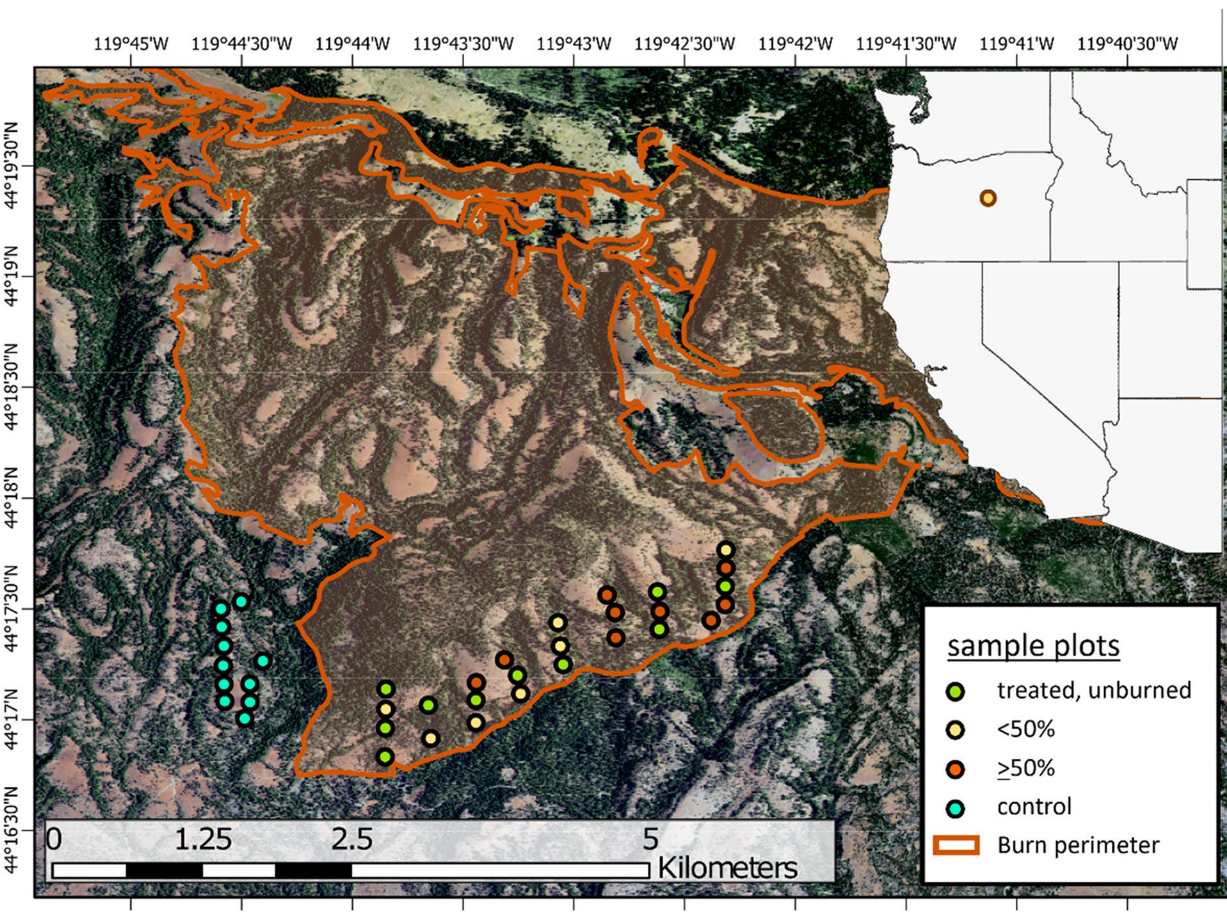

Fig. 1 Prescribed burn treatment area and location of vegetation transects. Transects are displayed by their burn category: control; treated, unburned; < 50% of transect burned; and ≥ 50% of transect burned. The study area was located within the Ochoco National Forest, Oregon, USA

investigate three problematic invasive annual grass species, cheatgrass, ventenata, and field brome (*Bromus arvensis*), and understory vegetation response to prescribed fire over 3 years following treatment. We ask the questions: (1) to what extent does annual grass cover at the time of burning influence prescribed fire spread, (2) how do three invasive annual grasses differ in their response to burning over time (1, 2, and 3 years postfire), and (3) how does understory composition change over time with invasion and fire? This study arose directly from conversations with land managers surrounding concerns regarding treating with prescribed fire in and near invaded areas.

Methods

Study area

The study was conducted in the Ochoco National Forest of central Oregon, USA (Fig. 1). The Ochoco National Forest is dominated by dry mixed conifer forests intermixed with large plateaus supporting pine and juniper woodlands, bunchgrass prairies, and sparsely vegetated, rocky sagebrush (*Artemisia* sp.) flats. Soils are primarily formed from volcanic-ash and wind-blown loess and vary in depth with surface topography (Paulson 1977). Elevation ranges from 1400 to 1800 m. The climate is strongly continental, with mean annual precipitation of 40 cm falling predominantly as snow between October and April (Western Regional Climate Center 2021). During the sampling period (2016–2020), annual precipitation ranged from 19 to 50 cm with the wettest month occurring in October 2016 and the driest period beginning in winter 2018 and extending to the end of the sample period (Fig. 2).

Plant communities vary with elevation, topography, and soils throughout the region (Fig. 3). The dominant tree species in this area is ponderosa pine (*Pinus ponderosa*) with scattered western juniper (*Juniperus occidentalis*) and interior Douglas fir (*Pseudotsuga menziesii subsp. glauca*). The understories of open forests (< 30% canopy cover) contain bunchgrasses including bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*). Denser forest understories are dominated by elk sedge (*Carex geyerii*), pinegrass (*Calamagrostis rubescens*), and perennial forbs including heartleaf arnica (*Arnica cordifolia*). Dwarf shrublands dominate shallow-soil plateaus throughout the forest mosaic, supporting stiff sagebrush (*Artemisia rigida*) and scattered shallow-rooted perennial bunchgrass including Sandberg bluegrass (*Poa secunda*) and native annual forbs. The invasive annual grasses ventenata, cheatgrass, and multiple species of invasive annual bromes (*Bromus* sp.) are present in forest openings, ecotones, and shrublands. Densely forested areas remain relatively uninvaded by shade-intolerant invasive grasses.

Fire history and restoration treatment

Historic fire regimes for the landscape were variable depending on topography and vegetation type. Prior to European settlement and the forced relocation of indigenous people to reservations in the late nineteenth century (Hessburg and Agee 2003), forests burned frequently with low and mixed severity fire, while low productivity shrubland patches rarely burned and helped slow

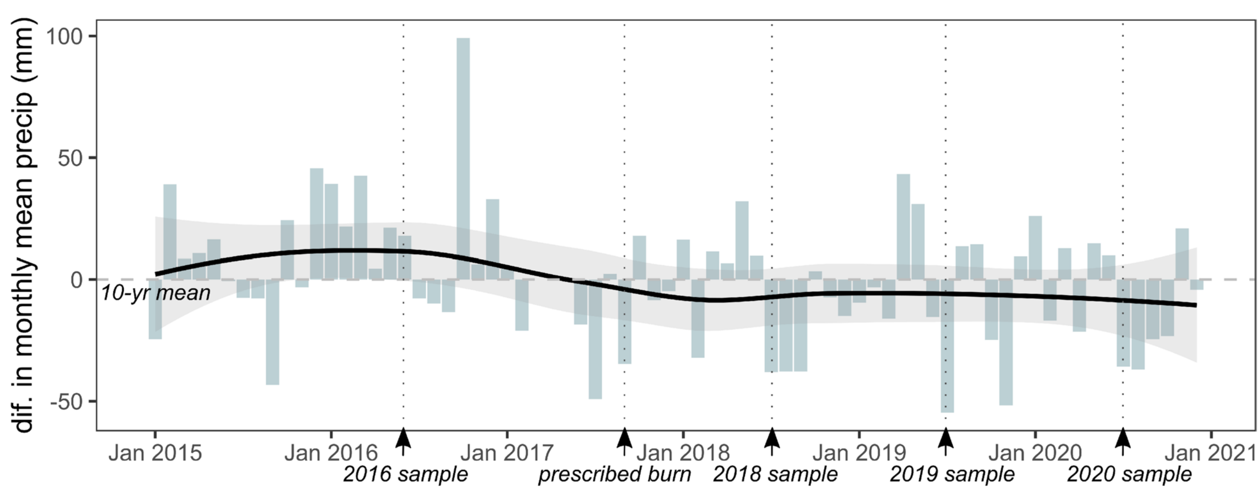

Fig. 2 Monthly mean precipitation (mm) divergence from the 10-year mean throughout the sampling period (2016–2020) including the mean divergence (solid line) and 95% confidence interval modeled using a loess smoother. Dotted lines indicate dates of vegetation sampling and the prescribed burn. Precipitation was recorded at Brer Rabbit, OR Remote Automatic Weather Station, at latitude 44° 19′N, longitude 119° 46′W, approximately 5 km WNW from the prescribed burn, 1743 m

Fig. 3 The 2017 prescribed fire burned through a forest mosaic landscape composed of patches of dwarf shrublands, open ponderosa pine, and closed canopy dry mixed conifer forests (**a**–**d**). Overall, the fire burned at low severity, primarily burning through litter and understory fuels (**c**, **d**). Photo credit: United States Forest Service

landscape-scale fire spread (Agee 1993; Heyerdahl et al. 2019; Johnson and Swanson 2005). Historically, ignitions were likely a mix of indigenous burning and lightning strikes. The cessation of burning along with a century of active fire suppression increased density and fuel loads in forests to outside the historic range of variability, increasing risk of high severity fire.

In an effort to restore ecosystem function and promote resistance and resilience, the majority of the study area was burned in a large prescribed fire in late September 2017, at the cool end of its prescription. The area was underburned by aerial ignition covering 1540 hectares. Fire was carried primarily by pine needles and grassy fuels and created low-severity mosaic effects (Fig. 3). There was very little tree canopy scorch, and mortality was estimated to be < 2% in mature trees, < 40% in small-diameter western juniper, and approximately 80% in conifer saplings growing in thickets. No mortality was evident in ponderosa pine > 0.5 m (21 in) diameter at breast height. Fire behavior was less active than intended due to shade cast by the smoke column (USDA Forest Service 2018).

Sampling

We used a Before-After-Control-Impact study design to evaluate the effect of burning on invasive grasses and understory vegetation. Before the burn, we installed 26 transects (plots) on a grid with a randomized starting location within the planned prescribed burn area in 2016 (Fig. 1). An additional 11 transects were installed as untreated controls just west of the treatment unit on similar soils, slopes, aspects, and vegetation communities (Fig. 1). The burn unit encompassed a mosaic of non-forest shrubland patches embedded in a forest matrix, including forested areas with dense tree canopy cover. Our study sites primarily fell within shrublands and areas with open tree canopy where invasive grasses were more prevalent (Fig. 1). Once in the field, transects were either established at the pre-determined grid-located starting points or relocated 46 m (150 ft) in a random direction if the transect was (1) within 15 m of a road, fence, water trough, salt lick, or other man-made object, or flowing water; (2) on a slope greater than 50%; or (3) comprised of ground cover > 10% bedrock or boulders. Transect starts were marked with rebar for relocation. Although much of the forest is grazed by cattle, we saw few signs of grazing within our study plots.

Vegetation was sampled prior to burning (year 2016), and 1, 2, and 3 years post burning (2018, 2019, and 2020) (Fig. 2) using a line point intercept method. All understory and overstory species were recorded every 1 m along each 40 m transect. Annual grasses were recorded more frequently, at every 0.5 m along the same transect to increase detection given some sparse and/or patchy populations. Less common, non-annual grass species may have lower representation in our study due to the lower frequency of transect readings. We calculated proportion understory and canopy cover as the number of positive hits divided by the total possible number of hits across all species. When we were unable to identify a species in the field, specimens were sampled and identified to the lowest taxonomic group possible using dichotomous keys. Non-native annual bromes (excluding cheatgrass) including field brome (*B. arvensis*), rattlesnake brome (*B. briziformis*), and corn brome (*B. squarrosus*), were lumped into a single "field brome" category for analysis given their inconsistent taxonomies, morphological and functional similarities, and that they are known to hybridize (Knowles 1944).

Within 1 month of the prescribed fire, a 10 m buffer was established along each transect (5 m on each side) and the area was assessed for visual burn evidence (e.g., litter and vegetation blackening or char, bole scorch). Transects were recorded as being "treated, unburned," "< 50% burned," or "≥ 50% burned" according to the proportion of the transect and buffer area that appeared to have burned.

Analysis

Invasion influence on burn extent

To examine how invasive annual grass cover in 2016 prior to burning influenced prescribed burn patterns, we modeled the probability of a transect (and 10 m buffer) within the burn perimeter being completely unburned, < 50% burned, or ≥ 50% burned with "burn evidence" as a three-level ordered response variable and total invasive annual grass (IAG) cover as a predictor variable. Ventenata, cheatgrass, and field brome covers were summed to calculate total IAG cover. To account for varying levels of overstory cover among transects (and the effect this might have on fire behavior), we included tree canopy cover as a fixed effect in the model. This analysis excluded the control transects for a final sample size of 26 plots.

Invasive annual grass response to burning and year

We investigated how the three IAG species responded to burning using logistic regressions with separate models for each species. Logistic regressions were used to account for our data being collected as counted proportions of positive hits along a transect, resulting in a non-normal distribution of errors. Transects were combined into two groups for analysis: "unburned" (including both control and treated, unburned transects) and "burned" (including transects with any burn evidence, < 50% or ≥ 50%). Fixed effects included burning (2-level factor: unburned vs. burned), time since fire (3-level ordered factor: 1, 2, 3 years), and their interaction. We also included a fixed covariate for each IAG species' 2016 cover (in their respective models) to account for pre-treatment invasion level, as we were particularly interested in the effect of propagule pressure on post-treatment invasion. Transect was included as a random effect to account for yearly repeated measures. We considered including other site level covariates in the models (e.g., tree canopy cover), but we did not have sufficient power. We investigated IAG species cover relationship to tree canopy cover separately in Appendix S1.

Plant community response to burning and year

We explored understory functional group composition pre-treatment (2016) and 3 years post-treatment (2020) with plots grouped by their burn evidence using non-metric multidimensional scaling (NMDS) ordinations with transects displayed as points oriented in species space. NMDS ordination was performed using the Bray-Curtis distance measure with two dimensions and random starting locations. Prior to NMDS, we removed rare species that occurred in fewer than 5% of transects, leaving 49 from the original 111 species. Species cover was square-root-transformed prior to analyses to reduce noise. To evaluate how species composition related to functional composition, we calculated functional group cover for each transect. Each understory species was assigned a functional group which included life form (graminoid/grass, forb, shrub, or subshrub), duration (annual or perennial), and Oregon native status (native or non-native) according to USDA plants database 2021 (Appendix S2). Transect functional group cover was calculated as the sum of species covers within each functional group at each transect, thus functional group cover could exceed 100%. We then fit the functional group vectors onto the ordination to display their linear relationship with the ordination axes.

We measured both how species composition differed between burn categories within a single year and between 2016 and 2020 within each burn category using Multiple Response Permutation Procedure (MRPP). MRPP provides a test of the degree to which groups are separated and outputs a change-corrected estimate of within-group homogeneity, A (Mielke and Berry 2001). If all transects are identical within a group, then $A = 1$. MRPP was performed using the Bray-Curtis distance measure with 999 permutations.

To examine how transect-scale diversity varied with burning over time, we modeled species richness and Shannon diversity response to burn evidence (unburned—control and treated, unburned combined; < 50% burned; ≥ 50% burned), post-treatment year (2018, 2019, 2020), and their interaction using separate linear mixed effects models. Pre-treatment diversity metrics were included as covariates to account for baseline levels of diversity. Transect was included as a random effect to account for repeated measures.

All analyses were performed in R version 4.1.1. Multinomial modeling was performed using the package "nnet" (Venables and Ripley 2002). We used the package "lme4" for mixed-effects modeling (Bates et al. 2015) and "vegan" for functional composition analyses and computing Shannon diversity (Oksanen et al. 2019). Interactions were evaluated using Wald chi-square tests with the "car" package (Fox and Weisberg 2018) and comparisons were performed with "emmeans" (Lenth, 2023).

Results

Invasion influence on burn extent

Of the 26 transects located within the burn unit, 9 were ≥ 50% burned, 7 were < 50% burned, and 10 remained unburned. The probability of a transect being ≥ 50% burned increased with increasing IAG cover after accounting for tree overstory cover (Fig. 4). At 20% IAG cover, it was nearly twice as likely that a transect was ≥ 50% burned compared to unburned or < 50% burned. The probability of burning at ≥ 50% was nearly 100% when IAG cover approached 60% (Fig. 4). Similarities between the < 50% and unburned groups may be in part due to the strategic avoidance of ignitions in nonforest dwarf shrubland patches where ventenata invasion was highest, potentially resulting in areas with higher IAG cover remaining unburned.

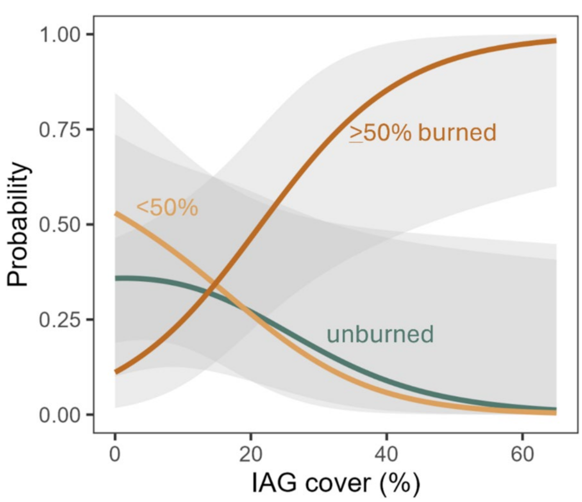

Fig. 4 Probability of a transect (and 10 m buffer) within the prescribed burn unit being unburned (green), < 50% burned (yellow), ≥ 50% burned (red) in relation to pre-fire invasive annual grass (IAG) cover. Gray shading represents 95% confidence intervals around the predicted probability. Tree overstory cover is held constant at 18% (mean overstory cover)

Prescribed burn effects

The prescribed burn primarily reduced understory cover and litter and had a slight effect on overstory tree cover (USDA Forest Service 2018; Figs. 3 and 5). Prior to treatment in 2016, overstory tree cover at our sample plots was highly variable, averaging 18.5% (SD = 19.1%). In 2018, following treatment, overstory cover was only slightly lower within the burn unit, and remained highly variable, averaging 15.7% (SD = 21.1%). We observed the largest difference in litter cover before and after treatment which declined about 1/3 from an average of 64.6% cover (SD = 21.7%) to 42.4% (SD = 20.3%) cover. Some ash and char were still visible in 2018, 1 year following the burn, although cover was generally low (mean cover = 7.1%, SD = 9.6%). We observed little change in moss and lichen cover before and after treatment (Fig. 5). As we were primarily interested in the understory response to burning, we did not measure sapling mortality post-treatment.

Invasive annual grass response to burning and time since fire

The three IAG species responded differently to burning over time (Fig. 6). Ventenata was the only species to have consistently lower average cover in burned than unburned transects. Averaging across the three post-treatment years, the probability of encountering ventenata on a transect hit was 72.4% lower in burned transects compared to unburned transects (odds ratio burned/unburned = 0.25, $p = 0.005$) after controlling for pre-treatment cover. Although even after burning, ventenata cover was higher on average than cheatgrass or field brome cover (Fig. 6). The effect of burning on ventenata cover did not vary with time since fire (Table 1; Fig. 6). Cheatgrass response to burning was highly variable between sites, but generally cheatgrass increased in burned plots with greater time since fire with the highest cheatgrass cover occurring in burned plots 3 years post-fire (Fig. 6). Burning had a weak and variable effect on field brome cover (Fig. 6). No IAG species demonstrated a strong relationship with tree canopy cover when tree cover was < 30%, and IAGs were generally absent from plots with over 30% overstory tree cover (Appendix S1).

Invasive annual grass response to sample year

Regardless of burning, the cover of all three IAGs increased over time. For all IAG species, time since fire (i.e., sample year) was the strongest predictor of occurrence (Table 1). When comparing 2016 to 2020 cover for both burned and unburned transects, ventenata cover was 2.0 times higher, cheatgrass was 1.5 times higher, and field brome was 1.9 times higher in 2020 on

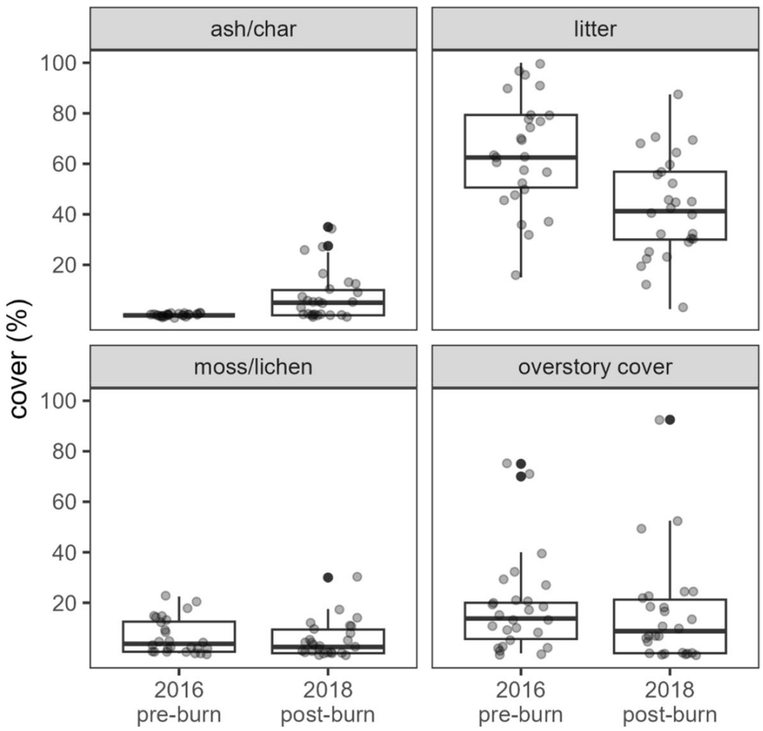

Fig. 5 Boxplots of ground cover (ash/char, moss/lichen, and litter) and overstory cover before (2016) and after (2018) the prescribed burn treatment for plots within the burn unit. Boxes display the interquartile range separated by a horizontal line representing the median. Vertical lines represent the minimum and maximum values (excluding outliers), and solid black points represent outliers. Raw data are displayed by transparent gray points. The prescribed burn took place in fall of 2017

average (Fig. 6). Species responded differently to specific years. Ventenata increased every sampling year except 2019, where the probability of occurrence decreased by 16% ($p=0.05$) in the unburned transects. In contrast, the probability of observing cheatgrass and field brome increased by 31% ($p=0.1$) and 165% ($p<0.0001$) during this same period, respectively. Ventenata increased the most between 2016 and 2018 (odds ratio = 3.3, $p<0.001$), but this trend was not reflected in field brome or cheatgrass which increased the most between 2018 and 2020 (Fig. 6).

Plant community response to burning and time since fire

Over the four sampling years, we identified 111 vascular plant species including 74 forb, 22 graminoid, 8 shrub, 4 subshrub, and 3 tree species (Appendix S2). Along with the three focal invasive annual grass species (ventenata, cheatgrass, and field brome), we also recorded scattered presence of the invasive annual grass, silky bentgrass (*Apera interrupta*), and non-native perennial grasses bulbous bluegrass (*Poa bulbosa*) and intermediate wheatgrass (*Thinopyrum intermedium*). Non-native forbs including yellow alyssum (*Alyssum alyssoides*), spring draba (*Draba verna*), jagged chickweed (*Holosteum umbellatum*), strict forget-me-not (*Myosotis stricta*), and yellow salsify (*Tragopogon dubius*) were present at low abundance throughout the study area.

We observed substantial overlap in species composition between burn categories both before (indicating similar composition before treatment) and after burning, indicated by strongly overlapping NMDS ellipses between groups (Fig. 7a; Table 2). Over the sampling period, transects shifted right along NMDS axis 1 and up along NMDS axis 2, indicating higher cover of invasive annual grasses and higher native perennials in 2020 than in 2016, regardless of burn evidence (Fig. 7b; Appendix S3). While species composition for all burn categories differed between pre-treatment and 3 years post-treatment (between 2016 and 2020) as indicated by MRPP results, these differences were strongest for the unburned transects (Table 2). We found no evidence to suggest that species richness or diversity differed markedly between years or burn categories (Table 3).

Discussion

Our case study indicated that invasive annual grasses vary in their response to a single low-severity fall prescribed fire in a dry forest-mosaic landscape in central

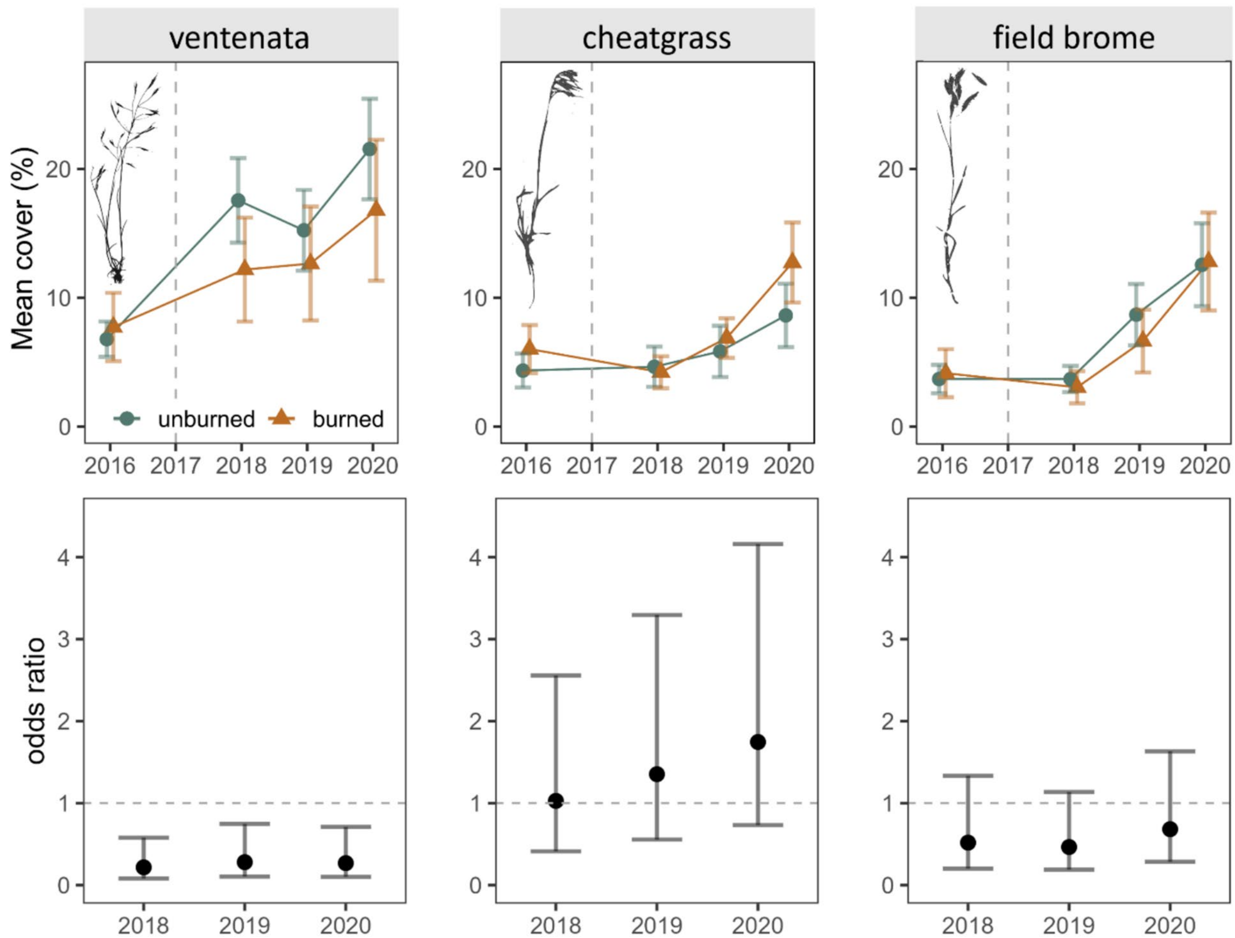

Fig. 6 Top row: Mean invasive cover and standard error for three invasive annual grass species (ventenata, cheatgrass, and field brome) by sample year and burn status: unburned (control and treated, unburned) and burned (< 50% and ≥ 50% burned). Prescribed burn took place in September 2017, indicated by vertical dashed line. Bottom row: Odds ratio (probability of occurrence burned/probability of occurrence unburned) with 95% confidence intervals by species for each post-treatment year given equal pre-treatment cover. Horizontal dashed line at 1 represents no difference in cover between burned and unburned transects. Points beneath 1 represent lower cover in burned plots than unburned plots and vice versa

Oregon. Increases in cheatgrass cover in burned transects 3 years after the prescribed burn indicate that burning may promote invasion at longer post-fire intervals. In contrast, low-severity prescribed fire slowed the rate of ventenata expansion in the short term compared to unburned areas. All three species recovered quickly after burning to pre-fire levels and increased substantially over the sampling period, suggesting that initial invasion level and annual growing conditions are better indicators of future invasion levels than low-intensity disturbance, at least in the short term (i.e., up to 3 years following disturbance).

We caution that the prescribed fire in this study was patchy and generally low severity (65% of the transects remaining unburned or < 50% burned), the forest canopy was already fairly open, and the fire did not substantially alter overstory cover. Shade-intolerant invasives may respond more strongly following higher severity fire with greater canopy loss (Kerns et al. 2020, 2006; Tortorelli et al. 2020). For example, fire severity was found to be a strong driver of cheatgrass, field brome, and medusahead cover in both open and closed canopy forests burned in large wildfires in the Blue Mountains ecoregion of Oregon, including the Corner Creek fire that burned adjacent to the prescribed burn unit in 2015 (Tortorelli et al. 2020).

IAG species responded differently to burning

Ventenata responded differently to burning than cheatgrass or field brome, reflecting previous work that found

Table 1 Analysis of deviance table from Wald chi-square tests for invasive annual grass logistic models

	Chisq	Df	*P* value
Ventenata			
Burn	7.78	1	0.005
Year	42.77	2	< 0.001
Ventenata 2016	42.27	1	< 0.001
Burn:year	2.59	2	0.274
Cheatgrass			
Burn	0.73	1	0.393
Year	87.35	2	< 0.001
Cheatgrass 2016	38.76	1	< 0.001
Burn:year	5.58	2	0.061
Field brome			
Burn	1.53	1	0.217
Year	180.47	2	< 0.001
Field brome 2016	27.88	1	< 0.001
Burn:year	4.13	2	0.127

ventenata to occupy different post-fire niches than other annual grass species (Tortorelli et al. 2020; Applestein and Germino 2022). Burning reduced the rate of ventenata expansion for 3 years following treatment, suggesting that low-intensity prescribed fire with little canopy loss may not immediately exacerbate ventenata invasion, a concern of treating invaded areas with prescribed fire. Previous studies reported that ventenata can be non-responsive to wildfire in heavily invaded non-forested areas such as dwarf-shrubland and bunchgrass prairies with similar abundances found in burned and unburned sites more than 4 years after burning (Tortorelli et al. 2020; Ridder et al. 2021). Additionally, Ridder et al. (2022) reported no effect of fall prescribed burning on ventenata invasion in the Zumwalt Prairie Preserve bunchgrass prairie in northeastern Oregon. It is important to note that the treatment in our study was a single burn with no follow-up. Repeated entry into treated areas may exacerbate invasions by moving propagules into disturbed areas and further opening tree canopy and increasing light in the understory.

In contrast to ventenata, burning appeared to exacerbate cheatgrass invasion by the third year after treatment, despite some uncertainty in the strength of these effects. Cheatgrass is often benefited by prescribed fire in dry pine forest ecosystems, particularly in sites with higher tree mortality (Merrill et al. 1980; Crawford et al. 2001; Kerns et al. 2006). Even in non-forest systems with little canopy cover, cheatgrass is readily exacerbated by disturbance-induced nutrient pulses (Leffler et al. 2016, Chambers et al. 2007), although it does not

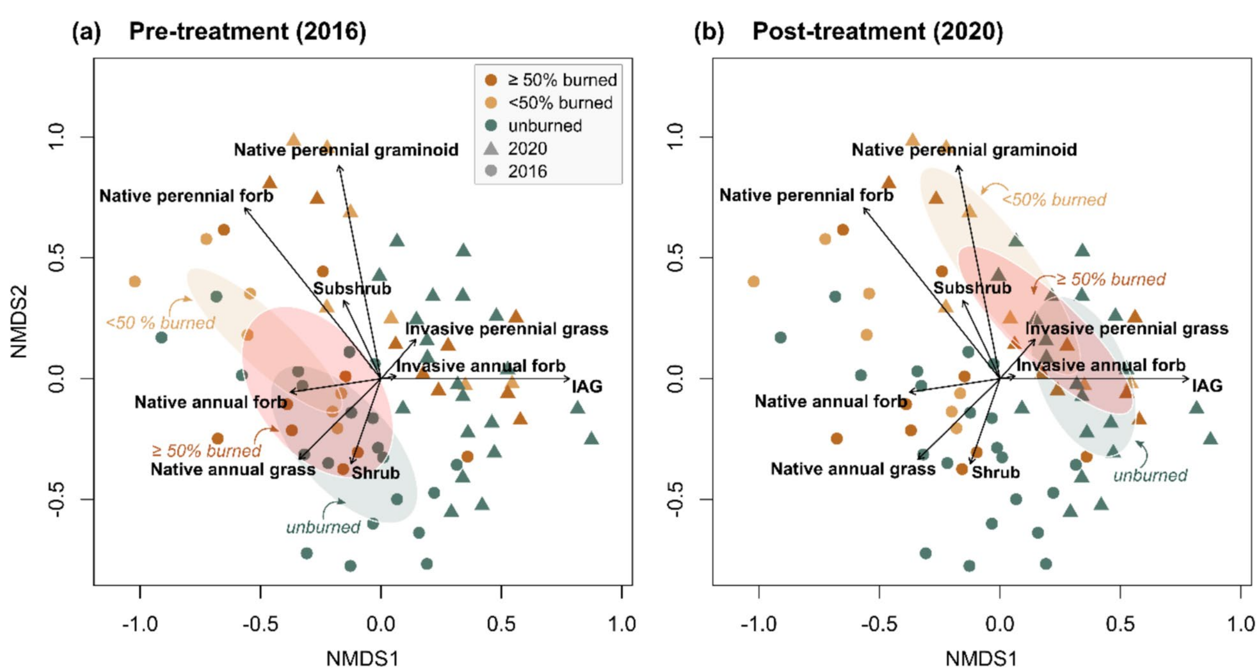

Fig. 7 Non-metric multidimensional scaling (NMDS) ordination of transects (points) in species space with dispersion ellipses representing the standard deviation of transect scores for each burn category: unburned (control and treated, unburned), < 50%, and ≥ 50%. (**a**) Pre-treatment in 2016 and (**b**) 3 years post-treatment in 2020. Points located closer together have more similar species composition and overlapping ellipses indicate little differentiation in species composition between groups. Arrow direction and length represent functional group linear relationships with ordination axes, scaled by r2. For example, points located farther to the right of NMDS1 have higher invasive annual grass (IAG) cover and points higher on NMDS2 have higher native perennial graminoid cover

Table 2 Multiple response permutation procedure (MRPP) analysis showing within-group homogeneity, *A statistic*, for understory species cover between and within burn categories pre- and post-treatment: unburned (control and treated, unburned), < 50% burned, and ≥ 50%

Comparison	A statistic	Delta (observed)	*P* value
2016: unburned [*n* = 21] vs. < 50% burned [*n* = 7] vs. ≥ 50% burned [*n* = 9]	0.030	0.678	0.010
2020: unburned [*n* = 21] vs. < 50% burned [*n* = 7] vs. ≥ 50% burned [*n* = 9]	0.036	0.651	0.008
Unburned: 2016 [*n* = 21] vs. 2020 [*n* = 21]	0.049	0.660	0.001
< 50% burned: 2016 [n = 7] vs. 2020 [*n* = 7]	0.046	0.668	0.06
≥ 50% burned: 2016 [*n* = 9] vs. 2020 [*n* = 9]	0.033	0.670	0.050

always require fire to invade and spread (Smith et al. 2023). Few studies have evaluated how field brome responds to fire, and those that have found fire to generally decrease abundance for up to 2 years, especially when burning is followed by periods of below-average precipitation (Whisenant 1990; Vermeire and Rinella 2009), as was the case in our study.

Different responses to burning among invasive annual grass species may be related to how susceptible seeds are to damage from fire and allocation of post-fire resources including nutrients and light, contributing to slower or more rapid post-fire recovery. Some studies have shown that cheatgrass increases the year following fire in open pine forests (Merrill et al. 1980). However, it is more common for cheatgrass to decrease in the first year following fire, owing to seeds being killed by fire when the litter layer is consumed (Young et al. 1987). Burning generally benefits cheatgrass 2 to 3 years following fire (Shinneman and Baker 2009) after seeds that survived the fire and those dispersed into burned areas have had time to respond to the release of post-fire nutrients, sunlight, and water from reduction in plant density (Brooks and Pyke 2002; Chambers et al. 2007).

We are not aware of any studies that have tested the effect of burning on ventenata seed banks explicitly; however, the negative effect of burning on ventenata occurrence observed here leads us to believe that the ventenata seed bank may be reduced by fire. Additionally, the persistent negative effect of burning on ventenata cover suggests that ventenata may not respond to the release of post-fire resources as strongly as cheatgrass. This reflects results from a field experiment where ventenata showed no response to the removal of above-ground biomass 1 year following the clipping treatment (Tortorelli et al. 2022). Clipping is not a direct surrogate for fire, which also boosts nutrient availability through ash production and pH shifts. Additionally, ventenata accumulated lower levels of foliar nitrogen than cheatgrass at both low and high soil-nitrogen levels in an experimental container study (James 2008), indicating that ventenata may benefit less from a post-fire influx of nitrogen through decomposition of fire-killed plants (Herman and Rundel 1989; Kauffman et al. 1994). Furthermore, ventenata exhibits higher shade tolerance than cheatgrass (Tortorelli et al. 2020) and, as such, may be less responsive to canopy loss following fire.

Table 3 Analysis of deviance table from Wald chi-square tests

	ChiSq	df	*P* value
Species richness			
Year	0.56	3	0.91
Burn category	2.08	2	0.35
Richness pre-fire (2016)	40.70	1	< 0.001
Year:burn category	8.37	6	0.21
Shannon diversity			
Year	2.34	3	0.51
Burn category	1.19	2	0.55
Shannon diversity pre-fire (2016)	46.21	1	< 0.001
Year:burn category	7.88	6	0.25

Invasion increased over time, regardless of burning

Overall, year and initial level of invasion had a much stronger influence on invasion trends than burning. Ventenata, cheatgrass, and field brome exceeded 2016 cover levels 1 to 2 years after the time of treatment, regardless of whether the transect burned. Additionally, cover of all species doubled (or nearly doubled) over the 5-year observation period. Steady increases in cover were likely driven by propagule pressure and existing seed banks, indicated by pre-treatment invasive annual grass cover coupled with suitable climatic conditions. All three species are prolific seed producers and can spread rapidly under suitable conditions. Thus, even where burning depleted the seed bank, surviving individuals could readily repopulate burned areas, quickly increasing invasion to above pre-fire levels. These findings reflect those of Keeley and McGinnis (2007), who found pre-fire cheatgrass cover to be a stronger predictor of post-fire invasion levels than fire intensity in a western dry pine forest. Our work also reinforces recent findings that annual grasses may not be as fire dependent as once thought for establishment and spread (Smith et al. 2023).

Interannual fluctuations in population abundance are likely dependent on climate conditions. Fall germinating winter annual grasses have been found to be strongly influenced by precipitation period and amounts. For example, cheatgrass cover is generally highest in years with above-average precipitation, especially when this precipitation lands in fall and/or spring (Chambers et al. 2007; Shinneman and Baker 2009; Boyte et al. 2016). Although early season precipitation followed by drought can cause cheatgrass mortality (Mack and Pyke 1984). Ventenata has been associated with higher fall and winter temperature and moderate winter precipitation (Nietupski et al. 2024, Nicolli et al. 2020). A study following a large sage-steppe fire in southeastern Oregon found that ventenata occupied higher elevations and benefited more from high winter/spring precipitation than cheatgrass or medusahead (Applestein and Germino 2022). Interestingly, in our study, ventenata cover increased between 2016 and 2018, but cheatgrass and field brome cover remained relatively constant over this same time period. This suggests that these species may respond differently to yearly climatic fluctuations. Annual bromes may have been more heavily impacted by below-average precipitation in February preceding the 2018 sampling. However, this same period had a similarly low precipitation in 2020, when all three IAG species cover increased substantially. It is also possible that ventenata responded to above-average precipitation the winter and spring preceding the 2016 sample more strongly than the annual bromes, and the effects of increased ventenata seed production in 2017 were still apparent in 2018. Understanding how different invasive annual grass species respond demographically to climatic fluctuations is important for predicting how and where invasions may occur in the future. Further long-term studies are needed to tease apart responses of these species to seasonal precipitation and temperature fluctuations.

Community response to invasion and burning over time

Overall, understory plant communities in the dry forest-mosaic were relatively unimpacted by the prescribed burn. Plant composition shifted towards invasive annual grass dominance over the study period regardless of burning, particularly in open areas, suggesting that these communities generally exhibit low invasion resistance. However, this shift in composition did not appear to result in lower species richness or diversity. Prescribed burns in dry forests can have mixed effects on understory plant diversity. Many studies found burning to have limited influence on diversity, with effects diminishing with time (Kerns and Day 2018; Scudieri et al. 2010; Zald et al. 2020). Although in Southwestern dry pine forests, burning combined with thinning increased both native and non-native cover and richness, with effects persisting over ten years following treatments during a 20-year megadrought (Springer et al. 2024).

The short-term resilient nature of understory community richness to invasion and low severity fire that we observed may be attributed to the abundance of deep-rooted perennial native grasses and forbs. These species may escape competitive effects of invasive species by resprouting from belowground energy stores (Pyke et al. 2010). Understory plant communities may be more heavily impacted over time if regeneration of perennial grasses and forbs from seeds is reduced by competition with invasive grasses. The dominant sagebrush species, *A. rigida* (non-sprouting obligate seeder), was largely absent from burned transects, reducing overall shrub cover in open patches within the forest mosaic. Losses in shrub cover and community structure may reduce soil nutrient input and wildlife habitat, especially when species lack the adaptations to recover quickly after fire (Nagy et al. 2021), as is the case for the dominant shrub species in our study.

Invasive annual grasses influence fire spread

Invasive annual grasses are a major concern across the American West where they increase fine fuel loads, ignitibility, and fire frequency in historically fuel-limited and fire-resistant ecosystems (D'Antonio and Vitousek 1992; Chambers et al. 2007; Brooks et al. 2004; Harrison et al. 2024). Frequent fire-adapted forests are thought to be relatively resistant to invasion-fire feedbacks and associated impacts. However, recent observations of ventenata expanding into forest-mosaics and forest ecotones, along with wildfire simulation modeling, have demonstrated that annual grasses can alter landscape-scale wildfire behavior in forest-mosaic ecosystems by facilitating spread across ecotones and into closed canopy forests (Tortorelli et al. 2023). Our findings suggest that invasion at > 20% cover facilitated prescribed fire spread, especially in non-forest patches and across forest ecotones that otherwise would not be expected to burn given extremely low fuel loads and continuity. Increased fire spread in dry-forest understories may help meet management goals of reducing woody fuel loads, especially if understory fuels are otherwise sparse. However, burning in invaded mosaic landscapes may hinder restoration goals by risking the loss of keystone sagebrush species from adjacent non-forest patches and exacerbating cheatgrass cover. Similar trade-offs have been documented in pinyon-juniper ecosystems where woody fuel treatments designed to reduce ladder fuels increased cheatgrass cover and fine fuel continuity (Williams et al. 2023).

Management implications

Managers are increasingly faced with difficult decisions in balancing the goals of preventing invasive species expansion and associated impacts against restoring forest structure and mitigating wildfire severity (Keeley 2006; Keeley and McGinnis 2007; Kerns et al. 2020). We demonstrate that low-severity, fall prescribed fire in a conifer forest-mosaic landscape of central Oregon may slow the rate of ventenata expansion in invaded areas (at least for 3 years following fire) but burning is unlikely to reduce invasion compared to pre-fire levels. Additionally, fall burning may benefit cheatgrass, although our evidence for this relationship was relatively weak. It is important to consider that, overall, the prescribed burn considered here was relatively low intensity with patchy areas of canopy loss. These findings may not generalize to burns with higher severity effects. Prescribed fire intensity has been associated with invasion in other dry forest systems (Jang et al. 2021; Kerns et al. 2006). Additionally, the burn was conducted in the fall, after all three species have typically dropped their seeds, and burning in other seasons may have different effects on invasive annual grass species (Kerns and Day 2017; Knapp et al. 2009). For example, fall burning was found to benefit non-native species, including cheatgrass, more strongly than spring burning in a dry western forest (Kerns and Day 2018; Zald et al. 2020; Knapp et al. 2009). This burn was conducted in September, likely before germination of winter IAGs. Even within fall, later burns may have different effects. While we did not observe notable signs of grazing within our study plots, it should be noted that the landscape in this study is frequently grazed by cattle. Livestock grazing can interact with prescribed burning through multiple pathways, with the potential to reduce understory resilience and exacerbate invasions by spreading seeds, reducing cover of competitive perennial bunchgrasses, and disturbing soils (Kerns and Day 2024). Although, much like with burning, understory response to grazing can vary dramatically depending on timing and intensity (Bates and Davies 2014; Davies et al. 2021; Williamson et al. 2020).

Regardless of burning, annual grasses increased over time, demonstrating the susceptibility of this dry forest-mosaic landscape to invasion. Given the high degree of invasion across Western landscapes, forest restoration plans might consider potential management strategies to reduce the initial abundance of invasives, especially where burn treatments and substantial tree canopy removal are planned. A holistic forest restoration approach which includes weed management coupled with fuel treatments may lead to greater overall ecosystem resistance and resilience (Kerns et al. 2020; Wollstein et al. 2022). The selective use of pre-emergent herbicides before burning may reduce seed-obligate invasive annual grasses and promote desirable perennial grasses and forbs which readily resprout after low-intensity fire (Pyke et al. 2014). Importantly, reducing annual grass cover in forest ecotones before burning may reduce fire spread from forests into adjacent, vulnerable sagebrush ecosystems and reduce the loss of shrub structure. Where pre-burn herbicide application is not possible, practitioners could consider limiting ignitions in and near heavily invaded areas to avoid undesirable fire effects, as was operationalized in this burn. Additional studies are needed to gain a better understanding of how integrated treatments influence fuels and restoration goals (Schroeder et al. 2022), particularly in recently invaded western dry forest-mosaics.

Abbreviation

IAG Invasive annual grass

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-026-00468-6.

Supplementary Material 1: Appendix S1. Relationship between invasive annual grass (IAG) cover and tree canopy cover before the prescribed fire treatment (2016) and three years following the burn (2018, 2019, and 2020) in burned and unburned plots.

Supplementary Material 2: Appendix S2. Species list and codes from USDA plants database (2021). Native status is relative to Oregon, U.S.A.

Supplementary Material 3: Appendix S3. Functional group vector correlation to NMS ordination axes.

Acknowledgements

We thank Moriah Young, Leila Giovannoni, and Simone Gibson for field assistance and Dustin Gannon and Ariel Muldoon for statistical guidance. Jill Welborn and Jeff Priest provided orientation and background that helped initiate this project. We acknowledge that our study area is located within the traditional homelands of the Northern Paiute, Wasco, and Warm Springs people. Today, living descendants of these people are a part of the Confederated Tribes of Warm Springs.

Authors' contributions

AD, BK, CT, and MK contributed to the formulation of overarching research goals and aims. BK and AD developed the methodology for sampling, and AD initiated the study and monitored the prescribed burn. CT collected field data, performed the analyses, and drafted the original manuscript. All authors contributed to the review and editing of the final manuscript.

Funding

Funding for this project was provided through the Joint Science Fire Project (USDA USFS Project #16-1-01-21), National Science Foundation Graduate Research Fellowship to CT, the Oregon Native Plant Society, and the Association for Fire Ecology.

Data availability

The datasets and code used in the study are available on GitHub at https://github.com/cmtortorelli/Prescribed-burn-IAG.

Declarations

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Received: 19 August 2025 Accepted: 2 March 2026
Published online: 07 April 2026

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