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Cheatgrass alters flammability of native perennial grasses in laboratory combustion experiments

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Abstract

Background The invasive annual grass cheatgrass (*Bromus tectorum*) increases fuel continuity, alters patterns of fire spread, and changes plant communities in sagebrush shrublands of the Great Basin (USA) and adjacent sagebrush steppe, but no studies have contrasted its flammability to native perennial grasses. Understanding cheatgrass flammability is crucial for predicting fire behavior, informing management decisions, and assessing fire risk in invaded areas. This study aimed to determine the flammability of cheatgrass compared to two native perennial grasses (Columbia needlegrass [*Achnatherum nelsonii*] and bluebunch wheatgrass [*Pseudoroegneria spicata*]) across a range of fuel moistures.

Results All three grass species had decreased flammability with increasing fuel moisture. Columbia needlegrass averaged 11% lower mass consumption than cheatgrass, and bluebunch wheatgrass had longer flaming duration and higher maximum temperatures than cheatgrass and Columbia needlegrass. The addition of cheatgrass to each perennial grass increased combined mass consumption, flaming duration, and flame heights. For these three attributes, the impact differed by the amount of cheatgrass in the mixture. Maximum and mean temperatures during perennial grass combustion were similar with and without cheatgrass addition. Some attributes of Columbia needlegrass flammability when burned with cheatgrass were higher than expected based on the flammability of each species, suggesting that Columbia needlegrass may be susceptible to pre-heating from combustion of cheatgrass. Conversely, the flammability of bluebunch wheatgrass and cheatgrass together had both positive and negative interactive effects, suggesting the impact on joint flammability from cheatgrass differs by perennial grass species.

Conclusions This study provides experimental evidence supporting previous qualitative observations of cheatgrass flammability. Cheatgrass increased perennial grass sustainability and consumption, suggesting that cheatgrass poses a significant fire threat to native grasses regardless of moisture content. The study provides species-specific insights into flammability, which could be used to inform efforts to prevent or mitigate cheatgrass-induced wildfires.

Keywords *Achnatherum nelsonii*, Bluebunch wheatgrass, *Bromus tectorum*, Cheatgrass, Columbia needlegrass, Fire behavior, Fuel moisture, Invasive species, *Pseudoroegneria spicata*, Rangeland, Sagebrush steppe

Resumen

Antededentes El pasto anual invasor conocido como bromo velloso o cheatgrass (Bromus tectorum), incrementa la continuidad de los combustibles vegetales, altera el patrón de propagación del fuego, y cambia las comunidades

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arbustivas de artemisia de la Gran Cuenca (Great Basin de los EEUU) y otros arbustales de estepas adyacentes. Sin embargo, ningún estudio ha contrastado su inflamabilidad en relación con otros pastos perennes nativos. El entender la inflamabilidad del bromo velloso es crucial para predecir el comportamiento del fuego informar sobre decisiones de manejo, y determinar el riesgo de incendio en áreas invadidas. Este estudio se basó en determinar la inflamabilidad del bromo velloso comparada con la de dos gramíneas nativas, el pasto aguja de la Columbia (Achnatherum nelsonii) y el agroapiro azul (Pseudoroegneria spicata) a través de un rango de distintos contenidos de humedad de esas especies.

Resultados Las tres especies de pastos decrecieron su inflamabilidad a medida que se incrementaba su contenido de humedad. El pasto aguja de la Columbia promedió un 11% menos de consumo de su biomasa que el bromo velloso, mientras que el agropiro azul tuvo una mayor duración de llama que el pasto aguja de la Columbia o el bromo velloso. La adición del bromo velloso a cada pasto perenne nativo incrementó el consumo de biomasa, y la duración y longitud de su llama. Para esos tres atributos, el impacto difirió en relación a la cantidad de bromo velloso en la mezcla. Las temperaturas máximas y medias durante la combustión de los pastos perennes fueron similares con o sin la adición del bromo velloso. Algunos atributos de la inflamabilidad del pasto aguja de Columbia, cuando se quemaba junto con el bromo velloso, fueron mayores a los esperados basados en la inflamabilidad de cada especie, lo que sugiere que el pasto aguja de Columbia puede ser susceptible al precalentamiento debido a la combustión del bromo velloso. Contrariamente, la inflamabilidad del agropiro azul junto con el bromo velloso tiene efectos interactivos tanto negativos como positivos, sugiriendo que el impacto de la inflamabilidad conjunta del bromo velloso difiere con la especie de pasto nativo de que se trate.

Conclusiones Este estudio provee de evidencia experimental que avala observaciones previas cualitativas sobre la inflamabilidad del bromo velloso. Esta especie incrementa la sostenibilidad y el consumo por el fuego, sugiriendo que el bromo velloso presenta una amenaza significativa para los pastos nativos independientemente de su contenido de humedad. Asimismo, este estudio provee de información especie-específica sobre inflamabilidad, lo que puede ser usado para informar sobre esfuerzos que deben hacerse para prevenir o mitigar los incendios inducidos por el bromo velloso.

Background

Biological invasions alter ecosystems worldwide by outcompeting native flora and fauna and leading to altered ecosystem processes (Mack and D'Antonio 1998; Ehrenfeld 2010). One of the most consequential impacts of invasive plants is their effect on fuel characteristics (including fuel moisture content, fuel volume, load, and packing ratios), which in turn affect fire behavior and often alter the frequency, intensity, extent, type, and seasonality of fires compared to non-invaded fuels (Brooks et al. 2004). Invasive plants often alter the natural fire regime to which native species have adapted (Stevens and Beckage 2009; Barnes et al. 2022). For example, the invasive succulent *Carpobrotus edulis* increases the moisture content of live fuels in postfire chaparral in maritime regions of California, causing less frequent and smaller fires (Odion and Davis 2000). In contrast, the invasive bunchgrass *Andropogon guyanus* in Australian savannas increases fuel loads, resulting in fires of greater intensity than in uninvaded areas (Rossiter et al. 2003). Fire regime changes in invaded areas often create ecological scenarios that favor the invaders, thus supporting continued invasion with numerous downstream impacts after fire events (D'Antonio & Vitousek 1992; Brooks et al. 2004).

A plant's flammability is influenced by a combination of chemical and physical traits, leading to variations across growth forms, species, and plant or fuel bed component(s) (Pausas et al. 2017). The flammability of a plant, plant parts, or many plants can be assessed using multiple techniques, including in field or laboratory-based combustion experiments. Laboratory experiments help control some of the variability found in natural fuel beds, such as microsite differences in moisture, and allow researchers to examine specific flammability traits under standardized conditions. These experiments have deepened our understanding of the heterogeneous nature of fuels by revealing how species characteristics and functional traits, like biomass, moisture content, and leaf surface-area-to-volume ratio, affect flammability (Grootemaat et al. 2015; Simpson et al. 2016; Fuentes-Ramirez et al. 2016). For instance, Cornwell et al. (2015) demonstrated the influence of species traits (primarily leaf size and resulting litter density) on surface fire behavior by comparing the flammability of litter fuel beds from 39 gymnosperm species. Laboratory combustion experiments also help identify drivers of geographical patterns in fire activity by analyzing fuels collected across a range of environmental conditions (Pausas et al. 2017). Prior et al. (2017) examined how precipitation, temperature,

and soil chemistry correlate with flammability patterns of grass and litter fuels across Australia. Additionally, such experiments can reveal how invasive species alter native fuel beds and affect fire activity. For example, the invasive forb *Lespedeza cuneata* decreases the flammability of native tallgrass prairies by increasing fuel bed density and moisture retention (Barnes et al. 2022). Isolating individual species or plant parts in controlled laboratory experiments can allow for a more specific classification of flammability which can be challenging to assess in heterogenous natural fuel beds. Blackhall and Raffaele (2019) assessed the ignitability of 31 native and invasive plants found in the wildland-urban interfaces of Patagonia to use in urban planning efforts to reduce fire risk. In summary, laboratory combustion experiments are valuable tools for advancing our understanding of flammability and its implications for fire management.

Flammability encompasses four phenomena: (1) *ignitability*-the likelihood or probability of ignition after a material is exposed to a known ignition source, (2) *sustainability*-how well the fuel continues to burn, (3) *combustibility*-how rapidly or intensely a material burns, and (4) *consumption*-the quantity of material that is consumed (Anderson 1970). Moisture content (and a plant's ability to retain moisture) is a major determinant of all four aspects of flammability, differs by plant species, changes throughout the season, and is sensitive to fine-scale changes, such as shaded microclimates or daily weather cycles (Rothermel 1972). Further, the flammability of two species burned together can be influenced not only by the flammability traits of the individual species but also by the interaction between the species (Van Altena et al. 2012; de Magalhães and Schwilk 2012; Blauw et al. 2015). Understanding species' flammability alone and in combination can contribute to knowledge of potential fire behavior with fuel beds containing target species.

Across western North America, annual grass invasions are credited with altering fire regimes, causing increased fire occurrence and frequency and overall creating a more flammable landscape (Balch et al. 2013; Fusco et al. 2019). Invasive annual grasses such as cheatgrass (*Bromus tectorum* L.), have a high fuel surface-to-volume ratio that readily ignites and rapidly carries wildfire even under wet early season conditions, and overall increases fine fuel continuity, which enables fire spread (Whisenant 1990; Balch et al. 2013; Fusco et al. 2019; Smith et al. 2023b). Annual grasses catalyze a shift in fire regime towards an increased invasive grass-wildfire feedback cycle, driven by increased fine fuel continuity, flammability of grasses, and faster postfire recovery of non-native species (D'Antonio and Vitousek 1992; Knapp 1996; Brooks et al. 2004; Balch et al. 2013). Areas dominated by annual grasses which then burn are more likely to remain in an annual-dominated state (Balch et al. 2013; Smith et al. 2023a). In addition, fires fueled by cheatgrass have greater emissions (CO_2 and particulate matter) than do fires without cheatgrass (Rennie et al. 2020). Invasive grass-fueled wildfires often occur earlier in the season than was common historically because cheatgrass cures, reducing stem and leaf moisture, before native plants senesce (Abatzoglou and Kolden 2011; Balch et al. 2013). More frequent fires can eliminate some sagebrush species, which are typically killed by fire and require long fire return intervals to reach maturity and produce seed (Whisenant 1990).

Invasive annual grass on the landscape can increase wildfire risk (Balch et al. 2013; Fusco et al. 2019; Pastick et al. 2021; Smith et al. 2023b). However, this increased risk is widely attributed to increased fuel load and continuity, and little is known about the species-level flammability of cheatgrass. No studies have quantified cheatgrass flammability, nor compared it to other native species present in the invaded ecosystem. To address this gap, we aimed to evaluate the flammability of cheatgrass and two native perennial bunchgrasses: Columbia needlegrass (*Achnatherum nelsonii* (Scribn.) Barkworth) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve). To assess flammability, we posed three research questions:

1. How does the flammability of cheatgrass compare to that of Columbia needlegrass and bluebunch wheatgrass across a range of fuel moistures?
2. What effect does the addition of cheatgrass have on the overall flammability of Columbia needlegrass and bluebunch wheatgrass?
3. When cheatgrass and Columbia needlegrass or bluebunch wheatgrass are burned together, does the combined flammability result from a simple combination of the individual species' attributes, or are there additional interactions between the two species that alter the overall flammability?

From these questions, we developed three research predictions:

1. Cheatgrass has higher flammability (ignitability, combustibility, consumption) than both Columbia needlegrass and bluebunch wheatgrass due to its high surface area to volume ratio and fine stems.
2. Columbia needlegrass and bluebunch wheatgrass have higher overall flammability (combustibility, sustainability) when burned with cheatgrass compared to when these perennial grasses are burned alone due to the differences in cheatgrass flammability.

3. When cheatgrass and Columbia needlegrass or bluebunch wheatgrass are burned together, the combined flammability is not a simple, additive function of the individual species' attributes; rather, is greater due to cheatgrass preheating perennial grasses, resulting in an increased overall flammability.

Methods

Collection and processing of plant materials

Cheatgrass, bluebunch wheatgrass, and Columbia needlegrass were selected for combustion experiments due to their dominance in sagebrush steppe ecosystems. Plant materials were collected at Rinker Rock Creek Ranch (Blaine County, Idaho) during the last week of June 2021. Grasses were clipped within 1 cm of the soil surface to obtain only aboveground plant material. All materials were oven-dried at 38 °C for 72 h and stored at room temperature until the initiation of the combustion experiments in July and August of 2021.

Prior to combustion experiments, samples were rehydrated, following methods from Blauw et al. (2015). Oven-dried samples were weighed to a standard mass (20 g for individual species trials and either 2.5, 5, 10, or 15 g for combined species trials), and water was added by weight to achieve the desired moisture content (MC) relative to dry mass. Samples were sealed in plastic bags for 48 h before sample combustion. This rehydration method allowed us to create different moisture contents, but these values should be considered relative to each other, and not representative of live fuel moisture. Cheatgrass was rehydrated to 5, 10, 15, 25, 35, 45, and 55% MC relative to dry mass. Perennial grasses were rehydrated to 15, 25, 35, 45, and 55% MC relative to dry mass. Prior to combustion, plants were weighed to obtain pre-burn wet mass and confirm MC. A minimum of five replicates of each MC for each species were burned.

Each perennial grass species was also burned in combination with cheatgrass. Perennial grass mass was kept consistent (20 g). Two target perennial grass MC were selected for combination experiments: a high (55%) and moderate (35%) MC. Four amounts of both cheatgrass mass (2.5, 5, 10, and 15 g) and MC (5, 15, 25, and 35%) were selected to reflect varying levels of cheatgrass invasion, from relatively low to high under different moisture conditions. Bluebunch wheatgrass combination trials were only burned with 2.5, 5, and 10 g of cheatgrass, at all four moisture levels. Four replicates of each annual and perennial grass combination at each MC were burned.

Combustion experiments

Combustion experiments were conducted inside a chamber at the University of Idaho's iFire laboratory (Moscow, Idaho). The chamber was constructed using a 10 cm diameter, 60 cm tall steel pipe, and elevated 2.5 cm above the ground to facilitate sample ignition (Fig. 1). For ventilation, approximately 15 holes, each with a diameter of 0.5 cm, were drilled into the walls of the chamber. Three Type K thermocouples (OMEGA Engineering) were inserted into the chamber at a height of 19, 33, and 48 cm from the base (Fig. 1). For analysis, we only used temperature data from the middle (33 cm height) thermocouple, to allow us to address our questions of how flammability differs by species rather than differences in temperature by height.

For each combustion trial, samples were weighed to the nearest 0.01 g pre-burn to assess moisture achieved from rehydration. For trials with two species, perennial and annual grasses were weighed separately since they had been independently rehydrated to achieve different MC. Grasses were burned upright inside the combustion chamber to best mimic natural fuel structure. Perennial and annual grass species mixtures were mixed homogeneously and loaded 5 cm diameter PVC pipes, cut longitudinally (Fig. 2). Both halves of PVC were closed around the sample and released into the chamber, positioned vertically (Fig. 2).

One mL of isopropyl alcohol was placed on a watch glass centered under the combustion chamber (Fig. 2). The alcohol was ignited using a remote charge through

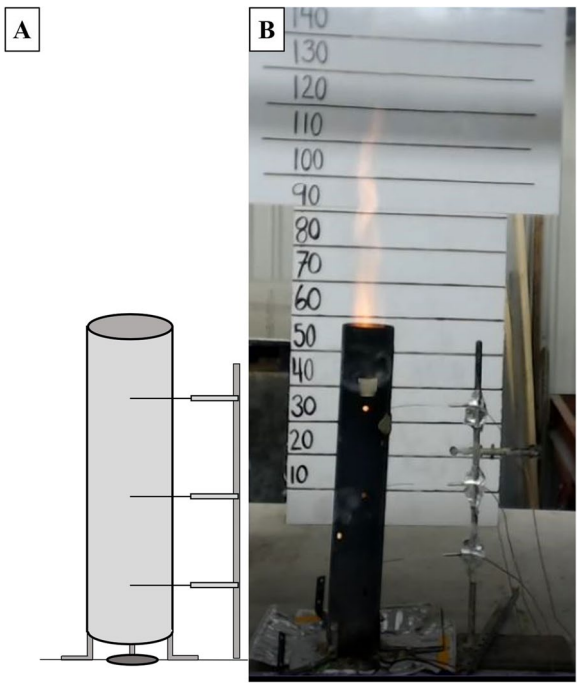


Fig. 1 Diagram (**A**) and photo (**B**) of the combustion chamber with three thermocouples (TC). The main chamber is a 10 cm diameter pipe raised 2.5 cm off the ground. Thermocouples extend into the center of the chamber at 19, 33, and 48 cm from the base

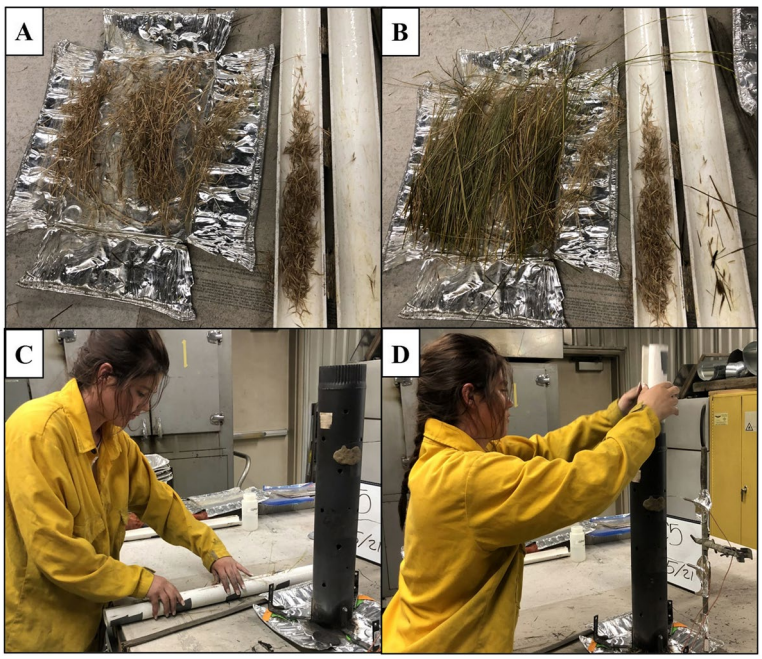


Fig. 2 Loading plant material into the combustion chamber. Panels **A** and **B** show combining annual (**A**) and perennial (**B**) grasses. Panels **C** and **D** show vertical sample loading into the combustion chamber

a wire. Each burn was recorded on video. A height board with 10 cm increments was placed behind the combustion chamber, and maximum flame height for each trial was recorded by viewing the videos (Fig. 1). Most flame heights exceeded the height of the chamber. However, for flames that were shorter than the chamber, their height was estimated within a range based on the visibility through chamber vent holes in the recorded video. Temperature was recorded for each thermocouple throughout the experiment at 0.5-s intervals. All temperature data were trimmed at a 100 °C temperature threshold, and temperatures measured after the maximum temperature was recorded were removed to exclude the cooling-off period (McGranahan 2020). Post-burn plant material was weighed to the nearest 0.01 g. For combined perennial and annual grass trials, post-burn weight was of both species combined.

Data analysis for individual and combined species trials

Data were summarized to assess four major phenomena of flammability. *Ignitability* was determined by assessing the probability of ignition, i.e., whether the sample ignited or not under standardized experimental conditions. This assessment was done visually during the trials and confirmed using video footage. Information from all trials was used to inform ignitability. For other attributes of flammability, temperature data from trials which ignited were used. *Sustainability* was assessed as flaming duration, which was the time in seconds that each thermocouple spent above 100 °C until the maximum temperature was reached. *Combustibility* was classified with three traits: maximum and mean temperature, and maximum flame height. Maximum temperature was calculated for each thermocouple. The mean temperature was the mean temperature between 100 °C and the maximum temperature, which excludes cooling off temperatures of the thermocouples. Maximum flame height was estimated by reviewing the trial videos and approximating the highest point from the high board to the nearest 10 cm. *Consumption* was calculated as percent mass loss (ML), using Eq. 1

$$\mathrm{ML}_{\%} = \frac{(M_i - M_e)}{M_i} \times 100 \tag{1}$$

where M_i is the initial mass and M_e is the end mass for each trial.

Differences in ignitability, sustainability, combustibility, and consumption were first examined across the three species (categorical variable for species identity) using ANOVAs. A Tukey post-hoc test was used if ANOVA results yielded significance. Next, differences in ignitability, sustainability, combustibility, and consumption were tested across MC for all three species, with MC as a continuous predictor variable using linear regression analysis. We also examined and reported

significant interactions between MC (categorical) and species (categorical) for each attribute of flammability.

Differences between combined species sustainability, combustibility, and consumption when cheatgrass was added to perennial grasses compared to perennial grass alone were tested using multiple ANOVA tests. For these analyses, each perennial grass species and level of perennial grass MC (35 or 55%) was examined separately. We tested for differences by cheatgrass amount (continuous) and moisture (categorical) using multiple ANOVA tests. To test for differences between the perennial grass alone (0 g of cheatgrass added) and perennial grasses with increasing amounts of cheatgrass, we used a Tukey post-hoc test. For all individual and combined species analyses, separate models were implemented for each combustion response variable.

Additive effects of combustion

To compare the sustainability, combustibility, and consumption of individual and combined fuel beds, the effect size of non-additivity was calculated using Eq. 2

$$\frac{(\text{Observed} - \text{Expected})}{\text{Expected}} \tag{2}$$

Observed values were obtained directly from trials involving two species, and the expected sustainability, combustibility, or consumption was calculated as a weighted average based on the results of individual species trials. Weights for each species were assigned based on their relative contribution to the total mass in the two-species trial.

Effect size was examined using a two-sided *t*-test and μ was set to zero to determine whether the mean effect size for each trial combination (perennial grass species × perennial grass MC × cheatgrass mass × cheatgrass MC) differed significantly from zero. A non-significant result suggests additivity of sustainability, combustibility, or consumption, meaning that the observed flammability does not differ significantly from what is expected based on individual species fuel beds. A significant effect size indicates a nonadditive interaction between the two species. Positive and negative values of the effect size indicate different directions of non-additivity, and the value represents the strength of the nonadditive effect. A negative effect size means that the observed values are lower than expected, indicating that the two species together reduce the sustainability, combustibility, or consumption compared to their individual responses. A positive effect size indicates that the two species together enhance the sustainability, combustibility, or consumption compared to their individual responses. Further, multiple linear regressions were used to examine whether non-additivity differed based on perennial grass species (categorical), perennial grass MC (categorical), cheatgrass mass (continuous), and cheatgrass MC (categorical). All statistical analysis was performed in R (version 4.0.3; R Core Team, 2023).

Results

Individual species flammability

All species maintained high ignitability across all moisture contents (MC) tested. All trials of individual species flammability had 100% ignition under our controlled experimental conditions, except for cheatgrass at 55% MC (45% ignition), and bluebunch wheatgrass at 25% (66% ignition), 35% (50% ignition), and 55% (50% ignition) MC. Bluebunch wheatgrass had greater sustainability (flaming duration) than cheatgrass (by 12.9 s on average; $p = 0.006$) and Columbia needlegrass (by 13.9 s on average, $p = 0.001$; Fig. 3A). Similarly, bluebunch wheatgrass had higher maximum temperatures than both cheatgrass and Columbia needlegrass by 129 and 160 °C, respectively ($p = 0.036$ and 0.003; Fig. 3B). Columbia needlegrass had 42 °C greater mean temperatures than did cheatgrass ($p < 0.001$), and cheatgrass had 50 °C greater mean temperature than did bluebunch wheatgrass ($p < 0.001$; Fig. 3C). Columbia needlegrass had 11 and 13 cm shorter flame heights than cheatgrass and bluebunch wheatgrass, respectively ($p = 0.003$; Fig. 3D). Similarly, Columbia needlegrass had 11% lower consumption on average than both cheatgrass and bluebunch wheatgrass (Fig. 3E, $p < 0.001$). All attributes of flammability except for duration ($p = 0.081$) decreased for all three species with increasing moisture ($p \leq 0.007$).

Combined species flammability

Some aspects of sustainability, combustibility, and consumption in combined perennial grass and cheatgrass fires were higher than when each perennial grass was burned alone, though this differed between the two perennial grass species (Fig. 4). Flaming duration and mass consumption of both perennial grass species with cheatgrass were greater than when each was burned alone (differences varied by cheatgrass mass, Fig. 4A and E; Table 1). Bluebunch wheatgrass with cheatgrass had greater flame heights than when bluebunch wheatgrass was burned alone (differences varied by cheatgrass mass, Fig. 4D; Table 1). There were no differences in the maximum nor mean temperature of perennial grass and cheatgrass combined trials compared to when each perennial grass was burned alone (Fig. 4B and C). There were some differences in combined flammability by annual grass MC, but only for Columbia needlegrass at 55% MC (duration $p = 0.012$; mean temp. $p = 0.026$; flame height $p = 0.015$; mass consumption $p < 0.001$; Table 1).

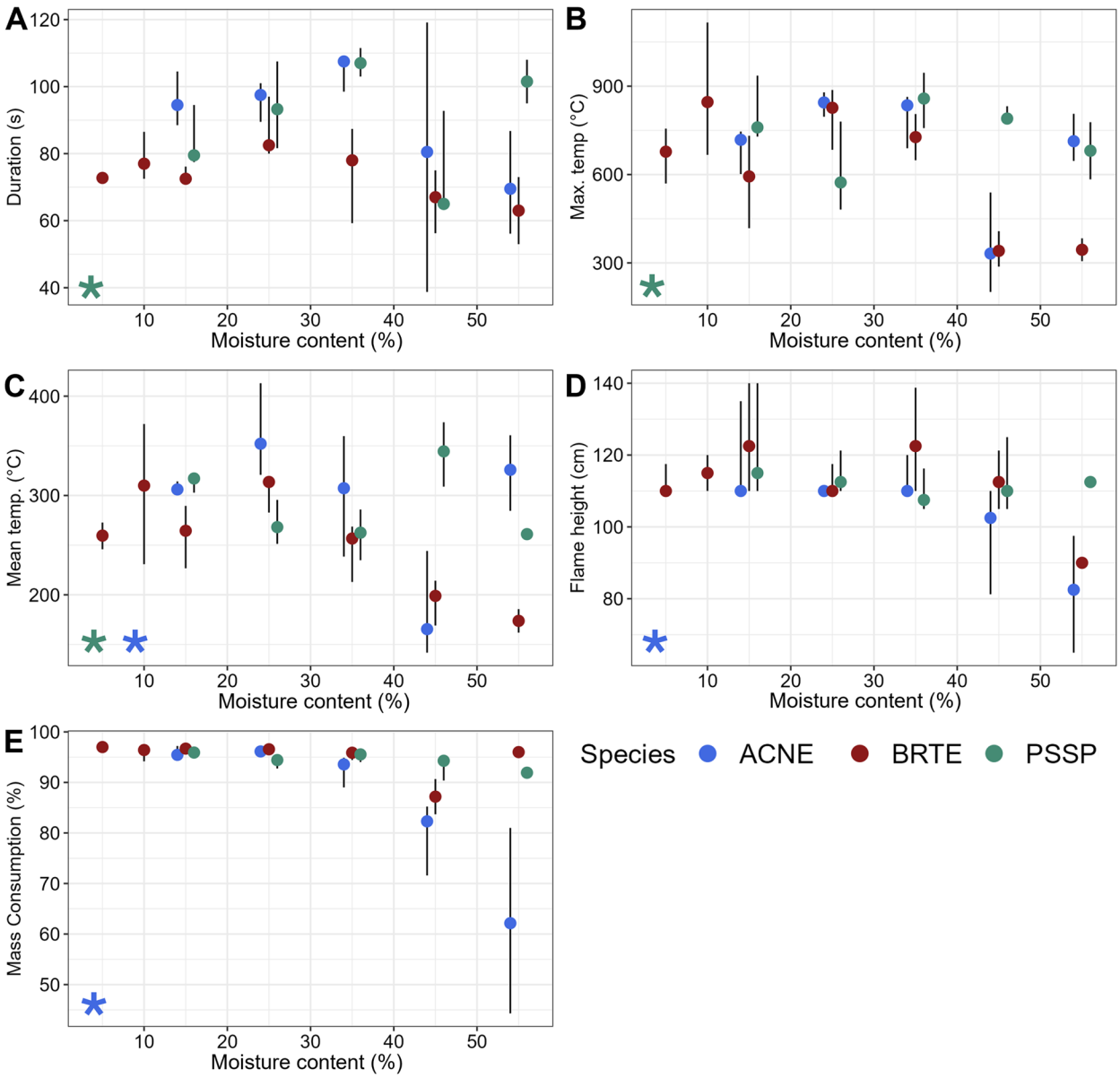


Fig. 3 Flammability (A = duration, B = maximum temperature, C = mean temperature, D = flame height, E = mass consumption) of individual species (ACNE = Columbia needlegrass, BRTE = cheatgrass, PSSP = bluebunch wheatgrass) with increasing percent moisture content (MC). Points represent median values, and black lines are the interquartile range for each median. Differences between each species' flammability were examined using multiple, one-way ANOVA tests: significant differences by species are indicated by colored * in bottom right

Additive effects of combined flammability

We observed additive effects in sustainability, some metrics of combustibility, and consumption, indicating that the combined flammability was different than expected based on the flammability of each species alone. For most attributes of flammability with both perennial grass species effect sizes either overlapped with 0, suggesting that the combined flammability of the perennial and annual grass matched expectations based on individual species flammability, or were negative, suggesting that combined flammability was less than what would be expected from individual species flammability (Fig. 5). The exception to this were the positive effect sizes for flaming duration of Columbia needlegrass at 55% MC with 10 and 15 g of annual grass (Fig. 5A), meaning that the combined flaming duration was greater than expected from each species individual flammability.

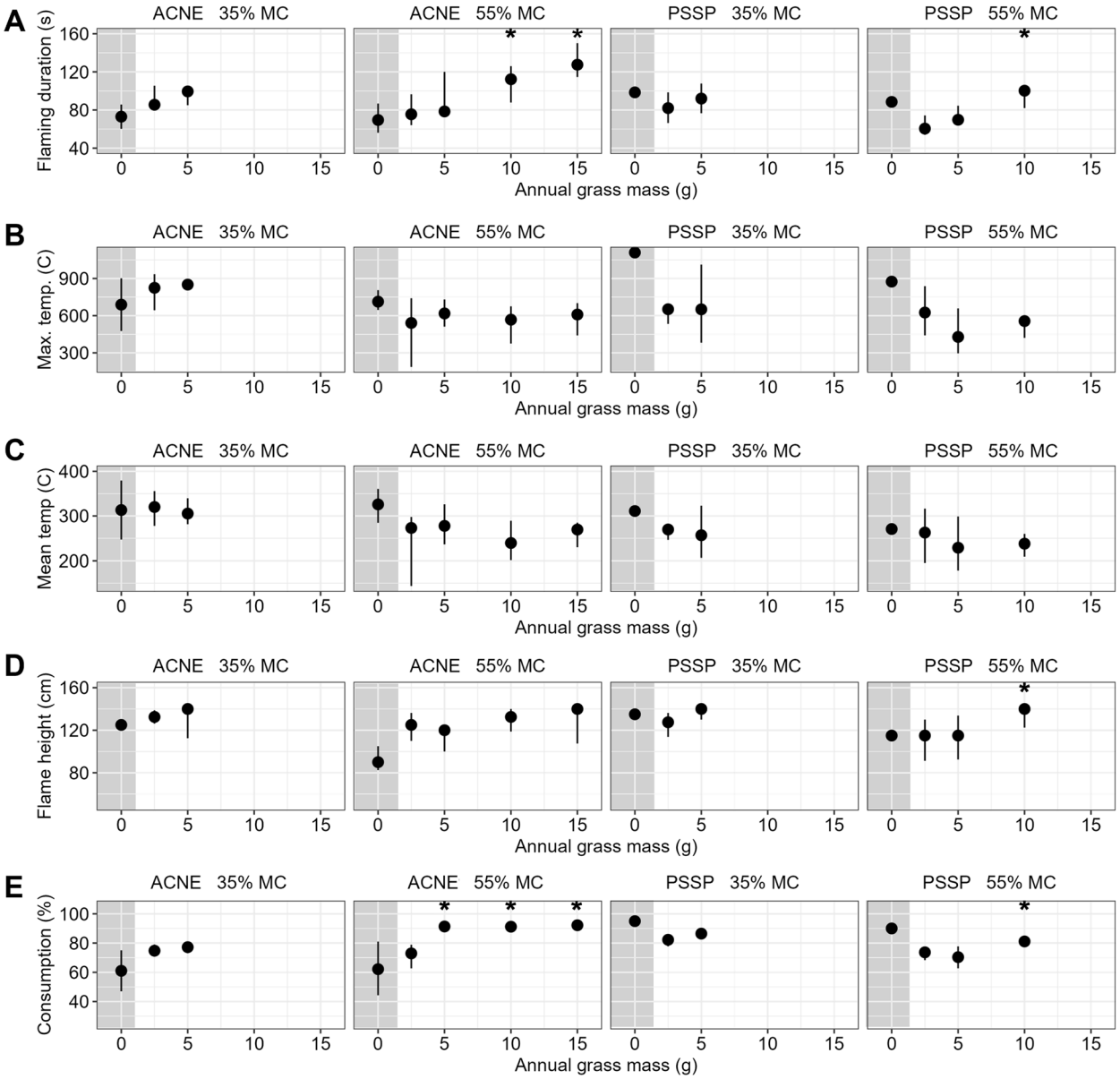


Fig. 4 Flammability (A = duration, B = maximum temperature, C = mean temperature, D = flame height, E = mass consumption) of perennial grasses (ACNE = Columbia needlegrass, PSSP = bluebunch wheatgrass) at 55% and 35% moisture content (MC) burned alone (gray boxes) and with increasing amounts of cheatgrass added to the mix. Points represent median values, and black lines are the interquartile range for each median. For each perennial grass species at both 35 and 55% MC, tests for differences in each flammability attribute were examined by annual grass mass and MC using an ANOVA test. Black asterisks indicate significant ($p < 0.05$) differences between the flammability of perennial grass when burned with cheatgrass compared to when burned alone. See Table 1 for differences by annual grass MC

Discussion

Experimental additions of cheatgrass to perennial grass increased overall flammability by increasing perennial grass sustainability, combustibility, and consumption. These findings provide experimental evidence supporting previous qualitative observations of high cheatgrass flammability (Link et al. 2006; Balch et al. 2013) and build on prior research of invasive grass flammability by Fuentes-Ramires et al. (2016). Our results broaden the scope of our understanding of invasive grass flammability by experimentally testing the impact of native and invasive grass fuel composition across a range of simulated moisture conditions.

First, we assessed differences in flammability by grass species. Cheatgrass exhibited either similar or lower flammability at the individual species level than

Table 1 Differences in combined flammability of Columbia needlegrass (ACNE) and bluebunch wheatgrass (PSSP) at two moisture content levels (MC; categorical covariate) by annual grass (AG) mass, and moisture content (MC, %) using multiple ANOVA tests. Significance codes for *p*-value: *** = < 0.001, ** = < 0.01, * = < 0.05

Flammability	PG Species	PG MC	Term	df	Sum Sq	Mean Sq	*f* value	*p* value	Sig
Duration	ACNE	35	AG MC	2	481.1	240.5	0.34	0.717	
			AG mass	1	857.5	857.5	1.22	0.293	
			Residuals	11	7717.8	701.6			
		55	AG MC	4	11,147.3	2786.8	3.66	0.012	*
			AG mass	3	23,016.2	7672.1	10.08	< 0.001	***
			Residuals	45	34,265.6	761.5			
	PSSP	35	AG MC	2	403.7	201.9	0.71	0.516	
			AG mass	1	924.5	924.5	3.27	0.104	
			Residuals	9	2545.6	282.8			
		55	AG MC	4	428.8	107.2	0.38	0.818	
			AG mass	2	7410.1	3705.1	13.27	< 0.001	***
			Residuals	30	8378.8	279.3			
Max. temp	ACNE	35	AG MC	2	34,747.2	17,373.6	0.27	0.770	
			AG mass	1	833.2	833.2	0.01	0.912	
			Residuals	11	715,316.5	65,028.8			
		55	AG MC	4	488,619.4	122,154.8	2.34	0.069	
			AG mass	3	113,700.3	37,900.1	0.73	0.542	
			Residuals	45	2,348,339.4	52,185.3			
	PSSP	35	AG MC	2	220,514.7	110,257.3	1.29	0.321	
			AG mass	1	11,604.5	11,604.5	0.14	0.721	
			Residuals	9	767,101.1	85,233.5			
		55	AG MC	4	403,718.2	100,929.6	1.89	0.138	
			AG mass	2	83,262.2	41,631.1	0.78	0.467	
			Residuals	30	1,599,449.5	53,315.0			
Mean temp	ACNE	35	AG MC	2	7107.4	3553.7	0.50	0.621	
			AG mass	1	2092.7	2092.7	0.29	0.599	
			Residuals	11	78,593.6	7144.9			
		55	AG MC	4	58,868.3	14,717.1	3.06	0.026	*
			AG mass	3	11,439.9	3813.3	0.79	0.505	
			Residuals	45	216,564.5	4812.5			
	PSSP	35	AG MC	2	2764.0	1382.0	0.53	0.604	
			AG mass	1	3.0	3.0	0.00	0.973	
			Residuals	9	23,276.1	2586.2			
		55	AG MC	4	19,296.3	4824.1	0.93	0.458	
			AG mass	2	2647.6	1323.8	0.26	0.776	
			Residuals	30	155,010.0	5167.0			
Flame height	ACNE	35	AG MC	2	1274.3	637.1	3.36	0.072	
			AG mass	1	35.7	35.7	0.19	0.673	
			Residuals	11	2083.3	189.4			
		55	AG MC	4	10,229.2	2557.3	3.46	0.015	*
			AG mass	3	928.7	309.6	0.42	0.740	
			Residuals	43	31,793.0	739.4			
	PSSP	35	AG MC	2	74.5	37.3	0.15	0.863	
			AG mass	1	112.5	112.5	0.45	0.519	
			Residuals	9	2243.8	249.3			
		55	AG MC	4	1262.6	315.7	0.74	0.574	
			AG mass	2	3751.3	1875.7	4.38	0.021	*
			Residuals	30	12,842.8	428.1			

Table 1 (continued)

Flammability	PG Species	PG MC	Term	df	Sum Sq	Mean Sq	*f* value	*p* value	Sig
Mass consumption	ACNE	35	AG MC	2	771.9	386.0	1.25	0.324	
			AG mass	1	312.3	312.3	1.01	0.336	
			Residuals	11	3398.8	309.0			
		55	AG MC	4	2064.8	516.2	7.45	< 0.001	***
			AG mass	3	3356.0	1118.7	16.15	< 0.001	***
			Residuals	45	3117.9	69.3			
	PSSP	35	AG MC	2	223.4	111.7	3.66	0.069	
			AG mass	1	36.4	36.4	1.19	0.303	
			Residuals	9	274.8	30.5			
		55	AG MC	4	545.9	136.5	2.68	0.050	
			AG mass	2	726.0	363.0	7.14	0.003	**
			Residuals	30	1525.4	50.8			

Columbia needlegrass and bluebunch wheatgrass. Specifically, bluebunch wheatgrass burned for longer and reached greater maximum temperatures than did cheatgrass and Columbia needlegrass. All three species had similar combustibility (maximum temperature and flame height) and were flammable, even at high moistures under laboratory conditions. This contradicts our initial prediction that cheatgrass would have higher flammability than native grasses across tested moistures due to its high surface area-to-volume ratio and fine stems. Our findings are in line with Link et al. (2019), who did not observe any differences in plot-level ignitability due to cheatgrass abundance when they experimentally ignited study plots that had been invaded by cheatgrass and replanted with large bunchgrasses. These results suggest that other plant traits, such as chemical composition or leaf size (Simpson et al. 2016; Cardoso et al. 2018), or fuels characteristics, such as packing ratio and fuel distribution (Fuentes-Ramirez et al. 2016), may explain differences in flammability observed on the landscape-scale in sagebrush shrublands due to cheatgrass.

The addition of cheatgrass to both perennial grass species resulted in fires with greater consumption, flaming duration, and flame heights compared to when the perennial grasses were burned alone. We predicted that the addition of cheatgrass would increase the overall flammability of the perennial grasses due to the higher fuel loads and lower moisture content of cheatgrass compared to the perennials. This prediction held true for some but not all attributes of flammability and the response differed by cheatgrass mass. When cheatgrass was added to each perennial grass species, the combined sustainability and consumption was higher than when perennials were burned alone. Most aspects of combustibility (maximum and mean temperature) for both perennial grass species when burned with cheatgrass did not differ from cheatgrass burned alone, though there were some differences in flame height. Our experimental conditions included mostly perennial grass mass with smaller amounts of cheatgrass. As cheatgrass mass increases, or even replaces perennial grass species, we would expect the resulting flammability to be more similar to when cheatgrass was burned alone. A similar phenomenon was observed by Barnest et al. (2022) in their examination of the invasive forb *Lespedeza cuneata* in native tallgrass prairie fuelbeds. Future studies could examine alternative ratios of native versus invasive fuels. Further, we assumed that both perennial grass species would behave similarly and did not anticipate the differences between the two perennial grass species. Another laboratory combustion experiment demonstrated differences in flammability by grass species (Simpson et al. 2016). These findings underscore the significance of comprehending the intricate dynamics between cheatgrass and native vegetation when evaluating flammability.

We also predicted that when burned together, combined flammability would not be a simple additive function of individual species' attributes; rather, there would be greater flammability due to cheatgrass preheating perennial grasses, resulting in an increased overall flammability. In most cases (perennial grass species, moistures, and flammability attributes), this prediction did not hold true. On the contrary, combined mixtures were less flammable than would be expected based on individual flammability. Blauw et al. (2015) similarly observed differences in combined flammability among species

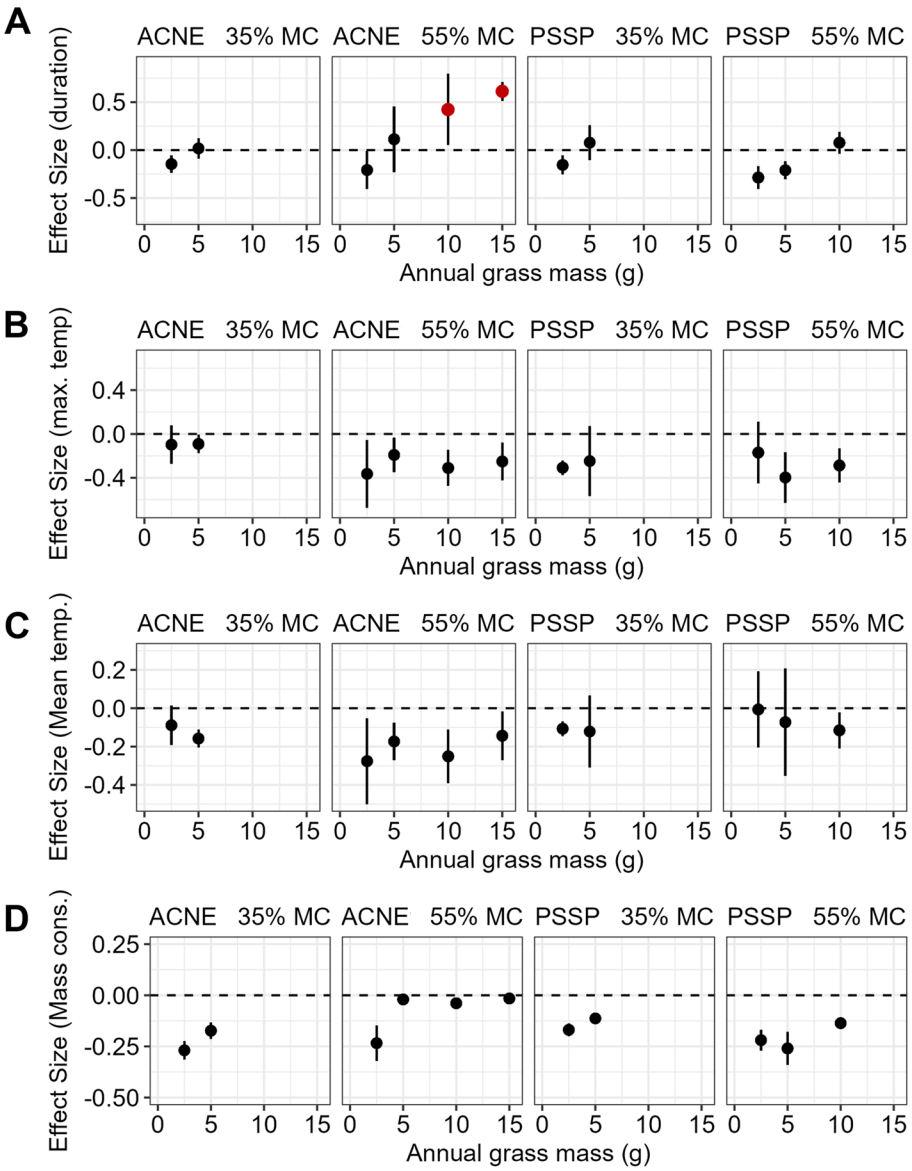


Fig. 5 Effect size between observed and expected flammability (A = duration, B = maximum temperature, C = mean temperature, D = mass consumption) of needlegrass (ACNE) and bluebunch wheatgrass (PSSP) at 55% and 35% moisture content (MC) with varying annual grass mass. Points represent mean values, and black lines are the interquartile range for each median. Effect sizes that do not overlap with 0 (horizontal dashed line) indicate the presence of nonadditivity. Red points indicate statistically significant ($p < 0.05$) positive effects

examined. There were some differences in observed verses expected flammability by perennial grass species, suggesting that these two perennial grass species may be differentially susceptive to pre-heating by cheatgrass. These findings are in congruence with Van Altena et al. (2012), who observed differences in flammability characteristics within two-species mixtures compared to those of monospecific fuel beds. Columbia needlegrass may be more easily ignited by cheatgrass pre-heating compared to bluebunch wheatgrass. These different pre-heating traits may be due to plant structure as Columbia needlegrass leaves have a greater surface area to volume ratio than bluebunch wheatgrass leaves. Columbia needlegrass leaves are narrower and more needle-like, whereas bluebunch wheatgrass leaves are wider and longer. Differences in perennial grass combined flammability could be an important consideration for seeding post-fire, post-disturbance, or within fuel breaks (Shinneman et al. 2019). However, our experimental design does not allow us to conclude that these increases

were attributable to cheatgrass specifically, or to an overall increase in the experimental fuel load, as occurs during cheatgrass invasion.

We considered the impact of both perennial and annual grass moisture content on joint flammability. There were no differences in total (annual and perennial grasses burned together) flammability due to perennial grass moisture. Similarly, the moisture of cheatgrass when added to perennial grasses was also largely unimportant in explaining combined flammability. These results were surprising given that we selected moistures (relatively low to moderate for annual grass and moderate to high for perennial grasses) that represented the mismatch in moisture conditions caused by cheatgrass curing earlier in the growing season than perennial grasses (D'Antonio and Vitousek 1992; Balch et al. 2013). These results suggest that the influence of cheatgrass on flammability may be more reliant on other physical or chemical traits of both annual and perennial grass species rather than moisture. Further, the ability of cheatgrass to alter flammability may be primarily contingent on its presence and less related to moisture during the growing season, which supports a relatively low threshold of cheatgrass abundance for altering the flammability of nearby species in line with the 10% cover threshold proposed by Pastick et al. (2021) in their analysis of remotely-sensed vegetation maps.

Another potential explanation for the lack of differences in combined flammability due to annual and perennial grass moisture content is the discrepancy between our experimental moisture content versus live fuel moisture conditions. We examined cheatgrass at 5–35% MC with perennial grasses, and our method of collecting grasses in the field, drying them, and then rehydrating them was consistent with other studies (Blauw et al. 2015) and provides repeatable measurements and experimental control. However, cheatgrass was mostly senesced and dry when collected, and our rehydration method involved sealing dried and senesced plants in water. Since this is not the same as intercellular water in live plants, our rehydration techniques would better represent precipitation on dead, fine fuels rather than late-fire season live fuel moistures. Our experimental moistures should be considered relative to each other, and not a reproduction of live moisture. Additional studies could examine differences in cheatgrass flammability throughout the season using live moisture conditions to better explore this phenomenon and relate observations to field conditions.

In this study, cheatgrass and perennial grasses were burned together in a homogenous mixture, with the plant material standing upright to simulate the structure of natural fuels. The main difference between the two fuel sub-layers was the natural height variation between perennials and annuals. However, the spatial distribution of fuels and the resulting fire spread between fuels was not examined. Cheatgrass and other invasive annual grasses create highly continuous fine fuel beds that facilitate fire spread between plants. Perennial grasses typically grow in tight bunches of live and dead plant material, while cheatgrass fills the plant interspaces (Pilliod et al. 2021). The flammability of each perennial grass species may vary depending on dead plant material within the bunch, which can be influenced by site climate, productivity, grazing, and decomposition rate (Bansal et al. 2014). For instance, a perennial grass surrounded by dry dead plant material, including attached and detached litter, could be more susceptible to ignition by cheatgrass in the interspaces. This pre-heating effect from cheatgrass and dead perennial grass material may contribute to increased flammability, as observed with Columbia needlegrass in our study, and warrants further investigations.

The flammability of cheatgrass was only examined in combination with two perennial grass species. To gain a more comprehensive understanding of cheatgrass flammability alongside other species, future research could explore the flammability of additional dominant sagebrush steppe species, including those commonly used within fuel breaks (Shinneman et al. 2019). Additionally, flammability experiments could consider the interaction of cheatgrass with other fuels, such as litter and lower shrub branches (Fuentes-Ramirez et al. 2016), since cheatgrass is often found in high density under shrub canopies. It is important to understand how annual and perennial grass species contribute to overall shrub flammability in sagebrush shrublands, as shrub components are a key driver of fire behavior in these ecosystems (Ellsworth et al. 2022).

Conclusions

While cheatgrass alone was not more flammable than the perennial grasses tested here, the addition of cheatgrass resulted in increased sustainability and consumption of the perennial grasses depending on cheatgrass mass. Cheatgrass more strongly increased the sustainability and consumption of Columbia needlegrass compared to bluebunch wheatgrass, indicating differing species-specific responses to the presence of cheatgrass. Grass species composition, not just the presence of cheatgrass, can influence overall flammability. The combined flammability of these perennial grasses did not differ by cheatgrass moisture, suggesting that grass abundance and physical traits matter more than moisture for combined flammability. Overall, these laboratory experiments allowed us to assess multiple attributes of flammability under

controlled conditions and different species responses indicate the complexity of landscape-scale fire risk.

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Authors' contributions
GH, TP, and ES conceived and designed the study with input from LJ and LE. GH led the acquisition, analysis, and interpretation of the data with contributions from all authors. GH led the writing of the manuscript. All authors contributed to the revising of the manuscript and have approved the submitted version.

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Data availability
The datasets used and analyzed during the current study are available from the corresponding author on request.

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Not applicable.

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The authors declare that they have no competing interests.

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