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Indaziflam reduces downy brome (*Bromus tectorum*) density and cover five years after treatment in sagebrush-grasslands with no impact on perennial grass cover

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Research Article

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Abstract

The invasive annual grass downy brome (*Bromus tectorum* L.) is a critical threat to the semiarid shrublands that characterize western North America. More abundant fine fuel after invasion typically increases fire frequency in plant communities adapted to relatively infrequent burning, reducing the likelihood of native plant persistence. Currently, imazapic is most often used to manage *B. tectorum*, but reinvasion from the seedbank after treatment is common. Indaziflam is a newer herbicide recently labeled for use in rangelands grazed by livestock, and many research trials have demonstrated its ability to deplete invasive annual grass seedbanks. We evaluated the effectiveness of indaziflam and imazapic for reducing *B. tectorum* density and cover over a period of approximately 5 yr (57 mo after treatment [MAT]) at two invaded sagebrush-grassland sites near Pinedale, WY. Treatments included three different indaziflam rates (51, 73, and 102 g ai ha^{-1}) and one imazapic rate (123 g ai ha^{-1}), and these treatments were reapplied to half of each plot at 45 MAT to evaluate the effects of two sequential applications. We also measured perennial grass cover, because positive perennial grass responses were observed after release from *B. tectorum* competition in other studies, and perennial grasses may provide resistance to *B. tectorum* reinvasion. Intermediate and high indaziflam rates (73 and 102 g ha^{-1}, respectively) reduced *B. tectorum* cover and density at 45 MAT, and perennial grass cover responded positively to some treatments, mostly early in the study (≤33 MAT). Imazapic reduced *B. tectorum* initially, but did not affect density or cover at either site beyond 21 MAT. Reapplication did not substantially improve *B. tectorum* control at 57 MAT in plots treated with intermediate and high indaziflam rates, suggesting that long-term control with a single indaziflam treatment may be possible in some cases.

Introduction

Downy brome (*Bromus tectorum* L.) invasion into the sagebrush-grasslands of western North America is one of the most critical threats facing these important rangelands (Clark 2020; DiTomaso et al. 2010; Smith et al. 2021). Variable germination timing (Beck 2009; Knapp 1996; Mack 1981), rapid growth (Arredondo et al. 1998), high seed production (Young et al. 1987), and acquisitive root morphology (Aguirre and Johnson 1991; Arredondo and Johnson 1999), help *B. tectorum* exploit important soil resources sooner than native plants and promote successful *B. tectorum* establishment. The altered fire regimes that typically follow invasion favor its increasing dominance, continued spread, and severe impacts to native plant communities (Clark 2020; Davies 2011; Davies et al. 2021b; West 1983).

Historical fire regimes are difficult to determine in relatively arid plant communities with few trees, but the long recovery time of big sagebrush (*Artemisia tridentata* Nutt.) suggests that fires were relatively infrequent in the past and limited in their extent (Miller et al. 2013; Schlaepfer et al. 2014). This fire regime is thought to have maintained a mosaic of shrub- and perennial grass–dominated plant communities in different phases of recovery from wildfire (Davies and Bates 2020; McAdoo et al. 2013), and supported a variety of different habitat types for the region's diverse wildlife (Burkhardt 1996; McAdoo et al. 2004). After invasion, more and more continuous fine fuel resulting from *B. tectorum* litter can substantially increase the likelihood of wildfire ignition and the rate of wildfire spread where and when *B. tectorum* occurs (Balch et al. 2013; Bradley et al. 2018; Davies and Nafus 2013). This is particularly the case when fine fuel accumulates over multiple years with above average precipitation (Pilliod et al. 2017).

Management Implications

The invasive winter annual grass *Bromus tectorum* (downy brome) has invaded vast expanses of sagebrush-grassland in western North America, and the fine fuel associated with invasion increases the frequency of wildfire such that native plants struggle to persist. Recent research suggests that *B. tectorum* invasion may expand across an even larger portion of the U.S. Intermountain West in the absence of effective and proactive management.

Imazapic is widely used to manage *B. tectorum*, but control often declines after 1 yr, and reinvasion is typical. Several trials have demonstrated that the newer herbicide indaziflam can selectively control annual grasses for 3 or more years, and past studies indicate that *B. tectorum* seedbanks are relatively short-lived in the field (≤5 yr). Thus, consecutive years of control with indaziflam may deplete *B. tectorum* seedbanks and increase the duration of control, but it is unclear whether this will require multiple applications.

A single indaziflam treatment at intermediate and high rates (73 and 102 g ai ha^{-1}, respectively) consistently reduced *B. tectorum* density and cover to very low levels (≤4.8 m^{-2} and ≤1.3%, respectively) at 45 mo after treatment (MAT), and only modest improvements in control were observed at 57 MAT with two treatments at these rates. Perennial grass cover responded positively to some treatments early in the study (≤33 MAT), but effects were inconsistent across years. Our results suggest that long-term *B. tectorum* control is possible with a single indaziflam treatment when applying herbicide to small plots, but managers should avoid assuming this outcome will be typical when applying indaziflam at larger scales. The intermediate indaziflam rate evaluated in our study aligns with the maximum single-use application rate permitted by the current grazing label (Rejuvra®, Bayer; 73 g ai ha^{-1}), suggesting that indaziflam may be a powerful tool for land managers tasked with mitigating the impacts of *B. tectorum* in grazed areas.

Frequent wildfires can be difficult for relatively slow-growing native perennials to cope with, but annual *B. tectorum* can recover rapidly (Humphrey and Schupp 2001; Perryman et al. 2020; Young and Evans 1978; Young et al. 1987), resulting in a destructive grass–wildfire feedback loop similar to what has emerged after nonnative grass invasion in many different arid and semiarid ecosystems (D'Antonio and Vitousek 1992; Fusco et al. 2019). Across 51 paired burned and unburned sagebrush sites, Swanson et al. (2018) found that native plant dominance declined after fire in all cases where pre-fire *B. tectorum* cover exceeded 15%, and Bradley et al. (2018) estimated that *B. tectorum* cover exceeds 15% over approximately 30% of the U.S. Intermountain West. Estimates suggest that the current extent of western North America's sagebrush steppe represents roughly half of what it was historically (Miller et al. 2011), in large part due to this destructive fire–invasion feedback loop.

The rate of *B. tectorum* expansion further clarifies the need for new tools and innovative approaches to annual grass management. Smith et al. (2021) estimated that the area of *B. tectorum*–dominated communities has increased 8-fold since 1990 in the Great Basin, with the most rapid expansion occurring in the most recent decade they considered (2011 to 2020). While relatively cold, high-elevation rangelands have long been considered more resistant to *B. tectorum* invasion (Chambers et al. 2014), this may be changing, and expansion into higher-elevation rangelands would allow *B. tectorum* invasion to continue unabated over an even larger portion of the region (Mealor et al. 2012; Smith et al. 2021). Unless effective management interventions are developed and deployed, *B. tectorum* is likely to continue severely impacting rangeland ecosystems in western North America, incurring substantial costs associated with wildland firefighting and restoring repeatedly burned landscapes (Davies et al. 2021b; Mack 2011; Perryman et al. 2018).

Existing approaches to manage *B. tectorum* often provide short-term reductions in abundance (≤2 yr after treatment [YAT]), but long-term control is difficult to achieve, and reinvasion is common without continued management (Mack 2011; Monaco et al. 2017). Imazapic is a broad-spectrum herbicide that inhibits the enzyme acetolactate synthase; it is selective against annual grasses at low use rates and is likely the most widely used herbicide for managing annual grasses because of its ability to provide both pre- and postemergent control (Kyser et al. 2013; Mangold et al. 2013). Imazapic has provided variable results (Applestein et al. 2018; Mangold et al. 2013), often reducing *B. tectorum* in the first year after treatment but having inconsistent long-term effects on *B. tectorum* abundance (Davison and Smith 2007; Elseroad and Rudd 2011; Morris et al. 2009; Munson et al. 2015).

Indaziflam, a recently labeled herbicide for use on rangelands grazed by livestock (USEPA 2020), provides multiyear *B. tectorum* control (Clark et al. 2020; Sebastian et al. 2016, 2017a). Indaziflam is a cellulose biosynthesis inhibitor with a unique site of action and no reported cases of resistance (Brabham et al. 2014; Tateno et al. 2016). This herbicide is uniquely suited to managing *B. tectorum* because of its selectivity and long period of residual activity (Clark 2020; Sebastian et al. 2016). Indaziflam binds tightly to soil organic matter and remains near the soil surface, where it can selectively inhibit root growth of germinating *B. tectorum* seeds without harming established perennials with deeper roots (Clark 2020; Sebastian et al. 2017a). Further, because it typically provides 3 or more years of control, and *B. tectorum* seedbanks are generally short-lived in the field (≤5 yr; Burnside et al. 1996; Sebastian et al. 2017b; Smith et al. 2008), indaziflam could deplete *B. tectorum* seedbanks with a single application or a sequence of applications spaced several years apart. While non-target impacts to native annual plants have been observed (Courkamp et al. 2022), field trials across the western United States have demonstrated indaziflam's effectiveness for controlling invasive annual grasses with no apparent impacts to established perennial plants (Clark et al. 2019, 2020; Hart and Mealor 2021; Sebastian et al. 2016, 2017a).

Perennial bunchgrasses are a key component of rangeland plant communities that increase resistance and resilience to annual grass invasion and wildfire, respectively (Applestein and Germino 2022; Blank et al. 2020; Chambers et al. 2014; Davies and Johnson 2017). Thus, proactively treating invaded areas that continue to support relatively abundant perennial grasses may represent a highly effective approach to *B. tectorum* management. While sagebrush-associated perennial grasses typically live longer than the expected period of residual activity from indaziflam treatment (Svejcar et al. 2014), they rely on recruitment from seed for long-term persistence (Hamerlynck and Davies 2019), which suggests that they may be sensitive to non-target impacts from repeated indaziflam treatments that extend residual activity over longer periods of time.

The primary objective of our study was to evaluate the long-term (57 mo) effectiveness of indaziflam (51, 73, and 102 g ai ha^{-1}) and imazapic (123 g ai ha^{-1}) for controlling *B. tectorum* in high-elevation sagebrush-grasslands where invaded communities continue to support abundant perennials. We also assessed treatment effects on co-occurring perennial grasses over this same span of time to evaluate the potential for non-target impacts and compared one and two applications of each herbicide treatment (45 mo between applications) to make the study more relevant to land managers considering multiple applications.

Materials and Methods

Site Description

The experiments were established in 2016 at two sites in Sublette County, WY. Site 1 (42.855°N, 109.655°W, approx. 2,250-m elevation) was located near Boulder Lake in the Bridger-Teton National Forest, and Site 2 (42.885°N, 109.739°W, approx. 2,250-m elevation) was located in the Half Moon Habitat Management Unit managed by the Wyoming Game and Fish Department. These study sites were approximately 8 km apart in the Cold Desert region of the North American Deserts ecoregion; Site 1 was characterized as a coarse upland ecological site (R043BY208WY), and Site 2 was characterized as a shallow loamy ecological site (R043BY162WY; USDA-NRCS 2021).

The soil at Site 1 was Pointer-Lateral complex (loamy-skeletal, mixed, superactive, Ustic Haplocryolls), which is characterized by a very cobbly sandy loam surface soil with 2.9% organic matter and 6.8 pH in the top 20 cm (USDA-NRCS 2021). The soil at Site 2 was Blackbear, rubbly-Branham, rubbly-Bobowic complex (loamy-skeletal, mixed, superactive, Pachic Agricryolls), which is characterized by cobbly or gravelly coarse sandy loam surface soil with 5.3% organic matter and 6.6 pH in the top 20 cm (USDA-NRCS 2021). Both sites had south-facing aspects, but Site 1 was slightly steeper than Site 2.

When treatments were applied, both sites supported plant communities dominated by native perennial bunchgrasses and shrubs, but invaded such that the majority of interspaces between established plants were infested by *B. tectorum*. The most common perennial grasses at both sites were needle and thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth] and bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Á. Löve], and the most common shrubs included antelope bitterbrush [*Purshia tridentata* (Pursh) DC], mountain big sagebrush [*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle], and mountain snowberry [*Symphoricarpos oreophilus* A. Gray]. The dominant forb at both sites was arrowleaf balsamroot [*Balsamorhiza sagittata* (Pursh) Nutt.]. A variety of less common native and nonnative plants existed at low abundance at the time of treatment.

Mean annual precipitation based on the 30-yr mean (1981 to 2010) was 294 mm for both sites based on the nearest weather station (located in Pinedale, 16 km from Site 1, 9 km from Site 2; WRCC 2021). Relative to this average, the 2017 and 2019 water years (October to September) were particularly wet (481 mm and 421 mm, respectively), and 2021 was particularly dry (250 mm). All other study years (2016, 2018, 2020) were within 10% of the 30-year mean (WRCC 2021).

An incidental, human-ignited wildfire (Boulder Lake Fire) burned Site 1 in August 2019. The fire was ignited on August 17, 100% contained on August 26, and declared out on September 17 (Teton Interagency Fire 2019). All study plots at this site were completely burned, and data from 45 and 57 mo after treatment (MAT) at Site 1 were collected approximately 9 and 21 mo after the fire, respectively.

Experimental Design

Initial herbicide treatments were applied at both sites on September 9, 2016, using a CO_2-pressurized custom-built backpack sprayer with 11002LP flat-fan nozzles (TeeJet® Spraying Systems, P.O. Box 7900, Wheaton, Il 60187) delivering 187 L ha^{-1} at 207 kPa. Along with an untreated control, four herbicide treatments were applied to 3 by 9 m plots in a randomized complete block design with four replications at each site. Herbicide treatments included three indaziflam rates (51, 73, and 102 g ha^{-1}; henceforth low, intermediate, and high rates, respectively) and imazapic applied at 123 g ha^{-1}. At the time of application, native plants were dormant, *B. tectorum* was 100% post–seed set, and no fall *B. tectorum* emergence was observed.

The same herbicide treatments were reapplied to half of each treated plot approximately 45 mo after initial herbicide application to evaluate long-term reductions in *B. tectorum* abundance with one and two applications of each treatment. This resulted in eight different herbicide treatments (one and two applications of four treatments, 3 by 4.5 m plots) along with an undivided control plot. Reapplication occurred on June 26, 2020, at Site 1 and June 27, 2020, at Site 2 using a CO_2-pressurized handheld research sprayer with 8002VS flat-fan nozzles (TeeJet® Spraying Systems) delivering 187 L ha^{-1} at 207 kPa. At the time of reapplication, native plants were still actively growing, and *B. tectorum* was nearing 100% post–seed set. All treatments (initial and reapplication) included a 0.25% v/v nonionic surfactant.

Treatment Evaluations and Data Analysis

To quantify herbicide treatment effects, we used 0.5-m^2 frames (Bonham et al. 2004) to measure *B. tectorum* density and perennial grass and *B. tectorum* absolute canopy cover (plant canopy relative to ground area; henceforth cover). We counted individual *B. tectorum* plants and recorded ocular estimates of cover to the nearest 1% in these frames. When *B. tectorum* was especially dense, plants were counted in only a portion of the larger frame to estimate density. Before herbicide reapplication, data were collected from five randomly located frames (subsamples) in each plot, and after reapplication, data were collected from three randomly located frames in each divided treatment plot. Data were collected at 9, 21, 33, 45, and 57 MAT (June 2017 to 2021), with data collection at 57 MAT occurring at 12 mo after reapplication.

To test treatment effects on *B. tectorum* density and *B. tectorum* and perennial grass cover before reapplication, we used the LME4 package in R. v. 3.6.2 (R Core Team 2019) to create linear mixed-effects models and ANOVA to test for treatment effects at $\alpha = 0.05$. Due to substantial interannual variability and environmental differences between sites, site and year were analyzed independently in all cases, with block included as a random factor. Visual inspection of quantile-quantile and fitted versus residual plots was used to verify that data met the assumptions of ANOVA. Cover data were arcsine square-root transformed, and density data were square-root transformed ($n + 0.5$) as necessary to meet these assumptions. When ANOVA indicated that significant differences existed between treatments, we used the EMMEANS package (R Core Team 2019) to obtain pairwise comparisons between treatment groups using a Tukey adjustment ($\alpha = 0.05$).

After reapplication, our experiment did not represent a true split-plot experimental design, because no sequential treatment was applied to the control plots, and these plots remained undivided. Thus, to analyze data from 57 MAT, each herbicide treatment and sequence (one or two applications) was considered a

Table 1. Results of ANOVA (α = 0.05) for treatment effects on *Bromus tectorum* density, *B. tectorum* cover, and perennial grass cover at Site 1 ($n = 4$) and Site 2 ($n = 4$).

	MAT[a]	Response[b]	F (numerator df, denominator df)	P > F[c]
Site 1	9 MAT	*B. tectorum* density	8.65 (4,12)	**<0.01**
		B. tectorum cover	19.41 (4, 12)	**<0.0001**
		Perennial grass cover	4.55 (4, 15)[d]	**0.013**
	21 MAT	*B. tectorum* density	10.87 (4, 15)[d]	**<0.001**
		B. tectorum cover	10.20 (4, 12)	**<0.001**
		Perennial grass cover	3.75 (4, 12)	**0.033**
	33 MAT	*B. tectorum* density	17.12 (4, 15)[d]	**<0.0001**
		B. tectorum cover	16.79 (4, 12)	**<0.0001**
		Perennial grass cover	7.82 (4, 12)	**<0.01**
	45 MAT	*B. tectorum* density	12.60 (4, 12)	**<0.001**
		B. tectorum cover	12.18 (4, 12)	**<0.001**
		Perennial grass cover	2.64 (4, 12)	0.086
	57 MAT	*B. tectorum* density	17.6 (8, 24)	**<0.0001**
		B. tectorum cover	6.16 (8, 24)	**<0.001**
		Perennial grass cover	1.48 (8, 24)	0.22
Site 2	9 MAT	*B. tectorum* density	6.2 (4, 12)	**<0.01**
		B. tectorum cover	8.83 (4, 12)	**<0.01**
		Perennial grass cover	7.16 (4, 12)	**<0.01**
	21 MAT	*B. tectorum* density	5.85 (4, 12)	**<0.01**
		B. tectorum cover	3.66 (4, 12)	**0.036**
		Perennial grass cover	0.75 (4, 12)	0.58
	33 MAT	*B. tectorum* density	12.27 (4, 12)	**<0.001**
		B. tectorum cover	5.67 (4, 12)	**<0.01**
		Perennial grass cover	1.26 (4, 12)	0.34
	45 MAT	*B. tectorum* density	50.25 (4, 12)	**<0.0001**
		B. tectorum cover	10.79 (4, 15)[d]	**<0.001**
		Perennial grass cover	2.59 (4, 12)	0.091
	57 MAT[e]	Perennial grass cover	0.64 (8, 27)[d]	0.74

[a]MAT, months after treatment.
[b]Density = number of individuals m^{-2}; cover = absolute canopy cover.
[c]Significant effects (P < 0.05) shown in bold.
[d]Random effect (block) was estimated as zero and removed from the model.
[e]Treatment effects on *B. tectorum* density and cover were not assessed at 57 MAT at Site 2 due to the near complete absence of *B. tectorum*.

single experimental treatment; data included eight herbicide treatments and an untreated control at 57 MAT. Because *B. tectorum* was nearly absent from all plots at Site 2 at this time, including nontreated controls, we only compared *B. tectorum* cover and density at 57 MAT at Site 1. Otherwise, data were analyzed using the same procedure used to compare treatments before reapplication. Results are presented in their original dimensions, means are reported with standard errors, and P-values reported in the text result from post hoc mean comparisons of treatments and untreated controls (Tukey's honest significant difference).

Results and Discussion

Bromus tectorum Density and Cover

Table 1 shows ANOVA results for *B. tectorum* density and cover. At Site 1, all treatments reduced *B. tectorum* density at 9 MAT, except the low indaziflam rate (imazapic P < 0.001; low P = 0.11; intermediate P = 0.041; high P = 0.017; Figure 1A), and all treatments reduced *B. tectorum* density at 21 MAT (P < 0.01; Figure 1A). At Site 2, responses to treatments at 9 MAT were more variable; *B. tectorum* density was only reduced compared with the nontreated control in plots treated with the low and high indaziflam rates (low P = 0.020; high P < 0.01; Figure 2A). However, similar to Site 1, all treatments reduced *B. tectorum* density at 21 MAT (imazapic P = 0.027; low P < 0.01; intermediate P = 0.032; high P = 0.014; Figure 2A). The more variable results at Site 2 may be the result of unexpected fall *B. tectorum* emergence occurring before herbicide application in September 2016. Indaziflam has no postemergence activity, so *B. tectorum* plants that emerged before application would not be controlled the following spring. While no fall emergence was detected at the time of treatment, dense *B. tectorum* litter was present at both sites, and this may have made emergence difficult to observe.

In contrast to the variability observed at 9 and 21 MAT, the intermediate and high indaziflam rates reduced *B. tectorum* density compared with the nontreated control at both sites at 33 and 45 MAT (P < 0.01; Figures 1A and 2A). The effects of imazapic and the low indaziflam rate were less consistent as the study progressed (Figures 1A and 2A). At Site 1, imazapic and the low indaziflam rate did not reduce *B. tectorum* density compared with the nontreated control at 33 MAT (imazapic P = 0.82; low P = 0.11) and 45 MAT (imazapic P = 0.85; low P = 0.13; Figure 1A). The effects of imazapic at Site 2 mirrored those of Site 1, with no effects on *B. tectorum* density at 33 MAT (P = 0.10) and 45 MAT (P = 0.11; Figure 2A). However, reductions in *B. tectorum* density were comparable for all indaziflam rates at Site 2, with significant reductions observed at 33 and 45 MAT (P < 0.01; Figure 2A).

The effects of treatment on *B. tectorum* cover were less consistent (Figures 1B and 2B). At Site 1, only the imazapic treatment reduced *B. tectorum* cover compared with the nontreated control at 9 MAT (P < 0.001); all treatments except the low indaziflam rate (P = 0.66) reduced *B. tectorum* cover at 21 MAT (imazapic P = 0.030; intermediate P = 0.033; high P < 0.001); and only the intermediate and high indaziflam rates reduced *B. tectorum* cover at 33 (P < 0.001) and 45 MAT (intermediate P = 0.013; high

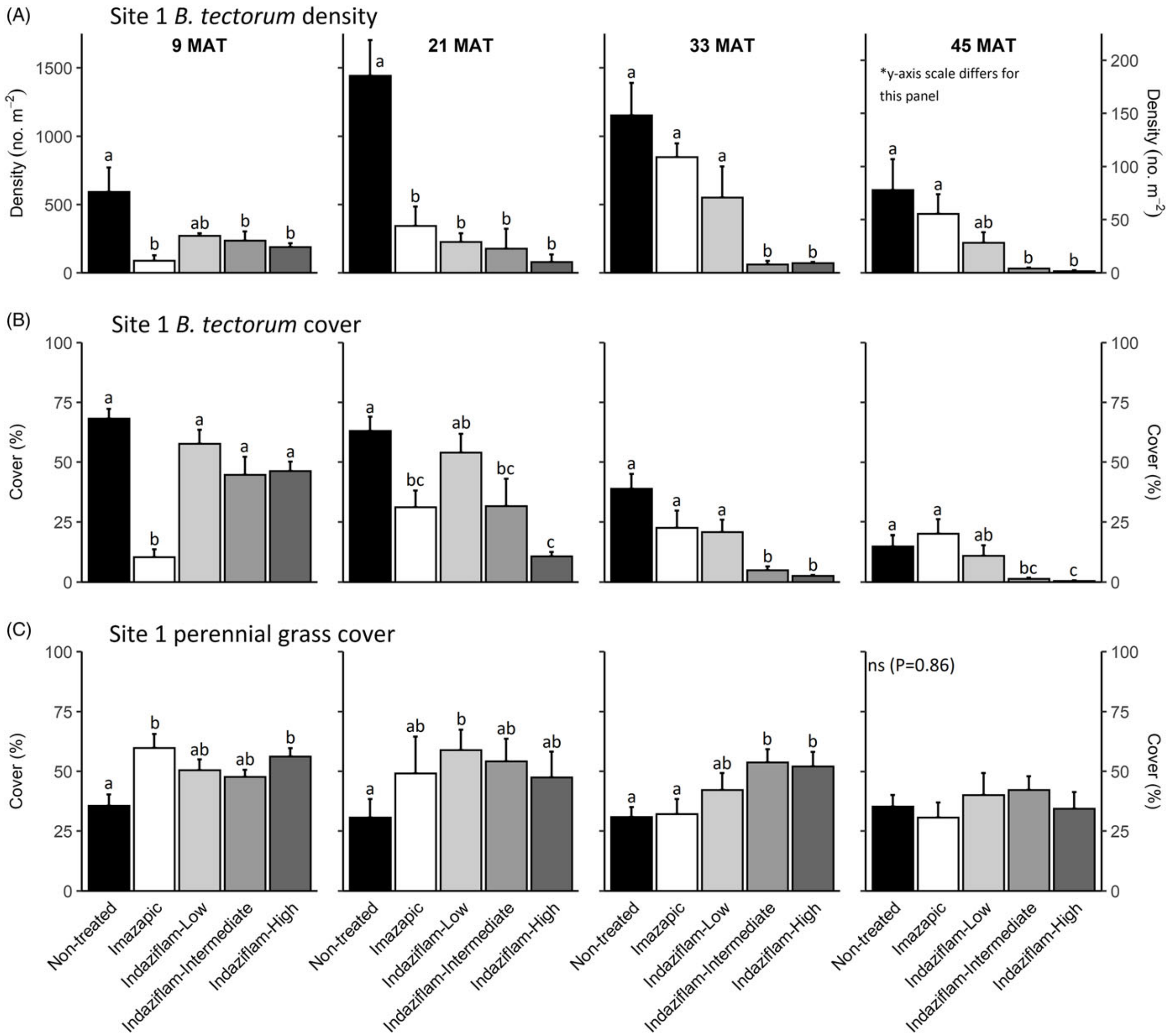

Figure 1. Mean (+1 SE) *Bromus tectorum* density (A), *B. tectorum* cover (B), and perennial grass cover (C) at Site 1 (Boulder Lake) at 9, 21, 33, and 45 mo after treatment (MAT; cover = absolute canopy cover). Herbicide treatments were applied in September 2016 when native plants were dormant and *B. tectorum* was 100% post–seed set. Letters indicate significant within-year differences among treatment means (Tukey's honest significant difference, α = 0.05, *n* = 4). Herbicide treatments are as follows: imazapic = imazapic 123 g ai ha^{-1}; indaziflam-low = indaziflam 44 g ai ha^{-1}; indaziflam-intermediate = indaziflam 73 g ai ha^{-1}; indaziflam-high = indaziflam 102 g ai ha^{-1}. All treatments included a 0.25% v/v nonionic surfactant. Note that *y*-axis scale is consistent across panel rows in all cases, except for *B. tectorum* density at 45 MAT (*).

P < 0.01; Figure 1B). At Site 2, all treatments except the intermediate rate of indaziflam (P = 0.62) reduced *B. tectorum* cover compared with the nontreated control at 9 MAT (P < 0.01); only the low indaziflam rate reduced *B. tectorum* cover at 21 MAT (P = 0.023); the low and high indaziflam rates reduced *B. tectorum* cover at 33 MAT (low P = 0.025; high P = 0.018), and all indaziflam treatments reduced *B. tectorum* cover at 45 MAT (P < 0.01; Figure 2B).

Variability in treatment effects on *B. tectorum* cover at 9 and 21 MAT (Figures 1B and 2B) is similar to what we observed for *B. tectorum* density (Figures 1A and 2A) and may also be explained by unexpected and undetected fall *B. tectorum* emergence the year of treatment. However, less consistent effects of indaziflam treatment on *B. tectorum* cover may also be influenced by the environmental conditions that *B. tectorum* individuals that escape control experience after indaziflam treatment eliminates most intraspecific competitors. Plants in dense monocultures often have only one or a few tillers, while solitary *B. tectorum* individuals in resource-rich environments often have many tillers and produce thousands of seeds (Hulbert 1955; Young et al. 1987; Zouhar 2003). These plants may also have large impacts on cover with minimal effects on density (Elzinga et al. 1998). While mean *B. tectorum* cover was very low in plots treated with intermediate and high indaziflam rates at both sites at 45 MAT (Figures 1B and 2B), we infrequently observed solitary *B. tectorum* individuals with 25+ tillers in indaziflam-treated plots, and these large plants may have contributed to the inconsistent treatment effects on *B. tectorum* cover we observed.

Based on prior research (Clark et al. 2020; Sebastian et al. 2016), we expected indaziflam to reduce *B. tectorum* cover and density for

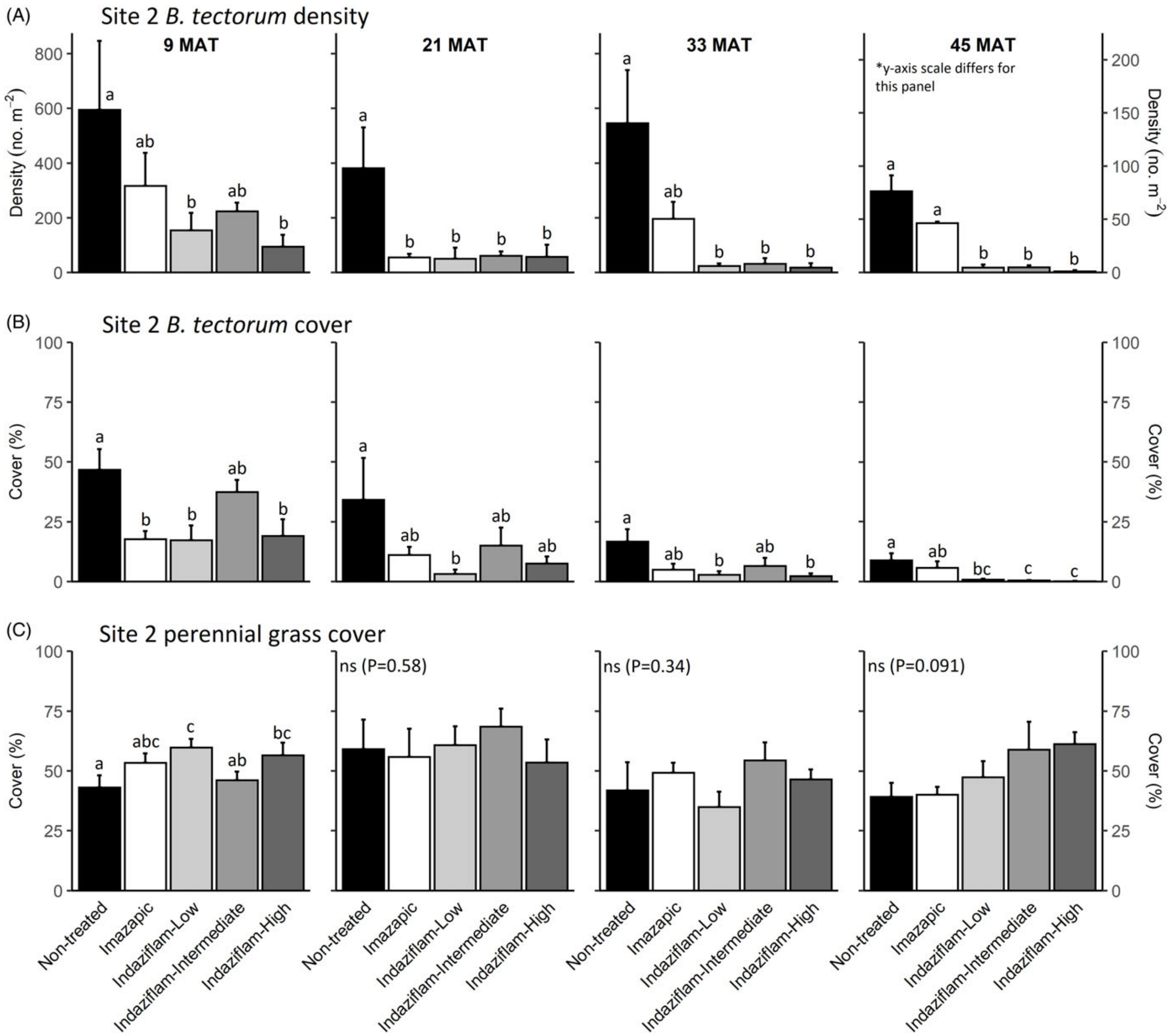

Figure 2. Mean (+1 SE) *Bromus tectorum* density (A), *B. tectorum* cover (B), and perennial grass cover (C) at Site 2 (Half Moon) at 9, 21, 33, and 45 mo after treatment (MAT; cover = absolute canopy cover). Herbicide treatments were applied in September 2016 when native plants were dormant and *B. tectorum* was 100% post–seed set. Letters indicate significant within-year differences among treatment means (Tukey's honest significant difference, $\alpha = 0.05$, $n = 4$). Herbicide treatments are as follows: imazapic = imazapic 123 g ai ha^{-1}; indaziflam-low = indaziflam 44 g ai ha^{-1}; indaziflam-intermediate = indaziflam 73 g ai ha^{-1}; indaziflam-high = indaziflam 102 g ai ha^{-1}. All treatments included a 0.25% v/v nonionic surfactant. Note that *y*-axis scale is consistent across panel rows in all cases, except for *B. tectorum* density at 45 MAT (*).

at least 3 yr, particularly at intermediate and high application rates, and imazapic to provide effective short-term control (1 to 2 YAT), but not long-term control (≥2 YAT). Consistent with this expectation, intermediate and high indaziflam rates consistently reduced *B. tectorum* density and cover to very low levels at 33 and 45 MAT at both sites, and imazapic was generally effective in the near term, but *B. tectorum* density and cover were not reduced in imazapic-treated plots beyond 21 MAT (Figures 1A and B and 2A and B). Importantly, the intermediate indaziflam rate evaluated in our study aligns with the maximum single-use application rate permitted by the current grazing label (Rejuvra®, Bayer; 73 g ai ha^{-1}; USEPA 2020), suggesting that indaziflam treatment at this rate may be a powerful tool for land managers tasked with mitigating the impacts of *B. tectorum* in grazed areas.

We observed an overall decline in *B. tectorum* abundance at our sites during the study. This decline is best reflected by *B. tectorum* cover, which steadily declined in nontreated control plots at both sites over the course of the study (Figures 1B and 2B). *Bromus tectorum* density remained high in nontreated control plots through 33 MAT at both sites (592 to 1,441 m^{-2} at Site 1 and 381 to 594 m^{-2} at Site 2), but it was much lower at 45 MAT (78 m^{-2} at Site 1 and 76 m^{-2} at Site 2; Figures 1A and 2A), and *B. tectorum* was nearly absent from all plots at 57 MAT at Site 2 (data not shown). This natural decline may reflect dry spring conditions; other research has observed temporary declines in *B. tectorum* abundance at high elevations related to periodic spring drought (Smith et al. 2021). In the months leading up to sampling at 57 MAT (June 2021), spring precipitation (March to June) in nearby Pinedale, WY, was reduced

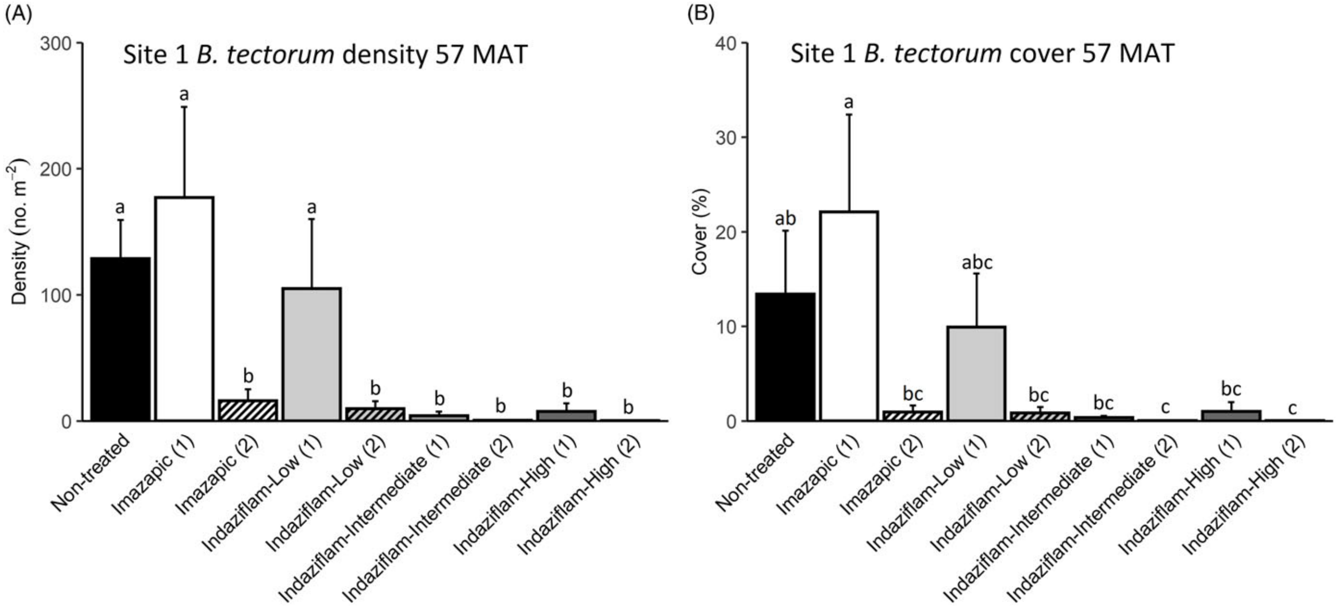

Figure 3. Mean (+1 SE) *Bromus tectorum* density (A) and *B. tectorum* cover (B) at Site 1 (Boulder Lake) at 57 mo after treatment (MAT; cover = absolute canopy cover). Treatment groups followed by a (1) received only one herbicide application, and treatment groups followed by a (2) received a sequence of two herbicide applications (diagonal line pattern). Initial herbicide treatments were applied in September 2016, and reapplications of the same treatments were made approximately 45 mo later in June 2020. Native plants were dormant and *B. tectorum* was 100% post–seed set when initial treatments were applied, and native plants were actively growing and *B. tectorum* was near 100% post–seed set when reapplication occurred. Letters indicate significant differences among treatment means (Tukey's honest significant difference, $\alpha = 0.05$, $n = 4$). Herbicide treatments are as follows: imazapic = imazapic 123 g ai ha^{-1}; indaziflam-low = indaziflam 44 g ai ha^{-1}; indaziflam-intermediate = indaziflam 73 g ai ha^{-1}; indaziflam-high = indaziflam 102 g ai ha^{-1}. All treatments (initial and reapplication) included a 0.25% v/v nonionic surfactant.

roughly 30% compared with the 30-yr mean (83 mm vs. 121 mm), with particularly dry conditions in June (4 mm vs. 31 mm; WRCC 2021).

Higher-elevation sagebrush communities are also thought to present greater challenges to *B. tectorum* invasion due to colder soil temperatures and more abundant perennial grasses (Chambers et al. 2014), and these same challenges could contribute to *B. tectorum* declines under the right circumstances. Local weed managers have noted declines in *B. tectorum* following cold spring conditions (J Kraft, personal communication), and one well-studied montane *B. tectorum* population located at a similar elevation (2,328 m) is known to have disappeared between 2005 and 2012 in Utah (Merrill et al. 2012). Both our sites are located at the same elevation (approx. 2,250 m), but the decline was more pronounced at Site 2, suggesting that elevation is likely not the only contributing factor. Differences between the sites may be related to differences in the degree of slope; both sites have south-facing aspects, but Site 1 may be slightly warmer due to its steeper slope, and this may favor *B. tectorum* by allowing it to begin growing earlier in the season, when resources are abundant and competition with native plants is minimal. We cannot completely explain the natural decline in *B. tectorum* abundance that occurred during our study, but it suggests that relatively high-elevation sagebrush-grasslands may not be highly suitable habitat for *B. tectorum* every year.

Due to the near absence of *B. tectorum* at 57 MAT at Site 2, we only analyzed *B. tectorum* cover and density after reapplication at Site 1 (Table 1). All treatments except single applications of imazapic ($P > 0.9$) and the low indaziflam rate ($P > 0.9$) reduced *B. tectorum* density compared with the nontreated control at 57 MAT ($P < 0.001$; Figure 3A), and there was no difference in *B. tectorum* density between treatment groups that received one or two applications of the intermediate and high indaziflam rates ($P > 0.9$; Figure 3A). Treatment effects on *B. tectorum* cover after reapplication were similar to those seen for density; the differences between treatment groups that received one or two applications of the intermediate and high rates of indaziflam were nonsignificant ($P > 0.9$; Figure 3B). However, *B. tectorum* cover was only reduced compared with the nontreated control at 57 MAT by two indaziflam applications at these same rates (intermediate $P = 0.028$; high $P = 0.027$; Figure 3B). Mean *B. tectorum* cover at 57 MAT was still very low in plots that received only one application of the intermediate and high rates of indaziflam (Figure 3B), but differences between these plots and the nontreated controls were only significant at the $\alpha = 0.10$ level (intermediate $P = 0.071$; high $P = 0.092$).

We expected reapplication to be necessary to maintain reductions in *B. tectorum* density and cover 3+ yr after initial treatment. This expectation was based on previous research showing that *B. tectorum* seedbanks can last 4 to 5 yr (Sebastian et al. 2017b; Young et al. 1987), and a companion study near Site 1 that detected only trace amounts of indaziflam in the soil at 37 MAT in plots treated aerially with the intermediate indaziflam rate (Courkamp et al. 2022). However, we also acknowledged that it may be possible to deplete *B. tectorum* seedbanks more quickly in some environments, because a variety of factors, including climate, fire history, and the specifics of the soil resource environment, can affect the likelihood of seed germination and seedbank longevity in the field (Baskin and Baskin 2014; Bazzaz 1996; Evans and Young 1975). One and two applications of the intermediate and high indaziflam rates resulted in comparable reductions in *B. tectorum* density and cover at 57 MAT at Site 1 (Figure 3A and B), suggesting that it may be possible to deplete *B. tectorum* seedbanks and achieve long-term control with only one herbicide application.

It is unlikely that indaziflam is still actively inhibiting *B. tectorum* at 45 and 57 MAT at our site (Courkamp et al.

2022), but if near-complete seedbank depletion occurs in the years immediately following application, control may continue until *B. tectorum* seeds disperse into treated areas from elsewhere. Further, relatively more precocious seed germination has been associated with *B. tectorum* populations collected in higher-elevation montane environments similar to our study sites (Allen and Meyer 2002; Meyer and Allen 1999), and this may promote more rapid seedbank depletion, because a greater fraction of the *B. tectorum* seeds present at the time of treatment are likely to germinate in the period of residual activity following a single application. Many factors can influence both *B. tectorum* seed longevity in field conditions (Baskin and Baskin 2014; Bazzaz 1996; Evans and Young 1975) and the likelihood of seed dispersal (e.g., Monty et al. 2013), thus we caution against assuming this outcome will be typical across different circumstances.

Our results demonstrate the potential of indaziflam for managing invasive annual grasses, but land managers should consider that our treatments were applied using a research sprayer that ensures consistent herbicide coverage in small plots. Even with this equipment, none of our treatments completely eliminated *B. tectorum*, and indaziflam is likely to be applied aerially and at much larger scales than our experimental plots. A companion study located near Site 1 (<200 m between study sites) evaluated aerial applications (helicopter) of the intermediate indaziflam rate to 2-ha plots (73 g ai ha^{-1} indaziflam with 47 L ha^{-1} of water as the carrier). Reductions in *B. tectorum* density and cover were more variable in these circumstances (Courkamp et al. 2022), suggesting that the risk of forgoing a second treatment and allowing *B. tectorum* to reestablish is worth considering. *Bromus tectorum* is known for rapid population growth (Humphrey and Schupp 2001; Perryman et al. 2020; Young and Evans 1978), and if less consistent herbicide coverage allows *B. tectorum* persistence in treated areas, it may rapidly replenish the seedbank after residual activity wanes and force land managers to start the process of depleting the seedbank for a second time. A sequence of two treatments may reduce this risk by increasing the consistency of treatment outcomes and the likelihood of achieving near-complete seedbank depletion at meaningful spatial scales, but future research is necessary to evaluate single and multiple indaziflam applications in operational settings. Land managers who use indaziflam in the near term will have to weigh the potential risk of reinvasion against the cost of indaziflam and make the best possible decision in each case given the resources available for treatment.

Perennial Grass Cover

We expected indaziflam treatments to have no observable impact on the cover of co-occurring perennial grasses based on previous research (Clark et al. 2020; Hart and Mealor 2021; Sebastian et al. 2016, 2017a). Consistent with our expectation, we did not observe any negative effects on perennial grass cover (Figures 1C and 2C). However, we observed positive effects on perennial grass cover early in the study, with perennial grass cover increasing relative to the nontreated control at 9 MAT in plots treated with imazapic and the high indaziflam rate at Site 1 (imazapic $P = 0.014$; high $P = 0.039$; Figure 1C), and plots treated with the low and high indaziflam rates at Site 2 (low $P < 0.01$; high $P = 0.024$; Figure 2C). Beyond 9 MAT, we observed no treatment effects on perennial grass cover at Site 2 ($P > 0.09$; Figure 2C), including at 57 MAT in plots where herbicide treatments were reapplied (19.8% to 32.0% mean perennial grass cover; data not shown). At Site 1, perennial grass cover was higher than in the nontreated control at 21 MAT in plots treated with the low indaziflam rate ($P = 0.026$), and the same was true at 33 MAT in plots treated with the intermediate and high indaziflam rates (intermediate $P < 0.01$; high $P = 0.015$; Figure 1C). Beyond 33 MAT, we observed no treatment effects on perennial grass cover at Site 1 ($P > 0.22$; Figure 1C), including at 57 MAT in plots where herbicide treatments were reapplied (27.0% to 40.9% mean perennial grass cover; data not shown).

Positive effects on perennial grass biomass following indaziflam treatment have been observed in some studies (Clark et al. 2020; Hart and Mealor 2021; Sebastian et al. 2017a), and resource preemption by *B. tectorum* is relatively well understood and can have substantial negative effects on perennial grass growth and vigor (Melgoza et al. 1990; Nasri and Doescher 1995; Ploughe et al. 2020). Consistent with this explanation, perennial grass cover at 33 MAT at Site 1 showed a positive response at intermediate and high indaziflam rates (Figure 1C), where *B. tectorum* density and cover were also lowest at this time (Figure 1A and B). These data support previous studies demonstrating that the positive perennial grass cover responses we observed probably resulted from reduced *B. tectorum* competition (Clark et al. 2020; Hart and Mealor 2021; Sebastian et al. 2017a).

If positive perennial grass cover responses were the result of reduced annual grass competition, it is not surprising that differences between treatments diminished over time at Site 2, where the natural decline in *B. tectorum* abundance that occurred during our study was most pronounced. At Site 1, the wildfire that occurred in August 2019 likely precluded our ability to detect treatment effects on perennial grass cover at 45 and 57 MAT. Our findings add to a growing number of studies demonstrating that indaziflam can selectively control annual grasses with minimal risk to established perennial plants (Clark et al. 2019, 2020; Fowers and Mealor 2020; Hart and Mealor 2021; Sebastian et al. 2016, 2017a; Seedorf et al. 2022), but future research should evaluate the potential for longer-term impacts to native perennials with repeated treatments. Impacts to *P. spicata* and *A. tridentata* seedlings have been observed in a grow room study (Clenet et al. 2019), and grazing managers have long understood the importance of allowing perennial grasses to complete their reproductive cycles in at least some years (Burkhardt and Sanders 2012), which suggests that the potential for longer-term impacts from repeated indaziflam treatments may be different.

We know of no published studies documenting annual grass reductions resulting from indaziflam treatment over a comparably long period of time (57 MAT), and our results reflect the variability that managers can expect to face when treating *B. tectorum* in the notoriously heterogeneous and unpredictable rangeland ecosystems of western North America (Boyd and Svejcar 2009; Svejcar et al. 2017). Land managers should be aware that short-term treatment outcomes may be inconsistent, and control may improve over time when using indaziflam alone, as was observed in our study. Seedorf et al. (2022) observed more consistent short-term (1 to 2 YAT) *B. tectorum* control when tank mixing indaziflam with imazapic compared with applying indaziflam on its own, and imazapic consistently reduced *B. tectorum* abundance at 9 MAT in our study (Figures 1A and B and 2A and B). Coupled with its selectivity against annual grasses at low use rates (Kyser et al. 2013), the short-term effectiveness of imazapic may make it a suitable tank-mix partner for indaziflam that can provide reliable short-term *B. tectorum* control.

Developing and implementing tools with the capacity to effectively manage annual grasses is critical to prevent the annual grass-fueled "downward spiral" of which researchers have long been aware (West 1983; Young and Evans 1978), and recent research suggesting that *B. tectorum* may be able to expand its dominance in higher-elevation sagebrush-grasslands only makes the necessity of confronting *B. tectorum* invasion more salient (Mealor et al. 2012; Smith et al. 2021). Expanded dominance in higher-elevation areas also suggests that the unexplained decline in *B. tectorum* abundance highlighted by our study is likely best understood as a temporary reduction in the density and cover of adult plants and not a durable transition back to a less-invaded state (Davies et al. 2021b; Smith et al. 2021). Proactive land managers seeking to preserve some of the resistance to invasion and resilience to wildfire conferred by perennial grasses may be able to use indaziflam to reduce *B. tectorum* where and when it co-occurs with these important rangeland plants, and this may represent a highly effective annual grass management strategy in sagebrush-grasslands.

While the intermediate and high indaziflam rates reduced density and cover to very low levels (Figures 1A and B and 2A and B), no treatment completely eliminated *B. tectorum*, which is notorious for its ability to rapidly recover from disturbance (Humphrey and Schupp 2001; Perryman et al. 2020; Young and Evans 1978; Young et al. 1987). The scale of *B. tectorum* invasion and the reality of limited resources for management also make it clear that *B. tectorum* needs to be managed as a permanent component of rangeland plant communities in western North America (Davies et al. 2021b; Perryman et al. 2018). In light of these challenges, future research should consider how best to prevent or delay *B. tectorum* reinvasion in treated areas and reduce the need for additional treatments after initial seedbank depletion (e.g., Davies and Sheley 2007). Researchers and land managers should also work together to determine how to best deploy indaziflam at landscape scales and combine indaziflam treatment with other practices (e.g., grazing to reduce fine fuels and safe sites for *B. tectorum* germination; Davies et al. 2016, 2021a; Perryman et al. 2020) and emerging restoration technologies (e.g., seed coatings and herbicide protection pods; Clenet et al. 2019; Holfus et al. 2021; Svejcar et al. 2022). Along with other studies (Clark et al. 2019, 2020; Hart and Mealor 2021; Sebastian et al. 2016, 2017a; Seedorf et al. 2022), our findings suggest that indaziflam may allow land managers to achieve objectives that were not feasible with other management tools and that indaziflam can play a significant role in efforts to mitigate the devastating impacts of annual grass invasion.

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