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RESEARCH ARTICLE

Herbicide effects on the establishment of a native bunchgrass in annual grass invaded areas: Indaziflam versus imazapic

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Abstract

1. Annual grass invasion is transforming the western United States and driving a need for restoration techniques that can both reduce exotic annual grass abundance and allow revegetation of native species. Pre-emergent herbicides can provide control of annual grasses, but when applied concurrently with direct seeding efforts, the herbicide can also impact seeded species. Indaziflam is a relatively new herbicide that may provide extended control of exotic annual grasses, but little is known about its effects when applied at the time of seeding.
2. In this study, we compared indaziflam to imazapic, a popular herbicide used in restoration efforts, to understand how indaziflam affects plant establishment of a native species, bluebunch wheatgrass *Pseudoroegneria spicata* (Pursh) Á. Löve. We created furrows on half our treatments to limit herbicide concentrations and potentially create a safe-site for seeding bluebunch wheatgrass.
3. During the 2-year study, indaziflam provided consistent control of the annual weed, downy brome *Bromus tectorum* L., whereas imazapic control decreased sharply with time. Indaziflam and imazapic decreased bluebunch wheatgrass seedling emergence by 96% and 46%, and 2-year plant density by 91% and 65%, respectively, compared to non-herbicide treatments. Both herbicides reduced aboveground biomass of bluebunch wheatgrass by over 85% 2 years after seeding/herbicide application.
4. Furrow treatments mitigated imazapic's effect on bluebunch wheatgrass, but did not limit the impacts by indaziflam.
5. Herbicide can be used in conjunction with direct seeding efforts, but mitigation of the effects to native seeds will depend on herbicide specifics such as mode of action and soil mobility.

KEYWORDS
bluebunch wheatgrass, Bromus tectorum, downy brome, furrow, invasive control, pre-emergent herbicide, restoration

1 | INTRODUCTION

Arid and semi-arid ecosystems comprise over one third of earth's terrestrial surface (Schlesinger et al., 1990), with many facing threat of exotic annual grass invasion (Brooks et al., 2004; D'Antonio & Vitousek, 1992). Annual grass invasions often lead to decreased plant and wildlife diversity through competition for soil moisture, accelerated fire cycles, and altered soil nutrient cycling (Bishop et al., 2019; Ehlert, 2019; Kerns & Day, 2017; Knapp, 1996; Peters & Bunting, 1994). The sagebrush steppe is an arid/semi-arid ecosystem in the United States vulnerable to invasion due to historic overgrazing (D'Antonio & Vitousek, 1992), altered fire regimes (Knapp, 1996), and fluctuations in precipitation patterns (Bradley & Mustard, 2005; Chambers et al., 2007; Davis et al., 2000). Invasion by annual grasses has transformed native plant communities in the semi-arid and arid systems such as the sagebrush steppe (Boyte et al., 2016; Chambers et al., 2007; Corbin & D'Antonio, 2004; Knapp, 1996). One prominent plant invader, downy brome *Bromus tectorum* L., is estimated to now cover more than 21 million hectares in the western United States, with an estimated 14% annual rate of spread (Bradley et al., 2018; Duncan & Clark, 2005). Innovative restoration techniques are needed to restore native vegetation to landscapes now dominated by invasive annual grasses.

Controlling invasive annual grasses proves vital to restoring native plant species, as invasives such as downy brome often outcompete native species after disturbance (St. Clair & Bishop, 2019) and quickly monopolize the seedbank, leaving a reduced opportunity for native species to re-establish (Humphrey & Schupp, 2001). Pre-emergent herbicides are commonly used to reduce downy brome abundance (Mangold et al., 2013), but when applied concurrently with seeding, this treatment can negatively impact the establishment of native shrubs (Owen, Sieg, & Gehring, 2011) and perennial grasses (Shinn & Thill, 2004). However, when herbicide effects are limited to the invasive annual grasses, herbicide can improve native plant establishment by reducing competition for resources (Eckert, 1974; Sheley, Carpinelli, & Morghan, 2007).

Seedbed preparation such as furrows could potentially mitigate harmful herbicide effects on native species (Eckert, Asher, Christensen, & Evans, 1974). If herbicide effect is lowered for non-target species, it could allow restoration seedings in systems that also need control of invasives. Usually, invasive plant control and seeding efforts occur as two events separated by many months or years, diminishing the opportunity to establish native plants in the environment with lowest invasive competition that occurs during active control efforts (Madsen, Davies, Mummey, & Svejcar, 2014). Furrows are a common practice in agriculture that improve water availability and may also have potential to limit exposure of non-target species to herbicide (Eckert et al., 1974). Creating a furrow after herbicide application side-sweeps surface soil that has been sprayed with herbicide, producing a potential safe site with low herbicide concentrations for desirable seeded species (Eckert, 1974). Furrows may also bury weed seed within the area where seeds are planted. Subsequently, this treatment may provide protection to seeded species without reducing weed control efficacy by herbicides.

Incorporating herbicide with direct seeding will require attention to specific attributes and mechanisms of the herbicide used. Imazapic is currently one of the most commonly used herbicides for invasive annual grass control on rangelands (Mangold et al., 2013). Imazapic kills plants by inhibiting activity of the enzyme acetohydroxy acid synthase (AHAS or ALS), an enzyme that is responsible for biosynthesis of the branched chain amino acids isoleucine, valine and leucine (Umbarger, 1978). Inhibiting ALS effectively starves the plant of these essential amino acids and is the herbicide's mode of action (Tranel & Wright, 2002). While imazapic provides strong control for 1 year, there is some evidence that it has limited soil residual activity, which results in inferior long-term control of invasive annual weeds (Sebastian et al., 2017a).

Short-term downy brome control poses a problem of re-invasion (Morris, Monaco, & Rigby, 2009). Long-term control is needed to decrease competition for young native plants that have been seeded and rely on spring soil moisture to survive summer heat and water stress (Melgoza, Nowak, & Tausch, 1990; Mulligan, Kirkman, & Mitchell, 2002). A new herbicide with pre-emergent action called indaziflam is now being tested for controlling annual grasses (Sebastian et al. 2017a). Indaziflam is an alkylazine herbicide that controls annual invasive grasses by inhibiting cellulose biosynthesis in susceptible species (Brabham et al., 2014). This herbicide has been shown to control downy brome up to 3 years after application (Sebastian, Sebastian, Nissen, & Beck, 2016b). Indaziflam's extended control is largely due to low soil mobility (K_{oc} = 497 mL/g OC) (Alonso, Koskinen, Oliveira, Constantin, & Mislankar, 2011; Jhala & Singh, 2012) and a longer soil half-life (>150 days) than many other pre-emergent herbicides, including imazapic (K_{oc} = 112 mL/g OC, soil half-life = 27–54 days) (Ulbrich, Souza, & Shaner, 2005).

Successful seeding efforts are commonly associated with high emergence, survival and growth of seeded species. Herbicides with pre-emergent activity can have different effects on each of these plant growth stages (Sebastian et al., 2017a, Shinn & Thill, 2004). Imazapic and indaziflam differ in their soil mobility, persistence, and mode of action, which may affect plant growth stages differently. It remains unknown if these differences make these herbicides more or less problematic for non-target injury to native species used in direct seeding efforts.

Some studies have compared invasive annual grass control by herbicide (Applestein, Germino, & Fisk, 2018; Clements, Harmon, Blank, & Weltz, 2017; Elseroad & Rudd, 2011; Sebastian, Nissen, Sebastian, Meiman, & Beck, 2017b), but few have examined potential ways to control invasive annual grasses while simultaneously allowing seeding of native species that are also susceptible to herbicide (Clark, Sebastian, Nissen, & Sebastian, 2020; Eckert et al., 1974). Here we study two herbicides that differ in mode of action, soil persistence, and soil mobility to identify potential strategies that control invasive grasses without harming native species seeded for restoration. Our first objective was to compare how these herbicides control downy brome. Our second objective was to understand how indaziflam and imazapic differentially affect a commonly seeded restoration species in the sagebrush steppe, bluebunch wheatgrass *Pseudoroegneria spicata* (Pursh) Á.

TABLE 1 Description of study sites detailing topography, climate, and soil properties of top 20 cm. MAT = mean annual temperature (30 yr. avg.) MAP = mean annual precipitation (30 yr. avg.) CEC = cation exchange capacity. Parentheses values represent percentage of 30 year mean precipitation

Site	Kious	Lehman	Provo
Slope	6%	9%	8%
Elevation (m)	2069	2041	1448
Aspect	East	Southeast	West
MAT (°C)	8.95	9.33	11.4
MAP (mm)	344.5	307.2	485.4
Lat (°N)	39.0130	38.9774	40.2479
Long (°W)	114.2154	114.1885	111.6340
2018 Precipitation (mm)	254 (64%)	236 (76%)	286 (59%)
2019Precipitation (mm)	394 (114%)	356 (115%)	659 (135%)
Soil type	Sandy loam	Sandy loam	Loam
Soil pH	5.75	6.51	7.34
Soil organic matter (%)	0.0180	3.0000	4.3000
Soil classification	Loamy-skeletal, mixed, superactive, frigid Aridic Argixerolls	Loamy-skeletal, mixed, superactive, mesic Aridic Argixerolls	Loamy-skeletal, mixed, superactive, mesic Pachic Calcixeroll
Cation exchange capacity (meq/100 g)	9.75	6.09	12.7
ppm NO_3-N	5.40	1.50	2.20

Löve. The herbicide's effect on bluebunch wheatgrass was assessed by measuring changes to seedling emergence, as well as plant density and aboveground biomass of established plants 2 years after planting. The third objective of this study was to determine if we could simultaneously reduce downy brome densities with herbicide while protecting our seeded species, bluebunch wheatgrass. We hypothesized that (1) indaziflam would provide superior downy brome control over a 2-year period based on results from other studies; (2) indaziflam would be more lethal to bluebunch wheatgrass than imazapic due to its low soil mobility and longer soil half-life; (3) the side sweep action of furrow creation would reduce herbicide effects by indaziflam on bluebunch wheatgrass more than imazapic due to indaziflam's lower soil mobility.

2 | MATERIALS AND METHODS

2.1 | Study sites

This study was conducted at three sites in the sagebrush steppe during 2017–2019. Two sites were located in the boundaries of Great Basin National Park, Nevada, USA, and the third site is located in Provo, Utah, USA. Sites varied in slope, elevation, soil characteristics and invasion extent (Table 1). Elevation between sites was 1448 m at the Provo site (Utah), 2013 m at Lehman flats site (Nevada), and 2135 m at the Kious Basin site (Nevada). Soils types across sites varied from stoney sandy loam (Lehman flats), to gravelly sandy loam (Kious basin) and gravelly loam (Provo). Downy brome comprised 40–80% relative herbaceous canopy cover at all sites. Vegetation at the Nevada sites was dominated by downy brome, but also contained several native species: *Elymus elymoides* Nutt., *Artemesia, tridentate* spp., *Pinus monophyla* Torr. & Frem., *Gutierrezia sarothrae* Pursh, and *Purshia tridentate* Pursh. Vegetation at the Provo site did not contain any abundant native species and consisted largely of downy brome and *Aegilops cylindrica* Host. Precipitation at the sites in 2018 consisted of an average spring (93–136% prcp. of 30 yr. avg.) and a dry summer (62–102% prcp. of 30 yr. avg.). In 2019 the precipitation consisted of a very wet spring (160–178% prcp. of 30 yr. avg.) and dry summer (46–51% prcp. of 30 yr. avg.) (DAYMET gridded climate dataset) (Thornton et al., 2014).

2.2 | Experimental design

Research plots were installed between 30 October 2017 and 5 November 2017. We tested establishment and growth of bluebunch wheatgrass in response to herbicide treatment using a 3 × 2 full factorial design. We had three herbicide treatments: imazapic, indaziflam, and no herbicide, accompanied by two post-herbicide planting methods: planting within a furrow and planting without a furrow. We created five replicate blocks, with each block was split into three sub-blocks, one treated with imazapic, one treated with indaziflam and one receiving no herbicide (Figure 1). Spatial arrangement of sub-block was randomized within each block. Immediately following herbicide applications, numbered markers were placed to designate rows for seeding. Furrows were created in half of the rows within each sub-block, and seeds were planted in both furrowed and non-furrowed rows. Each combination of seed and furrow (seed only, seed + furrow, furrow only and no seed or furrow) was replicated three times as

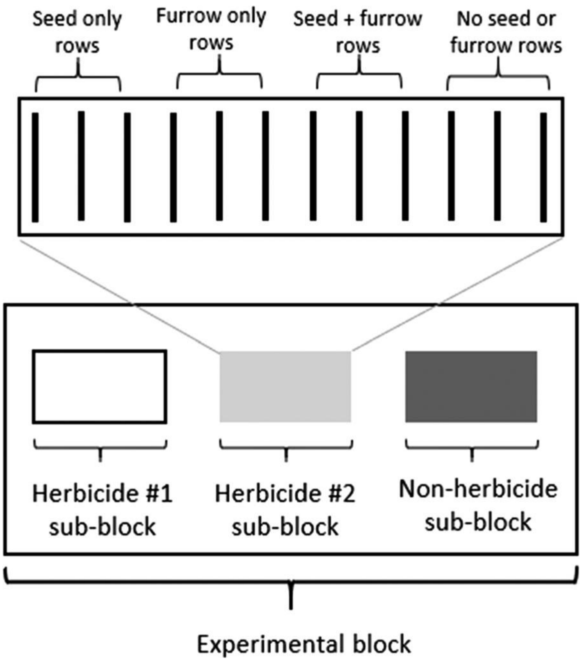

FIGURE 1 Experimental design of one study block

side-by-side rows in each herbicide treatment (sub-block) (Figure 1). Each sub-block measured 4.2 m long and 1 m wide. Within each block, the three sub-blocks were spaced 1.5 m apart to isolate herbicide effects and produced blocks that measured 15 m long × 1 m wide.

2.3 | Herbicide application

Herbicide treatments were applied as follows: no herbicide treatment (control), a mixture of imazapic and glyphosate at respective rates of 3.66 and 8.77 mL per 100 m^2 (350 and 840 a.e. per ha) and a mixture of indaziflam and glyphosate at the rates of 3.66 and 8.77 mL per 100 m^2 (350 and 840 a.e. per ha). Application rates were determined by label recommendations for downy brome control. Despite glyphosate being a part of both imazapic and indaziflam mixtures, they will be referred to as imazapic and indaziflam in the remainder of the study for simplicity and because they are the herbicides with pre-emergent capabilities that affect germination of the seeded native species. Herbicide was applied using a calibrated electric backpack sprayer that maintained a flow rate 1.9 L/min (model number: 63985, Chapin, Batavia, NY, USA). We used a single poly fan nozzle at an 80° angle. Herbicide was mixed to exceed the minimum carrier rate (minimum quantity of herbicide mixture per area) of 9 mL/m^2, being applied at a rate of 68 mL/m^2. Application was made using 15 s walks through each sub-block that was timed by a second researcher. A herbicide mixture was determined to deliver the correct rate of herbicide given the area of the sub-block, and the flow rate of the backpack sprayer. The flow rate was verified in the lab and the field using 15 s sprays into volumetric flasks. Herbicide application occurred on days with little to no wind, abundant sun and daily maximum temperatures exceeding 15–20°C.

2.4 | Furrows and planting

Furrows were created immediately following herbicide application. Furrows were 15 cm deep from soil surface and 35 cm wide. The depth and width were chosen based on the furrow creation capabilities on large-scale seedings with drill seeders using cultivator sweeps. Soil was excavated from the furrow with a garden hoe, placing the soil removed from the furrow in mounds between rows in efforts to replicate furrows created by cultivator sweeps in restoration settings. All rows (furrowed and non-furrowed) were spaced 35 cm apart and 1.2 m long. Bluebunch wheatgrass seeds were hand planted in the rows 1 cm below the soil surface (control) and covered with soil surrounding the seed (treated with herbicide) or covered in the bottom of the furrow with 1 cm of soil from the bottom of the furrow (untouched by herbicide). The seeding rate was doubled to account for harsh soil conditions as recommended by the USDA plant guide for bluebunch wheatgrass. Seeding occurred at all sites between 30 October 2017 and 5 November 2017 at a rate of 131 pure live seed per metre. Seeds were of the Anatone variety and were purchased from a commercial seed supplier (Granite Seed, Lehi, UT, USA) that obtained them from eastern Washington.

2.5 | Plant measurements

Bluebunch wheatgrass seedling emergence was characterized at the end of April 2018 by individually counting all live seedlings in each row of the entire plot. Bluebunch wheatgrass aboveground biomass was sampled and dried in late August 2019, 2 years after the initial planting. Biomass samples were collected by clipping all aboveground biomass at ground level. Downy brome cover was measured visually during the last week of May 2018 and May 2019. The bluebunch wheatgrass density was counted simultaneously as biomass was destructively sampled. Both bluebunch wheatgrass plant density and aboveground biomass were sampled once, 2 years after planting. All bluebunch wheatgrass sampling was done on the centre row of three side-by-side replicate rows to limit edge effect.

Downy brome cover estimates were made visually to the nearest 1% using a circular metal hoop (Bonham, Mergen, & Montoya, 2004). The hoop used was 1 m in diameter and placed over three side-by-side rows of the same treatment. The percentage of total ground area occupied by downy brome within the hoop was estimated visually using the total hoop area to the nearest percentage. These hoops were placed in the same position during both years of the study. Downy brome cover values were estimated for each treatment (four per sub-block) averaged to the sub-block level such that each herbicide treatment had one statistical repetition at the block level.

2.6 | Statistical methods

We used a mixed model linear regression for analysis of bluebunch wheatgrass and downy brome responses in our study. All analyses were done in R version 3.4.2 (R Core Team, 2019). Response variables for bluebunch wheatgrass were emergence (counts), plant density (plants per m^2) and total aboveground biomass (g/m^2). Fixed variables for each bluebunch wheatgrass model were herbicide type (imazapic, indaziflam, no herbicide), furrows and their interaction (furrow × imazapic, furrow × indaziflam). Random variables for all of the models were site and block, with block nested within site. Bluebunch wheatgrass plant density and emergence were both analysed using a Poisson error distribution with a log link function. Aboveground biomass was analysed using a normal distribution with a log transformation of the response variable. Data from all models met model assumptions for homogeneity of variance. Data from the Provo site includes only data for bluebunch wheatgrass seedling emergence and downy brome cover due to harsh drought conditions that killed all seedlings and resulted in no bluebunch wheatgrass plants in any sub-block after 2 years.

Response variables for downy brome were first- and second-year canopy cover. Herbicide type was the only fixed effect with three levels (imazapic, indaziflam and no herbicide). Random effects for downy brome analysis include block and site with block nested within site.

Pairwise comparisons of the bluebunch wheatgrass responses were done using a mixed linear model with a Tukey–Kramer adjustment. The model used the categorical treatments (no herbicide or furrow, imazapic, indaziflam, no herbicide with furrow, imazapic with furrow, indaziflam with furrow) as the fixed effects. Random effects were site and block, with block nested within site. Pairwise comparisons for downy brome were done exactly as the bluebunch pairwise comparisons, but the fixed effects were the three herbicide treatments.

3 | RESULTS

3.1 | Downy brome control

Imazapic and indaziflam reduced downy brome cover by 88% (to 4% cover) and 70% (to 10% cover) ($p < 0.001$) compared to non-herbicide control plots after 1 year (Figure 2). Despite imazapic providing stronger control than indaziflam in the first year, indaziflam provided superior control by year two (spring 2019) (Figure 2). Indaziflam maintained 70% downy brome control throughout the 2-year period ($p < 0.001$), whereas imazapic downy brome control decreased from 88% control in the first year, to only 20% in the second year ($p = 0.11$) (Figure 2).

3.2 | Bluebunch wheatgrass emergence

Imazapic and indaziflam application decreased bluebunch wheatgrass seedling emergence 46% and 96% compared to non-herbicide plots ($p < 0.001$) (Figure 3(a), Table 2). In non-herbicide plots, furrow treatments increased bluebunch wheatgrass emergence 32% ($p < 0.001$) compared to non-furrow treatments. Furrows reduced negative imazapic effects on bluebunch wheatgrass emergence such that seedling emergence observed in the imazapic + furrow treatments was the same as non-herbicide plots ($p = 0.99$) (Figure 3). This is further

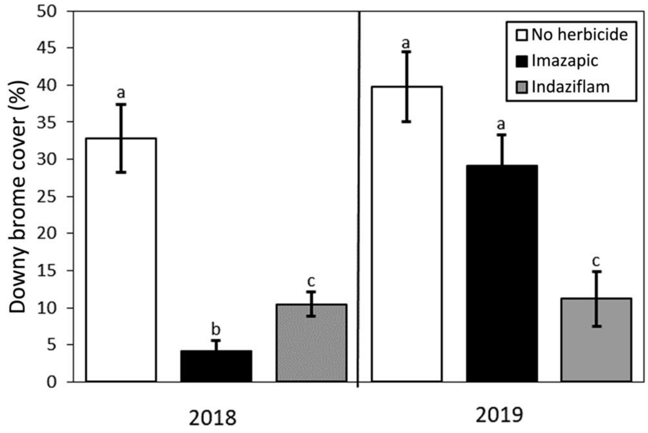

FIGURE 2 Absolute cover percentages of *downy brome Bromus tectorum* after a 2017 fall application of two pre-emergent herbicides (imazapic and indaziflam) and no herbicide at three sites in the sagebrush steppe. Letters indicate significant ($p < 0.1$) difference with comparisons made across other herbicide treatments of both years

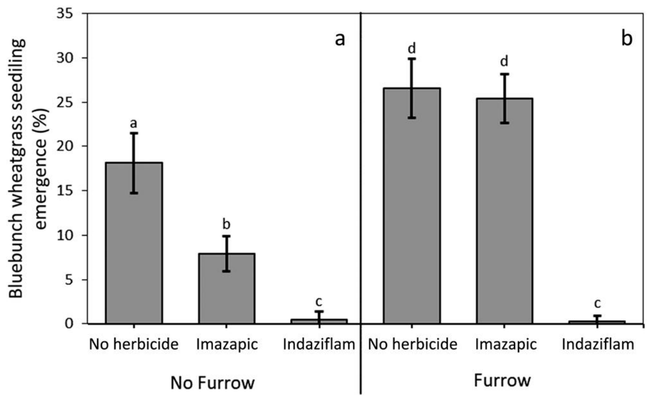

FIGURE 3 Seedling emergence (%) of *bluebunch wheatgrass Pseudoroegneria spicata* when planted in different herbicide-treated areas (imazapic, indaziflam and no herbicide) without furrows (a) and with furrows (b) at three sites in the sagebrush steppe. Letters indicate significant ($p < 0.1$) difference with comparisons made across all treatments (non-furrow and furrow)

indicated by the significant interaction between imazapic and furrow treatments (Table 2). In contrast, furrows did not protect bluebunch wheatgrass seeds from indaziflam, resulting in low seedling emergence that was unchanged with furrow treatments (Figure 3). Indaziflam also negated the positive furrow effect seen in non-herbicide plots as indicated by the negative indaziflam by furrow interaction coefficient (Table 2).

3.3 | Bluebunch wheatgrass plant density

Imazapic and indaziflam reduced bluebunch wheatgrass plant density 65% and 91% compared to non-herbicide controls ($p < 0.001$) (Figure 4(a), Table 2). Furrow treatments did not affect plant density in non-herbicide treatments (Table 2). Furrow treatments

TABLE 2 Summary of statistical regressions for all response variables. Mean and standard error values represent the mean of individual treatments for each response variable. Data comprises 2 years of data at three sites in the sagebrush steppe system. Degrees of freedom are excluded from our seedling emergence and plant density data due to the nature of mixed model regression with a Poisson error distribution

		Downy brome (*B. tectorum*)				
		Estimate	Standard error	DF	*T* value	Pr(> |*t*|)
First year cover (%)	Intercept (no herbicide)	5.50	0.59	3	9.29	0.004
	Imazapic	−3.93	0.41	40	−9.79	3.50E−12
	Indaziflam	−2.41	0.41	40	−6.01	4.60E−07
Second year cover (%)	Intercept (no herbicide)	6.15	0.45	9	13.75	1.40E−07
	Imazapic	−0.94	0.58	40	−1.62	0.11
	Indaziflam	−3.36	0.58	40	−5.81	8.70E−07
		Bluebunch wheatgrass (*P. spicata*)				
		Estimate	Standard error	DF	*Z* Value	Pr(> |*z*|)
Seedling emergence (#)	Intercept (seed only)	3.09	0.16	–	19.16	2.00E−16
	Imazapic	−0.68	0.09	–	−7.47	8.00E−14
	Indaziflam	−1.66	0.13	–	−12.53	2.00E−16
	Furrow	0.42	0.07	–	6.14	8.10E−10
	Imazapic × Furrow	0.75	0.11	–	6.89	5.50E−12
	Indaziflam × Furrow	−0.38	0.18	–	−2.06	0.04
		Estimate	Standard error	DF	*Z* Value	Pr(> |*z*|)
Plant density (plants/mš)	Intercept (seed only)	1.43	0.16	–	8.94	2.00E−16
	Imazapic	−0.91	0.29	–	−3.15	0.001
	Indaziflam	−1.34	0.34	–	−3.96	7.57E−05
	Furrow	−0.01	0.22	–	0.01	0.999
	Imazapic × Furrow	0.63	0.37	–	1.71	0.088
	Indaziflam ×Furrow	−0.45	0.53	–	-0.85	0.394
		Estimate	Standard error	DF	*T* Value	Pr(> |*t*|)
Aboveground Biomass (g)	Intercept (Seed Only)	1.15	0.25	54	4.66	2.13E−05
	Imazapic	−0.87	0.35	54	−2.49	0.016
	Indaziflam	−0.77	0.35	54	−2.21	0.031
	Furrow	−0.06	0.35	54	−0.16	0.875
	Imazapic ×Furrow	1.32	0.49	54	2.67	0.01
	Indaziflam × Furrow	−0.05	0.49	54	−0.11	0.915

mitigated the imazapic herbicide effect on bluebunch wheatgrass plant density, producing similar densities as non-herbicide treatments (Figure 4(b)). Furrows did not mitigate indaziflam herbicide effects on bluebunch wheatgrass plant density, resulting in similar low seedling emergence as indaziflam treatments without a furrow (Figure 4).

3.4 | Bluebunch wheatgrass biomass

Imazapic and indaziflam herbicide treatments reduced bluebunch wheatgrass aboveground biomass by over 98% after two growing seasons when planted without a furrow ($p < 0.001$) (Figure 5(a), Table 2). In the absence of herbicide, furrows did not significantly affect aboveground biomass of bluebunch wheatgrass compared to non-furrowed rows (Table 2). In herbicide applications, however, furrows mitigated the negative imazapic effects on aboveground growth, as indicated by the imazapic by furrow interaction. Furrow treatments within imazapic-treated plots produced 14-fold more aboveground biomass than non-furrow treatments in imazapic-treated plots ($p < 0.001$) (Figure 5, Table 2). Furrows in indaziflam treatments did not protect plants, as indicated by the lack of an interaction between indaziflam and furrow, resulting in very little aboveground biomass (Figure 5, Table 2).

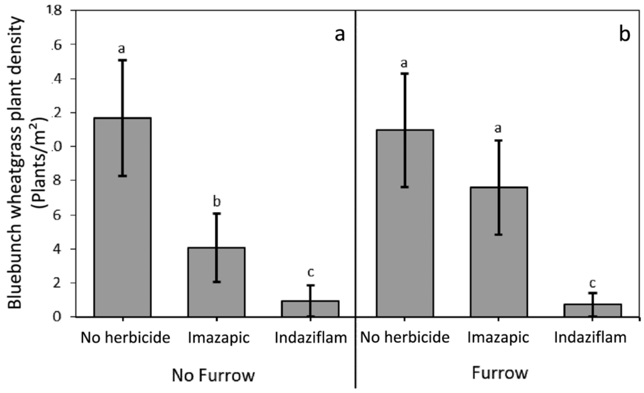

FIGURE 4 Average plant density (plants/m^2) of *Pseudoroegneria spicata (bluebunch wheatgrass)* after 2 years when planted in different herbicide-treated areas (imazapic, indaziflam, and no herbicide) without furrows (a) and with furrows (b) at two sites in the sagebrush steppe. Letters indicate significant ($p < 0.1$) differences with comparisons made across all treatments (non-furrow and furrow)

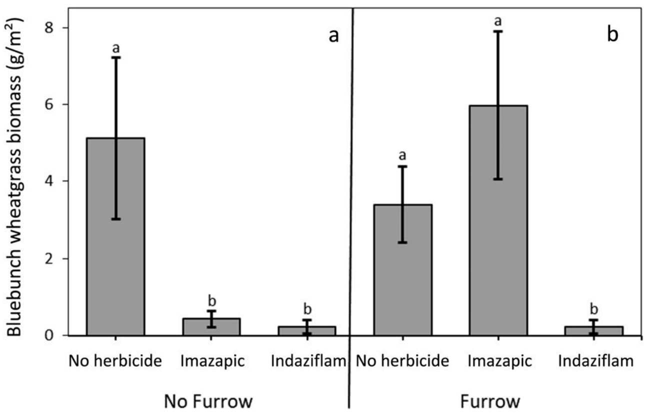

FIGURE 5 Aboveground biomass (g/m^2) of *Pseudoroegneria spicata* (bluebunch wheatgrass) after 2 years growth when planted in different herbicide-treated areas (imazapic, indaziflam, and no herbicide) without furrows (a) and with furrows (b) at two sites in the sagebrush steppe. Letters indicate significant ($p < 0.1$) differences with comparisons made across all treatments (non-furrow and furrow)

4 | DISCUSSION

Herbicide treatments had large effects on bluebunch wheatgrass and downy brome, which differed depending on herbicide type (Figure 3). Our results support our first hypothesis that indaziflam would provide better downy brome control 2 years after application, despite stronger control by imazapic in the first year. Our results partially support our second hypothesis. Without a furrow treatment, imazapic was less detrimental to bluebunch wheatgrass plant density than indaziflam (Figure 4 (a), but both imazapic and indaziflam applications resulted in similar bluebunch wheatgrass aboveground biomass (Figure 5(a). Our data do not support our third hypothesis, creating a furrow to limit herbicide effect on our planted seed was more effective with imazapic and showed no benefit when used with indaziflam.

4.1 | Herbicide effects on downy brome

Reinvasion of areas treated with imazapic occurred quickly, with downy brome recovering 2 years after the initial application (Figure 2). Imazapic is a strong control agent immediately following application, but due to higher soil mobility and a shorter soil half-life it may not completely control downy brome 1–2 years after application (Sebastian, Nissen, & De Souza Rodrigues, 2016a). We anticipate that reinvasion happened more quickly in our study system than it would in a large-scale imazapic application in post-fire conditions. Our herbicide treatments were only applied to the area where seed was planted, allowing large downy brome stands to grow at the edge of the herbicide-treated rows. This resulted in high propagule pressure, a major factor in invasion rates (Chambers et al., 2016; St. Clair & Bishop, 2019). In a large-scale application, high invasive propagule pressure occurs mostly near edges, whereas our small plots experienced pressure across the entire herbicide-treated area.

Indaziflam provided better long-term downy brome control than imazapic (Figure 2). As briefly described above, indaziflam has moderate to low mobility (Alonso et al., 2011) and readily persists in soil (Jhala & Singh, 2012). Comparatively, indaziflam has a longer half-life in soil than imazapic (>75 days) along with a significant residual activity that likely extends the duration of weed control (De Barreda, Reed, Yu, & Mccullough, 2013). With low soil mobility and high residual activity, indaziflam is well equipped to provide several years of downy brome control, a species that has high seed production (Hempy-Mayer & Pyke, 2008).

4.2 | Herbicide effects on bluebunch wheatgrass

Both herbicides reduced bluebunch wheatgrass aboveground biomass similarly after 2 years of growth in areas without furrows (Figure 5), but imazapic was less detrimental to plant density and seedling emergence than indaziflam (Figures 3 and 4). The reason imazapic was equally detrimental to aboveground growth compared to indaziflam, while being less detrimental to plant density and seedling emergence than indaziflam may be due to their different control mechanisms. Indaziflam reduces growth by inhibiting cellulose synthesis (Brabham et al., 2014), whereas imazapic kills by inhibiting synthesis of branched-chain amino acids (Tranel & Wright, 2002). Many seeds treated with imazapic emerged and survived but did not grow into large plants. We anticipate that many of the seeds survived the negative effects of imazapic (inhibited amino acid synthesis), but that the legacy effects from hindered early growth resulted in smaller plants after 2 years. Beyond reducing seedling emergence of the seeded species, herbicide legacy effects of imazapic and indaziflam applications may also affect perennial bunchgrass seeds in the native seedbank.

4.3 | Furrow effects

Furrow treatments improved emergence dramatically (Figure 3) in non-herbicide treatments, but the growth effect did not persist into the second year (Figures 4 and 5). High emergence of bluebunch wheatgrass may have led to increased intra-specific competition and resulted in reduced plant growth. A meta-analysis showed that intraspecific competition in grasses is four- to fivefold stronger than interspecific competition (Adler et al., 2018), though interspecific competition could also have reduced bluebunch wheatgrass growth due to fast reinvasion rates of downy brome in the imazapic sub-blocks and within non-herbicide sub-blocks. Also, furrows can slough in over time, potentially burying small seedlings.

Furrow treatments reduced herbicide effect on all stages of bluebunch wheatgrass growth in imazapic treatments but provided no protection in indaziflam treatments (Figures 3–5). We anticipate this difference is either due to (1) bluebunch wheatgrass physiology being more sensitive to indaziflam than imazapic or (2) the difference in soil mobility between the two herbicides is making the furrow treatment less effective in herbicide removal for indaziflam. The first possible explanation is supported by our emergence data outside of furrows, where indaziflam application resulted in less than 1% seedling emergence whereas imazapic application produced 8% emergence (Figure 3). In a study comparing the effects of indaziflam to imazapic, indaziflam caused higher invasive seed mortality than imazapic at the same rate (Sebastian et al., 2017a), but no study to date compares the effects of indaziflam to imazapic when seeding occurs simultaneously with herbicide application. One explanation of their different lethality towards invasives (and potentially seeded species) is the different mode of action each herbicide uses to kill plants. Herbicides inhibiting amino acid synthesis, such as imazapic, are slow to show visible injury to plants (Devlin & Cunningham, 1970). The mode of action of indaziflam, however, can act very quickly (Brabham et al., 2014). The complexity of cellulose biosynthesis makes it vulnerable to attack by indaziflam and may have more immediate negative effects than imazapic.

The second explanation that differing soil mobility of the two herbicides interact differently with the furrow is conceptually possible, where the two herbicides vary largely in their soil mobility. Herbicide with less soil mobility may affect seeds as the furrows sluff in over time, or more mobile herbicides could move to the soil surrounding the seed due to leaching after precipitation. Indaziflam is much less mobile than imazapic, largely due to lower water solubility (2.8 mg/L) and higher adsorption into organic matter than is seen with imazapic (Alonso et al., 2011; Sebastian et al., 2017a). Imazapic does not move much laterally but does leach vertically (De Souza, Ferreira, Da Silva, Ruiz, & Prates, 2000), so the vertical movement of imazapic away from the furrow may isolate furrow bottoms from the leaching pathway of imazapic. Whereas indaziflam, being less mobile, may persist in the upper soil longer (Perry, McElroy, Doroh, & Walker, 2011), leaching less than imazapic, and affect the seeds as the furrows sluff over time from wind and water erosion.

4.4 | Implications and recommendations

Here we show that pre-emergent herbicide may have a place in restoration seeding efforts. If pre-emergent herbicide injury can be limited to target species, invasive annual competition on seeded species is reduced to produce larger plants of seeded species at early growth stages. In general, restoration efforts including pre-emergent herbicides are challenging; the characteristics of indaziflam that lead to longer downy brome control than imazapic, also make it difficult to reduce injury to species seeded concurrently with herbicide efforts. In contrast, imazapic injury to seeded species can be limited, but downy brome control is short, resulting in eventual reinvasion.

Our results suggest that indaziflam applications strongly limit restoration of a native species (or potentially a native bunchgrass seedbank), and that it is likely best suited for control of invasive annual grasses alone. Sebastian et al. (2017) showed that indaziflam application to sites with mature native vegetation increased native species growth and provided three or more years of annual grass control. Imazapic can be used in restoration seeding efforts as long as measures are taken to limit seed exposure to the herbicide. To achieve long-term annual invasive grass control on restoration seeding sites, imazapic application alone will not suffice. One potential option is to apply imazapic prior to seeding, plant in a furrow made after herbicide application and then apply indaziflam 2 years later. Another option would be to wait (2–5 years) until the indaziflam activity level has decreased, and then seed native species. One study showed success seeding in the fall following a spring application of indaziflam (Clark et al., 2020). Both approaches could potentially lead to restoration seeding success, and long-term invasive annual grass control, but waiting to seed several years after herbicide application could potentially result in large areas of bare ground and eventual erosion on sloped or high wind areas. Our results show comparative effects of indaziflam and imazapic at sites that contain soils that are often found in the sagebrush steppe system, but herbicide mobility and persistence could vary when applications take place on soils with different organic matter, texture, annual rainfall and pH.

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AUTHORS' CONTRIBUTIONS

TT wrote the manuscript, collected and analysed the data; MM and SSC came up with the idea, helped with analysis and helped write the manuscript; RG and VA helped with experimental design and interpretation of results.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad digital repository [https://doi.org/10.5061/dryad.hdr7sqvgz] (Terry, Madsen, Gill, Anderson, & Clair, 2021)

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REFERENCES

Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, Meiners J. M., Tredennick A. T., & Veblen, K. E. (2018). Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. *Ecology Letters*, *21*(9), 1319–1329. https://doi.org/10.1111/ele.13098

Alonso, D. G., Koskinen, W. C., Oliveira JR., R. S., Constantin, J., & Mislankar, S. (2011). Sorption-desorption of indaziflam in selected agricultural soils. *Journal of Agricultural and Food Chemistry*, *59*, 13096–13101. https://doi.org/10.1021/jf203014g

Applestein, C., Germino, M. J., & Fisk, M. R. (2018). Vegetative community response to landscape-scale post-fire herbicide (imazapic) application. *Invasive Plant Science and Management*, *11*(3), 127–135. https://doi.org/10.1017/inp.2018.18

Bishop, T. B. B., Munson, S., Gill, R. A., Belnap, J., Petersen, S. L., & (2019). & St. Clair, S. B. Spatiotemporal patterns of cheatgrass invasion in Colorado Plateau National Parks. *Landscape Ecology*, *34*, 925–941 https://doi.org/10.1007/s10980-019-00817-8

Bonham, C. D., Mergen, D. E., & Montoya, S. (2004). Plant cover estimation: A contiguous Daubenmire frame. *Rangelands*, *26*, 17–22.

Boyte, S. P., Wylie, B. K., & Major, D. J. (2016). Cheatgrass percent cover change: Comparing recent estimates to climate change— driven predictions in the northern Great Basin. *Rangeland Ecology & Management*, *69*, 265–279. https://doi.org/10.1016/j.rama.2016.03.002

Brabham, C., Lei, L., Gu, Y., Stork, J., Barrett, M., & Debolt, S. (2014). Indaziflam herbicidal action: A potent cellulose biosynthesis inhibitor. *Plant physiology*, *166*, 1177–1185. https://doi.org/10.1104/pp.114.241950

Bradley, B. A., & Mustard, J. F. (2005). Identifying land cover variability distinct from land cover change: Cheatgrass in the Great Basin. *Remote Sensing of Environment*, *94*, 204–213. https://doi.org/10.1016/j.rse.2004.08.016

Bradley, B. A., Curtis, C. A., Fusco, E. J., Abatzoglou, J. T., Balch, J. K., Dadashi, S., & Tuanmu, M. N. (2018). Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. *Biological Invasions*, *20*, 1493–1506. https://doi.org/10.1007/s10530-017-1641-8

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., Hobbs, R. J., Pellant, M., & Pyke, D. (2004). Effects of invasive alien plants on fire regimes. *BioScience*, *54*, 677–688.

Chambers, J. C., Roundy, B. A., Blank, R. R., Meyer, S. E., & Whittaker, A. (2007). What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, *77*, 117–145. https://doi.org/10.1890/05-1991

Chambers, J. C., Germino, M. J., Belnap, J., Brown, C. S., Schupp, E. W., & (2016). & St. Clair S. B. Plant community resistance to invasion by Bromus species: The roles of community attributes, Bromus interactions with plant communities, and Bromus traits. In: M. J. Germino, J. C. Chambers, & C. S. Brown (Eds.), *Exotic brome-grasses in arid and semiarid ecosystems of the Western US* (pp. 275–304). Springer. https://doi.org/10.1007/978-3-319-24930-8_10

Clark, S. L., Sebastian, D. J., Nissen, S. J., & Sebastian, J. R. (2020). Evaluating winter annual grass control and native species establishment following applications of indaziflam on rangeland. *Invasive Plant Science and Management*, *13*, 1–11. https://doi.org/10.1017/inp.2020.23

Clements, C. D., Harmon, D. N., Blank, R. R., & Weltz, M. (2017). Improving seeding success on cheatgrass-infested rangelands in Northern Nevada. *Rangelands*, *39*(6), 174–181. https://doi.org/10.1016/j.rala.2017.10.003

Corbin, J. D., & D'Antonio, C. M. (2004). Competition between native perennial and exotic annual grasses: Implications for an historical invasion. *Ecology*, *85*, 1273–1283. https://doi.org/10.1890/02-0744

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics*, *23*, 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*, 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

De Barreda, D. G., Reed, T. V., Yu, J., & Mccullough, P. E. (2013). Spring establishment of four warm-season turfgrasses after fall indaziflam applications. *Weed Technology*, *27*, 448–453. https://doi.org/10.1614/WT-D-12-00168.1

De Souza, A., Ferreira, F., Da Silva, A., Ruiz, H., & Prates, H. (2000). Glyphosate and imazapyr leaching in soils with different textures and chemical composition. I-Bioassay method. *Planta Daninha*, *18*, 5–15. https://doi.org/10.1590/S0100-83582000000100001

Devlin, R. M., & Cunningham, R. P. (1970). The inhibition of gibberellic acid induction of α-amylase activity in barley endosperm by certain herbicides. *Weed Research*, *10*, 316–320. https://doi.org/10.1111/j.1365-3180.1970.tb00959.x

Duncan, C., & Clark, J. (2005). *Invasive plants of range and wildlands and their environmental, economical and societal impacts*. Weed Science Society of America.

Eckert, R. E. (1974). Atrazine residue and seedling establishment in furrows. *Journal of Range Management*, *27*, 55–56.

Eckert, R. E., Asher, J. E., Christensen, M. D., & Evans, R. A. (1974). Evaluation of the atrazine-fallow technique for weed control and seedling establishment. *Journal of Range Management*, *27*, 288–292.

Ehlert, K. A., Mangold, J. M., Menalled, F., Miller, Z., & Dyer, A. (2019). Seeding, herbicide, and fungicide impact on perennial grass establishment in cheatgrass infested habitats. *Ecological Restoration*, *37*(2), 67–70.Retrieved from https://www.muse.jhu.edu/article/725204

Elseroad, A. C., & Rudd, N. T. (2011). Can imazapic increase native species abundance in cheatgrass (*Bromus tectorum*) invaded native plant communities? *Rangeland Ecology & Management*, *64*, 641–648. https://doi.org/10.2111/REM-D-10-00163.1

Hempy-Mayer, K., & Pyke, D. A. (2008). Defoliation effects on *Bromus tectorum* seed production: Implications for grazing. *Rangeland Ecology & Management*, *61*, 116–123. https://doi.org/10.2111/07-018.1

Humphrey, L., & Schupp, E. (2001). Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist*, *61*(1), 85–92.Retrieved from http://www.jstor.org/stable/41717080

Perry, D. H., McElroy, J. S., Doroh, M. C., & Walker, R. (2011). Indaziflam utilization for controlling problematic turfgrass weeds. *Applied Turfgrass Science*, *8*, 1–7. https://doi.org/10.1094/ATS-2011-0428-01-RS

Jhala, A. J., & Singh, M. (2012). Leaching of indaziflam compared with residual herbicides commonly used in Florida citrus. *Weed Technology*, *26*, 602–607. https://doi.org/10.1614/WT-D-11-00161.1

Kerns, B. K., & Day, M. A. (2017). The importance of disturbance by fire and other abiotic and biotic factors in driving cheatgrass invasion varies based on invasion stage. *Biological Invasions*, *19*, 1853–1862. https://doi.org/10.1007/s10530-017-1395-3

Knapp, P. A. (1996). Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin desert: History, persistence, and influences to human activities. *Global environmental change*, *6*, 37–52. https://doi.org/10.1016/0959-3780(95)00112-3

Madsen, M. D., Davies, K. W., Mummey, D. L., & Svejcar, T. J. (2014). Improving restoration of exotic annual grass-invaded rangelands through activated carbon seed enhancement technologies. *Rangeland Ecology and Management*, *67*, 61–67. https://doi.org/10.2111/REM-D-13-00050.1

Mangold, J., Parkinson, H., Duncan, C., Rice, P., Davis, E., & Menalled, F. (2013). Downy brome (*Bromus tectorum*) control with imazapic on Montana grasslands. *Invasive Plant Science and Management*, *6*(4), 554–558. https://doi.org/10.1614/IPSM-D-13-00016.1

Melgoza, G., Nowak, R. S., & Tausch, R. J. (1990). Soil water exploitation after fire: Competition between Bromus tectorum (cheatgrass) and two native species. *Oecologia*, *83*, 7–13. https://doi.org/10.1007/BF00324626

Morris, C., Monaco, T. A., & Rigby, C. W. (2009). Variable impacts of imazapic rate on downy brome (Bromus tectorum) and seeded species in two rangeland communities. *Invasive Plant Science and Management*, *2*, 110–119. https://doi.org/10.1614/IPSM-08-104.1

Mulligan, M. K., Kirkman, L. K., & Mitchell, R. (2002). *Aristida beyrichiana* (wiregrass) establishment and recruitment: Implications for restoration. *Restoration Ecology*, *10*, 68–76. https://doi.org/10.1046/j.1526-100X.2002.10107.x

Owen, S., Sieg, C., & Gehring, C. (2011). Rehabilitating downy brome (*Bromus tectorum*)-invaded shrublands using imazapic and seeding with native shrubs. *Invasive Plant Science and Management*, *4*(2), 223–233. https://doi.org/10.1614/IPSM-D-10-00054.1

Peters, E. F., & Bunting, S. C. (1994). Fire conditions pre-and post-occurrence of annual grasses on the Snake River Plain. In: S. B. Monsen & S. G. Kitchen compsProceedings–Ecology and Management of Annual Rangelands; Boise, ID. Gen Tech. Rep. INT-GTR-313. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Citeseer.

R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Hueneke, L. F., Jarrell, W. M., Virginia, R. A., & Whitford, W. G. (1990). Biological feedbacks in global desertification. *Science*, *247*, 1043–1048. https://doi.org/10.1126/science.247.4946.1043

Sebastian, D. J., Nissen, S. J., & De Souza Rodrigues, J. (2016a). Preemergence control of six invasive winter annual grasses with imazapic and indaziflam. *Invasive Plant Science and Management*, *9*, 308–316. https://doi.org/10.1614/IPSM-D-16-00045.1

Sebastian, D. J., Sebastian, J. R., Nissen, S. J., & Beck, K. G. (2016b). A potential new herbicide for invasive annual grass control on rangeland. *Rangeland Ecology & Management*, *69*, 195–198. https://doi.org/10.1016/j.rama.2015.11.001

Sebastian, D. J., Fleming, M. B., Patterson, E. L., Sebastian, J. R., & Nissen, S. J. (2017a). Indaziflam: A new cellulose-biosynthesis-inhibiting herbicide provides long-term control of invasive winter annual grasses. *Pest management science*, *73*, 2149–2162. https://doi.org/10.1002/ps.4594

Sebastian, D. J., Nissen, S. J., Sebastian, J. R., Meiman, P. J., & Beck, K. G. (2017b). Preemergence control of nine invasive weeds with aminocyclopyrachlor, aminopyralid, and indaziflam. *Invasive Plant Science and Management*, *10*, 99–109. https://doi.org/10.1017/inp.2017.7

Sheley, R., Carpinelli, M., & Morghan, K. (2007). Effects of imazapic on target and nontarget vegetation during revegetation. *Weed Technology*, *21*(4), 1071–1081. https://doi.org/10.1614/WT-06-131.1

Shinn, S. L., & Thill, D. C. (2004). Tolerance of several perennial grasses to imazapic. *Weed Technology*, *18*, 60–65. https://www.jstor.org/stable/3989589

St. Clair, , B., S., & Bishop, T. B. (2019). Loss of biotic resistance and high propagule pressure promote invasive grass-fire cycles. *Journal of Ecology*, *107*, 1995–2005. https://doi.org/10.1111/1365-2745.13156

Terry, T. J., Madsen, M. D., Gill, R. A., Anderson, V. J., & (2021). St. Clair, S. B. Data from: Herbicide effects on the establishment of a native bunchgrass in annual grass invaded areas: Indaziflam vs. imazapic. Dryad Digital Repository. https://doi.org/10.5061/dryad.hdr7sqvgz

Thornton, P. E., Thornton, M. M., Mayer, B. W., Wilhemli, N., Wei, Y., Devarakonda, R., & Cook, R. B. (2014). *Daymet: Daily surface weather data on a 1-km grid for North America, Version 2*. Oak Ridge National Lab..

Tranel, P. J., & Wright, T. R. (2002). Resistance of weeds to ALS-inhibiting herbicides: What have we learned? *Weed Science*, *50*, 700–712.

Ulbrich, A., Souza, J., & Shaner, D. (2005). Persistence and carryover effect of imazapic and imazapyr in Brazilian cropping systems. *Weed Technology*, *19*(4), 986–991. https://doi.org/10.1614/WT-04-208R2.1

Umbarger, H. E. (1978). Amino acid biosynthesis and its regulation. *Annual Review Biochemistry*, *47*, 533–606. https://doi.org/10.1146/annurev.bi.47.070178.002533

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