EFFECTS OF VEGETATION HETEROGENEITY ON MULTIPHASIC TREATMENT OUTCOMES IN SAGEBRUSH STEPPE

by

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ABSTRACT

Exotic annual grass invasion into western North America has led to significant loss of native perennials, altering the structure and function of sagebrush-steppe ecosystems. Monitoring and assessment of necessary restoration treatments have provided mixed evidence of success. We hypothesized that treatment outcomes would be influenced by restoration strategy (e.g., the timing of herbicide or drill seeding) and by within-treatment vegetation heterogeneity. We evaluated exotic annual grass and exotic perennial forb response to three replicate treatments of the pre-emergent herbicides indaziflam and imazapic, and a combination treatment of both herbicides, followed with the broadleaf herbicide, aminopyralid, at a highly invaded site in Southern Idaho. A litter removal study was integrated to investigate the effects of thatch cover on herbicide application and two different revegetation methods, drill seeding and hand planting of native perennial seedlings, were nested into herbicide treatments. We accounted for vegetation heterogeneity within treatments by identifying pre-existing plant-community patch types and mapping their locations across the research site using high spatial resolution aerial imagery. We found that imazapic had no detectable effects on exotic annual grass cover, but significantly reduced exotic annual grass seedling density the first two years post-treatment. Indaziflam treatments effectively reduced exotic annual grasses for three years post-treatment, most notably the combination treatment of imazapic and indaziflam. Accounting for vegetation heterogeneity in our predictive models improved our ability to detect exotic annual grass response to treatment by a 5% change in cover.

None of the drill seeded plants emerged in either the treatments or controls for the duration of this study and all but a few native seedling plantings failed, precluding any meaningful revegetation comparisons between treatments. We were also unable to detect an influence of residual thatch on herbicide outcomes but did find that precipitation played a significant role in herbicide effectiveness. Overall, our findings suggest that indaziflam can be an effective tool for reducing exotic annual grasses in restoration, particularly when combined with imazapic, and that implementation of multiple sampling methods can provide greater insight into treatment outcomes. Additionally, our results indicate that accounting for plant-community patches in predictive models can improve model accuracy and therefore our ability to detect treatment effects.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.......... iv

ABSTRACT.......... vi

LIST OF TABLES.......... x

LIST OF FIGURES.......... xi

LIST OF ABBREVIATIONS.......... xiv

INTRODUCTION.......... 1

METHODS.......... 5

- Site Description.......... 5
- Experimental Design.......... 6
    - Main Treatments.......... 6
    - Subplots.......... 7
- Sampling Methods.......... 9
    - Line Point Intercept for Plant Cover.......... 9
    - Seedling Counts for Plant Density.......... 9
    - Density Counts for Large-Statured Exotic Forbs.......... 10
    - Mapping Plant-Community Patch Types.......... 10
- Data Analysis.......... 12
    - Main Treatments.......... 12
    - Subplots to Inform on Planting, Seeding, Litter, and Broadleaf Herbicide Effects.......... 13

RESULTS 14

Main Treatments 14

Response of Exotic Annual Grasses in Exotic Annual Grass Community Patch Types 14

Forb Response 15

Differences in Exotic Annual Grass Response Among Plant-Community Patch Types 15

Subplot Treatments 16

Aminopyralid Herbicide Subplots 16

Litter Removal (Raking and Re-treatment) Subplots 16

Drill Seeding and Hand Planting 17

DISCUSSION 18

Exotic Forb Response 19

Formal Assessment of Vegetation Heterogeneity 20

Litter Removal Effects and Yearly Precipitation Differences on Herbicide Effects 21

Aminopyralid Effects on Skeletonweed and Exotic Annual Grasses 22

Re-vegetation and Herbicide Treatments 23

Summary 23

Figures 25

Tables 34

REFERENCES 36

APPENDIX 43

LIST OF TABLES

Table 1 Post-Treatment Precipitation Totals and 20-Year Monthly Averages...... 34

Table 2 Model Comparisons for exotic annual grass cover by treatments............ 35

Table S1 Drill Seeding Mix for The 2018 And 2019 Drill Treatments.................. 47

LIST OF FIGURES

Figure 1 Map of the study site with classified RGB imagery acquired in August of 2019. Main herbicide treatments represented with numbers 1 – 5 replicated in three separate blocks. Treatments labeled 1 = controls, 2 = Indaziflam applied in 2018, 3 = Imazapic applied in 2018, 4 = Indaziflam applied in 2019, 5 = Indaziflam and Imazapic combined, applied in 2018. The three different colors represent the different plant-community patch types inferred from the aerial imagery. "CHJU" = skeletonweed (blue), "POBU" = bulbous bluegrass (yellow) and "EAG" = pre-treatment, EAG dominated (pink). Subplots were overlayed on top of main herbicide treatments either in strips (drill seeding) or marked 4x4 or 4x9 m plots...25

Figure 2 Precipitation (mm) accumulated by week relative to treatment application timing up to 8 weeks prior (-) and 8 weeks post (+) treatment. "Herbicide 2018" includes treatments of indaziflam, imazapic and the indaziflam and imazapic combinations applied in 2018. "Herbicide 2019" includes treatments of indaziflam applied in 2019. "Re-spraying 2019" includes 4x4m, unraked, subplots re-sprayed with the respective underlying treatments of indaziflam, imazapic and imazapic plus indaziflam applied in 2019 over top of treatments applied in 2018.......................................26

Figure 3 Precipitation accumulated within each month before or after treatment application and 30-year precipitation averages from 4-km^2 pixel PRISM data, 1991–2020). "Herb 2018" includes treatments of indaziflam, imazapic and the indaziflam and imazapic combinations applied in 2018. "Herb 2019" includes treatments of indaziflam applied in 2019. "Herb Re-treat 2019" includes 4x4m subplots re-sprayed with the respective underlying treatments of indaziflam, imazapic and imazapic plus indaziflam applied in 2019 over top of treatments applied in 2018. "Outplants" includes the hand planting of sagrbrush and perennial grass seedlings in 2 x 3 m subplots. "Drill 2018" and "Drill 2019" include the drill seeding treatments of native perennial grasses and forbs in 2018 and 2019 respectively. 27

Figure 4 Mean ± 95% CI cover predictions of exotic annual grasses by treatment and sample year. Predictions made from generalized linear mixed effects models with a beta distribution fitted with line-point intercept data. “Plant Patch Type” groups represent the three different plant-community patch types identified through imagery classification along with the base model (plant-community patch type not included as predictor). Indaziflam applied in 2019 was considered untreated for the 2019 monitoring year and excluded from the figure. 28

Figure 5 Mean ± 95% CI seedling count predictions ($1m^2$) of exotic annual grasses by treatment and sample time. Predictions made from generalized linear mixed effects model with a zero-inflated negative binomial distribution. “Plant Patch Type” groups represent the three different plant-community patch types identified through imagery classification of the site. 29

Figure 6 Mean ± 95% CI count prediction of exotic forbs in a $10m^2$ area. Predictions made using a generalized linear mixed effects model with a negative binomial distribution and fitted with density count data collected in summer of 2021 for exotic perennial forbs (n=15 per treatment). Starred treatments are significantly different from their respective controls based on 95% confidence interval overlap. 30

Figure 7 Mean ± 95% CI height predictions (cm) of exotic forbs. Predictions made using a generalized linear mixed effects model with a gamma distribution and fitted with density count data collected in summer of 2021 for exotic perennial forbs (n=15 per treatment type). Starred treatments are significantly different from their respective controls based on 95% confidence interval overlap. 31

Figure 8 Cover of skeletonweed or exotic annual grass cover by treatment type and sample year. Groups labeled “Treated” represent the 4x4m subplots where the herbicide aminopyralid was applied and “Untreated” represent the adjacent 4x4m subplots that were not treated with aminopyralid. 32

Figure 9 Exotic annual grass cover responses to raking prior to re-treatment of each herbicide type by sample year (2020, 2021). 33

Figure S1 Orthophotos from the UAV imagery in acquire in August of 2019, collected by Idaho State University and Donna Delparte, separated by Treatment Block. Block 3 (left), Block 1 (top right), and Block 2 (bottom right). 44

Figure S2 Confusion matrix for all treatment blocks. Numbers represent number of training points assigned to each classification category. Inaccuracy was highest between CHJU and EAG classes. The overall accuracy was 86% with a Kappa of .82 45

Figure S3 Seedling planting design for hand planted subplots. One subplot was applied per replicate treatment block (n=3 per treatment type). “ARTR” = sagebrush, “PSSP” = bluebunch wheatgrass, “ELEL” = squirrel tail, “POSE” = sandberg’s bluegrass and “ARPU” = purple three awn...........46

LIST OF ABBREVIATIONS

EAG	Exotic Annual Grass
CHJU	Chondrilla juncea (Skeletonweed)
POBU	Poa bulbosa (Bulbous bluegrass)
USGS	U.S. Geological Survey
UAV	Unmanned Aerial Vehicle
LPI	Line-Point Intercept

INTRODUCTION

The invasion of exotic annual grasses (EAGs) into western North America has been responsible for substantial loss of sagebrush steppe habitat (Mack 1981, Billings 1990). Exotic annual grasses create positive feedback loops with wildfire, decreasing natural fire return intervals and altering fire behavior by increasing the continuity of wildfire fuels and establishing more readily in burned areas (Balch et al. 2012, Brooks et al. 2004). Increased fire disturbance along with direct competition from exotic annual grasses has led to decreased plant biodiversity (Mahood and Balch 2019, Davies and Sheley 2011), reduced livestock forage (Pellant 1990, Major et al. 1960), and loss of wildlife habitat, particularly for steppe-obligate species (Rhodes et al. 2010, Knick and Rotenberry 200). Exotic annual grasses such as cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski) are widespread in arid and semi-arid deserts like those found in the Great Basin (D'Antonio and Vitousek 1992). Cheatgrass and medusahead directly compete with native perennial species by reducing available soil resources, creating microclimates from residual plant litter and by having short, early life cycles that take advantage of shallow soil moisture (Germino et al. 2016).

The most common treatment methods to restore invaded landscapes include herbicide application, reseeding of native vegetation, and vegetation or soil manipulation (e.g., plowing, mowing, or mechanical thinning; Pilliod et al. 2017). Herbicide treatments are implemented to decrease the occurrence of exotic plant species thereby reducing competition with surviving or seeded perennials, reducing fuel loads for wildfire, and slowing the spread of exotic species. Herbicides are either applied to soils to inhibit germination (pre-emergent) or to the foliar crowns or canopies to reduce growth or eradicate plants (post-emergent).

A commonly used herbicide on rangelands is the pre- or post-emergent herbicide imazapic, an acetohydroxyacid synthase (AHAS) inhibitor. Imazapic is perceived to have short-term control of exotic annual grasses with some studies providing evidence for a single year of control (Terry et al. 2021, Davies and Hamerlynck 2019) and other studies providing evidence for two years of control (Davies and Sheley 2011, Kyser et al. 2007, Davison and Smith 2007). Imazapic, an emerging herbicide that may overcome the perceived the short duration of control of imazapic, is a cellulose biosynthesis inhibitor that works exclusively as a pre-emergent, inhibiting root growth in germinants (Brabham et al. 2014). This herbicide is expected to have greater longevity in soils leading to longer term control of exotic annual grasses (Tateno et al. 2015). Studies comparing the longevity of indaziflam and imazapic have found that indaziflam maintains control of exotic annual grasses one to two years longer than imazapic (Clark 2020, Sebastian et al. 2016, Terry et al. 2021). Further studies have investigated whether combinations of indaziflam mixed with other (post-emergent) herbicides such as rimsulfuron, aminocyclopyrachlor or glyphosate, could be an even more effective option to controlling exotic annual grasses, but no current studies have tested the combination of indaziflam and imazapic together (Koby et al. 2019, Clark et al. 2019, Sebastian et al. 2016).

There are many challenges associated with restoring degraded landscapes and creating generalizable management plans (Svejcar et al. 2017). One challenge in the Great Basin stems from the spatial variability in climate, soil characteristics and topography, all of which can influence treatment outcomes (Boyd et al. 2012, Chambers et al. 2014). Despite accounting for these environmental factors, ecological models predicting vegetation response to treatment still have large amounts of variability unexplained by model predictors (Brudvig et al. 2017, Barnard et al. 2019). One possible source of variability could relate to inequivalent comparisons between controls and treated areas. Assuming, spatially, the controls and treatments are similar, there may still be differences between them in plant community composition and species cover which are not being accounted for during treatment evaluation. Another source of variation from vegetation could be explained by thatch layers left behind by senesced exotic annual grasses (particularly medusahead) prior to treatment. Plant litter has been hypothesized to intercept herbicides above the soil surface and restrict the amount of active ingredient reaching exotic annual grass seeds (Clark et al. 2019, Kyser et al. 2012). Thatch can also create microclimates favorable to annual grass germination and success while simultaneously suppressing native rangeland species (Evans and Young 1970). Few studies have looks at these effects. However, some of these studies have reported increased exotic annual grass control with various seed-bed preparations before herbicide including hand raking, tilling, and controlled burns, which remove the accumulated thatch layer (Kyser et al. 2007, Clark et al. 2019).

We applied a combination of different restoration treatments along with maps of pre-existing plant-community patch types to address the following questions: i) What is the longevity and effectiveness of the herbicide indaziflam and combination of indaziflam and imazapic for controlling exotic annual grasses and what are their secondary effects on non-target forbs? ii) Can the herbicide aminopyralid be an effective control agent for the exotic perennial forb skeletonweed and what are its non-target effects on exotic annual grasses? iii) Can residual thatch layers influence herbicide effects on exotic annual grasses? iv) Can mapping pre-existing plant communities account for vegetation heterogeneity within treatments and improve predictive models for evaluating treatment outcomes?

METHODS

Site Description

The study area, referred to as Top Hat, has burned in three separate wildfires with the most recent fire occurring in 1983 (WFIGS). The area was previously grazed by livestock for decades until several years prior to the study and is currently managed by the Idaho Department of Fish and Game (IDFG) in the foothills of the Idaho Batholith in the Boise Wildlife Management Area (lat 43°35’31.5”N, long 116°07’37.7”W). Top Hat is located at an elevation of 965 m with a soil type that is predominately vertisol (60% churning clay, 35% loamy 8-12, 5% loamy bottom 8-14; USDA-NRCS 2014). Annual average precipitation is 37.9 cm with a mean maximum temperature of 66 °C and a mean minimum temperature of 6 °C (PRISM; 4-km resolution, 30-year averages). This site is heavily invaded by medusahead, skeletonweed, and bulbous bluegrass among other non-native grass and forb species. Native species richness and abundance are low, and they include native perennial grasses such as purple three awn (*Aristada purpurea* Nutt.), sandbergs bluegrass (*Poa secunda* J. Presl), and squirrel tail (*Elymus elymoides* (Raf.) Swezey) and native perennial forbs such as common yarrow (*Achillea millefolium* L.), mexican whorled milkweed (*Ascelpias fascicularis* Decne.), and foothill death camas (*Zigadenus paniculatus* (Nutt.) S. Watson).

Experimental Design

Main Treatments

A full factorial of five different pre-emergent herbicide treatments with nested subplot treatments of broadleaf/post-emergent herbicide, drill seeding, hand planting, and litter removal were applied in three replicate blocks between 2018 and 2019 (Figure 1).

The main treatments included an untreated control, indaziflam (Rejuvra®) sprayed in the fall of 2018 or 2019 (73 g ai ha^{-1}, = 5 oz/acre, imazapic (Panoramic®) sprayed in fall 2018 (105 g ai ha^{-1}, = 6 oz/acre, and a tank-mixed treatment of both indaziflam and imazapic (73 g ai ha^{-1} + 105 g ai ha^{-1} = 5 + 6 oz/acre) in fall 2018. All treatments applied in 2018 occurred in late October. Temperature ranges were moderate around the time of treatment ranging from 41 - 71°C and with no precipitation accumulating in the month post-treatments (Weather Underground; Table 1). Indaziflam applied in 2019 occurred in late August. Temperatures near time of application were higher than the treatments applied in 2018, ranging from 52 – 99°C. Accumulated precipitation in the month post- treatment was also significantly higher (17.78 mm; Figure 2; Table 1). Main treatments were applied by Ada County Weed and Pest Department using trucks equipped with a 9- m wide boom sprayer and Raven's boom control (Raven Applied Technology, SD). All herbicides were sprayed with 187 L water ha^{-1} with 0.25% v/v non-ionic surfactant (Super Spread 7000®) to promote uniform coverage and absorption. Spraying was completed under ideal low-wind conditions.

Subplots

Aminopyralid Herbicide Subplots

To assess the effects of the broadleaf herbicide aminopyralid (Milestone®) on the invasive forb, skeletonweed, two, 4x4-m nested subplots were added to each main herbicide treatment in August of 2019 (Figure 1). Subplot locations were selected using high-spatial-resolution drone imagery collected in 2019 in which dense skeletonweed stands were evident and could be manually mapped. The subplots were arbitrarily placed within main treatments and mapped skeletonweed patches. Aminopyralid was then applied to each subplot with a 16-liter hand-pump backpack sprayer calibrated at a rate of 821 L ha^{-1} (122.5 g ai ha^{-1}). The non-ionic surfactant (SprayWet®) was added to the backpack sprayer at 0.25% v/v along with 15 mL of blue dye. There was 17.78 mm of accumulated precipitation in the month following herbicide treatment (Figure 2).

Litter Removal and Re-treatment Subplots

To assess the influence of litter on herbicide outcomes, we established two, paired, 4x4-m nested subplots within the main herbicide treatments in December of 2019 (indaziflam treatments applied in the same year (2019) were excluded; Figure 1). Litter removal subplot locations were selected using the same method as the aminopyralid subplots but targeted on dense exotic annual grass patches rather than skeletonweed patches. One of each of the paired subplots was manually raked to remove all standing and surface litter from the subplot and the adjacent subplot was left undisturbed (unraked). Both paired subplots were then retreated with their respective underlying main herbicide treatment at the same concentrations using a 16-liter hand pump backpack sprayer calibrated to 328 L ha^{-1} with the non-ionic surfactant (SprayWet®) added to the backpack sprayer at 0.30% v/v along with 15 mL of blue dye. Temperatures ranged from 28 - 51°C around the time of re-treatment, which was lower than the respective main treatment applications in fall of 2018. There was also a greater amount of precipitation in the month following the litter removal and re-spraying treatments compared to the underlying main treatments applied in 2018 with 19.05 mm total precipitation occurring after re-spraying in 2019 and 0 mm occurring after the main treatment were applied in 2018 (Figure 2; Table 1).

Drill Seeding Subplots

Drill seeding subplots were implemented to assess the effects of herbicide timing on drill seeding treatments. In fall of 2018, within a week of the main herbicide applications, three 5-m wide drill seeding strips containing a mix of native perennial grasses and forbs (37 kg ha^{-1}) were applied with a standard rangeland drill across all three replicate blocks (Figure 1). The same treatment was repeated in fall of 2019 with residual seed mix from 2018. The drill seeding in 2019 only installed a single, 5 m wide drill strip across the three treatment blocks. Both drill seeding treatments occurred in similar weather windows. Temperatures ranged from 16 °C to -7 °C in early November of 2018 and 16 °C to -9 °C in late December of 2019. Both drill seeding installations experienced freezing temperatures (< 0°C) and received precipitation in the month following application (17.02 mm and 33.27 mm respectively; Figure 3; Table 1).

Hand Planting Subplots

Sagebrush and perennial grass seedlings were hand planted to assess the effectiveness of this revegetation method as well as to examine the influence of herbicides on nursery stock seedlings. In the fall of 2019, nursery stock grass and shrub seedlings were hand planted into 2x3-m subplots within each main treatment (Figure 1). These species included Sandberg's bluegrass (POSE, *Poa secunda* J. Presl), bluebunch wheatgrass (PSSP6, *Pseudoregneria spicata* (Pursh) Á. Löve), bottleb squirreltail (ELEL5, *Elymus elymoides* (Raf.) Swezey), purple three-awn (ARPU9, *Aristida purpea* Nutt.) and basin big sagebrush (ARTRT, *Artemisia tridentata* Nutt. ssp. *tridentata*). All seedlings were grown for six months and were 98 cm^3 (grasses) or 164 cm^3 (shrubs) in size. In the month following seedling planting, temperatures ranged from 20 °C to -9°C and accumulated precipitation was very low, with a total of 5.3 mm (Figure 3; Table 1).

Sampling Methods

Line Point Intercept for Plant Cover

Plant cover was determined using a line-point intercept (LPI) method. Five, 20-m long transects were oriented diagonally across replicated main treatments and were monitored annually at the time of peak biomass (June) from 2019 to 2021. Incidences of litter (previous-year growth), bare soil or rock, and current-year growth to species for each canopy layer were recorded at 0.5-m intervals along the transects. Data was recorded directly into a database (USDA DIMA form, in Microsoft Access software) with Mesa2 field tablets (~3m accuracy, Juniper Systems, UT) and ESRI ArcGIS Collector software was used to aid in geo-locating plots and subplots, which were permanent.

Seedling Counts for Plant Density

Seedlings (new emergents) of all plant species were counted in the spring and fall (March or late November to early December, respectively) beginning in fall 2019 and ending in spring 2021. The number of emergent plants were counted by species in three

1-m^2 quadrats per monitoring plot in 2019 (resulting in 15 quadrats per replicated main treatment), but thereafter, in 2020 and 2021, sampling occurred in one 1-m^2 quadrat per monitoring plot. Species with high seedling densities were counted in smaller subquadrats within the designated 1-m^2 areas, specifically either in two 30x30-cm areas (e.g., large exotic forb skeletonweed) or in four 10x10-cm areas (e.g., small exotic annual grasses). Final calculations of seedling density for species were averaged by monitoring plot to a single value of seedling species per 1m^2.

Density Counts for Large-Statured Exotic Forbs

In the late summer of 2021, density counts of large-statured (i.e., plants 0.5 to >2 m height, depending on species) exotic forbs were recorded to investigate non-target herbicide effects on species unrepresented in LPI methods or spring/fall seedling density counts. The species skeletonweed, field bindweed (*Convolvulus arvensis* L.), prickly lettuce (*Lactuca serriolia* L.), yellow salsify (*Tragopogon dubius* Scop.), sunflower (*Helianthus annuus* L.), and moth mullein (*Verbascum blattaria* L) were counted in five monitoring plots per replicated main treatment. The number (count) and height of each species present within a plot was recorded incrementally beginning with a 1-m^2 plot and extending to 5.5, 9, or 13-m radius areas as needed until at least 3 individuals were detected. Total species density was extrapolated to a 10m^2 area per monitoring plot.

Mapping Plant-Community Patch Types

Accounting for vegetation heterogeneity within treatments was accomplished by first identifying and mapping dominant plant-community patch types using high spatial resolution imagery. In August of 2019 (one-year post-treatment) Idaho State University flew an unmanned aerial vehicle (UAV; operated by Donna Delparte) over the Top Hat site to create a 2.5-cm pixel resolution, red-green-blue orthophotograph (Figure 1). The imagery was delineated into a map of three different plant-community patch types using classification and regression trees (CART, Breiman et al. 1984) in the “classifier” package of Google Earth Engine, which assigned either “POBU” (bulbous bluegrass), “CHJU” (skeletonweed) or “EAG” (exotic annual grass) areas within the image.

To train our classifier, 30 randomly located 1-m radius plots were monitored at the time of image acquisition. Visual estimates of percent plant cover (to species) were recorded within each monitoring plot. Each plot was later designated as “POBU” or “CHJU” if their respective covers of bulbous bluegrass and skeletonweed were >25% or “EAG” if both bulbous bluegrass and skeletonweed cover was <25%. In the few cases where both species had >25% cover, the species with the highest percent cover was selected as the plant-community patch type for the classification.

To test the accuracy of our classified map, thirty additional sample areas were added as training points for validation. Using the same classifier package, a confusion matrix was created using the “errorMatrix” tool to test the accuracy of the classifier (Stehman 1997). The overall accuracy was 86% with a Kappa score of 0.82. Of 30 samples for each species, six CHJU were classified incorrectly as EAG, two POBU were classified incorrectly as EAG, and three and two EAG were incorrectly classified as CHJU and POBU, respectively.

Prior to treatment, the dominant species within the Top Hat site were bulbous bluegrass, skeletonweed and exotic annual grass. LPI data collected in 2019 suggested neither skeletonweed nor bulbous bluegrass were affected by treatments, therefore imagery of those two patch types obtained in 2019 would be representative of pre-treatment patches and all other areas were assumed to be dominated by exotic annual grasses. At the time the imagery was obtained (one-year post-treatment) exotic annual grass patches had been influenced by treatment and included cover from exotic annual grasses, perennial bunch grasses, bare soil, plant litter, and non-skeletonweed forbs.

Data Analysis

Main Treatments

To compare exotic annual grass cover responses to treatments we used a generalized linear mixed effects model (beta distribution) with the 'glmmTMB' package in R Studio (R Core Team 2021; Magnusson et al. 2017). Three different models for exotic annual grass (EAG) cover were compared to determine if plant-community patch type helped explain variability in treatment responses (Table 2): i) The "base model" included EAG cover (from LPI) as the response variable and treatment type (main treatments), sample year (year of monitoring; 2019-2021), and the interaction between the two as fixed effects; ii) The "block model" added random intercepts for treatment block and monitoring transect to the base model; iii) The "patch model" added plant-community patch type as a fixed effect to the block model.

To compare exotic annual grass density responses to treatments we used the same model formula from our cover analysis with a zero-inflated negative binomial distribution rather than a beta distribution. The zero-inflated model accounts for both the structural and sampling zeros in our seedling count data and creates a better fitting model for our data, which was over dispersed with many zero values (Blasco-Moreno et al. 2019).

To evaluate non-target effects of treatments on exotic forb height and density we used our block model with monitoring transect excluded as a random effect. The model for exotic forb height had a gamma distribution (log link) and the model for exotic forb density had a negative binomial distribution.

Model cover, density, and height predictions for EAG or exotic forbs were all made with the package ‘ggeffects’ (Lüdecke 2017). Akaike’s information criterion (AIC) was used to compare model fit and identify the best models. We also calculated root mean square error (RMSE) for each model type (base, block, and patch; Table 2).

Subplots to Inform on Planting, Seeding, Litter, and Broadleaf Herbicide Effects

Non-parametric Kruskal-Wallis tests (R package ‘dplyr’) were used to determine the significance of differences in plant cover among the treatments applied in subplots, compared to their respective control subplots, for each year (2020, 2021; no germinants from seeding in 2019), because the data were not normally distributed (Shapiro-Wilk, $P>0.05$).

RESULTS

Main Treatments

Response of Exotic Annual Grasses in Exotic Annual Grass Community Patch Types

Compared to controls, EAG cover was reduced by 20%, 51%, and 44% respectively, over all three years following the first (2018) indaziflam treatment (95% CI=9%, 8%, and 9%) and by 53% and 71% respectively, for the two years following the second (2019) indaziflam treatment (95% CI=8% and 7%; Figure 4). EAG cover was reduced 61%, 87%, and 84% respectively, over all three years following the combination treatment of indaziflam + imazapic (95% CI=6%, 2%, and 3%). All indaziflam treatments reduced EAG cover an additional 17% to 30% the second-year post-treatment. EAG cover in imazapic treatments was not significantly different from controls for any year post-treatment.

Unlike the treatment responses observed for EAG cover, EAG seedling densities (plants m^{-2}) were reduced 35%-40% by imazapic for the first two years post-treatment compared to controls (95% CI = 14%; Figure 5). No significant differences were observed in EAG seedling densities between controls and imazapic treatments the third-year post-treatment. Similar to EAG cover responses, EAG seedling densities were reduced most by the indaziflam + imazapic treatments, specifically 67%, 88% and 96%, respectively, all three years following treatment (95% CI = 11%, 5%, and 2%).

Indaziflam reductions of EAGs were again most evident two years following application, specifically with 34% greater reductions in the second compared to the first post- spray year (95% CI = 13%) (Figure 5).

Forb Response

Skeletonweed density was not significantly influenced by imazapic, indaziflam, or imazapic + indaziflam treatments, however skeletonweed heights were a mean 20 cm greater in all four treatments (95% CI= 5 cm; Figure 6). Sunflowers, on average, were 10-times denser (per 10 m^2) in imazapic + indaziflam treatments compared to controls and were 3- to 5-times denser in all other treatments other than treatments sprayed in 2019 with indaziflam. Mean sunflower heights were 23 cm greater in the imazapic + indaziflam and indaziflam treatments sprayed in 2019 than in unsprayed controls (95% CI = 25 cm). The exotic biennial forb prickly lettuce was on average 5-times denser within the imazapic treatments compared to the control and twice as dense in the imazapic + indaziflam treatments. Yellow salsify was found at higher densities (3- to 7-times denser) in all treatments except for the imazapic + indaziflam compared to controls.

Differences in Exotic Annual Grass Response Among Plant-Community Patch Types

Treatment effects on EAG cover were not uniform across the plant-community patch types within the main herbicide treatments and tended to be least in bulbous bluegrass (POBU) community patch types, intermediate in skeletonweed (CHJU) community patch types and greatest in EAG community patch types (Figure 4).

Compared to our base model, the inclusion of treatment block and monitoring transect as random intercepts accounted for 1% and 6% of model error, respectively and plant- community patch type explained and additional 2% of model error as indicated by the calculated RMSE (Table 2). Parsing treatment effects by plant-community patch type increased detectable treatment effect by a 5% change in EAG cover. EAG cover differed considerably amongst the community patch types irrespective of herbicide treatments, with 18% of the mean reduction in EAG cover attributed to the presence of bulbous bluegrass (confidence intervals did not overlap), and 12% reduction in EAG cover attributed to skeletonweed (95% CI=6%).

Subplot Treatments

Aminopyralid Herbicide Subplots

Aminopyralid treatments reduced skeletonweed cover by an average of 18% (SE untreated: 10%, treated: 5%) the first-year post-treatment (40% reduction compared to controls). By the second-year post-treatment there were no significant differences in skeletonweed cover between treated and untreated areas (Figure 7). Exotic annual grass cover was not significantly different between the treated and untreated subplots either year post-treatment (Figure 7). Additionally, we did not observe any significant interactions between aminopyralid and the underlying herbicide treatments.

Litter Removal (Raking and Re-treatment) Subplots

Within each main treatment, EAG cover was similar between the re-treated, raked and re-treated, unraked subplots for both years post-treatment (Figure 8). Re-treatments of all imazapic treatments (combination and singular treatments) greatly reduced EAG cover relative to the initial treatments. Imazapic only re-treatments (applied one year after first application) reduced EAG cover by 67.5% (SE = 5%) compared to the controls and re-treatments of imazapic and indaziflam combined reduced EAG cover by 99% compared to controls.

Drill Seeding and Hand Planting

her drill seeding nor hand planting treatments led to perennial plant recruitment (either for the 2018 or 2019 drill seedings) and there was nearly 100% mortality of hand planted individuals within one year post treatment. Only 3 of 108 sagebrush seedlings survived, and two were located within the herbicide treatment indaziflam + imazapic and another in the 2018 indaziflam treatment.

DISCUSSION

Our study site presented unique restoration challenges with unfavorable soil quality (churning clays), established populations of both invasive forb and grass species as well as a highly mosaiced and heterogenous plant-community structure across the site. Reducing exotic species while simultaneously increasing native perennials is a well-known challenge in heavily disturbed areas, with many cases of low success (e.g.

Knutson et al. 2014, Brabec et al. 2015, Monaco et al. 2005). In the case of this study, we observed multiple installations of drill seedings fail along with the hand plantings of greenhouse grown seedlings. The herbicide treatment direct effects were variable, with uneven control of EAGs within treatment. Indirect effects were also observed with the increased establishment of exotic forbs where resources were more readily available.

Variability in vegetation responses were not attributed to litter and were only partially attributed to the plant-community patch heterogeneity between treatment areas (i.e. ~5% error). Despite the variability observed within treatments, there were still significant differences in exotic annual grass control between the indaziflam and imazapic treatments. Indaziflam had the greatest control of EAGs when precipitation occurred within one-month post-treatment and our results suggested that the combination of indaziflam and imazapic is a more effective treatment than indaziflam alone. Indaziflam also provided a minimum of three years of EAG control compared to zero or one year of control from imazapic treated areas.

Our vegetation cover analysis did not provide evidence for EAG control from the imazapic treatments applied in 2018, however, we observed reduced EAG seedling densities from our count analysis for the first-year post-treatment. One explanation for the lack of cover reduction despite the decreased in density, is that the few EAGs that escaped imazapic grew larger foliar crowns, possibly due to greater soil-resource availability, thereby creating a similar canopy cover to those found in untreated controls. However, other studies have reported reductions in EAG cover following imazapic, including near our study site (Applestien et al. 2018, Germino et al. 2020, Lazarus et al. 2021

Similar to our results, studies have reported only a single year or no target effects when applied at similar rates as our study (70 g ai ha^{-1}; Clark et al. 2019, Sebastian et al. 2016, Koby et al. 2019). For example, Clark et al. (2020) did not see significant control of EAGs from imazapic only treatments, even with a greater application rate of 122 ai ha^{-1}. Alternately, Kyser et al. (2009) found that imazapic had moderate control at the same application rate, with subsequent, increased applications rates improving control, up to 210 g ai ha^{-1}. Comparatively, indaziflam treatments were still imparting close to maximum levels of EAG-density reduction in the third post-spray year, supporting the findings in studies conducted in other, wetter and more temperate grasslands (Sebastian et al. 2016, Clark et al. 2019, Terry et al. 2021).

Exotic Forb Response

Non-target effects of herbicides are another important factor to consider when evaluating the efficacy of an herbicide as a restoration treatment. A reduction in EAGscould potentially lead to a reduction in native forb abundance and richness, thereby reducing the benefit of EAG control. Additionally, the reduced abundance of otherwise dominant EAGs could also lead to an increase in exotic forb density, particularly for highly degraded areas where pre-existing exotic forb communities can easily spread and take advantage of soil resources without competition from grasses. The invasion of forbs after herbicide has been observed in several studies including Lazarus et al. (2021), Reid et al. (2009), and Pearson et al. (2016), however, we observed that exotic forb responses to the herbicides varied considerably among the species. Invaders such as prickly lettuce increased >10-fold in density in response to imazapic but not indaziflam, and invaders such as sunflower increased in response to both herbicides. Overall, imazapic had higher exotic forb invasion than the indaziflam only treatments, suggesting that the increased resource availability hypothesis for explaining post-emergent-herbicide invasion by exotic forbs cannot explain the full response.

Formal Assessment of Vegetation Heterogeneity

Prior to treatment, the Top Hat site was predominately a mosaic of bulbous bluegrass, medusahead and skeletonweed with plant-community patch sizes ranging from 2 to 50 m radii. We expected to observe improved predictive model accuracy by accounting for vegetation heterogeneity as a variable. However, including plant-community patch type as a fixed effect only marginally increased our model accuracy compared to our random effects (repeated transects). This suggests that there was variability occurring at the transect level that was not measured or accounted for in our model. Munson et al. (2015) also accounted for monitoring transect as a random effect and found that it explained more variability in vegetation cover than any of their fixed effects (excluding treatments). It is possible that classifying the site into only three community patch types was too course (i.e. insufficient categorical resolution) given the spatial diversity of plant-community patch types. Additionally, there was still 13% of error in model predictions of EAG response to treatments that was not explained by plant-community patch type or random effects. High model error is common in ecological systems as there are a multitude of biotic and abiotic factors to account for (Barnard et al. 2019, Brudvig et al. 2017). However, our in-sample model accuracy of 87% is above the standard (approx. 80% accuracy) for landscape-scale predictive models (Applestein et al. 2018b). The findings of our study as well as Dickens et al. (2015)

suggest that plant-community composition could be an important predictor for vegetation response to treatment, however more research is needed to fully understand how to capture this variability in a predictive model.

Litter Removal Effects and Yearly Precipitation Differences on Herbicide Effects

We expected, but did not observe, litter removal effects on herbicide re-treatments. However, other studies have shown significant differences in herbicide effect when a disturbance, such as raking, is used to expose the soil surface (Kyser et al. 2013). One possibility for our negative results could be that the layer of medusahead thatch was not thick enough to induce an effect on herbicide application within the treated areas, therefore not providing a significant difference in EAG cover between raked and unraked plots.

Interestingly, we did see imazapic re-treatment effects compared to initial treatments and controls. Whether this is due to accumulating more imazapic in the soil or some temporal factors such as weather causing the second spraying to be more effective is an important question. It's possible that higher precipitation after treatments applied in

2019 was the primary factor in herbicide success. Specifically, nearly 30 mm of precipitation was received preceding the 2018 treatments but none in the month after, which contrasted the nearly opposite patterns in 2019 (30mm of precipitation received after treatments and none in the month prior). Our findings that post-treatment precipitation is most likely to promote herbicide effectiveness contrasts with Morris et al. (2009) findings suggesting that pre-spraying moisture is a better predictor for treatment outcomes than post-treatment precipitation because infiltration of herbicides is greater in pre-wetted soils.

Aminopyralid Effects on Skeletonweed and Exotic Annual Grasses

Aminopyralid provided transient control of skeletonweed with only one year of cover reductions and quickly regained skeletonweed cover the second-year post-treatment. Other studies are mixed in whether they found aminopyralid control of skeleton weed (Spring et al. 2018, Thorne and Lyon. 2021). Specifically, Spring et al. (2018) observed strong control of skeletonweed two years post-treatment (97% and 84%, respectively) while Thorne and Lyon (2021) did not observe any significant control of skeletonweed from aminopyralid. Findings for aminopyralid control of EAGs is also mixed. Our study did not provide evidence for aminopyralid control of medusahead, whereas other studies have suggested that the broadleaf herbicide has potential for medusahead reduction (Kyser et al. 2012, Rinella et al. 2018). However, timing of aminopyralid application may be an important factor, for example Rinella et al. (2018) observed improved control of EAGs with spring applications vs. fall applications.

Re-vegetation and Herbicide Treatments

The failed drill seeding in our study precluded assessment of indaziflam effects on drill seeding, however, other re-vegetation studies have assessed the effects of indaziflam on perennial bunchgrass growth. Unfortunately, factors that commonly explain drill seeding failures were all observed in our study including below average precipitation years (drought; Hardegree et al. 2016), difficult soil types (churning clay), and competition from a large array of invasive species (Davies 2010, Young et al.

1999). The same seed mix was used for both years of application (2018 and 2019) and had a tested viability of 60-85% suggesting that variation in seeds or poor viability were unlikely to explain the results. Other studies have been done on indaziflam interactions with perennial grasses. A study by Terry et al. (2021) found negative impacts on seedling establishment when drill seeding was co-applied with a mix of indaziflam and glyphosate, although it is unclear which herbicide had this negative effect. Additionally, Koby et al. (2019) found minimal negative effects of indaziflam on established perennial species.

The second revegetation method (seedling hand planting) was followed by dry weather (Table 1) and seedlings were not watered in at the time of planting, which also may have contributed to the high mortality rate. Hand planting of seedlings may have had more success with improved environmental conditions.

Summary

Overall, our data suggests that indaziflam, particularly when combined with imazapic, can be an effective method for providing at least three years of exotic annual grass control, although methods of control for secondary invasions by non-target invaders may be necessary for more comprehensive restoration strategies. Additionally, a lack of revegetation success is highly problematic in sites where native perennials are scarce (such as Top Hat) and thus are weak sources for desired plant recovery. More intensive revegetation strategies and establishment of perennial bunchgrasses are vital to conservation and in preventing further invasion by exotic annual grasses and forbs (Davies and Svejcar 2008). Lastly, our results indicated that only some of the variability in treatment outcomes could be explained by vegetation heterogeneity between treatments and pre-existing plant-community effects. Further investigation is needed into the underlying causes of variation in treatment outcomes to improve predictions for vegetation response to treatment and to help inform successful management strategies.

Figures

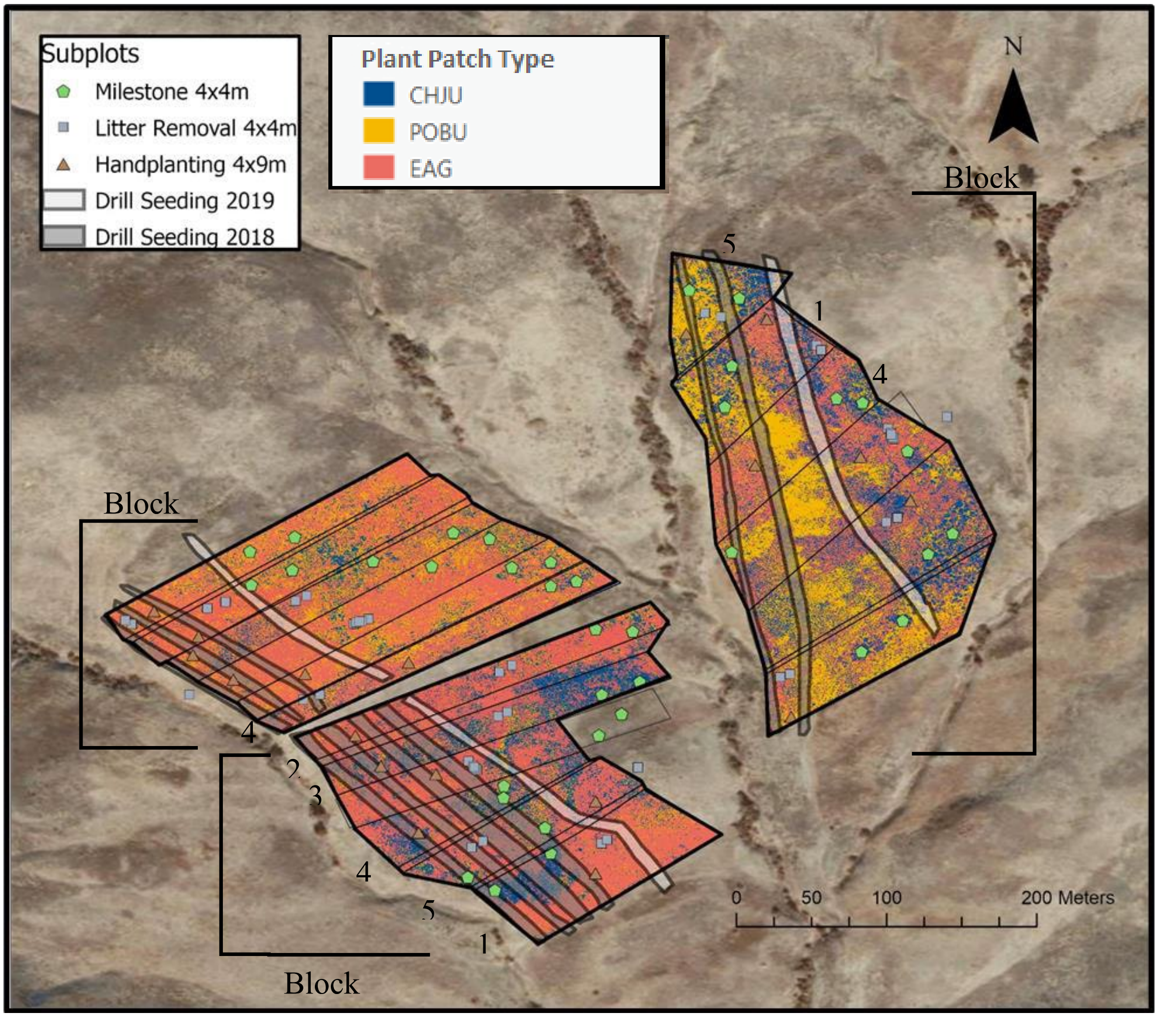

Figure 1 Map of the study site with classified RGB imagery acquired in August of 2019. Main herbicide treatments represented with numbers 1 – 5 replicated in three separate blocks. Treatments labeled 1 = controls, 2 = Indaziflam applied in 2018, 3 = Imazapic applied in 2018, 4 = Indaziflam applied in 2019, 5 = Indaziflam and Imazapic combined, applied in 2018. The three different colors represent the different plant-community patch types inferred from the aerial imagery. "CHJU" = skeletonweed (blue), "POBU" = bulbous bluegrass (yellow) and "EAG" = pre-treatment, EAG dominated (pink). Subplots were overlayed on top of main herbicide treatments either in strips (drill seeding) or marked 4x4 or 4x9 m plots.

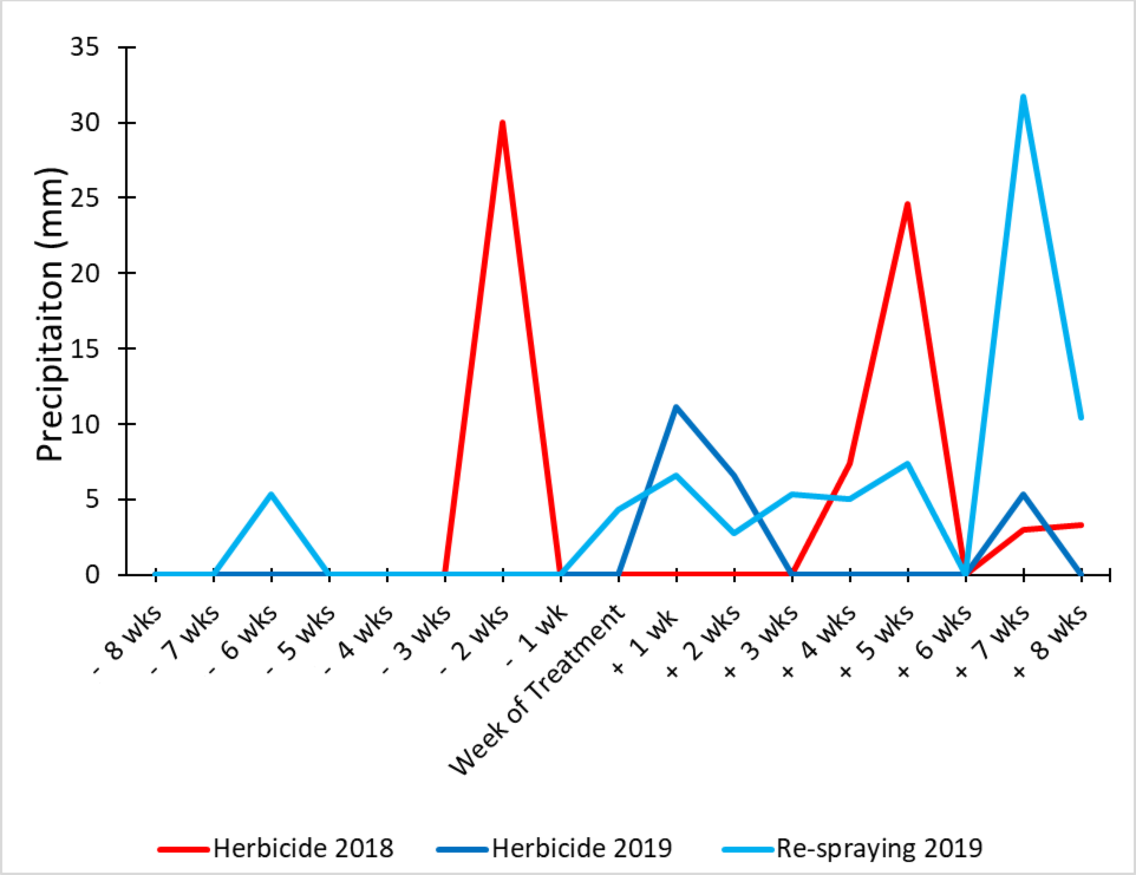

Figure 2 Precipitation (mm) accumulated by week relative to treatment application timing up to 8 weeks prior (-) and 8 weeks post (+) treatment. "Herbicide 2018" includes treatments of indaziflam, imazapic and the indaziflam and imazapic combinations applied in 2018. "Herbicide 2019" includes treatments of indaziflam applied in 2019. "Re-spraying 2019" includes 4x4m, unraked, subplots re-sprayed with the respective underlying treatments of indaziflam, imazapic and imazapic plus indaziflam applied in 2019 over top of treatments applied in 2018.

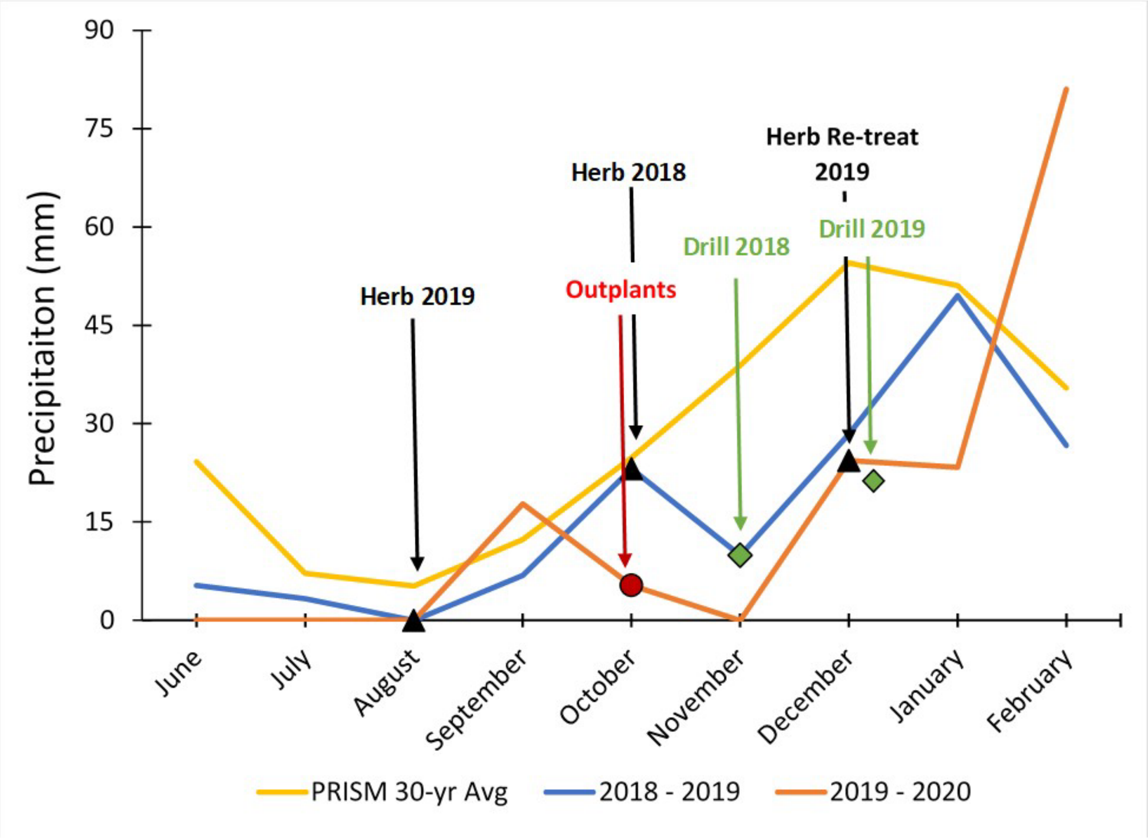

Figure 3 Precipitation accumulated within each month before or after treatment application and 30-year precipitation averages from 4-km^2 pixel PRISM data, 1991–2020). "Herb 2018" includes treatments of indaziflam, imazapic and the indaziflam and imazapic combinations applied in 2018. "Herb 2019" includes treatments of indaziflam applied in 2019. "Herb Re-treat 2019" includes 4x4m subplots re-sprayed with the respective underlying treatments of indaziflam, imazapic and imazapic plus indaziflam applied in 2019 over top of treatments applied in 2018. "Outplants" includes the hand planting of sagrbrush and perennial grass seedlings in 2 x 3 m subplots. "Drill 2018" and "Drill 2019" include the drill seeding treatments of native perennial grasses and forbs in 2018 and 2019 respectively.

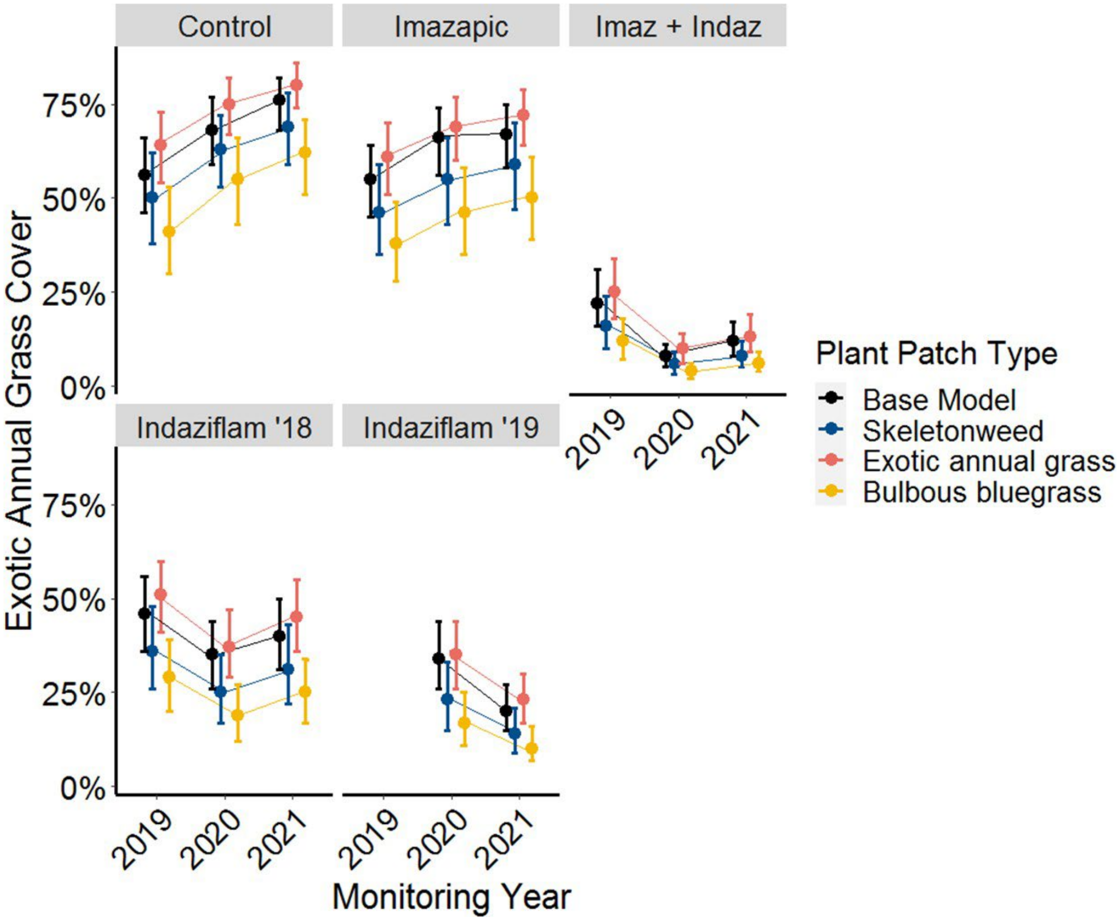

Figure 4 Mean ± 95% CI cover predictions of exotic annual grasses by treatment and sample year. Predictions made from generalized linear mixed effects models with a beta distribution fitted with line-point intercept data. "Plant Patch Type" groups represent the three different plant-community patch types identified through imagery classification along with the base model (plant-community patch type not included as predictor). Indaziflam applied in 2019 was considered untreated for the 2019 monitoring year and excluded from the figure.

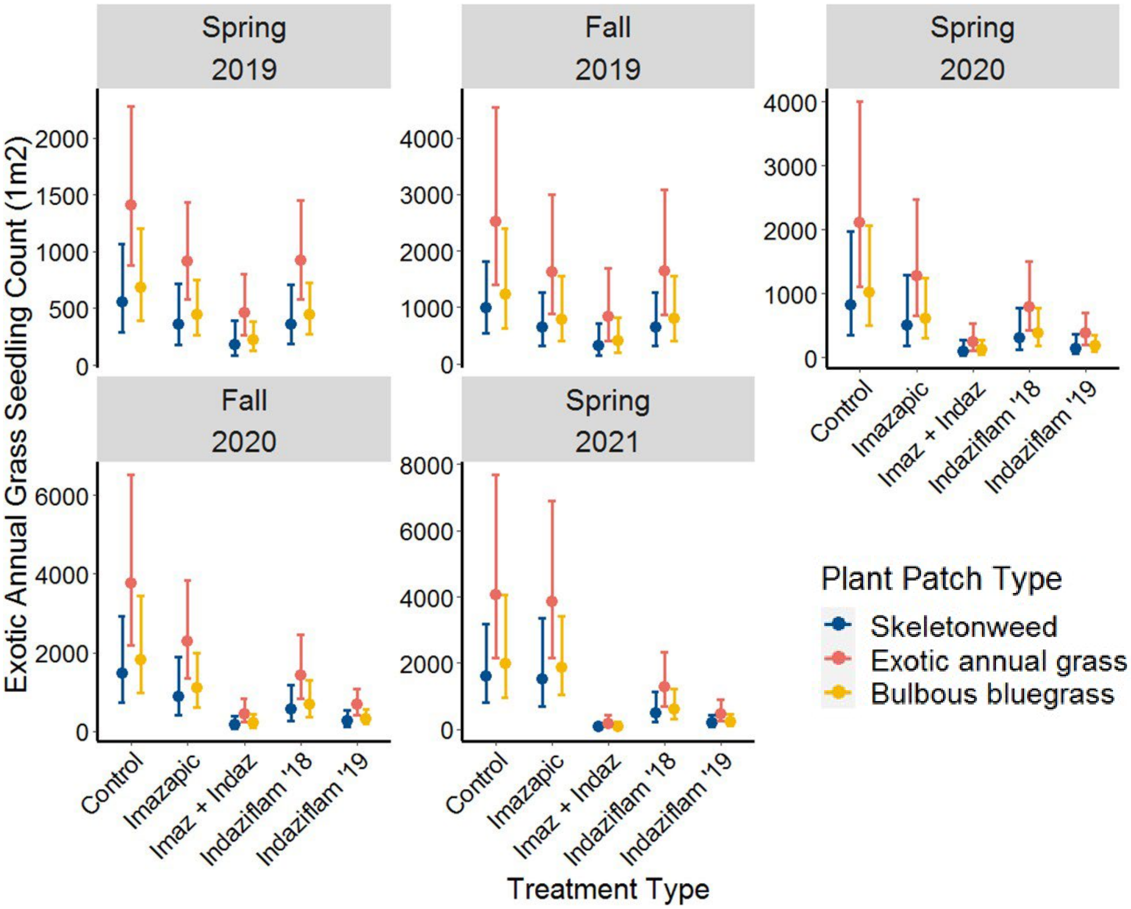

Figure 5 Mean ± 95% CI seedling count predictions ($1m^2$) of exotic annual grasses by treatment and sample time. Predictions made from generalized linear mixed effects model with a zero-inflated negative binomial distribution. "Plant Patch Type" groups represent the three different plant-community patch types identified through imagery classification of the site.

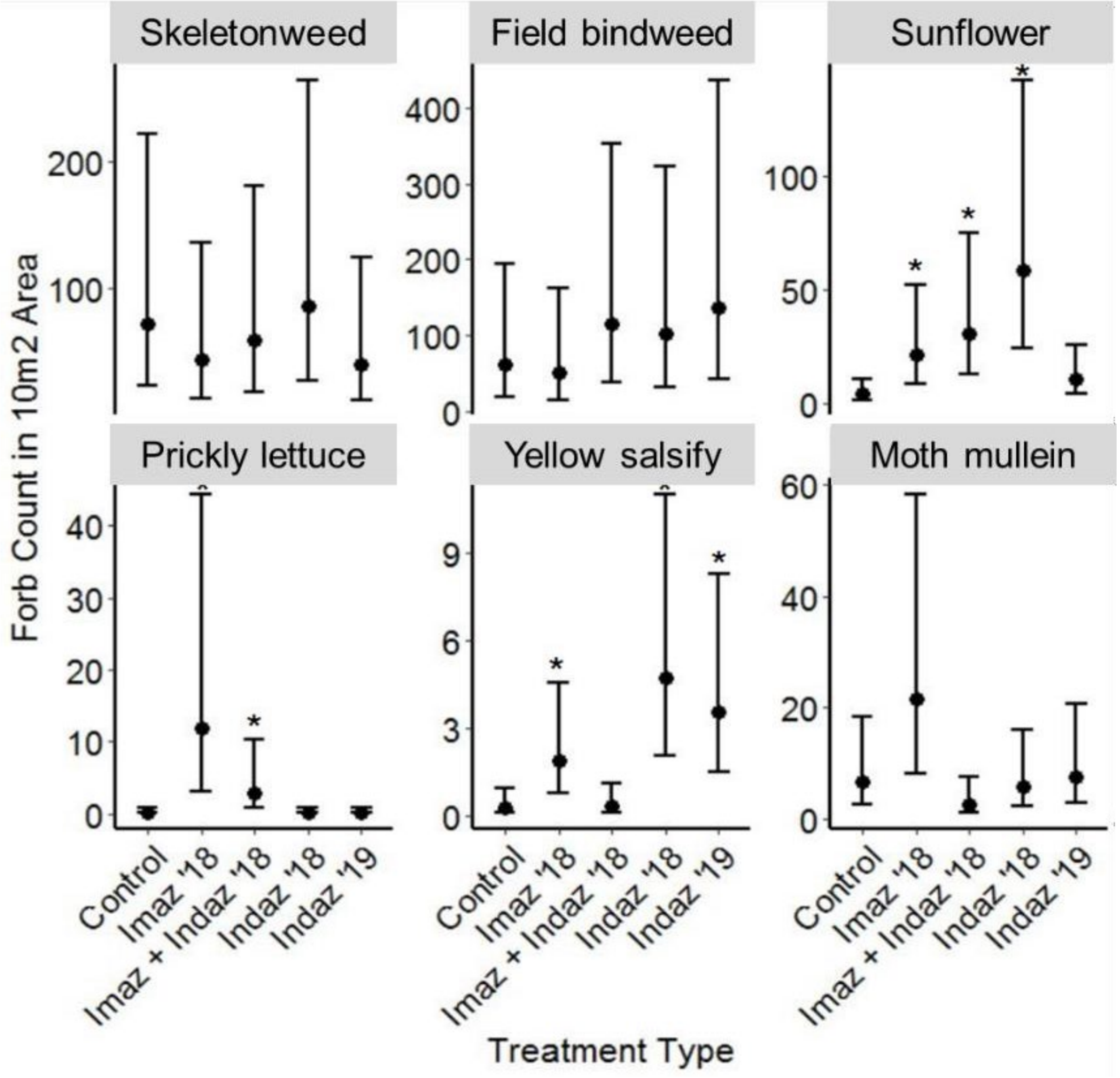

Figure 6 Mean ± 95% CI count prediction of exotic forbs in a $10m^2$ area. Predictions made using a generalized linear mixed effects model with a negative binomial distribution and fitted with density count data collected in summer of 2021 for exotic perennial forbs (n=15 per treatment). Starred treatments are significantly different from their respective controls based on 95% confidence interval overlap.

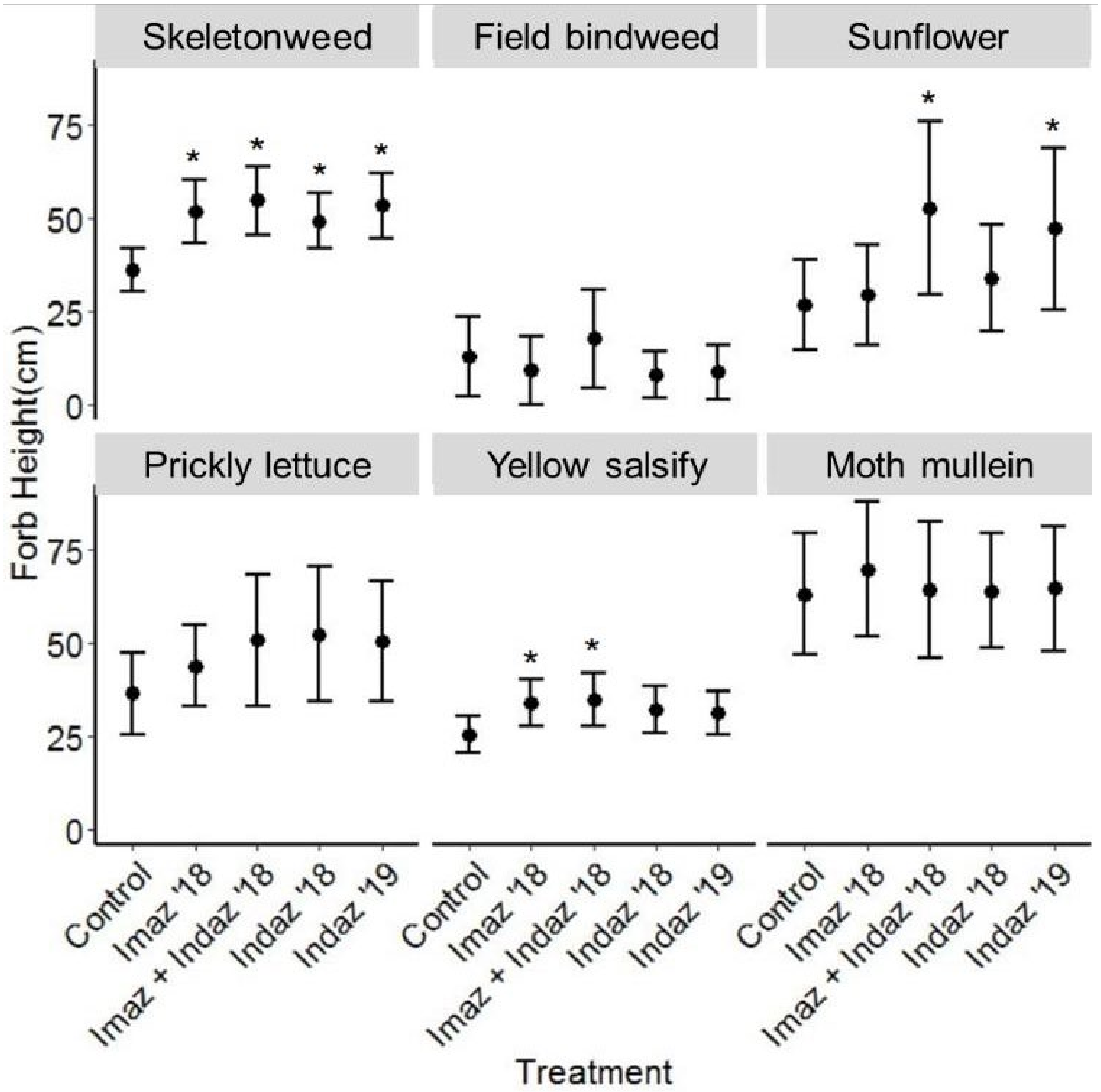

Figure 7 Mean ± 95% CI height predictions (cm) of exotic forbs. Predictions made using a generalized linear mixed effects model with a gamma distribution and fitted with density count data collected in summer of 2021 for exotic perennial forbs (n=15 per treatment type). Starred treatments are significantly different from their respective controls based on 95% confidence interval overlap.

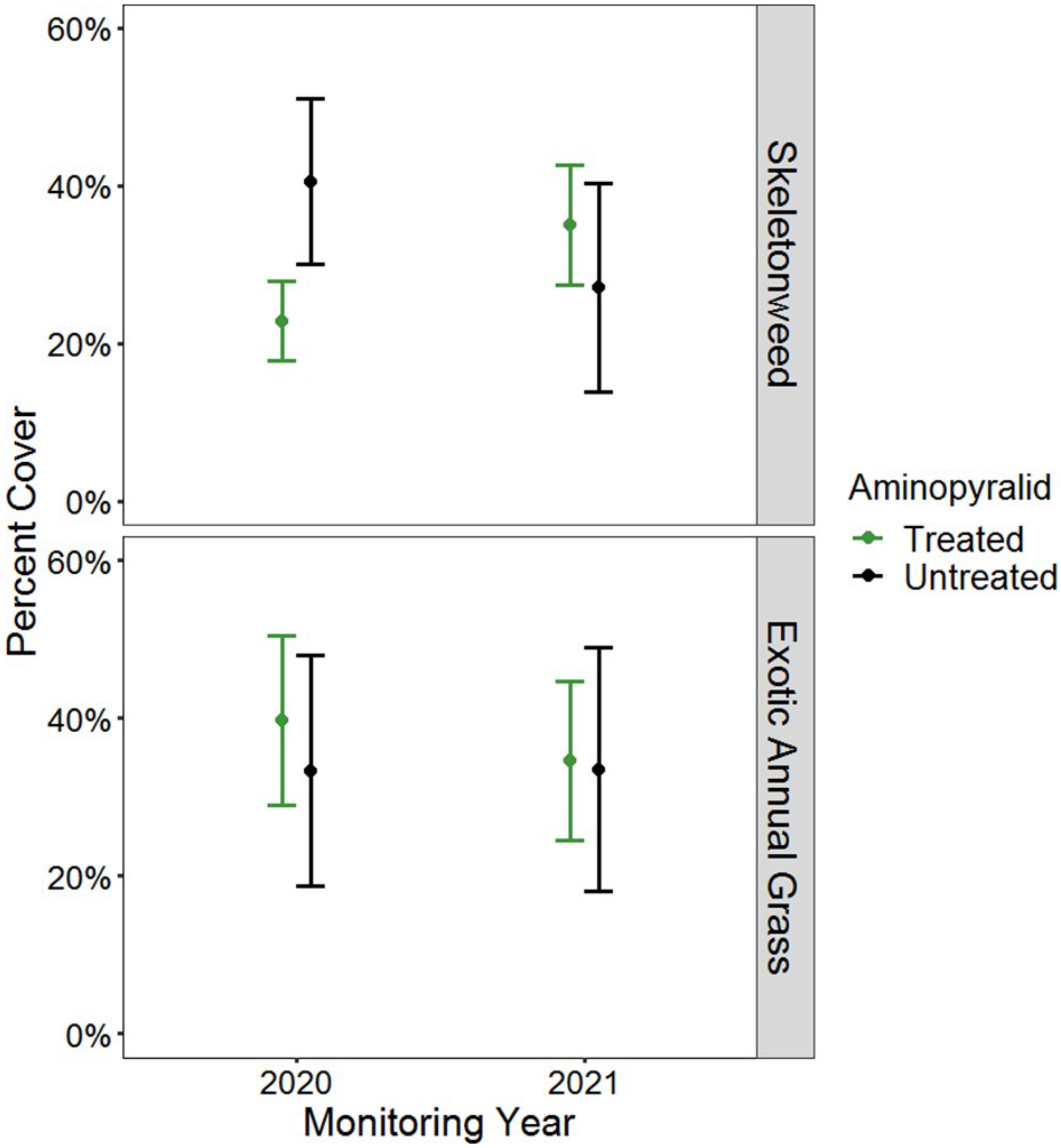

Figure 8 Cover of skeletonweed or exotic annual grass cover by treatment type and sample year. Groups labeled "Treated" represent the 4x4m subplots where the herbicide aminopyralid was applied and "Untreated" represent the adjacent 4x4m subplots that were not treated with aminopyralid.

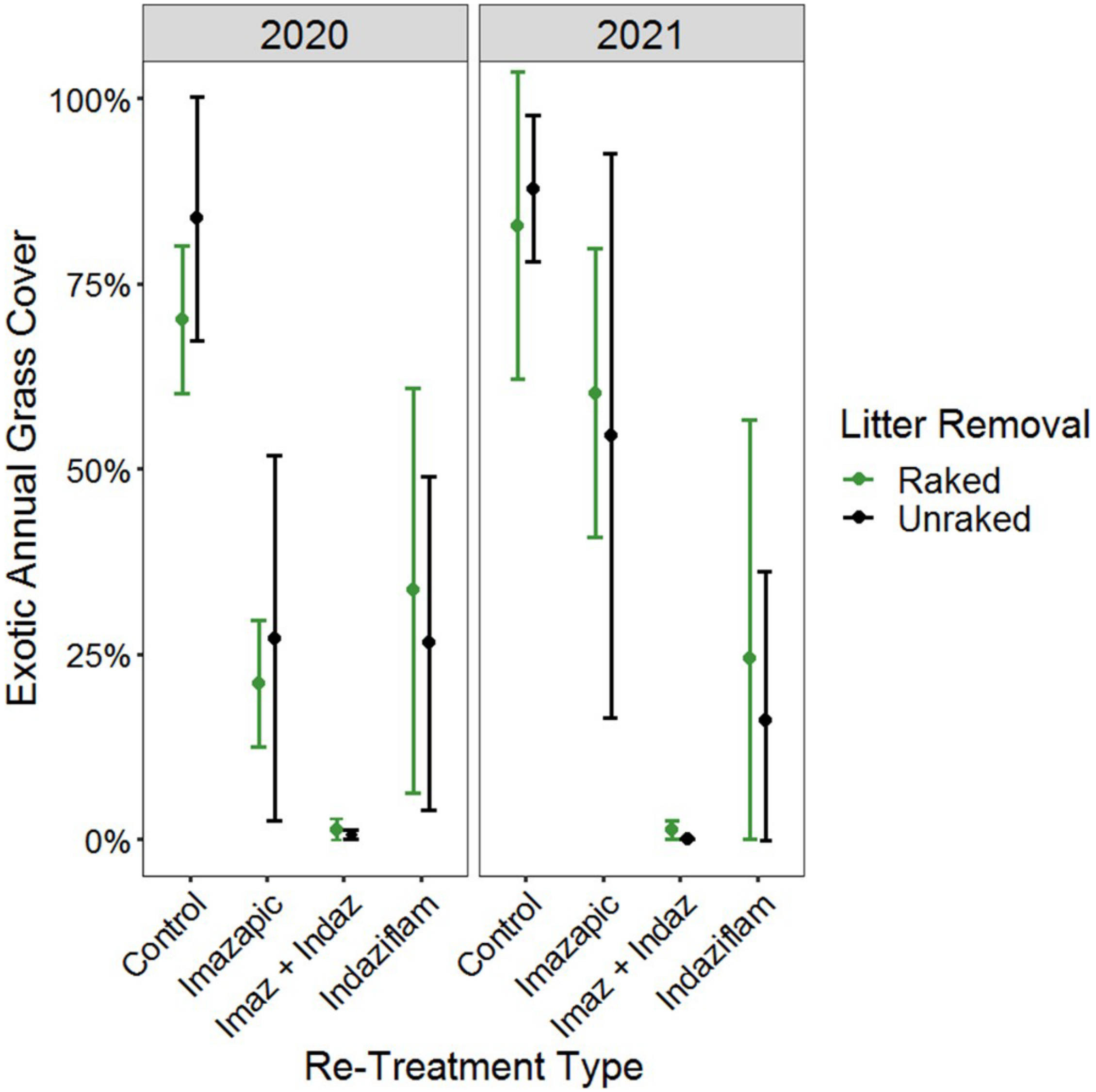

Figure 9 Exotic annual grass cover responses to raking prior to re-treatment of each herbicide type by sample year (2020, 2021).

Tables

Table 1 Post-Treatment Precipitation Totals and 20-Year Monthly Averages

Precipitation totals (mm) one month following treatment application and 30-year monthly total precipation averages. 30-year mean precipitation totals retrieved from PRISM climate group (4-km2 pixel PRISM data, 1991–2020) and post-treatment precipitation totals acquired from Weather Underground historical weather data for the Harris Ranch Station (located within 3 km of the Top Hat field site).

Treatment Name	20-yr Average Month	Application Date	30-yr mean precipitation Totals (mm)	Post-treatment precipitation Totals (mm)
Indaziflam '18, Imazapic '18, Imazapic + Indaziflam '18	November	10/25/2018	38.91	0
Handplanting		10/24/2019		5.33
Drill Seeding '18		11/4/2018		17.02
Indaziflam '19, Aminopyralid	September	8/28/2019	12.35	17.78
Litter Removal + Re- spraying	December	12/6/2019	54.52	19.05
Drill Seeding '19	January	12/18/2019	51.06	33.27

Table 2 Model Comparisons for exotic annual grass cover by treatments

Model descriptions for exotic annual grass density (negative binomial) and cover (beta). Both models are generalized linear mixed effects models fitted with a maximum likelihood estimation via 'TMB' (Template Model Builder). “Plant Patch Type” = three different plant communities identified through imagery classification of the site, “Year”= sample year, and “Season” = Fall or Spring sampling.

Model Name	**Distribution**	**Df**	**AIC**	**RMSE**
	negative binomial (zero - inflated)			
"Patch"	Treatment Type*Year + Plant Patch Type + Transect ID + Treatment Block	18	962.6	12.9
"Block"	Treatment Type*Year + Transect ID + Treatment Block	17	931.9	15.3
"Null"	Treatment Type*Year	16	- 929.6	21.7
	beta			
"Patch"	Treatment Type*Year + Plant Patch Type + Transect ID + Treatment Block	35	4424	1135.7
"Block"	Treatment Type*Year + Transect ID + Treatment Block	31	4455	1295.8
"Null"	Treatment Type*Year	32	4462	1300.7

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APPENDIX

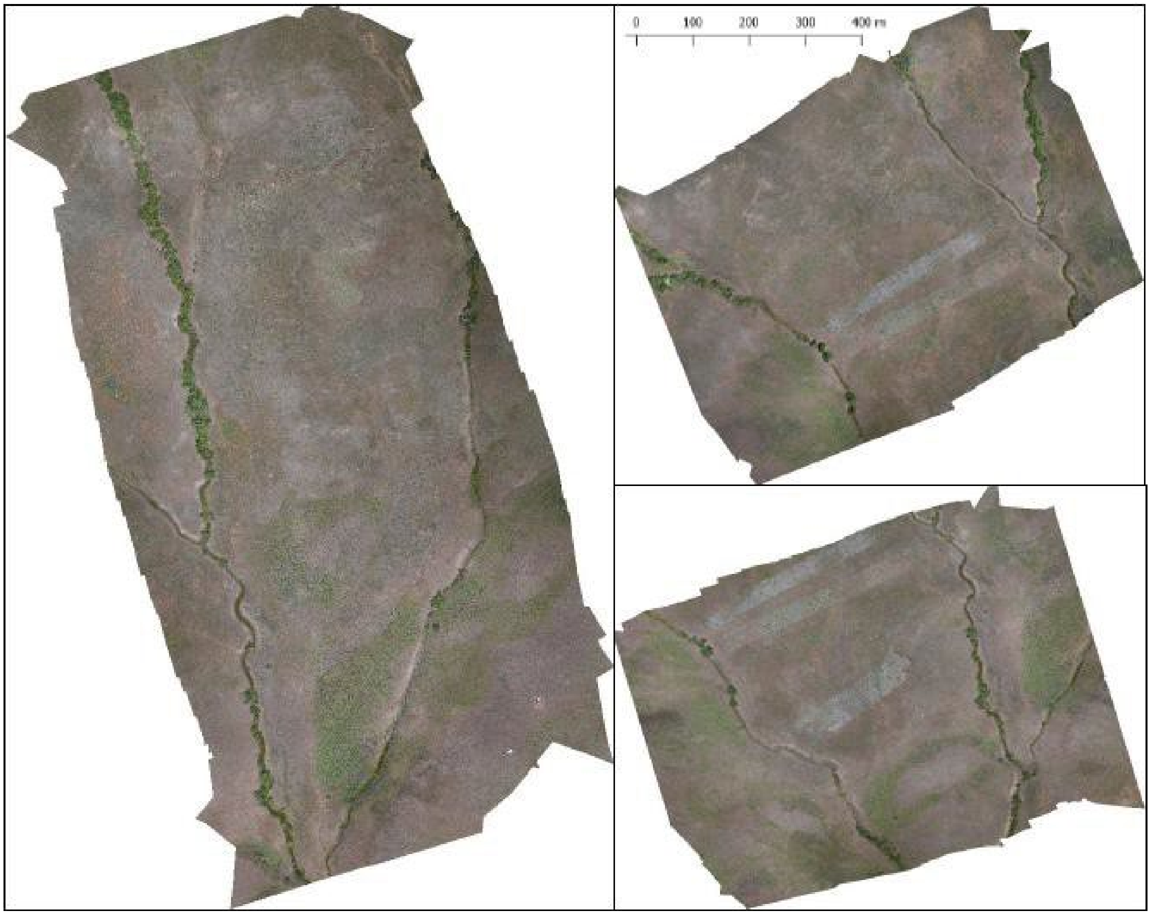
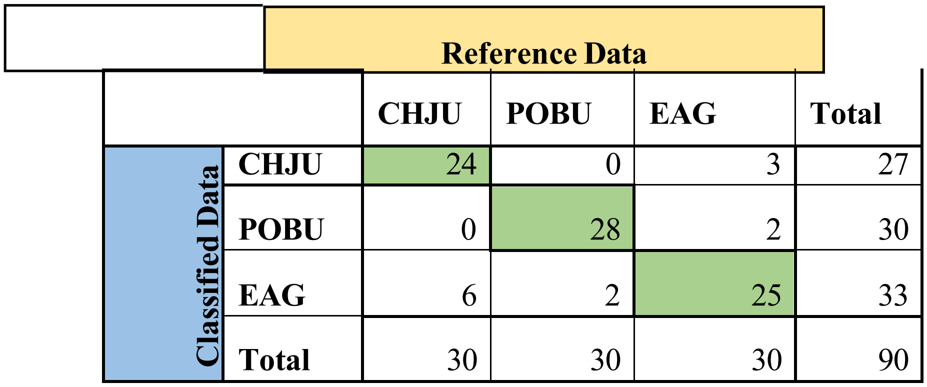


Figure S1 **Orthophotos from the UAV imagery in acquire in August of 2019, collected by Idaho State University and Donna Delparte, separated by Treatment Block. Block 3 (left), Block 1 (top right), and Block 2 (bottom right).**



		Reference Data			
		CHJU	**POBU**	**EAG**	**Total**
Classified Data	**CHJU**	24	0	3	27
	POBU	0	28	2	30
	EAG	6	2	25	33
	Total	30	30	30	90

Figure S2 Confusion matrix for all treatment blocks. Numbers represent number of training points assigned to each classification category. Inaccuracy was highest between CHJU and EAG classes. The overall accuracy was 86% with a Kappa of .82

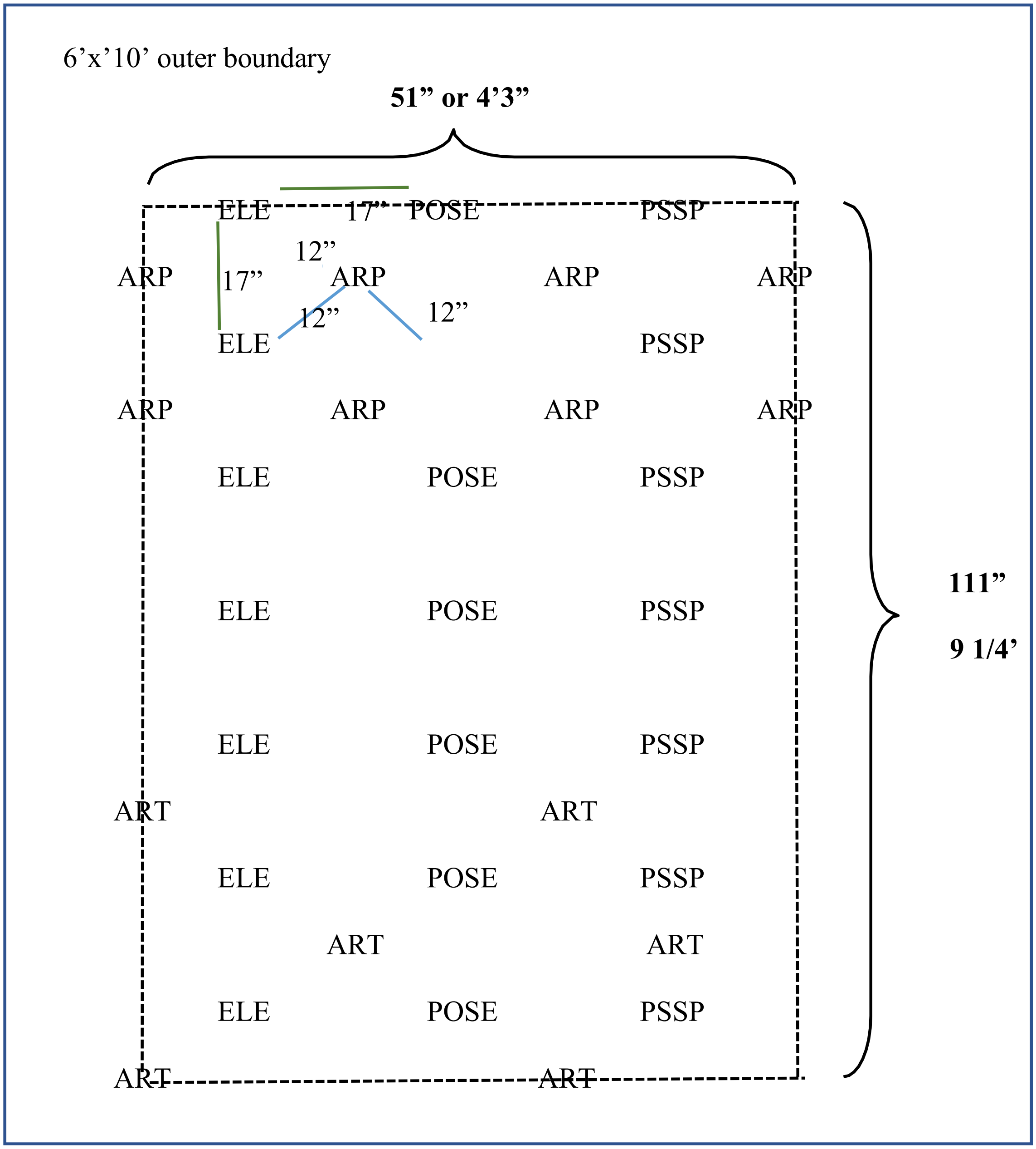


Figure S3 Seedling planting design for hand planted subplots. One subplot was applied per replicate treatment block (n=3 per treatment type). “ARTR” = sagebrush, “PSSP” = bluebunch wheatgrass, “ELEL” = squirrel tail, “POSE” = sandberg’s bluegrass and “ARPU” = purple three awn.

Table S1 **Drill Seeding Mix for The 2018 And 2019 Drill Treatments**

Treatments were applied at 33 lbs. per acre with a rangeland drill in late summer and fall respectively

Seed Proportion	**Common Name**	**Scientific Name**
0.449	Bluebunch wheatgrass	*Pseudoroegneria spicata* (Pursh) Á. Löve
0.189	Sandbergs bluegrass	*Poa secunda* J. Presl
0.199	Squirreltail	*Elymus elymoides* (Raf.) Swezey
0.09	Needle and thread	*Hesperostipa comata* (Trin. & Rupr.) Barkworth
0.013	Snakeriver wheatgrass	*Elymus wawawaiensis* J. Carlson & Barkworth
0.013	Munros globemallow	*Sphaeralcea munroana* (Douglas) Spach
0.003	Common milkweed	*Asclepias syriaca* L.
0.013	Lewis flax	*Linum lewisii* Pursh
0.015	Praire clover	*Dalea ornata* (Douglas ex Hook.) Eaton & J. Wright
0.006	Yarrow	*Achilliea millefolium*
0.01	Shaggy fleabane	*Erigeron pumilus*