IMPACTS OF A NON-NATIVE FORB, *ALYSSUM DESERTORUM* STAPF., AND NON-TARGET EFFECTS OF INDAZIFLAM IN THE SAGEBRUSH STEPPE OF YELLOWSTONE NATIONAL PARK

by

Jordan Meyer-Morey

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science
in
Land Rehabilitation

MONTANA STATE UNIVERSITY
Bozeman, Montana

January 2021

ACKNOWLEDGEMENTS

I would like to thank my primary advisor, Dr. Lisa Rew, for her continued support. This research and thesis would not have been possible without her guidance and patience. I would also like to thank the other members of my committee, Dr. Jane Mangold, Dr. Catherine Zabinski, and Dr. Matthew Lavin, for their expertise and counsel.

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Non-native plants can reduce biodiversity and disrupt essential ecosystem services and functions. For most non-native plant species however, quantitative evidence of negative effects is lacking, as are fundamental demographic details; such information can inform whether and at what growth stage to implement control. Control strategies can also negatively impact non-target native plant communities; therefore, evaluating the tradeoffs of management and understanding the actual impacts of the invader is essential. I sought to understand the life history, and evaluate the competitiveness and impacts of the non-native annual forb, *Alyssum desertorum* Stapf., as well as non-target effects of management, across an elevation gradient in a cool, mountain sagebrush (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle) steppe plant community.

Seed viability, fecundity, overwintering success, and likelihood of reaching reproductive maturity of *A. desertorum* all declined as elevation increased; all life stage transition rates were high, suggesting that targeting seed production or fall germination would be the most effective means for control of this species. Replacement series experiments revealed that *A. desertorum* is a weak competitor with functionally similar species. Additionally, in the field, the presence of *A. desertorum* did not affect species richness nor Shannon's diversity aboveground or in the soil seedbank, and functionally similar native annual forbs were not displaced in invaded areas.

I evaluated the efficacy and non-target effects of the pre-emergent herbicide, indaziflam, in diverse sagebrush steppe with localized infestations of *A. desertorum* across an elevational gradient. While indaziflam effectively controlled *A. desertorum* for two years, the richness and diversity of the surrounding community was reduced. Indaziflam inhibited recruitment of forbs, both in the field and in the seedbank. As indaziflam provides residual control of the soil seedbank for up to three years, my results suggest the future community composition may be altered, particularly native annual forb populations. Considering the weak competitive ability of *A. desertorum,* the species' minimal impacts to richness and diversity, and the negative effects of indaziflam to annual native forb species, I conclude that the non-target effects of indaziflam would outweigh any benefits to controlling *A. desertorum* in intact sagebrush steppe.

CHAPTER ONE

INTRODUCTION TO THESIS

Impacts of Non-Native Invasive Plants on Biodiversity

Invasive species are one of the leading direct causes of global biodiversity loss and can significantly alter ecosystem functions and services (Sala et al. 2000, Vilà et al. 2010). Invasive plants can modify native plant communities, resulting in altered disturbance regimes, transformed ecosystem functions, and an overall reduction in biodiversity (Elton 1958, Mack and D'Antonio 1998, Tilman 1999, Vilà et al. 2011). Ecosystem level effects can occur when the invasive plant differs from the resident plant species in resource acquisition, alters the trophic structure of the invaded area, or changes the disturbance frequency and/or intensity of the invaded area (Vitousek 1996). Most non-native species, however, do not become invasive or have ecosystem level effects (Williamson and Fitter 1996, Simberloff 2011), and the impacts of non-native plants are quite variable and species specific (Hejda et al. 2009, Vilà et al. 2011, Thompson 2014).

Non-native plants that do become invasive can have negative impacts on individual native plant species, leading to reduced native biodiversity (Vilà et al. 2011). At larger, global scales non-native plant invasions typically increase biodiversity, however at smaller, localized scales the effects can be positive or negative (Powell et al. 2011, Peng et al. 2019). Invasive non-native species can reduce the fitness and growth (Skurski et al. 2014) and suppress seed germination and seedling recruitment of native plants (Lesica and Shelly 1996), altering plant community species composition (Skurski et al. 2014) and increasing the abundance of non-native species. This dominance of non-native plants causes native species to become rare and results in a less diverse community (Parker et al. 1999, Hejda and Pyšek 2006). Ranked order of abundance can reveal a shift in species composition of a community as a result

of invasion, and this decline in native plant abundance following invasion could be a precursor to invasion-mediated species loss (MacDougall and Turkington 2005).

Changes in aboveground plant diversity also manifest in the soil seedbank. In a meta-analysis of 18 invasive non-native plants comparing invaded and uninvaded communities, Gioria et al. (2014) found that species richness and density of the native soil seedbank was lower in areas invaded by non-native plants. This reduction in native seedbank diversity can impact the aboveground plant community and make it difficult to rely on the seedbank for passive restoration once an invader is removed. However, these findings are largely driven by a few intensively studied species, and there is a need for more seedbank studies in invasion ecology (Gioria et al. 2014).

Understanding the impacts of individual non-native invasive plants is imperative, as effects on native plant communities differ between species (Hejda et al. 2009, Vilà et al. 2011). This is especially true because for most non-native species classified as invasive in North America, quantitative evidence of ecosystem alteration and impacts to species diversity due to invasion is either lacking or anecdotal (Blossey 1999, Hulme et al. 2013). Research focused on individual non-native species can help us to understand their unique attributes that promote invasion (Davis 2009) and to quantify their actual impacts (Hulme et al. 2013) in order that management can be prioritized, targeted and effective.

Invasion Ecology

Non-native species invasion is influenced by the properties of the environment, characteristics of both the native and non-native species, and available propagule pressure (Lonsdale 1999). Environments high in diversity are more resilient to stress and disturbance as functional redundancy allows for elasticity in species composition while maintaining ecosystem function (Peterson et al. 1998). Species and functional diversity reduce the impacts of invaders on resident species (Dukes 2001).

High diverse areas are more resistant to invasions as a result of niche saturation (Elton 1958, Chambers et al. 2014) and associated resource uptake. However, disturbance generally causes an increase in resource availability via the removal of existing plants (Davis et al. 2000), which can facilitate invasion of "opportunistic" disturbance-oriented species (both native and non-native; Prevéy et al. 2010) that grow rapidly, disperse high amounts of seed, and have short life spans. The long-term success of such species depends on whether the site is further disturbed, which will likely benefit similar early successional species. Conversely, if the site remains undisturbed, in which case it will likely be colonized by secondary successional species.

Non-native species that establish following a land disturbance may be considered passengers of change rather than direct drivers, and their impacts more symptomatic of the disturbance (MacDougall and Turkington 2005, Davis 2009). However, a subset of invasive plants ('transformer species') have the capacity to have large scale ecosystem impacts (Richardson et al. 2000), stressing that not all non-native plants are equal and have unique characteristics to facilitate invasion. The biological characteristics of invasive non-native plants play an important role in the invasion process (Lonsdale 1999, Radosevich et al. 2007). Examination of morphological, physiological, and life history traits that contribute to successful invasion (Thompson et al. 1995, Pyšek and Richardson 2007) can help improve understanding of the invasion process and increase success of control efforts. Baker (1974) provided a summary of 'ideal weed' characteristics, although these characteristics can also describe 'weedy' native species (Sutherland 2004) that are also able to colonize following disturbance.

Many non-native plants generate high propagule pressure that makes them highly successful in the presence of established native vegetation (Levine et al. 2003). Non-native species with high seed production (MacDougall and Turkington 2005, Radosevich et al. 2007) and rapid germination are able to establish early dominance after disturbance (Fischer et al. 2009, Gioria et al. 2014), although it should be

noted that some native species perform similarly. Seed production and germination rates are key stages of a species' life cycle along with seedbank longevity, seedling survival, length of time as immature and mature plant. Understanding a species' life stage transitions and sensitivity of these stages (elasticity analysis) allows for evaluation of stages that are most vulnerable to change (Pardini et al. 2009, James et al. 2012). However, there is a lack of life cycle models for many non-native plants in North America (Gioria et al. 2014).

Impacts of Non-Native Winter Annual Plants in Sagebrush Steppe

Across arid and semi-arid areas of the western United States, sagebrush ecosystems have been negatively impacted by invasive plants. This sagebrush steppe biome historically covered 529,000 km^2, however due to land use changes and non-native plant invasions it currently occupies about 56% of this historical range (Miller et al. 2011). Greater sage-grouse (*Centrocercus urophasianus* Bonaparte) is a keystone species in this biome and its habitat supports many other wildlife species, however degradation of the ecosystem threatens its survival (Connelly et al. 2004). Greater sage-grouse consume a variety of native plant species (Drut et al. 1994) and both food and cover are positively correlated with chick survival (Gregg and Crawford 2009). Many annual forb species provide critical early spring forage (Luna et al. 2018). The main motives to conserve and restore this habitat type are for protection of sage-grouse and other sagebrush dependent species, and sustainable grazing operations for ranchers.

Land use changes that have taken place in the sagebrush steppe have coincided with a proliferation of non-native winter annual plants that exploit an unused temporal niche. Most native plants in the sagebrush steppe are perennials or summer annuals that typically emerge in the spring. Winter annuals are characterized by a fall or winter germination and a dormancy period over the winter, and utilize resources immediately following the spring thaw (Grime 1979) when most native plants are

only beginning to grow. Non-native winter annual plants have the potential to reduce plant diversity, threaten rare and endangered species, reduce wildlife habitat and forage, alter fire regimes, increase erosion, and deplete soil moisture and nutrient levels in the sagebrush steppe (Billings 1994, DiTomaso 2000). Winter annual grasses specifically pose the greatest threat to sagebrush ecosystems, displacing native vegetation by altering fire regimes (Billings 1994, Balch et al. 2013), effectively competing for water, and increasing soil erosion (DiTomaso 2000). The resulting novel annual grasslands do not provide adequate habitat for wildlife or for grazing. While the impacts of invasive winter annual grasses in sagebrush ecosystems have been extensively studied (Germino et al. 2016), less attention has been given to winter annual broadleaf species that often co-occur.

Many invasive broadleaf species have expanded their range in the western U.S. due to soil disturbance by human activities and overgrazing (DiTomaso 2000). Invasive broadleaf species typically produce large numbers of seed and have long taproots that enable moisture extraction from deep in the soil (DiTomaso 2000). Anecdotal evidence suggests that annual grass invasion is often preceded by a dominant non-native annual forb community (Young and Clements 2005), such as *Alyssum desertorum* and other Brassicaceae, however further study is required. *Alyssum desertorum* acts as a facultative winter annual, meaning it can germinate in either the fall or the spring (Mosley 2014). Fall germination gives *A. desertorum* a competitive advantage over native annual forbs but little is known about its seedling overwintering success or other life cycle components.

Alyssum desertorum seeds disperse via ombrohydrochory, from water droplets which cause the activation of ballistic mechanisms in the plant (Liu et al. 2014). Seeds are also dispersed by vehicles (Rew et al. 2018) and by western harvester ants (*Pogonomyrtnex occidentalis*), which have a high preference for *A. desertorum* seeds (Crist and MacMahon 1992). *Alyssum desertorum* is classified as a weak invader and requires soil disturbance to establish (Jacobs 2012). Substantial increases of *A. desertorum*

populations have been observed following wildfire in sagebrush (Bates et al. 2004). Overall, there are significant knowledge gaps in the ecology and life stage demographics of *A. desertorum* that, if filled, may help better understand invasion in the sagebrush steppe and inform management decisions.

Managing Non-Native Plants

The success of non-native plants is driven by increased human disturbances, land use changes, and global climate change (Walther et al. 2005, Thuiller et al. 2007, Lenoir et al. 2010). The serious impacts non-native species can impose on all segments of society have driven the passage of multiple executive orders in the United States addressing the need to reduce these impacts and to prevent further invasions (Meyerson et al. 2019). Certain species have been deemed “noxious” and are considered so destructive that landowners and government agencies are legally required to control them. Understanding the invasiveness of individual non-native plant species can help direct management efforts towards those that are undoubtedly having negative impacts.

Techniques to manage non-native plants include physical, cultural, biological and chemical methods (Radosevich et al. 2007), however each technique has limitations and a combination of approaches should be applied. Some methods, such as the use of herbicides, can have negative effects on existing native communities in natural areas (Radosevich et al. 2007, Rinella et al. 2009, Wagner and Nelson 2014).

The motivation for non-native plant management in natural wildland areas is to preserve and protect the native plant communities and their ecosystem functions, therefore, potential negative impacts to native plants should be evaluated before active management is implemented. Rangelands present their own unique challenges for non-native plant management. Western rangelands are typically remote, arid, and experience extensive human driven disturbance, such as intensive cattle

grazing operations and recreational activities. The rugged and remote characteristic of rangelands make management of large non-native plant invasions difficult due to limited machinery access. Annual grasses are the most frequent target of management in the sagebrush, and herbicide, seeding and grazing are the most frequently used approaches in Wyoming, Colorado (Kelley et al. 2013) and Montana (Mangold, unpublished). The scale of herbicide application spans from backpack spray application for small patches to aerial application for larger or more inaccessible patches.

In order to successfully eradicate or control an invasive plant, the most sensitive life cycle transitions should be targeted (Radosevich et al. 2007, Ramula et al. 2008); in annual plants this is often seed production and/or longevity in the soil. Herbicides can deplete the seed bank, either by removing aboveground vegetation before the plant produces seeds (post-emergent) or by preventing seeds in the soil from emerging (pre-emergent). Pre-emergent herbicides can either disrupt germination or kill the germinating seedling. Herbicides with soil residual activity can provide pre-emergent control for several months to longer time periods depending on the herbicide, soil chemistry and climate.

The active ingredient indaziflam can provide long-term control of annual non-native grass and forb species (Sebastian et al. 2017a, Sebastian et al. 2017b, Clark et al. 2020). Originally developed in 2010 for turf and orchard use, indaziflam was approved under the trade name Esplanade™ for use in non-crop areas such as parks and open space, wildlife management areas, fire rehabilitation areas, and other non-grazed, wildland sites in 2016 by its developer, Bayer CropScience (Sebastian et al. 2017b). In June 2020 indaziflam was approved for further use in rangeland, CRP land and natural areas, including grazed areas (Bayer 2020) under the trade name Rejuvra™. Indaziflam is a member of the alkylazine herbicide family and has a unique mode of action as a cellulose biosynthesis inhibitor affecting the roots of germinating seeds. It potentially provides pre- and post-emergence control of both annual grass and

broadleaf weeds (Kaapro and Hall 2012). Its physical properties provide residual control on the top 3 cm of the soil for up to three years (Sebastian et al. 2017a).

Most field studies examining efficacy of indaziflam in wildlands have occurred in areas primarily dominated by invasive winter annual grasses with covers of 70 to 100 percent for *Bromus tectorum* (Sebastian et al. 2017a, Sebastian et al. 2017b, Clark et al. 2020). These studies show that the herbicide effectively controls *B. tectorum*, however to date there is only one study examining the effects of indaziflam on native vegetation that is not dominated by *B. tectorum* (Clark et al. 2019). This study showed no negative impacts to the established perennial native plant community where 33-35 native species were present, and pre-application cover of *B. tectorum* was between 30 and 70% cover (Clark et al. 2019).

The impacts of indaziflam to both native and non-native species in the seedbank should also be considered (Sebastian et al. 2017b). Herbicides with no soil longevity deplete the seedbank with annual applications; applying the non-selective herbicide glyphosate for five years reduced *B. tectorum* populations (Sebastian et al. 2016a). Indaziflam, which has soil longevity up to 3 years, can effectively suppress the non-native seed bank of both annual and perennial species in highly invaded areas (Sebastian et al. 2017b, Sebastian et al. 2017c). However, there have been no studies to date on effects on the native seed bank in intact areas with diverse vegetation. Since indaziflam targets the seedbank, seeds of native species are expected to be impacted along with non-native annual plants.

Indaziflam to Control Desert Alyssum in Yellowstone National Park

While *A. desertorum* is widespread in the sagebrush steppe of the northern range of Yellowstone National Park (YNP), it was recently discovered in diverse, intact sagebrush communities at elevations outside of its documented range. This prompted YNP land managers to evaluate potential

control methods, including the use of indaziflam, to eradicate these new populations and prevent further spread.

In YNP, non-native species represent about 15% of the total flora (Whipple 2001). In 2015 YNP land managers actively controlled 120 acres infested with non-native plants, 83% (100 acres) of which were treated with herbicides (Perrotti 2017). In the Gardiner Basin of YNP, an area with a long history of land disturbance (Hamilton and Hellquist 2012), land managers are using indaziflam to control non-native winter annual plants, including *A. desertorum*. Because there is little remaining native vegetation in these areas, it is likely the seedbank is depleted of native species. It is likely that indaziflam will be used to control non-native plants in other areas of the park that may have more intact native plant communities, prompting this research.

In Chapter 2, I evaluate life cycle transitions of *A. desertorum* and evaluate its competitiveness with two annual species, one spring germinating native annual forb species, *Microsteris gracilis*, and one fall germinating non-native annual grass, *B. tectorum*. In Chapter 3, I also evaluate how *A. desertorum* impacts the diversity of native plant communities, and assess the effects of indaziflam on the abundance of *A. desertorum* and all other plants over a 2-year period, and the effects of indaziflam on germination from the soil seedbank. This will provide more information on how indaziflam impacts surrounding native plant communities, including native annual forbs. In the final chapter, I bring together these results and place them in a broader management context.

References

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics **5**:1-24.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology **19**:173-183.

Bates, J., K. Davies, and R. Miller. 2004. Ecology of the Wyoming big sagebrush alliance in the northern Great Basin:2004 Progress Report. Burns, Oregon, USA: Eastern Oregon Agricultural Research Center. 65 pp.

Bayer. 2020. Rejuvra herbicide receives EPA approval. New herbicide is a long-term, economical solution for the control of invasive annual grasses, Bayer Environmental Science, 5000 CentreGreen Way, Suite 200, Cary, NC 27513.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. Proceedings-Ecology and Management of Annual Rangelands **313**:22-30.

Blossey, B. 1999. Before, during and after: the need for long-term monitoring in invasive plant species management. Biological invasions. **1**:301-311.

Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems **17**:360-375.

Clark, S. L., D. J. Sebastian, S. J. Nissen, and J. R. Sebastian. 2019. Effect of indaziflam on native species in natural areas and rangeland. Invasive Plant Science and Management **12**:60-67.

Clark, S. L., D. J. Sebastian, S. J. Nissen, and J. R. Sebastian. 2020. Evaluating winter annual grass control and native species establishment following applications of indaziflam on rangeland. Invasive Plant Science and Management **13**:199-209.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation asessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Cheyenne, Wyoming.

Crist, T. O., and J. A. MacMahon. 1992. Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. Ecology **73**:1768-1779.

Davis, M. A. 2009. Invasion Biology. Oxford University Press Inc.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of ecology. **88**:528-534.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. Weed Science **48**:255-265.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Technical Note: Diet and food selection of sage grouse chicks in Oregon. Journal of Range Management **47**:90-93.

Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. Oecologia **126**:563-568.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Springer, Boston, MA.

Fischer, J. L., W. A. Loneragan, K. Dixon, and E. J. Veneklaas. 2009. Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. Biological Conservation **142**:256-269.

Germino, M. J., J. C. Chambers, and C. S. Brown. 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications. 1st ed. 2016 edition. Cham: Springer International Publishing, Cham.

Gioria, M., V. Jaroˇsík, and P. Pyˇseka. 2014. Impact of invasions by alien plants on soil seed bank communities: Emerging Patterns. Perspectives in Plant Ecology, Evolution and Systematics **16**:132-142.

Gregg, M. A., and J. A. Crawford. 2009. Survival of greater sage-grouse chicks and broods in the northern Great Basin. The Journal of Wildlife Management **73**:904-913.

Grime, J. P. 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester.

Hamilton, E. W., and C. E. Hellquist. 2012. Yellowstone's most invaded landscape: vegetation restoration in Gardiner Basin. Pages 25-32 Yellowstone Science.

Hejda, M., and P. Pyšek. 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? Biological Conservation **132**:143-152.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology **97**:393-403.

Hulme, P. E., P. Pyšek, V. Jarošík, J. Pergl, U. Schaffner, and M. Vilà. 2013. Bias and error in understanding plant invasion impacts. Trends in Ecology & Evolution **28**:212-218.

Jacobs, J. S. 2012. Plant fact scheet for desert madwort (*Alyssum desertorum*).*in* U.-N. R. C. Service, editor., Bozeman State Office, MT.

James, J. J., M. J. Rinella, and T. Svejcar. 2012. Grass seedling demography and sagebrush steppe restoration. Rangeland Ecology & Management **65**:409-417.

Kaapro, J., and J. Hall. 2012. Indaziflam-a new herbicide for pre-emergent control of weeds in turf, forestry, industrial vegetation and ornamentals. Pak. F. Weed Sci. Res. **18**:267-270.

Kelley, W. K., M. E. Fernandez-Gimenez, and C. S. Brown. 2013. Managing downy brome (Bromus tectorum) in the Central Rockies: land manager perspectives. Invasive Plant Science and Management **6**:521-535.

Lenoir, J., J.-C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N. E. Zimmermann, S. Dullinger, H. Pauli, W. Willner, and J.-C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography **33**:295-303.

Lesica, P., and J. S. Shelly. 1996. Competitive effects of *Centaurea maculosa* on the population dynamics of Arabis fecunda. Bulletin of the Torrey Botanical Club:111-121.

Levine, J., M., M. Vilà, C. Antonio, M. D., J. Dukes, S., K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London. Series B: Biological Sciences **270**:775-781.

Liu, H., D. Zhang, X. Yang, Z. Huang, S. Duan, and X. Wang. 2014. Seed dispersal and germination traits of 70 plant species inhabiting the Gurbantunggut Desert in northwest China. Scientific World Journal **2014**:346405.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522-1536.

Luna, T., M. R. Mousseaux, and R. K. Dumroese. 2018. Common native forbs of the northern Great Basin important for Greater Sage-grouse. Gen.Tech.Rep. RMRS-GTR-387, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station; Portland, OR: U.S. Department of the Interiror, Bureau of Land Management, Oregon-Washington Region.

MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology. **86**:42-55.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.

Meyerson, L. A., J. T. Carlton, D. Simberloff, and D. M. Lodge. 2019. The growing peril of biological invasions. Frontiers in ecology and the environment. **17**:191-191.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Greater sage-grouse: ecology and conservation of a landscape specie and its habitats. Studies in Avian Biology **38**:145-184.

Mosley, J. 2014. Featured weed: yellow and desert alyssum. Big Sky Small Acres:4-5.

Pardini, E. A., J. M. Drake, J. M. Chase, and T. M. Knight. 2009. Complex population dynamics and control of the invasive biennial *Alliaria petiolata* (Garlic Mustard). Ecological Applications **19**:387-397.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological invasions. **1**:3-19.

Perrotti, P. 2017. Invasive Plants. URL:https://www.nps.gov/yell/learn/nature/invasive-plants.htm.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems **1**:6-18.

Prevéy, J. S., M. J. Germino, N. J. Huntly, and R. S. Inouye. 2010. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. Plant Ecology **207**:39-51.

Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: where do we stand? Pages 97-125 *in* W. Nentwig, editor. Biological Invasions. Springer Berlin Heidelberg, Berlin, Heidelberg.

Radosevich, S. R., J. S. Holt, and C. M. Ghersa. 2007. Ecology of weeds and invasive plants: relationship to agriculture and natural resource management. Third edition. John Wiley & Sons, Inc., Hoboken, New Jersey.

Ramula, S., T. M. Knight, J. H. Burns, and Y. M. Buckley. 2008. General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. Journal of Applied Ecology **45**:1124-1133.

Richardson, D. M., P. Pysek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions **6**:93-107.

Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. Ecological Applications **19**:155-162.

Sala, O. E., F. S. Chapin lll, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Sebastian, D. J., M. B. Fleming, E. L. Patterson, J. R. Sebastian, and S. J. Nissen. 2017a. Indaziflam: a new cellulose-biosynthesis-inhibiting herbicide provides long-term control of invasive winter annual grasses. Pest Management Science **73**:2149-2162.

Sebastian, D. J., S. J. Nissen, and J. De Souza Rodrigues. 2016. Pre-emergence control of six invasive winter annual grasses with imazapic and indaziflam. Invasive Plant Science and Management **9**:308-316.

Sebastian, D. J., S. J. Nissen, J. R. Sebastian, and K. G. Beck. 2017b. Seed bank depletion: the key to long-term downy brome (*Bromus tectorum* L.) management. Rangeland Ecology & Management **70**:477-483.

Skurski, T. C., L. J. Rew, and B. D. Maxwell. 2014. Mechanisms underlying nonindigenous plant impacts: a review of recent experimental research. Invasive Plant Science and Management **7**:432-444.

Sutherland, S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. Oecologia **141**:24-39.

Thompson, K., J. G. Hodgson, and C. G. R. Tim. 1995. Native and Alien Invasive Plants: More of the Same? Ecography **18**:390-402.

Thuiller, W., D. M. Richardson, and G. F. Midgley. 2007. Will climate change promote alien plant invasions? Pages 197-211 *in* W. Nentwig, editor. Biological Invasions. Springer Berlin Heidelberg, Berlin, Heidelberg.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology **80**:1455-1474.

Vilà, M., C. Basnou, P. Pyšek, M. Josefsson, P. Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, P. E. Hulme, and D. partners. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment **8**:135-144.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**:702-708.

Vitousek, P. M. 1996. Biological Invasions and Ecosystem Processes: Towards an integration of population biology and ecosystem studies. Pages 183-191 *in* F. B. Samson and F. L. Knopf, editors. Ecosystem Management: Selected Readings. Springer New York, New York, NY.

Wagner, V., and C. R. Nelson. 2014. Herbicides can negatively affect seed performance in native plants. Restoration Ecology **22**:288-291.

Walther, G.-R., S. Beißner, and C. A. Burga. 2005. Trends in the upward shift of alpine plants. Journal of Vegetation Science **16**:541-548.

Whipple, J. J. 2001. Annotated checklist of exotic vascular plants in Yellowstone National Park. Western North American Naturalist **61**.

Young, J. A., and C. D. Clements. 2005. Exotic and invasive herbaceous range weeds. Rangelands. **27**:10-16.

CHAPTER TWO

THE LIFE HISTORY OF *ALYSSUM DESERTORUM* AND ITS IMPACTS ON THE BIODIVERSITY OF A SAGEBRUSH STEPPE PLANT COMMUNITY

Introduction

Non-native plant invasions can have devastating effects on native plant communities and biodiversity (Sala et al. 2000, Vilà et al. 2010), though overall impacts of non-native plants are quite variable (Hejda et al. 2009, Vilà et al. 2011). Documented impacts range from reduced diversity aboveground (Vilà et al. 2011) and in the soil seed bank (Gioria et al. 2014), altered disturbance regimes and ecosystem structure (Billings 1994, DiTomaso 2000, Brooks et al. 2004), to negligible effects on species richness and diversity (Hejda and Pyšek 2006, Skurski et al. 2013). Understanding and monitoring the impacts of non-native plant species is critical to help determine whether and which species and populations to prioritize for management (Rew et al. 2007).

Though the majority of introduced non-native species fail to successfully establish and become invasive (Williamson and Fitter 1996), the few species that do can have devastating impacts. In the United States a series of executive orders have drawn attention to the importance of invasive species including invasive plants, leading to the passage of the Federal Noxious Weed Act (1990) and the Noxious Weed Control and Eradication Act (2004), which require control of certain species. Control efforts can damage desirable plant species (Rinella et al. 2009), sometimes more than the impacts of invaders themselves (Skurski et al. 2013). Therefore it is important to evaluate costs and benefits of management, and to understand the actual impacts of the invader and the management practice on the surrounding plant community (Rew et al. 2007). Unfortunately, quantitative evidence of ecosystem alteration and impacts to species diversity due to invasion is either lacking or anecdotal for most non-

native species classified as invasive in North America (Blossey 1999, Hulme et al. 2013). In addition to understanding the impacts of a non-native plant, understanding its life history can help inform management decisions. Life history models can determine which life stage transition contributes most to population growth and should therefore be targeted for control (Panetta et al. 2011).

Alyssum desertorum Stapf. Is a non-native winter annual forb widespread across North America. Native to Africa, Asia and Europe (Dudley 1968), this species was introduced to North America for medicinal purposes (Jacobs 2012). First documented in the United States in 1941 and Canada in 1955, *A. desertorum* is now prevalent in 37 U.S. states and seven Canadian provinces (Jacobs 2012). *Alyssum desertorum* prefers rocky dry sites and requires disturbance to establish (Jacobs 2012). Its historical elevational range is 792m to 1981m and has invaded Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) communities (Bates et al. 2004). In Yellowstone National Park (YNP), *A. desertorum* has been found above (2347m) this range in mountain big sagebrush *(Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) communities, which are generally higher in elevation than Wyoming big sagebrush communities. The recent spread of *A. desertorum* is likely facilitated by mild winters, severe droughts (Mosley 2014), land use changes and other factors that cause soil disturbance.

The ruderal habit and annual life cycle of *A. desertorum* enable it to exert high propagule pressure (Mosley 2014) and establish a robust annual soil seedbank of 3.1 seeds cm^{-2} (Hamilton and Hellquist 2012), however seed longevity in the soil is largely unknown (Mosley 2014). Liu et al. (2014) documented germination percentage of new seeds at 93% from a laboratory germination study, and anecdotal reports claim that most seeds germinate within a year (Mosley 2014). Little is known about life state transitions of *A. desertorum*, and such information would help determine which life stage is most susceptible, and therefore most appropriate, to target for control.

Alyssum desertorum acts as a facultative winter annual, meaning it can germinate in either fall or spring (Mosley 2014). Plants that germinate in fall lie dormant over winter and by spring the already established roots are able to utilize resources, however most native annuals in the sagebrush steppe do not germinate until spring, giving winter annuals a resource acquisition advantage. This unique temporal niche gives winter annuals such as *A. desertorum* a unique advantage in sagebrush steppe and the potential to have ecosystem effects (Vitousek 1996). *Alyssum desertorum* is purported to outcompete native plants and reduce biodiversity (Jacobs 2012, Mosley 2014), however there are no published studies assessing the direct impacts of *A. desertorum* on native communities. Studies conducted in highly disturbed systems attributed reduced diversity and establishment of planted species to competition from *A. desertorum* (Jacobs and Winslow 2018), however *A. desertorum* may be a passenger of disturbance rather than a driver (MacDougall and Turkington 2005). Hamilton and Hellquist (2012) found that soils invaded with *A. desertorum* had lower soil fauna diversity, however this was documented at a degraded Gardiner Basin site in YNP. There are no studies to our knowledge assessing the impacts of *A. desertorum* on intact native plant communities.

The first objective of this study was to quantify *A. desertorum* life history demographics across three elevations and determine the transition rates for each demographic component. I hypothesized that as elevation increases, all life stage transitions will decrease, as informed by other studies of non-native plant fitness at higher elevations (Monty and Mahy 2009). The second objective was to determine how *A. desertorum* competes with the non-native annual grass *Bromus tectorum* and the native annual forb *Microsteris gracilis* through replacement series experiments. *Bromus tectorum* is an invasive non-native annual grass of the sagebrush steppe (Billings 1994, Germino et al. 2016) and *M. gracilis* is a common early-successional native annual forb of the sagebrush found in disturbed soils (Brandt and Rickard 1994). I hypothesized that *A. desertorum* will be more competitive with *M. gracilis* than *B.*

tectorum. The third objective was to quantify effects of *A. desertorum* on the biodiversity of the native plant community. I hypothesized that *A. desertorum* will reduce species richness and species diversity of native, particularly annual forb species, both in the aboveground community as well as in the soil seedbank. This information collectively will help assess whether *A. desertorum* should be actively managed in diverse native sagebrush steppe.

Methods

Site Descriptions

Study sites were selected in northern Wyoming and southwestern Montana, U.S. along an elevational gradient ranging from 1450m to 2347m (Table 2.1). The lowest elevation site was located at the Montana State University Arthur Post Agronomy Farm (hereafter Post Farm) 8km west of Bozeman, Montana, and the other seven sites were in the northern range of Yellowstone National Park (YNP) (Appendix A Fig. A.1). The second lowest elevation site was located in the Gardiner Basin, an area that has experienced over a century of historical agricultural land use (Olliff et al. 2001) and is adjacent to YNP. The other six sites were within YNP, less disturbed and characterized as mountain big sagebrush (*Artemisia tridentata* ssp*. vaseyana;* Appendix E Table E.1.). These six sites were randomly chosen along an elevation gradient from a road-side survey of *A. desertorum* populations conducted with the aid of the YNP botanist.

Objective 1: Life History

The life-stages of *A. desertorum* were recorded to build a demographic population model. Germination rates and seed viability of *A. desertorum* were assessed with seeds collected in fall 2019 near the Mammoth site. To determine initial germination rates (***G***), seeds were assessed immediately after seed set and after a 4 week vernalization period at 4 °C. Seeds were surface sterilized prior to the

germination test by submerging in 5 ml of 70% ethanol for 30 seconds and then rinsing with 5 ml of sterilized deionized water for 30 seconds. Ten seeds were then placed in sterilized germination dishes, replicated three times. Each of the dishes contained a single sheet of blotting paper wetted with approximately 1 ml of sterilized deionized water and then sealed with Parafilm. Dishes were kept at 25 ˚C and exposed to 16:8 hours of light:dark, respectively. Germination was recorded daily for 14 days.

Table 2.1. Site environmental information. Temperature estimated from measurements at field sites, and from US Climate Data website (Data 2020) indicated with "*".

Site Name	lat., long.	Elevation (m)	Winter temp (°C)	Summer temp (°C)	Objective(s)
Post Farm	45.677153, -111.157403	1450	-1.93*	18*	1
Gardiner	45.052050 -110.762293	1588	-4.25*	26*	1
Mammoth	44.98448, -110.701070	1615	-6.43*	18.9	1,3
Blacktail	44.955921, -110.591039	1980	-3.40	16.8	3
Lamar	44.910876, -110.324971	1981	-0.40	18.5	3
Phantom	44.955555, -110.504886	2042	-6.43*	16.7	3
Swan	44.913451, -110.729714	2225	-3.4	16.2	1,3
Hayden	44.652375, -110.465486	2347	-6.43*	15.5	3

To estimate seed viability after one year in the soil (***V***), six nylon bags (6cm x 4cm), each with 30g sand and 50 *A. desertorum* seeds (sourced the same as above), were buried 1cm deep in the soil. Bags were buried in September 2019 along an elevational gradient at the Gardiner (1588m), Mammoth (1615m) and Swan (2225m) sites. After 1 year (September 2020), two bags from each site were collected, leaving the remaining four bags to be removed two and three years later. Seed viability was tested using the tetrazolium test of 1.0% tetrazolium solution after an 18-hr dark soak period at 30 °C.

Seed viability was determined using illustrations for Brassicaceae in *Seed Testing: Principles and Practices* (Elias et al. 2012).

To assess the other life stages of *A. desertorum,* two studies were conducted: one at Mammoth and Swan in YNP, and the other at the Post Farm. These studies were also established in September 2019. At the Post Farm, 10 pots (11.4cm^3) each sown with 25 *A. desertorum* seeds (collected from the Mammoth site) were buried to ground level, and a wire cage was placed over the pots to prevent predation. At each YNP site 10 wire rings (10cm diam.) were fixed to the ground around small groups (~5) of *A. desertorum* seedlings that had emerged that fall. For both studies seedlings were counted and rings/pots (hereafter plots) photographed in order to identify individual seedlings the following spring and summer.

All plots were surveyed the following spring (May 2020) to identify surviving overwintering individuals, and newly emerging individuals. Individuals were monitored monthly throughout the summer until senescence, to record the number that transitioned from overwintering or spring seedlings to reproductive maturity. There were only 9 spring seedlings that emerged from all plots and sites, therefore I was unable to confidently assess their transitions.

Fecundity was assessed for each site using the average number of fruits per plant in each plot, which was multiplied by the average number of seeds per fruit. The average number of seeds produced per fruit was estimated from 100 fruits collected from the Post Farm. These values were then multiplied by the germination rate (***G)*** to determine fecundity (***F***).

<u>Statistical Analysis</u> To calculate percent viability (**V**) of the soil seedbank, the number of seeds viable in the buried nylon bags after one year was divided by the number of seeds put in the bags (50). Vital rates calculated for each plot at each site were: $\boldsymbol{P_{fall}}$, probability of a seed produced that summer emerging in the fall; $\boldsymbol{P_{ow}}$, probability of overwintering survival; $\boldsymbol{P_{rep}}$, probability of reaching reproductive

maturity/fruiting. Probabilities were estimated by dividing the number of individuals that reached the next stage by the number of individuals in the previous stage, for example $\boldsymbol{P_{ow}} = n_{ow} / n_{fall}$. Only $\boldsymbol{P_{rep}}$ and $\boldsymbol{P_{ow}}$ were calculable for all three sites. Linear models were fit with **V**, $\boldsymbol{P_{ow}}$, and $\boldsymbol{P_{rep}}$ in response to site following a Gaussian distribution. A generalized linear model was fit with fecundity in response to site following a Poisson distribution. Sites were ordered by increasing elevation. Differences for all life history statistical models were evaluated with a two-way analysis of variance. Finally, to construct a life history diagram for *A. desertorum*, mean values were used across all sites for $\boldsymbol{V}$, $\boldsymbol{P_{ow}}$, $\boldsymbol{P_{rep}}$, and $\boldsymbol{F}$; $\boldsymbol{P_{fall}}$ was only from the Post Farm site, and ***G*** was only from the Mammoth site.

Objective 2: Competition

A replacement series competition experiment was conducted to assess how *A. desertorum* competes with a non-native annual grass (*Bromus tectorum)* and a native annual forb (*Microsteris gracilis*). In August 2019 *B. tectorum* seeds were collected near the Gardiner Basin (45.168325, -110.852305) and *M. gracilis* seeds were collected from the Hayden Valley of YNP (44.675449, -110.481931). Seeds of all species were stored in paper envelopes in a cold storeroom at ~5 °C for 4 months.

Five pots each of *B. tectorum* and *M. gracilis* were sown with *A. desertorum* for a total of 5 replicates per trial. The total target density for each pot was 24 plants pot^{-1} (210 plants m^{-2}), based on a preliminary study to determine at which point *B. tectorum* and *A. desertorum* experienced density-dependent competition; *M. gracilis* density was not assessed due to limited seed availability. The five density-combinations of *A. desertorum* with either *B. tectorum* or *M. gracilis* individuals were: 24:0, 18:6, 12:12, 6:18, 0:24 plants pot^{-1}. Seeds were sown into square pots (11.4cm^3) filled with equal parts loam, sand, and sphagnum peat moss. The soil was aerated steam pasteurized at 70 °C for 60 min. Seeds were systematically sown within a grid with 2cm spacing between seeds and from the edges of the pot.

Plants were grown in a greenhouse at the Plant Growth Center on the Montana State University-Bozeman campus (45.667979, -111.052532) at 18°C nighttime, and 22°C daytime temperatures with a 16-hr photoperiod. Two trials were conducted; the first from Jan-March, 2020, and the second from March-May, 2020. Pots were kept moist using moisture mats that were drip irrigated twice each day for 5 minutes. After 50 growing days, plants were harvested at the root crown (aboveground biomass) and roots were cleaned of soil (belowground biomass). Above and belowground biomass was dried for 48 hours at 43 °C and weighed to the nearest milligram.

Statistical Analysis Relative yield of each species pair was calculated using the proportion of the species in the mixture (P) and the mean plant biomass of the species in the mixture (A_{mix}) and monoculture (A_{mono}) (Cousens and O'Neill 1993).

$$RY = P * (A_{mix} / A_{mono})$$

A linear mixed model was fit with relative yield or proportional biomass of either *B. tectorum* or *M. gracilis* in response to the proportion of *A. desertorum,* including trial as a random effect and following a Gaussian distribution. Assumptions of normality and heteroskedasticity were evaluated and data transformed as needed. Significant differences were evaluated using Satterthwaite's approximation method.

Objective 3: Impacts to Biodiversity

To evaluate the effects of *A. desertorum* invasion on the diversity of the native plant community, the six study sites in YNP were used. All sites had an area with a considerable infestation of *A. desertorum* (> 10 individuals/m^2) adjacent to an area with low invasion (< 10 individuals/m^2): high and low invasion treatments were established in the respective areas. High invasion areas were typically located near roads and/or trails and had notable disturbance from native ungulates and/or human

activities such as trampling and construction. At five of the sites (Mammoth:M, Blacktail:B, Lamar:L, Phantom:P, and Swan:W) 18- 1m^2 plots were established in both high and low invasion areas. Twelve plots in each of the invasion treatments were sprayed with indaziflam and six control plots were left unsprayed. Half of the sprayed plots were originally targeted for seed addition, but this did not occur and these plots were considered "spray" plots for analysis. At the sixth site (Hayden:HD) 14 *1m^2 plots were established in both high and low invasion areas. Seven of the plots in each invasion treatment were sprayed with indaziflam, and seven plots were left unsprayed as controls. All spray plots were treated in August 2018 with 63g·ai·ha^{-1} indaziflam using a backpack sprayer fitted with a XR11002 flat spray nozzle (TeeJet® Spraying Systems, P.O. Box 7900, Wheaton, IL 60187). The timing of application targeted *A. desertorum* seedlings that had not yet emerged. In this chapter I will focus on the impacts of *A. desertorum* invasion and will address the impacts of indaziflam in Chapter Three.

Ocular estimates of canopy cover (to the nearest 0.5%) for each species and ground cover were conducted one and two years after treatment for each plot during the peak vegetative season, for the central 0.75m^2 of each plot to account for edge effects of the herbicide. Estimates were allowed to exceed 100% to account for understory canopy structure.

To assess the effect of *A. desertorum* on the seedbank, soil samples were collected from plots in high and low invasion areas at two sites (M, B) in April 2019. At each site, six soil cores (10cm dia. X 6cm deep) were collected from six control plots in areas of high and low invasion. The samples were taken between the 0.75m^2 and 1m^2 plot edges. Soil cores from the same plots were combined into one soil sample, for a total of one soil sample per plot, and an overall total of 24 samples (12 each high-control, and low-control).

Soil samples were spread out in trays (28cm x 13cm) on top of 2.5cm of sterilized soil (1:1:1 ratio of pasteurized mineral soil, sphagnum peat moss, and washed concrete sand) in the Montana State

University Plant Growth Center. Trays were set out in the greenhouse (22-18°C, 16-hr photoperiod) and watered twice each day for 5 minutes using a drip irrigation system. Seedlings that emerged were identified, counted, and then removed from the tray; those that were unidentifiable were repotted and grown until they were identifiable. Emerging graminoids were removed and not counted. There was no germination in the first month, therefore trays were moved to a cold, wet and dark stratification chamber (4 °C) for 30 days to break dormancy, after which the trays were returned to the greenhouse. Once germination diminished again (after about 6 months) the trays were put in the stratification chamber for 56 days and then returned to the greenhouse. The experiment was terminated after 17 months.

Statistical Analysis Percent cover estimates were used to calculate Shannon's diversity index, calculated as:

$$H = -\sum_{i=1}^{S} p_{i*} logb * p_i$$

where p_i is the proportion of species *I,* S is the number of species, and log*b* is the logarithm base 10. Richness and Shannon's diversity were calculated for native annual forbs, with and without *A. desertorum* in the dataset. Species richness was evaluated with generalized linear mixed-effects models (GLMM) following a Poisson distribution, and Shannon's diversity was evaluated with linear mixed models following a Gaussian distribution. Saturated models with all possible interactions were fit with invasion (high, low), herbicide treatment (spray, control), elevation, and year (2019, 2020) as main effects. To account for repeated measures of plots, the unique tag number for each plot was included as a random effect. The saturated model was

Response~Indaziflam*Invasion*Elevation*Year, random = Tag

with the response being either species richness or Shannon's diversity. Any significant interactions were maintained in the final models. Mammoth was the lowest site and used as the model intercept.

To assess differences in annual native forb abundance between levels of invasion, only the data from unsprayed plots were used. A linear mixed model was fit with annual native forb cover in response to level of *A. desertorum* invasion, elevation, and year with tag included as a random effect, following a Gaussian distribution. To compare differences in low and high invasions within sites, a new variable called "invasion.site" was created by combining invasion and site. A linear mixed model was fit similar to above, though with "invasion.site" replacing elevation and level of *A. desertorum* invasion. Differences in least squares means of annual forb cover between high and low invasion at each site were compared using Satterthwaite's approximation. To determine whether *A. desertorum* may be displacing the native annual forbs, rank abundance curves were constructed.

To evaluate impacts of *A. desertorum* on the soil seedbank, abundance and total proportion of native forbs (perennial and annual) established from the soil seedbank were analyzed using linear models with main effects as above. The model with abundance as the response was fit following a quasi-poisson distribution to account for overdispersion. To estimate the density of the soil seedbank for *A. desertorum*, the average number of *A. desertorum* seedlings per control tray was divided by the volume of soil collected per tray (18.8cm^3).

For all models, normality and heteroscedasticity assumptions were assessed, data were transformed when assumptions were not met, and differences were evaluated using a Type II ANOVA. Data for all objectives were analyzed and plotted using the statistical program R (Version 3.6.1, R Core Team, 2019) and the following packages: *BiodiversityR* (Kindt and Coe 2005), *car* (Fox and Weisberg 2019), *ggplot2* (Wickham 2016), *nlme* (Pinheiro et al. 2019), *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), and *vegan* (Oksanen et al. 2019).

Results

Life History

The initial germination rate (**G**) for vernalized *A. desertorum* was 30%, and zero for freshly shed seed due to innate dormancy. The viability of seeds in the soil after one year decreased as elevation increased (Appendix B Tables B.1 & B.2). Mean (±SE) seedbank viability after one year (***V***) was 34% (±14%) at the lowest site (G) and reduced to 1% (±1%) at the highest site (W) (Fig. 2.1a). The mean likelihood of a seedling emerging in the fall ($\mathbf{P_{fall}}$) was 0.59 (±0.1), though as noted above this was only documented for the Post Farm site. Overwintering success ($\boldsymbol{P_{ow}}$) and likelihood of reaching reproductive maturity ($\boldsymbol{P_{rep}}$) were lowest at the highest site (W; $p < 0.01$ and $p = 0.01$, respectively; Appendix B Table B.2) with mean overwintering success of 0.38 (±0.28). The mean overwintering success for the mid-elevation site was 0.61 (±0.23), and 0.80 (±0.15) for the lowest site, and only differed slightly from each other ($p = 0.06$; Fig. 2.1b; Appendix B Table B.2). There was no difference in mean probability of reaching reproductive maturity between the lower two sites (F and M) ($p = 0.57$), however the highest site (W) was significantly lower ($p = 0.01$; Fig. 2.2c; Appendix B Table B.2). Fecundity (***F***) was highest at the lowest site ($p<0.01$; Table 2.2). Mean fecundity per plant was 114 (±106) seeds at the lowest site (F) and 3 (±1) seeds at the highest site (Fig. 2.1d) (Appendix B Table B.2).

To construct a life history model for *A. desertorum*, means were calculated across all elevations for the transition probabilities detailed above. Mean(±SE) ***V*** was 0.2 (±0.07), $\boldsymbol{P_{ow}}$ was 0.6 (±0.05), $\boldsymbol{P_{rep}}$ was 0.7 (±0.06), and ***F*** was 41 (±15) seeds (Fig. 2.2). The Post Farm data were available for $\mathbf{P_{fall}}$, so that value was used in the model.

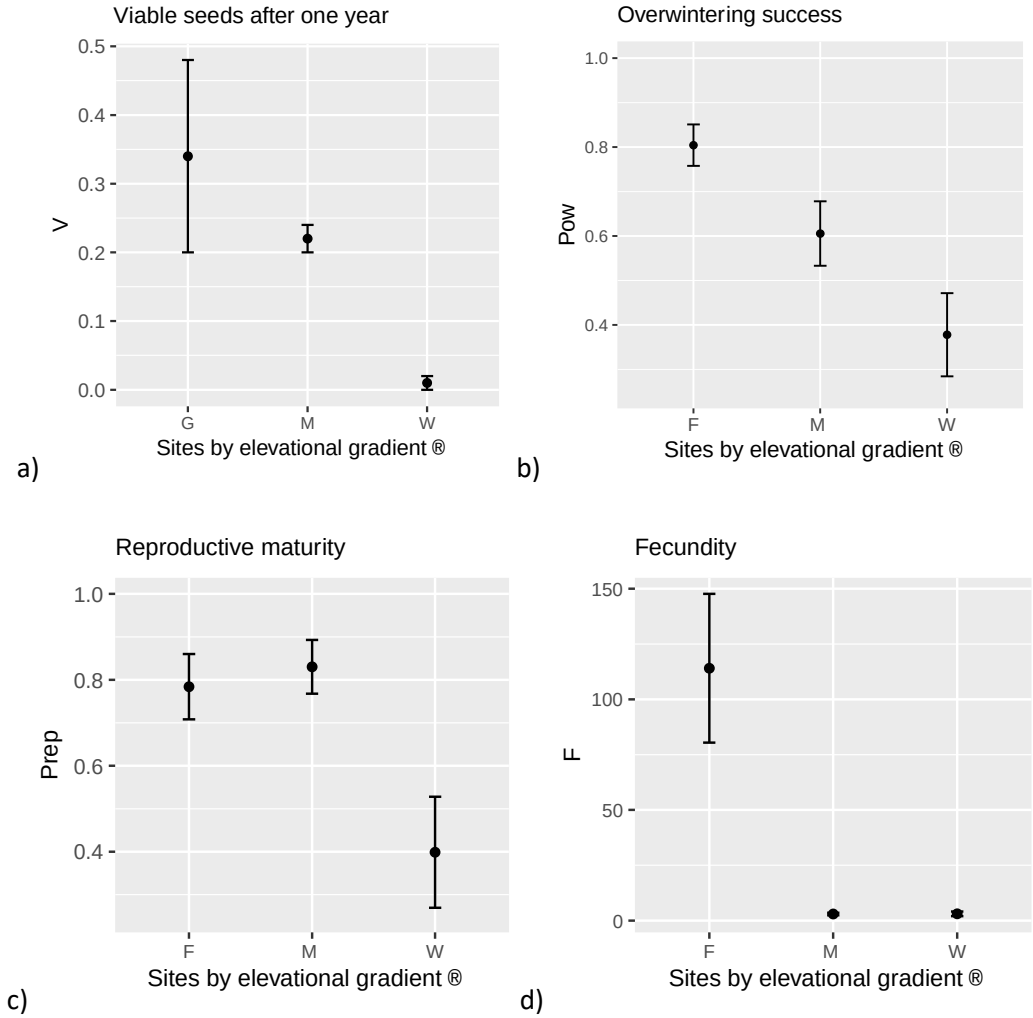


Figure 2.1. *Alyssum desertorum* mean (±SE) vital rates: a) *V* = seed viability after one year in the soil, b) P_{ow} = mean probability of overwintering success, c) P_{rep} = mean probability of reaching reproductive maturity, and d) *F* = fecundity. Data are from four sites across an elevational gradient (F = 1450m, G= 1588m, M = 1615m and W = 2225m).

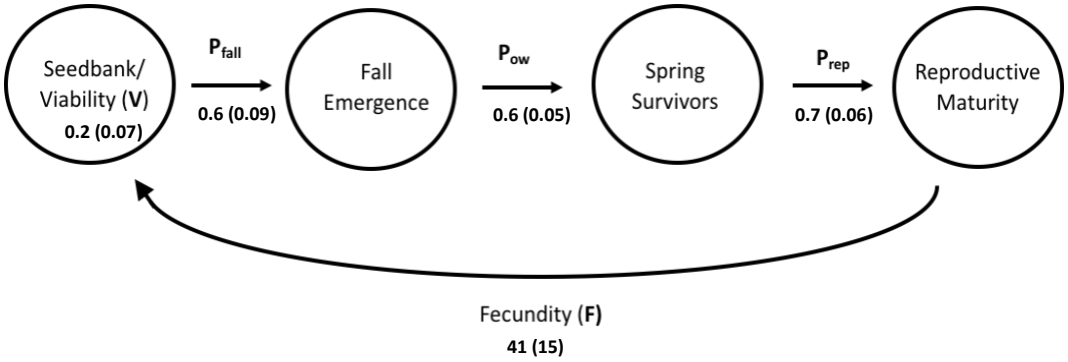


Figure 2.2. Life history model of *Alyssum desertorum* including the following mean (±SE) vital rate transition probabilities: *V* = seed viability in the soil after one year, P_{fall} = likelihood of a seed germinating in the fall; P_{ow} = probability of a fall seedling surviving over winter; P_{rep} = probability of seedling reaching reproductive maturity; and *F* = fecundity (average number of seeds produced per plant * germination rate G).

<u>*Alyssum desertorum* competition with *Bromus tectorum* and *Microsteris gracilis*</u>

Bromus tectorum experienced no negative interference from *A. desertorum* in relative yield above- or belowground, as the lines of observed yields for *B. tectorum* are almost identical to the lines of expected yields with no competition (Fig. 2.3). Additionally, the proportional biomass of *B. tectorum* both above- and belowground was increased by interspecific competition until the proportion of *A. desertorum* reached 0.75, where there was then a decrease in *B. tectorum* proportional biomass (Appendix B Fig. B.1). *Alyssum desertorum* was greatly reduced by interspecific interference when grown with *B. tectorum*. Both above- and belowground, the observed mean relative yields and proportional biomass of *A. desertorum* were far below the yields and biomass expected with no interference. (Fig. 2.3; Appendix B Fig. B.1).

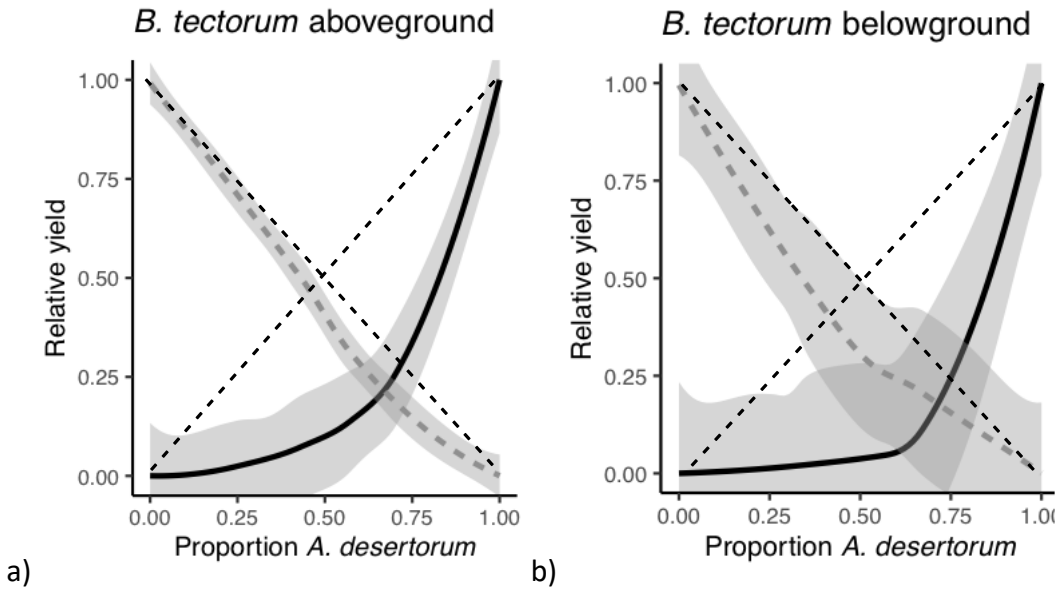


Figure 2.3. Effects of the proportion of Alyssum desertorum (solid) on the mean relative yield of Bromus tectorum (grey dash) a) aboveground and b) belowground. Black dashed lines represent expected yield trends when intra- and interspecific competition are equal. Grey bands represent standard error around the means

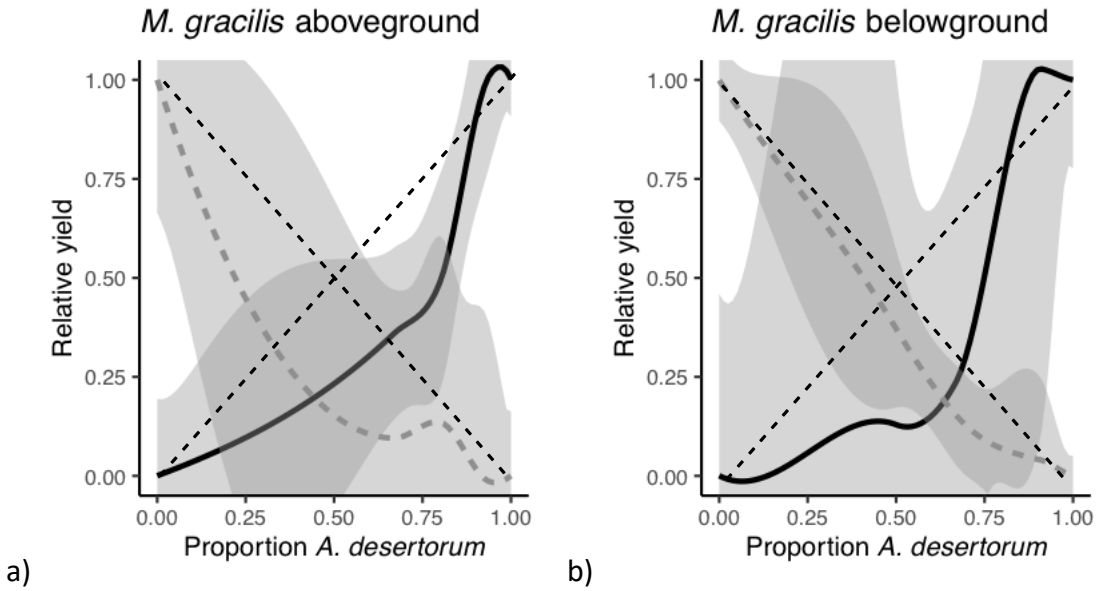


Figure 2.4. Effects of the proportion of *Alyssum desertorum* (solid) on the mean relative yield of *Microsteris gracilis* (grey dash) a) aboveground and b) belowground. Black dashed lines represent expected yield trends when intra- and interspecific competition are equal. Grey bands represent standard error around the means.

Aboveground relative yield of both *M. gracilis* and *A. desertorum* were reduced due to interspecific competition (Fig. 2.4a). Belowground relative yield was reduced more for *A. desertorum* than for *M. gracilis* (Fig. 2.4b); though I do acknowledge the large margins of error in these data. The proportional biomass of *A. desertorum* aboveground was much higher than expected, though belowground only slightly increased. *Microsteris gracilis* proportional biomass was reduced due to interspecific interference aboveground, though belowground there was little difference (Appendix B Fig. B.2).

Alyssum desertorum impacts on biodiversity of annual forbs

Annual forb richness response differed when *A. desertorum* was included or excluded from the data. When *A. desertorum* was included in the data, annual forb richness was lower in the high *A. desertorum* densities ($p < 0.01$) and differed by elevation ($p < 0.01$) and indaziflam ($p < 0.01$) though not by year ($p = 0.21$). However, when *A. desertorum* was removed from the data there was no longer a significant difference in annual forb richness ($p = 0.82$ between levels of invasion (Table 2.4; Appendix B Table 2). The difference in the estimate for mean species richness with and without *A. desertorum* is minimal (0.46 species) (Table 2.2).

Shannon's diversity of annual forbs differed significantly by invasion level only when *A. desertorum* was included in the analysis ($p < 0.01$; Table 2.5). Without *A. desertorum,* there was no difference in Shannon's diversity between invasion levels ($p = 0.28$). The pattern of differences in Shannon's diversity was similar for the other predictors regardless of including or excluding *A. desertorum* (Table 2.5; Appendix B Table 3).

The total cover of annual forbs (excluding *A. desertorum*) did not differ overall between levels of *A. desertorum* invasion ($p = 0.56$) or by year ($p = 0.88$), though as elevation increased cover also increased ($p < 0.01$; Appendix B Table B.3). At the lowest elevation mean (± SE) annual forb cover was

0.5 (±0.2) percent, and at the highest elevation mean annual forb cover was 9.9 (±0.9) percent. An analysis of differences of least squares means revealed a significant difference in annual forb cover between the high and low invasion areas at the highest (HD) elevation ($t_{61.7} = -2.97$, $p < 0.01$; Fig. 2.6).

The rank abundance curves of the native annual forb community in high and low invasion areas showed a similar general pattern. In the high invasion areas, *A. desertorum* dominated the rank abundance, though all other species were relatively evenly distributed along the rank abundance curve with no extreme declines in abundance between species. This pattern was similar to the rank abundance curve for native annual forbs in the low invasion areas, demonstrating that the high invasion of *A. desertorum* does not alter the abundances of native annual forbs (Appendix B Fig. B.3).

In the soil seedbank, there was no difference in the abundance of forb seedlings between high and low invasion samples ($p = 0.98$) nor by site ($p = 0.26$) however spray plots had fewer seedlings ($p = 0.04$). Proportion of seedlings was no different between high and low invasion samples ($p = 0.15$), though differed by site ($p = 0.04$) and indaziflam treatment ($p < 0.01$). Richness of seedlings did not differ by level of invasion ($p = 0.22$) though differed by site ($p < 0.01$) and by indaziflam treatment ($p < 0.01$). Shannon's diversity was no different between levels of invasion ($p = 0.74$), though differed by site ($p < 0.01$) and indaziflam treatment ($p < 0.01$; Appendix B Table B.4). The density of *A. desertorum* seeds in the soil seedbank was estimated to be 0.5 seeds cm^{-3}.

Table 2.2. Annual forb species richness and Shannon's diversity at study sites in Yellowstone National Park in response to the level of *Alyssum desertorum* invasion (high, low), elevation, indaziflam treatment (spray, control), and across two years (2019, 2020). Intercept is low invasion, control, 2019. Analysis with (+ALDE) and without (-ALDE) *A. desertorum* in the data. Results from a linear mixed model following a Gaussian distribution for richness and a Poisson distribution for Shannon's diversity. Values in bold indicate significant difference ($p < 0.05$).

Fixed effects							Random effects	
Response	Predictor	Est.	SE		z value	p(>)	Variance	
Richness							Tag	
Annual forbs (- ALDE) R^2=0.47	**Intercept**	**-3.45**	**0.92**		**-3.74**	**<0.01**	0.64± 0.80	
	Invasion	-0.04	0.18		0.23	0.82		
	Elevation	**1.8e-03**	**4.4e-04**		**4.03**	**<0.01**		
	Indaziflam	**-1.95**	**0.20**		**-9.89**	**<0.01**		
	Year	0.16	0.11		1.42	0.16		
Annual forbs (+ ALDE) R^2=0.52	**Intercept**	**-3.08**	**0.70**		**-4.39**	**<0.01**	0.32± 0.56	
	Invasion	**0.42**	**0.14**		**3.03**	**<0.01**		
	Elevation	**1.7e-03**	**3.3e-04**		**5.15**	**<0.01**		
	Indaziflam	**-1.85**	**0.15**		**-12.40**	**<0.01**		
	Year	0.14	0.09		1.46	0.14		
Response	Predictor	Est	SE	*df*	t-value	p(>)	Variance	
Shannon's diversity							Tag	Residual
Annual forbs (- ALDE) R^2= 0.67	Intercept	-0.29	0.18	204	-1.63	0.10	0.05± 0.23	0.05± 0.21
	Invasion	0.04	0.04	203	1.08	0.28		
	Elevation	**3.0e-04**	**8.6-e05**	**204**	**3.77**	**<0.01**		
	Indaziflam	**-0.35**	**0.04**	**204**	**-8.74**	**<0.01**		
	Year	0.03	0.02	204	1.53	0.13		
Annual forbs (+ ALDE) R^2=0.71	**Intercept**	**-0.43**	**0.20**	**204**	**-2.08**	**0.04**	0.07± 0.27	0.05± 0.23
	Invasion	0.06	0.04	203	1.37	0.17		
	Elevation	**4.4e-04**	**9.8e-05**	**203**	**4.46**	**<0.01**		
	Indaziflam	**-0.43**	**0.05**	**204**	**-9.55**	**<0.01**		
	Year	0.04	0.02	204	1.76	0.08		

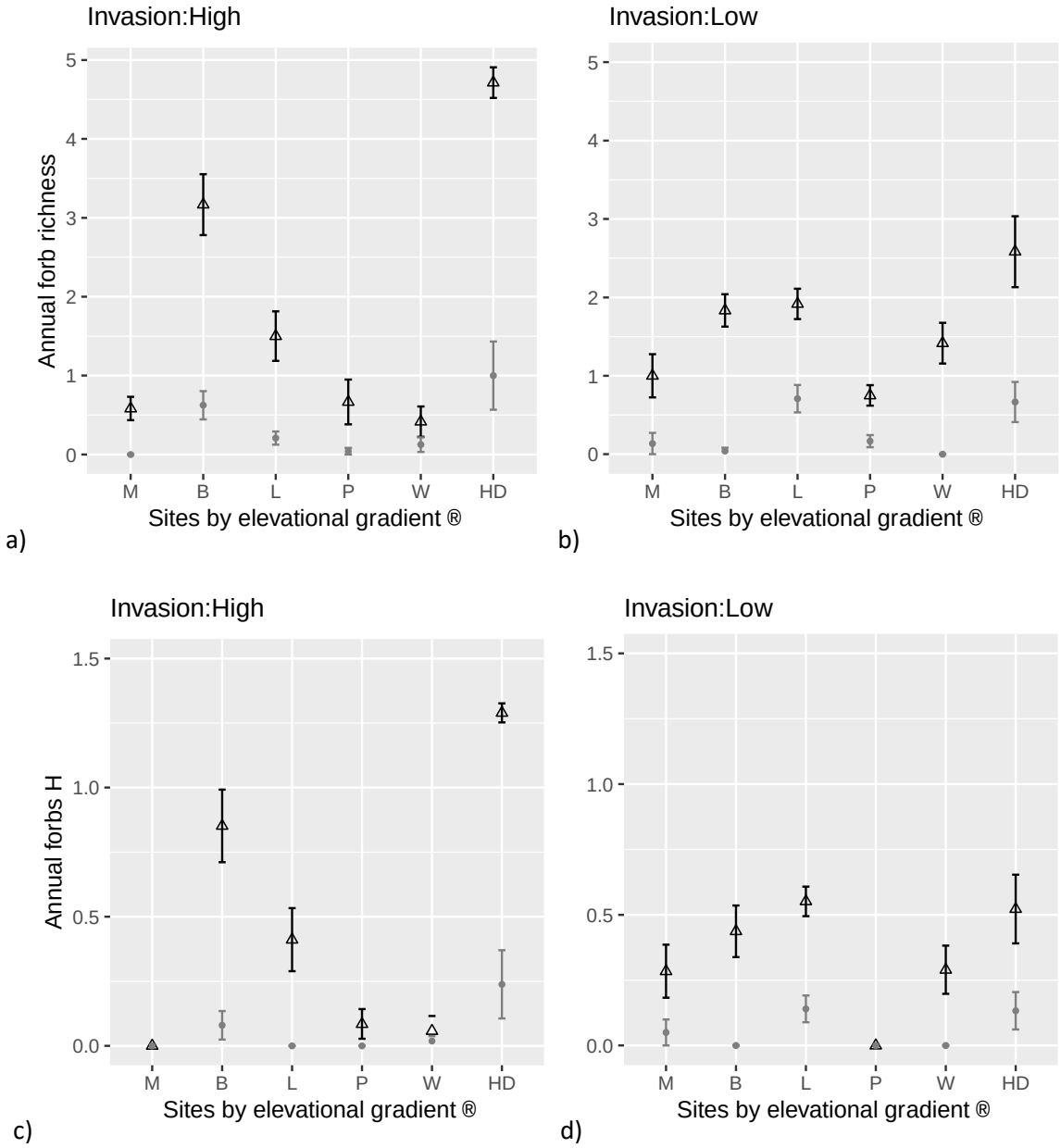


Figure 2.5. Annual forb mean (± SE) species richness (a, b) and Shannon's diversity (H) (c, d) post treatment (sprayed = ●, control = Δ) in high and low invasions of *Alyssum desertorum*, for two years across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and HD = 2347m). Data exclude *A. desertorum.*

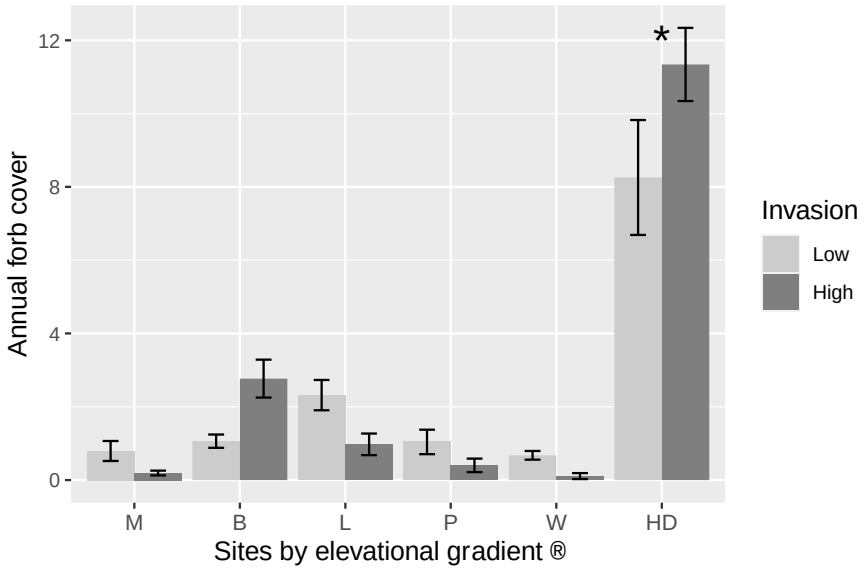


Figure 2.6. Mean (± SE) total cover of native annual forbs in high (dark grey) and low (light grey) invasions of *Alyssum desertorum*, across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and H = 2347m). Significant differences in cover between high and low invasion are represented by "*". Data exclude *A. desertorum.*

Discussion

I have broadened the scope of understanding of the non-native annual forb *A. desertorum*, by detailing the life history demographics, determining competitiveness with functionally similar species, and examining how this species affects the biodiversity of intact sagebrush steppe. The life history analysis of *A. desertorum* is the first of its kind; I measured five key demographic components. Seed viability in the soil bank after one year was 20% across all elevations, though declined abruptly as elevation increased; at the highest elevation seed viability was as low as 1%. Understanding a species' seed longevity in the soil is necessary to determine how long a treatment should last when soil seedbank suppression is the management goal, which is an effective approach in areas with dense infestations of non-native annual plants (Sebastian et al. 2017b). Seed production (fecundity) also

decreased as elevation increased, expanding upon the claims of Mosley (2004) that *A. desertorum* exerts a high propagule pressure and produces a high number of seeds.

The overwintering success (P_{ow}) of winter annuals is a key component of their competitiveness, particularly in ecosystems such as sagebrush steppe where they fill a unique temporal niche and utilize spring resources before most native plants. The overwintering rate of *A. desertorum* seedlings was lower with increasing elevation. While mean summer temperatures were similar between the low- and mid-elevation sites, the mean winter temperature was higher at the low site than the mid site (-1.93°C and -4.25°C, respectively). With milder winters, more *A. desertorum* seedlings will survive, at least at lower elevations. Additionally, considering that spring emergence was minimal at all sites, and the likelihood of fall germination (P_{fall}) was much higher (59%) than previously suggested by Mosely (2014), I can infer that the overwintering success of *A. desertorum* will be a key driver in the species' success. All the vital rate transitions measured (soil seedbank longevity, probability of fall emergence, overwintering success, probability of reproductive maturity, and fecundity) were lower at the higher elevations sites, which suggests that populations at higher elevations may not be as successful and abundant as those at lower populations, though with a warming climate *A. desertorum* may become more successful at higher elevations. Examining how this species responds to other environmental variables is required.

Alyssum desertorum was a weak competitor with two other annual plants, *B. tectorum* (a non-native grass), and *M. gracilis* (a native annual forb). *Bromus tectorum* was unaffected by *A. desertorum*, though *A. desertorum* yield and biomass were significantly reduced by *B. tectorum*. The interspecific competition between the two forbs resulted in reduced relative yield and proportional biomass for both species. Native plants can exhibit strong inhibitory effects on non-native plants that are functionally similar (Fargione et al. 2003), unless the invader has some other competitive advantage, such as the phenological advantage of winter annuals. My study suggests that when spring *A. desertorum* seedlings

emerge alongside *M. gracilis* seedlings, both species will experience interspecific competition, though it is unknown whether the more general fall *A. desertorum* seedlings would experience the same effects. Further studies examining how native forbs germinate and perform in the presence of established *A. desertorum* seedlings would be valuable, especially given the species' high fall germination rates and overwintering success.

At our six study sites along an elevational gradient, richness of the whole community and of native annual forbs was influenced by inclusion or exclusion of *A. desertorum* in the data set. Including the species of interest in the data can artificially inflate richness and diversity indices, and I compared results with and without *A. desertorum*. I found *A. desertorum* invasion had minimal impact on the whole community richness, but richness declined with elevation, as observed in other studies (Alexander et al. 2011, Haider et al. 2018).

Neither native annual forb community richness nor Shannon's diversity were affected by *A. desertorum* invasion. Neither did the richness or diversity of the soil seedbank differ between areas of high and low *A. desertorum* invasion, contrary to other studies documenting reduced seedbank diversity in invaded areas (Gioria et al. 2014). Furthermore, seed densities at my sites were not as high as Hamilton and Hellquist (2012), though their study was conducted in a highly degraded area. That there was no difference between areas of high and low invasion density in the native annual forbs aboveground or in all of the forbs in the soil seedbank suggests that *A. desertorum* is not impacting the native annual forb community. Our results indicate that *A. desertorum* can coexist with native annual forb species and is not displacing these species, but instead is occupying available soil niches aboveground and in the soil seedbank. Though as mentioned above in the competition study, *A. desertorum* can compete with annual forbs when grown alongside in high enough densities, and the competitiveness of *A. desertorum* fall seedlings with native annual forbs has yet to be evaluated.

Given the minimal impacts to the annual forb community and the requirement of soil disturbance for establishment (Mosley 2014, Mangold 2017), *A. desertorum* may be a passenger of disturbance rather than a driver of ecosystem change (MacDougall and Turkington 2005). The high invasion areas at our study sites were typically more prone than the low invasion areas to localized disturbance, such as trampling by humans or native ungulates, historical road construction, and vehicles. These disturbances may also influence the plant community composition and diversity, in addition to the presence of *A. desertorum* and other early successional annuals. It is likely that a robust native plant community will be resistant to degradation by *A. desertorum* if it is not severely damaged by human activities, such as construction or herbicide use. In areas that are degraded and have high infestations of *A. desertorum*, our estimate of seedbank longevity will help inform seedbank suppression efforts, and the high probabilities of fall germination and overwintering success suggest that control efforts in the fall may be the most effective.

In conclusion, I have filled knowledge gaps in the life history of *A. desertorum*, a non-native annual forb widespread in arid rangelands across the west. *Alyssum desertorum* has a high overwintering rate and a large majority of those survive to reproduce. However, after one year its viability in the seedbank is low, and declines rapidly with increasing elevation, as does fecundity. With a warming climate it is likely that the success of this species will increase at higher elevations. However, because *A. desertorum* is a weak competitor with functionally similar species and has minimal impacts to the native plant community both above and belowground, it is unlikely that this species alone has the potential to have broader ecosystem effects; perhaps *A. desertorum* should be tolerated rather than actively managed in intact sagebrush steppe.

References

Alexander, J. M., C. Kueffer, C. C. Daehler, P. J. Edwards, A. Pauchard, and T. Seipel. 2011. Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. Proceedings of the National Academy of Sciences **108**:656.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1-48.

Bates, J., K. Davies, and R. Miller. 2004. Ecology of the Wyoming big sagebrush alliance in the northern Great Basin:2004 Progress Report. Burns, Oregon, USA: Eastern Oregon Agricultural Research Center.65.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. Proceedings-Ecology and Management of Annual Rangelands **313**:22-30.

Blossey, B. 1999. Before, during and after: the need for long-term monitoring in invasive plant species management. Biological invasions. **1**:301-311.

Brandt, C. A., and W. H. Rickard. 1994. Alien taxa in the North American shrub-steppe four decades after cessation of livestock grazing and cultivation agriculture. Biological Conservation **68**:95-105.

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

Cousens, R., and M. O'Neill. 1993. Density dependence of replacement series experiments. Oikos **66**:347-352.

Data, U. S. C. 2020. U.S. Climate Data. URL:https://www.usclimatedata.com/climate/bozeman/montana/united-states/usmt0040.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. Weed Science **48**:255-265.

Dudley, T. R. 1968. Alyssum (cruciferae) introduced in North America. Rhodora **70**:298-300.

Elias, S. G., L. O. Copeland, M. B. McDonald, and R. Z. Baalbaki. 2012. Seed Testing: Principles and Practices. Page 48. Michigan State University Press East Lansing, MI

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences **100**:8916.

Fox, J., and S. Weisberg. 2019. An {R} Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. URL: https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Germino, M. J., J. C. Chambers, and C. S. Brown. 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications. 1st ed. 2016 edition. Cham: Springer International Publishing, Cham.

Gioria, M., V. Jaroˇsík, and P. Pyˇseka. 2014. Impact of invasions by alien plants on soil seed bank communities: Emerging Patterns. Perspectives in Plant Ecology, Evolution and Systematics **16**:132-142.

Haider, S., C. Kueffer, H. Bruelheide, T. Seipel, J. M. Alexander, L. J. Rew, J. R. Arévalo, L. A. Cavieres, K. L. McDougall, A. Milbau, B. J. Naylor, K. Speziale, and A. Pauchard. 2018. Mountain roads and non-native species modify elevational patterns of plant diversity. Global Ecology and Biogeography **27**:667-678.

Hamilton, E. W., and C. E. Hellquist. 2012. Yellowstone's most invaded landscape: vegetation restoration in Gardiner Basin. Pages 25-32 Yellowstone Science.

Hejda, M., and P. Pyšek. 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? Biological Conservation **132**:143-152.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology **97**:393-403.

Hulme, P. E., P. Pyšek, V. Jarošík, J. Pergl, U. Schaffner, and M. Vilà. 2013. Bias and error in understanding plant invasion impacts. Trends in Ecology & Evolution **28**:212-218.

Jacobs, J. S. 2012. Plant fact scheet for desert madwort (*Alyssum desertorum*).*in* U.N.R.C. Service, editor., Bozeman State Office, MT.

Jacobs, J. S., and S. Winslow. 2018. Comparing establishment and growth of five native grass species collected in Yellowstone National Park to those selected by the Plant Materials Program. Pages 1-5 *in* USDA-NRCS, editor., Bridger Plant Materials Center, Bridger PMC-NRCS, Montana.

Kindt, R., and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre(ICRAF), Nairobi. ISBN 92-9059-179-X.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. Tests in linear mixed effects models. Journal of Statistical Software **82(13)**:1-26.

Liu, H., D. Zhang, X. Yang, Z. Huang, S. Duan, and X. Wang. 2014. Seed dispersal and germination traits of 70 plant species inhabiting the Gurbantunggut Desert in northwest China. Scientific World Journal **2014**:346405.

MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology. **86**:42-55.

Mangold, J. 2017. October Weed Post: Yellow and desert alyssum (*Alyssum alyssoides* and *A. desertorum*). Montana State University Extension, Bozeman, MT.

Monty, A., and G. Mahy. 2009. Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. Oecologia **159**:305-315.

Mosley, J. 2014. Featured weed: yellow and desert alyssum. Big Sky Small Acres:4-5.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: community ecology package. R package version 2.5-6.

Olliff, T., R. Renkin, C. McClure, P. Miller, D. Price, R. Dan, and J. Whipple. 2001. Managing a complex exotic vegetation program in Yellowstone National Park. Western North American Naturalist **61**:347-358.

Panetta, F. D., O. Cacho, S. Hester, N. Sims-Chilton, and S. Brooks. 2011. Estimating and influencing the duration of weed eradication programmes. Journal of Applied Ecology **48**:980-988.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. Team. 2019. _nlme:Linear and Nonlinear Mixed Effects Models_. R package version 3.1-141.

Rew, L. J., E. A. Lehnhoff, and B. D. Maxwell. 2007. Non-indigenous species management using a population prioritization framework. Canadian Journal of Plant Science **87**:1029-1036.

Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. Ecological Applications **19**:155-162.

Sala, O. E., F. S. Chapin lll, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Sebastian, D. J., S. J. Nissen, J. R. Sebastian, and K. G. Beck. 2017. Seed bank depletion: the key to long-term downy brome (*Bromus tectorum* L.) management. Rangeland Ecology & Management **70**:477-483.

Skurski, T. C., B. D. Maxwell, and L. J. Rew. 2013. Ecological tradeoffs in non-native plant management. Biological Conservation **159**:292-302.

Vilà, M., C. Basnou, P. Pyšek, M. Josefsson, P. Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, P. E. Hulme, and D. partners. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment **8**:135-144.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**:702-708.

Vitousek, P. M. 1996. Biological Invasions and Ecosystem Processes: Towards an Integration of Population Biology and Ecosystem Studies. Pages 183-191 *in* F. B. Samson and F. L. Knopf, editors. Ecosystem Management: Selected Readings. Springer New York, New York, NY.

Williamson, M., and A. Fitter. 1996. The Varying Success of Invaders. Ecology **77**:1661-1666.

CHAPTER THREE

INDAZIFLAM CONTROLS *ALYSSUM DESERTORUM*, BUT ALSO AFFECTS NON-TARGET NATIVE PLANT COMMUNITIES OF SAGEBRUSH STEPPE

Introduction

Non-native plant invasions can have devastating impacts on native species by altering disturbance regimes, transforming ecosystem functions and reducing biodiversity (Elton 1958, Mack and D'Antonio 1998, Tilman 1999, Vilà et al. 2011). Chemical efforts to control non-native plants can also have adverse effects on existing native species (Crone et al. 2009, Rinella et al. 2009, Kettenring and Adams 2011), sometimes more than the effects from the invader itself (Ortega and Pearson 2011, Skurski et al. 2013). Understanding how herbicides affect both target and non-target vegetation is key to developing management strategies that achieve their goal of controlling invasive plants and increasing desired ones.

Controlling invasive plants in rangelands is critical to maintaining essential functions and services they provide to humans across the world (Lund 2007, O'Mara 2012). The sagebrush steppe rangeland in the western United States is a diverse ecological community that provides forage for livestock operations and provides habitat for wildlife species (Beck et al. 2012). This semi-arid ecosystem is threatened by land use changes, climate change, and subsequent non-native plant invasions (Knapp 1996, DiTomaso 2000, Vasquez et al. 2010). Invasive winter annual grasses such as *Bromus tectorum* L. alter fire regimes and disrupt ecosystem functions of the sagebrush steppe (Billings 1994, Young and Fay 1997, Balch et al. 2013), creating novel plant communities far less diverse than native communities (Allen and Knight 1984). Winter annual species occupy an unused temporal niche in the sagebrush

community; they germinate in the fall, lay dormant over the winter, and utilize resources immediately following the spring thaw (Grime 1979), when most native species are only beginning to grow.

One non-native annual species of the sagebrush steppe is the forb *Alyssum desertorum* Stapf (Noack 2020), which acts as a winter annual and is of growing concern to land managers (Mosley 2014). *Alyssum desertorum* commonly occurs in the sagebrush steppe at elevations from 792m to 1981m (Noack 2020), frequently alongside *B. tectorum* in disturbed areas (Young and Clements 2005). In Yellowstone National Park, *A. desertorum* has recently been found above its documented elevational range (at 2347m) primarily in areas disturbed by wildlife, by tourists walking off designated routes, or by recent construction (Anderson, pers. comm.). Anecdotal accounts claim that *A. desertorum* outcompetes native vegetation (Mosley 2014), though this species is unstudied. Active management to control the spread of *A. desertorum* using a newly approved herbicide, indaziflam (Bayer Crop Science), needs to be evaluated.

Indaziflam is a non-selective, pre-emergent herbicide that inhibits cellulose biosynthesis (Brabham et al. 2014) and was originally developed for use in turf and orchard systems (Kaapro and Hall 2012). Recently, indaziflam was approved for use in natural areas and grazed rangeland (Bayer 2020), and is being promoted as an option to control invasive annual grasses in sagebrush steppe (Sebastian et al. 2016b, Clark et al. 2020). Long-term control of these annual non-native grasses is desirable and may be achieved by using indaziflam to deplete the soil seedbank (Sebastian et al. 2017a, Sebastian et al. 2017b). Indaziflam shows great promise to reduce target species, as this herbicide remains active in the top few centimeters of soil for up to three years (Sebastian et al. 2016b) and would potentially require fewer applications than other less persistent herbicides (Sebastian et al. 2017a).

The efficacy of indaziflam in rangeland has been evaluated primarily in highly disturbed areas dominated by invasive annual grasses with little remaining native vegetation (Sebastian et al. 2017a).

The control of invasive annual grasses results in an increase in growth of existing perennial plants due to reduced competition (Sebastian et al. 2017a, Sebastian et al. 2020). Established perennial vegetation is largely unaffected by indaziflam (Clark et al. 2019), possibly because roots of perennial plants often extend below the zone of herbicide activity. New recruitment of a non-native perennial species was inhibited by indaziflam (Sebastian et al. 2017c) and it is likely that any germinating seeds in the zone of herbicide activity (0-2.5 cm depth) will not emerge, as indaziflam inhibits cellulose biosynthesis in the radicle (Brabham et al. 2014).

Seeds of both native and non-native species primarily reside in the top layer of soil or on the soil surface, so any germinating seeds will be impacted by indaziflam. Species with annual life-cycles and short-lived seed banks will be more impacted by indaziflam than perennial species that do not rely on annual germination. Only a couple indaziflam studies have examined impacts to annual forbs (Clark et al. 2019, Sebastian et al. 2020), and one of those found a slight increase in native annual cover after indaziflam treatment (Sebastian et al. 2020). This may suggest certain annual species are more tolerant of indaziflam, though further study is needed.

The goal of this study was to understand the effects of indaziflam on infestations of the non-native forb *A. desertorum*, and the native annual and perennial species co-occurring in diverse sagebrush steppe plant communities. The first objective was to determine whether indaziflam reduces *A. desertorum* abundance. I hypothesized that the herbicide would effectively control the non-native annual forb. The second objective was to assess whether indaziflam reduces richness and diversity of the whole plant community, distinguishing between perennial and annual species. I hypothesized that indaziflam would reduce annual species richness and diversity. For my final objective, to evaluate whether indaziflam reduces forb germination from the soil seedbank, I hypothesized that indaziflam would suppress all germination from the soil.

Methods

Field Study

The effects of indaziflam on non-native and native flora were evaluated at six study sites across the northern range of Yellowstone National Park (YNP); these sites were selected along an elevational gradient ranging from 1615m to 2347m (Appendix A Figure A.1). All sites were characterized as mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*). The six sites were randomly chosen to represent the elevation gradient from a road-side survey of *A. desertorum* populations within YNP, conducted with aid of the park botanist (H. Anderson).

To address potential temperature differences among the sites, two temperature probes were installed at each site: one at ground level and the other at ~0.5m, both probes were on the north side of a shrub. Hourly probe measurements were recorded at each site using Lascar EL-USB 1(Lascar Electronics) temperature data loggers. Temperature loggers were installed in September 2018 and were removed in August 2020; mean summer temperatures were calculated for May through September for each site (Appendix A Table A.1).

To address potential differences in soil moisture, at each site two GB-1 gypsum sensor blocks (Delmhorst Instrument Co.) were buried 10 cm deep between shrubs in areas without *A. desertorum*. Soil moisture was measured bi-weekly using a KS-D1 digital soil moisture tester (Delmhorst Instrument Co.) from June-September during 2019 and 2020. The first date of permanent wilting point was determined for each site, defined as the sample period soil moisture reached below -1.5MPa (Aho and Weaver 2008); Appendix A Table A.1). Finally, Soil samples from each site were analyzed for pH, soil organic matter (SOM), cation exchange capacity (CEC), and texture by Ward Laboratories (Kearney, NE), and soil names were determined using the Web Soil Survey (Soil Survey Staff) (Appendix A Table A.2).

All sites had a high and low invasion treatment, defined as areas with high levels of *A. desertorum* abundance (>10 individuals/m^2), and adjacent areas with low or no invasion (<10 individuals/m^2). At five of the sites (Mammoth:M, Blacktail:B, Lamar:L, Phantom:P, and Swan:W) 18-1m^2 plots were established each in high and low invasion areas. In each of the invasion treatments, twelve plots were sprayed with indaziflam and six control plots were left unsprayed. Half of the sprayed plots were originally targeted for seed addition but this did not occur and these plots were considered "spray" plots for analysis. At the sixth site (Hayden:HD), 14 -1m^2 plots were established each in high and low invasion areas. Seven of the plots in each invasion treatment were sprayed with indaziflam, and seven plots were left unsprayed as controls. All spray plots were treated in August 2018 with 63g·ai·ha^{-1} indaziflam using a backpack sprayer fitted with a XR11002 flat spray nozzle (TeeJet® Spraying Systems, P.O. Box 7900, Wheaton, IL 60187).

Ocular estimates of cover (to the nearest 0.5%) for each species and ground cover were conducted one and two years after treatment during peak vegetative season, for the central 0.75m^2 of each plot to account for potential edge effects of the herbicide. Estimates were allowed to exceed 100% to account for understory canopy structure.

Soil Seedbank Study

To assess the effect of herbicide on the seedbank, soil samples were collected from plots sprayed and not sprayed at two sites (M, B) in April 2019. At each site six soil cores (10cm dia. x 6cm deep) were taken in each of six seed-spray plots, and six control plots in areas of high and low invasion. The samples were taken between the 0.75m^2 and 1 m^2 plot edges. Soil cores from the same plots were combined into one soil sample, for a total of one soil sample per plot, and an overall total of 48 samples (12 each in high-spray, low-spray, high-control, and low-control). Soil samples were spread out in trays (28 cm x 13 cm). To prevent drying out and to avoid diluting the herbicide concentration in the soil the

samples were placed carefully on top of 2.5cm of sterilized soil (1:1:1 ratio of mineral soil, sphagnum peat moss, and washed concrete sand) in the Montana State University Plant Growth Center. Trays were placed in a greenhouse (22°-18°C, 16-hr photoperiod) and watered twice each day for 5 minutes using a drip irrigation system.

Seedling germination was recorded regularly. Seedlings that emerged were identified, counted, and then removed from the tray. Seedlings that were unidentifiable were repotted and grown until they were identifiable. Emerging graminoids were removed and not counted. There was no germination after one month, therefore trays were moved to a cold, wet and dark stratification chamber (4 °C) for 30 days to break dormancy, after which the trays were put back in the greenhouse. After germination diminished again (after about 6 months) the trays were put in the stratification chamber for 56 days and then returned to the greenhouse. The experiment was terminated after 17 months.

Statistical Analysis All analyses were completed using the statistical program R (Version 3.6.1, R Core Team, 2019) including the packages *BiodiversityR* (Kindt and Coe 2005), *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), *MuMIN* (Bartoń 2019), and *vegan* (Oksanen et al. 2019). *Alyssum desertorum* percent cover was analyzed as a separate response variable for our first objective but was included in the other response variable calculations. Percent cover estimates were used to calculate Shannon's diversity index for each plot. Shannon's diversity index was calculated as

$$H = -\sum_{i=1}^{S} p_i * logb * p_i$$

where p_i is the proportion of species *i,* S is the number of species, and log*b* is the logarithm base 10. In addition to the whole community, impacts to richness and diversity of perennial graminoids, perennial forbs and annual native forbs were examined.

To evaluate the effects of indaziflam alone on the abundance of *A. desertorum*, the high invasion data was subset and a linear mixed model following a Gaussian distribution was fit for objective

1. The saturated model included herbicide treatment (spray, control), elevation, and year (2019, 2020) as main effects. To account for repeated measures of plots between years, the unique tag number for each plot was included as a random effect. The saturated model for objective 1 was:

A. desertorum abundance ~ Indaziflam * Elevation * Year, random = Tag

For objective 2, indaziflam effects on the plant community, the full data set was used including both levels of *A. desertorum* invasion. Species richness was evaluated with generalized mixed-effects models (GLMM) following a Poisson distribution. Shannon's diversity was evaluated with linear mixed models following a Gaussian distribution. Saturated models with all possible interactions were fit with main and random effects as above and including invasion (high, low) as a main effect. The saturated model for objective 2 was:

Response ~ Indaziflam * Invasion * Elevation * Year, random = Tag

with the response being either species richness or Shannon's diversity. Any significant interactions were maintained in the final models. Normality and heteroscedasticity assumptions were assessed, and data transformed when assumptions were not met. Mammoth was the lowest site and used as the model intercept. A Type II ANOVA was used to evaluate treatment effects, with a post hoc Tukey's comparison to assess differences when necessary. To further assess changes in species composition between spray and control plots, rank abundance curves were created for all species at each site. Finally, for objective 3, impacts to the forbs in the soil seedbank, abundance, richness and Shannon's diversity were analyzed using the same modelling as above.

Results

Impacts of indaziflam on *A. desertorum* abundance

Indaziflam provided excellent control of *A. desertorum* one and two years after treatment within the high invasion plots at all sites ($p < 0.01$; Fig. 3.1; Appendix C Table C.1). There was no difference by

elevation nor year (p = 0.58; p = 0.15, respectively) however there were pair-wise interactions, and results will be discussed accordingly (Appendix C Table 1). The overall pattern was a reduction of mean *A. desertorum* cover in sprayed plots though there were differences in the magnitude of response across elevations between the two sampling years (Fig. 3.1). Only one site (L) showed a different pattern in that 2020 there was less *A. desertorum* in the control than sprayed plot (Fig. 3.1). Mean cover of *A. desertorum* averaged across all elevations in spray plots in 2019 was 0.1 (±0.43) and in 2020 was 0.2 (±0.08), and in control plots was 3.4 (±0.44) and 2.5 (± 0.32), respectively. In sprayed plots across all elevations mean *A. desertorum* cover was 97% less in 2019, and 91% less in 2020 than in control plots.

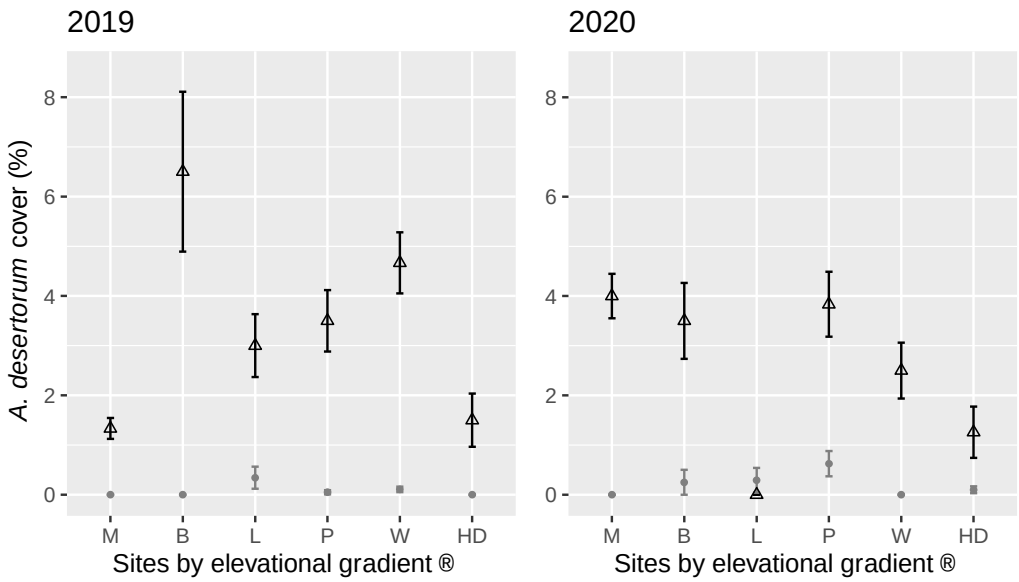


Figure 3.1. Mean (± SE) *Alyssum desertorum* cover after indaziflam treatment (sprayed = •, control = Δ) at sites in Yellowstone National Park across an elevational gradient (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m, and HD = 2347m) in 2019 and 2020. Data shown are from plots with high levels of *A. desertorum* invasion.

Impacts of indaziflam on the plant community

There were 146 native species: 93 perennial forbs, 28 perennial graminoids, 14 annual forbs, and 11 shrubs across all sites and invasion treatments. Also, there were very few non-native species: 4 perennial graminoids, 1 annual graminoid, 7 perennial forbs, 2 annual forbs (Appendix A Table A.1;

Appendix E Table E.1). Non-native species cover was low at all elevations, so these species were included in the whole community analysis. Total species richness ranged from 38 to 76 species at each site (Appendix A Table A.1).

For the whole plant community, mean species richness was reduced by indaziflam ($p < 0.01$) and elevation ($p < 0.01$), but did not differ by year ($p = 0.26$; Table 3.1; Fig. 3.2). There was moderate evidence to support a difference in richness between invasion levels ($p = 0.05$; Table 3.2), possibly explained by the highest elevation.

Richness was significantly lower in spray plots than control plots at all sites, except for two mid elevation sites (L and P, Tukey post-hoc $p = 0.06$ and $p = 0.99$, respectively). At the lowest site mean richness of low invasion control plots was 19.8 (±0.7) species with 18 (±0.8) in high invasion control plots, decreasing to 15 (±0.6) and 14 (±0.5), respectively when sprayed; a reduction of 22% and 29% respectively. At the highest site, mean richness of control plots in the low invasion treatment was 8 (±0.5) and 13 (±0.6) in the high invasion treatment, decreasing to 6 (±0.5) and 6 (±0.8) respectively when sprayed; a reduction in richness of 25% and 54%, respectively (Fig. 3.2).

Sprayed plots were less diverse than control plots ($p < 0.01$), and diversity decreased with elevation ($p < 0.01$) but did not differ between levels of invasion ($p = 0.40$) or by year ($p = 0.18$) (Table 3.2; Appendix C Fig. C.1). This reduction in diversity suggests that some species were more dominant in the sprayed plots, resulting in a less even distribution of species. To better understand these differences, changes in richness and diversity of perennial graminoids, perennial forbs, and annual forbs were analyzed separately.

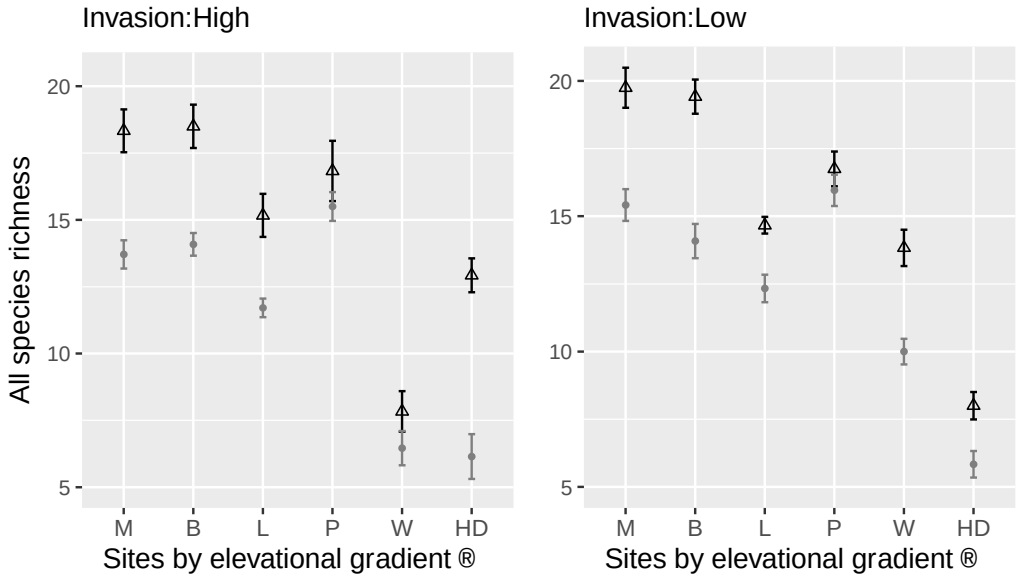


Figure 3.2. All species mean (± SE) richness after indaziflam treatment (sprayed = ●, control = Δ) in high and low invasions of *Alyssum desertorum* across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and HD = 2347m).

Perennial graminoids were largely unaffected by indaziflam. Mean richness did not differ between spray and control plots ($p = 0.96$), by level of invasion ($p = 0.08$), or by year ($p = 0.98$) However, richness differed by elevation ($p = 0.02$), and there was a significant interaction between elevation and invasion ($p = 0.01$; Table 3.1; Fig. 3.3). This interaction is likely due to the large difference in richness at the two highest elevations and patterns between low and high invasion (Fig. 3.3). At the highest elevation in the high invasion area, mean perennial graminoid richness of control plots (2.5±0.4) was greater than the sprayed plots (2±0.3), however in the low invasion area the inverse was true with fewer mean perennial graminoid species in control (1.6±0.3) than in the sprayed plots (2.3±0.2) (Fig. 3.3).

Shannon's diversity of perennial graminoids was also unaffected by indaziflam ($p = 0.50$), invasion level ($p = 0.28$), and year ($p = 0.86$), though differed by elevation ($p < 0.01$; Table 3.2). The higher elevations generally had lower perennial graminoid diversity than the lower elevations (Appendix C Fig. C.2).

Perennial forbs were affected by indaziflam. Mean perennial forb species richness was lower in spray plots compared to control ($p < 0.01$), in high invasion ($p = 0.02$), decreased with elevation ($p < 0.01$) and differed between years ($p = 0.01$; Table 3.1). A Tukey's post hoc test showed that the M and B sites had significant differences in perennial forb richness between spray and control plots ($t_{194} = 2.29$, $p < 0.01$ and $t_{194} = 2.35$, $p < 0.01$, respectively). At the lowest elevation (M), mean richness of control plots ranged from 11.4 (±0.54) in low invasion to 9.8 (±0.63) in high invasion areas, decreasing to 9.2 (±0.44) and 7.4 (±0.36) respectively when sprayed. At the next lowest elevation (B), mean richness of control plots ranged from 12.8(±0.60) in low invasion to 9.8 (±0.42) in high invasion, decreasing to 9.3(±0.52) and 8.6 (±0.43) respectively when sprayed. At the highest elevation perennial forb richness was the lowest; mean richness of unsprayed plots ranged from 2.8 (±0.3) in uninvaded to 3.5 (±0.33) in invaded, decreasing to 2.3(±0.67) and 2.6 (±0.59) respectively when sprayed (Fig. 3.4). Shannon's diversity of perennial forbs was less in the spray plots than the control plots ($p = 0.04$), slightly less in high invasion plots ($p = 0.05$), decreased with elevation ($p < 0.01$) and was lower in 2020 than 2019 ($p = 0.01$, Table 3.2; Appendix C Fig. C.3).

Relative rank abundance graphs for each species in spray and control plots elucidated which species were more dominant in the sprayed plots (Appendix D). Control plots in general had more middling abundant species and fewer dominant species compared to sprayed plots. Comparisons of total cover of perennial forb species in spray and control plots revealed a variety of responses among the sites; the most extreme differences will be discussed. At two sites a native forb was more abundant in sprayed than control: *Lupinus sericeus* at the lowest elevation (22.7 % vs 10.6% respectively) and *Arnica sororia* (17.2% and 0.9% respectively) at the second highest site. At the one mid elevation site (L) a native forb was less abundant in sprayed than control: *Arenaria congesta* (2% and 9% respectively); while at another (P), *Taraxacum laevigatum* was more dominant in the control than the spray plots

(17.5% and 23.6% respectively). One perennial forb species, *Geum triflorum,* was found only in control plots across all elevations.

Table 3.1 Effects of indaziflam (spray, control) on species richness of the whole plant community, perennial graminoids, perennial forbs, and annual forbs, controlling for level of *Alyssum desertorum* invasion (high, low), elevation, and year (2019, 2020). Intercept is control, low invasion, 2019. Results from mixed-effects models assuming a Poisson distribution. Values in bold indicate statistically significant differences ($p < 0.05$).

	Fixed effects					Random effect
Response	Predictor	Est.	SE	z-value	p(>)	Variance
						Tag
Richness						
Whole community	Intercept	4.55	0.16	28.92	<0.01	0.03±0.18
R^2=0.52	**Indaziflam**	**-0.24**	**0.04**	**-6.27**	**<0.01**	
	Invasion	-7e-03	0.04	-1.93	0.05	
	Elevation	**-9e-04**	**7.6e-05**	**-11.76**	**<0.01**	
	Year2020	-3e-03	0.03	-1.14	0.26	
Perennial graminoids	**Intercept**	**1.99**	**0.31**	**6.51**	**<0.01**	0.0±0.0
R^2=0.08	Indaziflam	2e-03	0.05	0.05	0.96	
	Invasion	-3e-04	2e-04	-1.76	0.08	
	Elevation	**0.96**	**0.43**	**2.25**	**0.02**	
	Year2020	1e-03	0.05	0.02	0.98	
	Elevation*Invasion	**-5e-04**	**2e-04**	**-2.55**	**0.01**	
Perennial forbs	**Intercept**	**4.90**	**0.22**	**22.17**	**<0.01**	0.09±0.29
R^2=0.56	**Indaziflam**	**-0.15**	**0.06**	**-2.59**	**0.01**	
	Invasion	**-0.13**	**0.06**	**-2.39**	**0.02**	
	Elevation	**-1e-03**	**1e-04**	**-12.98**	**<0.01**	
	Year2020	**-0.10**	**0.04**	**-2.59**	**0.01**	
Annual forbs	**Intercept**	**-3.08**	**0.70**	**-4.39**	**<0.01**	0.32±0.56
R^2=0.52	**Indaziflam**	**-1.85**	**0.15**	**-12.40**	**<0.01**	
	Invasion	**0.42**	**0.14**	**3.03**	**<0.01**	
	Elevation	**1e-03**	**2e-04**	**5.15**	**<0.01**	
	Year2020	0.14	0.93	1.46	0.14	

Table 3.2. Effects of indaziflam (spray, control) on Shannon's diversity of the whole plant community, perennial graminoids, perennial forbs, and annual forbs, controlling for level of *Alyssum desertorum* invasion (high, low), elevation, and year (2019, 2020). Intercept is control, low invasion, 2019 Results from mixed-effects models. Values in bold indicate statistically significant differences ($p < 0.05$).

		Fixed effects					Random effect	
Response	Predictor	Est.	SE	df	z-value	p(>)	Variance	
							Tag	Residual
Shannon's Diversity								
							0.11±	0.03±
Whole	**Intercept**	**4.24**	**0.23**	**204**	**18.62**	**<0.01**	0.33	0.16
community	**Indaziflam**	**-0.18**	**0.05**	**204**	**-3.71**	**<0.01**		
R^2=0.87	Invasion	-0.04	0.05	203	0.86	0.39		
	Elevation	**-1e03**	**1e-04**	**203**	**-9.18**	**<0.01**		
	Year	-0.02	0.02	204	-1.35	0.18		
Perennial							0.12±	0.03±
graminoids	**Intercept**	**3.00**	**0.24**	**204**	**12.67**	**<0.01**	0.34	0.18
R^2=0.83	Indaziflam	0.04	0.05	204	0.68	0.50		
	Invasion	-6e-02	0.05	203	-1.09	0.28		
	Elevation	**-9e04**	**1e-04**	**203**	**-8.31**	**<0.01**		
	Year	3e-03	0.02	204	-0.17	0.86		
	Elevation*Invasion	**3.00**	**0.24**	**204**	**12.67**	**<0.01**		
Perennial							0.21±	0.04±
forbs	**Intercept**	**3.90**	**0.32**	**204**	**11.51**	**<0.01**	0.46	0.19
R^2=0.88	**Indaziflam**	**-0.13**	**0.07**	**203**	**-2.02**	**0.04**		
	Invasion	-0.13	0.07	203	-1.94	0.05		
	Elevation	-1e-03	1e-04	203	-7.69	**<0.01**		
	Year	**-0.07**	**0.02**	**204**	**-3.47**	**<0.01**		
							0.07±	0.05±
	Intercept	**-0.43**	**0.20**	**204**	**-2.09**	**0.04**	0.27	0.23
Annual forbs	**Indaziflam**	**-0.43**	**0.05**	**204**	**-9.55**	**<0.01**		
R^2=0.71	Invasion	0.06	0.04	203	1.37	0.17		
	Elevation	**4e-04**	**10e-05**	**203**	**4.46**	**<0.01**		
	Year	0.04	0.02	204	1.76	0.08		

Figure 3.3. Perennial graminoids mean (± SE) species richness after indaziflam treatment (sprayed = ●, control = Δ) in high and low invasions of *Alyssum desertorum* across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and HD = 2347m).

There were 13 species of annual forbs at our sites, six were observed in both control and spray plots: *Alyssum desertorum, Collomia linearis* Nutt., *Draba nemorosa* L.*, Leptosiphon septentrionalis* (H. Mason) Porter & Johnson*, Microsteris gracilis* (Hook.) Greene*,* and *Polygonum douglasii* Greene. Annual forbs were greatly impacted by indaziflam. Mean species richness of annual native forbs decreased with indaziflam treatment ($p < 0.01$), and elevation ($p < 0.01$), increased in high invasion areas ($p < 0.01$), and did not differ between year ($p = 0.14$; Table 3.1). Species richness of annual forbs was reduced by at least 50% across all elevations in sprayed plots, however richness increased as elevation increased (Fig. 3.5). Shannon's diversity of annual forbs was also reduced by indaziflam ($p < 0.01$), though increased significantly with elevation ($p < 0.01$) and did not differ by year ($p = 0.08$) or level of invasion ($p = 0.17$) (Table 3.2).

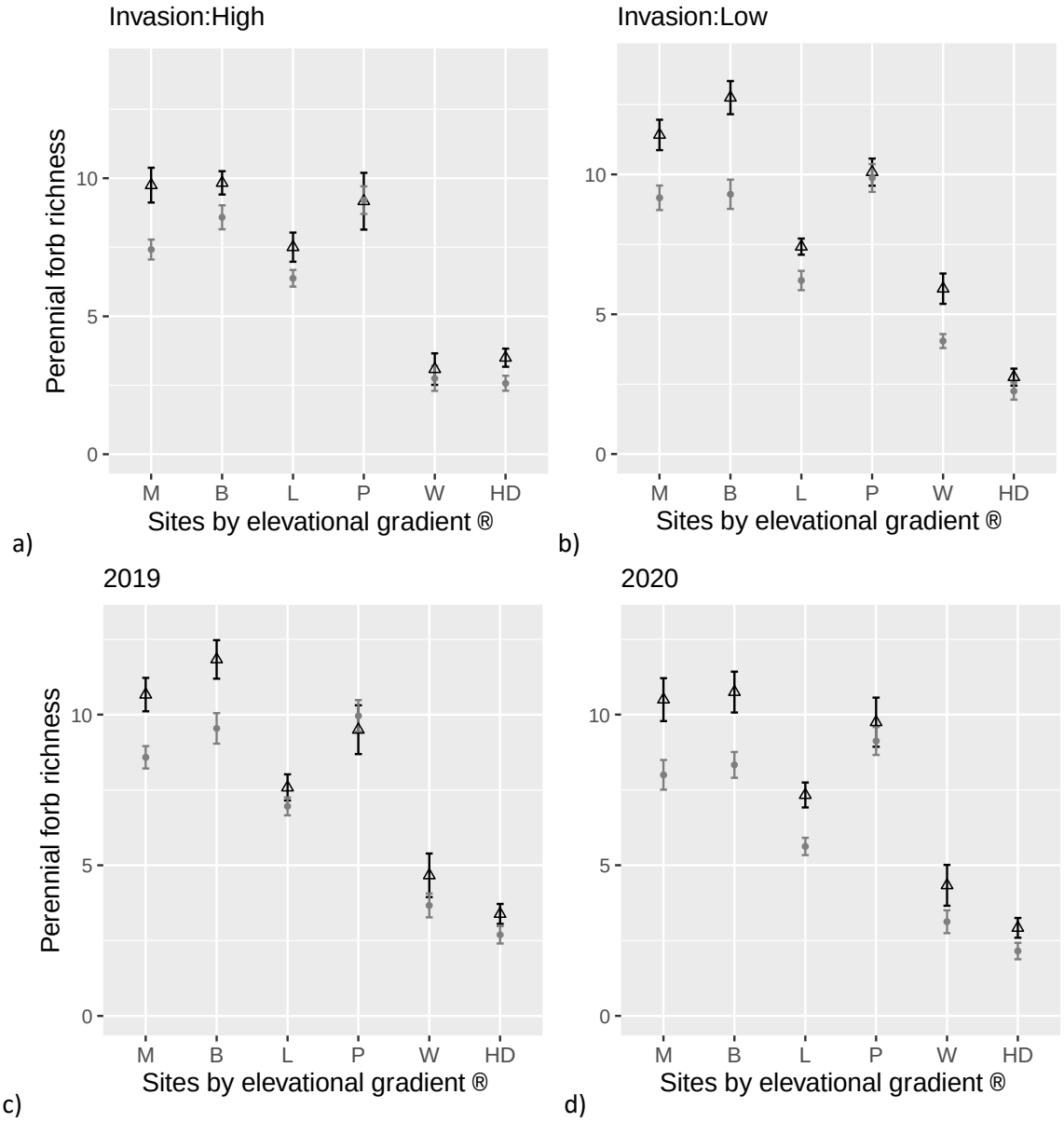


Figure 3.4 Perennial forb mean (± SE) species richness after indaziflam treatment (sprayed = ●, control = Δ) in a) high and b) low invasions of *Alyssum desertorum* and for two years a) 2019 and b) 2020 across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and H = 2347m).

a) b)

Figure 3.5. Annual forb mean (± SE) species richness after indaziflam treatment (sprayed = •, control = Δ) in a) high and b) low invasions of *Alyssum desertorum* across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and H = 2347m).

<u>Impacts of indaziflam on the soil seedbank</u>

There were 29 forb species that emerged from the soil seedbank. Species that emerged in the sprayed soils were *C. linearis, Descurania sophia* Webb ex Prantl*, D. nemorosa*, and *M. gracilis* (all annuals), though were very low in abundance compared to the unsprayed soils. Indaziflam greatly suppressed germination of both perennial and annual forbs from the soil seedbank. The abundance of seedlings differed in spray and control plots ($p < 0.01$), however was unaffected by level of invasion ($p = 0.52$) and site ($p = 0.41$; Fig. 3.6; Table 3.3). Mean abundance was 55.8 (±18.1) in the control, which was reduced to 1.1 (±0.83) when sprayed. Species richness ($p < 0.01$) was also significantly lower in the spray trays, though was higher at site B ($p < 0.01$). Mean richness from Mammoth and Blacktail controls was 3 (±0.51) species and 6 (±0.48) species, respectively, and was reduced to 0 (±0) and 0.5 (±0.34) when sprayed (Fig. 3.6-a). Shannon's diversity was also lower in spayed trays ($p < 0.01$) and increased in high invasion trays ($p < 0.01$; Table 3.3; Fig. 3.6-b).

Table 3.3. Effects of indaziflam on the abundance, species richness, and Shannon's diversity of seedlings emerged from the soil seedbank controlling for site and level of *Alyssum desertorum* invasion. Results from a linear model fit with a Poisson distribution for abundance and richness, and gaussian distribution for diversity. Intercept is control (no indaziflam treatment), site M, and low invasion. Values in bold indicate statistically significant difference ($p < 0.05$).

Response	Predictor	Est	SE	t-value	p-value
Abundance					
	Intercept	**4.0366**	**0.4148**	**9.731**	**<0.01**
	Indaziflam	**-3.9046**	**1.7065**	**-2.28**	**0.03**
	Site	-0.3957	0.4843	-0.817	0.42
	Invasion	0.3052	0.4806	0.635	0.53
Richness					
	Intercept	**0.8385**	**0.2254**	**3.720**	**<0.01**
	Indaziflam	**-2.881**	**0.4661**	**-6.181**	**<0.01**
	Site	**0.7603**	**0.2243**	**3.389**	**<0.01**
	Invasion	0.371	0.2127	1.768	0.08
Shannon's Diversity					
	Intercept	**0.73449**	**0.1091**	**6.726**	**<0.01**
	Indaziflam	**-0.89526**	**0.1091**	**-8.199**	**<0.01**
	Site	0.4014	0.1091	0.243	0.81
	Invasion	**0.02656**	**0.1091**	**3.676**	**<0.01**

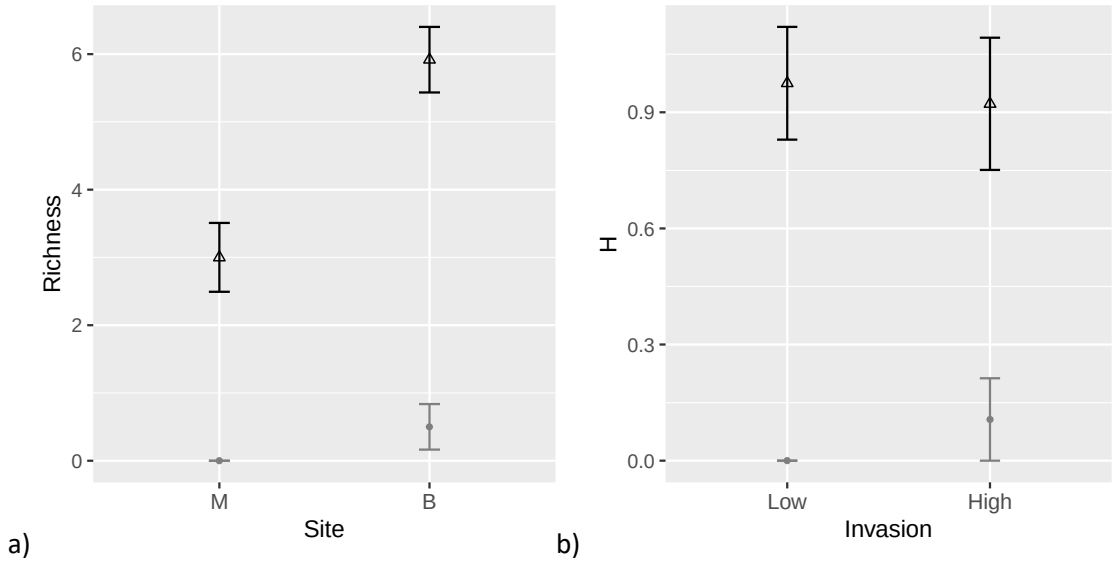


Figure 3.6. Soil seedbank mean (± SE) a) species richness at two low elevation sites in Yellowstone National Park (M= Mammoth, B= Blacktail) and b) Shannon's diversity (H) by level of *Alyssum desertorum* invasion (low, high) after indaziflam treatment (sprayed = ●, control = Δ).

Discussion

Herbicides are useful and effective tools to control non-native plants, however non-target effects on desirable vegetation must be considered when making management decisions. Our study examined impacts to the diversity of the non-target plant community as a result of using the pre-emergent herbicide indaziflam to control the non-native annual forb *Alyssum desertorum*. Additionally, I assessed the degree to which indaziflam impacts seed emergence for species naturally occurring in the soil seedbank from our field sites. Indaziflam controlled *A. desertorum,* but it also reduced species richness and abundance of perennial and annual forbs that emerged from the soil seedbank. Most previous indaziflam studies have focused on non-native winter annual grass control, as these species are the primary threat to rangelands of the western United States (Germino et al. 2016, DiTomaso et al. 2017), and are thus conducted in areas with high infestations of non-native grasses. The intact and diverse plant community at our study sites (total species richness ranged from 38 to 76 species) along with the patchy occurrence of *A. desertorum* provided an opportunity to assess the non-target effects of indaziflam on localized populations.

Indaziflam controlled the non-native winter annual forb *A. desertorum*, reducing cover by 97% one year post treatment, and by 91% two years following treatment. Results of the seedbank study showed almost no emergence of *A. desertorum* and other forbs in soils collected from sprayed plots, demonstrating the potential impact indaziflam can have in areas with a diverse plant community. Sebastian et al. (2017c) found that indaziflam combined with other herbicides provided 80% control of the perennial non-native forb *Linaria dalmatica* four years after application; herbicide without indaziflam did not provide similar control, therefore authors inferred that indaziflam prevented recruitment of *L. dalmatica* from the soil seedbank.

The whole plant community showed reduced species richness and Shannon's diversity in sprayed plots. The percent reduction of species richness between spray and control plots increased with elevation; the lowest site had a reduction of 22-29% and the highest site had a reduction of 27-52%, respectively. Our findings are contrary to other studies that found increased richness and abundance (Sebastian et al. 2020) and no effects on species richness (Clark et al. 2019) of the whole community one and two years after treatment, respectively. However as noted above, these other studies were conducted in areas with dense infestations of *B. tectorum* and the increased abundance and richness was attributed to release from competition (Clark et al. 2019, Sebastian et al. 2020).

Previous indaziflam studies have primarily focused on the response of perennial forbs and perennial grasses, as they are desirable components of rangeland plant communities; however, annual ephemeral forbs are also key components of rangelands. They provide critical spring forage for many wildlife species (Drut et al. 1994, Luna et al. 2018) and occupy an early successional niche. In our study annual forb richness was significantly reduced by indaziflam. These results are in contrast to another study that found no effect on annual forbs (Sebastian et al. 2020). This suggests that individual species of annual forbs may have differing sensitivities to indaziflam and demonstrates the need for species-specific research (Wagner and Nelson 2014). Three native annual forbs from our study emerged in both field plots and the greenhouse study sprayed treatments (*C. linearis, D. nemorosa*, and *M. gracilis)*. Native annual forbs have been shown to compete with non-native annuals (Uselman et al. 2015) and encourage establishment of planted species for restoration (Leger et al. 2014). Therefore, knowing which annual species are tolerant to indaziflam may be useful in restoration seed mixes after indaziflam application.

Indaziflam provides residual control in the soil for up to three years (Sebastian et al. 2016b) and while this attribute works to deplete the non-native annual grass seedbank (Sebastian et al. 2017b) and

suppress non-native forb species (Sebastian et al. 2017c), I have shown that native species in the soil seedbank will also be inhibited and the future community composition of sprayed areas may be altered. Perennial species populations may not be impacted as much by indaziflam since established individuals are unaffected and can potentially repopulate the soil seedbank after the herbicide has degraded. While perennial graminoids were largely unaffected as expected, perennial forb richness and diversity, and annual forb richness were both reduced by indaziflam and elevation. Reduced recruitment, rather than damage to established perennial vegetation, was likely the cause of perennial forb reduction. Annual species, however, rely on annual regeneration from the seedbank and depending on their rates of seed decay, may be particularly impacted by long lived residual non-selective pre-emergent herbicides like indaziflam. Unfortunately, the seed longevity of most native annual species in the sagebrush steppe is not known.

Indaziflam is a new herbicide to control invasive annual grasses and though it purportedly has no negative impacts to existing perennial vegetation, I have shown that the herbicide does prevent regeneration from the soil seedbank of *A. desertorum* and non-target perennial and annual forb species. In areas where the seedbank comprises mostly of non-native species, indaziflam may be a valuable tool to deplete the target species seedbank before active revegetation efforts. However, in areas with minimal invasions, an existing diverse plant community, and therefore likely a diverse seedbank, indaziflam may not be the most appropriate approach. Invasive plant management can be particularly difficult in arid rangelands, therefore evaluating the non-target effects on existing intact vegetation is

critical to developing management strategies to maintain and restore these areas and their ecosystem functions and services.

References

Aho, K., and T. Weaver. 2008. Measuring soil water potential with gypsum blocks: calibration and sensitivity. Intermountain Journal of Sciences **14**:51-60.

Allen, E. B., and D. H. Knight. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. The Southwestern Naturalist **29**:407-421.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology **19**:173-183.

Bartoń, K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.6. URL:https://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1-48.

Bayer. 2020. Rejuvra herbicide receives EPA approval. New herbicide is a long-term, economical solution for the control of invasive annual grasses, Bayer Environmental Science, 5000 CentreGreen Way, Suite 200, Cary, NC 27513.

Beck, J. L., J. W. Connelly, and C. L. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology & Management **65**:444-455.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. Proceedings-Ecology and Management of Annual Rangelands **313**:22-30.

Brabham, C., L. Lei, Y. Gu, J. Stork, M. Barrett, and S. DeBolt. 2014. Indaziflam herbicidal action: a potent cellulose biosynthesis inhibitor. Plant Physiology **166**:1177-1185.

Clark, S. L., D. J. Sebastian, S. J. Nissen, and J. R. Sebastian. 2019. Effect of indaziflam on native species in natural areas and rangeland. Invasive Plant Science and Management **12**:60-67.

Clark, S. L., D. J. Sebastian, S. J. Nissen, and J. R. Sebastian. 2020. Evaluating winter annual grass control and native species establishment following applications of indaziflam on rangeland. Invasive Plant Science and Management **13**:199-209.

Crone, E. E., M. Marler, and D. E. Pearson. 2009. Non-target effects of broadleaf herbicide on a native perennial forb: a demographic framework for assessing and minimizing impacts. Journal of Applied Ecology **46**:673-682.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. Weed Science **48**:255-265.

DiTomaso, J. M., T. A. Monaco, J. J. James, and J. Firn. 2017. Invasive plant species and novel rangeland systems. Pages 429-465 Rangeland Systems. Springer, Cham.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Technical Note: Diet and food selection of sage grouse chicks in Oregon. Journal of Range Management **47**:90-93.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Springer, Boston, MA.

Germino, M. J., J. C. Chambers, and C. S. Brown. 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications. 1st ed. 2016 edition. Cham: Springer International Publishing, Cham.

Grime, J. P. 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester.

Kaapro, J., and J. Hall. 2012. Indaziflam-a new herbicide for pre-emergent control of weeds in turf, forestry, industrial vegetation and ornamentals. Pak. F. Weed Sci. Res. **18**:267-270.

Kettenring, K. M., and C. R. Adams. 2011. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology **48**:970-979.

Kindt, R., and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre(ICRAF), Nairobi. ISBN 92-9059-179-X.

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.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. Tests in linear mixed effects models. Journal of Statistical Software **82(13)**:1-26. URL:https://doi.org/10.18637/jss.v18082.i18613.

Leger, E. A., E. M. Goergen, and T. F. de Queiroz. 2014. Can native annual forbs reduce *Bromus tectorum* biomass and indirectly facilitate establishment of a native perennial grass? Journal of Arid Environments **102**:9-16.

Luna, T., M. R. Mousseaux, and R. K. Dumroese. 2018. Common native forbs of the northern Great Basin important for Greater Sage-grouse. Gen.Tech.Rep. RMRS-GTR-387, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station; Portland, OR: U.S. Department of the Interiror, Bureau of Land Management, Oregon-Washington Region.

Lund, H. G. 2007. Accounting for the world's rangelands. Rangelands **29**:3-10.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.

Mosley, J. 2014. Featured weed: yellow and desert alyssum. Big Sky Small Acres:4-5.

Noack, R. 2020. Plant guide for desert madwort (*Alyssum desertorum*).*in* U.-N. R. C. Service, editor., Bridger Plant Materials Center. Bridger, MT

O'Mara, F. P. 2012. The role of grasslands in food security and climate change. Annals of Botany **110**:1263-1270.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: community ecology package. R package version 2.5-6. URL:https://CRAN.R-project.org/package=vegan.

Ortega, Y. K., and D. E. Pearson. 2011. Long-term effects of weed control with picloram along a gradient of spotted knapweed invasion. Rangeland Ecology & Management **64**:67-77.

Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. Ecological Applications **19**:155-162.

Sebastian, D. J., M. B. Fleming, E. L. Patterson, J. R. Sebastian, and S. J. Nissen. 2017a. Indaziflam: a new cellulose-biosynthesis-inhibiting herbicide provides long-term control of invasive winter annual grasses. Pest Management Science **73**:2149-2162.

Sebastian, D. J., S. J. Nissen, J. R. Sebastian, and K. G. Beck. 2017b. Seed bank depletion: the key to long-term downy brome (*Bromus tectorum* L.) management. Rangeland Ecology & Management **70**:477-483.

Sebastian, D. J., S. J. Nissen, J. R. Sebastian, P. J. Meiman, and K. G. Beck. 2017c. Preemergence control of nine invasive weeds with aminocyclopyrachlor, aminopyralid, and indaziflam. Invasive Plant Science and Management **10**:99-109.

Sebastian, D. J., J. R. Sebastian, S. J. Nissen, and K. G. Beck. 2016. A potential new herbicide for invasive annual grass control on rangeland. Rangeland Ecology & Management **69**:195-198.

Sebastian, J., J. Swanson, S. Sauer, S. Clark, and D. Sebastian. 2020. Pollinator community and floral resource response to cheatgrass control with Esplanade 200 SC (indaziflam) *in* Weed Science Society of America Western Society of Weed Science Joint Meeting, Maui, HI.

Skurski, T. C., B. D. Maxwell, and L. J. Rew. 2013. Ecological tradeoffs in non-native plant management. Biological Conservation **159**:292-302.

Soil Survey Staff. Web Soil Survey. Natural Resources Conservation Service, United States Department of Agriculture.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology **80**:1455-1474.

Uselman, S. M., K. A. Snyder, E. A. Leger, and S. E. Duke. 2015. Emergence and early survival of early versus late seral species in Great Basin restoration in two different soil types. Applied Vegetation Science **18**:624-636.

Vasquez, E. A., J. J. James, T. A. Monaco, and D. C. Cummings. 2010. Invasive plants on rangelands: a global threat. Rangelands **32**:3-5.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**:702-708.

Wagner, V., and C. R. Nelson. 2014. Herbicides can negatively affect seed performance in native plants. Restoration Ecology **22**:288-291.

Young, J. A., and C. D. Clements. 2005. Exotic and invasive herbaceous range weeds. Rangelands. **27**:10-16.

Young, J. A., and L. A. Fay. 1997. Cheatgrass and range science: 1930-1950. Journal of Range Management **50**:530-535.

CHAPTER FOUR

CONCLUSION TO THESIS

Non-native plant invasions can have devastating effects to native plant communities in natural areas worldwide (Sala et al. 2000, Vilà et al. 2010), though overall the impacts of non-native plants are quite variable (Hejda et al. 2009, Vilà et al. 2011) and quantitative evidence of ecosystem impact is largely lacking for most species (Blossey 1999). The impacts that have been documented are disproportionately represented by a select few species (Hulme et al. 2013), and more species-specific research is needed to understand the impacts of, and assess whether, a non-native species should be managed. Additionally, life history demographics are also largely unknown for most non-native species, and such information would aid in management decisions. Considering that control efforts can often have non-target impacts to the surrounding plant community (Rinella et al. 2009, Skurski et al. 2013, Wagner and Nelson 2014), sometimes more so than the invader themselves (Skurski et al. 2013), weighing the benefits and costs of herbicide use with the actual impacts of the invader is essential to determining the most appropriate control methods (Rew et al. 2007).

The goal of my research was to study the life history of the non-native annual forb *Alyssum desertorum*, evaluate its competitiveness with and impacts to the native plant community, and examine the non-target effects of the herbicide indaziflam to control localized populations of *A. desertorum* in diverse sagebrush steppe. Chapter Two detailed life stage transitions and built a life history model for *A. desertorum* to determine which life stages should be targeted for management. I quantified seed longevity in the soil seedbank, fall germination rates, reproductive maturity, overwintering success and fecundity. As elevation increased all vital rate transitions decreased, similar to other studies (Monty and Mahy 2009), suggesting that at higher elevations, which correlate with generally cooler and moister

conditions than lower elevations in the same region, this species may not be of concern. In southwest Montana, temperatures have increased by 0.19°C per decade since the 1950's (Whitlock et al. 2017). Under different climate scenarios, this warming pattern is predicted to continue and, interestingly, regional climate predictions suggest precipitation will increase by mid-century (Whitlock et al. 2017). These predictions suggest *A. desertorum* may become more successful at higher elevations if temperatures and precipitation increase.

I evaluated the competitive ability of *A. desertorum* through replacement series experiments with two annual species also common to the sagebrush steppe: the invasive annual grass *Bromus tectorum* and the native annual forb *Microsteris gracilis*. Overall *A. desertorum* was a weak competitor with both species, though the native annual forb was also impacted by interspecific competition, in line with other studies showing functionally similar native species compete with non-native species (Fargione et al. 2003). However, *A. desertorum* is a winter annual, which potentially gives this species a competitive phenological advantaged over native species; competition experiments with established *A. desertorum* and germinating annual forbs would further inform the impact and competitiveness of the species, especially considering the high rates of fall germination I documented. Current documents claim that *A. desertorum* outcompetes and displaces native plant communities, though I found no difference in richness or Shannon's diversity of native plant communities aboveground or in the soil seedbank between areas with high (>10/m^2) and low (<10/m^2) *A. desertorum* invasion. These results suggest that *A. desertorum* is perhaps a passenger of disturbance rather than an active driver of ecosystem degradation (MacDougall and Turkington 2005).

In the arid rangelands of the western United States, winter annual grass invasion is a monumental problem and these species have devastating impacts to sagebrush steppe plant communities, altering fire regimes and degrading ecosystem services and functions (Mack 1981). One

proposed action to control these non-native species is by soil seedbank suppression through the use of pre-emergent herbicides. Indaziflam is a recently approved pre-emergent herbicide that shows great promise in controlling these annual grasses (Sebastian et al. 2017b), however studies addressing the impacts to native plant communities are few and primarily in degraded areas (Sebastian et al. 2017a, Clark et al. 2019). In Chapter Three, the non-target effects of indaziflam were evaluated in the same diverse sagebrush steppe communities as above. The herbicide was applied to localized populations of *A. desertorum* and to adjacent uninvaded area, providing a unique opportunity to study the non-target effects of indaziflam to intact plant communities, in contrast to most studies examining indaziflam in near monocultures of invasive winter annual grasses (Sebastian et al. 2016a, Clark et al. 2019, Sebastian et al. 2020). I found that indaziflam effectively controls *A. desertorum,* however it also suppresses perennial and annual forb species in our observations above ground and of the soil seedbank. These results are contrary to previous studies documenting increases in perennial forb abundance, attributed to release from competitive annual grasses (Clark et al. 2019, Sebastian et al. 2020). My research suggests annual forb populations in relatively intact plant communities will likely be significantly impacted in areas treated with indaziflam, though more research on the seed longevity of these species would help to further understand the potential long-term impacts of indaziflam. Indaziflam provides residual control for up to three years (Sebastian et al. 2016b), therefore it is of great interest to monitor our study sites for a further three to four years after treatment. This information would further inform longer term impacts on indaziflam on the seedbank and future plant community.

Considering the weak competitive ability observed in controlled environments, minimal impacts to richness and diversity in field studies, and its ruderal habit, *A. desertorum* invasion does not seem poised to harm robust sagebrush steppe communities if they remain relatively undisturbed. The potential for indaziflam to suppress the soil seedbank threatens native species in areas with a diverse

native plant community, and perhaps its use should be limited to degraded areas where the seedbank is mostly comprised of non-native species. Therefore, the non-target effects of indaziflam would outweigh any benefits to controlling *A. desertorum* in intact sagebrush steppe. Our study has shown that not all non-native species negatively impact native systems, and that some non-target effects of management can be more destructive than the species being controlled.

References

Blossey, B. 1999. Before, during and after: the need for long-term monitoring in invasive plant species management. Biological invasions. **1**:301-311.

Clark, S. L., D. J. Sebastian, S. J. Nissen, and J. R. Sebastian. 2019. Effect of indaziflam on native species in natural areas and rangeland. Invasive Plant Science and Management **12**:60-67.

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences **100**:8916.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology **97**:393-403.

Hulme, P. E., P. Pyšek, V. Jarošík, J. Pergl, U. Schaffner, and M. Vilà. 2013. Bias and error in understanding plant invasion impacts. Trends in Ecology & Evolution **28**:212-218.

MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology. **86**:42-55.

Mack, R. N. 1981. Invasion of Bromus tectorum L. into Western North America: an ecological chronicle. Agro-Ecosystems **7**:145-165.

Monty, A., and G. Mahy. 2009. Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. Oecologia **159**:305-315.

Rew, L. J., E. A. Lehnhoff, and B. D. Maxwell. 2007. Non-indigenous species management using a population prioritization framework. Canadian Journal of Plant Science **87**:1029-1036.

Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. Ecological Applications **19**:155-162.

Sala, O. E., F. S. Chapin lll, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Sebastian, D. J., M. B. Fleming, E. L. Patterson, J. R. Sebastian, and S. J. Nissen. 2017a. Indaziflam: a new cellulose-biosynthesis-inhibiting herbicide provides long-term control of invasive winter annual grasses. Pest Management Science **73**:2149-2162.

Sebastian, D. J., S. J. Nissen, and J. De Souza Rodrigues. 2016a. Pre-emergence control of six invasive winter annual grasses with imazapic and indaziflam. Invasive Plant Science and Management **9**:308-316.

Sebastian, D. J., S. J. Nissen, J. R. Sebastian, and K. G. Beck. 2017b. Seed bank depletion: the key to long-term downy brome (*Bromus tectorum* L.) management. Rangeland Ecology & Management **70**:477-483.

Sebastian, D. J., J. R. Sebastian, S. J. Nissen, and K. G. Beck. 2016b. A potential new herbicide for invasive annual grass control on rangeland. Rangeland Ecology & Management **69**:195-198.

Sebastian, J., J. Swanson, S. Sauer, S. Clark, and D. Sebastian. 2020. Pollinator community and floral resource response to cheatgrass control with Esplanade 200 SC (indaziflam) *in* Weed Science Society of America Western Society of Weed Science Joint Meeting, Maui, HI.

Skurski, T. C., B. D. Maxwell, and L. J. Rew. 2013. Ecological tradeoffs in non-native plant management. Biological Conservation **159**:292-302.

Vilà, M., C. Basnou, P. Pyšek, M. Josefsson, P. Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, P. E. Hulme, and D. partners. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment **8**:135-144.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**:702-708.

Wagner, V., and C. R. Nelson. 2014. Herbicides can negatively affect seed performance in native plants. Restoration Ecology **22**:288-291.

REFERENCES CITED

Aho, K., and T. Weaver. 2008. Measuring soil water potential with gypsum blocks: calibration and sensitivity. Intermountain Journal of Sciences **14**:51-60.

Alexander, J. M., C. Kueffer, C. C. Daehler, P. J. Edwards, A. Pauchard, and T. Seipel. 2011. Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. Proceedings of the National Academy of Sciences **108**:656.

Allen, E. B., and D. H. Knight. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. The Southwestern Naturalist **29**:407-421.

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics **5**:1-24.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology **19**:173-183.

Bartoń, K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.6. URL:https://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1-48.

Bates, J., K. Davies, and R. Miller. 2004. Ecology of the Wyoming big sagebrush alliance in the northern Great Basin:2004 Progress Report. Burns, Oregon, USA: Eastern Oregon Agricultural Research Center.

Bayer. 2020. Rejuvra herbicide receives EPA approval. New herbicide is a long-term, economical solution for the control of invasive annual grasses, Bayer Environmental Science, 5000 CentreGreen Way, Suite 200, Cary, NC 27513.

Beck, J. L., J. W. Connelly, and C. L. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitats. Rangeland Ecology & Management **65**:444-455.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. Proceedings-Ecology and Management of Annual Rangelands:22-30.

Blossey, B. 1999. Before, during and after: the need for long-term monitoring in invasive plant species management. Biological invasions. **1**:301-311.

Brabham, C., L. Lei, Y. Gu, J. Stork, M. Barrett, and S. DeBolt. 2014. Indaziflam herbicidal action: a potent cellulose biosynthesis inhibitor. Plant Physiology **166**:1177-1185.

Brandt, C. A., and W. H. Rickard. 1994. Alien taxa in the North American shrub-steppe four decades after cessation of livestock grazing and cultivation agriculture. Biological Conservation **68**:95-105.

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

Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems **17**:360-375.

Clark, S. L., D. J. Sebastian, S. J. Nissen, and J. R. Sebastian. 2019. Effect of indaziflam on native species in natural areas and rangeland. Invasive Plant Science and Management **12**:60-67.

Clark, S. L., D. J. Sebastian, S. J. Nissen, and J. R. Sebastian. 2020. Evaluating winter annual grass control and native species establishment following applications of indaziflam on rangeland. Invasive Plant Science and Management **13**:199-209.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation asessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Cheyenne, Wyoming.

Cousens, R., and M. O'Neill. 1993. Density dependence of replacement series experiments. Oikos **66**:347-352.

Crist, T. O., and J. A. MacMahon. 1992. Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. Ecology **73**:1768-1779.

Crone, E. E., M. Marler, and D. E. Pearson. 2009. Non-target effects of broadleaf herbicide on a native perennial forb: a demographic framework for assessing and minimizing impacts. Journal of Applied Ecology **46**:673-682.

Data, U. S. C. 2020. URL:https://www.usclimatedata.com/climate/bozeman/montana/united-states/usmt0040.

Davis, M. A. 2009. Invasion Biology. Oxford University Press Inc., Oxford, UK.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of ecology. **88**:528-534.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. Weed Science **48**:255-265.

DiTomaso, J. M., T. A. Monaco, J. J. James, and J. Firn. 2017. Invasive plant species and novel rangeland systems. Pages 429-465 Rangeland Systems. Springer, Cham.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Technical Note: Diet and food selection of sage grouse chicks in Oregon. Journal of Range Management **47**:90-93.

Dudley, T. R. 1968. Alyssum (cruciferae) introduced in North America. Rhodora **70**:298-300.

Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. Oecologia **126**:563-568.

Elias, S. G., L. O. Copeland, M. B. McDonald, and R. Z. Baalbaki. 2012. Seed testing: principles and practices. Page 48. Michigan State University Press East Lansing, MI

Elton, C. S. 1958. The ecology of invasions by animals and plants. Springer, Boston, MA.

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences **100**:8916.

Fischer, J. L., W. A. Loneragan, K. Dixon, and E. J. Veneklaas. 2009. Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. Biological Conservation **142**:256-269.

Fox, J., and S. Weisberg. 2019. An {R} Companion to Applied Regression, Third Edition. Thousand Oaks CA: Sage. URL: https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Germino, M. J., J. C. Chambers, and C. S. Brown. 2016. Exotic brome-grasses in arid and semiarid ecosystems of the western US: causes, consequences, and management implications. 1st ed. 2016 edition. Cham: Springer International Publishing, Cham.

Gioria, M., V. Jaroˇsík, and P. Pyˇseka. 2014. Impact of invasions by alien plants on soil seed bank communities: emerging patterns. Perspectives in Plant Ecology, Evolution and Systematics **16**:132-142.

Gregg, M. A., and J. A. Crawford. 2009. Survival of greater sage-grouse chicks and broods in the northern Great Basin. The Journal of Wildlife Management **73**:904-913.

Grime, J. P. 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester.

Haider, S., C. Kueffer, H. Bruelheide, T. Seipel, J. M. Alexander, L. J. Rew, J. R. Arévalo, L. A. Cavieres, K. L. McDougall, A. Milbau, B. J. Naylor, K. Speziale, and A. Pauchard. 2018. Mountain roads and non-native species modify elevational patterns of plant diversity. Global Ecology and Biogeography **27**:667-678.

Hamilton, E. W., and C. E. Hellquist. 2012. Yellowstone's most invaded landscape: vegetation restoration in Gardiner Basin. Pages 25-32 Yellowstone Science.

Hejda, M., and P. Pyšek. 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? Biological Conservation **132**:143-152.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology **97**:393-403.

Hulme, P. E., P. Pyšek, V. Jarošík, J. Pergl, U. Schaffner, and M. Vilà. 2013. Bias and error in understanding plant invasion impacts. Trends in Ecology & Evolution **28**:212-218.

Jacobs, J. S. 2012. Plant fact scheet for desert madwort (*Alyssum desertorum*).*in* U.-N. R. C. Service, editor., Bozeman State Office, MT.

Jacobs, J. S., and S. Winslow. 2018. Comparing establishment and growth of five native grass species collected in Yellowstone National Park to those selected by the Plant Materials Program. Pages 1-5 *in* USDA-NRCS, editor., Bridger Plant Materials Center, Bridger PMC-NRCS, Montana.

James, J. J., M. J. Rinella, and T. Svejcar. 2012. Grass seedling demography and sagebrush steppe restoration. Rangeland Ecology & Management **65**:409-417.

Kaapro, J., and J. Hall. 2012. Indaziflam-a new herbicide for pre-emergent control of weeds in turf, forestry, industrial vegetation and ornamentals. Pak. F. Weed Sci. Res. **18**:267-270.

Kelley, W. K., M. E. Fernandez-Gimenez, and C. S. Brown. 2013. Managing Downy Brome (Bromus tectorum) in the Central Rockies: Land Manager Perspectives. Invasive Plant Science and Management **6**:521-535.

Kettenring, K. M., and C. R. Adams. 2011. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology **48**:970-979.

Kindt, R., and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre(ICRAF), Nairobi. ISBN 92-9059-179-X.

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.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. Tests in linear mixed effects models. Journal of Statistical Software **82(13)**:1-26. URL:https://doi.org/10.18637/jss.v18082.i18613.

Leger, E. A., E. M. Goergen, and T. F. de Queiroz. 2014. Can native annual forbs reduce *Bromus tectorum* biomass and indirectly facilitate establishment of a native perennial grass? Journal of Arid Environments **102**:9-16.

Lenoir, J., J.-C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N. E. Zimmermann, S. Dullinger, H. Pauli, W. Willner, and J.-C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography **33**:295-303.

Lesica, P., and J. S. Shelly. 1996. Competitive effects of Centaurea maculosa on the population dynamics of Arabis fecunda. Bulletin of the Torrey Botanical Club:111-121.

Levine, J., M., M. Vilà, C. Antonio, M. D., J. Dukes, S., K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London. Series B: Biological Sciences **270**:775-781.

Liu, H., D. Zhang, X. Yang, Z. Huang, S. Duan, and X. Wang. 2014. Seed dispersal and germination traits of 70 plant species inhabiting the Gurbantunggut Desert in northwest China. Scientific World Journal **2014**:346405.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522-1536.

Luna, T., M. R. Mousseaux, and R. K. Dumroese. 2018. Common native forbs of the northern Great Basin important for Greater Sage-grouse. Gen.Tech.Rep. RMRS-GTR-387, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station; Portland, OR: U.S. Department of the Interiror, Bureau of Land Management, Oregon-Washington Region.

Lund, H. G. 2007. Accounting for the world's rangelands. Rangelands **29**:3-10.

MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology. **86**:42-55.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.

Mack, R. N. 1981. Invasion of Bromus tectorum L. into Western North America: An ecological chronicle. Agro-Ecosystems **7**:145-165.

Mangold, J. 2017. October Weed Post: Yellow and desert alyssum (*Alyssum alyssoides* and *A. desertorum*). Montana State University Extension, Bozeman, MT.

Meyerson, L. A., J. T. Carlton, D. Simberloff, and D. M. Lodge. 2019. The growing peril of biological invasions. Frontiers in ecology and the environment. **17**:191-191.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Greater sage-grouse: ecology and conservation of a landscape specie and its habitats. Studies in Avian Biology **38**:145-184.

Monty, A., and G. Mahy. 2009. Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. Oecologia **159**:305-315.

Mosley, J. 2014. Featured weed: yellow and desert alyssum. Big Sky Small Acres:4-5.

Noack, R. 2020. Plant guide for desert madwort (*Alyssum desertorum*).*in* U.-N. R. C. Service, editor., Bridger Plant Materials Center. Bridger, MT

O'Mara, F. P. 2012. The role of grasslands in food security and climate change. Annals of Botany **110**:1263-1270.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: community ecology package. R package version 2.5-6. URL:https://CRAN.R-project.org/package=vegan.

Olliff, T., R. Renkin, C. McClure, P. Miller, D. Price, R. Dan, and J. Whipple. 2001. Managing a complex exotic vegetation program in Yellowstone National Park. Western North American Naturalist **61**:347-358.

Ortega, Y. K., and D. E. Pearson. 2011. Long-term effects of weed control with picloram along a gradient of spotted knapweed invasion. Rangeland Ecology & Management **64**:67-77.

Panetta, F. D., O. Cacho, S. Hester, N. Sims-Chilton, and S. Brooks. 2011. Estimating and influencing the duration of weed eradication programmes. Journal of Applied Ecology **48**:980-988.

Pardini, E. A., J. M. Drake, J. M. Chase, and T. M. Knight. 2009. Complex Population Dynamics and Control of the Invasive Biennial Alliaria petiolata (Garlic Mustard). Ecological Applications **19**:387-397.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological invasions. **1**:3-19.

Peng, S., N. L. Kinlock, J. Gurevitch, and S. Peng. 2019. Correlation of native and exotic species richness: a global meta-analysis finds no invasion paradox across scales. Ecology **100**:e02552.

Perrotti, P. 2017. Invasive Plants. URL: https://www.nps.gov/yell/learn/nature/invasive-plants.htm.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological Resilience, Biodiversity, and Scale. Ecosystems **1**:6-18.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. Team. 2019. _nlme:Linear and Nonlinear Mixed Effects Models_. R package version 3.1-141.

Powell, K., J. Chase, and T. Knight. 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. American journal of botany **98**:539-548.

Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasiveness in alien plants: where do we stand? Pages 97-125 *in* W. Nentwig, editor. Biological Invasions. Springer Berlin Heidelberg, Berlin, Heidelberg.

Radosevich, S. R., J. S. Holt, and C. M. Ghersa. 2007. Ecology of Weeds and Invasive Plants: Relationshiph to Agriculture and Natural Resource Management. Third edition. John Wiley & Sons, Inc., Hoboken, New Jersey.

Ramula, S., T. M. Knight, J. H. Burns, and Y. M. Buckley. 2008. General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. Journal of Applied Ecology **45**:1124-1133.

Rew, L. J., T. J. Brummer, F. W. Pollnac, C. D. Larson, K. T. Taylor, M. L. Taper, J. D. Fleming, and H. E. Balbach. 2018. Hitching a ride: Seed accrual rates on different types of vehicles. Journal of Environmental Management **206**:547-555.

Rew, L. J., E. A. Lehnhoff, and B. D. Maxwell. 2007. Non-indigenous species management using a population prioritization framework. Canadian Journal of Plant Science **87**:1029-1036.

Richardson, D. M., P. Pysek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and Invasion of Alien Plants: Concepts and Definitions. Diversity and Distributions **6**:93-107.

Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. Ecological Applications **19**:155-162.

Sala, O. E., F. S. Chapin lll, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Sebastian, D. J., M. B. Fleming, E. L. Patterson, J. R. Sebastian, and S. J. Nissen. 2017a. Indaziflam: a new cellulose-biosynthesis-inhibiting herbicide provides long-term control of invasive winter annual grasses. Pest Management Science **73**:2149-2162.

Sebastian, D. J., S. J. Nissen, and J. De Souza Rodrigues. 2016a. Pre-emergence control of six invasive winter annual grasses with imazapic and indaziflam. Invasive Plant Science and Management **9**:308-316.

Sebastian, D. J., S. J. Nissen, J. R. Sebastian, and K. G. Beck. 2017b. Seed bank depletion: the key to long-term downy brome (*Bromus tectorum* L.) management. Rangeland Ecology & Management **70**:477-483.

Sebastian, D. J., S. J. Nissen, J. R. Sebastian, P. J. Meiman, and K. G. Beck. 2017c. Preemergence control of nine invasive weeds with aminocyclopyrachlor, aminopyralid, and indaziflam. Invasive Plant Science and Management **10**:99-109.

Sebastian, D. J., J. R. Sebastian, S. J. Nissen, and K. G. Beck. 2016b. A potential new herbicide for invasive annual grass control on rangeland. Rangeland Ecology & Management **69**:195-198.

Sebastian, J., J. Swanson, S. Sauer, S. Clark, and D. Sebastian. 2020. Pollinator community and floral resource response to cheatgrass control with Esplanade 200 SC (indaziflam) *in* Weed Science Society of America Western Society of Weed Science Joint Meeting, Maui, HI.

Simberloff, D. 2011. How common are invasion-induced ecosystem impacts? Biological Invasions **13**:1255-1268.

Skurski, T. C., B. D. Maxwell, and L. J. Rew. 2013. Ecological tradeoffs in non-native plant management. Biological Conservation **159**:292-302.

Skurski, T. C., L. J. Rew, and B. D. Maxwell. 2014. Mechanisms underlying nonindigenous plant impacts: a review of recent experimental research. Invasive Plant Science and Management **7**:432-444.

Soil Survey Staff. Web Soil Survey. Natural Resources Conservation Service, United States Department of Agriculture. URL: http://websoilsurvey.sc.egov.usda.gov/.

Sutherland, S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. Oecologia **141**:24-39.

Thompson, K. 2014. Where do camels belong? . Profile Books LTD, London, Great Britain.

Thompson, K., J. G. Hodgson, and C. G. R. Tim. 1995. Native and alien invasive plants: more of the same? Ecography **18**:390-402.

Thuiller, W., D. M. Richardson, and G. F. Midgley. 2007. Will climate change promote alien plant invasions? Pages 197-211 *in* W. Nentwig, editor. Biological Invasions. Springer Berlin Heidelberg, Berlin, Heidelberg.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology **80**:1455-1474.

USDA NRCS. 2020. The PLANTS Database. National Plant Data Team, Greensboro, NC 27401-4901 USA. URL: http://plants.usda.gov.

Uselman, S. M., K. A. Snyder, E. A. Leger, and S. E. Duke. 2015. Emergence and early survival of early versus late seral species in Great Basin restoration in two different soil types. Applied Vegetation Science **18**:624-636.

Vasquez, E. A., J. J. James, T. A. Monaco, and D. C. Cummings. 2010. Invasive plants on rangelands: a global threat. Rangelands **32**:3-5.

Vilà, M., C. Basnou, P. Pyšek, M. Josefsson, P. Genovesi, S. Gollasch, W. Nentwig, S. Olenin, A. Roques, D. Roy, P. E. Hulme, and D. partners. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment **8**:135-144.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**:702-708.

Vitousek, P. M. 1996. Biological Invasions and Ecosystem Processes: Towards an Integration of Population Biology and Ecosystem Studies. Pages 183-191 *in* F. B. Samson and F. L. Knopf, editors. Ecosystem Management: Selected Readings. Springer New York, New York, NY.

Wagner, V., and C. R. Nelson. 2014. Herbicides can negatively affect seed performance in native plants. Restoration Ecology **22**:288-291.

Walther, G.-R., S. Beißner, and C. A. Burga. 2005. Trends in the upward shift of alpine plants. Journal of Vegetation Science **16**:541-548.

Whipple, J. J. 2001. Annotated checklist of exotic vascular plants in Yellowstone National Park. Western North American Naturalist **61**.

Whitlock, C., W. Cross, B. D. Maxwell, N. Silverman, and A. Wade. 2017. Montana climate assessment. Montana Institute on Ecosystems, Montana State University, and University of Montana, Bozeman and Missoula, Montana, USA.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology **77**:1661-1666.

Young, J. A., and C. D. Clements. 2005. Exotic and invasive herbaceous range weeds. Rangelands. **27**:10-16.

Young, J. A., and L. A. Fay. 1997. Cheatgrass and range science: 1930-1950. Journal of Range Management **50**:530-535.

APPENDICES

APPENDIX A

SITE DESCRIPTIONS

Table A.1. Site environmental characteristics for the six sites within Yellowstone National Park. Invasion level High represents areas with >10 individuals/m^2 *Alyssum desertorum* and Low represents areas with <10 individuals/m^2 of *A. desertorum*. Wilting point date is the approximate date soil moisture reached below -1.5MPa.

Site	# of Species	Elevation (m)	Mean summer temp C°(se)	Wilting Point Date	Invasion	Aspect	% Slope
Mammoth (M)	62	1615	18.9(2.6)	July 5	High	West	11
					Low	West	7
Blacktail (B)	72	1980	16.8(2.31)	July 5	High	South	2
					Low	South	2
Lamar (L)	61	1981	18.5(0.27)	July 5	High	North	4
					Low	North	9
Phantom (P)	76	2042	16.7(1.19)	July 5	High	South	22
					Low	South	6
Swan (W)	70	2225	16.2(1.18)	July 15	High	Flat	0.2
					Low	Flat	0.4
Hayden (HD)	38	2347	15.5(1.77)	July 15	High	South	27
					Low	South-East	17

Table A.2. Site soil characteristics for the six sites within Yellowstone National Park. Sites(elevation) are: M=Mammoth (1615m), B=Blacktail (1980m), L=Lamar (1981m), P=Phantom (2042m), W=Swan (2225m) and Hayden (2347m). For Invasion High represents areas with>10 individuals/m^2 of *A. desertorum* and Low represents areas with <10 individuals/m^2 of *A. desertorum*. SOM = soil organic matter; CEC = cation exchange capacity.

Site	Invasion	pH	SOM	CEC	%Sand	%Silt	%Clay	Texture	Soil Name
M	High	7.2	3.5	13.4	46	34	20	Loam	Hobacker-Libeg-Greyback families, complex
	Low	7.2	3.6	15.6	40	40	20	Loam	
L	High	7.2	4.6	15.5	47	33	20	Loam	Idmonton, Ledgefork families and Typic Cryaquolls, soils
	Low	7.2	4.5	14.4	49	33	18	Loam	Shook-Badwater-Passcreek families, complex
B	High	6.5	7.1	22.2	41	37	22	Loam	Shook-Badwater-Passcreek families, complex
	Low	6.5	6.7	16.4	49	33	18	Loam	
P	High	7.2	4.2	29.9	39	23	38	Clay Loam	Arrowpeak-Lionhead-Midfork families, complex
	Low	6.6	6.8	19.4	43	35	22	Loam	
W	High	7.2	6.4	28	45	35	20	Loam	Arrowpeak-Lionhead-Midfork families, complex
	Low	6.4	6.4	20.2	50	36	14	Loam	Shook-Badwater-Passcreek families, complex
HD	High	6.6	1.4	5.3	82	10	8	Loamy Sand	Shook, Sawpit and Kegsprings families, soils
	Low	6.0	1.5	8.1	88	6	6	Sand	Gallatin, family, Typic Cryaquolls and Grayslake family, soils

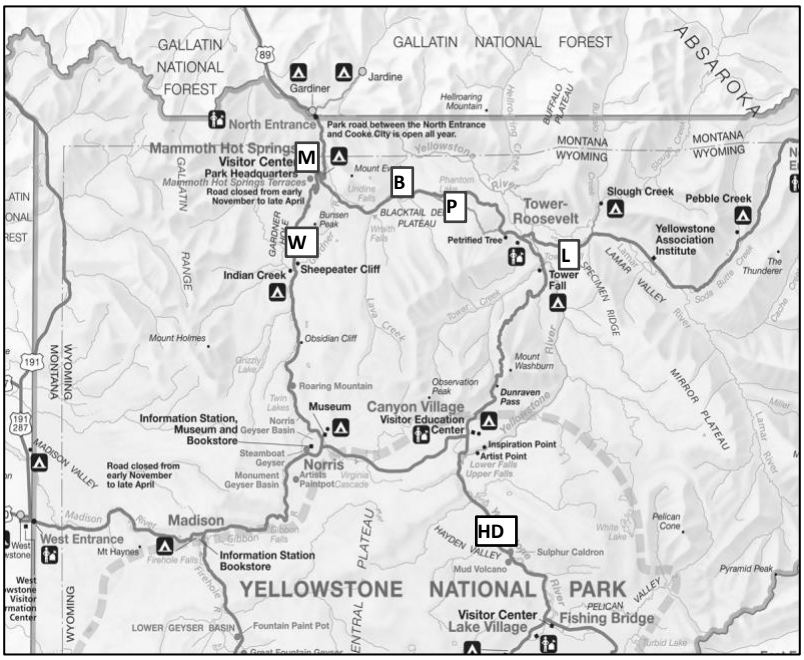


Figure A.1. Site locations in Yellowstone National Park. Mammoth:M, Blacktail:B, Lamar:L, Phantom:P, Swan:W , and Hayden:HD.

APPENDIX B

SUPPLEMENTAL MATERIALS

(CHAPTER TWO)

Table B.1. Mean (±SE) percent viability of *A. desertorum* seeds planted in soil after one year at three sites along an elevational gradient.

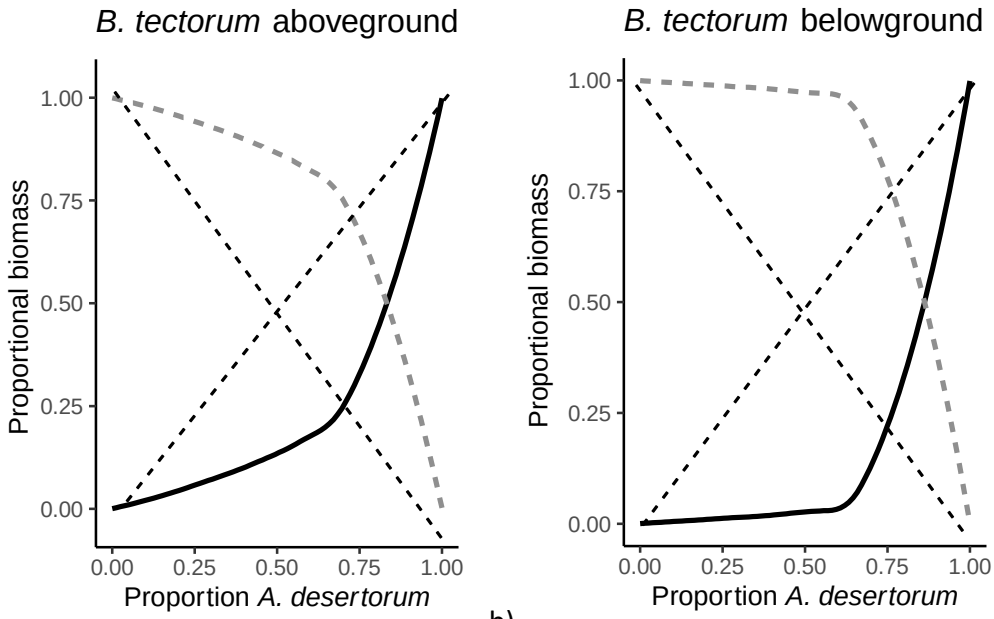
Site	Elevation (m)	Mean Summer Temp	Bag	# viable	% viable
Gardiner	1588	26	1	24	48
			2	10	20
Mammoth	1615	18.86	1	10	20
			2	12	24
Swan	2225	16.24	1	1	0
			2	1	2

Table B.2. Differences in vital rates of *Alyssum desertorum*: V = seed viability after one year in the soil, P_{ow} = mean probability of overwintering success, P_{rep} = mean probability of reaching reproductive maturity, and F = fecundity. Data are from four sites (F = 1450m, G= 1588m, M = 1615m and W = 2225m). Intercept for *V* is Site G, intercept for all others is Site F. Results from a linear model regression. Fecundity model followed a Poisson distribution, and all other responses followed a Gaussian distribution. Significant differences (p<0.05) are in bold.

Response	Predictor	Est	SE	t value	p(>)
V					
	Intercept	**34**	**8.19**	**4.15**	**0.03**
	Site M	-12	11.58	-1.04	0.38
	Site W	-33	11.58	-2.85	0.07
P_{ow}					
	Intercept	**0.80**	**7.0e-03**	**11.38**	**<0.01**
	Site M	-0.2	1	-1.99	0.06
	Site W	**-0.43**	**0.10**	**-4.15**	**<0.01**
P_{rep}					
	Intercept	**0.78**	**0.09**	**8.77**	**<0.01**
	Site M	0.05	0.13	0.37	0.72
	Site W	**-0.39**	**0.13**	**-2.97**	**<0.01**
F				z-value	
	Intercept	**4.74**	**0.03**	**159.94**	**<0.01**
	Site M	**-3.65**	**0.19**	**-19.63**	**<0.01**
	Site W	**-3.62**	**0.19**	**-18.44**	**<0.01**

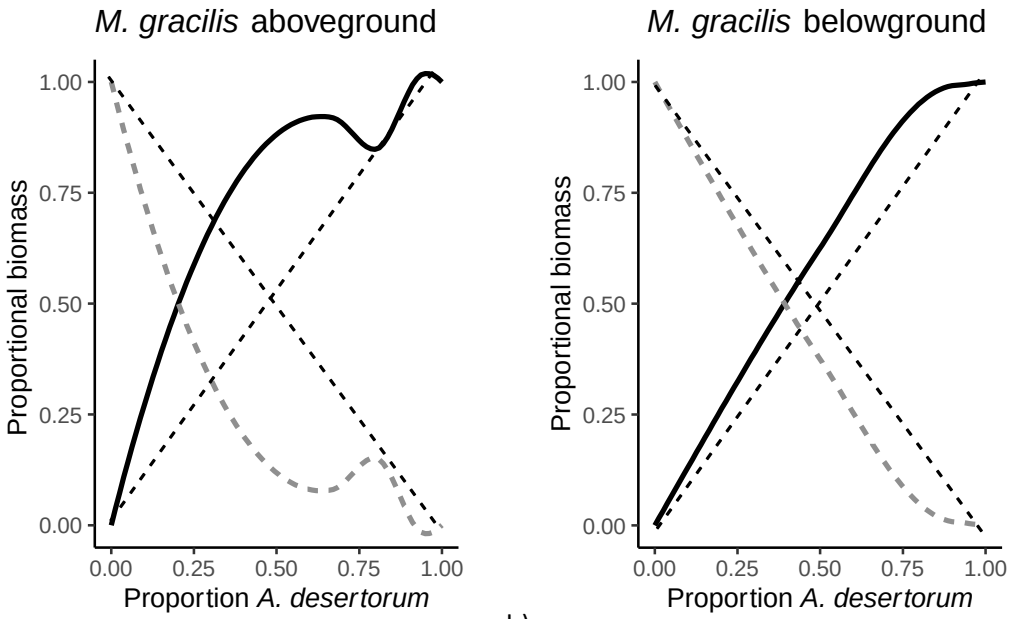
Table B.3. Results from linear mixed models used to assess the effects of proportion of *Alyssum desertorum* (Prop.ALDE) on the aboveground (AG) and belowground (BG) relative yield and biomass of *Bromus tectorum* and *Microsteris gracilis*. Satterthwaite's approximation was used to calculated p-values and degrees of freedom, and values in bold indicate significant difference (p < 0.05).

	Fixed effects						Random effects	
Response	Predictor	Est.	SE	*df*	t-value	p(>)	Variance	
							Trial	Residual
B. tectorum								
Relative Yield AG	**Intercept**	**0.96**	**0.03**	**2.7**	**36.12**	**<0.01**	0.00±0.02	0.00± 0.10
	Prop.ALDE	**-1.01**	**0.04**	**57**	**-28.12**	**<0.01**		
Relative Yield BG	**Intercept**	**0.90**	**0.06**	**27**	**14.16**	**<0.01**	0.14±0.37	0.14± 0.37
	Prop.ALDE	**-9.7**	**0.20**	**27**	**-8.47**	**<0.01**		
Biomass AG	**Intercept**	**1.37**	**0.02**	**2**	**19.14**	**<0.01**	0.01±0.07	0.01± 0.23
	Prop.ALDE	**-1.16**	**0.08**	**57**	**-13.78**	**<0.01**		
Biomass BG	Intercept	1.77	0.28	1	6.24	0.05	0.12±0.34	0.25± 0.50
	Prop.ALDE	**-1.61**	**0.26**	**26**	**-6.08**	**<0.01**		
M. gracilis								
Relative Yield AG	**Intercept**	**0.93**	**0.16**	**54**	**5.92**	**<0.01**	0.00±0.00	0.22± 0.47
	Prop.ALDE	**-0.97**	**0.18**	**54**	**-5.42**	**<0.01**		
Relative Yield BG	**Intercept**	**0.95**	**0.05**	**24**	**18.54**	**<0.01**	0.00±0.00	0.01± 0.11
	Prop.ALDE	**-0.97**	**0.06**	**24**	**-16.41**	**<0.01**		
Biomass AG	**Intercept**	**0.13**	**0.02**	**51**	**5.80**	**<0.01**	0.00±0.00	0.00± 0.07
	Prop.ALDE	**-0.12**	**0.02**	**47**	**-5.31**	**<0.01**		
Biomass BG	**Intercept**	**0.02**	**0.01**	**5**	**10.42**	**<0.01**	0.00±0.00	0.00± 0.00
	Prop.ALDE	**-0.02**	**0.01**	**24**	**-10.47**	**<0.01**		



a) b)

Figure B.1. Effects of *Alyssum desertorum* (solid) proportion on the biomass of *Bromus tectorum* (grey dash) a) aboveground and b) belowground. Black dashed lines represent expected yield trends when intra- and interspecific interference are equal.



a) b)

Figure B.2. Effects of *Alyssum desertorum* (solid) competition on the biomass of *Microsteris gracilis* (grey dash) a) aboveground and b) belowground. Black dashed lines represent expected yield trends when intra- and interspecific interference are equal.

Table B.4. Abundance of native annual forbs without (-) *A. desertorum* (ALDE) in the data set, in response to *A. desertorum* invasion level, elevation, indaziflam treatment, and year. Results from a linear mixed model following a Gaussian distribution. Values in bold indicate statistical significance (p<0.05).

Fixed effects							Random effects	
	Predictor	Est.	SE	*df*	t-value	p(>)	Variance	
Abundance							Tag	Residual
Annual								
forbs	**Intercept**	**-16.57**	**3.49**	**71**	**-4.74**	**<0.01**	9.88±	2.59±
(- ALDE)	Invasion	0.46	0.78	71	0.60	0.56	3.14	1.61
R^2= 0.85	**Elevation**	**0.01**	**1.7e-03**	**71**	**5.48**	**<0.01**		
	Year	0.04	0.27	72	0.15	0.88		

Table B.5 Differences in mean abundance and proportion of seedlings from the soil seedbank in response to level of *Alyssum desertorum* invasion (high, low), indaziflam treatment (spray, control), and site (M, B). Intercept is control, low invasion, and site M. Results from a linear regression. Abundance from a Quasi-Poisson distribution, proportion and Shannon's diversity from a Gaussian distribution, and richness from a Poisson distribution. P-values in bold indicate statistical significance (p < 0.05). No *A. desertorum* included.

Response	Predictor	Est	SE	t-value	p-value
Abundance					
R^2=0.38	**Intercept**	**4.09**	**0.43**	**9.55**	**<0.01**
	Invasion	0.01	0.53	0.03	0.98
	Site	-0.64	0.56	-1.14	0.26
	Indaziflam	**-3.71**	**1.75**	**-2.12**	**0.04**
Proportion					
R^2=0.48	**Intercept**	**0.64**	**0.10**	**6.78**	**<0.01**
	Invasion	-0.14	0.10	-1.48	0.15
	Site	**0.20**	**0.10**	**2.14**	**0.04**
	Indaziflam	**-0.55**	**0.10**	**-5.80**	**<0.01**
Richness					
R^2=0.77	**Intercept**	**0.55**	**0.26**	**2.11**	**0.04**
	Invasion	0.29	0.23	1.26	0.22
	Site	**0.99**	**0.26**	**3.80**	**<0.01**
	Indaziflam	**-2.71**	**0.48**	**-5.67**	**<0.01**
Shannon's					
diversity	**Intercept**	**0.59**	**0.11**	**4.19**	**<0.01**
R^2=0.63	Invasion	0.04	0.11	0.34	0.74
	Site	**0.47**	**0.11**	**4.17**	**<0.01**
	Indaziflam	**-0.79**	**0.11**	**-6.98**	**<0.01**

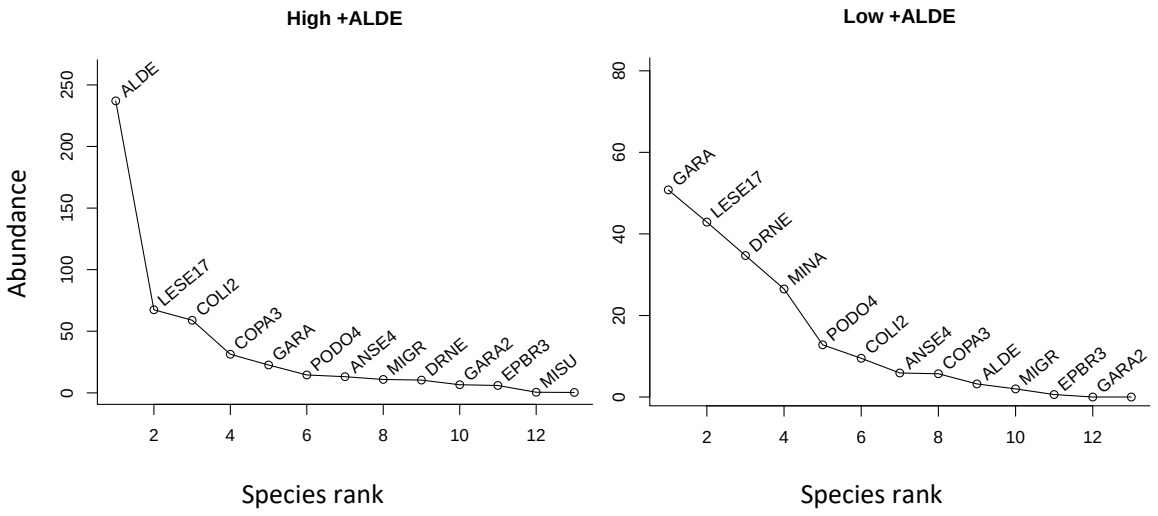


Figure B.3. Rank abundance (percent cover) of annual forbs in areas with high and low invasions of *A. desertorum*. Species codes defined in Appendix E.

APPENDIX C

SUPPLEMENTAL FIGURES

(CHAPTER THREE)

Table C.1. Percent cover of *Alyssum desertorum* (ALDE) in high invasion plots in response to indaziflam treatment (control, spray), elevation, and year (2019, 2020) Intercept is control, 2019. Results from a linear mixed model regression of p-values in bold indicate statistically significant difference (p<0.05).

Fixed effects							Random effect	
Response	Predictor	Est.	SE	df	t-value	p(>)	Variance	
							Tag	Residual
Cover ALDE	Intercept	2.66	1.30	184	2.06	0.41	0.65±	1.39±
R^2=0.64	**Indaziflam**	**-3.26**	**0.29**	**184**	**-11.15**	**<0.01**	0.80	1.18
	Elevation	3.5e-04	6.2e-04	184	0.56	0.58		
	Year	2.02	1.51	101	1.34	0.19		
	Indaziflam* Year	**0.97**	**0.34**	**101**	**2.83**	**<0.01**		
	Elevation* Year	**-1.4e-03**	**7.3e-04**	**101**	**1.96**	**0.05**		

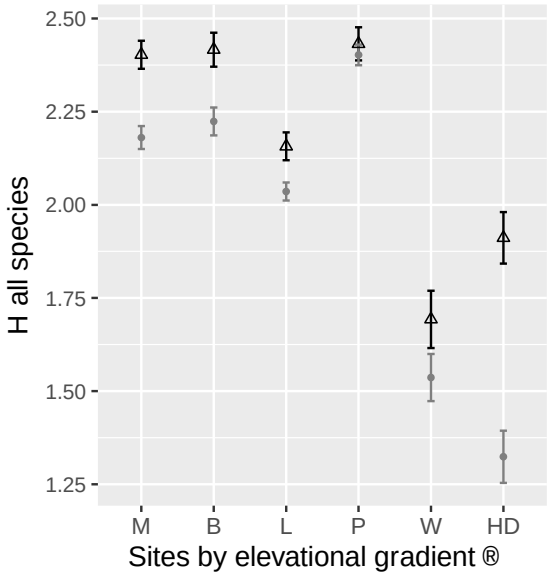


Figure C.1. Mean (± SE) Shannon's diversity (H) of all species post treatment (sprayed = ●, control = Δ) across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and HD = 2347m).

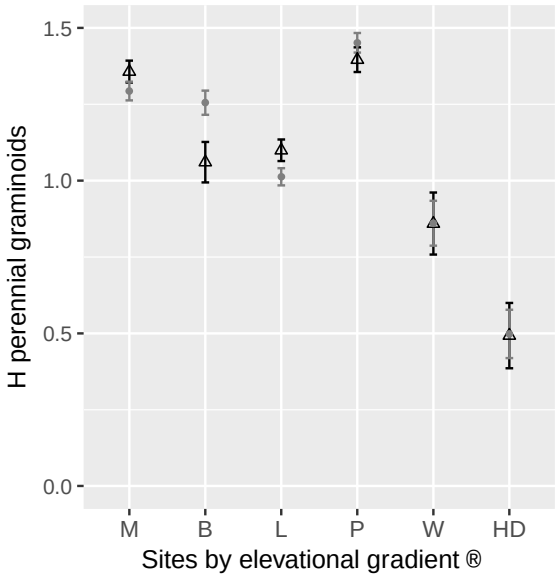


Figure C.2. Mean (± SE) Shannon's diversity (H) of perennial graminoids post treatment (sprayed = •, control = Δ) across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and H = 2347m).

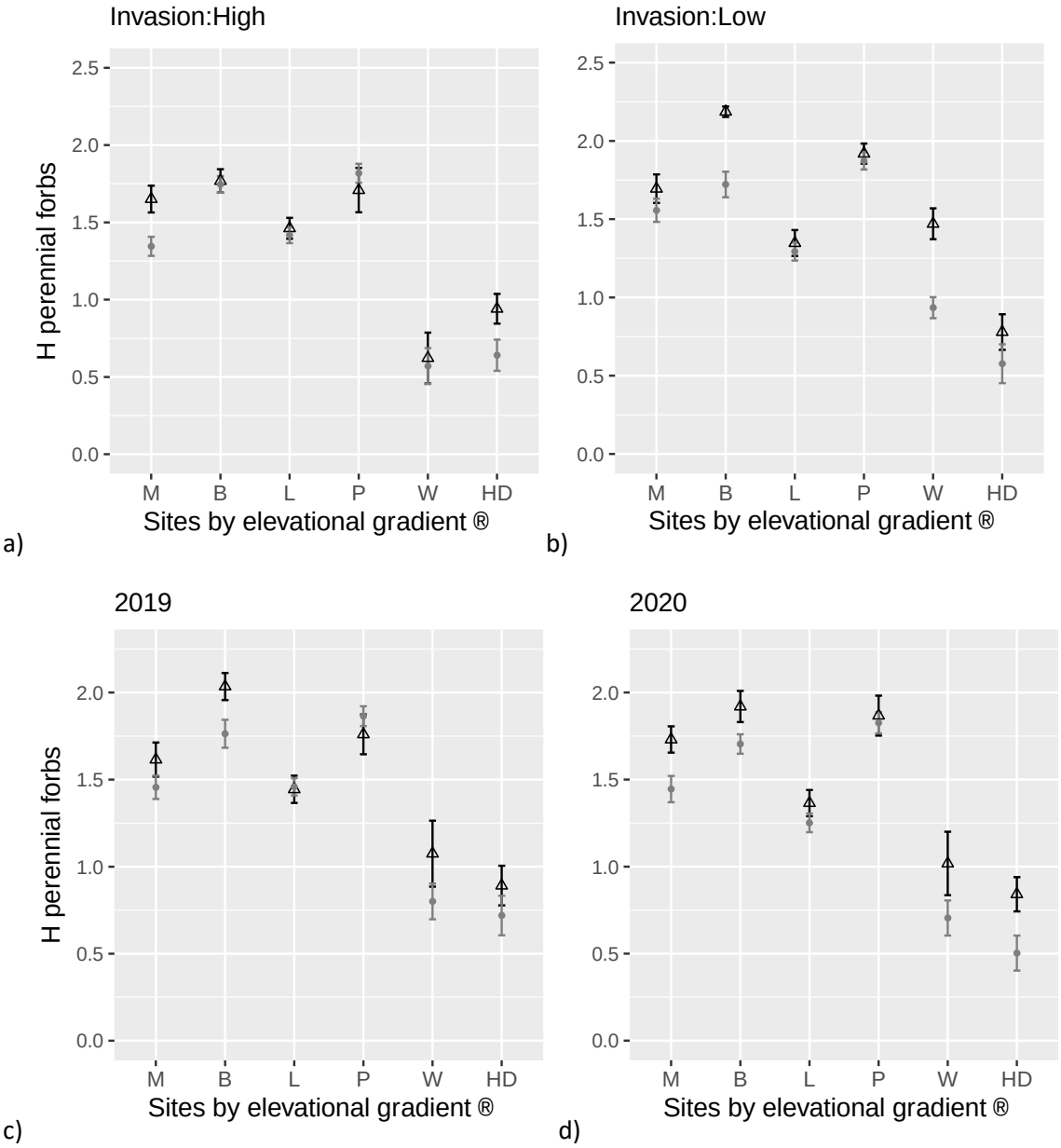


Figure C.3. Mean (± SE) Shannon's diversity (H) of perennial forbs post treatment (sprayed = ●, control = Δ) in a) high and b) low invasions of *Alyssum desertorum* and for two years c) 2019 and d) 2020 across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and H = 2347m).

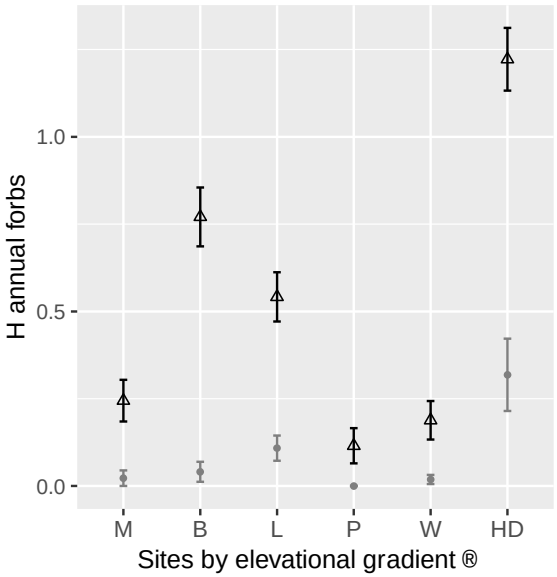


Figure C.4. Mean (± SE) Shannon's diversity (H) of annual forbs post treatment (sprayed = ●, control = Δ) across an elevation gradient in Yellowstone National Park (M = 1615m, B = 1980m, L = 1981m, P = 2042m, W = 2225m and H = 2347m).

APPENDIX D

RELATIVE RANK ABUNDANCE OF PERENNIAL FORBS

(CHAPTER THREE)

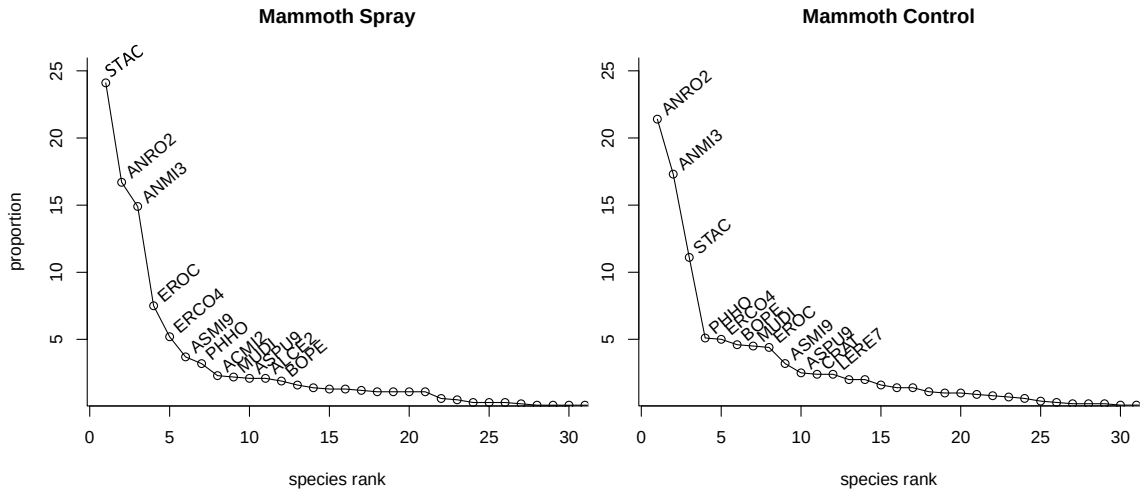


Fig. D.1. Rank abundance curves of perennial forb species post indaziflam treatment (spray, control) at Mammoth (1615m) site in Yellowstone National Park.

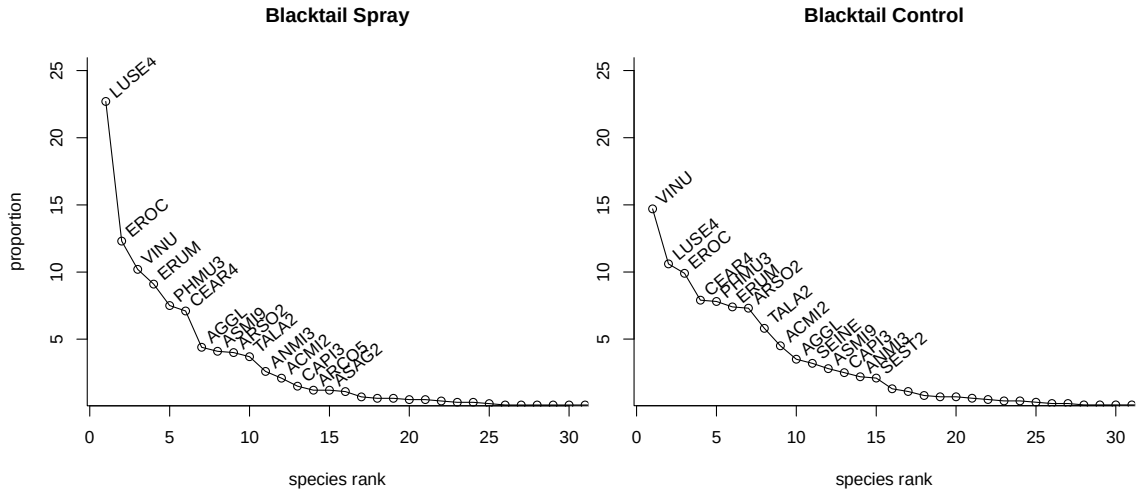


Fig. D.2. Rank abundance curves of perennial forb species post indaziflam treatment (spray, control) at Blacktail (1980m) site in Yellowstone National Park.

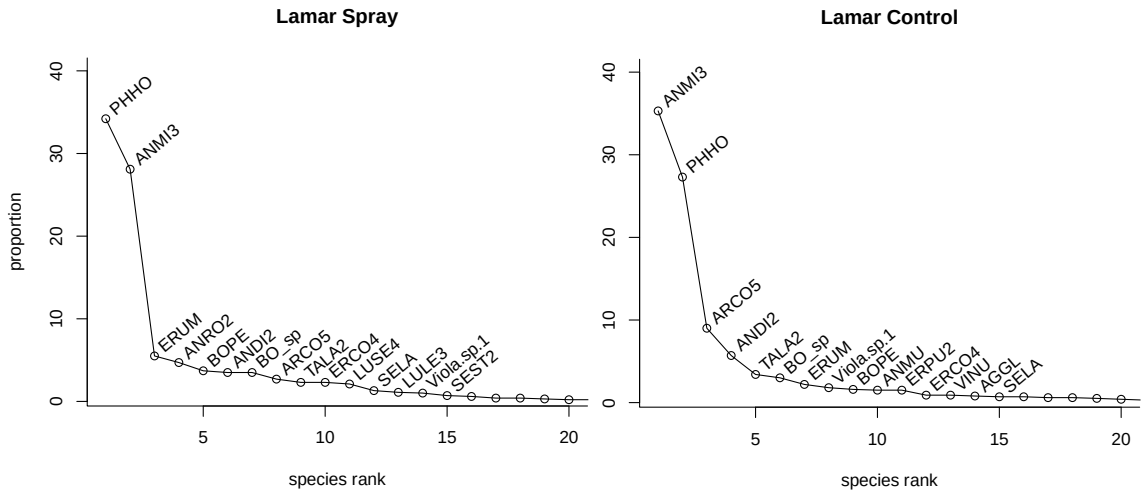


Fig. D.3. Rank abundance curves of perennial forb species post indaziflam treatment (spray, control) at Lamar (1981m) site in Yellowstone National Park.

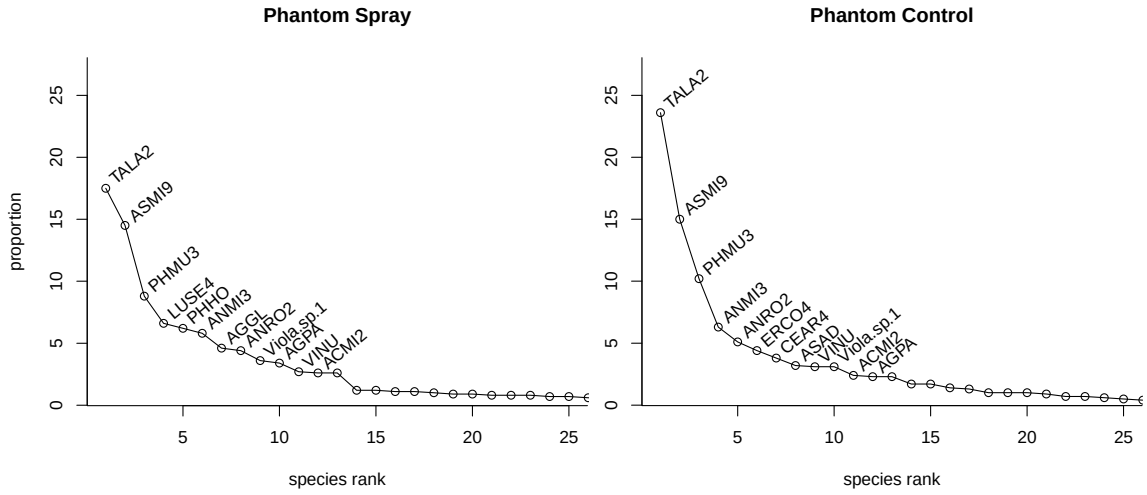


Fig. D.4. Rank abundance curves of perennial forb species post indaziflam treatment (spray, control) at Phantom (2042m) site in Yellowstone National Park.

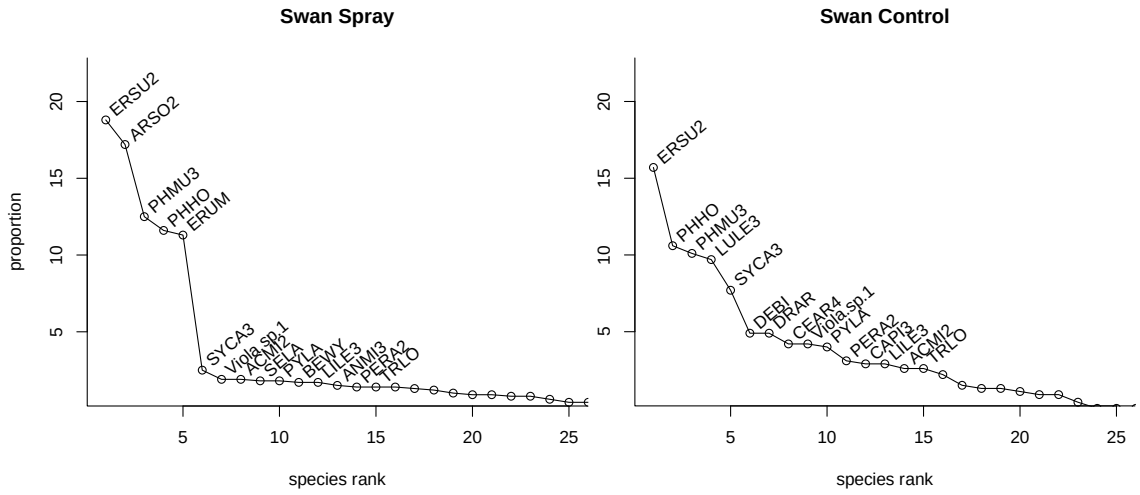


Fig. D.5. Rank abundance curves of perennial forb species post indaziflam treatment (spray, control) at Swan (2225m) site in Yellowstone National Park.

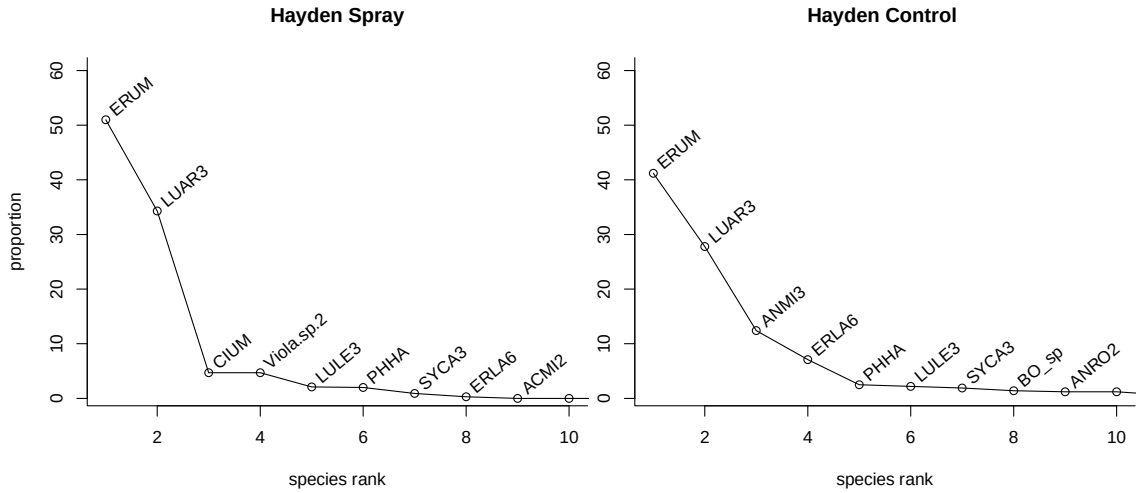


Fig. D.6. Rank abundance curves of perennial forb species post indaziflam treatment (spray, control) at Hayden (2347m) site in Yellowstone National Park.

APPENDIX E

SPECIES LIST AND CODES

Table E.1. Species list from all study sites in Yellowstone National Park. Species codes and full names from PLANTS.usda website(USDA NRCS 2020). Lifeform: P = perennial, A = annual; Nativity: N = native, I = non-native

PLANTS Code	Name	Lifeform	Nativity
		Forbs	
ACMI2	*Achillea millefolium*	P	N
AGGL	*Agoseris glauca*	P	N
AGPA	*Agoseris parviflora*	P	N
ALCE2	*Allium cernuum*	P	N
ALDE	*Alyssum desertorum*	A	I
ALTE	*Allium textile*	P	N
ANDI2	*Antennaria dimorpha*	P	N
ANMI3	*Antennaria microphylla*	P	N
ANMU	*Anemone multifida*	P	N
ANRO2	*Antennaria rosea*	P	N
ANSE4	*Androsace septentrionalis*	A	N
ARCO5	*Arenaria congesta*	P	N
ARNU	*Arabis nuttallii*	P	N
ARSO2	*Arnica sororia*	P	N
ASAD	*Astragalus adsurgens*	P	N
ASAG2	*Astragalus agrestis*	P	N
ASMI9	*Astragalus miser*	P	N
ASPU9	*Astragalus purshii*	P	N
BEWY	*Besseya wyomingensis*	P	N
BO_sp	*Boechera retrofracta*	P	N
BODI4	*Boechera divaricarpa*	P	N
BOMI3	*Boechera microphylla*	P	N
BOPE	*Boechera pendulocarpa*	P	N
BOST4	*Boechera stricta*	P	N
CADR	*Cardaria draba*	P	I
CAMI2	*Camelina microcarpa*	A	I
CAPI3	*Castilleja pallescens*	P	N
CARO2	*Campanula rotundifolia*	P	N
CEAR4	*Cirsium arvense*	P	N
CHDO	*Chaenactis douglasii*	P	N
CIUM	*Cistanthe umbellata*	P	N
COLI2	*Collomia linearis*	A	N
COPA3	*Collinsia parviflora*	A	N
COUM	*Comandra umbellata*	P	N
CRAC2	*Crepis acuminata*	P	N
CRAT	*Crepis atribarba*	P	N
CRMO4	*Crepis modocensis*	P	N
DEBI	*Delphinium bicolor*	P	N
DESO	*Desurainia sophia*	P	I

DOCO	*Dodecatheon conjugens*	P	N
DRAR	*Drymocallis arguta*	P	N
DRNE	*Draba nemorosa*	A	N
DRTH	*Dracocephalum thymiflorum*	P	N
EPBR3	*Epilobium brachycarpum*	A	N
ERCO4	*Erigeron compositus*	P	N
ERLA6	*Eriophyllum lanatum*	P	N
EROC	*Erigeron ochroleucus*	P	N
EROV	*Eriogonum ovalifolium*	P	N
ERPU2	*Erigeron pumilis*	P	N
ERSU2	*Erigeron subtrinervis*	P	N
ERUM	*Eriogonum umbellatum*	P	N
FIAR	*Filago arvense*	A	I
FRAT	*Fritillaria atropurpurea*	P	N
FRPU2	*Fritillaria pudica*	P	N
FRVI	*Fragaria virginiana*	P	N
GABI	*Galium bifolium*	A	N
GARA	*Gayophytum racemosum*	A	N
GARA2	*Gayophytum ramosissimum*	A	N
GETR	*Geum triflorum*	P	N
HEVI4	*Heterotheca villosa*	P	N
IOAL	*Ionactis alpina*	P	N
LERE7	*Lewisia rediviva*	P	N
LESE17	*Leptosiphon septentrionalis*	A	N
LIDA	*Linnaria dalmatica*	P	I
LILE3	*Linum lewisii*	P	N
LIPA5	*Lithophragma parviflorum*	P	N
LIRU4	*Lithospermum ruderale*	P	N
LOTR2	*Lomatium triternatum*	P	N
LUAR3	*Lupinus argenteus*	P	N
LULE3	*Lupinus leucophyllus*	P	N
LUPI	*Lupine* sp.	P	N
LUSE4	*Lupinus sericeus*	P	N
MACA2	*Machaeranthera canescens*	P	N
MEDI	*Medicago sativa*	A	I
MELU	*Medicago lupulina*	A	I
MIGR	*Microsteris gracilis*	A	N
MINA	*Mimulus nana*	A	N
MISU	*Mimulus suksdorfii*	A	N
MUDI	*Musineon divaricatum*	P	N
MYMI	*Myosotis micrantha*	A	I
OXLA2	*Oxytropis lagopus*	P	N
PEMO7	*Perideridia montana*	P	N
PERA2	*Penstemon radicosus*	P	N

PHHA	*Phacelia hastata*	P	N
PHHO	*Phlox hoodii*	P	N
PHLO2	*Phlox longifola*	P	N
PHMU3	*Phlox multiflora*	P	N
PODID	*Potentilla diversifolia* var. *diversifolia*	P	N
PODO4	*Polygonum douglasii*	A	N
POGR9	*Potentilla gracilis*	P	N
POMI	*Polemonium micranthum*	A	N
PYLA	*Pyrrocoma lanceolata*	P	N
RAGL	*Ranunculus glaberrimus*	P	N
RATE	*Ranunculus testiculatus*	A	I
RUPA	*Rumex paucifolius*	P	N
SEINE	*Senecio integerrimus* var. *exaltalus*	P	N
SELA	*Sedum lanceolatum*	P	N
SESE	*Senecio serra var. serra*	P	N
SEST2	*Sedum stenopetalum*	P	N
SIAL	*Sisymbrium altissimum*	A	I
SIDRD	*Silene drummondii* var. *drummondii*	P	N
STAC	*Stenotus acaulis*	P	N
SYCA3	*Symphyotrichum ascendens*	P	N
TALA2	*Taraxacum laevigatum*	P	I
TAOF	*Taraxacum officinale*	P	I
TRCA5	*Trifolium campestre*	A	I
TRDU	*Tragopogon dubius*	P	I
TRHY	*Trifolium hybridum*	P	I
TRLO	*Trifolium longipes*	P	N
VAED	*Valeriana edulis*	P	N
VEVE	*Veronica verna*	A	I
VINU	*Viola nuttallii*	P	N
Viola_1		P	N
Viola_2		P	N
Aster_3		P	
Aster_4		P	
Fabac_1		P	
Aster_5		P	
Fabac_2		P	
Forb_1		P	
Forb_2		P	
Aster_3		P	
Aster_4		P	
Forb_5		P	

Forb_6		P	
Forb_8		P	
AGIN	*Agropyron intermedium*	P	N
AGSM	*Agropyron smithii*	P	N
AGSP	*Agropyron spicatum*	P	N
AGTR	*Agropyron trachycaulum*	P	N
BRCA	*Bromus carinatus*	P	N
BRIN2	*Bromus inermus*	P	I
BRTE	*Bromus tectorum*	A	I
CADO	*Carex douglasii*	P	N
CAEL	*Carex eleocharis*	P	N
CAFI	*Carex filifolia*	P	N
CAIN	*Carex inops*	P	N
CAPE	*Carex pellita*	P	N
CAPR7	*Carex praticola*	P	N
CAPR5	*Carex praegracilis*	P	N
CASI	*Carex simluata*	P	N
DACA3	*Danthonia californica*	P	N
DANTH	*Danthonia intermedia*	P	N
ELEL	*Elymus elymoides*	P	N
FEID	*Festuca idahoensis*	P	N
JUBA	*Juncus balticus*	P	N
KOMA	*Koeleria macrantha*	P	N
MEBU	*Melica bulbosa*	P	N
MURI	*Muhlenbergia richardsonis*	P	N
PHPR3	*Phleum pratense*	P	I
POAR	*Poa arida*	P	N
POCO	*Poa compressa*	P	I
POFE	*Poa fendleriana*	P	N
POPR	*Poa pratensis*	P	I
POSE	*Poa secunda*	P	N
STCO	*Stipa comata*	P	N
STNE	*Stipa nelsonii*	P	N
STOC	*Stipa occidentalis*	P	N
STRI	*Stipa richardsonii*	P	N
STVI	*Stipa viridula*	P	N
		Shrubs	
ARCA13	*Artemisia cana*	P	N
ARFR4	*Artemisia frigida*	P	N
ARLU	*Artemisia ludoviciana*	P	N
ARTRV	*Artemisia tridentata* ssp. *vaseyana*	P	N
CHVI8	*Chrysothamnus viscidiflorus*	P	N

DAFR6	*Dasiphora fruticosa*	P	N
ERNA10	*Ericameria nauseosa*	P	N
KRLA2	*Krascheninnikovia lanata*	P	N
TECA2	*Tetradymia canescens*	P	N