RESTORATION AND POLLINATOR CONSERVATION: STRATEGIES FOR CONTROLLING INVASIVE ANNUAL GRASSES ON DEGRADED TRIBAL GRASSLANDS

by

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DEDICATION

I humbly dedicate this work to my family, you are the reason I strive to create a better world. To my beloved wife Suzy, thank you for your strength and patience through the long nights, the countless hours apart, and for your unwavering belief in me. Your unique blend of love truly has been my guiding star. To my mother whose love and support have shaped the person I am today. I am forever grateful. My beautiful daughter and granddaughters and the generations that follow this work is for you. It is my hope that the path I walk today will lead to a healthier and more vibrant land for you to walk tomorrow.

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ABSTRACT

Invasive annual grasses (IAG) threaten Intermountain foothill grasslands in northwestern Montana, and these grasslands are integral to the cultural and ecological well-being of the Séliš, Ksanka, and Ql'ispé Tribes. This project aimed to increase native vegetation cover and test the tolerance of native grasses and forbs to herbicides commonly used to control IAG. Three components were evaluated: a field study at two sites on Tribal grasslands, a greenhouse study of species tolerance, and a baseline bee survey at the two field sites. In the field study, six herbicides and nine species were tested, with herbicide treatments applied fall 2021 through summer 2022, depending on label recommended timings, and seeding occurring spring 2021. Canopy cover of all species was measured in 2022 and 2023. Rimsulfuron, sulfosulfuron, and indaziflam effectively reduced IAG (up to 96% control), while propoxycarbazone, imazapic, and glyphosate were less effective. Drill seeding largely failed. *Geranium maculatum*, *Cleomella serrulata*, and *Gaillardia aristata* were present in low numbers in 2022 but absent in 2023. The greenhouse study evaluated tolerance of 12 plant species to four herbicides, focusing on seedling emergence, biomass, and injury symptoms. Herbicides reduced emergence and reduced biomass for the majority of species compared to the non-sprayed check. All forbs showed high injury ranks except *Lupinus argenteus*, which ranked moderate across treatments. All grasses had high injury ranks across herbicides except *Thinopyrum intermedium*, which had the least injury of all species under sulfosulfuron. Although *T. intermedium* and *G. aristata* showed some emergence in indaziflam-treated soil, indaziflam prevented the emergence of all other species. A baseline bee survey conducted over three summer months in 2023 at the two field sites identified 42 bee species from 14 genera and five families. Species richness analysis predicted 48 species at one site and 74 species at the other site, indicating a relatively even distribution of species. To effectively manage IAG, rimsulfuron, sulfosulfuron, and indaziflam can be prioritized, but should be integrated with planting of specific native species to improve establishment and minimize non-target impacts. Restoration efforts should incorporate pollinator-friendly species and engage stakeholders to align management with cultural and ecological goals.

CHAPTER ONE

SETTING THE STAGE: STRATEGIES FOR GRASSLAND RESTORATION

Xest sx̣lx̣alt ~ kisuk kyukyit. Invasive annual grasses (IAG), in particular, cheatgrass (*Bromus tectorum* L.), Japanese brome (*Bromus japonicus*) Thunb., medusahead (*Taeniatherum caput-medusae* (L.) Nevski), and ventenata (*Ventenata dubia* (Leers) Coss. & Durieu), pose increasing ecological and economic threats in northwest Montana and the Inland Northwest. These IAG often dominate landscapes by quickly outcompeting native species for resources, namely water and nutrients, and they disrupt native ecosystems by altering fire cycles, reducing biodiversity, and lowering forage quality for livestock and wildlife. Their invasions have led to significant ecological and economic challenges, particularly in perennial grasslands, where they create monocultures that diminish land productivity and resilience. A comprehensive understanding of these species' behavior in various climates and disturbance regimes is crucial for developing effective management strategies in Montana and the surrounding region.

My research explored the responses of in-situ species, drill seeded species used for revegetation, and IAG to herbicide treatments on Tribal lands of the Confederated Salish and Kootenai Tribes (CSKT) within the Flathead Reservation. In the field I examined the effects of combining herbicide treatments for control of IAG with drill seeding for revegetation. In the greenhouse I evaluated whether herbicides used for IAG control would injure culturally important native seedlings used for restoration. I also established a baseline of bee species on the Flathead Reservation, helping to ensure that future management practices consider the impact on pollinators, which are vital to ecosystem resilience. Current management of IAG infestations largely relies on herbicide applications, which deepens the need for a better understanding of how both native bee and native plant species interact with restoration efforts. Much like the need for a deeper understanding of IAG traits in other regions, this research highlights the importance of refining control strategies that respect the cultural and ecological significance of native plant and pollinator species, while developing a more diverse array of management tools to protect and restore threatened grasslands.

Literature Review

The Inland Northwest, encompassing eastern Washington, northern Idaho, and western Montana, historically has been home to vast grasslands, yet has become increasingly threatened by IAG, necessitating focused efforts to protect and restore this vital grassland ecosystem through integrated management strategies (Maestas et al., 2022, 2023; Ehlert, 2017). The region's unique geography, climate, and ecological characteristics have shaped its cultural and natural history (Hessburg and Agee, 2003). Historical land use changes, particularly since European settlement, have significantly altered these ecosystems. The introduction of non-native plants, extensive livestock grazing, and agricultural development have altered native vegetation patterns and further disrupted ecological processes (Dukes and Mooney, 2004; Gordon, 1998).

The replacement of native plants with non-native species and the depletion of wildlife and pollinator habitat has marked a significant shift in the landscape (Ghisbain, 2021). Today contemporary issues such as climate change, land management policies, and ongoing pressures from development continue to impact grassland ecosystems. Addressing these challenges requires a multifaceted approach that integrates scientific research, traditional knowledge, and community involvement to restore ecological balance and support sustainable land use practices.

Climate change is expected to exacerbate the impacts from IAG because of changing precipitation patterns, increasing the frequency of extreme weather events, and further affecting plant and animal distributions (Finch et al., 2021; Runyon et al., 2012). Land management policies must adapt to these changing conditions integrating adaptive management approaches that account for the uncertainties of future climate scenarios to mitigate the widespread ecological and economic impacts of invasive grasses.

Cultural Connections

The Séliš (Salish), Ksanka (Kootenai), and Ql'ispé (Pend d'Oreille or Kalispel) Tribes of the Flathead Reservation have long maintained a deep connection with their ancestral lands, guided by traditional knowledge passed down for generations (personal communication Tim Ryan, 2023, Salish). These Tribes united to form the Confederated Salish and Kootenai Tribes (CSKT), while continuing to honor and preserve their unique cultural identities (CSKT, 2024). Traditional ecological knowledge (TEK) for the CSKT encompasses a holistic understanding of the land, plants, animals, and ecological processes developed through centuries of observation, experience, and spiritual connection (Inglebret and Wood, 2014; personal communications Finley, 2020, Salish; personal communications Durglo, 2024, Salish Pend d'Oreille; personal communications Dupuis, 2018, Kootenai; personal communications Decker, 2023, Salish; Ryan, 2022). This knowledge and value system are deeply embedded in their cultural practices, subsistence strategies, and land stewardship (Weart, 2022).

Unlike other Tribal nations where controlled burns were frequently used, the CSKT have traditionally focused on practices such as selective and honorable harvesting, plant cultivation, and seasonal migration to manage the landscape (Cajune, 2018; Dupuis, 2018; Tim Ryan, 2022).

Traditional ecological knowledge also involves "Spirit of Place" and language acknowledging the local flora and fauna, including the timing of flowering, seed collection, and animal behaviors (Decker, 2023).

One key example is the harvesting of xapi in Kootenai, or sxʷèʔli for the Salish, for English speakers camas (*Camassia quamash* (Pursh) Greene), an important root crop for the Tribes (Finley, 2020; Hart, Jeffrey Arthur, 1974). Honorable harvesting practices are timed carefully to ensure that the sxʷèʔli plants can regenerate for future years, thus balancing resource use with ecological sustainability. Another important example is the gathering of naqam¢u for the Kootenai, sp̓eƛ̓m for the Salish (Decker, 2023), and bitterroot in English (*Lewisia rediviva* Pursh). Naqam¢u is cherished and honorably harvested, guided by an intimate understanding of when the plant's roots are at their peak nutritional value and harvest will have the least ecological impacts, https://skclivinglandscapes.org/northwest/Principles/Northwest%20Principle%204/ (Andrews, 2019; Finley, 2020; Decker, 2023; Ryan, 2022; Weart, 2022). This honorable harvesting helps to ensure that plant populations remain healthy and viable over generations, supporting both the ecological integrity of the grasslands and the cultural traditions of the Tribes (Kimmerer, 2014; Decker, 2023).

Today the integration of TEK into modern land and resource management on the Flathead Reservation continues to play a vital role in preserving the region's biodiversity and ecological resilience. By maintaining these practices, the CSKT are not only protecting their environment but also ensuring the continuation of their cultural heritage and the well-being of future generations (Tim Ryan, 2023; Durglo, 2024). Their aboriginal territory originally spanned over 8,093,900 hectares at the time of the Hellgate Treaty of 1855, but the current reservation covers only 532,264 hectares, with just 352, 727 hectares of the land and surface waters under ownership of the Tribes and individual Tribal members (Wheeler, 2006; CSKT NRD 2024; Farrell et al., 2021). Therefore, controlling invasive species is a high priority to maintain Tribal food sovereignty and security as well as historical ecological resilience (Kapp, 2019; Montana Invasive Species Advisory Council, 2016).

Local initiatives should involve collaborative efforts, “from conception to completion,” with Indigenous communities to ensure that restoration projects honor traditional knowledge and address both ecological and cultural needs (Durglo, 2024; Chief et al., 2015). This collaboration would ensure that restoration projects honor Indigenous practices and contribute to the preservation of cultural heritage. By integrating traditional knowledge with modern scientific approaches, collaborative efforts strive to create resilient and sustainable rangeland ecosystems.

It has long been thought that European settlement dramatically transformed the grasslands of the Inland Northwest, introducing livestock grazing, agriculture, and invasive species that disrupted native ecosystems (Shinn, 1977; Gilio-Whitaker, 2019). However, Indigenous first people had already profoundly shaped these environments, and European settlers simply continued this process, albeit with different tools, species, and intentions (Norgaard and Fenelon, 2021; Wohl et al., 2017). This perspective challenges the narrative of European settlers as the sole agents of environmental change, recognizing that the land was already a humanized landscape, managed and shaped by Indigenous first people long before “it was discovered” in 1492 (Coughlan and Nelson, 2018; Finley, 2020; Durglo, 2024; Dupuis, 2018; Decker, 2023; Ryan, 2022). It also invites a reevaluation of how we understand the history of land use and its impacts on ecosystems in the Americas, acknowledging the complexity and longevity of human influence on these landscapes. This comparison suggests that the disruption of native ecosystems by European settlers wasn't a novel phenomenon but rather a continuation and acceleration of human-induced environmental change. The key difference lies in the scale, methods, and ecological outcomes. European settlement further altered our Intermountain foothill grassland ecosystems, often in ways that were less sustainable or beneficial than the practices of the Indigenous populations (Finley, 2020; Liebmann et al., 2016).

Invasive Annual Grasses

In the western U.S. notable invasive species include winter annual grasses such as *B. tectorum*, *B. japonicus*, *T. caput-medusae*, and *V. dubia*, which have spread extensively across millions of hectares (Bradley and Marvin, 2011; DiTomaso, 2000). Winter annual grasses typically germinate in the fall, survive the winter as seedlings, and continue growing in the spring before seeding and dying by early summer (Caudle and Baskin, 1968). Invasive annual grasses and other non-native plants can rapidly outcompete native vegetation, disrupting nutrient cycling, altering soil structure, and reducing habitat availability for native species (Beck, 2009; Fagúndez and Lema, 2019; Han et al., 2012). This, in turn, threatens overall biodiversity, alters ecosystems, impacts wildlife, and reduces forage for pollinators (Westbrooks 1998; Fagúndez and Lema 2019; D'Antonio and Vitousek, 1992; DiTomaso, 2000). Human migration, extensive cattle grazing, and the suppression of natural fires are aiding the spread of IAG across grassland, rangeland, and sagebrush steppe habitats in the western United States (DiTomaso, 2000; Davies et al., 2021; De Stefano et al., 2024). Invasive annual grasses often outcompete native seedlings during revegetation efforts, a challenge that may be exacerbated during drought years compared to wet years (Hart, Marshall T., 2022; Frost, 2023). As climate change intensifies, the

Intermountain foothill grasslands in the northwest US are projected to experience warmer and generally wetter conditions, potentially enhancing ecosystem processes like plant growth. However, shifting seasonal precipitation patterns characterized by reduced summer rainfall, diminished winter snowpack, and earlier snowmelt, which will alter hydrology, strain riparian systems, and increase the frequency of extreme events, pose significant challenges to restoration efforts (Polley et al., 2013).

Bromus tectorum is commonly referred to as cheatgrass or downy brome, and was first introduced to North America between 1889 and 1894 (Mack, 1981) either as a contaminant in agricultural seeds or through deliberate plantings (Mack, 1981; Thill et al., 1984). *Bromus tectorum* has a native range across Europe, the arid northern rim of Africa, and southwest Asia, with populations in southern Pakistan (Pierson and Mack, 1990). Recognized as one of the most significant plant invasions in North America, it has spread to every U.S. state in some capacity (D'Antonio and Vitousek, 1992; Molvar et al., 2024). *Bromus tectorum*, which thrives in arid and semi-arid ecosystems, covers an estimated 22 to 43 million hectares in the U.S. and is spreading at 14% annually (Beck, 2009). *Bromus tectorum* was first recorded in Montana around 1898, and within 100 years it had spread throughout all counties in the state (Hull and Pechanec, 1947; Menalled et al. 2008).

Bromus tectorum thrives in a variety of soil conditions and is particularly suited to disturbed or degraded lands (Monaco et al., 2016; Evans and Young, 1970; Young and Blank, 1995). Its ability to grow quickly and produce up to 5,000 seeds per plant enables it to rapidly dominate landscapes (Young et al., 1987). *Bromus tectorum* disrupts ecosystems by modifying fire regimes, and its highly flammable litter increase the frequency and intensity of fires, which leads to changes in plant community structures and a decline in native biodiversity (Hobbs and Huenneke, 1992; Reis et al., 2019). Management strategies for *B. tectorum* often involve a combination of herbicide applications and fire management practices (Brooks and Lusk, 2009). Pre-emergent herbicides are effective in reducing *B. tectorum* seedling establishment, while post-emergent treatments help manage established plants (Vicari et al., 1994). Controlling *B. tectorum* and other IAG can increase bare ground, which can lead to recolonization by IAG or other invasive species, or create an opportunity for successful revegetation with native species, depending on subsequent management efforts (Miller et al., 2014; Owen, Suzanne M. et al., 2011). Additionally, planting competitive native species and restoring native plant communities can reduce *B. tectorum* dominance and improve ecosystem function (Kettenring and Adams, 2011; Cox and Anderson, 2004).

Bromus japonicus, commonly known as Japanese or field brome, also native to Europe and Asia, was likely introduced to North America alongside *B. tectorum* in the 19th century through contaminated grain shipments (Beck, 2009; Hitchcock, 1935; Baskin and Baskin, 1981). Like *B. tectorum*, *B. japonicus* impacts native vegetation through competitive exclusion, altering soil properties, and shares a comparable lifecycle and invasive characteristics. *Bromus japonicus* outcompetes native species for resources, which leads to reduced diversity and altered ecosystem processes (Harmoney, 2007; Haferkamp et al., 1994). Like other IAG, *B. japonicus* is contributing to the decline of native flowering plants (Averett and Endress, 2022) and is rapidly expanding, posing a significant threat to the remaining Intermountain foothill grasslands in northwest Montana (Beck, 2009; Haferkamp and Heitschmidt, 1999). A single *B. japonicus* plant can generate an average of 1,885 seeds, which are easily spread by water or wind due to their lightweight nature, facilitating its rapid spread in disturbed habitats (Beck, 2009; Wang, 1986). *Bromus japonicus* seedling establishment is highly dependent on litter, particularly in years with low fall precipitation, while in years with high fall precipitation, litter has a much smaller impact (Whisenant and Uresk, 1985, 1990). Management strategies for *B. japonicus* are similar to those for other IAG, including the use of herbicides (both pre-emergent and post-emergent). Grazing that reduces litter production, as observed outside Badlands National Park in western South Dakota in the 1980s, can lead to lower *B. japonicus* density compared to areas with higher litter accumulation (Whisenant and Uresk, 1985, 1990). However, long-term control should be most effective when treatments are combined with the seeding of competitive native species (Beck, 2009; Mangold et al., 2013; Monaco et al., 2017).

Overall, the presence of non-native *Bromus* spp. alters several ecosystem properties, particularly biomass production and litter dynamics leading to altered fire regimes (Pilliod et al., 2017). While *Bromus* spp. may not consistently affect soil moisture, their impact on litter accumulation and decomposition rates could influence soil health over time (Belnap et al., 2016). Invasive *Bromus* spp. may reduce root system depth and density, potentially affecting soil stability, nutrient uptake, and water retention in grasslands dominated by perennial grasses (Ogle et al., 2003). Long-term annual *Bromus* management must be adaptive, taking into account site-specific ecological characteristics and the potential for resurgence in future years (Ashton et al., 2016).

Taeaniatherum caput-medusae, commonly known as medusahead, was first introduced to the U.S. from the Mediterranean region between the late 19th and early 20th centuries and has steadily spread across the western states (Meineke et al., 2024). Since its initial introduction, *T.*

caput-medusae has expanded its range by approximately 12% per year (Davies and Johnson, 2008). In Montana it was first reported in 2013, taking over a century to reach the state. Its spread continues to threaten native ecosystems across the region, now covering over 2.4 million acres across 17 western states (Kyser et al., 2014). *Taeaniatherum caput-medusae* invades grasslands and shrub steppe regions in the western U.S., displacing native vegetation and increasing fire frequency (Ploughe and Dukes, 2022). Similar to the previous two IAG species, *T. caput-medusae* contributes to soil degradation by forming dense litter layers that reduce water infiltration and hinder native plant germination (Nafus and Davies, 2014). The dominance of *T. caput-medusae* in invaded ecosystems is facilitated by the accumulation of litter, which can reduce microbial diversity, disrupt nutrient cycling, and create a physical barrier that prevents other plants from establishing, thereby benefiting *T. caput-medusae* by enhancing moisture retention and seed productivity (Cherr, 2009). The presence of the litter layer alters fire regimes and, because of its high silica content, reduces forage quality for both wildlife and livestock (Johnson et al., 2011; Swenson et al., 1964).

Taeniatherum caput-medusae seed production can vary depending on soil conditions and stand density. On valley bottom soils, plants generally produce one seed head per plant with an average of nine seeds per head, while on scabland soils, the average is around six seeds per head. In reduced competition, plants can produce more seed heads, typically between three and five per plant; although rare cases have observed 133 seed heads on a single plant (Cherr, 2009; Sharp and Tisdale, 1957). This fascinating seed production helps *T. caput-medusae* in creating dense litter with mat-like growth, often leading to the formation of monocultures (Betts, 2003).

Although herbicides can reduce *T. caput-medusae* populations, effective long-term control requires a multi-faceted approach that includes pre-emergent and post-emergent herbicide treatments, grazing management, litter removal, and revegetation (Bansal et al., 2014; Zhang et al., 2023; Evans and Young, 1970). A study in northern Utah assessed the effectiveness of prescribed burns followed by herbicide applications of sulfometuron and imazapic. Herbicide applications significantly improved *T. caput-medusae* control and increased bare ground, though results varied by site, season, and herbicide type (Monaco et al., 2005). Despite differences in litter levels between the low and high litter sites, no significant differences were found in perennial grass cover two years post-treatment. Several treatments maintained over 50% *T. caput-medusae* control in the second year, providing a critical opportunity to reintroduce perennial species through seeding (Monaco et al., 2005). Restoring native plant communities is essential to prevent the re-establishment of *T. caput-medusae* and to enhance ecosystem resilience (Uselman et al., 2014; Sheley and James, 2010).

Lastly, *Ventenata dubia,* commonly known as ventenata, native to Europe, Asia, and Africa, was introduced to the U.S. in the early 20th century and has become invasive across the Inland Pacific Northwest (Jones et al., 2020; Pavek et al., 2011). Although first identified in Washington in 1956, nearly 100 years after *B. tectorum* and *B. japonicus* (Old and Callihan, 1987), *V. dubia* has rapidly spread across various habitats (Jones et al., 2020). In northern Idaho and eastern Washington, *V. dubia* has been prevalent in Palouse prairie and canyon grasslands for over 30 years, reducing species richness and diversity (Jones et al., 2020). *Ventenata dubia* was initially recorded in Montana during the 1990s and has since been observed in 24 counties across the state, covering at least 22,258 hectares (Harvey and Mangold, 2018; Lesica et al., 2012).

Since the 1950s *V. dubia* has spread rapidly, affecting forage production, serving as a host for the barley yellow dwarf virus, and displacing *B. tectorum* in some regions (Ingwell and Bosque-Pérez, 2015). Managing *V. dubia* is challenging due to its rapid growth and prolific seed production. Under optimal conditions, *V. dubia* can produce up to 50 seeds/plant and 43,000 seeds/m^2, making it highly competitive (Pavek et al., 2011; Fryer, 2017). *Ventenata dubia* has impacts that are similar to those of other IAG and has the potential to influence fire dynamics (Fryer, 2017; Ridder et al., 2022) and reduce native plant diversity, although it has been studied less extensively (Harvey and Mangold, 2018; Wallace et al., 2015). *Ventenata dubia* exhibits resilience in the face of environmental changes and disturbances, thriving in areas where biocrust is present and even under conditions of trampling (Cellini, 2016). Its ability to alter water infiltration rates and reduce nutrient retention through competition with native vegetation and changes to soil properties highlights its role as a significant ecological disruptor in semiarid ecosystems (Cellini, 2016; Fryer, 2017). These soil changes create a feedback loop that favors further invasion of *V. dubia* and prevents the re-establishment of native species (Ridder et al., 2021).

Ventenata dubia appears to engage with arbuscular mycorrhizal fungi (AMF) relationships (Luedloff et al., 2022), unlike *B. tectorum*, which is generally non-mycorrhizal and tends to reduce AMF abundance (Busby et al., 2012). A study in central Oregon found that *V. dubia* roots were colonized by both AMF and dark septate endophytes, suggesting potential mutualistic benefits that may enhance its competitiveness and contribute to *V. dubia's* ability to thrive in stressful environments. However, the level of colonization varied significantly across different vegetation types, with the highest AMF colonization observed in wet meadows, indicating that environmental factors strongly influence fungal associations. Their findings suggest that *V. dubia* may use these fungal relationships to its advantage, potentially altering soil microbial communities and facilitating its invasion in a way distinct from other IAG, making it a unique challenge for restoration and control efforts (Luedloff et al., 2022).

Herbicide treatments have shown some effectiveness for *V. dubia* management. A study in the Pacific Northwest using rimsulfuron applied pre-emergent provided > 90% control after 10 months, while rimsulfuron and sulfosulfuron applied early post-emergence also had > 90% control after 9 months. Spring nitrogen (N) and nitrogen-phosphorus-potassium (NPK) fertilizers increased perennial grass cover and reduced *V. dubia* cover, suggesting that timing fertilizer applications during perennial grass growth can enhance integrated management strategies (Wallace and Prather, 2016). Adaptive and integrated management approaches will be vital for controlling all four of these IAG and reducing their ecological impacts (Bansal et al., 2014; Owen, Micheal DK. et al., 2015).

Chemical Control

Herbicides are widely used for managing invasive plants due to their effectiveness, ease of application, and visible outcomes (Kraehmer et al., 2014; Mangold et al., 2013; Sheley and Jacobs, 1997). Three modes of action are commonly used to control IAG, including; Group 2 herbicides (imazapic, rimsulfuron, sulfosulfuron, and propoxycarbazone-sodium), Group 9 (glyphosate), and more recently Group 29 (indaziflam). Group 2 herbicides, also known as acetolactate synthase (ALS) inhibitors, are a class of herbicides that disrupt the activity of the ALS enzyme in susceptible plant species (Tranel, 2002). Acetolactate synthase is an essential enzyme involved in the synthesis of branched-chain amino acids, and when the herbicides interfere with protein synthesis it leads to symptoms such as chlorosis (yellowing), stunted growth, and eventually plant death (Sharma, 2020; Das and Mondal, 2014). Despite their effectiveness, the prolonged use of Group 2 herbicides has led to the development of herbicide-resistant weed populations, including *B. tectorum* (Menalled et al., 2008; Park et al., 2005; Tranel, 2002). The presence of herbicide resistance underscores the need for integrating these herbicides with other management strategies to prevent resistance development and sustain long-term control (Park et al., 2005; Tranel, 2002; Ball et al., 2007).

Imazapic (Plateau®) is a selective herbicide in Group 2. Imazapic controls both annual and perennial grasses, including *B. tectorum*, and some broadleaf weeds (Terry, 2020). Imazapic provides residual control for one to two years, depending on the application rate and timing, making it a valuable tool for early-stage management of IAG, and where IAG dominate and require revegetation (Mangold et al., 2013; Sebastian et al., 2016). Several studies conducted on range and Conservation Reserve Program lands demonstrate imazapic's effectiveness on *B. tectorum*, especially when applied in the fall, regardless of litter presence, and greenhouse bioassays confirmed imazapic's persistence into spring (Mangold et al., 2013; Ehlert, 2013).

In split-plot field studies conducted at both an old-field and a rangeland site, the efficacy of three different rates of imazapic herbicide and eight seeding treatments was evaluated. The results showed that imazapic had effective control with a more than 95% reduction in *Bromus* spp. biomass (Orloff et al., 2015). At the old-field site, the herbicide controlled annual *Bromus* spp. for two growing seasons, while at the rangeland site, control lasted for one season (Orloff et al., 2015). Research conducted in Montana grasslands found that imazapic applied at the lowest labeled rate (105 g ai ha^{-1}) was able to control *B. tectorum* for at least one growing season, while minimizing non-target effects when applied at the optimal growth stage (Mangold et al., 2013). The same study showed pre-emergence applications were the least effective, achieving only 5-19% control. Post-emergence applications provided 25-77% control, while early post-emergence applications were the most effective, yielding 70-95% control. Applying imazapic to seedlings shortly after emergence (one- to two-leaf stage) was more effective than applying it to older seedlings (three- to four-leaf stage) (Mangold et al., 2013).

Another study was conducted at three sites in the sagebrush steppe, two within Great Basin National Park, Nevada and one in Provo, Utah. While imazapic initially controlled *B. tectorum*, its effectiveness declined sharply over time and led to significant reductions in the native perennial grass species *Pseudoroegneria spicata,* reducing seedling emergence by 46% and two-year plant density by 65%; however, it was less detrimental than indaziflam, which caused a 96% reduction in emergence and a 91% decrease in plant density (Terry et al., 2021). This underscores the importance of using imazapic and indaziflam with caution in conservation and restoration settings.

Rimsulfuron (Matrix® SG, DuPont™) is a sulfonylurea herbicide within the Group 2 ALS inhibitors. Rimsulfuron has proven effective in controlling IAG across diverse environments; although, field trials have shown mixed results (Hirsch et al., 2012; Sebastian et al., 2016). It has also caused significant injury to perennial grasses, a potential drawback for using in Intermountain foothill grasslands where IAG are invading (Sebastian et al 2016). In a study done in the foothills of the Bridger Mountain Range in southwestern Montana, rimsulfuron provided short-term control of *V. dubia*, but *V. dubia* increased in cover 20 months after treatment (Harvey, 2019; Mangold et al., 2024).

Rimsulfuron offers low soil persistence, which may reduce the impact on non-target species while attempting to control target grasses (Wallace and Prather, 2016). A study in the Intermountain Northwest showed rimsulfuron applied early post-emergence provided > 90% control 9 months after treatment (Wallace and Prather, 2016). A greenhouse study demonstrated that rimsulfuron significantly reduced the seed germination and seedling emergence of *B. tectorum* and *Agropyron cristatum*, with a greater impact compared to imazapic (Hirsch et al., 2012). Although rimsulfuron has limited residual soil activity, its effectiveness can be maximized through careful timing of application to coincide with weed emergence, and it is often combined with other herbicides to extend its range of control and prevent resistance (Sebastian et al., 2016; Onofri, 1996). Prolonged use of sulfonylureas also risks the development of herbicide-resistance, making it essential to rotate herbicides as part of a comprehensive management strategy (Prather et al., 2000; Holt and Lebaron, 1990).

Sulfosulfuron (Outrider® DG, Monsanto Company), another Group 2 herbicide, has been shown to control *V. dubia* and *B. tectorum* effectively in post-emergence applications (Harvey, 2019; Ribeiro et al., 2023; Butler et al. 2007; Shimizu et al., 2002). A study by Ribeiro et al. (2023) evaluated nine populations of *Bromus tectorum* for resistance to Acetyl-CoA Carboxylase (ACCase) inhibitors (e.g., clethodim, sethoxydim, fluazifop-P-butyl, and quizalofop-P-ethyl) key enzymes involved in fatty acid synthesis and lipid biosynthesis as well as the ALS inhibitor sulfosulfuron. The study found that all *B. tectorum* populations were resistant to ACCase inhibitors due to specific mutations. However, all populations were susceptible to sulfosulfuron, indicating its efficacy for controlling resistant *B. tectorum*. This study was the first to report specific mutations conferring resistance to ACCase inhibitors in *B. tectorum* and highlights different resistance mechanisms across populations (Ribeiro et al., 2023).

Field trials in Idaho demonstrated that sulfosulfuron (53 g ai ha^{-1}) provided over 90% control of *V. dubia* 9 months after treatment with minimal effects on the native perennial grasses *P. spicata* and *T. intermedium* (Wallace and Prather, 2016). This selectivity makes it a useful tool in areas where maintaining native perennial species is important. However, significant injury was observed in *Bromus inermis* and *Phleum pratense* when sulfosulfuron was applied early post-emergence (Wallace and Prather, 2016). In another study comparing the photosynthetic and growth responses of *B. tectorum* and *T. caput-medusae* along with twelve desirable grass species to sulfosulfuron (Monaco and Creech, 2004), sulfosulfuron consistently caused injury to wildryes and bromes, showing that rhizomatous grasses were more susceptible with minimal negative effects observed on bunchgrass and wheatgrass species (Monaco and Creech, 2004). Sulfosulfuron can be an effective short term option for managing IAG, although care should be taken with certain perennial grasses to minimize herbicide injury.

Propoxycarbazone-sodium (Lambient™) is a sulfonylaminocarbonyltriazolinone (SCT) herbicide, functioning similarly to sulfonylureas by inhibiting the ALS enzyme (Park et al., 2004). Propoxycarbazone-sodium has been used to control *B. tectorum* (Sbatella et al., 2011; Wallace and Prather 2016; Hirsch et al. 2012). Four and two year studies were conducted at multiple sites in Colorado, Nebraska, and Wyoming where propoxycarbazone-sodium showed promising results for controlling *B. tectorum* and seeding of desirable grasses, with effectiveness similar to or better than imazapic when followed by adequate rainfall after fall application (Sbatella et al., 2011). In terms of perennial grasses, propoxycarbazone-sodium and imazapic were generally well tolerated when applied 90 to 120 days before planting, with minimal biomass reduction for the cool season grasses *Agropyron cristatum* and *Thinopyrum intermedium*. However, tolerance varied by species; *Bromus inermis*, *Festuca ovina*, and *Dactylis glomerata* exhibited the least tolerance, particularly when herbicides were applied at or after planting. These findings suggest that propoxycarbazone-sodium may be an effective option for *B. tectorum* control while allowing for the reestablishment of certain perennial grass species under appropriate timing conditions (Sbatella et al., 2011).

In a study looking at herbicide control strategies for *V. dubia* in the Intermountain Pacific Northwest, propoxycarbazone-sodium provided moderate control of *V. dubia*, achieving 77–88% effectiveness in early post-emergence applications, though its performance was notably more variable compared to other herbicides like sulfosulfuron and rimsulfuron (Wallace and Prather 2016). While propoxycarbazone-sodium's control was significantly lower in pre-emergence applications, with rates ranging from 58–73%, it demonstrated improved efficacy when applied after *V. dubia* emergence. Despite its lower overall control, propoxycarbazone-sodium caused minimal injury (1–8%) to perennial grasses, making it a safer option for ecosystems where grass preservation is critical (Wallace and Prather 2016).

Studies have shown that *B. tectorum* metabolizes propoxycarbazone-sodium rapidly, thus effective control is achieved when applied at optimal stages of growth (Park et al., 2004). However, propoxycarbazone-sodium was found to be broken down in resistant biotypes within 72 hours, highlighting its rapid action (Park et al., 2004). Due to the rapid metabolism of propoxycarbazone-sodium in resistant biotypes of *B. tectorum*, there are concerns about the emergence of resistance in other species of IAG as well, underscoring the importance of integrating other management practices to sustain control over time.

Group 9 herbicides, also known as EPSP (5-enolpyruvylshikimate-3-phosphate) synthase inhibitors, are non-selective herbicides that inhibit the EPSP synthase enzyme, which is critical for the shikimate pathway in plants (Almeida et al., 2024). This pathway is essential for the production of aromatic amino acids like tryptophan, tyrosine, and phenylalanine (Dev et al., 2012). By inhibiting EPSP synthase, Group 9 herbicides disrupt protein synthesis, leading to growth cessation, chlorosis, and necrosis (Hess, 2018). Their non-selective nature makes them effective for controlling a broad range of invasive and weedy species, but it also requires careful application to prevent unintended damage to non-target vegetation. Over-reliance on EPSP inhibitors has resulted in herbicide-resistant weed species, which poses a significant challenge for land management (Heap and Duke 2018; Shaner, 2014).

Glyphosate (Roundup™ Monsanto) is the most common Group 9 herbicide (Vats, 2015). Glyphosate can be effective in controlling smaller *Bromus* plants, but its efficacy is highly dependent on the application rate and plant height. In one study glyphosate was generally less effective at reducing *Bromus* spp. biomass compared to tested graminicides (Metier et al., 2020). The low rate of glyphosate (0.42 kg ai ha−1) frequently performed the worst, especially for middle and taller height groups (8.5 cm, 11 cm, and 15.5 cm). High rates of glyphosate (0.56 kg ai ha−1) were more effective than low rates, but still often less effective than graminicides like fluazifop and quizalofop. Higher rates of glyphosate may be necessary for effective control, whereas graminicides, even at low rates, offer better control and may be preferable particularly in field settings where plant height can vary (Metier et al., 2020).

In a study evaluating control of *B. tectorum* using an integrated approach involving herbicides, grazing, and competitive perennial grasses, glyphosate (0.55 kg ai ha−1) and paraquat (0.6 kg ai ha−1) combined with intensive grazing provided effective control on rangeland (Whitson and Koch, 1998). Paraquat achieved over 90% control after two years, while glyphosate provided up to 97% control at one location after the first application. In the same study, seeding the perennial cool-season grasses *Apropyron trichophorum* and *Agropyron cristatum* in combination with herbicide and grazing effectively reduced *B. tectorum* reestablishment. The findings suggest that establishing competitive perennial grasses offers a more sustainable solution for *B. tectorum* management compared to herbicides alone or with grazing (Whitson and Koch, 1998).

In another study focused on glyphosate for annual *Bromus* spp. control on rangeland in eastern Montana, the use of low-dose glyphosate (210 g ha−1) applied once in fall reduced *B. tectorum* cover and seed bank density initially, but after a second year of treatment *B. tectorum* no longer responded to the herbicide. The seed bank of *B. japonicus* actually increased in areas treated with glyphosate over 2 years (Espeland and Kilian, 2015). Overall, glyphosate application proved unreliable for long-term control of annual *Bromus* spp., suggesting that it may not be an effective standalone solution for managing these invasions in the grasslands of the northern Great Plains.

Group 29 herbicides work by inhibiting the process of cellulose biosynthesis, which is essential for cell wall formation in plants (Kaapro and Hall, 2012; Chebli and Geitmann, 2017; Höfte and Voxeur 2017). This mode of action is especially effective on young plants, making Group 29 herbicides highly useful for controlling IAG and other weed species if applied pre-emergence and during early growth stages. Because they target cell wall formation, their effects are long-lasting and provide extended residual control in the soil, preventing the emergence of new seedlings for months or even years after application (Sebastian et al., 2017). However, this same prolonged activity can affect non-target species, particularly native forbs, which rely on seedling establishment from the soil seedbank (Clenet et al., 2019; Dutra et al., 2023). Overuse or improper application of Group 29 herbicides may reduce the regeneration capacity of beneficial seed bearing plant species, thereby impacting overall biodiversity (Terry et al., 2021).

Indaziflam (Rejuvra® Bayer) is a Group 29 herbicide (Cellulose Biosynthesis Inhibitor (CBI)) that inhibits the enzyme protoporphyrinogen oxidase (PPO) **(**Brabham et al., 2014; Sebastian et al., 2017). Indaziflam is a pre-emergent herbicide, targeting seeds at the time of germination by affecting the radicle as it emerges from the seed (Brabham et al., 2014; Pritchard et al., 2023). Indaziflam remains within the top few centimeters of the soil, impacting only plants with roots within that zone (González-Delgado and Shukla, 2020); therefore it shows promise as an effective herbicide for controlling annual weeds in perennial grasslands, targeting only shallow-rooted plants due to its localization in the top few centimeters of soil. (Fowers and Mealor, 2020).

Indaziflam provided significant long-term reduction in IAG biomass up to three years after treatment, outperforming imazapic, at multiple sites on the Colorado Front Range (Clark et al., 2020). In drill-seeded sites, indaziflam-treated plots showed cool-season grass frequency ranging from 37% to 69%, compared to only 0% to 26% in imazapic-treated plots. At the site with a remnant native plant community, indaziflam led to a three to four fold increase in native grass biomass. The findings suggest that indaziflam supports multiyear IAG control and aids in native species reestablishment through both drill seeding and enhancing remnant plant community response (Clark et al., 2020).

Indaziflam's ability to reduce invasive species competition makes it a powerful tool in areas with severe infestations (Crose, 2022; Meyer-Morey et al., 2021). While indaziflam is effective in reducing invasive species, it has been shown to reduce the richness and diversity of native forbs, particularly those that regenerate from the soil seed bank (Courkamp et al., 2022; Meyer-Morey et al., 2021). In the sagebrush-grasslands near Pinedale, Wyoming, indaziflam (73 g ai ha^{-1}) did not impact aboveground plant species diversity but significantly reduced the density and richness of native seeds in both shallow and deep seed banks (Courkamp et al., 2022). Meyer-Morey et al. (2021) reported decreases in both the native forb seed bank belowground and aboveground forb abundance, highlighting potential risks to native plant communities under some conditions. Despite seedbank reductions, Courkamp et al. (2022) found that all impacted species were still present in the aboveground plant community, suggesting that declines in native annual abundance might be temporary. These findings emphasize the importance of considering potential non-target impacts on seed banks to properly assess the trade-offs associated with indaziflam use in restoration efforts.

Litter and Bare Ground

Using herbicides to control IAG can lead to significant changes in litter accumulation and bare ground. While reducing IAG competition can promote desirable vegetation, these management practices may inadvertently result in heavy litter buildup, which can suppress germination and establishment of some plant species, or bare ground, which increases susceptibility to erosion and secondary invasion (Evans and Young 1970; Barnes, 2007; Pearson et al., 2016). Without sufficient propagules or seeds of desired species, an open niche left by IAG removal is likely to be pioneered by invasive plants, limiting natural recovery (Mangold, 2012). A five-year study in the northern Great Basin of the U.S. focusing on the effects of litter manipulation in sagebrush-steppe ecosystems invaded by IAG found that litter removal negatively impacted annual grass cover in dry conditions and perennial grass cover in wet conditions within the mixed community (Bansal et al. 2014). Significant effects on plant community composition were observed only with extensive litter removal (over 75%) and were dependent on the level of annual grass invasion, timing of litter removal, and seasonal precipitation patterns (Bansal et al., 2014). For the past 50 years, the litter layer has been recognized for its ability to modify soil microclimates and influence moisture retention and soil temperature, which in turn fosters the germination and establishment of annual weeds (Evans and Young, 1970). This process has contributed to the dominance of species like *B. tectorum* in rangeland ecosystems.

A study using an ACCase herbicide fluazifop-p-butyl plus litter removal was conducted to control *Bromus spp.* on farmlands abandoned for 20 years in southern California, and the results showed that native annuals increased in species richness following grass control, though their cover remained low except in two out of six years when rainfall was adequate (Allen et al., 2005). Removal of litter did not improve the response of native forbs, while two exotic species of *Erodium* benefitted most. Despite the dominance of *Erodium* spp., native forbs showed a positive response, suggesting less intense competition between native forbs and *Erodium* spp. compared to the invasive grasses. The invasive grasses began to recover after five years, indicating that ongoing management is needed. Additionally, shrubs from adjacent hills did not recolonize during the six-year period, suggesting that these valley bottoms may have always been forblands rather than shrublands. The study demonstrated that restoration efforts can help reveal the original vegetation of long-disturbed landscapes (Allen et al., 2005). Further research in grasslands is essential to explore how the litter layer affects the germination and establishment of native plant species and whether it similarly supports the overwintering of other IAG, as the differential impacts on native versus invasive species remain largely unexplored.

Bare ground, the absence of vegetation cover, is a critical factor in rangeland ecosystems. It plays a significant role in influencing plant community dynamics, as it can either provide opportunities for native species to establish or create a niche that invasive species may exploit (Weltz et al., 1998; Zobell et al., 2020). By maintaining areas of bare ground a reduction of competition from IAG can be seen; thereby, opening up space creating opportunities for native species to thrive (Veblen and Monaco, 2018; Hobbs, 1994; Hobbs and Huenneke, 1992). Evaluating the effects of herbicide treatments on bare ground is crucial for understanding their role in creating space for native seedlings and enhancing ecosystem resilience. (Everglades, Greater. Notes and Abstracts, 2004). Furthermore, assessing bare ground is essential because it is hypothesized to play a key role in providing habitat for many ground nesting bee species essential for pollination services (Antoine and Forrest, 2021; Ullmann et al., 2020). Approximately 70% of native bee species in the U.S. nest in the ground, often preferring sunny, bare soil areas (Harmon-Threatt, 2020). Therefore, while creating bare ground can aid in native plant restoration, it's vital to balance these efforts with the conservation of pollinator habitats to maintain overall ecosystem health (Winfree, 2010).

Restoring Native Plants

Revegetation combined with herbicide application is a widely used strategy to manage IAG (Orloff et al., 2015; Mangold et al., 2015), and efforts to study and implement revegetation practices have been ongoing since the mid-1900s (Hironaka, 1961; Hull, 1959). Controlling IAG alone may not suffice for restoring desired vegetation (Monaco et al., 2017; Rinella et al., 2012). Introducing propagules and promoting their persistence through targeted management increases the likelihood of long-term restoration success and ensures that management efforts produce lasting positive outcomes (Rinella et al., 2012; Mangold, 2012). Revegetation seeks to establish competitive, desired plant species that can suppress IAG growth and reduce their spread (Brooks and Lusk, 2009; Mangold et al., 2007). Typically, revegetation efforts involve drill-seeding native or desirable species following herbicide treatments (Rinella et al., 2012; Malone, 2015). This combined approach is more effective for providing long-term control of IAG compared to herbicide use alone (Monaco et al., 2016). The introduction of well-adapted vegetation enhances biodiversity and strengthens ecosystem resilience, making grasslands less prone to future invasions and disturbances (Johnson et al., 2011; Smith, 2004).

Additionally, reintroducing pollinator-friendly plants is crucial for restoring ecosystem function, as floral diversity supports wild pollinators throughout their foraging cycles (Tonietto and Larkin, 2018; Vaudo et al., 2015). Revegetation is a pivotal strategy in ecosystem restoration and invasive species management. By reestablishing native or desirable plant species, revegetation can enhance ecosystem functionality, improve soil health, and reduce the dominance of invasive species. Perennial grasses, in particular, are critical in revegetation efforts due to their long-term establishment, competitive ability, and contributions to soil stability and nutrient cycling and overall community composition (Davies et al., 2024; Hart and Mealor, 2021;

Wilson et al., 2010). However, despite its potential, revegetation often does not achieve the desired outcomes in the short term, particularly under extreme environmental conditions or without effective long-term management (Monaco et al., 2017). As a result, there is a need for continued management to improve the effectiveness of these approaches in sustaining desired plant communities and enhancing the resilience of restored grasslands.

Drill seeding is a method of sowing seeds directly into the soil using a specialized seeder, which creates furrows or grooves in the soil where seeds are deposited and covered. This technique is particularly useful for large-scale restoration projects and areas with compacted or disturbed soils. One of the main advantages of drill seeding is its ability to efficiently distribute seeds over a broad area, ensuring even coverage and increasing the likelihood of successful establishment (Shaw et al., 2020). Drill seeding offers several benefits for revegetation (Rinella et al., 2016). First, it allows for precise control over seeding depth, which is crucial for optimizing seed-to-soil contact and improving germination rates. Seeds planted too deep may not germinate, while those too shallow may be prone to desiccation or predation. By controlling the seeding depth, drill seeding can enhance seedling establishment and survival (Boyd and James, 2013). Second, drill seeding can incorporate seeds into the soil, which protects them from surface erosion and enhances their ability to access soil moisture and nutrients. Despite these advantages, drill seeding also has limitations. It is less effective on extremely rocky or uneven terrain, where soil preparation may be challenging. Furthermore, the technique requires proper calibration and maintenance of equipment to ensure accurate seed placement and avoid issues such as seed clogging or uneven distribution (Harvey, 2019). Successful drill seeding also depends on the choice of appropriate seed mixtures and the timing of seeding. For instance, seeding must be timed to coincide with favorable soil moisture conditions to promote germination and establishment. Using appropriate seed mixes could help achieve reference conditions effectively (Munson and Lauenroth, 2012, 2014). Using annual species like *Cleomella* (Rocky Mountain bee plant) and *Helianthus* (sunflowers) can help initiate early succession, providing rapid cover and improving soil conditions while giving perennials time to establish effectively (Mwangi et al., 2007).

<u>Pollination</u>

In the Inland Northwest, grasslands provide a mosaic of habitats that cater to the needs of different pollinator species, from wildflower meadows to sagebrush shrublands. Pollinators, including bees, butterflies, moths, flies, beetles, and birds, are critical to the reproduction of many plant species, particularly those that produce fruits, vegetables, and seeds. Approximately 75% of the world's flowering plants and 35% of global food crops rely on pollinators for reproduction (Klein et al., 2007; Van der Sluijs et al., 2016). Pollinators play an essential role in maintaining ecosystem health, agricultural productivity, and biodiversity (Katumo et al., 2022). Healthy pollinator populations support diverse plant communities, which in turn provide food, shelter, and nesting sites for a wide range of other species (Potts et al., 2016). Protecting and enhancing pollinator habitats in grasslands not only benefits biodiversity but also supports the resilience of agricultural systems dependent on these vital insects (Potts et al., 2009).

In Tribal grasslands the importance of pollination extends beyond ecological functions. Pollinators contribute to the vitality of plants that are used in traditional medicines, food sources, and cultural practices; therefore, having far-reaching consequences, not only for biodiversity and "earthly gifts" (Kimmerer, 2014) but also for the cultural practices and food security of

Indigenous communities (Carroll, 2023; Roué et al., 2015; Breslow et al., 2016). Native pollinators are integral to both cultural heritage and environmental sustainability. However, like pollinator populations worldwide, local pollinators are facing numerous threats, including habitat loss, climate change, pesticide exposure, and the spread of IAG; furthermore, the decline of pollinator populations due to so many threats highlights the need for comprehensive conservation strategies (Abrol, 2012; Elsayed, 2020). Collaborative efforts between scientists, land managers, and Indigenous communities are essential for developing effective strategies to protect pollinator habitats and maintain earthly gifts (Chief et al., 2015).

Threats to Pollinators

Pollinator populations worldwide are in decline due to a combination of factors. The loss of habitat, driven by IAG, land-use change, agriculture, and urbanization, are the most significant threats to pollinators (Abrol, 2012; Elsayed, 2020). As native habitats are fragmented or converted to other uses, pollinators lose access to the resources they need, such as flowering plants, nesting sites, and undisturbed ground (Vanbergen, 2013; Proesmans et al., 2019). Non-native plants like IAG can outcompete native vegetation, reducing the diversity and abundance of floral resources available to pollinators (Vanbergen et al., 2018). Grazing can significantly reduce the availability of native plants essential for pollinators; however, this could be from indirect effects, such as soil disturbance and nest destruction rather than reducing floral cover (Thapa-Magar et al., 2020). Thus, pollinator conservation in grasslands should focus on minimizing cattle impacts, especially during the early growing season to protect sensitive bee species. By using responsible grazing practices, such as moderate grazing, managers can support overall pollinator diversity, while reduced grazing in early spring may benefit specific early-season pollinators and bee-pollinated plants (Lazaro et al., 2016). Late season grazing has been found to enhance pollinator abundance by increasing flower availability (Sjödin et al., 2007).

Climate change is another major threat to pollinator populations (Forrest, 2017). Changes in temperature, precipitation patterns, and seasonal cycles can disrupt the timing of flowering and pollinator activity, leading to mismatches that negatively impact pollination services (Vasiliev and Greenwood, 2021). Additionally, extreme weather events, such as droughts and floods, can directly harm pollinator species by destroying their habitats or reducing their populations (Erenler et al., 2020; Nicholson and Egan, 2020). Given these numerous threats, it is imperative to collect baseline data on pollinator species abundance and diversity in order to assess the health of pollinator communities and track changes over time.

Baseline Survey of Pollinator Community

Establishing a baseline of pollinator species abundance and diversity is critical for grassland conservation on Tribal lands of the CSKT of the Flathead Reservation. A baseline survey will provide a snapshot of the current state of pollinator communities, allowing researchers to identify which species are present (Breeze et al., 2021). This information is essential for detecting declines in pollinator populations and understanding the factors contributing to those declines (Bartomeus et al., 2019; Popic et al., 2013). Without baseline data, it is difficult to assess the effectiveness of conservation efforts or to determine whether pollinator populations are recovering or continuing to decline (Roubik, 2001). Baseline data can be used to identify areas of high pollinator diversity and abundance that may serve as refuges or hotspots for pollinator conservation (Meiners et al., 2019). By identifying these areas, land managers and conservationists can prioritize them for protection and restoration efforts. For example, understanding which pollinators are most vulnerable to habitat loss associated with IAG, climate change, or pesticide exposure can help land managers make decisions about grazing practices, restoration projects, and pesticide use that minimize harm to pollinators (Abrol, 2012; Spiesman and Inouye, 2013). Additionally, baseline data can be used to track the success of restoration projects and adaptive management practices aimed at enhancing pollinator habitat (Barron, 2021).

Project Justifications and Objectives

Intermountain foothill grasslands in the Pacific Northwest face significant challenges from IAG. Controlling these species with herbicides is a critical component of effective grassland management. This research was conducted on the Flathead Reservation, located in northwestern Montana and owned and managed by the Confederated Salish and Kootenai Tribes (CSKT) (Figure 1.1). Understanding how herbicides control IAG as well as the impacts on non-target species and native species used in revegetation is critical for balancing effective IAG management with the restoration and preservation of native plant and pollinator communities. Three independent studies were conducted to this end, and they are presented in the chapters that follow.

Chapter two describes a field study where herbicides were integrated with no-till drill seeding to establish desirable species at two separate sites. I hypothesized that all herbicide treatments would reduce IAG compared to non-sprayed checks, with indaziflam providing superior efficacy, resulting in the lowest IAG canopy cover. Additionally, I expected that greater control of IAG would create more bare ground; thereby, increasing the abundance of seeded species, though indaziflam's post-seeding application would influence seeded species differently, and possibly more detrimentally, than other herbicides.

Chapter three describes a greenhouse study where I subjected native forb and grass species to herbicides under controlled conditions. Species and herbicides were mostly similar to those tested in the field study. I hypothesized that herbicide treatments would reduce seedling emergence and biomass across all treatments, with varying degrees of injury to seedlings. Specifically, I predicted that indaziflam would cause the greatest reduction in emergence and biomass, with the highest levels of seedling injury across species. Then, imazapic would significantly reduce emergence and biomass, with moderate to high injury to all species of seedlings, and rimsulfuron and sulfosulfuron would moderately suppress emergence and biomass with less injury,

Chapter four addresses the lack of knowledge of pollinator populations in grasslands threatened by IAG. I aimed to assess abundance, richness and evenness of bee populations on Tribal grasslands, providing critical data for managers to evaluate the success of future conservation measures and adapt management strategies as necessary. The concluding chapter summarizes key findings from each study, integrating the results to guide management practices for IAG and outlines potential directions for future research.

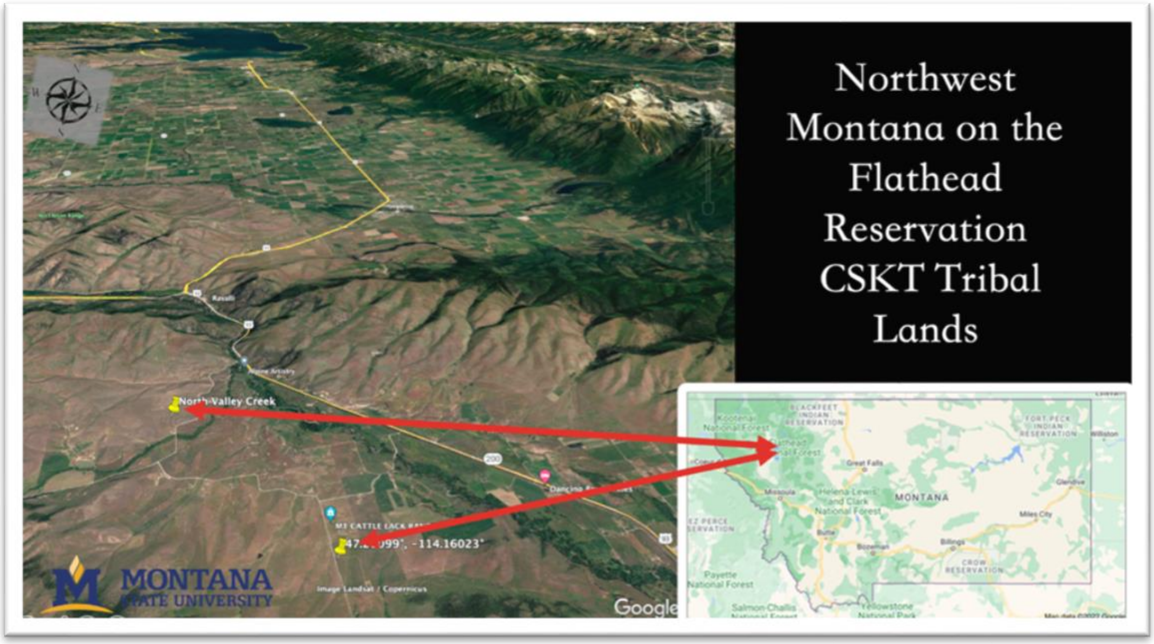

Figure 1.1 Map of study sites in northwest Montana on the Flathead Reservation.

CHAPTER TWO

ASSESSING HERBICIDE AND SEEDING TREATMENTS IN INTERMOUNTAIN FOOTHILL GRASSLANDS

Introduction

Intermountain foothill grasslands of the Confederated Salish and Kootenai Tribes (CSKT) or tribes in northwestern Montana have been impacted by cheatgrass (*Bromus tectorum* L.) since the end of the 19th century (Hull and Pechanec, 1947). Medusahead *(Taeniatherum caput-medusae* (L.) Nevski*)*, first identified in Montana on CSKT grasslands in 2013 (Christiansen personal communication, 2018), and ventenata *(Ventenata dubia* (Leers) Coss. & Durieu), identified on Tribal lands in 2008 (Soukala personal communication, 2018), have combined with other *Bromus* spp. specifically Japanese brome (*Bromus japonicus* Thunb.) to form an invasive annual grass (IAG) complex. Together these IAG are contributing to a lack of native flowering plants and perennial grass species (Davies, 2011). Invasive annual grasses are also rapidly expanding, further threatening CSKT grasslands and the last remaining Palouse prairie grasslands in the Inland Northwest (Averett, 2022, Dupuis personal communications, 2016; Germino and Lazarus, 2020).

The CSKT Intermountain foothill grasslands historically consisted of a diverse array of native perennial grasses, forbs, and shrubs. Rough fescue *(Festuca campestris* Rydb.) and bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) characterized these grasslands and they, along with other species of perennial grasses, would have been the most productive vegetative functional group before the grasslands were altered significantly by overgrazing, land conversion, and invasive plants (Mueggler and Stewart, 1981; Blankinship, 1905). Perennial grasses historically constituted 65-90% of total biomass, alongside a diverse forb community comprising 10-25%, and shrub species rarely exceeding 5% (Mueggler, 1980, 1983). Historic vegetation in the region not only provided good to excellent forage for wildlife and livestock, but also floral resources beneficial to local insect species (Mueggler, 1980; Dodson, 2007). Now these grasslands are much less diverse. For example, recent vegetative surveys indicate: annual grass canopy cover at 39-52%, perennial grasses at 21-31%, forbs 27-30%, and shrubs less than 1% (unpublished McRyhew). Additionally, forbs are primarily invasive and noxious weeds, and the existing perennial grasses are mostly introduced species. Furthermore, the invading species do not provide the same habitat and foraging resources for native wildlife and pollinators that native vegetation had historically (Pei et al. 2023; Ogilvie and Forrest, 2017). Given the current degraded state of CSKT's grasslands, there is a critical need to develop and implement effective restoration strategies (CSKT, 2020).

Invasive annual grasses typically germinate in the fall, overwinter in a vegetative state, and complete their lifecycle the following summer (Moore, 2020; Moore and Nelson, 2017; Thill et al., 1984). This life cycle allows for earlier germination and faster root elongation, giving them a competitive advantage over native perennial species that germinate and emerge in spring (De Stefano et al., 2024; Mummey et al., 2016; Hironaka 1961). One of the most widespread of these IAG is *B. tectorum*, covering an estimated 22 to 43 million hectares and spreading at 14% annually (Beck, 2009). *Bromus tectorum* has a native range across Europe (Novak and Mack, 2001) and was first recorded in Montana around 1898, and within 100 years it had spread throughout all counties in the state (Hull and Pechanec, 1947; Menalled et al., 2008). Similarly, *B. japonicus* also native to Europe and Asia, was likely introduced to North America alongside *B. tectorum* in the 19^{th} century through contaminated grain shipments (Beck, 2009). When *B. japonicus* was introduced in Montana is unknown; however, Haferkamp and Heitschmidt (1999) do not report either species of *Bromus* being common prior to the 1950s.

Taeniatherum caput-medusae, native to the Mediterranean and central Asia, is another highly invasive annual grass (Blank and Sforza, 2007). Since its initial introduction in North America attached to imported animals or their bedding, *T. caput-medusae* has expanded its range by approximately 12% per year (Davies and Johnson, 2008). In Montana it was first reported in 2013. Its spread continues to threaten native ecosystems across the region, now covering over 2.4 million acres across 17 western U.S. states (Kyser et al., 2014). Similar to the previous two IAG species, *T. caput-medusae* contributes to soil degradation by forming dense thatch layers that reduce water infiltration and hinder native plant germination (Nafus and Davies, 2014).

Ventenata dubia, native to Europe, Asia, and Africa, was initially recorded in Montana during the 1990s and has since been observed in 24 counties across the state, covering at least 22,258 hectares (Harvey and Mangold, 2018; Lesica et al., 2012). *Ventenata dubia* exhibits resilience in the face of environmental changes and disturbances, thriving in areas where biocrust is present and even under conditions of trampling (Cellini, 2016). *Ventenata dubia* appears to engage in arbuscular mycorrhizal fungi (AMF) relationships, unlike *B. tectorum*, which is generally non-mycorrhizal and tends to reduce AMF abundance (Busby et al., 2012; Alomran, 2019). This fungal relationship may give *V. dubia* an advantage, potentially altering soil microbial communities and facilitating its invasion in a way distinct from other IAG, making it a unique challenge for restoration and control efforts (Luedloff et al., 2022; Alomran, 2019; Pavithra and Yapa, 2018).

Chemical Management

Herbicides are widely used for managing IAG due to their effectiveness and ease of application, and while they offer control, most herbicides do not provide long-term efficacy (Monaco et al., 2017). Some herbicides commonly used to control IAG are imazapic (Plateau®, BASF Corporation), rimsulfuron (Matrix® SG, DuPont™), sulfosulfuron (Outrider® Monsanto), propoxycarbazone-sodium (Lambient™ Bayer Crop Science), glyphosate (Roundup ™ Monsanto), and indaziflam (Rejuvra® Bayer) (Wallace and Prather, 2016; Slopek and Lamb, 2017; Monaco et al., 2005; Hirsch et al. 2012; Vicari et al., 1994; Park et al., 2004; Sebastian et al., 2016, 2017). These herbicides target specific pathways in plant metabolism, disrupting essential enzyme activities and ultimately leading to plant death (Menon, 2021).

Imazapic is a group 2 pre- to post-emergent herbicide that has some residual activity in the soil, providing one or two-years of IAG control (Sebastian et al., 2016, 2017). Rimsulfuron is another group 2 post-emergent herbicide. Rimsulfuron has shown mixed results in field trials (Sebastian et al., 2016; Hirsch et al., 2012). It has also caused significant injury to perennial grasses, a potential drawback for using in Intermountain foothill grasslands where IAG are invading (Sebastian et al., 2016). Similar to rimsulfuron, another group 2 post-emergent herbicide is sulfosulfuron (Butler et al. 2007; Shimizu et al., 2002). Early post-emergent application of sulfosulfuron has achieved over 90% control of *V. dubia* with minimal impact on existing perennial grass species (Wallace, 2015). Propoxycarbazone-sodium has been used effectively to control *B. tectorum* (Sbatella et al., 2011; Wallace and Prather 2016; Hirsch et al., 2012). Roundup (Glyphosate™ Monsanto) is a non-selective, post-emergent systemic herbicide in group 9. High rates of glyphosate may be necessary for effective control of IAG particularly in field settings where plant height can vary (Metier et al., 2020). Indaziflam is a pre-emergent herbicide, targeting seeds at the time of germination by affecting the radicle as it emerges from the seed (Brabham et al., 2014; Pritchard et al., 2023). Indaziflam remains within the top few centimeters of the soil, impacting only plants with roots within that zone (González-Delgado and Shukla, 2020); therefore, it shows promise as an effective herbicide for controlling annual weeds in perennial grasslands (Fowers and Mealor, 2020).

Revegetation combined with herbicide application is a widely used strategy to manage IAG (Orloff et al., 2015; Mangold et al., 2015), and efforts to study and implement revegetation practices have been ongoing since the mid-1900s (Hull, 1959; Hopkins, 1953). Revegetation seeks to establish competitive, desired plant species that can suppress IAG growth and reduce their spread after disturbance (Brooks and Lusk, 2009; Mangold et al., 2007, 2012, 2015). Typically, revegetation efforts involve drill-seeding native or desirable species following herbicide treatments, and combining approaches is more effective for providing long-term control of IAG compared to herbicide use alone (Monaco et al., 2016; Rinella et al., 2012; Malone, 2015). The introduction of well-adapted vegetation enhances biodiversity and strengthens ecosystem resilience, making grasslands less prone to future invasions and disturbances (Johnson et al., 2010). Additionally, reintroducing pollinator-friendly plants is crucial for restoring ecosystem function, as floral diversity supports wild pollinators throughout their foraging cycles and gives them opportunity after frequent disturbance from restoration efforts (Tonietto and Larkin, 2018; Vaudo et al., 2015; Pokorny et al., 2004). However, despite its potential, revegetation often does not achieve the desired outcomes in the short term, particularly under certain environmental conditions or without effective long-term management (Monaco et al., 2017). As a result, there is a need for continued research and development to improve the effectiveness of these approaches in sustaining desired plant communities and enhancing the resilience of restored grasslands.

To address the threat posed by IAG to Intermountain foothill grasslands of CSKT in northwestern Montana, this research focused on integrating herbicides to suppress IAG and no-till drill seeding to establish desirable grasses, forbs, and shrubs. I hypothesized that all herbicides would reduce IAG compared to no treatment. I further hypothesized that seeded species frequency and density would be higher when the herbicide provided the most control of invasive annual grasses, leading to more open space (bare ground and litter) and reduced competitive vegetation cover.

Methods

The study was conducted over two years (2022-2023) on two sites, North Valley Creek (NVC) and Plant Lane (PL), on CSKT-owned Intermountain foothill grasslands on the Flathead Indian Reservation of northwestern Montana (Figure 1.1). The sites were fenced to exclude livestock grazing. The NVC site (47°14'1.93"N; 114°11'17.55"W) is at 911 meters elevation, the soils are primarily Belton silty loam at 8 to 15% slopes, and the annual precipitation ranges from 381- 483 millimeters (United States Department of Agriculture (USDA), Natural Resources Conservation Service, 2020). The historic vegetation would have comprised roughly 50% *F. campestra*, 26% *P. spicata*, 6% Idaho fescue (*Festuca idahoensis* Elmer.), 5% basin wildrye (*Leymus cinereus* (Scribn. & Merr.) A. Love), 2% prairie June grass (*Koeleria macrantha*

(Ledeb.) J.A. Schultes), 7% annual and perennial forbs, and 2% shrubs (Mueggler and Stewart, 1981; Mueggler, 1980). Invasive annual grass cover was approximately 45% at the start of the study and included *B. tectorum*, *B. japonicus, V. dubia*, and *T. caput-medusae*.

The PL site (47°12'2.90"N; -114° 9'38.17"W), approximately 6 km to the southwest of NVC, is at an elevation of 930 meters, the soils are McDonald silty clay loam at 4-8% slope, and annual precipitation is similar to that of NVC. The characteristic vegetation would have been 70% *F. campestris*, 10% *F. idahoensis,* 10% *P. spicata,* 5% Columbia needlegrass (*Achnatherum nelsonii* (Scribn.) Barkworth*)*, other perennial grasses at 5%, 10% annual and perennial forbs, and 5% shrubs (Mueggler and Stewart, 1981; Mueggler, 1980). Invasive annual grass cover was approximately 12% at the start of the study and included *B. tectorum, B. japonicus,* and *V. dubia*.

The study considered two main factors: herbicide treatments and seeded plant species treatments, hereafter referred to as herbicide and species. Treatments were arranged in a two-factor strip-plot design, with each herbicide and species combination replicated three times and blocked at each site. The main plots consisted of nine species and a non-seeded check, while the strip plots comprised seven herbicide levels, resulting in 70 subplots within each block. Species were drilled east to west, while herbicides were applied north to south. Both herbicide and species included a non-sprayed/seeded check. Species plots were 2.4 m wide and 3.4 m long, herbicide plots were 3.4 m wide and 2.4 m long, thus each subplot was 8.2 m^2.

Herbicides were applied starting in 2021 and ending in fall 2022 according to labeled rates and timings (Table 2.1). All but two of the herbicide treatments were applied on 19 October 2021. Glyphosate was applied in spring on 3 April 2022, as its mode of action requires contacting actively growing vegetation. Because indaziflam was applied after the first growing season, it was only sampled one year (2023) as opposed to other herbicide treatments that were sampled two years (2022 and 2023). This was done knowing the impact indaziflam can have if applied pre-seeding and to give seeded species an opportunity to germinate and grow for a single growing season before indaziflam was applied. Herbicides were applied using a 1982 John Deere tractor with attached 3 m boom sprayer with 48.3 cm nozzle spacing and delivered using TeeJet 8002, 80º even flat fan nozzles, and delivered with a water carrying capacity of 55.86 liters per hectare.

Table 2.1. Herbicide treatments applied at two sites North Valley Creek and Plant Lane on the Flathead Indian Reservation in northwestern Montana.

Herbicide Trade Name	**Active Ingredient**	**Product Rate a.i./ha**	**Date Applied**
Plateau®, BASF Corporation	Imazapic	105	19 Oct 2021
Matrix® SG, DuPont™	Rimsulfuron	53	19 Oct 2021
Outrider® Monsanto	Sulfosulfuron	53	19 Oct 2021
Lambient® Bayer	Propoxycarbazone-sodium	49	19 Oct 2021
Roundup® Bayer	Glyphosate	520	3 Apr 2022
Rejuvra® Bayer	Indaziflam	93	17 Aug 2022
No Spray	non-sprayed check	n.a.	n.a.

Seeding treatments were applied the spring following most of the herbicide applications (18 March 2022 at NVC; 19 March 2022 at PL). Seeding was done with a Flex II Truax™ no-till drill mounted on a Caterpillar® skid steer loader, and all species were drilled to a depth of 1.3 cm at USDA recommended rates (Table 2.2). Each species was seeded separately, with the drill being thoroughly cleaned between species with a vacuum cleaner. Treatments included nine species comprised of five forbs, two grasses, and two shrubs (Table 2.2). Species selection was based on their ecological significance in supporting grassland restoration and their cultural relevance to the local community. Additionally, the species were evaluated for their adaptability to the local climate and soil conditions, ensuring suitability for integration into long-term revegetation strategies. Further selection criteria included historic vegetation characteristics and flower accessibility for pollinator species.

Table 2.2. Seeding treatments applied at two sites, North Valley Creek and Plant Lane, in the Intermountain foothill grasslands on the Flathead Indian Reservation in northwestern Montana. (VNS=variety not stated)

Latin Name	**Common Name**	**Family**	**Seeding Rate Kg/ha**	**Cultivar/ Variety**
Lupinus argenteus Pursh	silver lupine	Fabaceae	0.8	Rubrucaulis
Gaillardia aristata Pursh	blanket flower	Asteraceae	0.8	Meriwether
Geranium maculatum Fisch & C.A. Mey.	wild Geranium	Geraniaceae	2.3	VNS
Cleomella serrulata (Pursh) Roalson & J.C. Hall (2015)	Rocky Mt. bee plant	Cleomeceae	1.9	VNS
Dalea purpurea Vent.	purple prairie clover	Fabaceae	0.8	Kaneb
Pseudoroegneria spicata (Pursh) Á. Love (1980)	bluebunch wheatgrass	Poaceae	1.6	Goldar
Festuca idahoensis Elmer.	Idaho fescue	Poaceae	0.7	Nezpurs
Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & G.I. Baird	rubber rabbitbrush	Asteraceae	0.6	VNS
Purshia tridentata (Pursh) D.C.	antelope bitterbrush	Rosaceae	0.3	VNS

In 2022 and 2023 (10 and 22 months after treatment (MAT), respectively) canopy cover of all species, litter, and bare ground were visually estimated to the nearest 1%. A one-meter stick was used to collect frequency and density of seeded species, and a 20cm x 50cm Daubenmire (1959, 1970) frame (hereafter referred to as quadrat) was used for estimating canopy cover (hereafter referred to as cover). Cover was allowed to exceed 100%. Plants often occupy different canopy layers (e.g., ground cover, mid-layer, and upper canopy), and this method ensures that all species are accurately represented regardless of their vertical position in the vegetation structure. Within each quadrat, species were identified, percent cover estimated, and data aggregated to calculate total abundance and average cover per square meter for every species, identifying the top 20 most abundant species at both sites. The quadrat was randomly placed corresponding with one drill line of each seeded species; this was done three times within each sub-plot and randomly placed corresponding with one drill line of each seeded species. The NVC site was sampled between 20 June to 14 July 2022 (24 days), and the PL site was sampled from 18 July to 4 August 2022 (18 days). In 2023 NVC was sampled from 11-14 July, and PL was sampled from 18-27 July. Sampling was timed to occur when the IAG were mature but before seed disarticulation.

We used a generalized linear model to evaluate the effect of herbicide treatments, site, and year. An analysis of deviance with a Chi-square test was conducted to evaluate the effects of herbicide, year, site, and their interaction on annual grass cover, bare ground, litter, and other in-situ functional groups (Okoye and Hosseini, 2024). Site was included as a random effect to account for variability between both sites, while treating herbicide and year as fixed effects. Total cumulative canopy cover for *B. tectorum*, *V. dubia*, *B. japonicus*, and *T. caput-medusae* were summed across treatments and blocks and analyzed together to provide broader overall assessment. Response variables were natural log transformed as needed to achieve normal distributions and homogeneity of variance; back-transformed means are reported. To compare the means of the treatments across groups and to the non-treated check, an emmeans Post-Hoc pairwise comparison was performed with a compact letter display used to graphically display treatment differences. All model selection and mean comparisons were done at $\alpha = 0.05$. Target seeded species were summed for frequency of individual seedlings found across herbicides.

These data were wrangled with Excel version 16.78, and statistical testing and graphical representation done in RStudio 4.3.1 (R Core Team, 2023). Packages used include; tidyverse (Wickham et al., 2019), dplyr (Wickham et al., 2021), tidyr (Wickham et al., 2020), ggplot2 (Wickham, 2016), ggthemes (Arnold, 2021), and emmeans (Lenth, 2022), multcomp (Hothorn et al., 2008) and multcompView (Graves et al., 2015).

Results

Invasive Annual Grass Cover

Herbicide treatments affected IAG cover ($\chi^2(6) = 10132.9$, $p < 0.001$), as did year ($\chi^2(1) = 4424.8$, $p < 0.001$) and site ($\chi^2(1) = 25238.1$, $p < 0.001$) (Table 2.3). The interaction between herbicide and year was also highly significant ($\chi^2(5) = 3742.4$, $p < 0.001$), indicating that the effects of herbicide varied across years.

Table 2.3. Analysis of deviance results showing the effects of herbicide, year, site, and their interaction on canopy cover of invasive annual grasses, litter, bare ground, invasive forbs, native forbs, perennial grasses, and seeded species.

Response Variable	Effect	Df	Deviance	Residual Df	Residual Deviance	Pr(>Chi)
Invasive Annual Grasses	Herbicide	6	10132.9	2333	78794	< 0.001***
	Year	1	4424.8	2332	74369	< 0.001***
	Site	1	25238.2	2331	49131	< 0.001***
	Herbicide:Year	5	3742.4	2326	45389	< 0.001***
Litter	Herbicide	6	2726.90	2333	44985	< 0.001***
	Year	1	588.23	2332	44397	< 0.001***
	Site	1	38.97	2331	44358	< 0.001***
	Herbicide:Year	5	1105.01	2326	43253	< 0.001***
Bare Ground	Herbicide	6	2528.79	2333	34494	< 0.001***
	Year	1	21.36	2332	34472	< 0.001***
	Site	1	297.99	2331	34174	< 0.001***
	Herbicide:Year	5	138.15	2326	34036	< 0.001***
Invasive Forbs	Herbicide	6	1382.69	2333	48977	< 0.001***
	Year	1	14.83	2332	48962	< 0.001***
	Site	1	1228.45	2331	47734	< 0.001***
	Herbicide:Year	5	76.7	2326	47657	< 0.001***
Native Forbs	Herbicide	6	962.9	2333	33465	< 0.001***
	Year	1	13014.4	2332	31175	< 0.001***
	Site	1	14070.4	2331	28658	< 0.001***
	Herbicide:Year	5	317.9	2326	28568	< 0.001***
Perennial Grasses	Herbicide	6	453.1	2333	65762	< 0.001***
	Year	1	848	2332	64914	< 0.001***
	Site	1	22482.3	2331	42432	< 0.001***
	Herbicide:Year	5	135.6	2326	42296	< 0.001***

At NVC in 2022 all herbicides reduced cover when compared to the non-sprayed check at 61.7% (95% CI: 60.3–63.2), with rimsulfuron resulting in the lowest cover at 2.6% (95% CI: 2.3–2.9) and sulfosulfuron the next lowest at 18.1% (95% CI:17.3–18.9) (Figure 2.1). Both rimsulfuron and sulfosulfuron were lower than all other herbicides tested. Glyphosate reduced IAG cover more so than imazapic and propoxycarbazone-sodium. Imazapic was only lower than propoxycarbazone-sodium. Propoxycarbazone-sodium resulted in mean IAG cover lower than the non-sprayed check but higher than all other herbicide treatments (Figure 2.1). By 2023 at NVC, indaziflam resulted in the lowest IAG cover at 19.1% (95% CI: 18.3–19.9) (Figure 2.1). The next highest reduction in IAG cover was rimsulfuron followed by sulfosulfuron. Imazapic had less IAG cover than propoxycarbazone-sodium, glyphosate, and the non-sprayed check. Propoxycarbazone-sodium was only lower than the non-sprayed check and glyphosate, which were similar to each other.

In 2022 at the PL site, IAG cover in the non-sprayed check was 15.7% (95% CI: 15.3–16.1), significantly higher than all herbicide treatments (Figure 2.1). Rimsulfuron resulted in the lowest cover at 0.7% (95%, CI: 0.6–0.7). Sulfosulfuron resulted in a mean cover of 4.6% (95% CI: 4.4–4.8), lower than glyphosate, imazapic, and propoxycarbazone-sodium. Glyphosate reduced IAG cover below that of propoxycarbazone-sodium and imazapic, and imazapic was lower than propoxycarbazone-sodium (Figure 2.1). In 2023 at PL, mean IAG cover in the non-sprayed check was 17.8% (95% CI: 17.3–18.3), which was similar to glyphosate at 18.3% (95% CI: 17.8–18.8), and propoxycarbazone at 17.0% (95% CI:16.5–17.4), and glyphosate had the highest cover of all herbicides (Figure 2.1). Sulfosulfuron and rimsulfuron reduced IAG cover relative to the non-sprayed check, and indaziflam resulted in the lowest IAG cover at 4.8% (95% CI: 4.6–5.1).

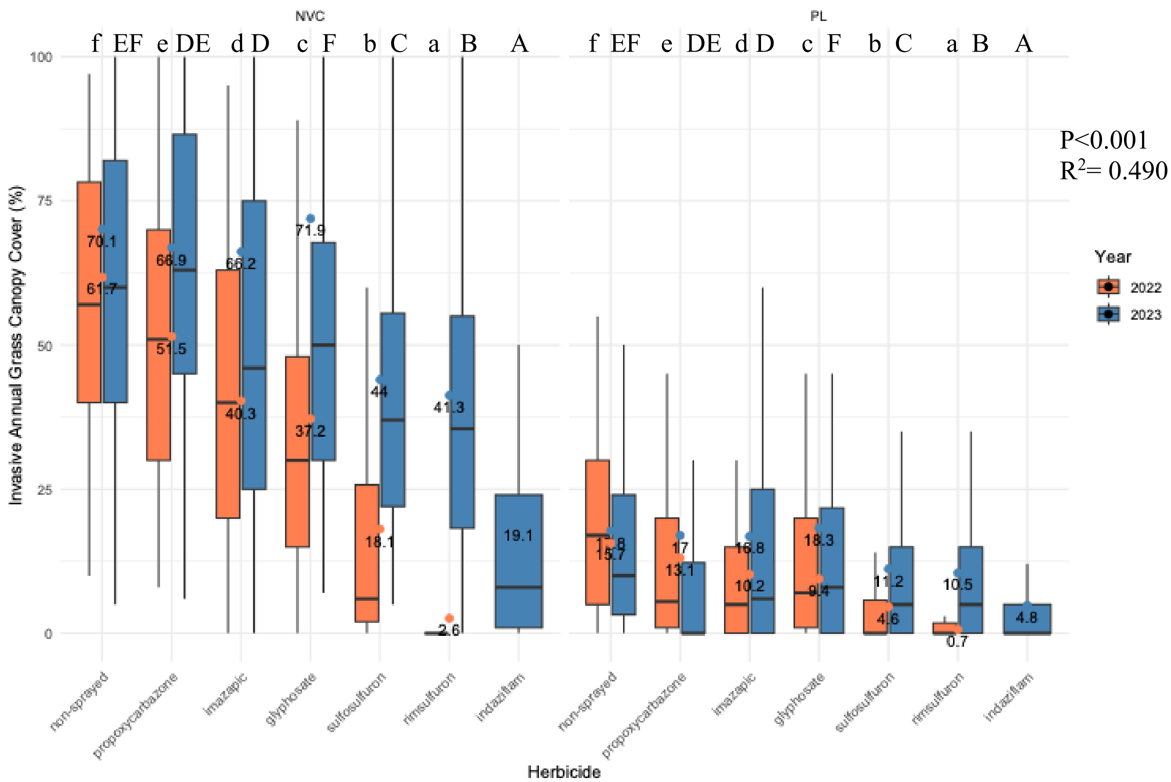

Figure 2.1. Invasive annual grass canopy cover (%) across herbicides and years (2022 and 2023) at two sites North Valley Creek (NVC, left) and Plant Lane (PL, right) in northwest Montana on the Flathead Reservation. The median is represented by the black line within the quartile box and the points for the estimated marginal mean values match the color of the year. Boxes indicate the interquartile range (IQR), covering the middle 50% of the data (25th to 75th percentile), while whiskers extend to the smallest and largest values within 1.5 times the IQR. Lower case letters are separating means across herbicide treatments within 2022 and within a site, and upper case letters separate means across herbicide treatments in 2023 and within a site.

<u>Litter Cover</u>

Herbicide treatments ($\chi^2(6) = 2726.90$, $p < 0.001$) and year ($\chi^2(1) = 588.23$, $p < 0.001$) explained variation in litter cover (Table 2.3). Site differences were also significant but accounted for a smaller portion of the deviance ($\chi^2(1) = 38.97$, $p < 0.001$). The interaction between herbicide and year was significant ($\chi^2(5) = 1105.01$, $p < 0.001$), suggesting that the effect of herbicide treatments varied across years.

At the NVC site in 2022, litter cover in the non-sprayed check was 6% (95% CI: 3.2–8.0) (Figure 2.2). All herbicides except propoxycarbazone-sodium increased litter cover, with rimsulfuron showing the highest cover at 20.4% (95% CI: 19.7–21.1). Glyphosate, imazapic, and sulfosulfuron all had similar litter cover, although sulfosulfuron was also similar to rimsulfuron. In 2023 litter cover for the non-sprayed check was 8.4% (95% CI: 6.0–10.8), and all herbicides except indaziflam were similar to each other and the non-sprayed check. Indaziflam had the highest litter cover at 21.1% (95% CI: 18.7–23.4) (Figure 2.2).

The PL site followed a similar trend as NVC in 2022, with all herbicides besides propoxycarbazone-sodium increasing litter cover compared to the non-sprayed check (Figure 2.2). Rimsulfuron and sulfosulfuron were similar to each other and had the highest cover, while imazapic and glyphosate were similar to each other and to sulfosulfuron (Figure 2.2). In 2023 litter cover for the non-sprayed check was 9.2% (95% CI: 8.7–9.6), which was similar to all herbicides except indaziflam. Indaziflam had the highest litter cover at 22.3% (95% CI: 21.6–23.1) (Figure 2.2).

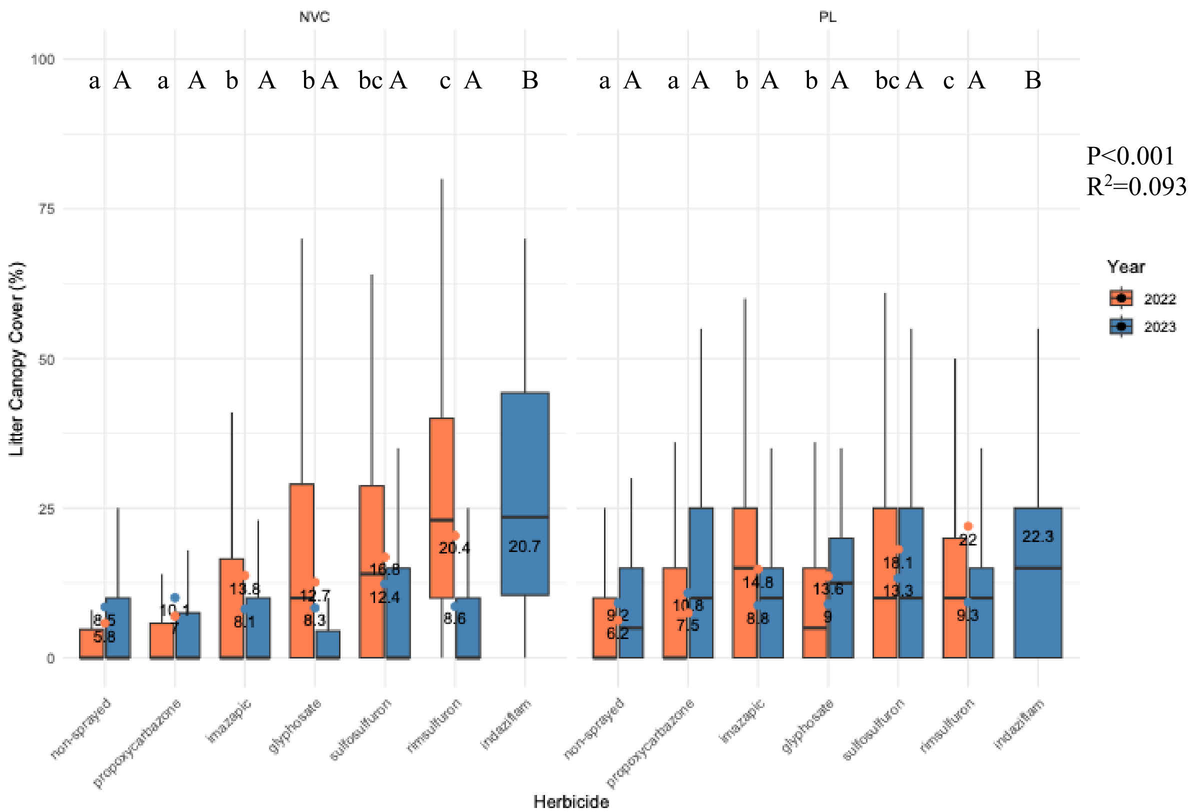

Figure 2.2. Litter canopy cover (%) across herbicides and years (2022 and 2023) at two sites North Valley Creek (NVC, left) and Plant Lane (PL, right) in northwest Montana on the Flathead Reservation. The median is represented by the black line within the quartile and the points for the estimated marginal mean values match the color of the year. Boxes indicate the interquartile range (IQR), covering the middle 50% of the data (25th to 75th percentile), while whiskers extend to the smallest and largest values within 1.5 times the IQR. Lower case letters are separating means across herbicide treatments within 2022 and within a site, and upper case letters separate means across herbicide treatments in 2023 and within a site.

<u>Bare Ground Cover</u>

Herbicide treatments ($\chi2(6)=2528.79$, $p<0.001$), year ($\chi2(1)=21.36$, $p<0.001$), and site ($\chi2(1)=297.99$, $p<0.001$) affected bare ground cover (Table 2.3). The interaction between herbicide and year was also highly significant ($\chi2(5)=138.15$, $p<0.001$), indicating that the effects of herbicide on bare ground varied across years.

At NVC in 2022, herbicide treatments were variable and none were similar to each other, but most herbicides increased bare ground compared to the non-sprayed check (Figure 2.3). Sulfosulfuron had the highest bare ground cover at 10.8% (95% CI: 10.3–11.4), followed by rimsulfuron and imazapic. Glyphosate had the lowest bare ground cover at 1.8% (95% CI: 1.6–2.0). In 2023 herbicides were still highly variable and only glyphosate and propoxycarbazone-sodium were similar to the non-sprayed check. Sulfosulfuron had the highest cover of bare ground 9.2% (95% CI: 8.7–9.7) followed by indaziflam and imazapic.

In 2022 PL showed similar trends as NVC, with sulfosulfuron having the highest bare ground cover at 7.7% (95% CI: 7.3–8.1), followed by rimsulfuron, imazapic, and propoxycarbazone-sodium (Figure 2.3). In 2023 sulfosulfuron was highest in bare ground cover at 6.6% (95% CI:6.2–6.9). Indaziflam was 5.2% (95% CI: 4.9–5.5) bare ground cover which was similar to imazapic at 4.7% (95% CI: 4.4–4.98), higher than all other treatments besides sulfosulfuron (Figure 2.3).

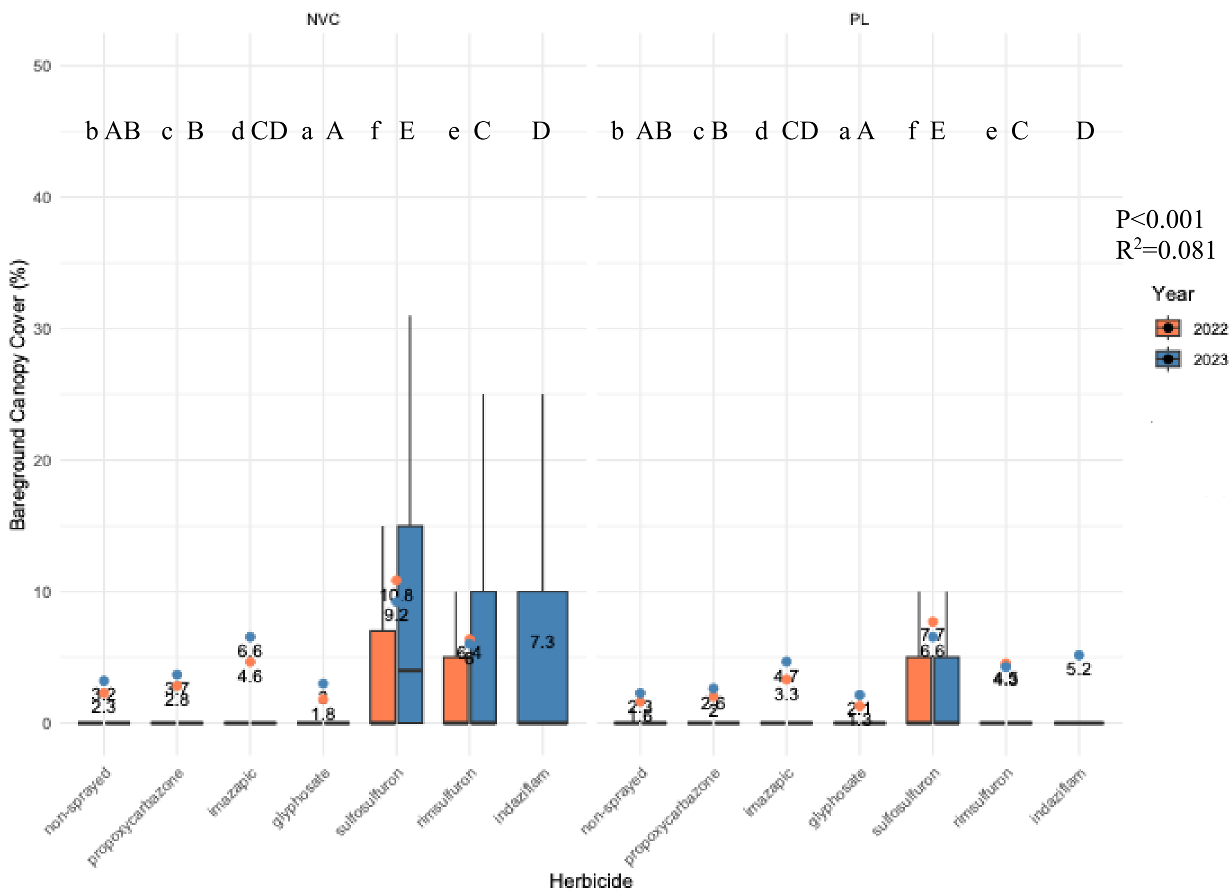

Figure 2.3. Bare ground canopy cover (%) across herbicides and years (2022 and 2023) at two sites North Valley Creek (NVC, left) and Plant Lane (PL, right) in northwest Montana on the Flathead Reservation. The median is represented by the black line within the quartile box and the points for the estimated marginal mean values match the color of the year. Boxes indicate the interquartile range (IQR), covering the middle 50% of the data (25th to 75th percentile), while whiskers extend to the smallest and largest values within 1.5 times the IQR. Lower case letters are separating means across herbicide treatments within 2022 and within a site, and upper case letters separate means across herbicide treatments in 2023 and within a site.

Invasive Forbs

Herbicide treatments significantly affected invasive forb cover ($\chi^2(6) = 1382.69$, $p < 0.001$), as did site ($\chi^2(1) = 1228.45$, $p < 0.001$) and year ($\chi^2(1) = 14.83$, $p < 0.001$) (Table 2.3). The interaction between herbicide and year was also highly significant ($\chi^2(5) = 76.70$, $p < 0.001$), indicating that the effects of herbicide on invasive forb cover varied across years.

At NVC in 2022, invasive forb cover was lowest in the non-sprayed check (20.4%, 95% CI: 19.8–21.1), imazapic (20.4%, 95% CI: 19.8–21.1), and glyphosate (21.6%, 95% CI: 21.0–22.3) (Figure 2.4). Rimsulfuron (30.9%, 95% CI: 30.1–31.8) resulted in the highest invasive forb cover across all treatments. In 2023 the non-sprayed check resulted in the lowest invasive forb cover at 18.6% (95% CI: 18.0–19.2). Glyphosate, sulfosulfuron, and imazapic were all similar to each other at about 21%. Indaziflam at 23.2% (95% CI: 22.5–23.9) and propoxycarbazone-sodium at 24.5% (95% CI: 23.8–25.3) both resulted in significantly higher invasive forb cover than the non-sprayed check, but rimsulfuron at 30.2% (95% CI: 29.4–31.0) had the highest invasive forb cover (Figure 2.4).

At PL in 2022, invasive forb cover followed a similar trend as NVC, with the non-sprayed check (27.1%, 95% CI: 26.3–28.0), imazapic (27.1%, 95% CI: 26.2–27.9), and glyphosate (28.6%, 95% CI: 27.8–29.5) all being similar to each other and resulting in the lowest invasive forb cover (Figure 2.4). Rimsulfuron invasive forb cover was 41.0% (95% CI: 40.0–42.1), which was highest of all the treatments. In 2023 invasive forb cover in the non-sprayed check was 24.6% (95% CI: 23.9–25.4), lower than all herbicide treatments (Figure 2.4). Glyphosate, sulfosulfuron, and imazapic all had similar invasive forb cover of about 27%. Indaziflam at 30.7% (95% CI: 29.8–31.6) and propoxycarbazone-sodium at 32.5% (95% CI: 31.6–33.5) both resulted in significantly higher invasive forb cover than the non-sprayed check, but rimsulfuron at 40.0% (95% CI: 39.0–41.1) had the highest invasive forb cover (Figure 2.4).

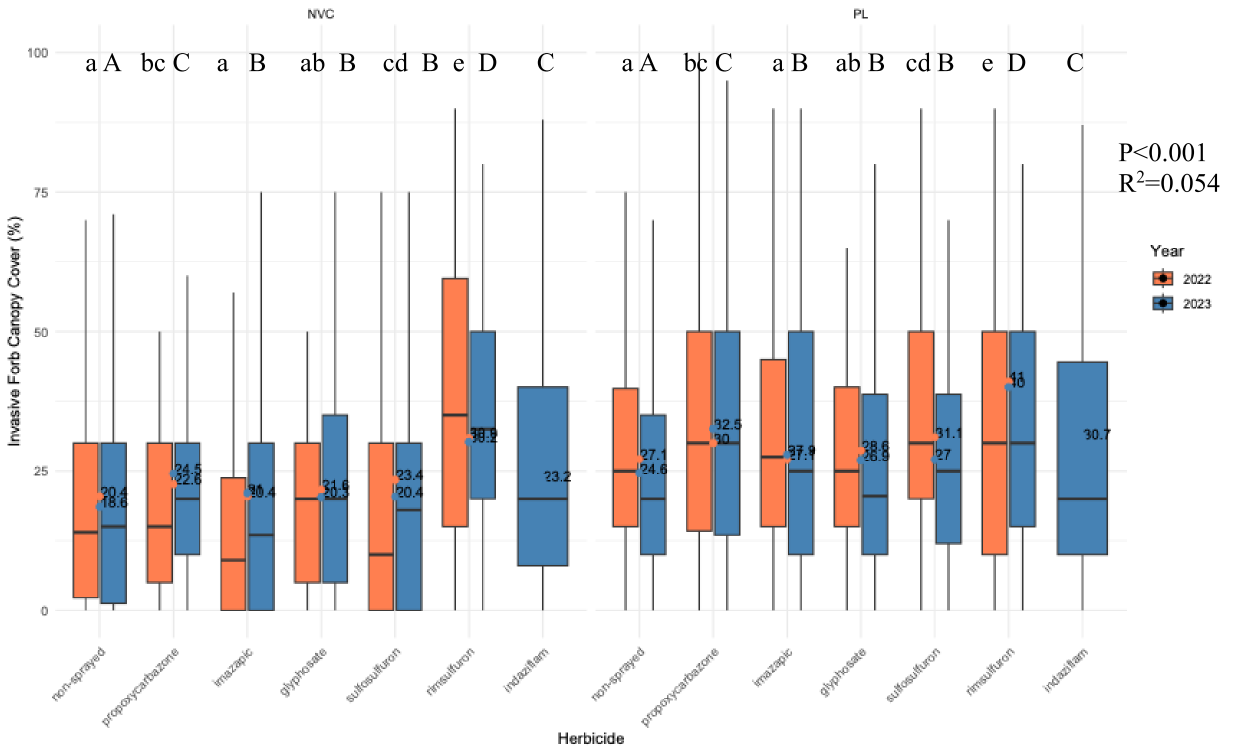

Figure 2.4. Invasive forb canopy cover (%) across herbicides and years (2022 and 2023) at two sites North Valley Creek (NVC, left) and Plant Lane (PL, right) in northwest Montana on the Flathead Reservation. The median is represented by the black line within the quartile box and the points for the estimated marginal mean values match the color of the year. Boxes indicate the interquartile range (IQR), covering the middle 50% of the data (25th to 75th percentile), while whiskers extend to the smallest and largest values within 1.5 times the IQR. Lower case letters are separating means across herbicide treatments within 2022 and within a site, and upper case letters separate means across herbicide treatments in 2023 and within a site.

Native Forbs

Herbicide treatments significantly reduced native forb cover ($\chi2(6)=2528.79$, $p<0.001$), as did year ($\chi2(1)=21.36$, $p<0.001$) and site ($\chi2(1)=297.99$, $p<0.001$) (Table 2.3). The interaction between herbicide and year was also highly significant ($\chi2(5)=138.15$, $p<0.001$), indicating that the effects of herbicide on native forbs varied across years.

In 2022 at NVC, native forb cover in the non-sprayed check was 11.6% (95% CI: 10.98–12.2) with sulfosulfuron, rimsulfuron, and propoxycarbazone all being similar and ranging from 10.4% to 12.4%. Glyphosate and imazapic resulted in higher native forb cover compared to the non-sprayed check, and similar to propoxycarbazone-sodium (Figure 2.4). By 2023 at NVC, native forb cover in the non-sprayed check was 3.8% (95% CI: 3.5–4.2), which was similar only to sulfosulfuron at 3.6% (95% CI: 3.3–3.9). Glyphosate (4.8%, 95% CI: 4.5–5.2) and propoxycarbazone-sodium (4.8%, 95% CI: 4.5–5.2) both had higher native forb cover than the non-sprayed check. Imazapic, rimsulfuron, and indaziflam resulted in the highest native forb cover and ranged from 6.1% to 6.7% (Figure 2.4).

At PL in 2022, native forb cover in the non-sprayed check, sulfosulfuron, rimsulfuron, and propoxycarbazone-sodium was similar and ranged from 4.2% to 5.0% (Figure 2.4). Glyphosate (5.2%, 95% CI: 4.9–5.5) and imazapic (5.3%, 95% CI: 4.97–5.6) had the highest native forb cover. By 2023 native forb cover in the non-sprayed check and sulfosulfuron was similar at 1.5% (95% CI: 1.4–1.7) and 1.4% (95% CI: 1.3–1.6), respectively. Glyphosate and propoxycarbazone-sodium (1.95%, 95% CI: 1.8–2.1) resulted in identical cover. Imazapic, rimsulfuron, and indaziflam were similar and had the highest native forb cover, ranging from 2.4% to 2.7% (Figure 2.4).

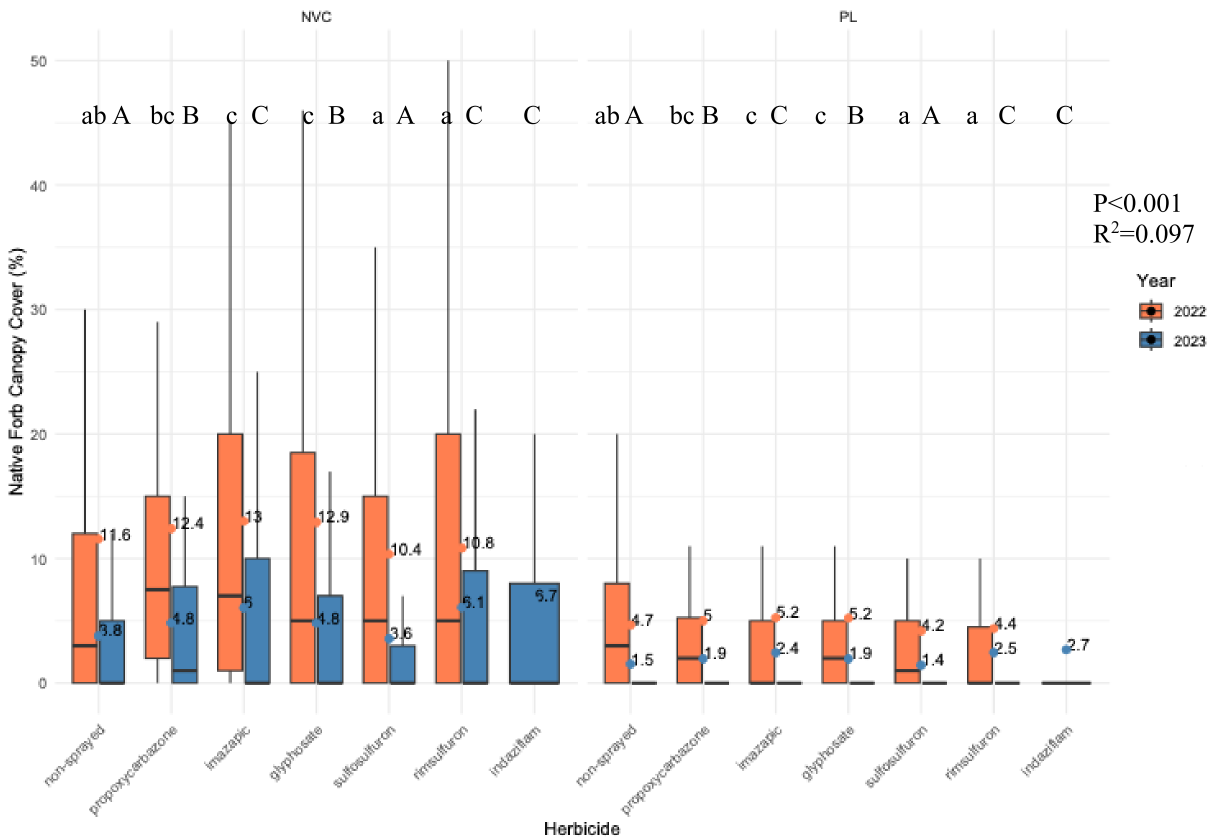

Figure 2.5. Native forb canopy cover (%) across herbicides and years (2022 and 2023) at two sites North Valley Creek (NVC, left) and Plant Lane (PL, right) in northwest Montana on the Flathead Reservation. The median is represented by the black line within the quartile box and the points for the estimated marginal mean values match the color of the year. Boxes indicate the interquartile range (IQR), covering the middle 50% of the data (25th to 75th percentile), while whiskers extend to the smallest and largest values within 1.5 times the IQR. Lower case letters are separating means across herbicide treatments within 2022 and within a site, and upper case letters separate means across herbicide treatments in 2023 and within a site.

Perennial Grasses

Herbicide treatments ($\chi2(6)=453.1$, $p<0.001$), as did year ($\chi2(1)=848.0$, $p<0.001$), and site ($\chi2(1)=22482.3$, $p<0.001$) affected perennial grass cover (Table 2.3). The interaction between herbicide and year was also highly significant ($\chi2(5)=135.6$, $p<0.001$), indicating that the effects of herbicide on perennial grass cover varied across years.

In 2022 at NVC, rimsulfuron resulted in the highest perennial grass cover at 10.6% (95% CI: 10.3–10.98) followed by sulfosulfuron, imazapic, and glyphosate that ranged from 8.9% to 9.4%. Propoxycarbazone-sodium at 7.8% (95% CI: 7.5–8.1) resulted in the lowest perennial grass cover across herbicides and was lower than the non-sprayed check. In 2023 perennial grass cover was highest in indaziflam at 13.0% (95% CI: 12.6–13.4), glyphosate at 12.3% (95% CI: 11.9–12.7), and the non-sprayed check at 12.8% (95% CI: 12.4–13.2). Rimsulfuron, sulfosulfuron, and imazapic were all similar and lower than the non-sprayed check. Propoxycarbazone-sodium (10.4%, 95% CI: 10.1–10.8) resulted in the lowest cover (Figure 2.5).

At PL in 2022, perennial grass cover was highest in the rimsulfuron treatment at 41.2% (95% CI: 40.1–42.4) followed by imazapic, glyphosate, and sulfosulfuron, and sulfosulfuron was similar to the non-sprayed check. Propoxycarbazone-sodium resulted in the lowest cover (30.3%, 95% CI: 29.3–31.3), even lower than the non-sprayed check (32.9%, 95% CI: 31.8–33.97). In 2023 indaziflam (50.4%, 95% CI: 49.09–51.74), glyphosate (47.8%, 95% CI: 46.5–49.1) and the non-sprayed check (49.6%, 95% CI: 48.3–51.0) had the highest perennial grass cover, while propoxycarbazone-sodium (40.5%, 95% CI: 39.3–41.7) again resulted in the lowest perennial grass cover (Figure 2.5).

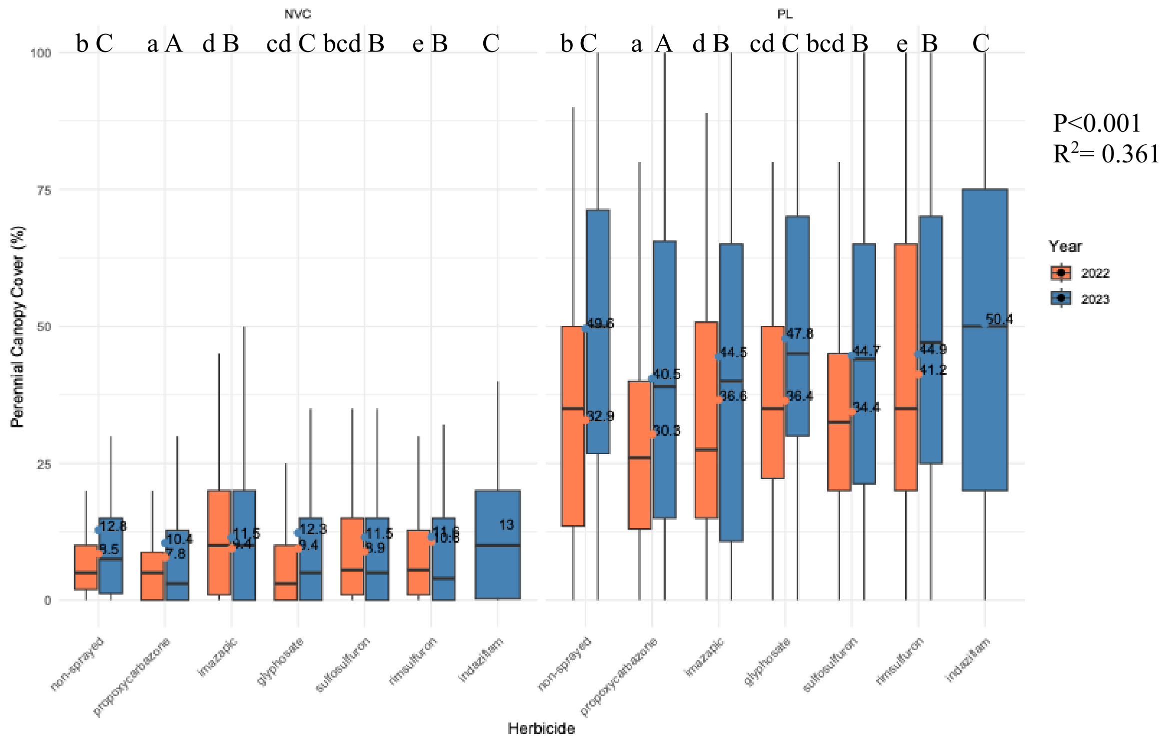

Figure 2.6. Perennial grass canopy cover (%) across herbicides and years (2022 and 2023) at two sites (North Valley Creek and Plant Lane) in northwest Montana on the Flathead Reservation. The median is represented by the black line within the quartile box and the points for the estimated marginal mean values match the color of the year. Boxes indicate the interquartile range (IQR), covering the middle 50% of the data (25th to 75th percentile), while whiskers extend to the smallest and largest values within 1.5 times the IQR. Lower case letters are separating means across herbicide treatments within 2022 and within a site, and upper case letters separate means across herbicide treatments in 2023 and within a site.

Seeded Species Frequency

Geranium maculatum had 12 seedlings in 2022, with five seedlings in the propoxycarbazone-sodium plots at NVC and seven seedlings at PL with three in the rimsulfuron plots and four in sulfosulfuron. Ten seedlings of *Cleomella serrulata* were found in 2022 and only in the rimsulfuron and sulfosulfuron treatments at NVC. *Gaillardia aristata* had six seedlings across both sites. *Pseudoroegneria spicata* was represented by one individual in 2022 in a glyphosate plot at PL. Only three individual seedlings of *F. idahoensis* were found at NVC in 2022; however, each seedling was found in a different treatment. *Dalea purpurea* had one seedling in 2022 at PL, and *L. argenteus* also only had one seedling but at NVC. No individuals of *P. tridentata*, or *E. nauseusa* were observed in either 2022 or 2023. No species were found in the imazapic or the indaziflam treatments, and no seedlings of any species were observed (within the frames) in 2023.

Ranked Abundance of In-situ Species

Both sites were dominated by non-native or noxious species, with *Potentilla recta*, *V. dubia*, *Poa compressa*, and *Centaurea stoebe* ranking highest in cover at 19%, 18.3%, 17.8%, and 10%, respectively. At NVC *V. dubia* had the highest abundance by cover at 27.9%, *P. recta* had 25.5%, *B. tectorum* at 10.0%, and *B. japonicus* at 9.1% (Figure 2.7). At PL *P. compressa had* 32.8% abundance by cover, and *C. stoebe* had 19.8%, *P. recta* was third highest in abundance at 13.4%, and V. dubia at 9%. The most abundant native species was *P. spicata*, ranking 11 overall, 15 at NVC (1% cover) and 8 at PL (3% cover). The least abundant native species was *F. idahoensis* ranking 55 (.0024% cover) across both sites.

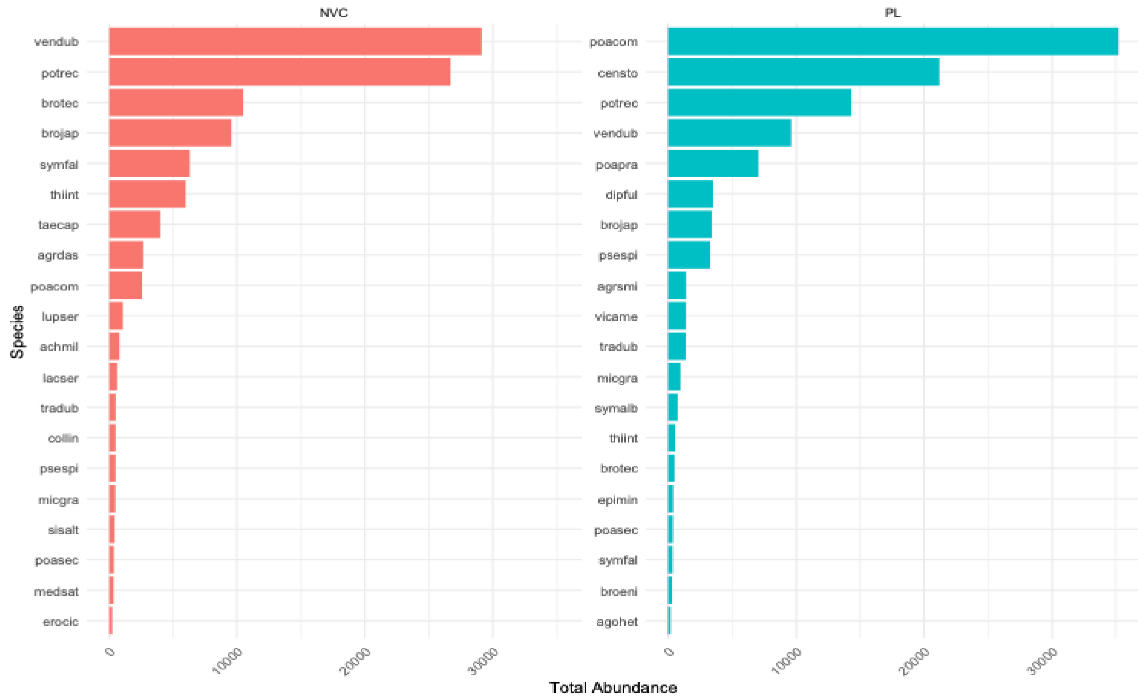

Figure 2.7. Top 20 most abundant plant species by total abundance (cover %) at two sites (North Valley Creek and Plant Lane) on the Flathead Reservation in northwest Montana. Bars represent the summed cover of each species across all herbicide treatments and years. Species are ordered by most abundant to least abundant. Species names corresponding to the six-letter codes on the y-axis (e.g. *Centaurea stoebe*=censto).

Discussion

Herbicides usually reduced IAG cover compared to the non-sprayed check, especially in 2022, supporting our hypothesis that herbicide treatments would lead to decreased IAG cover across treatments. Rimsulfuron consistently emerged as the most effective herbicide in reducing IAG cover and increasing litter. Rimsulfuron applied pre-emergence was particularly effective in the first growing season after application, demonstrating 96% control across both sites. In a previous study done in the Intermountain Pacific Northwest on *V. dubia*, rimsulfuron applied pre-emergence and early post-emergence provided over 90% control, demonstrating high efficacy in managing *V. dubia* in both application timings (Wallace and Prather 2016). Wallace and Prather (2016) also found negligible herbicide injury to *P. spicata* and *T. intermedium* within the rimsulfuron treatments. This suggests that rimsulfuron is effective for IAG control while being less injurious to certain perennial grass species making it a potentially suitable choice for integrated management strategies in invaded perennial grass systems.

In 2022 the sulfosulfuron treatment had the next most efficacious control at approximately 71% control across both sites. Field trials in Idaho demonstrated that sulfosulfuron (53 g ai ha^{-1}) provided over 90% control of *V. dubia* nine months after treatment with minimal effects on the native perennial grasses *P*. *spicata* and *T*. *intermedium* (Wallace and Prather, 2016). In other research sulfosulfuron consistently caused injury to wildryes (*Leymus* and *Psathyrostachys* spp.), and *Bromus inermis*, suggesting that rhizomatous grasses were more susceptible with minimal negative effects observed on wheatgrass species (e.g., *Agropyron* spp.) and bunchgrasses (Monaco and Creech, 2004).

In this study, first year control of IAG with glyphosate was 40%, substantially lower than what was anticipated. Better first year control and lower second year control was expected (Espeland and Kilian, 2015; Morris, 2016). A study in the Great Basin grasslands, with data collected over a two-year period, glyphosate alone reduced *B. tectorum* cover by 78% (from 45% to 10%), while the combination of glyphosate and imazapic achieved a 98% reduction (reducing cover to approximately 1%). Perennial grass cover was unaffected by glyphosate alone but initially reduced by imazapic, recovering by the second year (Morris, 2016). In a different study focused on glyphosate for annual *Bromus* spp. control on grassland in eastern Montana, the use of low-dose glyphosate (210 g ha−1) applied once in fall reduced *B. tectorum* cover and seed bank density initially, but after a second year of treatment *B. tectorum* no longer responded to the herbicide (Espeland and Kilian, 2015). In my study, similar to glyphosate, first year control for imazapic was only 35%, far lower than was expected. In field studies conducted at both an old-field and a rangeland site, imazapic had effective control with more than 95% reduction in *Bromus* spp. biomass (Orloff et al., 2015). The most underperforming herbicide in my study was propoxycarbazone-sodium where control was minimal at only 17% in the first year. In a study in the Intermountain Pacific Northwest, propoxycarbazone-sodium provided moderate control of *V. dubia*, achieving 77–88% effectiveness in early post-emergence applications, though its performance was notably more variable compared to other herbicides like sulfosulfuron and rimsulfuron (Wallace and Prather, 2016).

In regard to indaziflam and the assumption that it would exhibit superior efficacy in controlling IAG compared to other herbicides, it only achieved 71% control of IAG, much lower than levels of control reported in other field studies (Sebastian et al., 2016, 2017; Clark et al., 2020; Terry et al., 2021; Courkamp et al., 2022). Some studies have demonstrated that indaziflam provides superior and long-lasting control of IAG compared to glyphosate, imazapic, and rimsulfuron. For example, Sebastian et al. (2016) reported 89–100% control at 2 years after treatment (YAT) and 83–100% control at 3 YAT with indaziflam, while imazapic's effectiveness declined to 45–64% at 2 YAT and 10–32% at 3 YAT. Glyphosate and rimsulfuron under-performed both indaziflam and imazapic. However, another study conducted at three sites in the sagebrush steppe of Utah, reported that indaziflam reduced *B. tectorum* cover by 70% (to 10% cover) in the first year and maintained this level of control consistently over two years. In contrast, imazapic initially reduced *B. tectorum* cover by 88% (to 4% cover) but declined significantly to just 20% control by the second year, highlighting the longer-lasting efficacy of indaziflam; however, indaziflam caused a 96% reduction in emergence of *P. spicata* and a 91% decrease in plant density (Terry et al., 2021). Notably, in my study IAG control provided by indaziflam the first season after application (2023) was similar to that of sulfosulfuron and lower than that of rimsulfuron the first season after their applications (2022). It is important to recognize that indaziflam was sampled only once and applied post-seeding, offering a unique point of comparison on non-target effects than other herbicides evaluated. Long term monitoring would be helpful to inform managers of the impacts of indaziflam applied post seeding to the ability for seedlings to establish (Buell, 2021; González-Delgado and Shukla, 2020; Fowers and Mealor, 2020).

By 2023 both rimsulfuron and sulfosulfuron showed decreased effectiveness in reducing IAG cover, yet still provided some residual control into the second growing season at 41% and 37% control, respectively, relative to the non-sprayed check. However, without sustained depletion of the IAG seedbank, the risk of reinvasion remains high, potentially undermining the effectiveness of these treatments in the long term. Effective management of the IAG seedbank is essential to prevent reinvasion and achieve lasting control of IAG, as previous studies have demonstrated the challenges posed by seedbank persistence (Sebastian et al., 2017; Rinella et al., 2012). A field study in Colorado demonstrated that four to five consecutive years of glyphosate applications were necessary to effectively deplete the *B. tectorum* soil seed bank and prevent recovery (Sebastian et al., 2017). This multiyear approach not only controlled *B. tectorum* but also resulted in a 4 to 9-fold increase in perennial grass biomass, underscoring the importance of targeting the seed bank for sustainable IAG management.

All herbicides except propoxycarbazone-sodium resulted in higher litter accumulation compared to the non-sprayed check in 2022, and by the following year all herbicides were similar. Sulfosulfuron produced the most litter; however, litter production raises concerns about the potential for increased fire risk and challenges in native species establishment (Bansal et al., 2014; Fusco et al., 2019). Litter has been shown to play a role in the successful germination and establishment of *B. japonicus* (Baskin and Baskin, 1981). Abundant litter helps retain soil moisture, which compensates for low precipitation levels (Baskin and Baskin, 1981; Beck, 2009). Conversely, when both litter and precipitation are scarce, germination and subsequent seedling establishment of both IAG and desirable species can be reduced (Beck, 2009). The increase in litter production with sulfosulfuron indicates the necessity for integrated management strategies that include timely removal or incorporation of litter to promote the recovery of desirable vegetation (Bansal et al., 2014).

The non-sprayed check typically resulted in the least alteration to bare ground, as expected, providing a reliable baseline for comparison. Imazapic, rimsulfuron, and sulfosulfuron were the three herbicides that increased bare ground in 2022 and in 2023, demonstrating their efficacy in reducing vegetative cover. However, this increase was not accompanied by a rise in seeded species frequency or other functional groups, and bare ground levels remained generally low and minimally affected by treatment. While these findings suggest limited impact overall to bare ground, large increases in bare ground may raise concerns about soil erosion and habitat degradation, necessitating swift revegetation with desirable species (Scotton and Andreatta, 2021). Seemingly, we simply reduced IAG cover without much change in any other functional groups; highlighting the need for long term monitoring when concerned with temporal community composition changes or suitability of habitat (Adhikari, 2023; Monaco et al., 2017).

In our efforts to manage IAG, one of our primary concerns is ensuring that herbicides do not negatively impact any desirable non-target species co-occurring with IAG. Our results showed that the herbicides used had no adverse effects on perennial grass or native forb cover when compared to the non-sprayed check. This is an encouraging outcome, as it demonstrates the potential for using these herbicides to manage IAG while maintaining the integrity of desired perennial species, which are essential for long-term ecosystem resilience (Monaco et al., 2017). At the same time, perennial grasses did not increase consistently across herbicides in response to removal of IAG as has been shown in other research (Fowers and Mealor, 2020; Monaco et al., 2017). The study sites currently have significantly lower perennial grass cover compared to the historical range of 65-90% (Mueggler, 1980, 1983). The dominant perennial grass species at the sites are *T. intermedium*, *P. compressa*, and *P. pratensis*, all of which are introduced species. Herbicides can create an initial reduction in competition that allows perennial grass species to flourish and potentially suppress invasive plants, as observed in previous studies (Rose et al., 2001). However, invasive species often recover within one to five years especially if the area is not adaptively managed, indicating that herbicide treatments alone may not provide long-term control (Rinella et al., 2012). This highlights the importance of combining herbicide use with additional management strategies for sustained invasive suppression (Monaco et al., 2017).

Regarding the hypothesis that seedling abundance would be higher when herbicide treatment resulted in reduced IAG cover, seeded species frequency was consistently low to negligible across all herbicide treatments in 2022 and 2023, regardless of the reductions in IAG cover and higher bare ground and litter. The seeding treatment largely failed, with species not establishing in sufficient numbers preventing pairwise comparisons or a comprehensive statistical assessment of treatment effects on their frequency. Consequently, the hypothesis that seeded species would occur more frequently when herbicides reduced IAG and increased bare ground and litter was rejected. However, seeded species also did not establish in the non-sprayed check, which made it impossible to isolate treatment effect on seeded species abundance.

There are numerous factors that could have resulted in seeding failure, such as precipitation patterns, seed predation, and freeze/thaw cycles, all of which can hinder germination and growth (Mummey, 2016; Qasem, 2019). The warmer and drier conditions, early snowmelt runoff, and moderate drought conditions in northwest Montana during 2022-2023 likely had a substantial negative impact on our seeding efforts (Montana Department of Natural Resources and Conservation, 2023). The drier conditions were reflected in the observed decline of in-situ native forbs from 2022 to 2023, underscoring the need to consider ongoing site-specific climatic trends. Limited soil moisture and persistently dry conditions make it difficult for seeds of any kind to germinate and establish successfully (Belnap et al., 2016; Qasem, 2019).

Understanding the soil feedback interactions is crucial for developing effective restoration strategies that combine herbicide application with seeding of native species. To improve restoration success, various seeding technologies are being explored, including inoculations with arbuscular mycorrhizal fungi, which enhances plant nutrition and growth (Neuenkamp et al., 2019) while markedly improving resilience to drought and heavy metal stress (Pavithra and Yapa, 2018). The use of herbicide protection pods, seed coatings to improve germination rates and to shield seedlings from herbicide with extended soil activity, may be another promising tool for enhancing restoration efforts in annual grass-invaded grasslands by reducing early competition and fostering native perennial establishment (Clenet et al., 2019). By identifying and mitigating the factors limiting native species emergence, we can enhance the success of restoration efforts and achieve more resilient ecosystems that resist invasion by non-native species (Qinfeng et al., 2018; Mangold, 2012; Mangold et al., 2007, 2015).

Our study underscores the variability in herbicide effectiveness against IAG. Rimsulfuron, sulfosulfuron, and indaziflam were the most effective herbicides in reducing IAG, underscoring their potential as valuable management tools. These findings have important implications for land managers seeking to control IAG. However, because of the variability of natural ecosystems and the impacts herbicides have been shown to have on native seedlings (Clark, 2020; Crose, 2022), studies in more controlled conditions like a greenhouse are needed to isolate herbicide effects on seeded species and how they can potentially impact revegetation (Chapter 3). Future research should focus on understanding not just environmental factors influencing herbicide efficacy but exploring integrated management approaches combining chemical, mechanical, and biological control. This holistic approach will be necessary for sustainable management of invasive annual grasses (Harvey, 2019; Menalled et al., 2008; Orloff et al., 2015).

Given the limited, short-term effectiveness of our herbicide treatments and the challenges faced with successful seeding, future management efforts should prioritize the containment of IAG on CSKT’s Intermountain foothill grasslands. Since control measures provide temporary relief rather than a long-term solution, preventing the further spread of IAG becomes essential (Cherr, 2009; Blank and Sforza, 2007). Establishing containment zones could help restrict early populations to a small area within the state, working towards eventual eradication. Implementing early detection and rapid response (EDRR) strategies outside of this containment zone would be crucial for managing any new populations (Smith and Sheley, 2015; Davies and Johnson, 2008). Additionally, integrating forb, grass, and shrub restoration with invasive species control measures by tribal, state, federal, and private managers is vital to prevent IAG from dominating new areas, with an emphasis on minimizing damage to native species.

CHAPTER THREE

EVALUATING HERBICIDE IMPACTS IN A GREENHOUSE SETTING: NATIVE SEEDLING EMERGENCE, BIOMASS, AND INJURY RESPONSES

Introduction

The Intermountain foothill grasslands of northwest Montana, historically rich with diverse plant and animal life, remain ecologically significant despite facing increasing pressure from invasive annual grasses that threaten their biodiversity and disrupt their natural balance (Wallace and Prather, 2016; Wallace et al., 2015; Jones et al., 2020). Grasslands play a critical role in maintaining biodiversity, regulating nutrient cycling, supporting pollinator populations, and providing habitat for a wide range of plant and animal species (Habeck, 1987; Knight, 2014; Schickhoff, 2011). The Intermountain foothill grasslands have long provided vital sources of sustenance and spiritual connection for Indigenous communities, and they continue to support the livelihoods and well-being of the broader populations that now inhabit these lands (Anderson and Moratto, 1996; Stumpff et al., 2020; personal communication Frank Finley, 2020, Salish; personal communication Virgil Dupuis, 2018, Kootenai).

Invasive annual grasses (IAG) pose significant threats to the ecological balance of the grasslands and their associated cultural connection (Rai, 2022; Davies et al., 2015). Winter annual grass species like cheatgrass (*Bromus tectorum* L.) are among the most prevalent invaders in grasslands across western North America where millions of hectares have converted to near monocultures (Bradley et al., 2018; Molvar et al., 2024). Ventenata (*Ventenata dubia* (Leers)

Coss. & Durieu) and medusahead wildrye (*Taeaniatherum caput-medusae* (L.) Nevski) are increasingly co-occurring with *B. tectorum* and other annual *Bromus* spp. like *Bromus japonicus* Thunb. (Davies et al., 2015; Jones, 2018). Invasive annual grasses outcompete native plant species by exploiting environmental changes and efficiently utilizing resources such as sunlight, water, and nutrients, leading to reduced growth and reproduction in native plants, and in severe cases, displacement and biodiversity decline (Fagúndez and Lema, 2019; Westbrooks, 1998).

The loss of native plant diversity reduces forage for livestock and habitat for native wildlife and pollinators (Molvar et al., 2024). Invasive annual grasses can also alter soil composition, nutrient cycling, hydrological processes, and plant community structure (Baer, et al., 2003; Bansal et al., 2014). More specifically, rapid growth demonstrated by IAG leads to abundant biomass and accumulation of organic matter on the soil surface, forming a thick litter layer (Evans and Young, 1970; Bansal et al., 2014). Alternatively, attempts to control IAG can alter vegetation cover and soil microbial communities, which influence plant community dynamics by providing opportunities for either native species to re-establish, or more likely, further invasion by non-native species (Ralphs, 1995; Reitstetter and Rittenhouse, 2017). Addressing these challenges, including the disruption of nutrient cycling, alteration of soil structure, and increased vulnerability to further invasion, is essential for the conservation and restoration of threatened grassland ecosystems (Hobbs 1992; Gaskin et al., 2021).

Herbicides are commonly used to manage IAG because they are effective, simple to apply, and produce noticeable results (Sebastian et al., 2016, 2017; Wallace and Prather, 2016; Mangold et al., 2013). Some herbicides commonly applied to IAG are indaziflam (Rejuvra® Bayer), rimsulfuron (Matrix® SG, DuPont™), sulfosulfuron (Outrider® Monsanto), and imazapic

(Plateau®, BASF Corporation) (Nyamai et al., 2011; Barnes, 2007; Endress et al., 2012). Indaziflam, a non-selective Group 29 herbicide classified as a Cellulose Biosynthesis Inhibitor (CBI), targets seeds during germination by affecting the radicle as it emerges from the seed (Sebastian et al., 2016, 2017; Brabham et al., 2014). Rimsulfuron and sulfosulfuron are Group 2 herbicides that inhibit acetolactate synthase (ALS) enzyme activity, leading to the accumulation of toxic compounds in susceptible plants (Tranel, 2002; Butler et al., 2007; Shimizu et al., 2002). Imazapic is also a Group 2 herbicide and inhibits the synthesis of branched-chain amino acids by interfering with ALS enzyme activity (Tranel, 2002; Sharma, 2020).

Herbicides, including those used in IAG management, vary widely in their selectivity and persistence in the soil (Ismail and Kalithasan, 1997; Mangold et al., 2013). Some herbicides are highly selective, targeting specific plant types while sparing others, while others have broad-spectrum effects (Koning, 2019). Selectivity can also depend on the timing and frequency of application (Jablonkai, 2015). Herbicides with lower persistence offer shorter-term control compared to those with higher persistence (Upchurch, 1966). For example, imazapic, rimsulfuron, and sulfosulfuron may only provide one to two years of control (Wallace and Prather, 2016; Burnett and Mealor, 2015) while indaziflam has been shown to provide multiple years of control (Fowers and Mealor, 2020; Clenet et al., 2019; Mangold et al., 2024). While all herbicides discussed here offer valuable tools for integrated weed management in grassland restoration, indaziflam's higher soil persistence requires more cautious use in revegetation efforts. Its longer-lasting effects can benefit invasive species control yet demands consideration for potential impacts on native seedlings (Burnett and Mealor, 2015; Vicari, 1994; Eleftherohorinos, 2004; McManamen et al., 2018; Boutin, 2020; Gaskin et al., 2021).

Revegetation, particularly in areas with less than 20% native cover, is essential for restoring ecosystem function and structure, reducing conditions favorable to invasive species, and enhancing biodiversity (Mangold, 2012; Kettenring and Adams, 2011; Cavieres, 2021). Herbicides with higher selectivity and lower persistence may be more desirable when used during revegetation (Gaskin et al., 2021). Previous studies have shown that herbicides can impair the germination and biomass of native species, with particularly negative effects observed when seeding follows herbicide application rather than preceding it (Davies et al., 2024; McManamen et al., 2018). This timing difference suggests that applying herbicides after seeding may lead to higher establishment rates and improved plant health.

Despite these challenges, revegetating IAG-infested grasslands remains critically necessary, though success rates are often low (Madsen et al., 2013). It is important to understand how herbicides used to control IAG affect both target species and non-target native species during the vulnerable seedling stage. In a controlled greenhouse setting, I examined how four herbicides affect the emergence, biomass, and injury (rank 0-4), of 12 desirable, culturally important, and native species found in the Intermountain foothill grasslands in northwest Montana. Isolating the effects of different active ingredients on the emergence, biomass, and injury of native plant species in a greenhouse setting can inform management strategies in the field where additional factors like drought, predation, and competition might limit seeded species establishment. I hypothesized that, across all species, all herbicides would reduce seedling emergence and biomass and increase injury compared to the non-sprayed check. Additionally, I expected that the greatest reduction in emergence and biomass, as well as the highest injury levels, would occur with indaziflam, followed by imazapic, rimsulfuron, and sulfosulfuron.

Methods

The study was conducted over the course of four trials that occurred from 3 February 2023 to 5 January 2024 in a greenhouse in the Plant Growth Center (PGC) at Montana State University (MSU), Bozeman, Montana (45.6682° N, 111.0533° W). The study considered two main factors: herbicide treatments and seeded plant species treatments, hereafter referred to as herbicide and species, respectively. There were five levels of herbicide (including a non-sprayed check) and up to 12 levels of species, depending on the trial. Eight species were tested in trial 1, while trials 2-4 included 12 species (Table 3.1).

A restricted randomization complete factorial design was used, where all possible herbicide and species combinations were included and the assignment of treatment tray position on the greenhouse table was randomized at the beginning of each trial. There were four trials with each trial lasting 36-40 days, during which species were allowed to germinate, emerge, and develop under the specified conditions. Species were grown in 10 cm^3 “Cone-tainers”™ (hereafter referred to as cones) with 3-4 trays/herbicide, 96 cones/tray, 32 cones/species/tray, and 5 seeds/cone (n=640). In total, there are 15 trays in trial 1 and 20 trays in trials 2-4.

The herbicides included indaziflam (Rejuvra® Bayer) applied at 93 g a.i./ha, rimsulfuron (Matrix® SG, DuPont) applied at 53 g a.i./ha, sulfosulfuron (Outrider® Monsanto) applied at 53 g a.i./ha, and imazapic (Plateau®, BASF Corporation) applied at 105 g a.i./ha. Herbicides were chosen based on previous IAG chemical control research, common management practices, and followed the labeled application rates (Mangold et al., 2013; Rice and Toney, 1998; Wallace and Prather, 2016; Mangold et al., 2024). Herbicide was applied using a Generation III® research track sprayer (DeVries Manufacturing, Hollandale, MN) equipped with a TeeJet® 8002 EVS flat-fan spray nozzle (TeeJet Spraying Systems Co., Wheaton, IL), and calibrated to deliver 187 L ha^{-1} at 172 kPa. Trays were placed so that the tops of the cones were 36 cm from nozzle. All herbicides were applied directly to bare soil before seeding.

Species included up to 12 native plant species (Table 3.1). Each cone was planted with five seeds of a single species one day following herbicide application. Seeds were placed on top of the soil, covered with 1.0 cm of light sandy soil, and allowed to grow for 36-40 days, depending on the trial. Seeds of each species were purchased from Stevenson Intermountain Seed in Ephraim, Utah, and Bruce’s Seed Farm in Townsend, Montana. Species were chosen based upon their ecological and cultural relevance to grassland restoration efforts and to align with the species used in a field study (Chapter 2). Further selection criteria were based upon historic vegetation characteristics and flower accessibility for local pollinator species. For those species that required cold stratification (Shi et al., 2022), prior to each trial seeds were placed in sealed containers and refrigerated at 1.7°C for 37 days (Table 3.1).

Table 3.1. Latin name, common name, cultivar, and stratification requirements for selected plant species used in study along with trial number species were used. (VNS=variety not stated)

Latin Name & Authority	**Common Name**	**Cultivar**	**Strat**	**Trial**
Cleomella (Peritoma) serrulata (Pursh) Roalson & J.C. Hall (2015)	Rocky Mountain bee plant	VNS	yes	1, 2, 3, 4
Dalea purpurea Vent.	purple prairie clover	Kaneb	yes	1, 2, 3, 4
Gaillardia aristata Pursh	blanket flower	Meriwether	no	1, 2, 3, 4
Geranium maculatum Fisch & C.A. Mey.	Wild Geranium	VNS	yes	1, 2, 3, 4
Helianthus annuus L.	annual sunflower	VNS	no	2, 3, 4
Linum lewissi Pursh	Lewis flax	Maple Grove	yes	1, 2, 3, 4
Lupinus argenteus Pursh	Mountain lupine	Rubrucaulis	yes	1, 2, 3, 4
Festuca idahoensis Elmer.	Idaho fescue	Nezpurs	no	2, 3, 4
Leymus cinereus (Scribn. & Merr.) A. Love	basin wildrye	VNS	no	2, 3, 4
Pascopyrum smithii	western wheatgrass	VNS	no	2, 3, 4
Pseudoroegneria spicata (Pursh) Á. Love (1980)	bluebunch wheatgrass	Goldar	no	1, 2, 3, 4
Thinopyrum intermedium (Host) Barkworth & D.R. Dewey	Intermediate wheatgrass	VNS	no	1, 2, 3, 4

Each cone was filled with MSU PGC soil medium without any further amendments. The soil mixture includes equal parts (by volume) of loam soil, washed concrete sand, and Canadian Sphagnum peat moss with AquaGro 2000 G wetting agent blended in at approximately 0.6 kg m^{-3} of soil mix. The mix was aerated steam pasteurized at 70° C for 60 minutes. Trays were watered daily using a fogger with a flow rate of approximately 1.9 liters per minute, while waving the fogger in a circular fashion at the same height over the tray for 15 seconds each day at approximately 9 AM for the duration of the trials. Each tray was given approximately 0.5 liters daily, which equated to 19 liters total over the growing period. A 2.5 cm deep flow tray was placed underneath the trays that contained the cones to catch any herbicide or soil that was displaced by watering over the course of the study. A 16-hour photo period was maintained using

Philips SON-Agro 430-watt high pressure sodium bulbs, and day temperature was set to 22° C and an 18° C night temperature was maintained for each trial.

Cones were monitored daily. Seedling emergence was counted weekly and total emergence was counted for each cone at the end of each trial. At the end of each trial, aboveground biomass of all seedlings within a cone was clipped at 2.5 mm above the surface of the soil, placed in a paper bag, dried at 43º C for one week, and weighed to the nearest 0.001g. Seedling injury was visually rated per each individual cone before aboveground biomass was harvested. The injury scale ranged from 0 to 4, where 0 indicated no observable injury to the plant, 1 was low injury (slightly stunted growth, minor yellowing of leaves (chlorosis), minimal red or purple leaf veins, minor distorted leaf development, and low levels of crinkled leaves), 2 was moderate injury, 3 was high injury (severely stunted growth, severe chlorosis, obvious red or purple leaf veins, distorted leaf development, and high levels of crinkled leaves), and 4 was complete necrosis or plant death (Frans et al., 1986). Counts were tallied for each injury rank within each herbicide treatment group (imazapic, rimsulfuron, and sulfosulfuron) as well as the non-sprayed check. To facilitate comparison across herbicides, we calculated the percentage of plants falling into each injury severity ranking category by dividing the count of each rank by the total number of observations within each herbicide treatment.

I tested the main effects of herbicide treatment (imazapic, rimsulfuron, sulfosulfuron, and non-sprayed) on number of seedlings emerged, herbicide injury, and seedling biomass. Indaziflam was excluded from the overall analysis and comparisons among herbicides and was analyzed alone due to zero saturation issues, rendering accurate comparisons impossible. *Cleomella serrulata* was excluded from species comparisons due to lack of emergence in both sprayed and non-sprayed treatments. Analysis of variance was used with separate models for the emergence and biomass response variables. The fixed effects in the models included herbicide treatment (4 levels) and species (12 levels). I used an α-level of 0.05 to determine statistical significance and Bonferroni and Sadiki corrections for multiple mean comparison tests.

A generalized linear model (GLM) was used to analyze emergence with a Poisson distribution μ{Emergence ~ species * herbicide*trial, family='poisson'). Biomass was modeled with a linear mixed effects (LMER) model, μ{Biomass ~ species * herbicide | trial}. In the GLM for emergence, trial (4 levels) was included as a fixed effect, whereas in the LMER model for biomass and the CLM model for injury, trial was treated as a random effect to account for unobserved variability across trials and improve model generalizability. To meet assumptions of constant variance and normality, the response variables of emergence and injury were natural log-transformed and exponentiated for reporting. Given that the injury response variable is an ordinal categorical ranking from 0 to 4, I used a cumulative link mixed model (CLMM) fitted with the Laplace approximation as a function of species, herbicide, and the species*herbicide interaction, μ{Injury ~ species * herbicide (1|trial)}. Due to significant multicollinearity and zero saturation issues, a Bayesian approach was incorporated into the CLMM.

Emmeans package was used to compare the least square (LS) means of seedling emergence and injury across different herbicide treatments (Lenth, 2022). A Sadiki pairs test was used to compare LS means between each herbicide treatment and the non-sprayed check and identify significant differences in seedling injury levels among herbicide treatments (Lenth, 2016). A chi-square test was used to assess the independence between categorical variables to determine if there were significant associations between herbicide treatments and seedling emergence. These data were wrangled with Excel version 16.78, and statistical testing and graphical representation done in RStudio 4.3.1 (2023-10-31) (Lenth, 2020; R Core Team, 2023) Packages used included: tidyverse (Wickham et al., 2019), dplyr (Wickham et al., 2021), tidyr (Wickham and Girlich, 2023), ggplot2 (Wickham, 2016), ggthemes (Arnold, 2015) and ggpubr (Kassambara, 2020), emmeans (Lenth, 2021), multcomp (Hothorn et al., 2016) and multcompView (Gramsch and Sundberg, 2022).

Results

Herbicide treatment affected emergence ($p<0.0001$) and biomass ($p<0.0001$) across all species combined (Table 3.2). However, the significant interaction between species and herbicide treatment ($p<0.0001$) suggested that the impact of the herbicides on emergence varied depending on the species. The analysis of deviance for the biomass response variable revealed significant effects of species ($p < 0.001$), herbicide ($p < 0.001$), and their interaction ($p < 0.001$). All herbicide treatments showed reduction to seedling biomass when species were pooled for analysis ($p<0.001$) (Table 3.2).

Table 3.2. Analysis of variance results testing the effect of herbicide and species treatments on seedling emergence and biomass.

Response variable	**Factor**	**Degrees of Freedom**	**P-value**
Emergence	Species	10	<.0001
	Herbicide	3	<.0001
	Species: Herbicide	30	<.0001
	Species: Herbicide: Trial	70	0.3453
Biomass	Species	10	<.0001
	Herbicide	3	<.0001
	Species: Herbicide	30	<.0001

Emergence

For three of the forb species; Dalea purpurea, Gaillardia aristata, and Linum lewisii, emergence was reduced by herbicide treatments compared to the non-sprayed check, with limited differences among herbicides (Table 3.3). Dalea purpurea and G. aristata had 3.5 to 3.6 seedlings/cone, respectively, in the non-sprayed check, and herbicides reduced emergence to 2.2 to 2.8 seedlings/cone. Emergence for L. lewisii was 3.0 (95% CI: 2.7, 3.4) seedlings/cone in the non-sprayed check and 1.6 to 1.9 seedlings/cone when exposed to herbicide. Emergence for the other three forb species; Geranium maculatum, Helianthus annuus, and Lupinus argenteus, was not affected by any herbicide.

Grass species emergence was more variable across herbicide treatments and did not reveal any consistent trends (Table 3.3). *Thinopyrum intermedium* and *L. cinereus* tended to have the highest emergence of all the grasses. *Thinopyrum intermedium* was similar in the non-sprayed check to the sulfosulfuron treatments yet decreased in both imazapic and rimsulfuron. *Leymus cinereus* emergence was similar in the non-sprayed check to the rimsulfuron treatment followed by slight decreases in the imazapic and sulfosulfuron treatments. Compared to the non-sprayed check, *P. smithii* emergence was reduced only by rimsulfuron, and emergence was similar across imazapic and sulfosulfuron. *Pseudoroegneria spicata* and *F. idahoensis* were the only two grasses that responded to herbicide treatments similarly. For these two species, emergence was highest in the non-sprayed check and reduced to the same degree by all herbicides. For the indaziflam treatment, the only two species that emerged were *T. intermedium* and *G. aristata*. Mean emergence for *T. intermedium* was 3.4 seedlings/cone (95% CI: 2.86 3.95) and mean emergence for *G. aristata* was 2.2 seedlings/cone (95% CI: 1.55 2.76). Even for these species, emergence occurred only in trial one and was too variable to analyze further.

Table 3.3. Emergence of native forb and grass seedlings as affected by herbicide treatment. Values represent means with 95% confidence interval upper and lower limits shown in parentheses. Letters following means and confidence intervals separate means within a species and across herbicide treatments (α = 0.05).

Species	**Herbicide Treatment**			
	Imazapic	**Rimsulfuron**	**Sulfosulfuron**	**Non-sprayed**
Forbs				
Dalea purpurea	2.6 (2.2, 3.1) a	2.2 (1.9, 2.7) a	2.6 (2.3, 3.1) a	3.4 (3, 3.9) b
Gaillardia aristata	2.5 (0, 3) a	2.8 (2.5, 3.2) a	2.7 (2.3, 3.1) a	3.6 (3.2, 4) b
Geranium maculatum	1.3 (0.9, 2.0) a	1.6 (1.3, 2.1) a	1.6 (1.2, 2.1) a	1.5 (1.1, 1.9) a
Helianthus annuus	1.0 (0.2, 5) a	1.1 (0.6, 1.9) a	1.1 (0.5, 2.8) a	1.4 (1.1, 1.9) a
Linum lewisii	1.9 (1.5, 2.3) a	1.6 (1.2, 2.1) a	1.7 (1.3, 2.5) a	3.0 (2.7, 3.4) b
Lupinus argenteus	2.2 (1.8, 2.6) a	2.1 (1.8, 2.5) a	2.0 (1.7, 2.3) a	2.4 (2.1, 2.8) a
Grasses				
Festuca idahoensis	2.1 (1.7, 2.5) a	2.2 (1.7, 2.9) a	2.2 (1.7, 2.9)	3.6 (3.2, 4.1) b
Leymus cinereus	3.6 (3.1, 4.1) a	3.7 (3.3, 4.3) ab	3.6 (3.2, 4.2) a	4.4 (3.9, 5) b
Pascopyrum smithii	3.6 (3.1, 4.1) ab	3.4 (2.9, 3.9) a	3.6 (3.2, 4.2) ab	4.2 (3.7, 4.8) b
Pseudoroegneria spicata	3 (2.6, 3.4) a	3.3 (2.9, 3.7) a	3.4 (3.1, 3.9) a	4.5 (4, 4.9) b
Thinopyrum intermedium	3.5 (3.1, 3.9) b	2.8 (2.5, 3.2) a	4.1 (3.7, 4.6) c	4.7 (4.3, 5.3) c

Biomass

Three of the six forb species had reduced biomass from herbicide treatments compared to the non-sprayed check, with the extent of reduction varying by species (Table 3.4). *Gaillardia aristata* experienced the greatest reduction in biomass when compared to the non-sprayed check. Specifically, biomass was 0.13g (95% CI: 0.12, 0.14) in the non-sprayed check and as low as 0.04g (95% CI: 0.03, 0.05) in the rimsulfuron treatment and 0.05g (95% CI: 0.04, 0.06) in imazapic. For *H. annuus*, biomass was low overall at 0.04 (95% CI: 0.02, 0.05) in the non-sprayed check and reduced to 0.0 in all herbicides treatments. For *L. argenteus* there was some variation in biomass across herbicides, sulfosulfuron and imazapic were similar and both higher than rimsulfuron, yet all herbicides were lower than the non-sprayed check. *Dalea purpurea*, *G. maculatum*, and *L. lewisii* were the three forb species to have the same biomass in the non-sprayed check and herbicide-treated, and *G. maculatum* biomass was higher in sulfosulfuron than in imazapic and rimsulfuron (Table 3.4).

Grass biomass was reduced by herbicides in all species, but species exhibited variable responses with more pronounced reductions in some species like *T. intermedium* (Table 3.4). *Leymus cinereus*, *P. smithii*, and *P. spicata* showed consistent biomass reductions across all herbicide treatments compared to the non-sprayed check, while *Thinopyrum intermedium* and *F. idahoensis* exhibited the most substantial reductions under imazapic and rimsulfuron (Table 3.4). Interestingly, *F. idahoensis* biomass was higher under sulfosulfuron than in the non-sprayed check. When examining the effects of indaziflam on biomass for the two species that emerged in that treatment, all individuals of *G. aristata* had perished before they could be harvested for biomass measurements. For *T. intermedium* a mean biomass of 0.05g (95% CI: 0.04, 0.17), and a few outliers were observed, with one notable data point around 0.17g, suggesting that while most plants show low biomass, a few individuals might exhibit some level of tolerance to indaziflam.

Table 3.4. Biomass (grams) of native forb and grass seedlings as affected by herbicide treatment. Values represent means with 95% confidence interval upper and lower limits shown in parentheses. Letters following means and confidence intervals separate means within a species and across herbicide treatments (α = 0.05).

Species	Herbicide Treatment			
	Imazapic	**Rimsulfuron**	**Sulfosulfuron**	**Non-sprayed**
Forbs				
Dalea purpurea	0.01 (0, 0.02) a	0.01 (0, 0.02) a	0.01 (0, 0.02) a	0.02 (0.01, 0.03) a
Gaillardia aristata	0.05 (0.04, 0.06) a	0.04 (0.03, 0.05) a	0.07 (0.06, 0.08) b	0.13 (0.12, 0.14) c
Geranium maculatum	0.02 (0, 0.04) a	0.03 (0.02, 0.04) ab	0.05 (0.04, 0.06) ab	0.04 (0.03, 0.05) b
Helianthus annuus	0.01 (-0.06, 0.06) a	0.01 (-0.02, 0.03) a	0.01 (-0.03, 0.04) a	0.04 (0.02, 0.05) b
Linum lewisii	0.01 (0, 0.02) a	0.01 (0, 0.02) a	0.01 (0, 0.03) a	0.02 (0.01, 0.03) a
Lupinus argenteus	0.07 (0.06, 0.08) b	0.05 (0.04, 0.06) a	0.07 (0.06, 0.08) b	0.08 (0.07, 0.09) c
Grasses				
Festuca idahoensis	0.01 (0, 0.02) a	0.02 (0, 0.03) a	0.08 (0.07, 0.1) c	0.03 (0.02, 0.04) b
Leymus cinereus	0.03 (0.02, 0.03) a	0.02 (0, 0.03) a	0.02 (0.01, 0.03) a	0.10 (0.09, 0.1) b
Pascopyrum smithii	0.02 (0.01, 0.03) a	0.02 (0.01, 0.03) a	0.02 (0.01, 0.03) a	0.14 (0.13, 0.15) b
Pseudoroegn -eria spicata	0.04 (0.04, 0.05) a	0.03 (0.02, 0.03) a	0.03 (0.02, 0.04) ab	0.13 (0.13, 0.14) b
Thinopyrum intermedium	0.03 (0.02, 0.04) a	0.03 (0.02, 0.04) a	0.09 (0.09, 0.1) b	0.23 (0.22, 0.24) c

Injury

The Cumulative Link Mixed Model (CLMM) provided odds ratios for transitioning between injury levels (Table 3.5). The odds of a plant moving from minor injury (1) to moderate injury (2) were extremely low, with an odds ratio of 0.0009, suggesting that plants are highly likely to remain in the minor injury category rather than progressing to moderate injury under the conditions tested. Transitioning from moderate injury (2) to high injury (3) was slightly more likely, as reflected by an odds ratio of 0.0083, though this progression also remained rare. In contrast, the odds of a plant progressing from high injury (3) to severe injury or death (4) were much greater, with an odds ratio of 3.15, suggesting that once a plant reached a severe level of injury, the likelihood of progressing to death was much higher.

Table 3.5. Log-odds estimates, exponentiated estimates (odds ratios), standard errors, and z-values for injury rank from the cumulative link mixed model.

Injury Rank	Log Estimate	Exponentiated Estimate	Std. Error	z-value
1|2	-7.0345	0.000880959	0.469	-14.998
2|3	-4.7954	0.008267691	0.4547	-10.546
3|4	1.147	3.148732529	0.4318	2.656

Rimsulfuron showed the highest injury rates in Rank 3 with 81%, and a considerable portion also classified in Rank 4 (Table 3.6). Imazapic had 76% of cases classified as Rank 3, and sulfosulfuron displayed a slightly more varied distribution, with 64% of cases classified as Rank 3, and 19% in Rank 2 (Table 3.6). Among herbicides most observations were classified in Rank 3, with 73% of all cases showing high injury symptoms while moderate injury (Rank 2) made up just under 11%.

Table 3.6. Distribution of injury ranks for each herbicide treatment across all species, showing the counts and percentages of each rank for imazapic, rimsulfuron, and sulfosulfuron.

Herbicide	Injury	Count	Percentage	Herbicide	Injury	Count	Percentage
imazapic	1	11	0.966	rimsulfuron	1	25	2.25
imazapic	2	86	7.55	rimsulfuron	2	62	5.58
imazapic	3	860	75.5	rimsulfuron	3	897	80.7
imazapic	4	182	16	rimsulfuron	4	128	11.5
sulfosulfuron	1	71	6.61				
sulfosulfuron	2	207	19.3				
sulfosulfuron	3	685	63.8				
sulfosulfuron	4	111	10.3				

Forb species showed varying injury responses across herbicide treatments. For some species, like *D. purpurea* and *G. aristata*, mean injury rank was lowest under sulfosulfuron, while for other species, like *H*. *annuus* and *L*. *lewisii*, mean injury rank was highest under sulfosulfuron (Table 3.7). For four of the six forb species, mean injury rank was similar between imazapic and rimsulfuron. These species included *D*. *purpurea*, *H*. *annuus*, *L*. *lewisii*, and *L*. *argenteus*. *Lupinus argenteus* was the only species with a mean injury rank similar across all herbicides.

Mean injury rank for grass species was somewhat less variable than for forb species. For example, three of the grasses *P*. *spicata*, *T*. *intermedium*, and *F*. *idahoensis*, all had the lowest injury rank for sulfosulfuron and similar injury rank for imazapic and rimsulfuron (Table 3.7). Mean injury rank for *P*. *smithii* was lowest for imazapic and similar for rimsulfuron and sulfosulfuron. For *L*. *cinereus* mean injury rank was highest in sulfosulfuron. When looking at indaziflam in trial one, the injury rank of *T. intermedium* was 3.06, and 4.0 for *Gaillardia aristata.*

Table 3.7. Injury ranks of native forb and grass seedlings as affected by herbicide treatment. Values represent means with 95% confidence interval upper and lower limits shown in parentheses. Letters following means and confidence intervals separate means within a species and across herbicide treatments (α = 0.05). Non-sprayed check was removed from analysis due to multicollinearity and zero saturation issues.

Species	**Herbicide Treatment**		
	Imazapic	**Rimsulfuron**	**Sulfosulfuron**
Forbs			
Dalea purpurea	3.27 (2.75, 3.83) b	3.21 (3, 4) b	2.68 (2.25, 3.25) a
Gaillardia aristata	3.23 (3, 4) c	3.10 (2.5, 3) b	2.83 (2.25, 3.25) a
Geranium maculatum	3.26 (3, 4) ab	3.11 (2.5, 3) a	3.47 (3, 4) b
Helianthus annuus	3.44 (3, 4) a	3.43 (3, 4) a	3.82 (3.6, 4) b
Linum lewisii	3.18 (3, 4) a	3.26 (3, 3.5) a	3.54 (3, 4) b
Lupinus argenteus	2.52 (2, 3) a	2.61 (2.2, 3.0) a	2.43 (2.0, 2.83) a
Grasses			
Festuca idahoensis	3.15 (2.75, 3.5) b	3.26 (3, 3.6) b	3.01 (2.5, 3) a
Leymus cinereus	3.01 (2.5, 3) a	2.98 (2.5, 3.5) a	3.75 (3.5, 4.0) b
Pascopyrum smithii	3.04 (2.5, 3) b	2.81 (2.4, 3.2) a	2.86 (2.4, 3.2) a
Pseudoroegneria spicata	3.06 (2.5, 3.5) b	2.95 (2.5, 3.5) b	2.75 (2.25, 3.25) a
Thinopyrum intermedium	2.75 (2.25, 3.25) b	2.75 (2.25, 3.25) b	1.87 (1.5, 2.10) a

Discussion

The results of this study provide valuable insights into the effects of herbicides commonly used for IAG on a range of plant species used for revegetation in grassland ecosystems. I hypothesized that all herbicides would reduce emergence and biomass across species and increase injury compared to the non-sprayed check. Additionally, I expected that the greatest reduction in emergence and biomass, as well as the highest injury levels, would occur with indaziflam, followed by imazapic, rimsulfuron, and sulfosulfuron. My findings largely supported the hypotheses. The non-sprayed check consistently exhibited the highest emergence and biomass across all species. As predicted, indaziflam led to the greatest reduction in emergence and biomass. Imazapic, rimsulfuron, and sulfosulfuron all exhibited effects, depending on the species, but effects varied with some species showing more tolerance than others to specific herbicides.

We expected imazapic to cause significant suppression of emergence and reductions in biomass across most species, although its effects were more similar to rimsulfuron's than expected. Imazapic's impact on native species can be variable (Orloff et al., 2015; Sheley et al., 2007), and some research has indicated that certain species used for restoration can recover from initial injury caused by imazapic, although timing, rate of application, and environmental conditions play critical roles in determining seeding success (Sheley et al., 2007; Schantz et al., 2019; Sheley et al., 2012). For optimal restoration outcomes, imazapic may be most effective when integrated with site-specific preparations, such as burning and tilling, and combined with high seeding rates (Sheley et al., 2007). In particular, favorable outcomes have been observed in years with low winter temperature variability and high growing season precipitation, suggesting that restoration efforts should also consider weather patterns when planning imazapic application (Schantz et al., 2019). Thus, while imazapic can be an effective element of restoration, achieving consistent native species establishment requires careful planning and complementary practices (Sheley et al., 2012; Bekedam, 2004).

Rimsulfuron and imazapic both showed similar patterns of suppressing emergence and biomass, often causing moderate to high injury levels across most species. Both herbicides have demonstrated effectiveness for managing IAG, although their impacts on native species recovery differed slightly. For example, rimsulfuron was evaluated alongside other pre-emergence herbicides for controlling *B. tectorum* and *T. caput-medusae* in two sagebrush communities in northeastern California (Kyser et al., 2013). While rimsulfuron did not cause long-term harm to resident perennial grasses or annual forbs, its effectiveness was hindered by inconsistent precipitation, which also limited the establishment of seeded perennials. Similarly, imazapic continued to control IAG for up to two years and even supported increases in native forb cover over time. These results suggest that while both rimsulfuron and imazapic can be used to manage IAG, they may require careful timing to minimize injury to native vegetation and ensure effective revegetation (Kyser et al., 2013; Endress et al., 2012).

Of the four herbicides tested in my study, sulfosulfuron appeared to be the friendliest to seeded species. In a field study assessing grass tolerance to various roadside right-of-way herbicides, sulfosulfuron was found to support biomass accumulation and be one of the least injurious herbicide options (Baldos et al., 2010). The results from Baldos et al. (2010) coupled with my results suggest sulfosulfuron could be a candidate for revegetation projects aiming to establish native or desirable vegetation in similarly managed environments. Sulfosulfuron may deserve further attention for its use in revegetation of IAG-infested rangelands (Paporisch et al., 2020).

I expected that indaziflam, due to its persistence and non-selective properties, would result in the lowest emergence, and if emergence occurred, would have the highest injury levels among the tested herbicides (Dombro, 2024; Fowers and Mealor, 2020). Indaziflam exhibited severe impacts on emergence, with most species showing no emergence and subsequently, no biomass production. This is similar to a field study conducted in Wyoming where indaziflam was applied to a fallow field and 45 native species were seeded five and nine months later (Crose, 2022). Density of most seeded grasses and forbs was considerably lower in sprayed versus non-sprayed treatment one year after planting, and forb species appeared more impacted than grasses. In my study, *G. aristata* and *T. intermedium* showed some emergence, albeit inconsistent, and coincidentally the forb biomass could not be harvested and the grass produced minimal biomass. *Gallardia aristata* has been identified as a species potentially tolerant to indaziflam (Crose, 2022), and my results are the first to suggest *T. intermedium* may be another potentially tolerant species.

Some research indicates that while indaziflam can initially suppress emergence and early growth of certain species, its effects may vary depending on the plant species and specific conditions (Clark et al., 2019, 2020). In the short term and under greenhouse conditions, my study showed substantial reductions in seedling emergence under indaziflam. However, long-term re-establishment of desirable perennial species may be less impacted, and previous research suggests that the potential for recovery and eventual resilience after initial herbicide application is possible (Fowers and Mealor, 2020; Clark et al., 2019, 2020; Tilman and Downing, 1994).

Indaziflam demonstrates considerable potential for managing IAG in rangeland restoration, though its use in revegetation requires new strategies. For example, IAG could be controlled with a less persistent herbicide like imazapic or even glyphosate, desired species could be seeded and allowed to establish, then indaziflam applied to control IAG in the longer term. Alternatively, indaziflam could be applied initially, reduce the seed bank through at least two to three years of IAG control, then desired species seeded once indaziflam dissipates. Adjusting the seeding depth of desirable species has also been suggested and tested, with variable results (Crose, 2022). While indaziflam can be a very effective herbicide in IAG management, successful restoration will require tailored approaches that account for specific species' sensitivities.

No single species was immune to the effects of herbicide across all response variables (i.e., emergence, biomass, injury); therefore, it is difficult to identify the best candidate species for revegetation in IAG-infested grasslands. For example, *L. argenteus* emergence was not affected by herbicide treatment, but its biomass was reduced, and it exhibited moderate injury symptoms. Alternatively, *D. purpurea* biomass was consistent across herbicide treatments but its emergence was reduced, and it exhibited high injury symptoms. The differential responses observed across species and herbicide treatments in this study underscore the complex and nuanced impacts of herbicides on desirable species used for revegetation of plant communities (Merfield, 2022).

Recognizing the variability in species-specific responses to herbicides is important for land managers, especially in situations where the choice of herbicide is restricted by environmental regulations, budget constraints, or availability. For instance, if land managers can only apply one of these herbicides (indaziflam, imazapic, rimsulfuron, or sulfosulfuron), studies like this can guide managers in selecting species that are more likely to survive and establish under these treatments. For example, my results suggest that if sulfosulfuron is the herbicide of choice, candidate species to include in a seed mix should include *G. aristata*, *G. maculatum*, and *L. argenteus* for forbs and *F. idahoensis* and *T. intermedium* for grasses as these five species appeared least affected by sulfosulfuron across response variables measured. In this way, herbicide choice directly influences the success of revegetation efforts, and careful planning of species selection will maximize restoration outcomes while mitigating herbicide-induced damage (Baldos et al., 2010; Kyser et al., 2013). *Leymus cinereus*, *P. spicata*, and *P. smithii* showed some tolerance to rimsulfuron and sulfosulfuron, making them better suited for seeding in areas where these herbicides are applied. Seeding with these species could provide effective competition against invasives while supporting native plant recovery (Daehler, 2003). *Festuca idahoensis* is particularly sensitive to all herbicides in this study, suggesting that it should be seeded in areas without chemical control or alternatively managers could use glyphosate, which doesn't have any soil residual and could be applied to kill the IAG and seeded into without any ramifications for seeded species (Majeski et al., 2024).

Additionally, successional management, which modifies the processes of disturbance, colonization, and species performance, is key to developing and maintaining invasion-resistant plant communities and plays a crucial role in optimizing herbicide efficacy while minimizing collateral damage to desirable vegetation (Sheley and Mangold, 2003). Incorporating these considerations into grassland restoration plans can significantly enhance the success and sustainability of revegetation efforts. My study findings emphasize that carefully matching herbicide selection with species selection would allow managers to address disturbance by clearing invasive species, promote native species colonization by reducing competitive pressure, and enhance species performance by choosing herbicides that align with the resilience of desirable native plants (Sheley et al., 2006).

My results were obtained under ideal growing conditions in a greenhouse and without competition from invasive species, which does not fully represent field conditions and potentially limits their application. Yet, being able to control multiple external variables (e.g.

temperature, moisture) gives us the ability to isolate the effects of the herbicides, allowing for improved confidence in our conclusions (Boutin et al., 2004). Moving forward, integrated weed management approaches that incorporate specific herbicides with specific species offer the best chance of revegetation success on our degraded and threatened grassland ecosystems (Monaco et al., 2016). Notably, herbicides appeared to have a more pronounced effect on biomass than on emergence. Herbicides can reduce biomass by stunting plant growth after seedling emergence, leading to stable emergence but significantly diminished biomass (Cobb, 2022). Stable emergence with diminished biomass highlights the importance of considering herbicide impacts on multiple growth stages when assessing their overall effect on plant health and establishment (Ruffner and Barnes, 2010). Future greenhouse studies could extend the growth period after emergence to examine if initial impacts on biomass lessen over time. Future studies could also investigate the combined effects of herbicide application and competition from IAG to provide a more comprehensive understanding of herbicide impacts in more realistic scenarios.

In conclusion, this greenhouse study underscores the complexity of herbicide effects on native plant species used for revegetation in grassland ecosystems. While herbicides are essential tools for managing IAG, their indiscriminate use can have detrimental consequences for native plants used for revegetation in grasslands. By carefully evaluating the effects of herbicides on emergence, biomass, and injury of seeded species, this research provides valuable information for optimizing herbicide selection and choices of seeded species in grassland restoration projects.

CHAPTER FOUR

BASELINE SURVEY FOR POLLINATORS: ASSESSING ABUNDANCE, RICHNESS, AND DIVERSITY IN DEGRADED GRASSLANDS

Introduction

Grasslands are among the most imperiled ecosystems worldwide, and those within the Flathead Indian Reservation are no exception (Carbutt et al., 2017; Scholtz et al., 2022). Our pollinators are facing threats from habitat fragmentation and land-use changes leading to the degradation of biodiversity due to invasive plant species and overgrazing (Bardgett et al., 2021; Chawicha et al., 2023). The conversion of native grasslands alters the structure and composition of the landscape, introducing fences, crop monocultures, grazing pressure, and often reducing the availability of diverse flowering plants that bees rely on for forage (Magar, Khum Bahadur Thapa 2021; Mitchell, 2020). This can fragment habitats, disrupting the connectivity, making it harder for bees to find food and nesting sites (Osborne and Williams, 2001). Additionally, the invasion of invasive annual grasses (IAG) further fragments the ecological integrity of grasslands by replacing native species and altering biodiversity (Dogra et al., 2010). As stewards of these grasslands, Tribal managers recognize the importance of conserving pollinator communities to safeguard biodiversity and ecosystem services for present and future generations (Breslow et al., 2016; Rose et al., 2014; Thakur et al., 2016).

Within these grasslands pollinators play a vital role in maintaining ecosystem health and function and have a crucial role in the reproduction of flowering plants, which are essential for various economic, ecological, and cultural purposes (Ashworth et al., 2009; Potts et al., 2009). Insects like bees contribute significantly to global food production, supporting numerous native grassland plant species (Khalifa et al., 2021; Woodcock et al., 2014). Moreover, bees are vital for agricultural productivity, aiding in the production of crops that provide essential food, fiber, and medicine (Khalifa et al., 2021; Van der Sluijs and Vaage, 2016). This critical role not only sustains plant populations in grasslands but also fosters ecosystem functioning by enhancing plant reproduction, genetic diversity, and providing food and habitat for wildlife and livestock (Bendel et al., 2019; Seitz, 2020).

Despite their ecological importance, wild bees in grassland ecosystems face numerous threats that jeopardize their populations (Kearns et al., 1998). Habitat loss and degradation due to IAG are among the primary drivers of bee decline (Wesche et al., 2012; Carbutt, 2017). Additionally, intensive grazing has been shown to lead to invasive plant species like cheatgrass (*Bromus tectorum L.)* that further exacerbate the vulnerability of bee populations (Molvar et al., 2024; Williamson et al., 2020). All of these threats are leading to declines in species richness and abundance for native plants that bees depend on across North Americas grasslands (Molvar, 2024). There remains a significant gap in research regarding bee identity, abundance, and ecological roles. Global studies, including meta-analyses, emphasize the widespread deficiency in understanding pollinator communities, particularly in grasslands where habitat loss and invasive species are transforming ecosystems (Tonietto and Larkin, 2018; Winfree et al., 2011; Olynyk et al., 2021). This translates to a lack of baseline data, which complicates efforts to assess the impact of these threats, both locally and globally, leaving land managers with limited information to guide effective conservation strategies (Buchmann and Ascher, 2005; Kline and Joshi, 2020).

This chapter aims to provide Tribal managers with a baseline understanding of the community composition of pollinators abundance, richness, evenness, and diversity that occupy our threatened grassland ecosystems. My aim is to fulfill the pressing requirement for baseline surveys of pollinators in endangered grassland ecosystems, specifically focusing on tribal-owned grasslands in northwestern Montana. I systematically collected bees from two grassland sites degraded by IAG over the course of one growing season, and later analyzed the counts to determine the abundance, species richness, and diversity of pollinators. Baseline data serve as a reference point for future research, enabling managers to evaluate the success of conservation measures and adapt management strategies in response to emerging threats.

Methods

This research was conducted at two sites, North Valley Creek (NVC) and Plant Lane (PL), located in northwestern Montana, U.S.A., within a 60 km radius of Flathead Lake (47°42'8.64"N; 114° 8'14.61"W) in Lake County. The sites surveyed are within the Tribal-owned grasslands at the southern end of the Flathead Reservation, which is surrounded by two mountain ranges, the Mission Mountains to the northeast and the Salish mountains to the south and west. The NVC site (47°14'1.93"N; 114°11'17.55"W) is 911m in elevation and primarily consists of Belton silty loam soils, with slopes ranging from 8 to 15%. Annual precipitation averages 35 centimeters. Mean annual high temperature is 14°C and mean annual low temperature is 0°C (Western Regional Climate Center, 2024). Recent vegetation surveys show the dominant flowering forb species to be sulfur cinquefoil (*Potentilla recta* L.) (unpublished McRyhew).

Potentilla recta was first found in Montana in 1947 in Ravalli County and was listed as a noxious weed in 2017 (USDA PLANTS Database accessed 2024). The PL site (47°12'2.90"N; -114° 9'38.17"W) is at an elevation of 930m and features McDonald silty clay loam soils with slopes of 4-8%. Mean annual precipitation and daily temperature ranges are similar to that of NVC. Recent vegetation surveys showed the dominant flowering forb species at PL are spotted knapweed (*Centaurea stoebe* L.) and teazel (*Dipsacus fullonum* L.) (unpublished McRyhew), both non-native species. *Centaurea stoebe* was first found in Montana in 1920 in Ravalli County and declared noxious in the 1960s. *Dipsacus fullonum* has been naturalized since it was first cultivated in the 1800s (USDA PLANTS Database accessed 2024).

To collect a baseline of pollinator activity, I used established semi-permanent plots at each site (Chapter 2), where herbicides and seeding were applied to restore IAG infested grasslands. I used bee bowls, a widely adopted method for passively monitoring insect pollinators (Grundel et al., 2011; Shapiro and Minckley, 2014). The bee bowls were white, yellow, and blue UV-colored cups, filled halfway with soapy water, and placed at 18 locations per site, spaced every 9 paces. At the PL site, sampling occurred on five sampling days, starting in June and continuing until August, to capture seasonal variation in pollinator activity and species composition (Table 4.1). At the NVC site, bees were sampled on only one day in mid-July and did not match any of the PL sampling dates. As a result, no direct comparisons between the two sites were made to avoid misleading conclusions. The bee bowls were deployed between 9AM to 4PM allowing for the capture of foraging bees in optimal weather conditions. At the end of each sampling period, bees collected from the bee bowls were preserved in a freezer. The specimens were dried using a soft paper towel and a blow dryer to prevent damage and expedite the drying process (Figure 4.1).

Non-bee bycatch was logged but not identified or used in the baseline data. Bees were pinned, mounted (Figure 4.1), and transported to Utah State University, where expert entomologist Dr. Skyler Burrows identified them to species. The physical samples will be stored at the Salish Kootenai College Extension office for future access by students and land managers.

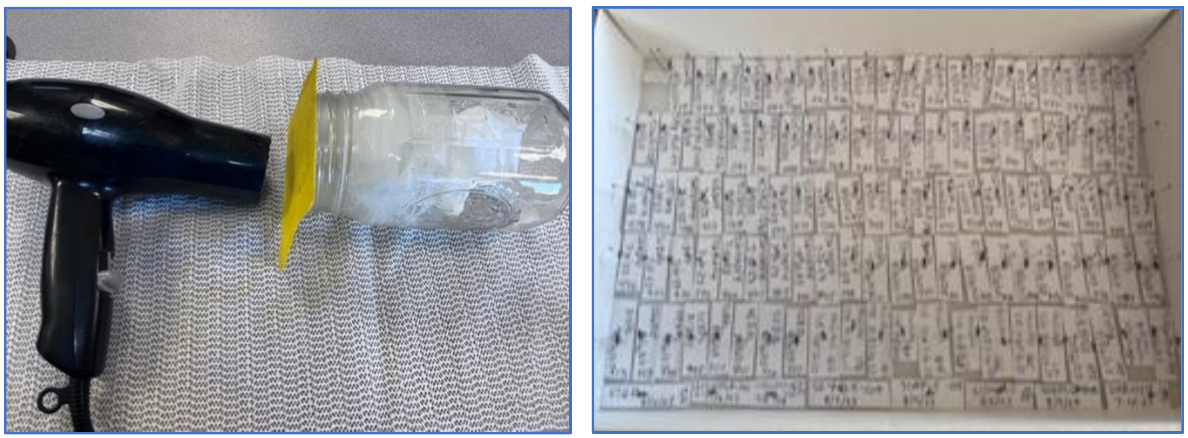

Figure 4.1 Example of pinned bee samples (*Lasioglossum incompletum*) and process of drying.

Several analyses were conducted to assess bee species abundance, diversity, and composition at the two sites and across multiple sampling dates. Species abundance and richness were calculated, with additional estimates provided by the Chao1 estimator to capture both observed and unobserved species richness (Chao, 1984). Shannon's Diversity Index was used to measure species diversity at each site, incorporating both the number of species and their relative abundances (Shannon, 1948). Along with Shannon's index, Pielou's Evenness was calculated to understand how evenly species were distributed within each site (Pielou, 1966). To further explore species composition differences, a Non-Metric Multidimensional Scaling (NMDS) ordination was performed. This method allowed for visualization of differences in species composition, both spatially and temporally across sampling dates, with stress values providing a measure of the accuracy of the ordination. These metrics provide valuable information about the health and stability of pollinator communities in Tribal grasslands (Cane et al., 2000). These data were wrangled with Excel version 16.78, and statistical testing and graphical representation done in RStudio 4.3.1 (2023-10-31) (Length, 2020; R Core Team). Packages used included; dplyr (Wickham et al., 2023), ggplot2 (Wickham, 2016), vegan package (Oksanen et al., 2022), and tidyr (Wickham & Girlich, 2023).

Results

A total of 42 bee species were collected across both sites, with 38 species at the PL site and 24 species at the NVC site (Table 4.1, Figure 4.2). The PL site contributed 381 individuals, while NVC accounted for 166 individuals (Figure 4.2). Individuals spanned 14 genera and five families, including mostly species that are wild and native; the exceptions were *Apis mellifera* and *Lasioglossum leucozonium,* (reviewed by Skyler Burrows 2024, see Table 1). Both sites shared 20 species, while 18 were found exclusively at PL and four were unique to NVC. The three most abundant species were *Lasioglossum incompletum* (137 individuals), *Halictus tripartitus* (112 individuals), and *Agapostemon foxauur angelicus* (98 individuals). Additionally, 12 species were represented by only a single individual (Table 4.1). The most species diverse genus across sites was *Lasioglossum* with 13 species, and the next highest diverse genera were *Halictus* with 6 species and *Bombus* with 4 species (Table 4.1).

Table 4.1. Bee species collected between 6 June 2023 and 16 August 2023 from two sites on the Flathead Reservation in northwest Montana: North Valley Creek (NVC) and Plant Lane (PL).

Common name	**Scientific name and authority**	**6 June 2023**	**14 June 2023**	**7 July 2023**	**26 July 2023**	**8 August 2023**	**16 August 2023**
Bicoloured sweat bee	*Agapostemon virescens,* Fabricius, 1775	PL	PL	NVC			
Angelic sweat bee	*Agapostemon foxauur angelicus*, Cockerell, 1924	PL	PL	NVC			PL
Texas sweat bee	*Agapostemon texanus*, Cresson, 1872					PL	PL
Purple miner bee	*Andrena prunorum*, Cockerell, 1896	PL	PL		PL		
Willow flower miner bee**	*Andrena salicifloris,* Cockerell, 1897			NVC			
Occidental digger bee**	*Anthophora occidentalis,* Cresson, 1869			NVC			
European honeybee *	*Apis mellifora,* Linnaeus		PL	NVC		PL	PL
Colorado black notched bumble bee	*Bombus bifarius,* Cresson, 1878					PL	
Yellow bumble bee	*Bombus fervidus,* Fabricius, 1798	PL		NVC		PL	PL
Nevada bumble bee	*Bombus nevadensis,* Cresson, 1874				PL	PL	
Red belted bumble bee	*Bombus rufocinctus,* Cresson, 1863				PL		
Edwards long horned bee	*Eucera edwardsii,* Cresson, 1878	PL					
Confused sweat bee	*Halictus confuses,* Smith, 1853					PL	
Wide striped sweat bee	*Halictus farinosus,* Smith, 1853	PL		NVC	PL	PL	
Ligated Gregarious sweat Bee	*Halictus ligatus,* Say, 1837	PL		NVC	PL	PL	PL
Confused sweat bee	*Halictus confusus,* Smith, 1853	PL		NVC		PL	PL
Polymorphic sweat bee	*Halictus rubicundus,* Christ, 1791		PL	NVC		PL	PL
Tripartite sweat bee	*Halictus tripartitus,* Cockerell, 1895	PL	PL	NVC	PL	PL	PL
White faced summer mason bee	*Hoplitis albifrans,* Kirby, 1837	PL		NVC		PL	
Hypocrite summer mason bee	*Hoplitis hypocrite,* Cockerell, 1906		PL	NVC			
White winged sweat bee	*Lasioglossum albipenne,* Robertson, 1890		PL				PL
Cooleys sweat bee	*Lasioglossum cooley,* Crawford, 1906	PL		NVC			PL

Metallic sweat bee	*Lasioglossum dialictus* spp., Cockerell, 1895			NVC	PL	PL	PL
A sweat bee	*Lasioglossum glabriventre,* Crawford, 1907	PL					
Weak veined bee**	*Lasioglossum hemihalictus*			NVC			
Incomplete sweat bee	*Lasioglossum incompletum,* Crawford, 1907			NVC	PL	PL	PL
White-banded sweat bee*	*Lasioglossum leucozonium,* Schrank, 1781		PL	NVC			
Nevada sweat bee	*Lasioglossum nevadense,* Crawford, 1907		PL			PL	PL
Hoary sweat bee	*Lasioglossum pruinosum,* Robertson, 1892			NVC			PL
Dimple bellied sweat bee	*Lasioglossum punctatovenra,* Crawford, 1907		PL	NVC			
Tansy mustard sweat bee	*Lasioglossum sisymbria,* Cockerell, 1895	PL	PL	NVC			
Titus's sweat bee	*Lasioglossum titusi,* Crawford, 1902		PL				
Three zoned sweat bee	*Lasioglossum trizonatum*		PL				
Furry leaf cutter bee	*Megachile perihirta,* Cockerell, 1898					PL	
Lupine long horned bee	*Melissodes lupina,* Cresson, 1878			NVC	PL		PL
Small long horned bee	*Melissodes microsticta,* Cockerell, 1905		PL			PL	
Paradise valley mason bee	*Osmia paradisica,* Sandhouse, 1924	PL					
mason bee**	*Osmia* spp.			NVC			
A mason bee	*Osmia trevoris,* Cockerell, 1897	PL	PL	NVC			
A miner bee	*Panurginus torchioi*	PL		NVC			
A cuckoo bee	*Sphecodes* sp. A						PL
A cuckoo bee	*Sphecodes* spp1						PL

*exotic
** Only found at North Valley Creek Site.
(NatureServe Network 2024; Dr. Skyler Burrows 2024)

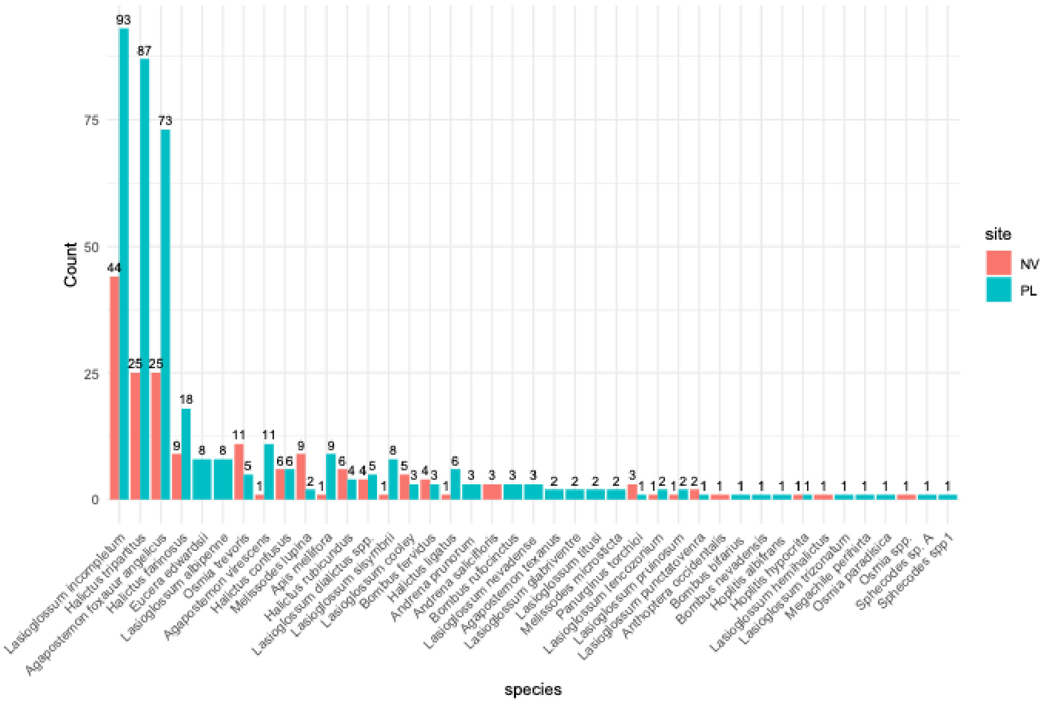

Figure 4.2. Count of each bee species collected from Plant Lane (PL) and North Valley Creek (NVC) sites on the Flathead Reservation in northwest Montana, with species ordered by descending abundance. Y-axis is the number of individual bee species.

<u>Abundance, Evenness, Richness</u>

At the PL site across five sampling dates, total bee abundance varied from 41 individuals on 26 July 2023 to 99 individuals on 9 August 2023. Species evenness, measured by Pielou's index, fluctuated between 0.773 on 6 June 2023 and 0.557 on 9 August 2023, suggesting variations in how equally the species were distributed within the community (Figure 4.3). Species richness ranged from 9 species on 26 July 2023 to 17 species on 16 August 2023. The PL site, sampled over multiple dates, showed distinct patterns of abundance, evenness, and richness across time, suggesting temporal variability in the bee community structure at this site (Figure 4.3). At the NVC site, sampled on 10 July 2023, 166 individuals were observed, representing 24 species (richness), with an evenness value of 0.771, indicating a relatively balanced species distribution.

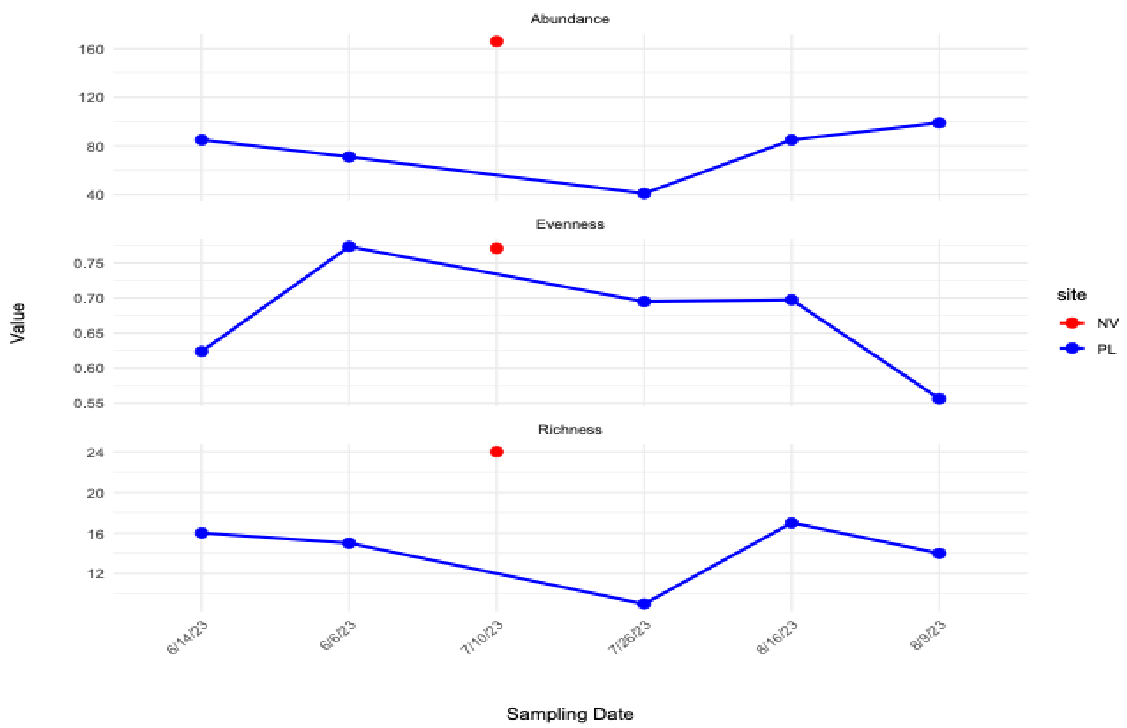

Figure 4.3. Seasonal trends in bee abundance (top), evenness (middle), and species richness (bottom) at the Plant Lane (PL) site and the North Valley Creek (NVC) site over six sampling dates in 2023. Abundance refers to the total number of bees sampled. Evenness represents how evenly individuals are distributed across species, calculated using Pielou's evenness index. Species richness indicates the number of distinct bee species sampled on each date. Sampling took place on 6 June, 14 June, 26 July, 16 August, and 9 August at PL, with an additional sampling point on 10 July at the NVC site.

Chao1 Richness Estimator

A species richness analysis using the Chao1 estimator was conducted for both sites. The estimated species richness at the PL site was 48 species with a (95% confidence interval (CI): 42.66, 53.92), indicating that additional species may be present but undetected in the current sample. At the NVC site, the Chao1 estimator predicted a species richness of 74 species, with a (95% CI: 64.70, 83.30). Pielou’s Evenness Index was approximately 0.7 for the PL site and 0.8

for the NVC site, reflecting the relatively even distribution of species at both sites. These results provide an estimate of the potential total species richness at each site, accounting for unseen species that may not have been sampled (Figure 4.4).

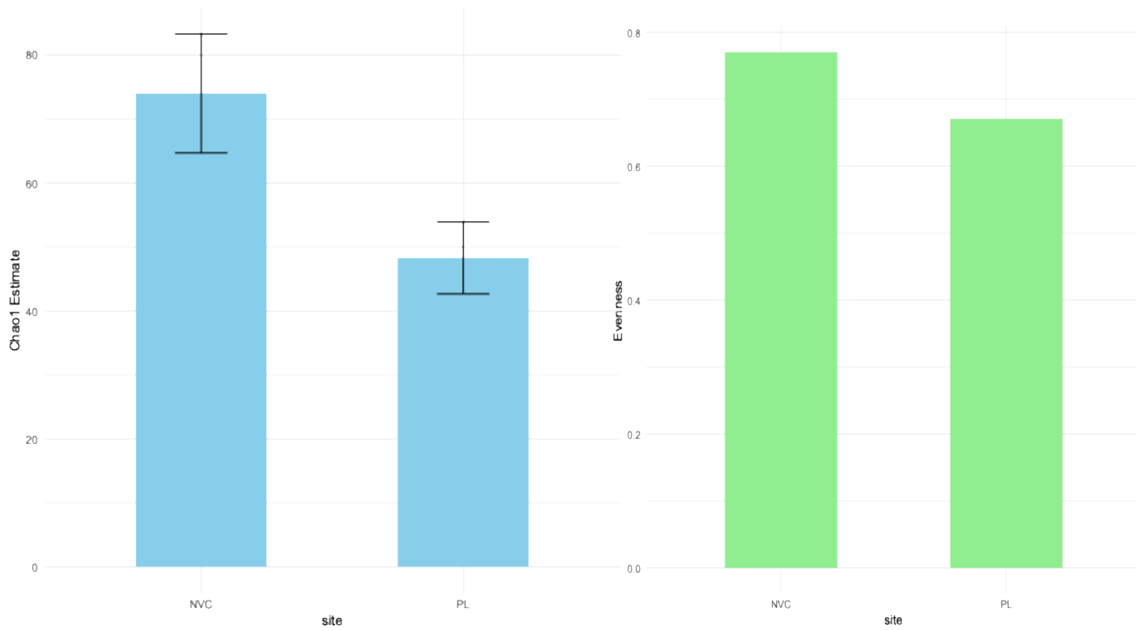

Figure 4.4. Species richness (Chao1 estimate) (left panel) with error bars representing 95% confidence intervals. The right panel illustrates species evenness based on Pielou's index, indicating the relative distribution of individuals among species at NVC and PL sites.

<u>Non Metric Multidimensional Scaling</u>

The Non-metric Multidimensional Scaling (NMDS) analysis using Bray-Curtis dissimilarities produced a two-dimensional ordination and a stress value of 0, indicating a perfect representation of the species data in two-dimensional space. Procrustes analysis comparing the ordination solutions revealed a best fit root mean square error of 0.0210 and a maximum residual of 0.0309, indicating that at least some of the NMDS solutions were highly similar and stable.

Several bee species contributed distinctively to the ordination, reflecting their varied presence across the samples. For example, *Eucera edwardsii*, *Hoplitis albifrans*, *Lasioglossum* *glabriventre* and *Osmia paradisica* were all positioned prominently in the ordination space, with positive associations on both NMDS1 and NMDS2 (0.2695; 0.5304), suggesting their abundance on specific dates or conditions. *Bombus nevadensis* and *Bombus rufocinctus* showed unique positioning (0.4392; -0.3395), indicating that these two species occur in conditions or communities that are positively associated with factors driving NMDS1 but negatively associated with factors affecting NMDS2. *Panurginus torchioi* (0.1169; 0.3416) and *Halictus farinosus* (0.2092 ; 0.2101) showed positive associations along NMDS1 and NMDS2. *Lasioglossum titusi* and *Lasioglossum trizonatum* were located at the negative end of NMDS1 (-0.7081; -0.0059), indicating their lower association with the sampling points. *Lasioglossum sisymbrii* (-0.4987 ; 0.0960) and *Hoplitis hypocrita* (-0.4317; 0.0728) were also found at the negative end of NMDS1, indicating their presence was less strongly associated with the factors driving the ordination in those dimensions. *Bombus fervidus* exhibited a positive position on NMDS2 (0.1233; 0.2901), suggesting a unique occurrence pattern compared to other species like *A. mellifera* (-0.0563; -0.1284), which had a negative association along NMDS1 and NMDS2, reflecting differing ecological preferences or abundance (Table 4.2).

Certain sampling dates at PL, 8 August 2023 and 16 August 2023, were positioned close together in the lower portion of the ordination (Figure 4.5), suggesting that the bee species composition during these dates was more similar. On the other hand, 6 June 2023 and 14 June 2023 at PL are positioned further away from these later dates, suggesting that the bee community in early June was notably different compared to later in the summer. This might reflect seasonal differences in species activity, with certain bees being more prevalent in early summer while others peak in mid-to-late summer (Figure 4.5).

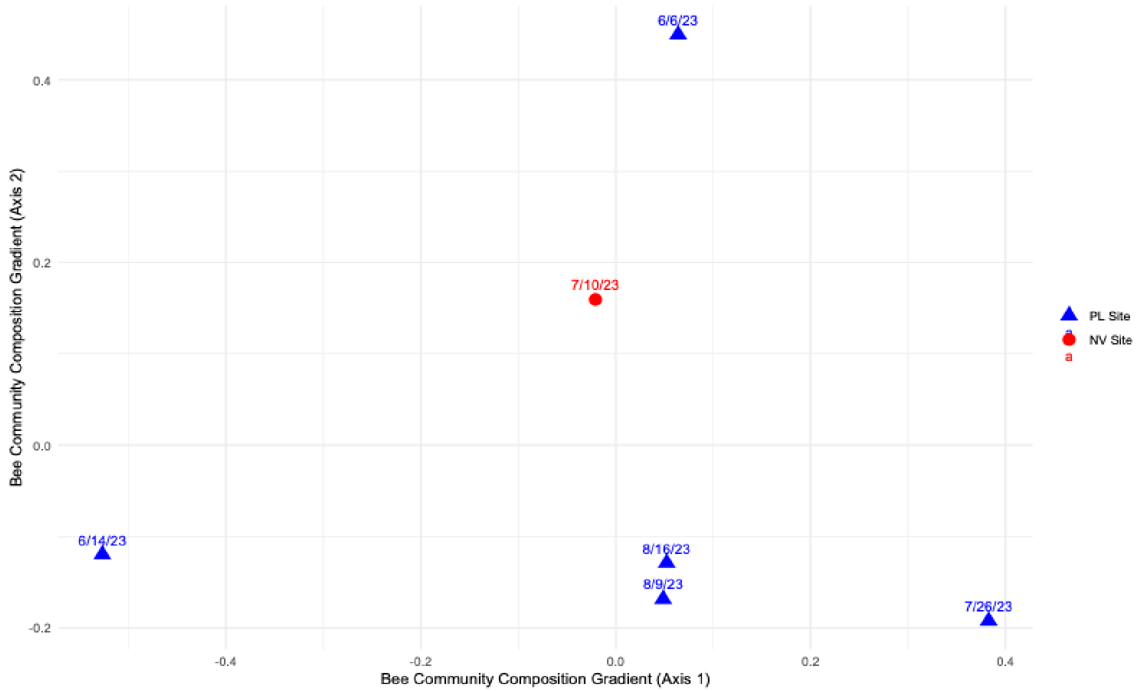

Figure 4.5. Ordination plot displaying the results of a multivariate analysis. Red circles North Valley Creek and blue triangles are Plant Lane. The axes represent gradients in species composition, with points closer together indicating more similar communities. Points closer to 0 suggest that these samples are more similar to one another.

The site scores provide a two-dimensional representation of the sampling dates and sites in the NMDS ordination (Table 4.2). The PL site on 6 June 2023 had a NMDS1 score of 0.20489 (moderately positive) and a NMDS2 score of 0.42544 (strongly positive) and was positioned in the upper-right quadrant of the ordination, indicating a distinct species composition along both NMDS1 and NMDS2. This suggests that the bee community at this site and date differs significantly from other sites along both axes. At the PL site on 14 June 2023 the NMDS1 score was -0.53835 (strongly negative) and the NMDS2 score was -0.00469 (close to zero) and was placed further to the left on the NMDS1 axis, indicating a strong difference in species composition along this axis compared to other dates. The NMDS2 score was close to zero, suggesting that this site shares similar characteristics with other sites along the NMDS2 axis (Table 4.2).

At Plant Lane on 26 July 2023 the NMDS1 score was 0.33393 (strongly positive) and the NMDS2 score was -0.27230 (moderately negative) and was located in the lower-right quadrant of the NMDS plot. This suggests the species composition is distinct along NMDS1, and the moderately negative NMDS2 score indicates a difference in species composition compared to other sites. For PL on 8 August 2023 the NMDS1 score was -0.01498 (close to zero) and the NMDS2 score was -0.20116 (moderately negative) and it was similar to other sites along NMDS1 (close to zero) but shows a moderate difference on NMDS2, placing it in the lower-left quadrant, indicating a different community structure or species composition along the NMDS2 axis. At PL on 16 August 2023 the NMDS1 score was 0.01556 (close to zero) and NMDS2 was -0.10388 (slightly negative) and is near the origin on NMDS1, indicating similarity to other sites along this axis, but the slightly negative NMDS2 score suggests a moderate difference in species composition along NMDS2 (Table 4.2).

Table 4.2 Non-metric multidimensional scaling (NMDS) site scores for bee species composition representing the coordinates for each sampling date and site in the ordination space.

NMDS1	**NMDS2**	**Site**	**Date**
-0.0010527	0.1566033	NVC	7 July 2023
-0.5383508	-0.0046963	PL	14 June 2023
0.20489494	0.42543723	PL	6 June 2023
0.3339267	-0.2723049	PL	26 July 2023
0.01555916	-0.1038793	PL	16 August 2023
-0.0149773	-0.20116	PL	8 August 2023

North Valley Creek single sampling day was 7 July 2023, which had a NMDS1 score of -0.00105 (very close to zero) and a NMDS2 score of 0.15660 (moderately positive) (Table 4.2) and is positioned near the origin of the NMDS1 axis suggests it shares some characteristics with other sites but is distinctly positive on the NMDS2 axis. This could indicate the bee species composition at this site and date is different from others. Overall, the differences in site scores across the dates suggest variability in bee species composition, with some dates showing strong distinctions (e.g., PL on 6 June 2023 and 26 July 2023) and others being more similar to one another (e.g., PL on 8 August 2023 and 16 August 2023). The NVC site 7 July 2023 is somewhat isolated from the PL site, aligning with its sampling on only one date, and reflects its distinct species composition (Figure 4.5).

Discussion

This survey presents the first baseline survey of bee species abundance, richness, and composition at two grassland sites on the Flathead Reservation in northwest Montana. Over one growing season, a total of 42 unique bee species were recorded. This information provides an understanding of the abundance of bee species present in this area and can be used for future monitoring and conservation efforts. Together, the measured factors—abundance, species richness, evenness, and composition—are needed to assess pollination services and maintain ecosystem resilience. Bees are essential for the health and resilience of grasslands, particularly in ecosystems facing degradation from invasive species and land-use changes (Sexton and Emery 2020).

The four most abundant species were *Lasioglossum incompletum* (137 individuals), *Halictus tripartitus* (112 individuals), *Agapostemon foxii angelicus* (98 individuals), and *Halictus farinosus* (27 individuals). These dominant species are critical for understanding the ecosystem's structure as they likely play significant roles in pollination activities. *Agapostemon* and some *Lasioglossum* species can display communal behavior with aggregative nesting habits, suggesting that these sites may be near one of these species' nesting aggregations or that the time of year we are sampling favors these particular species (Kueneman et al. 2024; Everaars et al. 2018). This variation could also be due to differences in habitat, floral resources, or other ecological factors (Novotny et al., 2021). Similarly, *H. tripartitus*, a common ground-nesting species, may also be benefiting from local habitat conditions, such as soil composition or floral availability, which support its nesting and foraging behaviors.

The presence of many species with lower counts (12) indicates a diverse community with numerous rare species, which are critical for maintaining ecological resilience (Lande, 1996). While a few species dominate the community, the numerous low-abundance species contribute to overall biodiversity and species richness. This balance of highly abundant and rare species contributes to the community's evenness and ecological stability. Interestingly, despite the high bee species richness, a single flowering species dominated at each site. Although greater floral diversity is often associated with better conditions for bees, some research suggests that areas with fewer types of flowers may actually provide sufficient foraging sites for bees and other pollinators (Liira and Jürjendal, 2023). This dominance of a single flowering species may reflect such conditions, providing optimal foraging resources for pollinators. It is important to highlight here that even if fewer in abundance, other flowering species were likely visited by bees (Mallinger et al., 2016).

The lack of studies on bee-plant associations in grassland ecosystems highlights the need for more research, which aims to understand how diverse floral morphology can support abundant and diverse bee populations (Burkle et al., 2020). Despite the degraded condition of our sites, the baseline data show high diversity, richness, and evenness indices values having moderate to high biodiversity. This unexpected diversity, richness, and evenness highlights the resilience of the bee community, which continues to thrive despite the prevalence of non-native and invasive species. These findings suggest that even in areas where restoration efforts have not fully re-established native plant communities, bees are still able to find adequate resources. Invasive forbs may be providing sufficient habitat and foraging opportunities, underscoring the adaptability of bees to altered landscapes (Roof et al., 2018; Burkle et al., 2019). If high richness and evenness are beneficial for ecosystem stability and resilience (Glenny et al. 2023), then both sites likely house bee communities that are providing pollination services. Since both sites exhibit moderately healthy bee diversity, conservation efforts should aim to maintain these levels. If there are any management practices unique to one site, understanding their impact could help improve or maintain biodiversity in the other site.

A potential limitation to consider is that these richness values represent data from just three months (June-August) in 2023. Given that interannual variation in bee abundance, richness, and community composition is common, it becomes challenging to define what "maintaining" these values would look like without conducting additional long-term monitoring. For instance, the composition of bumble bee communities varies across different landscape contexts, elevations, and seasons, highlighting the importance of considering habitat variability and sequential sampling, in conservation strategies (Hatten et al. 2013). Another potential limitation is with the use of bee bowl traps for sampling due to their inability to accurately capture true bee abundance and their bias in sampling different species unevenly. Bee bowl traps often fail to provide meaningful data for detecting population declines, as they are passive and influenced by environmental variables. To improve bee monitoring, alternatives such as molecular methods, nest censusing, mark-recapture studies, and targeted plant sampling are proposed to offer more reliable and precise assessments of bee population trends (Portman et al 2020; Larson et al. 2024; Packer and Darla-West 2021).

Interestingly, the NVC site on 7 July 2023, while isolated from the PL dates, positioning near the center of the species composition data suggests that while distinct, this community shares certain characteristics with the broader bee populations observed across the PL dates. The unique composition observed at NVC could be due to localized environmental factors, but without further sampling at NVC, firm conclusions about temporal dynamics at the site remain speculative. Meanwhile, the distribution of PL samples across different portions of the data emphasizes the dynamic shifts in bee communities over time. These shifts highlight the importance of environmental conditions in shaping bee activity and species composition. Such temporal variation is critical to ensuring pollination services and ecosystem resilience, especially when different plant species require pollination at different times (Roof et al., 2018; Burkle et al., 2019). Both sites have similar richness and evenness of species, suggesting a healthy and balanced bee community at each location.

Research in grassland ecosystems has demonstrated that bee species richness varies significantly based on habitat quality and restoration efforts. For instance, a study in eastern Nebraska compared wild bee communities across remnant tallgrass prairies, high-diversity prairie restorations, and low-diversity restorations or degraded grasslands (Lamke et al., 2022). The findings indicated that high-diversity restorations supported the highest average richness and abundance of both bees and native forbs during the midseason, while remnant prairies consistently supported bees throughout all seasons. In contrast, low-diversity restorations or degraded grasslands attracted fewer bee species, highlighting the impact of habitat quality on bee diversity (Lamke et al., 2022). Similarly, a meta-analysis of grassland restorations revealed that restored sites generally exhibited higher bee species richness compared to degraded grasslands (Sexton and Emery, 2020). The study emphasized that native prairie and grassland habitats, with their high forb richness and abundance, provide essential support for pollinator communities. However, widespread habitat destruction has led to significant declines in these ecosystems, underscoring the importance of restoration efforts in enhancing bee diversity (Sexton and Emery, 2020). These studies suggest that while invasive species and habitat degradation can negatively affect bee diversity, restoration efforts can significantly improve bee species richness in grassland ecosystems. The diversity and abundance of bees at our study sites, despite the presence of invasive species, align with findings from similar grassland habitats that have undergone restoration and still support diverse pollinator populations. This comparison suggests that despite the current state of degradation, these ecosystems retain enough habitat complexity to support a resilient bee community. By using this baseline as a reference point, Tribal managers can better assess the effectiveness of management interventions and adapt strategies to mitigate emerging threats to both pollinators and grassland ecosystems.

CHAPTER FIVE

CONCLUSIONS: REFLECTIONS AND RECOMMENDATIONS

The interconnectedness of the Séliš, Ksanka, and Ql'ispé people with their ancestral grasslands has been at the core of every step in this research. Throughout the study, each chapter has built upon a common goal: to restore balance and resilience to the Intermountain foothill grasslands of the Flathead Reservation that are being overrun with invasive annual grasses (IAG). By integrating a range of scientific methods, ecological principles, and cultural values, this work reflects the complexity and depth of the restoration challenge, underscored by the spiritual and cultural significance these lands hold for the Tribes. This project examined the effectiveness of different herbicide treatments combined with no-till drill seeding of native grasses and forbs to restore Intermountain foothill grasslands on the Confederated Salish and Kootenai Tribes' (CSKT) grasslands in northwestern Montana. These grasslands have been severely degraded by the invasion of *Bromus tectorum* (cheatgrass), *Ventenata dubia* (ventenata), *Taeniatherum caput-medusae* (medusahead), and *Bromus japonicus* (Japanese brome). These IAG have displaced native species and significantly altered ecosystem dynamics (Majeski et al., 2024; Sheley and Mangold, 2003). As part of this research, I explored the impact of various herbicides and seeding treatments on IAG control, as well as the ability of native grasses, forbs, and shrubs to establish under these conditions; furthermore, I wanted to understand what impacts that restoration tactics and management processes were having on populations of bees.

Chapter one provided the foundation by establishing the ecological context and the threats posed by IAG which have dramatically altered these grasslands. The literature review detailed the extensive research on IAG management and the delicate balance of using herbicides and revegetation. While herbicides show promise in controlling IAG in the short term, the challenge is not simply about reducing their populations (Monaco et al., 2017; Mangold et al., 2013; Wallace et al., 2015), but also about creating space for native species to reestablish dominance—species that have cultural and ecological value to the Tribes and others that depend upon these critical ecosystems (personal communications Dupuis, 2018). The review emphasized how historical land use, climatic change, and IAG have destabilized historic vegetation characteristics, necessitating a careful and deliberate approach to restoration (Maher et al., 2024; Polley et al., 2013; Ridder et al., 2021).

Chapter two focused on experimental efforts aimed at reestablishing desired native species in these invaded grasslands. The combination of herbicide treatments and seeding methods formed the core of this field study, seeking to determine which approaches would effectively control IAGs while simultaneously supporting the growth of native and culturally significant species of perennial grasses, forbs, and shrubs. The herbicides tested in this study varied widely in their efficacy against the four target IAGs. Rimsulfuron, sulfosulfuron, and indaziflam consistently emerged as the most effective, reducing IAG cover by 96%, 71%, and 71%, respectively, nine months after treatment. These results are consistent with previous findings that have reported significant reductions in IAG cover with rimsulfuron and sulfosulfuron application across different soil types (Crose, 2022; Hirsch et al., 2012; Wallace and Prather, 2016). However, despite the initial success of rimsulfuron and sulfosulfuron, their efficacy diminished in the second year, allowing IAG cover to rebound. Furthermore, initial seeding results showed that while certain herbicides reduced IAG cover, they were insufficient on their own to support the robust establishment of seeded species. This raised important questions about herbicide non-target effects and competition from IAGs and other invasive plants, pointing to the complexity of restoring such disturbed ecosystems. The failure of seeding treatments in this study highlights the need for more robust revegetation strategies. Future efforts should consider using a combination of treatments, including; scarification, soil amendments (e.g., arbuscular mycorrhizal fungi inoculation), increasing seed rates, using more desirable yet weedy early successional species, herbicide protective seed coatings, recycled paper mulch, and targeted irrigation to improve seed-to-soil contact and moisture availability, particularly in drought-prone regions like northwestern Montana (Neuenkamp et al., 2019; Luedloff et al., 2022; Holfus et al., 2021; Sheley et al., 2006).

Building on the field study, I recognized the need for a more controlled environment to test the effect of IAG herbicides on native species used for revegetation, leading to the greenhouse experiment outlined in Chapter three. At the Montana State University Plant Growth Center I aimed to understand more precisely how herbicide treatments interact with seeded species, free from the variability and unpredictability of field conditions. This chapter offered insights into the viability of different seeding and herbicide combinations and can help inform future field applications. *Gaillardia aristata* and *Thinopyrum intermedium* showed some tolerance to indaziflam, and with the proper timing these species/herbicide combinations could provide desired early successional planting. Our results also suggest that while indaziflam can effectively manage IAG its use in revegetation projects should be monitored closely due to its strong negative impact on seedling emergence, requiring careful consideration of species tolerance. Imazapic and rimsulfuron both significantly suppressed emergence and biomass, though their impacts were less severe than indaziflam. *Lupinus argenteus* showed the least overall injury across all treatments, while among grasses *Festuca idahoensis* exhibited the highest injury under rimsulfuron, and *Thinopyrum intermedium* had the least injury in sulfosulfuron. Given the variability in herbicide effects, site specific and tailored herbicide and species selection strategies are recommended for maximizing revegetation success in IAG-infested grasslands (Orloff et al., 2015). This greenhouse study was important for isolating the effects of herbicides on native seed emergence, biomass, and injury—all factors that are vital to long-term restoration success (Mangold et al., 2015; McManamen et al., 2018; Monaco et al., 2017). By understanding these dynamics better, we can refine our approaches to maximize native plant recovery without compromising the ecosystem's integrity.

An important aspect of my research was the need to establish a baseline for pollinator populations. Pollinators are essential to the ecological health of these grasslands, supporting the reproductive success of many native species (McNally, 2015). Chapter four explored how the loss of floral diversity due to IAG invasion has diminished habitat and resources for pollinators. A widely recognized hypothesis, supported by research across multiple studies (Mallinger et al., 2016; Liira and Jürjendal, 2023; Carman and Jenkins, 2016), is that the loss of native flowering forbs and shrubs has directly impacted pollinator diversity and abundance, highlighting the importance of restoring these plant species. The establishment of a pollinator baseline helps not only in tracking the recovery of these ecosystems but also in ensuring that restoration efforts consider the broader ecological networks essential to grassland health. This baseline can confirm questions of richness and evenness to allow managers to know if restoration efforts are affecting pollinators abundance. In a single growing season I was able to confirm that, although heavily degraded by both IAG and invasive forbs, my two study sites were still able to support a diverse and even population of wild bees.

Moving forward it is essential that we apply what we have learned from both the field and greenhouse studies to refine and adapt our management strategies. For instance, one of the key management recommendations is the integration of herbicide application with precise seeding strategies. Ensuring that seeded species have the best chance of establishment will require continual monitoring and adaptive management. Additionally, pollinator-friendly flowering plant species should be prioritized in restoration efforts, recognizing that pollinator health is a keystone for the broader ecosystem's recovery. This study contributes to a broader understanding of IAG management and restoration strategies, building upon existing literature (Hirsch et al., 2012; Mangold et al., 2013; Fowers and Mealor, 2020; Wallace and Prather, 2016). The results of this research offer valuable insights into the potential of herbicide applications for short term IAG control and the challenges associated with native species restoration in semi-arid grasslands.

The invasion of non-native species like *B. tectorum, B. japonicus, T. caput-medusaea,* and *V. dubia* represents more than an ecological disturbance—it disrupts the balance of a living, breathing landscape that has sustained the Tribes' cultural heritage for too many generations to count. The grasslands are more than ecosystems—they are sacred spaces, deeply woven into the spiritual and cultural fabric of the Tribes. Restoring these grasslands is an act of healing, a reclamation of ancestral stewardship and a commitment to future generations. The CSKT's relationship with the land is one of reciprocity and respect, deeply intertwined with traditional ecological knowledge and a profound understanding that the land provides when cared for, and in return, demands thoughtful guardianship. By combining modern restoration techniques with a respect for the wisdom of the land and the people who have lived in harmony with it, we move closer to a future where these grasslands continue to thrive, reflecting the enduring bond between the Tribes and their homeland. In this way, the restoration of these grasslands is a path toward renewed ecological balance, cultural resilience, and spiritual fulfillment for the CSKT, whose enduring connection to this land remains at the heart of this work.

In conclusion, effective grassland restoration requires a holistic approach, integrating multiple management strategies, including selective herbicide use and careful species selection, to enhance the success of revegetation efforts. Working with the knowledge that our efforts to restore the Intermountain foothill grasslands on the Flathead Indian Reservation is not only a scientific endeavor, but also a deeply spiritual and cultural journey; ultimately, I approached this work with respect and commitment. For the CSKT, these lands hold profound significance, embodying not only their history, but their identity, traditions, and future. These grasslands, though impacted and degraded by invasive species and disturbances, remain vibrant and resilient, continuing to provide essential resources for wildlife and pollinators, medicine for healing, and resources for the people who have stewarded this land for generations. There is a need for long-term commitment, not only to the science of restoration but also to the cultural connection that the Tribes have with their ancestral lands.

Lemlmtš ~ hu sukiɫq̓ukni

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