

USING ECOLOGICAL THEORY TO GUIDE THE IMPLEMENTATION  
OF AUGMENTATIVE RESTORATION

by

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## ABSTRACT

Invasive organisms are now considered the second worst threat to native biological biodiversity, behind habitat loss and fragmentation. Successful control of invasive plants can have unexpected impacts on native plants and wildland systems. Therefore, it is important for managers of invasive species to become increasingly concerned with more than target invaders, but also ecological mechanisms and processes like invasion resistance, environmental heterogeneity, and succession that direct plant community dynamics. Augmentative restoration is a management approach that augments existing ecological processes by selectively repairing and replacing those processes that are damaged or missing thereby directing plant communities in a desirable direction. Our overall objective was to test the concept of augmentative restoration. Our overall hypothesis was that successional processes occurring at high levels could be augmented by selectively repairing or replacing successional processes that occur at low levels to increase desired species composition. In a split plot design with 4 replications at 3 sites, 8 factorial treatment combinations from 3 factors (shallow tilling, watering, and seeding) were applied to whole plots, and 2,4-D was applied to sub plots. Cover and density of seeded species, *Centaurea maculosa*, and *Potentilla recta* as well as existing native and exotic forbs and grasses were sampled in 2002 and 2003 to produce pre-treatment and post-treatment data. ANCOVA was used to analyze cover and density data using pre-treatment data as a baseline covariate. Data indicated that areas with high percent bare ground required seeding and watering to increase seeded species and native forbs, while seeding and tilling increased seeded species and native forbs in areas of high soil moisture. *C. maculosa*, *P. recta*, and exotic forbs decreased in response to tilling and 2,4-D. Exotic and native grasses increased in response to tilling and 2,4-D indicating that grasses may have reproduced primarily vegetatively. This data provided evidence that augmentative restoration could provide managers with an ecological framework to develop restoration procedures that address invasion resistance, environmental heterogeneity, and succession in order to enhance native forbs and grasses as well as improve the emergence of seeded species to increase desired plant composition in wildlands damaged by invasive plants.

## CHAPTER 1

## INTRODUCTION

Invasive organisms are now considered the second worst threat to native biological biodiversity, behind habitat loss and fragmentation (Pimm and Gilpin 1989). In addition to displacing native plant species, invasive plants alter soil water dynamics by increasing erosion and reducing infiltration (Lacey et al. 1989), disrupt nutrient cycling (Chapin et al. 1997), and alter disturbance regimes (Vitousek et al. 1996). Invasive species cost states millions of dollars annually in control and lost production, and in Montana alone, spotted knapweed (*Centaurea maculosa* Lam.) costs the livestock industry \$11 million a year (Hirsch and Leitch 1996, Pimentel 2002). It is clear that invasive species have resulted in huge ecological and economic costs to society (Mooney and Hobbs 2000). The severity of these impacts prompted a 1999 Executive Order from the White House creating the National Invasive Species Council as well as a Biodiversity Treaty signed at the United Nations' 1992 Earth Summit that recognizes the threat that invading species pose to biodiversity.

At the global, federal, and state levels, several management tools have been implemented to control or eradicate invasive species. Control and eradication efforts have shown success in removing undesired invaders which may be promoting the recovery of native biodiversity (Myers et al. 2000). Despite this progress, these approaches often require indefinite investment of time, tools, and money to sustain control, and the existing or resulting plant community are not always considered (Sheley

et al. 1996). Consequently, successful control can have unexpected impacts on native species and wildland systems (Myers et al. 2000). For example, the control of one invader may provide the opportunity for other invasive species to establish (DiTomaso 2000), control tools may negatively impact desired native species in the system (Rice et al. 1997), or continual reinvasions may occur (Bussan and Dyer 1999). Sheley et al. (1996) has proposed using ecological understandings of whole wildland systems to improve the outcome of invasive plant management practices.

Augmentative restoration is an approach to managing invasive plant dominated wildlands that uses ecological mechanisms and processes to guide management practices in order to address the whole ecological system. Augmentative restoration is defined as a strategy that enhances existing ecological processes by selectively repairing and replacing those processes that are damaged or missing, thereby directing plant communities in a desirable direction (Bard et al. 2003). This approach incorporates ecological principles like invasion resistance and functional diversity, environmental heterogeneity, as well as succession.

### Invasion Resistance and Functional Diversity

Functionally diverse plant communities have been considered more resistant to invasion than less diverse communities because resource availability to invading species has been reduced (Tilman et al. 1997, Fargione et al. 2003). Functional characteristics of species, like differences in rooting depths, differences in resource demand throughout the growing season, or differences in nutrient preferences (nitrate versus ammonium versus

dissolved inorganic nitrogen) can influence resource use within a community (Hooper and Vitousek 1997). Greater native functional diversity can allow greater access to available resources increasing total resource uptake resulting in fewer resources available to invasive species.

Elton (1958) was first credited with stating the hypothesis that species-rich plant communities are less susceptible to invasion than are species-poor ones. Currently, the relationship between diversity and invasion resistance has been disputed where small-scale experiments have tended to support Elton's hypothesis, but regional scale studies have tended to show evidence for the reverse (Levine and D'Antonio 1999). Resolution of this contradiction has centered on making a distinction between population level effects of diversity from diversity effects occurring at the ecosystem level (Levine et al. 2002). Within an ecosystem, diversity covaries with environmental factors like disturbance, resource availability, and propagule supply. When environmental factors promote native species diversity, they may similarly favor the occurrence of invasive species diversity (Naeem et al. 2000). Therefore, two complementary hypotheses have resulted from this debate: 1) diversity increases invasion resistance at the population level and 2) diversity effects on invasion resistance can be weak relative to environmental factors that covary with diversity at the ecosystem level (Levine et al. 2002).

Augmentative restoration attempts to establish functionally diverse native plant communities in order to increase invasion resistance at the population level. At the ecosystem level, augmentative restoration attempts to address heterogeneity in environmental factors that may covary with diversity.

### Environmental Heterogeneity

Environmental heterogeneity is considered by many ecologists as a valuable ecological mechanism that can help explain and predict species composition and even maintain functionally diverse species in many systems (Huston 1994, Pickett and Cadenasso 1995, Loreau et al. 2003). Environmental heterogeneity includes variation in factors like resource availability (Pacala and Tilman 1994), disturbance (Ohsawa et al. 2002), propagule supply (Reed et al. 2000), and topography (Augustine 2003) that contribute to the structural complexity of the environment. These environmental factors influence the distribution and abundance of species, and variation in these factors can explain how different species can coexist (Crawley 1997). Huston (1994) explains that different functional types use different resources, use the same resources in different ways, or use the environment in a way that allows them to avoid competition with other functional types. Therefore, greater structural heterogeneity and more types of resources in an environment will increase the number of functional types that can be present (Huston 1994).

Heterogeneity in environmental factors can support an increase in the functional diversity of both native and invasive species (Levine 2000, Deutschewitz et al. 2003). Differential preferences in environmental factors can influence whether native versus invasive species are favored (Deutschewitz et al. 2003). For example, heterogeneity due to disturbance tends to support invasive species diversity more so than landscapes heterogeneous in other environmental factors (Pysek et al. 2002). Therefore, understanding how the heterogeneity in environmental factors differentially influence

native versus invasive species may be important in promoting desired species and limiting undesired species diversity at the ecosystem level. Augmentative restoration addresses the heterogeneity in successional mechanisms and processes in order to support environmental factors promoting native species diversity and limit environmental factors promoting invasive species diversity.

### Succession

Successional theory plays a considerable role in ecosystem preservation, management, and restoration (Bazzaz 1996, Whisenant 1999, Young et al. 2001, Walker and del Moral 2003). Succession is the recovery process of vegetation following any disturbance (Bazzaz 1996), and ecosystem restoration can be viewed as managed assistance with this process (Young et al. 2001). Ecologists have been developing successional theory for over 100 years producing several contrasting views (Walker and del Moral 2003). De Luc was first credited with the use of the word succession in 1806, but Clements (1916) provided the first conceptual framework of succession in which plant communities were considered deterministic and unidirectional moving toward a stable climatic endpoint. His ideas dominated successional theory for the next 50 years despite contrasting concepts offered by Gleason (1939) where succession was considered indeterminant and unpredictable depending on the properties of individual species. Finally in the 1950's, ecologists moved away from Clementsian succession and toward Gleason's reductionist approach. Successional studies began focusing on mechanistic explanations of succession based on data collected on individual species in particular

habitats (Pianka 1970, Pickett 1976, Harper 1977). A new wave of conceptual models resulted from successional experimentation including the r (rapid reproduction) and K (carrying capacity) strategist model (MacArthur 1972); the facilitation, tolerance, and inhibition models (Connell and Slatyer 1977); the ruderal, competitive and stress tolerant species model (Grime 1979); as well as the vital attributes model (Noble and Slatyer 1980). Pickett et al. (1987) further developed the concept of vital attributes by proposing a hierarchical list of ecological processes that may influence succession. Tilman (1988) proposed the resource ratio model suggesting that succession is driven by vegetation response to changing resource levels. Assembly rules have also been considered in order to explain species assembly into plant communities during succession (Drake 1990).

This review of successional theory indicates the complexity of ecosystems and plant community dynamics. Inevitably, validity can be credited to all of these theories depending on the questions being asked or the circumstances to which the theory is being applied. For restoration of invasive plant dominated wildlands, the successional framework proposed by Pickett et al. (1987) provides a basis for developing hypotheses, studying succession, and developing management strategies at different sites. This hierarchical framework includes a list of ecological processes that are grouped based on three general causes of succession (site availability, species availability, and species performance), and each of the processes is further delineated by specific ecological factors (Table 1). Manipulating the three causes of succession for resource management involves: 1) designing disturbances to create or eliminate site availability, 2) controlling colonization to promote or limit propagule availability and establishment of specific plant

species, and 3) controlling species performance to promote or limit the growth and reproduction of specific plant species (Luken 1990). This successional framework has been applied to invasive plant management (Sheley et al. 1996) and wildland restoration (Whisenant 1999). Augmentative restoration uses this framework to address the heterogeneity in environmental factors influencing successional processes that may promote native species diversity and limit invasive species diversity in order to establish and maintain functionally diverse, invasive species resistant plant communities.

Table 1.1. Causes of succession, contributing processes, and modifying factors. <sup>a</sup>

Causes of Succession	Contributing Processes	Modifying Factors
Site Availability	Disturbance	Size, severity, time intervals, patchiness, predisturbance history
Species Availability	Dispersal	Dispersal mechanisms and landscape features
	Propagules	Land use, disturbance interval, species life History
Species Performance	Resources	Soil, topography, climate, site history, microbes, litter retention
	Ecophysiology	Germination requirements, assimilation rates, growth rates, genetic differentiation
	Life history	Allocation, reproduction timing and degree
	Stress	Climate, site-history, prior occupants, herbivory, natural enemies
	Interference	Competition, herbivory, allelopathy, resource availability, predators, other level interactions

<sup>a</sup>Modified from Pickett et al. 1987

### Augmentative Restoration

Augmentative restoration is an approach to restoring desired plant communities on wildlands degraded by invasive species by using ecological mechanisms and processes to guide the development of restoration programs. We define augmentative restoration as a strategy that augments existing ecological processes by selectively repairing and replacing those processes that are damaged or missing, thereby directing plant communities in a desirable direction (Bard et al. 2003). This approach relies on a successional framework proposed by Pickett et al. (1987) which was modified by Luken (1990) for resource management and applied to invasive plant management by Sheley et al. (1996) as well as wildland restoration by Whisenant (1999). This framework guides the identification of key ecological processes within a particular wildland system that are influencing succession (site availability, species performance, and species availability). Often wildland systems are heterogeneous and ecological processes vary across the landscape. Therefore, measurement criteria are developed in order to survey this heterogeneity. Based on this survey, a restoration program is developed that augments existing ecological processes by selectively repairing or replacing damaged or missing ecological processes as they vary within the system. For example in some areas, site availability may already exist at high levels, but species availability and species performance occur at low levels. In this case, designing disturbances may not be required, but controlling colonization and controlling species performance may be required to increase desired species composition.

## Objectives

Our overall objective was to test the ecological framework and concept of augmentative restoration. We hypothesized that successional processes occurring at high levels can be augmented by selectively repairing and replacing successional processes that occur at low levels. The study was conducted to meet four specific objectives and test four specific hypotheses. The objectives and associated hypotheses were:

I. To determine the response of controlling colonization and controlling species performance in areas where site availability already occurred at high levels on the desired plant community. Our underlying hypothesis was that controlling colonization combined with controlling species performance would augment high site availability to increase desired species composition. More specifically, we hypothesized that dispersing desirable seeds combined with watering would augment high site availability to increase desired species composition.

II. To determine the response of designing disturbances and controlling colonization in areas where species performance occurred at high levels on the desired plant community. Our underlying hypothesis was that designing disturbances and controlling colonization would augment high species performance to increase desired species composition. More specifically, we hypothesized that shallow tilling and seeding would augment high species performance to increase desired species composition.

III. To determine the response of designing disturbances and controlling species performance in areas where species availability occurred at high levels on the desired plant community. Our underlying hypothesis was that designing disturbances and

controlling species performance would augment high species availability to increase desired species composition. More specifically, we hypothesized that shallow tilling and watering would augment high species availability to increase desired species composition.

IV. To determine the response of 2,4-D on *Centaurea maculosa* Lam. and *Potentilla recta* L. as well as the desired plant community. We hypothesized that 2,4-D would enhance seedling establishment of desired species by reducing competition from *C. maculosa* and *P. recta*.

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## CHAPTER 2

USING ECOLOGICAL THEORY TO GUIDE THE IMPLEMENTATION OF  
AUGMENTATIVE RESTORATION: RESPONSE OF SEEDED SPECIES AND  
TARGET INVASIVE SPECIESIntroduction

Current management of invasive species often focuses on control, with limited consideration of the existing or resulting plant community (Sheley et al. 1996). Successful control can have unexpected impacts on native species and wildland systems (Myers et al. 2000). For example, the control of one invader may provide the opportunity for other invasive species to establish (DiTomaso 2000), control tools may negatively impact desired native species in the system (Rice et al. 1997), or continual reinvasions may occur (Bussan and Dyer 1999). Therefore, managers of invasive species are becoming increasingly concerned with more than target invaders, but also the establishment and maintenance of desired plant communities (Zavaleta et al. 2001).

Land managers often consider the introduction and establishment of desirable competitive plants a worthwhile addition to their invasive plant management program. The revegetation process often follows traditional agricultural practices which is suitable for many non-native species (Harker et al. 1993), but can be inappropriate for native species (Wilson and Gerry 1995). For example, the application of fertilizers can be a common practice in revegetation programs, but native species are adapted to low nutrient conditions while invasive species are often adapted to high nutrient conditions (McLendon and Redente 1991). It is also becoming increasingly clear that the

establishment of plant populations does not necessarily restore ecosystem processes (Simenstad and Thorn 1996). Therefore, understanding ecosystem processes which promote native species and limit invasive species is critical to successfully establishing desired plant communities.

Augmentative restoration is an approach that uses ecological processes to guide management practices. Augmentative restoration is defined as a strategy that augments existing ecological processes by selectively repairing and replacing those processes that are damaged or missing, thereby directing plant communities in a desirable direction (Bard et al. 2003). This approach incorporates ecological mechanisms and processes like invasion resistance and functional diversity, environmental heterogeneity, as well as succession.

Establishing and maintaining invasion resistant plant communities involves restoring functionally diverse species that occupy a majority of the niches and promote continuous resource capture making fewer resources available for invasive species (Carpinelli 2000, Pokorny 2002, Fargione et al. 2003). Environmental heterogeneity is considered by many ecologists as a valuable ecological mechanism that can help explain and predict species composition and even maintain functionally diverse species in many systems (Huston 1994, Pickett and Cadenasso 1995, Loreau et al. 2003). Successional processes regulate plant community change over time. By manipulating successional processes, plant communities may be directed toward functionally diverse invasion resistant populations (Sheley et al. 1996, Whisenant 1999, Sheley and Krueger-Mangold 2003).

Augmentative restoration is based on a mechanistic successional framework proposed by Pickett et al. (1987) that includes three causes of succession (site availability, species availability, and species performance), processes that influence these causes, and factors that modify these processes. This framework can provide a basis for studying and designing successional management strategies at different sites.

Manipulating the three causes of succession involves: 1) designing disturbances to create or eliminate site availability, 2) controlling colonization to decrease or enhance availability and emergence of specific plant species, and 3) controlling species performance to decrease or enhance the emergence and establishment of specific plant species (Luken 1990).

This framework can be used to guide management across heterogeneous landscapes where ecological processes influencing site availability, species availability, and species performance vary. For example in some areas, processes influencing site availability may already exist at high levels, but species availability and species performance processes occur at low levels. In this case, designing disturbances may not be required, but controlling colonization and controlling species performance may be necessary to increase desired species composition.

Designed disturbances, controlled species performance, and controlled colonization can be accomplished in many ways depending on existing landscape conditions. Appropriate procedures must be selected specifically for a particular landscape. Where site availability is absent, shallow tilling could be used to design disturbances creating safesites for desirable species establishment with minimal release of

subsurface nitrogen (N). Deep tilling should be avoided, since it can promote high N availability which can favor invasive plant establishment (Tilman 1987, McLendon and Redente 1991, Herron et al. 2001). Watering could be used to control species performance shifting the competitive balance away from invasive species like *Centaurea maculosa* Lam. promoting the successful establishment of desired species (LeCain 2000). Where desirable species are absent or existing species are incapable of colonization, broadcast seeding could be an effective way to control colonization. Broadcast seeding could supplement the existing vegetation providing a seed source for functionally diverse native species (Whisenant 1999). Herbicide application could be used to design disturbances by opening niches filled by undesired species, control species performance by reducing the performance of undesired species, and/or control colonization by reducing seed sources of undesirable species. In many restoration studies, herbicides have been required to control weeds during the establishment phase (Borman et al. 1991, Carpinelli 2000), but it is unknown whether weed control is necessary in successional management for desired species establishment.

Our overall objective was to test the ecological framework and concept of augmentative restoration. We hypothesized that successional processes occurring at high levels can be augmented by selectively repairing and replacing successional processes that occur at low levels to increase seeded species. The study was conducted to meet four specific objectives and test four specific hypotheses. The first objective was to determine the effects of seeding and watering in areas of high percent bare ground due to vole disturbance on seeded species and target invasive species. We hypothesized that

dispersing desirable seeds combined with watering would augment high percent bare ground to increase seeded species and reduce target invasive species. The second objective was to determine the effects of shallow tilling and seeding in areas of high soil moisture on seeded species and target invasive species. We hypothesized that shallow tilling and seeding would augment areas with high soil moisture to increase seeded species and reduce target invasive species. The third objective was to determine the effects of shallow tilling and watering in areas of high percent cover native species on seeded species and target invasive species. We hypothesized that shallow tilling and watering would augment areas with high percent cover native species to increase seeded species and reduce target invasive species. The fourth objective was to determine the effects of 2,4-D on *Centaurea maculosa* and *Potentilla recta* L. as well as seeded species. We hypothesized that 2,4-D would enhance emergence and establishment of seeded species by reducing competition from *C. maculosa* and *P. recta*.

## Methods

### Study Area

Augmentative restoration was tested on the Kicking Horse Wildlife Mitigation Area south of Ronan, Montana (47° 29' N, 114° 5' W). This area was characterized by ephemeral prairie pothole wetlands. The soil was characterized as a deep, well drained silt loam and silty clay loam soil (glaciolacustrine deposits) with sodic properties within the top 76 cm. The slope varied from 2 to 15 percent and the elevation was 940 m.

Average annual precipitation ranged from 350-450 mm per year and average temperature was 7.6° C.

This area lies on a *Festuca scabrella*-*Agropyron spicatum* habitat type (Mueggler and Stewart 1980) dominated by *C. maculosa* and *P. recta*. Remnant stands of native species included *Achillea millifolium* L., *Agropyron smithii* Rydb., *Agropyron spicatum* (Pursh) Scribn. & Smith, *Festuca scabrella* Torr., *Gaillardia aristata* Pursh., *Geranium viscosissimum* F. & M., *Juncus balticus* Willd., *Koeleria cristata* Pers., *Lupinus sericeus* Pursh., *Monarda fistulosa* L., and *Poa sandbergii* Vasey. Historical disturbances associated with this site included grazing by cattle and intense meadow vole (*Microtis pennsylvanicus*) activity. The more palatable species of this habitat type, *Festuca idahoensis* Elmer and *A. spicata*, were far less common than the less palatable species, *F. scabrella*, *P. sandbergii*, and *Danthonia intermedia* Vasey.

Vole activity, hydrology, as well as propagule pools and dispersal were ecological processes specific to this site that influenced the three causes of succession (site availability, species availability, and species performance). Vole activity created disturbances influencing site availability, propagule pools and dispersal of different species influenced species availability, and the hydrology affected soil moisture levels influencing species performance. Vole activity provided tilled bare-soil microhabitats (55% bare ground) for colonization, while the colonization of these bare sites was constrained by the abundance and type of propagules available at the site (4-17% cover native species). Meanwhile, soil moisture gradients associated with the interspersed wetlands influenced the growth and reproduction of native or invasive species. LeCain

(2000) found that *C. maculosa* establishment and growth was inhibited in transitional zones between wetland and upland areas. The Kicking Horse Wildlife Mitigation Area was heterogeneous in these ecological processes.

### Experimental Sites

Three different experimental sites were established within the Kicking Horse Mitigation Area representing heterogeneity in the ecological processes influencing the three causes of succession (site availability, species performance, species availability). The heterogeneity was identified based on criteria that categorized ecological processes as occurring at low or high levels. The extent of vole activity (site availability) was measured by estimating percent bare ground, and  $\leq 10\%$  bare ground was considered low while  $\geq 30\%$  bare ground was considered high. Propagule supply (species availability) was measured by estimating percent cover of native species, and 0 to 5% cover native species was considered low, while 15 to 20% cover native species was considered high. Soil moisture (species performance) was first measured in May using a neutron probe (Hignett and Evett 2002), and 25 to 30% soil moisture integrated over the top 40 cm (upland areas) was considered low, while 30 to 35% soil moisture integrated over the top 40 cm (transition between upland and wetland areas) was considered high.

Based on these criteria, the landscape was surveyed and three experimental sites were identified. At site one, percent bare ground (55%) was high, while percent soil moisture (27%) and cover of native species (11%) were low (Figure 2.1). Percent soil moisture was high (33%), at the second site, while percent bare ground (4%) and percent

cover native species (4%) were low (Figure 2.2). At the third site, percent cover of native species was high (17%) while soil moisture (29%) and percent bare ground (2%) were low (Figure 2.3). Throughout this chapter, site one is represented by high site availability (SA), site two is represented by high species performance (SPP), and site three is represented by high species availability (SA).

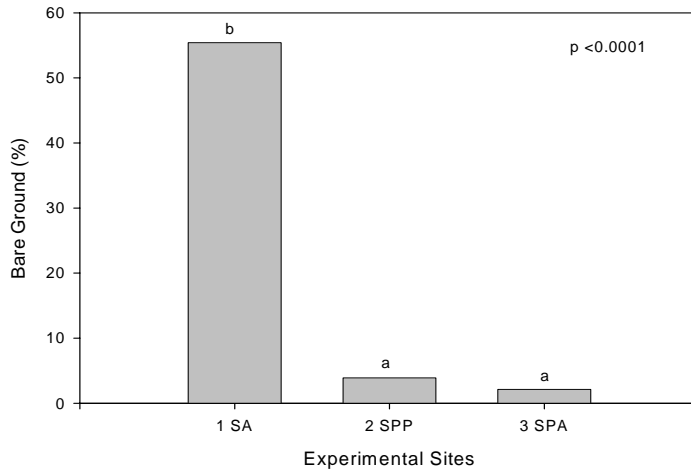


Figure 2.1. Percent bare ground at sites 1, 2, and 3. Analysis performed using ANOVA and Fisher's LSD procedure ( $\alpha = 0.05$ ) on square root transformed data. Non transformed means are presented.

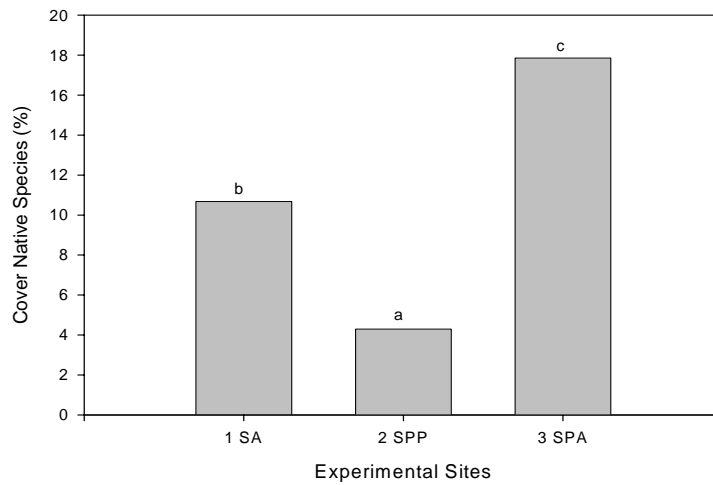


Figure 2.2. Percent cover native species at sites 1, 2, and 3. Analysis performed using ANOVA and Fisher's LSD procedure ( $\alpha = 0.05$ ) on square root transformed data. Non transformed means are presented.

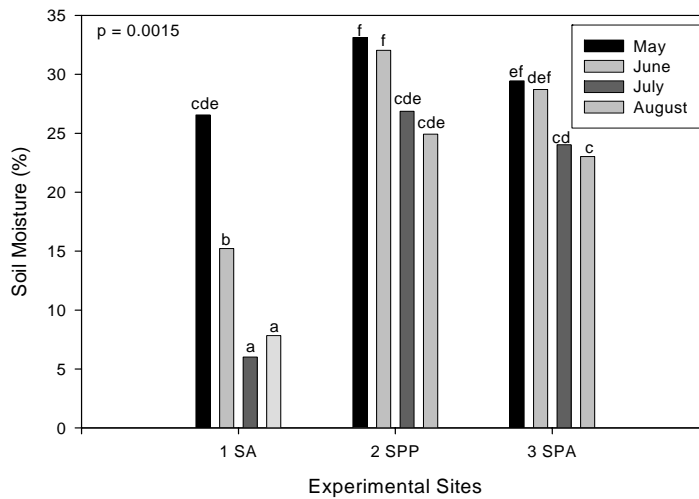


Figure 2.3. Percent soil moisture (upper 40 cm) in May, June, July, and August at sites 1, 2, and 3. Analysis performed using ANOVA and Fisher's LSD procedure ( $\alpha = 0.05$ ).

### Experimental Design

In a split plot design with four replications, 8 factorial treatment combinations from three factors: 1) shallow tilling or no shallow tilling, 2) watering or no watering, and 3) seeding or no seeding were applied to whole plots in three experimental sites. Sub plot treatments were application or no application of 2,4-D.

### Procedures

In May 2002, 32 plots (8 treatments replicated 4 times) were established within each of the three experimental sites generating a total of 96 plots. Plots were 1 by 2 m with 2 m between plots to ensure independence between plots. In late September 2002, 2,4-D was applied to half of every plot at a rate of 2 kg acid equivalence ha<sup>-1</sup> with a backpack sprayer. Conditions were clear with wind <5 mph and air temperature of 12.8°C. Two,4-D is a broad spectrum, broadleaf herbicide that provides about 90% control of *C. maculosa* and *P. recta* for up to one year. Its short half-life and soil binding properties make it an appropriate herbicide for this prairie pothole habitat (Dewey et al. 1997).

In mid October 2002, vole fences were constructed to prevent vole seed predation from occurring in plots (Maron and Simms 2001). Galvanized hardware cloth (0.625 cm mesh) attached to T fence posts every 3 m was buried 30 cm deep and extended 60 cm above ground. The fencing was topped with aluminum flashing (22.5 cm wide) to prevent voles from climbing over the top of the fences. Mouse traps were used to remove voles from within each fenced area.

Once voles were excluded, shallow tilling (site availability) and seeding (species availability) treatments were randomly applied to appropriate plots in late October 2002. Plots were rototilled to a depth of 5 cm. Following the tilling treatment, plots were broadcast seeded at a rate of 34 kg ha<sup>-1</sup>. The seed mixture consisted of six grasses (17 kg ha<sup>-1</sup>) and five forbs (17 kg ha<sup>-1</sup>) including *Agropyron spicatum* (5 kg ha<sup>-1</sup>), *Festuca scabrella* (5 kg ha<sup>-1</sup>), *Koeleria cristata* (1.75 kg ha<sup>-1</sup>), *Juncus balticus* (1.75 kg ha<sup>-1</sup>), *Poa sandbergii* (1.75 kg ha<sup>-1</sup>), *Agropyron smithii* (1.75 kg ha<sup>-1</sup>), *Gaillardia aristata* (3.4 kg ha<sup>-1</sup>), *Geranium viscosissimum* (3.4 kg ha<sup>-1</sup>), *Achillea millefolium* (3.4 kg ha<sup>-1</sup>), *Lupinus sericeus* (3.4 kg ha<sup>-1</sup>), and *Monarda fistulosa* (3.4 kg ha<sup>-1</sup>). These species represented key functional groups within the habitat type. Seed company, state of origin, and species variety for each seeded species are presented in Table 2.1. Germination and viability tests were performed on fifty seeds per species replicated four times to estimate percentage of seeds that will germinate and, of the seeds that did not germinate, percentage that are living or viable versus those that are not living or nonviable (Table 2.2).

In May, June, and July 2003, watering treatments (species performance) were randomly applied to appropriate plots. Water was added at a rate of one third (135 mm) the average annual precipitation (400 mm) based on NOAA weather data from a station located within 10 km from the study area. Water was applied on plots at a rate of 45 mm in a single watering event in early May, June, and July 2003. The timing of watering corresponded with the first three months of the growing season. Based on work by LeCain (2000), this water level should influence species performance adequately to shift

the competitive balance away from *C. maculosa* and promote successful establishment of seeded species.

Table 2.1. Seeded Species, Variety, Seed Company, and State of Origin.

Seeded Species	Variety	Seed Company	State of Origin
<i>Agropyron spicata</i>	Secar	Granite Seed Co. <sup>1</sup>	Washington
<i>Festuca scabrella</i>		Granite Seed Co.	Montana
<i>Koeleria cristata</i>		Wind River Seed <sup>2</sup>	Montana
<i>Juncus balticus</i>		Wind River Seed	Wisconsin
<i>Poa sandbergii</i>		Granite Seed Co.	Washington
<i>Agropyron smithii</i>	Rosana	Granite Seed Co.	Washington
<i>Gaillardia aristata</i>		Wind River Seed	Oregon
<i>Geranium viscosissimum</i>		Granite Seed Co.	Utah
<i>Achillea millefolium</i>		Granite Seed Co.	Washington
<i>Lupinus sericeus</i>		Native Seed Found. <sup>3</sup>	Idaho
<i>Monarda fistulosa</i>		Wind River Seed	Wyoming

<sup>1</sup>Granite Seed Co. 1697 W. 2100 N. Lehi, UT 84043; <sup>2</sup>Wind River Seed 3075 Lane 51 ½ Manderson, WY 82432; <sup>3</sup>Native Seed Foundation Star Route Moyie Springs, ID 83845.

Table 2.2. Germination and Viability of Seeded Species.

Species	Germination	Viable	Nonviable
<i>Agropyron spicata</i>	90%	4%	6%
<i>Festuca scabrella</i>	24%	2%	74%
<i>Koeleria cristata</i>	60%	12%	28%
<i>Juncus balticus</i>	63%	15%	22%
<i>Poa sandbergii</i>	67%	25%	8%
<i>Agropyron smithii</i>	88%	6%	6%
<i>Gaillardia aristata</i>	81%	2%	17%
<i>Geranium viscosissimum</i>	14%	50%	36%
<i>Achillea millefolium</i>	78%	2%	21%
<i>Lupinus sericeus</i>	0%	94%	6%
<i>Monarda fistulosa</i>	72%	1%	18%

### Sampling

Plots were sampled in 2002 prior to treatments and again in 2003 after treatments.

Plots were sampled for percent bare ground, percent cover and density of seeded species

and target invasive species, and soil moisture. Percent bare ground was sampled simultaneously with percent cover and density of plant species within a 20 cm by 50 cm frame placed randomly flat on the ground. Percent bare ground and percent cover plant species was estimated using a modified Daubenmire method (Daubenmire 1970). This method was modified to provide actual estimates of percent cover in order to obtain continuous rather categorical data. Density was determined by counting numbers of plants per species within the 20 cm by 50 cm frame. Prior to treatments, cover and density were estimated in mid July 2002 within three randomly placed frames per plot. After treatments, sampling occurred in mid July 2003 within two frames per sub plot providing four samples per plot. Volumetric water content in the upper 15 cm of the soil profile was measured at three random locations in each plot from May to August during 2003 using Time Domain Reflectometry to provide an indication of how the treatments influenced soil moisture (Jones et al. 2002).

### Analysis

Analysis of covariance was used to determine the effects associated with block, shallow tilling, seeding, watering, and 2,4-D on the cover and density of seeded species, *C. maculosa*, and *P. recta*. Pretreatment cover and density was used as a baseline covariate. To test our specific hypotheses, sites were analyzed separately. All main effects, two-way interactions, and three-way interactions were included in the model, and all four-way and five-way interactions were pooled in the error term. Square root transformations on cover and density data were used to meet the ANCOVA assumptions of normality and homogeneity of variance. The model was progressively reduced by

removing three-way interactions that were not significant ( $\alpha = 0.05$ ). The Fisher's LSD procedure ( $\alpha = 0.05$ ) was applied to compare interaction means.

Analysis of variance was used to determine the effects associated with site, block, month, shallow tilling, seeding, watering, and 2,4-D on soil moisture. Because the ANOVA assumptions of normality and homogeneity of variance were met, no transformation was required on percent soil moisture data. Fisher's LSD procedure ( $\alpha = 0.05$ ) was used to compare means.

## Results

### Seeded Species

Seeding alone increased seeded species cover and density at site one ( $p=0.0063$ ,  $p<0.0001$ ), site two ( $p=0.0006$ ,  $p<0.0001$ ), and site three ( $p=0.0059$ ,  $p<0.0001$ ) (Figure 2.4). Watering alone also increased seeded species cover and density at site one ( $p=0.0032$ ,  $p=0.0005$ ), site two ( $p=0.0002$ ,  $p=0.0088$ ), and site three ( $p=0.0006$ ,  $p=0.0017$ ) (Figure 2.5). Tilling alone resulted in no significant difference in seeded species cover and density at any site. At site one characterized by high percent bare ground, seeding in combination with watering increased seeded species cover ( $p=0.0273$ ) from 2 % to 9 % and density ( $p<0.0001$ ) from 18 to 120 stems  $m^{-2}$  (Figure 2.6).

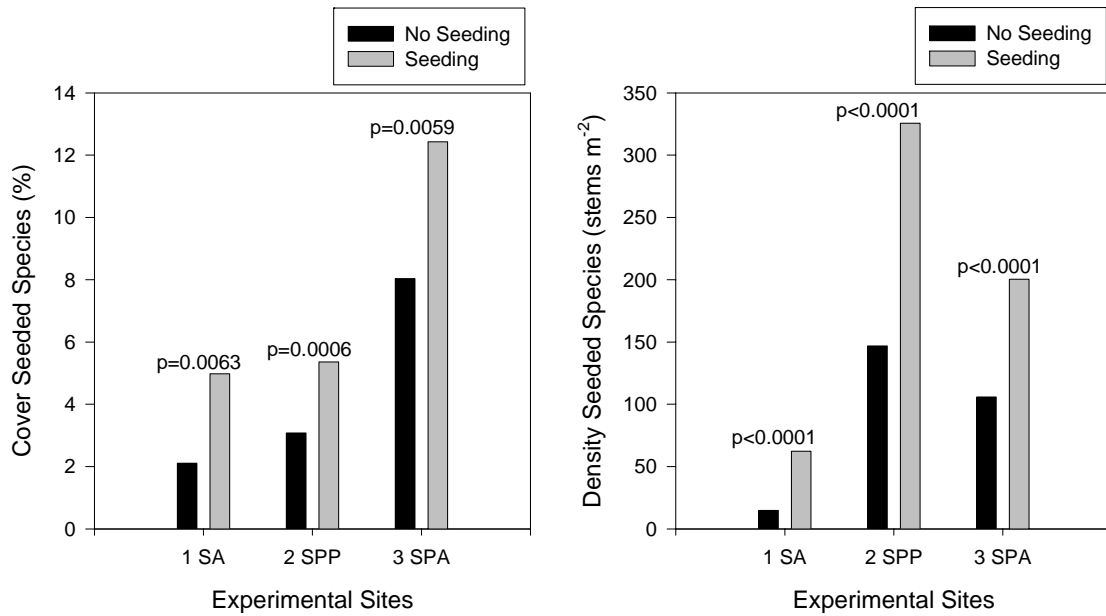


Figure 2.4. Percent cover and density of seeded species in response to seeding at sites 1, 2, and 3.

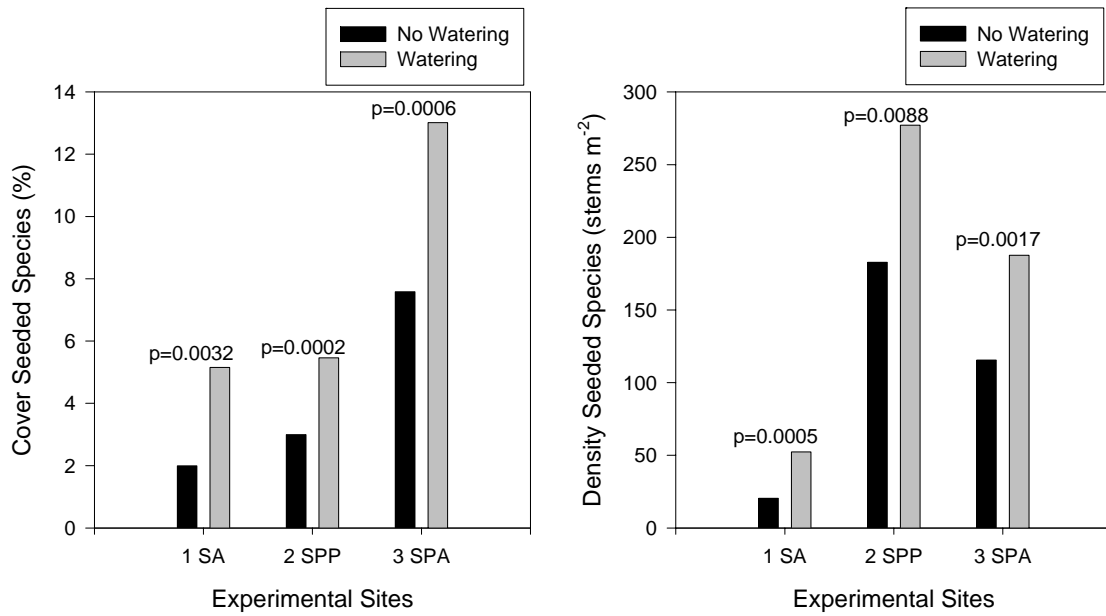


Figure 2.5. Percent cover and density of seeded species in response to watering at sites 1, 2, and 3.

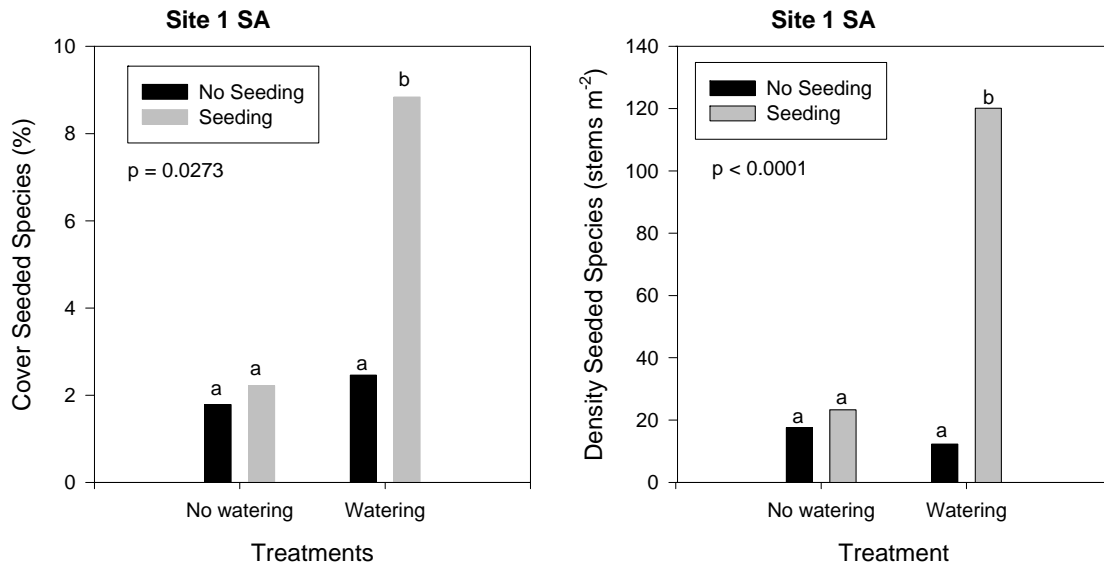


Figure 2.6. Percent cover and density of seeded species in response to seeding and watering at site 1.

At site two where soil moisture was considered high, seeding combined with tilling almost doubled the cover of seeded species as compared to the control ( $p=0.0085$ ). Without tilling there was no effect of seeding, but with tilling, seeding almost doubled seeded species cover (Figure 2.7). Watering in combination with tilling almost doubled the density of seeded species ( $p=0.008$ ) over the control at this site (Figure 2.7). Tilling, watering, and 2,4-D increased seeded species density ( $p=0.0099$ ) from 81 to 335 stems  $m^{-2}$ . Watering and tilling without 2,4-D was not different than watering without tilling in combination with 2,4-D on seeded species density (Figure 2.8).

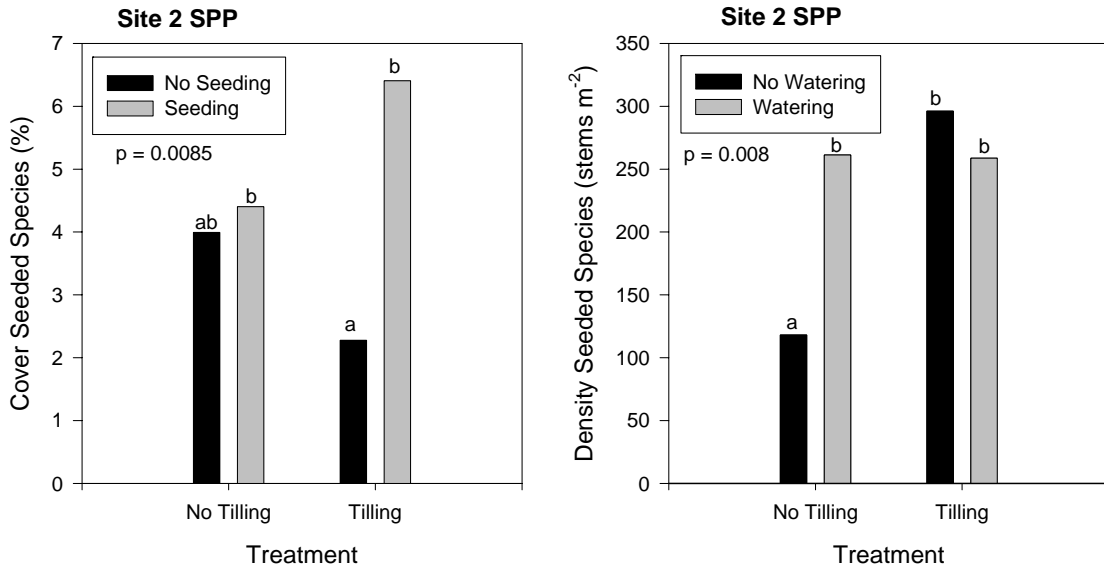


Figure 2.7. Percent cover of seeded species in response to seeding and tilling at site 2 and density of seeded species in response to watering and tilling at site 2.

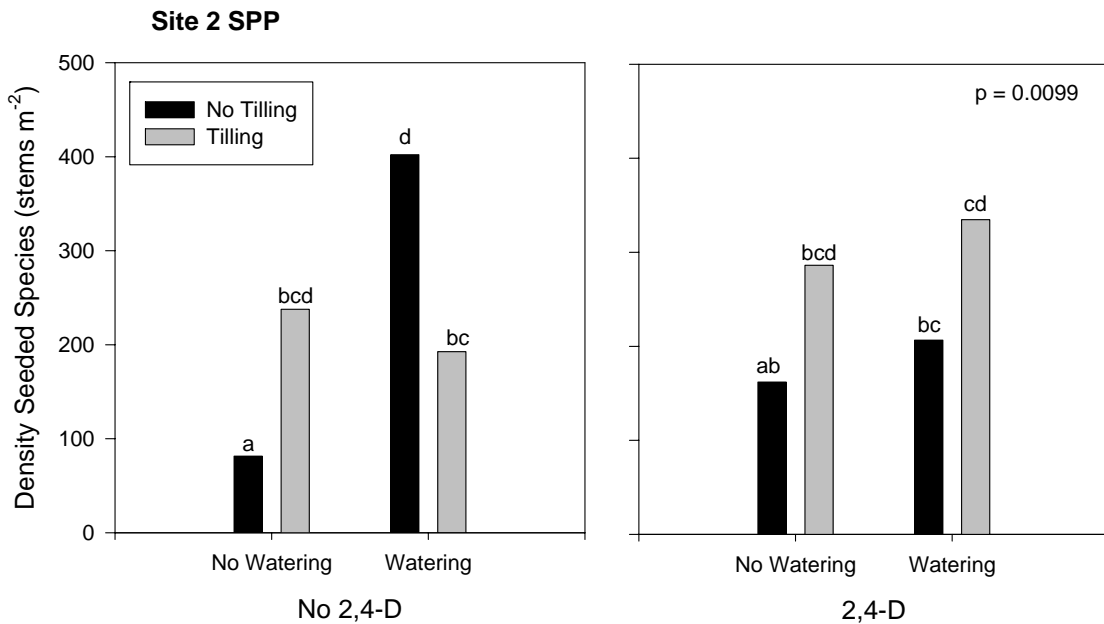


Figure 2.8. Density of seeded species in response to tilling, watering, and 2,4-D at site 2.

Where native species percent cover was considered high at site three, seeding and tilling increased ( $\alpha = 0.1$ ) seeded species cover from 10 to 13 % and increased ( $\alpha = 0.05$ ) seeded species density from 124 to 254 stems  $m^{-2}$ . For seeded species cover, there was a significant difference between seeding and no seeding only in the case where tilling occurred, but the tilling and seeding interaction was not different than the control (Figure 2.9). For seeded species density, a similar pattern occurred, but the tilling and seeding interaction significantly increased density as compared to the control (Figure 2.9).

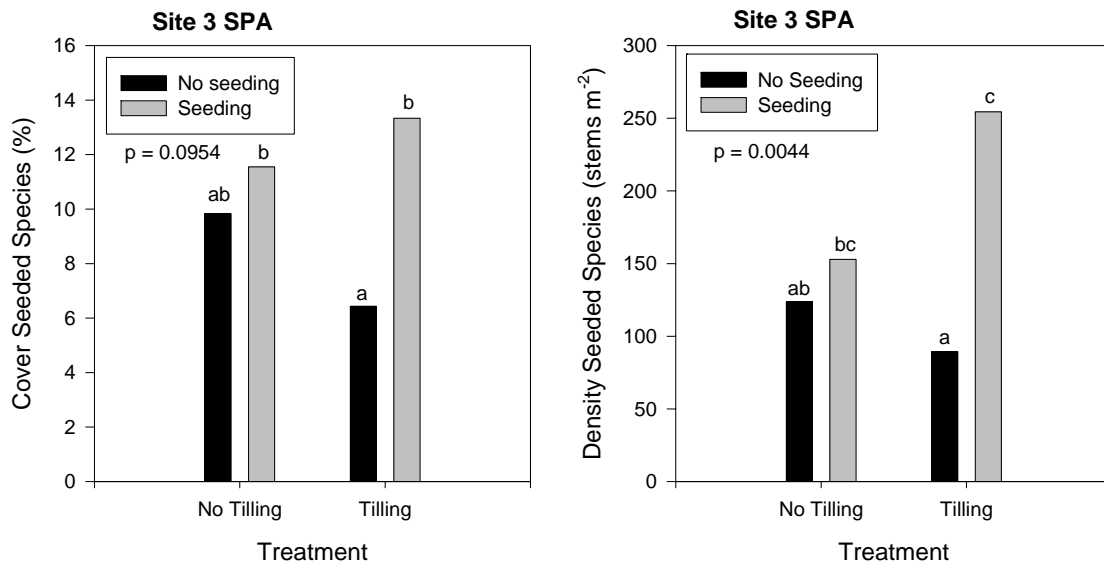


Figure 2.9. Percent cover and density of seeded species in response to seeding and tilling at site 3.

*C. maculosa* and *P. recta*

Tilling alone decreased the cover and density of *C. maculosa* and *P. recta* at all three sites, and watering alone increased the cover and density of *C. maculosa* and *P. recta* at sites two and three (Figure 2.10, Figure 2.11). Two,4-D decreased *C. maculosa* and *P. recta* cover ( $p < 0.0001$ ) and density ( $p = 0.0121$ ) by half of the control at site 2 (Figure 2.12). Tilling, watering, and 2,4-D maintained *C. maculosa* and *P. recta* densities ( $p = 0.005$ ) at the same level as the control. Without 2,4-D and no tilling, watering increased *C. maculosa* and *P. recta* density by four times the control. Without 2,4-D, tilling and watering resulted in no increase in *C. maculosa* and *P. recta* density. With 2,4-D, watering did not increase *C. maculosa* and *P. recta* density regardless of whether tilling occurred (Figure 2.13).

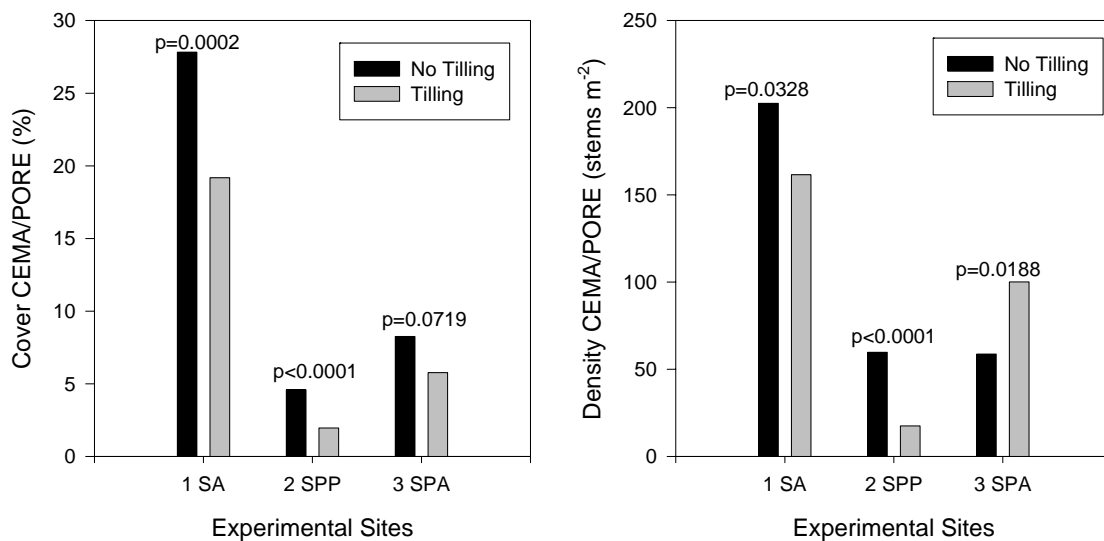


Figure 2.10. Percent cover and density of *C. maculosa* and *P. recta* in response to tilling at sites 1, 2, and 3.

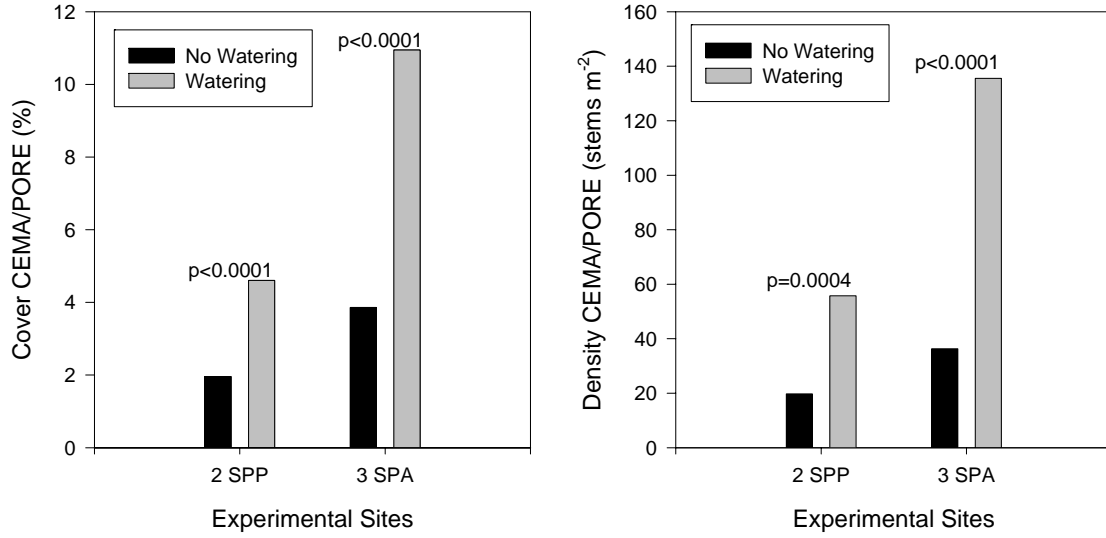


Figure 2.11. Percent cover and density of *C. maculosa* and *P. recta* in response to watering at sites 2 and 3.

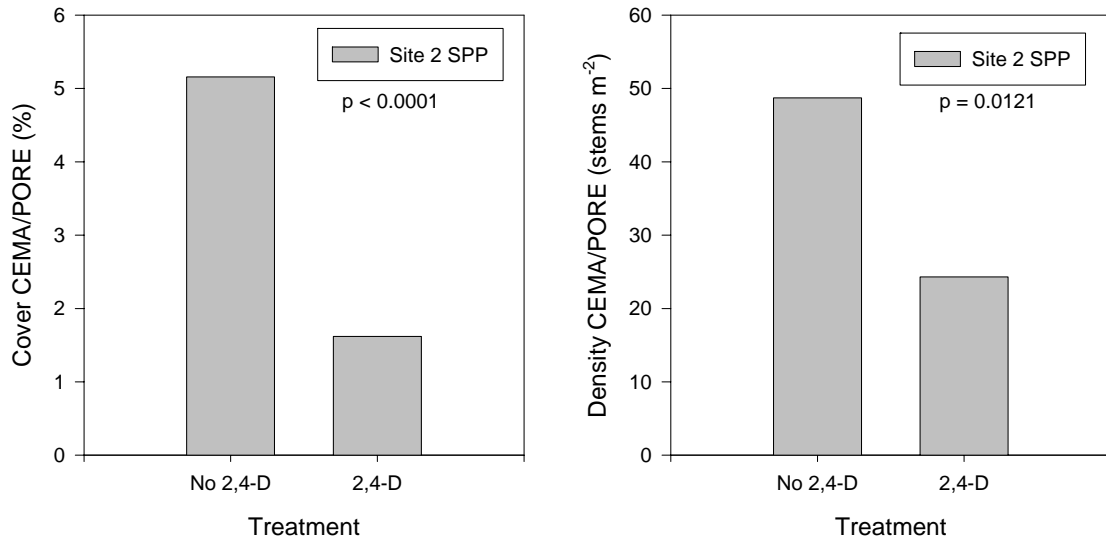


Figure 2.12. Percent cover and density of *C. maculosa* and *P. recta* in response to 2,4-D at site 2.

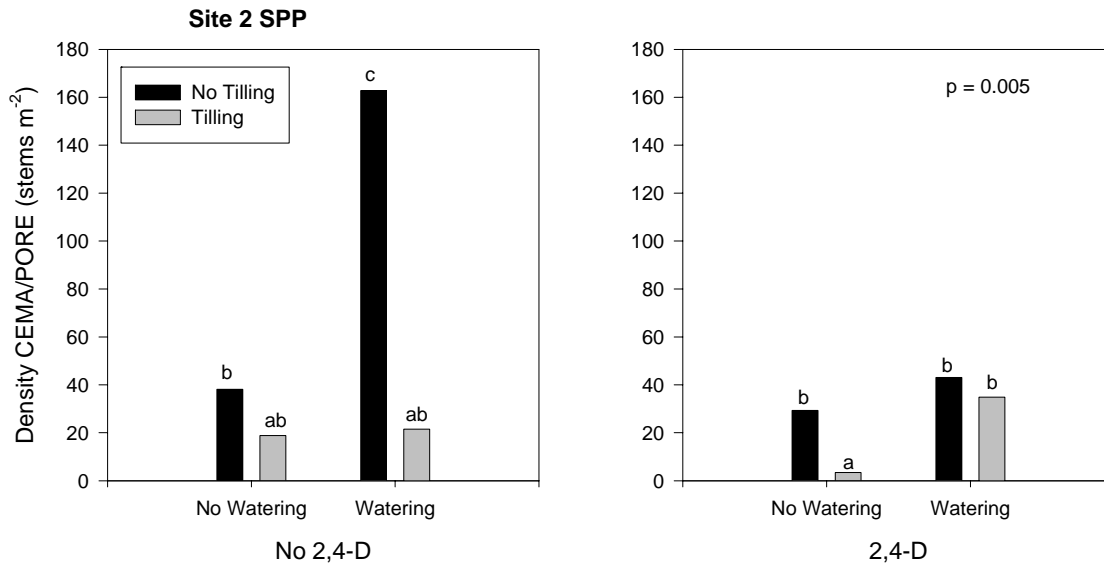


Figure 2.13. Density of *C. maculosa* and *P. recta* in response to tilling, watering, and 2,4-D at site 2.

### Soil Moisture

Conditions associated with site and month influenced percent soil moisture up to a 15 cm depth (Figure 2.14). Soil moisture at site one was lower in May (24.6%) and June (6.7%) than for site two (25.9%, 9.2%) and three (26.2%, 8.8%). In July, soil moisture at sites one (3.2%) and three (3.9%) were significantly lower than for site two (4.9%) and in August, soil moisture at site one (2.4%) was significantly lower than it was for the other two sites (3.7%, 3.9%).

Month and watering also influenced percent soil moisture (Figure 2.15). Percent soil moisture was significantly different between the months of May (~25%), June (~8%), July (~4%), and August (~3%). Watering increased percent soil moisture in May and June, but created no significant change in July and August. Shallow tilling and seeding treatments had no effect on percent soil moisture

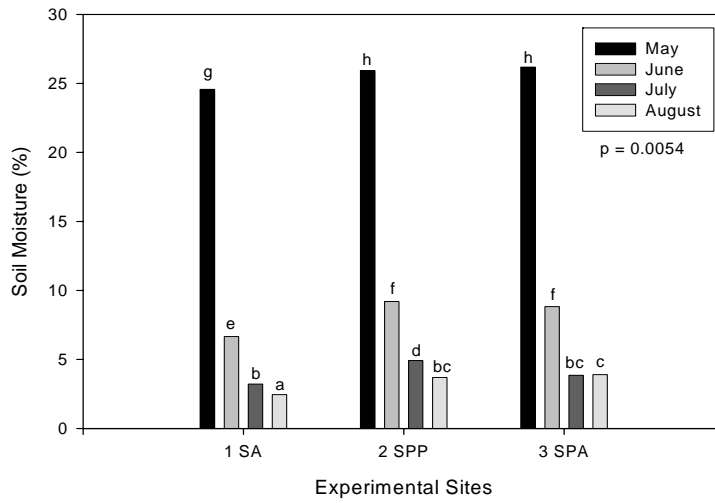


Figure 2.14. Percent soil moisture (upper 15 cm) response associated with site and month.

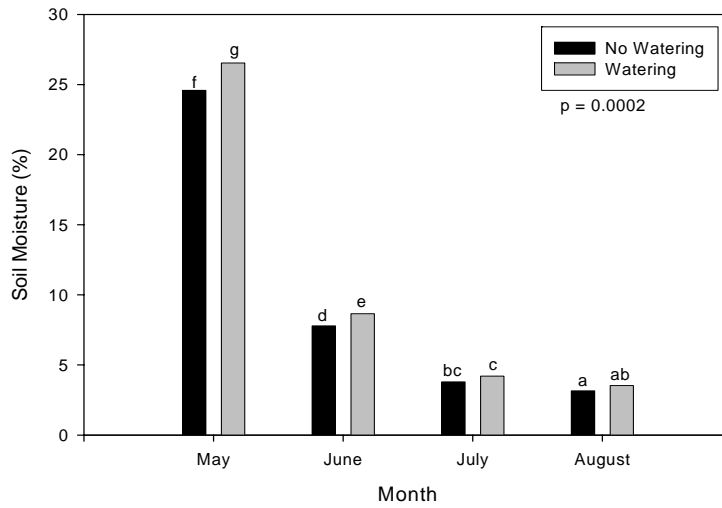


Figure 2.15. Percent soil moisture (upper 15 cm) response associated with month and watering.

## Discussion

Augmentative restoration attempts to use the heterogeneity in ecological processes that influence succession to increase desired species composition.

Succession is a long-term ecological process where long-term sampling of vegetation change can provide important information about the persistence of a particular trajectory (Wali 1999, Zedler and Callaway 1999). Emergence data represents the initial changes in plant community composition. Initial changes in plant community composition initiate and indicate the direction of successional dynamics (Whisenant 1999), and successful establishment of desired species often overcomes this critical barrier to successful restoration (Decker and Taylor 1985). By using the ecological principles that guide augmentative restoration, emergence of seeded species occurred at each of the three experimental sites.

Augmentative restoration provides a framework that allows managers to direct processes influencing all three causes of succession (Bard et al. 2003). We found that single treatments modifying processes influencing only one cause of succession did not create the most desirable outcome. For example, watering alone increased both seeded species as well as invasive plants, but watering combined with tilling and 2,4-D increased seeded species while controlling invasive plants. Tilling alone decreased invasive species in this study, but created no response in seeded species. Tilling in combination with seeding or watering increased seeded species. Similar results were produced by Sheley et al. (1999, 2005) where tilling and/or glyphosate were used to create safe sites and open niches to interact with broadcast seeding. Seeding alone may have increased seeded

species, but seeding combined with other treatments created an increase of greater magnitude. Similarly, Wilson and Gerry (1995) found seeding combined with herbicide and/or tilling created the highest native seedling densities. Combining treatments that augment ecological processes to influence all three causes of succession is critical to implementing augmentative restoration.

In most cases, we found evidence supporting our overall hypothesis that successional processes occurring at high levels can be augmented by selectively repairing and replacing successional processes that occur at low levels. For example, seeding combined with watering increased seeded species establishment in areas where vole activity increased site availability. Voles produce unpredictable episodic mounds that disturb the soil removing established plants and litter while changing soil conditions creating new opportunities for species establishment (Sousa 1984). Natural recolonization of vole mounds is limited by deep layer soil deposited on the surface containing low seed densities and covering seeds on the surface (Gutterman 1994). It has also been shown that mammal burrowing disrupts the physical structure of the soil which can decrease soil moisture (Huntley and Reichman 1994). These studies combined with our data support the hypothesis that seeding and watering can increase desired species composition, while tilling is unnecessary in areas disturbed by vole activity.

Additionally, where soil moisture was high influencing species performance, seeding (species availability) combined with tilling (site availability) significantly increased seeded species cover. ANOVA indicated that where remnant desired species were high, soil moisture was also high. In other words, where species availability was

high, species performance was also high and seeding combined with tilling significantly increased seeded species in these areas. Berlow et al. (2003) found that removal of sagebrush increased herbaceous biomass in mesic sites, but watering was required to increase herbaceous biomass in xeric sites. Soil moisture is highly variable and considered a critical limiting resource in arid and semiarid grasslands which can create strong spatial and temporal variation in herbaceous biomass (Burke et al. 1998). It is clear that understanding variation in soil moisture is critical to predicting successful establishment of seeded species. Our data supported our hypothesis that high soil moisture can be augmented by seeding and tilling, similar to that found by Berlow et al. (2003) for sagebrush removal.

We did not expect watering and tilling to increase the density of seeded species in areas with high soil moisture, but this outcome may indicate that this treatment combination promoted vegetative propagation of existing grasses. Belsky (1986) found that when grazing was eliminated which supported the growth of rhizomatous species, these vegetatively-reproducing species showed the greatest success in revegetating disturbances. In our study, shallow tilling created disturbances while watering may have supported the growth of rhizomatous grasses resulting in an increase in native grass density.

Assisting natural recovery of existing species is widely used in rangelands and forests where seed sources are available because it is a practical, low-cost alternative to planting or seeding (Barnett and Baker 1991). We expected that where percent cover native species was high, tilling combined with watering would increase desired species

establishment. It appeared that the remnant stands of desired species did not adequately provide propagules for natural colonization within the first growing season. Augmenting natural recovery of existing species from remnant stands often requires more time than establishing species by introduced seeds (Whisenant 1999). Data indicated that pre-existing soil moisture contributed more to increasing native forbs than colonization from remnant native stands. Site three was originally characterized by high native species cover, but analysis of pre-treatment soil moisture data indicated that this site had high soil moisture equivalent to site two. Therefore, data supported the hypothesis that high soil moisture could be augmented by seeding and tilling to increase native forbs at this site.

Our data indicated that developing appropriate criteria for characterizing site conditions is critical for designing appropriate augmentative restoration procedures. Developing threshold levels for ecological conditions based on a landscape survey and the ecological literature can be an effective approach to characterizing site heterogeneity. Ecological thresholds of plant species patterns and soil characteristics have been developed to determine whether jurisdictional wetland/upland boundaries coincide with ecological conditions (Kirkman et al. 1998). Environmental economists have been investigating ecological thresholds to guide conservation strategies (Eiswerth and Haney 2001, Muradian 2001). Ecological thresholds have also been explored for defining old-growth forest stands (Hunter and White 1997). When ecological conditions fall close to either side of a threshold, like the case of soil moisture for experimental site two and three, the threshold level may need to be adjusted to ensure that the heterogeneity is accurately characterized.

Decreasing *C. maculosa* and *P. recta* was dependent on creating disturbances by either shallow tilling or 2,4-D. Sheley et al. (1999, 2005) found that tilling or glyphosate doubled intermediate wheatgrass establishment and reduced *C. maculosa* compared to no disturbance. Similarly, Brown and Bugg (2001) found that seeded forb emergence was greatest when invasive plants were reduced with tilling. Our data indicated that tilling combined with seeding supported the establishment of seeded species while reducing invasive plants at sites two and three. Tilling provided safesites by opening niches once occupied by undesirable species (Sheley et al. 1999, Sheley et al. 2005). Tilling decreased invasive plants at site one, but had no effect on seeded species establishment. Vole disturbance at site one provided safesites for seeded species establishment and interference by invasive plants may have been minimal. This provides further support for the hypothesis that high site availability can be augmented by seeding and watering to increase desired species. Two,4-D effectively reduced invasive plants at site two. Two,4-D was required to prevent increases in *C. maculosa* and *P. recta* when water was added to support the emergence of seeded species. Seeded species may reduce *C. maculosa* and *P. recta* cover and density in subsequent growing seasons similar to what was found by Brown and Bugg (2001) and Carpinelli et al. (2004).

This study indicated that combining treatments influencing processes directing the three causes of succession is important for successfully establishing desired species while reducing *C. maculosa* and *P. recta*. Our data supported the applicability of the successional framework proposed by Pickett et al. (1987) to wildland management (Luken 1990, Sheley et al. 1996, Whisenant 1999). Successional management has not

yet been adapted for heterogeneous landscapes where the combination of treatments necessary can vary depending on existing site conditions. Where existing processes are functional, our data provided evidence that they can be augmented to assist restoration. Where existing processes are damaged, they can be repaired or replaced with selective successional management. We have found increasing evidence that augmentative restoration has the potential to preserve the existing heterogeneity and diversity to support the establishment of functionally diverse desired species.

Successful invasive plant management requires developing broad ecosystem restoration goals (Navas 1991, Zavaleta et al. 2001). Ecological principles like functional diversity and invasion resistance (Tilman et al. 1997, Fargione et al. 2003), environmental heterogeneity (Levine et al. 2002, Deutschewitz et al. 2003), and succession (Luken 1990, Sheley et al. 1996, Whisenant 1999) may be used to guide the restoration of invasive dominated wildlands to desired plant communities. Augmentative restoration may provide managers with an ecological framework to develop restoration procedures that address whole ecosystem processes in order to improve the establishment of desired plant communities in wildlands damaged by invasive species.

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## CHAPTER 3

USING ECOLOGICAL THEORY TO GUIDE THE IMPLEMENTATION OF  
AUGMENTATIVE RESTORATION: RESPONSE OF THE EXISTING  
PLANT COMMUNITYIntroduction

Managers of invasive species are becoming increasingly concerned with more than target plant invaders, but also the existing or resulting plant community (Sheley et al. 1996, Zavaleta et al. 2001). Restoration differs from many invasive plant management strategies in that the re-establishment of ecosystem structure and function is the focus rather than simply controlling or establishing particular species (Ehrenfeld and Toth 1997). Control tools can negatively impact existing desired species (Rice et al. 1997), and the establishment of particular plant populations does not necessarily restore ecosystem processes (Simenstad and Thorn 1996). Understanding the impact of restoration strategies on not only the target invasive species and seeded species, but also the existing plant community is critical to successfully restoring invasive plant dominated wildlands.

Directing vegetation change based on existing ecological processes may be an important alternative to full reconstruction of plant communities because site specific ecological processes may be preserved and a wider range of site-specific adapted species might be maintained (Whisenant 1999). Augmentative restoration is an approach that uses ecological processes to guide management practices and is defined as a strategy that augments existing ecological processes by selectively repairing and replacing those

processes that are damaged or missing, thereby directing plant communities in a desirable direction (Bard et al. 2003). This approach incorporates ecological principles like invasion resistance and functional diversity, environmental heterogeneity, and succession.

Establishing and maintaining invasion resistant plant communities involves restoring functionally diverse species that occupy a majority of the niches and promote continuous resource capture making fewer resources available for invasive species (Carpinelli 2000, Pokorny 2002, Fargione et al. 2003). Environmental heterogeneity is considered by many ecologists as a valuable ecological mechanism that can help explain and predict species composition and even maintain functionally diverse species in many systems (Huston 1994, Pickett and Cadenasso 1995, Loreau et al. 2003). Successional processes regulate plant community change over time. By manipulating successional processes, plant communities may be directed toward functionally diverse invasion resistant populations (Sheley et al. 1996, Whisenant 1999, Sheley and Krueger-Mangold 2003).

Augmentative restoration is based on a mechanistic successional framework proposed by Pickett et al. (1987) that includes three causes of succession (site availability, species availability, and species performance), processes that influence these causes, and factors that modify these processes. In Chapter 2, we manipulated the three causes of succession by: 1) designing disturbances to create or eliminate site availability, 2) controlling colonization to decrease or enhance availability and emergence of specific plant species, and 3) controlling species performance to decrease or enhance the

emergence of specific plant species (Luken 1990). We designed disturbances by shallow tilling to create safesites with minimal release of subsurface nitrogen so that desired species were favored rather than invasive species (Tilman 1987, McLendon and Redente 1991, Herron et al. 2001). Watering was used to control species performance by shifting the competitive balance away from invasive species like *Centaurea maculosa* Lam. promoting the successful establishment of desired species (LeCain 2000). Broadcast seeding was used to control colonization supplementing the colonization of existing vegetation by providing a seed source for functionally diverse native species (Whisenant 1999). Herbicide application was used to design disturbances by opening niches filled by undesired species, control species performance by reducing the performance of undesired species, and/or control colonization by reducing seed sources of undesired species to support the initial establishment of seeded species (Borman et al. 1991, Carpinelli 2000).

In Chapter 2, this framework was used to test the effects of successional management on seeded species and target invasive species across a heterogeneous landscape. Ecological processes influencing site availability, species availability, and species performance varied. For example in one area, processes influencing site availability already existed at high levels, but processes influencing species availability and species performance occurred at low levels. Our data indicated that in these areas of high percent bare ground, seeding (species availability) and watering (species performance) increased seeded species cover from 2 to 9% and density from 18 to 120 stems m<sup>-2</sup>. In another area that was characterized by high soil moisture influencing species performance, shallow tilling (site availability) and seeding (species availability)

increased seeded species cover from 10 to 13% and density from 124 to 254 stems m<sup>-2</sup>.

Our companion study suggested that, in most cases, successional processes occurring at high levels could be augmented by selectively repairing and replacing successional processes that occur at low levels to increase seeded species emergence. In this study, we investigated the influence of augmentative restoration on the existing plant community.

Our overall objective was to investigate the effects of augmentative restoration on the existing plant community. We hypothesized that successional processes occurring at high levels could be augmented by selectively repairing and replacing successional processes that occurred at low levels to increase native forbs and grasses. The study was conducted to meet four specific objectives and test four specific hypotheses. The first objective was to determine the effects of seeding and watering in areas of high bare ground due to vole disturbance on native forbs and grasses. We hypothesized that dispersing desirable seeds combined with watering would augment areas with high percent bare ground to increase native forbs and grasses. The second objective was to determine the effects of shallow tilling and seeding in areas of high soil moisture on native forbs and grasses. We hypothesized that shallow tilling and seeding would augment areas with high soil moisture to increase native forbs and grasses. The third objective was to determine the effects of shallow tilling and watering in areas of high cover native species on native forbs and grasses. We hypothesized that shallow tilling and watering would augment high cover native species to increase native forbs and grasses. The fourth objective was to determine the effects of 2,4-D applied in the fall on

native forbs and grasses. We hypothesized that 2,4-D application in the fall would not decrease native forbs and grasses.

## Methods

### Study Area

Augmentative restoration was tested on the Kicking Horse Wildlife Mitigation Area south of Ronan, Montana (47° 29' N, 114° 5' W). This area was characterized by ephemeral prairie pothole wetlands. The soil was characterized as a deep, well drained silt loam and silty clay loam soil (glaciolacustrine deposits) with sodic properties within the top 76 cm. The slope varied from 2 to 15 percent and the elevation was 940 m. Average annual precipitation ranged from 350-450 mm per year and average temperature was 7.6° C.

This area lies on a *Festuca scabrella*-*Agropyron spicatum* habitat type (Mueggler and Stewart 1980) dominated by *Centaurea maculosa* Lam. and *Potentilla recta* L. Remnant stands of native species included *Achillea millifolium* L., *Agropyron smithii* Rydb., *Agropyron spicatum* (Pursh) Scribn. & Smith, *Festuca scabrella* Torr., *Gaillardia aristata* Pursh., *Geranium viscosissimum* F. & M., *Juncus balticus* Willd., *Koeleria cristata* Pers., *Lupinus sericeus* Pursh., *Monarda fistulosa* L., and *Poa sandbergii* Vasey. Historical disturbances associated with this site included grazing by cattle and intense meadow vole (*Microtis pennsylvanicus*) activity. The more palatable species of this habitat type, *Festuca idahoensis* Elmer. and *A. spicata*, were far less common than the less palatable species, *F. scabrella*, *P. sandbergii*, and *Danthonia intermedia* Vasey.

Vole activity, hydrology, as well as propagule pools and dispersal were ecological processes specific to this site that influenced the three causes of succession (site availability, species availability, and species performance). Vole activity created disturbances influencing site availability, propagule pools and dispersal of different species influenced species availability, and the hydrology affected soil moisture levels influencing species performance. Vole activity provided tilled bare-soil microhabitats (55% bare ground) for colonization, while the colonization of these bare sites was constrained by the abundance and type of propagules available at the site (4-17% cover native species). Meanwhile, soil moisture gradients associated with the interspersed wetlands influenced the growth and reproduction of native or invasive species. LeCain (2000) found that *C. maculosa* establishment and growth was inhibited in transitional zones between wetland and upland areas. The Kicking Horse Wildlife Mitigation Area was heterogeneous in these ecological processes.

### Experimental Sites

Three different experimental sites were established within the Kicking Horse Mitigation Area representing heterogeneity in the ecological processes influencing the three causes of succession (site availability, species performance, species availability). The heterogeneity was identified based on criteria that categorized ecological processes as occurring at low or high levels. The extent of vole activity (site availability) was measured by estimating percent bare ground, and  $\leq 10\%$  bare ground was considered low while  $\geq 30\%$  bare ground was considered high. Propagule supply (species availability) was measured by estimating percent cover of native species, and 0 to 5% cover native

species was considered low, while 15 to 20% cover native species was considered high. Soil moisture (species performance) was first measured in May using a neutron probe (Hignett and Evett 2002), and 25 to 30% soil moisture integrated over the top 40 cm (upland areas) was considered low, while 30 to 35% soil moisture integrated over the top 40 cm (transition between upland and wetland areas) was considered high.

Based on these criteria, the landscape was surveyed and three experimental sites were identified. At site one, percent bare ground (55%) was high, while percent soil moisture (27%) and cover of native species (11%) were low (Figure 3.1). Percent soil moisture was high (33%), at the second site, while percent bare ground (4%) and percent cover native species (4%) were low (Figure 3.2). At the third site, percent cover of native species was high (17%) while soil moisture (29%) and percent bare ground (2%) were low (Figure 3.3). Throughout this chapter, site one is represented by high site availability (SA), site two is represented by high species performance (SPP), and site three is represented by high species availability (SPA).

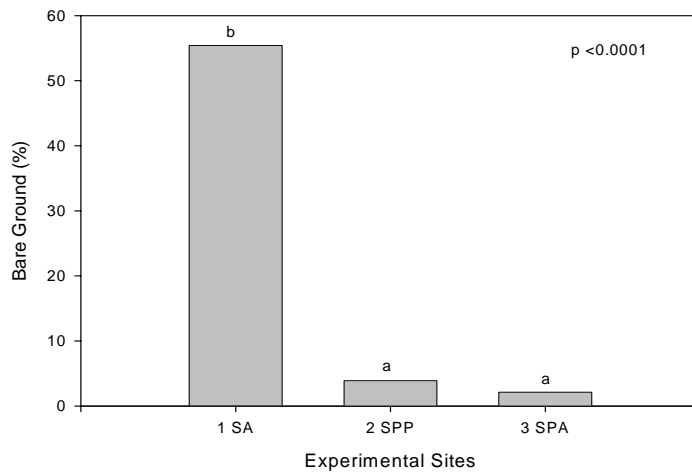


Figure 3.1. Percent bare ground at sites 1, 2, and 3. Analysis performed using ANOVA and Fisher's LSD procedure ( $\alpha = 0.05$ ) on square root transformed data. Non transformed means are presented.

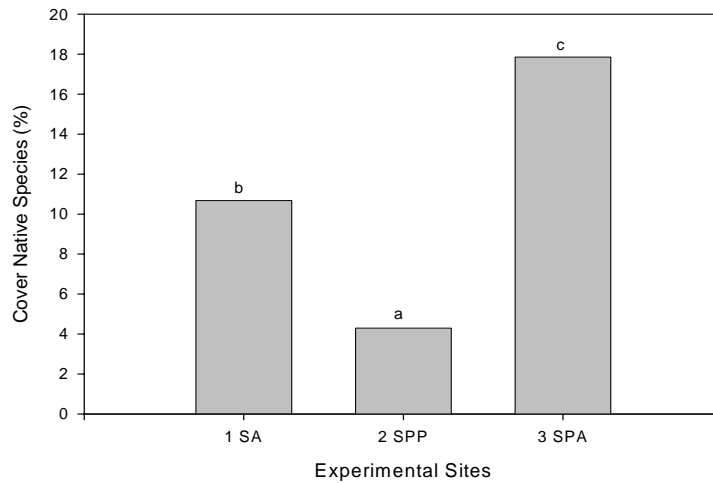


Figure 3.2. Percent cover native species at sites 1, 2, and 3. Analysis performed with ANOVA and Fisher's LSD procedure ( $\alpha = 0.05$ ) on square root transformed data. Non transformed means are presented.

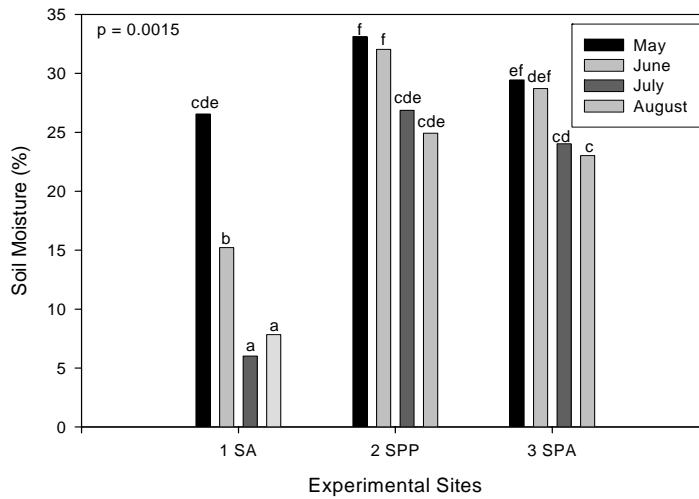


Figure 3.3. Percent soil moisture (upper 40 cm) in May, June, July, and August at sites 1, 2, and 3. Analysis performed using ANOVA and Fisher's LSD procedure ( $\alpha = 0.05$ ).

### Experimental Design

In a split plot design with four replications, 8 factorial treatment combinations from three factors: 1) shallow tilling or no shallow tilling, 2) watering or no watering, and 3) seeding or no seeding were applied to whole plots in three experimental sites. Sub plot treatments were application or no application of 2,4-D.

### Procedures

In May 2002, 32 plots (8 treatments replicated 4 times) were established within each of the three sites generating a total of 96 plots. Plots were 1 by 2 m with 2 m between plots to ensure independence between plots. In late September 2002, 2,4-D was applied to half of every plot at a rate of 2 kg acid equivalence  $\text{ha}^{-1}$  with a backpack sprayer. Conditions were clear with wind  $<5$  mph and air temperature of  $12.8^{\circ}\text{C}$ . Two,4-D is a broad spectrum, broadleaf herbicide that provides about 90% control of C.

*maculosa* and *P. recta* the year of application. Its short half-life and soil binding properties make it an appropriate herbicide for this prairie pothole habitat (Dewey et al. 1997).

In mid October 2002, vole fences were constructed to prevent vole seed predation from occurring in plots (Maron and Simms 2001). Galvanized hardware cloth (0.625 cm mesh) attached to T fence posts every 3 m was buried 30 cm deep and extended 60 cm above ground. The fencing was topped with aluminum flashing (22.5 cm wide) to prevent voles from climbing over the top of the fences. Mouse traps were used to remove voles from within each fenced area.

Once voles were excluded, shallow tilling (site availability) and seeding (species availability) treatments were randomly applied to appropriate plots in late October 2002. Plots were rototilled to a depth of 5 cm. Following the tilling treatment, plots were broadcast seeded at a rate of 34 kg ha<sup>-1</sup>. The seed mixture consisted of six grasses (17 kg ha<sup>-1</sup>) and five forbs (17 kg ha<sup>-1</sup>) including *Agropyron spicatum* (5 kg ha<sup>-1</sup>), *Festuca scabrella* (5 kg ha<sup>-1</sup>), *Koeleria cristata* (1.75 kg ha<sup>-1</sup>), *Juncus balticus* (1.75 kg ha<sup>-1</sup>), *Poa. sandbergii* (1.75 kg ha<sup>-1</sup>), *Agropyron smithii* (1.75 kg ha<sup>-1</sup>), *Gaillardia aristata* (3.4 kg ha<sup>-1</sup>), *Geranium viscosissimum* (3.4 kg ha<sup>-1</sup>), *Achillea millefolium* (3.4 kg ha<sup>-1</sup>), *Lupinus sericeus* (3.4 kg ha<sup>-1</sup>), and *Monarda fistulosa* (3.4 kg ha<sup>-1</sup>). These species represented key functional groups within the habitat type. Seed company, state of origin, and species variety for each seeded species are presented in Table 3.1. Germination and viability tests were performed on fifty seeds per species replicated four times to estimate

percentage of seeds that germinate and, of the seeds that did not germinate, percentage that are living or viable versus those that are not living or nonviable (Table 2.2).

Table 3.1. Seeded Species, Variety, Seed Company, and State of Origin.

Seeded Species	Variety	Company	State of Origin
<i>Agropyron spicata</i>	Secar	Granite Seed Co. <sup>1</sup>	Washington
<i>Festuca scabrella</i>		Granite Seed Co.	Montana
<i>Koeleria cristata</i>		Wind River Seed <sup>2</sup>	Montana
<i>Juncus balticus</i>		Wind River Seed	Wisconsin
<i>Poa sandbergii</i>		Granite Seed Co.	Washington
<i>Agropyron smithii</i>	Rosana	Granite Seed Co.	Washington
<i>Gaillardia aristata</i>		Wind River Seed	Oregon
<i>Geranium viscosissimum</i>		Granite Seed Co.	Utah
<i>Achillea millefolium</i>		Granite Seed Co.	Washington
<i>Lupinus sericeus</i>		Native Seed Found. <sup>3</sup>	Idaho
<i>Monarda fistulosa</i>		Wind River Seed	Wyoming

<sup>1</sup>Granite Seed Co. 1697 W. 2100 N. Lehi, UT 84043; <sup>2</sup>Wind River Seed 3075 Lane 51 ½ Manderson, WY 82432; <sup>3</sup>Native Seed Foundation Star Route Moyie Springs, ID 83845.

Table 3.2. Germination and Viability of Seeds by Species.

Species	Germination	Viable	Non-viable
<i>Agropyron spicata</i>	90%	4%	6%
<i>Festuca scabrella</i>	24%	2%	74%
<i>Koeleria cristata</i>	60%	12%	28%
<i>Juncus balticus</i>	63%	15%	22%
<i>Poa sandbergii</i>	67%	25%	8%
<i>Agropyron smithii</i>	88%	6%	6%
<i>Gaillardia aristata</i>	81%	2%	17%
<i>Geranium viscosissimum</i>	14%	50%	36%
<i>Achillea millefolium</i>	78%	2%	21%
<i>Lupinus sericeus</i>	0%	94%	6%
<i>Monarda fistulosa</i>	72%	1%	18%

In May, June, and July 2003, watering treatments (species performance) were randomly applied to appropriate plots. Water was added at a rate of one third (135 mm) the average annual precipitation (400 mm) based on NOAA weather data from a station

located within 10 km from study area. Water was applied on plots at a rate of 45 mm in a single watering event in early May, June, and July 2003. The timing of watering corresponded with the first three months of the growing season. Based on work by LeCain (2000), this water level should influence species performance adequately to shift the competitive balance away from *C. maculosa* and promote successful establishment of native forbs and grasses.

### Sampling

Plots were sampled in 2002 prior to treatments and again in 2003 after treatments. Plots were sampled for percent bare ground, percent cover and density of native and exotic forbs and grasses, as well as soil moisture. Percent bare ground was sampled simultaneously with percent cover and density of plant species within a 20 cm by 50 cm frame placed randomly flat on the ground. Percent bare ground and cover plant species were estimated using a modified Daubenmire method (Daubenmire 1970). This method was modified to provide actual estimates of percent cover in order to obtain continuous rather than categorical data. Density was determined by counting the number of plants of each species within the 20 by 50 cm frame. Prior to treatments, cover and density were estimated in mid July 2002 within three randomly placed frames per plot. After treatments, sampling occurred in mid July 2003 within two frames per sub plot providing four samples per plot. Volumetric water content in the upper 15 cm of the soil profile was measured at three random locations in each plot, once a month from May to August during 2003 using Time Domain Reflectometry to provide an indication of how the treatments influenced soil moisture (Jones et al. 2002).

### Analysis

Analysis of covariance was used to determine the effects associated with block, shallow tilling, seeding, watering, and 2,4-D on the cover and density of native and exotic forbs as well as native and exotic grasses. Pretreatment cover and density for each response was used as a baseline covariate. To test our hypotheses, sites were analyzed separately. All main effects, two-way interactions, and three-way interactions were included in the model, and all four-way and five-way interactions were pooled into the error term. Square root transformations on cover and density data were used to meet the ANCOVA assumptions of normality and homogeneity of variance. The model was reduced by progressively pooling three-way interactions that were not significant ( $\alpha = 0.05$ ) into the error term. The Fisher's LSD procedure ( $\alpha = 0.05$ ) was applied to compare interaction means.

Analysis of variance was used to determine the effects associated with site, block, month, shallow tilling, seeding, watering, and 2,4-D on soil moisture. Because the ANOVA assumptions of normality and homogeneity of variance were met, no transformation was required on percent soil moisture data. Fisher's LSD procedure ( $\alpha = 0.05$ ) was used to compare means.

### Results

#### Native Forbs

At all three sites, seeding alone and watering alone increased native forb cover and density (Figure 3.4, Figure 3.5). Tilling alone had no significant effect on native forb

cover or density at any site. At site one where percent bare ground was high, watering alone increased native forb cover from 5 to 11%, while watering combined with seeding increased native forb density from 15 to 116 stems  $m^{-2}$  (Figure 3.6). Watering, seeding, and tilling interacted to influence native forb cover ( $p = 0.0013$ ) and density ( $p = 0.0029$ ) at this site. Without watering, tilling or seeding had no effect on cover of native forbs. Native forb cover increased three-fold over the control with watering and seeding when no tilling occurred. With tilling added, native forb cover decreased below levels where seeding and watering were used (Figure 3.7). Native forb density responded in a similar pattern where watering and seeding without tilling resulted in an increased from 20 to 143 stems  $m^{-2}$ . With tilling, density decreased to 93 stems  $m^{-2}$  (Figure 3.8).

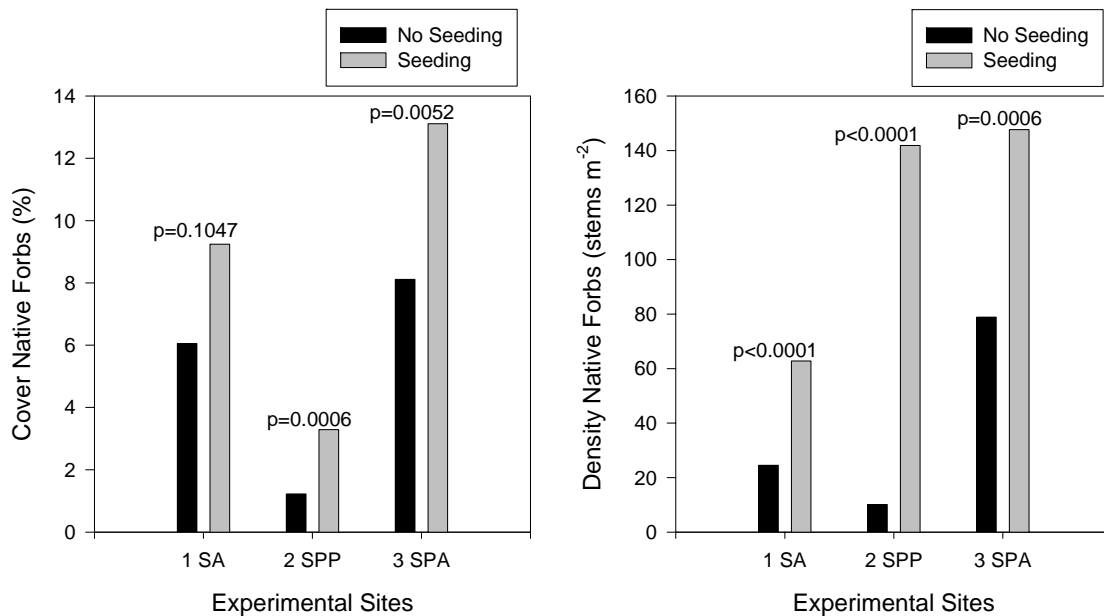


Figure 3.4. Percent cover and density of native forbs in response to seeding at sites 1, 2, and 3.

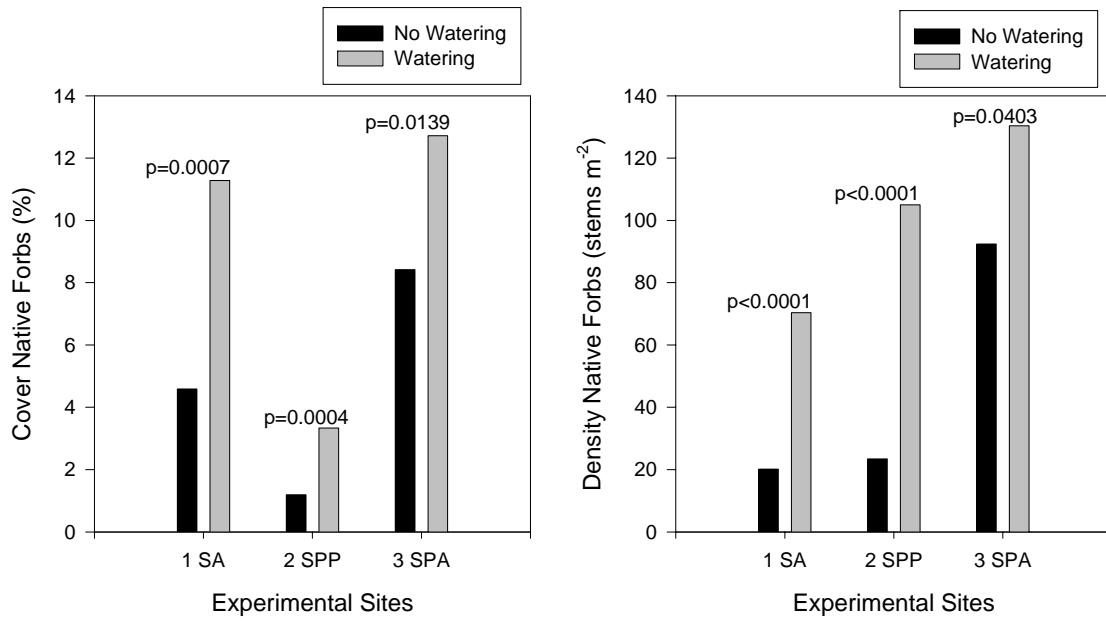


Figure 3.5. Percent cover and density of native forbs in response to watering at sites 1, 2, and 3.

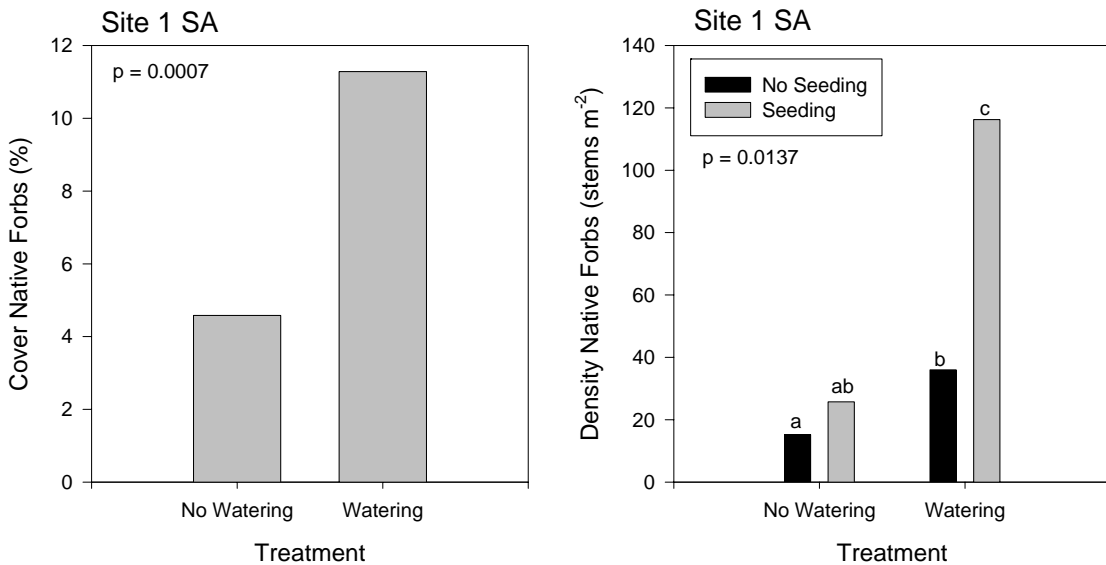


Figure 3.6. Percent cover of native forbs in response to watering at site 1 and density of native forbs in response to watering and seeding at site 1.

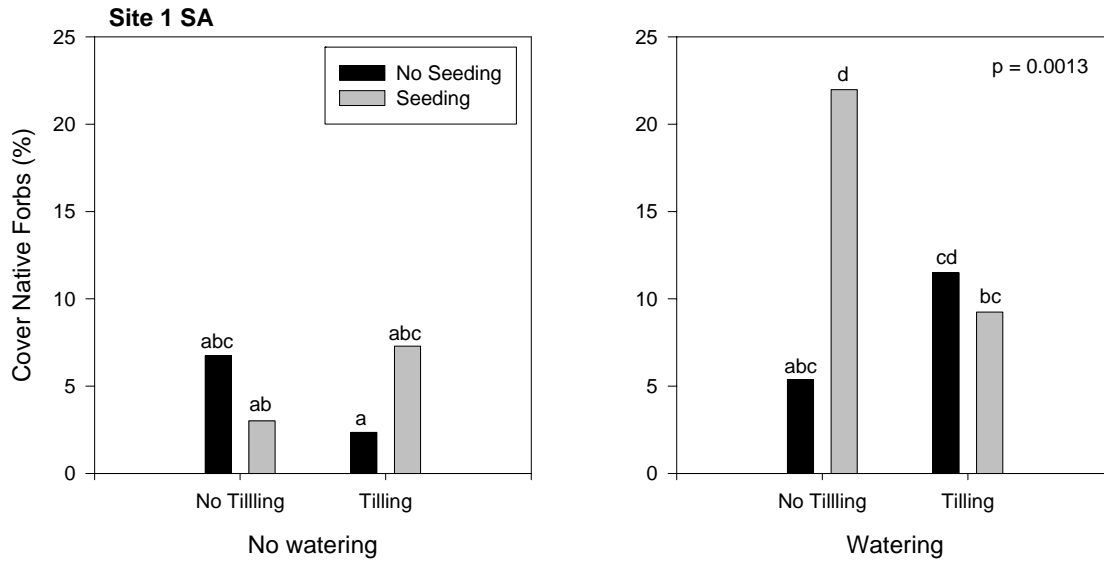


Figure 3.7. Percent cover of native forbs in response to watering, tilling, and seeding at site 1.

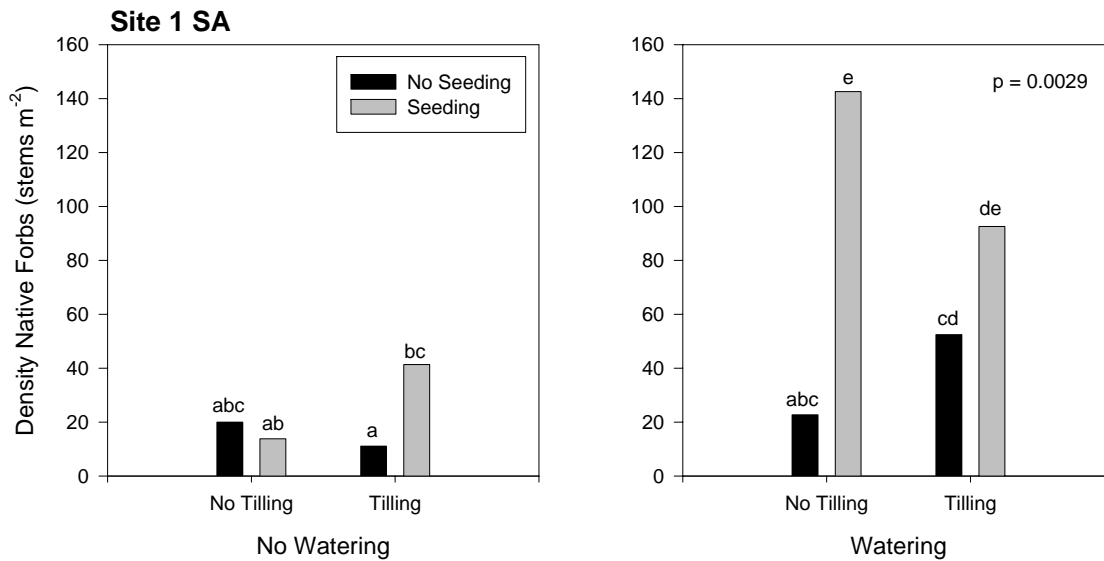


Figure 3.8. Density of native forbs in response to watering, seeding, and tilling at site 1.

At site two where soil moisture was high, seeding in combination with tilling increased native forb cover ( $p < 0.0001$ ) and density ( $p = 0.0016$ ). Without tilling, native

forb cover remained unchanged whether or not seeding occurred. With tilling, native forb cover decreased by more than one half of the control without seeding. Seeding was important when tilling was used to increase native forb cover back to the level of the control (Figure 3.9). Native forb density increased from 21 to 203 stems  $m^{-2}$  when tilling was combined with seeding and 21 to 92 stems  $m^{-2}$  when seeding occurred without tilling (Figure 3.9). Native forb cover ( $p=0.0022$ ) and density ( $<0.0001$ ) was also influenced by seeding and watering at site two. Seeding combined with watering increased native forb cover from 1 to 6% (Figure 3.10). Native forb density increased from 8 to 46 stems  $m^{-2}$  when seeding occurred without watering and 8 to 291 stems  $m^{-2}$  when seeding was combined with watering (Figure 3.10).

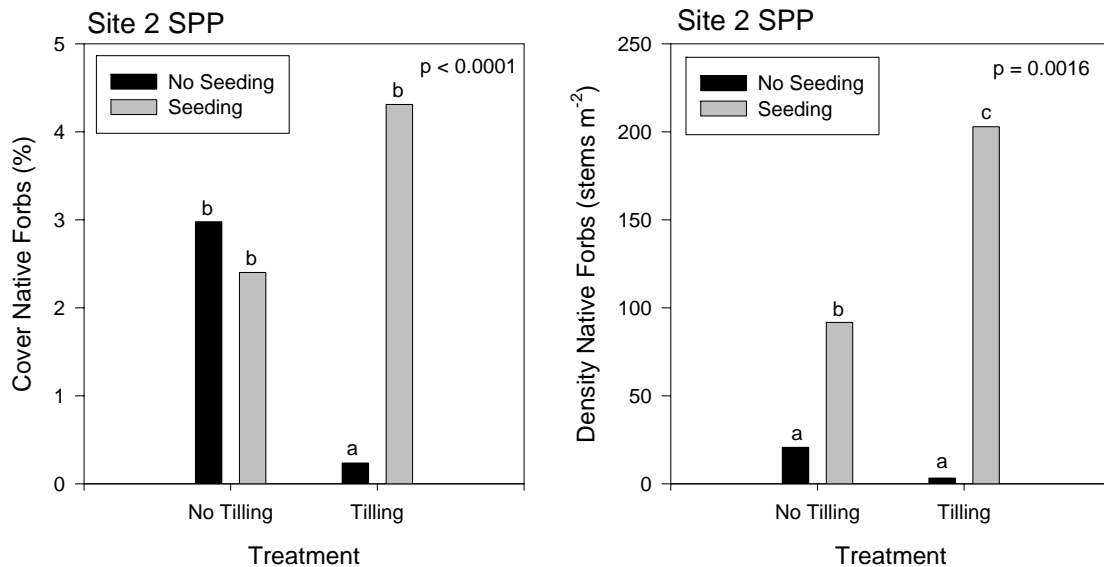


Figure 3.9. Percent cover and density of native forbs in response to tilling and seeding at site 2.

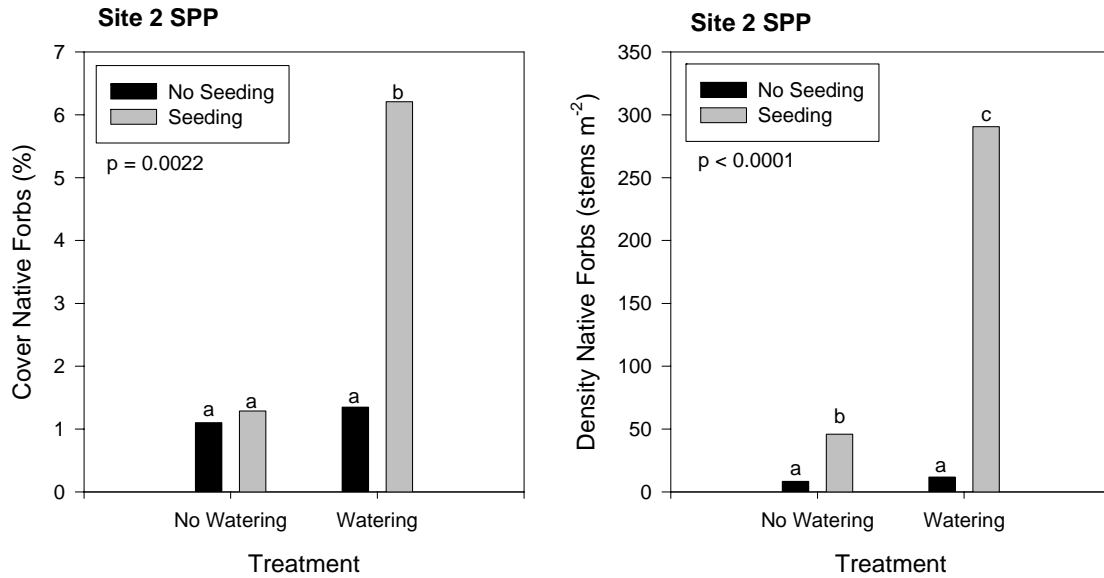


Figure 3.10. Percent cover and density of native forbs in response to watering and seeding at site 2.

At site three where native species cover was considered high, seeding combined with tilling influenced cover ( $p=0.001$ ) and density ( $p<0.0001$ ) of native forbs. Without tilling, seeding did not influence native forb cover. With tilling, native forb cover decreased from 12 to 5% without seeding but increased back to the level of the control with seeding (Figure 3.11). Native forb density increased from 130 to 200 stems  $m^{-2}$  when seeding was combined with tilling, while tilling alone decreased the density from 130 to 41 stems  $m^{-2}$  (Figure 3.11).

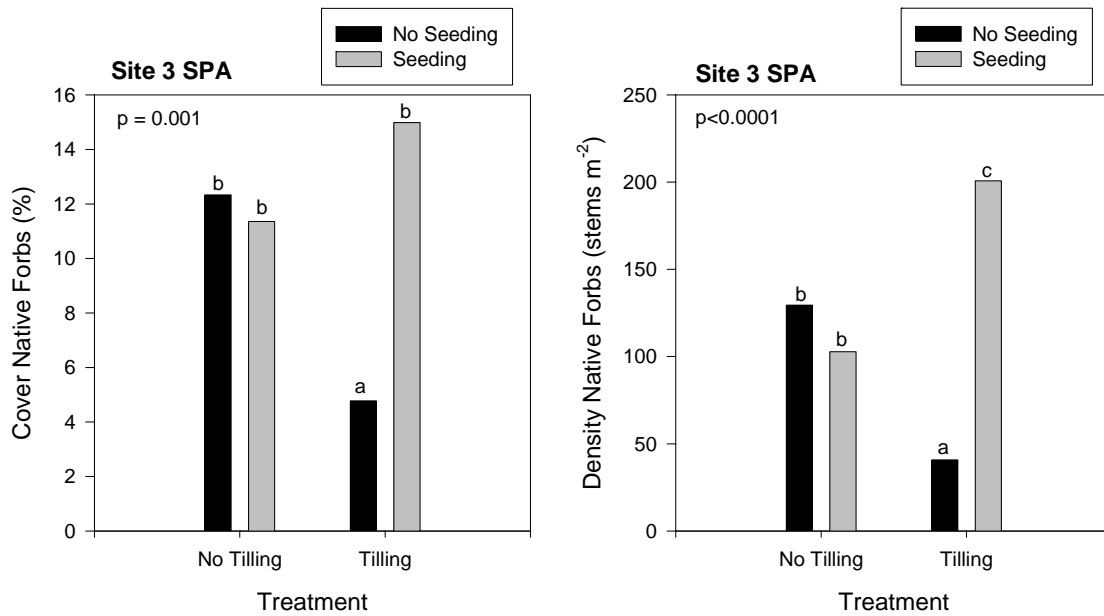


Figure 3.11. Percent cover and density of native forbs in response to tilling and seeding at site 3.

### Exotic Forbs

Watering alone increased exotic forb cover and density at site one ( $p=0.0419$ ,  $p=0.0024$ ), site 2 ( $p<0.0001$ ,  $p<0.0001$ ), and site 3 ( $p<0.0001$ ,  $p<0.0001$ ) (Figure 3.12). At site two where soil moisture was high, the combination of tilling and seeding reduced exotic forb cover ( $p<0.0001$ ) from 21 to 16% and density from 257 to 191 stems m<sup>-2</sup> (Figure 3.13). Exotic forb density increased from 151 to 426 stems m<sup>-2</sup> in response to watering, tilling, and 2,4-D ( $p = 0.0035$ ) at site two (Figure 3.14). At site three where native species cover was considered high, seeding alone ( $p=0.0032$ ) and tilling alone ( $p=0.0027$ ) increased exotic forb density from 77 to 149 stems m<sup>-2</sup> and 76 to 150 stems m<sup>-2</sup> respectively (Figure 3.15).

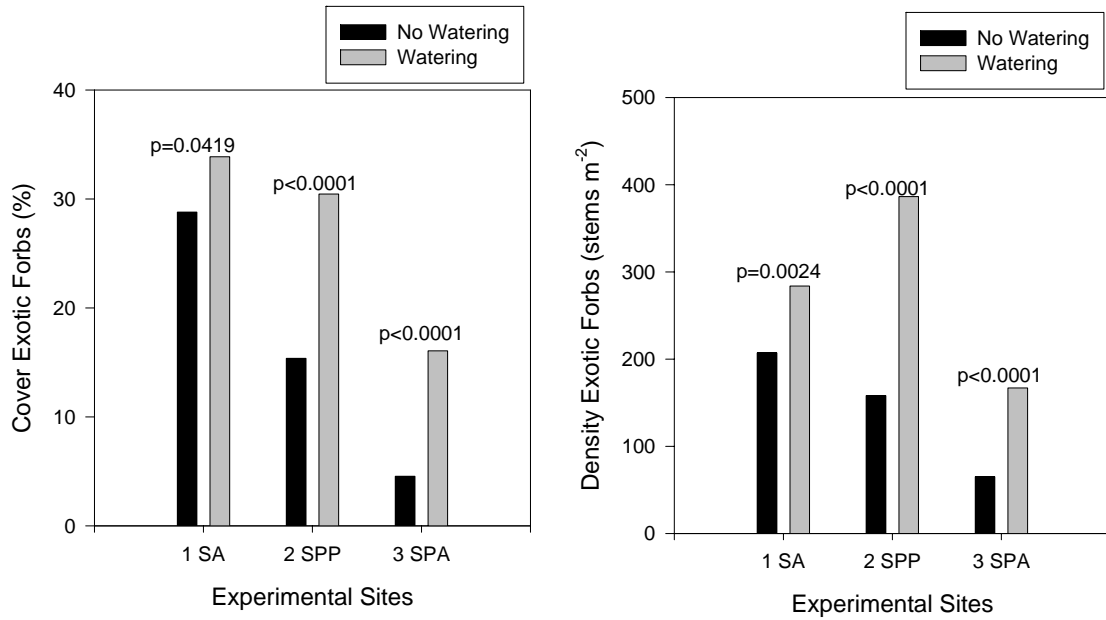


Figure 3.12. Percent cover and density of exotic forbs in response to watering at sites 1, 2, and 3.

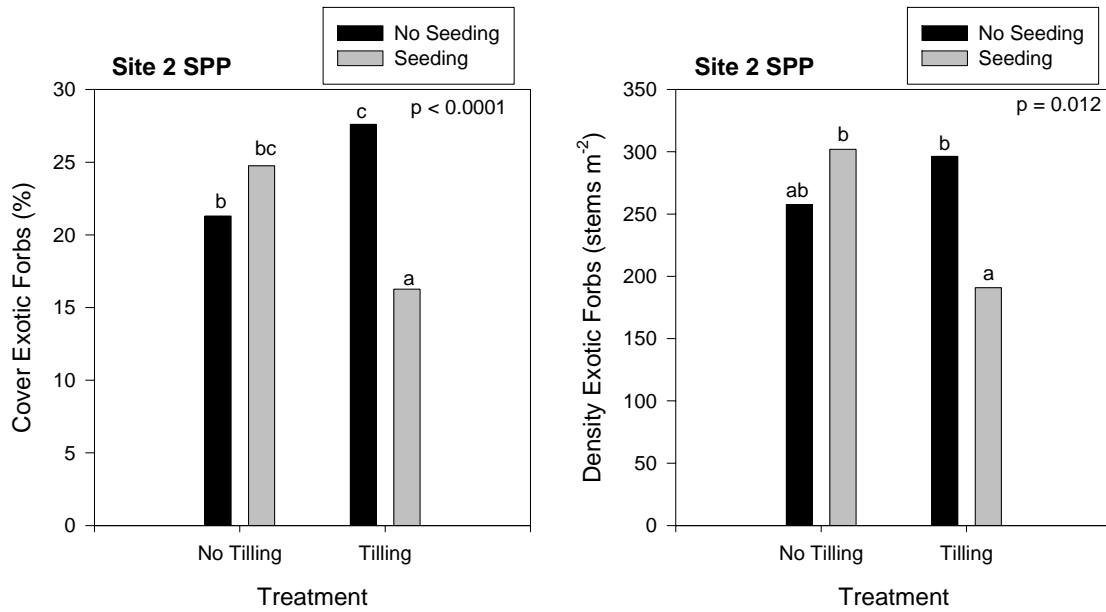


Figure 3.13. Percent cover and density of exotic forbs in response to tilling and seeding at site 2.

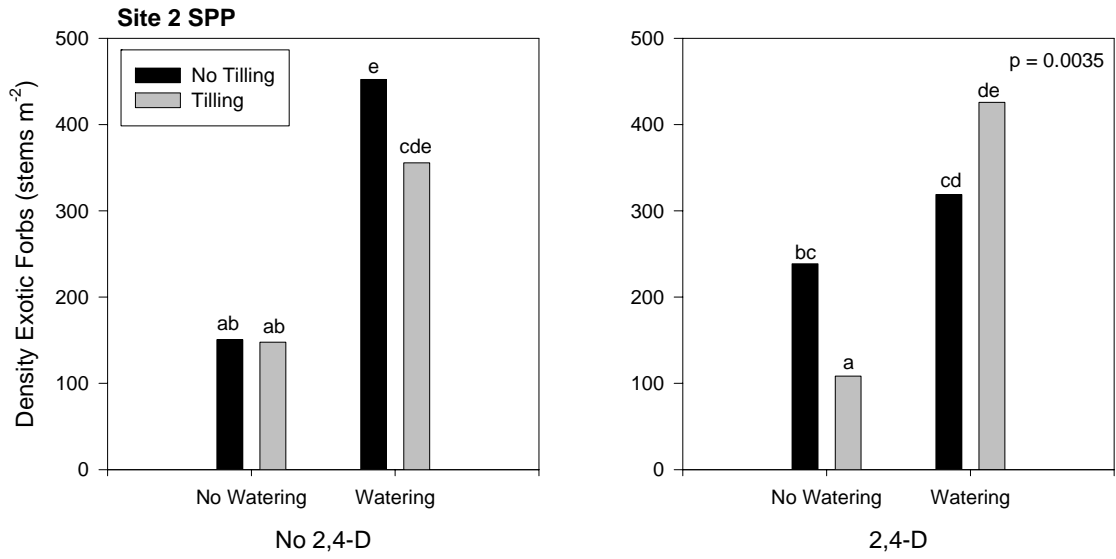


Figure 3.14. Density of exotic forbs in response to 2,4-D, watering, and tilling at site 2.

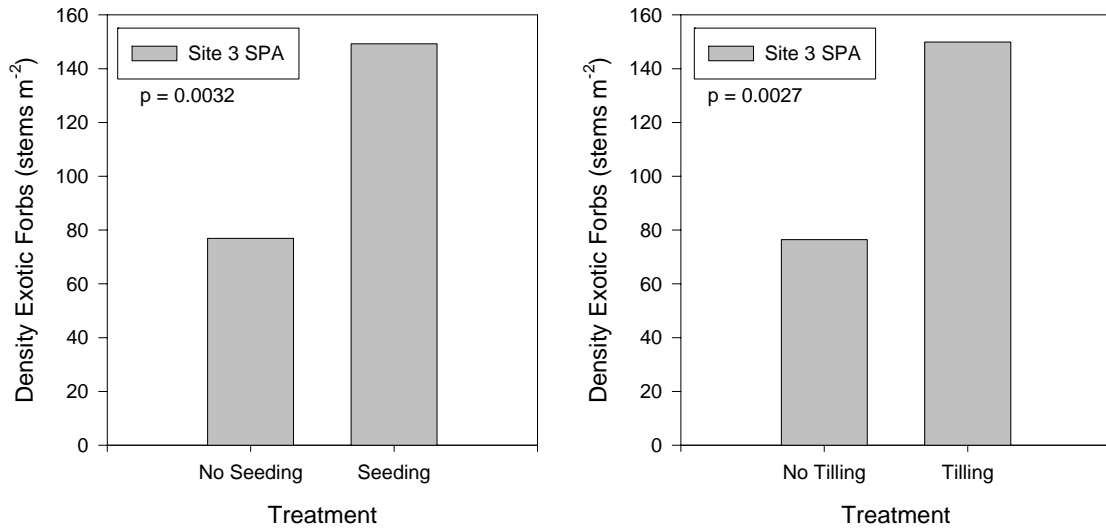


Figure 3.15. Density of exotic forbs in response to seeding alone and tilling alone at site 3.

### Native Grasses

At site two where soil moisture was high, native grass density increased ( $p=0.0243$ ) from 119 to 181 stems  $m^{-2}$  in response to 2,4-D (Figure 3.16). Native grass density also increased from 60 to 177 stems  $m^{-2}$  in response to watering, tilling, and 2,4-D ( $p = 0.0016$ ) at this site (Figure 3.17). At site three where native species cover was considered high, tilling alone decreased native grass density ( $p=0.016$ ) by about one half (Figure 3.18).

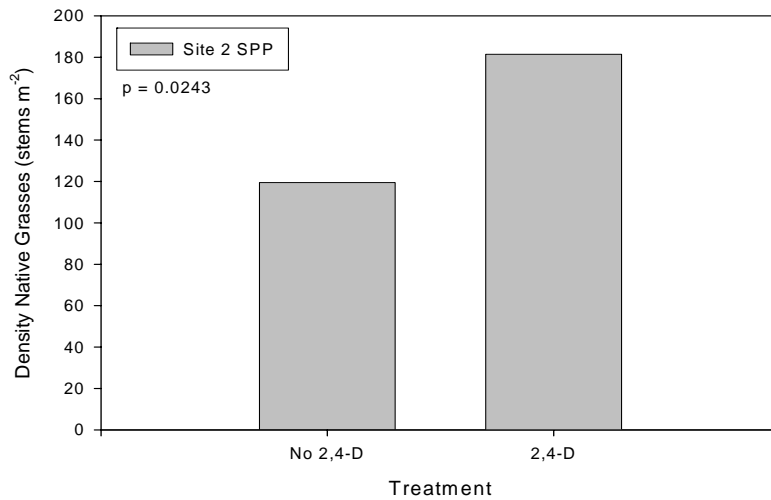


Figure 3.16. Density of native grasses in response to 2,4-D at site 2.

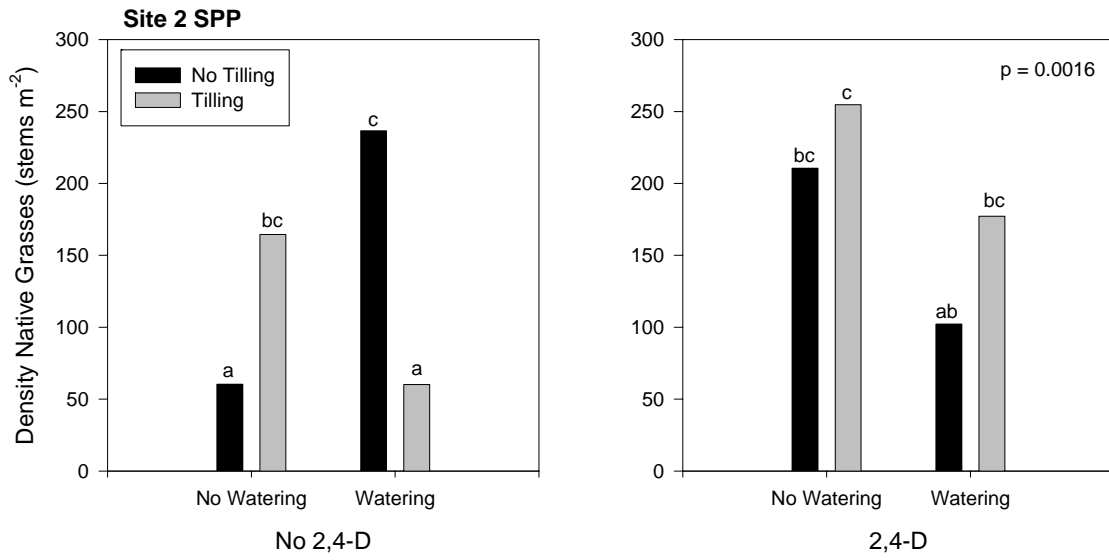


Figure 3.17. Density of native grasses in response to 2,4-D, watering, and tilling at site 2.

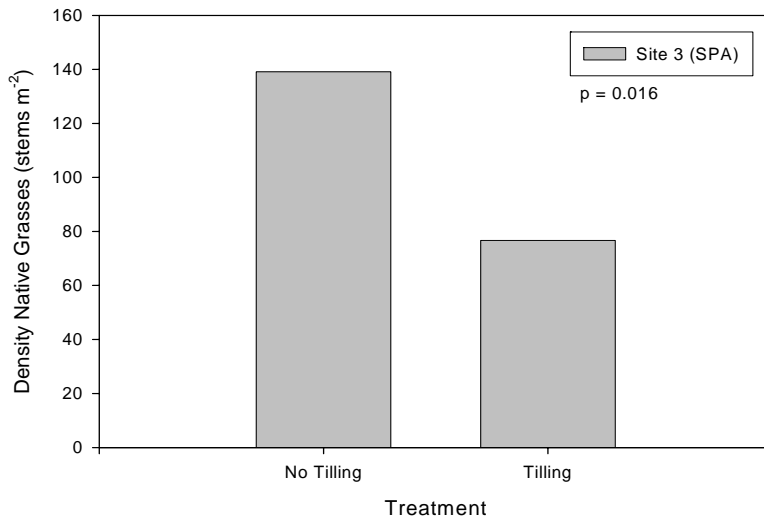


Figure 3.18. Density of native grasses in response to tilling at site 3.

### Exotic Grasses

At sites two and three, tilling alone decreased exotic grass cover (site 2  $p < 0.0001$ , site 3  $p = 0.0299$ ) and density (site 2  $p < 0.0001$ , site 3  $p = 0.0033$ ) (Figure 3.19). At site three, exotic grass density increased from 242 to 330 stems  $m^{-2}$  in response to watering ( $p = 0.0208$ ) and 243 to 329 stems  $m^{-2}$  in response to 2,4-D ( $p = 0.0234$ ) (Figure 3.20). Tilling combined with 2,4-D also influenced exotic grass cover ( $p = 0.0226$ ) and density ( $p = 0.0174$ ) at site three. Without tilling, 2,4-D had no effect on exotic grass cover and density. With tilling but without 2,4-D, the cover and density of exotic grasses decreased by one half as compared to the control. With tilling and 2,4-D, exotic grass cover and density increased back to levels similar to the control (Figure 3.21).

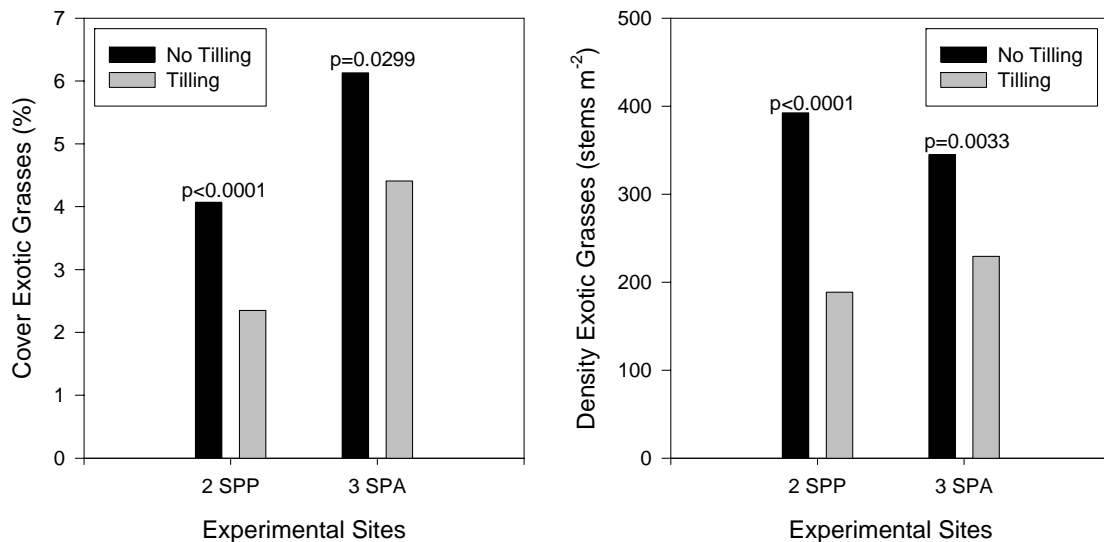


Figure 3.19. Percent cover and density of exotic grasses in response to tilling alone at sites 2 and 3.

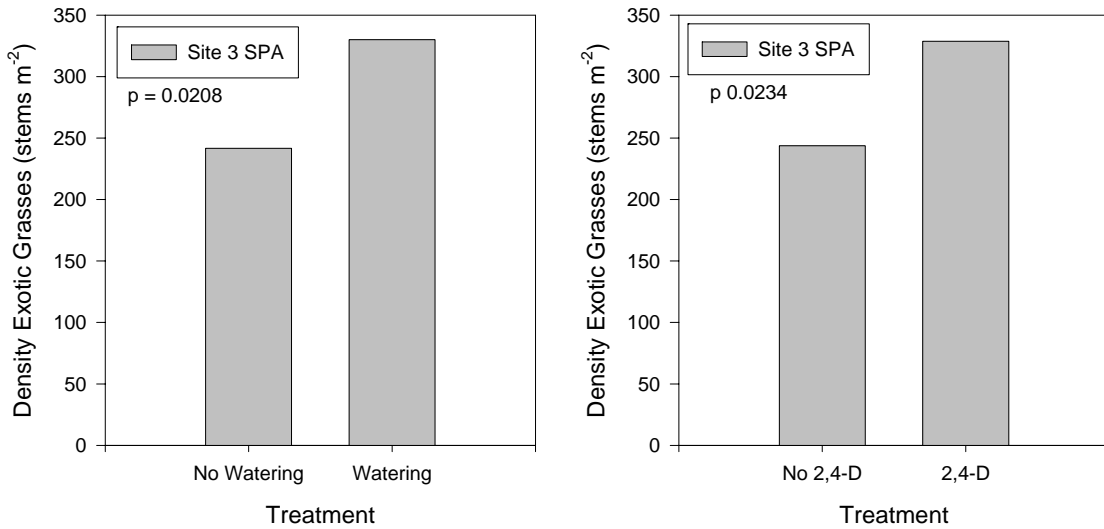


Figure 3.20. Density of exotic grasses in response to watering alone and 2,4-D alone at site 3.

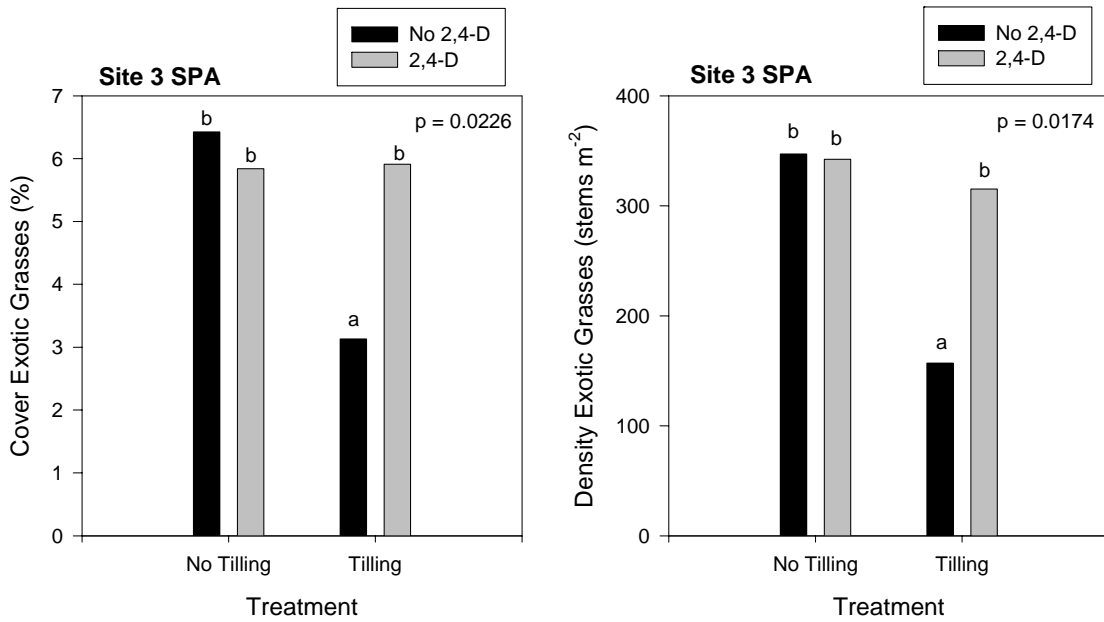


Figure 3.21. Percent cover and density of exotic grasses in response to tilling and 2,4-D at site 3.

## Soil Moisture

Conditions associated with site and month influenced percent soil moisture up to a 15 cm depth (Figure 3.22). Soil moisture at site one was lower in May (24.6%) and June (6.7%) than for sites two (25.9%, 9.2%) and three (26.2%, 8.8%). In July, soil moisture at sites one (3.2%) and three (3.9%) were significantly lower than for site two (4.9%) and in August, soil moisture at site one (2.4%) was significantly lower than it was for the other two sites (3.7%, 3.9%).

Month and watering also influenced percent soil moisture (Figure 3.23). Percent soil moisture was significantly different between the months of May (~25%), June (~8%), July (~4%), and August (~3%). Watering increased percent soil moisture in May and June, but created no significant change in July and August. Shallow tilling and seeding treatments had no effect on percent soil moisture

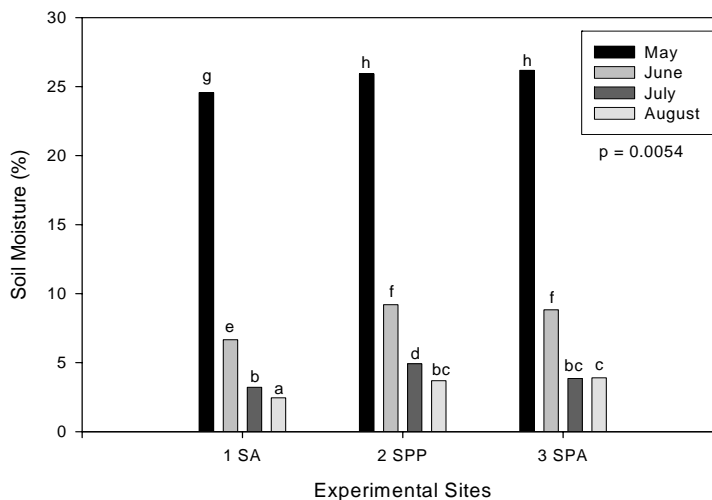


Figure 3.22. Percent soil moisture (upper 15 cm) response to site and month.

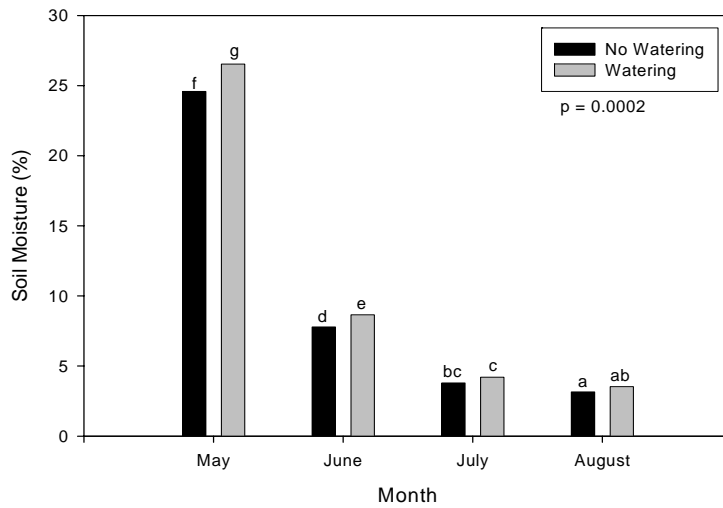


Figure 3.23. Percent soil moisture (upper 15 cm) response to month and watering.

### Discussion

The management of wildland systems degraded by invasive species must move towards the restoration of ecological processes that support the re-establishment of functioning, invasion resistant plant communities (Zavaleta et al. 2001, Sheley and Krueger-Mangold 2003). This shift in focus requires the consideration of the existing and resulting plant community when implementing restoration strategies (Sheley et al. 1996). Seeded species emergence has already provided support for augmentative restoration in our companion study. In this study, the response of the existing plant community to treatments continued to provide evidence supporting augmentative restoration and critical information for predicting long-term successional dynamics (Sheley et al. 1996, Ehrenfeld and Toth 1997, Rice et al. 1997).

The existing plant community was represented by native forbs, exotic forbs, native grasses, and exotic grasses. We first hypothesized that seeding combined with watering would augment areas with high percent bare ground caused by vole disturbance to increase native forbs and grasses. Sousa (1984) explained that vole mound building disturbs the soil creating new opportunities for species establishment. Boeken and Shachak (1998) provided evidence that mound revegetation was most affected by seed and resource limitations. Seeds can be limited on mounds because excavated soils with low abundance of germinable seeds covered seeds on the surface (Hobbs and Mooney 1985). Huntley and Reichman (1994) found evidence that mammal burrowing disrupts the physical structure of the soil which decreases soil moisture. Watering has been shown to increase revegetation rates on mounds (Rebollo et al. 2003) supporting the hypothesis that vegetation recovers more quickly from vole disturbance in mesic conditions (Goldberg and Gross 1988, Umbanhowar 1995).

Our companion study indicated that augmenting vole disturbed areas with seeding to influence species availability and watering to influence species performance increased seeded species cover and density. In this study, seeding and watering augmented vole disturbances to increase native forb cover, while the addition of tilling caused a significant decrease in native forb cover. Native forb density followed a similar pattern providing strong evidence for our hypothesis that tilling was not necessary and should even be avoided in areas with pre-existing high percent bare ground. Disturbances often promote invasive plant establishment (Tilman 1987, McLendon and Redente 1991, Randall 1999, Herron et al. 2001). Avoiding tillage while using pre-existing

disturbances could be a useful process oriented approach to supporting desired over invasive plant establishment. Exotic forbs could be reduced in response to seeding and watering in subsequent growing seasons because of interference caused by increased native forbs (Brown and Bugg 2001, Carpinelli et al. 2004).

Our second hypothesis was that shallow tilling and seeding would augment areas with high soil moisture to increase native forbs and grasses. Burke et al. (1998) explained that soil moisture can be highly variable and considered a critical limiting resource in semiarid grasslands creating strong spatial and temporal variation in herbaceous biomass. Other studies found patterns suggesting soil moisture can be a useful predictor of whether desirable plant cover/biomass will increase in response to the control of invasive plants in systems where water is a critical limiting resource (Giorgetti et al. 1997, Wright and Chambers 2002, Berlow et al. 2003).

Variation in soil moisture within our study area had a significant effect on vegetation response to treatments. Our companion study indicated that seeded species increased when areas with high soil moisture were augmented with seeding and tilling. In this study, we found support for our hypothesis that high soil moisture could be augmented with seeding and tilling to increase native forb cover and density. Exotic forb cover and density decreased with the same treatment combination. The upland site characterized by low soil moisture required watering and seeding to increase native forbs as discussed earlier. Seeding and watering also increased native forbs where soil moisture was high, but this treatment combination did not reduce exotic forbs. From the perspective of restoration, irrigation can be difficult to implement in many wildland

systems. Effectively predicting areas where water supplementation is unnecessary versus areas where irrigation can significantly improve desired species establishment may contribute to developing feasible and effective restoration strategies.

Our third hypothesis was that shallow tilling and watering would augment areas with high cover native species to increase native forbs and grasses. Assisting natural recovery of existing species is widely used in rangelands and forests where seed sources are available because it is a practical, low-cost alternative to planting or seeding (Barnett and Baker 1991). In this study, data indicated that remnant stands of native forbs did not adequately provide propagules for natural colonization within the first growing season. Augmenting natural recovery of existing species from remnant stands often requires more time than establishing species by introduced seeds, but regeneration from remnant stands could occur in future growing seasons (Whisenant 1999). Data indicated that pre-existing soil moisture contributed more to increasing native forbs than colonization from remnant native stands. Site three was originally characterized by high native species cover, but analysis of pre-treatment soil moisture data indicated that this site had high soil moisture equivalent to site two. Therefore, data supported the hypothesis that high soil moisture could be augmented by seeding and tilling to increase native forbs at this site.

Native and exotic grasses responded differently than native and exotic forbs to treatments in all areas. Grasses responded consistently to treatments causing disturbance. For example, the combination of tilling, watering, and 2,4-D increased native grass density, while 2,4-D alone increased exotic grass cover and density. These responses indicated that vegetative reproduction rather than recruitment from seed was more

important for grasses (Belsky 1986, Bullock et al. 1995, Berlow et al. 2003). Tilling and 2,4-D created open niches, while watering may have enhanced the vegetative propagation of native grasses. Belsky (1986) and Bullock et al. (1995) found that when grazing was removed, vegetatively-reproducing grasses showed greater success in revegetating disturbances than grasses from seeds. Berlow et al. (2003) found that perennial grass response to treatments after four years was likely due to vegetative growth rather than from seed. It was hypothesized that longer term monitoring may be necessary to determine community-level recruitment effects of perennial grasses from seed (Berlow et al. 2003). In addition, our germination and viability tests indicated that seeded grasses had lower germination and/or viability than the seeded forbs. Therefore, the response of native grasses to treatments was likely due to vegetative growth of existing perennial grasses rather than establishment of grasses from seeds.

The fourth hypothesis was that 2,4-D would not decrease native forbs and grasses. The timing of herbicide application has been widely recognized as a determinant of the effectiveness of the herbicide on target weeds and the likelihood of damaging surrounding desirable vegetation (Young et al. 1998, Bussan and Dyer 1999, DiTomaso et al. 1999b). Rice et al. (1997) found that herbicide application in late summer or fall minimized the exposure of desirable native species. In this study, 2,4-D was applied in the fall to prevent negative impacts on the native vegetation. Data provided evidence supporting our hypothesis that 2,4-D applied in the fall would not decrease native species cover and density.

This study indicated that combining treatments influencing processes directing the three causes of succession in a heterogeneous landscape supported an increase in native forb cover and density. In some cases, exotic forb cover and density were reduced. The initial changes in plant community composition support the applicability of the successional framework proposed by Pickett et al. (1987) to wildland management (Luken 1990, Sheley et al. 1996, Whisenant 1999). Successional management has not yet been adapted for heterogeneous landscapes where the combination of treatments necessary can vary depending on existing site conditions. Where existing processes are functional, our data provided evidence that they could be augmented to assist restoration. Where existing processes are damaged, they could be repaired or replaced with selective successional management. We have found increasing evidence that augmentative restoration has the potential to preserve the existing heterogeneity and diversity to support the establishment of functionally diverse desired species.

Successful invasive plant management requires developing broad ecosystem restoration goals (Navas 1991, Zavaleta et al. 2001). Ecological principles like functional diversity and invasion resistance (Tilman et al. 1997, Fargione et al. 2003), environmental heterogeneity (Levine et al. 2002, Deuschewitz et al. 2003), and succession (Luken 1990, Sheley et al. 1996, Whisenant 1999) may be used to guide the restoration of invasive dominated wildlands to desired plant communities. Our data provided increasing evidence that augmentative restoration could provide managers with an ecological framework to develop restoration procedures that address whole ecosystem processes in order to increase native forbs and grasses as well as improve the

establishment of seeded species to increase desired plant composition in wildlands damaged by invasive species.

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## CHAPTER 4

## SUMMARY

Augmentative restoration is defined as a wildland plant management strategy that augments existing ecological processes by selectively repairing and replacing those processes that are damaged or missing, thereby directing plant communities in a desirable direction (Bard et al. 2003). This study investigated the ecological framework and concept of augmentative restoration. Our overall objective was to determine whether successional processes occurring at high levels could be augmented by selectively repairing and replacing successional processes occurring at low levels to increase desired species composition.

In Chapter 2, we investigated the effect of augmentative restoration on the emergence of seeded species, while Chapter 3 focused on the effect of augmentative restoration on the existing plant community. The first underlying hypothesis was that controlling colonization combined with controlling species performance would augment areas with high site availability to support the emergence of seeded species as well as increase existing native forbs and grasses. More specifically, we hypothesized that dispersing desirable seeds combined with watering would augment areas with high percent bare ground to increase seeded species as well as existing native forbs and grasses. Data showed support for this hypothesis where seeded species cover increased from 2 to 9% and density from 18 to 120 stems  $m^{-2}$  in response to seeding and watering in areas with high percent bare ground. Native forb cover increased by three times the

control in response to seeding and watering without tilling, and native forb cover significantly decreased when tilling was added. Native forb density followed a similar pattern which provided further evidence supporting our hypothesis. *C. maculosa* and *P. recta* as well as other exotic forbs may be reduced in response to seeding and watering in following growing seasons due to interference caused by increased desired species (Brown and Bugg 2001, Carpinelli et al. 2004). Native grasses responded consistently to treatments causing disturbances like tilling and 2,4-D. Low representation of native grasses in the existing vegetation, low germination of seeded grasses, and evidence suggesting that vegetative propagation of grasses was important during the first growing season may explain why native forbs supported our hypothesis more strongly than native grasses.

The second underlying hypothesis was that designing disturbances and controlling colonization would augment areas with high species performance to support the emergence of seeded species as well as increase existing native forbs and grasses. More specifically, we hypothesized that shallow tilling and seeding would augment areas with high soil moisture to increase seeded species as well as native forbs and grasses. Data showed support for this hypothesis when percent cover of seeded species doubled in response to tilling and seeding at one site with high soil moisture. Also, seeded species cover increased from 10 to 13% and density from 124 to 254 stems  $m^{-2}$  in response to tilling and seeding at the other site with high soil moisture. Native forb cover and density also increased in response to tilling and seeding in both sites characterized by high soil moisture while exotic forbs decreased by the same treatment combination in one of the

high soil moisture sites. Native grasses responded similarly within these areas as described above.

The third underlying hypothesis was that designing disturbances and controlling species performance would augment areas with high species availability to support the emergence of seeded species as well as increase native forbs and grasses. More specifically, we hypothesized that shallow tilling and watering would augment areas with high species availability to increase seeded species as well as native forbs and grasses. Data indicated that the remnant stands of desired species did not adequately provide propagules for natural colonization within the first growing season. Augmenting natural recovery of existing species from remnant stands often requires more time than establishing species by introduced seeds (Whisenant 1999). Data indicated that pre-existing soil moisture contributed more to increasing native forbs than colonization from remnant native stands. This area was originally characterized by high native species cover, but analysis of pre-treatment soil moisture data indicated that this area had high soil moisture equivalent to the other high soil moisture area. Therefore, data supported the hypothesis that high soil moisture could be augmented by seeding and tilling to increase seeded species and native forbs.

The fourth hypothesis was that 2,4-D would enhance seedling establishment of seeded species by reducing *C. maculosa* and *P. recta*. We also hypothesized that a fall application of 2,4-D would not decrease native forbs and grasses. Two,4-D reduced *C. maculosa* and *P. recta* at one of the three experimental sites, but there was no indication

of this treatment enhancing seedling establishment of seeded species within the first growing season. Two,4-D did not decrease existing native forbs or grasses.

These studies indicated that combining treatments influencing processes directing the three causes of succession could support not only the emergence of seeded species but also an increase of existing forbs. In some cases, existing exotic forbs as well as the target exotic species were reduced. These initial changes in plant community composition supported the applicability of the successional framework proposed by Pickett et al. (1987) to wildland management (Luken 1990, Sheley et al. 1996, Whisenant 1999). Successional management has not yet been adapted for heterogeneous landscapes where the combination of treatments necessary could vary depending on existing site conditions. Where existing processes are functional, our data provided evidence that they could be augmented to assist restoration. Where existing processes are damaged, they could be repaired or replaced with selective successional management. Our data indicated that augmentative restoration has the potential to preserve the existing heterogeneity and diversity to support the establishment of functionally diverse desired species.

Successful invasive plant management requires developing broad ecosystem restoration goals (Navas 1991, Zavaleta et al. 2001). Ecological principles like functional diversity and invasion resistance (Tilman et al. 1997, Fargione et al. 2003), environmental heterogeneity (Levine et al. 2002, Deutschewitz et al. 2003), and succession (Luken 1990, Sheley et al. 1996, Whisenant 1999) may be used to guide the restoration of invasive dominated wildlands to desired plant communities. Our data

provided increasing evidence that augmentative restoration could provide managers with an ecological framework to develop restoration procedures that address whole ecosystem processes in order to increase native forbs and grasses as well as improve the establishment of seeded species to increase desired plant composition in wildlands damaged by invasive species.

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