Augmentative Restoration: Repairing Damaged Ecological Processes During Restoration of Heterogeneous Environments

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Heterogeneity in disturbance regimes, propagule pools, and factors affecting plant performance are a ubiquitous feature of wildlands. We tested a conceptual framework, termed augmentative restoration, aimed at identifying and selectively repairing or replacing damaged processes based on their predicted influence on the three causes of succession: site availability, species availability, and species performance. This framework was tested at three sites each with a different cause of succession naturally occurring in an ephemeral wetland dominated by invasive plants that had varying levels of disturbance (site availability), remnant native plants (species availability), and water availability (species performance). Our hypotheses were (1) seeding combined with watering would augment meadow vole disturbance to increase desired species composition, (2) shallow tilling combined with watering would augment remnant native species, and (3) shallow tilling combined with seeding would augment mesic soils to increase desired species composition. Shallow tilling, watering, and seeding were applied in a factorial arrangement at all three sites. These eight treatment combinations were applied in a split-plot design with four replications to generate 32 whole plots (2 m^2). The herbicide 2,4-D was applied on half of each whole plot to influence relative species performance. In two of the three sites, using augmentative restoration to guide our management approaches improved our decision as to the treatment combinations that would maximize seedling establishment. Selectively augmenting successional processes that remain intact by repairing or replacing processes occurring at inadequate levels can improve implementation of successional management and provide a refined process-based framework for restoration across heterogeneous landscapes. Besides the clear economic advantages of lower management inputs associated with augmentative restoration, avoiding unnecessary management inputs has the additional advantage of minimizing unintended negative impacts on ecosystem processes.

Nomenclature: 2,4-D; meadow vole, *Microtus pennsylvanicus* Ord.

Key words: Invasive plants, rangeland restoration, successional management.

Replacing and repairing damaged ecosystem processes at various scales is central to restoring degraded wildlands (Whisenant 1999). On landscapes degraded by invasive plants, repairing ecological processes is critical to correcting the cause of the invasion rather than continuously and periodically treating the symptoms (Sheley and Krueger-Mangold 2003). Successional management has been proposed as a process-oriented framework for developing ecologically-based invasive plant management strategies on rangelands (Sheley et al. 1996; Sheley and Krueger-Mangold 2003). Pickett et al. (1987) provided the theoretical basis for successional management by developing a hierarchical model that includes the general causes of succession, controlling ecological processes, and their modifying factors (Table 1). The three causes of succession include differential site availability (primary process: disturbance), differential species availability (primary process: colonization), and relative species performance (processes: resource acquisition rates, herbivory, competition, etc.) (Luken 1990; Pickett and Cadenasso 2005; Pickett et al. 1987). Based on what is known of the conditions, mechanisms, and processes controlling plant community dynamics, these causes of succession can be modified to allow predictable successional transitions toward desired plant communities (Bard et al. 2003; Sheley et al. 1996; Whisenant 1999).

DOI: 10.1614/IPSM-07-058.1

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Interpretive Summary

We developed and tested a novel restoration strategy, termed augmentative restoration, to improve restoration approaches of heterogeneous wildland systems. We hypothesized that using augmentative restoration, which enhances site-specific ecological processes occurring at sufficient levels by selectively augmenting ecological processes that are damaged, would result in greater seedling establishment than traditional restoration approaches. In two of the three sites, using augmentative restoration to guide our management approaches improved our decision as to the treatment combinations that would maximize seedling establishment. Augmentative restoration can improve decision making in a range of restoration settings, and has the economic and ecological advantage of lower management inputs.

This process-oriented theoretical framework has been successfully applied to guide the development of management strategies for invasive plants (Sheley et al. 2006b). In that study, the general hypothesis that successively modifying the factors influencing the causes of succession in an integrated fashion would favor the establishment and abundance of native grasses over singularly applied treatments was accepted. In addition to imposed factors, naturally occurring variation in disturbance regimes, propagule pools, and resource supply rates, herbivory and competition with associated species that affect establishment, abundance, and dominance are a pronounced and ubiquitous feature of wildland systems (Pickett and Cadenasso 1995; Schlesinger et al. 1996; Turnbull et al. 2000). For example, Foster et al. (2004) demonstrated that, along a productivity gradient, grassland species diversity and invasive plant establishment was seed-limited at unproductive sites but microsite-limited at productive sites. In contrast, Seabloom et al. (2003) found that native forb establishment in a grassland dominated by invasive annuals was seed-limited, regardless of soil resource supply rates or disturbance regime. In these invasive annual dominated systems, however, shrub seedling recruitment is restricted to areas disturbed by pocket gophers, whereas similar disturbance appeared to be less important for seedling recruitment in adjacent shrublands with a substantial amount of bare interspaces (DeSimone and Zedler 1999). Consequently, it may not be necessary or even desirable to uniformly incorporate all three causes of succession in efforts to restore many wildland systems if certain processes are already present and operating at sufficient levels.

While heterogeneity in disturbance, colonization, and factors that affect species performance have been widely identified in ecological theory as important mechanisms influencing community composition and diversity maintenance (Huston 1994; Loreau et al. 2003; Pickett and Cadenasso 1995), site-specific variation in these drivers of succession has not been incorporated into restoration programs. We propose a restoration strategy, termed augmentative restoration, which enhances site-specific ecological processes occurring at sufficient levels by selectively augmenting those processes that occur at inadequate levels as they vary across the landscape (Bard et al. 2004). Its goal is to maintain heterogeneity and improve the establishment and persistence of desired plant communities.

Little effort has been directed toward understanding how naturally occurring levels of disturbance, colonization, and species performance present at a particular site can be integrated with the current conceptual framework of successional management to improve restoration strategies of invasive-plant dominated wildlands. Our overall objective was to test the effectiveness of augmentative restoration in a heterogeneous, invasive-plant dominated community, relative to successional management approaches that uniformly address all causes of succession without regard to initial site conditions. To investigate this objective, establishment and enhancement of desired species were considered critical to initiating a favorable successional trajectory and in the long-term, controlling undesirable species by occupying a majority of available niches. We used the theoretical framework of successional management

Table 1. Causes of succession, contributing processes, and modifying factors.[a]

Causes of succession	Processes	Modifying factors
Site availability	Disturbance	Size, severity, time intervals, patchiness, predisturbance history
Species availability	Dispersal	Dispersal mechanisms and landscape features
	Propagule pool	Land use, disturbance interval, species life history
Species performance	Resource supply	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

[a] Modified from Pickett et al. 1987.

Table 2. Hypotheses for choosing combinations of restoration strategies aimed at addressing all three causes of succession based on which processes appeared to be occurring naturally (Luken 1990; Sheley et al. 1996).

General causes of succession		
Disturbance	Colonization	Species performance
Meadow[a] voles	Seeding	Watering
Tillage/2,4-D	**Remnant desired/ native species**	Watering
Tillage/2,4-D	Seeding	**High water table**

[a] Causes of succession deemed to be occurring naturally are bolded. Hypothetical treatments predicted to maximize desired species are not bolded.

(Pickett et al. 1987; Sheley et al. 1996) to identify damaged successional processes in our model semiarid grassland and to indicate necessary repair methods needed based on readily observed site characteristics. Our specific objectives were to determine the response of the desired plant community and target invasive species to treatments designed to influence processes associated with site availability (disturbance: shallow tillage and 2,4-D), species availability (colonization: seeding), and species performance (competition/resource acquisition: watering) in systems with (1) xeric soils, high meadow vole (*Microtus pennsylvanicus* Ord.) disturbance, and low remnant stand of native vegetation; (2) areas with xeric soils, low vole disturbance, but substantial remnant native species; and (3) mesic soils near a wetland, low vole disturbance, and low remnant vegetation. Based on the successional management framework, we hypothesized that (1) seeding combined with watering would augment meadow vole disturbance to increase desired species composition in xeric soils; (2) shallow tilling combined with watering would augment remnant native species to increase desired species composition in xeric soils; (3) shallow tilling combined with seeding would augment mesic soils to increase desired species composition; and (4) 2,4-D would enhance seedling establishment of desired species by reducing target invasive species abundance (Table 2).

Materials and Methods

Study Area. The study was conducted within the Kicking Horse Wildlife Mitigation Area located in the Mission Valley north of Missoula, MT (47°29′N, 114°5′W). This area was characterized by ephemeral wetlands and lies on a rough fescue (*Festuca campestris* Rydb.)–bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] habitat type (Mueggler and Stewart 1980), dominated by spotted knapweed (*Centaurea biebersteinii* DC.) and sulphur cinquefoil (*Potentilla recta* L.). Other exotic forbs include bur buttercup [*Ceratocephala testiculata* (Crantz) Bess], prickly lettuce (*Lactuca serriola* L.), and field pennycress (*Thlaspi arvense* L.). The two most common exotic grasses were Kentucky bluegrass (*Poa pratensis* L.) and downy brome (*Bromus tectorum* L.). Precipitation averages 400 mm (16 in) per year, and the mean annual temperature is 7.6 C (45.7 F). The soil is a well-drained silt loam and silty clay loam (glaciolacustrine deposits) with sodic properties within the top 76 cm. The slope varies from 2 to 15% and the elevation is 940 m (3,084 ft).

Study Sites. Three study sites were established within the Kicking Horse Wildlife Mitigation Area and were within 1 km (1,094 yd) of one another. The first site (Disturbed) was characterized by substantial meadow vole disturbance resulting in high percent bare ground. The second site (Remnant Native) was characterized by a relatively large remnant stand of native species. The third site (Wetland) was located adjacent to a wetland with high soil moisture. Site-specific data characterizing each site are presented in the Results section.

Treatments and Experimental Design. At all three sites, treatments included shallow tilling, watering, and seeding, which were applied alone and in combination to generate eight factorial treatment combinations (tillage, watering, seeding, tillage plus watering, tillage plus seeding, watering plus seeding, tillage plus watering plus seeding, and a control). These eight treatment combinations were applied in a split plot design with four replications to generate 32 whole plots (2 m^2). Half of each whole plot (1 m^2) received an application of 2,4-D. In late September 2002, 2 kg acid equivalence/ha of 2,4-D was applied to half of each plot with a backpack sprayer to control a broad spectrum of broadleaved plants. In late October 2002, appropriate plots were rototilled to a depth of 5 cm, and plots were broadcast-seeded at a rate of 34 kg/ha (30 lb/ac). The seed mixture consisted of six grasses (17 kg/ha) and five forbs (17 kg/ha), including *P. spicata* (5 kg/ha), rough fescue (*Festuca campestris* Rydb.) (5 kg/ha), prairie junegrass (*Koeleria cristata* auct. p.p., non Pers.) (1.75 kg/ha), baltic rush (*Juncus balticus* Willd.) (1.75 kg/ha), Sandberg bluegrass (*Poa secunda* J. Presl) (1.75 kg/ha), western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve] (1.75 kg/ha), common gaillardia (*Gaillardia aristata* Pursh) (3.4 kg/ha), sticky purple geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey.) (3.4 kg/ha), common yarrow (*Achillea millefolium* L.) (3.4 kg/ha), silky lupine [*Lupinus sericeus* Pursh ssp. *huffmanii* (C.P. Sm.) Fleak & D. Dunn] (3.4 kg/ha), and wild bergamot (*Monarda fistulosa* L.) (3.4 kg/ha). These species represented key functional groups within the habitat type. In May, June, and July 2003, watering treatments were applied so that a total of one-third (135 mm) of the average annual precipitation (400 mm) was added to the naturally occurring precipitation for the year.

Sampling. Plots were sampled for percent bare ground and percent soil moisture in 2002 before treatments were added and again in 2003 and 2004 after treatments were added. Percent bare ground was estimated in July within two randomly placed Daubenmire frames (0.10 m^2) per subplot. Percent soil moisture was sampled in three random locations per whole plot from May to August within the upper 15 cm of the soil profile using Time Domain Reflectometry (Jones et al. 2002). Cover and density of seeded species (*C. biebersteinii* and sulphur cinquefoil [*Potentilla recta* L.]), native forbs, exotic forbs, native grasses, and exotic grasses were estimated in July 2002 before treatments were added and again in July 2003 and 2004 after treatments were added. *Centaurea biebersteinii* and *P. recta* were collectively considered ''invasive species,'' whereas other nonindigenous forbs that do not appear invasive were called ''exotic.'' Percent cover and density of plant species were estimated within two randomly placed Daubenmire frames (0.10 m^2) in each subplot.

Data Analyses. ANOVA was used to determine differences between sites in percent soil moisture, bare ground, and cover of remnant native species before treatments were added. Analysis of covariance (ANCOVA) was used to determine the response of seeded species, *C. biebersteinii*, *P. recta*, native forbs, exotic forbs, native grasses, and exotic grasses to seeding, watering, and shallow tilling. Pretreatment cover and density data were used as a baseline covariate. Cover and density data were square root–transformed to meet assumptions of ANOVA and ANCOVA, and Fisher's Protected LSD test ($\alpha = 0.05$) was used to compare means. Back-transformed means are presented with letter to indicate differences among them. Data presented include only those treatments that were significant at the 0.05 level of significance, and means are averaged across factors that did not interact.

Results

Study Site Characteristics. The site identified as ''disturbed'' (by meadow voles) was about 55% percent bare ground, had about 14% soil moisture (averaged from May to August) due to its upland position, and had 11% cover of remnant native species (Figure 1). As it turned out, the site aimed at addressing ''colonization'' by possessing the most desired native species (18% cover) also had relatively high soil moisture (26% averaged from May to August), and only 2% cover of bare ground. The wetland site was used as an area where ''species performance'' favored desired species because it had 29% soil moisture (averaged from May to August), only 4% cover of bare ground, and 4% cover of native species. Research by Sheley et al. (2006b) indicated that native seeded species were favored in subirrigated wetlands, while *C. biebersteinii* was disfavored under these conditions.

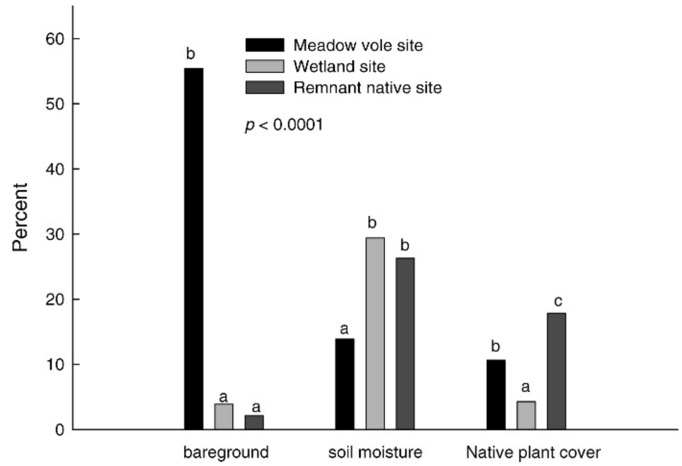

Figure 1. Study site characteristics used to indicate the degree to which the three general causes of succession were intact. Bare ground was used to quantify the level of natural disturbance. Soil moisture was used to indicate the degree to which moisture conditions would favor the performance of desired and native species over *C. biebersteinii* and *P. recta*. The cover of native species that could provide a seed source or vegetative reproduction was used to quantify colonization potential.

Site Availability/Disturbed Site (safe sites naturally existing). *Desired Species.* Seeding interacted with watering to influence the seeded species density in 2003 and 2004, native forb density in 2003, and native grasses in 2004. Tillage alone or in combination with any other factor did not affect these responses in either year ($P > 0.05$). In both years, the density of seeded species was greatest where seeding and watering were applied (Figures 2a and 2b). Cover of seeded species followed a similar pattern as density (data not shown). In 2003, native forb density followed a very similar pattern to that of all seeded species (Figure 2c), but not in 2004. In 2004, watering and seeding treatments alone produced native grass tiller density similar to that of the control (Figure 2d). However, seeding plus watering produced about 111 native grass tillers/m^2, while either treatment alone only produced about 29 native grass tillers/m^2.

Invasive Species. Centaurea biebersteinii and *P. recta* density and cover were influenced by the interaction of seeding, tilling, and 2,4-D in 2004 (Figures 3a and 3b). Water availability did not affect invasive species cover or density in either year ($P > 0.05$). Density of the two main invasive species decreased from 280 to 183 plants/m^2 in response to 2,4-D alone, but 2,4-D did not influence these species' density when 2,4-D was combined with any other treatment(s) (Figure 3a). Combined cover of *C. biebersteinii* and *P. recta* was lowest where 2,4-D alone, tillage alone, and seeding plus tillage plus 2,4-D were applied (Figure 3b). Of these treatments, only the seeding plus

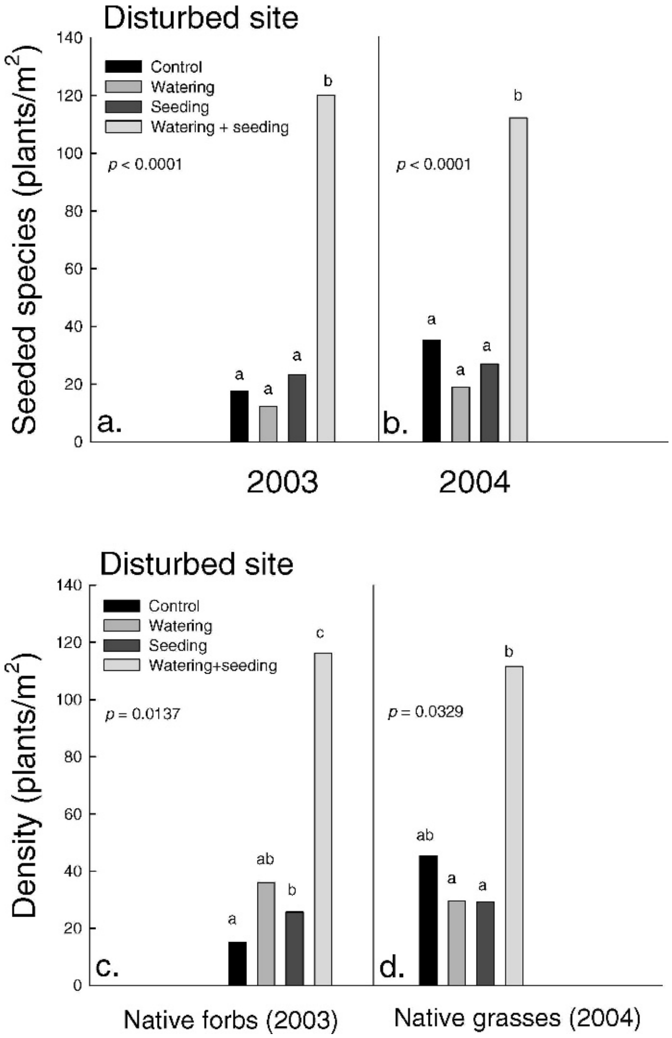

Figure 2. Interaction of seeding and watering on seeded species density in 2003(a) and 2004(b) as well as on native forbs in 2003(c) and native grasses in 2004(d) at the Disturbed site.

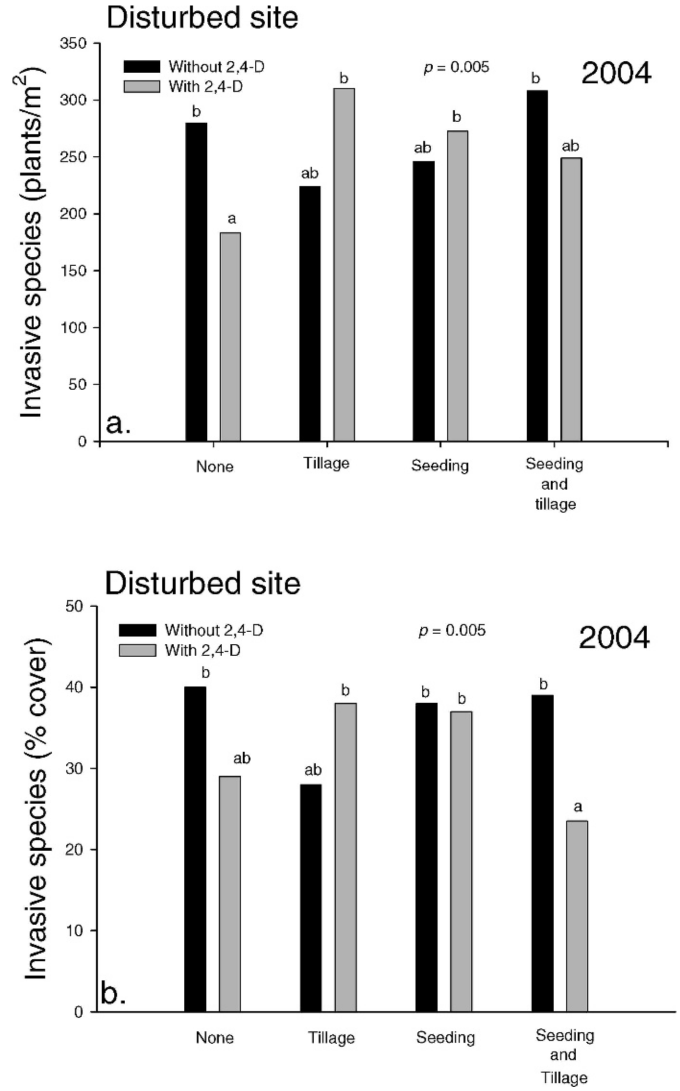

Figure 3. Interaction of seeding, tillage, and 2,4-D on invasive species density (a) and cover (b) in 2004 at the Disturbed site.

tillage plus 2,4-D combination had lower invasive species cover than the control, tillage plus 2,4-D, seeding (with or without 2,4-D), and seeding plus tillage without 2,4-D.

Other Exotic Species. In 2003, the only treatment influencing exotic forbs was watering. Across all treatments, exotic forb density increased from 207 to 284 plants/m^2 (P = 0.0024) and cover increased from 29 to 34% (P = 0.042) with watering. Exotic forb cover was influenced by the interaction of seeding, tilling, and watering in 2004 (Figure 4a). Exotic forb cover decreased from 53 to 37% in response to watering without seeding, from 53 to 30% in response to tilling without seeding, from 53 to 27% in response to seeding and watering, and from 53 to 27% in response to seeding, watering, and tilling (Figure 4a). Exotic forb density was not influenced by seeding, tilling, and watering in 2004 (P = 0.18). In 2004, the three-way combination of treatments was the only strategy that reduced exotic grass density, and the reduction was about threefold (Figure 4b).

Remnant Native Site (natural colonization of native plants possible). *Desired Species.* In 2003, seeding and tillage interacted to produce the highest density of seeded species (P = 0.004). Across treatments without seeding or tillage, seeded species density was 124ab plants/m^2. Tillage (89a plants/m^2) or seeding (153bc plants/m^2) did not alter seeded species density from that of the control that year. Combining these two treatments produced 254c plants/m^2, which was similar to plots only seeded. By 2004, seeding and tillage interacted with 2,4-D to influence seeded species density (Figure 5). The only treatment that had greater density than that of the control was seeding alone without 2,4-D, which produced about 440 plants/m^2. However, applying just 2,4-D produced a similar

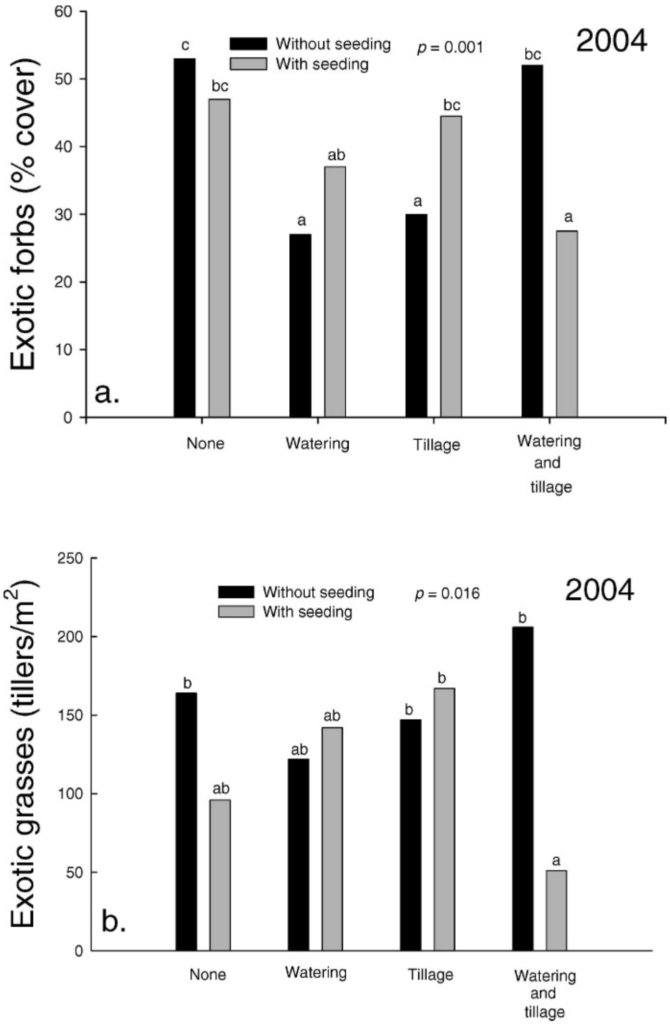

Figure 4. Interaction of watering, tillage, and seeding on (a) exotic forb cover and (b) exotic grass density in 2004 at the Disturbed site.

density of seeded species as seeding alone with 2,4-D. Tillage combined with 2,4-D was the only treatment combination that reduced seeded species density below that of the control. In 2003, seeding and tilling interacted to produce the highest native forb density and cover ($P = 0.001$ both years; means not shown). By 2004, the effects of seeding and tillage depended upon watering, but in all cases, native forb density was equal to or lower than that of the control ($P = 0.007$; means not shown).

Invasive Species. Centaurea biebersteinii and *P. recta* cover were influenced by the interaction of seeding, watering, and 2,4-D in 2003 ($P = 0.002$) and 2004 ($P = 0.023$). No treatment decreased the cover of invasive species below that of the control in either year (Table 3). Watering, watering plus seeding, and the combination of watering, seeding, and 2,4-D, produced higher invasive weed cover than the control in both years.

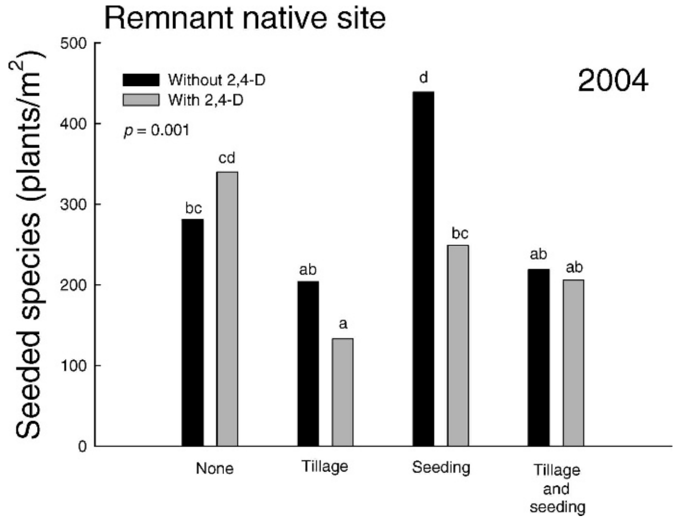

Figure 5. Interaction of tillage, seeding, and 2,4-D on seeded species density in 2004 at the Remnant Native site.

Other Exotic Species. Exotic forb cover was also affected by the interaction of seeding, watering, and 2,4-D in 2003 ($P = 0.001$) and 2004 ($P = 0.002$). In this case, all treatments except 2,4-D and seeding plus 2,4-D increased exotic forb cover over that of the control in both years (Table 4). The density of exotic grasses were influenced by the interaction of 2,4-D and tillage in 2003 ($P = 0.017$) and 2004 ($P = 0.017$). In 2003, tilling reduced exotic grass density from 347b (control) to 157a tillers/m^2. Application of 2,4-D alone and tilling plus 2,4-D produced 342b and 315b tillers/m^2, respectively that year. In 2004, the control, 2,4-D, and tillage produced 373a, 335a, and 373a tillers/m^2, respectively, whereas the combination of 2,4-D and tillage produced 604b exotic grass tillers/m^2.

Species Performance/Wetland Site (water favors desired species performance). *Desired Species.* In 2004, the effects of seeding on seeded species density depended upon tillage

Table 3. Interaction of 2,4-D; watering; and seeding on invasive species percent cover at the Remnant Native site.[a]

	2003	2004
Treatment	Cover (%)	Cover (%)
None	3.6 ab	7.0 ab
2,4-D	3.8 ab	7.7 ab
Watering	10.4 cd	12.3 bc
Watering + 2,4-D	6.8 bc	9.4 abc
Seeding	7.5 bc	13.0 bc
Seeding + 2,4-D	1.7 a	3.9 a
Seeding + Watering	10.1 c	12.9 bc
Seeding + Watering + 2,4-D	17.8 d	15.6 c

[a] Means followed by the same letter are not significantly different.

Table 4. Interaction of 2,4-D; watering; and seeding on exotic forb percent cover at the Remnant Native site.[a]

	2003	2004
Treatment	Cover (%)	Cover (%)
None	3.3 a	8.4 ab
2,4-D	5.4 ab	12.7 bc
Watering	14.8 d	19.3 cd
Watering + 2,4-D	11.8 c	15.9 cd
Seeding	8.6 bc	16.6 cd
Seeding + 2,4-D	2.1 a	5.9 a
Seeding + Watering	15.6 de	18.0 cd
Seeding + Watering + 2,4-D	23.0 e	23.9 d

[a] Means followed by the same letter are not significantly different.

and the application of 2,4-D (Figure 6a). Water addition alone or in combination with any other factor did not affect these responses in either year ($P > 0.05$). Tillage with 2,4-D and the three-way combination of treatments were the only management systems that increased seeded species density over that of the control. However, seeding plus 2,4-D and tillage plus seeding without 2,4-D produced the same densities of seeded species as those mentioned above. The effect of seeding on native grasses depended upon tillage and 2,4-D in 2004 (Figure 6b). On this wetland site, no treatment produced more native grass density than that of the control, and applying 2,4-D actually reduced native grass density below the control. Tillage with 2,4-D produced more native grass density than 2,4-D alone, tillage without 2,4-D, and either seeding with or without 2,4-D. Native forb density was influenced by the interaction of tillage and seeding in 2003 and 2004 (Figure 7). In both years, the combination of tillage plus seeding produced the highest native forb density. In 2003, seeding alone produced greater native forb density than tillage or the control, but that effect was removed by 2004.

Invasive Species. The only treatment effect on *C. biebersteinii* and *P. recta* at the wetland site was the main effect of 2,4-D ($P = 0.001$). The density of these two invasive species was reduced from 61.5 to 19.9 plants/m^2 after the application of this herbicide in 2004.

Other Exotic Species. Exotic forb density and cover followed a fairly consistent pattern in their response to tillage and seeding in both years. For example, the control produced about 296 exotic forb plants/m^2 in 2004. Neither tilling (378 plant/m^2), seeding (358 plant/m^2), nor their combination (262 plant/m^2) produced exotic forb densities different from that of the control. The only differences were that seeding plus tillage produced lower exotic forb density and cover than either treatment applied alone. Although no treatments influenced exotic grasses in 2003, seeding interacted with watering to affect exotic grass

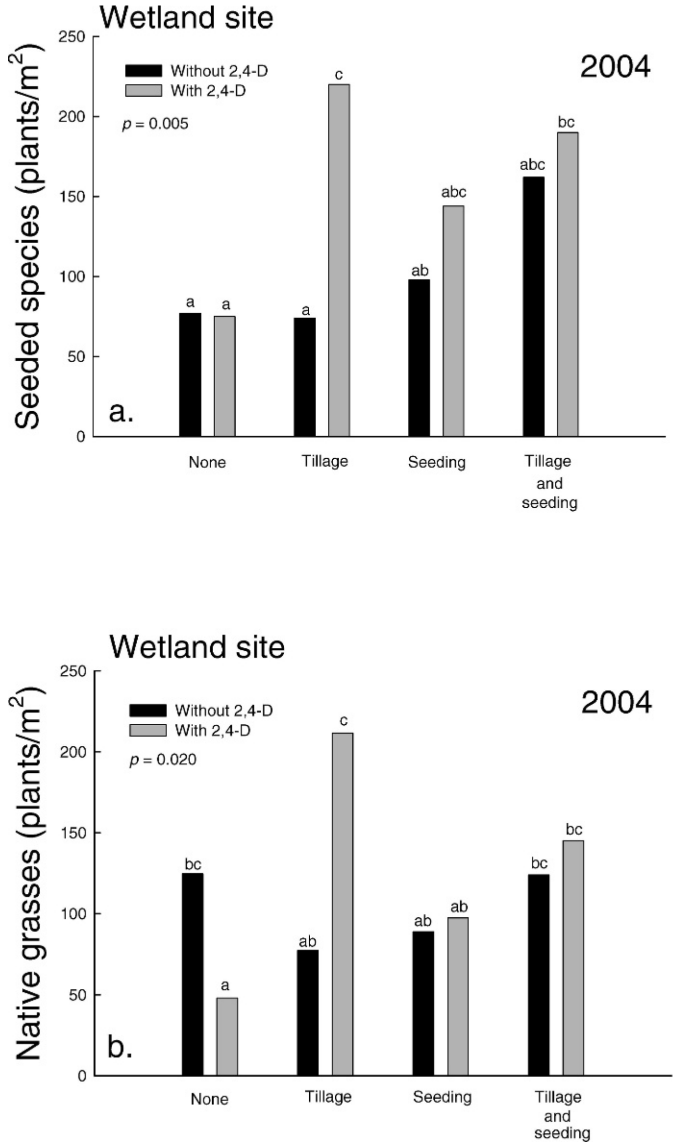

Figure 6. Interaction of tillage, seeding, and 2,4-D on (a) seeded species density and (b) native grass density in 2004 at the Wetland site.

density ($P = 0.001$) and cover ($P = 0.004$). Exotic grass density was highest in plots that were neither seeded nor watered (692c plant/m^2) and lowest where only water was applied (269a plants/m^2). Seed alone (421b plants/m^2) and seeding plus watering (471b plants/m^2) produced moderate levels of exotic grass density. Cover followed a similar trend with a maximum cover in the control plots of 15%.

Integrated Results

In order to provide an understanding of the overall results, means from treatments that produced the highest density of native grasses, native forbs, and the lowest invasive weeds for each site are presented (Table 5). Density is presented because establishment of desired species were considered critical to

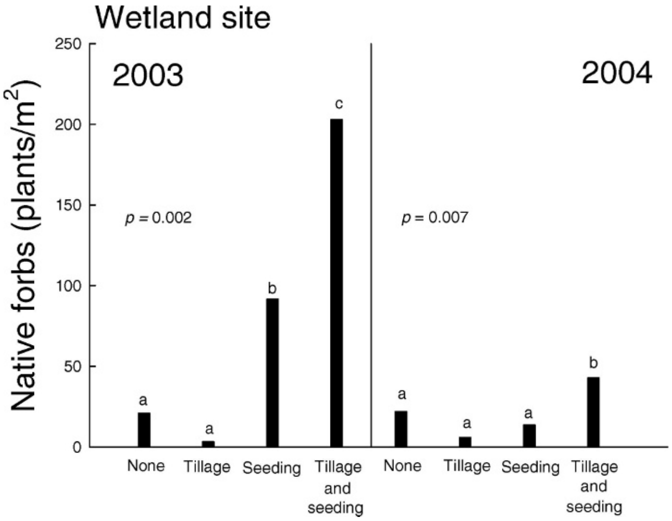

Figure 7. Interaction of tillage and seeding on native forb density in 2003 and 2004 at the Wetland site.

initiating a favorable successional trajectory and, in the long-term, controlling undesirable species by occupying a majority of available niches. Seeding and watering produced the highest native grass and forb density on the site disturbed by meadow voles. On the wetland site, tillage was important in the establishment or enhancement of native grasses and forbs. Combining tillage with 2,4-D favored native grasses, whereas combining tillage with seeding favored native forbs. Seeding favored native grasses and forbs on the site with a remnant native stand of desired species. In the short-term, 2,4-D decreased invasive weed density the most on the disturbed and wetland sites, but no treatment decreased weeds on the sites with remnant vegetation.

Discussion

Two major criticisms in restoration ecology are the lack of a general theory to allow the transfer of methodologies and knowledge from one situation to another (Halle and Fattorini 2004), and the need for process- and mechanistic-based principles that land managers can use to make decisions regarding implementation (Werner 1999). The search for models, frameworks, and principles that provide a bridge between ecological theory and the practice of restoration is well underway (Temperton et al. 2004) and is not new (Pickett et al. 1987). Pickett et al. (1987) proposed the ecological basis for a theoretical framework for developing invasive plant management that addresses the underlying cause of invasion (Sheley et al. 1996). This hierarchical model includes the general causes of succession, controlling ecological processes and mechanisms, and their modifying factors (Table 1). This mechanistic and process-based model offers potential for planning and predicting the outcome of integrated invasive plant management. In two prior companion studies, we found evidence to support the general hypothesis that, as weed management increasingly addresses the factors that modify the processes that influence the three general causes of succession (site availability, species availability, and species performance) in a complementary manner, the establishment and persistence of native desired species would increase (Sheley et al. 2006a).

Vegetation response to management differs among habitats (Vandvik et al. 2005). Thus, our ability to accurately predict management outcomes and choose appropriate management procedures depends on the level of knowledge about how a treatment modifies the processes directing succession (Sheley et al. 2006b; Werner 1999) and the specific environmental characteristics of sites and patches across the landscape (Burnett et al. 1998; Ludwig and Tongway 1995; Patten and Ellis 1995). Much of the focus on heterogeneity has been aimed at restoring it (Benton et al. 2003; Fuhlendorf and Engle 2004), while much less effort has been directed toward using existing heterogeneity to make restoration decisions across landscapes. In this study, we evaluated whether augmentative

Table 5. Treatments producing the highest density of native grasses and forbs and the lowest invasive weed density at each site.

Site	Native grasses	Native forbs	Invasive weeds
	(plants/m^2)		
Disturbed	Seeding + Watering	Seeding + Watering	2,4-D
	111 (22)[a]	118 (29)	175 (42)
Wetland	Tillage + 2,4-D	Tillage + Seeding	2,4-D
	220 (37)	201 (54)	20 (11)
Remnant native	Seeding	Seeding	—[b]
	435 (104)	100 (32)	
Control	18 (8)[c]	43 (21)	278 (71)

[a] Numbers in parentheses are SE of the mean.

[b] No treatment decreased invasive weeds on the site with remnant natives.

[c] Represents mean density across all sites.

restoration could advance traditional successional management approaches and provide a more effective ecologically-based framework to guide the implementation of restoration across heterogeneous landscapes dominated with invasive weeds (Bard et al. 2004).

Site Availability/Disturbed Site. *Seeded and Native Species.* We accepted our first hypothesis that seeding combined with watering would augment meadow vole disturbance to increase desired species composition. Seeded species density as well as native forb and grass density (including those not seeded) were highest where seeding and watering were applied together in this disturbed area. For example, seeded species density was about fourfold greater when seeding was applied with watering compared to either treatment alone. Additional disturbance with tillage or 2,4-D, however, did not increase seeded species density in either year. Similarly, pocket gopher disturbance has been shown to increase native seedling establishment in grasslands dominated by invasive annuals (DeSimone and Zedler 1999). The effect of this disturbance on seedling establishment, however, depends on soil moisture, with disturbance resulting in relatively greater establishment at sites with high soil moisture compared to sites with low soil moisture (Berlow et al. 2002). Thus, in many systems, current disturbance regimes (in our case maintained by meadow voles) may be adequate to create a sufficient number of safe sites for desired species so long as soil water is available in the upper portion of the profile.

Invasive and Exotic Species. Based upon the successional theory tested in this paper, we did not anticipate that tillage would be a major factor determining vegetation composition at the disturbed site because safe sites appeared to be created by meadow voles (Luken 1990; Rebollo et al. 2003). Tillage interacted with other treatments, including seeding, to influence exotic forbs and grasses, as well as the two invasive species at this site. In one study, cultivation to about 19 cm eliminated *C. biebersteinii* (Popova 1960), but in another study, tillage increased this weed's density while reducing its biomass (Sheley et al. 1999). Tillage can have species specific influence on performance (Légère and Sampson 2004), and it appears that seedlings and juvenile knapweed are susceptible to tillage (Popova 1960). Tillage appears to have a negative impact on other exotic forbs as well (Gordon et al. 2004).

The only treatment that decreased exotic grass density below that of the control was the combination of tillage, watering, and seeding at the disturbed site. The primary exotic grass was *B. tectorum*, which is well-known to be favored by disturbance alone (Mosley et al. 1999). In dry environments, this winter annual grass dominates because it uses winter precipitation before the later maturing bunchgrass and completes its life cycle when other later maturing species struggle (Harris 1967; Sheley and Larson 1994). Adding water may have favored establishing species and disfavored *B. tectorum* through competition by desired species with adequate moisture to establish, capture nutrients, and complete their life cycle.

Species Availability/Remnant Native Site. *Seeded and Native Species.* At the outset, it appeared that the augmentative restoration approaches we applied, based on successional management theory, were less useful in predicting the response of seeded species and desired native species in areas where native remnant plants existed and were expected to colonize the site. In this case, we hypothesized that creating a disturbance through tilling and/or 2,4-D combined with watering would augment remnant native species to increase desired species composition. Contrary to our hypothesis, seeding alone produced the highest density of seeded species. Seeding alone increased seeded species density about 1.5-fold. It is possible that 2,4-D affected newly emerging forbs, but since neither disturbance interacted with seeding there was probably a high availability of empty safe sites. These observations, however, are consistent with numerous seed addition studies that have demonstrated that seedling density and species diversity are seed-limited, even when remnant or established stands of native vegetation are present as a seed source. For example, a review by Turnbull et al. (2000) found that, among the seed addition studies conducted in arid and semiarid grasslands, seedling establishment was limited by seed availability in about 40% of the sites. While seed sources produced in intact native grasslands surrounding or adjacent to disturbed fields are generally insufficient to saturate safe sites available in disturbed areas (Kindscher and Tieszen 1998; Tilman 1990), even in intact native grasslands the seeding of desired species can increase seedling density up to fourfold without additional disturbance (Gross et al. 2005). Thus, at our Remnant Native site, it appears that enough safe sites existed naturally so that seedling establishment was seed limited, and that the propagule supply from the remnant native vegetation was insufficient to occupy a substantial proportion of the safe sites.

There is some evidence suggesting, however, that there was enough of a propagule pool in the soil seed bank at the Remnant Native site to respond to invasive weed control. For example, removal of invasive forbs with 2,4-D alone increased seeded species density as much as seeding alone. Once previously-occupied safe sites were open, it appeared that there was a sufficient native seed bank present to occupy at least some of these sites. Similar results have been found by other weed control experiments on *C. biebersteinii*, where a substantial residual understory of desired species was present (Davis 1990; Kedzie-Webb et al. 2002). Thus, although remnant vegetation can maintain a seed bank sufficient to support establishment in some safe sites, as predicted by the successional model, tillage appears to increase the rate of successional processes and magnitude of successional change, particularly with perennials that have low growth rates and are slow to recover following disturbance, as has been observed in other grasslands (Tilman 1990).

Invasive and Exotic Species. Many invasive weeds have rapid intrinsic growth rates (Radosevich et al. 1997) and experiments have demonstrated increased success of invaders following nutrient additions alone (Huenneke et al. 1990), although nutrient additions often interact with physical disturbance and water to promote invasion (Burke and Grime 1996; Duggin and Gentle 1998; Li and Norland 2001). Somewhat predictably, the two invasive species responded positively to watering or combinations including watering at the site where a remnant stand of desired species was present. At this upland site, water at one-third the annual precipitation may have been ideal for invasive weed growth. Although difficult to explain, it was interesting that watering, seeding, and 2,4-D increased weed cover. In this case, 2,4-D could have provided just enough control to lower weed density, but provided an increase in soil nutrients available to survivors.

Phenoxy herbicides are generally used to control broadleaved weeds common on rangeland (Bussan and Dyer 1999). There appeared to be a trade-off with respect to applying 2,4-D at the site with a remnant stand of desired species. Nearly all treatments without 2,4-D increased exotic forb cover, and nearly all combinations including 2,4-D produced the highest exotic grass density. Exotic grasses can metabolize phenoxy herbicides, which provide the basis for their selectivity (Bussan and Dyer 1999). In either case, managers can anticipate increases in either exotic group when using this phenoxy herbicide on upland sites with a remnant stand of desired species.

Species Performance/Wetland Site. Based on the successional management model (Table 1), we further predicted that, within our study system, shallow tilling combined with seeding would augment mesic soils at wetland sites to increase desired species composition because safe sites for establishment were not naturally abundant (Sheley et al. 1996). As hypothesized, tillage plus seeding, with or without 2,4-D, produced the highest density of seeded grasses and native forbs at the wetland site. At the Wetland site, water addition did not increase desired species establishment. Tillage combined with seeding had the largest effect on native forb functional group density at the Wetland site. This observation is also consistent with our predictions based on augmentative restoration, since remnant native forbs have substantially lower cover at this site than remnant native grasses. Thus, while both native forbs and grasses are microsite limited at wetland sites, the native forbs are substantially more seed-limited than the relatively more abundant native grasses. In addition to providing adequate water for germination and establishment of desired species, the subirrigated environment at the Wetland site may also have favored the performance of native grasses over *C. biebersteinii* (Sheley et al. 2006b).

Simultaneous seeding and application of a broadleaved herbicide has been successfully used to establish *P. spicata* in stands of *C. biebersteinii* (Sheley et al. 2001). We anticipated seeding combined with 2,4-D would also produce high densities of seeded species at the wetland site. This combination produced densities of seeded species similar to those of tillage plus seeding. Combining 2,4-D with seeding addressed disturbance and colonization similar to tillage and seeding (Sheley et al. 2005). In addition, tillage combined with 2,4-D produced high densities of seeded species by controlling broadleaved weeds while stimulating *P. smithii*, a rhizomatous perennial grass.

Invasive and Exotic Species. The response of invasive and exotic species was moderately predictable using the successional management model at the wetland site. As we expected, application of 2,4-D decreased invasive broadleaved weeds (Davis 1990). The interaction of seeding and tillage reduced exotic forbs, but not grasses, likely because their crowns remained somewhat intact with tillage. Adding water produced the lowest exotic grass density and cover. Since this site was on the water's edge, addition of water may have created conditions outside the exotic grasses' ecological amplitude (Sheley et al. 2006b).

Conclusion

Enduring restoration and rehabilitation of invasive plant dominated rangeland requires addressing the cause of the degradation (Whisenant 1999). Successional management provides a theoretical framework that conceptually allows managers to identify and repair processes influencing three general causes of community dynamics: disturbance, colonization, and relative species performance (Luken 1990), and has been proposed (Sheley et al. 1996; Sheley and Krueger-Mangold 2003) and tested for use on rangeland dominated by invasive species (Sheley et al. 2006b). Results from this study suggest that augmentative restoration can extend this successional management approach and can improve management approaches in restoring desired plant communities in heterogeneous environments with varying stages of disrepair or invasion by weeds (Bard et al. 2003).

Although the response of invasive weeds and other exotic species to factors driving succession were difficult to predict, augmentative restoration provided a robust conceptual framework for predicting desired species response to available sites (disturbance), available species (colonization), and techniques aimed at influencing relative species performance. In two of the three environments, using augmentative restoration based on successional theory and easily collectable criteria indicating the degree of site availability (disturbance by meadow vole activity), species availability (colonization by remnant native species) and relative species performance (increased water availability), improved our decision as to the treatment combinations that would maximize seedling establishment during restoration. The model only partially predicted the seeded species response at the site with a remnant stand of natives, although it appears that rapid establishment of desired species in many systems with remnant or intact stands of established desired species will likely be seed limited. A central goal of Ecologically Based Invasive Plant Management is to direct establishment of a healthy native plant community to alter the ecological processes allowing weeds to invade and persist, as opposed to management tools that only treat the symptoms of invasion. The conceptual framework of augmentative restoration was useful in establishing desired plant communities, which should in turn also address the major processes allowing invasions to persist.

Overall, these results strongly suggest that selectively augmenting succession processes that remain intact by repairing or replacing successional processes occurring at inadequate levels can enhance traditional successional management. This system could provide a useful process-based theory for restoration across heterogeneous landscapes. Besides the clear economic advantages of lower management inputs associated with augmentative restoration, avoiding unnecessary management inputs has the additional advantage of minimizing unintended negative impacts on ecosystem processes. In addition, the generality of this expanded conceptual framework has the potential to improve decision making in a range of restoration settings and facilitate transfer of methodologies and knowledge from one situation to another.

Acknowledgments

We thank the Confederated Salish and Kootenai Tribes for providing the site for conducting this research. We also thank the field assistants, Rene Kittle, Tamara Enz, Jen Anderson, Monica Pokorny, and Dr. Matt Rinella, who helped establish the plots, implement treatments, and collect data. In addition, we thank the anonymous reviewers who helped improved this manuscript.

Literature Cited

Bard, E. C., R. L. Sheley, and J. S. Jacobsen. 2003. Using ecological theory to guide augmentative restoration (Montana). Ecol. Restor. 21: 143–144.

Bard, E. C., R. L. Sheley, J. S. Jacobsen, and J. J. Borkowski. 2004. Using ecological theory to guide the implementation of augmentative restoration. Weed Technol. 18:1246–1249.

Benton, T. G., J. A. Vicery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18: 182–188.

Berlow, E. L., C. M. D'Antonio, and S. A. Reynolds. 2002. Shrub expansion in montane meadows: the interaction of local-scale disturbance and site aridity. Ecol. Appl. 12:1103–1118.

Burke, M. J. W. and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:776–790.

Burnett, M. R., P. V. August, J. H. Brown, and K. T. Killingbeck. 1998. The influence of geomorphological heterogeneity on biodiversity. I. A patch-scale perspective. Conserv. Biol. 12:363–370.

Bussan, A. J. and W. E. Dyer. 1999. Herbicide and rangeland. Pages 116–132 *in* R. L. Sheley and J. K. Petroff, eds. Biology and Management of Noxious Rangeland Weeds. Corvallis, OR: Oregon State University Press.

Davis, E. 1990. Spotted Knapweed (*Centuarea maculosa* Lam.) Seed Longevity, Chemical Control and Seed Morphology. Masters thesis. Bozeman, MT: Montana State University. 109 p.

DeSimone, S. A. and P. H. Zedler. 1999. Shrub seedling recruitment in unburned Californian coastal sage scrub and adjacent grassland. Ecology 80:2018–2032.

Duggin, J. A. and C. B. Gentle. 1998. Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest. For. Ecol. Manage. 109:279–292.

Foster, B. L., T. L. Dickson, C. A. Murphy, I. S. Karel, and V. H. Smith. 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. J. Ecol. 92:435–449.

Fuhlendorf, S. D. and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. J. Appl. Ecol. 41:604–614.

Gordon, T. A., D. A. Derksen, R. E. Blackshaw, R. C. Van Acker, A. Légère, P. R. Watson, and G. C. Turnbull. 2004. A multistudy approach to understanding weed population shifts in medium- to long-term tillage systems. Weed Sci. 52:874–880.

Gross, K. L. 1980. Colonization by *Verbascum thapsus* (Mullein) in an old field in Michigan: experiments on the effects of vegetation. J. Ecol. 68:919–927.

Gross, K. L., G. G. Mittelbach, and H. L. Reynolds. 2005. Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. Ecology 86:476–486.

Halle, S. and M. Fattorini. 2004. Advances in restoration ecology: insights from aquatic and terrestrial ecosystems. Pages 10–33 *in* V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, eds. Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. Washington, DC: Island.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecol. Monogr. 37:89–111.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71: 478–491.

Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge, UK: Cambridge University Press. 704 p.

Jones, S., J. M. Wraith, and D. Or. 2002. Time domain reflectometry measurement principles and applications. Hydrol. Processes. 16: 141–153.

Kedzie-Webb, S. A., R. L. Sheley, and J. J. Borkowski. 2002. Predicting plant community response to picloram. J. Range Manage. 55: 576–583.

Kindscher, K. and L. L. Tieszen. 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. Restor. Ecol. 6:181–196.

Légère, A. and N. Samson. 2004. Tillage and weed management effects on weeds in barley–red clover cropping systems. Weed Sci. 52: 881–885.

Li, Y. C. and M. Norland. 2001. The role of soil fertility in invasion of Brazilian pepper (*Schinus terabinthfolius*) in Everglades National Park, Florida. Soil Sci. 166:400–405.

Loreau, M., N. Mouguet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Ecology 100:12765–12770.

Ludwig, J. A. and D. J. Tongway. 1995. Spatial organization of landscapes and its function in semi-arid woodlands, Australia. Landscape Ecol. 10:51–63.

Luken, J. 1990. Directing Ecological Succession. New York: Chapman and Hall. 264 p.

Mosley, J. C., S. C. Bunting, and M. E. Manoukian. 1999. Cheatgrass. Pages 175–188 *in* R. L. Sheley and J. K. Petroff, eds. Biology and Management of Noxious Rangeland Weeds. Corvallis, OR: Oregon State University Press.

Mueggler, W. F. and W. L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. Ogden, UT: USDA Forest Service General Technical Report Int-66, Intermountain Forest and Range Experiment Station. 154 p.

Patten, R. S. and J. E. Ellis. 1995. Patterns of species and community distributions related to environmental gradients in an arid tropical ecosystem. Vegetation 17:69–79.

Pickett, S. T. A. and M. L. Cadenasso. 1995. Landscape ecology: spacial heterogeneity in ecological systems. Science 269:331–334.

Pickett, S. T. A. and M. L. Cadenasso. 2005. Landscape ecology: spacial heterogeneity in ecological systems. Science 269:331–334.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Model, mechanisms, and pathways of succession. Bot. Rev. 53:335–371.

Popova, A. Y. 1960. *Centaurea diffusa* Lam, a steppe pasture weed in the Crimea (English Translation). Botanicheskiy Zhurnal 45:1207–1213.

Radosevich, S. R., J. S. Holt, and C. M. Gharsa. 1997. Weed Ecology: Implications for Vegetation Management. New York: J Wiley and Sons. 608 p.

Rebollo, S., L. Perez-Camacho, J. Valenia, and A. Gomez-Sal. 2003. Vole mound effects and disturbance rate in a Mediterranean plant community under different grazing and irrigation regimes. Plant Ecol. 169:227–243.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364–374.

Seabloom, E. W., E. T. Borer, V. L. Boucher, R. S. Burton, K. L. Cottingham, L. Goldwasser, W. K. Gram, B. E. Kendall, and F. Micheli. 2003. Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecol. Appl. 13:575–592.

Sheley, R. L., P. B. Hook, and R. LeCain. 2006a. Establishment of native and invasive plants along a rangeland riparian gradient. Ecol. Restor. 24(3):173–181.

Sheley, R. L., J. S. Jacobs, and D. E. Lucas. 2001. Revegetating spotted knapweed infested rangeland in a single entry. J. Range Manage. 54: 576–583.

Sheley, R. L., J. S. Jacobs, and T. J. Svejcar. 2005. Integrating disturbance and colonization during rehabilitation of invasive weed-dominated grasslands. Weed Sci. 53:307–314.

Sheley, R. L., J. S. Jacobs, and R. P. Velagala. 1999. High seeding rates enhance intermediate wheatgrass establishment in spotted knapweed infested rangeland. J. Range Manage. 52:67–73.

Sheley, R. L. and J. Krueger-Mangold. 2003. Principles for restoring invasive plant infested rangeland. Weed Sci. 51:260–265.

Sheley, R. L. and L. L. Larson. 1994. Observation: comparative life history of cheatgrass and yellow starthistle. J. Range Manage. 47: 450–456.

Sheley, R. L., J. M. Mangold, and J. L. Anderson. 2006b. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. Ecol. Monogr. 76(3):365–379.

Sheley, R. L., T. J. Svejcar, and B. D. Maxwell. 1996. A theoretical framework for developing successional weed management strategies on rangeland. Weed Technol. 10:766–773.

Temperton, V. R., R. J. Hobbs, T. Nuttle, and S. Halle. 2004. Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. Washington, DC: Island. 424 p.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3–15.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238.

Vandvik, V., E. Heegaard, I. Maren, and P. Aarrestand. 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. J. Appl. Ecol. 42: 139–149.

Werner, P. 1999. Reflections on "mechanistic" experiments in ecological restoration. Pages 321–328 *in* W. R. Jordan III, M. E. Gilpin, and J. D. Aber, eds. Restoration Ecology: A Synthetic Approach to Ecological Research. Cambridge, UK: Cambridge University Press.

Whisenant, S. G. 1999. Repairing Damaged Wildlands: A Process Oriented, Landscape-Scale Approach. Cambridge, UK: Cambridge University Press. 328 p.

Received December 12, 2007, and approved September 20, 2008.