

POTENTIAL FOR SUCCESSIONAL THEORY TO GUIDE RESTORATION OF INVASIVE-PLANT-DOMINATED RANGELAND

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Abstract. Ecologists are searching for models, frameworks, and principles that provide a bridge between theory and the practice of restoration. Successional management has been proposed as a useful model for managing and restoring invasive-plant-dominated rangeland because it provides a framework in which ecological processes can be manipulated by managers to achieve a desired plant community. Successional management identifies three general causes of succession (site availability [disturbance], species availability [colonization], and species performance) and suggests that managers address the ecological process influencing each general cause in a coordinated fashion to direct plant community dynamics. We tested successional management using various techniques to restore invasive-weed-dominated rangeland. Our hypothesis was 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. Thus, we anticipated that the majority of responses to multiple treatments would be explained by higher order interactions, especially in the final year of the study (2004). To test this hypothesis, we used a model system within a *Festuca campestris*/*Pseudoroegneria spicata* habitat among pothole wetlands dominated by *Centaurea maculosa* and *Potentilla recta*, two invasive species. We used three herbicide treatments (none, 2,4-D, and picloram) to influence species performance; two seeding methods (imprinting, i.e., creating a small depression and broadcasting, and no-till drilling) to influence disturbance; three seeding rates (977, 1322, and 1557 seeds/m²) to influence colonization; and two cover crop treatments (with and without *Triticum aestivum*) to influence soil N and favor native grasses. Treatments were factorially arranged and replicated four times in a randomized complete block design in 2001 and sampled in 2002 and 2004. As predicted, plant response to treatments was dominated by two- and three-way interactions in 2004. The highest seeding rate (colonization) combined with no-till drilling (disturbance) produced the highest native grass density in 2002. These effects persisted into 2004 for *P. spicata*, but not for *F. campestris* or *F. idahoensis*. Combining picloram with no-till drill seeding also produced a high density of *P. spicata*. Drill seeding at 977 seeds/m² favored *F. idahoensis* density, while no-till drilling at 1322 seeds/m² favored its biomass in 2004. *F. idahoensis* established well after drill seeding with a cover crop and applying 2,4-D. Herbicides reduced native forb density and/or biomass, with early season forbs being more sensitive to picloram and summer forbs being more sensitive to 2,4-D. Herbicides increased exotic grasses' density and biomass but had no effect on native grasses. In most cases, integrating treatments that addressed multiple causes of succession favored a desired plant community. Thus, we accomplished our goal of using successional management to direct plant communities toward native desired species, but the treatments used did not improve species richness. Since naturally occurring native forbs did not respond favorably to any treatment combination, ecological restoration using successional management may best be thought of as an iterative procedure where various components and processes of the system are methodically repaired or replaced over time.

Key words: *Centaurea maculosa*; *Festuca campestris*; *Festuca idahoensis*; *invasive species*; *plant community dynamics*; *Potentilla recta*; *Pseudoroegneria spicata*; *restoration*; *successional management*.

INTRODUCTION

Invasive plants dominate and continue to spread throughout millions of hectares of rangeland in the western United States (Sheley and Petroff 1999). Invasive weeds alter the structure and function of ecosystems and threaten biological diversity (Randall

1996, Vitousek et al. 1996, Olson 1999). Invasive weeds have increased soil erosion, reduced infiltration (Lacey et al. 1989), and displaced native plant species (Belcher and Wilson 1989, Miller et al. 1994). During the 1990s, invasive weeds cost more than \$20 billion in control and lost production in the United States alone (Hirsch and Leitch 1996, Pimentel 2002).

Current management focuses on eliminating weeds rather than understanding and manipulating the ecological processes and mechanisms promoting invasion

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TABLE 1. Causes of succession, contributing processes, and modifying factors.

Cause of succession and process	Modifying factors
Site availability	
Disturbance	size, severity, time intervals, patchiness, predisturbance history
Species availability	
Dispersal	dispersal mechanisms, 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, quantity
Stress	climate, site history, prior occupants, herbivory, natural enemies
Interference	competition, herbivory, allelopathy, resource availability, predators, other level interactions

and species compositional changes (Hobbs and Humphries 1995). Managing invasive plants on rangeland generally emphasizes controlling weeds in order to increase grass production, which can be detrimental to native forbs (Sheley and Petroff 1999). This may exacerbate the weed problem by creating plant communities that lack functional diversity, thereby increasing their susceptibility to invasion (Levine and D'Antonio 1999, Naeem et al. 2000, Dukes 2001, Pokorny et al. 2005). Sustainable invasive plant management requires restoring diverse plant communities that function in maintaining ecological processes (Sheley et al. 1996, Sheley and Krueger-Mangold 2003).

It has been proposed that in order to achieve a diverse, desired plant community, invasive plant management must modify the processes and mechanisms directing plant community dynamics and structure (Sheley et al. 1996, Luken 1997, Sheley and Krueger-Mangold 2003). Traditional successional theory (Clements 1916) implied that plant communities were on a given trajectory for a particular climate, regardless of management. The traditional successional paradigm did not hold very much potential for guiding management of range and wild lands, but alternative models have been proposed since then that hold more promise (Connell and Slatyer 1977, Pickett et al. 1987b, Tilman 1988, Davis et al. 2000, Booth and Swanton 2002). One model of succession that lends itself to understanding and manipulating the mechanisms and processes directing plant community dynamics was proposed by Pickett et al. (1987b). The successional management model proposes three general causes of succession (site availability, species availability, and species performance), ecological processes primarily responsible for controlling the causes of succession, and factors that modify those processes (Table 1, after Pickett et al. [1987b]). Sheley et al. (1996) used the successional theory proposed by Pickett et al. (1987b) to develop a theory for invasive plant management that addresses the underlying cause of invasion. This model includes the general causes of succession, controlling ecological

processes and mechanisms, and their modifying factors (Table 1). Successional management is a mechanistic and process-based model that offers potential for planning and predicting the outcome of integrated invasive plant management.

Luken (1990) proposed using the successional model proposed by Pickett et al. (1987b) as a framework for formulating natural resource management strategies. Sheley et al. (1996) and Sheley and Krueger-Mangold (2003) proposed applying successional management to invasive-weed-dominated rangeland. Krueger-Mangold et al. (2005) expanded the model by incorporating multiple, mechanistic successional theories that provide further detail about successional processes. The potential of this successional theory to guide the development and implementation of effective restoration and invasive plant management is substantial, but largely untested.

Because information on establishing native species on invasive-weed-dominated land is scarce (but see Seabloom et al. 2003), and failures are commonly reported by managers, our overall goal was to investigate the initial response of vegetation to various restoration strategies applied within the context of successional management on rangeland dominated by invasive weeds. Our underlying hypothesis was that as weed management successively addressed the factors that modify or repair the processes influencing the three general causes of succession, i.e., site availability, species availability, and species performance, in a complementary manner, the establishment and persistence of native desired species would increase (Pickett et al. 1987a, Sheley et al. 1996). We expected that the majority of responses to various treatments aimed at addressing the three causes of succession would be explained by higher order interactions, especially in 2004, the final year of the study.

We tested the potential for using successional management to guide the establishment of native grasses on rangeland dominated by the invasive perennials *Centaurea maculosa* Lam. (spotted knapweed) and *Potentilla recta* L. (sulphur cinquefoil). *C. maculosa*

and *P. recta* are two of the most undesirable rangeland weeds in the northwestern U.S. (Rice 1991, Sheley et al. 1998, Sheley and Petroff 1999). One means of controlling these two species is broadleaf selective herbicides. Picloram (4-amino-3,5,6-trichloropicolinic acid), clopyralid (3, 6-dichloro-2-pyridine carboxylic acid), and 2,4-D (2, 4-dichlorophenoxy acetic acid), provide good control of *C. maculosa*, with picloram providing about three years of control (McKone et al. 1989, Lacey et al. 1999). *P. recta* does not respond to clopyralid, but is sensitive to picloram and 2,4-D (Rice 1999). The control provided by picloram limits competition with seeded grass species during the critical first years of establishment (Sheley et al. 2001). Application of 2,4-D provides short-term control and has a low soil residual (Bussan and Dyer 1999, Jacobs and Sheley 1999b).

There were several specific objectives and hypotheses associated with the various treatments. Our first objective was to test the effect different seeding methods had on native grass establishment. This objective addressed site availability through two seeding methods: no-till drill and broadcast seeding over small depressions. Based on the results of Sheley et al. (2001), we hypothesized that drill seeding would enhance seed soil contact, increase the likelihood that seeds occupy sites suitable for germination and emergence, and increase native grass establishment. The second objective was to test the influence of seeding rate on grass establishment. Seeding rate was used to modify species availability. We seeded a native three-species grass mix at three rates and hypothesized that, to the extent safe sites were available; establishment would be most successful at the highest rate. Objective three was to test the influence of two broadleaf selective herbicides, picloram and 2,4-D amine, on grass establishment as a specific test of modifying species performance. We hypothesized that picloram would reduce invasive weed competition long enough for the desired grasses to successfully establish. Species performance was also addressed by including a cover crop, *Triticum aestivum* L. (common wheat), or no cover crop treatment. Since Herron et al. (2001) found that including a cover crop of wheat shifted the competitive balance from *C. maculosa* in favor of *Pseudoroegneria spicata* Pursh (bluebunch wheatgrass), we hypothesized that *T. aestivum* would improve native grass establishment by giving a competitive advantage to the desired grasses.

We also quantified the response of the species growing in association with *C. maculosa* and *P. recta*. There were several hypotheses about the response of associated species to the various treatments. We hypothesized that the limited disturbance associated with the seeding techniques would have little influence on the associated species density, biomass, or species richness. We expected that the highest seeding rate would maximize establishment of native grasses, and thus, associated species density and biomass would be lowest because of competition. We hypothesized that both picloram and

2,4-D would increase associated grass density and reduce forb density, species richness, and diversity, but that picloram would reduce these parameters more than 2,4-D. We hypothesized that the cover crop *T. aestivum* would increase native associated species, but reduce exotic associated species by giving a competitive advantage to the desired grasses (Herron et al. 2001).

METHODS

Study site

This study was conducted on the Kicking Horse Wildlife Mitigation Area, south of Ronan, Montana, USA (47°29' N, 114°5' W) from 2001 through 2004. The site was a *Festuca campestris* Rydb. (rough fescue)/*Pseudoroegneria spicata* habitat type interspersed with ephemeral pothole wetlands (Mueggler and Stewart 1980). It was dominated by various exotic invasive plant species including *C. maculosa* and *P. recta*. The most common exotic grasses were *Poa compressa* L. (Canada bluegrass), *Poa pratensis* L. (Kentucky bluegrass), *Bromus tectorum* L. (cheatgrass), and *Dactylis glomerata* L. (orchardgrass). There were remnant stands of native plants, including *Achillea millefolium* L. (common yarrow), *Anemone cylindrical* Gray (candle anemone), *Antennaria* spp. (pussytoes), *Arnica sororia* Greene (twin arnica), *Castilleja pallescens* (Gray) Greenm. (pale Indian paintbrush), *Danthonia intermedia* Vasey (timber oatgrass), *F. idahoensis*, *Geum triflorum* Pursh (old man's whiskers), *Koeleria cristata* (L.) Pers. (prairie junegrass), *Lomatium triternatum* (Pursh) Coult. & Rose (nineleaf biscuitroot), and *Poa sandbergii* Vasey (Sandberg bluegrass). Historical disturbances associated with this site were grazing by cattle, limited agricultural practices, and intense meadow vole (*Microtus pennsylvanicus*) activity. *Festuca campestris* and *P. spicata* were less common than *F. idahoensis*, *P. sandbergii*, and *D. intermedia*.

The soil is a Post-Ronan-Water complex. It is a deep, 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. The average annual precipitation ranges from 350 to 450 mm per year and the average temperature is 7.6°C.

Experimental design

The study was conducted as a factorially (three herbicides × two cover crops × three seeding rates × two seeding methods = 36) arranged randomized complete block. Replications (four) were placed in three locations across the landscape, with one location containing two blocks. Blocks were greater than 10 m apart. We established 144 11.0 × 36.6 m plots, 36 in each of four blocks. The 36 treatment combinations were randomly assigned and applied as whole plot treatments. The three herbicide treatments were picloram at 0.28 kg/ha, 2,4-D amine at 2.2 kg/ha, and a control with no herbicide. (Active ingredient values are given for

herbicide mass.) The cover crop treatments included seeding with and without a cover crop of *T. aestivum*. We seeded a mix of three native grasses, *P. spicata*, *F. idahoensis*, and *F. campestris*, at three rates: low (977 seeds/m²), intermediate (1322 seeds/m²), and high (1557 seeds/m²) (Velagala 1996). The two different seeding methods utilized were no-till drill seeding and broadcast seeding following soil surface disturbance.

Procedures

Picloram was applied during the first week of November 2001. Approximately 241 L/ha of solution was applied with a single pass over the plot. Because of the lack of precipitation during August and September, very few adult *C. maculosa* or *P. recta* plants initiated fall regrowth. Since these were target weed species, the 2,4-D treatment was postponed until the following summer. When the seeded grass species reached the three to six leaf growth stage in the second week of July 2002, 2,4-D amine was applied using an ATV mounted pressurized sprayer with a spray width of 3.6 m. The unit delivered approximately 210 L/ha of solution.

Plots were seeded immediately following the application of picloram in November 2001. The native seed mix was blended to ensure the same number of live seeds of each species, *P. spicata*, *F. idahoensis*, and *F. campestris*, per kilogram of the seed mix. A Truax native seed, no-till range drill (New Hope, Minnesota, USA) was used for seeding. This drill created a continuous linear furrow ~12 mm deep and seeds were placed within the furrow. Furrows were closed by dragging heavy pipes behind the seeder. The cover crop was seeded at ~54 seeds/m². Although forbs are a critical component of restoration, especially where invasive plants dominate, we were interested in the response of naturally occurring forbs that might increase in abundance in response to our treatments. Thus, they were not included in the seed mix.

To disturb the soil, an AerWay duck foot imprinter (Norwich, Ontario, Canada) was pulled behind a tractor making approximately 18 holes/m² that were 9 × 9 × 10 cm in the soil to collect moisture during spring rains. Seeds were then broadcast over the plots from tubes connected to the seed box. The no-till drill planted seeds to a depth of 6–12 mm.

Sampling

For sampling purposes, plots were divided into three equal subplots in an attempt to capture variation within the plot. Since plant density and/or biomass could change as the sampling period progressed, all sampling was conducted block by block to account for any influence the time required to sample large plots may have made. Pre-treatment percentage cover of *C. maculosa* and *P. recta* was determined by estimation of the whole subplot in August 2001. Density of all species was determined during peak standing crop of the native grasses during 15–27 July 2002 and again in 2004. Density was determined by randomly placing two 0.2 ×

0.5 m Daubenmire frames in each subplot; all species within each frame were counted. Grass density was determined by counting each tiller within the frames. In 2004, biomass was determined by hand-clipping three randomly placed 1-m² square frames in each plot. Species that had been seeded were separated by each species. Other associated species were separated into functional groups. All plant material was dried at 60°C for three days and weighed.

Species richness is defined as the number of species found in each plot (Begon et al. 1996). Because the three seeded grasses, *P. spicata*, *F. campestris*, and *F. idahoensis*, are fundamental to the habitat type we were attempting to restore, they were included in the richness analysis, but *C. maculosa* and *P. recta* were not.

Analysis

A five-way ANOVA was used to determine the effects, seeding method, seeding rate, herbicide, and cover crop on the density of the seeded grasses, *C. maculosa*, *P. recta*, native grasses (other than those seeded), native forbs, exotic grasses, and exotic forbs (excluding the two invasive weeds). The complete ANOVA model included all main effects, two-, and three-way interactions. After analyzing the complete model for each group, three-way interactions that were not significant for any response variables within a group were removed. Mean comparisons were achieved using a Tukey's hsd comparisons at $\alpha = 0.05$; the standard error for each mean is presented in the figures.

ANCOVA was used to analyze density of seeded grasses using pre-treatment cover of *C. maculosa* and *P. recta* as the covariates. Pre-treatment cover of *C. maculosa* and *P. recta* did not affect any species density or biomass.

RESULTS

Seeded species

Main effects.—In 2002, seeding rate and seeding method influenced all three desired species' densities (Table 2). In all cases, seeding at the highest rate produced about three times the density of the desired species than seeding at the lowest rate. No-till drilling also increased density of desired species three-fold over broadcast seeding. Desired species densities ranged from ~5 to 36 plants/m² in plots receiving only seeding or seeding method treatments in 2002. No-till seeding decreased *C. maculosa* by ~5 plants/m² below those plots only broadcast seeded that year. Application of 2,4-D reduced *C. maculosa* from 46 to 4 plants/m² (hsd_{0.05} = 8.8) and *P. recta* from 58 to 6 plants/m² (hsd_{0.05} = 10.0). Picloram reduced invasive plant density by about one-half that of plants treated with 2,4-D in 2002.

The main effect of seeding rate on density alone persisted to 2004 on *P. spicata*, whereas the effect of seeding method alone persisted on *P. spicata* and *F. idahoensis* (Table 2) until 2004. *P. spicata* increased from

TABLE 2. List of *P* values for treatment main effects from ANOVA.

Source	df	<i>P. spicata</i>	<i>F. campestris</i>	<i>F. idahoensis</i>	<i>C. maculosa</i>	<i>P. recta</i>
Density (2002)						
Rate	2	0.001	0.001	0.001	0.382	0.235
Cover crop	1	0.080	0.990	0.980	0.768	0.743
Seeding method	1	0.001	0.001	0.001	0.043	0.080
Herbicide	2	0.225	0.218	0.001	0.001	0.001
Density (2004)						
Rate	2	0.001	0.638	0.053	0.331	0.871
Cover crop	1	0.583	0.734	0.845	0.087	0.107
Seeding method	1	0.001	0.081	0.005	0.496	0.989
Herbicide	2	0.031	0.093	0.653	0.001	0.002
Biomass (2004)						
Rate	2	0.010	0.217	0.445	0.117	0.591
Cover crop	1	0.223	0.217	0.965	0.597	0.078
Seeding method	1	0.186	0.110	0.363	0.682	0.282
Herbicide	2	0.802	0.110	0.410	0.011	0.754

Note: Values in boldface are statistically significant. Error df = 105 for all factors and years.

10 plants (977 seeds/m²) and 16 (1322 seeds/m²) plants/m² to 37 plants/m² where seeded with 1557 seeds/m² (*hsd*_{0.05} = 9.6) in 2004. *P. spicata* and *F. idahoensis* increased from 7 and 11.5 plants/m² to 35 and 33 plant/m², respectively, where they were seeded using a no-till drill rather than broadcast seeding.

In 2004, the main effect of seeding rate influenced *P. spicata* biomass (Table 2). *P. spicata* yielded 7 g/m² in plots seeded with 1557 seeds/m², which was higher than *P. spicata* in plots seeded with 977 seeds/m², but similar to plots seeded with 1322 seeds/m². Picloram or 2,4-D reduced *C. maculosa* from 120 g/m² to about 80 g/m² in 2004 (*hsd*_{0.05} = 30).

Two-way interactions.—In 2002, the effect of seeding rate on *P. spicata*, *F. scrabella*, or *F. idahoensis* depended upon seeding method (Fig. 1). Where seeds were broadcast, all three seeding rates produced similar desired-plant density. The highest seeding rate produced the highest density where no-till drilling occurred. No-till drilling combined with 1557 seeds/m² produced about twice the plant density as the 1322 seed/m² rate. No other two-way interactions were detected that year.

The interaction of seeding rate and seeding method on density persisted into 2004 for *P. spicata* and *F. idahoensis* (Fig. 2). In both cases, broadcast seeding produced similarly low plant density. As in 2002, the highest seeding rate produced the highest *P. spicata* density where it was no-till drilled (Fig. 2a). Conversely, the lowest seeding rate produced the highest *F. idahoensis* density where it was no-till drilled (Fig. 2b). The highest plant density was above 50 plants/m² for both species.

The influence of seeding method on *P. spicata* density also depended on the herbicide treatment in 2004 (Fig. 3). Where seeds were broadcasted, all three herbicide treatment rates produced similarly low *P. spicata* density. Plots treated with picloram produced the highest *P. spicata* density when seeds were no-till drilled.

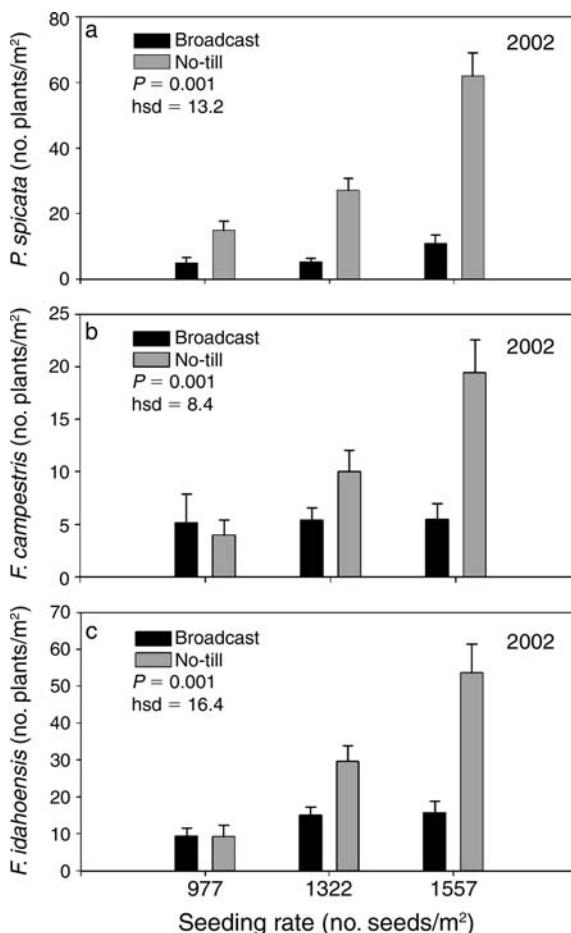


FIG. 1. Interaction of seeding rate and seeding method on densities (mean + SE) of three native perennial grass species in 2002. Tukey's *hsd* tests here and in all other figures were performed at $\alpha = 0.05$.

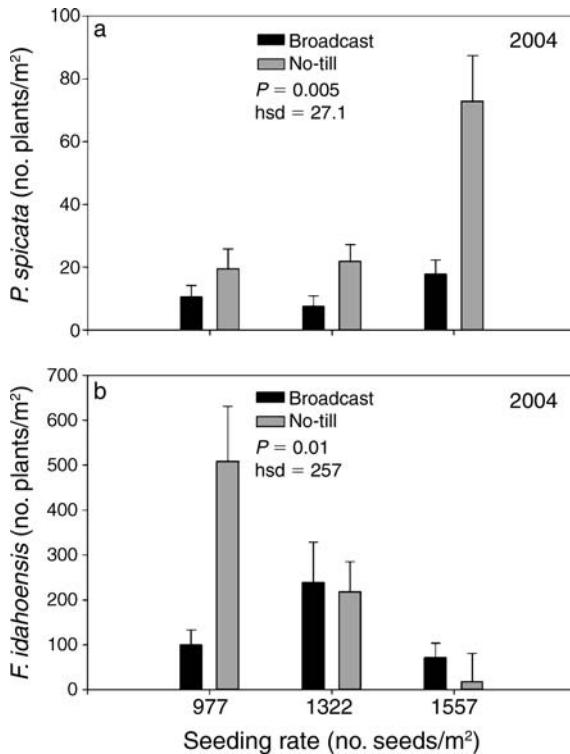


FIG. 2. Interaction of seeding rate and seeding method on densities (mean + SE) of two native perennial grass species in 2004.

Seeding rate interacted with herbicide treatment to influence *C. maculosa* density in 2004 (Fig. 4a). At 977 seeds/m², 2,4-D reduced *C. maculosa* density below that of the control or where picloram was applied. At seeding rates of 1322 seeds/m², picloram and 2,4-D produced similarly low *C. maculosa* densities, while the non-treated control produced the highest density of this invasive weed. At 1557 seeds/m², the density of *C.*

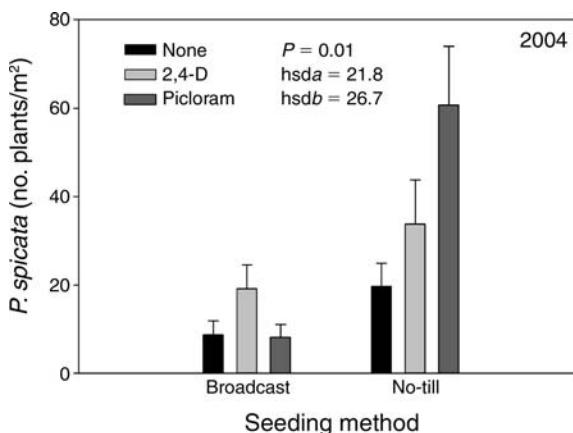


FIG. 3. Interaction of seeding method and herbicides on *P. spicata* density (mean + SE) in 2004. Tukey's *hsda* compares seeding method means within a herbicide treatment; *hsdb* compares different herbicide treatments.

maculosa was the same in the non-treated control as in plots treated with 2,4-D, which accounted for the interaction. The influence of seeding rate on *P. recta* density in 2004 depended on the presence or absence of a cover crop (Fig. 4b). All treatments produced similar *P. recta* density, except seeding at 1322 seeds/m² with a cover crop, which reduced *P. recta* density below that of any other treatment combination.

Seeding rate interacted with seeding method to influence *C. maculosa* biomass in 2004 (Fig. 4c). Seeding method did not influence *C. maculosa* biomass where

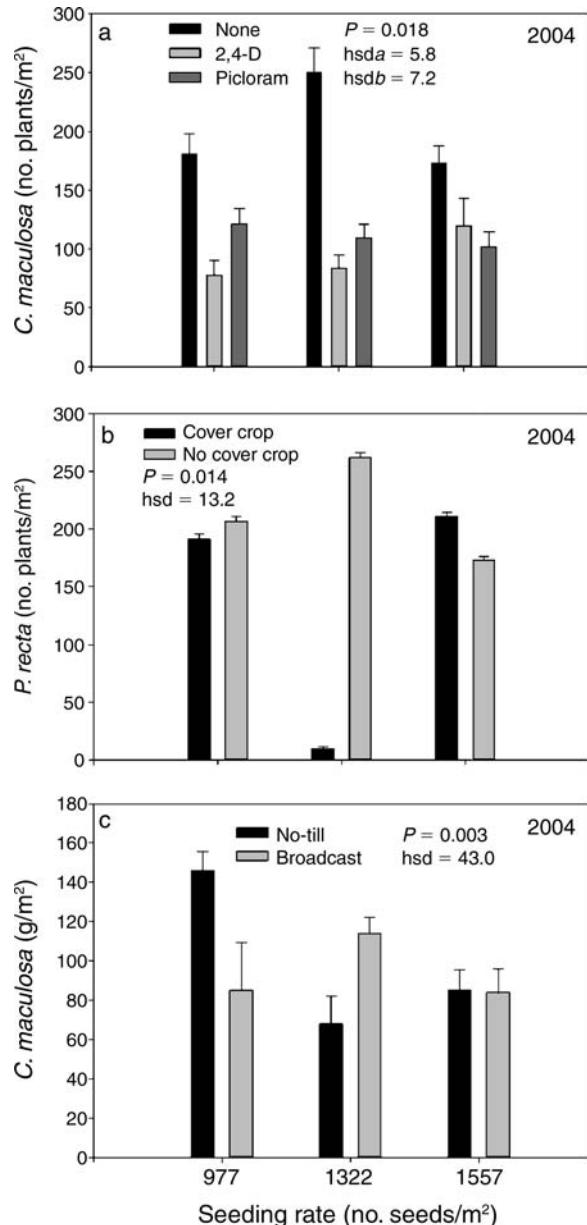


FIG. 4. Interaction of seeding rate and seeding method on the density (mean + SE) of *C. maculosa* and *P. recta* and the biomass of *C. maculosa* in 2004. In (a), Tukey's *hsda* compares within-herbicide means; *hsdb* compares different herbicides.

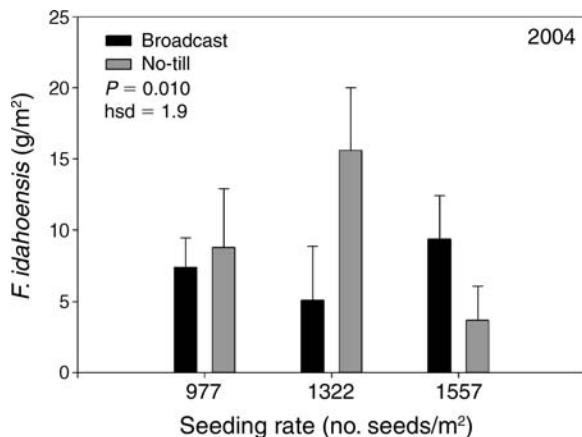


FIG. 5. Interaction of seeding rate and seeding method on *F. idahoensis* biomass (mean + SE) in 2004.

desired species were seeded at the highest rate (1557 seeds/m²), regardless of species. At the lowest seeding rate (977 seeds/m²), broadcast seeding yielded about 6 g/m² less of the weed than where the seeds were no-till drilled. On the other hand, no-till drill seeding yielded about 5 g/m² less *C. maculosa* than where seeds were broadcasted at 1322 seeds/m².

Seeding rate interacted with seeding method to affect *F. idahoensis* in 2004 (Fig. 5). At 977 seeds/m², no-till drill seeding yielded similar *F. idahoensis* biomass as broadcast seeding. No-till drill seeding at 1322 seeds/m² yielded about three-times as much *F. idahoensis* biomass as broadcast seeding at the same rate. At 1557 seeds/m², broadcast seeding produced about twice the *F. idahoensis* biomass of no-till drilling.

Three-way interactions.—The effect of seeding rate on *P. spicata* density depended upon the herbicide and presence or absence of a cover crop in 2002 (Fig. 6). The two lower rates produced similar density of *P. spicata*, which ranged between 8 and 22 plants/m². Addition of either an herbicide or cover crop did not influence *P. spicata* density in plots seeded at these rates. The density of *P. spicata* was slightly higher where seeded at 1557 seeds/m² than in areas seeded at lower rates where no herbicide was applied but a cover crop was present. At the highest seeding rate, *P. spicata* was over two times higher in 2,4-D treated plots where a cover crop was absent than where the cover crop was present.

The interaction of seeding method and cover crop on *F. idahoensis* density depended upon the herbicide treatment in 2004 (Fig. 7a). The highest number of *F. idahoensis* plants occurred where it was no-till drilled, sprayed with 2,4-D, and included a cover crop. Where *F. idahoensis* seeds were broadcasted, the highest density of that species occurred after application of picloram in the absence of a cover crop. The interaction of seeding method and cover crop on *F. idahoensis* biomass depended upon seeding rate that year as well (Fig. 7b). At 977 seeds/m², no-till drill seeding increased biomass by about nine times over broadcast seeding where a cover crop was present. In the presence of a cover crop, broadcast seeding increased *F. idahoensis* about four times that of no-till drilling where seeding was at 1322 seeds/m². At that seeding rate, no-till drill seeding tripled the *F. idahoensis* biomass compared to broadcast seeding in the absence of a cover crop.

The interaction of seeding method and cover crop on *C. maculosa* density and biomass depended upon the

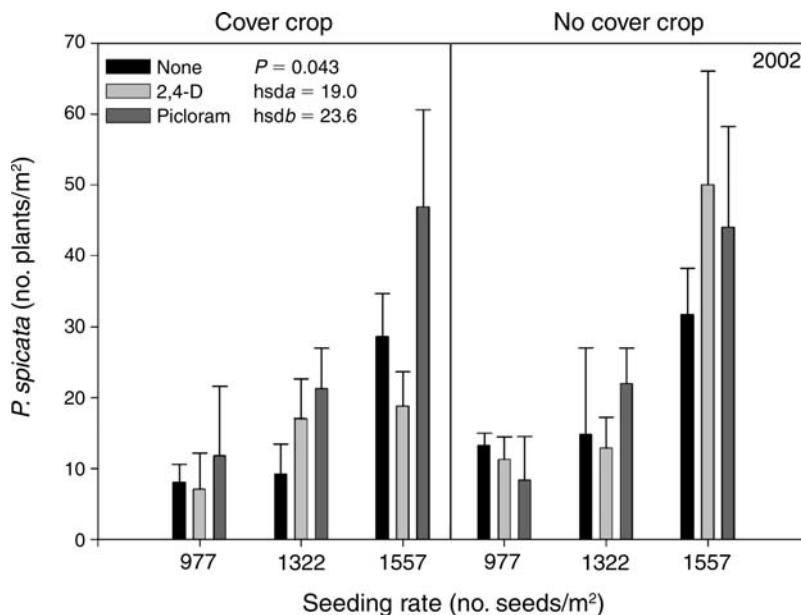


FIG. 6. Interaction of seeding rate, cover crop, and herbicides on *P. spicata* density (mean + SE) in 2002. Tukey's hsdA compares within-herbicide means; hsdB compares different herbicides.

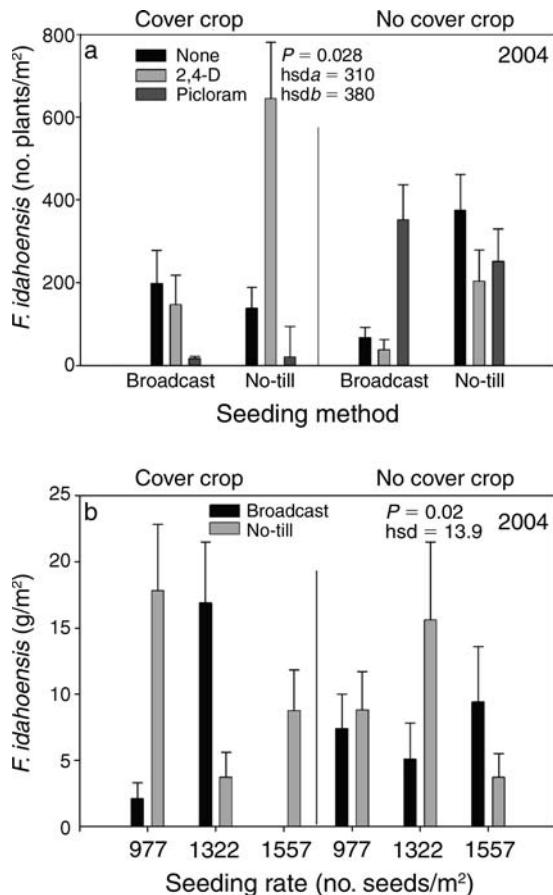


FIG. 7. (a) Interaction of seeding method, cover crop, and herbicides on *F. idahoensis* density (mean + SE) and (b) interaction of seeding rate, seeding method, and cover crop on *F. idahoensis* biomass (mean + SE) in 2004. In (a), Tukey's $hsda$ compares within-herbicide means; $hsdb$ compares different herbicides. Broadcast data for seeding rate 1557 are zero.

herbicide treatment in 2004 (Fig. 8). The highest *C. maculosa* density was produced where no herbicide was applied (Fig. 8a). Application of picloram reduced *C. maculosa* to about one-half that of the non-treated controls regardless of the presence or absence of a cover crop or seeding method. When broadcast seeding, *C. maculosa* was lower where a cover crop was absent than where it was present, when applied with 2,4-D.

With respect to *C. maculosa* biomass, no difference between the two herbicides was detected when no-till drilling occurred (Fig. 8b). When broadcast seeding and spraying with 2,4-D, the inclusion of a cover crop reduced *C. maculosa* biomass below that which did not include a cover crop.

The interaction of seeding method and cover crop on *P. recta* biomass depended upon the herbicide treatment in 2004, as well (Fig. 9). Neither picloram nor 2,4-D reduced *P. recta* biomass regardless of seeding method or the presence or absence of a cover crop. Where seeds were broadcasted and picloram was applied, a cover

crop reduced *P. recta* biomass from ~ 28 g/m² to ~ 3 g/m². Similarly, where seeds were drilled and 2,4-D was applied, a cover crop reduced *P. recta* biomass from ~ 22 g/m² to ~ 6 g/m².

Associated species

Native grasses.—Native grass (non-seeded species) density was not detectably affected by any treatment in 2002 ($P \geq 0.05$). In 2004, broadcast seeding increased associated grasses by 50 tillers/m² over plots drill seeded ($P = 0.033$). Conversely, no-till drilling increased native grass biomass from 10.9 g/m² in areas imprinted and broadcast seeded to 18.7 g/m² that year ($P = 0.044$).

Native forbs.—In 2002, the influence of herbicide on native forb density depended upon seeding rate. At 977 and 1322 seeds/m², 2,4-D produced less than one-third the forb density than that of the non-treated control (Fig. 10). On plots seeded with 1557 seeds/m², the control had about twice the number of forbs as in areas treated with 2,4-D. At the two higher seeding rates, picloram had no effect on native forbs, however at 977 plants/m², picloram reduced forb density by about one-half that of the control in 2002.

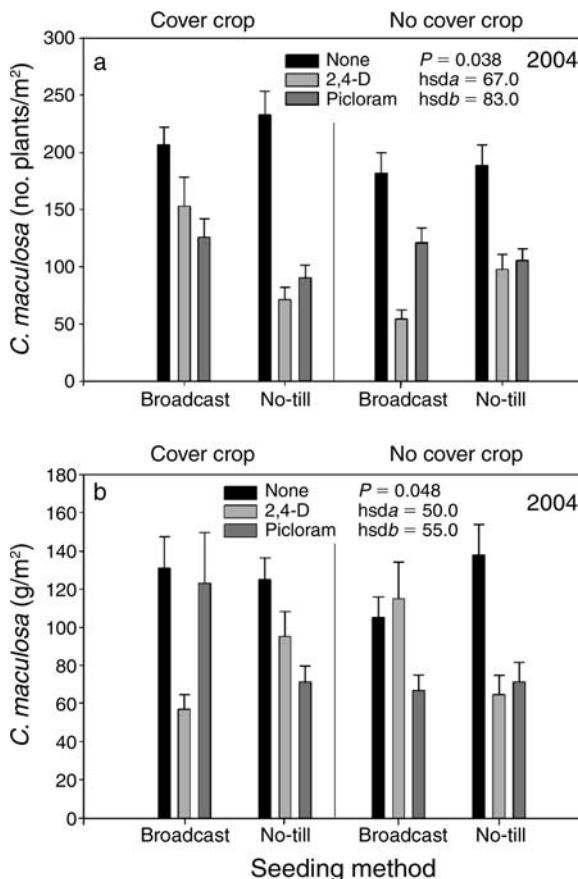


FIG. 8. Interaction of seeding method, cover crop, and herbicides on *C. maculosa* (a) density and (b) biomass (all values mean + SE). Tukey's $hsda$ compares within-herbicide means; $hsdb$ compares different herbicides.

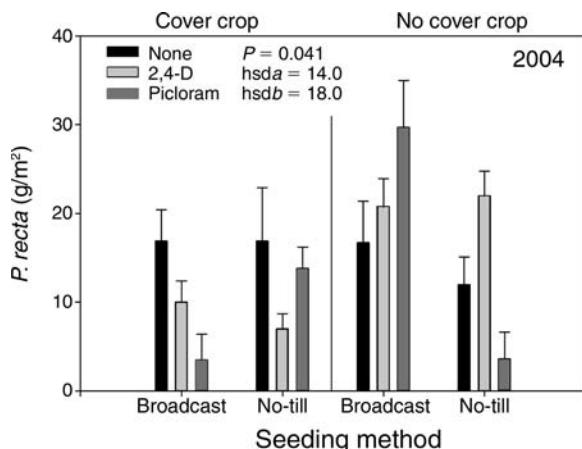


FIG. 9. Interaction of seeding method, cover crop, and herbicides on *P. recta* biomass (mean + SE). Tukey's hsd_a compares within-herbicide means; hsd_b compares different herbicides.

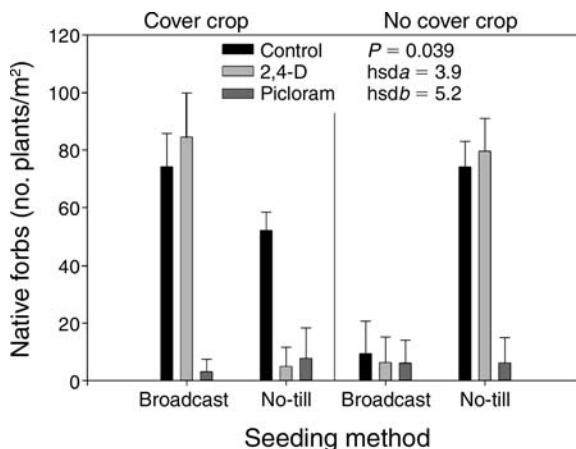


FIG. 11. Interaction of seeding method, cover crop, and herbicides on native forb density (mean + SE) in 2004. Tukey's hsd_a compares within-herbicide means; hsd_b compares different herbicides.

By 2004, both herbicides had reduced native forb density to one-sixth of the control (Fig. 11). The only exception was that forb density in the non herbicide-treated control plot, where grasses were broadcast seeded without a cover crop, was the same as that where either herbicide had been applied. This response accounted for the three-way interaction. In addition, the influence of seeding rate on native forb density depended upon the presence or absence of a cover crop in 2004 (Fig. 12). All seeding rates produced similar forb density where the cover crop was not included in the seed mixture. In plots with a cover crop, the low and high seeding rates produced about one-third to one-half the native forb density as seeding at the middle rate.

Exotic grasses.—In 2002, the influence of seeding method on exotic grass density depended upon the seeding rate (Fig. 13). Broadcast seeding and no-till drilling at 977 seeds/m² produced from 600 to 800 tillers/

m² of exotic grasses. No-till drilling, at either of the two higher seeding rates, produced fewer than 100 exotic grass tillers/m².

In 2004, the influence of seeding method on exotic grass density depended upon the herbicide treatment and the presence or absence of a cover crop (Fig. 14). Where native grasses were seeded without a cover crop, 2,4-D increased exotic grass density, regardless of sowing method. Without a cover crop, picloram increased exotic grass density where desired species were no-till drill seeded. Conversely, where native grasses were seeded with a no-till drill, application of 2,4-D or picloram did not alter exotic grass density from that of the control. Without an herbicide, exotic grass density was similar, regardless of seeding method or inclusion of a cover crop in 2004.

The effect of seeding method on exotic grass biomass depended upon the interaction of seeding rate and herbicide in 2004 (Fig. 15). Where seeds were broad-

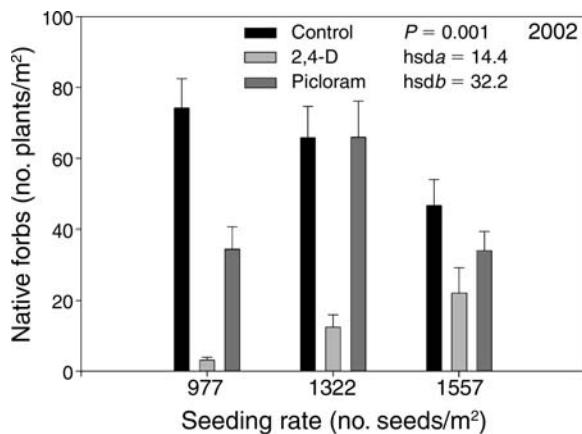


FIG. 10. Interaction of seeding rate and herbicides on native forb density (mean + SE) in 2002. Tukey's hsd_a compares within-herbicide means; hsd_b compares different herbicides.

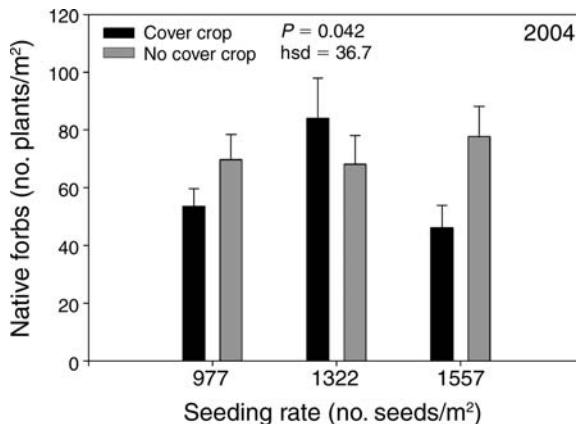


FIG. 12. Interaction of seeding rate and cover crop on native forb density (mean + SE) in 2004.

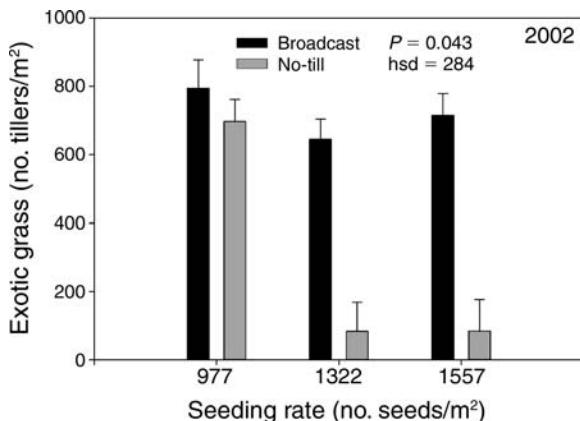


FIG. 13. Interaction of seeding rate and seeding method on exotic grass tiller density (mean + SE) in 2004.

casted at the lowest rate, herbicides did not influence exotic grass biomass. At 1322 seeds/m², 2,4-D increased exotic grass biomass over that of the control. At the highest seeding, both herbicides increased exotic grass biomass about four-fold over the control. Where seeds were no-till drilled at the 977 or 1322 seeds/m² rates, 2,4-D increased exotic grass biomass over that of the control, while at 1557 seeds/m², picloram increased this plant group's biomass higher than the control.

Exotic forbs.—Density of exotic forbs, other than *C. maculosa* or *P. recta*, was influenced by herbicides in 2002 and 2004. In 2002, no herbicide and picloram treatments produced ~155 and ~130 exotic forb plants/m², respectively ($P = 0.001$; $hsd_{0.05} = 36$). Application of 2,4-D reduced exotic forb density to ~22 plants/m². In 2004, both herbicides yielded exotic forb density similar to that of the control, which was ~71 plants/m². However, 2,4-D yielded ~55 exotic forbs/m², while

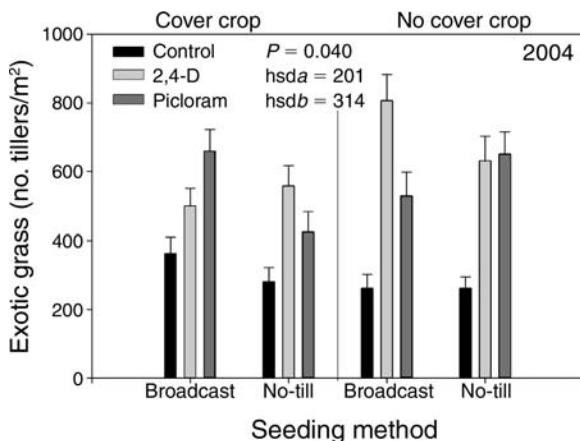


FIG. 14. Interaction of seeding method, cover crop, and herbicides on exotic grass tiller density (mean + SE) in 2004. Tukey's hsd_A compares within-herbicide means; hsd_B compares different herbicides.

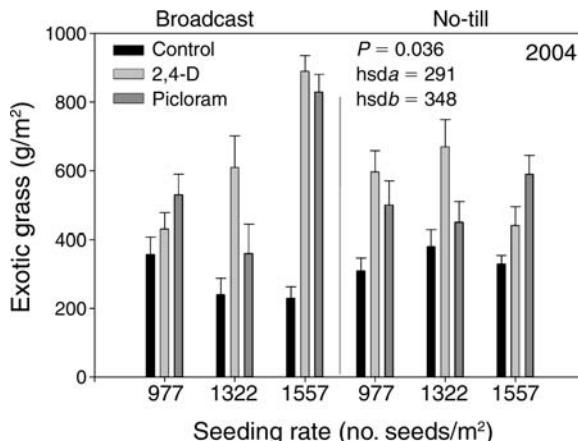


FIG. 15. Interaction of seeding rate, seeding method, and herbicides on exotic grass biomass (mean + SE) in 2004. Tukey's hsd_A compares within-herbicide means; hsd_B compares different herbicides.

picloram yielded 85 exotic forbs/m² ($P = 0.029$; $hsd_{0.05} = 29$).

In 2004, inclusion of a cover crop decreased exotic forb biomass from 22 to ~10 g/m² ($P = 0.002$). In addition, seeding method interacted with seeding rate to influence exotic forb biomass in 2004 (Fig. 16). At the lowest seeding rate (977 seeds/m²), no-till drill seeding produced about one-half the exotic forb biomass as broadcast seeding. Conversely, seeding at the middle seeding rate (1322 seeds/m²), broadcast seeding produced about one-half the biomass as no-till drill seeding. At the highest seeding rate, both seeding methods yielded similar exotic forb biomass.

Species richness.—In 2002, species richness depended upon herbicides ($P = 0.001$). Across all treatments, the non-treated control and picloram had a richness of 4.05 and 3.60, respectively ($hsd_{0.05} = 0.64$). Application of 2,4-D produced a richness of 1.84 that year. In 2004, no treatment or treatment combination affected species

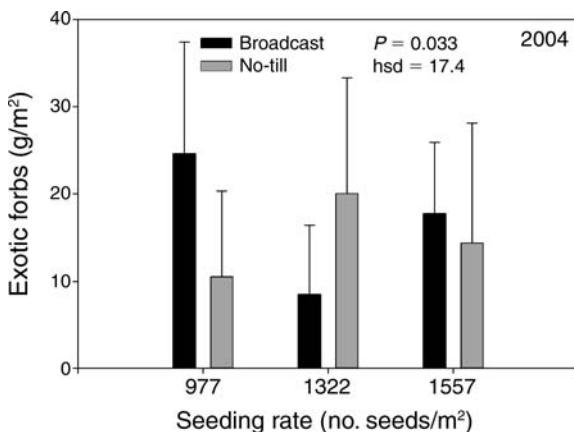


FIG. 16. Interaction of seeding rate and seeding method on exotic forb biomass (mean + SE) in 2004.

richness. Across all means, species richness was 3.15 (SE = 1.45) that year.

DISCUSSION

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). Successional management suggests that the mechanisms and processes influencing the three causes of succession can be manipulated in a coordinated manner to direct plant community trajectories (Pickett et al. 1987b, Luken 1990, Sheley et al. 1996). To the limits of our knowledge about how management strategies influence the causes of succession and their associated processes, managers could strategically integrate techniques in a manner that ensures that each successional cause is modified to favor a desirable plant community. As these general causes are increasingly and progressively addressed, the plant community should change from dominance by invasive weeds toward desired species. This implies that a singularly applied technique that modifies an individual process has less likelihood of stimulating desirable plant community dynamics than multiple techniques designed to modify multiple processes associated with all three causes of succession. Therefore, we hypothesized that the majority of responses to multiple treatments aimed at modifying the three causes of succession to shift dynamics in favor of native grasses and away from invasive weeds would be explained by higher order interactions, especially in the final year of the study (2004). In 2002, there were 10 significant main effects on native grass density, a seeding rate by seeding method interaction for each seeded grass species, a single three-way interaction influencing *P. spicata* density, and a three-way interaction influencing both invasive weeds. In 2004, five main effects on density remained significant and two main effects influenced biomass of any species. As we predicted, plant response to treatments was dominated by two- and three-way interactions in 2004. This provides some evidence suggesting that persistent and enduring effects on vegetation dynamics requires integrating various treatments to modify the processes that influence the causes of succession (Whisenant 1999, Sheley and Krueger-Mangold 2003).

Successional management may offer a guide to managers for integrating various treatments to establish native grasses and initiate restoration, but its usefulness will be based on its ability to predict the success or failure of various treatment combinations (Kedzie-Webb et al. 2001). We predicted that colonization and disturbance would interact to influence establishment of three native grass species. We thought that no-till drill seeding would maximize the likelihood of a seed germinating and the plant becoming established. Native perennial grasses have been successfully established using a no-till drill in the absence of invasive species across a wide array of environments (Doerr and Redente

1983, Jackson 1999, Montalvo et al. 2002). While the no-till drill maximized establishment for all the seeded grasses in 2002, by 2004 only the larger seeded species, *P. spicata*, still benefited from drill seeding. For this species, no-drill seeding created and placed the seeds in suitable, safe sites. Doerr and Redente (1983), Jackson (1999), and Montalvo et al. (2002) also found drill seeding to be more effective than broadcast seeding for establishing native grasses with relatively large seeds. No-till drill seeding also benefited *F. idahoensis* in 2004, but its response varied depending on the seeding rate, while *F. campestris* did not establish very well, regardless of seeding method. *Festuca idahoensis* has been shown to be slow and difficult to establish (Carrithers 1999, Jacobs et al. 1999, Sheley et al. 2001). Seedling establishment is influenced by a variety of factors, including seeding depth, soil temperature, soil texture, water availability, and light (Monsen et al. 2004). Determining the requirements of *Festuca* spp. and matching them to variable environmental conditions has proven difficult. The highly variable response of *F. idahoensis* and the poor establishment of *F. campestris* in our study support this notion. Small seeded species appear difficult to establish because their low seed mass may limit germination, seedling size, and seedling vigor (Zhang and Maun 1993).

We thought that higher seeding rates would maximize establishment because the second cause of succession, species availability, would be increasingly addressed with increasing seeding rate. Velagala et al. (1997) found grass establishment to improve as seeding rate increased when seeding into vegetation dominated by invasive species. This held true for *P. spicata*, but not for *F. idahoensis*. Drill seeding at the lowest rate favored the establishment of *F. idahoensis*, while no-till drilling at the moderate rate favored its biomass production. When *F. idahoensis* was sown with a cover crop, the lowest seeding rate again proved the most successful. This suggests that the lower seeding rates provided ample species availability for this species in this study. *F. idahoensis* seedling vigor is typically poor to fair, and they are not very competitive with seedlings of more aggressive species (Jacobs et al. 1999, Monsen et al. 2004). We think that seeding at lower rates may have reduced intra- and interspecific seedling competition, thereby increasing *F. idahoensis* establishment. Our ability to accurately predict management outcomes likely depends on the level of knowledge about how a treatment modifies the processes that elicit a particular positive response from individual species (Sheley et al. 1996, Sheley and Krueger-Mangold 2003).

In fact, predicting vegetation changes to higher order interaction is very complicated (Heil 2004). We accepted the hypothesis that picloram would reduce weed performance long enough for grass seedlings to become established because it produced the highest density of *P. spicata*. *F. idahoensis* established well where it was no-till drill seeded with a cover crop and 2,4-D was applied.

Although drill seeding a low rate of *F. idahoensis* successfully established this species, by 2004 it also established well where it was drill seeded with a cover crop and 2,4-D was applied. This provides some evidence supporting the hypothesis that *T. aestivum*, applied as a cover crop, would improve native grass establishment by giving a competitive advantage to the desired grasses (Herron et al. 2001). In a few cases, including a cover crop also produced high *F. idahoensis* biomass. On the other hand, at the highest seeding rate, *P. spicata* was reduced by including a cover crop and applying 2,4-D. Including a cover crop at high seeding rates may have increased competition between *T. aestivum* and seeded perennial grasses and resulted in their reduced establishment.

While forbs have been listed as diverse components of grassland communities (Daubenmire 1970, Sims et al. 1978, Mueggler and Stewart 1980, Jensen et al. 1988, Hogg 2001), they have not been a primary focus in classification and land management practices (Willoughby et al. 1998, Fuhlendorf and Engle 2001). More recently, ecologists have recognized native forbs as a critical management consideration because they can account for up to 83% of the richness and can represent a greater proportion of the total biomass than grasses in some rangeland systems (Pokorny et al. 2004). In addition, native forbs can provide substantial resistance to invasion, especially for invasive weeds having significant niche overlap (Pokorny et al. 2005). In the majority of cases in this study, 2,4-D and picloram reduced native forb density and/or biomass. In some cases, the reduction was one-fifth to one-sixth and the effects were most severe at the end of the study. Developing restoration strategies that minimize the negative effects on forbs is critical to developing enduring invasive weed management strategies (Pokorny et al. 2005).

Previous studies have found decreases in non-target forb density and cover following an application of picloram (Rice et al. 1997, Denny 2003), but picloram has also been found to have little effect on nontarget forb density (Bedunah and Carpenter 1989). In this study, the early season forbs appeared to be more sensitive to picloram than the summer forbs, while 2,4-D dramatically reduced the density of summer forbs. On the contrary, one year following treatment, Jacobs and Sheley (1999b) and Denny (2003) found native forb density to be unaffected by a summer 2,4-D application. The negative influence of 2,4-D on forbs could be mitigated by applying this herbicide later in the season when invasive weeds remain photosynthetically active, but native forbs are in summer dormancy.

Many native forbs and grasses do not compete directly for resources (Jacobs and Sheley 1999a), but applying herbicides to native forb dominated pastures often results in temporary increases in grass production. We did not expect the presence of a cover crop to reduce forbs. However, at the highest seeding rate in the

presence of a cover crop, enough negative interaction occurred between the two functional groups to reduce native forb density. A major factor influencing competition among plants is density (Yoda et al. 1963, Spitters 1983, Radosevich 1997). In this case, we believe the combined density of seeded grasses and *T. aestivum* was high enough to exert substantial competitive influence on native forbs (Newenhouse and Dana 1989).

Native grasses other than those that dominate these plant communities are another functional group important to functional diversity. Pokorny et al. (2004) documented 14 species of graminoids from just two sites within an *F. idahoensis*/*P. spicata* habitat type. We hypothesized that the limited disturbance associated with the seeding techniques would have little influence on the naturally occurring associated species density, biomass, or species richness. We rejected this hypothesis because native grasses (other than *P. spicata*, *F. idahoensis*, and *F. campestris*) responded differently to each seeding method. Imprinting and broadcast seeding increased associated grass density, while drill seeding increased their biomass. Size and severity of the disturbance dictate the amount of physical space available for colonization and greatly influence the timing and patterns of resource availability (Bazzaz 1983, 1984). Light and soil moisture profiles, soil nutrient content, and factors that modify the use of these resources, such as air and soil temperature, are affected by the extent of vegetation damage or removal (Collins et al. 1985, Runkle 1985). Apparently, imprinting creates substantially different conditions than drill seeding. Small depressions made by the imprinter could cause subtle differences in resource availability to newly emerging grasses, while the disking effect of the no-till drill could create occasional, but more severe, disturbances. The light, but commonly occurring disturbance may have promoted emergence, but too few resources might have been released to allow major biomass production. Conversely, drill seeding may have released larger amounts of resources in few locations. Thus, naturally occurring associated grasses that were established could gain biomass by using these newly released nutrients. In any case, knowledge of how management influences disturbance regimes could provide information necessary to design disturbance to favor desired species. It appears that creating disturbances that minimize nutrient release into the soil (e.g., shallow, light tillage vs. deep, heavy tillage), while providing adequate safe sites for native species to germinate and emerge would favor native over non-native species (Herron et al. 2001).

If the goal of restoration is to recover the organization, structure and function of plant communities, then understanding treatment effects on exotic species is central to determining appropriate weed management methods (Bradshaw 1983, 1996). Nearly all herbicide treatments increased exotic grass abundance. We hypothesized that native grasses would increase with

herbicide application, but given the increase in exotic grasses it is not surprising that native grasses did not increase. Exotic grass increases after herbicide applications may have occurred because they were more responsive to increased nutrients following weed control. Some exotic grasses have been found to be more responsive to nutrient pulses than native grasses (Cui and Caldwell 1997). Among our treatments, no-till drilling with a cover crop combined with herbicide application provided the lowest exotic grass abundance. Nothing conclusive could be deduced about the treatment effects on exotic forbs.

Restoring invasive-plant-dominated communities to functionally diverse systems is increasingly proposed as a central principle for managing invasive-plant-infested rangeland (Berger 1993, Sheley et al. 1996). Plant communities possessing high species richness may also resist invasion. Exotic plant species, including *C. maculosa*, were reduced and almost eliminated by increasing species richness (Carpinelli 2000, Kennedy et al. 2002, Sheley et al. 2005). In the California annual grasslands, invasion by *C. solstitialis* was minimized by increasing functional diversity, thereby reducing resource availability (Dukes 2001). No treatment influenced overall species richness by the end of this study. Moreover, richness remained low (about three to four species) compared to 83 species in a late-successional stage of a similar habitat type (Pokorny et al. 2004). The need for techniques to increase species richness during restoration of invasive-plant-dominated land is substantial.

As the three causes of succession are increasingly addressed in invasive plant management and desirable species' occurrence increases, the resulting plant community should contain lesser amounts of weedy species, in this case *C. maculosa* and *P. recta*. No-till drill seeding generally resulted in greater grass establishment; however no-till drill seeding did not consistently decrease *C. maculosa* and *P. recta* density and biomass. Herbicide treatment, seeding method, and whether or not a cover crop was seeded appeared to consistently influence the density and biomass of the two weedy species. Complex interactions influenced by densities of seeded species, cover crop, and weedy species, combined with species' response to herbicides determined plant community dynamics at this site. Further understanding of such interactions and their effect on plant community dynamics is necessary for successful implementation of successional management.

Integrated weed management has been applied by managers for decades (Radosevich et al. 1997). It is imperative that managers address the actual cause of the invasion and modify the processes that influence successional patterns in vegetation. Presently, integration is more of an intuitive art and is based on practical experience, rather than on scientific principles or laws. Successional management offers an ecological framework to use as a guide for managing invasive weed-

dominated rangeland in a manner that influences the actual cause of succession. Although it provides general direction into integrating invasive plant management strategies, its usefulness is limited by our lack of knowledge about how various mechanisms and processes influence plant community dynamics.

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 (Werner 1999). The goal of successional management is to direct infested plant communities on a trajectory toward a diverse group of desired species (Sheley et al. 1996). In this study, successional management was useful as a guide to establishing desired grasses, but the treatments used did not improve overall richness of the plant community. We believe that this mechanistic and process-based model offers potential for planning and predicting the outcome of restoration and invasive plant management. Since naturally occurring native forbs did not respond favorably to any treatment combination, ecological restoration using successional management may best be thought of as an iterative procedure where various components and processes of the system are methodically repaired or replaced over time.

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