

WEED CONTROL AND SOIL AMENDMENT EFFECTS ON RESTORATION PLANTINGS IN AN OREGON GRASSLAND

Russell T. Huddleston^{1,2} and Truman P. Young^{1,3}

ABSTRACT.—The restoration of perennial grasslands in western North America often depends on effective weed control. We took advantage of a grassland restoration site on the Nature Conservancy's Agate Desert Preserve in southern Oregon (TNC 1997), where 3 sites had been previously burned, mowed, or both. At these sites we carried out a series of controlled, replicated experiments designed to test the effectiveness of 3 weed control measures: (1) sawdust, (2) glyphosate herbicide, and (3) herbicide plus an alfalfa mulch. All plots were seeded with a mix of 3 native perennial grasses. The soils of the 3 areas differing in previous vegetation management were similar, with the exception of total available soil nitrogen, which was significantly lower in the 2 burned sites. The sawdust treatment reduced total available soil nitrogen, but only in the unburned site, and only in the first few months after application. In all 3 areas the alfalfa mulch significantly increased total available soil nitrogen. However, none of these soil nitrogen differences significantly affected the success of weeds or planted perennial grasses. The herbicide treatment reduced exotic annual grasses and forbs and greatly increased the success of native forbs and the planted perennial grasses. The herbicide increased both initial establishment of the native grasses and their absolute cover and biomass. These results suggest that neither nitrogen impoverishment nor nitrogen enrichment was a useful restoration technique at this site, but weed control by herbicides can be of considerable assistance in restoring native perennial grasses.

Key words: grassland restoration, weed control, glyphosate, soil impoverishment, *Achnatherum lemmonii*, *Festuca idahoensis*, *Pseudoroegneria spicata*, *Lomatium cookii*, *Limnanthes floccosa ssp. grandiflora*.

Many of the original native perennial grasslands in the California Floristic Province and parts of the Great Basin have been converted to communities dominated by Mediterranean annual grasses (Biswell 1956, Crampton 1974, Jackson 1985, Coupland 1992). Although the lack of accurate historical records makes the precise structure and composition of the original grassland communities speculative (Hamilton 1997), annual grasses presumably played only a minor role (Biswell 1956, Jackson 1985, Heady 1988). The conversion to (exotic) annual grasslands has resulted in alteration of grassland ecosystem properties, including changes in natural hydrologic regimes (Borman et al. 1992), disturbance pattern (D'Antonio and Vitousek 1992), nutrient availability (Bardgett et al. 1999), and competitive interactions (Dyer and Rice 1999, Hamilton et al. 1999).

This conversion is also considered detrimental to rangeland because it produces forage for a more limited time in the spring. Restoration of original grasslands is a desirable manage-

ment goal. It was once assumed that when livestock were removed, natural successional tendencies would restore the community to a pristine climax state, presumably dominated by perennials (George et al. 1992). In reality, the removal of grazing seldom results in the return to perennial grassland, and the communities tend to remain dominated by annual species in what is often referred to as either arrested succession or alternate stable states (Laycock 1991, Rietkerk and van de Koppel 1997, Rietkerk et al. 1997). Restoration to perennial grasslands appears to require more active intervention regardless of whether or not the eventual goal includes livestock utilization.

In their natural habitat, Mediterranean annual grasses may either be community dominants or occur in early successional stages, where they are eventually replaced by perennial species (Jackson 1985). Throughout the California Floristic Province and parts of the Intermountain Region, however, these same annual species have maintained dominance

¹Department of Plant Sciences, and Graduate Group in Ecology, University of California, Davis, CA 95616.

²Present address: CH2M HILL, 2485 Natomas Park Drive, Suite 600, Sacramento, CA.

³Corresponding author.

and have been found to inhibit the natural succession of native perennials (Evans and Young 1972, Heady et al. 1972, Heady 1988).

Invasion by exotic annual species can increase rates of grassland nutrient turnover, which tends to favor the persistence of annuals (Vinton and Burke 1995, Norton et al. 2004). Perennial grasses are adapted to low-nutrient conditions and tend to perform better than annual grasses in nitrogen-limited soils (Wilson and Gerry 1995, Claassen and Marler 1998). The use of organic materials with a high carbon content such as sawdust, bark, and straw may be useful in promoting soil microbial activity, may subsequently lead to increased nitrogen immobilization and a temporary reduction in the available soil nitrogen (Morgan 1994, Zink and Allen 1998, Reeve Morghan and Seastedt 1999), and may favor natives over weed species in restoration settings (Blumenthal et al. 2003).

Mulches are also used to conserve soil moisture, reduce soil erosion, and suppress weeds (Morgan 1997, Brown et al. 2000). Most often, wheat, barley, and rice straw are used. However, the use of native grass straw has been found to be an effective means of both mulching and seeding (Hujik 1999). The use of alfalfa straw has not been examined in the context of restoration. Alfalfa straw provides the benefits of mulching as well as a source of additional nitrogen fertilizer. Although nitrogen fertilization often leads to increased weed biomass, slow release of nitrogen may increase native seedling biomass (Brown et al. 2000). Additionally, if weed-control measures are used in conjunction with fertilization, native seedling density and vigor may be enhanced. Mulches should be weed-free to avoid introduction of more exotics and increased competition with native seedlings (Brown et al. 2000).

The careful and judicious use of herbicides can often be an effective means of reducing weed species in grassland ecosystems. Herbicides have been used to improve rangeland forage (Currie et al. 1987), manage natural grasslands (Rice and Toney 1998), and restore native grasses to woodlands (Christensen et al. 1974), rural roadsides (Bugg et al. 1997), and old fields (Wilson and Gerry 1995, Stromberg and Kephart 1996). Successful annual grass control can often be accomplished with fall applications of the post-emergent herbicide glyphosate following a prescribed burn (Anders-

son 1993, Morgan 1997). Application of post-emergence herbicides immediately prior to planting native species has been found to increase native seedling density and survivorship (Wilson and Gerry 1995, Stromberg and Kephart 1996).

Each of the techniques discussed above is commonly employed in grassland restoration to reduce competition with exotic species and enhance performance of perennial grasses. Successful weed control often requires an integrated approach using multiple techniques such as fire, mechanical disturbance, and herbicides to achieve maximum weed control and native seedling establishment (Anderson 1993, Gibbons and Youtie 1996). Restoration in natural areas specifically designed to preserve rare and endangered plant species poses a particular challenge. While the continued dominance by exotics results in poor habitat quality and can lead to reduced vigor and fecundity of the target species, restoration efforts aimed at reducing exotics must not significantly threaten nontarget species.

The purpose of this experiment was to examine how well these techniques decrease weedy species and increase the success of seeded native grasses in the context of the Agate Desert Preserve and its grassland community. In this study the effects of sawdust amendments, herbicides, and alfalfa straw mulch were specifically designed to maximize the success of planted perennial grasses while minimizing potential impact on the native forbs already present on the preserve. In particular, herbicide application was timed to catch early growth of exotics, but not native forbs.

STUDY SITE

This study was carried out at the Agate Desert (42°25'N, 122°52'W) located in the central Rouge Valley of southwestern Oregon. The Agate Desert (400 m asl) is dominated by a landscape consisting of irregularly shaped soil mounds approximately 1 m high with low, often rocky areas between the mounds forming seasonal vernal pools (Elliott and Sammons 1996). A 22-ha Nature Conservancy preserve is located in the northwestern part of the Agate Desert on the corner of Table Rock and West Antelope Roads, Medford, Oregon. The land had previously been leased for winter and spring cattle grazing, but cattle were removed from the site in March 1988.

The soils of the Agate Desert are a complex of the Agate-Winlow Series that occurs on fan terraces with patterned ground formed in alluvium from mixed sources. The surface layer is typically a gravelly clay loam about 10 cm thick with the lower 12–25 cm a gravelly clay. Effective rooting depth is 18–40 cm (SCS 1987).

Most of the precipitation falls from November through March, with only 25% of the precipitation falling during the remaining 7 months of the year. The average annual precipitation for the area is 478 mm. Monthly mean temperature ranges from 22.5°C in July to 3.2°C in December. During the wet winter months the inter-mound areas (vernal pools) fill with water. The years of the study were fairly representative. The study area received 419 mm of rain in 1999 and 478 mm in 2000. Temperatures during the study period were also similar to the long-term means.

The natural vegetation of the Agate Desert uplands was most likely dominated by a mixture of *Pseudoroegneria spicata* (bluebunch wheatgrass), *Festuca idahoensis* (Idaho fescue), *Poa secunda* (pine bluegrass), and assorted forb species. Earlier successional species may have included *Achnatherum lemmonii* (Lemmon's needlegrass), *Elymus elymoides* (squirrel-tail), and *Bromus carinatus* (California brome).

Nonnative annual grasses that currently dominate the upland areas of the mounded prairie throughout the Agate Desert have for the most part replaced native perennial grasses. These exotics include the grasses *Taeniatherum caput-medusae* (Medusahead), *Bromus hordeaceus* (soft chess), *Vulpia myuros* (rattail fescue), *Poa bulbosa* (bulbous bluegrass), and *Avena fatua* (wild oat), as well as forbs such as *Centaurea solstitialis* (yellow starthistle), *Tragopogon pratensis* (meadow salsify), *Lactuca serriola* (prickly lettuce), *Verbascum blattaria* (moth mullein), *Erodium cicutarium* (filaree), and *Hypericum perforatum* (Klamath weed). Native grasses are largely absent, with the exception of a few small patches. Two rare plant species endemic to southern Oregon, *Lomatium cookii* (Cook's desert parsley) and *Limnanthes floccosa* ssp. *grandiflora* (large-flowered wooly meadowfoam), occur in the Agate Desert.

METHODS

Five 1 × 4-m plots were randomly located within each of 3 areas differing in previous vegetation management: (1) burned in June

1998; (2) burned in June 1998 and mowed in May 1999; (3) mowed in May 1999. Plot locations within 1 m of a vernal pool were rejected, and all plots were at least 10 m distant from each other. Each plot was divided into four 1-m² subplots and randomly assigned 1 of 4 experimental treatments, for a total of sixty 1 × 1-m plots.

Native grass seed was collected by the Nature Conservancy in 1992 from extant populations occurring on the Agate Desert and was used to establish a native plant propagation program at the Oregon State University experiment station at Jacksonville, Oregon, and the Bureau of Land Management's seed orchard in Merlin, Oregon. Seeds of 3 native perennial grasses from these sources were harvested in June and July 1999: *Achnatherum lemmonii* from the Oregon State University experiment station; *Festuca idahoensis* from the Oregon State University experiment station; and *Pseudoroegneria spicata* from the Bureau of Land Management's seed orchard. Seeds from all 3 species were sieved and winnowed to remove chaff and cured at room temperature for several months. Lower seedling rates were used for *Pseudoroegneria spicata* (750 seeds · m⁻²) than for *Achnatherum lemmonii* (1000 seeds · m⁻²) and *Festuca idahoensis* (1200 seeds · m⁻²) due to limited seed availability.

On 4 December 1999 the upper soil surface in each of the plots was turned to a depth of approximately 5 cm using 4-pronged rakes. Then seed mixtures were evenly spread across each of the 1-m² plots and lightly mixed into the soils with the rakes. Each of the 4 subplots at each of the 15 experimental plots was randomly assigned to either a control or 1 of the following 3 treatments.

Sawdust Treatment

Sawdust from a local sawmill was thoroughly dried and then separated into 400-g allotments. On 4 December 1999, the same date that the seeds were sown, we evenly distributed an allotment of sawdust over a single 1-m² subplot in each plot and lightly mixed it into the upper soil surface with a 4-pronged rake. An additional 400 g of sawdust was added approximately midway through the experiment, on 26 February 2000, for a total rate of 800 g · m⁻². To avoid any additional disturbance to the vegetation, we spread the 2nd application of

sawdust evenly over the subplot but did not mix it into the soil.

Herbicide-only Treatment

Herbicide was applied to one 1-m² subplot in each plot on 28 November 1999, one week prior to seeding. Using the recommended rate, glyphosate (6 g of Roundup, Monsanto, San Ramon, CA, per gallon of water, or 2%) was applied to each unit using a hand-held sprayer at a delivery volume of approximately 0.5 L · m⁻² (7.8 kg glyphosate per ha). We applied the herbicide in the morning, under calm weather conditions, and were careful to avoid drift onto neighboring treatment units.

Glyphosate is a nonselective herbicide and in natural areas, or other sites with important native species components, the presence of nontarget species must be taken into account. Often this problem can be overcome by using selective herbicides (Rice and Toney 1998) or the use of wick application to target species (Anderson 1993). The advantage of using glyphosate is that it can be used to control both annual grasses and exotic forbs. Glyphosate is also relatively safe and poses minimal environmental risk as it is rapidly degraded by soil microorganisms and will not readily leach from the soils (Haney et al. 2000, Jonge et al. 2000).

Straw + Herbicide Treatment

We added alfalfa mulch to herbicide plots because supplemental nitrogen is known to favor exotics over natives (see Jaquemyn et al. 2003), and we wanted to know if, with the suppression of exotics, additional nitrogen enhanced the success of planted perennials. In the last 1-m² subplot in each plot, the same herbicide treatment described above was applied, followed by an alfalfa straw mulch. On 4 December 1999, once all plots had been seeded, straw was evenly spread over the plots. Approximately 1000 g of alfalfa straw per plot (1 m²) was used to cover the area to a uniform depth of approximately 4 cm.

Soil Sampling

Soil samples were collected on 7 November 1999 from each of the 3 pretreatment areas using a 3-cm-diameter soil-sampling probe. Three 0–15 cm soil cores were collected from each site and thoroughly homogenized. Samples were then dried and sieved through a 2-mm screen and sent to the Divi-

sion of Agriculture and Natural Resources Analytical Lab at the University of California, Davis, for analysis of pH, texture, organic matter, phosphorus, potassium, and total available soil nitrogen. Additional soil samples were collected on 26 February 2000 and 15 June 2000 and analyzed for nitrogen. Total available soil nitrogen (NO₃ and NH₄) was quantified using 50 g of fresh soil added to 100 mL of KCl solution, and run through a Carlson nitrogen analyzer (Carlson 1978, 1986).

Vegetation Sampling

At the time of the initial seeding (December 1999), vegetation in the burned areas was characterized by a dense cover of nonnative *Erodium cicutarium* and annual grass seedlings. Vegetation in the mow-only area was characterized by dense nonnative annual grass seedlings with a patchy distribution of *E. cicutarium* and *Lactuca serriola*. Native forbs, including *Lomatium utraculatum*, *Lupinus bicolor*, and *Plagiobothrys nothofulvus*, were present in all areas, but generally uncommon.

Percent cover by each plant species, bare ground, litter, and gopher disturbance was estimated on 9 May 2000 by placing an elevated 1-m² quadrat, divided into 20-cm² grid cells (each 4%), over each of the experimental plots. Seedling density in each plot was determined by counting the total number of seedlings of each of the native species present on 16 May 2001 inside a randomly placed 0.1-m² circular quadrat within each plot. All of the aboveground biomass within the quadrat was then removed for subsequent biomass analysis. Plot locations having greater than 10% cover of fresh gopher disturbance were rejected. Biomass samples were oven-dried, and the aboveground dry weight was determined for each of 4 groups of species: (1) planted native grasses, (2) native forbs, (3) nonnative annual grasses, and (4) nonnative forbs.

Statistical Analysis

The 3 planted native grasses were initially analyzed separately, but since they responded similarly to treatments and differed in previous vegetation management in all 3 areas, they were lumped (into “native grasses”) for the analyses presented here. Available soil nitrogen was compared within each of the 3 pretreatment areas. All other data from the controlled experiments were analyzed using 2-way

ANOVAs with treatments being fixed effects and vegetation management areas (random) block effects, and with 54 d.f. The data were highly right skewed and all data sets were log-transformed. Means were compared using Tukey tests for Honestly Significant Differences. The 3-month and 6-month soils data and the relative cover data from native and annual grasses failed to meet the assumptions of ANOVA, despite transformation of the raw data. These 4 data sets were therefore also analyzed using a nonparametric Wilcoxon rank scores test to compare treatment means (Sokal and Rohlf 1981). The statistical programs JMP (SAS 1996) and SAS (SAS 1999) were used for all statistical analyses.

RESULTS

Soils

The soils in the areas differing in previous vegetation management were similar for texture, pH, and most major nutrients. However, the 2 burned areas had 30% lower levels of total available soil nitrogen (NO_3 and NH_4) relative to the unburned area ($F = 6.44$, $P = 0.007$; Fig. 1). Three months into the experiment, the addition of sawdust significantly reduced total available soil nitrogen (NO_3 and NH_4) in the unburned, but not in the burned, plots (where soil nitrogen was already depleted). The addition of nitrogen-rich alfalfa straw significantly increased the total available soil nitrogen relative to the control and sawdust plots in all 3 areas. However, by 6 months after soil amendment, neither the sawdust treatment ($P = 0.07$) nor the alfalfa treatment ($P = 0.30$) exhibited total available soil nitrogen levels significantly different from controls (data not shown).

Relative Cover and Biomass

While the cover of seeded native grasses was somewhat higher in the burn and mow areas relative to the burn-only and mow-only areas, these differences were not significant (all $P > 0.15$; Fig. 2). Native grass cover was 10 times greater in the herbicide plots than in the control and sawdust plots ($F = 123$, $P < 0.0001$; Fig. 3). Neither the addition of sawdust to nonherbicide plots nor the addition of alfalfa to herbicide plots affected native grass cover (both $P > 0.15$; Fig. 3). These treatment effects were consistent across all 3 areas differing in previous vegetation management.

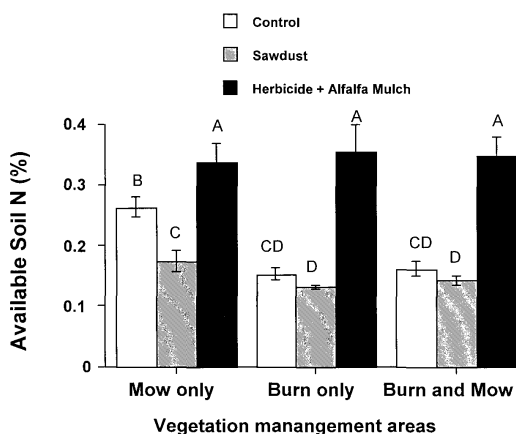


Fig. 1. Total available soil nitrogen (NO_3 and NH_4) 3 months after soil amendment. Across all treatments and vegetation management areas, bars sharing a letter are not significantly different ($P < 0.05$), based on analysis using log-transformed data. Error bars are standard errors.

The combination of burning and mowing reduced cover of nonnative annual grasses by nearly 40% relative to the burn-only and mow-only areas ($F = 3.69$, $P = 0.03$, Fig. 2). Nonnative annual grass cover was reduced by 80% in both herbicide treatments relative to the control and sawdust plots ($F = 37.9$, $P < 0.001$, Fig. 3). The addition of sawdust did not have a significant effect relative to the control plots ($P = 0.85$), and the addition of alfalfa straw made no difference in terms of nonnative grass cover when compared with the herbicide plot without alfalfa straw ($P = 0.49$; Fig. 3). These treatment effects were consistent across all 3 areas differing in previous vegetation management.

Native forb cover was somewhat lower in the burn-only and mow-only areas ($P = 0.12$; Fig. 2), and it was higher in the herbicide plots receiving alfalfa straw than in the control and sawdust plots ($P = 0.045$; Fig. 3). The difference in native forb cover in the herbicide treatments was due largely to increased cover of *Clarkia purpurea* and *Nemophila pedunculata*. One species, *Lomatium utriculatum*, had a slight (nonsignificant) decrease in cover in both herbicide plots relative to the control and sawdust plots. The remaining native forbs did not show any significant trends among treatments. These treatment effects were consistent across all 3 areas differing in previous vegetation management.

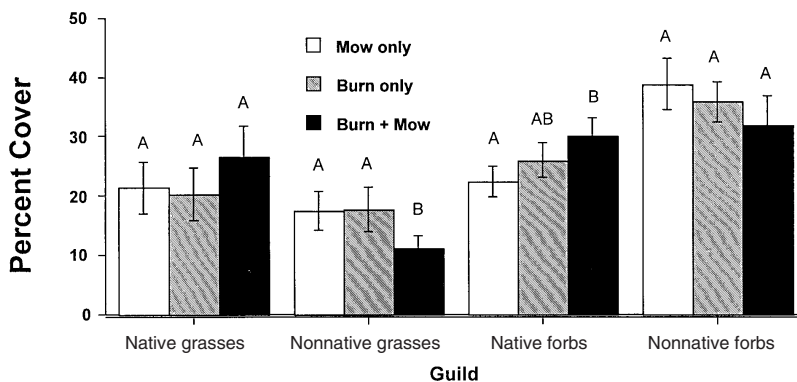


Fig. 2. Relative cover by previous vegetation management of the seeded perennial grasses, exotic annual grasses, native forbs, and nonnative forbs. Within each guild, bars sharing a letter are not significantly different ($P > 0.05$), based on analysis using log-transformed data. Error bars are standard errors.

Nonnative forb cover was similar across the pretreatment areas (Fig. 2). Herbicide treatments, both with and without alfalfa straw, reduced nonnative forb cover by 50%, most notably for *Erodium cicutarium* ($F = 18.9$, $P < 0.001$). Neither sawdust nor alfalfa straw had additional effects on nonnative forb cover (Fig. 3).

All of these patterns in relative cover were paralleled by similar differences in biomass. In fact, the correlation between relative cover and dry biomass across plots was significant for native grasses ($r = 0.76$, $P < 0.0001$), nonnative grasses ($r = 0.58$, $P < 0.0001$), and forbs (all forbs combined; $r = 0.28$, $P = 0.002$).

Native Grass Seedling Density

Seedling establishment 6 months after seeding was relatively high for all native bunchgrass species: *Achnatherum lemmonii* (18% of sown seeds established), *Pseudoroegneria spicata* (18%), and *Festuca idahoensis* (50%). Previous vegetation management had no effect on total native seedling density, but fall application of glyphosate prior to seeding resulted in 35%–50% greater native seedling density ($F = 7.84$, $P < 0.001$; Fig. 4). There were no additional differences associated with sawdust or alfalfa applications (Fig. 4). The individual species demonstrated similar responses to the treatments in all 3 vegetation management areas.

DISCUSSION

Pretreatment Areas

We did find some key differences between areas with different management histories. It

is logical that sawdust would reduce available soil nitrogen only in areas where nitrogen was not already volatilized by fire (Fig. 1), and that the combination of burning and mowing would favor natives over nonnatives (Fig. 2). However, these are not formally replicated treatment effects, but simply significant differences among sites that differed in management history. Because there may be other (unidentified) differences between these areas, we will be conservative here and discuss below only the results that came from the replicated controlled experiments.

Soils and Soil Amendments

The use of soil amendments to reduce available soil nitrogen can be inexpensive, can be easily applied over large areas, and can have minimal impacts on nontarget species. The results from our experiment, however, showed that the addition of sawdust had only a minimal effect on total soil nitrogen availability; a significant reduction in available soil nitrogen was seen only in the area where soil nitrogen had not been reduced previously by burning (Fig. 1). Even this effect was transient, and in any case it had no significant effect on the success of nonnative or native species or planted grasses.

The addition of nitrogen-rich mulch, in the form of alfalfa straw, resulted in slightly increased total soil nitrogen in all vegetation management areas 3 months after application (Fig. 1). After 6 months, however, this difference was no longer significant. It is not clear whether this is because of release from the soil

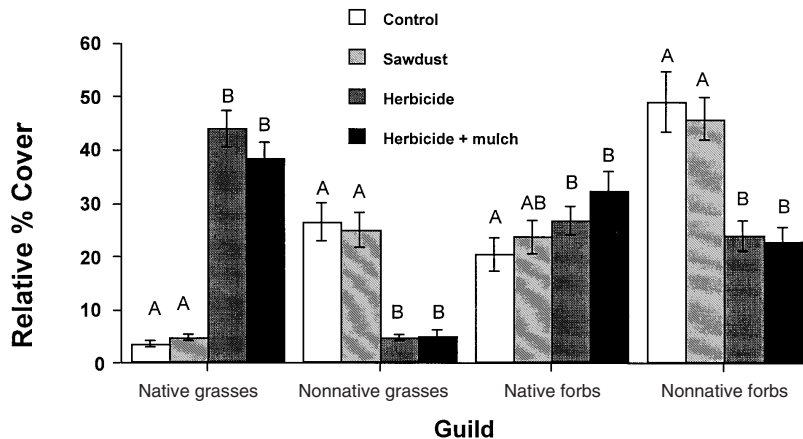


Fig. 3. Relative cover by experimental treatment of the seeded perennial grasses, exotic annual grasses, native forbs, and nonnative forbs. Within each guild, bars sharing a letter are not significantly different ($P > 0.05$), based on analysis using log-transformed data. Error bars are standard errors.

microbial environment or some other factor. Previous experiments with soil impoverishment have sometimes met with success (Paschke et al. 2000, Blumenthal et al. 2003), but they also often suggest only small, inconsistent, and short-term effects of carbon addition (Wilson and Gerry 1995, Zink and Allen 1998, Reeve Morghan and Seastedt 1999, Corbin and D'Antonio 2004).

Herbicide and Straw Mulch

Fall application of glyphosate prior to seeding produced the most promising results for native seedling establishment and control of annual grasses and forbs. In both the herbicide-only and herbicide-with-alfalfa-straw plots, there was a significant reduction in both nonnative annual grasses and forbs. Native seedling density, cover, and biomass were all considerably higher in the herbicide plots and were likely a result of the reduced competition from these exotic annual species. In general, alfalfa straw mulch provided little or no additional benefit in terms of total native seedling density, cover, or biomass, relative to the herbicide-only treatments.

These results suggest that competition with nonnative species reduced the density and, even more dramatically, the cover and biomass of planted perennial grasses. The increase in seedling density was 44%, but the increase in cover was nearly 10-fold. In other words, the demographic response of planted perennial grasses to herbicide was far exceeded by their

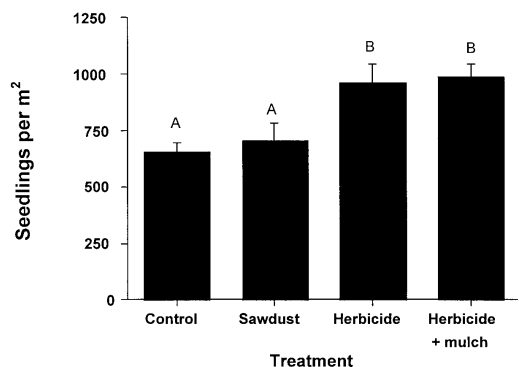


Fig. 4. Total native seedling density by treatment. Bars sharing a letter are not significantly different ($P > 0.05$), based on analysis using log-transformed data. Error bars are standard errors.

growth response. Our study examined only the first several months of growth of planted native grasses. However, the seedling stage is often limiting in plant populations (Harper 1977), and there is no reason to believe that these initial benefits to native grasses will not continue (Seabloom et al. 2003).

There was a significant increase in native forb cover in the alfalfa straw plots relative to the other treatments, but this was a result of the high abundance of a few species such as *Nemophila pedunculata* and *Clarkia purpurea*.

The responses of native and nonnative species to herbicide were inverse (Fig. 3), suggesting that competition with exotic annuals is

a major limiting factor in the establishment and success of native species (Evans and Young 1972, Heady et al. 1972, Heady 1988, Wilson and Gerry 1995). The application of glyphosate resulted in a reduction of nonnative annual grasses and forbs and improved native seedling establishment and cover of native forbs already present, but the effects on nontarget species is an important consideration. Glyphosate is a nonselective foliar herbicide affecting both grasses and forbs. Therefore the timing of application is an important factor in dictating the effects on nontarget species (Blackshaw et al. 2000). In this experiment herbicide was applied in the late fall, after some of the early annual species had germinated, but prior to the germination of many native forb species. This timing appeared to work well. Native forbs as a whole actually benefited from herbicide treatment. Previous experiments using glyphosate have also reported no negative impacts to native species and, in some cases, increased forb abundance and diversity (Whitson and Koch 1998, Washburn and Barnes 2000).

Although integrated approaches to weed control and the restoration of native perennial grasslands may be more successful than single-factor approaches (Anderson 1993, Gibbons and Youtie 1996), our results did not show this with these combinations of treatments. Our results suggest that well-timed herbicide application can be an effective treatment, at least for the initial establishment of native species. In contrast, both of our soil nitrogen amendments proved to be both transient and ineffective.

ACKNOWLEDGMENTS

We thank Kevin Rice, Darren Borgias, Molly Sullivan, Heather Bolstad, Kelly Koehn, Kari Veblen, Corinna Riginos, Rik Smith, Richard Evans, and Alison Berry for assistance of various kinds. Lynne Isbell and Karen Holl greatly improved the manuscript. This work was supported by The Nature Conservancy and the University of California at Davis.

LITERATURE CITED

- ANDERSON, J. 1993. Strategies for establishing native grasses. *Grasslands* 3:1–3.
- BARDGETT, R.D., J.L. MAWDSLEY, S. EDWARDS, P.J. HOBBS, J.S. RODWELL, AND W.J. DAVIES. 1999. Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. *Functional Ecology* 13:650–660.
- BISWELL, H.H. 1956. Ecology of California grasslands. *Journal of Range Management* 9:19–24.
- BLACKSHAW, R.E., G. SEMACH, X. LI, J.T. O'DONOVAN, AND K.N. HARKER. 2000. Tillage, fertiliser and glyphosate timing effects on foxtail barley (*Hordeum jubatum*) management in wheat. *Canadian Journal of Plant Science* 80:655–660.
- BLUMENTHAL, D.M., N.R. JORDAN, AND M.P. RUSSELLE. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13: 605–615.
- BORMAN, M.M., D.E. JOHNSON, AND W.C. KRUEGER. 1992. Soil-moisture extraction by vegetation in a Mediterranean maritime climatic regime. *Agronomy Journal* 84:897–904.
- BROWN, C.S., K.J. RICE, AND V. CLAASSEN. 2000. The effects of soil amendments and mulches on establishment of California native perennial grasses: a summary of selected results. *Grasslands* 10:1–17.
- BUGG, R.L., C.S. BROWN, AND J.H. ANDERSON. 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. *Restoration Ecology* 5:214–228.
- CARLSON, R. 1978. Automated separation and conductimetric determination of ammonia and dissolved carbon dioxide. *Analytical Chemistry* 50:1528–1531.
- . 1986. Continuous flow reduction of nitrate to ammonia with granular zinc. *Analytical Chemistry* 58:1590–1591.
- CHRISTENSEN, M.D., J.A. YOUNG, AND R.A. EVANS. 1974. Control of annual grasses and revegetation in ponderosa pine woodlands. *Journal of Range Management* 27:143–145.
- CLAASSEN, V.P., AND M. MARLER. 1998. Annual and perennial grass growth on nitrogen-depleted decomposed granite. *Restoration Ecology* 6:175–180.
- CORBIN, J.D., AND C.M. D'ANTONIO. 2004. Can carbon addition increase competitiveness of native grasses? A case study from California. *Restoration Ecology* 12:36–43.
- COUPLAND, R.T. 1992. *Natural grasslands*. Elsevier, Amsterdam and New York.
- CRAMPTON, B. 1974. *Grasses in California*. University of California Press, Berkeley.
- CURRIE, P.O., J.D. VOLESKY, T.O. HILKEN, AND R.S. WHITE. 1987. Selective control of annual bromes in perennial grass stands. *Journal of Range Management* 40:547–550.
- D'ANTONIO, C.M., AND P.M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- DYER, A.R., AND K.J. RICE. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80:2697–2710.
- ELLIOTT, M., AND D. SAMMONS. 1996. *Characterization of the Agate Desert*. Southern Oregon University, Department of Geology, Ashland.
- EVANS, R.A., AND J.A. YOUNG. 1972. Competition within the grass community. Pages 230–246 in V.B. Younger and C.M. McKell, editors, *The biology and utilization of grasses*. Academic Press, New York.
- GEORGE M.R., J.R. BROWN, AND W.J. CLAWSON. 1992. Application of nonequilibrium ecology to management of Mediterranean grasslands. *Journal of Range Management* 45:436–440.

- GIBBONS, S.T., AND B. YOUTIE. 1996. An examination of annual grass control methods for use on the Lawrence Memorial Grassland Preserve. *Bulletin of the Ecological Society of America* 77:162.
- HAMILTON, J.G. 1997. Changing perceptions of pre-European grasslands in California. *Madroño* 44:311–333.
- HAMILTON, J.G., C. HOLZAPFEL, AND B.E. MAHALL. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* 121:518–526.
- HANEY, R.L., S.A. SENSEMAN, F.M. HONS, AND D.A. ZUBERER. 2000. Effect of glyphosate on soil microbial activity and biomass. *Weed Science* 48:89–93.
- HARPER, J.L. 1977. *Population biology of plants*. Academic Press, New York.
- HEADY, H.F. 1988. Valley grassland. Pages 491–514 in M.G. Barbour and J. Major, editors, *Terrestrial vegetation of California*. California Native Plant Society, Sacramento.
- HEADY, H.F., J.W. BARTOLOME, M.D. PITT, G.D. SAVELLE, AND M.C. STROUD. 1972. California prairie. Pages 313–335 in R.T. Coupland, editor, *Ecosystems of the world: natural grasslands*. Elsevier, NY.
- HUIJK, P. 1999. Low-tech seeding technique for perennial bunchgrass yields promising results in the Lassen Foothills (California). *Ecological Restoration* 17:75–76.
- JACKSON, L.E. 1985. Ecological origins of California's Mediterranean grasses. *Journal of Biogeography* 12: 349–361.
- JACQUEMYN, H., R. BRYN, AND M. HERMY. 2003. Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. *Biological Conservation* 111:137–147.
- JONGE, H.D., L.W.D. JONGE, AND O.H. FACOBSEN. 2000. [14C] Glyphosate transport in undisturbed topsoil columns. *Pest Management Science* 56:909–915.
- LAYCOCK, W.A. 1991. Stable states and thresholds of range condition on North American rangelands—a viewpoint. *Journal of Range Management* 44:427–433.
- MORGAN, J.P. 1994. Soil impoverishment. *Restoration Management Notes* 12:55–56.
- . 1997. Plowing and seeding. Pages 193–215 in S. Packard and C.F. Mutel, editors, *The tallgrass prairie restoration handbook*. Island Press, Washington, DC.
- NORTON J.B., T.A. MONACO, J.M. NORTON, D.A. JOHNSON, AND T.A. JONES. 2004. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *Journal of Arid Environments* 57:445–466.
- PASCHKE, M.W., T. MCLENDON, AND E.F. REDENTE. 2000. Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* 3:144–158.
- REEVER MORGHAN, K.J., AND T.R. SEASTEDT. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. *Restoration Ecology* 7:51–55.
- RICE, P.M., AND J.C. TONEY. 1998. Exotic weed control treatments for conservation of fescue grassland in Montana. *Biological Conservation* 85:83–95.
- RIETKERK, M., AND J. VAN DE KOPPEL. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* 79:69–76.
- RIETKERK, M., F. VANDENBOSCH, AND J. VAN DE KOPPEL. 1997. Site-specific properties and irreversible vegetation changes in semi-arid grazing systems. *Oikos* 80:241–252.
- SAS. 1996. JMP. SAS Institute Inc, Cary, NC.
- . 1999. SAS. SAS Institute Inc., Cary, NC.
- SEABLOOM, E.W., W.S. HARPOOLE, O.J. REICHMAN, AND D. TILMAN. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Science* 100:13384–13389.
- SCS (SOIL CONSERVATION SERVICE). 1987. Soil survey of Jackson County area, Oregon. U.S. Department of Agriculture, Washington, DC.
- SOKAL, R.R., AND F.J. ROHLF. 1981. *Biometry*. W.H. Freeman and Company, New York.
- STROMBERG, M.R., AND P. KEPHART. 1996. Restoring native grasses in California old fields. *Restoration Management Notes* 14:102–111.
- TNC (THE NATURE CONSERVANCY). 1997. Agate Desert restoration plan. The Nature Conservancy, Medford, OR.
- VINTON, M.A., AND I.C. BURKE. 1995. Interactions between individual plant-species and soil nutrient status in shortgrass steppe. *Ecology* 76:1116–1133.
- WASHBURN, B.E., AND T.G. BARNES. 2000. Postemergence tall fescue (*Festuca arundinaceae*) control at different growth stages with glyphosate and AC 263,222. *Weed Technology* 14:223–230.
- WHITSON, T.D., AND D.W. KOCH. 1998. Control of downy brome (*Bromus tectorum*) with herbicides and perennial grass competition. *Weed Technology* 12:391–396.
- WILSON, S.D., AND A.K. GERRY. 1995. Strategies for mixed-grass prairie restoration: herbicide, tilling and nitrogen manipulation. *Restoration Ecology* 3:290–298.
- ZINK, T.A., AND M.F. ALLEN. 1998. The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. *Restoration Ecology* 6:52–58.

Received 14 September 2004

Accepted 29 December 2004