

Restoration of a Coastal California Grassland after Invasion by Nitrogen-Fixing Shrubs, French Broom (*Genista monspessulana*) and Scotch Broom (*Cytisus scoparius*)

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ABSTRACT

We studied the effect of two years of sawdust addition on the growth of native perennial grasses in a site where we manually removed two introduced nitrogen-fixing shrubs, French broom (*Genista monspessulana*) and Scotch broom (*Cytisus scoparius*) in central coastal California. We tested the hypothesis that sawdust addition to soil would reduce plant-available nitrogen levels, and thereby decrease the competitive effect of fast-growing exotic annual grasses on slower-growing native perennial grasses. After manual removal of broom, we planted three species of native grass seedlings alone or in combination with three species of exotic annual grasses, which were planted as seed. Half of all replicates received four applications of sawdust to the top 1 inch (3 cm) of mineral soil during the two-year experimental period. Plant-available nitrogen measured in laboratory aerobic incubations did not significantly decrease until the second year of sawdust application. Sawdust did not alter the competitive interaction between annuals and native perennials: native perennial grass seedlings were greatly suppressed by the presence of annuals and this was not changed by sawdust addition. In the absence of competition with annuals, we observed both direct stimulation and suppression by sawdust on native species. Annual grass biomass did not respond to sawdust addition. Nitrogen:carbon ratios of leaf tissue were similar across all species, suggesting that both annuals and perennials responded similarly to depletion of soil resources. Our results confirm that although it is possible to use sawdust to reduce nitrogen availability in broom-invaded soils, it is difficult to target the species that will benefit.

Keywords: *Cytisus scoparius*, *Genista monspessulana*, *Nassella pulchra*, nitrogen-fixer, nitrogen enrichment, sawdust

California coastal grasslands are currently undergoing widespread invasions by a suite of closely related nitrogen-fixing (N_2 -fixing) shrubs, commonly referred to as “brooms”—French broom (*Genista monspessulana*), Scotch broom (*Cytisus scoparius*), Spanish broom (*Spartium junceum*), Portuguese broom (*Cytisus striatus*), and gorse (*Ulex europaeus*). All of these species have been identified as “plant pests” in California (CalEPPC 1997). Restoration efforts have thus far focused on removal of above-ground biomass by pulling or cutting, and other treatments, such as burning, to reduce the extensive seedbanks of these species (Alexander and D'Antonio 2003). However, broom species also significantly increase soil nitrogen availability (Haubensak 2001), and some researchers have suggested that this change in soil chemistry may be particularly long lasting (Vitousek and others 1987). From a restoration perspective, an N-enriched soil may severely restrict the re-establishment of indigenous species by favoring fast-growing exotic species, which is exactly what a number of researchers have shown

in coastal California grasslands where N_2 -fixers have invaded (Maron and Jefferies 1999, Alexander and D'Antonio 2003).

Unlike Central Valley grasslands, where the composition is dominated by Mediterranean annual grasses, coastal California prairies have retained a strong native grass component (Heady 1988). Native grass cover declines, however, both during and after invasion of coastal prairie by broom (Haubensak, unpublished data). Following broom removal, annuals grasses may have an even greater advantage because high N-availability promotes their productivity as demonstrated in coastal California grasslands (Maron and Jefferies 1999, Alexander and D'Antonio 2003) and coastal sage scrub (Zink and Allen 1998). Experimental work from California grasslands demonstrates that these annual species directly suppress native grasses, such as purple needlegrass (*Nassella pulchra*), at the seedling stage (for example, Dyer and others 2000), although perennial grasses can be good competitors once they are established (Brown and Rice 2000a, Corbin and D'Antonio 2003). This body of work

suggests that a reasonable way to restore native grasses would be to decrease the performance of rapidly colonizing and fast-growing exotic annuals.

The addition of carbon (C) to soils is one technique for achieving such a result. By causing soil microbes to uptake and immobilize nitrogen, carbon amendments, such as sawdust, should have a stronger effect on the annual grasses and thereby reduce their competitive advantage over native perennials. While this assumption seems simple and straightforward, empirical evidence from numerous studies demonstrates that effects of C additions to soil are variable and often unpredictable (Shaver and Chapin 1980, Marion and others 1982, Wilson and Gerry 1995, Jonasson and others 1996a and 1996b, Schmidt and others 1997, Reeve-Morgan and Seastedt 1999, Corbin and D'Antonio 2004).

Here we report the results of a two-year experiment to determine the effects of sawdust addition on the competitive ability of fast-growing exotic annual grasses and native perennial grasses in an area that had been occupied and enriched by an N-fixing shrub for the previous ten years. We were interested in soil response as well as plant biomass response to the sawdust additions. We also separately evaluated the effect of sawdust on microbial activity in order to find support for the microbial immobilization mechanism that often goes untested in these experiments.

Methods and Materials

Study Site and

Experimental Design

Our study site is located in the Golden Gate National Recreation Area near Tennessee Valley, on the Marin Peninsula (Marin County), about 6 miles (10 km) north of San Francisco, California. The climate is Mediterranean, with the growing season beginning with autumn rains, and continuing until the termination of the rainfall period, typically in April. Temperatures during the annual summer drought are modified by coastal fog.

The study area consists of a series of ridge prairies within which are patches of

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coyotebush (*Baccharis pilularis*), the dominant native shrub, and small stands of French and Scotch broom, most of which were roughly 8-15 years old. These patches of broom range in size from several individuals to upwards of thousands of individuals, with patch diameters as large as 656 feet (200 m). Annual grasses, introduced from the Mediterranean region, co-dominate the herbaceous community with native perennial grasses and forbs. The dominant annual grasses are ripgut brome (*Bromus diandrus*), big quackinggrass (*Briza maxima*), slender oat (*Avena barbata*), and soft brome (*Bromus hordeaceus*). The dominant native grasses are California oatgrass (*Danthonia californica*), purple needlegrass and red fescue (*Festuca rubra*), all of which are perennial species. A small amount (less than 5 percent) of bare ground is present, the result of rodent activity (primarily by the meadow vole, *Microtus californicus*). The loamy isomesco soils were formed from sandstone and shale and contain 0.36-percent nitrogen (M. Ankovich unpublished data).

Broom species began to invade this area about 20-30 years ago. They are most abundant along trails, but patches have also established in open grassland. French broom is by far the most abundant and can produce from 8,800 to 10,200 seeds per year (Parker and Haubensack unpublished data). The density of plants within mature, monospecific broom patches at this site is 10.4 adult individuals per square meter—a density that produces an 80-100 percent canopy cover. Adult individuals have aver-

age stem diameters of about 1 inch (3 cm) and heights of 8.2 feet (2.5 m).

In December 1998, we used steel-bladed brushcutters to remove a dense stand of mature (roughly 8- to 10-year-old) broom individuals down to mineral soil from a 3,200-m² area. Root biomass was left in place, and we observed no regeneration or resprouting.

We established forty-two 2.25-m² plots (1.5 x 1.5 m) in the clearing. Plots were randomly assigned to one of the following treatments, with or without sawdust addition: 1) exotic annuals alone (annual-only); 2) native perennials alone (perennial-only); and 3) exotic annuals plus native perennials (annual-plus-perennial), for a total of six treatments with seven replicates each.

Species combinations of exotic annual grasses included slender oat, big quackinggrass, and ripgut brome at an initial planting density of about 12,000 seeds per square meter in both annual-only and annual-plus-perennial plots. This density was derived from Heady (1958), who estimated the initial densities of germinating grasses in California annual grassland at between 10,000-15,000 individuals per square meter. Perennial combinations were comprised of the following three native grass species common to this area: red fescue, purple needlegrass, and California melicgrass.

Perennial seedlings were started in the greenhouse in cone-tainers and planted out into "neighborhoods" of four, at an overall density of 70 individuals per square meter. This density is higher than that typically found in mature stands of native grasses because we wanted to minimize bare space in plots. Annuals were seeded into plots in early January 1999. Native perennial grass seedlings were six weeks old at the time of planting, which was about two weeks after the annuals germinated.

Sawdust was raked into the top inch (2-3 cm) of mineral soil at the same time as annuals were seeded, and again at the peak physiology of the annuals (April 1999). The first application was at the rate of 400 g/m², the second at 200 g/m², for a total of 600 g/m² for the first growing season. Two more subsequent applications were made during the 1999-2000 growing

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season, both at the rate of 200 g/m², for a total of 400 g/m² the second season. We estimated that these rates were about 200 percent and 100 percent of the C input to soil through aboveground net primary production for this site during 1999 and 2000, respectively (Haubensak 2001). We used a higher amount in the initial year of application because we expected nutrient release to be great immediately following broom removal. We used less the second year because of a difference in the type of sawdust available. The maple sawdust we used the second year was finer, denser, and more easily incorporated into the soil. We, therefore, did not need to apply the same amount to achieve a well-mixed effect.

To control for disturbance, all plots were raked whether or not they received sawdust. A subset of the perennial seedlings (n = 20 for each species) grown in the greenhouse was harvested at the time of outplanting, dried, and weighed for initial size. Means of these initial biomass values were subtracted from the final biomass values after harvests were conducted in June 1999. These initial biomass values were also subtracted from harvest values in June 2000.

Aboveground biomass of all plants was sampled in the field during June 16-20, 1999, from three quadrats (25 x 25 cm) randomly placed within each plot. For perennial-only plots, a "neighborhood" of four individuals of the same species was harvested separately. For annual-only plots, material from the three quadrats was combined. For annual-plus-

perennial plots, perennials were separated into species and annuals were combined. All plant material was dried in a 140°F (60°C) oven for 48 hours, then weighed. The same procedure was followed at the end of the following growing season, with sampling taking place in mid-June 2000.

At the end of the second growing season, all plants harvested that year were analyzed for total N and C. Native grass species were analyzed separately, while annuals were analyzed as a combination. After drying until constant weight at 140°F, plant tissue was ground in a Wiley Mill (mesh size #40), followed by grinding in a Wig-L-Bug amalgamator. Five milligrams of the dried, ground plant material were weighed into tin capsules for analysis of total N and total C by combustion on a Carlo Erba NA 1500 CHN analyzer.

At three time points during the 1999 growing season (February, April, and May), we collected soils from the top 4 inches (10 cm) of mineral soil (excluding litter layer), and brought them back to the laboratory for a seven-day aerobic incubation. This incubation provides an index of plant-available nitrogen (Binkley and Hart 1989). Soils were homogenized by hand to remove large (greater than 2 mm) stems, roots, and rocks. A subsample was used to determine gravimetric water content (g H₂O)/g dry soil). A second subsample was immediately extracted in 2M KCl and a third was incubated for seven days at field moisture levels and room temperature (22°C). Extractants from these last two subsamples were analyzed for ammonium (NH₄⁺) and nitrate (NO₃⁻), respectively, on a Lachat flow-injection ion analyzer. During the 2000 growing season, soils were analyzed for available N once during April, when annual grasses at this site experience their peak physiology.

In order to test the hypothesis that sawdust addition stimulates microbial activity, we measured CO₂ efflux from soils collected from dense (roughly ten adult individuals per square meter) broom stands immediately adjacent to the broom removal area. In March 2000, we used 2-inch (5-cm) diameter corers to collect the top 6 inches (15 cm) of mineral soil from ten different random locations. Soils were brought back to the laboratory for

analysis. We followed the methodology of Neff and others (2000).

Statistical Analyses

We used analysis of variance (ANOVA) to examine the effect of sawdust in mitigating the competitive effect of annuals when grown with perennials. Each time point for soil N availability was analyzed separately by ANOVA, with life-form group and sawdust as fixed main effects. Net mineralization and nitrification were analyzed separately. A repeated-measures ANOVA was used to analyze CO₂ efflux across six time points in soils, with sawdust addition as the main effect and time as the repeated measure. Differences among treatments were generally considered to be significant if p < 0.05. However, values of p < 0.10 are also reported here. All analyses were conducted using SYSTAT (SYSTAT 1997).

Results

Soil Response

In the first growing season, standing pool sizes of NH₄⁺ and NO₃⁻ were not significantly affected by sawdust addition at any time point (data not shown). Also, sawdust addition did not affect net mineralization or nitrification rates in seven-day, aerobic lab incubations across all three time points in 1999 (Table 1). Life-form group did, however, affect net nitrification rates in May 1999 with perennial-only plots having higher levels of net nitrification than annual-only or annual-plus-perennial plots (F_{2,30} = 6.916; p = 0.003) (Table 1). This effect was irrespective of sawdust, however. Net nitrification rates decreased almost five-fold during the growing season.

Gravimetric water content of the top 4 inches of soil was identical in sawdust addition and non-addition plots in February (F_{1,30} = 0.638; P = 0.431) and April (F_{1,30} = 0.013; P = 0.910) (data not shown). In May, however, sawdust-addition plots showed a small, but statistically significant, increase in gravimetric water content with a value of 8.6 percent for no-sawdust plots compared to 9.5 percent for plus-sawdust plots (F_{1,30} = 4.950; P = 0.034).

Table 1. Net mineralization and nitrification rate (7-day laboratory aerobic incubation) of soils collected from plots with different grass mixtures (annuals only, perennials only, and annuals + perennials), with and without sawdust, during 1999 and 2000 growing seasons. Analyses were conducted on the top 10 cm of mineral soil (litter material excluded). Values are means for each treatment (N = 7), followed by 1 standard error in parentheses.

		Mineralization rate (mg NH ₄ ⁺ -N + NO ₃ ⁻ -N kg soil ⁻¹ d ⁻¹)		Nitrification rate (mg NO ₃ ⁻ -N kg soil ⁻¹ d ⁻¹)	
		Minus sawdust	Plus sawdust	Minus sawdust	Plus sawdust
1999					
February	Annuals only	3.462 (1.219)	2.181 (0.419)	2.661 (0.626)	2.225 (0.313)
	Perennials only	1.811 (0.344)	1.692 (0.424)	2.289 (0.275)	1.931 (0.470)
	Annuals + Perennials	1.803 (0.414)	2.422 (0.590)	2.013 (0.342)	2.371 (0.515)
April	Annuals only	1.464 (0.605)	0.888 (0.238)	0.922 (0.173)	0.843 (0.218)
	Perennials only	0.629 (0.236)	0.880 (0.102)	0.752 (0.223)	0.980 (0.111)
	Annuals + Perennials	1.143 (0.396)	1.030 (0.192)	0.820 (0.194)	0.949 (0.190)
May	Annuals only	0.829 (0.782)	0.356 (0.163)	0.181 (0.088)	0.157 (0.039)
	Perennials only	1.040 (0.466)	0.475 (0.096)	0.471 (0.133)	0.360 (0.052)
	Annuals + Perennials	0.412 (0.108)	0.414 (0.101)	0.220 (0.083)	0.179 (0.048)
2000					
April	Annuals only	2.698 (0.638)	1.770 (0.710)	2.243 (0.433)	0.346 (0.359)
	Perennials only	5.489 (1.128)	1.646 (0.527)	4.830 (1.168)	0.306 (0.385)
	Annuals + Perennials	3.456 (0.906)	1.067 (0.169)	2.231 (0.776)	-0.088 (0.081)

By April, at the peak of the 2000 growing season, and after two additional sawdust applications, sawdust significantly decreased net nitrogen mineralization ($F_{1,34} = 15.992$, $P = 0.001$) and net nitrification ($F_{1,34} = 34.084$, $P = 0.001$) across all treatments (Table 1). Net mineralization was 1.5 to 3 times lower in sawdust-addition plots compared to no sawdust plots, while net nitrification was three to 15 times lower.

Plant Response

In 1999, the biomass of all three native perennial species was significantly reduced in the presence of annuals ($F_{1,23} = 50.28$, $P < 0.001$ for purple needlegrass; $F_{1,24} = 94.07$, $P < 0.001$ for red fescue; $F_{1,22} = 27.07$, $P < 0.001$ for California melicgrass) (Figure 1). This growth reduction of native perennials in the presence of annuals did not change with sawdust addition, which was indicated by a lack of significant "sawdust x annuals" interaction term for each species (Table 1). There was a generally positive influence of sawdust on growth of native species when grown without annuals, although this effect was significant only for red fescue

($F_{1,24} = 4.781$; $P = 0.039$). Red fescue was the largest of all the native grasses by the time of the 1999 harvest, and its average biomass was 40 percent greater in sawdust-addition plots compared to no-sawdust plots.

During the second season, most of the native grasses growing in the presence of annuals died regardless of sawdust addition. The growth of red fescue, the only native grass to survive the 1999-2000 growing season in the annual-plus-perennial plots, was negatively affected by both annuals and sawdust addition, with a significant "sawdust x annuals" term ($F_{1,21} = 5.139$, $P = 0.034$). Its growth was strongly reduced in sawdust-addition plots, but in the presence of annuals its growth was unaffected by sawdust addition (Figure 2).

The response of the three native species to sawdust in perennial-only plots was variable. Purple needlegrass growth increased slightly with sawdust addition, while California melicgrass had no significant response. Red fescue grew 40 percent smaller in sawdust-addition plots. As in 1999, the growth response in annual-only plots in 2000 was unaffected by addition of sawdust ($F_{1,21} = 0.741$, $P = 0.567$).

Microbial Activity

Carbon dioxide efflux (mg CO₂ g soil⁻¹ h⁻¹), a measure of microbial activity, was significantly greater in soils that received sawdust addition, but this effect varied over time (sawdust * time term, $F_{5,108} = 28.245$, $P < 0.001$) (Figure 3). Soil with sawdust addition had increasing CO₂ efflux over the incubation period, and had a high rate of activity at the end of the incubation. In contrast, soil without sawdust addition had almost no activity, peaking at about 20 percent the rate of the plus-sawdust soil by the midpoint of the incubation period (around 30 days), then decreasing to close to zero by the end of the incubation.

Restoration and Management Implications

Mitigating for nitrogen enrichment of soils by adding sawdust has two components: First, sawdust addition must have a greater direct effect on undesirable species than it does on desirable species. Second, desirable species should benefit from sawdust addition through competitive release. In the present study, we show that sawdust did decrease nitrogen availability, but undesirable fast-growing annuals were not disproportionately affected by the decrease. Furthermore, we observed direct negative effects of sawdust on the growth of desirable native grass species and these were not compensated for by release from annual grass competition.

Sawdust addition did have the intended effect of decreasing N availability across species by the second growing season. In the meantime, however, the suppressive effect of annuals on perennials was so dramatic that only red fescue survived in the presence of annuals through the end of the experimental period, irrespective of sawdust addition and the observed N decrease. This suggests that N availability was not the determining factor in growth of annuals when compared to perennials. The fact that there was 100-percent mortality of purple needlegrass and California melicgrass by the second year of the experiment is consistent with most of the literature from California

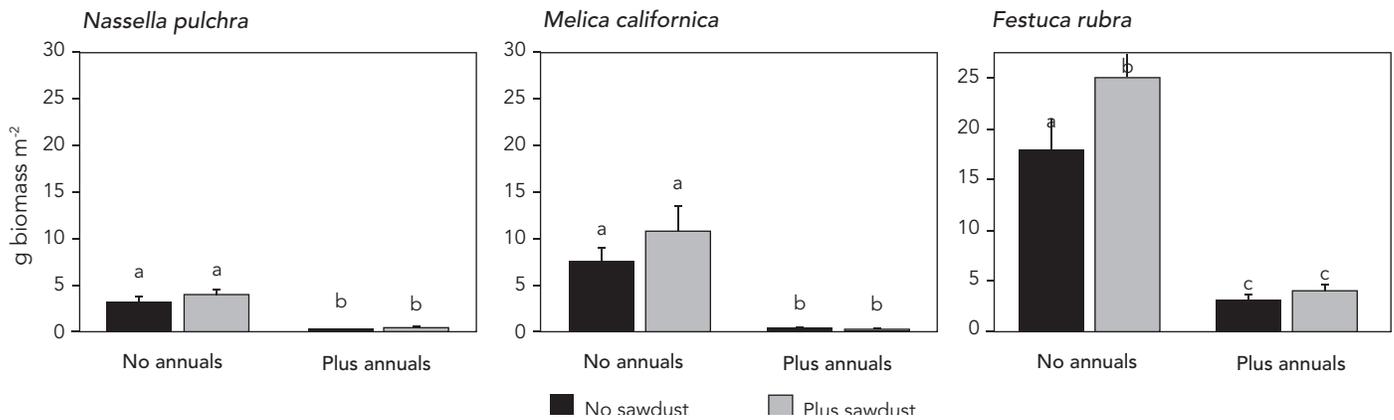


Figure 1. Growth response of three native grass species—red fescue (*Festuca rubra*), California melicgrass (*Melica californica*) and purple needlegrass (*Nassella pulchra*)—with and without sawdust addition, in the presence or absence of annual grass competition at the end of 1999 growing season. Bars represent means \pm one standard error ($n = 7$). For each species, different letters indicate significant differences between plus/no sawdust and plus/no annuals (Tukey HSD, $P < 0.05$).

annual grasslands. Only with addition of N fertilizer is there evidence that perennial grasses may overcome the suppressing effect of annual weeds (Brown and Rice 2000b)—an effect that is opposite to the rationale for adding carbon. Although it has been suggested anecdotally that annual grasses may facilitate the establishment of perennial grasses by protecting them from intense sun, heat, herbivores and frost (Brown and Rice 2000a), overwhelming evidence from field and greenhouse studies demonstrates that native perennial grasses have difficulty competing with introduced annual plants as seedlings in California grasslands (Bartolome and Gemmill 1981, Dyer and others 2000, Dyer and Rice 1999, Brown and Rice 2000a). Our results support this latter conclusion.

Because of mortality of purple needlegrass and California melicgrass, we could only evaluate the interaction of sawdust addition and annual grasses on the growth of red fescue by the end of our experiment. And in the case of that species, sawdust addition appeared to suppress its growth to the same extent that annual grasses did. Again, this suggests that the effect of competition from annuals was so strong that it overwhelmed any potential mitigating effect of sawdust addition. An alternative interpretation is that sawdust had such a negative effect on red fescue growth itself that suppression of annual grass competition did not matter. Growth from the

perennials-only plots supports the second interpretation: in the absence of competition from annuals, red fescue was 2.6 times smaller aboveground with sawdust addition compared to control plots. Similarly, Corbin and D'Antonio (2004) observed a direct negative effect of sawdust on purple needlegrass in a nearby coastal grassland community. Interestingly, we documented a positive direct effect of sawdust on purple needlegrass in this study, suggesting that responses of the same species may be variable across sites due to differences in factors, such as seed source or initial site fertility. The fact that we observed both negative and positive direct effects of sawdust on our non-target species underscores a central problem with this approach. That is, it is difficult to predict precisely which species or groups of species should respond directly (or most strongly) to sawdust addition based simply on broad life-history characteristics (annual or perennial). Our analysis of the nutrient use efficiencies (as N:C ratios, Vitousek 1982) of the three native grasses and the annuals (as a group) corroborates this conclusion further—all species were similar in their N use and thus responded similarly to the decrease in N availability despite the differences in life-histories. The similar N:C ratios of annual and perennial species that we documented may be due to the fact that at the seedling stage, perennial species may be capable of exhibiting the same nitrophilous behavior that fast-growing annual species are

expected to have under nutrient-enriched conditions. Alternatively, this similarity may also be a result of sampling error or the particular species that we chose to represent each group. In our study, there may be sufficient taxonomic distance among the species to mask a difference between the annual and perennial species that would otherwise be apparent.

The Legacy of Soil N Enrichment by Broom

One question to address when assessing the restoration potential of a site invaded by an N-fixer is: How long-lived is the enrichment effect, and how much does sawdust addition speed recovery to pre-enrichment/invasion levels? We conducted a reciprocal core transplant assay in 1999-2000 to test the importance of the broom canopy in maintaining a microenvironment for N mineralization (Haubensak 2001). We found that after broom removal, in the absence of N-rich broom litter or the microclimatic influence of broom cover on soils, mineralization rates are accelerated to the point of returning the N status of the soil to a pre-invasion state. We confirmed this by assaying nearby adjacent invaded and uninvaded areas at peak grass physiology in April 2000 and comparing those mineralization rates to those in our sawdust experiment measured at the same time. We found that even in soils untreated by sawdust addi-

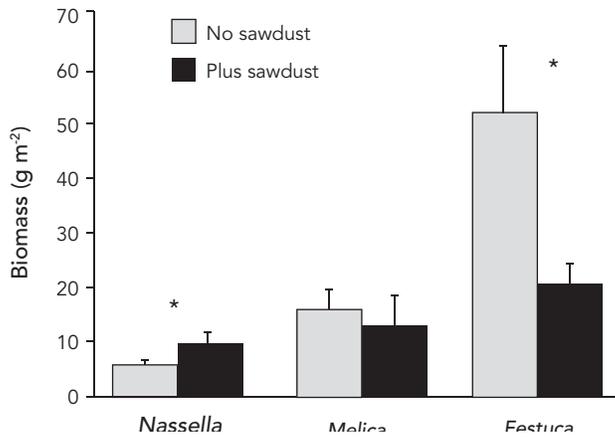


Figure 2. Biomass (g m^{-2}) of purple needlegrass (*Nassella pulchra*), California melicgrass (*Melica californica*), and red fescue (*Festuca rubra*) in perennial-only plots at the end of 2000 growing season, with and without sawdust addition. Bars represent means \pm one standard error ($n = 7$). An "*" denotes a significant effect of sawdust addition ($P < 0.05$).

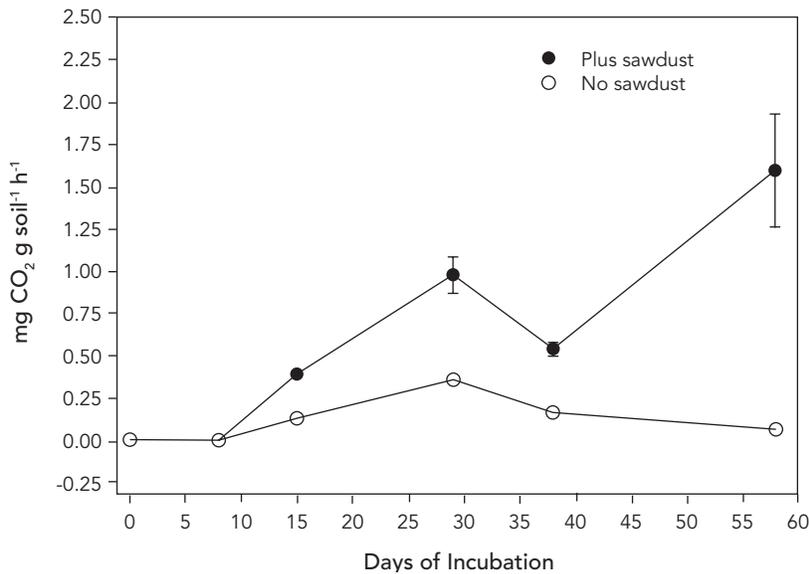


Figure 3. Carbon dioxide (CO_2) efflux in soils from broom stands collected during spring of second growing season, with and without sawdust addition, in $\text{mg C g soil}^{-1} \text{h}^{-1}$. Sawdust was added at approximately 50 percent higher rate than field additions. Each point represents the mean \pm one standard error ($n = 10$). Where standard error bars are not visible, they are hidden by the symbol.

tion, N availability had returned to pre-invasion levels one-and-one-half years after broom removal. Nitrogen enrichment by broom, then, may be a relatively transient effect. This idea, coupled with the results of this study, which suggest overall a relatively small role for N availability determining outcomes of plant performance, do not argue strongly for adding sawdust to soils following broom removal.

Conclusions and Recommendations

Carbon addition under conditions described here had no obvious beneficial effect for native perennial grasses and their restoration. On the other hand, survival of red fescue in this experiment underscores its high potential for revegetation and restoration projects, although Heady (1988) suggests that California fes-

cue was most likely the *Festuca* species that co-dominated the pristine California grassland. Restoration efforts in California often focus on purple needlegrass (Dyer and Rice 1997), but other perennial grasses have been shown to be effective at co-existing with exotic annual grasses, including meadow barley (*Hordeum brachyantherum* ssp. *brachyantherum*) (Bugg and others 1997) and Junegrass (*Koeleria cristata*) (Borman and others 1991). It is also important to keep in mind that prairie restoration is not complete without the establishment of both grasses and forbs (Carlsen and others 2000, Brown and Bugg 2001).

There are also a number of documented unintended effects of sawdust addition on target and non-target species. Sawdust addition can stimulate microbial activity and biomass growth, which may then be followed by a cycle of die-off and remetalization of that biomass (Schimel and others 1992) and increased net mineralization (Harmer and Alexander 1986). A pulse of nitrogen due to microbial biomass turnover would then result in increased plant growth in those plots. Our soil analyses were not conducted on a fine enough time scale to capture such dynamics; however, this would be one explanation as to why we observed much greater red fescue aboveground biomass with sawdust addition by the end of our experiment. Others have demonstrated a wide range of unintended effects of sawdust addition that have nothing to do with the mechanism of nitrogen availability. These include changes in the physical properties of soil (for example, water-holding capacity, total pore space, or bulk density) (Bugbee 1999). Some work has also shown that sawdust addition can increase fungal populations (Jonasson and others 1996b) that could then result in a change in the form of inorganic nitrogen that predominates (although our soil analyses do not necessarily suggest this particular outcome).

A lack of general understanding of carbon amendment effects is most likely the result of several factors that we gathered from a survey of the literature. First, the degree to which a site is nitrogen-enriched relative to its uninvaded or unaffected state is typically not known or

measured. It may be that in many cases (such as in ours) the enrichment effect is small or may decrease on its own. Indeed, in many sites, nitrogen availability (increased or not) may not be the most important factor that determines plant performance. Second, there is no standardized criterion on which the amount of carbon addition is based. For example, we used an estimate of carbon return to soil by means of aboveground NPP (measured onsite), while others doubled the amount applied in other studies, irrespective of any specific site information (for example, Alpert and Maron 2000). Third, most studies do not quantify the degree to which carbon amendments increase the soil carbon pool. There is likely to be a relationship between the initial carbon pool size, the amount of labile carbon added, and subsequent immobilization/mineralization cycles of the microbial biomass. In our case, adding carbon may have increased the soil carbon pool by about 30 percent, which may have been too small an increase to have large effects on annual grass biomass. If these parameters were known or measured, it would allow restorationists to compare and synthesize results of carbon amendment experiments more easily. It would also be a step toward developing a more generalized framework for predicting the efficacy of carbon amendments.

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