Can Carbon Addition Increase Competitiveness of Native Grasses? A Case Study from California

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Abstract

There is growing interest in the addition of carbon (C) as sucrose or sawdust to the soil as a tool to reduce plant-available nitrogen (N) and alter competitive interactions among species. The hypothesis that C addition changes N availability and thereby changes competitive dynamics between natives and exotics was tested in a California grassland that had experienced N enrichment. Sawdust (1.2 kg/m) was added to plots containing various combinations of three native perennial bunchgrasses, exotic perennial grasses, and exotic annual grasses. Sawdust addition resulted in higher microbial biomass N, lower rates of net N mineralization and net nitrification, and higher concentrations of extractable soil ammonium in the soil. In the first year sawdust addition decreased the degree to which exotic annuals competitively suppressed the seedlings of *Nassella pulchra* and, to a lesser extent,

Festuca rubra, both native grasses. However there was no evidence of reduced growth of exotic grasses in sawdust-amended plots. Sawdust addition did not influence interactions between the natives and exotic perennial grasses. In the second year, however, sawdust addition did not affect the interactions between the natives and either group of exotic grasses. In fact, the native perennial grasses that survived the first year of competition with annual grasses significantly reduced the aboveground productivity of annual grasses even without sawdust addition. These results suggest that the addition of sawdust as a tool in the restoration of native species in our system provided no significant benefit to natives over a 2-year period.

Key words: annual grass, coastal prairie grassland, grassland restoration, labile carbon, native perennial grass, nitrogen-enriched soils, sawdust.

Introduction

Ecosystem nitrogen (N) enrichment is a common barrier to plant community restoration. Past fertilization (Vitousek et al. 1997), atmospheric N deposition (Bobbink 1991), and invasion by N-fixing shrubs (Vitousek et al. 1987; Maron & Connors 1996) can all increase soil N availability and, in turn, can favor a few fast-growing species at the expense of slower growing species. Although general characteristics of non-native-invading plant species have proven elusive (Mack et al. 2000), N enrichment has been shown to favor invasive non-indigenous species in a variety of habitats (Huenneke et al. 1990; Vinton & Burke 1995; Maron & Connors 1996). Restoration in N-enriched habitats must therefore deal with the question of how to promote slower growing native species in competition with faster growing exotic species under high N conditions (Corbin et al. 2004).

Addition of C in the form of sucrose or sawdust has been suggested as a tool to reduce plant-available N and thereby increase the competitiveness of slower growing

natives (Morgan 1994; Alpert & Maron 2000; Paschke et al. 2000; Blumenthal et al. 2003). For this tool to work the addition of sucrose or sawdust must increase microbial N immobilization and decrease plant-available N. Under lower N conditions, growth of all vegetation would be expected to decrease, but if faster growing species are disproportionately affected by lower soil N concentrations, slower growing native species may benefit indirectly due to reduced competition from fast-growing exotic species.

Previous experimental tests of the benefits of C addition to native species have considered the impact of sucrose or sawdust on mixed plots of native and exotic plant species (Table 1). C addition has been shown to reduce inorganic N levels (Wilson & Gerry 1995; Zink & Allen 1998; Reever Morghan & Seastedt 1999; Paschke et al. 2000; Torok et al. 2000; Cione et al. 2002; Blumenthal et al. 2003) and exotic plant biomass (Reever Morghan & Seastedt 1999; Alpert & Maron 2000; Blumenthal et al. 2003). However C addition has not been shown to consistently benefit native species. Zink & Allen (1998) and Paschke et al. (2000) demonstrated positive effects of mulch and sucrose addition, respectively, on growth rates and relative abundances of native species, while other studies reported no benefit of sawdust addition to native species (Wilson & Gerry 1995; Reever Morghan & Seastedt 1999; Alpert & Maron 2000; Cione et al. 2002). C addition has been most successfully used by Blumenthal et al. (2003), who

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Table 1. Amendments of labile carbon (C) to reduce plant-available nitrogen and increase competitiveness of slower growing species.

Study	C Source Quantity and Form	Study Duration (years)
This study	1.2 sawdust	2
Blumenthal et al. (2003)	Various quantities of sucrose and sawdust	2
Cione et al. (2002)	2.5 cm depth leaf and bark mulch	1
Alpert & Maron (2000)	1.5 sawdust	2
Paschke et al. (2000)	1.1 sucrose	3
Torok et al. (2000)	0.1 sucrose $+ 0.03 \, kg/m^2$ sawdust	1
Reever Morghan & Seastedt (1999)	1.0 sucrose $+ 0.7 \, kg/m^2$ sawdust	1
Hopkins (1998)	$24 \, g \, C/m^2$ as sucrose and sawdust	3
Zink & Allen (1998)	3 cm depth pine bark, oat straw	3
Wilson & Gerry (1995)	0.4 sawdust	1
McLendon & Redente (1992)	1.1 sucrose	3

Quantity is kilogram of sawdust or sucrose per square meter added through the entire experiment. Frequency and method of application varied among studies.

reported that exotic biomass decreased and native biomass increased when a mixture of sucrose and sawdust was added to a tallgrass prairie restoration site. Sawdust remains an enticing tool for native restoration because of its ease of application and its cost effectiveness relative to sucrose. But if it decreases the production of all vegetation (natives and exotics), as has been reported in a number of studies, then sawdust would be less useful as a restoration tool than it would be if native biomass or competitiveness increases.

We tested the ability of sawdust addition to benefit native perennial grass species in competition with two different types of exotic grasses—exotic annual and exotic perennial grasses—in an ecosystem that had undergone N enrichment. We hypothesized that sawdust addition would lessen the competitive impact of exotic species on native species during the establishment phase. We expected that the impact of sawdust addition would be the strongest on native perennial, exotic annual interactions, because exotic annuals are known to be particularly responsive to changes in nutrient availability (Huenneke et al. 1990; Maron & Connors 1996) We chose an experimental design that permitted the examination of the relative impacts of native and exotic grasses on each other with and without sawdust addition. This represents a more complete test of the mechanisms of the benefits to native species of sawdust addition than previous studies. We further hypothesized that the effect of sawdust addition on native species in the absence of exotic competitors would be negative, indicating that the benefits of C addition to natives are mediated by the reduction in competitiveness of exotic species rather than by a direct positive effect of sawdust addition on growth of natives.

Methods

Study Area

This study took place at Tom's Point, a private nature preserve adjacent to Tomales Bay in Marin County, CA, U.S.A. (38° 13′ N, 122° 57′ W). Tomales Bay experiences highly seasonal rainfall patterns typical of Mediterranean climates. Annual rainfall is 790 mm per year, mainly falling between November and April. Peak growth for annuals is generally in late February through the end of March. For perennial species peak growth extends longer into the spring. Rainfall patterns vary among years, although typically the first rainfall events that stimulate germination occur in late October or November and the last events before the summer drought occur in April. Mean monthly temperature ranges from 13.9° C in March to 18.1° C in September. The soil at the study site was a Tomales Series sandy loam (fine, mixed, and mesic Ultic Paleustalf).

The site has not been grazed by livestock for at least 30 years. A portion of the reserve has been periodically dominated by *Lupinus arboreus* (bush lupine), a short-lived native N-fixing shrub that invades coastal grassland systems throughout central and northern California. At nearby Bodega Marine Reserve (BMR) *L. arboreus* has been shown to reduce native plant diversity through N enrichment of formerly native-dominated ecosystems (Maron & Connors 1996; Maron & Jefferies 1999). A portion of Tom's Point Preserve, where we established our experimental treatments, has become depleted of native species during repeated cycles of *L. arboreus* expansion and dieback. The high N content and low C:N ratio of the soils at our site (Table 2) is consistent with the pattern after *L. arboreus* colonization described by Maron and colleagues (Maron & Connors 1996; Maron & Jefferies 1999) at BMR. Few *L. arboreus* individuals were present at the beginning of the experiment due to widespread insect-driven dieback (Strong et al. 1995; Maron 1998),

Table 2. Mean (±SE) total nitrogen (N) and total carbon (C), and texture of the soil (top 10 cm) at the study site before the experiment.

Total soil N (mg N/g dry mass soil)*	4.1 (0.1)
Total soil C (mg C/g dry mass soil)*	49.5 (1.6)
C:N ratio	12.1 (0.05)
Sand (%)	83
Silt (%)	13
Clay (%)	5

*Carlo-Erba CHN autoanalyzer (Fisions Instruments, Milan, Italy).

and the area was dominated by introduced annual grasses including *Avena barbata* (slender wild oat), *Bromus diandrus* (ripgut brome), and *Vulpia myuros* (zorro fescue), introduced perennial grasses including *Festuca arundinacea* (tall fescue), *Holcus lanatus* (velvet grass), and *Phalaris aquatica* (harding grass) and such exotic annual and biennial forbs as *Carduus pycnocephala* (Italian thistle) and *Conium maculatum* (poison hemlock).

Experimental Design

Seeds of the introduced annual grasses *A. barbata*, *B. diandrus*, and *V. myuros*, the introduced perennial grasses *F. arundinacea*, *H. lanatus*, and *P. aquatica*, and the native perennial grasses *Agrostis idahoensis* (bent grass), *Festuca rubra* (red fescue), and *Nassella pulchra* (purple needle-grass) were collected by hand at Tom's Point Preserve in Spring 1998. Seeds of the introduced and native perennial grasses were planted in individual Conetainers (Stuewe and Sons, Corvallis, OR, U.S.A.) in September 1998 and allowed to germinate under greenhouse conditions.

In summer 1998, standing *C. pycnocephala* and *C. maculatum* individuals at Tom's Point Preserve were cut at ground level and removed. All remaining vegetation was sprayed with 5–10% glyphosate-based herbicide and removed, leaving bare soil. We established 70 1.5×1.5-m plots (with a 1–2 m buffer between plots) and assigned each plot to one of five treatments (Table 3). Because of the differences in size and longevity between exotic annual and exotic perennial grasses, it was not possible to equate the competitive environment experienced by native perennial grasses growing with each exotic group. Therefore we chose two different experimental designs to test the interactions between the native perennials and the exotics. We used an additive design in the case of the exotic annuals, whereby the density of individuals in plots containing both native perennials and exotic annuals was the sum of the number of individuals in single-group plots. In contrast, we used a replacement design in the case of the exotic perennials, whereby the density of individuals in each treatment remained constant (Table 3).

Annual seed densities applied in fall 1998 (Table 3) were chosen to fall within the range reported by Heady (1956) for Californian annual grasslands. Annual grass seeds were applied to appropriate plots in fall 1999 (second year) both

by allowing established plants from the previous growing season to set seed and by supplementing this natural seed rain with seed collected outside the experimental plots. Seeds were added at the same level as the previous season, with the exception that the number of *Vulpia* seeds was reduced to 7,750 seeds/plot. Perennial seedlings were transplanted from Conetainers between 5 and 14 January 1999 using a 2.5-mm soil corer to dig holes. Seedlings were planted in a 12×12 grid totaling 144 individuals per plot (Corbin & D'Antonio in press). Each plant was separated from its neighbors by 12 cm. The location of the species neighborhoods within each plot's grid was determined by randomly selecting grid location so that each species had the same number of individuals per plot. Plots were weeded of dicots and non-target grasses three times each year to maintain species composition and density.

We randomly selected six of the 14 plots to receive sawdust amendments, leaving eight plots that did not receive sawdust amendments. All plots were raked (top 2–4 cm) between 7 and 12 December 1998. We expected that frequent applications of sawdust would be more effective than a single large dose in influencing soil N cycling (Alpert & Maron 2000). Sawdust additions of $200 \, \text{g/m}^2$ were repeated in February (immediately before peak vegetation growth) and April 1999. Additions in the 1999–2000 growing season were performed in November 1999 (1 week after the first significant rains of the season), March 2000, and April 2000 at similar rates as in the previous growing season. All sawdust additions after the December 1998 application were cast onto the soil surface, rather than raked, so as to minimize the disturbance of the vegetation and soil matrix. The sawdust in the first season was a hardwood mixture obtained from a local lumber supply center; the following season the sawdust was obtained at a furniture-making store that used only maple wood (*Acer* sp.). Sawdust from both sources was finely textured and was observed to become well mixed into the top 10 cm of the soil during the experiment, though this effect was not quantified.

Plant Growth

Aboveground biomass of annual grasses was destructively sampled at peak biomass in Spring 1999 and 2000. All

Table 3. Treatments and initial planting densities (seeds or seedlings/2.25 m^2).

Treatment	Avena Seeds	Bromus Seeds	Vulpia Seeds	Native Perennial Seedlings	Exotic Perennial Seedlings
Annual only	3,400	1,750	9,000	0	0
Native perennial	0	0	0	144	0
Exotic perennial	0	0	0	0	144
Annual and native perennial	3,400	1,750	9,000	144	0
Exotic perennial and native perennial	0	0	0	72	72

Exotic annual seed densities were chosen to fall within the range reported by Heady (1956) for California grasslands.

aboveground vegetation was clipped in three randomly selected 0.25×0.25–m subsamples in each plot and separated by species. After drying ($60°$ C) to constant mass, each sample was weighed and returned to appropriate plots to decompose.

Aboveground biomass of perennial grasses was sampled twice each season using non-destructive methods. In the first season biomass was sampled 1 month after transplanting (March 1999) and in July 1999. Measurements were repeated in the fall (October 1999) and early summer (June 2000) of the second season to coincide with the minimum and maximum plant sizes, respectively. The basal diameter, height, and the number of flowering culms (where present) of 32 perennial grasses in each plot were sampled at each date. Allometric relationships between the three measures of plant size and aboveground biomass (clipped to <1 cm height) were constructed for each species by harvesting 29–45 individuals of each species representing a range of plant sizes (*A. oregonensis*: $n = 36$, $r^2 = 0.92$; *F. arundinacea*: $n = 32$, $r^2 = 0.92$; *F. rubra*: $n = 45$, $r^2 = 0.95$; *H. lanatus*: $n = 29$, $r^2 = 0.68$; *N. pulchra*: $n = 36$, $r^2 = 0.85$; *P. aquatica*: $n = 26$, $r^2 = 0.85$) (Corbin & D'Antonio in press). Each species' relationship between plant size and aboveground biomass was found to vary over time, so separate allometric equations were used in each growing season. Growth each season was calculated as the difference between each plant's biomass in the early summer and its biomass in March or October 1999.

Soil Analyses

Soil was analyzed for extractable ammonium and nitrate and net N mineralization in March, May, October, and November 1999 and in April 2000 to determine the impact of sawdust addition on soil mineral N. At each sampling period three 10 cm-deep $\times$ 2 cm-wide cores were collected from each plot, bulked, and sieved (<2 mm). One subsample of soil (10 g) was collected from each sample and immediately extracted with 50 mL of 2.0 M KCl for the determination of extractable ammonium and nitrate. Another soil sample was incubated in capped polyethylene vials at field moisture for 7 days at $25°$ C. The incubated samples were extracted with KCl as above. An additional subsample was weighed and dried overnight at >100° C for gravimetric water content (GWC) correction (calculated as [wet − dry]/ dry). At the time of the November 1999 and April 2000 sampling, additional subsamples of soil (10 g) were analyzed for microbial biomass N using the chloroform-fumigation extraction method (Brookes et al. 1985). One subsample was immediately extracted with 40 mg of 0.5M K_2SO_4 for determination of initial extractable N. The other subsample was fumigated with chloroform for 5 days. The fumigated subsamples were then extracted with K_2SO_4 as above. Organic N in the K_2SO_4 extracts was converted to NO_3-N in a sulfuric–salicylic acid Kjeldahl digestion (Howarth & Paul 1994).

Ammonium and nitrate concentrations in all extracts were measured using a Lachat flow-injection autoanalyzer at UC Berkeley, then converted to microgram of NO_3 and NH_4/g soil using GWC-corrected soil weights. Net mineralization of N was calculated as extractable nitrate + ammonium in the incubated sample minus extractable nitrate + ammonium in the initial extracts. Net nitrification was calculated as extractable nitrate in the incubated sample minus extractable nitrate in the initial extracts.

Statistical Analyses

The effect of sawdust addition on extractable ammonium and nitrate concentrations, net N mineralization rates, and GWC was tested using repeated measures ANOVA (SAS Institute 2000). The model used included Block, Sawdust, and Time, and the interaction between Sawdust and Time. The effects of Time and Sawdust $\times$ Time were analyzed with MANOVA using Roy's greatest root (Scheiner 1993). Where the analysis indicated different main effects in different time periods (i.e., significant Sawdust–Time interactions), ANOVA was run separately for each sample period. GWC was log transformed to meet the assumptions of ANOVA. The effects of the competition treatments and sawdust addition on the growth of each species were tested using ANOVA with a model including Block, Competition, Sawdust, and a Competition–Sawdust interaction. Native species responses to exotic annual and exotic perennial species were tested separately. Native biomass in June 2000 was also analyzed using ANOVA. The growth and biomass of each species were log transformed to meet the assumptions of ANOVA.

Results

Soil Responses to Sawdust Addition

Repeated measures ANOVA revealed significantly higher extractable ammonium levels in sawdust-amended plots ($F_{[1,58]} = 6.39$; $p < 0.02$) (Fig. 1). However, when the repeated measures ANOVA was performed excluding October 1999 (the only individual time in which extractable ammonium concentrations were significantly different between sawdust-amended and non-sawdust-amended plots (ANOVA: October 1999 $F_{[1,58]} = 14.32$, $p < 0.001$; all other sample times, $p > 0.1$), the effect of sawdust on ammonium concentrations was no longer significant. There was no effect of sawdust on extractable nitrate concentrations. Sawdust addition did decrease net N mineralization (repeated measures ANOVA: $F_{[1,58]} = 6.30$, $p < 0.02$) and net nitrification (repeated measures ANOVA: $F_{[1,58]} = 8.65$, $p < 0.01$), as we had predicted, though April 2000 was the only sample period in which either net N mineralization (ANOVA: $F_{[1,58]} = 44.94$, $p < 0.001$) or net nitrification (ANOVA: $F_{[1,58]} = 74.20$, $p < 0.001$) were significantly different among treatments (Fig. 1). As with the ammonium pool sizes, when this single date was excluded
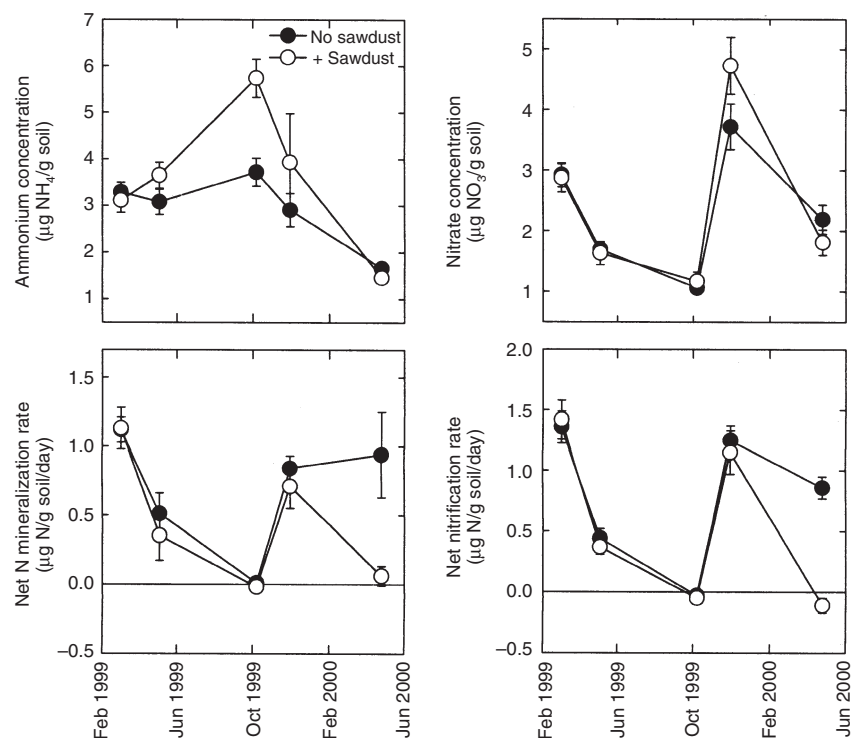
Figure 1. Extractable ammonium and nitrate concentrations, net nitrogen (N) mineralization rate, and net nitrification rate in unamended and sawdust-amended plots. Points represent mean ± 1 SE.

from the repeated measures ANOVA, the effect of sawdust on net N mineralization and net nitrification was not significant.

Microbial biomass N was significantly higher in sawdust-amended plots than non-sawdust plots in November 1999 (0.080 ± 0.003 versus $0.031 \pm 0.003 \, \mu g$ N/g soil [mean ± SE] and April 2000 (0.095 ± 0.005 versus $0.041 \pm 0.004 \, \mu g$ N/g soil) (repeated measures ANOVA: $F_{[1,58]} = 10.09$, $p < 0.01$). GWC was not significantly different in sawdust-amended plots as compared with non-sawdust-amended plots (repeated measures ANOVA: $F_{[1,58]} = 1.86$, $p > 0.15$).

Plant Responses to Sawdust Addition

The aboveground growth in the first growing season of all the three native species was negatively affected by competition with exotic annual species (Table 4; Fig. 2a). The effect of sawdust on one of the native species, *Nassella pulchra*, in that year was dependent on the presence or absence of annual species. When grown in the absence of annual competitors, sawdust had a negative effect on *N. pulchra*. When annuals were present, *N. pulchra* growth was greater with sawdust addition than without (annuals–sawdust interaction) (Table 4). Growth of one other native species, *Festuca rubra*, showed a trend toward the same pattern (Table 4). Competition with annual species reduced growth of *Agrostis oregonensis* and *F. rubra* in the second growing season (Fig. 2b), but any advantage

that sawdust may have provided for species competing with exotic annual species was no longer detectable: ANOVA revealed no significant interactions between sawdust and competition with annual grasses (Table 4). Furthermore none of the native species' aboveground biomass at the end of the 2-year experiment was significantly different between sawdust-amended plots and plots that did not receive sawdust ($p > 0.1$).

Competition with exotic perennials reduced the growth of all three native species in 1999, but there was no significant effect of exotic perennials on native growth in the second growing season (Table 4; Fig. 2). There was also no significant interaction between exotic perennial competition and sawdust for any of the native species in either season.

Among the exotic annual grasses, only *Vulpia myuros* was slightly affected by competition with native grasses in the first growing season, when its aboveground biomass was significantly lower with competition from native species (Fig. 3a). In contrast native species decreased annual grass production in the second season by over 50%, with all species showing significant declines (Fig. 3b). In neither season did sawdust addition influence the production of the three annual species or the total annual grass production.

The presence of native species did not reduce the growth of exotic perennial grasses in either year. In fact, *Festuca arundinacea* appeared to grow better with native

Table 4. ANOVA of effect of competition (with exotic annual and perennial grasses) and sawdust addition on native perennial grass growth in (A) 1998–1999 growing season and (B) 1999–2000 growing season.

	Agrostis		*Festuca rubra*		*Nassella*	
Source	$F_{[1,23]}$	p	$F_{[1,23]}$	p	$F_{[1,23]}$	p
(A) 1999						
Annuals	**19.24**	**0.0002**	**36.15**	**0.0001**	**18.19**	**0.0003**
Sawdust	0.40	0.5	0.72	0.4	1.31	0.3
Annuals × sawdust	0.11	0.7	3.10	0.092	**6.28**	**0.02**
Exotic perennials	**4.69**	**0.04**	**15.72**	**0.0006**	**3.90**	**0.06**
Sawdust	0.14	0.7	0.20	0.7	**3.69**	**0.07**
Exotic perennials × sawdust	0.83	0.4	0.03	0.9	1.87	0.2
(B) 2000						
Annuals	**22.64**	**0.0001**	**14.87**	**0.0008**	0.91	0.4
Sawdust	0.08	0.8	0.04	0.8	0.99	0.3
Annuals × sawdust	0.92	0.4	0.08	0.8	0.01	0.9
Exotic perennials	0.79	0.4	0.48	0.5	1.68	0.2
Sawdust	0.69	0.4	0.58	0.5	2.64	0.1
Exotic perennials × sawdust	0.01	0.9	0.71	0.4	0.17	0.7

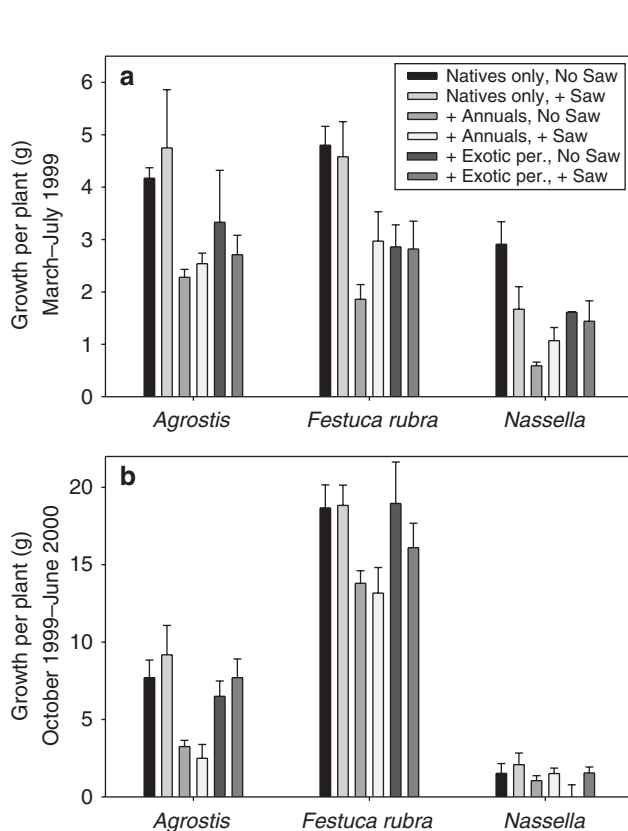Numbers in bold are significant.

Figure 2. Growth of each native perennial grass in 1999 (a) and 2000 (b). Competition treatments: native perennials only, natives with exotic annual grasses, and natives with exotic perennial grasses. Each competition treatment was crossed with sawdust addition. Bars represent mean ± 1 SE (See Table 4 for ANOVA).
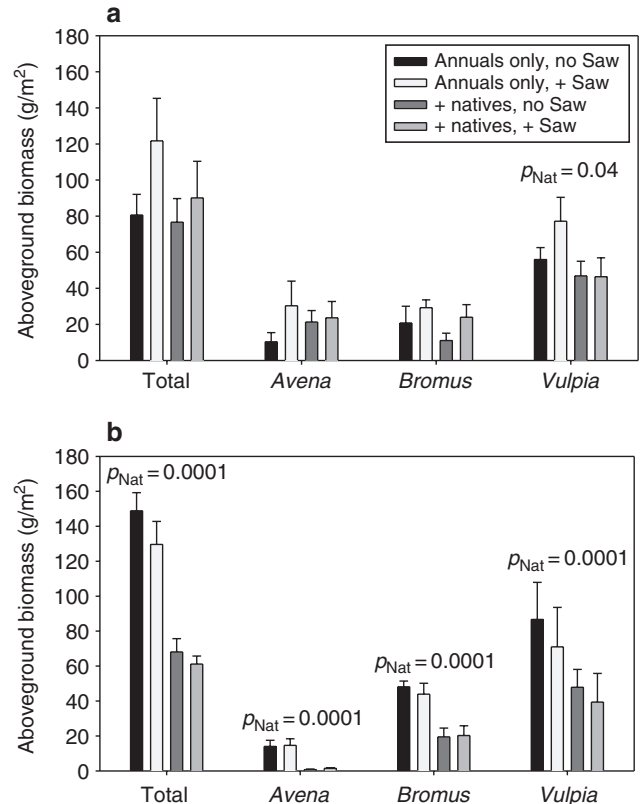

Figure 3. Biomass of each exotic annual species and total annual biomass in 1999 (a) and 2000 (b). Competition treatments: exotic annuals only and annuals with native perennial grasses. Bars represent mean ± 1 SE. Significant p values from ANOVA (model: biomass = block + native competition (Nat) + sawdust (Saw) + Nat × Saw) for each species are indicated.
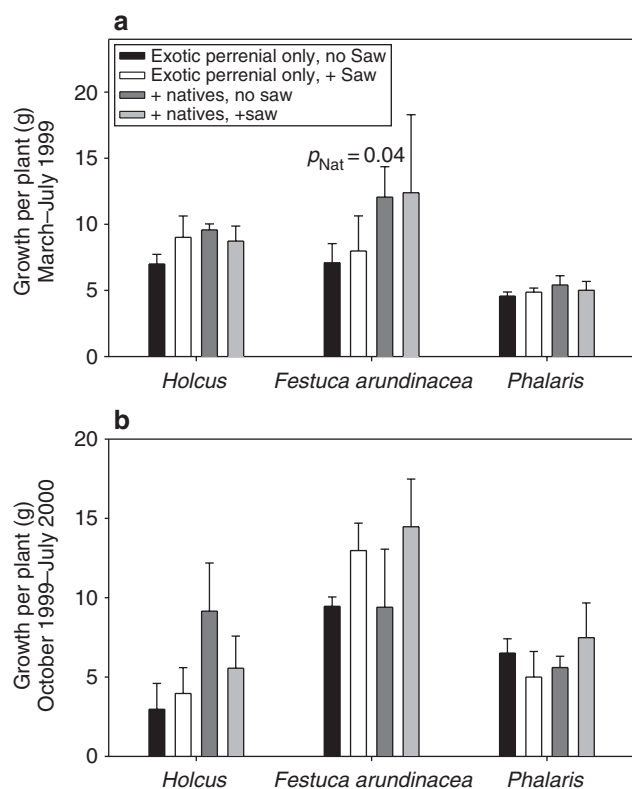
Figure 4. Growth of each exotic perennial grass in 1999 (a) and 2000 (b). Competition treatments: exotic perennials only and exotic perennials with native perennial grasses. Bars represent mean ± 1 SE. Significant *p* values from ANOVA (model: biomass = block + native competition

(Nat) + sawdust (Saw) + Nat × Saw) for each species are indicated.

perennial grasses than with other exotic perennial grasses in 1999 (Fig. 4). Growth of exotic perennials was not affected by sawdust addition in either growing season.

Discussion

In the first year, when natives were grown with exotic annual competitors, growth of *N. pulchra* and, to a lesser extent, *F. rubra* was greater in plots that received sawdust addition than in plots that did not receive sawdust addition. These results were consistent with our prediction that sawdust addition would benefit native species, particularly those competing with exotic annual grasses. In the second year, however, we did not find evidence that sawdust addition increased the competitiveness of natives. Instead, native species substantially reduced annual grass production regardless of whether sawdust was added or not. Sawdust addition did not influence the growth of native species competing with exotic perennial grasses in either growing season. At the end of the experiment the aboveground biomass of native species receiving sawdust addition was not greater than the biomass of natives that did not receive sawdust. We conclude therefore that the addition of sawdust as a tool in the restoration of native species

in our system, where target individuals were planted as seedlings and survival was high in all treatments, provided no significant benefit to natives over a 2-year period.

By the second growing season, sawdust additions had stimulated microbial immobilization of N, consistent with the findings of Torok et al. (2000), and had reduced rates of net N mineralization. We did not find evidence that sawdust addition decreased N availability or N cycling rates in the first growing season. Addition of sucrose and/ or sawdust has frequently been shown to reduce soil inorganic N levels in other systems (Zink & Allen 1998; Reever Morghan & Seastedt 1999; Blumenthal et al. 2003), though the efficacy of sawdust and sucrose may be dependent on initial soil fertility, quantity of C added, and the form of C added (e.g., sucrose versus sawdust) (Blumenthal et al. 2003). It is possible that the N enrichment from dying lupines in our coastal prairie site (Table 2) was high enough that the rate of sawdust addition was not sufficient to induce N limitation until the second year.

We did not find support for the expected mechanism by which lower N would impact native vegetation, namely by reducing competitors' production and indirectly benefiting natives' growth. Aboveground production of exotic annual or exotic perennial grasses was not affected by sawdust in either season and hence it is difficult to explain the impact of sawdust on natives competing with annual species in the first growing season. The effect of sawdust on one of the natives, *N. pulchra*, growing without exotic competitors was negative, but otherwise there was no evidence that sawdust negatively affected native growth. The possibility remains that shifting allocation to above- versus below-ground structures may have masked significant differences in the productivity of exotic annuals or exotic perennial species between plots receiving sawdust and plots that did not. It is, however, unlikely that sawdust addition had a direct facilitative effect on native growth, because sawdust addition did not increase the growth of natives in treatments without competitors.

Sucrose and sawdust addition to other systems has produced more lasting benefits to native species than we found. Paschke et al. (2000) and McLendon & Redente (1992) found that sucrose addition to two successional shortgrass steppe ecosystems favored slower growing perennial species over faster growing annual grasses such as *Bromus tectorum* (cheatgrass) and annual forbs. However sucrose is expensive relative to other C sources such as sawdust and therefore is less practical as a restoration tool (Reever Morghan & Seastedt 1999). Zink & Allen (1998) reported improved growth and survival of hand-planted *Artemisia californica* (California sagebrush) seedlings after 2 years of pine bark and oat straw addition to a California coastal sage scrub habitat. Sawdust addition (with or without sucrose addition) has been shown to negatively affect exotic competitors but has been less successful in benefiting native species (Wilson & Gerry 1995; Reever Morghan & Seastedt 1999; Alpert & Maron 2000;

Cione et al. 2002). However the ability to increase native growth may be a function of the quantity of sawdust added relative to site fertility. Blumenthal et al. (2003) reported decreasing availability of NO_3 and weedy biomass and increasing biomass of native species as the quantity of sucrose and sawdust input increased. They suggested, based on their data and a review of previous studies, that a threshold level of C likely must be added before decreases in soil N or increased competitiveness of native species is detected (Blumenthal et al. 2003). We cannot discount the possibility that greater quantities of sawdust addition, or a longer duration of sawdust application, may have led to different results in our study. Further investigations should examine whether the quantity of sucrose and/or sawdust that is added influences the outcome in other systems, as well.

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