

SOIL CARBON ADDITION CONTROLS WEEDS AND FACILITATES PRAIRIE RESTORATION

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Abstract. Soil nitrogen enrichment and consequent vigorous weed growth are thought to hinder the restoration of tallgrass prairie. Adding carbon to the soil may facilitate prairie restoration by inducing immobilization of plant-available nitrogen. Early attempts to use this method, however, have had mixed results. Success of C addition depends on three conditions: weeds must suppress prairie species in the absence of C addition, weeds must be nitrophilic relative to prairie species, and C addition must result in a large enough decrease in N to alter the balance of competition among weeds and prairie species. We examined these conditions by comparing productivity of 10 weeds and 11 tallgrass prairie species under 14 levels of C addition, ranging from 84 to 3346 g C/m². Carbon was tilled into the soil prior to planting. To control for non-N effects of C addition, N was added to a subset of plots. Relative to untreated plots, the highest level of C addition resulted in an 86% decrease in available NO₃-N, a 14× increase in early season light availability, a 54% decrease in weed biomass, and a sevenfold increase in prairie biomass. Nitrogen addition significantly reduced or reversed all of these effects. Significant species-specific responses to C addition included decreased biomass for six annual weeds and increased biomass for six prairie species, one annual weed, and three perennial weeds. These results suggest that C addition may be a useful tool for restoring N-limited plant communities.

Key words: carbon addition; carbon:nitrogen ratio; invasion, biological; nitrogen immobilization; prairie restoration; sawdust; sucrose; weed competition and control.

INTRODUCTION

The outcome of competition between native vegetation and weeds (undesirable, often exotic species) may often depend on N availability, with high levels of N increasing weed invasion and/or decreasing the success of native species (Huenneke et al. 1990, Bobbink et al. 1998, Smith et al. 1999). High N availability may be particularly problematic in the restoration of native plant communities, where prolific weed growth can delay or even preclude the reestablishment of native species (NRC 1992, Packard and Mutel 1997). For this reason, C addition has been suggested as a method for immobilizing plant-available N and increasing the success of native species (Morgan 1994). By increasing the soil C:N ratio, additions of organic C would be expected to induce soil microbes to immobilize available nitrogen. Decreased N, in turn, might reduce growth of nitrophilic weeds, thereby releasing native species from competitive suppression.

Results of early C addition experiments, however, have been decidedly mixed. Of the nine published stud-

ies we found, only two reported a significant increase in the success of native species with C addition. Zinc and Allen (1998) found that the addition of pine bark to the soil surface increased fungal activity, decreased available soil nitrate, and increased the establishment of the native shrub *Artemisia californica*. They suggest that N immobilization increased the ability of *A. californica* to compete against exotic annual weeds. Similarly, in a greenhouse study of two wetland species, sawdust addition increased biomass of the native sedge *Carex hystericina* by decreasing competition from the invasive grass *Phalaris arundinacea* (Perry 2001). C addition has been found to accelerate succession in both sagebrush (*Artemisia tridentata*) communities and shortgrass steppe in Colorado; however observed increases in native late-seral species were not significant (McLendon and Redente 1992, Paschke et al. 2000). A larger number of studies have found that C addition decreases the success of weeds but does not affect the growth of native species. This result has been observed in tallgrass prairie in Manitoba, mixedgrass prairie and shortgrass steppe in Colorado, and coastal grasslands in California (Morgan 1994, Reever Morghan and Seastedt 1999, Alpert and Maron 2000, Paschke et al. 2000). Finally, two studies reported little or no significant effect of C addition on either weeds or native species (Wilson and Gerry 1995, Hopkins 1998).

Given these varied results, particularly the common lack of response from native species, does C addition

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hold promise as method for facilitating native species establishment and growth? To answer this question it is necessary to examine the assumptions underlying the use of C addition as a management tool. For C addition to succeed, at least three conditions must be met: weeds must suppress native species in the absence of C addition, weeds must be nitrophilic relative to native species, and C addition must result in a decrease in available N sufficient in magnitude and duration to alter the balance of competition among native species and weeds.

With regard to the first condition, there are many instances in which weeds outcompete native species (Williamson 1996:137–143). If, however, C addition reduces the negative effect of weeds on prairie species but also suppresses native species directly, the net effect of C addition on native species would depend on the relative magnitude of these two processes. In such situations the facilitation of native species by C addition may depend on the presence of strong competitive interactions between weeds and native species.

Whether the second condition, that weeds are nitrophilic relative to native species, is met in any given situation would be expected to depend on the evolutionary history of both the weeds and the native species. Many plant communities were historically limited by N (Vitousek et al. 1997), and many species from N-limited plant communities compete effectively only when available N is low (Chapin 1980, Bobbink et al. 1998, Smith et al. 1999). Weeds have historically been thought of as plants adapted to disturbance, characterized by fast growth and abundant seed production (Baker 1965). Because this strategy depends on high availability of soil resources (Chapin 1980), weeds should compete well in high-N but not low-N habitats. Many weeds that are problematic in restoration, which often involves disturbance, would be expected to fit this definition. Although invaders of established plant communities exhibit more varied strategies (Crawley et al. 1989, Thompson et al. 1995, Daehler 1998), given the fact that many invasions occur in the context of N-enriched plant communities (Bobbink et al. 1998, Smith et al. 1999), one might also expect many of these species to be relatively nitrophilic.

The third assumption, a sufficiently large and lasting decrease in soil N, depends on initial soil conditions and the quantity of added C that becomes available over a given time period. It is well established that soil microbes will immobilize plant-available N given a sufficiently large pool of C (Tisdale et al. 1985:122–125). It is thus not surprising that many of the C addition studies, including one that found little response of vegetation to C addition (Wilson and Gerry 1995), observed decreases in soil N availability with C addition (Zink and Allen 1998, Reever Morghan and Seastedt 1999, Perry 2001). What is not known is the extent to which N must be lowered in order to affect the outcome of competition, and the quantity of C needed to achieve

that reduction. In the above studies there is no clear relationship between the quantity of C used and the observation of reduced N availability. This lack of relationship could be attributed to differences among studies in the availability of the C added, site fertility, or power to detect differences in N. There was, however, an apparent relationship between quantity of high-C organic matter (bark, sawdust, or sucrose) and the observation of plant responses. Organic matter addition rates in studies finding strong responses by vegetation ranged from 1500 to 7250 g organic matter per square meter (Reever et al. 1999, Albert and Maron 2000, Perry 2001) while those in studies finding little or no response by vegetation ranged from 72 to 800 g organic matter per square meter (McClendon and Redente 1992, Wilson and Gerry 1995, Hopkins 1998). This pattern suggests that, in certain studies, levels of C may have been too low to alleviate competitive suppression of native species.

Our primary objective in this study was to test whether C addition could facilitate native species' success given sufficient competition from weeds and sufficient quantities of added C. We also sought to determine whether responses of plant resources and vegetation to C addition were mediated by N immobilization.

METHODS

Study site

We conducted the experiment at the University of Minnesota Agricultural Experiment Station, St. Paul, Minnesota. In the five years prior to the study, the field was planted, respectively, to *Medicago sativa* L., *Zea mays* L., *Hordeum vulgare* L., *Glycine max* (L.) Merr., and *Z. mays*. The soil is a Waukegan silt loam with 2.19% C and 0.21% N in the topsoil, a C:N ratio of 10.4:1.

Experimental design

To examine the effect of C on plant growth and establishment, we used four replicates each of 14 levels of C addition (72 "C addition" plots). To control for non-N effects of C addition, we added N (in proportion to the quantity of C added) to an additional four replicates of five of the 14 levels of C addition (20 "C + N addition plots"). Plots were 2 × 2 m, separated by 1-m corridors (which served as buffers and walkways), and arranged in two randomized complete blocks. Following the addition of C and N, we seeded plots and corridors with both weed and prairie species.

Carbon/nitrogen addition

We added carbon as sucrose and sawdust (primarily pine and aspen; Mid-North Sawdust, Albertville, Minnesota). Each level of C addition comprised 5.9% sucrose and 94.1% sawdust. Sucrose (42% C) supplied readily available C, but was added in limited quantity to prevent fermentation. Sawdust (39% C and 0.21% N) supplied more recalcitrant C to increase the duration

of N immobilization. In order to examine both very low and very high levels of C addition, we increased the quantity of C exponentially. Total mass of C added per unit area for levels 0–13, respectively, was 0, 84, 133, 210, 333, 529, 666, 839, 1057, 1330, 1675, 2110, 2657, and 3346 g C/m². We applied sawdust and sucrose to the soil surface and tilled them in to a depth of 20 cm in late June of 1999.

The purpose of the N addition treatment was to counter the N-immobilization effect of C addition, and thereby control for effects of C other than N immobilization. We therefore added N only to plots that also received C addition, attempting to add enough N to replace the N anticipated to be lost due to immobilization. For this calculation, we assumed that sucrose and sawdust contained ~42% and 8% readily available C, respectively. To carbon levels 0, 3, 5, 9, and 13 we added 0, 8.5, 21.5, 54.1, and 136.0 g N/m², as a combination of readily available 34-0-0 ammonium nitrate fertilizer (10% of added N), and slow release, 40-0-0 Meister fertilizer (90% of added N; Chisso, Japan). We spread N on the soil surface and raked it into the soil within 2 wk of carbon addition. Because N addition plots were found to have high levels of available N relative to untreated control plots in the fall of 1999, we did not add additional fertilizer in 2000.

Study species/seed addition

We seeded a mix of prairie species that included (by mass), 35% *Andropogon gerardii* Vitm. (big bluestem), 25% *Schizachyrium scoparium* (Michx.) Nash (little bluestem), 25% *Sorghastrum nutans* (L.) Nash (Indian grass), 7.5% *Bouteloua curtipendula* (Michx.) Torr (side-oats gramma grass), 4% *Elymus canadensis* L. (Canada wild rye), and 3.5% *Panicum virgatum* L. (switch grass). Prairie forbs added were *Heliopsis helianthoides* (L.) Sweet (common ox-eye), *Liatris pycnostachya* Michx. (tall blazing star), *Monarda fistulosa* L. (wild bergamot), *Rattibida pinnata* (Vent.) Barnhart (yellow coneflower), and *Solidago rigida* L. (stiff goldenrod). Prairie seed (provided by Prairie Restorations, Princeton, Minnesota) included only local genotypes.

In order to create a uniform seedbank, which would allow us to measure the effect of C addition on individual species, we added weed species as well as prairie species and excluded extant weed species from the experiment. A limitation of this approach is that it did not allow us to measure the effects C addition on the presence of established perennial weeds or locally adapted species and genotypes. In particular, our results are unlikely to be generalizable to established perennial weeds, which might be relatively unaffected by C addition due to the presence of roots below the C addition zone. We added a combination of annual, biennial, and perennial weeds, all of which are listed on the Minnesota primary or secondary noxious weed lists (Durgan 1998): *Cirsium arvense* (L.) Scop. (Canada thistle), *Convolvulus arvensis* L. (field bindweed), *Eriochloa*

villosa (Thunb.) Kunth. (woolly cupgrass), *Hibiscus trionum* L. (Venice mallow), *Kochia scoparia* (L.) Schrader (kochia), *Silene latifolia* Poir. (white cockle), *Polygonum convolvulus* L. (wild buckwheat), *Setaria faberi* R. Herrm. (giant foxtail), *Sinapis arvensis* L. (wild mustard), and *Solanum nigrum* L. (black nightshade). At least two of these species are commonly problematic in prairie restoration: *C. arvense* and *S. faberi*. Weed seed (purchased from Valley Seed Service, Fresno, California, and V&J Seed Farms, Woodstock, Illinois) came from a variety of locations around the U.S. Seed of *C. arvense* was collected locally.

We mixed 3 g/m² of weed seed (0.3 g/m² of each species), and 3 g/m² of prairie grass seed with ~500 mL of perlite and 500 mL sand, and hand broadcasted the mixture into plots in early July 1999. To bury seed and increase seed-soil contact, we raked the soil lightly and packed it with a manual roller (1 m wide, filled with ~49 L of water). We then seeded prairie forbs (0.125 g seed/m² for each species) mixed with ~500 mL sand and 500 mL perlite, over the raked, packed soil. To avoid edge effects, we seeded corridors using the same methods, and the same densities of weed and prairie grass seed; to reduce expense, we did not add prairie forbs to corridors.

Study maintenance

Prior to the establishment of a vegetative cover, a severe thunderstorm moved the relatively buoyant slow release urea fertilizer among plots. This resulted in the loss of fertilizer from some plots, and the addition to plots which previously had none. To correct for this problem, we eliminated plots that gained or lost large quantities of fertilizer, and removed fertilizer granules (which were easy to see and collect) from plots that gained small quantities of fertilizer. A total of 12 plots were eliminated from the experiment. Treatments from which plots were eliminated (and numbers of plots eliminated) included C addition levels 0 (1), 1 (1), 7 (1), 9 (2), 10 (1), 11 (1), and C + N addition levels 0 (1), 5 (3), and 9 (1). To prevent further movement of fertilizer among plots, we dug 10 cm deep ditches in the center of the corridors.

Early in the season each year, we hand weeded species that were not part of the experiment (primarily *Chenopodium album* L.). To avoid influencing measurements of total weed biomass, we did not remove resident weeds emerging later in the season. We harvested these weeds with the experiment and included them in total weed biomass.

Data collection

Biomass.—To avoid edge effects, we harvested biomass only from the center of each 2 × 2 m plot. We included a 0.5-m buffer in the direction of tillage (north and south sides) and a 0.25-m buffer on the east/west sides. In September 1999, we harvested a 1 × 0.75 m subplot on the west side of each plot. In September

2000, we harvested a 1×0.5 m subplot on the east side of each plot. The smaller harvest area in 2000 resulted from the inclusion of an additional 0.25-m buffer between the area harvested in 1999 and that harvested in 2000. In each year, all plants were cut within 1 cm of the soil surface, separated by species, counted, dried at 60°C for 5 d, and weighed.

Light.—We measured light penetration (below canopy light intensity divided by above canopy light intensity) with a LI-COR Quantum line sensor (LI-COR, Lincoln, Nebraska, model LI-191 SA) and, for above canopy measurements only, a LI-COR Quantum point sensor (model LI-190 SA). Both sensors measured photosynthetic photon flux density over a period of 5 s. We averaged three below-canopy measurements to obtain below-canopy light intensity for each plot. We took all measurements within 2 h of solar noon on clear or mostly clear days.

Nitrogen and water.—We sampled available NO_3 and NH_4 45 and 60 d after C addition (23 and 38 d after seeding) in 1999 and in late June 2000. The resulting NO_3 and NH_4 concentrations are strongly affected by rates of loss (uptake, leaching) as well as supply (which is of primary interest to this experiment), and do not represent the overall quantity of N available to plants. Nevertheless, comparisons among C addition treatments can provide a qualitative measure of the effect of C addition on plant-available N, for the specific times that we sampled. We collected and mixed three 1.9 cm diameter, 15 cm deep soil cores from the buffer areas surrounding the biomass collection subplots. We extracted NO_3 and NH_4 with 2 mol/L KCl. We added 3 g of soil to 30 mL of KCl, shook the mixture for 1 h, and centrifuged it at $12\,500 \times 9.80665$ m/s² for 10 min. We then stored the supernatant at 8°C for several days before analysis for NO_3 and NH_4 in a flow injection analyzer (Zellweger Analytics, Milwaukee, Wisconsin). We determined soil water content by weighing the portion of soil not used for extraction before and after it was dried at 105°C for 10 d. Initial C and N contents of soil and sawdust were determined via combustion using a Leco CR12 analyzer (for total C) and a Leco FP528 analyzer (for total N) (Leco, St. Joseph, Michigan).

Data analysis

We analyzed data with Arc Version 1.03 (Cook and Weisberg 1999). We tested all data for significant heteroscedasticity and lack of fit, and used power transformations where necessary to reduce heteroscedasticity and nonlinearity. We examined effects of C addition separately for +N and -N plots by regressing response variables on the quantity of C added. To discover whether N addition significantly altered effects of C addition, we also regressed response variables on the quantity of C added with the presence or absence of N addition as a categorical predictor. Because control plots (no C addition) were common to +N and -N

treatments, we tested differences in slopes between +N and -N treatments assuming equal intercepts (Cook and Weisberg 1999). To simplify interpretation of graphs, we present data on untransformed axes, with regression lines backtransformed to fit the axes. We use log-transformed y-axes where necessary to display patterns on different scales within a single graph.

RESULTS

Soil nitrogen

Carbon addition significantly reduced available NO_3 at all sampling dates (Fig. 1). Because C addition also reduced plant biomass (and presumably NO_3 uptake), these results probably underestimate overall differences in plant-available NO_3 . Nitrate concentrations decreased at all C addition levels between 5 August and 10 September in 1999, and were once again low in June 2000. Nitrogen addition reduced (August 1999 and June 2000) or reversed (September 1999) the effect of C addition on NO_3 concentrations.

In contrast to the effect on NO_3 , NH_4 concentrations were unaffected by C addition alone (Fig. 2). At all sampling dates, however, NH_4 concentrations increased when both C and N addition were applied. Differences between N addition plots and control plots (no added C or N) were very large for NO_3 concentration in August 1999, and for both NH_4 and NO_3 concentrations in September 1999. By June 2000, however, differences between concentrations of NH_4 and NO_3 in N addition and control plots were small.

Light penetration

Due to incomplete early season data in 1999, light data are presented only for 2000. Our observations suggest that patterns were qualitatively similar in the two years. Light penetration through the canopy increased with increasing C addition (Fig. 3). The increase in light was most pronounced early in the season; light availability in plots with 3346 g/m² of C addition was more than 15 times that in control plots (Fig. 3A). As the season progressed, light penetration increased at lower levels of C addition and decreased at higher levels of C addition, resulting in a small but still significant difference in light penetration by late July 2000 (Fig. 3B). Nitrogen addition eliminated the effect of C addition on light penetration at both dates.

Water

Soil water content also increased with C addition, on all three dates of measurement (Fig. 4). Nitrogen addition reduced the positive effect of C addition on water content in September 1999, but did not affect water content in August 1999 or June 2000.

Weeds

Total weed biomass decreased with C addition in both 1999 and 2000 (Fig. 5). In both years, weed biomass at the highest level of C addition was <52% that

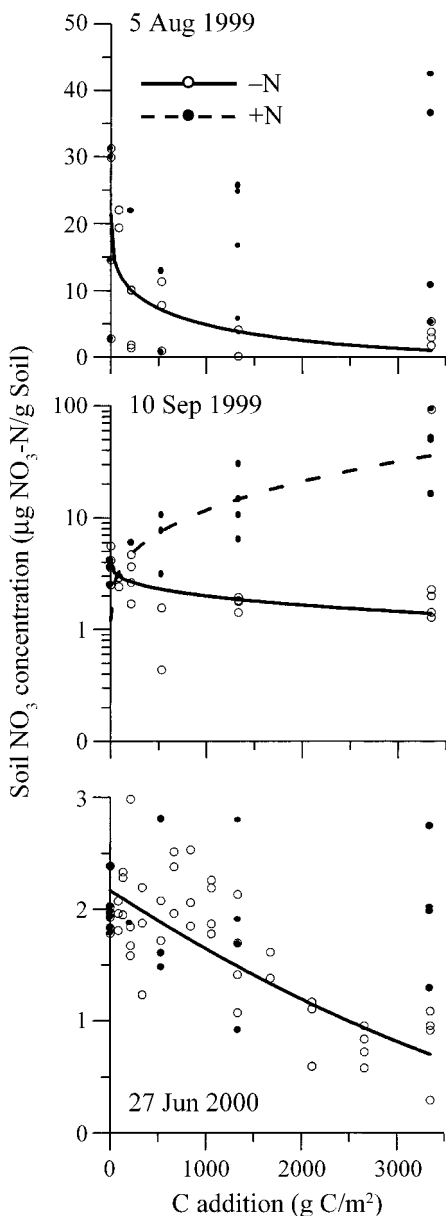


FIG. 1. Soil NO_3 concentration regressed against C addition, with N addition as a categorical predictor. Separate regressions of NO_3 concentration on +N and -N data were conducted when effects of N were significant: Aug 1999 ($P = 0.002$), Sep 1999 ($P < 0.001$), and June 2000 ($P < 0.001$). Regression lines are backtransformed from regressions conducted on transformed data and are shown for slopes significantly different from zero: Aug 1999 (-N, $P = 0.004$); Sep 1999 (-N, $P = 0.02$; +N, $P < 0.001$); Jun 2000 (-N, $P < 0.001$). Note differences in scale on y-axes, particularly the logarithmic scale used for Sep 1999. Degrees of freedom varied among analyses due to subsampling at some dates. Degrees of freedom for full, -N, and +N regressions, respectively, were 27, 17, and 12 (Aug 1999); 29, 18, and 13 (Sep 1999); and 59, 48, and 15 (Jun 2000). Transformations of carbon addition (C) and NO_3 concentration (NO_3) were $\text{C}^{0.33}$, $\text{NO}_3^{0.5}$ (Aug 1999); $\text{C}^{0.33}$, $\ln(\text{NO}_3)$ (Sep 1999); and C, $\text{NO}_3^{0.5}$ (Jun 2000).

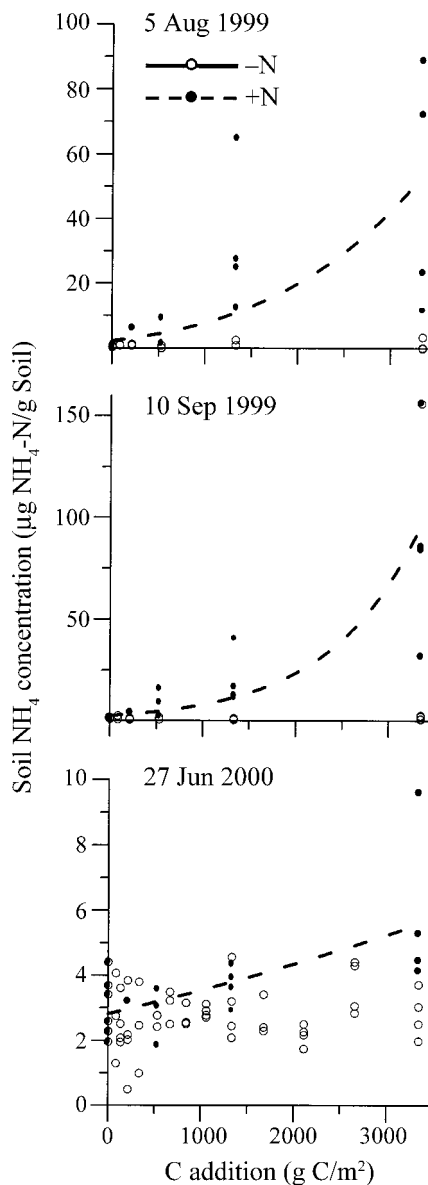


FIG. 2. Soil NH_4 concentration regressed against C addition, with N addition as a categorical predictor. Separate regressions of NH_4 concentration on +N and -N data were conducted when effects of N were significant: Aug 1999 ($P < 0.001$), Sep 1999 ($P < 0.001$), and Jun 2000 ($P = 0.001$). Regression lines are backtransformed from regressions conducted on transformed data and are shown for slopes significantly different from zero: Aug 1999 (+N, $P = 0.001$); Sep 1999 (+N, $P < 0.001$); Jun 2000 (+N, $P = 0.002$). Note differences in scale on y-axes. Degrees of freedom varied among analyses due to subsampling at some dates. Degrees of freedom for full, -N, and +N regressions, respectively, were 27, 17, and 12 (Aug 1999); 29, 18, and 13 (Sep 1999); and 59, 48, and 15 (Jun 2000). Transformations of carbon addition (C) and NH_4 concentration (NH_4) were $\text{C}^{0.33}$, $\text{NH}_4^{0.5}$ (Aug 1999); $\text{C}^{0.33}$, $\ln(\text{NH}_4)$ (Sep 1999); and C, $\text{NH}_4^{0.5}$ (Jun 2000).

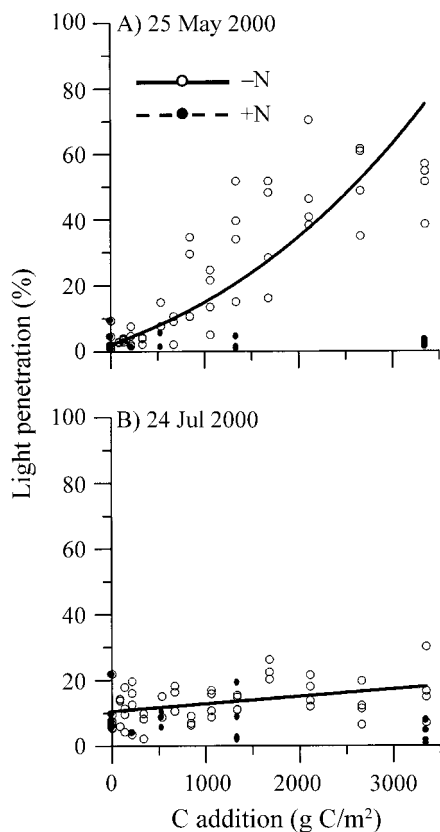


FIG. 3. Percentage light penetration (percentage of above-canopy light detected 2 cm above the soil surface) regressed against C addition, with N addition as a categorical predictor. Separate regressions of percentage light penetration on +N and -N data were conducted when effects of N were significant: May 2000 ($P < 0.001$) and Jul 2000 ($P < 0.001$). Regression lines are backtransformed from regressions conducted on transformed data and are shown for slopes significantly different from zero: May 2000 (-N, $P < 0.001$); Jul 2000 (-N, $P = 0.005$). Degrees of freedom for full, -N, and +N regressions, respectively, were 60, 49, and 15. Transformations of carbon addition (C) and percentage light penetration (L) were $C^{0.33}$, $\ln(L)$ (May 2000); C, L (Jul 2000).

of weed biomass in control plots. Weed biomass was somewhat lower in 2000 than in 1999, but weed growth was prolific in both years. The lowest total weed biomass measured in any plot in either year was 117 g/m² and the lowest percentage of plant biomass was 85%. Addition of both N and C eliminated the C addition effect in 1999 and reversed it in 2000. The difference between the two years appears to stem from lower overall weed growth in 2000 in all treatments except for the highest C + N addition treatment.

Because annual weeds made up the majority of plant biomass in both years, patterns of annual weed biomass were similar to those of total weed biomass. Annual weed biomass decreased with C addition in both years (Table 1). Nitrogen addition eliminated this effect in 1999 and reversed it in 2000. Biennial and perennial weeds exhibited the opposite pattern in both years, in-

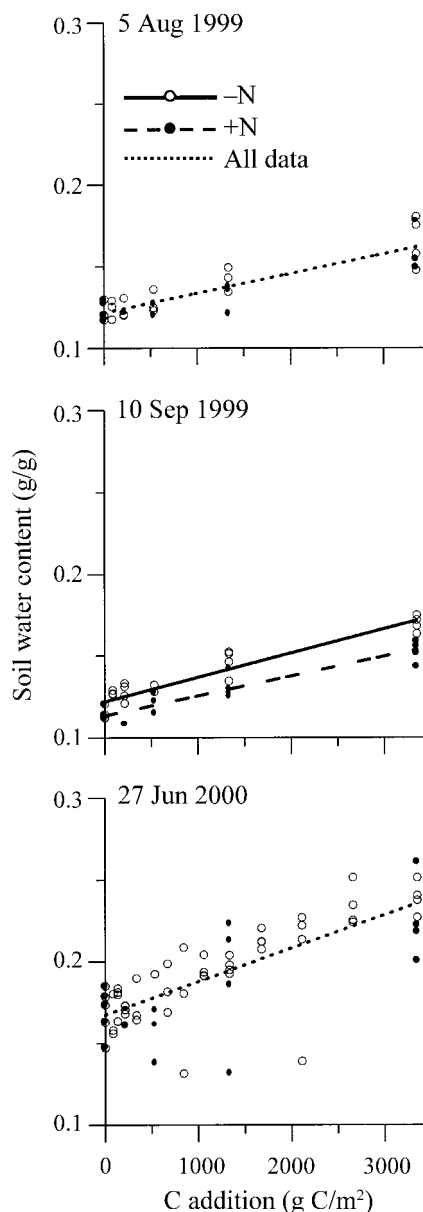


FIG. 4. Soil water content regressed against C addition, with N addition as a categorical predictor. Separate regressions of soil water content on +N and -N data were conducted when effects of N were significant: Sep 1999 ($P < 0.001$). Regression lines are shown for slopes significantly different from zero: Aug 1999 (all data, $P < 0.001$); Sep 1999 (-N, $P < 0.001$; +N, $P < 0.001$); Jun 2000 (all data, $P < 0.001$). Degrees of freedom varied among analyses due to subsampling at some dates. Degrees of freedom were 28 (Aug 1999); 29, 18, and 13 for full, -N, and +N regressions, respectively (Sep 1999); and 60 (Jun 2000).

creasing with C addition, but not with C + N addition (Table 1).

Power to detect species-specific responses of annual weeds to C and N addition was greater in 1999 than in 2000, due to the experimentally imposed seedbank. Results presented for annual species are therefore from

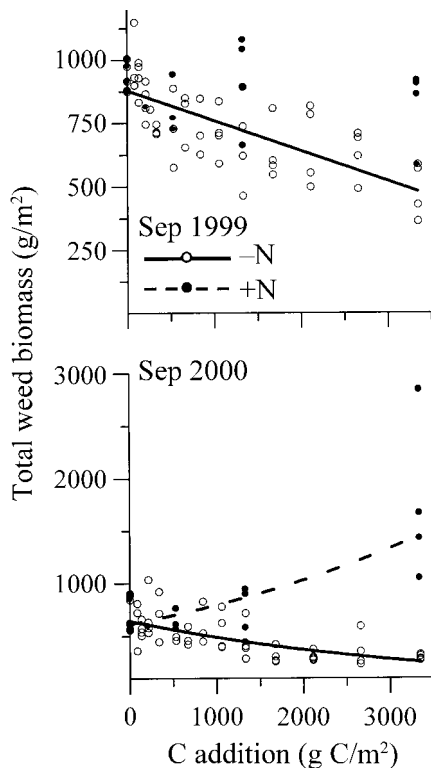


FIG. 5. Total weed biomass regressed against C addition, with N addition as a categorical predictor. Separate regressions of weed biomass on +N and -N data were conducted when effects of N were significant: Sep 1999 ($P < 0.001$) and Sep 2000 ($P < 0.001$). Regression lines are backtransformed from regressions conducted on transformed data and are shown for slopes significantly different from zero: Sep 1999 (-N, $P < 0.001$); Sep 2000 (-N, $P < 0.001$); (+N, $P < 0.001$). Note differences in scale on y-axes. Degrees of freedom for full, -N, and +N regressions, respectively, were 62, 51, and 15 (1999); 60, 49, and 15 (2000). Transformations of carbon addition (C) and weed biomass (B) were C, B (Sep 1999); C, $\ln(B)$ (Sep 2000).

1999, with the exception of results for *Polygonum convolvulus*, which germinated primarily in the second year of the experiment. Conversely, power to detect species-specific responses for perennial species was greater in 2000 than in 1999, due to the additional year of growth. Results presented for perennial species are therefore from 2000.

Biomass of six of seven annual weed species decreased with increasing C addition (Table 1). Sensitivity to C addition varied considerably within those five species, however (Fig. 6A, B). Biomass of *Solanum nigrum* and *Kochia scoparia* declined precipitously between 150 and 500 g C/m². Biomass of *Sinapis arvensis* and *P. convolvulus* declined more gradually, and that of *Setaria faberi* declined only slightly. *Eriochloa villosa*, which was observed only occasionally, showed no significant response to C addition. Of the annual weeds, only *Hibiscus trionum* increased in biomass with C addition, attaining more biomass than any other

species in the highest level of C addition. Biomass of all three biennial/perennial weed species increased with increasing C addition (Fig. 7). Biomass of *Silene latifolia*, which behaved as both a biennial and a perennial in this experiment, decreased above 2000 g C/m², however this decrease did not result in a significant lack of fit. Nitrogen addition significantly reduced or reversed the effect of C addition on biomass of all weed species except for *E. villosa*, *P. convolvulus*, and *S. arvensis* (Table 1).

Prairie species

Carbon addition facilitated prairie species establishment over the course of the experiment, increasing total prairie biomass in both years (Fig. 8). Nitrogen addition eliminated the facilitation of total prairie biomass by C addition in both years. Three of four prairie forbs were observed only occasionally, and they showed no significant patterns in response to any treatment. The biomass of all other prairie species increased with C addition (Fig. 9, Table 1). Nitrogen addition reduced or eliminated the effect of C addition for all prairie species. The quantity of C needed to facilitate establishment varied with functional group. All five C₄ prairie grasses produced little or no biomass below 1000 g C/m² (Fig. 9A). Conversely, the one C₃ prairie grass (*Elymus canadensis*) in the experiment and the one relatively abundant prairie forb (*Monarda fistulosa*) had substantial biomass at much lower levels of C addition (Fig. 9B). Among weed and prairie species that responded significantly to C addition, a significantly larger proportion of prairie species (seven of seven) than weed species (four of nine) responded positively to C addition ($\chi^2 = 6.09$, 1 df, $P = 0.014$).

DISCUSSION

In contrast to the results of many previous studies, we found that C addition greatly facilitated the growth of native species. With increasing levels of C addition we observed decreasing availability of NO₃, decreasing biomass of weeds, increasing light penetration, and increasing biomass of prairie species. Biomass of prairie species at the highest level of C addition was more than eight times that in control plots. Furthermore, adding N (in proportion to added C) reversed all of the above trends, suggesting that N immobilization accounted for the observed plant responses. Each of the three conditions needed for C addition to facilitate native species establishment—competition from weeds, relatively nitrophilic weeds, and sufficient N immobilization—appears to have been met. Below, we discuss each condition in more detail in order to explore the conditions under which C addition would and would not be expected to facilitate native species establishment.

That competition from weeds was sufficient to interfere with prairie establishment is suggested by the vigorous growth of weeds and the poor performance of prairie species. At the highest level of C addition,

TABLE 1. Transformations, *P* values, and directions of effects for regressions of annual and perennial weed biomass and individual species biomass on C and N addition in prairie restoration.

Species or group	Transformations		Significance of C and N addition effects				
	Dep. Variable	Ind. Variable	N-addition <i>P</i>	C addition without N		C addition with N	
	C = g C/m ²	B = biomass/m ²		Direction of slope	<i>P</i>	Direction of slope	<i>P</i>
Annual weeds							
Total annual weed mass 1999	C	B	<0.001	–	<0.001		NS
Total annual weed mass 2000	C	ln(B)	<0.001	–	<0.001	+	<0.001
<i>Eriochloa villosa</i>	C	ln(B)	NS		NS		NS
<i>Hibiscus trionum</i>	C	ln(B)	<0.001	+	<0.001	+	0.01
<i>Kochia scoparia</i>	C ^{0.33}	B ^{0.33}	<0.001	–	<0.001	–	0.04
<i>Polygonum convolvulus</i>	C	B ^{0.33}	NS		NS		NS
<i>Sinapis arvensis</i>	C	B		–	<0.001	–	0.004
<i>Setaria faberi</i>	C	B	<0.001	–	<0.04	+	0.003
<i>Solanum nigrum</i>	C	ln(B)	<0.001	–	<0.001		NS
Perennial weeds							
Total perennial weed mass 1999	C	B ^{0.33}	0.001	+	<0.001		NS
Total perennial weed mass 2000	C	B ^{0.5}	<0.001	+	<0.001	–	0.02
<i>Cirsium arvense</i>	C	B ^{0.25}	<0.001	+	<0.001	+	<0.001
<i>C. arvensis</i>	C ^{0.33}	B ^{0.25}	<0.001	+	<0.001	+	<0.001
<i>Silene latifolia</i>	C	B ^{0.25}	<0.001	+	0.04		NS
Prairie species							
<i>Andropogon gerardii</i> †	C	B ^{0.25}		+	<0.001		
<i>Bouteloua curtipendula</i> †	C ³	ln(B)		+	<0.001		
<i>Elymus canadensis</i>	C	B ^{0.25}	<0.001	+	<0.001		NS
<i>Monarda fistulosa</i>	C	B ^{0.33}	<0.001	+	<0.001	–	0.01
<i>Panicum virgatum</i> †	C ^{1.5}	ln(B)		+	<0.001		
<i>Schizachyrium scoparium</i>	C	ln(B)	<0.001	+	<0.001		NS
<i>Sorghastrum nutans</i>	C	ln(B)	<0.001	+	<0.001		NS

Notes: Biomass (transformed) was regressed against C addition (transformed), with “N addition” as a categorical predictor. The results of separate regressions, using only +N or –N data (“C addition” columns) show how C addition influences biomass with and without N addition.

† For species not observed in the N-addition plots, only the –N regression was analyzed. Degrees of freedom for the full regression, –N regression, and +N regression, respectively, were 62, 51, and 15 df in 1999, including weed biomass totals and all annual species except *P. convolvulus*; and 60, 49, and 15 df in 2000, including weed biomass totals, all perennial species, and *P. convolvulus*.

where prairie species were most successful, they still made up only 0.08% of aboveground plant biomass in 1999; with a second year of growth, they comprised 9% of plant biomass in 2000. At the other extreme, prairie species were virtually absent from control and N addition plots, making up 0.005% and 0.4% of total aboveground biomass in 1999 and 2000, respectively.

Our results do not prove that a release from competition caused the observed increases in the biomass of prairie species and some weeds. Given the suggestion of competition provided by the relative success of weeds and prairie species, however, it is useful to consider what resources might increase in availability with C addition. We found significant increases in both light penetration (Fig. 3) and soil water (Fig. 4) with C addition. Of the two changes, increasing light may be more likely to explain increases in biomass. N addition eliminated the effect of C addition on light penetration (Fig. 3), paralleling the response of increasing species (Figs. 7–9). Conversely, N addition reduced (at one of three sampling dates) but did not eliminate the observed increase in water content with C addition (Fig. 4).

Condition two, that weeds would be nitrophilic relative to native species, also appears to have been met in this experiment. Carbon addition, which lowered available NO₃, decreased weed biomass and increased prairie biomass (Figs. 5 and 8). Within the context of this experiment, the degree to which a species or group of species was considered to be nitrophilic was the inverse of its response to C addition. This definition considers affinity for N in the presence of competing species, and might not reflect a species' affinity for N if grown in isolation; it also assumes that the effects of C addition were mediated by N immobilization. The role of N immobilization in decreasing weed biomass and increasing prairie biomass is suggested by the reversal of both trends with C addition (Figs. 5 and 8). Effects of C addition other than N immobilization, such as direct chemical inhibition, or immobilization of nutrients other than N, could have played a role in plant responses. Such explanations, however, assume that the observed responses of weed biomass to N addition (Fig. 5) result from N limitation present in the absence of C addition. In 1999, total weed biomass did not increase with increasing levels of N addition, despite large in-

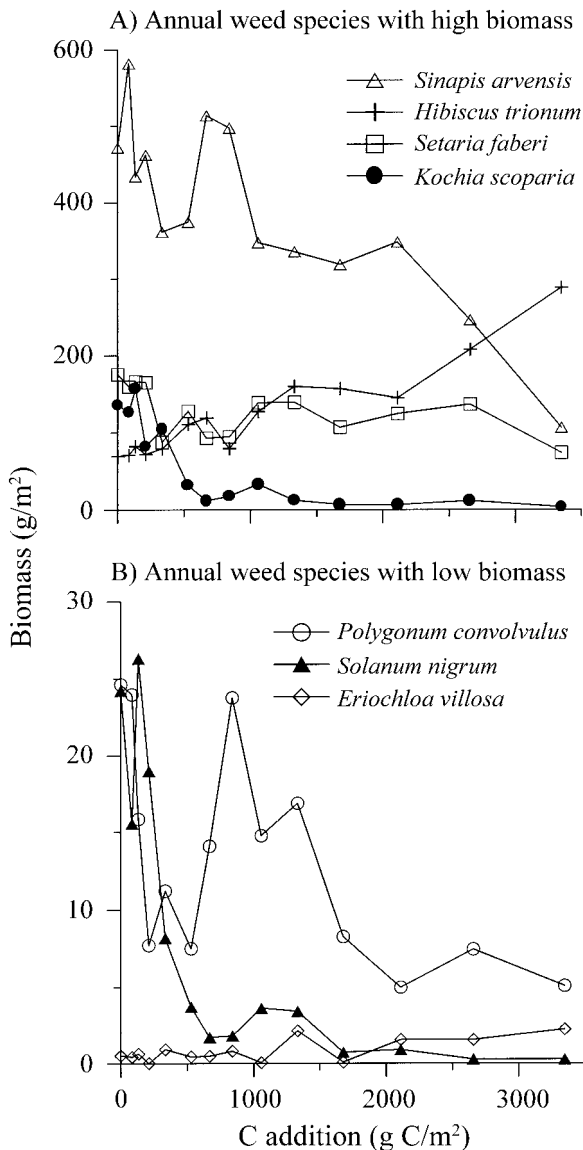


FIG. 6. Responses of annual weed species to C addition: (A) species with maximum mean biomass above 30 g/m², (B) species with maximum mean biomass below 20 g/m². Points represent means for C addition levels. For significance of C and N addition effects see Table 1.

creases in available N with N addition (Figs. 1 and 2), suggesting that (at least in 1999) N did not limit weed growth in the absence of C addition. Thus, while we cannot rule out other effects of C addition, the mitigation of plant responses to C addition by N addition strongly suggests that C addition influences weed and prairie biomass through N immobilization.

Results for individual species are also consistent with the hypothesis that weeds were nitrophilic relative to prairie species. A significantly larger proportion of prairie than weed species responded positively to C addition. Carbon addition reduced the biomass of most annual weed species (Fig. 6) and N addition signifi-

cantly reduced or reversed the effect of C addition for most annuals (Table 1). In contrast to the behavior of annual weeds, all biennial/perennial weed species and all prairie species increased with C addition but not with C + N addition. It is not clear, therefore, whether perennial weeds were nitrophilic relative to prairie species. Among perennial species, C₄ prairie grasses appeared to require the largest quantity of C to increase in biomass (Figs. 7 and 9), suggesting that these species may be less nitrophilic than either perennial weeds or other prairie species. To determine the relative affinity of prairie species and perennial weeds for N, however, N levels may need to be lowered further than they were in this experiment. It is important to note, furthermore, that the perennial weeds in this experiment were added as seed. Where established perennial weeds, especially deep-rooted perennial weeds, are the primary problem facing a restoration effort, incorporating C into the upper 10–20 cm of the soil might have little effect on the established weeds, while inhibiting the establishment of native species.

Condition three, a sufficiently large and lasting decrease in N to influence plant competition, appears to have been met only at higher levels of C addition. Carbon addition significantly reduced available NO₃ in both years, even though no new C was added in 2000 (Fig. 1). Given sufficient C, therefore, N immobilization appears to persist. The quantity of C needed to elicit a plant response varied considerably with species. The annual weeds *Kochia scoparia* and *Solanum nigrum* were very sensitive to C addition, exhibiting sharp declines in biomass at less than 500 g C/m² (Fig.

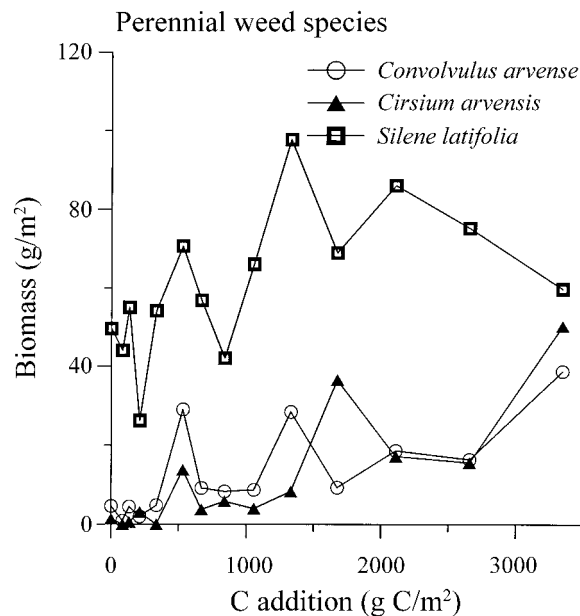


FIG. 7. Responses of perennial weed species to C addition. Points represent means for C addition levels. For significance of C and N addition effects see Table 1.



FIG. 8. Total biomass of prairie species regressed against C addition, with N addition as a categorical predictor. Separate regressions of prairie biomass on +N and -N data were conducted when effects of N were significant: Sep 1999 ($P < 0.001$) and Sep 2000 ($P < 0.001$). Regression lines are backtransformed from regressions conducted on transformed data and are shown for slopes significantly different from zero: Sep 1999 (-N, $P = 0.01$); Sep 2000 (-N, $P < 0.001$; +N, $P = 0.005$). Note differences in scale on y-axes. Degrees of freedom for full, -N, and +N regressions, respectively, were 62, 51, and 15 (1999); 60, 49, and 15 (2000). Transformations of carbon addition (C) and prairie biomass (B) were $C^{0.33}$, $B^{0.33}$ (Sep 1999); $C^{0.33}$, $B^{0.25}$ (Sep 2000).

6). At the other extreme, very little increase in biomass was observed for any of the C_4 prairie grasses at less than 1000 $g\ C/m^2$, and for all prairie grasses, the majority of the observed increase in biomass occurred at levels of C addition above 1500 $g\ C/m^2$ (Fig. 9). Furthermore, many of the trends, including those in total weed biomass in 1999, total prairie biomass in 2000, and biomass of all increasing species (except *Silene latifolia*), show no signs of leveling out, suggesting that further increases in C addition would yield additional shifts in species biomass.

The above results shed some light on which of these three conditions may not have been met in previous studies of C addition. In plant communities limited by resources other than N, weeds might not be expected to be nitrophilic relative to native species (condition 2). If native species are adapted to other resource lim-

itations, they might not differ substantially from weeds in their ability to compete for N. Alternatively, if resources other than N limit plant production during the course of an experiment, relative abilities to compete for N might not influence plant growth. Although, the role of other limiting resources in earlier C-addition studies is not clear, one author suggested that the overriding importance of water may have limited responses to C addition (Hopkins 1998).

Given the large quantities of C needed to elicit responses from the vegetation, it seems likely that previous studies did not add enough C (condition 3). Indeed, accounting for the quantities of C added, our results are similar to those reported in other studies.

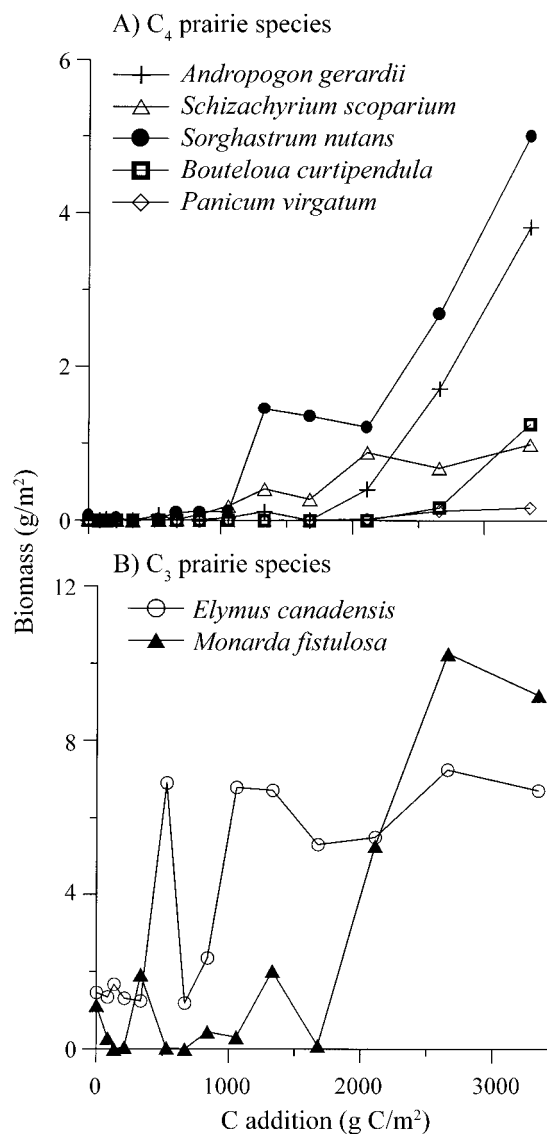


FIG. 9. Responses of prairie species to C addition: (A) C_4 prairie grasses, (B) C_3 prairie grass and prairie forb. Points represent means for C addition levels. For significance of C and N addition effects see Table 1.

As with previous studies adding less than 1350 g organic matter per square meter (McLendon and Redente 1992, Wilson and Gerry 1995, Hopkins 1998), we observed little change in vegetation below 1000 g organic matter (394 g C) per square meter. Previous studies that found C addition to inhibit weeds without facilitating native species added between 1500 and 1650 g organic matter per square meter (Reever Morghan and Seastedt 1999, Alpert and Maron 2000, Paschke et al. 2000). In that range, we observed decreases in the biomass of some annual weeds (Fig. 6), and little or no response from most prairie species (Fig. 9). Of the two studies that found C addition to facilitate native species establishment, one did not provide the mass of C used (Zink and Allen 1998), and the other used 7250 g organic matter per square meter (Perry 2001), within the range at which we observed substantial facilitation of native species.

The large quantity of C needed to elicit responses from native species raises the question of whether C addition is likely to be of practical use. The answer to this question will depend on numerous factors, the most important of which may be site fertility. The site we used had been fertilized regularly for many years prior to this experiment. On such fertile sites other methods of reducing N, such as herbage or topsoil removal, could be used to decrease available N prior to C addition. On less fertile sites, much lower quantities of C may be needed to immobilize enough N to facilitate prairie establishment. The practicality of C addition will also depend on the native and weedy species involved, the cost of obtaining and incorporating C (including the possibility of credits for C storage), and the interaction of C addition with other management techniques (e.g., mowing and/or burning). Despite these unknowns, the facilitation of prairie establishment by C addition in this experiment suggests that C addition holds promise as a tool for restoration of prairie and perhaps other historically N-limited plant communities.

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