



Carbon Addition as a Technique for Controlling Exotic Species in Pacific Northwest Prairies

Authors: Mitchell, Rachel M., and Bakker, Jonathan D.

Source: Northwest Science, 85(2) : 247-254

Published By: Northwest Scientific Association

URL: <https://doi.org/10.3955/046.085.0213>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Carbon Addition as a Technique for Controlling Exotic Species in Pacific Northwest Prairies

Abstract

Competition for soil resources is a driving force in plant community ecology. Therefore, amendments that alter soil resources should affect vegetation dynamics and are potential tools for controlling exotic species. We tested the effects of two types of carbon addition, sugar and activated carbon (AC), on an exotic-dominated grassland plant community. Sugar stimulates the microbial community and temporarily reduces plant available nitrogen (N), while AC adsorbs plant available N. Six experimental plots and three carbon treatments were used: sugar (1000 g m⁻²; 42% C), AC (420 g m⁻²; 100% C), and control. Treatments were applied in a split-plot design in spring 2008. Aboveground biomass, plant cover, species richness, and plant basal area were tracked for two growing seasons. Although total biomass was not affected by C addition, the distribution of biomass among life forms was affected: carbon addition reduced forb biomass but had no effect on grasses or legumes. Total cover was lower in sugar-treated plots, and sugar also altered the proportional composition of that cover by reducing the abundance of forbs, especially in the first year. Five species were particularly sensitive to sugar addition: *Myosotis discolor*, *Sonchus asper*, *Taraxacum officinale*, *Valerianella locusta*, and *Vulpia bromoides*. Sugar also reduced plant basal area in the first year. These results suggest that sugar and, to a lesser extent, AC could be useful management tools. Sugar could be applied to areas where herbicide use is undesirable, reducing the abundance of exotic forbs and providing a window of opportunity for native species establishment.

Introduction

How plants compete for resources is a fundamental question in ecology (Goldberg and Novoplansky 1997, Tilman 1999). Resource levels are spatially and temporally dynamic and can affect the outcome of competitive interactions (Tilman and Wedin 1991, Wedin and Tilman 1993). Consequently, intentional alterations of resources have been suggested as a management tool to reduce or prevent exotic plant invasion (Seabloom 2003, Corbin and D'Antonio 2004, Iannone et al. 2008). Alterations that favor native over exotic species could contribute to the restoration of ecosystems in which exotic plant species are a significant concern (Zink and Allen 1998, Kulmatiski and Beard 2006, Mangold and Sheley 2008).

In many temperate ecosystems, elevated levels of soil nitrogen (N) are an obstacle to increasing native diversity (Maron and Connors 1996, Kolb et al. 2002, Abraham et al. 2009). Fertilization (Vitousek et al. 1997), grazing (Hobbs 1996), N fixation by exotic species (Liao et al. 2008), and atmospheric deposition can all increase the level of N present in soils (Bobbink 1998). Increases in soil N have been shown to decrease

native plant diversity while favoring invasive species (Suding et al. 2005, Vinton and Goergen 2006, Clark 2007). Additions of carbon (C) to soil are expected to alter C:N ratios, increasing soil C content and reducing plant available N (Corbin and D'Antonio 2004), and therefore may negatively impact exotic species.

Pacific Northwest prairies are an extremely endangered North American grassland ecosystem. This unique ecosystem provides habitat for several rare and endangered species, including the streaked horned lark (*Eremophila alpestris strigata*), Taylor's checkerspot butterfly (*Euphydryas editha taylori*), island marble butterfly (*Euchloe ausonides insulanus*) and golden paintbrush (*Castilleja levisecta*). Presently, these prairies occupy less than 3% of their former acreage (Chappell et al. 2000). Remaining prairie fragments are often heavily invaded by exotic plant species (Dunwiddie et al. 2006) and have been degraded by agriculture and forest development. Scotch broom (*Cytisus scoparius*), a primary invader of these prairies, alters soil resources by increasing plant available N, depleting soil phosphorus, and inhibit the growth of competitors (Haubensak and Parker 2004, Shaben and Myers 2010).

Carbon addition to the soil surface is a reliable method for increasing soil C content (Perry et al. 2010). Furthermore, recent studies in grassland ecosystems

¹Author to whom correspondence should be addressed. E-mail: rachelmm@uw.edu

have demonstrated that C addition disproportionately affects non-N fixing, fast growing exotic annual species (Averett et al. 2004, Blumenthal et al. 2009), which often dominate high N-habitats and are typically benefited by increased N when compared to perennials. Using C addition as a restoration technique could reduce or eliminate the establishment and spread of exotic species (Alpert and Maron 2000, Eschen et al. 2007). This in turn could reduce the competition experienced by native species, creating bare-ground where naturally dispersed seeds can germinate, and provide a “window of opportunity” for the intentional establishment of native plants added through seeding or plugging. Ecosystems with a high diversity of native species are more resistant to invasion by exotic plants (Dukes 2001, Pokorny et al. 2005, Sheley and Carpinelli 2005, Hooper and Dukes 2010), suggesting that temporary “windows of opportunity” could have longer-term consequences for native plant establishment.

Carbon can be added to the soil in a number of forms. When added as sugar, it stimulates the uptake of inorganic N from soil into microbial biomass, thereby temporarily reducing plant available N (Morgan 1994, Morghan et al. 1999). When added as activated carbon (AC), the microbial community is not directly affected but the extremely high surface area to volume ratio of AC permits it to adsorb many times its own weight in organic compounds, including those containing N. A further advantage of AC is that it can also immobilize allelopathic compounds (Kabouw et al. 2010). AC is not widely used in restoration, and its effect on invasive exotic plants of Pacific Northwest prairies is not known. However, charcoal, a naturally occurring type of AC, is present in these ecosystems (Hegarty et al. 2011) because of intentional burning by Native Americans (Boyd 1999, Weiser and Lepofsky 2009).

Additions of C may impact specific plant life forms (e.g., grass, forb). For example, forb species have been shown to be sensitive to C addition in some systems (e.g., Blumenthal et al. 2009). Grasses can respond to C addition by increasing their allocation to roots (Eschen et al. 2006). Pacific Northwest prairies are invaded by a wide variety of exotic plants, with the dominant “problem” life forms varying by location. At present, it is unclear how C addition will affect Pacific Northwest grassland invaders. Understanding how C addition impacts different life forms could allow managers to selectively target them during restoration.

We hypothesized that amendments that increase soil C will have a strong negative effect on exotic Pacific Northwest prairie invaders. We specifically addressed

three questions: 1) How does C addition affect abundance (biomass, cover, richness, basal area) of exotic species (in total, by life form, and individually)? 2) Do sugar and AC perform similarly in an exotic dominated grassland ecosystem? 3) How long do effects of C addition last after application?

Methods

This experiment was performed at the Prairie Overlook site at Ebey’s Landing National Historical Reserve on Whidbey Island, Washington. The site is part of Ebey’s Prairie, which historically was the largest prairie-type ecosystem on Whidbey Island. Soils are derived from glacial outwash and are coarse textured and well drained. Fire has been excluded and the prairie converted to agricultural use since approximately 1850 (National Park Service 2006). Presently, the site is dominated by exotic grasses such as soft brome (*Bromus hordeaceus*) and orchard grass (*Dactylis glomerata*), and by exotic forbs such as hairy cat’s ear (*Hypochaeris radicata*) and narrow-leaf plantain (*Plantago lanceolata*). There are very few native species (six out of 47 total species) present on the site; the most common is Roemer’s fescue (*Festuca roemeri*), which was planted in two of the whole plots. Exotic species comprise the vast majority of cover at the site (~ 50% in the two whole plots planted with Roemer’s fescue but 100% in the other four whole plots), so our interest was in reducing their abundance.

Six whole plots (each 10 x 15 m) were utilized in this experiment. Plots were located on a hillside with slopes ranging from 5-20%. Each plot received one of three pre-treatments before the experiment began: 1) treated with herbicide, tilled, and planted with Roemer’s fescue, 2) treated with herbicide, tilled, and left unplanted, or 3) treated with herbicide, mowed, and left unplanted. Two plots per pre-treatment were included in this study so we could evaluate the effects of C addition across a range of restoration treatments, although there was insufficient replication to examine the effects of the pre-treatments themselves.

Carbon addition treatments were assigned following a split-plot design. Each 10 x 15 m whole plot was subdivided into three treatment plots, each 5 x 10 m. Treatment plots were oriented parallel to the slope to prevent mixing of treatments. Each treatment plot received one of three C addition treatments: 1) sugar (1000 g m⁻²; 42% C), 2) AC (420 g m⁻²; 100% C), or 3) control (no C addition). These application levels were chosen as they reduced exotic plant biomass in a greenhouse-based study (Eschen et al. 2006). Carbon

was hand applied to plots in three equal applications over a five-week period in spring 2008 (04/03/08 – 5/04/08), with total application rates equal to the above values.

Plant species identity, percent cover, and plant basal area were measured in eight 0.5 x 1 m quadrats per treatment plot. Percent cover was visually estimated for each species using the modified Daubenmire method. Plant basal area was estimated for the entire plant community using the same method. Data were collected in late spring for two years (06/12/08 and 5/30/09) after C addition. In addition, aboveground biomass was clipped each summer from four 0.1 x 1 m strips per treatment plot. Biomass was sorted by life form (grass, forb, or legume), dried at 60 °C for 10 days, and weighed.

Our response variables were biomass, cover, species richness, and plant basal area, all of which were averaged within each treatment plot. Total biomass, total cover, mean species richness per quadrat, and total plant basal area were analyzed as univariate responses to determine whether they differed among treatments. Biomass and cover data were then analyzed with multivariate techniques to determine whether the proportional allocation among life forms differed among treatments; we refer to these as ‘biomass distribution’ and ‘composition of cover’, respectively. Finally, the biomass and cover of each life form were analyzed individually. All analyses were conducted using the PERMANOVA+ add-on for the PRIMER-E software package (Anderson et al. 2008). PERMANOVA is a non-parametric, permutational technique that is analogous to classical ANOVA but makes no distributional assumptions about the data and can be applied to uni- and multivariate data (Anderson 2001, McArdle and Anderson 2001). Data were relativized by plot totals for multivariate analyses. Bray-Curtis distances were used for multivariate analyses and Euclidean distances for univariate analyses, with significance assessed using 9,999 permutations and $\alpha = 0.05$. We used a repeated measure ANOVA design with whole plots included as a blocking term to account for inter-plot variation. We focused on the Carbon main effect and the Carbon x Year interaction term. Significant Carbon main effects were followed by post-hoc analyses to determine which C treatments differed. Significant Carbon x Year interactions were followed by post-hoc analyses of individual years to identify which C treatments differed within a given year.

As reported below, sugar had a strong effect on plant cover. We therefore used Indicator Species Analysis (ISA) to identify species that differed strongly in abundance between control and sugar-treated plots. Each

whole plot was analyzed separately, and the results combined using meta-analytical techniques (Bakker 2008). Because of low sample size, significant indicators were assessed using $\alpha = 0.05$, regardless of the magnitude of their indicator values (IV).

Results

Total biomass was not affected by C addition, although biomass distribution among life forms was affected, particularly by the addition of sugar (Table 1). Subsequent analyses indicated that the addition of either sugar or AC significantly reduced forb biomass over both years (Figure 1) but had no effect on grasses or legumes (Table 1).

Total plant cover was reduced by sugar treatment in the first year, though post-hoc comparisons indicated that this difference was not statistically significant. The composition of cover was significantly affected by C addition, particularly by the addition of sugar, and was strongest in the first year. Subsequent analyses indicated that sugar addition significantly reduced forb cover, particularly during the first year (Figure 1) but did not affect grass or legume cover. Five species were significant indicators of control rather than sugar plots: *Myosotis discolor* ($P = 0.038$), *Sonchus asper* ($P = 0.016$), *Taraxacum officinale* ($P = 0.004$), *Valerianella locusta* ($P = 0.019$) and *Vulpia bromoides* ($P \leq 0.001$). These species were significantly less abundant on sugar treated than control plots.

There were significant Carbon x Year interactions for species richness and plant basal area. Although richness was lower in sugar treated than control plots during the first year, post-hoc comparisons indicated that this difference was not statistically significant (Figure 2). Plant basal area was lower in sugar-treated plots than in other C addition treatments during the first year (Figure 2; Table 1).

Discussion

Our primary question was whether C addition affected plant abundance in grassland communities; this was tested by examining the main effect of C addition without comparing types of C. Since we tested these treatments in an exotic dominated grassland, we hoped that the treatments would reduce plant abundance, and this was the case: C addition reduced plant abundance as measured by richness, cover, and plant basal area (Table 1). These results indicate that C addition may be a viable option for reducing the abundance of exotic species in PNW prairies.

TABLE 1. Results of PERMANOVA models testing the effects of Block, Carbon addition, Year, and the Carbon x Year interaction on biomass, cover, richness, and plant basal area. 'Distribution' and 'composition' are multivariate analyses of the biomass and cover, respectively, by life form; all other analyses are univariate. The pseudo-*F* (*F*) and permuted *P*-values (*P*) are reported for each factor along with the *R*² for the overall model. Significant effects ($\alpha = 0.05$) are in bold. Each model was assessed using 9,999 permutations.

	Block (df = 5, 25)		Carbon (df = 2, 25)		Year (df = 1, 25)		Carbon x Year (df = 2, 25)		<i>R</i> ²
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Biomass									
Total	13.1	<0.001	1.7	0.205	0.2	0.634	1.6	0.231	0.257
Distribution	8.9	<0.001	2.6	0.046	12.4	<0.001	1.7	0.155	0.275
Forb	7.0	<0.001	6.0	0.005	1.0	0.331	0.2	0.808	0.339
Grass	14.8	<0.001	0.1	0.924	3.5	0.067	0.8	0.453	0.240
Legume	1.2	0.333	0.5	0.668	3.5	0.083	0.5	0.510	0.684
Cover									
Total	2.7	0.039	1.2	0.313	8.5	0.008	3.8	0.035	0.435
Composition	8.1	<0.001	2.8	0.027	19.3	<0.001	3.7	0.006	0.254
Forb	7.1	<0.001	3.7	0.036	3.3	0.07	7.7	0.002	0.286
Grass	12.7	<0.001	0.3	0.742	13.2	0.001	0.5	0.571	0.241
Legume	2.2	0.082	2.1	0.144	21.9	<0.001	1.4	0.246	0.383
Richness	7.8	<0.018	5.0	0.604	9.2	<0.001	0.3	0.036	0.297
Basal Area	6.2	<0.001	0.2	0.824	21.3	<0.001	6.5	0.006	0.275

Furthermore, our results indicate that C addition affects life forms differently. We found that forbs were most strongly affected by sugar addition, which contradicts several previous studies (Eschen et al. 2006, 2007) reporting that grasses were more strongly affected by additions of sugar. A wide range of forbs appear to be affected, as the indicator species included perennial forbs (*T. officinale*, *S. asper*) and annual forbs (*M. discolor*, *V. locusta*). These species appear particularly sensitive to sugar addition, though further investigation would be necessary to determine the mechanisms behind this sensitivity.

One possible reason for the difference between our conclusions and those of studies that found grasses to be more sensitive to C addition (Eschen et al. 2006, 2007) may simply be the variables measured. For example, Eschen et al. (2006) found that grasses reduced their root:shoot ratio in response to C addition, but we did not measure this variable in our study. We did identify one annual grass (*V. bromoides*) that was much less abundant in sugar treated than control plots. It is possible that our C addition rates were not high enough to affect grasses, as some research has shown that higher rates (e.g., 3346 g m⁻² [Blumenthal et al. 2003]) yield stronger results, although we used the same rate as Eschen et al. (2006). Another possible reason for the difference is that our study was field-based while some of the others (e.g., Eschen et al. 2006) were greenhouse-

based. For example, perennial grasses in a field setting may have been established for several years and have fully developed root systems, allowing them access to water and nutrients not available to a newly established greenhouse-grown plant.

Neither sugar nor AC showed any significant effect on legume species. These results are not entirely surprising, as legumes are able to fix atmospheric N, and are unlikely to be as dramatically affected by increases in soil C content. There were seven legume species at the site, two of which were native (*Lotus micranthus* and *Vicia americana*) while five were exotic. Most of the legumes were annuals (5 species) and herbaceous (6 species); *Cytisus scoparius* was the only legume with a shrub growth form. These results suggest that a wide variety of legumes are unaffected by C addition treatments.

Sugar vs. Activated Carbon

Our second question was whether the two types of carbon, sugar and AC, differ in their effects. We found that sugar was a more effective amendment than AC in reducing the abundance of exotic species, particularly forbs. Sugar lends itself to restoration for a variety of reasons. It is readily available and easily dissolves in water allowing it to be sprayed or irrigated on to restoration sites. Sugar is non-toxic and can be applied in areas where herbicide use is prohibited or undesirable.

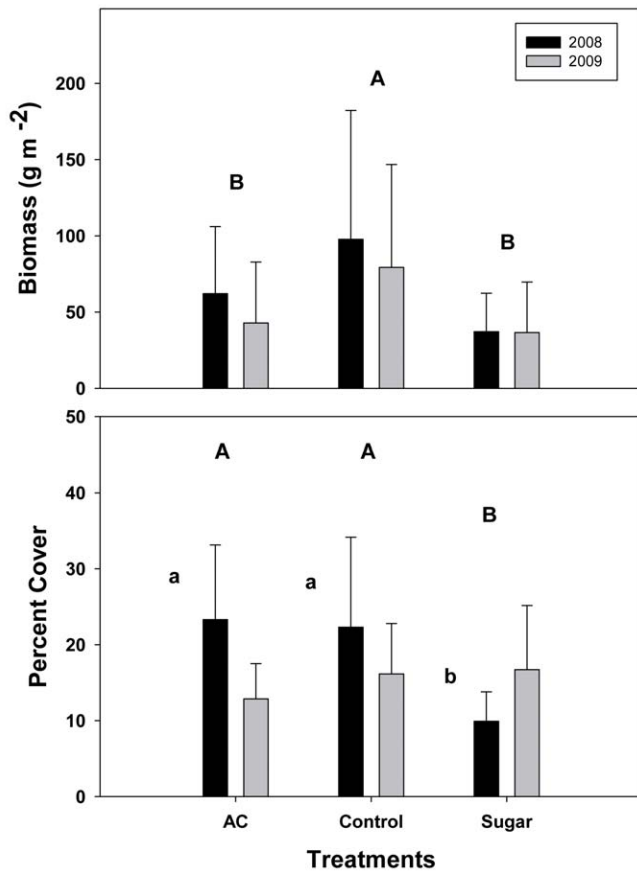


Figure 1. Aboveground biomass (top) and cover (bottom) (mean + standard deviation) of forbs in plots treated with activated carbon (AC), sugar, or left untreated (control) in 2008 and 2009. PERMANOVA results are summarized in Table 1. Significant carbon effects are indicated by uppercase letters. Significant Carbon x Year interactions were followed by post-hoc analysis of each year individually. Lowercase letters indicate treatments that differed significantly in 2008; treatments did not differ in 2009.

It is also short-lived in the environment, making it an ideal amendment for use as a pre-treatment, and for short-term restoration goals (e.g., rapid control of an emergent “problem” species).

Activated carbon, on the other hand, is long-lived in the environment; it is difficult for microbes to digest and therefore can remain in the soil for centuries, thus potentially permanently increasing soil C (Kulmatiski and Beard 2006). AC can adsorb organic molecules until its pore space is full, which can take months to years. AC is commonly used in agriculture, and is thus easily obtained and relatively inexpensive. In addition, it can be applied in a variety of ways, including dry surface applications, sprayed as a water-based slurry, or tilled into soil. Because AC is 100% C, it is non-toxic and can be used in areas where herbicides are not permitted.

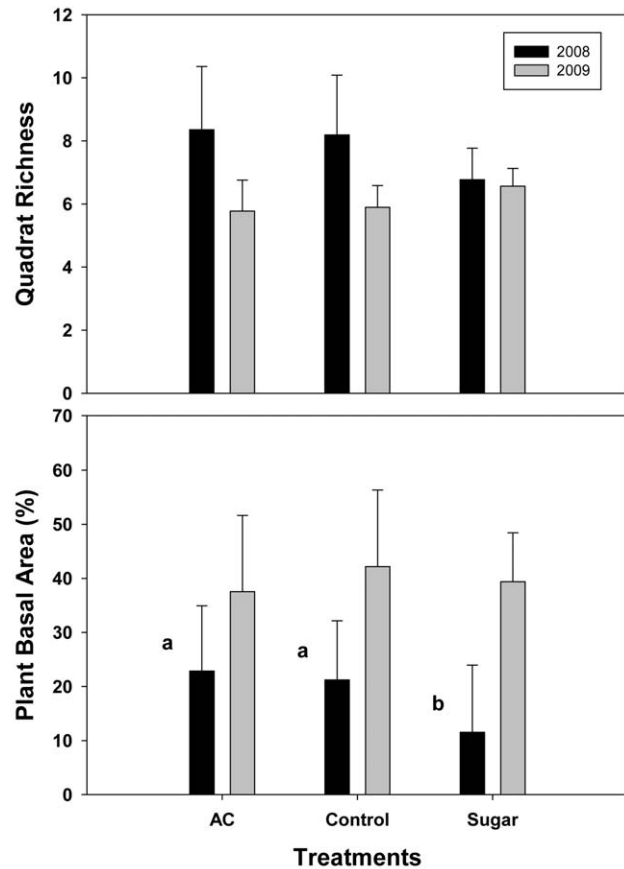


Figure 2. Quadrat-scale species richness (top) and plant basal area (bottom) (mean + standard deviation) in plots treated with activated carbon (AC), sugar, or left untreated (control) in 2008 and 2009. PERMANOVA results are summarized in Table 1. Significant Carbon x Year interactions were followed by post-hoc analysis of each year individually. Lowercase letters indicate treatments that differed significantly in 2008; treatments did not differ in 2009.

AC had a more limited effect on the plant community than sugar did, reducing only forb biomass. This may indicate that AC takes longer to affect the plant community than sugar, or that the method of application (dry addition to the surface) did not adequately introduce it to the system. The AC used in this study was of very fine particle size (< 150 μm) and our study site experiences high wind, which may have reduced the amount of AC penetrating the soil surface. C amendments tilled directly into the soil are accessed more rapidly than those applied to the surface (Biederman and Whisenant 2009), which may explain our lack of observed effects for AC. This fact may make AC of limited use in areas where tilling is impossible, such as prairie remnants. However, it may be useful in ex-arable, tilled fields or as a longer-lasting addition

to applications of short-lived C amendments, as AC affects soil N through adsorption, rather than through stimulation of the microbial community.

Overall, these results suggest that C addition, particularly in the form of sugar, negatively affected exotic forbs while leaving most grasses and legumes unaffected. This may be due to higher N requirements by forbs, or to differences in root position or the timing or uptake of soil N. However, it seems unlikely that C addition causes complete mortality of affected species, as species richness was not significantly affected. Instead, C addition seems to limit the growth of forbs.

Longevity of Carbon Addition

Our third question was how long C addition affects the plant community. Recent research indicates that C addition to the soil surface is the most reliable method for altering soil C:N ratios (Perry et al. 2010) and that, regardless of the C source used, alterations to the soil lose effectiveness rapidly after cessation of treatment (Prober and Lunt 2009; Kirkpatrick and Lubetkin 2011). Rapid loss of C effectiveness was supported in our study, as few significant effects remained detectable in the second growing season after application. If using C addition as the sole management tool, long-term reapplications would be necessary to have a lasting impact on the plant community. However, this short-term effect could also be capitalized on by, for example, applying sugar in a targeted fashion during early stages of plant invasion as a preventative measure. In addition, if there are phenological differences between desired and undesired species it may be possible to time sugar applications to capitalize on those differences.

Utility of Carbon Addition

The effect of C addition depends on the type of carbon, application rate, and method of application (Perry et al. 2010). In addition to sugar and AC, other carbon rich additives that have been examined include sawdust (e.g., Bleier and Jackson 2007), straw (e.g., Kaushik and Inderjit 2007), and wood-waste (Biederman and Whisenant 2009). At present, no general recommendation for application rates is available for C addition (Perry et al. 2010); a wide variety of rates have been used in previous studies (e.g., 84 – 3346 g m⁻² [Blumenthal et al. 2003]).

We have shown that C addition temporarily reduces the abundance of exotic forbs. This likely reduces competition from exotic species, and could provide a ‘window of opportunity’ for native species to establish

and compete in areas where they might otherwise be unable to do so (e.g., heavily invaded ecosystems). Recent research in Puget lowland prairies has indicated that treatment with sugar favors growth of transplanted native grasses and forbs (Kirkpatrick and Lubetkin 2011), making this an especially promising result. Combining sugar treatments with establishment of a diverse mixture of native prairie species through seeding or plugging could lead to improved native establishment and survival even in the presence of exotic invaders, although this has not yet been tested.

Future research directions should include testing a range of application methods, including tilling, spraying as slurry, combining with grass-specific herbicide (e.g., Fusilade), or repeated applications over a number of growing seasons. The effects of C addition on different plant life-stages should be investigated, as well as the mechanisms by which specific species are affected by C addition. Finally, future research should examine whether the strength of responses to C addition differs among communities and ecosystems. Although we were unable to obtain enough replicates of each pre-treatment to rigorously evaluate whether the response to C addition differed among pre-treatments, anecdotal evidence suggests that this was the case. For example, total cover was unchanged by sugar addition for those whole plots that were planted with fescue but was reduced by 68% in the other whole plots. Thus, our inclusion of multiple pre-treatments may have muted the overall response to C addition in our study. Furthermore, we worked in an exotic-dominated grassland while Kirkpatrick and Lubetkin (2011), working in native prairie, found that sugar addition had no effect on standing cover and enhanced the performance of native transplants within the first year after application. For C addition to become a viable management tool, we will have to understand when and where it is most effective.

Conclusions

Our research indicates that surface carbon applications, particularly of sugar, can temporarily reduce the abundance of exotic forbs while also reducing overall species richness and plant basal area. AC was of more limited use for weed control. The general applicability of sugar treatment makes it a useful tool for restoration projects facing invasion by exotic forbs. Further research is needed to determine what effect this treatment might have on desirable native forbs and how it might be integrated with restoration treatments, particularly the seeding or planting of native species.

Acknowledgements

We thank Laura Blume, Ryan Haugo, Andrea Blin, and Brandon Neuhaus for assistance with this research and Regina Rochefort, Janneke Hille Ris Lambers, Sarah Reichard and Soo-Hyung Kim for their advice

Literature Cited

- Abraham, J. K., J. D. Corbin, and C. M. D'Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density and order of emergence. *Plant Ecology* 201:445-456.
- Alpert, P., and J. L. Maron. 2000. Carbon addition as a countermeasure against biological invasion by plants. *Biological Invasions* 2:33-40.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.
- Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E, Plymouth, United Kingdom.
- Averett, J. M., R. A. Klips, L. E. Nave, S. D. Frey, and P. S. Curtis. 2004. Effects of soil carbon amendment on nitrogen availability and plant growth in an experimental tallgrass prairie restoration. *Restoration Ecology* 12:568-574.
- Bakker, J. D. 2008. Increasing the utility of indicator species analysis. *Journal of Applied Ecology*. 45:1829-1835.
- Biederman, L. A., and S. G. Whisenant. 2009. Amendment placement directs soil carbon and nitrogen cycling in severely disturbed soils. *Restoration Ecology* (online early view) doi:10.1111/j.1526-100X.2009.00564.x.
- Bleier, J. S., and R. D. Jackson. 2007. Manipulating the quantity, quality and manner of C addition to reduce soil inorganic N and increase C4:C3 grass biomass. *Restoration Ecology* 15:688-695.
- Bobbink, R. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86:717-738.
- Boyd, R. 1999. *Indians, Fire and the Land in the Pacific Northwest*. Oregon State University Press, Corvallis.
- Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13:605-615.
- Blumenthal, D. M. 2009. Carbon addition interacts with water availability to reduce invasive forb establishment in a semi-arid grassland. *Biological Invasions* 11:1281-1290.
- Chappell, C. B., M. S. Mohn Gee, B. Stephens, R. Crawford, and S. Farone. 2000. Distribution and decline of native grasslands and oak woodlands in the Puget Lowland and Willamette Valley ecoregions, Washington. In S. H. Reichard, P. Dunwiddie, J. Gamon, A. Kruckelberg and D. Salstrom (editors), *Washington Native Plant Society*, Seattle. Pp. 124-139.
- Clark, C. M., E. E. Cleland, S. L. Collins, J. E. Farigione, L. Gough, K. L. Gross, S. C. Pennings, K. N. Suding, and J. B. Grace. 2007. Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecology Letters* 10:596-607.
- Corbin, J. D., and C. M. D'Antonio. 2004. Can carbon addition increase competitiveness of native grasses? A case study from California. *Restoration Ecology* 12:36-43.
- Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia* 126:563-568.
- Dunwiddie, P., E. Alverson, A. Stanely, R. Gilbert, S. Pearson, D. Hays, J. Arnett, E. Delvin, D. Grosboll, and D. Marschner. 2006. The vascular plant flora of the south Puget Sound prairies, Washington, USA. *Davidsonia* 17:51-69.
- Eschen, R., H. Muller-Scharer, and U. Schaffner. 2006. Soil carbon addition affects plant growth in a species-specific way. *Journal of Applied Ecology* 43:35-42.
- Eschen, R., S. R. Mortimer, C. S. Lawson, A. R. Edwards, A. J. Brook, J. M. Igual, K. Hedlund, and U. Schaffner. 2007. Carbon addition alters vegetation composition on ex-arable fields. *Journal of Applied Ecology* 44:95-104.
- Goldberg, D., and A. Novoplansky. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85:409-418.
- Haubensak, K. A., and I. M. Parker. 2004. Soil changes accompanying invasion of the exotic shrub *Cytisus scoparius* in glacial outwash prairies of western Washington (USA). *Plant Ecology* 175:71-79.
- Hegarty, J., D. Zabowski, and J. D. Bakker. 2011. Use of soil properties to determine the historical extent of two western Washington prairies. *Northwest Science* 85:120-129.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695-713.
- Hooper, D. U., and J. S. Dukes. 2010. Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology* 98:764-777.
- Iannone, B. V., and S. M. Galatowitsch. 2008. Altering light and soil N to limit *Phalaris arundinacea* reinvasion in sedge meadow restorations. *Restoration Ecology* 16:689-701.
- Kaushik, S., and Inderjit. 2007. *Oryza sativa* straw restricts *Phalaris minor* growth: allelochemicals or soil resource manipulation? *Biology and Fertility of Soils* 43:557-563.
- Kirkpatrick, H. E., and K. C. Lubetkin. 2011. Responses of native and introduced plant species to sucrose addition in Puget lowland prairies. *Northwest Science* 85:255-268.
- Kolb, A., P. Alpert, D. Enters, and C. Holzappel. 2002. Patterns of invasion within a grassland community. *Journal of Ecology* 90:871-881.
- Kabouw, P., M. Nab, and N. M. van Dam. 2010. Activated carbon addition affects substrate pH and germination of six plant species. *Soil Biology and Biochemistry* 42:1165-1167.
- Kulmatiski, A., and K. H. Beard. 2006. Activated carbon as a restoration tool: Potential for control of invasive plants in abandoned agricultural fields. *Restoration Ecology* 14:251-257.
- Liao, C. Z., R. H. Peng, Y. Q. Luo, X. H. Zhou, X. W. Wu, C. M. Fang, J. K. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* 177:706-714.
- Mangold, J. M., and R. L. Sheley. 2008. Controlling performance of bluebunch wheatgrass and spotted knapweed using nitrogen and sucrose amendments. *Western North American Naturalist* 68:129-137.
- Maron, J. L., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105:302-312.

- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290-297.
- Morgan, J. P. 1994. Soil impoverishment: a little-known technique holds promise for establishing prairie. *Restoration Management Notes* 12:55-56.
- Morghan, K. J. R., and T. R. Seastedt. 1999. Effects of soil nitrogen reduction on nonnative plants in restored grasslands. *Restoration Ecology* 7:51-55.
- National Park Service. 2006. Ebey's Landing National Historical Reserve Final General Management Plan and Environmental Impact Statement. National Park Service, Seattle.
- Perry, L. G., D. M. Blumenthal, T. A. Monaco, M. W. Paschke, and E. F. Redente. 2010. Immobilizing nitrogen to control plant invasion. *Oecologia* 163:13-24.
- Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engle, J. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13:448-459.
- Prober, S. M., and I. D. Lunt. 2009. Restoration of *Themeda australis* swards suppresses soil nitrate and enhances ecological resistance to invasion by exotic annuals. *Biological Invasions* 11:171-181.
- Rashid, I., and Z. Reshi. 2010. Does carbon addition to soil counteract disturbance-promoted alien plant invasion? *Tropical Ecology* 51:339-345.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences* 23:13,384-13,389.
- Shabin, J., and J. H. Myers. 2010. Relationships between Scotch broom (*Cytisus scoparius*), soil nutrients and plant diversity in the Garry oak savannah ecosystem. *Plant Ecology* 207:81-91.
- Sheley, R. L., and M. F. Carpinelli. 2005. Creating weed-resistant plant communities using niche-differentiated non-native species. *Rangeland Ecology and Management* 58:480-488.
- Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences* 102:4387-4392.
- Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. *Ecology* 72:1038-1049.
- Tilman D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455-1474.
- Vinton, M. A., and E. M. Goergen. 2006. Plant-soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairie. *Ecosystems* 9:967-976.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7:737-750.
- Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient—initial conditions and mechanisms of competition. *Ecological Monographs* 63:199-229.
- Weiser, A., and D. Lepofsky. 2009. Ancient land use and management of Ebey's Prairie, Whidbey Island, Washington. *Journal of Ethnobiology* 29:184-212.
- Zink, T. A., and M. F. Allen. 1998. The effects of organic amendments on the restoration of disturbed coastal sage scrub habitat. *Restoration Ecology* 6:52-58.

Received 28 September 2010

Accepted for publication 18 March 2011