AN ABSTRACT OF THE DISSERTATION OF


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Abstract approved: ______________________________________________________________________________

Mark V. Wilson

Many studies suggest that weedy plant species are most successful when soil nitrogen is abundant. Consequently, I used soil nitrogen manipulations to determine if altering nitrogen would affect the establishment of both weedy and native plant species in a western Oregon wetland prairie. In two studies, we added carbon amendments (sucrose and sawdust) to the soil in order to decrease available soil nitrogen, and in one study we added nitrogen (ammonium nitrate). I show that weedy grasses (*Agrostis capillaris*, *Alopecurus geniculatus*, *Anthoxanthum odoratum*, *Holcus lanatus*, and *Lolium perenne*) were significantly suppressed in carbon-treated plots compared to control plots. Also, native grasses (*Deschampsia cespitosa* and *Danthonia californica*) yielded significantly more biomass in carbon plots than controls. These results suggest that carbon additions can deter weeds and promote native grasses during wetland prairie restoration.

Nitrogen-treated plots yielded significant increases in the biomass of both exotic and native grasses compared to controls. This increase in exotic grasses was expected due to the nitrophilous nature of these plants, but the increase in native grasses in these plots was unanticipated, since we expected these natives to be choked out by the weeds. We suggest that the native grasses were more
abundant in nitrogen treatments compared to controls because the very high levels of nitrogen in these plots reduced competition for belowground resources, allowing both plant groups to flourish.

The ratio of total native biomass to total weed biomass was high in carbon treatments across the hydrologic gradient, but was high in nitrogen treatments only in wetter plots.

We used monoculture and mixture plots to study the effects of hydrology on establishment and competitive ability of several native and exotic grasses. Our results show that three of the seven species (Danthonia californica, Beckmannia syzigachne, and Phalaris arundinacea) were excluded from growing in several mixture plots along the gradient, despite their successful establishment in adjacent monoculture plots. Furthermore, the exotic grasses showed low competitive abilities along the hydrologic gradient compared to the native grasses, indicating that invasive species are not competitively superior to native species, at least at the establishment and seedling stages.
The Effects of Nitrogen Manipulations and Hydrology on the Establishment and Competitive Abilities of Wetland Prairie Plant Species (Western Oregon)

by

Kimberly J. Davis

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Presented August 15, 2000
Commencement June 2001
I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.
Acknowledgements

There are many special people who have helped me in obtaining my degree. I would first like to thank my major professor Mark V. Wilson for showing me unlimited patience, attention, and support. He has been the best major professor a person could ask for. I also wish to thank Deborah L. Clark for being a supportive mentor and caring friend. I also thank the other members of our lab group, namely Mary Maret, Marilynn Bartels, Jennifer Goodridge, and Keli Kuykendall, for their scholarly advice as well as help in making field work fun! Also, a big thank you to my friend Brennan Ferguson for keeping me company in the lab on many a late evening.

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Most especially, I wish to thank my wonderful husband, Bill Henkel, for his love and support and for occupying Miles while I finish my dissertation.
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I dedicate this work to my husband and son.
Thank you for showing me what is truly important in life.
Chapter 1
Introduction

Oregon’s Willamette Valley once contained hundreds of thousands of acres of native prairie (Johanesson et al. 1971). Most of the valley, in fact, was prairie containing scattered oaks (mostly Quercus garryana) in hilly areas (Smith 1949, Boyd 1986). Willamette Valley prairie plant communities were maintained with the aid of the indigenous Kalapuya Indians. The Kalapuyas burned large tracts of prairies regularly in order to abet food harvesting and hunting practices (Boyd 1986). This burning ended in the 1840’s when the white settlers arrived.

The original species composition of these prairie plant communities is difficult to know for certain, since records are incomplete and grazing and exotic species have altered these prairies since the white settlers first arrived. The available evidence, however, suggests that wetland prairies were dominated by tall, perennial grasses, most notably Deschampsia cespitosa (tufted hairgrass) (Habeck 1961, Wilson 1998). Other common grass species were Danthonia californica (California oatgrass), Beckmannia syzigachne (American sloughgrass), Hordeum brachyantherum (meadow barley), and Agrostis exarata (spike bent grass). These prairies also contained a variety of forb species such as Camassia quamash (camas), Eriophyllum lanatum
(Oregon sunshine), Microseris laciniata (cut-leaf microseris), and *Plagiobothrys figuratus* (fragrant popcornflower).

Since the 1840's, the Willamette Valley floor has undergone dramatic changes. Wetland prairies have been almost completely destroyed by urbanization, agriculture, and the invasion of woody species due to the cessation of burning, with less than 1 percent of the original area of prairie remaining (Johanessen et al. 1971; Noss et al. 1995, Titus et al. 1996). As a result of this destruction, there are many Willamette Valley wetland prairie species threatened with extinction such as *Erigeron decumbens* var. *decumbens*, *Lomatium bradshawii*, and *Sidalcea nelsoniana*. In addition to those of the Willamette Valley, native prairies have also nearly disappeared in the Great Plains and in California (Schulenberg 1967, Bock & Bock 1995, Noss et al. 1995).

Despite the widespread destruction of these ecosystems, patches of wetland prairie do remain in the Willamette Valley. These prairies are not pristine, however, and in many cases the flora only vaguely resembles that of the early 1800's. Remnant wetland prairies have been heavily invaded by exotic plant species and these exotics often dominate the plant community. Some of the most rampant invasive species are *Agrostis capillaris* (colonial bentgrass, formerly *A. tenuis*), *Anthoxanthum odoratum* (sweet vernal grass), *Holcus lanatus* (velvetgrass), *Poa pratensis* (Kentucky bluegrass), and *Phalaris arundinacea* (reed canarygrass) (Franklin & Dyrness 1988, Wilson 1998). All of these species were introduced from Europe, although native genotypes of *Phalaris* probably existed in the Pacific Northwest before European cultivars were introduced.
Grasses as a group are probably the most widespread and detrimental of all invasive plants (Knops et al. 1995, D’Antonio et al. 1998).

Exotic species invasions create huge problems for land managers who attempt to conserve and protect native species and communities (Temple 1990, Berger 1993). Exotic species present problems because they can displace desirable native species and interrupt or alter ecosystem processes. Many invasive species are reported to have superior competitive ability and, thus, outcompete native species (Parker et al. 1993, Randall 1996, Parker & Reichard 1998). Invasive species also impact ecosystem functions by changing nutrient cycling rates (Versfeld & van Wilgen 1986, Vitousek & Walker 1989), altering the intensity and frequency of fire (Mack 1981, D’Antonio & Vitousek 1992), and changing plant-soil-water relations (Randall 1996).

The notion that invasive species are competitively superior to native species is, surprisingly, a subject that has received little study. Both D’Antonio and Vitousek (1992) and Parker and Reichard (1998) report that although many studies do suggest that native species are suppressed in the presence of invasive species, very few studies have tested the mechanism by which this occurs. Thus, there is little empirical evidence to support the widely accepted notion that invasive species are stronger competitors than native species.

The success of some invasive species has been attributed to changes in nitrogen cycling. Since invasive species are often fast-growing and “nitrogen-loving”, increases in nitrogen can promote these species (Aerts & Berendse 1988,
Berendse et al. 1992, Wedin & Tilman 1996). Increasing rates of nitrogen deposition due to agricultural runoff and air pollution have been blamed for the displacement of native species in other ecosystems (Bobbink & Willems 1987, Moore 1995, Pitcairn et al. 1995). Since nitrogen fertilizers are widely used in the Willamette Valley, it is possible that changes in nitrogen levels could be affecting plant interactions here.

In sum, Willamette Valley wetland prairies are threatened by many adversities such as habitat destruction, invasive species, and nitrogen pollution. What can be done to ensure that these prairies continue to exist? Many ecologists argue that protecting the native ecosystems that remain will not be enough to save these systems, since factors like pollution, invasive species, and others will continue to threaten and degrade these “protected” areas (Sinclair et al. 1995). Many ecologists argue that ecological restoration must be employed in order to protect threatened ecosystems. This ecological restoration is a two-fold process which entails (1) the re-establishment of native plants, and (2) the restoration of natural ecosystem functions (e.g., the re-introduction of fire, natural flooding, or the reduction of nutrient deposition) (Berger 1991, Hobbs & Humphries 1995, Randall 1996). These ecologists have suggested that without the restoration of natural ecosystem properties and functions, invasive species will continue to persist at the expense of native species.

Because of the potential for nitrogen pollution to alter Willamette Valley wetland prairies, one of the goals of my dissertation research was to explore the role of nitrogen in the interactions between native and exotic plant species. My
hypotheses were that (1) increasing available soil nitrogen would cause an
increase in the abundance of invasive species, and (2) reducing available soil
nitrogen would suppress the exotic species while promoting native plants. My
investigations of the effect of nitrogen levels are described in Chapters 2, 3 and 4.

I also researched the role of competition in my dissertation work, since
competition is a hugely debated topic in ecology, reported by some to greatly
influence the composition of plant communities (see Tilman 1982, Connell 1983,
Schoener 1983, Goldberg & Barton 1992), and few studies have examined the
role of competition between native and exotic plant species. In my research
(Chapter 5), I sought to determine the relative competitive abilities of several
common native and exotic grass species by growing and comparing these plants
under different hydrologic regimes. I predicted that their competitive abilities
would match my observations of their distribution in the field, i.e. that
*Anthoxanthum odoratum, Agrostis capillaris, and Holcus lanatus* would have the
highest competitive abilities in the driest zones, *Deschampsia cespitosa* would
have the highest competitive ability in the middle zones, and *Phalaris
arundinacea* would be the best competitor in the wettest zones.

In my final chapter (Chapter 6), I draw on my results on the role of
nitrogen and competition in wetland prairies to make suggestions for how these
important ecosystems might be restored.
References


Chapter 2
The Effects of Carbon Amendments on Species Establishment in an Oregon Wetland Prairie

Abstract

Soil carbon additions could be an effective site preparation tool in restoration if they reduce soil nitrogen levels via enhanced microbial immobilization, which in turn controls nitrophilous weedy plants. Previous studies have been limited to upland ecosystems and have yielded mixed results. We tested experimentally the effect of three levels of sugar and sawdust additions to a wetland prairie in western Oregon. Carbon additions resulted in significantly reduced levels of soil nitrogen, lower final aboveground biomass of unsown exotic grasses and a cosmopolitan weedy grass, and more aboveground biomass of the dominant native bunchgrass Deschampsia cespitosa sown into treatment plots. The increase in native plants seems to be from reduced competition by weedy grasses. These results demonstrate the potential of carbon additions as an effective tool in restoring degraded wetland prairies.
Introduction

Soil carbon amendments have recently been tested for controlling weeds and promoting native plants during ecological restoration. By adding carbon amendments to the soil, the carbon-limited microbial community proliferates and increases nitrogen immobilization. The resulting reduction in available soil nitrogen can influence species composition. In particular, native plants often grow slowly and have lower nitrogen affinities than their weedy, rapid-growing competitors (Bobbink & Willems 1987, Aerts & Berendse 1988, Berendse et al. 1992, Wedin & Tilman 1996), and reducing nitrogen availability through carbon additions may give native species an advantage over nitrophilous exotics.

While some experiments in soil carbon amendments have shown very limited or no success (Wilson & Gerry 1995, Seastedt et al. 1996, Hopkins 1998), other studies demonstrate that carbon additions are effective in decreasing weed growth and increasing native plant establishment (Morgan 1994, Zink 1994, Zink & Allen 1998). To our knowledge, all studies of this kind have been attempted in well-drained, upland communities, and not in wetlands.

We performed an experiment to see whether carbon additions might be useful in restoring a Willamette Valley wetland prairie. Our main objectives were to (1) determine whether we could reduce available soil nitrogen by adding sucrose and sawdust, (2) determine whether reducing soil N availability would suppress weed establishment, and (3) determine whether these treatments would aid in the establishment of native species. The results from this study pertain
directly to large areas of degraded wetland prairie in western Oregon. The results will also help resolve the issue of the role of soil carbon amendments in ecological restoration in general.

Natural History of Willamette Valley Wetland Prairies

The wetland prairies of western Oregon are poorly-drained grasslands that become saturated or inundated subsequent to autumn rains and remain wet through late spring. Prior to European settlement in the 1850's, this plant community was dominated by the native perennial grass Deschampsia cespitosa (tufted hairgrass), along with subdominant grasses such as Hordeum brachyantherum (meadow barley), Beckmannia syzigachne (American sloughgrass), Danthonia californica (California oatgrass) and Agrostis exarata (spike bent grass) (Habeck 1961, Wilson 1998). These grasses, with the exception of A. exarata, are bunchgrasses having tufted growth forms.

Urbanization, agriculture, exotic species invasion, and ecological succession have reduced Willamette Valley wetland prairies to less than 1% of their extent in the 1850's (Johanessen et al. 1971, Noss et al. 1995, Titus et al. 1996). Most degraded wetland prairies are now dominated by exotic grasses such as Holcus lanatus (velvetgrass), Agrostis capillaris (colonial bent grass), Alopecurus pratensis (meadow foxtail), Anthoxanthum odoratum (sweet vernal grass) and others. These grasses are seemingly fast-growing,
rhizomatous species that spread rapidly, characteristics that aid in their invasion of these wetland prairies.

Methods

Study Area

This study was conducted in a degraded wetland prairie, the Neilson Wetlands in the southern Willamette Valley west of Eugene, Oregon (44°3’30”N, 123°12’30”W). The site had been undisturbed since January 1994 when it was purchased by the U.S. Bureau of Land Management. Prior to that, the site was used for sheep grazing and may have also been cultivated for ryegrass production. The climate is temperate with average annual precipitation of about 107 cm and average annual air temperature of 11°C (Oregon Climate Service, Fern Ridge Dam, 1961-1990). Precipitation is highly seasonal, with approximately 90% occurring between October and May. The soils are of the Dayton silt loam (clay substratum series) and are very poorly drained (Soil Conservation Service 1987). Exotic, perennial plant species dominated the site, especially Holcus lanatus, Agrostis capillaris, and Hypochaeris radicata (rough cat’s-ear). The only native species that was common at the site was the rhizomatous grass Agrostis exarata. The native grasses Deschampsia cespitosa and Beckmannia sisygachne were present in very low abundance. (Plant nomenclature is concurrent with that of Hickman 1993.)
Experimental Design

In September 1996, we marked eight blocks across the study site and tractor-tilled these areas to a depth of roughly 30 cm. We next located eight, 0.5 x 0.5-m treatment plots within each block and randomly assigned each to one of eight carbon-sowing treatments.

The carbon-addition treatments ("high", "medium", "low", and control) and sowing treatments (sown and unsown) were applied in a factorial design. The high, medium, and low carbon treatments each received 1.0 kg/m² of both sucrose and sawdust on October 21, 1996. On May 18, 1997, the high carbon treatment received another 0.3 kg/m² sucrose, and the medium carbon treatment received another 0.1 kg/m² sucrose. These rates of carbon addition are similar to those used in other studies (Turner and Olson 1976, Morgan 1994, Wilson and Gerry 1995, Jonasson et al. 1996). The control treatments received no carbon. The sucrose and sawdust were spread uniformly across each treated plot, including a 0.25-m wide buffer. The first treatments were worked into the soil with a hand rake, while the second treatments were sprinkled on top of the soil.

Six native wetland prairie species were used in the sowing treatments: *D. cespitosa*, *B. syzigachne, Hordeum brachyantherum*, and the Asterid forb species *Eriophyllum lanatum* (Oregon sunshine), *Grindelia integrifolia* (Puget Sound grindelia), and *Microseris laciniata* (cut-leaf microseris). Sown plots were seeded with an equal mixture of all six species at 1 seed/cm² on October 28, 1996. Seeds were spread evenly across the plots and covered
with approximately 1 cm of soil. All seeds were collected from wetland prairies within a 50-km radius of our study site.

**Data Collection**

Samples were collected on May 29, 1997, from the upper 10 cm of soil. Thirty-two samples, one from each carbon treatment per block, were randomly selected and analyzed individually for available ammonium (NH$_4^+$), nitrate (NO$_3^-$), and extractable phosphates (P) in the laboratory. Soil NH$_4^+$ and NO$_3^-$ were extracted from still-moist, homogenized samples within 24 hrs of field collection by shaking approximately 10 g soil with 50 ml 2N KCl for 1 h. P was extracted similarly but using 3 g soil and 21 ml dilute acid fluoride (0.03N in NH$_4$F and 0.025N in HCl). During the extraction process, sub-samples were placed in pre-weighed tins and dried at 110° overnight to determine soil moisture content. The shaken soil-solution samples were filtered through Whatman no. 42 paper and the supernatant was analyzed colorimetrically using an Alpkem Rapid Flow Analyzer, Model 300 series. These measurements were adjusted to account for soil moisture.

Plant biomass was harvested from all treatment plots between July 14 and July 21, 1997. A 0.2 × 0.5-m quadrat was located in the center of each plot and all aboveground biomass in these quadrats was removed using a serrated knife. Plants were then separated into bags by species or group (named later), dried at 80°C for approximately 48 hrs, and weighed.
**Statistical Analyses**

All treatment-effect data were analyzed using analysis of variance (ANOVA) after data were transformed to meet statistical assumptions. For most data, an inverse transformation was used (e.g., $1/r + 10$). In cases where ANOVA analyses detected significant differences, Tukey's Honestly Significant Difference (HSD) Test was used to determine significant differences among groups (Day and Quinn 1989). All analyses were conducted with Statgraphics Plus for Windows version 4.0.

**Results**

*Effects of Carbon Additions on Soil Fertility*

Carbon treatments significantly affected nutrient availability (Table 2.1). Both ammonium and nitrate levels were lowest in the high carbon treatments, about one-fourth the levels in unmanipulated controls. Ammonium and nitrate were also significantly lower in the medium carbon treatments than in the low and control carbon treatments. Extractable phosphorus levels were significantly lower in the control plots than in the medium carbon treatment, but were indistinguishable from the high and low carbon treatments.
Table 2.1. Mean soil nutrient availability (µg/g dry soil) (with standard errors) after experimental addition of soil carbon in samples collected May 29, 1997.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>High</th>
<th>Medium</th>
<th>Low</th>
<th>Control</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ammonium</td>
<td>0.56a</td>
<td>0.79a</td>
<td>1.38b</td>
<td>2.20b</td>
<td>33.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nitrate</td>
<td>0.014a</td>
<td>0.061b</td>
<td>0.51c</td>
<td>0.63c</td>
<td>49.85</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Phosphate</td>
<td>9.49ab</td>
<td>10.64a</td>
<td>9.38ab</td>
<td>8.50b</td>
<td>6.15</td>
<td>0.001</td>
</tr>
</tbody>
</table>

The F and P value are from an analysis of variance. In the same row, means followed by the same letter are deemed not significantly different from each other by Tukey’s Honestly Significant Difference Test, α = 0.05.

**Treatment Effects on Plant Establishment**

Two of the three sown bunchgrasses established well in the sown plots. *Deschampsia cespitosa* and *Beckmannia syzigachne* established in most plots where sown, while *Hordeum brachyantherum* was present in just one of the 32 plots (Table 2.2). *Glyceria occidentalis* is a rare, native grass unsown by us that established in three of the 64 total plots. The establishment of native forbs was low, occurring in only 22% of the plots (14 out of 64), and exotic forbs were present in just 34% of the plots (22 out of 64).
Table 2.2. Plant taxa found in the experimental plots.

<table>
<thead>
<tr>
<th>Species or group</th>
<th>Description</th>
<th>Sown?</th>
<th>Frequency*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deschampsia cespitosa</td>
<td>Native bunchgrass, historically dominant species</td>
<td>Yes</td>
<td>32</td>
</tr>
<tr>
<td>Beckmannia syzigachne</td>
<td>Native bunchgrass, common but restricted to wetter prairies</td>
<td>Yes</td>
<td>24</td>
</tr>
<tr>
<td>Hordeum brachyantherum</td>
<td>Native bunchgrass, becoming uncommon in the Valley</td>
<td>Yes</td>
<td>1</td>
</tr>
<tr>
<td>Agrostis exarata</td>
<td>Native rhizomatous grass, common in the Valley</td>
<td>No</td>
<td>31</td>
</tr>
<tr>
<td>Glyceria occidentalis</td>
<td>Native grass, now uncommon in the Valley</td>
<td>No</td>
<td>1</td>
</tr>
<tr>
<td>Native forbs</td>
<td>The sown Eriophyllum lanatum, Grindelia integrifolia, and Microseris lacinia, and the unsown Lotus purshianus</td>
<td>Yes</td>
<td>11</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species or group</th>
<th>Description</th>
<th>Sown?</th>
<th>Frequency*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alopecurus geniculatus</td>
<td>Cosmopolitan, weedy perennial rhizomatous grass</td>
<td>No</td>
<td>25</td>
</tr>
<tr>
<td>Juncus bufonius</td>
<td>Cosmopolitan, weedy annual Rush</td>
<td>No</td>
<td>20</td>
</tr>
<tr>
<td>Exotic grasses</td>
<td>Rhizomatous perennials Agrostis capillaris, Holcus lanatus, &amp; Lolium perenne</td>
<td>No</td>
<td>19</td>
</tr>
<tr>
<td>Exotic forbs</td>
<td>Perennials Hypochaeris radicata &amp; Leontodon taraxacoides, with the annual Parentucellia viscosa</td>
<td>No</td>
<td>10</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species or group</th>
<th>Description</th>
<th>Sown?</th>
<th>Frequency*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exotic forbs</td>
<td>Perennials Hypochaeris radicata &amp; Leontodon taraxacoides, with the annual Parentucellia viscosa</td>
<td>No</td>
<td>10</td>
</tr>
</tbody>
</table>

* Number of plots in which the species or group was found at the time of sampling, out of 64 possible plots (32 sown plots and 32 unsown plots).

**D. cespitosa** and **Alopecurus geniculatus** were the most abundant species in the experimental plots; also abundant were the exotic grasses. All three varied significantly in biomass among carbon treatments (Tables 2.3 and 2.4). For the native bunchgrass **D. cespitosa**, biomass was four- and six-times higher in the medium and high carbon treatments, a statistically significant increase, compared to the control treatment (Table 2.5). The
effect was opposite for the cosmopolitan weed *A. geniculatus* and the exotic grasses, where biomass was significantly reduced to less than half the biomass in the control treatments (Table 2.5).

Sowing treatments did not significantly affect any of the plant groups that were not, themselves, sown. Sowing did affect (Table 2.4) the total amount of plant biomass in the plots, with the sown plots having more biomass (66.3 g/quadrat) than the unsown (47.7 g/quadrat) (Table 2.5).

*H. brachyantherum*, *G. occidentalis*, native forbs and exotic forbs had frequencies too low (establishment in fewer than 22 of 64 plots) for valid statistical analyses.

Table 2.3. Analysis of variance for treatment effects on final aboveground biomass for the two sown species *Deschampsia cespitosa* and *Beckmannia syzigachne*.*

<table>
<thead>
<tr>
<th>Term</th>
<th>d.f.</th>
<th><em>D. cespitosa</em></th>
<th><em>B. syzigachne</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS F P</td>
<td>MS F P</td>
</tr>
<tr>
<td>Block</td>
<td>7</td>
<td>0.00100</td>
<td>0.00168</td>
</tr>
<tr>
<td>Carbon Treatment</td>
<td>3</td>
<td>0.00238 5.21 0.008</td>
<td>0.00050 1.52 0.23</td>
</tr>
<tr>
<td>Residual</td>
<td>21</td>
<td>0.00046</td>
<td>0.00033</td>
</tr>
</tbody>
</table>

* Only sown plots were included in these analyses since these species were not present in unsown plots.
Table 2.4. Analysis of variance for treatment effects on final aboveground biomass for *Agrostis exarata*, *Alopecurus geniculatus*, *Juncus bufonius*, exotic grasses, and total biomass.

<table>
<thead>
<tr>
<th>Term*</th>
<th>d.f.</th>
<th><em>A. exarata</em></th>
<th></th>
<th><em>A. geniculatus</em></th>
<th></th>
<th><em>J. bufonius</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>P</td>
<td>MS</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Block</td>
<td>7</td>
<td>0.00054</td>
<td>0.0070</td>
<td>0.0029</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carbon</td>
<td>3</td>
<td>0.00086</td>
<td>2.59</td>
<td>0.08</td>
<td>0.0013</td>
<td>4.55</td>
<td>0.01</td>
</tr>
<tr>
<td>Treatment</td>
<td>1</td>
<td>0.00008</td>
<td>0.24</td>
<td>0.63</td>
<td>0.00017</td>
<td>0.57</td>
<td>0.46</td>
</tr>
<tr>
<td>Sowing</td>
<td>1</td>
<td>0.00033</td>
<td>0.00029</td>
<td>0.00052</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>52</td>
<td>0.00033</td>
<td>451.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Term*</th>
<th>d.f.</th>
<th>Exotic grasses</th>
<th>Total biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Block</td>
<td>7</td>
<td>0.0049</td>
<td>451.9</td>
</tr>
<tr>
<td>Carbon</td>
<td>3</td>
<td>0.0018</td>
<td>8.53</td>
</tr>
<tr>
<td>Treatment</td>
<td>1</td>
<td>0.00048</td>
<td>2.33</td>
</tr>
<tr>
<td>Sowing</td>
<td>52</td>
<td>0.00021</td>
<td>336.6</td>
</tr>
</tbody>
</table>

* All interaction terms (Block x Carbon, Carbon x Sowing, Sowing x Block) were insignificant and their mean squares have been incorporated in the residuals.
Table 2.5. Mean plant biomass (g per 0.1 m² quadrat) (with standard errors) for each carbon treatment.*

<table>
<thead>
<tr>
<th>Species</th>
<th>High</th>
<th>Medium</th>
<th>Low</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. cespitosa</em>*</td>
<td>42.0a</td>
<td>28.4a</td>
<td>23.6ab</td>
<td>7.1b</td>
</tr>
<tr>
<td></td>
<td>(9.7)</td>
<td>(9.2)</td>
<td>(6.6)</td>
<td>(2.6)</td>
</tr>
<tr>
<td><em>B. syzigachne</em>*</td>
<td>5.7</td>
<td>4.3</td>
<td>9.5</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>(2.4)</td>
<td>(2.8)</td>
<td>(4.6)</td>
<td>(2.4)</td>
</tr>
<tr>
<td><em>H. brachyantherum</em>*</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>(0.1)</td>
<td>(0.0)</td>
<td>(0.0)</td>
<td>(0.0)</td>
</tr>
<tr>
<td>*A. exarata</td>
<td>8.0</td>
<td>7.0</td>
<td>5.4</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>(1.4)</td>
<td>(1.8)</td>
<td>(1.5)</td>
<td>(1.1)</td>
</tr>
<tr>
<td>*G. occidentalis</td>
<td>0.1</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>(0.1)</td>
<td>(0.1)</td>
<td>(0.0)</td>
<td>(0.0)</td>
</tr>
<tr>
<td>Native forbs</td>
<td>0.3</td>
<td>0.4</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>(0.2)</td>
<td>(0.3)</td>
<td>(0.2)</td>
<td>(0.1)</td>
</tr>
<tr>
<td>*A. geniculatus</td>
<td>12.5a</td>
<td>19.7ab</td>
<td>15.7a</td>
<td>33.7b</td>
</tr>
<tr>
<td></td>
<td>(3.0)</td>
<td>(5.3)</td>
<td>(4.7)</td>
<td>(6.6)</td>
</tr>
<tr>
<td>*J. bufonius</td>
<td>4.6</td>
<td>7.9</td>
<td>11.0</td>
<td>2.5</td>
</tr>
<tr>
<td></td>
<td>(2.2)</td>
<td>(2.7)</td>
<td>(3.9)</td>
<td>(1.6)</td>
</tr>
<tr>
<td>Exotic grasses</td>
<td>5.6a</td>
<td>4.7a</td>
<td>5.1a</td>
<td>14.4b</td>
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<tr>
<td></td>
<td>(3.3)</td>
<td>(2.4)</td>
<td>(1.9)</td>
<td>(4.4)</td>
</tr>
<tr>
<td>Exotic forbs</td>
<td>0.4</td>
<td>0.7</td>
<td>0.2</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>(0.2)</td>
<td>(0.4)</td>
<td>(0.1)</td>
<td>(1.0)</td>
</tr>
<tr>
<td>Total biomass</td>
<td>55.4</td>
<td>56.7</td>
<td>54.2</td>
<td>61.8</td>
</tr>
<tr>
<td></td>
<td>(6.3)</td>
<td>(5.6)</td>
<td>(5.5)</td>
<td>(3.9)</td>
</tr>
</tbody>
</table>

* In the same row, means followed by the same letter are deemed not significantly different from each other by Tukey's Honestly Significant Difference Test. ** The unsown plots were excluded from these means.

Discussion

**Effects of Carbon Additions on Soil Fertility**

Our analyses show that carbon treatments effectively reduced available soil nitrogen and that nitrogen reduction increased with increased carbon input.

Other researchers have employed similar nitrogen-reduction techniques in old-fields (Wilson & Gerry 1995), semi-arid grasslands (Hopkins 1998), coastal sage scrub (Zink & Allen 1998), subtropical rainforests (Lamb 1980), and reclaimed
mining fields (Williamson & Johnson 1994). Nitrogen reduction trends due to our carbon additions in western Oregon wetland prairies appear to accord with these studies, despite our study area being the only wetland system.

Extractable phosphorus levels were affected by the carbon treatments in a way opposite to what we expected. Phosphorus levels were significantly lower in the control plots than in the medium carbon treatment plots. This contradicts other findings where both available phosphorus and nitrogen were significantly decreased in sugar and sawdust-treated plots in a mixed grassland-shrub ecosystem (Jonasson et al. 1996). That our experiment was conducted in a wetland system may be the reason we observed lower phosphate levels in non-carbon treated plots. It has been well documented that soluble phosphorus levels increase in wetlands that become anoxic as the ferric iron of ferric phosphates is reduced (Mitch & Gosselink 1993). Plots receiving added carbon are more likely to become anoxic than non-treated plots, and this may explain why carbon-treated plots showed higher phosphate levels. That phosphorus levels were increased by carbon additions, and not decreased, may be unimportant for the establishment of native versus weedy plants, since nitrogen, and not phosphorus, is generally the limiting nutrient in prairie (Risser 1985, Wilson & Tilman 1991) and wetland prairie (Morris 1991, Verhoeven et al. 1996) soils.
Treatment Effects on Plant Establishment

Carbon treatments significantly affected three plant groups in this study. *Alopecurus geniculatus* and exotic grass establishment decreased with the addition of carbon, while *Deschampsia cespitosa* establishment increased. The exotic grass species, *Agrostis capillaris*, *Holcus lanatus*, and *Lolium perenne*, are fast growing species (Hayes 1976, Grime et al. 1990, Poorter et al. 1995) with high nitrogen affinities (Olff et al. 1990, Olff & Bakker 1991). These grasses, along with *A. geniculatus*, were likely deterred from growing at their usual rapid pace because of the reduction in available soil nitrogen. *D. cespitosa*, in contrast, is a slowly growing species (Rahman 1976, Collet et al. 1996) which was not suppressed by the reduced nitrogen availability. That total biomass did not change across carbon treatments suggests that *D. cespitosa* benefited considerably from the reduced competition with the weedy grasses and exploited those available resources. These results indicate that carbon additions may be very effective in suppressing weedy grasses and promoting slower growing native grasses in Willamette Valley wetland prairies.

Carbon addition has been employed as a means for restoring degraded plant communities only in a handful of cases. When carbon additions have shown significant effects, exotic species were reduced in abundance compared to control plots, but native species remained unaffected (Morgan 1994, Seastedt et al. 1996). To our knowledge, an increase in growth of native California sagebrush seedlings with straw and bark soil amendments
(Zink & Allen 1998) is the only case other than our study in wetland prairies to show success in promoting native species via carbon additions.

The carbon treatments delivered in this study may have helped to return soil nitrogen conditions to their natural, pre-disturbed state. The native dominant grasses of the Willamette Valley wetland prairies are slow growing bunchgrasses, with dense, fibrous root systems. In the shortgrass steppe of Colorado, the vegetation is similar in that the dominant native plants are bunchgrasses while the dominant exotic plants are rhizomatous grasses that have less underground biomass than the bunchgrasses. In shortgrass steppe, native bunchgrasses shed more carbon from their root systems, support greater microbial biomass, and sustain lower nitrogen mineralization rates than do the rhizomatous grasses (Vinton & Burke 1995). Thus the native grasses appear to sustain their own slow-nitrogen-release system.

Conversely, the rhizomatous grasses release little carbon from their roots and sustain high nitrogen mineralization rates. In the Colorado site, rhizomatous grasses established 20 years earlier when fertilizers were added as part of a prior experiment. Nitrogen mineralization rates associated with native perennial bunchgrasses are lower than with exotic rhizomatous grasses in other systems as well (Wedin & Tilman 1990, 1996). Once nitrogen levels in disturbed soils are raised and exotic grasses become established, high rates of nitrogen turnover can serve as a "positive feedback" system that perpetuates high soil nitrogen levels (Vinton & Burke 1995, Jefferies & Maron 1997). If a similar phenomenon occurs in Willamette Valley prairies, with exotic
rhizomatous grasses, once established, maintaining soil nitrogen conditions that favor their own persistence, then carbon amendments should be useful in restoring soil conditions that favor native bunchgrasses.

Most Willamette Valley wetland prairies are dominated by dense, weedy rhizomatous grasses that resprout readily after disturbance. Extensive measures will be needed to control these pest species and make conditions more favorable for the natives to establish. Our study suggests that carbon additions may, indeed, be effective in wetlands for deterring weedy species and promoting desired natives.

Organic amendments besides sucrose and sawdust might be used instead of sucrose and sawdust to reduce soil nitrogen levels. Other studies have shown that soil nutrients can be effectively immobilized with the addition other materials, such as wheat straw and straw and rape residues (Powlson et al. 1985, Williamson & Johnson 1994, Wu et al. 1995) and oat straw and pine bark (Zink & Allen 1998). The use of these organic waste materials remains untested in wetland systems.

Acknowledgements

We heartily thank the U.S. Bureau of Land Management of Eugene, Oregon, for their generous support of this research and for the use of the Neilson Wetlands study site, with a special thanks to Jock Beall for his interest, support, and help in tilling our plots. We thank Carol Glassman for her assistance with soil nutrient analyses, Georgine Yorgey for help with field data collection and
Isaac Babcock for his help with initial set-up in the field. We are also grateful to Kate Lajtha, Don Zobel, David Myrold, Jeff Steiner, and Jack DeAngelis for their insightful comments and suggestions on this manuscript.
References


Chapter 3
Sugar, Carbon Treatment Kills Plants in Soil Impoverishment Experiment (Oregon)

Kimberly J. Davis and Mark. V. Wilson

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Summer 1997
Volume 15, Pages 80-81
Adding carbon to the soil, or “soil impoverishment” (Morgan 1994), has been hailed as a way to suppress nitrogen-loving weeds. The idea is to add large amounts of organic carbon, increase microbial activity and, thereby, decrease the available nitrogen in the soil. Various studies indicate that the low nitrogen condition starves out the weeds (Carson & Barrett 1988, Tilman & Wedin 1991). John Morgan (1994) reported that adding sugar and sawdust to plots sown with seeds of prairie species dramatically decreased weed abundance. Other prairie ecologists (Seastedt et al. 1995, Wilson and Gerry 1995) have reported mixed results with this method. Inspired by the possibility of a weed-free restoration, we began an experiment to learn whether carbon-rich soil amendments might suppress weedy exotics in our local wetland prairies—communities inundated or saturated for much of the winter and spring. To our knowledge, this nitrogen-reducing technique has never been tried in wetland prairies.

We began our experiment in a degraded wetland prairie within the Fern Ridge Natural Area in Eugene, Oregon. We established six test blocks across the prairie, each with a carbon-amended plot and a no-carbon (control) plot. These blocks were rototilled, treated, and retilled on September 13, 1995. The carbon-amended plots received a 50/50 mixture of sugar and sawdust at a rate of 2.0 kg/m². In November 1995, we hand-seeded subplots within the treated plots with a mix of five native wetland prairie species: American sloughgrass (*Beckmannia syzigachne*), California oatgrass (*Danthonia californica*), tufted hairgrass (*Deschampsia cespitosa*), Oregon sunshine (*Eriophyllum lanatum*), and cut-leaved microseris (*Microseris laciniata*). To compare the responses of exotics,
we also added six non-native species, including colonial bentgrass (*Agrostis tenuis*), sweet vernal grass (*Anthoxanthum odoratum*), velvet grass (*Holcus lanatus*), rough cat's ear (*Hypocharis radicata*), hairy hawkbit (*Leontodon nudicaulis*), and reed canary-grass (*Phalaris arundinacea*).

During the spring of 1996, we observed seedling growth and, in five of the six plots, it was easy to see which plants received the carbon treatments. Plants in those plots looked stunted and more yellow than plants in the control plots—evidence of nitrogen deficiency. We did not note, however, whether the carbon amendment affected exotic species any more than it affected the natives.

To sustain the effects of the nitrogen reduction, on May 12, 1996 we added another dose of sugar at a rate of 0.5 kg/m². The result was shocking! Nine days after we applied the additional carbon amendments, all the plants in these plots were dead. The sugar treatments, which were designed to favor prairie species in their competition with exotic weeds had, instead, killed all the species.

Immediately after the plants died, we collected 24 soil samples from all the plots and analyzed them for ammonium and nitrate levels. We found that ammonium levels were significantly lower (P = 0.02) in the carbon-treated plots (0.0064 mg NH₄/g soil) than the control plots (0.0138 mg NH₄/g soil), while nitrates did not differ significantly (0.0046 mg NO₃/g soil and 0.0040 NO₃/g soil). Thus, the carbon-addition treatments were successful in reducing nitrogen availability in these wetland prairie soils.

What went wrong? At this point, we can only speculate. We rejected the idea that a "sugar-loving" fungal pathogen was responsible because a pathogen
would have affected plants adjacent to the plots. Then, after noting that the soil in
the treated plots smelled strongly of hydrogen sulfide, we weighed the possibility
that the sudden, severe anaerobic conditions induced by rapid microbial growth
with the addition of the sugar adversely affected the plants. We concluded,
however, that a lack of oxygen, by itself, is not likely to have caused mortality
because these species are adapted to anaerobic conditions. It may also be the case
that the plants died due to the fact that the increased anaerobic respiration
generated a surge of toxic by-products, such as alcohols and organic acids. We
have also hypothesized that the plants may have become dehydrated due to
negative osmotic pressure caused by sugar in the soil.

Whatever the case, we have begun new experiments to determine whether
we can create nitrogen-reducing effects through carbon treatments without killing
the plants. In these experiments we plan to include separate spring and fall
treatments with various levels of organic matter being added, although some
spring treatments will receive no organic matter. We would appreciate any
comments or correspondence regarding this technique.
References


Chapter 4
The Effects of Soil Nitrogen Manipulation on the Establishment of Native and Weedy Plant Species in an Oregon Wetland Prairie

Abstract

Weedy plants are widely reported to be nitrophilous. Consequently, we used soil nitrogen manipulation (increasing nitrogen via ammonium nitrate additions and decreasing nitrogen via sucrose and sawdust additions), to test whether soil nitrogen levels would affect the biomass of weeds and desired native species in a western Oregon wetland prairie. Soil additions were added to tilled plots in December 1995, May 1996 and September 1996. Native species were sown into these plots in fall 1996, and all plant biomass was harvested in July 1997. Water table levels in these plots were also measured.

The carbon-addition treatments were effective in reducing both ammonium and total available soil nitrogen in 1996, and fertilizer additions strongly increased soil nitrogen levels during the whole study period. Soil treatments also significantly affected native grasses, exotic grasses, and relative native biomass (total native species/total weed species). The aboveground biomass of the natives in both the carbon and nitrogen treatments were seven times higher than in the control treatment. Biomass of the exotic grasses was highest in the nitrogen plots and least in the carbon plots. As a result, carbon treatments produced the highest ratio of native
biomass to total weed biomass. Relative native biomass was also high in the nitrogen treatments, but only along the wetter end of the water gradient. Plot wetness significantly affected the biomass of most plant groups, with exotic grasses and exotic forbs more abundant in drier plots, regardless of nitrogen manipulations. These results suggest that carbon additions can be effective in suppressing weeds and promoting native plants during wetland prairie restoration, especially in relatively wet plots.
Introduction

That weedy plants establish better than non-weedy plants under high nitrogen conditions has been widely reported (Berendse et al. 1987, Bobbink & Willems 1987, Heil & Bruggink 1987, Carson & Barrett 1988, Carson & Pickett 1990, McLendon & Redente 1991, Moore 1995, Pitcairn et al. 1995, Wedin & Tilman 1996). Weedy plants tend to grow fast and can assimilate available soil nitrogen before slower growing species, thus inhibiting the establishment of the slower growing plants (Bazzaz 1979, Grime 1979, McGraw & Chapin 1989, Carpenter et al. 1990, Huenneke et al. 1990, McLendon & Redente 1991). For these reasons, restoration ecologists have used nitrogen-reduction techniques to create soil environments that are unfavorable for weedy species, and thus more favorable for native plants. One technique to lower nutrient concentrations in the soil is to cut and remove aboveground vegetation when these tissues are rich with nitrogen (Oomes et al. 1996, Pfadenhauer & Grootjans 1999). Ecologists have also added different carbon sources to the soil, such as sucrose, sawdust, pine bark, and straw, to reduce available nitrogen (Morgan 1994, Wilson & Gerry 1995, Seastedt et al. 1996, Hopkins 1998, Zink & Allen 1998). In turn, these amendments enable the carbon-limited microbial community to proliferate and incorporate free soil nitrogen into microbial biomass, removing it from the available nitrogen pool.

In the Willamette Valley of western Oregon, restoration of native wetland prairies is challenging due to the presence of many weedy grasses and forbs. In the fall of 1995, we initiated a study using three soil treatments
(nitrogen added in the form of ammonium nitrate, nitrogen reduced by adding carbon in the form of sucrose and sawdust, and control treatments), and sowed a series of species mixtures into these treatment plots in order to measure their response the following year. We hypothesized that the weedy species would establish most successfully in the highest nitrogen treatments, and that the native species would perform best in the lowest nitrogen treatments. As it turned out, our second application of sucrose in the spring of 1996 caused the immediate death of all plants receiving that treatment (see Davis & Wilson 1997). This forced us to redesign our study. In the revised study we used the same treatment plots but sowed new seeds into new sowing plots. Our research question remained: What will be the effect of three nitrogen regimes on native and weedy species?

Methods

Study Area

The study site was a degraded wetland prairie, Horkelia Prairie, in the Fern Ridge Natural Area in the southern Willamette Valley west of Eugene, Oregon, USA (44°0'30"N, 123°15'W). Horkelia Prairie is owned and managed by the U.S. Army Corps of Engineers. Historically, the property was used for grazing and there are signs of attempts to change drainage and reduce flooding. The climate is temperate with average annual precipitation of 107 cm and average annual air temperature of 11°C (Oregon Climate
Service, Fern Ridge Dam, 1961-1990). The soils are the Natroy silty clay loam series and are poorly drained (Soil Conservation Service 1987). The site has a thick clay pan close to the surface that causes seasonal perching of the water table. Thus, the soils at Horkelia Prairie are saturated during much of the winter and spring, and are dry and cracked during the dry summer months.

Horkelia Prairie was dominated by a mixture of native and exotic species. The dominant native grasses were *Deschampsia cespitosa* (tufted hairgrass) and *Danthonia californica* (California oatgrass), both perennial bunchgrasses. Common native forbs included *Grindelia integrifolia* (Puget Sound grindelia), *Eriophyllum lanatum* (Oregon sunshine), *Microseris laciniata* (cut-leaf microseris), and *Prunella vulgaris* var. *lanceolata* (self-heal). The dominant exotic grasses included *Agrostis capillaris* (colonial bentgrass), *Anthoxanthum odoratum* (sweet vernal grass), *Holcus lanatus* (velvet grass), and *Phalaris arundinacea* (reed canary-grass), all rhizomatous perennials. Common exotic forb species included *Hypocharis radicata* (rough cat’s-ear), *Leontodon taraxacoides* (hawkbit), and *Mentha pulegium* (pennyroyal). *Panicum acuminatum* (western witchgrass) is a cosmopolitan weedy perennial that was also widely abundant.

**Experimental Design**

In September 1995, we located six 13-m × 5-m blocks across the study site while incorporating a range of elevations (a range of <20 cm). We then roto-tilled
these blocks to a depth of roughly 25 cm. We staked three 3.5-m × 3.5-m treatment plots within each block and randomly assigned the carbon, control, and nitrogen treatments to one plot each per block. The first soil treatments were added on October 14, 1995. The carbon plots received 1.0 kg sugar/m² plus 1.0 kg fir sawdust/m², the nitrogen plots received 25 g/m² ammonium nitrate, and the controls received no amendments. These additions were spread by hand and worked into the soil with a roto-tiller. On May 12, 1996, more soil amendments were added: 0.5 kg/m² sugar to the carbon plots and 15 g/m² ammonium nitrate to the nitrogen plots. These additions were carefully applied by hand sprinkling as low to the ground as possible (in order to avoid hitting the vegetation that was now present). On May 21, 1996, nine days after the second sugar addition all plants in the sugar-treated plots were dead (Davis & Wilson 1997).

For the revised study, we used the same blocks and treatment plots, and selected three new 0.5-m × 0.5-m sowing plots per treatment plot. On September 27, 1996 we removed all aboveground vegetation and any conspicuous root masses in the new 0.5-m × 0.5-m sowing plots by hand. We also hand spaded the soil to a depth of approximately 5 cm. We applied a final set of soil amendments to these plots and a 0.25-m buffer. To the carbon plots we added sugar in the quantity of 0.1 kg/m² and to the nitrogen plots we added 10 g/m² ammonium nitrate. The amendments were spread carefully and raked into the soil by hand.

In October 1996 we sowed each sowing plot with a mixture of five native species. We used three native grasses, Deschampsia cespitosa,
Danthonia californica, and Hordeum brachyantherum (meadow barley), and two native forbs, Eriophyllum lanatum and Microseris laciniata. Each plot received 100 seeds of each species for a total of 500 seeds. The seeds were spread carefully by hand and were covered with a thin layer (roughly 1 cm) of soil. These seeds were collected in summer 1996 in prairies within 50-km of the study site.

**Data Collection**

We collected soil samples for nitrogen analyses on three different dates. December 6, 1995 we analyzed soils for ammonium (NH$_4^+$) concentrations, and on both May 24, 1996 and May 26, 1997, we analyzed for both ammonium and nitrate (NO$_3^-$). In each case we collected 36 soil samples, 12 from each treatment type. Soil ammonium and nitrate were extracted from still-moist, homogenized samples within 24 hrs of field collection by shaking approximately 10 g soil with 50 ml 2N KCl for 1 h. During the extraction process, sub-samples were placed in pre-weighed tins and dried at 110°C for 24 hrs to determine soil moisture content. The shaken soil-solution samples were filtered through Whatman no. 42 paper and the supernatant was analyzed colorimetrically using an Alpkem Rapid Flow Analyzer, Model 300 series. These measurements were then adjusted to account for soil moisture.

Plant biomass was harvested from all of the 0.25 m$^2$-sowing plots between July 8 and July 12, 1997. All aboveground biomass in each plot was removed by
cutting all plants at soil level with a serrated knife. The plants were then
separated into bags by plant group, dried at 80°C for approximately 48 hrs, and
weighed. We defined eight plant groups: desired native grasses (hereafter
referred to as “native grasses”), native forbs, exotic grasses, exotic forbs, rushes,
_Panicum acuminatum_ (a native weedy grass), _Juncus bufonius_ (a cosmopolitan
weed), and shrubs.

Harvested plant groups included both sowed species and species
establishing without sowing (Table 4.1). The native grass group consisted
primarily of _Deschampsia cespitosa_ and _Danthonia californica_; no _Hordeum
brachyantherum_ established. The native forbs include the three species we
sowed, plus the liliaceous plants _Camassia quamash_ and _Brodiaea_ spp. which
likely resprouted from perennating bulbs, and the legume _Lotus purshianus_. The
exotic grasses that established were the perennial rhizomatous grasses _Agrostis
capillaris, Anthoxanthum odoratum, Holcus lanatus_, and _Phalaris arundinacea_,
and the annual grasses _Briza minor, Bromus hordaceus_, and _Aira caryophyllea_.
Exotic forbs that were present included the perennials _Hypochaeris radicata,
Leontodon taraxacoides, Mentha pulegium, Hypericum perforatum, Plantago
lanceolata_ and the annual species _Parentucellia viscosa_. The majority of plants
in the rushes group were _Juncus marginatus_, a weedy rhizomatous perennial that
has been recently introduced to the Willamette Valley and is now considered a
pest species (Guard 1995). A small number of shrub seedlings were found in only
three sowing plots, and the shrub group is not analyzed further. All plant
nomenclature is concurrent with that of Hickman (1993).
Table 4.1. Composition of each of the eight plant groupings in the experimental plots at Horkelia Prairie.

<table>
<thead>
<tr>
<th>Group</th>
<th>Composition in Harvest</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Desired Native Species</strong></td>
<td></td>
</tr>
<tr>
<td>Native grasses</td>
<td>High abundance of both <em>D. cespitosa</em> and <em>D. californica</em>; no <em>H. brachyantherum</em> established</td>
</tr>
<tr>
<td>Native forbs</td>
<td>Mostly <em>M. laciniata</em> and <em>E. lanatum</em>, with a few <em>G. integrifolia</em>, <em>C. quamash</em>, <em>L. purshianus</em>, and <em>Brodiaea</em> spp.</td>
</tr>
<tr>
<td>Weedy Species</td>
<td></td>
</tr>
<tr>
<td>Exotic grasses</td>
<td>Mostly <em>A. capillaris</em>, <em>A. odoratum</em>, and <em>H. lanatus</em>, with a few <em>P. arundinacea</em>, <em>B. minor</em>, <em>B. hordaceus</em>, and <em>A. caryophylllea</em></td>
</tr>
<tr>
<td>Exotic forbs</td>
<td>Mostly <em>H. radicata</em> and <em>L. taraxacoides</em>, with a few <em>M. pulegium</em> <em>P. viscosa</em>, <em>H. perforatum</em>, and <em>P. lanceolata</em></td>
</tr>
<tr>
<td>Rushes</td>
<td>Over 80% <em>J. marginatus</em>, with a few native <em>Eleocharis</em> sp. and <em>Carex</em> spp.</td>
</tr>
<tr>
<td><strong>Panicum acuminatum</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Juncus bufonius</strong></td>
<td></td>
</tr>
<tr>
<td>Shrubs</td>
<td><em>Rosa</em> spp., <em>Spiraea douglasii</em>, and <em>Crataegus douglasii</em></td>
</tr>
</tbody>
</table>

We also measured the water table of each block. During the 1995-1996 growing season, we made hydrological measurements biweekly from December 13, 1995 to June 1, 1996. When water was ponded, we made several measurements of water depth across all treatment plots and averaged these readings. When water levels were subsurface, we used water wells to record our measurements. Each block contained one water well constructed from PVC piping that enabled us to read water table measurements to a depth of 1 m.
**Statistical Analyses**

We used analyses of variance (ANOVA) to detect significant differences among soil nutrient data by using block and soil treatment as our independent variables. For our biomass data we used water level in place of block, because each water measurement represented one block. We used water levels and soil treatment, as well as their interaction, as our independent variables, in order to determine the effects of water as well as soil treatment on biomass. Residual and normality plots were constructed with each analysis and log transformations were made when warranted. When treatment effects were deemed significant at the 0.05 level, we used Tukey’s Honestly Significant Difference Test to detect specific treatment differences (Steel et al. 1997, Day & Quinn 1989). All analyses were performed using Statgraphics Plus for Windows version 4.0.

**Results**

*Effects of Treatments on Soil Nitrogen Availability*

Soil treatment significantly affected soil nitrogen concentrations (Table 4.2). Ammonium, nitrate, and total available soil nitrogen (ammonium + nitrate) levels were significantly highest in the plots that received ammonium nitrate. Ammonium and total available nitrogen levels were significantly lower in the carbon-treated plots than the control plots in May 1996. By May 1997, nitrogen levels were the same in the carbon-
treated plots and control plots, but still significantly higher in nitrogen-addition plots (Table 4.2).

**Table 4.2.** Means for soil nutrient availability (µg/g dry soil) after experimental addition of nitrogen and carbon in samples collected on three different dates.

<table>
<thead>
<tr>
<th>Form of N</th>
<th>Treatment</th>
<th>December 6, 1995</th>
<th>May 24, 1996</th>
<th>F</th>
<th>p*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>+Carbon</td>
<td>Control</td>
<td>+Nitrogen</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ammonium</td>
<td>25.0a</td>
<td>34.0a</td>
<td>96.1b</td>
<td>23.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nitrate</td>
<td>6.4a</td>
<td>13.8b</td>
<td>599.3c</td>
<td>152.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total available N†</td>
<td>11.3a</td>
<td>27.0b</td>
<td>625.7c</td>
<td>151.3</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

* The p value is from an analysis of variance. In the same row, means followed by the same letter are deemed not significantly different from each other by Tukey’s Honestly Significant Difference Test. † Total available N = ammonium plus nitrate.

**Water Effects on Plant Establishment**

Averages of bimonthly water measurements in each block ranged from –4.5 to –11.7 cm (the negative values indicate subsurface measurements). The aboveground biomass of the native grasses, native forbs, exotic grasses, exotic forbs, rushes and *J. bufonius* was significantly affected by water level (Table 4.3). Biomass of the native grasses, rushes, and *J. bufonius* significantly increased with increasing wetness (Table 4.3). Conversely, biomass of the exotic grasses, exotic forbs, and native forbs...
significantly decreased with increasing wetness (Table 4.3). There were no
significant interactions between water and soil treatment, except with the
ratio of total natives to total weeds.

**Soil Treatment Effects on Plant Establishment**

Soil treatments had significant effects on the aboveground biomass of
native grasses and exotic grasses (Table 4.3). The aboveground biomass of
native grasses was seven times higher in the carbon and nitrogen treatments
than in the control treatment (Table 4.4). Biomass of exotic grasses was five
times higher in the nitrogen treatments than in the controls, and least in the
carbon treatments (Table 4.4). Total biomass in the nitrogen plots was 70%
higher than in both the control and carbon plots, although this was not a
statistically discernable difference.

Soil treatment effects were also significant for the ratio of total
desired native biomass (i.e., native grasses + native forbs, hereafter referred
to as "total native biomass") to total weed biomass (Table 4.3), with the
proportion about seven and four times higher in carbon plots than in the
control and nitrogen plots, respectively (Table 4.4). There was a significant
interaction between hydrology and soil treatment, however (Table 4.4). An
examination of the interaction shows that the ratio of native to weed biomass
changes markedly with hydrology in the nitrogen-treated plots, less so in the
control plots, and remains constant in the carbon-treated plots (Figure 4.1).
Table 4.3. Analysis of variance results for soil treatment, water, and soil treatment x water effects on aboveground biomass.

<table>
<thead>
<tr>
<th>Plant Group</th>
<th>Water</th>
<th>Soil Treatment</th>
<th>Soil x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>b+</td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Native grasses</td>
<td>0.25</td>
<td>17.41</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Native forbs</td>
<td>-0.22</td>
<td>18.07</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Exotic grasses</td>
<td>-0.44</td>
<td>44.68</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Exotic forbs</td>
<td>-0.55</td>
<td>58.33</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>P. acuminatum</td>
<td>-0.04</td>
<td>0.70</td>
<td>0.40</td>
</tr>
<tr>
<td>Rushes</td>
<td>0.58</td>
<td>36.54</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>J. bufonius</td>
<td>0.48</td>
<td>21.24</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total biomass*</td>
<td>-0.02</td>
<td>0.34</td>
<td>0.56</td>
</tr>
<tr>
<td>Total native</td>
<td>+0.10</td>
<td>2.04</td>
<td>0.16</td>
</tr>
</tbody>
</table>

b is the fitted slope showing the relationship between aboveground biomass and water level. Positive values of b show increasing biomass with increasing water.

1 Tested using 1 degree of freedom and the residual M.S. 2 Tested using 2 degrees of freedom and the residual M.S.

*Includes all plant groups, including the small amount of shrubs. ** Total native biomass = native grasses + native forbs; Total weed biomass = exotic grasses + exotic forbs + P. acuminatum + rushes + J. bufonius + shrubs.

Table 4.4. Means for the aboveground plant biomass (g/0.25-m² quadrat) for each soil treatment. *

<table>
<thead>
<tr>
<th>Species</th>
<th>+Carbon</th>
<th>Control</th>
<th>+Nitrogen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native grasses</td>
<td>3.68a</td>
<td>0.52b</td>
<td>3.66a</td>
</tr>
<tr>
<td>Native forbs</td>
<td>0.33</td>
<td>0.71</td>
<td>0.085</td>
</tr>
<tr>
<td>Exotic grasses</td>
<td>1.60a</td>
<td>3.53b</td>
<td>17.9c</td>
</tr>
<tr>
<td>Exotic forbs</td>
<td>2.01</td>
<td>3.41</td>
<td>1.44</td>
</tr>
<tr>
<td>P. acuminatum</td>
<td>0.38</td>
<td>1.12</td>
<td>0.61</td>
</tr>
<tr>
<td>Rushes</td>
<td>9.96</td>
<td>10.61</td>
<td>8.20</td>
</tr>
<tr>
<td>J. bufonius</td>
<td>1.40</td>
<td>1.11</td>
<td>1.46</td>
</tr>
<tr>
<td>Total biomass</td>
<td>22.80</td>
<td>22.85</td>
<td>38.68</td>
</tr>
<tr>
<td>Total native biomass</td>
<td>0.60a</td>
<td>0.08b</td>
<td>0.16b</td>
</tr>
<tr>
<td>Total weed biomass</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* In the same row, means followed by the same letter are deemed not significantly different from each other by Tukey’s Honestly Significant Difference Test.
**Figure 4.1.** Biomass of native species relative to the biomass of weedy species along a wetness gradient in three different soil treatments. Lines show least-fit squares.

Discussion

*Effects of Treatments on Soil Nitrogen Availability*

In this experiment, we successfully reduced available soil nitrogen levels via the addition of sucrose and sawdust, with the strongest reduction in nitrogen levels recorded in May 1996. That ammonium levels were similar in carbon and control plots in December 1995 may be due to cooler weather conditions and thus slower microbial activity and uptake of nitrogen during that time. Similarities in
ammonium levels in carbon and control plots in May 1997 may have occurred because the effects of carbon additions had dissipated in the eight months from the last sucrose addition. Patterns such as these where nitrogen levels in carbon-treated plots slowly decrease and then return to control levels were observed in a similar study (Zink & Allen 1998).

Water Effects on Plant Establishment

Water levels significantly affected all species groups except *P. acuminatum* and total plant biomass. The native grasses and rushes (including the rush *J. bufonius*) produced more biomass in wetter blocks, while the exotic grasses, exotic forbs, and native forbs produced more biomass in the drier blocks, a phenomenon we have observed elsewhere (Steatfield & Frenkel 1997, M.V. Wilson unpublished results). That the rushes showed increased biomass in the wetter plots is not surprising since most rushes are hydrophilic species, but why the native grasses should show increased biomass in wetter plots, while native forbs, exotic grasses, and exotic forbs showed increased biomass in drier plots, is less obvious. These patterns may be the result of physiological limitations (e.g. low tolerance for poorly aerated soils) or ecological interactions (e.g. competition from neighboring plants), since both phenomena are known to dictate species composition in wetlands (Rahman 1976, Grace & Wetzel 1981, Chambers & Prepas 1990, Shipley et al. 1991). Results from our study at the Danebo Wetlands (Chapter 5) indicate that the causes for these patterns are more ecological than physiological, since both the native and exotic grasses grow very well along a
similar wetness gradient in the absence of competition. Because the primary objective of most wetland prairie restoration projects is to re-create a community dominated by native grasses, our results suggest that this might be most easily accomplished in the Willamette Valley on the wetter prairies.

**Soil Treatment Effects on Weedy Species Establishment**

Biomass of the exotic grasses was highest in the + nitrogen plots and lowest in the carbon-treated plots, matching our predictions that weedy species would be abundant where nitrogen is abundant, and less successful where nitrogen was reduced. Although theory suggests these patterns (Bazzaz 1979, Grime 1979, Carpenter et al. 1990), few studies have documented the suppression of weeds by the use of carbon additions. McLendon and Redente (1992) showed that weedy species were displaced in sucrose-treated plots when compared to nitrogen-treated and control plots, and Morgan (1994), Seastedt et al. (1996), and Zink and Allen (1998) have reported some success in suppressing weeds with carbon additions. These studies were in semi-arid or upland prairie ecosystems. The present study is the first demonstration of weed suppression by carbon additions to a wetland.

The rushes, namely *Juncus marginatus*, comprised a large portion of the weed biomass (44%) and were not significantly affected by the soil treatments. Thus, it should be noted that a major component of the weed biomass was not deterred by the carbon treatments. This indicates that carbon additions may be an
effective restoration tool for reducing weedy species in areas dominated by exotic grasses, but perhaps not in areas dominated by weedy rushes.

**Soil Treatment Effects on Native Species Establishment**

The native grasses, comprising 87% of the total native biomass, were significantly promoted in the carbon treatments compared to the controls. This follows our predictions, that native plants would show the most biomass in the carbon-treated plots because of their release from suppression by weedy, nitrophilous plants. These results indicate that carbon additions may be a useful tool for land managers attempting to restore native grasses to wetland prairie systems.

Most surprising to us was the performance of native grasses in the + nitrogen treatments, where native grass biomass equaled that of the carbon-treated plots (Table 4.3). We assumed that, because nitrogen levels would be favorable for the weedy plants in the nitrogen plots, these weeds would, in turn, suppress the native species in these treatments. The unexpected increase in native grass biomass in the nitrogen-treated plots may be the result of a decrease in belowground competition among the plants. The amount of soil nitrogen in these plots was very high compared to control levels (Table 4.2). Thus, it is reasonable to suggest that the native and exotic grasses were not in competition for nitrogen in the + nitrogen plots, which allowed both groups to have significantly higher biomass.
Ratio of Native to Weed Biomass

The ratio of native biomass to weed biomass within each soil treatment depended upon hydrology. In the wetter plots, the ratio of native to weed biomass was higher in both the carbon and nitrogen treatments compared to the controls (Figure 4.1). This pattern changed, however, as water levels decreased, with the ratio being much lower in the nitrogen treatments compared to the carbon treatments. Meanwhile, the ratio of native to weed biomass in the carbon treatments remained high across the water gradient.

These results suggest that carbon additions are effective in suppressing weed biomass and promoting native biomass regardless of position along the tested water gradient. Conversely, nitrogen effects on relative native biomass change with hydrology. We suggest that this change is due to growth patterns in the exotic grasses, which as a group comprised 60% of the weed biomass in the nitrogen treatments. As reported earlier (Table 4.3), exotic grass biomass decreased with increasing plots wetness. Furthermore, at the Danebo Wetlands, many of the same exotic grasses tolerated wetter conditions when grown in monocultures, but were greatly reduced when grown with native grasses (Chapter 5). These factors suggest that the exotic grasses are able to outcompete the native grasses under drier conditions, while the native grasses outcompete the exotic grasses when conditions are wetter.

Thus, the successful establishment of native species relative to weedy species is affected both by soil treatment and plot wetness, with the relative performance of native species being best in (a) carbon-treated plots because
weeds cannot tolerate the low nitrogen levels, and in (b) wet, nitrogen-treated
plots because the exotic grasses are out-competed under these conditions.

Acknowledgements

We are grateful to the U.S. Army Corps of Engineers of Fern Ridge, Oregon, for the use of the Horkelia Prairie study area, with a special thanks to Rick Hayes for his interest and help in the field. We thank Kate Lajtha and Carol Glassman for their assistance with soil nutrient analyses, Gorgine Yorgey for help with field data collection and biomass measurements, and Herb Huddleston for his guidance in the installation of our water wells. We are also grateful to Kate Lajtha, Don Zobel, Jeff Steiner, and Jack DeAngelis for their insightful comments and suggestions on this manuscript.
References


Chapter 5
A Comparison of the Establishment and Competitive Abilities of Three Native and Four Exotic Grass Species along a Hydrologic Gradient

Abstract

Plant species distributions in wetland prairies are often affected by species' physiological adaptations and their competitive abilities. In our study, we investigated the effects of a hydrologic gradient on the establishment of seven grass species in both monoculture and mixture plots. Two species, Beckmannia syzigachne and Phalaris arundinacea, were excluded from establishing in drier mixture plots, while Danthonia californica was excluded from the wetter mixture plots. The relative performance of seedlings of the native species was less suppressed by competition than was the exotic species. The exotic species Anthoxanthum odoratum, Holcus lanatus, and Phalaris arundinacea were the most sensitive to competition, while Danthonia californica (native), Deschampsia cespitosa (native) and Agrostis capillaris (exotic) showed strong competitive ability along most of the hydrologic gradient. These results contradict, at least for the establishment and seedling stages, the widely held notion that invasive species are superior competitors. Information from this study may be useful in decision making regarding species selection and exotic species control during wetland prairie restoration.
Introduction

Hydrology is a key component affecting plant distribution in many wetland prairies (Curtis 1955, Dix & Smeins 1967, Nelson & Anderson 1983, Streatfield & Frenkel 1997). The physiological response of plants with respect to water regime can vary widely from species to species. Some plant species may be limited to specific hydrologic conditions by their physiology. For instance, certain species are limited to wet habitats because they require inundated soils for seed germination (van der Valk et al. 1981, Coops & van der Velde 1995). In contrast, some plants may have very broad hydrologic tolerances because they have adaptations that enable them to maintain adequate oxygen supplies to their roots in low-oxygen soils (McKee et al. 1989, Mitsch & Gossilink 1993).

The distribution of plants along a gradient is also affected by interspecific competition. For example, a species may be limited to an even narrower hydrologic range than conferred by its physiology because it is outcompeted by other species (Rahman 1976, Grace & Wetzel 1981, Walter & Breckle 1985, Keddy et al. 1994, Coops et al. 1996). Thus, the ecological response of a species may be quite different from its physiological response.

In western Oregon wetland prairies, there are several invasive, non-native grasses such as *Agrostis capillaris* (colonial bentgrass), *Anthoxanthum odoratum* (sweet vernal grass), *Holcus lanatus* (velvetgrass), and *Phalaris arundinacea* (reed canary-grass) that now dominate much of the plant community and whose distribution varies across subtle changes in elevation. Higher and drier areas are often dominated by *Agrostis capillaris, Anthoxanthum odoratum*, and *Holcus*
lanatus. Meanwhile, moderately wet prairies are often dominated by the native bunchgrass *Deschampsia cespitosa* (tufted hairgrass), and even wetter areas are frequently overrun with *Phalaris arundinacea* (reed canary-grass).

Many assume that exotic plants such as these are competitively superior to native species, thus enabling their successful invasions of native habitats (Parker & Reichard 1998). However, as pointed out by both D’Antonio and Vitousek (1992) and Parker and Reichard (1998), few studies have actually documented competition between native and exotic plant species, and therefore the mechanisms by which exotic species carry out their invasions remain unclear. Improving our understanding of these mechanisms could be very helpful in the management and control of invasive plant species.

The goal of this study was to determine the effects of a hydrologic gradient on the establishment and growth of seven common grass species, three native and four exotic. We were interested in determining both the physiological response of each species as well as the ecological response, i.e. where each species would establish in the absence and presence of other competing species. We also wanted to compare the relative competitive abilities of these species to determine whether, indeed, native species are competitively inferior to exotic invaders. Information from this study may also be useful in decision making regarding species selection and exotic species control during wetland prairie restoration.
Methods

Study Site

This study was performed at the Danebo Wetlands in west Eugene, Oregon (123 10' 28" W and 44 03' 05''). The area is characterized by mild, wet winters and moderate, dry summers, with an average annual precipitation of roughly 107 cm (Oregon Climate Service, Fern Ridge Dam, 1961-1990). The soils of this site belong to the Natroy Series, indicating that they are poorly drained clay soils (Soil Conservation Service 1987). The soils of this site are generally saturated or ponded during the rainy season, from approximately November through May.

The Danebo Wetlands is a degraded wetland prairie owned and managed by the U.S. Bureau of Land Management, which is attempting to restore the area back to native prairie. Our study plots were located within a zone from which about 30 cm of topsoil was removed in the summer of 1995 in an attempt to remove the weedy seed bank. Thus, we initiated our study in an area that was ostensibly free of plants and any seed reserves.

Experimental Design

In fall 1995, we arranged twelve 2-m × 1-m blocks along a hydrologic (hillslope) gradient that was roughly 30 m long. We then randomly established seven 0.5-m × 0.5-m monoculture plots, one plot for each species, and one 0.5-m
× 0.5-m mixture plot within each block. The monoculture plots were designed for determining the physiological response of each species and the mixture plots were for determining ecological responses. Each monoculture plot was sown at a density of 1 seed/5cm², and the mixture plots were sown with an equal mixture of all seven species at a higher total density of 1 seed/1 cm². The seven species used in this study were the native bunchgrasses *Deschampsia cespitosa*, *Danthonia californica* (California oatgrass), and *Beckmannia syzigachne* (American sloughgrass) and the exotic rhizomatous grasses *Agrostis capillaris*, *Anthoxanthum odoratum*, *Holcus lanatus*, and *Phalaris arundinacea*. All plots were sown in October 1995 by first raking each plot by hand to a depth of approximately 1 cm, sprinkling the seeds carefully throughout the plot, and then covering the seeds with roughly 1 cm soil. All seeds were collected within a 30-mile radius of the study site during the summer of 1995.

Each monoculture plot was thinned to no more than ten plants the first year and eight plants the second year to reduce intra-specific competition, thus allowing the plants to grow at their maximum potential under each hydrologic regime. These densities appeared to eliminate at least competition for aboveground resources (i.e., light). Volunteer species not sown by us were removed from both monoculture and mixture plots by clipping those stems at the base and removing the cut material from the plot. All weeding occurred biweekly between March and August of 1996 (by August the plants had senesced), and between March and July of 1997.
We assessed the effect of competition on each species by comparing its relative performance in monoculture and mixture plots. Relative performance of a species is the average biomass per individual as a proportion of the combined average biomass per individual of all species. A competitively superior species will have a higher relative performance in mixtures than in monocultures. Using relative performance to evaluate competitive abilities has the advantage of accounting for inherent differences among species in individual plant sizes (see Goldberg 1987).

**Data Collection**

We measured the hydrology in each block biweekly from January through June in 1996 and 1997. Water levels were monitored in one of two ways. In ponded blocks we calculated water depth as the average of several direct measurements. In blocks that were not ponded, water wells installed in each block were monitored to measure the distance from the soil surface to the water table.

Aboveground tissues of all sown plants were harvested in July 1997. In the monoculture plots, each plant was clipped at the base and individually bagged. In the mixture plots, plants were bagged by species, with each bag containing one to hundreds of plants. These bags were then dried at 70°C to constant weight and their contents weighed.
Results

Hydrology

Water-depth measurements confirm the increasing wetness along the elevation gradient (Table 5.1). The first eight blocks increased gradually in wetness, while the lower four blocks were markedly wetter (Figure 5.1). Maximum inundation depths correspond with average water depths except for blocks 7 and 8. Duration of inundation was approximately 12 weeks for the first 8 blocks (except block 7), and at least twice this long in blocks 9 through 12.

Table 5.1. Hydrologic conditions recorded on 23 different days between January and June in 1996 and 1997 at the Danebo Wetlands.

<table>
<thead>
<tr>
<th>Block</th>
<th>Water Depth * (cm)</th>
<th>Maximum Inundation Depth (cm)</th>
<th>Approximate Period of Inundation (weeks)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-22.0</td>
<td>2.8</td>
<td>12</td>
</tr>
<tr>
<td>2</td>
<td>-19.0</td>
<td>8.0</td>
<td>12</td>
</tr>
<tr>
<td>3</td>
<td>-18.5</td>
<td>8.8</td>
<td>12</td>
</tr>
<tr>
<td>4</td>
<td>-16.0</td>
<td>15.2</td>
<td>12</td>
</tr>
<tr>
<td>5</td>
<td>-15.1</td>
<td>16.5</td>
<td>12</td>
</tr>
<tr>
<td>6</td>
<td>-13.1</td>
<td>18.5</td>
<td>12</td>
</tr>
<tr>
<td>7</td>
<td>-11.0</td>
<td>23.4</td>
<td>14</td>
</tr>
<tr>
<td>8</td>
<td>-10.9</td>
<td>21.0</td>
<td>12</td>
</tr>
<tr>
<td>9</td>
<td>3.5</td>
<td>43.9</td>
<td>24</td>
</tr>
<tr>
<td>10</td>
<td>5.5</td>
<td>45.0</td>
<td>24</td>
</tr>
<tr>
<td>11</td>
<td>10.4</td>
<td>51.2</td>
<td>27</td>
</tr>
<tr>
<td>12</td>
<td>17.1</td>
<td>59.6</td>
<td>27</td>
</tr>
</tbody>
</table>

* Negative numbers are the result of subsurface water measurements.
Seedling Establishment

Three of the seven grass species, *Beckmannia syzigachne*, *Danthonia californica*, and *Phalaris arundinacea*, established in the monoculture plots of all twelve blocks along the hydrological gradient (Figure 5.2). *Agrostis capillaris*, *Anthoxanthum odoratum*, *Holcus lanatus*, and *Deschampsia cespitosa* established only in the first eight blocks (with the exception of two small *Agrostis* plants in block nine). Thus the four wettest blocks contained essentially only three of the seven grass species, *Beckmannia syzigachne*, *Danthonia californica*, and *Phalaris arundinacea*.

Establishment patterns differed between mixture and monoculture plots for some species. In mixtures, *Beckmannia* and *Phalaris* did not establish in some of the dry blocks (Figure 5.2). Conversely, *Danthonia* established in all
twelve blocks along the gradient when grown in monoculture, while in mixture there was no seedling establishment in the wettest four blocks (9 through 12).

**Figure 5.2.** Presence and absence of seedling establishment in twelve blocks along the hydrological gradient. Solid diamonds indicate monoculture plots and asterisks indicate mixture plots.

**Relative Performance**

For *Anthoxanthum*, *Holcus*, *Phalaris*, and Total Exotic Species (calculated from the combined weights of the four exotic species), relative performance in mixture plots was generally lower than in monoculture plots across the hydrologic gradient (Figure 5.3) (The absolute biomass data used to compute relative performance is displayed in Appendix Tables A1 and A2). For *Agrostis*, *Danthonia*, *Deschampsia*, and Total Native Species (from the combined weights of the three native species), relative performance in mixture was generally higher.
than in monoculture. The relative performance of *Beckmannia* was slightly lower in mixture along the drier part of the gradient and was much higher in mixture along the wettest part of the gradient.

**Figure 5.3.** Relative performance (%) of each species in monoculture and mixture. Rectangles represent performances in monoculture and asterisks represent performance in mixture.

*Anthoxanthum odoratum*

![Graph for Anthoxanthum odoratum]

*Holcus lanatus*

![Graph for Holcus lanatus]
Phalaris arundinacea

Agrostis capillaris

Total Exotic Species
Danthonia californica

Deschampsia cespitosa

Beckmannia syzigachne
Discussion

Seedling Establishment

The seedling physiological and ecological responses were similar for some species and quite different for others. *Beckmannia syzigachne* and *Phalaris arundinacea* were physiologically capable of establishing along the entire hydrologic gradient when grown in monoculture, but were excluded from the driest plots under the crowded conditions of the mixture plots. This indicates that these species were out competed along the drier end of the gradient. It also suggests that attempts to restore *Beckmannia* to drier end prairies by sowing will fail unless interspecific competition is controlled. Similarly, threats of invasion by *Phalaris* seedlings in the drier end of wetland prairies is unlikely as long as other species are present. The native bunchgrass *Danthonia californica* established in all twelve monoculture plots along the gradient, but it did not appear in the four wettest blocks when grown in mixture. *Danthonia* is
uncompetitive in the wet end of the gradient and sowing of *Danthonia* into very wet areas should only be attempted if competition is controlled. The remaining four species showed similar establishment in both the monoculture and mixture plots along the gradient, indicating that competition did not prevent these species from establishing in any of the blocks (except for block 9 for *Agrostis*). These species are physiologically incapable of growing in the wettest conditions along the gradient.

**Relative Performance**

Relative seedling performance of the exotics *Anthoxanthum*, *Holcus*, and *Phalaris* and of Total Exotic Species was consistently lower in mixture plots than in monoculture plots across the hydrologic gradient, showing their susceptibility to competition. The opposite is true for *Agrostis*, *Beckmannia* (under wetter conditions), *Danthonia*, *Deschampsia*, and Total Native Species, which showed higher relative performance in the mixture plots than in the monoculture plots.

That the invasive, non-native species in this study were more suppressed by competition (except *Agrostis*) than were the native species contradicts the popular notion that invasive species are competitively superior. It also challenges the information reviewed by Parker and Reichard (1998), who found that exotic species often negatively interfered with the growth of native species, whereas native plants did not significantly interfere with exotics. Our results clearly demonstrate that native species, at the seedling stage, can interfere with the growth of exotic species.
Little competition information is available for the native species in our study, although Rahman (1976) did show that Deschampsia was a poor competitor compared to another perennial grass, Dactylis glomerata. Agrostis, Anthoxanthum, Holcus, and Phalaris, the exotic species in our study, are reported to be strong competitors (Mahmoud & Grime 1976, Remison & Snaydon 1978, Berendse 1982, Thorhallsdottir 1990, Turkington et al. 1993, Figiel et al. 1995, Rew et al. 1995, Wetzel & van der Walk 1998). Our results do not support these findings, at least at the seedling/juvenile stages and when grown in mixture with native grasses.

If the exotic species in our study are, indeed, not competitively superior to the native species, there must be alternative explanations for why these exotic species are such successful invaders. The success of some invasive species has been attributed, at least partially, to their reproductive strategies, e.g. abundant seed production, efficient seed dispersal, and other traits that enable plants to rapidly colonize disturbed areas (Shafroth et al. 1995, Rejmanek & Richardson 1996). It is possible that exotic species have been faster than native species at colonizing the disturbed areas so common in Oregon wetland prairies (Franklin & Dyrness 1988, Noss et al. 1995). These exotic species are also rhizomatous and can spread vegetatively, unlike the native bunchgrasses, which spread primarily by seed. Therefore, it is plausible that the exotic grasses have been able to establish more quickly in disturbed areas than the native species and, once in place, these mature plants compete strongly against emerging native seedlings.
If it is true that the exotic species in western Oregon wetland prairies rely more upon disturbance and reproductive strategy rather than competitive ability for their success, then land managers can focus on controlling disturbances in managed areas or make sure that native species are sown into disturbed areas quickly following a disturbance. Our evidence suggests that seedlings of native grasses have high competitive ability and should establish successfully when sown into areas where mature exotic grasses have been removed.

Acknowledgements

We heartily thank the U.S. Bureau of Land Management of Eugene, Oregon, for their generous support of this research and for the use of the Danebo Wetlands study site, with a special thanks to Jock Beall for his interest, support, and help in keeping our plots safe. We thank Gorgine Yorgey and Vega Tom for their help with field data collection and Herb Huddleston for his guidance in the installation of our water wells. We are also grateful to Don Zobel, Kate Lajtha, Jeff Steiner, and Jack DeAngelis for their insightful comments and suggestions on this manuscript.
References


## Appendix

**Table A1.** Average biomass (g) per plant (and standard errors) for each species in monoculture along the hydrologic gradient.

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Table A2. Average biomass (g) per plant for each species in mixture along the hydrologic gradient.

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Chapter 6
Final Summary

Effects of Carbon Additions

Many studies show that available soil nitrogen can be significantly reduced via the addition of carbon amendments (Lamb 1980, Williamson and Johnson 1994, Wilson and Gerry 1995, Hopkins 1998, Zink and Allen 1998), but none, to our knowledge, had been attempted in wetlands. My results show that carbon amendments are also effective in reducing soil nitrogen in wetland soils. Adding too much labile carbon (e.g., 0.5kg/m² sucrose), however, may create a strongly anoxic environment and/or other conditions that are deadly for plants (Chapter 3).

It is very possible that other types of carbon amendments might also aid in reducing available soil nitrogen. Products such as straw and plant wastes have been used successfully in other systems (Powlson et al. 1985; Williamson & Johnson 1994; Wu et al. 1995, Zink & Allen 1998), and are relatively inexpensive and widely available in the Willamette Valley (though the plant wastes would need to be free of weed propagules). Further trials using alternative carbon sources deserve study.

I predicted that reducing available soil nitrogen levels would result in the suppression of weedy plants and the promotion of native species. Indeed, plots receiving carbon additions did show significantly reduced biomass of exotic grasses, the most troublesome of all Willamette prairie invaders (Chapters 2 and
Other weedy species, such as the weedy rushes, were not affected by the soil treatments.

Carbon additions also promoted the growth of native grasses, namely *Deschampsia cespitosa* and *Danthonia californica* (Chapters 2 and 4). These important native species are both bunchgrasses, and bunchgrasses have been shown to maintain low nitrogen mineralization rates near their roots, while weedy, rhizomatous grasses perpetuate the rapid release of mineralized nitrogen (Wedin and Tilman 1990, Vinton & Burke 1995, Wedin and Tilman 1996). Bunchgrasses may benefit from carbon additions because they reduce nitrogen levels to pre-invasion conditions.

Many threatened native ecosystems are dominated by bunchgrasses, including both wetland and upland Willamette Valley prairies, the Great Central Valley grasslands of California, the shortgrass steppe of Colorado, and the Palouse Prairie and sagebrush steppe of the northern Great Basin (Vinton and Burke 1995, Barbour and Billings 2000). Each of these systems has been degraded by the invasion of annual and/or rhizomatous grasses. That my research shows carbon additions to effectively suppress weeds and promote bunchgrasses in Oregon wetland prairies, may mean carbon additions could be useful in other bunchgrass systems as well.

Invasive species are often one of the largest impediments to ecological restoration and enormous resources are spent on their control (Hobbs and Huenneke 1992, Berger 1993). My research supports the handful of other studies (Morgan 1994, Seastedt et al. 1996, Zink & Allen 1998) that indicate that carbon
additions may be a key tool for controlling invasive species during ecological restoration.

**Effects of Nitrogen Additions**

The ammonium nitrate additions at the Horkelia Prairie study yielded both anticipated and unanticipated results. The weedy, exotic grasses produced much more biomass in the nitrogen-treated plots compared to plots having lower nitrogen levels, a trend found in many other studies (e.g., Bobbink & Willems 1987, Aerts & Berendse 1988, Berendse et al. 1992, Wedin & Tilman 1996). Similarly, the native grasses produced significantly more biomass in the nitrogen treatments compared to the controls, however this was not a result we expected. This increase in native grass biomass in high-nitrogen plots may be the result of reduced competition among plants due to an excess of available nitrogen.

**Effects of Hydrology**

Our studies both at Horkelia Prairie (Chapters 3 and 4) and the Danebo Wetlands (Chapter 5) indicate that, overall, the native grasses we studied establish best in the mid to wetter end of the hydrologic gradient encountered in these prairies, while the exotic grasses establish most successfully in the drier end wetland prairies. Moreover, hydrologic conditions interact with the effects of carbon additions (Chapter 4) and competition (Chapter 5). These results indicate that restoration biologists in the Willamette Valley are more likely to be successful if they focus their efforts toward wetter end prairies.


**Competition**

At the Danebo Wetlands (Chapter 5), I showed that competition influences the establishment of sown grass species along a hydrologic gradient. Some species (*Beckmannia syzigachne*, *Danthonia californica*, and *Phalaris arundinacea*) when grown in species mixtures were completely displaced from establishing under certain wetness regimes. Other species (*Anthoxanthum odoratum*, *Holcus lanatus*, and *Deschampsia cespitosa*) were not excluded from any plots in which they were physiologically capable of growing. Such competitive displacement along hydrologic gradients has been observed elsewhere (Rahman 1976, Grace and Wetzel 1981).

Overall, the native seedlings were less suppressed by competition than the exotic seedlings when grown in crowded plots, a result I did not anticipate (Chapter 5). Originally, I had predicted that each species would prove to be a strong competition under the same hydrologic conditions where it was most abundant in the field, i.e. *Anthoxanthum odoratum*, *Agrostis capillaris*, and *Holcus lanatus* would have the highest competitive abilities in the driest zones, *Deschampsia cespitosa* would have the highest competitive ability in the middle zones, and *Phalaris arundinacea* would be the best competitor in the wettest zones. Indeed, *Agrostis* and *Deschampsia* were strong competitors in the drier and moderate zones, respectively. But, *Anthoxanthum* turned out to be most suppressed in the driest plots, *Holcus* was suppressed along the entire gradient, and *Phalaris* was suppressed along most of the gradient, especially in the wettest plots. Alternatively, *Danthonia californica* and *Beckmannia syzigachne*, species
that I did not predict would be competitively strong anywhere since these species are never dominant, turned out to be relatively immune to competition along much of the gradient.

My results contradict the common notion that invasive species are competitively superior to native species (Parker and Reichard 1998). My evidence indicates that when native and exotic wetland prairie grasses are sown simultaneously, it is the native plants that out compete the exotics. Whether *mature* individuals of these exotic grasses can out compete native seedlings or native adults is unknown to us and is a question that warrants investigating. Answers to these questions about competitive ability are important because they give insight about if and how exotic species might be controlled.
References


Bibliography


