THESIS

# NITROGEN AVAILABLITY EFFECTS ON EXOTIC, INVASIVE PLANT SPECIES

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY PETRA N. LOWE ENTITLED NITROGEN AVAILABLITY EFFECTS ON EXOTIC, INVASIVE PLANT SPECIES BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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# ABSTRACT OF THESIS

## NITROGEN AVAILABLITY EFFECTS ON EXOTIC, INVASIVE PLANT SPECIES

The invasion of ecosystems by exotic plant species is a serious concern for land managers and conservationists. One of the most universally recognized exacerbating factors of exotic species invasions is disturbance. Human alterations to the global nitrogen cycle have increased atmospheric nitrogen deposition to terrestrial ecosystems worldwide, a disturbance that may encourage the growth of exotic invasive species that are uniquely capable of growing quickly when excess nitrogen is available.

I undertook three experiments, one field and two greenhouse, to test the hypothesis that exotic invasive species are specifically adapted to take advantage of high nitrogen conditions, and outcompete natives as nitrogen availability increases, and that native species are better adapted to low nitrogen conditions and outcompete exotics when this nutrient is low. The field experiment examined the response of a disturbed shortgrass steppe community dominated by exotics to the addition of humus precursors and a labile carbon source intended to reduce plant available nitrogen. I was hypothesized that decreasing nitrogen availability would disadvantage the dominant exotic species and provide and advantage for the native species, returning the community to a vegetative structure more characteristic of undisturbed sites. Results of the experiment showed that decreasing nitrogen availability had no effect on native or exotic species density, richness, or basal cover.

A greenhouse study investigated the response of above and belowground biomass, plant height, and nitrogen tissue concentrations of two species, the native *Bouteloua gracilis*, and the exotic *Bromus tectorum*, to a gradient in nitrogen availability and competition. The two species were grown under five levels of nitrogen availability and five levels of competition. I hypothesized that the native species would compete better at the low nitrogen levels, but competitive advantage would shift to the exotic as nitrogen availability increased, as some research has shown native species grow better than exotics at low nitrogen levels whereas exotics are only able to support their rapid growth rates when high amounts of resources are available. The exotic species was the better competitor at all nitrogen levels.

A second greenhouse study investigated the above and belowground, height, and nitrogen tissue response of two native species, *Bouteloua gracilis* and *Agropyron smithii*, and four exotic species, *Bromus tectorum*, *Euphorbia esula*, *Cirsium arvense*, and *Centaurea repens*, to a gradient in nitrogen availability. I grew the six species individually under five levels of nitrogen availability. I hypothesized that the native plant species would gain more mass than the exotics at the low nitrogen levels, but the exotics would gain more mass at the high nitrogen levels. The native species failed to perform better than the exotics at the lowest nitrogen levels, but only two exotics performed better than the natives at the highest nitrogen levels. My results support the hypothesis that exotic species respond more readily to increasing nitrogen availability than native species, but do not support the hypothesis that all exotic species have a competitive advantage under high nitrogen conditions. Furthermore, my results do not support the hypothesis that native species have a competitive advantage over all exotic invasive weeds at low nitrogen conditions, as one of the exotics, *Bromus tectorum*, competed and grew comparatively better than the native species even at low nitrogen levels. The success of all exotic invasive weeds cannot be completely attributed to a rapid growth response to nutrient availability; it is likely that different species utilize a combination of strategies to outcompete native plant species.

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# DEDICATION

I would like to dedicate this work to my beloved father, Herb Lowe, who passed away September 4th, 1999

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# INTRODUCTION

The invasion of ecosystems by exotic plant species has long been recognized as a problem in ecology (Elton 1958, Baker 1986). The seriousness of exotic species invasions has increased to a such a level that it is considered an aspect of global environmental change (Vitousek et al. 1996). Exotic species invasions have a variety of negative effects including alteration of biogeochemical cycles (Vitousek 1986), alterations of disturbance cycles, specifically fire frequency (Billings 1990), and suppression of native species resulting in losses of biodiversity (D'Antonio and Vitousek 1992, Huston 1994). The most recognized cause and exacerbating factor of exotic species invasions is disturbance (Elton 1958, Orians 1986, Hobbs and Huenneke 1992). Human alteration of the global nitrogen cycle is an important cause of disturbance that facilitates exotic species invasions (Hobbs and Huenneke 1992).

Anthropogenic sources have doubled the amount of fixed nitrogen in the biosphere (Ayers et al. 1994) and as a result have increased atmospheric nitrogen deposition to both terrestrial and aquatic ecosystems (Schindler and Bayley 1993 Vitousek et al. 1997). Soil nitrogen has a major influence on plant species composition (Tilman 1987) and competition (Vitousek and White 1981). Several authors have hypothesized that weed species have evolved a host of shared characteristics which make them successful competitors for light under high resource conditions (Grime 1988, Baker 1986). Fertilization studies have supported this idea; increases in biologically available nitrogen promote the growth and community dominance of plant species adapted to take advantage of excess resource enrichment (Heil and Diemont 1983, Bobbinik et al. 1988, Hunneke et al. 1990, Milchunas and Lauenroth 1995, Burke and Grime 1996). The plants that come to dominate an area after enrichment with nitrogen are most often exotic, invasive weed species, which respond rapidly to increased resource enrichment with rapid growth rates, outcompeting the slower growing native plant species. Exotic species richness is positively correlated with soil nitrogen content (Stohlgren et al. 1999a, 1999b). Native, non-weedy plant species are able to compete under normal levels of nitrogen availability, as they are adapted well to local conditions. However, being adapted to tolerate low nitrogen levels in order to persist also means an inability to take full advantage of high nitrogen conditions when they occur (Grime 1979).

The overall hypothesis for my research is as follows:

> When nitrogen availability increases above the normal, ambient level, exotic weed species outcompete slower-growing native species because they are specifically adapted to maximize their growth under these conditions. Conversely, native, non-weedy species are better adapted to lower nitrogen conditions and outcompete exotic weed species at low nitrogen levels through tolerance of low resource availability.

Specific questions I will address under this hypothesis are:

1. Will reducing nitrogen availability reduce or eliminate exotic species density/dominance in a disturbed shortgrass steppe community?

2. Does reducing nitrogen availability reduce the competitive ability of *Bromus tectorum*, an exotic weed species, and enhance the competitive ability of *Bouteloua gracilis*, a native?
3. How does the nitrogen response of four exotic plant species, *Bromus tectorum*, *Centaurea repens*, *Cirsium arvense*, and *Euphorbia esula*, compare to that of two native species, *Bouteloua gracilis* and *Agropyron smithii*?

I have performed three experiments to address these specific questions. The first question is addressed in chapter one with a field experiment investigating the effects of a reduction in biologically available nitrogen on a disturbed shortgrass steppe community dominated by exotic species. This experiment tested the hypothesis that additions of humus precursors and sugar would disadvantage exotic weed species and favor native vegetation. The second question is addressed in chapter two with a greenhouse replacement series experiment investigating the effects of a nitrogen and competition gradient on an exotic species, *Bromus tectorum*, and a native species, *Bouteloua gracilis*. This experiment tested the hypothesis that decreasing nitrogen availability would decrease the competitive ability of the exotic species and enhance that of the native. The third question is addressed in chapter three with a nitrogen gradient greenhouse experiment investigating the nitrogen response of four exotic species and two native species. This experiment tested the hypothesis that the exotic plant species would perform comparatively better at the high nitrogen levels, while the native species would perform comparatively better at the low nitrogen levels.

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# CHAPTER 1

## AMELIORATION EFFECTS OF HUMUS PRECURSORS ON COMMUNITY INVASION BY EXOTIC SPECIES

### Introduction

One aspect of global environmental change of great concern to land managers and conservationists is the invasion of communities by aggressive, exotic plant species (Hobbs and Humphries 1995). Other aspects of global environmental change interact with, and exacerbate, the invasion of communities by exotic species, most notably land use changes that result in increases in ecosystem disturbance frequency and intensity (Vitousek et al. 1996). Ecologists have long recognized that exotic species invasions are exacerbated by disturbance (Elton 1958, Orians 1986, Huston 1994). Anthropogenic alteration of the global nitrogen cycle is a disturbance which may interact with and exacerbate exotic species invasions (Hobbs and Huenneke 1992).

Anthropogenic sources have doubled the amount of fixed nitrogen in the biosphere through a variety of pathways (Schindler and Bayley 1993 Ayers et al. 1994). As a consequence of this increase, atmospheric nitrogen deposition to both terrestrial and aquatic ecosystems worldwide has been enhanced (Vitousek et al. 1997). Several studies have shown that increased nitrogen availability enhances the dominance of plant species with the ability to respond rapidly to resource additions with rapid growth rates, over slower-growing, resource “conservative” plant species (Heil and Diemont 1983, Bobbinik et al. 1988, Hunneke et al. 1990, Wilson and Gerry 1995, Milchunas and

Lauenroth 1995, Burke and Grime 1996). Often, but not always, the plant species that respond quickly to resource additions with rapid growth rates are exotic weeds, who are superior competitors under conditions of resource enrichment, and are able to outcompete the slower growing native species. Researchers have found some native species appear to have a competitive advantage over exotic species in low nitrogen conditions (Wedin and Tilman 1990, Redente et al. 1992). If increased nitrogen availability favors exotic weed species, will reducing biologically available nitrogen reduce or eliminate this advantage in favor of native species? Can exotic species invasions be ameliorated by eliminating or reducing the excess resource enrichment these species have specifically evolved to exploit?

My objective for this study was to determine if the addition of humus precursors and a labile carbon source to a grassland ecosystem with areas of elevated nitrogen levels, will change community composition from its current dominance by exotic weeds back to dominance by native vegetation. I was also interested in assessing whether the addition of humus precursors and a labile carbon source would alter the seedbank of the experimental plots. The labile carbon source, sugar, may increase microbial immobilization of nitrogen, making the nitrogen unavailable for plant uptake on short time scales (Vitousek 1982, McLendon and Redente 1992). One of the least understood, but potentially important processes in terrestrial ecosystems is the capacity for the soil to store nitrogen in biologically unavailable forms via abiotic fixation is structures such as humus (Aber et al. 1989, Johnson 1992). Theories of humus formation all recognize lignin as an important substrate for humification, primarily because of its similar structure to humic acid (Stevenson 1994). Lignin has an extremely high C:N ratio, while humus has an extremely low ratio, implying that the process of humification results in increasing nitrogen concentrations in the most recalcitrant fraction of the soil organic matter pool. Indeed, studies have found that a significant amount of fertilizer N is sequestered in humic structures (Foster et al. 1985, Paul and Clark 1989), and that even newly added N in the soil is very stable (Kelley and Stevenson, 1985), and quickly incorporated into humic materials (He et al. 1988). The addition of humus precursors to the soil may result in a reduction of biologically available nitrogen by stimulating humification and the associated uptake and incorporation of nitrogen into biologically unavailable forms. I expect to find that the exotic weeds currently dominating my study site will fare poorly when the plant available nitrogen levels are depressed.

## Methods

I conducted the study at the Central Plains Experimental Range (CPER, 40°49' N latitude, 107°46'W longitude), which is 61 km northeast of Fort Collins, Colorado, USA. The mean monthly temperatures range from -3°C in January to 22°C in July; the mean annual precipitation is 321 mm (Lauenroth and Sala 1992). The dominant plant species in the shortgrass steppe is the perennial bunchgrass, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths. Other common species include *Buchloë dactlyoides* (Nutt.) Engelm., a perennial grass, *Artemisia frigida* Willd., a shrub, *Sphaeralcea coccinea* (Pursh) Rydb., a forb, and *Opuntia polyachantha* Haw., a succulent (nomenclature follows Great Plains Flora Association 1986). Exotic weed species are rare in undisturbed shortgrass steppe, flourishing primarily on roadsides (Kotanen et al. 1998).

I initiated the experiment on a historic study site. Prior researchers added treatments to this site consisting of control, water, nitrogen, and water plus nitrogen from

1971 to 1975 (Lauenroth et al. 1978). The historic experiment was a factorial combination of four treatments with two replicates, with each experimental unit being 1 ha in size. The water treatment consisted of maintaining the soil water potential above -.03 Mpa in the surface 10 cm of the soil during the growing season. The water treatment was applied with a sprinkler system, and the average water addition over the five year treatment period was 590 mm/yr. The nitrogen treatment consisted of maintaining a difference of 50 kg/ha of soil mineral nitrogen between the treatment and the control. Nitrogen was applied in the form of ammonium-nitrate, and the applications ranged from 100 to 150 kg $ha^{-1}yr^{-1}$ (Lauenroth et al. 1978). Researchers sampled the experimental plots for plant density, cover, and biomass production through 1974, and then again from 1982 to 1991. The initial sampling from 1970 to 1974 showed that the water and water plus nitrogen treatments had the strongest effect on plant community structure, both treatments increased biomass, and exotic weed species were noted on the water plus nitrogen treatment. Later sampling from 1982 to 1991 showed a ten-fold increase in exotic weed species on the water plus nitrogen plots as compared to the controls (Milchunas and Lauenroth 1995), a community change that has persisted on this site due to a chronic elevation of soil nitrogen caused by a plant tissue/soil organic matter feedback mechanism (Vinton and Burke 1995).

I superimposed six new treatments on the historic study site. The six new treatments were: control, sugar, lignin, sawdust, lignin and sugar, and sawdust and sugar. The lignin was obtained in a purified form from Capital Resin Corporation (Columbus, Ohio). The aspen sawdust was obtained from Delta Timber Company (Delta, Colorado).

The additions provided 350 g carbon $m^{-2}$ $yr^{-1}$, resulting in 1,061 g $m^{-2}$ of lignin, 777 g $m^{-2}$ sawdust, and 833 g $m^{-2}$ sugar being added to the study plots in 1998 and 1999.

I set up the study as a split-plot completely randomized design. I randomly located three transects within each 1 ha historic treatment, each one of these three transects was divided evenly into six 9 $m^2$ plots, to which I randomly assigned one of the six new treatments. The entire experiment consisted of two blocks of four historic treatments, and 3 transects of six new treatments for a total of 144 sample plots. Transect plots within each historic plot are statistically psuedoreplicates, resulting in two true replicates of each new treatment, one in each of the two historic replicate plots (Fig. 1.1).

I recorded density and basal cover by species within a centrally located 1$m^2$ plot within each 9 $m^2$ new treatment plot, in August 1997, 1998, and 1999. I determined basal cover using an inclined 10 point frame. I determined biomass for 1997-1999 every August utilizing a digital photographic technique (Paruelo et al. 2000), calibrated with 15 double sampled plots (both photographed and clipped).

To determine changes in the seedbank, I randomly located two 5 cm diameter soil cores, taken to a depth of 10 cm in each 9 $m^2$ new treatment subplot during the third week of April in 1998 and 1999. I combined the two cores and spread the mixture over a sterilized growth medium in plastic trays, which were placed in the greenhouse. I watered the samples daily and applied a 1/3 strength Hoagland's solution once a week. I identified seedlings and counted seedlings by species every two weeks for sixteen weeks. Once a seedling was identified to species it was removed from the growth tray.

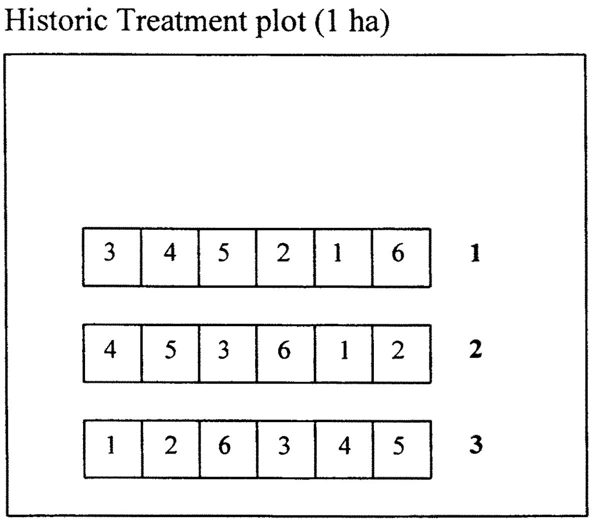


Fig. 1.1 Plot layout for experiment. This figure represents one of the four (control, nitrogen, water plus nitrogen, water) historic 1 ha wholeplot treatments. Inside each wholeplot historic treatment, three transects were randomly located. Each of these three transects was divided into six 9 $m^2$ plots and randomly assigned one of six new treatments: 1=control, 2=sugar, 3=lignin, 4=sawdust, 5=lignin plus sugar, 6=sawdust plus sugar.

I calculated exotic and native species richness for the seedbank as the number of different species for each group that germinated, and density as the total number of seedlings.

I analyzed both the field and seedbank data as a split-plot repeated measures analysis of variance utilizing the GLM procedure in SAS (SAS Institute 1988). The independent variables were historic treatment, new treatments, and year. The dependent variables for the field data were biomass, total species richness, exotic species richness, native species richness, exotic species density, exotic basal cover, native basal cover, and basal cover of *Bouteloua gracilis* (blue grama). Biomass data were log transformed to satisfy the assumptions of analysis of variance. The dependent variables for the seedbank data were exotic and native species richness and density.

## Results

### *Field Results*

There were no significant interactions among the independent variables. The historic treatments were significant for all dependent variables, but the new treatments were only significant for biomass and exotic species richness.

Aboveground biomass was significantly affected by all three of the independent variables (Table 1.1), but year had by far the largest effect, accounting for 81% of the variability in biomass from year to year. This is typical of the shortgrass steppe, as aboveground annual net primary production is strongly linked to precipitation (Lauenroth and Sala 1992). The historic treatments were significant, with the highest biomass occurring on the water plus nitrogen and the nitrogen plots, and the lowest biomass occurring on the control and water plots (Fig. 1.2a). The new treatments were also significant (p=.0455). Of the new treatments, the sugar treatment was the only one

Table 1.1. Field biomass (g m$^{-2}$), species richness (m$^2$), exotic species richness (m$^2$), native species richness (m$^2$) exotic species density (m$^2$), exotic species basal cover (m$^2$), native species basal cover (m$^2$), and *Bouteloua gracilis* basal cover (m$^2$) of the experimental plots. Richness data is based on species density.
Values with the same letter are not significantly different at P=0.05.

| | Biomass | Sp rich | Ex Sp rich | Nat Sp rich | Ex density | Ex BC | Nat BC | BOGR BC |
|---|---|---|---|---|---|---|---|---|
| Historical treatment | | | | | | | | |
| Control | 263.58a | 7.2a | .09a | 7.2a | .1a | 0.92a | 23.04b | 7.9a |
| Water | 278.70a | 6.7b | .89c | 5.8b | 7.59b | 0.55a | 18.91c | 4.7b |
| Nitrogen | 332.44b | 6.3b | .47b | 5.8b | 2.06a | 0.04b | 26.64a | 2.4b |
| Water + Nitrogen | 328.01b | 4.5c | 1.64d | 2.8c | 32.57c | 1.62a | 19.08c | 2.6b |
| New treatment | | | | | | | | |
| Control | 322.30a | 6.3a | 1.05a | 5.2a | 16.08a | 1.18a | 22.8a | 4.5a |
| Sugar | 275.62b | 6.2a | .79b | 5.4a | 9.76a | 0.41a | 23.23a | 5a |
| Lignin | 325.67a | 5.9a | .72b | 5.2a | 13.61a | 1.45a | 20.69a | 3.6a |
| Sawdust | 292.29a | 6.5a | .68b | 5.8a | 8.25a | 0.86a | 22.46a | 4.3a |
| Lignin + Sugar | 307.94a | 6.2a | .81b | 5.4a | 9.04a | 0.41a | 19.65a | 4.2a |
| Sawdust + Sugar | 280.28a | 5.9a | .59b | 5.3a | 6.75a | 0.38a | 22.74a | 4.8a |

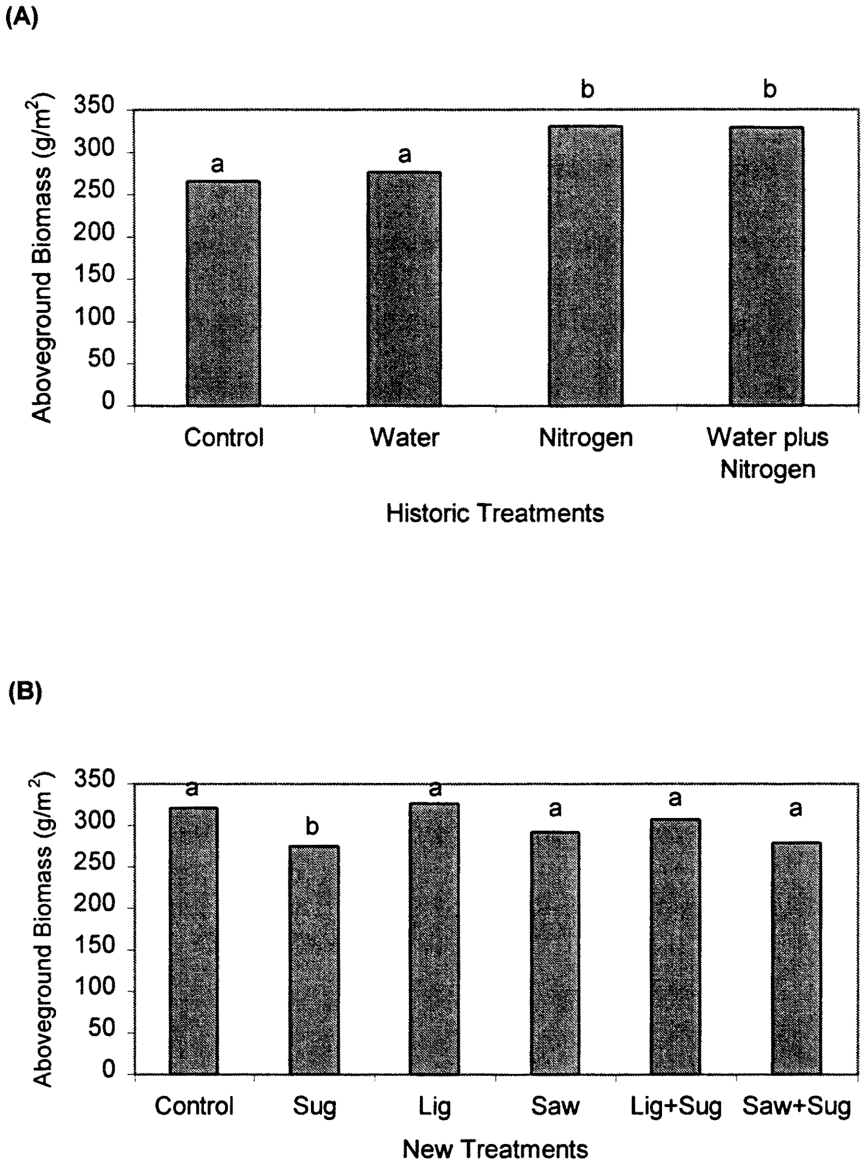


Fig 1.2. Aboveground plant biomass response to historic treatments, control, water, nitrogen, and water plus nitrogen, added from 1970 to 1975 to eight (one replicate of each treatment), 1 ha plots in northeastern Colorado.Data collected from 1997 to 1999.(A). Aboveground plant biomass response to new treatments, control, sugar, lignin, sawdust, lignin plus sugar, and sawdust plus sugar, added in 1998 and 1999 to two plots (one in each historic plot and replicate) and measured from 1997 in northeastern Colorado (B). Bars with the same letter are not significantly different at $p=0.05$.

significantly different from the control. The sugar treatment had significantly less biomass than the control (Fig. 1.2b).

The historic treatments had a strong effect on total species richness (Table 1.1). The greatest species richness occurred on the historic control plots, and the lowest species richness occurred on the historic water plus nitrogen plots (Fig. 1.3). The year was significant, but accounted for only 1 % of the variability in total species richness. The new treatments were not significant (p=.2715).

Exotic species richness was significantly affected by both the historic (p=.0001) and the new treatments (p=.0166) (Table 1.1). The new treatments accounted for only 2% of the variability in exotic species richness, while the historic treatments accounted for 33% of the variability. Exotic species richness was highest on the historic water plus nitrogen plots and lowest on the historic control historic (Fig. 1.4a). In the new treatments, exotic species richness was significantly higher on the control plots (Fig. 1.4b).

Only the historic treatments were significant in predicting native species richness (p=.0001), with the highest native species richness occurring on the control plots, and the lowest native species richness occurring on the water plus nitrogen plots (Table 1.1). The new treatments were not significant (p=.227).

Exotic species density was strongly related to the historic treatments. The highest exotic species density occurred on the water plus nitrogen plots, and the lowest on the historic control plots (Table 1.1). Exotic species density was also strongly related to year (p=.0001). The new treatments were not significant predictors of exotic species density (p=.2317). Basal cover of exotic species was significantly affected only by the historic

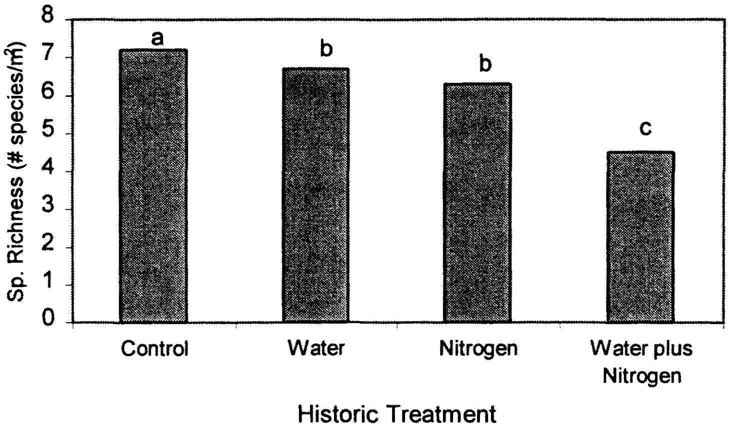
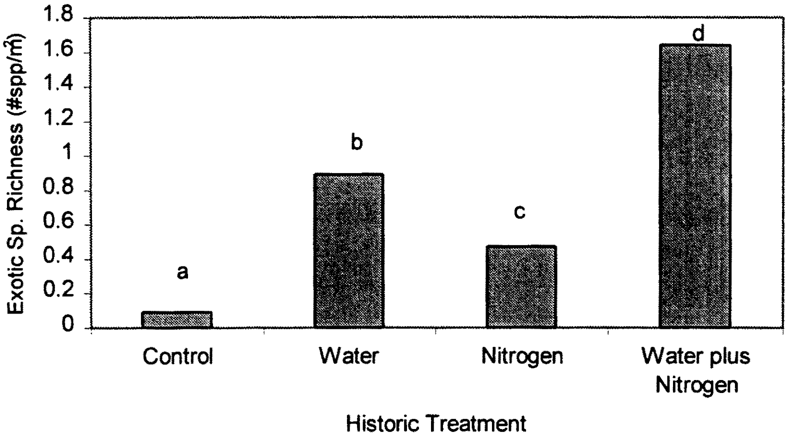


Fig 1.3. Total species richness response to historic treatments, control, water, nitrogen, and water plus nitrogen, added from 1970 to 1975 to eight (one replicate of each treatment), 1 ha plots in northeastern Colorado. Richness based on density data collected from 1997 to 1999. Bars with the same letter are not significantly different at $p=0.05$.

**(A)**



**(B)**

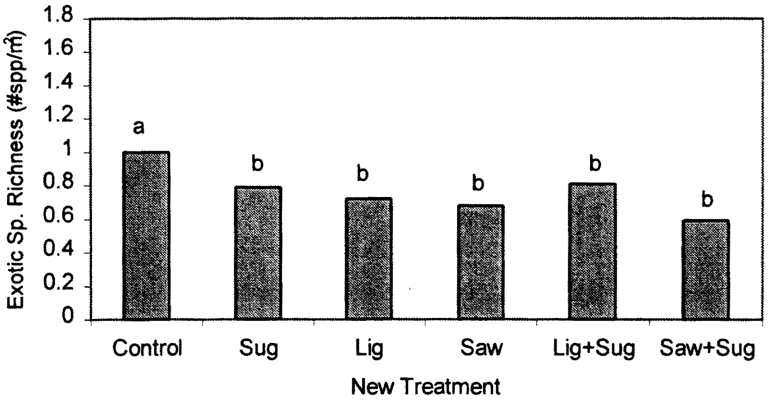


Fig 1.4. Exotic species richness response to historic treatments, control, water, nitrogen, and water plus nitrogen, added from 1970 to 1975 to eight (one replicate of each treatment), 1 ha plots in northeastern Colorado-data collected from 1997 to 1999.(A). Exotic species richness response to new treatments, control, sugar, lignin, sawdust, lignin plus sugar, and sawdust plus sugar, added in 1998 and 1999 to two plots (one in each historic plot and replicate) in northeastern Colorado (B). Exotic species richness is based on density data collected from 1997 to 1999. Bars with the same letter are not significantly different at p=0.05.

treatments, with highest exotic species basal cover occurring in the water plus nitrogen plots (Table 1.1). Native species basal cover was significantly affected by the historic treatments and year, with the highest amount of basal cover occurring on the nitrogen historic plots and in 1999. The new treatments were not significant (p=.5113). The *Bouteloua gracilis* (blue grama) basal cover response was very similar to that of native species basal cover, with the exception that the highest levels of blue grama basal cover occurred on the historic control plots. Again, the new treatments were not significant (p=.9489).

### *Seedbank Results*

Neither the new nor the historic treatments significantly affected the native species richness or density in the seedbank (Table 1.2). The historic treatments had a significant effect on exotic species richness and density (Table 1.2), but only explained 2% and 3% of the variability in these dependent variables, respectively. The new treatments did not significantly affect any of the seedbank dependent variables.

## Discussion

Biomass production was depressed by the addition of sugar, sawdust, sawdust and sugar, and lignin and sugar. Morghan and Seastedt (1999) found a similar depression of biomass production with the addition of sawdust and sugar over a three year period to a mixed-grass foothills community in Colorado. Morghan and Seastedt attributed the reduction in biomass they observed to a reduction in plant available nitrogen due to microbial immobilization.

Exotic species richness was the only community indicator to be significantly affected by the addition of the humus precursors and sugar; exotic species richness was

Table 1.2. Seedbank exotic species richness (# seedlings/m$^2$), native species richness (# seedlings/m$^2$), exotic species density (# seedlings/m$^2$), and native species density (# seedlings/m$^2$) on the experimental plots. Values with the same letter are not significantly different at P=0.05.

| | Ex Sp rich | Nat Sp rich | Ex density | Nat density |
|---|---|---|---|---|
| Historical treatment | | | | |
| Control | 31.69ab | 24.38a | 48.76a | 24.38a |
| Water | 23.16b | 24.38a | 36.57a | 24.38a |
| Nitrogen | 49.97a | 46.32a | 98.73a | 46.32a |
| Water + Nitrogen | 49.97b | 45.10a | 141.4b | 45.10a |
| New treatment | | | | |
| Control | 42.66a | 32.91a | 98.73a | 32.91a |
| Sugar | 37.78a | 37.78a | 54.85a | 37.78a |
| Lignin | 37.78a | 37.78a | 85.33a | 37.78a |
| Sawdust | 31.69a | 32.91a | 107.27a | 45.10a |
| Lignin + Sugar | 32.91a | 40.22a | 57.29a | 40.22a |
| Sawdust + Sugar | 49.97a | 32.91a | 82.89a | 32.91a |

highest on the plots that received no nitrogen reducing treatment. This is similar to results found by McLendon and Redente (1992) working on a semiarid sagebrush site in Colorado. They found that the addition of sucrose significantly reduced the abundance of two exotic Eurasian weeds, *Salsola iberica* and *Kochia scoparia,* which are the dominant exotic weeds on our site. Other researchers have found that additions of sawdust increased the establishment of native seedlings in a community that was dominated by exotics (Wilson and Gerry 1995).

The failure of the humus precursors to significantly reduce the dominance of the community by exotic weeds could be a result of several possibilities. The foremost of these possibilities is the limited duration of the study. The addition of carbon compounds to the soil may take time to translate into community changes aboveground, and even longer to translate into changes in the seedbank. Changes in species composition are slow in this semiarid system, large increases in exotic species on this site due to water and nitrogen additions which ended in 1975 were not noted until years later (Milchunas and Lauenroth 1995). Other researchers have found the addition of sugar and sawdust to be ineffective over a three year period in suppressing the growth of undesirable exotics (Morghan and Seastedt 1999).

Exotic weed species use a variety of mechanisms to outcompete other species (Baker 1986). It is possible that the success of the exotic invasive weeds at this study site is not due to rapid growth rates in response to elevated nitrogen levels, but to the expression of other successful competitive traits.

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# CHAPTER 2

# EFFECTS OF A NITROGEN AND COMPETITION GRADIENT ON THE GROWTH OF AN EXOTIC INVASIVE ANNUAL AND A SLOW-GROWING NATIVE PERENNIAL

## Introduction

Exotic plant invasions are a serious concern for land managers and conservationists. Anthropogenic influences are not only providing means of transport for the introduction of exotic species into new ecosystems, but are also providing favorable conditions for the growth and dominance of exotics through system disturbance and subsequent increased resource availability (Baker 1986, Huston 1994, Vitousek et al. 1996). Invasive plant species are thought to be successful in dominating new ecosystems partially because they differ from natives in their resource use efficiency (Vitousek 1990); often they have the ability to respond rapidly to increased resource availability with rapid growth rates, thus outcompeting native species (Grime 1977, Baker 1986). Anthropogenic changes to the global nitrogen cycle have increased atmospheric nitrogen deposition to terrestrial systems worldwide (Vitousek et al. 1997). It is possible that increased atmospheric nitrogen deposition into low nitrogen ecosystems could cause a shift in community composition from dominance by native plants to dominance by species that appear to have the intrinsic ability to exploit this enrichment (Willems et al. 1993); many of these species are exotic, invasive weeds (Hobbs and Huenneke 1992). Several field studies have shown that high nitrogen availability shifts community composition from dominance by native vegetation to dominance by resource exploitive, fast growing, exotic weed species (Hunneke et al. 1990, Milchunas and Lauenroth 1995, Wilson and Gerry 1995, Burke and Grime 1996).

In contrast to many other grassland systems, the shortgrass steppe of North America has experienced a minimal amount of invasion by exotic plant species (Kotanen et al. 1998). The resistance of the shortgrass steppe to exotic species invasion is thought to be due at least partially to the dominance by the native perennial bunchgrass *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, which accounts for 90% of the basal cover (Milchunas et al. 1989). The presence of *Bouteloua gracilis* on undisturbed shortgrass steppe appears to inhibit the establishment of exotic species seedlings (Milchunas et al. 1992), probably through competitive exclusion, as *Bouteloua gracilis* dominates the majority of belowground resources (Milchunas and Lauenroth 1989). Although undisturbed shortgrass steppe is apparently resistant to exotic species invasion, certain types of disturbances seem to facilitate and perpetuate this process. The addition of the two most limiting resources in the shortgrass steppe, water and nitrogen, in amounts far above what this system would normally experience, results in invasion and dominance by exotic plant species (Milchunas and Lauenroth 1995).

Several restoration experiments have attempted to ameliorate exotic species invasions by reducing the availability of soil nitrogen by the addition of varying carbon sources (McLendon and Redente 1992, Morgan 1994, Morghan and Seastedt 1999). This "reverse fertilization" (sensu Morgan 1994) reduces biologically available nitrogen by encouraging microbial immobilization, which is hypothesized to disadvantage exotic weedy species and provide an advantage to native species, which are better adapted to lower nitrogen availability (Wedin and Tilman 1990, Redente et al. 1992). Does decreasing biologically available nitrogen in the soil actually suppress the competitive advantage of exotic species and favor native species?

One of the most successful invasive exotics in the western United States is *Bromus tectorum* L., a Eurasian annual which, since its introduction about 110 years ago, has taken over millions of hectares in the intermountain western United States (Mack 1981). *Bromus tectorum* has not yet invaded the shortgrass steppe to any significant degree, but it is increasing in abundance along roadsides in this ecosystem (Kotanen et al. 1998). The importance of *Bromus tectorum* as an invasive species in the shortgrass steppe may increase in the future with changes in climate and increases in atmospheric nitrogen deposition. It is important to establish empirical baseline data on responses of this exotic species as compared to slow growing native dominant species in order to predict effects of high levels of nutrient availability on community dynamics.

My overall objective with this study was to determine the effects of nitrogen availability and competition on the growth of two grass species with contrasting life histories, a fast growing exotic annual species, *Bromus tectorum*, and a slow growing native, *Bouteloua gracilis*. Specifically, I was interested in testing the hypothesis that this exotic weedy species is physiologically capable of maximizing growth at high nitrogen levels, in contrast to the native species which I hypothesize is not capable of the same physiological plasticity, but will perform comparatively better at low nitrogen levels. This experiment utilizes one native species and one exotic species, which limits what inferences can be drawn from the results. However, the results may provide some insight into vulnerability of the system dominated by native *Bouteloua gracilis*, the shortgrass steppe, to invasion by the exotic *Bromus tectorum*. I expected to find the exotic species maximizing growth at the highest nitrogen levels, while the native species would maximize growth at a lower level of nitrogen. I also wanted to test the hypothesis that the competitive ability of the exotic species would decrease and the competitive ability of the native would increase at low nitrogen levels. I expected to find that *Bouteloua gracilis* would perform comparatively better at the lower nitrogen levels, but that this would quickly shift to an advantage to *Bromus tectorum* at high nitrogen levels.

## Methods

I conducted a replacement series experiment (de Wit 1960) with two species, five levels of competition, and five levels of nitrogen availability. All plants were grown in pots (15 cm x 16.5 cm) in a greenhouse. The two species were *Bromus tectorum* (cheatgrass) and *Bouteloua gracilis* (blue grama) (plant nomenclature follows the Great Plains Flora Association (1986)). Average annual net N mineralization in the shortgrass steppe is estimated to be 1.5-2.5 g $m^{-2}$ (Burke et al. 1997, Hook 1995). The nitrogen gradient was applied as g $m^{-2}$ equivalents because I thought that this unit of measurement would be more applicable to predictions about field conditions. The treatments were: 0 g N /$m^2$, 1 g N/$m^2$, 4 g N/$m^2$, 7 g N/$m^2$, and 10g N/$m^2$. The competition levels were monoculture, 1:4 (one individual of one species and 4 of the other), 2:3, 3:2, and 4:1. The total experiment included six levels of competition x five nitrogen treatments (0,1,4,7,10 g N/$m^2$) x 10 replicates of each combination of competition level and nitrogen treatment, for a total of 300 pots.

I collected *Bromus tectorum* seeds at the Central Plains Experimental Range (40°49' N latitude, 107°46' W longitude) in northcentral Colorado, a shortgrass steppe site. I obtained *Bouteloua gracilis* seeds from a seed dealer. Seeds of both species were sown in 3 l pots with a surface area of 191 cm$^2$, giving each individual plant 38 cm$^2$ of surface are and 600 cm$^3$ of substrate composed of 60% vermiculite and 40% washed sand by volume. I weeded the plants to final density one week after germination. I applied all micro and macro nutrients except nitrogen with a modified Hoagland's solution at the rate of 100 ml every two weeks. I applied nitrogen as a solution of ammonium nitrate, formulated to the correct treatment, in stages of 5 % of the total experimental treatment one week after germination, and every two weeks thereafter in dosages of 25 %, 35 %, 25 %, and 10%. The amount of nitrogen was staggered to provide the largest amount of nitrogen during the most rapid growth period. I watered the pots every two days to field capacity (approx. 700 ml of water).

The pots were maintained in an unshaded greenhouse for 70 days after weeding to final density from August 5th, 1998 to October 13th, 1998. At the end of the experiment, I harvested aboveground biomass by clipping each plant just above the root crown and drying the plant material at 55°C for 48 hours before weighing. I harvested belowground biomass by root washing only for the monoculture pots, as the roots in the combination pots proved impossible to separate into species. I ashed belowground biomass in a muffle furnace to correct values to an organic matter basis. I ground dried aboveground material in a ball mill, and analyzed a .1 g subsample for carbon and nitrogen content in a LECO CHN-1000 analyzer (St. Joseph, MI). There are only % N and C data for *Bouteloua gracilis* in the monoculture pots, as the aboveground growth of this species in the mixed ratio pots provided insufficient material for analysis.

I analyzed the data using the GLM procedure in SAS (SAS Institute 1989). I used 2-way analysis of covariance (ANCOVA) to test for the separate and combined effects of competition and nitrogen on aboveground biomass, height, and % N tissue concentration of *Bromus tectorum* and *Bouteloua gracilis*. I used ANCOVA to test for the effect of nitrogen on belowground biomass for both species. The average per plant aboveground biomass for both species was log-transformed to satisfy the assumptions of ANCOVA. ANCOVA was used over analysis of variance (ANOVA) because the independent variable nitrogen was continuous and competition was categorical. I used Fisher's least significant difference (LSD) procedure to compare the treatment means.

## Results

### *Responses to nitrogen*

The greatest average per plant height for *Bromus* and *Bouteloua* was achieved at the highest nitrogen levels and the smallest height at the lowest nitrogen levels (Fig. 2.1a,b). *Bouteloua* height had more of an asymptotic response to increasing nitrogen availability than *Bromus*.

The nitrogen x competition interaction was not significant for either species, but nitrogen levels significantly affected average per plant aboveground biomass in both species (Table 2.1, Table 2.2). *Bromus tectorum* aboveground biomass showed a stronger response to increasing nitrogen availability than *Bouteloua*, with the average per plant biomass increasing significantly until leveling out in the 7 g N/m$^2$ treatment (Fig. 2.1c). *Bouteloua gracilis* had a more asymptotic response, with average aboveground per plant biomass not changing significantly above 4 g N/m$^2$ (Fig. 2.1d). *Bromus tectorum*

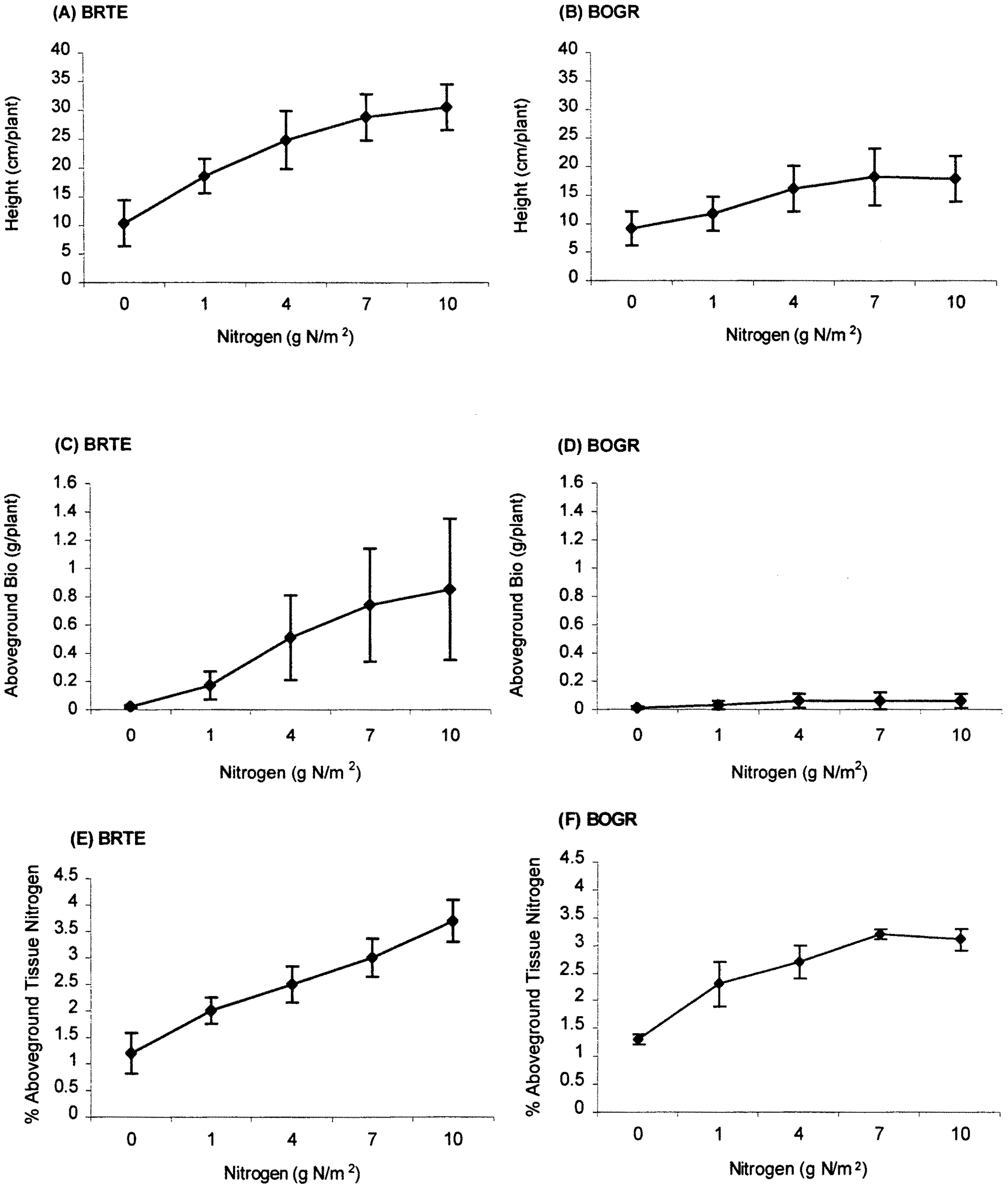

Fig. 2.1. Height, aboveground biomass, and % aboveground tissue nitrogen response of an exotic, *Bromus tectorum* (BRTE) (A,C,E), and a native, *Bouteloua gracilis* (BOGR) (B,D,F), grown from seed in a greenhouse for 70 days, to a gradient in nitrogen availability. Error bars are one standard deviation from the mean.

Table 2.1 ANCOVA table for *Bromus tectorum* showing the significance of the effects of a gradient in competition and nitrogen on the dependent variables of aboveground biomass, height, % nitrogen tissue concentration, and belowground biomass. Competition is missing from the belowground biomass analysis because roots in pots with both species could not be separated and identified.

| Response | Factor | df | MS | F | P | Partial $r^2$ |
|---|---|---|---|---|---|---|
| Aboveground bio | Competition | 4 | 8.612 | 20.74 | 0.0001 | 0.024 |
| | Nitrogen | 1 | 183.078 | 440.97 | 0.0001 | 0.323 |
| | Nitrogen x Nitrogen | 1 | 80.52 | 193.95 | 0.0001 | 0.0028 |
| | Competition x Nitrogen | 4 | 0.395 | 0.95 | 0.4351 | 0.145 |
| | Error | 221 | 0.4155 | | | 0.154 |
| Height | Competition | 4 | 110.5 | 6.22 | 0.0001 | 0.025 |
| | Nitrogen | 1 | 4171.56 | 234.65 | 0.0001 | 0.237 |
| | Nitrogen x Nitrogen | 1 | 1428.61 | 80.36 | 0.0001 | 0.0314 |
| | Competition x Nitrogen | 4 | 8.4 | 0.47 | 0.7549 | 0.0019 |
| | Error | 209 | 15.7 | | | 0.226 |
| N tissue conc | Competition | 4 | 0.45 | 4.46 | 0.0035 | 0.0346 |
| | Nitrogen | 1 | 3.95 | 39.14 | 0.0001 | 0.075 |
| | Nitrogen x Nitrogen | 1 | 0.106 | 1.05 | 0.309 | 0.002 |
| | Competition x Nitrogen | 4 | 0.022 | 0.23 | 0.9217 | 0.0017 |
| | Error | 53 | 0.1 | | | 0.102 |
| Belowground bio | Nitrogen | 1 | 11.31 | 10.12 | 0.0029 | 0.243 |
| | Nitrogen x Nitrogen | 1 | 6.14 | 5.5 | 0.0244 | 0.1502 |
| | Error | 38 | 0.35 | | | 0.6775 |

Table 2.2. ANCOVA table for *Bouteloua gracilis* showing the significance of the effects of a gradient in competition and nitrogen on the dependent variables of aboveground biomass, height, % nitrogen tissue concentration, and belowground biomass. Competition is missing as an independent variable in the N tissue concentration because not enough material was present for analysis. Competition is missing from the belowground biomass analysis because roots in pots with both species could not be separated and identified.

| Response | Factor | df | MS | F | P | Partial $r^2$ |
|---|---|---|---|---|---|---|
| Aboveground bio | Competition | 4 | 4.54 | 7.4 | 0.0001 | 0.0766 |
| | Nitrogen | 1 | 53.79 | 87.55 | 0.0001 | 0.2268 |
| | Nitrogen x Nitrogen | 1 | 27.12 | 44.15 | 0.0001 | 0.1144 |
| | Competition x Nitrogen | 4 | 0.724 | 1.18 | 0.3206 | 0.0122 |
| | Error | 220 | 0.6144 | | | 0.57 |
| Height | Competition | 4 | 45.06 | 2.92 | 0.0222 | 0.024 |
| | Nitrogen | 1 | 1325.66 | 85.81 | 0.0001 | 0.1759 |
| | Nitrogen x Nitrogen | 1 | 576.82 | 37.34 | 0.0001 | 0.0759 |
| | Competition x Nitrogen | 4 | 15.12 | 0.98 | 0.4198 | 0.003 |
| | Error | 224 | 15.44 | | | 0.461 |
| N tissue conc | Nitrogen | 1 | 2.64 | 22.4 | 0.0005 | 0.3346 |
| | Nitrogen x Nitrogen | 1 | 1.08 | 9.2 | 0.0104 | 0.1358 |
| | Error | 12 | 0.117 | | | 0.173 |
| Belowground bio | Nitrogen | 1 | 0.0246 | 0.85 | 0.3624 | 0.013 |
| | Nitrogen x Nitrogen | 1 | 0.001 | 0.06 | 0.8145 | 0.0007 |
| | Error | 38 | 0.029 | | | 0.8527 |

increased its aboveground biomass at roughly twice the rate of *Bouteloua gracilis* at the lower nitrogen levels (Table 2.3). At the higher nitrogen levels, *Bromus* continued to accumulate aboveground biomass at a similar rate, while the aboveground biomass accumulation rate of *Bouteloua* dropped off sharply, so much so, that *Bromus* at the higher nitrogen levels had a growth rate roughly five times higher than that of *Bouteloua.*

Nitrogen availability strongly affected nitrogen tissue concentrations in *Bromus tectorum* (Table 2.1). The response of *Bromus* nitrogen tissue concentrations to the nitrogen gradient (Fig. 2.1e) was very similar to the response of the aboveground biomass (Fig. 2.1c); both variables displayed almost a linear response to the nitrogen gradient. *Bouteloua* N tissue concentrations were significantly affected by the increasing nitrogen gradient (Table 2.2*).* *Bouteloua* nitrogen tissue concentrations had an asymptotic response to increasing N availability (Fig. 2.1f). *Bouteloua gracilis* increased nitrogen concentrations in its aboveground tissues at a faster rate than *Bromus* at the 1 g N/m$^2$ level (Table 2.3). At the other levels of nitrogen availability, the two species had very similar accumulation rates (Table 2.3).

Nitrogen did show an effect on the belowground accumulation of *Bromus tectorum* biomass (Table 2.1), but the response of *Bromus* belowground growth to the nitrogen gradient was significantly smaller compared to the response of the aboveground growth, which is to be expected as this species is an annual. The effect of nitrogen on the belowground growth of *Bouteloua gracilis* was not significant (Table 2.2).

Table 2.3. Growth and nitrogen accumulation rates of *Bouteloua gracilis* (BOGR) and *Bromus tectorum* (BRTE) in response to a nitrogen gradient. Data were calculated as change in aboveground biomass per plant or change in nitrogen tissue concentration over change in nitrogen availability.

| | Aboveground biomass | Aboveground biomass | %N | %N |
|---|---|---|---|---|
| Nitrogen (g N/ m$^2$) | BOGR growth rate | BRTE growth rate | BOGR N increase rate | BRTE N increase r |
| 1 | 0.15 | 0.272 | 1 | 0.7 |
| 4 | 0.135 | 0.332 | 0.35 | 0.3 |
| 7 | 0.053 | 0.274 | 0.271 | 0.25 |
| 10 | 0.046 | 0.217 | 0.18 | 0.25 |

*Responses to competition*

Competition significantly affected the average per plant aboveground biomass of both *Bromus tectorum* and *Bouteloua gracilis* (Table 2.1, Table 2.2). *Bromus* was very negatively affected by intraspecific competition. Per plant biomass was greatest for *Bromus* under the 4 *Bouteloua*:1 *Bromus* competition treatment and least in the monoculture pots (Fig. 2.2a), a trend that was exactly the same for *Bromus* height (Fig. 2.2b) and *Bromus* N tissue concentrations (Fig. 2.3). By contrast, *Bouteloua gracilis* was negatively affected by interspecific competition, *Bouteloua gracilis* height was greatest in the monoculture pots and least in the pots with the highest number of *Bromus tectorum* plants (1:4) (Fig. 2.2a). The trend in average per plant height was the same as that for aboveground biomass (Fig. 2.2b).

There was no significant nitrogen x competition interaction for either the exotic or the native species. The exotic species responded more strongly to increasing nitrogen availability, while the native species showed an asymptotic response. Nitrogen was not a significant predictor of belowground biomass accumulation in *Bouteloua*, but was for *Bromus*. *Bromus tectorum* and *Bouteloua gracilis* had opposite responses to intraspecific competition; *Bromus* had a strong negative response and *Bouteloua* had a positive response.

## Discussion

My results support the hypothesis that this exotic weedy species maximizes growth as nitrogen availability increases, but the native species does not have the physiological plasticity to increase its growth past a certain level. When the growth

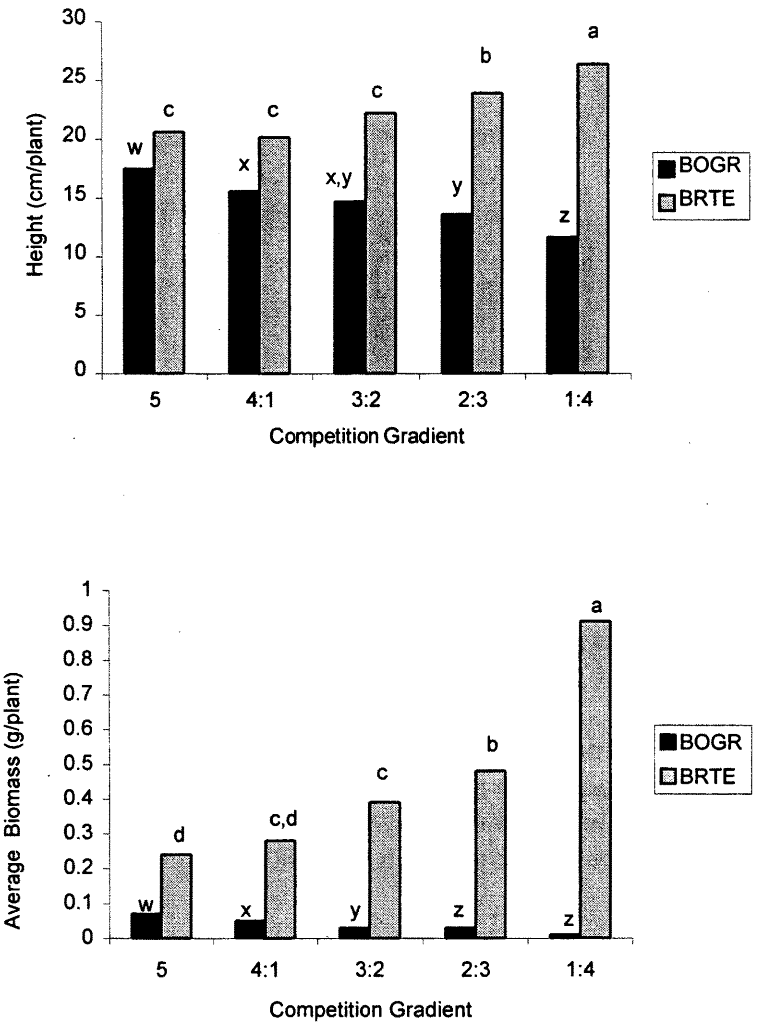

Fig. 2.2. Height (A) and aboveground biomass (B) response of native *Bouteloua gracilis* (BOGR) and exotic *Bromus tectorum* (BRTE), grown from seed in a greenhouse for 70 days, to a competition gradient. Competition gradient ratios are number individual plants of one species relative to number of individual plants of the other species in a single pot. Bars with the same letter are not significantly different at p=0.05.

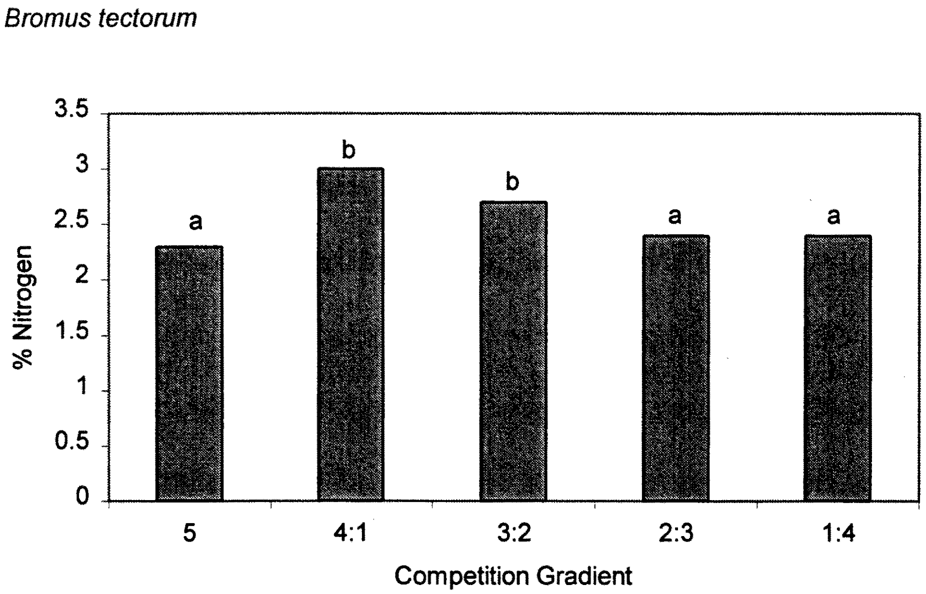

Fig. 2.3. Nitrogen tissue concentration response of the exotic, *Bromus tectorum,* grown from seed in a greenhouse for 70 days to a competition gradient. 5 is the monoculture, the other ratios are *Bouteloua gracilis*:*Bromus tectorum*. Means with the same letter are not significantly different at p=0.05.

at the highest nitrogen levels and the lowest nitrogen levels were compared, *Bromus tectorum* only gained 3% of the maximum mass possible at the low nitrogen levels while *Bouteloua gracilis* gained 13% of its maximum mass at the same levels, indicating the native species performed comparatively better at the lowest nitrogen levels. Nitrogen availability explained 34% of the variability in the belowground biomass accumulation and 45% of the variation in the aboveground biomass accumulation of *Bromus tectorum*, while it was not significant at all for the belowground biomass growth of *Bouteloua gracilis*, and explained only 34% of the variability in the aboveground biomass accumulation. *Bromus tectorum* is prepared to take advantage of high nitrogen availability, while *Bouteloua gracilis* is more capable of growing and persisting at lower nitrogen levels. Nitrogen availability was much more significant for the growth of *Bromus tectorum* than for *Bouteloua gracilis*, which exemplifies the different life histories of these two species. Field studies have found a strong correlation between soil nitrogen availability and exotic species richness (Stohlgren et al. 1999, Wiset et al. 1998).

The two species in this study fit well in the C-S-R conceptual model of plant strategies proposed by Grime (1977,1979). *Bromus tectorum* has characteristics of both a ruderal species and a competitor, as it has both a high resource allocation to reproduction and to growth. *Bouteloua gracilis* has characteristics of a stress-tolerator-slow growth rates, a long lifespan, and an inability to grow rapidly even when resources are in abundant supply. Other studies have shown that weedy ruderal-like species respond to high resource availability with greater growth than other plant species. Redente et al. (1992) found that *Salsola iberica*, a Eurasian exotic, had much higher aboveground biomass production in the greenhouse as nitrogen increased compared to four native plant species.

The positive response of *Bouteloua gracilis* to intraspecific competition found in this study is in contrast to a negative response of *Bouteloua gracilis* to intraspecific competition found by Richard and Redente (1995). It is important to consider however, that in the latter study, *Bouteloua gracilis* was grown under high and low nutrient conditions in the presence of another native species, *Buchloë dactyloides*, and at lower overall densities (two plants per pot) than used in this study. *Bouteloua gracilis* can be competitive with other species native to its own habitat, this is exemplified by the comparatively negative response to growth in monocultures when compared to growth in mixtures found in the Richard and Redente study. In our study, the growth of *Bouteloua* was significantly depressed as the number of *Bromus* individuals in the pot was increased, so a comparatively positive response to intraspecific competition was found. This indicates that *Bouteloua* is not inherently a poor competitor *per se*, but is vastly overshadowed by a species that has evolved a specific ability to maximize its growth when the opportunity exits. *Bromus tectorum* showed a significantly negative response to increasing intraspecific competition, possibly because this species is such a strong competitor against plants with stress tolerant life histories that the comparison between the species mixtures and monoculture pots was disproportionate. A negative response of *Bromus* to intraspecific competition was also found by Dakheel et al. (1994).

Exotic ruderal species like *Bromus tectorum* succeed by taking as much advantage of available nutrients as possible, while stress-tolerant species like *Bouteloua gracilis* succeed by just being able to survive and reproduce under resource depauperate conditions. Stress-tolerant species may make an evolutionary trade-off; they can survive low nutrient conditions, but are unable to take advantage of high resource conditions when they occur. This idea is exemplified by field studies that have found dramatic increases in weedy species and suppression of native species in response to nutrient enrichment (Wilson and Tilman 1991, McLendon and Redente 1991, McLendon and Redente 1992, Hobbs and Atkins 1988, Huenneke et al. 1990, Milchunas and Lauenroth 1995).

My results do not support the hypothesis that reducing available nitrogen will decrease the competitive advantage of the exotic weed species and increase the competitive advantage of the native species, when both species are grown from seed. Decreasing nitrogen availability depressed the growth of both species, but did not significantly alter the competitive relationship between *Bromus tectorum* and *Bouteloua gracilis*. This is evidenced strongly by the fact that at all nitrogen levels, *Bromus tectorum* only competed with itself, while the biomass accumulation of *Bouteloua gracilis* was strongly depressed by increasing competition from *Bromus*. Greenhouse studies have significant limitations, and I recognize that in many cases, an exotic weed such as *Bromus tectorum* will be competing with established individuals of *Bouteloua gracilis*. As such, extrapolation of these results to field conditions carries significant caveats. The two species in this study responded independently to increased and decreased nitrogen availability as was hypothesized given their life history characteristics. However, the deduction that reducing available nitrogen would ameliorate *Bromus tectorum*'s competitive ability was incorrect.

In the field, Morhghan and Seastedt (1999) found that the reduction of biologically available nitrogen by the addition of sugar and sawdust did not decrease exotic species, and failed to increase native, seeded species. Other researchers were able to reduce exotic weeds with the addition of sugar treatments in a semiarid sagebrush community in Colorado (McLendon and Redente 1992), or increase the success of native species seeded into a community dominated by exotics by the addition of sawdust (Wilson and Gerry 1995). My results suggest that restoration efforts attempting to reduce nitrogen availability would be ineffective in suppressing the growth of one exotic, *Bromus tectorum*.

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# CHAPTER 3

# THE EFFECT OF NITROGEN AVAILABLITY ON THE GROWTH OF EXOTIC, INVASIVE WEEDS

## Introduction

Exotic weedy plant species are theorized to share a host of specific life history traits; one of those characteristics is a rapid growth response to nutrient enrichment (Grime 1977, Baker 1986). Conversely, fast growing plant species, many but not all of which are exotic weeds, are thought to fare poorly under low nutrient conditions (Grime 1977, Chapin 1980, Shipley and Keddy 1988, Carson and Pickett 1990). The spread and persistence of invasive exotic weeds is of major concern to both land owners and conservationists as exotic plant invasion reduces biodiversity (Huston 1994), and alters ecosystem function (Vitousek 1986). High nitrogen availability has been shown to encourage the spread and dominance of exotic invasive weeds (Milchunas and Lauenroth 1995, Hunneke et al. 1990, Hobbs and Atkins 1988). Increases in atmospheric nitrogen deposition due to human alterations of the global nitrogen cycle may further exacerbate the spread of exotic species (Hobbs and Huenneke 1992).

Several exotic species, *Bromus tectorum* L. (cheatgrass), *Euphorbia esula* L. (leafy spurge), *Cirsium arvense* L. (Canada thistle), and *Centaurea repens* L. (Russian knapweed), have become of particular concern in the western United States due to their

Table 3.1. Species name, common name, growth form, photosynthetic pathway, place of origin, and date of introduction to North America, for the six plant species used in this study.

| Species | Common Name | Growth form | Photo pathway | Place of origin | Date of intro |
|---|---|---|---|---|---|
| Exotics | | | | | |
| *Bromus tectorum* | Cheatgrass | Annual grass | $C_3$ | Eurasia | 1850 |
| *Euphorbia esula* | Leafy spurge | Perennial forb | $C_3$ | Eurasia | 1829 |
| *Cirsium arvense* | Canada thistle | Perennial forb | $C_3$ | Europe | 1600 |
| *Centaurea repens* | Russian knapweed | Perennial forb | $C_3$ | Eurasia | 1898 |
| Natives | | | | | |
| *Bouteloua gracilis* | Blue grama | Perennial grass | $C_4$ | | |
| *Agropyron smithii* | Western wheatgrass | Perennial grass | $C_3$ | | |

aggressive invasion of large areas, their ability to displace native species, and the reduction in land use quality that accompanies the presence of these species. *Bromus tectorum*, an annual grass introduced from Eurasia, has taken over million of hectares in the intermountain West since its introduction in the mid 1800's (Mack 1981). *Bromus tectorum* establishes large monoculture stands that dry out early in the growing season, altering fire regimes by providing a large source of fine fuels, which appears to promote the dominance of *Bromus* by reducing competition from native species (Pellant 1990). *Euphorbia esula* is a perennial forb introduced from Eurasia that forms monoculture stands which displace native vegetation, degrade wildlife habitat, and significantly decrease forage availability and quality for domestic livestock. *Euphorbia esula* infests approximately 1.1 million hectares in the Great Plains of the U.S. and portions of Canada (Sheley and Petroff 1999). *Cirsium arvense* is a perennial forb introduced from Europe in the 1600's (Erickson 1983), which forms dense colonies via vegetative reproduction. *Centaurea repens*, a perennial forb introduced from Eurasia, infests 557,000 hectares in the western United States (Sheley and Petroff 1999). This species is a prolific seed producer as well as spreading vegetatively from root buds. Will increases in nitrogen availability favor the growth of these exotic weeds? Discerning the response of these species to varying nitrogen levels can help predict the impact of nitrogen additions on systems where these noxious weeds occur.

The objective of this study was to test the hypothesis that exotic, invasive weeds respond to increasing nitrogen availability with rapid growth rates, but cannot tolerate, or perform poorly at, low nitrogen availability when compared to native species.

## Methods

I set up the experiment in the greenhouse as a completely randomized design with six species and five levels of nitrogen availability. Two plant species represented native species and four represented invasive, exotic species. The native species were *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, a warm season perennial grass, and *Agropyron smithii* Rydb., a cool season perennial grass. *Bouteloua gracilis* was chosen because it dominates the shortgrass steppe, an ecosystem that has not been significantly invaded by exotic weeds (Kotanen et al. 1998). *Agropyron smithii* is a native species that has some weedy characteristics, for example, it grows readily in disturbed areas such as roadsides (Stubbendieck et al. 1981). The exotic, invasive weed species were *Bromus tectorum*, *Euphorbia esula*, *Cirsium arvense*, and *Centaurea repens*.. *Bouteloua gracilis* and *Agropyron smithii* seeds were obtained from a seed dealer. The seeds for the exotic invasive weeds were collected from locations around northern Colorado. The overall experimental design consisted of six species, five levels of nitrogen availability, and five replicates of each species at each level of nitrogen availability for a total of 150 pots. I sowed ten seeds from each species into each of 25 15-cm x 16.5-cm plastic pots with a substrate of 60% vermiculite 40% washed sand by volume. Ten days after first emergence, I thinned the seedlings in each pot to their final density of one plant per pot.

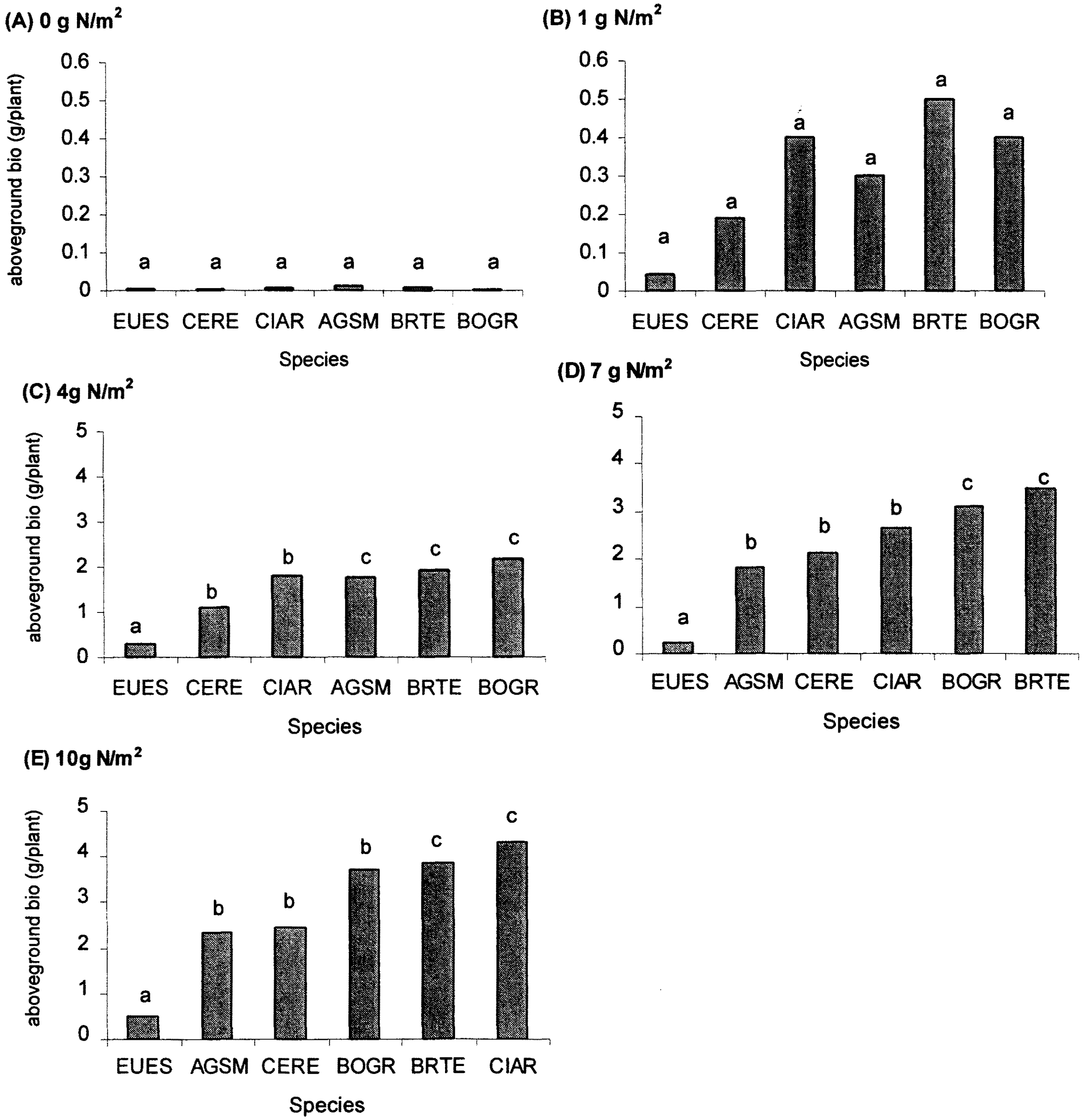
A nitrogen gradient was established with five levels of nitrogen availability equivalent to, 0 g N/m$^2$, 1 g N/m$^2$, 4 g N/m$^2$, 7 g N/m$^2$, and 10 g N/m$^2$. I applied the nitrogen treatments as a solution of ammonium nitrate in stages: 10% of the total ammonium nitrate application was applied the first 20 days after germination, and every two weeks thereafter I added dosages of 25%, 30%, 20%, and 5%. I organized the nitrogen additions this way so that the plants would receive the highest amounts of nitrogen during the early growth stages. I applied all micro and macro nutrients except nitrogen to the pots with a modified Hoagland's solution at a rate of 100 ml every week. I maintained the pots near field capacity by watering every day or every other day, depending upon need. I maintained the pots in an unshaded greenhouse for 75 days from July 8th, 1999 to September 21st, 1999.

At the end of the experiment, I harvested aboveground biomass by clipping each plant just above the root crown and drying the plant material at 55°C for 48 hours. I ashed belowground biomass in a muffle furnace; it is reported on an ash free basis. I measured plant height every two weeks. I ground the dried aboveground material in a ball mill and analyzed a 0.1 g subsample for carbon and nitrogen content in a LECO CHN-1000 analyzer (St. Josheph, MI).

I set up the experiment as a completely randomized design, and analyzed the data using the GLM procedure in SAS (SAS Institute 1989) with a one-way analysis of variance (ANOVA), nitrogen being the independent variable. The dependent variables were aboveground biomass, belowground biomass, height, and percent nitrogen in aboveground tissue. I used Fisher's least significant difference (LSD) procedure to compare treatment means.

## Results

Nitrogen was a significant predictor of aboveground biomass gain for all species. Nitrogen explained 74 and 76 % of the variability in aboveground biomass gain for the native species, *Bouteloua gracilis* and *Agropyron smithii*, explained 90 and 94 % of the



(A) 0 g N/m²

(B) 1 g N/m²

(C) 4g N/m²

(D) 7 g N/m²

(E) 10g N/m²

Fig. 3.1. Aboveground biomass response of two native species *Bouteloua gracilis* (BOGR), and *Agropyron smithii* (AGSM) and four exotic species, *Bromus tectorum*(BRTE), *Euphorbia esula* (EUES), *Cirsium arvense* (CIAR), and *Centaurea repens* (CERE), grown in a greenhouse from seed for 75 days to a nitrogen gradient of 0 g N/m$^2$ (A), 1 g N/m$^2$ (B), 4 g N/m$^2$ (C), 7 g N/m$^2$ (D), and 10 g N/m$^2$ (E). Bars with the same letter are not significantly different at p=0.05.

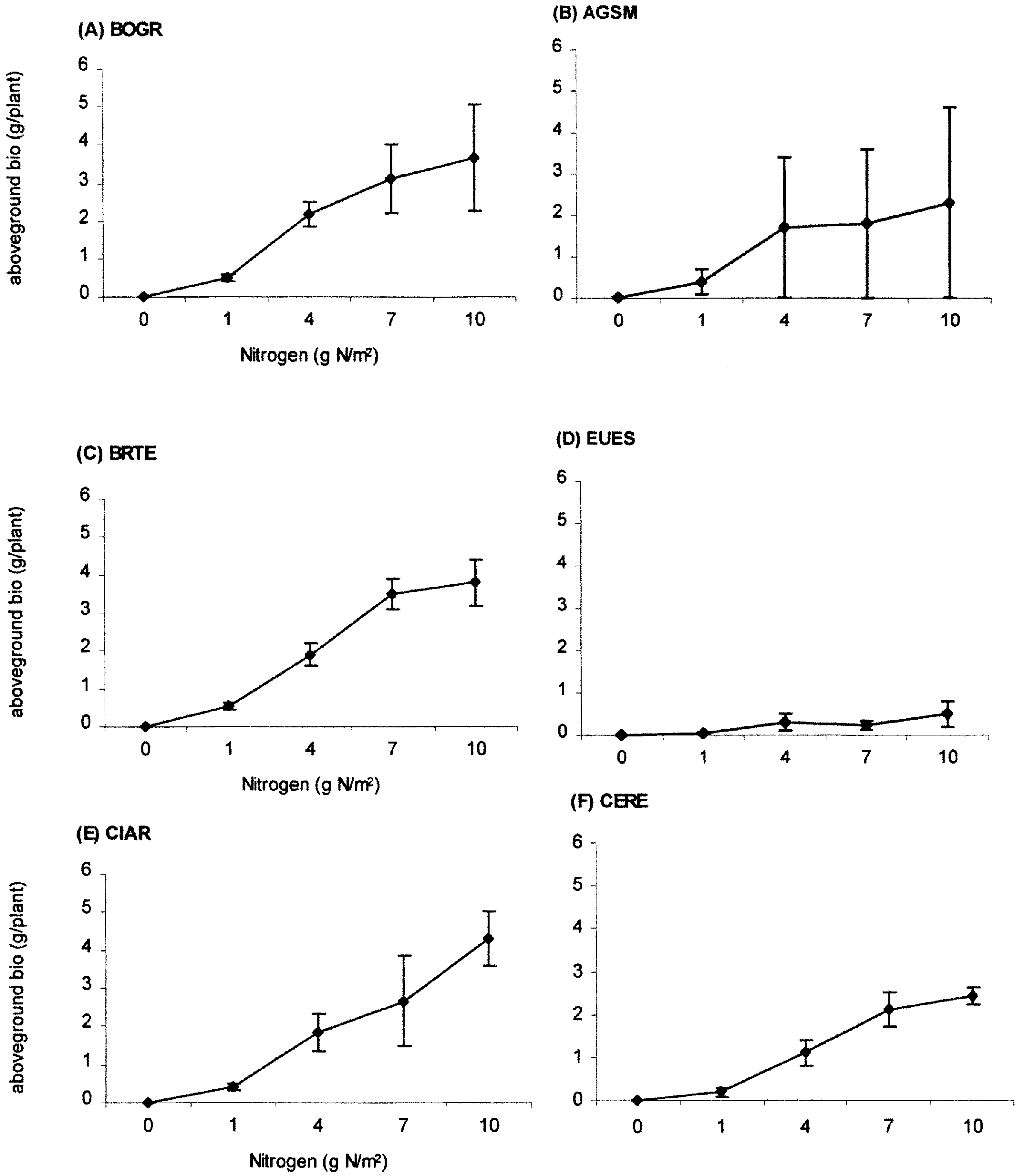


Fig. 3.2. Aboveground biomass response of two native species, *Bouteloua gracilis* (A) and *Agropyron smithii* (B), and four exotic species, *Bromus tectorum* (C), *Euphorbia esula* (D), *Cirsium arvense* (E), and *Centaurea repens* (F), grown from seed in the greenhouse for 75 days to a gradient in nitrogen availability. Error bars are one standard deviation from the mean.

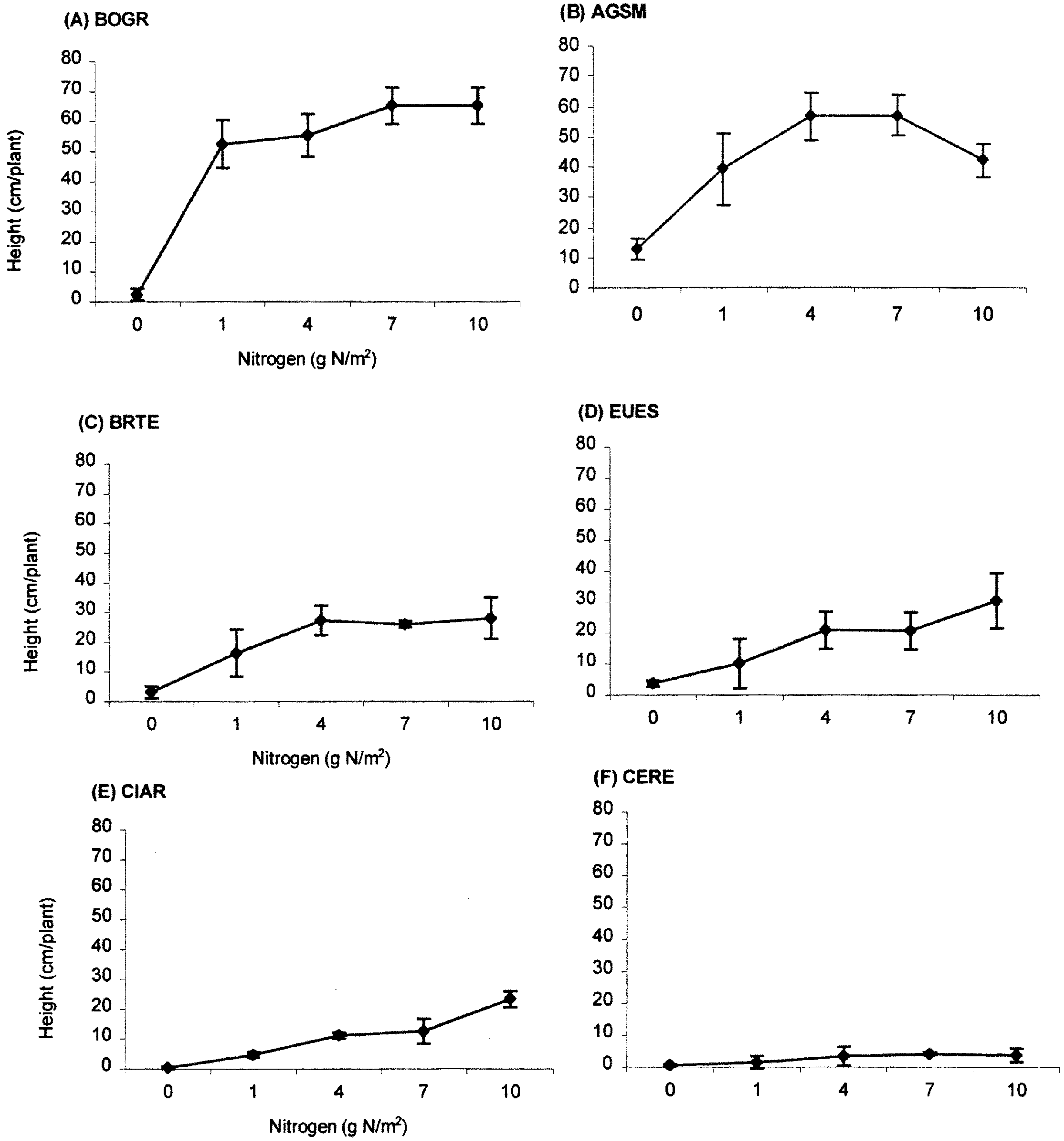


Fig. 3.3. Height response of two native species, *Bouteloua gracilis* (A), and *Agropyron smithii* (B), and four exotic species, *Bromus tectorum* (C), *Euphorbia esula* (D), *Cirsium arvense* (E), and *Centaurea repens* (D) grown from seed in the greenhouse for 75 days to a gradient in nitrogen availability. Error bars are one standard deviation from the mean.

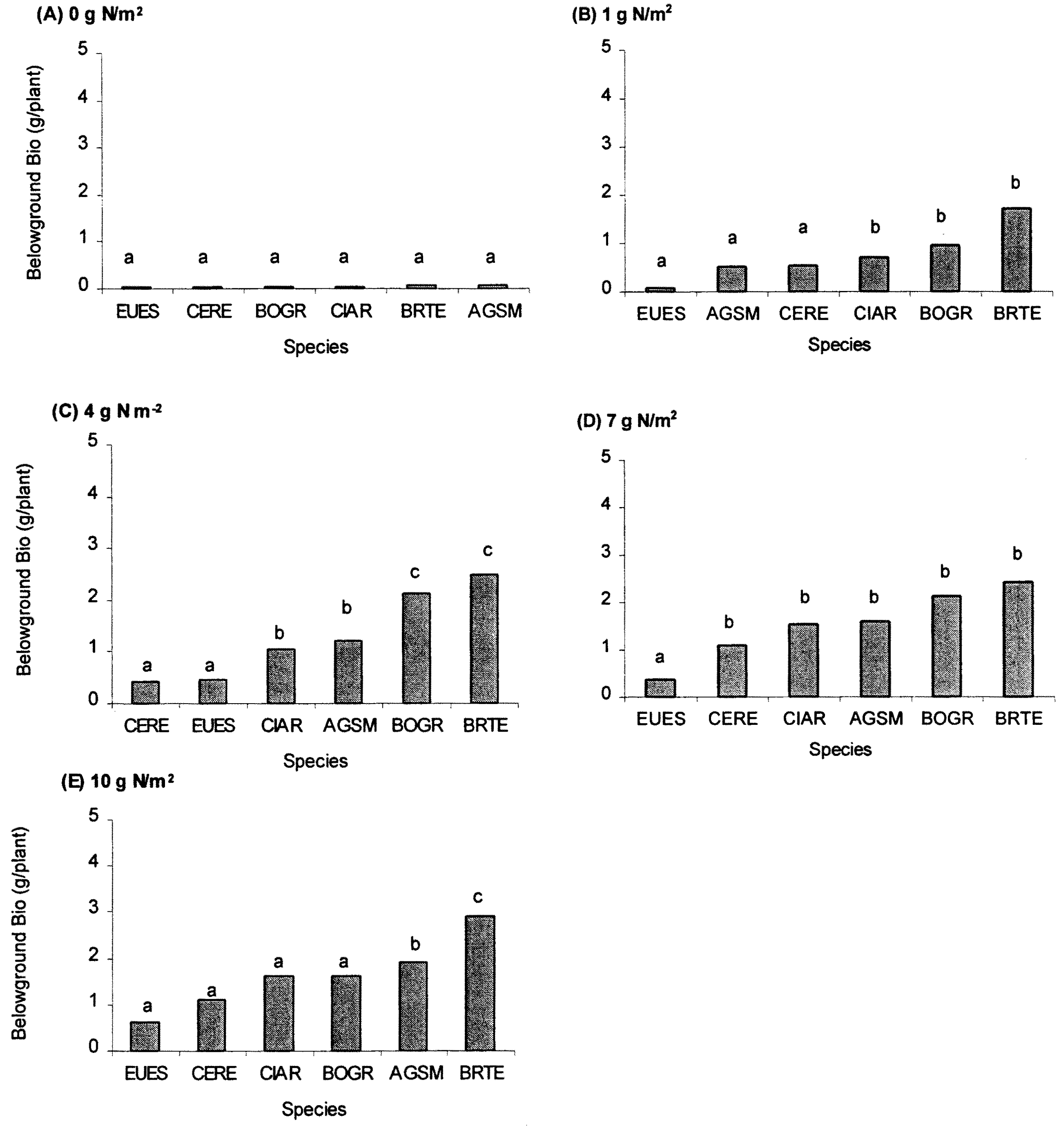


Fig. 3.4. Belowground biomass response of two native species, *Bouteloua gracilis* (BOGR), and *Agropyron smithii* (AGSM), and four exotic species, *Bromus tectorum* (BRTE), *Euphorbia esula* (EUES), *Cirsium arvense* (CIAR), and *Centaurea repens* (CERE), grown in a greenhouse from seed for 75 days to a nitrogen gradient of 0 g N/m$^2$ (A), 1 g N/m$^2$ (B), 4 g N/m$^2$ (C), 7 g N/m$^2$ (D), and 10 g N/m$^2$ (E). Bars with the same letter are not significantly different at p=0.05.

level of nitrogen availability, an exotic species, *Bromus tectorum*, had the greatest belowground biomass gain (Fig. 3.4 e). The two native species, and one exotic, *Centaurea repens*, continued to accumulate belowground biomass after 7 g N/m$^2$ (Fig. 3.5 a, b, f). *Euphorbia esula* and *Cirsium arvense* failed to gain belowground biomass above the 4 g N/m$^2$ level (Fig. 3.5 d,e), while *Bromus tectorum* failed to gain additional belowground biomass above 1 g N/m$^2$ (Fig. 3.5 c).

Tissue concentrations were not significantly affected by the nitrogen gradient for four species, one native, *Agropyron smithii*, and three exotics, *Euphorbia esula*, *Cirsium arvense*, and *Centaurea repens*. *Bouteloua gracilis* and *Bromus tectorum* tissue nitrogen concentrations were significantly affected by nitrogen availability. Nitrogen availability strongly affected *Bromus tectorum* tissue nitrogen concentrations, explaining 74% of the variability in this dependent variable. *Agropyron smithii* and *Euphorbia esula* did not increase their tissue nitrogen concentrations past the 1 g N/m$^2$ treatment (Fig. 3.6 b,d). *Bouteloua gracilis*, *Cirsium arvense*, and *Centaurea repens* increased their tissue nitrogen concentrations slightly past the 7 g N/m$^2$ treatment (Fig. 3.6 a,e,f), but *Bromus tectorum* increased its tissue nitrogen concentrations sharply past both the 4 and the 7 g N/m$^2$ treatment level (Fig. 3.6 c).

## Discussion

My data does not support the hypothesis that native species perform better than exotic species at low nitrogen levels. However, it is possible that the low nitrogen levels, 0 and 1 g N/m$^2$, were too low for any plant to perform well. It is noteworthy that at the

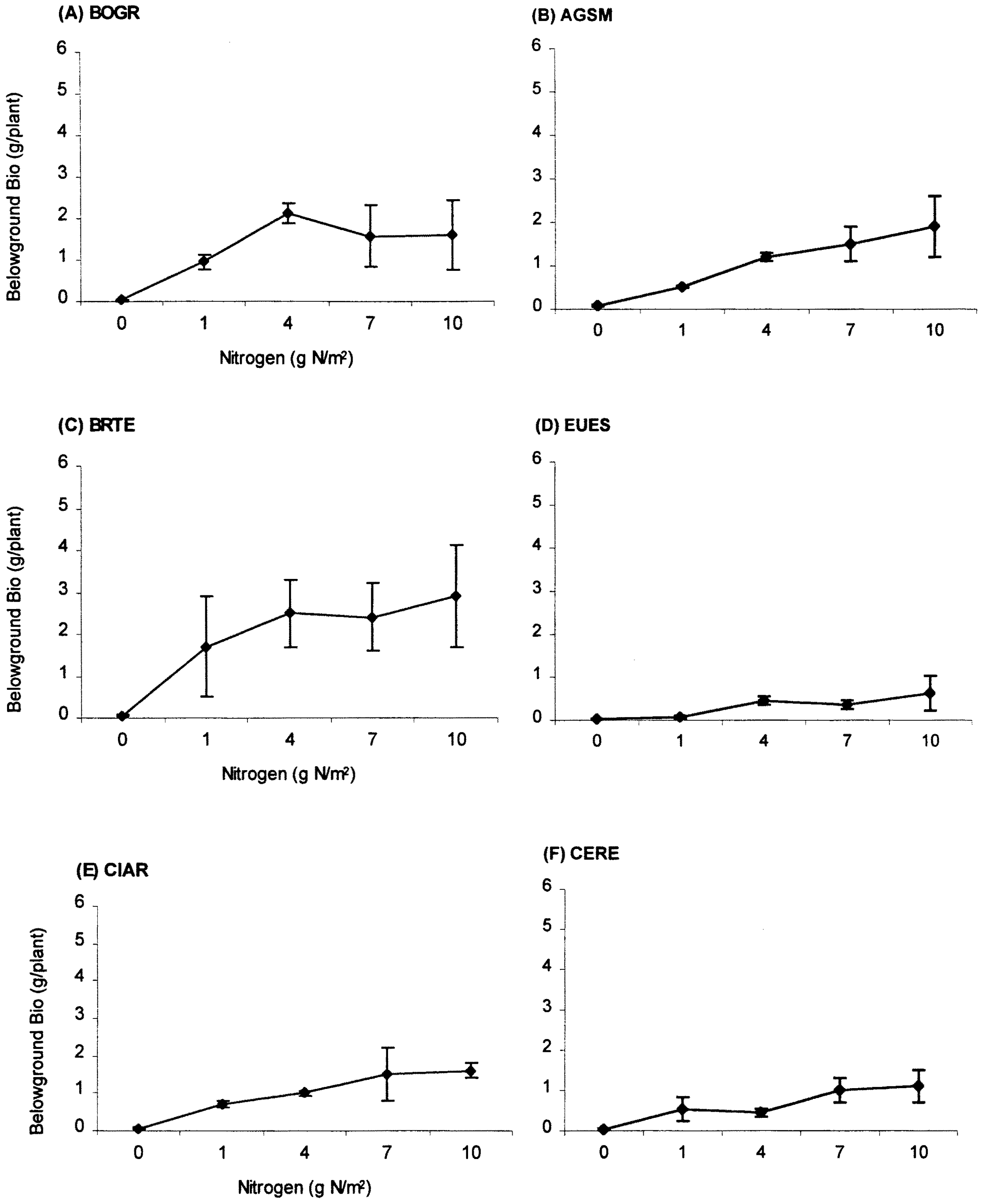


Fig. 3.5. Belowground biomass response of two native species, *Bouteloua gracilis* (A), and *Agropyron smithii* (B), and four exotic species, *Bromus tectorum* (C), *Euphorbia esula* (D), *Cirsium arvense* (E), and *Centaurea repens* (F), to a gradient in nitrogen availability. Error bars are one standard deviation from the mean.

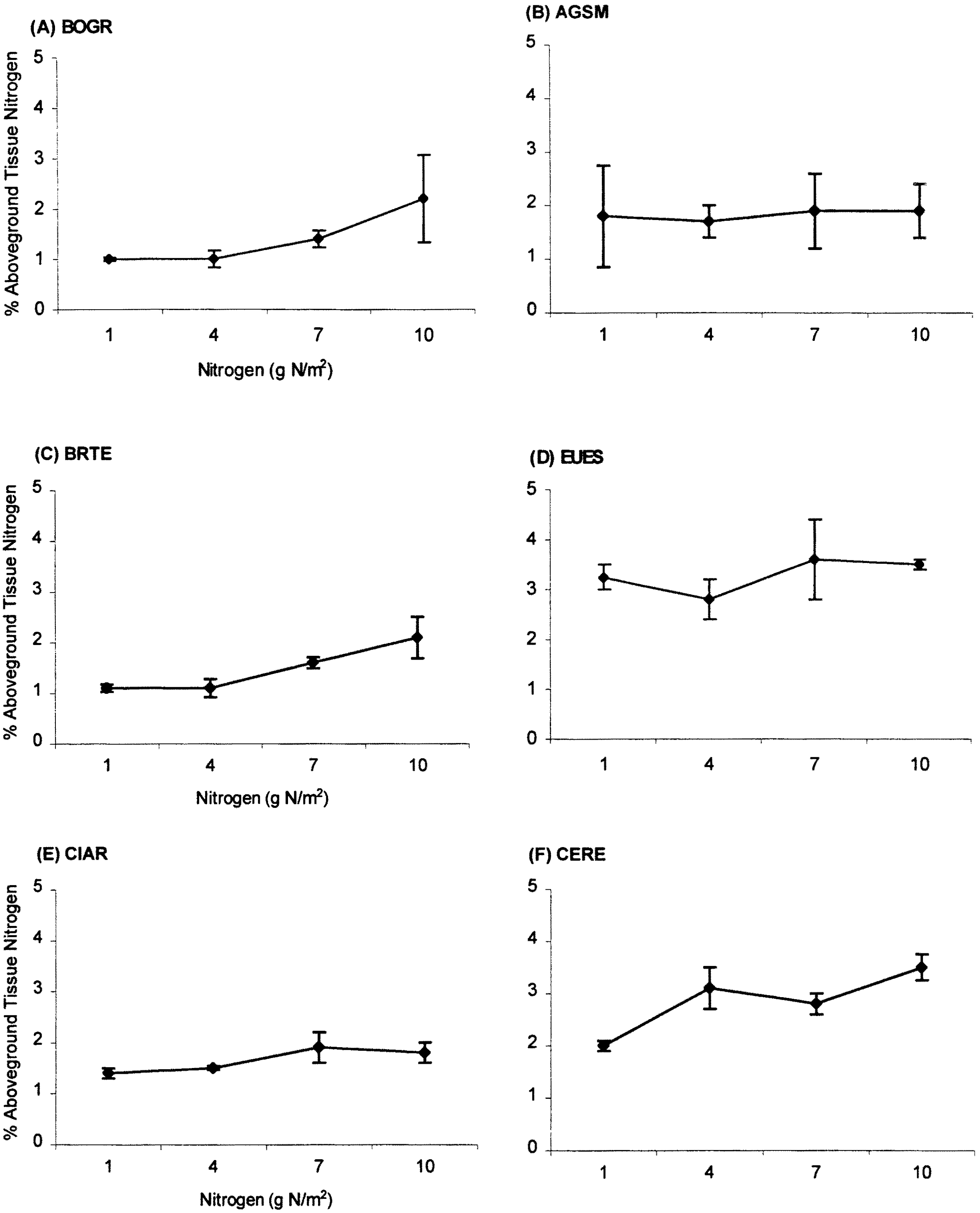


Fig. 3.6. Percent nitrogen in aboveground tissue response of two native species, *Bouteloua gracilis* (A), *Agropyron smithii* (B), and four exotics, *Bromus tectorum* (C), *Euphorbia esula* (D), *Cirsium arvense* (E), and *Centaurea repens* (F), grown from seed for 75 days in a greenhouse, to a gradient in nitrogen availability. Error bars are one standard deviation from the mean.

third level of nitrogen availability, 4 g $N/m^2$, the two natives gained more aboveground biomass than the exotics with the exception of *Bromus tectorum*. *Bromus tectorum*, a fast growing, exotic, invasive annual, performed as well or better than the native species at every level of nitrogen availability. The performance of *Bromus tectorum* is an exception to the theory that fast growing plant species fare poorly under low nutrient conditions (Shipley and Keddy 1988, Garnier et al. 1989). While this is in agreement with the findings from Chapter two, the performance of *Bromus* conflicts with the findings of Muller and Garnier (1990), who found the total biomass and relative growth rate of the fast growing annual *Bromus sterilis*, was significantly reduced by decreased nitrate availability, while the slow growing perennial *Bromus erectus* was not affected. However, it should be noted that in this experiment, nitrogen was added as ammonium, the preference of *Bromus tectorum* for ammonium as compared to nitrate is not known, but the related annual *Bromus sterilis* used in the aforementioned experiment showed no preference for one form of nitrogen over another (Muller and Garnier 1990). The tolerance of the fast growing exotic *Bromus tectorum* to low nitrogen levels is also different from the results found by Redente et al. (1992). Redente et al. grew four native species and one fast growing exotic species, *Salsola iberica*, under seven different nitrogen levels, and found the growth of *Salsola iberica* was significantly reduced at low levels of available nitrogen while the slow growing native species performed comparatively better. Although other researchers have found fast growing exotic species to be negatively affected by low nitrogen levels, my data do not support the generalization that all fast growing exotic species will be so affected.

The two native species, *Bouteloua gracilis* and *Agropyron smithii*, were expected to perform better than the exotics at low nitrogen levels, but perform much poorer than the exotics at high nitrogen levels. Two exotic species, *Bromus tectorum* and *Cirsium arvense* gained the most aboveground mass at the highest nitrogen levels, but the two native species gained the same amount or more mass than the other two exotics, *Euphorbia esula* and *Centaurea repens*. Padgett and Allen (1999) growing three exotic annuals and three native shrubs, hypothesized the same response, but also found the native plant species performed much better at high nitrogen levels than expected. In the field, *Bouteloua gracilis* frequency and basal cover has been found to decrease significantly with nitrogen fertilization (Samuel and Hart 1998, Lorenz and Rogler 1972), but *Bouteloua gracilis* height was found to increase with nitrogen fertilization (Samuel and Hart 1998). The decrease in frequency was attributed to increased competition from $C_3$ species which responded earlier to the excess nitrogen than the $C_4$ *Bouteloua gracilis*. In contrast, the frequency of *Agropyron smithii* in the field has been found to increase in response to nitrogen fertilization (Samuel and Hart 1998, Houston 1971).

My greenhouse data do support the hypothesis that at least some exotic species, when grown without competition, respond to increasing nitrogen with rapid growth rates, most notably *Bromus tectorum* and *Cirsium arvense*. The two native species stopped responding to increased nitrogen at the 4 g N/m$^2$ level, while the exotics continued to gain additional mass after 7 g N/m$^2$. Nitrogen was more important for the growth of two of the exotic species, *Bromus tectorum* and *Centaurea repens*, than it was for the two native species. Many field studies have shown strong shifts in community composition from dominance by native vegetation to dominance by exotic weeds with nitrogen enrichment (Milchunas and Lauenroth 1995, Hunneke et al. 1990, Hobbs and Atkins 1988). Exotic species richness is also positively correlated with soil nitrogen content in several North American grassland systems (Stohlgren et al. 1999). The dominance of exotic weeds under high nutrient conditions is attributed the rapid growth response of this functional group to additional resources. My data in part support this hypothesis, however, nitrogen availability was least important for the growth of one of the exotic plant species, *Euphorbia esula*, suggesting that a rapid growth response to nitrogen enrichment cannot explain the success of all exotic invasives. The success of exotic weeds is due to a multitude of factors; not all exotic species utilize a rapid growth response to nitrogen enrichment to outcompete other plants. Because the nitrogen response of the exotic species in this study varied so widely, I would conclude that anthropogenic nitrogen additions would favor some exotic weeds but not others.

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# CONCLUSIONS

I can now reexamine my three questions presented in the introduction.

1. Will reducing nitrogen availability reduce or eliminate exotic species density/dominance in the field?

The reduction of nitrogen availability on a disturbed shortgrass system failed to reduce the density and dominance of exotic species. I hypothesized that a reduction in biologically available nitrogen though the addition of humus precursors and a labile carbon source would disadvantage the exotic species currently dominating the study site, returning the site to more natural vegetation. This did not occur. The treatments failed to have any significant effect on exotic species density or dominance, possibly because the addition of carbon compounds takes time to translate into community changes, the treatments did not lower biologically available nitrogen to a sufficiently low level, or the relationship between exotic species success and nitrogen availability is not general.

2. Does reducing nitrogen availability reduce the competitive ability of *Bromus tectorum*, an exotic weed species, and enhance the competitive ability of *Bouteloua gracilis*, a native?

I found no evidence that reducing nitrogen availability reduces the competitive ability of the exotic *Bromus tectorum* and enhances that of the native *Bouteloua gracilis* in the greenhouse. Additionally, the field study (chapter 1) did not provide evidence that lowering nitrogen availability enhances the competitive ability of native species in general and decreases that of exotics.

3. How does the nitrogen response of four exotic plant species, *Bromus tectorum*, *Centaurea repens*, *Cirsium arvense*, and *Euphorbia esula*, compare to that of two native species, *Bouteloua gracilis* and *Agropyron smithii*?

I hypothesized that the exotic species would all perform well at the high nitrogen levels, but would perform poorly at the low nitrogen levels. I also hypothesized that the native species would perform comparatively better than the exotics at the low nitrogen levels, but would not be able to take advantage of the high nitrogen levels. The responses of the exotic species were mixed. *Bromus tectorum* responded strongly to high levels of nitrogen, but also grew better than the native species at low nitrogen levels. The two native species grew better than two of the exotics at high nitrogen levels, while nitrogen availability was least important overall for one of the exotics, *Euphorbia esula*.

I will now review the overall hypothesis for this research in light of the empirical evidence:

> When nitrogen availability increases above the normal, ambient level, exotic weed species are specifically adapted to maximize their growth under these conditions, and outcompete slower-growing native species. Conversely, native, non-weedy species are better adapted to lower nitrogen conditions and outcompete exotic weed species at low nitrogen levels through tolerance of non-optimal growing conditions.

Based on the empirical evidence gathered in this thesis I would conclude that some exotic weeds are specifically adapted to take advantage of high nitrogen conditions and outcompete natives as this nutrient increases, but other exotic weeds rely on a different life history strategy or a combination of strategies to outcompete native species. In other words, the success of all exotic invasive species cannot be completely explained by the possession of a rapid growth response to increasing nutrient enrichment.