DISSERTATION

CAUSES AND CONSEQUENCES OF EXOTIC SPECIES INVASION IN THE PONDEROSA PINE FORESTS OF COLORADO'S FRONT RANGE

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY E. CAROL ADAIR ENTITLED "THE CAUSES AND CONSEQUENCES OF EXOTIC SPECIES INVASION IN THE PONDEROSA PINE FORESTS OF COLORADO'S FRONT RANGE" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

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Biological invasions that succeed in altering the structure and composition of ecosystems can change the dynamics, storage, and efflux of carbon and nutrients within and from ecosystems. Understanding the causes and consequences of biological invasions is therefore of paramount concern to ecologists and managers.

I conducted three experiment intended to elucidate both the factors that cause or promote exotic species invasion and the biogeochemical consequences of these invasions. Two of my experiments investigate the effects of and interactions among environmental and disturbance factors in influencing the invasibility of ponderosa pine communities along Colorado's Front Range by exotic plant species. My first experiment explored the invasibility of this ecosystem by all identified exotic plant species, and the second experiment investigated invasion by *Bromus tectorum* specifically, as an example of a highly invasive and potentially damaging species. My final experiment investigated some of the consequences of *B. tectorum* invasion on pools of available and microbial carbon (C) and nitrogen (N), while attempting to control for variation in daily and seasonal time and water availability.

I found that exotic species are relatively successive along Colorado's Front Range. The main drivers of exotic and native species richness are largely similar, but thefactors that influence the success (percent cover) of exotic and native species do so in different directions or with varying strengths. The most important variable for predicting both native and exotic species richness was accessibility of the site from large population centers. Native and exotic richness increased with increasing human accessibility, which was estimated as shortest distance along roads from major population centers. The importance of accessibility to species richness could be due to the impact of historical and/or current high levels of physical disturbances related to land use and increased propagule pressure.

Successful invasion of *B. tectorum* was limited by N and water. Biomass at the end of the experiment was a saturating function of water and N. Even though plant mortality increased N availability, plant mortality had a generally negative impact on invasion success. This result may be sensitive to the drought conditions that persisted during this experiment.

In this ponderosa pine ecosystem, successful *B. tectorum* invasion seemed to have significant biogeochemical consequences. Averaged across the growing season, all labile and microbial pools of N and C were higher beneath *B. tectorum* than beneath perennial grass communities. Incorporating seasonal variation was crucial for detecting this pattern because this difference was not large or statistically significant at each sampling period within the growing season. As the growing season progressed, pools of C and N beneath

B. tectorum became increasingly larger than those beneath native grasses. This trend is probably due to the comparatively early senescence of *B. tectorum* versus native C_3 and C_4 grasses.

My research suggests that (1) spatial and temporal variation in environmental conditions, resource availability, and disturbances may interact to regulate the invasibility of a community and (2) the consequences of a successful invasion may have significant consequences for soil and microbial pools of C and N. Furthermore, if invasion by *B. tectorum* results in persistent increases in N availability, my results suggest that *B. tectorum* invasion could create a positive feedback loop between N availability and further *B. tectorum* or exotic plant invasion. Research that addresses the interactions between climatic variables, resources, disturbance types, and the causes and consequences of successful species establishment will hopefully increase our ability to understand, predict, and manage these complex events.

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DEDICATION

For Mike

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CHAPTER ONE

INTRODUCTION

Biological invasions can change the composition and structure of communities. If invasive species differ considerably from the native species that they replace (e.g., changing the dominant phenology or functional type), ecosystem processes such as productivity and nutrient cycling may be altered (Vitousek 1990, Lauenroth et al. 1993, Ehrenfeld 2003). Biological invasions can therefore represent one of the most fundamental changes that can occur to an ecosystem. Furthermore, the economic impacts of plant invasions are becoming startlingly clear. The annual cost of noxious weeds in the United States is estimated to be in excess of $20 billion a year (Cramer 1995, Pimentel et al. 2000).

The rapid rate at which plant species are transferred among and within continents virtually guarantees that no ecosystem type will be immune to the influx of exotic species. The potentially dramatic consequences of exotic plant invasion have made understanding the causes of invasion of vital importance for both land managers and scientists. The dual goals of my dissertation were to examine what drives the invasion of exotic species (chapters two and three) and to determine the consequences of an invasion that changed the dominant plant functional type and phenology of an ecosystem (chapter four).

The susceptibility of plant communities to invasion by exotic species has been linked to plant community diversity, disturbance, and resource availability (Elton 1958, Mack 1981, Mack 1986, D'Antonio and Vitousek 1992, Levine and D'Antonio 1999, Stohlgren et al. 1999, Davis et al. 2000). Probably the most consistent finding in invasion ecology is that disturbance increases the invasibility of plant communities by increasing the establishment and success of exotic species over that of native species (Burke and Grime 1996, Davis and Pelsor 2001, Gross et al. 2005). The varied types of disturbances that have been studied include small scale physical disturbances such as the alteration of physical soil conditions, plant mortality, and/or increases in resource availability (Hobbs and Huenneke 1992, Huston 1994, Davis et al. 2000, Shea and Chesson 2002, Williamson and Harrison 2002, Larson 2003), as well as anthropogenic activities associated with land use, trails, and roads, that may increase propagule pressure, create soil or plant mortality disturbances, or change resource availability independent of plant mortality (e.g., nitrogen deposition) (Vitousek et al. 1996, Lonsdale 1999, Davis et al. 2000).

Research in natural communities has indicated that the environmental factors that influence exotic success and richness may be the same as those that increase native plant richness and success (Levine and D'Antonio 1999, Stohlgren et al. 1999, Smith and Knapp 2001). If this is true, are there also certain types of disturbances that influence native and exotic species similarly in natural ecosystems, or are exotic species always promoted over native ones in the presence of a particular (or any) disturbance? Additionally, the same disturbance type may affect native and exotic species differently depending on abiotic conditions (King and Grace 2000, Becksted and Augspurger 2004, Leishman and Thomson 2005). For example, plant removal increased exotic success in a moist environment (Davis et al. 2000, Huston 2004), but decreased exotic success in a more arid climate, while soil disturbance increased success in both environments (Beckstead and Ausgpurger 2004). Understanding how various disturbance types interact with environmental factors to influence the presence and success of exotics in natural plant communities is crucial for determining which areas are susceptible to invasion and for understanding how management decisions influence exotic presence.

This is of particular importance in the ponderosa pine ecosystems of the Front Range, which are heavily impacted by anthropogenic activity and disturbance. How do disturbance and abiotic variables interact to influence exotic plant species invasion into ponderosa pine ecosystems? Do they influence natives and exotics similarly? In chapters two and three I investigated the environmental and disturbance drivers of exotic species invasion into ponderosa pine communities using various definitions of disturbance:

1. I investigated the factors that influence the success and richness of native and exotic species in the heavily impacted ponderosa pine ecosystems of Colorado's Front Range, with the hypothesis that native and exotic species are influenced similarly by environmental factors, but that exotic species are promoted by disturbance. Here, native and exotic species were examined on a

landscape scale and disturbance was defined by indices that characterize human land use and accessibility across the landscape (chapter two).

2. I then defined disturbance as plant mortality alone and investigated its effects and interaction with resource availability. I conducted experiments to examine the effects of gradients of resource availability (nitrogen (N) and water) and resident plant species mortality on the success of *Bromus tectorum*, a highly invasive annual grass, at four sites located in a natural ponderosa pine community. I hypothesized that plant mortality would increase N availability, and that disturbance and resource addition would therefore increase exotic success similarly (chapter three).

These two chapters address what abiotic and disturbance factors are most effective at promoting the invasion of a community by exotic species. I chose to focus on *B. tectorum* in chapter three, because it has been an extremely effective invader of semi-arid communities throughout the western United States, and it has enormous potential to alter ecosystem properties. In the western U.S., at least 40 million hectares of original sagebrush-perennial bunchgrass (C3 and C4) vegetation has been replaced by monocultures of *B. tectorum*, an annual C3 grass (D'Antonio and Vitousek 1992). In these areas, *B. tectorum* invasion drastically changed the fire regime (Whisenant 1990, Peters and Bunting 1994) and effectively blocked historical successional pathways (West 1979). *B. tectorum* has also been a successful invader of the understory of semi-arid pine ecosystems, including the ponderosa pine landscapes of Colorado's Front Range. Such invasions could have very large implications for changes in ecosystem function.

Most attempts to document if or how the invasion of *B. tectorum* affects soil nutrient and carbon pools have tried to capture overall or large-scale (spatial and/or temporal) changes in these pools by using "broad-brush," single point, temporally constricted, or laboratory measurements that do not control for daily and seasonal variation or differences in water availability. The results from these studies are often mixed, with some finding soils beneath *B. tectorum* to have lower levels of soil N and carbon (C) than beneath perennial grasses, and others finding higher levels beneath *B. tectorum* than perennial grasses, and yet others finding no difference (Bolton et al. 1990, Bolton et al. 1993, Vinton and Burke 1997, Evans et al. 2001, Booth et al. 2003). Examination of how nutrient pools beneath these species interact with water limitation and seasonal and daily variation may shed light on some of these disparate results. To address these potential interactions, in chapter three I evaluated how small water additions differentially affected soil pools of N, labile C, and microbial biomass C and N on a daily time scale, beneath invaded and non-invaded plants communities, where the invasive species has potentially different characteristics and phenology throughout a growing season (three times; in June, July and August). I hypothesized that soil C and N pools beneath each vegetation type (*B. tectorum* versus C3 and C4 perennial grasses) were water limited and would thus respond to small rainfall events, and that the response to water additions and the overall pool sizes would be different beneath the two different vegetation types and diverge with month due to phenological differences.

The goal of chapters two and three is to investigate the effects and interactions among environmental and disturbance factors in influencing the invasibility of ponderosa pine communities along Colorado's Front Range by exotics in general (chapter two) and by *B. tectorum* specifically (chapter three) as an example of a highly invasive and potentially damaging species. Chapter four investigates some of the consequences of *B. tectorum* invasion on pools of available and microbial carbon and nitrogen, while controlling for water availability and seasonal and daily variation. The final chapter summarizes my findings, and addresses how my results provide useful insights into invasion ecology and management.

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CHAPTER TWO

DISTURBANCE AND ENVIRONMENTAL FACTORS DRIVE NATIVE AND EXOTIC PLANT SPECIES RICHNESS IN THE PONDEROSA PINE FORESTES OF COLORADO'S FRONT RANGE

Abstract

Low-elevation ponderosa pine forests are some of the most heavily impacted forested ecosystems in Colorado, and have experienced a wide range of disturbances and land uses. I investigated several factors that influence the success and richness of native and exotic species in this heavily impacted ecosystem. Specifically, I tested the hypothesis that native and exotic species are influenced similarly by environmental factors (e.g., resource availability, slope, and elevation), but that exotic species are promoted by disturbance. I surveyed 32 south facing sites in ponderosa pine communities and found that exotic species are relatively successful in these communities along Colorado's Front Range. Of my 32 sites, no site was free of exotic species. At each site I collected data on native and exotic species cover and richness and various environmental variables including slope, elevation, % canopy (as a proxy for light availability), and total soil nitrogen (N). To index the relative impacts of anthropogenic disturbance, I measured the distance of each site from the nearest road and trail, and determined the shortest driving distance (in meters) of each site from the nearest large population center. This last measurement acted as a measure of the accessibility of each site to human use and interaction. Accessibility increased with decreasing driving distance. I found a significant positive relationship between native and exotic species richness, but was able to explain this relationship in terms of the effects of my measured explanatory variables (slope, elevation, total nitrogen, percent overstory canopy, time since fire, and three disturbance indicators). My results suggest that the main drivers of exotic and native species richness are largely similar. However, the factors that influence exotic and native species success (percent cover) do so with different strengths or in different directions. The most important variable for predicting both native and exotic species richness was driving distance. Both native and exotic richness increased with decreasing driving distance. The importance of this variable to species richness could be due to the impact of historical and/or current high levels of physical disturbances related to land use and increased native and exotic propagule pressure resulting from the long-term accessibility of sites close to urban areas. This result has important implications for the management of natural areas that are close to developing urban, suburban or exurban lands.

Introduction

The susceptibility of native plant communities to invasion by exotic species has been linked to resource availability, disturbance, and productivity (Mack 1986, D'Antonio and Vitousek 1992, Levine and D'Antonio 1999, Stohlgren et al. 1999a, Davis et al. 2000). These same factors are often invoked to explain patterns of total or native species richness and diversity (Connell 1978, Petraitis et al. 1989, Larson 2003, Lonsdale 1999, Sax and Gaines 2003, Foster and Dickson 2004, Gross et al. 2005, Huston 1994, Herbert et al. 2004, Waters et al. 2004). If native species richness and community invasibility are both determined by disturbance, resource availability, and productivity, it is perhaps unsurprising that research in natural systems has found some degree of positive correlation between exotic and native species richness (Levine and D'Antonio 1999, Kalkhan and Stohlgren 2000, Stohlgren et al. 2001, Shea and Chesson 2002). But do these factors influence the richness and success of native and exotic species in the same ways? Or are there certain factors, such as anthropogenic disturbance, that differentially influence the richness and success of exotic species versus native species?

The relatively consistent positive relationship between native and exotic richness found in observational studies suggests (1) that invaders and native resident species may be more similar than is often believed and (2) that the processes that allow for high levels of native species richness are the same as those that increase the susceptibility of an environment to invasive species (Levine and D'Antonio 1999, Stohlgren et al. 1999a, Smith and Knapp 2001). Recent work with null models lends credence to this hypothesis, by reproducing this positive relationship in the absence of any differences between exotic and native species (Fridley et al. 2004, Herben et al. 2004). In these models the strength and positive direction of the relationship between exotic and native species richness is solely dependent on, and increases with, the range of total richness or total number of individuals included in creating the relationship (Fridley et al. 2004, Herben et al. 2004). These models do not address why the total number of species or individuals that may persist in a given community changes, only that a positive relationship between exotic and native species richness is generated when it does change. Thus, the results of such modeling experiments (when independent of sampling area) are consistent with the hypothesis that the positive relationship between exotic and native species richness in natural systems is due to underlying factors that promote diversity in plant communities or environments, regardless of plant origin (Levin and D'Antonio 1999, Davis et al. 2000, Stohlgren et al. 1999a).

In contrast, one of the most consistent findings in invasion ecology is that disturbance increases the invasibility of plant communities by increasing the establishment and success of exotic species over that of native species (Burke and Grime 1996, Davis and Pelsor 2001, Gross et al. 2005). In plant communities, disturbance is typically defined as the removal or reduction of aboveground biomass, which facilitates the invasion of non-resident species by increasing the availability of resources (light, water, nutrients) or creating "safe sites" for germination (Hobbs and Huenneke 1992, Huston 1994, Davis et al. 2000, Shea and Chesson 2002, Williamson and Harrison 2002, Larson 2003). Disturbance has also been defined in terms of anthropogenic activities that increase propagule pressure, change land use or resource availability independent of plant mortality (e.g., nitrogen deposition) (Vitousek et al. 1996, Lonsdale 1999, Davis et al. 2000). Regardless of the exact definition, it is generally accepted that these types of anthropogenic disturbances typically increase the invasion and success of exotic species above that of native species.

In the western United States, the success of invading species has been intimately associated with disturbances such as fire, livestock grazing, and presence of roads and trails (Mack 1986, D'Antonio and Vitousek 1992, Mack et al. 2000, Larson et al. 2001, Larson 2003), but these interactions remain poorly characterized, particularly for western forested landscapes. This is of particular importance in the low elevation ponderosa pine ecosystems of the eastern slopes of the Colorado Front Range, which are heavily impacted by anthropogenic activity and disturbance. A large proportion of this low elevation forest is, and has historically been, affected by heavy interaction with populated areas along the Front Range and in the foothills. These forests have experienced logging, grazing, fire and fire suppression, suburban expansion, and recreational use beginning with Euro-American settlement in the 1870's (Fornwalt et al. 2003, City of Boulder Open Space and Mountain Parks 2005). Such activities have been linked to increases in both physical disturbance of the environment, propagule pressure, and changes in resource availability (D'Antonio and Vitousek 1992, Lonsdale 1999, Mack et al. 2000, Keeley et al. 2003), all of which are linked to the success of invading species (Lonsdale 1999, Davis et al. 2000).

My research objectives were therefore: (1) To determine the richness and success of exotic and native plant species in the ponderosa pine ecosystems of Colorado's Front Range; (2) To investigate how environmental variables and disturbance (time since fire and anthropogenic disturbance and/or accessibility of these areas) influence exotic and native success in this ecosystem; and (3) to determine if the variables that determine or influence exotic numbers and success (% cover) are the same that drive native richness and success.

To address my second and third objectives, I focused on environmental or abiotic variables that might act as drivers of richness (e.g., slope, elevation, resource availability). I did not include biotic variables such as % total cover or species richness. By focusing on environmental and disturbance variables, I was in effect hypothesizing that biotic interactions such as competitive exclusion or facilitation have little affect on patterns of exotic or native species richness in this across the landscape within this ecosystem. Because native and exotic richness in natural ecosystems across larger scales are often influenced by the same environmental variables, I hypothesized that exotic and native richness and cover would be influenced similarly by environmental variables but differentially by disturbance. Specifically, I hypothesized that exotic richness and cover would be increased by disturbance but that native richness and cover would have either a negative or neutral relationship with disturbance. Such results could be generated by disturbances that increase the success of exotic species over native species, perhaps by increasing the introduction of exotic seeds relative to native seeds and/or create or increase opportunities for new species to establish by freeing resources and creating safe sites for germination. In particular, I hypothesized that exotic success and richness would increase with anthropogenic disturbance measures and decrease with time since fire. Finally, I hypothesized that the commonly observed positive relationship between native and exotic species richness in natural systems is not due to biotic interactions, but to the fact that, on a landscape scale, similar environmental factors control the richness of both exotic and native species.

Methods

Study areas

I selected 32 sites with known fire histories in ponderosa pine forests along the Front Range of Colorado, USA (Figure 2.1). Fire history information was obtained from published work (Brown et al. 1999, Veblen et al. 2000 and pers comm, Huckaby et al. 2001) and communication with USDA forest service staff. All potential sites were stratified based on their N-S position along the Front Range and the number of years since last fire (0-3, 10-25, 25-75, and more than 125 years); I randomly chose my 32 sites from these categories. The exact sampling location was randomly selected from the south facing slopes within each of these sites. I chose to focus on south facing slopes because I observed that these areas are most commonly dominated by understory species and most commonly invaded by exotic species.

Variable selection and justification

The abiotic variables that I hypothesized would have a significant impact on native and/or exotic richness and cover were time since fire, % canopy (as a proxy for light availability), elevation, slope, total nitrogen (N), and three disturbance indicators that characterize the accessibility of these areas to anthropogenic activity: distance from trail, distance from nearest road, and driving distance from nearest population center.

All of these variables have been shown to influence native and/or exotic presence, richness, or success. Declines in light availability as a result of forest canopy cover or high levels of productivity decreases native and exotic richness and success (native diversity: Tilman and Pacala 1993, Huston and DeAngelis 1994, Abrams 1995, Stohlgren et al. 2001, exotic: Parendes and Jones 2000, Pierson et al. 1990). In the Colorado Rocky Mountains, native and exotic diversity have been shown to increase with total N and elevation (Stohlgren et al. 1999b, Stohlgren et al. 2001). I decided to include slope as a variable because it influences soil development and fertility (Schimel et al. 1985, Parton et al. 1987) and my sites included an extreme range of slopes, from 10 to 40%.

In this study, I characterized anthropogenic disturbance using three metrics: distance from nearest road, distance from nearest trail and the distance of the site from the nearest population center along established roads. Roads and trails act as corridors or agents for dispersal, provide suitable habitat and contain reservoirs of propagules for future episodes of invasion (Parendes and Jones 2000, Tyser and Worley 1992, Wilson et al. 1992, Lonsdale and Lane 1994, Forman and Alexander 1998, Patel and Rapport 2000). Because of the high level of interaction that this ecosystem experiences due to its proximity to major population centers (Figure 2.1), I chose a third metric, driving distance from the nearest population center, which characterizes each site's accessibility, both currently and historically, to anthropogenic activities. This is a landscape scale metric that represents the frequency and ease of access over longer time scales; areas that are very close to population centers by road are more likely to receive frequent use in the past and present.

Finally, fire is a major natural disturbance in this ecosystem (Brown et al. 1999, Veblen et al. 2000) and recent research in other fire-prone ecosystems has indicated that fire may cause exotic species richness and cover to increase (Evangelista et al. 2004, Keeley et al. 2003).

Data Collection

I estimated native, exotic, and total species richness and cover using a Modified-Whittaker style plot (20 x 50 m), placed with the long axis along the major elevation gradient (to maximize diversity in the plot) (Stohlgren et al. 1995, 1998). Nested within each 20 x 50 m plot, were ten 1 m^2 subplots systematically spaced along the inside border, two 10 m^2 subplots in alternate corners, and one 100 m^2 subplot located in the plot center. Percent cover for each species was recorded in the 1 m^2 subplots, and the presence of each species was recorded in the 10 m^2, 100 m^2, and 1000 m^2 plots. Exotic species were identified using the USDA Plants Database (USDA 2001). The location (UTM coordinates) of each plot was recorded using a GPS.

I determined elevation using a combination of GPS location and topographic maps. I measured the slope at each site using a clinometer. I estimated percent tree canopy at 5 points (at each corner and in the center of the plot, in four directions at each point) within each site using a spherical densiometer. I determined total soil nitrogen (N) from five soil samples taken under each of four types of vegetation randomly chosen from the present vegetation (a maximum of 20 samples): shrubs, perennial grasses, bare soil and *Bromus tectorum* (cheatgrass). Total soil N in each sample was determined by dry combustion (LECO CHN−1000 Element Analyzer, LECO Corporation, Saint Joseph, Mich., USA).

I found the nearest road and marked it with a GPS. If a trail was present within 5 km of the site, I measured the distance to it either manually with a tape measure or by marking the nearest point of the trail to the site using a GPS. Six sites did not have trails within 5 km. These sites were given the maximum distance of 5000 m.

I calculated driving distance from the nearest population center with a population greater than 3000 (according to the 1990 census) with GIS coverages of site locations, Colorado Front Range roads, and 1990 Colorado census data using ArcView GIS 3.2 (as described by Theobald 2003).

Data Analysis

Observational studies in natural systems that attempt to explain native and exotic richness and cover using only driving factors as independent variables (i.e., not using covarying community characteristics such as total cover or richness), typically explain relatively low amounts of the variation in the dependent variables (Waters et al. 2004, Stohlgren et al. 1999a, Bashkin et al. 2003). In such cases, the difference between competing hypotheses (or models) may not be great, and stepwise regression techniques, which are traditionally used to investigate these questions, may choose different models or variables depending on which stepwise technique is used (e.g., backward, forward), the order of the variables, autocorrelation of independent variables, and/or the chosen significance level (p-value) (Burnham and Anderson 2002). Often, the goal of linear and stepwise regression techniques is variable selection, that is, determining which of the explanatory variables under investigation is most important to predicting changes in the dependent variable. The variables excluded from the model chosen by stepwise regression are usually deemed biologically and statistically insignificant. However, because stepwise regression does not provide information on how much better the chosen model is from the rejected models (or the model chosen by a different stepwise technique) determining which model, or set variables, best explains the variation in the data can be difficult.

For these reasons, I chose to use an information-theoretic approach to rank my regression models and find the best model or set of models to predict exotic and native richness and cover (Burnham and Anderson 2002). This technique (1) allowed me to determine if there was a clear, best model or set of explanatory variables (model selection does not change with variable order) and (2) provided me with information about if the other models I tested were close competitors and if the unselected variables provided any biologically relevant information about the response variable.

This framework is based on parsimony, which is the trade-off between model fit and the number of parameters in the model, and favors the model with the least number of parameters that adequately describes the patterns in the data. Akaike's Information Criterion (AIC) estimates the information lost by using a model to approximate the unknown truth, and ranks a set of a priori models based on the support for each in the data. The difference between the AIC value of the best model and the values of the models ranked below it provides information on which models in the model set are close competitors. Generally speaking, models that are within 1-2 AIC points of the best model have substantial support in the data, models that are 4-7 points away have considerably less support, and models more than 10 points away have essentially no support in the data (Burnham and Anderson 2002). This methodology also provides information on model selection uncertainty by calculating Akaike weights (w_r). Akaike weights can be interpreted as the probability that the best model would again be selected as the best model, given the same set of models and a new set of similar data (Burnham and Anderson 2002).

If, as I suspected would be the case with my data, the selected models explain low proportions of the variance in the dependent variable (i.e., R^2 is low), there will likely be more than one best model (models within 2 AICc points of the best model) or many close competitors (models within 7 AICc points) and model selection uncertainty will be high (all models have low w_r's). If this is the case, AIC provides an alternative method for analyzing the importance of the chosen independent variables and making improved predictions about the dependent variables. First, Akaike weights can be used to assess the relative importance of each predictor variable in explaining variation in the dependent variable. This is done by summing the w_r's across all the models in the set that include the predictor variable ($w_+(x)$, where x is the predictor variable of interest) (Burnham and Anderson 2002).

Important variables will have a high $w_+(x)$ (near 1) because of that parameter's inclusion in the better models (which have high w_r's; the w_r's sum to 1 over all the models in the set).

Second, the model-averaged parameters and unconditional standard errors can be calculated to examine the direction (positive or negative) and magnitude (if the 95% confidence interval includes zero or not) of the effect of each variable (Burnham and Anderson 2002). Model-averaging consists of calculating a weighted estimate of the parameter for a given variable across all models in which it appears. Model averaging can also be used to calculate predictions of the dependent variable. This procedure is considered superior to making model predictions and inferences about variable importance based only on one best model when the second or third best model is nearly as well supported as the best model or when all models have nearly equal support (Burnham and Anderson 2004).

I developed a set of candidate models to explain the variation in exotic and native richness and cover based on all combinations of my eight abiotic and disturbance variables. However, because of the high correlation between percent canopy and time since fire ($R^2 > 40\%$), these two variables were never included in the same model. I did not attempt to develop interactions between the independent variables due to the small size of the data set (low degrees of freedom). Percent exotic cover and exotic richness were $\log_{10}(x+1)$ and $\log_{10}$ transformed (respectively) prior to analysis to improve normality. Distance to nearest trail (DT) was also $\log_{10}(x+1)$ transformed to increase the spread of values between 0 m (the minimum distance) and the maximum distance of 5000 m and improve normality. I fit regressions using the procedure for linear estimation for native cover and richness (proc REG) and the procedure for nonlinear estimation for exotic cover and richness (proc NLIN), to maintain the linear relationships between the dependent and independent variables (SAS Institute Inc., Cary, NC, USA). I calculated the AIC for each model, and corrected these values for bias due to small sample sizes (AICc) as described in Burnham and Anderson (2002).

For all my dependent variables, model selection uncertainty was high and there were no clear best models. Therefore, to more accurately evaluate the relative importance and influence of my variables, I calculated the $w_+(x)$, the model averaged parameter estimate, and associated unconditional standard error for each variable. Furthermore, to obtain the maximum inference that my data allowed, I calculated the model averaged predictions for native and exotic species richness and cover (Burnham and Anderson 2002, 2004).

In this way, rather than simply labeling a variable as statistically significant (therefore included in the final model) or statistically insignificant (therefore not included in the final model and considered biologically unimportant), the model averaging and variable ranking techniques described above allowed me to asses the relative ecological importance and influence of each of my variables on exotic and native species richness and cover. That is, in addition to determining the relative importance of each variable, I was able to examine the overall magnitude and direction of each variable's affect on exotic and native species richness and cover. This allowed me to determine if native and exotic species richness and cover were influenced by the same variables with similar strengths and directions, or if there were important differences in the how these variables influenced exotic and native species.

Percent canopy and time since fire (TF) were highly positively correlated ($R^2 = 0.481$). To examine the effect of time independent of % canopy, I reran the above analyses using the residuals from the regression of TF on percent canopy (TF_{res}), This analysis indicated that in most cases, the effect of TF on species richness and cover was due to the increase in % canopy with time. Results of this analysis are discussed below. The relationship between driving distance and elevation ($R^2 = 0.307$) was also of some concern, so I performed the same procedure on the residuals of the regression between driving distance (DD) and elevation (DD_{res}). Using DD_{res} did not change the results of the analysis, so these results are not included in my analysis.

Finally, I addressed the hypothesis that commonly observed positive relationship between native and exotic species richness in natural systems is due to environmental and/or disturbance factors that similarly control the richness of exotic and native species. I first regressed exotic richness against native richness to evaluate the strength of this relationship in my study. Native and Exotic richness were $\log_{10}$ transformed to fulfill normality assumptions for exotic richness and maintain linearity between exotic and native richness. After calculating the model averaged predictions (as described above) and residuals for exotic and native richness, I repeated this regression using the residuals from each analysis. The residuals are the difference between the observed data points and their model averaged predictions, and therefore represent the data with the variability due to the predictor variables removed. If the relationship between exotic and native species richness remained unchanged using the residuals (i.e., was still significant with a similar R^2), these abiotic variables would not be capable of explaining the observed relationship between native and exotic richness. The relationship between exotic and native species richness in this ecosystem might then be due to other, perhaps biotic, variables.

Results and Discussion

Richness and success of exotic and native plant species in the ponderosa pine forests of Colorado's Front Range

My results show that exotic species are successful in this ecosystem, accounting for an average of 13% and a maximum of 50% of total plant cover. I identified 35 exotic species within my sites. Exotic richness averaged 7 species per plot, but was as high as 16 species per plot. None of my sites were free of exotic species, and all plots contained at least two exotic species (Table 2.1).

Total cover of all sites ranged from 11 to 96%, with an average of approximately 50%. Understory species richness averaged was 56 species per plot, but ranged from 36 to 84 species (Table 2.1). I identified a total of 250 species; of these, 196 were identified as native species. Plot native richness ranged from 24 – 63 species, with an average of 41 species per plot. Native cover ranged from 11 to 72%, with an average of 42%. Native cover typically accounted for 76% of the total cover (Table 2.1). My results are consistent with other studies that have examined total, native and exotic richness and cover in ponderosa pine and dry meadow communities in Colorado, and are indicative of the generally moderate productivity of the understory of south facing slopes in this ecosystem versus more mesic communities in the area (Stohlgren et al. 1999a, Stohlgren et al. 2001, Fornwalt et al. 2003).

Drivers of native cover and richness

Although model selection revealed no clear best model for either native richness or cover, variable ranking and model averaged parameter estimates revealed that the most important variables in explaining native cover were elevation, total N, and percent canopy (Figure 2.2a). Native cover increased with elevation, a result that is consistent with other studies in the Rocky Mountains (Stohlgren et al. 2001). Consistent with results from other studies (Huston and DeAngelis 1994, Stohlgren et al. 1999b, Stohlgren et al. 2001, Waters et al. 2004, Bashkin et al. 2003), percent cover increased with total nitrogen and decreased with percent canopy.

The negative relationship between native cover and time since fire was due to the positive relationship between time since fire and percent canopy. Using the residuals of the time since fire – canopy relationship made time since fire the least important variable ($w_+(x) = 0.079$) and increased the importance of the negative relationship between percent canopy and native richness to above that of total N (Figure 2.2a). Slope had a moderate negative influence on % native cover, and, the three disturbance indicators had essentially no impact on native cover. My model averaged predictions explained 37.6% of the variation in native cover (Table 2.2).

These results are consistent with my hypothesis, that native species would be affected mainly by environmental variables and that disturbance indicators would have little influence.

My results for native richness, however, were decidedly contrary to this hypothesis. The most important variable for native richness was driving distance (the distance to the site by road from the nearest population center) (Figure 2.2b). The number of native species increased as driving distance decreased. While this result may seem initially counter-intuitive, native or total richness has been found to increase with moderate levels of disturbance (Caswell 1978, Connell 1978, Petraitis et al. 1989, Larson 2003) and with increased levels of propagule availability (Lonsdale 1999, Sax and Gaines 2003, Foster and Dickson 2004, Gross et al. 2005). The importance of this variable to native richness could therefore be due to the impact of historical or current levels of physical disturbance in accessible areas, or a result of increased propagule pressures resulting from the long-term access of areas close to, and accessible from, urban areas. Native richness also had a weaker negative relationship with distance from trail, indicated that richness declined with increasing distances from trails. This unexpected pattern could also be due to increased propagule pressure or disturbances that facilitate the establishment of native species. Although the relationship between native richness and distance to roads was what I expected (positive) the relationship was relatively weak (Figure 2.2b). Overall, my results are not consistent neither my original hypothesis nor with a number of studies that have found native richness to increase with distance from roads and trails, and increase generally with decreasing levels of anthropogenic disturbance (Larson et al. 2001, Larson 2003, Tyser and Worley 1992, Patel and Rapport 2000).

Native richness also had somewhat weak negative relationships with slope and time since fire and a positive relationship with total nitrogen (Figure 2.2b). In contrast to some research that has found a negative influence of fertility on native richness (Bashkin et al. 2003), our results agree with observational studies that have found higher native richness in areas with higher total N (Waters et al. 2004, Stohlgren et al. 1999b). There was essentially no effect (95% confidence interval included 0) of elevation or percent canopy on native richness, and using the residuals of the time since fire – canopy relationship did not change the overall results of this analysis (all variable rankings and $w_+(x)$'s remained within $^+/-$ 0.02 of the non-residual relationship). This indicates that for native richness, the moderate negative effect of time since fire on native richness is most likely independent of percent canopy. Model averaged predictions of native richness explained 30.45% of variation in native richness (Table 2.2), a result that is typical of observational studies that attempt to explain native richness as a function of abiotic and disturbance variables, particularly when the independent variables do not include non-driving variables such as total or native percent cover (Bashkin et al. 2003, Stohlgren et al. 1999b, Stohlgren et a. 2001, Waters et al. 2004).

Drivers of exotic cover and species richness

The primary controls on exotic cover and richness were resource availability (light and soil N) and disturbance indicators. As with native cover and richness, model selection did not result in a clear best model for exotic cover and richness, although my models did a slightly better job predicting exotic richness than cover. The best model predicted exotic richness as a negative function of driving distance (negative), distance to the nearest road (positive), total N (positive) and time since fire (negative). The second best model used all of these variables plus elevation (negative). Using the time since fire residuals resulted in very similar results, but percent canopy replaced time since fire. This indicated that, contrary to my hypothesis that exotic species success and richness would decrease with time since fire, the main effect of time since fire on exotic species richness is that percent canopy increases with time, decreasing light availability, and thereby decreasing exotic richness.

Variable ranking reinforced the model selection results by indicating that driving distance, total N and time since fire were most important variables in explaining exotic species richness, followed by distance from nearest road, elevation, and % canopy (Figure 2.2b). Using the time since fire residuals resulted in dramatically increasing the importance of % canopy ($w_+(x) = 0.944$), and decreasing time since fire ($w_+(x) = 0.044$), indicating that the main effect of time since fire on exotic richness is in increasing percent canopy (which decreases exotic richness).

In agreement with my hypothesis that disturbance would increase the richness of exotic species, exotic richness increased with decreasing driving distance (increasing accessibility). Exotic richness, like native richness, is affected by disturbance (Kotanen 1997, Williamson and Harrison 2002, Larson 2003) and increased levels of propagule availability (Lonsdale 1999, Smith and Knapp 1999, Williamson and Harrison 2002), so the importance of this variable to exotic richness would be for the same reasons: the impact of historical or current levels of physical disturbance in accessible areas and/or increased propagule pressures resulting from the long-term access of sites easily accessible from urban areas.

Exotic richness also increased with total soil N, which is consistent with most studies where increased productivity does not interfere with light availability (Huenneke et al. 1990, Stohlgren et al. 1999b, Thompson et al. 2001, Williamson and Harrison 2002, Waters et al. 2004). Slope and distance to trail were the least important variables (Figure 2.2b), increasing with slope and decreasing with distance from trail. My variables (model averaged) explained 61.97% of the variation in exotic richness (Table 2.2), which is more than is typically explained by studies that only include driving variables and similar to R^2 of studies that include variables such as native richness and exotic, native, or total cover as predictors (Waters et al. 2004, Stohlgren et al. 1999b, Bashkin et al. 2003).

Total nitrogen and distance to nearest trail were the most important variables for explaining exotic species cover, as indicated by variable ranking (Figure 2.2a). Total N increased exotic cover, which again, is consistent with other research, on exotic cover (Stohlgren et al. 1999b, Waters et al. 2004, Huenneke et al. 1990, Stohlgren et al. 2001). Consistent with my hypothesis, exotic cover increased with decreasing distance from trails. While most research on the influence of roads and trails have characterized only exotic richness (which usually increases with decreasing distance from trails), I found that distance from trails influenced percent cover of exotics similarly.

Elevation, slope, percent canopy and time since fire all had moderate negative affects on exotic cover. Using the residuals for the time since fire - percent canopy relationship did not change the overall results, but slightly increased the importance of percent canopy over time since fire. However, time since fire remained somewhat important, indicating that, consistent with my hypothesis, time since fire may have negative effects on exotic cover apart from increasing percent canopy or decreasing light availability. Driving distance and distance to the nearest road were the least important variables, having essentially no affect on exotic cover. Model averaged predictions explained 46.9% of variation in exotic cover (Table 2.2), which is consistent with most observational research that use only driving variables (Waters et al. 2004, Stohlgren et al. 1999b, Bashkin et al. 2003)

Differences and similarities – are the variables that determine or influence exotic success (% cover) and richness are the same that drive native species richness and success?

My results suggest that while the main drivers of exotic and native species richness are largely similar, the factors that influence the success (percent cover) of exotic and native species in this ecosystem are different, or have influence on native and exotic species with different strengths.

Contrary to my hypothesized negative or neutral relationship between native species and disturbance, both native and exotic cover and richness were influenced similarly by my disturbance indicators. Species richness (native and exotic) was strongly influenced by driving distance. I am relatively certain that the relationship of driving distance to all forms of richness is not a result of its moderate-low correlation with elevation, as re-running the analysis with the residuals from the regression of driving distance on elevation did not change the overall results or the strength of the relationship between driving distance and species richness. Rather, my interpretation is that driving distance is an indicator of the levels of human interaction along Colorado's Front Range. The high level of anthropogenic activity in these areas has most likely resulted in elevated levels of disturbance and high propagule pressure for native and exotic species. Exotic species were found in all plots and the effect of driving distance on both native and exotic richness appears to extend > 50 km, suggesting that the effect of the accessibility is a large scale process influencing overall invasibility, but also native richness, in this ecosystem. The main differences between how exotics and native species richness responded to disturbance were in the strength of their relationships with distance from nearest trail and road. Although the relationship between these variables and exotic and native species richness were in the same directions, distance to trail was approximately twice as important for native richness as for exotic richness. The reverse was true for distance to nearest road, which was about twice as important for exotic as it was for natives. However, the overall importance of these variables was moderate to low when compared to other variables included in the analysis.

Decreasing distance to trails positively influenced native but especially exotic cover, suggesting that its main effect may be increasing disturbances that provide increased resources or favorable conditions for the growth and success of populations of exotic species. Driving distance was not important to either native or exotic species cover, further suggesting that it reflects larger scale processes that affect the distribution of plant species throughout a landscape (i.e., richness), rather than the effects of localized disturbance, which is typically associated with effects of distance from roads and trails (Tyser and Worley 1992, Forman and Alexander 1998, Larson et al. 2001).

In this ecosystem, disturbance indicators seem to affect native and exotic species more similarly than do environmental variables. Although many of my environmental variables influence native and exotic species similarly (total N, percent canopy, and slope for percent cover), the influence of elevation and slope are more variable. Elevation was essentially unimportant for native species richness, but increased native percent cover and decreased exotic richness and cover. Slope, a variable of relatively low importance, increased exotic richness, but decreased native richness.

Explaining the exotic versus native species richness relationship

I found a moderate positive relationship between exotic and native species richness ($R^2 = 0.28$, Figure 2.3). Stohlgren et al. (1999a) found a much stronger relationship ($R^2 = 0.81$) between exotic and native richness across five different ecosystems in the Colorado Rocky Mts. The comparatively strong relationship of Stohlgren et al.'s (1999a) research versus mine is likely a result of the large range of total richness that occurs across the ecosystems they examined (e.g., from riparian to lodgepole pine) compared to the narrow range of total richness in the single ecosystem that I surveyed (Fridley et al. 2004, Herben et al. 2004). Indeed, these results are consistent with the results of the null or neutral models of Fridley et al. (2004) and Herben et al. (2004) that predict a positive relationship between exotic and native species richness at larger scales that increases in strength as the range of total richness or number of plants in sites included in the survey increases. The important result of these modeling studies is that a strong positive relationship is generated without accounting for biotic interactions between plants and in the absence of any differences between exotic and native species, therefore emphasizing that this relationship can occur when exotic and native species are exactly the same.

Thus, if total richness increases across an area, and native and exotic species are influenced similarly by the factors that increase total richness, the relationship between native and exotic richness could be caused by driving variables that increase both native and exotic species richness, such as intermediate levels of disturbance, resource availability, and propagule pressure. I found that my eight variables, and particularly the most important variables (Figure 2.2), influenced exotic and native species richness in largely similar ways. If I remove the influence of these variables, and the exotic versus native species richness remains significant, then it is likely that this relationship is not a result of the similar effects of the variables that I examined and may be the result of other (perhaps biotic) mechanisms or variables.

I examined the relationship between exotic and native species richness in the absence of my eight variables by regressing the residuals of the model averaged predictions of exotic richness against the residuals of the model averaged predictions for native richness. The removal of the effects of these variables from this relationship dramatically reduced the correlation between exotic and native species richness (Figure 2.3, $R^2 = 0.0871$, $P = 0.1009$). This suggests that the relationship between exotic and native richness may be explained by some or all of these eight variables, which act as drivers of both exotic and native species richness. The strong influence of my disturbance indicators to native and exotic species richness (particularly of driving distance), is the most likely factor in explaining this relationship.

Management Implications

Given my results, it seems that the question that needs to be addressed by ecologists is not so much "Why are species rich areas so invasible?" (because the factors that drive native richness also drive exotic richness; Stohlgren et al. 1999a) but more, what factors drive species richness, and therefore exotic richness, in the ecosystem or ecosystems of interest? In the ponderosa pine communities of Colorado's Front Range, the overall accessibility of a given site, as indexed by the driving distance of a site from the nearest population center, was the most important variable for explaining both exotic and native species richness. This has important implications for management practices that seek to control the spread and success of exotic species in this heavily impacted ecosystem.

Over the past few decades, Colorado's population has grown more rapidly than any other state in the United States (Baron et al. 2000). As a result, between 1960 and 1990, more than 10,000 km^2 of agricultural land and non-public forest lands were converted to urban, suburban, and exurban (low-density residential development that occurs outside of city limits) development and 1100 km^2 of agricultural land were converted to commercial and residential development every year between 1992 and 1997 (Baron et al 2000, Obermann, Carlson, and Batchelder 2000, Maestas et al. 2001). Recent projections call for up to a 51 percent population increase in Colorado over the next 25 years (Colorado Department of Local Affairs, 2001). Most of this population growth and coincident land use change is focused along Colorado's Front Range and nearby public forest lands and parks that often as "magnets" for development, i.e., along the edge of or within the ponderosa pine forest communities of Colorado's Front Range (Baron et al. 2000, Colorado Department of Local Affairs 2004).

My results suggest that the repercussions of this growth and the continued development of unprotected lands within ponderosa pine ecosystems could be large. Efforts to control the spread of exotic species should be focused in natural areas that are easily accessible from regions that are experiencing or have recently experienced population influxes and increased urbanization and development. Natural areas that will receive heavy interaction due to future development plans should also be targeted by management prevention measures.

While it is clear that the accessibility of natural areas influences the invasibility of the ponderosa pine communities along Colorado's Front Range, the mechanism that drives this relationship is less clear. Future research should focus on the factors that may drive this relationship such as land use history and propagule pressure.

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Table 2.1. Total, native, and exotic species richness and cover for 32 sites in ponderosa pine ecosystems along Colorado's Front Range

		Exotic	Native	Total
Species richness	Average	6.59	41.13	56.41
	Std error	0.63	1.58	2.18
	Max	16	63	84
	Min	2	24	36
% cover	Average	7.72	34.84	48.71
	Std error	1.81	2.85	3.99
	Max	34.20	72.50	96.95
	Min	0.00	10.95	11.60
% of total species	Average	11.24	73.07	
	Std error	0.84	0.92	
	Max	21.95	82.69	
	Min	3.85	58.54	
% of total cover	Average	12.63	75.53	
	Std error	2.60	3.24	
	Max	48.85	100.00	
	Min	0.00	29.89	

Table 2.2. Model averaged parameter estimates (PE), and unconditional standard errors (se) for native richness, exotic richness, native cover, and exotic cover. Italicized values have a $w_+(x)$> 0.50. Percent canopy and time since fire were italicized only if they were > 0.50 when the residuals of the time since fire vs. percent canopy relationship were used. "*" denotes where the 95% confidence interval for a variable parameter estimate includes zero.

Native richness

	PE (se)
Intercept	50.47 (7.64)
can	-0.0120 (0.0133)*
DD	*-1.89 E-04 (6.333 E-05)*
DnearR	0.00215 (7.82 E-04)
DTlog	-2.29 (0.571)
elev	-4.56 E-04 (0.00160)*
slp	-0.251 (0.0722)
TF	-0.0214 (0.00567)
TN	0.0191 (0.00575)

Model averaged R^2 = 0.3045

Exotic richness

	PE (se)
Intercept	10.87 (3.37)
can	*-0.0873 (0.00922)*
DD	*-7.39 E-05 (2.08 E-05)*
DnearR	0.00345 (7.76 E-04)
DTlog	-0.792 (0.114)
elev	-0.00408 (0.00102)
slp	0.0431 (0.0135)
TF	-0.0256 (0.00456)
TN	*0.0154 (0.00502)*

Model averaged R^2 = 0.6197

Native cover

	PE (se)
Intercept	0.0499 (22.51)
can	*-0.309 (0.0702)*
DD	1.959 E-05 (3.056 E-05)*
DnearR	-0.00114 (0.00134)*
DTlog	-2.36 (0.507)
elev	*0.0238 (0.00776)*
slp	-0.471 (0.130)
TF	-0.0816 (0.0134)
TN	*0.0657 (0.02037)*

Model averaged R^2 = 0.376

Exotic cover

	PE (se)
Intercept	10.90 (5.61)
can	-0.0533 (0.00873)
DD	7.78E-06 (8.33E-06)*
DnearR	-9.32 E-04 (4.53 E-04)*
DTlog	*-2.06 (0.601)*
elev	-0.00629 (0.00162)
slp	-0.133 (0.0309)
TF	-0.0211 (0.00487)
TN	*0.0249 (0.00896)*

Model averaged R^2 = 0.469

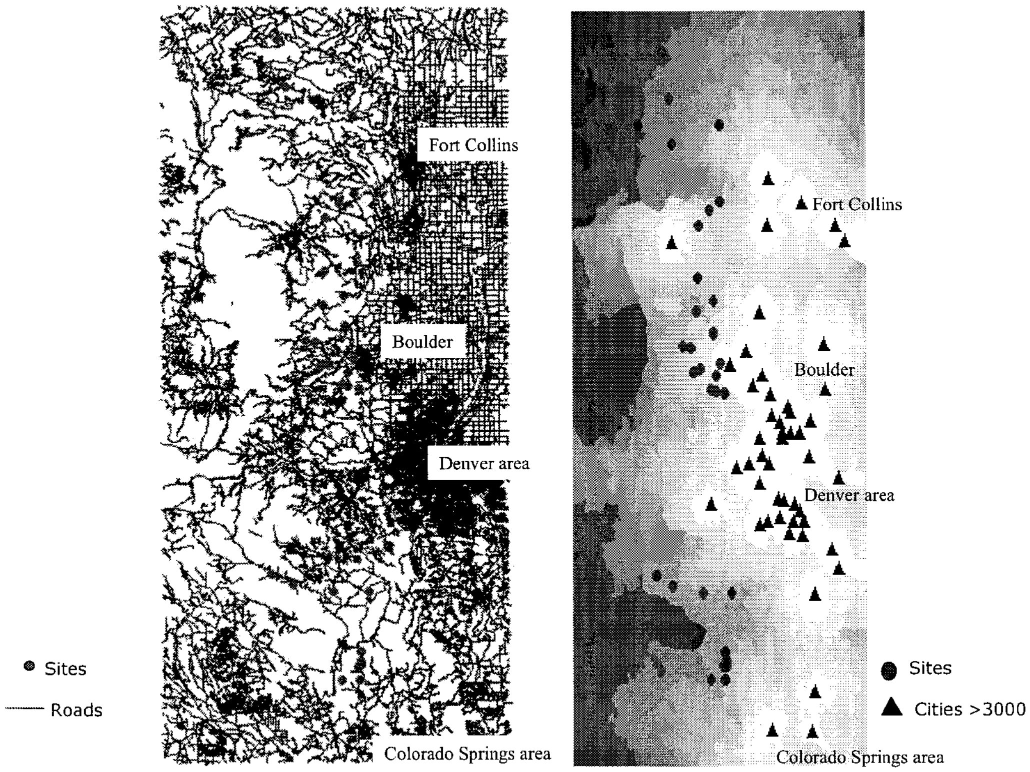

Figure 2.1. Site locations (a) with Front Range roads and (b) with driving distance from larger cities to all site locations along the Front Range (white to dark is shorter to longer driving distance in meters, i.e., decreasing accessibility).

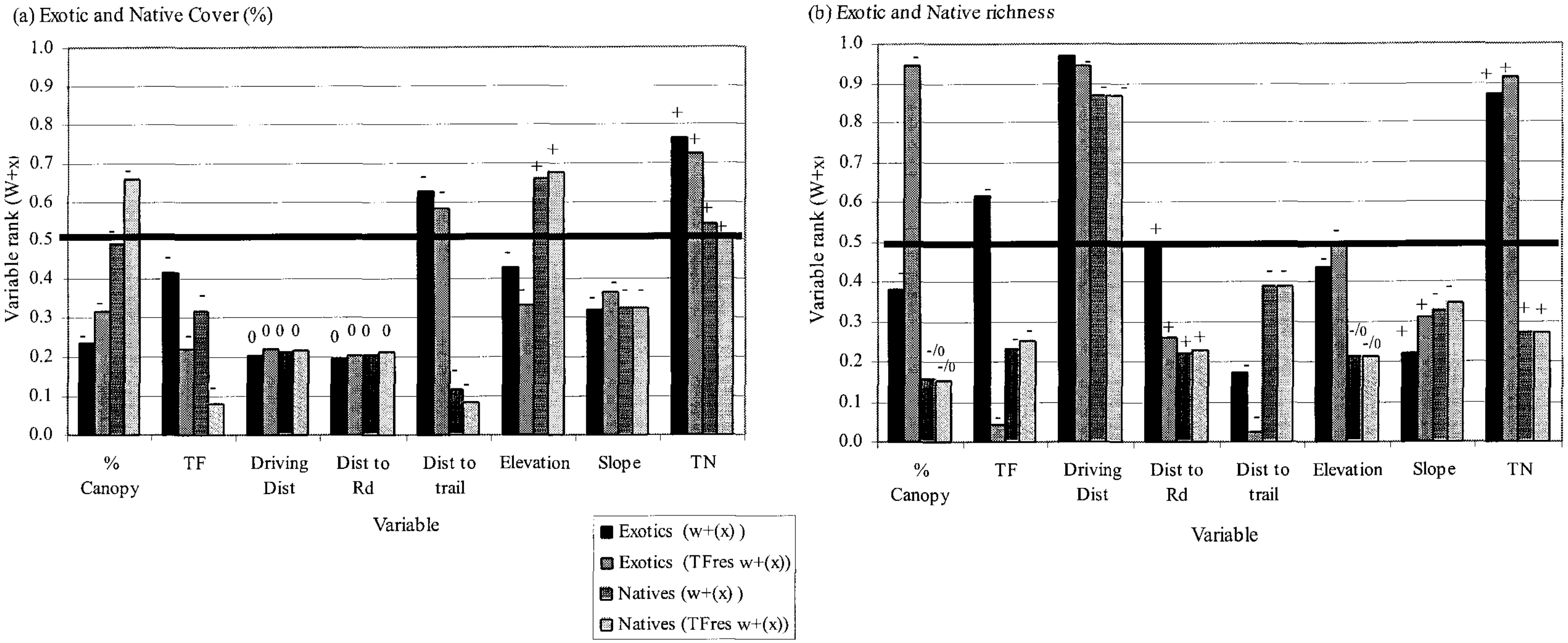

Figure 2.2. Variable ranking results for (a) exotic and native species richness and (b) exotic and native species cover (%). Values close greater than 0.5 and closer to 1 indicate variables of importance. Positive or negative signs above the bars indicate the direction of each variable's influence on the dependent variable. A zero indicates that the 95% confidence interval for the variable's parameter estimate includes zero. TF_{res} values are the rankings for the same analysis using the residuals from the time since fire versus percent canopy regression.

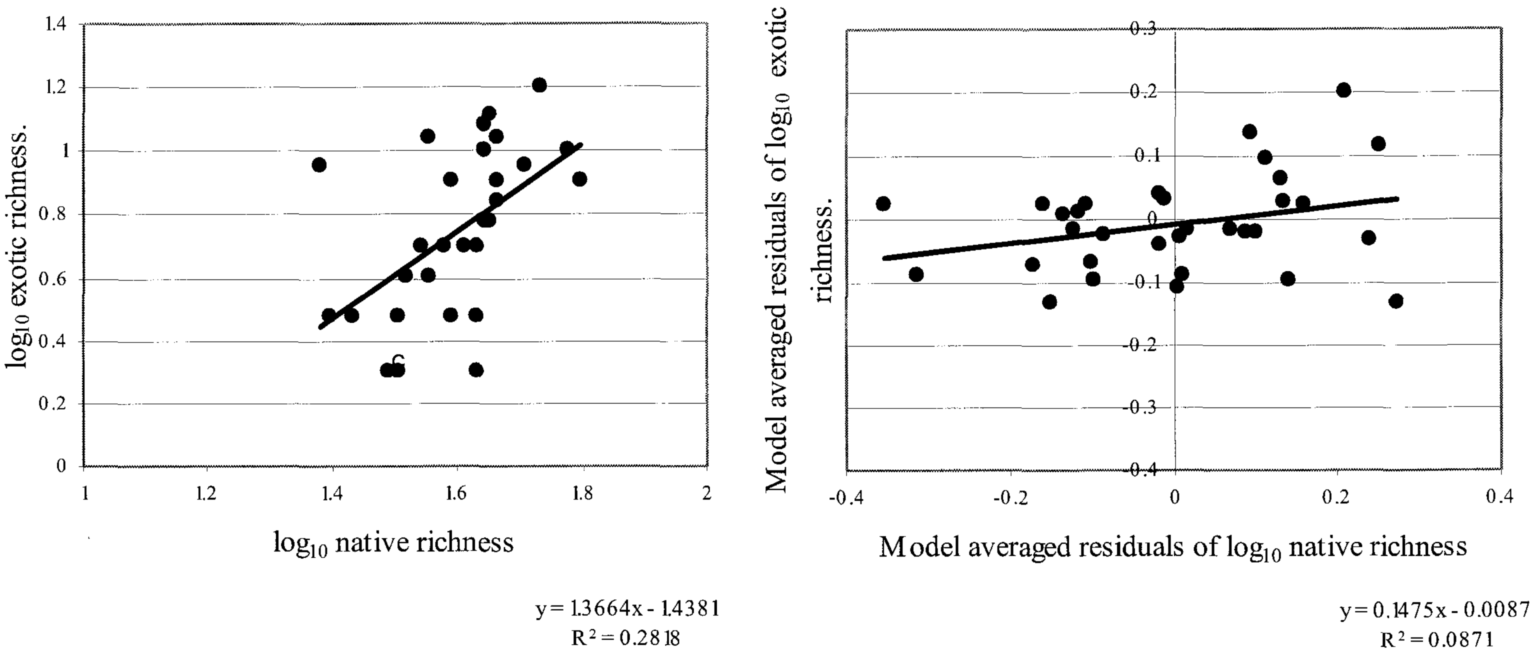

Figure 2.3. (a) Log_{10} exotic richness increases with $\log_{10}$ native richness in upland south facing ponderosa pine communities along the Front Range (P= 0.0018). (b) Residuals of the model averaged predictions for Log_{10} exotic richness do not increase significantly with $\log_{10}$ residuals of the model averaged predictions of native richness (P= 0.1009).

CHAPTER THREE

CONTRASTING EFFECTS OF RESOURCE AVAILABILILTY AND DISTURBANCE GRADIENTS ON PLANT COMMUNITY INVASION BY *BROMUS TECTORUM*

Abstract

The positive effect of disturbance on plant community invasibility is one of the more consistent results in invasion ecology. This is generally attributed to a coincident increase in available resources (due to the disturbance) that allows non-resident plant species to establish (the hypothesis of fluctuating resources; Davis et al. 2000). However, most research addressing this issue has been in artificial or highly modified plant communities. Additionally, disturbance has many definitions, but the form it usually takes in these experiments involves a combination of plant mortality and alteration of physical soil conditions (soil disturbance). These two disturbance types may have different or interacting effects on invasibility and one or both types may interact with climatic or abiotic factors, to result in different effects under different environmental conditions. To investigate the effects of, and interactions

among, resource availability and disturbance due to plant mortality alone in natural plant communities, I conducted an experiment to examine the effects of gradients of resource availability (nitrogen (N) and water) and resident plant species mortality on the success of *Bromus tectorum*, a highly invasive annual grass. I was interested in determining (1) if disturbance increased N availability, (2) if *B. tectorum* was limited (or co-limited) by N or water in this plant community, (3) how *B. tectorum* success changed with resource availability (linearly or with a saturating response), and (4) if plant mortality disturbances increase resource availability sufficiently to favor invasion. If this disturbance type increases resource availability and *B. tectorum* success responds similarly to increasing levels of resource availability and disturbance, the hypothesis of fluctuating resources would be supported. *B. tectorum* success was co-limited by N and water. Biomass at the end of the experiment was a saturating function of water, which determined maximum biomass, and N, which determined the rate at which maximum biomass was attained. Despite that fact that N availability increased with plant mortality, plant mortality disturbances had a generally negative impact on invasion success. My results may be due to the drought conditions that persisted during this experiment. Drought conditions create a stressful environment for plant establishment and growth. Under these conditions, plant mortality may have had other, negative effects (e.g., through the loss of plant/soil cover) or may not have released sufficient resources to promote the successful invasion of a non-resident species. Under more productive, wetter conditions (as was the previous year), plant mortality may have a larger impact on the invasion of plant communities by *B. tectorum*.

Introduction

There is much evidence linking diversity, disturbance, and resource availability to plant community invasibility (Levin and D'Antonio 1999, Stohlgren et al. 2001, Lonsdale 1999, Thompson et al. 2001), but most recent theories regarding exotic species invasion have focused on the role of resource availability, hypothesizing that community invasion is determined by spatial and temporal variation in resource availability (Davis et al. 2000, Foster and Dickson 2004). Any situation in which resident plants do not keep resources at uniformly low levels or that results in an increase in available resources, (e.g., nitrogen deposition or disturbance) increases the potential that an area may be invaded (Davis et al. 2000, Shea and Chesson 2002). However, with a few exceptions, resistance to invasion has been studied in artificial assemblages (Levin 2000, Prieur-Richard et al. 2000) or highly modified ecosystems (Burke and Grime 1996, Tilman 1997). Such experimentation has generated useful hypotheses about the role of, and interactions among, resource availability and disturbance in predicting the invasibility of plant communities, but these predictions need to be tested in experimental manipulations of natural systems.

Disturbances in natural ecosystems are diverse. Thus, the definitions of disturbance in observational and experimental studies are wide-ranging. Although this assortment of definitions is to some degree necessary to understand the equally wide-ranging effects of disturbance, the mechanisms by which "disturbance" promotes invasibility have been somewhat obscured by the plethora of definitions that accompany it. I assert that at its most basic level, disturbance in natural plant communities has two major forms: that of plant mortality and physical soil disturbance. Although these activities are often coincident, understanding the effects of each form of disturbance, in various ecosystems, is crucial to understanding what activities will promote community invasibility. In natural plant communities, the relationship between disturbance and resource availability is not well understood, and experiments that address the extent to which disturbance (plant mortality and/or soil disturbance) impacts community invasibility by increasing resource availability in natural plant communities are necessary.

The invasion of the annual grass *Bromus tectorum* into the western United States is one of the best-documented and most damaging plant invasions in human history (Mack 1981). At least 40 million hectares of original sagebrush-perennial bunchgrass vegetation has been replaced by monocultures of *B. tectorum* (D'Antonio and Vitousek 1992). *B. tectorum* invasion has drastically changed the fire regime (Whisenant 1990, Peters and Bunting 1994), and effectively blocked historical successional pathways in the sagebrush steppe region (West 1979). The spread and success of *B. tectorum* is thought to be due largely to the introduction of disturbances in the form of grazing and post-invasion changes in fire regimes (Mack 1986, D'Antonio and Vitousek 1992, Mack et al. 2000).

B. tectorum has also been a successful invader of the understory of semi-arid pine ecosystems, including the ponderosa pine landscapes of Colorado's Front Range. Such invasions could cause dramatic changes in ecosystem function. Because of its proximity to urban, suburban and exurban areas, the low elevation ponderosa pine ecosystems of the Colorado Front Range are heavily impacted by anthropogenic activity and associated disturbances. In addition to land use changes, the growth of urban areas along Colorado's Front Range has resulted in increases in N deposition (Baron et al. 2000), and models have predicted increases in precipitation and soil water availability as a result of irrigated land use along the Front Range (Stohlgren et al. 1998, Chase et al.1999). Determining how *B. tectorum* will respond to the varied and changing types and levels of disturbance and resource availability that impact this ecosystem is crucial for predicting the susceptibility of this ecosystem to invasion.

B. tectorum success has been linked to increases in nitrogen (N) (NPS 2000, Lowe et al. 2003, Monaco et al. 2003, Becksted and Augspurger 2004) and, in some cases, water (Link et al. 1995), but the nature of the response of *B. tectorum* to increasing levels of these resources is not known (e.g., linear or saturating). While the response of *B. tectorum* to increased resource availability seems to be generally positive, the exact role of disturbance in promoting the establishment and success of *B. tectorum* is less clear. The hypothesis of fluctuating resource availability predicts that if disturbance increases the availability of resources (N and/or water), it should increase *B. tectorum* invasion in the same way as increases in resource availability increase *B. tectorum* success (i.e., the shape of the response curve should be the same) (Davis et al. 2000). Either form of disturbance, plant mortality or soil disturbance, has the potential to increase resource availability. Plant mortality may increase available resources through a consequent decrease in plant uptake, while soil disturbance may increase available resources by increasing soil nutrient cycling rates by changing soil microclimate (aeration, moisture, temperature), microbial community structure, or making new substrate available for decomposition by breaking up soil aggregates (Elliot 1986, Kay 1990, Davis et al. 2000, Kristensen et al. 2000, Jackson et al. 2002). Understanding how *B. tectorum* will respond to such disturbances and changes in resource availability (particularly N and water) under natural conditions will be essential for maintaining ponderosa pine ecosystems.

My goal was to investigate the effects of water, nitrogen, and disturbance due to plant mortality on *B. tectorum* success in the ponderosa pine ecosystems of Colorado's Front Range. When disturbances due to plant mortality and alteration of soil conditions are allowed to interact, it may not be clear which disturbance type has (or even if both disturbance types have) a positive effect on resource availability and ultimately invasibility. I tested the following hypotheses: (1) disturbances that result in plant mortality increase N availability linearly by reducing plant uptake; (2) *B. tectorum* growth in this ecosystem is limited by both water and nitrogen (a hypothesis consistent with plant growth in semi-arid climates such as this one); (3) if *B. tectorum* growth is water and N limited, the successful invasion of *B. tectorum* will increase with water and nitrogen availability, either linearly (without reaching a maximum biomass) or with a saturating response (to a maximum biomass), due to limitation by other environmental or resource variables or plant characteristics (e.g., maximum growth rates; Figure 3.1a; Chapin et al. 1986); (4) if the main effect of plant mortality disturbance is to increase resource availability, disturbance, like resource addition, should release *B. tectorum* from resource limitation and increase invasion success in the same way as resource addition, i.e. in response to increasing levels of disturbance and resource availability *B. tectorum* success should increase with either a linear or saturating response (whichever response it shows to resource additions; Figure 3.1a). Alternatively, disturbance may not influence *B. tectorum* success in the same way as resource availability, perhaps creating adverse conditions for *B. tectorum* establishment, possibly through reducing plant cover and thereby increasing soil compaction, soil temperature, or soil and nutrient runoff and loss. In this case *B. tectorum* success may decrease linearly or increase to moderate levels of disturbance (plant mortality and cover loss) but decrease then at high levels of disturbance (intermediate disturbance hypothesis) (Table 3.1, Figure 3.1b).

Methods

Site locations and experimental design

I established four sites in ponderosa pine forests in the Arapaho-Roosevelt National Forest in Buckhorn Canyon, Larimer County, Colorado, USA. All sites were located in grassy openings within ponderosa pine forests, on south facing slopes. Although *B. tectorum* has invaded this canyon, all sites and plots were un-invaded. Sites were chosen randomly from all such sites located in the area.

At each site I set up three full factorial experiments: additions of N and/or water (NxW), N additions and/or disturbance (DxN), and water additions and/or disturbance (DxW). Each experiment consisted of all combinations of the four levels (including zero) of two of the three variables (water, N, and/or disturbance). I established 16 1-m^2 plots at each site for factorial experiment (a total of 48 plots per site). Each experiment had its own set of control plots (i.e., the zero levels of both treatments).

I added a total of 0, 1, 3, or 5 g N m^{-2} in three additions from September 2003 to May of 2004 (September 30, 2003, March 3, 2004, and May 5, 2003) as ammonium-nitrate. Levels of extractable inorganic N (point measurements throughout the 2003 growing season) for similar areas in this ecosystem average 0.07 g N m^{-2} (Adair unpublished data – will be in data Ch 3) and I used this value to represent the level of mineral N available in the 0 addition plots. My additions represent an increase in mineral N of up to approximately 100%.

I added water at rates of 0, 2, 5, or 10 mm week^{-1}. The 10 mm week^{-1} treatment doubled the amount of water in precipitation alone (~ 290 mm), as measured by two rain gauges I placed at sites one and two. I added water weekly for 5 weeks in the fall of 2003 (beginning September 30) and 10 weeks in the spring (beginning March 15, 2004). Water was transported to each site via foot or water pump and carefully applied with a watering can with pinhole-sized holes, to prevent soil compaction and runoff. Precipitation was measured weekly at sites 1 and 2 using All-Weather Rain Gauges. These data correlated well with data from the closest weather station located at Buckhorn Mountain (NCDC 2005). Rainfall measured by gauges at these sites over the duration of the experiment (October 2003 – June 2004) was 288 mm. I used this value as the amount of water received by 0 addition plots.

I created a gradient of plant mortality disturbances by removing 0, 20, 60, or 100% of the aboveground biomass in each plot. Biomass was removed by randomly selecting a 10 x 10 cm square in a frame placed over the plot. The plant occupying this section of the plot was removed. If the chosen plant removed more biomass than was required, another square was randomly selected. I clipped and sprayed plants with the herbicide glyphosate, N-(phosphono-methyl)-glycine, trade name Roundup® (Monsanto Co., St. Louis Missouri, USA), three weeks to one month prior to seeding the plots and beginning the experiment. The removed biomass was randomly chosen from existing biomass in 10 x 10cm areas. We chose to use this type of disturbance to investigate the effects of disturbances that are due to plant mortality, i.e., the freeing of resources through decreased competition. My disturbance attempted to free plant resources (used by resident plants) without adding resources through soil disturbance. Studies have found that these disturbance types may have different effects on *B. tectorum* success (e.g., Becksted and Augspurger 2004), and I was interested in determining if plant death alone results in adequate resources and conditions to promote *B. tectorum* success.

I planted *B. tectorum* seeds at a depth of 5 mm in a 50 x 50 cm area located in the center each plot using a grid system. I collected *B. tectorum* seed from local populations near each site. Coincident with the onset of *B. tectorum* germination, from September 23-27, 2003, I planted two seeds at each grid intersection (including the edges). Planting occurred approximately one month after I created the disturbance gradient. I began adding N and water after the planting. To minimize edge effects I applied treatments to the entire plot.

To characterize *B. tectorum* success in each plot, I harvested, air dried, and weighed all *B. tectorum* at the end of the experiment (after seed set when the plants began to cure) to obtain the *B. tectorum* biomass in each plot. *B. tectorum* was harvested on June 30 – July 2, 2004.

I monitored available mineral N in each treatment plot using Plant Root Simulator (PRS) probe–ion exchange membranes (Western Ag Innovations, Inc., Saskatoon, Canada). The PRS probes were sent to Western Ag Innovations, Saskatoon, Canada for extraction. At Western Ag, the probes were extracted with 17.5 mL of 0.5 M HCl for one hour in a zip lock bag, and the extractant was analyzed for NH_4^+ and NO_3^- using a Technicon autoanalyzer (Bran and Lubbe, Inc., Buffalo, NY). This allowed us to investigate not only how well N additions increased available N, but also how disturbance changed available N. I installed a pair of probes (one anion and one cation probe) in each plot on March 9, 2004 and left them in place until May 26, 2004, after *B. tectorum* had set seed. Results are reported as (μg 10 cm^{-2} probe surface area over the 79 day burial period).

Data Analysis

I analyzed the resulting data from each experiment to investigate how *B. tectorum* responds to combinations of disturbance and water, disturbance and N, and water and N. Using the N probe data, I used linear regression to test my hypothesis that N availability increases with plant mortality disturbance level (proc REG, SAS).

B. tectorum biomass was $\log(0.05 + x)$ transformed to improve normality. Because several of my hypotheses included nonlinear models with multiplicative effects among treatments, I chose to characterize the zero level of each treatment as either a naturally occurring amount (detailed above) or a very low level (the case for disturbance only; I used a value of 1%, insignificant in comparison to the treatment levels that are detailed above). If I used zero, many of the equations would = 0 due to multiplication effects. For example, in the equation $\log(wt) = \log(b_0 + b_1W(1-e^{(-b2*N)}))$, if W is zero, it cancels out the effect of N and causes the equation to equal to the log of the intercept (b_0); if N is zero it cancels out the effect of W and the equation is again equal to the $\log(b_0)$.

I used Akaike's Information Criterion (AIC) model selection to choose the model (linear, natural growth, or combined feedbacks) and combination of variables (N, water, and/or disturbance) that best explained the success of *B. tectorum* in each experiment. AIC estimates the information lost by using a model to approximate the unknown truth and is used to rank a set of a priori models based on the support for each in the data (Burnham and Anderson 2002). In essence, candidate models are ranked based on their relative distance from the unknown truth, which is represented by the data (it is assumed that the "unknown truth" generated the data). For these experiments I used AIC modified for small sample sizes (AICc). The difference between the AICc value of the best model and the values of the models ranked below it (Δr), provides information on which models in the model set are close competitors to the best model. The Δr of the best model is therefore zero; this indicates that it is the model closest to the unknown truth. Models with a $\Delta r < 2$ (that are within 1-2 AICc points of the best model and still relatively close to the "truth") have substantial support in the data, models with a Δr of 4-7 have considerably less support, and models with a $\Delta r > 10$ have essentially no support in the data (Burnham and Anderson 2002).

This methodology also provides information on model selection uncertainty by calculating Akaike weights (w_r) for each model in the a priori set. Akaike weights can be interpreted as the probability that the best model would again be selected as the best model, given the same set of candidate models and a new set of similar but independent data (Burnham and Anderson 2002)

I included site as a fixed variable in all models, but model selection was used to determine the placement of the site effect within the nonlinear models (e.g., affecting the intercept, b_0, maximum, b_1, or slope term, b_2, in the natural growth) (proc NLIN, SAS). I used bounds (limitations) on the parameter values in the natural growth equation to preserve the basic shape of the curve (i.e., an increasing function, Figure 3.1a). I selected models from each set that met the SAS default convergence criterion (proc NLIN, SAS), had a Δr of less than 3, and an R^2 of 0.2 or greater.

This analysis allowed us to determine if mineral N increased with disturbance, which (if either) resource (water or N) was more limiting to *B. tectorum* success and examine interactions between these resources, if and how *B. tectorum* biomass increased with water and nitrogen availability, and if disturbance increased resource availability sufficiently to favor invasion. If the main effect of disturbance is to increase resource availability, *B. tectorum* invasion (successful colonization) should respond similarly to both increasing levels of disturbance and nutrient availability. For example, if *B. tectorum* biomass increases linearly in response to increasing resource availability, it should also increase linearly with increasing disturbance (Figure 3.1a). If disturbance does not influence *B. tectorum* success in the same way as resource availability, *B. tectorum* biomass will not respond in the same way to increasing levels of resource availability and disturbance. If disturbance has negative effects on *B. tectorum* biomass, it may either decrease biomass linearly or increase it to moderate levels of disturbance but decrease it at high levels of disturbance (intermediate disturbance hypothesis) (Figure 3.1b). No response to N, water, or disturbance would indicate that these factors do not affect the invasibility of this ecosystem by *B. tectorum*. Additionally, if the invasion of *B. tectorum* is simply limited by propagule availability, it should be successful in all plots, whereas if *B. tectorum* is not successful in this ecosystem (at this time) it would not be successful in any plot.

Results

The effect of plant mortality disturbances on N availability

Disturbance increased the availability of mineral N when acting alone or in concert with N or water additions (Figure 3.2). Using the disturbance only treatments from the DxW and DxN factorial experiments revealed a positive effect of disturbance on N availability (linear), as indexed by the PRS cation and anion probes ($P < 0.0001$, $R^2 = 0.63$), but the strength of this relationship varied within experiments with the various water and nitrogen treatments (Figure 3.2).

In the DxW factorial experiment, available N increased with disturbance level, but this effect decreased as the amount of water a plot received increased (Figure 3.2a). In other words, adding water decreased the positive effect of disturbance on N availability. In this experiment, available N was best explained by a positive relationship with disturbance, a weak relationship with water (0 included in the 95% confidence interval), and a negative disturbance by water interaction term ($\Delta r = 0$, $R^2 = 0.4703$). The effect of water alone was not statistically significant ($P < 0.05$), but the DxW and disturbance effects were statistically significant. Additions of water did not appreciably decrease the amount of available N at any level of disturbance except for at 100% disturbance, where available N decreased considerably with increasing water additions ($R^2 = 0.4817$ for 100% disturbance plots only Figure 3.2a).

In the DxN factorial experiment disturbance also increased available N and this effect increased with increasing additions of N. Mineral N availability increased significantly ($P < 0.05$) with both the disturbance and N addition treatments (Figure 3.2b). Available N was best explained by a positive linear relationship with both N and disturbance ($\Delta r = 0$, $R^2 = 0.3832$).

Co-limitation of B. tectorum by N and water

B. tectorum was most successful in treatments that included both water and nitrogen, indicating that in this ecosystem (at this time), *B. tectorum* was limited by a combination of N and water availability. In the NxW experiment, the model that best explained *B. tectorum* success (biomass) was a natural growth equation (Table 3.2), with water and site influencing the maximum biomass term (b_1) and N influencing the rate of approach to the maximum (b_2) (Figure 3.3). In other words, N availability increased the rate at which *B. tectorum* approached its maximum biomass, while increasing water availability increased the maximum biomass that could be attained by *B. tectorum* (Figure 3.3). At low levels of water availability, *B. tectorum* biomass remained relatively low regardless of the amount of N added. However, *B. tectorum* biomass increased rapidly with added N as water availability increased.

Effects of, and interactions between, disturbance and resource availability on the success of B. tectorum

In the DxN factorial experiment, the negative effect of disturbance overwhelmed any positive influence that the increased availability of N might have had on *B. tectorum* success. The results of the disturbance by nitrogen factorial experiment were best explained by two models with Δr's < 0 (Table 3.2). At all sites, and in combination with all N treatments, disturbance had a linear negative effect on *B. tectorum* biomass. The first was a linear model with disturbance only (negative). The second best model was a linear model with disturbance (negative) and nitrogen (very slightly positive). Both models included site effects. Examination of the model parameters and resulting predictions from the models revealed that N had very little effect on the success of *B. tectorum*. This suggests that, of the two treatments, disturbance was the overwhelming predictor of *B. tectorum* success (Figure 3.4). However, there is considerable model selection uncertainty regarding the choice between these two models ($w_r = 0.473$ and 0.136 for D only and N + D respectively), suggesting that with another data set, N may be more important to *B. tectorum* biomass.

Disturbance increased *B. tectorum* success with no additions of water but as water additions increased, the effect of disturbance became neutral and then negative (Figure 3.5). Alternatively, the positive effects of water additions (positive with no disturbance) decreased with increasing levels of disturbance, and at the highest level of disturbance (100%), increasing the amount of water received by the plots actually decreased the success of *B. tectorum*. *B. tectorum* success in the DxW factorial experiment was best described by the positive linear combination of site, disturbance, and water, with a negative interaction term between disturbance and water (Figure 3.5; Table 3.2).

Discussion

N availability increased with plant mortality, indicating that this type of disturbance does act to increase resource availability. However, the combination of N and water had the largest positive effect on *B. tectorum* biomass/success compared to combinations of disturbance and either nitrogen or water. In most cases, plant mortality disturbance acted to decrease the success *B. tectorum*.

Maximum biomass was attained by *B. tectorum* in the high water and nitrogen treatments in the NxW factorial, suggesting that *B. tectorum* is limited by both water and N in this ecosystem. The model that best explained *B. tectorum* success in the NxW experiment reinforces this idea, as it explains biomass as a combination of water effects (on maximum biomass) and N effects (on the rate at which *B. tectorum* biomass increases to a maximum) (Figure 3.3). The maximum predicted *B. tectorum* biomass was similar between the DxN and DxW (approximately 0.4 g; Figures 3.4 & 3.5) factorial experiments, and was consistently lower than in the NxW experiment (maximum predicted biomass of 3.1 g; Figure 3.3). This also lends support to the co-limitation of *B. tectorum* by N and water, as neither resource alone nor in combination with disturbance was sufficient to increase biomass to the levels observed in the NxW experiment.

Contrary to my prediction that invasibility of this plant community by *B. tectorum* would increase with plant mortality disturbance due to increased resource availability, disturbance had primarily negative effects on *B. tectorum*, depending on which resource, water or N, it was combined with. Disturbance had a consistently negative effect on *B. tectorum* biomass in combination with N treatments and plant mortality increased the availability of N. This suggests that the availability of N alone is not sufficient to promote the success of *B. tectorum*. In combination with water treatments, disturbance had variable effects on *B. tectorum* success. At low levels of water addition, disturbance acted a bit like N, increasing *B. tectorum* success, but at higher levels of addition, disturbance decreased *B. tectorum* success (Figure 3.5). So, at some point (between 20 – 60% disturbance/plant cover removal), another factor associated with this type of disturbance, such as soil compaction or nutrient loss, reversed the positive influence of disturbance, and began to negatively affect *B. tectorum*, and by extension, decrease the invasibility of this system.

My results suggest that the plant mortality disturbance may have had other effects, perhaps on the microclimatic conditions in these plots that limited *B. tectorum* success. Although I did not measure soil water or temperature in response to my treatments, it could be that the reduction in plant cover that resulted from my disturbance treatments increased soil compaction and soil temperatures and concomitantly decreased the availability of soil water. Because *B. tectorum* in this series of experiments was limited by water, this could have resulted reducing the success of *B. tectorum* in the disturbance treatments.

Most experimental research on the interactions among disturbance and invasibility have found that disturbance has generally positive effects on plant community invasibility (Burke and Grime 1996, Smith and Knapp 1999, Gross et al. 2005), but other researchers have found that the effects of the variables that influence plant community invasibility (e.g., various disturbance types and propagule pressure) often vary with environmental conditions (Kotanen 1997, Wilsey and Polley 2003, Becksted and Augspurger 2004, Foster and Dickson 2004, Huston 2004). In productive environments, disturbed areas are generally more easily invaded than are undisturbed areas (Huston and DeAngelis 1994, Huston 2004). In such highly productive fertile environments, disturbances that remove plant biomass or cause plant mortality decrease competition, thereby increasing resource availability and making the environment more susceptible to invasion (Davis et al. 2000, Huston 2004). In such cases, the establishment of non-resident species (native or exotic) is considered to be limited primarily by competition for resources (Huston 2004, Foster and Dickson 2004). However, the degree to which invasion is limited by competition may vary along abiotic gradients of resource availability and climatic conditions, so that disturbances that remove native plant competition may facilitate invasion only in more productive sites (Huston 1999, Huston 2004, Foster and Dickson 2004, Leishman and Thomson 2005). Such gradients may be spatial, moving from dry to wet climates, or temporal, as a single community responds to wet, dry, or drought years. Whereas in productive environments or years, disturbance-caused mortality may reduce dominant species biomass and make critical resources, particularly light, available for smaller or invading plants (Huston 2004), in environments or times that are abiotically stressed, the same disturbance type may not release sufficient resources for invasion, and may simply remove plant biomass (assuming propagule availability) (Huston 2004, Leishman and Thomson 2005).

Alternatively, the removal of plant biomass without soil disturbance may have other effects, apart from increasing N availability, that result in reducing *B. tectorum* success. In harsher, less productive environments and times, different types of disturbances may have variable (positive or negative) effects by interacting with other factors or resources that affect invasibility (Kotanen 1997, King and Grace 2000, Becksted and Augspurger 2004, Leishman and Thomson 2005). Disturbances may reduce soil moisture by removing boundary layers (litter, plant biomass) and raising soil temperature, or change soil nutrient availability by increasing soil compaction, surface runoff, erosion, or leaching (Beckstead and Augspurger 2004, Leishman and Thompson 2005). For example, Beckstead and Ausgpurger (2004) found that in a Utah desert, different types of disturbances had different effects on *B. tectorum* success. Soil disturbance had a much larger effect on increasing *B. tectorum* establishment and success than did plant mortality alone (Beckstead and Ausgpurger 2004).

In studies of plant community invasibility, removal of competitors is often considered the primary factor leading to invasion success (Crawley 1987, Hobbs 1989). My results show that, in the ponderosa pine-grassland ecosystem of Colorado's Front Range, the simple removal of competition may not be enough to promote the invasibility of the plant communities by *B. tectorum*, a species that has been extremely successful throughout the western US. This experiment took place during a particularly dry period. The Palmer Drought Index for Front Range foothills was less than -1.5 for all months of the study, with five months of moderate drought conditions (< -2) and two months of severe drought (< -3), suggesting that this was a fairly stressful period for plant establishment and growth (NOAA 2005, CCC 2005). Under stressful climatic conditions, the freeing of resources through the removal of plant competition may not have been sufficient to promote the successful establishment and growth of *B. tectorum*. In fact the removal of neighboring plants may have exacerbated these stressful conditions by decreasing shade cover, which might otherwise lower soil temperatures and reduce losses of soil water.

The response of *B. tectorum* to water and N indicates that, under these stressful conditions, increasing N availability only increased *B. tectorum* success in the presence of sufficient water. When water is limiting, during periods of drought, disturbances that promote the availability of both water and nitrogen, versus the removal of nutrient competition alone, may be of considerably more concern for causing increases in the invasibility of these plant communities by *B. tectorum*. During average or above average precipitation years, it is possible that increasing available N through plant mortality alone may have significantly different or positive effects on *B. tectorum* success. Continuing research will hopefully take advantage of spatial and temporal variability to further elucidate the interactions among different disturbance types (soil disturbance and plant mortality) and climatic or abiotic conditions and stresses.

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Table 3.1. Mathematical expressions for hypotheses of linear and saturating increases in *B. tectorum* biomass with resource availability or disturbance (linear and natural growth equations), and for increased biomass to intermediate levels of disturbance and decreased at high levels of disturbance (combined feedbacks equation). In the natural growth equation, b1 describes the maximum biomass, and b2 describes the rate at which the curve approaches the biomass maximum, that is, how fast *B. tectorum* approaches its maximum biomass in response to increasing levels of resources. In the combined feedbacks equation, b1 is related to the rate of maximum increase in biomass with increasing disturbance, while b3 is the facilitation - inhibition term. B = log(wt) of *B. tectorum*, D = disturbance, R1 and R2 = N, water or disturbance, R3 = N or water only.

Linear increase with resource availability or disturbance

$$B = b_0 + b_iR_i$$

$$B = b_0 + b_1R_1 + b_2R_2$$

$$B = b_0 + b_1R_1 + b_2R_2 + b_3R_1R_2$$

Saturating increase with resource availability or disturbance

natural growth equation

$$B = b_0 + b_1(1\text{-}e^{(-b2R1)})$$

$$B = b_0 + b_1R_2(1\text{-}e^{(-b2R1)})$$

$$B = b_0 + b_1(1\text{-}e^{(-b2R1R2)})$$

Increase to intermediate levels of disturbance, decrease at high levels (disturbance only)

combined feedbacks equation

$$B = b_1(1\text{-}e^{(-b2D)}))$$

$$B = b_1R_3(1\text{-}e^{(-b2D)}))$$

Table 3.2. Best models, estimated parameters, and associated model selection criteria for each factorial experiment: Nitrogen (N) by water (W), disturbance (D) by N and D by W. *B. tectorum* success in the NxW experiment was best described by a natural growth equation including N and W, in the DxN experiment by a negative linear relationship with D alone (see results section for detailed discussion), and in the DxW experiment by a positive linear combination of D and W with a negative interaction term.

Equation form	Equation	Parameter estimates								
		b_0	water	N	disturbance	water*disturbance	R^2	AICc	delta r	w_r
natural growth	$B = \log(b_0 + (site + b_1)W(1-e^{(-b2N)}))$	0.1349	0.0006	0.3094			0.477	-115.91	0.00	0.60
linear	$B = \log(b_0 + b_iD)$	0.1719			-0.00165		0.417	-92.86	0.00	0.47
linear	$B = \log(b_0 + b_1D + b_2N)$	0.1713		0.00023	-0.00165		0.417	-90.37	2.49	0.14
linear with interaction	$B = \log(b_0 + b_1D + b_2W + b_3DW)$	-0.516	0.0019		0.00908	-0.00003	0.243	-99.08	0.07	0.58

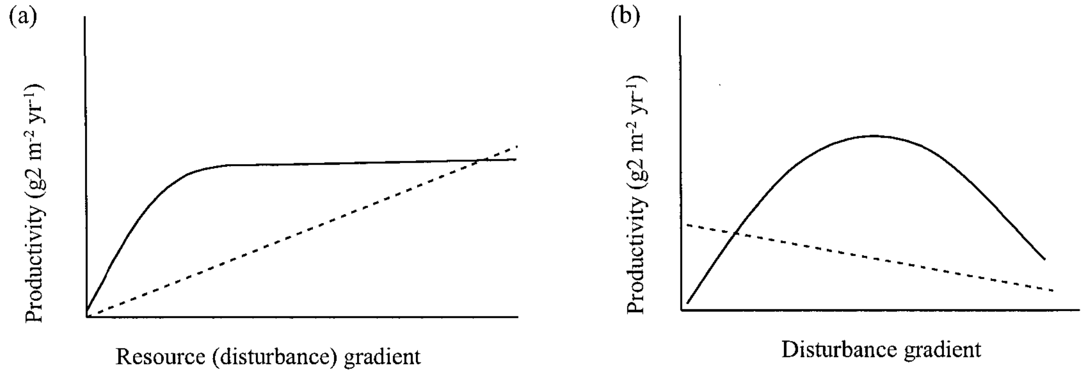

Figure 3.1 Hypothesized responses of *Bromus tectorum* biomass to increases in resource availability and plant mortality disturbance: (a) increases in resources as a result of either N and/or water additions or increasing levels of disturbance (due to plant mortality) will result in either a linear increase in *B. tectorm* biomass, dashed line, or a saturating increase, solid line; if disturbance does not increase resources sufficiently to consistently promote *B. tectorum* invasion, plant biomass will either (b) linearly decrease with increasing levels of disturbance (dashed) or increase to moderate levels, but decrease with high levels of disturbance (combined feedbacks, solid).

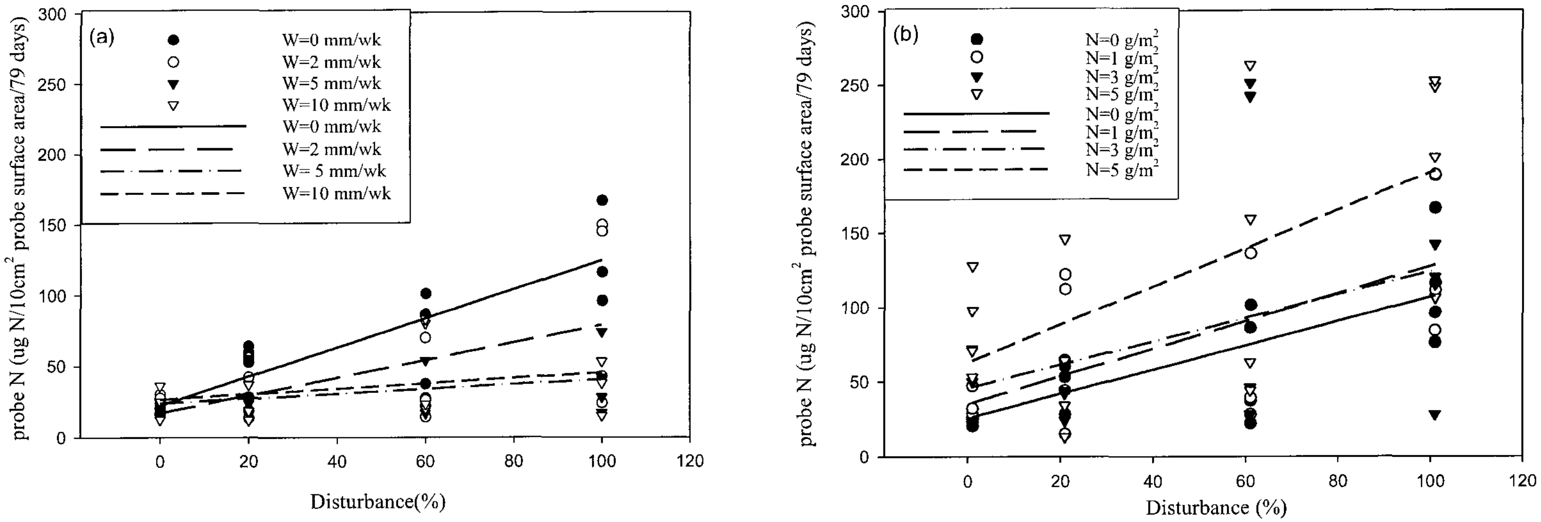

Figure 3.2. Available mineral nitrogen (N) increased with disturbance in two factorial experiments. Available mineral N was measured using PRS ion exchange resin soil probes and is presented in units of μg inorganic N / 10 cm^2 surface area / 79 day burial period. Each experiment has its own separate control plots. In the disturbance by water factorial experiment (a) available N increased with the level of disturbance at each level of water addition, but mineral N increased less as the level of water addition increased. In the disturbance by N factorial experiment (b) mineral N increased with disturbance at each level of N addition. Available N increased with increasing levels of N addition.

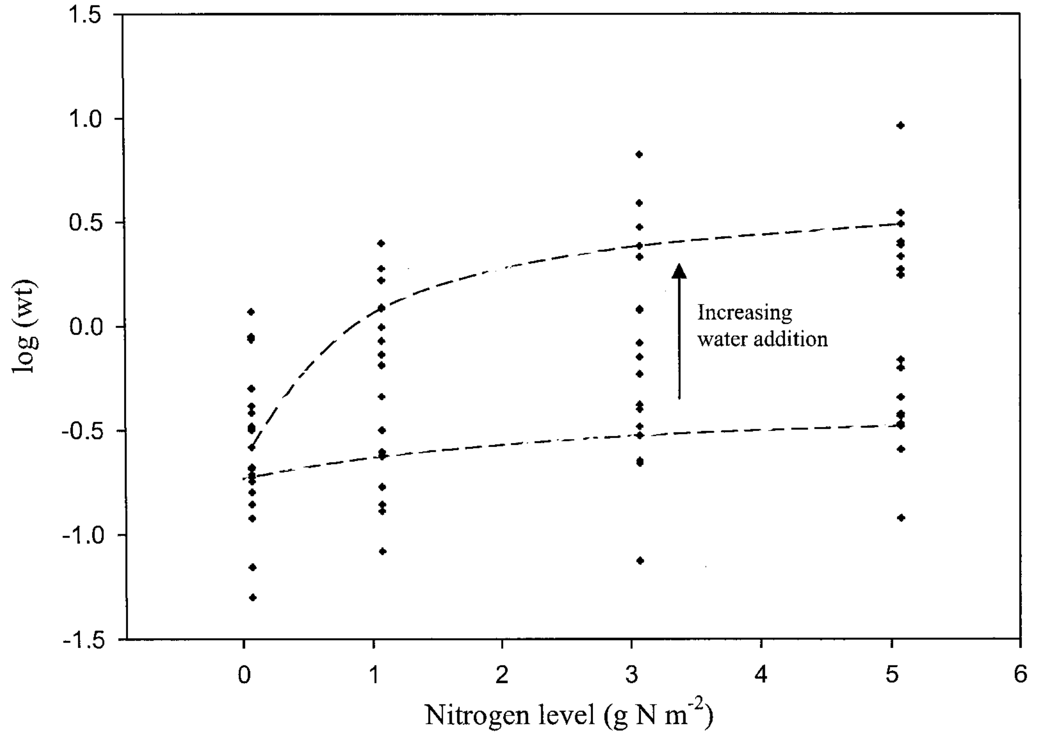

Figure 3.3. Best model for N by water factorial experiment. *B. tectorum* success was best explained by the natural growth equation, $\log(wt)=\log(b_0 + W(b_1 + site)(1-\exp^{(-b2N)}))$. Water additions increased maximum biomass and N additions increased the rate at which biomass approached the maximum. Upper and lower bounds of model predictions (dashed lines) with observed data (black circles).

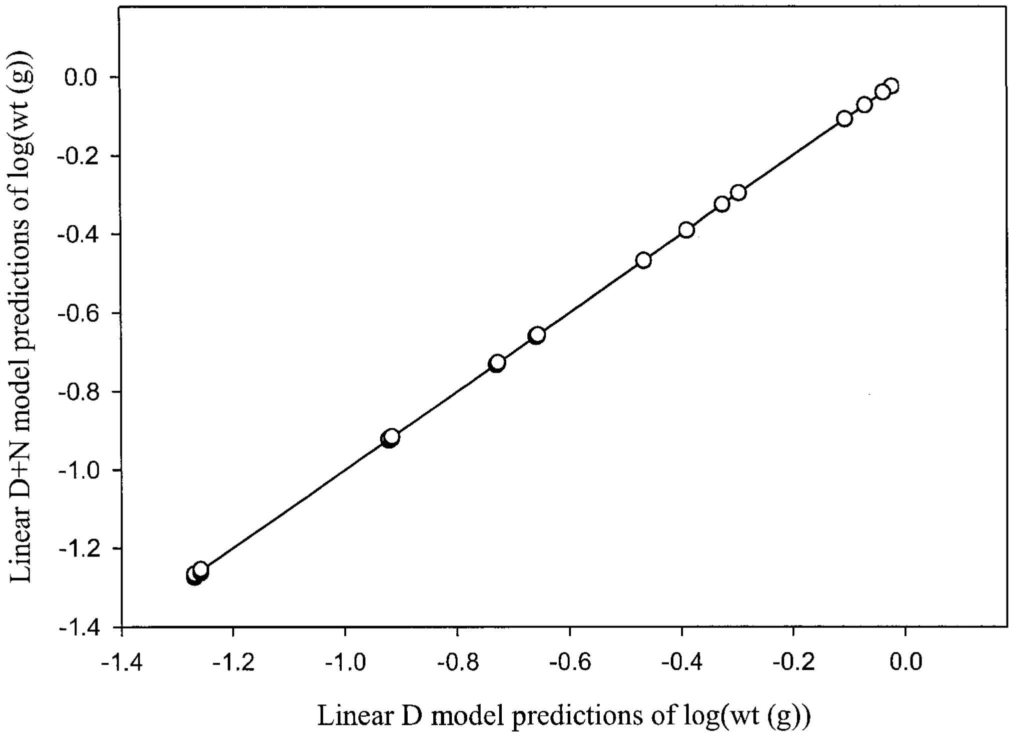

Figure 3.4. The two best models in the disturbance by N factorial experiment did not generate meaningfully different predictions of *B. tectorum* weight (g). Predictions of the linear model with disturbance (D) and nitrogen (N) are plotted against the linear model with D only (open circles). The solid line is a 1:1 line. All predictions fall on the 1:1 line, indicating that the more complicated linear D+N model does not significantly change the predictions of log(wt) from the simpler D only linear model.

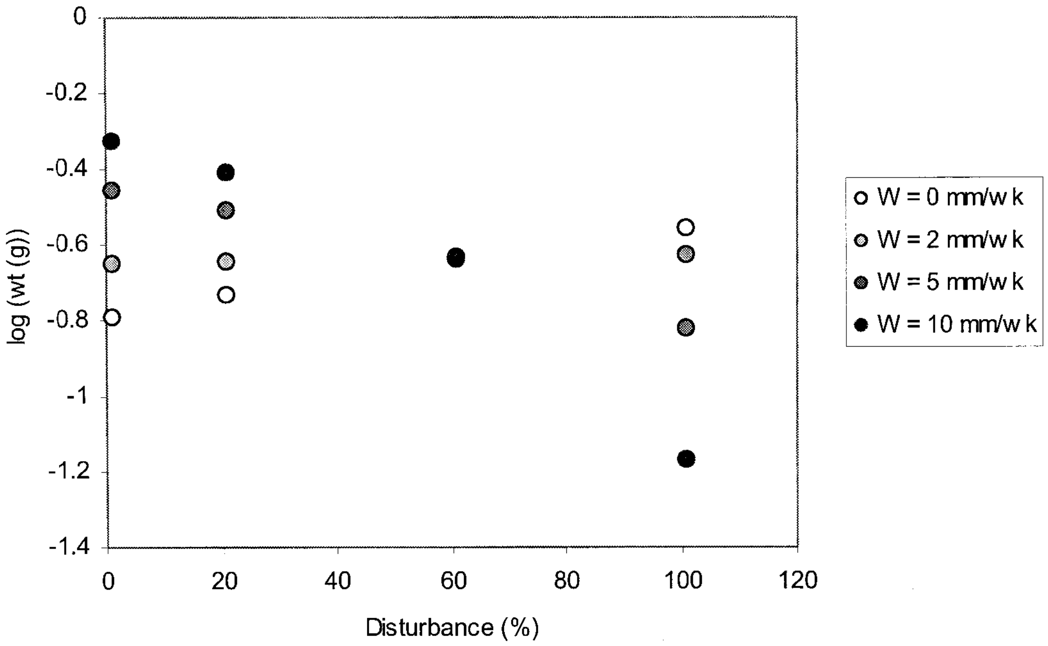

Figure 3.5. Results from the disturbance by water factorial model show that the effects of disturbance on *B. tectorum* success, which are initially positive, become negative with increasing levels of water addition (W = level of water addition per week). Predictions of *B. tectorum* biomass (wt(g)) from the best model, a linear combination of disturbance and water with interaction are shown without site effects for clarity.

CHAPTER FOUR

THE BIOGEOCHEMICAL CONSEQUENCES OF *BROMUS TECTORUM* INVASION INTO PONDEROSA PINE ECOSYSTEMS

Abstract

Along Colorado's Front Range, small rainfall events make up an important fraction of the water received by low elevation ponderosa pine ecosystems and may be ecologically significant triggers for biological and biogeochemical processes. At the same time, *Bromus tectorum*, an annual grass, is a common exotic invader of these ecosystems. *B. tectorum* invades and replaces C3-C4 perennial grass communities and may affect soil properties and processes by changing the timing of plant growth, resource uptake and litter deposition, or other species differences (e.g., litter quality). Although changes in timing and distribution of rainfall events (climate change) and plant community composition (exotic invasion) may separately affect ecosystem characteristics and processes, interactions between these processes may result in larger than expected impacts on ecosystem properties. I evaluated how small precipitation events (5 mm), species composition, time (daily and seasonal), and the interactions between them influence labile and microbial pools of C and N. I found

that while pools of labile N (inorganic and dissolved organic N) were largely unaffected by small rainfall events, labile carbon (C) and microbial biomass C/N ratios decreased after small events and microbial biomass C and N increased after rainfall events. Plant community composition had much larger effects on soil and microbial pools. Labile pools of N were one and a half times larger beneath stands dominated by *B. tectorum* than beneath perennial grasses. Microbial biomass C and N were also larger, and biomass C/N ratios lower, beneath *B. tectorum* than beneath perennial grasses. The effects of water additions and species composition on soil pools of C and N often changed throughout the growing season, but timing was more important for deciphering trends in soil pools as affected by species composition than for detecting responses to water additions. Timing only substantially affected the response of microbial biomass N and C/N ratios to water additions: C/N ratios were most responsive late in the growing season, while microbial N responded more during the first two months than the during the last. Labile C and N pools all increased through the growing season after plant community senescence, but often differences between pool sizes beneath *B. tectorum* and perennial grasses only became apparent later in the growing season. This was also the case for microbial biomass C/N. Conversely, trends in microbial biomass C and N were apparent early in the growing season, but disappeared in the last month of the study. These results suggest timing is important in determining the effects of small precipitation events and species composition. Additionally, for microbial pools, water additions had variable effects depending on the time within the growing season and the species composition, suggesting that invasion of *B. tectorum* could interact with changes in the distribution of small rainfall events to alter microbial processes in this ecosystem.

Introduction

Two major forces of human-driven global change are climate change and exotic species invasion. The effects of both of these processes receive widespread attention independently, but they may interact to change ecosystems to a larger degree than might be expected from the study of each process individually. Concern regarding climate change is mostly focused on large-scale changes in average temperatures or precipitation amounts, but climate change may affect more subtle patterns, such as the frequency, timing, or size of rainfall events (Gordon et al. 1992, Easterling et al. 2000, IPCC 2001).

In semiarid climates, like Colorado's plains and northern Front Range, small precipitation events make up the most consistent and frequent source of water (Noy-Meir 1973, Sala and Lauenroth 1982, Loik et al. 2004). Small rainfall events (< 5 mm) account for approximately 71% of daily events and provide 23% of the annual rainfall in Colorado's northern Front Range and foothills (NCDC 2005; Figure 4.1).

In these semiarid regions, water is the primary constraint on productivity and ecosystem processes, and very small rainfall events may support microbial activity (< 3 mm) and slightly larger events may increase plant nutrient uptake and photosynthesis (3-5 mm; Sala and Lauenroth 1982, Austin et al. 2004, Reynolds et al. 2004). The impacts of these common, small events on nutrient storage and cycling in natural systems have not been clearly determined. In laboratory and scarce field studies, rewetting of semiarid and arid soils often increases microbial biomass, nitrogen (N), and activity (e.g., decomposition and N mineralization) and changes composition (fungal biomass versus bacteria; Austin et al. 2004). Precipitation events may also change soil pools of carbon (C) and N by increasing microbial activity, leaching dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) from litter (Cleveland et al. 2004), disrupting soil aggregates (Lundquist et al. 1999, Austin et al. 2004), or releasing nutrients from microbial biomass (death during the dry period, lysis, or release of soluble microbial compounds during wet-up) (Bottner 1985, Halverson et al. 2000, Fierer and Schimel 2003, Austin et al. 2004). Determining whether small events (~5 mm) are sufficient to affect soil processes and pools in natural ecosystems is key to understanding how changes in precipitation regimes will affect semiarid ecosystem functioning.

If small events substantially influence soil pools and processes, then the distribution or timing of small events modified by climate change could have large consequences. Decreasing the frequency of small events and increasing event size, without changing the total amount of precipitation, reduced soil respiration and plant productivity in a Kansas grassland (Knapp et al. 2002, Harper et al. 2005) and decreased NPP, soil C, and available N in simulations using DayCent, the daily version of the Century ecosystem model (Parton et al.1998, Kelly et al. 2000, Del Grosso et al. 2001; Burke et al. unpublished). These results suggest that small events, and changes in their seasonal distribution, can have a large influence on ecosystem productivity and processes.

Changes in the plant species composition of an ecosystem can also have important consequences for ecosystem nutrient cycling. Plant species characteristics, such as plant structure, tissue chemical composition, carbon and nutrient allocation, and life span, have been shown to have significant effects on the size and dynamics of soil C and N pools (Melillo et al. 1982, Pastor et al. 1984, Wedin and Tilman 1990, Vinton and Burke 1995). The successful invasion of a non-resident or exotic species may therefore have large impacts on soil pools if it is sufficiently different from resident species in the community (Ehrenfeld 2003).

Exotic species have successfully invaded plant communities throughout the Rocky Mountains, altering plant community composition and potentially impacting soil pools and processes (Stohlgren et al. 1999, Fornwalt et al. 2003, Adair Ch 1). *Bromus tectorum*, a very successful and damaging exotic annual grass in the semi-arid western U.S., has been a particularly successful invader of Colorado's Front Range ponderosa pine ecosystems, invading and replacing native C3 and C4 perennial grasses (Mack 1981, Mack 1986, D'Antonio and Vitousek 1992). This replacement could have important effects on soil pools and processes, and many studies have attempted to document if or how native perennial grasses and introduced annual grasses differentially impact soil nutrient and carbon pools. The results from these studies are mixed, with some finding annual grasses (including *B. tectorum*) to have lower levels of various soil N and C pools than perennial grasses, and others finding higher levels beneath annual grasses than perennial grasses, and yet others finding no difference (Booth et al. 2003, Bolton et al. 1990, Bolton et al. 1993, Vinton and Burke 1997, Evans et al. 2001).

A potential explanation for this observed variability may be that the replacement of perennial grasses with *B. tectorum* may change not only the overall sizes of soil pools of C and N, but also the daily and/or seasonal dynamics of these pools. *B. tectorum* germinates in the fall, peaks in the early spring and senesces by early summer (Hulbert 1955, Abshapanek 1962, Finnerty and Klingman 1962, Baskin and Baskin 1981, Ogle and Reiners 2003). In contrast, the activity of perennial C3 and C4 grasses declines in the mid or late summer (respectively) (Singh et al. 1983) and they maintain root systems that store plant nutrients throughout the year (Ogle and Reiners 2003). The timing and quantity of these annual litter fluxes could have significant effects on seasonal pool sizes and fluxes (Woodmansee and Duncan 1980, Jackson et al. 1988, Wedin and Tilman 1990, Hart et al. 1993), but most of the studies mentioned above consist of single point, temporally constrained (short-term), or laboratory measurements that try to document overall or general changes in soil pools and do not control for daily and seasonal variation. Examination of how nutrient pools beneath these plant communities interact with time (seasonal and daily) may shed light on some of these disparate results.

Finally, there is the potential for interaction between changes in the timing of small rainfall events through climate change and changes in plant community composition as a result of exotic species invasion. Altering plant species composition may change the response of soil pools of C and N to small rainfall events through the growing season by changing the dominant phenology, plant resource use and uptake characteristics (e.g., the ability for rapid uptake of resources from temporally pulsed events; Duke and Caldwell 2001), and/or species responses to temperature and water stress (Huxman et al. 2004, Schwinning and Sala 2004). Changes in plant community composition may therefore interact with changes in the distribution or timing of small rainfall events to produce changes in ecosystem properties or functioning that are greater than might be expected from studying the response of ecosystems to each of these processes separately.

I conducted an experiment to examine how small precipitation events, species composition, time (daily and seasonal), and the interactions between them influence soil pools of C and N. I repeated the experiment, which took place over four to six days, three times throughout the growing season, in order to determine the seasonal and daily effect of plant community composition and small artificial rainfall events (5 mm) on soil pools of labile and microbial C and N, in *B. tectorum* dominated and native C3-C4 perennial grass communities. My hypotheses were:

(1) Time matters: soil pools of labile carbon and nitrogen (inorganic N, DOC and DON) and microbial biomass C and N change significantly at both daily and monthly time scales due to the high turnover rate of these pools and associated responsiveness to current soil conditions (temperature, moisture, and microbial substrate availability).

(2) Implicit in hypothesis is that DON is an important pool of labile N. DON is an important pool for both microbes (a substrate for microbial growth) and potentially important for plants (potential source of N). While pools of DON have been shown to be a substantial fraction of labile N in many ecosystems (e.g., (Jones et al. 2004), its importance in semi-arid ecosystems is unclear.

With this in mind, I hypothesized that DON would be a significant fraction of extractable soil N (relative to inorganic N pool size).

(3) As are many plants and soil processes in semi-arid climates, soil pools of labile and microbial C and N are water limited, and will therefore respond significantly to water additions on average and/or on a daily time scale. In addition to this general hypothesis, I made several specific predictions:

   a. DayCent predicts that inorganic N pools will decrease initially (due to plant uptake) and then increase linearly as soils dry and microbial activity increases, increasing decomposition and N mineralization.
   b. Microbial biomass C and N will increase with water additions (on average and initially) due to release from water limitation, but decrease with time since event as soils dry.
   c. C/N ratios will decrease, due to increased uptake of N with increased accessibility (due to water additions) or as a result of becoming more bacterially (rather than fungal) dominated (due to release from water limitation), and increase with time since event as soils dry and N becomes less accessible and/or bacterial activity declines due to water limitation.
   d. DOC and DON will increase on average, due to litter leaching, increases in microbial activity (decomposition), and/or soil structure disruption.

(4) *B. tectorum* invasion changes the size and response of soil pools of labile and microbial C and N to water additions. The responses of soil pools beneath each species group (*B. tectorum* versus C3-C4 plant communities) will diverge with month due to phenological differences; C4 grasses remain active

late in the growing season while *B. tectorum*, a C3 annual grass, becomes inactive and senesces. After *B. tectorum* senesces, microbial and soil N pools in *B. tectorum* dominated plots should be larger than in soils in adjacent perennial grass plots due to reductions in plant uptake and competition for soil resources.

Lastly, I examine the potential for interactions between changes in the timing of small rainfall events (climate change) and plant community invasion (*B. tectorum*).

Methods

Site selection and experimental design

I conducted this experiment in the ponderosa pine-grassland ecotone of the foothills of the Rocky Mountains (Horsetooth Mountain Park; Larimer County Parks, Larimer County, Colorado). The mean annual precipitation (MAP) of nearby weather stations is 430 mm and mean annual temperature (MAT) is 8.5 °C (NCDC 2005).

I randomly selected 4 sites from all potential south-facing sites that contained a mix of native C3 and C4 grasses that were free of *B. tectorum*, as well as adjacent areas dominated by *B. tectorum*. Native plots at sites 2-4 were dominated by a mixture of *Stipa comata*, *Bouteloua gracilis*, and *Andropogon gerardii*. The native plots at site 1 were dominated by a mixture of *Stipa comata*, *Stipa robusta*, *Bouteloua gracilis*, and *Bouteloua curtipendulum*. All sites were located between 1768-1817 m in elevation.

In June, I randomly selected 12 plots 1 m^2 at each site: half of the plots were established in native bunchgrass vegetation (C3/C4 mix) and half in areas dominated by > 80% *Bromus tectorum*. Of these plots, two from each vegetation type were randomly assigned to each experiment date. One of the two plots in each vegetation type was then randomly selected as the control. The other was assigned to the water treatment. At the beginning of each experiment, I applied 5mm of water to each treatment plot in the early morning (one in each vegetation type; two plots per site, a total of eight plots received water treatments). I conducted the experiment three times: in June, July, and August 2003.

Six hours after each water addition, and each day thereafter for four days in June and six days in July and August, I collected four soil samples from each plot with a 5 cm diameter core, from 0 – 5 cm depth. I transported soil samples back to the lab where they were processed and extracted within 6 hours of collection. Soils were mixed, sieved to remove large debris and gravel (#10, 2 mm sieve), and analyzed for gravimetric water content, extractable inorganic nitrogen, extractable dissolved organic carbon and nitrogen (DOC and DON), and microbial biomass carbon and nitrogen by the cholorform fumigation extraction method (Brookes et al. 1985). From each sample, I extracted a 20 g subsample with 100 mL of 0.5 M K_2SO_4. I fumigated another 20 g subsample with chloroform for 5 days and then extracted it with 0.5 M K_2SO_4. I analyzed both extracts for total organic carbon (extractable DOC) and total N using a Shimadzu DOC/TN analyzer (Shimadzu, Columbia, MD, USA). Microbial biomass C and N were calculated using a K_{ec} of 0.45 (Beck et al. 1997) and a K_{en} of 0.54 (Brookes et al. 1985). I analyzed nonfumigated extracts for inorganic N using an Alpkem autoanalyzer (Alpkem, College Station, TX). DON was calculated as the difference between total N and inorganic N.

I also analyzed soils from each site for texture using the hydrometer method (Day 1965). On average, all sites had sandy loam soils, with between 60-79% sand and 13-24% clay. There were no significant differences between native and exotic plots at the four sites in percent sand or clay content (paired t-test, all $P > 0.4$).

The 5 mm water addition treatments significantly raised percent soil water (0-5 cm) each month, with percent water declining with each day after the treatment (Table 4.1; Figure 4.2 and 4.3). There were no natural precipitation events during the three study periods. Most of the variation in percent soil water ($R^2 = 0.8413$) was explained by water treatment, plant community type, and time (day or month). Very little of the variation in soil water content was explained by other (unmeasured) site and plot differences (< 9 %; Table 4.1, Figure 4.3).

Data Analysis

I tested for the effects of plant community, water, and time (month and day), on DON, DOC, inorganic N, and microbial biomass C and N. I analyzed the results using a mixed model ANOVA with repeated measures (day) and site and plot as random effects (proc MIXED ANOVA, SAS). There were no significant 2-, 3-, or 4-way interactions between the random and fixed effects (plant community (pc), water (w), month (mo) and day (d)), so I did not include these effects in the final analysis ANOVA. I used Akaike's Information Criterion, adjusted for small sample size (AICc), to choose the most appropriate covariance structure for each of the response variables (autoregressive, autoregressive with heterogeneous variance, or compound symmetry). In all cases, either autoregressive or autoregressive with heterogeneous variance was selected (Table 4.1).

I calculated the R^2 for the ANOVA for each response variable with and without the random effects of site and plot. The difference between these values indicates the proportion of the variance that is due to random, and thus unpredictable, site and plot effects. The R^2 calculated in the absence of random effects is more closely related to the proportion of the variance that is predictable, i.e., that is explained by the applied treatments.

To examine the dynamics of soil pools of DON, DOC, inorganic N, and microbial C and N over all three months, as well as over the full course of sampled days, I analyzed the data in two separate sets: (1) All three months were analyzed over the first 4 days (because the June experiment was only run for 4 days); and (2) July and August were analyzed over all six days. However, the second analysis (6 days over 2 months) did not change the overall results except to remove some of month interactions. This was probably because June was wetter and cooler and thus not very similar to July and August, but July and August were both dry and warm. I therefore do not discuss the results of this analysis below.

Results

DON fraction of labile N

On average, soil DON was between 83 and 94% of extractable N (DON + inorganic N). Inorganic N and DON in control plots averaged 0.056 g N m^{-2} and 0.47 g N m^{-2}, respectively, over all three months. Average growing season levels of N and DON in the water treatment plots were similar, with DON averaging 0.44 g N m^{-2}, nearly 7 times greater than levels of inorganic N (0.065 g N m^{-2}).

The effect of time

All pools of labile and microbial biomass changed significantly on monthly time scales, and all pools except ammonium fluctuated significantly at daily time scales (Table 4.1). Inorganic N fluctuated significantly on a monthly time scale, increasing later in the growing season, but only nitrate-N changed significantly on daily time scales (Figure 4.4a-b, 4.5a-c). Although both ammonium and nitrate had significant interactions between day and month, this effect was stronger for nitrate, again suggesting that daily time scales are more important to explaining variation in nitrate than it was for explaining variation in ammonium, and that the way that nitrate changes by day changes during the growing season (significant month*day interaction; Table 4.1).

DON and DOC also changed significantly on monthly time scales, increasing throughout the growing season (Figure 4.4c and 4.6). Daily variation was also significant, and changed depending on time during the growing season (significant day*month interaction; Figure 4.6 d-f, Table 4.1).

Microbial biomass C and N decreased throughout the growing season (Figure 4.7a-b; Table 4.1). Both biomass C and N changed significantly with day, and daily variation changed with month (month*day interaction; Figure 4.8a-f). Microbial biomass C/N also changed significantly on daily and monthly times scales, with a month*day interaction, but C/N ratios increased throughout the growing season (Table 4.1, Figure 4.7c, Figure 4.8g-i).

The effect of water additions

Neither ammonium nor nitrate responded strongly to the water additions. However, nitrate had a significant three way interaction between water treatment, day, and month (Table 4.1), indicating that the water treatments did affect the daily levels of nitrate, but that the way water affected daily nitrate levels changed with month, increasing over (daily) time in June and August, but decreasing over time in July (Figure 4.5a-c). Although not significant on a monthly basis, soils that experienced water treatments seemed to have more ammonium in June and less ammonium in July and August than unwatered treatments and slightly more nitrate in all months (Figure 4.4a-b).

DON was also unresponsive to water additions and while daily variation was significant, it was not related to water treatments (Table 4.1). Although the water treatment did not have a significant effect on DON overall, DON was slightly higher in water treatment soils than in control soils during June, and water treatments slightly decreased DON in the other two months, particularly under *B. tectorum* stands (Figure 4.4c).

Water treatments significantly affected DOC, microbial biomass pools of C and N, and microbial biomass C/N ratios. Water treatments decreased the amount of DOC beneath both *B. tectorum* and perennial grasses in all months (Table 4.1; Figure 4.6). DOC also varied significantly with day, but the direction of variation was largely independent of water treatments (no day*water interaction). Microbial biomass C and N increased in response to water additions by increasing within two days of the event, followed by daily decreases (Figures 4.7a-b and 4.8a-f).

Microbial biomass C/N ratios were reduced by water additions, although this effect was more pronounced later in the growing season, when conditions were drier and warmer (Table 4.1; Figures 4.7c and 4.8g-i). Through time after an event (daily), the C/N ratios of the microbial biomass in the treatment soils initially declined and then increased as treatment soils dried and the C/N ratios of microbial biomass in the treatment and control soils converged (a significant water*day effect; Table 4.1, Figure 4.8g-i). This pattern was very clear in July and August, but when soils were wetter in June, there is very little or no effect of water additions (a significant water*day*month effect; Table 4.1, Figure 4.8g-i).

The effect of plant community

Plant community explained more variation in labile N pools than did the water treatments, which did not significantly affect ammonium, nitrate, or DON (Table 4.1).

Ammonium, nitrate-N, and DON were all higher under *B. tectorum*, particularly during July and August when soils were drier (Figure 4.4). DOC was greater in soils beneath *B. tectorum* than beneath perennial grasses throughout the growing season (Figure 4.6).

Microbial biomass C was generally greater beneath *B. tectorum* than perennial grass stands, but this difference decreased with month (sp*mo interaction; Table 4.1, Figure 4.7a). The response of microbial N was very similar to that of microbial biomass C. Microbial N was greater beneath *B. tectorum* than under perennial grasses, particularly during the first two months (Table 4.1, Figure 4.7b). Plant community differences were also significant for microbial C/N, but this difference was only truly apparent in the later two months, when native grasses had microbial biomass with a higher C/N ratio than *B. tectorum* (Figures 4.7c and 4.8g-i). Although there was not a significant species by water interaction, the decrease in the microbial biomass C/N ratios appears somewhat larger beneath perennial grasses than beneath *B. tectorum*, and this difference increases with time during the growing season (Figure 4.8g-i).

Unmeasured site and plot differences (the influence of random effects)

Overall, water treatment, plant community type, time, and random site and plot effects (the ANOVA model) explained over 70% of the variation in all soil pools except nitrate ($R^2 = 46.8\%$; Table 4.1). However, between 11 - 26% of the explained variation was due to unmeasured differences between sites and plots (random effects; Table 4.1). This suggests that, although water, plant community, and time explain a relatively large proportion of the variation in these soil and microbial pools (34-77%; Table 4.1), I did not measure all of the variables that controlled the between plot or site differences I observed in these pools.

Discussion

DON as a fraction of labile N

DON made up a significant fraction of the labile soil N pool, comprising up to 94% of extractable N. If we consider, as Jones et al. (2004) suggests, that only 10% of DON is truly labile, DON would still make up an average of 45% of labile N, which is still a substantial portion of the total amount of labile N. Concurrent declines in DON (although not statistically significant) with water additions and increases in Microbial biomass C and N (and decreases in microbial biomass C/N ratios), suggest that at least a small fraction of this DON may be available to microbial populations.

Effects of time, water, and plant community on labile soil and microbial pools of C and N

All labile and microbial pools of C and N varied on daily and monthly time scales, except ammonium, which was largely unaffected by day (Table 4.1). This may be due to the inability of my measurements or current procedures to capture the short term scale of variability in ammonium pools, which may cycle more quickly than daily measurements can capture (Van Miegroet 1995). All pools exhibited daily trends that varied depending on the month they were measured (significant mo*day interactions), suggesting that single point or daily measurements confined to a short portion of the growing season may not accurately represent how these pools change over time.

Contrary to my expectations, inorganic N and DON pools were largely unaffected by small rainfall events (water treatment). Although not statistically significant in the model, pairwise comparison of within month means showed some trends for ammonium, which seemed to increase with water additions in June but decrease after water additions in July and August, perhaps due to increased microbial immobilization (Figure 4.4b). The overall lack of a response from the inorganic soil N pools may partially reflect the inability of plants to respond to and utilize events of this size to take up available inorganic soil N (Austin et al. 2004, Schwinning and Sala 2004).

In contrast, DOC and microbial pools were very responsive to water additions (Table 4.1). This is consistent with research that suggests that microbial communities are the first and may be, if the event is very small (wetting soils only shallowly), the only pool to respond to respond to rainfall events (Austin et al. 2004, Schwinning and Sala 2004). DOC levels did not increase as I predicted, but decreased with water additions in all months (Figure 4.6). Microbial pools (biomass C, biomass N, and C/N ratios) responded to water additions as I expected: microbial biomass C and N increased with water additions, while C/N ratios decreased. The water-induced growth of microbial biomass C could explain coincident the decline in DOC with water additions. Combined with the somewhat lower (but statistically insignificant) levels of inorganic N and DON in the water treatment soils, the significant decrease in DOC could suggest that biomass is increasing through the utilization both of these of these soil pools. Overall, declines in DON with time and/or increases in microbial biomass may not be as obvious (or statistically significant) if only 10% of this pool is truly accessible to microbes (Jones et al. 2004).

Plant community type played a large role in explaining variation in all of the measured soil and microbial pools. Labile and microbial pools of C and N were all larger in soils beneath *B. tectorum* than beneath perennial grasses, suggesting that *B. tectorum* has a substantial influence on the size of these pools. Microbial biomass beneath perennial grasses had higher C/N ratios than biomass beneath *B. tectorum*. These results are consistent with research that has found soils under annual grasses *(Bromus japonicus* or *B. tectorum*) to have higher rates of nitrogen mineralization, higher levels of inorganic nitrogen, total nitrogen, soil microbial carbon and nitrogen, and soil respiration than soils beneath perennial bunchgrasses or shrubs (Bolton et al. 1990, Bolton et al. 1993, Vinton and Burke 1997).

Putting it together – fluctuations of soil and microbial pools in time and with treatment responses

The effects of water additions and species composition on soil and microbial pools of C and N changed throughout the growing season. However, timing, or seasonality, was more important for discovering how species composition affected labile and microbial pools of C and N.

DOC and microbial biomass C were responsive to water additions on average, with water decreasing and increasing these pools respectively, but daily dynamics were independent of the water treatment (no significant day*water interaction). Although labile pools of N were generally unresponsive to small water additions, what slight trends there were varied based on the month of the event (e.g., for nitrate with a significant w*mo*day interaction; Figures 4.4a and 4.5a-c). In July and August, DON and ammonium levels declined with water additions, but these trends were not statistically significant (Figure 4.4b-c).

Microbial Biomass N and C/N ratios were much more responsive to water additions than were labile pools. Water additions significantly altered daily variation in microbial biomass N and C/N ratios (day*water interaction), and this response often varied with time during the growing season. Microbial biomass C/N ratios became very responsive to water additions in July and August (significant w*mo*day interaction), when soils were warmer and drier than they were in June. This suggests that, when conditions were dry, small rainfall events either shifted the composition of the microbial community by increasing bacterial biomass over fungal biomass or increased the availability and uptake of N, which lowered the C/N ratio of microbial biomass. Although there was not a significant relationship between plant community and water treatments, this trend appears to be more pronounced beneath perennial grasses (Figure 4.8g-i).

Species composition had large effects on labile and microbial pools of C and N, but the effect of species composition on these pools often changed throughout the growing season. While labile pools of C and N were higher beneath *B. tectorum* than beneath perennial grasses throughout the growing season, the size of these pools, and often the differences between them, increased throughout the growing season as soils became warmer and drier and the plant communities senesced (Figures 4.4 and 4.6). This increase in labile pool sizes is clear across all months beneath *B. tectorum* but is only clear beneath perennial grasses in August, perhaps due to the early senescence of *B. tectorum* versus the later season decrease in activity and/or senescence of C3 and C4 grasses (Figure 4.4). These results are consistent with the results of Booth et al. (2003), who found that while inorganic N under perennial grasses and *B. tectorum* were similar in the spring, NO_3^- accumulated under *B. tectorum* after senescence.

Microbial pools of C and N were also larger in soils beneath *B. tectorum* than beneath perennial grasses, but pool size declined through the growing season (Figure 4.7). Although daily variation in labile soil or microbial pools did not depend on which plant community they were beneath, monthly variation in microbial pools did. Microbial pools of C and N were larger beneath *B. tectorum* stands than beneath perennial grasses, and the size of the difference between these pools beneath these communities became less pronounced as the growing season progressed (Figure 4.7a-b). Microbial biomass beneath perennial grasses had higher C/N ratios than biomass beneath *B. tectorum*, but this difference was not apparent until later in the growing season, as soils became drier and plant communities senesced. This difference in microbial C/N could suggest that perennial grasses may favor the development of fungal dominated communities. Alternatively, late in the growing season, soils beneath *B. tectorum* had higher levels of labile N (Figure 4.4) available for rapid immobilization by microbial populations reactivated by water additions.

Overall, the significant effect of plant community changed with month, and trends that were not apparent in one month, became very prominent at other periods in the growing season (e.g., nitrate, Figure 4.4a or microbial C/N, Figure 4.7c). This further supports the assertion that single point or very temporally constrained measurements may not capture potentially important differences or changes in soil properties with beneath different plant communities.

In this ecosystem, effects of small rainfall events and plant community characteristics on soil pools of labile and microbial C and N vary throughout the growing season. This suggests that plant phenology and/or seasonal change in environmental conditions probably have considerable influence on the daily and monthly dynamics of these pools.

Implications: changing the timing of small precipitation events and/or plant community type may interact to change ecosystem properties

My results suggest that increasing the amount of *B. tectorum* over perennial grass species could have several effects on ecosystem processes. Inorganic N was higher under *B. tectorum*, especially after *B. tectorum* senesced (reducing plant uptake) in June (Figure 4.4). As inorganic N levels increase, *B. tectorum* becomes a better competitor against native species such as *Bouteloua gracilis* (Lowe et al. 2003). In this way, *B. tectorum* could facilitate its own spread and domination of plant communities in this ecosystem. Alternatively, if *B. tectorum* increases, the resulting high levels of labile N during periods of low plant and microbial activity (July and August) could result in increased N losses due to gaseous losses or leaching and erosion during large late season rainfall events. Although relatively large (> 15 mm) events are common in this ecosystem during the late growing season (1-2 times a month per year in July and August; NCDC 2005), climate change-predicted increases in the occurrence of extreme (large) precipitation events (Gordon et al. 1992, Easterling et al. 2000, IPCC 2001) could exacerbate losses of labile N in *B. tectorum* dominated communities.

Finally, co-occurring changes in species composition and the distribution of small rainfall events may interact to affect microbial community composition and dynamics. Microbial pools were the most responsive to both species composition and rainfall events and the response these pools changed with the time of the growing season. Microbial pools and the response to water were larger beneath *B. tectorum* than beneath perennial grasses, particularly for microbial biomass N, Figures 4.7 and 4.8), but the size and response declined with month. Changing the distribution of small rainfall events throughout the growing season could therefore increase or decrease the overall response of the microbial community beneath *B. tectorum* to small events, relative to microbial communities beneath perennial grasses and the response that might occur during other months. Changing the seasonality of small rainfall events could therefore interact with changes in species composition to alter rates of ecosystem processes that are dependent on microbial biomass (e.g., decomposition and N mineralization).

My research suggests that investigation into how small events alter microbial community composition and associated processes (e.g., heterotrophic respiration or decomposition) on daily time scales throughout a growing season could shed light on how plant communities and changes in distribution or declines in small rainfall events may change ecosystem process rates. Additionally, investigation into how increasingly large rainfall events change the dynamics or size of soil pools of C and N throughout the growing season should aid in making predictions about how changes in precipitation regimes (such as increases in the frequency of large events) will interact to change ecosystem C and N storage and cycling. In short, if we can continue to further our knowledge about how important plant groups or species interact with precipitation events of variable size and timing to influence microbial communities and the availability and cycling of labile C and N, we may be able to better predict how changes in the timing of rainfall events or the invasion of a new species may affect the responses of an ecosystem.

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Table 4.1. Results of proc mixed repeated measure ANOVA with site and site*water*plant community*month (i.e., plot) as random effects and day as repeated measure. Fixed effects included day, month (mo), 5 mm water treatment (w), and plant community (pc; native C3 and C4 perennial grasses or Bromus tectorum). Response variables were percent water, nitrate nitrogen (N), ammonium-N, dissolved organic N (DON), dissolved organic carbon (DOC), microbial biomass C (MBC), microbial biomass N (MBN), and the C/N ratio of microbial biomass (MB C/N). Covariance structure was selected using AIC model selection and was chosen as autoregressive (AR(1)) or autoregressive with heterogeneous variance (ARH(1)) in all cases. Bold values are significant at a level of $p < 0.05$. R2 was estimated with and without random site and plot effects. The difference between these values is the proportion of the variance explained by unmeasured plot and site differences (random effects).

		F Values															R^2	R^2	**Proportion**
Variable	**Covariance Structure**	**water (w)**	**plant community (pc)**	**day (d)**	**month (mo)**	**w*pc**	**w*mo**	**pc*mo**	**w*d**	**pc*d**	**mo*d**	**w*pc*d**	**w*pc* mo**	**w*mo*d**	**pc*mo*d**	**w*pc* mo*d**	**with random effects**	**without random effects**	**of variation explained by random effects**
% water	AR(1)	**83.84**	**13.68**	**42**	**114.58**	0.01	1.05	**4.95**	**21.35**	0.28	**2.95**	0.82	0.11	0.34	1.15	0.26	0.9303	0.8413	0.089
Nitrate-N	ARH(1)	2.66	**15.28**	**12**	**22.26**	0.01	0.01	2.4	0.4	1.51	**11.1**	0.49	0.12	**2.42**	0.62	0.59	0.8053	0.587	0.2183
Ammonium-N	ARH(1)	0.42	**17.54**	1.4	**4.62**	2.12	2.12	0.17	2.21	0.95	**2.99**	1.19	3.5	0.45	1.23	1.31	0.468	0.3485	0.1195
DON	ARH(1)	0.43	**34.59**	**7.1**	**10.22**	0.02	2.92	0.03	1.4	0.81	**14.62**	1.14	2.34	0.25	0.58	1.05	0.7321	0.517	0.2151
DOC	ARH(1)	**5.44**	**30.08**	**8.1**	**3.5**	0.28	3.37	1.15	1.57	0.87	**14.05**	0.54	2.2	0.73	0.73	1.18	0.7379	0.4796	0.2583
MBC	AR(1)	**16.81**	**36.81**	**13**	**50.4**	2.35	1.05	**5.7**	2.4	1.15	**8.27**	0.72	1.76	1.24	0.62	0.25	0.8062	0.6861	0.1201
MBN	AR(1)	**2.3**	**38.03**	**19**	**83.52**	2.61	0.36	**4.66**	**5.96**	2.2	**7.53**	0.37	1.65	1.42	0.98	0.39	0.899	0.768	0.131
MB C/N	ARH(1)	**10.09**	**12.55**	**24**	**56.06**	0.75	2.85	**3.45**	**9.12**	0.21	**3.98**	1.24	1.8	**4.18**	0.18	1.38	0.9057	0.7072	0.1985

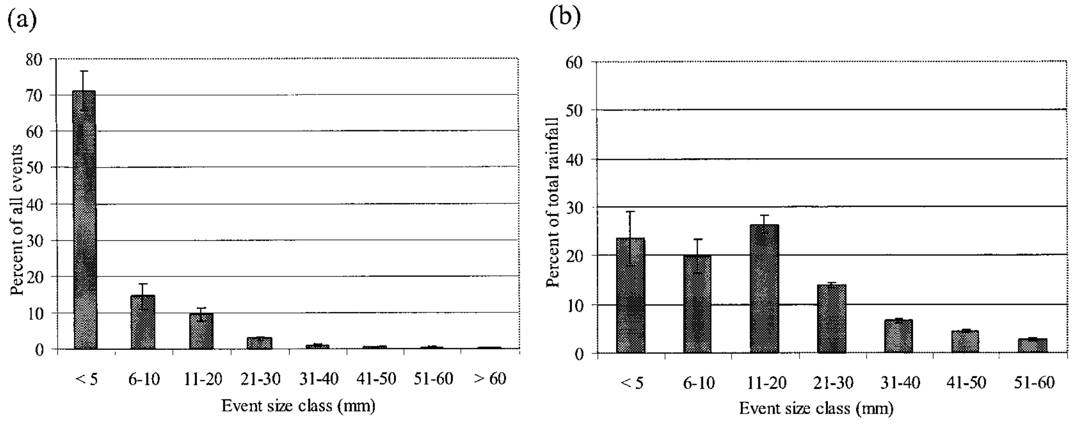

Figure 4.1. Precipitation patterns for eight sites in along northern Colorado's Front Range and foothills area in Larimer County (between 104 and 104 22'): (a) frequency of daily precipitation events in eight size classes and (b) percent of total rainfall in each size class for the same eight sites. Error bars are plus/minus one standard error.

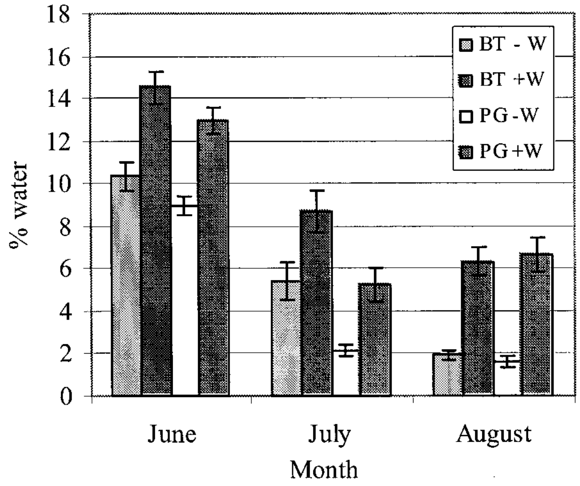

Figure 4.2. Average percent soil water per plant community (Bromus tectorum, *B. tectorum*, versus perennial C3 and C4 grasses, PG) and water treatment (additions, +W, versus control, -W) per month.

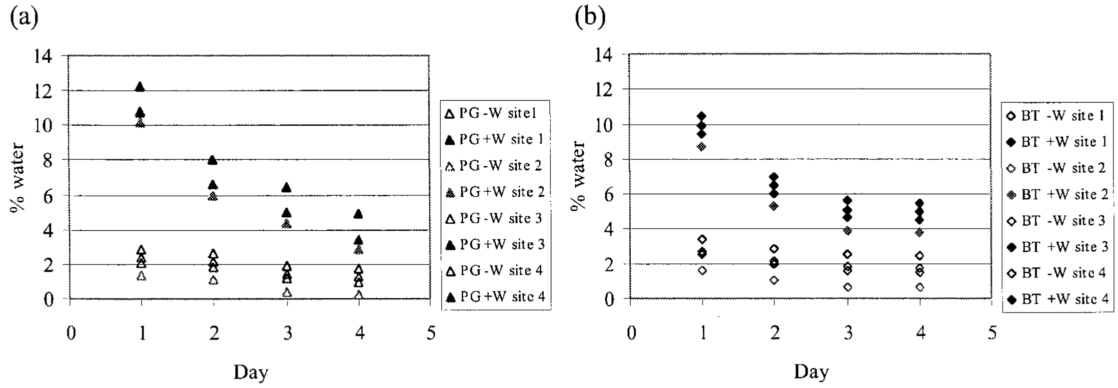

Figure 4.3. Daily fluctuations in August under perennial grasses (PG) and *B. tectorum* (BT) with and without water additions. Water additions increased soil water, which then decreased daily. Trend is the same for the months of June and July. Note that all sites respond similarly to the treatment or lack of treatment.

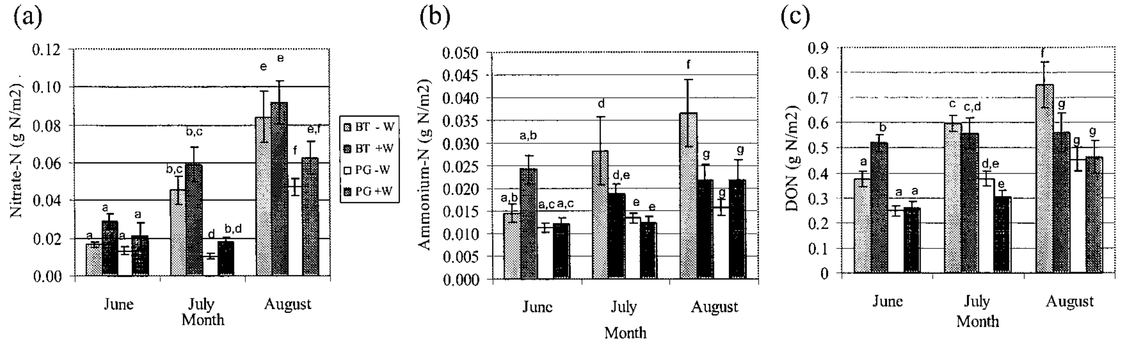

Figure 4.4. Mean (a) nitrate nitrogen (N) (b) ammonium-N and (c) dissolved organic N per treatment (plant community and water) per month. Letters denote significant differences (P<0.05). Mean comparisons are within month only.

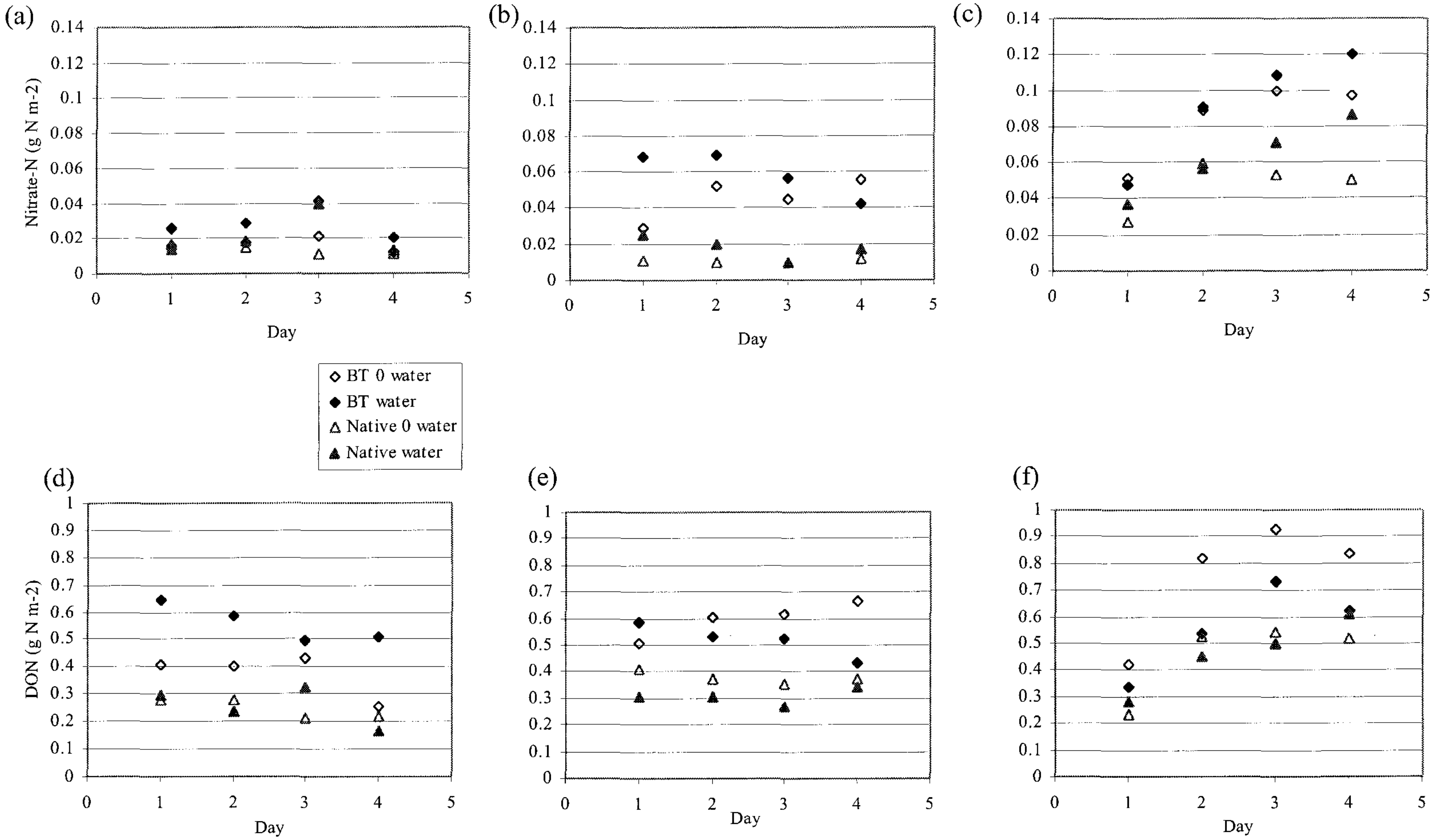

Figure 4.5. Daily fluctuations in labile N (inorganic and dissolved organic N): nitrate-N in (a) June (b) July and (c) August, and in dissolved organic N (DON) in (d) June (e) July and (f) August. Trends are shown without random effects (site and plot).

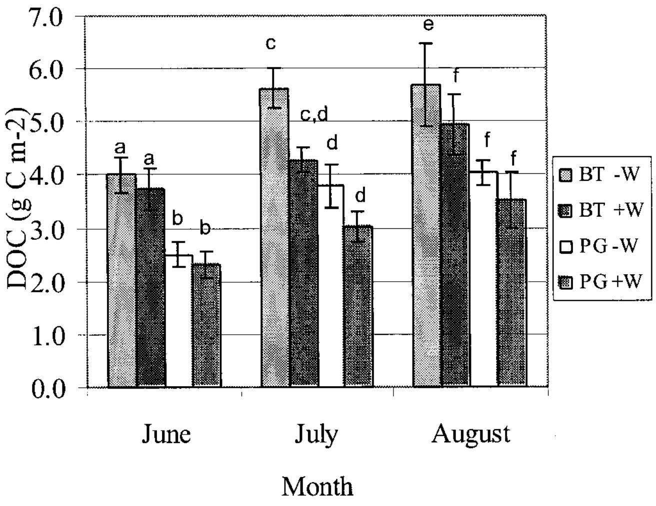

Figure 4.6. Average dissolved organic carbon (DOC) per plant community (Bromus tectorum, BT versus perennial grass, PG) treatment and water addition (+W) treatment versus control (-W) per month. Trends are shown without random effects. Letters denote significant differences (P<0.05). Mean comparisons are within month only.

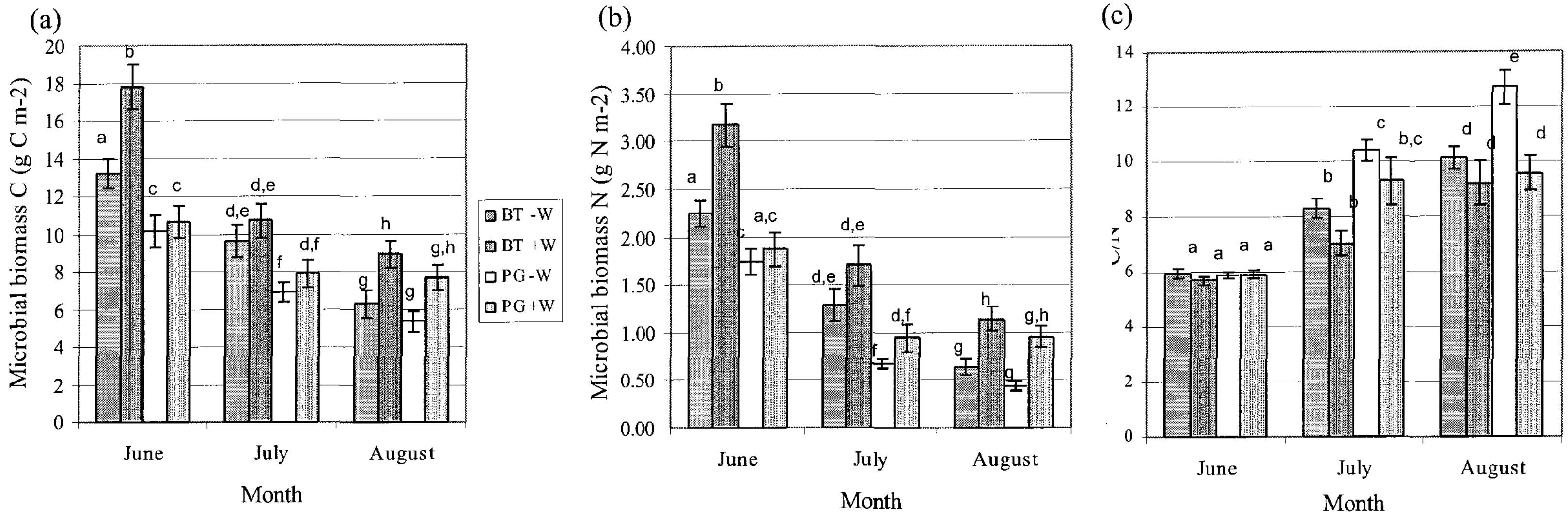

Figure 4.7. Average (a) micro microbial biomass, (b) microbial nitrogen (N), and (c) C/N ratio of microbial biomass per plant community (Bromus tectorum, BT versus perennial grass, PG) treatment and water addition (+W) treatment versus control (-W) per month. Trends are shown without random effects. Letters denote significant differences ($P<0.05$). Mean comparisons are within month only.

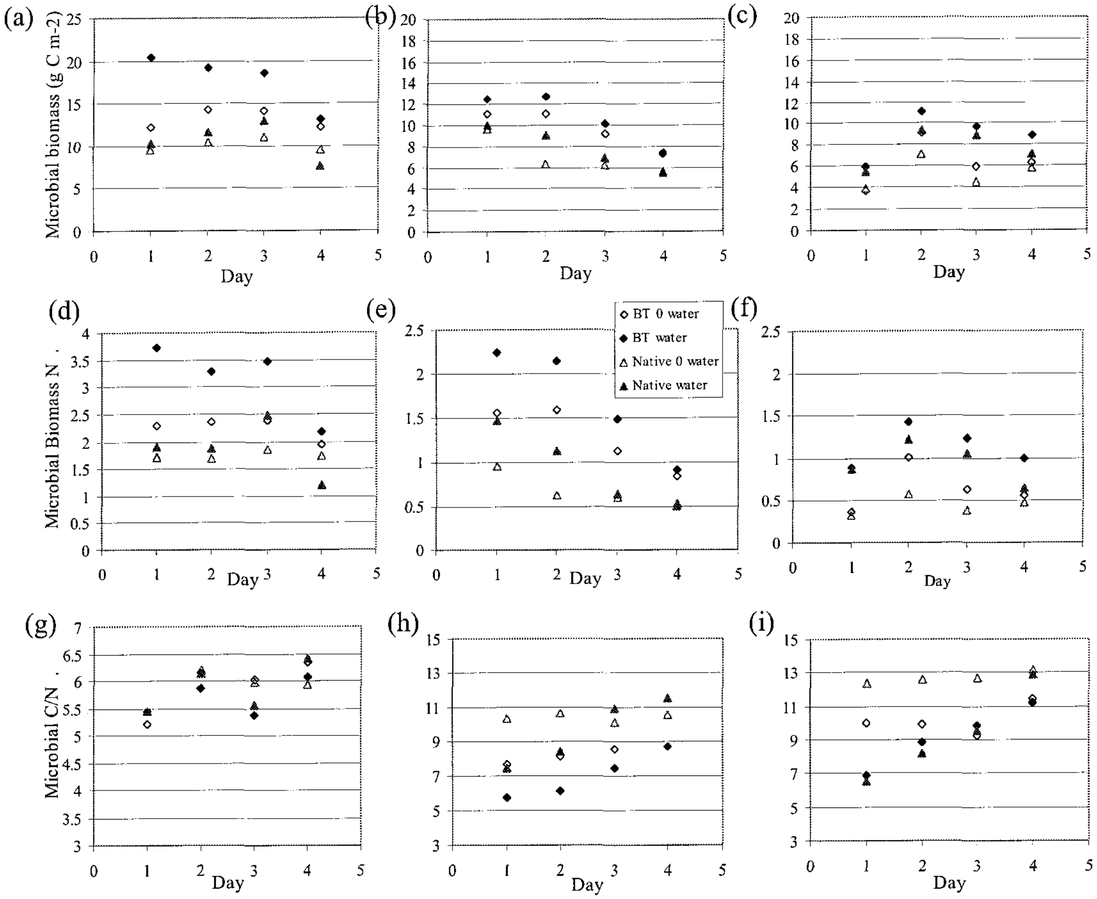

Figure 4.8. Daily fluctuations in microbial C and N pools: microbial biomass in (a) June (b) July and (c) August; microbial N in (d) June (e) July and (f) August; and microbial biomass C/N ratio in (g) June (h) July and (i) August. Trends are shown without random effects (site and plot). Note y-axis scale changes.

CHAPTER FIVE

CONCLUSION

Understanding the causes and consequences of exotic species invasion is of primary concern to both ecologists and land managers. One of the most consistent findings in invasion ecology is that disturbance increases the invasibility of communities (Burke and Grime 1996, Davis and Pelsor 2001, Gross et al. 2005). The ponderosa pine communities of Colorado's Front Range are subject to a wide range of disturbances, of both natural and human origin. The three studies I completed for my dissertation improve our current understanding of the causes and consequences of exotic species invasion, and provide potentially significant information for managing exotic invasion into the ponderosa pine forests of Colorado's Front Range.

In chapter two, I found that exotic species are successful in the ponderosa pine forests of Colorado's Front Range. In chapters two and three I examined the factors that influence the successful invasion of exotics into these communities. The results from these chapters suggest that resource availability is important to promoting exotic invasion. High light availability (low percent canopy) and high levels of soil nitrogen (N) (total in chapter two or available in chapter three) increased the richness (chapter two), cover (chapter two), and establishment (chapter three) of exotic species. The results of chapter three also identified available water as a potentially important co-limiting resource on exotic invasion.

Definitions of disturbance are quite diverse and include increased propagule pressure, increased resource availability, physical alteration of soil conditions, and plant mortality (Hobbs and Huenneke 1992, Huston 1994, Davis et al. 2000, Shea and Chesson 2002, Williamson and Harrison 2002, Larson 2003). My results coincide with a growing body of evidence that suggest complex interactions exist between various disturbance types and resource availabilities (as determined by climatic/environmental conditions) (King and Grace 2000, Becksted and Augspurger 2004, Huston 2004, Leishman and Thomson 2005). Furthermore, how do these disturbance types interact with one another?

In chapter two, I found that exotic richness was strongly influenced by accessibility from population centers (driving distance), but not by distance from trail or road. Conversely, distance to trail was the only important disturbance indicator for explaining variability in exotic species cover. This suggests that exotic richness is most affected by larger scale processes that affect the distribution of plant species throughout a landscape (i.e., historical and current land uses and accessibility), rather than by the effects of localized disturbances typically associated with roads and trails, while the reverse is true for exotic cover (Tyser and Worley 1992, Forman and Alexander 1998, Larson et al. 2001). Chapter three built on this result by showing that, in a particularly dry year, exotic plant establishment was favorably affected by resource availability (N and water), but not by small-scale resident plant mortality disturbances, even though this disturbance type increased levels of available N. This could imply that trails and roads influence exotic success by creating other types of disturbances (e.g., increased water availability from road runoff or soil disturbances). More likely, the effect of plant mortality has variable effects, depending on the current climate and availability of resources in the impacted community. The results of chapter three suggest that in this ecosystem, in dry years, disturbances that increase only N availability without also increasing water may not result in successful invasion, while a disturbance that increases both water and N in a dry year, or that increases N availability in a wet year, could have more dramatic consequences for exotic invasion. However, in chapter two I found that more fertile areas (where total soil N was greater) had higher exotic richness and cover, suggesting that disturbances that increase N availability over longer periods of time that encompass climatic variability (i.e., from N deposition or chronic fertilization) could result in more invadable communities.

Ultimately, my results suggest that attempts to control the invasion of exotic species may be best focused on (1) local disturbances that increase both water and N, that increase N in wet years, or that result in persistent increases in N, and (2) areas that are or will become easily accessible from established or developing population centers. Recently, propagule pressure has emerged as one of the best predictors of exotic species invasion (Lockwood et al. 2005). If more accessible areas are subject to higher levels of exotic propagules (Lonsdale 1999, Larson et al. 2001, Larson 2003), how do variable or increasing levels of propagule pressure interact with small scale disturbances such as plant mortality and/or soil disturbance, to affect exotic species invasion? Further research is needed to define the relationship between the accessibility of these natural areas and propagule pressure, as well as between propagule pressure and various physical disturbance types that may increase limiting plant resources.

Because invasions have been relatively successful in Colorado's Front Range ponderosa pine plant communities (chapter two), understanding the implications of exotic plant invasions is of at least equal importance to understanding its causes. If an invading species is significantly different (biologically speaking) from the resident species in phenology, structure, or responses to environmental variables, exotic dominance may result in changing the seasonal or daily dynamics of available nutrient pools (Ehrenfeld 2003). In chapter four I examined the consequences of one such plant invasion: the successful invasion of *B. tectorum* into the understory of ponderosa pine plant communities. My results showed that the seasonal availabilities of dissolved organic carbon (C), dissolved organic N, inorganic N, microbial carbon, and microbial N in soils beneath stands of *B. tectorum* were different (and greater) than in soils beneath stands of C3 and C4 perennial grasses.

The results of chapter four also suggest that there could be complex interactions between various human-influenced environmental changes; in this case between the invasion of *B. tectorum* and changes in the distribution of small rainfall events. Small water additions had variable effects on microbial N and C/N, depending on the time within the growing season and the species composition of the community. In other words, the effect of a small water addition increased or decreased when compared to either other months of the year (in the same plant community) or the native plant community (in the same month). This suggests that invasion of *B. tectorum* could interact with changes in the distribution of rainfall events to alter microbial processes in this ecosystem.

The overall goal of my dissertation was to provide ecological insights into the causes and consequences of exotic plant species invasion. My conclusions suggest that complex interactions between environmental conditions and various disturbance types may act to regulate the invasibility of a given community through space and/or time (given environmental variability). Furthermore, the consequences of successful invasion may also interact with environmental change to result in unanticipated changes in ecosystem functioning. Research that addresses the interactions between climatic variables, resources availabilities and dynamics, disturbance types, and the causes and consequences of successful species establishment and spread will hopefully increase our ability to understand, predict, and manage these complex events.

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