DISSERTATION

THE INFLUENCE OF CLIMATE, SOILS, AND LAND-USE ON PRIMARY PRODUCTIVITY AND CHEATGRASS INVASION IN SEMI-ARID ECOSYSTEMS

Submitted by
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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JOHN B. BRADFORD ENTITLED "THE INFLUENCE OF CLIMATE, SOILS AND LAND-USE ON PRIMARY PRODUCTIVITY AND CHEATGRASS INVASION IN SEMI-ARID ECOSYSTEMS" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

THE INFLUENCE OF CLIMATE, SOILS, AND LAND-USE ON PRIMARY PRODUCTIVITY AND CHEATGRASS INVASION IN SEMI-ARID ECOSYSTEMS

Although the influence of climatic conditions and soil properties on ecosystem processes is well documented and generally accepted, land-use practices have only recently been recognized as a potential driver of ecosystem processes and global change. The overall goal of my dissertation is to increase our understanding of how land-use contributes to global change in semi-arid areas and to identify the importance of these contributions in relation to the known control exerted by climate and soils.

Agricultural cultivation is a pervasive and widespread driver of global change in the U.S. Great Plains, yet few studies have estimated the consequences of cultivation for regional ecosystem processes. I quantified the ongoing impact of cultivation on net primary production and revealed that cultivation has substantially increased aboveground production while slightly decreasing belowground production, that the consequences of cultivation are concentrated in certain areas, and that a few specific crops account for much of the change in primary production. Comparing the influence of cultivation on spatial and temporal production and phenology with the influence of climate, soils and weather variations indicated that, despite a substantial importance of cultivation, climate retains primary control over spatial variability whereas cultivation and weather have roughly equivalent influence over temporal variation in ecosystem processes.

In the Great Basin, where biological invasions are an important facilitator of global change, I studied the invasion of cheatgrass, an exotic annual grass from Asia that has successfully invaded much of the Western U.S. My results suggest that multi-date multi-spectral imagery has the potential to detect and map cheatgrass distribution, although the inclusion of land-use information did not contribute to detection success. This result may prove a useful tool in future management and research endeavors. I utilized simulation models to examine the importance of climate, soils, disturbance regime and propagule pressure on cheatgrass invasion and concluded that climate dictates areas that are susceptible to cheatgrass invasion, disturbance frequency influences how severe the invasion will be and propagule pressure determines the speed of invasion. These conclusions suggest a general framework for understanding the potential future of cheatgrass invasion in un-invaded areas.

This work provides insight into the importance of land-use as a driver of global change processes in semi-arid ecosystems. The combination of these studies characterizes the important contributions of land-use to primary production and biological invasions in semi-arid regions, but also confirms the central role that climatic conditions play in influencing these ecosystem processes. This work represents one of the first attempts to directly compare the importance of human activities and environmental conditions on ecosystem processes across large scales.

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CHAPTER 1: INTRODUCTION

One of the central goals of ecologists is to understand what controls ecosystem processes and vegetation dynamics. The importance of climatic conditions and soil properties is well documented and generally accepted. Land-use practices, on the other hand, have only recently been recognized as a potential control over large-scale processes. As the human population grows, our impact on ecosystem structure and function increases and quantifying how the consequences of this global environmental change is a rising challenge for ecosystem scientists. Vitousek (1994) and Vitousek et al. (1996) identified the major processes that facilitate global change as: elevated atmospheric carbon dioxide, land-use change and biological invasions. The overall goal of my dissertation is to increase our understanding of how land-use contributes to global change in semi-arid areas and to identify the importance of these contributions in relation to the known control exerted by climate and soils.

There are two main semi-arid regions in the United States: the Great Plains and the Great Basin. The U.S. Great Plains extends from the Canadian border into South Texas and from the Rocky Mountains to the eastern deciduous forests. The U.S. Great Basin includes the area between the Pacific Coastal mountains and the Rocky Mountains. The Great Plains consists of relatively homogeneous semi-arid areas (Lauenroth and Burke 1995), while the Great Basin contains numerous smaller mountain ranges that create climatic variations and consequently, heterogenous vegetation patterns (West 1983). Although these regions both receive limited precipitation and are considered semi-arid, the seasonal timing of precipitation varies between the regions and this difference has a dramatic influence on the vegetation. The Great Plains receives precipitation primarily in the summer and its vegetation is dominated by warm season perennial grasses (Sims and Risser 2000). By contrast, precipitation in the Great Basin occurs mainly during fall, winter and spring months and vegetation consists largely of cool season perennial grasses and shrubs (West and Young 2000).

These climatic differences cause differences between these regions in their susceptibility to processes that facilitate global change. Summer precipitation in the Great Plains creates excellent conditions for agricultural cultivation. Consequently, the Great Plains is one of the most heavily cultivated areas in the world, with as much as 80% cropped in some counties and only 2% undisturbed areas throughout the region (Hannah et al. 1995). Cropping not only impacts vegetation composition, but can also alter carbon cycling rates, which, over a large area like the Great Plains, have the potential to influence the global carbon cycle. As a consequence, agricultural cultivation and its consequences on carbon cycling is likely the most consistent and widespread facilitator of global change in the Great Plains. In the Great Basin, cultivation is not as pervasive but, like many areas with primarily winter precipitation, the Great Basin has experienced remarkably widespread biological invasions that have had a dramatic effect on the native vegetation composition and functioning (West and Young 2000). Consequently, invasive species are probably the most important driver of global change in the Great Basin.

The overall goal of my dissertation is to examine the role of climate, soil and land-use on primary production in the Great Plains and biological invasions in the Great Basin. For the Great Plains, I quantify the impact of agricultural cultivation on net primary production and examine the relative importance of land-use practices relative to climate soil and weather. I compile 11 years of primary productivity and cultivation data for 630 counties to examine how regional primary production has been altered by cultivation. To generate spatial and temporal data of primary production at large scales, I develop estimates of grassland and cropland light use efficiency (**APPENDIX 1**) and combine them with remotely sensed measurements of photosynthetic activity. My objective for **CHAPTER 2** is to quantify the total regional consequences of cultivation for primary production, characterize specific areas within the Great Plains that have especially modified primary production, and identify particular crops that have the greatest impact on primary production. In **CHAPTER 3** I include climate, soil and weather observations in the dataset and my objective is to characterize the relative influence of agricultural cultivation on net primary production relative to the well-documented influence of climatic conditions, soil properties and weather patterns. This process involves dividing the observed variability in net primary productivity into spatial and temporal domains, and then further partitioning the variance into components that can be attributed to climate, soil, weather and land-use patterns. Variance partitioning and statistical modeling provides insight into the controls over ecosystem processes at large scale and represents a rare attempt to directly compare the importance of human land-use practices with naturally occurring conditions like climate.

In the Great Basin, I examine interactions between climate, soil, land-use and one particularly widespread invasive plant. The purpose of these studies is to determine the utility of remote sensing as a cheatgrass detection tool and to examine how climate, soil and land-use influence cheatgrass invasion. Cheatgrass (*Bromus tectorum L.*) is a cool season annual grass originally from Asia (Nowak and Mack 2001) that has successfully invaded huge parts of the Great Basin, causing dramatic modifications to vegetation composition (Knick and Rotenberry 1997, Anderson and Inouye 2000) and disturbance regimes (Meloza and Nowak 1991, D'Antonio and Vitousek 1992).

Environmental conditions exert strong control over the range and abundance of plant species. Plant distributions are dictated at large scales by patterns of precipitation and temperature and at smaller scales by soil, topographic and microclimatic conditions (Aber and Melillo 1991). Land-use practices can also influence patterns of plant distribution and invasion by altering vegetation structure (Houghton 1999) and creating disturbance that allows non-native species to become established (Hobbs and Huenneke 1992). The contribution of land-use to cheatgrass invasion was observed as early as 1932 by Pickford, who noted that cheatgrass was essentially limited to either burned or grazed areas. Subsequent studies have further characterized a strong link between disturbance conditions and cheatgrass invasion (D'Antonio and Vitousek 1992, Knapp 1996).

Despite the importance of cheatgrass in ecosystems semi-arid ecosystems, few studies have attempted to relate cheatgrass invasion to abiotic conditions (climatic, edaphic, land-use, etc) and synthesize these results into a model that simulates cheatgrass invasion. In addition, remote sensing may be able to provide a valuable method for mapping locations where cheatgrass has, and has not, successfully invaded. Obtaining accurate, reliable distribution information at large-scales is an essential first step to understandi how and why cheatgrass achieves invasive success. In **CHAPTER 4** my objective is to examine the possibility of utilizing optical remote sensing techniques to identify cheatgrass. Compared to native plants, cheatgrass displays a relatively early phenology (Thill et al. 1984) and this study employs multiple images throughout the growing season to detect cheatgrass. My objective in **CHAPTER 5** is to characterize the importance of climatic conditions, soil properties, disturbance regimes and propagule pressure on cheatgrass invasion. This chapter utilizes simulation models to estimate temporal dynamics of soil water potential and plant competition at three sites. The first two locations are well-studied research sites: one invaded area in the Great Basin and one uninvaded area in the Great Plains. These sites provide excellent validation information to confirm model predictions. The third location is a research site in Argentine Patagonia where cheatgrass has been observed but has not seriously invaded despite very similar climatic conditions and native vegetation to the Great Basin. Comparison of predicted invasion patterns between these locations increases understanding about how climate and soil can influence invasion, generates hypotheses about the potential importance of disturbance and popagule pressure for facilitating invasion, and provides insight into the potential future of cheatgrass invasion in Patagonia.

The combination of these studies provides insight into the general contribution of land-use to global change processes in the Western U.S. By including climate and soil properties in these analyses, I am able to expand my conclusions to include comparison of the importance of land-use relative to existing environmental conditions.

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CHAPTER 2: THE IMPACT OF CROPPING ON PRIMARY PRODUCTION IN THE U.S. GREAT PLAINS.

ABSTRACT

Land use and altered carbon dynamics are two of the primary components of global change. Consequently, the effect of land use on carbon cycling is a crucial issue in regional scale biogeochemistry. Previous studies have shown that climate and soil conditions control net primary production (NPP) at regional scales, and that agricultural land-use can influence NPP at local scales through altered water availability and carbon allocation patterns. However, few studies have attempted to quantify the effect of cultivation on NPP at regional scales, and no studies have examined this relationship for the most heavily cultivated region of the U.S.: the Great Plains. I quantified current regional above- and belowground productivity (including cultivation) for nine years on a county basis from two sources: 1) USDA agricultural census data and 2) STATSGO range site production values. By comparing these data with values of native vegetation NPP (pre-cultivation) derived from STATSGO, I estimated that cultivation is increasing regional NPP by approximately 10%, or 0.046 Pg Cyear$_{-1}$. In addition, I examined the relationship between cultivation of particular crops and NPP change between counties and characterized the influence of individual crops on primary productivity.

INTRODUCTION

Land use and altered carbon cycling are two major components of global change (Vitousek 1994). Land use practices often include dramatic modification of vegetation and are therefore one of the most direct and common ways that humans impact ecosystems (Houghton 1995, Houghton 1999). Cropping is a widespread component of land use, covering over 1.5 billion ha worldwide (Richards 1990). Although cropping has obvious effects on vegetation structure, it also influences ecosystem processes, including the magnitude and direction of the ongoing carbon flux between the atmosphere and the soil-vegetation system (Houghton et al. 1999). This flux of carbon (F_c) into the terrestrial biosphere can be simply expressed as:

$$F_c = NPP - D$$

where NPP is net primary production and D is decomposition. Although atmospheric circulation models can estimate regional F_c by examining patterns of carbon dioxide (e.g. Fan et al 1998), they provide no insight into the component processes. Understanding the influence of cropping on NPP and D is important because even relatively minor modifications of these fluxes may have substantial consequences on global carbon cycling when propagated through time and over vast cultivated areas. Subsequent alteration of the global carbon cycle can influence atmospheric carbon dioxide concentrations, providing potential positive or negative feedbacks to climate change.

Despite the potential impact of land use on ecosystem processes, few studies have attempted to quantify changes in long-term primary productivity of cultivated areas over large scales. Many regional-scale studies have focused on patterns in native plant production in relation to climatic and/or edaphic conditions (e.g. Lieth 1975, Sala et al

1988, Epstein et al 1997). Of the studies that have examined the relationship between land use and carbon cycling, most have either A) examined carbon release from initial land conversion (either into or out of cultivation) at large scales, B) quantified changes in carbon cycling processes at small scales or C) used ecological simulation models and/or remote sensing to estimate large-scale carbon cycling processes.

Studies of type A combine information about the amount of land converted with results about gain or loss of carbon (soil carbon or standing biomass) as a result of conversion (eg. Dale et al 1991, Houghton 1995, Dale 1997. Paustian et al. 1999.) For example, land conversion from native vegetation into cropping in the U.S. prior to 1945 is estimated to have released 27+-6 Pg of carbon, whereas subsequent abandonment, forest regrowth and fire suppression have sequestered approximately 2 PgC (Houghton et al 1999). Although this work provides insight into the initial impact of land conversion and subsequent carbon exchange, it does not help us to understand how land use practices influence the ongoing primary productivity in areas already converted. Only by quantifying how land use alters ecological processes long after conversion can we understand the continued impact of our land use legacies.

Studies of type B rely on site level measurements of productivity in cropped and uncropped comparisons to quantify the long-term changes in productivity. These results indicate that cropping in grasslands typically increases aboveground productivity (Buyanovsky et al 1987, Kucharik et al 2001), can decrease belowground productivity (D.P.Smith unpublished data), and almost always decreases soil carbon (reviewed by Burke et al. 1997). Although these studies provide valuable site level results and potential confirmation of larger scale studies, extrapolating these results to larger areas involves numerous scaling problems (Wiens 1989) and may ultimately require some estimates at multiple spatial scales (Wessman 1992). Understanding the influence of land use on global carbon cycling requires estimates at regional to global scales over at least several years and current methods of direct measurement only allow observations at relatively small scales.

Modeling and remote sensing exercises of type C have provided estimates of productivity at both global and regional scales (e.g. Parton et al 1993, Law and Waring, 1994, Field et al 1995, Moulin et al. 1998, Potter et al 1999). Potter (1993) used NDVI data constrained by weather observations to derive a global annual net primary productivity estimate of 56.4 PgC. Previously, these studies provided the only large-scale estimates of carbon cycling, and therefore the only means for quantifying the impact of land use on these processes. However, these results include major assumptions about scaling site level results (Wiens 1989) and have generally operated without validation of their large-scale estimates. In addition, these studies typically quantify processes under current conditions only, whereas understanding the ongoing impact of cropping on productivity requires accurate productivity estimates for current land-use patterns and estimates in the absence of cultivation.

With a growing worldwide population and subsequent increased need for food, cultivation is likely to increase in the future. Quantifying how cropping has modified the ongoing carbon fluxes at large scales and over long time periods is crucial for understanding the potential consequences of this widespread land use practice. In this study I quantified the relationship between cultivation and net primary productivity in the U.S. Great Plains by characterizing regional productivity both with and without cropping.

My specific objectives were to: 1) estimate regional net primary productivity and carbon allocation patterns in the absence of cropping, 2) include cropping information in these calculations to estimate current productivity and allocation, and 3) combine results from objectives 1 and 2 to quantify the influence of cropping on regional net primary productivity and 4) identify the direction and magnitude of influence of specific crops on productivity.

METHODS

Study site: Covering 23% of the contiguous U.S., the Great Plains region extends from the Canadian border to central Texas, and from the Rocky Mountains to approximately the 95th meridian. Annual precipitation occurs primarily during summer months, and varies from less than 400 mm in the west to approximately 1000 mm in the east. Mean annual temperature ranges from 3° to 21° C from north to south (Lauenroth and Burke 1995). The distribution of native plant communities is dictated by climatic conditions, and includes southern mixed prairie, shortgrass steppe, tallgrass prairie and northern mixed prairie (Lauenroth et al. 1999). Patterns of land-use follow the precipitation gradient, with primarily grazed native grassland and limited dryland and irrigated cropland in the west, wheat in the central part of the region and nearly contiguous cropland in the east.

For this study, I included counties that historically contained at least 70% of the following vegetation types: northern mixed grass prairie, shortgrass prairie, tallgrass prairie, tallgrass savanna, southern mixed grass prairie, desert savanna and floodplain forests. These restrictions identified 630 counties suitable for this study (Figure 2.1). I collected data for the years 1991-1999 for these counties.

Pre-cultivation productivity: Total net primary productivity (NPP) is the sum of aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP). Native ANPP estimates were derived from the USDA STATSGO database. NRCS has divided each state into "range sites", and for states in the western U.S. it has provided estimates of range site production based on measurements of aboveground biomass (SCS 1976). I entered these values and spatial locations into a GIS and used ARCINFO (ESRI 1996) to overlay a county map over the range site production map and calculate the area-weighted average range site production value for each county. Measuring BNPP involves quantifying root growth, and consequently is much more difficult than estimating ANPP (Lauenroth 2000). Although no widespread empirical BNPP data sources exist, recent work (Gill et al. 2002) has indicated that BNPP in grassland systems can be calculated from three other variables: maximum yearly instantaneous belowground biomass (BGB), maximum proportion of BGB that is alive during the year (liveBGB/BGB) and root turnover (T) according to the equation:

$$BNPP = BGB \times (\frac{liveBGB}{BGB}) \times T$$

Gill et al. used these relationships along with reported pairs of BNPP and ANPP values to generate equations to predict BNPP from ANPP and temperature in grasslands. Their results indicated that BGB, live BGB/BGB and T can be estimated from peak annual aboveground biomass (AGBIO) and mean annual temperature (MAT) as:

$$BGB = 79 \times AGBIO - 33.3(MAT + 10) + 1289$$

$$\frac{liveBGB}{BGB} = 0.6$$

$$T = 0.2884 \times e^{0.046 \times MAT}$$

I utilized these relationships to represent BGB, liveBGB/BGB, and T and calculated BNPP for each county. Since grassland ANPP in many areas can be equated to AGBIO (Lauenroth et al. 1986), we used our ANPP estimates as a surrogate for AGBIO. By dividing belowground production by aboveground production, I calculated a county-wide belowground to aboveground ratio that provides a simple indicator of how photosynthetic products are being allocated into plant components.

Current productivity: To quantify current productivity, I represented each county as a mixture of cropped areas and uncropped areas, which I assumed to be native vegetation. The USDA National Agricultural Statistics Service (NASS 1998) maintains records of acreage and economic yield for most crops produced in the U.S. Economic yield (ie. bushels or tons per unit area) were translated into ANPP and BNPP by using harvest index values (ratio of biomass harvested to total aboveground biomass) and resource allocation ratios (ratio of aboveground productivity to belowground productivity), respectively (e.g. Prince et al. 2001). I converted economic yield into biomass using information from Martin et al. (1976) and published harvest index values (Table 2.1) to calculate ANPP for cultivated areas. Since total county ANPP includes a mixture of cropped and uncropped areas, I calculated county ANPP as the area-weighted average of ANPP for each crop and native ANPP of the county in the absence of cropping (based on STATSGO data described above). To estimate whole county BNPP I estimated BNPP values for each crop and for native vegetation and calculated the area-weighted average.

I used published crop ANPP and BNPP values to determine allocation ratios for cultivated areas (Table 2.1) and utilized county ANPP and BNPP estimates from the pre-cultivation estimates above to estimate allocation for the remainder of the county. Total NPP is merely the sum of ANPP and BNPP.

Comparison of current and pre-cultivation productivity: Since the difference between my current and native estimates of productivity are entirely due to cropping practices, I calculated the effect of cropping on production in each county as current production minus native production. This result allowed me to examine both the spatial patterns and total magnitude of change in productivity, and integrated the effect of the proportion of the county cultivated and the effect of cropping a particular location on production. To further characterize the link between cropping and productivity change, I plotted change in ANPP, BNPP and NPP against cropping intensity for all counties. To quantify the current proportion of productivity that is derived from cropping, I compared NPP estimates from cropped areas with total current county NPP estimates for every county. Proportions for the entire region were obtained by summing cultivated NPP across the entire region and comparing it to current regional NPP.

Characterization of productivity change: To characterize the effect that specific crops have had on primary productivity, I performed separate multiple regressions with NPP, ANPP and BNPP as dependent variables and the proportion of the county planted in the five most common crops as independent variables. Corn, wheat, soybean, sorghum and hay were included in this analysis because they are the most commonly cultivated crops by area in the U.S. Great Plains. The crop coefficients produced by this process allowed me to identify both the direction of the influence that each crop has on productivity (positive sign indicates that the crop increases productivity and negative sign suggests that the crop decreases productivity.) and the magnitude of the influence (since the crop variables are all proportions of the county, the size of the coefficients indicate the magnitude of the effect.)

RESULTS

Pre-cultivation productivity: Pre-cultivation county ANPP estimates averaged 141 gC/m^2 and ranged from 39 gC/m^2 in the western part of the Great Plains to 336 gC/m^2 in the east (Figure 2.2: A, Table 2.2). Annual ANPP of native vegetation for the region was estimated at 0.253 PgC/yr. Estimates of pre-cultivation BNPP averaged 115 gC/m^2 and ranged from 86 gC/m^2 for counties in the southwest to 165 gC/m^2 in the eastern part of the region (Figure 2.2: D). I estimated yearly regional BNPP as 0.208 PgC/yr. Combining native ANPP and BNPP produced native NPP estimates averaging 256 gC/m^2 and ranging from 125 gC/m2 to 501 gC/m^2 with a yearly regional NPP estimate of 0.461 PgC/yr. As expected in water-limited systems, pre-cultivation NPP patterns were strongly linked to precipitation (Figure 2.3: A) and generally increased from west to east (Figure 2.2: G).

Current productivity: My estimates of current county ANPP averaged 177 gC/m^2 with a range of 42 to 620 gC/m^2 (Fig 2: C) and displayed spatial patterns that generally increase with precipitation from west to east. However, precipitation had a much weaker relationship with current NPP than it did with native NPP (Figure 2.3: B). County values of current ANPP combined to estimate a regional yearly ANPP of 0.319 PgC/yr. Current BNPP estimates ranged from 59 to 157 gC/m^2, averaged 105 gC/m2, and generally increased from southwest to northeast (Figure 2.2 E, F). Summing county BNPP results over the entire region yielded regional annual BNPP estimate of 0.188 PgC/yr. NPP estimates under current conditions averaged 282 gC/m^2 and ranged from 129 to 749 gC/m^2. (Figure 2.2: H, I). Over the entire region, I estimated current yearly NPP as 0.507 PgC/yr. My data indicate that 25.1% of this region is currently cropped, and that the percent of primary productivity accounted for by cropping for individual counties ranges between 0 and 95% and the regional total is 0.173 PgC/yr, or 34% of current productivity (Figure 2.4).

Comparison between pre-cultivation and current productivity:

Comparing county values of total current productivity with and without cropping suggested that cropping has had more positive than negative influences on carbon uptake (Figure 2.5). Examining aboveground productivity estimates from current crop statistics and native vegetation indicated that cropping has increased ANPP by an average of 37gC/m^2 with a minimum of –36 and maximum of 408gC/m^2. However, my results suggested a negative effect of cropping on BNPP, with an average change of -11 gC/m^2 (-62 – 23 g/m2). ANPP and BNPP combined to produce a positive effect on total NPP averaging 26 gC/m^2 (-86 – 411 g/m2) (Table 2.2). Not surprisingly, heavily cropped counties in the central part of the region displayed the greatest change (Figure 2.2 B, H.). For the calculations used in this study, I assumed uncultivated areas to be native vegetation, so the maximum potential change in productivity is related to the proportion of the county that is cropped. Consequently, counties with a high proportion of cropping (Figure 2.1) had a commensurately high potential for altered productivity, in the form of increased ANPP or decreased BNPP (Figure 2.6). The positive effect of cropping on ANPP and negative effect on BNPP combine to alter carbon allocation patterns to favor aboveground production. This result is especially evident in heavily cropped counties in the north-east part of the U.S. Great Plains (Figure 2.7). Combining all county values indicates a regional yearly increase of 0.066 PgC/yr for ANPP, decrease of 0.020 PgC/yr for BNPP and at increase of 0.046 PgC/yr for NPP.

Characterization of productivity change: All five of the major crops (corn, wheat, soybean, sorghum and hay) were significantly related to the estimated change in ANPP, BNPP and NPP, with $p<0.01$ in all cases except sorghum and NPP (Table 2.3). The complete models, which include all five crops and an intercept, explained 89% of the variance in ANPP change, 74% of the variance in BNPP change and 83% of the NPP change. Corn, wheat and sorghum are all positively related to ANPP change, with corn having the largest effect, followed by sorghum. Soybean and hay both have modest negative effects on ANPP (Table 2.3, A). BNPP change has small positive relationships with both corn and hay, but has negative relationships of larger magnitude with soybean, sorghum and wheat (Table 2.3, B). Total NPP change shows a very large positive correlation with corn, and smaller positive effects of sorghum and wheat (Table 2.3, C). On the other hand, NPP is negatively related to soybean and hay, with soybean indicating a large negative effect and hay a much smaller effect.

DISCUSSION

I compared estimates of current NPP and NPP in the absence of cropping to determine the ongoing impact of cropping on primary production in the U.S. Great Plains. I estimated that cultivation has increased ANPP by 0.066 PgC/yr, decreased BNPP by 0.020 PgC/yr, and increased NPP by 0.046 PgC/yr. These estimates represent a 26% increase in ANPP, a 10% decrease in BNPP and a 10% increase in total NPP. By comparison, estimates of the net carbon sink (net primary production minus decomposition) are 0.3-0.6 PgC/yr for the conterminous U.S. (Pacala, et al. 2001.)

My estimates of both native and current ANPP values and spatial patterns are consistent with prior studies of ANPP for native vegetation in the Great Plains (Sala 1988, Epstein et al. 1997, Lauenroth et al. 1999.) Similar to previous studies, I observed a positive linear relationship between precipitation and ANPP for grassland areas (Lauenroth 1979). The existence of a relationship between precipitation and current ANPP suggests that precipitation is still an important determinant of production, but the fact that the relationship is weaker than under native conditions indicates that cultivation is at least partially removing these grassland ecosystems from climatic constraints to productivity. My BNPP estimates are also consistent with empirical grassland BNPP measurements (reviewed by Gill et al. 2002). My NPP values are very similar to those of Prince et al. (2001), who also used crop-statistics to estimate production for counties in the eastern part of this region. Comparing these results to previous site level studies is inherently difficult because values from this study represent entire counties containing diverse land use types, whereas other studies typically measure NPP for specific sites within a county that may represent one or a few land use types. Lauenroth et al (2000) calculated ANPP of for winter wheat in 19 counties across a transect between northeast Colorado and northern Kansas and estimated ANPP at approximately 150gC/m2. My whole-county estimates for the same 19 counties averaged 144gC/m2; slightly lower because I included uncropped areas which are likely to have slightly lower ANPP.

My results indicate that many of the counties with especially large changes in primary production (Figures 2.5 and 2.6) and high current NPP relative to mean annual precipitation (Figure 2.3 B) are counties with substantial irrigation in cropped areas. This suggests that irrigation may be accounting for much of the change in primary productivity as a consequence of cropping practices. In semi-arid areas, water availability is crucially important for vegetation dynamics (Noy-Meir 1973) so it isn't surprising that widespread irrigation elevates primary production. Although my analysis didn't explicitly address the affects of fertilization, it is also reasonable to expect that fertilizer additions in cropped areas may contribute to my observations of increased net primary productivity.

My results suggest that 34% of the total primary productivity in this region is now accounted for by cultivation. Global estimates suggest that approximately one third of total primary production is utilized by all human activities (Vitousek et al 1986). However, more recent analyses of uncertainty have indicated that the actual value may lie somewhere between 10% and 55% and have identified large-scale agricultural production as a primary source of the uncertainty (Rojstaczer et al. 2001). My results provide a more accurate estimate of the fraction of regional primary production accounted for by cropping in this region. However, my estimate does not consider the primary production that is utilized by livestock grazing, a nearly ubiquitous practice in much of the uncultivated U.S. Great Plains, or other human endeavors. Consequently, I expect the actual value of total primary productivity appropriated by humans to be substantially greater than 34% for the U.S. Great Plains.

In addition to modifications of total primary production, my results indicate a large-scale alteration of carbon allocation patterns to favor aboveground biomass. This modification of allocation patterns as a result of cultivation has been previously observed at small scales (D.P. Smith, unpublished data) and may have consequences for long-term carbon storage of different decomposition rates for aboveground vs. belowground litter.

The relationships between specific crops and changes in productivity are consistent with expectations based on life history strategies and previous results. Corn is one of the most productive cereal crops grown in this region (Goudriaan et al. 2001), is a frequent choice for irrigated fields, and is therefore likely to cause increased productivity aboveground and total productivity. In the western part of the region, irrigation is primarily concentrated on corn crops, because these have the highest potential for economic return. Since hay plants are perennial and thus likely to invest substantial resources in belowground structures, it is logical to expect hay to have minimal impact on both ANPP and BNPP. Soybean, sorghum and wheat have intermediate biomass production, are not as commonly irrigated and because they are annuals they are unlikely to invest substantial resources belowground. Thus, the observed negative relationships between these crops and BNPP are not surprising. The positive relationship between both sorghum and wheat and ANPP is likely a consequence of these crops allocating most of their growth to aboveground structures and taking advantage of fertilization.

Soybean, on the other hand, has high energy content in the yield component and consequently has relatively small biomass production (Eastin et al. 1983) and is most likely to have negative consequences for ANPP.

The results suggest that the direction of relationships between specific crops and productivity change and magnitude of the observed effects varies among crops and individual crops can often have different, even opposing relationships with aboveground and belowground productivity change. Consequently, the localized impact of cultivation on productivity depends on the area and type of crops grown in the particular area as well as local climatic and edaphic conditions. To understand the relationship between cropping and primary production in large areas, future studies must examine the relative influence of cropping in the context of known controls over productivity such as climate and soil conditions. Identifying the implications of these results for atmospheric carbon budgets requires understanding of how cropping has influenced carbon storage and decomposition rates. Thus, combining these results with large-scale estimates of soil carbon pools may provide insight into the overall carbon consequences of cropping. Nevertheless, this study suggests that cropping has altered, and continues to alter, primary productivity in the U.S. Great Plains. These results are rare in their quantification of large-scale, long-term relationship between landuse practices and ecosystem processes.

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Figure 2.1: Cropping intensity for counties in the U.S. Great Plains and climatic conditions in the region.

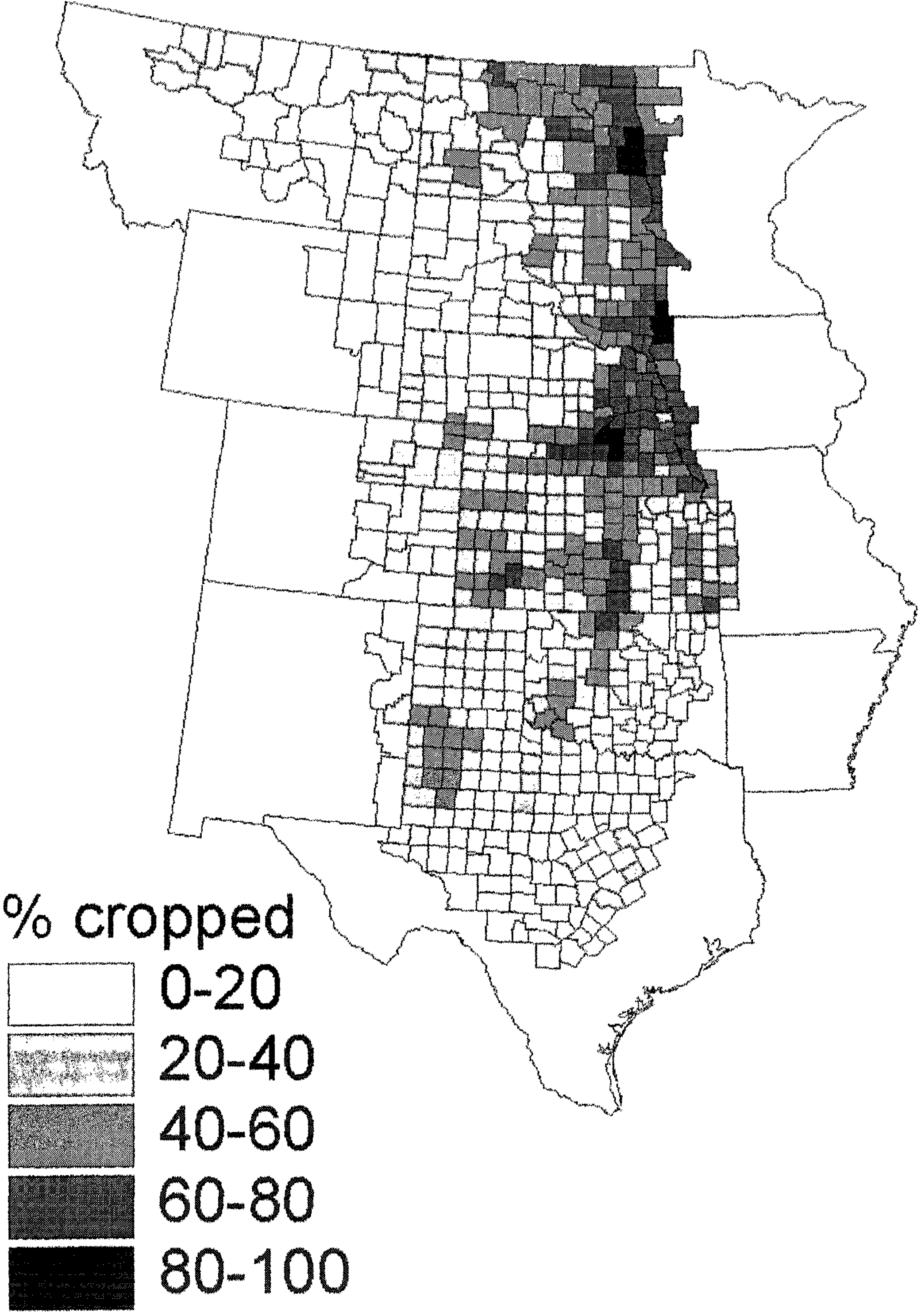

Figure 2.2: Pre-cultivation, current, and change in aboveground, belowground and total net primary productivity in the U.S. Great Plains by county.

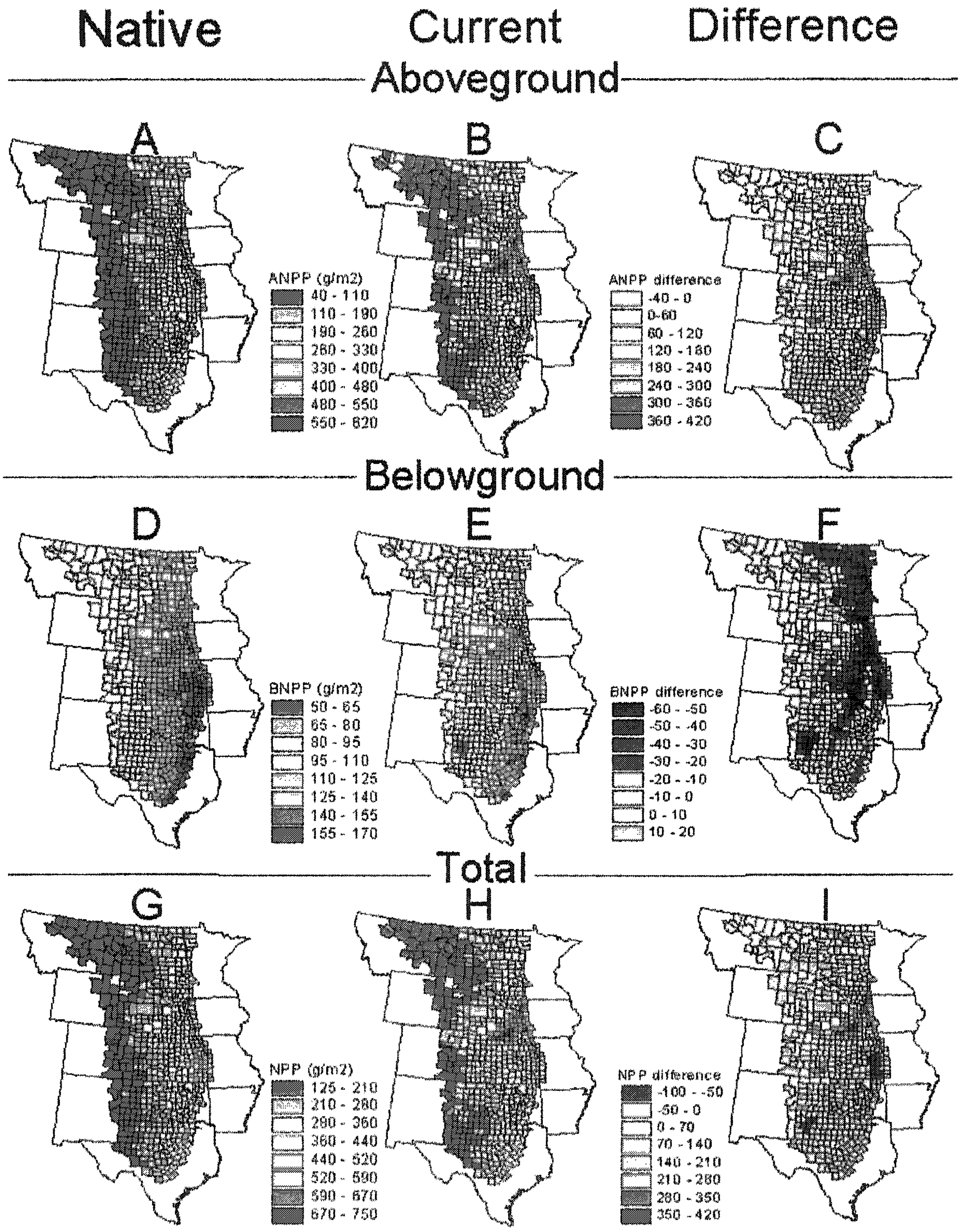

Figure 2.3: Aboveground productivity as a function of mean annual precipitation for counties in the U.S. Great Plains under pre-cultivation conditions (A) and native conditions (B). In B, each number represents a county and number values refer to the proportion of cropped area in each county that is irrigated. 0 indicates 0-10 % irrigated, 1 indicates 10-20% irrigated, etc.

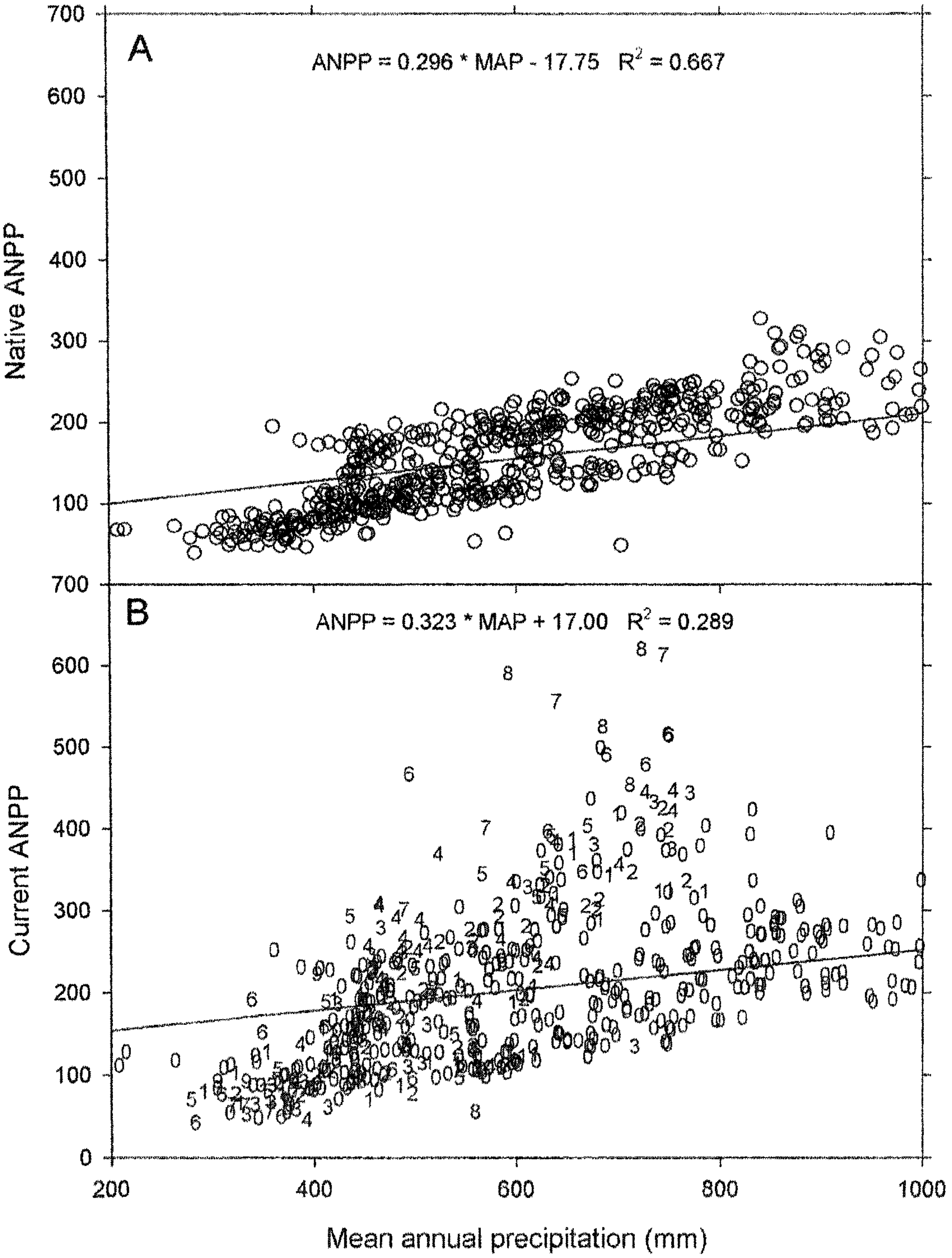

Figure 2.4: Proportion of current net primary production that is accounted for by cropping in counties of the U.S. Great Plains.

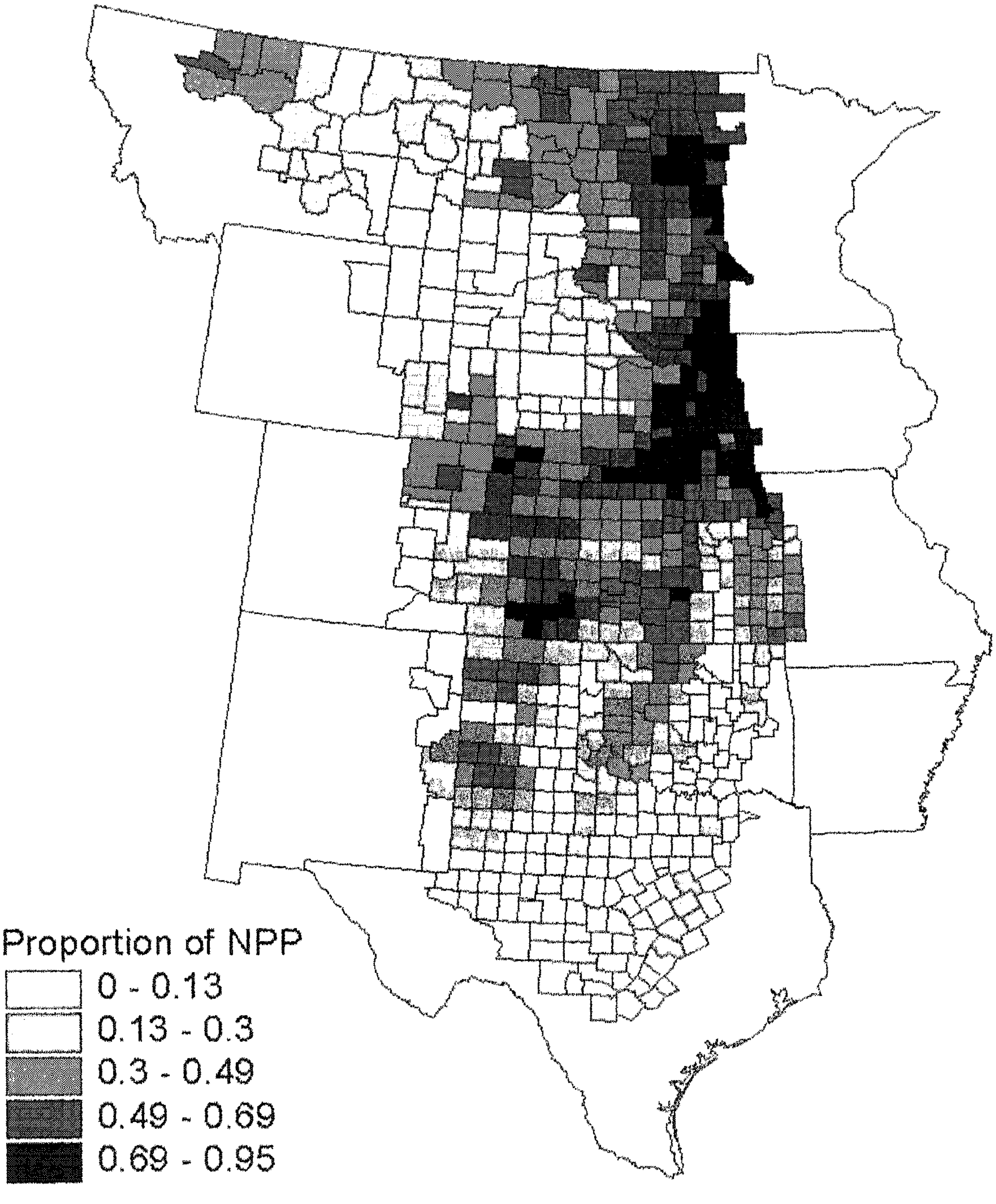

Figure 2.5: Pre-cultivation net primary productivity vs. current net primary productivity for counties in the U.S. Great Plains. Each number represents a county and number values refer to the proportion of cropped area in each county that is irrigated. 0 indicates 0-10 % irrigated, 1 indicates 10-20% irrigated, etc.

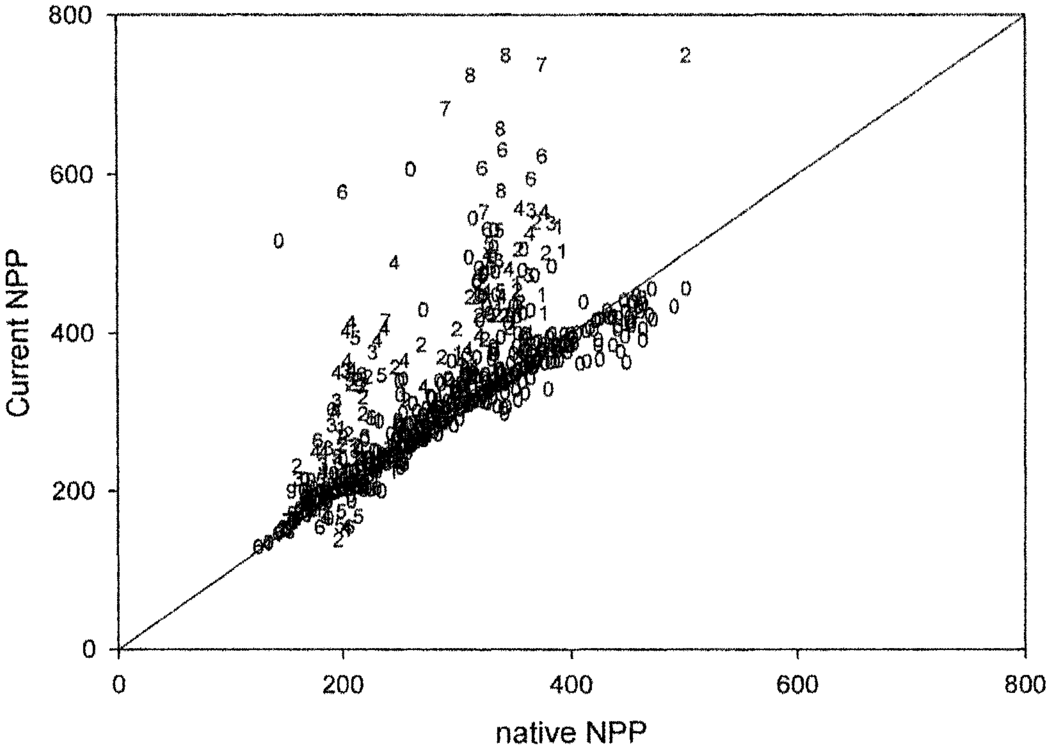

Figure 2.6: Change in net primary production (g/m^2) as a function of cropping intensity for counties in the U.S. Great Plains. Each number represents a county and number values refer to the proportion of cropped area in each county that is irrigated. 0 indicates 0-10 % irrigated, 1 indicates 10-20% irrigated, etc.

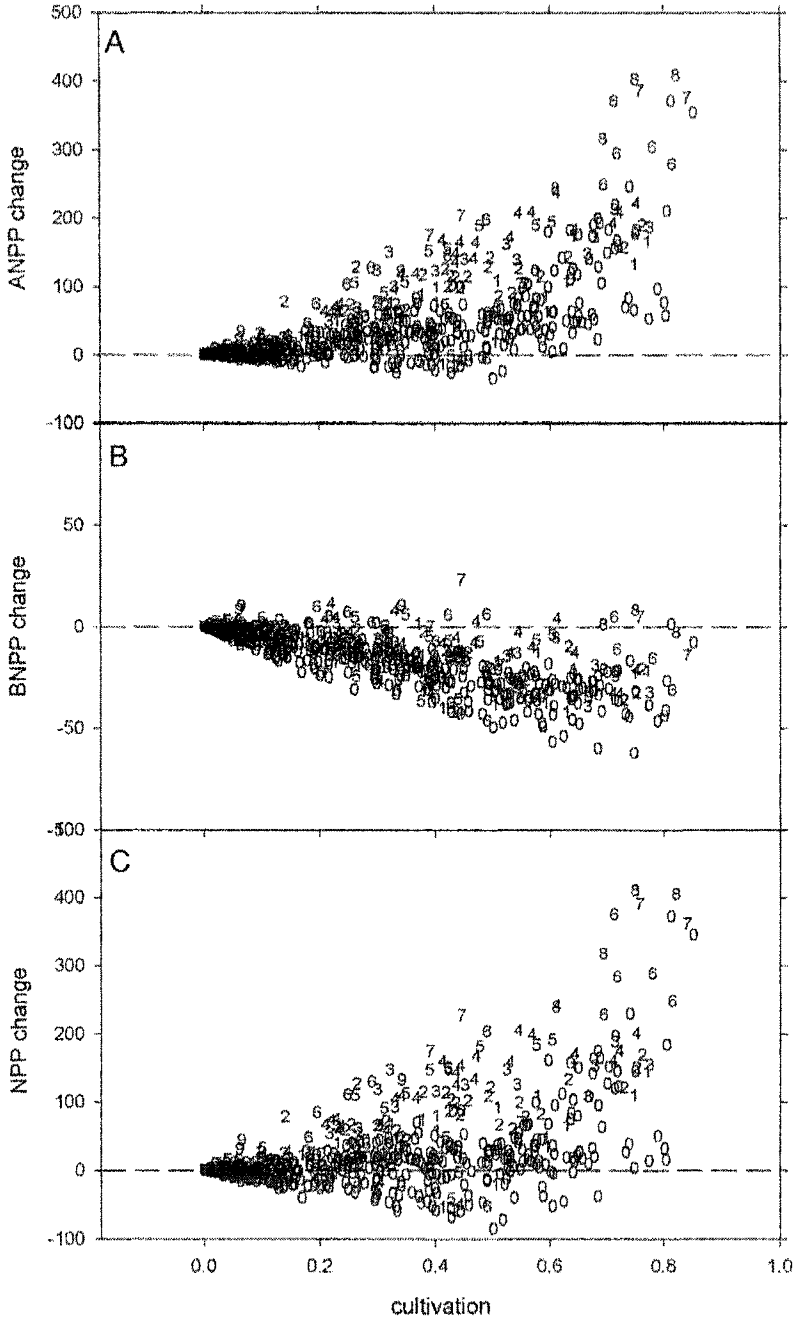

Figure 2.7: Carbon allocation ratio, expressed as belowground productivity divided by aboveground productivity for counties in the U.S. Great Plains under native and current (cropped) conditions.

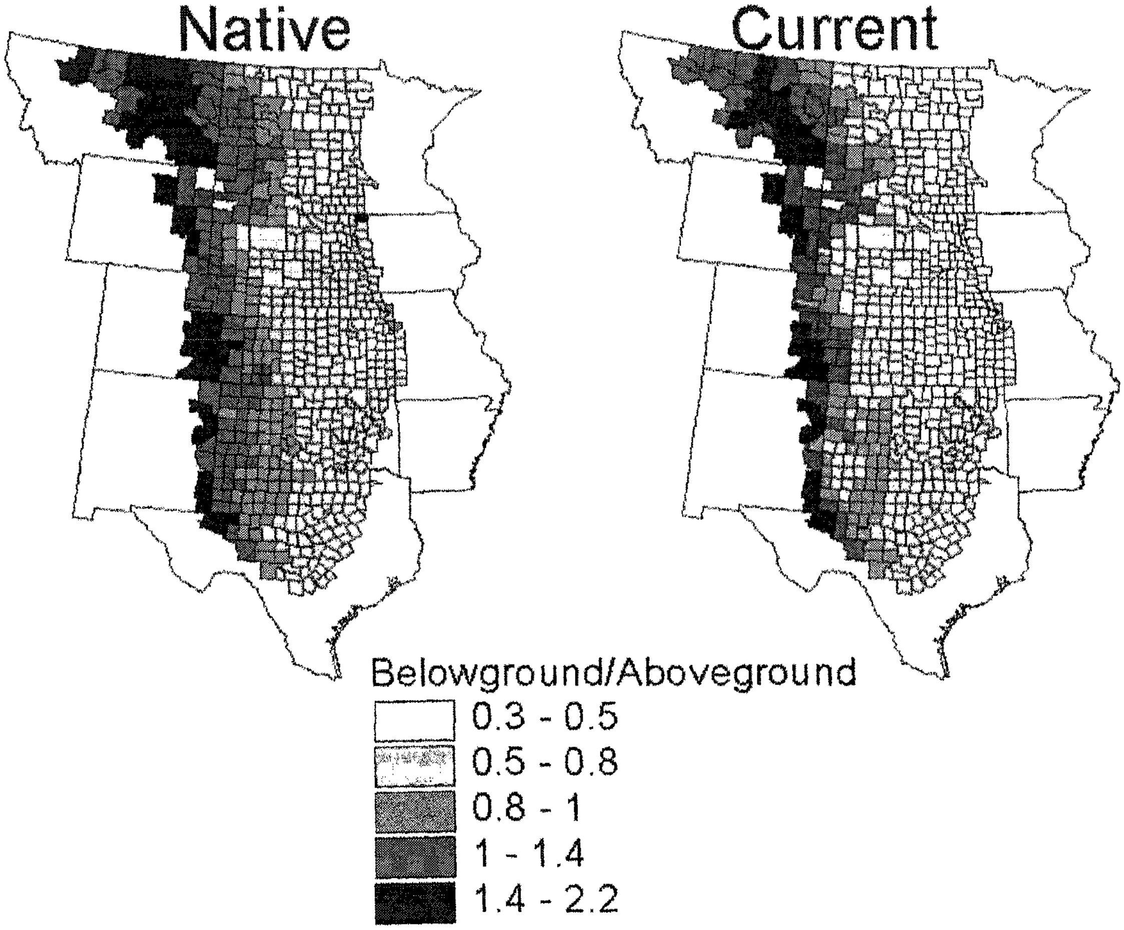

Table 2.1:References for allocation ratios and harvest indices for agricultural crops monitored.

Crop	Allocation	Reference	Harvest Index	Reference
Barley	0.50	Bolinder et al. 1997	0.49	Bridger et al. 1995 Nedel et al. 1993 Jedel et al. 1994 Bulman and Smith 1993 Hay 1995
Beans	0.26	Turpin et al. 2002 Crawford et al. 1997 Kloseiko et al. 2001	0.55	Scully and Wallace 1990
Corn	0.18	Allmaras et al. 1975 Anderson 1988	0.52	Dywer et al. 1994 Howell et al. 1998 Banziger et al. 1999 Edmeades et al. 1999 Kinery et al. 1997 Raun et al 1989 Prihar et al.1990 Hay 1995
Cotton	0.14	McMichael and Quisenberry 1991 Mauney et al. 1992 Kimball and Mauney 1993	0.55	Pettigrew and Meredith 1997 Mauney et al. 1992 Gerik et al. 1996 Heuer and Nadler 1999
Hay	0.87	Bray 1963		
Oats	0.40	Bolinder et al. 1997	0.52	Peltonen-Sainio 1994 Lynch and Frey 1993
Potato	0.10	Opena and Porter 1999 Jefferies 1993	0.55	Knowles and Botar 1992
Rye	0.24	Sheng and Hunt 1991	0.35	Giunta et al. 1999
Sorghum	0.09	Piper and Kukakow 1994	0.52	Prihar et al. 1991 Howell 1990 Prihar and Stewart 1990
Soybeans	0.15	Allmaras et al. 1975 Marvel et al. 1992 Silvius et al. 1977	0.42	Weilenmann de Tau and Luquez 2000 Salado-Navarro et al. 1993 Morrison et al. 1999 Ferris et al. 1999 Bhardwaj and Bhagsari 1991 Bhardwaj et al. 1990 Rao and Bhagsari 1996
Sunflower	0.25	Szaniawski 1983	0.40	Bange et al. 1997, 1998
Wheat	0.19	Bolinder et al. 1997 Sheng and Hunt 1991	0.39	Prihar and Stewart 1990 Sharma 1992 Beuerlein et al. 1991 Mulholland et al. 1998 Wheeler et al. 1996 Ferris et al. 1998 Hay 1995 Howell et al. 1990

Table 2.2: Estimates of aboveground (ANPP), belowground (BNPP) and total net primary production (NPP) for the U.S. Great Plains under native conditions in the absence of cropping, current conditions, and the difference between native and current conditions.

	Native				Current				Difference			
	Mean			Total (PgC)	Mean			Total (PgC)	Mean			Total (PgC)
		min	max			min	max			min	max	
ANPP	141	39	336	0.253	177	42	620	0.319	37	-36	408	0.066
BNPP	115	86	165	0.208	105	59	157	0.188	-11	-62	23	-0.020
NPP	256	125	501	0.461	282	129	749	0.507	26	-86	411	0.046

Table 2.3: Results from linear regressions of the change in total primary productivity (NPP), aboveground productivity (ANPP) and belowground productivity (BNPP) as a function of the cropping intensity of corn, soybeans, wheat, hay and sorghum.

NPP

Variable	Parameter Estimate	Step	Partial R-Square	Model R-Square	Value
Intercept	-4.70941				
corn	667.7249	1	0.7343	0.7343	<.0001
soybeans	-302.04904	2	0.0743	0.8086	<.0001
wheat	70.43418	3	0.0146	0.8231	<.0001
hay	-101.45166	4	0.0025	0.8257	0.0027
sorghum	76.83055	5	0.0016	0.8272	0.0176

ANPP

Variable	Parameter Estimate	Step	Partial R-Square	Model R-Square	Value
Intercept	-1.96976				
corn	631.53138	1	0.7946	0.7946	<.0001
wheat	131.20941	2	0.0583	0.8529	<.0001
soybeans	-170.43255	3	0.0234	0.8763	<.0001
hay	-122.52133	4	0.0095	0.8858	<.0001
sorghum	191.06806	5	0.0038	0.8896	<.0001

BNPP

Variable	Parameter Estimate	Step	Partial R-Square	Model R-Square	Value
Intercept	-2.73965				
soybeans	-131.61649	1	0.2578	0.2578	<.0001
wheat	-60.77523	2	0.3511	0.6088	<.0001
sorghum	-114.2375	3	0.0796	0.6885	<.0001
corn	36.19352	4	0.0474	0.7359	<.0001
hay	21.06966	5	0.0029	0.7388	0.0087

CHAPTER 3: CONTROLS OVER ECOSYSTEM PROCESSES: THE ROLE OF LAND-USE.

ABSTRACT

Identifying the conditions and mechanisms that control ecosystem processes is a central goal of ecosystem ecology. Ideas have ranged from single limiting-resource theories to co-limitation by nutrients and climate, to simulation models with edaphic, climatic and competitive controls. Although some studies have begun to consider the influence of land use practices, especially cropping, few studies have quantified the impact of cropping at large scales relative to other known controls over ecosystem processes. I utilized a 9-year record of productivity, phenology, climate, weather, soil conditions and cropping in the U.S. Great Plains to quantify the controls over spatial and temporal biomass patterns and estimate sensitivity to specific driving variables. I considered climate, soil conditions and long-term average cropping as controls over spatial patterns and weather and interannual cropping variations as controls over temporal variability. I found that variation in productivity is primarily spatial, whereas variation in phenology is more evenly split between spatial and temporal components. My models explained more of the variation in productivity than in phenology, and more of the spatial than the temporal patterns. My results indicate that although climate is the most important variable for explaining spatial patterns, cropping explains a substantial fraction of the

residual variability. Soil texture and depth contributed very little to my models of spatial variability. Weather and cropping deviation both made modest contributions to the models of temporal variability. These results suggest that the controls over phenology and temporal variation are not well understood. My sensitivity analysis indicates that productivity is more sensitive to climate than to weather and is very sensitive to cropping intensity. In addition to identifying potential knowledge gaps, these results provide insight into the probable long- and short-term ecosystem response to changes in climate, weather, and cropping.

INTRODUCTION

Predicting ecosystem response to global environmental change has become an important objective for ecosystem scientists, but robust predictions require understanding how environmental and land use conditions influence processes individually, and how these changing conditions combine and interact to modify processes.

Most efforts at understanding the controls over ecosystem processes have focused on relating them to climatic (e.g. Rosensweig 1968, Lieth 1975, Burke et al. 1997, Austin and Vitousek 1998), edaphic (Jenny 1941, Noy-Meir 1973) and weather (Burke et al. 1991, Tian et al. 1998, Potter et al. 1999) conditions. However, recent studies have attempted to examine how human land-use practices influence ecosystem processes (Vitousek 1992, Houghton et al. 1999). Although the consequences of human land-use for ecosystem processes have been examined at individual sites, few studies have attempted to quantify the magnitude and patterns of land-use effects on ecosystem processes at large spatial and temporal scales (e.g. Burke et al 2000).

As human population grows, the need for food will likely continue to increase, necessitating continued cropping in most currently cultivated agricultural areas and possible conversion of additional areas (Cassman 1999, Tilman et al. 2002). Insight into the relationship between cropping practices and spatio-temporal patterns of changes in ecosystem processes is essential to understanding the consequences of these practices. The widespread and pervasive nature of cropping practices means that cultivation may have a substantial impact on carbon cycling, potentially contributing to global environmental change by altering atmospheric carbon dioxide concentrations.

Ecological processes vary across space and time. Characterizing the patterns of this variation and understanding the controls over this variability has become a central goal of ecosystem scientists. In addition to strengthening basic knowledge of the controls of ecosystem structure and function, this understanding is crucial for predicting the consequences of changing climatic and land-use conditions. Since extrapolating site-level results to larger scales must overcome numerous challenges, including the potential for emergent properties and nonlinearities (O'Neill and Rust 1979, Wiens 1989, Wessman 1992, Levin 1992), there is a need for large-scale observations of the relationship between environmental conditions and ecosystem process (Wessman and Asner 1998). Some previous studies have used spatial variation in ecological processes and underlying environmental controls to provide insight into how these processes may respond to future environmental changes. However, there is some evidence that relationships may not be consistent between spatial and temporal domains (Lauenroth and Sala 1992). Consequently, studying the relationships between controlling factors and ecosystem processes over *both* space and time is essential.

In this study I quantify how environmental conditions and cropping practices influence net primary production and seasonality of aboveground biomass in a grassland ecosystem. Net primary productivity is the amount of carbon fixed by plants minus plant respiration and is, at least aboveground, one of the best-understood ecosystem process. Whereas net primary production is a measure of total annual ecosystem function, seasonal patterns of aboveground biomass provide insight into how ecosystems respond to fluctuations in environmental conditions within a year.

Grasslands are especially appealing for examining the relationship between environmental controls, land-use and ecosystem processes because grasslands typically have high cropping intensity and environmental influences on ecosystem processes of native vegetation is well established. Grasslands generally exist in areas of limited rainfall (Ripley 1992), where water availability exerts a relatively consistent control over grassland primary production (Lauenroth 1979). Precipitation is positively related to grassland productivity across space and through time, although the slope of the spatial relationship is greater, implying that at a particular location ecosystems may not immediately respond to altered conditions (Lauenroth and Sala 1992). The effect of temperature on primary productivity in grasslands depends on the interaction with precipitation and subsequent influence on water availability (Lauenroth 1979). In water-limited areas, warmer temperatures lower water availability and decrease production (e.g. Epstein et al. 1997 and Gill et al 2002). Recent studies have shown a negative relationship between temperature and agricultural yield, suggesting that the effect of temperature on productivity is not limited to native vegetation (Lobell and Asner 2003). However, in wetter areas, warmer temperatures have less influence on water availability, and can actually increase production by allowing longer growing seasons and faster photosynthetic rates (e.g. Lauenroth et al. 1999).

Soil properties can also influence productivity in grassland systems, although the nature of their influence is not consistent. Noy-Meir (1973) proposed an "inverse texture effect" that suggested that coarse textured soils allow greater water infiltration, have less evaporative water loss, thereby supporting higher productivity in dry areas than fine textured soils. By contrast, wetter areas that exhibit water loss primarily through drainage display higher productivity in fine textured soils with high water-holding capacity. Sala et al. (1988) contrasted ANPP with soil water-holding capacity and identified 370 mm/yr as the precipitation level below which coarse soils favor production, but subsequent analyses have suggested that this crossover point may occur at much higher precipitation levels (Epstein et al. 1997).

The effect of cropping on net primary production, in contrast to native vegetation, has received relatively limited attention, and generally only at small scales. Crops have typically been selected to maximize aboveground yield while only generating enough roots to obtain the necessary water and nutrient resources. Consequently, site-level studies have indicated that cropping generally increases aboveground production while having only modest effects on belowground production (Buyanovsky et al. 1987), and recent analysis has quantified this impact at regional scales (Chapter 1).

In general, the patterns and controls of grassland plant biomass seasonality have been much less studied than those for total annual productivity. Rathcke and Lacey (1985) identified three potential environmental controls over plant seasonal patterns: photoperiod, temperature, and moisture availability. Bonen (2002) suggested that temperature is the primary environmental control over plant seasonality in most ecosystems because metabolic processes only occur within specific temperature ranges. However, in water-limited systems, moisture availability can also restrict seasonal growth patterns (Jobbagy et al. 2002). Since temperature and precipitation generally dictate the start and end of the growing season in grasslands, I anticipate that these processes combine to exert primary control over the length of the growing season.

Cropping dramatically alters vegetation structure and function and thereby has potential to influence biomass seasonality, especially since many crops have been selected to display uniform seasonal development regardless of environmental conditions (Martin et al. 1976). The impact of cropping on aboveground biomass seasonality is readily apparent at small scales, but varies among crops so the cumulative effects at large scales are unclear. Single-species cropping of annual plants not only causes an abrupt start and end to the growing season, with consequences for growing season length, but also potentially influences the overall timing of growth patterns. For example, wheat is most often harvested early in the thermally defined growing season, and can display especially early seasonal biomass patterns when cultivated as a winter crop (fall planting and germination). Many other crops are planted only after soil temperatures rise to a particular level and thus initiate growth well after native plants (Martin et al. 1976).

The overall goal of this study was to model the relative importance of cropping in influencing net primary production and biomass seasonality relative to known controls such as climate (long-term conditions), weather (annual variation) and soil conditions. I used variance decomposition techniques to examine how environmental conditions and cropping practices relate to the observed variability in net primary production and aboveground biomass seasonality in grassland ecosystems. Specifically, my objectives were to: (1) partition the variance of productivity and biomass seasonality into spatial and temporal components and create statistical models for these variance components, (2) use the models to quantify the relative importance of cropping, climate, soil conditions and weather in understanding patterns in these ecosystem processes, and (3) combine the best spatial and temporal models to create an overall model and use it to predict the sensitivity of productivity and biomass seasonality to changes in climate, weather, soil conditions and cropping intensity.

METHODS

Study site: I conducted this study in the U.S. Great Plains, which includes 23% of the contiguous U.S. and extends from the Canadian border into south Texas and from the Rocky Mountains to approximately the 95th parallel (Figure 3.1). The Great Plains is ideal for this study because it contains a wide range of both cropping intensities and climatic conditions. Precipitation occurs primarily during the summer months and mean annual precipitation varies from under 400 mm in the west to nearly 1000 mm in the east. Mean annual temperature increases from 3° in the north to 21° C in the south (Lauenroth and Burke 1995). Land use is primarily agricultural, with grazed native grassland, dryland cropland, and irrigated cropland in the west, wheat in the central part of the region, and nearly contiguous corn/wheat in the east.

I included counties that historically contained at least 70% of the following vegetation types: northern mixed grass prairie, shortgrass prairie, tallgrass prairie, tallgrass savanna, southern mixed grass prairie, desert savanna, and floodplain forests.

These restrictions identified 630 counties within the Great Plains that are suitable for this study (Figure 3.1). I collected data for the years 1991-1998 for these counties.

Net primary production and biomass seasonality: I calculated monthly production and annual phenological characteristics for each county for the years 1990 through 1998. To estimate production, I used a modified version of the Carnegie Ames Stanford approach (CASA). CASA relies on methods developed by Monteith (1972, 1977) that allow estimation of plant productivity from observations of absorbed photosynthetically active radiation (APAR), and estimates of light use efficiency (LUE) according to:

$$NPP = APAR \times LUE \tag{1}$$

where APAR is the product of incoming photosynthetically active radiation (PAR) and the fraction of PAR that is absorbed by vegetation (FPAR). FPAR is related to the photosynthetic activity of vegetation and can be estimated via remotely sensed observations of the normalized difference vegetation index (NDVI) (Sellers et al. 1992). NDVI is a remotely sensed vegetation index that quantifies plant photosynthetic activity by measuring the difference between reflectance in the near-infrared wavelengths (NIR) and red wavelengths (RED) according to the formula:

$$NDVI = \frac{NIR - RED}{NIR + RED} \tag{2}$$

I used biweekly, 1x1 km NDVI data from NOAA's Advanced Very High Resolution Radiometer to estimate FPAR.

CASA has traditionally represented monthly LUE as

$$LUE = LUE * T_1 T_2 W \tag{3}$$

where LUE* is the maximum photosynthetic efficiency, T_1 and T_2 are reduction factors representing deviation from optimal temperature and deviation from 20°C, respectively, and W represents LUE reduction due to low soil moisture as determined by a soil water model (Potter et al. 1993, Field et al. 1995). Recent studies (see Appendix 1; Lobel et al. 2002) have suggested that vegetation type can substantially influence LUE* values, especially in cultivated areas. Consequently, I modified equation (3) to allow LUE* to vary according to the vegetation content of each county according to:

$$LUE^* = NLUE_N + C_3LUE_3 + C_4LUE_4 \qquad (4)$$

where LUE_N is 0.23 gC/MJ (the maximum LUE for native vegetation), LUE_3 and LUE_4 are observed photosynthetic efficiency values of 0.33 gC/MJ for C_3 croplands and 0.77 gC/MJ for C_4 croplands, (Appendix 1) and N, C_3 and C_4 are the proportions within the county of native vegetation, C_3 cropland, and C_4 cropland, respectively.

To partition the NPP estimates into aboveground and belowground productivity I calculated an allocation ratio for each county that is an area-weighted average of allocation in cropped areas and allocation in native grassland. For cropped areas, I used published allocation ratios for each crop (Appendix 3.1). For allocation ratios in uncropped areas I utilized relationships identified by Gill et al (2002) which suggest that grassland BNPP can be estimated from maximum yearly instantaneous belowground biomass (BGB), maximum proportion of BGB that is alive during the year (liveBGB/BGB) and root turnover (T) according to the equation:

$$BNPP = BGB \times (\frac{liveBGB}{BGB}) \times T \qquad (5)$$

Gill et al. indicated that BGB, live BGB/BGB and T can be estimated from peak annual aboveground biomass (AGBIO) and mean annual temperature (MAT) as:

$$BGB = 79 \times AGBIO - 33.3(MAT + 10) + 1289 \qquad (6)$$

$$\frac{liveBGB}{BGB} = 0.6 \qquad (7)$$

$$T = 0.2884 \times e^{0.046 \times MAT} \qquad (8)$$

I chose two indicators of biomass seasonality: the length of the growing season (LENGTH) and the date of maximum NDVI (DATEM). DATEM is an indicator of the time when photosynthetic activity is highest during the growing season (reported as the day of year) and provides insight into the timing of events within the active period. LENGTH was determined by estimating the beginning and end of the growing season and calculating the number of days between these dates. Reed et al. (1994) developed a method for determining these dates based on identifying a substantial change in the NDVI patterns through time. The start of the season is characterized as the date when NDVI first starts increasing in the spring and the end of the growing season is characterized as the date NDVI stops decreasing.

Data sources: My climate data were derived from a 30-year mean climate database of weather records archived by CLIMATEDATA (1988). I utilized soil texture (percent clay and sand) and depth information from the USDA STATSGO database (USDA 1989: http://www.ftw.nrcs.usda.gov/stat_data.html). Weather data for individual weather stations across the region were obtained from the National Climate Data Center at http://cdo.ncdc.noaa.gov/plclimprod/plsql/somdmain.somdwrapper?datasetabbv=TD3220&countryabbv=&GEORegionabbv=&Forceoutside for the years 1991 – 1999. Climate and weather information were entered into a GIS and interpolated from points (weather stations) into a surface covering the study area. I overlaid the climate and weather maps with soil information and extracted county means for the 630 counties in this study. I obtained cultivation data from the National Agricultural Statistics Service (NASS 1988: http://www.nass.usda.gov:81/ipedb/) which maintains records of crop area and yield for all U.S. counties.

Variance partitioning: The objective of the variance partitioning is to characterize the controls over spatial and temporal patterns in ANPP, BNPP, LENGTH and DATEM. Decomposing the observed variation into components and examining the controls over those variance components is one approach (Box et al. 1978). Total variation (σ^2_{total}) observed in an ecosystem processes over a region can be partitioned into spatial variation ($\sigma^2_{\mathrm{spatial}}$; differences from one location to another) and temporal variation ($\sigma^2_{\mathrm{temporal}}$; variation at a single location through time):

$$\sigma^2_{\mathrm{total}} = \sigma^2_{\mathrm{spatial}} + \sigma^2_{\mathrm{temporal}} \qquad (9)$$

The spatial and temporal components can be explained by examining the forces that dictate those sources of variability. However, since the driving variables included in the spatial or temporal models will not explain all of the observed variation, some residual process variability will exist. Spatial variation can be modeled by including sources of variation that change only across space and not through time:

$$\sigma^2_{\mathrm{spatial}} = \sigma^2_{\mathrm{model}} + \sigma^2_{\mathrm{residual}} = \sigma^2_{\mathrm{climate}} + \sigma^2_{\mathrm{soil}} + \sigma^2_{\mathrm{cropmean}} + \sigma^2_{\mathrm{residual}} \qquad (10)$$

where $\sigma^2_{\mathrm{model}}$ is the variation explained by any particular model, $\sigma^2_{residual}$ is the variation not explained by the model, $\sigma^2_{\mathrm{climate}}$, σ^2_{soil}, and $\sigma^2_{\mathrm{cropmean}}$ are the variation explained by variables representing climate conditions, soil properties and mean cropping intensity, respectively. Similarly, temporal variation can be modeled by including source of variation that fluctuate only in time:

$$\sigma^2_{\text{temporal}} = \sigma^2_{\text{model}} + \sigma^2_{\text{residual}} = \sigma^2_{\text{weather}} + \sigma^2_{\text{cropdev}} + \sigma^2_{\text{residual}} \quad (11)$$

where $\sigma^2_{\text{weather}}$ and $\sigma^2_{\text{cropdev}}$ are the variation explained by the variables representing weather deviations from the climatic means and deviation from the mean cropping intensity, respectively.

Generating overall predictions from spatial and temporal models requires combining them into a single model that explains the total observed variability. Total variation is also not completely accounted for by the driving variables, due to residual process variability, so it can be expressed as:

$$\sigma^2_{\text{total}} = \sigma^2_{\text{model}} + \sigma^2_{\text{residual}} = \sigma^2_{\text{climate}} + \sigma^2_{\text{soil}} + \sigma^2_{\text{cropmean}} + \sigma^2_{\text{weather}} + \sigma^2_{\text{cropdev}} + \sigma^2_{\text{residual}} \quad (12)$$

Modeling of spatial, temporal and overall variation: To characterize the influence of driving variables on variability in production and biomass seasonality, I first partitioned the variance into spatial and temporal components, and then generated independent predictive models for each type of variation. I calculated mean annual productivity and biomass seasonality values for each county and considered the differences among them to represent spatial variability. To represent temporal variability, I calculated the annual deviation from the mean productivity or biomass seasonality for each county. Since the magnitude of variation in both space and time depends on the spatial and temporal scales chosen, I utilized a 9-year record (1991-99) containing substantial inter-annual variation.

To determine the effect of climate, soil, weather and cultivation variables on productivity and biomass seasonality, a candidate set of *a priori* multiple linear regression models was developed for each combination of variation type (e.g. spatial or temporal) and response variable (e.g., ANPP, BNPP, LENGTH, DATEM). The spatial models included various combinations of parameters for climate (mean annual temperature and precipitation), soil texture (percent sand and clay and depth of the A horizon) and mean cropped area for the 5 major crops in the region from the (Table 3.1 & 3.2).

To compare these statistical models, I employed a method developed by Burnham and Anderson (2001) that relies on likelihood theory to quantify the amount of evidence for each model contained in the data. This method uses Akaike's Information Criterion (AIC) as an indicator of the information lost when a statistical model approximates truth and ranks models according to the support for each model contained in the observed data. The loglikelihood of each statistical model is calculated as

$$\log(\ell(\hat{\theta})) = -\frac{n}{2}\log(\hat{\sigma}^2) \tag{13}$$

where $\ell(\hat{\theta})$ is the likelihood of model $\hat{\theta}$ given the observed data and $\hat{\sigma}^2$ is the residual sum of squares divided by the sample size n. From these loglikelihood values, I calculated AIC$_c$ (AIC corrected for small sample size) for each statistical model as:

$$AIC_c = -2\log(\ell(\hat{\theta})) + 2K + \frac{2K(K+1)}{(n-K-1)} \tag{14}$$

where K is the number of estimated parameters (including an estimate of variance). Smaller values of AIC$_c$ indicate that the statistical model is closer to the truth (never known) and the best model has the lowest AIC$_c$ value. The difference between AIC$_c$ values (Δi) of competing models provides insight into the relative strength of support in the data for the various models, with differences of 1-2 AIC units suggesting substantial support, 3-7 AIC units indicating less support and >10 units implying no support in the data.

To avoid generating an excessively large number of spatial candidate models and to ensure that I generated conservative estimates of the importance of cropping, I used a hierarchical approach to model selection in which I first found the best model with only climate parameters, then held those parameters constant and chose the best model from various combinations of soil variables in addition to climate parameters. Last, I held climate and soil constant and included cropping information to choose the best overall model of spatial variability. Generating the statistical models in this order means that any covariance between variables will be attributed first to climatic variables and second to soil variables, minimizing the inferred importance of cropping. Temporal models were generated by selecting the best combination of weather parameters (calculated as temperature and precipitation deviation from the climate values) and then including deviations in cropped area for specific crops (deviation from the 9-year mean). Proc REG in SAS/STAT software (SAS 2001) was used to determine AIC for each model. (Appendix 3.1 and 3.2).

Impact of cropping: In addition to modeling the observed patterns in process variation, I examined how cropping alone influences the overall magnitude of spatial and temporal variability in productivity and biomass seasonality. I divided the counties into 9 classes based on cultivation intensity. Counties in class 0 are between 0 and 10 percent cultivated; counties in class 1 are between 10 and 20 percent cultivated, etc. No counties are more than 90% cropped, so only 9 classes exist (0 through 8). As an indicator of spatial variation, I used the 9-year mean cropping values to calculate a coefficient of variation for ANPP, BNPP, season length and date of maximum NDVI in each class. To quantify temporal variation, I calculated a coefficient of variation for each county based on the 9 observations from 1990 to 1998, and averaged those values across all counties in each cropping class to determine a single estimate of temporal variability for each class. I used linear regression to compare these spatial and temporal coefficients of variation against cropping intensity.

Sensitivity analysis: To generate an overall predictive model, I included independent variables from the best spatial and temporal models in the following categories: climate, soil properties, weather deviations and cropping practices (actual values for each year rather than mean values or deviations from the mean). For variables whose best spatial and temporal models had different parameters for cropping (i.e. individual crop proportions vs. C_3 and C_4 crop proportions) I used the parameters for the spatial model because those consistently explained a higher proportion of the overall variation.

I used this model to provide predictions of productivity and biomass seasonality as a function of the climate, soil, weather and cropping variables that were identified in the model selection process. By varying one of the driving variables while holding the remaining driving variables constant I estimated how each process responds to changes in those variables. I quantified the predicted response of productivity to changes in climate, soil, weather, and cultivation. In addition, because cropping intensity and cropping practices vary across the region, I divided the region into 9 subregions (Figure 3.2) and examined the effect of changes in cropping on productivity and biomass seasonality in each subregion.

RESULTS

Spatial vs. temporal variation: My results indicate that over 90% of the variation in ANPP occurs in the spatial domain, with only a small fraction occurring in the temporal domain (Table 3.3). The variation in BNPP was also predominantly spatial, although the discrepancy between spatial and temporal was not as dramatic. Similar to productivity, DATEM varied more over space that through time, although total variation was much more evenly split for DATEM. LENGTH was the only variable I examined that varied more though time than space, with 80% of total variation as temporal.

Effect of cultivation on process variance: I found that cultivation generally decreases the spatial and temporal variability of primary productivity and biomass seasonality, suggesting that cultivated areas have more consistent ecosystem processes from location to location as well as from year to year (Figure 3.3). The one exception to the general decrease in variability with cultivation is the relationship between spatial BNPP variability and cultivation, which my data suggest are positively related.

Spatial models: My best statistical model for spatial variability in aboveground productivity explained nearly all of the total variation in ANPP (Table 3.3). As a group, climate parameters (mean annual temperature and precipitation) were the most important set of independent variables, accounting for over half of overall variability. Cropping practices accounted for an additional 31% percent of spatial ANPP variation. Soil properties explained only a tiny fraction of ANPP variation. In the overall best model for spatial ANPP variation, my results indicate positive relationships between both MAP and MAT and ANPP. Both sand and clay were negatively related to ANPP when cropping practices are not included (climate and texture model) but these relationships become positive after accounting for cultivation. In addition to the effect of climate and soil properties, my results also indicate correlations between cropping practices and ANPP patterns. I found positive relationships between each of the 5 crops and ANPP, which is consistent with my expectation that cropping increases ANPP in part by altering carbon allocation ratios to favor aboveground structures (Chapter 1).

My best model for spatial variation in BNPP explained approximately two-thirds of the total variation, with cropping practices and climatic conditions accounting for 30% and 29% respectively. Soil properties contributed 5%. Similar to ANPP, I observed positive relationships between BNPP and both MAP and MAT, which are positively related in the U.S. Great Plains due to decreasing elevation and increasing precipitation from west to east. All three soil variables were negatively related to BNPP, implying greater belowground production in fine textured soils and soils with shallow A horizons than coarse soils or soils with deep A horizons. The best overall model for BNPP included total county-wide proportions of C_3 and C_4 crops, rather than proportions of individual crops. BNPP was negatively related to the abundance of C_3 crop but positively related to C_4 crops, a pattern consistent with the fact that C_4 crops, primarily corn and sorghum in this region, are extremely productive whereas the C_3 crops, primarily wheat and soybeans, are less productive.

The models for spatial variability did not perform as well for the aboveground biomass seasonality variables as they did for the production variables. The best model for LENGTH (length of the growing season) explained slightly over half of the overall variation, of which 40% was derived from climate parameters. Soil properties and cultivation practices only accounted for al very small fraction of the variation in LENGTH. LENGTH was positively related to MAP and negatively related to MAT, results that are both consistent with LENGTH limitation by late season water availability. Sand and clay are both negatively related to LENGTH, suggesting that coarse soils have higher water content than fine textured soils (with high silt content) late into the growing season. Four of the five crops were negatively related to the LENGTH season, which is to be expected since crops typically initiate growth later than native vegetation and are harvested before native vegetation stops growing.

For DATEM (the date of maximum NDVI), the best model explained over half of the observed variation, with the largest fraction coming from cropping practices, slightly less from climatic conditions and essentially nothing from soil properties. MAP is negatively related to DATEM when cultivation is included in the model, but positively related to DATEM in the absence of cultivation, whereas MAT is negatively related to DATEM. Clay displayed a negative relationship with DATEM, while the relationship with sand was small. Of the 5 crops examined, wheat and hay were both negatively related to DATEM.

Temporal models: My best model for temporal variability in ANPP explained less than half of the variation, with cropping accounting for most of the explained variation and weather explaining only 11%. Precipitation deviation is positively related to temporal variations in ANPP, as observed in grassland systems with some level of water limitation (Briggs and Knapp 1995). Temperature deviations were also positively related to ANPP but the slope of the relationship is much less that the slope of the precipitation relationship. Deviation in cropping intensity for all five crops was positively related to ANPP.

The best model for temporal variability in BNPP explained less than a third of the total variation, of which most is attributed to weather and only a small fraction to cropping. BNPP variation is positively related to precipitation deviation and negatively related to temperature deviation. The relationship between cropping and BNPP depends on the particular crop. Deviations in wheat, corn and sorghum are positively related to BNPP variations whereas hay and soybean deviations are negatively related. My best temporal models for both biomass seasonality variables explained only a small fraction of the total variation. The best model for LENGTH accounted for only 8% of the variation, most of which is due to weather. Similarly, the best model for the DATEM explained 7% of the variation.

Sensitivity analysis: My best models explained almost all of the variation in ANPP, over half of the variation in BNPP, approximately a third of the variation in DATEM, and only 16% of the variation in LENGTH (Table 3.3). Since these models were not particularly successful for the biomass seasonality variables, I conducted sensitivity analyses only for the response of productivity to changes in driving variables. I generated regional predictions of ANPP and BNPP for changes in mean annual precipitation, mean annual temperature, temperature, precipitation, soil percent sand and cropping intensity.

My analysis suggested that a 20% decrease in MAP would decrease ANPP and BNPP by 24 and 2.5 gm^{-2}, respectively (Figure 3.4). Since my MAP variable is log transformed, it has nonlinear effects on dependent variables. Consequently, my estimates of increases in ANPP and BNPP were only 19 and 2.3 gm^{-2}, respectively, slightly less than the decreases. By contrast, my models imply a much weaker response of productivity to twenty percent changes in annual precipitation with ANPP changing only 8.6 gm^{-2} and BNPP changing only 5 gm^{-2}.

In my analysis, MAT changes of ±2 °C caused modest increases for ANPP and BNPP of 2.9 and 2.8 gm^{-2}, respectively. Changing annual temperature by ±2 °C resulted in a similar positive ANPP change of 2.6 gm^{-2}, but produced a negative response in BNPP of 1.1 gm^{-2}. My analysis of the impact of altered soil texture predicts that ANPP is positively related to soil percent sand and clay with 20% decreases and increases in sand and clay causing a decrease of 14 gm^{-2} and increase of 15 gm^{-2}. BNPP, on the other hand, displayed a negative relationship with sand and clay, increasing by 4.1 gm^{-2} when sand and clay are lowered by 20% and decreasing by 4.5 gm^{-2} when sand and clay are increased by 20%.

In my models, modifications to cropping intensity had a large positive impact on ANPP, with predicted ANPP decrease of 26 gm^{-2} and increase of 27 gm^{-2} for 50% changes in cropping. I expect BNPP to have a very slight negative relationship with cropping intensity, with increases of 0.5 gm^{-2} and decreases of 0.7 gm^{-2} when cropping decreases and increases by 50%, respectively.

To further characterize the influence of cropping on productivity, I conducted sensitivity analyses for smaller areas within the U.S. Great Plains. I examined how changes of 50% in cropping intensity will impact ANPP and BNPP in 9 subregions (Figure 3.2). I used the same statistical model for all subregions, so differences among subregions are a consequence of spatial variation in crop distributions, not different models. All crops are positively related to ANPP, but the magnitude of the effect of changes in cropping depends on the type of crops in each subregion. My results suggest that changes in cropping will have the greatest effect on ANPP in the central and northeastern four subregions (Figure 3.5), and relatively minor effect in the remaining 5 subregions. BNPP is negatively related to C_3 crops but positively related to C_4 crops, meaning that both the direction and magnitude of BNPP changes will depend on crop type. My analysis predicts minor (effect sizes range from 1 to 4 gm^{-2}) decreases in BNPP for all subregions except CC, CE and SW. These areas have enough C_4 crops that the positive effect of C_4 crops on BNPP outweighs the negative effect of C_3 crops.

DISCUSSION

Spatial vs. temporal variability: By partitioning the observed process variation into spatial and temporal components, I discerned that variation in productivity occurs primarily in the spatial domain (more variation between locations than between years within a location), variation in the length of the growing season is mostly temporal (greater variability between years than between locations) and variation in the date of maximum NDVI is relatively evenly split between temporal and spatial domains. This result is consistent with previous studies of regional and site level productivity trends, which have shown very tight relationships between aboveground productivity and mean annual precipitation in grassland systems (Lauenroth 1979, Sala et al. 1988) but a weaker link, observed as a lag in recovery from drought, between interannual weather variations and productivity (Lauenroth and Sala 1992). The strong dependence of productivity on long-term (spatial) controls may be a consequence of the highly variable weather conditions and subsequent life history traits of dominant plants in the region I examined. The U.S. Great Plains encompasses climate regimes ranging from semiarid to subhumid, in which vegetation dynamics are heavily dependent on water availability and annual precipitation is extremely variable (Lauenroth and Burke 1995). Vegetation of the U.S. Great Plains contains several distinct communities dominated by perennial bunchgrasses that invest heavily in belowground structures and vegetation at any particular location is a combination of species that are adapted to long-term survival under conditions at that site. Interannual changes in precipitation, represented in this study as temporal weather fluctuations, alter conditions, but the species assemblage remains relatively constant. Consequently, the vegetation is unable to optimally respond to the altered conditions. On the other hand, spatial fluctuations in ecosystem processes represent ecosystem response to long-term mean conditions, in which the plant community is adapted to maximize productivity under those conditions. Paruelo et al (1999) compared the spatial and temporal relationships between precipitation and ANPP across a precipitation gradient in the Great Plains and found that ecosystems in the center part of the Great Plains are much more responsive to temporal precipitation variations than ecosystem on either end of the precipitation gradient. This suggests that elasticity through time is at least partially a function of plant community composition.

The relatively even split between spatial and temporal variation displayed by DATEM implies that this process is influenced by both short- and long-term controls. The large interannual variability of LENGTH suggests that the start and/or the end of the growing season (which combine to dictate the length) are strongly influenced by interannual processes, potentially weather. Early season temperature patterns can influence the onset of growth (Washitani and Masuda 1990) and precipitation has been shown to influence late-season developmental processes (Dickenson and Dodd 1976). Since the end of the growing season is controlled by the temporal dynamics of water availability, it is not surprising that LENGTH has larger temporal variability than the DATEM.

Effect of cropping on process variance: I found that spatial and temporal variability in ecosystem processes are generally lower in areas with high cropped proportion, with the exception of BNPP spatial variability. This result has been previously observed in temporal patterns (Buyanovsky et al 1987 and Lauenroth et al 2000) is not surprising since crops have been selected for consistent yield rather than for the ability to take advantage of especially favorable years or locations and a relatively small number of cultivars are utilized for each crop throughout the entire region (Martin et al. 1976). I anticipate that the negative relationship between BNPP spatial variability and cropping is the consequence of cropping generally having a negative impact on BNPP (Chapter1) and being most prevalent in highly productive areas (Figure 3.1). Decreasing BNPP in only part of productive areas causes high variability between cropped and uncropped sites and commensurately elevated spatial variability. This positive effect of cropping is not seen in temporal BNPP variation because the variability of interannual BNPP patterns is not increased by cultivation.

Controls over ANPP patterns: My statistical model for spatial ANPP patterns explained a very high proportion of the observed variation, and suggested that climatic conditions are the most important influences of ANPP, followed closely by cropping practices. In contrast to other recent analyses (Veron et al. 2002) soil properties explained only a small proportion of productivity variation, and thus contributed very little to my statistical models. The effect of MAP on ANPP has been observed in many previous studies (e.g. Lauenroth 1979, Sala 1988, Lauenroth et al 2000), but the positive relationship between MAT and ANPP is contradictory to some previous studies. Epstein et al (1996, 1997) found a negative relationship between MAT and ANPP of native grasslands and Veron et al (2002) observed a negative relationship between MAT and ANPP for winter wheat. Modeling temporal variability as a function of deviations in weather and cropping indicated that weather conditions account for the largest proportion of temporal BNPP and LENGTH patterns, cropping is the most important determinant of ANPP, and cropping and weather are equally important for DATEM.

Since silty soils are favored for cultivation, the higher ANPP observed for fine textured soils may simply be a consequence of those soils being more heavily cropped. When cropping is included in the model, it explains much of the ANPP patterns in the relatively moist and productive central, east and northeast parts of the region (Figure 3.1), leaving soil texture to account for ANPP variations in more xeric areas. In these semiarid locations, the inverse texture effect (Noy-Meir 1973) predicts that coarse textured soils will allow greater water penetration, minimize evaporation losses and therefore have higher productivity than fine textured soils. In an analysis of a smaller area within the U.S. Great Plains, Paruelo et al (2001) found that land use was the most important predictor of ANPP. My result that climate is slightly more important is very likely a consequence of the greater spatial extent, and therefore greater overall climatic variation in my dataset.

My temporal ANPP model indicated positive effects of both precipitation and temperature. Although temporal precipitation trends are known to positively influence ANPP, (Lauenroth and Sala 1992, Briggs and Knapp 1995), the temperature result is surprising since higher temperatures should decrease water availability, and thus have a negative impact on productivity. I observed that cultivation deviation for all five crops was positively related to ANPP, possibly as a result of increased carbon allocation to aboveground structures and/or increased resource availability as a consequence of irrigation and fertilization.

Controls over BNPP patterns: My spatial model for BNPP explained nearly two thirds of the observed variation. I found a positive relationship with MAP, which is consistent with general observations of total productivity and water availability in this region (Lauenroth et al. 1999). Lower BNPP in coarse textured soils is difficult to understand, but may be a consequence of the inverse texture effect causing coarse soils to have greater water availability and subsequently less belowground inputs in xeric areas while also causing coarse soils in mesic areas to have less water availability and decreased total productivity. The negative effect of soil depth is likely a consequence of cropping simultaneously decreasing soil depth through water and wind erosion and decreasing BNPP through altered carbon allocation (Chapter 1). My temporal BNPP model indicated a positive relationship between BNPP and precipitation but a negative relationship between BNPP and temperature. These results are likely a consequence of higher precipitation increasing water availability while higher temperatures decrease water availability.

Controls over biomass seasonality: Although my spatial models for phenological processes were relatively successful, the temporal models of both phenological processes explained an extremely small proportion of the observed variation. My observations of the end of the growing season are actually estimates of the time when plants lose green biomass as a consequence of switching from vegetative to reproductive growth. For native plants, the timing of this switch is somewhat elastic, and will be controlled by either temperature or precipitation, depending on which of these conditions first becomes limiting. Consistent with these expectations, I observed a positive relationship between MAP and LENGTH and a negative relationship between MAT and LENGTH. The positive relationship between MAP and LENGTH is likely a consequence of higher MAP increasing water availability late in the season causing longer growing seasons (Jobbagy et al. 2002). Although warmer temperatures are likely to cause earlier start of the growing season, thereby potentially lengthening the growing season, the strong effect of high temperatures on decreased water availability late in the season may outweigh this positive effect and cause shorter seasons (Jobbagy et al. 2002). I found that the abundance of most of the crops was negatively related to LENGTH, which is to be expected since crops typically initiate growth later than native vegetation and, relative to native plants, display consistent and uniform development that allows predictable harvest schedules.

I found that the influence of MAP on DATEM depends on weather the effects of cultivation are included in my model. The positive relationship between in the absence of cultivation has been previously observed (Jobbagy et al. 2002) and can be attributed to increased water availability causing increased growth later in the season. The negative relationship when cultivation is accounted for is unexpected, but may be a result of MAP influencing native vegetation more than crops. Since productivity in native vegetation is more tightly linked to MAP than in cultivated areas (Lauenroth et al 2000, Chapter 1) and native vegetation tends to have earlier seasonal development than most crops, areas with higher MAP have exhibit proportionally more early season growth than late season growth. I found that MAT is negatively related to DATEM, probably because warmer temperatures facilitate earlier start of the growing season (Jobbagy et al. 2002) as well as more rapid decrease in available water. Wheat is cultivated as a winter crop in much of the region and consequently has very early spring development (Martin et al. 1976). Hay consists of perennial plants that do not grow from seed like many other crops and thus have relatively rapid initial growth that can lead to early DATEM. By contrast, corn, soybeans and sorghum are all related to later DATEM, probably because these crops require warmer soil conditions and are planted and harvested relatively late in the season.

In general, my models performed better for spatial patterns than temporal patterns, and better for productivity than biomass seasonality. This may imply that the controls over temporal variation and biomass seasonality may not be as well understood as those that influence spatial patterns and productivity and may warrant more attention in the future. At the very least, it suggests that temporal variation and biomass seasonality do not respond to the environmental controls as I represented them in this study. I might have had better success in the temporal domain and with biomass seasonality if I had divided both climate and weather into seasonal components (e.g.. early season temperature, mid and late summer precipitation) and/or represented soil properties as indices with known relevance to water dynamics (i.e. soil water holding capacity) rather than simple measures of soil texture. In addition, my independent variables for temporal patterns only included weather and cropping conditions for the current year, and it is possible that conditions in previous years may influence both productivity and biomass seasonality.

Sensitivity analyses: I utilized the best overall models for productivity to estimate how changes in environmental conditions could impact ANPP and BNPP. These sensitivity analyses suggest that ANPP is most susceptible to variations in precipitation and cropping, whereas BNPP is equally sensitive to changes in climate, weather and soil conditions. Although the predicted response of ANPP to changing precipitation and temperature are not surprising, my results do indicate substantial sensitivity of ANPP to cropping intensity. Changes in cropping intensity of fifty percent produce ANPP changes greater than those predicted for 20% changes in MAP, implying that productivity in the U.S. Great Plains is highly sensitive to changes in cropping and that long-term predictions of carbon cycling in this region should consider the impact of cropping.

My models imply markedly different productivity response to changes in climate as opposed to changes in weather, a result that identifies potential limitations of studies that use spatial patterns to predict ecosystem responses to temporal changes. Previous studies have observed greater ecosystem response to climate than weather, and have suggested that this lag effect is a consequence of vegetation structure requiring time to respond to altered conditions (Lauenroth and Sala 1992). I predicted dramatically different magnitudes of ANPP responses to altered long-term vs. inter-annual precipitation and even different directions of BNPP responses to long-term vs. inter-annual temperature, implying that relationships in the spatial domain may not accurately predict the immediate response of productivity to climate change. These discrepancies have implications for the commonly used "space for time" substitution, in which spatial patterns are used to gain insight into the consequences of temporal changes.

I examined productivity response to altered cropping intensity in smaller areas within the U.S. Great Plains and found that although ANPP increases in all areas, the magnitude is highly variable and BNPP can have very small positive or negative changes. These variations in productivity response between subregions illustrates that the effect of cropping on ecosystem processes depends on the specific cropping practices in an area. In addition, they provide insight into the relative importance of different driving variables on ecosystem processes. As expected, climate patterns and weather conditions both account for a substantial proportion of process variation. This study is one of the first to consider the impact of land-use on large-scale ecosystem processes and my results indicate that cropping has a substantial impact on these processes, in many cases proving to be more important than climate or weather.

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Figure 3.1: Mean annual precipitation and temperature, soil percent sand and cropping intensity for 630 counties in the U.S. Great Plains.

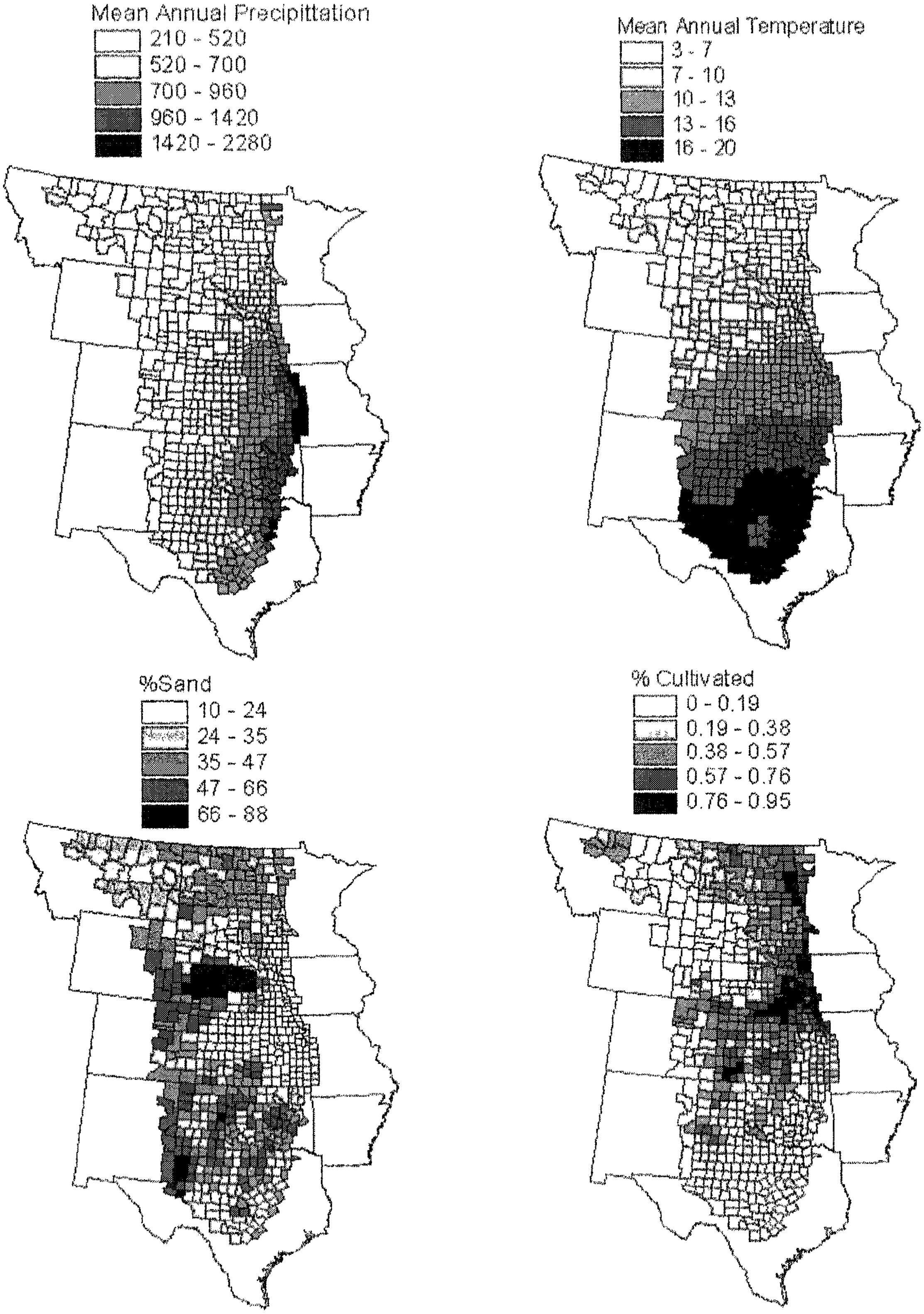


Table 3.1: Names, meanings and units for independent variables used in statistical models of spatial and temporal variability of net primary productivity and biomass seasonality.

domain	independent variable name	meaning
spatial	map	mean annual precipitation (mm)
	lmap	log(map)
	mat	mean annual temperature (°C)
	mapmat	interaction of map and mat
	clay	soil percent clay
	sand	soil percent sand
	ahor	depth of soil A horizon (cm)
	specific crops	percent of county harvested in each crop
	cultivation	total percent of the county that is cultivated
	C_3crops	percent of the county cultivated in C_3 crops
	C_4crops	percent of the county cultivated in C_4 crops
temporal	pptdev	precipitation for each year (mm)
	tempdev	temperature for each year (°C)
	*crop*dev	deviation from mean cultivation of *crop*
	cultdev	deviation from mean percent cultivated
	C_3cropsdev,	deviation from mean percent cultivated in C_3 crops
	C_4cropsdev	deviation from mean percent cultivated in C_4 crops

Figure 3.2: Subregions within the U.S. Great Plains. Letters refer to the location of each subregion (NW = northwest, etc.)

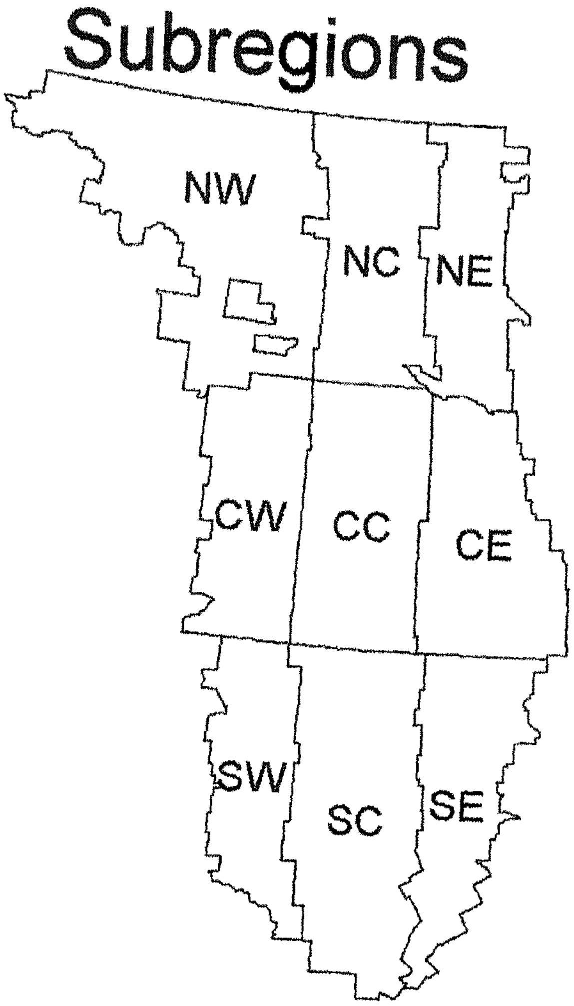


Table 3.3: Productivity and aboveground biomass seasonality variance partitioning into spatial and temporal components and partitioning of those components into driving variables.

Component	ANPP	BNPP	Length	Maximum
Components of variation				
Spatial	0.93	0.70	0.20	0.58
Temporal	0.07	0.30	0.81	0.42
Proportion of spatial variation explained				
Climate	0.59	0.29	0.41	0.26
Soil	0.04	0.06	0.02	0.01
Cultivation	0.31	0.31	0.11	0.29
Residual	0.06	0.35	0.47	0.44
Proportion of temporal variation explained				
Weather	0.11	0.19	0.07	0.03
Cultivation	0.28	0.11	0.01	0.03
Residual	0.61	0.70	0.92	0.93
Overall variation (spatial and temporal) explained by best model				
R^2	0.90	0.53	0.16	0.35
Residual	0.10	0.47	0.84	0.65

Figure 3.3: The relationship between cropping intensity and spatial (A) and temporal (B) coefficient of variability in above- and belowground productivity and spatial (C) and temporal (D) coefficient of variability in the length of the growing season and date of maximum NDVI.

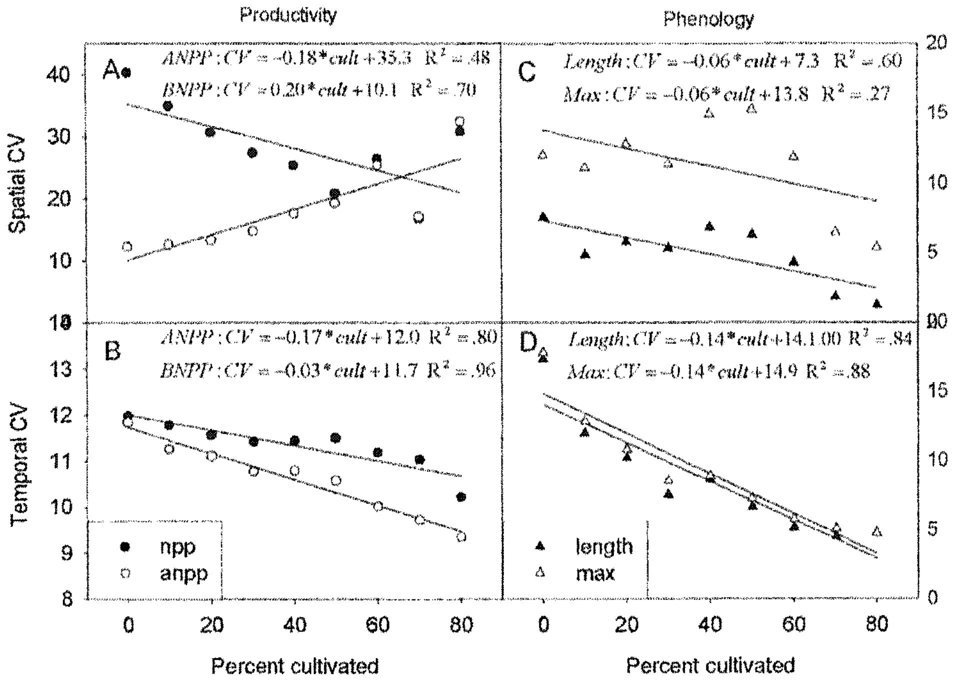


Figure 3.4: Sensitivity of above- and belowground productivity to changes in mean annual precipitation (A), mean annual temperature (B), annual precipitation (C), annual temperature (D), soil percent sand and clay (E) and cultivation proportion (F) in the U.S. Great Plains.

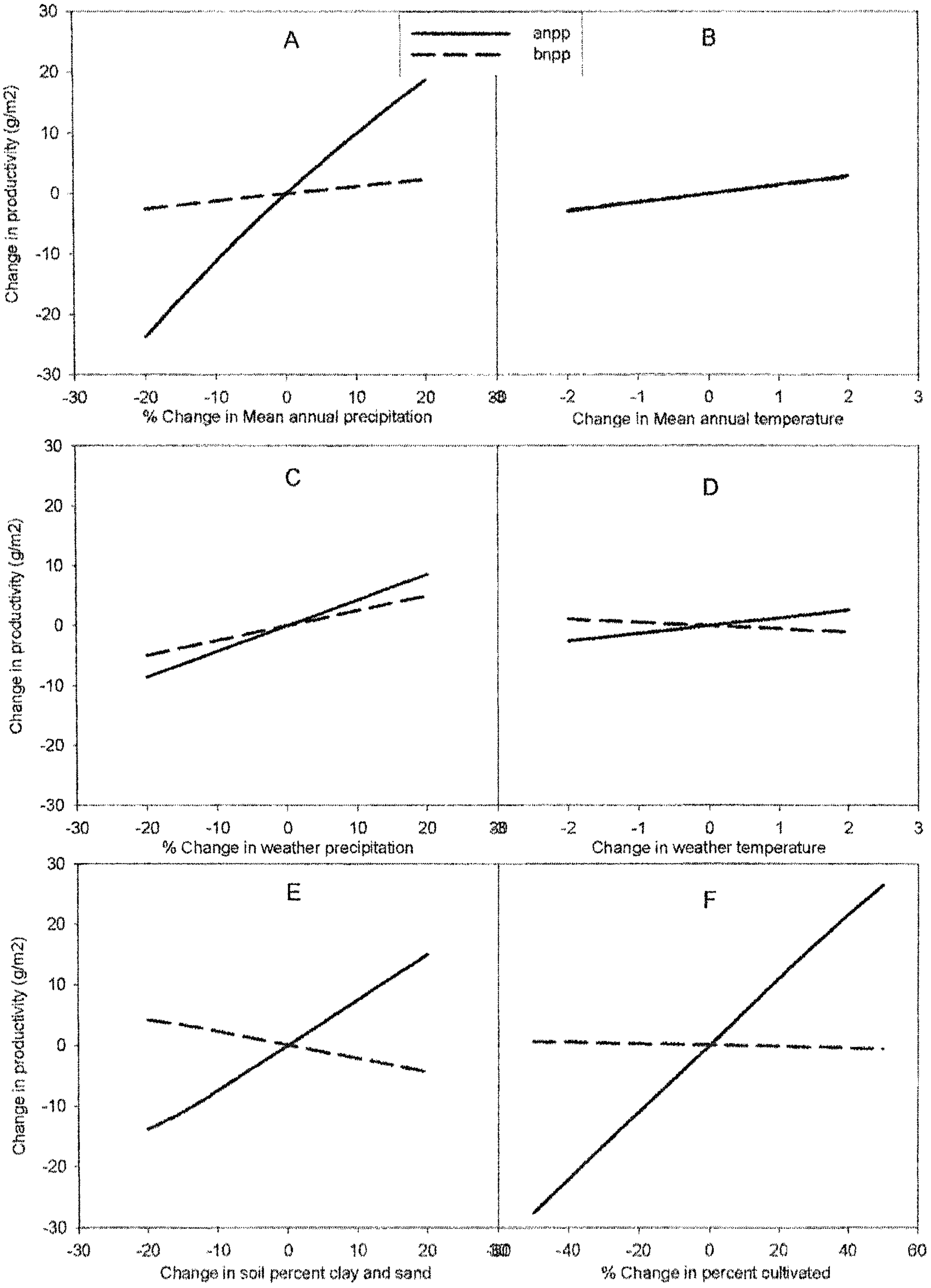
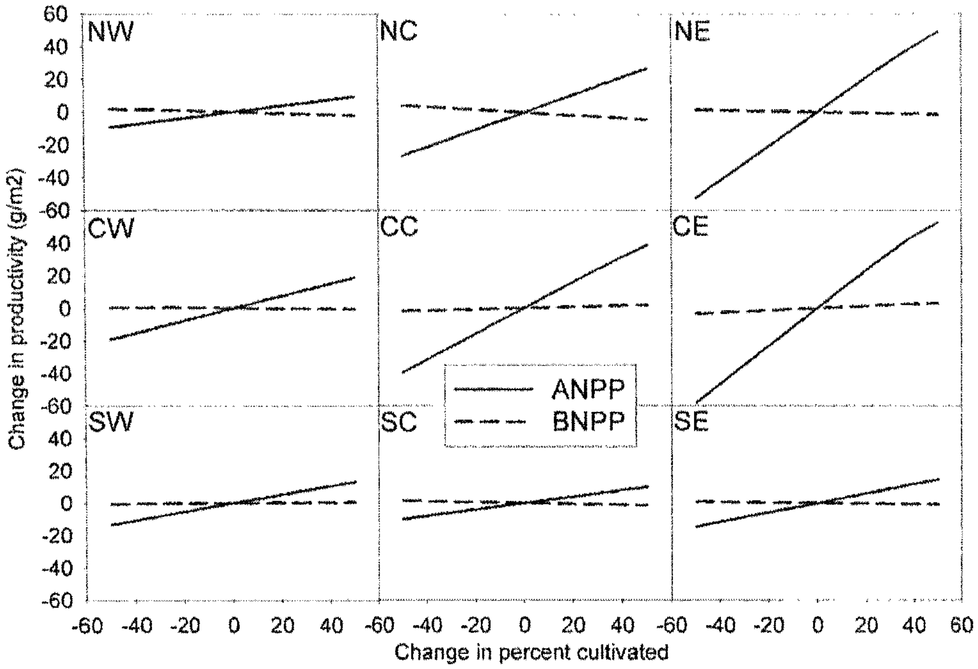


Figure 3.5: Sensitivity of above- and belowground productivity to changes in cropping intensity for 9 subregions within the U.S. Great Plains.



Appendix 3.1:References for allocation ratios for agricultural crops monitored.

Crop	Allocation ratio	Reference
Barley	0.50	Bolinder et al. 1997
Beans	0.26	Turpin et al. 2002 Crawford et al. 1997 Kloseiko et al. 2001
Corn	0.18	Allmaras et al. 1975 Anderson 1988
Cotton	0.14	McMichael and Quisenberry 1991 Mauney et al. 1992 Kimball and Mauney 1993
Hay	0.87	Bray 1963
Oats	0.40	Bolinder et al. 1997
Potato	0.10	Opena and Porter 1999 Jefferies 1993
Rye	0.24	Sheng and Hunt 1991
Sorghum	0.09	Piper and Kukakow 1994
Soybeans	0.15	Allmaras et al. 1975 Marvel et al. 1992 Silvius et al. 1977
Sunflower	0.25	Szaniawski 1983
Wheat	0.19	Bolinder et al. 1997 Sheng and Hunt 1991

Appendix 3.2: Model selection results for candidate models representing spatial variation in productivity and phenology

Category	Model	Number of parameters	AIC	Δ AIC	likelihood	model weight
		Length of the growing season				
climate	map	2	3093.43	375.75	2.56E-82	2.56E-82
	log(map)	2	3113.62	395.94	1.06E-86	1.06E-86
	mat	2	3097.20	379.52	3.88E-83	3.88E-83
	climate	3	2873.34	155.66	1.58E-34	1.58E-34
	climate and interaction	4	2851.19	133.51	1.02E-29	1.02E-29
climate with soil properties	climate & clay	5	2845.58	127.90	1.69E-28	1.69E-28
	climate& sand	5	2852.72	135.04	4.75E-30	4.75E-30
	climate & ahor	5	2849.40	131.72	2.50E-29	2.50E-29
	climate & texture	6	2845.93	128.25	1.42E-28	1.42E-28
	climate & clay and depth	6	2841.11	123.43	1.58E-27	1.58E-27
	climate & sand and depth	6	2850.78	133.09	1.26E-29	1.26E-29
	climate & texture and depth	7	2840.82	123.14	1.82E-27	1.82E-27
climate and soil with cultivation practices	climate, soil & two dominant crops	9	2761.41	43.72	3.20E-10	3.20E-10
	climate, soil & major crops	12	2717.68	0.00	1	1
	climate, soil & cultivation	8	2801.47	83.78	6.41E-19	6.41E-19
	climate, soil & C_3/C_4 crops	9	2751.24	33.55	5.18E-08	5.18E-08
		Date of maximum NDVI				
climate	map	2	3986.46	491.86	1.6E-107	1.561E-107
	log(map)	2	3982.76	488.17	9.9E-107	9.9154E-107
	mat	2	3829.36	334.77	2.03E-73	2.02602E-73
	climate	3	3814.81	320.21	2.93E-70	2.92869E-70
	climate and interaction	4	3799.32	304.72	6.78E-67	6.78E-67
climate with soil properties	climate & clay	5	3798.16	303.56	1.21E-66	1.21E-66
	climate& sand	5	3801.19	306.59	2.66E-67	2.66E-67
	climate & ahor	5	3797.68	303.08	1.54E-66	1.54E-66
	climate & texture	6	3799.29	304.69	6.89E-67	6.89E-67
	climate & clay and depth	6	3797.61	303.01	1.60E-66	1.60E-66
	climate & sand and depth	6	3799.61	305.01	5.86E-67	5.86E-67
	climate & texture and depth	7	3798.96	304.36	8.11E-67	8.11E-67
climate and soil with cultivation practices	climate, soil & two dominant crops	9	3575.72	81.12	2.42E-18	2.42E-18
	climate, soil & major crops	12	3494.60	0.00	1	1
	climate, soil & cultivation	8	3775.14	280.54	1.21E-61	1.21E-61
	climate, soil & C_3/C_4 crops	9	3663.11	168.51	2.56E-37	2.56E-37

Appendix 3.3: Model selection results for candidate models representing temporal variation in productivity and phenology

Model	Number of Parameters	AIC	Δ AIC	likelihood	model weight
Aboveground net primary productivity					
precipitation	2	35272.62	2148.11	0	0
temperature	2	35918.50	2794.00	0	0
weather	3	35265.56	2141.06	0	0
weather & two dominant crops	5	33620.56	496.06	1.91E-108	1.91E-108
weather & major crops	8	33124.50	0.00	1	1
weather & cultivation deviation	4	34003.37	878.87	1.43E-191	1.43E-191
weather & deviation of C_3crops and C_4crops	4	33185.1363	60.63	6.81E-14	6.81E-14
Belowground net primary productivity					
precipitation	2	27422.94	798.22	4.67E-174	4.67E-174
temperature	2	28492.32	1867.60	0	0
weather	3	27419.69	794.96	2.38E-173	2.38E-173
weather & two dominant crops	5	26976.19	351.46	4.79E-77	4.79E-77
weather & major crops	8	26624.72	0.00	1	1
weather & cultivation deviation	4	27291.33	666.61	1.77E-145	1.77E-145
weather & deviation of C_3crops and C_4crops	4	26700.2106	75.49	4.06E-17	4.06E-17
Length of the growing season					
precipitation	2	36223.44	209.07	3.99E-46	3.71E-46
temperature	2	36179.00	164.63	1.79E-36	1.66E-36
weather	3	36056.05	41.68	8.89E-10	8.26E-10
weather & two dominant crops	5	36057.96	43.59	3.42E-10	3.17E-10
weather & major crops	8	36061.34	46.97	6.32E-11	5.87E-11
weather & cultivation deviation	4	36019.49	5.12	7.73E-02	7.18E-02
weather & deviation of C_3crops and C_4crops	4	36014.37	0.00	1	1
Date of maximum NDVI					
precipitation	2	33965.58	310.63	3.53E-68	3.53E-68
temperature	2	33883.58	228.63	2.26E-50	2.26E-50
weather	3	33850.86	195.90	2.89E-43	2.89E-43
weather & two dominant crops	5	33719.73	64.78	8.59E-15	8.59E-15
weather & major crops	8	33654.96	0.00	1	1
weather & cultivation deviation	4	33842.59	187.63	1.80E-41	1.80E-41
weather & deviation of C_3crops and C_4crops	4	33776.42	121.46	4.21E-27	4.21E-27

CHAPTER 4: CHEATGRASS ABUNDANCE ESTIMATION FROM MULTI-DATE MULTI-SPECTRAL IMAGERY

ABSTRACT

Non-native plant species have invaded many terrestrial ecosystems and previous studies have suggested that these invasions can modify energy flow and nutrient cycling as well as plant species compositions. To quantify the overall impact of these invasions, we need to understand the spatial distribution and abundance of the invaders. Consequently, obtaining accurate and reliable distribution maps for invasive plants has become a crucial step in both research and management efforts in invaded ecosystems. I tested the ability of multi-date LANDSAT imagery to detect cheatgrass (*Bromus tectorum*), an annual cool season grass originally from Asia and Europe that has spread throughout much of western North America and dramatically altered many ecosystems in these areas. Cheatgrass displays early seasonal development compared to most native species. By comparing ground measurements of plant species cover with spectral response at multiple times throughout the growing season, I quantified the extent to which this phenological difference can facilitate cheatgrass detection. Using a model selection approach to determine the best transformation of the spectral data and the best statistical relationship between spectral response and ground observations, I found a significant relationship between spectral response and cheatgrass abundance ($R^2 = 0.647$).

This relationship indicates that cheatgrass detection is possible with multi-spectral imagery, and could be used to create cheatgrass distribution maps. I suggest that the strength of this relationship could be improved by either obtaining higher spatial resolution imagery that more accurately captures cheatgrass patches or by utilizing hyperspectral imagery that would allow subpixel unmixing of the observed spectra.

INTRODUCTION

In the past two centuries humanity has facilitated biological invasions by removing natural barriers to dispersal (Mack and Lonsdale 2001). Whereas physical barriers once kept species geographically isolated, intercontinental travel now transports organisms around the world, placing species into entirely different ecosystems, biomes and continents (Vitousek et al. 1996). The consequences of these introductions are diverse and widespread and include altered nutrient cycling (Vitousek 1990), modified disturbance regimes (Mack and D'Antonio 1998) and increased extinction rates (D'Antonio and Vitousek 1992). As ecologists attempt to understand the causes and consequences of these invasions, and land managers strive to identify prevention and control strategies, developing methods for detecting particular invasive species has become an important goal for both scientists and managers. For plant invasions, optical remote sensing is one technique with potential for mapping the distribution of invasive plants (Roughgarden et al. 1991). Compared to alternative detection techniques (i.e. long-term field sampling and monitoring), remote sensing has several advantages, notably low cost for wide coverage and data consistency across multiple years. However, in order to successfully identify individual species, remote sensing requires the target species be a locally widespread invader, to exist in reasonably abundant patches, and most importantly to display different reflectance spectra than other plant species in the area (Cochran 2000).

One of the most important invasive species in western North America in terms of area covered and impact on native plant communities is cheatgrass (*Bromus tectorum L).* A winter annual cool season grass originally from Asia and Europe (Novak and Mack 2001), cheatgrass has become prevalent throughout much of the western United States. It is a promising candidate for detection with remote sensing because it has a unique phenology for this region. Cheatgrass germinates and grows rapidly throughout the fall, assumes a semi-dormant state for the winter, produces seedheads in the spring and senesces in early summer (Thill et al. 1984). Fall germination allows cheatgrass to utilize winter and early spring precipitation that is typical in much of the intermountain region of the U.S. (Knapp 1996), and creates a distinct developmental signature that may prove useful as a detection tool for remotely sensed imagery acquired at multiple times during the growing season (e.g. Knick et a. 1997.) Cheatgrass reaches maximum photosynthesic activity in late spring, whereas native vegetation reaches maximum photosynthetic activity in early to mid summer (Paruelo and Lauenroth 1995).

Remotely sensed observations of plant function have mapped vegetation structure in the U.S. Great Basin (Paruelo and Lauenroth 1995) and other areas (Lloyd 1990, Paruelo et al. 1993). Kremer and Running (1993) examined the ability of imagery with 1km pixel size to detect cheatgrass and found that although the remotely sensed phenological signature of cheatgrass was statistically separable from native shrubs, the classification accuracy was confounded by subpixel variation in topographic and soil reflectance. In this study, I attempt to address some of the issues identified in Kremer and Running (1993) by employing imagery with higher spatial resolution and including available information on soil variability.

My general goal in this study was to determine how well widely available LANDSAT imagery detect cheatgrass. Specifically, my objectives were 1) to compare the strength of the statistical relationship between various combinations of multi-date, multi-spectral imagery and cheatgrass abundance, 2) to quantify the extent to which including available soil and vegetation disturbance information can strengthen these relationships, and 3) to examine the predictive ability of the best statistical relationship and other techniques including supervised classification and spectral mixture analysis.

METHODS

Study site: The Snake River Birds of Prey National Conservation Area (BOP) on the Columbia Plateau in southwestern Idaho is located approximately 70km southwest of Boise, Idaho. BOP (116°E, 43°N) covers ~240,000 ha of semi-arid mixed shrubs, grasses and agricultural land around the Snake River. Elevation at the canyon rim is approximately 1000m. Hot, dry summers and moist, mild winters typify the climate (Figure 4.1). Plant communities are dominated by big sagebrush (*Artemisia tridentata*) in the north and a combination of winterfat (*Ceratoides lanata*) and saltbush (*Atriplex* spp.) toward the south. Native bunchgrasses included bluebunch wheatgrass (*Agropyron spicatum*) and western wheatgrass (*Agropyron smithii*) (West 1983), but currently consist primarily of bottlebrush squirreltail (*Sitanion hystrix*), Sandberg's bluegrass (*Poa secunda*) and six-weeks fescue (*Vulpia octoflora*). Widespread wildfires in the 1980s have facilitated a patchy conversion to plant communities dominated by cheatgrass, Bur buttercup (*Ranunculus testiculatus*) and Russian thistle (*Salsola iberica*) (Kochert and Pellant, 1986). Grazing and military exercises are the primary land-use practices on BOP.

LANDSAT data: I obtained 4 LANDSAT ETM images acquired on March 30, June 2, June 18 and Oct 8 2000 (Figure 4.2 and 4.3). These images were referenced to RMS error of less than 30 meters and atmospherically corrected using ACORN Version 3.12 (Acorn 2001), which considers radiance arriving at the sensor as

$$L_t = \frac{F_0}{\pi}\left(R_a + \frac{RT_dT_u}{1-SR}\right)$$

where L_t is total radiance arriving at the sensor, F_0 is solar irradiance at the top of the atmosphere, R_a is the reflectance of the atmosphere, T_d and T_u are the downward and upward transmittance of the atmosphere, S_r is the downward reflectance of the atmosphere and R is the spectral reflectance of the surface. Solving for R yields:

$$R = \left(\left(\frac{F_0T_dT_u}{\pi} \Big/ \frac{L_t - F_0R_a}{\pi}\right) + S\right) - 1$$

ACORN uses sensor properties (gain, offset, wavelength) and empirically measures solar irradiance information to approximate F_0, T_d, T_u, R_a and S and calculate R.

I calculated the following vegetation indices for each image: the normalized difference vegetation index (NDVI) (rouse et al. 1973), the soil adjusted vegetation index (SAVI) (Huete 1988), the modified soil adjusted vegetation index (MSAVI) (Qi 1994), the transformed soil adjusted vegetation index (TSAVI) (Baret et al. 1989) and the tasseled cap transformation (Kauth and Thomas 1976) (Table 4.1). Both SAVI and MSAVI incorporate a parameter (L) relating to vegetation abundance where values of L range from 0 for abundance vegetation to 1 for sparse vegetation (Huete 1988, Qi 1994). Since my study site contains sparse vegetation I set L equal to 1.0.

Vegetation data: I utilized vegetation data from 162 transects in the BOP area (J.L.Downs, personal communication). The transects were 100 meters long and point-intercept aerial cover was recorded every meter for the length of the transect. These vegetation transects were all sampled during the summer of 2000. The location of the start of each transect was measured to 5m accuracy using a global positioning system receiver and the direction recorded to allow transfer into a geographic information system. I obtained soil classification data from the USDA State Soil Geographic database (STATSGO: USDA 1989). Although relatively coarse in spatial resolution, the STATSGO soil data represented the only available information about soil conditions within the study site. The vegetation transects exist on the Orchard Training Area, a military installation, and the Department of Defense records disturbances that occurs on the transects from military exercises. I utilized these data as a general indicator of vegetation disturbance in my analysis by including the number of points along the transect that were visibly disturbed (i.e. vegetation removed or killed) in the year 2000. Disturbance level, along with soil class, was included in the regression analysis described below.

Data analysis 1 – Statistical models: My first objective was to examine statistical relationships between cheatgrass abundance and spectral features. I entered the transects into a geographic information system and overlayed them on the images. I extracted the mean reflectance value of all bands and vegetation indices for each transect into a database to use for statistical analysis. Based on these vegetation indices and band reflectance values, I created a set of candidate statistical models of the multispectral data to compare with cheatgrass abundance.

I generated candidate statistical models by combining 6 methods for transforming the observed reflectance values (Table 4.1) into indicators of vegetation with 16 different combinations of the transformed reflectance data (Table 4.2). The 6 methods of transforming reflectance included the 5 vegetation indices mentioned above and the untransformed reflectance values. For each of these 6 transformations, I conducted multiple linear and logit-transformed regressions of cheatgrass abundance against the transformed reflectance values. Regressions on logit-transformed data use a simplified version of the logistic function and are commonly employed for representing response variables that range from 0 to 1 (Legendre and Legendre 2000). I employed logit transformation to represent spectral response data according to the following formula:

$$y = \frac{1}{(1+e^{x})}$$

where y = predicted cheatgrass abundance and

$$x = \beta_0 + \beta_1 band_1 + \beta_2 band_2 + \beta_3 band_3 + \beta_4 band_4 .... \beta_{24} band_{24}$$

Since transects with consistent reflectance are less likely to contain a mixture of high and low cheatgrass areas, I conducted weighted and unweighted regressions using the inverse of the spatial reflectance variability as a weight for each transect (number of pixels per transect = 3 – 5). To examine the potential improvement that including soil and/or disturbance information in the analysis could make to these relationships, I included statistical models with soil, disturbance and both soil and disturbance in each candidate set of statistical models.

To compare these statistical models, I employed a method developed by Burnham and Anderson (2001) that relies on likelihood theory to quantify the amount of evidence for each model contained in the data. This method uses Akaike's Information Criterion (AIC) as an indicator of the information lost when a statistical model approximates truth and ranks models according to the support for each model contained in the observed data. The loglikelihood of each statistical model is calculated as

$$\log(\ell(\hat{\theta})) = -\frac{n}{2}\log(\hat{\sigma}^2)$$

where $\ell(\hat{\theta})$ is the likelihood of model $\hat{\theta}$ given the observed data and $\hat{\sigma}^2$ is the residual sum of squares divided by the sample size n. From these loglikelihood values, I calculated AIC_c (AIC corrected for small sample size) for each statistical model as:

$$AIC_c = -2\log(\ell(\hat{\theta})) + 2K + \frac{2K(K+1)}{(n-K-1)}$$

where K is the number of estimated parameters (including an estimate of variance). Smaller values of AIC_c indicate that the statistical model is closer to the truth (never known). The difference between AIC_c values (Δ_i) of competing models provides insight into the relative strength of support in the data for the various models, with differences of 1-2 AIC units suggesting substantial support, 3-7 AIC units indicating less support and >10 units implying no support in the data. Model weights are interpreted as the weight of evidence in favor of a model, and for a set of n candidate models are calculated as

$$weight_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{1}^{n}\exp\left(-\frac{1}{2}\Delta_i\right)}$$

This method has the advantage that it utilizes models created prior to data analysis and contains a penalty for each parameter included, thereby minimizing the possibility of identifying spurious results (Burnham and Anderson 2001). Avoiding spurious results that are specific to an individual dataset is especially appealing for my analysis because I was interested in identifying representations of the multi-spectral data that have the general ability to predict cheatgrass, rather than characterizing a relationship between spectral features and vegetation composition that is specific to this dataset.

I compared my set of *a priori* statistical models against the cheatgrass abundance data using SAS/STAT (SAS System for Windows 2001) and calculated the model weights. I also calculated the adjusted coefficient of determination for each model in order to quantify the strength of the relationship between the multi-spectral data and cheatgrass abundance. To quantify the predictive ability of the best statistical model, I cross validated my results by removing 10% of the transects, recalculating the regression parameters using the best model and using these parameter values to predict cheatgrass abundance in the 10% of transects that were not used in the analysis. By repeating this analysis 10 times, omitting a different 10% of the transects each time, I obtained predictions for all of the transects. This method provides insight into the ability of the model to predict cheatgrass abundance for pixels not included in the dataset from which parameters were estimated.

Data analysis 2 – spectral unmixing: I examined the potential of spectral unmixing to predict cheatgrass adunance. Spectral unmixing techniques are based on the concept that an observed spectrum can be decomposed into the sum of pure spectra (endmembers) from multiple surfaces and this technique has been successfully performed with multi-date, multi-spectral imagery (Adams et al 1995, Smith et al. 1990). To conduct spectral unmixing, I utilized the mixture tuned matched filtering (MTMF) procedure in ENVI (Environment for Visualizing Images 2001), which treats the spectrum of each pixel as a mixture of multiple pure spectra, or endmembers. MTMF can unmix the spectra for each pixel into proportions of all endmembers identified or based on the proportion of a single endmember. Since I was only interested in cheatgrass abundance, I unmixed the spectra for a single endmember. I attempted two independent methods to create this endmember. First, I averaged the spectra for the 3 transects with highest cheatgrass abundance and unmixed the image for that spectra. Second, I ran the pixel purity index routine in ENVI (Environment for Visualizing Images 2001), to identify the 0.5% of pixels that are most likely to be pure (i.e. contain a single endmember). I examined these pixels and calculated the mean spectral response of three pixel clusters that display spectral features consistent with my expectations for cheatgrass (i.e. high blue and red absorption early in the season followed by decreased absorption late in the season.) I unmixed the image based on each of these three spectra independently and compared the predictions with observed cheatgrass abundance. I only present the results for the spectra with the best performance.

Data analysis 3 – classification: I quantified the predictive ability of the multispectral data to characterize cheatgrass density with classification and spectral unmixing routines using all 24 ETM bands. I divided the transects into 3 classes of cheatgrass abundance (high, medium and low, corresponding to <=10, 11-40 and >40 cheatgrass observations within the transect) and divided the transects in each class into training and test groups. I used the training groups to conduct supervised classifications using both Bayesian maximum likelihood and feed-forward neural network classifiers (Richards and Jia 1994) in ENVI. I then examined how well the classified images predicted cheatgrass abundance in the test groups and created error matrices and overall accuracy estimates for each classification. The 76 validation transects consisted of 45 low, 17 medium and 14 high. To quantify the accuracy of both classification techniques and of the best regression model, I created error matrices, determined omission and commission errors for each class, and calculated overall accuracy (percent of transects correctly classified) and the K_{hat} coefficient, which is a separate measure of overall accuracy determined by KAPPA analysis that includes omission and commission errors and indicates whether the classification results are significantly different from a random result (i.e. K_{hat} coefficient values less than or near 0 indicate a result only slightly better than a random result (Congalton 1991). To facilitate comparison of the predictive ability of the best regression model with the classification routines described below, I divided transects into the same 3 classes and generated a prediction error matrix and overall accuracy estimate for the best regression model.

RESULTS

Statistical models: Of the statistical models I compared, the best model employed a logit-transformed regression and used untransformed reflectance values (Table 4.3: logit model in BANDS). Although the best model did not include weighted regression, soil, or disturbance information, I observed some support (models with $\Delta_i < 10$ where Δ_i is the difference between the model AIC and the AIC of the best model) in the data for the linear model (linear), the linear model with disturbance (linear_d) and the logit transformed model with disturbance (logit_d). My data indicate essentially no support for any of the other 94 models I examined. The best model displayed a coefficient of determination between observed cheatgrass abundance and predicted cheatgrass abundance of 0.647 with a 80% confidence interval width of approximately 18% cheatgrass abundance (Figure 4.4).

The regression model correctly classified 79 of the 97 transects in the low cheatgrass abundance class (Table 4.4). Of the remaining 18 transects, 14 were identified as medium and 4 as high cheatgrass abundance. Twenty of the 52 transects in the medium class were correctly classified by the regression model, with 18 mistakenly classified as low and 14 mistaken as high cheatgrass abundance. Of the 18 transects with high cheatgrass abundance, 12 were correctly identified by the regression model, 5 were classified as medium and 1 as low abundance. These results produced omission error rates of 19%, 49% and 60% and commission rates of 19%, 62% and 33% for the low, medium and high classes, respectively. My regression model generated an overall prediction accuracy of 66% and a K_{hat} coefficient of 0.409.

Spectral unmixing: The spectral unmixing procedure estimates the proportion that the target endmember comprises of the observed spectra. I identified 4 spectral signatures as potential cheatgrass endmembers (1 from transects with high cheatgrass abundance and 3 "pure" endmembers with early phenological characteristics) and unmixed the image relative to those endmembers. Although none of these endmembers are likely to represent pure cheatgrass, it is reasonable to expect that they contain many spectral features in common with cheatgrass dominated areas, and therefore their proportion within each pixel's observed spectra may correlate with cheatgrass abundance. None of the predictions of cheatgrass abundance from the spectral unmixing displayed reliable relationships with observed cheatgrass abundance.

Classifications: The maximum likelihood classifier correctly classified 35 of the 45 transects in the low class (Table 4.4). Of the ten remaining transects, 9 were misidentified as medium and 1 as high. Eight of the 17 medium transects were correctly classified while the remaining 9 where classified as low. The maximum likelihood classifier didn't correctly identify any of the transects in the high class, classifying 5 low and 9 as medium. These results indicate omission errors of 22%, 53% and 100% for low, medium and high classes, respectively. Commission errors were similar with values for low, medium and high of 29%, 69% and 100%. The overall accuracy of the maximum likelihood classifier was 57%, with a K_{hat} coefficient of 0.194.

The neural network classifier correctly identified only 16 of the 45 low transects and classified 11 of the remainder as medium and 18 as high. Of the 17 medium transects, only 5 were correctly classified, 8 were identified as low and 4 as high. Four of the 14 high transects were correctly classified, while 7 were misidentified as low and 3 as medium. The neural network classifier produced omission error rates for the low, medium and high classes of 64%, 71% and 71%, with commission error rates of 48%, 74% and 85%. The overall accuracy was only 33% with a K_{hat} coefficient of –0.049.

DISCUSSION

My model selection results indicate that the untransformed reflectance values were more useful for predicting cheatgrass abundance than any of the vegetation indices I examined. I expected the unique phenology displayed by cheatgrass to cause heavily invaded areas to have earlier seasonal development observable by vegetation indices. The fact that the untransformed values were superior to any of the vegetation indices suggests that variation in cheatgrass abundance influences spectral response in ways not necessarily captured by temporal trends in overall vegetation structure as measured by vegetation indices. Of the vegetation indices I examined, the tasseled cap transformation was the most successful, followed by NDVI and SAVI, which produced extremely similar results, MSAVI and TSAVI. Although my study areas contained sparse vegetation and consequently a strong signal from soil, the vegetation indices that were specifically designed to control for soil variability (SAVI, MSAVI, TSAVI) performed no better than NDVI, a vegetation index that does not include any soil adjustment factors. In addition, the best model I identified did not include information about soil properties or disturbance condition. Nor did my best model employ a weighted regression method, indicating that using spectral variability as an indicator of consistency of cheatgrass abundance may not be work or that the consistency of cheagrass abundance within a transect does not influence the ability of remote sensing methods to quantify it.

I observed that the logit-transformed regression performed better than linear regression for all 6 reflectance transformations, implying that the relationship between cheatgrass abundance and spectral response is non-linear. This non-linearity has previously been observed between vegetation density and spectral response (Myneni et al. 1997) and is likely a consequence of very small amounts of cheatgrass having essentially no influence on spectral response until cheatgrass abundance reaches a intermediate level. The observation that my best model tends to overestimate abundance in low cheatgrass areas and underestimate abundance in high cheatgrass areas (Figure 4.4) indicates that the model is not sufficiently responsive to either very high or very low cheatgrass abundance and may suggest that alterative non-linear functions might yield better fit between predictions and observations. In addition, errors in the independent variables (i.e. unaccounted variation in the remote sensing data) may contribute to this lack of fit (Curran and Hay). These results suggest a threshold effect, in which cheatgrass is undetectable at very low abundances, but has an approximately linear effect on spectral response at intermediate and high abundances. Non-linearity between cheatgrass abundance and spectral response may explain the general failure of the spectral unmixing routine, which assumes that the observed spectrum is a mixture of multiple endmembers that are linearly related to the abundance of the endmembers on the ground (Smith et al. 1990). Non-linearities between cheatgrass density and its reflectance would cause substantial problems with this technique.

My best regression model produced better predictions than either of the classification techniques I examined. Both the classifications and the regression model had difficulty correctly classifying transects with high cheatgrass abundance. This difficulty may be a consequence of transects with high cheatgrass also having high abundance of other plants, making the task of separating the cheatgrass signal from other species more difficult than areas of low total vegetation. My data did show a positive relationship between cheatgrass abundance and NDVI (not shown), which supports the idea that cheatgrass abundance is generally related to total vegetation abundance.

I anticipate that more accurate predictions could be generating by addressing two potential sources of error in my methods. First, the spatial patterns of cheatgrass abundance may not correspond with the spatial resolution of the ETM imagery I utilized. If cheatgrass patches are small enough that most pixels are a mixture of cheatgrass patches and other patches of other vegetation, all remote sensing techniques will have greater difficulty accurately characterizing the ground cover (Grunblatt, 1987). Specifically, homogeneous cheatgrass patches with a diameter less than twice the pixel size may produce a spectral response that is a mixture of multiple cheatgrass abundance signals and may be difficult to accurately cheatgrass abundance on the ground. I attempted to control for this complication by weighting the influence that the transects have on the regression analysis by the inverse of the spatial spectral variability but found that the weighted regression technique did not improve the statistical relationship between cheatgrass abundance and spectral response. I suggest obtaining spectra from numerous areas with known vegetation abundance and composition, including leaf level spectra from cheatgrass and other species. Comparisons of spectra from areas with similar soil and other plant species but with different cheatgrass abundance will provide further quantification of the ways in which cheatgrass abundance alters the observed spectra of an entire scene.

The second potential complication is the confounding effects of soil reflectance variability on the overall observed spectrum. Since my study site contains very sparse vegetation with low leaf area, the spectral response includes a substantial component from soil that isn't blocked by vegetation. Soil properties can cause variations in soil reflectance (Huete 1987), which can dramatically influence the total observed reflectance in areas with low vegetation canopy closure (Asner 1998). Despite my attempts to address this problem by utilizing vegetation indices specifically designed to separate vegetation signal from soil signal (Table 4.1: SAVI, MSAVI, TSAVI, tasseled cap), the best statistical model did not utilize any of these indices. Consequently, I expect that soil reflectance variability is influencing my results. I suggest that further studies address this issue directly by obtaining spectra of soil as well as several of the prevalent plant species at multiple times throughout the growing season and use these data to un-mix the observed spectrum. If acquired throughout the growing season, these spectra could quantify the separability of cheatgrass from native plant species based on phenology (e.g. Michelson et al 1998, Key et al. 2001). Ideally, these spectra would be obtained with a hyperspectral instrument to facilitate investigation of the possibility of cheatgrass identification though spectral features not observable with multi-spectral imagery (Goetz et al 1985, Cochran 2000). My efforts at subpixel unmixing focused only on modeling the abundance of the cheatgrass endmember rather than the all components of the image, and the endmembers I identified as potentially cheatgrass may not have been sufficiently representative of cheatgrass spectra. In addition, Okin et al (2001) suggested that vegetation cover must exceed 30% for successful spectral unmixing of hyperspectral imagery, so my lack of success with this technique may stem from insufficient vegetation cover for unmixing with ETM data.

Despite the limitations of these results, my best statistical relationship displayed a promising relationship with cheatgrass abundance and I was able to utilize this relationship to generate predictions of cheatgrass distribution in my study site (Figure 4.5). In addition, my results identify further studies that may be able to strengthen the relationship between remotely sensed information and cheatgrass abundance. Although the applicability of the detection techniques utilized here to other areas invaded by cheatgrass remains untested, this method may prove a useful tool for mapping cheatgrass distribution and abundance.

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Figure 4.1: Mean monthly precipitation (mm) and temperature (°C) for the Birds of Prey National Conservation area in SW Idaho.

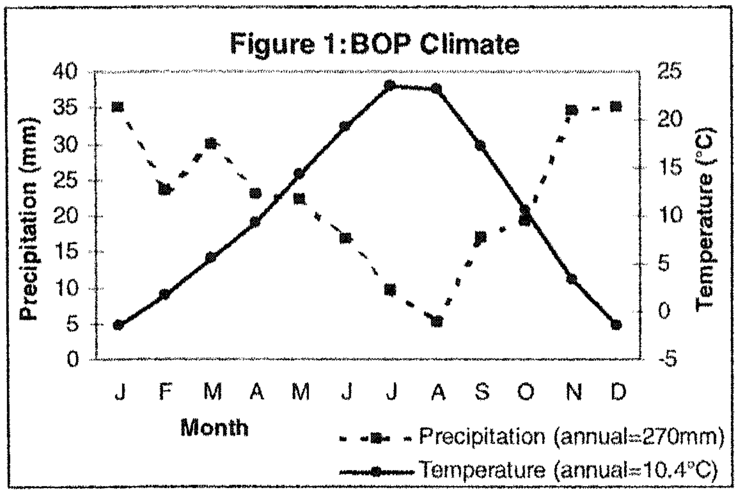


Figure 4.2: Annual patterns of live biomass for cheatgrass and native plants in the U.S. Great Basin (Hulbert 1955, Harris 1967) and dates of LANDSAT image acquisition for this study.

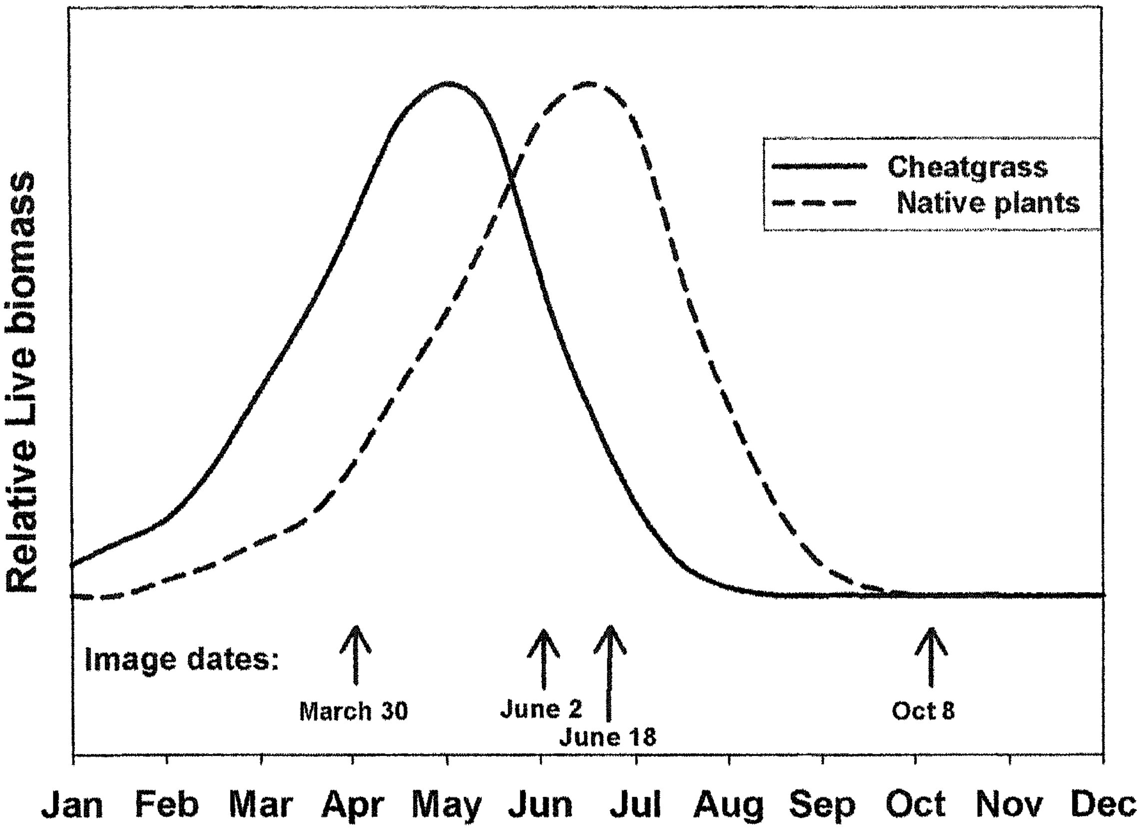


Figure 4.3: Infrared color composite LANDSAT ETM image of the study are in and around the Birds of Prey National Conservation Area in SW Idaho.

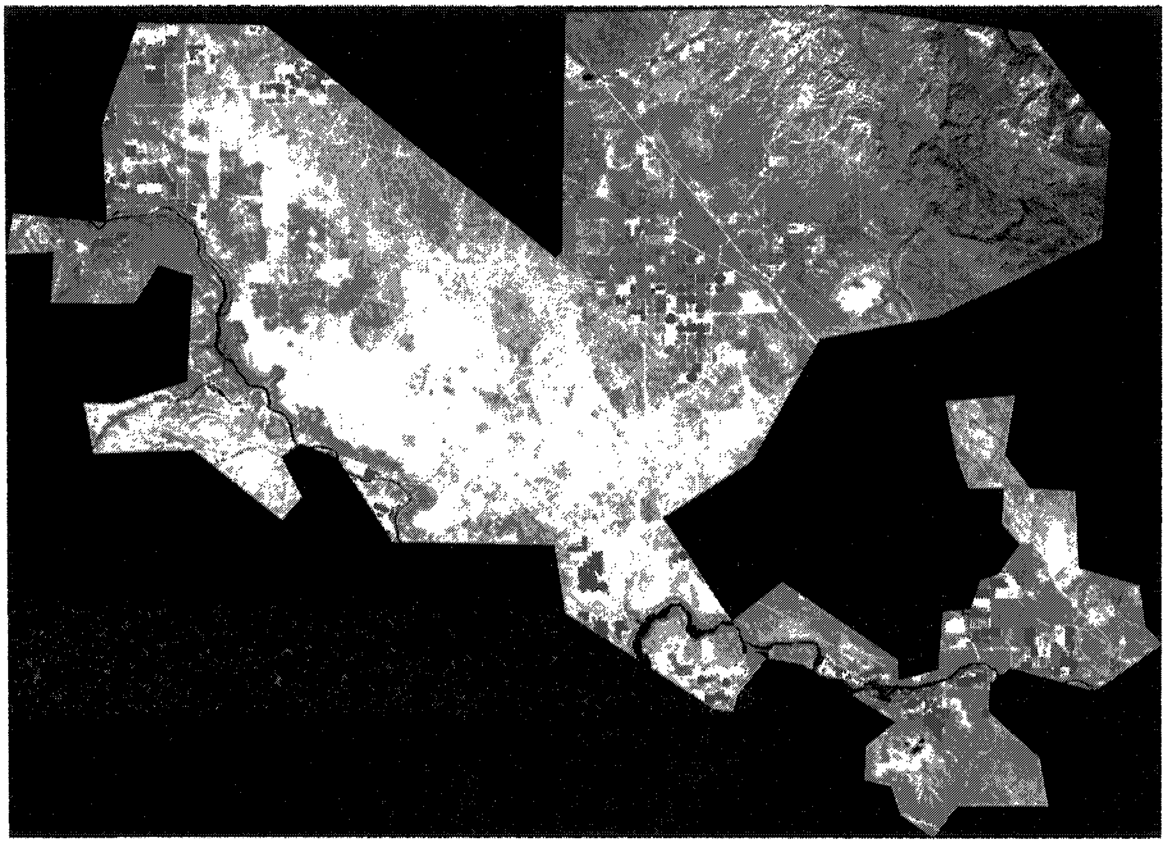


Table 4.1: Spectral transformations applied to the LANDSAT ETM data prior to implementing statistical models for predicting cheatgrass abundance at the Birds of Prey National Recreation area in SW Idaho.

Abbreviation	Name	Reference
NDVI	Normalized Difference Vegetation Index	Rouse et al. (1973)
SAVI	Soil Adjusted Vegetation Index	Huete, A. R. (1988)
MSAVI	Modified Soil adjusted Vegetation index	Qi et al. (1994)
TSAVI	Transformed soil adjusted vegetation index	Baret et al. (1989) Baret and Guyot (1991)
Tasseled cap	Tasseled Cap Transformation	Kauth and Thomas (1976)
Bands	Atmospherically corrected reflectance values for LANDSAT ETM bands 1-5 and 7	

Table 4.2: Statistical models applied to each spectral transformation to generate candidate models for predicting cheatgrass abundance from LANDSAT imagery acquired over the Birds of Prey National Recreation area in SW Idaho..

Abbreviation	regression technique	soil type information included?	weighted by reflectance variability ?	disturbance information included?
linear	linear	No	No	No
linear_w	linear	No	Yes	No
linear_s	linear	Yes	No	No
linear_ws	linear	Yes	Yes	No
linear_d	linear	No	No	Yes
linear_wd	linear	No	Yes	Yes
linear_sd	linear	Yes	No	Yes
linear_wsd	linear	Yes	Yes	Yes
logit	logit transformed	No	No	No
logit_w	logit transformed	No	Yes	No
logit_s	logit transformed	Yes	No	No
logit_ws	logit transformed	yes	Yes	No
logit_d	logit transformed	No	No	Yes
logit_wd	logit transformed	No	Yes	Yes
logit_sd	logit transformed	Yes	No	Yes
logit_wsd	logit transformed	Yes	Yes	Yes

Table 4.3: Model selection results for models generated to predict cheatgrass abundance from multi-date LANDSAT imagery at the Birds of Prey National Recreation area in SW Idaho..

Reflectance transformation	Statistical representation	loglikelihood	R^2	K	AIC	AICc	Δi	model likelihood	model weight
NDVI	linear	310.584	0.359	6	-609.1682	-608.6432	50.14	1.29E-11	1.01E-11
	linear_w	309.927	0.355	6	-607.8535	-607.3285	51.46	6.70E-12	5.22E-12
	linear_s	317.450	0.409	13	-608.9003	-606.5212	52.26	4.48E-12	3.49E-12
	linear_ws	316.523	0.404	13	-607.046	-604.6669	54.12	1.77E-12	1.38E-12
	linear_d	310.766	0.360	7	-607.5321	-606.8277	51.96	5.22E-12	4.06E-12
	linear_wd	309.860	0.355	7	-605.7205	-605.0161	53.77	2.11E-12	1.64E-12
	linear_sd	317.590	0.410	14	-607.1805	-604.4174	54.37	1.56E-12	1.22E-12
	linear_wsd	316.478	0.404	14	-604.9551	-602.192	56.59	5.14E-13	4.00E-13
	logit	312.780	0.376	6	-613.5599	-613.0349	45.75	1.16E-10	9.05E-11
	logit_w	311.762	0.369	6	-611.5236	-610.9986	47.79	4.20E-11	3.27E-11
	logit_s	320.244	0.429	13	-614.4873	-612.1082	46.68	7.31E-11	5.69E-11
	logit_ws	318.763	0.420	13	-611.5257	-609.1466	49.64	1.66E-11	1.30E-11
	logit_d	312.783	0.376	7	-611.5658	-610.8614	47.92	3.92E-11	3.05E-11
	logit_wd	310.458	0.361	7	-606.917	-606.2126	52.57	3.84E-12	2.99E-12
	logit_sd	320.281	0.429	14	-612.5627	-609.7995	48.99	2.31E-11	1.80E-11
	logit_wsd	318.653	0.419	14	-609.306	-606.5429	52.24	4.52E-12	3.52E-12
SAVI	linear	310.583	0.359	6	-609.1668	-608.6418	50.14	1.29E-11	1.01E-11
	linear_w	309.926	0.355	6	-607.852	-607.327	51.46	6.70E-12	5.22E-12
	linear_s	317.449	0.409	13	-608.8988	-606.5197	52.27	4.47E-12	3.48E-12
	linear_ws	316.522	0.404	13	-607.0445	-604.6654	54.12	1.77E-12	1.38E-12
	linear_d	310.765	0.360	7	-607.5307	-606.8263	51.96	5.21E-12	4.06E-12
	linear_wd	309.860	0.355	7	-605.719	-605.0146	53.77	2.11E-12	1.64E-12
	linear_sd	317.589	0.410	14	-607.179	-604.4158	54.37	1.56E-12	1.22E-12
	linear_wsd	316.477	0.404	14	-604.9536	-602.1905	56.60	5.13E-13	4.00E-13
	logit	312.779	0.376	6	-613.5589	-613.0339	45.75	1.16E-10	9.05E-11
	logit_w	311.761	0.369	6	-611.5226	-610.9976	47.79	4.20E-11	3.27E-11
	logit_s	320.243	0.429	13	-614.4862	-612.1071	46.68	7.31E-11	5.69E-11
	logit_ws	318.762	0.420	13	-611.5249	-609.1458	49.64	1.66E-11	1.29E-11
	logit_d	312.782	0.376	7	-611.5648	-610.8604	47.93	3.92E-11	3.05E-11
	logit_wd	310.458	0.361	7	-606.9159	-606.2114	52.57	3.83E-12	2.99E-12
	logit_sd	320.281	0.429	14	-612.5616	-609.7984	48.99	2.30E-11	1.79E-11
	logit_wsd	318.653	0.419	14	-609.3052	-606.542	52.24	4.52E-12	3.52E-12
MSAVI	linear	310.389	0.357	6	-608.7778	-608.2528	50.53	1.06E-11	8.29E-12
	linear_w	309.738	0.354	6	-607.4761	-606.9511	51.83	5.55E-12	4.32E-12
	linear_s	317.162	0.407	13	-608.3232	-605.9442	52.84	3.35E-12	2.61E-12
	linear_ws	316.258	0.402	13	-606.5153	-604.1362	54.65	1.36E-12	1.06E-12
	linear_d	310.554	0.358	7	-607.1072	-606.4028	52.38	4.22E-12	3.29E-12
	linear_wd	309.664	0.354	7	-605.3273	-604.6229	54.16	1.73E-12	1.35E-12
	linear_sd	317.283	0.408	14	-606.5668	-603.8037	54.98	1.15E-12	8.96E-13
	linear_wsd	316.197	0.402	14	-604.395	-601.6318	57.15	3.88E-13	3.02E-13
	logit	313.578	0.381	6	-615.1552	-614.6302	44.16	2.58E-10	2.01E-10
	logit_w	312.602	0.375	6	-613.2044	-612.6794	46.11	9.73E-11	7.58E-11
	logit_s	321.006	0.434	13	-616.0127	-613.6336	45.15	1.57E-10	1.22E-10
	logit_ws	319.595	0.426	13	-613.1896	-610.8105	47.98	3.82E-11	2.98E-11
	logit_d	313.582	0.381	7	-613.1631	-612.4587	46.33	8.71E-11	6.79E-11
	logit_wd	311.364	0.368	7	-608.7281	-608.0237	50.76	9.49E-12	7.39E-12
	logit_sd	321.051	0.434	14	-614.1024	-611.3392	47.45	4.98E-11	3.88E-11
	logit_wsd	319.510	0.425	14	-611.0197	-608.2566	50.53	1.07E-11	8.30E-12

Table 4.3 continued

Reflectance transformation	Statistical representation	loglikelihood	R^2	K	AIC	AICc	Δi	model likelihood	model weight
TSAVI	linear	293.465	0.213	6	-574.9305	-574.4055	84.38	4.75E-19	3.70E-19
	linear_w	292.425	0.204	6	-572.8496	-572.3246	86.46	1.68E-19	1.31E-19
	linear_s	300.549	0.277	13	-575.0982	-572.7191	86.07	2.05E-19	1.59E-19
	linear_ws	298.454	0.260	13	-570.9088	-568.5297	90.26	2.52E-20	1.96E-20
	linear_d	293.661	0.215	7	-573.3226	-572.6182	86.17	1.95E-19	1.51E-19
	linear_wd	292.494	0.205	7	-570.9875	-570.2831	88.50	6.05E-20	4.71E-20
	linear_sd	300.745	0.278	14	-573.4891	-570.7259	88.06	7.55E-20	5.88E-20
	linear_wsd	298.510	0.261	14	-569.0202	-566.2571	92.53	8.08E-21	6.30E-21
	logit	293.769	0.216	6	-575.5386	-575.0136	83.77	6.44E-19	5.02E-19
	logit_w	292.586	0.206	6	-573.172	-572.647	86.14	1.97E-19	1.54E-19
	logit_s	301.852	0.288	13	-577.7039	-575.3248	83.46	7.53E-19	5.86E-19
	logit_ws	299.554	0.269	13	-573.1085	-570.7294	88.06	7.56E-20	5.89E-20
	logit_d	293.868	0.217	7	-573.7358	-573.0314	85.75	2.39E-19	1.86E-19
	logit_wd	293.016	0.225	7	-572.0321	-571.3277	87.46	1.02E-19	7.95E-20
	logit_sd	301.891	0.288	14	-575.7828	-573.0197	85.77	2.38E-19	1.85E-19
	logit_wsd	298.849	0.263	14	-569.698	-566.9348	91.85	1.13E-20	8.84E-21
Tasseled Cap	linear	328.392	0.482	14	-628.7843	-626.0211	32.76	7.68E-08	5.98E-08
	linear_w	326.124	0.471	14	-624.2488	-621.4856	37.30	7.95E-09	6.19E-09
	linear_s	333.292	0.511	21	-624.5848	-618.2124	40.57	1.55E-09	1.21E-09
	linear_ws	330.980	0.500	21	-619.9602	-613.5878	45.20	1.53E-10	1.19E-10
	linear_d	328.608	0.483	15	-627.2163	-624.0375	34.75	2.85E-08	2.22E-08
	linear_wd	326.353	0.472	15	-622.7057	-619.5269	39.26	2.99E-09	2.33E-09
	linear_sd	333.449	0.512	22	-622.8982	-615.8704	42.92	4.80E-10	3.74E-10
	linear_wsd	331.120	0.501	22	-618.2393	-611.2116	47.57	4.67E-11	3.64E-11
	logit	333.133	0.512	14	-638.2651	-635.502	23.28	8.79E-06	6.85E-06
	logit_w	330.340	0.505	14	-632.6806	-629.9174	28.87	5.39E-07	4.19E-07
	logit_s	337.215	0.536	21	-632.4302	-626.0578	32.73	7.82E-08	6.09E-08
	logit_ws	334.965	0.530	21	-627.9294	-621.557	37.23	8.24E-09	6.42E-09
	logit_d	334.367	0.519	15	-638.7334	-635.5546	23.23	9.02E-06	7.03E-06
	logit_wd	331.655	0.514	15	-633.309	-630.1302	28.66	5.99E-07	4.67E-07
	logit_sd	338.472	0.542	22	-632.9444	-625.9167	32.87	7.29E-08	5.67E-08
	logit_wsd	336.169	0.538	22	-628.3389	-621.3112	37.47	7.29E-09	5.67E-09
Bands	linear	356.805	0.631	26	-661.6105	-651.5819	7.20	2.73E-02	0.021
	linear_w	355.211	0.625	26	-658.4224	-648.3938	10.39	5.54E-03	0.004
	linear_s	357.945	0.636	33	-649.8909	-633.0187	25.77	2.54E-06	1.98E-06
	linear_ws	355.950	0.629	33	-645.9008	-629.0286	29.76	3.45E-07	2.69E-07
	linear_d	356.858	0.631	27	-659.7152	-648.8375	9.95	6.91E-03	0.005
	linear_wd	355.252	0.625	27	-656.5032	-645.6255	13.16	1.39E-03	0.001
	linear_sd	357.987	0.636	34	-647.9731	-629.9428	28.84	5.46E-07	4.25E-07
	linear_wsd	355.951	0.629	34	-643.9025	-625.8722	32.91	7.13E-08	5.55E-08
	logit	360.407	0.647	26	-668.8144	-658.7858	0.00	1.00E+00	0.779
	logit_w	353.874	0.624	26	-655.7476	-645.719	13.07	1.45E-03	1.13E-03
	logit_s	361.545	0.652	33	-657.0901	-640.2179	18.57	9.29E-05	7.24E-05
	logit_ws	353.604	0.628	33	-641.2085	-624.3363	34.45	3.31E-08	2.58E-08
	logit_d	360.408	0.647	27	-666.8163	-655.9386	2.85	2.41E-01	0.188
	logit_wd	354.294	0.626	27	-654.5889	-643.7112	15.07	5.33E-04	4.15E-04
	logit_sd	361.546	0.652	34	-655.0926	-637.0623	21.72	1.92E-05	1.49E-05
	logit_wsd	353.736	0.628	34	-639.4722	-621.4419	37.34	7.78E-09	6.06E-09

Figure 4.4: Observed cheatgrass abundance vs. predicted cheatgrass abundance derived from the best regression model generated from multi-date LANDSAT imagery of the Birds of Prey National Recreation area in southwest Idaho. Confidence intervals shown are 80%, 90% and 95%.

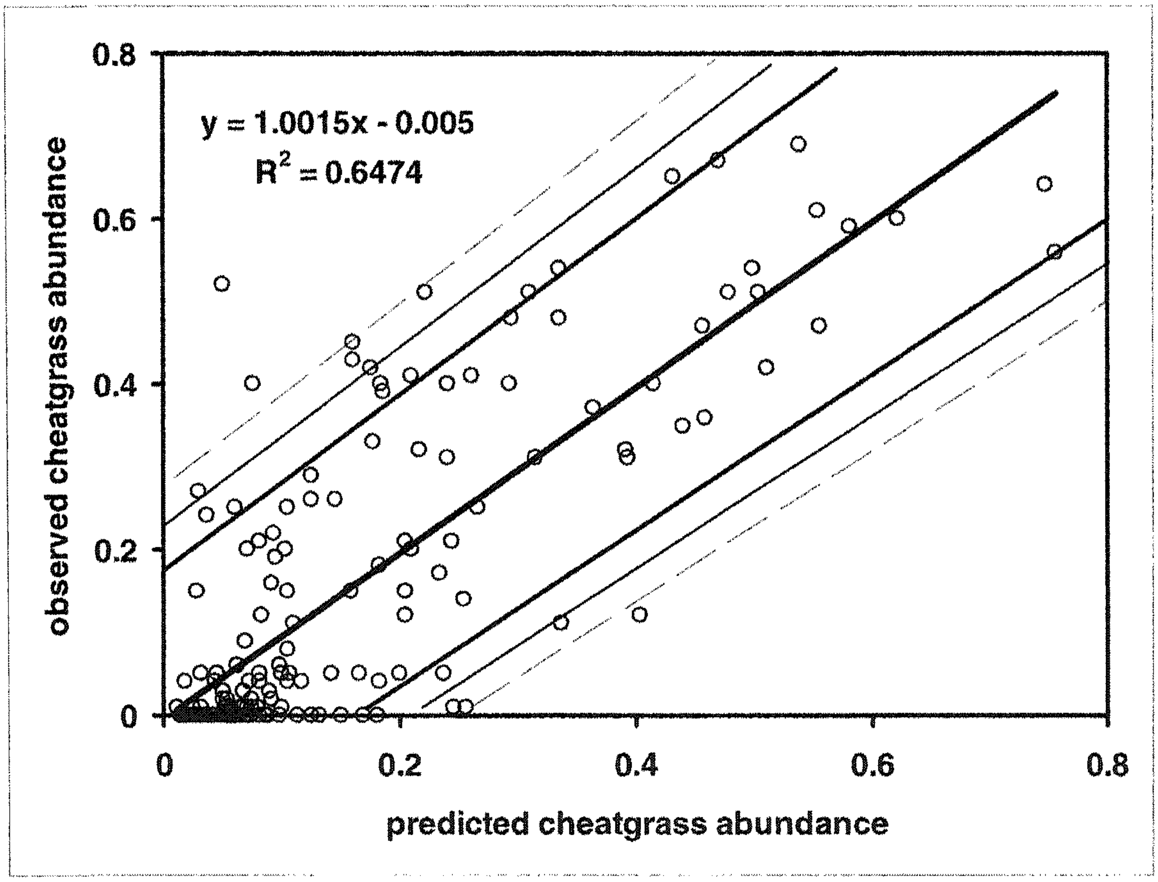
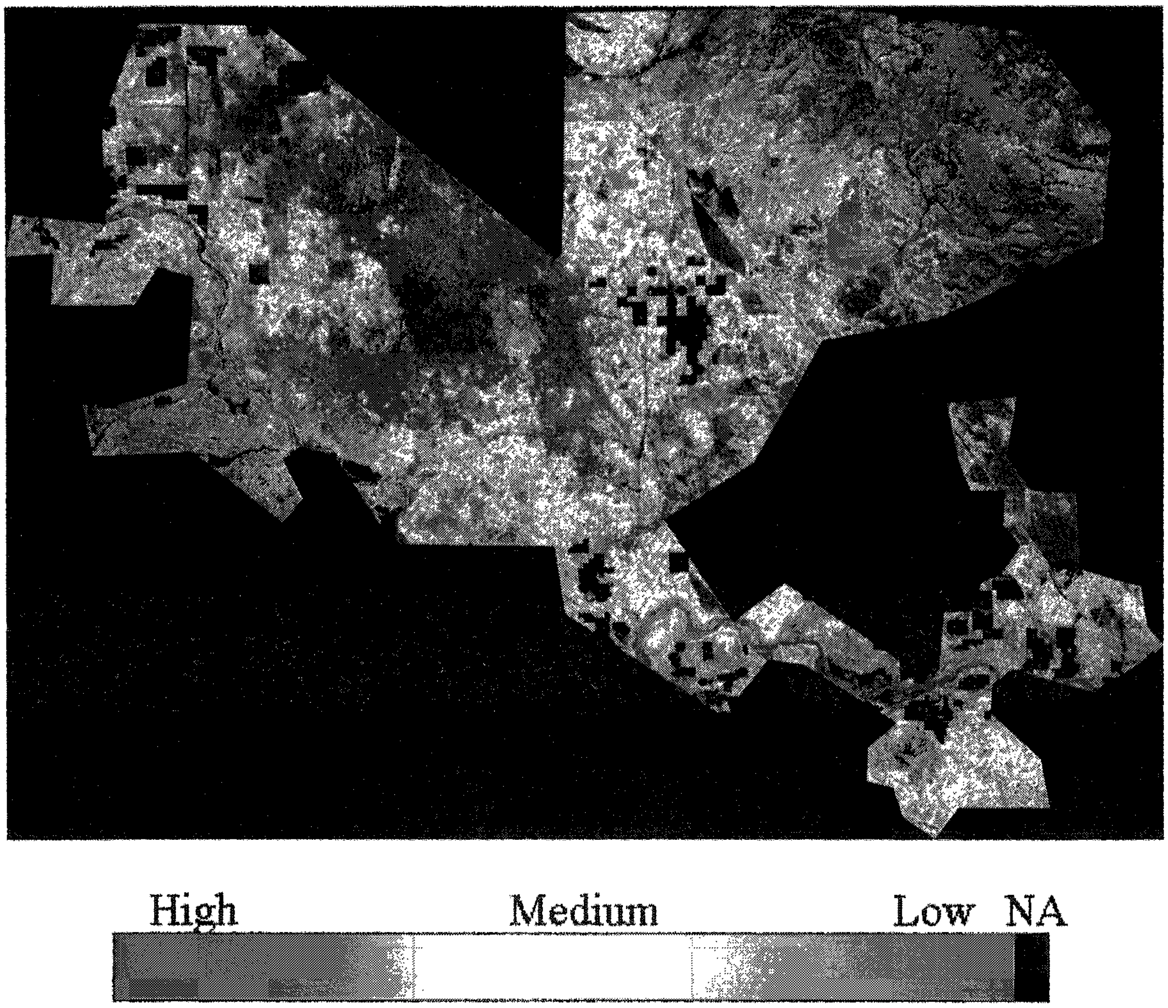


Table 4.4: Error matrices, ommission/comission errors and overall accuracy estimates for three techniques employed to predict cheatgrass abundance from multi-date LANDSAT imagery of the Birds of Prey National Recreation Area in SW Idaho.

Method	Error Matrix						Errors			Accuracy	khat
Maximum likelihood			Observed								
		Class	Low	Med	High	Total	Class	ommission	comission	0.566	0.195
		Low	35	9	5	49	Low	0.22	0.29		
	Predicted	Medium	9	8	9	26	Medium	0.53	0.69		
		High	1	0	0	1	High	1.00	1.00		
		Total	45	17	14						
Neural Network			Observed								
		Class	Low	Med	High	Total		ommission	comission	0.329	-0.049
		Low	16	8	7	31	Low	0.64	0.48		
	Predicted	Medium	11	5	3	19	Medium	0.71	0.74		
		High	18	4	4	26	High	0.71	0.85		
		Total	45	17	14						
Regression			Observed								
		Class	Low	Med	High	Total		ommission	comission	0.665	0.409
		Low	79	14	4	97	Low	0.19	0.19		
	Predicted	Medium	18	20	14	52	Medium	0.49	0.62		
		High	1	5	12	18	High	0.60	0.33		
		Total	98	39	30						

Figure 4.5: Predicted cheatgrass abundance for the Birds of Prey National Recreation Area in southwest Idaho.



CHAPTER 5: CONTROLS OVER CHEATGRASS INVASION: THE IMPORTANCE OF CLIMATE, SOILS, DISTURBANCE AND SEED AVAILABILITY

ABSTRACT

Predicting the future intensity and distribution of invasive plant species requires understanding how they will respond to the environmental conditions of the new location. Quantifying the importance of environmental conditions and disturbance patterns for a particular invasive species involves gaining insight into the consumption of multiple resources over both space and time. In arid and semi-arid ecosystems where water is a primary limiting resource, these interactions can be simplified by focusing on the acquisition and utilization of water. I utilized a soil water model to simulate how variations in climatic and soil properties influence temporal soil water dynamics, and quantified how this variation is likely to affect the establishment of cheatgrass, a cool-season annual grass that has successfully colonized much of the U.S. Great Basin. In addition, I utilized a gap dynamics model to simulate the impact of disturbance regime and seed availability on competition between cheatgrass and native plants. My results suggest that climate is extremely important, but that soil properties do not significantly influence the probability of observing conditions suitable for cheatgrass establishment. The plant competition

results indicate that frequent disturbance causes more cheatgrass in invaded areas and higher seed availability causes faster invasion. These results suggest that climatic conditions dictate which areas are susceptible to invasion, disturbance regime dictates the severity of invasion and seed availability dictates the speed of invasion.

INTRODUCTION

Biological invasions can have dramatic effects on the structure and function of terrestrial ecosystems. The consequences of invasions by exotic plants can include changes in plant community composition and biodiversity, modified carbon, nutrient energy and water cycles, altered fire regimes and potentially decreased economic agricultural yield. As a result of these impacts, biological invasions have recently become recognized as a major component of global environmental change (Vitousek et al 1996).

One invasive plant that has had a dramatic impact on semiarid ecosystems in North America is cheatgrass (*Bromus tectorum L.*), a cool season annual grass, originally from Asia (Novak and Mack 2001), that has achieved remarkable success in the western United States (Morrow and Stahlman 1984, Knapp 1996). First introduced to North America in the late 19th Century, and with invasion partly facilitated by heavy grazing (Pickford 1932) and plowing (Knapp 1996), cheatgrass rapidly spread across the continent (Mack 1981) and continues to colonize new areas (Hunter 1991). Cheatgrass is the dominant plant species on over 20% of the sagebrush steppe in the Great Basin region of the U.S.(Knapp 1996). In heavily invaded areas, cheatgrass has modified plant community composition (Anderson and

Inouye 2000), decreased forage quality for livestock and wildlife (Thill et al. 1984, Young et al 1987, Ganskopp and Bohnert 2001), changed soil seedbank contents (Humphrey and Schupp 2001), drastically increased fire frequency (Meloza and Nowak 1991, D'Antonio and Vitousek 1992) and potentially altered energy, water and nutrient cycling (Hinds 1975, Evans et al. 2001, Svejcar and Sheley 2001).

A common explanation for why cheatgrass has been able to outcompete native plants in Great Basin ecosystems focuses on the synchrony between cheatgrasses phenology and water availability. Cheatgrass is a winter annual, germinating in the fall, growing throughout the winter as temperature and water availability permit and producing seeds in late spring (Thill et al. 1984). Most locations where cheatgrass has successfully invaded are arid to semiarid and receive precipitation primarily during the winter and spring months (Knapp 1996). Other semiarid regions in North America, notably the Great Plains, receive most of their precipitation during the summer (Lauenroth and Burke 1995), and have not experienced substantial cheatgrass invasion. Although cheatgrass is present in Great Plains ecosystems, it appears to be essentially confined to disturbed areas and rarely, if ever, achieves dominance (Betz 2001). These observations lead to the hypothesis that cheatgrass is able to outcompete native plants only in areas with consistent water availability during fall, winter, and early spring. In arid and semi-arid regions, water is the primary limiting resource, and the acquisition and utilization of water is considered the central component of plant competition (Noy-Meir 1973). Early phenology allows cheatgrass to utilize available water during the winter, completing its life cycle before dry summer conditions and possibly decreasing the soil water available to other plants, causing a direct negative impact on native vegetation (Harris 1962).

Other explanations for the invasive success of cheatgrass have been proposed, including the possibility that cheatgrass can display unusual phenotypical plasticity in response to variable environmental conditions (Anderson 1996), that cheatgrass has greater water and/or nitrogen use efficiency (Rice et al. 1992, Link et al 1995, Lowe et al. 2002), or that cheatgrass is more suited than native plants to frequent disturbance regimes (D'Antonio and Vitousek 1992). There is substantial evidence that both wildfires and plowing for cultivation positively influences cheatgrass invasion (Melgoza and Nowak 1991, Knapp 1996). Cheatgrass invasion typically results in more frequent fires, and the fires create a positive feedback to invasion by killing the perennial plants that comprise most of the native vegetation (D'Antonio and Vitousek 1992). As an annual grass that has produces seeds by the onset of summer, cheatgrass provides fuel for wildfires and is not seriously impacted by the burning. By contrast, perennial native shrubs and bunchgrasses are killed by the fires and take at least several years to recover.

The strong influence of both climate and disturbance regime on cheatgrass invasion suggests that important interactions may exist between climate and disturbance. Climate may dictate areas that are potentially susceptible to cheatgrass invasion, while disturbance conditions might determine whether the invasion occurs. Sound predictions about the future of cheatgrass invasion requires understanding the consequences and potential interactions of both climate and disturbance regime.

One unanswered question about cheatgrass invasion relates to the potential for invasion in South America. Certain areas in Argentine Patagonia have climatic conditions that are similar to heavily invaded parts of the Great Basin in North American (Adler 2003). Despite these climatic similarities and the fact that cheatgrass does exist in these Patagonian ecosystems, cheatgrass has not substantially invaded these areas, and it represents only a very minor component of the vegetation (Soriano et al. 1983). By understanding the variables that impact competition between native plants and cheatgrass, land managers can identify areas that are susceptible to cheatgrass invasion and determine what land-use practices would help minimize the invasion in susceptible areas. For example, if cheatgrass invasion is determined primarily by climate and the resultant temporal patterns of water availability, potential invasion in Patagonian ecosystems should be predictable based on climate and soil conditions. If, on the other hand, specific disturbance regimes are necessary for cheatgrass invasion, Patagonian ecosystems may remain uninvaded.

My overall goal in this study is to examine how climate and soil influence the soil water conditions needed for cheatgrass establishment, and how disturbance and seed availability combine to influence cheatgrass competition with native plants. I employ two simulation models to address this goal. I utilize a soil water model to simulate daily soil water dynamics as a function of climate and soil variables (Parton 1978). In arid and semiarid regions, water is the primary limiting resource and understanding temporal patterns of water availability provides substantial insight into how specific plants vegetation dynamics in these systems (Noy-Meir 1973). Soil water models are commonly used to simulate the movement and storage of subsurface water (e.g. Eitzinger et al. 2004) and the effects of this water flow on vegetation establishment and competition (e.g. Lauenroth et al. 1994, Peters 2000). I also use an individual plant based model to simulate resource acquisition and plant competition (Coffin and Lauenroth 1990). Simulation modeling has been used to gain insight and generate testable hypotheses about interspecific competition (Biondini 2001, Peters 2002), resource utilization (Lauenroth et al. 1994), plant response to climate change (Prentice et al. 1992, Starfield and Chapin 1996) and biological invasions (Higgins et al. 1996, Kriticos et al. 2003).

My objectives are to 1) examine the potential importance of climate and soil conditions on cheatgrass establishment by simulating the probability of suitable soil water availability in 9 combinations of weather and soils from the 3 sites and quantify how parameters defining suitable conditions influence these results and 2) simulate competition between cheatgrass and native plants at all three sites and estimate the consequences of varying the frequency of disturbance and cheatgrass propagule pressure. I simulate cheatgrass invasion at three sites: a heavily invaded Great Basin site, a Patagonian site with superficially suitable climatic conditions that nevertheless remains uninvaded, and a Great Plains site that, based on precipitation timing, should not be invadable and has very little cheatgrass.

METHODS

Study sites: I simulated soil water dynamics for three locations: the shortgrass steppe ecosystem of NE Colorado, USA (40.8° N, 107.8° W), the sagebrush steppe ecosystem of eastern Washington, USA (46.6°N, 119.6°W) and the Patagonian steppe of the Chubut province in southern Argentina (45.4°S, 70.3°W). To represent the shortgrass steppe (SGS), I utilized climatic and vegetation data from the Central Plains Experimental Range (CPER). Located approximately 60 km northeast of Fort Collins, CO, climate at the CPER is semiarid (321mm mean annual precipitation) with most of the precipitation (Figure 5.1) and plant growth (Table 5.1) occurring during the summer months. Monthly temperatures at the CPER average 8.8° C and range from –5° C in January to 22° C in July (Lauenroth and Milchunas 1992). Vegetation at the CPER is dominated by C_4 perennial grasses, primarily *Bouteloua gracilis* and *Buchloe dactyloides*, but also includes annual grasses, forbs and shrubs (Lauenroth and Milchunas 1992). Annual net primary production averages 130 g/m2 with substantial interannual variability in response to annual precipitation (Lauenroth and Sala 1992). For my SGS simulations I modeled a sandy loam soil common at the CPER, with information about the soil profile provided by Smith (2003) (Table 5.2).

For information about the sagebrush-steppe ecosystem I utilized data from the Arid Lands Ecology Reserve (ALE) on the U.S. Department of Energy's Hanford Reservation, located northwest of Richland, WA. Climate at ALE is arid, with an average of 160mm of annual precipitation, 80% occurring during between October and May (Figure 5.1). Monthly temperatures at ALE average 11.7°C and range from 24.7°C in July to –1.4°C in January (Rickard 1988). Vegetation at ALE consists chiefly of C_3 perennial grasses and shrubs, most commonly *Agropyron spicatum* and *Artemisia tridentate*. Net primary production averages 110 g/m2 (Rickard and Vaughan 1988). Soils at ALE consist mainly of silt loams (Wildung and Garland 1988) and I obtained profile texture data from Adler (2003).

My Patagonian steppe research site (PAT) was the Rìo Mayo Experimental Station of the Instituto Nacional de Tecnologia Agropecuaria, located in southwest Chubut province. PAT receives 154mm of mean annual precipitation, primarily during the winter and monthly temperatures range from 1.7°C to 15.6°C with an average of 8.6°C (Figure 5.1) (INTA 2003). Vegetation at PAT is very similar to ALE, composed of mixed perennial grasses, including *Stipa speciosa*, *Stipa humilis* and *Poa ligularis* and shrubs, primarily *Mulinum spinossum* (León et al. 1998). Annual net primary production at PAT is approximately 90 g/m2 (Paruelo et al. 1998). I utilized texture information for the soil profile at PAT provided by Adler (2003) for a loamy sand soil common in the Patagonian Steppe.

Soil water model description: I used SOILWAT, a soil water model originally designed to simulate water dynamics in the shortgrass steppe (Parton 1978). SOILWAT requires input information in three general categories 1) weather conditions, including daily maximum and minimum temperature, precipitation, and monthly relative humidity, wind speed and cloud cover, 2) monthly values of aboveground biomass, litter and % of aboveground vegetation that is live, and 3) soil texture, bulk density, field capacity, wilting point and relative proportions of evaporation and transpiration for each layer in the soil profile. Using these inputs, SOILWAT simulates water interception by aboveground vegetation and litter, water infiltration and flow through the soil profile, evaporation, and transpiration for each soil layer on a daily basis. A detailed description of the original model is presented in Parton (1978). With the exception of modifying input parameters to represent ecosystems other than the shortgrass steppe, the only major modification I made to the model was to alter the procedure for calculating the amount of water intercepted during precipitation events by aboveground biomass and litter (Appendix 1). To create daily weather data, I used a first-order Markov weather generator that uses actual weather observations to estimate the distribution of temperature and precipitation values and the probability of precipitation occurring as a function of date and conditions on the previous day. I parameterized these distributions and probabilities with 30 years of data for the SGS site and 12 years of data for both the ALE and PAT sites.

Individual plant model description: STEPPE is a yearly time-step individual-based gap-dynamics model that simulates plant growth, competition and reproduction on a yearly basis as a function of resource availability. To estimate resource availability, STEPPE compares monthly soil-layer specific transpiration estimates from SOILWAT with plant phenology and root distribution (Table 5.4). These parameters combine to define a two-dimensional plant activity and potential resource acquisition space that can be used to conceptually define and differentiate between plant functional groups (Figure 5.2). I defined 7 plant functional groups to simulate with STEPPE: warm season perennial grasses (PGW), cool season perennial grasses (PGC), warm season annual grasses (AGW), cool season annual grasses (AGC), shrubs, warm season forbs (FORW) and cool season forbs (FORC). The AGC group is used to represent cheatgrass in my simulations. STEPPE uses information about plant life history characteristics, including maximum growth rates, maximum size, life span, and reproductive strategy (Table 5.5) to simulate interactions among individual plant which is then translated in to growth, reproduction and/or mortality as a consequence of the amount of water available for transpiration. Further details about STEPPE are available in Coffin and Lauenroth (1990) and Coffin et al (1993). Relative rooting distribution (proportion of a total roots in a layer) is multiplied by relative phenological activity (proportion of total annual activity in a month) to determine an active rooting quantity for each species in each month in each soil layer.

Model scenarios for objective 1: My first objective was to quantify the importance of climatic and soil properties on the probability of conditions suitable for cheatgrass establishment. I simulated soil water dynamics near the soil surface throughout the year at the three study sites and quantified the probability of soil water potential and weather conditions being suitable for cheatgrass establishment. I ran 12 simulations at each of the three sites for 1000 years and used these replicates to quantify variability between sites and as a general indicator of variability between runs. To quantify the affect of soil and weather on the probability of conditions suitable for cheatgrass establishment, I conducted SOILWAT runs for 9 scenarios, consisting of all factorial combinations of soil properties and weather patterns from the three study sites. I simulated 1000 years for each scenario and quantified the number of years when conditions were suitable for cheatgrass establishment. Since cheatgrass is a winter annual that can germinate during fall or spring, I quantified the probability of suitable conditions separately for these two seasons. Initial estimates of the parameters for the soil water availability and weather conditions required for cheatgrass establishment (Table 5.3) were obtained from detailed studies of cheatgrass life history traits conducted by Hulbert (1955) and Harris (1967). Since cheatgrass is a cool season annual grass, I assumed that cheatgrass germination was possible during the first and last 90 days of the year. To examine the consequences of soil properties and weather on soil water dynamics I averaged 100 years of daily soil water potential estimates to create a long-term seasonal soil water potential by layer. I quantified the relative importance of climatic and soil conditions on establishment probability by running a complete factorial analysis of variance in the ANOVA procedure in SAS (SAS 2001). Since the model results do not contain a random component, the F-value results are meaningless, so I present only the mean squares results, which provide insight into how variation in the response relates to variation in driving variables.

To quantify how sensitive my results from objective 1 were to the parameters that specify conditions suitable for cheatgrass establishment, I used 12 parameters to define the conditions that I considered suitable for cheatgrass establishment. Since the values of these parameters will directly influence the estimated establishment probability and thus possibly have dramatic effect on my results, I examined how my establishment results varied as I changed each parameter (Table 5.7). These parameters specify soil water and temperature conditions for germination and establishment as well as the timing of these two events (Table 5.3). I ran model simulations to quantify both spring and fall establishment probabilities for all three sites (i.e. no factorial combinations of climate and soil as employed in objective 1) for three levels of each parameter that span the range of reasonable values. To quantify the influence of each parameter on establishment, I calculated a sensitivity index, the mean difference in establishment between simulations with higher and lower parameter values across both seasons and all three sites. This provided a general index of how much a changing a single parameter altered the establishment results.

Model scenarios for objective 2: To simulate plant competition and cheatgrass invasion, I used STEPWAT to simulate 50 replicates (equivalent to simulating 50 0.125 m^2 plots) at all three sites. Each simulation included only native vegetation for 100 years. I then introduced cheatgrass by allowing establishment of a single cheatgrass seed on each plot at a probability of 0.1 per year. Simulations were run for 400 years after allowing cheatgrass invasion and disturbance was not included in these initial simulations.

Disturbance was included in the model by killing all the plants in a plot at a certain frequency. This approach allowed me to examine the consequences of variable disturbance frequencies, but does not provide insight into the impact of disturbances of varying intensity or type. I examined the consequences of disturbing the plots every 5, 10, 25, 50 and 100 years. To examine the consequences of variations in seed availability, I modified the probability of cheatgrass germination that was not accounted for by of seeds from the seedbank. This probability was also simulated at 5 levels: 0.01, 0.05, 0.1, 0.25, 0.5. I simulated scenarios at each site for all combinations of the 5 disturbance levels with the 5 seed availability levels. To provide insight into the model predictions of overall plant community structure with and without cheatgrass, I quantified plant community composition for the 100 years prior to cheatgrass invasion as well as for the final 100 years of each disturbance level (at the intermediate of the 5 seed availability levels.) As a measure of eventual cheatgrass invasive success, I calculated the mean cheatgrass biomass for the final 100 years as an indicator of overall invasion success and I determined the first year than cheatgrass biomass exceeded $40 g/m^2$ as an indicator of invasion speed. I ran a factorial analysis of variance to determine the relative contributions of disturbance and seed availability to the variation in both biomass and the year biomass reached $40 g/m^2$ and present only the results for mean squares.

RESULTS

Cheatgrass establishment: In my initial comparison of the three sites I found that conditions suitable for cheatgrass establishment were most rare at the SGS site, where an average of 7.5 years out of 1000 in the spring and 110 years out of 1000 in the fall contained suitable conditions for cheatgrass establishment (Figure 5.2). By contrast, my model results suggested that soil water conditions at the ALE site were suitable for cheatgrass establishment in 720 out of 1000 years in the spring and 254 years out of 1000 in the fall. Conditions at the PAT site were suitable for 564 years in the spring and 510 years out of 1000 in the fall.

The most striking observation from the soil water potential results is the marked increase in soil water potential (indicating greater soil water content and greater water availability) during the fall, winter and spring months at both the ALE and PAT sites. This dramatic increase in soil water occurred at ALE and PAT regardless of soil type, although soil properties do appear to have some influence on the magnitude of this drop in soil water potential – for instance, at the PAT site simulations using ALE soils and simulations using either SGS or PAT soils produced slightly different seasonal soil water dynamics. The negative effect of ALE soils on the winter increase in soil moisture is more pronounced under the PAT climate than under the ALE climate.

These seasonal patterns of soil water potential were translated into the suitable cheatgrass establishment conditions and I observed that establishment varied more with climate than soil. My ANOVA results suggest that climatic conditions account for almost all of the variability in spring, fall, and total establishment, whereas soil conditions account for only a small proportion of the variation (Table 5.4). I observed higher establishment success for both ALE and PAT climates than the SGS climate regardless of soil type. Spring season establishment under the SGS climate was essentially nothing, with 5 or less years out of 1000 producing suitable conditions for all soil types. Fall conditions at SGS yielded roughly 100 years suitable for establishment. Out of 1000 runs, simulations with ALE climate had suitable conditions in greater than 700 and 200 years during the spring and fall, respectively. Establishment for simulations with PAT climate was slightly more dependent on soil properties, with the highest total establishment occurring under ALE soils but the highest spring establishment and lowest fall establishment occurring under the SGS soil. The scenario with PAT climate and PAT soil produced intermediate, but fairly high values of 391 and 499 years out of 1000 for spring and fall establishment, respectively.

Importance of establishment parameters: Of the 12 parameters, I identified four that have a substantial influence on the estimated establishment (Figure 5.4). In order of estimated importance, the parameters are: the soil depth considered important for establishment (depth), the maximum (negative) soil water potential necessary for establishment (estabswp), the minimum number of days between germination and establishment (minbtw) and the minimum temperature necessary for establishment (mintempestab). The effect of any of the other 8 parameters was less than half of that of mintempestab.

Overall community structure: In the absence of annual cool season grasses, the model simulated an SGS plant community dominated by warm season perennial grasses, with a sizable component of cool season perennials and very small amounts of shrubs, warm season annuals and forbs (Figure 5.6 A). At both ALE and PAT, plant communities simulated without cool season annual grasses consisted primarily of cool season perennials and shrubs with a modest warm season annual component, a very small amount of warm season perennials and essentially no forbs (Figure 5.6 B and C). Including cool season annual grasses in these communities caused very little change in the SGS community, but did influence the ALE and PAT communities. At the SGS, warm season perennial grasses dominated the plant communities at all disturbance levels except the 2 year frequency, where all the groups displayed very low but comparable biomass. Overall biomass also decreased at ALE and PAT as disturbance frequency inreased, although the decline was less pronounced. The plant community composition at ALE and PAT appeared more responsive to disturbance frequency, with shrubs and perennial cool season grasses becoming less prevalent while annual grasses, especially cool season annuals, becoming more prevalent as disturbance frequency increased.

Disturbance and seed availability: My simulations indicated essentially no cheatgrass invasion in the SGS regardless of the frequency of disturbance or the number of cheatgrass seeds available (Table 5.7). None of the SGS scenarios predicted that cheatgrass biomass would reach the arbitrary threshold of 40g/m2 at any point during the 500 year simulations.

By contrast, the model simulated substantial cheatgrass invasion for all scenarios examined at both the ALE and PAT sites. For all levels of seed availability, simulations at both ALE and PAT estimated the highest cheatgrass biomass for scenarios with disturbance events every 10 years, and biomass decreased as disturbance frequency decreased. The lowest cheatgrass biomass values were observed in scenarios with disturbance every 2 years. Seed availability had a comparatively small influence on simulated cheatgrass biomass. For any disturbance frequency, biomass estimates displayed only minor variations for scenarios with different probability of cheatgrass establishment. However, the number of years required for cheatgrass biomass to reach the threshold was influenced by seed availability. In general, scenarios with low probability of cheatgrass establishment required more years than scenarios with high seed availability, although the years required was more variable for simulations with low seed availability. ANOVA results indicate that most of the variation in biomass is influenced by disturbance, with a very small fraction attributed to propagule pressure (Table 5.8). By contrast, the time required to reach the biomass threshold was influenced primarily by seed availability and secondarily by disturbance frequency. My results indicate that the interaction between disturbance frequency and seed availability has only very minor influence on the variability of either response variable.

DISCUSSION

Importance of climatic conditions and soil properties: I observed large differences among all six of the site by season combinations. My site-level results are consistent with expectations, in that the heavily invaded ALE site displayed high establishment probabilities and the relatively uninvaded SGS site produced very few years with conditions suitable for cheatgrass establishment. The correspondence between simulated establishment probabilities and observed cheatgrass success supports my overall hypothesis that, climate patterns and soil conditions can serve as general predictors for areas potentially susceptible to cheatgrass invasion.

In general, I observed higher probability of establishment conditions at ALE and PAT than SGS, and the differences were much greater during the spring than during the fall. These results indicate that climatic conditions, specifically the seasonal timing of precipitation, is of central importance for determining the probability of observing conditions suitable for cheatgrass establishment. Although I didn't examine it in this study, it is reasonable to expect that precipitation regime has a strong influence on life history stages after establishment, including growth, reproduction and mortality (Hulbert 1955). Precipitation timing appears to impact both the overall probability of establishment at different sites and the balance between spring and fall germination. The lack of precipitation during the winter at the SGS leads to extremely dry winter and spring conditions, which explains why establishment probabilities at the SGS are so small during the spring. At both ALE and PAT, relatively wet winters create moist spring soil conditions and produce much higher spring establishment probabilities and presumably more favorable growing conditions for a cool season annual grass. Although both ALE and PAT displayed higher fall establishment probabilities than SGS, the differences were not as great as in the spring. This is likely a consequence of fall soil water conditions being influenced by summer precipitation patterns. High precipitation during the summer at the SGS can occasionally store enough water to create suitable establishment conditions during the fall. This storage capability of SGS soils is illustrated by the widespread cultivation of winter wheat (a fall germinating winter annual typically planted on a field that was fallow during the summer) in the SGS ecosystem (NASS). Likewise, the dry summers of both ALE and PAT produce extremely dry soil conditions in early fall, requiring substantial rainfall to wet the soil prior to establishment.

Comparisons of the temporal dynamics of soil water potential among the 9 combinations of climate and soil for each site suggests that climate plays a dominant role in influencing soil water conditions. Regardless of the type, soils at the SGS are never consistently wet at any time of year. This is not surprising for a system in which the bulk of the precipitation occurs during the warm season, when it is highly susceptible to evaporative loss. By contrast, both the ALE and PAT sites have consistently high soil water availability during the fall, winter and spring months and this result is relatively independent of the soil conditions considered. ALE and PAT both receive the bulk of their precipitation during the coolest months, when evaporative demand is low and the water is able to accumulate in the soil, creating a time of favorable growing conditions that is consistent over many years. The importance of overlap between seasonal temperature and precipitation patterns has been previously recognized as an important driver of ecosystem structure and function in arid and semiarid systems. Sala et al (1997) identified this overlap, along with soil texture, as the two primary environmental conditions that combine to influence competitive interactions between grasses and shrubs. My results are consistent with the general model proposed by Sala et al (1997) and suggest that the seasonal timing of precipitation may play a central role in influencing cheatgrass invasion.

It is worth noting that I observed higher establishment probabilities at both ALE and PAT despite the fact that the SGS site receives nearly twice as much annual precipitation as either ALE or SGS. This indicates that the timing of precipitation can be a more important driver of establishment probability than even the total amount of precipitation.

Influence of establishment parameters: The identity of the four most influential establishment parameters provides insight into which conditions are more tenuous and which parameters require further characterization through field and observational experiments. The importance of the soil depth that is considered relevant for establishment is not especially surprising, since my soil water potential results indicate strong differences in the soil water potential of deep soil layers among sites and soil types. Simulations with SGS climate and soils showed high negative soil water potential (low water availability) in deep layers compared to all other scenarios. This suggests that the importance of moisture content of deep soil layers may vary with both climate and soil conditions. Previous studies have observed that cheatgrass can send roots to depths well over 1 meter, deeper than I simulated in this study (Harris 1967 and Hulbert 1955). Obtaining realistic estimates of the importance and necessity of deep roots is difficult, but my sensitivity analysis suggests that it may be necessary in order to accurately predict the potential success of cheatgrass.

The second most influential parameter is the estabswp, which suggests that achieving high water availability for establishment is possibly more limiting than sustaining favorable water availability conditions for several days (i.e. notice the relative lack of importance of the minimum number of wet days prior to establishment.) The most important timing parameter is minbtw, implying that the amount of time required between germination and establishment is a crucial value to characterize. Specifying this parameter is confounded by the complication of defining when a plant has become established. Since many annual grasses can produce seeds under extremely poor conditions, often while remaining very small, the question of defining when cheatgrass is "established" may require further characterization. The fourth important parameter was mintempestab, which served to limit establishment during extremely cold periods.

Possibly the most important result of my exploration of parameter importance is that the differences among sites was relatively insensitive to changes in the parameters. This lends support to my general conclusions about the importance of climatic and soil conditions for generating conditions suitable for cheatgrass establishment. Reasonable modifications to my input parameters were not sufficient to overwhelm the positive impact of both the ALE and PAT climates on cheatgrass establishment probabilities.

Model predictions of plant community dynamics: In general, the model estimates of plant community composition do not contradict existing knowledge about these ecosystems. Previous studies have found that the vegetation at the SGS is dominated by warm season perennial grasses (Lauenroth and Milchunas 1993, Sims and Risser 2000) whereas vegetation at ALE and PAT consists primarily of shrubs and cool season perennial grasses (Rickard and Vaughan 1988, Soriano et al 1983, West 1983). The observation that adding cool season annuals to ALE and PAT plant communities increases overall biomass suggests that this group is utilizing some otherwise unused resources, rather than simply taking resources from other groups. This is not unexpected, since my model simulated only 7 plant function groups it is entirely possible that water resources during certain periods in some soil layers were not being fully utilized in the absence of cool season annuals. Model estimates of substantial invasion at ALE and essentially no invasion at SGS are consistent with the general observation that cheatgrass has become a major part of the vegetation in the U.S. Great Basin while remaining relatively unimportant in the U.S. Great Plains.

This coherence between STEPPE model predictions and field observations lends credibility to conclusions based on model output and suggests that STEPPE results may provide insight into the potential invasion at PAT.

Importance of disturbance and seed availability: My results suggest that the frequency of disturbance exerts substantial control over the magnitude or severity of cheatgrass invasion but only moderate influence over the rate of invasion. I simulated that more frequent disturbances have higher cheatgrass biomass, which is consistent with previous studies that have shown a strong relationship between cheatgrass invasion and disturbance (D'Antonio and Vitousek 1992, Knick and Rotenberry 1997). Wildfires, heavy grazing or plowing may cause more severe invasion by removing established perennial plants and creating available resources for cheatgrass (Melgoza and Nowak 1991). The observation that undisturbed locations at ALE can remain relatively uninvaded despite close proximity to nearby seed sources supports the conclusion that disturbance conditions influence the magnitude of invasion (Rickard and Vaughan 1988).

I found that seed availability did not dictate the eventual amount of cheatgrass, but did substantially influence how fast cheatgrass invaded. Previous studies have suggested that human actions that increase seed availability, most notably cultivation with contaminated seed or heavy road traffic from invaded areas are believed to have facilitated invasion in the Great Basin (Mack 1981).

Controls over cheatgrass invasion in PAT: These results suggest an overall conceptual framework for predicting cheatgrass invasion in which climatic conditions specify regions that are susceptible to invasion, disturbance regime dictates how severe the invasion will be, and seed availability influences how fast the invasion occurs. The importance of an interaction between climate and disturbance appears to be crucial in understanding the dynamics of cheatgrass invasion. For example, these conclusions imply that the PAT site is susceptible to invasion, but that disturbance and seed availability will be important for understanding the magnitude and speed of invasion. My results suggest that climatic patterns exert the primary control over soil water dynamics and subsequently over plant community composition. Since I did not find soil conditions to be important and PAT has a climate similar to ALE, an area than has experienced heavy cheatgrass invasion over the past 100 years, it seems reasonable to conclude that PAT is susceptible to substantial cheatgrass invasion. The fact that PAT remains uninvaded is likely a consequence of having different disturbance regime than ALE, or at least different availability of seeds. Thus, the future of cheatgrass invasion in PAT, and other potentially susceptible areas, depends on both natural and human manipulations of seed sources and disturbance conditions.

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Table 5.1: Monthly parameter values for aboveground litter, biomass and percent live for the 3 study sites simulated by SOILWAT. SGS refers to the shortgrass steppe Long Term Ecological Research site in NE Colorado, ALE refers to the Arid Land Ecology Research in Central Washington and PAT refers to Rio Mayo area in Argentine Patagonia.

	SGS			ALE and PAT		
	Litter	Biomass	% live	Litter	Biomass	% live
January	75	150	0	100	150	0.05
February	80	150	0	100	170	0.05
March	85	150	0.1	100	135	0.1
April	90	170	0.2	110	140	0.2
May	50	190	0.4	120	150	0.4
June	50	220	0.6	140	150	0.45
July	50	250	0.4	160	140	0.25
August	55	220	0.6	150	140	0.12
September	60	190	0.4	150	140	0.12
October	65	180	0.2	140	140	0.1
November	70	170	0.1	140	130	0.1
December	75	160	0	120	130	0.05

Table 5.2: Input parameter values for soil conditions and evaporation/transpiration coefficients for the 3 sites simulated by SOILWAT. SGS refers to the shortgrass steppe Long Term Ecological Research site in NE Colorado, ALE refers to the Arid Land Ecology Research in Central Washington and PAT refers to Rio Mayo area in Argentine Patagonia.

	Max Depth (cm)	Bulk Density	Field Capacity	Wilting point	Evaporation coefficient	Transpiration Coefficient	Percent Sand	Percent Clay
SGS	3	1.46	0.2012	0.0333	0.5	0.1	0.768	0.144
	15	1.46	0.2012	0.0333	0.28	0.149	0.768	0.144
	30	1.61	0.25141	0.08912	0.22	0.339	0.611	0.248
	45	1.43	0.28874	0.07084	0	0.186	0.541	0.331
	60	1.43	0.28874	0.07084	0	0.114	0.541	0.331
	75	1.43	0.28874	0.07084	0	0.112	0.541	0.331
	90	1.43	0.28874	0.07084	0	0	0.541	0.331
	120	1.43	0.28874	0.07084	0	0	0.541	0.331
	150	1.43	0.28874	0.07084	0	0	0.541	0.331
	240	1	1.1	1	0	0	0.01	0.01
ALE	3	1.33	0.24	0.09	0.5	0.1	0.41	0.085
	15	1.33	0.24	0.09	0.35	0.25	0.41	0.085
	30	1.33	0.24	0.09	0.15	0.3	0.41	0.085
	45	1.33	0.24	0.09	0	0.2	0.41	0.085
	60	1.33	0.24	0.09	0	0.1	0.41	0.085
	75	1.33	0.24	0.09	0	0.05	0.41	0.085
	90	1.33	0.24	0.09	0	0	0.39	0.07
	120	1.33	0.24	0.09	0	0	0.39	0.07
	150	1.33	0.24	0.09	0	0	0.39	0.07
	240	1.33	0.24	0.09	0	0	0.39	0.07
PAT	3	1.55	0.16	0.05	0.5	0.1	0.89	0.07
	15	1.55	0.16	0.05	0.35	0.25	0.89	0.07
	30	1.55	0.16	0.05	0.15	0.3	0.89	0.07
	45	1.55	0.16	0.05	0	0.2	0.89	0.07
	60	1.55	0.16	0.05	0	0.1	0.89	0.07
	75	1.55	0.16	0.05	0	0.05	0.89	0.07
	90	1.55	0.16	0.05	0	0	0.89	0.07
	120	1.55	0.16	0.05	0	0	0.89	0.07
	150	1.55	0.16	0.05	0	0	0.89	0.07
	240	1.55	0.16	0.05	0	0	0.89	0.07

Table 5.3: Soil water and timing parameters for determining conditions suitable for cheatgrass establishment in simulations at the shortgrass steppe, the sagebrush steppe and the patagonian steppe.

Abbreviation	Parameter description	Value	Reference
depth	Soil depth affecting establishment (cm)	30	Harris (1967) and Hulbert(1955)
germswp	Soil water potential in top 3 cm required for germination (-bars)	12.5	Harris (1967)
estabswp	Soil water potential required for establishement (-bars)	5	Harris (1967)
minwetgerm	Minimum consecutive wet days for germination	2	Harris (1967) and Hulbert(1955)
maxdry	Maximum consecutive dry days after germination but before establishment	40	Harris (1967)
minwetestab	Minimum consecutive wet days after germination before establishment	5	Harris (1967)
minbtw	Minimum days between germination and establishment	15	Hulbert(1955)
maxbtw	Maximum days between germination and establishment	75	Harris (1967) and Hulbert(1955)
mintempgerm	Minimum temperature for germination (°C)	5	Harris (1967) and Hulbert(1955)
maxtempgerm	Maximum temperature for germination (°C)	15	Harris (1967) and Hulbert(1955)
mintempestab	Minimum temperature for establishment (°C)	0	Harris (1967)
maxtempestab	Maximum temperature for establishment (°C)	20	Harris (1967) and Hulbert(1955)

Table 5.4: Proportion of phenological activity in each month and proportion of roots in each soil layer for plant functional groups simulated at the shortgrass steppe, the sagebrush steppe and the patagonian steppe.

Phenological Activity	Month				Group			
		PGC	PGW	AGC	AGW	SHRUB	FORC	FORW
	1	0.025	0	0.05	0	0.0125	0	0
	2	0.075	0	0.1	0	0.0125	0.05	0
	3	0.15	0	0.15	0.05	0.1	0.1	0
	4	0.2	0.05	0.2	0.1	0.125	0.2	0.1
	5	0.25	0.15	0.3	0.25	0.15	0.3	0.25
	6	0.2	0.4	0.05	0.35	0.25	0.15	0.35
	7	0.075	0.2	0	0.15	0.15	0.1	0.2
	8	0	0.15	0	0.1	0.1	0.05	0.1
	9	0	0.05	0	0	0.0625	0.025	0
	10	0	0	0.05	0	0.0125	0.025	0
	11	0.0125	0	0.05	0	0.0125	0	0
	12	0.0125	0	0.05	0	0.0125	0	0

Root distribution	Layer				Group			
		PGC	PGW	AGC	AGW	SHRUB	FORC	FORW
	1	0.2	0.2	0.35	0.3	0.05	0.05	0.15
	2	0.35	0.5	0.275	0.4	0.2	0.2	0.3
	3	0.25	0.2	0.15	0.2	0.25	0.4	0.35
	4	0.15	0.1	0.125	0.1	0.25	0.3	0.2
	5	0.05	0	0.1	0	0.15	0.05	0
	6	0	0	0	0	0.1	0	0

Table 5.5: STEPWAT parameter values for each functional group included in the simulations of plant community dynamics at the shortgrass steppe, the sagebrush steppe and the patagonian steppe.

Parameter	Site	Group						
		PGC	PGW	AGC	AGW	SHRUB	FORC	FORW
initial resource space	SGS	0.07	0.51	0.02	0.05	0.07	0.08	0.2
	ALE	0.4	0.025	0.1	0.05	0.35	0.05	0.025
	PAT	0.3	0.025	0.1	0.05	0.4	0.1	0.025
typical individuals per plot	SGS	0.333	1	1	2	0.02	0.1	0.1
	ALE	0.4	0.03	0.1	0.05	0.35	0.05	0.02
	PAT	0.3	0.025	0.1	0.05	0.4	0.1	0.025
maxium age		75	75	1	1	100	35	35
intrinsic annual growth rate		0.474	0.474	0.947	0.947	0.4	0.426	0.426
proportion of intrinsic growth rate to set as maximum		0.9	0.9	0.9	0.9	0.9	0.9	0.9
num of years pre-mortality		2	2	2	2	2	2	2
*probability of establishment**		*0.125*	*0.125*	*0.1*	*0.1*	1	1	0.015
maximum individuals that may establish per year		2	2	NA	NA	1	3	3
biomass at establishment		0.5	0.605	0.02	0.02	2	0.035	0.035
biomass at maturity		12	12	1	0.5	100	0.707	0.707
vegetative reproduction		y	y	n	n	n	n	n
seedlings per vegetative reproduction		3	3	0	0	3	0	0
temperature class		2	1	2	1	2	2	1

Table 5.6: Analysis of variance results for the probability of conditions suitable for cheatgrass establishment in the spring, fall, and both seasons.

Dependent variable	Source	df	Sum of Squares	Mean Square
Spring	Climate	2	799699	399849
	Soil	2	6613	3306
	Interaction	4	7645	1911
Fall	Climate	2	163742	81871
	Soil	2	13841	6920
	Interaction	4	33525	8381
Total	Climate	2	1408517	704258
	Soil	2	7133	3566
	Interaction	4	20189	5047

Table 5.7: Mean cheatgrass biomass and mean year that biomass reached 40 g/m2 for the final 100 years of each simulation for varying levels of disturbance frequency and establishment probability. SGS refers to the shortgrass steppe Long Term Ecological Research site in NE Colorado, ALE refers to the Arid Land Ecology Research in Central Washington and PAT refers to Rio Mayo area in Argentine Patagonia.

	Site	Disturbance Frequency	Probability of establishment (cheatgrass only)				
			0.01	0.05	0.1	0.25	0.5
Biomass	SGS	2	1.9	2.3	2.3	2.4	2.5
		10	0.1	0.1	0.1	0.1	0.1
		25	0.0	0.0	0.0	0.0	0.0
		50	0.0	0.0	0.0	0.0	0.0
		None	0.0	0.0	0.0	0.0	0.0
	ALE	2	37.8	40.3	39.1	36.6	33.8
		10	95.7	99.1	99.4	95.7	89.7
		25	61.0	63.9	64.8	62.3	60.2
		50	48.5	48.8	48.8	49.6	48.2
		None	38.2	38.4	38.2	37.1	37.0
	PAT	2	36.4	41.8	40.6	37.9	35.4
		10	125.4	133.3	130.5	122.5	111.9
		25	91.5	96.3	93.2	91.5	86.7
		50	82.0	87.0	83.4	82.2	75.9
		None	76.2	74.3	71.9	73.2	71.0
Year	SGS	2	never	never	never	never	never
		10	never	never	never	never	never
		25	never	never	never	never	never
		50	never	never	never	never	never
		None	never	never	never	never	never
	ALE	2	200	128	116	108	104
		10	151	111	105	102	102
		25	151	126	125	102	102
		50	151	140	105	102	101
		None	274	147	145	116	105
	PAT	2	216	130	118	110	104
		10	133	107	104	102	101
		25	127	123	103	102	101
		50	151	113	105	102	101
		None	190	109	109	105	101

Table 5.8: Analysis of variance results for simulated cheatgrass biomass and years required to reach a 40g/m2 biomass threshold as a function of disturbance, seed availability, and the interaction.

Dependent variable	Source	df	Sum of Squares	Mean Square
Biomass	disturbance	4	19089	4772
	seed availability	4	204	51
	interaction	16	95	6
Threshold	disturbance	4	4030	1007
	seed availability	4	23219	5805
	interaction	16	6631	414

Figure 5.1: Long-term climatic conditions at the three sites simulated. SGS refers to the shortgrass steppe Long Term Ecological Research site in NE Colorado, ALE refers to the Arid Land Ecology Research in Central Washington and PAT refers to Rio Mayo area in Argentine Patagonia.

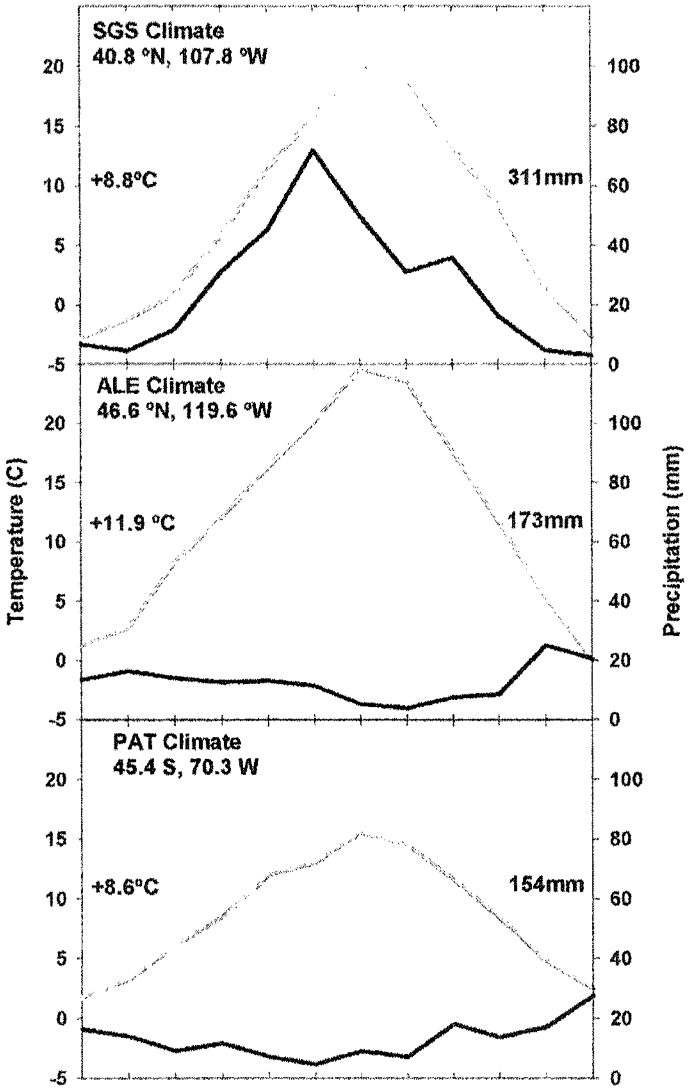


Figure 5.2: Resource space occupied by each plant functional group as defined by annual phenology and root distribution within the soil. PGC and PGW are cool and warm season perennial grasses, respectively. AGC and AGW and cool and warm season annual grasses, respectively. FORC and FORW are cool and warm season forbs, respectively.

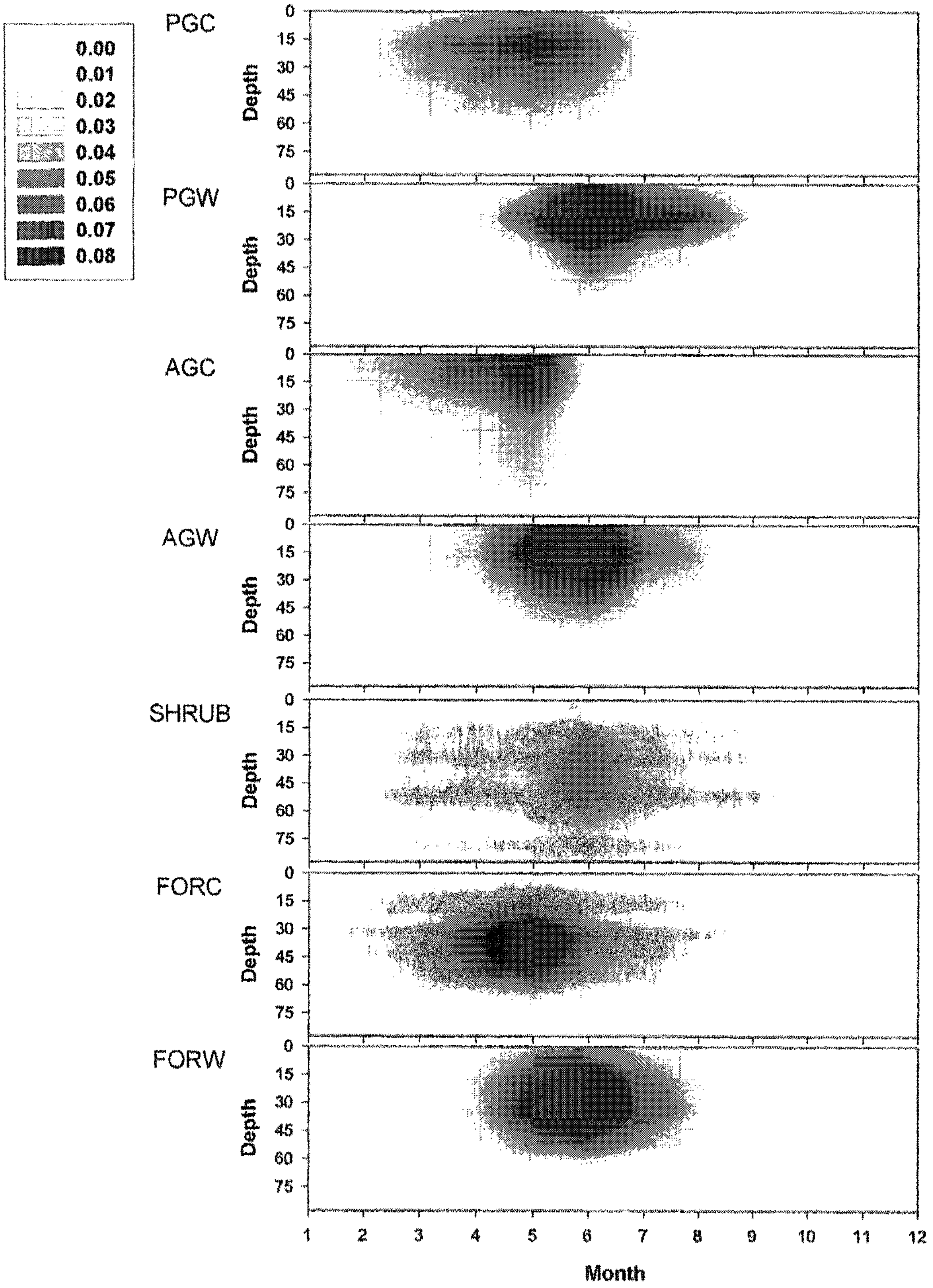


Figure 5.3: Establishment results for the spring and fall at SGS ALE and PAT. Values shown are number of years out of 1000 with conditions suitable for establishment. SGS refers to the shortgrass steppe Long Term Ecological Research site in NE Colorado, ALE refers to the Arid Land Ecology Research in Central Washington and PAT refers to Rio Mayo area in Argentine Patagonia.

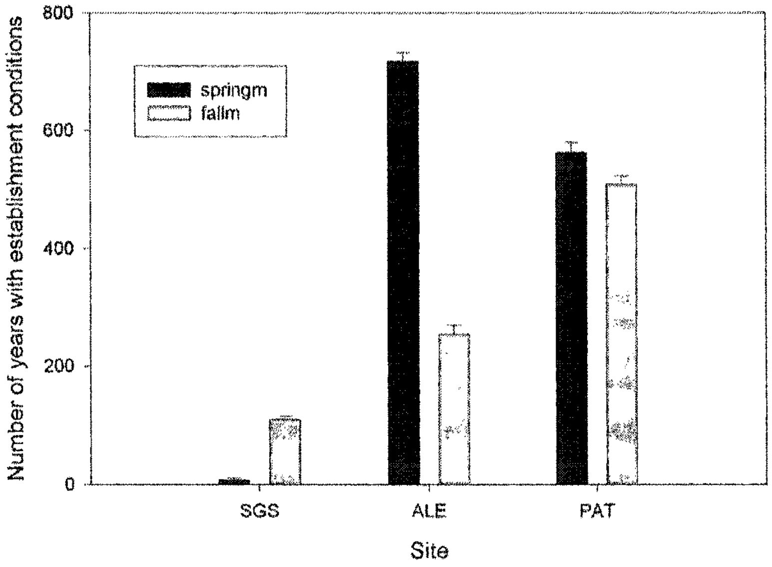


Figure 5.4: Daily precipitation (vertical bars), soil water potential and number of years out of 1000 with conditions suitable for cheatgrass establishment. Values in upper left and right are number of years with suitable conditions in spring and fall, respectively. SGS refers to the shortgrass steppe Long Term Ecological Research site in NE Colorado, ALE refers to the Arid Land Ecology Research in Central Washington and PAT refers to Rio Mayo area in Argentine Patagonia.

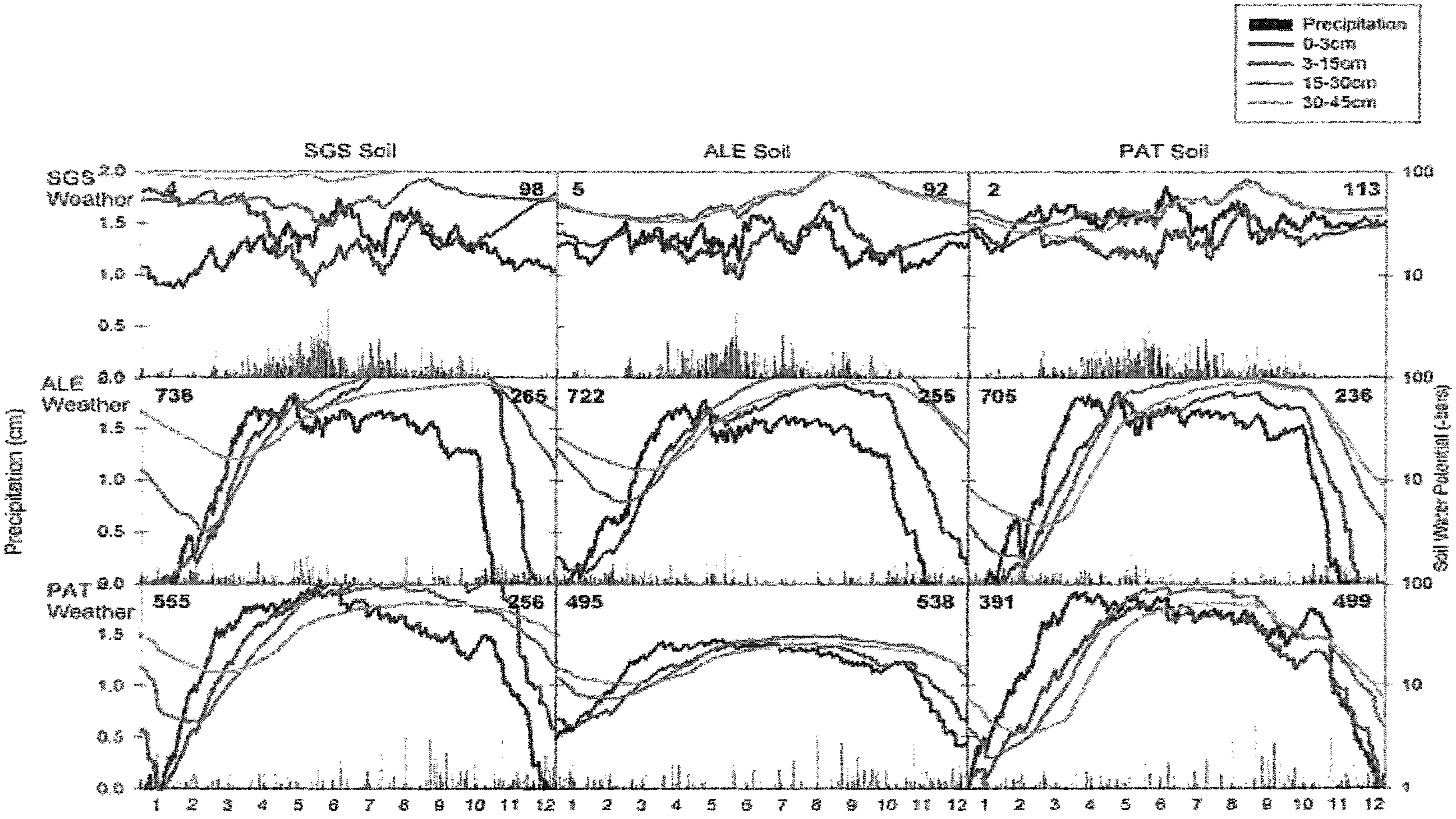


Figure 5.5: Deviation in years with suitable establishment conditions as a result of parameter modification for the 12 parameters that define suitable conditions.

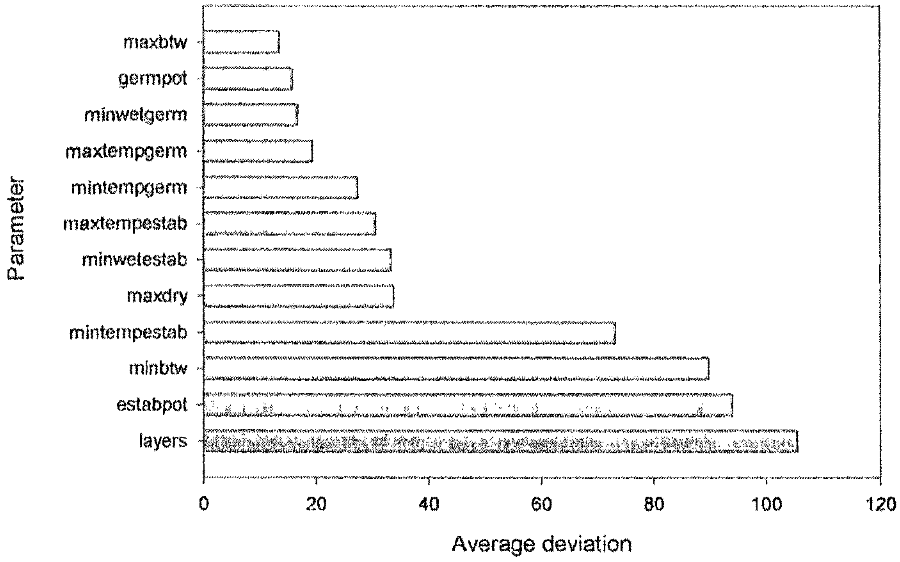
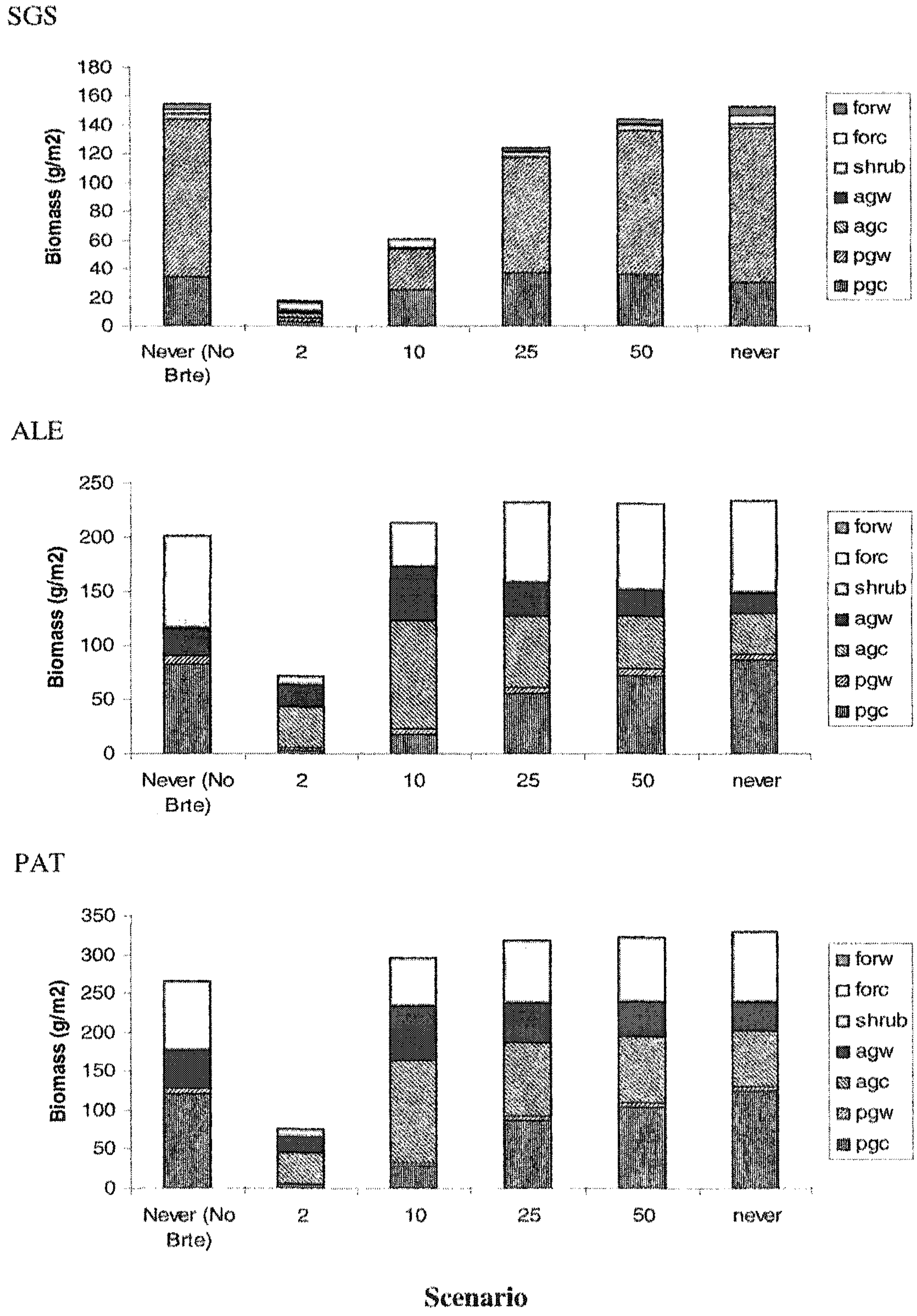


Figure 5.6: Mean biomass of functional groups for scenarios without cheatgrass, and with cheatgrass under 5 disturbance frequencies. SGS refers to the shortgrass steppe Long Term Ecological Research site in NE Colorado, ALE refers to the Arid Land Ecology Research in Central Washington and PAT refers to Rio Mayo area in Argentine Patagonia.



APPENDIX 5.1: MODIFICATIONS TO THE SOILWAT MODEL

Method for estimating rainfall interception by aboveground biomass and litter: Rainfall interception aboveground vegetation was calculated as a function of live biomass, litter, canopy height and LAI using relationships identified by Corbett and Crouse (1968). Corbet and Crouse quantified the amount of water held by grasses and shrubs for a range of vegetation conditions and precipitation event sizes. These observations allowed Corbet and Crouse to estimate the parameters (slope and intercept) for linear equations relating canopy interception to precipitation event size. Since Corbet and Crouse reported the parameters for predicting interception for multiple levels of live biomass and litter, I was able to create linear equations representing how both the slope and intercept change with vegetation cover (Figure 5A.1). Rainfall interception is calculated in the SOILWAT model as a function of vegetation cover (percent cover * canopy height) and litter biomass (g/m2) using these equations. Because vegetation and litter conditions change throughout the year, interception also varies seasonally (Figure 5A.2).

Figure 5A.1: Regression lines for estimating the slope and intercept of the line relating precipitation intercepted by aboveground biomass (A) and aboveground litter (B) to vegetation cover and litter biomass, respectively.

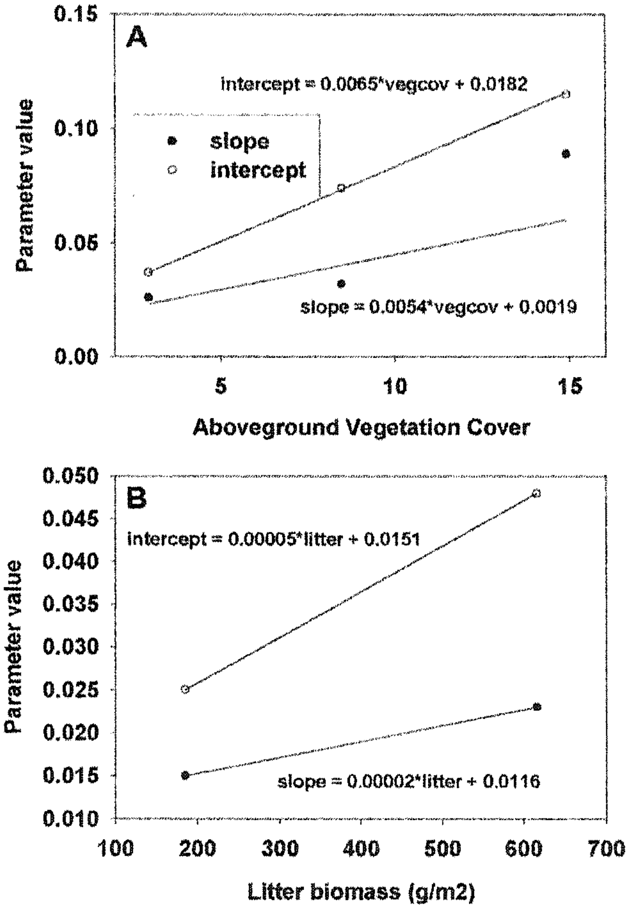
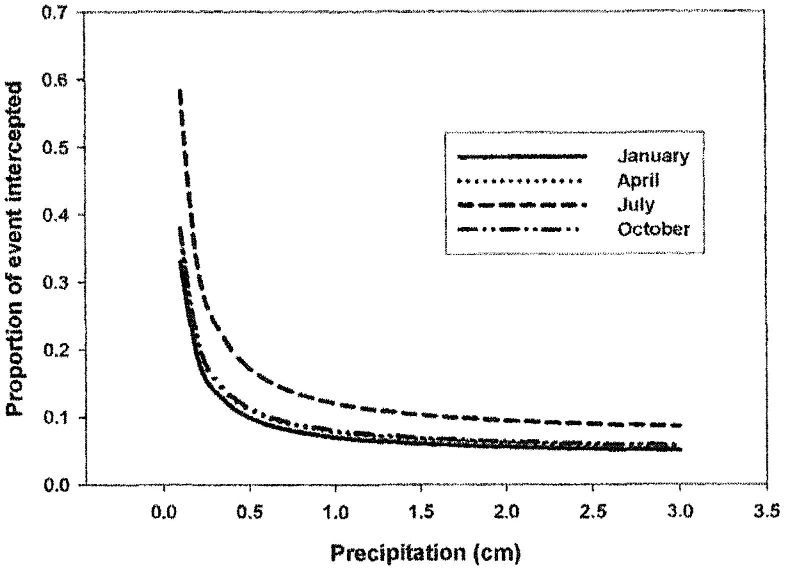


Figure 5A.2: Proportion of a precipitation event that is intercepted by both aboveground biomass and litter as a function of event size for four times during the year.



CHAPTER 6: CONCLUSIONS

These studies represent new understanding of the large-scale impact of human activities on natural systems as well as ecological insight into the relative influence of environmental conditions and land-use practices on ecosystem processes.

In **CHAPTER 2**, my examination of the consequences of land-use patterns in the Great Plains revealed that cultivation has increased aboveground primary production by 26%, decreased belowground production by 10% and created a total regional increase of 10% or approximately 0.046 PgC/yr. These results represent the first quantification of the ongoing consequences of cultivation for primary production and may provide useful information for model validation. Previous studies have examined the effect of land-use practices upon carbon cycling (e.g. Burke et al. 1989, Houghton et al. 1999), and utilized simulation models for extrapolating these processes to regional scales (e.g. Sala et al. 1988, Burke et al. 1990, 1991, Parton et al. 1987, Burke et al. 1997). Although these models have been tested at individual locations, the validity of the models at a regional scale can only be determined by comparison of the model results with actual regional estimates of net primary production and community structure. This study provides a regional estimate of how land-use affects primary production in the Great Plains, which is necessary for testing the validity of these models.

My analysis in **APPENDIX 1** of photosynthetic activity measurements indicates that cultivated areas have much higher light use efficiency than native grasslands, and that this variation influences large-scale ecosystem light use efficiency. My results imply that including cultivation information in the formulation of light use efficiency estimates is crucial for obtaining accurate estimates of primary production from remotely sensed data. The values of light use efficiency for native grassland, C_3 crops and C_4 crops that I provide may prove valuable for future attempts to estimate primary production in mixed grassland-agricultural areas.

In **CHAPTER 3** I used these light use efficiency values to quantify how spatial and temporal patterns of primary production respond to environmental controls as well as land-use practices. I considered climate, soil conditions and long-term average cultivation as spatial controls and weather and interannual cultivation variations as temporal controls. I found that variability in primary production occurs primarily in the spatial domain, whereas variation in phenology is relatively evenly divided between spatial and temporal components. My models explained more of the variation in productivity than phenology and more of the spatial than the temporal patterns, suggesting that the controls over phenology and temporal processes are not well understood. These results indicate that although climate is the most important variable for predicting spatial variation in productivity and phenology, cultivation explains a substantial fraction of the residual variability. Soil conditions contributed very little to my models of spatial variation. Weather and cultivation deviation both made modest contributions to the models of temporal variation in productivity and phenology. A sensitivity analysis indicated that primary productivity is more sensitive to climate than weather and is very sensitive to cultivation intensity. This study identified potential knowledge gaps and provided insight into the probable long- and short-term ecosystem response to changes in climate, weather, and cultivation.

In **CHAPTER 4** I examine the potential of multi-date multi-spectral remotely sensed data to detect a cheatgrass in the Great Basin. I utilized an information-theoretic approach to model selection to determine the best transformation of the spectral data and the best statistical relationship between spectral response and ground observations. I found a significant relationship between spectral response and cheatgrass abundance ($R^2 = 0.647$). This relationship indicates that cheatgrass detection is possible with multi-spectral imagery, and could be used to create cheatgrass distribution maps. These results may prove useful for both land management and research efforts (e.g. Young and Clements 2003) that require accurate and consistent cheatgrass distribution information at large scales (Roughgarden et al. 1991).

In **CHAPTER 5** I use simulation models to examine how climate, soil, disturbance regime and propagule pressure influence cheatgrass invasion. I found that climatic conditions exert primary control over the temporal dynamics of soil water conditions, and therefore influence the suitability of a particular site to invasion. My results suggest an overall conceptual framework for predicting cheatgrass invasion in which climatic conditions specify regions that are susceptible to invasion, disturbance regime dictates how severe the invasion will be, and propagule pressure influences how fast the invasion occurs. This general understanding of the controls over cheatgrass invasion should provide insight into the question of future cheatgrass invasion in areas that have not yet experienced widespread invasion, such as Argentine Patagonia (Soriano et al. 1983). My results indicate that Patagonia is susceptible to invasion but suggests that land-use practices may influence the severity and speed of invasion.

As a whole, my dissertation provides some insights into the importance of land-use as a driver of global change processes in semi-arid ecosystems. These studies quantified the impact of land-use on global change processes and placed these impacts in the context of control exerted by environmental factors. I found that while land-use practices exert substantial influence on both primary production in the Great Plains and biological invasions in the Great Basin, my results indicate that climatic conditions retain primary control over these processes while soil properties are only minimally important. This work represents one of the first attempts to directly compare the importance of human activities and environmental conditions on ecosystem processes across large scales.

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APPENDIX 1: THE RELATIVE IMPORTANCE OF LIGHT USE EFFICIENCY MODIFICATIONS FROM WEATHER AND CULTIVATION FOR ESTIMATION OF LARGE-SCALE NET PRIMARY PRODUCTIVITY

ABSTRACT

Net primary production is the amount of carbon fixed into biomass by vegetation and understanding spatial and temporal variation in net primary production has become a central goal of ecosystem ecologists. Optical remote sensing techniques can help address this need by providing accurate, consistent and reliable approximations of photosynthetic activity at large scales. However, converting photosynthetic activity into net primary production requires estimates of light use efficiency, which is has been known to vary between vegetation types. In this study, we compare remotely sensed photosynthetic activity measurement with ground based net primary productivity estimates to determine appropriate light use efficiency values for grasslands and croplands. We contrast the performance of models with and without both cultivation information and light use efficiency down-regulation due to inclement weather conditions. Our results suggest that including cultivation information in light use efficiency calculations causes dramatically better fit between ground and remotely sensed estimates of primary production. We observed only modest improvements as a consequence of including environmental down-

regulation, which may be a result specific to grassland and cropland systems. In addition to illustrating how crops and native grasslands have variable light use efficiency at large scales, these results present a suite of approaches to approximating light use efficiency that may prove useful in future studies of grassland and cropland primary production.

INTRODUCTION

Ecosystem structure and function vary across both space and time, and accurately representing this variation is essential for understanding ecological processes at large spatial and temporal scales (Levin 1992). Obtaining measurements that capture process variation has become one of the primary challenges for large-scale ecological studies (Wessman and Asner 1998). Although some processes may be amenable to direct scaling or simulation modeling efforts, these techniques often include aggregation errors (O'Neill and Rust 1979, Rastetter et al. 1992) or assumptions about driving variables (e.g. Leith 1975, Parton et al. 1993). Remotely sensed spectral reflectance data are unique in their ability to provide consistent large-scale observations that can be related to ecological processes (Roughgarden et al. 1991). .

One fundamental ecological process that may be measurable at large scales via remote sensing is plant productivity. Obtaining consistently accurate estimates of plant productivity has become crucial because production influences carbon cycling and elevated atmospheric carbon dioxide may be partly responsible for observations of warming climatic trends (IPCC 2001.) The direction and magnitude of the atmosphere-biosphere carbon flux is dictated by the balance between net primary production (NPP: flux to the biosphere) and decomposition (flux to the atmosphere.) Although neither carbon flux nor decomposition are easily measured over large areas (but see Goulden et al. 1996), NPP is related to plant photosynthetic activity and can be estimated by observing patterns of light absorption via remote sensing (Sellers 1995). Consequently, remote sensing techniques that quantify light absorption have emerged as the primary source of large-scale NPP information, and the only actual observations of carbon cycling processes at regional or global extents. Monteith (1972, 1977) developed methods for estimating plant productivity from observations of absorbed photosynthetically active radiation (APAR), and estimates of light use efficiency (LUE):

$$NPP = APAR \times LUE \tag{1}$$

where NPP is net primary productivity ($gm^{-2}time^{-1}$), APAR is absorbed photosynthetically active radiation ($MJm^{-2}time^{-1}$) and LUE is photosynthetic efficiency ($gCMJ^{-1}$). APAR can be calculated from the product of incoming photosynthetically active radiation (PAR) and the fraction of PAR that is absorbed by vegetation (FPAR.) FPAR is related to the photosynthetic activity of vegetation and can be determined from remotely sensed observations of surface reflectance. These methods have gained popularity in large-scale ecosystem studies because they produce NPP estimates from relatively modest inputs.

Regional and global scale NPP studies require accurate estimates of both APAR and LUE. Although spatial and temporal variations in APAR can be consistently quantified through remote sensing techniques (Sellers et al. 1992), photosynthetic efficiency is not yet easily assessable by remote sensing (although see Barton et al. 2001 and Boegh et al. 2002). LUE is known to exhibit both spatial variation across vegetation types (Gower et al. 1999, Turner et al. 2002) and temporal variation at individual sites

(Nouvellon et al. 2000, Campbell et al. 2001). Consequently, generating valid representations of LUE is especially difficult in regions with substantial cultivation because native vegetation and crops often have different LUE values (Gower et al. 1999), which creates spatial heterogeneity not captured by the remotely sensed input data. One approach is to utilize a single LUE value for the entire study area, including cultivated and uncultivated areas. Although this solution has the advantage of simplicity and modest data requirements, it may produce substantial errors due to systematic misrepresentation of LUE. Other methods incorporate information about vegetation type or weather conditions in LUE calculation (e.g. Ruimy et al. 1994). One such technique is the Carnegie Ames Stanford Approach (CASA) for estimating NPP from remote sensing data. CASA is a widely recognized NPP model that downregulates photosynthetic efficiency in response to cold temperatures or dry soil conditions (Potter et al. 1993). Despite documented variability of LUE between crops and native grasses (Gower et al. 1999, Lobell et al. 2002), the CASA approach to NPP estimation typically does not consider cultivation patterns in their formulation of LUE.

A recent study that quantified cropland LUE at large scales is the work of Lobell et al. (2002), in which LUE estimates for corn and wheat were estimated by fitting crop harvest statistics to remote sensing observations using the CASA model. This study concluded that cultivated areas have different LUE than native vegetation and that those estimates can be utilized to improve large-scale estimates of NPP that are derived from remote sensing. My study differs from that of Lobell et al. in both objectives and methods. One important difference is that I determined cropland LUE by fitting ground-based estimates of NPP for entire counties with remote sensing NPP estimates for the same counties and years. By contrast, Lobell et al. relied upon a classification of AVHRR pixels (Hansen 2000) into cultivated or uncultivated and only used the cultivated pixels to estimate LUE. Other differences include the fact that Lobell et al. assumed that belowground productivity was a constant proportion of aboveground productivity regardless of the crop whereas I calculated belowground productivity as a flexible proportion of aboveground productivity that depends on published crop-specific carbon allocation ratios. Both of these approaches have potential disadvantages: the classification that Lobell et al utilized must contain some errors, since no 1 km^2 area in entirely cultivated, and likewise my estimates of whole-county LUE assume that uncultivated areas are native vegetation. Comparison of the results from these two approaches can provide valuable validation of the resultant LUE estimates.

In addition to examining how cultivation can influence ecosystem LUE and subsequent estimates of NPP, this study quantifies the importance of modifying LUE based on environmental (e.g. reducing LUE for low temperatures or water availability) limitations. Although environmental modification of LUE may provide improved NPP estimates, the magnitude of the improvement and the relative benefits of LUE modifications from environmental conditions versus cultivation remains unclear because independent validation data are rare. This study represents one of the first attempts to understand the extent to which environmental LUE modifications improve remote sensing NPP estimates.

Understanding how LUE responds to spatial variations in vegetation type and temporal variations in weather provides insight into the necessity and value of performing these LUE modifications. In this study I calculate NPP from APAR and LUE with different representations of LUE and quantify the importance of including environmental conditions and cultivation intensity in LUE by comparing these estimates to independent ground measurements of NPP. This analysis allows us to characterize the extent to which LUE modifications from environmental conditions and cultivation intensity actually improve NPP estimates. My specific objectives are 1) characterize the discrepancies between NPP estimates from the existing CASA model and ground level data, 2) address these discrepancies by inverting equation 1 to estimate grassland and cropland LUE values for remote sensing NPP algorithms with and without LUE limitation due to environmental conditions and cultivation practices and 3) use these results to quantify the importance of the environmental and cultivation LUE modifications in grassland and cropland systems.

METHODS

Study site: I conducted this study in the U.S. Great Plains, which comprises the area between the Rocky Mountains and the Mississippi River, from the Canadian border into south Texas (Figure 1). Native vegetation includes southern mixed prairie, shortgrass steppe, tallgrass prairie and northern mixed prairie. Land-use is dominated by grazed native grassland and cropland. Precipitation occurs primarily in the summer and mean annual precipitation ranges from less than 400 mm in the west to approximately 1000 mm in the east. Mean annual temperature ranges from 3° to 21° C from north to south (Lauenroth and Burke 1995).

I chose counties for this study based on availability of range site production data from the USDA Natural Resource Conservation Service's (NRCS) STATSGO database

(SCS 1976) and vegetation type as defined by Kuchler (1964). STATSGO provides range site production values only for states to the west of and including the Dakotas, Nebraska, Kansas, Oklahoma and Texas. Within this area I included counties that historically contained at least 70% of the following vegetation types: northern mixed grass prairie, shortgrass prairie, tallgrass prairie, tallgrass savanna, southern mixed grass prairie, desert savanna and floodplain forests. These restrictions identified 630 counties within the Great Plains that were suitable for this study (Figure 1). I collected data for the years 1991-1998 for these counties. The Great Plains region is ideal for this study because it contains a wide range of cultivation intensities and native vegetation is primarily grassland. The range of cultivation intensities allows us to examine the influence of cultivation and crop photosynthetic pathway on LUE. Remote sensing methods, based on NDVI, have been used to estimate NPP in grasslands (Tucker et al. 1986, Paruelo et al. 1993, Paruelo et al. 1997, 1999, Potter et al. 1999) and croplands (Aase and Siddoway 1981, Hatfield 1983, Daughtry et al. 1992, Moulin et al. 1998).

Ground estimates of NPP: Whole-county NPP estimates must include estimates from a mixture of cultivated and non-cultivated areas. To quantify county-level primary productivity from ground-based measurements, I assumed all non-cultivated areas are native grassland, and considered each county as a mixture of cultivated areas and native grasslands. Cultivated area was determined from USDA crop harvest statistics (NASS 1998). Within each county, I estimated aboveground NPP (ANPP), belowground NPP (BNPP), and overall NPP (the sum of ANPP + BNPP) for both cultivated areas and native grasslands. Ground estimates of whole-county NPP were calculated as the area-weighted average of NPP from cultivation and NPP from native grasslands on the remainder of the county.

For ANPP in native areas I utilized data from the STATSGO database. NRCS has divided each western state into range sites, and measured range site production, defined as ANPP (Joyce et al. 1986). I used ARCINFO (ESRI 1996) to overlay a county map over the range site production map and calculate the area-weighted average range site production value for each county.

Estimating native belowground net primary productivity (BNPP) is more difficult than estimating ANPP (Lauenroth 2000). Consequently, no empirical datasets for regional BNPP exist. However, Gill et al. (2002) have reasoned that BNPP can be estimated as a function of maximum yearly instantaneous belowground biomass (BGB), maximum proportion of BGB that is alive during the year (liveBGB/BGB) and root turnover (T) according to the equation:

$$BNPP = BGB \bullet (\frac{liveBGB}{BGB}) \bullet T$$

Gill et al. (2002) used these relationships along with reported pairs of BNPP and ANPP values to generate equations to predict BNPP from ANPP and temperature in grasslands. Their results indicate that BGB, live BGB/BGB and T can be estimated from aboveground biomass (AGBIO) and mean annual temperature (MAT) as:

$$BGB = 79 \bullet AGBIO - 33.3(MAT + 10) + 1289$$

$$\frac{liveBGB}{BGB} = 0.6$$

$$T = 0.0009 \bullet ANPP + 0.25 \qquad \text{"direct function"}$$

or

$T = 0.2884e^{0.046 \times MAT}$ "exponential function"

I utilized these relationships to represent BGB and liveBGB/BGB. For turnover, I calculated regional BNPP using both the direct and exponential functions. Although these methods produced differences in the spatial BNPP patterns, the regional BNPP totals were extremely similar. For further analyses, I calculated BNPP using the exponential function because its spatial patterns were closer to observed patterns within the Great Plains than were estimates using the direct function.

To estimate NPP in cultivated areas, I utilized data from The USDA National Agricultural Statistics Service (NASS 1998). NASS maintains records of acreage and economic yield for most crops produced in the U.S. Economic yield (ie. bushels or tons) can be translated into ANPP and BNPP by using harvest index values (ratio of biomass harvested to total aboveground biomass) and resource allocation ratios (ratio of aboveground productivity to belowground productivity), respectively (e.g. Prince et al. 2001, Zheng et al 2003). I used published harvest index values (Table A.1) to calculate ANPP for cultivated areas. To estimate BNPP I calculated a whole-county allocation ratio and multiplied it by ANPP estimates (both from NDVI and crop statistics) to determine BNPP. I used published ANPP and BNPP values for crops to determine allocation ratios (Table A.1) for cultivated areas and assumed that uncultivated areas are native vegetation.

Initial comparison of CASA and ground estimates: For my initial comparison between remotely sensed NPP and ground level NPP I used the CASA model, with a minor modification, to estimate NPP. The CASA model uses semimonthly measurements of the normalized difference vegetation index (NDVI) from NOAA's Advanced Very High

Resolution Radiometer (AVHRR) to measure FPAR. NDVI is a commonly used remotely sensed vegetation index that quantifies plant photosynthetic activity by measuring the difference between reflectance in the near-infrared wavelengths and red wavelengths according to the formula:

$$NDVI = \frac{NIR - RED}{NIR + RED}$$

Chlorophyll in live green vegetation reflects a greater proportion of light in the infrared wavelength than the red wavelength, creating positive NDVI values. As a result, NDVI has been strongly correlated with the fraction of absorbed photosynthetically active radiation (FPAR) in native vegetation (Law and Waring 1994, Goward et al. 1994, Goward and Huemmrich 1992) as well as crops (Gallo et al. 1985, Daughtry et al. 1983). Seasonal NDVI signatures can provide an estimate of annual FPAR, which combines with empirical measurements of incoming (PAR) to estimate APAR. CASA represents LUE as a single global maximum value that is reduced during times of unfavorable temperature or water availability. Monthly LUE is determine as:

$$E = LUE^{*} \bullet T_1 \bullet T_2 \bullet W$$

where E* is the maximum photosynthetic efficiency, T_1 and T_2 are reduction factors representing deviations from site-specific optimal temperature and deviation from 20°C, respectively and W represents reduction from low soil moisture as determined by a simple soil water model (Potter et al. 1993, Field et al. 1995). Lobell et al. (2002) recently showed that cultivated areas, even at very large scales, have different LUE values than native grasslands. In an attempt to account for this variation and thus generate the most realistic CASA-derived NPP estimates given current understanding of LUE values, I modified CASA determination of LUE slightly by using Lobell et al's results to represent LUE* as an area weighted average of native area, C_3 cropland area and C_4 cropland area:

$$LUE^* = N \bullet LUE_N + C_3 \bullet LUE_3 + C_4 \bullet LUE_4$$

where LUE_N is the LUE for native vegetation, LUE_3 and LUE_4 are previously observed photosynthetic efficiency values for 0.29 for C_3 croplands and 0.66 for C_4 croplands, (Lobell et al. 2002) and N, C_3 and C_4 are the proportions within the county of native vegetation, C_3 cropland and C_4 cropland, respectively. I examined results from CASA using two different estimations of LUE for native vegetation. In the first version, I used the LUE value of 0.435 traditionally employed by CASA, whereas in the second version I determined the native vegetation LUE by finding the native LUE value that minimized squared errors between ground NPP data and the CASA NPP estimates for the 158 counties with less than 10% cultivation. For both approaches, I utilized Lobell's LUE values for C_3 and C_4 LUE. I employed both of these modified CASA models to estimate NPP for each county for the years 1990-1998, calculated 9-year county means and compared these means with the ground NPP estimates described above.

Formulating alternative LUE representations: To examine how modifications to LUE from environmental (weather and subsequent soil moisture) conditions and land use patterns impact the ability of remotely sensed techniques to measure NPP county, I formulated 6 models that estimate NPP using eq. 1 with varying methods for representing LUE (Table A.2). To examine the importance of limiting LUE based on environmental conditions, three of the models use the weather LUE limitations calculated by the CASA method and three assume constant LUE through time. To examine the influence of variations in sensitivity to vegetation type, each set of three models contains one model that uses a single value of LUE for the entire county, one model that calculates LUE as a spatially weighted average of the cultivated and native areas within the county, and one model that calculates LUE as a weighted average of native vegetation area, C_3 cultivated area and C_4 cultivated area.

Determining LUE values for each model: Since NPP equals APAR times LUE, I used my ground-level county NPP data (STATSGO/Crop harvest) and NDVI-derived APAR to solve for LUE values. To determine new photosynthetic efficiency values for each NDVI-based model, I performed a linear regression for each model to determine the LUE value or values. For the models with a single LUE value, ground-level NPP is the independent variable, APAR is the dependent variable, and LUE is the coefficient determined by the regression. For the models with multiple LUE values, NPP divided by APAR is the independent variable and proportion of the county in different vegetation types (native and total cultivated or native, C_3 crops and C_4 crops) are the dependent variables. I used the REG procedure with the no intercept option in SAS Version 8.0 (SAS 1999) to perform these regressions with mean NPP, APAR and land use data from the years 1990 to 1998.

Assessing the importance of LUE modifications: The validity of each NDVI-derived model is quantified by the extent to which the NPP predicted by the model fits the NPP calculated from ground estimates. Because the LUE values for each model were determined by regression of APAR onto observed NPP, the slope and intercept of the relationship between the subsequent model predictions and the observed NPP values are 1 and 0, respectively. Consequently, the R^2 values for each model measure only the degree of similarity between predictions and observations and quantify the accuracy of the model. Since the NDVI models used in this study differ only in the formulation of county LUE, comparison of model R^2 values indicate how the various formulations can influence model validity.

RESULTS AND DISCUSSION

CASA NPP vs. ground NPP: I used two modified CASA representations that relied on LUE values derived by Lobell (2002) for C_3 and C_4 crops and calculated a LUE value for each county based on spatially weighted averages of native vegetation and crops. This method allowed us to partially account for differences in LUE based on cultivation practices. Comparisons of NPP from the version of CASA with native LUE of 0.405 and ground estimates indicate that this CASA model consistently predicts higher county NPP than ground-level NPP estimates based on STATSGO data and crop harvest statistics (Figure A.2). Of the 630 counties examined in this study, 580 have higher NPP estimates from CASA, whereas only 50 have higher estimates from ground level measurements. The difference between CASA and ground-level county NPP estimates range from 316 to -141 g/m2. For the entire region, CASA estimates NPP to be 0.705 $PgCyr^{-1}$, compared to a ground level estimate of 0.507 $PgCyr^{-1}$. The difference between these estimates is 0.198 $PgCyr^{-1}$. For comparison, the best estimates of the net carbon sink (the difference between the net carbon fixed by vegetation (NPP) and the release of carbon to the atmosphere through processes such as decomposition) for the conterminous US is 0.3-0.6 $PgC\ yr^{-1}$ (Pacala, et al. 2001.) Furthermore, the difference between CASA and ground estimates is negatively related to cultivation intensity. Although the CASA model was originally calibrated on NPP measurements from multiple biomes, including native grasslands (Potter et al.1993), counties with very low cultivation (and hence a high proportion of native grassland) show a consistent positive difference between CASA and ground estimates. This study, along with other recent work (Lobell et al. 2002), represent the first attempts to calibrate CASA to individual biomes. My results suggest that the CASA model overestimates productivity in native grasslands (Figure A.2 A). Since the algorithms for calculating APAR from NDVI are well established (Sellers et al.1992), this discrepancy is likely a result of overestimating LUE for native vegetation. Counties with higher levels of cultivation, on the other hand, have lower, and in some cases negative, differences between CASA and ground NPP estimates. The fact that heavily cultivated counties display a better fit between CASA and ground estimates may suggest that the county-specific LUE values used in this modified CASA representation are closer to the LUE of cultivated areas than the LUE of native vegetation (Table A.2).

To examine how NPP estimates from CASA could be improved by altering the value of LUE for native vegetation I determined a new native LUE by least squares regression on counties with very low levels of cultivation (<10% cultivated). Using this approach, I identified an optimum native vegetation LUE estimate of 0.246 gC/MJ (Table A.2), substantially lower than the LUE value of 0.405gC/MJ that was calibrated from measurements in multiple ecosystems and originally utilized by CASA (Potter et al. 1993). This difference may account for much of the discrepancy between CASA NPP estimates and ground NPP estimates (Figure A.2 B). NPP estimates using this LUE representation are closer to ground NPP estimates than NPP estimates generated with a native LUE of 0.405 gC/MJ (Figure A.2 A vs. B), increasing the R^2 value of the regression between predictions and observation from 0.506 to 0.803 (Table A.2). Differences between county level ground NPP and CASA NPP using this method range from -123 g/m2 to 749 g/m2, with 361 counties greater than the ground estimate and 269 counties lower than the ground estimates. This method estimates regional NPP of 0.502 $PgCyr^{-1}$, only slightly less than the ground estimate of 0.507 $PgCyr^{-1}$(Table A.2). My results indicate that modifying the LUE value for native grasslands in the CASA model from 0.405 gC/MJ to 0.246 gC/MJ dramatically improved the fit between NPP estimates from CASA and ground observations, implying that 0.405 gC/MJ is higher than the actual LUE of native grasslands.

LUE values for independent LUE models: To further explore the possibility for improving NPP estimates and provide independent validation for the cropland LUE values derived by Lobell et al (2000), I generated 6 algorithms for representing county LUE and used the ground-level NPP estimates along with APAR data to determine the LUE values appropriate for each algorithm (Table A.2). When I represent LUE as a single value, I estimate LUE to be 0.301gC/MJ when environmental limitation is included and 0.202gC/MJ when weather limitation is not included (Table A.2, A and D). These results suggest an overall weather-limited LUE of 0.301gC/MJ.

Representing county LUE as an area-weighted average of native grassland and cultivated areas (Table A.2: B and E) produced weather-limited LUE estimates for native and cultivated areas of 0.218gC/MJ and 0.498gC/MJ, respectively, and non-limited LUE estimates for native and cultivated areas of 0.139gC/MJ and 0.351gC/MJ, respectively. In algorithms 3 and 6, I represented LUE as a function of native grassland area, C_3 cropland area and C_4 cropland area. When I included weather limitations on LUE, I found LUE for native areas, C_3 crops and C_4 crops to be 0.234 gC/MJ, 0.332 gC/MJ and 0.770 gC/MJ, respectively. The native LUE value of 0.234 gC/MJ is very close to the 0.246 gC/MJ native LUE value that I determined using only counties with less than 10% cultivation. My weather limited algorithm with separate LUE values for native, C_3 and C_4 crops is should produce results comparable to Lobell et al. (2002), who estimated LUE values corn (the primary C_4 crop) and wheat (the primary C_3 crop) of 0.66gC/MJ and 0.29gC/MJ, respectively. The discrepancies between the results of Lobell et al. (2002) and my results are likely a consequence of 2 differences in how I obtained my LUE estimates. First, I calculated LUE for all C_3 and C_4 crops, rather than specifically corn and wheat. Wheat is only modestly productive and may not display LUE representative of other C_3 crops. This may explain why my C_3 estimate is slightly higher than Lobell et al's wheat LUE. Second, my estimates are based on weighted averages for entire counties, rather than individually identified pixels as utilized by Lobell et al. (2002). Lobell et al's (2002) approach of fitting LUE values to entire AVHRR pixels that have been classified as cultivated may produce slightly lower LUE estimates for C_3 and C_4 crops because each pixel that is classified as cultivated is likely to contain some native vegetation. Since native vegetation has lower LUE these unaccounted mixtures will decrease the observed LUE values for croplands, possibility explaining my slightly higher estimates of LUE for C_3 and C_4 croplands compared to Lobell et al's (2002) estimates. The differences in methods employed by these two approaches to estimating LUE makes comparisons between the approaches valuable for validation. Although the approaches do not yield exactly identical LUE values, the differences are modest and suggest that the estimates are good approximations of the actual LUE values for specific land use types.

Not including weather limitations yielded LUE estimates of 0.150gC/MJ, 0.231gC/MJ and 0.548gC/MJ for native areas, C_3 crops and C_4 crops, respectively. I observed a general pattern of highest LUE in C_4 crops, lower C_3 crops and lowest LUE in native grasslands; this pattern is also documented in previous studies (Ruimy et al. 1994, Gower et al. 1999). However, my LUE values, even those that include limitation due to weather and soil moisture conditions, are generally lower than previous results. Gower et al. (1999) reviewed published studies of LUE and observed a range of 2.85 to 5.07gC/MJ in C_4 crops, 1.02 to 5.2gC/MJ in C_3 crops and 0.07 to 2.00gC/MJ in grasslands. In a similar review, Ruimy et al.(1994) calculated a value of 2.07 gC/MJ for cultivated crops and 1.26gC/MJ for grasslands. In my best NPP algorithm I observed LUE values of 0.77gC/MJ in C_4 crops, 0.33gC/MJ in C_3 crops and 0.23gC/MJ in grasslands. The consistent discrepancy between my results and those from previous studies may be a consequence of different spatial scales, temporal durations and methods of calculating LUE. Many previous studies have quantified LUE for short time periods (i.e., growing season or shorter) and at plot scales, whereas my study calculates annual LUE from NPP and APAR observations of entire counties, including non-vegetated or other low-productivity areas.

Not surprisingly, the algorithms that allow LUE limitation from environmental conditions (weather and soil moisture) produced higher LUE values than the algorithms that did not limit LUE based on weather. The weather limitation lowers LUE during months when conditions are either too dry or too cold to allow maximum photosynthetic efficiency. This requires that the LUE values used in calculating NPP be increased to allow good fit between predicted and observed NPP values. The LUE predicted by algorithms that incorporate environmental limitations are an estimate of the maximum attainable photosynthetic efficiency. Algorithms that do not include weather limitation of LUE, on the other hand, will always yield lower LUE values because those LUE values must produce the same productivity estimates but are never reduced during times of adverse conditions. These LUE values may prove useful for future NPP studies in large grassland and cropland areas.

Importance of LUE modifications: To quantify the strength of the relationship between NPP predicted by each remote sensing algorithm and NPP estimated by ground data I calculated R^2 for each comparison. Since my 6 algorithms for calculating NPP from APAR and LUE differ only in their representations of LUE, comparison of R^2 values provides insight into the importance of the LUE modifications for improving model fit. Representing LUE as a single value yielded R^2 values of 0.279 when LUE included weather limitation and 0.162 without weather limitation (Table A.2). These low R^2 values are not surprising considering the substantial differences in observed LUE between native grasses and crops. Cultivated plants have been selected for consistent growth (e.g. Boukerrou and Rasmusson 1990, Edmeades et al. 1999) and are often irrigated and/or fertilized, limiting the effect of resource limitation on cropland LUE and allowing some croplands to have higher LUE values than native grasslands. Counties with extremely heavy cultivation had much higher NPP values from ground estimates than from remote sensing estimates for these algorithms, suggesting that the LUE used in these counties was too low (Figure A.3: A and D). Consequently, a single value cannot adequately represent LUE in a region with variable cultivation intensity. The algorithm that included weather limitation was more successful at NPP prediction than the algorithm without weather limitation. The improvement appears to be most evident in counties with low productivity, indicating that temporal weather limitation is most important in less productive, typically dry, areas that are subjected to more frequent and drastic drought events (Lauenroth and Burke 1995). The single LUE algorithms with and without weather limitation overestimated total regional annual NPP predictions by 0.024 and 0.035 $PgCyr^{-1}$ compared to the ground data.

Including information about the total area cultivated in the calculation of LUE increased the R^2 to 0.671 with weather limitation and 0.602 without weather limitation (Figure A.3: B and E). This is a substantial improvement in the relationship between predictions and ground observations over the algorithms that treated LUE as a single value. Compared to the algorithms with a constant LUE, determining separate values for native and cropland LUE produced lower values for native LUE and higher values for cropland LUE compared to the single LUE. This variability allows the LUE used for each county to more accurately represent the actual LUE patterns throughout the region and therefore improve predicted NPP. In particular, these algorithms appear to have improved NPP predictions for counties with low productivity (i.e., counties on the left of Figure A.3:B and E are centered over the identity line, as opposed to counties on the left of Figure A.3:A and D, which are consistently above the identity line.) Since the unproductive counties tend to have low cultivation intensity, these counties are primarily native grassland, are assigned lower LUE values, and are predicted to have lower NPP. These lower NPP predictions are closer to the ground data than NPP estimates with a single LUE value. Likewise, counties with heavy cultivation get assigned a high LUE value and subsequently have higher NPP predictions (compare the tail of outliers in Figure A.3 A and D with the outliers in Figure A.3:B and E), again strengthening the fit with ground data. Despite this improvement, NPP predictions for many counties with extremely heavy cultivation are still consistently lower than the ground estimates. The algorithm that included weather limitation yielded slightly better results than the algorithm without weather limitation. The algorithms utilizing separate values for native and cropland LUE also showed improvement in regional NPP estimation compared to the algorithms with constant LUE. The difference between predicted and observed regional NPP is 0.005 and 0.009 $PgCyr^{-1}$ for weather limited and non-limited algorithms, respectively.

Representing LUE as an area weighted average of native area, C_3 cropland and C_4 cropland produced the best relationship between NPP predictions and observations (Table A.2, algorithms C and F.) I calculated R^2 values of 0.840 and 0.793 for the algorithms with and without weather limitation, respectively (Figure A.3: C and F). The LUE values determined for C_4 crops are substantially higher than either the native and C_3 cropland LUE in these algorithms or the overall cropland LUE in algorithms B and D. Since many of the extremely productive counties contains high proportions of corn, a common C_4 crop, this high LUE for C_4 crops elevates the predicted NPP for these counties to levels very close to the ground-level NPP (ie. counties on the right of Figure A.3:C and F are close to the identity line.) Representing LUE in terms of native, C_3 and C_4 areas also improved regional NPP estimates. Regional NPP from the algorithms with and without weather limitation are only 0.001 and 0.005 $PgCyr^{-1}$ higher than regional NPP from the ground data, indicating improvement over algorithms with LUE values for native and cultivated areas only (Table A.2). Including environmental limitation improved NPP predictions for algorithms with this LUE representation, but again the improvement was minor compared to the effect of separating cropland into C_3 and C_4 crops.

My results indicate that temporal modifications to LUE from weather and soil moisture conditions provide modest improvements in NPP predictions. This conclusion may be specific to grassland ecosystems. Environmental LUE limitation may not be especially important for modeling NPP in grasslands because the shallow rooting, short lifecycles and limited water storage capacity of grasses may cause tighter coupling between environmental conditions and light absorption. Water is the primary limiting resource in grasslands (Noy-Meir 1973), and grassland plants respond quickly to changes in water availability. Unlike coniferous trees, which maintain photosynthetic pigments throughout the winter, or deciduous trees, which use deep root systems and water reservoirs in their trunks to maintain photosynthetic activity during brief droughts, grasses are quickly and dramatically impacted by soil moisture conditions. If the formation and degradation of photosynthetic pigments in grass leaves is closely linked to actual photosynthetic activity, then APAR observations will accurately measure NPP, minimizing the need to separately model LUE reduction due to environmental conditions. Alternatively, the soil water model employed by CASA may not realistically represent the moisture conditions in the relatively shallow soil surface layer accessed by grass roots.

CONCLUSIONS

Previous studies (e.g. Lobell et al 2002) have determined that cultivated areas can have LUE values different from native vegetation and that these differences can influence remote sensing estimates of NPP. I found that the CASA NPP model, including estimates of cropland LUE from Lobell et al. (2002) produced consistently higher NPP estimates than my ground data in native grasslands, and to a lesser extent, in croplands. I were able to dramatically reduce the discrepancies between CASA estimates and ground estimates of NPP using a smaller native LUE that I determined by fitting CASA NPP to ground NPP in counties with very low cultivation. In addition to this modification to CASA's LUE calculations, I formulated six other representations for LUE and compared NPP estimates using those representations with ground NPP estimates. My statistically determined constant LUE value for the entire region was lower than the LUE used by CASA, accounting for CASA's general NPP overestimation. Representing LUE as a mixture of native and cultivated area indicated higher cultivated LUE and even lower native LUE. When I divided LUE into three components (native vegetation, C_3 cropland and C_4 cropland), I found similarly low native LUE, intermediate values for C_3 cropland LUE and very high C_4 cropland LUE. Although my LUE values are generally lower than estimates from physiologically based LUE studies, LUE trends between C_4 crops, C_3 crops and native grasses that are consistent with previous results.

My results provide future investigators with a suite of grassland and cropland LUE estimates for remote sensing NPP estimation methods. Although I identify LUE values with and without LUE modification from weather and crop type, the specific values applicable to a particular situation depend on the availability of weather and cultivation data for the areas and time periods of interest. Comparisons between my algorithms for representing LUE suggest that NPP predictions of remote sensing models are substantially improved by modifying LUE based on the total area cultivated, and are further improved by including information about the proportion of C_3 and C_4 crops within the cultivated area. I also quantified the importance of incorporating LUE limitations from adverse environmental conditions and determined that these modifications produced only minor improvement in NPP predictions. Nevertheless, LUE limitations from adverse weather and soil moisture conditions produced modest though consistent improvements in NPP predictions, especially for low productivity counties in models without cultivation information. Currently, many large-scale NPP estimation models that are based on remote sensing include weather limitation, but do not include information about cultivation practices. My results indicate that, as least in the grassland systems I studied, these methods don't necessarily require environmental limitations but they might achieve dramatically enhanced predictions by incorporating cultivation information.

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Table A.1:References for allocation ratios and harvest indices for agricultural crops monitored.

Crop	Allocation	Reference	Harvest Index	Reference
Barley	0.50	Bolinder et al. 1997	0.49	Bridger et al. 1995 Nedel et al. 1993 Jedel et al. 1994 Bulman and Smith 1993 Hay 1995
Beans	0.26	Turpin et al. 2002 Crawford et al. 1997 Kloseiko et al. 2001	0.55	Scully and Wallace 1990
Corn	0.18	Allmaras et al. 1975 Anderson 1988	0.52	Dywer et al. 1994 Howell et al. 1998 Banziger et al. 1999 Edmeades et al. 1999 Kinery et al. 1997 Raun et al 1989 Prihar et al.1990 Hay 1995
Cotton	0.14	McMichael and Quisenberry 1991 Mauney et al. 1992 Kimball and Mauney 1993	0.55	Pettigrew and Meredith 1997 Mauney et al. 1992 Gerik et al. 1996 Heuer and Nadler 1999
Hay	0.87	Bray 1963		
Oats	0.40	Bolinder et al. 1997	0.52	Peltonen-Sainio 1994 Lynch and Frey 1993
Potato	0.10	Opena and Porter 1999 Jefferies 1993	0.55	Knowles and Botar 1992
Rye	0.24	Sheng and Hunt 1991	0.35	Giunta et al. 1999
Sorghum	0.09	Piper and Kukakow 1994	0.52	Prihar et al. 1991 Howell 1990 Prihar and Stewart 1990
Soybeans	0.15	Allmaras et al. 1975 Marvel et al. 1992 Silvius et al. 1977	0.42	Weilenmann de Tau and Luquez 2000 Salado-Navarro et al. 1993 Morrison et al. 1999 Ferris et al. 1999 Bhardwaj and Bhagsari 1991 Bhardwaj et al. 1990 Rao and Bhagsari 1996
Sunflower	0.25	Szaniawski 1983	0.40	Bange et al. 1997, 1998
Wheat	0.19	Bolinder et al. 1997 Sheng and Hunt 1991	0.39	Prihar and Stewart 1990 Sharma 1992 Beuerlein et al. 1991 Mulholland et al. 1998 Wheeler et al. 1996 Ferris et al. 1998 Hay 1995 Howell et al. 1990

Table A.2: Models for calculating NPP from NDVI-derived APAR and LUE values with statistically determined LUE values and standard errors by vegetation type for the CASA model, the CASA model with statistically determined native LUE, and other models with and without environmental LUE limitation and NPP estimates by county for STATSGO/Crop data. Values reported are coefficients of determination for comparisons between predicted and ground NPP, mean, min and max county NPP as well as regional NPP.

Algorithm	LUE representation		LUE estimation results			R^2	NPP ($gCm^{-2}yr^{-1}$)			Total $PgCyr^{-1}$
	Environmental limitation	Cultivation information	vegetation type	Estimate	SE		Mean	Min	Max	
CASA	Yes	C_3 and C_4 crops	native	0.4345	NA*	0.506	425.1	210.2	645.6	0.705
			C_3 Crops	0.29	NA*					
			C_4 Crops	0.66	NA*					
CASA with native	Yes	Only counties with < 10% cultivation	native	0.246	0.002	0.8031	308.5	127.6	613.6	0.496
			C_3 Crops	0.29	NA*					
			C_4 Crops	0.66	NA*					
A	Yes	None	All vegetation	0.301	0.003	0.279	316.7	156.5	482.4	0.531
B	Yes	Total cultivation	native	0.219	0.004	0.671	318.6	113.4	516.3	0.512
			cultivated	0.498	0.007					
C	Yes	C_3 and C_4 crops	native	0.234	0.003	0.842	319.9	121.5	705.2	0.508
			C_3 Crops	0.332	0.009					
			C_4 Crops	0.770	0.013					
D	No	None	All vegetation	0.202	0.002	0.162	317.0	190.4	442.0	0.542
E	No	Total cultivation	native	0.139	0.003	0.603	317.5	132.9	493.6	0.516
			cultivated	0.351	0.006					
F	No	C_3 and C_4 crops	native	0.150	0.002	0.793	318.7	143.6	682.9	0.512
			C_3 Crops	0.231	0.007					
			C_4 Crops	0.548	0.009					
Ground Data							318.4	128.7	749.2	0.507

*These LUE values are based on previous studies rather than estimated in this study, so standard error values are not available.

Figure A.1: The U.S. Central Great Plains region with temperature and precipitation gradients.

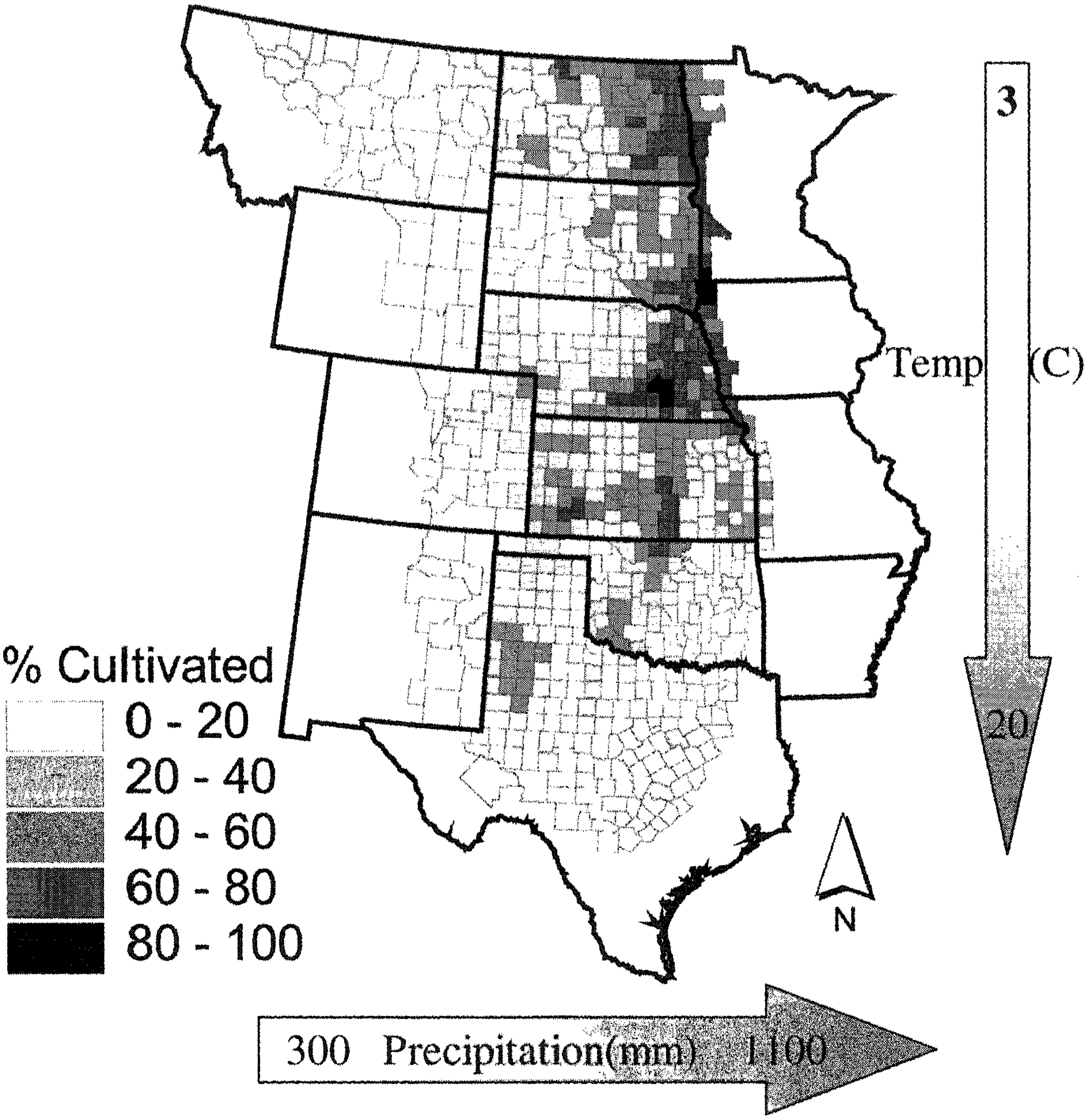

Figure A.2: Scatterplot of county NPP estimates in the U.S. Great Plains from (A) the CASA model vs. ground estimates and (B) the CASA model with native LUE determined by lease squares. Each symbol represents a county and numerical values indicate cultivation intensity (0 = 0-10% cultivated, 1 = 10-20% cultivated, etc.) Solid lines are the identity lines.

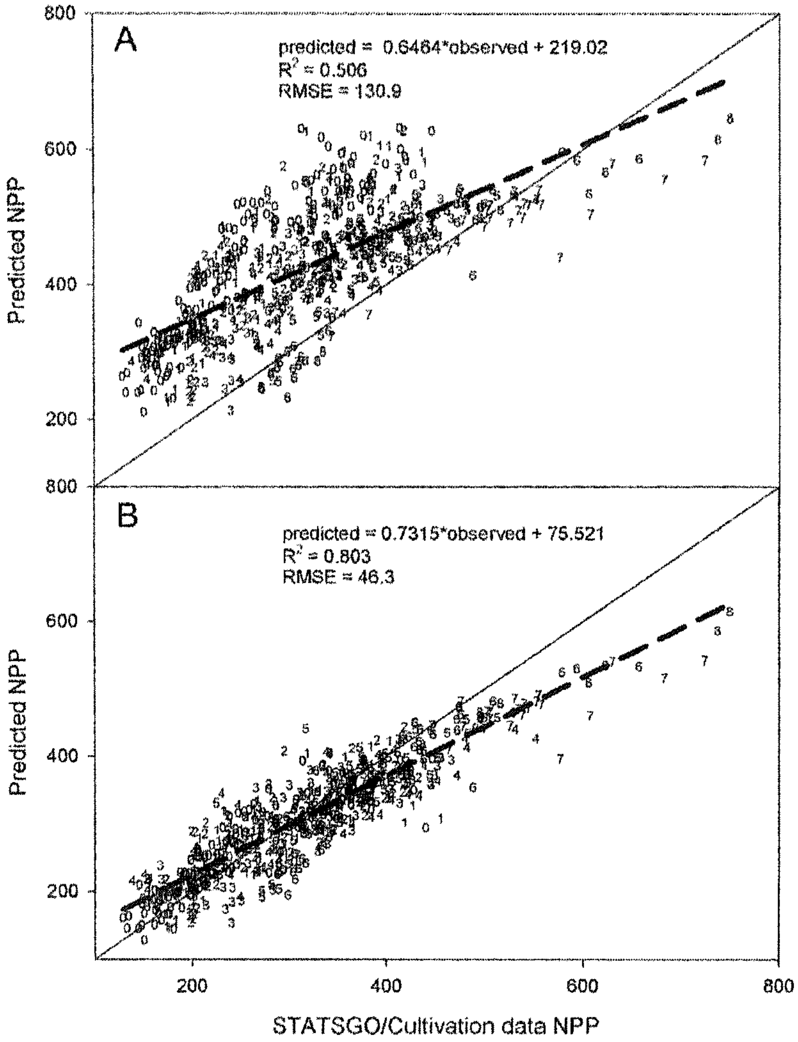

Figure A.3 Scatterplots of predicted vs. observed county NPP in the U.S Great Plains for remote sensing NPP methods containing LUE alrogithms with and without environmental limitation on LUE at 3 levels of vegetation type determination. A-F are prediction from algorithms A-F in Table A.2. Each symbol represents a county and numerical values indicate cultivation intensity (0 = 0-10% cultivated, 1 = 10-20% cultivated, etc.) Solid lines are the identity lines.