The Influence of Climate, Soils, Weather, and Land Use on Primary Production and Biomass Seasonality in the US Great Plains

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ABSTRACT

Identifying the conditions and mechanisms that control ecosystem processes, such as net primary production, is a central goal of ecosystem ecology. Ideas have ranged from single limiting-resource theories to colimitation by nutrients and climate, to simulation models with edaphic, climatic, and competitive controls. Although some investigators 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. We used a 9-year record of productivity, biomass seasonality, climate, weather, soil conditions, and cropping in the US Great Plains to quantify the controls over spatial and temporal patterns of net primary production and to estimate sensitivity to specific driving variables. We considered climate, soil conditions, and long-term average cropping as controls over spatial patterns, while weather and interannual cropping variations were used as controls over temporal variability. We found that variation in primary production is primarily spatial, whereas variation in seasonality is more evenly split between spatial and temporal components. Our statistical (multiple linear regression) models explained more of the variation in the amount of primary production than in its seasonality, and more of the spatial than the temporal patterns. Our results indicate that although climate is the most important variable for explaining spatial patterns, cropping explains a substantial amount of the residual variability. Soil texture and depth contributed very little to our 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 seasonality and temporal variation are not well understood. Our sensitivity analysis indicates that production is more sensitive to climate than to weather and that it is very sensitive to cropping intensity. In addition to identifying potential gaps in out knowledge, these results provide insight into the probable long- and short-term ecosystem response to changes in climate, weather, and cropping.

Key words: primary production; carbon; land use; agriculture; climate; weather; soil; seasonality; cropping; grassland; US Great Plains.

INTRODUCTION

Predicting ecosystem response to global environmental change has become an important objective for ecosystem scientists, but robust predictions require an understanding of how environmental and land-use conditions influence ecosystem processes. Most efforts to improve our understanding of the controls over ecosystem processes have focused on relating them to climatic (for example, Rosenzweig 1968; Lieth 1975; Burke and others 1997; Austin and Vitousek 1998), edaphic (Jenny 1941; Noy-Meir 1973), and weather (Burke and others. 1991; Tian and others 1998; Potter and others 1999) conditions. However, recent studies have attempted to examine how land-use practices—notably, agricultural cropping—influence ecosystem processes (Vitousek 1992; Houghton and others 1999; Guerschman and others 2003). Although the consequences of agricultural land use for ecosystem processes have been examined at individual sites, few studies have attempted to quantify the magnitude and nature of land-use effects at large spatial and temporal scales (for example, Burke 2000). As human population grows, the need for food will continue to increase, necessitating continued cropping in current agricultural areas and the conversion of additional areas (Cassman 1999, Tilman and others 2002). Insight into the relationships among cropping practices, environmental conditions, and spatiotemporal patterns of changes in ecosystem processes is essential to understanding the consequences of these practices.

In this study, we quantified how environmental conditions and cropping practices influence net primary production (NPP) and seasonality of aboveground biomass in the US Great Plains. Net primary production is the amount of carbon fixed by plants minus plant respiration and is, at least above ground, one of the best-understood ecosystem processes. Whereas NPP is one 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.

The US Great Plains is well suited for examining the relationship among environmental controls, land use and ecosystem processes because this area has high cropping intensity and the environmental influences on the ecosystem processes of its native vegetation are well established. Precipitation is positively related to grassland production across space and through time, although the slope of the spatial relationship is greater, implying that at a particular location ecosystems may not respond immediately to altered conditions (Lauenroth and Sala 1992). The effect of temperature on primary production in grasslands depends on the interaction with precipitation and subsequent influence on water availability (Lauenroth 1979). In water-limited areas, warmer temperatures can lower water availability and decrease the production of native grasslands (for example, Epstein and others 1997; Gill and others 2002) and agricultural areas (Lobell and Asner 2003). However, in wetter areas, warmer temperatures have less influence on water availability and can increase production by promoting longer growing seasons and faster photosynthetic rates (for example, Lauenroth and others 1999). Environmental conditions also influence biomass seasonality by dictating photoperiod, temperature, and water availability (Rathcke and Lacey 1985; Bonen 2002; Jobbagy and others 2002).

Soil properties can also influence production in grasslands, although the nature of their influence is not consistent. Noy-Meir (1973) proposed an ''inverse texture effect'', which suggests that coarse-textured soils enable greater water infiltration, and have less evaporative water loss, thereby supporting higher production in dry areas than fine-textured soils. By contrast, wetter areas in which water loss occurs primarily via drainage support higher production in fine-textured soils with high water-holding capacity (Sala and others 1988; Epstein and others 1997).

The effect of cropping, in contrast to native vegetation, on NPP, has received relatively limited attention and has generally been investigated only at small scales. Crops have typically been selected to maximize aboveground yield while generating only enough roots to obtain the necessary water and nutrient resources. Consequently, site-level studies have shown that cropping generally increases aboveground production while having only modest effects on belowground production (Buyanovsky and others 1987), and recent analyses have quantified this impact at regional scales (Guerschman and others 2003, Bradford and others 2005b). The impact of cropping on aboveground biomass seasonality is readily apparent at small scales, but it varies among crops; thus, 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. Some crops are planted only after soil temperatures rise to a particular level and thus initiate growth well after native plants, whereas other crops are harvested before native plants cease growth (Martin and others 1976).

The overall goal of this study was to create statistical models of the relative importance of cropping on NPP and its seasonality relative to known controls such as climate (long-term conditions), weather (annual variation), and soil conditions. We used variance decomposition techniques to examine how environmental conditions and cropping practices relate to the observed variability in NPP and its seasonality in the grassland ecosystems of the Great Plains. Specifically, our objectives were to (a) partition the variance of production and biomass seasonality into spatial and temporal components and create statistical models for these variance components; (b) use the models to quantify the relative importance of cropping, climate, soil conditions, and weather to our understanding of the patterns in these ecosystem processes; and (c) combine the best spatial and temporal models to create an overall model that could be used to predict the sensitivity of production and biomass seasonality to changes in climate, weather, soil conditions, and cropping intensity.

METHODS

Study site

We conducted this study in the US Great Plains, which includes 23% of the contiguous United States and extends from the Canadian border into south Texas and from the Rocky Mountains to approximately the 95th parallel (Figure 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 (MAP) varies from under 400 mm in the west to nearly 1,000 mm in the east. Mean annual temperature (MAT) increases from 3°C 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.

We included counties that historically contained at least 70% of the following vegetation types: northern mixed-grass prairie, shortgrass steppe, tallgrass prairie, tallgrass savanna, southern mixed-grass prairie, desert savanna, and floodplain forests. Using these restrictions we identified 630 counties within the Great Plains that were suitable for this study (Figure 1). We collected data for the years 1991–98 for these counties.

Net Primary Production and Biomass Seasonality

We calculated annual production and its seasonality for each county for the years 1990 through 1998. To estimate production, we used a modified version of the Carnegie Ames Stanford approach (CASA). CASA relies on methods developed by Monteith (1972, 1977) that enable estimates of plant production from remotely sensed observations (8-km resolution AVHRR data) of absorbed photosynthetically active radiation (APAR) and estimates of light-use efficiency (LUE). We used the APAR estimates from CASA described in Hicke and others (2002) and the LUE estimates from Bradford and others (2005a) to generate county-level NPP data for the years 1990–98.

To partition the NPP estimates into aboveground and belowground production, we calculated an allocation ratio for each county. This ratio is an area-weighted average of allocation to cropped areas and allocation to native grassland. For cropped areas, we used published allocation ratios for each crop (see Appendix 1 at http://www.springerlink.com). For allocation ratios in uncropped areas, we used relationships identified by Gill and others (2002), which suggest that grassland belowground NPP can be estimated from maximum yearly instantaneous belowground biomass, belowground live biomass fraction, and MAT, as calculated by Bradford and others (2005b).

We chose two indicators of seasonality: the length of the growing season and the date of maximum Normalized Difference Vegetation Index (NDVI). Date of maximum NDVI is an indicator of the time when photosynthetic activity is highest during the growing season (reported as the day of the year) and provides insight into the timing of events within the active period. Growing-season length was determined by estimating the beginning and end of the growing season and calculating the number of days between these dates. Reed and others (1994) developed a method for determining these dates that is based on identifying a substantial change in the NDVI patterns through time. The start of the season is defined as the date in the spring when the NDVI begins to increase; the end of the growing season is defined as the date when the NDVI stops decreasing.

Data Sources

Our climate data were derived from a database of 30-year monthly weather records from over 200 weather stations archived by CLIMATEDATA
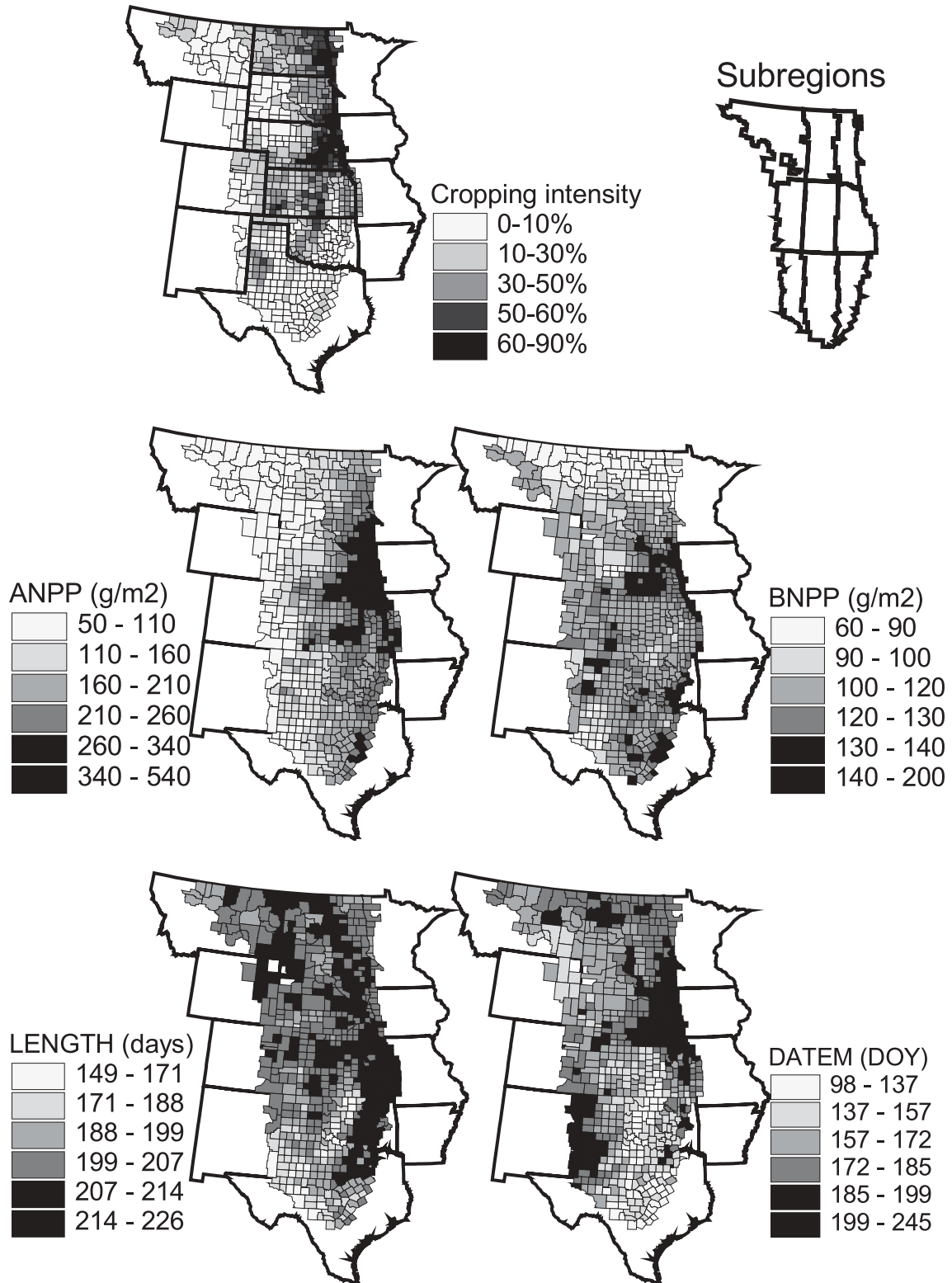
Figure 1. The US Great Plains region, with general patterns of mean annual precipitation and mean annual temperature, cropping intensity (average percent of each county under cultivation), subregion boundaries (indicated on small map), spatial patterns (averaged over all years) of the four response variables. ANPP, aboveground net primary production; BNPP, belowground net primary production; LENGTH, length of growing season; DATEM date of maximum Normalized Difference Vegetation Index (NDVI).

(1988). We used soil texture (percent clay and sand) and depth information from the USDA STATSGO database (USDA 1989; also see http://www.ftw.nrcs.usda.gov/stat_data.html). Monthly weather data for over 200 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=&GEO-Regionabbv=&Forceoutside for the years 1990–98. Climate and weather information were entered into a GIS and interpolated into a 1-km GRID using the trend surface method in ArcInfo (ESRI 1996) from points (weather stations) into a surface covering the study area. We overlaid the climate and weather maps with soil information and extracted county means for the 630 counties in this study. We obtained cultivation data from the National Agricultural Statistics Service (NASS 1988; also see http://www.nass.usda.gov:81/ipedb/), which maintains records of crop area and yield for all US counties.

Partitioning Variability into Space and Time

Our objective of variance partitioning was to characterize the variation in aboveground NPP (ANPP), belowground NPP (BNPP), growing-season length, and date of maximum NDVI. Decomposing the observed variation into spatial and temporal components and examining the controls over those variance components is one approach (Box and others 1978). Total variation (σ^2_{total} observed in ecosystem processes over a region can be partitioned into spatial variation ($\sigma^2_{\text{spatial}}$, or differences from one location to another averaged across all years) and temporal variation ($\sigma^2_{\text{temporal}}$, or variation at a single location through time):

$$\sigma^2_{\text{total}} = \sigma^2_{\text{spatial}} + \sigma^2_{\text{temporal}} \qquad (1)$$

The spatial and temporal components can be explained by examining the forces that dictate those sources of variability. Spatial variation is modeled by including sources of variation that change only across space and not through time:

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

where σ^2_{model} is the variation explained by any particular model; $\sigma^2_{\text{spatial residual}}$ is the variation not explained by the spatial model; and $\sigma^2_{\text{climate}}$, σ^2_{soil}, and $\sigma^2_{\text{cropmean}}$ are the variation explained by variables representing climate conditions, soil

properties, and mean cropping intensity, respectively. Similarly, temporal variation can be modeled by including sources of variation that fluctuate only through time:

$$\sigma^2_{\text{temporal}} = \sigma^2_{\text{model}} + \sigma^2_{\text{residual}} = \sigma^2_{\text{weather}} + \sigma^2_{\text{cropdev}}$$
$$+ \sigma^2_{\text{temporal residual}}$$
$$(3)$$

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.

To generate overall predictions from spatial and temporal models, it is necessary to combine them into a single model that explains the total observed variability. Total variation can be expressed as:

$$\sigma^2_{\text{total}} = \sigma^2_{\text{model}} + \sigma^2_{\text{residual}} = \sigma^2_{\text{climate}} + \sigma^2_{\text{soil}} + \sigma^2_{\text{cropmean}}$$
$$+ \sigma^2_{\text{weather}} + \sigma^2_{\text{cropdev}} + \sigma^2_{\text{total residual}}$$
$$(4)$$

Statistical Modeling of Spatial, Temporal, and Overall Variation

To characterize the influence of driving variables on variability in production and biomass seasonality, we first partitioned the variance into spatial and temporal components, and then generated independent predictive models for each type of variation. We calculated mean annual production and biomass seasonality values for each county and considered the variability in the set of individual deviations from the overall mean to represent spatial variability. To represent temporal variability, we calculated the annual deviation from the mean production or biomass seasonality for each county. Because the magnitude of variation in both space and time depends on the spatial and temporal scales chosen, we used a 9-year record (1990–98) that includes substantial inter-annual variation.

To determine the effect of climate, soil, weather, and cultivation variables on production and biomass seasonality, a candidate set of a priori multiple linear regression models was developed for each combination of variation type (for example, spatial or temporal) and response variable (for example, ANPP, BNPP, growing-season length, and date of maximum NDVI). The spatial models included various combinations of parameters for climate (MAT and MAP), soil texture (percent sand and clay and depth of the A horizon), and mean crop-

Table 1. 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 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

ped area for the 12 major crops in the region (Tables 1 and 2). Temporal models were generated by selecting the best combination of weather parameters (calculated as deviation in temperature and precipitation from the climate values) and then including deviations in cropped area for specific crops (deviation from the 9-year mean). The results presented here used mean annual values for both climate and weather variables. Although we attempted analyses with seasonal and monthly representations of temperature and precipitation (results not shown), the mean annual values proved to be more useful for explaining both spatial and temporal patterns in primary productivity and biomass seasonality. We used actual measures of precipitation and temperature rather than an index of drought severity or water availability for the following reasons: First, in the Great Plains, where water is limiting and precipitation occurs primarily in the summer, MAP is strongly related to NPP (Lauenroth 1979; Sala and others 1988; Burke and others 1997; Lauenroth and others 2000), and MAT and soil properties explain much of the remaining variation (Epstein and others 1997; Gill and others 2002). Second, because the objective of this work was to understand the explanatory power of land use in the context of past work that related ecosystem processes to precipitation and temperature variables, we needed to use the same variables as previous studies.

To compare these statistical models, we used 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. Smaller values of AIC_c (AIC corrected for bias due to small sample size) indicate that the statistical model is closer to the truth (never known); thus, 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; differences of 1–2 AIC_c units suggest substantial support, 3–7 AIC_c units indicate less support, and more than 10 units imply no support in the data (Burnham and Anderson 2001).

We used a hierarchical approach to model selection in which we 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. Finally, we 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. Proc REG in SAS/STAT software (SAS 2001, ver.8002; Cary, NC, USA) was used to determine AIC_c for each model (See Appendices 2 and 3 at http://www.springerlink.com).

Table 2. Candidate Models for Spatial and Temporal Variation in Country-level Productivity and Aboveground Biomass Seasonality for the US Great Plains

Domain	Category	Model	Variables
Spatial	Climate	MAP	MAP
		Log (MAP)	LMAP
		MAT	MAT
		Climate	LMAP, MAT
		Climate and interaction	LMAP, MAT, MAPMAT
	Climate with soil properties	Climate & clay	Best climate parameters, clay
		Climate & sand	Best climate parameters, sand
		Climate & Ahor	Best climate parameters, Ahor
		Climate & texture	Best climate parameters, clay, sand
		Climate & clay and depth	Best climate parameters, clay, Ahor
		Climate & sand and depth	Best climate parameters, sand, Ahor
		Climate & texture and depth	Best climate parameters, clay, sand, Ahor
	Climate and soil with cultivation practices	Climate, soil & two dominant crops	Best climate and soil parameters, corn, wheat
		Climate, soil & major crops	Best climate and soil parameters, corn, wheat, soybeans, hay, sorghum
		Climate, soil & cultivation	Best climate and soil parameters, cultivation
		Climate, soil & C_3/C_4 crops	Best climate and soil parameters, C_3 crops, C_4 crops
Temporal	Weather	Precipitation	Pptdev
		Temperature	Tempdev
		Weather	Pptdev, Tempdev
	Weather with cultivation	Weather & two dominant crops	Best weather parameters, corndev, wheatdev
		Weather & major crops	Best weather parameters, corndev, wheatdev, soybeansdev, sorghumdev, haydev
		Weather & Cultivation deviation	Best weather parameters, cultdev
		Weather & deviation of C_3 crops and C_4 crops	Best weather parameters, C_3 cropsdev, C_4 cropsdev

Impact of Cropping

We divided the counties into nine classes based on cultivation intensity. Counties in class 0 are between 0% and 10% cultivated, counties in class 1 are between 10% and 20% cultivated, and so on. Because no counties are more than 90% cropped, only nine classes exist (0 through 8). Dividing the counties into nine cultivation classes creates smaller subregions, each with unique cultivation intensity. For each class, we quantified spatial and temporal variation in response variables (productivity and biomass seasonality). As an indicator of spatial variation, we 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, we calculated a coefficient of variation for each county based on the nine 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. We used linear regression to compare these spatial and temporal coefficients of variation against cropping intensity.

Sensitivity Analysis

To generate an overall predictive model, we 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 (that is, individual crop proportions versus C_3 and C_4 crop proportions), we used the parameters for the spatial model because they consistently explained a higher proportion of the overall variation.

We used this model to provide predictions of production 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,

Table 3. Variance Partitioning Results for Productivity and Phenology Variables

Component	Aboveground Productivity	Belowground Productivity	Length of Growing Season	Date of Maximun NDVI
	Mean County Value ($n = 5670$)			
	203 g/m^2	117g/m^2	203 days	Day 171
	Average Deviation from Mean			
Spatial	69.3 g/m^2	14.3 g/m^2	8.9 days	18.8 days
Temporal	17.5 g/m^2	9.8 g/m^2	15.6 days	13.4 days
	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

NDVI, Nomalized Difference Vegitation Index.
Mean values are shown for each variables along with the average deviation in the spatial domain (mean deviation between long-term average county values) and the temporal domain (mean deviation between county values for individual years and long-term county averages). Also shown is the amount of overall variation occuring in the spatial and temporal domains, the proportion of variation that can be attributed to specific driving variables and the amount of overall variation that is explained by the best statistical regression models.

we estimated how each process responds to changes in those variables. We quantified the predicted response of production to changes in climate, soil, weather, and cultivation. In addition, because cropping intensity and cropping practices vary across the region, we divided the region into nine subregions (Figure 1) and examined the effect of changes in cropping on production and biomass seasonality in each subregion.

RESULTS

Spatial versus Temporal Variation

An overwhelming majority of the variation in both ANPP and BNPP occurred in the spatial domain, with only a fraction in the temporal domain (Table 3). Similar to productivity, growing-season length varied more over space than through time, but total variation was much more evenly split for date of maximum NDVI. Season length was the only variable we examined that varied more through time than space, with 80% of total varia-

tion occurring between times rather than between locations.

Effect of Cultivation on Process Variance

Cultivation generally decreased the spatial and temporal variability of primary production and biomass seasonality, suggesting that cultivated areas have more consistent ecosystem processes from location to location as well as from year to year (Figure 2). The one exception to the general decrease in variability with cultivation was the relationship between spatial BNPP variability and cultivation, which our data suggested are positively related.

Spatial Models

Spatial variability in aboveground production explained nearly all of the total variation in ANPP (Table 3). As a group, climate parameters (MAT and MAP) were the most important set of independent variables, accounting for over half of overall variability in ANPP, whereas cropping
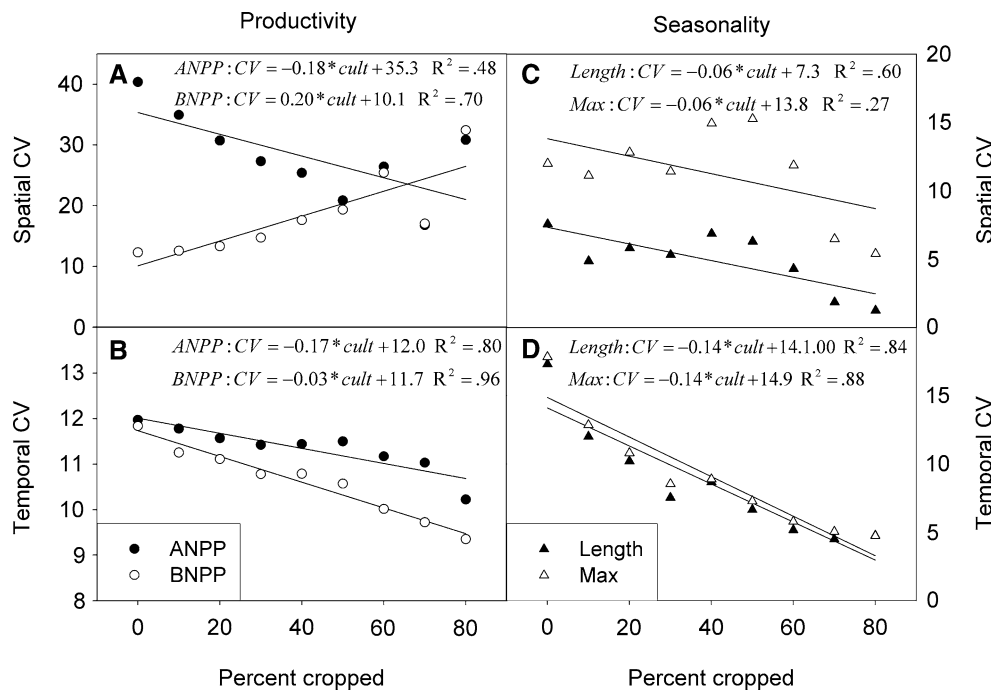
Figure 2. Relationship between cropping intensity and spatial (**A**) and temporal (**B**) coefficient of variability (CV) in above- and belowground production and spatial (**C**) and temporal (**D**) CV in the length of the growing season and date of maximum Normalized Difference Vegetation Index (NDVI). ANPP, aboveground net primary production; BNPP, belowground net primary production; LENGTH, length of growing season; DATEM, date of maximum NDVI.

intensity accounted for an additional 31% and soil properties explained only a tiny fraction. In the overall best model for spatial ANPP variation, our results indicated positive relationships between both MAP and ANPP and MAT and ANPP. Both sand and clay were negatively related to ANPP when cropping practices were not included (climate and texture model), but these relationships became positive after accounting for cultivation. In addition to the effect of climate and soil properties, our results also indicated positive correlations between spatial cropping practices and ANPP patterns.

Spatial variation in BNPP explained approximately two-thirds of the total variation, with cropping practices and climatic conditions accounting for 30% and 29%, respectively, whereas soil properties contributed 5%. We found positive relationships between BNPP and both MAP and MAT, whereas all three soil variables were negatively related to BNPP, implying that belowground production was greater in fine-textured soils and soils with shallow A horizons than in coarse soils or soils with deep A horizons. The best overall model for BNPP included countywide proportions of C_3 and C_4 crops, rather than proportions of individual crops. Belowground NPP was negatively related to the abundance of C_3 crops but positively related to C_4 crops—a pattern consistent with the fact that C_4 crops, (primarily corn and sorghum), are extremely productive, whereas C_3 crops, (primarily wheat and soybeans), are less productive.

Models for spatial variability did not perform as well for the seasonality variables as they did for the production variables. The best model for growing-season length explained slightly over half of the overall variation, of which 40% was derived from climate parameters. Soil properties and cultivation practices accounted for only a very small fraction of the variation in season length. Season length was positively related to MAP and negatively related to MAT, results that are both consistent with growing-season regulation by limited late-season water availability. Sand and clay were both negatively related to season length. Four of the five crops were negatively related to season length, which is to be expected because crops typically initiate growth later than native vegetation and are harvested before native vegetation stops growing.

For 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. When cultivation is included in the model, MAP is negatively related to date of maximum NDVI, but it is positively related in the absence of cultivation, whereas MAT is negatively related to date of maximum NDVI. Clay displayed a negative relationship with date of maximum NDVI, whereas the relationship with sand was small. Of the five crops examined, wheat and hay were both negatively related to date of maximum NDVI.
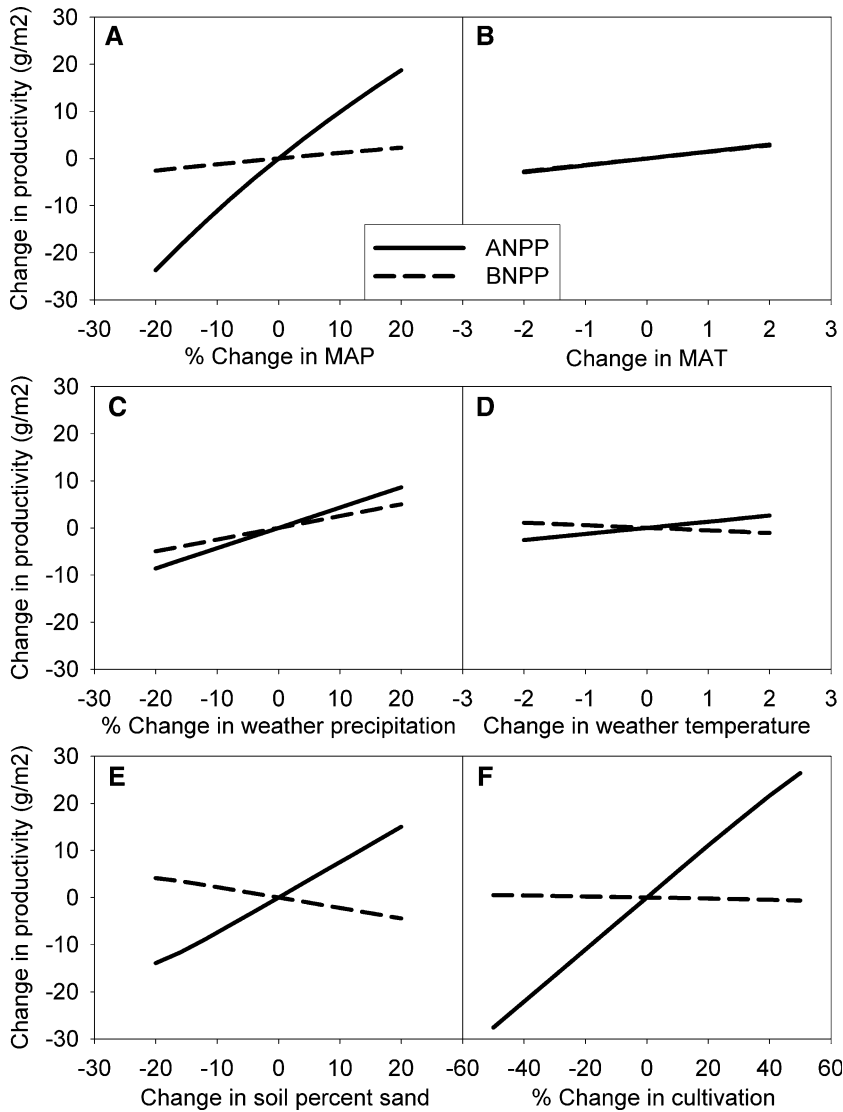
Figure 3. Sensitivity of above- and belowground production to changes in mean annual precipitation (MAP) (**A**), mean annual temperature (MAT) (**B**), annual precipitation (**C**), annual temperature (**D**), soil percent sand and clay (**E**), and percent of area under cultivation (**F**) in the US Great Plains.

Temporal Models

Our best model for temporal variability in ANPP explained less than half of the variation; cropping accounted for most of the explained variation, and weather explained only 11%. Precipitation deviation was positively related to temporal variations in ANPP. Temperature deviations were also positively related to ANPP, but the slope of the relationship was lower than the slope of the precipitation relationship. Temporal patterns of cropping intensity of all five crops were positively related to ANPP.

The best model for temporal variability in BNPP explained less than a third of the total variation, most of which was attributed to weather, with only a small fraction due to cropping. Variation in BNPP was positively related to precipitation deviation and negatively related to temperature deviation. The relationship between cropping and BNPP depended on the particular crop. Cropping intensity of wheat, corn, and sorghum was positively related to BNPP variations, whereas cropping intensity of hay and soybean was negatively related. Our best temporal models for both seasonality variables explained only a small fraction of the total variation. The best model for growing-season length accounted for only 8% of the variation, most of which is due to weather. Similarly, the best model for date of maximum NDVI explained 7% of the variation.

Sensitivity Analysis

Because our models were not particularly successful for the seasonality variables, we conducted sensitivity analyses only for the response of
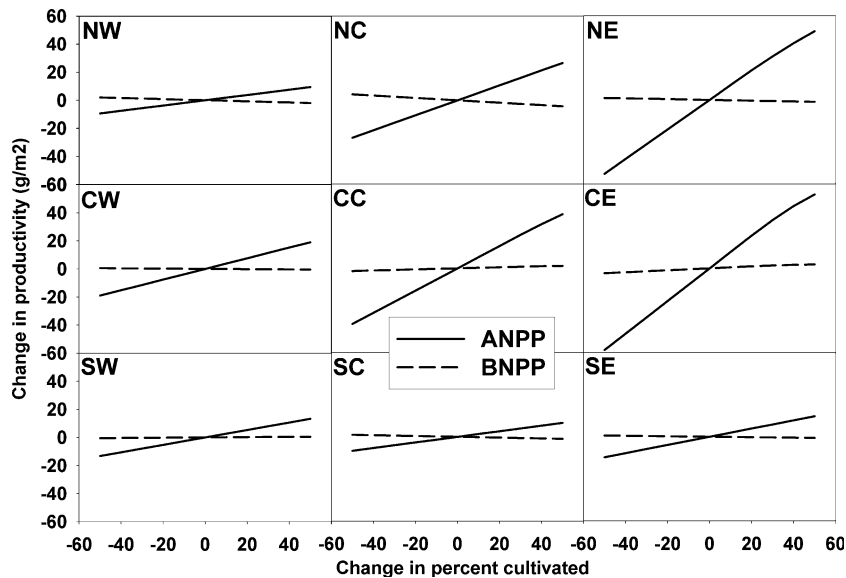
Figure 4. Sensitivity of above- and belowground production to changes in cropping intensity for nine subregions within the US Great Plains. ANPP, aboveground net primary production; BNPP, belowground net primary production.

production to changes in driving variables. We generated regional predictions of ANPP and BNPP for changes in MAP, MAT, temperature, precipitation, soil percent sand, and cropping intensity.

Our analysis suggested that a 20% decrease in MAP would decrease ANPP and BNPP by 24 and 2.5 g m^{-2}, respectively (Figure 3). Because our MAP variable is log-transformed, it has nonlinear effects on dependent variables. Consequently, our estimates of increases in ANPP and BNPP were only 19 and 2.3 g m^{-2}, respectively, or slightly less than the decreases. By contrast, our models implied a much weaker response of production to 20% changes in annual precipitation, with ANPP changing only 8.6 g m^{-2} and BNPP changing only 5 g m^{-2}.

Changes in MAT of ±2°C caused modest increases for ANPP and BNPP of 2.9 and 2.8 g m^{-2}, respectively. Changing annual temperature by ±2°C resulted in a similar positive ANPP change of 2.6 g m^{-2}, but produced a negative response in BNPP of 1.1 g m^{-2}. Our analysis of the impact of altered soil texture predicted that ANPP was positively related to soil percent sand and clay, and 20% decreases and increases in sand and clay caused a decrease of 14 g m^{-2} and an increase of 15 g m^{-2} respectively. On the other hand, BNPP showed a negative relationship with sand and clay, increasing by 4.1 g m^{-2} when sand and clay were lowered by 20% and decreasing by 4.5 g m^{-2} when sand and clay were increased by 20%.

Modifications to cropping intensity had a large positive impact on ANPP, with a predicted ANPP decrease of 26 g m^{-2} and an increase of 27 g m^{-2} for 50% changes in cropping. We expect BNPP to have a very slight negative relationship with cropping

intensity, with increases of 0.5 g m^{-2} or decreases of 0.7 g m^{-2} when cropping decreases or increases by 50%, respectively.

To further characterize the influence of cropping on production, we conducted sensitivity analyses for smaller areas within the US Great Plains. We examined how changes of 50% in cropping intensity would impact ANPP and BNPP in nine subregions (Figure 1). We 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 were positively related to ANPP, but the magnitude of the effect of changes in cropping depended on the type of crops in each subregion. Our results suggested that changes in cropping would have the greatest effects on ANPP in the central and northeastern four subregions (Figure 4) and relatively minor effects in the remaining five subregions. Belowground NPP was negatively related to C$_3$ crops but positively related to C$_4$ crops, meaning that both the direction and magnitude of BNPP changes depends on crop type. Our analysis predicted minor (effect sizes range from 1 to 4 g m^{-2}) decreases in BNPP for all subregions except CC, CE, and SW subregions (see Figure 4). These areas have enough C$_4$ crops that the positive effect of C$_4$ crops on BNPP outweighed the negative effect exerted by C$_3$ crops.

DISCUSSION

Spatial versus Temporal Variability

By partitioning the observed process variation into spatial and temporal components, we found that

variation in production 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 the temporal and spatial domains. The perceived importance of spatial versus temporal controls over ecosystem processes is always a function of the extent (both spatial and temporal) of the data set examined. Because this study examined a relatively large area over only 9 years, it may be biased toward finding spatial controls to be more important. Nevertheless, our results are consistent with previous studies of regional- and site-level production trends, which have shown very tight relationships between aboveground production and long-term MAP in grasslands (Lauenroth 1979; Sala and others 1988) but a weaker link, observed as a lag in recovery from drought, between weather variations and production (Lauenroth and Sala 1992). The strong dependence of primary production on long-term (spatial) controls may be a consequence of the highly variable weather conditions in the US Great Plains (Lauenroth and Burke 1995) and the life history traits of the dominant plants, which are generally perennial and heavily invested in belowground structures. At any particular location, the vegetation is a combination of species that are adapted to survive under the long-term climatic conditions extant at that site. Interannual weather fluctuations alter current conditions, but species assemblages remain relatively constant and the vegetation is unable to respond optimally to the altered conditions. By contrast, spatial fluctuations in ecosystem processes represent the ecosystem's response to long-term climatic conditions, in areas where the vegetation is adapted to maximize production under those conditions. When Paruelo and others (1999) compared the spatial and temporal relationships between precipitation and ANPP across a precipitation gradient in the Great Plains, they found that ecosystems in the center of the Great Plains precipitation gradient are more responsive to temporal variation in precipitation than ecosystems on either end of the gradient. This suggests that responsiveness through time is at least partially a function of plant community composition.

The relatively even split between spatial and temporal variation shown by date of maximum NDVI implies that it is influenced by both short- and long-term controls. The large interannual variability of growing-season 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). Because the end of the growing season is often controlled by water availability, it is not surprising that growing-season length has greater temporal variability than the date of maximum NDVI.

Effect of Cropping on Process Variance

We found that, with the exception of spatial variability in BNPP, the magnitude of spatial and temporal variability in ecosystem processes are generally lower in areas with heavy cropping intensity. Similar findings for areas of high-intensity cropping have also been reported in studies of temporal patterns (Buyanovsky and others 1987; Lauenroth and others 2000). These results are not surprising because crops have been selected for consistent yield rather than their ability to take advantage of especially favorable years or locations, and a relatively small number of cultivars are used for each crop throughout the entire region (Martin and others 1976). We anticipate that the negative relationship between BNPP spatial variability and cropping is the consequence of cropping generally having a negative impact on BNPP (Bradford and others 2005b) and being most prevalent in highly productive areas (Figure 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 Aboveground Net Primary Production Patterns

Our 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 on ANPP, followed closely by cropping practices. In contrast to the findings of other recent analyses (Veron and others 2002), soil properties explained only a small fraction of production variation and thus contributed very little to our statistical models. The effect that MAP exerts on ANPP has been reported in many

previous studies (for example, Lauenroth 1979; Sala and others 1988; Lauenroth and others 2000), but the positive relationship that we observed between MAT and ANPP is contradictory to some previous studies. For example, Epstein and others (1996, 1997) found a negative relationship between MAT and ANPP in native grasslands, and Veron and others (2002) reported a similar result for winter wheat.

Because silty soils are often 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 1), leaving soil texture to account for ANPP variations in more xeric areas. Contrary to our observation of higher productivity on fine-textured soils, the inverse texture effect (Noy-Meir 1973) predicts that, in semi-arid ecosystems, coarse-textured soils will enable greater water penetration, minimize evaporation losses, and therefore be more productive than fine-textured soils. In an analysis of a smaller area within the US Great Plains, Paruelo and others (2001) found that land use was the most important predictor of ANPP. Our finding that climate is slightly more important is very likely a consequence of the greater spatial extent, and therefore the greater overall climatic variation, in our data set. The weak relationship between soil properties and ANPP is at least partly a consequence of the fact that we examined a relatively dry region, where water limitation is of central importance. Soil properties are likely to be more important in wetter areas that are less limited by water. The positive relationship between cropping intensity of the five major crops and ANPP is consistent with our expectation that cropping would increase ANPP by altering carbon allocation ratios to favor aboveground structures (Bradford and others 2005b).

Our temporal ANPP model indicated that both precipitation and temperature had positive effects. Although temporal trends in precipitation are known to have a positive influence on ANPP, (Lauenroth and Sala 1992; Briggs and Knapp 1995), the positive effect found for temperature is surprising because higher temperatures should decrease water availability and thus have a negative impact on productivity. We observed that cropping intensity for all five crops was positively related to ANPP, possibly as a result of increased carbon allocation to aboveground structures and/or in-creased resource availability as a consequence of irrigation and fertilization.

Controls over Belowground Net Primary Production Patterns

Our spatial model for BNPP explained nearly two thirds of the observed variation. We found that BNPP had a positive relationship with MAP, which is consistent with general observations of total production and water availability in this region (Lauenroth and others 1999). Lower BNPP in coarse-textured soils is difficult to understand, but it may be a consequence of the inverse texture effect, which causes coarse soils in xeric areas to have greater water availability and subsequently less belowground inputs 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 via water and wind erosion and decreasing BNPP via altered carbon allocation (Bradford and others 2005b).

When we modeled temporal variability as a function of deviations in weather and cropping, we found that weather conditions accounted for the largest proportion of temporal BNPP patterns. Our model for temporal variation in BNPP indicated that there was a positive relationship between BNPP and precipitation but a negative relationship between BNPP and temperature. These results are likely a consequence of the fact that higher precipitation increases water availability whereas higher temperatures decrease water availability.

Controls over Biomass Seasonality

Although our spatial models for biomass seasonality were relatively successful, the temporal models of both seasonality variables explained only a small fraction of the observed variation. Our calculations 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 change is somewhat elastic and will be controlled by either temperature or precipitation, depending on which of these conditions first becomes limiting. Consistent with the expectations implied by these controls, we observed a positive relationship between MAP and growing-season length and a negative relationship between MAT and growing-season length. The positive relationship for MAP is likely a consequence of the fact that a higher MAP will increase water availability late in

the season, causing longer growing seasons (Jobbagy and others 2002). Although warmer spring temperatures are likely to promote earlier vegetative growth, thereby potentially lengthening the growing season, high temperatures late in the season will decrease water availability, and this, strong negative effect may outweigh that positive effect, thereby causing a shorter growing season (Jobbagy and others 2002). We found that the abundance of most of the crops was negatively related to growing-season length, which is to be expected because crops typically initiate growth later than native vegetation and, relative to native plants, are characterized by a consistent and uniform development that enables predictable harvest schedules.

The influence of MAP on date of maximum NDVI depended on whether the effects of cultivation were included in the model. A positive relationship between MAP and NDVI in the absence of cultivation has been reported previously (Jobbagy and others 2002) and can be attributed to the fact that increased water availability causes increased growth later in the season. The negative relationship when cultivation is accounted for was unexpected, but may be a result of MAP having a greater influence on native vegetation than on crops. Because production is more tightly linked to MAP in native vegetation than in cultivated areas (Lauenroth and others 2000; Bradford and others 2005b) and native vegetation tends to develop earlier than most crops, areas with higher MAP have proportionally more early-season than late-season growth.

We found that MAT is negatively related to date of maximum NDVI, probably because warmer temperatures facilitate an earlier start of the growing season (Jobbagy and others 2002) as well as a more rapid decrease in available water. In agreement with other recent work (Guerschman and others 2003), our results indicate that the impact of cultivation on biomass seasonality depends on the specific crop. Wheat is cultivated as a winter crop in much of the region, has very early spring development (Martin and others 1976), and was correlated with an early date of maximum NDVI. Hay consists of perennial plants that, unlike many other crops, do not grow from seed and thus has relatively rapid initial growth that can lead to an early date of maximum NDVI. By contrast, corn, soybeans, and sorghum have all later date of maximum NDVI, probably because these crops require warmer soil conditions and are therefore planted and harvested relatively late in the season.

In general, our models performed better for spatial patterns than temporal patterns, and better for production than biomass seasonality. This result implies that the controls over temporal variation and seasonality are not as well understood as those that influence spatial patterns and production and therefore 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 we represented them in this study. We might have had better success in the temporal domain and with biomass seasonality if we had divided both climate and weather into seasonal components (for example, early-season temperature, mid- and late-summer precipitation) and/or represented soil properties as indices with known relevance to water dynamics (that is, soil water-holding capacity) rather than simple measures of soil texture. In addition, our independent variables for temporal patterns included only weather and cropping conditions for the current year, and it is possible that conditions in previous years influence both production and biomass seasonality.

Sensitivity Analyses

We used the best overall models for production to estimate how changes in environmental conditions could impact ANPP and BNPP. These sensitivity analyses suggest that ANPP is more 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 is not surprising, our results do indicate that ANPP has substantial sensitivity to cropping intensity. Changes in cropping intensity of 50% produce ANPP changes greater than those predicted for 20% changes in MAP, implying that production in the US Great Plains is highly sensitive to changes in cropping; thus, long-term predictions of carbon cycling in this region should take the impact of cropping into consideration.

Our models suggest that production responds in a markedly different way to changes in climate than it does to changes in weather—a result that demonstrates the potential limitations of studies that use spatial patterns to predict ecosystem responses to temporal changes. Previous investigators have reported that ecosystems respond more strongly to climate than to weather, and have suggested that this delayed response, or lag effect is a consequence of vegetation structure requiring time to respond to altered conditions (Lauenroth and Sala

1992). We predicted dramatically different magnitudes of ANPP response to changes in long-term versus interannual precipitation and even different directions in the BNPP response to long-term versus interannual temperature, implying that relationships in the spatial domain may not accurately predict the immediate response of production 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.

We examined production response to altered cropping intensity in smaller areas within the US 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 production response between subregions show that the effect of cropping on ecosystem processes depends on the specific cropping practices followed in a given 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 accounted 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 our results indicate that cropping has a substantial impact on these processes, which in many cases proved to be more important than climate or weather. Although we did not explicitly examine the importance of practices linked to cropping—notably, irrigation and fertilization—our conclusion that cropping is a major driver of ecosystem processes provides strong evidence that the large-scale and long-term consequences of these practices warrant further investigation.

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REFERENCES

Allmaras RR, Nelson WW, Vorhees WB. 1975. Soybean and corn rooting in southeastern Minnesota: II. Root distributions and related water inflow. Soil science society of America Journal 39:771–77.

Anderson EL. 1988. Tillage and N fertilization effect on make root growth and rootshoot ratio. Plant and Soil 108:245–51.

Austin AT, Vitoiujek PM. 1997. Nutrient dynamics on a precipitation gradient in Hawaii. Oecologia 113:519–29.

Bolinder MA, Angers DA, Dubuc JP. 1997. Estimating shoot to root ratios and annual carbon inputs in soils for cereal crops. Agriculture, Ecosystems and Environment 63:61–6.

Box GEP, Hunter WG, Hunter JS. 1978. Statistics for experimenters. New York: Wiley and Sons.

Bradford JB, Hicke JA, Lauenroth WK. 2005. The relative importance of light use efficiency modification from environmental conditions and cultivation for estimation of large-scale net primary productivity. Remote Sensing of Environmental 96:246–55.

Bradford JB, Lauenroth WK, Burke IC. 2005. The impact of cropping on primary production in the U.S. Great Plains. Ecology 86:1863–72.

Bray JR. 1963. Root production and the estimation of net productivity. Canadian Journal of Botany 41:65–72.

Briggs JM, Knapp AK. 1995. Interannual variability in primary production in allgrass prairie: climate soil moisture, topographic position, and fire as determinants of aboveground biomass. American Journal of Botany 82:1024–30.

Burke IC. 2000. Landscape and Regional Biogeochemistry Approaches. In Sala O.E, Jackson R.B, Mooney H.A, Howarth R.W, editors, Methods in Ecosystem Science. Springer-Verlag, New York. pp 277–88.

Burke IC, Kittel TGF, Lauenroth WK, Snook P, Yonker CM, Parton WJ. 1991. Regional analysis of the central great plains, sensitivity to climate variability. 41:685–92.

Burke IC, Lauenroth WK, Parton WJ. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology 78:1330–40.

Burnham KP, Anderson DR. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research 28:111–119.

Buyanovsky GA, Kucera CL, Wagner GH. 1987. Comparative analyses of carbon dynamics in native and cultivated ecosystems. Ecology 68:2023–31.

Cassman KG. 1999. Ecological intensification of cercal production systems: yield potential, soil quality, and precision agriculture. Proceedings of the National Academy of Sciences, USA 96:5952–59.

CLIMATEDATA. 1988. Climatedata User's Manual. U.S. West Optical Publishing, 90 Madison St. Suite 200, Denver, CO. 80206.

Crawford MC, Grace PR, Bolloti WD, Oades JM. 1997. Root production of a barrel medic (Medicago truncatula) pasture, a barley glass (Hordeum leporiurn) pasture and a fababean (Vicia faba) crop in southern Australia. Australian Journal of Agricultural Research 48:1139–50.

Dickenson CE, Dodd JL. 1976. Phenological pattern in the shortgrass prairie. Amercian Midland Naturalist 96:367–78.

Epstein HE, Lauenroth WK, Burke IC. 1997. Effects of temperature and soil texture on aboveground net primary production in the U.S. Grent Plains. Ecology 78:2628–31.

Epstein HE, Lauenroth WK, Burke IC, Coffin DP. 1996. Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. Journal of Vegetation Science 7:777–88.

Gill RA, Kelly RH, Parton WJ, Day KA, Jackson RB, Morgan JA, Scurlock JMO, Tieszen LL, Castle JV, Ojima DS, Zhang XS. 2002. Using simple environmental variables to estimate belowground productivity in grasslands. Global ecology and biogeography. 11:79–86.

Guersehman JP, Paruelo JM, Burke IC. 2003. Land use impacts on the normalized difference vegetation index in temperate Argentina. Ecological Application 13:616–28.

Hicke JA, Asner GP, Randerson JT, Tucker C, Los S, Birdsey R, Jenkins JC, Field C. 2002. Trends in North American net primary productivity derived from satellite observations. 1982–1998. Global Biogeochemical Cycles 16:#1019.

Houghton RA, Hackler JL, Lawrence KT. 1999. The U.S. carbon budget: Contributions from land-use change. Science 285:574–8.

Jefferies RA. 1993. Cultivar responses to water stress in potato: effects of shoot and roots. New Phytologist 123:491–98.

Jenny H. 1941. Factors of soil formation. New York, New York, USA: McGraw-Hill.

Jobbagy EG, Sala OE, Paruelo JM. 2002. Patterns and controls of primary poruddion in the Patagonian Steppe: a remote sensing approach. Ecology 83:307–19.

Kimball BA, Mauney JR. 1993. Response of cotton to varying CO_2, irrigation, and nitrogen: Yield and Growth. Agronomy journal 85:706–712.

Kloseiko J, Mandre M, Ruga I. 2001. Biomass nitrogen, sulfur, and phosphorus contents of beans grown in limed soil in response to foliar application of HNO_3 or H_2SO_4 mists. Journal of Plant Nutrition 24:1589–1607.

Lauenroth WK. 1979. Grassland primary production: North American grasslands in perspective. In: French NR, Eds. Perspectives in grassland ecology. Ecological Studies, Vol 32. New York, NY, USA: Springer-Verlag. pp 3–24.

Lauenroth WK, Burke IC. 1995. Great Plains, Climate variability,. In: Nierenberg WA, Eds. Encyelopedia of Environmental Biology. New York: Academic Press. pp 237–49.

Lauenroth WK, Burke IC, Gutmann MP. 1999. The structure and function of ecosystems in the central North American grassland region. Great Plains Research 9:223–59.

Lauenroth WK, Burke IC, Paruelo JM. 2000. Pattern of production and precipitation-use efficiency of winter wheat and native grasslands in the Central Great Plains of the United States. Ecosystems 3:344–51.

Lauenroth WK, Sala OE. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2:397–403.

Lieth H. 1975. Modeling the primary productivity of the world. In: Lieth H, Whittaker RH, Eds. Primary productivity of the biosphere. New York, NY, USA: Springer-Verlag. pp 237–63.

Lobell DB, Asner GP. 2003. Climate and management contribution to recent trends in US. agricultural yields. Science 299:1032.

Martin JH, Leonard WH, Stamp DL. 1976. Principles of field crop production. New York, NY, USA: Publishing CO., Inc.

Marvel JN, Beyrouty CA, Gbur EE. 1992. Response of soybean growth to root and canopy competition. Crop Science 32:797–801.

Mauncy JR, Lewin KF, Hendrey GR, Kimball BA. 1992. Growth and yield of cotton expose to free-air CO_2 enrichment. Critical reviews in plant sciences. 11:213–222.

McMichael BL, Quisenberry JE. 1991. Genetic variation for root-shoot relationships among cotton germplasm. Environmental and experimental botany 31:461–470.

Melgoza G, Nowak RS, Tausch RT. 1990. Soil-water exploitation after fire - competition between *bromus-tectorum* (cheatgrass) and 2 native species. Occologia 83:7–13.

Monteith JL. 1977. Climate and the efficiency of crop produption in Britain. Phi1osophioal transactions of the royal society of London. Ser B 281:277–94.

Monteith JL. 1972. Solar Radiation and productivity in tropical ecosystems. Journal of Applied Ecology 9:747–66.

NASS. 1988. Acreage. Publication number CrPr 2-5 (6-98). USDA, Washington, DC. USA: National Agricultural Statistics Service (NASS).

Noy-Meir I. 1973. Desert ecosystem: environment and producers. Annual review of ecology and systematics 4:25–51.

Opena GB, Porter GA. 1999. Soil management and supplemental imgation effects on potato: II. Root growth. Agronomy Journal 91:426–31.

Paruelo JM, Burke IC, Lauenroth WK. 2001. Land-use impact on ecosystem functioning in eastern Colorado, USA. Global change biology 7:631–39.

Paruelo JM, Lauenroth WK, Burke IC, Sala OE. 1999. Grassland precipitation-use efficiency varies across a resource gradient. Ecosystems 2:64–8.

Piper JK, Kilakow PA. 1994. Seed yield and biomass allocation in Sorghum bicolor and F1 and backcross generations of S. bicolor x S. habpense. Canadian Journal of Botany 72:468–74.

Potter CS, Klooster S, Brooks V. 1999. Interannual variability in terrestrial net primary production: exploration of trends and controls on regional to global scales. Ecosystems. 2:36–48.

Ratheke B, Lacey EP. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16:179–214.

Reed BC, Brown JF, Darrel V, Lovcland TR, Merchant JW, Ohlen DO. 1994. Measuring phonological variability from satellite imagery. Journal of Vegetation Science 5:703–14.

Rosenzweig ML. 1968. Net primary production of terrestrial communities: prediction from climatological data. American Naturalist 102:67–74.

Sala OE, Parlon WJ, Joyce LA, Lauenroth WK. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–5.

Seghicri J, Floret C, Pontanier R. 1995. Plant phenology in relation to water availability: herbaceous and woody species in the savannas of northern Cameroon. Journal of Tropical Zoology 11:237–254.

Sheng Q, Hunt LA. 1991. Shoot and root dry weight and soil water in wheat, triticale and rye. Canadian Journal of Plant Science 71:41–49.

Silvius JE, Johnson RR, Peters DB. 1977. Effect of water stress on carbon assimilation and distribution in soybean plants at different stages of development. Crop Science 17:713–6.

Szaniawski RK. 1983. Adaptation and functional balance between shoot and root activity of sunflower plants grown at different root temperatures. Annals of Botany 51:453–9.

Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich III JVK, Moore B, Vorosmarty CJ. 1998. Effect of interannual climate variability on carbon storage in Amazoman ecosystems. Nature 396:64–7.

Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S. 2002. Agricultural sustainability and intensive production practices. Nature 418:671–7.

Turpin JE, Robertson MJ, Hillcoat NS, Herridge DF. 2002. Fababean (Vicia faba) in Australia's northern grainy belt: canopy development, biomass, and nitrogen accumulation and partitioning. Australian Journal of Agricultural Research 53:227–37.

USDA Soil Conservation Service. 1989. STATSGO Soil Maps. National Cartographic Center. TX, USA: Fort Worth.

Veron SR, Paruelo JM, Sala OB, Lauenroth WK. 2002. Environmental control of primary production in agricultural systems of the Argentine Pampas. Ecosystems 5:625–35.

Vitousek PM. 1992. Global environmental change: an introduction. Annual Review of Ecology and Systematics 23:1–14.

Washitani I, Masuda M. 1990. A comparative study of the germination characteristics of seeds from a moist tall grassland community. Functional Ecology 4:543–557.