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Environmental Controls of Primary Production in Agricultural Systems of the Argentine Pampas

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ABSTRACT

We studied the aboveground net primary productivity (ANPP) of wheat crops in the Argentine Pampas. Our specific objectives were to determine (a) the response of ANPP to changes in water availability (b) the regional patterns of ANPP and (c) the interannual variability and environmental controls of ANPP. We used ground and satellite data to address these questions. Wheat ANPP was calculated as the ratio between grain yield and harvest index. We developed a simple model that took into account environmental and genetic improvement effects upon harvest index. We used the normalized difference vegetational index (NDVI) as a surrogate for ANPP at the county level. Straight-line regression models were fitted to single-year and average values of ANPP and precipitation to derive temporal and spatial models for wheat. For grasslands, we used spatial and temporal models already published. At any given site, there was no difference between modeled wheat and grassland average ANPP. The response of ANPP to changes in interannual water availability decreased along the precipitation gradient when vegetation structure (for example, species composition, density, and total cover) was held constant (wheat crops). Wheat ANPP and total production variability, estimated from remotely sensed data, decreased as mean annual precipitation (MAP) increased. The percentage of soils without drainage problems was the variable that explained most of the wheat ANPP spatial variability as shown by stepwise linear regression. Precipitation variability accounted for 49% of wheat ANPP variability. Remotely sensed estimates of ANPP variability showed lower and wheat ANPP higher temporal variability than annual precipitation.

Key words: primary production; variability; wheat; grasslands; vegetational constraints; biogeochemical constraints; normalized difference vegetation index (NDVI); Argentine Pampas.

INTRODUCTION

The environmental controls of aboveground net primary production (ANPP) and its spatial and temporal variability have been a topic of considerable interest in grassland ecology for decades. In 1939, Walter first documented a positive linear relationship between ANPP and mean annual precipitation (MAP). The same type of relationship was later found for many grasslands around the world (Rosenzweig 1968; Lauenroth 1979; Rutherford 1980; Le Houerou and others 1988; Sala and others 1988; McNaughton and others 1993). The correla-

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tive models fitted for different regions were remarkably similar (McNaughton and others 1993), with the slope of the relationship often associated with the precipitation use efficiency of the system (PUE) (Le Houerou 1984). PUE refers to the ratio between ANPP and precipitation and is usually expressed in g m^{-2} mm^{-1}. At a finer spatial resolution, Sala and others (1988) and Epstein and others (1997) showed that soil texture and temperature accounted for a significant portion of the variability not associated with MAP in the Central Great Plains of the United States.

The slope of the relationship between ANPP and precipitation is different for temporal and spatial series of precipitation and ANPP data (Lauenroth and Sala 1992). Spatial models are constructed by using aboveground primary production and precipitation for different sites averaged over a number of years (Sala and others 1988). Temporal models, on the contrary, consider annual series of precipitation for single sites (Lauenroth and Sala 1992; Briggs and Knops 1995). In general, the proportion of the variability accounted for by temporal models is lower than in the case of spatial models.

Using empirical data and remotely sensed estimates of ANPP, Paruelo and others (1999) found that the slope of the temporal model was lower than the slope of the spatial model at both extremes of the typical precipitation gradient of temperate grassland areas (100–1000 mm) and similar at intermediate levels. They described the change of the ratio between the slope of the temporal and spatial models across the MAP gradient using a double logistic equation. The ratio between the temporal and spatial slopes peaks at 462 and 491 mm of MAP depending on the source of ANPP data (field and remote-sensed estimates, respectively). Paruelo and others interpreted this pattern as the result of changes in the relative importance of the two components of structural constraints to the response of ANPP to interannual changes in precipitation. They hypothesized that vegetational constraints decrease and biogeochemical constraints (for example, nutrient limitation) increase along a MAP gradient. Thus, at each site, a combination of vegetational and biogoechemical constraints define a boundary within which ANPP varied in response to changes in water availability. At a continental scale, Knapp and Smith (2001) reported that maximum variability in ANPP occurs in biomes where low vegetational constraints are combined with moderate variability in precipitation.

Vegetational constraints are related to a set of plant attributes that let an individual survive, grow, and develop under low resource availability. At the same time, these constraints reduce the maximum relative growth rate of the plant (RGR_{max}, the dry weight increase per unit of biomass and per unit of time, under optimal conditions). Most of the characteristics associated with drought resistance (low shoot–root ratio, low specific leaf area, low stomatal conductance, and so on) constrain maximum photosynthesis and growth rate (Orians and Solbrig 1977). This finding corresponds with the idea of a tradeoff between RGR_{max} and drought resistance (Tilman 1988; Keddy 1992; Grime 1997). Del Pino (1999) found a positive relationship between the relative growth rate of 18 grass species and the MAP of the habitat where the species are dominant. At the driest extreme of the precipitation gradient, the dominance of low RGR_{max} species positively influences its fitness under adverse conditions but also diminishes the potential growth (Lambers and others 1998). Vegetation from dry sites has low seed and tiller densities, which further diminish the response to years of high precipitation.

Vegetational constraints would represent the result of the adjustment of the plant community structure of a particular site to the modal resources availability. An analysis of the relationship between precipitation (as a surrogate for water availability) and primary productivity based on long-term data across an environmental gradient would reflect such adjustment at the level of carbon gains. Two sites differing in their MAP are expected to reach different adjustments between water availability and vegetation structure (species composition, total cover, spatial pattern). It would be incorrect to expect similar primary productivity at sites with different MAP, even if, in the same year, they receive identical amounts of precipitation. This caveat highlights the risks of space-for-time substitutions in ecological studies. However, most models of plant productivity assume this relationship is valid (for example, Parton and others 1987).

Biogeochemical constraints, on the other hand, are related to the magnitude of nutrient or light limitation. Precipitation affects both nutrient demand—via changes in species composition—and nutrient offer—through its effects on weathering and leaching. Austin and Vitousek (1998) found that at humid sites the effects of precipitation on leaching exceeds its effects on weathering and deposition.

One of the main problems in studying the sensitivity of aboveground primary productivity to changes in resource availability is the difficulty of finding areas that differ in MAP and have the same vegetation structure or biogeochemical constraints. The expansion of the area devoted to wheat production in the Pampas region of Argentina during the last century has homogenized the ecosystem structure along a precipitation gradient. Wheat crops offer a particularly useful system for the study of the temporal and spatial relationship between aboveground primary productivity and water availability because this type of system minimizes the variation in vegetation structure.

There are some differences to be considered when comparing cropped land ANPP to grassland ANPP. During the last century, crop yields improved significantly due to the intensification of agricultural practices. This process has basically relied on two factors: better crop management and genetic improvement (for example, see Cassman 1999). The former strategy includes better agronomic practices and increased external inputs, mainly in the form of nitrogen (N). The impact of genetic improvements on grain yield was largely accounted for by an increase in the harvest index (the ratio between grain yield and total aboveground biomass) (Slafer and Kernich 1996). Additional effects on aboveground primary productivity are associated with fertilizer application or irrigation in recent years. Resource addition in the study area is relatively less important than it is in other agricultural areas of the world (Ghersa and León 1999). In the Pampas, the goal of crop management practices (for example, better sowing dates, improved fallowing techniques, and so on) was to achieve a better match between the existing resources and the most common crop requirements rather than producing an increment in absolute resources.

In this article, we analyze different aspects of the carbon gain of wheat systems—namely, the response of ANPP to changes in water availability, the regional patterns of ANPP, and the interannual variability and environmental controls of ANPP. Our specific objectives were: (a) to compare the spatial relationship between ANPP and MAP of wheat fields and grasslands across a precipitation gradient, (b) to study the changes in the year-to-year response of ANPP to precipitation in a system with a homogeneous vegetation structure (wheat crops), (c) to identify the controls of the spatial and temporal variability of wheat ANPP, and (d) to characterize and compare the interannual variability of wheat and total production along a precipitation gradient.

The study provides information to evaluate the hypothesis that at low precipitation sites vegetation structural constraints limit ANPP sensitivity to changes in water availability. The analysis of the interannual variability of production was based on estimates derived from wheat fields and estimates based on remotely sensed data.

Methods

We developed spatial and temporal models using wheat ANPP values. Wheat ANPP was calculated from grain yield data and monthly records of precipitation for 48 counties distributed across the Pampas region of Argentina (located between 28° and 40°S and 68° and 57°W) from 1970 to 1997 (Figure 1). Grain yield data were obtained from the records of the Agriculture Department of Argentina. Precipitation data for the same period were collected from the Instituto Nacional de Tecnología Agropecuaria (INTA), the Servicio Meteorológico Nacional, the Ministerio de Asuntos Agrarios de Buenos Aires, and the Secretaria de Estadísticas de La Pampa. Mean annual temperature (MAT) data were taken from J. P. Guerschman (unpublished), who estimated them from the Leemans and Cramer (1991) database (http://www.ngdc.noaa.gov/seg/eco/cdroms/gedii_a/datasets/a03/lc.htm). The temperature database was assembled from observations between 1931 and 1960; even if it does not reflect recent global warming, it adequately represents the spatial gradient in MAT. We checked the correspondence between the data from Leemans and Cramer and more recent means (Servicio Meteorologico Nacional 1992) for 15 sites and found it satisfactory ($r^2 = 0.95$, $n = 15$). In the analyses, all years with missing data on grain yield or precipitation were ignored.

Straight-line regression models were fitted for the relationship between wheat average ANPP and MAP (spatial models) (objective a). We also fitted straight-line regression models to wheat ANPP and annual precipitation for each site (temporal models) (objective b). The slopes of the regression models are estimates of the response of wheat ANPP to spatial or interannual changes in precipitation. Ten sites with a MAP of more than 1000 mm were not analyzed because wheat ANPP decreased with further increases in MAP, possibly as a result of indirect negative effects of high MAP upon harvest conditions or diseases.

We calculated wheat ANPP as peak biomass. Peak biomass was derived from the ratio of wheat grain yield to harvest index (HI). For the available data series, it is possible to identify two main sources of interannual variability for the harvest index: genetic improvement and environmental conditions (Fischer 1975; Slafer and Andrade 1989). We developed a simple model that took into account both sources of variability to estimate HI changes

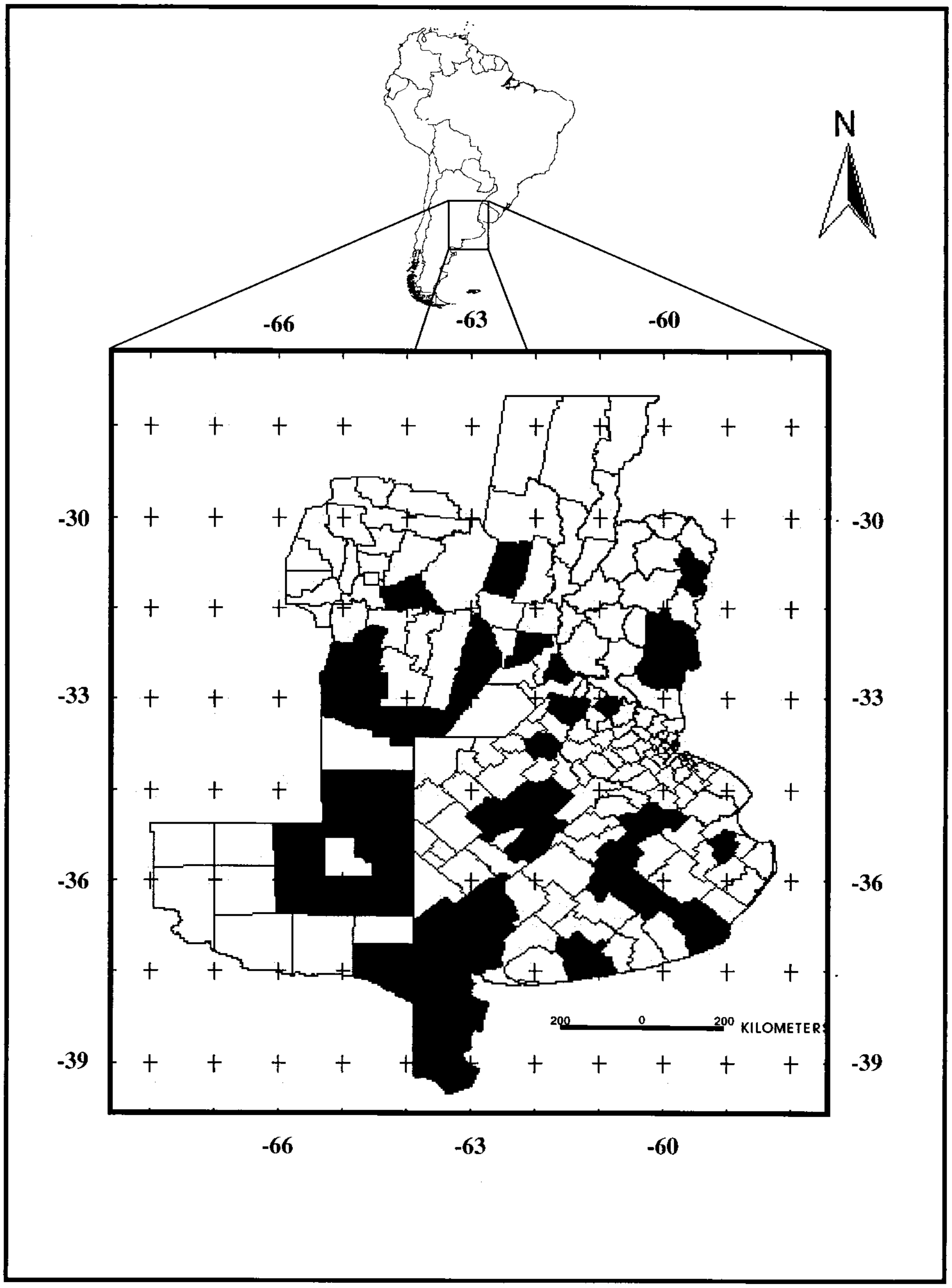

Figure 1. Map of the region under study. Climatic and edaphic data were obtained for the black-colored counties (departments) throughout the region.

through time. Genetic improvement effects upon potential harvest index (HI_p) were estimated from the exponential relationship between HI and the year of release found by Calderini and others (1995). The relationship they found for seven wheat cultivars representative of those used from 1920 to 1990 in the Pampas and grown under no nutritional or water stress was:

$$PHI_j = \frac{2.19 \cdot 10^{-8}\ j\ e^{0.01072\ j}}{100}$$

where j is the year and PHI is the potential harvest index for the j year. To take into account changes in environmental conditions among years, we developed an environmental index (EI). The EI was calculated as the ratio between the HI for a single year and place and the maximum HI for the same place.

Sadras and Connor (1991) showed that wheat HI was mainly related to the proportion of water transpired after anthesis in a curvilinear form:

$$HI_{ij} = (\beta_{ij}/[1 - (0.58 - 1.68^{*}\ \beta_{ij})]$$

where HI_{ij} is the harvest index for the i place in the j year, β_{ij} is the amount of water transpired after

Table 1. Variables Considered in the Forward Stepwise Regression Analysis and Their Maximum and Minimum Values

Variables	Maximum Value	Minimum Value
Average wheat ANPP (g/m^2)	757	335
Wheat ANPP coefficient of variation	0.49	0.15
1st quarter precipitation (mm)	419	135
2nd quarter precipitation (mm)	280	85
3rd quarter precipitation (mm)	229	60
4th quarter precipitation (mm)	391	84
Mean annual temperature	18.6°C	13.5°C
% SWDP	97	0
% SwSaP	40	0
% SwSoP	99	0
Precipitation coeficient of variation	0.38	0.15

% SWDP, % SwSaP, and % SwSoP = proportion of soils of each county without drainage problems, with salinity problems, and with sodicity problems.

anthesis expressed as fraction of total water transpired for the i place and the j year, 0.58 is the potential contribution of preanthesis assimilates to wheat yield, and 1.68 is an empirically derived parameter that describes the form of the curve. We used precipitation as a surrogate for transpiration (G. A. Slafer personal communication) because transpiration data were not available and at this stage, wheat canopy cover approximates 100% (Satorre and Slafer 1999) and rainfall is lower than potential evapotranspiration (FAO 1985). The ratio between the precipitation from October to December (anthesis to maturity) and from May to December (total crop cycle plus a follow month) was obtained to estimate the proportion of water transpired after anthesis. Finally, we obtained the actual HI for a single place and year as follows:

$$HI_{actual\ ij} = EI_{ij} \times PHI_j$$

Among the potential controls of spatial and temporal wheat ANPP variability, we explored climatic and edaphic factors (objective c). The climatic database was the same one that we used for objective a. Soil data were obtained from J. P. Guerschman (unpublished) based on the digital version of the Atlas de Suelos de la República Argentina (SAGPyA 1990). Soil data are the proportion of the county area occupied by soils with different drainage, sodicity, and salinity characteristics. Forward stepwise regression analyses (Kleinbaum and Kupper 1978) were used to study the relationship between wheat ANPP spatial and temporal variability and environmental variables across the studied area. Climatic and edaphic data were our independent variables (Table 1).

To achieve the fourth objective, we used estimates of production derived from two sources: wheat yields and remotely sensed data. A remotely sensed surrogate for ANPP was calculated for each county using the annual integral of the normalized difference vegetation index (NDVI-I) (Tucker and others 1985; Paruelo and others 1997). NDVI was computed from the reflectance in the red (channel 1) and near-infrared (channel 2) bands of the NOAA/AVHRR satellite as: NDVI = (channel 2 − channel 1)/(channel 1 + channel 2). NDVI-1 is a good estimator of the amount of photosynthetic active radiation intercepted by the canopy and hence of ANPP (Sellers and others 1992). The amount of photosynthetic active radiation intercepted is linearly related to the aboveground primary production. The coefficient of proportionality can be affected by nutrient or water availability. NDVI data were obtained from the Pathfinder AVHRR Land database (James and Kalluri 1994). The temporal and spatial resolutions are 10 days and 64 km^2, respectively, from 1982 to 1993. To calculate the NDVI-I value for a specific year and county, we averaged all the county's pixels over the 36 annual images (January to December). To characterize the temporal variability of wheat ANPP, NDVI-I, and annual precipitation, we calculated the coefficient of variation (CV) over 12 years (1982–93). The CV has been used extensively as an index of variability of both climatic and ecological data sets (Le Houerou and others 1988; Frank and Inouye 1994; Lauenroth and Burke 1995; Paruelo and Lauenroth 1998).

We took special care to evaluate biases related to the number of missing data in each of the sites in-

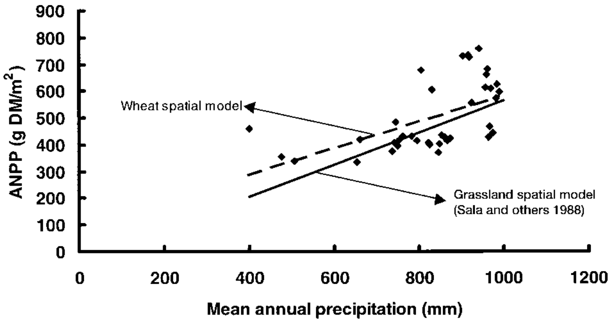

Figure 2. Relationship between wheat ANPP (*broken line*) and MAP (spatial model) ($ANPP_w$ (g/m^2) = 0.5 × MAP + 86.32; $r^2 = 0.32$; $P < 0.001$; $n = 38$. The solid line represents the spatial model for natural grasslands published by Sala and others (1988): ANPP (g/m^2) = 0.6 × MAP − 34.

cluded in the analyses or the time periods considered. For the wheat spatial model and the relationship between the CV of wheat ANPP and MAP, we progressively removed sites with decreasing numbers of missing data from the data set and recalculated the regression model. The parameters of both regression models were relatively insensitive to the set of sites included in each analysis (data not shown).

Results

The spatial model for the peak biomass of wheat crops (our ANPP estimator) was similar to the one presented by Sala and others (1988) for grasslands:

$$ANPP_w\ (\mathrm{g\ m^{-2}}) = 0.5 \times MAP + 86 \quad (r^2 = 0.32,\ P < 0.001)$$

$$ANPP_g\ (\mathrm{g\ m^{-2}}) = 0.6 \times MAP - 34 \quad (r^2 = 0.90,\ P < 0.01)$$

(Sala and others 1988)

The slope of the wheat model was slightly lower than the grassland model while the y intercept was higher, but neither was significantly different ($n = 38$; $P > 0.05$ by *t*-test) (Figure 2). The difference is even lower if we consider the equation presented by McNaughton (1985) that has a slope of 0.48 g m^{-2} mm^{-1}. The difference between the coefficients of determination of both models may be due to the different extent of the independent variable considered. Wheat crops in the Pampas are restricted to areas with more than 400 and less than 1000 mm of MAP, whereas Sala's grassland model considers a larger MAP gradient (100–1200). Thus, at this regional scale, there must be factors other than MAP controlling wheat ANPP.

The forward stepwise regression analysis showed that edaphic and climatic variables explained 63% of the spatial variability in wheat ANPP (Table 2). A substantial proportion of this variability (36%) was accounted for by an edaphic variable: the percentage of soils without drainage problems (SWDP). Precipitation and temperature explained the rest. SWDP synthesizes many edaphic characteristics of the soil, such as texture, profile depth, and topography. Precipitation during the second and first quarter explained 15% and 5% of the variance, respectively, whereas MAT explained 7% of the spatial variability of ANPP. ANPP was negatively related to MAT.

The temporal models of the relationship between wheat ANPP and annual precipitation for individual sites showed a broad range of slopes, from −0.48 to 0.47 g m^{-2} mm^{-1} y^{-1} for sites with MAP of 400 and 905 mm, respectively. None of the slopes of the temporal models was higher than the slope of the spatial model. Values close to zero or negative values may show a lack of response in carbon gain, since precipitation increases mainly due to the indirect negative effects of increased moisture on harvest conditions or disease incidence. To compare these results with the equation presented by Paruelo and others (1999), we expressed this relationship as the ratio between the slope of the temporal model and the slope of the spatial model along the precipitation gradient (Figure 3). This ratio decreased as MAP increased, according to the following equation:

$$\mathrm{Ratio} = -0.0013 \times MAP + 1.29 \quad (r^2 = 0.24;\ P < 0.01)$$

The negative relationship between the ratio of the slopes and MAP was still significant ($P < 0.05$) when we either replaced negative values by zero or removed negative values.

On a temporal basis, wheat ANPP variability was associated with precipitation variability and MAT. Precipitation variability accounted for 49% of wheat ANPP variability, whereas MAT explained 10% (Table 2).

The relative variability of wheat ANPP and of the NDVI-I decreased as MAP increased (Figures 4a and b). Wheat ANPP variability was almost always higher than NDVI-I variability. The CVs of both wheat ANPP and NDVI-I were positively related to precipitation variability. However, the integral of NDVI showed less temporal variability than precipitation because all points fall below the 1:1 line (Figure 5b). There was not a clear pattern for wheat

Table 2. Forward Stepwise Regression Analysis Results for the Two Dependent Variables Considered (Average Wheat ANPP and Wheat ANPP Coefficient of Variation) and for the Entire Data Set (n = 46)

Dependent Variable	Intercept	R^2	F	Independent Variables	Regression Coefficient	Partial R^2	P
Average Wheat ANPP (g/m^2)	749.61	0.63	17.53	% SWDP	1.58	0.36	<0.001
				2PPT	0.8	0.15	<0.001
				MAT	−40.4	0.07	<0.001
				1PPT	0.58	0.05	<0.05
Wheat ANPP CV	0.064	0.59	15.88	PPT CV	0.425	0.49	<0.01
				MAT	0.022	0.10	<0.01

ANPP = aboveground net primary production. R^2, F, partial r^2, and P = the coefficient of determination, the ratio between the model's mean square and the mean square error, the partial coefficient of determination of each single variable and to the level of probability of the F, respectively. % SWDP = percentage of soils without drainage problems within a county. 1PPT, 2PPT, and MAT = first and second quarter precipitation and mean annual temperature, respectively. PPT CV = the precipitation coefficient of variation.

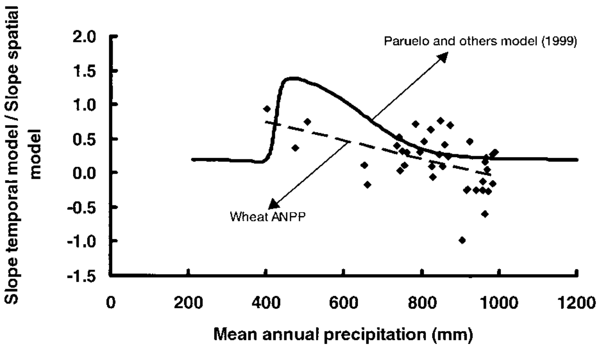

Figure 3. Slope of the regression between wheat ANPP and annual precipitation fitted for each site (temporal model) divided by the slope of the spatial model for wheat (0.5), along the MAP gradient of the Pampas (*broken line*). The solid line corresponds to the double logistic model presented by Paruelo and others (1999) for natural grasslands ($y = 0.2 + 1.307/(1 + e^{-0.1304 \times (MAP - 424)} - 1.307/(1 + e^{-0.0132 \times (MAP - 644)})$.

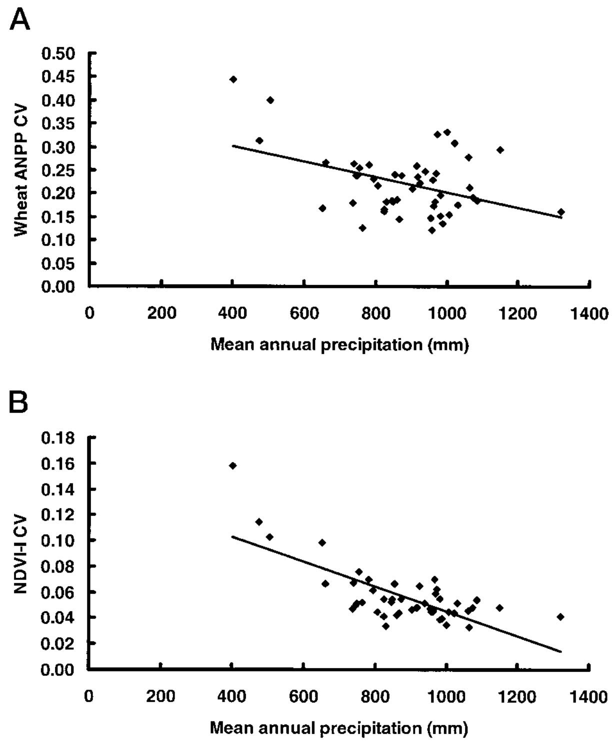

Figure 4. (**A**) Relationship between MAP (1970–97) and the CV of wheat ANPP ($CV_w = -0.0002 \times MAP + 0.367$; $r^2 = 0.17$; $P < 0.001$; $n = 48$) for the period between 1982 and 1993. (**B**) Relationship between MAP (1970–97) and the CV of the annual integral of the NDVI (NDVI-I) ($CV_{NDVI\text{-}I} = -0.0001 \times MAP + 0.141$; $r^2 = 0.53$; $P < 0.001$; $n = 48$) for the period between 1982 and 1993.

ANPP (points were equally distributed around the 1:1 line) (Figure 5a).

The patterns found when we plotted wheat ANPP CV and NDVI-I CV against precipitation CV remained the same independent of the time periods considered (July to June, September to May, September to December). The only exception was when we considered wheat ANPP CV and September to December precipitation CV, where most of the points fall below the 1:1 line. However, this pattern is in accordance with the results of the forward stepwise regression model. First and second quarter precipitation (January to March and April to June) would contribute to the stabilization of wheat ANPP by increasing the amount of water stored in the soil. We concluded, then, that there was only a small bias associated with the particular time periods used in the analyses.

Discussion

Wheat crops had almost the same aboveground productivity as grasslands, based on the estimates derived from correlative models (Figure 2). Our data showed that the conversion of natural grass-

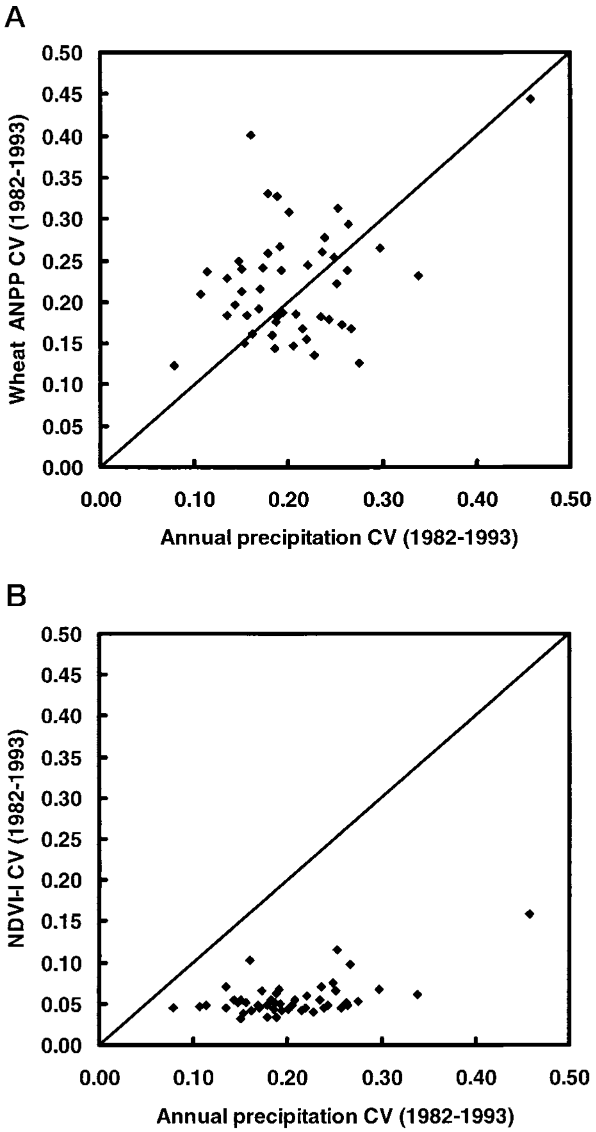

Figure 5. (**A**) Relationship between the coefficient of variation (CV) of annual precipitation and the CV of wheat ANPP. The solid line corresponds to the 1:1 line. Annual precipitation CV and wheat ANPP CV were calculated from 1982 to 1993. (**B**) Relationship between the CV of annual precipitation and the CV of the annual integral of the NDVI (NDVI-I) for the period 1982–93. The solid line corresponds to the 1:1 line.

lands into wheat crops did not result in an increase in ANPP. However, if we consider the difference in belowground–aboveground biomass ratio between wheat and grasslands, the expansion of agriculture may imply a reduction in total production. According to earlier reports in the literature, wheat crops have a belowground–aboveground biomass ratio in the range of 0.1 to 0.4 (O'Toole and Bland 1987; Siddique and others 1990); whereas for grasslands, this ratio ranges between 0.73 and 10 (Sims and others 1978; Milchunas and Lauenroth 1995).

Lauenroth and others (2000) found that, in the Central Great Plains of the United States, on average just 0.2 g m^{-2} of wheat ANPP are produced for each millimeter of MAP, as compared to 0.6 g m^{-2} for grasslands. In the Pampas, the slopes of wheat crops and grasslands are quite similar (Figure 2). We believe that the difference between the North and South American grassland regions is due to the characteristics of their respective agricultural systems. In the US Central Great Plains, wheat is cropped under summer fallow management practices (one crop every 2 years). Water stored during the fallow period may be responsible for the low sensitivity of wheat to an increase in annual precipitation.

The negative relationship between the ratio of temporal and spatial slopes of the precipitation (PPT)-ANPP model for wheat and MAP (Figure 3) suggests that as MAP increases, the response of net primary productivity to interannual changes in precipitation decreases. This result supports the hypothesis of Lauenroth and Sala (1992) and Paruelo and others (1999) that the maximum response to changes in water availability is found at the driest extreme of the precipitation gradient if vegetational constraints are held constant and minimum. For eastern Colorado and eastern Kansas, the slopes for the wheat temporal models were, in general, lower than the spatial model slope, and—as we found—the slopes of the temporal models decreased across the MAP gradient (Lauenroth and others 2000). Because both studies fixed the structure of the vegetation, the reduced response should be associated with biogeochemical restriction—that is, the increase in the rate of mineralization is less than the increase in water availability. Burke and others (1997) found that ANPP, soil organic matter (SOM) and N limitation increased with increasing precipitation. They suggested that with high contents of SOM, higher proportions of organic matter are sequestered in passive pools unavailable for mineralization and plant uptake. In the semiarid Argentine Pampas, Diaz-Zorita and others (1999) found that wheat yields were related to both soil water retention and total organic carbon in dry years, whereas they were related to total N and Phosphorus (P) contents in wet years.

The correlation between precipitation during the first and second quarters of the year and crop yield agrees with studies from Rebella and Zeljkovich (1980), Hall and others (1992), and Satorre and Slafer (1999). In the Pampas, rainfall distribution tends to be monsoonal, with the maximum occurring between December and March (summer) and the minimum in July to August (winter) (Hall and others 1992). Wheat crops, which are sown between the end of May and the beginning of August, frequently coincide with water shortage during the vegetative and early reproductive phases (Savin and others 1995). Under these conditions, the amount of water stored in the soil at the time of sowing has a critical role in determining wheat ANPP and grain yield.

The results of the forward stepwise regression analysis suggest that precipitation is the main determinant not only of ANPP but also of its interannual variability. Paruelo and Lauenroth (1998) found a similar pattern for the grasslands and shrub lands of North America. The decreasing variability of wheat ANPP as MAP increases (Figure 4) may be related to the negative relationship between precipitation interannual variability and mean annual precipitation (PPT CV $= -0.0001 \times$ MAP $+ 0.34$; $r^2 = 0.24$, $P < 0.05$) (not shown) (Lauenroth and Burke 1995). A low proportion (10%) of the variance of wheat ANPP variability was accounted for by the differences in MAT among different sites. Temperature may affect ANPP variability indirectly by increasing potential evapotranspiration and soil evaporation. Thus, the capacity of the soil to transfer water received during fallow to the crop-growing period diminishes, making the system more dependent on current precipitation.

The relative variability of wheat ANPP was higher than the relative variability of PPT. The opposite was found for the relationship between NDVI-I and PPT CVs (Figure 5a and b). We interpret this pattern as a consequence of the different areal aggregation levels of both ANPP estimates. Wheat ANPP variability integrates ANPP values of a single crop; for example, it does not include the effect of weed communities that may coexist with the crop or be present during the fallow period. NDVI, by integrating into a single pixel different crops and plant communities, provided an ANPP estimate from a more diverse system at the landscape level.

CONCLUSION

The model fitted to the relationship between average ANPP and MAP for wheat fields across the Pampas was quite similar to the models developed worldwide for grassland areas (Sala and others 1988; McNaughton and others 1993; Paruelo and others 1998). For wheat fields in the Pampas, however, MAP is not the main control of the spatial variability of ANPP. Soil characteristics related to the texture, depth, and topography explained a substantial fraction of the spatial variation in the ANPP of wheat systems.

As has also been described for grasslands (Paruelo and others 1999), the sensitivity of ANPP to changes in water availability decreased across the MAP gradient considered in this study. We found this pattern in a system (wheat crops) with a low and constant level of structural vegetational constraints. The highest response occurred at the driest extreme of the MAP gradient. The lowest response of ANPP to interannual changes in precipitation at the wettest end of the gradient would be associated with biogeochemical constraints. The differential response of ANPP to changes in precipitation across a MAP gradient found for grasslands and their replacement communities needs to be incorporated into models that describe the functional response of this ecosystem to environmental changes.

ANPP variability was positively related to precipitation variability. Given the same variability in precipitation, ANPP was more variable among years in warmer than in cooler areas. Temperature increases evapotranspiration rates, reducing the water-buffer capacity of the soil. A monospecific crop such as wheat amplified precipitation variability at the functional level (ANPP). More complex and diverse systems (including several crops, grassland communities, old fields, and so on.) were able to dampen climatic fluctuations. The interannual variability (coefficient of variation) of ANPP estimates derived from remotely sensed data over areas including several crops and grassland communities was lower than the interannual variability of precipitation.

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