

Grassland Precipitation-Use Efficiency Varies Across a Resource Gradient

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ABSTRACT

Aboveground net primary production (ANPP) is positively related to mean annual precipitation, an estimate of water availability. This relationship is fundamental to our understanding and management of grassland ecosystems. However, the slope of the relationship between ANPP and precipitation (precipitation-use efficiency, PUE) has been shown to be different for temporal compared with spatial precipitation series. When ANPP and precipitation are averaged over a number of years for different sites, PUE is similar for grasslands all over the world. Studies for two US Long Term Ecological Research Sites have shown that PUE derived from a long-term dataset (temporal model) has a significantly lower slope than the value derived for sites distributed across the US central grassland region (spatial

model). PUE differences between the temporal model and the spatial model may be associated with both vegetational and biogeochemical constraints. Here we use two independent datasets, one derived from field estimates of ANPP and the other from remote sensing, to show that the PUE is low at both the dry end and the wet end of the annual precipitation gradient typical of grassland areas (200–1200 mm), and peaks around 475 mm. The intermediate peak may be related to relatively low levels of both vegetational and biogeochemical constraints at this level of resource availability.

Key words: precipitation-use efficiency; primary production; grasslands; normalized difference vegetation index (NDVI); satellites; gradients.

INTRODUCTION

Aboveground net primary production (ANPP), which is a key attribute of grassland ecosystems, integrates in its value different aspects of ecosystem structure and functioning, such as secondary production or herbivore biomass (McNaughton and others 1989). The positive relationship between ANPP and mean annual precipitation (MAP) has been documented for many areas around the world (Walter 1939; Rosenzweig 1968; Lauenroth 1979; Rutherford 1980; Le Houerou and others 1988; Sala and others 1988; McNaughton and others 1993). The models fitted for different areas of the world are

remarkably similar (McNaughton and others 1993; Paruelo and others 1998). The slope of this relationship [precipitation-use efficiency, PUE (Le Houerou 1984)] has been shown to be different for temporal precipitation series (PUE_t) compared with spatial precipitation series (PUE_s) (Lauenroth and Sala 1992). Spatial models are constructed by using ANPP and precipitation data for different sites averaged over a number of years. They are represented by a single straight line with a unique PUE and account for a large fraction of the variability in ANPP (Sala and others 1988).

For two US LTER sites (KONZA and CPER) (Lauenroth and Sala 1992; Briggs and Knapp 1995), temporal models based on long-term ANPP typically have lower slopes than spatial models (Sala and

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others 1988). These empirical data suggest that PUE_t is lower than PUE_s at both extremes of the precipitation gradient. Substituting space for time will lead to an overestimation of ANPP in wet years and an underestimation in dry years. A generalization of these results suggests that PUE_t is always lower than PUE_s . PUE differences between temporal and spatial models may be associated with vegetational and biogeochemical constraints (Lauenroth and Sala 1992). If these constraints are constant, PUE_t will be lower than PUE_s and relatively similar along the resource gradient. However, vegetational and biogeochemical constraints may vary in intensity across the gradient.

Vegetational constraints are associated with the time constant of the response of dominant plants to changes in resource availability. Vegetational constraints will be high if the rate of change of leaf-area index (LAI) of the dominant plants per unit of resource is low. The ability of the ecosystem to respond to changes in precipitation will be greater for systems dominated by mesophytic grasses than for systems dominated by shrubs or xerophytic grasses. Given the same change in precipitation, mesophytic grasses will show greater changes in ANPP than will shrubs or xerophytic grasses. The rate of change of LAI and/or carbon gain per unit of resource will be related to the relative growth rate and maintenance costs of the dominant species.

Biogeochemical constraints are related to the magnitude of nutrient limitation. Nutrient limitation should be higher toward the wet end of a precipitation gradient than at the dry end (Austin and Vitousek 1998). We hypothesize that vegetational constraints decrease and biogeochemical constraints increase along a MAP gradient. From this hypothesis, it follows that PUE_t will peak at intermediate values of MAP.

Our objective was to identify the pattern of change in the temporal sensitivity of ANPP to annual precipitation (PUE_t) across the typical precipitation gradient found in temperate grasslands. We based our study on long-term data of ANPP and annual precipitation for individual sites available in the literature or from the Internet. We did not perform a formal meta-analysis (Arnqvist and Wooster 1995), but by changing the extent of the individual studies we were able to identify general patterns not evident from the single-site analysis.

METHODOLOGY

To analyze changes in PUE_t along a precipitation gradient, we conducted two separate analyses. In the first, we assessed PUE for 11 temperate grassland sites worldwide (seven US and four Eurasian

sites) by using data on ANPP and annual precipitation for at least 4 years. Data were obtained from the literature or from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC at http://www-eodis.ornl.gov/npp/npp_home.html).

In the second analysis, we estimated PUE by using remotely sensed estimates of ANPP for 19 grassland sites across the central grassland region of North America by using the annual integral of the normalized difference vegetation index (NDVI-I) as an estimate of ANPP (Tucker and others 1985; Paruelo and others 1997). Sites were selected based on their size (to allow for a proper identification on the images) and the absence of major human disturbances. NDVI was computed from the reflectance in the red (channel 1) and near-infrared (channel 2) bands of the NOAA/AVHRR 11 satellite ($NDVI = \text{channel 2} - \text{channel 1} / (\text{channel 1} + \text{channel 2})$). NDVI-I is a good estimator of the amount of photosynthetically active radiation intercepted and hence of ANPP (Sellers and others 1992). To calculate the annual integral, we used 1-km-resolution biweekly maximum NDVI composites for 1990, 1991, 1992, and 1993 (Eidenshink 1992; Paruelo and others 1997). Images were obtained from the EROS Data Center in Sioux Falls, South Dakota (USA). We did not use NDVI databases that cover a longer period (for example, the Pathfinder AVHRR Land database) because the size of the pixel (64 km²) is greater than many of the selected sites. Both the NDVI images and the study-site coordinates were converted to the Lambert Azimuthal Equal Area map projection coordinates. The annual integral (NDVI-I) was calculated by summing the products of NDVI for each date and the proportion of the year represented by that date ($\sum^n NDVI_i \cdot T_i$, where n is the total number of composites per year, $NDVI_i$ is the i th composite, and T_i is the proportion of the year covered by the i th composite: usually 15 days). Annual precipitation data for each study site were obtained either from the ORNL DAAC site or from the Earthinfo database.

We fit straight-line regression models for the relationship between field estimates of ANPP and annual precipitation (PPT) and between NDVI-I and PPT (temporal models) for each site. The slopes of the regression models are estimates of PUE_t for each site. Because we used ANPP and NDVI-I data, the slopes of the models derived from each dataset had different units. To allow for comparison between the field and remotely sensed data, we normalized the slopes of the regression models fitted for each site by dividing them by the slope of the respective spatial models.

For each dataset, we calculated the spatial models from the average ANPP and MAP for each site. The

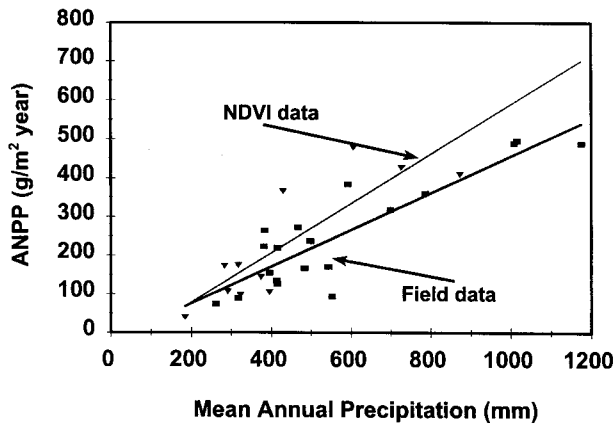


Figure 1. Relationship between aboveground net primary production (ANPP) and mean annual precipitation (MAP) for the field (squares) and normalized difference vegetation index (NDVI, triangles) datasets. Each point corresponds to the average ANPP and MAP for a particular site. The lines correspond to the regression models fit to each dataset (spatial models). $ANPP = -49.4 + 0.64 \times MAP$ ($F = 34$, $r^2 = 0.73$, $n = 11$, $P < 0.001$) for the field-based dataset, and $ANPP = -19.7 + 0.48 \times MAP$ ($F = 59$, $r^2 = 0.78$, $n = 19$, $P < 0.001$) for the NDVI dataset.

slope of the linear model fit to the data was our estimate of PUE_s . For comparison purposes, site-average NDVI-I data were converted into ANPP values by using $ANPP = 3803 \cdot NDVI-I^{1.9028}$ (Paruelo and others 1997). Both datasets are available on the Internet at <http://www.IFEVA.edu.AR/ANPP>.

RESULTS AND DISCUSSION

The spatial models based on field estimates and satellite data were quite similar (Figure 1):

$$ANPP = -49.4 + 0.64 \times MAP$$

$F = 34$, $r^2 = 0.73$, $n = 11$, $P < 0.001$ (ANPP dataset)

$$ANPP = -19.7 + 0.48 \times MAP$$

$F = 59$, $r^2 = 0.78$, $n = 19$, $P < 0.001$ (NDVI dataset)

Both the spatial slopes (PUE_s) and the proportion of the variance accounted for by MAP were within the range found by other authors (Rosenzweig 1968; Lauenroth 1979; Rutherford 1980; Le Houerou and others 1988; Sala and others 1988; McNaughton and others 1993).

The temporal models for the individual sites showed a broad range of PUE_t (Figure 2). For the dataset based on field data, the highest PUE_t was 0.77, that is, 20% higher than the PUE_s (0.64) (slope of the spatial model). For the NDVI based dataset, the highest PUE_t was 81% higher than the respec-

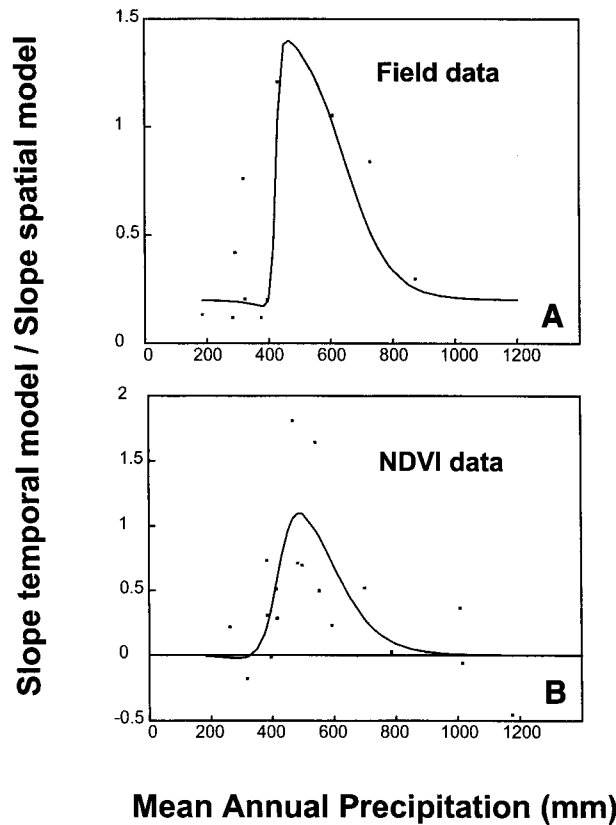


Figure 2. A Slope of the regression between ANPP and annual precipitation fitted for each site (temporal model) divided by the slope of the spatial model (0.64), along a mean annual precipitation gradient. The solid line corresponds to a double logistic model fitted to the data: $y = 0.2 + 1.307/(1 + e^{-0.1304x(MAP - 424)}) - 1.307/(1 + e^{-0.0132x(MAP - 644)})$ ($r^2 = 0.76$, $F = 28.54$, $P < 0.0005$). B Slope of the regression between the normalized difference vegetation index (NDVI-I) and the annual precipitation fitted for each site divided by the slope of the spatial model (0.48), along a mean annual precipitation gradient. The solid line corresponds to a double logistic model fitted to the data: $y = 1.585/(1 + e^{(-0.0366x(MAP - 419))}) - 1.585/(1 + e^{(-0.0130x(MAP - 580)})}$ ($r^2 = 0.50$, $F = 16.7$, $P = 0.0008$).

tive PUE_t (0.48). A double logistic model accounted for 76% ($P = 0.0005$) (Figure 2A) and 50% ($P = 0.0008$) (Figure 2B) of the variance in the ratio between the temporal slope and the spatial slope of the ANPP and the NDVI datasets, respectively (see the Figure 2 legend). The pattern derived from the NDVI dataset was weaker than the one derived from field data. The use of just 4 years of NDVI data to fit the temporal model may account for the scatter in these data. Sites with a PUE_t greater than that of the spatial model had a MAP between 420 and 600 mm (Figure 2). The double logistic models predicted a maximum slope for the temporal models for sites with a MAP of 462 mm for the ANPP dataset and of

491 mm for the NDVI-I dataset. The MAPs corresponding to the inflection points of the ascending part of the double logistic models were very similar between datasets (424 mm for field estimates of ANPP and 419 mm for the NDVI-I dataset). The second inflection points (descending part of the curve) occurred at MAPs of 644 mm and 580 mm for the ANPP and NDVI-I datasets respectively.

We interpreted the pattern of PUE_i across the MAP gradient as the result of changes in the relative magnitude of vegetational and biogeochemical constraints. At the driest extreme of the MAP gradient, the dominance of species with low relative growth rates (RGRs) likely constrains the response of ANPP to interannual changes in precipitation. There are unavoidable trade-offs between RGR and drought resistance in plants since most characteristics associated with drought resistance such as high root:shoot ratio, low specific leaf area, and low stomatal conductance necessarily constrain maximum photosynthesis and growth rates (Tilman 1988; Keddy 1992; Grime and others 1997). In a semiarid environment, the response of ANPP to extremes of water availability may require significant changes in plant cover that often involve changes not only in individual plant size but also in the number of individuals or in species composition. Additionally, the recruitment rate of new individuals is often low in semiarid regions and requires favorable conditions for a number of processes that usually take place over a relatively long period (seed production, seed dispersion, germination, and establishment) (Aguilar and Sala 1994; Lauenroth and others 1994). Vegetational constraints become even more important in arid and semiarid environments if we take into account that interannual variability in precipitation increases with decreasing annual precipitation.

At the wettest extreme of the gradient, the dominance of species with high relative growth rates combined with relatively low interannual variability in precipitation reduces the magnitude of the vegetational constraint. These species (that is, tallgrasses) can adjust total cover or LAI faster than can the dominant species at semiarid sites (that is, shortgrasses or shrubs). However, an increase in biomass or LAI may result in an increase in nutrient (or light) limitation. The increase in nitrogen-use efficiency with increased water availability (Vinton and Burke 1995) indicates a potential for N limitation (Vitousek 1982) and consequently for an increase in biogeochemical constraints.

The variability displayed by the ANPP-PPT slopes (PUE) may be partially related to the dependence of the constraints on other factors. The relative importance of vegetational constraints is associated with

species composition, and MAP is not the only control on the relative abundance of plant species. Disturbance regime (both natural or anthropogenic), seasonality of precipitation, mean annual temperature, and soil texture also affect the relative abundance of plant functional types or species (Paruelo and Lauenroth 1996; Epstein and others 1997; Sala and others 1997). Biogeochemical constraints are related to the soil organic carbon and nitrogen pools. In addition to MAP, temperature and soil texture have a strong influence on the size of these pools (Burke and others 1989, 1997).

The description of the variability of ANPP sensitivity to water availability across a spatial gradient of precipitation represents an important improvement in our understanding of ecosystem functioning. It also has consequences for how we interpret the dynamics of the relationship between temperate grassland structure and function. Our results suggest differential time lags in structural and functional adjustments of the ecosystem across a water-availability gradient. Reaching an ANPP in equilibrium with a new level of water availability requires a modification in the ecosystem structure. How long will this adjustment take? The lag may differ, depending on whether the structural constraints are vegetational or biogeochemical. For example, an ecosystem located in the middle portion of the gradient that experiences an increase in MAP will have a soil organic carbon pool out of equilibrium with this climatic condition. In this case, the magnitude of the biogeochemical constraint will be greater than for an ecosystem in equilibrium with the MAP. The adjustment will involve an increase in soil organic matter, which may take a long time (Schlesinger and others 1990; Burke and others 1995). An ecosystem located in the drier portion of the gradient that experiences an increase in MAP will have a plant cover and species composition (depending on the magnitude of the change in MAP) out of equilibrium with the new environment. The time lag required for adjustment may be longer than if there had been a reduction in MAP. This suggests the potential for hysteresis in ecosystem adjustment to new environmental conditions.

The pattern of ANPP sensitivity to PPT (PUE) may also have important applications. A model describing the changes in PUE across the MAP gradient may improve the estimates of carrying capacity over extensive rangeland areas such as parts of western North America, southern South America, or northeastern Asia. A reliable description of PUE may help, for example, in analyzing the relationship between historical forage availability and grazing pressure of domestic herbivores on these rangelands. Based on

the knowledge of a variable PUE, we may also improve predictions of grassland ecosystem responses to climatic changes. The use of a spatial model allows us to predict only steady-state conditions. A proper representation of transient scenarios is crucial to understand the response of ecosystems to global change in a time frame of decades (Seastedt and Knapp 1993). An understanding of the time lags generated by vegetational and biogeochemical constraints will help us to represent these transitions better.

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