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Inter-annual variation in primary production of a semi-arid grassland related to previous-year production

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Abstract. Mean annual precipitation accounts for a large proportion of the variation in mean above-ground net primary production (ANPP) of grasslands worldwide. However, the inter-annual variation in production in any grassland site is only loosely correlated with precipitation. The longest record of variation in production and precipitation for a site corresponds to a shortgrass steppe in Colorado, USA. A previous study of this record showed that current-year precipitation accounted for 39% of the inter-annual variation in ANPP. In this note, we show that ca. one third of the unexplained variation is related to previous-year ANPP: ANPP per mm of precipitation was higher in years preceded by wet, more productive years than in years preceded by average years; similarly, ANPP per mm of precipitation was lower in years preceded by dry, less productive years than in years preceded by average years. Since previous-year ANPP was, in turn, associated with precipitation of a year before, current-year ANPP was also explained by precipitation of two previous years. Our finding not only increases our predictive ability, but it also changes our understanding of how ANPP responds to fluctuations in precipitation. If ANPP is thought to vary according to current-year precipitation only, it will simply track annual precipitation in time. According to this new result, however, ANPP fluctuations are buffered if wet, more productive years alternate with dry, less productive years, and they are amplified if wet or dry sequences of several years take place.

Keywords: Above-ground net primary production; Climate; Drought; Precipitation.

Abbreviation: ANPP = Above-ground net primary production.

Introduction

There has been significant progress in understanding controls of primary production of grasslands at a regional scale. At this large scale, mean above-ground net primary production (ANPP) of widely different systems is strongly correlated with their mean annual precipitation (Walter 1939, cited by Rutherford 1980; Lauenroth 1979; McNaughton 1985; Sala et al. 1988). For example, in the North American grassland region, mean annual ANPP increases at a rate of 0.6 g/m^2 per mm of mean annual precipitation, and this variable accounts for 90% of the regional variation in ANPP (Sala et al. 1988; Lane et al. 1998).

Much less is known about the controls of the temporal, inter-annual variation of productivity at a given site. Lauenroth & Sala (1992) gathered a unique data set to explore the relationship between annual ANPP and precipitation across a 52-yr series in a single shortgrass steppe site. Three of their major results were that (1) there was a linear relationship between annual ANPP and precipitation of the same year, (2) the slope of the relationship was lower than the slope of the regional model, and (3) the dispersion of the data around the temporal model was larger than the dispersion of data around the regional model (precipitation explained 39% of the variation in ANPP among years, contrasting with 90% of the regional model). Addition to the model of up to four variables describing the distribution of precipitation events into size classes did not increase significantly the fraction of explained variance: a four-variable model explained only 6% more variance than the simple univariate model based on annual precipitation.

Regarding the finding that the slope of the function relating ANPP to precipitation was lower in the temporal than in the spatial model, Lauenroth & Sala (1992) suggested that this was an indicator of structural constraints to primary production: along a spatial precipitation gradient, different structural features of vegetation (ranging from canopy cover, and plant density to species composition) would be in equilibrium with climate, but each vegetation unit would not be able to track year-to-year variations in precipitation as closely as the longer process of adjusting structure to prevailing climate did. Lauenroth & Sala (1992) pointed out that an interesting feature of their data set was that after each of two years of severe drought (1954 and 1964) ANPP did not recover the following year, as their precipitation-based model would predict. They suggested that structural changes produced by drought might have hampered the ability to respond to the re-establishment of average or wet conditions.

In the present paper we present a new analysis of Lauenroth & Sala's (1992) data set. Our objective was to explore if previous-year conditions accounted for part of the unexplained variation of the relationship between current-year production and current-year rainfall. This previous-year effect has been proposed in the past for perennial grasslands and shrublands (Webb et al. 1978; Smoliak 1986; Rundel & Gibson 1996; Jobbágy & Sala 2000). However, in some cases it has not been demonstrated, whereas in others it has accounted for only a small proportion (5%) of the inter-annual variation in primary production. Webb et al. (1978) analysed the relationship between primary production and actual evapotranspiration of two shortgrass-prairie sites and a cold desert (two, six, and two years of data respectively). Since the variation in annual production was better explained by the summed evapotranspiration of the current and the previous year than by any of them individually, the authors concluded that there was a carry-over of production potential from the previous year. However, their data set combined the production-evapotranspiration relationship of three sites that differed in mean annual evapotranspiration by more than 200 mm. This, together with the fact that there were only two years of data for two of the sites, suggests that they assessed the spatial rather than the temporal, production-precipitation relationship, and that the combination of two years of evapotranspiration was simply a better assessment of the site mean. Smoliak (1986) analysed a 50-yr record of forage production in a mixed-grass prairie. Current-year precipitation explained 54% of the variation in ANPP, and precipitation from the previous September plus precipitation during the April-July period slightly increased the proportion explained to 59%. Rundel & Gibson (1996) analysed a 9-yr record in the Rock Valley desert and found no correlation between production and rainfall for either the current or the previous calendar year. However, they only found a significant correlation with rainfall of the ‘hydrologic year’, which integrated the period from October through September. Finally, using a 15-yr data set for a Patagonian steppe, Jobbágy & Sala (2000) found that current-year precipitation accounted for approximately the same proportion of the inter-annual variation in shrub production as precipitation of the current plus the previous year. In contrast, grass production was not accounted for by precipitation during any period.

Methods

We analysed the data published by Lauenroth & Sala (1992). They gathered a 52-yr record of ANPP for the Central Plains Experimental Range (CPER) in North Central Colorado, USA (40° 49' N, 104° 46' W). ANPP was estimated from biomass sampled at the end of the growing season by harvesting live and standing dead biomass from 0.19-m^2 quadrats. The site has a mean annual precipitation of 321 mm and a mean annual temperature of 8.6 °C. Seasonal patterns of precipitation and temperature are correlated, with maxima during the summer and minima in winter. The grassland is dominated by *Bouteloua gracilis*, which accounts for approximately 90% of basal cover and plant production.

The data set consisted of an almost continuous record of annual primary production from 1939 to 1990. We considered up to four variables as candidates to explain the residuals of the temporal relationship between current-year ANPP and precipitation: ANPP and precipitation of the first and second previous year. Since the series was continuous for precipitation data, but it had two gaps for production, inclusion of ANPP of one or two previous years reduced the number of data points available for the analysis. Thus, instead of a complete stepwise multiple regression including all possible independent variables, with the subsequent confounding association between variable addition and data loss, we performed three stepwise regressions. First, we added previous year production with the subsequent loss of two data points: 1941 and 1981, which lacked data from their previous year ($N = 47$). Second, we explored the association with precipitation of the first and second previous year ($N = 49$). Finally, we considered all four variables, including the production of the second previous year, with the subsequent loss of two more data points: 1942, and 1982 ($N = 45$).

Results

As Fig. 1 shows, the dispersion of the data around the model fitted by Lauenroth & Sala (1992) appears to be associated with the ANPP of the previous year. In general, ANPP in years preceded by low production years (open squares) was overestimated by the model, whereas ANPP in years preceded by above-average production (closed squares) was underestimated by the model. The residuals of the model are then clearly related to previous-year production. Addition of previous-year ANPP raised the proportion of explained variance from 0.39 to 0.58 (Table 1). This indicates that ANPP of a given year is positively related not only with current precipitation, but also with previous-year production.

Precipitation of the first previous year significantly increased the proportion of explained variance of the original model, but it was slightly less important than previous-year production ($r^2 = 0.54$). However, a model including current year, first previous year, and second previous year precipitation essentially explained the same proportion of variance as the model based on current-year precipitation and previous-year ANPP

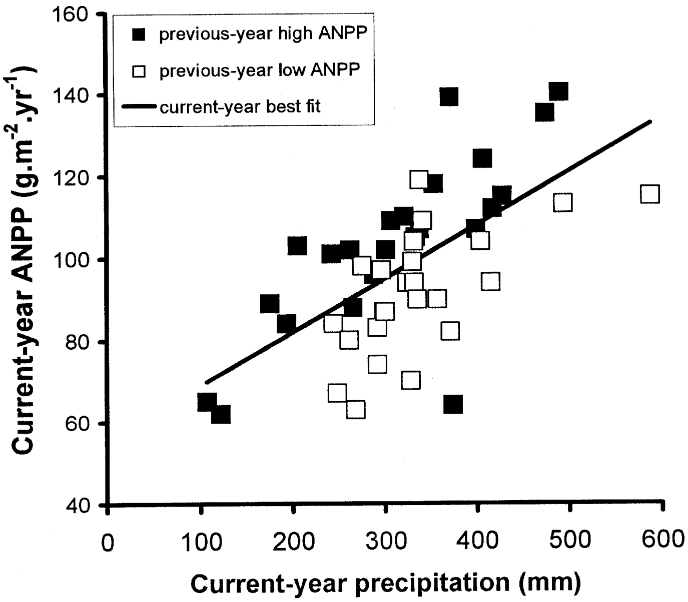

Fig. 1. Relationship between current-year ANPP and current-year precipitation at the Central Plains Experimental Range site. The best-fit line corresponds to Lauenroth & Sala's (1992) model (see Table 1). Closed squares indicate years preceded by a year with ANPP above the mean, usually a wetter than average year. Open squares indicate years preceded by a year with ANPP below the mean, usually a drier than average year.

(Table 1). When all variables were available to be entered into the model, including ANPP of two years before the current year, the best model was, again, the one based on current-year precipitation and previous-year production (Table 1). Finally, current year precipitation and previous year precipitation were not associated ($r^2 = 0.01$).

In addition to better explaining the ANPP variations of Lauenroth & Sala's (1992) data set, the previous-year production model makes different predictions about the response of ANPP to precipitation fluctuations from year to year. Not surprisingly, the responses of ANPP predicted by Lauenroth & Sala's (1992) model simply track precipitation (Fig. 2). In contrast, our model based on previous-year production predicts different responses according to precipitation history. If precipitation fluctuates alternatively above and below the mean each year, our model predicts a more buffered behaviour of ANPP than Lauenroth & Sala's model: a dry year preceded by a wet year in such alternated sequence will suffer less reduction in ANPP, and a wet year preceded by a dry one will experience a smaller increase in ANPP (Fig. 2). However, if there is a sequence of either dry or wet years, the new model amplifies the effect of the change in precipitation compared to the original model: wet years preceded by wet years will have higher ANPP per unit precipitation and ANPP will then be higher than predicted by the original model; conversely, dry years preceded by dry years will have lower ANPP per unit precipitation and ANPP will then be lower than predicted by the original model (Fig. 2). In nature, as shown by Lauenroth & Sala (1992), precipitation is only rarely consistently above or below the mean for more than two or three years, so both buffering and amplifying effects should be seen depending on the particular sequence.

Table 1. Alternative models that account for the interannual variation in current-year above-ground net primary production of the shortgrass prairie at the CPER site. The first row corresponds to the model obtained by Lauenroth & Sala (1992), and it is included here as a reference. The other rows correspond to three stepwise regressions with different sets of variables. The models only include those variables that had a significant effect when added to the model. ANPP indicates above-ground net primary production (g. m^{-2}. yr^{-1}); *pp* indicates annual precipitation (mm); (t), ($t-1$), and ($t-2$) indicate current year, first-previous year, and second- previous year respectively.

Possible variables	**Model**	r^2	***F* (df)**	***P***
$pp_{(t)}$ (Lauenroth & Sala 1992)	$\mathrm{ANPP}_{(t)} = 55.8 + 0.13\, pp_{(t)}$	0.39	31.0 (1, 48)	0.0001
$pp_{(t)}, pp_{(t-1)}, pp_{(t-2)}, \mathrm{ANPP}_{(t-1)}$	$\mathrm{ANPP}_{(t)} = 14.8 + 0.13\, pp_{(t)} + 0.41\, \mathrm{ANPP}_{(t-1)}$	0.58	30.4 (2, 44)	0.0001
$pp_{(t)}, pp_{(t-1)}, pp_{(t-2)}$	$\mathrm{ANPP}_{(t)} = 9.98 + 0.13\, pp_{(t)} + 0.08\, pp_{(t-1)} + 0.05\, pp_{(t-2)}$	0.60	22.1 (3, 45)	0.0001
$pp_{(t)}, pp_{(t-1)}, pp_{(t-2)}, \mathrm{ANPP}_{(t-1)}, \mathrm{ANPP}_{(t-2)}$	$\mathrm{ANPP}_{(t)} = 16.7 + 0.13\, pp_{(t)} + 0.40\, \mathrm{ANPP}_{(t-1)}$	0.57	27.3 (2, 42)	0.0001

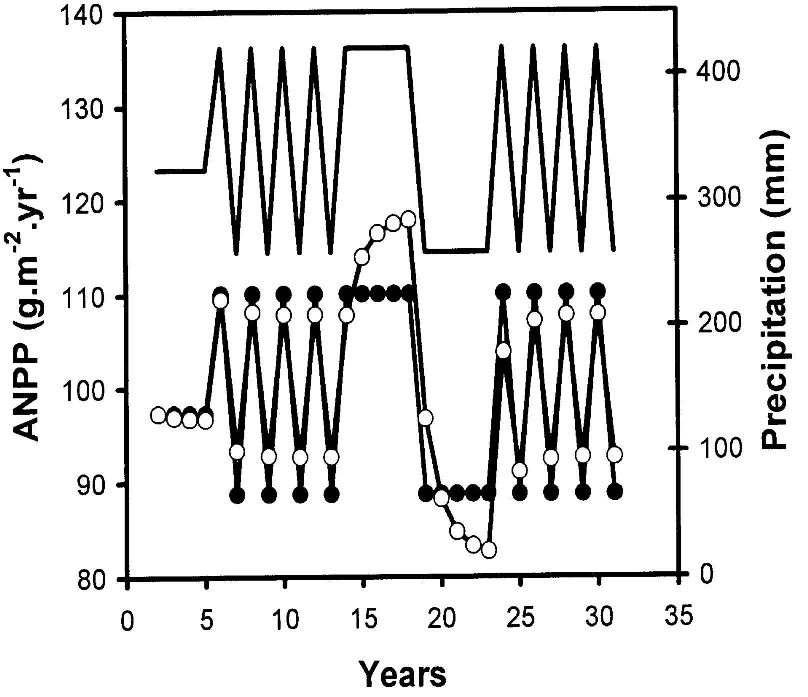

Fig. 2. Simulations of precipitation (solid line without symbols) and ANPP fluctuations predicted by Lauenroth & Sala's model (closed circles) and our model (open circles). From left to right, a sequence of average years, alternating wet and dry years (30% above and below the mean), a wet sequence, a dry sequence, and alternating wet and dry years.

Discussion

Our re-analysis of Lauenroth & Sala's (1992) data set produce the following changes in our understanding: (1) it provides a better model of the temporal variation of ANPP for the grassland site with the longest record of annual production of the world, (2) it suggests, but does not prove, a causal relationship between previous-year production and the response of this grassland to annual variations in precipitation, and (3) it implies that previous-year effects both buffer and amplify the response of ANPP to changes in precipitation depending on the sequence of dry or wet years.

There are indications that the difference between spatial and temporal models of grassland production is a general phenomenon (Paruelo et al. 1998), and that lag effects may play an important role (Webb et al. 1978; Smoliak 1986; Rundel & Gibson 1996; Jobbágy & Sala 2000). In annual grasslands, lag-effects are commonly found because of the close, causal relationship between seed production and community dynamics (Hobbs & Mooney 1995). Unfortunately, it is difficult to explore the generality of our findings for perennial grasslands because a long series of data is required to detect such a complex relationship between productivity and precipitation. Smoliak (1986) analysed a 50-yr series of forage production and meteorological data for a mixed grass prairie in southeastern Alberta. Current-year production was related to annual precipitation (r^2 = 0.54) and addition of four variables describing seasonal patterns of temperature and precipitation only explained an additional 9% of variation (r^2 = 0.63). We analyzed the effect of including either previous-year production or previous-year precipitation to the current-year precipitation model for this mixed-grass prairie (losing three data points because of gaps in the series). Inclusion of either previous-year variable was significant (P < 0.001) and explained 12% of variation (combined r^2 = 0.66). The effect was in the same direction as in the shortgrass steppe: production per unit of current-year precipitation was positively related with previous-year production or precipitation. A re-analysis of the 22-yr data set from the more humid tallgrass prairie (Briggs & Knapp 1995; Knapp et al. 1998) showed that primary production was independent of previous-year production or precipitation for different topographic positions and burning regimes. We do not know whether this lack of association reflects intrinsic ecosystem differences or simply results from the shorter time encompassed by the data set.

We have simply revealed a pattern that may result from a variety of potential mechanisms. An intuitive first explanation would propose that carry-over of water from one year to the next could be responsible for the pattern that we observed. However, this is unlikely in the system under study. Annual potential evapotranspiration exceeds precipitation by a factor of 4, precipitation is concentrated during the growing season, and the residence time of water in the soil is very short (Sala et al. 1992). The only time in a previous year in which precipitation is not at least matched by evaporation is November-December, a period with an average precipitation of no more than 10 mm, less than 3% of annual precipitation. Furthermore, most of the inter-annual variability in precipitation is accounted for by the occurrence of summer storms (Sala et al. 1992).

Thus, we can speculate on general, structural or functional mechanisms. Structural attributes, such as seed, plant, and tiller density, leaf area, or root biomass may be reduced after a year with low precipitation and production and, thus, may either constrain the ability of ecosystems to respond to a subsequent increase in water availability or aggravate the response to another year with low precipitation. In turn, high precipitation may increase the same attributes and can either ameliorate the response to a subsequent year with low precipitation or potentiate the response to another year with high precipitation through an increase in resource exploration (Nobel & Franco 1986; Harrington 1991; Busso & Richards 1993; Qi & Redmann 1993; Lauenroth et al. 1994; Fox 1995). Ecosystem functional attributes may also account for these responses. Organic matter decomposition and nutrient mineralization are limited by water availability (Schimel & Parton 1986). Thus, years with low precipitation will result in low rates of nutrient release into the soil solution, whereas the opposite effect will be observed in years with above-average precipitation.

Regardless of the mechanisms involved, the evidence that primary production is positively related with previous-year production and precipitation has consequences on the way these semi-arid grasslands may be understood and managed. With a few months of anticipation to many decisions related to livestock or wildlife management, managers may count now with a better assessment of the potential response of forage production to current-year precipitation. As more data sets are gathered in long-term studies, and remote sensing records become longer, we will be able to test the generality of this pattern.

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