

Do Grasslands Have a Memory: Modeling Phytomass Production of a Semiarid South African Grassland

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ABSTRACT

We analyzed data sets on phytomass production, basal cover, and monthly precipitation of a semiarid grassland in South Africa for good, medium, and poor rangeland condition (a) to investigate whether phytomass production per unit of basal cover differed among rangeland conditions, (b) to quantify the time scales of a carryover effect from production in previous months, and (c) to construct predictive models for monthly phytomass. Finally, we applied the best models to a 73-year data set of monthly precipitation data to study the long-term variability of grassland production. Our results showed that mean phytomass production per unit of basal cover did not vary significantly among the rangeland conditions—that is, vegetated patches in degraded grassland have approximately the same production as vegetated patches in grassland in good condition. Consequently, the stark decline in production with increasing degradation is a first-order effect of reduced basal area. Current-year precipitation accounted for 64%, 62%, and 36% of the interannual variation in phytomass production for good, me-

dium, and poor condition, respectively. We found that 61%, 68%, and 33%, respectively, of the unexplained variation is related to a memory index that combines mean monthly temperature and a memory of past precipitations. We found a carryover effect in production from the previous 4 years for grassland in good condition and from the previous 1 or 3S month for grassland in medium and poor condition. The memory effect amplified the response of production to changes in precipitation due to alternation of prolonged periods of dry or wet years/months at the time scale of the memory. The interannual variability in phytomass production per unit basal cover (coefficient of variation [CV] = 0.42–0.50 for our 73-year prediction, CV = 0.57–0.71 for the 19-year data) was greater than the corresponding temporal variability in seasonal rainfall (CV = 0.29).

Key words: basal cover; climate; carryover effect; desertification; drought; grassland conditions; long-term data set.

INTRODUCTION

Primary production is a fundamental aspect of ecosystem functioning that sets the energy available for

other trophic levels (McNaughton and others 1989). For example, both herbivore consumption and biomass have a strong correlation with primary production (McNaughton and others 1989; Oesterheld and others 1992). Additionally, primary production is a strong regulator of the flow of elements within the biosphere (Mooney 1991). It is particularly important for the management of semiarid

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ecosystems where rangelands are the main source of forage for livestock to understand the factors that control phytomass production.

Significant progress has been made in understanding the controls of rangeland primary production. Mean aboveground net primary production (ANPP) of widely different arid and semiarid systems is strongly correlated with mean annual precipitation (for example, see Sneva and Hyder 1962; Noy-Meir 1973; Lauenroth 1979; McNaughton 1985; Le Houérou and others 1988; Sala and others 1988a; Paruelo and others 1999). Additional factors that control ANPP include temperature (Christie 1981; Epstein and others 1997), evapotranspiration (Snyman 1998), soil water-holding capacity (Sala and others 1988a; Epstein and others 1997; Snyman 2000), nutrient availability (Chapin 1991; Du Preez and Snyman 1993), species composition (Milchunas and Lauenroth 1993), grazing (O'Connor and Roux 1995; Oesterheld and McNaughton 2000), and fire (Oesterheld and McNaughton 2000). Most of these analyses described the controls of the spatial variability of ANPP. In general, the relationships of ANPP with environmental variables were derived from long-term averages for many sites distributed across environmental gradients ("spatial models"). Much less is known about the controls of the temporal, interannual variation of productivity at a given site ("temporal models") (Paruelo and others 1999).

The degradation of semiarid grasslands follows a general pattern where grazing alters the species composition from long-lived perennials to annuals or short-lived perennials (O'Connor and others 2001). Changes in species composition are correlated with a decline in basal cover. Because of lower cover, larger runoff, and soil and nutrient loss, overall productivity declines with increasing degradation, a pattern that is widely found in grasslands (Snyman and Fouché 1991, 1993; Du Preez and Snyman 1993; Milchunas and Lauenroth 1993; O'Connor and Roux 1995; O'Connor and Bredenkamp 1997; Snyman 1998; McNaughton and others 1989; O'Connor and others 2001) and other semiarid vegetation types (Danckwerts and Nel 1989; O'Connor 1994; Hoffman and Ashwell 2001). This decline in production may be primarily caused by basal cover decline, and production per unit of basal cover may not change with degradation. If this null model is not met, an overproportional decline in production might be caused by factors such as edge effects (that is, in more fragmented grasslands, more tufts are exposed to marginal conditions at the edges of larger patches of bare ground where micro conditions are less favorable) and changes in species

composition. The interesting question therefore is whether or not a reduction in production is proportional to basal cover reduction (that is, the pure effect of basal cover loss), or if additional "fragmentation" effects give rise to an overproportional loss in production. The analogous question of the relative effects of habitat loss and fragmentation for animal populations has also been a controversial topic of discussion (for example, see Kareiva and Wennergren 1995; Fahrig 1997, 2002; Flather and Bevers 2002).

Memory and carryover effects might play an important role in the functioning of semiarid rangelands by buffering fluctuations in phytomass production if wet, more productive years alternate with dry, less productive years and by amplifying fluctuations if wet or dry sequences of several years take place (Goward and Prince 1995; Oesterheld and others 2001). In the past, such carryover effects have been demonstrated for a few perennial grasslands and shrublands (for example, see Paulsen and Ares 1962; Hanson and others 1982; Smoliak 1986; Gibbens and Beck 1988; Snyman and Fouché 1991; Jobbágy and Sala 2000; O'Connor and others 2001; Oesterheld and others 2001). Determining the time scale of the memory of rangelands is important not only for increasing our predictive ability, but also for enhancing our understanding of how phytomass production (or changes in basal cover) responds to fluctuations in precipitation. Earlier attempts to investigate carryover and memory effects considered mostly production from previous years as additional independent variables in a linear regression model (for example, see Oesterheld and others 2001; O'Connor and others 2001; but also see Gibbens and Beck 1988; Goward and Prince 1995; Anderson and Inouye 2001). However, there is no reason to restrict the memory to an annual time scale. In short-lived vegetation, it is more probable that a carryover effect acts on a monthly time scale, whereas in perennial vegetation it may act on a yearly, or even longer, time scale. Also, using production for the previous year as an independent variable is impractical for predictive purposes because data on production are usually less available than precipitation data. We thus propose to substitute production history with a "memory" index based on the rainfall history of the site. Our indices are basically a weighted running mean of monthly effective precipitation where the weighting factor declines exponentially with time.

The general aim of this study was to obtain an understanding of factors determining phytomass production in the semiarid grasslands. We used two data sets on phytomass production from South Af-

rica, one comprising monthly production from the 1995–96 growing season to the 1998–99 growing season and a second one comprising total seasonal production from the 1977–78 to the 1995–96 growing season. Both data sets included data for three rangeland conditions (good, medium, and poor), monthly rainfall, and annual basal cover. More specifically, (a) we investigated whether phytomass production per unit of basal cover differed among rangeland conditions, or if “fragmentation effects” or changes in species composition introduced an over proportional decline in production relative to basal cover loss; (b) we built indices based on monthly rainfall and mean monthly temperature to describe the memory of the grassland; and (c) we constructed predictive models for monthly phytomass production per unit of basal cover using these indices. Finally, we applied the best models to a 73-year data set of monthly precipitation data to study the long-term variability of grassland production.

METHODS

Site Description

The short-term monthly production data set was collected in Bloemfontein (28°50'S, 26°15'E; 1,350 m a.s.l.); the long-term seasonal production data set was collected on the Sydenham farm of the University of the Free State 15 km southeast of Bloemfontein, South Africa (29°06'S, 26°67'E; 1,350 m a.s.l.). The long-term precipitation data set was obtained from Glen (28°57'S, 25°20'E; 1,304 m a.s.l.), approximately 30 km northeast of Bloemfontein. For the 1975–96 period, the monthly rainfall between Glen and the Sydenham farm was highly correlated ($r = 0.91$, $P < 0.001$). The study sites are situated in the semiarid summer rainfall region (annual average, 560 mm) of South Africa within a *Themeda triandra*–*Cymbopogon plurinodis* grassland ecosystem (Acocks 1953) (plant nomenclature follows Arnold and De Wet 1993). The soil is a fine sandy loam of the Valsrivier form (Goedemoed family—1121) (Soil Classification Working Group 1991) and is representative of the semiarid grassland. Rain falls almost exclusively during summer (October to April), with an average of 78 days of precipitation per year. Mean maximum monthly temperature ranges from 17°C in July to 33°C in January, but extremes of 41°C in January and 28°C in July have been recorded. On average, frost occurs 119 days per year (Schulze 1979).

Data Collection

In the semiarid grassland ecosystems of South Africa, species composition and basal cover are used to characterize rangeland condition (O'Connor and others 2001). Prior to the experiments, three compositional states reflecting good, medium, and poor rangeland condition were created. These three states closely reflect the distinct composition and basal cover that could arise as a result of different grazing histories of this grassland (Mostert 1958; Van den Berg and others 1975; O'Connor and others 2001). Conditions of the long-term experiment were maintained from 1977–78 to 1995–96; those of the short-term experiment were maintained from 1995–96 to 1998–99. The good-condition grassland was dominated by the perennial bunchgrass *Themeda triandra* and had the highest basal cover; the medium condition grassland was dominated by perennial bunchgrasses of *Eragrostis* species; the poor condition grassland was dominated by the stoloniferous perennial *Tragus koelerioides* and the short-lived bunchgrass *Aristida congesta* and had the lowest basal cover. For more details on the mean percentage contribution to cover of the total of 14 species present at the study sites, see O'Connor and others (2001). All species were indigenous, perennial C₄ species.

The experimental layout was a fully randomized design consisting of three treatments (good, medium, poor condition) and three replicates. The experiments were established on an area that was initially in good condition and was not grazed during the experiment. The good-condition treatment was left as found. The medium- and poor-condition treatments were created and maintained by selectively pulling out individual tufts of species that were not characteristic of that condition, keeping soil disturbance to a minimum. Few plants had to be removed after the first 3 years. Each of the nine experimental units was 2 × 15 m, with average slopes of 4% and 3.5% for the long-term and short-term experiment, respectively. Soil was uniform across plots. Species composition was determined by recording the plant nearest to 500 points in each unit during April using a bridge-point apparatus (adapted from Levy and Madden 1933). Basal cover was determined as the percentage strikes of these points.

In the short-term experiment, monthly accumulated aboveground phytomass production was determined for each experimental unit by clipping a 10-m² plot (that had not been harvested before) to a height of 30 mm at the end of each month. In the long-term experiment, the seasonal aboveground

Table 1. Indices Used for Predicting Monthly Phytomass Production per Unit of Basal Cover

Symbol	Formula	Meaning
$T(m)$		Temperature index for month m
$R(m)$		Precipitation for month m
$RT(m)$	$= R(m) T(m)$	Effective precipitation, the precipitation weighted by the temperature index
$VigR(m, c)$	$VigR(m) = VigR(m-1)c + R(m-1)(1-c)$	Precipitation memory index
$VigRT(m, c)$	$VigRT(m) = VigRT(m-1)c + RT(m-1)(1-c)$	Effective precipitation memory index
$SumR(m)$	$= \sum_{i=September}^m R(i)$	Accumulated precipitation from September to month m
$SumRT(m)$	$= \sum_{i=September}^m R(i)T(i)$	Accumulated effective precipitation from September to month m
$SumVR(m, c)$	$= \sum_{i=September}^m R(i)VigR(i, c)$	Accumulated precipitation to month m , weighted by the precipitation memory index $VigR$
$SumVRT(m, c)$	$= \sum_{i=September}^m RT(i)VigRT(i, c)$	Accumulated effective precipitation to month m , weighted by the effective precipitation memory index $VigRT$

phytomass production of each experimental unit was harvested to a height of 30 mm, the effective stubble height, at the end of the growing season after the first frost. End-of-season standing crop may underestimate ANPP because of tissue senescence (Sala and others 1988b).

STATISTICAL ANALYSES

Differences between Compositional States

For analyses of the short-term experiment, we used the data on monthly phytomass production per unit of basal cover $h(s, y, m)$ at compositional state s , year y , and month m , and the accumulated data from September up to month m :

$$p(s, y, m) = \sum_{i=September}^m h(s, y, i) \quad (1)$$

For analyses of the long-term data set, we used the data on total seasonal phytomass production per unit of basal cover, $p(s, y, April)$. Note that the growing season starts in September and ends in April. Finally, we calculated $P(s, y, April)$, the total seasonal phytomass production per hectare as:

$$P(s, y, April) = p(s, y, April) b(s, y) \quad (2)$$

where $b(s, y)$ is the corresponding basal cover at state s and year y . To investigate whether phytomass production per unit of basal cover differed among compositional states, we compared the means of $p(s, y, m)$ (short-term data) and the means of $p(s, y, April)$ (long-term data) among compositional states. To investigate whether phytomass production of grasslands in different compositional

states responds differently to rainfall, we calculated for the long-term data set the slopes of the linear relations between total phytomass production per unit of basal cover and precipitation during the growing season (total rainfall from September to April) and tested with a t -test for significant differences among the slopes.

Indices for Predicting Phytomass Production

To develop predictive models for long-term monthly phytomass production we hypothesized indices that summarize the effects of monthly rainfall, mean monthly soil temperature, and "memory" of past rainfall events (Table 1). To obtain the best model, we built several regression models with these indices and the data on phytomass production per unit of basal cover. To relate our approach to previous analyses (O'Connor and others 2001), we also constructed models that included production of the previous year as an additional independent variable.

In the first step of our analysis, we included precipitation of month m , $R(m)$, or accumulated precipitation from September (the beginning of the growing season) up to month m , $SumR(m)$. In the next step, we introduced a temperature index, $T(m)$, scaled to values between 0 and 1, which is based on monthly average soil temperature taken at 14:00 at 50-mm depth, averaged over the four seasons from 1995–96 to 1998–99—that is, each month is assigned a set value that is related to its average relative temperature (Snyman 2000). By multiplying the temperature index $T(m)$ and precipitation $R(m)$, we obtained an index of effective precipitation, because both low temperature and

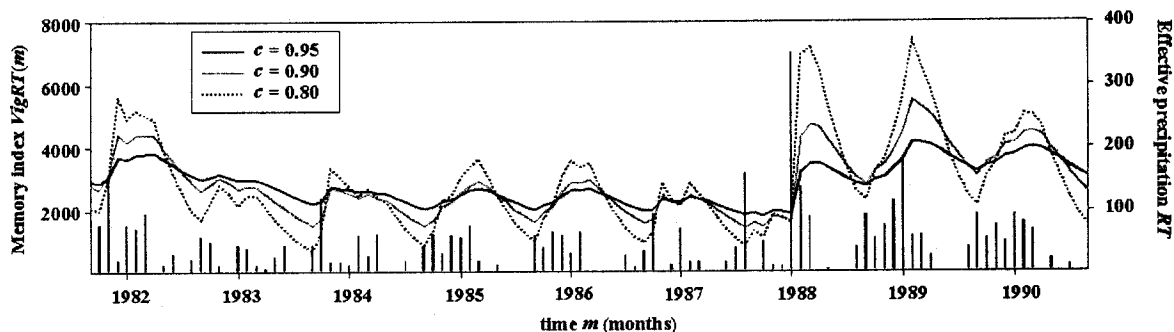


Figure 1. Example of effective precipitation memory indices $VigRT$ between 1982 and 1990, plotted together with monthly precipitation. Dashed line, $c = 0.8$; solid gray lines $c = 0.9$; solid black line, $c = 0.95$.

precipitation constrain phytomass production (for example, high rainfall during the cold season does not stimulate much phytomass production because C_4 grasses have high temperature optima for photosynthesis) (Ehleringer and Bjorkman 1977). For predictions of total phytomass production in the long-term experiment, we used the accumulated seasonal rainfall during the growing season (from September to April), $SumR(m = April)$, or the analogous index with effective rainfall $SumRT(m = April)$ (Table 1).

In the final step, we introduced a precipitation memory index $VigR(m, c)$ for month m with parameter c that describes the dependence on past precipitation. We used this memory index, analogously to the temperature index, as a weighting factor for monthly precipitation $R(m)$ and hypothesized that the accumulated weighted seasonal rainfall $Sum VR(m = April, c)$ would explain seasonal phytomass production better than accumulated seasonal rainfall $SumR(m = April)$.

We defined the precipitation memory index $VigR(m, c)$ iteratively as:

$$VigR(m, c) = c VigR(m - 1, c) + (1 - c) R(m - 1) \quad (3)$$

where c is a parameter that ranges between 0 and 1. $VigR$ is an iterative index because the value from last month, $VigR(m - 1, c)$, is used to calculate the index for the present month m . Our precipitation memory index weights precipitation of the last month with coefficient $(1 - c)$ and the index of the last month with coefficient c (Eq. [3]). We will thereafter refer to c as the memory coefficient because it determines the duration of the memory in $VigR$. This can be seen by iterating Eq. (3). With initial value $VigR_0$ at month $m = 0$, we obtained for the 1st month $VigR(1, c) = c VigR_0 + (1 - c) R(0)$;

after iterating m times, the precipitation memory index yields:

$$VigR(m, c) = VigR_0 c^m + (1 - c) [c^{m-1} R(0) + c^{m-2} R(1) + c^{m-3} R(2) + \dots + c^0 R(m-1)] \quad (4)$$

Equation (4) shows that the initial condition $VigR_0$ contributes with coefficient c^m to the current memory index, and that precipitation at month $m = 0$ contributes with coefficient $(1 - c) c^{m-1}$. Thus, the memory fades away with time in an exponentially declining manner (Figure 1). For small values of c , the memory is short. In the extreme case of $c = 0$, $VigR(m, c)$ become equal to $R(m-1)$ (Eq. [3]). On the other hand, for larger values of c , the memory persists longer (Figure 1), and in the extreme case of $c = 1$ the memory index is constant (Eq. [3]), which corresponds to an infinite memory where the contribution of the last month is infinitesimally small (that is, no memory). We obtained an effective precipitation memory index $VigRT$ (Table 1) analogously to Eq. (3) by using effective monthly precipitation $R(m)T(m)$ instead of monthly precipitation $R(m)$.

Because the memory indices $VigR$ and $VigRT$ depend on the initial condition (Eq. [4]), we used monthly precipitation data for the period 1923 to 1977 to determine the initial values $VigR_0$ or $VigRT_0$. These long-term data were taken from the weather station in Glen in the vicinity of the sites where the production data were collected (see "Application of Our Model to a Long-term Precipitation Data Set"). We determined the value of the memory coefficient c indirectly through adjustment with our data—that is, we searched the value of c that maximized the R^2 value of the corresponding regression model.

Regression Models for Predicting Monthly Phytomass Production

In the first analysis, we investigated whether monthly phytomass production was directly related to monthly (effective) precipitation. This is an important prerequisite for our memory indices for predicting seasonal production (Table 1). To test our model assumption, for each compositional state we built a linear model with monthly phytomass production $h(s, y, m)$ as the dependent variable and monthly precipitation $R(m)$, or effective monthly precipitation $RT(m)$, as the independent variable ("monthly models"). In the next step, we repeated the same analysis, but with the accumulated production up to month m [that is $p(s, y, m)$, as the dependent variable and accumulated precipitation up to month m [that is $Sum R(m)$, as the independent variable ("accumulative models"). In this step, we did not introduce indices related to memory because 4 years of data were not enough to discern memory effects.

Regression Models for Predicting Long-term Phytomass Production

For each compositional state, we built three different regression models to predict $p(y)$, the long-term seasonal phytomass production per unit of basal cover at year y . The first model considers only seasonal rain $SumR$ as an independent variable, the second model also includes the production for the last year $p(y-1)$ (for example, see O'Connor and others 2001; Oesterheld and others 2001), and the independent variable of the third model is the index $SumVR$ (Table 1) that considers our memory index. The third model contains one unknown parameter, the memory index c . We applied this model for different values of c and for each compositional state we determined the value c_{best} that maximized the R^2 value. To test our hypothesis that inclusion of effective precipitation $R(m)T(m)$ instead of precipitation $R(m)$ will improve performance of our models, we repeated the three models with the analogous indices based on effective precipitation (that is, $SumRT$ instead of $SumR$, and $SumVRT$ instead of $SumVR$).

Evaluation of the Long-term Model with the Short-term Data

We evaluated the model for long-term phytomass production using the short-term data set. To this end, we determined the indices (that is, $SumVR$ or $SumVRT$) and the memory coefficients c_{best} that yielded the best fit of our long-term data. Next, we built the corresponding accumulative models with

the data from the short-term experiment and compared the regression coefficients between corresponding models. With this procedure, we tested whether or not the regression coefficients of our best models were independent of the specific time period chosen to calibrate the model.

Application of Our Model to a Long-term Precipitation Data Set

Some important aspects of ecosystem functioning in arid and semiarid areas can only be examined properly by using long-term data. These issues include the relationship between rainfall variability and primary production, and how this relationship changes among compositional states. Using a 73-year time series of monthly precipitation data from Glen in the vicinity of the sites where the production data were collected, we predicted monthly phytomass production per unit of basal cover using our best models. We were able to use the rainfall data set from Glen to extrapolate our model on phytomass production because the monthly rainfall between Glen and the Sydenham farm was highly correlated ($r = 0.91$, $P < 0.001$) for the 1975–96 period where both data sets overlap. We calculated descriptive statistics of the precipitation data set and the resulting long-term predictions for phytomass production per unit of basal cover in the three compositional states. Finally, we compared the resulting frequency distribution of the predicted total phytomass production among the compositional states.

RESULTS

Differences among the Compositional States

Mean phytomass production per unit of basal cover varied little among the compositional states but showed a tendency to decline from good to medium to poor condition (Table 2). Variations between months (short-term series) and years (long-term series) were much larger than differences between compositional states (Table 2). Consequently, for the short-term series, the t -test for equality of means yielded P values of 0.151, 0.026, and 0.37 for differences between good and medium, good and poor, and medium and poor, respectively. For the long-term series, it yielded P values of 0.074, 0.216, and 0.632 for differences between good and medium, good and poor, and medium and poor, respectively. Thus, we detected significant differences in mean phytomass production per unit of basal cover only for the short-term series between the good and poor conditions. For the long-term experiment, the linear relations between annual phyto-

Table 2. Descriptive Statistics for Phytomass Production per Unit of Basal Cover for the Different Compositional States

Condition	Mean	Std Dev	CV	Minimum	Maximum	No. Cases	Mean Basal Cover (%)
Monthly phytomass production per unit of basal cover from 1995–96 to 1998–99							
Good	30.9	30.0	0.97	-1.1	111.1	96 ^a	8.3
Medium	25.2	24.8	0.98	-11.4	96.0	96 ^a	6.4
Poor	21.9	25.6	1.17	-13.9	101.0	96 ^a	2.9
Yearly phytomass production per unit of basal cover from 1985–86 to 1995–96							
Good	147.9	83.8	0.57	41.6	347.6	57 ^b	8.6
Medium	119.7	81.2	0.68	24.9	352.3	57 ^b	6.5
Poor	127.4	89.9	0.71	4.4	350.7	57 ^b	3.1

Units for phytomass production per unit of basal cover are kg ha^{-1} per unit of basal cover.

^aEight months, 4 years, and three replicates

^bNineteen years and three replicates

mass production per unit of basal cover [$p(s, y, \text{April})$] and precipitation during the growing season [$\text{SumR}(\text{April})$] yielded slopes ($\pm \text{SE}$) of 0.39 (± 0.04), 0.37 (± 0.04), and 0.32 (± 0.06) $\text{kg ha}^{-1} \text{mm}^{-1}$ per unit basal cover for good-, medium-, and poor-condition grassland, respectively. The slopes were significantly different from zero and did not differ significantly among compositional states, indicating that the long-term response of phytomass production per unit of basal cover to precipitation did not differ significantly among compositional states. However, because of the stark differences in basal cover among compositional states (Table 2), there were significant differences among total seasonal phytomass production per hectare among compositional states (O'Connor and others 2001). This indicates that loss of basal cover was the main mechanism responsible for the decline in total phytomass production with increasing degradation.

Predicting Monthly Phytomass Production

In all cases, except for the poor-condition scenario, we found a highly significant linear relation between monthly (effective) precipitation and monthly production per unit basal cover ($P < 0.001$). For the good condition, $R^2 = 0.51$ [with $R(m)$] and $R^2 = 0.57$ [with $RT(m)$]; for the medium condition, $R^2 = 0.41$ [with $R(m)$] and $R^2 = 0.45$ [with $RT(m)$]; but for the poor condition, $R^2 = 0.09$ [with $R(m)$] and $R^2 = 0.12$ [with $RT(m)$]. Including the effective precipitation index improved the model performance in all cases.

For the accumulated data, the models improved considerably because accumulating evened out monthly noise and the marked seasonal pattern. For the good condition, $R^2 = 0.93$ [with $R(m)$] and $R^2 = 0.94$ [with $RT(m)$]; for the medium condition,

$R^2 = 0.93$ [with $R(m)$] and $R^2 = 0.92$ [with $RT(m)$]; whereas for the poor condition, $R^2 = 0.87$ [with $R(m)$] and $R^2 = 0.85$ [with $RT(m)$].

Predicting Long-term Phytomass Production

Figure 2 summarizes the results of our analyses of the long-term data set. We varied the memory coefficient c over its entire range ($0 \leq c \leq 1$) and determined the R^2 value of the linear regressions for the three compositional states and for the two cases with and without effective rainfall. Note that models without memory (that is, the indices SumR and SumRT) correspond to the case $c = 1$ (Eq. [3]). For each of these six models, we determined the value of the memory coefficient c indirectly by maximizing R^2 . Considering effective rainfall (that is, the index SumRT instead of SumR) improved the regression models in all cases considerably; for the best models, R^2 increased 13% for the good condition, 19% for the medium condition, and 13% for the poor condition (Figure 2 and Table 3). Including memory (that is, $c < 1$) improved the regression models additionally by some 9% for the good condition and 7% for the medium and poor condition (Table 3 and Figure 2). The memory of the good condition was long-lasting ($c_{\text{best}} = 0.95$) (Figure 2); after 4 years (48 months), the coefficient c^{48} of the memory dropped below 10%. In contrast, the memory of the medium condition ($c_{\text{best}} = 0.4$) (Figure 2) comprised only one season, after 3 months the coefficient c^3 of the memory dropped below 10%, and the memory of the poor condition ($c_{\text{best}} = 0.1$) (Figure 2) was even shorter; after 1 month the coefficient c^1 of the memory dropped to 10%.

Our best models explained 86%, 88%, and 57% of the variation in production for the good, medium, and poor conditions, respectively (Figure 3).

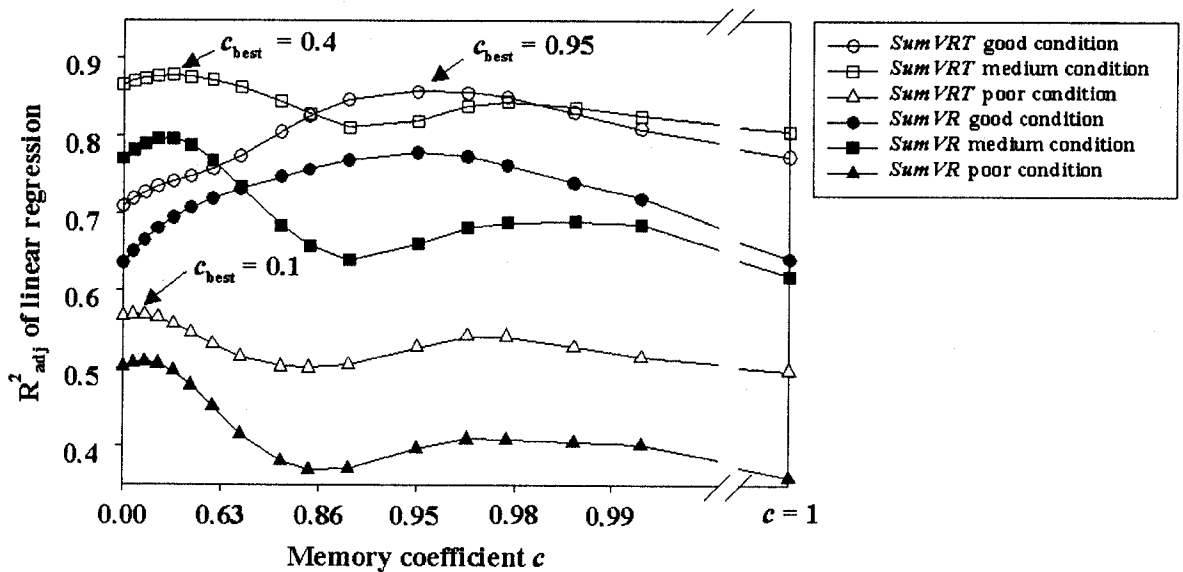


Figure 2. Analysis of the long-term data set. The x-axis shows the memory coefficient c and the y-axis the R_{adj}^2 value of the linear regressions with seasonal phytomass production per unit of basal cover as the dependent variable and the independent variable $\text{SumVRT}(m = \text{April}, c)$ (open symbols) or $\text{SumVR}(m = \text{April}, c)$ (black symbols). Circles indicate results for the good-condition state; square symbols, medium; triangles, poor. Note that the models for $c = 1$ correspond to the case without memory because the memory indices are constant in this case.

The fit for the poor condition is relatively low, mainly due to outliers in the 1994–95 season with high production (Figure 3C). After removing the outlier for 1994–95, our model explained 79% of the variation in production. The 1994–95 growing season was a dry season with only 366 mm precipitation (the average seasonal precipitation from 1973–74 to 1999–2000 was 531 mm), which followed a wet season with 843 mm precipitation.

To test the effectiveness of the memory models based on precipitation history, we built regression models with the two independent variables accumulated seasonal (effective) precipitation SumR (SumRT) and production for the last year $p(y-1)$ instead of the models with a single independent variable SumVR (or SumVRT) that considered memory. Production for the last year did not improve the regression models for the three states by more than 1% (Table 3). This result indicates that the index SumVRT effectively described the effects of precipitation, temperature, and memory on production.

Evaluation of the Long-term Model with the Short-term Data

The three models constructed with the short-term data set were in agreement with the corresponding models for the long-term data set; the variation in the coefficients b was fully within the range given by the standard error of the coefficients (Table 4),

and the intercepts a were small. Thus, we found that 4 years of data on monthly phytomass production are enough to calibrate a model for long-term phytomass production with sufficient precision for this environment. Prerequisite, however, is that the memory coefficient c_{best} is known. Figure 4 shows, exemplarily for the good condition state, the predicted values of accumulated monthly phytomass per unit basal cover and the data from the short-term and long-term experiments.

Because the regression coefficients are practically identical, we cannot detect an underestimation of ANPP (the accumulated monthly production of the short-term experiment) when measuring end-of-season standing crop (the data of the long-term experiment) that may arise because of tissue senescence (O'Connor and others 2001).

Application of Our Model to a Long-term Precipitation Data Set

The seasonal precipitation $\text{SumR}(\text{April})$ between 1922 and 1995 averaged 513.1 mm (SD = 149.7 mm, CV = 0.29), and the effective seasonal precipitation $\text{SumRT}(\text{April})$ averaged 376.5 mm (SD = 109.6 mm, CV = 0.29). As expected, the mean predicted phytomass production per unit of basal cover was highly variable among years (Figure 5). It averaged 175, 131, and 138 kg/ha per unit of basal cover for the good, medium, and poor conditions,

Table 3. Comparison of Different Regression Models for Predicting $p(y)$, the Long-term Seasonal Phytomass Production per Unit of Basal Cover

Regression Model	Regression Coefficients			
	R^2_{adj}	$a \pm SE$	$b \pm SE$	$d \pm SE$
Good				
$p(y) = a + b \text{ SumR}^a$	0.64	-44** \pm 21	0.39*** \pm 0.04	—
$p(y) = a + b \text{ SumR} + d p(y-1)$	0.76	-112** \pm 21	0.42*** \pm 0.03	0.39*** \pm 0.07
$p(y) = a + b \text{ SumVR}(c_{best} = 0.95)^a$	0.78	-37* \pm 15	0.87*** \pm 0.06	—
$p(y) = a + b \text{ SumRT}^a$	0.77	-58** \pm 16	0.58*** \pm 0.04	—
$p(y) = a + b \text{ SumRT} + d p(y-1)$	0.87	-113*** \pm 15	0.61*** \pm 0.03	0.32*** \pm 0.05
$p(y) = a + b \text{ SumVRT}(c_{best} = 0.95)^a$	0.86	-26* \pm 11	1.67*** \pm 0.09	—
Medium				
$p(y) = a + b \text{ SumR}^a$	0.62	-65** \pm 21	0.37*** \pm 0.04	—
$p(y) = a + b \text{ SumR} + d p(y-1)$	0.65	-86*** \pm 23	0.38*** \pm 0.04	0.18* \pm 0.08
$p(y) = a + b \text{ SumVR}(c_{best} = 0.4)^a$	0.80	-15 \pm 9	0.39*** \pm 0.03	—
$p(y) = a + b \text{ SumRT}^a$	0.81	-86*** \pm 15	0.58*** \pm 0.04	—
$p(y) = a + b \text{ SumRT} + d p(y-1)$	0.82	-100*** \pm 16	0.58*** \pm 0.04	0.14* \pm 0.06
$p(y) = a + b \text{ SumVRT}(c_{best} = 0.4)^a$	0.88	19** \pm 7	0.62*** \pm 0.03	—
Poor				
$p(y) = a + b \text{ SumR}^a$	0.36	-27 \pm 30	0.32*** \pm 0.06	—
$p(y) = a + b \text{ SumR} + d p(y-1)$	0.46	-64* \pm 30	0.31*** \pm 0.05	0.33** \pm 0.10
$p(y) = a + b \text{ SumVR}(c = 0.2)^a$	0.51	38* \pm 15	0.31*** \pm 0.04	—
$p(y) = a + b \text{ SumRT}^a$	0.49	-50 \pm 26	0.51*** \pm 0.07	—
$p(y) = a + b \text{ SumRT} + d p(y-1)$	0.56	-75* \pm 26	0.48*** \pm 0.07	0.27* \pm 0.09
$p(y) = a + b \text{ SumVRT}(c_{best} = 0.1)^a$	0.57	41** \pm 14	0.48*** \pm 0.06	—

Independent variables were the (effective) seasonal rain SumR (SumRT), the production for the last year $p(y-1)$, and SumVR (SumVRT), the accumulated (effective) seasonal rain weighted with the (effective) precipitation memory index.

In February 1988, abnormally high rainfall occurred (475 mm, = or 85% of the long-term annual average). Because much of it was lost as runoff, we used a lower value (300 mm) for our analysis. For regression models with SumVR and SumVRT as an independent variable, we determined the value of the memory coefficient c indirectly by selecting the value of c that maximized the R^2 value.

Boldface indicates the best models constructed with a memory index.

* $P < 0.05$

** $P < 0.005$

*** $P < 0.0005$

^aThe models were constructed with only 18 years of data (the 1st year was excluded) to make the m comparable to the models where production of the last year $p(y-1)$ entered.

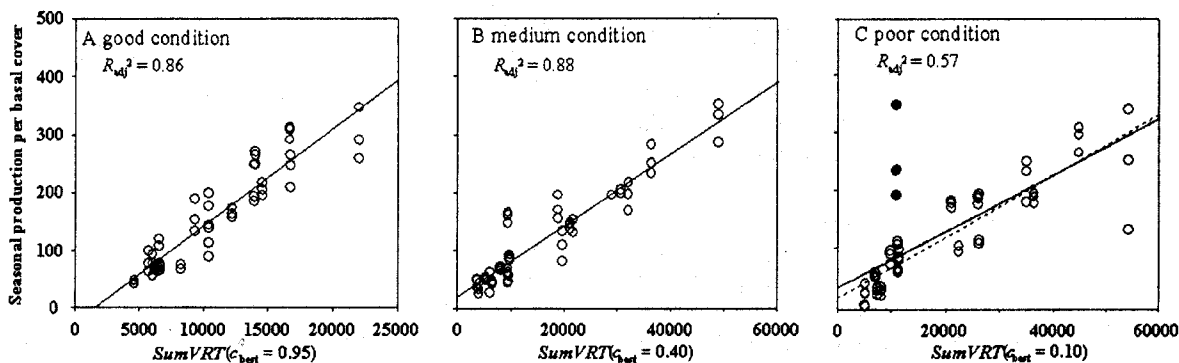


Figure 3. The best regression models $p(y) = a + b \text{ SumVRT}(c_{best})$ predicting seasonal phytomass production per unit of basal cover with memory coefficients $c = 0.95$, 0.4 , and 0.1 for the good (A), medium (B), and poor conditions (C), respectively. The open circles show the data for all three replicates; the solid lines show the best regression models. After removal of the outliers (black dots, 1994–95 growing season) the model for the poor condition [$y = 0.51 * \text{SumVRT}(c = 0.1) + 22.1$, dashed line] explained 79% of the variation in production. The very dry 1994–95 growing season followed a very wet season.

Table 4. Evaluation of the Long-term Models with the Short-term Data Set

		Condition		
		Good	Medium	Poor
Long-term	c_{best}	0.95	0.40	0.10
Short-term	R^2_{adj}	0.86	0.88	0.57
Long-term	R^2_{adj}	0.96	0.86	0.79
Short-term	a	-26.5 ± 10.9	$19.3^* \pm 6.6$	$40.8^* \pm 13.5$
Long-term	a_s	5.8 ± 3.6	$43.5^{***} \pm 4.1$	$37.3^{***} \pm 4.3^{***}$
Short-term	b	$1.67^{***} \pm 0.09$	$0.62^{***} \pm 0.03$	$0.48^{***} \pm 0.06$
Long-term	b_s	$1.73^{***} \pm 0.04$	$0.64^{***} \pm 0.03$	$0.43^{***} \pm 0.02$

If the regression coefficients of the best models constructed with the long-term data set (Table 3) are independent of the specific time period chosen, the corresponding models $p(s, y, m) = a_s + b_s \text{SumVRT}(c_{best}, m)$ constructed with the short-term data set and memory coefficient c_{best} yield the same regression coefficients (that is, $a_s = a$, and $b_s = b$).

Given are the R^2_{adj} values of the regressions and the regression coefficients \pm SE for the corresponding models for the long-term and the short-term data sets.

*** $P < 0.0001$

** $P < 0.001$

* $P < 0.01$

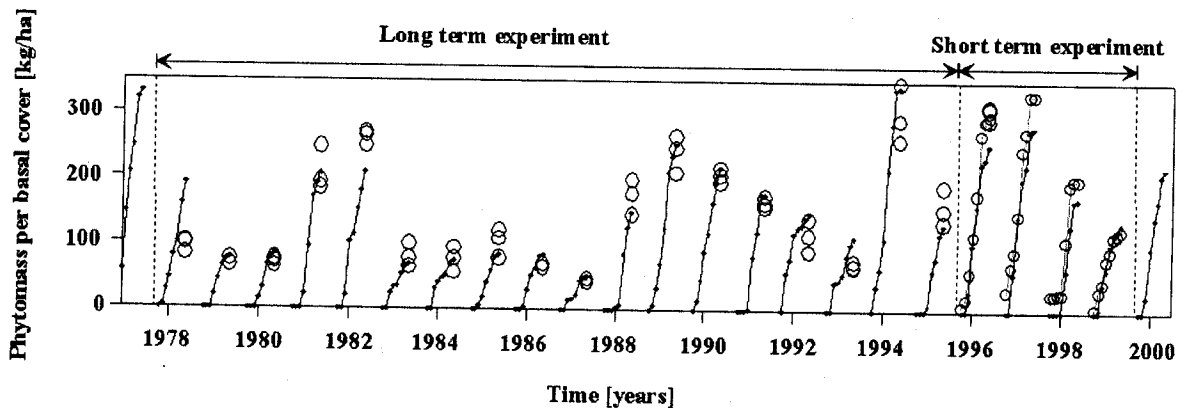


Figure 4. Predicted accumulated monthly phytomass production per unit of basal cover (solid lines with small black dots, monthly values) for the good condition and field data on phytomass production (open circles). For the short-term experiment (1995–96 to 1998–99), we show the monthly accumulated data.

respectively, and yielded CV of 0.43, 0.51, and 0.43, respectively. Thus, the variability in annual predicted production was some 50%–70% greater than the corresponding variability in annual rainfall. For the data from the long-term experiment, we obtained slightly higher figures—CV = 0.57, 0.68, and 0.71, for the good, medium, and poor conditions, respectively (Table 2).

To understand why the variability in (predicted) production was higher than the variability in effective precipitation, we investigated the autocorrelation structure of effective precipitation at the yearly scale (that is, the correlation between SumRT at lags of 1–15 years) and at the monthly scale (that is, the correlation between $\text{RT}(m)$ at a lag of 1 month, but only taken during the growing season). Effective seasonal precipitation over 73 years was (weakly)

positively correlated at a lag of 1 year ($r = 0.18$, $P = 0.108$) and significantly negatively correlated at lags of 9 years ($r = -0.27$, $P = 0.021$), 10 years ($r = -0.49$, $P < 0.001$), and 11 years ($r = -0.35$, $P = 0.003$). This result indicates that there are 10-year cycles of alternating periods of wet and dry years (Figure 5). Monthly effective precipitation during the growing season was significantly positively correlated at a lag of 1 month ($r = 0.15$, $P = 0.001$, $n = 524$). Thus, at the yearly scale, prolonged periods of wet and dry years alternated, and the memory index VigRT was above mean during periods of wet years and below mean during periods of dry years. This caused predicted phytomass production to increase during a period of wet years and to drop during a period of dry years. A similar mechanism was true for the short-lasting memory because of

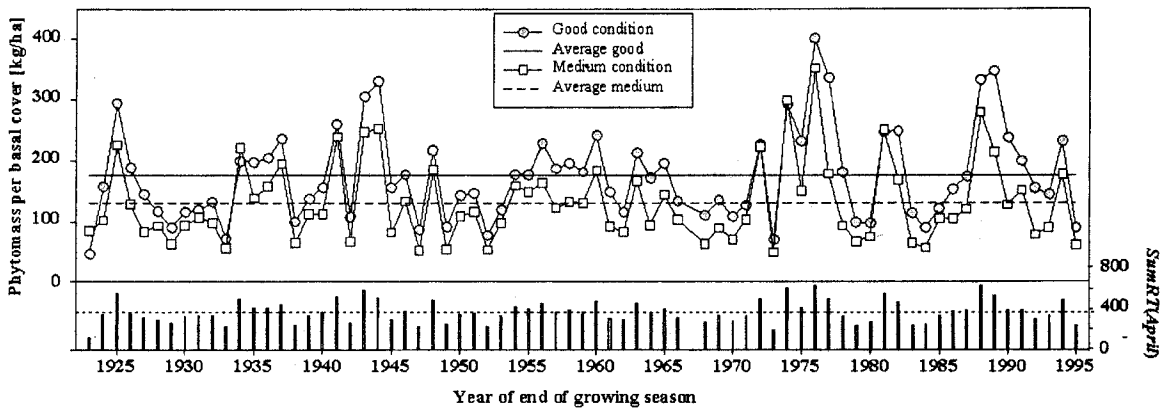


Figure 5. Extrapolation of our best models for phytomass production per unit of basal cover (Table 3) on a 73-year long-term precipitation data series from the same area. The predictions for the good condition are indicated by gray circles; the long-term average is given as a solid line. The predictions for the medium condition are indicated by open squares; the long-term average is given as a dashed line. The bottom of the figure shows the effective accumulated seasonal precipitation $SumRT(April)$; the dashed horizontal shows its average.

the positive correlation of monthly effective precipitation at a lag of 1 month; the memory index $VigRT$ was high after consecutive months of high effective rainfall (see Figure 1), which amplified the variability in the predictive production.

Calculation of the frequency distribution of the predicted total seasonal production (we multiplied the prediction for seasonal phytomass production per unit of basal cover with the average basal cover 8.6%, 7.5%, and 3.1% for good, medium, and poor, respectively) showed the stark impact of compositional state on production (Figure 6). Although seasonal production in the good-condition state dropped only in 6% of all years below 700 kg/ha, it was 49% for the medium condition and 90% for the poor condition. In only 10% of all years, the predicted production of medium-condition grassland exceeded the average predicted production of that in good condition (1,500 kg/ha); in only 6% of all years, poor-condition grassland reached half of the average of the good condition.

DISCUSSION

Most of our knowledge about the controls and temporal variability of grassland primary production concerns an annual time scale (Lauenroth 1979; Sala and others 1988a; McNaughton and others 1993; Epstein and others 1997; Paruelo and others 1999). Because we were working with a model that operated on a monthly basis, and we were using both monthly and yearly data on phytomass production, our study provides new insights into the characteristics and environmental controls of car-

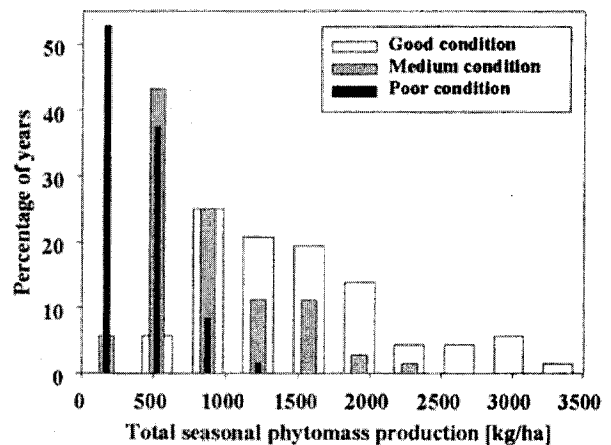


Figure 6. Frequency distribution of predicted total seasonal phytomass production for the three compositional states based on the 73-year long-term precipitation data set and our best models (Table 3). To obtain total seasonal phytomass production, we multiplied the prediction per unit of basal cover by the average basal cover of the long-term data set (Table 2).

bon gains in grassland areas. Our analysis of two phytomass production data sets of South Africa semiarid grasslands suggests that (a) mean phytomass production per unit of basal cover varies little between compositional states but shows a trend to decrease with declining condition; (b) the system has a memory of past precipitation; (c) the memory causes carryover effects in production from the previous 4 years if the grassland is in good condition (dominated by perennial *T. triandra*) and effects

from the previous 1 or 3 months if the grassland is in medium or poor condition (dominated by short-lived grasses); (d) the memory effect both buffers and amplifies the responses of production to changes in precipitation, depending on the sequence of dry or wet years/month; and (e) phytomass production in the South African grassland amplifies the variability in seasonal rainfall. The latter result is consistent with many previous studies of arid and semiarid ecosystems (Le Houérou and others 1988), but it is contrary to findings in some grassland and shrubland systems (for example, Lauenroth and Sala 1992; Paruelo and others 1998) where variability in phytomass production was smaller than that of rainfall.

Phytomass Production Relative to Basal Area

Clearly, reduction in basal cover will reduce phytomass production. Bare soil evaporation, runoff, soil erosion, and nutrient losses will increase as total cover decreases. A change in the spatial pattern of a grassland—that is, fragmentation and clumping of patches (Aguiar and Sala 1999; Reynolds and others 1999) resulting from degradation—may result in either increases or decreases in phytomass production/basal cover. A reduction may result from “edge effects” in the degraded, more fragmented grassland (for example, a larger proportion of the tufts suffer a harsher microclimate at the edge of bare soil patches) or because species adapted to harsher environments are less productive than species adapted to good conditions. An increase will result from a concentration of resources in the remaining clumps of vegetation (“fertility islands,” per Whitford 1995). All these processes may operate simultaneously, and the observed patterns will result from the relative contribution of the different processes. However, our results suggest that the net effect of these processes cancel, such that net production depends primarily upon percentage basal cover of grasses.

The Memory of the Grassland

Our results showed that there are linear relationships between monthly phytomass production and the product of monthly precipitation (R), a temperature index (T), and a precipitation memory index ($VigRT$). Thus, the memory index acts as a weighting factor that amplifies or reduces production according to the precipitation history and describes the ability of the grassland to respond to a given monthly precipitation. The advantage of our approach is that it relies, without losing explanative

power, only on rainfall data (and average long-term monthly temperatures) and not on production of the past years. Our model can therefore be widely applied if monthly long-term precipitation data (and average monthly temperature data) are available. We used the memory index as a weighting factor for monthly precipitation. In this, our conceptual model on phytomass production (that is, the indices $SumVR$ and $SumVRT$) differs from similar approaches (for example, Gibbens and Beck 1988; Goward and Prince 1995; Anderson and Inouye 2001) that related phytomass production (or basal cover) directly to a memory index σ of the general form:

$$\sigma = b_t\sigma_t + b_{t-1}\sigma_{t-1} + \dots + b_0\sigma_0 \quad (5)$$

where σ_t gives the environmental effect on vegetation in time step t ; t is the current time step ($t-1$ is the previous time step, and so on), and b_i are the individual time step weights (Goward and Prince 1995). The general memory index in Eq. (5) covers, as special cases, antecedent precipitation from the last m time steps (for example, see Gibbens and Beck 1988), precipitation in a previous year (that is, lag effects) (Anderson and Inouye 2001), as well as our memory index (Eq. [4]).

We hypothesized that using effective precipitation instead of precipitation would improve the performance of our models for predicting phytomass production. For the summer rainfall grassland studied here, we assumed a simple model for effective precipitation by weighting precipitation with a temperature index that accounts for the high temperature optima of C_4 grasses for photosynthesis. Our results supported this hypothesis (see Figure 2). The percentage of variation in production per unit of basal cover explained by the best models increased by 13%–19%. Note that our simple model for effective precipitation does not consider the effect of temperature on soil water availability, which would require a water balance model to obtain actual evapotranspiration. We did not include a water balance model because we intended to keep our model simple. Our model for effective precipitation improved the predictions for production considerably (Table 3 and Figure 2), and a small possible improvement in predictive ability does not justify the use of a more complex approach. The use of monthly temperature data instead of the long-term averages, however, may generate the need to calculate actual evapotranspiration or to include a nonlinear effect of temperature (a saturation function instead of a multiplicative effect) because very high temperatures may reduce water availability due to soil evaporation and reduce monthly precip-

itation use efficiency. In other semiarid grasslands, analogous models for effective precipitation (or "biologically usable" water) might be different and require the inclusion of actual evapotranspiration, depending, for example, on the physiological characteristics of the grass species and the climatic characteristics of the site (for example, winter rainfall versus summer rainfall).

Weighting effective precipitation (RT) with the effective precipitation memory index ($VigRT$) further increased the percentage of the explained variation in production from 77% to 86%, from 81% to 88%, and from 49% to 57% for the good, medium, and poor conditions, respectively (Table 3). Without considering the temperature index, the effect of including the memory index was larger (Table 3). Both temperature and memory dampen the effect of exceptionally high precipitation events outside the growing season. The damping effect of the memory index was associated with the low frequency of 2 successive months with high precipitation outside the growing season. The temperature index damping effect was associated with the effect of low temperatures on plant growth.

The use of a model that operated at a monthly basis allowed us to identify the time scale of the memory, and this represents an important gain over previous attempts (but see Gibbens and Beck 1988). We found that the grassland in good condition, which is dominated by perennial *T. triandra*, has a memory that lasts up to 4 years, whereas the memory of the grasslands in medium and poor conditions, which are dominated by shorter-lived and annual grass species, lasts for only 1 or 3 months. However, for the medium and poor conditions, we found two maxima in the $c-R^2$ plot (Figure 2), a local maximum for a long-lasting memory, and an absolute maximum at the short-lasting memory. This pattern is explained by the fact that a given compositional state comprises several species, and the medium-condition grassland still retains some long-lived climax perennials. One of the dominant species in the poor-condition grassland, *T. koelerioides*, is a stoloniferous perennial that lives about 4 years and that could account for the long-term memory of the poor condition, whereas other dominant species, such as the annual *A. congesta*, might account for the dominant short-term memory.

Carryover effects can be related to "soil memory," "population dynamics memory," or "plant memory." In some systems, the soil acts as a "capacitor," and water from one year is transferred to the next one. In other systems, features of plant population dynamics (for example, initiation of buds in the

previous growing season, a seed bank, establishment of a cohort of perennial plants) (Goward and Prince 1995), or plant structural factors related to changes in biomass, storage organs, or cover (for example, see Gibbens and Beck 1988; Anderson and Inouye 2001) may explain the memory of the system. By analyzing phytomass per unit of basal cover instead of phytomass, we excluded the potential memory in basal cover that may be caused by a combination of recruitment pulses and the perennial lifespan of grasses. Such an effect was observed by Gibbens and Beck (1988). They determined the memory of grasslands in southern New Mexico, USA, on a monthly scale by maximizing the R^2 of linear regressions relating total perennial grass basal area to accumulated precipitation from the preceding months. Gibbens and Beck (1988) found that 3–4 years of antecedent precipitation was significantly associated with perennial grass basal area.

By repeating the analysis of Gibbens and Beck (1988), we found similar results. For grassland in good and medium condition, basal cover was most strongly related to 6 years of antecedent effective precipitation ($R^2 = 0.57$ and 0.42 for the good and medium conditions, respectively). Grassland in poor condition showed two maxima, one for 28 months ($R^2 = 0.29$) and another for 4 months ($R^2 = 0.24$). However, the analogous analysis with our memory indices $SumVRT$ instead of antecedent effective precipitation yielded much poorer fits ($R^2 < 0.22$ for all three compositional states).

This result indicates that different memory mechanisms may operate for phytomass production per unit basal cover and for basal cover and that an adequate description of them may require different indices. Some studies reported lag effects in the responses of species or functional group cover to precipitation patterns. For example, by analyzing a 45-year data set, Anderson and Inouye (2001) found that total cover (or cover of shrubs or perennial grasses) of a sagebrush steppe in Idaho, USA, did not correlate with precipitation received in the year preceding the sample year, but rather with precipitation received from 3 to 5 years earlier. Similar lags were reported for arid shrublands in south Australia by Noble (1977), who attributed the long carryover effects of some species to shoot longevity.

A possible explanation for our finding of a perennial memory of grassland in good condition regarding phytomass production is that the dominant species *T. triandra*, which has deeper roots than the dominant species in the other compositional states (Snyman 2000), can access water from deeper soil

layers that has been stored in past months. Although more than 80% of the root mass of perennial grasses was found in the top 150–200-mm soil layer (Snyman 2000) and this mass is primarily responsible for production, the importance of the contribution of deeper roots to the survival of plants during water stress must not be underestimated (Snyman 2000). Climax grasses are known to withdraw water from layers deeper than 2 m during drought periods (Snyman 1994). In contrast, shorter-lived species with shallow root systems only have access to water in higher soil layers, which is stored from only a few months earlier (see Snyman 2000).

Using a 52-year record of phytomass production at a shortgrass steppe site in north central Colorado, USA, a site with a mean annual precipitation of 321 mm, Oesterheld and others (2001) found a significant carryover effect from the previous year's production. However, they speculated that this was unlikely to be due to soil water storage. Rather, it was probably due to structural or functional mechanisms produced by drought, which might have hampered the ability of the system to respond to the reestablishment of average or wet production conditions.

Variation in Annual Production versus Variation in Precipitation

Despite the importance of data on year-to-year variation in functional aspects of ecosystems, they are extremely limited (Mooney 1991; Knapp and Smith 2001; Jobbagy and others 2002; Veron and others 2002). An important open question in this respect is how the temporal variability in climate affects the variability of ecosystem processes in grassland and shrubland areas?

We found a pattern in production versus precipitation variability (the CV of phytomass production is higher than that of rainfall) that is consistent with many studies in arid and semiarid ecosystems (for example, Le Houérou and others 1988). We identified a mechanism that acts as a memory of past precipitations and can inflate the variability in rainfall. More specifically, this mechanism was caused by a positive correlation of precipitation at the scale of the memory of the grassland that amplified the variability in precipitation: Production was higher during a sequence of several wet years or months and lower during a sequence of several dry years or months. This mechanism could explain the contradictory results of other studies in South and North America (Fernández and others 1991; Lauenroth and Sala 1992; Paruelo and others 1998) in which the CV of production was smaller than that of pre-

cipitation. At the shortgrass steppe, which has a memory at an annual scale (Oesterheld and others 2001), precipitation is only rarely consistently above or below the mean for more than 2 or 3 years (Lauenroth and Sala 1992). In areas where there are no prolonged periods of dry and wet years, a dry year after a wet year will yield more production than expected by precipitation alone, and a wet year after a dry year will yield less production than expected by precipitation alone—a pattern that will buffer the variability in precipitation. Using satellite data, Paruelo and others (2000) showed that the relative variability of phytomass production is highly dependent on the spatial scale. The CV decreased exponentially as the size of the experimental plots increased. Differences in the size of the experimental plots between the earlier studies and our analysis may account for part of the differences in the results.

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REFERENCES

- Acocks JPH. 1953. Veld types of South Africa. 3rd ed. *Memoirs of the Botanical Survey of South Africa*, No. 28. . . .
- Aguiar MR, Sala OE. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends Ecol Evol* 14:273–7.
- Anderson JE, Inouye RS. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecol Monogr* 71:531–56.
- Arnold TH, De Wet BC. 1993. *Plants of Southern Africa: names and distribution*. *Memoirs of the Botanical Survey of South Africa*, No. 62. . . .
- Chapin FS. 1991. Effects of multiple environmental stresses on nutrient availability and use. In: Mooney HA, Winner WE, Pell EJ, Eds. *Responses of plants to multiple stresses*. San Diego (CA): Academic Press. p 67–88.
- Christie EK. 1981. Biomass and nutrient dynamics in a C4 semiarid Australian grassland community. *J Appl Ecol* 18:907–18.
- Dankwerts JE, Nel LO. 1989. The effect of frequency of defoliation on *Themeda triandra* in the false thornfeld of the Eastern Cape. *J Grassland Soc S Afr* 6:32–6.
- Du Preez CC, Snyman HA. 1993. Organic matter content of a soil

- in a semi-arid climate with three long-standing veld conditions. *Afr J Rangeland Forage Sci* 10:108–10.
- Ehleringer JR, Bjorkman O. 1977. Quantum yields for CO₂ uptake in C₃ and C₄ plants: dependence on temperature, CO₂, and O₂ concentrations. *Plant Physiol* 59:86–90.
- Epstein HE, Lauenroth WK, Burke IC. 1997. Effects of temperature and soil texture on ANPP in the U.S. Great Plains. *Ecology* 78:2628–31.
- Fahrig L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *J Wildlife Manag* 61:603–10.
- Fahrig L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecol Appl* 12:346–53.
- Fernández RJ, Sala OE, Golluscio RA. 1991. Woody and herbaceous aboveground production of a Patagonian steppe. *J Range Manage* 44:434–7.
- Flather CH, Bevers M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *Am Nat* 159:40–56.
- Gibbens RP, Beck RF. 1988. Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. *J Range Manage* 41:186–92.
- Goward SN, Prince SD. 1995. Transient effects of climate on vegetation dynamics: satellite observations. *J Biogeog* 22:549–63.
- Hanson CJ, Wright JR, Smoliak S. 1982. Use of historic yield data to forecast range herbage production. *J Range Manage* 35: 614–6.
- Hoffman MT, Ashwell A. 2001. *Nature divided: land degradation in South Africa*. Cape Town: UCT Press.
- Jobbagy E, Sala OE. 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecol Appl* 10:541–9.
- Jobbagy EG, Sala OE, Paruelo JM. 2002. Patterns and controls of primary production in the Patagonian steppe: a remote sensing approach. *Ecology* 83:307–19.
- Kareiva P, Wennergren U. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373:299–302.
- Knapp AK, Smith MD. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–4.
- Lauenroth WK. 1979. Grasslands primary production: North American grasslands in perspective. In: French NR, Eds. *Perspectives in grassland ecology*. Ecological Studies. New York: Springer-Verlag. p 3–24.
- Lauenroth WK, Sala OE. 1992. Long-term forage production of North American shortgrass steppe. *Ecol Appl* 2:397–403.
- Le Houërou HN, Bingham RL, Skerbek W. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *J Arid Environ* 15:1–18.
- Levy EB, Madden EA. 1933. The point method of pasture analysis. *NZ J Agric* 46:267–27.
- McNaughton SJ. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecol Monogr* 55:259–94.
- McNaughton SJ, Oesterheld M, Frank DA, Williams KJ. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341:142–4.
- McNaughton SJ, Sala OE, Oesterheld M. 1993. Comparative ecology of African and South American arid to subhumid ecosystems. In: Goldblatt P, Eds. *Biological relationships between Africa and South America*. New Haven (CT): Yale University Press. p 548–67.
- Milchunas DG, Lauenroth WK. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol Monogr* 63:327–66.
- Mooney HA. 1991. Biological responses to global change: an agenda for research. *Ecol Appl* 1:112–7.
- Mostert JWC. 1958. Studies of the vegetation of parts of the Bloemfontein and Brandfort districts. *Memoirs of the Botanical Survey of South Africa*, No. 31. . . . pp 311–226.
- Noble IR. 1977. Long-term biomass dynamics in an arid chenopod shrub community at Koonamore, South Australia. *Aust J Bot* 25:639–53.
- Noy Meir I. 1973. Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:25–41.
- O'Connor TG. 1994. Composition and population responses of an African savanna grassland to rainfall and grazing. *J Appl Ecol* 31:155–71.
- O'Connor TG, Roux PW. 1995. Vegetation changes (1949–71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *J Appl Ecol* 32:612–26.
- O'Connor TG, Bredenkamp GJ. 1997. Grassland. In: Cowling R, Richardson D, Pierce S, Eds. *Vegetation of Southern Africa*. Cambridge (UK): Cambridge University Press. p 215–57.
- O'Connor TG, Haines LM, Snyman HA. 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *J Ecol* 89:850–61.
- Oesterheld M, McNaughton SJ. 2000. Herbivory in terrestrial ecosystems. In: Sala OE, Jackson RB, Mooney HA, Howarth R, Eds. *Methods in ecosystem science*. New York: Springer-Verlag. p 151–7.
- Oesterheld M, Sala OE, McNaughton SJ. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature* 356:234–6.
- Oesterheld M, Loreti J, Semmartin M, Sala OE. 2001. Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *J Veget Sci* 12:137–42.
- Paruelo JM, Jobbagy E, Sala OE, Lauenroth W, Burke IC. 1998. Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecol Appl* 8:194–206.
- Paruelo JM, Lauenroth WK, Burke IC, Sala OE. 1999. Grassland precipitation use efficiency across a resource gradient. *Ecosystems* 2:64–9.
- Paruelo JM, Oesterheld M, Di Bella CM, Arzadum M, Lafontaine J, Cahuepe M, Rebella CM. 2000. A calibration to estimate primary production of subhumid rangelands from remotely sensed data. *Appl Veget Sci* 3:189–95.
- Paulsen HA Jr, Ares FN. 1962. Grazing values and management of black-grama and tobosa grasslands and associated shrub ranges of the Southwest. Technical Bulletin No. 1270. Washington (DC): US Department of Agriculture
- Reynolds JF, Virginia RA, Kemp PR, DeSoyza AG, Tremmel DC. 1999. Impact of simulated drought on resource islands of shrubs in the Chihuahuan desert: effects of species, season, and degree of island development. *Ecol Monogr* 63:69–106.
- Sala OE, Biondini ME, Lauenroth WK. 1988b. Bias in estimates of primary production: an analytical solution. *Ecol Model* 44:43–55.
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK. 1988a. Primary

- production of the central grassland region of the United States. *Ecology* 69:40–5.
- Schulze ER. 1979. Climate of South Africa. Part 8. General Survey. Pretoria: Weather Bureau.
- Smoliak S. 1986. Influence of climatic conditions on production of *Stipa-Bonteloua* prairie over a 50-year period. *J Range Manag* 39:100–3.
- Sneva FA, Hyder DN. 1962. Estimating herbage production on semi-arid ranges in the Intermountain Region. *J Range Manag* 15:88–93.
- Snyman HA. 1994. Evapotranspiration, water-use efficiency and quality of six dryland planted pasture species and natural vegetation, in a semi-arid rangeland. *Afr J Rangeland Forage Sci* 11:82–8.
- Snyman HA. 1998. Dynamics and sustainable utilization of rangeland ecosystems in arid and semi-arid climates of southern Africa. *J Arid Environ* 39:645–66.
- Snyman HA. 2000. Soil-water utilisation and sustainability in a semi-arid grassland. *Water SA* 26:333–41.
- Snyman HA, Fouché HJ. 1991. Production and water-use efficiency of semi-arid grasslands of South Africa as affected by veld condition and rainfall. *Water SA* 17:263–8.
- Snyman HA, Fouché HJ. 1993. Estimating seasonal herbage production of a semi-arid grassland based on veld condition, rainfall and evapotranspiration. *Afr J Rangeland Forage Sci* 10:124–30.
- Soil Classification Working Group. 1991. Soil classification: a Taxonomic system for South Africa. Pretoria: Department of Agriculture Development.
- Van den Berg B, Roberts BR, Vorster LF. 1975. The effect of seasonal grazing on the cover and composition of *Cymbopogon-Themedra* veld. *Proc Grassland Soc S Afr* 10:111–7.
- Veron SR, Paruelo JM, Sala OE, Lauenroth WK. 2002. Environmental controls of primary production in the Argentine pampas. *Ecosystems* 5:625–35.
- Whitford WH. 1995. Desertification: implications and limitations of the ecosystem health metaphor. In: Rapport DJ, Gaudet CL, Calow P, Eds. *Evaluating and monitoring the health of large-scale ecosystems*. New York: Springer-Verlag. p 273–93.