Probabilistic model predicts dynamics of vegetation biomass in a desert ecosystem in NW China

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The temporal dynamics of vegetation biomass are of key importance for evaluating the sustainability of arid and semiarid ecosystems. In these ecosystems, biomass and soil moisture are coupled stochastic variables externally driven, mainly, by the rainfall dynamics. Based on long-term field observations in northwestern (NW) China, we test a recently developed analytical scheme for the description of the leaf biomass dynamics undergoing seasonal cycles with different rainfall characteristics. The probabilistic characterization of such dynamics agrees remarkably well with the field measurements, providing a tool to forecast the changes to be expected in biomass for arid and semiarid ecosystems under climate change conditions. These changes will depend—for each season—theon the forecasted rate of rainy days, mean depth of rain in a rainy day, and duration of the season. For the site in NW China, the current scenario of an increase: of 10% in rate of rainy days, 10% in mean rain depth in a rainy day, and no change in the season duration leads to forecasted increases in mean leaf biomass near 25% in both seasons.

Significance

The temporal dynamics of vegetation biomass are of vital importance for evaluating the sustainability of arid and semiarid ecosystems. Field observations indicate that soil moisture and plant biomass fluctuate stochastically with the occurrence of rainfall events. Based on long-term field observations, we find that the dynamics of the vegetation biomass can be quantified by their analytically derived time-dependent probability distribution. This allows for the study of the impact of climate change scenarios on vegetation cover and plant water resource competition. It is found that in a restored desert ecosystem in northwest (NW) China, the growing season leaf biomass is expected to increase by nearly 25% compared to the present.

Ecosystem Characteristics: Climate, Soil, and Vegetation

Long-term detailed measurements of vegetation dynamics were carried out at the plant level in four plots located at the Shapotou Desert Research and Experiment Station in NW China. Meteorological 60-y records at the station provide an adequate characterization of the rainfall dynamics at the site. The mean annual rainfall is 182.6 mm, of which 82% falls in the rainy season (May 1–September 30) with an observed range between 60 mm and 270 mm and a SD of 57.1 mm. The mean rainfall during the wet season is 149.1 mm and during the dry season is 33.5 mm, with SDs of 51.5 mm and 16.9 mm, respectively.

The arrival of rainfall events is modeled as a Poisson process in which the rate $\lambda_0$ (d$^{-1}$) is constant over the course of a season, but varies between seasons. After accounting for interception (which acts as a censoring process), the rainfall arrival rate is transformed into the infiltration arrival rate $\lambda$ (2); $\lambda$ inherits the seasonal characteristics of $\lambda_0$, namely constant intraseason and variable interseason values.

The temporal structure within each rainfall event is ignored, with all water modeled as arriving in an instantaneous pulse with random depth. For values of the arrival rate typical of water-limited systems (such as those here), it will be rare for such a process to produce multiple arrivals in a given day, and so the continuous-in-time Poisson process can be correctly understood at the discrete daily scale. In this case, $\lambda_0$ (d$^{-1}$) represents the probability of having rain on a given day, and the distribution of rain depth during a pulse arrival is equivalent to the distribution of rain depth on any rainy day (6); in particular, this distribution is taken to be exponential with mean $\mu$ (2). The fluctuations of $\lambda_0$ and $\mu$ for both seasons at the site for the period 1956–2015 are shown in Fig. S1.

A detailed description of the field site, its climate, soil, and vegetation is given in Field Site and Vegetation. Based on the analysis...
of the meteorological data, the mean rainfall arrival rate, \( \lambda_0 \), in the wet season is 0.231 d\(^{-1}\). For the dry season it is 0.073 d\(^{-1}\). The mean daily rainfall depth for a wet day in the wet season is 4.2 mm, and for the dry season it is 2.1 mm (Table S1).

The dominant vegetation is the drought-tolerant shrub *Artemisia ordosica*; photographs of the broader site and this shrub in particular are shown in Fig. 1. Field measurements to estimate the biomass at the end of each season as well as the shrub in particular are shown in Fig. 1. Field measurements to estimate the biomass at the end of each season as well as the plant parameters needed in the analytical computations are described in Methods. The values of the climate, soil, and plant parameters are reported in Tables S1 and S2.

The Theoretical Model. The temporal evolution of vegetation biomass per canopy area \( B \) may be described by the differential equation

\[ \dot{B} = (\alpha \eta - \beta) B, \]

where \( \beta \) is the per-unit biomass loss rate, \( \alpha \) is the non–water-limited per-unit assimilation rate, and \( \eta \) is an inhibition function that captures the dependence on water availability for transpiration and assimilation, both modulated by the stomata. In our previous work (3, 7), \( B \) has denoted various plant tissue types, but here we are modeling only the leaf component of the vegetation. (Details on the derivation of these dynamics, especially the resolution of and interaction between different tissue types, are given in Theoretical Model.) This equation requires a description of the dynamics of water availability for closure, which are provided specifically by a water balance equation for the root zone of the vegetation:

\[ A_r n Z_r \frac{dS}{dt} = -E_m \rho \eta A_c B + A_r I. \] [2]

The left-hand side above gives the rate of change of the water volume in the soil. \( A_r \) is the root coverage area (i.e., the amount of land surface area with roots beneath it) within the measurement plot, \( n \) is the soil porosity, and \( Z_r \) is the rooting depth, so that the product \( A_r n Z_r \) is the pore space volume available to store water in the root zone; and \( S \), the relative moisture content, is the fraction actually occupied by water. On the right-hand side, the depth of rain entering the soil per unit time \( I \) is multiplied by the root area to give the volumetric input; output (i.e., loss) \( E_m \rho \eta A_c B \) represents transpiration: The weight of leaf biomass per canopy area \( B \) is multiplied by the canopy area of the plot \( A_c \) to give the total leaf weight in the plot; this in turn is multiplied by the leaf area per weight constant \( \rho \) to give the total plot leaf area; the result is multiplied by the transpiration rate per unit leaf area, given as a maximum rate \( E_m \) times the same water limitation factor \( \eta \) that appears in the assimilation rate, which we now write explicitly as a function of soil moisture \( \eta(S) \), as in Eq. S28.

Rearranging yields

\[ \dot{B} = (\alpha \eta(S) - \beta) B \]

\[ \dot{S} = -\gamma B \eta(S) + I, \] [4]

where \( \gamma = (A_c / A_r)(E_m \rho / n Z_r) \) and \( I \) is given as units of soil storage fraction per time. The values for the derived parameters are given in Table 1. The stochasticity of this infiltration process, with arrival rate \( \lambda \) and a rescaled mean infiltration depth \( 1/\theta \) (again, expressed as a fraction of the root zone water storage volume), induces a probability density function (pdf) on the biomass–soil moisture state space.

Schaffer et al. (3) showed that for constant rainfall parameters this system allowed for an exact, closed-form steady-state pdf, but also, in recognition of the fact that convergence to this state might take longer than the length of a typical (constant parameter) season, derived an approximation of the system’s transient behavior. This approximation exploits the fact that biomass varies on a much slower timescale than soil moisture, so that changes in biomass on an interval of interest (such as a season) involve an integration that tends to average out the soil moisture fluctuations in that interval, allowing for a simple estimation of the marginal pdf of biomass. Formally, this estimate is obtained by setting \( \dot{S} = 0 \) in the above system, and substituting the soil moisture equation into the biomass equation yields

\[ \dot{B} = \alpha I - \beta B \] [5]

so that each unit of infiltrating water is converted immediately to biomass (hence the name given in ref. 3, “no-storage limit”)

Table 1. Values of the reduced plant, soil, and climate parameters needed to specify the joint dynamics in Eqs. 3 and 4 and the “no storage” dynamics in Eq. 5 and appearing also in Eqs. 6 and 7

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Units</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \alpha )</td>
<td>d(^{-1})</td>
<td>0.0196</td>
</tr>
<tr>
<td>( \beta )</td>
<td>d(^{-1})</td>
<td>0.0071</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>m(^2) g(^{-1}) d(^{-1})</td>
<td>(4.44 \times 10^{-5})</td>
</tr>
<tr>
<td>( s_w )</td>
<td>m(^3)</td>
<td>0.02</td>
</tr>
<tr>
<td>( s^* )</td>
<td>m(^3)</td>
<td>0.099</td>
</tr>
<tr>
<td>( \lambda )</td>
<td>d(^{-1})</td>
<td>0.182 (wet), 0.045 (dry)</td>
</tr>
<tr>
<td>( 1/\theta )</td>
<td>m(^3)</td>
<td>0.022 (wet), 0.011 (dry)</td>
</tr>
<tr>
<td>( T )</td>
<td>d</td>
<td>153 (wet), 212 (dry)</td>
</tr>
</tbody>
</table>
with the conversion ratio—essentially a water use efficiency—of \( \alpha/\gamma \). This single equation is obtained exactly in the parameter limit where (for given efficiency) the transpiration and assimilation coefficients in the system of Eqs. 3 and 4 are taken to be arbitrarily large, and so it can be considered merely as a simplified, albeit convenient, governing equation for a subset of the parameter space, which is largely how it was discussed in ref. 3. However, this limit has an alternate (and more meaningful) interpretation. The biomass dynamics certainly depend on the availability of water, which may be characterized by the average root zone soil moisture \( S \) as in Eq. 3; this assumes that the transpiration does not depend on the distribution of moisture, so that a single hydrological state variable is sufficient, and the system is closed using the water balance Eq. 4 as discussed. An alternative approach is to note that, for the given (constant) water-to-biomass conversion ratio, each storm represents an injection of potential biomass, and the problem is to determine the amount of it that will be realized and when. The amount is determined by the assumption that, postinterception, all water infiltrating the root zone will be transpired, which is equivalent to saying that transpiration dominates leakage and evaporation within the root zone. The timing of this transpiration is assumed instantaneous, which reflects the fast nature of the soil moisture variations relative to those of the biomass. These two assumptions allow the dynamics to be resolved by a single state variable as in Eq. 5, without assumptions on the distribution of the root zone soil moisture. Thus, Eq. 5 represents not just a simplification of the two-state-variable model, but also an alternate closure condition. The theory for the underlying dynamics is further elaborated in Theoretical Model.

Analysis
Comparison of Field Measurements with Analytical Results. The modeling approach described above is used to examine the biomass response to an alternating regime of wet and dry seasons, as found at the study site. Schaffer et al. (3) showed that for typical dryland parameter values, the end-of-season biomass would be significantly different from that of the constant-parameter steady state (a similar calculation is performed in ref. 8). The system did not have time to adjust to a given season before it ended and the wet–dry cycle started over again. This was also confirmed for the site specifically (Fig. S2). Thus, it is the transient results of ref. 3, corresponding to Eq. 5, that form the departure point for the analysis here.

The equations describing the pdfs of biomass at any particular time in a wet or dry season and after a given number of consecutive seasonal–annual cycles have taken place are given in Eqs. S18–S21 and plotted in Fig. 2 for the site.

After infinitely many such cycles, the system will have converged to a “seasonal” steady state, where the statistics depend on the point in the year at which measurements are made (i.e., end of wet season, end of dry season), but not on the year in question. Fig. 2 also addresses the question, How long does it take for the seasonal regime to establish itself? This will necessarily depend on the initial state, because a more extreme state will persist for a longer time, but the steady-state distribution provides a useful baseline. To be explicit, suppose the system were exposed to wet (or dry) season conditions for an infinitely long time, allowing it to equilibrate to a sort of upper (or lower) bound on the vegetation state. How many dry–wet cycles will it take to effectively converge from these reference levels? Explicit formulas for the convergence of the moments are given in ref. 3 and in Eqs. S22–S24, but it is clear graphically from Fig. 2 that the impact of the alternating regime is well established after about 3 y and so beyond this point the seasonal steady state can be said to prevail. The mean and variance of the seasonal steady-state distributions are especially informative and their analytical expressions are given here in Eqs. 6 and 7. The quantities

\[ p_b = e^{-\beta(T)} T \]

\[ \alpha_d = 64.2 \text{ g m}^{-2} ; \mu_w = 183.1 \text{ g m}^{-2} \text{ and } \sigma_d = 15.5 \text{ g m}^{-2} ; \sigma_w = 45.6 \text{ g m}^{-2} \text{, respectively.} \]

Using the parameter values in Table 1, the analytical mean and SD of leaf biomass (leaves, new shoots) per unit of canopy area at the end of dry season and at the end of the wet season are \( \mu_d = 64.2 \text{ g m}^{-2} ; \mu_w = 183.1 \text{ g m}^{-2} \text{ and } \sigma_d = 15.5 \text{ g m}^{-2} ; \sigma_w = 45.6 \text{ g m}^{-2} \text{, respectively.} \]

The field measurements of leaf biomass per unit canopy area at the end of wet season are presented in Table S3 for each of the four plots used in this study.

The mean and SD of the biomass at the end of the wet season estimated using all four plots and their different years of measurements are \( \mu_w = 185.0 \text{ g m}^{-2} \text{ and } \sigma_w = 37.6 \text{ g m}^{-2} \text{, which are both remarkably close to those analytically predicted. (The estimate of the variance is in fact a slight underprediction due to the correlation between measurements made in successive years, although this effect is largely negligible. See Methods for details.) The slight overprediction of the variance is to be expected, as}
the no-storage model removes any temporal buffering effect the soil might have on the rainfall process; a water storage capacity within the plant tissues would also have a buffering, variance-reducing effect not captured by our model. Fig. 3 compares the cumulative distribution function of the leaf biomass data at the end of the wet season with that resulting from the theoretical distribution describing the seasonal steady state at that moment. Again, there is a remarkable agreement between the theory and the data.

There were no previous measurements of biomass at the end of the dry season and thus we performed individual biomass measurements in each of 22 well-established shrubs located in a different 10-m \( \times \) 10-m plot at the end of April 2016. The observed results of leaf biomass per unit canopy area at the end of the dry season are shown in Table S4. Because only a single year of dry season data is available, we cannot compute meaningful statistics or form the empirical distribution function. Whereas there is some variability from shrub to shrub, this is not attributable to random hydrological forcing, because each shrub in a small spatial area such as the plot is driven by the same rainfall process. Still, the single-year mean plot biomass may be computed, resulting in \( \mu_d = 68.4 \text{ g m}^{-2} \), which, perhaps fortuitously, is quite close to the predicted value. Additionally, the interplant variability (which indicates both species-inherent and spatial variability) can be compared with the predicted variability induced by the intermittent rainfall model to determine the relative size of these effects; in Methods, we show specifically that interplant contribution to the total variance is small.

The soil moisture was not a major focus of this study, and measurements are not currently available, but because the methodology of ref. 3 provides for it (Eqs. S26–S29), as a final item we compute the theoretical predictions of the soil moisture distributions that correspond to the end of season biomass states discussed above. These are shown in Fig. 4. Both seasons are characterized by very dry soils (with an overwhelming probability of being at less than 20% saturation), although end of wet season moisture content is higher. This is again indicative of the difference between the seasonal steady state and the “true” steady state, because infinitely long seasons would balance the change in rainfall with a change in transpiring biomass, resulting in the same mean soil moisture for either season.

Impact of Climate Change on Biomass and Soil Moisture Dynamics.

The theoretical framework described above allows us to study the impact of climate change on the leaf biomass dynamics arising from changes in the vegetation or climate characteristics. We assume that the type of plants at the site under analysis remains the same and that climate will follow the scenario described in the recent study of Gao et al. (9), which finds a likely increase in the total annual rainfall at the site between 10% and 25%. We also assume that most of the impact on biomass will arise from changes in the rainfall dynamics that in the modeling framework are controlled by the rate of arrival of wet days in each season \( (\lambda_0) \), the mean rainfall depth in a rainy day in each season \( (\alpha) \), and the seasons durations \( (T) \). The climate scenario to be studied retains the same length of seasons and increases by 10% the \( \lambda_0 \) and the \( \alpha \) values for each season. This leads to a total annual rainfall of 219 mm, which is about 21% above the present conditions and in the range found in the climate change study (9). The interception loss is assumed the same (\( \Delta = 1 \text{ mm} \)). Many other combinations of changes between \( \lambda_0, \alpha, \) and \( T \) could also be studied and this topic is being pursued for a number of regions throughout the world. Fig. 5 shows the seasonal steady-state pdfs for biomass at the end of the wet and dry seasons under the conditions of the new climate scenario. They should be compared with those in Fig. 2 describing the present conditions. The mean values and SDs are now \( \mu_w = 226.6 \text{ g m}^{-2}, \mu_d = 80.1 \text{ g m}^{-2} \) and \( \sigma_w = 53.2 \text{ g m}^{-2}, \sigma_d = 18.2 \text{ g m}^{-2} \). The steady-state pdfs for soil moisture under the conditions of the above climate change scenario experience very little change with respect to the present ones shown in Fig. 4; the additional rainfall predicted under climate change is largely offset—from the point of view of the soil water balance—by the larger amount of transpiring vegetation. Thus, the first-order effects of climate change would be on the vegetation, with the soil moisture experiencing second-order effects.

Finally, we point out that these predictions ostensibly address the biomass and soil moisture properties that would occur if the climate change scenario prevailed in place of the current one. We have not explicitly discussed the (temporally structured) transition from one regime to another, but in practice this distinction is of little consequence. The characteristic biomass adjustment timescale is on the order of \( 1/\beta \) (with full adjustment
even from a relatively extreme state occurring in <3 yr, as in Fig. 2), whereas the climate is predicted to change on the decadal scale, so the biomass at future times will tend to stay well adjusted to the climate at those times; e.g., Eqs. 6 and 7 for the mean and variance in a given year would be well determined by using the parameters prevailing in that year, the longer history being “forgotten” by the biomass process before the climate could change very much. However, we may add the caveat that the biomass considered here is the leaf biomass; the dynamics of seed germination/new plant emergence and wood growth might occur on timescales comparable to the climate change timescale.

Discussion

The analytically derived mean and SD of leaf biomass at the end of the wet season matches very closely with those measured in the field. Our single year of dry season data are also consistent with the data, although by itself it does not permit a good estimate of the distribution. Moreover, the analytical cumulative distribution of leaf biomass at the end of the wet season also agrees very well with the long-term data. This close agreement gives confidence to the values predicted under the climate change scenario studied for the site. In the wetter conditions considered in the scenario the mean biomass at the end of the wet season is 24% larger than the present one. For the dry season the change in mean biomass is 25%. The predicted increase in leaf biomass is thus very significant and carries important consequences for the structure of the ecosystem and for the future reforestation of other sites in the region. The predicted increase in the SD of leaf biomass is about 17% for each season and thus the coefficient of variation is reduced by near 6% for each season.

The above predictions are assuming that the increase in total rainfall results from an increase of 10% in both $\lambda_t$ and $\alpha$ for both seasons and that the duration of the seasons as well as the plant characteristics remain the same. Other scenarios can also be studied. If one wished to study a scenario where $\lambda_t$ and $\alpha$ remain the same and the 21% forecasted increase in annual rainfall results from an increase of 30.4% in the duration of the wet season, the predicted biomass at the end of the wet or dry season would be 205.0 g m$^{-2}$ and 84.3 g m$^{-2}$, respectively, which is quite different from that under the scenario considered here. This illustrates the importance of understanding the statistical structure of the rainfall and not just its mean values. We emphasize that this structure affects not only the shape of the biomass distribution (i.e., its higher-order moments), but also the mean biomass value; the nonlinear, threshold-type nature of the interception results in a greater fraction of water reaching the root zone when the mean rainfall depth increases, so that the mean biomass increases superlinearly (hence the 24% predicted increase with a 21% increase in annual rainfall, as discussed in the previous section).

Methods

Field Observations of the Desert Shrub Ecosystem. Four experimental plots of $10 \times 10$ m$^2$—identified by the year when revegetation was initiated—were studied in regard to their changes in plant biomass throughout the years. The shrub canopy projection area was calculated by taking the longest and shortest diameters through the center of the fullest part of the canopy. The biomass per unit canopy projection area at the end of wet season is calculated from a site-specific previously established empirical relationship between leaf biomass and canopy projection area (10, 11). The characterization was carried out at the individual plant level for the four plots in the years between 1981 and 1998. The percentage of the canopy coverage over the total area of the plot is the sum of the canopy areas divided by the plot area. No similar data were available for biomass at the end of the dry season. Thus, a preliminary estimation was carried out in this case for 2016. The biomass at the end of the dry season of the year 2016 was estimated by direct harvesting of one plot ($10 \times 10$ m$^2$) outside the long-term vegetation-monitoring plots because such a harvesting method is prohibited in those plots. With the measured leaf biomass and from the canopy projection area we calculate the leaf biomass per unit area of canopy coverage (10, 11). The measured biomass per unit canopy area and the canopy coverage area at the end of the wet season for the period 1981–1998 are given in Table S3 for all four plots. The corresponding values at the individual shrub level corresponding to the end of the dry season in 2016 are given in Table S4.

The active root zone depth ($Z_r$) where over 90% of the roots are contained was measured by ditches to a depth of 2 m with a width of 0.5 m across the center area where the shrubs grow. During this process observations were made of the root distribution. Saturated soil conductivity ($K_s$) was obtained via in situ infiltration measurements through a tension disk infiltrometer (12).

Canopy interception loss ($\Sigma = 1$ mm) was estimated as the difference between open-field rainfall and throughfall (13).

The transpiration rate ($E$) and photosynthesis rate ($P_o$) were measured on clear sunny days from the sunrise time at around 6 AM (local time) to the sunset time around 7 PM at time intervals of 1 h. Each measurement was taken on three mature shrubs. For each shrub, three labeled leaves from the top, middle, and low canopy positions were selected under non-water-limited conditions. Using a portable Li-6400 gas analysis system, the uptake of CO$_2$ of each labeled leaf was estimated (Li-Cor Inc.) and leaf area of the labeled leaves was obtained using the Li-3000 area meter after the gas exchange experiment was concluded. Thus, the $P_o$ and $E$ per unit leaf area were then calculated. The maximum $P_o$ and $E$ needed for the analytical calculations were then determined from the hourly variations of $P_o$ and $E$ from 6 AM to 7 PM. $P_o$ is the rate of the uptake of CO$_2$ per unit leaf area, and thus the net assimilation ($A_{\text{net}}$) per unit leaf area is calculated by subtracting the weight of carbon from the total molecular weight of CO$_2$ on the basis of the maximum $P_o$. The maximum daily transpiration, $E_{\text{max}}$ and maximum daily net assimilation, $A_{\text{max}}$ are then scaled to the daily duration of transpiration and photosynthesis activities, which is estimated in 13 h for the study area.

The root respiration coefficient, $R_o$, the fraction of daily assimilation lost in respiration by roots per unit mass of roots, was calculated from root respiration rates (obtained using the portable Li-6400 gas analysis system) and dry root weights. The other plant traits, e.g., the specific leaf area ($\phi$), leaf mass ratio (LMR), growth yield (Y$_g$), and senescence rate ($q$), were determined during the field survey (14). More details about the procedures are given in “Field Observations.” The values of the parameters are shown in Table S2.

Correcting the Variance. We have mentioned in passing two corrections to the variance that might arise, due to the variability between individual plants (i.e., a spatial correction), as well as to the interannual corrections.
of the measurements (i.e., a temporal correction). We address both types here and show that they are small.

We begin with the interplant variability. The most likely source of such variability in our model is that each plant may have a different value of the term \( \alpha / \gamma \), reflecting either variability in the efficiency of the plant (the amount of biomass realized per unit of water) or, more likely, variability in the horizontal spread of the root zone, which translates into a variability in the amount of water provided to the plant by each rainfall event. As shown in Eqs. S35 and S36, variability in this quantity scales the biomass of the corresponding plant by a fixed amount, but otherwise does not change its probabilistic behavior in time. If we let \( B_i(t) \) denote the biomass corresponding to the values \( \alpha / \gamma \) used previously, we can write for plant \( i \)

\[
B_i(t) = Z_iB_i(t),
\]

where \( Z_i \) is the relative efficiency, now permitted to have a spread around the reference value (i.e., the mean value) of unity. Each measurement of biomass at a given point of time involves an averaging over \( n_p \) plants,

\[
B(t) = \frac{1}{n_p}\sum_{i=1}^{n_p} B_i(t) = \mu Z(t),
\]

seen above to separate as a product of the average relative efficiency with the reference biomass (which is, to reiterate, the one corresponding to the efficiency value used throughout this paper). The total variance is obtained by conditioning on the value of the random variable \( \mu Z \), using the law of total variance (see Eqs. S35–S40 for details):

\[
\text{Var}(\theta) = \sigma^2 + \text{Var}[\mu Z] + \mu^2 \sigma^2 = \sigma^2(1 + \mu^2 \frac{1}{n_p} \frac{\sigma_Z^2}{\sigma_\theta^2}).
\]

Here, \( \sigma^2 \) is the analytical variance induced by the stochastic rainfall process. The second term in the parentheses is the fractional variance correction due to the interplant variability, which depends on two new quantities: the variance of the relative efficiency \( \sigma^2_Z \), determined by the detailed, plant-by-plant measurements made in the dry season of 2016 as \( \sigma^2_Z \approx 0.056 \), and also the number of plants \( n_p \) used to determine each year’s biomass. The plot in which the 2016 dry season measurements were made had 22 plants, and the other plots had a comparable number, so that the variance correction from this source is about 1%.

We turn now to the temporal correction; because of the interannual correlations of the measurements, the standard estimate of the variance will be biased. In particular, because the correlations are positive, it will on average yield an underestimate. The standard estimator of the variance for \( n \) independent measurements \( X_i \) is

\[
\hat{\sigma}^2 = \frac{1}{n-1} \sum_{i=1}^{n} (X_i - \bar{X})^2.
\]

Taking the expectation of both sides gives

\[
\text{Var}[\hat{\sigma}^2] = \sigma^2 - \frac{1}{n\bar{T}} \left[ \sum_{i=1}^{n} \sigma^2 + \sum_{i=1}^{n} \sum_{j=1}^{n} \sigma^2 \right],
\]

where \( \bar{T} \) is the number of growing seasons for which measurements were made. As shown in Eq. S33, the autocovariance between measurements \( i, j \) is \( \rho_{ij} \), where as before \( \rho_{ij} \) is a decay factor (Eqs. 6 and 7). Substituting and summing the resultant geometric series gives the result in Eq. 13, whence we see that the error is about 1% (with \( n = 14 \), using all data shown in Table S3):

\[
\text{Var}(\hat{\sigma}^2) \approx \sigma^2 \left( 1 - \frac{2\rho_{ij}}{\bar{T}} \right).
\]

[13]

Determining the Rainfall Parameters. As a final point, we address the question of how to accurately determine the rainfall parameters. The values used thus far were obtained by averaging over a relatively long time period, 1956–2015, whereas our biomass measurements were made over the shorter period 1989–1998, with the bulk of the measurements in 1989–1998 when all four plots were incorporated. To justify this, let us consider what would happen if we tried to determine the rainfall parameters from a more targeted time interval, e.g., the 10 y of 1989–1998. To be concrete, let us consider the determination of the wet season rainfall arrival rate \( \lambda_{w} \). Suppose the true value were as estimated above, \( \lambda_{w} = 0.231 \frac{d}{d^{-1}} \); then we can compute the sampling error as follows. The variance over time \( T \) of the number of rainfall arrivals for such a Poisson process is

\[
\sigma^2_{\lambda_w} = \lambda_{w} T
\]

and the variance in the corresponding estimate \( \hat{\lambda}_{w} = N/T \) is

\[
\sigma^2_{\hat{\lambda}_w} = \frac{\lambda_{w} T}{T^2} = \frac{\lambda_{w}}{T}.
\]

If we made this estimate over 10 y of wet seasons, then \( T = 10 T_w \), and we would find that \( \lambda_{w} T = 0.0723 \frac{d}{d^{-1}} \); and so the size of the 2σ range would be 21% of the true value, which is rather large. Thus, in using the full rainfall history to estimate the parameters, we have made a tradeoff: We reduce this statistical imprecision of the determination, but we necessarily risk averaging out genuine variations. A more detailed climatological history is beyond the scope of this work, although any reader concerned by this method may be assuaged by the fact that if we did restrict our estimation window to, e.g., 1989–1998, we would get for the (wet, dry) season, respectively a \( a = 43.32, 2.41 \) mm, \( \lambda_{w} = 0.221, 0.0778 \) d⁻¹, \( \lambda = 0.175, 0.0514 \) d⁻¹, yielding the biomass prediction \( \mu Z = (184.5, 71.6) \text{ g m}^{-2} \), \( n_p = (46.2, 17.6) \text{ g m}^{-2} \); these values are almost identical to the stated results.

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Field Site and Vegetation

The field campaigns and measurements were conducted at Shapotou Desert Research and Experiment Station of the Chinese Academy of Sciences (37°32' N, 105°02' E), with an elevation of 1,300 m above mean sea level, bordering the Tengger Desert, which is the fourth largest desert in China. The study site is part of the Inner Mongolian Highland Region and is at the extreme southeast end of the Tengger Desert. The climate of the site is characterized by arid to semiarid conditions. Mean annual precipitation is 182.6 mm (during the years 1956–2015) with 82% of the rain falling in the wet season of approximately 153 d between May and September. The monthly average temperature is highest in July at 24.6 °C and lowest in January at −5.6 °C. During the growing/wet season, the rainfall dynamics are characterized by a large variation in total precipitation between 60.0 mm and 269.5 mm, and the daily rainfall events vary between 21 mm and 52 mm. The mean daily temperature varies between 12.9 °C in April and 17.7 °C in July, with a maximum value of 24.6 °C in July. The dune sands characteristic of the site consist mainly of fine sand, 0.05–0.25 mm, and clay content of about 0.2%. The sand is classified as Typic Psammaquents (15). Groundwater is found at a depth below 50 m in the 80-m-thick sand. Soil moisture content is restricted by the very modest and fluctuating annual precipitation, which dominates and constrains the number and size of plant species. Rainfall dynamics are characterized by the rate of rainy days, λa, and the mean rainfall in a rainy day, s, as described in the main text. The fluctuations of these two parameters from 1956 through 2015 are shown in Fig. S1. Climate and soil parameters used in the analysis are shown in Table S1. To protect the Baotou–Lanzhou railway against encroaching sand dunes in the Shapotou area, straw checkboards (spacing 1 × 1 m²) were established by inserting straws vertically into the soil to a depth of 15–20 cm, protruding approximately 10–15 cm above the dune surface to stabilize the shifting sand dunes by increasing the surface roughness (16). Desert shrub seedlings (e.g., Salix gordejevii, Calligonum arborescens, Atraphaxis bracteata, Caragana korshinskii, A. ordosica, and Hedysarum scoparium) were then planted in straw checkboard plots in the 1950s, the 1960s, and subsequent years. Over time, a seminatural desert ecosystem dominated by dwarf-shrub A. ordosica associated by annual grasses of Bussia dasypila and Eragrostis poaeoides was established (4). The success of this effort has not only ensured the safe operation of the railway in the sand dune area, but has also played an important role in the restoration of the local eco-environment (17).

The desert shrub A. ordosica has a stomatal behavior adaptable to survive drought-prone environments and it is a superior competitor in the site conditions via fluctuations in stomatal conductance, transpiration, and photosynthetic rate (14, 18, 19). It also presents a high regeneration capacity of seedling clones (5) and an adaptive distribution of the root system that concentrates in the shallow soil layers (17).

Field Observations

Four long-term vegetation dynamics monitoring plots (10 m × 10 m each) were established. They are identified in accordance with the years of their revegetation. The shrub canopy projection area was calculated by taking the longest and shortest diameters through the center of the fullest part of the canopy.

The estimation of biomass is carried out via allometric equations, a commonly used nondestructive alternative where the estimation is done on the basis of easily measured growth attributes (10, 11, 20–23). Here, the leaf biomass per unit canopy projection area at the end of the wet season is estimated from the empirical relationship between the biomass and the canopy projection area (10, 11) at the plant level for the four plots in the years between 1981 and 1998. The percentage of the canopy coverage over the total area of the plot is the sum of the canopy area divided by the plot area (Table S3). The leaf biomass at the end of dry season of the year 2016 is estimated directly in the field by a harvesting method at one plot (size 10 m × 10 m) outside the abovementioned long-term vegetation dynamic monitoring plots for the reason that using the harvesting methods to measure biomass in these plots is prohibited. The individual plant measurements at the end of the 2016 dry season are given in Table S4.

The active root zone depth (Zr) where most of the roots are contained was observed from a number of ditches to a depth of 2 m below the ground, with a width of 0.5 m across the center area where the shrub grows. During this process we took casual observation of the root distribution. Saturated soil conductivity (Ks) was obtained by in situ infiltration measurements from a tension disk infiltrometer (12).

The wilting point for A. ordosica was estimated as the difference between open-field rainfall and throughfall. It relies on a least-squares regression of below-canopy precipitation against open-field rainfall under natural conditions (13).

The transpiration rate (E) and photosynthesis rate (Pn) were measured on a clear sunny day from the sunrise time at around 6 AM (local time) to the sunset time at around 7 PM (local time) with intervals of 1 h. Every measurement was taken in three mature shrubs. Measurements were carried out for three labeled leaves from the top, middle, and low positions in the canopy. Measurements for nonlimited water conditions were carried out using a portable Li-6400 gas analysis system (Li-Cor Inc.), monitoring the CO2 concentration to determine the uptake of CO2 of the labeled leaf inside of the leaf chamber of the Li-6400. The leaf areas of the labeled leaves were measured using a Li-3000 area meter (Li-Cor Inc.) after the gas exchange experiment to calculate the Pn and E per unit leaf area (18). The maximum Pn and E were then determined according to the daily variation of Pn and E from 6 AM to 7 PM. Pn is the rate of the uptake of CO2 per unit leaf area, and thus, the net assimilation, An, per unit leaf area is calculated by subtracting the weight of carbon from the total molecular weight of CO2. The maximum transpiration rate and net assimilation rate were then scaled to daily values using 13 h/d as the period of duration of photosynthetic and assimilation activities.

The soil respiration rate (Rr) during the growing season was measured under non–water-limited conditions, using a closed-chamber portable Li-6400 gas analysis system as described by Norman et al. (24). Rr is made up of root respiration and microbial respiration (Rm). Root respiration refers to root-derived CO2 that combines root respiration and rhizosphere respiration. Rm refers to that from soil organic matter. Root respiration is then estimated as the difference between Rr and Rv [Kucera and Kirkham (25)]. The linear relationship between the root respiration rate and root biomass yields the root respiration coefficient (Rr), which is the fraction of daily assimilation lost in respiration by roots per unit mass of roots [Gifford (26)].
The canopy-to-root ratio \( A_c/A_r \) was estimated from ref. 27. [Taking the ratio of mean plant canopy area \( A_c = 0.97 \text{ m}^2 \) to the average root area in the outer root band between 0.8 m and 1 m, so \( A_c = (\pi (0.8^2 + 1^2)/2) \text{ m}^2 = 2.576 \text{ m}^2 \), and then \( A_c/A_r = 0.38 \).] This parameter is difficult to estimate precisely, as \( A_r \) is the catchment area of the roots, which depends on the distribution of fine roots as well as coarse roots, and varies as the square of the root radius, complicating the uncertainty. When there is uniform (nonpatchy) vegetation coverage—as in, e.g., a dense grassland—this difficulty disappears, as then the canopy and root areas are equal to the plot or reference area, but this is not the case here.

The other plant traits such as the specific leaf area (ratio of leaf area to dry leaf mass, \( \rho \)), leaf mass ratio (ratio of leaf dry mass to plant mass, \( f_L \)), growth yield (\( Y_g \)), and senescence rate (\( \phi \)) were determined during the field survey (14).

To estimate the root senescence rate, the sequential coring method was used, measuring living root and dead root biomass. Dead roots were identified by changes in shape, color, and elasticity. The senescence ratio was then estimated by dividing the annual root necromass by the mean biomass (28).

The above parameter measurements are summarized in Table S2.

**Theoretical Model**

The theory of the vegetation dynamics is discussed, especially focusing on the simplifications needed to obtain them and the resulting interpretations of the parameters appearing in the main text. The necessary parameter values are provided in Tables S1–S4.

**Vegetation Dynamics—Allometries, Biomass Types, Partitioning.** Our prior work (e.g., ref. 3) was largely theoretical and did not delve into the details of the plant physiology, focusing rather on the structure of the distributions generated by interacting biomass and soil moisture. To compare with specific field observations, it is worth revisiting the derivation of the fundamental equations to remove any ambiguity about the meaning of their terms. *A. orodosica* is a shrub with fine root, leaf, and woody tissues, and its description in time could in principal require three nontrivial biomass state variables, with the dynamics generated by

\[
\frac{dB}{dt} = A_m Y_g \rho \eta(B, S) [B_L - \beta_i^*(B, S) B_i + \sum_{j \neq i} \Omega_{i,j}(B, S)] \quad i \in \{L = \text{"leaf"}, r = \text{"root"}, w = \text{"wood"}\}. \tag{S1}
\]

The meanings of the various terms are as follows. Carbon gains are given by a gain rate per unit of leaf biomass \( A_m Y_g \rho \), multiplied by the amount of leaf biomass present in the system, where \( A_m \) is the maximum assimilation rate per leaf area, \( \rho \) is the specific leaf area, and \( Y_g \) is the growth yield—the fraction of carbon available after paying the respiration costs of the assimilation/photosynthesis process. Consider the system to include all biomass of the species under consideration in the plot, so that the expression \( B \) appearing in Eq. S1 is a total biomass, in grams, rather than a per-unit-area biomass of any kind (in the main text \( B \) is redefined per unit canopy area, as discussed below).

\( B \) is the biomass state variable, which now is a vector with the different biomass components (\( B_i \), without the vector sign, denotes the total scalar biomass: i.e., \( B = B_{Lr} + B_{Lr} + B_{w} \)). The factor \( \eta \) has its usual meaning as the inhibition function for assimilation (or transpiration), although the most general case is indicated above in which it can depend on the biomass state in addition to the soil moisture, because, e.g., for any given saturation level, the density of the roots or the conductance of the xylem can affect the ease of removing water from the soil. This additional dependency on \( B \) will actually not change much theoretically for the no-storage model, because \( \eta \) is eliminated anyway by using the soil moisture equation later on or, as described in this paper, the details of the water uptake rate following a rainfall infiltration will not matter provided the correct amount of water is accounted for. The terms \( \beta_i^* \) are losses of (or from) each tissue type to the surrounding system, which are distinct from the whole plant loss rate \( \beta \) we have typically used (as described below), and hence the asterisk.

There are two terms here that we have not previously explicitly written. The factor \( \xi \), gives the fraction of assimilated carbon that is partitioned into each tissue type, which in principle can depend on the total state of the plant \( B \) as well as the soil moisture state. The relation between \( \xi \) and the allometric fractions we previously used, \( f_L \), depends on the assumptions made to reduce this system of equations, as detailed below. The other new term is \( \Omega_{i,j} \), which is a carbon (i.e., biomass) transfer term into tissue type \( i \) from \( j \); we have implicitly used the existence of such terms before, namely to maintain our linear allometric relationship between root and leaf biomass.

The question now becomes, How do we reduce the set of equations given in [S1] to a single biomass equation such as that given in Eq. 3, and what are the implications for how we interpret the parameters? The first step is to assume the loss coefficients are constant, so that losses are linear with respect to biomass. This implies the following:

- Losses are strictly per unit, with no whole-plant effects. That is, a gram of root tissue experiences a loss rate (due to, e.g., senescence and respiration) that is unrelated to the rest of the plant state, such as amount of leaf coverage or wood/xylem health.
- No dependence of \( \beta \) on the soil moisture state means that we are essentially considering a carbon-starvation model, in which biomass loss from lack of water occurs because there is insufficient carbon to pay the metabolic costs. This is in contrast to models in which lack of water creates low water potential leading to tissue damage, the repair of which dominates the carbon deficit. Thus, asserting \( \beta \neq \beta(S) \) implies that the plant tissue is very drought tolerant.

We now want to isolate an equation for the leaf biomass dynamics while preserving tractability, and the typical choice is to assume (Linear Allometries) a set of allometric relationships. This is the approach used in this paper, although it is interesting to note that an equation of the same form is obtained for an opposite extreme of plant behavior: Rather than assuming the plant has perfect top–down management and reallocation of its biomass, specifically designed to maintain the allometries, we can assume (Independent Leaves) that leaf biomass evolves completely independently of the other two types.

**Linear Allometries.** We can proceed from Eq. S1 by summing the three component equations. By conservation of mass, the partition fractions must sum to unity (\( \sum_i \xi_i = 1 \)), and the transfer terms must sum to zero (\( \sum_{i,j \neq i} \Omega_{i,j} = 0 \)), because all newly assimilated carbon must go to one of the three components, and the transfer terms move only mass within the plant, but cannot change the total. The resulting equation is

\[
\frac{dB}{dt} = A_m Y_g \rho \eta(B, S) [B_L - \sum_i \beta_i^* B_i]. \tag{S2}
\]
This is a mixed equation, and we can use the allometric assumption to reduce it to a single-state biomass variable. Even though the transfer terms have disappeared, we specify that they are calibrated so that the plant is continuously pushing biomass around between the tissue types according to the linear allometry

\[ B_i = f_i B \quad i \in \{ L, r, w \}. \]  

Substituting into Eq. S2 gives a single-biomass equation:

\[ \frac{dB}{dt} = A_m Y_r \rho f_L \eta(B, S) B - \sum_{i \in \{ L, r \}} f_i \beta_r^* B. \]  

The reduced gain and loss rates have been identified in the above as respectively \( \alpha \) and \( \beta \). Note that the loss coefficient \( \beta = \sum_i f_i \beta_r^* \) is the weighted sum of the tissue-specific loss coefficients, but that the net coefficient for a given tissue type under the allometric assumption is now different because of the transfer terms we needed for the allometric approach in the first place. To be concrete, we can multiply Eq. S4 by \( f_i \) to express it in terms of leaf biomass:

\[ \frac{dB_L}{dt} = \alpha \eta(B_L, S) B_L - \beta B_L. \]  

The leaf biomass has the same loss coefficient as the overall biomass, namely \( \beta \), rather than \( \beta_r^* \). In other words, the leaves experience their proportional share of total plant losses, whatever those might be, rather than losses incurred specifically by leaf tissue. Eq. S5 is nominally identical to that used for the analysis in this paper, although we should be a bit careful when it comes to physically understanding the transfer terms. It is physically realistic that the plant has some ability to perform such transfers, perhaps by cannibalizing the tissue in the fine roots to free up carbon/energy for the leaves. However, wood tissue is a sunk investment; a plant under stress loses its leaves/roots, but cannot reallocate its own trunk to become a smaller, unstressed tree. Thus, it does not make sense for wood tissue to be part of the allometry on the timescales of interest. We can assume that the wood is completely static and inert (characteristic perhaps of a mature shrub), so that it has no transfer terms, receives no newly assimilated carbon, and causes no losses, and restrict attention only to the roots and leaves, in which case we have the final equation (for the leaves)

\[ \frac{dB_L}{dt} = \alpha \eta(B_L, S) B_L - \beta B_L \quad \alpha = A_m Y_r \rho f_L, \quad \beta = \sum_{i \in \{ L, r \}} f_i \beta_r^*, \]  

which is the same as Eq. S5, except that the wood fraction \( f_w = 0 \), which is equivalent to renormalizing the mass fractions for roots and leaves only. Alternatively, we could allow for some fraction of new carbon to be allocated to wood, but for the wood to not otherwise interact with the dynamics (no transfers, no losses per se), which would give the equation

\[ \frac{dB_L}{dt} = \alpha \eta(B_L, S) B_L - \beta B_L \quad \alpha = A_m Y_r \rho f_L, \quad \beta = \sum_{i \in \{ L, r \}} f_i \beta_r^*, \]  

which is the same as Eq. S6, except that the gain rate \( \alpha \) is reduced by fraction \( \xi_{L+r} < 1 \) of its original value, because the remaining fraction is going to wood. In summary, Eqs. S6 and S7 are the proper ones for use in the sort of analysis performed here under the allometric approach, with [S5] applying only if the wood is “flexible” to reallocation. In either case, we assume losses are dominated by leaves and roots, so that

\[ \beta = f_r \beta_r^* + f_i \beta_L^* = (1 - f_L)(R_r + q_r) + f_L q_w, \]  

where \( R_r \) [d\(^{-1}\)] is the root respiration coefficient, \( q_r \) [d\(^{-1}\)] is the root senescence rate, and \( q_L \) [d\(^{-1}\)] is the leaf senescence rate. It is observed (through the direct field observations of X.-p.W.) that under conditions of low water stress, \( q_L \) is very small compared with the dominant loss term (root respiration), and we estimate it as equal to the root senescence rate \( q_L = q_r \equiv q \); the effect of this assumption on the overall loss rate is minimal.

There is a subtle point here, which is that even though we determine \( \beta \) for a small value of \( q_L \), we are not neglecting the possibility of more pronounced leaf senescence. Rather, the measurements made of the root turnover and respiration (as described previously) fully capture the metabolic costs of maintaining plant tissues, including the leaves, when these measurements are made under nonstressed conditions. When water stress occurs due to the intermittent nature of the rainfall or the transition to the dry season, these costs remain the same, except that their expression is shifted from respiration, associated with tissue maintenance, to senescence as the (leaf) tissue dies. Thus, the parameter \( \beta \) is calculated as

\[ \beta = f_r \beta_r^* + f_i \beta_L^* = (1 - f_L)R_r + q. \]  

**Independent Leaves.** As an alternative approach, we can go all the way back to the general dynamics in Eq. S1 and consider the leaf biomass component (dropping the wood transfer term, which as argued above should vanish)

\[ \frac{dB_L}{dt} = A_m Y_r \rho \xi_L (\bar{B}, S) \eta(\bar{B}, S) B_L - \beta_L^* B_L + \Omega_{L+r}. \]  

Rather than assuming a high degree of coordination with the roots to maintain a given biomass proportion, we could assume the leaves function independently: They exchange no biomass \( \Omega_{L+r} = 0 \), and they do not account for the state of the rest of the plant (or the soil moisture) when “deciding” what fraction of assimilated carbon \( \xi_L \) to keep, so that \( \xi_L \) is a constant, resulting in the equation

\[ \frac{dB_L}{dt} = A_m Y_r \rho \xi_L \eta(\bar{B}, S) B_L - \beta_L^* B_L. \]  

This has the same form as Eqs. S6 and S7, but with \( \xi_L \), the partition fraction, appearing in the definition of \( \alpha \) rather than \( f_L \) or \( \xi_{L+r} f_L \), and with \( \beta_L^* \), the leaf loss coefficient, due only to tissue-specific loss mechanisms (leaf metabolism, leaf senescence), rather than being
the leaf fraction of the whole-plant loss coefficient. This approach is, to our knowledge, uncommon; we identify it to make the point that there are several physiological models that give rise to the same form of differential equations and that the allometric approach involves nontrivial assumptions.

Inhomogeneous Coverage and Water Balance. No matter which approach is used to define the biomass equation, the system requires a soil moisture equation. Because the shrubs do not form a continuous cover, there is some root area \( A_r < A \), where \( A \) is the reference plot area (here equal to 100 m\(^2\)). The roots are occupying a “total bucket” of volume \( V_r = A_r n Z_r \), so the water balance equation is (compare Eq. 2 of the main text)

\[
A_r n Z_r \frac{dS}{dt} = -E_m \rho \eta(\vec{B}, S) B_L + A_r I. \tag{S12}
\]

This equation can be reexpressed, as shown below, to cast it in the desired form. However, we first emphasize a subtle point about the water balance: The term \( A_r \) multiplying the infiltration rate \( I \) represents the plot area from which incident water enters the root zone (which we call of the root catchment area), and this in principle may differ from the definition of \( A_r \) as the coverage area of the roots. In particular, a system that exhibited overland flow due to unsaturated runoff would have two distinct values, and the root catchment area would be larger or smaller than the root coverage area, depending on whether the net effect of the overland flow were to shunt water into or away from the vegetation. In the site considered here, such a flow is not observed—a feature consistent with the high-permeability sandy soil and the small amount of water in each rainfall event—and so we assume a single value of \( A_r \).

Rescaling Eq. S12, we have the full system

\[
\begin{align*}
\dot{B}_L &= \alpha \eta B_L - \beta B_L \quad \alpha = \left( \frac{A_m Y_p \rho f_L}{\xi_{L+r} A_m Y_p \rho f_L} \right) \beta = \left( \sum_{i \in \{L,r\}} \frac{f_i B_i^*}{\beta_i^*} \right) \\
\dot{S} &= -\eta \gamma B_L + I \quad \gamma = \frac{1}{A_r n Z_r} \tag{S13} from [S12]
\end{align*}
\]

These equations describe the total leaf biomass in the plot and the soil moisture within the span of the shrub root zones, which may be overlapping (although assumed nonoverlapping or at least noninteracting with other species). Because it is extremely difficult to directly measure the root area \( A_r \), we instead assume a fixed ratio between \( A_r \) and the canopy area \( A_c \), which can be measured, and renormalize the biomass accordingly:

\[
\begin{align*}
\dot{\bar{B}}_L &= \alpha \eta (B_L/A_c) - \beta (B_L/A_c) \quad \alpha = \left( \frac{A_m Y_p \rho f_L}{\xi_{L+r} A_m Y_p \rho f_L} \right) \beta = \left( \sum_{i \in \{L,r\}} \frac{f_i B_i^*}{\beta_i^*} \right) \\
\dot{\bar{S}} &= -\eta \gamma (B_L/A_c) + I \quad \gamma = \frac{A_r}{A_c} \frac{E_m \rho}{n Z_r} \tag{S14} from [S12]
\end{align*}
\]

This gives the result for biomass/soil moisture dynamics per unit canopy area, as in the main text, using the first of the three parameter interpretations above for the biomass dynamics. It is essential to note we assume canopy and root areas are constant with respect to the dynamics in both of these cases, where “constant” means that they are defined by the spatial extent of the wood tissue (branches and coarse roots), which varies more slowly than the leaves and fine roots.

Alternate Model—Spatial Growth. As mentioned, the above results assume that new leaf growth and water uptake are happening within an area already defined (external to the dynamics), by either the canopy or the root coverage areas. As a final comment in this section, we propose that the same basic equations can be used to describe a sparsely vegetated landscape in which canopy (and root) radii are variable, so that the noise term is multiplicative. This actually has the same form we have been using, because (defining \( U \equiv B^{1-p} \)) we have

\[
\dot{\bar{B}} = \alpha B^p I - \beta B \quad 0 < p < 1 \tag{S15}
\]

so that the noise term is multiplicative. This actually has the same form we have been using, because (defining \( U \equiv B^{1-p} \)) we have

\[
\dot{\bar{U}} = (1 - p) \alpha I - (1 - p) \beta U \tag{S16}
\]

which is the same as our current model except with a transformed state variable and \( \beta U = (1 - p) \beta \), \( \alpha U = (1 - p) \alpha \); this again corroborates our observation that there are several systems and interpretations to which the form of our dynamics applies.

Statistics of the No-Storage Limit—Analytical Results

As discussed in the main text, the biomass dynamics can be simplified in the limit where incoming water is immediately transpired, so that (from Eq. 5)

\[
\dot{\bar{B}} = \frac{\alpha}{\gamma} I - \beta B. \tag{S17}
\]

The justifications for this approximation are discussed rather extensively in our previous work [Schaffer et al. (3)], in which we also derive many of the analytical results used here for the probability distributions. Here we briefly rewrite the key analytical results for ease of reference (results below are from this reference unless otherwise indicated). These take the form of the probability distributions of biomass and soil moisture.

To quote ref. 3 verbatim, “We consider distinct climate epochs with each epoch corresponding to a year made up of a wet and a dry season with distinct rainfall parameters \( (\lambda_w, \lambda_d) \) and \( (\theta_w, \theta_d) \) and durations \( (T_w, T_d) \). Suppose for concreteness that each year \( j \) consists of a dry season followed by a wet season, the initial biomass at the start of year \( j = 1 \) is distributed as an arbitrary variable \( B_0 \),
and that the biomass evolves under these dry/wet fluctuations into year \( j = J^* \) (ref. 3, p. 14). We call \( B_{j,d}(t) \) and \( B_{j,w}(t) \) the biomass after time \( t \) has passed in the dry (wet) season of the final year \( J \). The pdfs of these two random variables are easier to express through the Laplace transforms of the scaled biomass \( B' = \theta_p B \) and the ratio \( r = \theta_d/\theta_w = \theta_d/\theta_w \), where \( \theta = (\gamma/\alpha)\theta_w \).

\[
\tilde{f}_{B_{j,d}(t)}(z) = \left( \frac{r + p z}{r + z} \right)^q \prod_{j=1}^{J-1} \left( 1 + p_w p_{w-1} p z \right)^q \left( \frac{r + p_d p_{d-1} p z}{r + p_d p z} \right)^q \tilde{f}_{B_d}(p_d^{-1} p z)
\]

[S18]

\[
\tilde{f}_{B_{j,w}(t)}(z) = \left( \frac{1 + p z}{1 + z} \right)^q \tilde{f}_{B_{j,w}(t)}(z) \prod_{j=1}^{J-1} \left( 1 + p_d p_{d-1} p z \right)^q \left( \frac{r + p_d p_{d-1} p z}{r + p_d p z} \right)^q \tilde{f}_{B_d}(p_d^{-1} p d p z)
\]

[S19]

where \( p = p(t) = e^{-\beta t} \) and \( p_{\{j\}} = p(T_1) \) for \( \{j \in \{a, w, d\} \). For both the wet and dry cases, the initial value \( B_0 \) is taken to follow the corresponding wet or dry steady-state distribution, so that the initial distributions (in scaled units) correspond to

\[
\tilde{f}_{B_d}(z) = \begin{cases} \left( \frac{1}{1 + \tau} \right)^q d \\ \text{wet initial condition} \\ \left( \frac{\beta \tau}{\tau + \beta} \right)^q d \\ \text{dry initial condition} \end{cases}
\]

[S20]

The inversion may be performed with respect to the variable \( B' \), and the distribution in the physical biomass units can be recovered by rescaling:

\[
f_{B_{j,d}(t)}(b') = \mathcal{L}^{-1} \left[ \tilde{f}_{B_{j,d}(t)}(z) \right](b')
\]

[S21]

The above Eqs. S18–S21 are used to generate the plots in Figs. 2, 3, and 5 of the main text.

The behavior of the time-dependent cumulants (recall that the cumulants are equivalent to the moments; the first cumulant is the mean, and the second is the variance) of such a biomass distribution is given explicitly in ref. 3 as

\[
\kappa_n(B_{j,d}(t)) = \left( e^{-\gamma \alpha t} (1 - p_w^{n(J-1)}) \left( \frac{\kappa_n(Y_{(d,w)}(t))}{\theta_w} + p_w^n \kappa_n \left( \frac{Y_{(d,T_d)}}{\theta_d} \right) \right) + \kappa_n \left( \frac{Y_{(d,t)}}{\theta_d} \right) \right)
\]

[S22]

\[
\kappa_n(B_{j,w}(t)) = e^{-\gamma \alpha t} \kappa_n(B_{j,d}(T_d)) + \kappa_n \left( \frac{Y_{(w,t)}}{\theta_w} \right)
\]

[S23]

where \( Y_{(d,w)} \) has cumulants defined by

\[
\kappa_n(Y_{(d,w)}(t)) = \frac{\lambda (d,w)(n-1)!}{\beta^{(d,w)}} \left( 1 - e^{-\gamma \alpha (d,w) t} \right)
\]

[S24]

The nonseasonal steady-state pdf for the biomass (i.e., when a single pair of values \( \lambda, \alpha \) persists indefinitely) has an exact expression for the inverse transform:

\[
f_{B}(b) = \hat{\theta}^{-\beta} \hat{\lambda}^{q-1} \hat{\theta}^{-\theta} \hat{\lambda} \hat{\theta} \equiv \frac{\lambda}{\beta} \hat{\theta} \equiv \frac{\gamma}{\alpha} \hat{\theta}
\]

[S25]

This may be understood as a limit toward which infinitely long seasons converge. Finally, the soil moisture distribution associated with the no-storage limit corresponds to the soil moisture dynamics generated by

\[
\hat{S}_{d,w} = -\gamma \mu_{d,w} \eta(S) + 1
\]

[S26]

in which the transpiration term takes the mean biomass of the corresponding season as a constant parameter. The resulting distribution is

\[
f_{\hat{S}}(s) = \frac{C_s}{\eta(s)} e^{-\theta_s + \frac{\Delta s}{\alpha} + \frac{\psi}{\pi(\gamma)} \frac{\theta_s}{\pi(\gamma)}}
\]

[S27]

In contrast to ref. 3, we use a piecewise linear form here for \( \eta \),

\[
\eta(s) = \begin{cases} 0 & s < s_w \\ s-s_w & s_w < s < s^* \\ 1 & s > s^* \end{cases}
\]

[S28]

so that the explicit form of the distribution becomes (using the translated variable \( x = s - s_w \))

\[
f_{\hat{x}_{d,w}}(x) = \left( \theta^{-\psi} \Gamma(\psi) \Gamma'(\theta s^*, \psi) \left( \theta - \psi + x^* \right)^{-1} \right) \left( \frac{x^* - 1}{\theta - \psi + x^*} \right) \left( \frac{x^* - 1}{\theta - \psi + x^*} \right) \left( \frac{\lambda x^*}{\gamma \mu_{d,w}} \right)
\]

[S29]

which is the expression used to create Fig. 4. Note that \( \Gamma \) is the usual gamma function, and \( \Gamma_i \) is the lower incomplete gamma function

\[
\Gamma_i(x, a) \equiv \frac{1}{\Gamma(a)} \int_0^x \tau^{a-1} e^{-\tau} d\tau.
\]

[S30]
Finally, we need two results relating to the determination of the variance. The first of these is the autocovariance function needed to compute the expectation of the variance estimator in the main text (Methods). It is a general result for two random variables \( X_i, X_j \) that if they are linearly related, i.e., by
\[
X_i = aX_j + Z
\]  
and \( X_i \) and \( Z \) are independent, then \( \sigma_{ij}^2 = a^2 \). In the present case, \( Z \) is the net new biomass assimilated by rainfall over a time period, \( X_j \) is the initial biomass, and \( X_i \) is the final biomass, as in ref. 3,
\[
B(t + t_0) = e^{-\int_{t_0}^{t} \beta(t') \, dt'} B(t_0) + \frac{\alpha}{\gamma} \int_{t_0}^{t} e^{-\int_{t_0}^{t'} \beta(t'') \, dt''} I(t') \, dt',
\]
where the rightmost term is a function only of the rainfall after \( t_0 \) (and so independent of \( B(t_0) \)). If \( \beta \) is assumed constant as here, and the interval is indexed by the starting year \( j \) and ending year \( t \), then
\[
\sigma_{ij}^2 = e^{-\beta[i-j]} \, Z = p_a[i-j].
\]
It follows that
\[
E[\sigma^2] = E\left[ \frac{1}{n-1} \sum_{i=1}^{n} (X_i - \hat{\mu})^2 \right] = \sigma^2 - \frac{1}{n(n-1)} \sum_{i=1}^{n} \sum_{j \neq i} \sigma_{ij}^2,
\]
where the second equality follows using the definition of \( \hat{\mu} \), reflecting either variability in the efficiency of the plant (the amount of biomass realized per unit of water) or, more likely in our case, variability in the horizontal spread of the root zone, which translates into a variability in the amount of water provided to the plant by each rainfall event. Eq. S32 shows that once the effect of the arbitrary initial conditions has vanished, all plants experiencing the same rainfall process \( I \) will have the same biomass, up to the factor of \( \alpha/\gamma \equiv W \). Thus, for plants \( i \) and \( j \) (note that these are indexes of the plant, not of time)
\[
B_i(t) = \frac{W_i}{W_0} B_j(t),
\]
if we define \( W_0 \) as the reference efficiency value (i.e., that corresponding to the value of the parameters \( \alpha, \gamma \) used throughout this paper, which we assume is the correct mean value), then we can write
\[
B_i = \frac{W_i}{W_0} B_0 \equiv Z_i B_0,
\]
where \( Z_i \) is the efficiency of plant \( i \) relative to the reference level, and this is now interpreted as a random variable; it is assumed independent from plant to plant, and its mean is equal to unity by definition of the reference level. We are considering now the variability among plants \( i = 1, \ldots, n_p \) at a single point in time, so the argument \( t \) has been suppressed. The sample variance among the different plants becomes
\[
\hat{\sigma}_B^2 = \frac{1}{n_p-1} \sum_{i=1}^{n_p} (B_i - \hat{\mu}_B)^2 = \frac{1}{n_p-1} \sum_{i=1}^{n_p} (Z_i - \hat{\mu}_Z)^2 B_0^2,
\]
where the second equality follows using the definition of \( \hat{\mu}_B \) as the sample mean and substituting in the result of Eq. S36. The sample coefficient of variation is
\[
\hat{C}\!V_B = \frac{\hat{\sigma}_B}{\hat{\mu}_B} = \sqrt{\frac{1}{n_p-1} \sum_{i=1}^{n_p} (Z_i - \hat{\mu}_Z)^2 B_0^2} = \hat{C}\!V_Z = \hat{\sigma}_Z,
\]
where the result follows for a sufficiently large sample by the law of large numbers \( \hat{\mu}_Z \approx E[\hat{\mu}_Z] = 1 \). Thus, given a mean of interplant statistics at a single time point, we can characterize the variability of the quantities \( Z_i \); these statistics are furnished by the detailed plant measurements made in the 2016 dry season, yielding the values \( \hat{\mu}_B = 68.4 \text{ g m}^{-2}, \hat{\sigma}_B = 16.2 \text{ g m}^{-2}, \), and \( C\!V_B = 0.237 \approx \hat{\sigma}_Z \). With this characterization in hand, we can use the law of total variance to decompose the variance into its temporal part—i.e., that induced by the random rainfall process and treated throughout this paper—and the interplant part. The biomass measured at any point \( t \) is an average over \( n_p \) plants,
\[
B(t) = \frac{1}{n_p} \sum_{i=1}^{n_p} B_i(t) = \hat{\mu}_Z B_0,
\]
and, as seen above, this becomes a product of the average relative efficiency with the reference biomass (which is, to reiterate, the one corresponding to the efficiency value used throughout this paper). The total variance is obtained by conditioning on the value of the random variable \( \hat{\mu}_Z \) (recall the law of total variance states that \( \text{Var}[X] = E[Y] \text{Var}[X|Y] + \text{Var}[E[X|Y]] \)):
\[
\text{Var}[B] = \text{Var}[\hat{\mu}_Z B_0] = E[\hat{\mu}_Z \hat{\sigma}_B^2] + \text{Var}[\hat{\mu}_Z \hat{\mu}_B] = \hat{\sigma}_B^2 \left( 1 + \frac{\hat{\mu}_B^2}{n_p} \frac{1}{\hat{\sigma}_Z^2} \right).
\]

Tables S1–S4 provide the requisite raw and derived parameter values, and Figs. S1 and S2 describe the site and analysis.
Fig. S1. (A–D) The variation of rainfall arrival rate $\lambda_0$ in the wet season (A) and the dry season (B) and the variation of the mean daily rainfall depth $a$ in the wet season (C) and the dry season (D) over the years from 1956 to 2015. Dashed lines indicate the average values.

Fig. S2. (A and B) Comparison of time-dependent—but nonseasonal—mean (A) and variance (B) of biomass with the steady-state values.

Table S1. Climate and soil parameters at Shapotou Desert Research and Experiment Station used in analytical expressions

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean annual rainfall</td>
<td>Wet season: 182.6 mm</td>
</tr>
<tr>
<td>SD annual rainfall</td>
<td></td>
</tr>
<tr>
<td>Mean rainfall</td>
<td>Wet season: 149.1 mm</td>
</tr>
<tr>
<td>SD rainfall</td>
<td>Wet season: 51.5 mm</td>
</tr>
<tr>
<td>Season duration $T$</td>
<td>Wet season: 153 d</td>
</tr>
<tr>
<td>Rainfall arrival rate $\lambda_0$</td>
<td>Wet season: 0.231 d$^{-1}$</td>
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<tr>
<td>Mean rainfall depth $a$</td>
<td>Wet season: 4.2 mm</td>
</tr>
<tr>
<td>Interception depth $\Delta$</td>
<td>Wet season: 1.0 mm</td>
</tr>
<tr>
<td>Infiltration arrival rate $\lambda$</td>
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</tr>
<tr>
<td>Normalized rainfall depth $1/\theta = a/nZ_r$</td>
<td>Wet season: 0.022</td>
</tr>
<tr>
<td>Porosity $n$</td>
<td>Wet season: 0.39</td>
</tr>
<tr>
<td>Root zone soil depth $Z_r$</td>
<td>Wet season: 500 mm</td>
</tr>
<tr>
<td>Saturated soil conductivity $K_s$</td>
<td>Wet season: 337 cm d$^{-1}$</td>
</tr>
<tr>
<td>Soil conductivity exponent $c$</td>
<td>Wet season: 10</td>
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</table>
Table S2. Vegetation parameters at Shapotou Desert Research and Experiment Station used in analytical expressions

<table>
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<th>Parameters</th>
<th>Values</th>
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<tr>
<td>Biomass growth factor $\alpha$</td>
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<tr>
<td>Biomass loss rate $\beta$</td>
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<td>Saturation uptake rate $\gamma$</td>
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<tr>
<td>Incipient stomatal closure $s^*$</td>
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<td>Maximum daily transpiration $E_m$</td>
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<tr>
<td>Maximum daily net assimilation $A_m$</td>
<td>13.20 g m$^{-2}$ d$^{-1}$</td>
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<td>Wilting saturation $s_w$</td>
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<tr>
<td>Specific leaf area $\rho$</td>
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<td>Leaf mass ratio $f_L$</td>
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<td>Canopy to root ratio $A_c/A_r$</td>
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<td>Growth yield $Y_g$</td>
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<td>Root respiration coefficient $R_r$</td>
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<td>Senescence rate $q$</td>
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Table S3. The percentage of the canopy coverage over the total area of the plot ($C$) and the biomass per unit canopy area ($B$) at the end of wet season

<table>
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<tr>
<th>Year</th>
<th>C, %</th>
<th>$B$, g m$^{-2}$</th>
<th>C, %</th>
<th>$B$, g m$^{-2}$</th>
<th>C, %</th>
<th>$B$, g m$^{-2}$</th>
<th>C, %</th>
<th>$B$, g m$^{-2}$</th>
<th>C, %</th>
<th>$B$, g m$^{-2}$</th>
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Table S4. Dry weight, canopy projection area, and biomass per unit canopy area at the end of dry season in 2016

<table>
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<tr>
<th>Shrub no.</th>
<th>Dry weight, g</th>
<th>Canopy projection area, m²</th>
<th>Biomass, g·m⁻²</th>
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