Title
Ecohydrological controls on grass and shrub above-ground net primary productivity in a seasonally dry climate

Permalink
https://escholarship.org/uc/item/70z9t8m6

Journal
ECOHYDROLOGY, 8(8)

ISSN
1936-0584

Authors
Parolari, AJ
Goulden, ML
Bras, RL

Publication Date
2015-12-01

DOI
10.1002/eco.1605

License
CC BY 4.0

Peer reviewed
Ecohydrological controls on grass and shrub above-ground net primary productivity in a seasonally dry climate

Anthony J. Parolari,1,2* Michael L. Goulden3 and Rafael L. Bras4,5

1 Nicholas School of the Environment, Duke University, Durham, NC, USA
2 Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, MA, USA
3 Department of Earth System Science, University of California, Irvine, CA, USA
4 School of Civil and Environmental Engineering, Georgia Institute of Technology, Atlanta, GA, USA
5 School of Earth and Atmospheric Sciences, Georgia Institute of Technology, Atlanta, GA, USA

ABSTRACT

Seasonally dry, water-limited regions are often co-dominated by distinct herbaceous and woody plant communities with contrasting ecohydrological properties. We investigated the shape of the above-ground net primary productivity (ANPP) response to annual precipitation ($P_a$) for adjacent grassland and shrubland ecosystems in Southern California, with the goal of understanding the role of these ecohydrological properties on ecosystem function. Our synthesis of observations and modelling demonstrates grassland and shrubland exhibit distinct ANPP-$P_a$ responses that correspond with characteristics of the long-term $P_a$ distribution and mean water balance fluxes. For annual grassland, no ANPP occurs below a 'precipitation compensation point,' where bare soil evaporation dominates the water balance, and ANPP saturates above the $P_a$ where deep percolation and runoff contribute to the modelled water balance. For shrubs, ANPP increases at a lower and relatively constant rate across the $P_a$ gradient, while deep percolation and runoff account for a smaller fraction of the modelled water balance. We identify precipitation seasonality, root depth, and water stress sensitivity as the main ecosystem properties controlling these responses. Observed ANPP-$P_a$ responses correspond to notably different patterns of rain-use efficiency (RUE). Grass RUE exceeds shrub RUE over a wide range of typical $P_a$ values, whereas grasses and shrubs achieve a similar RUE in particularly dry or wet years. Inter-annual precipitation variability, and the concomitant effect on ANPP, plays a critical role in maintaining the balance of grass and shrub cover and ecosystem-scale productivity across this landscape. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS soil moisture dynamics; seasonal climates; primary production; rain-use efficiency

Received 10 July 2014; Revised 10 January 2015; Accepted 15 January 2015

INTRODUCTION

Semi-arid ecosystems are often characterized by a patchwork of plant communities, such as the herbaceous and woody vegetation mosaic found in regions with seasonally dry climate. Because of their socio-economic importance and vulnerability to change under future climate and land use conditions (Schlesinger et al., 1990; Rietkerk et al., 2004; Reynolds et al., 2007; Schneider et al., 2007), a mechanistic understanding of the structure and function of such water-limited ecosystems is essential to their proper management. Extensive research has highlighted both bottom-up (i.e. competition for soil moisture and nutrients) and top-down (i.e. fire and herbivory) controls on the productivity of semi-arid woody and herbaceous vegetation (Scholes and Archer, 1997).

The link between primary productivity and precipitation is an important indicator of dryland function. At the scale of an individual site, the response of above-ground net primary productivity (ANPP) to annual precipitation ($P_a$) varies substantially with soil type, plant functional type (PFT) and climate. ANPP generally increases with $P_a$, with evidence for both linear (Briggs and Knapp, 1995; Huxman et al., 2004; Hsu et al., 2012) and nonlinear (saturating) (Hsu et al., 2012) ANPP-$P_a$ responses. However, ANPP-$P_a$ correlations are often weak, and in some cases, ANPP is insensitive to $P_a$ (Sala et al., 2012).

Previous analyses of the ANPP-$P_a$ relation have been relatively descriptive, and the ecohydrological basis for these patterns has yet to be explored in detail. Because of nonlinearity in the surface hydrological response to precipitation, interaction between the soil water balance and vegetation productivity may be one factor that controls the shape of the ANPP-$P_a$ response. Annual evapotranspiration, the water flux that facilitates productivity, tends to saturate with increasing annual precipitation (Budyko, 1974).
In addition, root depth places a fundamental constraint on soil water availability. Shallow root profiles are associated with increased non-productive water fluxes, runoff and leakage and decreased water storage volume (Sala et al., 1988; Laio et al., 2001b). Lastly, asynchronous precipitation and energy availability in seasonally dry climates may limit ecosystem water availability. In these ecosystems, a large fraction of precipitation occurs before the growing season and is susceptible to non-productive evaporation and leakage losses before roots can effectively compete for available soil moisture. Therefore, soil, climate and vegetation factors that affect the soil water balance response to precipitation may explain observed variability in ANPP-\(P_a\) patterns.

The link between \(P_a\), soil moisture, and ANPP may also help explain the coexistence of woody and herbaceous vegetation under similar climate, soil, and disturbance regimes. To date, observations of ANPP-\(P_a\) responses have been reported for a single PFT at a given site (e.g. Briggs and Knapp, 1995) or for multiple PFTs across sites (e.g. Sala et al., 1988; Huxman et al., 2004; Hsu et al., 2012; Jin and Goulden, 2014). Modelling studies quantified soil water balance effects on ecological success and generally focused on simulated water stress, transpiration, or primary productivity as key indicators of vegetation patterns (Schwinning and Ehleringer, 2001; van Wijk and Rodriguez-Iturbe, 2002; Scanlon and Albertson, 2003; Ivanov et al., 2008a, 2008b; Viola et al., 2008; Hwang et al., 2009; del Jesus et al., 2012; Feng et al., 2012). While water stress is difficult to validate, ANPP is a commonly measured ecological property that combines information on resource availability and competitive advantage. The integration of ANPP observations and ecohydrological models offers an opportunity to advance mechanistic understanding of how woody and herbaceous vegetation communities may coexist under similar environmental conditions.

This paper is focused on the ecohydrological mechanisms connecting ANPP and \(P_a\) in the seasonally dry, semi-arid climate of coastal Southern California. We address the following questions: How do ANPP-\(P_a\) patterns differ between adjacent grass and shrub communities that grow in the same soil and climate environment? Does interaction between precipitation, the soil water balance and productivity explain these observed ANPP-\(P_a\) patterns and their differences? And, finally, how do ANPP-\(P_a\) patterns inform understanding of grass–shrub coexistence in seasonally dry environments? Our analysis is based on results from multi-year rainfall manipulation experiments in two distinct communities, one dominated by annual grasses and the other by drought-deciduous shrubs. The two communities are immediately adjacent to each other, and historical aerial photographs demonstrate this pattern has been stable for at least 70 years. In addition to climate and disturbance history (i.e. fire), topographic and edaphic factors are consistent between these communities. First, we analyse the ANPP-\(P_a\) response for both PFTs, demonstrating distinct linear and nonlinear responses in the shrub and grass communities, respectively. Second, we apply a simple model coupling ANPP to soil moisture dynamics to investigate the role of ecohydrological processes in generating these ANPP-\(P_a\) patterns. Last, the observed ANPP-\(P_a\) patterns are used as a basis for understanding how inter-annual \(P_a\) variability facilitates the co-occurrence of grass and shrub communities at this site.

LOMA RIDGE EXPERIMENT

The Loma Ridge rainfall manipulation experiment was established in 2007 and is located in central Orange County, California (33.742°N, 117.704°W). The site consists of distinct annual grass (Bartolome et al., 2007) and drought-deciduous shrub communities (Rundel, 2007) (Figure 1). Loma Ridge experiences a seasonal climate with, on average, 90% of annual rainfall occurring in the winter between November and April (Figure 2). The local soil is homogeneous and characterized as sandy loam.

Experimental plots

Rainfall manipulation was conducted in the grass and shrub communities for 6 years (2007–2012) and 4 years (2009–2012), respectively. In each community, 24 rectangular plots are divided into eight replicates of three water input treatments: ambient, ambient minus 40% (dry), and ambient plus 40% (wet). Plot dimensions are 6.1 × 8.5 m (grass) and 12.2 × 18.3 m (shrub). Rainfall is excluded from dry plots with retractable clear polyethylene roofs that were closed during approximately half of the rain events (<5% of the days during a year). Water draining from the roofs was collected in polyethylene tanks for subsequent application to the wet plots using pressure compensated drip tubing. Excluded events and irrigation rates were chosen to simulate observed patterns in storm frequency and intensity. Roof operation and irrigation are identical for the grass and shrub plots. Ambient water input was measured half-hourly by tipping bucket.

Above-ground net primary productivity was measured at the end of each growing season. Grassland ANPP was determined in late April or May by harvesting two 14 × 50 cm strips in each plot. The samples were oven-dried at 60 °C for 4 days and subsequently weighed. Late season herbaceous growth (generally from May through July) accounted for less than 10% of ANPP and was not considered in our analysis.

Shrub ANPP was determined from direct measurements of the annual crown volume increase of the four most common species: Artemisia californica (ARCA), Malosma laurina (MALA), Salvia mellifera (SAME) and Acmispon...
**glaber** (ACGL). Averages of 6 ARCA, 9 MALA and 19 SAME shrubs were identified and permanently tagged in each shrub plot in October 2008 (a total of 807 plants). The volume of each shrub was recorded at the end of each growing season of each year (during August to October) using a ruler to measure the plant’s width \( w \), depth \( d \) and height \( h \). Plant volume was calculated as the product \( v = wdh \ been converted to mass \( m \), using allometric equations determined by harvest at the site (ARCA: \( m = 0.0002v + 37.6, r^2 = 0.8787 \); MALA: \( m = 0.001v + 6.18, r^2 = 0.8699 \); and SAME: \( m = 0.0009v + 19.5, r^2 = 0.9536 \)). ACGL biomass was determined from annual measurements of ACGL fractional cover and density (mass per ground area) in each plot. Fractional cover was measured along an 18.3 m transect in each plot. Density was determined by harvesting and drying ACGL from each plot after measuring plant area.

We accounted for the ANPP of the remaining shrub species at the site (species other than ARCA, MALA, SAME and ACGL) based on cover measurements of all species in each plot (Kimball et al., 2014). We assumed a species’ ANPP was proportional to its ground cover; this factor increased overall ANPP an average of 12%. Additionally, our measurements did not include litterfall, which we accounted for based on observations at a nearby, floristically similar shrubland (Vourlitis et al., 1997). We assumed the allocation to biomass increment (mostly stems and other longer-lived tissues) relative to litter production (mostly leaves, flowers and twigs) was similar between sites; this factor increased ANPP by an average of 42%. The resulting shrub ANPP reflects the primary production by perennial woody plants only; it does not include the production by herbaceous plants within shrub plots.

The entire site, including all the grass and shrub plots, burned in the October 2007 Santiago wildfire. The fire had a significant effect on plant species composition for 1–2 years, increasing the abundance of forbs in the grassland and decreasing the abundance of grasses (Goulden et al., in prep). Similarly, the fire increased the abundance of herbaceous plants and ACGL in the shrubland for 3–4 years and decreased the cover of ARCA, MALA and SAME (Kimball et al., 2014). The abundance
of grasses and forbs offsets, such that annual grassland ANPP was largely unaffected by the fire and fire recovery. Likewise, ACGL cover offsets ARCA, MALA and SAME cover, which reduced the effect of fire and recovery on coastal sage ANPP.

Climate data
Loma Ridge climate was characterized using several data sources, including daily and annual precipitation and daily potential evapotranspiration. The long-term distribution of annual precipitation was based on a composite of nearby rain gauges (Tustin Irvine Ranch COOP, Santa Ana Fire Station COOP) and the Loma Ridge site rain gauges, resulting in an 83-year record (1929–2012, with the water year defined September through August). All data sources were adjusted to the Loma Ridge observations by linear regression based on overlapping periods. Distributions of daily storm depth and inter-storm duration were estimated from a 104-year record of daily precipitation totals (1906–2010, Santa Ana Fire Station COOP). Lastly, energy availability for evapotranspiration was estimated as daily reference evapotranspiration ($ET_0$) estimated over a nearby well-watered grassland (CIMIS Irvine, Station 075, 1987–2012). This estimate uses a modified Penman approach.

ANPP MODEL
Above-ground net primary productivity is modelled by linking plant carbon fluxes to the soil water balance. We assume photosynthesis, respiration, and mortality are entirely dependent on root zone soil moisture ($s$). Therefore, $s$ is effectively treated as an integrated indicator of the effects of all growth and stress factors (i.e. water, temperature, and nutrient supply). Although each of these factors contributes to ANPP, nutrient supply rates and temperature are closely related to $s$ in dryland ecosystems.

Soil water balance
The soil water balance is defined at the daily scale for a flat vegetated patch overlying a vertically homogeneous soil column with porosity $n$ ($m^3/m^3$) and active root zone depth $z_r$ ($m$),

$$\frac{dz_r}{dt} = P_e - E - T - L. \quad (1)$$

Water entering the soil column is denoted the effective precipitation ($P_e$), or precipitation minus canopy interception and surface runoff. The modelled soil moisture losses are bare soil evaporation ($E$), transpiration ($T$) and leakage below the soil column [$L$; all in units of $(mm/Day)$]. Each of these water fluxes depends on $s$, and we follow common parameterizations described in the succeeding text (Laio et al., 2001a). The model is forced with synthetically generated daily precipitation time series (described in the Section on Meteorological Forcing) and integrated numerically.

Precipitation is assumed to infiltrate instantaneously at the beginning of each wet day. Canopy interception is first subtracted from the total storm depth $[h \ (mm)]$ and is defined as the product of the vegetated ground fraction ($v$; Equation (5)) and a parameter describing the water storage capacity of the canopy, $c_{max}$ (mm). Only saturation-excess runoff is considered, which is modelled as the depth of precipitation in excess of the soil storage capacity at the time of the event. With these assumptions, $P_e$ is

$$P_e = \min[h - \min(h, c_{max} v), n z_r (1 - s)]. \quad (2)$$

Evaporation and transpiration are defined as (e.g. Montaldo et al., 2005),

$$E + T = E_p [k_s (1 - v) \beta_s + k_v v \beta_v], \quad (3)$$

where $E_p$ ($mm/day^{-1}$) is the climate-derived potential evapotranspiration, $k_s$ and $k_v$ are dimensionless coefficients that represent physical limits to actual evapotranspiration due to local soil or vegetation conditions, and $\beta_s$ and $\beta_v$ represent the reduction in $E$ or $T$ resulting from soil moisture deficit. We assume the $\beta_i$’s follow piecewise linear functions,

$$\beta_s = \begin{cases} 0 & s \leq s_h \\ \frac{s - s_h}{s_f - s_h} & s_h < s \leq s_f \\ 1 & s > s_f \end{cases}, \quad (4a)$$

and

$$\beta_v = \begin{cases} 0 & s \leq s_w \\ \frac{s - s_w}{s^* - s_w} & s_w < s \leq s^* \\ 1 & s > s^* \end{cases}, \quad (4b)$$

where $s_h(\cdot)$ is the hygroscopic point, $s_f$ is the field capacity, $s_w$ is the permanent wilting point, and $s^*$ is the incipient stress point.

Total ET is partitioned between $E$ and $T$, assuming available energy is extinguished exponentially with leaf area. Therefore, the ground fraction contributing to $T$ is

$$v = 1 - \exp(-k L_a), \quad (5)$$

where $k$ ($m^{2} m^{2}$) is the light extinction coefficient and $L_a$ ($m^2$) is the leaf area index. $L_a$ is assumed to scale linearly with above-ground biomass, according to the specific leaf area, $(m^2/leaf g\ C^{-1})$, assumed constant. It follows that the ground fraction contributing to $E$ is $(1 - v)$.
Lastly, leakage below the root zone is assumed to depend on \( s \) similar to the unsaturated hydraulic conductivity,

\[
L = K_s \exp \left[ \frac{\gamma(s - s_f)}{\gamma(1 - s_f)} - 1 \right],
\]

where \( K_s \) (mm day\(^{-1} \)) is the saturated hydraulic conductivity, \( c = 2b + 3 \) represents the decay of conductivity with saturation, where \( b \) is the soil pore size distribution index, and \( \gamma = 2b + 4 \).

**Vegetation carbon balance**

The vegetation carbon balance, including photosynthesis, respiration and water stress-induced mortality, generally follows SVM3 (Montaldo et al., 2005; see also Istanbulluoglu et al., 2012 and references), a relatively simple model shown to perform well in their evaluation of several dynamic vegetation models. The only difference between our model and SVM3 is that we do not explicitly include temperature effects.

The above-ground vegetation carbon balance is

\[
\frac{dC_a}{dt} = f_a NPP - S = f_a (A - R_g - R_m) - S,
\]

where \( C_a \) (g C m\(^{-2} \)) is the above-ground plant carbon pool, \( f_a(\cdot) \) is the fraction of \( NPP \) allocated to above-ground growth, and the carbon fluxes are gross photosynthesis (\( A \)), growth and maintenance respiration (\( R_g \) and \( R_m \)), and senescence \( S \); all in units of (g C m\(^{-2} \) day\(^{-1} \)).

Photosynthesis is linked to the water balance through the coupled stomatal transport of CO\(_2\) and H\(_2\)O. We model \( A \) in a fashion similar to \( T \) as a piecewise linear function of \( s \),

\[
A = p_{\text{max}} \beta_s \nu,
\]

where \( p_{\text{max}} \) (g C m\(^{-2} \) day\(^{-1} \)) is the maximum daily scale photosynthesis rate for a fully vegetated surface and \( \beta_s \) is given by Equation (4b). \( p_{\text{max}} \) can be interpreted as a constant parameter integrating the light, temperature, and vapour pressure deficit functions in Montaldo et al., (2005).

Respiration is separated into two components, corresponding to the energy requirements for growth of new plant tissue and maintenance of existing live tissue. \( R_g \) is the rate of incoming photosynthate used for new growth, assumed as a constant fraction, \( k_g \), of \( A \). \( R_m \) is the rate of incoming photosynthate used to maintain existing tissue, assumed as a constant fraction, \( k_m \), of \( C_a \). These assumptions give the following expression for \( NPP \) (Thornley 1970):

\[
NPP = y_g A - k_m C_a,
\]

where \( y_g = 1 - k_g(\cdot) \) is the growth yield parameter and \( k_m \) (day\(^{-1} \)) is a biomass-specific maintenance respiration rate.

For drought-deciduous species, such as the grasses and shrubs found at Loma Ridge, senescence is driven by the simultaneous accumulation of water deficit and temperature stresses at the beginning of the summer. We model the role of soil moisture in this process as (Collins and Bras, 2010),

\[
S = m(1 - \beta_s)^q C_a,
\]

where \( m \) (day\(^{-1} \)) is the maximum biomass-specific mortality rate and the exponent \( q \) represents nonlinearity in the water stress response.

Combining Equations (7)–(10), the above-ground vegetation carbon balance is,

\[
\frac{dC_a}{dt} = f_a y_g p_{\text{max}} \beta_s \nu - \left[ k'_m + m(1 - \beta_s)^q \right] C_a,
\]

where \( k'_m = f_a k_m \) and the effect of soil moisture is evident in the balance of growth and senescence terms. To be consistent with the experimental methodology, modelled grass ANPP is defined as the peak \( C_a \) simulated in each year and modelled shrub ANPP is defined as the cumulative sum of \( NPP \) and \( R_m \) simulated in each year. We assume dry matter production is approximately 0.5 g DM g\(^{-1} \) CO\(_2\) (Scholes and Walker, 1993).

**Meteorological forcing**

The model is forced with synthetic precipitation and \( ET_0 \) time series based on long-term statistics. For precipitation, we use a Monte Carlo approach. Simulations for each soil and vegetation parameter set are forced by a 10 000-year time series of rainfall generated as follows. Each year is split into two seasons: a wet winter and a dry summer (Figure 2). The wet season length is denoted \( T_w \), and the dry season length is \( 365 - T_w \). For each wet season, a total precipitation volume, \( P_a \) (mm), is sampled from a uniform distribution between 0 and 800 mm, while each dry season is assumed to produce zero rainfall. Within each wet season, a series of rain events is then sampled. We assume storm depths, \( h \), and inter-storm durations, \( t_s \), are independent and exponentially distributed with mean storm depth, \( \alpha \) (mm), and mean inter-storm duration, \( \lambda^{-1} \) (day). At Loma Ridge, \( \alpha \) and \( \lambda \) vary with \( P_a \) such that wetter years are characterized by increased frequency of storms and increased storm intensity (Figure 3).

This behaviour is fit by the following relations:

\[
\alpha = m_0 \sqrt[1/2]{P_a},
\]

and

\[
\lambda = (m_0 T_w)^{-1} \sqrt[1/2]{P_a},
\]

where \( m_0 \) (mm\(^{-1/2} \)) is a parameter that controls the contribution of \( \alpha \) and \( \lambda \) to \( P_a \); \( m_0 \) is estimated as 0.65 for Loma Ridge. Using this sampling scheme, the statistics of modelled ANPP and soil water fluxes reflect variability in the timing and intensity of rain events within each wet season and not the distribution of annual precipitation.

The seasonal cycle of $E_p$ is assumed to follow the observed long-term average for each day. A sinusoidal curve is fit to the time series of daily averages,

$$E_p(t) = E_p - \Delta E_p \sin(2\pi\omega t),$$  

(13)

where $E_p = 3.45$ (mm day$^{-1}$) is the average daily $E_p$ for all days, $\Delta E_p = 2.0$ (mm day$^{-1}$) is the amplitude of the seasonal cycle, and $\omega^{-1} = 365$ (day) is the period. $t=0$ corresponds to October 1.

**Model calibration**

The model was parameterized using typical values found in the literature, as summarized in Tables I and II, and by calibrating the photosynthesis and stress-induced turnover parameters, $p_{\text{max}}$ and $m$. The model was calibrated to measurements of 15-cm volumetric water content and surface CO$_2$ and H$_2$O fluxes measured by eddy covariance. The calibration methodology and results are presented and discussed in the Supporting Information.

**RESULTS AND DISCUSSION**

**Observed ANPP-$P_a$ responses**

The annual grass and drought-deciduous shrub PFTs at Loma Ridge exhibit distinct ANPP-$P_a$ responses (Figure 4). Grass ANPP increases rapidly with increasing $P_a$ for $P_a < 240$ mm and saturates at a constant value for $P_a > 240$ mm. Interestingly, this transition point corresponds roughly to the long-term median $P_a$. Shrub ANPP also increases with $P_a$, but at a lower, nearly constant rate across all values of $P_a$. Grasses and shrubs achieve a similar range of ANPP with a maximum of approximately 600 g DM m$^{-2}$ year$^{-1}$ (DM, dry matter). Grass ANPP exceeds shrub ANPP for intermediate $P_a$ (i.e. $200 < P_a < 500$ mm), whereas ANPP is similar for grasses and shrubs in dry and wet years outside this range.

The ANPP-$P_a$ relations were quantified by regression, with linear and logistic models, and by the ANPP model. The logistic model is defined as

$$ANPP = a_{\text{max}} \left\{ 1 + \left[ \frac{1-f}{f} \right] \exp\left[-r(P_a - P_f)\right] \right\}^4,$$  

(14)

where $a_{\text{max}}$ (g DM m$^{-2}$) is the saturating value of ANPP, $r$ (mm$^{-1}$) is a biomass-specific rainfall use efficiency, and $f(\cdot)$ is the fraction of $a_{\text{max}}$ at $P_f$. Both grass and shrub ANPP sensitivity to $P_a$ are best described by the logistic model, as supported by their respective $r^2$ values (Table III). Grass ANPP clearly responds to $P_a$ in a logistic fashion, while the logistic model fit for shrubs is nearly linear (Figure 4, Table III).

Above-ground net primary productivity model results are consistent with observations and the logistic model fit (Figure 5). However, compared to the linear and logistic fits, the ANPP model suggests a stronger saturation of shrub ANPP for $P_a > 500$ mm. Performance of the ANPP model is evaluated in the attached Supporting Information. In the next section, the ANPP model results are explored.

---

**Table I. Soil hydraulic and climate parameters estimated for Loma Ridge.**

<table>
<thead>
<tr>
<th>Parameter(^a)</th>
<th>Units</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Porosity</td>
<td>$n$</td>
<td>0.43</td>
</tr>
<tr>
<td>Hygroscopic point</td>
<td>$s_h$</td>
<td>0.14</td>
</tr>
<tr>
<td>Field capacity</td>
<td>$s_c$</td>
<td>0.56</td>
</tr>
<tr>
<td>Pore size distribution index</td>
<td>$\beta$</td>
<td>4.39</td>
</tr>
<tr>
<td>Saturated hydraulic conductivity</td>
<td>$K_s$</td>
<td>cm day$^{-1}$</td>
</tr>
<tr>
<td>Bare soil evaporation efficiency(^b)</td>
<td>$k_s$</td>
<td>0.5</td>
</tr>
</tbody>
</table>

\(^a\) Soil properties and soil moisture thresholds are those reported by Laio et al. (2012) for sandy loam.\(^b\) Surface evaporation efficiency is calibrated to observed soil moisture time series and is similar to those reported by Istanbulluoglu et al. (1955).
further, particularly with respect to the correspondence between ANPP and the soil water balance.

Soil water balance controls on ANPP-$P_a$ responses

The coupled ANPP and soil water balance model results provide a mechanistic interpretation of the observed ANPP-$P_a$ relations. We identify three regimes that highlight the importance of interaction between ecological and hydrological processes in the ANPP response to $P_a$.

**Precipitation compensation point.** A minimum precipitation volume, $P_{min}$, is required to support non-zero productivity. This value was previously defined as ‘ineffective precipitation’ or the ‘zero-yield intercept’ (Noy-Meir, 1973). Modelling results suggest grasses and shrubs exhibit a similar $P_{min}$, which is approximately 100 mm (Figure 5), and $P_{min}$ is controlled by the temporal separation between the wet season and the growing season. Below $P_{min}$, the soil water balance is entirely partitioned to bare soil evaporation (Figure 6). This non-productive loss is likely concentrated during the initial rainy period, when canopy cover and transpirational demand are low and bare soil and interception evaporation dominates total ET (Eastham et al., 1999). $P_a$ must therefore exceed the early season evaporation demand to support non-zero productivity.

**Constant rain-use efficiency.** In the second regime, ANPP scales linearly with $P_a$. Here, transpiration represents an important fraction of the water balance, while evaporation remains constant, and ANPP is truly ‘water-limited’ (Figures 5 and 6). The width of this regime is different for grasses and shrubs. Grass ANPP varies linearly between $P_{min}=100$ mm and $P_{max}=260$ mm, where grass ANPP saturation is very well-defined above $P_{max}$. Shrub ANPP observations suggest a nearly linear increase across the entire range of observations, up to at least 600 mm. Alternatively, model results suggest shrub ANPP may saturate at approximately 500 mm of rainfall. In either case, this regime of the shrub ANPP-$P_a$ curve is characterized by a lower slope and a wider $P_a$ range than that for grasses.

The slope of the ANPP-$P_a$ curve in this regime is equivalent to the maximum rain-use efficiency (RUE) (LeHouerou, 1984). Loma Ridge RUEs estimated from the logistic model fits are 2.1 g DM m$^{-2}$ mm$^{-1}$ H$_2$O for grasses

### Table II. Vegetation parameters estimated for Loma Ridge.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Grass</th>
<th>Shrub</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Above-ground allocation fraction</td>
<td>$f_a$</td>
<td>0.77</td>
<td>0.57</td>
<td>Arora and Boer (2005); Harpole et al. (2007)</td>
</tr>
<tr>
<td>Maximum photosynthesis rate</td>
<td>$p_{max}$ g C m$^{-2}$ day$^{-1}$</td>
<td>25</td>
<td>20</td>
<td>Calibrated</td>
</tr>
<tr>
<td>Biomass yield</td>
<td>$y_g$</td>
<td>0.75</td>
<td>0.75</td>
<td>Dewar (1996); Istanbuluoglu et al. (2012)</td>
</tr>
<tr>
<td>Maintenance respiration coefficient</td>
<td>$k_m$ day$^{-1}$</td>
<td>0.01</td>
<td>0.01</td>
<td>Dewar (1996)</td>
</tr>
<tr>
<td>Biomass-specific mortality rate</td>
<td>$m$ m$^2$ leaf g C$^{-1}$</td>
<td>0.02</td>
<td>0.02</td>
<td>Calibrated</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>SLA m$^2$ leaf g C$^{-1}$</td>
<td>0.01</td>
<td>0.01</td>
<td>Montaldo et al. (2008); Istanbuluoglu et al. (2012)</td>
</tr>
<tr>
<td>Wilting point</td>
<td>$s_w$</td>
<td>0.18</td>
<td>0.18</td>
<td>Laio et al. (2001a)</td>
</tr>
<tr>
<td>Incipient stress point</td>
<td>$s$</td>
<td>0.46</td>
<td>0.30</td>
<td>Laio et al. (2001b); Montaldo et al. (2008)</td>
</tr>
<tr>
<td>Water stress exponent</td>
<td>$q$</td>
<td>3</td>
<td>3</td>
<td>Laio et al. (2008a)</td>
</tr>
<tr>
<td>Transpiration efficiency</td>
<td>$k_v$</td>
<td>1</td>
<td>1</td>
<td>Istanbuluoglu et al. (1955)</td>
</tr>
<tr>
<td>Root depth</td>
<td>$z_r$ cm</td>
<td>30</td>
<td>125</td>
<td>Hellmers et al. (1955); Holmes and Rice (1996); Schenk and Jackson (2002)</td>
</tr>
<tr>
<td>Growing season start date</td>
<td>$t_0$</td>
<td>45</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>
and 0.9 g DM m⁻² mm⁻¹ H₂O for shrubs. These values are consistent with those previously reported for water-limited ecosystems, which typically range between 0.5 and 2 g DM m⁻² mm⁻¹ H₂O (Noy-Meir, 1973; LeHouerou, 1984; Sala et al., 1988). Loma Ridge RUE also falls within the range expected for C₃ grasses and shrubs. Photosynthetic water use efficiency of C₃ grasses typically ranges between 2 and 5 mmol CO₂ mol⁻¹ H₂O, while that of C₃ shrubs may be as high as 11 (Lammers et al., 2008). Assuming growth and maintenance respiration accounts for approximately half of carbon assimilated by photosynthesis (Cannell and Thornley, 1974) and dry matter production is approximately 0.5 g DM g⁻¹ CO₂ (Scholes and Walker, 2012), then 1.2 < RUE < 3 for grasses and 1.2 < RUE < 6.6 for shrubs.

**ANPP saturation.** Finally, grass and possibly shrub ANPP saturate at high Pₐ. The modelled water balance suggests that the saturation point, Pₘₐₓ, is related to progressively increasing non-productive leakage and runoff losses. Pₘₐₓ is associated with the point where leakage plus runoff is approximately 15% of the water balance for both PFTs. The fraction of the modelled water balance partitioned to non-productive leakage and runoff losses increases with Pₐ for both PFTs (Figure 6). Both fluxes are overall higher for

---

Table III. Linear and logistic model fits to Loma Ridge above-ground net primary productivity (ANPP) data.

<table>
<thead>
<tr>
<th>Community</th>
<th>Model</th>
<th>ANPP</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass</td>
<td>Linear</td>
<td>ANPP = 0.785Pₐ + 170</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>ANPP = 547(1 + 9 exp[-0.025(Pₐ - 66)])⁻¹</td>
<td>0.83</td>
</tr>
<tr>
<td>Shrub</td>
<td>Linear</td>
<td>ANPP = 0.855Pₐ - 9.5</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>Logistic</td>
<td>ANPP = 821(1 + 9 exp[-0.005(Pₐ - 23)])⁻¹</td>
<td>0.81</td>
</tr>
</tbody>
</table>

Figure 5. Modelled ANPP-Pₐ relation for Loma Ridge grasses (top) and shrubs (bottom). The dashed line corresponds to the mean over 10,000 precipitation realizations, and the grey region corresponds to two standard deviations around this mean. Observations are indicated by open symbols (μ ± SE, n = 8). The three ANPP regimes are marked by the letters: A = precipitation compensation point, B = constant rain-use efficiency and C = ANPP saturation. ANPP, above-ground net primary productivity; Pₐ, annual precipitation.

Figure 6. Modeled mean annual water balance components as a function of annual precipitation for modeled grasses (top) and shrubs (bottom). E: evaporation; T: transpiration; L: leakage; R: runoff. Model forcing is the same as that in Figure 5.
grass, which has a smaller root zone depth (Table II). Because leakage and runoff depend strongly on soil moisture, these fluxes are most important early in the growing season when the soil is more saturated. Similar to early season evaporation in dry years, leakage and runoff represent a fraction of \( P_a \) that the ecosystem cannot utilize to support productivity. It is also possible that productivity is limited by other factors such as light or nutrients in wet years.

**Evaporation-transpiration partitioning in seasonally dry climates**

In addition to the aforementioned interpretation of interannual ANPP variability, the model results provide an estimate of the partitioning of total ET into the individual contributions of \( E \) and \( T \). Across the precipitation gradient, \( E \) is typically greater than \( T \) for both grasses and shrubs, with the exception of shrubs in wet years (Figure 6). Under well-watered conditions, the ratio \( T/ET \) is approximately 0.40 for grasses and 0.54 for shrubs. These values are consistent with recent estimates from stable isotope and experimental studies that place \( T/ET \) between 0.35 and 0.80 (Coenders-Gerrits et al., 2014; Wang et al., 2014). However, data from seasonally dry climates is notably absent in these estimates.

There is reason to hypothesize \( T/ET \) ratios in seasonally dry climates fall at the lower end of the estimated range. Of the studies analysed by Wang et al. (2014), three have characteristics similar to the Loma Ridge site. In two semi-arid shrublands in the North American monsoon region, \( T/ET \) ratios were 42% and 47% (Cavanaugh et al., 2011). In a seasonally dry, semi-arid Eucalypt woodland, \( T/ET \) was measured at 53% and 22% in the summer and winter, respectively (Mitchell et al., 2009). In winter-sown, rain-fed crops in a seasonally dry climate, the \( T/ET \) ratio was 50% and 46% for two different row spacings (Eberbach and Pala, 2005). As mentioned in the previous text, low \( T/ET \) ratios in these environments may be related to asynchrony of rainfall and productivity (e.g. Eastham et al., 1999), a pattern consistent with our simulations.

**Resource use strategies, ANPP-\( P_a \) responses and climate**

The observed and modelled ANPP-\( P_a \) patterns suggest a specific role for ecohydrological mechanisms in interannual ANPP variability at Loma Ridge. In dry years, productivity is constrained by asynchrony between the wet and growing seasons and the resulting seasonality of bare soil evaporation. In wet years, productivity is constrained by root zone soil moisture storage and its effect on leakage and runoff. Productivity scales directly with precipitation only in intermediate rainfall years. The relative importance of these controls across a precipitation gradient varies with resource use strategy, as supported by the comparison between Loma Ridge grass and shrub observations. This interaction between resource use strategies, ANPP and climate is now discussed, specifically in relation to root depth, water stress tolerance, and respiration.

Root zone depth (\( z_r \)) regulates a trade-off between the total volume of plant available water and the carbon cost of below-ground productivity. The shallow grass \( z_r \) constrains plant available water and increases non-productive losses, modelled here as leakage and saturation-excess runoff. On the other hand, the deeper shrub \( z_r \) is associated with increased moisture storage and access to moisture stored at deeper soil layers, which effectively limits non-productive losses. Because of these effects, \( z_r \) controls the main features of the modelled ANPP-\( P_a \) response, predicting a trade-off between the precipitation compensation point (\( P_{\text{min}} \)) and the saturating ANPP (\( a_{\text{max}} \)), all other parameters being equal (Figure 7a). Water stress limits productivity in dry years, and therefore, \( P_{\text{min}} \) increases with \( z_r \) as the modelled \( a_{\text{max}} \) decreases. The modelled \( a_{\text{max}} \) also increases.
with $z_r$. Measuring the growing season length as the time to maximum biomass, the model predicts an increased growing season length with $z_r$ (Figure 7b). Deep-rooted plants have access to a larger store of water, allowing a longer period of growth before the wilting point is reached and, therefore, higher $a_{\text{max}}$. Considering variation in $z_r$ alone, the model suggests a lengthened growing season comes at the expense of a higher precipitation requirement for positive productivity. This modelling result provides a physical basis for productivity-resource responses previously hypothesized (Pastor and Bridgham, 1999). However, the cost of deep roots, including increased below-ground allocation and root maintenance respiration, may compromise the ability of shrubs to achieve the predicted increase in $a_{\text{max}}$. Indeed, in wet years, Loma Ridge grasses and shrubs reach a similar maximum ANPP (Figure 4), while shrub gross ecosystem exchange is typically twice that of grasses (Figure S3).

Deep-rooted species may compensate for increased $P_{\text{min}}$ through a lower sensitivity to water stress. The point of incipient water stress ($s^*$) is typically lower for woody species than for herbaceous species (Scholes and Walker, 1993; Williams and Albertson, 2004), which improves function under chronically low soil moisture levels. Further, because woody plants maintain a coarse root structure between years, they may be better able to adapt the depth of root water uptake and to integrate deep stored moisture with intermittent infiltration at the surface to improve productivity in dry years (Sivandran and Bras, 2013). Our model confirms that increased resilience of productivity under water stress, represented by lower $s^*$, offsets the increased $P_{\text{min}}$ associated with deep roots.

Rain-use efficiency and ecosystem organization

Grasses and shrubs demonstrate different RUE patterns across the precipitation gradient, which the model suggests results from the combined effects of root depth, below-ground allocation, respiration, and water stress on ANPP. The slope of the ANPP-$P_a$ curve in intermediate precipitation years indicates that shrub RUE is approximately half of grass RUE. Therefore, assuming RUE is a good indicator of ecological success, it can be concluded grasses are at an advantage in this ecosystem under typical precipitation conditions. Although shrub RUE is less than grass RUE during most years, shrubs achieve a comparable RUE in dry or wet years (Figure 8). This suggests these unlikely rainfall years may be critical to the maintenance of shrub populations at Loma Ridge. Along the Kalahari transect, another savanna-like ecosystem, the mixed tree–grass ecosystem state was shown to maximize a combined measure of transpiration and water stress across a wider range of $P_a$ than either homogeneous community (Caylor et al., 2009). In addition, the observed relative tree–grass cover in this ecosystem is associated with a soil water balance that simultaneously limits water stress and leakage (Scanlon and Albertson, 2003). The data presented here support these previous conclusions and demonstrate that efficient use of the soil water balance is fundamentally related to the ANPP-$P_a$ curves of the component PFTs. At Loma Ridge, shrubs are sub-optimal under typical rainfall conditions but achieve a competitive RUE during infrequent dry and wet years, whereas grasses appear to exploit the most likely climatic conditions.

The observed relations between ANPP, RUE and the long-term $P_a$ distribution may indicate an underlying organization between climate, ecosystem resource use efficiency, and biogeography. First, note that grass ANPP saturates and grass RUE are maximum at the observed median $P_a$ (Figures 4 and 8). Grass ANPP saturation may be related to the emergence of a biogeochemical constraint to productivity, such as nitrogen supply, under high rainfall conditions (Yahdjian et al., 2011). If grass ANPP saturation at Loma Ridge was indeed the result of a biogeochemical constraint, our results would indicate that these constraints are linked with climate. For example, nutrient supply rates in Loma Ridge grassland may be such that the maximum, nutrient-limited ANPP is achieved under average climate conditions. Therefore, we might expect the saturation point, $P_{\text{max}}$, for similar PFTs to vary with the mean $P_a$ across climates and soil types. Secondly, grass–shrub co-occurrence may be viewed as a mechanism by which ecosystem-scale ANPP and RUE are maximized across a wider range of $P_a$ than either community can achieve in isolation. We hypothesize the presence of shrubs allows for a deeper root depth in high rainfall years beyond that which could be achieved with annual grasses alone. In a mixed ecosystem, the physiological constraint of limited
grass root depth is compensated by the addition of deep-rooted shrubs, a viable solution to an optimization problem constrained by PFT traits and availability.

CONCLUSIONS

We analysed the ANPP response to annual precipitation in annual grassland and drought-deciduous shrubland in a seasonally dry, semi-arid climate. A multi-year rainfall manipulation experiment revealed a nonlinear, saturating ANPP-$P_a$ response in grassland and a contrasting linear response in shrubland. We applied a simple ANPP model based on the soil water balance to explore the mechanisms by which the land surface response to precipitation modulates inter-annual ANPP variability. Assuming transpiration and soil moisture deficit as the primary controls on ANPP, the coupled ANPP-soil water balance model reproduced the general features of the ANPP-$P_a$ relation in both communities. From a mechanistic viewpoint, the model suggests several ecohydrological factors govern this relation: (1) asynchrony between the wet season and the growing season, which promotes bare soil evaporation; (2) root depth, which controls infiltration rates, soil water storage, root water access and growing season length; and (3) incipient stress point, which controls the resilience of productivity under water stress. Together, these factors suggest that although shrubs are less efficient water users under average precipitation, their increased below-ground allocation and respiration demand are offset by resilience under water stress and a longer growing season, possibly conferring shrubs’ competitive advantage in dry and wet years. Because rain-use efficiency was asymmetric across the experimentally imposed precipitation gradient, inter-annual precipitation variability may be critical to grass–shrub coexistence in this ecosystem.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge support from the U.S. Department of Energy through grant FG02-05ER64021, the National Science Foundation through grant EAR 0962253, and the Kuwait-MIT Center for Natural Resources and the Environment. We also thank the anonymous reviewers for helpful comments on previous versions of this manuscript.

REFERENCES
