Biogeosciences Discuss., 11, 7575–7613, 2014 www.biogeosciences-discuss.net/11/7575/2014/ doi:10.5194/bgd-11-7575-2014 © Author(s) 2014. CC Attribution 3.0 License.



This discussion paper is/has been under review for the journal Biogeosciences (BG). Please refer to the corresponding final paper in BG if available.

Continental-scale impacts of intra-seasonal rainfall variability on simulated ecosystem responses in Africa

K. Guan^{1,2}, S. P. Good³, K. K. Caylor¹, H. Sato⁴, E. F. Wood¹, and H. Li⁵

¹Department of Civil and Environmental Engineering, Princeton University, Princeton, NJ, USA ²Department of Environmental & Earth System Science, Stanford University, Stanford, CA 94025, USA

³Department of Geology and Geophysics, University of Utah, Salt Lake City, UT 84112, USA ⁴Department of Environmental Geochemical Cycle Research, Japan Agency for Marine-Earth Science and Technology (JAMSTEC) 3173-25 Showamachi, Kanazawa-ku, Yokohama, 236-0001, Japan

⁵Department of Earth and Planetary Sciences, Rutgers University, Piscataway, NJ 08854, USA

Received: 9 April 2014 - Accepted: 1 May 2014 - Published: 27 May 2014

Correspondence to: K. Guan (kaiyug@stanford.edu)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Discussion P	BGD 11, 7575–7613, 2014						
ner I Discussion	Ecological Impacts of intra-seasonal rainfall variability K. Guan et al.						
ם חמס	Title Page						
) D T	Abstract	Introduction					
-	Conclusions	References					
	Tables	Figures					
sion	14	►I					
Pun	•	•					
D	Back	Close					
	Full Screen / Esc Printer-friendly Version						
n Paner							

Abstract

Climate change is expected to result in an increase of intra-seasonal rainfall variability, which has arisen from concurrent shifts in rainfall frequency, intensity and seasonality. Changes in intra-seasonal rainfall variability are likely to have important ecologi-

- ⁵ cal impacts for terrestrial ecosystems, and quantifying these impacts across biomes and large climate gradients is required for a better prediction of ecosystem services and their responses to climate change. Here we use a synthetic weather generator and an advanced vegetation dynamic model (SEIB-DGVM) to virtually conduct a series of "rainfall manipulation experiments" to study how changes in the intra-seasonal
- rainfall variability affect continent-scale ecosystem responses across Africa. We generated different rainfall scenarios with fixed total annual rainfall but shifts in: (i) frequency vs. intensity, (ii) seasonality vs. frequency, (iii) intensity vs. seasonality. These scenarios were fed into the SEIB-DGVM to investigate changes in biome distributions and ecosystem productivity. We find a loss of ecosystem productivity with increased rain-
- ¹⁵ fall frequency and decreased intensity at very low rainfall regimes (<400 mm year⁻¹) and low frequency (<0.3 day⁻¹); beyond these very dry regimes, most ecosystems benefit from increasing frequency and decreasing intensity, except in the wet tropics (>1800 mm year⁻¹) where radiation limitation prevents further productivity gains. This finding reconciles seemingly contradictory findings in previous field studies on the di-
- 20 rection of rainfall frequency/intensity impacts on ecosystem productivity. We also find that changes in rainy season length can yield more dramatic ecosystem responses compared with similar percentage changes in rainfall frequency or intensity, with the largest impacts in semi-arid woodlands. This study demonstrates that not all rainfall regimes are ecologically equivalent, and that intra-seasonal rainfall characteristics play
- a significant role in influencing ecosystem function and structure through controls on ecohydrological processes. Our results also suggest that shifts in rainfall seasonality have potentially large impacts on terrestrial ecosystems, something that should be explicitly examined in future studies of climate impacts.



1 Introduction

Due to increased water holding capacity in the atmosphere as a consequence of global warming (O'Gorman and Schneider, 2009), rainfall is projected to vary in intensity and frequency across much of the world (Easterling et al., 2000; Trenberth et al., 2003;

- ⁵ Chou et al., 2013), in conjunction with complex shifts in rainfall seasonality (Feng et al., 2013; Seth et al., 2013). This indicates a large increase in the frequency of extreme events and variability in rainfall (Easterling et al., 2000; Allan and Soden, 2008), and many of these changes may be accompanied with little changes in total annual rainfall (Knapp et al., 2002; Franz et al., 2010). Meanwhile, regions sharing similar mean
- climate state may have very different intra-seasonal dynamics, and the ecological significance of second-order climate statistics has been largely overlooked previously in terrestrial biogeography (Good and Caylor, 2011). For example, ecosystems in West Africa and Southwest Africa (Fig. 1) share similar total annual rainfall, but West Africa has much more intense rainfall events within a much shorter rainy season, while South-
- ¹⁵ west Africa has a longer and less intense rainy season. The same amount of total rainfall can come in very different ways, which may cause distinctive ecological responses and landscape. Understanding the impacts of these regional differences in intra-seasonal rainfall variability and their possible future changes on terrestrial ecosystems is critical for maintaining ecosystem services and planning adaptation and miti-20 gation strategies for ecological and social benefits (Anderegg et al., 2013).

The changes in intra-seasonal rainfall characteristics, specifically frequency, intensity and seasonality, have critical significance to ecosystem productivity and structure (Porporato et al., 2001; Weltzin et al., 2003; Williams and Albertson, 2006; Good and Caylor, 2011; Guan et al., 2014), but previous studies on this topic (summarized in

Table 1) have their limitations in the following aspects. First, existing field studies on this topic mostly focus on a single ecosystem, i.e. grasslands, and subsequently only low rainfall regimes have been examined to date (mostly below 800 mm year⁻¹, see Table 1). Grasslands have the largest sensitivity to hydrological variabilities among all



ecosystems (Scanlon et al., 2005; Guan et al., 2012), however inferences drawn from a single ecosystem are limited in scope and difficult to apply to other ecosystems and rainfall regimes. Second, even within grasslands, different studies have seemingly contradictory findings (see Table 1), and there is a lack of a comprehensive framework to resolve these inconsistencies. Specifically, whether increased rainfall intensity with decreased rainfall frequency has positive (Knapp et al., 2002; Fay et al., 2003; Robertson et al., 2009; Heisler-White et al., 2009) or negative impacts (Heisler-White et al., 2009; Thomey et al., 2011) on grassland productivity is still debatable. Third, previ-

- ous relevant studies mostly focus on the impacts of rainfall frequency and intensity (Table 1 and Rodríguez-Iturbe and Porporato, 2004), and largely neglect the possible changes in rainfall seasonality. Rainfall frequency and intensity mostly describe rainfall characteristics within the rainy season, but do not account for the impacts of interplay between rainy season length and dry season length (Guan et al., 2014). For ecosystems predominately controlled by water availability, rainy season length constrains the
- temporal niche for active plant physiological activities (van Schaik et al., 1993; Scholes and Archer, 1997), and large variations in rainfall seasonality can lead to significant shifts in biome distribution found from paleoclimate pollen records (e.g. Vincens et al., 2007). Given changes in rainfall seasonality have been found in various tropical regions (Feng et al., 2013) and have been projected in future climate (Biasutti and So-
- ²⁰ bel, 2009; Shongwe et al., 2009; Seth et al., 2013), studies investigating their impacts on terrestrial ecosystem are relatively rare, and very few field studies are designed to address this aspect (Table 1, Bates et al., 2006; Svejcar et al., 2003; Chou et al., 2008). Finally, there is an increasing trend of large-scale studies addressing rainfall variability and ecological responses using satellite remote sensing (Fang et al., 2005;
- ²⁵ Zhang et al., 2005, 2013; Good and Caylor, 2011; Holmgren et al., 2013) and flux network data (Ross et al., 2012). These large-scale studies are able to expand analysis to more types of ecosystems and different climate conditions, and provide valuable observation-based insights. However there are very few theoretical modeling works to corroborate this effort. All these above issues call for a comprehensive modeling



study to investigate different aspects of intra-seasonal rainfall variability on terrestrial ecosystems spanning environmental gradients and various biomes.

In this paper, we aim to study ecological impacts of intra-seasonal rainfall variability on terrestrial ecosystems. In particular, we design virtual "rainfall manipulation experi-

- ⁵ ments" to concurrently shift intra-seasonal rainfall characteristics without changing total annual rainfall. We focus on the impacts of these different rainfall scenarios on ecosystem productivity (e.g. Gross Primary Production, GPP) and biome distributions in the African continent, simulated by an advance dynamic vegetation model SEIB-DGVM (Sato and Ise, 2012). Previous modeling approaches in this topic (Gerten et al., 2008;
- Hély et al., 2006) designed various rainfall scenarios by rearranging (halving, doubling or shifting) the rainfall amount based on the existing rainfall observations. In contrast to these approaches, we design a weather generator based on a stochastic rainfall model (Rodríguez-Iturbe et al., 1999), which allows us to implement a series of experiments by synthetically varying two of the three rainfall characteristics (rainfall intensity,
- rainfall frequency, and rainy season length) while fixing total annual rainfall at the current climatology. We choose Africa as our test-bed mostly because the following two reasons: (1) the rainfall regimes and biomes have large gradients varying from extremely dry grasslands to highly humid tropical evergreen forests, and thereby provide a large pool of different biomes; (2) Africa is a continent usually assumed to have few
- temperature constrains (Nemani et al., 2003), which will help to isolate the impacts of precipitation from temperature, as one challenge in attributing climatic controls on temperate ecosystems or Mediterranean ecosystems is the superimposed influences from both temperature and precipitation. The overarching science question we will address is: *How do African ecosystems respond to possible changes in intra-seasonal rainfall*
- variability (i.e. rainfall frequency, intensity and rainy season length)?



2 Materials and methods

2.1 Methodology overview

Table 1 summarizes previous field-based rainfall manipulation experiments, such as Knapp et al. (2002) that concurrently increasing rainfall frequency and decreasing rain-

- ⁵ fall intensity while fixing total rainfall for a grassland. The central idea of our study is to design similar rainfall manipulation experiments but test them virtually in the model domain across large environment gradients. We manipulate rainfall changes through a stochastic weather generator based on a parsimonious model of rainfall processes: statistically for the daily rainfall record, the mean annual precipitation (MAP) is a prod-
- ¹⁰ uct of the three rainfall characteristics for the wet season, rainfall frequency (λ , day⁻¹), rainfall intensity (α , mm), and rainy season length (T_w , days), normalized by f_w (the fraction of wet-season rainfall to the MAP) to account for the contribution from dry season rainfall (MAP = $\alpha\lambda T_w/f_w$). Thus it is possible to simultaneously perturb two of the rainfall characteristics away from their climatological values while preserving the MAP unchanged (Fig. 2). We then feed these different rainfall scenarios into a well-validated
- dynamic vegetation model (SEIB-DGVM, Sect. 2.2) to study simulated ecosystem response. Detailed experiments design is described in Sect. 2.5.

2.2 SEIB-DGVM model and its performances in Africa

We use a well-validated vegetation dynamic model SEIB-DGVM (Sato et al., 2007)
 as the tool to study ecosystem responses to different rainfall variabilities. This model follows the traditional "gap model" concept (Shugart, 1998) to explicitly simulate the dynamics of fine-scale ecosystem structure and function for a set of virtual vegetation patches as a surrogate to represent large-scale ecosystem states. Thus individual trees are simulated from establishment, having competition with other plants, to death which creates "gaps" in which different plant function types (PFTs) to develop. The SEIB-DGVM includes mechanical-based and empirical-based algorithms for land



physical processes, plant physiological processes, and plant dynamic processes. The SEIB-DGVM contains algorithms that explicitly involve the mechanisms of plant-related water stress (Fig. 3, Sato and Ise, 2012). Similar to previous studies (e.g. Milly, 1992; Porporato et al., 2001), the current SEIB model implements a continuous "water stress factor" (Eq. 2) based on the soil moisture status (Eq. 1), scaling from 0 (most stress-ful) to 1 (with no stress), which then acts to scale the stomatal conductance for plant transpiration and carbon assimilation.

 $\text{stat}_{\text{water}} = (S - S_{\text{w}})/(S_{\text{f}} - S_{\text{w}})$

5

10

Water stress factor = $2 \cdot \text{stat}_{water} - \text{stat}_{water}^2$

where S, S_w and S_f refer to the fraction of volumetric soil water content within the rooting depth, at the wilting point, and at field capacity, respectively. The SEIB-DGVM also allows the development of annual and perennial grasses as well as multiple life cycles of grass at one year based on environmental conditions, and multiple life cycles

- of tree growth per year are possible in theory but rarely happen in simulations (Sato and Ise, 2012). In particular, life cycles of grass are under prominent control of soil moisture status. The previously defined "water stress factor" and other environmental conditions co-determine the optimum LAI of the grass layer, which influences maximum daily NPP and the leaf phenology. When optimum LAI exceeds 0 for preceding 7
- ²⁰ days, the dormant phase changes into the growth phase; while when optimum LAI falls below 0 for preceding 7 days, the growth phase changes into the dormant phase (Sato et al., 2007). SEIB-DGVM also explicitly simulates the light conditions and competitions among different PFTs in the landscape based on its simulation of 3-D canopy structure and radiative transfer (Sato et al., 2007).
- The SEIB-DGVM has been tested both globally (Sato et al., 2007) and regionally for various ecosystems (Sato et al., 2010; Sato, 2009; Sato and Ise, 2012), which compared favorably with ground observations and satellite remote sensing measurements in terms of ecosystem composition, structure and function. In particular, the SEIB-DGVM has been successfully validated and demonstrated its ability in simulat-



(1)

(2)

ing ecosystem structure and function in the Africa continent (Sato and Ise, 2012). For woody species, two plant function types (PFTs) of tropical woody species are modeled in Africa: tropical evergreen trees and tropical deciduous trees, which distinguish in their phenology, with the former having leaves all year around, and the latter shed-

- ⁵ ding leaves during dry season, which is mostly controlled by root-zone moisture status (Sato and Ise, 2012). Trees and grasses coexist in a cell, with the floor of a virtual forest monopolized by one of the two grass PFTs, C_3 or C_4 grass, the type of which is determined at the end of each year by air temperature, precipitation, and CO_2 partial pressure (Sato and Ise, 2012).
- The SEIB model was run at a one degree spatial resolution and at a daily temporal resolution. It was spun-up for 2000 years driven by the observed climate (1970–2000) for the soil carbon pool to reach steady state, followed by 200 years simulation driven by the forcings based on the experiment design in Sect. 2.4. Because our purpose is to understand the direct impacts of intra-seasonal rainfall variability, we turned off
- the fire component of the SEIB model to exclude fire-mediated feedbacks in the results. Though we are fully aware of the important role of fire in interacting with rainfall seasonality and thus in influencing Africa ecosystem productivity and structures (Bond et al., 2005; Lehmann et al., 2011; Staver et al., 2012), studying these interactions is beyond the scope of this work. For the similar reason, we fixed the atmospheric CO₂ concentration at 380 ppmv to exclude possible impacts of CO₂ fertilization effects.

2.3 Synthetic weather generator

25

The synthetic weather generator used here consists of two major components: (i) to stochastically generate daily rainfall based on a rainfall model, and (ii) to conditionally sample all other environmental variables from historical records to preserve the covariance among climate forcing inputs.

The rainfall model can be statistically expressed as MAP = $\alpha \lambda T_w/f_w$, and we set f_w to be 0.9, i.e. the period including 90% of total annual rainfall is defined as "wet season" (exchangeable with "rainy season" hereafter). The "wet season" and "dry season"



rainfall time series are respectively modeled using the Marked Poisson Process. In this rainfall model, any day can be either rainy or not, and a rainy day is counted as one rainy event; rainfall events occur as a Poisson Process, with the parameter $1/\lambda$ being the mean intervals between rainfall events, and rainfall intensity α for each rainfall

- ⁵ event following an exponential distribution, with α being the mean rainfall intensity per event (Rodríguez-Iturbe et al., 1999). The wet season length is modeled as a beta distribution bounded from 0 to 1, scaled by 365 days. All climatological values of these rainfall characteristics (including the mean and variance of rainfall frequency, intensity and length of wet and dry seasons) were derived from the satellite-gauge-merged rain-
- ¹⁰ fall measurement from TRMM 3b42V7 (Huffman et al., 2007) for the period of 1998 to 2012, based on the above assumptions for the rainfall process. The two steps of the synthetic weather generator are described as below:

Step 1: Model the daily rainfall following the Marked Poisson process described above. In particular, for a specific year, we first stochastically generate the wet season length by sampling from the beta distribution, and the dry season length is determined accordingly. Then we generate the daily rainfall for wet and dry season respectively.

15

Step 2: Based on the simulated daily rainfall time series in Step 1, we conditionally sample temperature, wind, and humidity from the Global Meteorological Forcing Dataset (GMFD, Sheffield et al., 2006), as well as cloud fraction and soil temperature from the Climate Foregoet System Beanalysis (CFSP) from National Contern for Fault

- from the Climate Forecast System Reanalysis (CFSR) from National Centers for Environmental Prediction (NCEP) (Saha et al., 2010). For each day, a sample is randomly drawn from a pool that covers all the historical record within a 21-day time window centered at the sampling day. From the sampling pool, we find the day such that the historical rainfall amount of the chosen day is within (100–30) % to (100+30) % of the
- simulated daily rainfall amount. We then draw all other environmental variables on that sampled day to the new climate forcing. If we can find a sample from the pool, this sampling is called "successful". When there is more than one suitable sample, we randomly select one. When there is no suitable sample, we randomly select one day within the



pool. The mean "successful" rate for all the ensembles and all the experiments across Africa is 83 %.

The GMFD data (Sheffield et al., 2006) blends reanalysis data with observations and disaggregates in time and space, and is available from 1948 to 2008, with 1.0-degree spatial resolution and daily temporal resolution. The CFSR data (Saha et al., 2010) provides cloud fraction and simulated soil temperature from three soil layers for the SEIB model. The CFSR version that we used is from 1979 to 2010, and the original 0.3° spatial resolution and 6 hourly temporal resolution are aggregated to 1.0° and daily.

To test the validity of the synthetic weather generator, we ran the SEIB model using the historical climate record ($S_{climatology}$) and the synthetic forcing ($S_{control}$), with the latter generated using the weather generator based on the rainfall characteristics derived from the former. Figure A1 shows that the SEIB model simulations driven by these two different forcings generate similar biome distributions with a Cohen's Kappa coefficient of 0.78 (Cohen, 1960), and similar GPP patterns in Africa, with the linear fits of annual GPP: GPP($S_{control}$) = 1.03 GPP($S_{climatology}$) + 0.215 (R^2 = 0.89, P < 0.0001). Both biome and GPP patterns are consistent with observations (Sato and Ise, 2012). These results provide confidence in using the synthetic weather generator and SEIB-DGVM to conduct the further study.

2.4 Experiment design

²⁰ Three experiments are designed as follows, and are shown in the conceptual diagram (Fig. 2):

Exp 1 (Perturbation of rainfall frequency and intensity, and the experiment is termed as $S_{\lambda-\alpha}$ hereafter, with S referring "Scenario") Simulations forced by the synthetic forcings with varying λ and α simultaneously for wet season (20% increases of λ and

²⁵ corresponding decreases of α to make MAP unchanged; 20 % decreases of λ and corresponding increases of α to make MAP unchanged; no change for dry season rainfall characteristics) while fixing T_w at the current climatology;



Exp 2 (Perturbation of rainfall frequency and rainy season length, termed as $S_{T_w-\lambda}$) Simulations forced by the synthetic forcing with varying T_w and λ simultaneously for wet season (20% increases of T_w and corresponding decreases of λ to make MAP unchanged; 20% decreases of T_w and corresponding increases of λ to make MAP unchanged; no change for dry season characteristics) while fixing α at the current climatology;

Exp 3 (Perturbation of rainy season length and intensity, termed as $S_{T_w-\alpha}$) Simulations forced by the synthetic forcing with varying T_w and α simultaneously for wet season (20% increases of T_w and corresponding decreases of α to make MAP unchanged; 20% decreases of T_w and corresponding increases of α to make MAP unchanged; no

change for dry season characteristics) while fixing λ at the current climatology. Because λ and T_w have bounded ranges ($\lambda \sim [0, 1]$ and $T_w \sim [0, 365]$), if the updated

value exceeds the range, we would force the new updated value to be the upper bound, and rearrange the other variable to ensure MAP unchanged. For example in Exp 1, if after 10% increase the updated λ is larger than 1, we would force the updated λ to be 1, and recalculate the changes in α to keep MAP the same as before. All the scenarios have six ensemble runs differentiated in their synthetic forcings to account for the stochasticity of the synthetic weather generator.

3 Results

10

- ²⁰ We present the differences in simulated biome distributions of the three experiments (i.e. $S_{\lambda-\alpha}$, $S_{T_w-\lambda}$, $S_{T_w-\alpha}$) in Fig. 4 (and Figs. A2 and A3 for their spatial patterns), and the differences in simulated soil moisture and GPP in Figs. 5 and 6. These differences indicate the simulated ecosystem sensitivity to the slight perturbation away from the current climatology of intra-seasonal rainfall characteristics. We present the differences between +20% and -20% changes in each experiment. We also assessed shifts of
- ± 10 %, and found that these responses are similar with only smaller magnitudes and thus not shown here. Figure 6 plots the difference in simulated GPP as a function of



mean annual precipitation and the climatological value of a perturbed rainfall characteristic, paired with the standard error (SE) between simulations to indicate the uncertainty of the result, as $SE = \sigma/\sqrt{n}$, where σ and n refer to the standard deviation and the sample size in each bin respectively. Thus changes in GPP and their associated standard ⁵ errors are calculated for each climatological bin; where the bin size for MAP, rainfall frequency, rainfall intensity and rainy season length are 100 mm year⁻¹, 0.05 day⁻¹, 1 mm and 15 days respectively. We recognize that there are large heterogeneity in soil texture, altitude and other factors which can influence simulation results at local scale, and using the current approach essentially lumps these factors and highlights the impacts from our interested variables (i.e. rainfall characteristics). A series of illustrations in Fig. 7 were generalized from the simulated time series, and will be used to explain the underlying mechanisms.

3.1 Ecosystem sensitivity to rainfall frequency and intensity (Experiment $S_{\lambda-\alpha}$)

The experiment S_{λ-α} shows that the simulated biome distributions, after increasing
rainfall frequency λ and decreasing its intensity α (λ↑, α↓) under a fixed total annual rainfall, have small differences in the low rainfall regime (around 500 mm year⁻¹, Fig. 4a), with a small portion of regions converting from woodland to grassland, indicating a negative impact of increasing rainfall frequency when total rainfall is very low. In the high rainfall regime (around 1500 mm year⁻¹, Fig. 4a), increasing rainfall frequency significantly converts tropical evergreen forests into woodlands. In the intermediate rainfall regime (600–1000 mm year⁻¹), there are little changes in biome distributions. We further check the spatial patterns of differences in annual mean soil moisture and annual total GPP (Fig. 5a and b). We find that GPP increases with increasing rainfall frequency across most of the Africa continent, except in very dry end (in the southern and eastern Africa) as well as very wet regions (in central Africa and northeastern)

Madagascar). This GPP pattern mostly mirrors the soil moisture change (Fig. 5b), except the wet tropics where the changes of soil moisture and GPP are in the reversed signs.



Figure 6a shows the GPP sensitivity as a function of MAP and the climatological rainfall frequency, and we find three major patterns stand out:

Pattern 1.1: Negative GPP sensitivity shows up in the very dry end of MAP regime (MAP < 400 mm year⁻¹) and with very low rainfall frequency ($\lambda < 0.3 \text{ day}^{-1}$), i.e. GPP decreases with more frequent but less intense rainfall in this low rainfall regime, without changes in the total rainfall amount.

Pattern 1.2: Across most rainfall regimes (MAP from 400 mm year⁻¹ to 1600 mm year⁻¹), increasing frequency of rainfall (and simultaneously decreasing rainfall intensity) lead to positive GPP sensitivity. This positive GPP sensitivity peaks at the low range of rainfall frequency (~0.35 day⁻¹) and around the MAP of 1000 mm year⁻¹.

Pattern 1.3: At the high range of MAP (>1800 mm year⁻¹) with low rainfall frequency $(\sim 0.4 \text{ day}^{-1})$, GPP decreases with increased rainfall frequency.

10

15

The GPP sensitivity with respect to MAP and rainfall intensity (Fig. 6c) contains more uncertainties and shows more complex patterns, mostly because the space that most pixels cluster (Fig. A4c) also has large variance (Fig. A4d). Thus we will not over-interpret the pattern in Fig. 6c.

Illustrative time series in Fig. 7a and b explain the above Pattern 1.1 and Pattern 1.2, respectively. Figure 7a shows that when rainfall events are small and very infrequent, increasing rainfall frequency while decreasing intensity would cause more

- frequent downcrossings of soil moisture at the wilting point S_w , which subsequently would reduce the effective time of carbon assimilation and plant growth (i.e. when soil moisture is below S_w , plants would be in the extreme water stress and stop physiological activity). It is worth noting that this case only happens when MAP is very low with low frequency, where the biome is dominantly grasslands, which explains the spatial
- patterns of negative soil moisture and GPP sensitivity in Fig. 5a and b. This result also corroborates the field findings of the negative impacts from increasing rainfall frequency in Heisler-White et al. (2009) and Thomey et al. (2011) at low rainfall regimes.

Figure 7b explains the positive sensitivity of soil moisture and GPP with increasing rainfall frequency over most Africa continent (Pattern 1.2). Once individual rainfall event



has enough intensity and rainfall events are frequent enough, downcrossings of S_w would not easily happen; instead, the accumulative rainy-season water stress (shaded areas between S_{w} and S^{*}, Porporato et al., 2001) becomes the dominant source of growth stress for plants; and increasing rainfall frequency can lead to a significant 5 decrease in this type of plant water stress. This conclusion drawn from our numerical modeling is consistent with previous findings in Rodríguez-Iturbe and Porporato (2004) based on stochastic modeling. We also find that this positive impact reaches to its maximum in the intermediate total rainfall (\sim 1000 mm year⁻¹) and relatively low rainfall frequency ($\sim 0.35 \, \text{day}^{-1}$), indicating that in these regimes increasing rainfall freguency could most effectively decrease plant water stress and create marginal benefits 10 of GPP to the increased rainfall frequency. Either too large total annual rainfall or too high rainfall frequency may uplift soil moisture status in general, which would reduce the sensitivity to water stress with fewer downcrossings of soil moisture critical point S^{*}: and once the soil moisture is always ample (i.e. above S^{*}), the changes in either MAP or rainfall frequency would not alter plant water stress. 15

There is another negative GPP sensitivity shown in Pattern 1.3, but the mechanism is different from the previous negative GPP case. In regions with total rainfall usually more than 1800 mm year⁻¹, SEIB-simulated tropical forests exhibit radiation-limitation rather than water-limitation during wet season. Increase of rainfall frequency at daily scale would enhance cloud fraction and suppress plant productivity in these regions (Graham et al., 2003). Thus even though soil moisture still increases (Fig. 5a), GPP decreases with increased rainfall frequency. This mechanism also explains why tropical evergreen forests shrink its area with increased rainfall frequency (Fig. 4a).

It is worth noting that the magnitude of GPP changes due to rainfall frequency and intensity is relatively small in most of the woodlands, but can be relatively large for drylands with MAP below 600 mm year⁻¹ (up to 10–20% of annual GPP). This pattern also explains why only modest changes in biome distribution happen for the transitional area between woodlands and grasslands (Fig. 4a).



3.2 Ecosystem sensitivity to rainfall seasonality and frequency (Experiment $S_{T_w-\lambda}$)

The experiment $S_{T_w-\lambda}$ shows that the simulated biome distribution, after increasing rainy season length and decreasing rainfall frequency (i.e. $T_w \uparrow, \lambda \downarrow$) under a fixed total annual rainfall, has an increase of area in tropical evergreen forests, which are converted from woodlands, an area increase of woodlands converted from grasslands in the northern Africa, and a small expansion of grasslands into woodlands in the African Horn region (Fig. 4b). Figure 5c and d show that increasing rainy season length T_w and decreasing frequency λ would significantly increase annual mean soil moisture and GPP (up to 30%) in most woodland area, meanwhile decreased soil moisture and GPP are found in the southern and eastern Africa, and tropical evergreen forest regions have little response. We further explore the GPP sensitivity space in Fig. 6e and g, and find the following interesting patterns, which are mostly robust due to the

¹⁵ **Pattern 2.1**: The negative GPP sensitivity tends to happen where MAP is mostly below 1000 mm year⁻¹ with long rainy season length ($T_w > 150$ days) and low rainfall frequency ($\lambda < 0.35$ day⁻¹), which is a unique rainfall regime that sporadically spread rain events for a long rainy season.

small standard errors shown in Fig. 6f and h:

Pattern 2.2: When MAP and rainfall frequency are both larger than certain ranges (MAP > 1000 mm year⁻¹ and $\lambda > 0.4 \text{ day}^{-1}$), trading the decrease of λ for the increase of T_w would significantly increase GPP. The maximum positive GPP sensitivity happens in the rainfall regime with the intermediate MAP range (1100–1500 mm year⁻¹) and the high rainfall frequency ($\lambda \sim 0.7 \text{ day}^{-1}$).

Pattern 2.3: There exists an "optimal rainy season length" for relative changes in
 ²⁵ ecosystem productivity at different MAP ranges (the white area between the red and blue space in Fig. 6e). For the same MAP, longer than this length, rainy season length-ening would decrease GPP; while shorter than this length, rainy season lengthen-



ing would increase GPP. This "optimal rainy season length" increases with MAP until 1400 mm year⁻¹.

Figure 7c explains the negative GPP sensitivity in Pattern 2.1. In the situation with low MAP and infrequent rainfall events, decreasing rainfall frequency to extend rainy
season length (i.e. *T*_w ↑, *λ* ↓) would lead to longer time between rainfall events and possibly longer excursion below *S*_w, which would restrain continuous plant growth and have detrimental effects on ecosystem productivity. It is worth noting that long rainy season in dryland (Fig. 6e) is usually accompanied with low rainfall frequency (Fig. 6g). The southern African grasslands typically fall in this category and thus have negative GPP sensitivity (Fig. 5c and d); these regions also correspond to the small biome conversion from woodlands to grasslands in the low range of MAP (~300 mm year⁻¹) as shown in Fig. 4b.

Figure 7d explains the positive GPP sensitivity in Pattern 2.2, which shows that when rainfall is ample enough to maintain little or no water stress during rainy season, in-¹⁵ creasing the interval of rainfall events may introduce little additional water stress but can significantly extend the growing season. This situation mostly happens in woodlands, where limited water stress exists during growing season, and dry season length is the major constraint for plant growth. Thus increase of rainy season length extends the temporal niche for plant growth, and significantly modifies the biome distribution, which leads to large wood encreachment to grasslands and also conversion of wood-

²⁰ which leads to large wood encroachment to grasslands and also conversion of woodlands to tropical evergreen forests, as shown in Fig. 4b.

The little GPP sensitivity in tropical evergreen forest regions is mostly attributed to the long rainy season length already existed in this type of ecosystem. Thus further increasing T_w may reach to its saturation (365 days) and thus have little impact to ²⁵ ecosystem productivity. Similar reason also explains why the GPP sensitivity has the maximum response in the intermediate MAP range rather than the high MAP range, at which GPP sensitivity has been saturated.

The finding of "optimal rainy season length" across different rainfall regimes (Fig. 6e) is consistent with our previous empirical finding about the similar pattern of "optimal



rainy season length" for tree fractional cover in Africa derived based on a satellite remote sensing product (Guan et al., 2014). Two distinctive GPP sensitivities separated by the "optimal rainy season length", with this optimal length increasing with MAP, fully demonstrate the importance to explicitly consider the non-linear impacts of rainy season length on ecosystem productivity under climate change, which has been largely

overlooked before.

3.3 Ecosystem sensitivity to rainfall seasonality and intensity $(S_{T_w-\alpha})$

The results of the experiment $S_{T_w-\alpha}$ have many similarities with those of $S_{T_w-\lambda}$, including the similar changes in biome distributions (Fig. 4), soil moisture and GPP patterns (Fig. 5e and f). We further find that the GPP sensitivity space with MAP and rainy season length (Fig. 6i) is also similar with that of $S_{T_w-\lambda}$ (Fig. 6e). One new pattern is that rainfall intensity has little impacts on the GPP sensitivity, as the contour lines in Fig. 6k are mostly parallel with y-axis (rainfall intensity); in other words, the tradeoff between T_w and α is mostly a function of MAP and T_w , but not α , and the largest marginal effects happen in the intermediate range of MAP, similar as in $S_{T_w-\lambda}$.

Figure 7e and f explain the governing hydrological mechanisms for the patterns of $S_{T_w-\alpha}$, which also have many similarities with $S_{T_w-\lambda}$. For the negative case (Fig. 7e), decreasing rainfall intensity to extend rainy season in very low MAP regime may possibly lead to more downcrossings of S_w and interrupt continuous plant growth. The positive case (Fig. 7e) is similar as that in Fig. 7d, i.e. the repartitioning of excessive rainy-season water to the dry season for an extended growing period would significantly benefit plant growth and possible increase tree fraction cover.

4 Discussion and Conclusion

In this paper we provide a new modeling approach to systematically understand the ecological impacts from changes in intra-seasonal rainfall characteristics (i.e. rainfall



7592

frequency, rainfall intensity and rainy season length) across biomes and climate gradients in the African continent.

4.1 Limitation of the methodology

Though the modeling framework that we used is able to characterize the diverse ecosystem responses to the shifts in different rainfall characteristics, it nevertheless has its limitations. The current rainfall model only deals with the case of single rainy season per year, and approximates the case of double rainy seasons per year to be single rainy season case. This assumption may induce unrealistic synthetic rainfall patterns in the equatorial dryland regions, in particular the Horn of Africa, thus the resulting sensitivity of these regions may be less reliable. We also assume that rainfall frequency and intensity are homogenous throughout wet and dry seasons, but in reality they still

- have seasonal variations. We only consider rainy season length for rainfall seasonality, and neglect the possible temporal phase change; actually rainfall seasonality change usually has length and phase shifts in concert. These rainfall-model-related limitations
- ¹⁵ can be possibly overcame by simulating smaller intervals of rainfall processes (e.g. each month has their own α and λ) rather than simulating the whole wet or dry season using one fixed set of α and λ . Besides, only using one ecosystem model also means that the simulated ecosystem sensitivity can be model-specific, though we believe the sensitivity patterns (e.g. Figs. 5 and 6) should mostly hold as the necessary
- 20 ecohydrological processes have been incorporated in the SEIB-DGVM, magnitudes or thresholds in these patterns may vary depending on different models. For example, GPP in tropical evergreen forests (Figs. 5b and 6a) is less sensitive to radiation limitation as shown in satellite-based observation than in the SEIB simulation in Africa (Guan et al., 2013). We recognize that to exclude fire impacts in the current simulation
- may bring some caveats in interpreting the results, as evidence shows that many savanna regions can be bistable due to fire effects (Staver et al., 2011; Hirota et al., 2011; Higgins and Scheiter 2012; also see for a possible rebuttal in Hanan et al., 2013) and changes in rainfall regimes may not only have direct effects on vegetation productivity



but also indirect effects through influencing fire regimes, and rapid biome shifts may be a consequence. These feedbacks can be important in situations where the growing season length changes, which are related to fuel loads, fuel moisture dynamics and hence fire intensity (Lehmann et al., 2011). Quantifying these fire-rainfall feedbacks will be the important future direction to pursue.

4.2 Clarifying the impacts of rainfall frequency and intensity on ecosystem productivity

In this paper we have resolved the previous debate about whether increasing rainfall intensity (or equivalently decreasing rainfall frequency, i.e. λ ↓, α ↑) has positive or negative impacts on above-ground primary productivity with a fixed annual rainfall total. We identify that negative GPP sensitivity with increased rainfall frequency is possible at very low MAP range (~400 mm year⁻¹) with very low rainfall frequency (<0.35 day⁻¹) (Fig. 6a), due to the increased downcrossings of soil moisture wilting point, which restricts plant growth (Fig. 7a). Our derived MAP threshold to distinguish different GPP sensitivities with rainfall frequency is consistent with our meta-analysis based on the previous field studies (Table 1), which shows a threshold of MAP at 340 mm year⁻¹ separates positive and negative impacts of more intense rainfall on ANPP. Our findings are also consistent with others about increased tree encroachments with increased rainfall intensity in very low rainfall regime (<544 mm year⁻¹, Kulmatiski and Beard, 2013), which essentially follows the same mechanism as identified in Fig. 7a.

In addition, we thoroughly investigated the ecosystem responses across all the ranges of rainfall in Africa, and we find that beyond the very low rainfall range below 400 mm year⁻¹, most grasslands and woodlands would benefit from increasing rainfall frequency, which also corroborate the previous large-scale findings about the positive effects of increased rainfall frequency (and decreased rainfall intensity) for tree fractions

effects of increased rainfall frequency (and decreased rainfall intensity) for free fractions across the African continent (Good and Caylor, 2011). The only exception happens at the very wet end of MAP (~1800 mm year⁻¹) where cloud-induced radiation-limitation may suppress ecosystem productivity with increased rainfall frequency. We also find



that changes in rainfall frequency and intensity mostly affact grassland-dominated savannas (changes of GPP up to 20%), and the corresponding effects are much smaller in woodlands and have little impact on woodland distribution. Though this work is only based on a single model, it provides a primary assessment for understanding of interactive changes between λ and α in ecosystem functioning, which expands to the full spectra of rainfall ranges compared with previous studies (e.g. Porporato et al., 2004).

4.3 Ecological importance of rainy season length

The results involving rainy season length (i.e. $S_{T_w-\lambda}$ and $S_{T_w-\alpha}$) have fully demonstrated the ecological importance of rainfall seasonality. The magnitudes of changes in soil moisture, GPP and biome distribution in $S_{T_w-\lambda}$ and $S_{T_w-\alpha}$ are much larger than those of $S_{\lambda-\alpha}$, with almost one order of magnitude difference. These disproportional impacts of T_w indicate that slight changes in rainy season length could modify biome distribution and ecosystem function more dramatically compared with the same percentage changes in rainfall frequency and intensity. We also notice that $S_{T_w-\lambda}$ and $S_{T_w-\alpha}$ have similar results, which is because that both λ and α describe rainfall characteristics within wet season, while T_w describes rainfall characteristics of both dry season and wet season.

Given the importance of rainy season length, its ecological impacts under climate change are largely understudied, though substantial shifts in rainfall seasonality have ²⁰ been projected in both Sahel and South Africa (Biasutti and Sobel, 2009; Shongwe et al., 2009; Seth et al., 2013). Here we only address the rainfall seasonality in terms of its length, and future changes in rainfall seasonality may modify their phase and magnitude in concert. The climate community has focused on the increase of extreme rainfall events (Field et al., 2012), which could be captured by the changes in λ or α towards heavier tails in their distribution. However, explicit and systematic assessments and projection on rainfall seasonality changes (including both phase and magnitude) are still limited even in the latest Intergovernmental Panel on Climate Change (IPCC)





BGD



to these changes and their ecological implications are required for future hydroclimateecosystem research.

4.4 Not all rainfall regimes are ecologically equivalent

As Fig. 1 gives a convincing example that the same total annual rainfall may arrive in a very different way, our results further demonstrate that ecosystems respond differently to the changes in intra-seasonal rainfall variability. For example, with similar MAP, West Africa and Southwest Africa can have reversed responses to the same changes in intra-seasonal rainfall variability. As shown in the experiments of $S_{T_w-\lambda}$ and $S_{T_w-\alpha}$, increasing T_w while decreasing λ or α generates slightly positive soil moisture and GPP sensitivity in West Africa (Fig. 5c and d), but would cause relatively large GPP decrease in Southwest Africa. The prior hydroclimate conditions of these two regions can explain these differences: West Africa has much shorter rainy season with more intense rainfall events, which is totally contrary to Southwest Africa, which has a long rainy season but many small and sporadic rainfall events. As a result, under a fixed annual rainfall to-

- tal, slightly increasing rainy season and meanwhile decreasing rainfall intensity would 15 benefit plant growth in West Africa, but the same change would lengthen dry spells in Southwest Africa and bring negative effects to the ecosystem productivity. We further deduce that the rainfall use efficiency (RUE, defined as the ratio of plant net primary production and total rainfall) in these two drylands could be different: West Africa may
- have lower RUE, and the intense rainfall could lead to more infiltration-excess runoff, 20 and thus less water would be used by plants; while Southwest Africa can have higher RUE, because its sporadic and feeble rainfall events would favor grass to fully take the advantage of the ephemerally existed water resources. This conclusion is partly supported by Martiny et al. (2007) based on satellite remote sensing. We further hy-
- pothesize that landscape geomorphology in these two drylands may be different and 25 therefore reflect distinctive rainfall characteristics. More bare soil may exist in West Africa grasslands due to intense-rainfall-induced erosion, while Southwest Africa may

have more grass fraction and less bare soil fraction. Testing these interesting hypotheses is beyond the scope of this paper, but is worthy the further exploration.

Acknowledgements. K. Guan and E. F. Wood acknowledge the financial supports from the NASA NESSF fellowship. S.P. Good and K. K. Caylor acknowledge the financial supports from the National Science Foundation through the Grant EAR-0847368. The authors thank Ignacio Rodríguez-Iturbe for his valuable inputs and discussion.

References

10

20

25

- Anderegg, L. D. L., Anderegg, W. R. L., and Berry, J. A.: Not all droughts are created equal: translating meteorological drought into woody plant mortality, Tree Physiol., 33, 701–712, 2013.
- Bates, J., Svejcar, T., Miller, R., and Angell, R.: The effects of precipitation timing on sagebrush steppe vegetation, J. Arid Environ., 64, 670–697, 2006.
- Biasutti, M. and Sobel, A. H.: Delayed Sahel rainfall and global seasonal cycle in a warmer climate, Geophys. Res. Lett., 36, L23707, doi:10.1029/2009GL041303, 2009.
- ¹⁵ Bond, W. J., Woodward, F. I., and Midgley, G. F.: The global distribution of ecosystems in a world without fire, New Phytol., 165, 525–537, 2005.
 - Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., and Mearns, L. O.: Climate extremes: observations, modeling, and impacts, Science, 289, 2068–2074, 2000.
 - Fang, J., Piao, S., Zhou, L., He, J., Wei, F., Myneni, R. B., Tucker, C. J., and Tan, K.: Precipitation patterns alter growth of temperate vegetation, Geophys. Res. Lett., 32, L21411,
 - doi:10.1029/2005GL024231, 2005.
 - Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., and Collins, S. L.: Productivity responses to altered rainfall patterns in a C₄-dominated grassland, Oecologia, 137, 245–251, 2003.

Feng, X., Porporato, A., and Rodriguez-Iturbe, I.: Changes in rainfall seasonality in the tropics, Nature Climate Change 3, 811–815, 2013.

Field, C., Barros, V., Stocker, T., Qin, D., Dokken, D., Ebi, K., Mastrandrea, M., Mach, K., Plattner, G.-K., Allen, S., Tignor, M., and Midgley, P. (eds.): IPCC, 2012: Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK, and New York, NY, USA, 2012.



Franz, T. E., Caylor, K. K., Nordbotten, J. M., Rodríguez-Iturbe, I., and Celia, M. A.: An ecohydrological approach to predicting regional woody species distribution patterns in dryland ecosystems, Adv. Water Resour., 33, 215–230, 2010.

Gerten, D., Luo, Y., Maire, G. L., Parton, W. J., Keougn, C., Weng, E., Beier, C., Ciais, P.,

⁵ Cramer, W., Dukes, J. S., Hanson, P. J., Knapp, A. A. K., Linder, S., Nepstad, D., Rustad, L., and Sowerby, A.: Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones, Global Change Biol., 14, 2365–2379, 2008.

Good, S. P., and Caylor, K. K.: Climatological determinants of woody cover in Africa, P. Natl. Acad. Sci. USA, 108, 4902–4907, 2011.

¹⁰ Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G., and Wright, S. J.: Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons, P. Natl. Acad. Sci. USA, 100, 572–576, 2003.

Guan, K., Wood, E. F., and Caylor, K. K.: Multi-sensor derivation of regional vegetation fractional cover in Africa, Remote Sens. Environ., 124, 653–665, 2012.

- Guan, K., Wolf, A., Medvigy, D., Caylor, K., Pan, M., and Wood, E.: Seasonal coupling of canopy structure and function in African tropical forests and its environmental controls, Ecosphere, 4, 35, http://dx.doi.org/10.1890/ES12-00232.1, 2013.
 - Guan, K., Wood, E. F., Medvigy, D., Pan, M., Caylor, K. K., Sheffield, J., Kimball, J., Xu, X., and Jones, M. O.: Terrestrial hydrological controls on vegetation phenology of African savannas and woodlands, J. Geophys. Res., doi:10.1002/2013JG002572, 2014.
 - Hanan, N. P., Tredennick, A. T., Prihodko, L., Bucini, G., and Dohn, J.: Analysis of stable states in global savannas: is the CART pulling the horse?, Global Ecol. Biogeogr., 23, 259–263, 2013.

20

Harper, C. W., Blair, J. M., Fay, P. A., Knapp, A. K., and Carlisle, J. D.: Increased rainfall vari-

- ²⁵ ability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem, Global Change Biol., 11, 322–334, 2005.
 - Heisler-White, J. L., Blair, J. M., Kelly, E. F., Harmoney, K., and Knapp, A. K.: Contingent productivity responses to more extreme rainfall regimes across a grassland biome, Global Change Biol., 15, 2894–2904, 2009.
- Hély, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M. T., and Guiot, J.: Sensitivity of African biomes to changes in the precipitation regime, Global Ecol. Biogeogr., 15, 258–270, 2006.
 Higgins, S. I. and Scheiter, S.: Atmospheric CO₂ forces abrupt vegetation shifts locally, but not globally, Nature, 488, 209–212, 2012.



- Hirota, M., Holmgren, M., Nes, E. H. V., and Scheffer, M.: Global resilience of tropical forest and savanna to critical transitions, Science, 334, 232–235, 2011.
- Holmgren, M., Hirota, M., van Nes, E. H., and Scheffer, M.: Effects of interannual climate variability on tropical tree cover, Nature Climate Change 3, 755—758, doi:10.1038/nclimate1906, 2013.
- Huffman, G. J., Bolvin, D. T., Nelkin, E. J., Wolff, D. B., Adler, R. F., Bowman, K. P., and Stocker, E. F.: The TRMM Multisatellite Precipitation Analysis (TMPA): quasi-global, multiyear, combined-sensor precipitation estimates at fine scales, J. Hydrometeorol., 8, 38–55, 2007.
- ¹⁰ Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., Harper, C. W., Danner, B. T., Lett, M. S., and McCarron, J. K.: Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland, Science, 298, 2202–2205, 2002.
 - Kulmatiski, A. and Beard, K. H.: Woody plant encroachment facilitated by increased precipitation intensity, Nature Climate Change 3, 833–837, doi:10.1038/nclimate1904, 2013.
- Lehmann, C. E. R., Archibald, S. A., Hoffmann, W. A., and Bond, W. J.: Deciphering the distribution of the savanna biome, New Phytol., 191, 197–209, 2011.
 - Martiny, N., Camberlin, P., Richard, Y., and Philippon, N.: Compared regimes of NDVI and rainfall in semi-arid regions of Africa, Int. J. Remote Sens., 27, 5201–5223, 2006.

Miranda, J., Armas, C., Padilla, F., and Pugnaire, F.: Climatic change and rainfall patterns: effects on semi-arid plant communities of the Iberian Southeast, J. Arid Environ., 75, 1302–1309, 2011.

- Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J., Myneni, R. B., and Running, S. W.: Climate-driven increases in global terrestrial net primary production from 1982 to 1999, Science, 300, 1560–1563, 2003.
- O'Gorman, P. A. and Schneider, T.: The physical basis for increases in precipitation extremes in simulations of 21st-century climate change, P. Natl. Acad. Sci. USA, 106, 14773–14777, 2009.
 - Porporato, A., Laio, F., Ridolfi, L., and Rodríguez-Iturbe, I.: Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress – III. Vegetation water
- ³⁰ stress, Adv. Water Resour., 24, 725–744, 2001.

5

20

Porporato, A., Daly, E., and Rodríguez-Iturbe, I.: Soil water balance and ecosystem response to climate change, Am. Nat., 164, 625–632, 2004.



7599

- Robertson, T. R., Bell, C. W., Zak, J. C., and Tissue, D. T.: Precipitation timing and magnitude differentially affect aboveground annual net primary productivity in three perennial species in a Chihuahuan Desert grassland, New Phytol., 181, 230–242, 2009.
- Rodríguez-Iturbe, I. and Porporato, A.: Ecohydrology of Water-Controlled Ecosystems: Soil
 Moisture And Plant Dynamics, Cambridge University Press, Cambridge, United Kingdom, 2004.
 - Rodríguez-Iturbe, I., Gupta, V. K., and Waymire, E.: Scale considerations in the modeling of temporal rainfall, Water Resour. Res., 20, 1611–1619, 1984.
 - Rodríguez-Iturbe, I., Porporato, A., Ridolfi, L., Isham, V., and Cox, D. R.: Probabilistic modelling
- of water balance at a point: the role of climate, soil and vegetation, P. Roy. Soc. A-Math. Phy., 455, 3789–3805, 1999.
 - Ross, I., Misson, L., Rambal, S., Arneth, A., Scott, R. L., Carrara, A., Cescatti, A., and Genesio, L.: How do variations in the temporal distribution of rainfall events affect ecosystem fluxes in seasonally water-limited Northern Hemisphere shrublands and forests?, Biogeosciences, 9. 1007–1024. doi:10.5194/bg-9-1007-2012. 2012.
- ¹⁵ 9, 1007–1024, doi:10.5194/bg-9-1007-2012, 2012.
 Saha, S., Moorthi, S., Pan, H.-L., Wu, X., Wang, J., Nadiga, S., Tripp, P., Kistler, R., Woollen, J., Behringer, D., Liu, H., Stokes, D., Grumbine, R., Gayno, G., Wang, J., Hou, Y.-T., Chuang, H.-Y., Juang, H.-M. H., Sela, J., Iredell, M., Treadon, R., Kleist, D., Delst, P. V., Keyser, D., Derber, J., Ek, M., Meng, J., Wei, H., Yang, R., Lord, S., Dool, H. V. D., Kumar, A., Wang, W.,
- Long, C., Chelliah, M., Feng, Y., Huang, B., Schemm, J.-K., Ebisuzaki, W., Lin, R., Xie, P., Chen, M., Zhou, S., Higgins, W., Zou, C.-Z., Liu, Q., Chen, Y., Han, Y., Cucurull, L., Reynolds, R. W., Rutledge, G., and Goldberg, M.: The NCEP climate forecast system reanalysis, B. Am. Meteorol. Soc., 91, 1015–1057, 2010.
 - Sato, H.: Simulation of the vegetation structure and function in a Malaysian tropical rain forest using the individual-based dynamic vegetation model SEIB-DGVM, Forest Ecol. Manag.,
- using the individual-based dynamic vegetation model SEIB-DGVM, Forest Ecol. Manag 257, 2277–2286, 2009.
 - Sato, H. and Ise, T.: Effect of plant dynamic processes on African vegetation responses to climate change: analysis using the spatially explicit individual-based dynamic global vegetation model (SEIB-DGVM), J. Geophys. Res., 117, G03017, doi:10.1029/2012JG002056, 2012.
- ³⁰ Sato, H., Itoh, A., and Kohyama, T.: SEIB-DGVM: a new dynamic global vegetation model using a spatially explicit individual-based approach, Ecol. Model., 200, 279–307, 2007.



BGD 11, 7575–7613, 2014 **Ecological Impacts of** intra-seasonal rainfall variability K. Guan et al. **Title Page** Abstract Introduction Conclusions References **Tables Figures** Back Close Full Screen / Esc **Printer-friendly Version** Interactive Discussion

Discussion

Paper

Discussion

Paper

Discussion Paper

Discussion Paper

Sato, H., Kobayashi, H., and Delbart, N.: Simulation study of the vegetation structure and function in eastern Siberian larch forests using the individual-based vegetation model SEIB-DGVM, Forest Ecol. Manag., 259, 301–311, 2010.

Scanlon, T. M., Caylor, K. K., Manfreda, S., Levin, S. A., and Rodriguez-Iturbe, I.: Dynamic

response of grass cover to rainfall variability: implications for the function and persistence of savanna ecosystems, Adv. Water Resour., 28, 291–302, 2005.

Shugart, H. H.: Terrestrial Ecosystems in Changing Environments, Cambridge University Press, UK, 1998.

Scholes, R. J. and Archer, S. R.: Tree-grass interactions in savannas, Annu. Rev. Ecol. Syst., 28, 517–544, 1997.

Seth, A., Rauscher, S. A., Biasutti, M., Giannini, A., Camargo, S. J., and Rojas, M.: CMIP5 projected changes in the annual cycle of precipitation in monsoon regions, J. Climate, 26, 7328–7351, 2013.

Sheffield, J., Goteti, G., and Wood, E. F.: Development of a 50-year high-resolution global

- dataset of meteorological forcings for land surface modeling, J. Climate, 19, 3088–3111, 2006.
 - Shongwe, M. E., van Oldenborgh, G. J., van den Hurk, B. J. J. M., de Boer, B., Coelho, C. A. S., and van Aalst, M. K.: Projected changes in mean and extreme precipitation in africa under global warming. Part I: Southern Africa, J. Climate, 22, 3819–3837, 2009.
- ²⁰ Staver, A. C., Archibald, S., and Levin, S. A.: The global extent and determinants of savanna and forest as alternative biome states, Science, 334, 230–232, 2011.
 - Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P. M. (eds.): IPCC, 2013: Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovern-

²⁵ mental Panel on Climate Change, Cambridge University Press, Cambridge, UK and New York, NY, USA, 2013.

- Svejcar, T., Bates, J., Angell, R., and Miller, R.: The influence of precipitation timing on the sagebrush steppe ecosystem, in: Changing Precipitation Regimes and Terrestrial Ecosystems, edited by: McPherson, G. and Weltzin, J., University of Arizona Press, Tucson, AZ, 2027 pp. 2002
- ³⁰ 237 pp., 2003.

10

Thomey, M. L., Collins, S. L., Vargas, R., Johnson, J. E., Brown, R. F., Natvig, D. O., and Friggens, M. T.: Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland, Global Change Biol., 17, 1505–1515, 2011.

- Trenberth, K. E., Dai, A., Rasmussen, R. M., and Parsons, D. B.: The changing character of precipitation, B. Am. Meterol. Soc., 84, 1205–1217, 2003.
- van Schaik, C. P., Terborgh, J. W., and Wright, S. J.: The phenology of tropical forests: adaptive significance and consequences for primary consumers, Annu. Rev. Ecol. Syst., 24, 353–377, 1993.

5

Vincens, A., Garcin, Y., and Buchet, G.: Influence of rainfall seasonality on African lowland vegetation during the Late Quaternary: pollen evidence from Lake Masoko, Tanzania, J. Biogeogr., 34, 1274–1288, 2007.

Weltzin, J. F., Loik, M. E., Schwinning, S., Williams, D. G., Fay, P. A., Haddad, B. M., Harte, J.,

Huxman, T. E., Knapp, A. K., Lin, G., Pockman, W. T., Shaw, M. R., Small, E. E., Smith, M. D., Smith, S. D., Tissue, D. T., and Zak, J. C.: Assessing the response of terrestrial ecosystems to potential changes in precipitation, BioScience, 53, 941–952, 2003.

Williams, C. A. and Albertson, J. D.: Dynamical effects of the statistical structure of annual rainfall on dryland vegetation, Global Change Biol., 12, 777–792, 2006.

- ¹⁵ Zhang, X., Friedl, M. A., Schaaf, C. B., Strahler, A. H., and Liu, Z.: Monitoring the response of vegetation phenology to precipitation in Africa by coupling MODIS and TRMM instruments, J. Geophys. Res., 110, D12103, doi:10.1029/2004JD005263, 2005.
 - Zhang, Y., Moran, M. S., Nearing, M. A., Campos, G. E. P., Huete, A. R., Buda, A. R., Bosch, D. D., Gunter, S. A., Kitchen, S. G., McNab, W. H., Morgan, J. A., McClaran, M. P.,
- Montoya, D. S., Peters, D. P., and Starks, P. J.: Extreme precipitation patterns and reductions of terrestrial ecosystem production across biomes, J. Geophys. Res.-Biogeo., 118, 148–157, 2013.



Table 1. Summary of previous representative studies on assessing the impacts of rainfall characteristics (i.e. rainfall frequency, intensity and seasonality) on the structure and function of terrestrial ecosystem.

Focus	Methods	Spatial Scale	Time scale	MAP (mm year ⁻¹)	Ecosystem type	Major Conclusion	Reference
freq; int	RS	Africa continent	intra-annual climatology	[0,3000]	Africa all	(int-) woody cover	Good and Caylor (2011)
freq; int	RS	US		[163,1227]	US	(int–) ANPP greatest in arid grassland (16 %) and Mediterranean forest (20 %) and less for mesic grassland and temperate forest (3 %)	Zhang et al. (2013)
freq; int	RS	Pan-tropics (35° N to 15° S)	inter-annual	[0,3000]	Tropical ecosystems	(CV+) wood cover in dry tropics; (CV-) wood cover in wet tropics	Holmgren et al. (2013)
freq; int	RS	Northern China	intra-annual	[100,850]	temperate grassland and forests	(int-) NDVI for temprate grassland and broadleaf forests, not for coniferous forest	Fang et al. (2005)
freq; int	Flux	Northern Hemisphere	intra-annual	$[393 \pm 155, 906 \pm 243]$	shrubland and forest	(int-) GPP, RE and NEP	Ross et al. (2012)
seas	RS	Africa continent	climatology	[0,3000]	Africa all	rainy season onset and offset controls vegetation growing season	Zhang et al. (2005)
freq; int (fix MAP)	Field	plot (Kansas, USA)	intra-annual	615	grassland	(int-) ANPP	Knapp et al. (2002)
freq; int (fix MAP)	Field	plot (Kansas, USA)	intra-annual	835	grassland	(int-) ANPP	Fay et al. (2003)
increase seasonal rainfall	Field	plot (Taxes, USA)	intra-annual	365	grassland	(int-) ANPP	Robertson et al. (2009)
freq; int	Field	plot (Kansas, USA)	intra-annual	[320,830]	grassland	(int-)ANPP for MAP=830 mm year ⁻¹ ; (int+)ANPP for MAP=320 mm year ⁻¹	Heisler-White et al. (2009)
freq; int	Field	plot (New Mexico, USA)	intra-annual	250	grassland	(int+) ANPP	Thomey et al. (2011)
freq; int (fix MAP)	Field	plot (Kansas, USA)	intra-annual	834	grassland	(int–) soil CO ₂ flux	Harper et al. (2005)
freq; int (fix MAP)	Field	plot (Kruger National Park, South Africa)	intra-annual	544 savanna	sub-tropical	(int+) wood growth; (int-) grass growth	Kulmatiski and Beard (2013)
sea (fix MAP)	Field	plot (Oregon, USA)	intra-annual	[140,530]	grassland	impact biomass and bare soil fraction	Bates et al. (2006), Svejcar et al. (2003)
sea	Field						
freq; int; MAP	Field	plot (South Africa)	intra-annual	[538,798]	grassland	(int-) ANPP	Swemmer et al. (2007)
MAP; sea	Field	plot (Spain)	intra-/inter- annual	242	grassland	Mediterranean dryland ecosystem has more resilience for intra- and inter-annual changes in rainfall	Miranda et al. (2008)

Focus: frequency (freq); intensity (int); seasonality (sea); variation (CV).

Methods: Field Experiments (Field); Remote Sensing (RS); Flux Tower (Flux).

Major Conclusion: increasing rainfall intensity (or decreasing frequency) has positive impacts (int+); increasing intensity (or decreasing frequency) has negative impacts (int-); increasing rainfall CV has positive impacts (CV+); increasing rainfall CV has negative impacts (CV-).



Discussion Paper

Discussion Paper

Discussion Paper

Discussion Paper





Figure 1. (**a** and **b**) Spatial pattern of the rainfall characteristics in Africa: (**a**) MAP; (**b**) rainfall intensity; (**c**) rainfall frequency; (**d**) rainy season length. The black-line identified areas refer to two savanna regions in West and Southwest Africa. (**e** and **f**) Normalized histograms of the rainfall characteristics in two savanna regions of West and Southwest Africa. (**e**) MAP; (**f**) rainfall intensity; (**g**) rainfall frequency; (**h**) rainy season length.



Figure 2. Conceptual diagram of the experiment designs for three experiments $(S_{\lambda-\alpha}, S_{T_w-\lambda}, S_{T_w-\alpha})$.





Figure 3. Schematic diagram of water stress factor ranging from 0 (most stressful) to 1 (no stress), which acts to reduce transpiration and carbon assimilation. The red dotted line is based on Porporato et al. (2001) with a reversed sign, and the SEIB model has a nonlinear implementation (blue solid line, Sato and Ise, 2012).





Figure 4. Differences in simulated dominated biomes in the three experiments (i.e. $S_{\lambda-\alpha}$, $S_{T_w-\lambda}$, $S_{T_w-\alpha}$).





Figure 5. Simulated changes in annual mean soil moisture (0–500 mm, first column) and annual mean GPP (second column) for different experiments. Please note that the scales of $S_{\lambda-\alpha}$ is much smaller than those of $S_{T_w-\lambda}$ and $S_{T_w-\alpha}$. The two areas with black boundaries in each panel are West African grassland and Southwest African grassland associated with Fig. 1. The spatial patterns shown here are smoothed by 3 × 3 smoothing window from the raw data.





Figure 6. Differences in simulated annual GPP as a function of mean annual precipitation and one of the perturbed rainfall characteristics in all the three experiments (i.e. $S_{\lambda-\alpha}$, $S_{T_w-\lambda}$, $S_{T_w-\alpha}$) in the left column. The right column shows the correspondent standard errors (SE, calculated as $SE = \sigma/\sqrt{n}$, where σ refers to the standard deviation within each bin, *n* is the sample size in each bin, and *n* and σ are shown in Fig. A4), with larger values associated with more uncertainties and requires more caution in interpretation. The contours are based on the binned values, with for each 100 mm year⁻¹ in MAP, each 0.05 day⁻¹ in rainfall frequency, each 1 mm in rainfall intensity and each 15 day in rainy season length.







Figure A1. Comparison of biomes and annual GPP between Sclimatology and Scontrol to test the validity of the synthetic weather generator. The biome definition follows Sato and Ise (2012).





Figure A2. Simulated biomes for different experiments.





Figure A3. Normalized histograms of three simulated dominating biomes in the three experiments.





Figure A4. The sample size (*n*) in each bin (left column) and standard deviation (σ) in each bin (right column), corresponding to Fig. 6. In Fig. 6 right column, standard deviation (SE) is calculated as SE = σ/\sqrt{n} .

