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Extreme precipitation patterns and reductions of terrestrial ecosystem production across biomes

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[1] Precipitation regimes are predicted to shift to more extreme patterns that are characterized by more heavy rainfall events and longer dry intervals, yet their ecological impacts on vegetation production remain uncertain across biomes in natural climatic conditions. This in situ study investigated the effects of these climatic conditions on aboveground net primary production (ANPP) by combining a greenness index from satellite measurements and climatic records during 2000–2009 from 11 long-term experimental sites in multiple biomes and climates. Results showed that extreme precipitation patterns decreased the sensitivity of ANPP to total annual precipitation (P_T) at the regional and decadal scales, leading to decreased rain use efficiency (RUE; by 20% on average) across biomes. Relative decreases in ANPP were greatest for arid grassland (16%) and Mediterranean forest (20%) and less for mesic grassland and temperate forest (3%). The cooccurrence of heavy rainfall events and longer dry intervals caused greater water stress conditions that resulted in reduced vegetation production. A new generalized model was developed using a function of both P_T and an index of precipitation extremes and improved predictions of the sensitivity of ANPP to changes in precipitation patterns. Our results suggest that extreme precipitation patterns have substantially negative effects on vegetation production across biomes and are as important as P_T. With predictions of more extreme weather events, forecasts of ecosystem production should consider these nonlinear responses to altered extreme precipitation patterns associated with climate change.

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1. Introduction

[2] Climate change involves rising global mean temperatures and more extreme precipitation patterns with a higher frequency of larger storms and longer intervening dry periods [*Easterling et al.*, 2000; *Intergovernmental Panel on Climate Change* (*IPCC*), 2007; *Groisman and Knight*, 2008; *Allison et al.*, 2009]. There is growing evidence that precipitation regimes have become more extreme at global, regional, and local scales [*Easterling et al.*, 2000]. Such altered intra-annual precipitation patterns, along with warmer temperature, will affect vegetation production, water balance, and biodiversity and result in changes in the structure and functioning of terrestrial ecosystems [*Sala et al.*,

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2000; *Knapp et al.*, 2002]. Even if total annual precipitation (P_T) remains unchanged in an ecosystem, changes in rainfall event frequency and distribution will alter the soil water available to the terrestrial ecosystem [*Knapp et al.*, 2002; *Weltzin et al.*, 2003]. Hence, understanding and quantifying the impacts of these infrequent climate conditions on terrestrial ecosystems are critical to scientific and public interests.

[3] Most studies to date have focused on the effects of changes in total precipitation amounts [*Knapp et al.*, 2008]. The importance of total precipitation amount on ecosystem production has been assessed widely and aboveground net primary production (ANPP) usually increases across biomes with increasing mean annual precipitation (MAP) [*Sala et al.*, 1988; *Knapp and Smith*, 2001; *Huxman et al.*, 2004a]. However, evidence is mounting that terrestrial ecosystem processes are sensitive to intra-annual precipitation patterns even in the absence of changes in annual precipitation quantity [*Knapp et al.*, 2002, 2008]. In addition, RUE, commonly described as the ratio of ANPP to P_T, is a critical indicator for assessing ecosystem responses to altered precipitation patterns [*Huxman et al.*, 2004a; *Bai et al.*, 2008]. Therefore, studies of the ecological consequences of climate change should be based not only on annual averages but also on the predicted changes in intra-annual precipitation patterns.

[4] Field manipulated experiments that investigate the effects of precipitation patterns independent of precipitation amount are commonly used to understand responses of ecosystems to the infrequent changes in precipitation patterns. These studies usually have been conducted either on an individual ecosystem or over short-term periods, which render comparisons difficult across biomes. Changes in precipitation patterns (increasing extreme events) have shown mixed effects in grasslands. For example, ANPP for tallgrass prairie was reduced [*Knapp et al.*, 2002], but increased ANPP in semiarid grassland was also observed [*Heisler-White et al.*, 2008]. *Miranda et al.* [2009] showed that there was little to no effect on plant production in semiarid Mediterranean grassland. Because total rainfall amount and large storms are strongly interrelated in natural settings, manipulated experiments may not reflect these mixed effects and highly nonlinear responses of vegetation in natural conditions [*Sala et al.*, 1992; *Huxman et al.*, 2004b]. Long-term measurements of natural variability in field settings, supported by manipulative experiments, are considered the best approach for determining the impact of infrequent extreme precipitation patterns on vegetation production [*Weltzin et al.*, 2003].

[5] Collectively, in spite of the emerging research on responses of biological process to more extreme climate regimes [*Knapp et al.*, 2008; *Smith*, 2011], our understanding and quantification of the effects of more extreme precipitation regimes across biomes is lacking [*Weltzin et al.*, 2003; *Heisler-White et al.*, 2009]. Few studies have addressed the influences of extreme precipitation events on ecosystem production across biomes in the natural climate conditions at the regional scale [*Weltzin et al.*, 2003; *Knapp et al.*, 2008]. An alternative to manipulated experiments is to analyze these effects on ecosystem processes in natural field settings with long-term measurements across biomes [*Huxman et al.*, 2004b].

[6] In this study, we focused on a 10-year data set of Moderate Resolution Imaging Spectroradiometer (MODIS) enhanced vegetation index (EVI; an index of canopy photosynthetic capacity) [*Huete et al.*, 2002] as an indicator of ANPP in combination with field observations from 11 long-term experimental sites in the conterminous United States. Our primary goal was to examine the impacts of interannual variability in precipitation on vegetation production across biomes, with particular focus on (1) quantifying the direction and magnitude of ANPP responses to extreme precipitation regimes and (2) developing a cross-biome relationship between vegetation production and extreme precipitation patterns at the regional scale.

2. Materials and Methods

2.1. Study Sites and Data Selection

[7] We focused our study on 11 U.S. Department of Agriculture (USDA) experimental sites across the conterminous United States. These sites included different precipitation regimes and biomes representative of ecosystems ranging from arid grasslands to temperate forest. They represent a broad range of production, climatic and soil conditions, and life history characteristics of the dominant species. At each site, a location was selected in an undisturbed vegetated area of size at least 2.25×2.25 km (Table 1). According to Köppen-Geiger climate classification [*Peel et al.*, 2007], arid grassland (DE, JE, WG, SR, and CP) and Mediterranean forest (CC) experience a climate with a dry season and are seasonally water limited, whereas mesic grassland (SP and

Table 1. Descriptions of the Sites in This Study[a]

Site and Location	Latitude (°)	Longitude (°)	Land Cover	MAP[b] (mm)	Maximum Temperature[b] (°C)	Code
Desert Experimental Range, Utah	38.547	−113.712	Arid grassland	163 (53)	19 (1.1)	DE
Jornada Experimental Range, New Mexico	32.589	−106.844	Arid grassland	242 (78)	25 (0.7)	JE
Walnut Gulch Experimental Watershed, Arizona	31.736	−109.938	Arid grassland	311 (85)	25 (1.0)	WG
Santa Rita Experimental Range, Arizona	31.846	−110.839	Arid grassland	447 (129)	29 (0.7)	SR
Central Plains Experimental Range, Colorado	40.819	−104.748	Arid grassland	363 (85)	16 (1.4)	CP
Southern Plains Experimental Range, Oklahoma	36.614	−99.576	Mesic grassland	586 (153)	22 (0.9)	SP
Little Washita River, Oklahoma	34.918	−97.956	Mesic grassland	796 (195)	24 (1.2)	LW
Little River Watershed, Georgia	31.537	−83.626	Temperate conifer forest	1148 (257)	25 (0.6)	LR
Mahatango Creek, Pennsylvania	40.731	−76.592	Temperate broadleaf forest	1058 (179)	16 (0.9)	MC
Bent Creek Experimental Forest, North Carolina	35.500	−82.624	Temperate mixed forest	1227 (239)	19 (0.6)	BC
Caspar Creek, California	39.337	−123.748	Mediterranean forest	1054 (301)	16 (0.7)	CC

[a]Precipitation and temperature for the 40-year period 1970–2009 were available for all sites except JE and DE, for which data were available for the 32-year period of 1978–2009 for JE and for the 66-year period of 1935–1984 and 1994–2009 for DE. [b]Average MAP and average annual mean maximum temperature with standard deviation in parentheses.

LW) and temperate forest (LR, MC, and BC) experience humid climates and can be light limited.

[8] The climate data set used in this study was constructed from in situ daily precipitation and daily maximum air temperatures measured at the local weather station representative of each site from 1970 to 2009, except for JE and DE. Daily data were available from 1978 to 2009 for JE. For DE, there were only daily precipitation data from 1935 to 1984 and from 1994 to 2000 and annual data from 2000 to 2009 at the local station. Therefore, we used the closest NOAA weather station with longer-term and consistent daily data series as a surrogate to calculate extreme indices for the 2000–2009 time period, while the annual precipitation data were still used for the analysis. Long-term (40 years) in situ precipitation data sets were used to identify climate extremes within the past decade. Among several statistical methods to diagnose extreme events, we focused on the extreme indices as proposed by *Frich et al.* [2002], which are widely used and adopted as standard output data in the IPCC AR4 report [*IPCC*, 2007]. In this study, we considered a set of extreme precipitation indices (Table 2). Extreme precipitation indices include R95pToT, R95p%, SDII, and CDD (Table 2). CDD represents the length of dry spell. SDII expresses the intensity of extreme precipitation. R95pToT is defined as annual precipitation amounts due to daily precipitation exceeding the 95th percentile of the 1970–2009 period, and R95p% represents the fraction of P_T due to the events above 95th percentile (R95p% represents the frequency of heavy storms). Because absolute P_T and amounts of extreme events vary significantly from arid grassland to forest, we used R95p% (i.e., R95pToT normalized by P_T) for analysis to make this index comparable across sites, whereas R95pToT was used to analyze the absolute correlation with P_T. Extreme precipitation indices considered for the analysis are calculated for each year and for each site. Annual values were based on the hydrologic year extending from 1 October to 30 September.

2.2. EVI Data

[9] The EVI data set was derived from the MODIS land product subset (MOD13Q1) with 16-day and 250 m resolutions for the period of 2000–2009. To compare EVI with in situ climatic measurements, we averaged the EVI data over an area of ~2.25 × 2.25 km (9 × 9 pixels) based on the coordinates for each site in Table 1. A total of 230 scenes (23 per year for 10 years) were obtained for each of the 11 sites. To eliminate the noise of low-quality cloud- and aerosol-contaminated pixels, a pixel-based quality assurance (QA) control was applied to generate a less noisy time series data set. The software TIMESAT was used to smooth the QA-filtered time series of EVI as well as to estimate the vegetation and phenology parameters [*Jönsson and Eklundh*, 2004]. An integrated EVI was then computed to represent the total vegetation production over the growing season. This large integral of MODIS EVI measurements (referred to as iEVI hereafter) was used as our surrogate measure of ANPP (Figure 1a). Remote sensing vegetation indices [normalized difference vegetation index (NDVI) and EVI] have been widely used as a proxy of ANPP because they are strongly correlated with terrestrial ANPP [*Field et al.*, 1995; *Prince and Goward*,

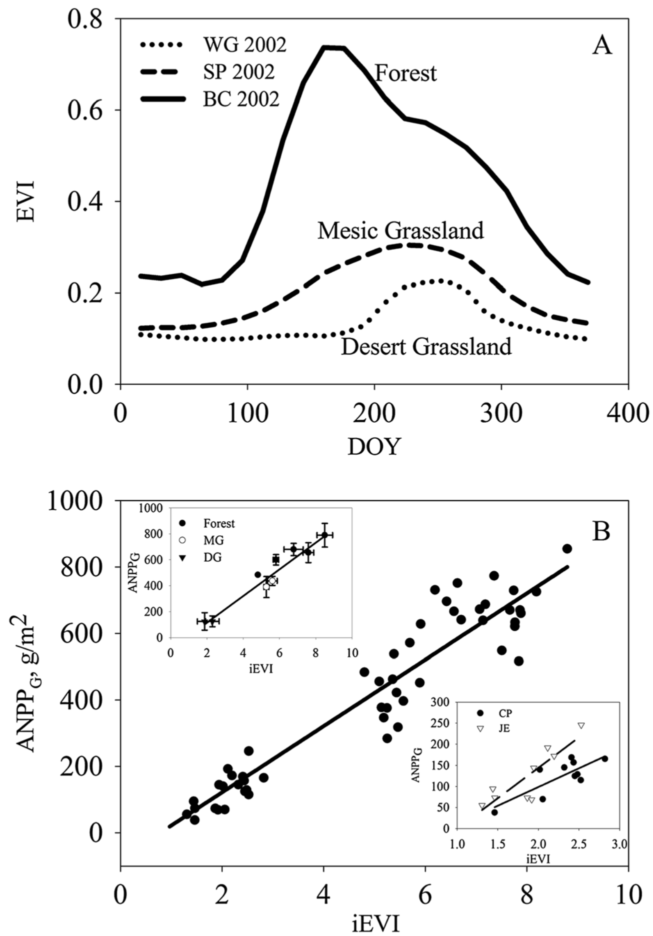

Figure 1. (a) An example of 1-year smoothed EVI time series for desert grassland (DG), mesic grassland (MG), and forest. (b) Relationship between annual $ANPP_G$ and the corresponding iEVI derived from MODIS data during the 2000–2009 period for nine selected sites across biomes. The solid line shows the linear regression ($R^2 = 0.90$; $P < 0.0001$; RMSE = 82.60). The top inset shows the site average of ANPPG and iEVI (regression model, $R^2 = 0.94$; $P < 0.0001$; RMSE = 65.87). Error bars are the standard deviations. The bottom inset shows the relationships at sites CP and JE ($R^2 = 0.50$ and 0.74; RMSE = 29.29 and 36.89, respectively; $P < 0.01$).

Table 2. Extreme Indices Used in This Study

Index	Description	Abbreviation	Units
1	Annual precipitation due to daily rainfall >95th percentile	R95pTOT	mm
2	Precipitation fraction of annual total precipitation due to daily rainfall ≥95th percentile of present daily precipitation during 1970–2009	R95p%	%
3	Simple precipitation intensity index: P_T divided by the number of days with daily rainfall ≥1 mm/d	SDII	mm/d
4	Annual maximum number of consecutive days with daily rainfall <1 mm	CDD	days

1995; *Paruelo et al*., 1997; *Myneni et al*., 2001; *Fang et al*., 2005; *Bunn and Goetz*, 2006; *Beck and Goetz*, 2011]. MODIS EVI has been reported to be more sensitive to ANPP than NDVI, especially at higher biomass regions [*Huete et al*., 2002, 2006]. To validate the relation between iEVI and annual ANPP for the data set in this study, ground measurements of ANPP ($ANPP_G$; g/m^2) during the period 2000–2009 were compiled for nine sites across the United States (Table 3). A strong relationship [Equation (1)] between $ANPP_G$ and the corresponding iEVI was derived across biomes for these long-term experimental sites (Figure 1b):

$$ANPP_G = 102.2526 \times iEVI - 101.3382, \quad R^2 = 0.90, \quad P < 0.0001 \tag{1}$$

[10] The site-specific comparison with ANPP from the ground measurements showed generally good agreement across the sites (Figure 1b). The ratio of root mean square error (RMSE) of simulated ANPP to the mean of the measured ANPP ranged from 0.05 to 0.39 (mean ratio of 0.20) across all sites. The relationship between ANPP and iEVI at site scale (two grassland sites included in Table 1) also showed similar temporal variations during 2000–2009 (Figure 1b, inset). Hence, iEVI can be used to accurately quantify the dynamics of ANPP with confident and provide consistent sensitivity across biomes ranging from arid grassland to forest. In the following results and discussion, the trends in iEVI are interpreted to represent the cross-biome behavior of ANPP.

2.3. Climate Data Analysis

[11] There were complex interactions between P_T and extreme events, which made it difficult to separate the relative effects of each other in field studies occurring under natural rainfall regimes. Across all sites, P_T was strongly related to R95pToT and SDII events, and total rainfall amounts and large storms were strongly related across biomes (Table 4). Although the frequency of extreme events was far less than small events (Figure 2a), R95p% was up to 50% with an average of 22% across all the sites (Figure 2b, inset). P_T increased as the amounts of extreme events increased ($R^2 = 0.66$; $P < 0.01$; Figure 2b). A similar relation between P_T and SDII was found. Wet years were usually related to the presence of a few large rainfall events. Because R95pToT and SDII were strongly correlated (Table 4), we reported only the results for the index R95p%, although we found quite similar results for both R95p% and SDII (SDII results not reported here).

Table 4. Pearson Correlations of Extreme Indices Combining All the Data Sets[a]

	R95pToT	SDII	CDD	P_T
R95pToT	1.00			
SDII	**0.76**	1.00		
CDD	−0.28	−0.22	1.00	
P_T	**0.81**	**0.81**	**−0.40**	1.00

[a]Bold values are significant at the $P < 0.01$ level (two-tailed t test). P_T, hydrologic annual precipitation.

[12] To isolate effects of precipitation patterns (extreme events size and rainfall intensity) from effects of P_T, we proposed a new approach of precipitation data analysis with respect to the ANPP-P_T relation. We split the total data set (11 sites and 10 years) into two groups based on R95p% (Figure 2b, inset). Based on the distribution of R95p% frequency (Figure 2b, inset), we set a threshold of 20% to split the groups with a similar number of points for each group. The groups were labeled "Low" for R95p% < 20% and "High" for R95p% ≥ 20% (Figure 2b, inset). Because R95p% of the Low group was less than or close to the mean of R95p% (22%), we referred to years in the Low group as normal years and those in High group as extreme years. Therefore, we split the 10-year data set into two groups for each site. There were at least 2 years for any of the two groups for each site. For instances, there were 3 years in Low group and 7 years in High group at Jornada site, whereas there were 8 years in Low group and 2 years in High group at Little River site. The MAP amounts for each group are presented in Table 5. Then, we conducted the precipitation analyses in two ways to study the effects of extreme precipitation patterns on ecosystem production.

[13] First, to evaluate the variations in the responses of ANPP to extreme precipitation patterns between biomes

Table 3. Sites With In Situ ANPP Measurements Within the Period of 2000–2009 for Validation With iEVI

Site[a]	Biome and Location	Period	Mean annual ANPP (g/m^2)	Source
Jornada LTER	Arid grassland, New Mexico	2000–2009	124.3	*Huenneke et al*. [2002], *Peters et al*. [2012]
Central Plains Experimental Range	Grassland, Colorado	2000–2008	85.7	Jack A. Morgan (personal communication, 2012)[a]
Cedar Creek LTER	Grassland, Minnesota	2000–2007	389.5	*Clark and Tilman* [2008]
Konza Prairie LTER	Grassland, Kansas	2000–2002	436.8	*Turner et al*. [2006]
Harvard Forest	Mixed forest, Massachusetts	2000–2009	654.6	*Munger and Wofsy* [1999]
Metolius Intermediate Pine	Evergreen needleleaf forest, Oregon	2001	483.3	*Law et al*. [2003]
Park Falls	Deciduous broadleaf forest, Wisconsin	2000, 2004	599.7	*Burrows et al*. [2003]
Ohio Hills FFs	Mixed forest, Ohio	2001–2002	789.7	*Chiang et al*. [2008]
University of Michigan Biological Station	Deciduous broadleaf forest, Michigan	2000–2006	679.4	*Gough et al*. [2008]

[a]Estimates of ANPP of shortgrass steppe vegetation were obtained from harvests of total aboveground biomass at the USDA Agricultural Research Service Central Plains Experimental Range taken near the time of peak aboveground biomass in late July or early August from 2000 to 2008. Four permanent transects in the pasture allowed a systematic sampling of pasture 23 W, a long-term moderately grazed pasture. Each transect comprised fifteen 1 × 1 m^2 exclosure cages (60 total) that are moved each spring. Aboveground biomass was harvested from a 0.1 m^2 quadrant in the center of each exclosure. Biomass was harvested from every fifth cage for a total of 12 cages each year. Standing biomass was separated into the following functional groups: C_3 perennial grasses, C_3 annual grasses, forbs, subshrubs, blue grama/buffalo grass (dominant C_4 perennial grasses), other C_4 grasses, and standing dead trees. Biomass was dried at 60 °C for a minimum of 48 h and weighed.

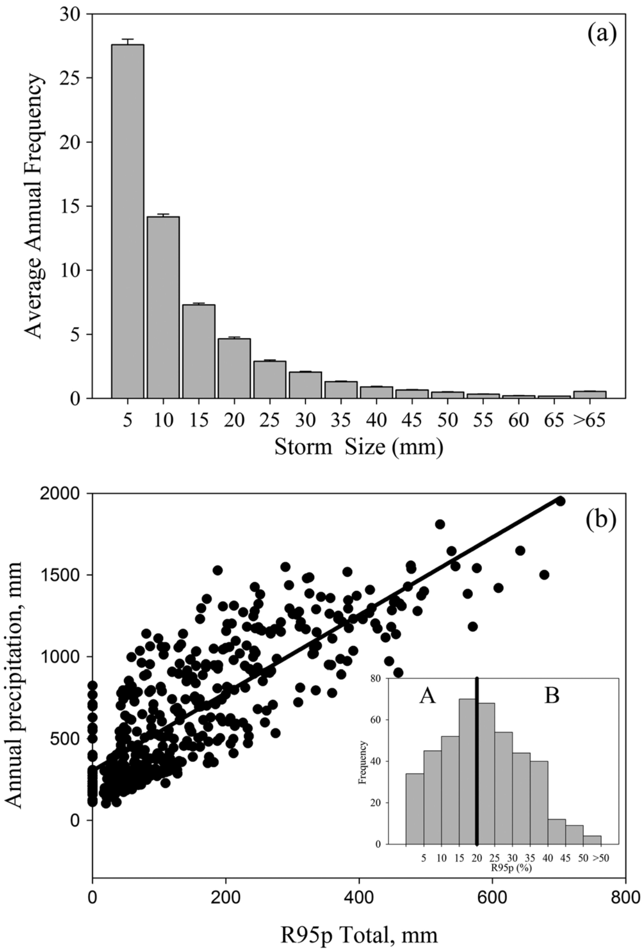

Figure 2. (a) Frequency analysis of size of precipitation events for the whole site year data set. (b) The contribution of extreme rainfall events to total precipitation for the whole data set. The regression coefficient of correlation (r^2) is 0.66 ($P < 0.01$), as stated in Table 3. The inset shows the frequency of R95p%. The thick solid line within the inset indicates the threshold to define the two groups based on R95p% of all site year data.

Table 5. Average Annual Precipitation (mm) During All the Years in Two R95p% Groups Across the Biomes[a]

Biomes	Low	High	Difference (%)
DG	237 (25)	276 (25)	16.4
MG	624 (11)	982 (9)	57.4
TF	1011 (15)	1249 (15)	23.6
MF	866 (5)	1217 (5)	40.6

[a]Average difference combined into biome types. DG, arid grassland sites (DE, JE, WG, SR, and CP); MG, mesic grassland sites (SP and LW); TF, temperate forested sites (LR, MC, and BC); MF, Mediterranean forested site (CC). The numbers in parentheses represent the number of site year data points in each group.

independent of annual rainfall amounts, we selected years with similar P_T (±5%) but different R95p% groups for each site (Table 6). We found at least 1 year in Low group and 1 or more corresponding year with similar P_T in High group for each site (Table 6). At some sites, we found two or more pairs in the two R95p% groups. For example, for the 2 years in High group at Little River, we found 2 corresponding years with similar P_T (±5%) in Low group, respectively (resulting in two pairs; Table 6). Then, the relative differences of iEVI were compared for these years across 11 sites. In addition, the average results were combined into biome types similar to those used by *Knapp and Smith* [2001].

[14] Second, to assess the overall effects of extreme precipitation patterns on relations between ANPP and P_T across biomes, we compared the sensitivity of relations for different groups for R95p% across all sites, respectively. An F test was used to compare the statistical significances between the two curves of ANPP-P_T relations across biomes. Further, average RUE was also compared for the different R95p% groups across sites. RUE is an effective measure for the responses of primary production to precipitation [*Huxman et al.*, 2004a]. Here, RUE was estimated directly as the ratio of iEVI to the corresponding P_T [*Bai et al.*, 2008]. A Pearson correlation analysis and Duncan's multiple range tests were used to determine significant differences in extreme indices and iEVI among groups using the SAS version 9.1 (SAS Institute, Cary, North Carolina).

3. Results

3.1. Differential Responses to Extreme Precipitation Patterns Between Biomes

[15] Among all sites, the effects of fewer but larger rainfall events on ANPP were negative for seven sites (DE, JE, WG, SR, CP, BC, and CC; $P < 0.01$), and not significantly different from zero for four sites (SP, LW, LR, and MC; $P > 0.05$). This suggests that a shift to more extreme precipitation patterns, with no changes in P_T, resulted in different responses of vegetation production between ecosystems (Figure 3). Combined into biome types, increased heavy precipitation events caused significant reduction of ANPP for arid grassland sites and Mediterranean forested sites, whereas there was no significant reduction in ANPP for mesic grassland and temperate forested sites (Figure 3). As R95p% increased from 11% to 33% (Table 6) for arid grassland sites, the mean annual iEVI decreased by 16% (Figure 3). The mean annual iEVI of the Mediterranean forested site (CC) was reduced by 20% when R95p% increased from 15% to 28%. For the mesic grassland sites and temperate forested sites, mean annual iEVI showed no significant decreases ($P > 0.05$), although R95p% increased from ~15% to 30% (Figure 3; Table 6). The concurrence across four arid grassland sites in ANPP reduction indicates that arid grasslands are more sensitive to the infrequent extreme precipitation regimes than other biomes.

3.2. Cross-Biome ANPP-P_T Relation Due to Extreme Precipitation Patterns

[16] Across biomes, the relation between ANPP and P_T differed significantly between years with low extreme precipitation patterns and high extreme years with larger and more infrequent precipitation events (Figure 4). Biome-level patterns of ANPP responses to extreme precipitation patterns were reflected by significantly altered curvilinear relationship slopes of ANPP-P_T for Low and High groups of R95p% (Figure 4). Overall, across the range of biomes, the ANPP-P_T relations behaved significantly different for the two groups

Table 6. Comparison of Mean P_T (mm), CDD, and R95p% Differences for Years With Similar Annual Precipitation But Different R95p % Group (Years in the Low and High Groups)[a]

		P_T			R95p%		CDD		R95p%		CDD	
Biome	Site	Low	High	Difference (%)	Low	High	Low	High	Low	High	Low	High
DG	DE	145 (2)	140 (2)	−3.1	4.6	23.8	41	43	10.8	33.6	54	68
	JE	254 (1)	249 (3)	−2.1	8.7	37.7	53	69				
	WG	295 (1)	305 (2)	3.4	15.0	38.7	68	88				
	SR	341 (3)	342 (3)	0.1	8.0	31.5	65	100				
	CP	331 (3)	332 (3)	0.3	17.4	36.3	43	40				
MG	SP	594 (2)	578 (3)	−2.6	14.9	33.6	43	45	11.7	30.2	40	40
	LW	648 (2)	674 (3)	3.9	8.5	26.8	38	35				
TF	LR	1042 (2)	1095 (2)	5.1	17.0	33.6	26	23				
	MC	1163 (2)	1200 (2)	3.1	17.1	29.7	15	17	15.4	30.5	27	22
	BC	1140 (1)	1193 (2)	4.6	11.9	28.4	39	26				
MF	CC	947 (2)	972 (3)	2.6	14.9	28.0	59	93	14.9	28.0	59	93

[a]See Table 2 for R95p%. The numbers in parentheses represent the number of selected years in each group that had similar P_T. For example, for the 2 years in the High group at Little River, we found two corresponding years with similar P_T (±5%) in the Low group, respectively. The last two columns represent the average values by biome type (see Table 5). Biome type codes were defined in Table 5, and site codes were defined in Table 1.

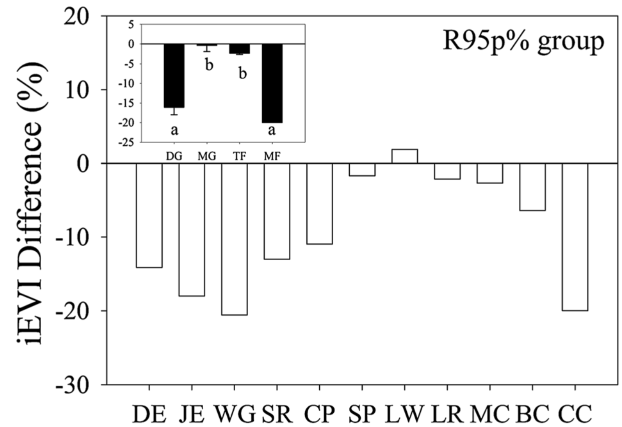

Figure 3. Comparison of iEVI relative difference of years with similar annual precipitation but different R95p% group (years in the Low and High groups; iEVI difference = $(iEVI_{High} - iEVI_{Low}) / iEVI_{Low} \times 100$ across 11 sites. For each site, the years with similar annual precipitation were selected to compare the iEVI differences in the two groups. The inset shows the average iEVI difference combined into biome types. Different letters indicate significant differences at $P < 0.05$.

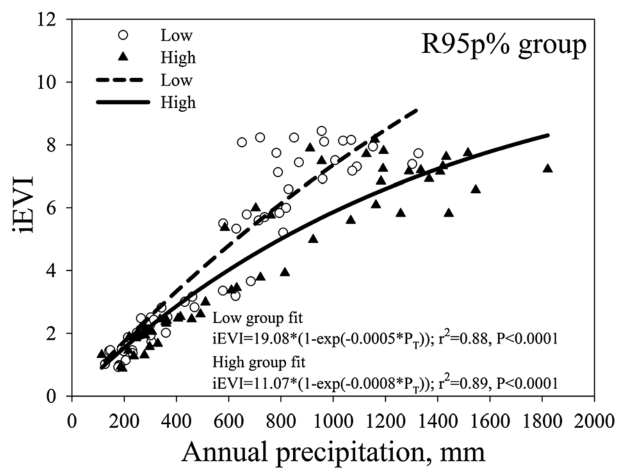

Figure 4. Relation of production across precipitation gradients for 11 sites for two groups (Low: R95p% < 20%; High: R95p% ≥ 20%). See Table 2 for R95p% definitions. The relations were significantly different for the two groups ($F_{2,106} = 18.51$; $P < 0.0001$).

representing low and high R95p% ($P < 0.005$; Figure 4) during the 2000–2009 periods. The main effect of R95p% on the ANPP-P_T relation was significant ($F_{2,106} = 18.51$, $P < 0.0001$; Figure 4). When years with more extreme precipitation patterns were chosen for analysis, the ANPP-P_T relation shifted to the right so that a year with more extreme events would have less ANPP and the function would also asymptote at a larger P_T (Figure 4). Such significant shifts in sensitivity represent negative influences of altered precipitation patterns across the range of biomes, even if P_T amounts increased with more extreme events. These results suggest that once the dependence of ANPP on P_T amount is determined, sites with more extreme precipitation patterns show reductions of ANPP. The result also highlights that a generalized pattern of ANPP responses to extreme precipitation patterns could be developed across biomes along a broad precipitation gradient.

[17] The shifting pattern of sensitivity relations with different precipitation patterns can be further illustrated by a decreasing mean annual RUE with increases in larger rainfall events (Figure 5; Table 7). In general, the years with more extreme rainfall events had lower mean annual RUE for all biomes on average compared with years with fewer extreme events. The reductions ranged from 3.2% (LW) to 34.8% (CC) with an average of 16.8%. The general decreasing trend for RUE still held true when site-level data were aggregated by vegetation types (Figure 5, inset). At the biome level, grassland sites showed the least reduction, especially mesic grasslands, whereas forested sites had the biggest reduction ($P < 0.05$; Figure 5, inset; Table 7). On average, a shift to fewer but larger rainfall events caused a reduction of 6.4% of annual RUE for mesic grassland sites, and an overall decrease of 12.6% for arid grassland sites. For forested sites, the reduction of RUE was even greater with 24.2% and 34.8% for temperate forested and Mediterranean forested sites,

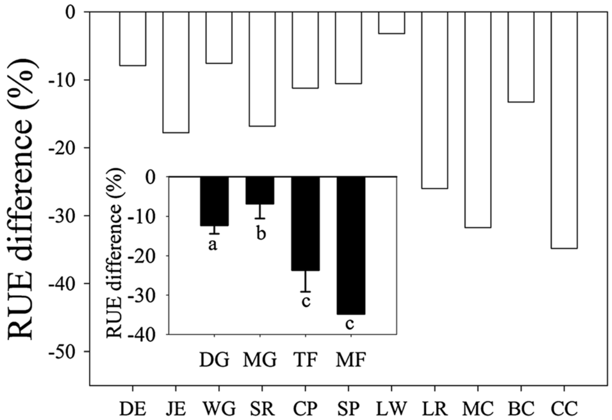

Figure 5. Comparison of RUE (iEVI/P_T) difference of years in the two R95p% groups (years in the Low and High groups; RUE difference = ($RUE_{High} - RUE_{Low}$) / RUE_{Low} 100) across 11 sites. The inset shows the average iEVI difference combined into biome types. Different letters indicate significant differences at $P < 0.05$.

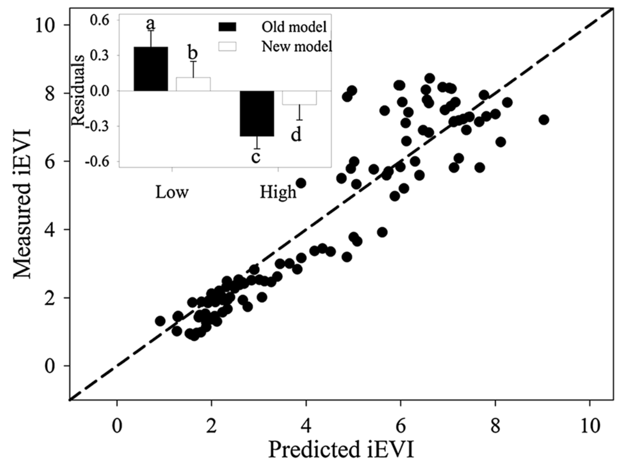

Figure 6. Comparison between predicted and measured iEVI with the new model [Equation (3)] across all sites. The inset shows the comparisons of the mean residual for Low and High groups (Figure 1b) with the old [Equation (2)] and new [Equation (3)] models. Different letters indicate significant differences at $P < 0.05$.

Table 7. Average Rainfall Use Efficiency (iEVI/Precipitation) During All Years in Two R95p% Groups Across the Biomes[a]

Biome	Low	High	Difference (%)
DG	77.91	68.11	−12.6
MG	70.13	65.67	−6.4
TF	79.07	59.96	−24.2
MF	74.07	48.28	−34.8

[a]Average difference combined into biome types (see Table 5). The MODIS EVI values were scaled by a factor of 10,000 before calculating rainfall use efficiency.

respectively (Figure 5, inset). This indicates that, during the years with more extreme events, mesic grassland ecosystems were less affected than all other biomes.

3.3. Development of a General Model With Extreme Precipitation Index and Annual Precipitation

[18] In previous studies, the overall relation (old model) between ANPP and P_T was expressed as an exponential relation of the form ANPP = a($1 - e^{bPT}$) [e.g., *Huxman et al.*, 2004a]. Using iEVI as a surrogate for ANPP and the measurements of P_T (mm) from all sites in this study, a model of this form was obtained:

$$iEVI = 10.9157 * (1 - e^{-0.00086*P_T}) \quad R^2 = 0.83, \quad P < 0.001, \quad n = 110 \tag{2}$$

[19] Given the significant effects of extreme precipitation patterns observed in this study, a multiple nonlinear regression model of iEVI (new model) was derived as a function of R95p% and annual precipitation:

$$\text{iEVI} = (15.6665 - 0.0973 \times R95p\%) \times (1 - e^{-0.00066*P_T}) \quad R^2 = 0.88, \quad P < 0.001, \quad n = 110 \tag{3}$$

where R95p% represents the precipitation extreme index (Table 2). R95p% and P_T together explained 88% of the variance in observed ANPP across biomes. The strong relation between ANPP and both variables of P_T and R95p% across diverse sites is evidence that a regional model could be developed to predict ANPP responses to extreme precipitation patterns (Figure 6). The rate constants of the exponent in these two models were not significantly different, whereas the negative coefficient of R95p% in Equation (3) represents the negative effects of extreme precipitation patterns on ANPP. We compared the new model [Equation (3)] with the old model [Equation (2)] and found a significant improvement in predicting ANPP responses for both less (Low group) and more (High group) extreme precipitation patterns across biomes (Figure 6, inset). When we compared these two models with an F test, Equation (3) was significantly better than Equation (2) ($F_{1,107} = 17.21$; $P = 0.0007$). Moreover, the mean residual (MR) of predicted and measured iEVI with Equation (2) was 0.37 and -0.43 for Low and High groups during 2000–2009 periods, respectively (Figure 6, inset). In contrast, the average residuals with Equation (3) were significantly decreased for Low and High groups, where MR = 0.11 and -0.14, respectively ($P < 0.05$; Figure 6, inset). The lower residuals observed using the new model with the extreme index and P_T relative to the old model with P_T alone provides evidence that the combined model may improve the predictions of responses of vegetation growth in altered precipitation patterns with more extreme rainfall events.

4. Discussion

[20] Understanding how ANPP responds to extreme precipitation patterns, characterized by fewer and larger rain events and longer intervening dry periods, is crucial for assessing the impacts of climate change on terrestrial ecosystems. Quantifying the ecological consequences of extreme precipitation events has been difficult [*Reynolds et al.*, 2004], and we know little about how these patterns affect production beyond experimental conditions [*Smith*, 2011]. Strong relations between ANPP and P_T have been

reported by *Huxman et al*. [2004a], with vegetation types ranging from arid grassland to tropical forest. Our results indicate that combining P_T and extreme precipitation patterns can improve predictions of ecosystem production. It is possible that extreme precipitation patterns are just as important as total precipitation amount. The study shows that the years with increased less frequent but larger extreme events had lower RUE across all biomes on average compared with normal years with less extreme events. The regional lowered vegetation production and RUE across biomes suggests that extreme precipitation patterns do not benefit vegetation carbon uptake across biomes but rather result in significant reductions in carbon uptake. The lower RUE may reflect the inability of plants to effectively use precipitation in the years with more extreme events. Apparently, there is an upper threshold on the size of events that contributed effectively to ANPP given that larger events do not increase production [*Swemmer et al*., 2007]. The effective response of plants to water inputs is optimum at moderate event size and precipitation from larger events is less effective and therefore reduces RUE [*Huxman et al*., 2004b] and hence vegetation production.

[21] Among biomes, the intensity of the ANPP response to extreme precipitation patterns differed between water-limited and mesic sites (Figure 3, inset). These different responses highlight the relative importance of both larger rainfall event size and longer dry interval in precipitation patterns. For arid grassland and Mediterranean forested sites, the significant reduction in ANPP with intense precipitation patterns when total P_T did not change is likely due to increased water deficits due to the combination of more extreme events and longer drought interval. When precipitation patterns are more extreme, a smaller fraction of rainfall infiltrates into the soil water, and runoff increases lead to water losses to streams [*Arora et al*., 2001]. Thus, effective rainfall available for stimulating biological processes is decreased [*Porporato et al*., 2002]. The extended drought intervals caused even more extreme water stress. This also explained the inconsistency between our results and the short-term experimental studies of *Heisler-White et al*. [2008, 2009] in semiarid grassland. The dry interval between rain events in their experiments was only 10–30 days [*Heisler-White et al*., 2008, 2009], which likely resulted in lower drought stress. However, in our study, the drought intervals were longer (Table 6), which resulted in greater water stress at our scale (~2.25×2.25 km) than their plot scale experiments. The decline of ANPP in our sites is consistent with the reduction of plant production and mortality for arid grasslands due to recent drought in the southwestern United States [*Scott et al*., 2010; *Munson et al*., 2012].

[22] In contrast, we found no significant responses in ANPP to more extreme rainfall patterns in mesic grassland and temperate forest sites irrespective of P_T during the 2000–2009 period. It is likely that this discrepancy is due to differences of water stress experienced with more extreme precipitation patterns among the ecosystems. In the arid grassland and Mediterranean sites, where soil and plants are usually seasonally water limited, increased intense events were accompanied by more extended dry periods. Mean CDD increased from 54 to 68 days for arid grasslands sites and from 59 to 93 days for the Mediterranean forested site (Table 6). This means that the extreme rainfall years were coupled with more severe drought conditions in arid grassland and Mediterranean forest sites during 2000–2009 periods. As a result, these ecosystems may be subject to more severe and longer periods of water stress. In contrast, for mesic grassland and temperate forested sites that usually maintain a relatively unstressed state, the increases of infrequent larger rainfall events did not result in soil and plant water stress due to no significant changes in dry intervals (or drought periods) between events (i.e., CDD did not change; Table 6). This implies that the cooccurrence of larger rainfall events and longer dry intervals resulted in greater water stress conditions and reduction of vegetation production for arid grassland and Mediterranean forest sites.

[23] Even with the variable intensity of the ANPP response to extreme precipitation patterns among biomes, we found a generalized negative pattern of ANPP response across biomes. Biome-level responses to more extreme precipitation patterns without changing P_T have an overall negative impact on ecosystem RUE and vegetation production at regional scales. This negative sensitivity of ANPP responses is supported by a recent study for shrublands and forests with FLUXNET data [*Ross et al*., 2012]. They also found that more extreme rainfall regimes, characterized by fewer and larger events, had strong negative effects on vegetation production of these ecosystems. It appeared that, although the variance of responses to more extreme precipitation patterns was greater between sites, convergence in overall pattern and control across biomes was indicated by this analysis in naturally occurring climate conditions. The downshift of ANPP-P_T relations across biomes indicates that, although ANPP increases across biomes with increasing MAP, this increase is somewhat dampened or offset by extreme precipitation patterns across biomes, which illustrates the important role of precipitation patterns in influencing vegetation growth across biomes. This also implies that climatic variables such as MAP are useful to predict average ecological response to climate change across climatic gradients [*Huxman et al*., 2004a; *Knapp and Smith*, 2001], whereas precipitation patterns may predict some variability in these responses [*Knapp et al*., 2002; *Heisler-White et al*., 2008, 2009]. As a result, regional-scale models between ANPP and precipitation [*Huxman et al*., 2004a] may change substantially under infrequent extreme precipitation regimes.

[24] Thus, a generalized model for quantifying the effects of extreme precipitation patterns was developed in which only P_T and R95p% are required [Equation (3)]. The resulting relationship has the general form of the old model [Equation (2)] but also represents the negative influences of extreme precipitation events. It has been suggested that the responses of ANPP to precipitation across biomes require a complex model including not only P_T but also other factors such as precipitation patterns [*Knapp and Smith*, 2001]. Our new model could be used to predict the regional ecological consequences of altered climate change with more extreme precipitation patterns. At regional and longer timescales, with increased extreme events in altered precipitation patterns, the shift in ANPP-precipitation relations is important because it indicates that altered rainfall patterns have the potential to modify ANPP responses to future climate change. The new model can serve as a practical tool to quantify this effect at regional scales. The statistical comparison of our new model with the old one implied a significant improvement in prediction of responses of ecosystem production to more extreme

precipitation patterns. However, it should be pointed out that, due to data limitations, our research did not include some biomes (e.g., tropical forest and steppe); therefore, it is necessary to validate this model using other sites and biomes with ongoing MODIS and climatic measurements in the future.

5. Conclusions

[25] The present study has important implications for understanding and predicting the impacts of more extreme precipitation regimes on terrestrial ecosystem under future climates. A shift to larger rainfall events with longer intervening dry intervals is predicted global climate change scenarios and has been recently reported [*Easterling et al.*, 2000; *Groisman and Knight*, 2008]. The results from this study illustrate the importance of extreme precipitation patterns, not just precipitation amount, on vegetation production across biomes [*Knapp and Smith*, 2001; *Huxman et al.*, 2004a]. Cross-biome and between-biome comparisons indicated that the intensity of terrestrial ecosystem production response to extreme precipitation patterns is greater for water limited than mesic sites. Of particular importance for our assessment of sensitivity are analyses conducted to explore the effects of extreme rainfall events size and frequency in natural climatic conditions. Our study provides new evidence of the impact of extreme precipitation patterns on vegetation production in natural settings across biomes and suggests that long-term measurements in natural field conditions are needed to determine this impact in addition to those imposed by rainfall manipulation experiments.

[26] Given the importance of ANPP in the global C cycle and its feedback to climate change, our results suggest that increases in extreme precipitation events have the potential to substantially reduce ecosystem production and carbon uptake across biomes under climate changes. Future increases in frequency of extreme events and drought periods, together with reducing P_T in the southwestern United States, as projected by some models [*Seager et al.*, 2007; *Cayan et al.*, 2010], are expected to induce more water deficits and reduction in grassland vegetation production. Our findings not only provide insight for experimental studies on terrestrial ecosystems but also highlight the need to take intra-annual precipitation patterns into account in climatic and ecological models for future climate change.

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