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Positive impacts of precipitation intensity on monthly CO_2 fluxes in North America

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ABSTRACT

Precipitation is one of the most important climate factors that can affect the gross ecosystem production (GEP) of terrestrial ecosystems. Positive impacts of precipitation on annual GEP have been reported for vegetated areas worldwide. However, little is known about the influence of precipitation intensity on GEP, especially at the monthly to seasonal temporal scale. Here we show that monthly GEP is insensitive to the sum of monthly total precipitation (P_s, mm), but positively correlated to precipitation intensity (P_a, mm), defined as the average precipitation per event from half-hourly measurements over a month. Different plant functional types (PFTs) exhibit substantial differences in the sensitivity of monthly GEP to P_a. PFTs of water-limited regions responded more intensely than those in mesic environments, as demonstrated by a negative correlation between the slope of the GEP-P_a regression line and average P_a. Furthermore, this slope increases with latitude, indicating higher sensitivity of GEP to P_a for boreal ecosystems than for temperate regions. Therefore, we anticipate increased intensity of storms, as projected by some climate models, may impart a previously overlooked positive impact on precipitation intensity on GEP.

1. Introduction

Terrestrial ecosystems play a dynamic role in the global carbon (C) cycle as their carbon balance is highly sensitive to climatic change (Knapp and Smith, 2001; Piao et al., 2008). Climate variation affects photosynthesis and respiration processes in vegetation and therefore, climate is a major determinant of vegetation production of terrestrial ecosystems. As climatic and atmospheric changes are expected to accelerate in the near future, it is imperative that we improve the capability of estimating these factors (e.g., temperature, precipitation) on carbon budgets in support of scientific investigation and policy formulation (Chen et al., 2003).

While climatic change such as the increase in temperature and the elevated CO_2 concentration in the atmosphere, has been demonstrated to have large effects on terrestrial ecosystem production (Norby et al., 2005; Piao et al., 2008; Beer et al., 2010; Zhao and Running, 2010; Wu et al., 2012a), precipitation has been suggested to have an even profound impact on ecosystem dynamics than the single or combined effects of rising CO_2 and temperature, especially in arid and semiarid environments for the determination of the distribution, structure, and diversity of plants (Easterling et al., 2000; Houghton et al., 2001; Knapp et al., 2002; Weltzin et al., 2003).

The spatial pattern of precipitation in future, as projected by most general circulation models (GCMs), will increase in tropics and at middle and high latitudes and decrease in subtropical latitudes (Easterling et al., 2000). However, unresolved discrepancies exist among diverse models for specific regions, probably because of the difficulty in dealing with cloud microphysics and precipitation processes (Weltzin et al., 2003). Despite the uncertainties in feedbacks between annual precipitation variability and vegetation productivity, there are evidences that projected variation in future precipitation patterns are likely to alter the responses of the carbon cycle, though it may differ across biomes (Fang et al., 2001; Knapp and Smith, 2001; Wu and Chen, 2012; Wu et al., 2012b).

The underlying mechanism of the impacts of annual variability of precipitation on CO_2 uptake may differ across plant functional types (PFTs) and is difficult to evaluate globally due to the unavailability of data and model limitations. In addition, previous research conducted at the annual or seasonal temporal scales may have not fully addressed the effects of precipitation on vegetation biogeochemistry as precipitation is an environmental factor of high temporal heterogeneity (Chahine, 1992; Weltzin et al., 2003). Future precipitation regimes are characterized by larger sizes while also longer interval dry periods, it is thus important to understand how vegetation productivity responds to different frequencies and intensities of precipitation and how the sensitivities of such responses vary across different PFTs. Therefore, multi-year observations of study sites with long-term observations of productivity and precipitation are especially useful in

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quantifying the influence of long-term climate change on carbon sequestration of terrestrial ecosystems (Knapp and Smith, 2001; Huxman et al., 2004). In this study, we provide an analysis of the relationship between the gross ecosystem production (GEP) and monthly precipitation patterns using multi-year data (CO_2 flux and meteorological measurements) across eight PFTs in North America and ask:

1) How are monthly precipitation quantity and intensity related?
2) What is the relationship between monthly GEP and precipitation quantity and intensity?
3) How do these relationships vary by site characteristics?

2. Methods

2.1. Study sites

The data employed in this study were selected from the AmeriFlux (http://public.ornl.gov/ameriflux/dataproducts.shtml) and Fluxnet-Canada (http://www.fluxnet-canada.ca) archives. The rules for site selection were mainly regulated by the data availability, data quality and data time duration (e.g., minimum number of years of data was set to six) as these criteria can better support the mechanical analysis of long-term precipitation on productivity. As a result, data from 20 AmeriFlux and Fluxnet-Canada tower sites located across North America were chosen (Fig. 1 and Table 1). These sites cover eight PFTs in North America, including grassland (GRA, 2 sites), wetland (WET, 2 sites), deciduous broadleaf forest (DBF, 4 sites), crops (CRO, 2 sites), evergreen needle-leaf forest (ENF, 4 sites), mixed forest (MF, 2 sites), evergreen broadleaf forest (EBF, 2 sites), and woody savannas (WSA, 2 sites). This broad range of sites provided a wide dynamical range of both GEP and precipitation. While there are a larger number of AmeriFlux sites available, the sites selected here have a long gap-filled time series of GEP and coincident high quality precipitation and volumetric soil moisture data collected on-site. Broadly, the selected sites are representative of many North American biomes.

2.2. Flux, climate and canopy structure data

For Canadian sites, a standard procedure was used to estimate annual net ecosystem production (NEP) and to partition NEP into components of GEP and ecosystem respiration (R_e) from gap-filled half-hourly measurements (Barr et al., 2004). For AmeriFlux sites, level-4 GEP and products were used and these data were gap-filled with the Artificial Neural Network (ANN) method (Papale and Valentini, 2003) and/or the Marginal Distribution Sampling (MDS) method (Reichstein et al., 2005).

Previous work of Desai et al. (2008b) indicated that different decomposition techniques generally have a moderate impact on the modeled GEP, though most methods tended to cluster on similar results to within 10%, suggesting the reliability of multiple site comparisons and syntheses in this study when using a consistent method across all sites. This also agrees with the general understanding that biases associated with different gap filling methods tend to be small (Moffat et al., 2007).

Precipitation data for the sites were obtained from half-hourly meteorological measurements collected by on-site tipping bucket

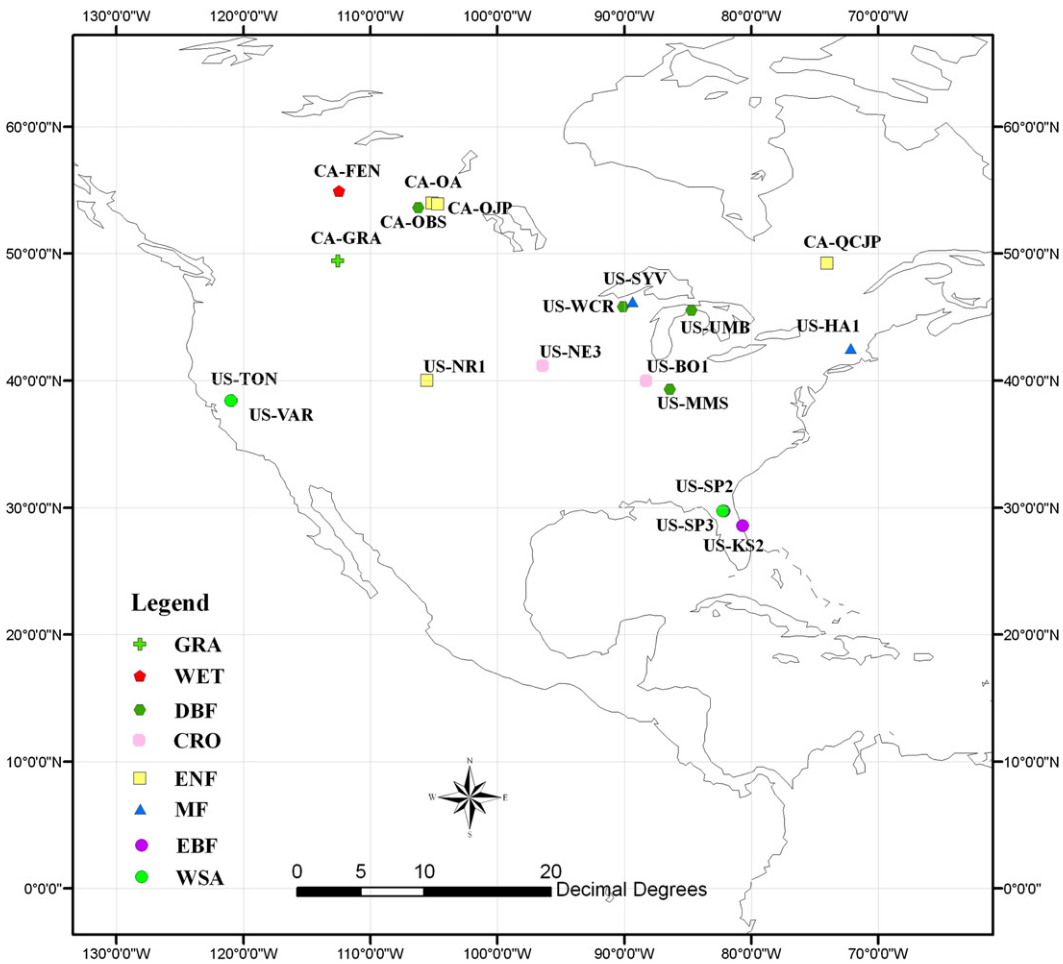

Fig. 1. Locations of the 20 flux sites in North America that cover eight PFTs. GRA, WET, DBF, CRO, ENF, MF, EBF, and WSA, represent grassland, wetland, deciduous broadleaf forest, crops, evergreen needle-leaf forest, mixed forest, evergreen broadleaf forest, and woody savannas, respectively.

Table 1
Detail descriptions of 20 sites in this analysis.

Sites	Latitude	Longitude	Land cover	Year	References
US-VAR	38.4133	−120.9507	GRA	2002–2007	Ryu et al. (2008)
CA-GRA	49.4300	−112.5600	GRA	1998–2006	Flanagan and Johnson (2005)
CA-FEN	54.9538	−112.4669	WET	2004–2009	Flanagan and Syed (2011)
CA-BOG	45.4094	−75.5187	WET	2004–2009	Admiral and Lafleur (2007)
US-UMB	45.5598	−84.7138	DBF	1999–2006	Curtis et al. (2002)
US-MMS[a]	39.3231	−86.4131	DBF	1999–2006	Dragoni et al. (2007)
US-WCR	45.8059	−90.0799	DBF	1999–2006	Cook et al. (2004)
CA-OA	53.6289	−106.1978	DBF	2002–2008	Barr et al. (2004)
US-NE3	41.1797	−96.4397	CRO	2002–2008	Suyker and Verma (2008)
US-BO1[b]	40.0062	−88.2904	CRO	1997–2006	Meyers et al. (2006)
US-NR1	40.0329	−105.5460	ENF	2000–2007	Yi et al. (2008)
CA-OBS	53.9872	−105.1178	ENF	1999–2008	Margolis et al. (2006)
CA-OJP	53.9163	−104.6920	ENF	2000–2007	Margolis et al. (2006)
CA-QCJP	49.2671	−74.0365	ENF	2002–2009	Margolis et al. (2006)
US-SYV	46.2420	−89.3477	MF	2001–2006	Desai et al. (2008a)
US-HA1	42.5378	−72.1715	MF	2001–2006	Urbanski et al. (2007)
US-SP3	29.7548	−82.1633	EBF	1999–2004	Powell et al. (2008)
US-KS2	28.6086	−80.6715	EBF	2001–2006	Powell et al. (2008)
US-TON	38.4316	−120.9660	WSA	2002–2007	Ma et al. (2007)
US-SP2	29.7648	−82.2448	WSA	1999–2004	Gholz and Clark (2002)

[a] Missing data for 2004.
[b] Missing data for 2000 (GRA, WET, DBF, CRO, ENF, MF, EBF, and WSA, represent grassland, wetland, deciduous broadleaf forest, crops, evergreen needle-leaf forest, mixed forest, evergreen broadleaf forest, and woody savannas, respectively).

sensors. Missing data was gap-filled using the observations from nearby climate stations (Jassal et al., 2009). These data were summed to derive monthly precipitation (P_s, mm). We also calculated the number of time periods with precipitation (n = number of half-hours with recorded precipitation in the month) and the maximum precipitation of a single rain event (P_{max}, mm) from the half-hourly observations. These values were then used to obtain our estimate of precipitation intensity or average precipitation per rainfall event (P_a, mm) by dividing P_s by *n*.

Three further steps were adopted for preparing the monthly precipitation and GEP data. First, by the definition of P_a, months with no precipitation for all sites were excluded from the analysis. Second, for each site, months with differences between individual P_a and monthly average P_a larger than three times of the standard deviation (SD) of all P_a for this site were deemed as "outliers" (Ruan et al., 2005). Third, for all PFTs, we were focused on the growing season which was constrained by months with positive values in the mean air temperature (T_a). However, due to differences in this growing season length as well as data availability across PFTs, certain criteria were also adopted. For example, for GRA and CRO, months from May to September were used (Flanagan and Johnson, 2005; Suyker and Verma, 2008), while months from April to October were excluded for Mediterranean sites, such as US-VAR and US-TON (Ma et al., 2007; Ryu et al., 2008).

For analysis of relationships between GEP and P_a or P_s, we also analyzed site-level soil moisture. Soil water content (SWC, %) was measured by the time-domain reflectometry (TDR) type probes at 0–30 cm for AmeriFlux sites. For Canadian sites, SWC was calculated as the average values of sampled data by depth to at least 50 cm. The variation of soil water content (VSWC) in *i* month is defined as the difference of mean SWC in current month and the previous month,

$$VSWC_i = SWC_i - SWC_{i-1}. \tag{1}$$

The difference of soil water content (DSWC) was calculated as

$$DSWC_i = abs(VSWC_i). \tag{2}$$

Finally, we further analyzed our relationships against maximum measured leaf area. We also searched in the above two data systems and literature sources for leaf area index (LAI, m^2m^{-2}) data. At some sites, time series of monthly LAI was derived either as the average value from multiple observations (if available) or a single measurement per month.

3. Results

3.1. Relationship between P_s and P_a

Monthly observations of precipitation total (P_s) and precipitation intensity (P_a) were compared for all sites (Fig. 2). In general, P_a increases as P_s increases, with a linear fit between the two variables having a R^2 of 0.24 ($p<0.001$). Some non-linearity was present in the end and the fit was improved with such a fit with coefficient of determination (R^2) of 0.27 ($p<0.001$). The non-linear relationship indicates that P_a had a larger relative dynamical range than P_s. The importance of larger relative dynamic range for P_a is demonstrated in Fig. 3, which shows the averaged values of P_s and P_a for the eight PFTs that span wide ranges of monthly GEP and precipitation. For example, while no difference in P_s was observed between mixed forest (MF) and evergreen broadleaf forest (EBF) (91.61 and 91.67 mm, respectively), P_a varied considerably (0.89 mm and 1.61 mm, respectively), which correlates well with the large variation in GEP for these two groups (125 and 157 g C/m^2/month, respectively). In this perspective, statistically speaking, P_a is likely to provide a better predictor of GEP than P_s and a thus greater potential for characterizing temporal and spatial patterns of vegetation production.

3.2. Relationship between monthly GEP and P_s, P_a

On an individual site basis, only three sites (CA-OBS, CA-OJP and US-SP3) had significant correlations between GEP and P_s (Fig. 4). This result indicates that this relationship differs from its counterpart at the annual scale where GEP is significantly associated with precipitation over 40% of the vegetated land, although with substantial variations across PFTs and spaces (Beer et al., 2010). In contrast, we find that monthly GEP was significantly correlated with P_a for all sites in our sample, with coefficients of determination (R^2) ranging from 0.59 ($p<0.001$) to 0.09 ($p=0.012$) (Fig. 5).

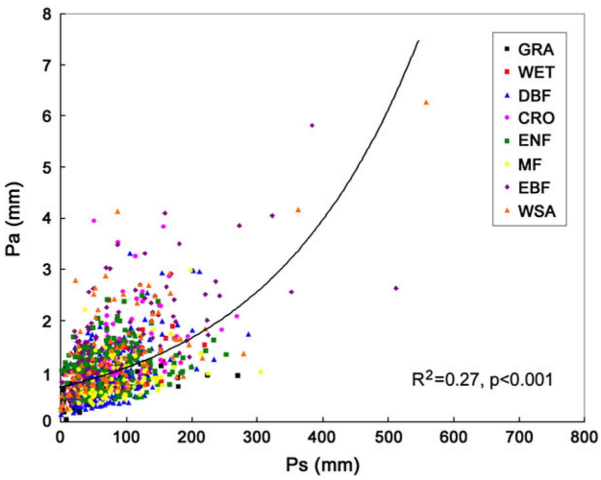

Fig. 2. Relationship between P_s and P_a for the eight plant functional types. The regression line for overall data is y = 1.82 exp [(2.24e^{-3})x]-1.07. GRA, WET, DBF, CRO, ENF, MF, EBF, and WSA, represent grassland, wetland, deciduous broadleaf forest, crops, evergreen needle-leaf forest, mixed forest, evergreen broadleaf forest, and woody savannas, respectively.

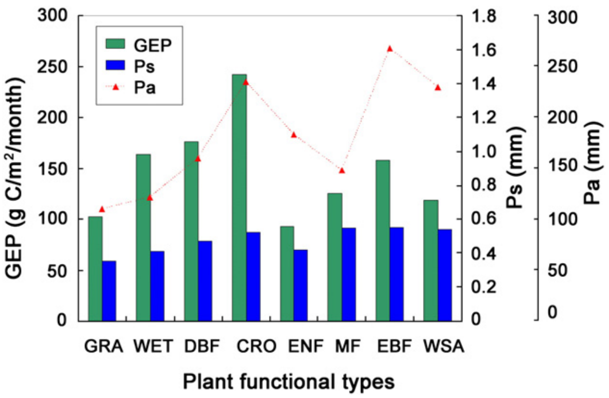

Fig. 3. Average values of monthly GEP, P_s and P_a for the eight PFTs, GRA, WET, DBF, CRO, ENF, MF, EBF, and WSA, represent grassland, wetland, deciduous broadleaf forest, crops, evergreen needle-leaf forest, mixed forest, evergreen broadleaf forest, and woody savannas, respectively.

We substantiate this newly discovered relationship between GEP and P_a from both the canopy structure and the hydrologic perspectives. First, LAI is typically correlated to GEP, and here we find that similarly P_a is a better predictor of LAI variability than P_s (Fig. 6a, b). While a significant correlation (R^2 equals to 0.26) is observed between P_a and LAI for all sites, the correlation differs across PFTs. The linear regressions are found to be the best fit for sites with relatively low LAI (e.g., GRA). However, for dense canopies (e.g., the EBF), the relationship breaks down at LAI greater than 6 (Table 2).

Second, the fate of precipitation includes interception, infiltration, and runoff (Chahine, 1992). In vegetated areas, a considerable part of the precipitation may be intercepted by the canopy and returned to the atmosphere via rapid evaporation. The remainder reaches the ground surface as throughfall and stemflow. Soil moisture is the direct link between precipitation and ecological processes, and only that part of precipitation that reaches the soil, i.e. net precipitation, can increase the soil moisture, either in the top layer or the entire root zone by hydrologic redistribution (Reynolds et al., 1999; Ryel et al., 2003; Gash and Shuttleworth, 2007; Muzylo et al., 2009). For sites where SWC data were available (N = 55%), we find that GEP is independent of mean SWC but negatively correlated to the monthly variation of the absolute difference in soil water content (DSWC, %) across PFTs, $R^2 = 0.10$; $p < 0.001$ (Fig. 6c, d). Despite the small R^2, this finding indicates that vegetation growth likely benefits from a relatively stable SWC (e.g., a variation within 5%, Fig. 6f) at the monthly temporal scale because water typically reduces GEP during drought conditions, whereas when water is sufficient radiation availability is typically the limiting factor on GEP.

3.3. Sensitivity analysis of relationship between GEP and P_a

It is apparent from Fig. 5 that the sensitivity of GEP to P_a varies among the PFTs. Factors underlying this different sensitivity are explored in Fig. 7. The slopes derived from the linear regression for each biome were found to be negatively correlated with P_a ($R^2 = 0.48$, $p < 0.001$), indicating that an increase in P_a has greater influence on GEP of PFTs in xeric regions than that in mesic environments (Fig. 7a). This result is consistent with the evolutionary and ecological views that species in water-limited regions with high production potentials (e.g., GRA, WET) would be very sensitive to the water availability, while biomes in mesic environments with high production potentials (e.g., EBF) are less sensitive (Huxman et al., 2004). Such different sensitivities are indirectly supported by recent research of both single site evaluations in mixed deciduous forest (Newman et al., 2006) and grasslands (Thomey et al., 2011) and multi-site studies across PFTs (Zha et al., 2010).

Dependence of the changes in this sensitivity on DSWC further supports these differences. Due to the lack of available SWC data some sites were excluded from the analysis (CA-FEN, US-UMB, US-NE3, US-HA1, US-SP3 and US-SP2). Water limited PFTs, GRA for example, are characterized by the low P_a that leads to large variations in both DSWC and monthly GEP. However, for regions with high P_a (e.g., EBF), DSWC is small, resulting in a relatively stable monthly GEP. The positive correlation between DSWC and the coefficient of variation (CV) of GEP for sites with available SWC supports our analysis (Fig. 7b; $R^2 = 0.55$, $p < 0.001$). This is because when water becomes abundant, resources other than water (e.g., soil nitrogen, light) may act as more important limiting factors for production (Huxman et al., 2004). These two different responses imply a decrease in the amplitude of GEP variation at high P_a and explain the negative correlation between the slope and P_a.

We further analyzed GEP-P_a sensitivity as a function of latitudinal gradient. A coefficient of determination (R^2) of 0.49 ($p < 0.001$) was obtained between the slopes of the GEP-P_a relationship and latitude for all sites (Fig. 8a), implying boreal ecosystems have a higher sensitivity than that of temperate regions. P_a is also better correlated with GEP of sites located at high latitudes, which is evidenced by the relationship between R^2 of GEP-P_a relationship and latitude (Fig. 8b). A negative correlation between R^2 and average monthly P_s for all sites (Fig. 8c; $R^2 = 0.57$, $p < 0.001$) highlights that the use of P_a to evaluate future precipitation intensity on GEP would be more suitable for drought-prone regions.

3.4. Precipitation intensity covariation with air temperature and global shortwave radiation

Since temperature and radiation are important factors of GEP, we also analyzed their covariance with precipitation intensity (Table 3). We found that monthly mean temperature was significantly correlated with P_a except for the grassland sites and the coefficients of determination also showed substantial variations among PFTs. WET ecosystem had the highest correlation with R^2 of 0.47 ($p < 0.001$) and the lowest R^2 of 0.10 ($p = 0.025$) was observed at CRO sites. Relationship between P_a and R_g was much lower (below 0.20) compared to that of P_a and T_a and they were only significantly correlated at WET, MF, EBF and WSA ecosystems. These analyses indicate that for most of these ecosystems, the temperature may co-control the vegetation production with the precipitation intensity. However, the influence of radiation is much smaller than that of temperature.

4. Discussion

To the best of our knowledge, these are the first results showing the additional important and overlooked impact of precipitation intensity on GEP at the monthly temporal scale. These results are consistent with previous research showing that while most aspects of terrestrial ecosystem structure and function are vulnerable to hydrologic changes caused by precipitation, the response may be less dependent on changes in annual precipitation quantity but more reliant on precipitation variability (Mearns et al., 1997; Knapp et al., 2002). P_a in our analysis, although being derived from the total half-hourly measurements, holds the potential as an indicator of the precipitation variability that best relates to GEP variability. These results are also consistent with previous experimental work altering rain amount in grasslands (Heisler-White et al., 2008) and observational studies (Thomey et al., 2011), which report a significant increase of above ground net primary production (ANPP) for grasslands with a single large rainfall event compared to multiple small events with equal total rainfall amounts.

Our analyses suggest that there is a relationship between maximum production and VSWC. Although not fully understood yet, the function between monthly GEP and VSWC can be conceptually illustrated by Fig. 9. Soil water content stability means values may fall in the [−5, 5] for example, so why do these samples have a relatively higher monthly GEP? Large negative values (left region of VSWC = −5%) mean

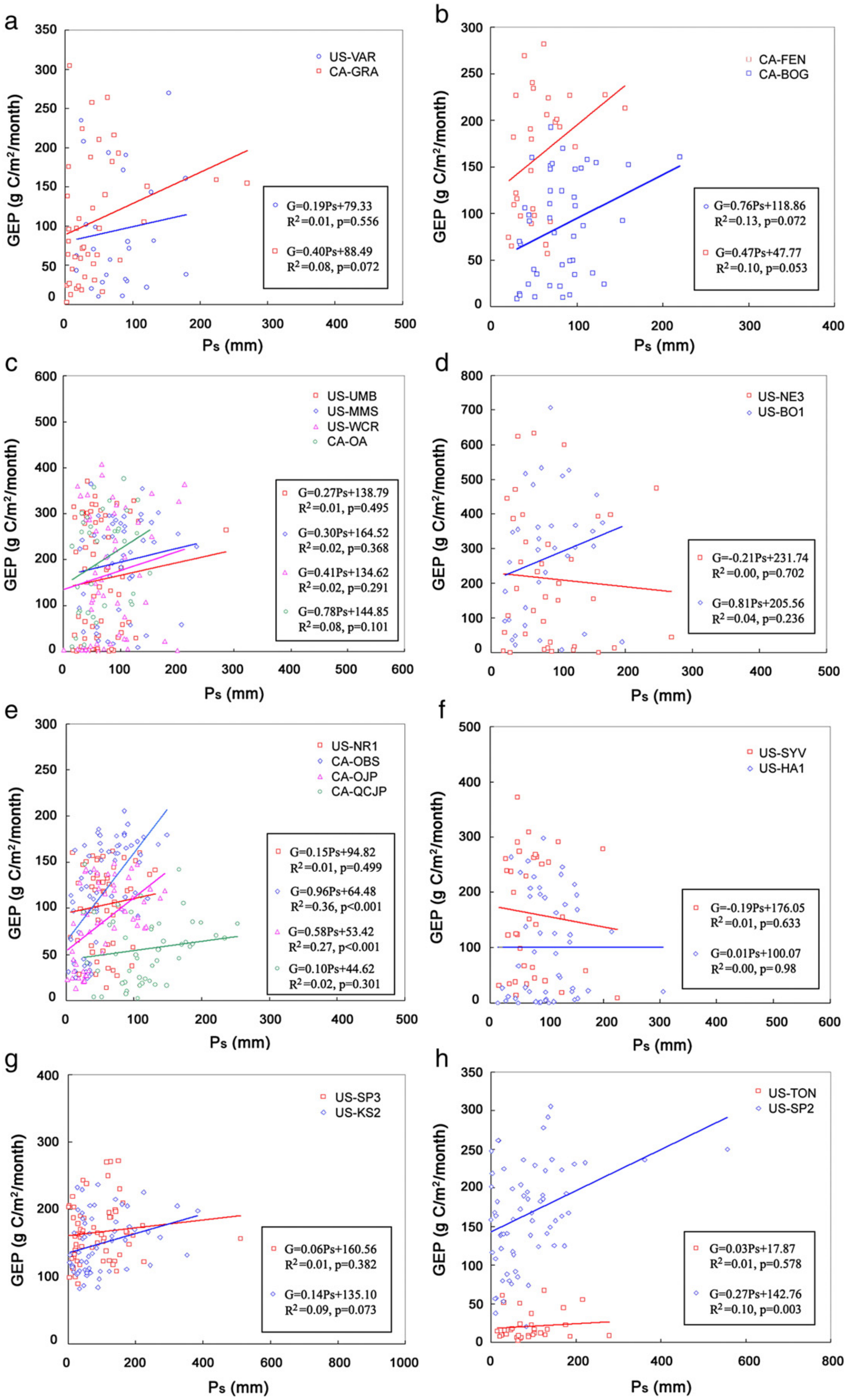

Fig. 4. Relationship between the monthly sum of precipitation (P_s, mm) and monthly GEP ($g\cdot C\cdot m^{-2}$) for 20 sites in North America. a, b, c, d, e, f, g and h represent the GRA, WET, DBF, CRO, ENF, MF, EBF, and WSA, respectively (see the text for details).

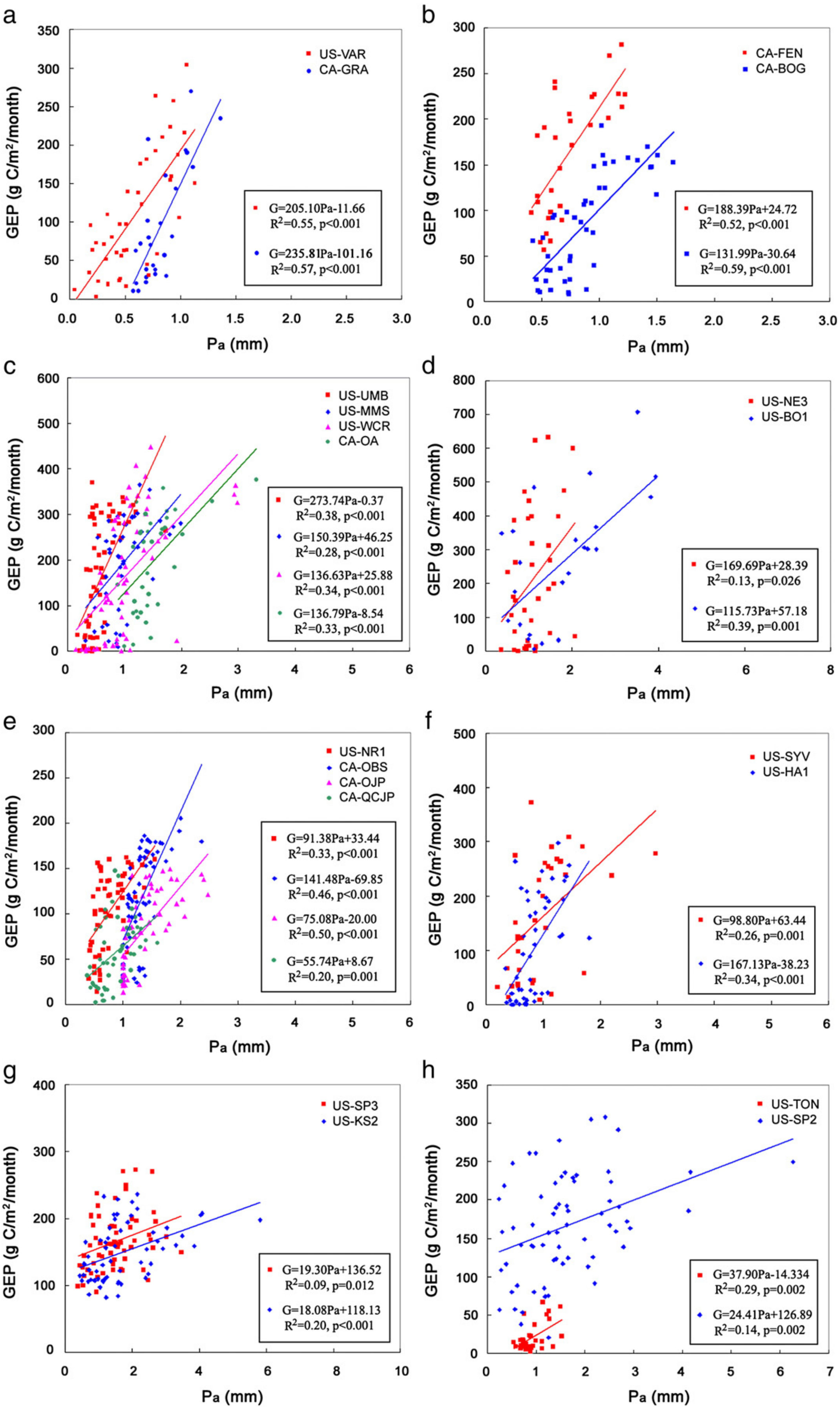

Fig. 5. Relationship between the monthly average precipitation per event (P_a, mm) and monthly GEP ($g \cdot C \cdot m^{-2}$) for 20 sites in North America. a, b, c, d, e, f, g and h represent the GRA, WET, DBF, CRO, ENF, MF, EBF and WSA, respectively (see the text for details).

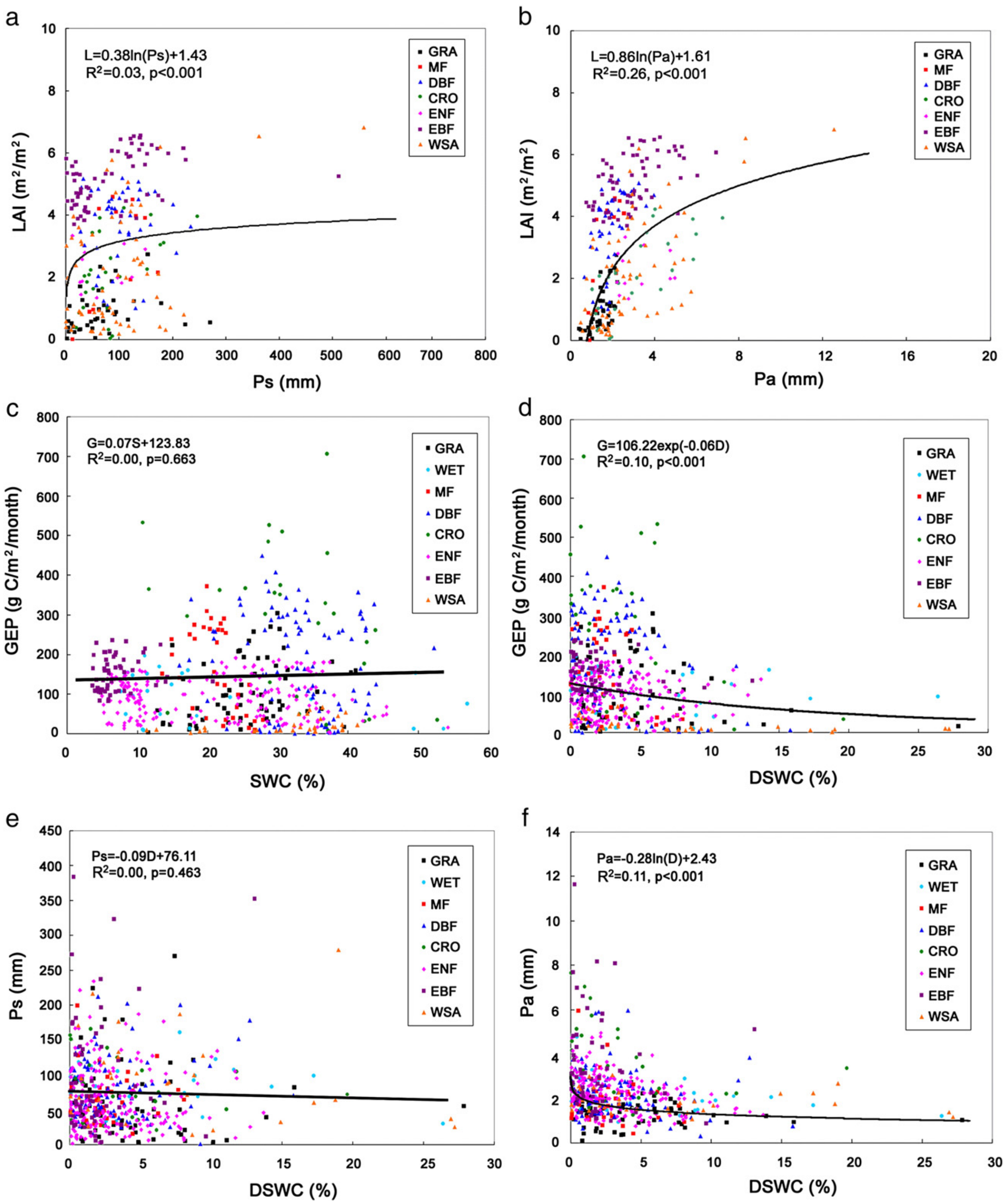

Fig. 6. Relationships between precipitation patterns and monthly GEP, canopy structural and soil water variables. a, correlation between leaf area index (LAI) and P_s. b, correlation between leaf area index (LAI) and P_a. c, correlation between monthly GEP and the mean soil water content (SWC). d, correlation between monthly GEP and the DSWC. e, correlation between P_s and the DSWC. f, correlation between P_a and the DSWC. GRA, WET, DBF, CRO, ENF, MF, EBF, and WSA, represent grassland, wetland, deciduous broadleaf forest, crops, evergreen needle-leaf forest, mixed forest, evergreen broadleaf forest, and woody savannas, respectively.

drought and the decrease of monthly GEP is caused by the water shortage. On the other hand, large positive variations (right region of VSWC = 5%) in SWC are caused by the increase in the number of periods of precipitation (n). However, increase in n will also result to low radiation which can also reduce the monthly GEP. These assumptions are supported by our data (Fig. 10). Both low and high values of n can lead to large VSWC. Average n (n_ave) for VSWC below −5% and above 5% are 56 and 102, respectively. Months with VSWC variations within 5% have a medium n_ave of 70. However, high n values can give rise to sharp decreases in the radiation for all observations with R^2 equals to 0.20 ($p<0.001$). Previous research also suggests that water availability will play a limiting role for production in drought conditions, while other resources

Table 2
Correlations between P_a and available LAI across plant functional types.

PFTs	Equations	R^2 (p-value)	No. (n)	LAI_ave ($m^2 \cdot m^{-2}$)	SD ($m^2 \cdot m^{-2}$)
GRA	$L=1.67P_a-0.31$	0.42 (p<0.001)	37	0.87	0.65
DBF	$L=1.68\ln P_a+3.87$	0.26 (p<0.001)	43	3.72	1.18
CRO	$L=1.64\ln P_a+1.62$	0.56 (p<0.001)	26	2.11	1.26
ENF	$L=0.21\ln P_a+2.16$	0.08 (p=0.781)	12	2.25	0.65
MF	$L=4.08P_a-0.53$	0.58 (p=0.006)	11	2.83	1.68
EBF	$L=0.85\ln P_a+4.90$	0.26 (p<0.001)	63	5.14	0.84
WSA	$L=1.10P_a+0.57$	0.41 (p<0.001)	63	2.17	1.78

(SD is the standard deviation; GRA, DBF, CRO, ENF, MF, EBF, and WSA, represent grassland, deciduous broadleaf forest, crops, evergreen needle-leaf forest, mixed forest, evergreen broadleaf forest, and woody savannas, respectively).

(e.g., light, nitrogen) will become the constraint role when water is sufficient (Weltzin et al., 2003). Therefore, samples with a medium VSWC are expected to enhance monthly GEP.

This conceptual model is also useful in explaining the positive correlation between P_a and GEP. In natural environments, it is difficult to maintain the desired stable state of VSWC because of constant changes in environmental factors (precipitation, evaporation, etc.). A significant logarithmic decrease of P_a with DSWC is found from the available data (as shown in previous Fig. 6f), suggesting that larger P_a values promote a more stable net precipitation, which leads to a relatively more stable SWC, supporting enhanced GEP. This reasoning is

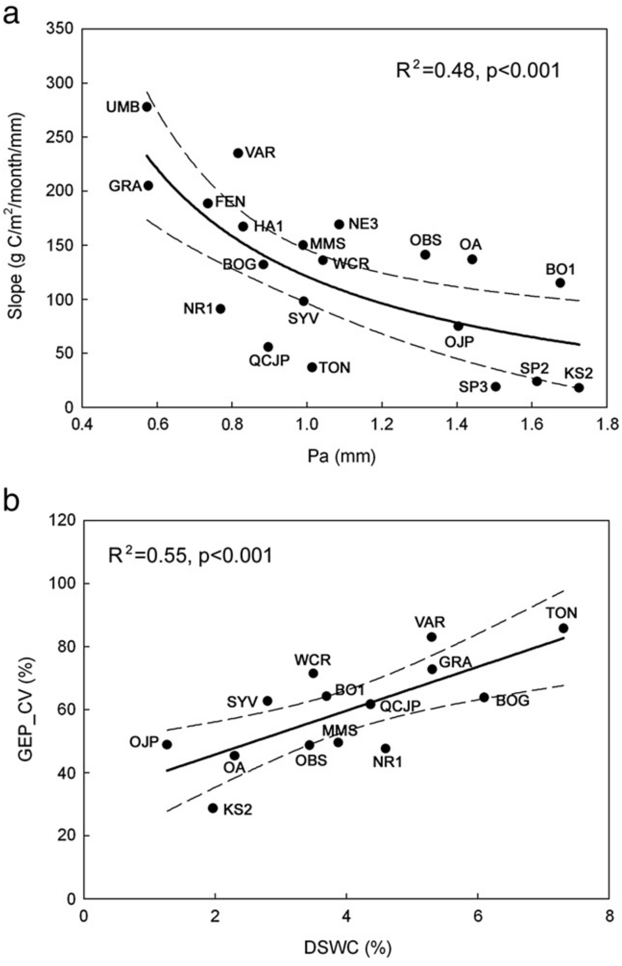

Fig. 7. a, Correlation between P_a and the slope of GEP-P_a relationship for all sites; b, Correlation between DSWC and the coefficient of variation (CV) of GEP for sites with available SWC (CA-FEN, US-UMB, US-NE3, US-HA1, US-SP3 and US-SP2 are excluded due to unavailable of SWC data).

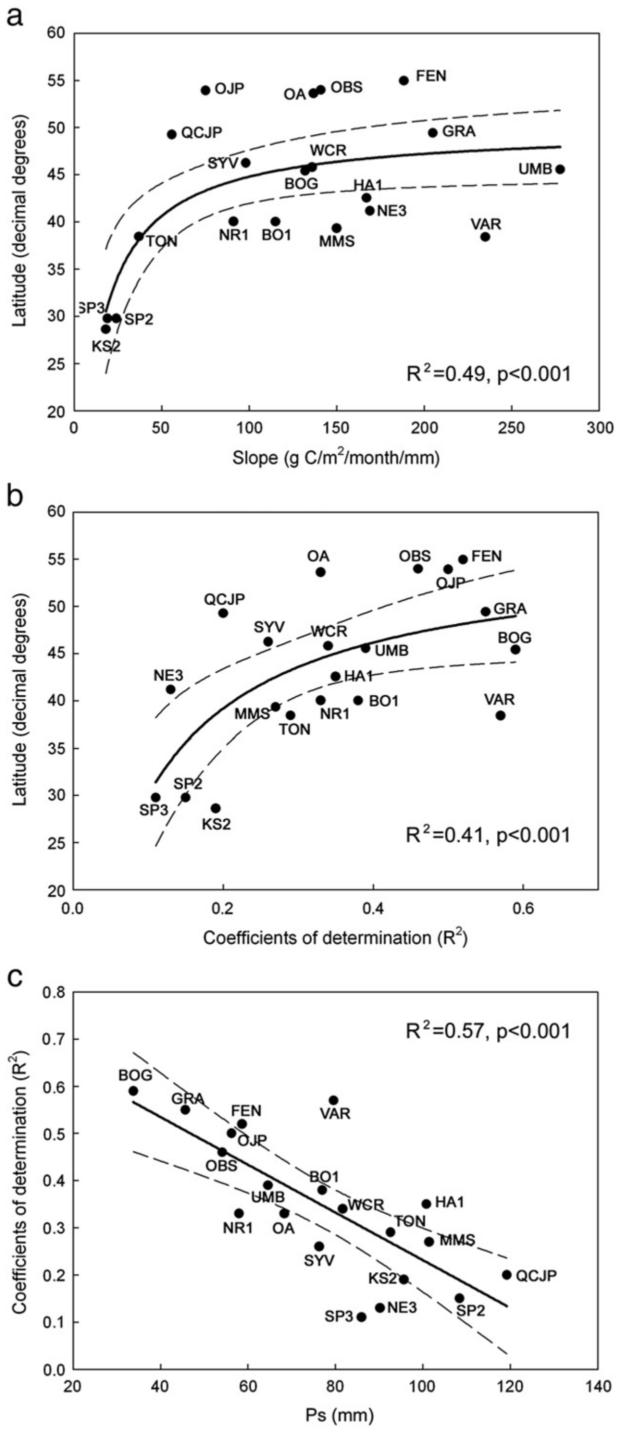

Fig. 8. Latitudinal patterns of (a) the slope of GEP-P_a correlation and (b) R^2 of GEP-P_a correlation for all sites; (c) relationship between R^2 of GEP-P_a correlation and average P_s for all sites.

supported by our available datasets showing that less than 6% (5 out of 88) observations have SWC variations over 5% for P_a above 1.5 mm, whereas for P_a below 1 mm this proportion rises to 31% (68 out of 221). We believe that it is this result that best explains the observed positive influence of increased precipitation intensity on monthly GEP.

Since P_a is related to both LAI and GEP, it is also worthwhile to consider whether variation in LAI over the growing season would potentially affect the correlation between P_a and GEP. We standardized GEP by LAI using the ratio GEP/LAI as one way to remove this effect. Detailed monthly LAI data were available at five sites, and the correlations

Table 3
Relationships between precipitation intensity (P_a, mm) and monthly mean air temperature (T_a, °C), global shortwave radiation (R_g, MJ/m^2/month).

Plant functional types		T_a (°C)	R_g (MJ/m^2/month)
P_a (mm)	GRA	NS	NS
	WET	$R^2=0.47$, $p<0.001$	$R^2=0.11$, $p=0.005$
	DBF	$R^2=0.27$, $p<0.001$	NS
	CRO	$R^2=0.10$, $p=0.025$	NS
	ENF	$R^2=0.36$, $p<0.001$	NS
	MF	$R^2=0.35$, $p<0.001$	$R^2=0.18$, $p<0.001$
	EBF	$R^2=0.35$, $p<0.001$	$R^2=0.12$, $p<0.001$
	WSA	$R^2=0.34$, $p<0.001$	$R^2=0.16$, $p<0.001$

GRA, WET, DBF, CRO, ENF, MF, EBF, and WSA represent grassland, wetland, deciduous broadleaf forest, crops, evergreen needle-leaf forest, mixed forest, evergreen broadleaf forest, and woody savannas, respectively. NS indicates no significant correlation was observed.

between P_a and GEP/LAI for these sites are shown in Fig. 11. While positive correlation was obtained at the grassland site (CA-GRA, $R^2=0.11$, $p<0.001$) and the deciduous forest site (US-MMS, $R^2=0.21$, $p<0.001$), both the crop site (US-NE3) and woody savannas site (US-SP2) have shown negative correlations with both R^2 of 0.31 ($p<0.001$). No correlation was obtained for an evergreen broadleaf forest site (US-SP3). The underlying mechanism of these equivocal correlations is not well understood at present, but still suggests the influence of precipitation intensity on vegetation productivity and should be explored in future analysis.

Our evaluation on the relationships between P_a and temperature and radiation shows that the effect of P_a on monthly GEP should be considered with other factors influencing GEP. This agrees with the assumption that the roles of climate variables on vegetation production could change with both time and PFTs. More importantly, it supports the suggestion that the pattern of precipitation (e.g., intensity) could have more important effect than the quantity. This is meaningful for the regional carbon budget since we have many cases where predictions of vegetation production are substantially different among various ecosystem models (Beer et al., 2010). One explanation of such difference could be the unknown effects of certain variables (e.g., precipitation patterns) that affect GEP, but their mechanisms are not well understood and thus not being included in models. Our results from precipitation intensity may be a potential solution to know the missing processes or feedback mechanisms that attenuate the vegetation production to climate (Beer et al., 2010). Given the difficulty in climate models predicting future precipitation, one particular useful implication of our analysis is that future ecosystem models for the analysis of precipitation effects might take this precipitation intensity into consideration to improve the ability of climate models to predict quantitative ecosystem responses in future climate scenarios. However, for the operational

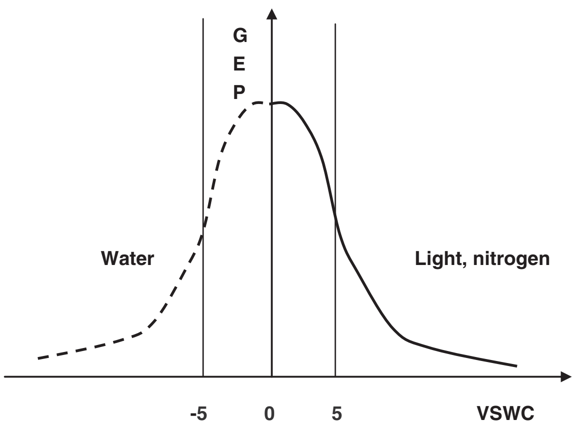

Fig. 9. The conceptual model of maximum production as a function of VSWC.

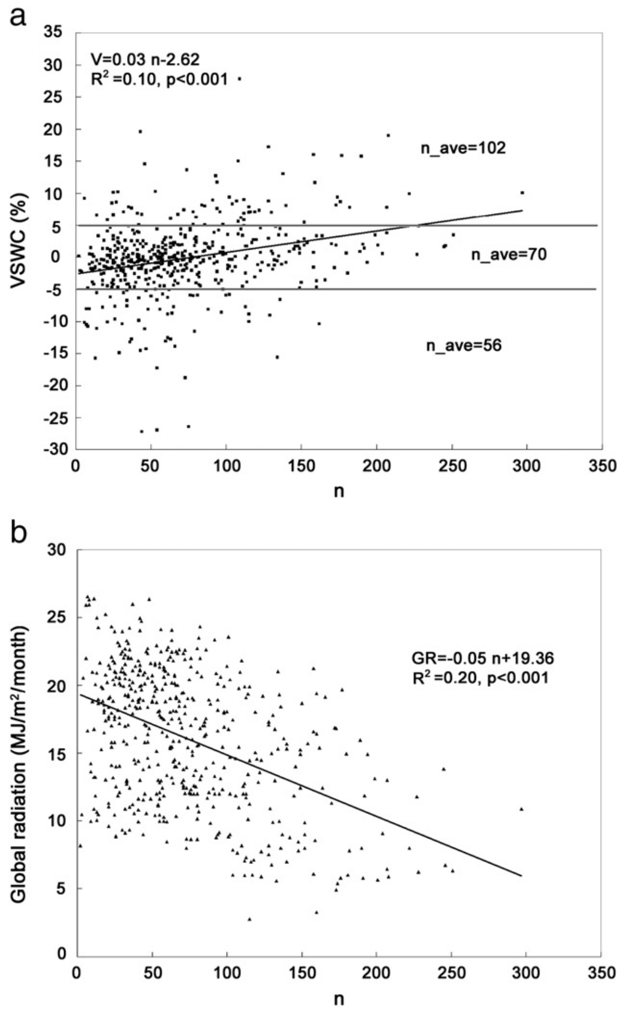

Fig. 10. a, Relationship between precipitation times (n) and the variation in soil water content (VSWC). The two gray lines indicate the variations with ±5%. Black line represents the regression equation. Average n (n_ave) for VSWC below −5%, within 5% and above 5% are 56, 70 and 102, respectively. b, Relationship between the precipitation times (n) and the monthly global shortwave radiation.

applications of P_a, the effects of other meteorological variables (e.g., temperature, radiation) on vegetation production should be also considered as their covariation with precipitation intensity.

Two extreme conditions also need to be discussed in the application of P_a. First, for months with no precipitation, P_a will not make sense for the evaluation of water availability. The production of vegetation can either be very low (US-VAR) or even higher (US-TON) and it may be dependent on the synchronization between vegetation growing season and precipitation period. In this case, other factors, such as the soil water content, soil texture and the precipitation of the last month may have potential use for the analysis of water status and production (Ryel et al., 2003; Weltzin et al., 2003). A second consideration is the "outlier" months that have P_a departing far from the average values that are often due to unusual and rarely occurring storms. For example, P_a for site US-BO1 reached 9.5 mm in September 2004 because there were only two ($n=2$) rainfalls that occurred in that month and one of which had a precipitation amount of 18 mm ($P_{max}=18$ mm), almost equal to P_s (19 mm). This unusual P_a value is almost five times larger than the SD of P_a after subtracting the P_a averages of all months for this site. This "outlier", in a statistical perspective, would happen in natural ecosystems because precipitation is a stochastic environmental factor that can change dramatically. However, for the month, both GEP and soil water content are not

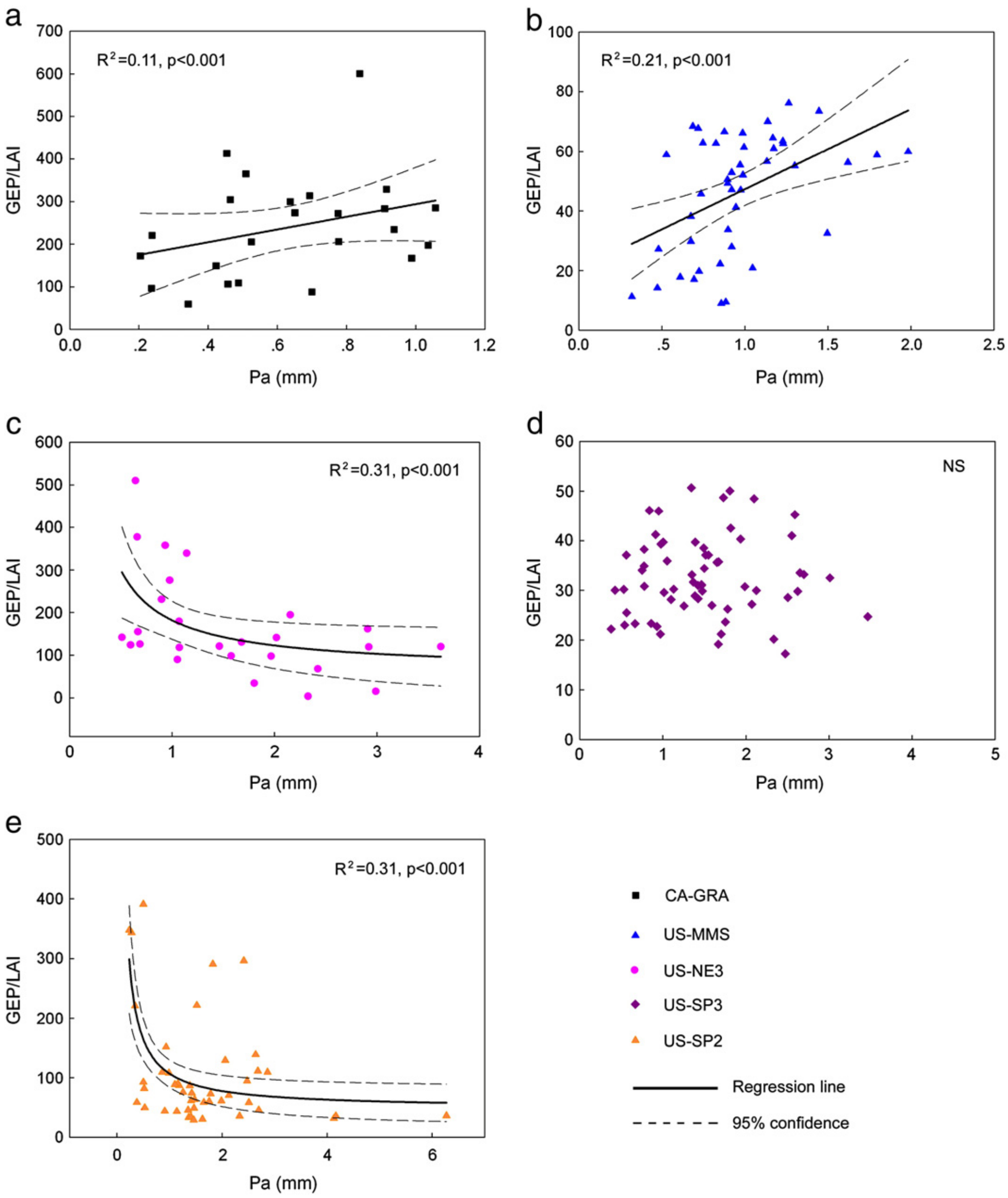

Fig. 11. Relationship between P_a and GEP/LAI for (a) CA-GRA, (b) US-MMS, (c) US-NE3, (d) US-SP3 and (e) US-SP2.

significantly different from other months of the same period because high values of P_a may not imply large amount of monthly precipitation. This uncertainty points to the need of incorporation of other variables (e.g., precipitation intervals) in order to better characterize the frequency and intensity of precipitation events.

5. Conclusions

There are several broad implications of this newly developed relationship between our precipitation intensity metric (P_a) and gross ecosystem photosynthesis (GEP). First, P_a highlights the importance of precipitation temporal patterns rather than the quantity alone. It provides insights to improve the accuracy of GEP estimates by ecosystems models that do not incorporate such mechanisms. Second, the correlation between GEP and P_a can bridge previous experimental results on carbon components under manipulated precipitation patterns to natural settings, in order to improve our understanding of the role of precipitation variability (Knapp et al., 2002). Third, this correlation provides a method to link GEP to changes of precipitation at the monthly temporal scale. Previous results that are obtained at the annual scale may be improved using P_a, which would be especially useful in climate change research because temporal heterogeneity of precipitation can lead to substantial differences in monthly precipitation even if the annual precipitation totals are relatively stable. Lastly, the higher correlation coefficients at water limited sites indicate that P_a would be most useful for the arid, semi-arid and drought susceptible regions that occupy about 30% of the world's land surface and support about one billion people (Weltzin et al., 2003). As projected by climate change models, drought is likely to become more severe at subtropical latitudes, thus we may expect that the area suitable for P_a application will increase. There is an urgent need for models to assess this dependence of vegetation production on precipitation patterns at different temporal scales and substantiate our claim of superior performance of P_a over P_s under relatively dry climate conditions and its importance in estimating the global terrestrial productivity and carbon cycle under future climate change scenarios.

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