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Contrasting responses of terrestrial ecosystem production to hot temperature extreme regimes between grassland and forest

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Abstract. During the past several decades, observational data have shown a faster increase in hot temperature extremes than the change in mean temperature. Increasingly high extreme temperatures are expected to affect terrestrial ecosystem function. The ecological impact of hot extremes on vegetation production, however, remains uncertain across biomes in natural climatic conditions. In this study, we investigated the effects of hot temperature extremes on vegetation production by combining the MODIS enhanced vegetation index (EVI) data set and in situ climatic records during the period 2000 to 2009 from 12 long-term experimental sites across biomes and climate. Our results show that higher mean annual maximum temperatures (T_{max}) greatly reduced grassland production, and yet enhanced forest production after removing the effect of precipitation. The relative decrease in vegetation production was 16 % for arid grassland and 7 % for mesic grassland, and the increase was 5 % for forest. We also observed a significantly positive relationship between interannual aboveground net primary production (ANPP) and T_{max} for the forest biome ($R^2 = 0.79$, $P < 0.001$). This line of evidence suggests that hot temperature extremes lead to contrasting ecosystem-level responses of vegetation production between grassland and forest biomes. Given that many terrestrial ecosystem models use average daily temperature as input, predictions of ecosystem production should consider such contrasting responses to increasingly hot temperature extreme regimes associated with climate change.

1 Introduction

The observed global temperature showed a warming of 0.85°C (0.65 to 1.06°C) over the period of 1880 to 2012, and the number of warm days and nights has increased at the global scale (IPCC, 2013). Future temperature is expected to continue to warm more rapidly over land than ocean, and there will be more frequent hot and fewer cold temperature extremes over most land area (IPCC, 2013). Terrestrial ecosystems are strongly impacted by climate and climate change (Nemani et al., 2003), and hence this trend towards hot temperature extremes would have important consequences on terrestrial ecosystems (IPCC, 2012). Numerous modeling and observational climate warming studies have shown the general enhancement of vegetation growth or increases in vegetation greenness in northern terrestrial ecosystems (e.g., Keeling, et al., 1996; Myneni, et al., 1997; Zhou et al., 2001; Neigh et al, 2008; Wu et al., 2011). However, knowing the general response of ecosystems tells us little about how the ecosystem in a particular location will respond or how different ecosystem responds to hot temperature extremes. For example, Peng et al. (2013) recently reported that the growing-season greenness was positively correlated with the maximum daily temperature (T_{max}) in northwestern North America and Siberia but negatively correlated in drier temperate regions such as western China, central Eurasia, and central and southwestern North America.

Usually, field manipulated experiments have been conducted to investigate the effects of climatic warming on ecosystem (Alward et al., 1999; Shaver et al., 2000; Wu et al., 2011). Such experimental manipulations are important to understand and quantify the individual contribution of climatic

Table 1. Descriptions of the sites in this study[a].

Site and location	Latitude (degree)	Longitude (degree)	Land cover	MAP (mm)[b]	Max. temperature (°C)	Code
Desert Exp. Range, UT	38.547	−113.712	Arid grassland	216 (65)	19 (1.1)	DE
Jornada Exp. Range, NM	32.589	−106.844	Arid grassland	242 (78)	25 (0.7)	JE
Walnut Gulch Exp. Watershed, AZ	31.736	−109.938	Arid grassland	311 (85)	25 (1.0)	WG
Santa Rita Exp. Range, AZ	31.846	−110.839	Arid grassland	447 (129)	29 (0.7)	SR
Central Plains Exp. Range, CO	40.819	−104.748	Arid grassland	381 (91)	16 (1.4)	CP
Southern Plains Exp. Range, OK	36.614	−99.576	Mesic grassland	586 (153)	22 (0.9)	SP
Little Washita Creek, OK	34.918	−97.956	Mesic grassland	796 (195)	24 (1.2)	LW
Little River Watershed, GA	31.537	−83.626	Temperate conifer forest	1148 (257)	25 (0.6)	LR
Mahatango Creek, PA	40.731	−76.592	Temperate broadleaf forest	1058 (179)	16 (0.9)	MC
Cutfoot Experimental Forest, MN	47.4264	−94.0141	Temperate broadleaf forest	665 (101)	11 (1.1)	CF
Bent Creek Exp. Forest, NC	35.500	−82.624	Temperate mixed forest	1227 (239)	19 (0.6)	BC
Caspar Creek, CA	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, for which data were available for a 32-year period 1978–2009.

[b] Average annual sum of precipitation (MAP) and average annual mean max temperature with standard deviation in parentheses.

warming on vegetation growth by controlling other global change factors. However, these studies have usually been conducted either on an individual ecosystem or over short-term periods, which render the comparisons across biomes that may differ between regions and ecosystem difficult. A main problem with these experiments is that they do not incorporate the entire micro- and macro-environmental aspects of variable weather. In addition, the long-term responses of ecosystem function are difficult to capture in warming experiments most of which were short term (< 5 years) (Wu et al., 2011). In other words, manipulated experiments are spatially and temporally restricted. The results from these manipulated studies are needed to understand in the context of long-term experiments in the natural field settings. 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., 2004).

Although individual grassland or forest sites have been conducted for their response to climatic warming or extremes (Wu et al., 2011; Smith, 2011), there is still no consensus on how ecosystem production will respond to temperature extremes across biomes from arid grassland to forest. Furthermore, many comparison studies used ecosystem production from a compilation of in situ measurements from long-term experimental sites (Huxman et al., 2004). However, the measuring procedures of vegetation production are not consistent across sites, and in some cases, not consistent over time at a given site (Sala et al., 1988), and this will result in some uncertainties. As a result, we are lacking generalizations about the regional behavior of terrestrial ecosystem with more hot temperature extreme regimes.

The last decade has witnessed dramatic global warming: 9 of the 10 warmest years on record have occurred during the 21st century (NOAA, 2013). These conditions are similar to those expected due to climate change (IPCC, 2013). In par-

ticular, the United States has warmed faster than the global rate since the late 1970s, and heat waves in 2005, 2006, and 2007 broke all-time records for high maximum and minimum temperatures (NOAA, 2013). Therefore, this recent climatic condition provides an opportunity to study the functional response of biomes to hot temperature extremes with respect to future climate change.

In this study, we used a 10-year data set of MODerate resolution Imaging Spectroradiometer (MODIS) enhanced vegetation index (EVI) (Huete et al., 2002) as an indicator of aboveground net primary production (ANPP), in combination with field observations from 12 long-term experimental sites in the conterminous United States. The primary objective of this study was to examine the response of vegetation production to hot temperature extremes, with particular focus on quantifying the direction and magnitude of ANPP long-term response across biomes from semi-arid grassland to temperate forest. We first assessed the changes in annual ANPP due to higher temperature extremes across biomes. Then, we examined the link between temperature extremes and annual ANPP after controlling the effects of precipitation and low temperature.

2 Materials and methods

2.1 Study sites and meteorological data

Twelve USDA experimental sites across the conterminous United States were used. These sites included different precipitation regimes and biomes representative of ecosystems ranging from arid grassland 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 at least 2.25 km × 2.25 km in size (Table 1).
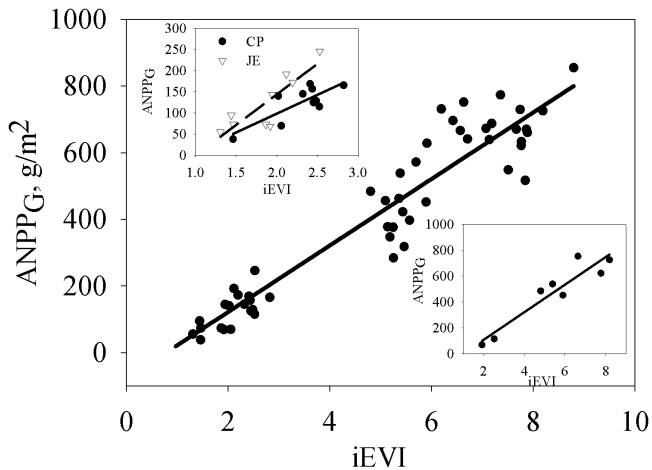
Figure 1. Relationship between annual ground measurements of ANPP ($ANPP_G$) and the corresponding iEVI derived from MODIS data during the period between 2000 and 2009 for nine selected sites across biomes ($R^2 = 0.90$, $P < 0.0001$; Table 2). The upper inset shows the relationship at two sites of CP and JE ($R^2 = 0.63$ and 0.74, respectively, $P < 0.01$). The lower inset shows the relationship between $ANPP_G$ and iEVI for the year 2001 across the 9 sites ($R^2 = 0.88$, $P < 0.001$).

According to Köppen–Geiger climate classification (Peel et al., 2007), arid grassland (DE, JE, WG, and SR) and Mediterranean forest (CC) sites experience a climate with a dry season and are seasonally water-limited, whereas mesic grassland (CP, SP, and LW) and temperate forest (LR, MC, BC, and CF) sites experience humid climate and can be temperature-limited.

The climate data set used in this study was from in situ daily precipitation and maximum and minimum air temperature measured at the local weather station representative of each site from 1970 to 2009 except for JE, for which data were available from 1978 to 2009. Long-term (40-year) in situ temperature data sets were used to identify climate extremes within the past decade. In this study, we considered two extreme temperature indices. Maximum temperature index (T_{max}) represents annual mean daily maximum temperature, and minimum temperature index (T_{min}) represents annual mean daily minimum temperature. Annual values were based on the hydrologic year extending from 1 October to 30 September. The interannual variability of temperature extremes was represented by the anomaly, which was calculated as the departure of a given year from the mean of the period between 1970 and 2009 divided by the standard deviation. Positive anomaly means higher T_{max} above the long-term average, and vice versa for negative anomaly.

2.2 Satellite data

We used satellite observations of the EVI from the MODIS as a proxy for annual ANPP. 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 $\sim 2.25\,km \times 2.25\,km$ (9×9 pixels) based on the coordinates for each site in Table 1. A total of 230 scenes (23 scenes × 10 years) was obtained for each of the 12 sites. In order 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 based on the quality flag in MOD13Q1 product (Ponce-Campos et al., 2013). Then the software TIMESAT was used to smooth the QA-filtered time series of EVI as well as to estimate the vegetation parameters such as EVI integrals of the growing season (Jönsson and Eklundlh, 2004). The large integral of MODIS EVI measurements (referred to as iEVI hereafter) over the whole year was used as our surrogate measure of ANPP (Fig. 1). The MODIS iEVI has been used to quantify the dynamics of ANPP across biomes ranging from arid grassland to forest (Zhang et al., 2013; Ponce-Campos et al., 2013). For this study, to validate the relation between iEVI and annual ANPP for the data set in this study, ground measurements of ANPP ($ANPP_G$) during the period 2000–2009 were compiled for nine sites (53 years in total) across the United States (Table 2). A strong relationship (Eq. 1) between $ANPP_G$ and the corresponding iEVI was derived across biomes for these long-term experimental sites (Fig. 1):

$$ANPP_G = 100.97 \times iEVI - 85.28 \qquad (1)$$
$$R^2 = 0.90 \quad P < 0.001 \quad (n = 53).$$

It should be noted that Eq. (1) is a spatiotemporal relationship between $ANPP_G$ and iEVI across biomes. At the site scale, the temporal relationship between $ANPP_G$ and iEVI is not as strong as Eq. (1), but the site-specific comparison with $ANPP_G$ from the plot-scale ground measurements at two sites in Table 1 (CP and JN) showed generally good agreement during the period between 2000 and 2009 (Fig. 1 inset, $R^2 = 0.70$, $P < 0.01$) in spite of the scale differences between measurements of iEVI and $ANPP_G$. Hence iEVI could show the interannual variability of vegetation growth. On the other hand, the spatial correlation is also significantly positive between $ANPP_G$ and the corresponding iEVI, as shown in Fig. 1 (inset) for the year of 2001 across biomes ($R^2 = 0.88$, $P < 0.001$). Therefore, we assumed that the iEVI can be a reasonable surrogate for ANPP interannual variability and provide consistent sensitivity across biomes ranging from arid grassland to forest in our analyses.

2.3 Data analysis

To investigate the sensitivity of ANPP to temperature extreme (T_{max}) across biomes, we compared the iEVI measured during years with extremely high temperatures with the mean iEVI of all other years during 2000–2009 for each site. Years

Table 2. Sites with "in-situ" ANPP measurements within the period of 2000–2009 for validation with iEVI.

Site	Biome and Location	Period	Source
Jornada LTER	Arid grassland, New Mexico	2000–2009	http://www.lternet.edu/sites/
Sevilleta LTER	Arid grassland, New Mexico	2002–2003	http://www.lternet.edu/sites/
Shortgrass Steppe LTER	Grassland, Colorado	2000–2009	http://www.lternet.edu/sites/
Cedar Creek LTER	Grassland, Minnesota	2000–2007	http://www.lternet.edu/sites/
Konza Prairie LTER	Grassland, Kansas	2000–2002	http://www.lternet.edu/sites/
Harvard Forest	Mixed forest, Massachusetts	2000–2006	http://www.lternet.edu/sites/
Metolius Intermediate Pine	Evergreen needleleaf forest, Oregon	2001	http://public.ornl.gov/ameriflux/
Park Falls	Deciduous broadleaf forest, Wisconsin	2000, 2004	http://public.ornl.gov/ameriflux/
Ohio Hills FFs	Mixed forest, Ohio	2001–2002	Chiang et al. (2008)
University of Michigan Biological Station	Deciduous broadleaf forest, Michigan	2000–2006	Gough et al. (2008)
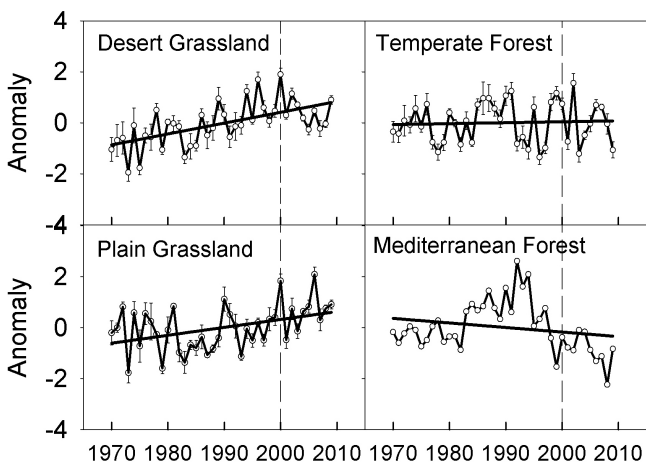
Figure 2. Long-term trends of the anomaly of T_{max} during 1970–2009 for different biome types. DG, arid grassland sites (DE, JE, WG, SR, and CP in Table 1); MG, mesic grassland sites (SP and LW in Table 1); TF, temperate forested sites (LR, MC, BC, and CF in Table 1); MF, Mediterranean forested site (CC). The dotted line shows the year of 2000 for the starting year of the MODIS EVI data set.

with extremely high temperatures were defined as those for which the T_{max} anomaly was ≥ 1 or the maximum anomaly year when there is no anomaly > 1 during 2000–2009. Since both precipitation and temperature (T_{max} and T_{min}) have limitations on vegetation production (iEVI) and they covary with one another, we also used partial correlation analysis to assess the relationship between iEVI and T_{max} by removing the effects of precipitation and T_{min}. Partial correlation analysis is widely used to isolate the relationship between two variables by removing the effects of many correlated variables. A Duncan multiple range test was used to determine significant differences in temperature and iEVI among groups.

3 Results and discussion

3.1 Long-term trends of the anomaly of T_{max}

Figure 2 shows the long-term trends of T_{max} for the four biome types (Table 1). For desert grassland, annual mean maximum temperature increased by 1.66 °C ($P < 0.0001$) during the 40-year period from 1970 and 2009 (Fig. 2). For mesic grassland, T_{max} increased by 1.21 °C ($P < 0.0001$) during 1970–2009 (Fig. 2). There was no significant trend for T_{max} for temperate forest sites. In contrast, T_{max} decreased slightly for Mediterranean forest even though not statistically significant for the whole 40-year period (Fig. 2, $P > 0.1$). However, Fig. 2 shows that there were two different periods for T_{max} at the Mediterranean forest site (CC in Table 1). T_{max} increased by 1.86 °C ($P < 0.0001$) before the earlier 1990s but then dropped dramatically by -3.46 °C ($P < 0.0001$) after 1992 (Fig. 2). The temperature rises observed in desert and mesic grassland are consistent with the observation in the southwestern US and the Great Plains (US-GCRP, 2009; MacDonald, 2010). However, the unchanged annual mean T_{max} in the temperate forest sites is not consistent with the regional temperature rise in the eastern US (USGCRP, 2009).

3.2 Contrasting responses to T_{max} between grassland and forest biomes

Figure 3 shows that annual iEVI was significantly correlated with T_{max} ($R^2 = 0.79$, $P < 0.001$) across the temperature gradient of forested sites, and a stronger relation was identified between the decadal maximum T_{max} and corresponding iEVI ($R^2 = 0.95$, $P < 0.005$; Fig. 3). Because the slopes of these two relations are not significantly different (F test, $P > 0.05$; Fig. 3), this confirms that forest production increases with elevated temperature across the temperature gradient (Magnani et al., 2001; Wullschleger et al., 2003; Huxman et al., 2004). This also suggests that the decadal maximum T_{max} may not affect the overall sensitivity of interannual ANPP to mean annual temperature. Figure 3 also
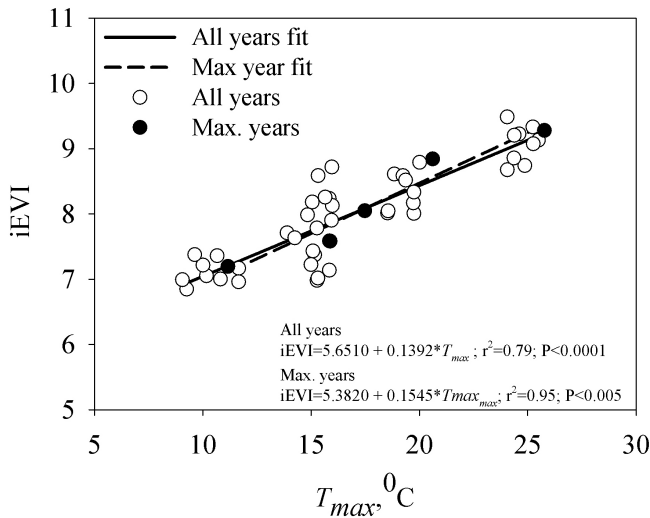
Figure 3. Relationship between iEVI and T_{max} and their maximum-year T_{max}–iEVI relationship for five forested sites. The dotted line shows the linear relationship between maximum-year T_{max} and the relevant iEVI for all the sites.

Figure 4. Comparison of iEVI differences between the extreme years and average of all other years of T_{max} across sites. Extreme years mean that the years of T_{max} anomaly are ≥ 1. The inset denotes the average differences by biome type. DG, arid grassland sites (DE, JE, WG, and SR in Table 1); MG, mesic grassland sites (CP, SP, and LW in Table 1); TF, temperate forested sites (LR, MC, BC, and CF in Table 1); MF, Mediterranean forested site (CC). Different letters indicate significant differences at $P < 0.05$.

suggests that maximum temperature can explain 80 % of the variability of vegetation production across these forest sites. For the grassland sites, however, there is no significant correlation between mean annual iEVI and T_{max} ($R^2 = 0.05$, $P = 0.64$). This is consistent with the fact that vegetation production is more controlled by water availability for grasslands in arid and semi-arid regions and interannual ANPP being related to soil moisture variability (Knapp and Smith, 2001; Knapp et al., 2002; Cherwin and Knapp, 2012). On the other hand, the forest biome is more temperature-limited with regard to productivity, particularly in regions that are not constrained by water, and climatic warming can stimulate vegetation growth through enhancing summer photosynthesis (Churkina and Running, 1998; Nemani et al., 2003; Piao et al., 2007).

Within sites, however, the interannual iEVI was not correlated with interannual variations in T_{max} at any forest site ($P > 0.05$). The differences between spatial and temporal patterns of forest ANPP responses to T_{max} reflect different underlying mechanisms at regional and local scale. The regional pattern of forest ANPP is determined primarily by temperature, while the temporal pattern for a given ecosystem is most likely affected by interactions between temperature and nutrient availability. Several studies have found limited forest production response to warming alone but significant response to warming with fertilization (Parsons et al., 1994; Press et al., 1998; Rustad et al. 2001; Strömgren and Linder 2002; Xu et al. 2011).

Among biomes, higher T_{max} with an anomaly > 1 had a direct negative effect on vegetation production in grassland ecosystems, especially for arid grassland, but a positive effect on forest ecosystems (Fig. 4, $P < 0.05$). On average, the de-
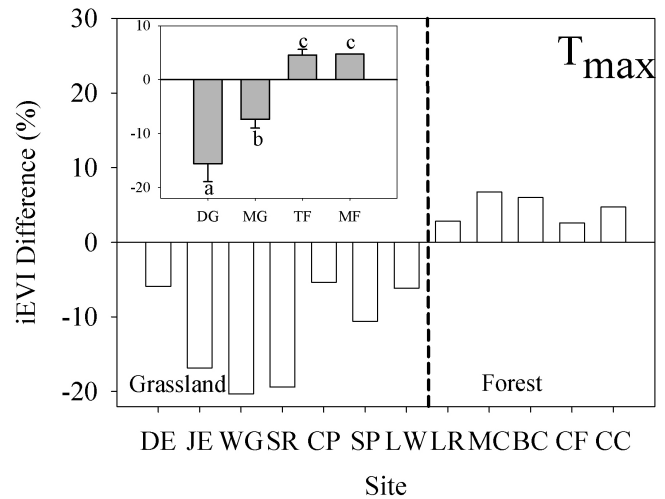
creases in iEVI were up to 7 % for mesic grassland, and 16 % for arid grassland (Fig. 4, inset). This may be attributed to the negative effects of warming temperatures on water availability through enhanced evapotranspiration (Seager and Vecchi, 2010). In contrast, higher T_{max} enhanced mean annual iEVI by 5 % for both temperate and Mediterranean forest sites (Fig. 4). There were larger, positive responses of ANPP to higher temperatures for forested sites in colder environments, which are the sites of BC and MC (Fig. 4).

The results stated above demonstrate the effects of hot temperature extreme on vegetation production without considering the confounding effects of other variables such as precipitation and T_{min}. There is a highly positive correlation between T_{max} and T_{min}. To isolate the role of T_{max} from precipitation and T_{min}, we alternately investigated the apparent responses of iEVI to T_{max} with partial correlation analyses to remove the confounding effects. Figure 5 shows how interannual iEVIs respond to variations in interannual T_{max} across sites. After removing the effects of T_{min} and precipitation in the partial correlation analyses, the individual T_{max} interannual changes again show the contrasting effects on the interannual iEVI between grassland and forest sites (Fig. 5). For desert grassland sites, interannual iEVI is negatively correlated with interannual T_{max} with statistical significance at the 0.05 level ($R = 0.35$). There is no significantly partial correlation between T_{max} and annual iEVI for mesic grassland sites (Fig. 5), implying little or no response of ecosystem production to T_{max} after removing the effects of T_{min} and precipitation. In contrast, interannual
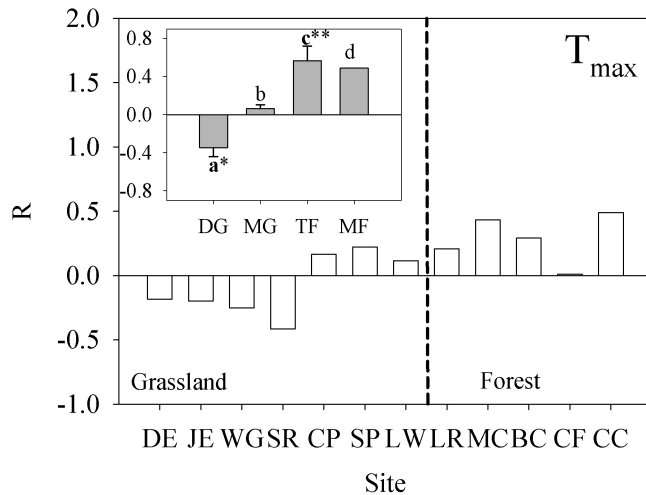
Figure 5. Partial correlations between iEVI and T_{max} after controlling the effects of T_{min} and precipitation across sites. (1) Statistically significant at the 95 % ($P < 0.05$) level; (2) statistically significant at the 99.9 % ($P < 0.001$) level.

T_{max} variations exhibit significantly positive partial correlations with interannual iEVI changes for temperate forest sites ($R = 0.57$; $P < 0.001$). For the Mediterranean forest site of Caspar Creek, it also shows positive partial correlations between interannual T_{max} and iEVI but without statistical significance ($R = 0.49$; $P = 0.22$) due to fewer data sets from only site. This opposite response of interannual iEVI to T_{max} between wet and dry temperate regions of the North America agrees well with a recent global study by Peng et al., 2013, in which remarkable spatial patterns of the partial correlations between growing-season greenness and T_{max} over the Northern Hemisphere were shown.

In all, the two approaches in the present study suggest that hot temperature extremes imposed a negative effect on vegetation production for grassland, especially desert grassland in the southwestern US, while it has a positive effect on forest (Figs. 4 and 5). This difference in response between grassland versus forest may be related to the adaptations of dominant species in terms of their response to warming temperature. Higher T_{max} and warming climate would imply drier soils through increased evaporative demand (Manabe and Wetherald, 1986) and decreased production due to decreases in stomatal conductivity, down-regulation of the photosynthetic processes, and increased allocation to roots in arid and semi-arid regions (Chaves et al., 2002). Our results agree well with the results of previous studies (Braswell et al., 1997; Piao et al., 2006; Munson et al., 2012) that higher temperatures may have directly negative effects on vegetation growth in arid and semi-arid grassland. With more atmospheric carbon dioxide in the future, however, such warming desiccation effects would be likely modified at least for arid grasslands as shown by Morgan et al. (2011). For forest, the positive effect is consistent with the results reported by

Rustad et al. (2001) and McMahon et al. (2010) for ANPP in ecosystem warming experiments that higher T_{max} would have a positive impact on forest production (Boisvenue and Running, 2006). Previous studies have also shown that higher temperatures favor tree growth by enhancing photosynthesis (Lukac et al., 2010) and nutrient uptake (Weih and Karlsson, 2002), especially in sites where trees were not typically constrained by moisture stress. Thus, these contrasting responses to T_{max} in different ecosystems could have different effects on regional vegetation carbon uptake (Braswell et al., 1997). However, it should be noted that, due to data limitations, only 12 sites were used in this study. We need more data from all terrestrial ecosystems to test whether the contrasting effect of temperature extremes is a general behavior in forest and grassland ecosystems. Furthermore, the results reported here may be temporal, and the long-term impact of temperature extremes on ecosystem functional integrity across biomes is yet unknown. The ongoing field measurements of carbon flux and meteorological data from eddy covariance flux method for different ecosystem may provide an opportunity to validate the assumption in this study.

4 Conclusions

Understanding how vegetation production responds to extreme warm temperature regimes is crucial for assessing the impacts of climate change on terrestrial ecosystem. Recent record-breaking high temperatures in the contiguous US provide the opportunity to study such effects. Our study offers a generalization of the functional response of ecosystem to hot extreme conditions predicted with climate change across biomes in the natural climatic conditions. By using satellite and in situ meteorological data, we found a contrasting response of terrestrial ecosystem to extreme warm temperature anomalies between grassland and forest biomes in natural settings. The opposite direction and magnitude of response indicates different sensitivities across ecosystems to hot temperature extremes. A recent study has shown that there is a continuous increase in hot extremes over land, despite the slowed rate of increase in annual global mean temperature (Seneviratne et al., 2014). Hence, the sensitivity of ecosystem production in response to hot extremes across biomes found here has important implications. Current terrestrial ecosystem models usually utilize daily mean or monthly temperature data as input, and hence they may neglect the response of vegetation to extreme warm temperature (T_{max}). To some extent, the effects of hot extremes are more relevant for climate change impacts than global mean temperature on ecosystems (IPCC, 2012, 2013). Hence, this work further strengthens our understandings of the ecosystem-level response to extreme warm temperatures across biomes. This study also clarifies the value of long-term experimental sites together with continuing satellite-based observations such as EVI in future studies. This compelling result in a

natural setting at the ecosystem level should play a role in future climate change impact studies.

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