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

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Abstract

Observational data during the past several decades show faster increase of hot temperature extremes over land than changes in mean temperature. Towards more extreme temperature is expected to affect terrestrial ecosystem function. However, the ecological impacts of hot extremes on vegetation production remain uncertain across biomes in natural climatic conditions. In this study, we investigated the effects of hot temperature extremes on aboveground net primary production (ANPP) by combining MODIS EVI dataset and in situ climatic records during 2000 to 2009 from 12 long-term experimental sites across biomes and climates. Our results showed that higher mean annual maximum temperatures (T_{\max}) greatly reduced grassland production, and yet enhanced forest production after removing the effects of precipitation. Relative decreases in ANPP were 16 % for arid grassland and 7 % for mesic grassland, and the increase were 5 % for forest. We also observed a significant positive relationship between interannual ANPP and T_{\max} for forest biome ($R^2 = 0.79$, $P < 0.001$). This line of evidence suggests that hot temperature extreme leads to contrasting ecosystem-level response of vegetation production to warming climate between grassland and forest. Given that many terrestrial ecosystem models use average daily temperature as input, predictions of ecosystem production should consider these contrasting responses to more hot temperature extreme regimes associated with climate change.

1 Introduction

The observed global temperature shows a warming of 0.85 (0.65 to 1.06) °C over the period of 1880 to 2012, and the number of warm days and nights has increased on the global scale (IPCC, 2013). Future temperatures are expected to continue to warm more rapidly over land than oceans, and there will be more frequent hot and fewer cold temperature extremes over most land area (IPCC, 2013). This towards hot temperature extremes would have important consequences on terrestrial ecosystems (IPCC, 2012).

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5 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). Knowing, however, the general response of ecosystems tells us little about how the ecosystems in a particular location will respond or how different ecosystem responds to hot temperature extremes. For example, Peng et al. (2013) recently showed that growing-season greenness is positively correlated with the maximum daily temperature (T_{\max}) in northwestern North America and Siberia while negatively correlated in drier temperate regions such as western China, central Eurasia, central and southwestern North America.

10 Usually, field manipulated experiments have been conducted to investigate the effects of climate warming on ecosystems (Alward et al., 1999; Shaver et al., 2000; Wu et al., 2011). These studies usually have been conducted either on an individual ecosystem, or over short-term periods, which render comparisons difficult across biomes that may differ between regions and ecosystems. A main problem with these experiments is that they do not incorporate the entire micro- and macro-environmental aspects of variable weather. In addition, long-term responses of ecosystem function are difficult to capture in warming experiments most of which are short term (< 5 years) (Wu et al., 2011). Despite the research on responses of biological process to more extremely warm temperature (Smith, 2011), our understanding and quantification of the effects of more hot temperature extreme regimes *across* biomes is lacking. 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).

25 The last decade has witnessed dramatical global warming in that 9 of the 10 warmest years on record have occurred during the 21st century (NOAA, 2013). These conditions are similar to those expected with climate change (IPCC, 2013). In particular, 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 temper-

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atures (NOAA, 2013). Therefore, this recent climatic conditions provide 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 dataset of MODerate resolution Imaging Spectroradiometer (MODIS) Enhanced Vegetation Index (EVI) (Huete et al., 2002) as an indicator of ANPP, in combination with field observations from 12 long-term experimental sites in the conterminous United States. Our primary goal was to examine the response of vegetation production to hot temperature extremes, with particular focus on quantifying the direction and magnitude of ANPP responses across biomes.

2 Materials and methods

2.1 Study sites and meteorological data

Twelve USDA experimental sites were used 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 km × 2.25 km (Table 1). According to Köppen–Geiger climate classification (Peel et al., 2007), arid grassland (DE, JE, WG, SP, and CP) and Mediterranean forest (CC) experience a climate with a dry season and are seasonally water-limited, whereas mesic grassland (SP and LW) and temperate forest (LR, MC, BC and CF) experience humid climates and can be temperature-limited.

The climate dataset used in this study was constructed from in situ daily precipitation, maximum and minimum air temperatures measured at the local weather station representative of each site from 1970–2009 except for JE, for which data were available from 1978–2009. Long-term (40 years) in situ temperature datasets were used to identify climate extremes within the past decade. In this study, we considered two ex-

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treme 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 1970–2009 periods, 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 dataset 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 $\sim 2.25 \text{ km} \times 2.25 \text{ km}$ (9×9 pixels) based on the coordinates for each site in Table S1 (see Supplement). A total of 230 scenes (23/year \cdot 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 dataset. 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 Eklundh, 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 dataset in this study, ground measurements of ANPP (ANPP_G) during the period 2000–2009 were compiled for 10 sites 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):

$$\text{ANPP}_G = 99.8249 \cdot \text{iEVI} - 78.0621, \quad R^2 = 0.90, \quad P < 0.0001 \quad (1)$$

Therefore, 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 sections, the trends in iEVI are interpreted to represent the cross-biome behavior of ANPP.

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 with extremely high temperatures were defined as those years for which the T_{\max} anomaly ≥ 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's multiple range tests were used to determine significant differences in temperature and EVI among groups.

3 Results and discussion

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

Figure 2 show the long-term trends of T_{\max} for four biome types. For desert grassland, annual mean maximum increased by 1.66°C ($P < 0.0001$) during the 40 year period

from 1970 to 2009 (Fig. 2). For mesic grassland, T_{\max} increased by 1.21°C ($P < 0.0001$) during 1970–2009 (Fig. 2). For temperate forest, there was no significant trend for T_{\max} . 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. 1 shows that there are two different periods for T_{\max} at the Mediterranean forest sites. T_{\max} increased by 1.86°C ($P < 0.0001$) before earlier 1990s but then dropped dramatically by -3.46°C ($P < 0.0001$) after 1992 (Fig. 2). The temperature rise observed in desert and mesic grassland is consistent with the observation in the southwestern US and the Great Plains (USGCRP, 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

Annual iEVI is significantly correlated with T_{\max} ($R^2 = 0.79$, $P < 0.001$; Fig. 3) across temperature gradients 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 temperature gradients (Magnani et al., 2001; Wullschlegel et al., 2003; Huxman et al., 2004). This also suggests that decadal maximum T_{\max} may not affect the overall sensitivity of interannual ANPP to mean annual temperature. The results suggest that maximum temperature can explain 80 % of the variability of vegetation production across these forest biomes. For grassland sites, however, there is no significant relationship between mean annual iEVI and T_{\max} ($R^2 = 0.05$, $P = 0.64$). This is consistent with that vegetation production is more controlled by water availability for grasslands in arid and semi-arid regions while forest biomes are temperature-limited in wet areas (Churkina and Running, 1998). Within sites, however, the interannual iEVI was not correlated with interannual variations in T_{\max} at any site ($P > 0.05$). The differences between spatial and temporal patterns of forest ANPP responses to T_{\max} reflect different underlying

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mechanisms on regional and local ecosystem scales. 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 found limited forest production response to warming alone, but significant response to warming with fertilization (Parsons et al., 1994; Press et al., 1998).

Among biomes, higher T_{\max} with anomaly > 1 had a direct negative effect on vegetation growth in grassland ecosystems, especially for arid grassland, yet a positive effect on forest ecosystems (Fig. 4; $P < 0.05$). On average, the decreases of 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. There were larger, positive responses of ANPP to higher temperature for forested sites in colder environments (BC and MC, Fig. 4).

The results stated above demonstrated the effects of hot temperature extreme on vegetation production without considering the confounding effects of other variables such as precipitation and T_{\min} . In addition, there is a high 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 iEVI respond to variations of interannual T_{\max} across biomes. After removing the effects of T_{\min} and precipitation in the partial correlation, the individual T_{\max} interannual changes again show contrasting effects on the interannual iEVI between grasslands and forest (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 significant 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 T_{\max} exhibits significant positive partial

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correlations with interannual iEVI 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 less data points. This opposite responses of interannual iEVI to T_{\max} between wet and dry temperate regions of the North America agrees well with a recent global study (Peng et al., 2013) in which they showed remarkable spatial patterns of the partial correlations between growing-season greenness and T_{\max} over Northern Hemisphere.

In all, the two approaches in the present study suggest that hot temperature extreme impose 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 vs. forest may be related to 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 temperature may have directly negative effects on vegetation growth in arid and semi-arid grasslands. 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 across biomes that higher T_{\max} will 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).

4 Conclusions

Understanding how vegetation production responds to extreme warm temperature regimes is crucial for assessing the impacts of climate change on terrestrial ecosystems. Recent breaking-record high temperature in the contiguous US provide the opportunity to study this effect. By using long-term satellite and in situ meteorological data, we found a contrasting response of terrestrial ecosystems to extreme warm temperature anomalies between grassland and forest in natural settings. The opposite direction and magnitude of response indicate distinguished sensitivities across ecosystems to hot temperature extremes. Recent study shows that there is a continuous increase of 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 we 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 strength our understanding of the ecosystem-level responses to extreme warm temperature across biomes. These compelling results in a natural setting at the ecosystem level should play a role in future climate change impacts studies.

Supplementary material related to this article is available online at <http://www.biogeosciences-discuss.net/11/5997/2014/bgdc-11-5997-2014-supplement.pdf>.

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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.

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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 Needle-leaf Forest, Oregon	2001	http://public.ornl.gov/ameriflux/
Park Falls	Deciduous Broad-leaf 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)

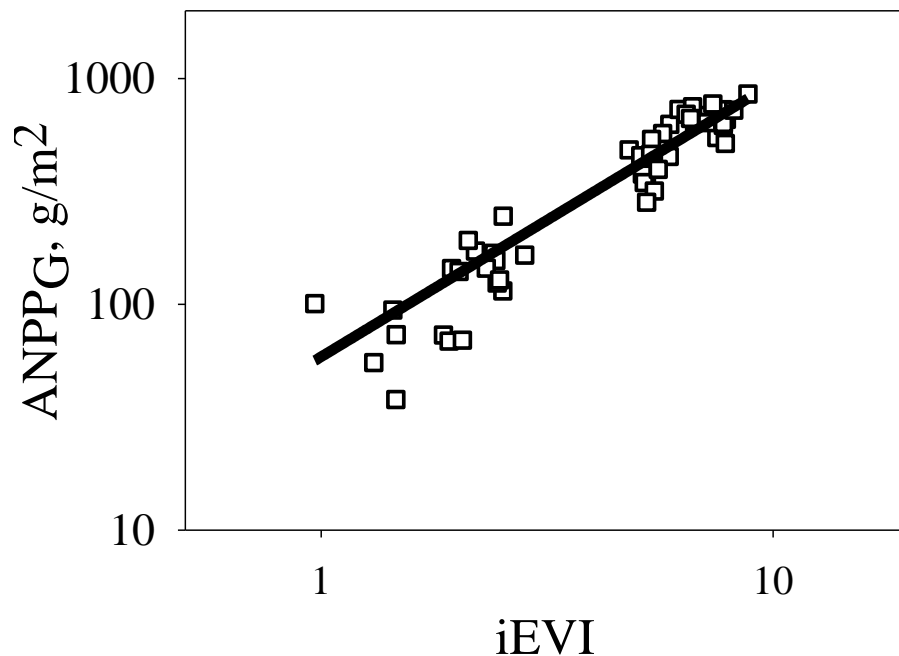


Fig. 1. Relationship between annual ANPP_G and the corresponding iEVI derived from MODIS data during 2000–2009 period for 11 selected sites across biomes. Solid line shows the linear regression ($R^2 = 0.90$, $P < 0.0001$).

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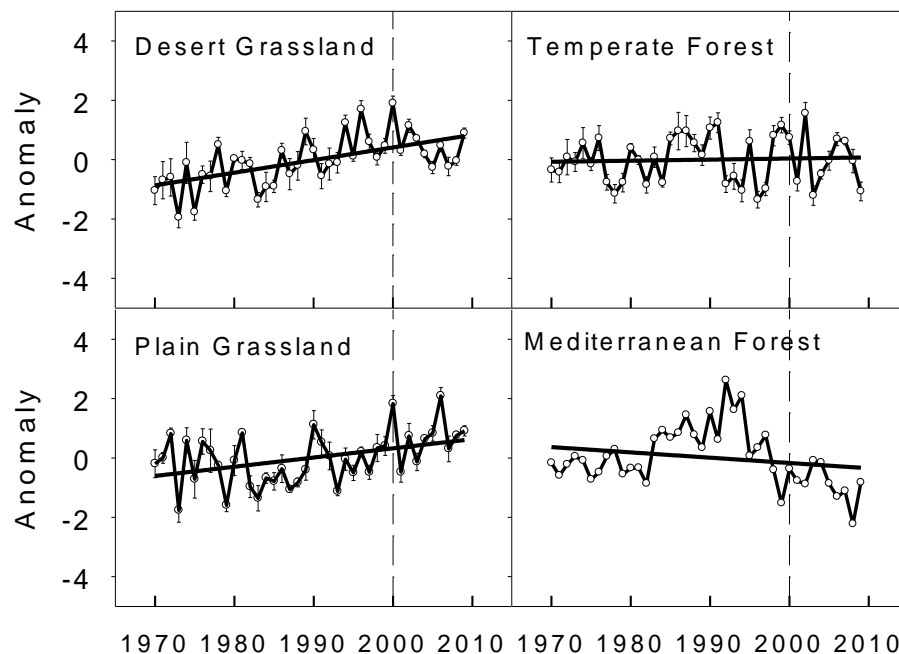


Fig. 2. Long-term trends of the anomaly of T_{\max} during 1970–2009 for different biome type. DG, arid grassland sites (DE, JE, WG, SR, and CP); MG, mesic grassland sites (SP and LW); TF, temperate forested sites (LR, MC, BC, and CF); MF, Mediterranean forested site (CC).

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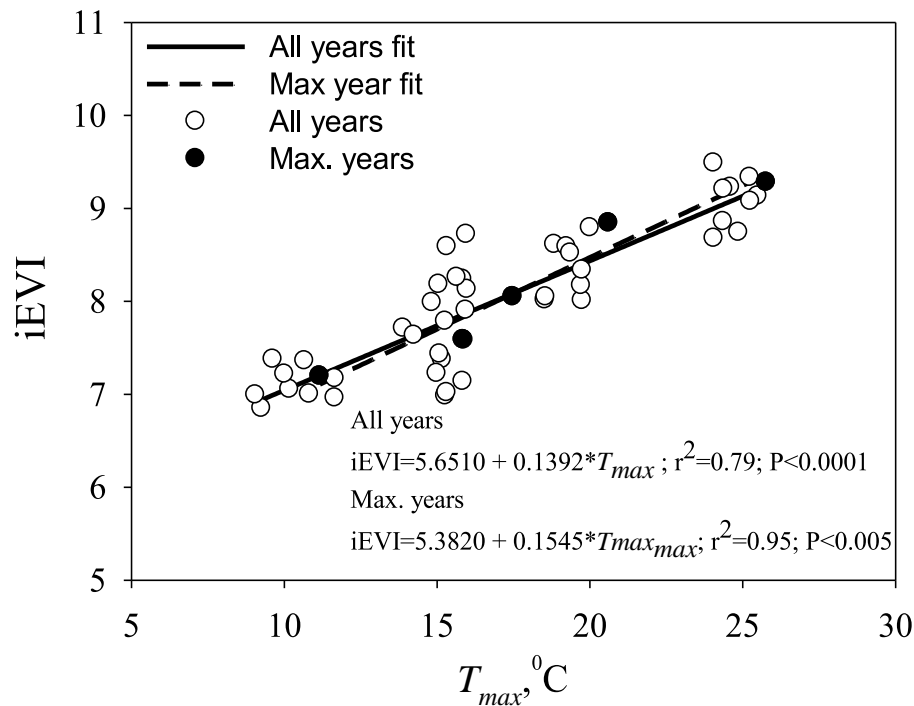


Fig. 3. Relations between iEVI and the indices of T_{max} across precipitation regimes and their maximum index-iEVI relation for 4 forested sites. Solid line shows the linear relation between maximum index value and the relevant iEVI for all the sites.

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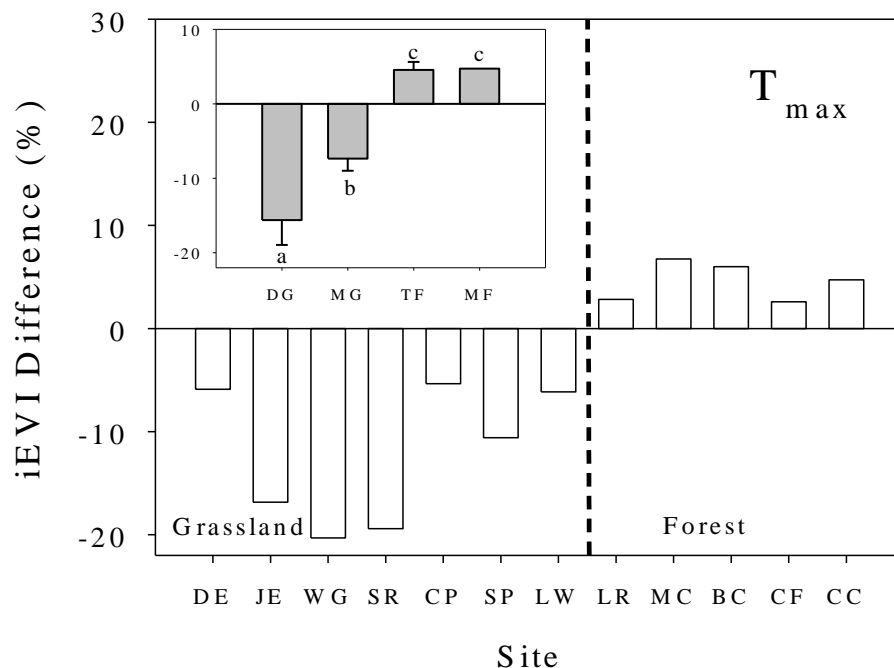


Fig. 4. Comparison of iEVI difference between extreme years and average of all other years for T_{max} across sites. Extreme years mean that T_{max} anomaly is ≥ 1 . The inset denotes the average difference by biome type. DG, arid grassland sites (DE, JE, WG, SR, and CP); MG, mesic grassland sites (SP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

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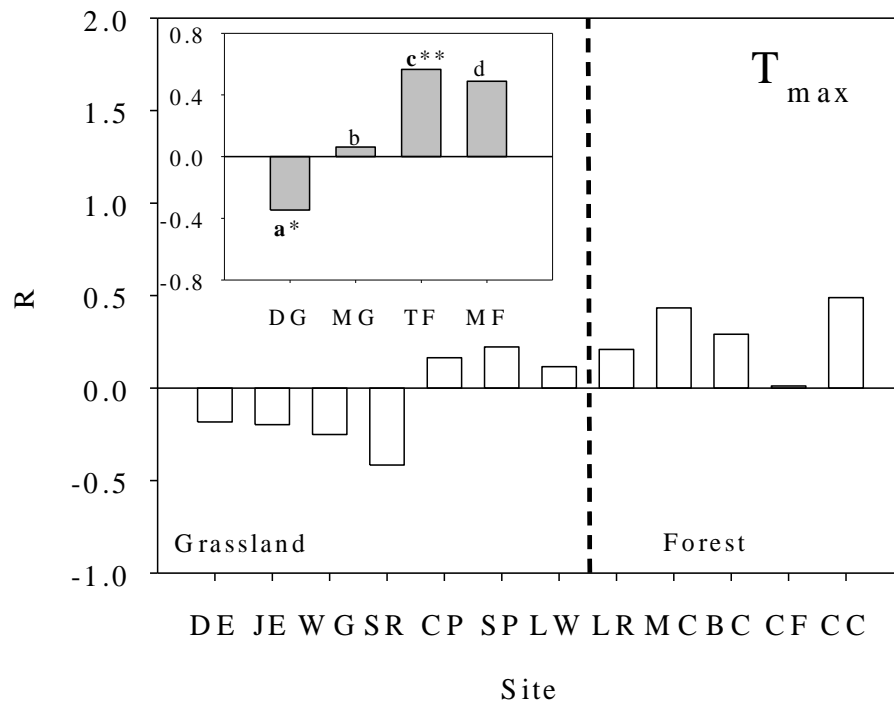


Fig. 5. Partial correlation between iEVI and T_{\max} after controlling for T_{\min} and precipitation across sites. * Statistically significant at the 95 % ($P < 0.05$) level; ** statistically significant at the 99.9 % ($P < 0.001$) level.

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