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

Running title: Response of ecosystem production to hot extremes

Y. Zhang[1*], M. Voigt[1], and *H. Liu*[2]

[1]Institute for Space Sciences, Freie Universität Berlin, 12165 Berlin, Germany;
[2]Changjiang River Scientific Research institute, Changjiang Water Resources commission, 430010 Wuhan, China

** Corresponding author, phone: +49-(0)30-83859025, fax: +49-(0)30-83856664,*
E-mail: yongguang.zhang@wew.fu-berlin.de

ABSTRACT: During the past several decades, observational data has 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 investigate the effects of hot temperature extremes on vegetation production by combining MODIS EVI dataset and *in situ* climatic records taken during 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 ANPP and T_{max} for forest biome ($R^2 = 0.79$, $P < 0.001$). This line of evidence suggests that hot temperature extremes lead to contrasting ecosystem-level response of vegetation production between grassland and forest. 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.

Keywords: ANPP, Biomes, Hot Temperature Extremes, EVI, T_{max}

1. INTRODUCTION

The observed global temperature showed a warming of 0.85 (0.65 to 1.06) ℃ 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). This 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 showed that the growing-season greenness was 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.

Usually, field manipulated experiments have been conducted to investigate the effects of climate warming on ecosystem (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 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). 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).

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 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 temperature (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 dataset 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. 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 response across biomes.

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 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, 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 dataset used in this study was constructed from *in situ* daily precipitation, maximum and minimum air temperature measured at the local weather station representative of each site from 1970-2009 except for JE, for which data was 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 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 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 ~2.25×2.25 km (9×9 pixels) based on the coordinates for each site in Table 1. A total of 230 scenes (23/year *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 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 & 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 dataset in this study, ground measurements of ANPP ($ANPP_G$) during the period 2000-2009 were compiled for 9 sites (53 years totally) 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):

$$ANPP_G = 100.9716 * iEVI - 85.2766$$
$$R^2 = 0.90 \quad P < 0.0001 \quad (n = 53) \tag{1}$$

It should be noted that Eq. 1 is a spatio-temporal 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 from the ground measurements at two sites in Table 1 (CP and JN) showed generally good agreement during 2000-2009 periods (Fig.1 inset, around R^2=0.70, P<0.01). Hence iEVI could show the inter-annual 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 argue that 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 findings for iEVI are discussed in relation to ANPP, using the two terms interchangeably.

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 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. For desert grassland, annual mean maximum temperature increased by 1.66 ℃ ($P<0.0001$) during the 40-year period from 1970 to 2009 (Fig. 2). For mesic grassland, T_{max} increased by 1.21 ℃ ($P<0.0001$) 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, Figure 2 shows that there were two different periods for T_{max} at the Mediterranean forest site (CC). T_{max} increased by 1.86 ℃ ($P<0.0001$) before the earlier 1990s but then dropped dramatically by -3.46 ℃ ($P<0.0001$) 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 was significantly correlated with T_{max} ($R^2 = 0.79$, $P < 0.001$; Fig. 3) 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 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 suggests that maximum temperature can explain 80% of the variability of vegetation production across these forest biomes. For the 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 biome is 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 forest site ($P > 0.05$). The differences between spatial and temporal patterns of forest ANPP responses to T_{max} reflect different underlying mechanisms on regional and local ecosystem 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).

Among biomes, higher T_{max} with 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 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 (Fig. 4). There were larger, positive responses of ANPP to higher temperature for forested sites in colder environments which are 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 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 iEVI respond to variations of interannual T_{max} across biomes. 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 T_{max} exhibits significantly positive partial 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 fewer data points. 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 (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 (Fig. 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 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} 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). It should be noted that, however, due to data limitations, only 12 sites were used in this study. We need more data from all ecosystems to test whether the contrasting effect of temperature extremes is a general behavior on forest and grassland ecosystem. 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 breaking-record high temperature in the contiguous US provides the opportunity to study this effect. By using long-term satellite and *in situ* meteorological data, we found a contrasting response of terrestrial ecosystem to extreme warm temperature anomalies between grassland and forest in natural settings. The opposite direction and magnitude of response indicates different 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 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 strengths our understandings of the ecosystem-level response to extreme warm temperature across biomes. This compelling result in a natural setting at the ecosystem level should play a role in future climate change impacts studies.

ACKNOWLEDGMENTS

The work by YZ and MV has been funded by the Emmy Noether Programme (GlobFluo project) of the German Research Foundation. Thanks to Anthony R. Buda, David D. Bosch, Stacey A. Gunter, Stanley G. Kitchen, W. Henry McNab, Jack A. Morgan, Mitchel P. McClaran, Diane S. Montoya, Debra P.C. Peters, and Patrick J. Starks for providing the climatic data. We also thank the EcoTrends Project www.ecotrends.info for access to multi-site, long-term data. This work used biological data acquired by LTER network. We acknowledge the Oak Ridge National Laboratory (ORNL), Distributed Active Archive Center (DAAC) for making these data available. We thank Dr. Bai Yang, Dr. Jyh-Min Chiang, Dr. Beverly Law, and Dr. Arlyn Andrews for providing suggestions about the ANPP data. We also thank the principal investigators, information managers, scientists and technicians responsible for measuring ANPP at the LTER sites. The authors also gratefully acknowledge the valuable suggestions made by Dr. Christopher Kyba at Freie Universität Berlin.

REFERENCES

Alward, R. D., J. K. Detling, and D. G. Milchunas (1999), Grassland vegetation changes and nocturnal global warming. Science 283, 229–231.

Braswell, B.H., D.S. Schimel, E . Linder, B. Moore, (1997), The response of global terrestrial ecosystems to interannual temperature variability. *Science,* 238, 870–872.

Boisvennue, C., and S.W. Running (2006), Impacts of climate change on natural forest production- evidence since the middle of the 20th century. *Global Change Biology*, 12, 862-882.

Chaves, M.M., J.S. Pereira, J.P. Maroco, *et al.* (2002), How plants cope with water stress in the field: photosynthesis and growth. *Annals of Botany*, 89, 907-916.

Chiang, J,M., R.W. McEwan, D.A. Yaussy, and K.J. Brown (2008), The effects of prescribed fire and silvicultural thinning on the aboveground carbon stocks and net preimary production of overstory trees in an oak-hickory ecosystem in southern Ohio. *Forest Ecol. Manag.*, 255, 1584-1594.

Churkina, G., and S.W. Running (1998), Contrasting climate controls on the estimated production of global terrestrial biomes. Ecosystems, 1, pp. 206–215.

Gough, C.M., C.S. Vogel, H.P. Schmid, H.B. Su, and P.S. Curtis (2008), Multi-year convergence of biometric and meteorological estimates of forest carbon storage. *Agric. For. Meteorol.*, 148, 158-170.

Keeling, R. F., S. C. Piper, and M. Heimann (1996), Global and hemispheric CO2 sinks deduced from changes in atmospheric O2 concentration. Nature, 381, 218–221.

Lukac, M., C. Calfapietra, A. Lagomarsino, F. Loreto (2010), Global climate change and tree nutrition: effects of elevated CO_2 and temperature. *Tree Physiology*, 30, 1209-1220.

MacDonald, G.M. (2010), Water, climate change, and sustainability in the southwest. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 21256–21262.

Manabe, S., and R.T. Wetherald (1986), Reduction in summer soil wetness induced by an increase in atmospheric carbon dioxide. *Science*, 232,626– 628.

McMahon, S.M., G.G. Parker, and D.R. Miller (2010), Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences of the United States of America* 107, 3611–5.

Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, R. R. Nemani (1997), Increased plant growth in the northern high latitudes from 1981 to 1991. Nature, 386, 698–702.

Myneni, R.B., J. Dong, C. J. Tucker, et al. (2001) A large carbon sink in the woody biomass of northern forests. *Proceedings of the National Academic Sciences of the United States of America*, 98, 14784–14789.

NOAA National Climatic Data Center, State of the Climate: Global Analysis for Annual 2013, published online December 2013, retrieved on February 21, 2014 from http://www.ncdc.noaa.gov/sotc/global/2013/13.

Huete, A.R., K. Didan, T. Miura, E.P. Rodriguez, X. Gao, L.G. Ferreira (2002), Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, 83, 195–213.

Huxman, T.E., M.D. Smith, P.A. Fay, *et al.* (2004), Convergence across biomes to a common rain-use efficiency. *Nature*, 429, 651-654.

IPCC, 2012: Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change [eds Field, C. et al.]. Cambridge University Press, Cambridge, UK, and New York, NY, USA, 582 pp.

IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, et al. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.

Jonsson, P., and L. Eklundh (2004), TIMESAT–a program for analyzing time-series of satellite sensor data. *Computers & Geosciences*, 30, 833-845.

Parsons, A.N., J.M. Welker, P.A.Wookey, M.C. Press, T.V. Callaghan, J.A. Lee (1994), Growth responses of four dwarf shrubs to simulated climate change. *Journal of Ecology*, 82, 307-318.

Peel, M.C., B.L. Finlayson, T.A. McMahonl (2007), Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633–1644.

Peng, S., S.L. Piao, P. Ciais, R. Myneni, et al. (2013), Asymmetric effects of daytime and night-time warming on Northern Hemisphere vegetation. Nature 501, 88–92, doi:10.1038/nature12434

Piao, S.L., A. Mohammat, J.Y. Fang, Q.Cai, J.M. Feng (2006), NDVI-based increase in growth of temperate grasslands and its responses to climate change in China. *Global Environmental Change*, 16, 340-348.

Press, M.C., J.A. Potter, M.J.W. Burke, T.V. Callaghan, J.A. Lee (1998), Responses of a sub-arctic dwarf shrub community to simulated environmental change. *Journal of Ecology*, 86, 315-327.

Ponce, Campos G.E., M.S. Moran, A. Huete, Y. Zhang, et al. (2013), Ecosystem resilience despite large-scale altered hydroclimatic conditions. Nature, 494, 349–352.

Rustad, L.E., J.L. Campbell, G.M. Marion, *et al.* (2001), A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126, 543-562.

Seager, R., and G.A.Vecchi (2010), Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences of the United States of America* 107, 21277–21282.

Seneviratne, S.I., M.G. Donat, B. Mueller, L.V. Alexander (2014), No pause in the increase of hot temperature extremes. Nature Climate Change 4(3), 161-163.

Shaver, G.R., J. Canadell, F.S. III Chapin, et al. (2000), Global warming and terrestrial ecosystems: a conceptual framework for analysis. Bioscience, 50, 871–882.

Smith, M.D. (2011), The ecological role of climate extremes: current understanding and future prospects. *Journal of Ecology*, 99, 651-655.

USGCRP (2009), Global Climate Change Impacts in the United States . Karl, T.R., J. M. Melillo, and T. C. Peterson (eds.). United States Global Change Research Program. Cambridge University Press, New York, NY, USA.

Weih, M., and P.S. Karlsson (2002), Low winter soil temperature affects summertime nutrient uptake capacity and growth rate of mountain birch seedlings in the subarctic, Swedish lapland. *Arctic, Antarctic, and Alpine Research*, 34, 434-439.

Wu, Z., P. Dijkstra, G.W. Koch, J. Peñuelas, B.A. Hungate (2010), Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology, doi:10.1111/j.1365-2486.2010.02302.x

Wullschleger, S.D., P.J. Hanson, D.E. Todd (2003), Forest water use and the Influence of precipitation change. in North American temperate deciduous forest responses to changing precipitation regimes, edited by Hanson PJ and Wullschleger SD.Springer, New York, USA.

Zhang, Y., M.S. Moran, M.A. Nearing, Campos G.E. Ponce, et al. (2013), Extreme precipitation patterns and reductions of terrestrial ecosystem production across biomes. Journal of Geophysical Research: Biogeosciences, 118, 1-10, doi:10.1029/2012JG002136.

Zhou, L. M., C. J. Tucker, R. K. Kaufmann, D. Slayback, N. V. Shabanov, and R. B. Myneni (2001), Variations in northern vegetation activity inferred from satellite data of vegetation indexduring 1981 to 1999. Journal of Geophysical Research, 106,20069–20083.

List of Tables

List of Figures

Figure 1. Correlation between annual $ANPP_G$ and the corresponding iEVI derived from MODIS data during 2000-2009 periods for 9 selected sites across biomes (R^2=0.90, *P*<0.0001). The upper lower inset shows the relationships 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 site (R^2=0.88, P<0.0001).

Figure 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).

Figure 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.

Figure 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.

Figure 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.

Table 1 Descriptions of the sites in this study*.

Site and location	*Latitude (degree)*	*Longitude (degree)*	*Land cover*	*MAP (mm) ***	*Max. Temperature (℃)*	*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

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

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/*
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*

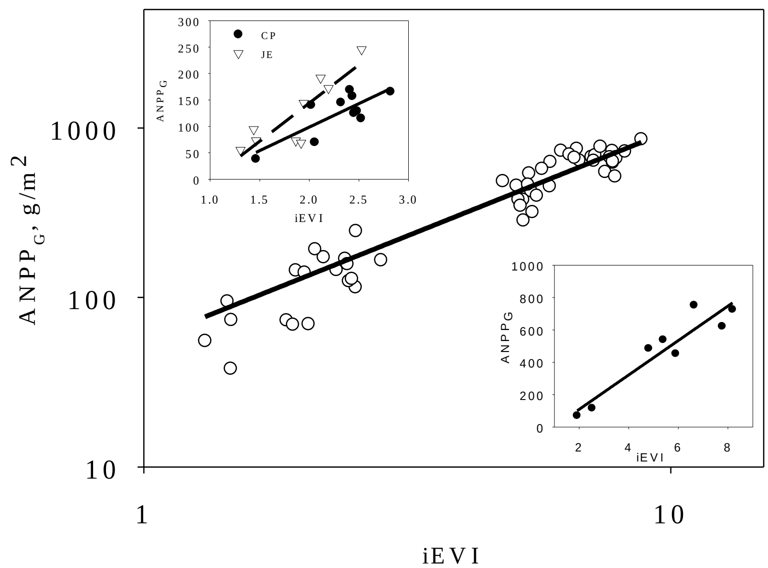

Figure 1. Correlation between annual $ANPP_G$ and the corresponding iEVI derived from MODIS data during 2000-2009 periods for 9 selected sites across biomes (R^2=0.90, P<0.0001). The upper lower inset shows the relationships at two sites of CP and JE (R^2=0.63 and 0.74, respectively, P<0.01). The lower inset shows the relationship between $ANPP_G$ and iEVI for the year 2001 across site (R^2=0.88, P<0.0001).

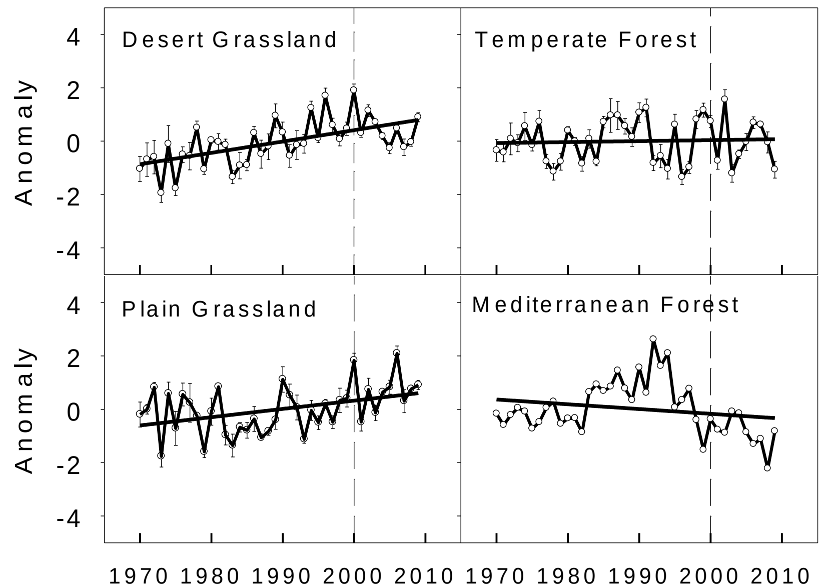

Figure 2. Long-term trends of the anomaly of T_{max} during 1970-2009 for different biome type. DG, arid grassland sites (DE, JE, WG, SR, and CP); MG, mesic grassland sites (SP and LW); TF, temperate forested sites (LR, MC, BC, and CF); MF, Mediterranean forested site (CC). The dotted line shows the year of 2000 for the starting year of the EVI dataset.

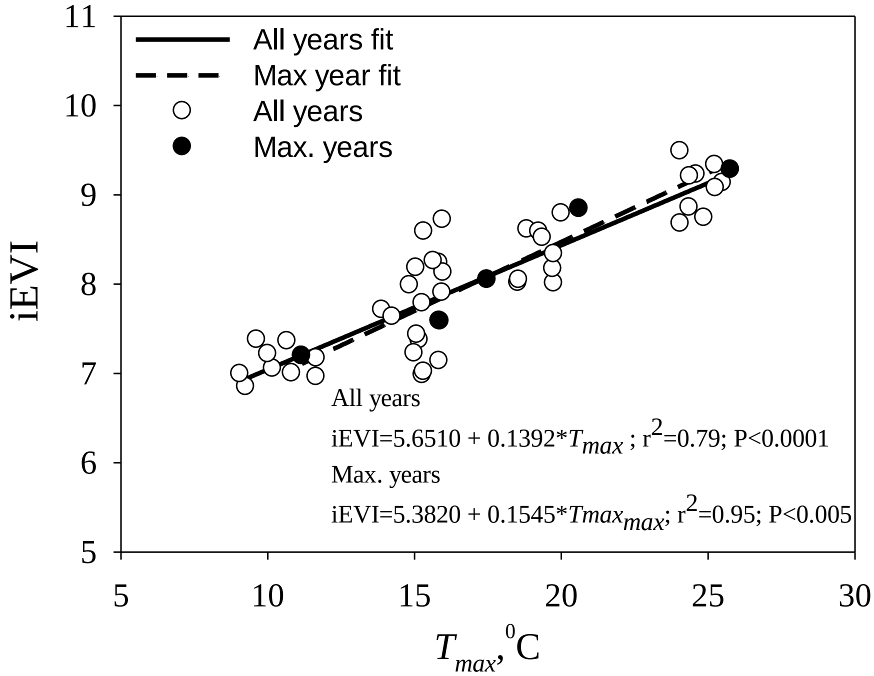

Figure 3. Relations between iEVI and the indices of T_{max} across precipitation regimes and their maximum index-iEVI relation for 4 forested sites. Solid line shows the linear relation between maximum index value and the relevant iEVI for all the sites.

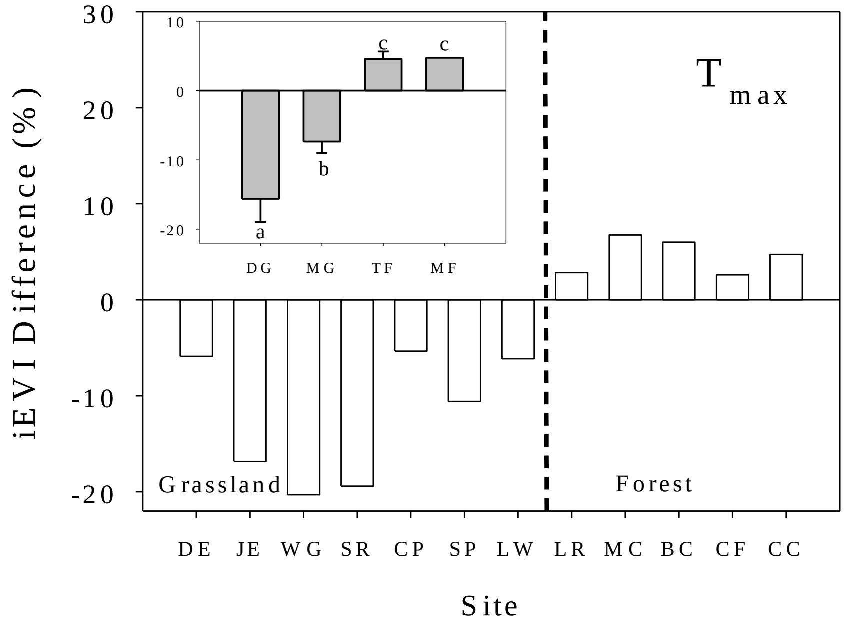

Figure 4. Comparison of iEVI difference between extreme years and average of all other years for T_{max} across sites. Extreme years mean that T_{max} anomaly is ≥1. The inset denotes the average difference by biome type. DG, arid grassland sites (DE, JE, WG, and SR); MG, mesic grassland sites (CP, SP,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

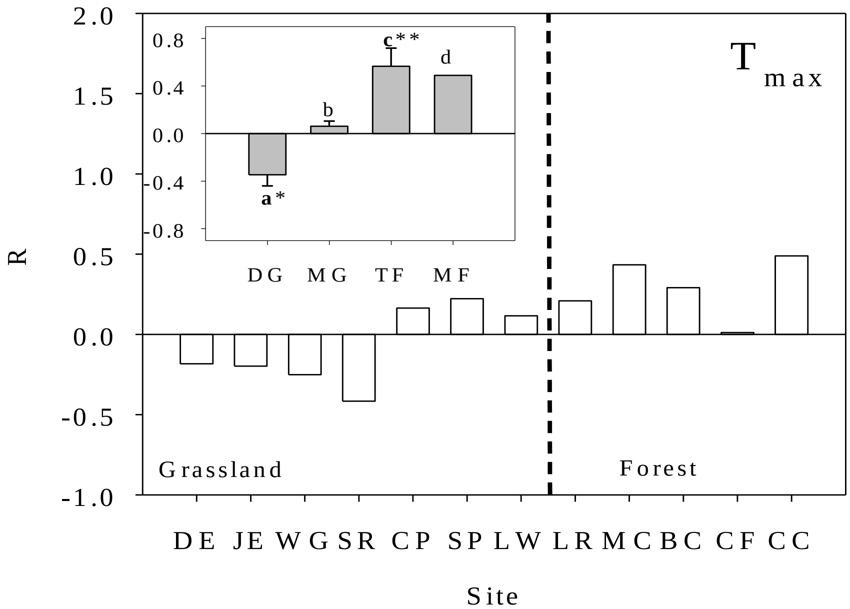

Figure 5. Partial correlation between iEVI and T_{max} after controlling for T_{min} and precipitation across sites. * Statistically significant at the 95% (P<0.05) level; ** statistically significant at the 99.9% (P<0.001) level.