



Short communication

Diverse responses of vegetation production to interannual summer drought in North America

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ABSTRACT

Droughts are projected to occur more frequently with future climate change of rising temperature and low precipitation. However, its impact on regional and global vegetation production is not well understood, which in turn contributes to uncertainties to model carbon sequestration under drought scenarios. Using long-term continuous eddy covariance measurements (168 site-year), we present an analysis of the influences of interannual summer drought on vegetation production across 29 sites representing diverse ecoregions and plant functional types in North America. Results showed that interannual summer drought, which was evaluated by the increase in summer temperature or decrease in soil moisture, would cause reductions of both summer gross primary production (GPP) and net ecosystem production (NEP) in non-forest sites (e.g., grasslands and crops). On the contrary, forest ecosystems presented a very different pattern. For evergreen forests, lower summer soil moisture decreased both GPP and NEP; however, higher summer temperature only reduced NEP with no apparent impacts on GPP. Furthermore, summer drought did not show evident impacts on either summer GPP or NEP in deciduous forests, suggesting a better potential of deciduous forests in resisting summer drought and accumulating carbon from atmosphere. These observations imply diverse responses of vegetation production to interannual summer drought and such features would be useful to improve the strengths and weaknesses of ecosystem models to better comprehend the impacts of summer drought with future climate change.

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1. Introduction

Summer drought is one of the extreme climate events that have shown tremendous impacts on ecosystem processes from both local to regional and global scales (Phillips et al., 2009; Fensharm et al., 2009; Zhao and Running, 2010; Mishra and Singh, 2010; Ledger et al., 2011). The most pronounced drought has reduced 30% of gross primary production (GPP) and resulted in a net carbon source (negative net ecosystem production, NEP) over the whole Europe in 2003 (Ciais et al., 2005).

While the importance of summer drought has been recognized, it is still one of the least understood issues in global environmental change, especially considering its impact on vegetation production (Breshears et al., 2005; Piao et al., 2009; Sowerby et al., 2008; Ledger et al., 2011). A global reduction in net primary production (NPP) has been reported, which is particularly attributed to the frequent drought attacks in the Southern Hemisphere during the last decade

(Zhao and Running, 2010). This report also gives rise to debates on the mechanistic links between drought and vegetation production, which is probably due to the lack of explicit soil moisture dynamics (Samanta et al., 2011). Therefore, there is a pressing need to better understand the drivers of drought as well as their impacts on ecosystem productivity across regions and plant functional types (Mishra and Singh, 2010).

Summer drought can be indicated by extreme weather observations, including the high air temperature, low precipitation, low soil moisture and strong radiation (Peñuelas et al., 2007; Ciais et al., 2005; Easterling et al., 2000; Mishra and Singh, 2010; Wu et al., 2012). Among these indicators, air temperature and soil moisture may exhibit first order on summer drought as evidenced by the correlation between air temperature and radiation as well as the more direct effect of soil moisture on ecosystem processes than precipitation (Weltzin et al., 2003; Knapp et al., 2002; Piao et al., 2009). With long-term (168 site-year) eddy covariance (EC) measurements, we present an analysis on the relationships between summer drought (indicated by temperature and soil moisture) and vegetation production in North America with objectives to (1) understand the impacts of drought on both summer GPP and NEP, and (2) to evaluate such responses across different plant functional types and ecoregions.

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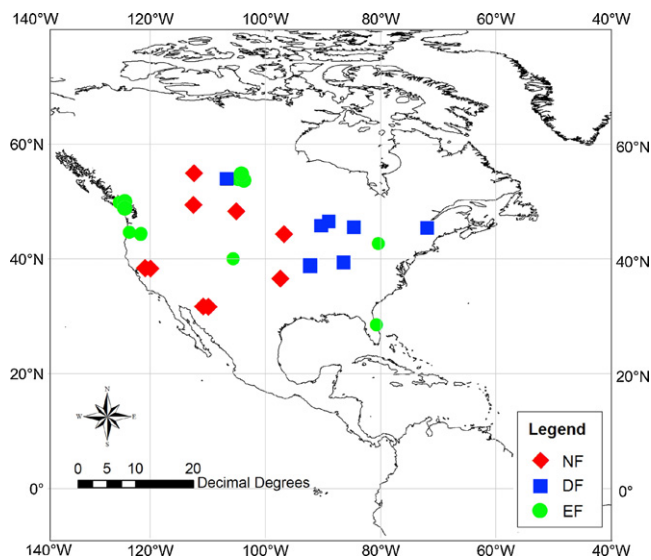


Fig. 1. Spatial distribution of the flux sites in this study. The NF (♦), DF (■) and EF (●) represent non-forests, deciduous forests and evergreen forests, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

2. Materials and methods

2.1. Study sites

The availability of soil water content (SWC, %) restricts the analysis and we therefore identified 29 sites that could provide sufficient data to analyze the influence of summer drought on carbon sequestration in North America (Fig. 1 and Table 1). This broad range of sites provided a wide dynamical range of both carbon fluxes (summer GPP and NEP in ranges of 0–1200 g C m⁻², –200 to 700 g C m⁻², respectively) and meteorological variables (summer temperature and SWC in ranges of 10–28 °C, 4–45%, respectively) and the vegetation can be generally classified into three plant functional types, including the non-forest (NF), deciduous forest (DF) and the evergreen forest (EF) ecosystems. Broadly, the selected sites are representative of many North American biomes.

2.2. Flux measurements and statistical analyses

The flux data for each site employed in this study were downloaded from the AmeriFlux (<http://public.ornl.gov/ameriflux/dataproducts.shtml>) and Fluxnet-Canada Data Information System (<http://www.fluxnet-canada.ca>). For each year, calculations of both carbon fluxes and meteorological measurements were performed from June to August were applied.

For the Canadian sites, a standard procedure was used to estimate NEP and to partition NEP into components of GPP and ecosystem respiration (R_e) from gap-filled half-hourly measurements (Barr et al., 2004). Empirical regressions of nighttime NEE to temperature and daytime GPP to photosynthetically active radiation (PAR) were used to estimate GPP and R_e and fill gaps as discussed in more detail in Barr et al. (2004). For the AmeriFlux sites, level-4 monthly products were used to determine summer GPP, NEP. 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). Flags with information regarding the quality of the original and gap-filled data were also added. Site-level air temperature (T_a , °C) was consistently measured from tower meteorological sensors and on-site SWC was also determined by the gravimetric

methods or time-domain reflectometry (TDR) type probes at a general depth around 0–30 cm, which would slightly differ in individual sites. The mean values from June to August for these two variables were calculated to represent the summer temperature and SWC.

The impacts of interannual summer drought on carbon fluxes were analyzed using year-to-year anomalies of both variables considering their different dynamic ranges across sites and regions. The pairwise Pearson coefficient (r) and p -value were used to evaluate these correlations. In particular, these correlations were also separated by plant functional types, i.e., both for all NF sites (33 site-year), DF sites (31 site-year) and EF sites (74 site-year).

3. Results

Summer drought showed evident impacts on the carbon fluxes in NF ecosystems (Fig. 2). Significant negative correlations were acquired between temperature anomaly and both GPP ($r = -0.48$, $p = 0.003$) and NEP ($r = -0.47$, $p = 0.004$) anomalies. Generally, high summer temperature dramatically reduced both GPP and NEP at the rates of 35.8 g C m⁻² and 20.9 g C m⁻² per degree increase in temperature. Soil moisture was also found to be closely correlated with carbon fluxes with r of 0.60 ($p < 0.001$) and 0.61 ($p < 0.001$) for summer GPP and NEP, respectively. One percentage decrease in SWC would lead to reductions in both GPP and NEP by 13.7 g C m⁻² and 8.1 g C m⁻² in summer.

Forest ecosystems showed complex patterns in the responses to summer drought. Deciduous forest sites exhibited unexpected patterns when summer temperature and SWC were explored to correlate with both GPP and NEP (Fig. 3). With our dataset, no significant correlations were observed between carbon fluxes and either of these two variables, potentially implying that both GPP and NEP are insensitive to interannual variations in temperature and soil moisture. In contrast, the responses of carbon fluxes to summer drought in evergreen forests depended on the drought indicators (Fig. 4). While no relationship was identified between interannual variability in GPP and temperature, interannual NEP showed an evident decrease in warmer summers ($r = -0.45$, $p < 0.001$). When considering the soil moisture, it showed consistent positive impacts on both GPP and NEP with r of 0.39 ($p < 0.001$) and 0.48 ($p < 0.001$), respectively, indicating that the decrease in SWC also reduces GPP and NEP.

4. Discussion and conclusions

Modeling drought impacts needs sophisticated understanding of the role of soil moisture in regulating ecological processes, which is probably not well considered in existing ecosystem models (Samanta et al., 2011). This consideration also helps to better interpret carbon fluxes under drought scenarios. Our regional analysis based on flux measurements indicates that the soil moisture is a better indicator than the temperature in linking interannual summer drought and ecosystem carbon fluxes as higher correlations were observed, excluding both weak performances for deciduous forests. The temperature alone seems insufficient to address summer drought, probably due to more evident impacts of water stress than temperature on photosynthesis in summer (Garbulsky et al., 2008). This is consistent with previous studies emphasizing the importance of SWC in explaining summer drought (Piao et al., 2009; Weltzin et al., 2003). An interesting result is that for non-forest and evergreen forest where the SWC is correlated with both GPP and NEP, the relative rate of decrease NEP in relative to GPP is very similar with ratio of 59.1% and 59.7%, respectively. This observation suggests that the proportion of GPP being transferred into NEP during summer drought is quite close,

Table 1
Descriptions of study sites in this analysis.

| Site ID | Land cover | Latitude | Longitude | Regional climate | Data range |
|---------------------|-----------------------|----------|-----------|---------------------------|------------|
| CA-GRA | Grassland | 49.43 | -112.56 | Temperate-Continental | 1999–2005 |
| US-FPE | Grassland | 48.31 | -105.10 | Dry (arid and semi arid) | 2003–2006 |
| US-TON | Savanna | 38.43 | -120.97 | Subtropical-Mediterranean | 2001–2007 |
| US-VAR | Grassland | 38.41 | -120.95 | Subtropical-Mediterranean | 2001–2007 |
| CA-FEN | Wetland | 54.95 | -112.47 | Boreal | 2006–2008 |
| US-WKG | Grassland | 31.74 | -109.94 | Dry (arid and semi arid) | 2004–2007 |
| US-ARM | Crop | 36.61 | -97.49 | Subtropical-Mediterranean | 2003–2006 |
| US-BKG | Grassland | 44.34 | -96.84 | Temperate | 2004–2006 |
| US-SRM | Savanna | 31.82 | -110.87 | Dry (arid and semi arid) | 2004–2006 |
| US-SYV | Deciduous broad-leaf | 46.24 | -89.35 | Temperate-Continental | 2002–2006 |
| CA-OAS | Deciduous broad-leaf | 53.63 | -106.19 | Boreal | 2002–2009 |
| US-MOZ | Deciduous broad-leaf | 38.74 | -92.20 | Subtropical-Mediterranean | 2004–2007 |
| US-BAR | Deciduous broad-leaf | 44.06 | -71.29 | Temperate-Continental | 2004–2006 |
| US-MMS ^a | Deciduous broad-leaf | 39.32 | -86.41 | Subtropical-Mediterranean | 2003–2008 |
| US-UMB | Deciduous broad-leaf | 45.56 | -84.71 | Temperate-Continental | 2002–2006 |
| US-WCR | Deciduous broad-leaf | 45.8 | -90.08 | Temperate-Continental | 1999–2006 |
| US-NR1 | Evergreen needle-leaf | 40.03 | -105.55 | Boreal | 2002–2005 |
| CA-OBS | Evergreen needle-leaf | 53.99 | -105.12 | Boreal | 1999–2009 |
| CA-OJP | Evergreen needle-leaf | 53.92 | -104.69 | Boreal | 2000–2008 |
| US-ME2 | Evergreen needle-leaf | 44.45 | -121.56 | Subtropical-Mediterranean | 2002–2010 |
| US-ME3 | Evergreen needle-leaf | 44.31 | -121.61 | Subtropical-Mediterranean | 2004–2008 |
| CA-DF49 | Evergreen needle-leaf | 49.87 | -125.33 | Temperate | 1999–2009 |
| CA-DF88 | Evergreen needle-leaf | 49.53 | -124.90 | Temperate | 2002–2009 |
| CA-DF00 | Evergreen needle-leaf | 49.87 | -125.29 | Boreal | 2001–2009 |
| US-KS2 | Evergreen broad-leaf | 28.61 | -80.67 | Subtropical-Mediterranean | 2003–2006 |
| CA-TP39 | Evergreen needle-leaf | 42.71 | -80.36 | Temperate | 2003–2007 |
| CA-HJP94 | Evergreen needle-leaf | 53.91 | -104.66 | Boreal | 2002–2005 |
| CA-HJP02 | Evergreen needle-leaf | 53.94 | -104.65 | Boreal | 2004–2008 |
| US-MRF | Evergreen needle-leaf | 44.65 | -123.55 | Subtropical-Mediterranean | 2007–2009 |

^a Data unavailable for 2005.

irrespective of different magnitudes in either GPP or NEP between non-forest and evergreen forest ecosystems. We still cannot explain this observation, which possibly implies some unknown mechanisms that regulate drought and carbon sequestration.

Our results show that the responses of carbon fluxes to summer drought differ substantially among plant functional types. Carbon fluxes in non-forest ecosystems show the highest sensitivity to interannual variations of summer drought, either from the

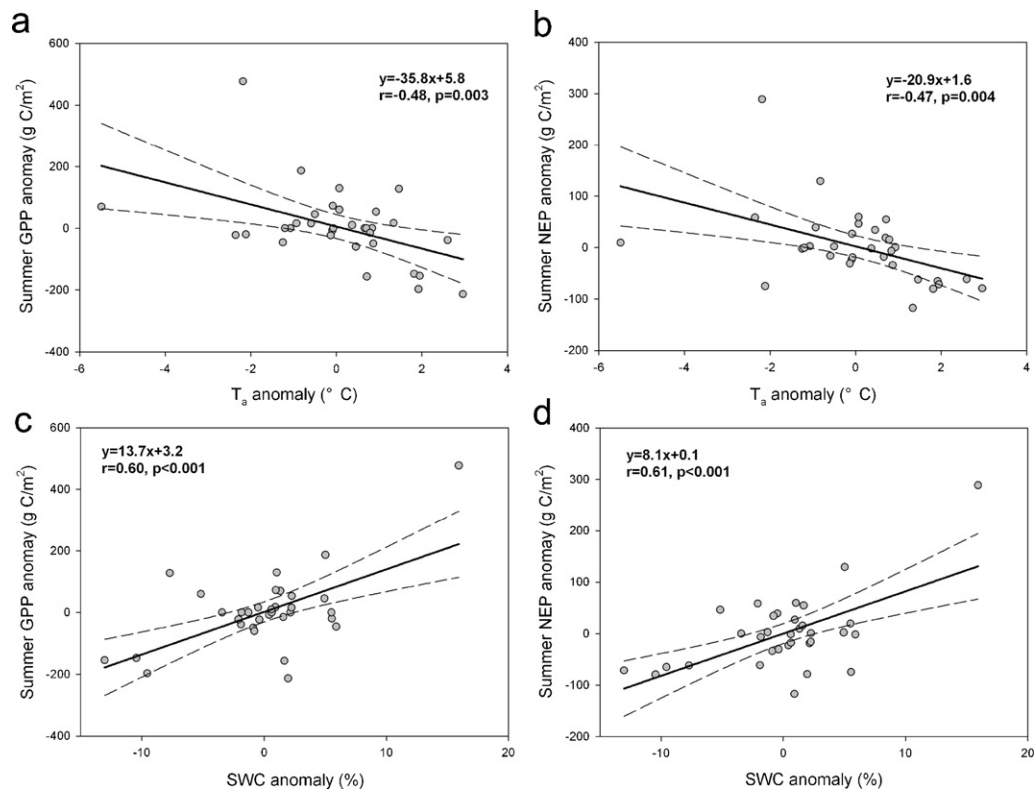


Fig. 2. Relationships between summer temperature anomaly and (a) summer gross primary production (GPP) anomaly, (b) summer net ecosystem production (NEP) anomaly in non-forest ecosystems; relationship between summer soil water content (SWC) anomaly and (c) summer GPP anomaly, (d) summer NEP anomaly in non-forest ecosystems.

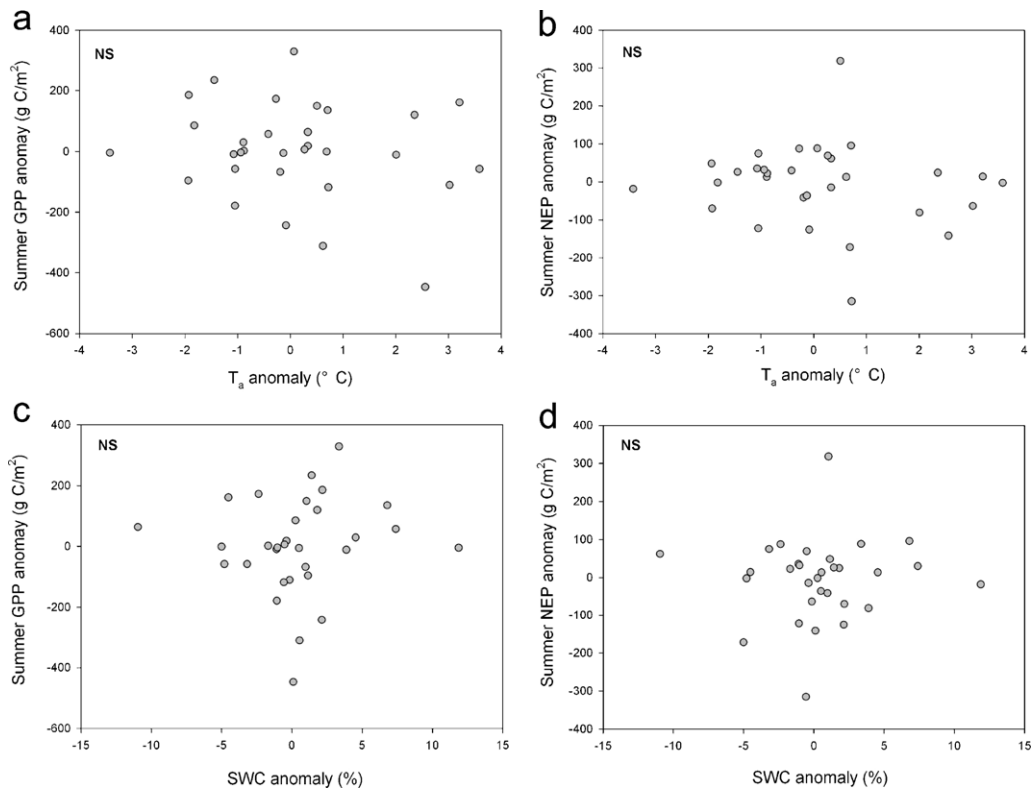


Fig. 3. Relationships between summer temperature anomaly and (a) summer gross primary production (GPP) anomaly, (b) summer net ecosystem production (NEP) anomaly in deciduous forest ecosystems; relationship between summer soil water content (SWC) anomaly and (c) summer GPP anomaly, (d) summer NEP anomaly in deciduous forest ecosystems. NS represents no significant correlation.

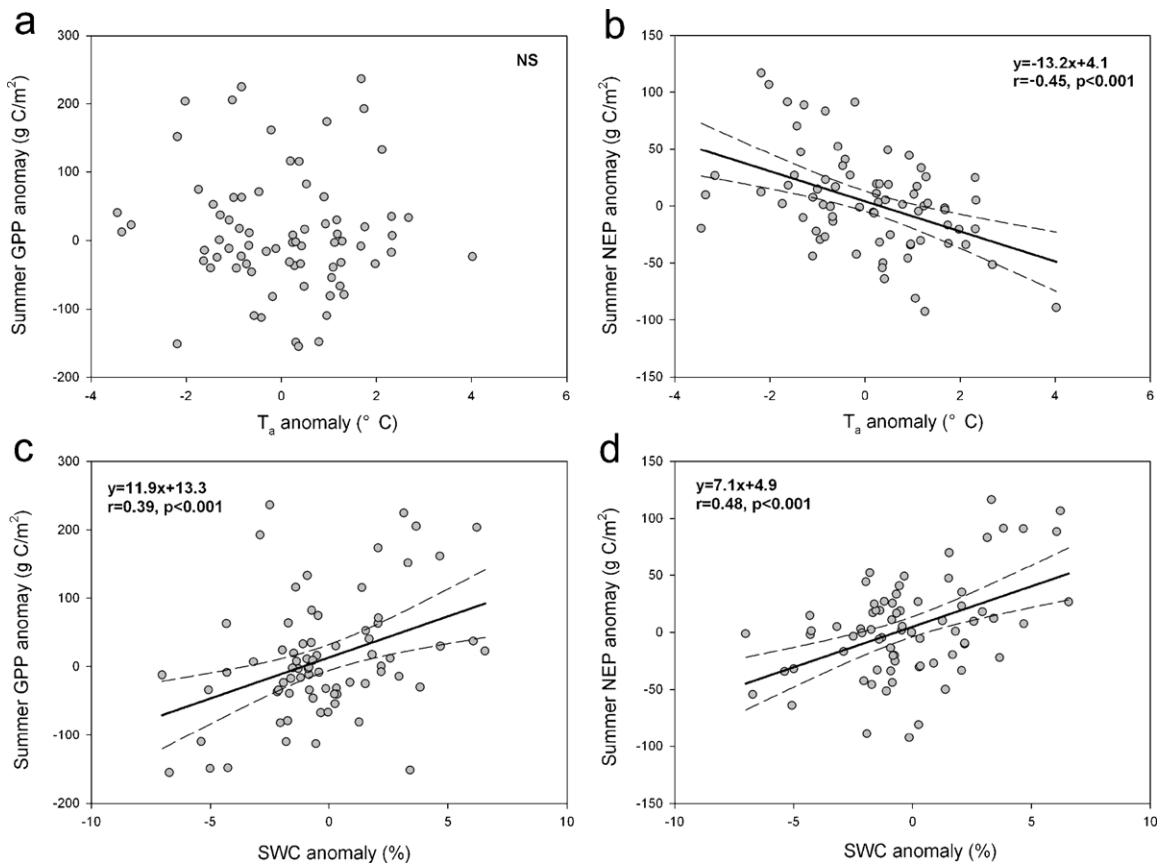


Fig. 4. Relationships between summer temperature anomaly and (a) summer gross primary production (GPP) anomaly, (b) summer net ecosystem production (NEP) anomaly in evergreen forest ecosystems; relationship between summer soil water content (SWC) anomaly and (c) summer GPP anomaly, (d) summer NEP anomaly in evergreen forest ecosystems. NS represents no significant correlation.

perspective of temperature or soil moisture, which can be supported from larger slopes of the respective correlations. Some reasons are provided to interpret such responses. Non-forest ecosystems (e.g., grasslands and crops) do not have much capability in resisting severe drought and they are water sensitive. For example, they cannot obtain water from deeper soil layers with their shadow roots during summer drought compared with forest ecosystems and thus carbon fluxes (both GPP and NEP) would be greatly reduced. For summers with sufficient soil moisture and favorable temperatures, they also tend to respond more rapidly and both GPP and NEP will increase. This high sensitivity has been demonstrated in previous study of Huxman et al. (2004) and would contribute in two aspects, the larger slopes of these correlations as well as much stronger relationships.

Different forest types also lead to the diverse responses of carbon fluxes to summer drought, especially considering the deciduous forests that show low insensitivity to interannual variation of summer drought. Previous report from Welp et al. (2007) also indicates the different sensitivity between deciduous and evergreen forests to summer drought and suggests a greater variation of carbon balance in deciduous forests. However, with our dataset from a wider range of sites and regions, it is difficult to predict the directions of either GPP or NEP with only summer temperature or SWC, indicating a distinct feature of deciduous forests in resisting drought stress. Furthermore, this feature may also be greatly influenced by site specific soil properties, including soil structures, chemical compositions (Ledger et al., 2011). Interannual variability of GPP in evergreen sites does not seem to be correlated with summer temperature, but we observe a reduction in the summer NEP, suggesting an increase in the ecosystem respiration which, on the contrary, is not supported by the data ($r=0.15$, $p=0.207$). These observations imply the high spatial heterogeneity of carbon sequestration to summer drought, even when such analysis is restricted to forest landscape, which agrees with the previously reported nonuniform effects of growth rates during summer drought both at sites (Pasho et al., 2011) and regions (Anchukaitis et al., 2006).

One useful implication from different responses in forests is that the deciduous forests may hold the potential to be more resistant to interannual summer drought without evidently losing the capability of sequestration carbon from atmosphere. However, the evergreen forests would reduce such potential greatly as evidenced by the correlations between NEP anomaly and both temperature and SWC anomalies. We suggest that this response probably adds more weights on the claim that future climate change would favor deciduous forests over evergreen forests in the perspective of phenology (Richardson et al., 2009). Most importantly, these analyses suggest the diverse responses of interannual carbon sequestration to summer drought across plant functional types, contributing difficulties in analyzing drought effects globally. However, such knowledge would be useful in assessing future drought properly and gain a better understanding of underlying mechanisms related to summer drought that can improve the strengths and weaknesses of future ecosystem models.

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