LETTER

Divergent responses of ecosystem water use efficiency to drought timing over Northern Eurasia

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Abstract

Warming has resulted in increases in frequency, intensity and/or duration of droughts in most land regions over the globe. Nevertheless, knowledge on how ecosystem water use efficiency (WUE) responds to extreme drought stress and whether the responses are affected by drought timing is still limited. In this study, we examined the changes in ecosystem WUE under extreme drought years over Northern Eurasia during 1982–2011 and further assessed WUE responses to droughts with separate groupings designed to characterize the timing of extreme drought stress. We found that drought timing indeed influenced the responses of ecosystem WUE under extreme drought years. Negative impacts of extreme drought stress during the dry season on ecosystem WUE were more remarkable than those from extreme drought stress during the wet season. Particularly, impacts of droughts on ecosystem carbon–water interactions differed among ecosystem types due to the specific hydrothermal condition of each biome. The information provided by our analyses plays an important role in identifying water use strategies of terrestrial vegetation in response to drought stress and will help improve our understanding and predictions of the response of ecosystem WUE to global environmental change.

1. Introduction

Since the pre-industrial, global mean surface temperature has increased by about 0.87 °C with a more remarkable warming in global land surface temperature (1.53 °C) (IPCC 2018). Confronted by climate change, the frequency, intensity and/or duration of droughts has increased in some regions including the Mediterranean, North Africa and Middle East (Vicente-Serrano et al 2014, Spinoni et al 2015, Dai and Zhao 2017, Páscoa et al 2017), northeastern China (Spinoni et al 2019), parts of South America (Fu et al 2013) and much of sub-Saharan Africa (Masih et al 2014, Dai and Zhao 2017). These changes have dramatically impacted terrestrial ecosystems, food security and land processes including greenhouse gas fluxes, and could bring about severe challenges for vegetation growth, especially in northern high latitudes where vegetation growth is sensitive to climate change (Vitasse et al 2009, Wolkovich et al 2012, Buitenwerf et al 2015).

Water use efficiency (WUE), which is usually represented as an integrated physiological metric for monitoring the changes in carbon and water exchanges (Huang et al 2015, Frank et al 2015a, Yang et al 2016), largely determines whether vegetation could survive under severe drought stress. At the leaf level, transpiration and photosynthesis are tightly coupled via leaf stomatal conductance and the various stress factors (e.g. soil drought, frost, heatwave) that affect leaf functioning (Sun et al 2015). The ratio of instantaneous photosynthesis to transpiration defines
leaf-scale WUE, which is a critical indicator of the amount of carbon assimilation per unit of water loss (Keenan et al. 2013, Medlyn et al. 2017). At the ecosystem scale, WUE is generally defined as the ratio of gross primary productivity (GPP) and evapotranspiration (ET) (Ponton et al. 2006, Yu et al. 2008, Beer et al. 2009, Hu et al. 2010, Zhu et al. 2011, Huang et al. 2015, 2016). It indicates the coupling of the carbon and water gross exchanges between ecosystem and the atmosphere, and reflects the adaptability of an ecosystem to variable climate conditions (Huang et al. 2015).

Previous studies have concluded a significant positive trend in WUE in most areas of terrestrial ecosystems over the globe, as a result of the increasing atmospheric CO2 concentration and climate change during the past several decades. At the same time, extreme climatic events, such as drought, extreme precipitation, heat wave etc. occurred in a large part of the globe with increasing frequency and intensity as suggested above (IPCC 2019). These changes have likely altered the ecological functioning of terrestrial ecosystems and the structure of plant communities, potentially affecting the coupling relationship between terrestrial carbon and water cycles. Recently, many attempts have been implemented to examine drought impacts on carbon–water interactions (e.g. Yang et al. 2016, Peters et al. 2018, Ahmadi et al. 2019, Boese et al. 2019, Zhang et al. 2019, Green et al. 2020, Wang et al. 2020a). However, the relationships between ecosystem WUE and droughts vary dramatically across different vegetation types and environmental conditions. For instance, annual WUE increased under drought in Northeast China and central Inner Mongolia but decreased in Central China (Liu et al. 2015). For Eurasian temperature grasslands, which locates in the middle Eurasia continent, drought enhanced ecosystem WUE for over 65% of this region (Chen et al. 2017). Using two observational WUE datasets, Yang et al. (2016) further provided a global synthesis of ecosystem WUE responses to drought and highlighted an obviously contrasting WUE responses to drought across ecosystems. They showed that WUE increases with drought in arid ecosystems but decreases in semi-arid/sub-humid ecosystems, which can be attributed to different sensitivities of ecosystem processes to changes in hydro-climatic conditions (Yang et al. 2016).

particularly, several studies have indicated a ‘two-stage’ WUE-drought relationship in certain regions. For example, Lu and Zhuang (2010) found that ecosystem WUE in the conterminous United States tended to increase under moderate drought but decrease under severe drought. In North China, slight and moderate drought enhanced ecosystem WUE while severe and extreme drought resulted in WUE reductions regardless of different hydroclimatic conditions and biomes (Xu et al. 2019). For South China, however, moderate and extreme drought reduced annual WUE and severe drought slightly increased annual WUE, suggesting a ‘turning point’ in WUE-drought relationship (Liu et al. 2015). In contrast, positive WUE responses to severe and extreme drought occurred across land biomes in California (Malone et al. 2016) and in the forest ecosystem in Southwest China (Zhou et al. 2018). Spatially coherent increases in intrinsic WUE were also observed over the Northern Hemisphere during severe droughts that affected Europe, Russia and the United States in 2001–2011 (Peters et al. 2018). Despite low likelihood of occurrence, extreme drought can have dramatic impacts on ecosystems and pose a threat to vegetation growth. But our current knowledge on how terrestrial ecosystem WUE responds to extreme drought remains controversial and is incomplete for a range of systems, because the results are primarily based on local- to regional-scale observations and data.

More importantly, the mode, direction, as well as magnitude of drought impacts on ecosystems could vary greatly due to the pronounced seasonal cycle of many ecosystem and land use (Misson et al. 2010, 2011, Camarero et al. 2015b, Huang et al. 2018). More recently, evidence emerged from regional-scale studies indicating divergent responses of ecosystem WUE to seasonal droughts (Song et al. 2019, Wang et al. 2020a). For example, Wang et al. (2020a) reported divergent responses of ecosystem WUE to extreme droughts according to the occurrence time by comparing WUE variations under the 2009/2010 autumn–spring drought and the 2011 summer drought in Southwest China. They observed that WUE increased during the early stage of autumn–spring drought and then decreased during the peak period, whereas summer drought led to negative WUE anomalies nearly throughout the drought duration (Wang et al. 2020a). These findings suggest that the expected magnitude of drought impacts on WUE possibly depends on the timing of droughts. Even so, drought timing influence on the WUE-drought relationships and its underlying mechanism are still poorly understood.

Northern Eurasia is undergoing significant changes associated with climate warming and is among regions that are projected to warm most by the end of 21st century (IPCC 2013). Drought could become more severe over Northern Eurasia in the future, potentially exerting profound impacts on the carbon-water coupling of terrestrial ecosystems. Unfortunately, a consensus of WUE responses to extreme droughts has not been achieved across multiple ecosystems over this region, and little information is known about the effects of drought timing.

In this study, we examined how WUE responded to extreme drought stress over Northern Eurasia. We attempted to address the following questions: (a) how ecosystem WUE responses to extreme drought stress differ among ecosystem types? (b) do drought effects on ecosystem WUE vary among drought stresses with different timing? (c) if so, how does drought
timed impact and the magnitude of drought impacts on WUE? Addressing these questions will help improve current understanding of drought impacts on vegetation growth, and is of great importance to improving projecting impacts of extreme drought stress on terrestrial ecosystems under future climate change.

2. Data and methods

2.1. Study region

This study focuses on the vegetated regions over Eurasia north of 30° N, generally covering the Northern Eurasia region which accounts for ~20% of the global land mass. In this region, biogeophysical and biogeochemical feedbacks from changes in surface energy, water, and carbon budgets under climate change play an important role in global changes.

2.2. Climate dataset and drought metric

As one of the most biologically relevant drought variables aiming to characterize drought impacts in terms of plant water stress, climatic water deficit (CWD) has been widely used as a climatic indicator for aridity and to predict vegetation presence and growth rates (Stephenson 1998, Lutz et al 2010, Anderegg et al 2015). In this study, we first calculated CWD as drought metric using gridded precipitation and potential ET (PET) datasets from Climatic Research Unit (CRU). Monthly precipitation and PET data were both derived from CRU TS v4.03 datasets (Harris et al 2014) for the period 1901–2018 at the spatial resolution of 0.5° × 0.5°. Considering the available datasets for WUE calculation (see also section 2.4), this study only focuses on the entire period of overlap for all datasets (i.e. from 1982 to 2011). Monthly CWD values were then calculated as monthly precipitation minus monthly PET during 1982–2012, and then aggregated to obtain annual CWD values. Although climatic water balance can also be measured by precipitation minus ET (P−ET), we did not adopt this metric since P−ET are generally used to assess changes in runoff (hydrological drought) rather than soil moisture (agricultural) drought that is closely related to vegetation growth (Vogt et al 2018, Liu et al 2020). To examine changes in temperature during extreme drought years, the mean annual temperature during 1982–2011 was derived from monthly temperature data from CRU TS v4.03 dataset with a spatial resolution of 0.5° × 0.5°.

2.3. Detection of extreme drought stress and its timing

To detect drought year, for each pixel in the gridded CWD map, we obtained the detrended anomalies of drought metric (i.e. CWD) series during 1982–2011. Following Zscheischler et al (2013, 2014), long-term linear trend was removed from the CWD series with the aim of removing the change in mean climate state and focusing on interannual CWD variations for extreme drought detection. Thereafter an ‘extreme drought year’ is defined as the year with detrended anomaly of CWD exceeding two standard deviations (2-SD dry anomaly) (Anderegg et al 2015, Huang et al 2018), indicating the bottom 2.3% of CWD anomalies during the study period assuming a normal distribution. To verify the universality and reliability of this approach of extreme drought detection, one pixel was selected from Europe (47° N, 6° E). Using this approach, the Europe-wide extreme heat and drought in 2003 (Ciais et al 2005, Leuzinger et al 2005, Revetez et al 2006) was successfully and correctly captured (figure S1 (available online at stacks.iop.org/ERL/16/045016/mmedia)).

Extreme drought years detected above were divided into three groups according to whether each extreme drought year was induced by water stress during the dry and/or wet season. Note that in this study, the (relatively) dry/wet season was determined by water availability for vegetation using CWD because most of the study region does not have a typical monsoon climate with clear dry and rainy seasons. Following Li and Fu (2002), for each pixel, the dry season arrives at the first month when the monthly CWD value is detected to change from above to below the annual mean CWD, and vice versa for the wet season arrival (Li and Fu 2002). Based on this, monthly CWD values were averaged over the dry (wet) season to get the annual series mean CWD during dry (wet) season. In this condition, an extreme drought year was classified into three categories according to whether the detrended anomaly of mean CWD during dry and/or wet season exceeds one standard deviation (1 SD dry anomaly). These three categories included: (a) extreme drought years with both dry and wet season droughts (DS + WS droughts), (b) extreme drought years with only dry season droughts (DS droughts), and (c) extreme drought years with only wet season droughts (WS droughts).

2.4. Quantification of WUE and its response to extreme drought stress

Ecosystem WUE, as an indicator of the adjustment of vegetation photosynthesis to water loss at ecosystem scale, is defined as the ratio between GPP and ET as widely used in previous studies (e.g. Zhu et al 2011, Huang et al 2015, Sun et al 2015, Yang et al 2016, Xu et al 2019). Here, GPP refers to the sum of gross carbon uptake by vegetation photosynthesis (Chapin et al 2011). ET, which is the sum of transpiration, canopy interception evaporation, and soil evaporation, is used as the indicator of ecosystem water loss considering the infeasibility of distinguishing these three components (Huang et al 2016, Wang et al 2020b).

Global gridded datasets of estimated GPP and latent heat (LE) were downloaded from the Department
of Biogeochemical Integration of Max Planck Institute (MPI) (www.bgc-jena.mpg.de/geodb/projects/Data.php) with a 0.5° × 0.5° spatial resolution and a monthly temporal resolution from 1982 to 2011. The GPP/LE data from MPI is the so far only data-oriented GPP/LE product with continuous spatial coverage and the longest time span (i.e. 1982–2011). Model tree ensemble approach was applied for GPP/LE estimation based on monthly FLUXNET eddy-covariance observations (Jung et al 2015). It is a machine learning model that upscales flux tower measurements of GPP/LE to the global scale using satellite fraction of absorbed photosynthetic active radiation global time varying maps, climate fields, and land-cover datasets (Jung et al 2015). Following Tang et al (2014), ET was converted from LE units based on the formula \( ET = LE/\lambda \) (\( \lambda = 2454 \text{ J g}^{-1} \)) and then used for WUE calculation. Monthly GPP/ET values were aggregated over the course of each year to obtain annual GPP/ET values for annual WUE calculation as this study aims to examine the impacts of extreme drought years on annual WUE.

In order to quantify the WUE response to extreme drought years, for each grid cell and each extreme drought year, we calculated the standardized anomaly of WUE during the extreme drought year. To explore the effects of drought timing on WUE responses to extreme droughts, standardized WUE anomalies were averaged across all extreme drought events for each of the three types of extreme drought years. Analysis of variance was conducted to determine whether there is a statistically significant \( P < 0.05 \) difference regarding WUE responses between different drought types. Note that only single drought (no extreme drought year detected within 3 years before or post an extreme drought year) were considered in this study.

2.5. Land cover types classification

Land cover types were defined based on the International Geosphere–Biosphere Program (IGBP) based on a MODIS land cover classification (https://webmap.ornl.gov/wcsdown/wcsdown.jsp?dg_id=10011_1) when comparing WUE responses for different land cover types. Land cover types from IGBP were first reclassified into seven vegetation types: evergreen needle-leaved forest (ENF), deciduous needle-leaved forest (DNF), deciduous broadleafed forest (DBF), mixed forest (MF), grassland, shrubland and cropland (CRO). Then, grassland was further subdivided into temperate grassland (TGR), boreal and arctic grassland (BGR), and shrubland was further subdivided into temperate (TSH) and boreal shrubland (BSH) following the global climate map of Köppen–Geiger climatic classification (Kottek et al 2006). Urban and build-up regions were excluded in our analysis using IGBP land cover data. The grid cells with an annual mean normalized difference vegetation index (NDVI; derived from the advanced very high resolution radiometer sensors) being less than 0.1 are excluded from analyses in order to remove areas with very low ecosystem productivity.

3. Results and discussions

3.1. WUE responses to extreme drought stress over Northern Eurasia

Extreme drought years can be detected over 40% of the study area during 1982–2011. The majority (90%) of these regions experienced only one extreme drought year during the study period, while only a small part of these regions showed more than two extreme drought events (figure 1(a)). Further analyses show that the annual total precipitation is markedly lower than normal for almost all regions during detected extreme drought years, with about 55% of these regions showing precipitation anomalies exceeding two SD (figure 1(b)). For about 21% of the regions with detected extreme droughts, extreme drought years were accompanied by anomalous high temperature stresses (annual mean temperature anomalies exceeding one SD) (figure 1(c)). Particularly, extreme drought years with extreme high temperatures (temperature anomalies exceeding 1.5 SD) can be observed in parts of Western Siberia, Northeast China and parts of Northern and Eastern Europe.

Ponce-Campos et al (2013) pointed out that ecosystem WUE (defined as the ratio between above-ground net primary production to ET) is conservative across different biomes. They also found higher WUE in drier years with WUE increasing to a maximum value during drought and decreasing to a minimum value in wet years. Their research also indicates hydroclimatic thresholds, beyond which the ecosystem resilience breaks down as biomes endure the significant drought-induced mortality under extreme drought conditions (Ponce-Campos et al 2013).

This study examined changes in the ecosystem WUE during the detected extreme drought years over Eurasia north of 30° N (figure 2). Ecosystem WUE decreased below one SD over about 26% of these regions, among which negative WUE anomalies over two SD are mainly found in Central Asia, parts of Western and Central Europe, Western Siberia and Northeast China. This result is in support of findings by Ponce-Campos et al (2013) that extreme drought would reduce ecosystem WUE. Further analyses combing changes in ecosystem WUE, GPP and ET (figure S2) during extreme drought years suggest divergent underlying processes of WUE responses to extreme droughts across the study area. Overall, WUE responses to extreme droughts seems to be generally reflected by GPP changes under extreme drought stresses (figure 2(b)). For regions with decreased WUE during extreme drought years, GPP were much more remarkably influenced by droughts than ET and eventually resulted in decreased WUE. This may be because the water availability is a primary limitation...
Figure 1. Spatial distribution of the numbers of extreme drought years detected during 1982–2011 (a) and the standardized anomalies of precipitation (b) and temperature (c) during extreme drought years. The extreme drought year was detected based on climatic water deficit (CWD) values, which is calculated as precipitation minus potential evapotranspiration. Change in precipitation (temperature) during extreme drought years compared with normal years is indicated by the standardized anomaly of total precipitation (mean temperature). Black points mark regions with very low ecosystem productivity that are excluded in this study. For panel (b) and (c), 0.5, 1, 1.5, 2 positive (negative) standardized anomalies refer to the top (bottom) 30%, 15.9%, 6.7%, 2.3% anomalies during 1982–2011 assuming a normal distribution.

for vegetation growth in these regions with relatively dry climatic conditions (Knapp and Smith 2001, Nemani et al 2003, Bai et al 2008). In this case, extreme drought further aggravated water stresses or even led to plant mortality (Eamus et al 2013), therefore largely reducing vegetation productivity (Ciais et al 2005, Leuzinger et al 2005, Brêda et al 2006, Schwalm et al 2012).

By contrast, it should be noted that increased ecosystem WUE above normal ranges (exceeding one SD) are also observed in northern high latitudes (north of 50° N), such as parts of Northern Europe as well as Western and Central Siberia (figure 2(a)). Composing maps in figure 2(b) show that such higher than for normal years ecosystem WUE was also dominated by more significantly enhanced GPP than ET during droughts. In these regions, high temperature events concurrent with droughts (figure 1(c)) possibly leaded to melting of frozen soil, consequently mitigating soil water stress and increasing nutrient availability (Mazzarino et al 1991). Decreased precipitation (figure 1(b)) in extreme drought years also suggests increased solar radiation reaching the land surface. These may partly alleviate limitations to vegetation photosynthesis due to low temperature and insufficient solar radiation in these high latitude regions (Nemani et al 2003) and thus benefits ecosystem WUE despite droughts.
3.2. Influences of drought timing on WUE responses to extreme drought stress

Several recent researches have pointed out that the expected magnitude of drought impacts on terrestrial ecosystem likely depends on the timing of drought events (Camarero et al. 2015b, Huang et al. 2018). In this study, we further compared whether ecosystem WUE responses differ according to drought timing over the study region. We show that DS droughts had a significantly ($p < 0.05$) larger negative effects on ecosystem WUE than DS + WS droughts (figure 3(a)). On average, the negative WUE departure from DS droughts ($-0.459$) was more than twice the magnitude of WUE departure from DS + WS droughts ($-0.202$). By contrast, ecosystem WUE was slightly above the mean value (0.085 SD) under WS droughts during the study period.

However, there may still exist a risk that the drought timing effects on the WUE responses to extreme drought stress may be confounded by plant phenology, considering that for more than 80% of the study area with detected extreme drought years, at least 60% of the length of DS overlapped with the growing season of the local vegetation. Therefore, we further compared WUE changes between drought years with different drought timing only for regions where the dry season overlaps with the period photosynthesis (Zhu et al. 2016) for local vegetation for less than 70% of dry season (31% of the current study area). Similar results are observed as shown in figure S3, suggesting our conclusion is robust to interactions between growing season and dry/wet seasons.

Combining GPP and ET changes during the three different types of extreme drought years (figures 3(b) and (c)), DS + WS droughts suppressed GPP more remarkably than ET, hence leading to the observed negative WUE anomalies during these periods. During DS droughts, the negative WUE anomalies resulted from relatively decreased GPP and increased ET under extreme drought stress. The inhibitions of ecosystem productivity from DS and DS + WS droughts are more profound compared with WS droughts (figure 3(b)) could result from the fact that dry season overlaps with the period of active vegetation growth more than wet season across most of the study area (figure S4). During WS droughts, positive WUE anomalies were due to slightly increased GPP but decreased ET during these periods. On the one hand, due to the relatively more sufficient water availability during the wet season, drought stresses would not exceed the hydroclimatic threshold that may break down the coupling relationship between carbon and water cycle as suggested by Ponce-Campos et al (2013). According to their results, the plant water use strategies are not changed, that is, for individual plants, the amount of photosynthetic assimilation per
unit of water loss through leaf transpiration is kept consistent or even slightly increased. On the other hand, reduced precipitation during the wet season suggests decreased water loss from canopy interception and evaporation from bare soil, eventually ET (figure 3(c)). All these processes could lead to the positive WUE anomalies during WS droughts.

3.3. WUE responses to extreme drought stress for different land cover types

WUE responses to extreme drought stress could be largely divergent among ecosystems considering their different background climate conditions. Hence, we further compared ecosystem WUE responses to extreme drought stress for nine major land cover types (see section 2) across the study regions (figure 4). The results suggest that grassland ecosystems (TGA and BGA, mainly in drylands of the middle part of the Eurasian continent) experienced substantially reduced WUE with more profound suppression in GPP than ET during extreme drought years compared with normal years. This result contrasts with that from Chen et al (2017), which suggests that WUE over temperate Eurasian Steppe tended to increase under drought due to larger reduction of ET than GPP. Such distinction may result from the fact that Chen et al (2017) investigated WUE changes along with a temporally drying trend, whereas our analyses focused on extreme drought years, which could largely reduce plant photosynthesis within a short period (Ciais et al 2005, Leuzinger et al 2005, Schwalm et al 2012) through reduced CO₂ supply to Rubisco due to stomata closure (Chaves et al 2009, Misson et al 2010, Konings and Gentine 2017), by suppressing mesophyll conductance to CO₂ diffusion (Keenan et al 2010, Misson et al 2010), by decreasing the activity and concentrations of photosynthetic enzymes (Misson et al 2010) and/or by drought-induced plant mortality/dieback (Anderegg et al 2013). Consistent results that high atmospheric vapor pressure deficit and low soil moisture inhibited photosynthesis and therefore suppressed WUE for grassland are also found by Zhang et al (2019) based on ecosystem intrinsic WUE (iWUE, which excludes the contribution of bare and canopy ET changes to WUE).

WUE of cropland (CRO) dropped below normal-year values due to largely depressed ecosystem carbon assimilation. Although the resistance of croplands to drought could be promoted by crop improvement,
Figure 4. Comparison of the standardized anomalies of ecosystem water use efficiency (WUE) during extreme drought year between different land cover types. Nine major land cover types involved in this study are reclassified based on land cover types from IGBP (see section 2). Black points in panel (a) mark regions with very low ecosystem productivity that are excluded in this study. Only gridded pixels with extreme drought years detected are shown here. In panel (b), the error bars indicate the standard deviation. In panel (c), the symbol ‘+’ represents positive standardized anomalies of WUE (GPP or ET), while ‘−’ refers to negative standardized anomalies of WUE (GPP or ET) during the extreme drought year.

and water-saving irrigation technology (Zhang et al 2019), extremely water deficit can still break down the carbon–water coupling along with dramatically reductions of ecosystem productivity. Our results are consistent with Xu et al (2019) who also report severe and extreme drought caused WUE declines for cropland in North China.

Conversely, most forest and shrubland ecosystems, which are mainly distributed north of 50° N, generally show positive WUE anomalies during extreme drought years. For most forest ecosystems (ENF, DNF, DBF and MF), higher ecosystem WUE during extreme drought years than normal years, in supporting of findings in Zhang et al (2019). Further analyses suggest that such enhancement in forest WUE are dominated by relatively increased GPP in spite of during droughts. On the one hand, forests are suggested to be most resistant to drought (Xu et al 2019), because forests with extensive root system tend to absorb moisture from deeper soil layer to relieve water stress under drought (Chapin et al 2011). Therefore, ecosystem productivity of forest is less likely to be negatively affected by severe droughts as grassland. On the other hand, relatively increased temperature and less precipitation along with drought could partly alleviate the temperature- and radiation limitations for ecosystem productivity over these boreal forest regions (Nemani et al 2003). Increased soil moisture and available nutrients for plant (Mazzarino et al 1991) resulting from melting of permafrost could also benefit for photosynthetic capacity over these regions.

Shrubland ecosystem (TSH and BSH) experienced enhanced WUE in extreme drought years but
the underlying driving factors are different. Positive WUE anomalies in TSH, which is in lower latitudes with less annual precipitation and higher aridity (Abatzoglou et al 2018) than BSH, are accompanied by reduced ET due to limited water supply for ET during severe droughts. By contrast, enhanced WUE for BSH is mainly attributed to higher GPP than ET sensitivity to water availability changes because of the relatively more favorable ambient conditions for vegetation photosynthesis induced by drought.

Influences of drought timing on WUE responses to extreme drought stress were also investigated for the nine major land cover types over the study area (figure 5). Our results suggest that, for dryland ecosystems (TGR, BGR and TSH), DS droughts had much more remarkable negative influences on
ecosystem WUE than either DS + WS droughts or WS droughts. This could be attributed to the most profound drought-induced reductions in GPP during DS droughts since dry season for these ecosystems largely overlaps with the vegetation growing season (figure S4). Such dramatically reduced WUE during DS droughts was also observed for cropland (CRO). It should be noted that ET was less sensitive to droughts for CRO than for grassland probably due to agricultural irrigation and land use management (Teuling et al 2019, Padrón et al 2020, Wang et al 2020b). Even though, vegetation photosynthesis largely decreased during extreme drought years, especially DS droughts, for CRO. For BSH, which is mainly distributed over northern high latitudes (figure 4(a)), all the three drought types resulted in positive WUE responses with DS droughts having the most remarkable positive influences on WUE as well as GPP and ET. For this ecosystem, we found that the dry season generally starts from April to May, that is, the summertime for the Northern Hemisphere with relatively higher temperature and water availability. Droughts occurring during this period suggest increased solar radiation, soil moisture and/or nutrient availability for vegetation growth, eventually enhancing vegetation productivity and ecosystem WUE.

For forest ecosystems, more remarkable positive WUE responses were observed during either DS + WS droughts or DS droughts than during WS droughts for ENF as the environmental conditions during DS (generally overlaps summertime for these regions) could significantly contribute to increase in plant photosynthesis. In terms of DNF, which is mainly distributed in Central and Eastern Siberia, WS droughts results in the most significant increases in WUE than normal years across different drought event types with higher sensitivity of GPP than ET to extreme drought for these regions. For other land cover types, the existing evidence seems cannot fully explain the WUE responses during different drought event types. Much future work is still needed to improve our understanding for underlying processes of WUE responses to extreme droughts.

4. Concluding remarks

In conclusion, we examined the impacts of extreme drought years on ecosystem WUE during 1982–2011 across Northern Eurasia, with particular focuses on investigating the drought timing effects and distinguishing responses of different land cover types.

- Ecosystem WUE respond to extreme drought stress differ among ecosystem types. For forest and boreal shrubland ecosystem over northern high latitudes (north of 50° N), hot days and increasing solar radiation were usually concurrent with droughts, which to some extent eliminate the limitations of low temperature and insufficient light on photosynthesis. In this case, vegetation productivity was substantially enhanced, possibly resulting in slightly increased ecosystem ET. Higher ecosystem WUE during drought years than during normal years are therefore observed due to more significantly enhanced GPP than ET during droughts.

- By contrast, for temperate shrubland and cropland ecosystems over arid/sub-arid climate conditions in relatively lower latitudes (30–50° N), extreme drought years tended to further aggravate the water stress for vegetation growth. Consequently, in these regions, vegetation photosynthesis was largely suppressed with significantly negative ecosystem WUE anomalies observed.

- Our results also suggest that the timing of drought is a crucial factor determining its impacts on ecosystem WUE responses to drought stresses. Extreme droughts induced by drought in dry season have significantly more remarkable negative influences on ecosystem WUE than those induced by drought in wet season, especially for grassland, temperate shrubland and cropland ecosystems.

Although some general goals have been achieved, we recommend several considerations for future research on WUE related to variability in ecological strategies and responses to climate extremes. Previous studies suggest that ecosystem responses can exceed the duration of the climate impacts via lagged effects on the ecosystem processes (Anderegg et al 2015, Frank et al 2015b, Huang et al 2018). Our study, however, only describes the direct, current impacts of the extreme drought years on ecosystem WUE, without considering other lagged and/or indirect drought impacts. Moreover, ecosystem WUE responses to extreme drought stress could differ among different stages of drought development as a result of different sensitivities of carbon/water cycle processes to changes in hydro-climatic conditions. For instance, Wang et al (2020a) found that ecosystem WUE increased in the early stage of extreme autumn-spring drought in 2009/2010 but decreased in the peak period, by satellite-derived data in South-west China. Accordingly, responses of seasonal WUE to subseasonal/interannual soil moisture variabilities require further observation-based investigations to improve the predictions of the ecosystem responses to global change in the further.

Data availability statements

The data that support the findings of this study are available upon reasonable request from the authors.
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