Environmental Research Letters

LETTER

The collapse points of increasing trend of vegetation rain-use efficiency under droughts

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Keywords: rain-use efficiency, drought, tipping point, SPEI, global biome

Abstract

The vegetation rain-use efficiency (RUE) represents the ability of an ecosystem to use rainfall and is an important descriptor of ecological functions of terrestrial system. Although studies have been conducted to investigate the impact of droughts on vegetation, we still lack critical understanding of how exactly RUE responds to droughts of different time scales and intensities. Here, we present evidence for a rapid response in RUE, and collapse points of RUE increase trend during droughts by using multi-source meteorological data and satellite-derived vegetation indices. The highest correlation was found consistently between RUE and computed drought index at time scale of 1 month for all biome types and climate regimes. We further discovered that RUE increased significantly with amplification of drought intensity to a maximum RUE, especially for semi-arid and arid biomes. As drought is prolonged, RUE increased till a tipping point was reached across all biomes and climatic conditions, indicating that the long-term droughts weaken the sensitivities of RUE to drought and threaten the resilience of ecosystem. This study comprehensively provides a satellite-based evaluation of RUE response to different drought features. We envisage that the findings would contribute to the development of drought early warning from an ecological perspective and to provide the sustainable environmental management.

1. Introduction

Terrestrial ecosystem, a major sink in the global carbon cycle, accounts for the absorption 25%–30% of anthropogenic carbon dioxide emissions (Reichstein et al 2013). Although they are profoundly modulated by variability in external forcing (Allen et al 2010, Ponce Campos et al 2013), identifying how terrestrial ecosystems respond to varying hydroclimatic conditions is a research question of global concern (Seddon et al 2016). Changes in precipitation patterns, including the magnitude, intensity and frequency, and the stochasticity, are reflected by changes in the physiology, phenology and distribution of the vegetation (Chesson 2000, Weltzin et al, 2003, Chen et al 2020). Also, heterogeneous changes of local temperature in both space and time have an apparent influence on vegetation productivity (Choat et al 2012) by altering photosynthetic function (Wu et al 2011) and length of the growing season (Jeong et al 2011, Wang et al 2011). Consequently, such climate induced changes could influence the global sequestration of terrestrial carbon (Reichstein et al 2013).

Drought is commonly defined by a marked deficiency of precipitation and supernormal high temperature (Vicente-Serrano et al 2010, Lu et al 2011, Luo et al 2017). The concept of a drought is useful in comprehensively representing hydroclimatic conditions of precipitation, evapotranspiration and water availability under the climate change (Trenberth et al 2014). The intrinsic system sensitivity of vegetation functions as a consequence of droughts has been of particular interest to ecologists, climatologists and hydrologists (e.g. Fang et al 2019, Lawal et al 2019, Deng et al 2020). Moreover, there is mounting evidence of drought-related damage to vegetation, which
demonstrates the ability of droughts to slow vegetation growth (Pasho et al. 2011), to reduce productivity (Ciais et al. 2005), to reshape the distribution of species and communities (Engelbrecht et al. 2007), and to produce regional vegetation die-off events (Breshears et al. 2005, Adams et al. 2009, Anderegg et al. 2012). One of the important consequences of droughts associated with climate change is that a small shift in the frequency or severity of droughts could flip the vegetation system from a net carbon sink to a significant carbon source, creating sizable positive feedbacks to global warming (Choat et al. 2012, Reichstein et al. 2013).

Rain-use efficiency (RUE) is commonly defined as the ratio of net primary production (NPP) to precipitation over a given period (Le Houérou 1984, Prince et al. 1998). Based on the ecosystem-specific relationship between NPP and precipitation, RUE has been used as a descriptor of ecosystem functioning (Huxman et al. 2004, Yan et al. 2014) and land degradation (Prince et al. 1998, Kaptué al., 2015). Yet RUE is a more complicated indicator of ecosystem resilience than we expected. For instance, both experimental and modeling studies have shown that spatial RUE could vary greatly among different types of vegetation due to differences in vegetative constraints (Huxman et al. 2004) and edaphic factors (Yang et al. 2010). Across some precipitation gradient, the RUE has been reported to exhibit positive (Bai et al. 2008), unimodal (Paruelo et al. 1999, Yang et al. 2010) and negative (Hu et al. 2010) relationships with mean annual precipitation (MAP).

Climate change will lead to increases in drought duration and intensity, and ultimately to a new hydroclimatological regime for most regions of the globe (Dai 2011, Lehner et al. 2017). Within this context, increased studies have focused on this natural hazard in recent years, and made great efforts to monitor and quantify droughts at the regional or even global scales with considering the drought time scale (e.g. Vicente-Serrano et al. 2013, Norman et al. 2016, Lawal et al. 2019, Sun et al. 2019).

In view of its close relationship with climates, vegetation RUE is expected to change noticeably under the aggravated drought (Huxman et al. 2004, Ponce Campos et al. 2013). Therefore, it is imperative to understand the response of vegetation RUE to droughts of different time scales. Such in-depth understanding may help to more accurately predict the vegetation function and resilience under climate change (Xu et al. 2013, Du et al. 2018), and meanwhile may serve as an additional indicator to drought early warning system (Bachmair et al. 2018). Nevertheless, what remains to be established is how vegetation RUE exactly responds to droughts at a global scale. More importantly, it is not clear whether information on drought time scale and intensity will yield specific tipping points that mark the collapse of ecological system. Although the long-term measurements in field setting can provide site-level mechanisms (e.g. Ponce Campos et al 2013, Zhang et al. 2014, Yan et al. 2014), an overall picture is lacking on the sensitivity of ecosystem to droughts with different time scales and the critical point of ecological collapse across a broad range of global biomes and climatic settings. Recent progress in satellite remote sensing has made available various datasets concerned with climatic and ecological related variables (Huette 2016). These data offer us opportunities to conduct a quantitative global assessment of drought effect on all terrestrial ecosystems.

The aim of this study is to investigate how RUE behaves in response to drought across global biomes at a monthly time scale and to discover whether critical thresholds of RUE under different drought intensities and time scales exist before ecosystems collapse. With vegetation indices and multi-source meteorological data, we first estimate NPP by using Carnegie-Ames-Stanford Approach (CASA) carbon model and compute the global monthly values for RUE for the period of 1982 to 2015. We then examine the global relationships between RUE and droughts of different time-scale (1–24 months) represented by Standardized Precipitation Evapotranspiration Index (SPEI) and its bioclimatic distribution using Pearson correlation analysis and probabilistic risk analysis. We also quantify the critical drought time scale and intensity values that are associated with abrupt RUE changes across different climatic regimes and biome types. An overview of the datasets, procedures and models is given in the flow chart (figure 1).

2. Materials and methods

2.1. Meteorological data

In this study, we acquired the global data with 0.5° × 0.5° grid size and monthly temporal resolution for the period of 1982 to 2015. Temperature, precipitation and potential evapotranspiration were retrieved from the Climatic Research Unit (CRU) (Harris et al. 2014) (http://www.cru.uea.ac.uk/). Solar radiation data were obtained from ERA-Interim (https://www.ecmwf.int/) produced by the European Centre for Medium-Range Weather Forecasts (ECMWF) (Dee et al. 2011). Meteorological data for 1980 and 1981 were also used for computing water deficit before study period.

2.2. Vegetation indices

We used the AVHRR GIMMS3g.v1 Normalized Difference Vegetation Index (NDVI) data at a spatial resolution of 8 km for the period of 1982 to 2015 (Tucker et al. 2005) (http://ecocast.arc.nasa.gov/data/pub/gimms). The original NDVI data (15 day interval) were aggregated to monthly scale using a maximum value composite (MVC) approach (Holben 1986). We obtained satellite estimates of annual
terrestrial NPP by using MOD17A3 at 1 km resolution from 2000 to 2014 (Running et al 2011) (https://lpdaac.usgs.gov/products/mod17a3v055/). The MOD17A3 product has been validated at the global scale ($R^2 = 0.77$) (Zhao et al 2005) and is therefore considered as a verification dataset for this study. To be consistent with the pixel resolution of meteorological data, both NDVI data and MOD17A3 product were spatially resampled using the nearest-neighbor approach. For further validation data, we also made use of NPP field measurements from 900 individual points across the world (figure S1(c) (stacks.iop.org/ERL/15/104072/mmedia)) (https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=615), which were produced by Ecosystem Model-Data Intercomparison (EMDI) (Olson et al 2013). Each point NPP measurement offers an annual NPP estimate computed as an average over the overall temporal coverage from 1931 to 1996 (this coverage does not include all years for all sites).

In addition to characterize the spatial distribution of world biomes, we combined the GLC2000 land cover/use classification (Bartholomé and Belward 2005) (https://www.gvm.jrc.it/glc2000) with Köppen-Geiger climate classification (Kottek et al 2006) (http://koeppen-geiger.vu-wien.ac.at/) at a spatial resolution of 0.5° (figures S1(a) and (b)). As required by NPP model, seven land cover classes, including evergreen broadleaf forest (EBF), deciduous broadleaf forest (DBF), evergreen needleleaf forest (ENF), deciduous needleleaf forest (DNF), mixed forest (MF), shrubland (Shrub), grassland (Grass), and cropland (Crop), were obtained from the map and further considered in the analyses.

2.3. SPEI
Using CRU monthly gridded precipitation (P) and potential evapotranspiration (PET) as the input data, we computed monthly SPEI at the time scale ranging from 1 to 24 months to identify the spatiotemporal
pattern of drought (Vicente-Serrano et al 2010). The calculation of SPEI mainly relies on the difference (D) between P and PET:

$$D_n^k = \sum_{i=0}^{k-1} (P_{n-i} - PET_{n-i}), n \geq k$$ (1)

where $k$ is the time scale, and $n$ is the calculation number.

Time scale, referring to time period that water deficit accumulates, is a crucial factor in drought characterization (Liu et al 2017). Moreover, annual SPEI is defined as the SPEI value in December with time scale of 12 months (SPEI-12Dec) for each year (Vicente-Serrano et al 2020). A negative value of SPEI represents a water deficit, whereas a positive value represents water surplus (Vicente-Serrano et al 2013). In this study, we applied a broad definition of drought (i.e. SPEI < 0), which is basically equivalent to dryness. We thought that RUE in some biomes would exhibit abrupt change under the relatively mild drought condition (SPEI ~ −0.5). And a strict drought definition such as SPEI < −1, may cause us to ignore the RUE tipping point of some biomes.

2.4. NPP model

We estimated monthly NPP by using the CASA model, which was developed based on the light use efficiency concept (Potter et al 1993, Field et al 1995). The model calculates NPP as a function of the absorbed photosynthetically active radiation (APAR) and a maximum light use efficiency variable ($\epsilon_{max}$) that is modified by stress scalars for temperature ($T_c$) and moisture ($W_c$):

$$NPP = PAR \times FPAR \times (\epsilon_{max} \times T_c \times W_c)$$ (2)

In the CASA model, APAR is the product of photosynthetically active radiation (PAR) and the fraction of PAR absorbed by green vegetation (FPAR). Besides, mean annual NPP estimated by CASA model is shown in figure S2(a).

2.5. Analytical methods

We assessed the influence of drought on RUE with means of the Pearson correlation coefficient between monthly values of RUE (12 series) and SPEI for time scale from 1 to 24 months for the period of 1982 to 2015. For each pixel, we carried out 288 (12 × 24) correlation analyses. Furthermore, to remove the impact of vegetation phenology on results, the monthly correlations were summarized annually by retaining only the annual minimum correlation coefficient (Vicente-Serrano et al 2013). Subsequently, SPEI time scale and month of the year corresponding to the annual minimum correlation coefficient were obtained (figure S3).

Meanwhile, to validate the results based on the Pearson coefficient, we also performed a probabilistic risk analysis by using the probability distributions for all variables (Van Oijen et al 2013). We computed the difference in monthly RUE between hazardous (SPEI < 0) and non-hazardous (SPEI > 0) environmental conditions with broadly different (1–24 months) SPEI time scales:

$$\Delta RUE = E(RUE|SPEI < 0) - E(RUE|SPEI > 0)$$ (3)

where $E(RUE|\cdot)$ is expectation the conditional value.

Additionally, we further calculated $[E(RUE|SPEI < 0) - E(RUE|SPEI > 0)]/E(RUE|SPEI > 0)$ for eliminating the influence of spatial difference of RUE value. Two sets of monthly results were both summarized annually by extracting only the annual maximum value.

In order to identify the drought condition corresponding to the RUE tipping point at the biome scale, we employed binned average analysis to minimize the uncertainty created by spatial heterogeneity that randomly impacts RUE (Huang et al 2015). Binned averages of RUE and SPEI were determined with every 0.05 bins of SPEI in the range of −3 to 3. The RUE binned averages with statistical populations of less than 25 were excluded in the analyses. Besides, when detecting the RUE tipping point, only the RUE-SPEI relationships in the range of SPEI < 0 (i.e. drought condition) were taken into account because we solely examined the effect of drought on vegetation RUE. Considering different SPEI time scales and biomes, 960 (24 × 40) binned average results were obtained in this study. It should be noted that when performing binned average analysis, we focused on the month at which the minimum correlation coefficient is found for each biome (table S2). By limiting the analysis to the month with the strongest response to drought for each biome, we could largely reduce the effect of seasonality.

As a comparison test, we computed the slope of linear regression for binned averages of annual RUE and SPEI-12Dec across 40 biomes using model-simulated NPP and MOD17A3, respectively (figure S9). Results based on two datasets exhibit a good agreement ($R^2 = 0.49, P < 0.001$), supporting to some extent the reliability of our findings obtained by using CASA-estimated NPP.

3. Results and discussion

We used the CASA, a remote sensing-based carbon model (Potter et al 1993, Field et al 1995), to estimate the global NPP (See Materials and methods). NPP decreases latitudinally from the equator to polar regions. The highest values are associated with tropical rainforests (e.g. Amazon Rainforest, Congo Rainforest and Southeast Asian Rainforest) as being shown in the long-term average annual NPP for the period
of 1982 to 2015 (figure S2(a)). It seems that spatial pattern of annual NPP is temporally stable, and thus our result is consistent with previous literature focusing on different study periods such as 1988–1993 (Awaya et al, 2004), 2000–2009 (Zhao and Running et al, 2010), and 2000–2014 (Tum et al, 2016).

Our global estimates of NPP were also evaluated through comparisons with independent datasets of ground-based EMDI (Olson et al 2013) and satellite-based MOD17A3 (Zhao et al 2005). For 900 ground observation points and 42,935 collocated pixels, our estimated NPP generally agrees well with the EMDI ($R^2 = 0.73, P < 0.001$) and MOD17A3 datasets ($R^2 = 0.69, P < 0.001$) (figures S2(b) and (c)). The global RUE pattern exhibits a rich spatial structure with relatively high values in those regions with a MAP of approximately 400 mm (figure 2). RUE values tend to be smaller in both dryer and wetter areas along the precipitation gradient. This kind of unimodal pattern in RUE associated with dry/wet conditions has been confirmed in several recent regional studies (e.g. Paruelo et al 1999, Hu et al 2010, Yang et al 2010). Low mean values in RUE under humid conditions are explained by biogeochemical limitations (such as nitrogen and light, Paruelo et al 1999, Huxman et al 2004), or a decrease in effective precipitation owing to runoff, groundwater recharge and soil water storage (Ponce Campos et al 2013). At the dry extreme, drought resistance actions of vegetation including reducing specific leaf areas and stomatal conductance, may constrain maximum photosynthesis and growth rates (Grime et al 1997), resulting in a lower RUE in arid environments.

To better understand the effect of droughts on RUE, we performed a Pearson correlation analysis between monthly values of RUE and SPEI for time scale of 1 to 24 months (See Materials and methods). A significant negative relationship between the RUE-SPEI correlation and drought time scale exists with a logarithmic distribution ($R^2 = 0.99, P < 0.001$). With an increase in the time scale of droughts, the absolute value of minimum correlation coefficient between RUE and SPEI decreases and tends to be zero irrespective of the global average (figure 3(b)) or different biome types (figure 3(c)). These results indicate that RUE responds to droughts with a fast rate initially and weakens as the drought persists (figure S3(b), 96.3% of the world vegetated areas exhibit the highest RUE-SPEI correlation at 1 month SPEI time scale).

Spatially, regions exhibiting significant negative correlations ($P < 0.01$) between RUE and SPEI-1 (1 month drought) represent 98.6% of the global vegetated land, except for certain cold-region steppes and desert margins with non-significant relationships (figure 3(a)). Few-month hysteresis was reported to broadly exist in the response to droughts for vegetation coverage (e.g. Ji and Peters 2003, Hua et al 2017, Xu et al 2018) and primary productivity (e.g. Pasho et al 2011, Chen et al 2013). Results here indicate that the adjustment in RUE during the first month of droughts is timely and rapid.

Furthermore, we examined the robustness of these observations with an independent approach involving probabilistic distribution (See Materials and methods). We computed the difference in RUE ($\Delta$RUE) between drought (i.e. SPEI < 0) and non-drought conditions (i.e. SPEI > 0) at different time scales by using conditional response distribution (Van Oijen et al 2013) (figures 3(d) and S4(a)). We also calculated the difference ratio (i.e. relative $\Delta$RUE) to eliminate uncertainty associated with the spatial variation in RUE value (figures 3(e) and S4(b)). Results
here confirm the same features of RUE response to droughts. Thus, biomes appear to be sensitive to the initial onset of dry conditions, reflected by rapid changing values of RUE. This behavior represents the inherent capacity of vegetation to accommodate disturbances, in order to retain its functionality and feedback.

Subsequently, we tried to reveal the relationship between RUE and drought intensity (SPEI-1) by using binned average method (Huang et al. 2015) (See Materials and methods). We illustrated specific results using DBF biomes as an example (figure 4). RUE in 3 types of climatic conditions (i.e. Cwa, BSh, and Aw) exhibits an initial increase and a subsequent decrease with increasing drought intensity, and peaks around $-1$ of SPEI-1 value, which is an apparent tipping point of drought-induced RUE increase trend at the biome scale. However, in other three types of climatic conditions (i.e. Cfa, Dfb, and Dfc), RUE increases continuously along the drought intensity without an upper limitation. Combining with statistical results across 34 biomes (figure S5), we found that the tipping point for drought intensity (ranging from $-1.55$ to $-0.55$ as the SPEI-1 value) is only associated with arid and semi-arid biomes (mean annual water balance lower than 0 mm per year) (table S3).
These results suggest that humid biomes are capable of retaining sensitivity to more severe drought than arid ones. This behavior is likely related to the diverse response mechanisms of vegetation under different climatic conditions, allowing to survive under drought stress (Chaves et al. 2003). In general, vegetation in arid settings is equipped to mitigate the water shortage condition during droughts (Mcdowell et al. 2008). Thus, arid biomes respond to drought in a plastic manner, relying on physiological, anatomical and functional strategies to prevent damage due to water deficits (Vicente-Serrano et al. 2013). Examples of such vegetation responding mechanism include suppression of photosynthesis, and limiting gas exchange to reduce leaf water loss and respiration cost (Pivovaroff et al. 2015, Xu et al. 2018).

Nonetheless, humid biomes can effectively sustain primary production during droughts because of its low sensitivity to variation in water availability (Chen et al. 2013, Seddon et al. 2016). Furthermore, differences in tipping point for drought intensity among biomes are closely related to biome type and mean annual temperature (figure S6), representing the consensus among researchers that biotic (Isbell et al. 2015) and abiotic factors (Stuart-Haëntjens et al. 2018) have distinct effects on ecosystem resistance.

We also examined the relationship between RUE and drought time scale for different biomes. For DBF biomes, the change gradient in RUE decreases to a convergent point (RUE-SPEI slope equals zero) along with the increase in drought time scale across all climatic conditions (figure 3). This feature of RUE

Figure 4. (a) Spatial distribution of mean annual water balance for the period of 1982–2015. Regions circled by thick solid box are denoted as the typical deciduous broadleaf forest (DBF) regions. (b–g) Relationship between binned averages of RUE and SPEI-1 for deciduous broadleaf forest biomes under different climatic regions based on the Köppen-Geiger climate classification (see figure S1(b) and table S1). Circles (blue) are binned averages of RUE and SPEI-1 with every 0.05 bins of SPEI-1 in the range of -3 to 3. The RUE binned averages with statistical population less than 25 are excluded in the analyses. Results of the regression by means of the coefficient of determination are also shown in graphs.
reveals that long-term drought weakens the increase in RUE induced by water deficit, which is corroborated by previous results that ecosystem resilience decreases with prolonged drought (Ponce Campos et al. 2013). Based on statistical results across 40 biomes (figures 5 and S7), we quantified the threshold value of drought time scale (table S4) by identifying SPEI time scale corresponding to a zero RUE-SPEI slope during droughts (i.e. SPEI < 0). Biomes that are not shown in table S4 may sustain to long-lasting droughts (>24 months), or would have experienced the shifts in species composition as a result of severe droughts (Craine et al. 2013). In addition, the quantified tipping point for drought time scale of ranging from 10 to 24 months of SPEI time scale is positively correlated with MAP ($R^2 = 0.49$, $P = 0.024$) for biomes under MAP of over 500 mm (figure S8). This can be explained by lower constraint of water availability on more humid biomes (Nemani et al., 2003). However, for specific biomes such as shrublands, MAP has negative effect on tipping point for drought time scale. Although semi-arid shrubland biomes are well adapted to deal with water deficit condition (expressed as higher threshold value of drought time scale), extreme drought may still lead to widespread growth decline and vegetation mortality in semi-arid areas due to damage to physiological function during droughts (Jia et al. 2016).

It is worth noting that we applied a relatively broad drought definition (i.e. SPEI < 0), compared with previous studies (e.g. Vicente-Serrano and Begueria 2016, Deng et al 2020, Li et al 2020). Due that RUE tipping point exists objectively, our conclusions are not influenced by the selection of SPEI threshold. Moreover, as we expected, the results confirmed that RUE tipping points for drought intensity in various biomes differ noticeably, and are within a very wide range, from $-1.55$ to $-0.55$ (SPEI value) (figures 4 and S5). Thus, such broad drought definition can prevent us from ignoring some RUE tipping points which occur under mild drought condition (SPEI ~ $-0.5$).

By determining the quantitative relationship of RUE response to drought and subsequent revelation of the RUE tipping point for drought, our results have direct implications for deepening understanding of ecosystem change amid global climate change. Meanwhile, they are also meaningful for improving drought early warning systems, such as the European Drought Observatory (EDO), the US Drought Monitor (USDM), and the South Asia Drought Monitoring System (SADMS). First, many existing drought early warning systems rely mostly on meteorological indicators with little regard for additional factors, and thus may not accurately quantify the drought condition (Caccamo et al. 2011, Bachmair et al. 2018). Second, these systems cannot directly translate the drought hazard into the occurrence and severity of drought impacts (Sutanto et al. 2019), leading to the inadequate preparation for drought-induced economic and agricultural losses (Farahmand et al 2015). Third, these systems usually develop the similar

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**Figure 5.** Relationship between SPEI time scale and the slope of linear regression for binned averages of RUE and SPEI during drought (i.e. SPEI < 0) for six typical deciduous broadleaf forest (DBF) biomes. As for the biomes exhibiting apparent tipping point under drought intensity, only the trend of RUE prior to the tipping point is taken into consideration. The inset in each graph shows the relationship between binned averages of RUE and SPEI of multiple time scales (1, 2, 3, 4, and 5 months) corresponding to circles shaded in grey. Colors represent the different SPEI time scales in the six graphs. Arrows indicate the general trend of RUE-SPEI relationship along with the SPEI time scale.
drought strategies without the consideration of local conditions (Giordano et al 2013). According to the conclusion of general rapid response of RUE to drought (figure 3), we could indirectly monitor the regional dry-wet changes by collecting and analyzing vegetation RUE information. And quantifying the response of RUE to drought essentially is the linkage between drought impact and drought hazard. Furthermore, RUE tipping points for various biomes reported here (figures 4 and 5) could help customize drought risk assessment and management, which is appropriate to the local condition. Therefore, this study demonstrates that incorporating vegetation RUE information into the existing system is a feasible way to improve local to regional drought early warning capacity. Subsequently, we took Horn of Africa as an example for a more detailed illustration. During the last few decades, Horn of Africa has been struck by multiple droughts (Gies et al 2014, Funk et al 2019). This region mainly includes three kinds of biomes: GRA(Aw), GRA(BSh) and GRA(BWh). According to the fact that RUE increase trend induced by drought, the drought onset can be identified by examining whether vegetation RUE exceeds a threshold. The approximate RUE thresholds in exuberance period for these three biomes are 1 gCm$^{-2}$ mm$^{-1}$, 4 gCm$^{-2}$ mm$^{-1}$, and 5 gCm$^{-2}$ mm$^{-1}$, respectively. Besides, GRA(BWh) is detected to be more prone to collapse along with the drought intensification compared with other two biomes, suggesting that GRA(BWh) is the key biome needed to be comprehensively managed.

Droughts bring on a rapid response with increase in RUE across diverse biomes, while such increase would proceed to some threshold as the drought intensifies and continues. Although this study has presented unique behaviors in biomes responding to droughts, further studies are still needed to examine how other factors such as altered species composition, and dynamic growing season could complicate the specific processes, which maintain the ecosystem resilience. Because more frequent and severe droughts are expected under warming climates into the foreseeable future, our findings here represent a step forward in fully understanding the functionality of vegetative communities under external environmental disturbances, contributing to the development of sustainable adaptation strategies for maintaining the vulnerable ecological zones as well human well-being.

Acknowledgments

This work was jointly supported by the National Science Foundation of China (51979071, 517779073), the Distinguished Young Fund Project of Jiangsu Natural Science Foundation (BK20180021), the National ‘Ten Thousand Program’ Youth Talent, and the Six Talent Peaks Project in Jiangsu Province. Meanwhile, thanks to several institutions for making their data freely available. Cordial thanks are extended to the editor, Mr. Johnathan Keen, and two anonymous referees for the valuable comments which greatly improve the quality of the paper.

Data availability statement

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

Justification

1. What are the new results or developments reported in your article?

This paper investigated the exact response pattern of vegetation rain-use efficiency to droughts of different time scales and intensities at the global scale. It revealed the existence of critical thresholds of vegetation rain-use efficiency during droughts, and identified corresponding drought intensity and duration across a broad range of biomes and climatic settings, which has never been precisely qualified in previous studies.

2. In what way are these new results or developments timely?

Awareness of the exact response pattern of vegetation to droughts is essential towards addressing the current problems involving pasture degradation, and forest die-off events. Considering the occurrence of more prolonged and severe droughts under global warming, new findings reported in this paper are urgently needed worldwide to minimize such drought-related damage to vegetation, and even terrestrial ecosystem.

3. Why are these new results or developments significant?

These new findings are valuable for fully understanding the function properties of vegetation communities contributed to ecosystem resilience when facing external environmental disturbance. Furthermore, they would contribute to the development of drought early warning from an ecological perspective and to provide the sustainable environmental management.

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