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Meta-analysis shows non-uniform responses of above- and belowground productivity to drought

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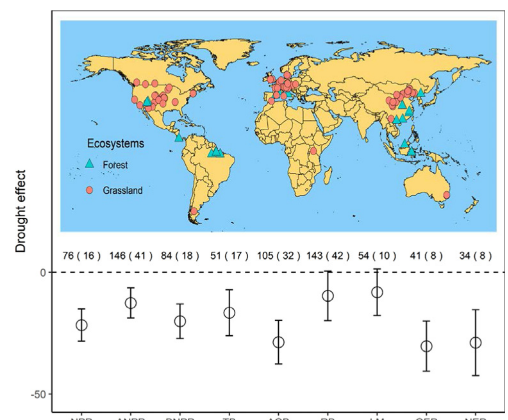
HIGHLIGHTS

- Drought had negligible effects on litter mass on a global scale.
- Soil pH influenced the response of terrestrial productivity to drought.
- The effects of drought on productivity were consistent between biomes.

GRAPHICAL ABSTRACT



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ABSTRACT

Terrestrial productivity underpins ecosystem carbon (C) cycling and multi-trophic diversity. Despite the negative impacts of drought on terrestrial C cycling, our understanding of the responses of above- and belowground productivity to drought remains incomplete. Here, we synthesized the responses of terrestrial productivity and soil factors (e.g., soil moisture, soil pH, soil C, soil nitrogen (N), soil C:N, fungi:bacteria ratio, and microbial biomass C) to drought via a global meta-analysis of 734 observations from 107 studies. Our results revealed that the productivity variables above- and belowground (i.e., net primary productivity, aboveground net primary productivity, belowground net primary productivity, total biomass, aboveground biomass, root biomass, gross ecosystem productivity, and net ecosystem productivity) were decreased across all ecosystems. However, drought did not significantly affect litter mass across all ecosystems, and the responses of above- and belowground productivity to drought were non-uniform. Furthermore, the responses of these productivity variables to drought were more pronounced with drought intensity and duration, and consistent across ecosystem types and background climates. Drought significantly decreased soil moisture, soil C concentrations, soil C:N ratios, and microbial biomass C, whereas it enhanced soil pH values and fungi:bacteria ratios. Moreover, the negative effects of drought on above- and belowground productivity variables were correlated mostly with the response of soil pH to drought among all soil factors. Our study indicated that litter biomass, which mostly represents productivity levels via traditional ecosystem models, was not able to predict the responses of terrestrial ecosystem productivity to drought.

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The strong relationship between the responses of soil pH and terrestrial productivity to drought suggests that the incorporation of soil pH into Earth system models might facilitate the prediction of terrestrial C cycling and its feedbacks to drought.

1. Introduction

Climate change, which is characterized by global warming has been decreasing the amount of precipitation worldwide (IPCC, 2013; Knapp et al., 2015). Further, global climate models have forecast increases in the magnitude and frequency of drought events (Sun et al., 2020b; Tan et al., 2018). Drought is anticipated to directly impact plants and soil processes (He and Dijkstra, 2014; Sardans et al., 2008; Sun et al., 2020a), both of which greatly influence terrestrial carbon (C) cycling, and in turn, feedback positively or negatively on future global scale change (Frank et al., 2015; Song et al., 2019; Wu et al., 2011). Although ecosystem productivity plays a decisive role in terrestrial C cycling and ecosystem functionality (Knapp et al., 2017), our understanding of drought on above- and belowground productivity remains elusive (Doughty et al., 2015; Hulshof et al., 2020). An improved elucidation of the responses of terrestrial productivity to drought is vital for predicting the consequences of more severe drought events on terrestrial ecosystems.

To date, investigations into drought scenarios across a variety of ecosystems have demonstrated modifications in terrestrial above- and belowground productivity; however, the responses of productivity variables to drought are themselves highly variable (Deng et al., 2017; Jin et al., 2018; Liu et al., 2015; Wilcox et al., 2017; Wu et al., 2011; Zhou et al., 2016). For example, drought stress may reduce net primary productivity (NPP) (Jin et al., 2018), or have negligible effects on aboveground net primary productivity (ANPP) (Doughty et al., 2015), or even positive effects on litter biomass (St Clair et al., 2009). The inconsistent results of previous studies are largely ascribable to the effects of drought intensity, experimental duration, ecosystem attributes (e.g., species composition and vegetation structures), and climate (e.g., mean annual temperature and precipitation) (Liu et al., 2018; Sardans et al., 2008; Sun et al., 2020b). A quantitative synthesis of results across various studies may assist with confirming the general effects of drought on terrestrial productivity, while identifying the sources of variations (Gurevitch et al., 2018).

Drought intensity and duration may interact to influence productivity variables, and these interactions likely fluctuate with ecosystem type and within the context of climate (Sun et al., 2020b). For example, a recent global meta-analysis has demonstrated that grassland ANPP responded strongly to elevated drought intensity over brief temporal scales, but not over longer timescales (Gao et al., 2019). Conversely, forest ANPP is more sensitive to prolonged drought, albeit less responsive to short-term drought, which is predominantly the result of tree mortality (DeSoto et al., 2020; Reichstein et al., 2013). Assessing how drought intensity and duration interact is critical for improving our capacity to evaluate the impacts of future drought scenarios.

Terrestrial productivity is also sensitive to soil factors (Deng et al., 2017; Knapp et al., 2017; Rawat et al., 2020), where above- and belowground productivity may decrease with drought through reduced soil moisture (Xu et al., 2013), as plant growth is constrained under water stress (Knapp et al., 2017). Additionally, soil pH is a key driver behind productivity patterns at regional and global scales (Ordoñez et al., 2009; Rawat et al., 2020). Meanwhile, decreased soil C, N, and C:N ratios induced by drought (Sun et al., 2020b) are likely to reduce productivity, due to the lower accumulation of soil C and N pools (Chen and Chen, 2019). Drought also regulates microbial communities, while impacting both microbial C use efficiencies and nutrient supplies to soils, which consequently influences productivity (Deng et al., 2017). Drought has been revealed to have negative effects on productivity, while influencing soil properties and microbial communities that regulate ecosystem processes (Sun et al., 2020a; Zhou et al., 2018). Consequently, to what extent soil properties and microbial communities interact to reduce terrestrial productivity under drought stress requires quantitative synthesis.

Over the last decade, several meta-analyses have focused specifically on the effects of drought on terrestrial productivity (Gao et al., 2019; Song et al., 2019; Wu et al., 2011; Zheng et al., 2020; Zhou et al., 2016). The results showed a general decrease in above- and belowground productivity; however, these studies were limited in scope and did not concentrate on edaphic controls in the reduction in terrestrial productivity under drought stress. For this study, we posed two questions. (i) Does the above- and belowground productivity of terrestrial ecosystems respond uniformly to drought? (ii) Do the divergent responses in above- and belowground productivity result from variations in drought intensity, experimental duration, ecosystems, climate, and soil factors?

To address these two questions, we developed a global dataset that integrated 734 observations derived from 107 field-based publications in the literature (Fig. 1) to investigate the responses of above- and belowground productivity to drought. We hypothesized that: (i) Above- and belowground productivity respond uniformly to drought between different productivity variables. (ii) The effects of drought are dependent on drought intensity, experimental duration, ecosystem type, background climate, and soil factors.

2. Materials and methods

2.1. Data collection

We searched peer-reviewed studies (2000–2019) that examined the effects of drought on terrestrial productivity, employing Google Scholar, ISI Web of Science, and the China Knowledge Resource Integrated Database. Different combinations of keywords were employed for our comprehensive search, including (rainfall reduction OR decreased rainfall OR throughfall reduction precipitation exclusion OR decreased precipitation OR water stress) AND (C fluxes OR productivity OR production OR accumulation OR biomass OR mass OR respiration OR ecosystem). Studies were incorporated only if they met the following criteria: (a) drought experiments were conducted in the field using rain shelters; (b) drought treatments were under the same biotic and abiotic conditions as the control; (c) the magnitudes of precipitation reductions and experimental duration were clearly reported; (d) no other forcing factors (e.g., warming, N addition, etc.) were applied during the drought treatments; (e) productivity variables were measured for at least one-growing season. Up to December 2020, a total of 734 observations from 107 published studies (Fig. 1) met the criteria above and were included in this meta-analysis.

Following a previous study (Song et al., 2019), extracted productivity variables included net primary productivity (NPP) and its above- and belowground compartments (ANPP and BNPP); total, aboveground, and root biomass (TB, AGB, and RB); litter mass (LM); and gross and net ecosystem productivity (GEP and NEP). Data were obtained directly from tables or figures using WebPlotDigitizer software (Burda et al., 2017). Aside from the data on productivity variables, corresponding

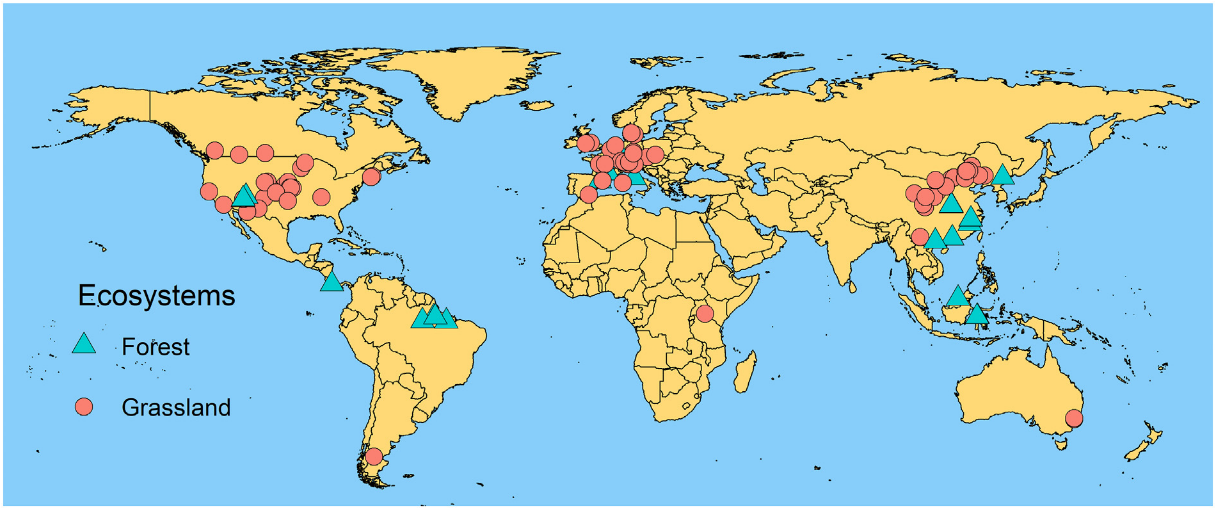

Fig. 1. Global locations of the 107 studies included in this meta-analysis. Aqua triangles and magenta circles represent forests and grasslands, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

geographical variables [ecosystems (forests and grasslands), mean annual temperature and precipitation (MAT and MAP)], soil moisture, soil pH, soil C and N concentrations, soil C:N ratios, and soil microbial communities [fungi:bacteria and microbial biomass C (MBC)] were also collected. Grasslands included meadows, shrublands, and grasslands, whereas forests included natural and planted forests.

Additionally, for the reported soil moisture content (%) in the treatment and control groups of each study, we converted this to a change in soil moisture as drought intensity (DI), which was measured by: [(moisture content of control group - moisture content of drought treatments)/(moisture content of control group)] (Sun et al., 2020b; Sun et al., 2020c). Drought duration (ED) referred to number of days between the initiation of the experiment and subsequent measurements.

2.2. Data analysis

All statistical analyses were performed in R 3.6.0 (R Development Core Team, 2020). We employed the natural log response ratio (lnRR) to examine the responses of productivity variables to drought treatments following Hedges et al. (1999):

$$\text{lnRR} = \ln\ (X_{treatment}/X_{control}) \quad (1)$$

where, $X_{treatment}$ and $X_{control}$ are the mean values of given productivity variables under drought treatments and control groups, respectively. Similar to previous research (Sun et al., 2020b; Sun et al., 2020d), we used the number of replications for weighting: $Wi = (n_t \times n_c) / (n_t + n_c)$, where Wi is the weight associated with each observation, n_t and n_c are the replication numbers in the drought treatments and control groups, respectively.

A linear mixed-effect model was applied to test whether the responses of individual productivity variables to drought treatments differed from zero. The mixed-effect model was fitted with the maximum likelihood method employing the *lme4* package, with study as random factor, and *Wi* as the weight for each lnRR observation (Bates et al., 2015). The log response ratio and its corresponding 95% confidence interval (CI) were derived from mixed-effect models for each individual productivity variable. For ease of interpretation, the lnRR and its corresponding CI were transformed to change percentages as (e^{lnRR} - 1) × 100%. If the 95% CI did not overlap with zero, this indicated that terrestrial productivity responses to drought treatments were significant.

Mixed-effect models were performed to test whether the lnRR of productivity variables or soil factors varied with DI and ED using the following model structure:

$$\text{Y} = \beta_0 + \beta_1\ \ln\ (\text{DI}) + \beta_2\ \ln\ (\text{ED}) + \pi_{study} + \varepsilon \quad (2)$$

where, Y represents the lnRR of each productivity variable or soil factors; β_{0-2}, π_{study}, and ε are model coefficients, and the random effect of "study" accounts for the autocorrelation between observations within each study and sampling error, respectively. To meet a linearity assumption, we compared linear, natural log-transformed terms, and the addition of interaction terms for both (Chen et al., 2020), We found that the models based on Eq. (2) always had lower Akaike information criterion values (Table S1), which were consequently employed as parsimonious models. Further, the continuous variables (DI and ED) in Eq. (2) were scaled (observation minus the mean and divided by standard deviation) to facilitate comparisons between productivity variables or soil factors that had different DI and ED: thus, β_0, β_1, and β_2 represented the responses of productivity or soil factors to drought, DI, and ED, respectively (Cohen et al., 2013).

Finally, to test the biogeographic effects on the productivity variables, we compared the Akaike information criterion values of models with or without interaction terms of DI × biogeographic factors (e.g., ecosystems, MAT, or MAP) and ED × biogeographic factors, and found that models without interaction terms possessed lower Akaike information criterion values (Table S2). Thus, we added the individual terms for ecosystem type and background climate (MAT and MAP) to Eq. (2), respectively (Chen and Chen, 2019; Sun et al., 2021). Moreover, to gain mechanistic insights into the responses of productivity to drought, we used regression analysis to assess the associations between the responses of productivity variables and those of soil factors.

3. Results

Across all terrestrial ecosystems, the NPP was decreased significantly by 21.7%, on average (95% confidence intervals, −28.3 to −15.1%; $p < 0.001$), ANPP by 12.6% (−18.8 to −6.4%; $p < 0.001$), and BNPP by 20.1% (−27.2 to −13.0%; $p = 0.001$), under drought stresses compared to the means of the control groups (Fig. 2a). Furthermore, drought stress decreased the TB by 16.7% on average (−26.1 to −7.2%; $p = 0.006$), AGB by 28.7% (−37.6 to −19.8%; $p < 0.001$), RB by 9.7% (−19.9 to 0.1%; $p = 0.05$), GEP by 30.4% (−40.7 to −20.1%; $p = 0.003$), and NEP by 28.9% (−42.4 to −15.4%; $p = 0.02$). The LM exhibited no significant

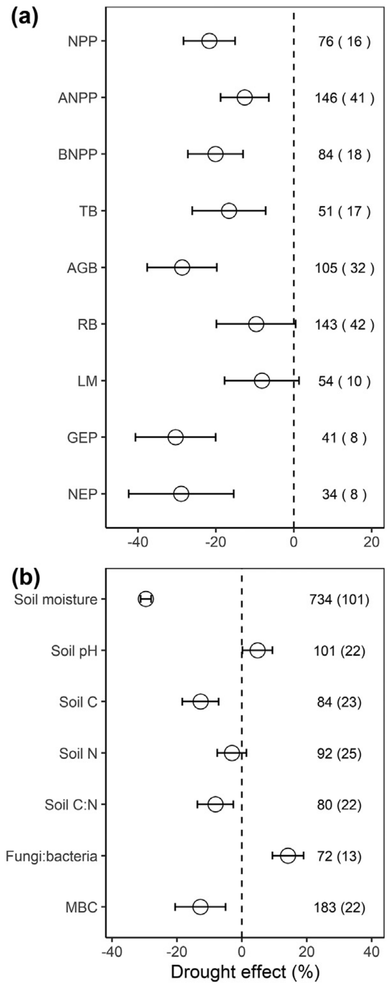

Fig. 2. Log response ratio of productivity variables (a) and soil factors (b) under drought stress. Values (estimated β_0 in Eq. (1)) are expressed as means ±95% confidence intervals. The numbers outside and within parentheses represent the numbers of observations and studies, respectively. NPP = net primary productivity; ANPP = aboveground net primary productivity; BNPP = belowground net primary productivity; TB = total biomass; AGB = aboveground biomass; RB = root biomass; LM = litter mass; GEP = gross ecosystem productivity; NEP = net ecosystem productivity; soil C = soil organic carbon; soil N = soil total nitrogen; and MBC = microbial biomass carbon.

responses to drought stress ($p = 0.11$). In addition, drought stress decreased the soil moisture by 29.6%, on average (−31.2 to −27.9%; $p < 0.001$), soil C by 12.8% (−18.4 to −7.2%; $p < 0.001$), soil C:N by 8.2% (−13.7 to −2.6%; $p = 0.01$), and MBC by 12.8% (−20.6 to −5.0%; $p < 0.001$), whereas they increased the soil pH by 4.8% (0.2 to 9.4%; $p = 0.04$) and fungi:bacteria ratio by 14.2% (9.4 to 19.1%; $p < 0.001$) (Fig. 2b). The soil N exhibited no significant responses to drought stress ($p > 0.05$).

With greater drought intensity and experimental duration, the lnRR of all productivity variables decreased, with the exception of LM (both $p > 0.1$) (Fig. 3). Further, the effects of drought on productivity variables were not altered significantly between ecosystems (forests and grasslands), MAT, and MAP (all $p > 0.05$; Table S3), which indicated globally consistent productivity responses to drought across ecosystems and background climates.

The lnRR of all productivity variables, except for LM, were negatively correlated with the lnRR of soil pH (all $p < 0.05$; Table 1). Moreover, biogeographic factors (e.g., ecosystems, MAT, or MAP) had no significant influences on the relationship between the responses of productivity and soil pH (all $p > 0.05$; Table S4). Additionally, TB and RB were positively correlated with the MBC and negatively correlated with the fungi:bacteria ratio (all $p < 0.05$).

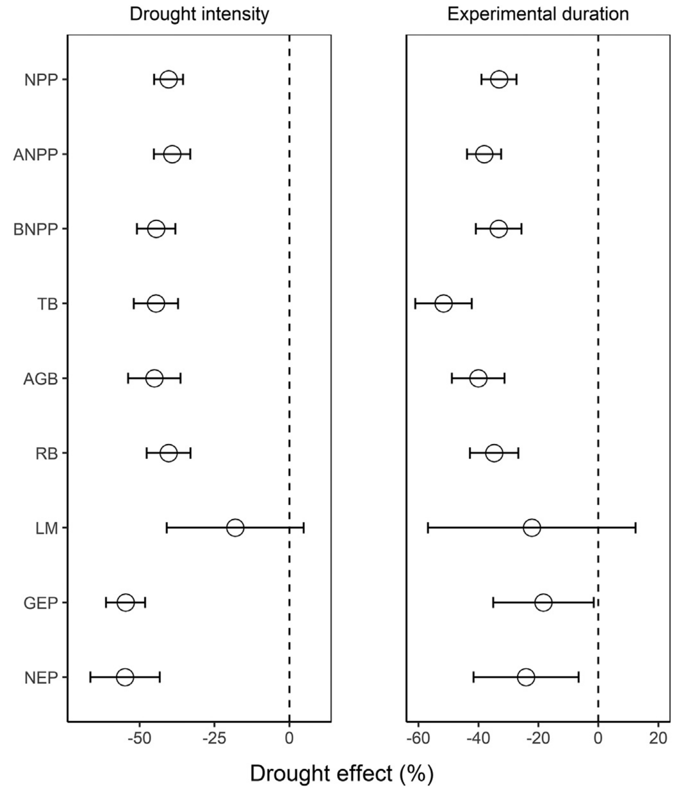

Fig. 3. The lnRR as a function of drought intensity (estimated β_1 in Eq. (1)) and experimental duration (estimated β_2 in Eq. (1)) on productivity variables. NPP = net primary productivity; ANPP = aboveground net primary productivity; BNPP = belowground net primary productivity; TB = total biomass; AGB = aboveground biomass; RB = root biomass; LM = litter mass; GEP = gross ecosystem productivity; and NEP = net ecosystem productivity.

4. Discussion

Based on our comprehensive meta-analysis, we investigated the responses of terrestrial productivity to drought with a focus on the interactions of drought intensity, experimental duration, ecosystem type, and background climate on a global scale. Our analyses revealed that drought had non-uniform effects on terrestrial productivity, with negative effects on NPP, ANPP, BNPP, TB, AGB, RB, GEP, and NEP, but no significant influences on LM. Further, the effects of drought on productivity

Table 1
The relationships (*F* values) between the lnRR of soil factors and lnRR of productivity variables under drought treatments. Significant positive and negative relationships are shown in bold ($p < 0.05$) and symbolized by (+) and (−), respectively. Regressions were not performed when the sample sizes were fewer than 5. NPP = net primary productivity; ANPP = aboveground net primary productivity; BNPP = belowground net primary productivity; TB = total biomass; AGB = aboveground biomass; RB = root biomass; LM = litter mass; GEP = gross ecosystem productivity; NEP = net ecosystem productivity; soil C = soil organic carbon; soil N = soil total nitrogen; and MBC = microbial biomass carbon.

Variable	Soil pH	Soil C	Soil N	Soil C:N	MBC	Fungi:bacteria
NPP	**(−) 16.02**		8.72		0.14	
ANPP	**(−) 5.81**	2.21	1.99	1.57	0.13	0.77
BNPP	**(−) 6.04**	2.27	1.48	0.77	0.15	1.11
TB	**(−) 12.09**	0.01	2.57	0.21	**(+) 18.71**	**(−) 12.23**
AGB	**(−) 7.56**	1.65	1.37	2.94	0.87	0.23
RB	**(−) 8.73**	3.56	4.64	0.06	**(+) 12.85**	**(−) 5.75**
LM	3.02	0.06	1.05	1.68	0.12	
GEP	**(−) 19.05**	1.94	1.09	0.03	1.76	
NEP	**(−) 11.71**	3.98	0.20	2.27	0.99	

variables were more pronounced with intensity and duration. However, the responses of productivity to drought were globally consistent. More importantly, we found that the responses of productivity variables were most strongly associated with the response of soil pH to drought.

4.1. Global patterns of productivity under drought

The finding that LM remained unaltered under drought treatments on a global scale was unexpected (Fig. 2a) and inconsistent with a recent meta-analysis, which reported that drought significantly reduced LM (Song et al., 2019). Several potential mechanisms might justify the unaltered responses of LM to drought. Firstly, one possible explanation was that soil water availability had not fallen below the lowest threshold required to sustain minimal physiological processes (Brando et al., 2008). Secondly, drought-affected forest dwelling trees may respond via the premature shedding of stress-induced leaves only after a latency phase that may be longer than leaf lifespans (Moser et al., 2014). Thirdly, the divergence in LM between the two studies may have been attributed to different sample sizes for LM (54 in our study vs. 14 in Song et al. (2019))). This pattern indicated a temporary mismatch of LM and ANPP in response to drought events, which highlighted the non-uniform influences of drought on different productivity variables (Knapp et al., 2008). Furthermore, the potential disconnects between productivity and decomposition processes might offer avenues for future comparative research, which may uncover novel mechanisms for ecosystem C cycling (Song et al., 2019).

As anticipated, we found that drought significantly reduced terrestrial productivity (Fig. 2a), which confirmed the conclusions derived from previous forest (Moore et al., 2018; Ogaya and Peñuelas, 2007) and grassland (Ansley et al., 2013; Jin et al., 2018) studies across spatial and temporal gradients (Gao et al., 2019; Song et al., 2019; Wilcox et al., 2017; Wu et al., 2011). One possible explanation was that, under drought stress, plant growth was constrained and the growth rate of dominant herbs was decreased in grasslands (Jin et al., 2018). In forests, the photosynthetic rate (Xu et al., 2018) and development (Deng et al., 2017) of tree canopies were depressed, which was considered as a conservative strategy to adapt to water stress (Brando et al., 2008). Additionally, Gao et al. (2019) conducted a global synthesis and suggested that decreased photosynthesis, due to reduced stomatal conductance, resulted in the reduction of ANPP across multiple ecosystems.

Our results revealed that the effects of drought on terrestrial productivity variables increased with drought intensity and duration (Fig. 3). Decreased above- and belowground productivity under greater drought intensity and duration were anticipated since photosynthetic activity decreases under higher experimental drought intensities for extended durations (Arend et al., 2016). Therefore, our analysis indicated that a lack of the effects of drought on productivity variables in certain studies might have been due to low drought intensities and brief experimental timelines (Chen et al., 2019). Collectively, our results suggested enduring and deepening effects of drought on terrestrial productivity under increased intensity and duration.

As individual ecosystems often provide few observations with little statistical power (Button et al., 2013), we tested their overall effects (Sun et al., 2020d; Zhang et al., 2018) and found that the responses of terrestrial above- and belowground productivity did not change spatially (Table S3). Although disparities in the biogeographic factors between ecosystems (i.e., vegetation structures, plant communities, and soil nutrients) may have resulted in the observed variable productivity (Gao et al., 2019; Song et al., 2019), our analysis indicated similar responses on a global scale after controlling for drought intensity and experimental duration. As there are few studies that investigate GEP and NEP, there remain several uncertainties regarding the effects of drought on terrestrial productivity. Therefore, we suggest that our global synthesis will inspire new experiments to further explore these meaningful domains.

4.2. Relationships between productivity and soil factors under drought

Soil properties (e.g., soil moisture, pH, and C availability) and microbial communities (e.g., fungi:bacteria and microbial biomass) mediate the relationships between plants and soils (Zhou et al., 2018), thereby supporting the productivity of terrestrial biomass (Rawat et al., 2020). Our results demonstrated that drought significantly increased soil pH (Fig. 2b), which might have consequently altered the responses of above- and belowground productivity to drought (Table 1). This was likely because soil pH controls the availability of many critical soil nutrients (e.g., phosphorus and potassium) for plants and soil microbes (Catovsky and Bazzaz, 2002). A previous global synthesis found that soil resident organic C had significant effects on the productivity of biomass in response to drought (Deng et al., 2021), which was not detected in our analysis. A probable explanation was that, under drought, soil pH might potentially confound the effects of soil organic C (Sun et al., 2020a). There remain significant uncertainties regarding the simultaneous responses of multiple soil factors on the responses of terrestrial productivity to drought, as most studies included only one or two soil factors. Thus, we recommend future drought experiments incorporate the responses of multiple soil factors.

We found a positive association between the responses of MBC and plant biomass to drought (Table 1), which was consistent with previous evidence (Chen et al., 2019; Craven et al., 2020; Rawat et al., 2020). This positive relationship suggested a coherent plant-soil-microorganism system response to drought (Sun et al., 2020b). Moreover, our results indicated that the response of plant biomass was negatively correlated with the response of fungi:bacteria ratio, likely because fungi are more competitive than bacteria in low-nutrient environments (Chen et al., 2019; Sun et al., 2020a). Overall, our results suggested that the response of soil microbial communities is key to the response of terrestrial productivity to drought.

4.3. Implications

Understanding the patterns and controls of terrestrial productivity under drought conditions is important for the modeling of C cycling and its feedbacks to changing climates (Zheng et al., 2020). Traditional ecosystem models mostly use LM to represent productivity levels (McGroddy et al., 2004). The implicit assumption of these models is that above- and belowground productivity responds uniformly, which might not be correct. To accurately predict how terrestrial biogeochemical C cycling responds to climate change may require a comprehensive consideration of the non-uniform responses of above- and belowground productivity variables to environmental change.

Our results highlighted the importance of soil pH for controlling above- and belowground productivity (Table 1), which extended the previous notion that soil pH drives global patterns of soil fungi (Tedersoo et al., 2014), bacteria (Fierer and Jackson, 2006), and microbial metabolic quotients (Xu et al., 2017). This perspective provides a basis for the model parameterization of terrestrial C cycling. Models that include soil pH may significantly improve the estimation of terrestrial productivity by incorporating correlations between soil pH, drought intensity, and experimental duration. Thus, the incorporation of soil pH into Earth system models is urgently required to more accurately predict C budgets and their feedbacks to climate change (Li et al., 2019).

5. Conclusion

The implied assumption of existing models is that above- and belowground productivity responds uniformly, which may not be the case in terms of drought. To accurately predict how terrestrial biogeochemical C cycling responds to climate change may require a comprehensive consideration of the modifications in above- and belowground productivity variables and the role of soil pH in mediating the responses of productivity to environmental change.

Data accessibility statement

The data used to support the findings of this study are available in Figshare. (https://doi.org/10.6084/m9.figshare.13109582).

CRediT authorship contribution statement

Cuiting Wang: Data curation, Writing – original draft. **Yuan Sun:** Visualization, Investigation, Software. **Han Y.H. Chen:** Writing – review & editing. **Jinyan Yang:** Writing – review & editing. **Honghua Ruan:** Conceptualization, Methodology, Supervision.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.146901.

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