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Drought-induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials

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Abstract

Extreme drought is likely to become more frequent and intense as a result of global climate change, which may significantly impact plant root traits and responses (i.e., morphology, production, turnover, and biomass). However, a comprehensive understanding of how drought affects root traits and responses remains elusive. Here, we synthesized data from 128 published studies under field conditions to examine the responses of 17 variables associated with root traits to drought. Our results showed that drought significantly decreased root length and root length density by 38.29% and 11.12%, respectively, but increased root diameter by 3.49%. However, drought significantly increased root:shoot mass ratio and root cortical aerenchyma by 13.54% and 90.7%, respectively. Our results suggest that drought significantly modified root morphological traits and increased root mortality, and the drought-induced decrease in root biomass was less than shoot biomass, causing higher root:shoot mass ratio. The cascading effects of drought on root traits and responses may need to be incorporated into terrestrial biosphere models to improve prediction of the climate–biosphere feedback.

KEYWORDS

C sequestration, drought, root biomass, root morphology

1 | INTRODUCTION

Increasing global temperature is expected to change the amount, intensity, and frequency of precipitation as well as evapotranspiration in most regions of the Earth (IPCC, 2013). Severe and frequent droughts may have strong and widespread impacts on plants, which could further threaten the biodiversity and stability of terrestrial ecosystems (Bai, Xu, Blumfield, & Reverchon, 2015; Frank et al., 2015).

Drought-induced effects on plants are closely associated with the response of rooting systems and their function to water limitation, leading to altered plant nutrient uptake (Anderegg, 2012). Root system plasticity is critical to plant acclimation and survival under environmental stress, especially drought (Pierik & Testerink, 2014). Therefore, understanding the responses of root systems to drought is crucial for terrestrial biosphere models to better project vegetation dynamics and ecosystem carbon (C) cycling under climate change (Fisher, Huntzinger, Schwalm, & Sitch, 2014).

Previous studies have demonstrated that root traits play important roles in plant growth and terrestrial biogeochemical cycles via interactions with microorganisms within the rhizosphere (Bardgett, Mommer, & De Vries, 2014; Chapman, Miller, Lindsey, & Whalley, 2012; Nie, Lu, Bell, Raut, & Pendall, 2013). Root traits are mainly assessed in regards to their architecture (e.g., rooting depth), morphology (e.g., root diameter [RD]), and physiology (e.g., root respiration [Ra], Bai et al., 2010; Nie et al., 2013; Bardgett et al., 2014). Drought potentially affects root traits and responses in many ways by reducing soil water and nutrient availability (Brunner & Godbold, 2007; Chaves, 2002; Yang, Wang, Yang, & Guo, 2012). The altered root traits induced by drought may exhibit positive or negative effects on leaf physiology, plant growth, and plant community composition (Frank et al., 2015), leading to changes in ecosystem structure and function (Bardgett et al., 2014). Root traits and responses are thus considered as key drivers in regulating ecosystem belowground processes (Bardgett et al., 2014).

Over the past decades, a large number of studies have been conducted to examine the effects of drought on root traits and responses, which have considerably improved our understanding of the mechanisms underlying the drought effects (Brunner & Godbold, 2007; Chaves, 2002). For example, drought could contribute plant to produce thinner and deeper roots to improve water and nutrient acquisition (Chapman et al., 2012; Fuentealba et al., 2015; Ma et al., 2018). Fast-growing species with more resource acquisitive strategy may exhibit higher specific root length (SRL, i.e., root length [RL] per unit root weight), root nitrogen (N) uptake, and N content but lower C concentration and root lifespan compared with slow-growing species with the resource-conservative strategy (Roumet et al., 2006). In addition, drought-tolerant species often have a high investment in root biomass (RB), whereas drought-avoiding species produce greater SRL by increasing root surface area (RA; Chaves, 2002; Lavinsky et al., 2015). However, current understanding about the global patterns of root traits in response to drought remains highly uncertain due to the lack of large and complete datasets (Bardgett et al., 2014; Ostle et al., 2009; Warren et al., 2015).

Drought effects on root traits and responses investigated in previous individual studies are highly contradictory (Chapman et al., 2012; Chaves, 2002). For example, drought may affect RL with decrease (Guha, Rasineni, & Reddy, 2010), increase (Chiatante, Di Iorio, & Scippa, 2005; Manoharan et al., 2010), or no effect (Mori & Inagaki, 2012; Yang et al., 2012). Similarly, the responses of other root traits (e.g., RD, SRL) to drought also varied (Asfaw & Blair, 2012; Eldhuset et al., 2013; Fotelli, Geßler, Peuke, & Rennenberg, 2001). These highly diverse results may result from the difference in extent of drought and speed at which soil moisture is depleted (Chapin, Matson, & Mooney, 2002; Comas, Becker, Cruz, Byrne, & Dierig, 2013). The drier soil environment could contribute to faster root mortality (RM) than those with higher moisture (Chapin et al., 2002). The responses of root traits to drought may also change with experimental duration due to the difference of physicochemical properties in soils (Chapin et al., 2002; Gaul, Hertel, Borken, Matzner, & Leuschner, 2008). Meanwhile, the current contradictory responses of root traits to drought may be associated with the differences of plant functional types (Kashiwagi et al., 2005). For instance, drought decreased RB of oaks (*Quercus robur* L.) by about 33% (Kuster, Arend, Günthardt-Goerg, & Schulin, 2012), but it reduced RB in rice (*Oryza sativa* L.) by about 95% (Asch, Dingkuhn, Sow, & Audebert, 2005). In addition, greenhouse results may differ from those in field trials, due to the artificial environmental conditions, especially light levels that are often too low and causes plants to use water differently (Chapin et al., 2002). These shortcomings may pose great challenge for us to profoundly understand the response of root traits to drought and predict climate-C cycle feedback from ecosystem to global scale (Bai et al., 2010; Brunner & Godbold, 2007; Fisher et al., 2014). Therefore, it is necessary to integrate available data from different sources to reveal the patterns and mechanisms of root traits in response to drought with a unified view.

To help extrapolate results from individual studies to unravel a central tendency, a meta-analysis, which is a quantitative, scientific synthesis tool to provide reliable conclusion (Gurevitch, Koricheva, Nakagawa, & Stewart, 2018), was conducted from 128 studies from field-based experiments with 17 root traits and responses to evaluate the responses of root traits to drought. Specifically, our objectives were (a) to examine global patterns of drought-induced changes in root traits and responses and (b) to investigate regulation of functional types (e.g., woody and herb) and experimental conditions (e.g., drought duration and intensity) on root traits and related responses in response to drought.

2 | MATERIALS AND METHODS

2.1 | Data sources

Peer-reviewed journal articles published before November 2017 were searched using Web of Science and China Knowledge Resource Integrated Database (CNKI). The following search term combinations were used: (water or rain or precipitation or drought or dry stress) and (root) and (biomass or length or diameter or volume or density or area or production or turnover or mortality or morphology or physiology or architecture) and (xylem or conduit or vessel or cortical or aerenchyma). Five criteria were set to select studies and avoid bias in our selection, including that (a) experiments were conducted under the field conditions and had at least one set of paired data (under control and drought treatment) for selected variables; (b) to avoid short-term noise, experiments with duration less than one growing season were excluded; (c) initial environmental and climate conditions, soil parameters, and species compositions in the control and drought treatments were the same; (d) the field experiments were carried out at the same temporal and spatial scales in both control and drought treatments; and (e) the means, standard deviations (SD) or standard errors (SE),

and replicates (*n*) of the selected variables (see below for the detailed description) could be directly extracted or calculated from the chosen data. In total, the 128 published studies reporting about field studies were selected from 2,600 publications based on the four criteria.

Measurements under different drought magnitudes and plant functional types were considered as independent observations if more than one drought magnitude or plant functional type available from the same study (Nie et al., 2013). If more than one measurement of the chosen variables presented from the same experiment at different temporal scales, we extracted measurement data from the latest sampling (Lu et al., 2011).

The selected studies also had at least one of 17 response variables to be included in the database. The chosen 17 root traits and responses were grouped into five categories in our compiled database. The categories included (a) root morphological traits (i.e., RD, root volume [RV], RA, SRL, specific RA, root tissue density [RDen], root length density [RLDen]); (b) root production and turnover rate (root production rate, root turnover rate, RM, and Ra); (c) RB (total RB, fine RB [roots, ≤2 mm in diameter], coarse root biomass [CRB, roots >2 mm in diameter], root:shoot mass ratio [R/S], and fine:coarse root ratio); (d) root anatomical traits (i.e., xylem conduit diameter, xylem vessel density, and root cortical aerenchyma); and (e) growth responses (RL). Meanwhile, three environmental variables including latitude, mean annual temperature, and mean annual precipitation (MAP) were also recorded directly from papers if they were listed in the paper or, in the cases where they were not reported, the data were extracted from the global climate database (available at http://www.worldclim.org/) using site geographical coordinates information.

We classified plants into 10 plant functional groups with five pairs, including herbs and woody plants, forbs and grasses, deciduous and evergreens plants, annual and perennial herbs, nonleguminous and leguminous plants. Forcing and environmental variables included latitude (43.65°S–62.78°N, Figure 1), drought duration (7–3,650 days), and drought intensity (decreases of water inputs 5–100%). Drought intensity was expressed as the percentage changes of precipitation or irrigation between control and drought treatments. In addition,

when control and drought treatments were manipulated to maintain a certain level of soil water content, drought intensity was calculated by the percentage changes of soil water content between control and drought treatments.

2.2 | Data analysis

In this study, we used a meta-analysis to combine available data from different sources to examine responses of root traits to drought with a unified view (Hedges, Gurevitch, & Curtis, 1999; Lu et al., 2011). The response ratio (RR) is a common approach, which is used to reflect the effects of drought on root traits (Hedges et al., 1999). The RR is defined as the natural log of the ratio of the mean value of a given variable in the treatment group ($\overline{X}t$) to that in the control group ($\overline{X}c$), which is used to represent the magnitude of changes in the variables as below.

$$RR = Ln(\overline{X}t/\overline{X}c) \tag{1}$$

The mean, *SD* or *SE* ($SE = SD/\sqrt{n}$), and *n* for each treatment were extracted to calculate the variance (*v*) from the following equation.

$$v = \frac{s_t^2}{n_t \overline{x}_t^2} + \frac{s_c^2}{n_c \overline{x}_c^2} \tag{2}$$

The reciprocal of variance $\left(w = \frac{1}{v} \right)$ was considered as the weight (W) of each RR based on statistical precision. Weighted response ratio (RR++) was calculated using the following equation.

$$RR_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k}w_{ij}RR_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{k}w_{ij}} \tag{3}$$

where *m* is the group number (e.g., different plants) and k_i is the number of comparisons in the *i*th group. The weighted *SE* was followed by
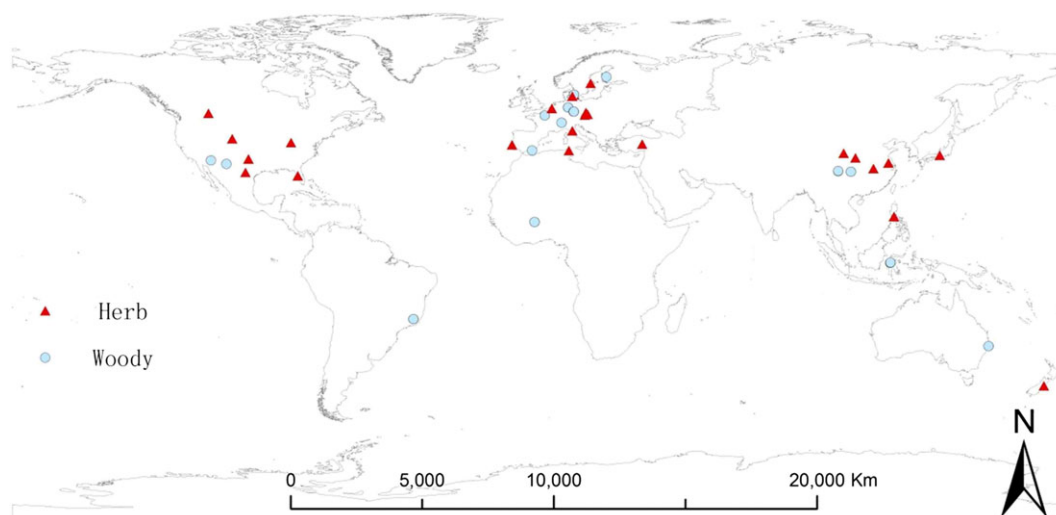

FIGURE 1 Global distribution of drought experiments in this meta-analysis. The selected studies were group into herb and woody species

$$S(RR_{++}) = \sqrt{\frac{1}{\Sigma_{i=1}^{m} \Sigma_{i=1}^{ki} w_{ij}}}. \qquad (4)$$

The frequency distribution of RRs was tested by the normal test and described by a Gaussian function using Equation (5) in SigmaPlot software (Systat Software Inc., CA, USA).

$$y = \alpha exp\left[-\frac{(x-\mu)2}{2\sigma 2}\right], \qquad (5)$$

where x is the RR of root traits, y is the frequency (i.e., the number of RR values), α is a coefficient showing the expected number of RR values at x = μ, and μ and σ are the mean and variance of the frequency distributions of RR, respectively.

We used bootstrapping method to obtain the lowest and highest 2.5% values to derive the 95% confidence interval (95% CI) based on 5,000 iterations (Adams, Gurevitch, & Rosenberg, 1997). In case the 95% CI of RR_{++} for a root trait overlapped with zero, drought had no significant impact on the variable. Otherwise, variables were statistically different (Luo, Hui, & Zhang, 2006). The percentage change of a variable by drought was calculated from the RR_{++} by [exp (RR_{++}) −1]×100%. The effects of latitude, mean annual temperature, MAP, drought duration, drought intensity, and soil volume on the RR of variables were examined by Pearson correlation analysis in SPSS 17.0 software (SPSS, Inc., Chicago, IL, USA).

3 | RESULTS

3.1 | Effects of drought on root morphological and growth traits

Across all studies for root morphological traits, drought significantly decreased RV, RL, SRL, and RLDen by 21.17%, 38.29%, 5.46%, and 11.12%, respectively, but increased RD by 3.49% (Figure 2; Table S1). Among these variables, RL showed the largest decrease in response to drought compared with other variables (Figure 2). In contrast, drought had no significant effects on RA, specific root area, and RDen (Figure 2). In addition, drought significantly increased RM, xylem conduit diameter, and root cortical aerenchyma (Figure 3) and decreased xylem vessels density but had no effect on root production, root turnover rate, and Ra (Figure 3; Table S1).

3.2 | Effects of drought on RB and its relationship with morphological traits

Our meta-analysis showed that drought had a significant effect on RB (Figure 4; Table S1). Specifically, drought significantly decreased total RB, fine RB, and CRB by 9.23%, 9.06%, and 41.01%, respectively, whereas increased R/S and fine:CRB ratio by 13.54% and 9.93%, respectively (Figure 4; Table S1). Response ratios of RB to drought were positively correlated with RL, RD, and RLDen but negatively with SRL (Figure 5). Relationships of RB with RL RDen, and SRL were not
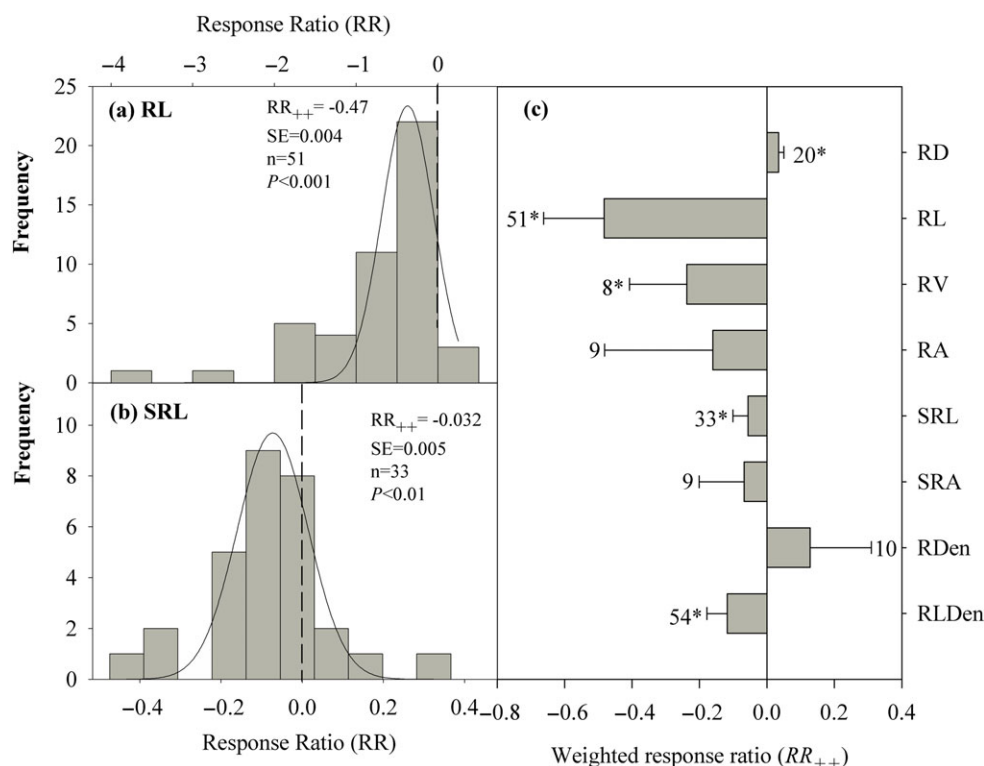

FIGURE 2 Frequency distributions of the response ratio (RR) of (a) root length (RL) and (b) specific root length (SRL) under drought and (c) weighted response ratio (RR_{++}) to drought for eight variables related to root morphology. RR_{++} was calculated by log RR and weights of the individual studies based on statistical precision, representing the changing magnitude induced by drought. RR_{++} > 0, <0, and =0 represents positive, negative, and neutral effects, respectively. Bars represent RR_{++} ± 95% confidence intervals. The vertical line was drawn at RR_{++} = 0. Number values for each bar indicate the sample size. RD: root diameter; RV: root volume; RA: root surface area; SRA: specific root area; RDen: root tissue density; RLDen: root length density [Colour figure can be viewed at wileyonlinelibrary.com]
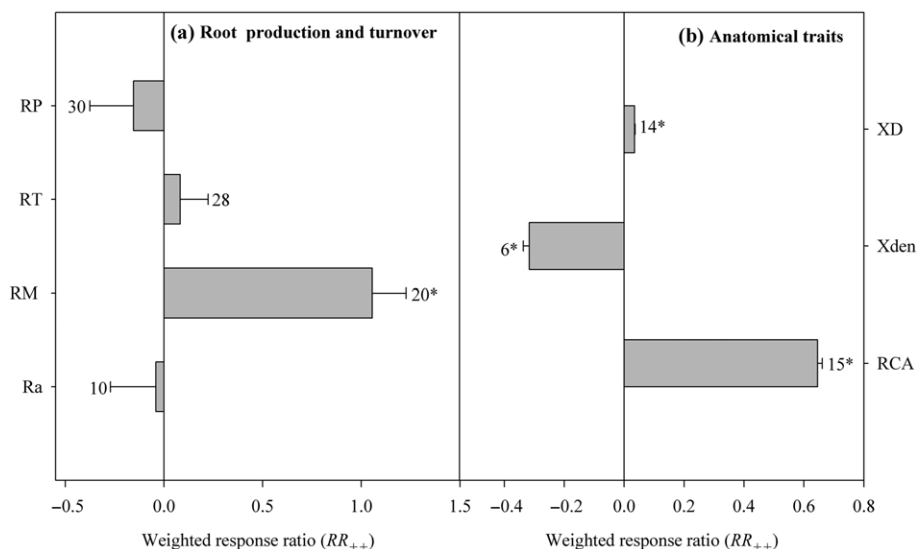
FIGURE 3 Weighted response ratio (RR_{++}) to drought for four variables related to (a) root production and turnover rates and (b) anatomical traits. Bars represent $RR_{++} \pm 95\%$ confidence intervals. The vertical line was drawn at $RR_{++} = 0$. Number values for each bar indicate the sample size. XD: xylem conduit diameter; XDen: xylem vessel density; RCA: root cortical aerenchyma; RP: root production rate; RT: root turnover rate; RM: root mortality; Ra: root respiration [Colour figure can be viewed at wileyonlinelibrary.com]
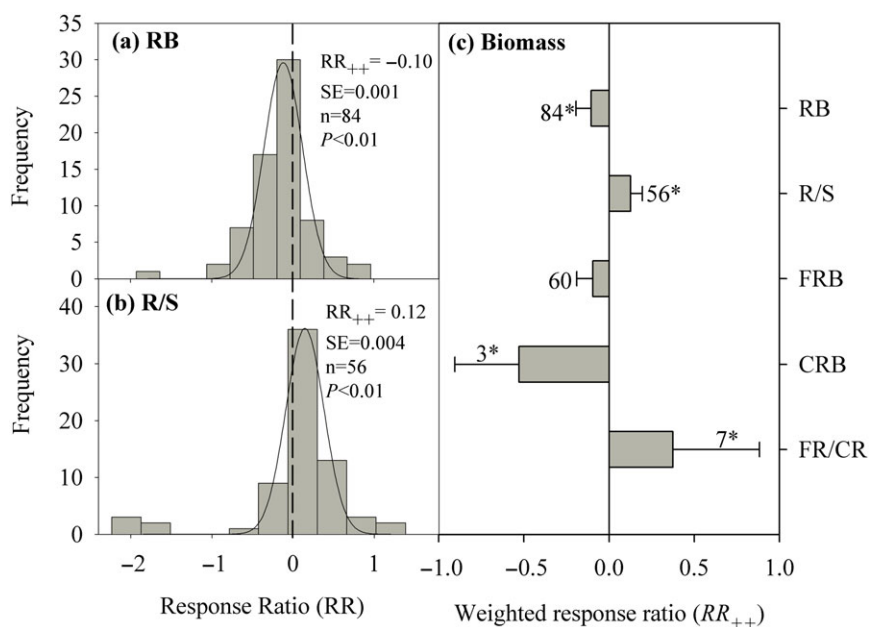

FIGURE 4 Frequency distributions of response ratios (RR) of (a) root biomass (RB) and (b) root:shoot ratio (R/S) under drought. (c) Weighted response ratio (RR_{++}) to drought for five variables related to RB. Bars represent $RR_{++} \pm 95\%$ confidence intervals. The vertical line was drawn at $RR_{++} = 0$. Number values for each bar indicate the sample size. FRB: fine root biomass; CRB: coarse root biomass; FR/CR: fine root:coarse root ratio [Colour figure can be viewed at wileyonlinelibrary.com]

altered by plant functional type. However, no significant correlation between RB and RD for either herbs or woody plants were observed, although they showed significant correlation when combined together (Figure 5).

3.3 | Influences of plant functional types, experimental condition, drought duration, and intensity

Plant functional types affected the overall magnitude and even direction of the RRs_{++} of RB, R/S, RL, and SRL to drought (Figure 6). Specifically, drought had significant negative effects on total RB for all plant functional types (−9.23%, Figure 6a). This negative effect was also significant for herb (−8.25%), woody (−18.22%), and grass (−8.25%) plants when analysed separately. However, RB of forbs showed

positive responses (+2.93%) to drought. Drought significantly increased R/S for all plant functional types including woody plant (+18.93%) and grass (+10.35%). However, forbs showed the opposite response to drought with decreased R/S of −4.24%. Deciduous and evergreen woody plants showed opposite effects on the response of R/S to drought as well as annual versus perennial herbs (Figure 6b). Drought had negative effects on RL for all plant functional types but with different magnitudes (Figure 6c). In addition, drought significantly decreased SRL of forbs and grasses by 7.98% and 6.42%, respectively, but increased that of woody plants by 30.03%.

Our meta-analysis also showed that drought duration and intensity affected the responses of RB, R/S, RL and RLDen to drought (Figure 7). The responses of RB to drought with more than 1 year (>1) showed greater decreases than treatments under 1 year. RLDen showed positive responses to drought with >1 year, whereas it
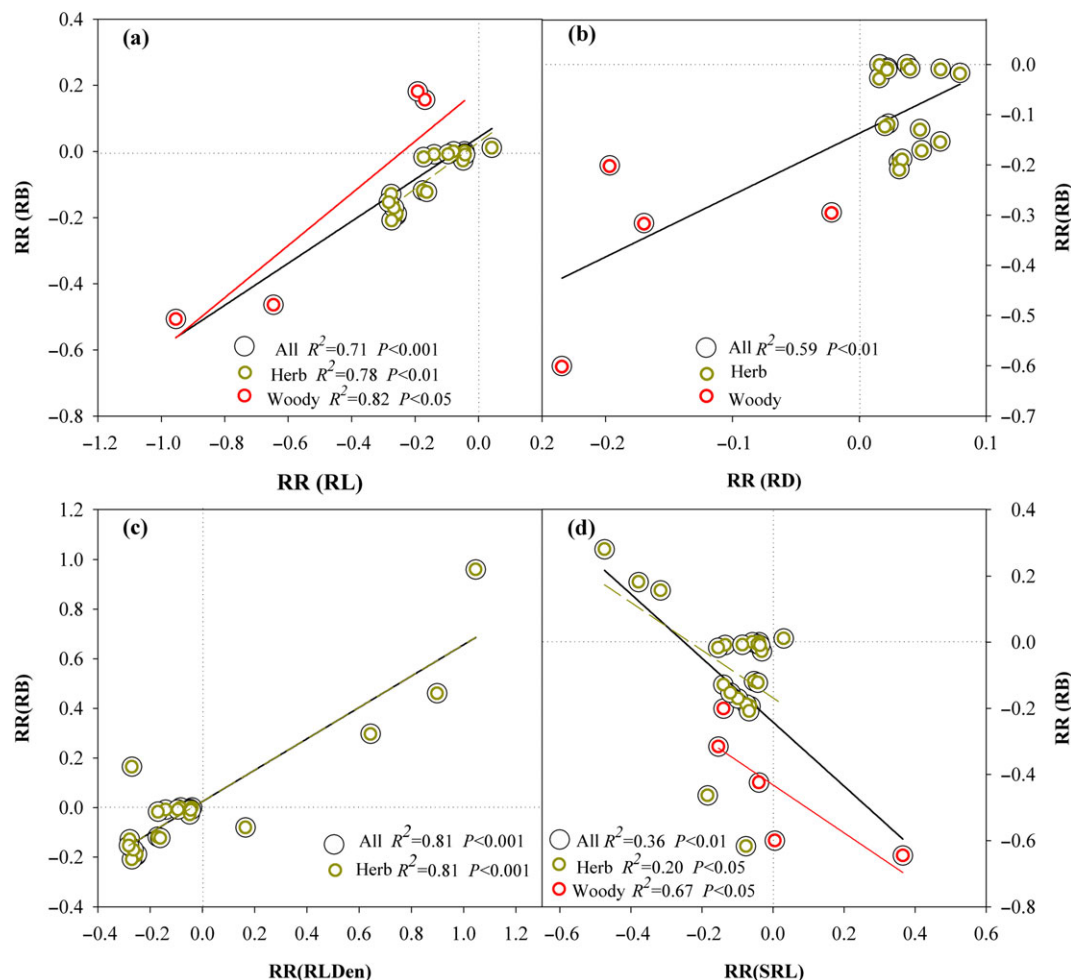
FIGURE 5 Response ratio relationships between (a) root length (RL), (b) root diameter (RD), (c) root length density (RLDen), and (d) specific root length (SRL) with root biomass (RB), respectively. All represents the data for all functional type—black closed circles; herb-Dk—yellow closed circles; woody—red closed circles

exhibited a negative response to drought under <0.5 and 0.5–1 years. Meanwhile, both RB and RL under drought intensity of >50% showed the largest negative response to drought than those than under <25% and 25–50% intensity. Both R/S and RLDen under <25% intensity showed a negative response to drought but increased them under 25–50% and >50% intensity. In addition, drought intensity exhibited a significant negative correlation with RL and a positive correlation was observed between MAP and SRL (Table S2).

4 | DISCUSSION

4.1 | Drought-induced changes in root morphological and growth traits

Drought is one of the major global change factors (e.g., drought, warming, and elevated CO_2) that significantly affects root traits in terrestrial ecosystems (Wasson et al., 2012; Wright, Rao, & Farquhar, 1994). Our meta-analysis showed that drought significantly decreased RL, RV, SRL, and RLDen (Figure 2). The decreased RL might be attributed to the decreased C allocation to roots due to the reduction of aboveground plant production induced by drought (Comas et al.,

2013; Gaul et al., 2008; Moser et al., 2010). Specifically, the drought would decrease nutrients and water availability, leading to reduced RB and increased RM (Figure 4; Wright et al., 1994). Plant damage induced by drought is also likely to decrease root elongation, resulting in significant reduction of RLDen and root area. It has been shown that drought may have a negative effect on root metabolism and storage of nutrients, leading to smaller RA for exchange of resources at the plant–soil interface (Chapin et al., 2002).

Similarly, our results indicated that drought caused a significant increase in RD but a decrease in SRL at the global scale (Figure 2). Due to the limited absorption capacity for water and nutrients, the drought would decrease SRL to adapt the environment (Chapin et al., 2002; Yu, Liu, Yang, & Huang, 2015). Decreased SRL would further lead to increased root lifespan and decreased root growth rate in response to drought (Marshall, 1986; Perez-Harguindeguy et al., 2013). Drought-induced decrease in RD may be associated with the greater embolism, leading to higher RM (Chapin et al., 2002; Chaves, 2002; Roumet et al., 2006). We also found that the responses of RL and SRL to drought differed significantly among plant functional groups (Figure 6), which may be attributed to the difference in strategies of different groups to obtain nutrients and water to support their growth in response to drought stress (Daryanto, Wang, & Jacinthe,
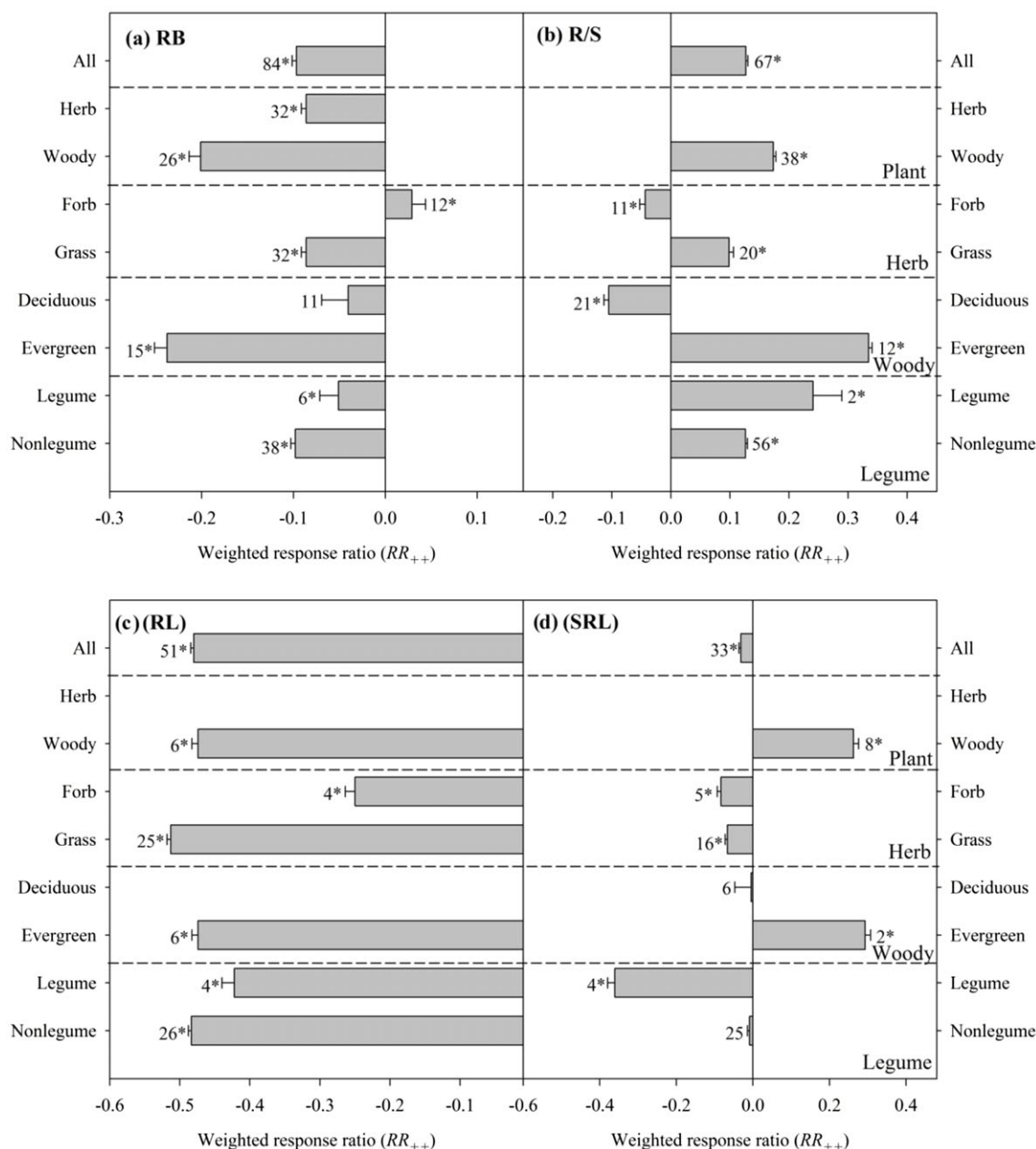
FIGURE 6 Weighted response ratios (RR_{++}) for the responses of (a) root biomass (RB), (b) root:shoot mass ratio (R/S), (c) root length (RL), (d) and specific root length (SRL) to drought for all plant functional types included in the meta-analysis. Bars represent RR_{++} ± 95% confidence intervals. The vertical line was drawn at RR_{++} = 0. Number values for each bar indicate the sample size [Colour figure can be viewed at wileyonlinelibrary. com]

2017). For example, herbs may have stronger C-use efficiency than woody plants under low drought intensity because thinner RD of herbs may benefit plants to enhance the ability to leverage photosynthetic C by reducing reliance on mycorrhizae (Ma et al., 2018). These results indicate that herbs may trigger greater survivorship strategies than woody plants in response to drought when the stress intensity is low (Struik, 1965; Thorne & Frank, 2008).

4.2 | Drought-induced changes in RB and its relationships with morphological traits

Because suites of root traits are linked to plant growth rate (Comas, Bouma, & Eissenstat, 2002), responses of root morphological traits

to drought are closely connected with root production and turnover, leading to larger changes in RB than the control (Figures 3, 4, Gaul et al., 2008; Fiala et al., 2009; Moser et al., 2010). Our meta-analysis showed that drought had no significant effects on root production but significantly increased root morality (Figure 3). These results might be attributed to the following mechanisms. First, drought stress could directly increase RM by depleting starch and sugar reserves (Maguire & Kobe, 2015) and indirectly inhibit photosynthate transportation to the root system (Hasibeder, Fuchslueger, Fritz, Richter, & Bahn, 2014; Marshall, 1986). Second, to ensure a relatively high capacity to acquire water and nutrients under drought, plants might shed their older fine roots and produce new fine roots (Naghavi, Toorchi, Moghaddam, & Shakiba, 2015), which further increases RM and
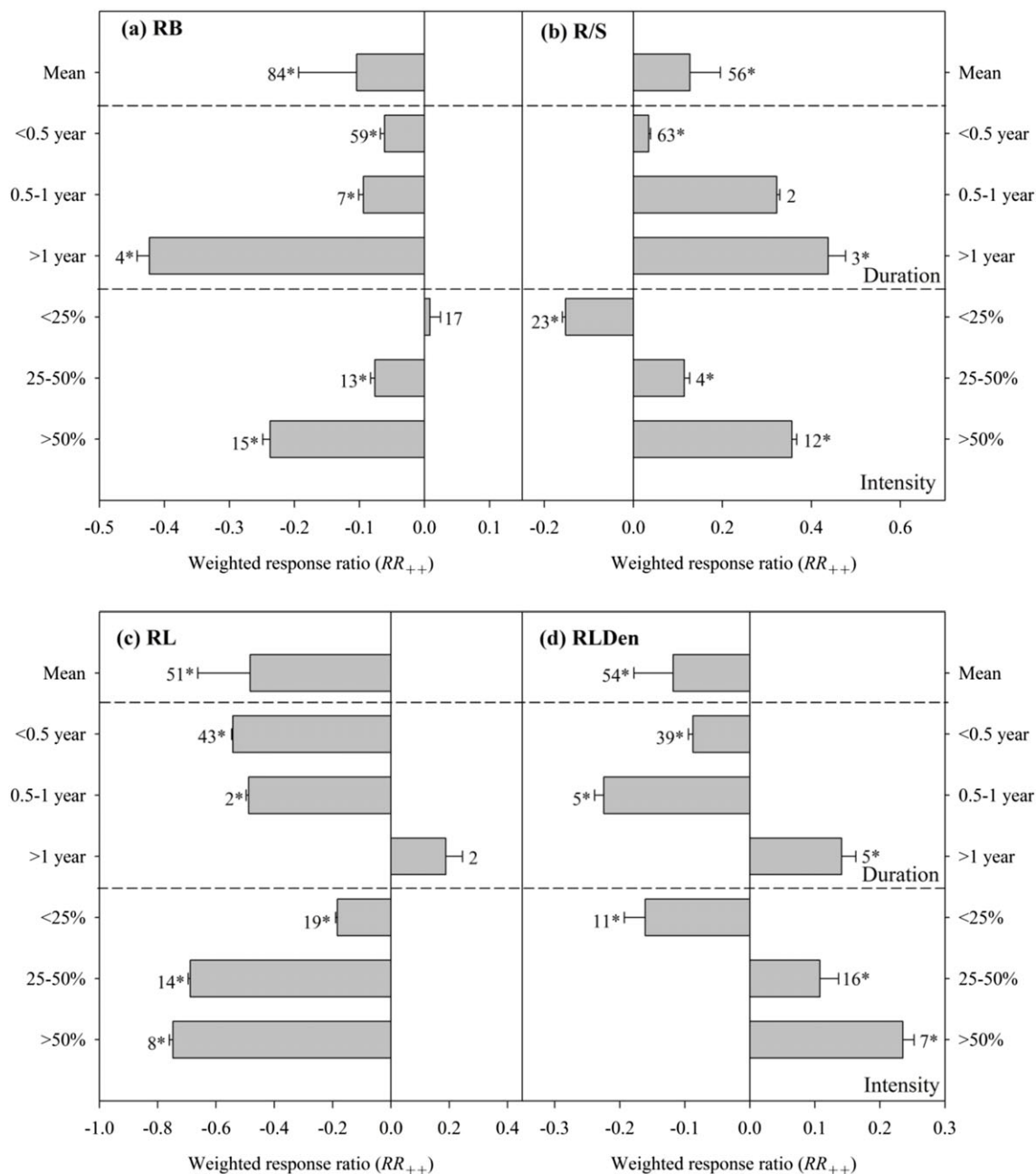
FIGURE 7 Weighted response ratios (RR_{++}) for the responses of (a) root biomass (RB), (b) root:shoot mass ratio (R/S), (c) root length (RL), (d) and root length density (RLDen) to drought under experimental duration and drought intensity. Bars represent RR_{++} ± 95% confidence intervals. The vertical line was drawn at RR_{++} = 0. Number values for each bar indicate the sample size [Colour figure can be viewed at wileyonlinelibrary.com]

decreases root production (Eldhuset et al., 2013; Nagajothi, Sheeba, & Bangarusamy, 2014).

Our meta-analysis also found that drought significantly increased R/S (Figure 4c; Table S1), which was consistent with the results from Pallardy and Rhoads (1993) and Aspelmeier and Leuschner (2006). Increased R/S is a plant avoidance mechanism in response to drought when drought increases the proportion of RB relative to aboveground biomass (Hermans, Hammond, White, & Verbruggen, 2006; Hodge, 2009; Zhou et al., 2017). Meanwhile, the response of R/S to drought varied among plant functional types (Figure 6), which might be attributed to the different strategies of plant functional types to obtain water and nutrients and distribution of RB at different soil profile (Daryanto et al., 2017). For example, more C can be easily allocated

into roots in response to drought due to thinner RD in herbs than woody plants (Ma et al., 2018).

4.3 | Factors regulating the responses of root traits to drought

Environmental factors (e.g., experimental conditions, drought duration, and intensity) have been shown to affect the responses of root traits to drought (Wright et al., 1994; Fiala et al., 2009; Kano-Nakata et al., 2013). We found that drought-induced decrease in RB was more significant under drought duration of >1 year than those under 1 year, which may relate to less photosynthetically fixed C inputs to belowground roots in longer term drought compared with those in short

term (Chapin et al., 2002). Meanwhile, drought led to the largest decrease in RB and RL under drought intensity of >50% than those under <25% and 25–50% intensity (Figure 7). These changes may contribute to greater difficulty in nutrient absorption and transport for plants under higher drought intensity, leading to decreased RL and RB (Chapin et al., 2002; Gaul et al., 2008). Furthermore, a positive correlation between the response of SRL to drought and MAP was observed in this study (Table S2). The plant productivity in wetter regions is usually greater than those in drier areas, and therefore, the actual response of SRL to drought may have been masked, causing the positive correlations (Chapin et al., 2002). In addition, the response of root traits to drought under field conditions differ from those in greenhouse conditions (data not shown), which may be due to the difference in water, wind conditions, and growth space (Chapin et al., 2002; Wright et al., 1994).

4.4 | Implications for manipulative experiments and model development

Currently, most regions are experiencing increased frequency of severe drought, which not only threatens the biodiversity and stability of terrestrial ecosystems but also alters ecosystem structure and function (Bardgett et al., 2014; van der Molen et al., 2011). In this study, we observed that changes in RB induced by drought largely result from altered root morphological traits at a global scale. Our results may thus offer some suggestions for the development of global C cycle models as well as the design of manipulative experiments in the future, at least in three aspects. First, our study found that drought significantly decreased RL and SRL and then affected RB (Figures 2–4). However, root dynamics (e.g., SRL) in current land surface models are noticeably absent in simulating global biogeochemical cycling, especially under drought conditions (Bardgett et al., 2014; Warren et al., 2015), which may lead to overestimation or underestimation in global C feedback to climate change. For example, the current dynamic global vegetation models completely bypass RB (usually calculated by a ratio of shoot biomass) when simulating the effects of drought on vegetation production (Ostle et al., 2009). Root biomass may be used as a specific unique marker to determine plant sensitivity or tolerance to drought (Warren et al., 2015). Therefore, future Earth system models may need to take roots into account for better forecasting the responses and feedback of terrestrial ecosystems to climate change.

Second, drought-induced decreases in root morphological traits caused considerable changes in root production and RB (Figures 2–4), demonstrating the close relationships among different root traits (e.g., morphology, biomass, and production) under drought (Figure 5). However, most of the current drought experiments only measured one or few root traits, which makes it difficult for us to examine the drought-induced interaction of diverse root traits and ecosystem processes (Bardgett et al., 2014). Well-designed experiments are thus necessary to comprehensively examine the response of diverse root traits and other ecosystem processes to drought (Fotelli et al., 2001). Third, global climate change often incorporates simultaneous changes in multiple environmental factors (e.g., rising temperature, precipitation, nitrogen addition, and elevated CO_2), which may interactively influence root traits (Zhou et al., 2017).

However, despite the fact that our current study indicated the importance of drought on root traits, the interactions between drought and multiple climate factors on root traits in terrestrial ecosystems still remained uncertain. Hence, there is urgent need to undertake more multifactor with extreme drought studies with long-term experiments to examine the responses of root dynamics in terrestrial ecosystems to future climate change.

5 | CONCLUSIONS

Root traits play an important role in the plant acclimation and/or adaptation to drought. Our results showed that drought had a marked impact on root traits and responses across the globe. Specifically, drought significantly affected root morphological traits and increased RM. Drought-induced decrease in RB was less than shoot biomass, leading higher R/S. However, some variables (e.g., root production and Ra) were not affected significantly by drought. The drought duration and intensity affected the responses of root traits to drought to some degree. Importantly, both RL and SRL were the main two forcing variables to predict responses of RB to drought. Our results highlighted the importance of drought effects on root traits, especially RL and RB, which may need to be incorporated into regional and global models for predicting effects of climate drought on global root traits and assessing the climate–biosphere feedback.

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SUPPORTING INFORMATION

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