C:N:P stoichiometry of plants, soils, and microorganisms: Response to altered precipitation

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Abstract Precipitation changes modify C, N, and P cycles, which regulate the functions and structure of terrestrial ecosystems. Although altered precipitation affects above- and belowground C:N:P stoichiometry, considerable uncertainties remain regarding plant–microbial nutrient allocation strategies under increased (IPPT) and decreased (DPPT) precipitation. We meta-analyzed 827 observations from 235 field studies to investigate the effects of IPPT and DPPT on the C:N:P stoichiometry of plants, soils, and microorganisms. DPPT reduced leaf C:N ratio, but increased the leaf and root N:P ratios reflecting stronger decrease of P compared with N mobility in soil under drought. IPPT increased microbial biomass C (+13%), N (+15%), P (26%), and the C:N ratio, whereas DPPT decreased microbial biomass N (−12%) and the N:P ratio. The C:N and N:P ratios of plant leaves were more sensitive to medium DPPT than to IPPT because drought increased plant N content, particularly in humid areas. The responses of plant and soil C:N:P stoichiometry to altered precipitation did not fit the double asymmetry model with a positive asymmetry under IPPT and a negative asymmetry under extreme DPPT. Soil microorganisms were more sensitive to IPPT than to DPPT, but they were more sensitive to extreme DPPT than extreme IPPT, consistent with the double asymmetry model. Soil microorganisms maintained stoichiometric homeostasis, whereas N:P ratios of plants follow that of the soils under altered precipitation. In conclusion, specific N allocation strategies of plants and microbial communities as well as N and P availability in soil critically mediate C:N:P stoichiometry by altered precipitation that need to be considered by prediction of ecosystem functions and C cycling under future climate change scenarios.

KEY WORDS

Climate zone; Ecological stoichiometry; Precipitation change; Plant-soil interactions; Soil microbes; Terrestrial ecosystems; Global change

1 | INTRODUCTION

Global warming and extreme weather events have large impacts on global precipitation patterns (Maurer et al., 2020; Smith et al., 2023). Precipitation changes can shift the magnitude and frequency of extreme precipitation events (Deng et al., 2021; Stocker, 2014), and affect plant growth, litter production quality and quantity. Precipitation changes can also alter soil pH, aggregate stability, and cation exchange capacity, and consequently modify plant and microbial community stability (Austin & Vitousek, 2000; Khalili et al., 2016; Ma et al., 2016). These changes have a large influence on carbon (C), nitrogen (N), and phosphorus (P) cycles, as well as their stoichiometry (Prommer et al., 2019; Sierra et al., 2017; Thakur et al., 2015). Therefore, clarifying the changes of C:N:P stoichiometry to altered precipitation is essential to predict the impacts of climate change on ecosystem functions.

Ecological stoichiometry has been widely used to study the balance of energy and nutrients at the level of individual organisms, communities and ecosystems (DeMott & Pape, 2005). Changes in stoichiometry of nutrients reflect the ecosystem limitations and consequently, the response to any environmental factors (e.g. N or P deposition), and also to future global change (Sardans et al., 2012; Yue et al., 2017). Ecosystem C:N:P stoichiometry mainly affect the primary productivity, nutrient cycling and food webs in ecosystems (McGroddy et al., 2004). The C:N:P stoichiometry are related to litter decomposition, N_2 fixation and leaching, plant diversity, and the ability of organisms to adapt to environmental stresses (Heuck et al., 2015; Nielsen & Ball, 2015). An asymmetric model of the relationship between the aboveground net primary production (ANPP) and altered precipitation (Knapp et al. 2017) indicated positive and negative asymmetry responses of ANPP to the precipitation variability (Knapp et al., 2017). The positive asymmetry indicates that the ANPP change to increased precipitation (IPPT) is higher than to decreased precipitation (DPPT). The negative asymmetry indicates that the negative impact of extreme DPPT on ANPP is far greater than the positive effects of extreme

IPPT (Knapp et al., 2015; Zhou et al., 2018). The asymmetric reactions of terrestrial C:N:P stoichiometry to IPPT or DPPT, however, are still unknown, which limit our predictions on the C balance of terrestrial ecosystems to precipitation changes.

The results of altered precipitation on plant, soil and microbial C:N:P stoichiometry are inconsistent (Sardans et al., 2021). For example, an increase in plant biomass N:P ratio by DPPT due to a larger decrease in plant P concentration than N concentration (He and Dijkstra, 2014). A meta-analysis generalized that DPPT increases plant N:P ratios (Yuan & Chen, 2015), owing to that P is far more immobile than N, and drought decrease the uptake of P more than that of N (Sardans et al., 2021). Two meta-analyses have demonstrated contrasting results on soil microorganisms, i.e., one reported microbial biomass C:N ratio decreased with increased precipitation (Xu et al., 2020), but the other reported the increase of C:N ratio (Deng et al., 2021). These inconsistences were attributed to: (1) magnitude of precipitation manipulation (Ren et al., 2017; Wilcox et al., 2017); (2) duration of precipitation manipulation (Canarini et al., 2017; Zhou et al., 2018); (3) differences in local climate [e.g., mean annual temperature (MAT) and mean annual precipitation (MAP)] (Wu et al., 2011; Xu et al., 2020). These studies, however, have mainly focused on the effects of altered precipitation on a single indicator (e.g., C, N, or C:N) of plant, soil or microbial C:N:P stoichiometry. The comprehensive effects of precipitation changes on plant-soil-microbial system were rarely studied. Furthermore, the extent of the magnitude, duration, and climate factors on plant, soil and microbial C:N:P stoichiometry is still unclear.

To generalize the response of plant-soil-microbial C:N:P stoichiometry to altered precipitation, we conducted a synthesis from precipitation manipulation experiments in three groups of ecosystems: grasslands, shrublands and forests. We meta-analyzed 828 observations from 236 studies to answer the following questions: (1) how do C:N, C:P, N:P ratios of plants, soil and microorganisms respond to IPPT and DPPT? (2) How do these responses and sensitivity depend on climate and ecosystem types? and (3) Which factors affect the response of C:N:P stoichiometry to altered precipitation?

2 | MATERIALS AND METHODS

2.1 | Data compilation and extraction

A comprehensive search of primary studies with experimental precipitation manipulation (i.e., increased precipitation and/or drought) published before MAY 2022 were selected. These studies evaluated the effects of increased (IPPT) and decreased (DPPT) precipitation on C:N:P ratios in plants, soils, and microbial biomass. We obtained the published papers from Google Scholar (*www.scholar.google.com*), Web of Science (*www.webofscience.com*), and China Knowledge Infrastructure (CNKI; *www.cnki.net*). The following search terms were used: (“altering precipitation” OR “changing precipitation” OR “altering rainfall” OR “changing rainfall” OR “drought” OR “decreasing precipitation” OR “increasing precipitation” OR “precipitation variation” OR “water addition” OR “water reduction” OR “precipitation experiment”) and (“C” OR “N”, “P”, OR “C:N” “C:P” OR “N:P” OR “C:N:P”). We filtrated the published papers using the following criteria in the dataset:

(1) the studies were conducted in the field, including control and altered precipitation (IPPT or DPPT); cropland and laboratory studies were excluded,

(2) the numbers of replicates (≥ 3), means, and standard deviations (SD) or standard errors (SE) of C:N:P ratios were presented in the original paper,

(3) magnitude and duration of precipitation change were clearly described,

(4) the control and altered precipitation treatments were at the same initial experimental conditions,

(5) for multifactorial experiments, other manipulation factors (e.g., warming, nutrient addition, etc.) and their interactions were excluded in the precipitation treatments.

Using these criteria, a total of 386 IPPT and 442 DPPT independent paired sites (Supporting Information Dataset S1) from 236 articles were selected for further analyses. For the studies reported only the response of the element (C, N or P) concentration, we calculated the corresponding element ratios. For the studies that do not provide standard deviation (SD), we used the "Bracken1992" method to estimate it using "*metagear*" package in R software (Benítez-López et al., 2017). The observations were collected mainly in North America, Europe and Asia (Figure 1). The studies that fitted our criteria were located between 45.7° S and 76.5° N, with MAT ranging from −11.3 to 28 °C and MAP from 81 to 3, 990 mm (Supporting Information Dataset S1). The magnitude of precipitation treatments ranged from −100% to +100%, the duration of precipitation treatments ranged from 1 to 15 years.

To standardize the level of precipitation manipulation in each study, all the operate levels were converted to percentage of annual precipitation changes [ΔPPT (%)]. For IPPT, treatments manipulations were implemented through two methods:

1) A constant water amount was added each year. For this situation, we recorded the annual precipitation data of each research year, and then calculated ΔPPT.

2) The precipitation was collected from the water shelter, and then was discharged into the IPPT experimental plots, or the water was added to a fixed proportion after each rainfall event.

In these cases, the ΔPPT were calculated based on Equation (1), of which PPT was the precipitation during the manipulation period, the ΔPPT is the annual precipitation change. For the DPPT that were conducted by the establishment of a rainout shelter, the ΔPPT was calculated as the percentage of the rainout-shelter area to the total plot ($PER_{shelter}$) if the DPPT was performed throughout the year; or if the DPPT was seasonal, DPPT was calculated using the method of (Hoover et al., 2018). In Equation (1), APPT is the annual amount of precipitation, PPT_{TP} was the total amount of precipitation among the experimental period.

$$\Delta PPT = PER_{shield} \times \frac{PPT_{TP}}{APPT} \quad (1)$$

Figure 1

2.2 |Factors affecting the response of C:N:P stoichiometry

Several factors affect the response of C:N:P stoichiometry of plants, soil and microbial biomass to altered precipitation. These factors include climate variables (i.e., MAT, MAP), ecosystem type (Ecosystem Type), change of precipitation levels (Magnitude), and duration of precipitation manipulation (Duration). These variables were recorded directly from the original or referenced papers. If the original climate information (MAT, MAP and potential evapotranspiration) was not available, the global climate database (WorldClim, version 2.0, http//:www.worldclim.org) was used. The humidity index (HI) was calculated as the ratio of mean annual precipitation to mean annual potential evapotranspiration. The graphical data were obtained digitalized by the free software Webplotdigitizer software (Burda et al., 2017) to extract the means and SDs or SEs.

2.3 | Statistical analysis

We evaluate the responses ratio (RR) of C:N:P stoichiometry in each study followed the methods of (Hedges et al., 1999) to altered precipitation:

$$RR = \ln (X_e / X_c) = \ln X_e - \ln X_c \quad (2)$$

The variance (v) of each RR was calculated as follows:

$$v_i = (S_e / X_e)^2 / n_e + (S_c / X_c)^2 / n_c \quad (3)$$

where X_c and X_t are the means of a specific variable in the control and the treatment groups, respectively; n_c and n_t are the number of replicates of the in the control and altered precipitation groups, respectively. S_e and S_c are the SD in the control and altered precipitation groups of each observation, respectively.

The “*metafor*” package in R software was used to calculate the weighted response ratio (ln

RR_{++}) and its 95% confidence interval (CI) using weighted regressions and random-effects models. The weighted mean response ratio (RR_{++}) was calculated using Equation (4):

$$RR_{++} = \sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij} RR_{ij} / \sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij} \quad (4)$$

where, *m* is the number of groups, *k* is the number of comparisons in the i_{th} group, and w_{ij} is the weight of each response ratio. The weight (w_{ij}) was calculated according to Equation (5):

$$w_{ij} = 1/(v_i+\tau^2) \quad (5)$$

Two variances are considered to calculate the weighted factors (w_{ij}) and RR in the mixed effect model, including the within-study (*v*) and among-study (τ^2) variances (Benítez-López et al., 2017).

A variance linked to RR_{++} was calculated using Equation (6):

$$SE(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij}}} \quad (6)$$

The weighted response ratio (RR_{++}) and 95% confident interval (CI) were calculated by "*rma.mv*" function in the "*metafor*" package. If 95% CI of weighted lnRR did not include zero, the effect of precipitation manipulation was considered as significant (p <0.05).

The effect sizes of the terrestrial C:N:P stoichiometry were grouped by the type of moderator variables (for example, the ecosystem type, humidity, and precipitation magnitude, etc.) in response to the direction and the size of altered precipitation. To test whether the response ratio between the sub-groups differ, we conducted the heterogeneity test (Q_m test). When the Q_m value was significant (p <0.05), the response ratio between each group (ecosystem type, humidity, and precipitation magnitude, etc.) was accepted as different. The weighted response ratio and its 95% confidence interval (CI) were converted to the percentage of changes by altered precipitation to facilitate explanation (as shown in the equation 7) and understanding effects. The weighted RR_{++} greater than 0 indicates the positive effect of altered precipitation on the analyzed variable, and lower than 0 means negative effects.

$$\text{Percentage change} = (e^{RR_{++}} - 1) \times 100\% \quad (7)$$

The sensitivity of each variable is standardized by the magnitude of precipitation change, which helps to evaluate the response of plants, soil and microorganisms. The sensitivity was calculated as follows:

$$\text{Sensitivity} = \frac{RR}{\Delta \text{PPT}} \quad (8)$$

The absolute value of sensitivity reflects the size of sensitivity, positive and negative symbol represents the response direction. The variance (*v*, sensitivity) of sensitivity is calculated using Equation (9).

$$\text{Vsensitivity} = \frac{V_{RR}}{\Delta \text{PPT}^2} \quad (9)$$

The sensitive weighted average (sensitivity_{++}) and the calculation method of its SE are the same as RR_{++}.

The single meta-regression was used to check the relationships between the RR and continuous variables (e.g., magnitude and duration). To examine the heterogeneity of each variable across subgroup categories (plants, soil, microorganisms), we calculated the between-group heterogeneity (Q_m) among ecosystem types (grassland, shrubland and forest), climate humidity (dry and humid) and magnitude of precipitation (slight, medium and extreme). The results of between-group heterogeneity of humidity were classified by HI = 0.65 (Table S2-S4). The relative importance of all possible combinations of the environmental variables was identified to analyze the most important predictors of the effects of altered precipitation on C:N:P stoichiometry using "*glmulti*" package in R software (4.0). The relative importance of each predictor was calculated the sum of Akaike weights containing all models including this predictor using corrected Akaike's Information Criteria (AIC). These values can be considered to the overall effect of each variable in all models. A cutoff of 0.8 was set to distinguish between nonessential and important predictors. The funnel plots were used to explore the possibility of publication bias (Figure S7-S12).

3 | Results

3.1 | Responses of C:N:P stoichiometry to altered precipitation

IPPT had no effects on leaf C, N and P concentrations, but elevated leaf and shoot C:P ratios across all ecosystem types (Figure 2e). DPPT decreased leaf C:N ratio, but increased leaf N:P, litter N (7.5%), root N (4%) and root N:P ratio across all ecosystem types (Figure 2b and f). Compared with ambient precipitation, IPPT increased soil C (4.4%) and N (3.5%) concentration; and C:P ratio, but DPPT reduced soil C (4.4%), N (5.2%) concentrations, and C:P ratio (Figure 2a, b, and e). IPPT increased microbial biomass C, N, and P by 13%, 15%, and 26%, respectively (Figure 2a-c), but DPPT reduced microbial biomass N (12%) and N:P ratio (Figure 2b and f).

Figure 2

3.2 | Response of plant, soil and microbial C:N:P stoichiometry to altered precipitation in dry and humid climates

IPPT and DPPT have opposite impacts on plant-soil-microbial C:N:P stoichiometry in dry and humid areas (Figure 3). In dryland, IPPT increased leaf and soil C:P by 7.8% and 4.8% (Figure 3e), respectively. Similarly, IPPT increased C and N concentration of soil (4.6% and 3.7%) and microbes (16% and 19%) in dryland. IPPT raised the C and N concentration in microbial biomass 4-6 times greater than in soil in drylands (Figure 3a and b). DPPT had no effect on plant, soil and microbial C:N:P except increased leaf N concentration in dryland (Figure 3b). In humid climate, DPPT decreased soil N and N:P by 6.7%, 13%, respectively, but increased leaf N and N:P by 19%, 13%, respectively (Figure 3b and f).

Figure 3

3.3 | Sensitivity of plant, soil and microbial C:N:P stoichiometry to altered precipitation

Leaf C:N and N:P were sensitive to medium DPPT because of N concentration was sensitive to medium DPPT (Figure 4b, d and f), but leaf C:P was sensitive to medium IPPT (Figure 4e). Soil C:P were sensitive to medium IPPT owing to the sensitivity of soil C to medium IPPT (Figure 4a and e). Soil C, N, C:N, C:P and N:P were sensitive to medium DPPT (Figure 4a, b, d-f), whereas soil N, C:P and N:P sensitive to slight DPPT (Figure 4a, e and f). In contrast, microbial biomass C, N, and C:N were sensitive to slight IPPT (Figure 4a-d). Microbial biomass C:N were sensitive to extreme DPPT the sensitivity of microbial biomass N (Figure 4b and d).

When the data is grouped by dry and humid ecosystems, the plants, soil, and microorganisms respond differently to altered precipitation (Table S1). C and C:P of plants in dry ecosystems were sensitive to medium IPPT, but not sensitive to DPPT (Table S1). In contrast, N, C:N and N:P of plants in humid ecosystem were sensitive to medium DPPT, but not sensitive to IPPT (Table S1). Soil C:N:P were majorly sensitive to medium IPPT in dry and humid ecosystem. N, C:N and N:P of soil microorganisms were sensitive to slight IPPT in dry and humid ecosystem, but not sensitive to DPPT (Table S1). In addition, microbes were majorly sensitive to extreme IPPT in dry ecosystem (Table S1).

Figure 4

3.4 | Factors influencing the response of plant-soil-microbial C:N:P stoichiometry to altered precipitation

Model (summed Akaike weights) selection analysis demonstrated that plant N, C:N and N:P were best explained by MAP and MAT, but none of the variables reached the Akaike threshold of 0.8 on C, P and C:P to altered precipitation (Table 1). In contrast, precipitation magnitude was the most important factor affecting soil and microbial C:N, C:P and N:P ratios.

Linear regression analysis confirmed that leaf and root N concentrations as well as N:P ratio elevated with increasing MAP, but leaf and root C:N declined with increasing MAP (Figure S1b, c and f). Soil C, N, C:P and microbial biomass C and N:P elevated with the increasing precipitation magnitude, but microbial biomass C:N decreased with increasing precipitation magnitude (Figure S2a,b, d-f).

4 | Discussion

4.1 | Response of C:N:P stoichiometry to altered precipitation

Altered precipitation affects plant and microbial growth by changing the soil water availability, and altering the fate of C sequestration (Abbasi et al., 2020b; Beier et al., 2012; Rousk et al., 2013). DPPT decreased leaf C:N, and increased leaf N:P, litter N, root N and N:P. DPPT decreased soil water content, and consequently the capacity of uptake of P more than the capacity to take up N by plants, thus diminishing proportionally more the leaching losses of soil N than of P and resulting in increased N:P ratio in plant communities. Higher plant N:P ratio can favor species with low growth rate, and is favorable for adapting to arid environments (Sardans et al., 2021). Decreased C:N ratio in leaves, litters and roots by DPPT were mostly attributed to a loss of N use efficiency due to more severe water limitation and decreased activity of key enzymes involved in photosynthesis (e.g., ribulose 1,5-bisphosphate carboxylase/oxygenase) in plants (Flexas et al., 2006; Zhou et al., 2016). DPPT decreased the leaf C:N ratio in forest ecosystems and humid regions (Figure 3d and 6d), demonstrating that N is accumulated in leaves of trees (Figure 3). The possible mechanisms were that plants have closer symbiotic associations with AM fungi to increase N and P uptake and water use efficiency under drought stress (Figure 6; Mariotte et al., 2017). This situation reduced soil nutrient concentrations, which was supported by that DPPT decreased soil C, N and C:P compared with ambient precipitation owing to P uptake is more seriously limited than that of N under drought (Figure 2a, b and e). Similarly, DPPT reduced microbial biomass N and N:P (Figure 2b and f), and the possible mechanism is that drought led to the dieback of microbial cells, and decreased microbial biomass N concentration (Gu et al., 2019). These changes prompted the decline of microbial N use efficiency, and decreased microbial activities (Zeglin et al., 2013).

Compared with ambient precipitation, IPPT effects on plant, soil and microbial C:N:P stoichiometry were of minor importance than the observed under DPPT except elevated leaf and shoot C:P (Figure 2 a-f). This could be mainly related to that IPPT increased P use efficiency, litter inputs and P mineralization consistent with previous studies (Austin et al., 2000), which altered the balance of C and P in leaf and shoot. IPPT increased soil and microbial biomass C and N concentration (Figure 2a and b) because IPPT increased plant biomass (Figure S4), and provided more litter input belowground and rhizodeposition (Figure 6, Clark et al., 2009; Khalili et al., 2016). The increased C resource enhanced the availability of soluble substrates for microbial communities (Figure S5, Clark et al., 2009; Khalili et al., 2016). Subgroup analysis found that IPPT mainly affected microbial biomass C:N:P in dry areas and grasslands (Figure 3), indicating microbial communities in dry ecosystems are susceptive to increased precipitation. Increased precipitation increased litter input and decomposition rates, which provided the nearest photosynthate to soil microbes (Austin & Vitousek, 2000; Hao et al., 2017). Medium precipitation stimulates exudation of root metabolites, which act as enzymes leading to rapid decomposition of organic material and release of labile C (Clark et al., 2009; Zhou et al., 2018). IPPT declined the microbial biomass C:N ratio, which was related to the shifts in microbial communities to higher precipitation (Zhou et al., 2018). Increasing soil water availability increased the growth of bacteria with high C:N (Hess & Austin, 2017; Li et al., 2020).

Figure 6

Figure 7

Plants and microbes can maintain or alter their biomass nutrient composition to adapt to changes of nutrient availability in soil by precipitation changes. Leaf N:P increased with soil N:P, indicating that the leaf N:P is plastic (S = 0.78, Figure 7f). Leaves with high N and P concentrations tend to be short lived and structurally fragile, with high specific leaf area and photosynthetic activity (Sardans et al., 2012). Strong stoichiometric homeostasis of soil microbes under altered precipitation with the non-significant relationships between soil C:N:P stoichiometry and microbial biomass C:N:P (Figure 7d-f). Soil microbes actively adjusted physiologically to adapt to changes in soil N and P resources despite changing soil moisture (Yang et al., 2011; Xu et al., 2013). Homeostasis regulation is essential for microbial growth, which is a critical physiological regulation in maintaining microbial biomass production (Heuck et al., 2015; Sterner & Elser, 2002). Most soil microbes are heterotrophic and thought to exhibit stronger homeostasis behavior at the organic level than autotrophs (Clark et al., 2009). Decreased precipitation increases fungi and decrease bacterial abundance, because fungi have stronger anti-drought stress cell walls and extended hyphal structure to efficiently extract water, leading to higher C:N (Ullah et al., 2021). Therefore, altered precipitation shift the microbial homeostasis through altering microbial community composition (Clark et al., 2009; Delgado-Baquerizo et al., 2017).

4.2 | Sensitivities of C:N:P stoichiometry to precipitation changes

Leaf N concentration, C:N and N:P ratios were sensitive to medium DPPT (Figures 4b, d and f), further confirmed that DPPT mainly affected the N cycle of plants. Drought can increase plant N uptake in humid areas (Wu et al., 2022), thus with high sensitivity of leaf N concentration, C:N and N:P ratios to DPPT in humid regions (Table S1). One important possible mechanism is that drought can diminish N losses by leaching (Austin & Vitousek, 2000; Hao et al., 2017). Specially, humid area has high soil moisture, and medium drought could increase soil aeration can favor root activity and increase N uptake by roots from soil (Deng et al., 2021; Farooq et al., 2009; Hertel et al., 2013). Subgroup analysis further revealed that soil C and N concentrations, and C:N, C:P and N:P ratios were sensitive to medium DPPT (Table S1). These results were consistent with the response of forests to DPPT (Figure S6), suggesting that forests are more vulnerable to drought. The possible mechanism is that long-term drought increased the mortality of single trees, and forests need more water for their greater stand biomass are the biomes more affected by drought, thus it takes longer to fully restore the level before the stress owing to the stomatal and/or photochemical limitation. These results were consistent with the decreased annual precipitation in most subtropical regions (Harper et al., 2005).

Soil microbial biomass C and N concentrations, and C:N ratio were sensitive to slight IPPT (Figure 4a-d), and microbial biomass N concentration and C:N ratio were also sensitive to extreme DPPT (Figure 4b and d). Similarly, microbial biomass C, N and P concentrations and C:N ratio respond to IPPT, not to DPPT (Figure 5), and the response of microbial biomass N concentration to IPPT (15%) is greater than that to DPPT (12%). These results were consistent with the prediction of the double asymmetric model proposed by Knapp et al. (2017). Soil water availability after severe drought reduce solute diffusivity and inhibit microbial growth due to the inability to access substrates under dry conditions (Ren et al., 2017; Schimel et al., 2007). In dry areas, DPPT reduced soil microbial activities, which in turn are more susceptible to water availability (Schimel et al., 2007; She et al., 2018).

Soil microbes (N, C:N and N:P) were sensitive to slight IPPT in dry and humid ecosystem (Table S1). Slight IPPT can increase water availability and relieve water stresses for soil microorganisms, promoting microbial nutrient absorption and growth (Huxman et al., 2004). Small precipitation events, especially in dry ecosystems, eliminated water-induced substrate limitation and increases microbial biomass C, N and P concentrations as observed in previous studies (Davidson et al., 2012; Evans & Wallenstein, 2014; Wang et al., 2021). Therefore, precipitation change regimes alter water sensitivity and ultimately influencing microbial growth in terrestrial ecosystems.

Figure 5

4.3 | Driving factors of C:N:P stoichiometry response to altered precipitation

Plant, soil and microbial C:N:P stoichiometry responses to altered precipitation were affected by climate factors and precipitation magnitude. This study found that the response ratio of leaf and root N concentration and C:N ratio were related to MAP (Figure S1b and d), indicating that plant N was closely related to MAP changes to altered precipitation. This relationship can be attributed to the gradients of ecosystem N cycle along environmental and experimental factors (Xu et al., 2020; Yue et al., 2017). Plant growth depends on the net photosynthetic rate, photosynthetic efficiency, which mainly directly affected by climate factors (Farooq etal., 2009). N is a component of chlorophyll and an essential element for photosynthetic enzymes, and MAP can directly or indirectly increase N absorbed by the roots and their ability to transport to plant organs by changing vegetation composition and soil biogeographic processes (Sardans et al., 2012; Yue et al., 2019). In addition, the N cycle between plants and soil is faster in low-latitude bio communities with high MAP, accompanied by high N gas or leaching losses, and biological nitrogen fixation capacity, such as subtropical and tropical forests (Deng et al, 2018). Different ecosystems dominate species distributions due to differences in climate factors. Ecosystem type influenced plant N concentration (Table S2, $Q_m = 9.67$, $p = 0.02$) and C:N ratio (Table S2, $Q_m = 11.87$, $p = 0.008$) ratios under DPPT, but not in grasslands and deserts ecosystems (Figure S6). This differential response is that plant functional types (e.g., nitrogen-fixing species) differ between ecosystem types (Pugnaire et al., 2019). Consequently, leaf stoichiometry to altered precipitation is specific across sites with climate conditions.

Leaf N, soil C and microbial biomass C concentrations, C:N, and N:P ratios were related to the magnitude of altered precipitation (Figure S2a, d and f). These results were consistent with previous meta-analysis (Knapp et al., 2015; Zhou et al., 2018). Increased precipitation elevated soil water availability, and accelerates microbial decomposition of soil organic matter in arid ecosystems (Wang et al., 2021; Zeglin et al., 2013). Decreased precipitation leads to a linear relationship between plant and microbial responses with precipitation changes (Abbasi et al., 2020; Dijkstra et al., 2012). These relationships result from the normal range of treatment magnitudes in most precipitation experiments worldwide (Wang et al., 2021). When combined with extreme precipitation, the responses of other plant-microbial processes deviated from the linear relationship with precipitation variation amplitude (Luo et al., 2017). Extreme drought results in impaired photosynthesis, decreased microbial nutrient mineralization, and even death of plants and microorganisms, while extreme precipitation brings excess water, restricted soil oxygen, and limit plant and soil microbial growth (Wang et al., 2020). Therefore, more extreme precipitation (⩾67%) and multiple levels of precipitation experiment should be performed to assess whether these linear relationships hold under extreme conditions in the future.

4.4 | Implications of precipitation changes for C cycle and future research

The N-related variables of plants, soil and microbes were sensitive to altered precipitation (Figure 6), which suggested that N cycles altered the growth and metabolism of plants and microbes. Previous studies have demonstrated that N limited plant primary productivity and C sequestration in various ecosystems (Elser et al., 2007; Vitousek et al., 2010). In general, N rapidly accumulates from the atmosphere through biological N fixation that dominate the early stages of ecosystem development (Delgado-Baquerizo et al., 2017; Sardans et al., 2021). But, N accumulates slowly from the atmosphere through atmospheric deposition and biological fixation and tend to become less limiting in more advanced successional stages (DeMott & Pape, 2005; Luo et al., 2017). Most free-living microbial communities are N-limited, and secreted N acquiring-extracellular enzymes that catalyzed organic matter decomposition (Hewins et al., 2016; Mariotte et al., 2017). These processes can construct plant and microbial cell walls, depolymerize macromolecules, and ultimately provide soluble substrates for microbial assimilation (Henry et al., 2005; Kaiser et al., 2014). Therefore, altered precipitation not only affect the N-related leaf photosynthesis, and net primary productivity (Nielsen & Ball, 2015), but also influence the soil extracellular enzyme activities by microbes involved in N mineralization, and ultimately affect the accumulation of soil organic carbon (Waldrop et al., 2004; Yuan & Chen, 2015).

Precipitation manipulation experiments have been conducted across the world, but there are some limitations and uncertainties in experimental studies of precipitation change. Available data for some parameters or processes are still limited, for example, the number of studies of leaf C, N, and P concentrations, C:N, C:P, and N:Pratios in shrubland ecosystems is less than 10 (Figure 3). The distribution of sampling points is also an important factor that increases the uncertainty of meta-analysis. Most of the experiments are in the northern Hemisphere, such as China, Europe and the United States (Figure 1). Savanna ecosystems in the Southern Hemisphere, particularly from tropical and subtropical regions of Africa, contributed to uncertainty in the analysis of this study. Overall, although the meta-analysis identified the importance of ecosystem type, rainfall intensity, and climate on plant-soil-microbial C:N:P stoichiometry, most of the studies had short experimental periods (< 10 years). As a result, a comprehensive understanding of how precipitation affects plant-soil-microbial nutrient dynamics over time scales of more than a decade is still lacking (Yue et al., 2019). The rewetting process during the precipitation treatment period (early or late vegetation season), precipitation period and the first precipitation after precipitation also had important effects on plant-soil-microbial C:N:P stoichiometry dynamics.

5 | Conclusions

The systematic response of C, N and P concentration and consequently the C:N:P stoichiometry to altered precipitation across the globe provides unparalleled insights into ecosystem biogeochemical processes by increased and decreased precipitation. Drought increased leaf C:N ratio, but increased leaf N:P ratio on a global scale. Increased precipitation elevated soil C, and N concentrations, while DPPT decreased them. Increased precipitation increased microbial biomass C, N and P concentrations, whereas drought reduced microbial biomass N concentration and N:P ratio due to the changes in microbial community composition. Plant communities were more sensitive to decreased precipitation than to increased precipitation, especially in humid areas. Soil and microbes were more sensitive to increased precipitation than to decreased precipitation, especially in dry areas. MAP and precipitation magnitude regulated the response of plant-soil-microbial C:N:P stoichiometry to altered precipitation. Consequently, incorporating the specific aspects of precipitation intensity and N-related traits into the framework of global climate predictions could tribute to a deeper understanding of precipitation mediated C dynamics.

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Author contributions

J.L. and L.D. designed the research, J.L. and L.D. collected the data, J.L. performed the research, J.L., L.D., J.P., and Y.K. analysed the data, J.L., L.D. and J.W. visualized the figures, and J.W., L.D. J.P., J. S., S.Z., and Y.K. wrote the paper.

Declaration of Competing Interest

All the authors declare no competing interests.

Supplementary information

Appendix table S1-S4 and Appendix figures S1-S12.

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Tables and Figures:

Table 1 Model-averaged importance of the predictors of the effects of altered precipitation on plant, soil, and microbial C, N, P, concentrations, C:N, C:P and N:P ratios.

	Variables	MAT	MAP	HI	Ecosystem type	Duration	Magnitude
Leaf	C	0.2324	0.3457	0.2889	0.1026	0.2166	0.5436
	N	**0.9919**	**0.9996**	**0.9853**	0.1090	0.3604	0.4409
	P	0.2267	0.3862	0.535	0.086	0.2454	0.6695
	C:N	0.4691	**0.8228**	0.6106	0.2598	0.5273	**0.8051**
	C:P	0.3468	0.3479	0.2331	0.0880	0.2118	0.6027
	N:P	**0.8412**	**0.8123**	0.4925	0.3584	0.6629	0.2339
Soil	C	0.6647	0.4293	0.3293	0.5690	0.2681	**1**
	N	0.5464	0.3439	0.5094	**0.9676**	0.2612	**0.9957**
	P	0.2475	0.5597	0.3501	0.6661	0.3780	**0.9629**
	C:N	0.2491	0.2894	0.4183	0.0747	0.4285	0.7165
	C:P	0.2919	0.4678	0.5714	0.1984	0.3314	**1**
	N:P	0.2959	0.4393	0.3565	0.1581	0.3421	**1**
Microbial biomass	C	0.4381	0.3453	0.3092	**0.8624**	0.2717	**1**
	N	0.2836	0.2810	0.2668	0.2118	0.2822	**1**
	P	0.2858	0.2737	0.2628	0.1295	0.3439	**0.8116**
	C:N	0.2810	0.4105	0.3440	0.2895	0.3242	**1**
	C:P	0.0074	0.0002	0.1786	0.0542	0.0518	0.0006
	N:P	0.2375	0.2376	0.2323	0.0650	0.4812	0.3898

Importance is estimated from the sum of Akaike weights based on model selection analysis using corrected Akaike's Information Criteria (AIC). Cutoff is set at 0.8 to explore the most essential variables. MAP, mean annual precipitation; MAT, mean annual temperature; HI, humidity index. The black bold values indicate the cutoff values >0.8.

Figure captions:

Figure 1 Geographical distribution of the studied sites included in this meta-analysis. The subset figure indicated the whole range of mean annual precipitation (MAP) and mean annual temperature (MAT) of the study sites and the respective ecosystems.

Figure 2 Responses of C (a), N (b), P (c) concentrations, C:N (d), C:P (e), N:P (f) ratios in leaves, shoots, litter, soil, and microbial biomass to altered precipitation. Values are weighted effect sizes and their 95% confidence intervals. Values represent the strength of the effect of altered precipitation on response variables relative to the control, numbers indicate the number of observation data. The effect of precipitation treatments is considered significant if the 95% CI of the effect size does not overlap with zero. IPPT, increased precipitation; DP, decreased precipitation. The solid symbols indicate significant response to altered precipitation, and hollow symbols indicate no significant response to altered precipitation.

Figure 3 Responses of C (a), N (b), P (c) concentrations, C:N (d), C:P (e), N:P (f) ratios in leaves, soil, and microbial biomass to altered precipitation in dry (HI < 0.65) and humid climates (HI > 0.65). Values are weighted effect sizes and their 95% confidence intervals. Values represent the strength of the effect of altered precipitation on response variables relative to the control, numbers indicate the number of data observations. The effect of precipitation treatments is considered significant if the 95% CI of the effect size does not overlap with zero. IPPT, increased precipitation; DPPT, decreased precipitation. The solid symbols indicate significant response to altered precipitation, and hollow symbols indicate no significant response to altered precipitation.

Figure 4 The sensitivity of C (a), N (b), P (c) concentrations, C:N (d), C:P (e), N:P (f) ratios in leaves, soil and microbial biomass to ΔPPTs binned by slight (≦ 33%), medium (33% ~ 67%) and extreme (≥ 67%) IPPT and DPPT. The error bars represent 95% confidence intervals; the numbers above the error bars represent the observation numbers for each estimate; and the following asterisks indicate significant responses (the 95% confidence intervals do not overlap with zero). IPPT, increased precipitation; DPPT, decreased precipitation. The solid symbols indicate significant response to altered precipitation, and hollow symbols indicate no significant response to altered precipitation.

Figure 5 A conceptual framework for the double asymmetric responses of plant, soil and microbial biomass C:N:P stoichiometry to altered precipitation in the globe. The solid lines indicate significant response to altered precipitation, and hollow lines indicate no significant response to altered precipitation.

Figure 6 Potential mechanisms of the influences of altered precipitation on ecosystem processes driving plant, soil and microbial C:N:P stoichiometry in the globe. WUE, water use efficiency; DOC, dissolved organic carbon; NH_4^+–N, ammonia nitrogen concentration, and NO_3^-–N, nitrate nitrogen concentration. The blue short arrows (↑↓) represent increase and decrease in response to IPPT, red short arrows (↑↓) represent increase and decrease in response to DPPT. ①Wu et al., (2011), ②Zhou et al. (2016), ③Deng et al. (2021).

Figure 7 Relationships between plant, microbial and soil C:N:P stoichiometry by altered precipitation. *S* represents the slope of the regression between plant or microbial communities (C:N, C:P or N:P) and resource stoichiometry (soil C:N, C:P, or N:P). Plant or soil microbial communities are strong stoichiometric homeostasis whhen the S was not significant ($p > 0.05$). The data with significant regressions were classified as homeostatic plastic ($S > 0.75$), weakly plastic ($0.5 < S < 0.75$), weakly homeostatic ($0.25 < S < 0.5$), or homeostasis ($0 < S < 0.25$) (Sterner, & Elser, 2002).

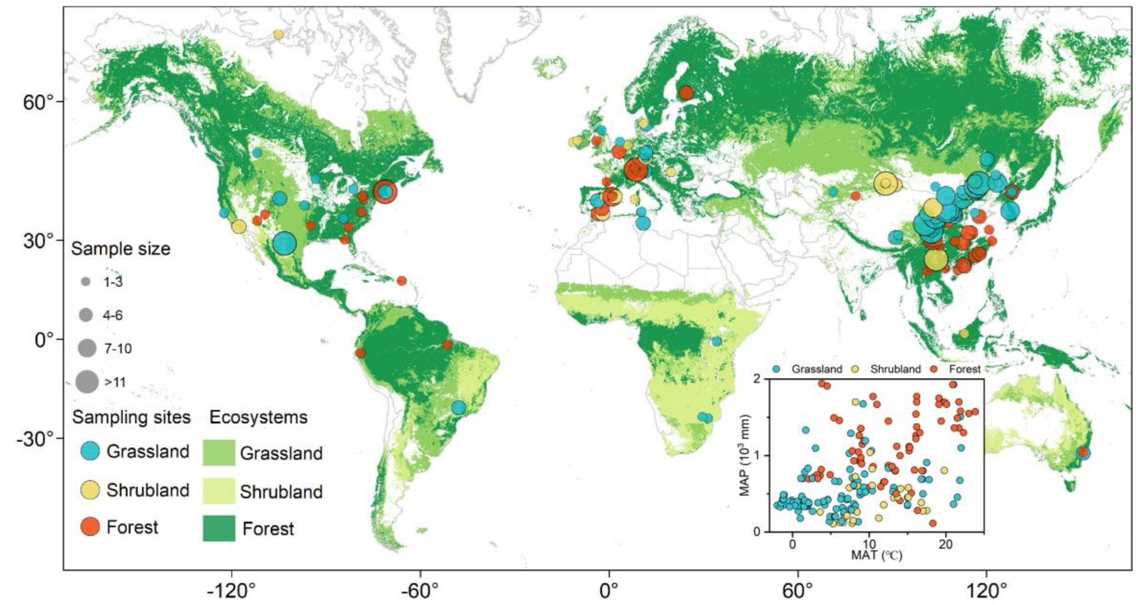

Figure 1 Geographical distribution of the studied sites included in this meta-analysis. The subset figure indicated the whole range of mean annual precipitation (MAP) and mean annual temperature (MAT) of the study sites and the respective ecosystems.

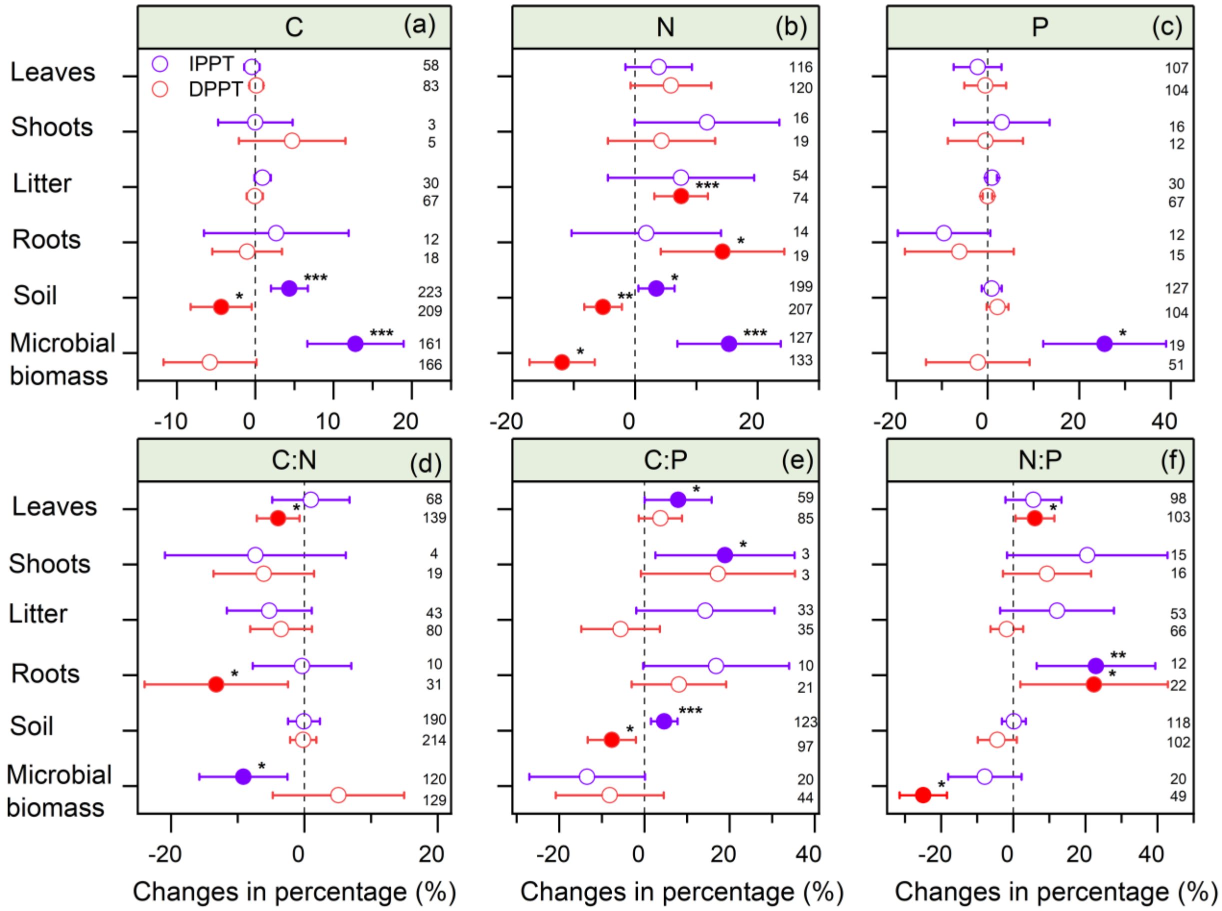

Figure 2 Responses of C (a), N (b), P (c) concentrations, C:N (d), C:P (e), N:P (f) ratios in leaves, shoots, litter, soil, and microbial biomass to altered precipitation. Values are weighted effect sizes and their 95% confidence intervals. Values represent the strength of the effect of altered precipitation on response variables relative to the control, numbers indicate the number of observation data. The effect of precipitation treatments is considered significant if the 95% CI of the effect size does not overlap with zero. IPPT, increased precipitation; DPPT, decreased precipitation. The solid symbols indicate significant response to altered precipitation, and hollow symbols indicate no significant response to altered precipitation.

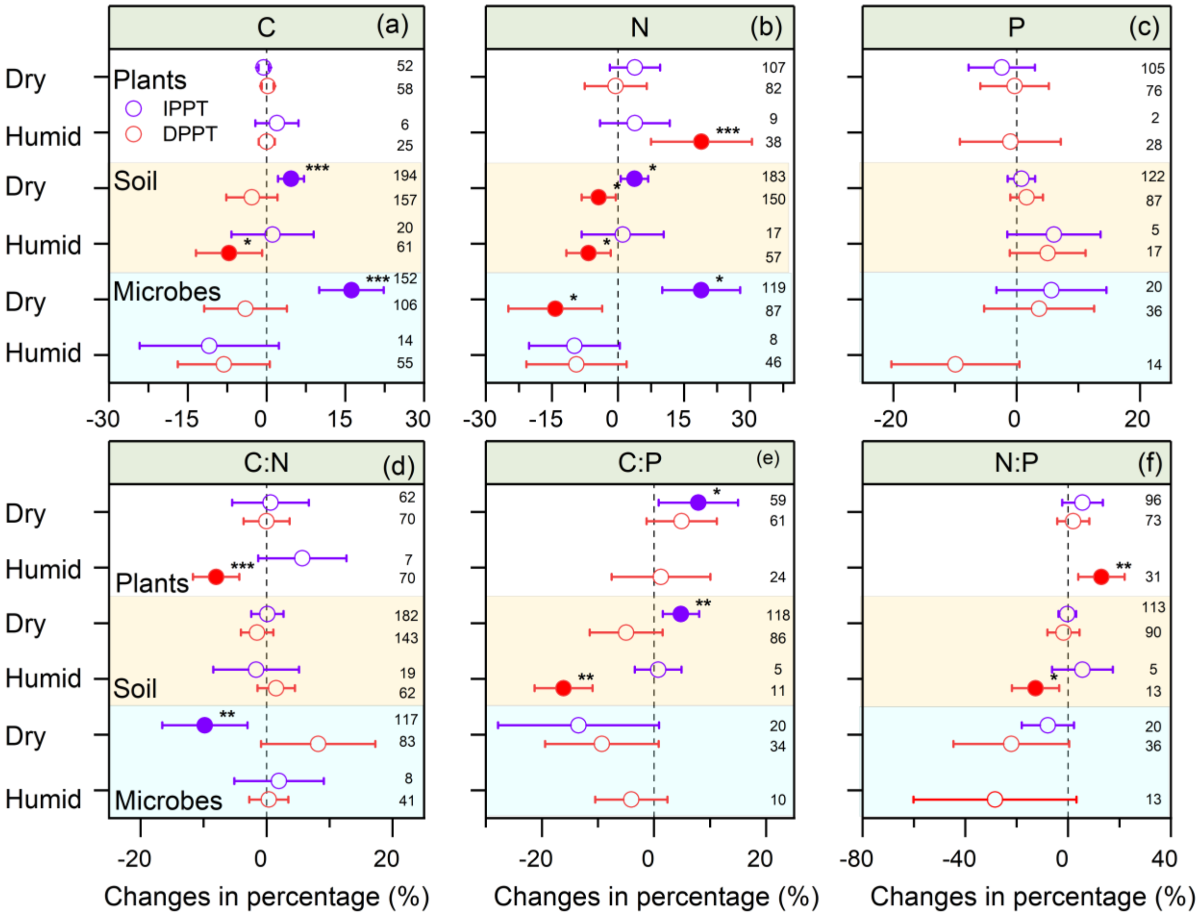

Figure 3 Responses of C (a), N (b), P (c) concentrations, C:N (d), C:P (e), N:P (f) ratios in leaves, soil, and microbial biomass to altered precipitation in dry (HI < 0.65) and humid climates (HI > 0.65). Values are weighted effect sizes and their 95% confidence intervals. Values represent the strength of the effect of altered precipitation on response variables relative to the control, numbers indicate the number of data observations. The effect of precipitation treatments is considered significant if the 95% CI of the effect size does not overlap with zero.IPPT, increased precipitation; DPPT, decreased precipitation. The solid symbols indicate significant response to altered precipitation, and hollow symbols indicate no significant response to altered precipitation.

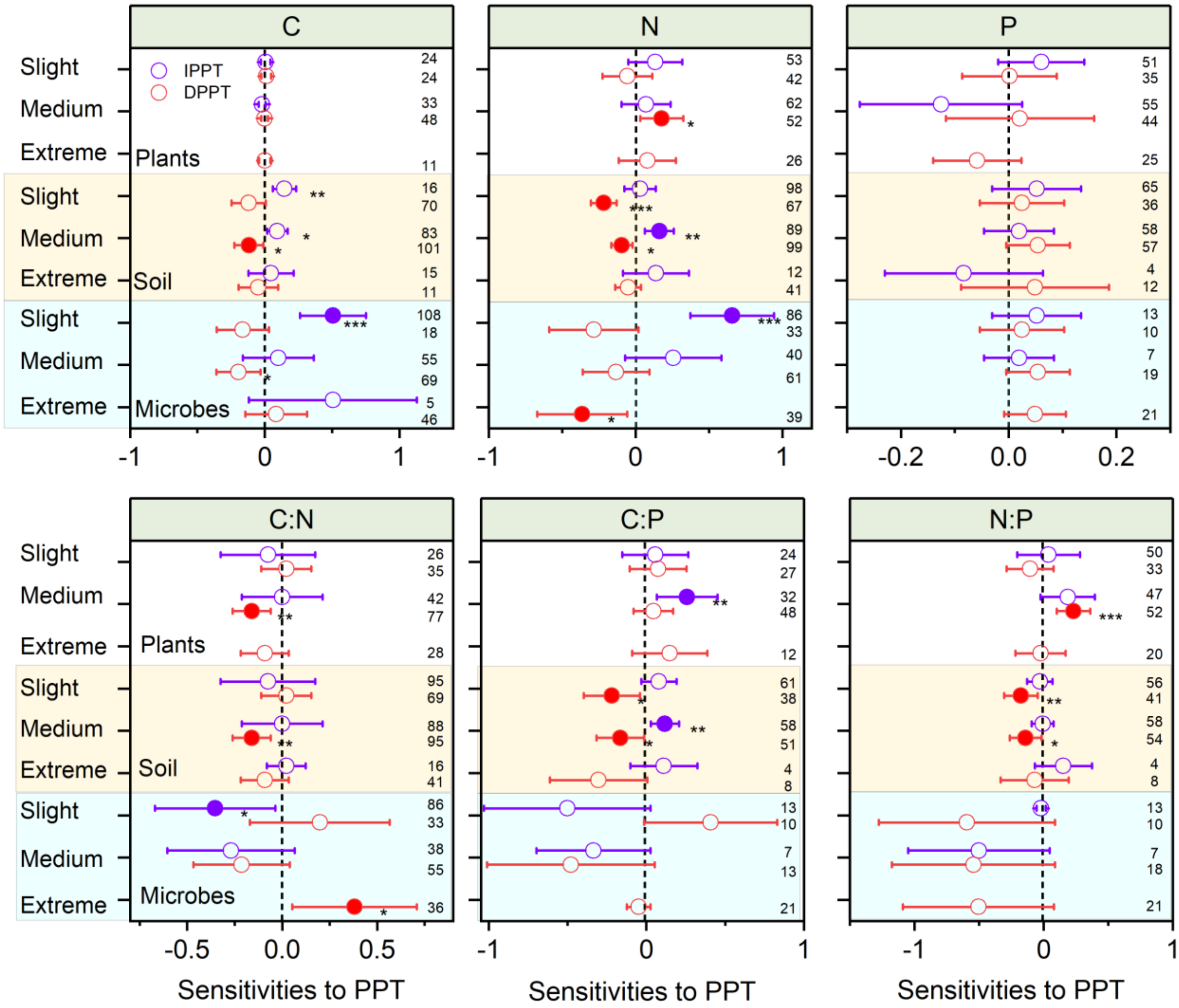

Figure 4 The sensitivity of C (a), N (b), P (c) concentrations, C:N (d), C:P (e), N:P (f) ratios in leaves, soil and microbial biomass to ΔPPTs binned by slight (≦ 33%), medium (33% ~ 67%) and extreme (≥ 67%) IPPT and DPPT. The error bars represent 95% confidence intervals; the numbers above the error bars represent the observation numbers for each estimate; and the following asterisks indicate significant responses (the 95% confidence intervals do not overlap with zero). IPPT, increased precipitation; DPPT, decreased precipitation. The solid symbols indicate significant response to altered precipitation, and hollow symbols indicate no significant response to altered precipitation.

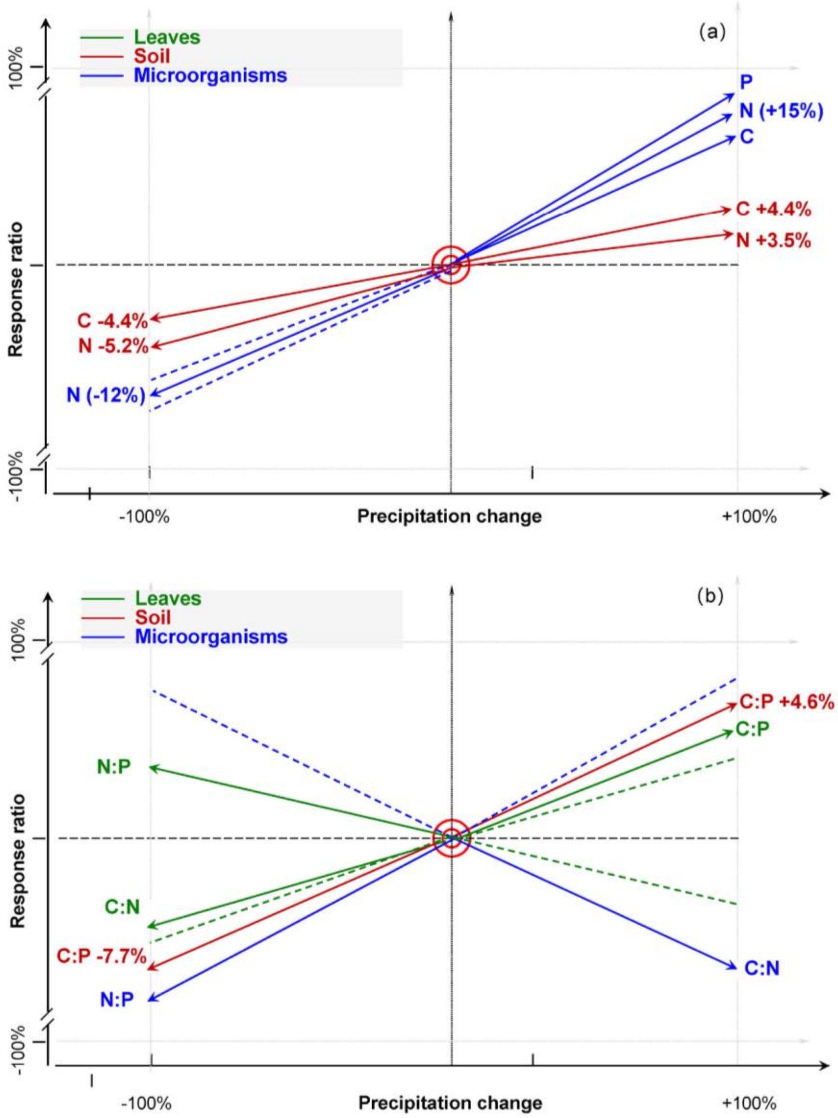

Figure 5 A conceptual framework for the double asymmetric responses of plant, soil and microbial biomass C:N:P stoichiometry to altered precipitation in the globe. The solid lines indicate significant response to altered precipitation, and hollow lines indicate no significant response to altered precipitation.

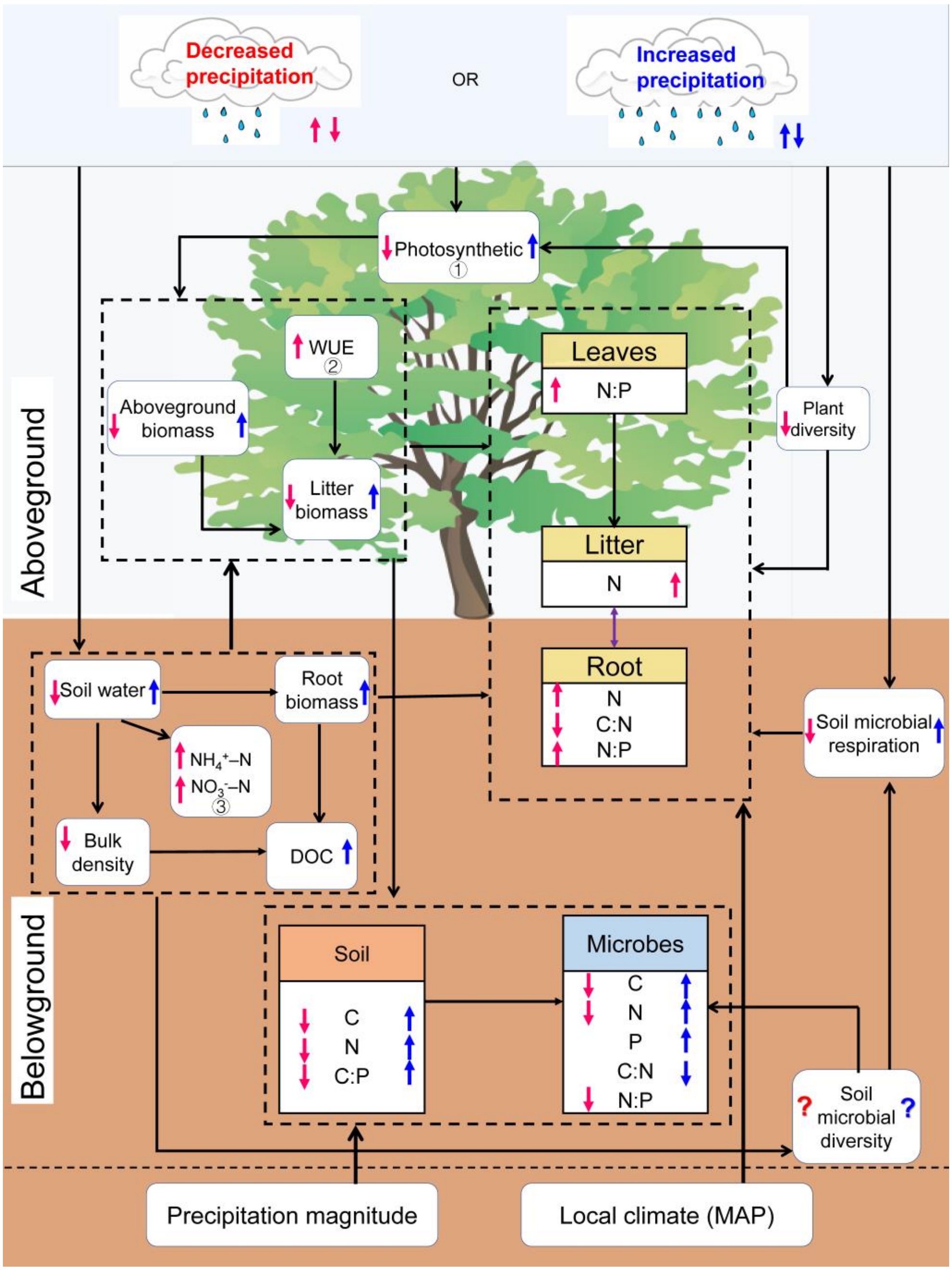

Figure 6 Potential mechanisms of the influences of altered precipitation on ecosystem processes driving plant, soil and microbial C:N:P stoichiometry in the globe. WUE, water use efficiency; DOC, dissolved organic carbon; NH_4^+–N, ammonia nitrogen concentration, and NO_3^-–N, nitrate nitrogen concentration. The blue short arrows (↑↓) represent increase and decrease in response to IPPT, red short arrows (↑↓) represent increase and decrease in response to DPPT. ①Wu et al., (2011), ②Zhou et al. (2016), ③Deng et al. (2021).

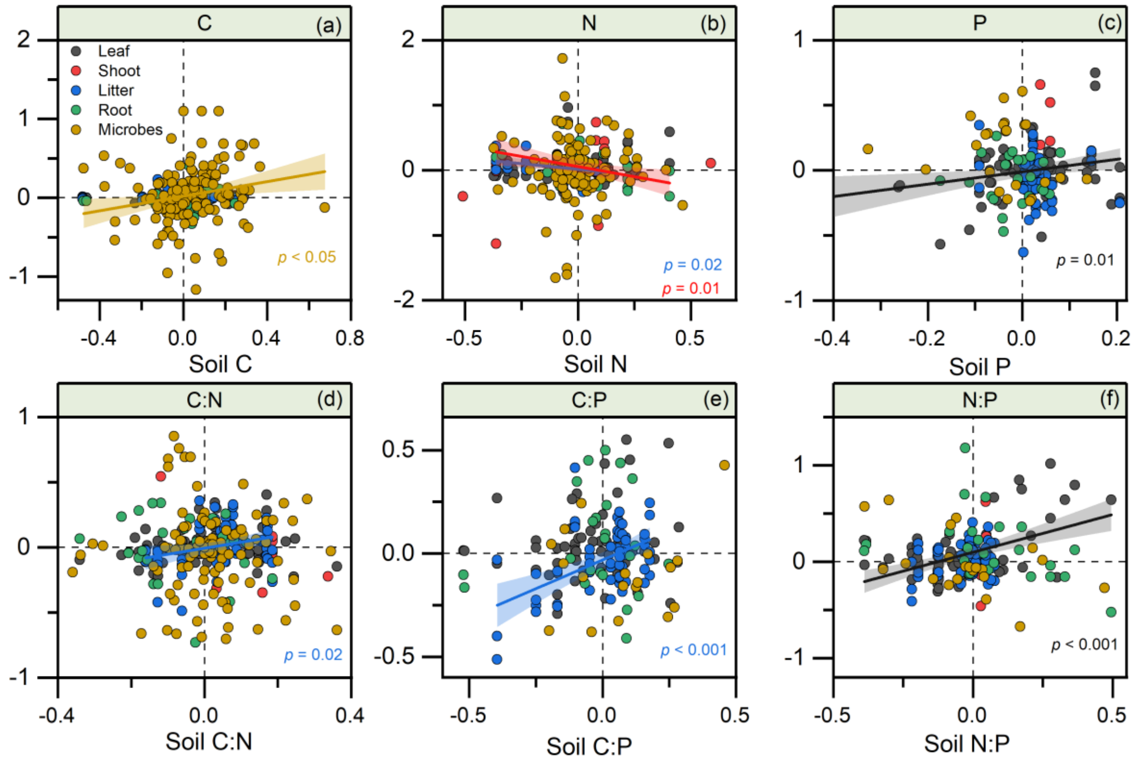

Figure 7 Relationships between plant, microbial and soil C:N:P stoichiometry by altered precipitation. S represents the slope of the regression between plant or microbial communities (C:N, C:P or N:P) and resource stoichiometry (soil C:N, C:P, or N:P) responses ratio (RR). Plant or soil microbial communities are strong stoichiometric homeostasis whhen the S was not significant ($p > 0.05$). The data with significant regressions were classified as homeostatic plastic ($S > 0.75$), weakly plastic ($0.5 < S < 0.75$), weakly homeostatic ($0.25 < S < 0.5$), or homeostasis ($0 < S < 0.25$) (Sterner, & Elser, 2002).