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# High adaptability of *Pinus sylvestris* var. *mongolica* to drought-induced soil nutrient deficiency

Jingling Zhang<sup>1,3</sup>, Guigang Lin<sup>1,2\*</sup>, Qiong Zhao<sup>4</sup> and De-Hui Zeng<sup>1,2\*</sup>

## Abstract

**Background:** Drought can exert a profound influence on soil nutrient availability, and understanding whether and how tree species adapt to this change is a critical priority for predicting the consequence of climate change on forest structure and function. The objective of this study was to examine the adaptability of Mongolian pine (*Pinus sylvestris* var. *mongolica*) to drought-induced changes in soil nutrient availability from the perspective of root functions.

**Methods:** We conducted a 7-year precipitation manipulation experiment with three levels of throughfall reduction (0%, 30%, and 50%) to simulate different drought intensities. We measured soil physicochemical properties and fine-root nutrient concentrations and biomass, and calculated the stoichiometric homeostatic regulation coefficient ( $1/H$ ) of fine roots.

**Results:** Drought reduced soil organic carbon (C), nitrogen (N), phosphorous (P) and inorganic N concentrations, as well as ratios of total N to total P, and available N to available P in the 0–20 cm soil layer. In contrast, drought had no significant effect on fine-root N and P concentrations, and fine-root biomass in the 0–40 cm soil layer. Fine roots displayed high homeostatic regulation coefficients of N (with  $1/H$  values of 0.19 and 0) and P (with  $1/H$  values of 0.33 and 0) concentrations in 0–20 and 20–40 cm soil layers, respectively.

**Conclusions:** Our results indicate that drought leads to soil nutrient deficiency and the decoupling between N and P cycling, and provide evidence that Mongolian pine has high adaptability to drought-induced decrease in soil nutrient availability by maintaining great fine-root biomass to ensure sufficient nutrient uptake.

**Keywords:** C:N:P stoichiometry, Fine-root biomass, Stoichiometric homeostasis, Throughfall reduction

## Introduction

Drought is a great threat to ecosystem health in many regions around the world, and likely to be more frequent, severe, and longer duration in the future under the context of climate changes (Ault 2020), with significant consequences for forest ecosystem services (Sardans and Peñuelas 2012; Shi et al. 2014). Until now, most studies have largely concentrated on aboveground response to

drought (de Meira Junior et al. 2020; López et al. 2021; Vargas et al. 2021); however, few studies have systematically explored the dynamic interactions between roots and soil physicochemical properties (Phillips et al. 2016; Tauca et al. 2020). Thus, it is critical to uncover the belowground responses to drought for better predicting the effects of future climate change on forest ecosystem functions.

Ecological stoichiometry represents the balance of multiple chemical elements, especially for carbon (C), nitrogen (N) and phosphorus (P), and reflects the interactions of soil environment with plants, providing a critical perspective for assessing how belowground systems respond

\*Correspondence: lingg@iae.ac.cn; zengdh@iae.ac.cn

<sup>1</sup> CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China  
Full list of author information is available at the end of the article

to drought stress (Austin and Vitousek 2012; Sterner and Elser 2002). Stoichiometric homeostasis is a central concept of ecological stoichiometry, which is defined as the ability of plants to maintain relatively constant elemental concentrations or ratios irrespective of soil environment changes (Yu et al. 2015). High stoichiometric homeostasis in organs means the great adaptability of plants in responses to changes in soil nutrient availability induced by drought (Yu et al. 2010).

Drought stress has significant effects on soil nutrient availability, especially for N and P. Soil N mainly derives from atmospheric N fixation, and its availability is largely controlled by biological processes, such as N mineralization, nitrification and denitrification processes (Yang et al. 2020). In contrast, soil P availability depends not only on biological processes such as immobilization and mineralization of organic P, but also on geochemical processes including weathering and adsorption/desorption of inorganic P (Hou et al. 2018; Jiao et al. 2016). Drought can alter soil N and P availability through inhibiting soil microbial activity and promoting the lysis of dead and live cells of soil microorganisms (Gao et al. 2020; Zhang et al. 2020). With increasing aridity, soil N and P cycles could become decoupled due to the different degrees in the effect of drought on N-related and P-related processes (Delgado-Baquerizo et al. 2013). Indeed, numerous studies have reported that drought reduced soil total N concentration, but not total P concentration in forest ecosystems (Delgado-Baquerizo et al. 2018; Sardans et al. 2020; Sun et al. 2020).

Fine roots are the primary pathway for water and nutrient uptake by trees (Ostonen et al. 2011), and play a crucial role in maintaining tree growth and forest ecosystem functions (Lin and Zeng 2017). Fine-root nutrient concentrations reflect tree nutritional and growth status, and nutrient homeostasis in fine roots reflects the adaptability of trees to drought and is a critical mechanism to maintain forest ecosystem stability (Elser et al. 2010). Soil nutrient availability regulates fine-root nutrient concentrations by changing root nutrient uptake capacity under drought conditions (Zang et al. 2021). Tree's nutrient storage, remobilization and foraging strategies can help to maintain fine-root nutrient homeostasis under drought (Rennenberg et al. 2006; Schlesinger et al. 2016). Dead fine-root biomass, live fine-root biomass, and turnover rates are important indicators for understanding the belowground ecological processes in response to environmental changes (Hu et al. 2021; Jackson et al. 1997). Plant can increase root biomass by allocating more photosynthates to roots under drought, which can improve root nutrient uptake capacity (Brunner et al. 2015; Liu et al. 2017; Zhou et al. 2020). Therefore, evaluating fine-root nutrient status, stoichiometric homeostasis and

biomass could improve our understanding of whether tree species can adapt to drought-induced changes in soil nutrient availability (Sardans et al. 2021).

In this study, we aimed to explore the effect of drought on soil N and P availability and to examine the adaptability of Mongolian pine (*Pinus sylvestris* var. *mongolica*) to this change in soil nutrient availability from the view of root functions. To achieve this aim, we conducted a 7-year precipitation manipulation experiment with three levels of throughfall reduction (0, 30, and 50%) to simulate different drought intensities in a Mongolian pine plantation at the Horqin Sandy Lands, Northeast China. We measured soil physicochemical properties and fine-root nutrient concentrations and biomass, and calculated the stoichiometric homeostatic regulation coefficient of fine roots. Based on this experiment design, the following hypotheses were tested: (1) drought would reduce soil N and P availability by inhibiting microbial activities, and this inhibitory effect would be stronger for N than P because soil P availability is also partly controlled by geochemical processes; and (2) as drought-resistant species (Zhu et al. 2008), Mongolian pine would have high nutrient homeostasis under drought through maintaining great fine-root biomass to ensure sufficient nutrient uptake. This study could have important implications for understanding the adaptation of trees to changes in nutrient availability induced by climate change from the perspective of root functions.

## Materials and methods

### Study site and experiment design

This study was conducted at the Daqinggou Ecological Station (42°58'N, 122°21'E, 260 m above sea level) in the south-eastern Horqin Sandy Lands, Northeast China. This study site has a dry sub-humid temperate climate with mean annual temperature of 6.4 °C. The mean annual precipitation is 450 mm with most precipitation occurring between June and August. The mean annual evapotranspiration and aridity index (1–precipitation/reference evapotranspiration, Whitford 2002) are 1780 mm and 0.75, respectively. Mongolian pine plantation was established using 4-year-old seedlings with 2 × 5 m spacing on the slope degree of less than 2° in 2003. Tree height and diameter at breast height were measured in October 2019, with average values being 7.49 m and 13.56 cm, respectively. Dominant understory species include *Artemisia scoparia*, *Agropyron cristatum* and *Lepedeza davurica* (Hu et al. 2019).

The throughfall manipulation experiment was initiated in May 2013. The experiment was designed with three treatments: control, a 30% throughfall reduction and a 50% throughfall reduction. Each treatment had three replicates. Nine 15 × 15 m plots were established in the

Mongolian pine plantation. Replications of all the three treatments were arranged randomly in the nine plots. In order to prevent interference between plots, an approximately 5 m wide buffer zone was established between adjacent plots. A 40 cm deep buffer ditch was excavated and lined with 5 mm thick  $\times$  50 cm high PVC boards to inhibit lateral water movement and interflow.

Throughfall reducing facilities were composed of rain shields, support frames and drain pipes. The V-shaped transparent acrylic plate of 3 mm thick and 5 m long was used as the rain shield. Nine support frames (without drain pipes) were arranged in the control (Fig. 1a), and the rain shield was inverted V-shaped (56 rain shields), so as to eliminate the effects of rain shield on the light interference. The plots with 30% throughfall reduction (Fig. 1b) had nine support frames with fixed V-shaped rain shield, and the number of rain shield was 56, which can cover 30% of the ground area and reduce throughfall by approximately 30%. The plots with 50% throughfall reduction (Fig. 1c) had nine support frames with 107 V-shaped rain shields, which can cover 50% of the ground area and reduce throughfall by approximately 50%. The reduced throughfall was drained from plots through the drain pipes.

#### Rainfall measurement

Rainfall amount data were derived from the weather station of the Daqinggou Ecological Station. We recorded the rainfall events based on the daily rainfall amount during the growing season (May–October) in 2013–2019,

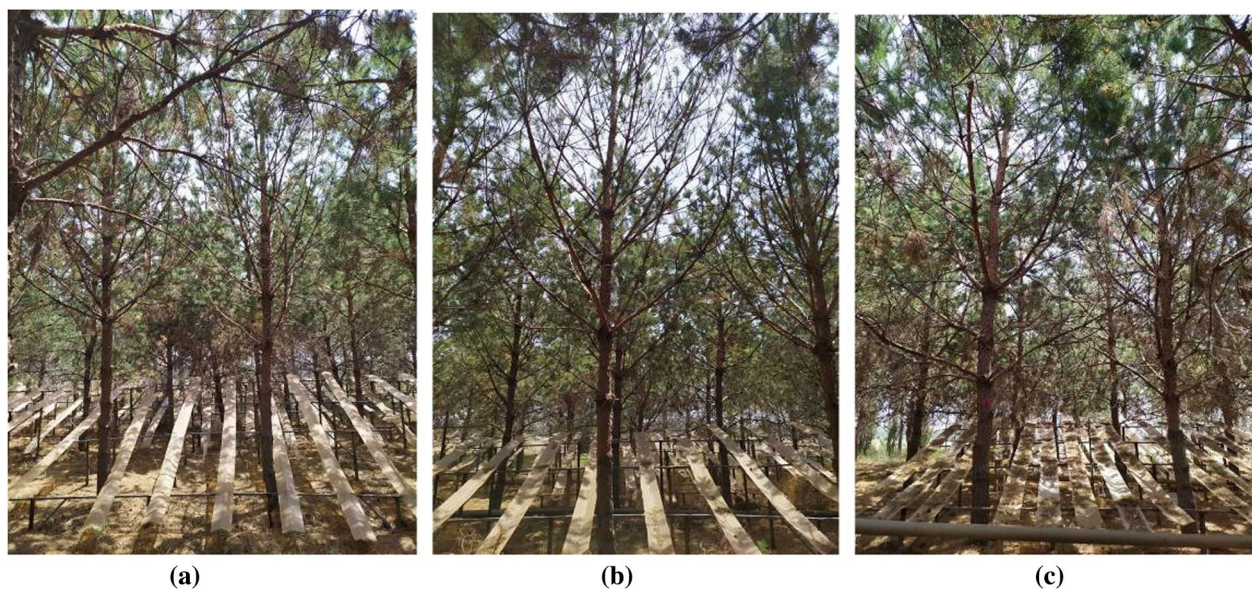
and classified it into six levels including 0–5, 5–10, 10–15, 15–20, 20–25 and 25–50 mm (Wei et al. 2017).

#### Soil and root sampling and measurement

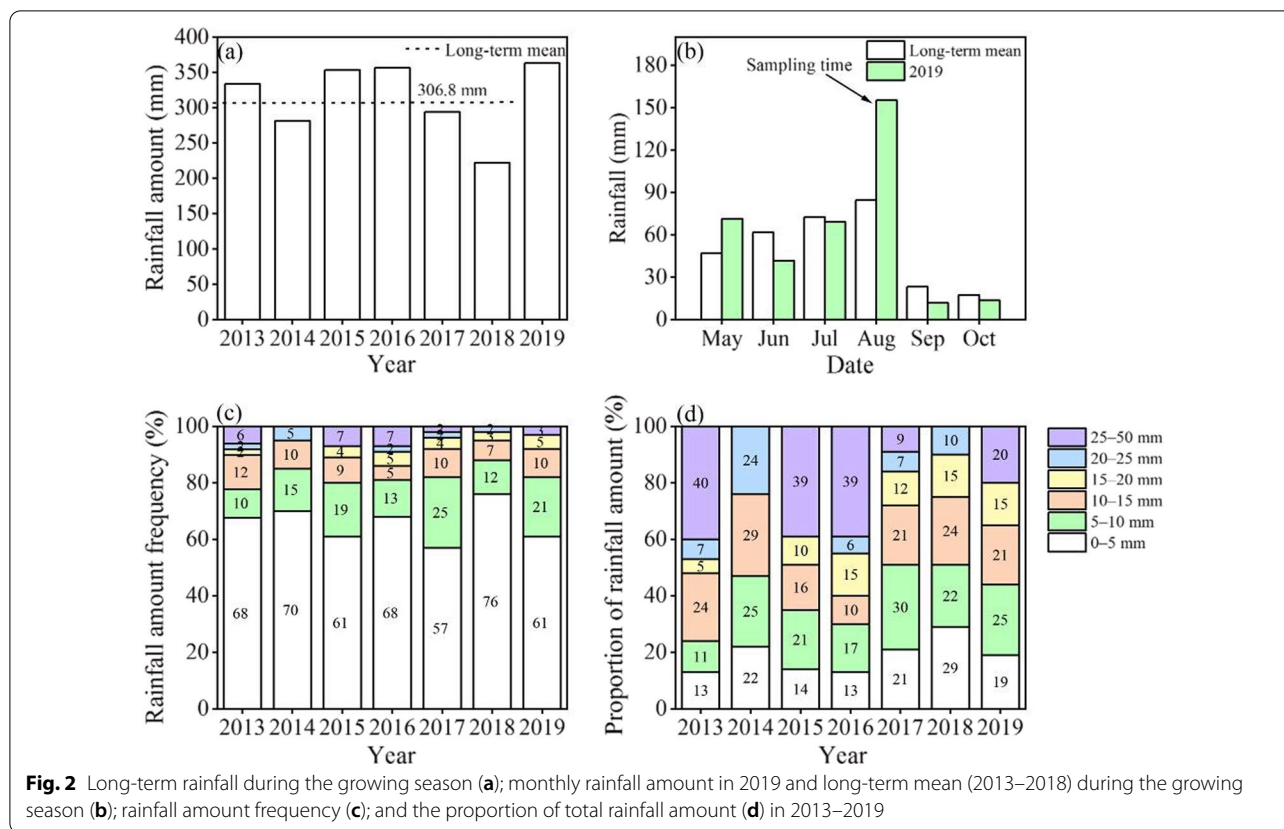
Soil and root samples were collected in August 2019. Soil cores (inner diameter 6 cm) were sampled at two depth intervals of 0–20 and 20–40 cm, and a total of 12 soil cores were randomly chosen for analysing soil physico-chemical and fine-root properties in each plot. Each soil core was gently loosened to pick out intact root branches and broken root segments. After that, soil samples were sieved by a 2 mm mesh. Collected soil and root samples were transported to a laboratory within 2 h and frozen at  $-18^{\circ}\text{C}$  for further analyses.

Collected root samples were gently washed with deionized water, and understory (e.g. grasses and forbs) roots were identified and then discarded based on the differences between Mongolian pine roots and understory roots in morphology, architecture and colour. In this study, roots  $\leq 2$  mm in diameter were defined as fine roots and coarse roots (e.g.  $> 2$  mm in diameter) were picked out and discarded. After that, total fine roots were classified into dead and live fine roots based on their differences in morphology, toughness and colour (Vogt and Persson 1991). Dead and live fine-root samples were weighed after oven drying at  $65^{\circ}\text{C}$  for 72 h. Then, live fine roots were ground by a ball mill for chemical analyses.

Soil water content was measured by oven drying at  $105^{\circ}\text{C}$  to constant weight. The measured soil chemical properties included soil inorganic N ( $\text{NH}_4^+\text{-N}$  and



**Fig. 1** Three throughfall reduction treatments in a Mongolian pine plantation: control (a), no throughfall exclusion; 30% drought (b), 30% of throughfall exclusion area; 50% drought (c), 50% of throughfall exclusion area



NO<sub>3</sub><sup>-</sup>-N), Olsen-P, organic C, total N and P concentrations. Soil inorganic N concentration was determined by a continuous-flow autoanalyzer (AutoAnalyzer III, Bran + Luebbe GmbH, Germany) after extracting with 2 M KCl. Soil Olsen-P concentration was measured using the molybdate blue method after extracting with 0.5 M NaHCO<sub>3</sub> (Olsen et al. 1953). Soil organic C and fine-root C concentrations were determined using the K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub>-H<sub>2</sub>SO<sub>4</sub> wet oxidation method (Nelson and Sommers 1996). Soil and fine-root total N and P concentrations were determined by the continuous-flow autoanalyzer after digesting with H<sub>2</sub>SO<sub>4</sub>.

**Calculation and statistical analysis**

To assess the homeostatic regulation ability of Mongolian pine in response to drought, we calculated the homeostatic regulation coefficient (1/H) using the nutrient concentrations of fine roots and soils according to the following equation (Sterner and Elser 2002):

$$\lg y = \lg c + 1/H \times \lg x$$

where *y* represents fine-root N or P concentrations, *x* represents soil total N or P concentrations in each soil layer, and *c* is a constant. If the regression relationship is not significant (*P* > 0.05), then 1/H is set at zero, and the organism is considered as ‘strictly homeostatic’. If the regression relationship is significant (*P* < 0.05), then 1/H > 0 was interpreted as follows: 0 < 1/H ≤ 0.25, ‘homeostatic’; 0.25 < 1/H ≤ 0.50, ‘weakly homeostatic’; 0.50 < 1/H ≤ 0.75, ‘weakly plastic’; 1/H > 0.75, ‘plastic’ (Bai et al. 2019; Persson et al. 2010).

All data were tested for normality and variance homogeneity separately using the Shapiro–Wilk test and the Levene’s test. If data did not satisfy the normality and variance homogeneity assumptions, they were log<sub>10</sub>-transformed prior to analyses. Two-way ANOVA was performed to test the effects of drought treatment, soil depth, and their interaction on soil and fine-root properties. Moreover, one-way ANOVA was separately conducted to analyse whether there were significant differences in soil and root properties among drought treatments in 0–20 and 20–40 cm soil layers. Independent

**Table 1** Two-way ANOVA test (*F* values) for the effects of drought treatment (D), soil depth (SD), and their interaction (D × SD) on soil water content and nutrient availability, fine-root nutrients and biomass

Variables	D	SD	D × SD
Soil water content	15.68***	12.72**	0.45
NH <sub>4</sub> <sup>+</sup> -N	0.39	54.83***	0.90
NO <sub>3</sub> <sup>-</sup> -N	7.97**	24.09***	3.39*
Inorganic N	4.79*	40.50***	2.71
Olsen-P	1.99	97.49***	1.02
Available N:P	3.82*	10.84**	0.77
Soil organic C	11.86***	112.90***	3.02
Soil total N	10.81***	56.79***	3.15
Soil total P	10.12***	68.59***	3.67*
Soil C:N	2.42	3.71	1.37
Soil C:P	1.80	47.70***	0.34
Soil N:P	4.56*	15.59***	1.26
Root C	0.54	6.11*	0.34
Root N	1.14	124.14***	1.65
Root P	0.90	40.62***	0.65
Root C:N	4.23*	95.26***	4.43*
Root C:P	1.21	17.19***	0.71
Root N:P	0.12	0.06	0.05
Dead fine-root biomass	0.34	72.22***	2.30
Live fine-root biomass	3.00	55.87***	0.90
Total fine-root biomass	1.44	81.64***	0.23

\**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001

*t*-tests were performed to analyse the differences in soil and root properties between 0–20 cm and 20–40 cm soil layers across each drought treatment. Post hoc mean comparison was performed by the least significant difference. Redundancy analyses (RDA) were separately conducted to analyse whether variation in fine-root nutrient concentrations and biomass can be explained by soil physicochemical properties in 0–20 cm and 20–40 cm soil layers. The RDA was carried out using the Canoco 5.0, and ANOVAs using the SPSS Statistics 21. Significant level of all analyses was set at  $\alpha = 0.05$ .

## Results

### Rainfall conditions

During the growing season (May–October) of 2013–2018, the rainfall amount ranged from 222.4 to 356.2 mm, with a mean value of 306.8 mm (Fig. 2a). The rainfall amount in 2019 when we collected soil and root samples was 363.0 mm, representing 118.3% of the long-term mean rainfall amount with an increase mainly occurring in August (Fig. 2b). The daily rainfall amount mainly

distributed in 0–5 mm, and the frequency ranged from 57 to 76%, followed by the 5–10 mm (10%–25%) in growing seasons over the past 7 years (2013–2019, Fig. 2c). In addition, the proportion of 0–10 mm rainfall amount in total rainfall amount (May–October) was 24–51% in 2013–2019 (Fig. 2d).

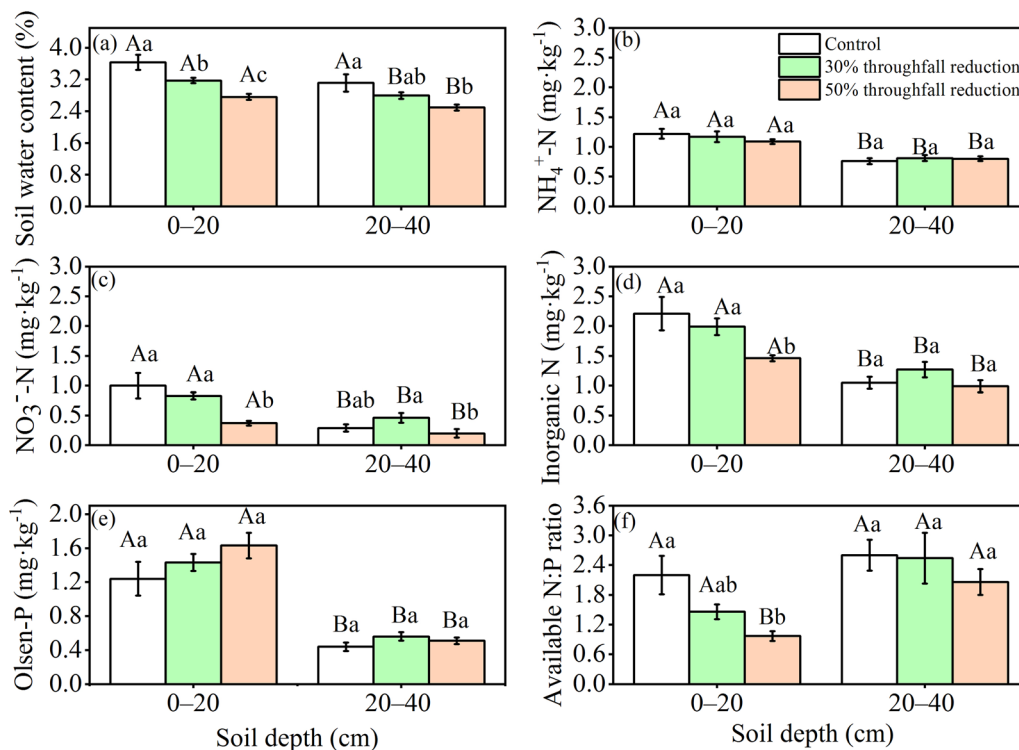
We recorded 61 rainfall events from May to October 2019. The rainfall amount mainly distributed in 0–5 mm with 37 rainfall events, and the frequency was 61%, followed by the 5–10 mm (13 rainfall events, 21%). There were only 2 rainfall events (3%) higher than 25 mm. Moreover, the proportion of 0–10 mm rainfall amount in total rainfall amount was 44% in 2019.

### Soil water content and nutrient availability

Soil water content was significantly affected by drought and soil depth, but not by their interaction (Table 1). Generally, soil water content was decreased by throughfall reduction across the two soil layers. Meanwhile, soil water content was higher in 0–20 cm than in 20–40 cm soil layers in drought treatments but not in the control treatment (Fig. 3a).

Drought significantly decreased soil nutrient availability, and exhibited a greater inhibitory effect on soil N availability than P availability. Specifically, soil NH<sub>4</sub><sup>+</sup>-N concentration was not significantly affected by drought, but significantly by soil depth with higher values in 0–20 cm than in 20–40 cm soil layers (Table 1, Fig. 3b). Soil NO<sub>3</sub><sup>-</sup>-N (Fig. 3c) and inorganic N (Fig. 3d) concentrations were significantly decreased by drought in the 0–20 cm soil layer with a greater inhibitory effect in the treatment of 50% throughfall reduction. In the 20–40 cm soil layer, soil NO<sub>3</sub><sup>-</sup>-N concentration was highest in the 30% throughfall reduction treatment, followed by the control and 50% throughfall reduction treatments. Moreover, soil NO<sub>3</sub><sup>-</sup>-N and inorganic N concentrations were higher in 0–20 cm than 20–40 cm soil layers. Soil Olsen-P concentration was not significantly influenced by drought treatment, and was significantly lower in 20–40 cm than 0–20 cm soil layers (Table 1, Fig. 3e). Drought significantly reduced soil available N:P ratio in the 0–20 cm but not in the 20–40 cm soil layers (Fig. 3f).

Soil organic C, total N, total P concentrations were significantly affected by drought and soil depth, and only total P concentration was affected by their interaction (Table 1). The 30 and 50% throughfall reduction treatments separately decreased soil organic C concentration by 9.0 and 28.6%, total N concentration by 15.8 and 36.2%, and total P concentration by 8.9 and 26.7% relative to the control treatment (Fig. 4a–c). In the 20–40 cm



**Fig. 3** Effect of drought on soil water content,  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ , inorganic N, Olsen-P concentrations and available N:P ratio (mean  $\pm$  SE,  $n=3$ ) in different soil depths. Different uppercase letters above the bars indicate significant differences between soil layers at each drought treatment, and different lowercase letters above the bars indicate significant differences among three drought treatments at each soil depth

soil layer, drought had no significant effect on total soil nutrients. Additionally, soil organic C, total N and total P decreased with increasing soil depth. Soil C:N ratio was not affected by drought, soil depth and their interaction (Fig. 4d). Soil C:P ratio (Fig. 4e) decreased with increasing soil depth. Soil N:P ratio decreased with increasing soil depth, and was lower in the 50% throughfall reduction treatment relative to the control treatment in the 0–20 cm soil layer (Fig. 4f).

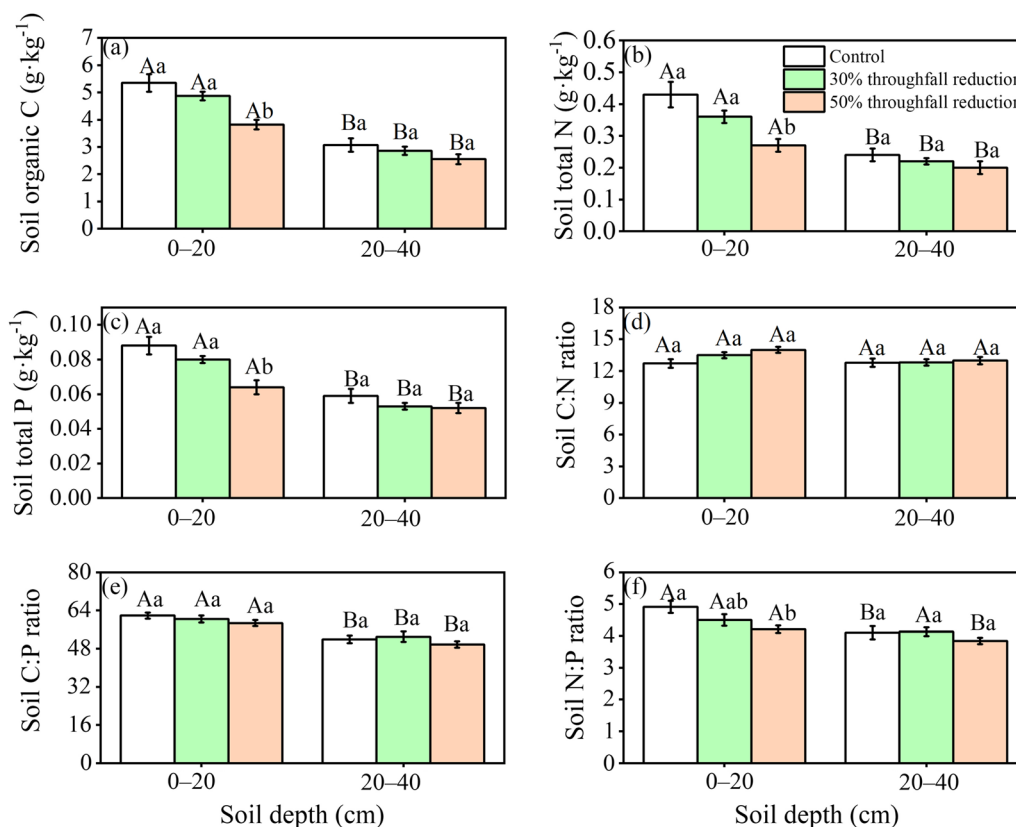
#### Fine-root nutrients and biomass

In contrast with soil physicochemical properties, fine-root nutrients and biomass were not significantly influenced by drought except root C:N ratio (Table 1). In each treatment, there was no significant difference between 0–20 cm and 20–40 cm soil layers in fine-root C concentration (Fig. 5a). Across the three treatments, fine-root N (Fig. 5b) and P (Fig. 5c) concentrations significantly decreased with increasing soil depth. Conversely, fine-root C:N and C:P ratios were significantly higher in 20–40 cm than 0–20 cm soil layers (Fig. 5d–e). Moreover,

fine-root C:N ratio was significantly influenced by drought in the 20–40 cm soil layer (Fig. 5d). Fine-root N:P ratio was not affected by drought, soil depth and their interaction (Fig. 5f). Across the three treatments, dead fine-root biomass (Fig. 6a), live fine-root biomass (Fig. 6b) and total (dead + live) fine-root biomass (Fig. 6c) were significantly higher in 0–20 cm than 20–40 cm soil layers.

#### Relationships of fine-root nutrients and biomass with soil physicochemical properties

Fine-root nutrients showed strong homeostasis in response to drought. Specifically, ‘homeostasis’ and ‘strict homeostasis’ were found in root N concentration in 0–20 cm and 20–40 cm soil layers, respectively. Root N homeostatic regulation coefficients ( $1/H$  value) were 0.19 and 0 ( $P>0.05$ ) in 0–20 cm and 20–40 cm soil layers, respectively (Fig. 7a–b). ‘Weak homeostasis’ and ‘strict homeostasis’ were found in root P concentration with  $1/H$  values of 0.33 and 0 ( $P>0.05$ ) in 0–20 cm and 20–40 cm soil layers, respectively (Fig. 7c–d).



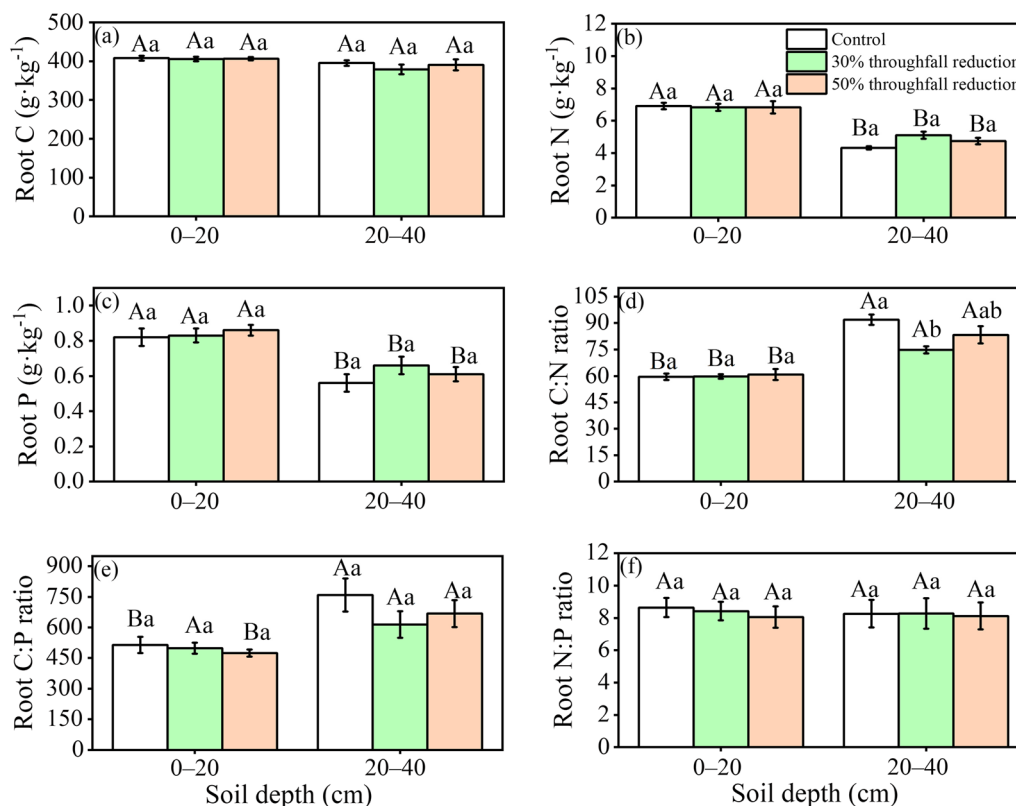
**Fig. 4** Effect of drought on soil organic C, total N, total P concentrations, C:N ratio, C:P ratio and N:P ratio (Mean ± SE,  $n = 3$ ) in different soil depths. Different uppercase letters above the bars indicate significant differences between soil layers at each drought treatment, and different lowercase letters above the bars indicate significant differences among three drought treatments at each soil depth

The RDA analyses showed that all 11 measured soil properties did not explain the variation in fine-root nutrients and biomass in the 0–20 cm soil layer (Monte Carlo test:  $F = 1.3$ ,  $P = 0.338$ , Fig. 8a). However, in the 20–40 cm soil layer, 11 soil properties explained 72.4% of the variation in fine-root nutrients and biomass (adjusted explained variation is 52.2%; Monte Carlo test:  $F = 3.6$ ,  $P = 0.006$ ). Moreover, the 11 soil properties accounted for 71.3% and 0.7% of the correlations with fine-root traits on the first and second axis, respectively (Fig. 8b). Soil water content was the only significant factor that explained 27.9% of variation in fine-root nutrients and biomass.

## Discussion

### Increasing aridity reduced soil nutrients and decoupled N and P cycling

Our result observed that drought significantly reduced soil  $\text{NO}_3^-$ -N and inorganic N concentrations in the 0–20 cm soil layer, which was consistent with the findings of Ren (2012). Two main reasons might be responsible for these results. First, drought can inhibit soil microbial activity by decreasing soil water content, leading to the reduction in soil N transformation rates (Homyak et al. 2017). Second, nitrite-oxidizing bacteria may recover more slowly from stressful conditions than ammonia-oxidizing bacteria (Tappe et al. 1999), and the resultant decreases in nitrification rates might reduce



**Fig. 5** Effect of drought on fine-root C, N, P concentrations, C:N ratio, C:P ratio and N:P ratio (Mean  $\pm$  SE,  $n = 3$ ) in different soil depths. Different uppercase letters above the bars indicate significant differences between soil layers at each drought treatment, and different lowercase letters above the bars indicate significant differences among three drought treatments at each soil depth

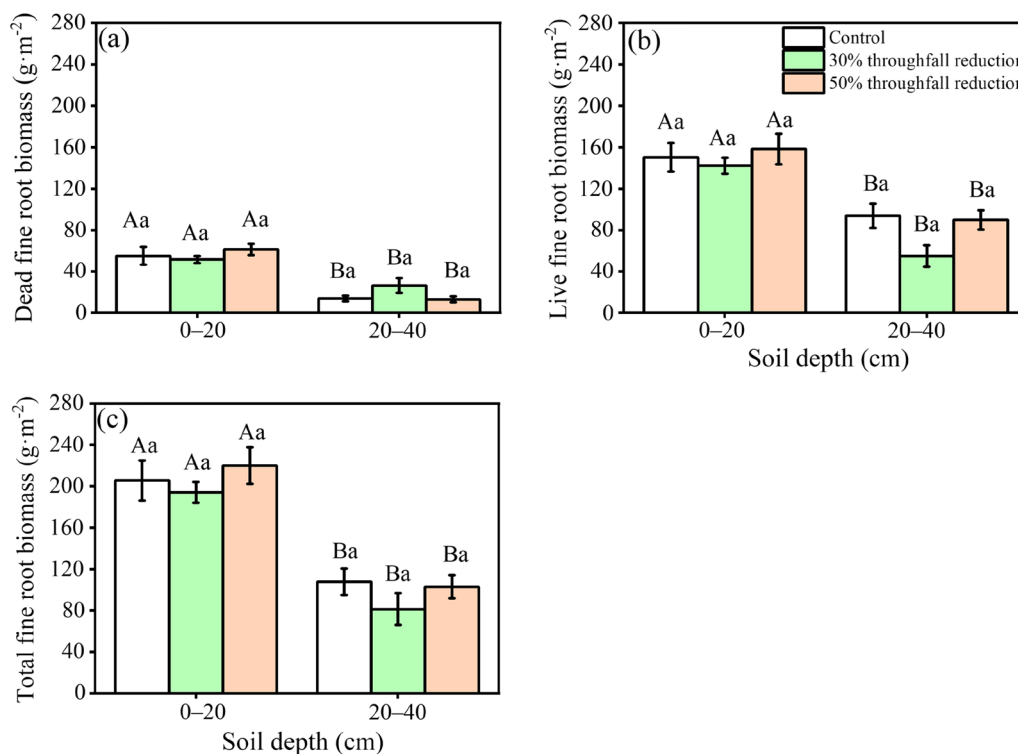
$\text{NO}_3^-$ -N concentration under drought. In the 20–40 cm soil layer, drought caused a higher  $\text{NO}_3^-$ -N concentration in the 30% throughfall reduction than in control and 50% throughfall reduction, which may be due to the increase in N inputs from the lysis of dead soil microorganisms and the decomposition of dead roots (Gao et al. 2020). Indeed, we observed that dead fine-root biomass was slightly higher in 30% throughfall reduction than in control and 50% throughfall reduction in the 20–40 cm soil layer, although not statistically significant (Fig. 6a).

Our result showed that soil total C, N and P concentrations decreased with increasing throughfall reduction, indicating that exacerbated drought might lead to soil nutrient deficiency and degradation (Vitousek 2004). This result is consistent with a previous study showing the decrease in soil nutrients with increasing aridity in a desert ecosystem, north-western China (Zhang et al. 2019). In our study site, the aridity index value is 0.75, indicating that biotic factors might play dominant roles in regulating soil nutrient dynamics (Wang et al. 2019).

Drought-induced decrease in soil organic C concentration might be because drought decreases C input from plants to soil through reducing tree photosynthesis rates (Boyer 1976). The decrease in soil total N and P concentrations especially in the 50% throughfall reduction may be due to the slow transformation of N and P from forest floors to mineral soils under drought conditions (Attiwill and Adams 1993; Deng et al. 2021). Indeed, our previous study has found that drought reduced litter decomposition rates (Xie et al. 2019), thus resulting in the slow return rates of N and P from forest floors to mineral soils under drought.

Our result also showed that soil N and P cycling was decoupled with increasing drought intensities in the 0–20 cm soil layer, which might be owing to the greater reduction in total N than that in total P concentrations. This result is consistent with a study conducted in northern China (Jiao et al. 2016), which demonstrates that decreases in precipitation for most of the temperate grasslands could lead to a soil C–N–P decoupling.



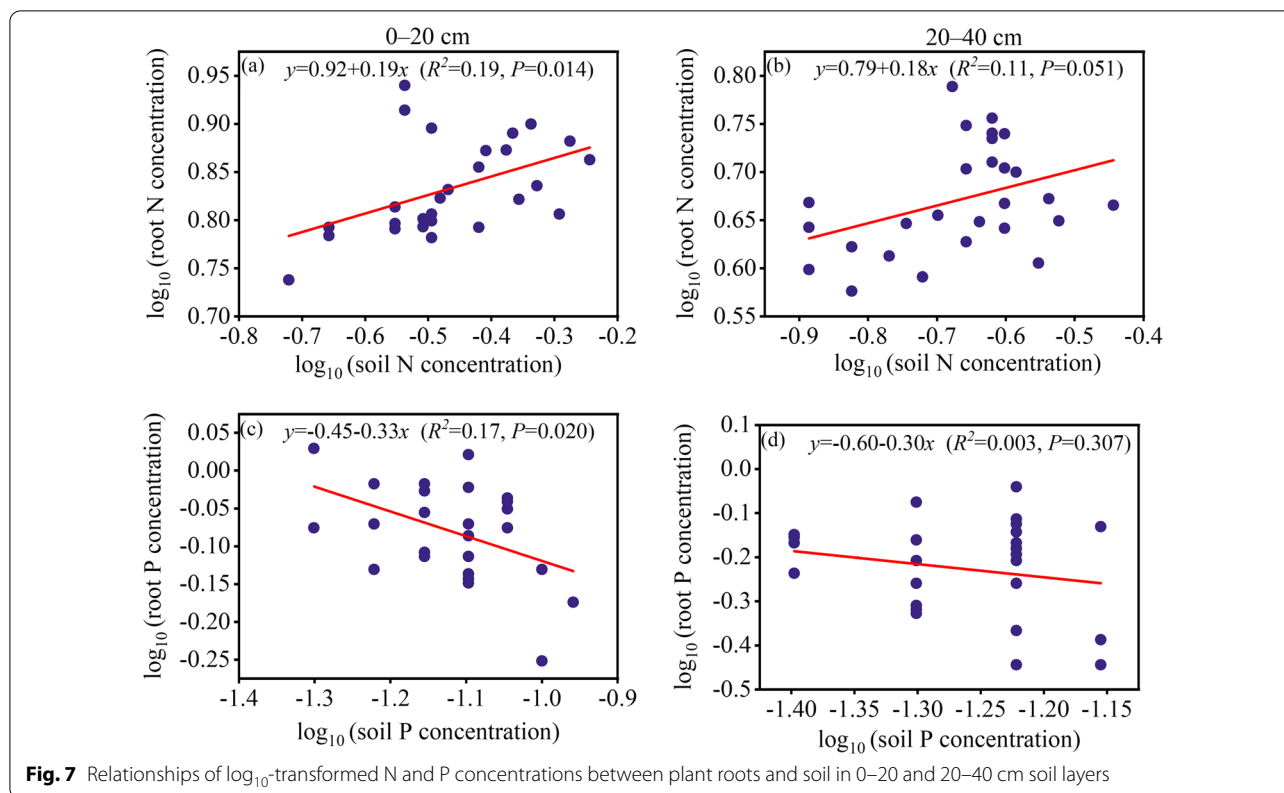


**Fig. 6** Effect of drought on dead, live and total fine-root biomass (mean  $\pm$  SE,  $n = 3$ ) in different soil depths. Different uppercase letters above the bars indicate significant differences between soil layers at each drought treatment, and different lowercase letters above the bars indicate significant differences among three drought treatments at each soil depth

### Mongolian pine exhibited high nutrient homeostasis in response to drought-induced soil nutrient deficiency

Our study showed that drought did not significantly affect fine-root nutrients and biomass in the 0–40 cm soil layer except for the fine-root C:N ratio in the 20–40 cm soil layer. In line with our study, Ji et al. (2020) also reported that root C, N, and P concentrations of three temperate tree species were not significantly influenced by drought stress, but by soil substrates. The no response of fine-root nutrient concentrations to drought may be explained from the perspective of plant adaptation. Plants can acclimate to short-term drought by adjusting phenotypic plasticity and adapt to long-term drought through slow genetic variation (Brodribb et al. 2020; Fang and Xiong 2015). Phenotypic plasticity is the key mechanism for plant adaptation to drought (Richter et al. 2012), which might include the following two aspects in our study. On the one hand, Mongolian pine may increase water uptake and use efficiency through using these three strategies. First, gross rainfall is partitioned into throughfall, interception loss and stemflow through the foliage,

branches and trunk in forest ecosystems (Molchanov 1963). Mongolian pine may increase foliage water uptake from canopy interception and transport to the root system (Liu et al. 2021; Schreel and Steppe 2020). In our study site, the rainfall amount frequency mainly distributed in 0–10 mm (82%), and the rainfall amount proportion of 0–10 mm in total rainfall amount was 44% in 2019 (Fig. 2c–d). The low rainfall amount of 0–10 mm might increase tree canopy interception capacity (Gash 1979). In addition, our studied Mongolian pine plantation was 21 years old and had long needle leaves, large branch angle with high stand density (1156–1422 trees ha<sup>-1</sup>), and thus resulted in high canopy interception capacity (Li et al. 2015). Second, when water availability decreases, Mongolian pine may improve its water-use efficiency under drought through decreasing stomatal conductance (Song et al. 2019). Third, when soil water content does not meet the water requirement of tree growth, Mongolian pine may increase root construction in deep soil to obtain water from groundwater besides soil water. Indeed, Song et al. (2020) showed that groundwater



could contribute up to 30% of water used by Mongolian pine in the summer in our study site, such that the sufficient groundwater supply may ensure root growth.

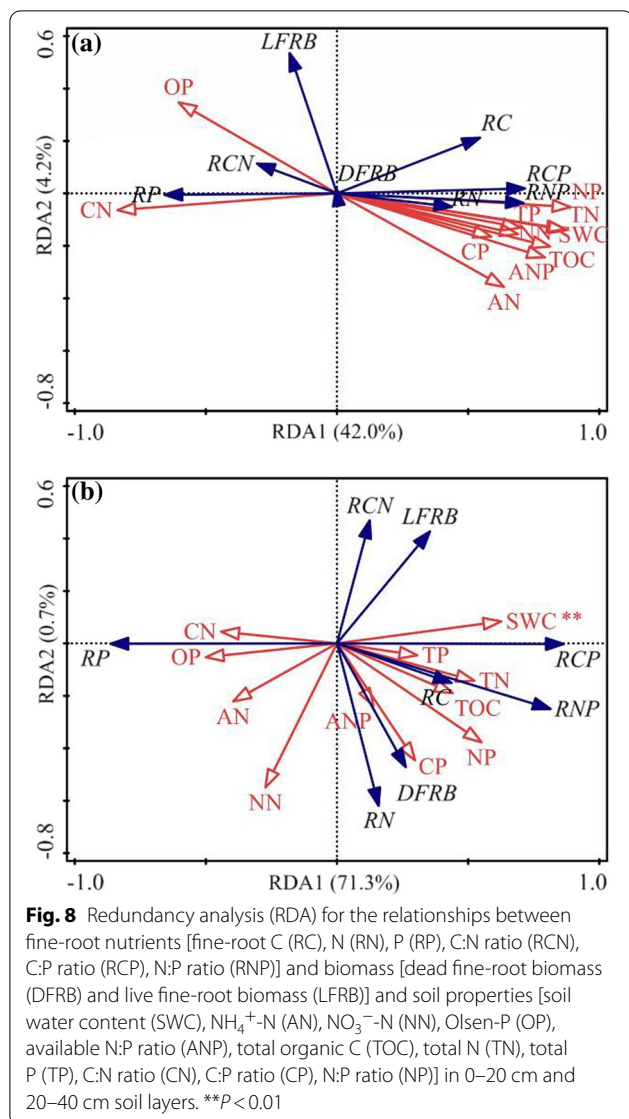
On the other hand, Mongolian pine can maintain nutrients by using the different strategies of nutrient conservation and acquisition. First, Mongolian pine may maintain N and P concentrations through high N and P resorption efficiency (57–60%, Zheng et al. 2020), which is considered as an important strategy of nutrient conservation under stressed conditions (Vitousek 1982). Second, the no response of fine-root biomass to drought in our study indicates that Mongolian pine may maintain high nutrient foraging capacity to ensure sufficient nutrient uptake. Furthermore, plants are able to adjust their nutrient demands to maintain diverse functions under climate change (Tian et al. 2019), and thus Mongolian pine might reduce its nutrient demand when facing short-term drought events.

A high nutrient homeostasis plays an important role in plant adaptation to climate change, which can remain relatively stable plant biomass or increase productivity under stress conditions (Viciedo et al. 2019; Wang et al. 2018). In our study, Mongolian pine

exhibited a relatively high N and P homeostasis in response to drought-induced soil nutrient deficiency, which might indicate the strong adaptation of Mongolian pine to drought (Mariotte et al. 2021). In consistent with our study, Wang et al. (2021) found that the high N and P homeostasis of *Ulmus pumila* and *Populus alba* improved their adaptation to arid and nutrient-deficient environment. The maintained high fine-root biomass under drought that ensure sufficient nutrient uptake may be the reason for the high N and P homeostasis of Mongolian pine.

## Conclusions

This study aimed to explore the effect of drought on soil N and P availability and to examine the adaptability of Mongolian pine to this change in soil nutrient availability from the view of root functions. After 7 years of drought manipulation, our results revealed that throughfall reduction significantly decreased soil nutrient availability and resulted in the decoupling between N and P cycling. In contrast, fine-root nutrient concentrations and biomass did not significantly respond to drought. Collectively, our findings highlight that drought could lead to soil nutrient deficiency and



degradation, and suggest that Mongolian pine has high adaptability to this soil nutrient deficiency by maintaining high fine-root biomass to achieve sufficient nutrient uptake. Our study could have important implications for selecting tree species when conducting afforestation of drought prone areas under climate change. In these areas, tree species that can sustain robust root function under drought may be the priorities.

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#### Author contributions

All authors contributed to the study's conception and design. Material preparation, data collection and analysis, manuscript draft were performed by JZ. The manuscript was reviewed and edited by D-HZ, GL and QZ. All authors read and approved the final manuscript.

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#### Data availability

The datasets used or analysed during the current study are available from the corresponding author on reasonable request.

#### Declarations

#### Ethics approval and consent to participate

Not applicable.

#### Consent for publication

Not applicable.

#### Competing interests

The authors declare that they have no competing interests.

#### Author details

<sup>1</sup>CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China. <sup>2</sup>Daqinggou Ecological Station, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China. <sup>3</sup>University of Chinese Academy of Sciences, Beijing 100049, China. <sup>4</sup>School of Resources and Environmental Engineering, Anhui University, Hefei 230601, China.

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