Contrasting nutrient-mediated responses between surface and deep fine root biomass to N addition in poplar plantations on the east coast of China

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ABSTRACT

Dynamics of fine root biomass (FRB) is fundamental to understanding carbon allocation and storage in forests. However, our understanding of FRB responses and its vertical distribution with respect to atmospheric nitrogen (N) deposition is limited. In this study, we applied five N addition rates (0, 5, 10, 15, and 30 g m^{-2} yr^{-1}) to explore effects of N addition on FRB and its distribution patterns along soil profile (0–100 cm) in poplar plantations on the east coast of China. We found that N addition significantly decreased total FRB and altered its vertical distribution. Specifically, N addition decreased FRB in the surface (0–20 cm) and increased it in the deep (20–100 cm) soil layers. Structural equation models (SEM) showed that soil available nutrients dominantly regulated FRB and its vertical distribution in poplar plantations. Decreased FRB and increased root distribution to deep soil layers indicate that trees can not only regulate carbon allocation between above- and below- ground tissues, but also optimize nutrient uptake by redistributing their roots vertically under different nutrient environments.

1. Introduction

Fine roots play a critical role in carbon (C) cycling in terrestrial ecosystems, absorbing soil nutrients and water for sustainable plant production and releasing C through root litter and rhizo-deposition (Norby and Jackson, 2000; Hendricks et al., 2006; Xia et al., 2015). It is estimated that fine roots (diameter ≤ 2 mm) represent <2% of the total ecosystem biomass, but contribute as much as 30–70% of the global annual net primary production (NPP) (Jackson et al., 1997; Hendricks et al., 2006; Bai et al., 2015). Nitrogen (N) deposition has increased roughly three to five times over the course of the 20th century (IPCC, 2013) and is predicted to continue to increase by more than half again by 2030 relative to 2000, exceeding 50 kg N ha^{-1} yr^{-1} in southeastern China (Liu et al., 2013; Yu et al., 2019). The great N deposition is anticipated to have a large effect fine root biomass (FRB) by inducing soil acidification, altering availability of soil nutrients and nutrient balances, among other processes (e.g., Lu et al., 2014; Yuan and Chen, 2015; Vanguelova and Pitman, 2019). However, knowledge of the responses of FRB to N deposition remains limited, especially at various soil depths with its vertical distribution along the soil profile, hindering an accurate projection of future ecosystem functions under global change.

Studies that explore fine root responses to N addition in forest ecosystems have undoubtedly advanced our understanding in recent decades, but results are inconclusive. Among these studies, results indicate that N addition may increase (e.g., Bai et al., 2008; Kou et al., 2018), decrease (e.g., Li et al., 2015; Peng et al., 2017; Wang et al., 2019), or have little impact (e.g., Ostertag, 2001; Gao et al., 2011) on fine root dynamics (including fine root production and FRB). The inconsistency in responses of fine roots to N addition may partly result from differences in nutrient limitation, sampling depths, N addition rates (and others) among studies (e.g., Gao et al., 2011; Xu et al., 2017; Yan et al., 2019).

Soil nutrient limitation, especially the availability of N and phosphorus (P), for plant growth are common among terrestrial ecosystems (Kou et al., 2015; Wang et al., 2017). One important way that N deposition affects FRB is through increasing soil N availability and unbalancing soil nutrients (Galloway et al., 2004). Increased soil N availability under N addition may cause a preferential shift in biomass allocation between roots and shoots based on optimal allocation theory (Chapin et al., 1987; Eissenstat and Yanai, 1997), leading to decreases in belowground NPP (e.g., Gong et al., 2014; Wang et al., 2019). Plants

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allocate photosynthetic products more to branches when aboveground resources decline (e.g., CO_2 and light) and more to roots when belowground resources (e.g., water and nutrients) are limited (Poorter et al., 2012). Additionally, increased soil N availability under N addition could alter plant P acquisition strategies by influencing soil properties such as pH and phosphatase activity, subsequently affecting FRB (e.g., Penuelas et al., 2013; Deng et al., 2017; Zhao and Zeng, 2019). N and P soil cycles are coupled with biological demand (Sistla and Schimel, 2012; Huang et al., 2019). For example, N addition increases tree growth in temperate and northern forests limited by N, while in subtropical and tropical forests limited by P, N application has little effect on tree growth (Tian et al., 2018). However, we know little about the role that P plays in mediating effects on N addition on FRB in forest ecosystems.

Understanding FRB distribution at various soil depths is essential in understanding forest dynamics (Li et al., 2020). Although plant roots tend to be most abundant in topsoil and to decrease sharply with increasing soil depth (e.g., Peek et al., 2004; Zhang et al., 2018), the function of deep roots cannot be ignored (Pries et al., 2018). For example, hydraulic lift is the process where deep rooted plants can absorb water from the low soil layers and transport it to the dry upper layer (Horton and Hart, 1998; Meier et al., 2018). Additionally, Yan et al. (2017) found N addition reduced the surface FRB (0–20 cm) and increased the deep FRB (20–40 cm) in boreal forests. However, our current understanding of the vertical distribution of fine roots along the soil profile (0–100 cm) in temperate forests to cope with resource variation is far from comprehensive. Moreover, the 95% rooting depth is considered as a key variable to quantify the interaction among plants, soil and climate (Cihlar, 1997; Xu et al., 2014). Although there have been a large number of manipulative global change experiments around the world, few have studied vertical distribution pattern of fine roots along the soil profile in response to N addition in forest ecosystems (Smithwick et al., 2013). Therefore, to accurately evaluate the soil C dynamics, further research on fine root response to N deposition requires an examination of deep root behavior.

Poplar is one of the major planted tree species in China, covering an area of >7.5 million ha. Poplar plantations play an important role in C sequestration in China (Fang et al., 2008; Wang et al., 2015). N deposition has increased dramatically in the eastern coast areas of China in recent decades, but we know little of responses of poplar plantations to N deposition, especially the belowground (Yu et al., 2014). We thus conducted our N addition experiments to explore the effects of N addition on FRB and its vertical distribution in poplar plantations at the Dongtai Forest Farm on the east coast of China. We hypothesized that: (1) N addition reduced FRB and changed the vertical distribution pattern according to the optimal allocation theory (Chapin et al., 1987); and (2) soil available nutrients regulated FRB and its distribution along soil profile because the productivity of poplar plantation in the area is largely restricted by soil nutrient availability.

2. Materials and methods

2.1. Experimental site and design

Our experimental site locates at the Dongtai Forest Farm in Yancheng, Jiangsu Province, China (120°49′E, 32°52′N). The forest farm was established in 1965 and covers an area of approximately 3000 ha^{-1}. It has an oceanic and monsoon climate with mean annual temperature is 13.7 °C and precipitation is 1051 mm (Wang et al., 2015). The soil of the forest farm is sandy loam with a pH value around 8 (Bian et al., 2019). Poplar (*Populus deltoids*) is one the most widely planted species on the farm.

We established an N addition experiment on an 8-year old pure poplar (*Populus deltoids* cv. 'I-35′) plantation in May 2012. Stand density was 333 trees hm^{-2} with the mean diameter at breast height (1.3 m height, DBH) of 23.12 cm in May 2012. The plantation had uniform site conditions that allowed us to implement precise management of sites

chosen as our plots. We created a randomized block design with a five level gradient of N addition (N0: 0, N1: 5, N2: 10, N3: 15, and N4: 30 g N m^{-2} yr^{-1}) in four replicate blocks (25 × 190 m^2). Each N treatment plot was approximately 25 × 30 m^2 with a 10 m buffer zone between adjacent plots and a minimum 500 m between replicate plots. We chose a range of N addition rates relative to an ambient N deposition rate of approximately 50 kg N ha^{-1} year^{-1} for this area (Zhu et al., 2016). Liu et al. (2013) predict that critical loads of N deposition in Jiangsu province could exceed 200 kg N ha^{-1} year^{-1}. In each month of the growing season (May to October) from 2012 to 2018, we calculated the annual NH_4NO_3 deposition and dissolved the one-sixth of this amount in 20 L water that was sprayed evenly under the canopy using a backpack sprayer to simulate natural N deposition. Each control plot received 20 L of water without NH_4NO_3.

2.2. Microclimate

Air temperature and precipitation data were derived from the National Meteorological Information Center, China Meteorological Administration. Soil temperature (ST) in the top 20 cm was measured using a thermocouple connected to an Li-Cor 6400 portable infrared gas analyzer (IRGA) (LI-COR Inc., Lincoln, NE, USA). Soil water content (SWC) in the top of 20 cm was measured using HydroSense II (HS2) (HydroSense II, Campbell Scientific, Logan, UT, USA). Soil temperature and volumetric soil water content were usually measured once in non-growing and twice in growing seasons every year.

2.3. DBH measurement and leaf and soil sampling

In June 2017 and 2018, DBH of each Poplar tree in our plots was measured with a breast-diameter ruler at the vertical height of 1.3 m above the ground from the base of the trees (Liu et al., 2018). In July 2018, we randomly selected three healthy Poplar trees in the center of each plot and collected fresh green leaves using homemade bow and arrow. The foliar samples were then mixed evenly to obtain a composite sample. Fresh green foliar samples were first deactivated of enzymes for approximately half an hour at 105 °C and, transported in several coolers to our laboratory at Nanjing Forestry University, and oven-dried for 48 h at 65 °C. Three soil samples were randomly collected using a soil corer with an inner diameter of 4 cm to a depth of 100 cm in each subplot in July 2018. The 100 cm soil cores were then evenly divided into ten layers, each of 10 cm. The three samples from each layer were combined and homogenized to obtain a representative soil sample for each subplot, which were transported in coolers to our lab for further analyses. In the lab, composite soil samples, with rocks, roots and other debris removed, were air-dried and pressed through a 2 mm sieve for soil physicochemical analysis. The concentration of total C and N in the leaf and surface fine roots (0–20 cm) were measured using an elemental analyzer (Li et al., 2018) (Elementar, Vario EL III, Elementar Analysen Systeme GmbH, Germany). We did not measure C and N contents of the fine roots from 20 to 100 cm due to the limited amount of root biomass. Soil available N (soil AN) was determined by the alkali dispersion method (Gai et al., 2021). Soil available P (soil AP) was extracted using microwave digestion and a $NaHCO_3$ solution then measured using the Mo-Sb colorimetric method (Zhang et al., 2020). Soil pH was measured at a soil to water ratio of 1: 2.5 air dried soil (10 g) was added into deionized water (25 ml) and shaken for 90 s with a magnetic stirrer, then the pH was measured after 30 min with lightning magnetic PHS-25 (Kou et al., 2018).

2.4. Fine root biomass and its distribution estimation

Fine root biomass was estimated using the soil coring method (Xu et al., 2013; Feng et al., 2018). Root samples were randomly collected using a soil coring with an inner diameter of 4 cm to a depth of 100 cm in each subplot in June and November each year in 2017 and 2018. Similar
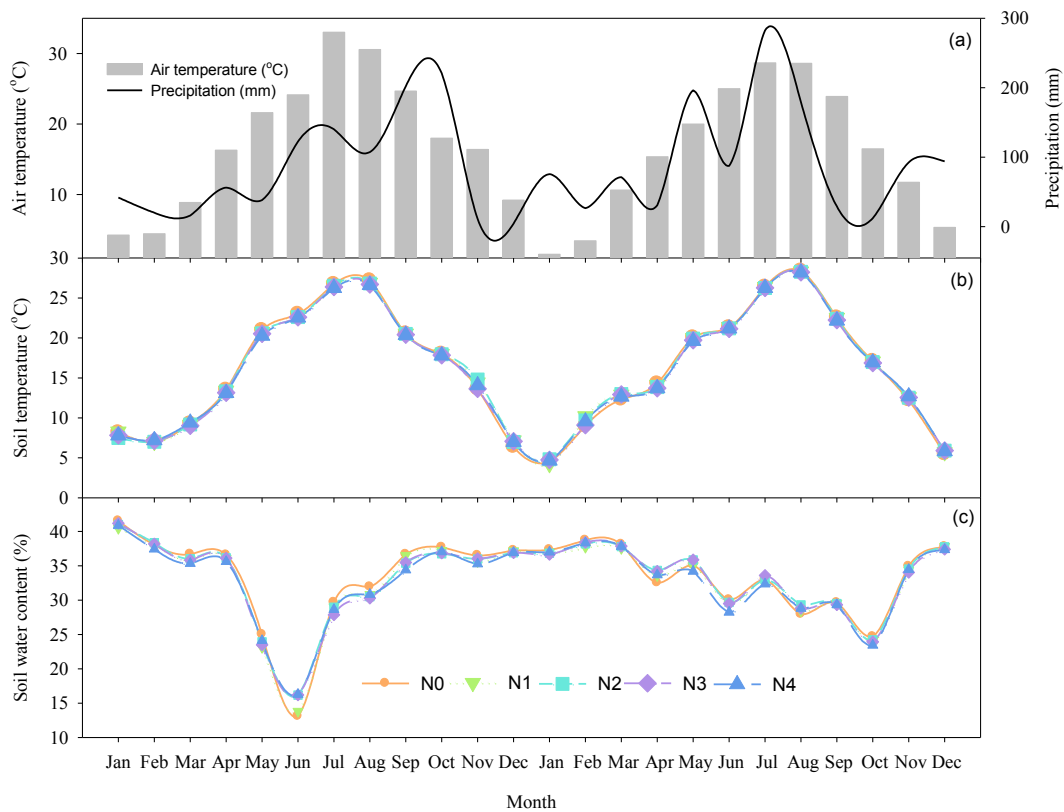
Fig. 1. Seasonal variation of air temperature and precipitation (a), soil temperature (b) and moisture (c) across N addition treatments.

to the soil samples, root cores were also evenly divided into ten layers, transported to our laboratory, and stored at −20 °C before analysis. Root cores were carefully washed by wet sieving (0.5 mm) under gently flowing water and then all roots were picked out with forceps. Living fine roots (≤2 mm in diameter) were collected, oven-dried at 65 °C for 48 h, and weighed to estimate FRB (Persson, 1983; Pregitzer, 2002; Feng et al., 2018).

The vertical distribution of fine roots was quantified using a coefficient (β) based on the asymptotic single-parameter global model (Gale and Grigal, 1987):

$$Y = 1 - \beta^d \tag{1}$$

where Y is the cumulative root fraction, calculated as the proportion of FRB from the soil surface to any depth (e.g. 0–20, 0–50 cm) to total FRB (0–100 cm). d is the soil depth (cm), and β is the fitted coefficient of rooting distribution. Higher β values indicate a greater proportion of fine root biomass at depth, and lower β values imply a greater proportion of fine root biomass near the soil surface. We used nonlinear regression to fit the parameter β, and used the coefficient of determination (r^2) to evaluate the fit.

2.5. Statistical analyses

Prior to testing trial responses, we used the Shapiro-Wilk statistic to test for data normality and the Levene's test for homogeneity of variance. For data that do not conform to the normality hypothesis based on the Shapiro-Wilk test, in order to reduce the violation of the normality hypothesis and improve the coefficient estimation of small samples, we bootstrapped the fitted coefficients of all models by 1000 iterations using the boot package.

Because we measured FRB in plots repeatedly among sampling times and sampled roots in layers within each plot, we used a linear mixed-effect model to test the effects of N addition, sampling times (T), and

soil depth (D) using formula:

$$Y_{ijkl} = N_i + T_{j(l)} + D_{k(l)} + N_i \times D_{j(l)} + N_i \times D_{k(l)} + T_{j(l)} \times D_{k(l)} + N_i \times T_{j(l)} \times D_{k(l)} + e_l \tag{2}$$

where Y_{ijkl} is the FRB, β values, soil environment or soil properties, N_i (i = 1, 2, …, 5) is the N addition rates, $T_{j(l)}$ (j = 1, 2, …, 4) is the sampling times (June and November in 2017 and 2018), $D_{k(l)}$ (k = 1, 2, …, 10) is the soil depth as a factor variable (0–10, 10–20, …, 90–100 cm), and e_l is the random plot effect (l = 1, 2, …, 4). To test the effects of N addition and sampling time on root vertical distribution (parameter β) and soil environment (including ST and SWC), the term "D" in Eq. (2) was excluded. Similarly, in order to test the effects of N addition and soil layer on soil properties, including soil AN, AP, N: P and pH, the term "T" in Eq. (2) was not included. To compliment Eq. (2), where N was treated as a categorical variable, we also analyzed our data by treating N as a continuous variable. Both analyses were qualitatively similar (Figs. S1 and S2). We performed the linear mixed effect analysis using restricted maximum likelihood estimation within the lme4 module.

Structural equation modeling (SEM) was conducted to determine the effects (direct and indirect) of the soil environment (including ST and SWC), soil pH and soil nutrients (including AN, AP and N: P) on the responses of FRB and β values to N addition. Based on previous knowledge and our results from statistical analysis and linear regression, we proposed a priori model of hypothesized relationships within a path diagram, allowing a causal interpretation of the model outputs. Path coefficients were obtained using the maximum likelihood estimation technique. The Chi-square (χ^2) test was used to evaluate overall goodness of fit for this model. A non-significant χ^2 test ($p > 0.05$) and a root mean square error of approximation (RMSE) < 0.05 indicate the model is acceptable. Additionally, due to strong correlations between the soil factors, we conducted a principal component analysis (PCA) to create a multivariate functional index before building the SEM. The first

Table 1
Results of mixed model ANOVA (F-tests) for the effects of nitrogen addition (N), soil depth (D), sampling time (T) and their interactions on fine root biomass (FRB) and percentage of fine root biomass (%FRB), of N, T and their interactions on vertical distribution parameter β, soil temperature (ST) and water content (SWC), and of N, D and their interactions on soil available nitrogen (AN), soil available phosphorus (AP), soil available N:P ratio and soil pH under simulated plots of N addition in poplar plantations. ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, ns: $p > 0.05$.

	ST (°C)		SWC (%)		Soil AN (g/kg)		Soil AP (g/kg)		Soil N:P		pH		FRB (g/m²)		%FRB (%)		β values	
	df	F, p	df	F, p	df	F, p	df	F, p	df	F, p	df	F, p	df	F, p	df	F, p	df	F, p
N	4	0.82 ns	4	0.44 ns	4	51.92***	4	2.59*	4	11.64***	4	4.06*	4	20.47***	4	4.54**	4	20.30***
D	—	—	—	—	9	183.94***	9	181.99***	9	1.12ns	9	61.90***	9	338.72***	9	366.49***	—	—
T	23	1204.25***	23	75.48***	—	—	—	—	—	—	—	—	3	1.98ns	3	1.59ns	3	5.00**
N*D	—	—	—	—	36	4.32***	36	3.89***	36	1.03ns	36	0.89ns	36	14.40***	36	4.55***	—	—
N*T	92	0.23 ns	92	0.13 ns	—	—	—	—	—	—	—	—	12	0.49ns	12	0.39ns	12	1.76ns
D*T	—	—	—	—	—	—	—	—	—	—	—	—	27	4.27***	27	3.59***	—	—
N*D*T	—	—	—	—	—	—	—	—	—	—	—	—	108	1.21ns	108	1.30ns	—	—

principal component (PC1) explained 60.0% and 73.9% of the total variance for soil environment and nutrients, respectively. All figures were prepared using Sigma plot 10.0 (Systat Software, San Jose, CA) and all statistical analyses were performed using R 3.5.1 (http://cran.r-project.org). All the SEM analyses were conducted using AMOS 22.0 (Amos Development Corporation, Chicago, IL, USA).

3. Results

3.1. Microclimate, DBH, soil properties, plant C and N

Air temperature, precipitation, soil temperature and moisture across treatments showed clear seasonal dynamics (Fig. 1). Mean annual air temperature was 16.38 °C in 2017 and 15.96 °C in 2018 (Fig. 1a). Mean annual precipitation was 980 and 1177 mm in 2017 and 2018, respectively (Fig. 1a). ST increased from January to August and then decreased from August to December in 2017 and 2018 (Fig. 1b). SWC was the lowest in June 2017 and October 2018 (Fig. 1c). We found that neither N addition nor the interactions of N addition and sampling time had a significant effect on ST and SWC (all $p > 0.05$, Table 1). N addition and sampling time both significantly increased DBH (all $p < 0.01$, Fig. S3a), but the interactions between N addition and sampling time had no significant effects on DBH ($p > 0.05$, Fig. S3a). In addition, we found that the C concentration in green leaves increased significantly, while that in fine roots decreased with increasing N addition rates ($p < 0.01$, Fig. S3c). N addition increased soil AN, AP and N: P and decreased pH (all $p < 0.05$, Table 1, Fig. S4). With increasing soil depth, soil AN and AP decreased while pH increased (all $p < 0.05$, Table 1, Fig. S4). The interactive effects of N addition and soil depth had a significant effect on soil AN and AP (all $p < 0.001$, Table 1, Fig. S4), but not on N: P ratio and pH (all $p > 0.05$, Table 1, Fig. S4).

3.2. Effects of N addition on FRB and its vertical distribution

N addition significantly decreased FRB ($p < 0.01$, Table 1, Fig. 2). Compared with N_0, for example, N_1, N_2, N_3, N_4 decreased FRB by 7.7, 14.9, 26.9 and 39.4% in June 2017, respectively. Along the soil profile, both FRB and its proportional distribution to total FRB were consistently affected by N addition, soil depth, and interactions with N addition and soil depth and with soil depth and sampling time (all $p < 0.01$, Table 1). However, sampling time, its interaction with N addition, and the interaction of N addition, soil depth, and sampling time had no significant effect on FRB (all $p > 0.05$, Table1). With increasing N addition rates, FRB in the surface soil layer (0–20 cm) decreased whereas FRB in deep soil layer (20–100 cm) increased ($p < 0.01$, Table 1, Fig. 3). In June 2017, FRB in the deep soil layer was much higher than that at the other three sampling times ($p < 0.01$, Table 1, Fig. S5). In addition, FRB in general decreased significantly with increasing soil depth ($p < 0.01$, Table 1, Fig. S5). We found that β increased significantly with increasing N addition rates and was much higher in June 2017 than at the other three sampling times (all $p < 0.01$, Table 1, Fig. 4).

3.3. Relationships of FRB and β with microclimate and soil properties

We found FRB in the poplar plantation was regulated negatively by the mix of soil nutrients represented by PC1 ($p < 0.001$, Fig. 5a) and positively by soil pH ($p < 0.001$, Fig. 5c), but had no significant correlation with PC1 of the soil environment parameters ($p > 0.05$, Fig. 5b). β was correlated positively with PC1 of the soil nutrients ($p < 0.001$, Fig. 5d) and negatively with PC1 of the soil environment ($p < 0.05$, Fig. 5e) and soil pH ($p < 0.05$, Fig. 5f). SEM analyses showed that FRB was largely determined by soil available nutrients and β was predominantly regulated by soil available nutrients and soil environment (Fig. 6).
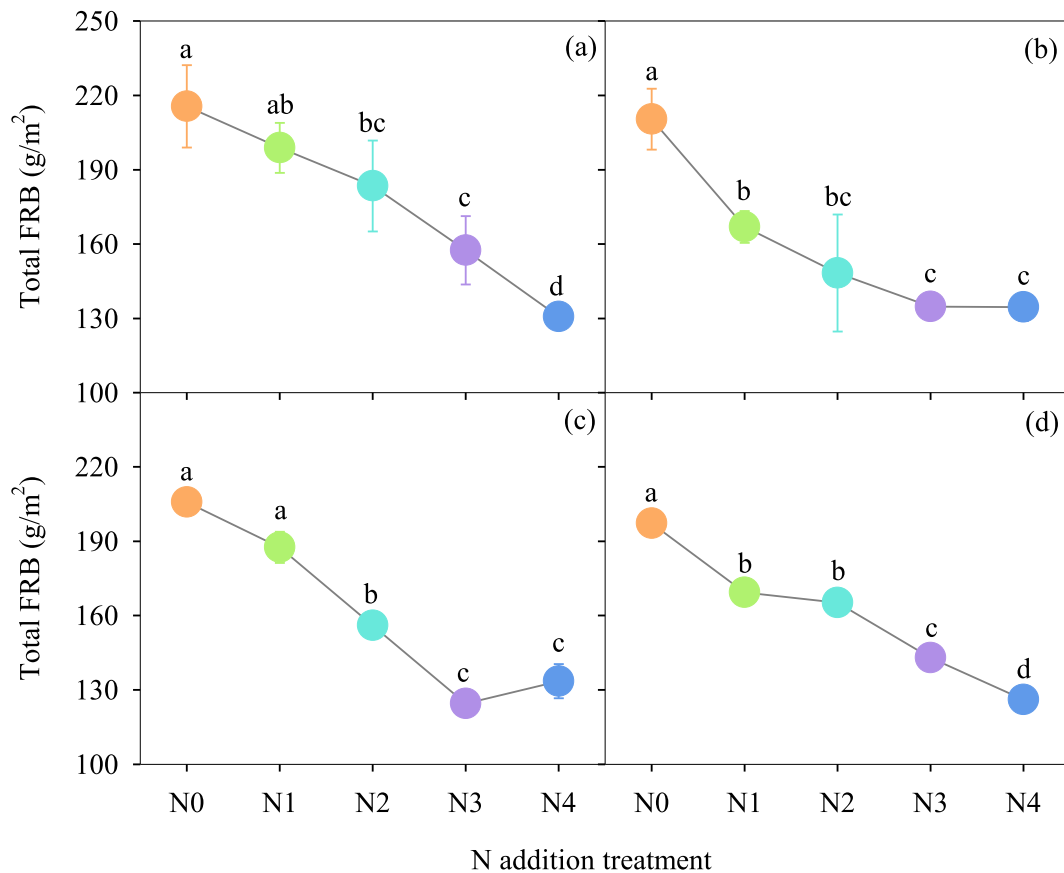
Fig. 2. Variation in fine root biomass across N addition treatments. (a): June 2017; (b): November 2017; (c): June 2018; (d): November 2018. Lowercase letters indicate significant differences at $p = 0.05$ among N addition treatments.

4. Discussion

4.1. Effects of N addition on FRB

Fine roots are usually sensitive to N addition (King et al., 2002; Yuan and Chen, 2015). In line with many previous findings (Yan et al., 2017; Wang et al., 2019), our results showed that N addition, in general, decreased FRB in poplar plantation. Plants can improve the efficiency of resource acquisition by increasing the growth of fine roots in the absence of soil nutrients (Iversen, 2010; Wang et al., 2013). Therefore, when the availability of soil nutrients is improved (e.g., increased AN (0–100 cm) and AP (0–20 cm) ($p < 0.01$, Table 1, Fig. S2 a and b) at our study site), plants need fewer roots and less active root area to meet nutrient demands (Helmisaari et al., 2007). This can be also explained in terms of cost-benefit theory, which suggests that plants would invest less C in fine roots and can maximize nutrient uptake when soil nutrients are rich (Eissenstat and Yanai, 1997; Peng et al., 2017).

Indirectly, N addition may have induced changes in soil nutrient availability that altered plant physiological processes and C allocation patterns. Optimal C allocation theory indicates that if N is abundant in soil, plants would reduce their C investment in roots (Chapin et al., 1987; Eissenstat and Yanai, 1997). The theoretical foundation of optimal C allocation theory is that soil is limited by N (Kobe et al., 2010; Peng et al., 2017). This is the case in the saline-alkali soils of coastal eastern China that are usually limited by N (Xia et al., 2019). Moreover, our finding that N addition increased poplar leaf C content and DBH while decreased root C content are in accordance with the theory, which partly explained the observed decreases in FRB.

### 4.2. N addition effects on FRB vertical distribution

Quantifying the vertical distribution of FRB is essential to understand below-ground ecological processes such as water and nutrient uptake of roots (Xu et al., 2014; Zhang et al., 2019). Our results showed that poplar FRB decreased significantly with increasing soil depth across treatments, which agrees with many previous findings (e.g., Arndal et al., 2018; Zhang et al., 2019; Houde et al., 2020). The decrease in FRB may relate to the sharp decrease in soil nutrients with increasing soil depth, one of the dominant controlling factors of vertical root distribution (all $p < 0.05$, Table 1, Fig. S4). Interestingly, we found FRB decreased in surface (0–20 cm) versus deep (20–100 cm) soil layers under N addition. Similarly, Yan et al. (2017) reported that N addition significantly reduced FRB in the 0–20 cm soil layer and increased in the 20–40 cm soil layer. Modeling studies also indicate that N addition allows fine roots to spread more widely into deep soil layers (Iversen, 2010). N addition may alleviate N limitation through the whole soil profile, but other nutrients, such as soil P, may respond inconsistently to N addition among soil layers (Gress et al., 2007; Li et al., 2016). We found that N addition increased P availability in the surface soil layer, but had little effect on P in the deep soil layer ($p < 0.01$, Table 1, Fig. S4b). Therefore, investing in fine roots in the surface soil is less beneficial for plants when the nutrient limitation of the surface soil is alleviated with N addition (Jackson et al., 1996; Van Wijk, 2011), leading to lower FRB in the surface soil layer. In contrast, increased N availability in the deep soil layer caused P limitation, which stimulated root growth to absorb more P.

By fitting models, we found N addition significantly increased the vertical distribution parameter β, indicating that N addition promoted the distribution of fine roots to deeper soil layers. This new distribution pattern may be the biological result of plants' adaptation to changes in
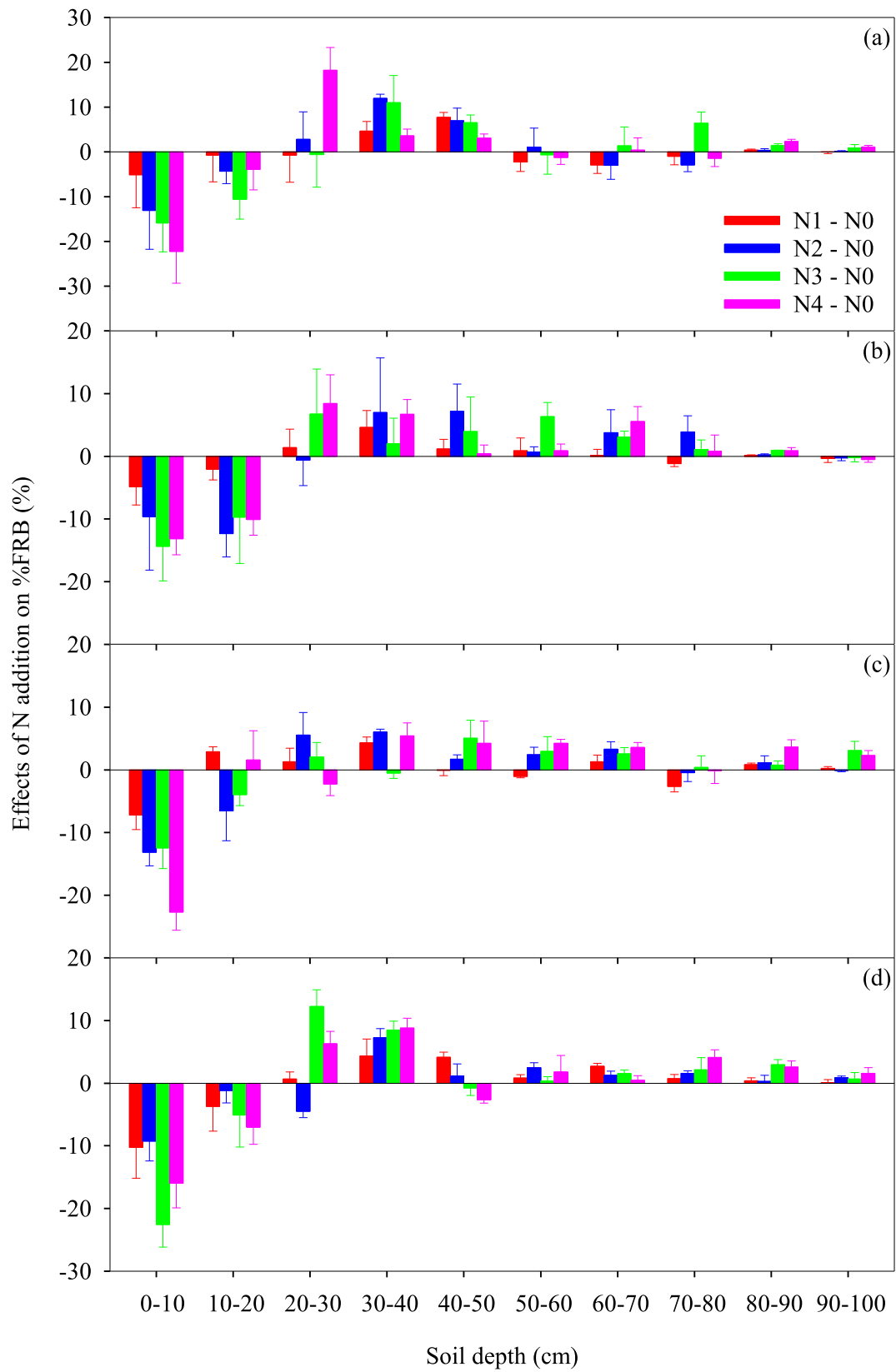
Fig. 3. Effects of N addition on the vertical distribution of fine root biomass along the soil profile from 2017 to 2018. (a): June 2017; (b): November 2017; (c): June 2018; (d): November 2018. FRB% represents the percentage of root biomass of a specific soil layer (e.g. 0–10 cm) to the total fine root biomass (0–100 cm).
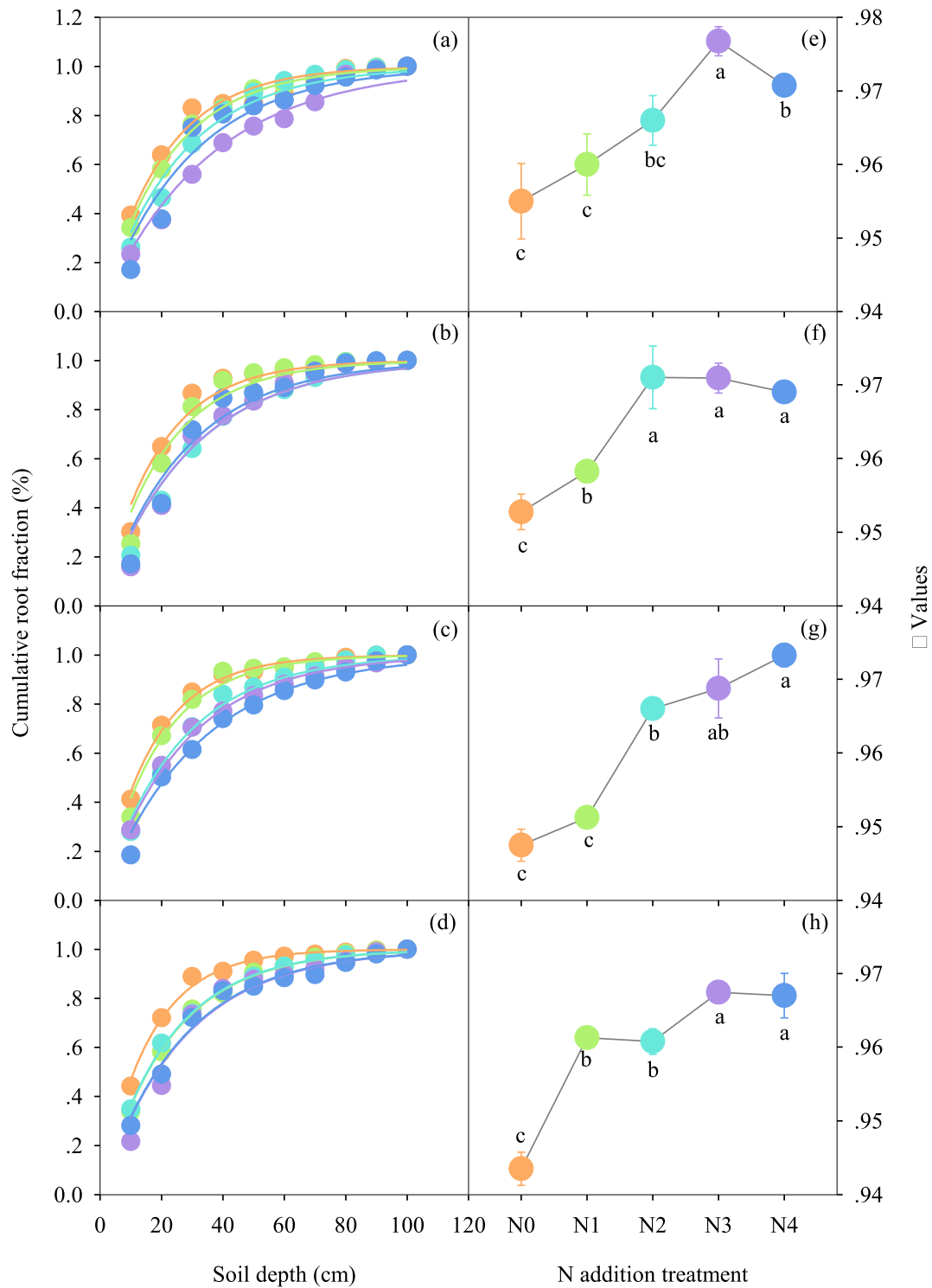
Fig. 4. Cumulative root biomass fraction along the soil profile (a-d) and variation in root vertical distribution parameter (*β*) (e-h) across N addition treatments. (a, e): June 2017; (b, f): November 2017; (c, g): June 2018; (d, h): November 2018. Lowercase letters indicate significant differences at *p* = 0.05 among different N addition treatments.

the external environment. It has been reported that N leaching occurs along the soil profile under N addition (e.g., Panagopoulos et al., 2007; Turner and Henry, 2010; Crowley and Lovett, 2017), indicating the transfer of N to deep soil layers, which nevertheless remain N-limited (Weintraub et al., 2017). According to the optimal allocation principle, this suggests that C is allocated to the deep root system to maximize N absorption (Chapin et al., 1987; Eissenstat and Yanai, 1997). In addition, studies at the same site found N addition decreased turnover with few

impacts on fine root production in deep soil layers. These findings indicate that roots could continue to grow as long as the benefits of nutrient acquisition exceeded the C value of surviving roots (Burton et al., 2000; Peng et al., 2017), leading to increased FRB in deep soil layers. Overall, different responses of fine root growth at different soil depths to N addition indicate that FRB as well as its vertical distribution is sensitive to N addition and trees can optimize nutrient uptake by redistributing their roots vertically under different nutrient
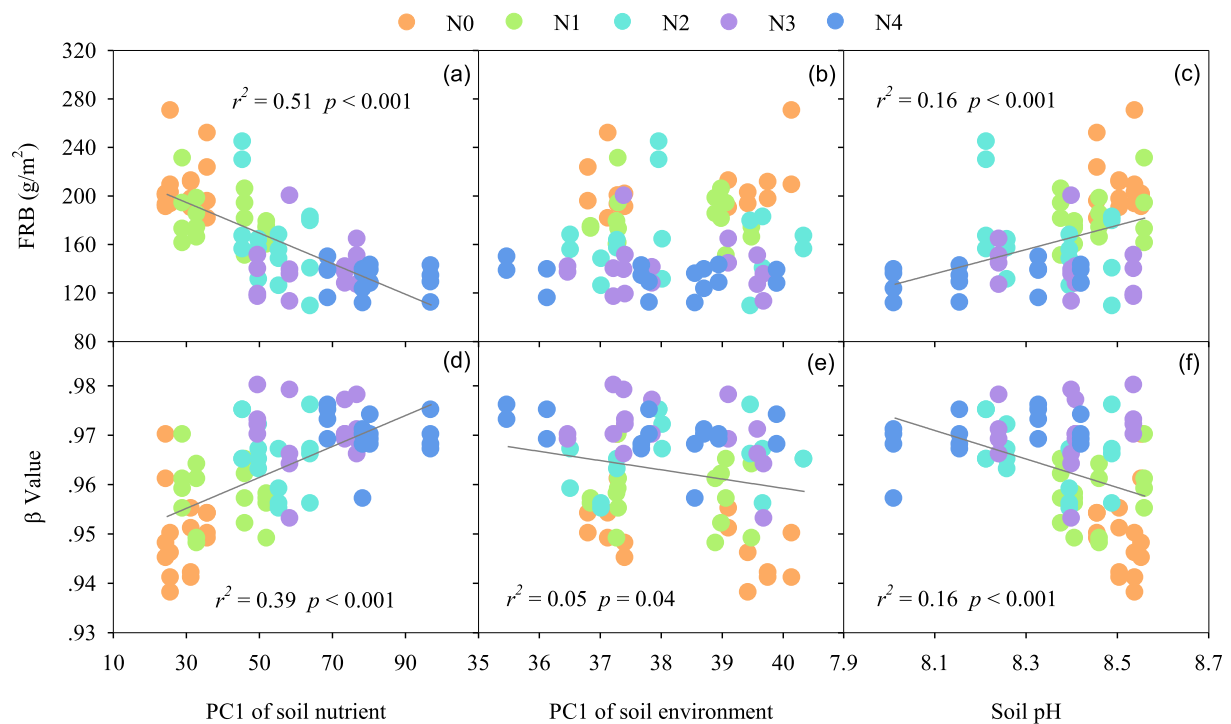
Fig. 5. Bivariate relationships of fine root biomass and root vertical distribution parameter (β) with PC1 of soil nutrient (a, d), PC1 of soil environment (b, e) and soil pH (c, f) across N treatments.

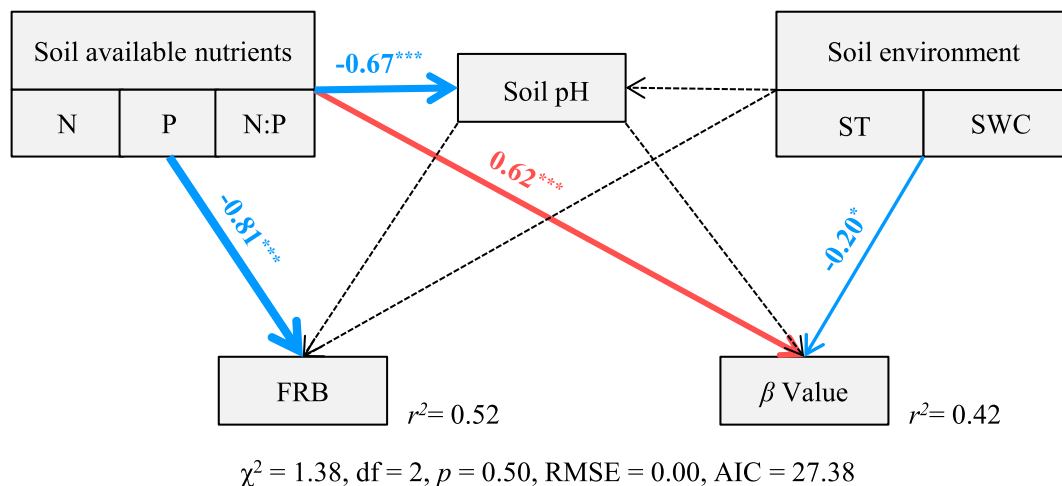$$\chi^2 = 1.38, \, df = 2, \, p = 0.50, \, RMSE = 0.00, \, AIC = 27.38$$

Fig. 6. Structural equation modeling (SEM) analysis performed to evaluate pathways of N addition influence on the fine root biomass of poplar and root vertical distribution parameter (β). Variables are soil nutrients, soil environment and soil pH. Blue and red arrows indicate significantly ($p < 0.05$) negative and positive relationships, respectively. Dotted lines refer to insignificant relationships ($p > 0.05$). Numbers on arrows represent standardized path coefficients, and the width of the arrows is proportional to the strength of the path coefficients. r^2 values associated with response variables indicate the proportion of variation explained by relationships with other variables. (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$). ST: soil temperature; SWC: soil water content; AN: soil available N; AP: soil available P; N:P: soil available N:P; FRB: fine root biomass; β: the vertical distribution parameter of fine roots; χ^2: chi-square; df: degrees of freedom; RMSE: root mean square error of approximation; AIC: Akaike's Information Criteri. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

environments.

In addition, we found that β in June 2017 was higher than that in the other three sampling times, which may be caused by lower soil water content. Studies have shown that plant roots often extend into deep soil layers to achieve water resources in arid and semiarid, tropical, and subtropical ecosystems (Brando et al., 2008). Similarly, our results demonstrated that deep fine roots can be of pivotal importance to alleviate water stress in temperate environments. Moreover, deep fine roots associated with the advantage of lower maintenance costs to offset the

higher construction costs, can absorb more water compared with surface fine roots (Joslin et al., 2006; Germon et al., 2016). Thus, plant developed new fine roots in the vertical direction especially in deep soil layers, which would be considered as an effective solution in coping with drought stress.

4.3. Regulation of FRB and its vertical distribution

We found that soil pH positively regulated FRB across N treatments.

Low soil pH may inhibit root growth by increasing aluminum and iron plasma concentrations (Bai et al., 2015; Yan et al., 2017). However, consistent with previous findings (Wang et al., 2019), our results showed that FRB dynamics in poplar plantations with N addition was dominantly regulated by soil available nutrients. Soil available nutrients are considered to be one of the most frequent controlling factors on plant root productivity (Peng et al., 2017; Ding et al., 2020). The regulation of FRB by soil available nutrients aligns with the optimal allocation theory and cost-benefit relationship, which indicates that trees trade-off nutrient uptake and C investment for root production and maintenance (Bakker et al., 2008). Additionally, recent studies have shown that soil nutrient availability drives the root economics spectrum. This is usually represented by the negative relationship between root N, P concentration and root tissue density, describing the trade-off between conservation and acquisition in root resource uptake (Ostonen et al., 2017; Ding et al., 2020). In conclusion, the change of soil available nutrients may alter the C allocation pattern and the physiological functions of fine roots, and further affect FRB, which is an effective strategy for trees to adapt to different habitat conditions.

Soil available nutrients not only controlled FRB in poplar plantations but also regulated the vertical distribution of the root system. Our SEM results showed that there were two important pathways through which the vertical distribution of fine roots was mediated. First, the soil environment negatively regulated β. Studies have shown that increases in surface soil temperature usually make fine roots distribute deeper (Li et al., 2017; Zhang et al., 2019; Courchesne et al., 2020). Additionally, soil moisture strongly determines the root distribution in terrestrial ecosystems, which may be due to N addition induced increases in transpiration reduce surface soil water use efficiency (Huang et al., 2016; Lu et al., 2018). Second, soil available nutrients positively regulated β, consistent with the results of a recent study that the expansion of deep roots is closely related to nutrient availability (Newman et al., 2020). The regulation of soil available nutrients in β also agreed with the cost-benefit relationship (Iversen, 2010). C gains may shift the cost-benefit balance in favor of root production in deeper soil layers and the benefits of smaller resource gains may have previously been outweighed by C costs (Iversen, 2010). Intense competition with surface microbes in addition to intra- and interspecific interactions with roots from neighboring plants can further increase the value of deep root penetration and increase the microbial immobilization of available nutrients (Fierer et al., 2003; Li et al., 2014). Our results may provide a scientific basis for the management of soil environment and nutrients of the plantation ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions: All authors contributed intellectual input and assistance to this study and manuscript preparation. X.X. conceived the idea and designed the study. Q. G. collected and analyzed the data with help from X.X. Q. G. and X.X. wrote the paper with input from all authors.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119152.

References

Arndal, M.F., Tolver, A., Larsen, K.S., Beier, C., Schmidt, I.K., 2018. Fine root growth and vertical distribution in response to elevated CO 2, warming and drought in a mixed heathland–grassland. Ecosystems 21, 15–30.

Bai, W., Guo, D., Tian, Q., Liu, N., Cheng, W., Li, L., Zhang, W.H., 2015. Differential responses of grasses and forbs led to marked reduction in below-ground productivity in temperate steppe following chronic N deposition. J. Ecol. 103, 1570–1579.

Bai, W.M., Wang, Z.W., Chen, Q.S., Zhang, W.H., Li, L.H., 2008. Spatial and temporal effects of nitrogen addition on root life span of Leymus chinensis in a typical steppe of Inner Mongolia. Funct. Ecol. 22, 583–591.

Bakker, M.R., Jolicoeur, E., Trichet, P., Augusto, L., Plassard, C., Guinberteau, J., Loustau, D., 2008. Adaptation of fine roots to annual fertilization and irrigation in a 13-year-old Pinus pinaster stand. Tree Physiol. 29, 229–238.

Bian, H., Geng, Q., Xiao, H., Shen, C., Li, Q., Cheng, X., Luo, Y., Ruan, H., Xu, X., 2019. Fine root biomass mediates soil fauna community in response to nitrogen addition in poplar plantations (Populus deltoids) on the East Coast of China. Forests 10, 122.

Brando, P.M., Nepstad, D.C., Davidson, E.A., Trumbore, S.E., Ray, D., De Camargo, P.B., 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philos. Trans. Royal Soc. B 363, 1839–1848.

Burton, A.J., Pregitzer, K.S., Hendrick, R.L., 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. Oecologia 125, 389–399.

Chapin, F.S., Bloom, A.J., Field, C.B., Waring, R.H., 1987. Plant responses to multiple environmental factors. Bioscience 37, 49–57.

Cihlar, J., Barry, T., Ortega Gil, E., Haeberli, W., Kuma, K., Landwehr, J., ... Solomon, A., 1997. GCOS/GTOS plan for terrestrial climate-related observation. GCOS 32, version 2.0: WMO/TD-796, UNEP/DEIA/TR, 97-7.

Courchesne, D.N., Wilson, A.Z., Ryser, P., 2020. Regional distribution patterns of wetland monocots with different root turnover strategies are associated with local variation in soil temperature. New Phytol. 226, 86–97.

Crowley, K.F., Lovett, G.M., 2017. Effects of nitrogen deposition on nitrate leaching from forests of the northeastern United States will change with tree species composition. Can. J. For. Res. 47, 997–1009.

Deng, Q., Hui, D., Dennis, S., Reddy, K.C., 2017. Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: A meta-analysis. Glob. Ecol. Biogeogr. 26, 713–728.

Ding, J., Kong, D., Zhang, Z., Cai, Q., Xiao, J., Liu, Q., Yin, H., 2020. Climate and soil nutrients differentially drive multidimensional fine root traits in ectomycorrhizal-dominated alpine coniferous forests. J. Ecol.

Eissenstat, D.M., Yanai, R.D., 1997. The ecology of root lifespan. Adv. Ecol. Res. 27, 1–60.

Fang, S., Xie, B., Liu, J., 2008. Soil nutrient availability, poplar growth and biomass production on degraded agricultural soil under fresh grass mulch. For. Ecol. Manage. 255, 1802–1809.

Feng, C., Wang, Z., Zhu, Q., Fu, S., Chen, H.Y.H., 2018. Rapid increases in fine root biomass and production following cessation of anthropogenic disturbances in degraded forests. Land Degrad. Dev. 29, 461–470.

Fierer, N., Allen, A.S., Schimel, J.P., Holden, P.A., 2003. Controls on microbial CO2 production: a comparison of surface and subsurface soil horizons. Glob. Change Biol. 9, 1322–1332.

Gai, X., , Z.Z., , X.Z., , F.B., , C.Y., 2021. Effects of chicken farming on soil organic carbon fractions and fungal communities in a Lei bamboo (Phyllostachys praecox) forest in subtropical China - ScienceDirect. Forest Ecology Management 479.

Gale, M., Grigal, D., 1987. Vertical root distributions of northern tree species in relation to successional status. Can. J. Forest Res. 17, 829–834.

Galloway, J.N., Dentener, F., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., 2004. Nitrogen cycles: past, present, and future. Biogeochemistry 70, 153–226.

Gao, Y.Z., Chen, Q., Lin, S., Giese, M., Brueck, H., 2011. Resource manipulation effects on net primary production, biomass allocation and rain-use efficiency of two semiarid grassland sites in Inner Mongolia, China. Oecologia 165, 855–864.

Germon, A., Cardinael, R., Prieto, I., Mao, Z., Kim, J.H., Stokes, A., Dupraz, C., Laclau, J., Jourdan, C., 2016. Unexpected phenology and lifespan of shallow and deep fine roots of walnut trees grown in a silvoarable Mediterranean agroforestry system. Plant Soil 401, 409–426.

Gong, X.Y., Berone, G.D., Agnusdei, M.G., Palma, R.M.R., Schaufele, R., Lattanzi, F.A., 2014. The allocation of assimilated carbon to shoot growth: in situ assessment in natural grasslands reveals nitrogen effects and interspecific differences. Oecologia 174, 1085–1095.

Gress, S.E., Nichols, T.D., Northcraft, C.C., Peterjohn, W.T., 2007. Nutrient limitation in soils exhibiting differing nitrogen availabilities: what lies beyond nitrogen saturation? Ecology 88, 119–130.

Helmisaari, H., Derome, J., Nojd, P., Kukkola, M., 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiol. 27, 1493–1504.

Hendricks, J.J., Hendrick, R.L., Wilson, C.A., Mitchell, R.J., Pecot, S.D., Guo, D., 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. J. Ecol. 94, 40–57.

Horton, J.L., Hart, S.C., 1998. Hydraulic lift: a potentially important ecosystem process. Trends Ecol. Evol. 13, 232–235.

Houde, S., Thivierge, M.-N., Fort, F., Bélanger, G., Chantigny, M.H., Angers, D.A., Vanasse, A., 2020. Root growth and turnover in perennial forages as affected by management systems and soil depth. Plant and Soil.

Huang, J., Liu, L., Qi, K., Yang, T., Yang, B., Bao, W., Pang, X., 2019. Differential mechanisms drive changes in soil C pools under N and P enrichment in a subalpine spruce plantation. Geoderma 340, 213–223.

Huang, Z., Liu, B., Davis, M.R., Sardans, J., Penuelas, J., Billings, S.A., 2016. Long-term nitrogen deposition linked to reduced water use efficiency in forests with low phosphorus availability. New Phytol. 210, 431–442.

IPCC, 2013. The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. 2013. There is no corresponding record for this reference.[Google Scholar], 33-118.

Iversen, C.M., 2010. Digging deeper: fine-root responses to rising atmospheric CO2 concentration in forested ecosystems. New Phytol. 186, 346–357.

Jackson, R.B., Canadell, J.G., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389–411.

Jackson, R.B., Mooney, H.A., Schulze, E.D., 1997. A global budget for fine root biomass, surface area, and nutrientcontents. Proc. Natl. Acad. Sci. U. S. A. 94, 7362–7366.

Joslin, J.D., Gaudinski, J.B., Torn, M.S., Riley, W.J., Hanson, P.J., 2006. Fine-root turnover patterns and their relationship to root diameter and soil depth in a 14C-labeled hardwood forest. New Phytol. 172, 523–535.

King, J.S., Albaugh, T.J., Allen, H.L., Buford, M.A., Strain, B.R., Dougherty, P.M., 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. New Phytol. 154, 389–398.

Kobe, R.K., Iyer, M., Walters, M.B., 2010. Optimal partitioning theory revisited: Nonstructural carbohydrates dominate root mass responses to nitrogen. Ecology 91, 166–179.

Kou, L., Guo, D., Yang, H., Gao, W., Li, S., 2015. Growth, morphological traits and mycorrhizal colonization of fine roots respond differently to nitrogen addition in a slash pine plantation in subtropical China. Plant Soil 391, 207–218.

Kou, L., Jiang, L., Fu, X.L., Dai, X.Q., Wang, H.M., Li, S.G., 2018. Nitrogen deposition increases root production and turnover but slows root decomposition in Pinus elliottii plantations. New Phytol. 218, 1450–1461.

Li, C., Yan, K., Tang, L., Jia, Z., Li, Y., 2014. Change in deep soil microbial communities due to long-term fertilization. Soil Biol. Biochem. 75, 264–272.

Li, F.L., McCormack, M.L., Liu, X., Hu, H., Feng, D.F., Bao, W.K., 2020. Vertical fine-root distributions in five subalpine forest types shifts with soil properties across environmental gradients. Plant Soil 456, 129–143.

Li, W., Jin, C., Guan, D., Wang, Q., Wang, A., Yuan, F., Wu, J., 2015. The effects of simulated nitrogen deposition on plant root traits: a meta-analysis. Soil Biol. Biochem. 82, 112–118.

Li, X., Simůnek, J., Shi, H., Yan, J., Peng, Z., Gong, X., 2017. Spatial distribution of soil water, soil temperature, and plant roots in a drip-irrigated intercropping field with plastic mulch. Eur. J. Agron. 83, 47–56.

Li, Y., Chen, Han, Y.H., Song, Qianyun, Liao, Jiahui, Ziqian, Huang, Shide, 2018. Changes in Soil Arthropod Abundance and Community Structure across a Poplar Plantation Chronosequence in Reclaimed Coastal Saline Soil. Forests.

Li, Y., Niu, S., Yu, G., 2016. Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: a meta-analysis. Glob. Change Biol. 22, 934–943.

Liu, C., Xing, Y., Duanmu, J., Tian, X., 2018. Evaluating different methods for estimating diameter at breast height from terrestrial laser scanning. Remote Sensing 10, 513.

Liu, X., Zhang, Y., Han, W., Tang, A., Shen, J., Cui, Z., Vitousek, P., Erisman, J.W., Goulding, K., Christie, P., 2013. Enhanced nitrogen deposition over China. Nature 494, 459–462.

Lu, X., Mao, Q., Gilliam, F.S., Luo, Y., Mo, J., 2014. Nitrogen deposition contributes to soil acidification in tropical ecosystems. Glob. Change Biol. 20, 3790–3801.

Lu, X., Vitousek, P.M., Mao, Q., Gilliam, F.S., Luo, Y., Zhou, G., Zou, X., Bai, E., Scanlon, T.M., Hou, E., 2018. Plant acclimation to long-term high nitrogen deposition in an N-rich tropical forest. PNAS 115, 5187–5192.

Meier, I.C., Knutzen, F., Eder, L.M., Mullerhaubold, H., Goebel, M., Bachmann, J., Hertel, D., Leuschner, C., 2018. The deep root system of Fagus sylvatica on sandy soil: structure and variation across a precipitation gradient. Ecosystems 21, 280–296.

Newman, G.S., Coble, A.A., Haskins, K.E., Kowler, A.L., Hart, S.C., 2020. The expanding role of deep roots during long-term terrestrial ecosystem development. J. Ecol.

Norby, R.J., Jackson, R.B., 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytol. 147, 3–12.

Ostertag, R., 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. Ecology 82, 485–499.

Ostonen, I., Truu, M., Helmisaari, H., Lukac, M., Borken, W., Vanguelova, E., Godbold, D.L., Lohmus, K., Zang, U., Tedersoo, L., 2017. Adaptive root foraging strategies along a boreal–temperate forest gradient. New Phytol. 215, 977–991.

Panagopoulos, I., Mimikou, M., Kapetanaki, M., 2007. Estimation of nitrogen and phosphorus losses to surface water and groundwater through the implementation of the SWAT model for Norwegian soils. J. Soil Sediment 7, 223–231.

Peek, M.S., Leffler, A.J., Ivans, C.Y., Ryel, R.J., Caldwell, M.M., 2004. Fine root distribution and persistence under field conditions of three co-occurring Great Basin species of different life form. New Phytol. 165, 171–180.

Peng, Y., Guo, D., Yang, Y., 2017. Global patterns of root dynamics under nitrogen enrichment. Glob. Ecol. Biogeogr. 26, 102–114.

Penuelas, J., Poulter, B., Sardans, J., Ciais, P., Der Velde, M.V., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., 2013. Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. Nat. Commun. 4, 2934.

Persson, H.Å., 1983. The distribution and productivity of fine roots in boreal forests. Plant Soil 71, 87–101.

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta analyses of interspecific variation and environmental control. New Phytol. 193, 30–50.

Pregitzer, K.S., 2002. Fine roots of trees – a new perspective. New Phytol.

Pries, C.E.H., Sulman, B.N., West, C., O'Neill, C., Poppleton, E., Porras, R.C., Castanha, C., Zhu, B., Wiedemeier, D.B., Torn, M.S., 2018. Root litter decomposition slows with soil depth. Soil Biol. Biochem. 125, 103–114.

Sistla, S.A., Schimel, J.P., 2012. Stoichiometric flexibility as a regulator of carbon and nutrient cycling in terrestrial ecosystems under change. New Phytol. 196, 68–78.

Smithwick, E.A.H., Eissenstat, D.M., Lovett, G.M., Bowden, R.D., Rustad, L.E., Driscoll, C.T., 2013. Root stress and nitrogen deposition: consequences and research priorities. New Phytol. 197, 712–719.

Tian, D., Du, E., Jiang, L., Ma, S., Zeng, W., Zou, A., Feng, C., Xu, L., Xing, A., Wang, W., 2018. Responses of forest ecosystems to increasing N deposition in China: A critical review. Environ. Pollut. 243, 75–86.

Turner, M.M., Henry, H.A., 2010. Net nitrogen mineralization and leaching in response to warming and nitrogen deposition in a temperate old field: the importance of winter temperature. Oecologia 162, 227–236.

Van Wijk, M.T., 2011. Understanding plant rooting patterns in semi-arid systems: an integrated model analysis of climate, soil type and plant biomass. Glob. Ecol. Biogeogr. 20, 331–342.

Vanguelova, E.I., Pitman, R.M., 2019. Nutrient and carbon cycling along nitrogen deposition gradients in broadleaf and conifer forest stands in the east of England. For. Ecol. Manage. 447, 180–194.

Wang, G., Fahey, T.J., Xue, S., Liu, F., 2013. Root morphology and architecture respond to N addition in Pinus tabuliformis, west China. Oecologia 171, 583–590.

Wang, G., Liu, F., Xue, S., 2017. Nitrogen addition enhanced water uptake by affecting fine root morphology and coarse root anatomy of Chinese pine seedlings. Plant Soil 418, 177–189.

Wang, J., Gao, Y., Zhang, Y., Yang, J., Smith, M.D., Knapp, A.K., Eissenstat, D.M., Han, X., 2019. Asymmetry in above-and belowground productivity responses to N addition in a semi-arid temperate steppe. Glob. Change Biol. 25, 2958–2969.

Wang, S., Tan, Y., Fan, H., Ruan, H., Zheng, A., 2015. Responses of soil microarthropods to inorganic and organic fertilizers in a poplar plantation in a coastal area of eastern China. Appl. Soil Ecol. 89, 69–75.

Weintraub, S.R., Brooks, P.D., Bowen, G.J., 2017. Interactive effects of vegetation type and topographic position on nitrogen availability and loss in a temperate montane ecosystem. Ecosystems 20, 1073–1088.

Xia, J., Ren, J., Zhang, S., Wang, Y., Fang, Y., 2019. Forest and grass composite patterns improve the soil quality in the coastal saline-alkali land of the Yellow River Delta, China. Geoderma 349, 25–35.

Xia, M., Talhelm, A.F., Pregitzer, K.S., 2015. Fine roots are the dominant source of recalcitrant plant litter in sugar maple-dominated northern hardwood forests. New Phytol. 208, 715–726.

Xu, X., Luo, Y., Shi, Z., Zhou, X., Li, D., 2014. Consistent proportional increments in responses of belowground net primary productivity to long-term warming and clipping at various soil depths in a tallgrass prairie. Oecologia.

Xu, X., Sherry, R.A., Niu, S., Li, D., Luo, Y., 2013. Net primary productivity and rain-use efficiency as affected by warming, altered precipitation, and clipping in a mixed-grass prairie. Glob. Change Biol. 19, 2753–2764.

Xu, Z., Ren, H., Li, M.-H., Brunner, I., Yin, J., Liu, H., Kong, D., Lü, X.-T., Sun, T., Cai, J., 2017. Experimentally increased water and nitrogen affect root production and vertical allocation of an old-field grassland. Plant Soil 412, 369–380.

Yan, G., Chen, F., Zhang, X., Wang, J., Han, S., Xing, Y., Wang, Q., 2017. Spatial and temporal effects of nitrogen addition on root morphology and growth in a boreal forest. Geoderma 303, 178–187.

Yan, X.-L., Jia, L., Dai, T., 2019. Fine root morphology and growth in response to nitrogen addition through drip fertigation in a Populus× euramericana "Guariento" plantation over multiple years. Ann. Forest Sci. 76, 13.

Yu, G., Chen, Z., Piao, S., Peng, C., Ciais, P., Wang, Q., Li, X., Zhu, X., 2014. High carbon dioxide uptake by subtropical forest ecosystems in the East Asian monsoon region. PNAS 111, 4910–4915.

Yu, G., Jia, Y., He, N., Zhu, J., Chen, Z., Wang, Q., Piao, S., Liu, X., He, H., Guo, X., 2019. Stabilization of atmospheric nitrogen deposition in China over the past decade. Nat. Geosci. 12, 424–429.

Yuan, Z., Chen, H.Y., 2015. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. Nat. Clim. Change 5, 465–469.

Zhang, B., Cadotte, M.W., Chen, S., Tan, X., You, C., Ren, T., Chen, M., Wang, S., Li, W., Chu, C., 2019. Plants alter their vertical root distribution rather than biomass allocation in response to changing precipitation. Ecology 100.

Zhang, J., Feng, L., Ouyang, Y., Hu, R., Wang, J., 2020. Phosphate-solubilizing bacteria and fungi in relation to phosphorus availability under different land uses for some latosols from Guangdong, China. Catena 195, 104686.

Zhang, Z., Huang, M., Zhang, Y., 2018. Vertical distribution of fine-root area in relation to stand age and environmental factors in black locust (Robinia pseudoacacia) forests of the Chinese Loess Plateau. Can. J. Forest Res. 48, 1148–1158.

Zhao, Q., Zeng, D., 2019. Nitrogen addition effects on tree growth and soil properties mediated by soil phosphorus availability and tree species identity. For. Ecol. Manage. 449, 117478.

Zhu, J., Wang, Q., He, N., Smith, M.D., Elser, J.J., Du, J., Yuan, G., Yu, G., Yu, Q., 2016. Imbalanced atmospheric nitrogen and phosphorus depositions in China: Implications for nutrient limitation. J. Geophys. Res. 121, 1605–1616.