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RESEARCH PAPER

Fine root morphology and growth in response to nitrogen addition through drip fertigation in a *Populus × euramericana* "Guariento" plantation over multiple years

Xiao-Li Yan[1] · Liming Jia[2] · Tengfei Dai[2]

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Abstract

• ***Key message*** **Nitrogen addition through drip fertigation to a poplar plantation (*Populus × euramericana* "Guariento") promoted fine root growth only in the early period. The relationship between root growth and soil N content was positive in the first 2 years, but became negative in the third year when the soil N availability had substantially increased.**

• ***Context*** Nitrogen (N) deficiency is common in forest soils, and N addition is sometimes applied in the case of intensive plantations. There is a need to better document the impact of N addition through the high-efficiency fertilization technique on fine root morphology and growth, given their importance for the uptake of nutrients and for tree growth.

• ***Aims*** We aimed to quantitatively investigate the responses of fine roots in morphology and growth to N addition through surface drip fertigation over multiple years in a *Populus × euramericana* "Guariento" plantation.

• ***Methods*** A field experiment that included four drip fertigation treatments with N addition levels (0, 60, 120, and 180 kg N ha^{-1} $year^{-1}$) was conducted for three successive years. A coring method was used to sample soils and quantify the root morphological traits and soil N content along 0–60-cm profiles.

• ***Results*** The root biomass density, length, surface area, specific length, and tissue density were significantly higher in the N addition treatments than those in the control after the first year, but the positive effect decreased in the second year. In the third year, root biomass in the N addition treatments was even lower by 11–39% than that in the control. The relationship between root growth and soil N content was also positive in the first 2 years and negative in the third year.

• ***Conclusion*** N addition promoted fine root growth mainly in the shallow soil and in the early period of experiment. The relationship between root growth and soil N content became negative in the third year when the soil N availability had substantially increased. It is suggested that fine roots adjust their growth and morphology in response to N availability varying along the soil profile and with the fertilization duration.

Keywords Nitrogen addition · Fine root · Root morphology · Vertical distribution · Drip fertigation · *Populus × euramericana* "Guariento"

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Contribution of the co-authors XL Yan and LM Jia designed and coordinated the research. XL Yan and TF Dai conducted the experiment. XL Yan wrote the manuscript. All members reviewed the manuscript.

✉ Liming Jia
jlm@bjfu.edu.cn

[1] College of Forestry, Fujian Agriculture and Forestry University, Fuzhou 350002, China

[2] Ministry of Education Key Laboratory of Silviculture and Conservation, Beijing Forestry University, Beijing 100083, China

1 Introduction

Root systems can adjust their morphological traits in response to the local heterogeneity of soil nutrients (Fort et al. 2015; Kou et al. 2015; Liu et al. 2017; Ostonen et al. 2007). In particular, fine roots play a crucial role in regulating plant and ecosystem functions through acquiring nutrients. Recent studies have shown that fine root morphological traits vary widely across nutrient patches, water resources, and plant species (Eissenstat et al. 2015; Kou et al. 2015; Liu et al. 2015; Wang et al. 2016). Increasing evidence suggests that trees optimize their resource uptake by modifying fine root growth and morphological traits (Mou et al. 2013; Wang et al. 2013;

Wang et al. 2016). Several morphological and physiological traits have been used as potential indicators of nutrient absorption ability of trees (Ostonen et al. 2007). Among those, root biomass density is the most commonly investigated parameter in the context of fertilization effects (Ostertag 2001). The root length density is assumed to be proportional to the resource acquisition potential (Aerts and Chapin 1999; Eissenstat et al. 2000; Wurzburger and Wright 2015). The specific root length is used to characterize the economic aspects of root systems (Fitter et al. 1991). Overall, previous studies emphasized the responses of fine roots to climate changes or nutrient patches. Investigations of the responses of fine roots in the field have been infrequent (Wang et al. 2016). Knowledge of potential effects of fertilization management on fine root morphological characteristics based on long-term field experiments is still insufficient. Understanding their spatial and temporal response characteristics could not only contribute to the elucidation of nutrient absorption mechanism but also help efficient management practices in forest plantations.

Forest ecosystems are commonly limited by soil nitrogen availability (Kou et al. 2015; Lebauer and Treseder 2008; Wang et al. 2017). Improvement of available N in intensively managed forests has yielded substantial increase in production (Clemensson and Persson 1995; Holopainen and Heinonentanski 1993; Wang and Liu 2014). However, more studies have found that enriched available N resulted in decreases in biomass, length, and the number of fine roots (Li et al. 2015; Nadelhoffer 2000; Van Diepen et al. 2010; Wang et al. 2013). Further investigation is thus needed to clarify how fine roots change their growth and morphological traits in response to N addition in forest plantations, especially to the recent highly increasing anthropogenic N deposition (Galloway et al. 2008; Kou et al. 2016). Previous studies on nitrogen management have been performed either on pot-grown specimens or on field-grown trees with conventional fertilization techniques (Coleman 2007; Yan et al. 2018). Long-term field experiments with high-efficiency fertilization techniques should be of great significance to our limited understanding of the effects of nitrogen addition on fine roots within a soil profile.

Poplar plantations are one of the most widely planted commercial forests, and China has the largest area in the world (Dickmann 2006; Perry et al. 2001; Yan et al. 2018). High-efficiency fertilization techniques such as fertigation have been increasingly applied to the cultivation of plantations to meet their high nutrient requirements around the world (O'Neill et al. 2014; Rennenberg et al. 2010; Wang et al. 2015). Although previous studies have shown that fertigation can significantly promote the growth and production of polar plantations (Wang et al. 2015; Yan et al. 2018; Yan et al. 2016), the responses of root systems were not reported. Several studies investigated fine root characteristics in poplar (Alafas et al. 2008; Dickmann et al. 1996; Douglas et al. 2010; Heilman et al. 1994; Mulia and Dupraz 2006; Pregitzer et al. 2000), but those on root morphological traits in response to N addition through long-term field experiments were relatively few (but see Coleman 2007; Dickmann et al. 1996). It remains unclear how fine roots of poplar adjust their morphology in balance with absorption in response to increased N availability.

The aim of this study was to quantitatively examine the responses of fine root growth and morphological traits to nitrogen addition through surface drip fertigation over multiple years. The specific objectives were (i) to identify whether the fine root morphology would be affected by the N addition through surface drip fertigation, (ii) to explore whether the fine root growth and biomass would be promoted by N addition and positively related to N dosage, and (iii) to determine whether such an effect is constant across years.

2 Materials and methods

2.1 Site description and plant material

The experiment was conducted at a research field in Shunyi District, a northern suburb of Beijing, China (40° 05′ 48.7″ N, 116° 49′ 35.6″ W, 28 m above sea level). The site is characterized by a warm temperate continental climate with an annual mean temperature of 11.5 °C, precipitation of 625 mm, and a frost-free period of approximately 195 days. The soil is a sandy loam, and the total nitrogen, available N, available phosphorus, and potassium contents at the beginning of the experiment were 0.58 g kg^{-1}, 12.79 mg kg^{-1}, 4.89 mg kg^{-1}, and 195.31 mg kg^{-1}, respectively. Detailed information of soil physical properties has been presented in Yan et al. (2018).

The plantation was established in the spring of 2011 with 3-year-old saplings that were cultured from cuttings of a fast-growing poplar clone (*Populus* × *euramericana* "Guariento"). Saplings were planted in alternating wide (12 m) and narrow (6 m) rows at an intra-row spacing of 4 m, resulting in an overall planting density of 300 trees ha^{-1}. Surface drip irrigation pipes were laid along the tree rows, and each pipe roughly supplied water at a flow rate of 2 L h^{-1} during operation.

2.2 Experimental design

The field experiment comprised four N application treatments each with three replicates (0.13 ha each) that were arranged in a randomized block design. N addition treatments through surface drip fertigation (DF) were applied in the growing seasons over three successive years (2012–2014). Urea (CH_4N_2O) in three doses (totally 60, 120, and 180 kg N ha^{-1} year^{-1}, denoted as DFN_{60}, DFN_{120}, and DFN_{180}, respectively) was applied through six times each year by dissolving it in water. The fourth treatment was the control, representing the conventional management in this region. Because the N addition treatments have water inputs during the surface drip fertigation, an equal amount of water was also applied simultaneously to the control by drip irrigation. Furrow irrigation was applied to both the control and treatments to promote leaf expansion at the beginning of the growing season. The actual water amount was determined by reading the meters after irrigation. Errors might exist among the four treatments. The total irrigation amounts for the four treatments in 2012, 2013, and 2014 were 354.4–398.1 mm, 389.8–429.7 mm, and 363.6–386.5 mm, respectively, approximating 56–68% of the mean annual precipitation in the region. The six N application times were May 5, June 1, June 21, July 8, August 2, and August 29 in 2012; April 28, May 20, June 13, June 30, July 26, and August 17 in 2013; and April 21, May 12, June 7, July 7, August 2, and August 28 in 2014.

2.3 Root sampling and measurements of root morphological traits

Sampling of fine roots was conducted using a soil coring method in October of each growing season. Six trees of average size were selected from each block to locate the root sampling spots. The soil core was taken at a 1-m distance from the trunk of the selected sample tree and directly below the drip irrigation nozzle. Six soil cores (10-cm internal diameter, 10-cm height) were sampled in the 0–60-cm soil layer (i.e., 0–10, 10–20, 20–30, 30–40, 40–50, and 50–60 cm) at each spot. A total of 432 soil cores were collected. Each soil sample was gently wet sieved using fresh water to rinse the soil and other materials from the roots with two sieves (0.8 and 0.125-mm mesh) to avoid losing fine roots. Live roots were distinguished from dead roots by their lighter color and greater resilience (Xi et al. 2013). All live roots were stored in tightly sealed valve bags and kept frozen until root morphological measurements were made.

Root morphology was determined using an Epson Twain Pro high-quality scanner. Using forceps and dissecting needles, all the fine root segments were carefully spread out on a transparent plastic sheet without overlap and abutments. Images at 400 dpi were obtained and saved in a tagged image file format. The length, surface area, volume, and average diameter of roots were determined using the image analysis software WinRHIZO (Regent Instruments Inc., Quebec, Canada). The roots with a diameter > 2 mm were excluded from calculations in this study. After morphological trait measurements, the roots were dried at 65 °C to a constant weight for the determination of dry mass.

2.4 Soil nitrogen content

Field sampling for soil nutrient analyses was conducted at the beginning of the experiment (March 2012) and in October at the end of each growing season at a 1-m distance from the trees corresponding to those for fine root sampling. Core samples were taken to a 60-cm depth at 20-cm intervals (i.e., 0–20, 20–40, and 40–60 cm) at each location. N concentrations were analyzed using the Kjeldahl method.

2.5 Data analysis

The root biomass density (RBD, g m^{-3} soil), root length density (RLD, m m^{-3} soil), and root surface area (RSA, m^2 m^{-3} soil) data were calculated as total dry mass, root length, and surface area of a sample/soil core volume, respectively. The specific root length (SRL, m g^{-1}) was calculated from the total fine root length in each soil core divided by their dry weight. The root average diameter (RAD, mm) was calculated from the mean of total roots in each soil core. The root tissue density (RTD, g cm^{-3} root) was the ratio of the sample root dry mass to its volume.

Table 1 The *p* values of repeated-measurement ANOVA for responses of root biomass density (RBD), root length density (RLD), root surface area (RSA), specific root length (SRL), root average diameter (RAD), and root tissue density (RTD) to N dose, soil depths, the year of experiment, and their interactions

Source of variation	df	*p* value and significance level					
		RBD (g m^{-3} soil)	RLD (m m^{-3} soil)	RSA (m^2 m^{-3} soil)	SRL (m g^{-1})	RAD (mm)	RTD (g cm^{-3} root)
N dose	3	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.200NS	< 0.001***
Soil depths	5	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.024*	0.013*
Year of experiment	2	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***
N dose × soil depths	15	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.066NS	0.001**
N dose × year of experiment	6	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.053NS	< 0.001***
Soil depths × year of experiment	10	< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.001**
N dose × soil depths × year of experiment	30	< 0.001***	< 0.001***	< 0.001***	0.001**	0.016*	0.001**

Significance of analysis of variance factor: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

NS not significant

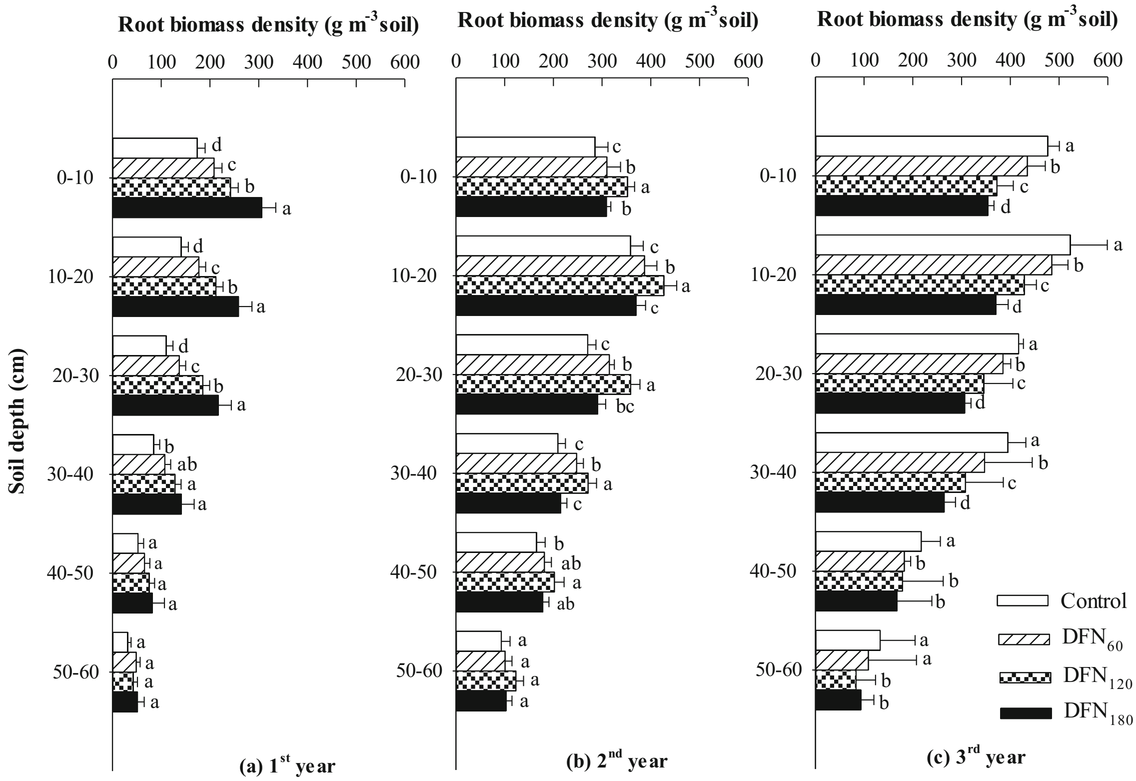

Fig. 1 Root biomass density (RBD) under different N addition treatments during 3 years of experiment. Values are expressed as means and standard errors (SE). Different letters within the same soil layer indicate significant difference among N addition treatments

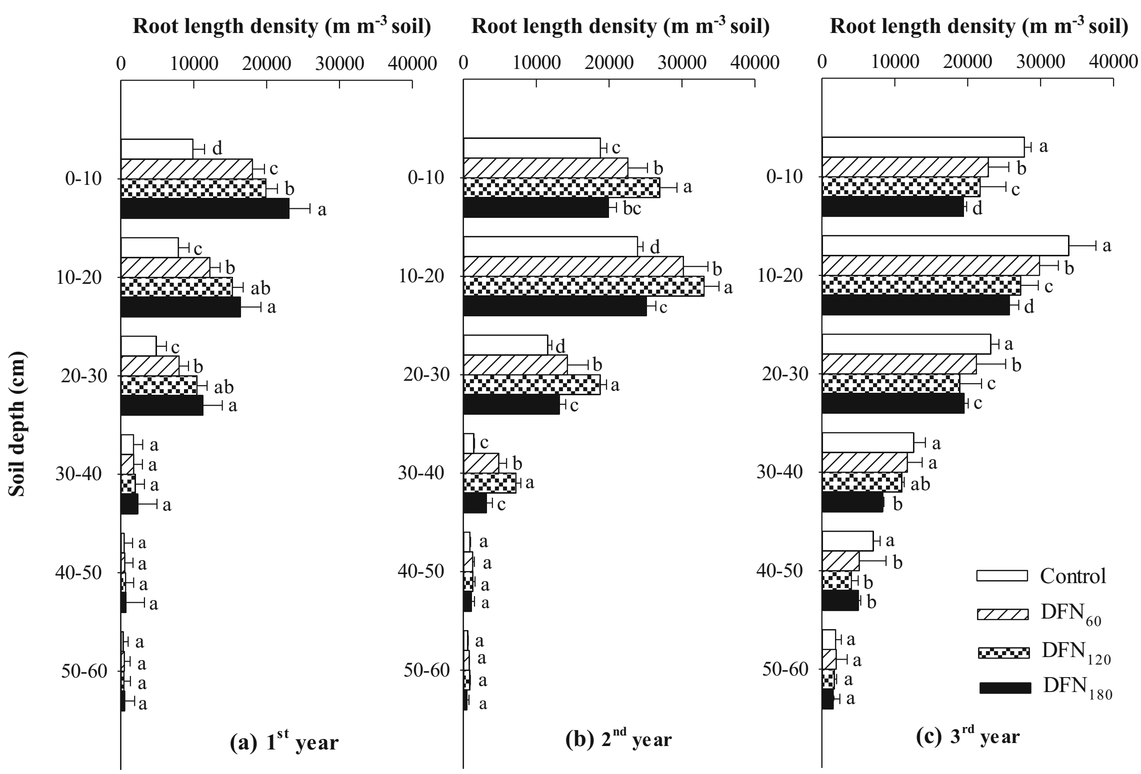

Fig. 2 Root length density (RLD) under different N addition treatments during 3 years of experiment. Values are expressed as means and standard errors (SE). Different letters within the same soil layer indicate significant difference among N addition treatments

All statistical analyses were conducted using SPSS 22.0 for Windows (SPSS Inc., Chicago, IL, USA). The three-way repeated-measure ANOVA was used to examine the effects of the N addition, soil depth, year of experiment, and their interactions on the RBD, RLD, RSA, SRL, RAD, and RTD. Multiple comparison among N addition treatments within each soil layer was conducted using the Tukey's test (significance level was set at $p = 0.05$). Prior to the ANOVA, all data was tested to satisfy the assumptions of normality ($p > 0.05$) and homogeneity of variance ($p < 0.05$). The relationships between RLD, RSA, RBD, and soil N content were analyzed by the linear regression method for mean values using SigmaPlot 12.5.

3 Results

3.1 Effects of N dosage, soil depth, year of the experiment, and their interactions on root morphological traits and biomass

The RBD, RLD, RSA, and SRL varied across N dosage, soil depth, and year of the experiment (Table 1). The effects of N dosage, soil depth, year of the experiment, and their interaction on RBD, RLD, SRL, and RSA were all statistically significant ($p < 0.001$ or $p < 0.01$). The RAD was statistically different among soil depths ($p < 0.05$) and among the years of experiment ($p < 0.001$), but the effects from N dosage and the interactions between N dosage and either of the other two factors were not significant ($p > 0.05$). The effects on RTD were significant ($p < 0.05$) for all the factors, and those affected by N dosage, year of the experiment, and various interaction effects reached high significance ($p < 0.001$ or $p < 0.01$).

3.2 Vertical distribution of fine roots in response to N addition

Experiments over 3 years showed that the RBD, RLD, RSA, SRL, and RTD were much higher in the top 30-cm layers in both the treatments and the control, and they decreased with the soil depth (Figs. 1, 2, 3, 4, and 5). Taking the RBD as an example, their distribution percentages in the 0–30-cm soil layer were as high as 70–74%, 66–67%, and 66–67% in the three successive years, respectively. The difference in RAD

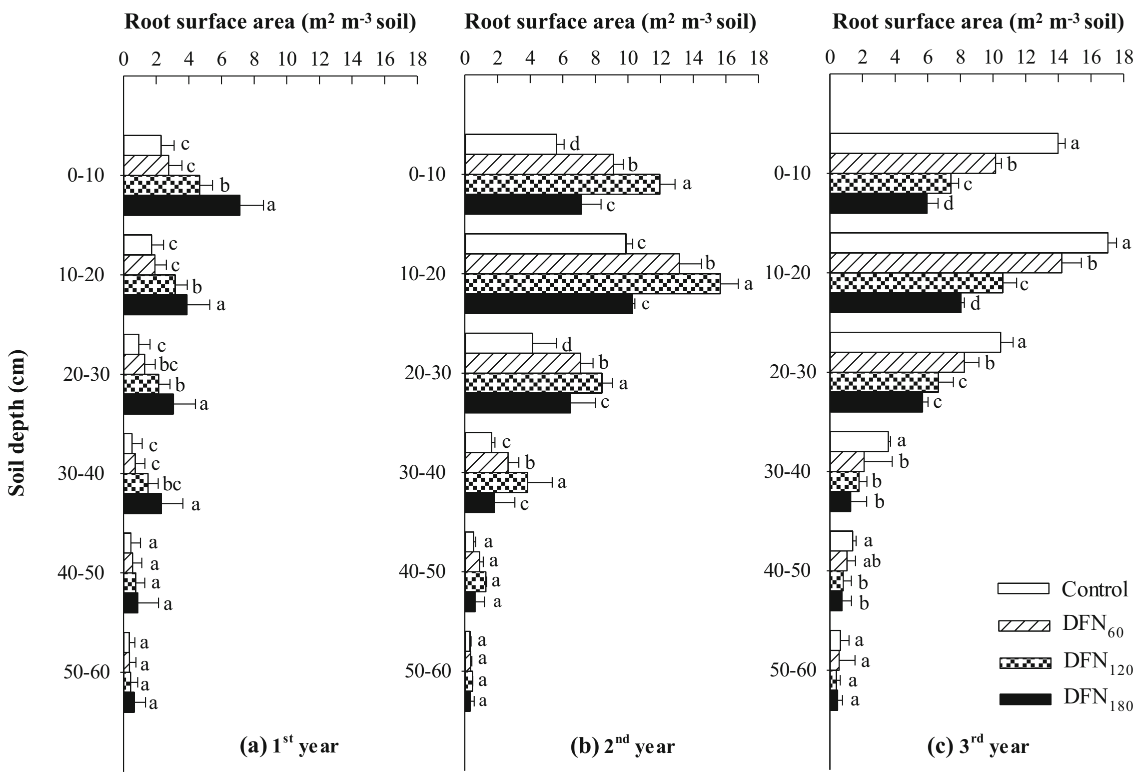

Fig. 3 Root surface area (RSA) under different N addition treatments during 3 years of experiment. Values are expressed as means and standard errors (SE). Different letters within the same soil layer indicate significant difference among N addition treatments

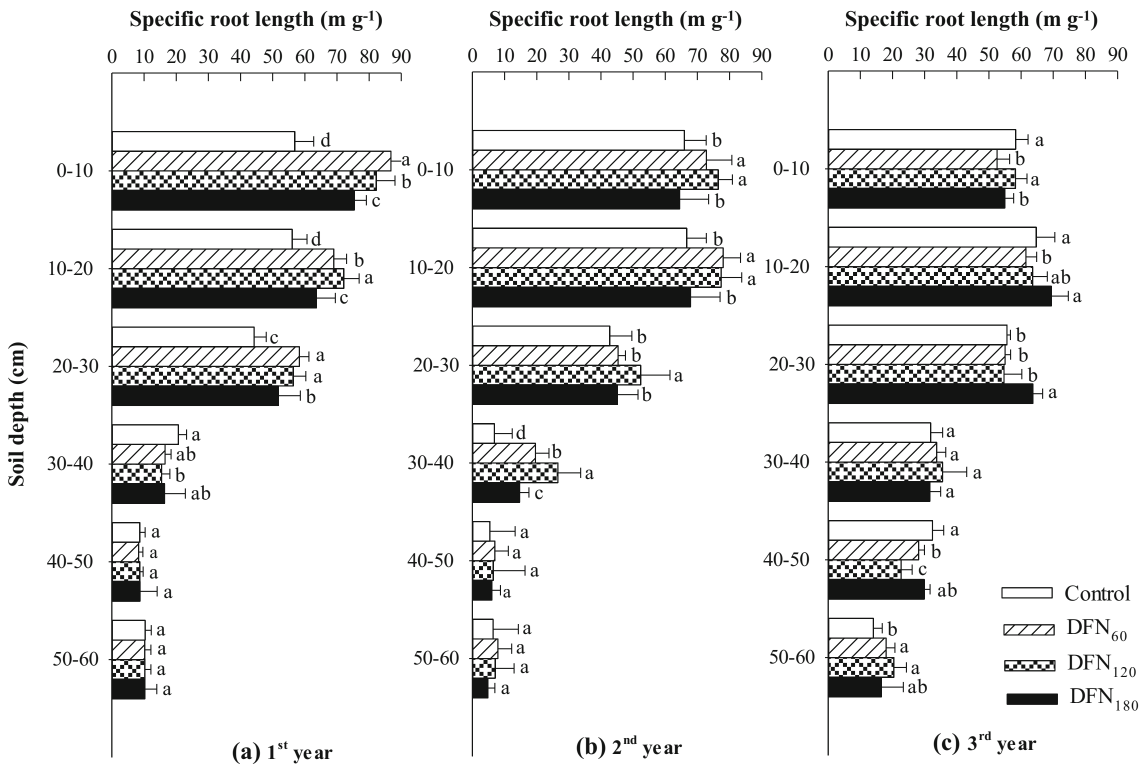

Fig. 4 Specific root length (SRL) under different N addition treatments during 3 years of experiment. Values are expressed as means and standard errors (SE). Different letters within the same soil layer indicate significant difference among N addition treatments

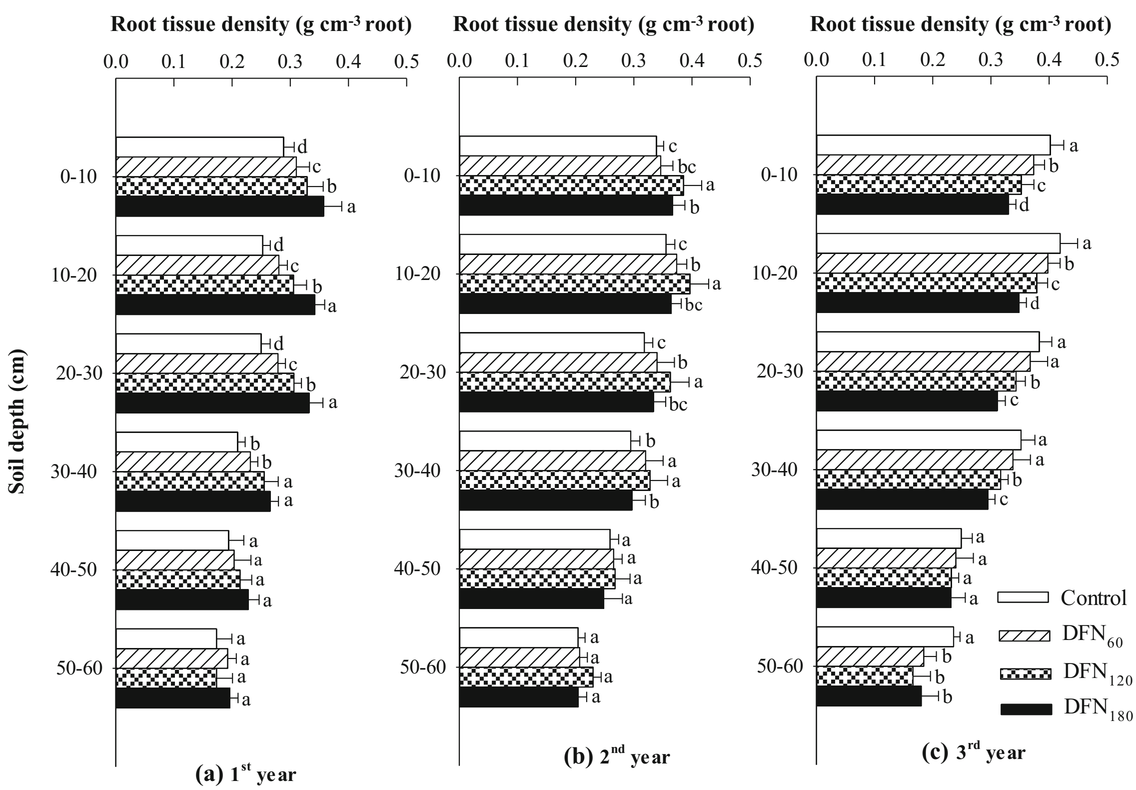

Fig. 5 Root tissue density (RTD) under different N addition treatments during 3 years of experiment. Values are expressed as means and standard errors (SE). Different letters within the same soil layer indicate significant difference among N addition treatments

among soil depths was also statistically significant ($p < 0.05$) according to the results of ANOVA (Table 1).

3.3 Fine root morphological traits and biomass in response to N addition

In each of the three experimental years, all the fine root morphological traits and biomass showed differences between the N addition treatments and control in the upper soil layers, though they were not always statistically significant between any two treatments (Figs. 1, 2, 3, 4, and 5). In the first year, the RBD, RLD, RSA, SRL, and RTD in the N addition treatments were significantly higher than those of the control, especially in the surface soil of 0–30 cm in depth ($p < 0.05$). Compared with the control, the N addition treatments enhanced the RBD, RLD, RSA, SRL, and RTD by 23–84%, 169–224%, 21–184%, 21–36%, and 5–35%, respectively (Figs. 1a, 2a, 3a, 4a, and 5a). However, the positive effect decreased in the second year, and there was no significant difference between DFN_{180} treatments and the control ($p > 0.05$) (Figs. 1b, 2b, 3b, 4b, and 5b). In the third year, the RBD, RLD, RSA, and RTD in most of the soil layers under the N addition treatments were significantly lower than the control (Figs. 1c, 2c, 3c, and 5c). For example, the RBD was 11–39% lower in the N addition treatments than those in the control (Fig. 1c). Additionally, the RAD did not show significant differences among the N addition treatments and the control throughout the three successive years of the experiment (Fig. 6).

The specific relationships between the N content in soil and root morphological traits were investigated for the 3 years (Fig. 7). Overall, the figures clearly show that upper soil contains higher N contents and greater values for the fine root parameters. Among the treatments and the control, the root morphological traits were linearly correlated with the soil N contents in each soil layer, with the extent of change (i.e., slope of regressions) decreasing in deeper soil. The regressions showed a decreasing trend of the positive correlation with the treatment year as expressed by the regression slopes. In particular, the correlations were even negative in the third year, coinciding with the information from Figs. 1, 2, and 3.

4 Discussions

4.1 Effects of N addition through surface drip fertigation on root morphology and growth vary with years of the experiment

Fine root growth was promoted by N addition and positively related to N dosage in the first year of the experiment. However, such a positive relationship was not observed from the second year. The fine root biomass was significantly higher

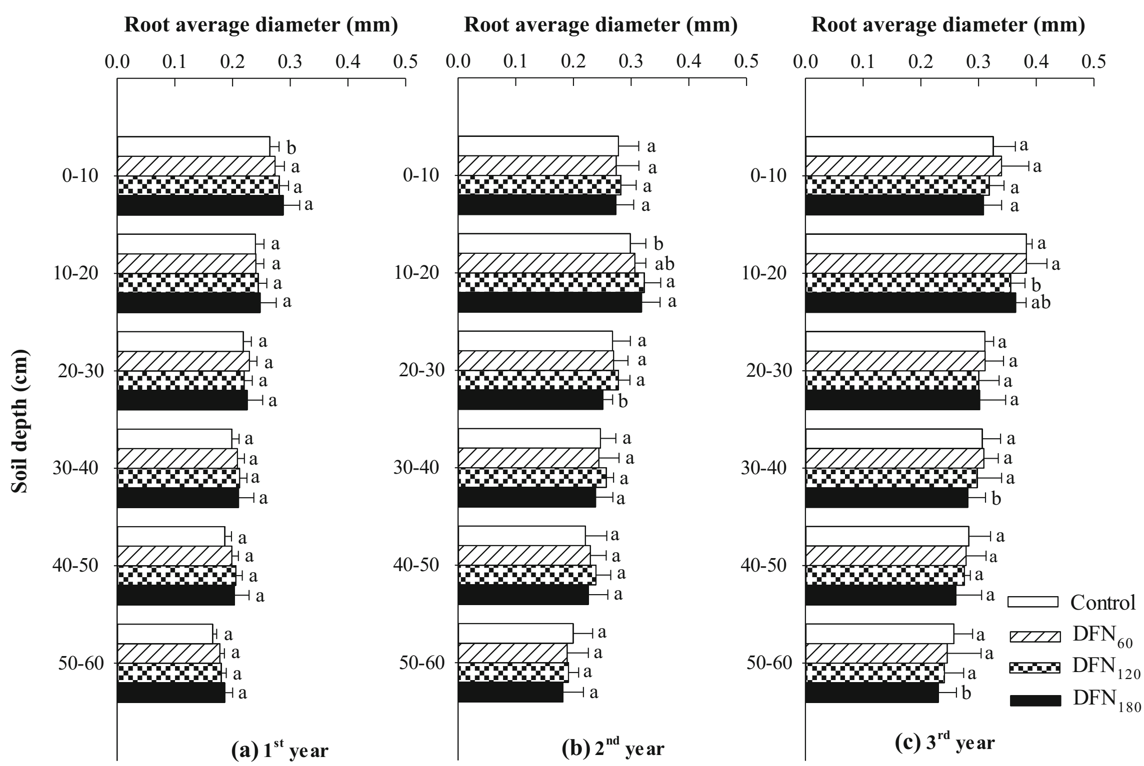

Fig. 6 Root average diameter (RAD) under different N addition treatments during 3 years of experiment. Values are expressed as means and standard errors (SE). Different letters within the same soil layer indicate significant difference among N addition treatments

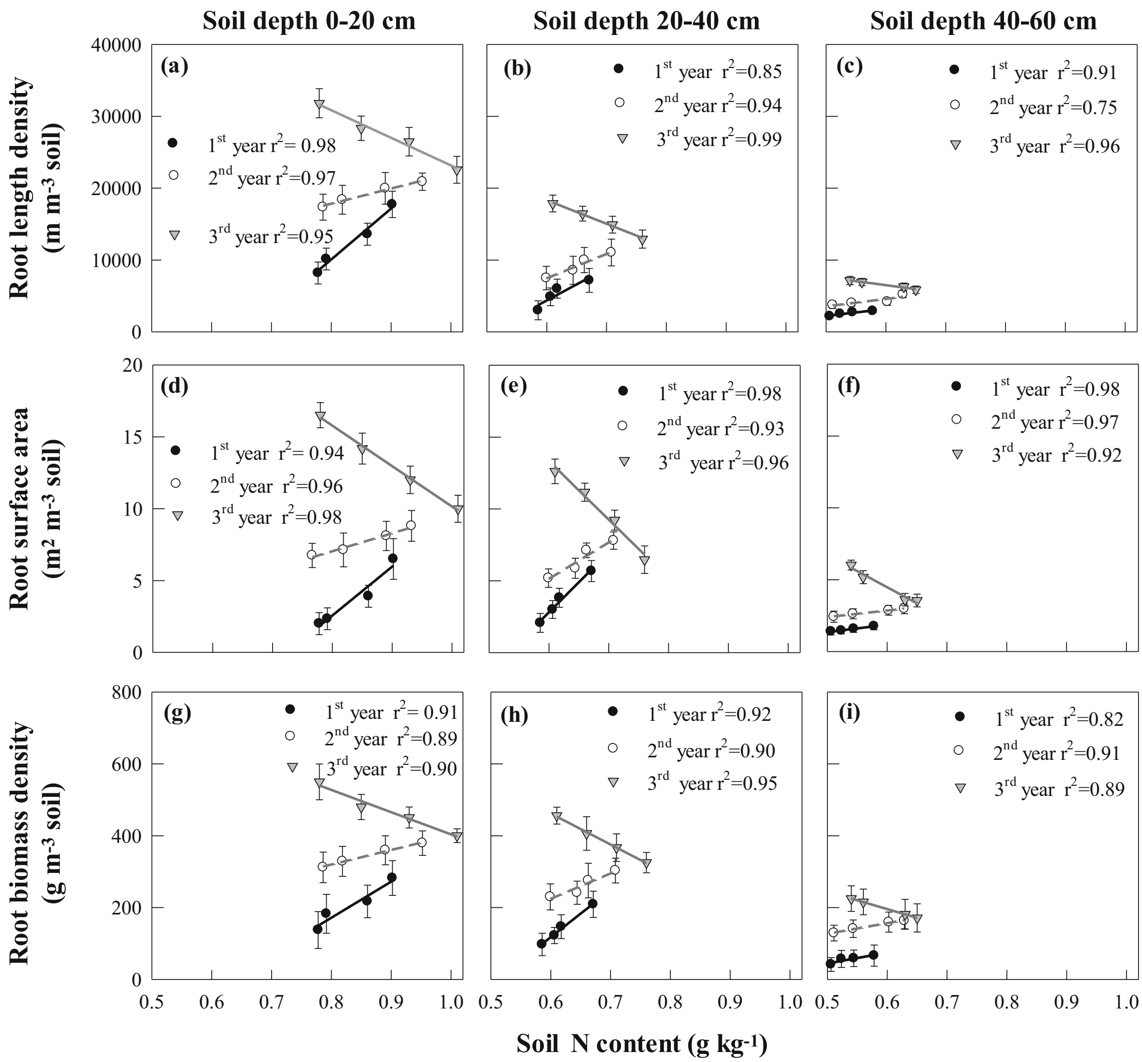

Fig. 7 Relationships between root length density (RLD), root surface area (RSA), root biomass density (RBD), and soil N content in different soil depth during 3 years of experiment. Lines are fitted linear relationships; black circle and sold line indicate the first-year relationship; white circle and dashed line indicate second-year relationship, and gray triangle and gray line indicate the third-year relationship

in the control than in the N addition treatments in the third year, showing a negative relationship between the root growth parameters and N dosage (Figs. 1c and 7). These suggest that the effects of N addition on fine root growth vary over time. There have been reports of positive, negative, and no effect of N addition on fine root biomass. While some studies showed an increase in fine root biomass following N addition (Liu et al. 2017; Nadelhoffer 2000; Noguchi et al. 2013; Pregitzer et al. 1993; Wang et al. 2016), others showed that N addition and higher N availability reduced fine root production and turnover in forests (Burton et al. 2000; Li et al. 2015; Peng et al. 2017; Tateno et al. 2004; Wang et al. 2012; Wurzburger and Wright 2015). Moreover, some studies even showed that N fertilization had no effect on fine root biomass or length density (Genenger et al. 2003; Pregitzer et al. 1995; Tingey et al. 1996). Based on the 3-year experiment, our results suggest that these inconsistent responses should be related to different soil N conditions and plant species.

In the first year of our study, a positive effect of N addition was clearly observed, yielding 25–78% higher RBD than those in the control (Fig. 1a). This is consistent with the condition of the relatively young trees whose root systems have not fully developed and thus could not absorb and utilize water and nutrient resources from deep soil. Therefore, fine roots tended to expand and proliferate in the surface soil where water and nutrient conditions were improved by drip fertigation. Young trees are generally considered to have relatively inadequate root systems that would be more likely to show a strong positive response to the addition of N (Chen and Brassard 2013; Peng et al. 2017). In addition, trees should be more sensitive to nutrients under low nutrient conditions; it is thus reasonable that N addition accelerates root growth in the first year of an experiment.

In the second year of N addition treatments, only medium and low levels of N dosage showed increasing effects on the RBD, whereas the RBD for high N dosage was not significantly different from the control (Fig. 1b). In the third year, fine root biomass, length, surface area, and tissue density were even significantly lower in the N addition treatments compared to the control (Figs. 1c, 2c, 3c, and 5c). Such results can be explained by the influence of stand age and experimental duration on the responses of fine roots to N addition (Peng et al. 2017). After the study site has been fertilized with N for a period, trees should experience lower levels of N limitation than they did originally. After 3 years of surface drip fertigation, the N contents in the 0–20 and 20–40-cm soil layers of this experiment were approximately 6–28% and 8.2–25% higher for the soils treated with fertigation than for the control (Fig. 8). The "law of the minimum" theory suggests that a plant should not necessarily increase the proportion of C to roots if it is not N-limited (Peng et al. 2017). A similar response pattern in which N-induced changes in root biomass were negatively correlated with experimental duration was also reported by Bobbink et al. (2010) and Phoenix et al. (2012). Ostertag (2001) noted that the long-term effects of N fertilization on the fine root biomass differ from short-term effects. Previous studies suggest that RTD tends to increase to adapt to water shortage and nutrient-poor conditions and high level of soil N fertility would cause a decrease of RTD (Eissenstat et al. 2000; Ostonen et al. 2011). The changing trend of RTD in this study was similar to that of RBD and most other parameters, which implies that the reduction of RTD appears only when the N availability exceeds a threshold level.

Additionally, with increasing age, trees have more complete and deeper root systems, and they can uptake water and nutrient resources in the deeper soil layer. This is in accordance with the trade-off between cost and profit, i.e., plant roots tend to maximize benefits while minimizing costs during resource uptake and utilization (Eissenstat and Yanai 1997). One important cost is tissue construction for building absorptive surfaces for water and soil nutrients. The poplar trees in this study might have lower construction costs per unit of fine root biomass in the first year of the experiment and thus showed greater root proliferation. Conversely, in the third year of the experiment, fine root parameters would hardly change under the N-rich condition following high doses of N addition or as N addition exceeds a threshold. These results also imply that the poplar clone changes its root system to adapt to fluctuating soil nitrogen conditions.

4.2 N addition through the drip fertigation technology affected fine root growth in shallow soil rather than in deep soil

N addition through surface drip fertigation promoted fine root growth, especially in the surface 0–30-cm layer. The first reason should be the concentrated distribution of fine roots in the surface soil layer in most forests, and shallow roots can benefit from their better soil nutrient and physical conditions. In addition to the higher concentration of nutrients, the aeration and texture for root growth are also better in topsoil than in deeper layers (Chen and Brassard 2013; Jobbagy and Jackson 2001; Schenk and Jackson 2002). The occurrence of more fine roots

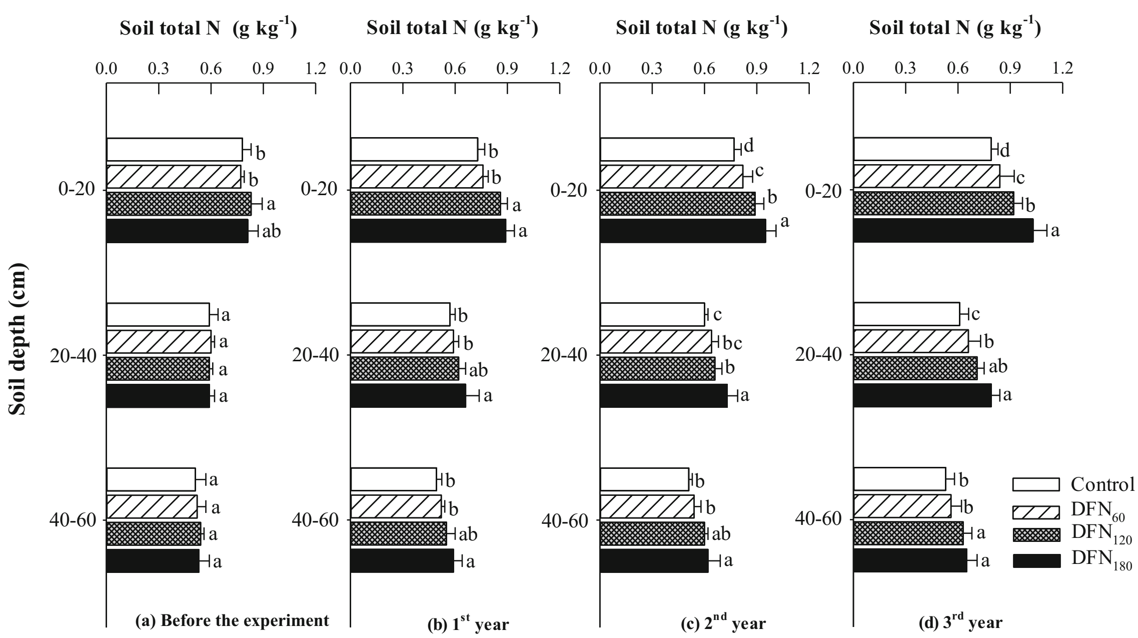

Fig. 8 Soil total N content in the 0–20, 20–40, and 40–60-cm soil layers before the experiment and after each growing season of the 3-year experiment. Values are expressed as mean ± standard errors (SE). Different letters within the same soil layer indicate significant difference among N addition treatments

in the surface soil is reasonable especially under this high N condition (Bennett et al. 2002; Zewdie et al. 2008). Second, N addition through surface drip irrigation in our study should have percolated slowly to approximately 50 cm in depth (Xi et al. 2013; Yan et al. 2016); fine roots in the topsoil layer should have priority access to nutrients (Chang et al. 2012; Vogt et al. 1981). The effect of fertigation management on soil N content should have gradually moved downward in the soil as N addition continues.

5 Conclusions

Nitrogen addition through surface drip fertigation affected fine root growth positively in the early period in a *Populus* × *euramericana* "Guariento" plantation, and there was a positive correlation between root growth and soil N content. The positive effect was greater in shallow soil than in deep soil, and varied with time. Root growth under the N addition treatments decreased in the third year when the soil N availability had substantially increased, and the relationship between root growth and soil N content became negative. It is suggested that the fine roots adjust their growth and morphology in response to N availability varying along the soil profile and with the fertilization duration.

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Data availability statement The datasets generated and/or analyzed during the current study are available in the Dryad repository (Yan et al. 2018). Datasets not peer-reviewed. Yan XL, Jia LM, Dai TF (2018) Data from: Fine root morphology and growth in response to nitrogen addition through drip fertigation in a Populus × euramericana "Guariento" plantation over multiple years. Dryad Digital Repository. [Dataset] https://doi.org/10.5061/dryad.3h41m6v

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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