



Response of density-related fine root production to soil and leaf traits in coniferous and broad-leaved plantations in the semiarid loess hilly region of China

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Received: 9 February 2021 / Accepted: 18 April 2021
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Abstract Fine roots are the most active and functional component of root systems and play a significant role in the acquisition of soil resources. Density is an important structural factor in forest plantations but information on changes in fine roots along a density gradient is limited. In this study, plantations of black locust (*Robinia pseudoacacia* L.) and Chinese pine (*Pinus tabulaeformis* Carr.) with four density classes were analyzed for the influence of soil and leaf traits on fine root growth. Fine root biomass increased with stand density. High fine root biomass was achieved through increases in the fine root production and turnover rate in the high-density black locust plantations and through an increase in fine root production in the pine plantations. In the high-density Chinese pine stand, there was a high fine root turnover which, coupled with high fine root production,

contributed to a high fine root biomass. Overall, fine root production and turnover rate were closely related to soil volumetric water content in both kinds of plantations, while fine root biomass, especially the component of necromass, was related to soil nutrient status, which refers to phosphorous content in black locust plantations and nitrogen content in Chinese pine plantations. There was a close linkage between leaf area index and fine root dynamics in the black locust plantations but not in the pine plantations.

Keywords Fine roots · Black locust · Chinese pine · Semiarid · Soil moisture · Leaf area index

Introduction

In forest plantations, stand density is a major index representing resource use conditions and interactions among and between trees and environments; thus, it is of major consideration in management practices. Stand density determines stand spatial structure and directly affects the distribution of light, heat, moisture, and other ecological factors affecting the growth of individual trees and of the plantation (Cai et al. 2016; Hakkenberg et al. 2016; Bo et al. 2018). The effect of stand density on fine root dynamics has been studied in natural forests coupled with species richness (He et al. 2005; Marquard et al. 2009; Zeng et al. 2020). In plantations, the effects of stand density on fine root biomass, production, and turnover rate have been reported less frequently.

Fine roots, generally defined as ≤ 2 mm in diameter, are one of the most physiologically active organs of the tree, owing to their short lifespan and large absorption capacity (Liu et al. 2014; Wells and Eissenstat 2001). Although fine roots account for less than 10% of the total forest biomass (Olesinski et al. 2012), they account for approximately a

Project funding: The study was financially supported by the National Key R & D Program of China (2017YFC0504601).

The online version is available at <http://www.springerlink.com>.

Corresponding editor: Zhu Hong.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11676-021-01358-0>.

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third of the annual net primary production in forest ecosystems (Finer et al. 2019; Wang et al. 2019). Because of their crucial role in energy and matter fluxes and the essential function of soil resource acquisition in the biosphere (Stewart and Frank 2008), fine root dynamics have been widely studied. However, most studies have focused on the upper soil layers no more than 30 cm deep where fine roots are believed to be the most abundant (Yuan and Chen 2010; Pickles and Pither 2014). Fine roots in deeper soil profiles have been reported to have a disproportionate impact on soil resource acquisition when trees cope with stress such as seasonal drought (Binkley 2015; Yang et al. 2017; Wasyliv and Karst 2020). Due to the heterogeneous spatiotemporal distribution of fine roots (Wang et al. 2013b), and the difficulty of directly observing underground processes (Finer et al. 2011), knowledge about fine root dynamics remains limited.

The effects of soil factors on fine root growth have been extensively studied. Soil nutrients and water have been reported to affect age-related fine root biomass but not fine root production in plantations on the Loess Plateau (Chen et al. 2016). Zhou and Shangguan (2007) reported that soil water is a key factor in fine root vertical distribution, whereas the effect of inorganic nitrogen (N) is relatively limited. Soil surface layers are believed to have higher nutrient concentrations, low soil strength, and high water availability, which would promote the proliferation of roots with a more acquisitive strategy (Prieto et al. 2015). However, a contrasting hypothesis suggested that fine roots might grow rapidly in order to more efficiently exploit soil resources in poor soil (Weemstra et al. 2017). Given that both theories have been corroborated and refuted with empirical data (Leuschner et al. 2004; Hertel et al. 2013; Wang et al. 2013a), more field data are needed from semiarid regions.

Just as fine roots do belowground, leaves serve as absorption and interface organs aboveground (Jia et al. 2015). Fine roots provide nutrients and water for photosynthesis in the leaves and in return, leaves provide carbohydrate products for fine roots (Jackson et al. 1997). The two active organ systems are closely linked through material exchange and their activities and biomass are interdependent as predicted by the functional balance theory (Vanninen and Makela 1999; Albaugh et al. 2006). Leaves and roots show similar resource acquisition strategies based on previous evidence (Diaz et al. 2004; Liu et al. 2010), and leaf functional traits may be partially extrapolated to corresponding root traits (Fort et al. 2013; Li and Bao 2015). Fine root traits, such as biomass, morphology, and physiology, were found to be associated with leaf traits within and among species (Withington et al. 2006; Hajek et al. 2013; Meng et al. 2018). Leaf nutrients are considered plastic traits that change with plant response to environmental variability (Pugnaire 2001). For example, carbon (C) contents reflect the adaptation strategy, to

some extent, of plants to the environment (Zhao et al. 2018), nitrogen (N) contents reflect the ability of plants to capture resources through enzymatic processes, and phosphorus (P) contents determine the energy available for metabolism (Agren 2008; Li and Bao 2015). Cote et al. (2003) reported that fine root production was negatively correlated with leaf N and P concentrations. The sensitivity of the shoot-to-root ratio to foliage N decreased with increasing root biomass in Japanese red pine seedlings (Chiwa et al. 2012). Moreover, carbon allocation to roots was found to be mediated by foliar N in black spruce seedlings (Campagna and Margolis 1989).

The Loess Plateau is a vast ecologically fragile area in China (Fu et al. 2017). Since the launch of the Grain-for-Green Program in 1999, 16,000 km² of rain-fed cropland has been converted to planted vegetation, resulting in an increase of 25% in vegetation cover in the region (Feng et al. 2016). Plantation forests are the main contributors to ecological restoration in this area. Black locust (*Robinia pseudoacacia* L.) and Chinese pine (*Pinus tabulaeformis* Carr.) are the major plantation species in this area and have high environmental adaptability and stress resistance (Zhou and Shangguan 2007; Chen et al. 2016). In this study, we investigated fine root biomass, fine root production, fine root turnover rate, and fine root necromass of four stand density classes in black locust and Chinese pine plantations in the loess hilly region. It was hypothesized that: (1) the effect of stand density on soil and leaf characteristics is inconsistent in the two plantation species due to different nutrient utilization strategies; and, (2) broad-leaved and coniferous plantations differ in their root-leaf linkages and responses of fine root production to soil properties.

Materials and methods

Site characteristics

This study was conducted in southern Yan'an, Shaanxi Province, China. This area is characterized by a temperate semi-arid climate in the “forest to forest-steppe” ecosystem transition zone (Yamanaka et al. 2014). The landforms are mainly loess hills and gullies. Mean annual precipitation is 537.9 mm, mostly occurring in July and August, and the annual mean temperature is 10.0 °C based on the Yan'an city meteorological station data for 1956–2015 (Cheng et al. 2020). The growing season is from April to October. The main soil type is calcic Cambisols according to the FAO classification system (Yamamoto and Endo 2014). The study area comprised black locust and Chinese pine plantations established in large areas during the past decades (Yamanaka et al. 2014). Shrubs and grasses are sparse in the understory layer of both plantations.

Experimental design and vegetation survey

Two types of plantations (black locust and Chinese pine) were selected along a stand density gradient. Stand density was classified into four classes (Table 1). All plots were converted from croplands with similar history and management. In the early spring of 2017, the study plots were established 0.5–5 km apart. The plots were 400 m² (20 m × 20 m), except for a few at 100 m² (10 m × 10 m) because of terrain conditions. Only two replicates were established in each density class due to few classes sharing similar age and site conditions. The vegetation survey was conducted yearly at the end of the growing season. Stand age was determined from tree rings of core samples. Details of the sampling plots are presented in Table 1.

Soil sampling and measurements

In 2017, soil samples from depths of 0–20, 20–40, 40–60 and 60–80 cm were collected in each plot using a cylindrical soil core sampler (4 cm in diameter). Six sites were chosen for sampling within each plot and were divided into two groups, on the left and on the right, each including upper, middle, and lower locations along the slope. For each group, samples from the same soil layer were thoroughly mixed to form a representative sample. Two soil samples were collected as replicates for each depth in each plot. The samples were cleaned of rocks and plant fragments, air-dried, ground and sieved through a 0.25 mm mesh. Organic C content was measured by wet combustion with K₂Cr₂O₇ (Chinese standard GB 7857–87), total N content was determined by the Kjeldahl acid-digestion method, and total P content quantified using molybdenum-blue colorimetry (National Agricultural Technology Extension Service Center 2006). The nutrient concentrations in the horizon (0–80 cm) were calculated by averaging those of the four layers.

In each plot, two representative sites at the upper and lower positions were chosen as replicates, and 3-m Tecnat[®]

plastic tubes with an internal diameter of 42 mm were placed for repetitive measurements of soil moisture. Volumetric soil water content was measured using a time-domain reflectometry system (TRIME; IMKO Micromodultechnik, Ettlingen, Germany). Measurements began one year after installation. Soil water content was measured at 20-cm intervals along the profile, and the average for each layer obtained from the replicated tubes. During the growing season, three measurements were carried out: before the rainy season (May), during the rainy season (August), and after the rainy season (October). The average of the three measurements was taken as the plot soil water content used in the analysis.

Leaf sample collection and measurement

To collect leaf samples, representative trees were selected in each plot and healthy, mature leaves were collected from the upper and middle crowns. Three groups of leaf samples were collected from each plot and brought to the laboratory for nutrient content analysis. To determine the specific leaf area (SLA, m² kg⁻¹), 10–20 mature leaves without disease symptoms and insect pests were scanned to full size images. Samples were oven-dried at 105 °C for 30 min and then at 65 °C to a consistent weight. Leaf surface area was determined from the leaf images using Image J (National Institute of Health, Washington DC, USA). The specific leaf area was calculated as the ratio of leaf area to dry leaf weight.

Oven-dried leaves were ground to powder and sieved through a 0.15 mm sieve. Organic C content was measured using the same method as used for soil samples. The powdered samples were initially digested with H₂SO₄ and H₂O₂, and leaf N and P contents were determined using the semi-micro Kjeldahl method and colorimetry assays, respectively.

Leaf area index (LAI, m² m⁻²) was calculated from litterfall data from three litter traps (50 cm × 50 cm) in each plot. Leaf litter was sorted by species, dried at 65 °C for approximately 48 h to a constant weight, and weighed to the nearest 0.01 g. Leaf area index was estimated by the tree

Table 1 Information on the plots of the plantations

Species	Stand density (ind. ha ⁻¹)	Stand density class	Altitude (m)	Age (a)	Slope (°)	pH	DBH (cm)	H (m)
Black locust (<i>Robinia pseudoacacia</i>)	<2500	I	1150	17	22	8.7	9.1 ± 4.3	7.0 ± 2.6
	2500–3000	II	1295	19	19	8.6	8.1 ± 3.3	6.5 ± 2.1
	3000–3500	III	1290	19	20	8.7	7.2 ± 3.6	7.6 ± 2.6
	>3500	IV	1150	17	19	8.6	6.4 ± 3.2	8.4 ± 2.7
Chinese pine (<i>Pinus tabulaeformis</i>)	<2500	I	1171	36	18.5	8.4	20.9 ± 4.5	12.5 ± 1.3
	2500–3000	II	1222	40	22	8.4	12.2 ± 9.4	9.1 ± 2.8
	3000–3500	III	1171	36	19	8.3	14.4 ± 3.7	13.5 ± 2.1
	>6500	IV	1222	40	23	8.4	8.3 ± 3.3	9.4 ± 1.9

DBH is diameter of breast height; H is tree height. The data represent Mean ± SD

leaf litter biomass and mean specific leaf area for the two plantations (Henderson and Jose 2005).

Estimates of fine root biomass, production, and turnover rate

Fine root biomass and necromass were measured using soil cores. Seven soil cores at representative locations were collected from each plot in July 2017. A soil auger was used to collect soil cores at 20-cm intervals to a depth of 80 cm. Fine root production was estimated using ingrowth cores established at seven representative points in each plot in August 2017. Ingrowth cores made of nylon net bags (6.5 cm diameter) were set up after soil columns were removed and filled with root-free original soil at the same depth. All ingrowth cores were extracted after one year (August 2018) by carefully removing the soil around the cylinder and separated into four layers at 20-cm intervals to collect roots that had grown into the core during the year. Soil cores were placed in plastic bags and transported to the laboratory to separate the roots. Fine roots were removed from the soil using forceps, and the remaining root segments in the soil were gently washed in a 0.1 mm sieve. All fine roots were washed to remove affixed soil residue and divided into living and dead roots. Fine roots that were brown or black in color, rigid and inelastic, and in some cases had decaying tissue were regarded as dead roots, whereas those that were white or light brown in color, were elastic and flexible were classified as live (Yuan and Chen 2012; Ding et al. 2019). After classification, fine roots were oven-dried at 70 °C to a constant mass and weighed to the nearest 0.001 g.

Fine root production ($\text{t ha}^{-1} \text{a}^{-1}$) was estimated from root biomass growing into the ingrowth cores—both live and dead roots were counted because of the short root longevity—divided by the growth time (one year). Fine root turnover rate (a^{-1}) was defined as the ratio of fine root production to fine root biomass (Aber et al. 1985; Yuan and Chen 2012).

Data analysis

Individual soil and leaf samples from each plot were treated as subsamples and used for statistical analysis. Averaged values were used in diagrams created with Sigmaplot 14.0. One-way analysis of variance (ANOVA) tested the differences in soil, leaf, and fine root characteristics. Two-way ANOVA analyzed the effect of stand density and species on fine root traits. The association between fine root characteristics and soil and leaf properties was assessed by Pearson correlation analysis. Statistical analyses were performed using SPSS 21.0 for Windows (version 21.0; SPSS Inc., Chicago, IL, USA). Stepwise regression analysis was conducted using RStudio (version 3.6.2; R Core Team 2019, [https://](https://www.r-project.org/)

www.r-project.org/). Significant differences were evaluated at the 0.05 probability level.

Results

Soil properties and leaf traits

In black locust plantations, soil C and N contents were higher in density class II than in class I and the differences among classes II, III, and IV were not statistically significant (Fig. 1a, b). Soil P content and volumetric water content decreased with increasing stand density (Fig. 1c, d). In Chinese pine plantations, soil C, N, and P contents were significantly higher in stand density class III than in other density classes (Fig. 1a–c). Soil volumetric water content decreased as stand density increased (Fig. 1d).

Leaf C content did not change significantly with stand density in either plantation (Fig. 2a). In black locust plantations, leaf N content was maximized in density class III and minimized in class II (Fig. 2b). P contents in the leaves increased with stand density (Fig. 2c). There was no apparent change in leaf N and P contents with stand density in Chinese pine plantations (Fig. 2b, c). Leaf N content was highest in density class II and lowest in class III, while leaf P content was highest in density class IV and lowest in class I. Specific leaf area and leaf area index increased with stand density and maximized in density class III in black locust plantations (Fig. 2d, e). A similar trend was found in leaf area index, while specific leaf area was the lowest in density class II and highest in class IV in Chinese pine plantations.

Fine root biomass, production, turnover rate, and necromass

Greater fine root biomass, production, turnover rate, and necromass were found in higher stand density classes in both types of plantations, but differences between the adjacent classes were not statistically significant, particularly between class III and class IV (Fig. 3). Overall, more significant differences were found among density classes in black locust plantations than in pine plantations, especially for fine root turnover rate (Fig. 3d).

Fine roots were influenced by stand density and species (Table 2). The interaction between species and stand density had no effect on fine root production and biomass, but did have a significant effect on fine root turnover rate. Fine root production and biomass of Chinese pine were higher than those of black locust in each stand density class (Fig. 3a, c), while the fine root turnover rate of Chinese pine was lower than that of black locust along the stand density class spectrum.

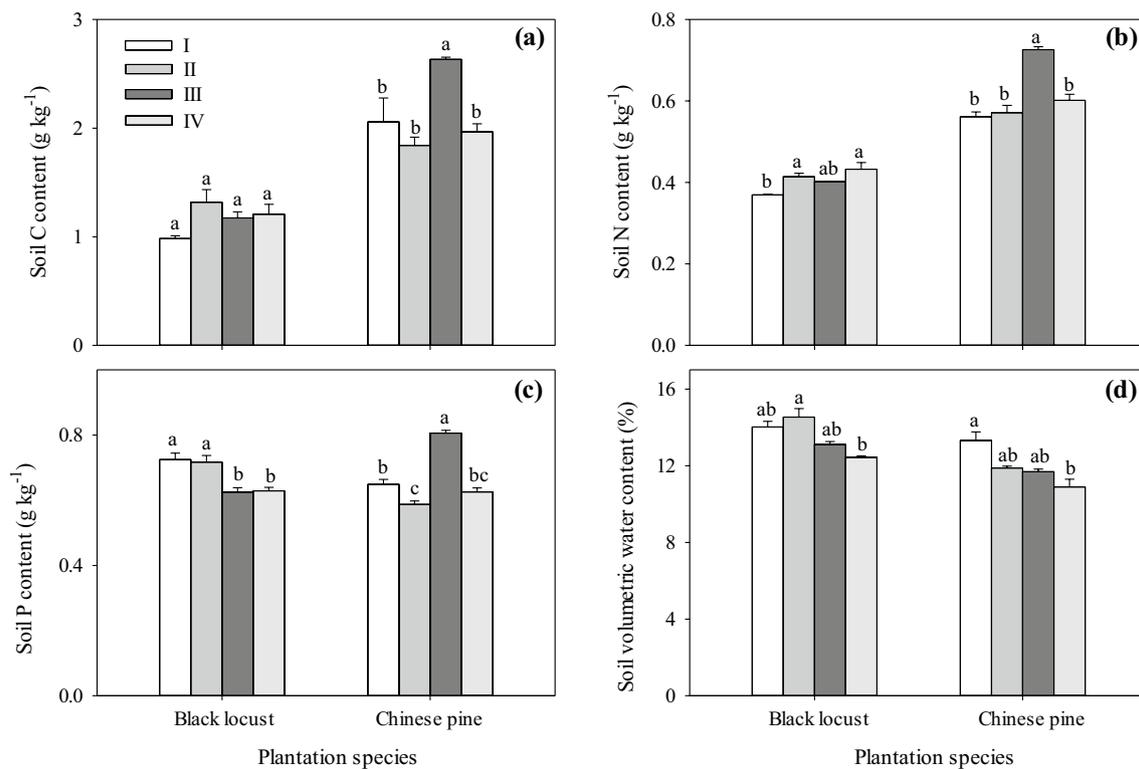


Fig. 1 Soil properties of the two plantations along a stand density gradient. I, II, III, and IV represent four stand density classes; data bars are means and standard deviations. Different lowercase letters are statistically different ($P < 0.05$) among density classes within the same plantation

Effects of soil properties on fine roots

Pearson correlation analysis on fine root characteristics and soil properties in black locust plantations showed that fine root biomass and necromass were significantly related to soil N and P contents, whereas fine root production and turnover rate were related to soil P and volumetric water content. In Chinese pine plantations, fine root biomass and necromass were significantly related to soil N and volumetric water content, while fine root production and turnover rate were significantly related only to soil volumetric water content (Table 3).

Relationships between leaves and fine roots

In black locust plantations, fine root biomass, production, and turnover rate were correlated with leaf area index. In addition, fine root production and turnover rate were also correlated with leaf P contents (Table 4). In Chinese pine plantations, fine root biomass was correlated with specific leaf area and leaf area index, fine root production was correlated with leaf C and P contents and specific leaf area, and fine root turnover rate was correlated with leaf C and P contents. We did not find any relationships between necromass and leaf traits in the two plantations.

Influence of multiple factors on fine roots

The relationships between fine roots and multiple factors (including soil and leaf properties) were further analyzed by stepwise regressions (Table 5). The results showed that fine root biomass in black locust could be explained by soil P and leaf area index, and fine root production and turnover rate was closely related to soil volumetric water and leaf area index. Fine root necromass was related to soil P. In Chinese pine plantations, fine root biomass could be explained by soil N and volumetric water contents. Fine root production and turnover rate were related to soil volumetric water and leaf C contents, and fine root necromass to soil N. In the two plantations, fine root biomass and necromass were closely related to soil nutrient contents (N or P), while fine root production and turnover rate shared similar major explanatory variables.

Discussion

Changes in soil and leaf traits along the stand density gradient

Stand density influences soil environments by affecting the availability of nutrients (Bo et al. 2018), and is regarded as

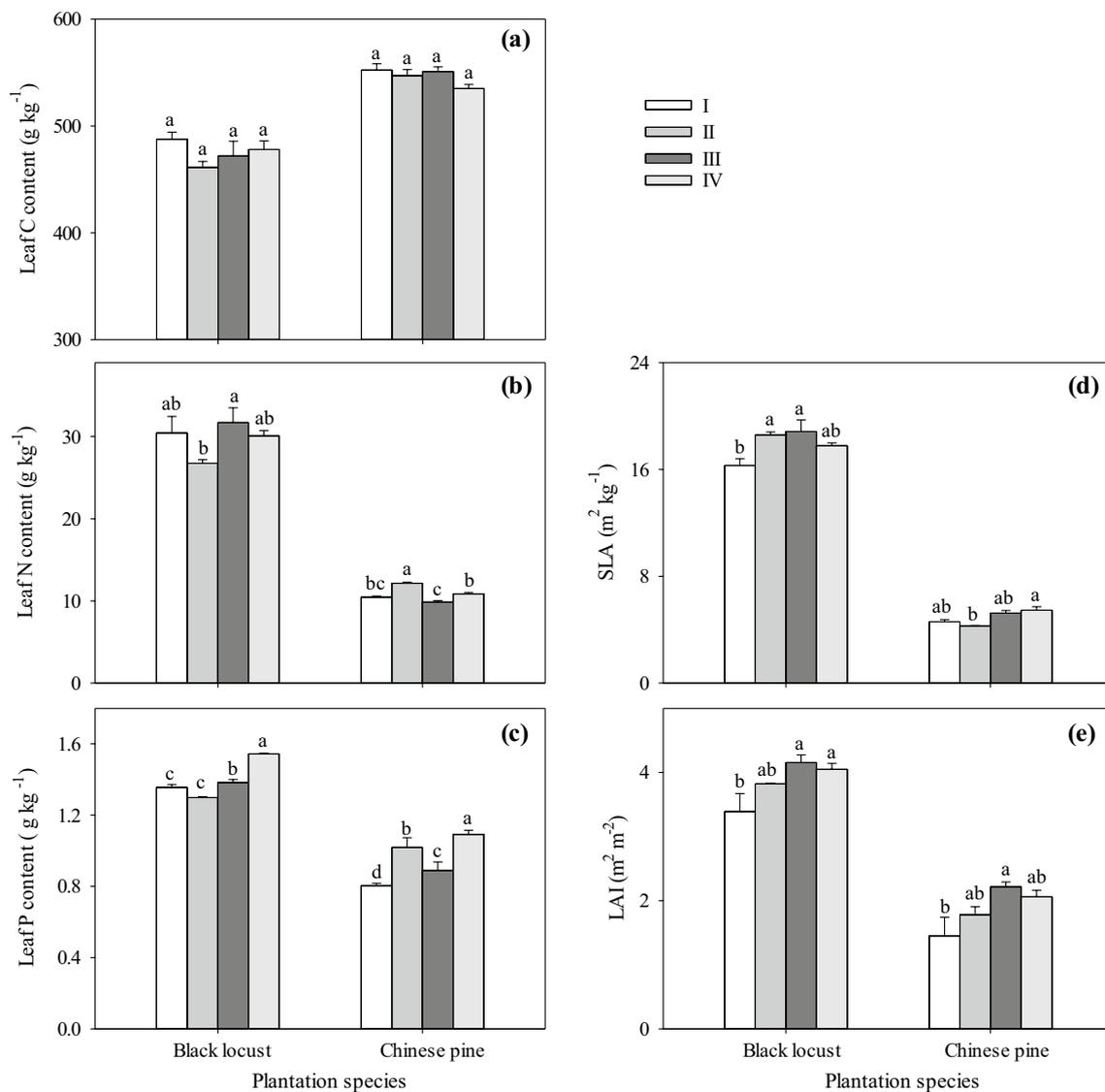


Fig. 2 Leaf properties of the two plantations along a stand density gradient. I, II, III, and IV represent four stand density classes; data bars are means and standard deviations; different lowercase letters are

statistically different ($P < 0.05$) among stand density classes within the same plantation

one of the most significant factors influencing nutrient fluctuations (Zheng et al. 2020). In black locust plantations, soil C and N contents showed a cumulative trend in low stand densities, peaked at density class III, then decreased slightly with increasing density. Organic C and N content were closely related on a small scale to stand density (Chen 2006). A possible reason may be that more sunlight and throughfall are available in relatively lower density stands, which would result in greater litterfall decomposition rates. In forests with N-fixing species, such as black locust, rapid litterfall decomposition often results in the accumulation of organic matter and N in the soil (Tateno et al. 2007). The results of this study suggest that this promotional effect was weakened with increasing stand density. Soil P content decreased with

increasing density, which is consistent with results reported previously (He et al. 2005; Zeng et al. 2020). This may be because N-fixation is accompanied by high energy costs and increases the P demand required to synthesize the energy product ATP, a molecule that carries energy within cells (Reed et al. 2011; Schleuss et al. 2020). High consumption and insufficient sources caused a decline in soil P content with increasing stand density. In Chinese pine plantations, there were no clear trends in changes of soil nutrients with stand density. The ectomycorrhizal mycobiont of the root system of Pinaceae, which is involved in nutrient uptake and circulation (Chu et al. 2016), may counteract the effect of stand density on soil nutrients, although stands planted at higher densities are believed to have a larger demand for

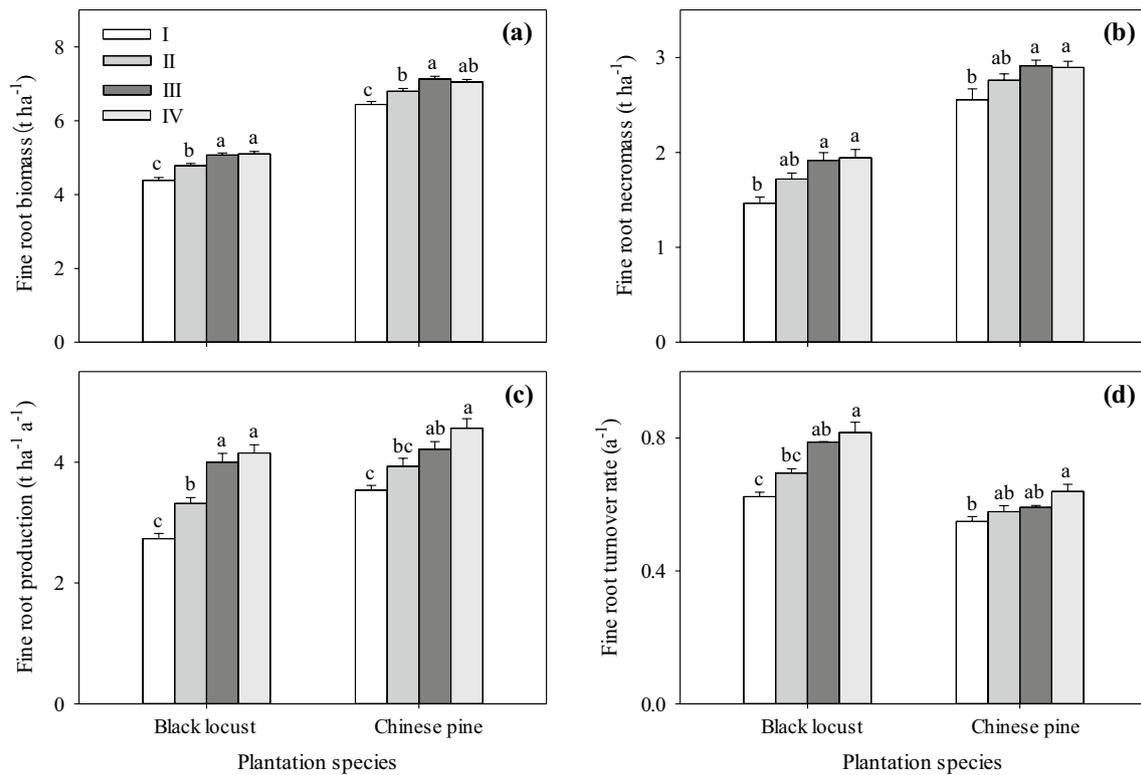


Fig. 3 Fine root characteristics in the two plantations along a stand density gradient. I, II, III, and IV represent four stand density classes; bars are means and standard deviations, different lowercase letters are statistically different ($P < 0.05$)

Table 2 Two-way ANOVA summary of the effects of stand density and tree species on fine root variables

Source of variation	Df	FRB	FRP	FRT	FRN
Tree species	1	0.000**	0.000**	0.000**	0.000**
Stand density	3	0.000**	0.000**	0.000**	0.000**
Stand density × Tree species	3	0.857	0.107	0.027*	0.839

FRB is fine root biomass; FRP is fine root production; FRT is fine root turnover rate; FRN is fine root necromass. Data represent P -values unless otherwise indicate

* and ** represent $p < 0.05$ and $p < 0.01$, respectively

soil resources (Will et al. 2005). Compared with deciduous leaves, the poor decomposition of needle litter slows down the recycling of nutrients (Yuste et al. 2005). In high density stands, this is often accompanied by a higher interception of precipitation in crowns and interception of throughfall in thicker litterfall layers on the soil surface. The lack of water replenishment in the soil, coupled with the high consumption in high density stands, caused the decline in soil volumetric water content with increasing density.

In this study, leaf nutrient contents did not show a clear trend with stand density. Forest nutrient cycling is governed by numerous inter-related processes and factors (Paluch and

Table 3 Pearson correlation coefficients between fine root characteristics and soil properties in the two plantations

Species	Variables	SC	SN	SP	SW
Black locust	FRB	0.380	0.715*	-0.762*	-0.667
	FRP	0.239	0.598	-0.794*	-0.771*
	FRT	0.176	0.515	-0.777*	-0.780*
	FRN	0.331	0.712*	-0.789*	-0.611
Chinese pine	FRB	0.332	0.744*	0.406	-0.849**
	FRP	0.102	0.533	0.090	-0.869**
	FRT	0.016	0.392	-0.069	-0.800*
	FRN	0.350	0.713*	0.258	-0.711*

FRB is fine root biomass; FRP is fine root production; FRT is fine root turnover rate; FRN is fine root necromass; SC is soil carbon content; SN is soil nitrogen content; SP is soil phosphorus content; SW is soil volumetric water content

* and ** represent $p < 0.05$ and $p < 0.01$, respectively

Gruba 2010). Leaf nutrient content is a result of complex processes combined with nutrient uptake, allocation, and resorption (Wright and Westoby 2003; Tsujii et al. 2020). However, tree species have specific physiological and biological processes, and coupled with environmental conditions, influence nutrient content in leaves that vary with adaptation and resilience (Cao et al. 2018). Therefore, stand

Table 4 Pearson correlation coefficients between fine root characteristics and leaf properties in the two plantations

Species	Variables	LC	LN	LP	SLA	LAI
Black locust	FRB	-0.346	0.081	0.600	0.621	0.834*
	FRP	-0.210	0.248	0.727*	0.586	0.860**
	FRT	-0.158	0.330	0.751*	0.587	0.870**
	FRN	-0.458	-0.144	0.495	0.388	0.652
Chinese pine	FRB	-0.507	-0.081	0.560	0.712*	0.771*
	FRP	-0.753*	0.077	0.709*	0.740*	0.566
	FRT	-0.816*	0.155	0.738*	0.662	0.418
	FRN	-0.702	0.061	0.590	0.565	0.533

LC is leaf carbon; LN is leaf nitrogen; LP is leaf phosphorus; SLA is specific leaf area; LAI is leaf area index; FRB is fine root biomass; FRP is fine root production; FRT is fine root turnover rate; FRN is fine root necromass

* and ** represent $p < 0.05$ and $p < 0.01$, respectively

Table 5 Stepwise regressions for the effects of soil and leaf properties on fine root characteristics in the two plantations

Species	Regressions	R^2	P
Black locust	FRB = 0.5288LAI - 2.4491SP + 4.4492	0.7953	<0.01
	FRP = 1.1271LAI - 0.3237SW + 3.5869	0.9113	<0.01
	FRT = 0.1545LAI - 0.0455SW + 0.7503	0.9397	<0.01
	FRN = 3.8719 - 3.1310SP	0.5593	0.020
Chinese pine	FRB = 2.0778SN - 0.2045SW + 8.01824	0.9257	<0.01
	FRP = 16.8907 - 0.2922SW - 0.0171LC	0.8256	<0.01
	FRT = 1.9278 - 0.0201SW - 0.0020LC	0.7968	<0.01
	FRN = 1.8464SN + 1.6416	0.4271	0.046

SN is soil nitrogen; SP is soil phosphorus; SW is soil volumetric water; LC is leaf carbon; LAI is leaf area index; FRB is fine root biomass; FRP is fine root production; FRT is fine root turnover rate; FRN is fine root necromass

density may be a relatively weak factor affecting leaf nutrient content. Specific leaf area and leaf area index showed clear, similar trends with stand density in the two plantations. Individual trees may adapt to decreasing light levels caused by high stand density by increasing single leaf area and leaf quantity. Higher specific leaf area is in line with the poorer conservation of the acquired resources and stronger nutrient return, thus leading to faster nutrient cycling (Wright et al. 2002). The forest canopy has sufficient sunlight, competition between individuals is weak, and the demand for photosynthetic carbohydrates is lower in low density stands, so leaf area is relatively small. As stand density increases, sunlight in the forest weakens and competition between individuals increases. A larger leaf area is required to increase the interception of sunlight. When the stand density is excessive, leaves may divert more energy and nutrients toward the synthesis of defense compounds to resist and adapt to the stress caused by weak sunlight and neighbor competition, which explains the decrease in both leaf area index and specific leaf area.

Effect of stand density on fine roots

Along the density gradient, the increasing tendencies of fine root biomass, necromass and production were similar in both plantations. This could be attributed to the stands were in early stage of development (Table 1). At this stage, low competition promotes production, leading to higher fine root production in higher density stands (He et al. 2005; Li et al. 2011). However, this effect would be negligible when the stand density exceeds a threshold value (He et al. 2005). This might explain the insignificance in fine root biomass and production between density classes III and IV.

The vertical distribution of fine roots followed similar patterns in these plantations. Both fine root production and biomass gradually decreased along the soil profile (0–80 cm) in each density class (Appendix Figs. S1, 2). In both plantations, there were larger significant differences among the density classes in the upper soil layers than in the deeper layers. Allocation percentage of fine roots in deeper soil layers increased with increasing stand density, suggesting that intensified competition by increased stand density would result in more roots being forced into the deeper soil to acquire resources (Prieto et al. 2015).

Unlike biomass and production, the response of fine root turnover rate to stand density showed subtle differences. In Chinese pine plantations, fine root turnover rate did not increase significantly (classes I to III, stand density <3500 ind. ha⁻¹) until the density was excessive (class IV, >6500 ind. ha⁻¹). However, there were larger significant differences among density classes in fine root turnover rate in black locust plantations, which may have been caused by differences in genetics and/or adaptation to environmental changes between species (Eissenstat and Yanai 2002; Wang et al. 2020). Black locust is considered a fast-growing species (Campagnaro et al. 2018; He et al. 2020), and therefore has a higher turnover rate. However, Chinese pine is a species which has a relatively conservative growth strategy (Yan

et al. 2006). These results suggest that black locust ensures high fine root biomass by increasing fine root production and turnover rate with increasing stand density, whereas Chinese pine does so by increasing fine root production; only when stand density increases significantly, does the fine root turnover rate increase significantly.

Response of fine roots to soil properties

The availability of soil resources is a key driver of production and ecosystem processes (van der Sande et al. 2018). There were significant correlations between fine root biomass, fine root production, and soil resources in the two plantations. Fine root biomass and necromass were affected by soil N and P content, especially N according to the results of stepwise regressions (Tables 3 and 5) in black locust plantations. The weak relationships between soil N, fine root production, and fine root turnover rate may be attributable to specific N fixation characteristics, resulting in less N limitation (Tateno et al. 2007). In addition, fine root production and turnover rate were negatively related to soil P content. These results support the hypothesis that plants preferentially allocate more resources to roots on sites with low soil moisture and poor nutrients (Garnier 1991; Gao et al. 2020). In Chinese pine plantations, the positive relationship between soil N and fine root biomass could be explained by the conservation nutrient use strategies employed by Chinese pine. As Chinese pine has lower leaf N and P contents, longer leaf life, and slower litter decomposition than those of black locust, the nutrient-use strategy by Chinese pine is more conservative than black locust (Yan et al. 2006; Chen et al. 2018). Lower N utilization and leaf N content, and slower nutrient cycling allow Chinese pine to be beneficial in infertile habitats. In the two plantations, there were negative relationships between both fine root production and turnover rate and soil volumetric water content. A more likely explanation might be that plants resisting drought stress would allocate more biomass to roots (Davis et al. 2004) by promoting the proliferation of fine roots to efficiently exploit the soil resources. Our results are consistent with the optimal resource partitioning theory (Hertel et al. 2013). Nevertheless, these relationships between fine root biomass, production, and turnover rate and soil properties are not constant because fine roots grow and turnover rapidly as available nutrients increase, which would result in a decline in net fine root biomass (Yuan and Chen 2010).

Correlation between fine roots and leaf traits

Leaves and fine roots share attributes that suggest they may have similar trait syndromes: a relatively short life span, a primary function of resource acquisition, and typical determinate growth (Eissenstat and Yanai 1997; Withington et al.

2006). In the black locust plantations, fine root biomass and production were positively related to stand leaf area index. In forests, leaf area is the trade-off interface between photosynthetically active organs of the vegetation and the atmosphere, and affects the light, thermal, and hydric conditions within the canopy (Wright et al. 2004; Kalacska et al. 2005). Therefore, larger leaf area had greater light interception, resulting in more energy for root activity. However, fine root turnover rate was not only related to leaf area index, but was also explained by leaf P content. Black locust is known for its N-fixation properties which may result in P being a limiting factor for photosynthesis (Reed et al. 2011). The production of photosynthesis, however, drives fine root activity (Du and Fang 2014; Meng et al. 2018), which seems to be a more likely explanation. In contrast to black locust plantations, fine root production and turnover rate were closely related to leaf C content in Chinese pine plantations. Leaves are the main organ for C assimilation, and their C content reflects their adaptability to the external environment (Wright et al. 2004). Evergreen needles are believed to sequester carbon concurrently with needles of the previous year, directly providing C to maintain growth (Cao et al. 2018). Therefore, leaf C content is an important factor in the physiological processes of Chinese pine. This might explain the close correlation between fine root dynamics (fine root production and turnover rate) and C content in needles. In addition, a feedback loop has been proposed between leaf nutrient contents, fine root production, and soil nutrient conditions (Cote et al. 2003); more relevant information is needed to complement this loop.

On the other hand, the spatio-temporal heterogeneity of fine roots in the plantations and the relatively small number of plots might result in some limitations in this study. Although the relationships between density-based fine roots and soil and leaf characteristics were analyzed, we were unable to analyze these along the stand density gradients. In consideration of this limitation, the number of plots in each stand density class should be increased in future investigations, and the relationships between fine roots, soil and leaves with density gradients analyzed more comprehensively.

Conclusions

In the black locust plantations, soil carbon and nitrogen accumulated with stand density at relatively lower densities, while soil phosphorous and volumetric water contents constantly decreased. In the Chinese pine plantations, carbon, nitrogen and phosphorous contents did not show a clear trend with stand density. The changing trend of soil volumetric water contents was similar to that in the black locust plantations. In the black locust plantations, high fine

root biomass in the higher density stand was maintained by increasing fine root production and turnover rate with increasing stand density. In the Chinese pine plantations, fine root biomass increased with stand density was achieved by increasing the fine root production. When stand density was excessive, fine root turnover rate increased significantly to ensure higher biomass. Fine root biomass, especially necromass, was related to soil phosphorous content in the black locust plantations and nitrogen content in the Chinese pine plantations, and fine root production and turnover rate were related to soil moisture in the two plantations. Fine root biomass, production and turnover rate were closely correlated to leaf area index in the black locust stands. In the Chinese pine plantations, fine root production and turnover rate were related to leaf carbon contents.

Acknowledgements We gratefully acknowledge our group members, mainly graduate students from Northwest A & F University and the University of Chinese Academy of Sciences for their contributions to the field investigations.

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