Responses of absorptive root and mycorrhizal colonization of Chinese fir (*Cunninghamia lanceolata*) to varied environmental conditions

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Received: 12 July 2021 / Accepted: 11 July 2022 / Published online: 3 August 2022
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Abstract Root branching and mycorrhizal symbioses are two major mechanisms for soil resource acquisition by trees. Understanding the relationship between these two mechanisms and their responses to varied environmental conditions is crucial for predicting the responses of foraging strategies of roots to environmental changes. This study was conducted in 11 Chinese fir (*Cunninghamia lanceolata*) plantations distributed in different environmental conditions in Subtropical China to assess the relationship between root tip traits related to nutrient foraging (branching ratio of 1st-order roots to 2nd-order roots, arbuscular mycorrhizal (AM) colonization) and their environmental variables, including mean annual precipitation (MAP), mean annual temperature (MAT), soil C, soil N, soil P, and soil pH. Root branching was more sensitive to environmental conditions than mycorrhizal symbioses. The branching ratio and AM colonization

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of Chinese fir were significantly related to several environmental variables. The branching ratios were positively correlated with MAT, but negatively correlated with soil C, soil N, and soil pH \( (P < 0.05) \), suggesting that harsh environmental conditions can promote absorptive root branching. To our surprise, the AM colonization of absorptive roots was not as sensitive to environmental factors as branching ratio. However, the AM colonization of absorptive roots was positively correlated with soil pH \( (P < 0.1) \), indicating that soil acidity controls mycorrhizal symbioses. Moreover, the branching ratio was significantly negatively correlated with AM colonization \( (P < 0.05) \). Our results confirmed that environmental conditions significantly regulate fine root branching and its mycorrhizal symbioses, but with different controlling variables. The negatively correlated relationship of branching ratio and AM colonization shows that environmental factors regulate absorptive root traits in different ways.

Keywords Absorptive roots · Branching ratio · Arbuscular mycorrhizal (AM) colonization · Chinese fir · Environmental conditions

Introduction

Fine roots play key roles in soil resource acquisition (Johnson et al. 2003; Guo et al. 2008). They are plastic and their functional traits vary widely across plant species and environmental conditions (Guo et al. 2008; Holdaway et al. 2011). The morphology of fine roots is often directly related to physiological functions (Eissenstat 2000; Pregitzer et al. 2002), and the development of an efficient fine root system is crucial for trees to ensure sufficient nutrient uptake in various conditions (Ostonen et al. 2013).

Fine roots are composed of absorptive fine roots (usually referred to as the first- and second-order roots) and transport fine roots (higher orders in the branching hierarchy), with the uptaking capacity of nutrients and water declining with increasing root order (McCormack et al. 2015). Root tips (first-order root) and their mycorrhizal symbioses (the association between the fungi and the roots) are the most metabolically active parts of absorptive fine roots. Their traits are good indicators of the adaptability of root systems to environmental conditions (Ostonen et al. 2017). The changes of root tip traits are expressions of the plastic responses to their environmental conditions (Ostonen et al. 2013; Kong and Ma 2014; Eissenstat et al. 2015; Soudzilovskaia et al. 2015).

Absorptive fine root traits such as diameter, surface area, branching ratio, specific root length (SRL), tissue density, and mycorrhizal colonization are crucial for resource acquisition of trees (Eissenstat et al. 2015; Wang et al. 2016; Yan et al. 2019). However, studies showed that root traits can be divided into two major dimensions: (1) mycorrhizal colonization which is related to root construction, maintenance, and persistence and (2) branching architecture which is related to root plastic responses to the environment (Kong et al. 2014). Plants may choose to allocate resources to root tips or mycorrhizal fungi in different environmental conditions (Hodge and Storer 2015).

Plant root branching is a critical root trait (Liese et al. 2017) and is paramount for the acquisition of adequate soil water and nutrients (Duque et al. 2019). The plasticity of root systems in terms of the variations in the size, shape, and surface area of the roots (Xie and Yu 2003; Motte and Beeckman 2019) was largely associated with root branching (Nibau et al. 2008). The capacity of root branching can improve the adaptation of plants to environmental conditions by anchoring and foraging in the soil (Motte and Beeckman 2019). Usually, proliferating a predominance of absorptive roots requires greater C allocation of trees to root formation (Ostonen et al. 2017). Contrary to prolific root branching, mycorrhizal colonization enhances the nutrient absorption of plants through the large surface area of mycelium (Smith and Read 2008). Nearly 67.4% of mycorrhizal associations of vascular plants belong to Arbuscular Mycorrhiza (AM) fungi (Brundrett 2009). This inoculation of AM fungi of roots assists plants in obtaining nitrogen (N), phosphorus (P), and many other nutrients, as well as water from the soil (Clark and Zeto 2000; Jakobsen et al. 2005; Chen et al. 2016; Liese et al. 2017; Frew et al. 2018) to promote the growth of plants (Muthukumar and Udayan 2006; Kong et al. 2014).

Due to significant influences to belowground and aboveground growth of plants, fine root traits related to resource investment and acquisition (branching ratio and the rate of mycorrhizal colonization) were considered as two important root traits in association with resources acquisition (Kong et al. 2014;
Zemunik et al. 2015; Liese et al. 2017; Chen et al. 2018). Thus, it is important to understand the relationship between these two fine root traits and environmental conditions, which is essential to understand belowground resource acquisition of trees. In the past several decades, studies have found that branching architecture and mycorrhizal colonization showed large variations within species growing in different environmental conditions (Johnson et al. 2003; Loudet et al. 2005; Cudlin et al. 2007; Osmont et al. 2007). For example, plants allocate more biomass for root proliferation when growing together in interspecific plant competition (Hodge et al. 1999; Liao et al. 2019), which resulted in the increase of absorptive root biomass (Guo et al. 2004; McCormack and Guo 2014).

Since Chinese fir (Cunninghamia lanceolata) is widely distributed in Subtropical China (N21°41′–N34°03′, E101°30′–E121°53′, and 70-2900 m in altitude) (Bian et al. 2014) and is the most important commercial plantation tree species in China, we chose Chinese fir as our study object. The broad distribution of Chinese fir plantations provides a good opportunity of studying the responses of absorptive root and mycorrhizal colonization to varied environmental conditions. According to the previous study (Piao and Liu 2011; Li et al. 2019), Chinese fir is colonized with arbuscular mycorrhizal (AM) fungi and not colonized with ectomycorrhizas (EM). The main research objective of the study was to determine the relationship between these two mechanisms (root branching and root tip AM colonization) and environmental conditions (MAP, MAT, soil C, soil N, soil P, and soil pH) using Chinese fir plantation forests located in Subtropical China. We hypothesized that (1) environmental variables were the main factors causing the variations of these two mechanisms, and (2) environmental conditions with limited resources (e.g., low soil N and soil P) resulted in the increase of AM colonization, as observed by Jakobsen et al. (2005) and Liu et al. (2015).

**Materials and methods**

**Site description**

We collected the absorptive root samples in 11 Chinese fir plantations with the average age of 23 years located in different areas with different soil pH, different soil nutrients, and different climatic conditions in Subtropical China from October to November of 2013 (Huitong, Shaxian, Taihe, Tongling, and Pingxiang) and from November of 2017 to January of 2018 (Zhenxiong, Zhengan, Yuexi, Shangcheng, Guangmingcun, and Xinfeng additionally) (Fig. 1). The detailed information regarding the locations is presented in Table 1.

**Root sampling**

In each location, we chose 9 Chinese fir individuals at random for root sampling. For each tree, six main lateral roots including the first five root orders were tracked by carefully removing surface soil (0–20 cm) at the base with a shovel and a fork. According to Pregitzer’s study, the most terminal branch was defined as the first-order roots (Pregitzer et al. 2002). The soil adhering to the roots was carefully removed and the intact roots were collected. Three of the lateral root samples were immediately placed into sealed polyethylene bags and placed on ice in a cooler and then transported to the laboratory and stored in a freezer at −40 °C to limit live tissue degradation (Clemensson-Lindell and Persson 1992) before root morphology measurements. Another three lateral root samples were immediately put into Formalin-Aceto-Alcohol (FAA) solution (90 ml of 50% ethanol, 5 ml of 100% glacial acetic acid, and 5 ml of 37% formalin) for AM colonization assessments. The intact root branches for estimating branching ratios and AM colonization from each location were pooled as one composite sample separately (27 branches for estimating branching ratios and 27 branches for estimating AM colonization).

**Root branching ratio**

The frozen roots were then thawed, cleaned, and immediately sorted. The root samples from each location were classified by root branch orders (with root tips as the first-order roots) and the 1st- and 2nd-order roots were separated from the root samples. Root branching ratio was calculated as the number of the 1st-order roots divided by the number of the 2nd-order roots in this study.
Root AM colonization

Acid fuchsin staining (Giovannetti and Mosse 1980) was used to measure root AM colonization. After the root samples stored in FAA solution were washed with deionized water, the 1st-order root segments were selected and were cleared in hot 10% (w/v) KOH solution at 90 °C for 50 min, acidified in 2% HCl at room temperature for 5 min, and stained with 0.05% (w/v) acid fuchsin at 90 °C for 20 min (Liu et al. 2015). Then AM colonization of 50 1-cm-long root segments from each site was measured at ×200 magnification (Leica DM 2500; Leica Mikrosysteme Vertrieb GmbH, Bensheim, Germany) using the line-intersect method described by McGonigle et al. (1990). Arbuscules, vesicles, non-septate, and pink-colored hyphae within the roots were all considered as evidence of AM colonization, and overall colonization is calculated as the following formula:

\[
\text{AM colonization (\%)} = \frac{\text{Number of AM segments scored}}{\text{Total number of segments}} \times 100\%.
\]

Fig. 1 Locations of Chinese fir sampling sites used in this study. More details are shown in Table 1

Data analysis

Root branching ratio and AM colonization were tested for normality using Shapiro–Wilk tests. Homogeneity of variance was checked using F tests. Linear regression was used to test possible relationships between root traits (Root branching ratio and AM colonization) and environmental conditions (MAP, MAT, soil C, soil N, soil P, and soil pH, \(n = 11\)). Statistical tests were considered significant at \(P < 0.05\). All analyses were conducted using SPSS 16.0 and SigmaPlot 12.5 statistical software.
### Table 1  Stand characteristics of the 11 Chinese fir locations

| Location       | Soil pH | Stand age (y) | Longitude (E) | Latitude (N) | Altitude (m) | MAP* (mm) | MAT* (℃) | Density (trees ha⁻¹) | DBH (cm) | AM colonization (%) | Branching ratio | Root diameter of the 1st order roots (mm) | Soil C (mg/g) | N (mg/g) | P (mg/kg) |
|----------------|---------|---------------|---------------|--------------|--------------|-----------|-----------|----------------------|----------|----------------------|----------------|-------------------------------------------|-----------|---------|----------|
| Yuexi          | 5.2     | 23            | 116°23'       | 30°72'       | 275          | 1506      | 15.3      | 1477                 | 19.0     | 46.0                 | 2.3            | 0.52                                        | 24.8      | 1.9     | 143.4    |
| Shangcheng     | 5.1     | 33            | 115°36'       | 31°43'       | 781          | 1376      | 13.4      | 1041                 | 28.3     | 47.0                 | 2.2            | 0.51                                        | 55.2      | 4.0     | 249.0    |
| Shaxian        | 5.0     | 21            | 117°43'       | 26°30'       | 200          | 1653      | 20.6      | 1716                 | 20.9     | 70.1                 | 2.8            | 0.71                                        | 24.6      | 1.6     | 273.3    |
| Tongling       | 4.8     | 20            | 117°59'       | 30°56'       | 430          | 1370      | 17.0      | 950                  | 16.1     | 57.1                 | 2.6            | 0.66                                        | 19.4      | 1.9     | 464.3    |
| Guangmingcun   | 4.8     | 25            | 112°67'       | 27°21'       | 404          | 1564      | 16.4      | 2084                 | 15.2     | 57.0                 | 3.1            | 0.49                                        | 24.1      | 1.7     | 114.0    |
| Zhengan        | 4.8     | 16            | 107°53'       | 28°16'       | 970          | 1154      | 14.1      | 2427                 | 15.4     | 57.0                 | 3.3            | 0.46                                        | 17.0      | 1.4     | 227.8    |
| Zhenxiong      | 4.7     | 17            | 105°19'       | 27°60'       | 1243         | 1018      | 14.2      | 2202                 | 15.0     | 33.0                 | 2.7            | 0.50                                        | 34.1      | 2.3     | 165.6    |
| Taihe          | 4.7     | 30            | 115°04'       | 26°44'       | 100          | 1453      | 19.4      | 2245                 | 15.5     | 53.5                 | 3.6            | 0.53                                        | 7.0       | 0.9     | 109.8    |
| Xinfeng        | 4.6     | 21            | 115°18'       | 25°24'       | 278          | 1598      | 18.7      | 1163                 | 27.0     | 26.0                 | 3.3            | 0.64                                        | 24.6      | 1.8     | 139.8    |
| Pingxiang      | 4.6     | 20            | 106°52'       | 22°03'       | 570          | 1275      | 23.2      | 1383                 | 15.3     | 23.7                 | 4.1            | 0.62                                        | 19.6      | 1.3     | 218.8    |
| Huitong        | 4.5     | 23            | 110°08'       | 27°09'       | 500          | 1360      | 17.6      | 1483                 | 23.5     | 20.6                 | 4.0            | 0.64                                        | 13.7      | 1.3     | 223.0    |

*MAT and MAP are given for 1961–2015 in the locations (http://data.cma.cn/data/cdcdetail/dataCode/A.0029.0005.html)
Results

The relationship between root branching ratio and environmental conditions

The root branching ratios were varied from 2.1 to 4.0 across the 11 locations (Table 1). Root tips were sensitive to environmental conditions and were significantly affected by MAT, soil C, soil N, and soil pH. High temperature promoted more root tips as the branching ratios of Chinese fir were positively and significantly correlated to MAT ($P < 0.05$) (Fig. 2). In contrast, root tips were significantly constrained by soil nutrients and soil pH as the branching ratios were negatively correlated with soil C, soil N, and soil pH ($P < 0.05$) (Fig. 2). In other words, poor nutrient conditions could promote more root tips or branching.

The relationship between absorptive root AM colonization and environmental conditions

The mean AM colonization of absorptive roots differed and varied from 23.7% to 70.1% across the 11 locations (Table 1). The regression analysis
between the AM colonization and environmental variables showed that AM colonization of absorptive roots was not sensitive to climatic conditions (MAT, MAP) and soil nutrients (soil C, soil N, and soil P) ($P > 0.05$). But to our surprise, soil pH was positively correlated with the AM colonization of absorptive roots ($P < 0.10$) (Fig. 3), suggesting that soil pH might be an exclusive environmental factor regulating the AM colonization in our study region.

**Discussion**

Our results indicated that environmental variables are decisive in regulating absorptive root branching ratios and AM colonization in our studied forests. The branching ratios and AM colonization of the same tree species varied across locations with different environmental conditions. This was consistent with our first hypothesis that environmental variables were the main factors causing the variations of absorptive root branching ratios and AM colonization.

Our study showed that root tips are sensitive to climate and soil nutrients. The branching ratios were

**Fig. 3** Linear regressions of AM colonization and environmental factors ($N=11$) (values are means of individual locations)
positively correlated with MAT, but negatively correlated with soil N and soil pH (Fig. 2). The positive correlation of branching ratio and MAT proved that temperature was a significant climatic factor (Abbas Al-Ani and Hay 1983; McMichael and Quisenberry 1993) which could enhance the production of root tips (Nagel et al. 2009). The negative correlation of branching ratio with soil N was consistent with the results from Zhang et al. (2007) and Chun et al. (2005) who showed that high N concentrations inhibited root tip meristem activity since plants do not need more root tips for the acquisition of N (Zhang et al. 2007). The root branching ratios were also negatively correlated with soil pH and were high in the locations with low soil pH (e.g., Huitong and Pingxiang in Table 1; Fig. 2). The reason might be that the increase of soil acidity can result in lower nutrient mobility in soil solution (Freschet et al. 2017), the decline of soil microbial biomass C, N, and nitrification (Kemmitt et al. 2006), which could lead to the deficiency of soil nitrogen availability, and consequently led to more root tips for increasing nitrogen absorption. The relationships of branching ratios and environmental conditions suggested that more carbon resources were allocated to root tips to enhance the acquisition of soil water and nutrients under harsh environmental conditions (e.g., low soil nutrients and high soil acidity) (Duque and Lynch 2018).

In contrast, the absorptive root AM colonization of Chinese fir was not so sensitive to climatic conditions and soil nutrients (Fig. 2 and Fig. 3) in our study. The AM colonization did not show any significant relations with MAT, MAP, soil C, soil N, and soil P. The reason might be that our study locations are in Subtropical China with similar climate and soil properties. However, we found that mycorrhiza was positively related to soil pH ($P < 0.10$) (Fig. 3). This result is consistent with the results from previous studies that root AM fungi of plants was pH sensitive (Kawahara et al. 2016; Rajasree et al. 2016) and reduces in acidic soils (Clark 1997; Frater et al. 2018).

The relationship between root traits and environmental conditions in this study showed that soil acidity is an important environmental driver for the shifting of root foraging strategies of Chinese fir in Subtropical China. Both root tips and AM fungi were sensitive to soil pH in spite of their opposite directions (Fig. 4). The negative relationship of branching ratio and AM colonization in our study was consistent with the results from Price et al. (1989) and Hetrick et al. (1991) who showed that root branching could be reduced by AM fungal colonization, with the increasing mycorrhizal dependence for nutrients. Ostonen et al.’s (2017) study also showed that from temperate to boreal forests, the biomass of root tips increased, whereas the biomass of mycorrhizal fungi decreased.

Our study showed that several other environmental factors such as MAT, soil C, and soil N also played important roles in affecting root traits. The absorptive roots of Chinese fir increased either the branching of lower-order roots or AM colonization in different environmental conditions. Usually, either of these two traits dominates. But in harsh or stressed conditions, plants have evolved mechanisms that can compensate for lower nutrient availability (e.g., coldness and acid soils) and could depend on different strategies (Zadworny et al. 2016). For example, both the branching ratio and the AM colonization of absorptive roots were high in Taihe (Table 1). This might be related to high MAT, low soil nutrients (soil N and soil P), and high soil acidity in this area. To attain enough resources, the absorptive roots have to develop both root tips and mycorrhizal fungi.

**Conclusion**

Our study showed that absorptive root traits of Chinese fir had large variations spatially in response to various environmental conditions. Soil nutrients (soil C and soil N) and climatic factor (MAT) were
important variables for fine root branching, but not for the AM colonization. Soil acidity was determined as an exclusive factor for regulating both the AM colonization and fine root branching. Those results provide important insights for predicting absorptive root traits in a future changing environment. Future studies are needed to include more environmental gradients and cover more tree species to advance our understanding of the relationship between root nutrient foraging strategies and environmental conditions.

Author contributions YCL, XWW, and HMW conceived the ideas and designed methodology for the study; YCL and LL collected data; HBF, HLD, WFL, and JLL led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Funding This study was financially supported by the National Natural Science Foundation of China (31960308) and the Science and Technology Project of Jiangxi Education Department (GJJ201906).

Declarations

Conflict of interest The authors have not disclosed any competing interest.

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