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Spatial and temporal effects of nitrogen addition on root morphology and growth in a boreal forest

Guoyong Yan[a,b,1], Fei Chen[b,1], Xin Zhang[a], Jianyu Wang[b], Shijie Han[c], Yajuan Xing[a,d,*], Qinggui Wang[a,b,**]

[a] College of Agricultural Resource and Environment, Heilongjiang University, 74 Xuefu Road, Harbin 150080, China
[b] School of Forestry, Northeast Forestry University, 26 Hexing Road, Harbin 150040, China
[c] Institute of Applied Ecology, Chinese Academy of Sciences, 72 Wenhua Road, Shenyang 110016, China
[d] Institute of Forestry Science of Heilongjiang Province, 134 Haping Road, Harbin 150081, China

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ABSTRACT

The production and turnover of fine roots play a critical role in regulating underground carbon (C) cycling of terrestrial ecosystems, which are a biological feature in regulating the capacity of plant to capture soil nutrients. Although the importance of fine root production (FRP) and turnover (FRT) to whole-plant and ecosystem C cycling is increasingly recognized, their response to nitrogen (N) deposition remains unclear. To understand how N addition affects the FRP and FRT of fine roots, a field experiment was conducted with four N treatment levels (0, 2.5, 5.0, and 7.5 $g\,N\,m^{-2}\,yr^{-1}$) to quantify the effects of N deposition on fine root dynamics and vertical allocation in a boreal forest using the minirhizotron technique. Our results showed that N deposition significantly decreased total number of live and dead fine roots and total surface area of live fine roots in topsoil layers (0–20 cm soil depth), while increased in subsoil layers (20–40 cm soil depth) during 2015–2016. Average diameter of fine root was increased by N addition particularly in subsoil layers. The FRP rate was reduced by N addition in the topsoil, but increased in the subsoil layers, whereas patterns of their seasonal changes were not affected in both soil layers. The FRT rate tended to decrease under N addition compared with control in both soil layers during the observation years, potentially indicating a slower underground C cycle with N addition. Moreover, fine roots distributed more deeply in the soil due to N addition, indicating fine roots may through self-regulation and change of growth strategy to face environment stressor.

1. Introduction

Fine roots (< 2 mm in diameter) could contribute as much as 30–75% of global annual net primary production, despite representing $< 2\%$ of the total ecosystem biomass (Nadelhoffer and Raich, 1992; Jackson et al., 1997; Gill and Jackson, 2000; Hendricks et al., 2006; Gaudinski et al., 2010). This implies that fine roots may represent an important part of ecosystem carbon (C) input into soils. Additionally, previous studies suggested that respiration of live roots and decomposition of dead roots make a significant contribute to soil C emission (Gordon and Jackson, 2000; Zhang and Wang, 2015). Those results suggested that fine root production (FRP) and turnover (FRT) have important effects on soil dynamic of C (Nie et al., 2013). However, some studies showed that FRP and FRT were sensitive to changes of soil nitrogen (N) availability (Burton et al., 2000; Tateno et al., 2004; Noguchi et al., 2013; Wang et al., 2013; Wurzburger and Wright, 2015). Thus, FRP and FRT may be altered by changes of soil N availability due to atmospheric N deposition. With the fossil fuel combustion, application of N fertilizer and N fixing plants cultivation, atmospheric N deposition has increased by approximately four-fold over the past century (IPCC, 2013), resulting in increased biologically available N across various ecosystems (Lu et al., 2011; Ring et al., 2011). A large amount of N deposition has been found to significantly affect plant growth and nutrient cycling, which may change carbon sequestration in plant biomass, soil C pools and ecosystem C cycle (Magnani et al., 2007; Pregitzer et al., 2008; Reay et al., 2008; Thomas et al., 2010). Although the effects of N deposition on soil C cycle have been studied extensively in past decades, these effects are not well understood, particularly with referenced to how fine root dynamics respond to N deposition. Thus, examining how effects of simulate N deposition on FRP and FRT is

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* Correspondence to: Y. Xing, College of Agricultural Resource and Environment, Heilongjiang University, 74 Xuefu Road, Harbin, 150080, China.
** Correspondence to: Q. Wang, School of Forestry, Northeast Forestry University, 26 Hexing Road, Harbin 150040, China.
E-mail addresses: xingyajuan@163.com (Y. Xing), qgwang1970@163.com (Q. Wang).

[1] These authors contributed equally to this work.

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essential for a better understanding of soil C cycle under future scenarios of increasing N deposition (Yuan and Chen, 2012).

Atmospheric N deposition influences fine roots directly by damaging root tissues and mycorrhiza, and indirectly by increasing soil N availability and nutrient imbalances (Nadelhoffer, 2000; Galloway et al., 2004). Many experiment studies have showed that fine root biomass decreased as the N deposition increased (Hendricks et al., 2006; Mei et al., 2010; Wang et al., 2013). The meta-analysis also showed that simulated N deposition significantly decreased fine root biomass (Li et al., 2015). Decrease of fine roots biomass indicated that plants may adjust resource foraging strategy to adjust environmental change (Ostonen et al., 2011). Previous studies showed that plants may increase fine root growth to improving resource foraging efficiency, when soil nutrients are deficient (Ostonen et al., 2011). Thus, fine root biomass may decrease when soil nutrients become abundant (Wang et al., 2013). Plants also may adjust resource foraging strategy by modifying fine root morphological traits, such as root diameter and total live fine roots surface area (Rasse, 2002; Wang et al., 2013). Helmisaari et al. (2007) found that less active root area is needed to meet the plant's nutrient demand when soil nutrients become abundant. Thus, total live fine roots surface area may be decreased under N deposition. In addition, FRP and FRT may be altered due to increase in atmospheric N deposition (Mei et al., 2010; Li et al., 2015; Peng et al., 2016). However, effects of N deposition on FRP and FRT are inconsistent. The addition of N deposition may significantly increase (Son and Hwang, 2003; Bai et al., 2008; Li et al., 2015), substantially decrease (Burton et al., 2000; Mei et al., 2010; Peng et al., 2016) or lack of influence (Ostertag, 2001; Baldi et al., 2010) on FRP and FRT. These different results illustrated that variations in climate, tree species, and variable methodology may influence the response of roots to the N addition (McCormack and Guo, 2014; Peng et al., 2016). For example, Mei et al. (2010) reported that N fertilization did not significantly alter FRP and FRT rate estimated by the sequential soil cores, but did reduce FRP and FRT rate estimated by the ingrowth core method. Each method which have been used to quantity FRP and FRT has both advantages and disadvantages (Vogt et al., 1998). However, compared with the ingrowth core method and the sequential soil cores, the minirhizotron technique has advantages in monitoring root dynamics in suit under different treatment (Vogt et al., 1998).

Although effects of N deposition on FRP and FRT have received extensive attention, but relatively few studies have considered depth distribution pattern of fine roots respond to N deposition in boreal forest (Smithwick et al., 2013). Lifespan of fine root is related with soil depth (Baddeley and Watson, 2005). Previous studies found that the effects of N deposition on lifespan of fine roots in different depth were different (Adams et al., 2013). In order to accurately assess the soil C dynamics, improved understanding of fine roots of different depth responses to N deposition is needed.

Following rapid economic growth, the average annual bulk deposition of N increased from approximately 13.2 kg of N per in the 1980s to 21.1 kg of N per hectare in 2000s in China (Liu et al., 2013). In addition, the annual N deposition rate was found to be 12 kg N hm^{-2} yr^{-1} in coniferous forest, and a highly significant ($P < 0.001$) increase in bulk N deposition was found in northern China (Zhao et al., 2009; Liu et al., 2013). In order to reveal how FRP and FRT response to N deposition in boreal forest, we conducted an experiment with four N treatment levels (0, 2.5, 5, and 7.5 g N m^{-2} $year^{-1}$) to quantify the effects of N deposition on fine root dynamics and vertical allocation using the minirhizotron technique in a larch (*Larix gmelinii*) forest in northern China. In the boreal forest, *Larix gmelinii* is dominant plant species with extensive distribution in northern China. As the productivity of boreal forest is restricted by nutrient deficiency in northern China, we hypothesize that (1) simulated N deposition will decrease fine root number, total fine root surface area and FRP based on optimal C allocation theory (Chapin et al., 1987); and (2) FRT may display different responses to different levels of simulated N addition based on previous studies (Burton et al., 2000; Peng et al., 2016).

2. Materials and methods

2.1. Field site and experimental design

The study was carried out in a *Larix gmelinii* forest, located in Nanwenghe National Natural Reserve in the Greater Khingan Mountains, Northeastern China (51°05′-51°39′ N, 125°07′-125°50′ E). Climate is characterized by a cold temperate continental climate, mean annual temperature is − 2.4 °C, the maximum mean monthly temperature is about 18.6 °C occurring in July, and the minimum mean temperature is − 26.3 °C occurring in January. The mean annual precipitation is about 489 mm, 70–80% of which falls during short season from July to August. The soil type of the study areas is mainly sandy loam in 0–20 cm and gravelly sand in 20–40 cm. The plant community at the experimental site is dominated by *Larix gmelinii* (29 year). Stand density at the study site was 2852 ± 99 trees hm^{-2}, and a mean diameter at breast height (1.3 m height, DBH) of 8.98 ± 0.32 cm. The understory plants are *Rhododendron simsii Planch.*, *Vaccinium spp.* and *Ledum palustre L.*

To investigate the effects of N deposition on soil C dynamic, the simulated N addition experiment was established with a randomized complete block design, and the N addition field experiment began in May 2011. Total three blocks were established and each block was divided into four 20 × 20 m plots with the buffer strips between any two plots > 10 m to avoid disturbing nearby plots. Total 12 plots were established. According to the northern N deposition rate of 2.5 g N m^{-2} yr^{-1} in the China (Liu et al., 2013), the widely used method (double and triple the local N deposition rate) in previous studies simulating N deposition (Song et al., 2016), three N addition treatments, low-N (2.5 g N m^{-2} yr^{-1}), medium-N (5.0 g N m^{-2} yr^{-1}), high-N (7.5 g N m^{-2} yr^{-1}) and a control (no added N) were conducted randomly in four plots of each blocks. NH_4NO_3 was applied in this study as form of N addition. The additions were done monthly with a backpack sprayer during the growing season (total five times from May to September). Before each application, the NH_4NO_3 was weighed according to the N addition rate, mixed with 32 L of water and sprayed evenly onto the forest floor of each plot. The control plots received 32 L water without NH_4NO_3.

2.2. Minirhizotron installation and image collection

To investigate fine root dynamics, minirhizotron tubes (external 7 cm in diameter, internal 6.4 cm in diameter and 100 cm in length) was installed. Five tubes were randomly buried in each plot. Total 60 minirhizotron tubes were installed. All tubes were buried at an angle of 30° to the vertical to a tube depth of 84 cm (equals to a vertical soil depth of 42 cm). The portion of each tube exposing aboveground was first wrapped with black tape to isolate sunlight and then with yellow tape to minimize heat exchange. The top end of each tube was capped using a white-tape-wrapped cap and a ziplock bag to reduce water vapor (Kou et al., 2016).

A lag period of up to 12 months is required to stabilize the density of fine roots, after installing minirhizotron tubes (Joslin and Wolfe, 1999). Thus, minirhizotron tubes were installed in June 2014, and image collection did not begin until May 2015. We captured digital images consecutively at a month interval in growth season (from May to September) during 2015 and 2016. Root images (21.6 × 19.6 cm, 300 dpi) were captured at two tube depths (0–20 cm and 20–40 cm soil depth) using a scanner (CI-600 Root Scanner, CID Bio-Science, Inc., USA) which was exactly matched to the tube size according to the schematic described by Maeght et al. (2013).