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The effects of warming and nitrogen addition on fine root exudation rates in a young Chinese-fir stand

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ABSTRACT

Despite the perceived importance of root exudates in forest ecosystem function, few studies have simultaneously examined the effects of elevated temperature and nutrient availability on root exudates, especially in the tropical and subtropical regions. This limits our ability to predict belowground C allocation and nutrient cycling in response to global change at a global scale. In this study, we used a complete randomized block design with factorial soil warming (ambient, ambient + 4 °C) and nitrogen (N) addition (ambient, ambient + 40 Kg N ha^{-1} yr^{-1}) to examine their effects on in situ fine root exudates and sapling growth in a young Chinese fir (*Cunninghamia lanceolata*) stand. We found that soil warming and N addition each had negative effects on root exudation rates. Moreover, there was a negative interactive effect of soil warming and N addition on fine root exudation rates (i.e., further reduction), likely due to altered fine root morphological and chemical properties, soil characteristics and belowground C allocation. Root exudation rates negatively related to soil inorganic N concentrations, but positively related to fine root diameter, specific root length, N concentration and non-structural carbohydrate concentration. Reducing root exudation rates may be a physiological adjustment of the Chinese fir stand to high soil nutrient availability associated with warming and N addition. Collectively, the results indicate that the effects of warming on root exudation rates are dependent on soil fertility and moisture. Reduced exudation rates under warming plus N addition may decrease the flux of labile C from the roots to the soil suggesting that N deposition may mitigate warming-enhanced SOM decomposition. These findings provide new insights into belowground C dynamics and root-soil interactions in response to soil warming and N addition.

1. Introduction

Warming and N deposition are two important aspects of global change that have profound effects on ecosystem structure and functions (Corre et al., 2003; Butler et al., 2012; Ramirez et al., 2012; Yu et al., 2016). The average global surface temperature has increased 0.78 ℃ in the past 100 years, and is expected to further increase 1.5–3.7 ℃ by the end of this century (IPCC, 2013). Recently, studies have examined the combined effects of warming and N deposition on soil carbon (C) sequestration, microorganism and plant distribution (Chen and Brassard, 2013; Camenzind et al., 2014; Sendall et al., 2015). Few studies, however, have explored the effects of warming and N deposition on the root system, although the root system plays a key role in ecosystem C cycling (Matamala et al., 2003; Li et al., 2015).

Root exudates are an important source of belowground carbon (C) input accounting for 5%-21% of annual photosynthetic production (Baetz and Martinoia, 2014). A substantial proportion of root-derived labile C that fuels soil microbial activity is derived from the release of recent photosynthates through root exudates (Phillips et al., 2009, 2011). Root exudates directly affects the growth of rhizosphere

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microorganisms and the soil organic matter (SOM) decomposition (Bengtson et al., 2012). Root exudates have also been suggested to affect SOC pools via inducing priming effects in the rhizosphere (Shahzad et al., 2015). Because root exudates are released into a narrow zone of soil around roots and are rapidly assimilated by soil microbes, they are among the most poorly quantified components of the belowground C cycle (Wardle, 2002; Paterson, 2003). The lack of a thorough understanding of root exudates represents an important knowledge gap on the effects of warming and N deposition on important rhizosphere processes.

The rate of root exudation and the composition of root exudates are affected by many biotic and abiotic factors (Phillips et al., 2011; Yin et al., 2013a). Studies have illustrated the role of biotic factors, such as plant species, photosynthesis rate, phenology and plant nutritional status, on the quantity and quality of root exudates (Kuzyakov, 2002; Zhang et al., 2004; Gärdenäs et al., 2011). Some studies have also examined the role of abiotic factors, such as CO_2 concentration and temperature, on regulating root exudates (Phillips et al., 2009; Yin et al., 2013a). Rising temperature and changes of N availability have major impacts on root exudates. Increases of soil temperature directly affect the physiological status of plant roots, and thus affect the quantity and chemical composition of root exudates (Drake et al., 2011). Studies have shown that warming increased root exudation, possibly through increases in belowground C allocation and changes in root morphology (Uselman et al., 2000; Yin et al., 2013a,b). In terms of soil N status, plants tend to invest more photosynthetic products into the belowground components in soils with low N availability relative to soils with high N availability (Dijkstra et al., 2008; Phillips et al., 2009). Some studies indicated that root morphological and chemical properties (e.g., tissue N content and root length) were highly variable in different developmental stages and environmental conditions (Wells and Eissenstat, 2002; Ostonen et al., 2007). However, the relationship between root exudates and fine root morphological and chemical properties under warming and enhanced N deposition conditions is not well understood.

Because of the complexity of rhizosphere ecological processes and the limitation of research methods, studies on the effects of soil warming and N addition on root exudates are limited, and most of which concentrated in the temperate region (Yin et al., 2013a). Relatively little is known about the tropical and sub-tropical (sub/tropical) regions, which limits our understanding of how forest rhizosphere processes respond to change at the global scale. Compared to temperate and boreal forests, sub/tropical forests have relatively high soil N availability (Russell and Raich, 2012; Zhang et al., 2013) and rapid nutrient cycling (Chapin, 1990). Thus, the effects of N addition on fine root exudates, which is to a large degree dependent on nutrient availability, can vary considerably among forests of different regions. In addition, fine root growth in sub/tropical forests is less temperature-limited compared to that in temperate and boreal forests so that the effects of soil warming on fine root exudates are likely also different between sub/tropical forests and temperate and boreal forests. Although there are increasing efforts examining fine root exudates in relation to warming and N addition (but mostly focused on one of the two) in the tropics and subtropic, field-based manipulative experiments are rare (Zhou et al., 2013). It has been suggested that manipulative warming experiments in tropical forests are urgently needed (Cavaleri et al., 2015). Warming and increased N deposition co-occur in many parts of the world. Concurrent changes in temperature and N deposition may have interactive effects on root exudates (Pinder et al., 2012) that cannot be adequately inferred from single-factor experiments (Dermody et al., 2006).

Chinese fir (*Cunninghamia lanceolata*) is the most important timber species in China, accounting for 6% of the world's plantations by area and playing an important role in forestry and forest C sequestration in China (Piao et al., 2009). It remains unclear how fine root physiology of Chinese-fir plantations will vary with soil warming and N addition. Knowledge of the responses of fine root exudates of Chinese-fir plantations to soil warming and N addition can contribute to better predict feedbacks of terrestrial C cycling to climate change. To our knowledge, there have been no field experiments that examined the combined effects of soil warming and N deposition on fine root exudates of Chinese-fir plantations. In this study, we used a factorial experiment combined with a modified culture-based cuvette system to study in situ root exudation rates in response to soil warming and N addition. Specifically, we addressed the following questions. First, how will soil warming and N addition affect fine root exudation rates? Second, are there interactive effects between soil warming and N addition on fine root exudation rates? Third, what kind of factors, endogenous or exogenous, affect fine root exudation rates in the Chinese-fir stand? Through addressing these questions, we tested the following hypotheses. First, based on the results of previous studies that warming had positive effects on fine root exudates (Uselman et al., 2000; Yin et al., 2013a), we hypothesized that warming would increase fine root exudation rates (H_1). Second, because previous studies found that N addition reduced root exudates in soils with high N availability (Paterson and Sim, 2000; Phillips et al., 2011) and our study site has high N availability (Zhang, 2013), we hypothesized that N addition would reduce fine root exudation rates (H_2). Third, because of the hypothesized opposite effects of warming and N addition, we hypothesized that warming plus N addition would have minimal effects on fine root exudation rates (H_3). Fourth, because studies have shown that some fine root properties (e.g., root diameter, SRL, and N concentration) and belowground biomass are related to root exudation rates (Groleau-Renaud et al., 1998; Darwent, 2003; Badri and Vivanco, 2009; Sun et al., 2017), we hypothesized that belowground C allocation, root morphological and chemical traits are significantly related to root exudation rates (H_4).

2. Materials and methods

2.1. Study site description

This study was conducted at the Chenda Observation Study Site (26°19′N, 117°36′E) of Sanming Forest Ecosystem and Global Change Research Station in Fujian Province, China. The study area is characterized by a typical mid-subtropical monsoonal climate with a mean annual temperature (MAT) of 19.1 °C. The mean annual precipitation (MAP) is 1750 mm, with approximately 75% occurring during the period from March to August. Mean annual air temperature and annual precipitation during the study period were 18.8 °C and 1198 mm, respectively, which were lower than the long-term averages (Fig. 1a). The relative humidity (RH) is 81%, and the mean annual evapotranspiration is 1585 mm. The growing season is relatively long, with an annual frost-free period of approximately 300 days. The elevation of the study site is 300 m above sea level. The parent material of the soil is granite and the soil is classified as red soils, equivalent to Oxisol in the USDA Soil Taxonomy and OrthicArisol in the FAO taxonomy system (FAO, 1985; State Soil Survey Service of China, 1998; Soil Survey Staff of USDA, 2014).

2.2. Experimental design

A complete randomized block design, with warming and N addition as fixed factors, was established in a young Chinese-fir stand in August 2014. There were four treatments, each with six 2.5 m × 2.5 m replicates (plots): control (CT), soil warming (W, +4 °C), N addition (N, +40 kg N ha^{-1} yr^{-1}), and soil warming plus N addition (WN, +4 °C and +40 kg N ha^{-1} yr^{-1}). The experiment was carried out on a flat area that was not significantly affected hydrologically by adjacent forests. In addition, the understory vegetation within the experimental plots was removed periodically to minimize the effects of understory vegetation. In the soil warming plots, soil heating cables (Nexans type