



Strong root respiration response to nitrogen and phosphorus addition in nitrogen-limited temperate forests

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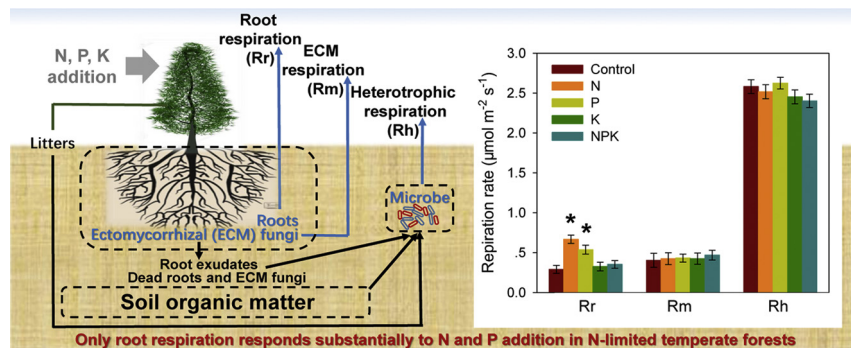
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HIGHLIGHTS

- Only root respiration responds greatly to N and P addition in N-limited temperate forest.
- The response of soil respiration and its components to nutrient addition don't fluctuate greatly over different years.
- The significant inter-annual variation may obscure the impact of fertilization.
- Soil temperature and moisture controlled the inter-annual variations of soil respiration.

GRAPHICAL ABSTRACT



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ABSTRACT

Nutrient availability is one of the key regulator of the global forest carbon balance. The use of fossil fuels and fertilizers has increased the amount of biologically reactive nitrogen (N) in recent decades and N fertilization also changes the availability of other nutrients such as phosphorous (P) and potassium (K). The increased soil nutrient availability is known to stimulate forest growth, but we currently lack comprehensive understanding of the response of soil respiration and its three components (roots, microbes, and ectomycorrhizal (ECM) fungi) to the increased soil N, P and K availability. We conducted a 4-year field fertilization experiment with N, P and K addition in an N-limited temperate forest and separated ECM fungi respiration (Rm), root respiration (Rr) and heterotrophic microbial respiration (Rh) from total soil respiration. Our results showed that Rr increased with N and P addition while Rh and Rm did not respond to nutrient addition. Rm, Rr and Rh varied substantially from year to year, but their responses to nutrient addition did not fluctuate in different years. Our results indicate that in N-limited forest ecosystems, Rh and Rm may not respond substantially to future changes in nutrient addition and that inter-annual variation in climate may be the determinant of soil CO₂ efflux in response to global changes.

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1. Introduction

Forest soil respiration (Rs) is the primary pathway by which plant-fixed carbon dioxide (CO₂) is released back to the atmosphere (Högberg and Read, 2006; Gaumont-Guay et al., 2009). Rs arises from the autotrophic respiration of roots (Rr), their associated ectomycorrhizal (ECM) fungi (Rm) and of heterotrophic microbial

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respiration (Rh) (Hanson et al., 2000; Subke et al., 2006). Rr represents a major source of CO₂ loss from plants (Rodeghiero and Cescatti, 2006). Rh is an integrator of the decomposition of soil organic matter and is important in soil organic carbon (SOC) stabilization (Janssens et al., 2010). ECM fungi are regarded as vital modulators in SOC dynamics under the scenario of global changes (Talbot et al., 2008; Cairney, 2012). ECM fungi consume carbohydrate from their host plant, among which 47–89% of photosynthate allocated to mycorrhizas is respired to support the maintenance of existing fungal tissue and the process of nutrient uptake, contributing to CO₂ emissions from soil to the atmosphere (Heinemeyer et al., 2007). In recent years, researchers have begun to recognize the substantial contribution of ECM fungi to Rs (Phillips et al., 2012; Neumann and Matzner, 2014) and have suggested that Rm is larger than Rr (Heinemeyer et al., 2007, 2012). However, in most cases, Rm typically remains within the Rr component when assessing the response of Rs to global change (Janssens et al., 2010). In order to estimate the fate of atmospheric CO₂ under the projected increases in the upcoming century (up to 20% and >200% compared with current concentrations (Pachauri and Reisinger, 2007)), it is crucial to separate the respective contributions of Rm, Rr and Rh to total Rs.

Nutrient availability is one of the key regulator of the global forest carbon (C) balance in the context of global nitrogen (N) deposition (Fernández-Martínez et al., 2014). A recent meta-analysis suggested that N deposition reduces forest Rs when N is not limiting to microbial growth (Janssens et al., 2010). Kang et al. (2016) observed that the response of forest Rs to nutrient addition depends on the site fertility. There is substantial evidence that N enrichment spectacularly affects the activity of the rhizosphere, and of mycorrhizal root symbionts in particular (Treseder, 2004). Under high N deposition conditions, plants tend to reduce reliance on ECM hyphae and obtain N using their roots (Jones and Smith, 2004; Neuhauser and Fargione, 2004) thus potentially causing the decrease of Rm and the increase of Rr. In addition, N deposition increases soil acidity and decreases microbial biomass and extracellular enzyme activities (Ramírez et al., 2010; Phoenix et al., 2012), consequently resulting in the decrease of Rh.

Nitrogen deposition was also observed to shift temperate forests from N limitation to phosphorus (P) limitation (Vitousek et al., 2010). In N-limited temperate forests, P addition may increase ECM hyphae growth and root growth to enhance N uptake (Wallander and Thelin, 2008; Zeng and Wang, 2015), thus possibly increasing Rm and Rr. Moreover, P addition may also decrease extracellular enzyme production especially phosphatase production (Brooks et al., 2011), thus decreasing the microbial decomposition of P-containing minerals and Rh. Extra N input will also cause potassium (K) deficiency because the availability of K ions is low owing to the strong mineral adsorption of K ions (García and Zimmermann, 2014). Early laboratory experiments have shown that K addition increased ECM fungal production (Ericsson, 1995), but little data are available concerning the response of Rm, Rr and Rh to K addition (Potila et al., 2009). Most previous studies have focused on the effects of N deposition on Rs and its components (Hasselquist et al., 2012; Vallack et al., 2012). However, we still lack a comprehensive mechanistic understanding of Rs and its three components responses to N, P and K addition.

The responses of Rs and its three components to nutrient addition may also fluctuate greatly over different years. Year-to-year fluctuations in the factors such as soil temperature and moisture, biomass, composition and function of microbial community, root biomass and N concentration may lead to great changes in Rs and its three components (Heinemeyer et al., 2007; Heinonsalo et al., 2015). Thus, Rs and its three components may show distinct inter-annual variations in responses to background abiotic and biotic factors. Moreover, the effect of fertilization treatments may also result in the variation of Rs and its three components. The background variations from year to year may complicate our understanding of the responses to fertilization treatments. For instance, background inter-annual variation in microbial community was reported to have a larger magnitude than global change

effects, and this variation appeared to constrain the responses of fertilization treatment in a California annual grassland (Gutknecht et al., 2012). Therefore, it is possible to observe a lag between the initiation of a treatment and the time that the response becomes significant (Sherry et al., 2008). However, the responses of Rs and its three components to nutrient addition over longer timescales are rarely studied (Hasselquist et al., 2012).

In order to better understand the effects of nutrient addition on Rs and its three components in temperate forest ecosystems, we conducted a 4-year field fertilization experiment with N, P and K addition in an N-limited coniferous pine forest. A mesh-trenching method was used to separate Rm, Rr and Rh from Rs. We measured major abiotic (soil temperature, soil water content and soil pH) and biotic attributes (microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), the ratio of fungal and bacterial biomass, potential extracellular enzyme activities, root C concentration, root N concentration and fine root biomass) influencing Rm, Rr and Rh. We aimed to answer two scientific questions: (1) what are the responses of Rm, Rr and Rh to N, P, and K addition; and (2) whether the responses fluctuate substantially among different years. We hypothesized the following. (1) Rm would decrease and Rr would increase with N addition owing to the reduced reliance on ECM hyphae under conditions of high N availability. In contrast, Rh would decrease because of the increased soil acidity, decreased microbial biomass and extracellular enzyme activities as a result of N addition. With P and K addition, Rm and Rr would increase because of the increased ECM hyphae growth and root growth in order to obtain N. Moreover, Rh would decrease because of the decreased extracellular enzyme production. (2) The responses of Rm, Rr and Rh to N, P and K addition would vary among different years as a result of the combination of substantial inter-annual variation and the fertilization treatments.

2. Materials and methods

2.1. Site description

The study site was located in Saihanba Forestry Center, Hebei Province, northern China (42°10′–42°50′N, 117°12′–117°30′E, 1400 m a.s.l.). This region is characterized by a semi-arid and semi-humid temperate climate, with annual mean air temperature of -1.4°C and precipitation of 450.1 mm. The growing season is relatively short, beginning in mid- to late-May and ending in early October. The soils are classified as aeolian sandy soils according to the Chinese Soil Taxonomy (similar to cambisols defined by the World Reference Base for Soil Resources (WRB)). Soil pH ranged from 5.8 to 6.3 with the averaged concentration of 1.3% in SOC and 0.1% in soil total N at 0–10 cm soil depth. The region covers the largest area of plantations in China and primary forests were almost completely removed during the 1950–60s and replaced by coniferous species in reforestation and afforestation programs (Fang et al., 2001; Wang et al., 2013). The arborous layer is dominated by evergreen *Pinus sylvestris* var. *mongolica* (Mongolia pine, 85%) and deciduous *Larix principis-rupprechtii* (Prince Rupprecht's larch, 15%). Both tree species form symbiotic relationships with ECM fungi. Fire suppression management has resulted in an approximately 2.5 cm thick forest litter layer and relatively sparse herbaceous layer with the dominant species being *Carex rigescens*, *Thalictrum aquilegifolium*, *Galium verum*, *Geum aleppicum*, *Artemisia tanacetifolia* and *Agrimonia pilosa*. Fertilization experiments were conducted in an approximately 35-year-old stand, with an average diameter at breast height of 12.9 cm. Tree height averaged 10.5 m and the tree density was between 3500 and 4000 trees ha⁻¹.

2.2. Fertilization experimental treatments

At the beginning of August 2010, experimental plot was set up with an area of 10 × 10 m, separated by a 5 m buffer zone. We designed five treatments including control (no nutrient addition, received water

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