



Negative effect of nitrogen addition on soil respiration dependent on stand age: Evidence from a 7-year field study of larch plantations in northern China

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ABSTRACT

Increasing anthropogenic nitrogen (N) deposition will affect the global carbon (C) cycle, although the mechanisms and magnitudes of its effects are not yet fully understood. Soil respiration (Rs) and its components (i.e., heterotrophic (Rh) and autotrophic (Ra) respiration) represent the largest flux of carbon dioxide (CO₂) from terrestrial ecosystems to the atmosphere. However, the potentially interactive effect of N addition and stand age on Rs in forests remains unclear. We conducted a 7-year (2010–2016) field experiment in three differently-aged larch plantations (11-, 20-, and 45-year-old, representing sapling, intermediate, and mature stands) to investigate the effects of different N addition rates (control: no N addition; low-N addition, N20: 20 kg N ha⁻¹ year⁻¹; and high-N addition, N50: 50 kg N ha⁻¹ year⁻¹) on Rs. We found significant seasonal variation in Rs, Rh, and Ra, with levels highest in summer and lowest in autumn. Rs correlated strongly with soil temperature and weakly with soil moisture, and Rs, Rh, and Ra increased exponentially with soil temperature. The temperature sensitivity (Q₁₀) of Rs was lowest in the mature stand, which suggests that it will sequester relatively more C in a warmer climate. The Q₁₀ of Ra was higher than that of Rh, indicating that it contributed proportionally more to the total soil CO₂ efflux. N addition had no significant effect on Q₁₀. Rs in the intermediate stand was significantly lower than Rs in the sapling and mature stands, which may be due to its lower soil temperature and poorer substrate quality. N addition decreased Rs by an average of 9%, but significant effects were only observed in the sapling and intermediate stands. The negative influence of N addition on Rs was largely dependent on soil temperature, with more negative effects observed in the summer when temperatures were higher, and attributable to a reduction in either Ra in the intermediate stand or Rh in the sapling stand. We hypothesize that N limitation in the young trees was alleviated by fertilization, which decreased C allocation to roots, whereas N addition may have exerted a more negative influence on soil microbial activity in the sapling stand. In summary, our results highlight the importance of stand age in regulating the negative effects of N addition on Rs and its components, which has implications for projecting the global C–climate feedback in the future.

1. Introduction

During the past century, anthropogenic nitrogen (N) deposition originating from human activities such as N fertilization and fossil fuel combustion has increased substantially. Indeed, ~210 Tg of reactive N was created from anthropogenic sources in 2005 (IPCC, 2013).

Moreover, annual global N deposition is predicted to increase by a factor of 2.5 by the end of this century under the assumed IPCC SRES A2 scenario (Galloway and Cowling, 2002; Lamarque et al., 2005). Due to the strong coupling between carbon (C) and N, high rates of atmospheric N deposition could drastically affect C cycling, especially in N-limited temperate ecosystems (Magnani et al., 2007; Pregitzer et al.,

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2008; Sun et al., 2014). For example, Thomas et al. (2010) reported that N deposition stimulated aboveground forest growth by 61 kg of C per kg atmospheric N deposition in the US, with total global C storage expected to increase by 0.31 Pg C year⁻¹ due to N deposition. Janssens et al. (2010) estimated that a reduction in soil carbon dioxide (CO₂) efflux (i.e., soil respiration (Rs)) of 36 g C occurs for each gram of N added, mainly driven by decreased heterotrophic respiration (Rh) in forest ecosystems.

Rs is the largest CO₂ source from terrestrial ecosystems to the atmosphere, accounting for 70–90% of total ecosystem respiration (Raich and Schlesinger, 1992). There are two components to Rs: heterotrophic respiration (Rh) and autotrophic respiration (Ra). Rh represents CO₂ released during the decomposition of dead organic matter by free-living microbes and fauna, and Ra represents CO₂ released by roots, mycorrhizal fungi, and other rhizosphere organisms that rely directly on the recently allocated C from photosynthesis in the belowground environment (Hasselquist et al., 2012; Heinemeyer et al., 2007). Even small changes in Rs may dramatically alter the atmospheric CO₂ concentration and global C balance, with consequent feedbacks on climate change (Betts, 2000; Peng et al., 2009; Piao et al., 2008; Rustad et al., 2000).

Experimental evidence derived from previous studies has demonstrated that N addition can exert positive (Tu et al., 2013; Zhang et al., 2014), negative (Bowden et al., 2004; Sun et al., 2014), or no (Lee and Jose, 2003; Liu and Greaver, 2010) effect on Rs. This conspicuous absence of consistency highlights the importance of evaluating the effects of N addition on Rs. Furthermore, the durations of these experimental studies were relatively short (always less than 3 years) (Laganière et al., 2012; Sun et al., 2014; Wang et al., 2017). In a longer-term study, Bowden et al. (2004) observed an initial increase of Rs in the first year following N addition in a temperate forest, no significant influence in the second year, and a reduction of 41% after 13 years of continuous N addition. The initial increase is attributed to the increase in tree productivity, which in turn resulted in more C allocation to roots and mycorrhizal fungi. In contrast, belowground allocation and soil microbial activity eventually decreased with the continuous N addition (Bowden et al., 2004; Maaroufi et al., 2015). Taken together, medium- and long-duration studies are urgently needed to clarify the effects of chronic N deposition on soil C dynamics (Bowden et al., 2004; Maaroufi et al., 2015; Peng et al., 2017), especially for partitioning Rs to different components (i.e., Rh and Ra).

Many studies have revealed that Rs is mainly influenced by soil temperature, soil moisture, and substrate supply in forest ecosystems (Bowden et al., 2004; Chen et al., 2014; Janssens and Pilegaard, 2003; Laganière et al., 2012; Saiz et al., 2006). The effects of these abiotic and biotic factors on soil CO₂ emission might vary within a season (Du and Fang, 2014; Ma et al., 2014; Saiz et al., 2006). Therefore, a better understanding of how soil respiration and its components change over time during the growing season would improve our ability to model the C balance of forest ecosystems. Furthermore, stand age is one of the most important characteristics of a forest and can exert a great influence on net primary productivity (He et al., 2012), biomass density (Fang et al., 2014; Yan et al., 2017), and soil CO₂ efflux (Ma et al., 2014; Saiz et al., 2006). For example, Saiz et al. (2006) showed that Rs in Sitka spruce plantations in central Ireland initially decreased with stand age and then leveled out in older stands, whereas Ma et al. (2014) showed that stand age regulated the response of Rs in larch plantations to temperature in northern China using the same study sites that we report on in this paper. However, to date, the combined effects of N addition and stand age on Rs and its components remain unclear, as do the potential underlying mechanisms. Such an incomplete understanding of Rs limits our ability to accurately predict the response of forest ecosystems to climate change. Therefore, a better understanding of the impact of N addition and stand age on Rs and its components will help us accurately include the influence of afforestation on the global C cycle and balance.

Globally, the area of plantation forests increased from 1.68×10^8 ha in 1990 to 2.78×10^8 ha in 2015 (or by 4.06–6.95% of the total forest area), with the most rapid increase occurring in temperate zones, especially in China (Payn et al., 2015). China accounts for about one third of the global area of plantation forest. As the most dominant timber species in north China (Mason and Zhu, 2014; Yan et al., 2017, 2018a), larch (*Larix* spp.) plantations have both valuable climatic (e.g., C sequestration) and economic (e.g., timber production) implications (Gao et al., 2016; Yan et al., 2017, 2018a). In this study, we measured Rs and its components (i.e., Rh and Ra) during the growing season for 7 years, following N addition in three age categories (11-, 20-, and 45-year-old stands, representing sapling, intermediate, and mature stands, respectively) in *Larix principis-rupprechtii* plantations in north China. Our objectives were to determine (1) seasonal patterns of Rs; (2) responses of Rs and its components to soil temperature and soil moisture; (3) the effects of N addition and stand age on Rs and its components and their sensitivities to soil temperature; and (4) the cumulative CO₂ effluxes during the growing season.

2. Materials and methods

2.1. Site description

The study was conducted at the Saihanba ecological station (42°24.723'N, 117°14.844'E, 1505 m a.s.l.) of Peking University, which is situated in Saihanba National Forest Park, Hebei Province, north China. The climate is semi-humid, with long and cold winters (November–March) and short springs and summers. The growing season lasts from May to October. From 1971 to 2010, the mean annual temperature was -1.4 °C (the lowest and highest monthly mean temperatures were -21.8 and 16.2 °C in January and July, respectively), the mean annual precipitation was 450 mm, and the frost-free duration was 81 days (Ma et al., 2014a). The monthly mean air temperature and precipitation from January to December during 2010–2016 can be seen in Fig. 1. The well-drained soils are predominantly sandy, and the topography is relatively flat. Snowfall begins in mid-October, and snow melt occurs in early April. Typically, the depth of snow accumulation is less than 30 cm in winter. The ambient N deposition is 13 kg ha⁻¹ year⁻¹ (Sun et al., 2016).

2.2. Experimental design

In August 2009, we selected three larch plantation stands of different ages, i.e., 11-, 20-, and 45-year-old stands, representing sapling, intermediate, and mature stands, respectively. At the same time, all

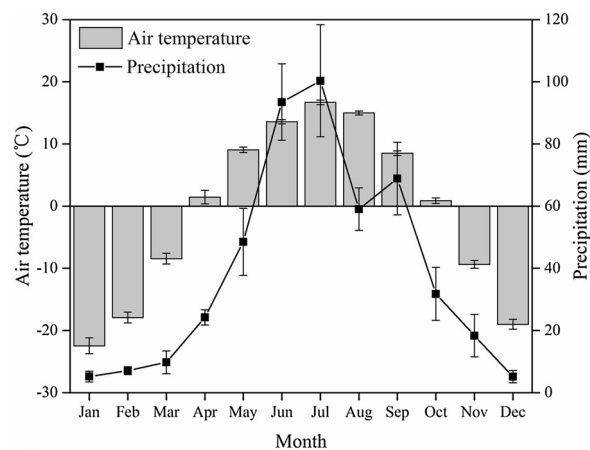


Fig. 1. Mean monthly air temperature (°C) and precipitation (mm) between 2010 and 2016. Data were obtained from the nearest climate station (the distance between the station and study plot is less than 3.5 km).

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