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Biotic community shifts explain the contrasting responses of microbial and root respiration to experimental soil acidification

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ABSTRACT

Soil respiration is comprised primarily of root and microbial respiration, and accounts for nearly half of the total CO_2 efflux from terrestrial ecosystems. Soil acidification resulting from acid deposition significantly affects soil respiration. Yet, the mechanisms that underlie the effects of acidification on soil respiration and its two components remain unclear. We collected data on sources of soil CO_2 efflux (microbial and root respiration), above- and belowground biotic communities, and soil properties in a 4-year field experiment with seven levels of acid in a semi-arid Inner Mongolian grassland. Here, we show that soil acidification has contrasting effects on root and microbial respiration in a typical steppe grassland. Soil acidification increases root respiration mainly by an increase in root biomass and a shift to plant species with greater specific root respiration rates. The shift of plant community from perennial bunchgrasses to perennial rhizome grasses was in turn regulated by the decreases in soil base cations and N status. In contrast, soil acidification suppresses microbial respiration by reducing total microbial biomass and enzymatic activities, which appear to result from increases in soil H^+ ions and decreases in soil base cations. Our results suggest that shifts in both plant and microbial communities dominate the responses of soil respiration and its components to soil acidification. These results also indicate that carbon cycling models concerned with future climate change should consider soil acidification as well as shifts in biotic communities.

1. Introduction

Soils across the globe have experienced or are experiencing enhanced acidification because of acid deposition (Zhao et al., 2009) and anthropogenic reactive N inputs (Galloway et al., 2008). Continuous soil acidification remains a major concern in developing countries of East Asia (Zhao et al., 2009; Yang et al., 2012). For instance, the pH of the surface soil layer dropped from 7.5 to 5.0 during decade of N enrichment in a semi-arid Inner Mongolia grassland (Lan and Bai, 2012). This reduction in soil pH may lead to declines in biodiversity, rates of biogeochemical cycles, and ecosystem functioning (Stevens et al., 2010; Chen et al., 2013a). Soil acidification has also been suggested to be an underlying mechanism that decreases CO_2 efflux and soil organic carbon turnover and therefore increases the storage of soil organic carbon in forest ecosystem (Kemmitt et al., 2006; Janssens et al., 2010; Oulehle et al., 2011). However, how soil acidification affects belowground carbon cycling via shifts in plant and soil microbial communities in terrestrial ecosystems is still unclear.

Soil respiration represents CO_2 release from soil as a consequence of soil microbial respiration associated with litter decomposition and root respiration of live roots and their symbionts (Kuzyakov, 2006). Soil respiration is one of the largest carbon effluxes between the atmosphere and terrestrial ecosystems and plays a vital role in regulating atmospheric CO_2 concentration and climate on Earth (Davidson et al., 2002). Accurate determination of both soil microbial respiration and root respiration is critically important to predict the net ecosystem carbon balance (Hanson et al., 2000; Kuzyakov, 2006). It is well documented that soil

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acidification decreased soil respiration (Lohm et al., 1984; Lettl and Hýsek, 1994; Vanhala et al., 1996; Evans et al., 2012) or microbial respiration (Bååth et al., 1980; Lettl and Hýsek, 1994; Oulehle et al., 2011) in forest ecosystems. However, few studies have directly assessed the effects of soil acidification on both the microbial and root respiration in semi-arid grasslands, and this lack of information and understanding hinders our capacity to predict the impact of future acidification on ecosystem carbon balance (Evans et al., 2012).

Because soil pH is a major factor regulating soil nitrogen transformations (Aciego Pietri and Brookes, 2008), the availability of base cations (Currie et al., 1999; Bowman et al., 2008), plant and microbial communities (Rousk et al., 2010; Stevens et al., 2010; Rousk et al., 2011), and soil respiration (Bååth et al., 1980; Oulehle et al., 2011; Evans et al., 2012). A number of reports have describe and summarize the pathways by which soil acidification changes soil microbial respiration and root respiration (Supporting information, Fig. S1). First, the high concentration of soil H^+ associated with acidification alters soil base cations often leads to changes in plant and microbial compositions and activities (Kochian, 1995; Rousk et al., 2010; Van Den Berg et al., 2005). second, high concentrations of H^+ can directly alter N availability for plants and microbes (Aciego Pietri and Brookes, 2008; Chen et al., 2013a; Van Den Berg et al., 2005). Finally, these soil acidification-induced changes in soil microbes and plants inevitably affect the microbial and root respiration (Phillips and Fahey, 2007; Janssens et al., 2010). In addition, previous studies concerning these pathways have largely focused on soils of acidic origin. However, the relative contributions of these pathways to soil acidification-induced changes in soil respiration and its components have not been carefully examined in soils of alkaline origin (Janssens et al., 2010).

Semi-arid Inner Mongolia grasslands, part of the Eurasian Steppe, are suffering rapid soil acidification (Yang et al., 2012) because the expansion of industrial, vehicular, and agricultural activity in this region has greatly increased energy consumption and SO_2 and NO_X emissions (Zhao et al., 2009). Here, we conducted a 4-yr field experiment in the semi-arid grassland to quantitatively evaluate the directions and magnitudes of diverse effects induced by soil acidification on soil respiration and its two components. Specifically, we attempt to address three research questions. First, how will soil acidification affect plant and soil microbial communities, soil cations, and N status? Second, how will soil acidification affect soil respiration and its components? Third, what will be the major pathways mediating soil acidification-induced changes in soil respiration and its components?

2. Materials and methods

2.1. Study site

This study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 43°38′N, 116°42′E) of the Chinese Academy of Sciences, which is located in the Xilin River Basin of Inner Mongolia, China, at an altitude of approximately 1200 m a.s.l.. The semi-arid continental climate is characterized by a mean annual (1982–2009) precipitation of 334 mm and a mean annual temperature of 0.9 °C. Precipitation mainly falls in the growing season (June–August), which is coincident with high temperatures. The site has a dark chestnut soil (Calcic Chernozem according to ISSS Working Group RB, 1998), with a loamy-sand texture. Before the experiment began, the plant community was dominated by *Leymus chinensis* (Trin.) Tzvel., a C_3 perennial rhizomatous grass that is widely distributed in the Eurasia steppe region.

2.2. Soil acidification experiment

The establishment of the soil acidification experiment was described by Chen et al. (2013a, 2015) and is briefly described here. In 2009, a 15-m × 20-m location with fairly uniform vegetation was designated within the permanent research plots of IMGERS. The location was divided into 35 plots; each plot was 2-m × 2-m and was surrounded by an iron sheet fence that extended 20 cm into the soil and 5 cm above the soil. Plots were also separated by 1-m walkways. Five replicate plots for each of seven treatments were established in a randomized block design. The treatments included seven rates of addition of a sulfuric acid solution: 0, 2.76, 5.52, 8.28, 11.04, 13.80, and 16.56 mol H^+ m^{-2}. Acid was added at these rates three times (September 2009, June 2010, and September 2010). At each time, each dose of 98% sulfuric acid was diluted in 80 L of well water. The low anthropogenic acid deposition (ca. 0.2 mol H^+ m^{-2} yr^{-1}) of the Inner Mongolia steppe have decreased the surface soil pH by 0.63 units during the last two decade (Yang et al., 2012). It is projected to have acid deposition up to 0.5 mol H^+ m^{-2} yr^{-1} in 2030 for this steppe (Zhao et al., 2009).

2.3. Trenching of subplots and measurement of soil CO_2 efflux

Trenching was used to estimate total soil CO_2 efflux and to separate its sources into soil microbial and root respiration (Kuzyakov, 2006). In this approach, soil CO_2 efflux is measured in plots with roots (both soil microbial and root respiration) and in plots without roots (only soil microbial respiration). In April 2010, one trenched subplot (0.5-m × 0.5-m) was established in each plot (2-m × 2-m). Each trenched subplot was prepared by making vertical cuts in the soil along the boundaries to 50 cm depth such that all roots crossing the boundaries of the trenched subplots were severed but not removed. Pieces of 0.3-cm-thick polyethylene board were then inserted into the vertical cuts to prevent roots from growing into the subplots. Roots in the trenched subplots were killed by weekly cutting of all the aboveground parts of plants in the subplots at the litter surface. In late August 2012 (about 2 years after trenching treatment), we did not find living or dead roots (0–50 cm depth) in any of the trenched subplots. We also found there was no difference in soil moisture and total microbial biomass (assessed by analysis of phospholipid fatty acids) between trenched and un-trenched subplots (Fig. S2). Therefore, after 2 years trenching treatment, using soil CO_2 efflux in the trenched subplots as an indicator of microbial respiration could be ideal in this semi-arid grassland ecosystem.

In June 2012, two steel, square collars (30-cm × 30-cm and 5 cm in height) were placed in each plot (2-m × 2-m), one in the trenched subplot and the other outside the trenched subplot. The steel collars were inserted into the soil to a depth of 3 cm for measurement of soil CO_2 efflux. To minimize the effect of acid neutralization on soil CO_2 efflux from carbonates in deep soil, we measured soil CO_2 efflux during growing season (June to August) of 2012 after about 2 years of trenching treatment. Soil CO_2 efflux was measured on three consecutive replicate days for each month (during 20th–29th) using three Li-Cor 840 infrared gas analyzers (IRGAs) (Li-Cor, Inc., Lincoln, Nebraska, USA), each of which was attached to a removable soil CO_2 efflux chamber (30-cm × 30-cm and 30 cm in height). All soil CO_2 efflux measurements were completed within one replicate day between 9:00 am and 11:00 am. Each measurement usually required 3 min.

2.4. Measurement of specific root respiration

To elucidate the effects of shifts in plant species on root respiration, in late August 2012 we measured the specific root