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Timing patterns of nitrogen application alter plant production and CO_2 efflux in an alpine meadow on the Tibetan Plateau, China

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ABSTRACT

Nitrogen (N) availability is an important factor that determines ecosystem productivity and respiration, especially in N-limited alpine ecosystems. However, the magnitude of this response depends on the timing and amounts of N input. Moreover, we have only a limited understanding of the potential effects of the timing of N fertilization on ecosystem carbon (C) and N processes, and activities of the soil microbes. A nitrogen fertilization experiment was conducted in an alpine meadow on the Tibetan Plateau to determine how plant productivity and ecosystem respiration (*RE*) respond to the timing and amount of N application. In this study, half of the N was added either in the early spring (ES), before the growing season, or in the late fall (LF), after the growing season. All treatments received the other half of the N in mid-July. Three N levels (10, 20, 40 kg N hm^{-2} yr^{-1}) were used for each of two N treatments, with no N addition used as a control. Plant aboveground biomass, ecosystem respiration (*RE*) and soil respiration (*RS*) were measured for the 2011 and 2012 growing seasons. The LF treatment enhanced ecosystem CO_2 efflux compared with the ES treatment at high N addition levels, resulting from an increase of soil dissolved organic C (DOC) and soil microbial activity. The ES treatment resulted in increased plant aboveground biomass when compared with LF during both growing seasons, although this increase accounted for little variation in ecosystem and soil respiration. Overall, the ES treatment is likely to increase the ecosystem C pool, while the LF treatment could accelerate ecosystem C cycling, especially for the high N treatment. Our results suggest that supplying N during the early stage of the growing season benefits both forage production and soil C sequestration in this alpine ecosystem.

Introduction

More than half of the grasslands that cover around 40% of the Earth's land surface have been converted to grazing ecosystems; a substantial portion of this grazing land has already been degraded (White et al. 2000; Guo et al. 2012). Degraded grasslands are often characterized by low species diversity, vegetation cover and productivity, and are dominated by less palatable plant species (Asner et al. 2004). This severely threatens the development of farming and animal husbandry, and degrades the environment in general. Nitrogen (N) fertilization, which has been widely employed as a management tool for increasing plant production and improving grassland forage quality, promotes the recovery of degraded grasslands (Schellberg et al. 1999; Conant et al. 2001; Bai et al. 2010). The timing of N application has been used in agricultural ecosystems to maximize crop yield (Weisz et al. 2001; Bly and Woodard 2003; Blackshaw et al. 2004; Randall and Vetsch 2005; Terry et al. 2012), improve grain quality (Johansson et al. 2004; Brown and Petrie 2006) and evaluate greenhouse gas emissions (Phillips et al. 2009; Drury et al. 2012). For example, an experiment using ^{15}N labeled N revealed that ryegrass absorbed much more fertilizer when N had been applied in late winter and early spring rather than in autumn, leading to higher seed yield (Cookson et al. 2001). Although N fertilization has been widely and effectively used in grassland management, the effects of the timing of N application on plant production and ecosystem CO_2 fluxes remains unclear. Moreover, the underlying mechanisms need to be discovered.

A lack of available N severely limits plant growth and soil microbial activity in a N-limited ecosystem (Bowman et al. 1993; Kaye and Hart 1997; Cao and Zhang 2001), and strong competition

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exists for available N between plants and soil microbes in these ecosystems (Jaeger et al. 1999; Song et al. 2007; Sorensen et al. 2008). Temporal differentiation in the use of limiting resources is an important mechanism that minimizes severe competition between plants and soil microbes (Jaeger et al. 1999; Kuzyakov and Xu 2013). For instance, microbial biomass declined dramatically in early spring, and this death of microbes made nutrients available for plant growth in an alpine meadow on Niwot Ridge, Colorado (Brooks et al. 1998; Ryan et al. 2000; Edwards et al. 2006). In contrast, plants wither in late fall, which provides a C source for soil microbes (Jaeger et al. 1999; Lipson et al. 1999). In addition, plants can modulate N availability by allocating photosynthetic carbon (C) to belowground pools, which provides a labile C source for soil microbes. Carbon input stimulates soil microbial activity and enhances mineralization of soil organic matter, which in turn provides available N for plant growth (Jaeger et al. 1999; Kuzyakov and Xu 2013). Plant growth and soil microbial activity respond differently to the timing of N application, which in turn probably results in differences in ecosystem and soil respiration. Here, we hypothesize that N application in early spring is beneficial to plant growth, which increases their investment of photosynthetic C to aboveground biomass. Meanwhile, N application in late autumn favors soil microbes but not plants. In the following growing season after N application in the previous autumn, plants increase their investment of photosynthetic C to belowground pools and this results in high levels of microbial activity and release of available N.

To our knowledge, no empirical research addresses the question of how exogenous N addition in fall and spring shapes the relationship between roots and microorganisms, and consequently affects plant productivity and ecosystem respiration later in the growing season. To address this question, an N addition experiment was conducted in an N-limited alpine meadow on the Tibetan Plateau starting in early July 2010. Nitrogen application time was manipulated in two types of treatment, i.e. early spring and late fall treatments, plus a control treatment. In the early spring treatment (hereafter designated as ES), a half dose of N was added in early spring in May before seedling establishment. In the late fall treatment (LF), a half dose of N was added in late September after plants had withered. For both of the treatments, another half does of N was added in mid-July, at the peak of the growing season. Three levels of N fertilization were experimentally applied each time N was added, with two treatments each having three N levels, for a total of seven treatment combinations including a control. During the growing seasons of 2011 and 2012, we measured ecosystem and soil respiration, aboveground biomass and soil microbial biomass C and N. The goal was to: (1) investigate the effects of N application time on patterns of ecosystem respiration and soil respiration during the growing season, and (2) analyze the relationships between aboveground biomass, soil microbial biomass C with the ecosystem and soil CO_2 fluxes under different N application rates and timing. Soil microbes can immobilize large amounts of N late in the growing season (Jaeger et al. 1999; Lipson et al. 2002). We hypothesized that (1) N addition in late fall enhances biomass and metabolic activity of soil microbes and would thus stimulate CO_2 fluxes in the following growing season, and (2) N addition in early spring provides a plentiful supply of available N for seedling establishment and thus would boost plant production during the entire growing season.

Materials and methods

Study site

An N fertilization experiment was carried out in an alpine meadow in Damxung County (91°05′ E, 30°51′ N, 4333 m a.s.l.) in the southwestern part of the Qinghai-Tibetan Plateau. The continental monsoon from the Pacific Ocean primarily controls the climate giving it long cold winters and short cool summers (Shi et al. 2006). The mean annual temperature is 1.3 °C, with a minimum of −10.4 °C in January and a maximum of 10.7 °C in July (Ma et al. 2010). Annual precipitation is 477 mm, about 85% of which falls from June to August. *Kobresia pygmaea* C. B. Clarke var. *pygmaea*, *Stipa capillacea* Keng and *Carex montis-everestii* Kükenth dominate the meadows, accompanied by other tussock sedges, grasses and herbs, all of which provide about 50% vegetation cover (Ma et al. 2010; Zong et al. 2012). The Mat-Gryic Cambisol soil corresponds to a Gelic Cambisol. Table 1 provides soil characteristics; N deposition in this region is about 7.0 kg N ha^{-1} yr^{-1} (Lü and Tian 2007).

Table 1
Soil characteristics at the study site, an alpine meadow in Damxung County, Tibet, China. Means ± S.E. were given (*N* = 4).

Soil characteristics	Means ± S.E.
pH	6.95 ± 0.75
Bulk density (g cm^{-3})	1.13 ± 0.17
Soil organic matter (%)	1.94 ± 1.03
Total soil N (%)	0.12 ± 0.07
Total soil P (%)	0.05 ± 0.02
Dissolved organic C (g kg^{-1})	0.015 ± 0.004
Inorganic N (g m^{-2})	1.99 ± 0.06

N fertilization experiment

A 50 m × 50 m area of alpine meadow with uniform vegetation cover was selected for the N fertilization experiment in early July 2010. Two treatments using N application timing were conducted with three levels of N addition for each treatment, i.e. early spring and late fall treatments, plus a control (no N addition) for a total of seven tests. In the ES treatment, half of the N was added in early spring in May before the seedling establishment. In the LF treatment, half of the N was added in late September after plants had withered. For both of these types of treatments, another half dose of N was added in mid-July, at the peak of the growing season. In each N application treatment, we set up the following N levels, 10, 20 and 40 kg N ha^{-1} yr^{-1}, coded as LN (low), MN (medium) and HN (high), respectively. No N addition was used for the control. The seven treatments were coded as ES-LN, ES-MN, ES-HN, LF-LN, LF-MN, LF-HN, and control. The random block design used in this experiment employed four blocks and seven 3 m × 3 m plots within each block with 2-m aisle as a buffering zone (Bowman et al. 2006; Jiang et al. 2013). The seven treatments were randomly arranged with seven plots in each block and each treatment had four replications. Nitrogen levels of 10, 20 and 40 kg N ha^{-1} yr^{-1}, roughly equal to 1.5, three, and six times the ambient N deposition in this area; the level of N deposition is projected to increase to 40 kg N ha^{-1} yr^{-1} by 2050 on the Qinghai-Tibetan Plateau (Galloway et al. 2004). This winter rangeland meadow is grazed in the non-growing season but not in growing season (May–September).

A NH_4NO_3 aqueous solution was sprayed in each plot as fertilizer as described above. Plots for control treatment received the same amount of water without N. Water added in each plot was equivalent to 6.0 mm precipitation, or approximately 1.2% of the annual precipitation, which is well within the magnitude of interannual variation (20.3% during 1981–2010).

Ecosystem respiration measurements

CO_2 efflux with aboveground plants measured in a dark chamber was considered to be ecosystem respiration (Jiang et al. 2013), and CO_2 efflux without aboveground plants was soil respiration. Before initiation of each measurement, a 20 cm diameter and 5 cm tall PVC collar was inserted into the soil at a depth of 3 cm in each plot for the