



Do rhizosphere priming effects enhance plant nitrogen uptake under elevated CO₂?



Ming Nie^{a,*}, Elise Pendall^b

^a Ministry of Education Key Lab for Biodiversity Science and Ecological Engineering, The Institute of Biodiversity Science, Fudan University, #2005 Songhu Road, Shanghai 200438, China

^b Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith NSW 2751, Australia

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ABSTRACT

Numerous studies suggest that rhizosphere priming can mediate decomposition of soil organic matter (SOM), but direct evidence of priming-induced soil SOM decomposition on plant N uptake under elevated CO₂ (eCO₂) is very rare. By using a continuous dual labelling technique with ¹³C-depleted CO₂ and ¹⁵N-enriched soil, we investigated priming of SOM decomposition and its relationship with plant N uptake of C4 and C3 grasses from a grassland ecosystem under eCO₂. We observed that eCO₂ induced increases in plant biomass, plant N uptake, rhizosphere priming, and total SOM decomposition in both grasses at an early plant life stage. Increased total SOM decomposition was positively related with plant N uptake by both C4 and C3 grasses under eCO₂. However, the C3 grass was more dependent on N acquired from rhizosphere priming of SOM than the C4 grass. Our findings highlight that plant N uptake could be enhanced under eCO₂ via accelerated SOM decomposition, and rhizosphere priming effects on SOM decomposition could play a more important role in N availability of the C3 grass in comparison with the C4 grass.

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1. Introduction

Plants play important roles in exchanging ecosystem-atmosphere C and regulating climate (Le Quéré et al., 2015). Elevated CO₂ (eCO₂) has been found to increase plant production and promote C allocation to plant rhizospheres, which could help to mitigate rising atmospheric CO₂ concentration (Luo et al., 2006; Nie et al., 2013a). As suggested by the progressive nitrogen limitation hypothesis, however, the positive response of plants to eCO₂ may decline over time as soil N becomes increasingly limiting under eCO₂ (Luo et al., 2004). As a result, sustained growth of plants under eCO₂ might require supply of exogenous N to meet the high N requirement of plants.

Recent studies suggest that interactions between plant roots and soil can increase SOM decomposition, thereby enhancing N mineralization from SOM under eCO₂ (Dijkstra et al., 2008; Phillips et al., 2011). This positive feedback of soil N cycling to eCO₂ is mainly explained by eCO₂-induced increase in plant rhizodeposition coupled with an increase in belowground decomposition activity (Kuzyakov 2002; Cheng et al., 2014). Therefore, priming of

SOM decomposition may considerably affect soil N supply and feedback to plant N availability (Hu et al., 2001). However, most experiments testing rhizosphere priming effects have focused primarily on soil respiration and the ecosystem C budget (Kuzyakov, 2002; Cheng et al., 2014). Our understanding of the effect of priming-induced change in SOM decomposition on plant N availability is limited, despite its importance for long-term ecosystem sustainability under climate change (Gardenas et al., 2011; Dijkstra et al., 2013; Cheng et al., 2014).

A growing body of evidence suggests that plant priming effects have positive effects on plant N availability in various ecosystems under eCO₂. For example, Phillips et al. (2011) found that an eCO₂-induced increase in root-derived C was positively correlated with microbial release of extracellular enzymes involved in N mineralization in a pine forest. Zak et al. (2011) applied an inorganic ¹⁵N dilution method to show a positive feedback of soil N cycling to increased plant productivity due to eCO₂ in northern forests. In addition, Carrillo et al. (2014) found that eCO₂-induced change in SOM decomposition can alter plant tissue N concentration and its stoichiometry in a grassland. However, direct evidence of effects of priming-mediated SOM decomposition on plant N uptake which largely determines N availability is very rare (Gardenas et al., 2011; Cheng et al., 2014). Efforts to disentangle the feedbacks of plant N

* Corresponding author.

E-mail address: mnie@fudan.edu.cn (M. Nie).

uptake to eCO₂ would greatly improve our understanding of the close linkage between rhizosphere priming effects and plant N availability under climate change.

Grassland ecosystems, covering 40% of the Earth's land surface, support many productive agricultural and natural areas, and provide habitat and food for livestock and humans (Morgan et al., 2008; Gibson, 2009). In particular, the continued ability of grasslands to provide sufficient nutrients to livestock as climate changes is uncertain (Morgan et al., 2008). For example, in a North American grassland, eCO₂ altered soil N dynamics and above- and below-ground stoichiometry, leading to changes in grass performance (Dijkstra et al., 2010; Carrillo et al., 2014). However, C3 and C4 grasses have contrasting responses to eCO₂ in terms of their productivity, nutrient use efficiency, and digestibility of herbage available to grazing livestock (Morgan et al., 2004; Soussana and Luescher, 2007; Lattanzi et al., 2010). Therefore, understanding of eCO₂-induced shifts in N uptake of C3 and C4 grasses should throw a new light on rangeland use and management under climate change.

By using a novel dual-isotope continuous labelling technique with ¹³C-depleted CO₂ and ¹⁵N-enriched soil, we conducted a laboratory microcosm experiment with two common North American grasses (C4 *Bouteloua gracilis* and C3 *Hesperostipa comata*), to test whether priming-mediated SOM decomposition under eCO₂ can affect plant N uptake and whether C3 and C4 grasses have different responses of rhizosphere priming to eCO₂.

2. Materials and methods

2.1. Experimental setup

The C4 *B. gracilis* and C3 *H. comata* we selected in this experiment are widespread grasses of the central and southern Great Plains, USA, and are utilized by wildlife as well as domestic cattle and sheep (Lecain et al., 2000; Derner et al., 2006). The soil we used was enriched in ¹⁵N (0.5 g m⁻² ¹⁵N applied as 99.9 atom% ¹⁵N ammonium nitrate in April 1997) from a prior experiment in a shortgrass prairie at the USDA-ARS Central Plains Experimental Range, Colorado, USA (Dijkstra et al., 2008). About 15 years after ¹⁵N was added (and 9 years after the completion of the original experiment), soil was collected from the top 15-cm and sieved (mesh size 2 mm) to remove roots and homogenize the soil. The soil is a Remmit fine sandy loam (Ustollic Camborthid) with 0.8% organic C in the top 15 cm. We leached the soil with DI water in large buckets with small waterspouts to decrease nutrient availability. After that, the soil was air-dried and passed through a 2-mm sieve to further remove plant residues, soil fauna and other coarse materials, and then homogenized to attain a composite sample. Before our experiment, the initial soil inorganic N (NH₄⁺ + NO₃⁻) content was determined on 2-M KCl extracts measured on an Alpkem Flow Solution IV Automated wet chemistry system. Soil inorganic δ¹⁵N was determined using the diffusion method with (precombusted) GF/D glass fiber filter

papers (Brooks et al., 1989). All samples were analysed for C, N, ¹³C and ¹⁵N on a Thermo Finnigan Delta Plus XP mass spectrometer with a Costech 4010 elemental analyser inlet (or gas bench for respiration samples) (Thermo Finnigan, Bremen, Germany). Soil organic N was estimated as the difference between total and inorganic N, and soil organic δ¹⁵N was determined by mass balance. The initial soil inorganic N (NH₄⁺ + NO₃⁻) and organic N concentrations were 0.14 ± 0.002 and 0.41 ± 0.03 mg g⁻¹, respectively (n = 8; t-statistic < 0.0001). The proportion of inorganic N is somewhat higher than in a similar undisturbed soil (Carrillo et al., 2012), possibly owing to mineralization during long-term storage. The δ¹⁵N values of inorganic and organic N of initial soil were 445.7 ± 12.5 and 587.5 ± 10.8‰, respectively (n = 8; t-statistic < 0.0001). Therefore, we took advantage of the distinct δ¹⁵N values to estimate the relative sources of plant N (N from the original inorganic pool vs. N mineralized from SOM).

The experiment was carried out at the University of Wyoming, USA. After emergence of the second leaves on moist filter paper in glass Petri dishes, two seedlings of each grass were transferred to a pot filled with 600 g of soil (dry weight). We used a total of 15 pots (two grasses × five replicates + five unplanted pots) under each CO₂ treatment (ambient CO₂ and elevated CO₂). During the first week of the experiment, all pots (including unplanted plots) were rewetted to 25% gravimetric soil moisture content to enhance seedling growth. After that, the gravimetric water content in each pot was maintained at 15% (approximately 50% water holding capacity) using DI water, with no fertilizer additions. To simulate field conditions during the growing season, the climate-controlled chambers (Percival PGC-9/2, Percival Scientific, Perry, IN, USA) were set to a 14 h daytime period with light intensity of 700 μmol m⁻² s⁻¹. The daytime and night-time temperatures were 25 °C and 18 °C, respectively. We used a Li-250 light meter (LI-COR, Lincoln, NE, USA) and Telaire 7001 m (Telaire, Goleta, CA, USA) to ascertain the reliability of light intensities and temperatures of the chambers every day. To achieve continuous ¹³C-labelling of plant tissues, the chambers were modified to receive an influx of ¹³C-depleted CO₂ (δ¹³C = -33.1‰) combined with an external air input which had been scrubbed by a soda lime column (Cheng and Dijkstra, 2007). The CO₂ concentrations inside the chambers were calibrated by infrared CO₂ sensors (GMM220, Vaisala, Helsinki, Finland) and continuously monitored by Telaire 7001 m (ambient CO₂ concentration: 371.9 ± 2.1 ppm (mean ± se)); elevated CO₂ concentration: 702.9 ± 8.7 ppm. The elevated CO₂ concentration was chosen because it is a scenario of climate change without emission control or reasonable management by the end of this century ("business as usual," IPCC, 2007). The δ¹³C values of CO₂ inside chambers were continuously monitored by a Picarro G2101i ¹³CO₂ analyzer (Picarro, Sunnyvale, CA, USA). The chamber systems we used were shown to have high reliability and stability during comparative studies of plant genetics and eco-physiology (Haselhorst et al., 2011; Nie et al., 2015). Throughout the experiment, the δ¹³C values of CO₂ were stable (ambient CO₂: -25.0 ± 0.2‰; elevated CO₂: -24.9 ± 0.2‰), and there was no significant daily difference in the δ¹³C values of experimental chambers.

Table 1

δ¹³C (‰) values of plant tissue, CO₂ respired from roots grown in soil organic matter-free sand, soil organic matter without plants (n = 6 at ambient and elevated CO₂, note that slightly depleted δ¹³C value respired from unplanted pots at eCO₂ resulted from diffusion of more depleted CO₂ into the soil), and the soil respiration from planted pots. The δ¹³C value of SOM was -20.4 ± 0.6‰ and inorganic C was not present.

Plant functional type	CO ₂	Plant tissue δ ¹³ C	se	Root CO ₂ δ ¹³ C	se	SOM CO ₂ δ ¹³ C	se	Soil Resp CO ₂ δ ¹³ C	se
C3	aCO ₂	-44.52	0.82	-47.8	0.68	-20.2	1.76	-26.4	0.34
C4	aCO ₂	-30.48	0.11	-36.1	0.82	-20.2	1.76	-23	0.68
C3	eCO ₂	-48.48	0.61	-50.4	0.6	-22.4	0.49	-27.6	1.46
C4	eCO ₂	-36.16	0.35	-41.9	0.44	-22.4	0.49	-26.3	0.59

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