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Rhizodeposition-induced decomposition increases N availability to wild and cultivated wheat genotypes under elevated CO_2

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ABSTRACT

Elevated CO_2 may increase nutrient availability in the rhizosphere by stimulating N release from recalcitrant soil organic matter (SOM) pools through enhanced rhizodeposition. We aimed to elucidate how CO_2-induced increases in rhizodeposition affect N release from recalcitrant SOM, and how wild *versus* cultivated genotypes of wheat mediated differential responses in soil N cycling under elevated CO_2. To quantify root-derived soil carbon (C) input and release of N from stable SOM pools, plants were grown for 1 month in microcosms, exposed to ^{13}C labeling at ambient (392 μmol mol^{-1}) and elevated (792 μmol mol^{-1}) CO_2 concentrations, in soil containing ^{15}N predominantly incorporated into recalcitrant SOM pools. Decomposition of stable soil C increased by 43%, root-derived soil C increased by 59%, and microbial-^{13}C was enhanced by 50% under elevated compared to ambient CO_2. Concurrently, plant ^{15}N uptake increased (+7%) under elevated CO_2 while ^{15}N contents in the microbial biomass and mineral N pool decreased. Wild genotypes allocated more C to their roots, while cultivated genotypes allocated more C to their shoots under ambient and elevated CO_2. This led to increased stable C decomposition, but not to increased N acquisition for the wild genotypes. Data suggest that increased rhizodeposition under elevated CO_2 can stimulate mineralization of N from recalcitrant SOM pools and that contrasting C allocation patterns cannot fully explain plant mediated differential responses in soil N cycling to elevated CO_2.

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1. Introduction

The rise in atmospheric CO_2 concentrations stimulates photosynthesis in most plants, leading to an increase in plant production by approximately 20% (Ainsworth and Long, 2005; de Graaff et al., 2006). The stimulation of plant production should enhance soil C input, which in turn may increase soil C sequestration, thereby counterbalancing the rise in atmospheric CO_2 (Gifford, 1994). However, the extent to which elevated CO_2 stimulates soil C storage has proven hard to predict, because it is unclear whether the plant growth response to elevated CO_2 can be sustained in the long-term (de Graaff et al., 2006; Reich et al., 2006; Van Groenigen et al., 2006).

Due to increased growth rates under elevated CO_2, plant N demands increase (Luo et al., 2006). In addition, the greater soil C inputs associated with enhanced plant production lead to enhanced soil microbial N demands (de Graaff et al., 2006, 2007). Consequently more N is retained in both plant tissues and soil pools under elevated CO_2, which may result in progressive N limitation (PNL; Luo et al., 2006). The PNL concept posits that in unfertilized ecosystems, N availability progressively decreases under elevated CO_2, because N retention in soil and vegetation is stimulated. This ultimately leads to a decline in plant growth and a concomitant decrease in soil C sequestration (Luo et al., 2004; de Graaff et al., 2006).

In a synthesis of results on plant growth and soil nutrient cycling under elevated CO_2 in long-term field experiments, however, we showed that under low N availability elevated CO_2 still stimulated plant production by ~10%, even though data suggested that PNL had developed in these ecosystems (de Graaff et al., 2006). In addition, plant production and soil C contents continue to increase under elevated CO_2 in the Duke FACE experiment, despite there being no evidence of increased net N mineralization or nutrient-use efficiency (Finzi et al., 2001; Johnson, 2006; Finzi et al., 2006). This suggests that an unexplained internal source of N can alleviate PNL in unfertilized ecosystems exposed to long-term elevated CO_2.

Hungate and Chapin (1995) postulated that if mineral nutrients are scarce in soils, microbes utilize rhizodeposits as a carbon-source, and decompose more SOM in order to acquire nutrients. More N is then moved into the active N pool in the soil where,

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eventually, they may be made available to plants. This process is referred to as priming, which is defined as the stimulation of soil organic matter (SOM) decomposition caused by the addition of labile substrates (Jenkinson et al., 1985; Dalenberg and Jager, 1989). Since elevated CO_2 frequently stimulates rhizodeposition – an important contributor to labile soil C inputs – (Billes et al., 1993; Cotrufo and Gorissen, 1997) and increases decomposition of SOM (de Graaff et al., 2006; Carney et al., 2007), priming of more recalcitrant SOM may be the mechanism partially responsible for alleviating PNL under elevated CO_2 in low N environments. However, increased root-derived soil C input under elevated CO_2 and increased rates of N mineralization due to decomposition of recalcitrant SOM have never been directly linked.

Accumulation of SOC requires a positive imbalance between inputs to and outputs from SOM stocks (Jastrow et al., 2007). Thus, enhanced soil C sequestration under elevated CO_2 can only occur if the rate of soil C decomposition lags behind the CO_2-induced increase in soil C input (Raich and Schlesinger, 1992). Several authors have reported a decrease in soil C as a result of increased native SOM decomposition (i.e. priming) under elevated CO_2 (Cardon et al., 2001; Pendall et al., 2003; Hoosbeek et al., 2004). If rhizodeposition-induced decomposition of recalcitrant SOM actually is an important mechanism that increases N availability to plants under elevated CO_2, its concurrent effect on native C mineralization has to be measured to elucidate its potential impact on net soil C sequestration. Namely, the question ultimately is whether N mineralization induced by rhizodeposition promotes plant growth and a concomitant input of soil C sufficiently to counterbalance the increase in C decomposition.

Plant species differ in mediating changes in soil N cycling in response to global change, but these differences have not been predictable from a knowledge of species' biology (Hungate et al., 1996). To predict plant species' impacts on soil nutrient cycling under elevated CO_2, they have been classified into broad groups relying on a broad suite of related plant traits that may generalize how they respond to environmental changes (Eviner and Chapin, 2003). However, such classifications have yet provided limited understanding of how plant species affect plant and microbial N acquisition under elevated CO_2 (Hungate et al., 1996; Zak et al., 2000). Using plants with genetic similarity, but contrasting C-allocation patterns may provide another approach for elucidating why plants vary in mediating soil N availability under elevated CO_2. Namely, C allocation to roots is a key plant trait for explaining differential responses in N cycling as it affects both rhizodeposition and nutrient uptake, and genetic similarity minimizes the number of other plant traits that can influence a plants' response to climate change.

With this study, we aimed at determining how elevated CO_2 affects rhizodeposition of C and how this feeds back to N release from recalcitrant SOM under both wild (*Triticum turgidum* subsp. *diccocoides*) and cultivated genotypes (*Triticum turgidum* subsp. *durum*) of wheat. The wild and cultivated genotypes of wheat are expected to have contrasting C allocation patterns, since modern agriculture developed cultivars that function well in favorable soil environments but lack traits necessary for growth in low-resource environments (Rengel and Marschner, 2005). Thus, selection for increased yield under high-input agricultural systems produced cultivars with smaller root systems (Chapin et al., 1989; Siddique et al., 1990; Jackson, 1995) and greater C partitioning to shoots (Gifford et al., 1984).

We hypothesized that elevated CO_2 increases the inputs of root-derived C thereby stimulating decomposition of recalcitrant SOM and concurrently increasing soil N availability and plant N uptake. In addition, we hypothesized that greater C allocation to the roots of the wild wheat genotypes results in greater rhizodeposition-induced N mineralization from stable SOM pools under elevated CO_2. To quantify root-derived soil carbon (C) input and release of N from stable SOM pools, plants were grown for 1 month in soil microcosms containing ^{15}N predominantly present in recalcitrant SOM pools while being exposed to ^{13}C labeling at ambient (392 μmol mol^{-1}) and elevated (792 μmol mol^{-1}) CO_2 concentrations.

2. Materials and methods

2.1. Pre-treatment of the soil

The soil used for the experiment was derived from the Swiss Free Air Carbon dioxide Experiment (FACE) in March of 2003. This soil had received ^{15}N fertilization treatments for 10 consecutive years, which has lead to incorporation of a significant amount of the ^{15}N into the more stable SOM pools (de Graaff et al., 2008). The samples were taken to a depth of 25 cm from both ambient and elevated CO_2 field plots under *L. perenne* that had received N fertilization (140 kg N ha^{-1} y^{-1}), with an atom% ^{15}N excess of 0.3841 in 1995 and 1.0602 from 1996 to 2003. No differences in total N, C or fertilizer derived N were observed between the ambient and elevated CO_2 treatments after 10 years (Van Kessel et al., 2006).

The soil of the ambient and elevated CO_2 treatments was composited, air dried and sieved to 2 mm. Next, sterile sand (30% to dry weight) was added, to increase its volume and to facilitate root extraction at termination of the experiment. Water-holding capacity of the soils was determined by calculating the difference in weight of soils at saturation point and oven-dry weight (100 °C). Water was added to obtain 60% of water-holding capacity. Subsequently, the soils were incubated at 30 °C for 145 days in ten plastic filters (Nalgene Filter model 7111; Becton Dickinson Labware, Lincoln Park, NJ, USA) at 35 °C (Kaye et al., 2002). A glass fiber filter (Whatman GF/A, Whatman Inc., Ann Arbor, MI, USA), and an "extra thick" glass fiber prefilter (Gelman Sciences, Ann Arbor, MI, USA) were used to replace the filter originally in the filter unit.

To deplete the soil from labile N and ^{15}N, the soils were leached at days: 1, 8, 25, 43, 58, 86, 100, 120 and 145, with a leaching solution containing all essential nutrients except for N (Stanford and Smith, 1972; Nadelhoffer, 1990; Kaye et al., 2002). At each leaching event, 1 L of the N-free leaching solution was added to the top of the filter, allowed to equilibrate with the soil for 45 min. and then drawn through the filter with a weak vacuum until all the leachate was collected (Kaye et al., 2002). Leaching was terminated when the rate of labile ^{15}N efflux from the soil was near zero ($6.8 * 10^{-5}$ μg^{-1} g^{-1} day^{-1}) for the last three leaching events. The soil was removed from the filters and composited, after which it was transferred to the containers. Three pots with 25 g of control soil were placed in the chambers in closed specimen cups in order to confirm that ^{15}N mineralization was insignificant in the absence of plants.

2.2. Experimental design and growing conditions

Plants were exposed to two (392 and 792 μmol mol^{-1}) atmospheric CO_2 concentrations in two controlled environment chambers for 32 days. The chambers were located in the Greenhouse Facility at UC-Davis. They were constructed from clear Plexiglas, had a volume of 2000 L and were entirely sealed for the duration of the experiment, to allow for continuous labeling with $^{13}CO_2$-gas. Carbon dioxide concentrations were measured with an IRGA (model 820-LC, LI-COR, Lincoln, NE, USA) in a closed air circulating system. The IRGA was connected to an automatic burette, which was pulsed if the IRGA-reading fell below the threshold