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Carbon allocation in grassland communities under drought stress followed by ^{14}C pulse labeling

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ABSTRACT

Although extreme climatic events such as drought have important consequences for belowground carbon (C) cycling, their impact on the plant-soil system of mixed plant communities is poorly understood. Our objective was to study the effect of drought on C allocation and rhizosphere-mediated CO_2 fluxes under three plant species: *Lolium perenne*, *Festuca arundinacea* and *Medicago sativa* grown in monocultures or mixture. The conceptual approach included $^{14}CO_2$ pulse labeling of plants grown under drought and optimum water conditions in order to be able to follow above- and belowground C allocation. After ^{14}C pulse labeling, we traced ^{14}C allocation to shoots and roots, soil and rhizospheric CO_2, dissolved organic carbon (DOC) and microbial biomass.

Drought and plant community composition significantly affected assimilate allocation in the plant-soil system. Drought conditions changed the source sink relationship of monocultures, which transferred a relatively larger portion of assimilates to their roots compared to water sufficient plants. In contrast, plant mixture showed an increase in ^{14}C allocation to shoots when exposed to drought.

Under drought stress, root respiration was reduced for all monocultures except under the legume species. Microbial respiration remained similar in all cases showing that microbial activity was less affected by drought than root activity. This may be explained by strongly increased assimilate allocation to easily available exudates or rhizodeposits under drought. In conclusion, plant community composition may modify the impact of climatic changes on carbon allocation and belowground carbon fluxes. The presence of legume species attenuates drought effects on rhizosphere processes.

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1. Introduction

The influence of climate on the plant soil system is complex and the interactions are poorly understood. Short-term events may have much stronger impacts on pools and/or fluxes in ecosystems compared with long-term trends (Kuzyakov and Gavrichkova, 2010). Climatic modification may concern mostly plant–soil interactions due to its impact on carbon (C) allocation and root activity (Cheng and Kuzyakov, 2005).

Roots of higher plants are key functional components of belowground systems and the zone of soil around roots – rhizosphere – plays an important role in the soil C cycle. The rhizosphere has been considered as one of the key fine scale components in global carbon cycle research (Coleman et al., 1992). In the rhizosphere, soil organic matter (SOM) decomposition and mineralization are controlled by root litter inputs, but also through root–microbial interactions i.e. rhizosphere effects influencing (1) nutrient availability, (2) physical and chemical environment, (3) availability of organic substrates and (4) priming (Hinsinger et al., 2009; Cheng and Kuzyakov, 2005). Moisture conditions may significantly alter rhizosphere effects on decomposition. While root exudation was increased following water limitation, priming effects were found to be reduced (Dijkstra and Cheng, 2007). In agricultural systems, as consequence of agricultural monocultures, most studies on rhizosphere effects have been limited to plants grown individually, although species mixtures were found to respond differently to environmental stress such as drought. For example, at low water levels, rhizosphere effects of plant species grown in mixture were found to reduce SOM decomposition and plant N uptake compared to monocultures (Dijkstra et al., 2010). Potential activity of enzymes involved in the C cycle tended to increase in soil under plant mixtures, while they were unchanged or decreased under monocultures (Sanaullah et al., 2011).

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CO_2 efflux from soil constitutes a major component of the global carbon cycle and is likely to be altered by climate change. The evolution of CO_2 is a sensitive indicator of crop residue decomposition, SOM turnover and ecosystem disturbance (Paul et al., 1999). Summer drought was found to decrease soil CO_2 efflux and to alter its sources (Joos et al., 2010). Under wheat plants, the amount of assimilates lost as CO_2 respired from soil was found to be enhanced following water limitations (Palta and Gregory, 1997). Soil CO_2 efflux originating from assimilates is the result of two distinct processes controlling rhizosphere respiration: (1) root respiration and (2) microbial respiration from the metabolism of rhizodeposits (Andrews et al., 1999; Cheng and Kuzyakov, 2005). These distinctions are important for interpreting the sources of CO_2 and the fate of carbon within soils and ecosystems. At present, we lack a detailed understanding of the rhizosphere processes of single species as well as plant mixtures that occur in response to drought stress.

Therefore, in this study, we tested the effect of drought on belowground C allocations and rhizosphere-mediated soil respiration in grassland soil under grassland species grown in monoculture or mixture. Our conceptual approach included pulse labeling of plants with $^{14}CO_2$ and partitioning of the labeled carbon in plant and soil carbon dioxide fluxes. The aim of this study was to evaluate the changes of rhizosphere processes occurring in response to drought.

2. Materials and methods

2.1. Soil

The soil samples were taken from the top 20 cm of a loamy Cambisol under flat temporary grassland established since more than 50 years. The site is part of the long-term observatory for environmental research (ORE-ACBB) of INRA, France. It is located near Lusignan in the south-west of France (46°25′12,91″ N; 0°07′29,35″ E). The soil is carbonate-free and has the following characteristics: pH 6.4, organic C (C) 1.4%, nitrogen (N) 0.16%, sand 11%, clay 17%, silt 72% (Chabbi et al., 2009). After sampling the soil was air-dried and passed through a 5 mm sieve.

2.2. Experimental design and growth conditions

In order to study interactive effects of plant community composition and water availability on belowground C allocation and root-derived CO_2, a two factorial experiment was established. We used seeds of *Lolium perenne*, *Festuca arundinacea* and *Medicago sativa*, which were grown for five days in petri dishes. Thereafter, the plants were planted in microcosms containing 500 g of soil. The experimental setup included planting (i) as 6 plants of the same species (monocultures) or (ii) as 2 × 2 × 2 plants (mixture) of each species. To assure 3 replicates for each treatment combination (individual plant species, mixture or unplanted soil and two different water levels), in total 24 microcosms with planted soil and 6 microcosms with unplanted soil (control) were incubated for 70 days. The plants were grown at 26–28 °C day and 22–23 °C night temperature with a day-length of 14 h and light intensity of approximately 400 μmol m^{-2} s^{-1} at the top of canopy.

During the first 30 days of plant growth, optimum water level (70% of the available field capacity) was maintained for all plants. After one month of plant development, the soils were adjusted to two water levels: (1) optimum conditions (70% of the field capacity) and (2) drought conditions (30% of the field capacity) for 40 days. The unplanted soil control was maintained for both moisture levels.

2.3. Plant ^{14}C labeling

After 40 days of growth under different moisture conditions, carbon allocation patterns were determined using ^{14}C labeling. The detailed procedure for plant ^{14}C labeling is given in previous studies (Kuzyakov and Siniakina, 2001; Kuzyakov et al., 1999). Briefly, the labeling apparatus consisted of two compartments. The lower compartment was used for soil and plant roots and the upper compartment for the shoots and $^{14}CO_2$ generation. One day before labeling, each hole in the lid of the lower compartment containing one plant was sealed with silicon paste. Three hours before labeling, pots were flushed with CO_2-free air to remove CO_2 evolved prior to labeling. Each species was labeled separately. 1480 kBq of ^{14}C as $Na_2^{14}CO_3$ solution was put in a test tube in the upper compartment of the chamber and the chamber was then closed. Three ml of 5 M H_2SO_4 was added to the $Na_2^{14}CO_3$ solution in the test tube through a Teflon tube. This allowed the complete evolution of $^{14}CO_2$ into the chamber atmosphere. Assimilation took place within 3 h after the pulsing of $^{14}CO_2$. After the labeling period of 3 h, trapping of CO_2 from the upper compartment was started to remove the remaining unassimilated $^{14}CO_2$ by pumping the air through 15 ml of 1 M NaOH solution. Thereafter, the top of the chamber was removed.

2.4. Carbon mineralization and analysis of plant material, soil as well as microbial biomass

Throughout the experiment, which lasted 120 h, CO_2 evolved from the soil–root compartment was trapped in 15 ml of 1 M NaOH solution by continuous pumping (100 cm^3 min^{-1}) with a membrane pump. The CO_2 trap was changed every 6 h starting immediately after the labeling. Total content of CO_2–C collected in the NaOH solution was measured by titration with 0.01 M HCl against phenolphthalein, after addition of 2 M $BaCl_2$ solution (Kuzyakov and Cheng, 2001).

Five days after the labeling, the soil–root chamber was destructively sampled. Shoot material was separated from roots and roots were separated from soil and washed by dipping them into water. Shoots, roots and soil were dried at 60 °C, homogenized and pulverized in a ballmill (Retsch) prior to further analysis. For total C analysis the plant shoots, roots and soil were combusted and the CO_2 evolved trapped in NaOH and the CO_2–C measured as described above.

A subsample of fresh soil was used for microbial biomass determination by $CHCl_3$ fumigation-extraction (Vance et al., 1987). After fumigation, 10 g of the fumigated and an unfumigated sample were extracted with 40 ml of 0.05 M K_2SO_4 solution. Briefly, the mixture was shaken for 30 min at 300 rev min^{-1}. Thereafter it was centrifuged (8000 × G, 10 min), the supernatant recovered by filtration and analyzed for TOC and ^{14}C. The microbial biomass C and ^{14}C were calculated as the difference between fumigated and non-fumigated soil samples after correcting for extraction efficiency ($k = 0.45$) (Vance et al., 1987).

Dissolved organic carbon contents were determined as the sum of C in the K_2SO_4 extract of unfumigated samples and C in water remaining after root washing. The ^{14}C activity of both fractions were accepted as ^{14}C in DOC (Kuzyakov and Domanski, 2002). The total C and N contents in water after root washing and in K_2SO_4 extracts were determined with Multi C/N 2100 (Analytik Jena, Germany).

2.5. ^{14}C activity measurements

^{14}C activities of DOC and CO_2 in NaOH from respiration as well as of bulk plant shoot, roots and soil were measured by mixing 1 ml of this solution with 2 ml of scintillation cocktail (Rotiszint EcoPlus, Carl

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