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Short Communication

Zea mays rhizosphere respiration, but not soil organic matter decomposition was stable across a temperature gradient

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ABSTRACT

In a greenhouse experiment, we grew maize plants at different densities. We added fertilizer to half of the pots and created a temperature gradient. After 10 weeks of plant growth, we measured soil CO_2 efflux (SCE) and determined rhizosphere respiration (R_{rhizo}) and the decomposition rate of soil organic matter (R_{SOM}) using the different $\delta^{13}C$ of the C_3 soil and C_4 plants. Whereas R_{rhizo} remained stable across the temperature gradient, R_{SOM} significantly increased with growth temperature. Neither plant density, nor the fertilizer treatment affected the relation between R_{rhizo} or R_{SOM} and growth temperature. Although R_{rhizo} might still increase with temperature in the short term, long term exposure to higher temperatures revealed full thermal acclimation of R_{rhizo}, but not of R_{SOM}.

It was previously suggested that rhizosphere respiration (R_{rhizo}) and soil organic matter decomposition (R_{SOM}) respond differently to temperature (Boone et al., 1998; Hartley et al., 2007a; Moyano et al., 2007). Boone et al. (1998) found a higher temperature sensitivity of R_{rhizo} as compared to R_{SOM}, but this temperature response of R_{rhizo} was strongly affected by seasonal variations in plant phenology and photosynthetic substrate supply. Other studies suggested lower temperature sensitivity for R_{rhizo} than for R_{SOM} (Bhupinderpal-Singh et al., 2003; Hartley et al., 2007a; Moyano et al., 2007), whereas Baath and Wallander (2003) and Schindlbacher et al. (2009) found similar temperature effects on R_{SOM} and R_{rhizo}. More research is obviously needed to verify that models need to apply different temperature responses for R_{SOM} and R_{rhizo}. In particular, the confounding effects of seasonal variations in, e.g., root growth should be excluded, as they can substantially influence apparent temperature responses (Curiel Yuste et al., 2004; Davidson et al., 2006). Also studies using trenching or girdling as partitioning method face important shortcomings, decreasing the reliability of their results (Kuzyakov, 2006). In the current study, we avoided seasonal variations and used the ^{13}C natural abundance technique (growing C_4 plants in a soil with C_3 plant-derived organic matter) to determine effects of growth temperature on R_{rhizo} and R_{SOM}. In addition, we tested for effects of plant density and fertilizer addition.

We grew *Zea mays* in 40 pots (20 l) containing a homogenized soil mixture (20% silt, 80% sand; 5% organic matter was added as plant-derived compost; bulk density was 1.3 g cm^{-3}). To obtain a gradient in root mass and activity, which would be detectable in R_{rhizo}, we planted one, three, or six plants per pot. Furthermore, two nutrient treatments were created by adding 12 g slow-release fertilizer (Osmocote; N/P/K/Mg: 15/4.8/10.8/1.2; trace elements: B, Cu, Fe, Mn, Mo, Zn; Scotts Australia Pty Ltd) to half of the pots. All pots were irrigated roughly every 48 h (water was added until it leached out at the bottom) and always in the evening prior to a measurement campaign. We placed all pots randomly in a greenhouse, where plants were grown at roughly 25 °C during daytime and 15 °C during night time. Because the experiment was conducted in winter with cooler ambient temperatures, the greenhouse was permanently heated. The heater was located at one end of the greenhouse, thus creating a temperature gradient with soil temperatures in the afternoon around 28 °C near the heater and below 20 °C at the other end of the greenhouse (Supplementary Information 1). Thus, pots growing near the heater were exposed to higher temperatures for the entire three-month duration of the experiment.

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The experiment was ended when the first plants started to initiate flowers (10 weeks after the start of the experiment). During the last two days of the experiment we measured the soil CO_2 efflux (SCE), using a closed dynamic infrared gas analysis system, consisting of a home-made soil chamber (10.2 cm diameter, 12.3 cm height) and a Li-6200 (LICOR Inc, Nebraska, USA). Attached in parallel to the system was a two-litre stainless steel collector to collect air samples for isotopic analysis. The airflow through the system was diverted through this collector when taking air samples for isotope analysis. During flux measurements, the collector was always by-passed. The soil chamber was equipped with a pressure equilibration tube (0.76 mm inner diameter, 0.7 m long) to mitigate potential pressure gradients. Diffusion of CO_2 through this tube was negligible because during the measurements the CO_2 concentration difference between the chamber headspace and the atmosphere went from −25 to +25 ppm. Inside the soil chamber, air was mixed with a horizontally blowing fan mounted on top of the chamber. Fan speed was reduced so that air speed near the soil surface was $<0.1\ m\ s^{-1}$.

All measurements were made within two consecutive days and in a predetermined random order. Furthermore, each pot was measured twice when the flux rates differed less than 5%. In case of larger differences, we made two extra measurements (immediately after the first two measurements) and used the mean of the four fluxes as the final value. Estimates of R_{SOM} and R_{rhizo} were based on the difference in $\delta^{13}C$ between the C_3 plant-derived organic matter ($\delta^{13}C$ around −25‰) and the C_4 maize root-derived carbon (circa −14‰). We calculated R_{SOM} and R_{rhizo} with a basic mixing equation (Balesdent et al., 1987):

$$R_{SOM} = SCE^{*}(\delta^{13}C_{SCE} - \delta^{13}C_{Rrhizo})/(\delta^{13}C_{RSOM} - \delta^{13}C_{Rrhizo}), \quad (1)$$

where SCE is the measured soil CO_2 efflux, $\delta^{13}C_{SCE}$ is the isotopic signature of the soil-respired CO_2 and $\delta^{13}C_{RSOM}$ and $\delta^{13}C_{Rrhizo}$ are the isotopic signatures of the soil carbon-derived CO_2 and the root carbon-derived CO_2, respectively. Rhizosphere respiration was estimated as the difference between SCE and R_{SOM}. Detailed information on the partitioning method is given in Supplementary Information 1. In Fig. 1, we demonstrate that R_{rhizo} increased with increasing root biomass, which substantiates the methodology of our separation technique.

Regressions of SCE, R_{SOM} and R_{rhizo} versus soil temperature were fitted in Matlab (7.2.0.232, The Mathworks, Natick, MA, USA). Further statistical analyses were performed in SAS (SAS system 9.2, SAS Institute, Cary, NC, USA). We used two-way Ancova analysis, with soil temperature as a covariable, to test for fertilization and plant density effects on the temperature responses of SCE, R_{SOM} and R_{rhizo}. Soil temperature data are shown in Table 1.

Soil respiration significantly increased with growth temperature, but this increase was solely due to the temperature response of R_{SOM}, as R_{rhizo} did not change with growth temperature (Fig. 2). The decreasing temperature response of SCE with increasing plant density (Table 2), and thus with increasing contribution of R_{rhizo} to SCE, further confirmed that R_{rhizo} was less sensitive to growth temperature than R_{SOM} and adds additional support to our methodology. Similarly, Heinemeyer et al. (2007) found that heterotrophic respiration was the main process responsible for the exponential relation between SCE and temperature. We further observed that, although both plant density and fertilization significantly affected root biomass (Supplementary Information 2) and thus R_{rhizo}, the temperature response of R_{rhizo} remained unaffected (Table 2).

Increased labile soil carbon inputs with increasing root biomass could affect the temperature response of R_{SOM} (Davidson and Janssens, 2006), but this was not the case in our experiment

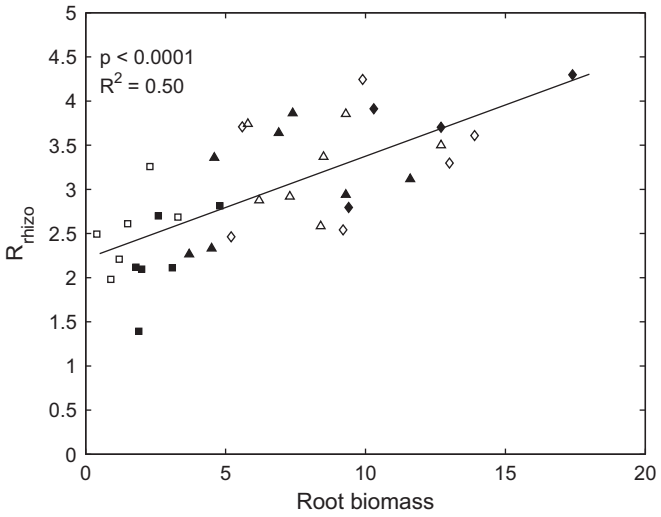

Fig. 1. Rhizosphere respiration (R_{rhizo}; μmol CO_2 $m^{-2}\ s^{-1}$) versus root biomass (g pot^{-1}). White and black symbols represent the unfertilized and fertilized treatment, respectively. Squares are pots with one plant, triangles are pots with three plants and diamonds represent pots with six plants. The line represents the linear regression fitted through the data, and the *p* value indicates the significance of this regression. The high R_{rhizo} at zero root biomass probably indicates the fraction of rhizosphere that remains in the soil when roots are extracted.

where the response of R_{SOM} to growth temperature was unaffected by plant density (Table 2). Possibly, soil microbes were not carbon-limited, in which case additional substrate supply would not alter the temperature response of R_{SOM}. Alternatively, the additional labile soil carbon in the high density pots was utilized in the weeks before our measurements. The latter is supported by the measurements of soil organic carbon content, showing no difference among the treatments (Supplementary Information 2).

The obvious zero-effect of growth temperature on R_{rhizo} suggests full thermal acclimation, which was clearly not the case for R_{SOM} (although we cannot exclude the possibility of partial acclimation of R_{SOM}). Several studies have reported thermal acclimation of autotrophic respiration (e.g., Rook, 1969; Bryla et al., 1997; Atkin et al., 2000, 2005; Ow et al., 2008). Whereas in plants thermal acclimation allows the maintenance of a positive carbon balance (Atkin and Tjoelker, 2003), for soil microorganisms, there is no obvious benefit of reduced activity with increasing

Table 1
Soil temperature (°C) of all replicates for the different plant densities ($D = 1$: one plant per pot, $D = 3$: three plants per pot; $D = 6$: six plant per pot) and for unfertilized (UF) and fertilized (F) pots. Note that one outlier value for the soil CO_2 efflux ($D = 6$, F) was removed from the analyses.

	Replica	$D = 1$	$D = 3$	$D = 6$
UF	1	18	19.5	19
	2	22.2	22.3	20
	3	23	23.9	21.7
	4	24.7	24.9	22.15
	5	24.75	25.2	23.75
	6	27.5	28.1	26.7
	7		28.5	27.5
F	8	21.7	21.3	24.2
	9	21.7	22.7	25.6
	10	21.8	24.45	26.3
	11	23.6	24.9	27.2
	12	27.5	26.1	
	13	28.5	26.3	
	14		27.45	