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Effect of repeated drying–rewetting cycles on microbial biomass carbon in soils with different climatic histories

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ABSTRACT

There are contrasting results regarding the effect of repeated drying–rewetting (DRW) cycles on microbial biomass carbon (MBC), and two fundamentally different mechanisms have been postulated. The first is a microbial stress mechanism which will reduce MBC as stress-sensitive microbes die, and the second is a substrate supply mechanism which will increase MBC through the release of a microbial substrate from non-biomass soil organic carbon (C). However, the balance of these two mechanisms has not been fully examined for various soils with different climatic histories, especially for soils from humid areas. We hypothesized that soils subjected to fewer DRW events would be largely affected by the stress mechanism. Therefore, the effect of repeated DRW cycles on MBC and C dynamics was investigated and compared to that of a moist control treatment for four soils with different DRW histories. The first DRW significantly reduced the MBC for soils with less DRW but not for soils with more DRW. However, when comparing the sizes of MBC after 28 days of four DRW cycles and the moist treatment, the result was not related to the microbial resistance of each DRW. Cumulative respired CO_2-C over a 4-day moist period after each DRW was always significantly greater than that in the moist treatment even when the MBC was not reduced by the DRW. The results with no change in MBC suggested that the substrate supply mechanism rather than the stress mechanism would be essential for the effect of repeated DRW cycles on MBC and C dynamics.

1. Introduction

The response of the terrestrial carbon (C) cycle to climate change is one of the largest uncertainties affecting future climate change projections (Carvalhais et al., 2014). Compared to temperature, the effect of soil moisture on the terrestrial CO_2 flux was less mechanistically predicted (Carvalhais et al., 2014). Global climate models predict that many regions may experience longer periods of drought and more intense precipitation events in the future (Christensen et al., 2007). Therefore, many surface soils may experience more frequent and/or intense rewetting by rainfall events that occur following dry conditions (Borken and Matzner, 2009). Such drying–rewetting (DRW) cycles of soils would affect microbial biomass C (MBC) and the mineralization of soil organic C (SOC) by microbes. Therefore, understanding the effect of repeated DRW cycles on MBC and soil C cycle is essential for future climate change projections.

There are contrasting results regarding the effect of repeated DRW cycles on MBC (Xiang et al., 2008; Butterly et al., 2009; Bapiri et al., 2010), and two fundamentally different mechanisms, probably having opposite effects on MBC, have been postulated. The first is a microbial stress mechanism, which should reduce MBC since the amount of stress-sensitive microbes would be decreased due to DRW stress (Van Gestel et al., 1993). The second is a substrate supply mechanism, which may increase MBC since microbial substrates would be increased through the breakdown and physical release of occluded SOC from soil aggregates (Denef et al., 2001). Because these two mechanisms would occur simultaneously, MBC would be affected by the balance of the two mechanisms during repeated DRW cycles. The balance might be different among various types of soils with different climatic histories. However, studies about the effect of repeated DRW cycles on MBC have typically focused on semi-arid and Mediterranean soils (Xiang et al., 2008) but not on soils from humid regions that had subjected to fewer and less intense DRW events, although it is predicted that soils from humid areas, such as Southeast Asia and Japan, may be more affected by future DRW events (Christensen et al., 2007).

We hypothesized that soils from humid areas that had rarely experienced DRW events would be largely affected by the microbial stress mechanism when the soils were subjected to DRW, because our

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previous study clearly showed that one DRW treatment caused a significant reduction in MBC for such soils due to less resistance to DRW stress (Sawada et al., 2016). In addition, we hypothesized that the microbial stress would be decreased with an increasing number of DRW cycles, because the microbes surviving the DRW cycles may be more resistant to subsequent DRW events (Butterly et al., 2009). However, to test these hypotheses, parallel incubations with continually moist control compared to incubations with repeated DRW cycles would be needed (Meisner et al., 2015), since our previous study did not have an appropriate control treatment (Sawada et al., 2016).

The rewetting of dried soils often causes an increase in microbial respiration (rewetting respiration pulses) and extractable organic C (EOC) contents. In our previous study, respiration rates were measured at high temporal resolution after rewetting (e.g. 1 h) (Sawada et al., 2016). As a result, we showed that the DRW of soils with less DRW from humid areas resulted in C-saturated conditions for surviving microbes, in which the respiration rates within 2 h after rewetting were not significantly different from those with the glucose addition because available substrate C would be released from the cells due to the death of microbes (Sawada et al., 2016). However, we did not investigate the effect of repeated DRW cycles on the relationship between rewetting respiration pulses and available substrate C.

The objective of this study is to investigate the influence of repeated DRW cycles on MBC and EOC related to rewetting respiration pulses in various types of soils that had experienced different DRW histories. For this purpose, four soils were sampled from sites with different climatic histories, including humid areas, and the MBC, EOC, and microbial respiration rates were measured over time during an incubation with four DRW cycles and during a continually moist incubation.

2. Materials and methods

2.1. Soils

Soil samples were collected from four sites under different climatic and land-use conditions in Thailand, Japan, and Kazakhstan. In northern Thailand, forest and cropland soils (hereafter referred to as THf and THc, respectively) were collected from the village of Du La Poe, Mae Hong Son Province, northern Thailand, where a traditional style of shifting cultivation is still used. This region is characterized by a mean annual temperature of about 20.2 °C and an annual precipitation of about 1220 mm, with soils classified as Ustic Haplohumults (by USDA soil taxonomy) (Funakawa et al., 2006). THf soil was collected from natural forests, while THc soil was collected from an upland rice field that had been cultivated for 2 months following slash and burn agricultural practices. The soils were the same as in Sawada et al. (2016), but the sampling times were different. In Japan, a paddy soil (JPp) was collected from a paddy field in the Experimental Farm of Kyoto University, Osaka, where the mean annual temperature is about 17.0 °C and the annual precipitation is about 1260 mm (Experimental Farm, Kyoto University, 2011). This soil developed on the alluvial fan of a small river and is classified as Typic Fluvaquents (by USDA soil taxonomy). In northern Kazakhstan, a cropland soil (KZc) was collected from an oat field in the Experimental Farm of Barayev Kazakh Research and Production Center of Grain Farming, Shortandy, where the mean annual temperature is about 2 °C and the annual precipitation is about 300 mm. This soil is classified as Typic Haplustolls (by USDA soil taxonomy).

The sites in Japan and Thailand have humid climates, while the site in Kazakhstan has a drier climate than the other sites. In addition, the THf soil would have been subjected to fewer DRW events than the THc soil because of the presence of a litter layer and canopy shading (Fierer and Schimel, 2003).

Mineral soil samples were collected from several points in each site to a depth of 10 cm after the removal of plant debris and organic horizons, then pooled to form a composite sample for each site. Freshly collected soil samples were sieved through a 2 mm sieve, homogenized, and stored at field moisture and 5 °C until use. Subsamples of the soils were air-dried and then analyzed for organic C, total N, soil pH, and clay contents as previously described (Sawada et al., 2009) (Table 1). The soils were pre-incubated for 1 week at about 50% of their water-holding capacity (WHC) and 25 °C to reduce the influence of disturbances resulting from collection and sieving.

Table 1
Basic soil properties.

Soil name	Site	pH (H_2O)	Organic C (mg C g^{-1} soil)	Total N (mg N g^{-1} soil)	Clay content (%)
THf	Thai forest	4.8	61	5.0	41
THc	Thai cropland	6.7	32	2.2	41
JPp	Japanese paddy	5.9	33	3.0	24
KZc	Kazakh cropland	7.9	27	1.7	37

2.2. Soil incubation

We determined the effect of four DRW cycles on MBC, K_2SO_4-extractable organic C (EOC), and microbial respiration rates with the incubation experiment consisting of four soils and two treatments (DRW and constantly moist). Following the pre-incubation, MBC and EOC were measured with three replicates at the beginning of the incubation experiment. Then soils were exposed to DRW or moist treatment for four weeks at 25 °C.

For the moist treatment, three subsamples (100 g oven-dried soil) were placed in a 300 mL flask and kept constantly moist at 50% of WHC. Ten grams of soil was collected from each flask at 7, 14, 21, and 28 days to measure the MBC. Five grams of soil was collected at 21 days to measure the EOC. In addition, two subsamples (10 g oven-dried soil) were placed in a 100 mL flask and kept constantly moist at 50% of WHC. The respiration rate was measured using the flask at 0, 7, 14, 21, and 28 days.

For the DRW treatment, three subsamples (200 g oven-dried soil) were subjected to four DRW cycles. A DRW cycle was initiated by 3 days of soil drying, thinly spread on a plastic tray, which was performed for 2 days at 40 °C, and then temperature-equilibrated for 1 day at 25 °C. After that, the soil sample was rewetted to 50% of WHC by spraying deionized water onto the soil and subjecting it to moist incubation for 4 days at 25 °C in 500 mL flasks. The DRW cycle was repeated four times. Ten grams of soil was collected from each flask at 3, 7, 10, 14, 17, 21, 24, and 28 days (i.e., at 0 and 4 days after each rewetting) to measure the MBC. Ten grams of soil was collected from two of three flasks randomly selected at 3, 10, 17, and 24 days (i.e., immediately after each rewetting) to measure the respiration rate during a 4-day moist period after the rewetting. Five grams of soil was collected at 3 and 24 days to measure the EOC. The soil moisture was periodically adjusted based on the weight loss over the entire incubation period.

2.3. Analysis

The MBC was estimated by the substrate-induced respiration (SIR) method (Anderson and Domsch, 1978) according to the method described by Sawada et al. (2016) with a minor modification. Briefly, aliquots of each soil (10 g oven-dried soil) were placed in 100 mL plastic cups, then amended with glucose powder at 1000 μg C g^{-1} soil, which would be sufficient to obtain the initial maximum respiration rates (Anderson and Domsch, 1978). Samples were subsequently homogenized by mixing for 1 min with a spatula. Homogenized soil samples were placed in 100 mL Erlenmeyer flasks. Then each flask was