Immediate and subsequent effects of drying and rewetting on microbial biomass in a paddy soil

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ABSTRACT

Many surface soils in Japan may experience more frequent and intense drying–rewetting (DRW) events due to future climate changes. Such DRW events negatively and positively affect microbial biomass carbon (MBC) through microbial stress and substrate supply mechanisms, respectively. To assess the MBC immediately after DRW and during the incubation with repeated DRW cycles, two laboratory experiments were conducted for a paddy soil. In the first experiment, we exposed the soil to different drying treatments and examined the MBC and hourly respiration rates immediately after the rewetting to evaluate the microbial stress. In the second experiment, we compared microbial growth rates during the incubation of the partially sterilized soil with a continuously moist condition and repeated DRW cycles to evaluate the contribution of the substrate supply from non-biomass soil organic C on MBC. First, all drying treatments caused a reduction in MBC immediately after the rewetting, and higher drying intensities induced higher reduction rates in MBC. A reduction of more than 20% in MBC induced the C-saturated conditions for surviving microbes because sufficient concentrations of labile substrate C were released from the dead MBC. Second, repeated DRW cycles caused increases in the microbial growth rates because substrate C was supplied from non-biomass organic C. In conclusion, MBC decreased immediately after DRW due to microbial stress, whereas MBC increased during repeated DRW cycles due to substrate C supplied from non-biomass organic C.

1. Introduction

The Japan Meteorological Agency (2013) has projected that both the annual number of dry days with daily precipitation of less than 1 mm and the annual frequency of hourly precipitation exceeding 50 mm will increase in Japan by the end of the twenty-first century, in combination with an increase of about 3°C in the annual mean temperature. Therefore, many surface soils may experience more frequent and/or intense rewetting by rainfall events that occur following dry conditions due to the future climate changes (Borken and Matzner 2009). Such drying–rewetting (DRW) events often lead to an immediate reduction in microbial biomass carbon (MBC) due to microbial stress (Marumoto et al. 1982) and an increase in labile carbon (C) available for microbes, producing a pulse of respiration rates (Birch 1958).

The respiration rates over time immediately after rewetting of dried soils measured at a high time resolution (e.g., 1 h) generally show two types (Göransson et al. 2013; Meisner et al. 2013, 2015, 2017; Sawada et al. 2016; Rath et al. 2017). In the first type (type 1), respiration rates are highest immediately after rewetting and subsequently decrease exponentially. In the second type (type 2), they remain stable for less than 16 h, then are sometimes followed by a secondary increase. Respiration rates depend on both the concentrations of available substrate C and the amounts of living MBC, which determines the microbial capacity to mineralize substrate C (Smith et al. 1985). Therefore, the type 1 response will occur when the microbial capacity does not limit the mineralization of substrate C due to low substrate C availability, whereas the type 2 response will occur when the microbial capacity limits the mineralization due to high substrate C availability, resulting in C-saturated conditions for microbes. Therefore, it was often observed that the type 2 response occurred when large portions of MBC were reduced and turned to labile substrate C by DRW due to microbial stress (Meisner et al. 2015; Sawada et al. 2016). In addition, we showed that initial respiration rates immediately after rewetting in type 2 were not significantly different from those after the addition of glucose as a model substrate of labile C (i.e., substrate-induced respiration (SIR) rates) due to C-saturated conditions (Sawada et al. 2016, 2017). Therefore, we assumed that the ratio of respiration rate without glucose addition to that with glucose addition immediately after the rewetting of dried soils (referred to as \( R_{\text{No/Gluc}} \)) should be used as an indicator of the impact of DRW on microbes, and an \( R_{\text{No/Gluc}} \) of 100% should indicate C-saturated conditions for microbes (Sawada et al. 2017). In addition, we observed that hourly respiration rates over time after rewetting under C-saturated conditions were not fitted by exponentially decaying functions, which are often employed in soil organic carbon (SOC) dynamic models (Sawada et al. 2016).

The reduction rates in MBC by DRW have been shown to be higher in soils subjected to fewer DRW events because the microbes in such soils have not yet adapted to the DRW stress (Van Gestel et al. 1993; Butterly et al. 2009). We found that
Drying treatments for soils with a history of less DRW resulted in C-saturated conditions for the surviving microbes due to the increases in labile C from dead MBC (Sawada et al., 2016, 2017). Drying treatments, such as the duration of drying periods (e.g., Meisner et al., 2015), drying temperatures (e.g., Haney et al., 2004), and the duration of moist incubation periods before drying (e.g., Yu et al., 2014), also affect MBC and respiration rates after rewetting. Meisner et al. (2015) observed that drying periods of <2 weeks resulted in a type 1 response, whereas drying periods of >4 weeks resulted in a type 2 response. However, it was not clear how drying treatments would affect the rewetted microorganisms and induce a C-saturated condition for surviving microbes, although higher drying intensities should lead to a larger release of labile C from dead MBC.

It is reasonable to expect that repeated DRW cycles of soil lead to a reduction in MBC compared to the condition of moist incubation, because DRW should reduce MBC, which turns to labile substrate C, and only a fraction of substrate C is used to increase the MBC due to respiratory loss. However, there were several observations that repeated DRW cycles caused increases in MBC compared to moist incubation (Denef et al., 2001; Xiang et al., 2008). We also found that the size of MBC after 28 days of incubation with four DRW cycles was slightly but significantly larger than that after 28 days of moist incubation in a Japanese paddy soil (Sawada et al., 2017). This was probably because substrate C was released from non-biomass soil organic C (SOC) through a substrate supply mechanism during repeated DRW cycles (Xiang et al., 2008). The substrate supply mechanism results from physicochemical processes such as the breakdown of aggregates and the increases in water-extractable organic C by drying-induced mineral-surface acidification (Kaiser et al., 2015). However, in our previous study using the freshly collected Japanese paddy soil, the increases in MBC by repeated DRW cycles was much lower than those in other studies using Mediterranean soils with more drying histories (Xiang et al., 2008), because the first and second DRW to such a Japanese soil with less drying histories significantly reduced the MBC immediately after rewetting. In other words, the increases in MBC derived from non-biomass SOC through the substrate supply mechanism should be hampered by the decreases in MBC by the first and second DRW through the microbial stress mechanism. Therefore, in this study, we initially sterilized the vast majority of soil microbes by drying at 70°C and then compared the growth of surviving microbes during incubation under a continuously moist condition and repeated DRW cycles in order to confirm the contribution of substrate C supplied from non-biomass SOC other than dead MBC by repeated DRW cycles to MBC.

The objective of this study was to evaluate the immediate and subsequent effects of DRW on MBC through the responses to microbial stress and/or substrate supply mechanisms for a paddy soil. For this purpose, (1) we evaluated the effect of different drying treatments on MBC and the hourly respiration rates and microorganisms immediately after the rewetting and (2) we confirmed whether substrate C supplied from non-biomass SOC during repeated DRW cycles would positively affect the growth of surviving microbes in the partially sterilized soil.

2. Materials and methods

2.1. Soil

A soil was collected from a paddy field in the Experimental Farm of Kyoto University, Osaka (Experimental Farm, Kyoto University 2011) in March, before irrigation. The soil was the same as the JP soil in Sawada et al. (2017). The soil pH was 5.9, organic C was 33 mg C g⁻¹ soil, total N was 3.0 mg N g⁻¹ soil, and the clay content was 24%. Freshly collected soil sample was sieved through a 2 mm sieve, homogenized, and stored at field moisture and 5°C until use. The soil was pre-incubated for 1 week at 50% of the maximum water-holding capacity (WHC) at 25°C to reduce the influence of disturbances resulting from collection and sieving.

2.2. Experiment 1: immediate effect of different drying treatments

We examined the effect of different drying treatments on MBC and hourly respiration rates immediately after the rewetting. Following pre-incubation (referred to as ‘Initial’ hereafter), the soil was subjected to various drying treatments and rewetted back to 50% of the maximum WHC. Drying treatments included 7 days of drying at 25°C (Dry 25°C); 2 days of drying at 40°C, followed by temperature equilibration for 1 day at 25°C (Dry 40°C); 1 day of drying at 70°C, followed by 1 day at 25°C (Dry 70°C); 30 days of drying at 25°C (Dry 30d); and 60 days of drying at 25°C (Dry 60d). The Dry 70°C treatment was conducted to evaluate the effect of sterilization of vast majority of microbes. As controls, moist incubation at 50% of the maximum WHC for 7 days (Moist 7d) and 30 days (Moist 30d) were included. In addition, to evaluate the effect of the moist incubation duration before drying, moist incubation for 30 days, followed by 7 days of drying at 25°C (Dry aft LMI (i.e., long moist incubation)), was also included. For drying treatments, soil samples were dried by being thinly spread on plastic trays at a depth of approximately 1 cm. These samples were subsequently rewetted by spraying deionized water to 50% of the maximum WHC. Immediately after the rewetting of dried soil, hourly respiration rates without and with glucose addition were measured as described in the following section (2.4. Analysis).

2.3. Experiment 2: effect of three DRW cycles on microbial growth

We evaluated the effect of repeated DRW cycles on microbial growth. After pre-incubation, soil was initially exposed to a Dry 70°C treatment as mentioned above to sterilize the vast majority of soil microbes. The dried soil was rewetted and then incubated in a continuously moist condition or three DRW cycles for 25 days at 25°C according to Sawada et al. (2017) with a minor modification to compare the growth of surviving microbes on substrate C supplied from non-biomass SOC other than dead MBC. Briefly, for the moist incubation, three subsamples (100 g of oven-dried soil) were placed in 300 mL flasks and kept constantly moist at 50% of WHC. Ten grams of soil was collected from each flask at 0, 4, 11, 18, and 25 days to
measure hourly respiration rates with glucose addition. In addition, two subsamples (10 g of oven-dried soil) were placed in 100 mL flasks and kept constantly moist. The respiration rates without glucose addition were measured hourly until 12 h and then at 4, 11, 18, and 25 days using the flasks. For the incubation with three DRW cycles, three subsamples (200 g of oven-dried soil) were incubated for 4 days at 50% of WHC in 500 mL flasks. Then the soil was exposed to a Dry 40°C treatment as detailed above. After that, the soil sample was rewetted to 50% of WHC and moist incubated for 4 days. The DRW cycle was repeated three times. Ten grams of soil was collected from each flask at 7, 11, 14, 18, 21, and 25 days (i.e., at 0 and 4 days after each rewetting) to measure hourly respiration rates with glucose addition. Ten grams of soil was collected from two of three flasks randomly selected at 7, 14, and 21 days (i.e., at 0 days after each rewetting) to measure the hourly respiration rates without glucose addition until 12 h and then at 4 days during the moist incubation after rewetting.

2.4. Analysis

The respiration rates with glucose addition were measured and MBC was estimated using the SIR method (Anderson and Domsch 1978) according to Sawada et al. (2017). Briefly, aliquots of each soil (10 g of oven-dried soil) were amended with glucose powder at 1000 μg C g⁻¹ soil. The concentration of added glucose was determined to be sufficient to obtain the initial maximum respiration rates but not to suppress those by excess concentration (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. Each flask was aerated for 20 min with air that had been passed through a 2 mol L⁻¹ NaOH solution to achieve a low background CO₂ concentration (approximately 50 μL CO₂ L⁻¹). The flask was then closed with a rubber septum for 40 min, followed by measuring the headspace CO₂ concentration using an infra-red gas analyzer (ZFP9, Fuji Electric Systems, Tokyo, Japan). The same procedure was repeated hourly for 4 h. The CO₂ evolution rate (μg CO₂-C g⁻¹ soil h⁻¹) at each sampling time was calculated after subtracting the background CO₂ concentration. The average of 3-hourly respiration rates over 4 h was used as the SIR rate for each sample, since the hourly respiration rates were almost kept constant during 4 h. The MBC was calculated using the SIR rate according to Anderson and Domsch (1978) after correcting for temperature at 25°C to 22°C.

The respiration rates without glucose addition (μg CO₂-C g⁻¹ soil h⁻¹) were also measured hourly for 12 h and sometimes at 4 days after rewetting and mixing with spatula in the same way as for the respiration rates with glucose addition, but without the glucose addition.

2.5. Statistics

All data are expressed as the means and standard deviations on an oven-dried soil-weight basis (105°C, 24 h). Significant differences in the means of two variables were identified using a Student’s t-test. Significant differences in means among multiple variables were identified using Tukey’s multiple comparisons at a significance level of p < 0.05.

Nonlinear exponential regression analyses (Eq. 1) were used to describe the respiration rates over a 12 h moist period after the rewetting of dried soils by the least-squares method using Sigmaplot 2002 for Windows Version 8.0 (Inc 2002) (Sawada et al. 2016):

\[
y = A \exp(-kt) + y_0
\]

where \(y\) is the respiration rate (μg CO₂-C g⁻¹ soil h⁻¹), \(k\) is the first-order rate constant for a labile (i.e., exponentially decaying) pool (h⁻¹), \(t\) is time after rewetting (h), and \(y_0\) is the asymptotic value that respiration approaches (μg CO₂-C g⁻¹ soil h⁻¹).

3. Results

3.1. Experiment 1: immediate effect of different drying treatments

All drying treatments with different intensities caused significant reductions in the sizes of MBC (Fig. 1). The reduction rates in MBC by DRW were calculated as the difference of MBC between immediately before drying and after rewetting divided by the MBC immediately before drying, and ranged from 7 to 93% (Fig. 1). The reduction rates increased with the increasing temperature of drying (i.e., Dry 25°C, Dry 40°C, and Dry 70°C) and increasing duration of the drying period (i.e., Dry 25°C, Dry 30d, and Dry 60d) (Fig. 1). When comparing the duration of the moist incubation period before drying, the reduction rate (7%) for soil dried at 25°C immediately after pre-incubation (Dry 25°C) was significantly lower than that (29%) for soil dried at 25°C after further moist incubation for 30 days following pre-incubation (Dry aft LMI) (p < 0.001). In contrast, moist incubation (i.e., Moist 7d and Moist 30d) had no significant effect on MBC (Fig. 1).

Initial respiration rates after rewetting without glucose addition were significantly lower than the SIR rate (i.e., initial respiration rate after glucose addition) for Dry 25°C and Dry 30d (Fig. 2A,D), whereas they were not significantly different from the SIR rates for other drying treatments (i.e., Dry 40°C, Dry 70°C, Dry 60d, and Dry aft LMI), indicating C-saturated conditions (Fig. 2B–F). Therefore, the ratios of the initial respiration rate without glucose addition to the SIR rate (\(R_{\text{No/}}\text{Gluc}\)) were near 100% for Dry 40°C, Dry 70°C, Dry 60d, and Dry aft LMI but were below 80% for Dry 25°C and Dry 30d (Fig. 3). Hourly respiration rates for 12 h after rewetting increased over time for Dry 70°C, whereas they decreased over time for other drying treatments (Fig. 2). The rates over time for Dry 25°C, Dry 40°C, and Dry 30d were well described (p < 0.001) as exponential decaying rates approaching a constant value (Eq. 1), but this was not the case for other drying treatments (Dry 70°C, Dry 60d, and Dry aft LMI) (Fig. 2).

The relationship between the \(R_{\text{No/}}\text{Gluc}\) and the reduction rates in MBC by DRW was assessed for this study and the previous two studies, in which a wide range of soils from different climatic and land use conditions were exposed to different drying treatments (Sawada et al. 2016, 2017) (Fig. 3). The result indicated that the \(R_{\text{No/}}\text{Gluc}\) increased with the increasing reduction
rates of MBC and was near 100% when the reduction rates were above 20%, resulting in C-saturated conditions.

3.2. Experiment 2: effect of three DRW cycles on microbial growth

The Dry 70°C treatment sterilized the vast majority of MBC as well as in Experiment I, and thus the initial size of MBC was about 40 μg C g⁻¹ soil (Fig. 4A). The MBC increased over time during moist incubation after the initial rewetting (Fig. 4A). The MBC also increased over time during incubation with three DRW cycles (Fig. 4A). When comparing the MBC between moist incubation and three DRW cycles, the sizes of MBC in the DRW cycles at 4 days of moist periods after the first, second, and third DRW (i.e., at 11, 18, and 25 days) were 1.3, 1.5, and 1.4 times larger than those in moist incubation, respectively (Fig. 4A).

Hourly respiration rates after the initial rewetting of soil dried by the Dry 70°C treatment increased exponentially, followed by steep decreases, and then were relatively stable for 25 days during moist incubation (Fig. 4B). For the incubation with three DRW cycles, hourly respiration rates increased over time during the 12 h moist period after the first DRW, whereas they decreased slowly after the second and third DRW (insert in Fig. 4B). These rates were not fitted by Eq. 1 (Fig. 4B). The initial respiration rates after the first and second DRW were

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**Figure 1.** MBC with different treatments (see text). Bars indicate standard deviations. Bars followed by the same letters do not differ significantly among treatments at *p* < 0.05. Figures (%) indicate the reduction rates in MBC by DRW.

**Figure 2.** Respiration rates over time (black) after the rewetting of dried soils for Dry 25°C A, Dry 40°C B, Dry 70°C C, Dry 30d D, Dry 60d E, and Dry aft LMI F. Initial respiration rates (white) after the glucose addition (i.e., SIR rates) are also shown. Bars indicate standard deviations. NS and *** indicate not significant and *p* < 0.001, respectively, between with and without glucose addition. Lines show fitting to Eq. (1) \( y = A \exp (-kt) + y_0 \).
not significantly different from the SIR rates, indicating C-saturated conditions, whereas that after the third DRW was significantly lower than the SIR rate (Fig. 4B).

The amounts of total CO$_2$-C ($\mu$gC g$^{-1}$) respired during the 25 days of moist and DRW incubation were calculated by cumulating the respiration rates, assuming that the respiration rates during the drying periods for the DRW incubation were 0. As a result, the cumulative respired CO$_2$-C were 1050 and 1090 $\mu$gC g$^{-1}$ for the moist and DRW incubation, respectively, although that for the DRW incubation must be underestimated due to the assumption of 0 for the respiration rates during the drying periods.

4. Discussion

4.1. Immediate effect of different drying treatments

All drying treatments significantly reduced the size of MBC, indicating the death of a substantial portion of microbes due to microbial stress (Fig. 1). In total 93% of MBC was reduced by the Dry 70°C treatment and should be at least partly turned into labile substrate C. Therefore, the addition of glucose as a model substrate of labile C did not increase the initial respiration rate, indicating the C-saturated condition for surviving microbes (Fig. 2C). In addition, since the labile substrate C was used by surviving microbes, the respiration rates increased exponentially due to the microbial growth and thus showed the type 2 response (Fig. 2C).

The reduction rates in MBC by all drying treatments except Dry 70°C ranged from 7 to 37% (Fig. 1), which is within the range of 5 to 66% observed in six Asian soils (Sawada et al. 2016) and that of 3 to 68% observed in 17 New Zealand soils (Sparling et al. 1986). The drying treatments with higher intensities (i.e., higher drying temperatures and longer drying periods) induced higher reduction rates in MBC, which is consistent with other studies (Navarro-García et al. 2012; Meisner et al. 2015). In addition, the longer duration of moist incubation before drying (i.e., Dry aft LMI) induced higher reduction rates, probably because microbial substrate C used as the energy to survive drying conditions was depleted during moist incubation (Yu et al. 2014).

The Dry 25°C and Dry 30d treatments reduced 7% and 12% of MBC, respectively (Fig. 1), but did not induce the C-saturated conditions (Fig. 2A,D) with an $R_{No/Gluc}$ of below 80% (Fig. 3). Therefore, hourly respiration rates over time after rewetting can be fitted to Eq. 1 and showed the type 1 response (Fig. 2A,D). In contrast, the Dry 40°C, Dry 60d, and Dry aft LMI treatments reduced 20%, 37%, and 29% of MBC, respectively (Fig. 1), and induced C-saturated conditions (Fig. 2B–E) with an $R_{No/Gluc}$ of nearly 100% (Fig. 3). When all of the data obtained in this study and the previous two studies (Sawada et al. 2016, 2017) were used, the $R_{No/Gluc}$ values were related to the reduction rates in MBC by DRW, and the reduction of more than 20% of MBC induced C-saturated conditions with an $R_{No/Gluc}$ of nearly 100%, even when a wide range of soils were exposed to different drying treatments (Fig. 3).

Hourly respiration rates over time after rewetting under C-saturated conditions for the Dry 70°C, Dry 60d, and Dry aft LMI treatments could not be fitted to Eq. 1, which is consistent with the previous study (Sawada et al. 2016). In addition, although those rates could be fitted to Eq. 1 for the Dry 40°C C treatment under C-saturated conditions, an initial respiration rate at time 0 calculated as shown in (Fig. 2B) (i.e., 6.09 * exp...
\((-0.27 \times 0) + 2.63 = 8.72 \mu g CO_2-C g^{-1} soil h^{-1}\) was higher than the SIR rate (i.e., 7.18 \(\mu g CO_2-C g^{-1} soil h^{-1}\)), which should be a maximum respiration rate for microbes, and thus appeared to be overestimated by Eq. 1. Therefore, our study clearly showed that hourly respiration rates under C-saturated conditions cannot be simulated by most SOC models with first-order kinetics because they are regulated by the microbial capacities, and thus it is important to incorporate microbial parameters into SOC models on DRW events (Lawrence et al. 2009). In addition, our study suggested that the reduction of more than 20\% of MBC due to microbial stress by various disturbances such as freezing and thawing and pesticide application as well as DRW may induce C-saturated conditions, and thus the respiration rates may not be simulated by most SOC models with first-order kinetics (Fig. 3).

**4.2. Effect of repeated DRW cycles on microbial growth**

The MBC increased over time during 25 days of moist incubation after the vast majority of microbes were killed by the Dry 70°C treatment, indicating that surviving microbes grew on labile substrate C derived from dead MBC (Fig. 4A). The MBC also increased over time during 25 days of incubation with three DRW cycles (Fig. 4A). The MBC in the DRW incubation was significantly higher than those in the moist incubation throughout the experiment (Fig. 4A). For the incubation with three DRW cycles, hourly respiration rates increased over time during 12 h of moist conditions after the first DRW (insert in Fig. 4B), and the MBC increased during 4 days of moist conditions after the first DRW (i.e., from 7 to 11 days) (Fig. 4A), suggesting that microbes grew on labile substrate C. However, hourly respiration rates decreased over time during 12 h of
5. Conclusion

We evaluated MBC immediately after DRW and during incubation with repeated DRW cycles for a paddy soil and found that MBC was affected by different mechanisms between immediately after DRW and during repeated DRW cycles. DRW usually results in the reduction in MBC immediately after rewetting through the microbial stress mechanism (Fig. 1). In addition, hourly respiration rates over time immediately after rewetting were affected by the reduction rates in MBC by DRW (Fig. 2, 3). In contrast, MBC was positively affected by the substrate C supplied from non-biomass SOC during several days of incubation with repeated DRW cycles (Fig. 4). These results suggested that SOC may be negatively affected by increasing numbers of DRW events in the future due to the respiratory loss caused by microbial stress immediately after DRW and the release of substrate C from non-biomass SOC during repeated DRW cycles.

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Sawada et al. (2017) found that the size of MBC after 28 days of four DRW cycles was only 1.1 times larger than that after moist incubation for the same but fresh soil without the Dry 70°C treatment. The increase in MBC for the fresh soil was much lower than that in this study with the Dry 70°C treatment because of the negative impact of initial DRW events on the MBC due to microbial stress. Recently, there has been increasing interest in understanding the factors relating to the release of non-biomass SOC during repeated DRW cycles for various types of soils, such as aggregate formation and breakdown, enzymatic activities, and organic matter composition (Kaiser et al. 2015). For this purpose, soil samples have often been sterilized to separate cellular metabolism and extracellular depolymerization (Blankinship et al. 2014; Daou et al. 2016). Similarly, our study showed that examining the effect of repeated DRW cycles on the growth of surviving microbes after sterilization of the majority of microbes is a promising approach to evaluating the contribution of non-biomass SOC to MBC. However, since the sterilization method as drying at 70°C used in our study would result in an artifact of drying treatment, further studies with the other sterilizing methods such as chloroform fumigation, gamma irradiation, and autoclaving is necessary (Blankinship et al. 2014). In addition, it remains unknown through what mechanisms the substrate C was supplied from non-biomass SOC. Therefore, further study is needed to assess the effect of repeated DRW cycles on MBC for various types of soils, for example, using labeled substrates to divide the sources into MBC and non-biomass organic matter (Jenkinson and Powlson 1976).
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