



Weaker priming and mineralisation of low molecular weight organic substances in paddy than in upland soil



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ABSTRACT

Although soil organic matter (SOM) and microbial biomass pools in flooded paddy soils are generally larger than they are in upland soils, the processes (i.e., slower mineralisation, other types of C stabilization, and a negative priming effect) underlying higher SOM stocks in paddy soil are unclear. To elucidate these processes, three ¹³C labelled low molecular weight organic substances (¹³C-LMWOS) (i.e., glucose, acetic acid, and oxalic acid) were incubated in upland and paddy soils under simulated field conditions. Within 30 days of incubation, acetic acid exhibited the highest mineralisation in both soils. The amount of mineralisation of glucose in upland soil was higher than that of oxalic acid ($p < 0.05$), whereas the opposite was observed for paddy soil. Mineralisation of all three LMWOS was lower in paddy soil than that in upland soil ($p < 0.05$), illustrating that the molecular structure of the LMWOS as well as soil management determined the mineralisation rate. The priming effect evoked by oxalic acid and glucose was lower in paddy than in upland soil ($p < 0.05$). Therefore, the generally weaker mineralisation and priming effect of LMWOS observed in paddy soil contributed to higher carbon accumulation than they did in upland soil. Priming effect was positively correlated with fungal abundance, which was lower in paddy soil than in upland soil. Thus, slow organic C turnover in paddy soil is partly attributed to the suppression of fungal activity by flooding.

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1. Introduction

Terrestrial ecosystems play an important role in the global carbon (C) cycle. Low molecular weight organic substances (LMWOS), e.g., sugars, carboxylic acids, and amino acids, are derived from root exudates [1,2], leached litter products [3,4], microbial residues, and metabolic products [5]. The rapid mineralisation and turnover of LMWOS appears to dominate the total CO₂ emission of soil, despite

their low concentration of these substances [4,6]. The mineralisation rates of LMWOS are generally very fast, ranging from minutes to days [7–9]. For example, in one study [10], 50% of glucose-C was observed to have been released as CO₂ within 20 days (d) in grassland soil, and more than 50% of applied ¹³C amino acids (alanine and glutamate) were observed to have been mineralised after 10 d in an arable soil in another study [11]. Mineralisation is LMWOS-specific, e.g., a higher proportion of amino acids (19.4% of the total ¹⁴C added) than of glucose (14%) are mineralised to CO₂ within 2 d in arctic tundra soil [12]. Moreover, C in a –COOH group oxidizes to CO₂ faster than C in a –CH₃ group [7]. Thus, the –CH₃ group contributes more to the formation of soil organic matter (SOM) than does the –COOH group. In short, the chemical nature of LMWOS largely

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determines their mineralisation processes in soil [9].

LMWOS may evoke the priming effect, which could be positive or negative [13,14]. Microbial activation by LMWOS is one of the causes of the priming effect, where positive priming could result from microbial growth and the concomitant increased production of enzymes that degrade SOM [15,16]. Nobili et al. [17] suggested that some microorganisms invest low amounts of energy in maintaining a cellular state of “metabolic alertness”, and they react more rapidly to substrates than to dormant cells. The input of LMWOS in soil accelerates the turnover of bacteria, especially that of *r*-strategists, thus triggering a positive priming effect [18]. Some microbial groups that preferentially utilize poorly available substrates from bacterial necromass remain alive after the exhaustion of easily available organics [19]. These organisms are considered to be *K*-strategists [20], which are stimulated by moribund bacteria and their lysates, thereby continuing to promote the decomposition of SOM and the positive priming effect. However, sometimes the exhaustion of microbially available substrates and the subsequent decrease in enzymatic activities can lead to negative priming [21,22].

In China, paddy fields account for approximately 26% of the farmlands and are primarily distributed in subtropical regions [23]. Under the same geomorphic units and climatic conditions, organic C content in surface-flooded paddy soil is greater than it is in upland soil [24]. In comparison to upland agro-ecosystems, flooded paddy ecosystems have specific physical and chemical soil properties and associated microbial communities [25]. Compared with upland soil, the processes—e.g., higher organic carbon input, slower mineralisation, other types of C stabilization, slower turnover, and negative priming effect—that lead to higher SOM stocks in paddy soil are unclear. The objective of this study was to distinguish the mineralisation and priming effects of three ¹³C-LMWOS (glucose, acetic acid, and oxalic acid) in upland and paddy soils based on a simulated field experiment. The working hypotheses for this study were (1) the mineralisation differs among the three ¹³C-LMWOS owing to their discrepancies in the types and numbers of their functional groups and microbial utilization [7,11]. (2) The slower turnover rate of SOM in anaerobic paddy soil will lead to a lower proportion of mineralised ¹³C-LMWOS in paddy soil than that in upland soil, thus resulting in the accumulation of SOM in paddy soil [25]. (3) Lower microbial metabolic quotient ($q\text{CO}_2$, the ratio of CO_2 production per unit microbial biomass C) in paddy soil leads to a weaker priming effect than that in upland soil [26–29].

2. Materials and methods

2.1. Soil sampling and preparation

Surface soils (0–15 cm depth) were collected from an upland field (29°15′49.7″N and 111°31′57.5″E) and a paddy field (29°15′22.0″N and 111°31′38.1″E) in the fallow season, in Pantang, Hunan Province, China. The fields have been under tillage for at least 30 years. The upland field was under crop rotation with cotton and canola, and the paddy field was under mono cropping with rice (drainage in fallow season). Fresh soils were sieved (<2 mm) and mixed, and visible roots, plant residues, and rocks were removed. The soils were subsequently stored at 4 °C prior to the incubation experiment. Basic soil properties are listed in Table 1.

2.2. Experimental design and soil incubations

Four treatments were applied to upland and paddy soils: the addition of each of the three ¹³C-labelled LMWOS—glucose, acetic acid, oxalic acid—and a control treatment that did not contain any

exogenous LMWOS. The rationale for choosing these substances was based on the following considerations: (1) Carbohydrates and organic acids are relatively abundant LMWOS of root exudates. (2) Acetic and oxalic acids contain different numbers of chemical functional groups (i.e., one or two –COOH, respectively), which could affect microbial activity and SOM mineralisation. All three ¹³C-labelled substances, i.e., ¹³C-glucose (U-¹³C, 99 atom%), ¹³C-acetic acid (1, 2-¹³C₂, 99 atom%), and ¹³C-oxalic acid (1, 2-¹³C₂, 99 atom%), were purchased from Cambridge Isotope Laboratories (Tewksbury, MA, USA), and were mixed with their corresponding unlabelled substances, resulting in 5.1 atom% ¹³C of glucose, 4.46 atom% ¹³C of acetic acid, and 6.01 atom% ¹³C of oxalic acid.

Experiments were conducted under open-air field conditions. A certain amount of sampled soil (equivalent to 200 g dry soil) was weighed and added to each polyvinylchloride (PVC) tube (hereafter referred to as ‘soil columns’: 20 cm height × 5 cm diameters; the thickness of soil in PVC tube was approximately 8 cm). During the pre-incubation (2 weeks) and incubation (30 d) periods, the water-holding capacity was gravimetrically controlled at approximately 40% in upland soil, while the paddy soil was maintained under flooding conditions (with 3 cm water) by supplementing with distilled water. At the beginning of incubation, 1 mL of ¹³C-LMWOS solution was injected into each column with a syringe. The injection of each LMWOS solution was performed at 5 vertical points in each soil column (approximately every 1.5 cm), with each injection point receiving 0.2 mL of solution. The amount of applied tracer was equal to 20 mg C (about 20% of the C stored within the microbial biomass in paddy soil) [30]. Subsequently, 5 mg N was added as an $(\text{NH}_4)_2\text{SO}_4$ solution to all the treatments for microbial growth. A plastic cover was used to prevent rainfall for the 30 d of experiments. At 0.25, 0.5, 1, 2, 5, 10, 20, and 30 d of incubation, redox potential (Eh) in paddy soil was measured by inserting the probe of an InLab Redox sensor (Mettler Toledo Columbus, OH, USA) to a depth of 4–5 cm below the soil surface, and the Eh (mV) was recorded until the value was stable. Next, the water layer on paddy soil samples was removed using syringes, and separate columns for upland and paddy soils were destructively sampled. Each soil sample was divided into two subparts for the measurement of different properties: (1) one subpart was used to analyse microbial biomass C (MBC) within 24 h, and (2) the other subpart was stored at –80 °C to analyse microbial abundance and the microbial community.

2.3. CO_2 flux

The flux and the ¹³C atom% of the released CO_2 were analysed at 0, 0.25, 0.5, 1, 2, 5, 10, 15, 20, 25, and 30 d after the addition of the LMWOS (i.e., glucose, acetic acid, and oxalic acid). CO_2 flux was determined using the static chamber chromatography method [31]. Briefly, CO_2 gas was sampled between 9:00 and 11:00 a.m. on each sampling day. Prior to sampling, the concentration and ¹³C atom% of CO_2 in each column were maintained at ambient levels. Then, CO_2 in the ambient air was taken as a background value (0 min). After sealing the column for 30 min within a chamber (the volume of the chamber was approximately 300 mL), two 30 mL samples were collected from each chamber using a syringe and were subsequently injected into separate pre-evacuated 12-mL vacuum bottles fitted with butyl-rubber lids to measure CO_2 concentrations and $\delta^{13}\text{C}$ values. CO_2 concentration was analysed using a gas chromatograph (Agilent 7890A; Agilent Technologies, Santa Clara, CA, USA) equipped with a flame ionization detector for CO_2 analyses at 250 °C. The $\delta^{13}\text{C}$ value of CO_2 was determined using an ultra high-resolution isotope ratio mass spectrometer (MAT 253; Thermo Scientific, Waltham, MA, USA). The CO_2 flux (F) ($\text{mg d}^{-1} \text{kg}^{-1}$ soil) was calculated as follows:

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