Geoderma 305 (2017) 219–227

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Soil respiration and microbial biomass in multiple drying and rewetting cycles – Effect of glucose addition

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ARTICLE INFO

Keywords:
Glucose
Microbial biomass
Respiration flush
Rewetting frequency

ABSTRACT

Previous studies showed that the respiration flush upon rapid rewetting of dry soil decreases with increasing number of drying and rewetting (DRW) cycles which is thought to be due to various factors, for example, lower substrate availability or microbial biomass or changes in microbial community structure. To investigate if the reduction of respiration flush with increasing cycle number is due to lack of available substrate upon rewetting, incubation experiments with four DRW cycles were conducted where glucose solutions of different concentrations, low (50 μg C g^{-1} soil), medium (250 μg C g^{-1} soil) and high (500 μg C g^{-1} soil) were added either in all four cycles or only in cycle 1, 2, 3 or 4 (the other cycles rewetted with water). Additional treatments included a constantly moist control (CM, 70% of maximum water-holding capacity) and DRW treatments with only RO water. When dry soil was rewetted only with RO water, the respiration flush upon rewetting was about twice as high in the first two cycles than in cycles 3 and 4. Soil microbial biomass C (MBC) one day after rewetting remained stable until cycle 3 after which it decreased by about 20%. In all glucose treatments, the glucose-induced increase in respiration rate was greater in earlier than later cycles, irrespective of whether glucose was added to one cycle only or in all cycles. But when expressed relative to CM, the respiration rate was greater in the last two cycles. Single glucose addition increased MBC only in the cycle in which it was added whereas repeated glucose addition increased MBC over time. Glucose addition and DRW increased the metabolic quotient, thus reduced C use efficiency. In treatments with glucose added in all four cycles, the metabolic quotient increased with DRW cycle number which indicates lower efficiency in later cycles. It is concluded that lower substrate availability can be one of the reasons for the decrease in respiration flush upon rewetting with cycle number.

1. Introduction

The organic C pool in terrestrial ecosystems (1550 Pg) is more than twice that of the atmospheric pool of 755 Pg and about three times that stored in vegetation (550 Pg) (Lal and Follett, 2009). However, the majority of soil organic C is not readily decomposable by soil microorganisms (Hoyle et al., 2008) and organic C is generally thought to be the primary limiting nutrient for soil organisms (Anderson and Domsch, 1978; Maraun and Scheu, 1995; Smith, 2005). This conclusion is based on the increase in soil respiration after adding trace amounts of easily-available C substrates, either in single (Sparling et al., 1981) or multiple additions (De Nobili et al., 2001; Hoyle et al., 2008).

One third of the land cover on earth is arid, semi-arid or seasonally arid, where droughts and episodic rewetting events are common (Schimel et al., 2007). As soils dry, water and nutrient diffusion become limiting (Killham and Firestone, 1984). In order to survive or maintain activity during drought, soil microorganisms have developed strategies such as adjustment of cellular water potential by accumulating solutes or switching to a dormant state (Schimel et al., 2007). Dormancy was suggested to be a preferred strategy to cope with low soil water content, especially in areas that frequently experience fluctuations in moisture content, such as semi-arid regions (Manzoni et al., 2014). Rapid rewetting of dry soils is another environmental stress, causing cell rupture or forcing microbes to release osmolytes accumulated during drying to minimize water influx into the cells (Schimel et al., 2007). The CO_2 flush upon rewetting is ascribed to utilisation of a range of sources, including dead microbes, released osmolytes and organic matter previously inaccessible to microbes (Borken and Matzner, 2009; Jin et al., 2013; Schimel et al., 2007). When exposed to several drying and rewetting cycles, the respiration flush upon rewetting usually decreases

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http://dx.doi.org/10.1016/j.geoderma.2017.06.010
Received 23 January 2017; Received in revised form 6 June 2017; Accepted 9 June 2017

with increasing DRW cycle number (Baumann and Marschner, 2013; Butterly et al., 2010; Fierer and Schimel, 2002; Mikha et al., 2005). One explanation for this decrease is the depletion of available substrates, other factors include decreased size of microbial biomass and changes in microbial community structure (Fierer et al., 2003; Kim et al., 2012; Van Gestel et al., 1993). If the lack of available substrate is the reason for decreasing respiration flush upon rewetting in multiple drying and rewetting (DRW) cycles, the flush should not decrease when readily available C is added at rewetting. In our study, glucose was used as readily available soil amendment, as it is present in root exudates and in freshly added crop residues and is immediately available to a broad range of soil microorganisms (Elmajdoub et al., 2014; Nakatsu et al., 2005). Further, if substrate availability decreases with DRW cycle number, the addition of readily available C should have a greater effect in later compared to earlier cycles. To our knowledge, this has not been investigated before. The aim of this study was to determine the influence of addition of easily available organic C upon rewetting on respiration and microbial biomass in DRW cycles. Soil was exposed to four DRW cycles and glucose was added at rewetting at different concentrations and in different cycles. We hypothesised that (i) when glucose is added only once, the stimulation of respiration will be greater when glucose is added in later compared to earlier cycles, (ii) the effect of a single glucose addition on respiration and microbial biomass will be confined to the cycle at which glucose was added, and (iii) the addition of glucose at all four cycles will prevent the decrease in respiration flush with cycle number.

2. Materials and methods

2.1. Soil

The soil was collected from 0 to 10 cm depth in the Waite Long-term Rotation Trial, Urrbrae (Longitude 138°38′3.2″ E, Latitude 34°58′0.2″ S) in South Australia. The semi-arid region has a Mediterranean climate with cool, wet winters and hot, dry summers; mean annual rainfall of 545 mm, mean annual temperature of 17 °C and is about 50 m above sea level. Most of the precipitation occurs in winter (May–August), rainfall events in summer are rare and separated by long periods of hot and dry weather. The soil is a Red-brown Earth in the Australian soil classification system (Isbell, 2002) or a Rhodoxeralf according to US Soil Taxonomy. Four locations were sampled within the plot which had been managed as a wheat-fallow rotation continuously for over 80 years. The samples were pooled and carefully mixed to give one composite sample.

The soil was collected in summer and therefore dry; it was passed through a 2 mm sieve and stored air-dried. Stones and visible plant material were removed manually. The soil had the following properties (Shi and Marschner, 2014): sand 274 g kg^{-1}, silt 499 g kg^{-1}, clay 227 g kg^{-1}, EC 0.1 dS m^{-1}, pH 5.7, maximum water-holding capacity (WHC) 358 g kg^{-1}, total organic C (TOC) 18.9 g kg^{-1}, total N 0.7 g kg^{-1} and C/N ratio 27. Details about the measurement of soil properties are given in Shi and Marschner (2013). Briefly, soil particle distribution was measured by the hydrometer method, soil pH and EC in a 1:5 soil to reverse osmosis (RO) water ratio after one hour end-over-end shaking. Maximum water-holding capacity (WHC) was determined by placing the soil in rings in sintered glass funnel attached to a 100 cm water column ($\Psi m = -10$ kPa), then the soil was wetted to saturation and drained for 48 h. The dry soil was weighed after drying in a fan-forced oven at 105 °C for 24 h. Total organic C concentration was determined by dichromate oxidation (Walkley and Black, 1934) and total N concentration by micro-Kjeldahl digestion (Ma and Zuazaga, 1942).

2.2. Experimental design

Before the onset of the experiment, the soil was pre-incubated for 10 days at 70% of WHC to reactivate the microbes and stabilise soil respiration after rewetting of air dry soil (Setia et al., 2011). This water content was based on a previous study where we found that 70% of WHC is the optimum water content for respiration in this soil (Shi et al., 2015). The pre-incubation was carried out by placing 20 g soil (dry weight basis) immediately after wetting in PVC cores (height 5 cm and diameter 3.7 cm) with the bottom covered by a nylon mesh (7.5 μm, Australian Filter Specialist). The soil was then adjusted to a bulk density similar to that in the field (1.35 g cm^{-3}) by pressing the soil to a certain height using the following formula:

$$\text{Bulk density} = \frac{M}{\pi r^2 h}$$

where M = soil mass (g), r = radius of the cores (cm), h = height in the core (cm). The cores were placed on a tray in the dark at constant temperature (22 °C). The tray was covered loosely with a lid to minimize water loss. Soil water content was checked every 2–3 days, and reverse osmosis (RO) water was added if necessary to maintain the water content at 70% of WHC. The pre-incubation in the cores was done to minimize interference of soil disturbance with the effect of soil drying on microbial activity at the beginning of the experiment. After pre-incubation, the soil cores were transferred into 1 L glass jars (Ball®, Jarden Corporation) with gas-tight lids to measure CO_2 release.

Two incubation experiments were carried out. The aim of the first experiment was to determine soil respiration rate, total cumulative respiration and microbial biomass C (MBC) concentration one day after rewetting over four DRW events in which glucose was added in all four cycles or only in cycle 1, 2, 3 or 4 with other cycles rewetted with RO water. Three glucose concentrations were used: low (50 μg C g^{-1} soil), medium (250 μg C g^{-1} soil) and high (500 μg C g^{-1} soil). These concentrations were chosen based on a preliminary experiment in which the soil was rewetted with a wide range of glucose concentration (0.05, 0.1, 0.5, 1, 2, 4, 6, 8 and 10 mg C g^{-1} soil). The respiration flush one day after rewetting increased from 0.05 to 0.5 mg C g^{-1} soil, and didn't increase further at higher glucose concentrations. The amount of glucose added in our study was within the range of 5 and 5000 μg per g soil which had been used in previous studies (Hoyle et al., 2008; Šantrůčková et al., 2004).

There were 17 treatments in total, with five drying and rewetting (DRW) treatments for each glucose concentration: glucose added in all 4 cycles, or only in cycle 1, 2, 3 or 4, water was used for rewetting in the other three DRW events (see also Fig. 1). Additional treatments included four rewetting events with RO water and a constantly moist (CM) control with soil water content maintained at 70% of WHC throughout the experiment. Fifteen replicates were set up per treatment to allow destructive sampling for MBC concentration determination one day after rewetting at each cycle (three replicates per sampling date).

Experiment 2 was conducted to investigate short-term changes in microbial biomass after rewetting. Microbial biomass C concentration was determined daily during the three-day moist period in cycles 1 and 4 without or with glucose addition at rewetting. Only the medium glucose concentration was used (250 μg C g^{-1} soil) which was added in all four cycles. Thus, there were three treatments: CM, four DRW cycles with addition of either water or medium glucose concentration. Eighteen replicates per treatment were prepared for destructive measurement of microbial biomass C concentration on days 1, 2 and 3 after rewetting in cycles 1 and 4 (three replicates per sampling date).

Experimental conditions and length were similar in both experiments. In each DRW cycle, there were five dry days and three moist days. To ensure rapid and complete soil drying, a pouch with self-indicating silica gel (BDH Chemicals) was placed in each jar on the first day of each dry period and exchanged daily for five days. Previous tests had shown that the silica gel did not absorb measurable amounts of CO_2 (Butterly, personal communication). For regeneration, the pouches were dried at 105 °C overnight in a fan-forced oven. After addition of the silica pouches, the jars were sealed immediately with gas-tight lids