Soil Biology & Biochemistry 112 (2017) 269–276

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Partial drying accelerates bacterial growth recovery to rewetting

Annelein Meisner [a, b, *], Ainara Leizeaga [a], Johannes Rousk [a], Erland Bååth [a]

[a] Microbial Ecology, Department of Biology, Lund University, Ecology Building, SE-223 62 Lund, Sweden
[b] Sections of Microbiology and Terrestrial Ecology, Department of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark

ARTICLE INFO

Article history:
Received 21 December 2016
Received in revised form
8 May 2017
Accepted 16 May 2017
Available online 29 May 2017

Keywords:
Drying-rewetting
Bacterial growth
Respiration
Birch effect
Climate change
Drought

ABSTRACT

Fluctuations in soil moisture create drying-rewetting events affecting the activity of microorganisms. Microbial responses to drying-rewetting are mostly studied in soils that are air-dried before rewetting. Upon rewetting, two patterns of bacterial growth have been observed. In the Type 1 pattern, bacterial growth rates increase immediately in a linear fashion. In the Type 2 pattern, bacterial growth rates increase exponentially after a lag period. However, soils are often only partially dried. Partial drying (higher remaining moisture content before rewetting) may be considered a less harsh treatment compared with air-drying. We hypothesized that a soil with a Type 2 response upon rewetting air-dried soil would transform into a Type 1 response if dried partially before rewetting. Two soils were dried to a gradient of different moisture content. Respiration and bacterial growth rates were then measured before and during 48 h after rewetting to 50% of water holding capacity (WHC). Initial moisture content determined growth and respiration in a sigmoidal fashion, with lowest activity in air-dried soil and maximum above ca. 30% WHC. Partial drying resulted in shorter lag periods, shorter recovery times and lower maximum bacterial growth rates after rewetting. The respiration after rewetting was lower when soil was partially dried and higher when soils were air-dried. The threshold moisture content where transition from a Type 2 to a Type 1 response occurred was about 14% WHC, while >30% WHC resulted in no rewetting effect. We combine our result with other recent reports to propose a framework of response patterns after drying-rewetting, where the harshness of drying determines the response pattern of bacteria upon rewetting dried soils.

1. Introduction

Moisture is an important determinant of microbial activity in soil (Manzoni et al., 2012a). Fluctuations in moisture conditions create drying and rewetting events, which affect microbial growth rates and soil respiration rates (Kieft et al., 1987; Blazewicz et al., 2014), and it is well known that a pulse of carbon dioxide (CO_2) often is observed after rewetting a dry soil (Jarvis et al., 2007; Sponseller, 2007; Kim et al., 2012). Most studies of drying-rewetting events assess completely air-dried soils that are rewetted to optimal moisture (Chowdhury et al., 2011; Barnard et al., 2015; Meisner et al., 2015), but soil moisture content will vary spatially (Rey et al., 2017) and temporally (Cregger et al., 2012). Thus, the moisture content before rewetting will vary and is frequently much higher than in air-dried soils (Lado-Monserrat et al., 2014). The increase in respiration rate induced by rewetting has been shown to be less evident when soil is partially dried before rewetting (Kim et al., 2010; Yan and Marschner, 2014) and is only detectable when soil is dried to a moisture content below a threshold level (Fischer, 2009). Thus, rewetting completely air-dried soils could be considered a harsher perturbation than rewetting partially dried soils. It is generally assumed that the size of the respiration pulse will correlate with the amount of microorganisms killed by the drying-rewetting event (Kieft et al., 1987; Blazewicz et al., 2014; Fraser et al., 2016), although mobilization of carbon (C) released from soil organic matter (Xiang et al., 2008; Schimel et al., 2011) or the accumulation of osmolytes in microbial biomass (Warren, 2014; but see Boot et al., 2013) will also contribute to the respiration pulse.

Two patterns of bacterial growth have been observed upon rewetting a dry soil (Fig. 1). In the first pattern ("Type 1 response"; Fig. 1), bacterial growth rates increase linearly from low values

* Corresponding author. Microbial Ecology, Department of Biology, Lund University, Ecology Building, SE-223 62 Lund, Sweden.
E-mail addresses: annelein.meisner@biol.lu.se (A. Meisner), ainara.leizeaga@biol.lu.se (A. Leizeaga), johannes.rousk@biol.lu.se (J. Rousk), erland.baath@biol.lu.se (E. Bååth).

http://dx.doi.org/10.1016/j.soilbio.2017.05.016

upon rewetting without a lag period (Iovieno and Bååth, 2008). In the second pattern ("Type 2 response"; Fig. 1), bacterial growth rates start to increase exponentially after a clear lag period of up to 20 h of very low levels of bacterial growth (Göransson et al., 2013). These differences in growth patterns also result in a shorter recovery time for the Type 1 response, and higher rates of maximal growth in the Type 2 response (Meisner et al., 2015). Previous work showed that a prolonged drying period can shift the response pattern from a Type 1 to a Type 2 within the same soil (Meisner et al., 2013, 2015). It was hypothesized that a lower survival of microbes due to prolonged drying was the reason for this shift in response pattern (Meisner et al., 2015), suggesting that a harsher treatment would result in a Type 2 response with increasingly longer lag periods.

Since partial drying could be considered a less harsh treatment than air-drying, we hypothesized that a soil with a Type 2 response to rewetting air-dried soil would transform into a Type 1 response if dried only partially before rewetting (Fig. 1). As such, the aims of the current study were: (1) to test how partial drying affect the bacterial growth response upon rewetting a soil with a Type 2 response; (2) to determine at what moisture level the transition from a Type 2 into a Type 1 occurs. We expected that partial drying before rewetting would result in shorter lag periods before the increase of bacterial growth, lower maximum growth rates after rewetting and a shorter recovery time to values matching those in a constantly moist soil compared to air drying. In addition, we expected that partial drying before rewetting would result in a lower CO_2 release upon rewetting. A prerequisite for our study was that respiration and bacterial growth rates are reduced at lower water contents before rewetting (Iovieno and Bååth, 2008; Manzoni et al., 2012a).

2. Material and methods

2.1. Soil

Selected soils exhibited a Type 2 response after rewetting following 4 days' air drying, with an increase in bacterial growth after lag periods of around 15–20 h at 17 °C. Soil from Greenland was collected in August 2014 at Østerlien, which is located close to the Arctic Station, Qeqertarsuaq, Disko Island in Central West Greenland. The soil at this site was formed by quaternary deposits on pre-quaternary formations of crystalline, breccia and plateau-basalt lavas, of the order Gelisols (USDA, 1992) or Cryosols (FAO, 1989). The soil was sampled from the A-horizon (pH_{water} = 6.7; SOM = 5.7%). Soil from the U.K. was collected in August 2014 at the Henfaes Experimental Research Station, which is located 12 km east of Bangor, U.K. The soil was a fine loamy brown earth over gravel (pH_{water} = 5.3; SOM = 8.4%) classified as a Dystric Cambisol (FAO, 1989) or a Fluventic Dystrochrept (USDA, 1992) and was collected under ca. 12 year old Alder (*Alnus glutinosa*) or Beech (*Fagus sylvatica*) monocultures describes previously (Göransson et al., 2013). All soils were sieved (<2.8 mm) fresh, and stones and roots were picked out by hand. Soils were stored at 4 °C until use.

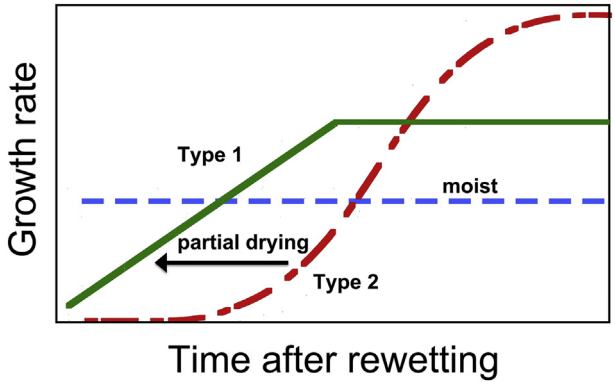

Fig. 1. Schematic overview of the two response patterns of bacterial growth found after drying-rewetting. In a Type 2 response (red stippled line), bacteria increase their growth rates after a clear lag period, whereas in a Type 1 response (green line), bacteria increase their growth rate linearly immediately after rewetting. The blue line indicates the bacterial growth rate in the constantly moist control soil. The arrow indicates the hypothesis that partial drying before rewetting changes the Type 2 into a Type 1 response. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Experiments

Four experiments were made. For the U.K. soils, the alder and beech forest soils were treated as replicate experiments. The Greenland soil was only sampled at one place, but two separate experiments with this soil were made in order to replicate the experiment. We combined non-independent experimental assessments of the same location for curve fitting.

2.2.1. Drying of soils

The soils were dried at room temperature (22–23 °C) under a fan until they reached the intended range of water contents. Before drying, 50 g field moist soil was placed into 500 ml microcosms and adjusted to 50% of its maximum water holding capacity (WHC). The time to reach the desired water content varied from 0 h (for 50% WHC) to 2 days (for air-dried soils). Once the approximate moisture content was reached, the microcosms were lidded and the water content was determined gravimetrically.

All the microcosms were placed at 17 °C and kept with lids closed for 1–4 days. Then bacterial growth and respiration were measured in the moisture gradient of soils one day before rewetting to estimate the direct effect of moisture content on growth and activity. The growth rate assessments used 1 h incubations and the respiration rate assessments used 24 h.

2.2.2. Rewetting of soils

Dried soils were rewetted to 50% WHC and incubated at 17 °C together with a moist control always kept at 50% WHC. Upon rewetting, bacterial growth was measured every 2–3 h during 48 h. To allow this sampling scheme, two sets of soils were prepared from each microcosm on the day of rewetting by placing 15 g subsamples of soil into 150 ml plastic vials. One set was rewetted in the evening and one set the following morning to allow for response curves with a high temporal resolution as has been performed previously (Meisner et al., 2013, 2015).

2.3. Microbial analyses

2.3.1. Bacterial growth

Bacterial growth was measured by the incorporation of ^{3}H-Leucine (Leu) into extracted bacteria (Bååth et al., 2001). Briefly, at each time point, one gram of soil was mixed with 20 ml demineralized water by vortexing for 3 min. The supernatant with a bacterial suspension was sampled after low speed centrifugation (1000 *g* for 8 min) and the incorporation of Leu was measured in 1.5 ml aliquots of the bacterial suspension. A combination of non-radioactive and tritiated Leu ([^{3}H]Leu, 37 MBq ml^{-1}, 5.74 TBq mmol^{-1}, Perkin Elmer, USA) was added to yield a final concentration of 275 nM. The extracted bacteria were incubated for 1 h at 17 °C. The samples were washed (Bååth et al., 2001) and the radioactivity of the incorporated Leu was measured on a liquid