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# Prolonged drought changes the bacterial growth response to rewetting

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ABSTRACT

Rewetting a dry soil can result in two response patterns of bacterial growth and respiration. In type 1, bacterial growth starts to increase linearly immediately upon rewetting and respiration rates are highest immediately upon rewetting. In type 2, bacterial growth starts to increase exponentially after a lag period with a secondary increase in respiration occurring at the start of the exponential increase in growth. We previously observed that the type 1 response occurred after rewetting 4-day dried soil and type 2 for 1-year dried soil. Here we studied in detail how the duration of drought related to the two types of responses of bacterial growth and respiration to rewetting. Soil was air dried for different time periods from 4 days up to 48 weeks. Upon rewetting, bacterial growth and respiration was measured repeatedly at 17 °C during one week. Drought periods of ≤2 weeks resulted in a type 1 response whereas drought periods of ≥4 weeks resulted in a type 2 response. The lag period increased with drought duration and reached a maximum of ca. 18 h. The bacterial growth response was also affected by incubation of moist soil before drying–rewetting. The lag period increased with duration of moist soil incubation before the 4-day drying–rewetting event and reached also a maximum of ca. 18 h. The exponential growth increase in the type 2 response coincided with a secondary increase in respiration, which increased in magnitude with increasing drought duration. Cumulative respiration increased with drought duration and was ca. 4 times higher after 48 weeks of drought compared to 4 days. Thus, prolonged drought affected the response type of bacterial growth and respiration to rewetting, and also increased lag period, the magnitude of the secondary increase in respiration and total C release. The effect of drought was, however, modified by incubation period of moist soil before drought, suggesting that soil conditions before a drying–rewetting event need consideration when evaluating microbial responses.



## 1. Introduction

Rewetting a dry soil will result in a pulse of $CO_2$ (Schimel et al., 2011; Kim et al., 2012; Placella et al., 2012). This phenomenon has been named the Birch effect after one of its first observers (Birch, 1958). The $CO_2$ pulse is large enough to be observed at field-scales when dry soil is moistened by rainfall events (Jenerette et al., 2008) and can contribute to a significant part of heterotrophic respiration in ecosystems (Yuste et al., 2005; Fan et al., 2015). The $CO_2$ pulse has been observed in many different ecosystems, including desert (Sponseller, 2007), agriculture (Priemé and Christensen, 2001), forest (Fierer and Schimel, 2002), and grassland soils (Warren, 2014). Respiration rates are often highest immediately upon rewetting, decreasing exponentially over time (Li et al., 2010; Kim et al., 2012; Meisner et al., 2013), but a secondary respiration increase has also been observed, with maximum rates reached around one day after rewetting (Göransson et al., 2013; Meisner et al., 2013). This secondary increase has been associated with more extensive drying (Meisner et al., 2013) or heating treatments (Haney et al., 2004) and may be involved in the increased release of $CO_2$ with more extensive drying (Chowdhury et al., 2011; Meisner et al., 2013; Barnard et al., 2015). As drying–rewetting events can affect soil C cycling, the microbial mechanisms that underlie the respiration response are of interest.

Two patterns of bacterial growth have been observed upon rewetting dry soil (Fig. 1). In the type 1 pattern, bacterial growth

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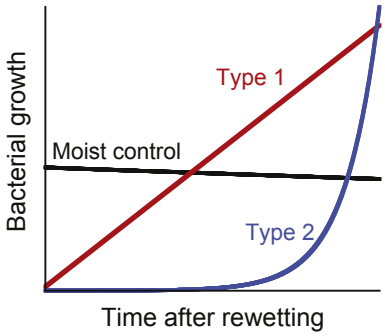


**Fig. 1.** Schematic overview of a type 1 and a type 2 response of bacterial growth upon rewetting a dry soil.

starts immediately upon rewetting and increases linearly with time (Iovieno and Bååth, 2008). This pattern has the highest respiration immediately after rewetting, and thus microbial growth dynamics do not coincide with respiration. In the type 2 response (Fig. 1) the initial bacterial growth is very low after rewetting, and starts increasing exponentially only after a pronounced lag period. The exponential growth coincided with a secondary increase in respiration (Göransson et al., 2013). Bacterial growth, which previously was observed to have a type 1 response, was changed into a type 2 response after rewetting soils dried for one year instead of four days (Meisner et al., 2013). However, the question remains if the transition from the first to the second response type is gradual or occurs after a threshold time of drying.

Here we study how prolonged drought affects the transition from the type 1 to the type 2 pattern after rewetting to determine if there is a threshold of drought for this transition, and if the relationship saturates toward longer durations of drought. The aim was thus to determine how a gradient of drought durations influenced bacterial growth and the respiration responses in soil upon rewetting. We hypothesized that a longer drought period before rewetting (1) would change the bacterial growth from a linear growth increase upon rewetting (type 1) to an exponential growth increase after a lag period (type 2), (2) would increase the lag-period when a type 2 response was present, and (3) would increase the total $CO_2$ released from soil. In addition, we expected a secondary increase in respiration rate to coincide with the bacterial growth increase in type 2 responses, with increasing levels with increasing drought periods.

We performed a series of experiments where a soil, which initially had a type 1 response when rewetted after a 4-day period of drought, was dried for 4 days up to 48 weeks. We measured bacterial growth and respiration rates at high temporal resolution upon rewetting. During the study, it was found that the incubation time of moist soil before the start of the drying period affected the microbial response. We thus also studied how the interaction between incubation time of moist soil and duration of drought affected respiration and bacterial growth responses after rewetting.

## 2. Materials and methods

### 2.1. Soil

Soil was collected from managed grassland in South Sweden in the autumn of 2012. The soil is classified as a sandy loamy brown earth soil (Cambisol, FAO; Inceptisol, USDA). This is a well-mixed soil without any conspicuous organic horizon and thus a composite sample was taken from approx. 0–20 cm depth. The soil had 15.6% soil organic matter (determined as loss on ignition at 600 °C) and a $pH_{water}$ of 6.5. The soil was sieved fresh prior to the experiments to remove stones and roots, and the water content was adjusted to 50% of water holding capacity. This soil was used in previous experiments (Meisner et al., 2013), and fresh soil was shown to have a type 1 rewetting response after 4 days air-drying. Fresh soil was also sampled in autumn 2013 to verify that the type 1 response still remained in fresh soil.

### 2.2. Experiments

Moist soil was put into 500 ml microcosms containing lids to prevent water loss, and microcosms were incubated at room temperature (approx. 22 °C). They were regularly aerated and water was added to adjust to 50% WHC when needed. At different time points, the lid was removed and microcosms were put under a ventilator to dry (Fig. 2). They were then incubated dry without lids under the same conditions as microcosms with moist soil. The mean moisture content of dried soils before rewetting was 3.1 ± 0.1% WHC (mean ± SEM), and did not vary systematically with duration of drought. Rewetting was performed for all samples of an experiment at the same time. Therefore, the soils had not only different periods of drought, but also different periods of incubation in moist conditions before drying (Fig. 2). All treatments were replicated three times.

Three experiments were set up that ran for different periods. The results from the different experiments were combined to be able to analyze both (i) soils with different drought periods but constant incubation time with moist soil, and (ii) constant drought periods and different incubation times.

Experiment 1 was set up in autumn 2012 and ran for 19 weeks (Fig. 2). 18 microcosms were prepared with 120 g of soil in each. Microcosms were sampled two times. At the first sampling (Exp. 1a), soil had been air dried for 0 (continuously moist), 4 days, 1, 2, 4 and 8 weeks. At the second sampling (Exp. 1b), soil had been air dried for 9, 13 and 17 weeks.

Experiment 2 was set up in January 2013 and ran for 26 weeks (Fig. 2). 12 microcosms were prepared with 60 g of soil in each. Soil was air dried for 0 (continuously moist), 4 days, 4, 6 and 26 weeks before rewetting.

Experiment 3 was set up in autumn 2012 and ran for 48 weeks (Fig. 2). 15 microcosms were prepared with 60 g in each. Soil was air dried for 0 (continuously moist), 4 days, 8, 12, 24 and 48 weeks before sampling.

### 2.3. Rewetting

Responses of respiration and bacterial growth were measured after rewetting at a minimum of 10 time points during one week at 17 °C. Soil was divided into two sets for each replicate the day before rewetting and incubated in the dark at 17 °C (the expected summer soil temperature in the region). On the day of rewetting one set was rewetted up to 50% WHC in the morning and one in the evening. The two sets were used to allow response curves with high temporal resolution as was done previously (Meisner et al., 2013). The soil was rewetted with demineralized water using a pipette, after which the soil was mixed thoroughly with a spatula. The two sets per replicate are combined in the graphs.

### 2.4. Measurements

#### 2.4.1. Respiration

For experiment 1, 3 g of soil was put in a 20 ml glass vial, purged with pressurized air, sealed and incubated at 17 °C. 4 ml air was sampled and stored in a 3 ml Exetainer® vial until analysis on a GC



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