



The impact of salinity on the microbial response to drying and rewetting in soil



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ABSTRACT

In saline soils, the severity of drought for the soil microbial community is exacerbated by accumulating concentrations of salts during drying. In this study we investigated how bacterial growth and respiration responses to drying-rewetting were affected by salinity. To do this, we adjusted a non-saline soil to four different salinities (0, 2, 7 and 22 mg NaCl g⁻¹), followed by addition of plant material and a one-month incubation. Following the incubation period, we assessed the moisture dependence of respiration and growth, as well as the responses of bacterial growth and respiration to a cycle of air-drying followed by rewetting to optimal moisture. The inhibition of bacterial growth and respiration by reducing moisture increased with higher salt concentrations. As such, salinity was shown to increase the negative impact of drying on bacterial growth and alter the bacterial growth and respiration dynamics after rewetting. Drying-rewetting of soils with low salinity resulted in an immediate onset and gradual resuscitation of bacterial growth to levels similar to before drying. In contrast, in soils with higher salinity growth increased exponentially after a lag period of several hours. The duration of the lag period induced by salinity increased with the amount of salt added. The observed lag period matched previously reported results observed in response to more severe drying by e.g. longer duration of drought and drought combined with starvation. In treatments with a salt concentration ≤ 7 mg NaCl g⁻¹ a high respiration pulse occurred immediately after rewetting and subsequently respiration declined. In the most saline treatment the initial respiration was reduced below the level of continuously moist soil to later increase exponentially in parallel with the increase in bacterial growth. We conclude that soil salinity increases the inhibition of microbial activity by low moisture, that fundamentally different responses to drying-rewetting cycles can be induced, and that high salt concentrations can substantially delay the pulse of respiration induced by rewetting dry soil.

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1. Introduction

Rewetting dried soil generally results in one of two types of responses of respiration and microbial growth (Fig. 1), during which respiration and bacterial growth rates have been found to be uncoupled (Meisner et al., 2013). In the first type of response (henceforth “type 1 response”) a linear increase in growth rate starts immediately after rewetting, recovering growth rates to levels similar to those before drying within hours. This coincides with a respiration rate that is highest immediately after

rewetting and subsequently decreases exponentially towards rates similar to before drying within days (Fig. 1). In the second type of response (henceforth “type 2 response”), an initial lag period of almost no growth occurs, lasting for up to 20 h, followed by an exponential increase of growth to levels far exceeding those before drying. This response coincides with elevated respiration rates that remain high for an extended duration and that are sometimes followed by a secondary increase that occurs simultaneously with the exponential increase in growth (Fig. 1). Whether the growth response to drying and rewetting in a particular soil follows a type 1 or a type 2 response has been proposed to be influenced by the severity of drying. For instance, a lag period in growth rates after rewetting can be induced by increasing the duration of drought before rewetting, as well as by a prolonged period of storage of soil samples prior

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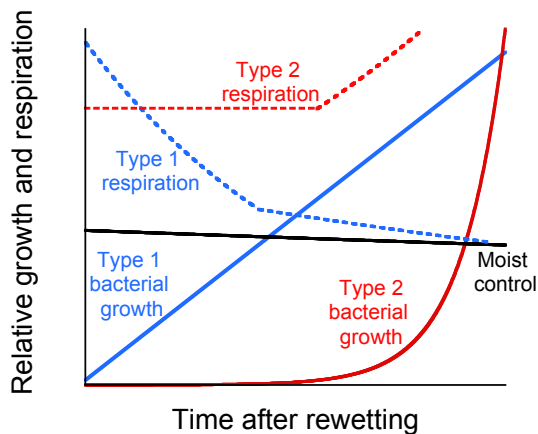


Fig. 1. Schematic illustration of type 1 (blue) and type 2 (red) responses of bacterial growth (solid line) and respiration (dashed line) to drying-rewetting. A type 1 response after drying-rewetting is characterized by a linear increase in bacterial growth, accompanied by an initial high respiration pulse that decreases exponentially over time. A type 2 response is characterized by a lag period of almost no growth together with elevated respiration rates, followed by an exponential increase in growth rate which coincides with an extended duration of elevated respiration rates and sometimes a secondary increase in respiration. The black line marks the continuously moist control for both bacterial growth and respiration, which decrease slightly over the course of the experimental period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to drying-rewetting which is thought to induce starvation (Meisner et al., 2015).

During drying of soil, the concentration of ions in the soil solution increases. High salt concentrations in soils are known to negatively impact microbial activity (Rath and Rousk, 2015). The combination of low soil water content and high salt concentrations could interact and exacerbate the negative effect of the individual factors on the soil microbial community. Even though saline soils are widespread in arid and semi-arid areas of the world, where droughts are a common occurrence, to date the effects of drying and rewetting (drying-rewetting) on the microbial community have been mainly studied in non-saline soils. In fact, only a handful of studies have looked at the combined effect of low water content and high salinity on the response of respiration and microbial growth to drying-rewetting (Chowdhury et al., 2011a, 2011b; Mavi and Marschner, 2012; Kakumanu and Williams, 2014).

This study consisted of a two-part experiment. Microcosms were set up by adjusting a non-saline soil to different salinities through addition of different amounts of NaCl. The microcosms were also supplied with additions of plant material, in order to provide the microbial communities with additional resources to fuel adaptation to salinity. First, we dried soils of different salinities and monitored the moisture dependences of respiration and bacterial growth during drying. Second, we rewetted dried soils of different salinities to study the influence of salinity on the dynamics of microbial growth and respiration after rewetting. We hypothesized (i) that the severity of drying experienced by the soil microbial community would increase with salinity (H1), and (ii) that higher severity of drying in the more saline soils would induce a shift from a type 1 response to a type 2 response of bacterial growth and respiration (H2).

2. Material and methods

2.1. Soil

Soil was collected in May and June 2015 from a permanent grassland site in Vomb, south Sweden (55° 40' 27" N, 13° 32' 45" E).

The soil is a well-drained sandy grassland soil and classified as a Eutric Cambisol (IUSS Working Group WRB, 2006) or Inceptisol (Soil Survey Staff, 1999). Multiple soil samples were collected with a spade from pits dug to a depth of ca. 20 cm and combined into composite samples, homogenized, and sieved (<2.8 mm). The soil had a water content (gravimetric, 24 h at 105 °C) of ca. $28 \pm 0.4\%$ dry weight (dw) (mean ± 1 SE of three replicates), a water holding capacity (WHC) of $65 \pm 2\%$ dw and an organic matter content (loss on ignition, 600 °C for 12 h) of $19.6 \pm 0.6\%$ dw. In a 1:5 soil:water mixture the pH was 6.1 ± 0.02 and the electrical conductivity was 0.09 ± 0.005 dS m⁻¹. Soil properties did not differ between soil sampled in May and June. Experiment 1 was performed on soil sampled in May only, whereas experiment 2 was performed on soil samples collected in both May and June.

2.2. Microcosm setup

Soil (250 g) was weighed into 1-l plastic containers with airtight lids and adjusted to four different salinity levels through the addition of different amounts of NaCl (0, 2.5, 7.3 and 22.2 mg NaCl g⁻¹ soil) together with 100 µl of H₂O per g soil. These salt additions resulted in a salt concentration of 0, 12, 31 and 98 mg NaCl per g H₂O in moist soil. Electrical conductivity in the four treatments, measured in a 1:5 soil:water mixture (EC_{1:5}), was 0.1, 1.1, 2.8 and 6.8 dS m⁻¹. This corresponds to an electrical conductivity in saturated paste ranging from ca. 1–90 dS m⁻¹ (Rengasamy, 2006). For each level of salinity three replicate microcosms were set up. A complete set of 12 microcosms was set up with each of the soil samples collected in May and June. The soils were then incubated in the dark for 3 weeks at 18 °C with 15 mg 1:1 wheat straw –alfalfa g⁻¹ soil that was mixed into the soil by prolonged shaking on a vortex mixer. The added plant material had a C content of ca. 45% and a C/N ratio of ca. 45 (Dumas dry combustion, VarioMAX CN, Elementar, Hanau Germany). The particle size of the ground and sieved plant material was between 250 and 630 µm. Previously it was found that straw with a high C/N ratio predominantly stimulated fungal growth, whereas alfalfa with a lower C/N ratio predominantly stimulated bacterial growth (Rousk and Bååth, 2007). A mixture of both straw and alfalfa should therefore stimulate both fungal and bacterial growth. A water content of ca. 60% WHC was maintained throughout the incubation period and microcosms were regularly aired and mixed to prevent anoxic conditions. Previous experiments showed that three weeks incubation time after salt addition was a sufficiently long time period for the community to adapt to the increased salt concentrations, as was shown by an induced community tolerance occurring within ca. 1 week following salt exposure (Maheshwari, 2015).

2.3. Experiment 1: direct moisture dependence of respiration and bacterial growth

After an incubation period of three weeks at different salinities (see above) a subset of soil from each microcosm was gradually air-dried at 23 °C under a fan over a period of 3–4 days. Water content was monitored by weighing of microcosms and once a target soil water content was reached, subsamples of soil were collected and stored at 5 °C in closed vials for later analysis of respiration and microbial growth rates (see section 2.5.). The drying continued until the microcosms reached a constant weight, i.e. the soil was completely air-dried at a water content of ca. 1% WHC. The selected target soil water contents covered a range of soil water contents from moist soil to completely air-dried soil. All samples were analyzed simultaneously after the end of the experiment.

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