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Bacterial growth and respiration responses upon rewetting dry forest soils: Impact of drought-legacy

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ABSTRACT

Longer periods of drought and droughts of higher intensity are expected to become increasingly frequent with future climate change. This has implications for the microbially mediated turnover of soil organic matter (SOM), which will feedback to the global C cycle. In this study, we addressed the microbial dynamics underlying the pulse of respiration following rewetting of dry soil, and how the drought-legacy of the soil modulated this response. We studied the microbial dynamics upon rewetting of dry soils from a field-experiment in a temperate forest soil exposed to two seasons of experimental summer-drought, or ambient conditions, by rewetting air-dried soil samples, and monitoring the respiration and bacterial growth responses. The respiratory responses in drought-exposed soils were slower and reached lower rates than control soils, translating to less C mineralised one week after rewetting. While the bacterial growth in drought-exposed soil also was slower, this was only a delayed response, and no differences in cumulative bacterial growth one week after rewetting could be established between drought-exposed and control soils. The pulse in respiration and microbial growth following the rewetting appeared to be due to facilitated microbial C availability caused by physical perturbation of the soil induced by the rewetting event. Reduced C input by trees during drought probably contributed to differences between drought-treated and control soils. Our results indicate that a history of drought increases the microbial C-use efficiency during a rewetting, suggesting a negative feedback to climate warming.

1. Introduction

Changes in land-use and use of fossil fuels have strongly affected the global carbon (C) cycle to date (Le Quéré et al., 2009) with subsequent effects also on the global climate. These changes are also associated with increasing temporal variability of climatic factors and the frequency and risk for extreme events (Meehl and Tebaldi, 2004; Heimann and Reichstein, 2008). Longer periods of drought and droughts of higher intensity (Meehl et al., 2007) as well as heat spells (Ganguly et al., 2009; Fischer and Schär, 2010) are expected to grow increasingly frequent. These changes will also influence the turnover of the soil organic matter (SOM), which plays an important role in the global C cycle as a major component of the world's surface C reserves (Gruber et al., 2004). Soil respiration accounts for approximately two-thirds of total C loss from terrestrial ecosystems (Schimel, 1995; Luo and Zhou, 2006) and is principally governed by the factors temperature and moisture (Waksman and Gerretsen, 1931; Davidson and Janssens, 2006).

In soil, the turnover of SOM is dominated by the soil microbial community, composed primarily of bacteria and fungi. The influence of drying–rewetting events on the overall decomposer function of the microbial community has been frequently assessed (e.g. Birch, 1958; Bloem et al., 1992; Fierer and Schimel, 2003; Xiang et al., 2008). It is well-known that rewetting dry soil results in a pulse of respiration of a much higher rate than the basal respiration of the moist soil. The phenomenon has been named "the Birch-Effect" in recognition of its first documentation (Birch, 1958). Surprisingly, the microbial mechanisms underlying the dynamics of the Birch-effect remain only rudimentarily understood to date. There have been assessments of the endpoints of drying–rewetting cycles on the soil microbial community, including indications of reductions in microbial biomass (Wu and Brookes, 2005), changes in the composition of the microbial biomass (Fierer et al., 2003; Steenwerth et al., 2005; DeAngelis et al., 2010) and different effects on fungi and bacteria (Gordon et al., 2008; Bapiri et al., 2010). Moreover, progress has been made regarding how drought and

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dry-wet cycles affect microbial processes based on assessments of enzyme activities in the soil (Alarcón-Gutiérrez et al., 2010; Tiemann and Billings, 2011; Evans and Wallenstein, 2012). This has resulted in forwarding the hypothesis that the microbial release of osmo-regulatory low molecular weight dissolved organic matter components, including amino acids, underlie the respiratory pulse following rewetting (Williams and Xia, 2009). However, reports on the direct effects on the primary agent of biogeochemical cycles during the Birch-effect, the active microbial community itself, are still rare. Especially, high-resolution assessments of the dynamics of the active microbial community during the course of the Birch-effect respiration pulse are lacking from the literature. Likely, this is due to a lack of suitable methods to assess the actively growing microbial community (Rousk and Bååth, 2011). The single attempt to date to measure both the microbial growth rate and respiration during the course of a rewetting event, to monitor the microbial dynamics underlying the Birch-effect, was reported by Iovieno and Bååth (2008). There, as expected, respiration increased immediately upon rewetting dry soil to maximal levels far exceeding those in a continually moist soil, and, while decreasing exponentially following these maxima, rates remained higher than those of a moist control soil for several days. In contrast, bacterial growth only gradually increased to slowly converge with rates similar to those in a continually moist soil only after about 8 h. Thus, the bacterial growth response was found to be decoupled from the respiration response during the first few days after rewetting. While this case-study demonstrated a way forward to generate an understanding for the microbial mechanisms in the regulation of the C mineralisation during rewetting of dry soils, this has to date not been translated into comprehensive assessments of drought-exposed soils.

The increasing variability of soil moisture caused by droughts and an intensification of the hydrological cycle (Meehl and Tebaldi, 2004; Heimann and Reichstein, 2008) combined with the powerful effect of dry–wet cycles on soil respiration, will make drying–rewetting events increasingly important to consider in achieving an overall C budget of terrestrial systems (Suseela et al., 2012). Moreover, the coupled responses of the decomposer microbial community will be important to address both to enable a mechanistic understanding of the underlying microbial dynamics behind the Birch-effect, and to identify long-term consequences of it. The latter of these statements can be illustrated by the basis for a method developed to estimate microbial biomass (Blagodatskii et al., 1997), where the difference in soluble N between dried and moist soil samples is used to estimate viable microbial biomass-N, implying a very destructive influence by dry conditions that will impair decomposer function, at least transiently.

In this study, we addressed the microbial dynamics underlying the Birch-effect, and how the drought-legacy of the soil modulated this response. To do this, we used soils from a field-experiment in a temperate forest to assess the "Birch-effect" in soil exposed to two seasons of experimental summer-drought or to ambient conditions. We hypothesized that (i) bacterial growth (gradual) and respiration (immediate) dynamics upon rewetting would be decoupled over the first 24 h after rewetting, (ii) that variation in low molecular weight components of the dissolved organic carbon in soil solution would correlate with the respiratory responses, suggesting a connection to microbial release of osmo-regulatory compounds, and (iii) that the history of drought would influence the microbial dynamics and respiratory response following rewetting. More precisely, we predicted that forest soils previously exposed to summer drought would release (i.e. respire) less C compared to the C used for bacterial growth, suggesting a bacterial community acclimatised to drought conditions. To test this, we air-dried soil samples from the field experiment, and subsequently monitored the respiration and bacterial growth following a rewetting event at high resolution for one week.

2. Materials and methods

2.1. Soils and field experiment

The study site was located at the Henfaes Experimental Research Station (53°14′N, 4°01′W) on the coastal plain, about 12 km east of Bangor, Wales, UK. The climate is Hyperoceanic, with average annual rainfalls of about 1000 mm. The soil at Henfaes is a fine loamy brown earth over gravel (Rheidol series) classified as a Dystric Cambisol (FAO, 1989) or a Fluventic Dystrochrept (USDA, 1992). The aspect is north-westerly, at an altitude of 13–18 m a.s.l. The depth of the water table ranges between 1 and 6 m.

The field experiment that our soil samples were collected from consisted of 8 experimental plots, half of which were roofed to reduce rain during the growing season (see below) to create experimental summer-drought conditions. The experimental plots were 8 m in diameter and located in the buffer zone of 2 former control plots (no treatment) previously used in the Free Air Carbon dioxide Enrichment experiment "BangorFACE". We used soil samples from plots where either beech (*Fagus sylvatica*) or alder (*Alnus glutinosa*) were planted at 80 cm spacing in a hexagonal design (Fig. S1). At the start of drought experiment the trees were 9 years old and had a mean basal diameter at about 1.3 m from the ground of 43 ± 1.6 mm in alder and 13 ± 0.5 mm in beech, corresponding to a basal area of 27 ± 2.0 and 2.4 ± 0.2 m^2 ha^{-1}, respectively. The fine root biomass in the top 10 cm of the soil, on the other hand, was similar in alder and beech soils, with 112 ± 53 and 102 ± 70 g m^{-2} respectively.

A transparent plastic roof was mounted between the tree rows on a wooden frame on the drought plots. The roof was 0.4–0.7 m above the soil surface with the highest part along a ridge in the middle allowing the water to flow into gutters along two sides. The gutters ended in buckets connected to outfalls leading the water at least 10 m away from the roof. The roofs covered approximately 70% of the area leaving open strips along the tree rows. Each subplot of 2.6 m^2 consisted of 9 trees and was surrounded by ample buffer zones of roofed area (Fig. S1). The roofs were mounted on the 10th of June 2010 and removed during the first week of November 2010 and then mounted again 14th of April and removed 13th of September 2011. Unroofed plots of an otherwise identical design were used as treatment controls for ambient conditions. Soil moisture and soil temperature was measured at 5 cm soil depth daily in-between the alder and the beech plots using TDR probes (Decagon Devices, Washington; see Fig. S1). Soil samples were also collected about bi-monthly and analysed gravimetrically (24 h at 105 °C) to verify TDR measurements and that different tree stand plots were not dissimilar in water content.

2.2. Laboratory rewetting experiment

We collected soil samples at the termination of the field drought experiment in September 2011. Using a 1 cm in diameter soil auger to 10 cm soil depth, five samples were combined into one composite sample in each of the four replicate plots of beech and alder. Samples were collected under the roofs in the drought-experiment. The samples were air-dried at room temperature until water content was completely reduced (i.e. no longer decreasing; for approx. 1 week), and subsequently stored dry for approximately two months until used in our experiments. For soil properties before rewetting see Table 1. To ensure the lack of any artefacts in measurements or treatments over the course of our