

Microbial response to drying and rewetting: osmotic and matric effects

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The pulse of CO₂ produced by rewetting a dry soil has long been the focus of field and laboratory experiments (Birch 1958). Many studies have probed the mechanism involved and how it may respond to differences in the size (Chen et al. 2009), and frequency (Fierer et al. 2003; Yao et al. 2011) of water input; and to the differing physical characteristics of plant community and soil types (Kim et al. 2010; Saetre and Stark 2005; Wang 2003). A consensus is yet to emerge for the mechanisms that are responsible for this pulse, but progress is certainly being made. The source of the respiration pulse following a drying-rewetting (DRW) event is thought to be newly available substrate, which comes from either microbial release of osmoregulatory compounds and/or labile organic matter released from physical protection (Xiang et al. 2008). In response to shifts in physical structure and substrate availability, DRW events often elicit a change in the composition and/or function of the microbial community (Chowdhury et al. 2011b; Gordon et al. 2008).

Stresses experienced by microbes during a DRW event are mediated through changes in water potential. The potential energy of water consists of contributions from gravitational, matric and osmotic

components. In soil, gravitational effects are minor, whereas osmotic effects (solute concentration) and matric effects (capillarity and adhesion) are the main contributors to overall water potential. In this issue, Chowdhury and colleagues take an interesting look at the interplay between water and salt content of soil; how those factors affect the size of CO₂ pulse, and the composition of the microbial community following a DRW cycle(s) in an artificially saline soil. The study investigated if more saline soils would produce larger CO₂ pulses, and if the microbial community in more saline soil would be more resistant to compositional changes when subject to DRW events.

Soils with three different salt contents (the original soil and two with added NaCl) were supplemented with ground wheat straw and subjected to one, two or three cycles of DRW. The addition of ground wheat straw was to reduce substrate limitation following multiple DRW cycles. Theory states that microbes respond to osmotic stress by accumulating intracellular solutes. The expected result of inducing greater osmotic stress by increasing soil salt content was a larger CO₂ pulse in soils with higher salinity. Results were mixed. At the highest salt content, overall microbial activity was reduced and cumulative C respired was the same for the low and intermediate salt content by the end of the experiment. However, at the intermediate salt content there was a greater respiration pulse relative to the low level following the third DRW cycle. Microbial community composition (as evaluated by phospholipid fatty acid

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content) from soils with higher salinity was expected to be more resistant to DRW cycles, because it was already adapted to low water potential. Here results were not as expected; community structure changed in response to DRW cycles regardless of starting salt content, and maintained altered community structure until the end of the incubation (63 days) relative to a continuously moist control.

What are the controls on these processes? Why would microbes in soil with intermediate salinity respire more cumulative C following the third DRW cycle? Or, more generally, what are the potential explanations for any change in C respired by microbes in a ‘stressful situation’? The answers to these questions are a combination of factors including: total microbial biomass, total substrate availability and the use efficiency of available carbon by the existing biomass. In this study, the data indicated overall biomass did not change in response to either the DRW treatments or to the different levels of salinity. As hypothesized by the authors, an increased availability of substrate, potentially due to larger osmolyte pools at intermediate salinity, is a reasonable explanation; however, a more efficient use of the same size C pool with equivalent microbial biomass cannot be ruled out.

In this study, why does community composition shift in response to DRW events regardless of salt content, and can the explanations invoked be applied to other types of sudden stress events? Whenever I think of microbial community composition I am tempted to extrapolate to the macro-organism scale in search of a conceptual framework. With regard to soil DRW events, the habitat that comes to mind is the intertidal zone. In the intertidal, the plants and animals living there must cope with drastic daily extremes in turbulence, temperature, salinity and water content. In soil, the dimension of turbulence is removed, and the temperature effect is modulated, but the extremes in water content are of the same scale, i.e. almost completely dry to saturated. In the above-ground world, a specialized and highly adapted community exists in the intertidal environment. Belowground, at the micro-scale, there may or may not be a specialized community that can cope with sudden stress depending on the environment. While microbial populations can be spatially distinct with some known predictors of biogeographical patterns (Fierer et al. 2009; Martiny et al. 2006) the resistance and resilience of these communities is still a question

where more work is needed. Perhaps a better way to pose the question of why microbial communities shift due to stress events is not by looking for resistance or resilience in the native communities, but by looking for similarities in those that survive/respond to environmental stressors. In the study by Chowdhury et al. in this issue, their data do fall along these lines with more similarities overall among the communities subjected to DRW events than with those that remained continuously moist.

The ability of microbes to tolerate or respond to matric and osmotic stress, and substrate characteristics, were likely the determining factors of microbial community structure in this study. At the start of the experiment, salt contents of the soil were adjusted; they were pre-incubated, and then were amended with wheat straw, so the extant microbial community had access to very similar substrate chemistry. No matric stress was induced in continuously moist controls, so the gradient of osmotic stress along with changing substrate quantity and quality over the course of the incubation likely caused community composition to diverge. When subject to DRW events, microbes that were able to respond to/survive the combination of matric and osmotic stress were less variable than those that could tolerate osmotic stress alone. Further, the microbes in the moist controls had access to the variety of products from continuous decomposition of soil organic matter. In the DRW treatments, however, the microbial community was limited to less diverse substrates: either wheat straw or those produced via DRW events from osmolyte production/aggregate disruption, further constraining the active community (Goldfarb et al. 2011). Although community structure was not more resistant to DRW events at higher salinities as expected, the authors recognized that because salinity was induced rapidly two weeks prior to the onset of the experiment, the pre-incubation time may not have been long enough for development of a halotolerant/halophilic microbial community.

Chowdhury and colleagues have recently published additional studies that seek to separate the effects of matric and osmotic potential on microbial community response and structure (Chowdhury et al. 2011a, b). Overall, low matric potential was found to be a greater stress than low osmotic potential. In addition, high osmotic stress was more damaging to fungi than to bacteria, and high matric stress was

more damaging to bacteria than to fungi. They also found that total microbial biomass generally decreased until water potential reached a threshold value of -2 MPa, below which the level of biomass was maintained. Maintenance of biomass at this level indicated the adapted/remaining microbial community was tolerant to the associated matric and osmotic stresses. These types of threshold data are critical for developing a larger-scale understanding and predictive ability that can be translated to other ecosystems or climatic regimes (Li et al. 2010).

All three of the studies by Chowdhury and colleagues (this issue; Chowdhury et al. 2011a, b) contribute data to the underexplored question of how microbes respond to osmotic stress in saline soils, and add useful information on consequences of low matric potential in dry ecosystems. Based on their data, the mechanisms for this response seem to be distinct under matric and osmotic stress. In soils with high osmotic stress but sufficient moisture, solute concentration is high but there is still liquid water present. In soils with high matric stress, microbes are consolidated into tight water films surrounding soil particles or capillary water at particle junctions. The thickness of water films depends on soil particle structure, but at low water potentials (< -1.5 MPa) estimates are on the order of 10s to 100s of nm (Or et al. 2007). With the average dimensions of *E. coli* at $2\text{ }\mu\text{m}$ length and $0.5\text{ }\mu\text{m}$ thickness, it is unlikely that bacteria are immersed in water films on soil particles. Instead, microbes are likely maintained in a matrix of extracellular polymeric substances (EPS). The exact composition of EPS has been difficult to determine, but it is known to be a complex mixture of polysaccharides, proteins, organic acids, and extracellular DNA (Steinberger and Holden 2005). Returning to the intertidal conceptual framework, the function of EPS is akin to the mucus that surrounds intertidal organisms protecting them from desiccation. Indeed, EPS has been shown to modulate microbial survival by retaining water and maintaining nutrient gradients (Roberson and Firestone 1992). Future studies that are seeking to address questions of matric stress and possibly osmotic stress as well, would do well to consider the impact of EPS on microbial survival.

The state of our knowledge on microbial response to DRW events, like that of any scientific question, breaks down to what we think we know, and what we are still trying to figure out. We know the CO_2 pulse

following a DRW event is a combination of microbially derived and liberated labile organic matter. We know the microbial community generally shifts in response to a DRW event. We know we can describe the pulse dynamics reasonably well with modeling. The work of Chowdhury and colleagues adds information that was lacking on the response of saline soils to DRW events, and contributes to our understanding of the matric and osmotic affects on the microbial community. Continuing work should enhance our understanding the functional response of the microbial community and its resistance/resilience to DRW events. These data can then be applied to shifting climatic patterns and how changes in the size and frequency of DRW events will impact C storage in future climate scenarios.

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