The Biogeochemistry of Drought

Joshua Schimel[1], Claudia Boot[1], Patricia Holden[2], Dad Roux-Michollet[2], Sophie Parker[1], Sean Schaeffer[1], and Kathleen Treseder[3]

[1]Dept. Ecology, Evolution, and Marine Biology. University of California Santa Barbara. Santa Barbara, CA 93106. USA. Schimel@lifesci.ucsb.edu
[2]Bren School of Environmental Science & Management. University of California Santa Barbara. Santa Barbara, CA 93106. USA.
[3]Dept. Ecology & Evolutionary Biology. University of California Irvine. Irvine, CA 92697. USA.

Abstract

At least 1/3 Earth's land experiences regular drought, and climate models suggest this will increase. However, the biological processes occurring during the dry season have only been studied by inference from what happens when the rains return. Important dry soil phenomena remain unexplained, such as the "Birch Effect"--the pulse of respiration on rewetting a dry soil. Important and surprising processes occur during the dry season. For example, during the California summer, in grasslands, soils are dry and plants are dead, but the biomass and population size of several important groups of microorganisms increase, even though their activity is very limited. These changes appear to result from a combination of microbial drought survival physiology and disconnections in soil water films in dry soil and limit substrate diffusion and organismal movement. This talk will discuss the current state of knowledge on microbial drought and dry/wet cycle dynamics.

Keywords

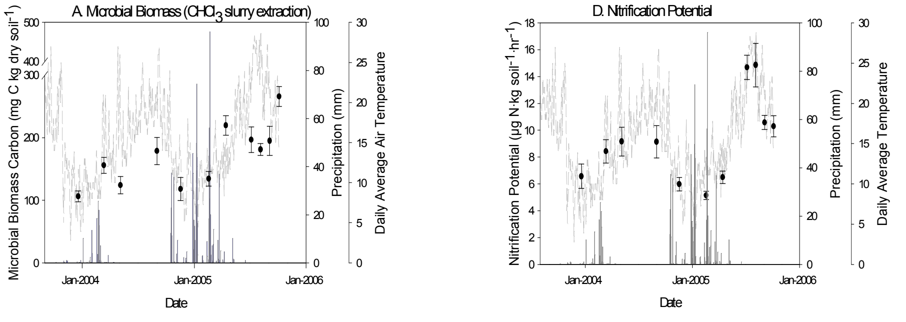
Drought, biogeochemistry, California, grassland

Introduction

The world is a dry place: roughly 1/3 of the terrestrial land surface has arid, semi-arid, or Mediterranean climates that are characterized by long droughts. Climate models also suggest that drought is likely to become more prevalent with climate warming. However, the biogeochemistry of the dry season has usually been studied only implicitly– as "antecedent conditions" that regulate the pulses of biological activity that occur with the early rains or the chemical characteristics of streamflow. However, rarely have the biogeochemical processes that occur during the dry season been studied explicitly to understand what creates the conditions at the beginning of the wet, "growing season."

In California, summer can go 6 months without any rain. During the summer, temperatures can exceed 40° C. It has always been assumed that the "non-growing season" was a period of dormancy and mere survival: native grasses senesce, some native shrubs are partially drought-deciduous, and microbial respiration rates drop to levels of 0.1 to 0.3 g C/m^2/d as soils dry to as low as 5% H_2O (Xu *et al.* 2004).

Surprisingly, however, over the summer, microbial biomass increases (Figure 1a; Parker 2006) as do the potentials for nitrification and denitrification (Figure 1d) and even denitrification potentials more than doubled (Figure 1e). These surprising results beg an explanation. Why, at a time when activities are lowest and conditions appear worst, does it appear that many groups of organisms are doing best?



We hypothesized that these surprising summertime dynamics result from two micro-scale phenomena: a) the physiology of microbial drought survival and b) the hydrological disconnectivity of the "microbial landscape." As soils dry, microbes experience direct physiological stress, resource limitation from drying, and hydrological disconnections in their environment. On the other hand, microbes may experience reduced predation pressure (Gorres *et al.* 1999) because microbial predators also rely on a connected landscape for foraging.

As water potentials decline, cells must accumulate solutes to reduce their internal water potential to avoid dehydrating and dying. As their primary osmolytes, microorganisms are thought to use simple organics as osmotic agents. In culture, bacteria have been shown to use amino compounds such as proline, glutamine, and glycine betaine (Csonka 1989), while fungi use polyols such as glycerol, erythritol, and mannitol (Witteveen & Visser 1995). Although bacteria are able to accumulate K^+, they only do this after they have exhausted their ability to synthesize or take up preferred compounds (Killham & Firestone 1984).

Accumulating osmolytes however, is energetically expensive. Bacteria can accumulate amino acids to between 7 and 20% of total bacterial C (Killham & Firestone 1984) and between 11 and 30% of bacterial N. In fungi, polyols can account for over 10% of cell mass (Tibbett *et al.* 2002). When extrapolated to an ecosystem scale, the amounts are large. For example, in a grassland soil, osmolyte production to survive a single drought event could conservatively account for 20 g C/m^2, compared to an NPP in the range of 300 - 600 g/cm^2/y. The proportional values for N are larger, 0.75 g N/m^2 or more, equivalent to 10-40% of annual net N mineralization.

If summers are stressful, however, it is thought that the rewetting in the fall could be even more damaging, causing up to 50% mortality (Kieft *et al.* 1987). This is in line with the "Birch Effect," the flush of respiration and mineralization on rewetting a dry soil.

In our research, we have explored the dynamics of dry season biogeochemistry, with specific questions being:

What are the changes in microbial populations and processes through the dry summer?
How important are these dynamics in annual C and N cycles?
What mechanisms are responsible for these changes?
What happens on rewetting?
What are the physical and biological mechanisms that regulate drying/rewetting dynamics?

Materials & Methods

Our core research site is at the Sedgwick Reserve in the Santa Ynez Valley of Central California. This is an area with a Mediterranean Climate—cool wet winters and hot dry summers. The soils are Mollisols, typically argixerolls, with pachic argixerolls dominating on valley floors. The vegetation is a mix of open annual grassland, dominated by Mediterranean invasive species dominated by *Bromus diandrus* and *Avena fatua.*

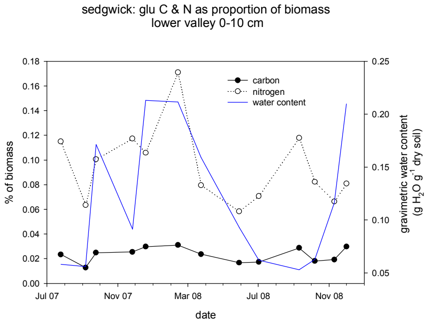
We measured biogeochemical parameters by regular soil sampling throughout several summers. Soil cores were collected to 20 cm depth and returned to the laboratory for analysis. Microbial biomass was measured by a $CHCl_3$ slurry method (Fierer and Schimel 2003). Mineralization potentials were measured by sealing jars and measuring headspace CO_2 accumulation; periodically samples are harvested and analyzed for NH_4^+ and NO_3^-. Nitrification potentials were measured by chlorate slurry (Belser and Mays 1980). Cellular amino acids (osmolytes) were analyzed by HPLC on the $CHCl_3$ extracts. *In situ* fungal growth was measured using minirhizotrons with a microscopic camera and image analysis to evaluate the turnover of individual fungal hyphae. Drying/Rewetting experiments were done in the laboratory with soil samples in canning jars. Soils were allowed to air dry for varying periods of time and then were rapidly rewet.

Results and Discussion

While in situ respiration rates are minimal during the dry summer (data not shown), all indices of microbial biomass and potential are typically highest at the end of the dry season; these include microbial biomass, short-term respiration potential, and nitrification potential. Fungal growth is slow during the summer, averaging < 2 new hyphae /m^2/month. Certain bacterial populations, notably proteobacteria, on the other hand, crash with the onset of summer. Pools of NH_4^+ and extractable organic C (EOC) increase through the summer but crash with the first rains of autumn, the NH_4^+ rapidly being nitrified.

We postulate that NH_4^+ and EOC pools increase because some exo-enzymatic and microbial processes continue in thin water films even in dry soils, but that diffusion is so limited that these materials remain unavailable until soils wet up. What remains unclear is why overall microbial populations increase during the dry summer. We hypothesize that this is because bacteria and fungi that survive the initial dry-down are drought tolerant and so while they maintain low rates of activity and growth, those rates aren't zero. Predation by protozoa and other microfauna, on the other hand, should be even more sensitive to moisture than is microbial growth. Protozoa require water-filled pores to forage. Thus, in a dry soil, death rates may decline even more extremely than do growth rates, allowing populations to increase.

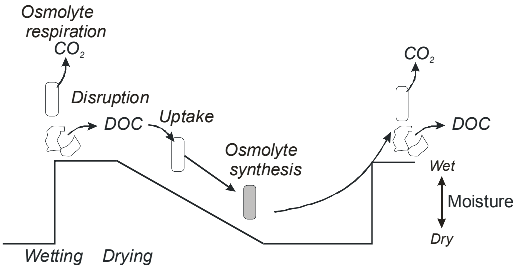
We measured the *in situ* concentrations of cellular amino acids throughout the year, anticipating that concentrations of known amino acid osmolytes (proline and glutamate) would increase over the summer. In fact, proline was never measurable, while glutamate remained a relatively constant proportion of the totat microbial biomass throughout the year, changing little between summer and winter. Thus, amino acids do not appear to be used as osmolytes in this microbial community. We are measuring other possible compounds, but it also remains possible that in a natural soil, where C is a limiting resource, that microbes are forced to rely on inorganic osmolytes or that a large fraction of the community uses glutamate as a constitutive osmolyte.



When dry soils are finally rewet, there is a large flush of respiration. An isotope equilibration experiment, in which ^{14}C-glucose is added to soil and incubated into the microbial biomass prior to dry-down and rewet, indicated that the CO_2 released is dominated by microbial material, although a substantial amount of extractable organic C was also released (Fierer and Schimel 2003). However, in a number of studies, we have found that through multiple dry-wet cycles microbial biomass does not decline, and may actually increase dramatically (Xiang *et al*. 2008). Additionally, through multiple dry-rewet cycles, more CO_2 may be released than was present in the biomass. Thus, while the C released in a single dry-rewet cycle may be dominated by microbial material, over multiple cycles, the C must be released by physical processes, such as aggregate disruption, desorption, and diffusion of otherwise unavailable material to microbes.

Thus, these results raise some conundrums that are difficult to reconcile: the apparent lack of identifiable organic osmolytes, the apparent microbial source for CO_2 respired in the rewetting flush, and the multiple-cycle requirement that it is soil organic matter that fuels successive rewetting pulses. Our current working hypothesis to tie together these different results is that physical and biological processes are closely coupled through multiple dry-rewet cycles.

We hypothesize that during drought, several critical processes occur: 1) microbes accumulate cellular materials that may be respired on rewetting, and 2) desorption, exoenzymes, and microbial turnover produce a pool of easily respired material that accumulates because of diffusion limitation. On rewetting, several processes occur: 1) microbes respire some measure of the cellular material, 2) the accumulated soil material becomes bioavailable and is rapidly metabolized, and 3) mass rewetting redistributes organic materials throughout the soil, overcoming native diffusion limitation, and 4) desorption and aggregate disruption release an additional fraction of otherwise unavailable soil organic matter. The newly-available resources are used by microbes and accumulate as cellular materials as a new drying cycle begins. Thus, while it is physical processes that ultimately drive C from the soil through multiple dry-rewet cycles, these are proximally mediated by microbial processes associated with stress tolerance and the release from stress.



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