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DE-SC0008208:
Climate Change Feedbacks from Interactions Between New and Old Carbon

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EXECUTIVE SUMMARY

Title: **Climate Change Feedbacks from Interactions Between New and Old Carbon**

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Priming effects, or responses of SOM decomposition rates to inputs of new, labile carbon (C), have the potential to dramatically alter projections of ecosystem C storage. Priming effects occur in most ecosystems, are significant in magnitude, and are highly sensitive to global changes. Nevertheless, our mechanistic understanding of priming effects remains poor, and this has prevented the inclusion of these dynamics into current Earth system models (ESMs).

We conducted two manipulative experiments in the field to quantify how priming effects influence SOM dynamics. Specifically, we asked: *To what extent do inputs of "new" root-derived carbon (C) influence "older" C in SOM, and are the magnitude and direction of these effects sensitive to climate?* We addressed these questions within the Boston-Area Climate Experiment - an old-field ecosystem that has been subjected to three precipitation treatments (ambient, -50%, and +50% of each precipitation event during the growing season) and four warming treatments (from ambient to +4°C) since 2008.

In the first experiment, we installed root and fungal ingrowth cores into the plots. Each core was filled with SOM that had an isotopic signature (of its C compounds) that differed from the vegetation in the plots such that inputs of "new" C from roots/fungi could be quantified using the change in isotopic signatures of C in the cores. Further, we used cores with different mesh sizes to isolate root vs. mycorrhizal fungal inputs. We found that belowground C fluxes were dominated by root inputs (as opposed to mycorrhizal inputs), and that root-derived inputs were greatest in the plots subjected to experimental warming. Given that that the warming-induced increase in belowground C flux did not result in a net increase in soil C, we conclude that the warming treatment likely enhanced priming effects in these soils.

In the second experiment, we experimentally dripped dissolved organic C compounds into soils in the BACE plots to simulate root-derived C fluxes. Specifically, we constructed artificial roots attached to an automated peristaltic pump to deliver the compounds to soil semi-continuously during the peak of the growing season. We found that changes in exudate quality had small but significant effects on microbial activities, often interacting with N availability and temperature-induced changes. These results further underscore the importance of priming effects, especially under warming conditions.

Collectively, our results provide some of the first field-based estimates of how soil moisture and temperature can directly and indirectly alter root-induced changes in SOM dynamics. This exploratory project lays the groundwork for further research on priming that incorporates effects of plant species and microbial communities to global changes. Such information should enable the development of more mechanistic and better predictive models of SOM decomposition under increased greenhouse gas levels, with the ultimate goal of reducing the level of uncertainty in projections of future climate.

Project Goals, Objectives, and Accomplishments

Background

There is a need to better represent belowground processes in Earth system models (Ostle et al. 2009); these include limitations to plant growth from nutrient availability, and responses of the various components of soil respiration to environmental changes (Heimann and Reichstein 2008, Arneth et al. 2010). We characterized how precipitation patterns affect new C release via roots and mycorrhizae, and subsequent "priming effects" (PE) in a field context. Priming effects, the process by which new additions of labile C stimulate microbial decomposition of SOM, have the potential to accelerate recalcitrant SOM loss, potentially complicating common model assumptions about SOM pool turnover rates. **The goal of this project was to help identify the extent to which precipitation changes (and warming) modify PE, with the assumption that soil moisture will be the main driver of differences in both cases.** Strong responses to changes in precipitation and warming would suggest that the development of a more mechanistic representation of interactions between new and old C could improve model projections.

Our overarching goal was to contribute to improved climate projections. The best current projections of future climate come from Earth system models, which can dynamically simulate feedbacks to climate change from marine and terrestrial systems. Many sources of uncertainty limit the quality of current projections. Currently, some of the most uncertain feedbacks to climate change involve belowground terrestrial processes (Arneth *et al.* 2010). For instance, relatively few Earth system models permit nutrient constraints to limit the effects of CO_2 fertilization on plant growth (Wang and Houlton 2009), and representations of the response of heterotrophic respiration to warming in models often omit important seasonal patterns (Suseela *et al.* 2011). Accurate representation of C loss from soils (e.g., through heterotrophic respiration of litter and SOM) is critical, since twice as much C is stored in soils as in vegetation (Dixon 1994).

Long-term C storage in terrestrial ecosystems depends on the balance between C gains and losses in plant biomass and soil pools (Schlesinger & Lichter 2001). Most research to date has focused on factors that control C sequestration in plants (Dixon 1994). A fundamental challenge to studying changes in soil C storage is that the inputs are small relative to pool sizes, and that spatial heterogeneity (horizontal and vertical) constrains our ability to detect significant changes in C gains and losses. Additionally, processes that influence net primary productivity (NPP) often interact non-linearly with processes that control decomposition and nutrient release (Shaver *et al.* 2000). For this reason, ecosystem models make many simplifying assumptions about the factors controlling the fate of C inputs to soils (Schimel *et al.* 1994).

Current model structures represent SOM loss as functions of temperature, typically as first-order decay constants modified by soil moisture (Bauer *et al.* 2008, Reichstein and Beer 2008). To better represent responses of SOM decomposition to environmental changes, future model structures are likely to incorporate a more detailed understanding of the individual processes involved (Allison *et al.* 2010, Conant *et al.* 2011). Priming effects are not incorporated in most current models, likely due to a lack of understanding of their importance across systems; although the rhizosphere has been referred to as the "new frontier for soil biogeochemistry" (Hinsinger *et al.*, 2006), there is

a dearth of information on the ecological significance of PE and many other rhizosphere processes (Cardon & Whitbeck, 2007).

Paradoxically, many CO_2 enrichment experiments have failed to detect C accumulation (Lichter *et al.* 2008; Talhelm *et al.* 2009; Drake *et al.* 2011), and in some cases have found soil C losses (Carney *et al.* 2007), despite large increases in aboveground and belowground productivity. This pattern has been attributed to PE. Although PE are widely invoked as a mechanism to explain enhanced soil C loss (Hoosbeek *et al.* 2004; Carney *et al.* 2007; Paterson *et al.* 2008; Megonigal *et al.* 2009; Drake *et al.* 2011), few experiments have characterized PE in the field (Kuzyakov 2010). Given that PE have the potential to influence feedbacks to climate forcing through increased CO_2 fluxes to the atmosphere (positive feedback) and enhanced nitrogen (N) availability to plants (negative feedback), understanding the underlying mechanisms and biogeochemical consequences of PE is necessary if we are to realistically simulate terrestrial feedbacks to the increasing greenhouse gas concentrations (Heimann & Reichstein 2008) and changing climate.

Two common assumptions about PE are that the process is fueled by labile C from decomposing leaf litter (Hoosbeek *et al.* 2004; Carney *et al.* 2007; Megonigal *et al.* 2009; Sayer *et al.* 2011), and that the C released from priming originates from recalcitrant SOM that is hundreds to thousands of years old (Fontaine *et al.* 2004; Fontaine *et al.* 2011). However, roots contribute significant amounts of labile C to soils in the form of soluble exudates, sloughed cells and rhizodeposits (Grayston *et al.* 1996). Such inputs accelerate decomposition by providing rhizosphere microbes (including mycorrhizal fungi) with energy to synthesize SOM-degrading extracellular enzymes (Cheng & Kuzyakov 2005). Moreover, the rapid turnover and high N content of rhizosphere microbes (Rousk & Baath 2011) and mycorrhizal hyphae (Staddon *et al.* 2003) indicate that microbial necromass may be decomposed preferentially relative to more recalcitrant SOM (Kuzyakov 2010).

In the coming decades, model projections suggest Earth's climate will warm, and precipitation regimes will change (IPCC 2007). While the exact changes will vary over space and time, warming will tend to dry soils over much of the land surface, while precipitation changes will exacerbate or alleviate that drying. Increases in CO_2 concentration will lead to water savings in some locations, offsetting some of the drying effects of warming (Morgan *et al.* 2011). Although model algorithms currently adjust many respiration-related process rates based on soil moisture, PE are typically not included. Given that root and mycorrhizal fungal activities are generally greater in wet soils and rhizosphere PE may increase the temperature sensitivity of decomposition (Zhu & Cheng 2011), an improved understanding of the responses of PE to soil moisture changes will contribute to more accurate representations of ecosystem C cycling under global change (Ostle *et al.* 2009; Gardenas *et al.* 2011).

<u>Project activities</u> (including objectives, methods and hypotheses)

Our objectives were to understand how root exudation and PE respond to changes in soil moisture and temperature in the field (Fig. 1). Conducting this project at the BACE allowed us to take advantage of the broad spectrum of belowground research that has been conducted at the site. Further examination of the relationships between exudation

and other variables over the course of the 2012 and 2013 growing seasons provided context about the biotic and abiotic factors that control this process.

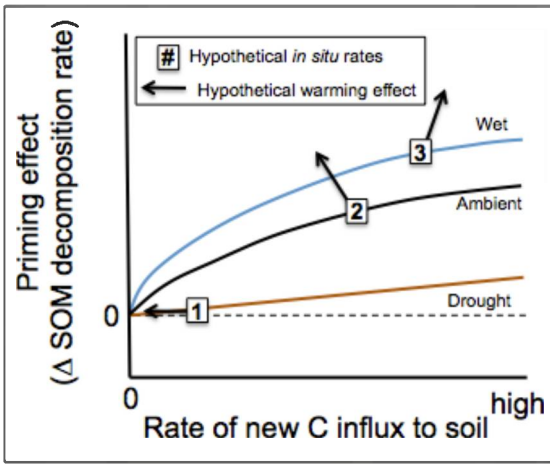

Fig. 1. Conceptual diagram of the hypothetical responses of priming effects to root and mycorrhizal C inputs under different precipitation regimes (drought, brown curve; ambient precipitation, black curve; wet treatment, blue curve). Numbered boxes show hypothetical values of cumulative annual C input and priming *in situ* under drought (1), ambient (2), and wet (3) treatments. Arrows show hypothetical changes in these values with warming. We expect the pattern of responses to depend strongly on N availability; for instance, values on the y-axis might be expected to scale with the inverse of N availability.

Objective I: To quantify the effects of elevated and reduced precipitation on root-derived C fluxes to soil.

Background. Belowground C fluxes have long been considered a "black box" in soils research, and little is known about the effects of soil moisture on rhizosphere processes in field soils (Grayston *et al.*, 1996). Previous work with loblolly pine trees by co-PI Phillips suggested that increases in root-derived C inputs are related to low resource availability (Phillips et al, 2011).

Hypothesis 1: Elevated precipitation will increase and reduced precipitation will decrease root-derived fluxes (Figure 1), with the magnitude of this effect being greatest in the warmed plots.

Approach (Brief methods)

We quantified root and mycorrhizal inputs to soil using a modification of the ^{13}C natural abundance technique (Staddon 2004). Soils with $\delta^{13}C$ signatures derived from C4 plants (which were uncommon at the BACE site) were transplanted into each plot. To partition the contribution of root and mycorrhizal fungal inputs, we placed these C4 soils into one of three types of in-growth cores: one with a mesh permitting the penetration of both roots and fungal mycelium (2 mm diameter), one with a mesh size allowing for penetration by fungal mycelia only (50 µm), and one with a mesh that restricted all root and fungal ingrowth (1 µm). To test different approaches to restricting all root and fungal growth, we also separately compared soils in cores made of 1 µm mesh, solid PVC, and a 50 µm mesh that was rotated 360 degrees every two weeks to break any mycelia that were growing. To facilitate growth of mycorrhizal fungi and not saprotrophic fungi, we ensured the soils had low C content (by mixing with sand; final content 0.6% C, Wallander *et al.* 2001; Hendricks *et al.* 2006), and placed cores in the zone of soil where mycorrhizal hyphae are dominant (upper 15 cm of mineral soil, Lindahl *et al.* 2007). We installed these ingrowth cores for two periods: an initial short-term experiment in late summer and early fall of 2012, and a subsequent one-year "main" experiment.

In the short-term ingrowth core experiment, we found that roots accounted for 90% of C inputs across all treatments and seasons (as determined by subtracting C inputs in 50 µm cores from those in 2 mm cores; Figure 2).

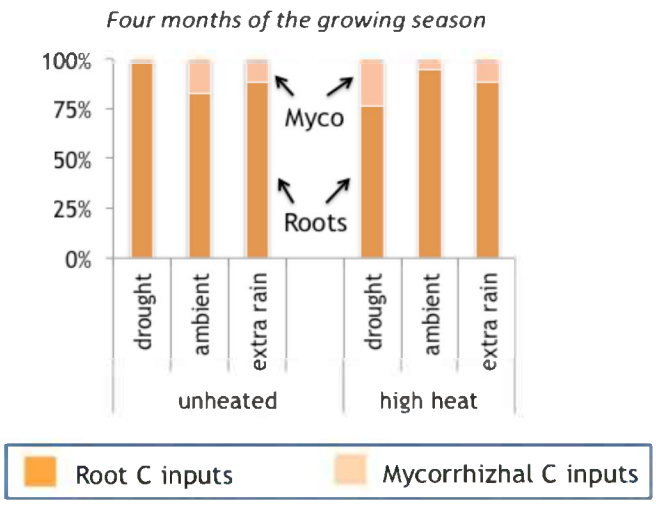

Fig. 2. Root and mycorrhizal contributions of "new" (i.e., recently-fixed) C, as detected by isotopic differences in 13C inside the ingrowth cores. Ingrowth cores were installed from July to October in 2012. On average, 89% of inputs were from roots. No differences among the treatments ($P > 0.05$)

Additionally, we found two times as much root C input in heated vs. unheated treatments in the final four months of the 2012 growing season (warming effect $p < 0.05$; precipitation treatment and warming x precipitation were not significant), and no interactive effects of warming and soil moisture on root-derived C (Figure 3).

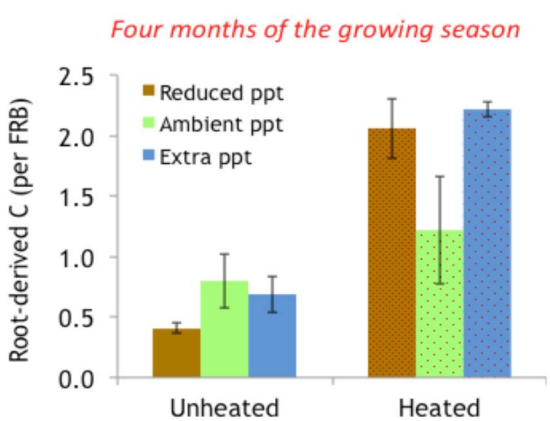

Fig. 3. Root-derived inputs of C were significantly greater in experimentally warmed soils than in controls ($p < 0.05$). There were no precipitation (ppt) effects or warming by precipitation interactions ($P > 0.05$). Ingrowth cores were installed from July to October in 2012.

Greater belowground inputs with warming may have resulted from increased water or nutrient limitation, or because of accelerated tissue turnover or exudation. We then explored the consequences of the variation in root-derived C fluxes for microbial functions by quantifying microbial biomass and turnover of C, N and P inside the ingrowth cores at the end of the experiment. No relationships were observed for C input and net N mineralization or the activity of enzymes involved in C and N-acquisition. However, belowground inputs strongly increased two indices of P availability: bicarbonate extractable and phosphatase enzyme activity. In both cases, more root-derived C was positively correlated with enhanced P cycling (Figure 4).

The main experiment was conducted from November 2012 to November 2013. Similar to the short-term experiment, roots accounted for 89% of C inputs across all

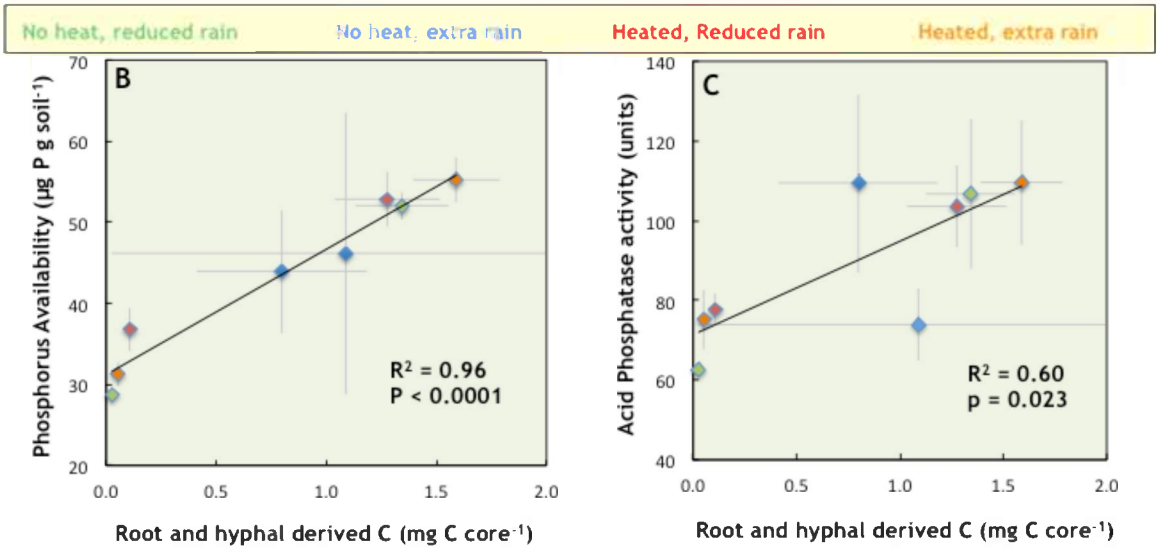

Fig. 4. Belowground inputs strongly increased two indices of P availability: bicarbonate extractable (B), and phosphatase enzyme activity (C). Ingrowth cores were installed from July to October in 2012.

treatments and seasons, and the percentage of allocation to roots vs hyphae was not affected by environmental treatments. We saw a temperature effect of similar magnitude as in the short-term experiment, but there was also a temperature by moisture interaction such that the effects of heating were greatest in the ambient moisture treatment, and not apparent in the wettest treatment. Thus, we did not find support for our initial hypothesis that the greatest root C flux occurred in the warm and wet (i.e., irrigated) soils.

We quantified microbial biomass and turnover of C, N and P inside the ingrowth cores after one year. Across the treatments, we found positive relationships between the amount of root-derived carbon and the amounts of microbial biomass ($r^2 = 0.82$), net N mineralization ($r^2 = 0.41$), and extractable P ($r^2 = 0.74$).

We used the data from aboveground and belowground production (including root-derived C inputs to soil) in a simple modeling exercise. First, we coupled a plant allocation model (FUN; Fisher et al. 2010) with a soil C process model

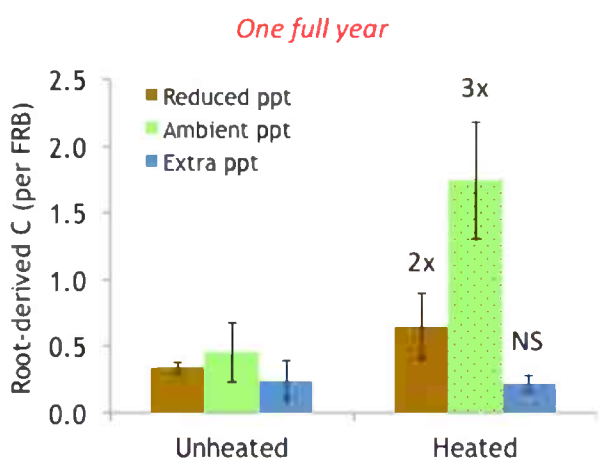

Fig 5. Root-derived inputs of C after one year were significantly greater in experimentally warmed soils than in controls ($p < 0.05$), similar to the results fromt he four month experiment. However, unlike the previous experiment, there was a significant precipitation by warming interaction. Ingrowth cores were installed from November 2012 to November 2013.

(CORPSE; Sulman et al. 2014). We forced the model with climate data from the BACE, ramping up the warming treatment to 4 degrees C over 30 years, and incorporating the precipitation treatments from the start. We examined how differences in root-derived C inputs (owing to the experimental treatments) would influence priming effects and soil C losses over a 30-year window. Our model simulations indicate that despite greater inputs of root-derived C in the warming treatments, net soil C losses may be small in plots where soil moisture limits microbial activity (Figure 6). Similarly, despite no net changes in root-derived C in the warmed plots, net losses of C may be large if there is sufficient soil moisture to stimulate microbial activity e.g., in our warmed and irrigated plots). Thus, microbial sensitivity to soil moisture is the critical determinant of how exudate fluxes will impact decomposition and priming. Crucially, our model results show that in dry soils, no amount of exudation can offset the loss of soil C that would occur when conditions are more favorable (i.e., wetter) for microbial decomposition.

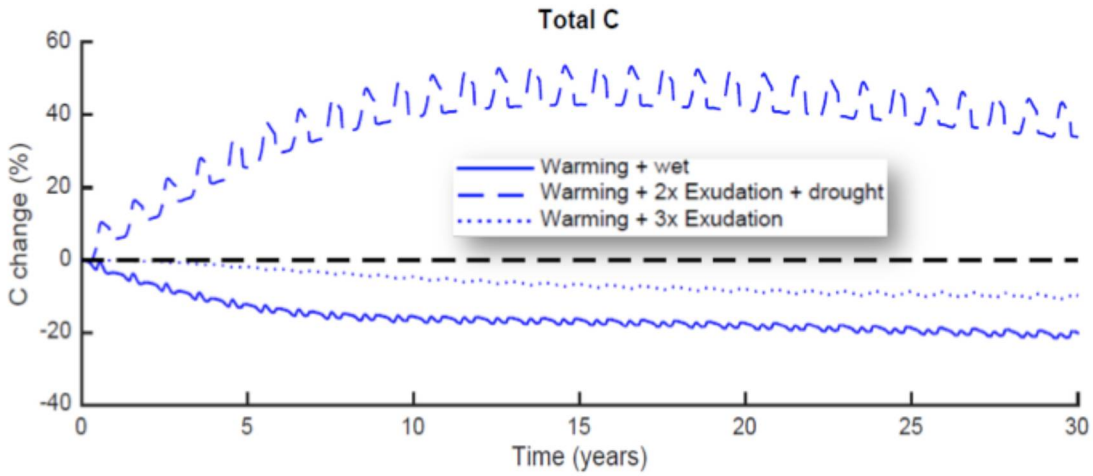

Fig. 6. Modeled consequences of changes in belowground inputs (owing to experimental warming) on soil C content, as predicted by CORPSE. The model was spun up to equilibrium and run for 30 years using climate data from the BACE plots.

Objective II: To quantify the effects of root-derived C inputs on decomposition via PE

Background. Root exudates have been shown to affect SOM decomposition in a temperature-sensitive manner (e.g., Kuzyakov et al. 2007, Zhu & Cheng 2011) and greenhouse experiments suggest a strong relationship between exudation, soil moisture and priming in some soils (Dijkstra and Cheng 2007). Mycorrhizal fungi increase SOM decomposition through the release of exo-enzymes from extramatrical mycelium (Read, 1992), and this C flux may contribute up to 50% of the dissolved organic C in forest soils (Hogberg & Hogberg, 2002). We hypothesized that greater rates of C allocation to roots and mycorrhizae under elevated precipitation would increase SOM decomposition in the rhizosphere by priming SOM decomposition and accelerating microbial turnover. As seen in Objective 1, the premise for this hypothesis was not borne out; we found that rhizosphere C inputs were more strongly affected by warming than precipitation.

Hypothesis 2: The magnitude of root and mycorrhizal PE will depend upon the degree to which soil moisture influences soil N availability. Reductions in N availability owing to dry soil conditions or intense plant-microbe competition will result in greater belowground C allocation. In dry soils, PE will be reduced while in wet soils PE will be enhanced (Figure 1).

Approach (Brief methods)

To assess the relationship between exudate amount and PE, we used "rhizosphere simulators" (Fig. 7) to slowly inject different concentrations and compositions of exudate solution into soils in the BACE plots. Specifically, we released exudate solutions that contained the same amount of C (~ 3% of mean annual NPP), but varying amounts of N to achieve a molar C:N ratio of 10, 50 and 100. After four weeks of adding these compounds, soils around the simulators (within 1cm of "roots") were collected, and a suite of microbial and biogeochemical processes were quantified.

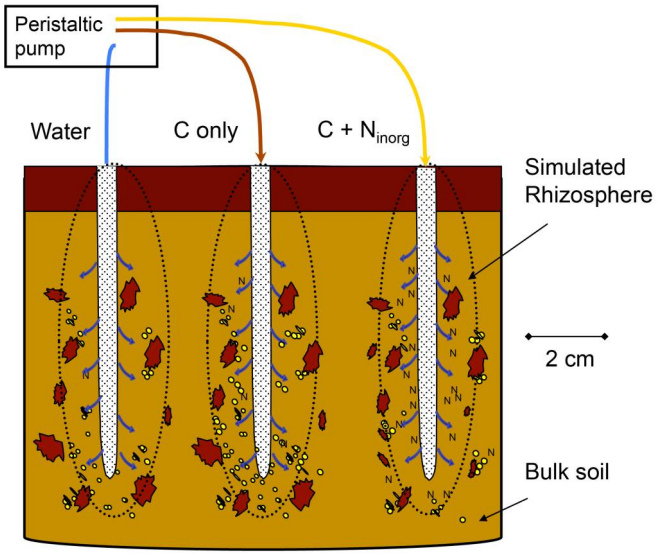

Fig. 7. Soil cross-section showing the ceramic microlysimeters that served as "rhizosphere simulators."

We found that root exudates increased microbial respiration, with the greatest magnitude of effects occurring for exudates with a C:N of 50 (52% increase) and 100 (56% increase). This effect was not influenced by warming or altered precipitation (i.e. interactions with C quality: $p > 0.05$). Increasing rhizosphere N availability had little effect on microbial biomass and P availability, and greater inputs of N increased N mineralization, but only in unheated soils (Figure 8). Enzymes involved in the acquisition of C and P from SOM were increased by N inputs, but only in warm and wet soils (*data not shown*). We initiated a follow-up exudate injection experiment that was intended to run for a longer duration, but the sudden and unexpected departure of the technician maintaining this experiment left the project unfinished and unrecoverable.

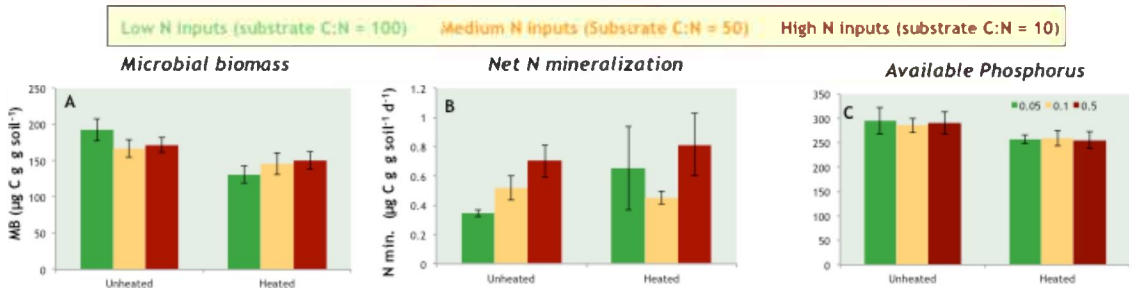

Fig. 8. Consequences of *in situ* exudate additions on microbial biomass, and N and P availability over a four-week period at the BACE plots.

Conclusion and Products Developed

Belowground processes mediate the flux of energy and materials in terrestrial ecosystems and mediate feedbacks to climate change through their effects on ecosystem C storage and nutrient cycling (Aber & Melillo, 1991). Despite their importance, several critical components of the belowground subsystem remain poorly understood owing to methodological challenges of studying temporally dynamic and spatially heterogeneous processes. Thus, there is a clear need for novel methods and new studies examining fundamental aspects of belowground C and N cycling – as well as their interactions – in order to better understand ecosystem consequences of global environmental change (Pendall *et al.*, 2004). Our exploratory research examined responses of PE to warming and soil moisture changes, providing insights into the ecosystem-scale consequences of root-microbial interactions in the rhizosphere. Results were presented at annual meetings of the Ecological Society of America (Phillips et al. 2013, 2015, and are currently being written up for publication.

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