Response of microbial communities to water stress in irrigated and drought-prone tallgrass prairie soils

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Received 14 December 2006; received in revised form 10 May 2007; accepted 19 May 2007
Available online 26 June 2007

Abstract

To better understand how water stress and availability affect the structure of microbial communities in soil, I measured the change in phospholipid fatty acids (PLFA) and the incorporation of $^{13}$C-labeled glucose into the PLFA following exposure to water stress. Overlaid on the laboratory water stress treatment, samples were collected from drought-prone and irrigated (11 years) tallgrass prairie soil (0–10 cm depth). In the laboratory, soils were either incubated at $-250$ kPa or dried steadily over a 3-d period to $-45$ MPa. On the fourth day, the dried samples were brought up to $-250$ kPa and then all samples received $250 \mu$g of glucose-C (+4000 $\delta^{13}$C-PDB) solution that brought them to $-33$ kPa matric water potential. Samples were then extracted for PLFA following 6 and 24 h of incubation ($25 \pm 1 ^\circ$C). Non-metric multidimensional scaling (NMS) techniques and multi-response permutation procedure (MRPP) showed that the largest effect on the mol% distribution of PLFA was related to the field scale water addition experiment. In response to irrigation, the PLFA 16:1$\omega_5$, 18:1+, and 18:2$\omega_6,9$ showed increases, and a15:0, a17:0, and cy19:0 showed decreases in their respective mol%. Effects related to the induction of laboratory water stress were predominantly associated with a decrease in the mol% distribution of the putative fungal biomarker (18:2$\omega_6,9$) with little to no change in the mol% distribution of the bacterial biomarkers. Interestingly, the flow of C to the microbial community was not strongly related to any single PLFA, and differences were rather subtle, but multivariate MRPP detected change to the community structure related to the laboratory water stress treatment but not related to the 11 years of field irrigation. Our results suggest that both the total and the actively metabolizing bacterial community in soil were generally resistant to the effects of water stress brought by rewetting of dry soil. However, more research is needed to understand the nature of the fungal response to drying and rewetting in soil.

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Keywords: $^{13}$C-PLFA compound-specific isotope analysis of microbial communities; Drying–rewetting

1. Introduction

Water dynamics and stress exert a major influence on microbial physiology and function (Harris, 1981; Yancey et al., 1982; Kempf and Bremer, 1998), however, there is still considerable debate about how water stress affects soil microbial communities, their biomass, and their overall activity. One of the primary factors influencing microbial responses to soil water cycling is the situation of feast or famine that occurs in most ecosystems. The vast majority of ecosystems undergo short- and long-term droughts, which cause soil water contents to drastically decrease.

Eventually, water stress is alleviated either through rainfall or from irrigation (e.g. agro-ecosystems). While there is widespread agreement that drying and rewetting results in large immediate changes in nutrient cycles (Sorensen, 1974; Bottner, 1985; Appel, 1998), there is still considerable debate about the nature of abiotic and biotic responses that can mechanistically explain measured changes in soil processes. There is evidence for instance, that both microbial and non-microbial pools of C contribute to changing C and N pools and mineralization rates (Schimel et al., 1999; Denef et al., 2001; Steenworth et al., 2005; Cosentino et al., 2006). While both of these mechanisms are useful for explaining results from various studies, there have been relatively few definitive mechanistic explanations that can be used to explain the soil microbial response to...
drying and rewetting (Killham and Firestone, 1984; Kieft et al., 1987; Schimel et al., 1989; Scheu and Parkinson, 1994; Halverson et al., 2000; Fierer et al., 2002).

It has been hypothesized that soils that naturally experience climatic conditions that promote high degrees of variability in water availability may be more adapted to water stress and may thus show a more limited response to drying and rewetting induced water stress. For instance, a drought-prone grassland soil responded much less to drying and rewetting than an oak-dominated soil that tend to have naturally more moderate variability in water potential (Fierer and Schimel, 2003). Other studies with soils taken from soil with naturally contrasting soil moisture regimes have shown, anecdotally, that this hypothesis may have widespread merit (van Gestel et al., 1993; Lundquist et al., 1999; Franzluebbers et al., 2000).

It has also been hypothesized that active and growing members of microbial communities may be more susceptible to the effects of water stress than the whole and predominantly inactive or dormant microbial community. This hypothesis follows from the fact that soils are a low-nutrient environment and that a large number of microorganisms are in a physiologically inactive or starvation state that should be expected to afford some protection from environmental disturbance (Chen and Alexander, 1973). The one attempt at understanding the response of actively growing soil microorganisms was only capable of resolving rRNA structural differences in bacterial communities, which were small if non-existent to the effects of water stress (Griffiths et al., 2003).

The objective of our study was to trace the movement of $^{13}\text{C}$ from glucose into the microbial PLFA to determine if the activity of the microbial community in continuously moist soil differed from that of soil exposed to drying and rewetting. Overlaid on this experiment, we also wanted to determine if there was altered response of the microbial community to water stress following 11 years of irrigation in a tallgrass prairie. By understanding the nature of the microbial community response, we can better explain the relative importance of drying and rewetting on community structure and turnover, and gain insight into the factors that contribute to flushes of C and nutrients following drying and rewetting.

2. Materials and methods

2.1. Site description

The experiment was conducted in a native (annually burned in spring) upland tallgrass prairie located at the Konza Prairie Biological Station near Manhattan, KS, USA. Soils of the upland summit topographic position are dominated by mesic Typic Hapludolls (Benfield silty clay loam). Vegetation on the site was a mixture of C$_3$ and C$_4$ species, dominated by big bluestem (Andropogon gerardii) and Indian grass (Sorghastrum nutans (L.) Nash). Previously, it has been shown that average peak aboveground biomass (1993–2000) was approximately 575 and 455 g m$^{-2}$ in continuously moist and drought-prone transects, respectively, of which 35–50 g m$^{-2}$ was forbs (Knapp et al., 1998). Standing root biomass did not differ between treatments and was approximately 785 g m$^{-2}$ in the top 10 cm of soil (Williams, 2001). Many of the dominant grasses and forbs responded to irrigation through increased biomass production, but forbs showed the largest response (http://climate.konza.ksu.edu/).

Established in 1990 and 1993, the irrigation pipelines traversed a 70-m long by 30-m wide transect in the upland (280 m MSL) topographic position. Penman equations and meteorological data were used to calculate plant water demand, and water was added during the months of May/June through September (Penman, 1948; Knapp et al., 1998; Williams, 2001). During the other months of the year, precipitation exceeds evapotranspiration. In the driest year of 1991, an additional 470 mm of water was added in the irrigated treatments, whereas in the wettest year of 1993, only 80 mm of water was added. On average, 245 mm of water was added in each growing season, an amount equivalent to 60% of the average total rainfall during the 4-month period. The year of 2003 was a typically dry year with only 500 mm of rainfall recorded during the peak growing season months of May through September, resulting in an additional 245 mm of water added via irrigation (http://climate.konza.ksu.edu/). Four replicate irrigation plots (1.0 m$^2$) were interspersed by four un-watered control plots. Details of the irrigation transects in the Konza Prairie LTER and their experimental design have been published previously (O’Lear and Blair, 1999; Todd et al., 1999; Williams and Rice, 2007). Soils that were irrigated were maintained at water potentials consistently above approximately −1500 kPa during the growing season, whereas soils that receive only natural rainfall inputs often drop well below −5000 kPa for extended periods of time (Williams, 2001).

Twenty 2.2-cm dia by 10-cm deep soil cores were collected from each plot in late September 2003. After collecting, soils were immediately passed through a 4-mm mesh sieve, meticulously hand-cleaned of roots and organic debris, and stored at 4 °C for less than 2 weeks. Several natural rainfalls occurred during September, and as a result all soils had soil water contents between 32% and 34%. The relationship between soil water content and soil water (matric) potential was estimated using standard methods on freshly sieved soils that were repacked to the original bulk density (~1.0 g cm$^{-3}$). The first method utilizes a porous ceramic plate that is used to make contact between a soils sample and a pressure differential up to −1500 kPa (Klute, 1986) in a closed system. The second method, known as the filter paper method, also measures water potential in a closed system. In this case, a Whatman #41 filter paper was incubated with a soil sample of known water content for 6 d. The amount of water adsorbed to the filter paper could be measured by an analytical balance and
then used to estimate water potential as described by McInnes et al. (1994).

2.2. Pre-incubation and addition of $^{13}$C-glucose to the soils

Field-moist soils (15 g dry weight) were weighed into 160-ml serum bottles and brought up to $-250$ kPa soil water content and incubated for 3 d ($25^\circ$C). One set of soils was kept moist at $-0.25$ MPa, and two sets were slowly and linearly dried over a 3-d period to $-45$ MPa. On the 4th day, the dried soils were brought back to $-250$ MPa over a 20-s period with a single addition of 5.5 g deionized water. A 0.5-ml solution of D-glucose ($U$-$^{13}$C, $\delta^{13}$C-PDB = +4000) containing 250 $\mu$g glucose C was immediately and evenly added to all of the soils resulting in a matric potential of $-33$ kPa. The continuously moist soil was extracted after 6 h, and the dried and rewetted soils were incubated for 6 and 24 h and then extracted for PLFA. Preliminary experiments suggested that the glucose was catabolized during a 6-h period. There were no significant changes in the mol% of total and glucose-derived PLFA-C between sampling times, so results from the 6-h incubation and extraction are presented.

2.3. Extraction and analysis of soil PLFA

Lipids were extracted according to the procedure of White and Ringelberg (1998) as modified by Butler et al. (2003). Briefly, portions of soil (15 g wet weight) were extracted overnight in a mixture of chloroform, methanol and 50 mM phosphate buffer (pH 7.1). Lipids were extracted the following day by centrifugation and filtration. Dried lipid extracts were re-dissolved in chloroform and separated into neutral, glyco- and phospholipids on solid phase silica columns (Supelco, Inc., Bellefonte, PA) with a 30-m HP Innowax column (internal diameter, 0.25 mm; film thickness, 0.25 $\mu$m) connected to a Europa 20–20 mass spectrometer (Europa Scientific, Cheshire, England). During the methylation step, an ORCHID on-line combustion interface in line with a Europa 20–20 mass spectrometer (Europa Scientific, Cheshire, England). During the methylation step, an additional C atom is added to the fatty acid molecule. Notations: “Me,” “cy,” “i,” and “a” refer to methyl group, cyclopropane groups, and iso- and anteiso-branched fatty acids, respectively. Fifteen PLFA comprised $\sim$95% of the PLFA, and were each present in sufficient quantity to obtain accurate $\delta^{13}$C values. Other indicator fatty acids such as hydroxy fatty acids and long chain fatty acids ($\geq$C20) were either below the limit of accurate detection, or present in amounts too small to get accurate $\delta^{13}$C values. Two fatty acids (16:1$\omega$7 and 10Me16:0) merged (denoted as 16:1+) into one peak, as did 18:1$\omega$7 and 10Me18:0 (denoted as 18:1+).

$\delta^{13}$C values of individual PLFA were determined as described by Butler et al. (2003) with an Agilent 6890 gas chromatograph (Agilent Inc., Palo Alto, CA) equipped with a 30-m HP Innowax column (internal diameter, 0.25 mm; film thickness, 0.25 $\mu$m) connected to a Europa ORCHID on-line combustion interface in line with a Europa 20–20 mass spectrometer (Europa Scientific, Cheshire, England). During the methylation step, an additional C atom is added to the fatty acid molecule. This additional C atom, of known $\delta^{13}$C value ($\sim$44%), was corrected for the $\delta^{13}$C values of the PLFA with the following equation:

$$\delta^{13}C_{PLFA} = \frac{[C_{PLFA} + 1] \times \delta^{13}C_{FAME} - \delta^{13}C_{MeOH}}{C_{FAME}}$$

where $C_{PLFA}$ and $\delta^{13}C_{PLFA}$ refer to the number of C atoms and the $\delta^{13}$C value, respectively, of the PLFA; $C_{FAME}$ and $\delta^{13}C_{FAME}$ refer to the number of C atoms and the $\delta^{13}$C value of the FAME after derivitization, and $\delta^{13}C_{MeOH}$ refers to the $\delta^{13}$C value of the methanol used for methylation.

We calculated the proportion of residue derived PLFA-C for each individual PLFA by using the following equation:

$$F_i = \frac{M_c (\delta_n - \delta_i)}{(\delta_n - \delta_i)}$$

where $F_i$ is the relative fraction of C in each PLFA composed of enriched $^{13}$C residue, $M_c$ is the relative percentage of C in each PLFA to that of the total PLFA, $\delta_i$ represents the $\delta^{13}$C of the PLFA-C derived from the $^{13}$C enriched residue, $\delta_n$ represents the $\delta^{13}$C of the PLFA-C derived from un-enriched residue, and $\delta_n$ represents the $\delta^{13}$C of the labeled residue.

The mol% or proportion ($P_{Fi}$) of glucose derived C for each PLFA to that of the total glucose derived PLFA-C for all fatty acids was then calculated for each fatty acid using the following equation:

$$P_{Fi} = \frac{F_i}{\sum F_i} \times 100.$$

Standard nomenclature is used to describe PLFA. The number before the colon refers to the total number of C atoms; the number(s) following the colon refers to the number of double bonds and their location (after the “$\omega$”) in the fatty acid molecule. Notations: “Me,” “cy,” “i,” and “a” refer to methyl group, cyclopropane groups, and iso- and anteiso-branched fatty acids, respectively. Fifteen PLFA comprised $\sim$95% of the PLFA, and were each present in sufficient quantity to obtain accurate $\delta^{13}$C values. Other indicator fatty acids such as hydroxy fatty acids and long chain fatty acids ($\geq$C20) were either below the limit of accurate detection, or present in amounts too small to get accurate $\delta^{13}$C values. Two fatty acids (16:1$\omega$7 and 10Me16:0) merged (denoted as 16:1+) into one peak, as did 18:1$\omega$7 and 10Me18:0 (denoted as 18:1+).

2.4. Statistical analyses

The ordination and multivariate analysis of the data utilized the PC-ORD version 4 software (MJM Software, Gleneden Beach, OR) and followed the recommendations of McCune and Grace (2002). The effects of field irrigation and laboratory drying and rewetting were analyzed using mol% of total and new C in the 15 dominant PLFA. Multivariate analysis was carried out using the multi-response permutation procedure (MRPP). The MRPP is a non-parametric procedure for testing the hypothesis of no
difference between two or more groups of entities. Non-
metric multidimensional scaling (NMS), also a non-
parametric method, was used to provide graphical ordina-
tion of the mol% PLFA-C and mol% new PLFA-C data. Matrix dissimilarity was measured using the Sorenson
distance measure. The preferred solution, based on the
lowest stress and instability was two dimensional, resulting
in a final stress of 12.4.

Mol% for each individual and biomarker PLFA were
analyzed using the univariate method of Proc Mixed (SAS
Institute, 1996). The experiment was input as a strip plot
design with the strip factors of field irrigation and
laboratory drying–rewetting. LSD tests were used to
determine where significant differences occurred (α = 0.05).

3. Results

3.1. Microbial community structure in response to field and
laboratory water stress

Data presented in Fig. 1 show the mol% distribution of
15 analytically distinguishable PLFA extracted from soil. The distribution of PLFA-C between the laboratory water
treatments were significantly different in only two specific
cases, with drying and rewetting resulting in a mol% reduction in 10me17:0 and 18:2ω6,9 (Fig. 1a vs 1b). The
MRPP analysis of mol% PLFA-C indicated no difference
in how soils that were continuously moist for 11 years or
were drought prone responded to wetting and drying in the
laboratory. However, compared to the drought-prone soil,
the field treatment of 11 years of continuously high water
availability resulted in mol% reductions of α15:0, α17:0
and cy19:0 and increases in 16:1ω5, 18:1+ and 18:2ω6,9.
The extent of the effect of field irrigation compared to that of
laboratory wetting and drying can also be seen in Fig. 2.
Corroborating the univariate analysis noted in Fig. 1, the
NMS and MRPP analysis show significant differences
between the field water treatment with no effect of
laboratory drying and rewetting on the multivariate spread
of the data. There was no interaction effect between the
field and laboratory water treatments.

3.2. Water availability and stress effects on glucose C
incorporation into the microbial community

MRPP analysis showed that there was a significant effect
of the laboratory but not the field level water addition
experiment on the mol% distribution of PLFA-C derived
from glucose. The two-dimensional NMS representation of
this relationship can most easily be seen in Fig. 3. There
were, however, no specific PLFA that showed significant
differences between the different treatments (Fig. 4). In this
regard, it is important to note the lower amount of
variability attributed to Axis 2 than Axis 1. There was no
interaction affect between the field and laboratory water
treatments.

4. Discussion

It was found that overall microbial community structure
was altered more by the field level manipulation of water
than by drying and rewetting induced water stress. I
hypothesize that the change was related to the ongoing and
cumulative differences that define the field level manipula-
tion of water. These differences can be attributed to indirect
effects, such as changing amounts of C input related to greater belowground plant biomass productivity in the continuously moist soils, in addition to any direct affects of water regime. Indeed, both C availability and water regime have been implicated as major determinants of soil microbial community structure in both laboratory and field-based experimental manipulations (Zhang and
Zak, 1998; Frey et al., 1999; Wilkinson et al., 2002;
Drenovsky et al., 2004).
With both types of water stress, whether through natural drought cycles common to tallgrass prairie or through the induction and alleviation of water deficit in the laboratory, there was ~25% reduction in the mol% of the fungal PLFA marker (18:2\text{\omega}6,9) compared to situations where water availability was kept more or less constant. Greater fungal to bacterial biomass ratios were previously reported to occur throughout the growing season as a result of 7 years enhancement of water availability in tallgrass prairie soil (Williams and Rice, 2007). While fungal microorganisms have traditionally been touted as highly resistant to water stress and are known to grow at relatively low water potentials (Harris, 1981; Schimel et al., 1989), these results suggest that perhaps there are groups in soil that may be particularly susceptible to soil water status and stress. Suffice it to say, the ability to grow at low water potential does not necessarily translate into the capacity to withstand the osmotic upshock that follows rewetting of dry soil. Fungal biomass reductions related to drying and rewetting stress have been noted by other researchers (Denef et al., 2001), suggesting that the generalization that fungi are
relatively resistant to water stress is in need of further verification.

In light of the fact that the microbial biomass in the prairie soils are dominated by fungi (Bailey et al., 2002; Williams and Rice, 2007), the reduction in the mol% of the fungal biomarker to water stress, which could suggest fungal turnover resulting from cell lysis, could also be representative of a substantial change in fungal community structure. This would be the case if certain types or groups of fungi were sensitive to osmotic upshock. Unfortunately, PLFA analysis is not capable of resolving these possible differences. In contrast, the bulk of the PLFA, not including the 18:2ω6,9 and 18:1ω9, are probably most representative of bacterial communities (Bossio and Scow, 1998; Bailey et al., 2002). The lack of significant change in mol% distribution in these PLFA is in agreement with recent reports that bacterial communities in soils appear to be relatively resilient and/or adaptable to the effects of drying and rewetting (Wilkinson and Anderson, 2001; Fierer et al., 2002; Griffiths et al., 2003). Other studies of soil prokaryotic communities suggest that some soil bacterial communities can be sensitive to drying and rewetting (Fierer et al., 2002; Pesaro et al., 2004). However, with these latter studies it is difficult to garner a sense of the magnitude of the community change compared to that of other environmental drivers.

In the context of the response of the fungal PLFA (18:2ω6,9) to rewetting of dry soil, it was interesting to note that, regardless of treatment, only a small fraction of new C (mol% ~1) flowed into this PLFA. This result would seem to suggest that only a small subset of the fungal community responded to the glucose addition. If only a small component of the community was actively growing on the glucose, this limits extrapolation as to how the broader fungal community might respond to water stress. We cannot rule out the possibility, furthermore, that this low response by the fungal community may be analogous to the negative influence that tillage may have on fungal communities (Wardle, 1995). As such, the fungal biomass response to drying and rewetting may have been partially precipitated by the disturbance initiated by the sampling and sieving of the soil, and may have inadvertently increased their susceptibility to water stress and lowered the response of the fungi to glucose addition. While we tried to strike a balance between pre-incubation of the soils before initiation of the experiment to help offset disturbance effects, we also did not want to over-incubate the soils and risk changing the conditions that might then override or mask the effects manifested in the field experiment. It is also important to note that the degree of drying that we inflicted on the soil and its community members was not a typical yearly drying scenario, but more an extreme that would occur in the driest years, perhaps two to three times per decade (Garcia, 1992; Williams, 2001). Hence, a more typical water deficit in soil may not have the same detrimental effect on the fungal biomass. More research using several different levels of water stress and using undisturbed soil will help resolve these questions.

By utilizing high-resolution isotope techniques and focusing on the most active, growing, and presumably the most sensitive subset of the community we expected to see changes in the way that the metabolically active community members utilized glucose, a molecule that is constitutively utilized by a widespread set of microorganisms. In this way, for example, we expected to see that some biomarkers, such as those of less dilution stress tolerant gram-negative microorganisms (16:1ω7, 18:1ω7, cy17:0, cy19:0) to show marked reductions in the amount of glucose-C, while gram-positive types (i15:0, a15:0 i16:0, i17:0) which have been shown to be more water stress tolerant would show definitive increases in glucose-derived C (Harris, 1981; Halverson et al., 2000). However, even with the significant change in the structure of the actively growing microbial community in response to drying and rewetting, there were no specific changes in PLFA, and the structural alterations seemed small and unremarkable compared to the overall similarities in the distribution of glucose-C within the community. In contrast to communities derived from soils in more humid and moist regions, it has been previously hypothesized that communities derived from arid and dry-mesic type systems, such as the tallgrass prairie, may be naturally resistant and adaptable to drying–rewetting induced water stress (van Gestel et al., 1993; Fierer et al., 2002; Pesaro et al., 2004), a view that is generally supported by our work.

The small but structurally similar change in the actively growing community in response to drying and rewetting stress by both field water availability treatments makes sense in light of the soil conditions at sampling. When sampled in late September, the water contents and presumably other environmental factors such as temperature were similar between the continuously moist and drought-prone soils. While it was shown that the structure of the total microbial community with contrasting water regimes are distinctive from each other, the response of the actively metabolizing community may be more closely related to the immediate environmental conditions rather than historical treatment effects. Indeed, previous research that studied the functional response of the cultivable community bears this possibility out (Griffiths et al., 2003; Williams and Rice, 2007). Presuming that the two active microbial communities were similar, it is then no surprise that the drought-prone and continuously moist field soils responded similarly to drying and rewetting induced water stress under laboratory conditions.

Based on observations for glucose-responsive community members, and the overall dynamic nature of soil microbial communities related to seasonal influences, the response of the active community members needs further study. Indeed, even the small non-specific change that we
noted in the flow of C to PLFA may be more indicative of physiological rather than structural community change. However, if it turns out to be a broad truism that microbial community structure does not change or changes very little in response to drying and rewetting induced water stress, then other mechanisms are needed that can account for fluxes of C and N that typically follow the wetting of dry soil. One popular hypothesis suggests that microorganisms in soil are responding and adapting to the drying phase of water stress through the accumulation of organic cytoplasmic solutes (alcohols, amino acids). Upon rewetting, these solutes are expelled from the biomass and redistributed into the extracellular soil matrix where they are quickly mineralized (Kieft et al., 1987; Halverson et al., 2000; Fierer and Schimel, 2003). This hypothesis has merit in that a microbial response of this type has been widely measured in cultured systems (Tschicholz and Truper, 1990; Schleyer et al., 1993; Halverson et al., 2000). It also has the advantage of helping to explain both the increase in carbon dioxide and N production rates that typically occur immediately following the rewetting of dry soil. Lastly, it also helps to explain the resilience of the microbial community structure by invoking a known physiological adaptation to sudden and large water potential changes that occur in most soils. This hypothesis does not rule out the possible contributions of non-microbial sources of mineralizable C such as that released through physical slaking or the breakdown of aggregates that have been shown to follow drying and rewetting (Degens and Sparling, 1995; Denef et al., 2001; Cosentino et al., 2006). Indeed, there is still evidence that both microbial and non-microbial sources play an important role in contributing to the nutrient flushes released when rewetting of dried soil (Mikha et al., 2005; Wu and Brookes, 2005).

The results of this study have interesting implications regarding the mechanisms of community response to drying and rewetting. In the light of other research, and if the broader PLFA results can be said to be representative of the general community response, soil microbial communities as a whole appear to be rather well adapted to water stress. By exclusion this would suggest that process changes (e.g., C and N fluxes) that can be attributed to soil biology might be best explained by physiological and functional changes rather than structural changes in communities. However, more research is needed to understand the nature of the microbial, and especially the fungal response to drying and rewetting in soil.

Acknowledgments

I appreciate the field and laboratory support provided by Jami Schaffner and Amy Thompson. This research was funded by a competitive grant from the Soil Processes Division within USDA-NRI. Special thanks is extended to the Konza Prairie Biological Station for providing access to their long-term irrigation experiment.

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