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Responses of the soil microbial community to nitrogen fertilizer regimes and historical exposure to extreme weather events: Flooding or prolonged-drought

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ABSTRACT

Extreme weather events, including flooding and prolonged-drought, may establish long-lasting effects on soil biotic and abiotic properties, thus influencing ecosystem functions including primary productivity in subsequent years. Nitrogen (N) fertilizer addition often improves soil fertility, thereby potentially alleviating legacy effects on soil function and plant productivity. The soil microbial community plays a central role in mediating soil functioning; however, little is known about the legacy impacts of extreme weather events and N fertilizer addition on soil bacterial communities and the key processes involved in carbon (C) cycling. Here, the potential legacy effects of waterlogging, prolonged-drought and N fertilizer addition (0, 100, 200 and 300 kg N/ha) on soil bacteria and microbial respiration were investigated. The abundance, diversity and composition of the bacterial community, and basal and induced-respiration rates, in a farming soil system were examined, using quantitative PCR, high-throughput DNA sequencing, and MicroResp™. Soils *previously* exposed to short-term waterlogging events and prolonged-drought (by air-drying for 4 months) were used in our study. Prolonged drought, but not waterlogging, had a strong legacy effect on the soil bacterial community and microbial respiration. The addition of N fertilizer up to 300 kg N/ha could not fully counteract the legacy effects of prolonged-drought on soil bacteria. However, N addition did increase bacterial abundance and diversity, and inhibited soil microbial respiration. Significant correlations between microbial respiration and bacterial community structure were observed, but N addition weakened these relationships. Our results suggest that the resilience (rate of recovery) of soil bacterial communities and functions to prolonged-drought is limited in farming systems, and therefore, may take a long time to recover completely. Subsequently, this should be explicitly considered when developing adaptation strategies to alleviate the impacts of extreme weather events.

1. Introduction

The frequency and intensity of extreme weather events are projected to increase under future climatic conditions which can significantly impact ecosystem functions, including biogeochemical cycling and productivity of farming systems (IPCC, 2007). Extreme drought and waterlogging can impact ecosystems directly via altered water supply to plant and microbial communities and indirectly via changes in soil physico-chemical properties. For example, soil nutrient availability may be affected by a change in soil structure and pH which can alter the rate of soil processes catalysed by soil microbial communities (Ponnamperuma, 1984; Yang et al., 2016). Similarly, prolonged drought and water deficit stress can limit substrate diffusion to such an extent that microbial access and activities are reduced (Stark and Firestone, 1995; Voroney, 2007; Brunner et al., 2015). Soil microbes exposed to drought periods may alter their rates of function due to physiological stresses, potentially changing the rate and pathways of C and N transformation (Schimel et al., 2007). Microbes survive by accumulating solutes such as amino acids when moisture is limiting, to decrease their internal water potential and avoid dehydration and

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death (Harris, 1981). However, the cost of accumulating solutes is energetically expensive (Schimel et al., 2007).

Our understanding of the direct effects of environmental variables (e.g. temperature, water) on microbial communities and functions has improved recently (Rousk et al., 2013; Liu et al., 2017). For example, changes in soil moisture due to water stress are well known to affect microbial abundance (Gordon et al., 2008), structure (Placella et al., 2012) and process rates (Placella et al., 2012; Göransson et al., 2013). In addition, microbial responses to environmental disturbances may relate to their historical conditions (Schimel et al., 2007; Evans and Wallenstein, 2012). However, we have limited knowledge whether extreme weather events have legacy impacts on the resilience (rate of recovery) of the microbial community (abundance, composition and diversity) and their contribution to ecosystem functioning (Rousk et al., 2013; de Vries et al., 2012), but this information is critical to fully understand their role in natural and agricultural systems (Martiny et al., 2017). The responses of microbial community and functions to environmental disturbances may vary (Allison and Martiny, 2008). For example, (1) microbial community composition can be resistant or resilient to disturbances (Bowen et al., 2011; Shade et al., 2011); (2) shifts in microbial community composition due to stress exposure do not affect ecosystem functions (Wertz et al., 2007); and (3) microbial function, but not community composition, respond to disturbance (Agrawal, 2001). If the resilience of the microbial community is low (i.e. slow rate of recovery), it is important to identify the consequences for ecosystem functioning including C cycling, which could affect C fluxes to the atmosphere and accelerate climate change (Martiny et al., 2017; Treseder et al., 2012; Trivedi et al., 2016). For agricultural systems, any legacy impact will have important consequences for farm productivity via the impact on the rate of nutrient cycling.

Soil processes involved in C cycling may be altered in response to extreme weather events (Baldwin et al., 2015; Sánchez-Andrés et al., 2010; Meisner et al., 2015; Liu et al., 2017). Shifts in microbial communities and the links to soil C processes upon exposure to extreme weather events have been observed in previous studies (Liu et al., 2017). Although extreme weather events may initiate legacy effects on soil processes, biota and plant growth (Meisner et al., 2013a; Cavagnaro, 2016; Banerjee et al., 2016), less is known about the legacy effects on soil processes involved in C cycling. Extreme weather events, including flooding and prolonged-drought, alter soil moisture conditions which is a key factor influencing C and nutrient cycling in soils (Martins et al., 2016; Liu et al., 2017). Soil microbial communities are the main drivers of ecosystem functioning (Delgado-Baquerizo et al., 2016a), including processes directly involved in C cycling (Singh et al., 2010; Trivedi et al., 2016) and nutrient cycling, and exposure to extreme weather events may have long-lasting effects on these processes in subsequent years (Meisner et al., 2013a). Previous studies have suggested different vulnerabilities of different soil microbiota to drought and flooding stresses (Graff and Conrad, 2005; Schimel et al., 2007; Chodak et al., 2015); however, little is known about the taxonomic structure and diversity of soil bacterial communities in response to the legacy effects of extreme weather events.

N fertilizer supply is used globally to enhance soil fertility and hence improves plant productivity during conventional farming practices (Lu et al., 2015; Nkebiwe et al., 2016). An increased rate of N fertilizer may be used to mitigate negative effects of extreme weather events on soil fertility. However, evidence for the response of soil bacterial communities to N fertilizer addition remains contradictory (Marschner et al., 2003; Ogilvie et al., 2008; Lupwayi et al., 2011; Roberts et al., 2011). For example, microbial community composition was reported to be unresponsive to N addition in crop soils (Roberts et al., 2011), whereas others have observed a shift in community structure and a decrease in bacterial diversity in grassland soils (Zeng et al., 2016). Ramirez et al. (2012) found consistent responses of soil biota, particularly shifts in bacterial composition, to N amendment across a wide range of ecosystems. Additionally, whether legacy impacts of extreme weather events on microbial communities may be moderated by N fertilization remains largely unknown, but remains critical for understanding C and nutrient cycling in agricultural systems.

Carbon cycling in soils play a critical role in maintaining soil nutrients which are directly related to crop productivity (Gougoulias et al., 2014). Thus, it is imperative to examine the response of C cycling processes to the legacy effects of extreme weather events and determine whether this can be modulated by different rates of N fertilizer. Soil microbial respiration (a proxy for soil organic C decomposition) in response to altered precipitation may be highly variable and dependent on ecosystem type (Borken et al., 2006; Cleveland et al., 2010; Van Straaten et al., 2010). This process is an important flux in the soil C cycle and linked to soil organic C pools (Gougoulias et al., 2014). In some studies, N fertilizer addition often inhibits soil microbial respiration rates in natural and agricultural systems (Kowalenko et al., 1978; Bowden et al., 2004; Treseder, 2008; Gagnon et al., 2016), thereby potentially increasing C sequestration rates (Ramirez et al., 2012). Above findings support the nutrient mining theory (i.e. when N is limiting, the microbial community “mines” soil organic matter (SOM) to secure their N requirement, potentially leading to loss of soil C via increased microbial respiration) (Moorhead and Sinsabaugh, 2006). However, we have limited knowledge regarding potential modification of this relationship via the legacy impacts of extreme weather events. This knowledge is particularly important if the response of microbial community composition to extreme weather events (flooding vs drought) is divergent. This divergence in community composition will have consequences for total metabolic activities, including the rate of soil respiration (Singh et al., 2010), which is currently not well-known. Additionally, the underlying mechanism of microbial respiration response to extreme weather events under different rates of N fertilizer remains relatively unclear (Ramirez et al., 2010), but important for formulating environmentally sustainable farming.

In this study, we examined the response of the soil bacterial community and microbial respiration to the legacy effects of extreme weather events and different rates of N fertilizer addition in agroecosystems, using cotton as a model system. Given differential response of microbial communities to flooding and drought, we hypothesized that (1) soil bacterial communities will have lower resilience to historical prolonged-drought than to waterlogging exposure; and (2) N fertilization will modulate the response of the microbial community and respiration to historical extreme weather events through altered soil physicochemical properties. Our hypotheses are based on previous findings, which reported a consistent impact of drought on soil microbial communities and activities, and some have even reported strong legacy impacts of drought on plant-microbial interactions (Meisner et al., 2013a, 2013b; de Vries et al., 2012). The impact of waterlogging on microbial communities and activities are known, but impacts seem to be transient (Bossio and Scow, 1995; Unger et al., 2009) or less pronounced than other factors such as land-use types (Drenovsky et al., 2010). Additionally, in dryland farming, microbial diversity, abundance, and activities are limited by water availability (Martins et al., 2016; Maestre et al., 2015) and further loss of soil water under drought treatment can generate a stronger legacy impacts.

2. Materials and methods

2.1. Glasshouse experimental setup and soil sampling

A glasshouse experiment was conducted at Western Sydney University (WSU), Australia for approximately 7 months, using soils collected from a cotton field which had been exposed to waterlogging events in 2013–2014, simulated by running furrow irrigation for 120 h at an early and late flowering stage of cotton crop at the Australian Cotton Research Institute (ACRI) in Narrabri (30.31^{o}S, 149.78^{o}E), New South Wales (NSW), Australia. This region represents a semi-arid ecosystem and experiences hot summers with maximum and