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Do organic inputs alter resistance and resilience of soil microbial community to drying?

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ABSTRACT

Grassland ecosystems in south-eastern Australia are important for dairy and livestock farming. Their productivity relies heavily on water availability, as well as the ecosystem services provided by soil microbial communities including carbon and nutrient cycling. Management practices such as compost application are being encouraged as a means to improve both soil water holding capacity and fertility, thereby buffering against the impacts of increasing climate variability. Such buffering consists of two complementary processes: resistance, which measures the ability of an ecosystem to maintain community structure and function during a period of stress (such as drying); and resilience, which measures the ability of an ecosystem to recover community structure and function post-stress. We investigated the effects of compost on the resistance and resilience of the grassland soil ecosystem under drying and drying with rewetting events, in a terrestrial model ecosystem. Overall, compost addition led to an increase in soil moisture, greater plant available P and higher plant $\delta^{15}N$. Soil C:nutrient ratios, mineral N content (NH_4^+ and NO_3^-) and soil microbial PLFA composition were similar between amended and unamended soils. Rainfall treatment led to differences in soil moisture, plant above-ground and below-ground biomass, plant $\delta^{15}N$, soil mineral N content (NH_4^+ and NO_3^-) and microbial biomass C, N and P composition but had no effects on soil C:nutrient ratios, plant available P and soil microbial PLFA composition. There was little interaction between rainfall and compost. Generally, the soil microbial community was resistant and resilient to fluctuations in rainfall regardless of compost amendment. However, these properties of the soil microbial community were translated to resilience and not resistance in soil functions. Overall, the results below-ground showed much greater response to rainfall than compost amendment. Water was the key factor shaping the soil microbial community, and nutrients were not strong co-limiting factors. Future projections of increasing rainfall variability will have important below-ground functional consequences in the grassland, including altered nutrient cycling.

1. Introduction

South-eastern Australia generally experiences high climatic variability. Grassland ecosystems form an important part of this landscape, where 350 million ha are grazed for livestock and dairy production (ABS, 2013). Drought is a natural, periodic characteristic that shapes such landscapes, and although native perennial pastures are generally well-adapted to this high variability, improved pastures containing exotic, fast growing annual pastures such as ryegrass are widespread and much more susceptible to drought and other stresses (White et al., 2000). Because the quantity and timing of rainfall influence patterns of plant production (Dukes et al., 2005) and carbon storage and loss (Chou et al., 2008), effects on soil biota and their processes can be magnified beyond that caused solely by water deficit, which create further feedback that alters above-ground biota (Wardle et al., 2004).

As climate projections suggest a future with greater frequency and severity of drought and extreme rainfall events (Hennessy et al., 2008; Alexander and Arblaster, 2009), the ability of soil microbial

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communities to withstand or adapt to the changes remain unclear. Some studies have observed that soil microbial communities in grassland ecosystems were resistant and resilient to climatic extremes, suggesting the presence of communities adapted to regular, seasonal fluctuations in temperature and rainfall experienced by such ecosystems (Griffiths et al., 2003; Waldrop and Firestone, 2006; Cruz-Martínez et al., 2009). In a review by Allison and Martiny (2008), soil microbial composition was found to be sensitive and not immediately resilient to elevated CO_2, mineral fertilisation, temperature changes and carbon amendments. They suggested that functional redundancy is overestimated and different communities are not functionally similar. As such, changes in microbial composition may cascade into changes in soil ecosystem services as the soil microbial community is a key player in soil processes.

Nutrient availability is also an important driver of soil ecosystem function and carbon cycling. Modern agriculture is heavily dependent on regular fertiliser inputs and this trend is likely to continue in the coming decades, although some fertilisers, such as phosphorus and potassium, are derived from finite resources (Vitousek et al., 1997; Cordell et al., 2009; Odegard and van der Voet, 2014). The addition of organic amendments (OA) may offer an option to supplement/augment inorganic fertilisers and support sustainable, biologically regulated nutrient supply systems. Previous studies have shown that inputs of OA affect soil biota, plants and biogeochemical cycling (Bastida et al., 2008; Ippolito et al., 2010; Ryals and Silver, 2013). OA has been observed to improve primary productivity and net ecosystem C storage (Ryals and Silver, 2013; Ryals et al., 2014). Microbial biomass and activity often increase with addition of OA (Bastida et al., 2008) and improvements in soil organic matter with OA can persist for over a decade (Ippolito et al., 2010).

Organic amendments are proposed to improve soil resilience to disturbance (Griffiths and Philippot, 2013). Organic matter amended soils have been observed to exhibit less pronounced changes in microbial phospholipid fatty acid or PLFA (total PLFA, bacterial PLFA, saturated and monounsaturated PFLA) compared to unamended soils under drought conditions (Hueso et al., 2012). Severe disturbances can lead to poor but stable and resistant states that require external inputs to provide a source of energy and nutrients to allow biological colonisation and increase microbial activity (Ohsowski et al., 2012). Besides energy and nutrients, OA may also improve soil structure, cation exchange capacity and water holding capacity, which combined with slow-release of nutrients may benefit below- and above-ground resilience to disturbance (Hargreaves et al., 2008; Ryals and Silver, 2013; Ryals et al., 2014). With these expected benefits to the soil on addition of compost, compost may increase both the resistance and resilience of grassland soil microbial communities, and therefore soil functions, to drying and rewetting cycles that are projected to increase in frequency and severity in the region.

With this aim in mind, this study identified the responses of an intensively grazed grassland ecosystem to altered rainfall and organic amendment, focussing on soil microbial community responses. To do so, we determined (1) the above-ground and below-ground responses to drying and rewetting and, (2) examined if compost alters the resistance and resilience of the soil microbial community to drying and rewetting cycles. Specifically, we examined the hypothesis that compost amendment increases the resistance and resilience of the soil microbial community to altered rainfall; and therefore, similarly increase the resistance and resilience of the processes of C, N and P cycling that they govern to altered rainfall. We also tested the hypothesis that grassland soil microbial activity is more responsive to drying-rewetting than soil microbial community composition, i.e. resistance and resilience of soil microbial composition are greater than resistance and resilience of soil functions. Any increase in the resistance and resilience of the soil microbial community following compost amendment would be indicated either by a stable microbial community composition in response to drying (resistance), or the ability of the community composition to recover post drying-rewetting (resilience). Correspondingly, any increase in the resistance and resilience of the soil C, N and P processes with compost amendment would be indicated by stable level of soil processes in response in response to drying (resistance), or the recovery in process rates (as indicated by microbial activity) post drying-rewetting (resilience).

2. Materials and methods

2.1. Soil, experimental design and sampling

In a terrestrial model ecosystem experiment, we collected intact soil cores from an intensively grazed grassland in the Toomuc Valley at Pakenham (38°0′ S, 145°28′ E). The field site was covered predominantly by ryegrass (*Lolium* sp.) and some ribwort plantain (*Plantago lanceolata*), carpet grass (*Axonopus affinis*) and finger grass (*Digitaria* sp.). The soil was a Brown Chromosol with 7.5% organic matter, C:N ratio of 11.1, $\delta^{13}C$ of −29.5‰, $\delta^{15}N$ of 3.9‰ and pH of 5.39 (H_2O). Intact soil cores (40 cm length*15 cm diameter), including the living vegetation, were then housed in carts connected to a cooling unit and placed within a glasshouse. Such a terrestrial model ecosystem setup simulates natural processes and interactions while allowing control over some environmental variables such as rainfall (see Knacker et al., 2004 for details of terrestrial model ecosystem approach).

We used a fully factorial design with two compost application rates and three rain regimes. The green waste was collected from municipal green waste and composted following the method of Ng et al. (2014). Its characteristics were: total C (16.9%), total N (1.49%), total P (2440 mg/kg), $\delta^{13}C$ (−27.8‰); $\delta^{15}N$ (7.3‰), NO_3^- (485 mg/kg), NH_4^+ (30 mg/kg) and pH 8.36 (H_2O). Compost was applied to the soil surface at the rate of 30 ton/ha (based on dry mass), which was equivalent to 86 g (wet weight) per core. The control amendment treatment received no compost.

Rain treatments were based on rainfall data from 1948 to 2012 for Pakenham from the Australian Bureau of Meteorology (2012) weather station at Scoresby, located 32 km to the northwest. The frequency of rain was determined by calculating the median number of rain events and the number of days where the rainfall was greater than 1 mm, followed by random number generation using R 2.15.1. A rain event was defined by any precipitation in a day or over consecutive days. Accordingly, in this experiment, rain was applied once at each rain event for March and April and over two consecutive days for each rain event in May. For normal rain, which is the control rain treatment, we determined total amount of rain from the decile 5 (median) rainfall for each autumn month (March, April and May) over the period 1948 to 2012. This corresponds to 47.8 mm, 65.0 mm and 83.2 mm for March, April and May, respectively. For the drying (drought) treatment, we used the lowest rainfall recorded over the same period. This corresponds to 4.0 mm, 18.4 mm and 12.4 mm for March, April and May respectively. The rewetting (heavy rainfall) after drought treatment on day 87 (150 mm in a day) was based on record high rainfalls in Victoria.

Cores were assigned in a randomised complete block design. Each full set of treatments was housed in a temperature-regulated cart and each treatment was replicated five times. The cores were equilibrated for 2 weeks and maintained under normal rain conditions using deionised water. The cores were organised into randomised blocks, housed within a controlled environment glasshouse. The photoperiod was 16 h day/8 h night. Day temperature was maintained at maximum 24 °C, 20 °C and 16 °C,