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E.-L. Ng, A.F. Patti, M.T. Rose, C.R. Schefe, R.J. Smernik, T.R. Cavagnaro

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Authors: [1, 2] [*]Ng, E-L; [2]Patti A.F; [1, 2]Rose M.T., [3]Schefe C.R., [4]Smernik, R. [4]Cavagnaro T.R.

[1]School of Biological Sciences, [2]School of Chemistry, Monash University, Victoria 3800, Australia. [3]Department of Environment and Primary Industries, Victoria, Australia, [4]School of Agriculture, Food and Wine, University of Adelaide Waite Campus, Urrbrae, South Australia 5064, Australia

[*] Corresponding author. Tel.: +613 99051660; Fax: +613 9905 5613.

E-mail address: eeling.ng@monash.edu

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.

Keywords: carbon cycling; 13-C NMR; PLFA; microbial activity; grassland soil microbial community

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 (Alexander and Arblaster, 2009; Hennessy et al., 2008), the ability of soil microbial communities to withstand or adapt to the changes remain unclear. Some studies have observed that soil microbial community in grassland ecosystems were resistant and resilient to climatic extremes, suggesting presence of communities adapted to regular, seasonal fluctuations in temperature and rainfall experienced by such ecosystem (Cruz-Martínez et al., 2009; Griffiths et al., 2003; Waldrop and Firestone, 2006). 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 fertilization, 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 fertilizer inputs and this trend is likely to continue in the coming decades, although some fertilizers, such as phosphorus and potassium, are derived from finite resources (Cordell et al., 2009; Odegard and van der Voet, 2014; Vitousek et al., 1997). 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 et al., 2014; Ryals and Silver, 2013). 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 et al., 2014; Ryals and Silver, 2013). With these expected benefits to the soil on addition of compost, compost may increase both the resistance and

resilience of grassland soil microbial community, 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, focusing 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 soil microbial community to altered rainfall; and therefore, similarly increase the resistance and resilience of the processes of C, N and P that they govern to altered rainfall. We also tested the hypothesis that grassland soil microbial activity is more responsive to drying-rewetting compared to soil microbial community composition, i.e. resistance and resilience of soil microbial composition are greater than that of soil functions. Any increase in the resistance and resilience of the soil microbial community with compost amendment would be indicated by a stable microbial community composition in response to drying, and the ability of the community composition to recover post drying-rewetting respectively. 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, and the recovery in process rates (as indicated by microbial activity) post drying-rewetting respectively.

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 (40cm length*15cm diameter), including the living vegetation, were then housed in carts connected to a cooling unit and placed within a glasshouse. Such 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 on the surface at the rate of 30 ton/ ha (based on dry mass), which was equivalent to 86 g (wet weight) per core. The control 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 is greater than 1 mm, followed by random number generation using R 2.15.1. A rain event is 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 1948 to 2012. This corresponds to 47.8 mm, 65.0 mm and 83.2 mm for March, April and May, respectively. For 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, respectively, for March, April and May. The cores were destructively sampled after 3 months. Samples were taken from the 0-5 cm depth and sieved to less than 2 mm. Subsamples were kept at 4 °C for enzyme analysis or -20 °C for other analyses, followed by air drying of the remaining sample for chemical analysis.

2.2 Soil physical and chemical properties

Unamended and amended soil samples were analysed for a suite of chemical properties. A high-frequency induction furnace (LECO Pty Ltd) was used to measure total soil C and N. Mineral N was extracted with 2 M KCl (1:4 soil extractant) and measured colorimetrically

following Forster (1995) and Miranda et al. (2001) for NH_4^+ and NO_3^-, respectively. NH_4^+ was determined by reaction with salicylate and hypochlorite in a buffered alkaline solution in the presence of sodium nitroprusside. NO_3^- was determined by reduction of nitrate using vanadium (III) combined with detection by acidic Griess reaction. Total soil P was determined by method 17C1 in Rayment and Lyons (2011). Air-dried soil was subjected to aqua regia block digestion followed by measurement using ICP-AES. Plant available P, measured as Colwell P was extracted with 0.5 M $NaHCO_3$ (1:100 soil extractant) and measured following D'Angelo *et al.* (2001) using malachite green colorimetric procedure

2.3 Plant Biomass

The above-ground biomass was obtained by cutting the grass close to the soil surface. Roots were extracted by wet sieving using 1 mm and 0.25 mm sieves. Samples were dried at 40 °C for 3 days. Plant C, N, $\delta^{13}C$ and $\delta^{15}N$ content were determined on an ANCA GSL2 elemental analyser interfaced to a Hydra 20-22 continuous-flow isotope ratio mass spectrometer (Sercon Ltd., UK). Stable isotope data are expressed in the delta notation ($\delta^{13}C$ and $\delta^{15}N$), relative to the stable isotopic ratio of Vienna Pee Dee Belemnite standard (R_{VPDB}= 0.0111797) for C and atmospheric N_2 (R_{Air} = 0.0036765) for nitrogen.

2.4 Microbial community analyses

Soil microbial biomass C, N and P were determined by the chloroform fumigation-extraction technique as described by Vance et al (1987), but using 4 g of fresh soil for both

fumigated and un-fumigated sub-samples. Microbial biomass C was quantified by dichromate digestion of fumigated and unfumigated samples as described by Cai *et al*. (2011). Microbial biomass N was determined using the method of Joergensen and Brookes (1990) to quantify ninhydrin-reactive N, and microbial biomass P was determined via the method of Jeanotte *et al*. (2004) using malachite green colorimetric procedure.

Soil microbial phospholipid fatty acid (PLFA) was extracted using a method modified from Bligh and Dyer (1959) using citrate buffer (Nielsen & Petersen 2000) and alkaline methanolysis of phospholipids (Bossio and Scow, 1998). The PLFA profile was identified using a Varian CP 38/00 gas chromatograph fitted with 5 % phenyl:95 % methylsiloxane column (Varian, Walnut Creek CA, USA). The fatty acids i15:0, a15:0, 15:0, i16:0, 16:1ω7, i17:0, a17:0, 17:0cy, 17:0, and 19:0cy were chosen as bacterial biomarkers and linoleic acid (18:2ω6,9) was chosen as the biomarker for decomposer fungi (see Frostegård and Bååth, 1996 and references therein).

2.5 Microbial activity

We assayed the activities of five enzymes in soil. β-glucosidase (BGL), phosphatase (PHOS) and polyphenol oxidase (PPO) activities were determined according to procedures modified from Allison and Jastrow (2006). We have found these assays to provide a good indication of soil microbial community activity in our earlier work on the impact of organic amendments to the soil (Ng et al., 2014). Peroxidase (POX) was assayed using a method modified from Frey *et al.* (2000) and Johnsen and Jacobsen (2008). Urease (URE) was assayed following a method modified from Kandeler and Gerber (1988). 0.5 mL of homogenised soil

slurry in sodium acetate buffer (pH 5, 50 mM; 5g in 50 mL) was combined with 0.5 mL of substrate solution made using the acetate buffer. BGL, PHOS, URE, PPO and POX were incubated for 2h, 2h, 5h, 1h and 10 mins, respectively. A background soil control and a substrate control were analysed for all enzymes. For URE, an additional 0.01 mL of toluene was added in all replicates and controls. At the end of incubation, NH_4^+ was extracted using 4 M KCl and NH_4^+ measured using the Forster (1995) method modified for a 96-well microplate.

2.6 Statistical Analysis

Randomised block design ANOVA was performed. Where assumptions of normality and homoscedasticity were not met, transformations were carried out and compared to results of untransformed data. Where similar statistical significance was obtained, results of the untransformed data were presented. Transformation was retained for the analysis of the following: log (n+1) transformation for aboveground biomass for May and $\delta^{15}N$, and rank transformation for BGL and PHOS. Post-hoc multiple comparisons were carried out using a least significant difference (LSD) test with *p*-values adjusted using Bonferroni.

To assess the resistance of the soil microbial communities (i.e. their ability to resist change following a disturbance), we calculated the difference in soil microbial structure between drying and control relative to the control using bacterial biomass, fungal biomass and bacteria-to-fungal ratio (B:F ratio). To assess the resilience of the microbial communities (i.e. their ability to recover after disturbance), we calculated the difference between the rewetting and control relative to the control using bacterial biomass, fungal biomass and B:F ratio. The resistance of microbial activities (BGL, PHOS, PPO, POX, URE), as indicators of soil functions, was

calculated as the difference of soil function between drying and control relative to the control. Therefore, the resistance of soil functions was examined with respect to controls. The resilience of the soil functions was calculated as the difference between the rewetting and control treatments relative to the control treatments. Compost-amended soils under normal rainfall were used as controls for amended samples and unamended soils under normal rainfall were used as controls for unamended samples. Randomised block design ANOVA was carried out as above on the actual response variables for all treatments to minimise introduced errors due to multiple one-way ANOVAs.

Multivariate analysis was carried out using standardised data. Microbial biomass and PLFA data were standardised using chord transformation. Kendall τau (τ) was used to examine correlation between fatty acids. Most fatty acids were correlated. Five fatty acids had < 50% correlation with other variables. Sequential addition of fatty acids to the analysis did not add meaningful patterns to the ordination. Therefore these five fatty acids were sufficient for the final nonmetric multidimensional scaling (NMDS). All results were checked by using chi-square transformation, cluster analysis and principal component analysis (PCA). Cluster analysis was done using Ward's hierarchical clustering on the Bray-Curtis dissimilarity matrix. The results were generally the same and only NMDS and cluster analysis are shown.

Data analysis was carried out on R 2.15.1 (R Core Team 2012) using the alr3 package (Weisberg, 2005) and the agricolae package (Mendiburu, 2012) for randomised block ANOVA and LSD test, respectively. Ordinations were carried out using the vegan package (Oksanen et al., 2012).

3. Results

3.1 Soil physical and chemical properties

Soil moisture differed across the different rainfall treatments applied (Fig. 1; $F_{2,22}$ = 204.1, p <0.001). Soil moisture was highest in rewetting, followed by normal rainfall and drying treatments. Additionally, amended soils had consistently higher soil moisture than unamended soils ($F_{1,22}$ = 10.4, p = 0.039). Soil C:N, C:P and N:P ratios were similar across treatments (Fig. 1). Mineral N content (NH_4^+ and NO_3^-) was different only between rain treatments (Fig. 1; $F_{2,22}$ = 11.4, p <0.001 for NH_4^+; $F_{2,22}$ = 53.9, p <0.001 for NO_3^-). Soil NH_4^+ and NO_3^- were higher in the drying and rewetting treatments compared to normal rain. Plant available (Colwell) P was only different between amended and unamended treatments ($F_{1,22}$ = 6.4, p = 0.019). Compost amended soils had higher Colwell-P compared to unamended soils.

3.2 Plant biomass and elemental content

Plant biomass was mainly affected by rain treatment (Fig. 2; $F_{2,22}$ = 37.3, p <0.001 in April; $F_{2,22}$ = 65.3, p <0.001 in May; $F_{2,22}$ = 8.2, p = 0.002 for roots), where above-ground biomass was higher under normal rain in the second and third months of the experiment. Root biomass was also higher under normal rain compared to drying, but similar when compared to rewetting. The addition of OA also affected above-ground biomass at the end of the experiment (May) ($F_{1,22}$ = 12.1, p = 0.002); specifically, above-ground biomass was lower in compost amended than unamended soils.

Plant aboveground C content was affected by OA only under normal and rewetting treatments (Fig 2B; $F_{2,22}$ = 5.5, p = 0.013). Under normal rain, there was higher plant C in unamended compared to compost amended soil but the reverse was found in the rewetting treatment, i.e. plant biomass C was higher in compost amended soil compared to unamended soil. Plant $\delta^{13}C$ varied over a narrow range between -27 and -29 ‰ (Fig. 2C). Plant aboveground N content was similar across all treatments (Fig. 2D). However, their $\delta^{15}N$ value was affected by rain treatment ($F_{2,22}$ = 3.6, p = 0.04) and addition of OA (Fig. 2E; $F_{1,22}$ = 18.5, p <0.001). Specifically, plant $\delta^{15}N$ was more similar between drying and rewetting treatments compared to normal rainfall. Plant $\delta^{15}N$ was also higher with addition of OA; this is consistent with the OA having a higher $\delta^{15}N$ than the soil.

3.3 Soil microbial composition and structure

Soil microbial biomass C, N and P composition under normal and rewetting treatments were more similar than for the drying treatment (Fig. 3A). Additionally, cluster analysis indicated that soil microbial biomass C, N and P composition was more similar between amended soil under rewetting and soils under normal rain (Fig. 3C). Soil microbial PLFA composition showed no clear pattern with regards to the treatments (Fig 3B). OA altered the resistance of bacterial biomass to drying ($F_{2,22}$ = 15.7, p < 0.001, Fig. 4A). Bacterial biomass in unamended soil was resistant to drying. The addition of compost further increased the bacterial biomass even with drying. Fungal biomass was resistant to drying regardless of OA treatment ($F_{1,22}$ = 0.8, p = 0.371, Fig. 4A). The B:F ratio was similarly resistant to drying regardless of OA treatment ($F_{1,22}$ = 2.2, p = 0.152, Fig. 4A).

With rewetting, the resilience of bacteria to drying differed between amended and unamended soil ($F_{2,22}$ = 15.7, p < 0.001, Fig. 4B). With the addition of OA, bacterial biomass after rewetting was similar to that of normal rain levels. The addition of OA did not alter the resilience of fungal biomass or B:F ratio. Fungal biomass under the rewetting regime was similar to that of normal rainfall regardless of the addition of OA ($F_{1,22}$ = 0.8, p = 0.371, Fig. 4B). The B:F ratio was higher in rewetting compared to drying treatment regardless of OA treatment ($F_{2,22}$ = 13.8, p < 0.001, Fig. 4B).

3.4 Microbial activities

β-glucosidase (BGL), phosphatase (PHOS), polyphenol oxidase (PPO) and peroxidase (POX) activities had low resistance to drying (Fig. 4C; $F_{2,22}$ = 4.2, p = 0.029; $F_{2,22}$ = 9.5, p = 0.001; $F_{2,22}$ = 7.5, p = 0.003; $F_{2,20}$ = 35.4, p < 0.001). This was indicated by the observed lower than control microbial activity with drying. The addition of OA did not alter the resistance of BGL, PPO or POX to drying but improved PHOS resistance to drying. URE was unaffected by drying regardless of the amendment treatment ($F_{2,22}$ = 0.9, p = 0.406).

BGL was resilient to drying with or without OA ($F_{2,22}$ = 4.2, p = 0.029, Fig. 4D). PPO was similarly resilient to drying with or without OA ($F_{2,22}$ = 7.5, p = 0.003, Fig. 4D). Both BGL and PPO returned to control levels with rewetting in both amended and unamended soils. PHOS resilience was low but the addition of OA improved PHOS resilience to drying ($F_{2,22}$ = 9.5, p = 0.001, Fig. 4D). URE was unaffected by rewetting regardless of the amendment treatment ($F_{2,22}$ = 0.9, p = 0.406, Fig. 4D). The addition of OA reduced the resilience of POX to drying ($F_{2,20}$ = 5.9, p = 0.009, Fig. 4D).

4. Discussion

Overall, compost addition led to an increase in soil moisture, greater plant available Colwell-P and higher plant $\delta^{15}N$. Soil C:nutrient ratios, mineral N content (NH_4^+ and NO_3^-) but 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 $\delta^{15}N$ content, 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 Colwell-P and soil microbial PLFA composition. There was little interaction between rainfall and compost amendment, which was found to affect only plant above-ground C content, bacterial biomass, POX activity and microbial biomass C, N and P composition. We expected that compost amendment would improve the resistance and resilience of the soil microbial community to drying and rewetting cycles. Bacterial biomass was resistant to drying and bacterial biomass further increased with compost despite drying, but the resistance and resilience of fungal biomass and B:F ratio to drying were unaffected by compost addition. Compost addition also did not alter the resistance and resilience of most soil functions to drying and rewetting.

Cluster analysis of soil microbial biomass C, N and P composition indicated a possible interaction effect of rainfall and OA treatments, where the analysis indicated two main groups. One group consisted of compost amended soil under rewetting, and both amended and unamended soils under normal rainfall. The other group consisted of unamended soil under rewetting, and both amended and unamended soils under drying. Given these differences in microbial biomass elemental composition between amended and unamended soil under rewetting

occurred while their microbial PLFA composition and B:F ratio remained similar, this may indicate that the compost amendment altered soil microbial behaviour and physiology (Blagodatskaya et al., 2007; Manzoni et al., 2010). Prior studies have also found physiological responses to rewetting without changes in microbial community composition (Griffiths et al., 2003).

The low B:F ratio under drying and the high B:F ratio after rewetting indicated a rapid change in microbial structure. Fungi can be resistant to drying and are less sensitive to changes in moisture although they tend to decrease when the soil becomes saturated (Drenovsky et al., 2004; Unger et al., 2009; Yuste et al., 2011). We did not observe water saturation in our soils but we did observe lower fungal biomass with rewetting compared to soils under drying conditions. In a mild rewetting study using two soils, an inconsistent response from fungal biomass was observed whereby one soil had higher fungal biomass with rewetting while the other did not respond to rewetting (Steenwerth et al., 2005). Changes in other physicochemical properties of the environment and interactions of microbes with other soil biota have been proposed to be at play. Furthermore, we measured these changes less than three days after the rewetting and soil moisture remained higher in the rewetting treatment, so these differences in microbial structure may merely reflect the temporal dynamics in the soil physicochemical environment. Interestingly, bacterial biomass in the compost amended soils returned to control levels with rewetting but unamended soil had a significantly higher bacterial biomass. It is unclear what could have caused this response and this is worthy of further investigation.

We expected soil microbial activity to be more responsive to drying and rewetting compared to soil microbial composition or structure. Indeed we observed that soil functions changed with rainfall regimes, with a general decline in all enzyme activities under drying.

However, microbial activity returned rapidly to that of control levels with rewetting, indicating soil functional resilience. Upon rewetting, rapid resuscitation of the soil microbial community, together with an immediate increase in activity, maximises the temporal pulse in resource availability (Dijkstra et al., 2012; Placella et al., 2012). The increases in microbial activity, however, did not alter the available N content in soils that experienced rewetting, which were similar in both amended and unamended soils, and similar to that of soils which experienced drying. As URE activity was unaffected by rainfall or compost, N was unlikely to be limiting in this system.

As microbial activity is sensitive to drying, we expected that the addition of compost may improve resistance and resilience of soil functions to drying. However, we found that BGL, PHOS and PPO were only affected by rainfall. The only interaction effect observed for soil functions was POX activity. The addition of compost did not improve the resistance of POX to drying but it reduced POX resilience to drying. POX activity has been reported to decrease with drying and this decline has been associated with reductions in fungal biomass and species richness but these observations did not extend beyond a drought period (Toberman et al., 2008). Besides fungi, actinomycetes are central to the production of phenol oxidase and peroxidases for the degradation of phenolic compounds indicative of more recalcitrant organic matter (Kirk and Farrell, 1987; Sinsabaugh, 2010). As we observed fungal biomass was similar between amended soil that experienced rewetting and its normal rainfall control, actinomycetes may have an important role in our ecosystem. It is unclear why POX resilience to drying should be reduced with compost addition. It could be a simple case of the soil microbes preferentially exploiting the sudden pulse of labile resources from compost and plant exudates. Measures of POX over a longer period post-rewetting would be necessary to test this possibility.

The similarity of the overall microbial PLFA composition across compost amendment and rainfall variations, the general resistance and resilience of microbial structure and resilience of soil functions in this grassland can be attributed to various factors. First, the chemical nature of the compost is an important determinant of its decomposition and transformation (Fontaine et al., 2011; Kallenbach and Grandy, 2011; Pascault et al., 2013). For example, prior study has shown that the carbon composition of the OA strongly influences microbial PLFA composition and activity through changes in soil carbon composition (Ng et al., 2014). The carbon composition of the soil organic matter influences its chemical, physical and biological interaction within the soil matrix and determines its stability and accessibility to the soil microbial community (Kögel-Knabner et al., 2008). We found that the soil carbon composition, as determined by ^{13}C-solid state NMR, was relatively similar across all our treatments (see supplementary Fig S1). As compost is a form of stabilised organic matter, its chemical nature makes it palatable only to a subset of the soil microbial community (Fontaine et al., 2003; Pascault et al., 2010). As such, depending on the environment and therefore organo-mineral interactions, the decomposition of compost may be slow. In one field study, it has been observed that only 12% of compost was decomposed 3 years after amendment (Ryals and Silver, 2013). This slow rate of decomposition means that hysteresis may have an important role that cannot be addressed within the time scale of this study.

Second, previous studies have reported that soil microbial communities inhabiting environments that regularly observe great fluctuations in environmental conditions are relatively resistant and resilient to such fluctuations in their environment (Fierer et al., 2003; Griffiths et al., 2003). This in part is attributed to physiological properties of the soil inhabitants and in part to permanent changes in the physical domain of the soil with such fluctuations. For example, the

collapse of macro- and meso-pores in soil or organic matter aggregates when hydrogen-bonded water is lost is irreversible with rewetting. These can explain the similarity in responses from soil microbial communities of different farming systems in California's hot, rain-free summer to soil drying and re-wetting (Lundquist et al., 1999). Combined with a history of intensive land use, a soil microbial community that is resistant and resilient to disturbances may have evolved earlier to inhabit this habitat (Ge et al., 2008; Martiny et al., 2006; Ohsowski et al., 2012). A comparison of microbial communities across eight land use across California has found that agricultural management had larger effects on microbial composition than elevation or precipitation regime (Drenovsky et al., 2010). Furthermore, the biotic legacy and site history also influences soil physicochemical properties which have important effects on microbial community composition and physiology (Griffiths and Philippot, 2013). As our study site is an intensively grazed grassland with moderate nutrient availability, this may explain the lack of microbial activity response to compost amendment.

Third, the timing of rainfall, rather than quantity has been proposed to be critical to grassland community response (Chou et al., 2008; Cruz-Martínez et al., 2009; Weltzin et al., 2003; Zeglin et al., 2013). Following 5 years of rainfall addition in a grassland experiment, soil bacteria and archaea were found to be relatively similar to those found under ambient rainfall conditions (Cruz-Martínez et al., 2009). The changes that were subsequently observed during the sixth and seventh year occurred only when additional rainfall exacerbated or alleviated periods of aberrant conditions in the ambient climate. When rainfall occurs over a cold winter, lower evaporation rates translate to increased soil water, less oxygen and translocation of oxides of iron and aluminium leading to lower soil redox potential (Berhe et al., 2012). When rainfall occurs in a warmer spring, an increase in plant growth leads to higher evaporation rates and soil redox

potential (Berhe et al., 2012). These changes in soil chemical properties affect soil organic matter stabilisation, and may help to explain some of the responses seen in the microbial communities that rely on soil organic matter to support their activity for cell growth and maintenance.

The addition of compost did not improve the resistance of plant growth responses to drying. Both plant above-ground and below-ground productivity were negatively affected by drying, although plant $\delta^{13}C$ showed no clear indication of drought stress. Despite the differences in availability of mineral N and indications from $\delta^{15}N$ that the plants did utilise the N from OA, this was not translated to higher plant N in compost amended soils, although there seemed to be a trend of higher plant N with compost amendment. In fact, the above-ground N content of plants indicated that they were marginally deficient despite compost amendment. We do not discuss plant resilience here as this study focuses on soil microbial community, and therefore we have measured rewetting responses less than three days post-wetting. This duration is insufficient for examining plant resilience. However, it is important to note that while semi-arid grasslands are adapted to moisture limitation, a study on semi-arid shortgrass steppe in Colorado, USA, found that it took more than 4 to 7 years of drought before significant differences in plant species composition were observed (Evans et al., 2011). The Victoria region of study has just emerged in mid-2010 from a 13-year period drought, and therefore this study presents an interesting insight into the state of ecosystem processes post prolonged stress.

In this study, we found that the grassland soil microbial communities are generally resistant and resilient to fluctuations in rainfall regardless of compost amendment. These properties of the soil microbial community were translated to resilience but not resistance in soil functions. Overall, the results below-ground showed much greater response to rainfall than

compost amendment. This indicates that in this grassland, water is the main limiting factor for the soil microbial community, and nutrients are not strong co-limiting factors.

Such robustness observed in grassland soil microbial community to rainfall alteration is not seen in overlying macro-organisms (Cruz-Martínez et al., 2009). In our study, we observed that plant growth was sensitive to rainfall and compost amendment, but interaction among main treatments were rare, or at least not discernible based on our measures. It also appeared that soil fertility and climate factors differ in their relative importance as drivers for the above- and below-ground communities.

Rainfall and organic amendment impact plant-soil interactions across a range of spatial and temporal scales, at which the potential for decoupling increases with increasing scale (Bardgett et al., 2013). For example, at physiological level, rainfall affects photosynthetic rate and the production of plant exudates. On a higher level, it may lead changes in plant community composition, thereby altering the amount and quality of plant exudates entering the soil (Bardgett et al., 2013). Such differences in above- and below-ground responses may lead to decoupling between below- and above-ground dynamics and affect biogeochemical cycling (Bardgett et al., 2013; Cruz-Martínez et al., 2009). On the other hand, others have found that microbial and plant processes can be synchronised following a water pulse (Dijkstra et al., 2012). We have also observed in our study that both soil functions and plant productivity was similarly poor in resistance to drying despite organic input, but soil functions were resilient to drying. There is possible that plant processes are similarly resilient in this ecosystem. Given there may be a time lag and longer duration in plant-microbial feedback that cannot be captured in our study, such interpretations remain to be confirmed by future studies. This study represents one of the few studies examining interactions between organic matter amendment and environmental change.

Such studies, particularly if longer-termed, will allow us to identify climate-management-plant-soil microbial interactions and identify ways forward to sustainable management of productive ecosystems under global change.

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Figures

Fig. 1 Chemical and moisture properties of soil with compost treatment (mean ± standard error) under different rainfall. All bar plots are similarly grouped from left to right for drying, normal and rewetting treatments. (+) = compost amended soils, (-) = unamended soils.

Fig. 2(A) Plant aboveground in March, April and May, and root biomass in May; where (+) = compost amended soils, (-) = unamended soils. (B,D) Plant C and N contents and, (C,E) Plant $\delta^{13}C$ and $\delta^{15}N$ in May.

Fig. 3 Variations in soil microbial composition with amendment treatment under variations in rainfall. Nonmetric multidimensional scaling (NMDS) plots of (A) microbial biomass C, N and P composition and (B) microbial PLFA composition. Distances among points express relative dissimilarities in microbial composition. (C) Cluster analysis of microbial biomass C,N and P composition. (+) = compost amended soils, (-) = unamended soils.

Fig. 4 (A,C) Effects of compost on resistance of soil microbial PLFA composition and microbial activity to drying. (B,D) Effects of compost on resilience of microbial composition and microbial activity following rewetting. Abbreviations stand for bacterial-to-fungal ratio (B:F ratio), B-glucosidase (BGL), phosphatase (PHOS), polyphenol oxidase (PPO) and peroxidase (POX). (+) = compost amended soils, (-) = unamended soils.