



Short communication

Rhizosphere effects on functional stability of microbial communities in conventional and organic soils following elevated temperature treatment

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ABSTRACT

The resistance and resilience of soil function may be increased through selection of crops and organic matter inputs. Soil from paired organic or conventional plots was left unplanted or used to grow barley. Substrate induced respiration (SIR) and community level physiological profiles (CLPP) were significantly different in both planted and unplanted systems and in conventional and organically-managed farming systems with no interaction; planted and organic systems had higher SIR. Following heat treatment (30 min at 70 °C), CLPP of planted and unplanted soils in both farming systems changed; a small short-lived decline in SIR only occurred in the planted soils. Differences in the response of these microbial communities to stress may be related to the relative proportions of active and dormant organisms; an increase in functional diversity did not necessarily reflect changed soil function.

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No dominant factor drives functional stability of soil microbial communities in semi-natural systems (Orwin et al., 2006). However, selection of crops and organic matter inputs in agricultural systems leads to differences in the amount and quality of soil organic matter (SOM; Murphy et al., 2011). Often soils in organic farming systems have been shown to have higher SOM and biological fertility compared to conventional systems – this is driven by choices in farm management. Gregory et al. (2009) showed that long-term farm management was related to resistance and resilience in physical and biological function; hence farmers may be able to mitigate soil function against climate change (Stockdale and Watson, 2009). Grime (2001) showed that plant species growth pattern was linked to community stability. Soil micro-organisms can also be grouped by growth rate (Fontaine et al., 2003) and the functional stability of microbial communities may be regulated similarly (Botton et al., 2006; Orwin et al., 2006). In contrast resistance and resilience in soil function have been positively correlated (Gregory et al., 2009). Short-term responses to stress may be mediated largely by the response of fast-growing micro-organisms (Bottner, 1985), while slow-growing/dormant micro-organisms may affect measured microbial community structure with little impact on function (Rousk et al., 2011). Consequently,

microbial community structure is as important for soil functional stability as diversity *per se* (Griffiths et al., 2004). The resilience of soil function may also depend on the availability of resources immediately before disturbance, which drives both the size and community structure of soil micro-organisms (Bosatta and Berendse, 1984). Functional redundancy within the soil microbial community also means that significant change in diversity can take place following a stress, without an impact on overall soil function.

Semi-arid agricultural soils of Western Australia are characterized by hot, dry summers with surface soil temperatures (0–10 cm) typically reaching 30–40 °C (Barton et al., 2011) and cooler, wet winters. Burning continues to be a common management practice in Western Australia to address disease carry over, weed control and easier passage of seeding equipment (Hoyle and Murphy, 2006). Hence intense short-term heat treatment represents an annual stress (Banning and Murphy, 2008). Farming systems with contrasting long-term organic matter inputs (organic/conventional soil) were subjected to a pre-treatment (planted/unplanted system) to alter the balance between fast-growing and less-active micro-organisms. Functional stability was assessed in relation to the capacity of the soil microbial community to utilize low-molecular-weight organic molecules (Anderson and Domsch, 1978; Degens et al., 2001). We hypothesized that: (i) organic soil has greater soil microbial activity, resistance and resilience than conventional soil; (ii) planted/unplanted systems show responses to stress as

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a result of the altered balance of fast-growing (rhizosphere) and less-active (bulk soil) micro-organisms which are able to utilize a wide range of substrates.

The Alternative Farming System trial at Morawa Agricultural College, Western Australia has field plots in rotation with crops and annual pasture managed in accordance with the National Association for Sustainable Agriculture, Australia (NASAA) standards (organic) or in arable cropping (wheat-chick pea rotations, conventional). Both systems were managed with minimum tillage. Following 10 years of the trial a composite soil sample (0–10 cm; 30 kg) was collected in each farming system during summer fallow (field water content 0.005 g g^{-1}) following oat/peas (organic) or wheat (conventional) and sieved ($<4 \text{ mm}$). The soil is a shallow red earth (McArthur, 1991; Ferralic Cambisol, FAO; sandy loam texture). The organic and conventional soils had organic carbon (C) contents (Walkley Black) 1.09 and 0.91% C, pH (CaCl_2) 6.5 and 5.3, available phosphorus (Colwell) 33 and 54 mg P kg^{-1} , available potassium (Colwell) 521 and 297 mg K kg^{-1} and water holding capacity (WHC) 23 and 18 g g^{-1} respectively.

Four replicate pots (2 kg, organic or conventional soil, without nutrient amendment) were either planted (barley, 9 plants per pot) or left unplanted at 75% WHC in a glasshouse for 8 weeks until roots and associated rhizosphere micro-organisms occurred throughout the soil. Plants were cut 1 cm above the soil surface; soil and root material was then mixed thoroughly by hand (unplanted systems were also mixed). Two subsamples from each replicate pot (200 g oven dry equivalent) were placed into 1 L glass jars and incubated (25°C for 48 h) allowing basal respiration to stabilize. One subsample (unsealed) was then placed in a pre-heated oven (70°C) for 30 min. Actual soil temperature was recorded using a data logger (Signatrol, UK; Fig. 1); water loss during heat treatment was $<1.1\%$ of the total. Sterilized water was added to account for this minimal loss and jars were then returned to incubate for a further 240 h with the other sub-samples where no heat treatment had been applied (25°C , 75% WHC).

Substrate induced respiration (SIR) was used to assess the functional capacity of the heterotrophic micro-organisms in the absence of C limitation (Anderson and Domsch, 1978). Briefly 1 g soil (oven dried equivalent) was weighed into McCartney bottles (27.7 mL) on seven occasions after the heat treatment (0, 24, 48, 72, 144, 192, 240 h) and 0.75 mM of glucose–C added. After 4 h incubation, CO_2 concentrations in headspace samples were determined (against $4.95 \pm 0.10\%$ CO_2 in He, BOC Ltd.) by infra-red gas analysis. Use of the absolute data allowed consideration of the overall response of soil functions to stress (Gregory et al., 2009). Resistance

and resilience of SIR rates were also expressed in relation to untreated controls (Orwin et al., 2006); systems were considered to have recovered when the resilience index reached zero (Banning and Murphy, 2008).

At the end of the incubation (240 h), C substrate-utilization (Degens et al., 2001) based on community level physiological profiles (CLPP) was used to determine if catabolic diversity had recovered after heat treatment. Briefly, 25 different organic substrates (Stevenson et al., 2004; 2 mL adjusted to soil pH) were each added to soil prepared as for SIR; CO_2 production was determined as described above. Catabolic evenness was calculated using the Simpson–Yule index (E ; Magurran, 1988). A higher index value indicates greater catabolic diversity within the active microbial population (Degens et al., 2001); in this study the maximum value is therefore 25.

Differences in SIR were tested by analysis of variance with two fixed factors: farming system (organic or conventional) and pre-treatment (planted or unplanted; GenStat, 2001). CLPP data were standardized using the total substrate response of each soil. Distance matrices were based on Manhattan distance, conferring better robustness to outliers (Clarke and Warwick, 2001). Test of the multivariate null hypotheses of no difference between the *a priori* defined treatments was examined using permutation multivariate analysis of variance (PerMANOVA; Anderson, 2001a). PerMANOVA tests used 4999 permutations of raw data from residuals under a reduced model (Anderson, 2001b). To visualize the differences, ordinations were performed by principal coordinate analysis (PCA).

SIR followed a non-constant but parallel path in all farming systems and pre-treatments (planted/unplanted) during the incubation period (Fig. 2a–d). Where no heat treatment had been applied, average SIR was significantly higher ($P < 0.001$) throughout the incubations in both the organic (4.5 compared with $3.7 \mu\text{g CO}_2\text{-C g}^{-1} \text{ soil h}^{-1}$) and planted systems (4.4 compared with $3.8 \mu\text{g CO}_2\text{-C g}^{-1} \text{ soil h}^{-1}$) with no interaction. Fließbach et al. (2007) also found higher microbial biomass, activity and catabolic diversity in soils from organic farming systems. In our study the organic soil had higher SOM and pH as a result of increased C inputs and an absence of acidifying mineral fertilizers. Similarly Jangid et al. (2008) found that SOM levels and pH determined microbial population size and community structure. CLPP was also different in farming system ($P = 0.002$) and pre-treatment ($P = 0.003$) with no interaction. Organic soils had a significantly greater E (15) than conventional (12; $P < 0.05$), but there was no difference with pre-treatment (planted/unplanted). Short-term inputs of relatively simple C compounds in the rhizosphere or crop residues increase microbial biomass and activity through stimulation of fast growing bacteria (Kowalchuk et al., 2002) but do not change catabolic diversity (Bending et al., 2002). PCA of the CLPP data showed clear differences where no heat treatment was applied (Fig. 3). Organic and conventional soils separated along Axis 1 of the ordination plot with smaller separation between planted and unplanted systems; the largest component of the variance observed in the CLPP is therefore likely to be linked to microbial resource availability/utilization.

On average, heat treatment caused a small but significant decline in SIR ($P = 0.013$). These soils experience an annual summer fallow (drought) period of 4–6 months where soils experience desiccation (Barton et al., 2011). We hypothesize that this has led to a microbial community resistant to extreme environmental conditions. Gregory et al. (2009) also found that SIR decreased by 0–40% and not all soils were affected by short-term heat treatment. We found no difference in the response of SIR to heat treatment between organic and conventional soils, despite the absolute differences in SIR and CLPP. However, the micro-organisms responsible for SIR in the planted

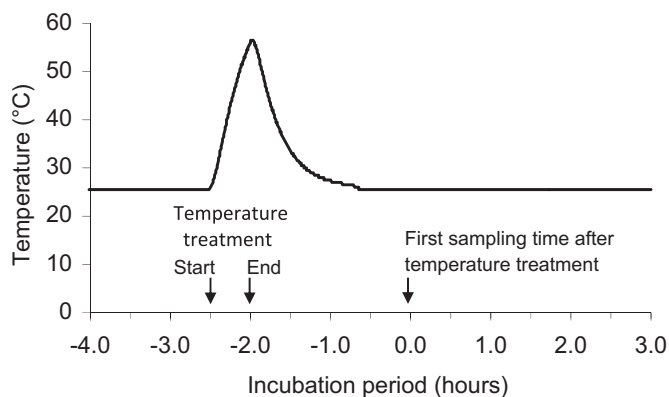


Fig. 1. Soil temperature trace taken from a temperature logger inserted in the centre of the soil sample for the experimental period -4 h to $+3 \text{ h}$ where time = 0 h refers to the first sampling of soils. The start and end of the 30 min temperature treatment is shown.

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