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Research paper

The importance of plants to development and maintenance of soil structure, microbial communities and ecosystem functions

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ABSTRACT

Soil ecosystem functions depend on the development, activity and maintenance of soil biology which in turn depends on plants because they add important carbon resources through litter fall, root exudates, mucilage and root remnants, and root activity for the aggregates formation. Correspondingly, our hypothesis was that maintaining high inputs of plant-derived carbon is important to the formation and stabilisation of soil structure, and this in-turn may support a greater diversity of habitats for microbial communities thereby ensuring more robust soil ecosystem function. To test this hypothesis we measured the physical, chemical and biological characteristics of soil from a long-term field trial. The trail was initiated in Spring 2000 on a silt loam soil (Udic Dystocrept, USDA) in Canterbury, New Zealand and includes a combination of crop and tillage treatments: permanent pasture [PP], permanent fallow [PF], rotation of barley, wheat and peas under intensive [Ii], minimum [Mm] and no tillage [Nn]. Soil aggregate profiles (size class, distribution, mean weight diameter – MWD), total organic carbon and nitrogen (TOC, and TN), along with metabolic and PLFA data were analysed using a multi-phase experimental design to investigate the effect of different plants and soil management practices on soil structure, microbial metabolic diversity and activity. The PP treatment had the most complex soil structure (MWD between 3.6 and 2.8 depending on depth) with 61% of aggregates in the 8.000 2.000 mm size class compared with PF (MDW between 1.8 and 0.5) that had only 14% of aggregates in this size class. There was strong evidence for maintenance of good soil structure within the no tillage treatment (Nn) which had higher proportions of the 8.000 2.000 mm aggregates (45%) compared to Mm (40%) and Ii (35%). Similar relationships were observed in TOC and TN data. PP had superior metabolic activity with approximately 5 μg CO_2-C g^{-1} soil (dry weight) produced in the 0–7.5 cm depth for all C-source groups. These superior indicators of soil ecosystem function for PP was attributed to the lack of soil disturbance, continual supply of carbon and a stable microbial community with an enrichment of bacteria compared to fungi at the surface. We conclude that continuous growth of plants in combination with low soil disturbance promoted greater macroaggregate scale structure, added more carbon and promoted greater microbial biomass, metabolic diversity and capacity to execute soil ecosystem function.

1. Introduction

Plants are the primary source of organic matter and energy that support soil microbial activity and maintain many important soil ecosystem functions (Beare et al., 1995; Kuzyakov and Blagodatskaya, 2015; Ponge, 2015). The organic matter supplied by plants includes that sourced from root exudates and root turnover as well as plant residues deposited on the soil surface (Rees et al., 2005). Plants also play a key role in soil structure development, including the formation of biopores from root growth and turnover and the stabilisation of soil aggregates (Oades, 1993). Soil macroaggregates (i.e. > 0.250 mm) are formed and stabilized by the physical entanglement of roots and fungal hyphae, including those of vesicular-arbuscular mycorrhizae (VAM), and the deposition of microbial and plant mucilages, particularly polysaccharides (Tisdall and Oades, 1982; Lynch and Bragg, 1985; Gupta and Germida, 1988; Oades 1993; Puget et al., 1999). These

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stabilizing agents tend to be transient in nature and require continuous inputs of organic materials and microbial activity to maintain stability (Tisdall and Oades, 1982; Blankinship et al., 2016).

The formation and stabilisation of macroaggregates facilitates some of the fundamental ecosystem functions that the soil performs, which is improving water infiltration and storage along with partitioning of water flow within the environment (Larson and Pierce, 1991). The pore spaces between the aggregates also support other ecosystem functions because the pores allow the infiltration of air and water and the diffusion of gases and substrates that are important for maintaining and regulating soil microbial activity (e.g. element transformations). These interactions play a key role in regulating soil fertility and plant productivity (Doran and Zeiss, 2000) in self-reinforcing positive feedback loops. The development of complex soil structure, composed of pores and aggregates of different sizes serves to create a wide range of habitats that support a diversity of microorganisms and functions (Beare et al., 1995; Kuzyakov and Blagodatskaya, 2015) that contribute to the overall ecosystem services provided by the soil.

Plant roots and corresponding macroaggregate development associated with greater root biomass and activity should also increase the number of "microbial hotspots", as defined by Kuzyakov and Blagodatskaya (2015). This is because there will be a greater abundance of organic compounds and debris distributed throughout a larger volume of soil profile to fuel microbial processes. In each microbial hotspot it is possible to have distinct soil ecosystem functions like nutrient or carbon transformations and hotspots have higher rates of biological activity when compared to bulk soil.

The cultivation of soils to grow crops tends to result in a decline in aggregate stability and a loss of macroaggregates (Elliott, 1986). The breakdown of macroaggregates has been attributed to the direct physical disturbance imposed by tillage and/or the indirect effects of tillage on soil organic matter decomposition and a decline in the supply of stabilizing agents (e.g. roots, fungal hyphae, polysaccharides) (Six et al., 2004). Physical disturbance through tillage also tends to break up the macroaggregates into microaggregates (< 0,250 mm diameter). Soil where structure consists predominantly of microaggregates has less capacity to support soil ecosystem functions like water and air transport and generally has lower carbon contents and biology activity. Structurally impacted soil presents a less favorable environment for soil organisms and microbial hotspots created during plant growth can be destroyed. Evidence also suggests that tillage changes the genetic composition of the microbial community (Cookson et al., 2008). As soil microbial community function is dependent on abiotic factors like carbon sources, air and water flows, the microbial community in the same spatial area can be quite different, even in the presence of the same plant (Kuzyakov and Blagodatskaya, 2015), because localized physicochemical conditions are disrupted by tillage (Six et al., 2004).

In this context, we hypothesised that maintaining high inputs of plant-derived carbon is important for the formation and stabilisation of soil structure, and this in-turn may support a greater range of habitats for microbial communities thereby ensuring more robust soil ecosystem function. To test these hypotheses we analysed the size distribution, organic matter content and microbial community structure and metabolic activity of water-stable aggregates from a long-term field trial that had differing inputs of organic matter depending on the agricultural plants grown, crop rotation and different tillage intensities. Our aim was to evaluate the role of the plants and soil management in shaping soil structure and ecosystem functions.

2. Material and methods

2.1. Experimental site and field trial

A long-term tillage trial site was used called the Millennium Tillage Trial which was initiated in Spring 2000 on a Wakanui silt loam (Udic Dystocrept, USDA) at Lincoln, Canterbury, New Zealand (43°40′S latitude, 172°28′E longitude; mean annual air temperature 11.4 °C, mean annual rainfall 867 mm). Prior to trial establishment, the site was sheep-grazed, irrigated permanent pasture (PP) that had not been cultivated for at least 14 years.

Three tillage methods applied in Spring and Autumn seasons were evaluated, these being; No-tillage (Nn): no cultivation, seeds direct drilled; Minimum tillage (Mm): the top 100 mm cultivated using a spring tined implement, followed by secondary cultivation (harrowing and rolling twice); Intensive tillage (Ii): cultivation to ~200 mm using a mouldboard plough, followed by secondary cultivation (one pass with a spring tined implement followed by harrowing and rolling twice). All tillage operations were carried out using standard commercial equipment.

Spring-sown main crops rotation included *Hordeum vulgare* (barley), *Triticum aestivum* (wheat), and *Pisum sativum* subsp. *arvense (pea)*. They were followed by winter-grazed (sheep) cover crops (oats or forage brassicas). All crops were sown using a Great Plains direct drill. Fertiliser (N and P) were applied to the spring crops to ensure these nutrients were not limiting. Plots representing the original ryegrass-clover pasture were maintained within the trial as a control. To balance the trial design, these plots were split into subplots; permanent pasture (PP), and permanent fallow (PF). The PP sub-plots were grazed with sheep (typically 10 times per year; 20 sheep per plot). The main fertiliser applied to the PP plot was superphosphate. The PF subplots received no fertiliser and had no animal or vehicle trafficking throughout the trial. Herbicide (Glyphosate) was used to maintain the PF subplots plant free. Management (irrigation, fertiliser, grazing regime) of the PP plots remained the same as before the trial. All treatments (i.e. Arable crops, PP and PF) were irrigated in summer to ensure that water was not limiting to pasture or crop growth. Treatments were replicated three times in an incomplete Latin square. The plot size was 28 m x 9 m. Further trial details can be obtained from Fraser et al. (2013).

2.2. Soil sampling and processing

Soil samples were collected in February 2013 and involved 10 cores (32 mm diameter) per plot taken in a V-shape and composited (bulked) by depth as follows: 0–7.5 cm, 7.5–15.0 cm and 15.0–25.0 cm). Subsamples of each composited soil were frozen at −20 °C, after which portions were freeze-dried for PLFA analysis (described below), with long term storage of freeze-dried soil also at −20 °C. The remaining soil was gently crumbled by hand until fragments could pass through an 8 mm sieve and were stored field-moist at 4 °C until further analysis. Each soil sample was air-dried (20 °C) for 48 h before wet aggregate size distribution analysis.

2.3. Wet aggregate size distribution, total organic carbon (TOC) and total nitrogen (TN)

The aggregate size distributions were analysed using a wet-sieving apparatus described by Beare and Bruce (1993) using sieves with apertures of 2.000, 0.250 and 0.053 mm diameter. The apparatus was operated for 20 min with a frequency of 0.8 oscillations s^{-1} and 0.16 g soil (dry weight equivalent) cm^{-2}. This process captured 4 aggregate size classes: 8.000–2.000, 2.000-0.250, 0.250–0.053 and < 0.053 mm with near complete recovery of all particle fractions from individual samples. Four replicates of each field-moist sample were wet-sieved. Separated aggregate fractions from three of the four replicates were combined by size class and the excess water was removed using Büchner funnels lined with Whatman 42 filter paper discs atop sidearm flasks attached to a vacuum manifold. A two gram aliquot of wet soil was taken from each aggregate size class after excess water was removed and was oven dried (105 °C) to calculate moisture content for use in carbon substrate utilisation studies. Aggregate size classes collected from the remaining replicate were oven dried (105 °C) and the proportion of aggregates in each size class and the Mean Weight