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Quantifying the impact of microbes on soil structural development and behaviour in wet soils

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ABSTRACT

There is evidence that microbial populations play an important role in altering soil pore geometry, but a full understanding of how this affects subsequent soil behaviour and function is still unclear. In particular the role of microorganisms in soil structural evolution and its consequence for pore morphological development is lacking. Using a combination of bio-chemical measurements and X-ray Computed Tomography (CT) imaging, a temporal comparison of microscale soil structural development in contrasting soil environments was made. The aim was to quantify the effect of microbial activity in the absence of other features likely to cause soil deformation (e.g. earthworms, roots etc.) on soil structural development in wet soils, defined by changes in the soil porous architecture i.e. pore connectivity, pore shape and pore volume during a 24 week period. Three contrasting soil textures were examined and changes compared between field soil, sterilised soil and a glucose enhanced soil treatment. Our results indicate that soil biota can significantly alter their microhabitat by changing soil pore geometry and connectivity, primarily through localised gaseous release. This demonstrates the ability of microorganisms to modify soil structure, and may help reveal the scope by which the microbial-rich rhizosphere can locally influence water and nutrient delivery to plant roots.

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1. Introduction

Our understanding of the spatiotemporal nature of soil structure remains limited, despite its importance for nutrient availability to plant roots, gaseous exchange through the soil profile and movement of solutes through pore networks (Hinsinger et al., 2009). It has long been acknowledged that soil microbial activity and function are closely linked to structure (Oades, 1984; Six et al., 2004; Crawford et al., 2012), with processes related to soil biological activity such as: i) the microbial exudation of secondary metabolites and binding agents (Bossuyt et al., 2001; Six et al., 2006); and ii) particle enmeshment by fungal communities (Tisdall, 1994; Moreno-Espíndola et al., 2007) both increasing adhesion between soil particles and generating particle aggregation. However, the rate, nature and scale by which changes occur remains uncertain.

Soil microstructure is known to regulate microbial function (Young and Ritz, 2000), largely through influencing the spatial distribution of soil biota (Nunan et al., 2006). Distinct local microenvironments associated with microbial communities cause highly variable biological activity throughout the soil matrix (Fenchel, 2003), with evidence for microorganism patchiness confined to specific niches recorded at hundred μm scales (e.g. Nunan et al. (2003)). The consequence of microorganism patchiness in altering the functional response of soil systems has helped to elucidate driving factors responsible for ecological community development (Parkin, 1993). For example, enrichment of substrate through organic matter at the soil surface enables microbial proliferation of the upper soil horizons, inducing enhanced soil aggregate size and stability (Bossuyt et al., 2001; De Gryze et al., 2006a). However, knowledge regarding the degree and timescales over which soil structural development takes place in terms of aggregation and pore evolution is still unclear, mainly due to the issue of scale and access to appropriate technology to probe this. The majority of previous work in this area has focused on soil

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structural development at the macroscale (>150 μm) largely due to the resolution of the equipment available at the time (e.g. Atkinson et al. (2009)). Macroaggregate formation and re-stabilisation rates have been correlated with microbial activity, increasing with the addition of microbial substrate and decreasing rapidly as the substrate is utilised (De Gryze et al., 2006b). More recent investigations have successfully quantified the influence of microbial activity on soil aggregate formation for various mycorrhizal fungal treatments (Hallett et al., 2009), roots (Martin et al., 2012) and clay mineralogy (Barré and Hallett, 2009), demonstrating the diverse nature of microbe-soil-plant interactions. However, macroscale quantification of soil structure is perhaps not the most relevant scale for investigations of the soil microbial community. It follows that when investigating soil aggregate and subsequent pore formation, quantification at the microscale can provide a more rigorous assessment of microbial-induced aggregation due to the microscopic changes to structure anticipated, that may be missed at coarser resolutions. At this smaller scale, changes to pore size distributions within individual aggregates (Feeney et al., 2006) and aggregate formation under wheat residue addition (De Gryze et al., 2005) indicate the potential for microbial driven structural changes that can occur in just a few weeks. Likewise Crawford et al. (2012) demonstrated an increase in porosity and surface connectivity in samples harbouring fungal activity over a 25 day incubation, but no significant effect of bacterial activity in isolation or bacteria and fungi combined on soil structure at a resolution of 53 μm. However, quantification of the microbial impact on soil morphological development at smaller pore scales, its impact over longer timeframes, and subsequent consequences for the overall connectivity of pore systems, remains unknown.

Previous research exploring the impact of microorganisms in the evolution of soil structure has been limited by our inability to non-invasively visualise the soil environment. Advances in industrial X-ray micro CT (Computed Tomography) in the last five years, in particular, provide a higher image quality and resolution, with shorter scan times resulting in more samples analysed in a given time period. In this paper, we present a fully replicated experiment with multiple time points from three contrasting microbial treatments. Three different soil types per microbial treatment were each held at a water content higher than the air entry potential, simulating soil water contents found in moist field soils. The aims were to quantify the temporal influence of microbial activity on soil structure and pore morphology development (defined by changes in porosity, pore connectivity, volume, and shape during the incubation period), by selectively inhibiting and promoting microbial growth. We examined the potential for soil microorganisms to i) alter the physical architecture of soil over time in the absence of other biotic features liable to cause soil deformation (e.g. earthworms, roots); ii) influence the surface connected pore architecture of initially unconnected pore space in homogenised soil; iii) alter the size, shape and nature of pore space; and iv) alter soil structure in the absence of abiotic factors e.g. localised wetting and drying cycles. We hypothesise that microbial populations in carbon enhanced soils will have significantly higher biomass (Joergensen and Raubuch, 2002) and activities (Bossuyt et al., 2001; Steinbeiss et al., 2009) than those in field soil, which will alter the physical soil matrix to a more porous state.

2. Methods

2.1. Soil column preparation and sampling

A loamy sand soil from the Newport series (sand 83.2%, silt 4.7%, and clay 12.1%; pH 6.35; organic matter 2.93%; FAO Brown Soil) taken from the University of Nottingham farm at Bunny, Nottinghamshire, UK (52.8586°, −1.1280°), a silty clay loam soil from the Batcome series (sand 18.3%, silt 49.0%, and clay 32.7%; pH 5.76; organic matter 7.02%; FAO Chromic Luvisol) taken from Rothamsted Highfield Arable plot, UK (51.8047°, −0.3628°), and a clay loam soil from the Worcester series (sand 35.6%, silt 31.5%, and clay 32.9%; pH 6.50; organic matter 5.19%; FAO Argillic Pelosol) also taken from the University of Nottingham farm at Bunny, were sieved at field moisture to <2 mm. A sub-section of each soil texture was γ-irradiated at 27 kGy (Isotron, Daventry, UK) to sterilise the soil. Irradiation at this level is reported to eliminate all fungi, actinomycetes, algae, invertebrates and bacteria from the soil (McNamara et al., 2003). Four sterile replicate columns (25 mm diameter × 70 mm height) for each soil texture were uniformly packed to a bulk density of 1.2 Mg m^{-3} for three microbial treatments: i) Unaltered 'field' soil; ii) γ-irradiated 'sterile' soil; and iii) Glucose amended 'enhanced activity' soil. Columns were packed in four layers, and the surface of each layer scarified prior to additional layers being added, in order to prevent compaction layers being produced (confirmed later by X-ray imaging). All columns were saturated with sterilised (autoclaved) deionised water and left to drain for three days to reach a notional field capacity (confirmed with water release curve data, Fig. S1). Micropore tape was placed over the macrocosms to reduce water loss and prevent sample contamination, whilst still enabling gaseous exchange. Macrocosms were incubated for 24 weeks in a glass fronted incubator at 16 °C. The water status of the columns was maintained (determined by weight) by addition of sterile deionised water every 1–2 days in equal amounts to the top and bottom of the columns. To the glucose enhanced soil, glucose was added in equal measures to the top and bottom of the macrocosm every 2 days totalling 0.05 mg C g^{-1} soil day^{-1}, a rate which is reported to be similar to rhizodeposition (Preston et al., 2001). A sterile control was used solely to ascertain the influence of the watering regime on the resultant temporal changes to soil porosity.

2.2. X-ray Computed Tomography (CT)

CT scanning was conducted using a Phoenix Nanotom 180NF scanner (GE Sensing and Inspection Technologies, Wunstorf, Germany) set at 120 kV and 100 μA, with a 0.1 mm Cu filter. The voxel size was set at 12.38 μm, with the centre of the macrocosm 55 mm from the X-ray source and each scan taking 33 mins to complete. The total number of projection images for each column was 720 per scan at a detector size of 2304 × 2304 pixels, creating *ca.* 5 GB file sizes when reconstructed as 8-bit volumes. Four replicate columns per soil texture per microbial treatment (36 in total) were repeatedly scanned at weeks 0, 2, 4, 8, 16 and 24 of incubation, generating a total of 180 scans over the course of the investigation (the scanner was unavailable for week 16 of the glucose treatment). The precise positioning of the scanner manipulator stage and reconstructed region in all subsequent scans ensured that each column was repeatedly scanned and analysed in exactly the same location throughout the investigation, enabling direct comparisons of porosity and pore characteristics to be made over time. Samples were scanned in a random order at each sampling interval to minimise the influence of short-term diurnal changes in pore development. The dose to the centre of each macrocosm was calculated at 3.9 Gy for each scan, equating to a total of 23.1 Gy over the course of the 24 week investigation. This is well below the limit of ~10 kGy reported to cause damage to soil-borne microbial populations (McNamara et al., 2003; Zappala et al., 2013).

2.3. Image processing, segmentation and analysis

Raw grey-scale X-ray CT images were processed using ImageJ 1.44 (http://rsbweb.nih.gov/ij/). A uniform contrast enhancement was applied to 1% of saturated pixels in order to improve image

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