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Residues with varying decomposability interact differently with seed or root exudate compounds to affect the biophysical behaviour of soil

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Abstract

Plants have a large impact on the physical behaviour of soil, partly due to seed and root exudates that alter mineral:organic matter associations. In this study we explored how the decomposability of residues in soil interacts with seed or root exudate compounds to influence microbial respiration, mechanical behaviour and hydrological properties. Sandy loam and clay loam soils were amended at a rate of 40 t ha^{-1} with ground green barley (7.13 mg C g^{-1}), barley straw (7.26 mg C g^{-1}) or poultry manure (5.22 mg C g^{-1}), and either chia seed exudate at 1.84 mg C g^{-1} soil or root exudate compounds at 14.4 mg C g^{-1} soil. On cores packed to 1.3 g cm^{-3}, uniaxial compression, penetration resistance, water sorptivity, water retention and porosity were measured at time 0, after 14 days of incubation at 20 ^{o}C, and then after subjecting incubated soils to three cycles of wetting and drying to simulate weathering. These time increments and weathering were intended to simulate a newly germinated seed or tip of a root, through to a more mature system. Application of seed and root exudate increased carbon dioxide (CO_2) emissions from 0.31 ± 0.01 to 15.11 ± 0.71 μg C-CO_2 g soil^{-1} hour^{-1} for the sandy loam soil and from 0.171 ± 0.01 to 10.56 ± 0.78 C-CO_2 g soil^{-1} hour^{-1} for the clay loam soil. There were large changes in soil physical properties caused by seed or root exudate amendment coupled with residues, their decomposition and weathering. After incubation and weathering, soils with added seed or root exudates and their interactions with organic residues were more mechanically stable, as measured by penetration resistance (22 to 58% increase) and compression index (25 to 43% decrease) compared to soils amended only with organic residue. Water sorptivity and porosity diminished with the addition of the exudate. Exudates in combination with organic residues better protected soils against structural destabilization by increasing particle cementation, and decreasing rapid wetting and porosity.

Introduction

A major strategy in soil management is the use of organic residues to improve fertility and soil physical conditions (Lal, 1990; Scotti et al., 2013). Application of organic residues as soil amendments can influence soil physical properties that enhance root growth and contribute to mitigation of global climate change from its slow return of CO_2 to the atmosphere (Lehmann, 2007; Agegnehu et al., 2016). Studies have shown that decomposed organic residues maintain and increase soil organic matter content (Iovieno et al., 2009; Tejada et al., 2009), which impacts physical properties important for soil functioning and plant growth. Physical impacts include improved soil structure by aggregation (Scotti et al., 2013; Arthur et al., 2014) that alters pore geometry and continuity so that water infiltration and root penetration through the soil profile increases (Zhu et al., 2016). There are also enhanced chemical characteristics through the release of plant nutrients (Swift, 2001; Leifeld et al., 2002), and stimulation and enhancement of the soil biotic community (Bekele et al., 2015).

The importance of organic matter to soil physical structure has been known for millennia (Lal 1990), with considerable research published showing carbon inputs to mostly improve stability and aggregation (Hernandez et al., 2017; Pausch and Kuzyakov 2017). Moreover, organic residues added to soils may become physically protected in the soil matrix through aggregation (Chevallier, 2014; Aminiyan et al., 2015). More recent research has shown that root exudates can impact on the rate of soil organic matter (SOM) decomposition, a process termed 'priming' (Keiluweit et al., 2015; Rousk et al., 2015). In the course of decomposition, large amounts of soil-derived carbon as CO_2 or methane as CH_4 and nitrogen as N_2O can be released in a very short time (Kuzyakov et al., 2000; Shahzad et al., 2018). Nannipieri et al. (2008) has shown that soil respiration is strictly linked to organic C mineralization and provides a suitable parameter used in determining microbial activities in the rhizosphere.

Moreover, interactions between root exudates and organic residues may influence soil physical functioning differently. The stability of aggregates and hydraulic transport may be influenced differently. To date, there is little information on these interactions. One challenge is the collection and preservation of root exudate in sufficient quantities, so many studies have used model exudates in various forms in laboratory studies, such as mucilages extracted from the seed coatings of *Salvia sp*. (Chia) (Kroener et al., 2014) or *Capsella sp*. (Deng et al., 2015), and chemical diffusible fractions, such as polygalacturonic acid (Czarnes et al., 2000; Traoré et al., 2000), or a model exudate root cocktail (Paterson et al., 2007; de Graaff et al., 2010).

The decomposition of exudate fractions has been reported to influence soil physical properties (Sun et al., 2017). Traoré, et al. (2000) applied a range of exudate compounds to soils and found an increase in soil aggregation. The stability of aggregates can have large impacts on soil structure, thereby affecting the movement of water and plant nutrients (Franzluebbers, 2002; Bronick and Lal, 2005), microbial activities (Yazdanpanah et al., 2016) and root growth (Six et al., 2004). Other studies observed similar impacts on soil physical properties from the application of organic residues (Scotti, et al., 2015; Abd El-Halim and Lennartz, 2017).

Wang et al. (2017) and Yazdanpanah et al. (2016) emphasized changes to structural properties from the application of many organic amendments to soils. These have quantified soil pore structure or aggregate stability, but they have not explored the interactive effects of organic residue/amendments and plant derived exudates into soil. Other studies have explored how biological exudates on their own influence a range of hydrological and mechanical soil properties (Czarnes et al., 2000; Peng et al., 2011). The interaction of root exudate and organic residues in a soil system, and the subsequent influence on biochemical and physical processes within the soil system, underpin rhizosphere structure formation and function. There is a gap in quantitative data on mechanical and hydrological properties that occur in soil as seeds germinate and roots grow through soil to form the rhizosphere.

Our objective was to explore how the rate of microbial decomposition is influenced by the interactions of exudates and organic residue with varying decomposability, and the impact of these interactions on soil physical behaviour during rhizosphere formation. To do this we added chia seed mucilage or a root exudate cocktail to sandy-loam and clay-loam soils amended with either green barley, barley straw or poultry manure, then quantify microbial mineralization and the corresponding impact on mechanical stability and hydraulic properties. We hypothesized that the exudates and microbial mineralization will increase soil stability by mechanical and hydrological changes. By studying the soil before and after incubation, and then after cycles of wetting and drying, we simulated conditions at a freshly growing root tip or geminating seed through to more mature conditions after weathering in the rhizosphere. To quantify physical changes induced by these treatments, we measured penetration resistance and compression characteristics and a range of hydrological properties. Compared to visual examinations of pore structure or structural stability, these tests quantify underpinning physical processes in rhizosphere structural formation, stability and physical functioning.

Materials and methods

Soil

Sandy loam and clay loam top soils (0-20cm) were sampled from fields under different management practice at Bullion field in James Hutton Institute, Dundee, UK (56.27N 3.40W). The sandy loam soil is a Dystric Cambisol and the clay loam soil is a Gleyic Cambisol (FAO classification). Bulk samples of these soils were air-dried at 30^{o}C to 1 % moisture, passed through a 2mm sieve and then stored at 4^{o}C. Table 1 lists the soil, chia exudate and organic residue characteristics.

Table 1

Exudate components

An artificial root exudate cocktail was produced after Paterson et al. (2007) by combining common sugars, organic acids, and amino acids found in root exudates (Rovira and McDougall, 1967; Jones, 1998; Hütsch et al., 2002). Seed exudate was extracted from chia (*Salvia sp*.) by the same method described in Oleghe, et al. (2017).

Organic residues

Three organic residues, green barley, barley straw and poultry manure were used as they have different decomposability and organic carbon to nitrogen ratios (Table 1). They were air dried and ball milled for 3 minutes to a fine powder (Retsch PM100 Ball Mill, Retsch GmbH, Germany).

Samples were prepared by mixing 15.5 mg g^{-1} dry weight organic residue to 100 g of air dried soil. These rates are approximately equivalent to 40 t ha^{-1} of organic amendment, assuming a soil bulk density of 1.3 g cm^{-3} and a 20 cm plough depth. The residue amended samples were further amended with the root exudate cocktail at 14.4 mg C g^{-1} soil or seed exudate at 1.84 mg C g^{-1} soil. Deionised water was added to bring the soils to the equivalent of -10 kPa as described in Table 2. This was determined on a duplicate batch of samples that were packed as described in the next section and then equilibrated on a tension plate (Ecotech

Bonn, Germany). Soil samples without exudate and organic residue treatments were used as controls.

Table 2

Soil cores preparation and incubation

40 g of each soil, residue and exudate treatment were packed in 0.5 cm layers into plastic cores (height = 2 cm, diameter = 5 cm) to a bulk density of 1.3 g cm^{-1} and placed in sealed respiration chambers. Five replicates of each treatment were incubated at 20 ^{o}C in a SANYO plant culture incubator (SANYO electric co. Ltd, Japan). The water contents of all samples were adjusted and maintained at field capacity with deionised water for 14 days and the hourly rates of microbial respiration were measured in air column, extracted at days 0, 1, 3, 7 and 14, and then analysed for carbon dioxide (CO_2) nitrous oxide (N_2O) and methane (CH_4^+) concentrations using a gas chromatograph (GC; systems Agilent 6890, GC System, USA).

Mechanical and hydrological measurements

Penetrometer resistance (P_R) was determined from cone penetration tests at day zero, within one hour after placing samples in respiration containers using a 1 mm diameter, 30^{o} full cone opening miniature penetrometer attached to a 5 kN load cell, at a loading rate of 0.3 mm min^{-1} on a mechanical test frame (Zwick All Round Z5, Zwick-Roell, Ulm, Germany). This loading rate provides a balance between minimising the impacts of dynamic loading (Bengough and Mullins, 1990) and allowing for an adequate throughput of samples. After fourteen days decomposition, the samples were saturated and drained to -10 kPa matric potential using a tension table at 4 ^{o}C to minimise microbial decomposition. Gravimetric water content and water sorptivity were measured before cone penetration measurements were repeated on the same samples. Water sorptivity was measured using a mini-infiltrometer technique with the apparatus described by Hallett et al. (2003). Each sample was placed in contact with the infiltrometer tip constructed from a standard 200 µl pipette tip and with a head of -10 mm. Liquid uptake by the soil from the infiltrometer reservoir was logged from a balance at 2 s intervals for 140 s. After about 20 s, the water flow rate was steady and used to calculate sorptivity. After this, three cycles of wetting and drying from saturation to -50 kPa were then imposed to simulate natural weathering, followed by returning the soil to field capacity at -10 kPa. Gravimetric water content, water sorptivity and cone penetration measurements were repeated. The samples were then rewetted and dried again to -50 kPa, followed by compression to 600 kPa on the same mechanical test frame using approaches described in Oleghe et al. (2017).

Calculations and statistics

The experiment was setup as a four-way factorial design with three levels of added exudates, four levels of organic amendment, two soil textures and three decomposition stages. Each treatment had five replicates. In our statistical analysis, we did not consider the soil texture as a factor due to significant differences in both texture and organic matter content, so each soil was analysed independently. Statistical analysis and graphics were done using the 'R statistical computing language' (R Core Team, 2018).

Results

Microbial respiration

Table 3

The incubation of soils amended with organic residue and artificial root exudates had a small, but significant effect on CO_2 and N_2O emission (Figure 1), but CH_4 emissions were very low and not affected by any amendments (data not shown). The concentrations of CO_2 and N_2O were increased ($P < 0.001$) by the organic residue in the sandy soil, whereas, the results show that CO_2 concentration was only increased by barley residue in the clay loam soil. This indicates that the impact of organic residue on microbial decomposition was enhanced more in the sandy loam than in clay loam soil. Additionally, the root exudates caused greater variability in CO_2 concentration than seed exudate for both soils.

However, microbial activities varied more from the interaction of seed or root exudates with the organic residues in both soils. CO_2 and N_2O emissions were significantly increased ($P < 0.001$) from the interaction of exudates and residues compared to results for just exudate or organic residue treatments (Table 4).

The microbial activities for the sandy loam soil showed a lag phase before the start of exponential growth, which was only visible for poultry residue and root exudate interaction on the clay loam soil. Also, we observed a stationary phase for the control clay loam soil, although this effect was quickly countered with the interactions of organic residue and exudates. The carbon mineralization rate was greatest for green barley, followed by poultry manure, barley straw and then the control (Figure 1).

Figure 1

Soil pore characteristics

Volumetric water content, θ, and air filled porosity, f_a, measured at -10 kPa varied markedly from the application of organic residue (Table 5). Generally, the organic residue caused an increase in water content, but these effects were significantly greater ($P < 0.05$) with green barley powder and barley straw residues on both soils. Furthermore, microbial decomposition and wetting-drying cycles caused a significantly greater increase ($P < 0.05$) in water content for all organic residue treatments.

The honest significant difference (HSD) between arithmetic means of the volumetric water content revealed that seed exudate had greater water retention capacity than root exudates or the control for both soils. In general, the interactions of exudate and organic residue resulted in greater water retention from 0.235 – 0.381 $cm^3\ cm^{-3}$ of those observed for exudate or residue on their own (Table 4). The interaction of both green barley powder and barley straw residues and seed exudate showed greater increases ($P < 0.005$) in θ at -10 kPa for both soils. The wetting-drying cycles increased the effect of these interactions on water retention significantly more ($P < 0.05$) in the clay loam soil compared to the sandy loam soil.

Organic residue and exudate treatments had a significant effect ($P < 0.05$) on water sorptivity, S_w for both soils (Table 3). The barley straw residue increased sorptivity on incubated sandy loam soil, but this effect was quickly lost over the wetting-drying cycles. Thereafter, water sorptivity decreased significantly with residue treatments compared to the control. This show that in organic residue amended soils, water infiltration increases with the number of wetting cycles (Table 5).

Seed and root exudates had no impact on S_w in the sandy loam soil, but caused a decrease in S_w in the clay loam soil (Table 5). The water sorptivity, decreased noticeably in all treatment interactions compared to the control except for the treatment interactions of exudates and poultry manure residue on sandy loam soil (Table 4). The treatment interactions of root and barley residue had the smallest water sorptivity of 0.232 mm $s^{-1/2}$ compared to 0.698 mm $s^{-1/2}$ for the control soils.

Soil strength

Adding green barley or barley straw increased penetrometer resistance P_R, but poultry manure had no impact (Figure 2, Tables 5 and 6). For P_R, the larger the value, the greater the particle cementation and soil strength. With Tukey's HSD post hoc tests, the soils amended with root exudate were found to have increased soil strength, with penetrometer resistance increases of 58% for the sandy loam and 23% for the clay loam soils ($P < 0.05$). Penetrometer resistance for the exudate and organic residue interactions increased significantly ($P < 0.05$) for both soils. However, greater resistances were caused by root exudate interactions with organic residue in the sandy loam soil, while increases in the strength of clay loam soils were directly linked to the interactions of the seed exudate treatment with organic residues (Figure 2). Generally, root exudate interactions with green barley and barley straw amendments showed the most significant increases in penetration resistance with values >0.4 MPa. The influence of wetting-drying cycles had no impact on the strength of incubated soils.

Figure 2

A smaller compression index, C_c, indicates greater resistance to compaction as less pore volume is lost for a given compaction stress. Adding any form of residue to either the sandy loam or clay loam soil had no impact on C_c. Root or seed exudates significantly increased the resistance to deformation stress at -50 kPa matric potential ($P < 0.05$) compared to unamended soils (Figure 3, Tables 5 and 6). In the sandy loam soil, the root exudate had the greatest impact on soil deformation, while seed exudate caused a similar effect in the clay loam soil. The interactions of organic residues and exudates increased the soil strength and subsequent resistance to deformation from compaction stress ($P < 0.05$).

Figure 3

Discussion

The hypothesis that exudate and organic residue interactions will stimulate microbial activities and mechanical stability of soil was confirmed in this study. The added substrates increased microbial activities, with the quality and source of carbon in exudates and organic residue having a large impact on the rate of microbial mineralization (De Graaff, 2010). The interaction of easily available organic compounds caused expected increases in the rate of microbial activities at different times, measured from respiration of CO_2 and N_2O (Jones, 1998) (Table 3; Figure 1). Surprisingly, cumulative respiration was only affected by added residues and/or exudates for the clay loam soil (Table 5). The exudate interactions with organic residue likely increased the susceptibility of these substrates to microbial decomposition, although this would require isotopic labelling to confirm (Table 4). Increased microbial population and activities could result in the production of microbial mucilages, dissolved organic carbon, exudates or organic material components that are chemically too complex to undergo continuous microbial mineralization (Morel et al., 1991; Rillig et al., 2015). This could impact the bonding properties of the soil, with implication for water retention and physical stability. We found increased physical stability in our soil with impact on some hydraulic properties following microbial decomposition.

The biochemical changes to exudate and organic residue composition likely promoted increased water retention (Table 5). Exudates, microbes, microbial mucilage and other organic compounds in soil could provide changes to pore properties, and under wetting could improve the water holding capacity of the soil. Albers (2008) also found increased moisture saturation following mineralization of organic compounds in soils. We assume that capillarity increased with micro-porosity and pore connectivity at -10 kPa. Thus, water sorptivity, S_w diminished as the degree of saturation increases. In addition, dissolved organic compounds and mucilage may clog micro pores or flow into pores, which directly impact movement and retention of soil water (Hallett et al., 2003; Albalasmeh and Ghezzehei 2014).

Soil strength

Microbial decomposition of exudates and organic residues affected soil hydrological and mechanical properties (Figure 2 and 3). These effects were likely driven by particle cementation and the formation of mechanically stable aggregates (Zhang et al., 2005) influenced by hydraulic changes from wetting and drying (Dexter, 1988; Hofmockel and Bach 2015; Kallenbach et al., 2016). We found that soil strength benefited from microbial decomposition of exudate on its own, while the organic amendment on its own disrupted the stability of pores and mineral particles (Figure 2). However, the interactions of seed or root exudate with the organic residue countered the disruptive impact and resulted in larger increases in penetration resistance, with the increases sustained over wetting-drying cycles. Some earlier studies have also shown that microbial activities and associated organic products from these interactions may drives changes in soil stability (Morel et al., 1991; Watt et al., 1993; Traoré, et al., 2000). The implication for root laterals might be increased penetration resistance within the modified zone, but the levels measured are not restrictive to root growth (Bengough and Mullins, 1990).

Further evidence of differing mechanical stabilisation between seed and root exudates, and organic residue amendments provided by the compression index also suggest increased biogenic cementation of soil particles (Figure 3). An overall summary of the findings are illustrated in Figure 4. The resistance to compaction stress of 600 kPa for both seed and root exudates indicates that exudate associated biogenic cementation decreased the susceptibility of the soils to compaction stress. A positive relationship between the exudates and soil stability has been observed after microbial mineralization (Oades, 1993, Naveed et al., 2018). Part of this will be due to a direct correlation between soil strength and the mineralization of exudates, which can produce microbial metabolites that have a greater capacity to bind soil particles (Morel et al., 1991; Watt et al., 1993; Traoré, et al., 2000). Increased void space decreases the total bond area, as reflected in the compression index that measures the combined impacts of particle cementation and pores to soil strength. Unlike Zhang et al. (2005), who found that the amendment of soils with peat as a particulate organic matter analogue increased susceptibility to compaction, we found a combination of either root or seed exudates with organic residue, increased compaction resistance. There was no impact from adding exudates on their own.

Figure 4

To simulate exudate released by a germinating seed or real plant root, we used exudate analogues in homogeneously packed soils in this experiment. We demonstrated that seed exudate applied at 1.84 mg C g^{-1} soil or root exudate compounds at 14.4 mg C g^{-1} soil caused biogenic consolidation. This was further enhanced if soils were also amended with organic residues of green barley, barley straw or poultry manure at an equivalent rate of 40 t ha^{-1}. These results in a model system suggest that biological and physical properties of the soil volume surrounding a growing seed or root can be enhanced substantially by exudate components interacting with organic residues. The observed differences between the type and nature of exudates were pronounced. In addition, the magnitude in biophysical modifications induced by the exudates, were influenced by the nature and chemical composition of the organic residue. Whilst our results represent many processes involved in the stabilizing effect of root and seed exudates, there are limitations to this model study. We ground residues to allow for homogeneous mixing with the soil, but organic amendments would be in larger forms and more sparsely distributed in natural soils. Moreover, the exudates used allowed for testing of large soil volumes, but soil conditions and plant species will create large differences in composition. Interesting possibilities exist for similar experiments using real growing plant roots and a range of soil conditions. Pore structure changes could be explored in greater detail with non-invasive imaging. Additionally, there is room to understand the magnitude and nature of microbial carbon mineralization (‘priming’) from the chemical and physical soil properties and considering its impact in flocculation of organic matter and clay fractions at the micro scale.

Conclusion

Organic residue incorporation is common practice to improve soil physical conditions, but this study has demonstrated that the impacts are affected considerably by the presence of exudates produced by plants. At different stages of decomposition and weathering the impacts varied, with exudates generally causing greater mechanical stabilisation than residues. Exudates are surface active and react directly with interparticle bonds, so this would be expected. Interestingly, the effects of root exudates were attenuated when added in combination with poultry manure, showing that some residues may counter-act stabilising mechanisms of exudates.

Bulk porosity was not affected by either residues or exudates, but they caused more water storage in the available pores, particularly when added in combination. This suggests pore clogging, which tied in with decreased water sorptivity in the presence of exudates or residues in the clay loam soil. Within the pores, swelling of mineralised exudates under wetting likely influenced micro porosity and pore structure re-orientation under weathering, which increased moisture capture and diminished sorptivity. As the sandy loam soil had more air-filled pores to take up water, as shown by f_a, pore clogging was possibly not great enough to affect sorptivity.

The amount of the physical changes were affected by the nature of the exudate, C/N ratio of the organic residue and the stage of microbial mineralisation. This research demonstrates the changes to soil structure imposed by germinating seed or root growth to aid favourable soil physical conditions for growth. Moreover, it demonstrates that simple experiments that add individual organic substrates may produce results that are far different than could be experienced in natural systems, where residue incorporation, native organic matter and plant exudates work together to affect soil physical behaviour. The next step should be to extend this research to glasshouse and field experiments to compare the interactions of different plants and residue incorporation on physical properties of bulk soil and the rhizosphere.

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Table 1: Characteristics of the experimental soils, chia exudate and organic residue. Mean ± s.e.m. of 3 replicates.

Soil texture	Clay	Silt	Sand	Carbon	Nitrogen	pH	C:N	Concentration
	(g. 100 g^{-1})			(mg/g)	(mg/g)	($CaCl_2$)		(mg/g)
Sandy loam	16	24	60	2.25 ± 0.14	0.16 ± 0.03	5.48 ± 0.07	16:1	-
Clay Loam	26	30	44	2.95 ± 0.12	0.23 ± 0.02	5.15 ± 0.04	13:1	-
Chia exudate	-	-	-	3.75 ± 0.11	0.11 ± 0.003	-		9.2 ± 0.26
Organic residue								
Green barley	-	-	-	47.14 ± 0.04	3.98 ± 0.02	-	12:1	-
Barley straw	-	-	-	46.32 ± 0.13	0.56 ± 0.05	-	82:1	-
Poultry manure	-	-	-	33.87 ± 0.09	4.43 ± 0.01	-	8:1	-

Table 2: Gravimetric water content (%) at -10 kPa for soils treated with organic residue applied at 40 t/ha. Mean ± s.e.m. of 3 replicates.

Soil texture	Control	Green barley	Barley straw	Poultry manure
Sandy loam	17 ± 0.004	20 ± 0.006	20 ± 0.007	18 ± 0.003
Clay loam	19 ± 0.003	23 ± 0.003	25 ± 0.012	21 ± 0.012

Table 3: Summary of the analysis of variance for microbial respiration CO_2 and N_2O for sandy loam and clay loam soils.

Microbial respiration		Sandy loam			Clay loam		
Source of variation	[a]df	Sum Sq	F ratio	*P*	Sum Sq	F ratio	*P*
CO_2							
Exudate	2	0.368	19.893	< 0.001	0.651	52.411	< 0.001
Amendment	3	0.913	32.933	< 0.001	0.980	52.553	< 0.001
Time(Days)	4	15.683	424.403	< 0.001	4.579	184.200	< 0.001
Exudate:Amendment	6	0.304	5.492	< 0.001	0.148	3.960	< 0.001
Exudate:Time(Days)	8	4.134	55.934	< 0.001	1.754	35.286	< 0.001
Amendment:Time(Days)	12	1.854	16.720	< 0.001	1.305	17.493	< 0.001
Exudate:Amendment:Time(Days)	24	0.914	4.123	< 0.001	0.948	6.355	< 0.001
Residuals	240	2.217	-	-	1.492	-	-
N_2O							
Exudate	2	0.0002	9.383	< 0.001	0.0002	4.428	0.013
Amendment	3	0.0004	14.482	< 0.001	0.0007	9.237	< 0.001
Time(Days)	4	0.0022	56.073	< 0.001	0.0006	6.071	< 0.001
Exudate:Amendment	6	0.0002	3.844	0.001	0.0004	2.665	0.016
Exudate:Time(Days)	8	0.0006	7.215	< 0.001	0.0003	1.556	0.139
Amendment:Time(Days)	12	0.0010	8.075	< 0.001	0.0010	3.333	< 0.001
Exudate:Amendment:Time(Days)	24	0.0008	3.318	< 0.001	0.0010	1.669	0.029
Residuals	240	0.0024	-	-	0.0059	-	-

[a]Degrees of freedom.

Table 4: Summary of the analysis of variance for volumetric water content, θ, air filled 'f_a' and total porosity, 'f' (m^3 m^{-3}), and water sorptivity S*w* (mm $s^{-1/2}$) for sandy loam and clay loam soils.

Source of variation		Sandy loam			Clay loam		
Volumetric water, θ	[a]df	Sum of squares	F value	*P*	Sum of squares	F value	*P*
Exudate	2	0.0072	10.430	< 0.001	0.0036	4.237	0.016
Amendment	3	0.0364	35.040	< 0.001	0.0766	60.237	< 0.001
SoD	2	0.0037	5.315	0.006	0.3718	438.502	< 0.001
Exudate:Amendment	6	0.0067	3.228	0.005	0.0046	1.825	0.098
Exudate:SoD	4	0.0003	0.222	0.926	0.0025	1.489	0.209
Amendment:SoD	6	0.0097	4.674	< 0.001	0.0068	2.677	0.017
Exudate:Amendment:SoD	12	0.0037	0.897	0.552	0.0035	0.691	0.758
Residuals	144	0.0499	-	-	0.0610	-	-
Air porosity, f_a							
Exudate	2	0.0073	10.668	< 0.001	0.0036	4.296	0.015
Amendment	3	0.0364	35.476	< 0.001	0.0766	60.558	< 0.001
SoD	2	0.0034	4.909	0.009	0.3684	436.597	< 0.001
Exudate:Amendment	6	0.0067	3.261	0.005	0.0046	1.821	0.099
Exudate:SoD	4	0.0003	0.212	0.931	0.0026	1.521	0.199
Amendment:SoD	6	0.0097	4.739	< 0.001	0.0068	2.675	0.017
Exudate:Amendment:SoD	12	0.0037	0.911	0.537	0.0035	0.683	0.766
Residuals	144	0.0492	-	-	0.0608	-	-
Total porosity, f							
Exudate	2	0.0049	3.146	0.047	0.0044	3.717	0.028
Amendment	3	0.0027	1.148	0.334	0.0013	0.718	0.544
SoD	1	0.0619	78.895	< 0.001	0.2412	404.415	< 0.001
Exudate:Amendment	6	0.0045	0.953	0.461	0.0014	0.390	0.884
Exudate:SoD	2	0.0049	3.146	0.047	0.0044	3.717	0.028
Amendment:SoD	3	0.0027	1.148	0.334	0.0013	0.718	0.544
Exudate:Amendment:SoD	6	0.0045	0.953	0.461	0.0014	0.390	0.884
Residuals	96	0.0753	-	-	0.0573	-	-
Water sorptivity, S_W							
Exudate	2	0.6118	13.456	< 0.001	0.6118	13.456	< 0.001
Amendment	3	1.3509	19.808	< 0.001	1.3509	19.808	< 0.001
SoD	1	2.3945	105.329	< 0.001	2.3945	105.329	< 0.001
Exudate:Amendment	6	3.0386	22.277	< 0.001	3.0386	22.277	< 0.001
Exudate:SoD	2	0.1994	4.385	0.015	0.1994	4.385	0.015
Amendment:SoD	3	0.4027	5.905	0.001	0.4027	5.905	0.001
Exudate:Amendment:SoD	6	0.4663	3.419	0.004	0.4663	3.419	0.004
Residuals	96	2.1824	-	-	2.1824	-	-

[a]df, Degrees of freedom. SoD = Stage of decomposition

Table 5: Mean values of interaction effects for exudate and organic residue treatments on sandy and clay loam soils.

		Cumulative Respiration				Mechanical properties				Pore properties							
Sandy loam		CO_2 (µg)		N_2O (µg)		P_R (MPa)		C_c (-)		θ (m3/m3)		f_a (m3/m3)		f (m3/m3)		S_W (mm $s^{-1/2}$)	
Residue	**Exudate**	**LSMean**	**.Group**	**LSMean**	**.Group**	**LSMean**	**.Group**	**LSMean**	**.Group**	**LSMean**	**.Group**	**LSMean**	**.Group**	**LSMean**	**.Group**	**LSMean**	**.Group**
	Control	1.813	a	0.033	ab	0.259	abc	0.382	ef	0.235	a	0.274	h	0.540	-	0.698	b
Zero	Seed	2.099	ab	0.047	abc	0.323	abcdef	0.307	abcd	0.250	bcd	0.260	efg	0.524	-	0.676	b
	Root	2.812	ab	0.020	a	0.411	def	0.299	abcd	0.247	abc	0.262	fgh	0.532	-	0.537	ab
	Control	3.507	ab	0.074	cd	0.320	bcde	0.351	b def	0.267	de g	0.242	cde	0.533	-	0.460	ab
Barley	Seed	3.793	ab	0.088	d	0.380	cdef	0.275	a c	0.282	f h	0.227	ab	0.517	-	0.438	ab
	Root	4.506	b	0.061	bcd	0.470	f	0.267	a c	0.279	efgh	0.230	abcd	0.525	-	0.299	a
	Control	2.469	ab	0.033	ab	0.292	bcd	0.350	cdef	0.266	def	0.243	b de	0.539	-	0.483	ab
Straw	Seed	2.755	ab	0.047	abc	0.355	cdef	0.275	ab	0.281	gh	0.229	a c	0.524	-	0.461	ab
	Root	3.468	ab	0.020	a	0.444	ef	0.267	ab	0.278	efgh	0.231	abcd	0.532	-	0.321	a
	Control	3.222	ab	0.047	abcd	0.173	a	0.408	f	0.243	ab	0.267	gh	0.546	-	0.666	b
Poultry	Seed	3.508	ab	0.061	abcd	0.236	ab	0.332	abcde	0.257	cd	0.252	ef	0.530	-	0.644	b
	Root	4.221	ab	0.034	abc	0.325	bcd	0.325	abcde	0.254	bcd	0.255	efg	0.539	-	0.505	ab
Clay loam																	
	Control	1.054	ab	0.023	ab	NS	NS	0.474	cde	0.315	ab	0.194	g	0.561	-	0.568	h
Zero	Seed	1.393	a c	0.046	abcd	NS	NS	0.327	a	0.326	abcd	0.184	e	0.546	-	0.406	d fg
	Root	2.398	cde	0.019	a	NS	NS	0.365	ab	0.317	a c	0.192	e	0.551	-	0.395	b efg
	Control	2.930	cdef	0.077	cde	NS	NS	0.455	bcde	0.358	cde	0.151	f	0.557	-	0.405	cdefg
Barley	Seed	3.270	defg	0.101	e	NS	NS	0.308	a	0.369	e	0.140	d	0.542	-	0.243	ab
	Root	4.275	g	0.074	b de	NS	NS	0.346	a	0.361	b de	0.149	ab	0.547	-	0.232	a
	Control	1.887	abcd	0.037	abcd	NS	NS	0.502	de	0.370	de	0.139	a	0.564	-	0.425	fg
Straw	Seed	2.227	abcdef	0.061	abcde	NS	NS	0.355	ab	0.381	e	0.129	c	0.550	-	0.263	abc e
	Root	3.231	efg	0.033	abcd	NS	NS	0.392	abc	0.372	de	0.137	d	0.555	-	0.251	a cd
	Control	2.278	cde	0.032	ab	NS	NS	0.511	e	0.343	abcde	0.167	a	0.565	-	0.509	gh
Poultry	Seed	2.618	b def	0.056	abcd	NS	NS	0.364	ab	0.353	abcde	0.156	a	0.551	-	0.347	abcdef
	Root	3.623	fg	0.029	a c	NS	NS	0.402	abcd	0.345	abcde	0.165	bc	0.556	-	0.336	abcdef

.Group = means with the same letter(s) are not statistically different, P_R = penetration resistance, C_c = compression index, θ = volumetric water content, f_a = air filled porosity, f = Total porosity and S_W = water sorptivity.

Table 6: Summary of the analysis of variance for penetrometer resistance 'P_R' (MPa) and compression index 'C_c' for sandy loam and clay loam soils.

Source of variation		Sandy loam			Clay loam		
***Penetration resistance* $\mathbf{P_R}$**	[a]df	Sum of squares	F value	Pr(>F)	Sum of squares	F value	*P*
Exudate	2	0.6974	113.076	< 0.001	0.2148	47.457	< 0.001
Amendment	3	0.5497	59.417	< 0.001	0.0098	1.450	0.231
SoD	2	2.7590	447.361	< 0.001	5.1234	1131.736	< 0.001
Exudate:Amendment	6	0.5545	29.972	< 0.001	0.2353	17.329	< 0.001
Exudate:SoD	4	0.3600	29.187	< 0.001	0.2873	31.730	< 0.001
Amendment:SoD	6	0.0621	3.354	0.004	0.2672	19.674	< 0.001
Exudate:Amendment:SoD	12	0.8462	22.867	< 0.001	0.2167	7.977	< 0.001
Residuals	144	0.4440	-	-	0.3259	-	-
Compression index C_c							
Exudate	2	0.0845	15.953	< 0.001	0.2334	33.965	< 0.001
Amendment	3	0.0349	4.394	0.008	0.0294	2.855	0.047
Exudate:Amendment	6	0.0559	3.515	0.006	0.0454	2.201	0.059
Residuals	48	0.1272	-	-	0.1649	-	-

[a]df, Degrees of freedom

SoD = Stage of decomposition

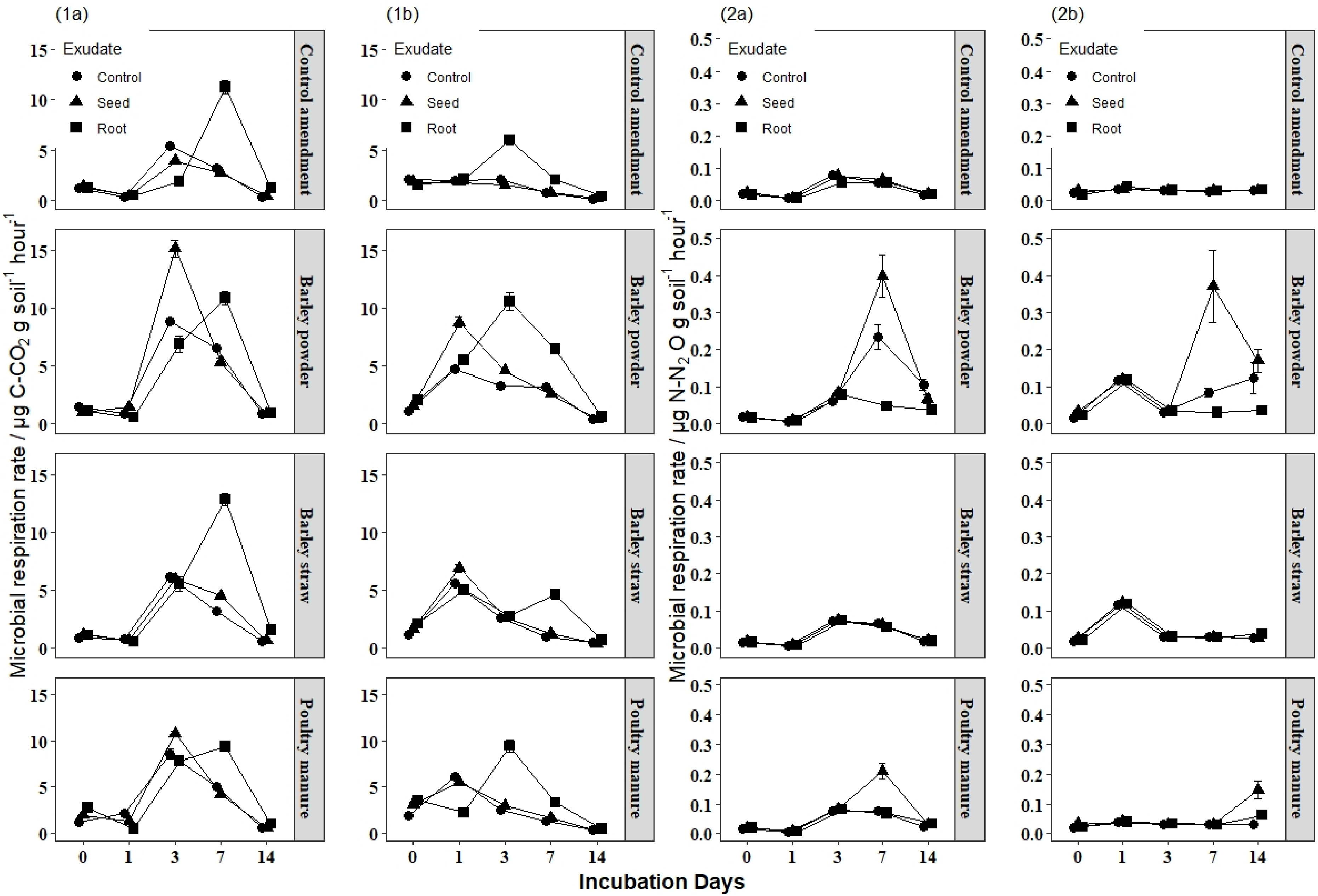
Figure captions

Figure 1: Microbial mineralisation of added exudate and organic residue, rate of decomposition were determined for: (1), CO_2 ($C\text{-}CO_2.g^{-1}.hour^{-1}$). (2), N_2O ($N\text{-} N_2O.g^{-1}.hour^{-1}$). on. (a), sandy loam. (b), clay loam soil.

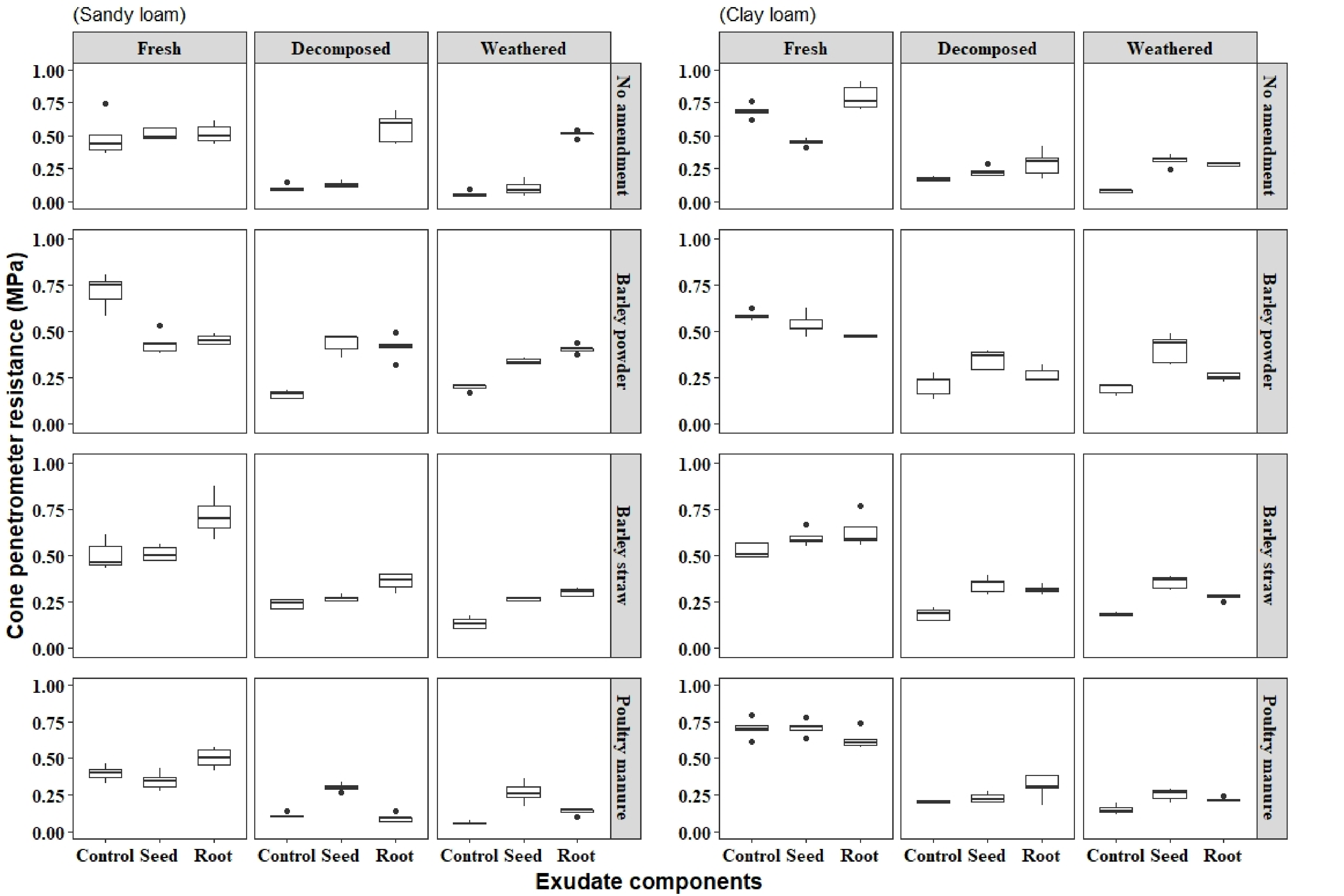
Figure 2: Cone penetration resistance at -10 kPa matric potential relationship to exudate components in soils when fresh, incubated and weathered on sandy and clay loam soils, treated with four organic residue: (a) sandy and (b) clay loam soils.

Figure 3: Compression index at -50 kPa matric potential relationship to exudate components in soils when weathered on sandy loam and clay loam soils, treated with four organic residue: (a) sandy and (b) clay loam soil.

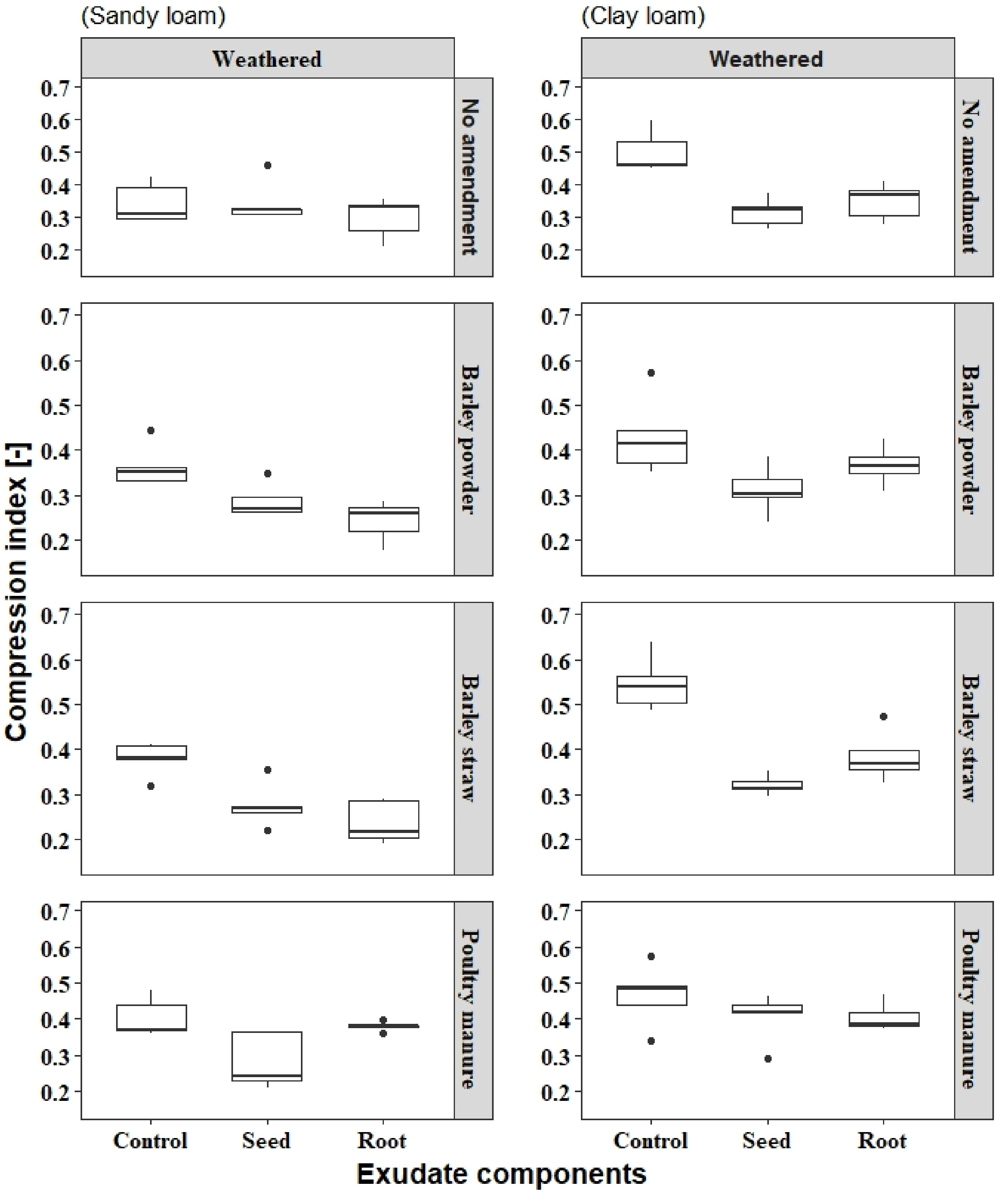
Figure 4: Biological mechanisms of soil aggregate formation illustrating our hypothesis that the impact of exudates and organic residue interactions on soil physical properties will be influencial decomposition and wetting-drying cycles.



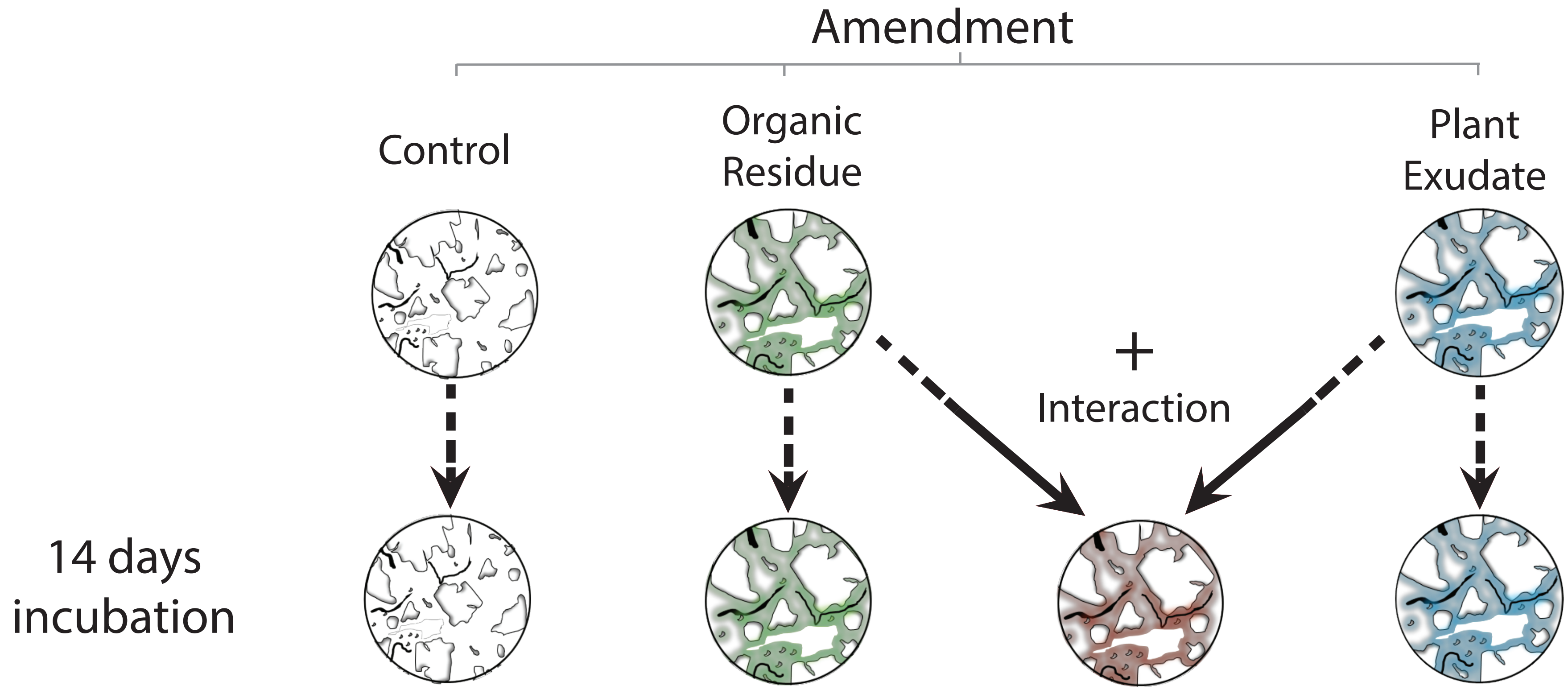
(1a)
(1b)
(2a)
(2b)
Exudate
Control
Seed
Root
Control amendment
Barley powder
Barley straw
Poultry manure
Microbial respiration rate / µg C-CO2 g soil-1 hour-1
Microbial respiration rate / µg N-N2O g soil-1 hour-1
Incubation Days



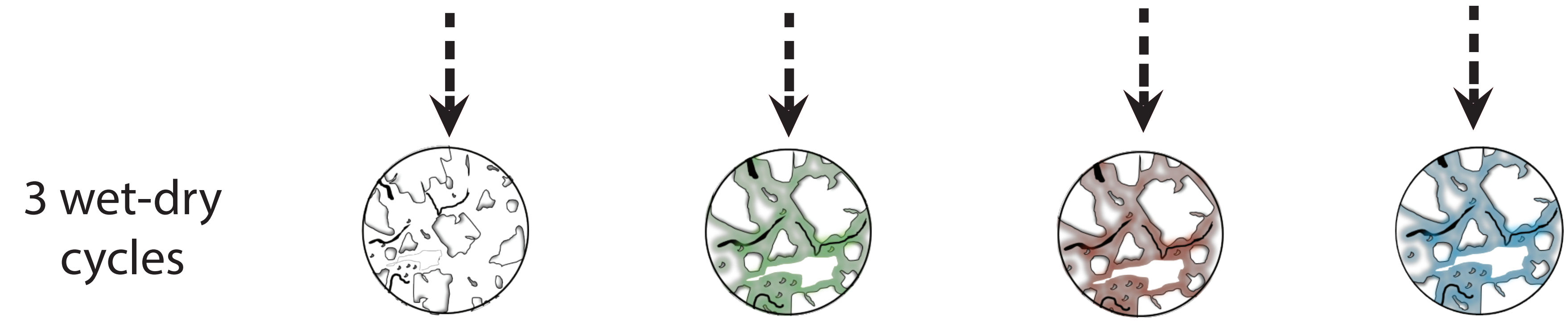
(Sandy loam)
(Clay loam)
Fresh
Decomposed
Weathered
No amendment
Barley powder
Barley straw
Poultry manure
1.00
0.75
0.50
0.25
0.00
Control
Seed
Root
Cone penetrometer resistance (MPa)
Exudate components



(Sandy loam)
(Clay loam)
Weathered
Weathered
No amendment
Barley powder
Barley straw
Poultry manure
0.7
0.6
0.5
0.4
0.3
0.2
Compression index [-]
Control
Seed
Root
Exudate components



Microbial activity	Low	Increase	Very high	High
Water retention	Small increase	Increase	Very high	High
Soil strength	Low	Low	Very high	Very high



Water retention	Small increase	Increase	Very high	High
Soil strength	Low	Low	Very high	Very high
Water sorptivity	Very high	High	Very low	Very low