

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

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24 **Abstract**

25 Plants have a large impact on the physical behaviour of soil, partly due to seed and root  
26 exudates that alter mineral:organic matter associations. In this study we explored how the  
27 decomposability of residues in soil interacts with seed or root exudate compounds to influence  
28 microbial respiration, mechanical behaviour and hydrological properties. Sandy loam and clay  
29 loam soils were amended at a rate of 40 t ha<sup>-1</sup> with ground green barley (7.13 mg C g<sup>-1</sup>), barley  
30 straw (7.26 mg C g<sup>-1</sup>) or poultry manure (5.22 mg C g<sup>-1</sup>), and either chia seed exudate at 1.84  
31 mg C g<sup>-1</sup> soil or root exudate compounds at 14.4 mg C g<sup>-1</sup> soil. On cores packed to 1.3 g cm<sup>-3</sup>,  
32 uniaxial compression, penetration resistance, water sorptivity, water retention and porosity  
33 were measured at time 0, after 14 days of incubation at 20 °C, and then after subjecting  
34 incubated soils to three cycles of wetting and drying to simulate weathering. These time  
35 increments and weathering were intended to simulate a newly germinated seed or tip of a root,  
36 through to a more mature system. Application of seed and root exudate increased carbon  
37 dioxide (CO<sub>2</sub>) emissions from 0.31 ± 0.01 to 15.11 ± 0.71 µg C-CO<sub>2</sub> g soil<sup>-1</sup> hour<sup>-1</sup> for the  
38 sandy loam soil and from 0.171 ± 0.01 to 10.56 ± 0.78 C-CO<sub>2</sub> g soil<sup>-1</sup> hour<sup>-1</sup> for the clay loam  
39 soil. There were large changes in soil physical properties caused by seed or root exudate  
40 amendment coupled with residues, their decomposition and weathering. After incubation and  
41 weathering, soils with added seed or root exudates and their interactions with organic residues  
42 were more mechanically stable, as measured by penetration resistance (22 to 58% increase)  
43 and compression index (25 to 43% decrease) compared to soils amended only with organic  
44 residue. Water sorptivity and porosity diminished with the addition of the exudate. Exudates in  
45 combination with organic residues better protected soils against structural destabilization by  
46 increasing particle cementation, and decreasing rapid wetting and porosity.

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49

## 50 **Introduction**

51 A major strategy in soil management is the use of organic residues to improve fertility  
52 and soil physical conditions (Lal, 1990; Scotti et al., 2013). Application of organic residues as  
53 soil amendments can influence soil physical properties that enhance root growth and contribute  
54 to mitigation of global climate change from its slow return of CO<sub>2</sub> to the atmosphere (Lehmann,  
55 2007; Agegnehu et al., 2016). Studies have shown that decomposed organic residues maintain  
56 and increase soil organic matter content (Iovieno et al., 2009; Tejada et al., 2009), which  
57 impacts physical properties important for soil functioning and plant growth. Physical impacts  
58 include improved soil structure by aggregation (Scotti et al., 2013; Arthur et al., 2014) that  
59 alters pore geometry and continuity so that water infiltration and root penetration through the  
60 soil profile increases (Zhu et al., 2016). There are also enhanced chemical characteristics  
61 through the release of plant nutrients (Swift, 2001; Leifeld et al., 2002), and stimulation and  
62 enhancement of the soil biotic community (Bekele et al., 2015).

63 The importance of organic matter to soil physical structure has been known for  
64 millennia (Lal 1990), with considerable research published showing carbon inputs to mostly  
65 improve stability and aggregation (Hernandez et al., 2017; Pausch and Kuzyakov 2017).  
66 Moreover, organic residues added to soils may become physically protected in the soil matrix  
67 through aggregation (Chevallier, 2014; Aminiyan et al., 2015). More recent research has  
68 shown that root exudates can impact on the rate of soil organic matter (SOM) decomposition,  
69 a process termed ‘priming’ (Keiluweit et al., 2015; Rousk et al., 2015). In the course of  
70 decomposition, large amounts of soil-derived carbon as CO<sub>2</sub> or methane as CH<sub>4</sub> and nitrogen  
71 as N<sub>2</sub>O can be released in a very short time (Kuzyakov et al., 2000; Shahzad et al., 2018).  
72 Nannipieri et al. (2008) has shown that soil respiration is strictly linked to organic C  
73 mineralization and provides a suitable parameter used in determining microbial activities in the  
74 rhizosphere.

75 Moreover, interactions between root exudates and organic residues may influence soil  
76 physical functioning differently. The stability of aggregates and hydraulic transport may be  
77 influenced differently. To date, there is little information on these interactions. One challenge  
78 is the collection and preservation of root exudate in sufficient quantities, so many studies have  
79 used model exudates in various forms in laboratory studies, such as mucilages extracted from  
80 the seed coatings of *Salvia sp.* (Chia) (Kroener et al., 2014) or *Capsella sp.* (Deng et al., 2015),

81 and chemical diffusible fractions, such as polygalacturonic acid (Czarnes et al., 2000; Traoré  
82 et al., 2000), or a model exudate root cocktail (Paterson et al., 2007; de Graaff et al., 2010).

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

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

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

113 examinations of pore structure or structural stability, these tests quantify underpinning physical  
114 processes in rhizosphere structural formation, stability and physical functioning.

115

## 116 **Materials and methods**

### 117 *Soil*

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

124

**Table 1**

### 125 *Exudate components*

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

### 130 *Organic residues*

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

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

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

144 **Table 2**

145

146 *Soil cores preparation and incubation*

147 40 g of each soil, residue and exudate treatment were packed in 0.5 cm layers into  
148 plastic cores (height = 2 cm, diameter = 5 cm) to a bulk density of 1.3 g cm<sup>-1</sup> and placed in  
149 sealed respiration chambers. Five replicates of each treatment were incubated at 20 °C in a  
150 SANYO plant culture incubator (SANYO electric co. Ltd, Japan). The water contents of all  
151 samples were adjusted and maintained at field capacity with deionised water for 14 days and  
152 the hourly rates of microbial respiration were measured in air column, extracted at days 0, 1,  
153 3, 7 and 14, and then analysed for carbon dioxide (CO<sub>2</sub>) nitrous oxide (N<sub>2</sub>O) and methane  
154 (CH<sub>4</sub><sup>+</sup>) concentrations using a gas chromatograph (GC; systems Agilent 6890, GC System,  
155 USA).

156 *Mechanical and hydrological measurements*

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

173 kPa. Gravimetric water content, water sorptivity and cone penetration measurements were  
174 repeated. The samples were then rewetted and dried again to -50 kPa, followed by compression  
175 to 600 kPa on the same mechanical test frame using approaches described in Oleghe et al.  
176 (2017).

### 177 *Calculations and statistics*

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

184

## 185 **Results**

### 186 *Microbial respiration*

187

#### **Table 3**

188 The incubation of soils amended with organic residue and artificial root exudates had a small,  
189 but significant effect on CO<sub>2</sub> and N<sub>2</sub>O emission (Figure 1), but CH<sub>4</sub> emissions were very low  
190 and not affected by any amendments (data not shown). The concentrations of CO<sub>2</sub> and N<sub>2</sub>O  
191 were increased ( $P < 0.001$ ) by the organic residue in the sandy soil, whereas, the results show  
192 that CO<sub>2</sub> concentration was only increased by barley residue in the clay loam soil. This  
193 indicates that the impact of organic residue on microbial decomposition was enhanced more in  
194 the sandy loam than in clay loam soil. Additionally, the root exudates caused greater variability  
195 in CO<sub>2</sub> concentration than seed exudate for both soils.

196 However, microbial activities varied more from the interaction of seed or root exudates with  
197 the organic residues in both soils. CO<sub>2</sub> and N<sub>2</sub>O emissions were significantly increased ( $P <$   
198  $0.001$ ) from the interaction of exudates and residues compared to results for just exudate or  
199 organic residue treatments (Table 4).

200 The microbial activities for the sandy loam soil showed a lag phase before the start of  
201 exponential growth, which was only visible for poultry residue and root exudate interaction on  
202 the clay loam soil. Also, we observed a stationary phase for the control clay loam soil, although  
203 this effect was quickly countered with the interactions of organic residue and exudates. The

204 carbon mineralization rate was greatest for green barley, followed by poultry manure, barley  
205 straw and then the control (Figure 1).

206 **Figure 1**

207

208 *Soil pore characteristics*

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

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

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

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



235

236 *Soil strength*

237 Adding green barley or barley straw increased penetrometer resistance  $P_R$ , but poultry manure  
238 had no impact (Figure 2, Tables 5 and 6). For  $P_R$ , the larger the value, the greater the particle  
239 cementation and soil strength. With Tukey's HSD post hoc tests, the soils amended with root  
240 exudate were found to have increased soil strength, with penetrometer resistance increases of  
241 58% for the sandy loam and 23% for the clay loam soils ( $P < 0.05$ ). Penetrometer resistance  
242 for the exudate and organic residue interactions increased significantly ( $P < 0.05$ ) for both soils.  
243 However, greater resistances were caused by root exudate interactions with organic residue in  
244 the sandy loam soil, while increases in the strength of clay loam soils were directly linked to  
245 the interactions of the seed exudate treatment with organic residues (Figure 2). Generally, root  
246 exudate interactions with green barley and barley straw amendments showed the most  
247 significant increases in penetration resistance with values  $>0.4$  MPa. The influence of wetting-  
248 drying cycles had no impact on the strength of incubated soils.

249

**Figure 2**

250

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

259

260

261

**Figure 3**

262

263 **Discussion**

264 The hypothesis that exudate and organic residue interactions will stimulate microbial  
265 activities and mechanical stability of soil was confirmed in this study. The added substrates  
266 increased microbial activities, with the quality and source of carbon in exudates and organic  
267 residue having a large impact on the rate of microbial mineralization (De Graaff, 2010). The  
268 interaction of easily available organic compounds caused expected increases in the rate of  
269 microbial activities at different times, measured from respiration of CO<sub>2</sub> and N<sub>2</sub>O (Jones, 1998)  
270 (Table 3; Figure 1). Surprisingly, cumulative respiration was only affected by added residues  
271 and/or exudates for the clay loam soil (Table 5). The exudate interactions with organic residue  
272 likely increased the susceptibility of these substrates to microbial decomposition, although this  
273 would require isotopic labelling to confirm (Table 4). Increased microbial population and  
274 activities could result in the production of microbial mucilages, dissolved organic carbon,  
275 exudates or organic material components that are chemically too complex to undergo  
276 continuous microbial mineralization (Morel et al., 1991; Rillig et al., 2015). This could impact  
277 the bonding properties of the soil, with implication for water retention and physical stability.  
278 We found increased physical stability in our soil with impact on some hydraulic properties  
279 following microbial decomposition.

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

289

### 290 *Soil strength*

291 Microbial decomposition of exudates and organic residues affected soil hydrological  
292 and mechanical properties (Figure 2 and 3). These effects were likely driven by particle  
293 cementation and the formation of mechanically stable aggregates (Zhang et al., 2005)  
294 influenced by hydraulic changes from wetting and drying (Dexter, 1988; Hofmockel and Bach  
295 2015; Kallenbach et al., 2016). We found that soil strength benefited from microbial

296 decomposition of exudate on its own, while the organic amendment on its own disrupted the  
297 stability of pores and mineral particles (Figure 2). However, the interactions of seed or root  
298 exudate with the organic residue countered the disruptive impact and resulted in larger  
299 increases in penetration resistance, with the increases sustained over wetting-drying cycles.  
300 Some earlier studies have also shown that microbial activities and associated organic products  
301 from these interactions may drives changes in soil stability (Morel et al., 1991; Watt et al.,  
302 1993; Traoré, et al., 2000). The implication for root laterals might be increased penetration  
303 resistance within the modified zone, but the levels measured are not restrictive to root growth  
304 (Bengough and Mullins, 1990).

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

#### 320 **Figure 4**

321 To simulate exudate released by a germinating seed or real plant root, we used exudate  
322 analogues in homogeneously packed soils in this experiment. We demonstrated that seed  
323 exudate applied at 1.84 mg C g<sup>-1</sup> soil or root exudate compounds at 14.4 mg C g<sup>-1</sup> soil caused  
324 biogenic consolidation. This was further enhanced if soils were also amended with organic  
325 residues of green barley, barley straw or poultry manure at an equivalent rate of 40 t ha<sup>-1</sup>. These  
326 results in a model system suggest that biological and physical properties of the soil volume  
327 surrounding a growing seed or root can be enhanced substantially by exudate components

328 interacting with organic residues. The observed differences between the type and nature of  
329 exudates were pronounced. In addition, the magnitude in biophysical modifications induced by  
330 the exudates, were influenced by the nature and chemical composition of the organic residue.  
331 Whilst our results represent many processes involved in the stabilizing effect of root and seed  
332 exudates, there are limitations to this model study. We ground residues to allow for  
333 homogeneous mixing with the soil, but organic amendments would be in larger forms and more  
334 sparsely distributed in natural soils. Moreover, the exudates used allowed for testing of large  
335 soil volumes, but soil conditions and plant species will create large differences in composition.  
336 Interesting possibilities exist for similar experiments using real growing plant roots and a range  
337 of soil conditions. Pore structure changes could be explored in greater detail with non-invasive  
338 imaging. Additionally, there is room to understand the magnitude and nature of microbial  
339 carbon mineralization ('priming') from the chemical and physical soil properties and  
340 considering its impact in flocculation of organic matter and clay fractions at the micro scale.

341

## 342 **Conclusion**

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

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

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

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559

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

560

Soil texture	Clay (g. 100 g <sup>-1</sup> )	Silt	Sand	Carbon (mg/g)	Nitrogen (mg/g)	pH (CaCl <sub>2</sub> )	C:N	Concentration (mg/g)
Sandy loam	16	24	60	2.25 $\pm$ 0.14	0.16 $\pm$ 0.03	5.48 $\pm$ 0.07	16:1	-
Clay Loam	26	30	44	2.95 $\pm$ 0.12	0.23 $\pm$ 0.02	5.15 $\pm$ 0.04	13:1	-
<i>Chia exudate</i>	-	-	-	3.75 $\pm$ 0.11	0.11 $\pm$ 0.003	-		9.2 $\pm$ 0.26
<i>Organic residue</i>								
Green barley	-	-	-	47.14 $\pm$ 0.04	3.98 $\pm$ 0.02	-	12:1	-
Barley straw	-	-	-	46.32 $\pm$ 0.13	0.56 $\pm$ 0.05	-	82:1	-
Poultry manure	-	-	-	33.87 $\pm$ 0.09	4.43 $\pm$ 0.01	-	8:1	-

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

<b>Soil texture</b>	Control	Green barley	Barley straw	Poultry manure
Sandy loam	17 $\pm$ 0.004	20 $\pm$ 0.006	20 $\pm$ 0.007	18 $\pm$ 0.003
Clay loam	19 $\pm$ 0.003	23 $\pm$ 0.003	25 $\pm$ 0.012	21 $\pm$ 0.012

564

565 **Table 3:** Summary of the analysis of variance for microbial respiration CO<sub>2</sub> and N<sub>2</sub>O for sandy  
 566 loam and clay loam soils.

567

<b>Microbial respiration</b>							
Source of variation	<sup>a</sup> df	Sandy loam			Clay loam		
		Sum Sq	F ratio	P	Sum Sq	F ratio	P
<b>CO<sub>2</sub></b>							
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	-	-
<b>N<sub>2</sub>O</b>							
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	-	-

568 <sup>a</sup>Degrees of freedom.

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

<b>Source of variation</b>	<b>Sandy loam</b>				<b>Clay loam</b>		
<b><i>Volumetric water, <math>\theta</math></i></b>	<b><sup>a</sup>df</b>	<b>Sum of squares</b>	<b>F value</b>	<b><i>P</i></b>	<b>Sum of squares</b>	<b>F value</b>	<b><i>P</i></b>
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	-	-
<b><i>Air porosity, <math>f_a</math></i></b>							
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	-	-
<b><i>Total porosity, <math>f</math></i></b>							
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	-	-
<b><i>Water sorptivity, <math>S_w</math></i></b>							
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	-	-

572 <sup>a</sup>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.

<i>Sandy loam</i>		Cumulative Respiration				Mechanical properties				Pore properties							
		CO <sub>2</sub> (µg)		N <sub>2</sub> O (µg)		P <sub>R</sub> (MPa)		C <sub>c</sub> (-)		θ (m <sup>3</sup> /m <sup>3</sup> )		f <sub>a</sub> (m <sup>3</sup> /m <sup>3</sup> )		f (m <sup>3</sup> /m <sup>3</sup> )		S <sub>w</sub> (mm s <sup>-1/2</sup> )	
Residue	Exudate	LSMean	.Group	LSMean	.Group	LSMean	.Group	LSMean	.Group	LSMean	.Group	LSMean	.Group	LSMean	.Group	LSMean	.Group
Zero	Control	1.813	a	0.033	ab	0.259	abc	0.382	ef	0.235	a	0.274	h	0.540	-	0.698	b
	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
Barley	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
	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	abcc	0.525	-	0.299	a
Straw	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
	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	abcc	0.532	-	0.321	a
Poultry	Control	3.222	ab	0.047	abcd	0.173	a	0.408	f	0.243	ab	0.267	gh	0.546	-	0.666	b
	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
<i>Clay loam</i>																	
Zero	Control	1.054	ab	0.023	ab	NS	NS	0.474	cde	0.315	ab	0.194	g	0.561	-	0.568	h
	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
Barley	Control	2.930	cdef	0.077	cde	NS	NS	0.455	bcde	0.358	cde	0.151	f	0.557	-	0.405	cdefg
	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
Straw	Control	1.887	abcd	0.037	abcd	NS	NS	0.502	de	0.370	de	0.139	a	0.564	-	0.425	fg
	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
Poultry	Control	2.278	cde	0.032	ab	NS	NS	0.511	e	0.343	abcde	0.167	a	0.565	-	0.509	gh
	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

574 **.Group** = means with the same letter(s) are not statistically different, P<sub>R</sub> = penetration resistance, C<sub>c</sub> = compression index, θ = volumetric water content, f<sub>a</sub> =

575 air filled porosity, f = Total porosity and S<sub>w</sub> = water sorptivity.

576 **Table 6:** Summary of the analysis of variance for penetrometer resistance ' $P_R$ ' (MPa) and  
 577 compression index ' $C_c$ ' for sandy loam and clay loam soils.  
 578

Source of variation	Sandy loam				Clay loam		
<i>Penetration resistance <math>P_R</math></i>	<sup>a</sup> df	Sum of squares	F value	Pr(>F)	Sum of squares	F value	<i>P</i>
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	-	-
<i>Compression index <math>C_c</math></i>							
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	-	-

579 <sup>a</sup>df, Degrees of freedom

580 SoD = Stage of decomposition



581 **Figure captions**

582

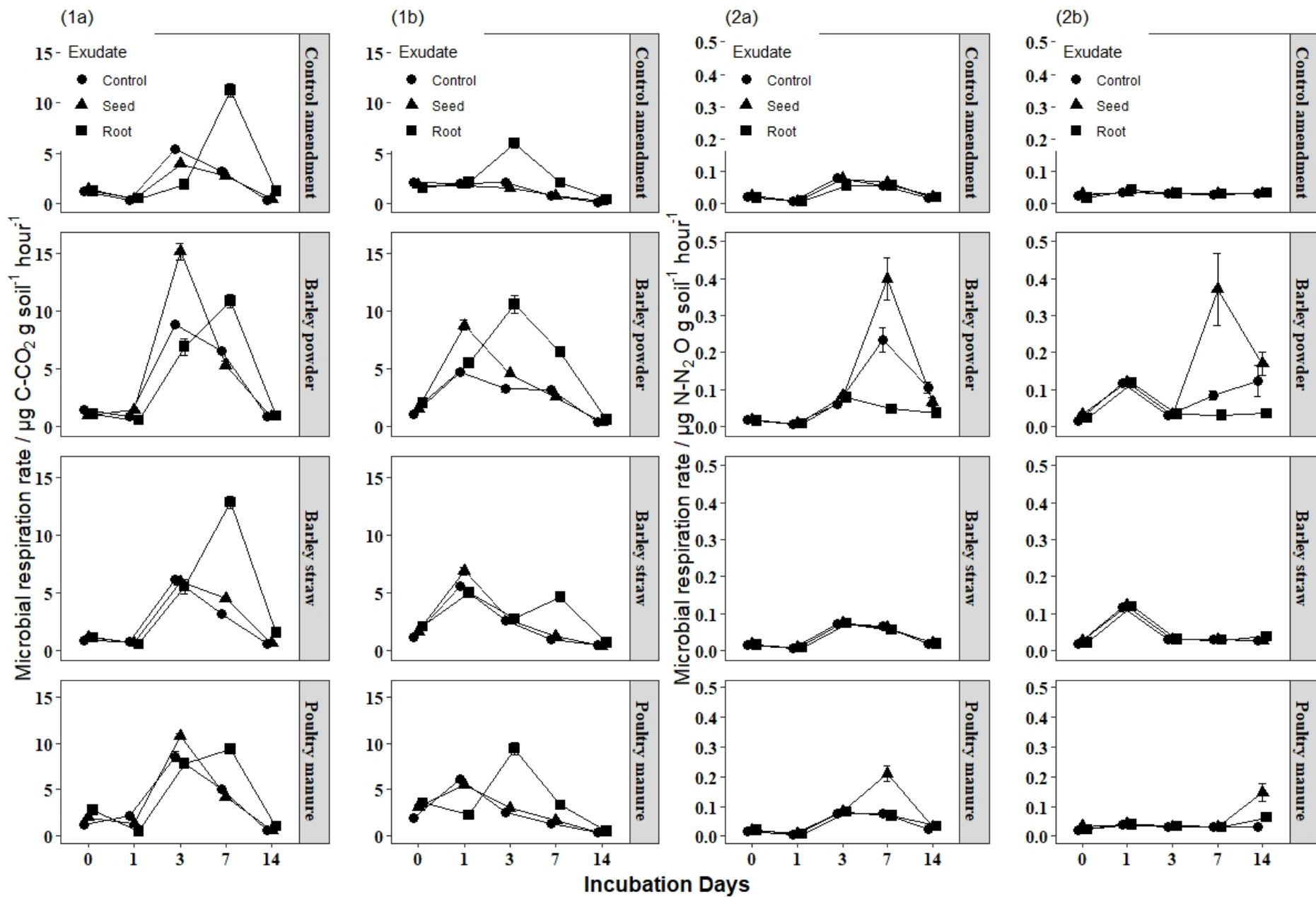
583 **Figure 1:** Microbial mineralisation of added exudate and organic residue, rate of  
584 decomposition were determined for: (1), CO<sub>2</sub> (C-CO<sub>2</sub>.g<sup>-1</sup>.hour<sup>-1</sup>). (2), N<sub>2</sub>O (N- N<sub>2</sub>O.g<sup>-1</sup>.hour<sup>-1</sup>).  
585 on. (a), sandy loam. (b), clay loam soil.

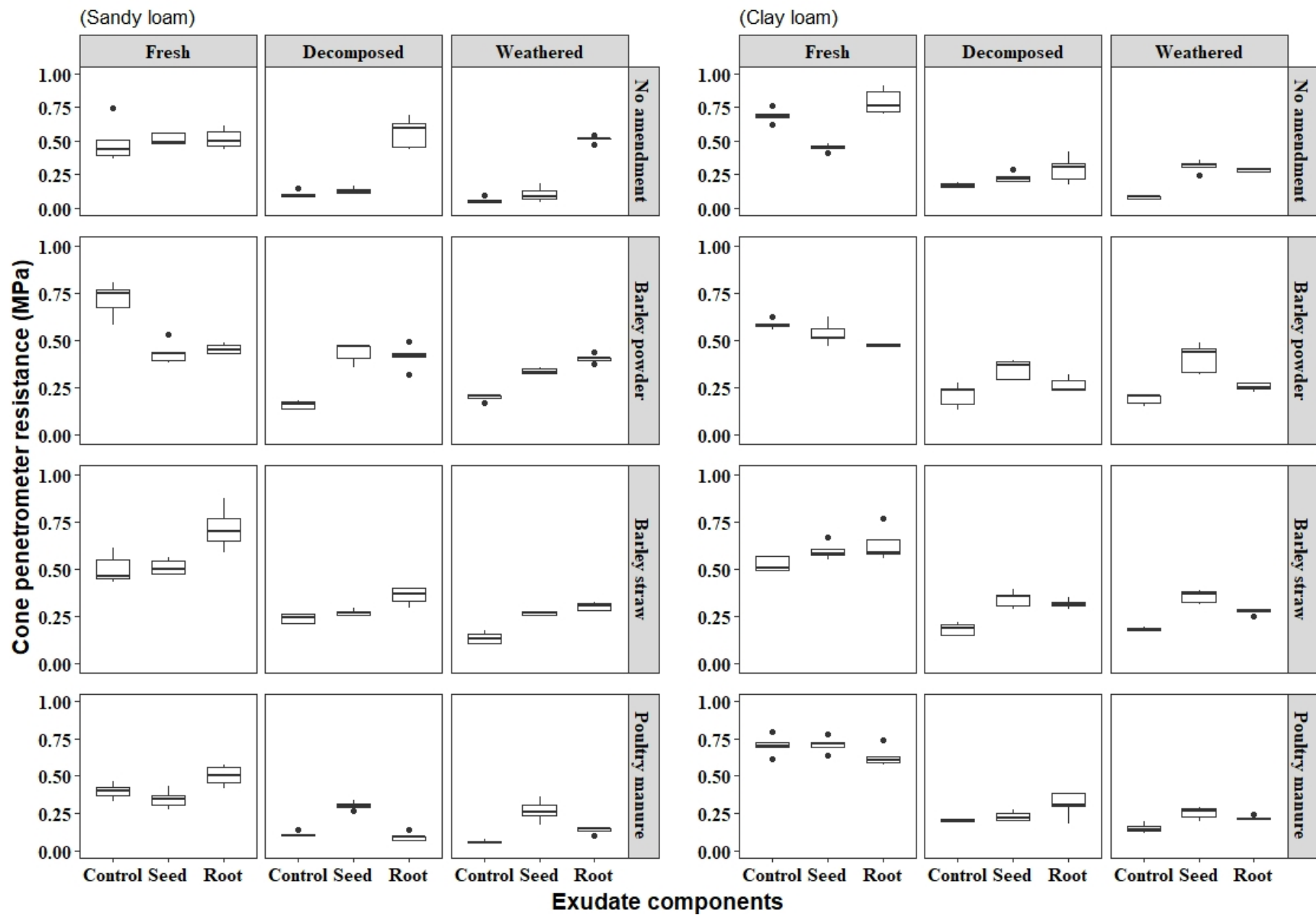
586 **Figure 2:** Cone penetration resistance at -10 kPa matric potential relationship to exudate  
587 components in soils when fresh, incubated and weathered on sandy and clay loam soils, treated  
588 with four organic residue: (a) sandy and (b) clay loam soils.

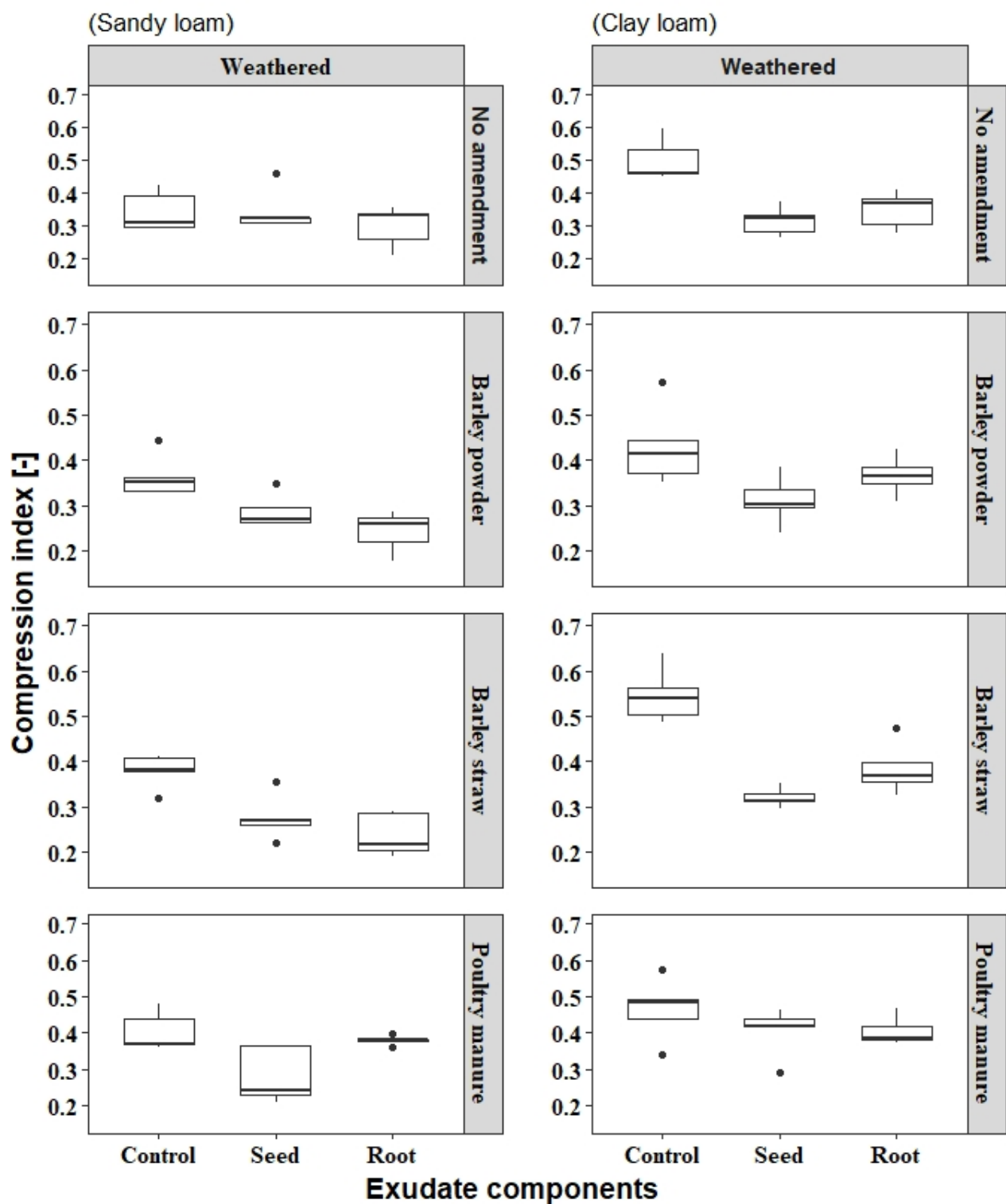
589 **Figure 3:** Compression index at -50 kPa matric potential relationship to exudate components  
590 in soils when weathered on sandy loam and clay loam soils, treated with four organic residue:  
591 (a) sandy and (b) clay loam soil.

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

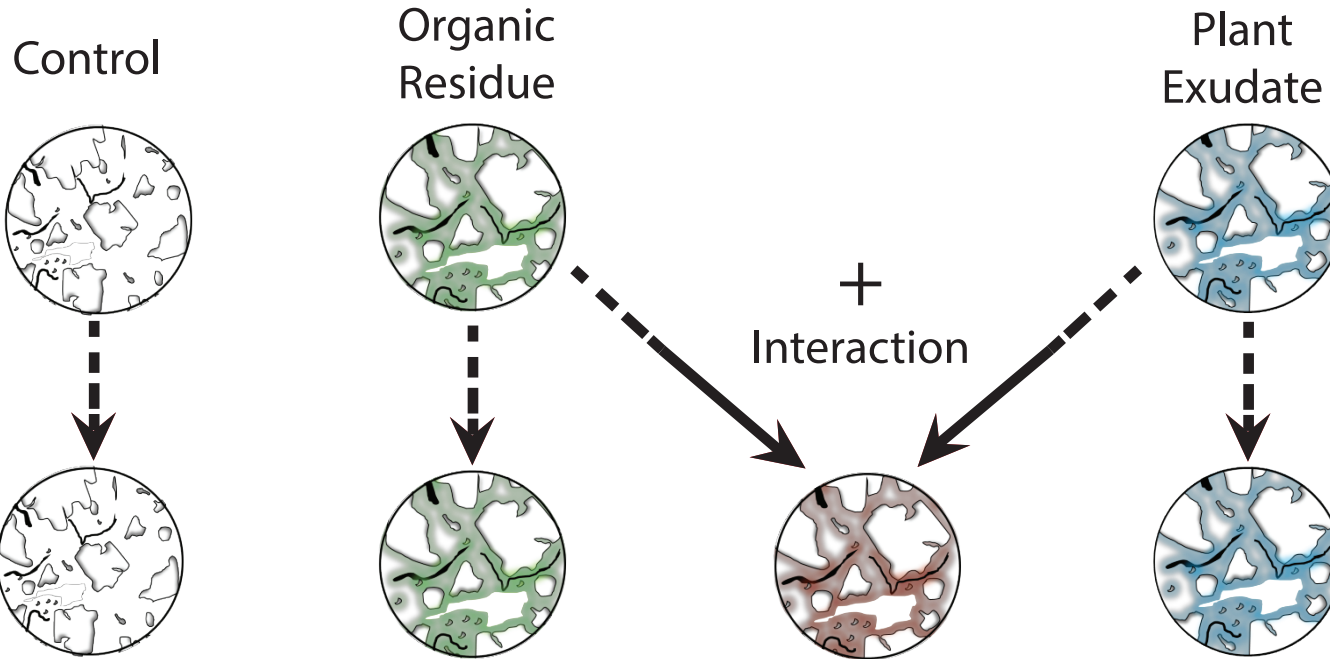
595







# Amendment



14 days incubation

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

3 wet-dry cycles

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