

## Highlights

Root hairs and rhizodeposits are root traits that vary between plant species and crop genotypes and have a large impact on both plants and soils.

Targeting these traits may benefit both plants and soil, improving food and environmental security at the same time. Soils may store more carbon (greenhouse gas mitigation), trap more water (drought tolerance) and nutrients, and resist erosion.

From limited research, rhizosphere size has been maintained or improved in modern crop varieties, but potential exists to increase it further. Whether this will lead to improved yield or soil properties, however, requires greater field testing to verify.

Laboratory and glasshouse research using root trait ideotypes has found marked impacts on soil biophysical properties. Rhizodeposits vary in behaviour between species from hydrogels to surfactants, and as soil dispersers (miners) or aggregators (builders).

## 1 **Building soil sustainability from root-soil interface traits**

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13 **Keywords:** rhizosphere; soil; soil structure; exudate; mucilage; root hair

### 14 15 **Abstract**

16 Great potential exists to harness plant traits at the root-soil interface, mainly  
17 rhizodeposition and root hairs, to “build” soils with better structure that can trap more  
18 carbon and resources, resist climate stresses and promote a healthy microbiome. These  
19 traits appear to have been preserved in modern crop varieties, but scope exists to improve  
20 them further as they vary considerably between genotypes and respond to environmental  
21 conditions. From emerging evidence, rhizodeposition can act as a disperser, aggregator  
22 and/or hydrogel in soil, and root hairs expand rhizosheath size. Future research should  
23 explore impacts of selecting these traits on plants and soils concurrently, expanding from  
24 model plants to commercial genotypes, and observing whether impacts currently limited to  
25 glasshouse studies occur in the field.

## 26 27 **Building soil sustainability from root-soil interface traits**

28 By reversing our thinking of how root-soil interface traits affect the functioning of the  
29 rhizosphere, there is considerable opportunity to restore degraded soils [1], mitigate  
30 greenhouse gases [2] and enhance biodiversity [3]. These are some of the grandest  
31 challenges facing humanity [4], which by focussing on root-soil interface traits, plant  
32 breeding may help address while also underpinning another grand challenge - food security.

33 Breeding crop varieties with the target of improving soil health and reducing soil  
34 degradation will produce better conditions for crop growth through more efficient resource  
35 utilisation and stress tolerance, so a win-win is possible where both yield and soil are  
36 improved and could be the cornerstone of regenerative agriculture.

37 Whilst considerable research has explored root exudation and the rhizosphere microbiome  
38 [3,5-7], the lack of integrated research with other disciplines has failed to capture wider  
39 benefits of root-soil interface traits on soils. If soils are improved by optimising rhizosphere  
40 function, then plants may benefit from both direct and indirect impacts. Direct impacts have  
41 been studied extensively, focussed primarily on the suppression of pathogens [3,8] and the  
42 capacity of plants to capture resources from soil, such as through manipulation of nutrient  
43 cycling by microorganisms [9]. This review focusses on indirect impacts that are less well  
44 studied, specifically on the capacity of roots to restructure soil.

45 By targeting soil structure building root traits, abiotic stress resistance of both plants and  
46 soils could increase through microbial habitat formation to improve nutrient cycling,  
47 stabilisation of soil against erosion, a greater capacity of soil to absorb, store and drain water  
48 [10]. Such improvements to soil structure driven by plants may improve carbon storage  
49 [11,12] and may mitigate against soil compaction damage that prevents deep-rooting  
50 cultivars penetrating through hard layers of soil and capturing otherwise lost resources [13].  
51 Plants are known to have a huge impact on soil properties, but these processes are  
52 generally ignored in plant breeding, where the primary focus is yield, either directly from  
53 plant productivity or indirectly from biotic and abiotic stress tolerance [10]. With the shift  
54 towards reduced tillage and smaller inputs of agrochemicals, a plant's capacity to alter soil  
55 structure [14] and the rhizosphere microbiome [3] will become increasingly important.  
56 Given that root-soil interface traits that benefit soils may also benefit plants, perhaps  
57 favourable traits have been inadvertently selected in modern varieties, so we seek evidence  
58 from past research.

59

## 60 **Plants as architects of soil**

61 The capacity of plants to manipulate soils has been long appreciated, forming the basis of  
62 good rotation design and biological tillage [15]. A considerable body of research has shown

63 plant roots to be a major driver of the soil microbiome [5,6] and soil physical structure [16].  
64 The mechanisms used by plant roots to navigate and modify structurally heterogenous soil  
65 were discussed by Jin et al. [13], who also argued that optimising root-soil interactions could  
66 improve food and soil sustainability. Starting at the root tip, compression of soil by an  
67 elongating and expanding root can be eased by sloughed off cells [17] and exuded mucilage  
68 [18] (Figure 1). Extending along the root, primarily to the elongation zone, exudates are  
69 released that enhance nutrient capture [19]. All of these compounds secreted by roots  
70 provide a major burst of substrate, producing a 'hot spot' or 'hot moment' at the root soil  
71 interface [20]; this has profound effects on the diversity and functioning of the surrounding  
72 microbiome [7].

73 A hot opportunity may exist to manipulate mucilages and exudates from roots to improve  
74 soil properties at the root-soil interface, producing a unique biophysical environment and  
75 niche for microbes and their functions. These compounds interact with microbial by-  
76 products and the physical action of the expanding, drying and wetting root to form the  
77 rhizosphere [14]. Rhizosphere size is difficult to define and varies rapidly over time, but it  
78 can have chemical influences extending 3 mm and physical influences extending over 10  
79 mm into the soil. A volume of soil under cereals has been estimated to be 2% roots and  
80 about 50% rhizosphere [21], but there is scope through breeding to extend this further.  
81 Properties of the rhizosphere can vary markedly to the surrounding soil, with a range of  
82 benefits to plant productivity and the environment (Box 1). It forms the interface of all  
83 materials captured by the plant from soil and the habitat where microorganisms interact to  
84 cycle plant nutrients and compete against pathogens and is therefore a critical zone of  
85 global significance.

86

### 87 **Plant breeding and root-soil interface traits**

88 Modern agriculture has degraded soils through depleting soil carbon, acidification,  
89 increasing salinity (irrigation and removal of trees), mining of elements, enhancing erosion  
90 and decreasing microbial diversity [4]. To some extent, these threats can be mitigated by  
91 improved agronomy, but perhaps plant breeding exacerbated soil degradation by focussing  
92 on yield and resource capture in fertilised soils? Fertilisers decrease the benefit of root-soil  
93 interface traits such as exudates and root hairs [22,23] to capture nutrients, arguably

94 making them more dispensable for the plant. Coupled with this, modern crop cultivars may  
95 have root systems that are smaller, steeper and reach deeper than older varieties [24,25],  
96 so they would be expected to return less carbon to soils. However, even when root system  
97 biomass has decreased over time with cultivar development, net effects on rhizodeposition  
98 may be minimal and therefore the long-term impact on soil carbon is uncertain [26].

99 Furthermore, under less ideal conditions of drought [24] or compaction [27], modern  
100 varieties may be more responsive at reaching deeper soil [28] where rhizodeposits  
101 decompose more slowly, resulting in more effective carbon storage [29]. In a study of over  
102 100 wheat genotypes, Mathew et al. [30] concluded that root biomass could be selected  
103 along with grain yield to satisfy both soil carbon sequestration and food security.

104 By growing deeper in soil, root architecture offers exciting opportunities to improve crop  
105 resistance to stress and soil carbon storage at the same time [28]. This comes at a metabolic  
106 cost, so there is emerging interest in altering root anatomy such as tissue structure for  
107 greater metabolic efficiency [31]. Compared to system architecture, however, root-soil  
108 interface traits can offer far greater metabolic efficiency for capturing resources from soil  
109 [32,33]. Under constrained conditions of nutrients, water or temperature, root hair  
110 abundance increases [34] and exudates containing more efficient enzyme signatures can be  
111 produced [35]. Exudates and root hairs work in tandem to improve metabolic efficiency  
112 [12], driving improved soil conditions for the plant in the rhizosphere [36].

113 As the rhizosphere is difficult to define and separate from soil, soil that adheres to roots to  
114 form a rhizosheath [14] is often measured as it has defined boundaries and is easier to  
115 sample. While this operationally defined trait does not encompass the entire rhizosphere, it  
116 is a good proxy for rhizosphere size and properties [37]. From the little data that exists  
117 comparing landraces to different eras in modern crop breeding, it appears that rhizosheath  
118 size has been maintained or improved over time (Table 1).

119 The size of the rhizosheath differs considerably between species [38] and also between  
120 genotypes of the same species. But would targeting rhizosheath size in breeding lead to a  
121 yield reduction? A comparison of rhizosheath size to yield finds little impact (Figure 2), and  
122 one of the few field studies on root hair impacts on rhizosheath size found a positive impact  
123 on yield in dry years [39]. Potential therefore exists to target genotypes with a greater  
124 ability to physically manipulate soils, possibly with improved crop productivity too.

125 Could this offer a new tool in a plant breeders' arsenal? Quantitative trait loci (QTLs) related  
126 to rhizosphere size have been found and the genetic controls may be relatively simple [40].  
127 Between 144 elite genotypes of *Hordeum vulgare* grown in soil mesocosms, rhizosphere size  
128 was found to vary by over 500%, with the upper quartile varying by about 175% [41].  
129 However, it is not only the genotype but also the environment that affects rhizosphere size.  
130 Poor soil phosphorus availability and root-soil contact tends to create larger rhizospheres  
131 [42], so selecting crops for rhizosphere size could infer greater abiotic stress resistance with  
132 plasticity from responsiveness in degraded soils. Drought can increase rhizosphere size and  
133 its ability to store and transmit water, particularly in drought tolerant genotypes [16].  
134 Investment in the rhizosphere or rhizosphere may give a direct pay off to the plant through  
135 improved resource acquisition to counteract stress [5,12,16,43], but it may also indirectly  
136 pay off by improving soil structure. It is interesting to note that the species which were first  
137 noted for having rhizospheres were desert grasses that survived in extremely poor soils low  
138 in organic matter content [44]. Plants appear to be investing in improving their soil  
139 conditions at the root-soil interface and buffering themselves against hostile environments.  
140 The recent surge in understanding of how specific root-soil interface traits manipulate root-  
141 soil interactions has been enabled by a range of new technologies. From milligram samples  
142 of precisely extracted rhizosphere soil, molecular approaches have unravelled contrasting  
143 microbiomes between plant species and genotypes [6,8]. Rhizosphere properties can be  
144 measured in intact soil samples using high resolution physical and chemical measurements  
145 [45], including 3D visualisation of how root traits impact soil pore structure [46]. By  
146 combining the technologies enabling shoot-root phenotyping [47] with molecular biology of  
147 plants and soil microorganisms[6], studies of the rhizosphere offer a great opportunity to  
148 understand below-ground interactions and their genetic drivers that could be harnessed to  
149 improve soil conditions at a spatially and temporally meaningful scale.

150

### 151 **Root-soil interface traits for more sustainable plants**

152 The emerging understanding of root-soil interface traits demonstrates the great capacity of  
153 plants to manipulate the soil environment and has potential to inform new crop genotypes.  
154 Roots produce larger and more stable volumes of soil at their surface, mainly by root hairs  
155 and rhizodeposits (Figure 1), that work together to affect the environment surrounding the

156 root, producing the equivalent of intestinal villi and secretions to enhance nutrient capture  
157 and support a microbiome. Jethro Tull's [48] assertion 250 years ago that 'roots are but as  
158 guts inverted... that spew out what is superfluous' captures these processes eloquently,  
159 although mucilages and exudates are certainly not superfluous.

160 Compared to the study of the gastrointestinal tract, however, the presence of soil creates a  
161 major challenge to the study of root traits. Gut biology is complicated, but the 3D dynamic  
162 pore structure, diverse chemistry and vast biodiversity of soil produces a much more  
163 complex system. Just as in gut biology, rhizosphere research focuses on the microbiome [6],  
164 but unlike gut biology where habitat is fixed by organ structure, the rhizosphere microbiome  
165 interacts with soil particles, the growing root, root hairs and rhizodeposits to continuously  
166 produce new habitat over time and space. With emerging evidence of the underlying  
167 processes that drive this habitat creation comes growing confidence that crop genotypes or  
168 species can be selected for their ability to physically manipulate soils. One impact is  
169 decreased abiotic stress from drought through rhizodeposits restructuring soil to trap more  
170 water [13] and easing deep root penetration through compacted soil [18]. Water stress  
171 alters rhizodeposit chemistry thus influencing microbial diversity [5] and function such as  
172 exopolysaccharide production by roots and microbes improving water retention [49].

173 However, the understanding of the physical processes underpinning rhizosphere formation  
174 and its impacts on plants is only just emerging and is constrained by the challenge of direct  
175 sampling of rhizodeposits from soil [19]. An alternative is to harvest exudates and other  
176 rhizodeposits in soil-free systems such as hydroponics [50], sterile and inert matrices to  
177 simulate soil [51], or directly from exuding brace roots or seedling root tips [52,53].

178 Measurements of directly harvested rhizodeposits have helped to unravel processes that  
179 lead to the development and functioning of the rhizosphere. Building on research exploring  
180 the chemistry of root mucilage, Read & Gregory [54] found that these compounds were  
181 highly surface active and viscous. By being surface active, root mucilage can decrease the  
182 surface tension of water by over 30%, with an expected easing of water capture from  
183 surrounding soil [55]. Viscous rhizodeposits, on the other hand, are more resistant to  
184 drainage. This may aid water uptake [33] and produce microhydrological niches that could  
185 buffer roots and microorganisms from the wetting and drying stresses of surrounding soil  
186 [56]. Viscous rhizodeposits may also help fill gaps that emerge between drying roots and soil

187 [57], further enabling greater water uptake [56], but potentially leading to the development  
188 of a hydrophobic rhizosphere that rewets poorly following drought [58]. The surface activity  
189 of other rhizodeposits can help mitigate hydrophobicity, producing greater rewetting rates  
190 [43]. Experimental evidence using model rhizodeposits has suggested that they may also  
191 decrease water movement rates in dry soil [59], although much of this has been limited to  
192 sandy soils where this impact is exacerbated [55].

193 So, it is not just the chemical composition of rhizodeposits that improves root-soil  
194 interactions, but also their physical properties and this needs to be considered when  
195 exploring root traits. The viscosity and surface activity of rhizodeposits varies between plant  
196 species [54,55] resulting in different impacts to soil [60]. *Hordeum vulgare* has a greater  
197 proportion of organic acids to sugars in its rhizodeposits compared to *Zea mays*, resulting in  
198 a lower viscosity and greater surface activity [50]. This suggests that when these  
199 rhizodeposits are added to soil, *Hordeum vulgare* eases water extraction by its exudates  
200 acting as a surfactant whereas *Zea mays* exudates improve water storage by acting as a  
201 hydrogel [60]. Mechanical measurements of soils amended with these rhizodeposits found  
202 *Hordeum vulgare* to weaken and disperse soil particle bonds, which has been speculated to  
203 improve nutrient release, ease root growth and catalyse changes to the rhizosphere [50].  
204 *Zea mays* rhizodeposits have the opposite effect of strengthening and gelling soil particle  
205 bonds. Rapid microbial degradation of rhizodeposits produces secondary compounds  
206 [19,49], so their physical impacts may change quickly. Microbes have been found to change  
207 *Hordeum vulgare* rhizodeposits from dispersing into gelling compounds [50] with  
208 diminished surface activity [60] that aggregate soil to create more favourable habitats for  
209 microbes and plants. This might improve the sustainability of soil as a more stable and  
210 aggregated structure will be more effective at storing and cycling water, carbon and  
211 nutrients.

212 The different properties of *Zea mays* and *Hordeum vulgare* rhizodeposits could reflect the  
213 environments where they evolved. It is fascinating to think that environmental variability may  
214 have played out in subtle changes to exudate quality that lead to opposing strategies to  
215 cope with a deficit of water or nutrients, giving us a range of rhizosphere strategies to  
216 challenge the problems posed by drought and soil degradation. Likewise, desert plants are  
217 being used to inform QTLs controlling rhizosphere formation [44,49], which could be



218 extended to common crop species as more evidence of contrasting rhizodeposit properties  
219 emerges. Harvesting of rhizodeposits and performing quick measurements of their physical  
220 behaviour augmented by modelling approaches of root-water uptake could provide a high-  
221 throughput approach to screen large numbers of genotypes to identify favourable traits.  
222 This would complement emerging understanding of chemical components of rhizodeposits  
223 [36] and rapid screens to assess their adhesive properties that aggregate soil [61].

224 These direct physical measurements of the capacity of rhizodeposits to disperse and  
225 aggregate soils were visually apparent in decades old scanning electron micrographs of the  
226 rhizosphere [62]. With the emergence of noninvasive 3D imaging of root-soil interactions,  
227 coupled with increased computing power, leaps in understanding should eventually inform  
228 crop breeding [16,47]. For example, synchrotron imaging at sub-micron resolution has  
229 visualised the tortuous pathways through soil pores that root hairs penetrate to increase  
230 the zone of influence of the root and its capacity to capture resources [46,63]. Such  
231 technology is unravelling how traits such as increased root hair length lead to greater P  
232 capture [42] and yield under limited conditions (Figure 3) [64]. Sophisticated numerical  
233 models can use synchrotron imaging of the sub-micron scale 3D structure of root hairs [65]  
234 and their interaction with soil pores [46] to predict resource capture. Other models begin to  
235 explore how microbial traits interact with the physical, chemical and biological properties at  
236 these pore scales [66]. The combined experimental knowledge and modelling approaches  
237 will deepen our understanding of rhizosphere properties, potentially offering an exciting  
238 new tool to simulate optimum root trait ideotypes.

239 High resolution 3D imaging has also revealed that root hairs can restructure the root-soil  
240 interface to counteract compaction from roots expanding radially and axially as they grow  
241 [46]. This early work visualising how root hairs and soil structure interact has been limited to  
242 seedlings of *Hordeum vulgare* and *Triticum aestivum* [65] and different water stresses.  
243 Findings have been contradictory [46,63], likely due to soil properties, and different  
244 genotypes have yet to be explored, so considerable potential exists for follow-on research.  
245 Direct visualisation of root hairs in soil has also questioned the value of measuring root hairs  
246 in artificial conditions as there may be limited similarity to abundance and length when  
247 grown in soil [67]. Processes leading to greater resource capture by root hairs also require  
248 greater investigation. In an elegant study using a root pressure chamber [68], root hairs

249 were found to buffer the drying gradient (water potential flux) at the root-soil interface,  
250 enabling greater transpiration rates from drying soil [69]. This led to questioning of  
251 accepted concepts of plant hydraulics, where stomatal closure under water stress has been  
252 argued to be driven by soil hydraulic properties at the root-soil interface rather than xylem  
253 vulnerability [70]. Expanding the zone of soil influenced by roots through root hairs may  
254 therefore offer another plant trait to improve drought tolerance.

255 Root hairs also improve anchorage between roots and surrounding soil [34]. This has been  
256 observed to increase pull-out resistance, potentially decreasing root lodging by wind,  
257 uplifting by grazing animals and improved establishment of seedlings upon soil disruption  
258 [61,71,72]. Another role of root hairs is bracing the root against soil, improving penetration  
259 into compacted soils [73]. From the perspective of the plant, root hairs improve nutrient  
260 and water capture, anchorage and penetration, but from the perspective of soil there are  
261 further potential positive impacts summarised in Box 1.

262

### 263 **Root-soil interface traits for more sustainable soils**

264 An over-arching impact of root hairs and rhizodeposition traits on soil is carbon [11,12],  
265 which underpins a broad range of environmental processes that feed back to plant  
266 productivity and stress tolerance. It has been estimated that 2.4x more carbon is  
267 contributed by roots than shoots to soils [29]. Between different genotypes of the same  
268 crop, rhizodeposition chemistry and its knock-on impact to soil carbon storage can vary  
269 markedly [74]. Just as dabbing paint with a brush allows it to penetrate into nooks and  
270 crannies on surfaces, root hairs can aid the influence of plant roots by penetrating into soil  
271 pores that are too small for roots and distributing rhizodeposits into a greater volume of soil  
272 [29]. This creates the adhered soil that makes up the rhizosheath [75], which is postulated  
273 to be a major process that aggregates carbon and makes it more recalcitrant to  
274 decomposition by microorganisms [29].

275 The studies discussed thus far provide convincing arguments of the potential to select  
276 rhizodeposition and root hairs to build more stable and aggregated soils. However, it is less  
277 clear if they result in meaningful impacts in the field. Even in a laboratory study, hairless  
278 root mutants of *Hordeum vulgare* had a similar capacity to stabilise soil against erosion as

279 their wildtype parent, but root system architecture confounded interpretation [76]. As in  
280 this work, many other studies have used hairless mutants to disentangle mechanisms, but  
281 meaningful data for crop breeders needs to contrast commercially viable varieties with  
282 differing root hairs and rhizodeposition [77]. One of the few field studies exploring root  
283 hairs compared two commercial *Hordeum vulgare* varieties with a range of root hair  
284 mutants of one of the varieties [39]. Longer root hairs were correlated with bigger  
285 rhizosheaths, but the commercial varieties did not differ enough to provide a contrast.  
286 Further field experiments using a broader range of contrasting rhizosphere trait genotypes  
287 of different crops are needed to verify that postulated impacts from laboratory studies have  
288 meaningful impact. These experiments need to consider longer-term impacts to soil,  
289 particularly carbon dynamics, physical structure and microbial populations that are the  
290 cornerstone of soil health.

291

## 292 **Concluding Remarks and Future Perspectives**

293 Modern varieties and crop breeding lines can have vastly different root hair and  
294 rhizodeposit properties that need to be scrutinised more closely for their combined impacts  
295 on plants and soils (see Outstanding Questions). Studies on the microbiology, chemistry and  
296 physical properties of the rhizosphere have shown large plasticity caused by stresses from  
297 drought, soil compaction or nutrient availability. A genotype's capacity to engineer  
298 favourable soil properties at the root surface could enhance its fitness under variable field  
299 conditions.

300 We have shown evidence that selecting genotypes for favourable root-soil interface traits  
301 can also improve yield with minimal metabolic cost. There is potential through crop rotation  
302 for the root-soil interactions of preceding crops to benefit follow-on crops. Moreover,  
303 longer-term improvements to soil could result, that benefit both the crop and the  
304 environment. The impact of plant roots on soils has been appreciated for centuries, but it is  
305 only now that new technologies are emerging that are unravelling the mechanistic  
306 processes of how plant root traits form the rhizosphere and impact both plants and soils.  
307 We are only at the beginning of understanding whether rhizodeposition and root hairs could  
308 be selected for more sustainable soils, but the emerging evidence is positive and compelling  
309 (see also outstanding questions).

310

## 311 **Acknowledgements**

312 This research was supported by the NERC/BBSRC Soil Security Programme (NE/M005747/1)  
313 and projects in its portfolio (BB/L026058/1, BB/L025892/1, NE/P014208/1 and  
314 NE/P014224/1). The contribution of TSG was also supported with the financial support of  
315 the Rural & Environment Science & Analytical Services Division of the Scottish Government

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## 317 **References**

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- 319 1. Brainard, J. (2018) Alarm over land degradation. *Science* 359, 1444-1444
- 320 2. Rumpel, C. *et al.* (2018) Boost soil carbon for food and climate. *Nature* 553, 27-27
- 321 3. Mauchline, T.H. and Malone, J.G. (2017) Life in earth - the root microbiome to the  
322 rescue? *Curr. Opin. Microbiol.* 37, 23-28. 10.1016/j.mib.2017.03.005
- 323 4. Scherer, L. *et al.* (2020) Global priorities of environmental issues to combat food  
324 insecurity and biodiversity loss. *Sci. Total Environ.* 730, 9.  
325 10.1016/j.scitotenv.2020.139096
- 326 5. Williams, A. and de Vries, F.T. (2020) Plant root exudation under drought:  
327 implications for ecosystem functioning. *New Phytol.* 225, 1899-1905.  
328 10.1111/nph.16223
- 329 6. Sasse, J. *et al.* (2018) Feed your friends: do plant exudates shape the root  
330 microbiome? *Trends Plant Sci.* 23, 25-41. 10.1016/j.tplants.2017.09.003
- 331 7. Pieterse, C.M.J. *et al.* (2016) The soil-borne supremacy. *Trends Plant Sci.* 21, 171-173.  
332 10.1016/j.tplants.2016.01.018
- 333 8. Hilton, S. *et al.* (2018) Preceding crop and seasonal effects influence fungal, bacterial  
334 and nematode diversity in wheat and oilseed rape rhizosphere and soil. *Appl. Soil*  
335 *Ecol.* 126, 34-46. 10.1016/j.apsoil.2018.02.007
- 336 9. Schmidt, J.E. *et al.* (2020) Impacts of directed evolution and soil management legacy  
337 on the maize rhizobiome. *Soil Biol. Biochem.* 145, 13. 10.1016/j.soilbio.2020.107794
- 338 10. Gregory, P.J. *et al.*, eds (2013) *Rhizosphere Engineering by Plants: Quantifying Soil–*  
339 *Root Interactions (Enhancing Understanding and Quantification of Soil–Root Growth*  
340 *Interactions, Vol. enhancingunder)* (Vol. Advances in Agricultural Systems Modeling,
- 341 11. Pausch, J. and Kuzyakov, Y. (2018) Carbon input by roots into the soil: Quantification  
342 of rhizodeposition from root to ecosystem scale. *Global Change Biology* 24, 1-12.  
343 10.1111/gcb.13850
- 344 12. Holz, M. *et al.* (2018) Root hairs increase rhizosphere extension and carbon input to  
345 soil. *Ann. Bot.-London* 121, 61-69. 10.1093/aob/mcx127
- 346 13. Jin, K.M. *et al.* (2017) Shaping an optimal soil by root-soil interaction. *Trends Plant*  
347 *Sci.* 22, 823-829. 10.1016/j.tplants.2017.07.008
- 348 14. York, L.M. *et al.* (2016) The holistic rhizosphere: integrating zones, processes, and  
349 semantics in the soil influenced by roots. *J. Exp. Bot.* 67, 3629-3643.  
350 10.1093/jxb/erw108
- 351 15. Chen, G.H. and Weil, R.R. (2010) Penetration of cover crop roots through compacted  
352 soils. *Plant Soil* 331, 31-43. 10.1007/s11104-009-0223-7

- 353 16. Rabbi, S.M.F. *et al.* (2018) Plant roots redesign the rhizosphere to alter the three-  
354 dimensional physical architecture and water dynamics. *New Phytol.* 219, 542-550.  
355 10.1111/nph.15213
- 356 17. Bengough, A.G. *et al.* (2011) Root elongation, water stress, and mechanical  
357 impedance: a review of limiting stresses and beneficial root tip traits. *J. Exp. Bot.* 62,  
358 59-68. 10.1093/jxb/erq350
- 359 18. Oleghe, E. *et al.* (2017) Plant exudates improve the mechanical conditions for root  
360 penetration through compacted soils. *Plant Soil* 421, 19-30. 10.1007/s11104-017-  
361 3424-5
- 362 19. Oburger, E. and Jones, D.L. (2018) Sampling root exudates - Mission impossible?  
363 *Rhizosphere* 6, 116-133. 10.1016/j.rhisph.2018.06.004
- 364 20. Kuzyakov, Y. and Blagodatskaya, E. (2015) Microbial hotspots and hot moments in  
365 soil: Concept & review. *Soil Biol. Biochem.* 83, 184-199.  
366 10.1016/j.soilbio.2015.01.025
- 367 21. Bengough, A.G. (2012) Water dynamics of the root zone: rhizosphere biophysics and  
368 its control on soil hydrology. *Vadose Zone J.* 11,
- 369 22. Wissuwa, M. and Kant, J. (2021) Does half a millimetre matter? Root hairs for yield  
370 stability. A commentary on 'Significance of root hairs for plant performance under  
371 contrasting field conditions and water deficit'. *Ann. Bot.-London* 128, iii-v.  
372 10.1093/aob/mcab027
- 373 23. Wen, T.J. and Schnable, P.S. (1994) Analyses of mutants of 3 genes that influence  
374 root hair development in *Zea-mays* (Gramineae) suggest that root hairs are  
375 dispensable. *American Journal of Botany* 81, 833-842. 10.2307/2445764
- 376 24. Friedli, C.N. *et al.* (2019) Modern wheat semi-dwarfs root deep on demand:  
377 response of rooting depth to drought in a set of Swiss era wheats covering 100years  
378 of breeding. *Euphytica* 215. 10.1007/s10681-019-2404-7
- 379 25. Aziz, M.M. *et al.* (2017) Five decades of selection for yield reduced root length  
380 density and increased nitrogen uptake per unit root length in Australian wheat  
381 varieties. *Plant Soil* 413, 181-192. 10.1007/s11104-016-3059-y
- 382 26. Van de Broek, M. *et al.* (2020) The soil organic carbon stabilization potential of old  
383 and new wheat cultivars: a (CO<sub>2</sub>)-C-13-labeling study. *Biogeosciences* 17, 2971-2986.  
384 10.5194/bg-17-2971-2020
- 385 27. Correa, J. *et al.* (2019) Soil compaction and the architectural plasticity of root  
386 systems. *J. Exp. Bot.* 70, 6019-6034. 10.1093/jxb/erz383
- 387 28. Thorup-Kristensen, K. *et al.* (2020) Digging deeper for agricultural resources, the  
388 value of deep rooting. *Trends Plant Sci.* 25, 406-417. 10.1016/j.tplants.2019.12.007
- 389 29. Rasse, D.P. *et al.* (2005) Is soil carbon mostly root carbon? Mechanisms for a specific  
390 stabilisation. *Plant Soil* 269, 341-356. 10.1007/s11104-004-0907-y
- 391 30. Mathew, I. *et al.* (2019) Selection of wheat genotypes for biomass allocation to  
392 improve drought tolerance and carbon sequestration into soils. *J. Agron. Crop Sci.*  
393 205, 385-400. 10.1111/jac.12332
- 394 31. Lynch, J.P. *et al.* (2021) Root anatomy and soil resource capture. *Plant Soil* 466, 21-  
395 63. 10.1007/s11104-021-05010-y
- 396 32. Brown, L.K. *et al.* (2013) A conceptual model of root hair ideotypes for future  
397 agricultural environments: what combination of traits should be targeted to cope  
398 with limited P availability? *Ann. Bot.-London* 112, 317-330. 10.1093/aob/mcs231

- 399 33. Ahmed, M.A. *et al.* (2014) Mucilage exudation facilitates root water uptake in dry  
400 soils. *Functional Plant Biology* 41, 1129-1137. 10.1071/fp13330
- 401 34. Vissenberg, K. *et al.* (2020) Hormonal regulation of root hair growth and responses  
402 to the environment in Arabidopsis. *J. Exp. Bot.* 71, 2412-2427. 10.1093/jxb/eraa048
- 403 35. Zhang, X.C. *et al.* (2020) Rhizosphere hotspots: Root hairs and warming control  
404 microbial efficiency, carbon utilization and energy production. *Soil Biol. Biochem.*  
405 148. 10.1016/j.soilbio.2020.107872
- 406 36. Galloway, A.F. *et al.* (2020) Cereal root exudates contain highly structurally complex  
407 polysaccharides with soil-binding properties. *Plant Journal* 103, 1666-1678.  
408 10.1111/tbj.14852
- 409 37. Pang, J.Y. *et al.* (2017) Unwrapping the rhizosheath. *Plant Soil* 418, 129-139.  
410 10.1007/s11104-017-3358-y
- 411 38. Brown, L.K. *et al.* (2017) The rhizosheath - a potential trait for future agricultural  
412 sustainability occurs in orders throughout the angiosperms. *Plant Soil* 418, 115-128.  
413 10.1007/s11104-017-3220-2
- 414 39. Marin, M. *et al.* (2020) Significance of root hairs for plant performance under  
415 contrasting field conditions and water deficit. *Ann. Bot.-London.*  
416 10.1093/aob/mcaa181
- 417 40. James, R.A. *et al.* (2016) Rhizosheaths on wheat grown in acid soils: phosphorus  
418 acquisition efficiency and genetic control. *J. Exp. Bot.* 67, 3709-3718.  
419 10.1093/jxb/erw035
- 420 41. George, T.S. *et al.* (2014) Understanding the genetic control and physiological traits  
421 associated with rhizosheath production by barley (*Hordeum vulgare*). *New Phytol.*  
422 203, 195-205. 10.1111/nph.12786
- 423 42. Haling, R.E. *et al.* (2013) Root hairs improve root penetration, rootsoil contact, and  
424 phosphorus acquisition in soils of different strength. *J. Exp. Bot.* 64, 3711-3721.  
425 10.1093/jxb/ert200
- 426 43. Ahmed, M.A. *et al.* (2018) Engineering rhizosphere hydraulics: pathways to improve  
427 plant adaptation to drought. *Vadose Zone J.* 17. 10.2136/vzj2016.09.0090
- 428 44. Price, S.R. (1911) The roots of some north african desert-grasses. *New Phytol.* 10,  
429 328-340
- 430 45. Veelen, A. *et al.* (2020) Root-induced soil deformation influences Fe, S and P:  
431 rhizosphere chemistry investigated using synchrotron XRF and XANES. *New Phytol.*  
432 225, 1476-1490. 10.1111/nph.16242
- 433 46. Koebernick, N. *et al.* (2017) High-resolution synchrotron imaging shows that root  
434 hairs influence rhizosphere soil structure formation. *New Phytol.* 216, 124-135.  
435 10.1111/nph.14705
- 436 47. Tracy, S.R. *et al.* (2020) Crop improvement from phenotyping roots: highlights reveal  
437 expanding opportunities. *Trends Plant Sci.* 25, 105-118.  
438 10.1016/j.tplants.2019.10.015
- 439 48. Tull, J. (1762) *Horse-hoeing husbandry: or, an essay on the principles of vegetation*  
440 *and tillage.* A. Millar
- 441 49. Ndour, P.M.S. *et al.* (2020) The rhizosheath: from desert plants adaptation to crop  
442 breeding. *Plant Soil* 456, 1-13. 10.1007/s11104-020-04700-3
- 443 50. Naveed, M. *et al.* (2017) Plant exudates may stabilize or weaken soil depending on  
444 species, origin and time. *Eur. J. Soil Sci.* 68, 806-816. 10.1111/ejss.12487

- 445 51. Boeufremblay, V. *et al.* (1995) Influence of mechanical impedance on root  
446 exudation of maize seedlings at 2 development stages. *Plant Soil* 172, 279-287.  
447 10.1007/bf00011330
- 448 52. Zickenrott, I.M. *et al.* (2016) An efficient method for the collection of root mucilage  
449 from different plant species-A case study on the effect of mucilage on soil water  
450 repellency. *J. Plant Nut. Soil Sci.* 179, 294-302. 10.1002/jpln.201500511
- 451 53. Read, D.B. *et al.* (1999) Physical properties of axenic maize root mucilage. *Plant Soil*  
452 211, 87-91
- 453 54. Read, D.B. and Gregory, P.J. (1997) Surface tension and viscosity of axenic maize and  
454 lupin root mucilages. *New Phytol.* 137, 623-628. 10.1046/j.1469-8137.1997.00859.x
- 455 55. Read, D.B. *et al.* (2003) Plant roots release phospholipid surfactants that modify the  
456 physical and chemical properties of soil. *New Phytol.* 157, 315-326.  
457 doi.org/10.1046/j.1469-8137.2003.00665.x
- 458 56. Benard, P. *et al.* (2019) Microhydrological niches in soils: how mucilage and eps alter  
459 the biophysical properties of the rhizosphere and other biological hotspots. *Vadose*  
460 *Zone J.* 18, 10. 10.2136/vzj2018.12.0211
- 461 57. Carminati, A. *et al.* (2009) When roots lose contact. *Vadose Zone J.* 8, 805-809
- 462 58. Ahmed, M.A. *et al.* (2016) Drying of mucilage causes water repellency in the  
463 rhizosphere of maize: measurements and modelling. *Plant Soil* 407, 161-171.  
464 10.1007/s11104-015-2749-1
- 465 59. Zhang, W.C. *et al.* (2021) Physical properties of a sandy soil as affected by incubation  
466 with a synthetic root exudate: Strength, thermal and hydraulic conductivity, and  
467 evaporation. *Eur. J. Soil Sci.* 72, 782-792. 10.1111/ejss.13007
- 468 60. Naveed, M. *et al.* (2019) Surface tension, rheology and hydrophobicity of  
469 rhizodeposits and seed mucilage influence soil water retention and hysteresis. *Plant*  
470 *Soil* 437, 65-81. 10.1007/s11104-019-03939-9
- 471 61. Eldridge, B.M. *et al.* (2021) A centrifuge-based method for identifying novel genetic  
472 traits that affect root-substrate adhesion in *Arabidopsis thaliana*. *Front. Plant Sci.* 12,  
473 13. 10.3389/fpls.2021.602486
- 474 62. Dorioz, J.M. *et al.* (1993) The role of roots, fungi and bacteria on clay particle  
475 organization - an experimental approach. *Geoderma* 56, 179-194. 10.1016/0016-  
476 7061(93)90109-x
- 477 63. Koebernick, N. *et al.* (2019) Imaging microstructure of the barley rhizosphere:  
478 particle packing and root hair influences. *New Phytol.* 221, 1878-1889.  
479 10.1111/nph.15516
- 480 64. Gahoonia, T.S. and Nielsen, N.E. (2004) Barley genotypes with long root hairs sustain  
481 high grain yields in low-P field. *Plant Soil* 262, 55-62.  
482 10.1023/B:PLSO.0000037020.58002.ac
- 483 65. Keyes, S.D. *et al.* (2013) High resolution synchrotron imaging of wheat root hairs  
484 growing in soil and image based modelling of phosphate uptake. *New Phytol.* 198,  
485 1023-1029. 10.1111/nph.12294
- 486 66. Portell, X. *et al.* (2018) Microscale heterogeneity of the spatial distribution of organic  
487 matter can promote bacterial biodiversity in soils: insights from computer  
488 simulations. *Front. Microbiol.* 9, 16. 10.3389/fmicb.2018.01583
- 489 67. Nestler, J. *et al.* (2016) Root hair formation in rice (*Oryza sativa* L.) differs between  
490 root types and is altered in artificial growth conditions. *J. Exp. Bot.* 67, 3699-3708.  
491 10.1093/jxb/erw115

- 492 68. Deery, D.M. *et al.* (2013) Uptake of water from a Kandosol subsoil. II. Control of  
493 water uptake by roots. *Plant Soil* 368, 649-667. 10.1007/s11104-013-1736-7
- 494 69. Carminati, A. *et al.* (2017) Root hairs enable high transpiration rates in drying soils.  
495 *New Phytol.* 216, 771-781. 10.1111/nph.14715
- 496 70. Carminati, A. and Javaux, M. (2020) Soil rather than xylem vulnerability controls  
497 stomatal response to drought. *Trends Plant Sci.* 25, 868-880.  
498 10.1016/j.tplants.2020.04.003
- 499 71. Choi, H.S. and Cho, H.T. (2019) Root hairs enhance *Arabidopsis* seedling survival  
500 upon soil disruption. *Sci. Rep.-UK* 9, 10. 10.1038/s41598-019-47733-0
- 501 72. Zenone, A. *et al.* (2020) Biological adhesion in seagrasses: The role of substrate  
502 roughness in *Posidonia oceanica* (L.) Delile seedling anchorage via adhesive root  
503 hairs. *Mar. Environ. Res.* 160, 9. 10.1016/j.marenvres.2020.105012
- 504 73. Bengough, A.G. *et al.* (2016) Root hairs aid soil penetration by anchoring the root  
505 surface to pore walls. *J. Exp. Bot.* 67, 1071-1078. 10.1093/jxb/erv560
- 506 74. Mwfulirwa, L. *et al.* (2016) Barley genotype influences stabilization of  
507 rhizodeposition-derived C and soil organic matter mineralization. *Soil Biol. Biochem.*  
508 95, 60-69. 10.1016/j.soilbio.2015.12.011
- 509 75. Burak, E. *et al.* (2021) Root hairs are the most important root trait for rhizosheath  
510 formation of barley (*Hordeum vulgare*), maize (*Zea mays*) and *Lotus japonicus* (Gifu).  
511 *Ann. Bot.-London.* 10.1093/aob/mcab029
- 512 76. Burak, E. *et al.* A mesocosm-based assessment of whether root hairs affect soil  
513 erosion by simulated rainfall. *Eur. J. Soil Sci.*, 9. 10.1111/ejss.13042
- 514 77. Wissuwa, M. and Kant, J. (2021) Does half a millimetre matter? Root hairs for yield  
515 stability. A commentary on 'Significance of root hairs for plant performance under  
516 contrasting field conditions and water deficit'. *Ann. Bot.-London.*  
517 10.1093/aob/mcab027
- 518 78. Adu, M.O. *et al.* (2017) Quantifying variations in rhizosheath and root system  
519 phenotypes of landraces and improved varieties of juvenile maize. *Rhizosphere* 3, 29-  
520 39. <https://doi.org/10.1016/j.rhisph.2016.12.004>
- 521 79. McDonald, G.K. *et al.* (2018) Responses to phosphorus among barley genotypes.  
522 *Crop Pature Sci.* 69, 574-586. 10.1071/cp17406
- 523 80. Delhaize, E. *et al.* (2015) The genetics of rhizosheath size in a multiparent mapping  
524 population of wheat. *J. Exp. Bot.* 66, 4527-4536. 10.1093/jxb/erv223
- 525 81. Delhaize, E. *et al.* (2012) Aluminium tolerance of root hairs underlies genotypic  
526 differences in rhizosheath size of wheat (*Triticum aestivum*) grown on acid soil. *New*  
527 *Phytol.* 195, 609-619. 10.1111/j.1469-8137.2012.04183.x
- 528 82. Okano, N. *et al.* Spanish spelt is unique germplasm for improvement of root hair  
529 length in hexaploid wheat. *Plant Soil*, 14. 10.1007/s11104-020-04555-8
- 530 83. Liu, T.Y. *et al.* (2019) Comparative metabolite profiling of two switchgrass ecotypes  
531 reveals differences in drought stress responses and rhizosheath weight. *Planta* 250,  
532 1355-1369. 10.1007/s00425-019-03228-w
- 533 84. Brown, L.K. *et al.* (2012) What are the implications of variation in root hair length on  
534 tolerance to phosphorus deficiency in combination with water stress in barley  
535 (*Hordeum vulgare*)? *Ann. Bot.-London* 110, 319-328. 10.1093/aob/mcs085
- 536

537



538 **Glossary**

539 **Biological tillage:** fragmentation and aggregation of soil through the action of plant roots,  
540 soil fauna and microorganisms.

541 **Exudate:** substances secreted by roots, comprised of a mix of sugars, amino acids, organic  
542 acids and other organic substances.

543 **Microhydrological niches:** discrete spatial regions in soil where biological compounds alter  
544 water holding and transport properties.

545 **Mucilage:** polysaccharide rich compounds secreted at the root tip that are viscous.

546 **Quantitative trait loci (qtls):** genes that influence specific traits.

547 **Rhizodeposits:** collective term for all materials exchanged from the plant to soil, dominated  
548 by exudates, mucilages and sloughed cells.

549 **Rhizosheath:** soil that adheres strongly to the root through the action of root hairs and  
550 rhizodeposits. It provides a rapid and easy approach to sample soil affected by plant roots.

551 **Rhizosphere:** soil at the interface of plant roots that has been influenced by rhizodeposits.  
552 All resources capture by a plant from soil enters through the rhizosphere. It generally has  
553 greater carbon, biological activity and stability than surrounding soil.

554 **Root hairs:** single cell outgrowths from the root epidermis that increase root surface area  
555 and soil exploration.

556 **Soil structure:** the spatial arrangement of soil particles and pores, driven primarily by  
557 aggregation and dispersion from roots and soil biology.

558

559 **Table 1.** Rhizosheath size of landraces and released varieties of four crop species, along with  
560 the data source

Species	Rhizosheath size (g m <sup>-1</sup> ) <sup>a</sup>			Soil		Soil pH	Soil P (mg kg <sup>-1</sup> )	Soil water content	Refs.
	Era I	Era II	Era III	WRB	Texture				
<i>Zea mays</i>	2.38	2.58	2.09	Acrisols	Sandy Loam	6.1	26.1	70% FC	[78]
<i>Hordeum vulgare</i>	4.37	4.54	4.37	Luvisols	Sandy Loam	9.2	5 (Colwell P)	75% FC	[79]
<i>Triticum aestivum</i>	-	4.60	3.86	Acrisols	N/A	6.2	N/A	90% FC	[80,81]
<i>Triticum aestivum</i>	1.69	-	1.13-2.54	Andosols	N/A	N/A	14.4	80% FC	[82]
<i>Panicum virgatum</i>	-	0.80	2.40	N/A	N/A	N/A	N/A	30% FC	[83]

561 <sup>a</sup>Rhizosheaths are expressed as gram per metre of root, including weights of both the fresh  
562 root and the moist soil. **Era I:** landraces; **Era II:** earlier varieties of *Zea mays* (1983-1998),  
563 *Hordeum vulgare* (1951-1986), *Triticum aestivum* (1932-1972) and *Panicum virgatum*

564 (1963); **Era III**: later varieties of *Zea mays* (2006-2013), *Hordeum vulgare* (1996-2013),  
565 *Triticum aestivum* (1993-2006) and *Panicum virgatum* (1973-1978). WRB is the Reference  
566 Soil Group of the World Reference Base for soil resources.

567

568

## 569 **Figure legends**

570 **Figure I.** How root surface traits influence soils.

571 **Figure 1.** Formation of the physical environment at the root-soil interface through the  
572 combined impacts of root hairs, root tip mucilage (blue) and root exudates (yellow).  
573 Bacteria (red dots) and arbuscular mycorrhizal fungi (green lines) populations increase along  
574 the root and produce secondary compounds from rhizodeposits that have further physical  
575 impacts.

576

577 **Figure 2.** Relationship between rhizosphere size and yield of *Hordeum vulgare*, including 20  
578 varieties from McDonald et al. [79] (black circles) and 4 genotypes differing in root hair  
579 length of cv Optic from Brown et al. [84] (white circles). Each genotype under P-limited  
580 conditions is represented as a percentage of achievable yield for the same genotype under  
581 unlimited P conditions.

582

583 **Figure 3.** Relationship between root hair length and P uptake (A), yield (B) for 11 cultivars of  
584 *Hordeum vulgare* under P-limited conditions, from Gahoonia and Nielsen [64]. Each cultivar  
585 under P-limited conditions is represented as a percentage of achievable P uptake/yield for  
586 the same cultivar under unlimited P conditions.

587

## 588 **Box 1. Rhizosphere traits that benefit plants and soils**

589 Plant roots are ecosystem engineers that are highly responsive to the soil environment [13].  
590 Through rhizodeposition, roots massively influence a thin zone of soil at their surface that is  
591 expanded by root hairs (see Figure I). Improved properties for plants emerge in the  
592 rhizosphere, which is teaming with microbial life in mutualistic, symbiotic and parasitic  
593 interactions with plants [3]. Everything a plant captures from soil passes through the

594 rhizosphere, which also serves as a store that captures and releases water and nutrients  
595 better than the surrounding soil [70].

596 The benefits to the plant from the rhizosphere also benefit the soil. Carbon is the primary  
597 driver, which provides substrate for microbial activity that underpins nutrient cycling and  
598 particle aggregation [6]. A range of root and microbial derived compounds aggregate soil,  
599 capture water as hydrogels and ease water extraction by their surface activity. Root hairs  
600 further bind the soil together, improving anchorage of roots and possibly soil resistance to  
601 erosion.

602 Between different genotypes of the same crop, rhizodeposition and root hair properties  
603 differ and the QTLs driving these traits are being identified [41]. Rhizodeposition and root  
604 hairs also adapt to the soil environment, increasing plant resistance to drought [5] and  
605 nutrient capture when fertility is poor [38]. Targeting root traits that influence the  
606 rhizosphere could therefore make both soils and food production more sustainable.

607

608

## Outstanding Questions

Are root traits influencing rhizosphere characteristics improved or degraded in modern crops compared to landraces?

What are the fundamental processes driving the biophysical structuring of rhizosphere properties and how are they influenced by root traits?

Can we improve root-soil interactions for crops by learning from wild plants that have evolved in contrasting environments?

Are there specific QTLs to link crop genotypic and root-soil interface traits that can benefit breeding programmes?

Can we integrate the complex information on rhizospheres, plant physiology and the soil environment to develop models to identify traits that benefit both plants and soils?

How does the plasticity of root hair growth, rhizodeposition and the rhizosphere microbiome to environmental stress alter the biophysical properties of soil?

How do root traits and rhizospheres impact soils and ecosystem services such as water, nutrient and carbon storage over the long-term in the field?

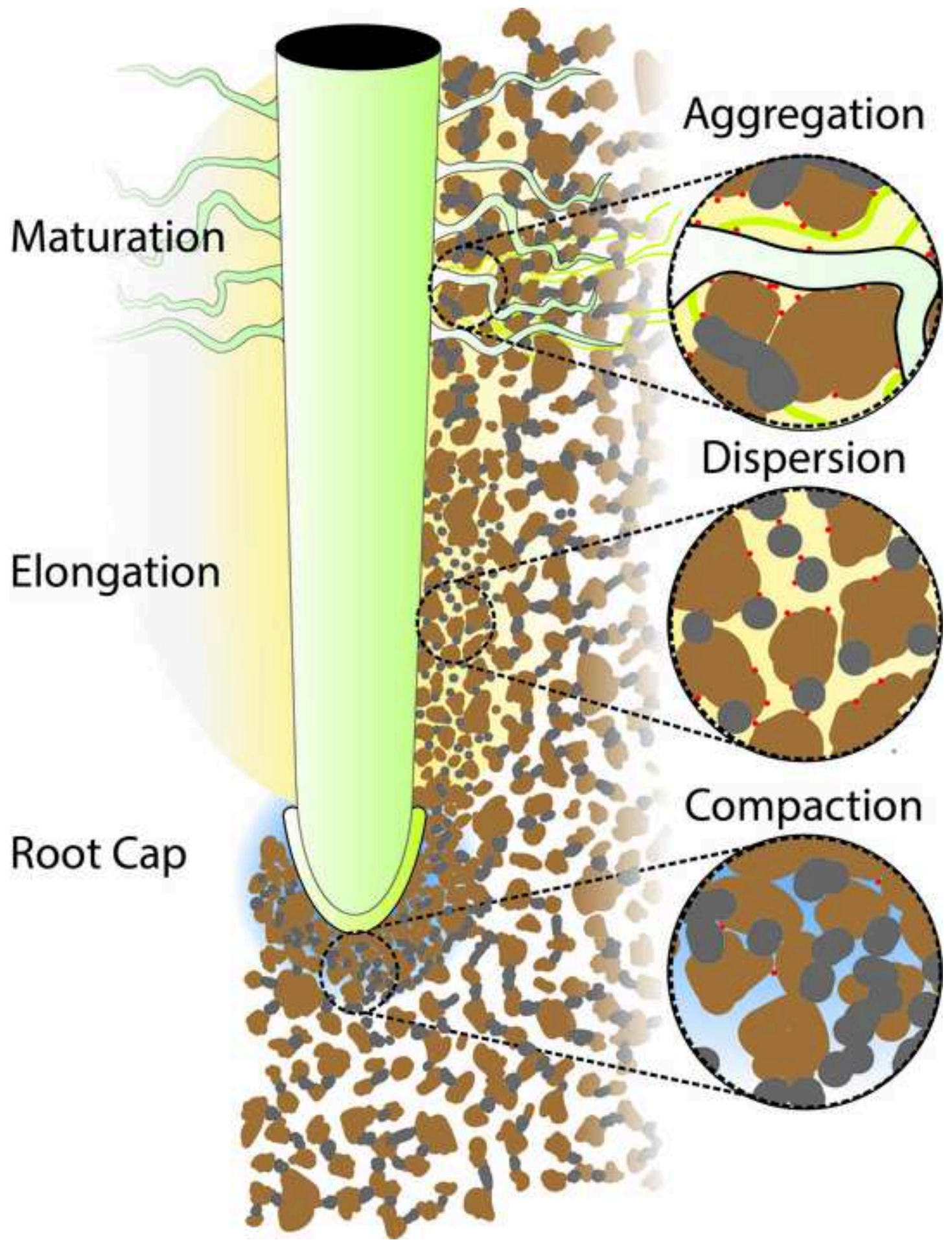


Figure 2

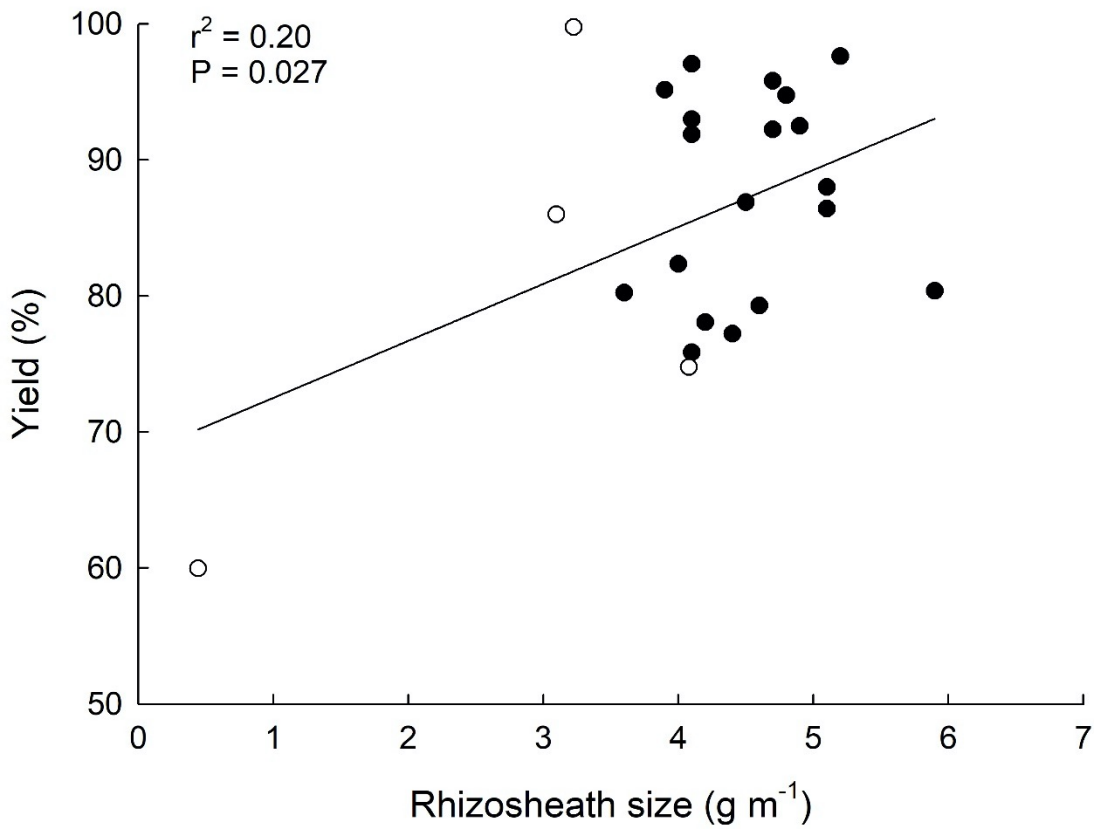


Figure 3

