

Trends in Plant Science

Building soil sustainability from root-soil interface traits

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

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).

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

2

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12

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14

15 **Abstract**

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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
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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 rhizospheres, 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

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316

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- 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 ⁻¹) ^a			Soil		Soil pH	Soil P (mg kg ⁻¹)	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 ^aRhizosheaths 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 rhizosheath 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?

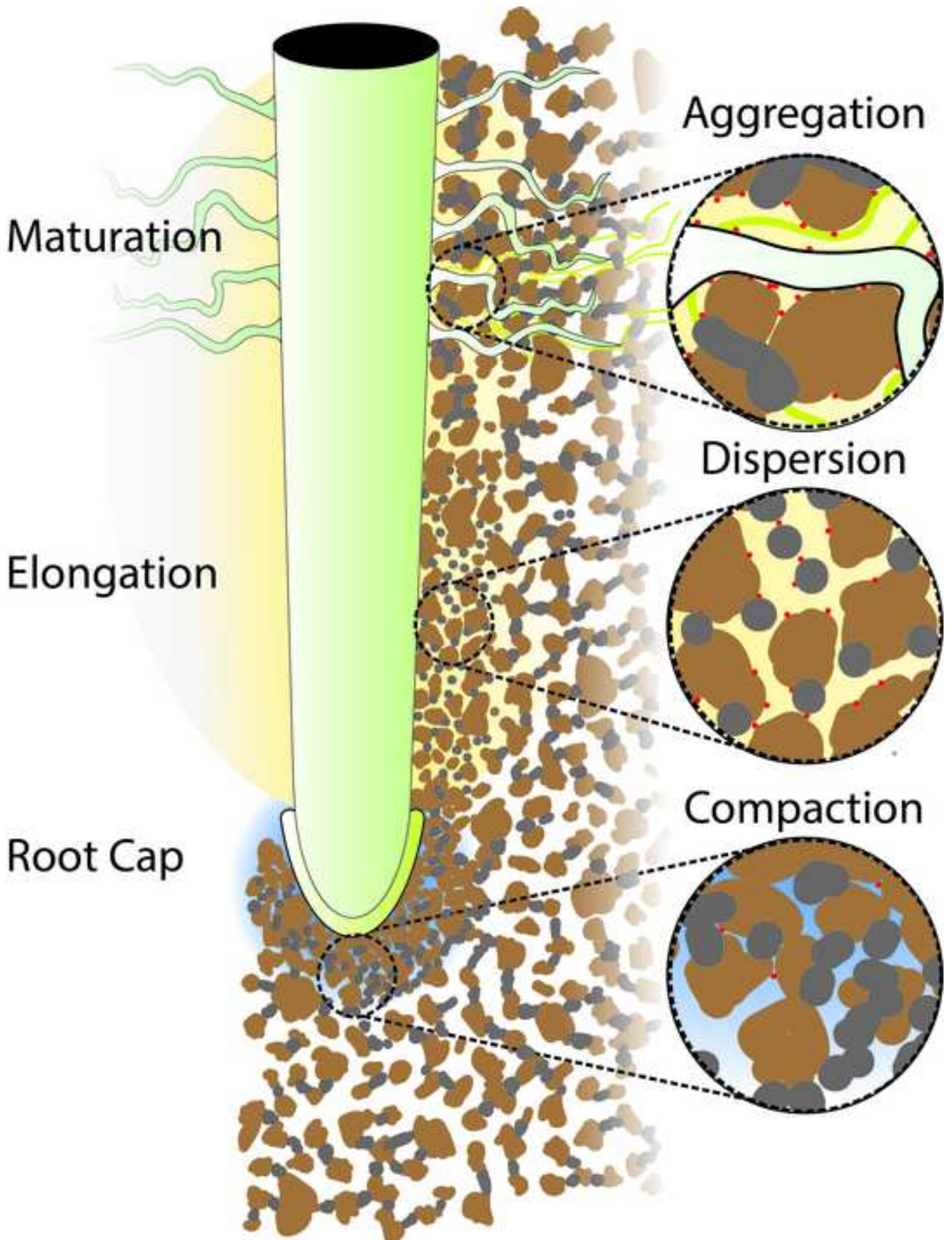


Figure 2

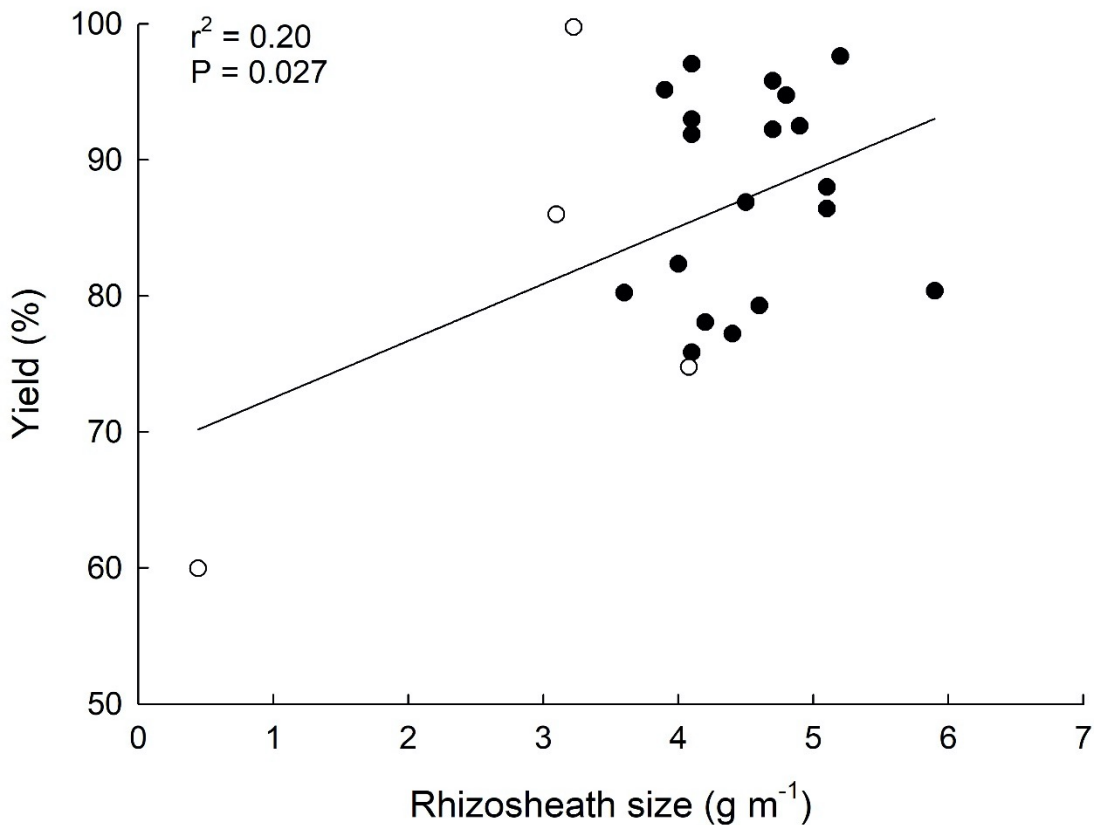


Figure 3

