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The ability of maize roots to grow through compacted soil is not dependent on the amount of roots formed

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Revised manuscript with changes accepted:

1 **Title:** The ability of maize roots to grow through compacted soil is not dependent on
2 the amount of roots formed

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20

21 **Abstract**

22 **Highlights:**

- 23 • Soil compaction influenced the proportion of coarse roots (i.e. > 1 mm diameter)
24 of maize in a genotype-dependent manner
- 25 • Rooting depth was reduced and root distribution within the soil profile changed
26 when grown in compacted soil
- 27 • Rooting depth and total root length, total coarse root length and total fine root
28 length were not correlated with each other in compacted soil
- 29 • The ability of roots of different genotypes to reach a certain depth was not
30 related to the amount of roots formed

31 **Keywords**

32 Impedance; compaction; root length; root distribution; compensatory growth

33

34 **Abstract**

35 Mechanical impedance is a primary constraint to root growth and hence the capture
36 of soil resources. To investigate whether rooting depth and root length under
37 mechanical impedance caused by compaction are correlated we evaluated 12 maize
38 lines at two field sites. To distinguish between lateral and nodal roots, roots were
39 sorted into different diameter classes. Coarse roots had diameters >1 mm and
40 represent nodal root axes. Greater proportions of coarse roots on compacted plots
41 were found at both field sites however results were driven by genotypic variation. Soil
42 compaction reduced total rooting depth (in all diameter classes) and coarse rooting
43 depth at both sites compared to non-compacted plots. Root distribution was influenced
44 by compaction with greater root length densities closer to the soil surface. Root length
45 and root depth were not related to each other under impeded conditions. Coarse roots
46 of some genotypes became obstructed on the compacted plots, while other genotypes
47 were capable of growing through the impeding soil and reached deeper soil strata
48 resulting in differential distribution of roots through the soil profile. On compacted plots
49 we observed genotypes with similar root depths but with contrasting coarse root
50 lengths. The ability of roots to grow through compacted soils is therefore not
51 dependent solely on the coarse root length formed by the root system.

52 **1. Introduction**

53 The ability of plants to acquire nutrients and water is dependent on soil exploration.
54 Mechanical impedance can lead to reduced total root length and/or a redistribution of
55 root length within the soil profile (Pfeifer *et al.*, 2014a; Shierlaw and Alston, 1984),
56 which could affect the acquisition of water and nutrients. As soils get denser and
57 stronger with depth, due to overburden pressure (Gao *et al.*, 2012, 2016), mechanical
58 impedance will often restrict deeper rooting root phenotypes more than topsoil foraging
59 root phenotypes. Periodic droughts are common in many ecosystems and drier soils
60 are generally harder (Gao *et al.*, 2012; To and Kay, 2005; Vaz *et al.*, 2011; Whalley *et al.*,
61 2005; Suralta *et al.*, 2018). However, plants with root systems that grow deeper
62 are in general better adapted to drought (Chimungu *et al.*, 2014a; Lilley and
63 Kirkegaard, 2016; Lynch, 2013; Zhan *et al.*, 2015). Certain soils offer very large
64 mechanical impedance to roots, for example hard-setting soils in Australia (Mullins *et al.*,
65 1987) or rainfed lowland rice cultivation systems (Suralta *et al.*, 2018). Different
66 agricultural management approaches can also introduce compaction and plough pans
67 by wheeled traffic or trampling (Batey, 2009; Hamza and Anderson, 2005). Depending
68 on the soil textural characteristics, suboptimal soil conditions during trafficking (such
69 as high moisture contents) will exacerbate compaction (Horn *et al.*, 1995; Raper,
70 2005). Roots can become confined to surface soil strata when not capable of
71 penetrating through a hard soil layer such as a plough pan (Barraclough and Weir,
72 1988; Ehlers *et al.*, 1983). Root systems are able to compensate root growth by
73 exploiting the lesser impeded regions of the soil, as illustrated by split pot experiments
74 (Bingham and Bengough, 2003; Pfeifer *et al.*, 2014a) or layered pot systems (Shierlaw
75 and Alston, 1984). Roots of maize (Chimungu *et al.*, 2015), rice (Chandra Babu *et al.*,

76 2001; Clark *et al.*, 2000, 2002; Yu *et al.*, 1995), wheat (Botwright Acuña and Wade,
77 2005; Kubo *et al.*, 2006) and common bean (Rivera *et al.*, 2019) show substantial
78 genotypic variability for penetrating strong wax layers simulating mechanical
79 impedance.

80 Root systems consist of distinct root classes which vary by taxa, for example many
81 dicot taxa have a dominant taproot, while monocots, such as cereals, form nodal roots
82 from shoot nodes (Hochholdinger *et al.*, 2004; Lynch and Brown, 2012; Rich and Watt,
83 2013). Adult maize root systems consist of primary, seminal, crown (belowground
84 nodal) and brace (aboveground nodal) roots, all these classes form lateral roots. For
85 monocotyledons, nodal roots are the main parent axes of lateral roots present at depth
86 as these laterals proliferate from nodal roots (Cairns *et al.*, 2004; Nagel *et al.*, 2012).

87 Genotypic variation for lateral root phenotypes has functional consequences in maize
88 (Postma *et al.*, 2014; Zhan *et al.*, 2015; Zhan and Lynch, 2015; Jia *et al.*, 2018). Root
89 classes have different elongation rates that vary greatly as a function of time. For
90 maize, lateral roots have been found to elongate at 2.2 cm day⁻¹ for 2.5 days, while
91 nodal roots elongated at a rate of 3 cm day⁻¹ over a 5 week period (Cahn *et al.*, 1989).
92 Under non-impeded conditions primary roots of maize elongated at 4.8 cm day⁻¹, while
93 seminals only elongated at 3.2 cm day⁻¹ (Veen and Boone, 1990). Differences in
94 elongation rates between root types can lead to soils being differentially explored with
95 time by each root type and could affect the volume and depth of bulk soil that can be
96 explored within a certain time by different root types. Biomechanical properties also
97 vary according to root class, with seminal roots being stronger than lateral roots
98 (Loades *et al.*, 2013). Whether this translates to specific penetration ability under
99 impeded soil conditions according to root class remains to be investigated. It has been
100 hypothesised that the contrasting phenotypes of distinct root classes adds to a plants'
101 plasticity and flexibility when interacting with different environments (Chochois *et al.*,
102 2015; Wu *et al.*, 2016) but the functional implications of the differential effects of
103 mechanical impedance on distinct root classes are poorly understood.

104 Root system size differs among genotypes and different soil conditions (Gao and
105 Lynch, 2016; Nakhforoosh *et al.*, 2014). Root system size, expressed as total root
106 length or root length density, can be split between coarse and fine roots (Cahn *et al.*,
107 1989; Steinemann *et al.*, 2015; Varney *et al.*, 1991). Small grain cereals such as wheat
108 or barley are characterised by fine axial roots, maize has thicker axial roots, while
109 dicots and perennials have very coarse axial roots. But for all these species, a
110 distinction between a main root axes and smaller diameter lateral roots can be made.
111 Coarser roots are needed in order to deploy finer roots within the soil profile. Studies
112 on wheat suggest that wheat genotypes with more root axes had greater penetration
113 of wax layers (Whalley *et al.*, 2013).

114 Mechanical impedance not only affects root growth, it also has an impact on shoot
115 growth. Root to shoot ratios can decrease under compaction (Andrade *et al.*, 1993;
116 Hoffmann and Jungh, 1995; Pfeifer *et al.*, 2014a). Aboveground plant growth is
117 impacted as leaf elongation rates can be reduced (Andrade *et al.*, 1993; Young *et al.*,

118 1997) and the rate of leaf appearance decreases (Beemster and Masle, 1996) when
119 roots experience mechanical impedance. The reduction of shoot and root growth due
120 to mechanical impedance can result in decreasing yield (Kirkegaard *et al.*, 1992
121 ;Tuzzin de Moraes *et al.*, 2020).

122 Better root growth under mechanical impedance can be attributed to different traits.
123 For instance, the frictional component of mechanical impedance is reduced when roots
124 produce mucilage or border cell sloughing (Iijima *et al.* 2000, 2004; Bengough and
125 McKenzie, 1997). Smaller root tip radius to length ratios are linked to greater
126 elongation rates under mechanical impedance (Colombi *et al.*, 2017b). Another
127 beneficial trait is the presence of root hairs which can provide anchorage for roots to
128 cross from loose to harder soil layers (Bengough *et al.*, 2011; Haling *et al.*, 2013). Root
129 hairs also maintain water uptake when soils dry (Carminati *et al.*, 2017). Root
130 anatomical traits such as greater cortical cell diameter have been linked to reduced
131 energy costs under impeded conditions (Colombi *et al.*, 2019). It has been suggested
132 that smaller outer cortical cells prevent buckling, which facilitate penetration of harder
133 layers (Chimungu *et al.*, 2015).

134 Genotypes can adjust their root distribution with depth in response to compaction
135 (Barracough and Weir, 1988) however few studies have compared different
136 genotypes and their redistribution of roots under compaction. Little is known about root
137 system size for those root systems that do manage to grow deeper in compacted soils.
138 The hypothesis that rooting depth and root length are not related to each other on
139 compacted plots was tested for deeper rooting genotypes.

140 **2. Material and Methods**

141 **2.1. Plant material and growth conditions**

142 Twelve maize (*Zea mays* L.) recombinant inbred lines from a study by Chimungu *et*
143 *al.* (2015) were selected for different levels of root penetrability of a wax layer. These
144 genotypes were planted in a split-plot design in order to study their root growth in
145 compacted conditions at two field sites. Seeds were obtained from Dr. Shawn
146 Kaepler (University of Wisconsin, Madison WI, USA – Genetics Cooperations Stock
147 Center, Urbana, IL, USA). Genotypes were grown at the Apache Root Biology Centre
148 (ARBC), Willcox Arizona, USA (32°01'N, 109°41'W), planted on June 16, 2016, and
149 the Russell E. Larson Agricultural Research Center in Rock Springs (further referred
150 to as PSU), Pennsylvania, USA (40°42'N, 77°57'W), planted on July 10, 2017. Field
151 sites differed in soil texture, the ARBC site has a soil classified as a Grabe series
152 (coarse-loamy, mixed, superactive, calcareous thermic Torrifuvent) and has a clay
153 loam texture, while the PSU site is classified as a Hagerstown series (silt-loam, fine,
154 mixed, semiactive, mesic Typic Hapludalf) and has a silt-loam texture. Compaction
155 was introduced by passing over the treated plots with heavy machinery. At ARBC a 4
156 wheel tractor (4 tonnes with 8 passes) and at PSU a 3-axle truck (20 tonnes with 4
157 passes) were used. Penetration resistance (Figure 1) as well as an increase of dry
158 bulk density were measured over the soil profile in order to verify increased soil

159 strength and soil density. A FieldScout SC900 Compaction Meter (Spectrum
160 Technologies Inc., Aurora, IL, USA) fitted with a 1/2 inch cone was used to measure
161 the penetration resistance. Dry bulk density was calculated as the mass of oven dried
162 soil per unit soil sample volume (Blake and Hartge, 1986). Soil was oven dried at
163 105°C until a constant weight was achieved. Irrigation was managed on the basis of
164 soil moisture content to avoid water deficit stress (PR2/6-tubes at ARBC (Delta-T
165 Devices Ltd, Cambridge UK) and multiplexed TDR-100 probes at PSU (Campbell
166 Scientific Inc., Logan, UT, USA). PR2/6-tubes were installed on both the compacted
167 and non-compacted plots at ARBC, while TDR-100 probes were installed at a nearby
168 field site on non-compacted conditions to determine if irrigation was needed (Figure
169 S1: gravimetric water contents were calculated from volumetric water contents and
170 soil dry bulk density). As the ARBC field site was based in the desert, the plots were
171 heavily irrigated, while PSU plots did not require any supplemental irrigation. Nutrients
172 and pesticides were applied based on standard agronomic practices (Table S1).

173 **2.2. Root sampling**

174 When all genotypes were tasselling (55 and 51 days after planting for ARBC (coarse-
175 loam) and PSU (silt-loam) respectively) one soil core was taken from each subplot.
176 Coring tubes (60 cm deep, 5.1 cm diameter) fitted with a plastic sleeve (4.5 cm
177 diameter) were driven into the soil between 2 plants in a row (Trachsel *et al.*, 2013).
178 Cores were stored at 4° C until root washing could be carried out, up to a maximum of
179 2 weeks. Cores were divided into six 10 cm increments and roots were washed out of
180 the soil over a 850 µm sieve for each depth profile. Roots were temporarily stored in
181 75% ethanol in water (v/v). Root length per section was measured by scanning roots
182 on a flatbed scanner (Epson Perfection V700 photo, Epson America, Inc., Long Beach,
183 USA) and analysis was carried out with WinRHIZO Pro 2013e system (Regent
184 Systems Inc., Quebec, Canada). Each core increment was captured by images taken
185 at a resolution of 400 dpi (15.75 pxls/mm), speed priority setting off and dust removal
186 on high. Axial roots (nodal, primary, seminal) and lateral roots have been identified
187 as having a diameter >0.6 cm and <1.0 cm for maize respectively (Cahn *et al.*, 1989;
188 Varney *et al.* 1991, Hund *et al.* 2009) and are therefore used instead of the Böhm
189 classification (Böhm, 1979). Using root diameter classes 0 – 0.5, 0.5 – 1.0, 1 – 1.5,
190 1.5 – 2.0, 2.0 – 2.5, 2.5 – 3.0, 3.0 – 3.5, 3.5 – 4.0, >4 mm permitted discrimination of
191 coarse (> 1 mm diameter) and fine (< 1 mm diameter) roots and attributed coarse roots
192 to nodal root classes from the third node and upward. However individual nodal root
193 classes could not be distinguished from cores as there is no reference to root crown
194 position. Root length measurements (total, coarse and fine) and proportions (coarse
195 and fine) were made for the entire soil core. Root distributions were compared on the
196 basis of root length densities measurements within 10 cm increments. D₉₅ and D₇₅ are
197 the rooting depth above which 95 and 75% of the total root length within a core were
198 located. These rooting depth measurements were calculated by linear interpolation
199 (Schenk and Jackson, 2002). When applied to the coarse root fraction in the core, in
200 order to calculate the coarse rooting depth, these measurements are indicated as D_{95c},

201 D_{75c}. An overview of the different measurements directly measured or calculated from
202 the winRHIZO scans and their definition can be found in Table 1.

203 **2.3. Plant sampling**

204 Two plants per subplot (4 replicate subplots per compaction treatment) were sampled
205 at tasselling using the 'shovelomics' method (Trachsel *et al.*, 2011). Subsequent
206 measurements per subplot were obtained by averaging between the two harvested
207 plants per subplot. Root crowns were carefully washed and removed from the stem
208 above the brace roots, brace roots not reaching the soil were clipped off at the base
209 of the stem to expose the crown roots. Root crowns were then imaged to obtain
210 information about the root angle in order to establish that root angle did not affect
211 rooting depth (Figure S2). We used a Nikon D70s camera with a sigma DC 18-50mm
212 lens which produced 4000 x 6000 pxl images. Illumination was achieved by white
213 fluorescent indoor lighting with a white cloth cover for light diffusion. Root angle from
214 the horizontal was manually measured in ImageJ (Schneider *et al.*, 2012). Above
215 ground plant parts were dried at 60° C for 3 days and dry weight of the biomass
216 recorded (Figure S3).

217 **2.4. Statistical Analysis**

218 Genotypes were planted in a completely randomised split-plot design with compaction
219 treatment at the whole-plot level (167.26 m²) and twelve genotypes as subplots,
220 replicated four times in each field site. Each subplot was 3.05 m x 4.57 m and ordering
221 of genotypes (subplots) was randomised within each whole-plot. Every subplot was
222 then planted with 4 rows of the appropriate genotype, with 23 cm within row spacing
223 and 76 cm between row spacing reaching a planting density of approximately 57500
224 plants per hectare. This planting density is sparser than standard agronomic practices
225 which reduced intra-plant competition and aided sampling. All root distribution
226 variables derived from coring (1 soil core per subplot) were transformed using a Box-
227 Cox transformation to achieve normality before analysing the data in a split plot
228 ANOVA. Total root length per genotype was plotted against averaged penetration
229 resistance across both field sites. Root proportions per genotype were plotted per field
230 site and post-hoc comparisons between compacted and non-compacted treatments
231 were carried out using a Tukey HSD test. The same was done for coarse and total
232 rooting depth, where additionally a linear regression was tested between these
233 measurements. A generalised linear model was applied to assess the effect of field
234 site, compaction and genotype and coarse and total root lengths on rooting depth.
235 Relationships between variables were first assessed by correlation plots on pooled
236 data across all genotypes. For the relationship between D₇₅ and D_{75c} an analysis of
237 covariance (ANCOVA) was performed, followed by linear regression. As genotypic
238 effects were identified by the split plot analysis on certain variables, individual linear
239 regressions were made on the averaged genotypic values. Rooting depth data (coarse
240 and total) and total root length averaged per genotype were normally distributed within
241 impedance level and field site datasets. Root proportional data was analysed by using
242 a beta regression (Cribari-Neto and Zeileis, 2015). To further analyse the variable

243 relationships among each other, a principal component analysis (PCA) was conducted
244 within field site – compaction treatment combinations. Principal components were
245 retained based on eigenvalues greater than 1. In order to investigate different types of
246 root distributions under compacted conditions rooting depth data was plotted against
247 total root length data and genotypes with either similar root length and contrasting
248 depth or with similar depth and contrasting root length were identified. An ANOVA was
249 used to test the effect of genotype, compaction, total rooting depth (D_{75}), total coarse
250 rooting depth (D_{75c}), total root length (TRL) and total fine root length (TRL_f) on
251 aboveground biomass. Graphpad Prism (Graphpad Software, 2017) was used for
252 visualising data and R version 3.5.0 (R Core Team, 2018) was used for data analysis.

253 3. Results

254 3.1. Decrease in root length on compacted soil depends on field site

255 Total root length (TRL) from ARBC (coarse-loam) soil cores was greater than the total
256 root length in PSU (silt-loam) cores in both compacted and non-compacted plots
257 (Figure 2, S4). On coarse-loam (ARBC) total root length was reduced by 47.4% on
258 average across all genotypes when grown on the compacted plots and total root length
259 was clearly reduced for each genotype (Figure 2, Table 2). As total coarse root length
260 represents only a small part of the total root length (Figure 2), total root length
261 reduction on coarse-loam (ARBC) is mainly due to reduced total fine root length
262 (Figure 2, Table 2). In contrast, on silt-loam (PSU), compaction did not significantly
263 alter total root length (Table 2), possibly due to greater penetration resistance on both
264 compacted and non-compacted plots in comparison with the coarse-loam (ARBC)
265 plots (Figure S4).

266 Total coarse root length (TRL_c) was differentially affected by the compaction treatment
267 at both field sites (Figure 2, Table 2). A compaction x genotype interaction was present
268 on coarse-loam (ARBC), but not on silt-loam (PSU) (Table 2). The overall average of
269 total coarse root length decreased from $48.9 \text{ cm} \pm 3.4 \text{ (se)}$ to $39.0 \text{ cm} \pm 3.3 \text{ (se)}$ under
270 compaction on coarse-loam (ARBC), while it increased from $16.3 \text{ cm} \pm 2.2 \text{ (se)}$ to 23.7
271 $\text{cm} \pm 3.3 \text{ (se)}$ under compaction on silt-loam (PSU). Total fine root length (TRL_f) was
272 negatively affected by the compaction treatment on coarse-loam (ARBC) (decreasing
273 from $1755.9 \text{ cm} \pm 77.9 \text{ (se)}$ to $809.1 \text{ cm} \pm 37.3 \text{ (se)}$), but was not affected on silt-loam
274 (PSU) (Table 2). At both field sites no genotypic differences were present for total fine
275 root length (Table 2). A positive effect of compaction was noted on overall coarse root
276 proportion (P_c) at ARBC (coarse-loam) with an increase from 2.8% to 4.4% under
277 compacted soil conditions (Table 2, Figure 3). At PSU (silt-loam) we observed an
278 increase from 3.4% to 4.4% for P_c , (Figure 3) although no compaction treatment effect
279 was noted (Table 2). Genotype had significant effect on the proportion of coarse roots
280 (P_c) and fine roots (P_f) at both field sites and for coarse-loam (ARBC) there was an
281 interaction between compaction treatment and genotype present (Table 2).
282 Compaction increased the proportion of coarse roots for most genotypes (Figure 3).
283 The only genotype that had greater P_c under impeded conditions at both field sites
284 was IBM051. Other genotypes manifesting increased P_c under impeded conditions

285 were OhW122, OhW119, NyH126, IBM146 and IBM059 at ARBC (coarse-loam), but
286 these did not show increased P_c in silt-loam (PSU). In silt-loam (PSU) other genotypes
287 such as OhW128 and IBM284 increased their P_c , while they did not in coarse-loam
288 (ARBC). A genotype that did not have greater coarse root proportions in response to
289 compaction in either location was IBM086, this genotype had similar coarse root
290 proportions in coarse-loam (ARBC), while in silt-loam (PSU) the coarse root
291 proportions appeared smaller under compaction.

292 **3.2. Total rooting depth versus coarse rooting depth**

293 Absolute and relative measures of root length density per depth increment provided
294 insight into how roots were growing within the soil profile and how root distributions
295 change in response to compaction (Figure 4). Root distribution changes became
296 clearer when relative root length density measures were considered (Figure 4B-D).
297 Distributions of coarse root length density and root length density differed (Figure 4)
298 illustrated by differences in values of D_{95} and D_{75} (rooting depth considering all roots
299 diameter classes) versus D_{95c} and D_{75c} (rooting depth considering coarse roots) (D_{75}
300 and D_{75c} shown in figure 4, 5). Total rooting depth and coarse rooting depth
301 measurements were correlated (Figure 5F). D_{75} and D_{75c} were significantly reduced
302 by compaction at both locations, while D_{95} and D_{95c} were only reduced at ARBC
303 (coarse-loam) (Table 2). A genotypic effect on rooting depth was present in coarse-
304 loam (ARBC), but absent in silt-loam (PSU) (Table 2). On coarse-loam (ARBC) some
305 genotypes had significantly shallower total and coarse rooting depths under impeded
306 conditions (IBM014, IBM059, IBM146, OhW119, OhW122) (Figure 5A-C). Other
307 genotypes such as OHW128 had shallower total root length under impeded conditions,
308 but coarse rooting depth was not significantly reduced (Figure 6C). In contrast,
309 IBM323, IBM178, IBM284 and IBM086 had shallower coarse rooting depth under
310 compaction, but total rooting depth was not reduced (Figure 5A-C). On silt-loam (PSU)
311 an effect of compaction was present on D_{75c} and D_{75} (Table 1), however only
312 genotype, IBM059, showed significantly shallower coarse root distributions (Figure
313 5B).

314 **3.3. Relationships between root distribution variables**

315 Relationships between the different variables can be further explored through the
316 correlation plot across all genotypes (Figure S5, S6, S7) as well as the PCA plots per
317 field site with treatment combination (Figure S8). Individual linear regressions between
318 root distribution variables depicting the different genotypes can be found in Figures 6,
319 S6 and S7. Across all field sites and levels of compaction rooting depth variables (D_{95} ,
320 D_{75} , D_{95c} and D_{75c}) positively correlated to each other (Figure S8). Likewise root length
321 variables total root length (TRL), total fine root length (TRL_f) and total coarse root
322 length (TRL_c) correlated strongly with each other (Figure S8). Relationships between
323 rooting depth and the other root distribution variables are discussed below.

324 **3.3.1. The relationship between total rooting depth and other root distribution** 325 **variables**

326 A negative relationship between total root length and total rooting depth was found
327 under ARBC (coarse-loam) non-compacted conditions at a probability of 0.10 (Figure
328 6A, S5). General linear modelling indicated integrative effects of field site and
329 compaction on the relationship between total root length and total rooting depth (Table
330 3). As total root length mainly consists of fine roots, a relationship persists between
331 total fine root length and total rooting depth (Figures S6). No such relationship was
332 seen on silt-loam (PSU) or under compaction (Figures 6B, S6). No relationship was
333 found for total rooting depth and total coarse root length (Figure S6C-D) and coarse
334 root proportion (Figure S6E-F) under any scenario.

335 **3.3.2. The relationship between coarse rooting depth and other root distribution** 336 **variables**

337 A positive relationship between coarse root proportion and coarse rooting depth (D75_c)
338 was present under non-compacted conditions at the coarse loam (ARBC) field site
339 (Figure 6C). This correlation was not observed under compacted conditions, nor at the
340 other field site (Figure 6C-D). Coarse rooting depth was also not correlated with total
341 root length, total coarse root length or total fine root length under any of the field site
342 with compaction treatment combinations (Figures 6E-F, S7). This could also be
343 deduced from the general linear model (Table 3).

344 **3.4. Root length density distributions show field-site dependent genotypic** 345 **adjustments to compacted conditions**

346 Genotype had an effect on coarse rooting depth on coarse-loam (ARBC) but on silt-
347 loam (PSU) (Table 2). Coarse (Figure 7) and total (Figure S9) root length distributions
348 over the soil profile at PSU (silt-loam) had smaller root length densities than on coarse-
349 loam (ARBC). Distribution differences with depth between genotypes were less
350 evident on silt-loam (PSU) (Figure 7), no significant statistical effect of genotype alone
351 was noted on D₇₅ or D_{75c} (Table 2), which could be attributed to larger standard errors
352 at PSU (Figure 5D) and generally less roots found. The general linear model (Table
353 3) shows that genotype in combination with other factors did have a significant effect
354 on D_{75c}. Different genotypes were found from each field site that showed similar
355 coarse root length but contrasted in root depth or showed similar coarse root depth
356 but contrasted in total root length. (Figure S10). For these measurements we observed
357 genotypes with similar total coarse root length, but different rooting depths
358 representing shallow and deeper root systems with similar root system sizes (IBM284
359 versus IBM323 for coarse loam (ARBC) and IBM051 and OhW122 for silt-loam (PSU))
360 (Figure 8A). A similar analysis was carried out based on total root length and depth
361 (Figure S11, S12).

362 **3.5. Relationship between root distribution variables and aboveground** 363 **biomass**

364 Compaction influenced aboveground biomass significantly (Figure 9, S2) but could
365 also be related to other root measurements derived from coring. For both coarse-loam
366 (ARBC) and silt-loam (PSU) soils, plant biomass was higher when coarse roots were

367 able to grow deeper due to being less impeded (Figure 9). In coarse-loam (ARBC)
368 however TRL_f also played a role, while in silt-loam (PSU) greater plant biomass was
369 reached on non-compacted plots without TRL_f having a role.

370 **4. Discussion**

371 In this study, on two different soils with compacted and non-compacted plots, we found
372 total root length reduction due to compaction f was field site dependent (Figures 2,
373 Table 2). Coarse root proportions were influenced by genotype at both field sites
374 (Figure 4, Table 2). Rooting depth of coarse and total roots were strongly correlated
375 (Figure 5). Root length and rooting depth variables were not correlated when plants
376 were grown on compacted plots (Figures 6, S5, S6, S7, S8). Our results support the
377 hypothesis that the ability of roots to grow to depth through compacted soils is not
378 dependent on the amount of roots formed by the root system. Furthermore, we
379 propose that root length density distributions are either characterised by avoidance or
380 by adaptive strategies for different genotypes when grown in compaction.

381 **4.1. Root phenotypes show high levels of plasticity**

382 **4.1.1. Field site effects on root systems**

383 Total root lengths (TRL), total fine root lengths (TRL_f) and total coarse root lengths
384 (TRL_c) were greater on coarse-loam (ARBC) than on silt-loam (PSU) (Figures 2, S6).
385 The significant reduction of the fine root length due to compaction on coarse-loam
386 (ARBC) could influence the proportions of fine and coarse roots. Greater changes in
387 coarse root proportions were observed at ARBC (coarse-loam) versus PSU (silt-loam)
388 (Figure 3), which could potentially be driven by a disproportionately greater reduction of
389 total fine root length versus that of total coarse root length (causing a shift towards
390 greater proportion of coarse roots). Rooting depths $D75$ and $D75_c$ were different at the
391 two field sites (Figures 5, S6, S7, Table 3). Differences between field sites for
392 observations considering root length, root proportions and root depth could be related
393 to differences in soil parameters. Maize seedlings had significantly longer seminal
394 roots in a sandy loam versus a sandy clay loam (Panayiotopoulos *et al.*, 1994) while
395 rooting depths of grapevines were deeper in coarse textured soils than fine textured
396 soils (Nagarajah, 1987). Greater root length was possibly attained on coarse-loam
397 (ARBC) because of the greater sand fraction in the soil versus silt-loam (PSU).
398 Another possible explanation for the root length differences between coarse- and silt-
399 loam could be a difference in root-soil contact between the field sites. On the non-
400 compacted plots of PSU (silt-loam), smaller dry bulk densities could mean reduced
401 levels of root-soil contact, which in turn reduces water and nutrient uptake (Veen *et*
402 *al.*, 1992). The coarse-loam field site (ARBC) consisted of a more uniform, less
403 structured soil, while the silt-loam field site (PSU) had more pronounced soil structure
404 in terms of aggregation observed in the field. Roots can take advantage of cracks or
405 bio-pores from earthworms or old root channels present to bypass compacted layers
406 (Atwell, 1993; Hatano *et al.*, 1988; Stirzaker *et al.*, 1996). Cracks and pores will impose
407 lower axial pressures on roots than bulk soil (Jin *et al.*, 2013). It is likely that the

408 presence of such low-resistance channels in the soil structure at PSU (in silt-loam)
409 could have permitted deeper rooting than at ARBC (coarse-loam).

410 **4.1.2. Compaction influences root system distribution**

411 Compaction influenced root growth at both field sites, but more significantly at ARBC
412 (coarse-loam), where all rooting variables were significantly affected (Table 2). At both
413 field sites the compaction treatment influenced the average total coarse root length
414 across genotypes in different ways (Figure 3, Table 2). Total coarse root length
415 decreased on coarse-loam (ARBC), which could be due to the effect compaction had
416 on root system size in general. Total and fine root length were more significantly
417 reduced than total coarse root length under compaction (Table 2, Figure 2).
418 Reductions in root length in compacted soil has been reported for different species
419 including maize (Grzesiak, 2009; Iijima and Kono, 1991). At PSU (silt-loam) total and
420 fine root length were not significantly affected by compaction (Table 2) and total coarse
421 root length increased (Figure 3, Table 2). Increased total coarse root length could
422 potentially be caused by radial expansion as roots generally increase in diameter when
423 experiencing mechanical impedance. Elongation is slowed compared to elongation
424 rates at lower levels of mechanical impedance, which in turn decreases root length
425 (Bengough *et al.*, 2006; Bengough and Mullins, 1991; Bengough and Young, 1993).
426 While all root length measures decreased on coarse-loam (ARBC), these observations
427 on root length were different on silt-loam (PSU) where fine and coarse roots were
428 differentially affected by the compaction treatment. Coarser roots such as seminal or
429 nodal root axes were more impeded than lateral roots possibly reflecting the fewer
430 macropores present under compacted conditions. Such effects have been found in
431 barley growing in glass ballotini of different sizes, with larger pores only restricting
432 seminal growth and smaller pores restricting both laterals and seminal growth of barley
433 (Goss, 1977). Laterals capable of growing in pores larger than their own diameters
434 would encounter less impedance than those laterals forced to grow through bulk soil
435 or smaller pores (Iijima and Kono, 1991).

436 Under compaction both rooting depth (D_{75}) and rooting depth of coarse roots (D_{75c})
437 decreased at both field sites (Tables 1, 2; Figures 5, 6, S6, S7). Reduction of D_{75c} due
438 to compaction could be linked to reduced aboveground biomass (Figure 9). Shallower
439 rooting depths probably reflect slower root elongation rates, so it will take longer for a
440 root to reach deep soil strata. Smaller differences in rooting depth of compacted and
441 non-compacted plots at PSU (silt-loam) (Figure 5) could be due to the smaller
442 differences in penetration resistance with increasing depth versus ARBC (coarse-
443 loam) (Figure 1). Roots at the PSU field site (silt-loam) would initially experience
444 greater levels of mechanical impedance, but once they pass this zone should be able
445 to elongate more normally. The reduction in rooting depth under compaction is in
446 agreement with observations with wheat (Barraclough and Weir, 1988; Chen *et al.*,
447 2014). Compaction altered root distribution, generally shifting root distribution to
448 shallower strata (Figures 4, 5, 7, S9). Multiple studies have described similar
449 redistributions of roots under impeded field conditions for various crops (Barraclough

450 and Weir, 1988; Brereton *et al.*, 1986; Chen and Weil, 2011; Chen *et al.*, 2014). For
451 maize specifically, roots of 2-3 week old plants were confined to surface layers under
452 compaction (Veen and Boone, 1990). A similar observation was made during a 4 week
453 growing period for maize grown in root boxes (Iijima *et al.*, 1991) and in the field up to
454 tasselling (Laboski *et al.*, 1998). Soil compaction reduces soil porosity, hydraulic
455 conductivity and air permeability and this increases the risk of hypoxia (Laboski *et al.*,
456 1998; Kuncuro *et al.*, 2014; Xiong *et al.*, 2020). In this set-up of compacting entire field
457 sites, the stress caused by impedance and hypoxia cannot be mutually excluded.
458 Therefore hypoxia might also have played a role in reducing growth of the root system.
459 A recent studies by Xiong *et al.* (2020) illustrates that higher moisture contents
460 negatively influenced root growth in compacted soils.

461 **4.1.3. Compaction influenced genotypes differently**

462 Under compaction at both field sites most genotypes had a greater proportion of
463 coarse roots (Figure 3) and genotypes differed in this response (Table 3). An
464 increased proportion of coarse roots could either be attributed to (1) the reduction of
465 the fine root proportion, (2) the increase in diameter of roots grown under impeded
466 conditions due to thickening or (3) a combination of the two. On coarse-loam (ARBC),
467 total fine root length was significantly reduced (Table 3, Figure 2), which in turn would
468 influence root proportions. However, as there was no such reduction of total fine root
469 length on silt-loam (PSU), root thickening, which is the increase in radial diameter of
470 the roots, is probably the main cause of a shift in root proportions on silt-loam.

471 Genotypic differences were found for total and coarse rooting depth variables (Figures
472 5, 7, 8, S6, S7, Tables 2, 3). No relationship between root length variables existed
473 (with the exception of negative relationship between total root length and total rooting
474 depth under non-compacted conditions at ARBC (coarse-loam)). Deeper rooting was
475 not associated with root system size. Root phenes that have been found to contribute
476 to overcoming impedance include anatomical traits such as reduced cell file number
477 and increased levels of aerenchyma (Lynch and Wojciechowski, 2015; Vanhees *et al.*,
478 2020) and is thought to be linked to reduction of metabolic costs, reduced energy
479 and/or facilitating O₂ diffusion (Hanbury and Atwell, 2005; Lynch, 2015; Colombi *et al.*
480 *et al.*, 2019). It has also been suggested that anatomical traits such as smaller outer
481 cortical region cells will stabilize a root during the penetration of a harder soil layers
482 (Chimungu *et al.* 2015). Other phenes are sharper root tip shape, the presence of root
483 hairs, the production of mucilage, root cap sloughing and steeper growth angles
484 (Bengough *et al.*, 2011; Colombi *et al.*, 2017b; Haling *et al.*, 2013; Iijima *et al.*, 2000,
485 2004; Jin *et al.*, 2013, Lynch and Wojciechowski, 2015). How all these phenes can
486 synergistically work together is worthy of further investigation. Other studies have
487 shown that plasticity could play a role, for instance for rice it was observed that upon
488 rewetting after drought differences in nodal root elongation through a hardpan were
489 present between genotypes (Suralta *et al.*, 2018).

490 **4.2. The relationship between root length and root depth varies among** 491 **genotypes**

492 Root length and rooting depth are not related under impeded conditions (Figures 6,
493 S6, S7, S8). Coarse rooting depth, representing nodal roots, responded differently to
494 compaction among genotypes. Genotypes such as IBM059 or IBM323 at ARBC
495 (coarse-loam) or IBM086 at PSU (silt-loam) grew deeper under non-compacted
496 conditions but reduced their coarse root length under compaction (Figure 5A-B).
497 IBM178 grew intermediately deep in coarse-loam (at ARBC), and deep in silt-loam (at
498 PSU) but did not reduce its coarse rooting depth to the same extent as the
499 aforementioned genotypes (Figure 5A-B). This suggests that coarse roots of some
500 genotypes were obstructed by the compaction treatment while coarse roots of other
501 genotypes were capable of growing through.

502 We found genotypes with similar root system size that reached different rooting depths
503 (Figure 8A, S12) as well as genotypes with similar deeper coarse rooting depth but
504 with different total coarse root length (Figure 8B, S12). Coarse rooting depths can thus
505 be reached in different ways as the root system with smaller values for coarse root
506 length densities were able to grow as deep as the root systems that have greater
507 coarse root length density at depth. Shoots can be sustained by different root system
508 sizes and rooting depths as long as water and nutrients are available. Therefore
509 rooting depth under compaction is not simply related to the amount of roots formed. In
510 the following section we discuss how each type of root distribution with depth could
511 sustain plant growth.

512 **4.2.1. Root systems with equal coarse root length reach different depths**

513 Coarse roots of some genotypes were obstructed, while others managed to grow
514 through impeded soil domains and reached deeper strata (Figure 8A). If nodal roots
515 are sufficiently impeded, these and any laterals roots emerging from them will
516 automatically be located within the upper soil strata. However laterals may grow
517 downwards from a shallow starting point when they experience less impedance than
518 nodal roots by, for instance, making use of smaller pores (Goss, 1977). Increased
519 lateral branching has been observed in the non-impeded parts of the soil (Montagu *et*
520 *al.*, 2001) and will enable a plant to extract water and nutrients when root length is
521 maintained and sufficient soil resources are available in the unimpeded soil
522 (Barraclough and Weir, 1988). Compensatory root growth introduces more roots in the
523 less impeded domains, often in the upper soil strata (Barraclough and Weir, 1988;
524 Materechera *et al.*, 1993; Nosalewicz and Lipiec, 2014; Pfeifer *et al.*, 2014a). A similar
525 redistribution can be seen in the compacted plots (Figures 7, S9). Compensatory
526 mechanisms may influence nutrient and water acquisition.

527 Rooting depth has been linked to water acquisition, especially under drought
528 conditions where deeper rooting increases yield (Gao and Lynch, 2016; Hund *et al.*,
529 2009; Lynch, 2013, 2018; Chimungu *et al.*, 2014a, 2014b; Lynch *et al.* 2014; Zhan *et*
530 *al.*, 2015). Our study did not employ a water deficit, but it has been shown that
531 compaction can make water deficit stress more severe (Grzesiak *et al.*, 2014): even
532 without the presence of water deficit stress, increased water uptake from the topsoil
533 can be present on compacted soils. This in turn will increase the penetration resistance

534 within the topsoil and further limit access to the deeper soil layers (Colombi *et al.*,
535 2018). A root system that is limited to shallow soil strata will thus be more at risk for
536 water deficit both in terms of reduced access, as well as increased water depletion in
537 its local soil environment. It is likely that in the coarse soil (ARBC) compacted
538 treatment the air-filled porosity was often <10% in the surface 20cm, but generally
539 >10% in the other treatments. The root system might therefore have been influenced
540 by poor oxygen availability (hypoxia) however this can be seen as common feature of
541 compacted soils in the field where porosity is reduced. Clear shifts in root distribution
542 occurred in our field sites, we observed changes in root proportion, changes in rooting
543 depth, and changes in root distribution (Figures 3, 5, 7, S9). How these shifts influence
544 resource acquisition under impeded field conditions merits further investigation.

545 Stresses such as waterlogging have been found to have a more severe impact in
546 impeded soils (Grzesiak *et al.*, 2014). Environmental effects such as temperature
547 fluctuations or soil drying by direct evaporation pose additional threats to more shallow
548 root systems (Lynch, 2018). Overall compensatory root growth can be seen as a stress
549 avoidance strategy as plants come less into direct contact with the impeded soil
550 regions and grow where impedance is lower. This can be considered as an indirect
551 adaptation or response to the impeding conditions. As soils are a typically
552 heterogeneous, roots could take advantage of cracks or pores present to bypass
553 compacted layers (Hatano *et al.*, 1988; Atwell, 1993; Stirzaker *et al.*, 1996) which
554 would be another avoidance strategy. Rasse and Smucker (1998) showed that maize
555 can make use of root-induced macropores from a previous alfalfa crop. Preferential
556 growth towards artificial pores has been observed in compacted soils (Stirzaker *et al.*,
557 1996; Pfeifer *et al.*, 2014b; Colombi *et al.*, 2017a; Atkinson *et al.*, 2020) but whether
558 this is due to oxytropism or locally reduced penetration rates is still under debate,
559 although promising attempts have been made to model the process (Landl *et al.*,
560 2017). Roots adapted to impedance are characterised by traits that help them
561 overcome impedance, enabling them to grow better in harder soils. Those genotypes
562 capable of rooting deeper and of overcoming impedance stress are at less at risk of
563 nutrient deficiencies, of lack of access to water and of other environmental stresses.

564 **4.2.2. Equal depths can be reached by root systems of different sizes**

565 We observed genotypes that contrasted in root system size (measured as total coarse
566 root length) were able to reach similar depths on compacted plots (Figure 8B, S12).
567 Greater amounts of coarse roots (measured as greater TRL_c) would be found when a
568 maize plant forms more root axes per nodal position, additionally greater amounts of
569 coarse roots may also be caused by root thickening. We found that no rooting depth
570 measure correlated with TRL_c (Figures 6E-F, S6A-D, S7). The ability of a root system
571 to grow deeper in compacted soils is therefore not dependent on the amount of roots
572 formed as both large and parsimonious root systems can reach similar depths on
573 compacted plots at both field sites. This is in contrast with observations on wheat,
574 where penetrability of a harder wax layer was related to amount of root axis formed
575 (Whalley *et al.*, 2013), or that denser root systems of lupin are deeper rooting (Chen

576 et al., 2014). On the other hand, comparisons between species show that species with
577 a larger number of roots in the top layers of a layered medium did not automatically
578 have greater penetration rates through the compacted layer (Materchera *et al.*,
579 1993). A field study with two rice varieties showed that varieties with a greater root
580 density were able to root deeper under control conditions, but under greater
581 penetrometer resistances became more strongly affected than others with lower
582 rooting densities (Cairns *et al.*, 2004).

583 The formation of more roots can have benefits such as increased foraging for water
584 and nutrients or reduced risk of root loss due to pests and diseases (Lynch, 2003,
585 2018, 2019). Increased root formation can however come at a substantial costs (York
586 *et al.*, 2013, Lynch, 2003). Greater elongation rate, greater root diameter, increased
587 branching or greater formation of axial roots increase the metabolic cost of the root
588 system (York *et al.*, 2013, Lynch, 2018). Second, the formation of too many roots will
589 introduce competition for internal and external resources (Lynch, 2018). Excessive
590 root formation not only induces intraplant competition for resources, it also increases
591 root maintenance and formation costs. Other traits, such as increased aerenchyma
592 formation, large cortical cell size, reduced cortical cell file number or reduced crown
593 root number bring costs down (Lynch, 2003, 2018) which would enable these plants
594 to allocate resources elsewhere. For instance, it has been shown that maize with fewer
595 crown roots are able to allocate roots deeper (Saengwilai *et al.*, 2014; Gao and Lynch,
596 2016, Lynch 2018). Recent experiments by Guo and York (2019) showed excising
597 nodal roots stimulated greater shoot biomass and root length at depth under low N
598 conditions as biomass was reallocated to lateral and early nodal roots. Under impeded
599 conditions, metabolic cost reduction might be significant. A recent study by Colombi
600 (2019) found energy costs were linked to cortical cell diameters, with greater cell
601 diameters reducing the metabolic cost under impeded conditions. As both large as
602 well as parsimonious root systems were able to reach similar coarse root depth
603 (Figures 8B, S12B) we suggest that parsimonious phenotypes could potentially
604 allocate more resources to shoot growth. This effect could be apparent under high
605 input systems, where improved conversion of soil resources to yield would be greater
606 for parsiminous phenotypes (Lynch and Brown, 2012; Lynch, 2018).

607 **Conclusions**

608 Rooting depth and root length were not correlated under impeded conditions. Different
609 coarse rooting depths were reached by genotypes characterised by similar root
610 system sizes. We suggest genotypes better adapted to impedance (and therefore
611 rooting deeper) are less at risk of additional stresses such as nutrient deficiency, soil
612 drying, lack of access to water and other environmental conditions. We hypothesise
613 that excessive root formation will introduce greater competition for internal and
614 external resources, furthermore larger root systems have greater metabolic costs
615 associated with them. We also suggest that parsimonious phenotypes will be able to
616 steer resource allocation to shoot growth and improved yields. We found that the

617 amount of roots formed by the root system does not determine the ability of those roots
618 to grow deeper under impeded conditions.

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626

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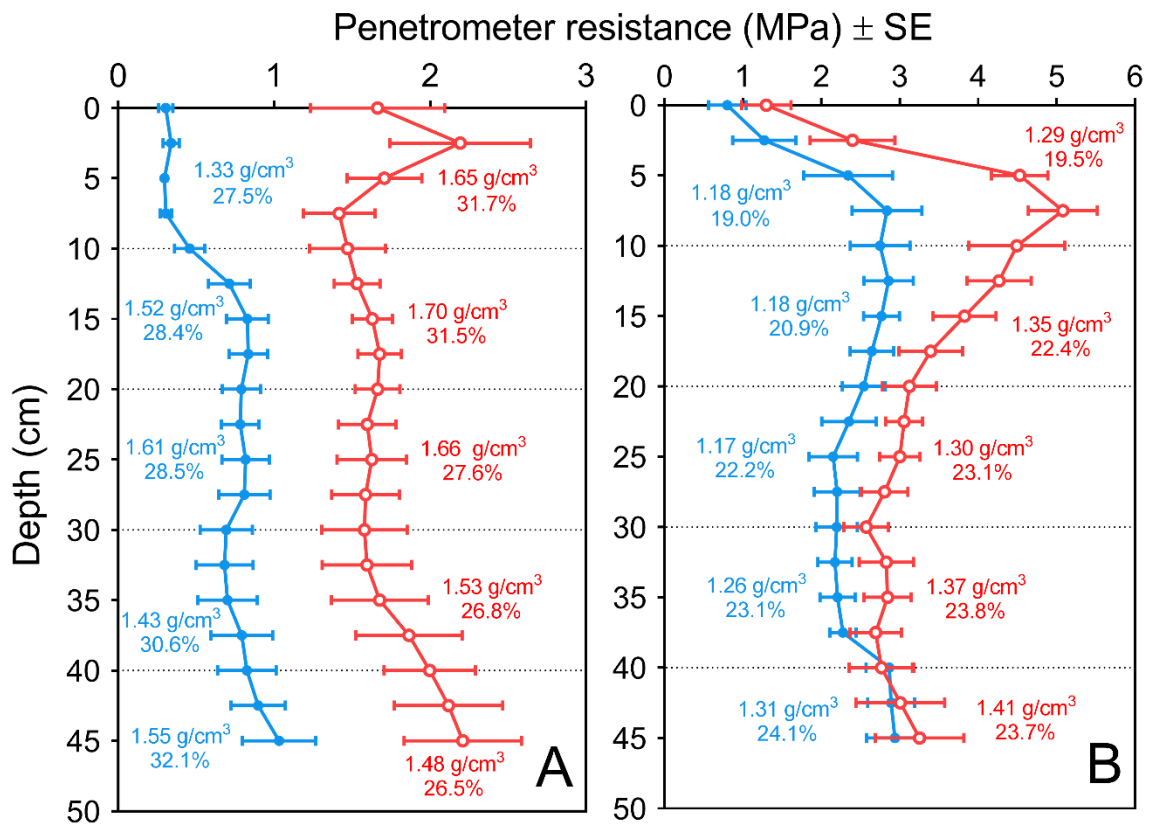
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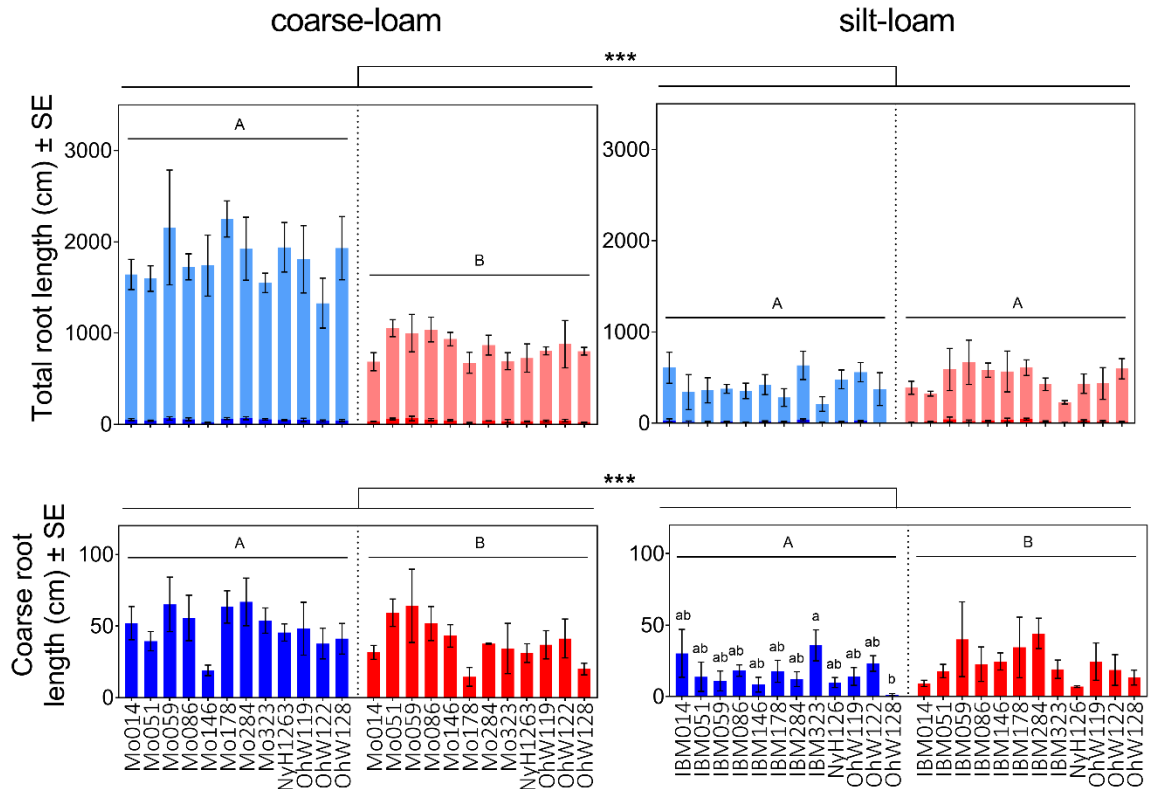
1018 Figures



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1020 **Figure 1** – Average penetrometer resistances ± SE for compacted (red) and non-
1021 non-compacted (blue) treatments at (A) the ARBC field site (coarse-loam) and (B) the PSU
1022 field site (silt-loam) before planting. Mean soil moisture content (v/v) was measured
1023 for each 10 cm increment, together with soil dry bulk density, both written on graph
1024 within relevant depth ranges. Figure adopted from Vanhees *et al.* (2020).

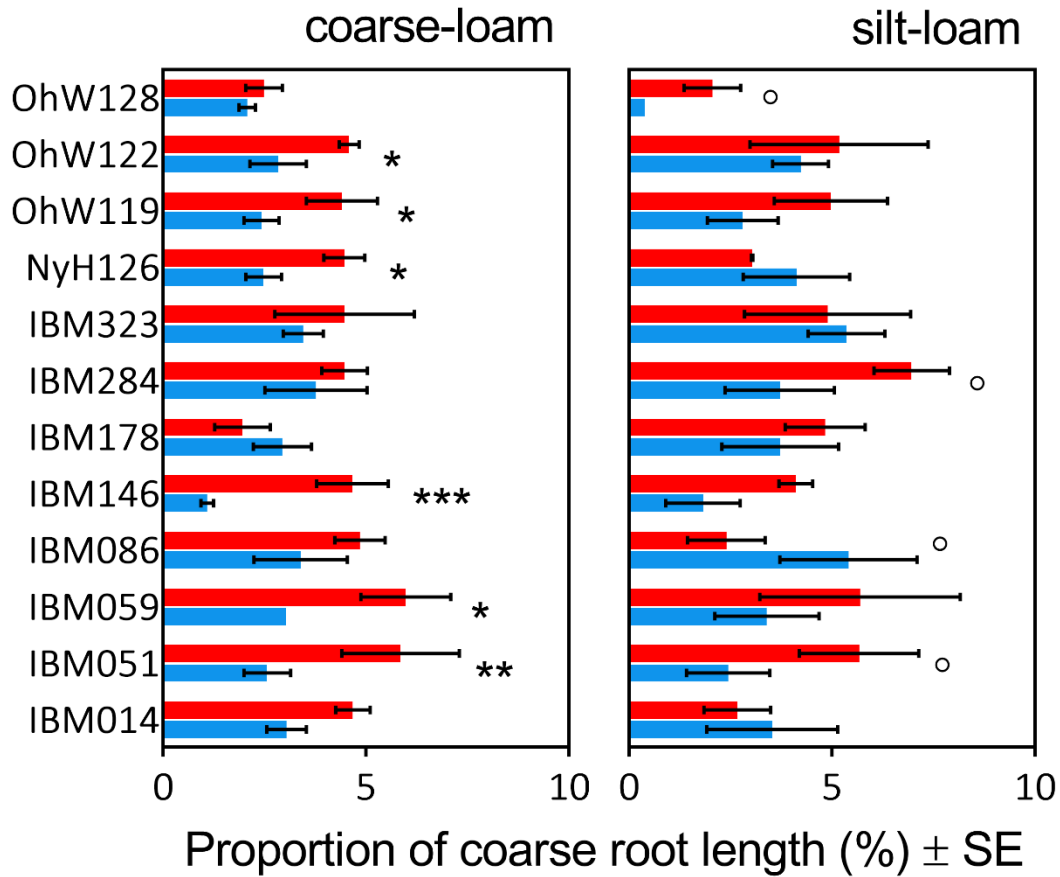
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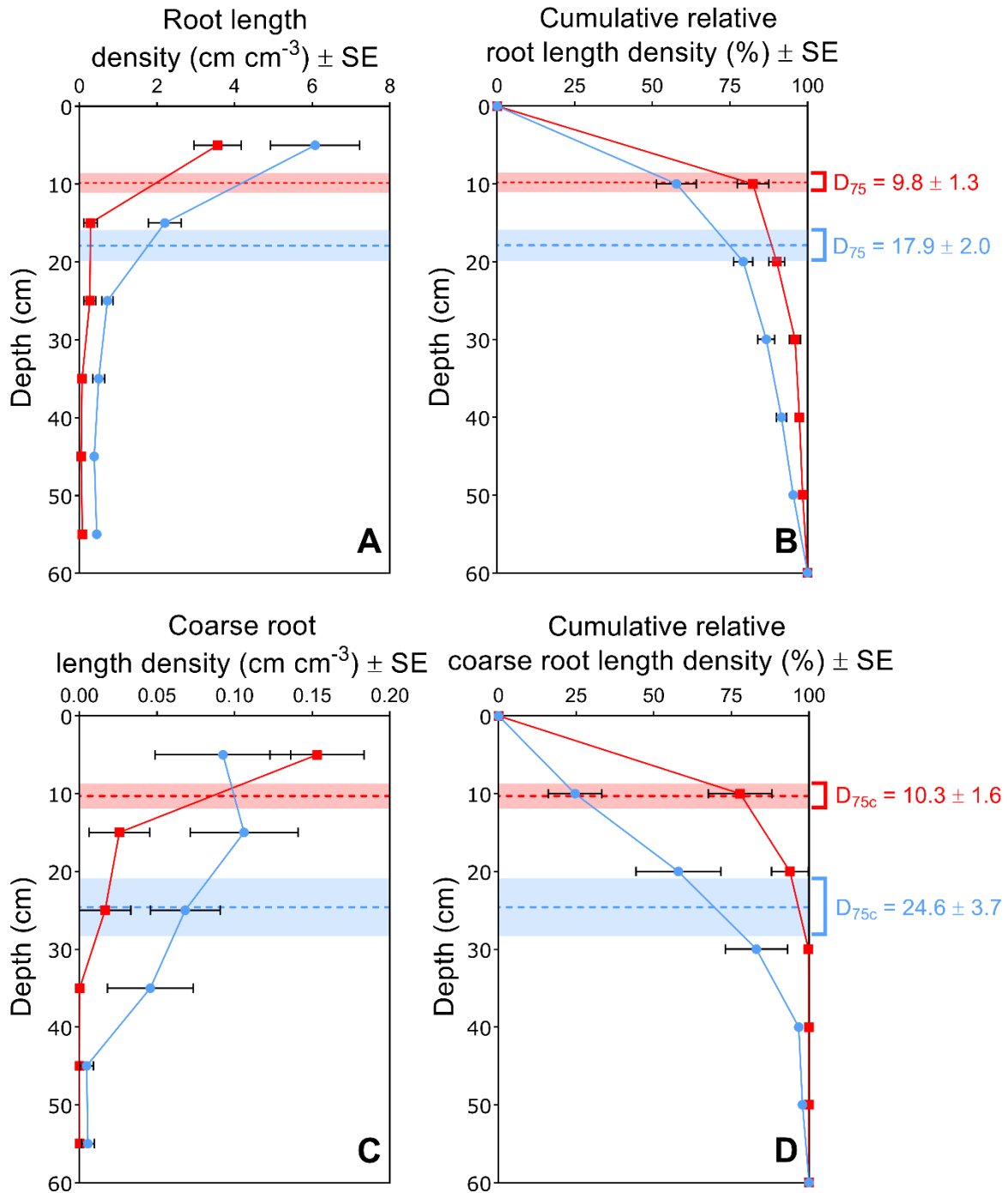
1027 **Figure 2** - Average total root length (cm) ± SE split into coarse (dark blue, dark red)
 1028 and fine (light blue and light red) root length (cm) for maize genotypes tested at
 1029 acoarse-loam (ARBC) versus silt-loam (PSU) field site. Coarse roots are defined as
 1030 having diameters larger than 1 mm, while fine roots are those with diameter smaller
 1031 than 1 mm. Compacted measurements in red, non-compacted measurement in blue.
 1032 Error bars represent standard deviations. If differences between the field sites (***, p
 1033 ≤ 0.001), treatments (A/B, $p \leq 0.05$) and genotypes (a/ab/b, $p \leq 0.05$) were present.

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Figure 3 – Proportions of coarse (>1.0 mm diameter) root length (%) ± SE found in cores of different genotypes in two field sites. Non-compacted data in blue, compacted data in red. IBM059 (coarse-loam at ARBC) and OHW128 (silt loam at PSU) have such small standard errors they could not be visualised. Post-hoc Tukey comparisons within field site indicate when treatment effect was significant for each genotype at significance level ° $P \leq 0.10$, * $P \leq 0.05-0.01$, ** $P \leq 0.01-0.001$, *** $P \leq 0.001$.



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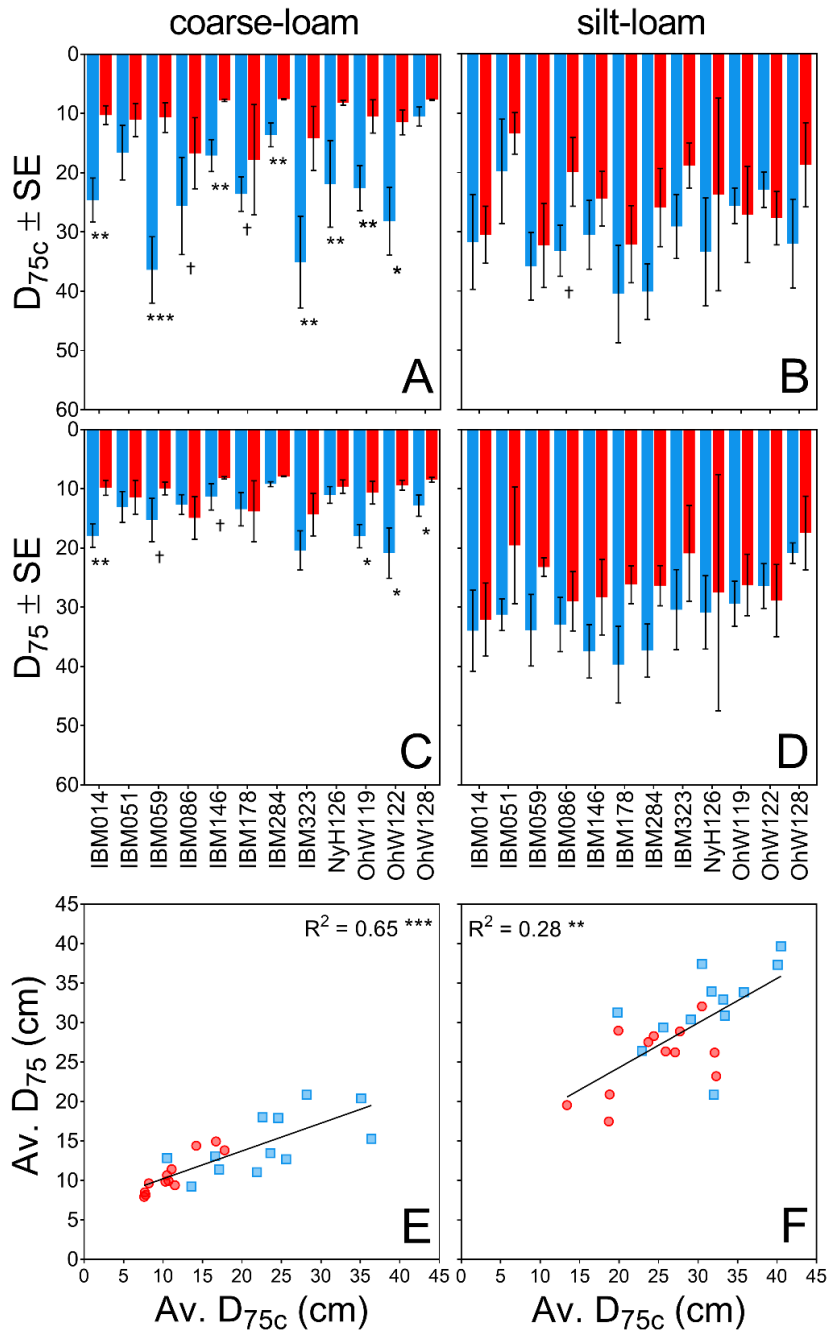
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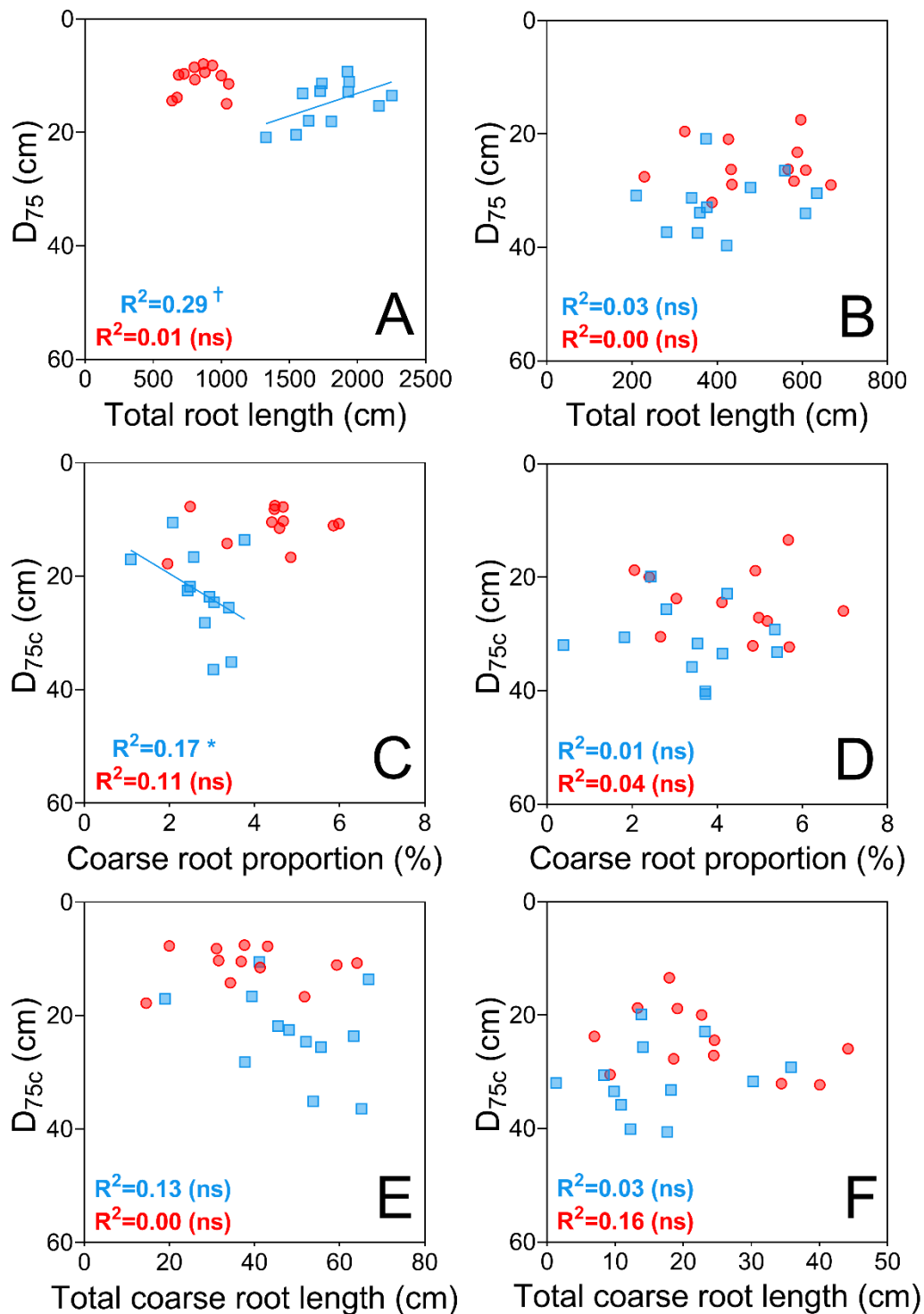
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Figure 4 – Illustration of difference between absolute versus relative root length density distributions for genotype IBM014 considering total root length and coarse root length at the coarse-loam field site (ARBC). (A) + (C) Absolute distributions of root length densities, (B) + (D) Relative distributions of root length densities. Compacted data in red and non-compacted data in blue. Error bars represent standard errors. The rooting depth (cm) ± SE where 75% of the total root length (D_{75}) or coarse root length (D_{75c}) was visualised by the striped line, coloured region represents SE for the depth measurements. No error bars shown when standard error was too small to visualise.



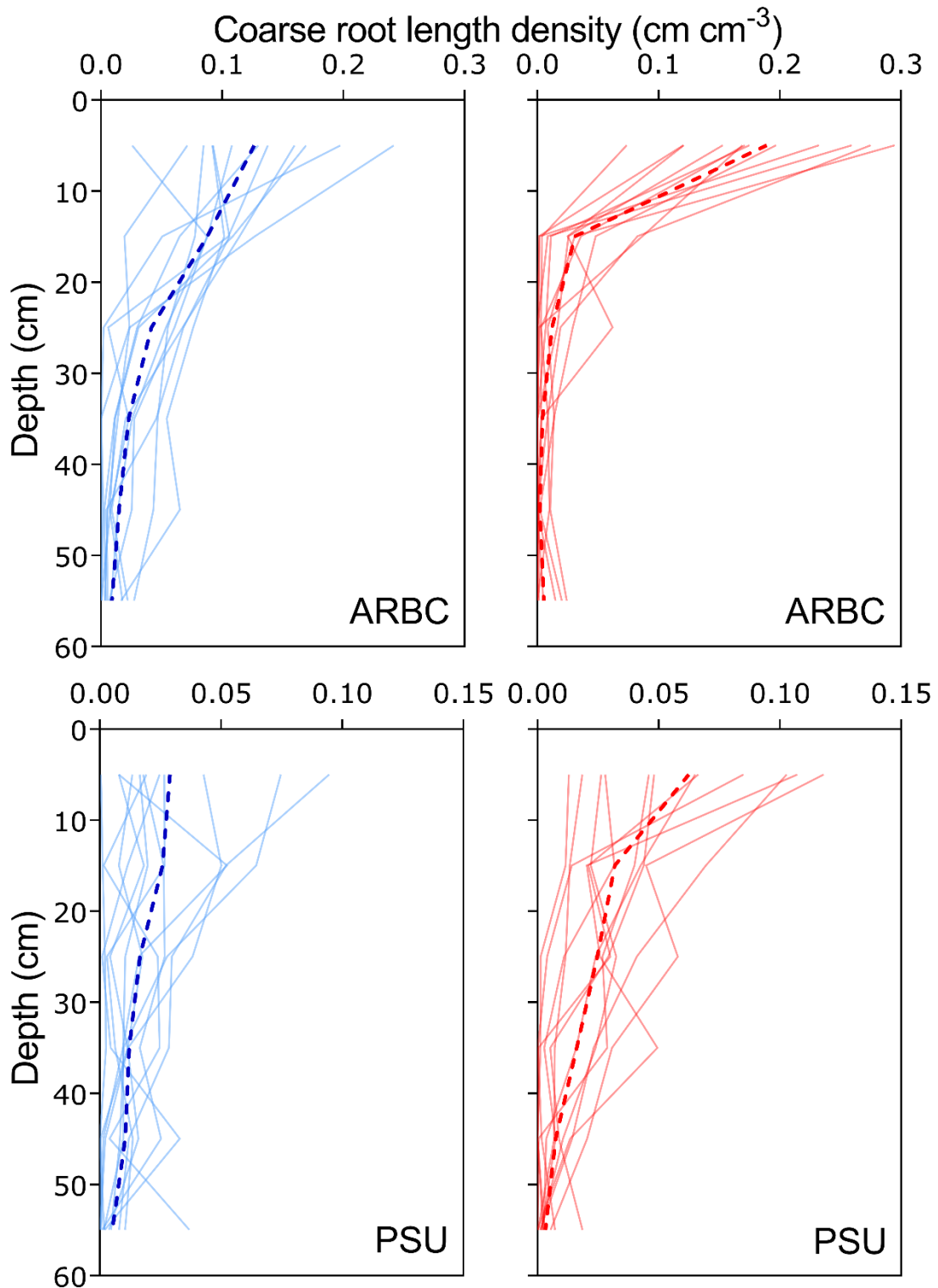
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1054 **Figure 5** – Coarse and total rooting depth and their correlation for both field sites under
 1055 compaction (red) and non-compacted (blue) conditions.. (A) + (B) Average coarse
 1056 rooting depth (D_{75c}), (C) + (D) Average total rooting depth, (E) + (F) Correlation
 1057 between D_{75} and D_{75c} . Error bars represent standard errors. (A) + (C) + (E): ARBC
 1058 field site (coarse-loam) and (B) + (D) + (F): PSU field site (silt-loam). Post hoc Tukey
 1059 comparisons between compaction and noncompaction within each field site for each
 1060 genotype were carried out on rooting depth data (panels A-D). Coarse and total rooting
 1061 depth are correlated (E-F) Levels of significance + $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$, ***
 1062 $P \leq 0.001$.



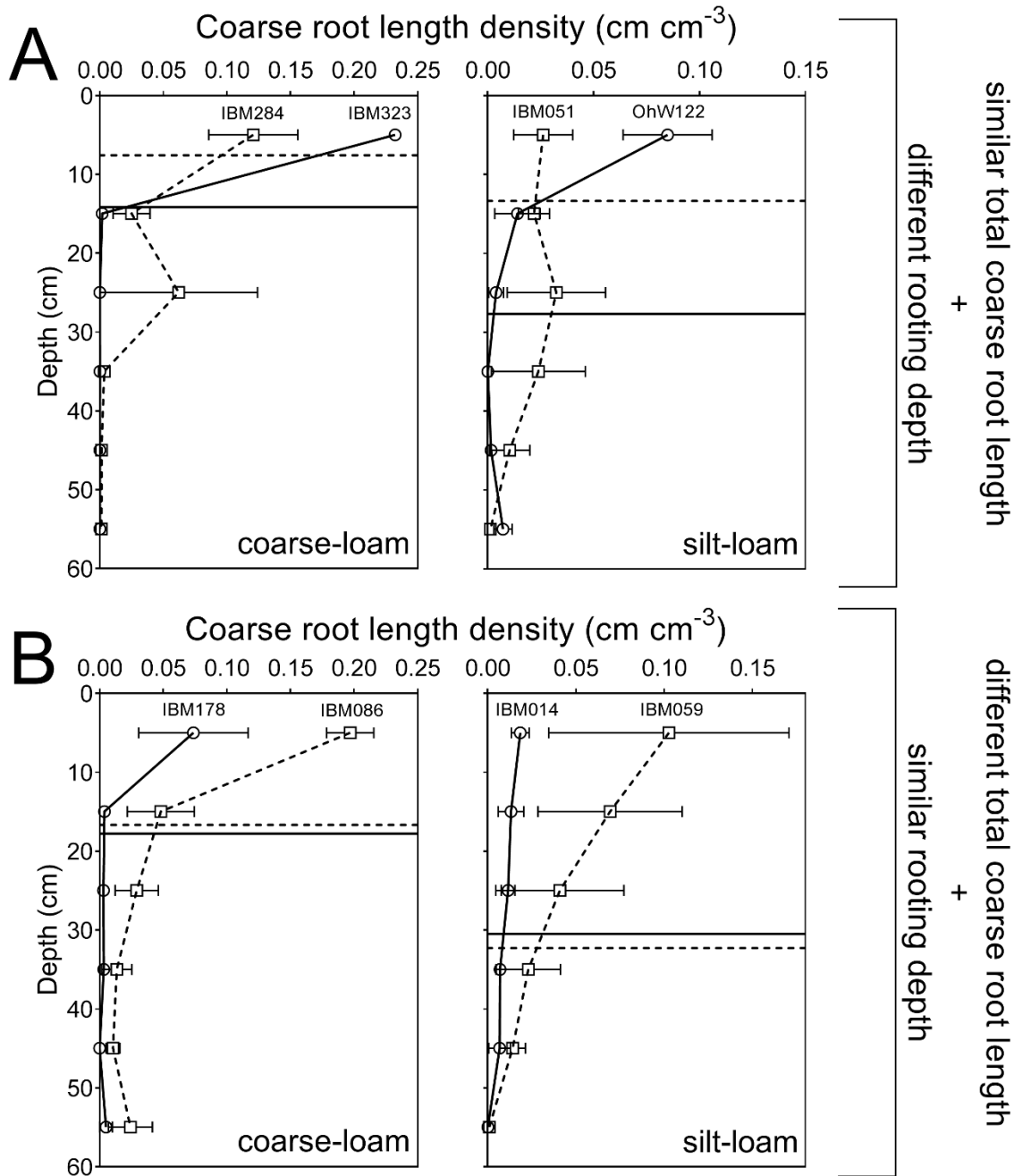
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Figure 6 – Linear regressions between root distribution variables at the two different field sites. Field site ARBC (coarse-loam) visualised in A, C, E and field site PSU (silt-loam) visualised in B, D, F. Compacted data (red) and non-compacted data (blue). Each datapoint represents the averaged value across the replicates for each genotype tested. Normal linear regression was used for A–B and E–F, and a betaregression was used for C–D as data was proportional. When a significant relationship was found this was at a level of significance of † $P \leq 0.10$ or * $P \leq 0.05$.



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 1072 **Figure 7** - Genotypic variation in the coarse root length density (cm cm⁻³) per depth
 1073 increment across two field sites and two compaction treatments. Non-compacted data
 1074 in blue and compacted data in red. The ARBC field site (coarse-loam) and PSU field
 1075 site (silt-loam) had different soil textures. The striped lines are the averages across all
 1076 genotypes, lighter coloured lines are the average for individual genotypes tested.
 1077 Similar plots for total root length density distributions can be found in Figure S9.

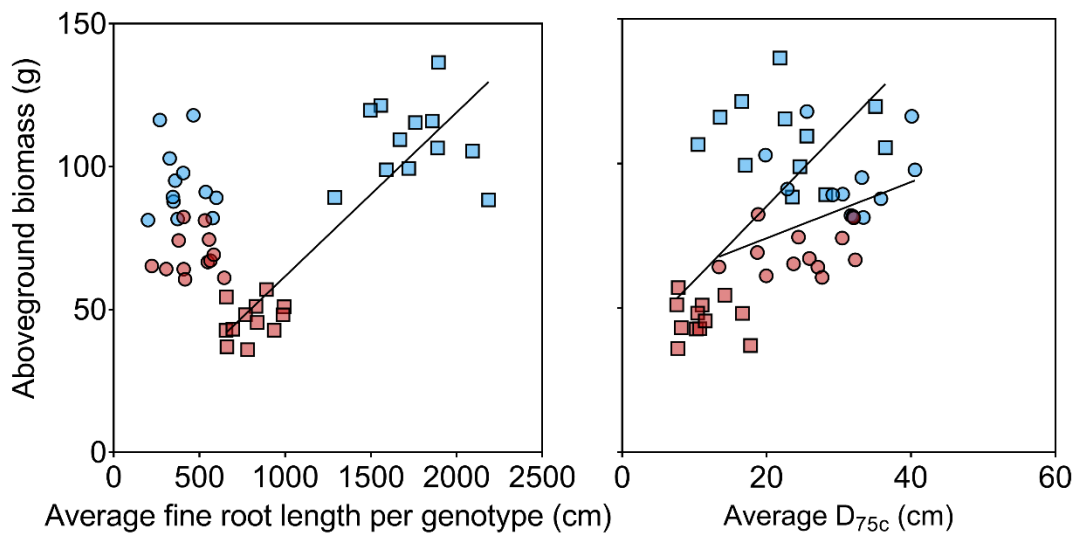
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Figure 8 – Coarse root length densities (cm cm^{-3}) \pm SE distributions with soil depth on compacted plots comparing (A) two genotypes per field site (coarse loam at ARBC and silt-loam at PSU) with similar total coarse root length but with different associated rooting depths and (B) two genotypes with similar rooting depths but with different total coarse root lengths. For (A) striped lines stands for the deeper rooting genotype and associated D_{75c} , while the solid line stands for the shallower rooting genotypes and associated D_{75c} . For (B), the solid line is used for the genotype that produces less roots but reaches equally deep as the genotype that produces more roots (striped lines). No error bars shown when standard error was too small to visualise. Selection comparison can be found in Figure S10. Similar plots for total root length density distributions can be found in Figure S12.

ARBC: Biomass ~ Genotype + D75 _c + D75 + TRL _f + TRL _c + Compaction		
	F-value	p-value
Genotype	1.144	ns
D75 _c	140.93	***
D75	0.231	ns
TRL _f	37.629	***
TRL _c	2.287	ns
Compaction	5.83	*
PSU: Biomass ~ Genotype + D75 _c + D75 + TRL _f + TRL _c + Compaction		
	F-value	p-value
Genotype	0.649	ns
D75 _c	14.491	**
D75	5.244	ns
TRL _f	0.083	ns
TRL _c	3.75	ns
Compaction	9.713	*



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1093 **Figure 9** – Relationships between average biomass and root distribution values and
 1094 are visualised in the accompanied plots where squares are data from the ARBC
 1095 (coarse-loam) field site while circles are data from the PSU (silt-loam) field site.
 1096 Compacted data in red, non-compacted data in blue. Level of significance in the
 1097 ANOVA analysis are *** $p < 0.001$, ** $p < 0.01$ and * $p < 0.05$.

1098 **Tables**

1099 **Table 1** – Definitions of the different measurements obtained after WinRHIZO analysis of the soil cores.

Measurement	Abbreviation	Definition	Unit
Total root length	TRL	The summation of all individual root sections per 10 cm increment of the entire soil core	cm
Total coarse root length	TRL _c	The summation of all individual root sections per 10 cm increment with a diameter greater than 1 mm over the entire soil core	cm
Total fine root length	TRL _f	The summation of all individual root sections per 10 cm increment with a diameter smaller than 1 mm over the entire soil core	cm
Coarse root proportion	P _c	The ratio of total coarse root length versus total root length	%
Fine root proportion	P _f	The ratio of total fine root length versus total root length	%
Root length density	-	The root length found in the soil volume of a 10 cm increment of the soil core and this including all root diameter classes	cm cm ⁻³
Coarse root length density	-	The total coarse root length found in the soil volume of a 10 cm increment of the soil core	cm cm ⁻³
Relative root length density	-	The ratio of total root length density of a single 10 cm increment versus the sum of the total root length density found over the entire core	%
Relative coarse root length density	-	The ratio of coarse root length density of a single 10 cm increment versus the sum of the coarse root length density found over the entire core	%
Rooting depth	D ₉₅	The rooting depth above which 95% of the total root length is located	cm
	D ₇₅	The rooting depth above which 75% of the total root length is located	cm
Coarse rooting depth	D _{95c}	The rooting depth above which 95% of the total coarse root length is located	cm
	D _{75c}	The rooting depth above which 75% of the total coarse root length is located	cm

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1102 **Table 2** F-values for split plot analysis results of the different root distribution variables
 1103 at the two field sites. P-values tested at the following levels of significance: † p ≤ 0.10, *
 1104 p ≤ 0.05, ** p ≤ 0.01, *** p ≤ 0.001. Subscript c stands for coarse and f stands for fine
 1105 when measurements are made on a separate root class. TRL stands for total root
 1106 length, P stands for proportion of coarse or fine roots. D75 and D95 stand for rooting
 1107 depth at which 75 and 95 percent of the total root length can be found.

		ARBC (coarse-loam)	PSU (silt-loam)
TRL	Compaction	77.12 ***	1.37
	Genotype	0.67	0.54
	Compaction x Genotype	0.87	0.85
TRL _c	Compaction	4.59 †	3.61 †
	Genotype	1.58	1.12
	Compaction x Genotype	2.11 *	1.35
TRL _f	Compaction	78.81 ***	1.25
	Genotype	0.67	0.56
	Compaction x Genotype	0.81	0.83
P _c	Compaction	18.29 **	3.43
	Genotype	2.60 **	1.97 *
	Compaction x Genotype	2.12 *	1.34
P _f	Compaction	18.62 **	2.63
	Genotype	2.46 *	1.77 †
	Compaction x Genotype	1.93 †	1.30
D _{75c}	Compaction	76.53 ***	4.65 †
	Genotype	3.15 **	1.67
	Compaction x Genotype	0.71	0.55
D _{95c}	Compaction	42.29 ***	0.78
	Genotype	3.86 ***	0.65
	Compaction x Genotype	1.33	0.60
D ₇₅	Compaction	17.31 **	6.78 *
	Genotype	2.74 **	1.08
	Compaction x Genotype	0.87	0.36
D ₉₅	Compaction	25.02 ***	1.56
	Genotype	2.70 **	1.11
	Compaction x Genotype	1.33	0.33

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1110 **Table 3** – Summary of general linear model results for the linear regression of total or
 1111 coarse rooting depth (D_{75} or D_{75c}) with total root length (TRL) or total coarse root length
 1112 (TRL_c). P-values tested at the following levels of significance: † $p \leq 0.10$, * $p \leq 0.05$, **
 1113 $p \leq 0.01$ and *** $p \leq 0.001$.

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$D_{75} \sim \text{TRL} + \text{Field site} + \text{Compaction} + \text{Genotype}$		
	F-value	p-value
Field site	57.36	***
Compaction	12.21	*
Genotype	1.22	
Total root length	3.09	†

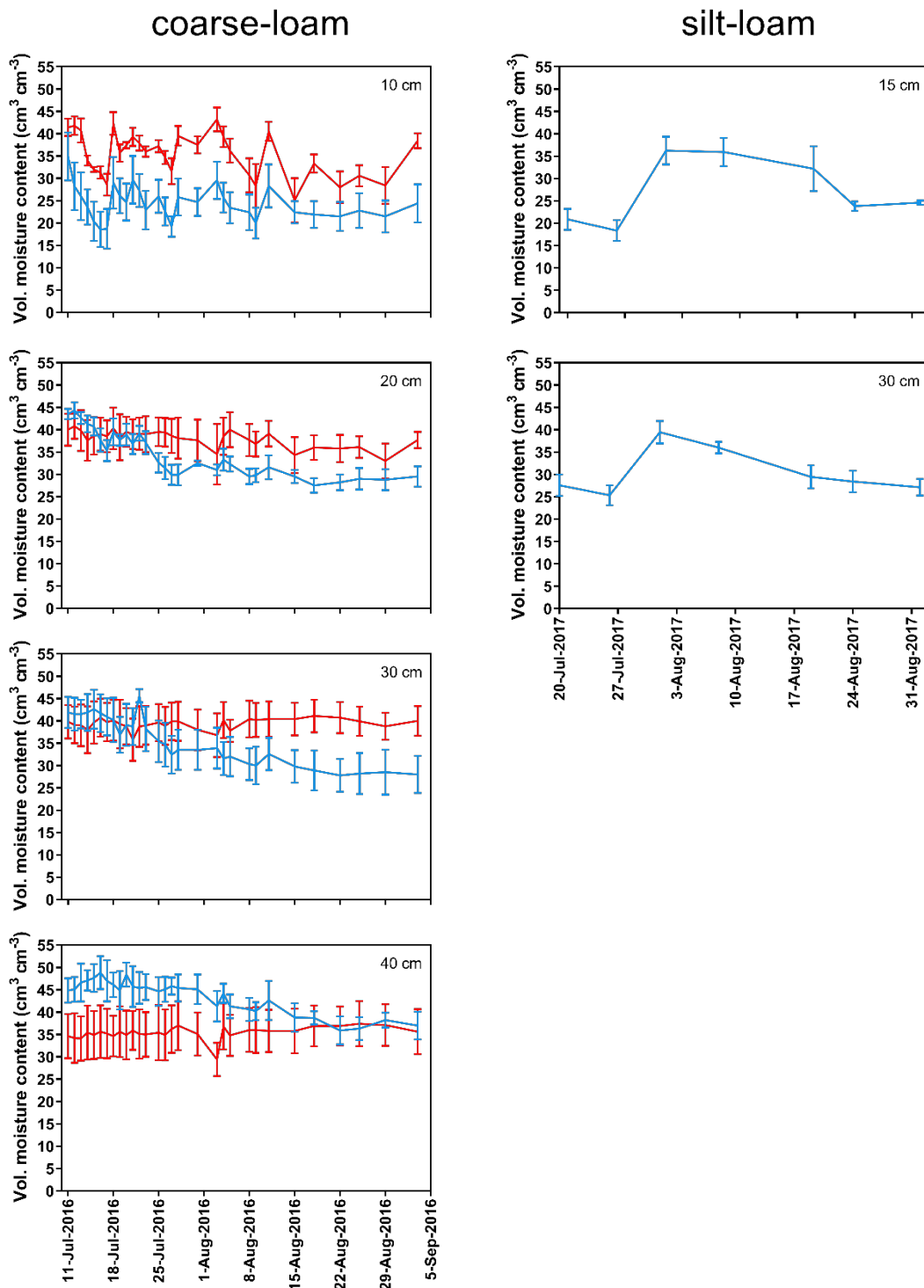
$D_{75} \sim \text{TRL}_c + \text{Field site} + \text{Compaction} + \text{Genotype}$		
	F-value	p-value
Field site	106.37	***
Compaction	10.2	*
Genotype	1.17	
Total root length	0.34	

$D_{75c} \sim \text{TRL} + \text{Field site} + \text{Compaction} + \text{Genotype}$		
	F-value	p-value
Field site	35.83	***
Compaction	25.51	***
Genotype	2.12	*
Total root length	2.73	

$D_{75c} \sim \text{TRL}_c + \text{Field site} + \text{Compaction} + \text{Genotype}$		
	F-value	p-value
Field site	41.39	***
Compaction	34.77	***
Genotype	1.99	*
Total root length	1.39	

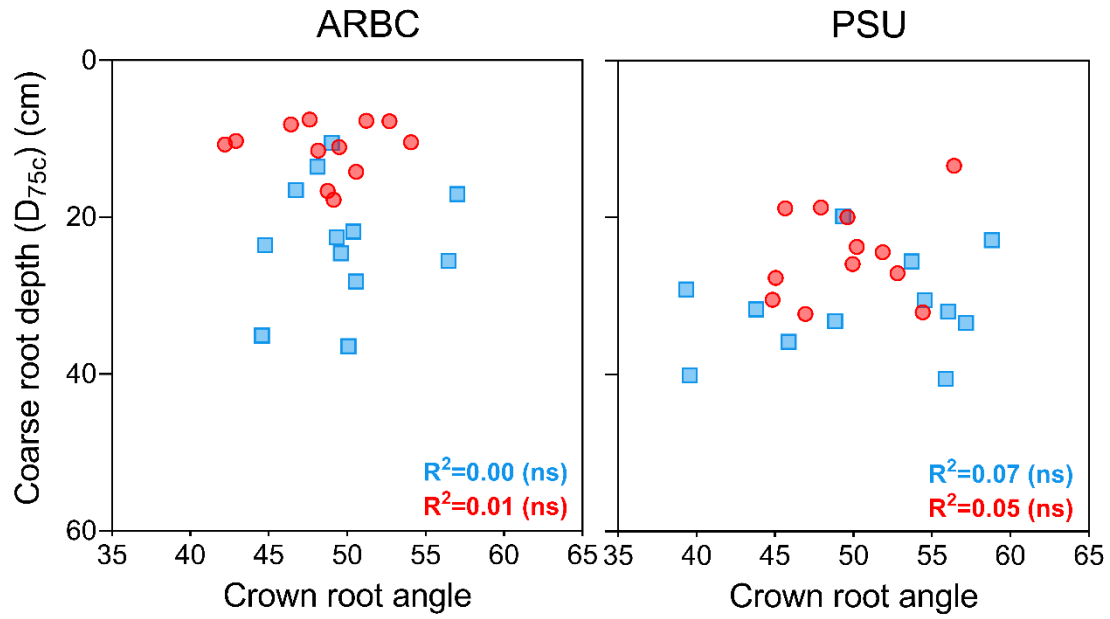
1115 Appendices

1116 Supplementary data



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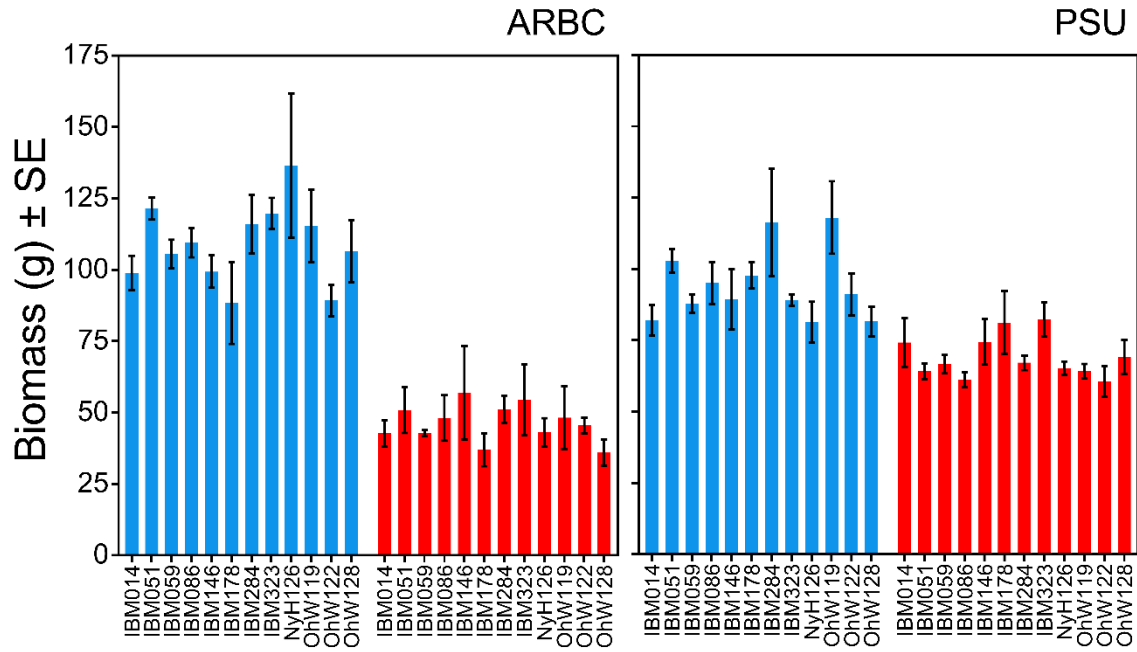
1118 **Figure S1** – Volumetric water content was used to steer irrigation (ARBC, coarse-loam
1119 field site) or to decide if irrigation was needed (PSU, silt-loam field site). On coarse-
1120 loam PR2-tubes were installed while on silt-loam TDR-probes were used to measure
1121 volumetric water content; gravimetric water content was calculated from this and the
1122 dry bulk density. Compacted site (red), non-compacted (blue).



1123 **Figure S2** – Relationship between crown root angle and coarse rooting depth for
 1124 ARBC (coarse-loam) and PSU (silt-loam) field sites. Figures adjusted from
 1125 supplementary Figure 1 from Vanhees *et al.* (2020). Compacted site (red), non-
 1126 compacted (blue).

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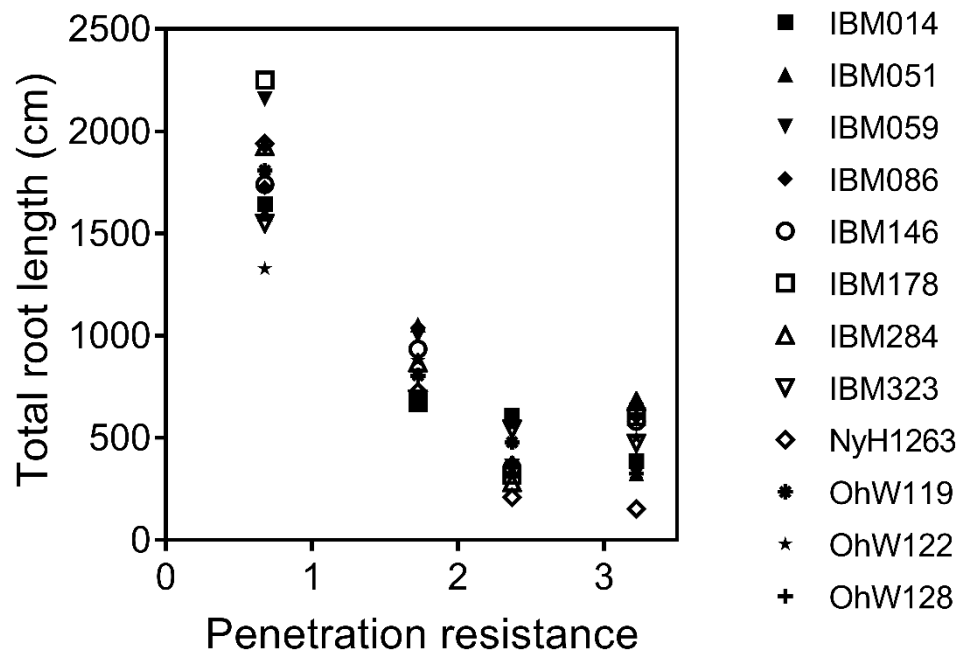
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1130 **Figure S3** – Biomass \pm SE at both field sites under compacted (red) and non-
 1131 compacted (blue) conditions for each genotype. The ARBC field site has a coarse-
 1132 loam soil while the PSU field site has a silt loam soil texture. Figure adjusted from
 1133 supplementary Figure 3 from Vanhees *et al.* (2020).

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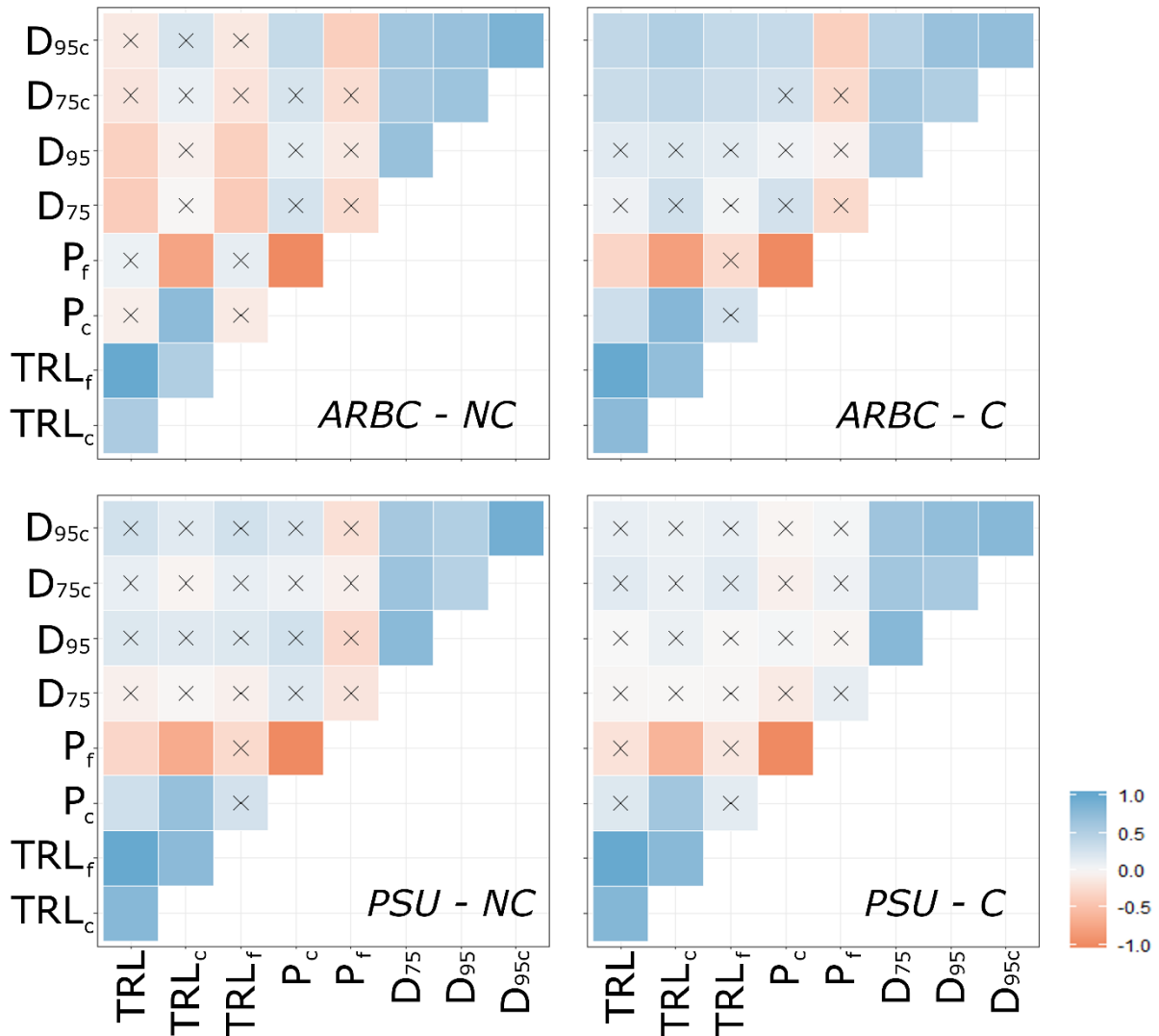


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1136 **Figure S4** – Total root length of each genotype plotted at the averaged penetrometer
 1137 resistance of the 2 field trial compaction treatment combinations.

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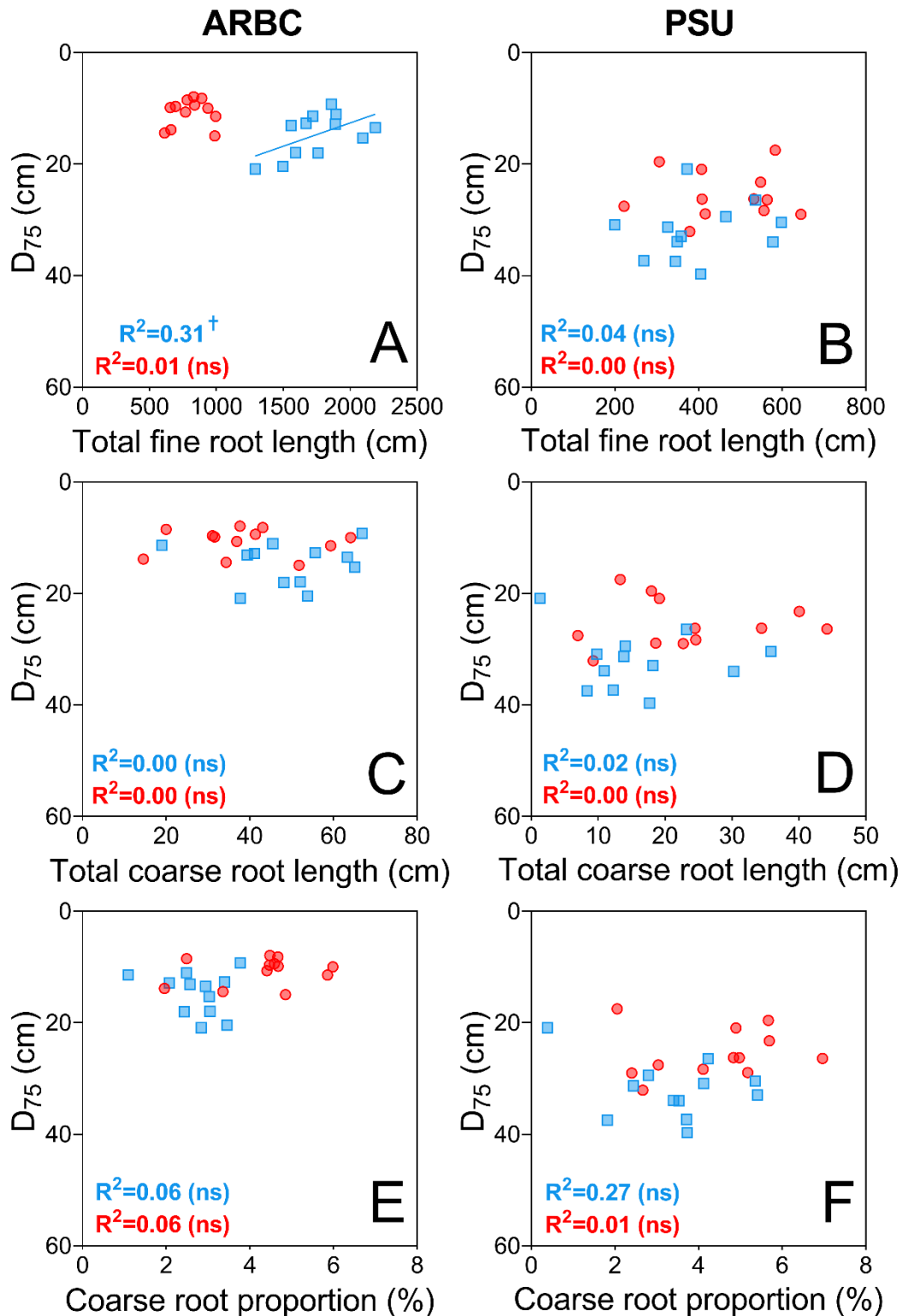
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1141 **Figure S5** – Correlation plots between tested variables averaged over all genotypes
 1142 across field sites (ARBC (coarse-loam) or PSU (silt-loam)) and compacted (C) or non-
 1143 compacted plots (NC) combinations. The correlation coefficient is visualised by the
 1144 scale bar, negative correlations are orange and positive correlations are blue. A cross
 1145 represents a non-significant correlation at significance $p \leq 0.05$.

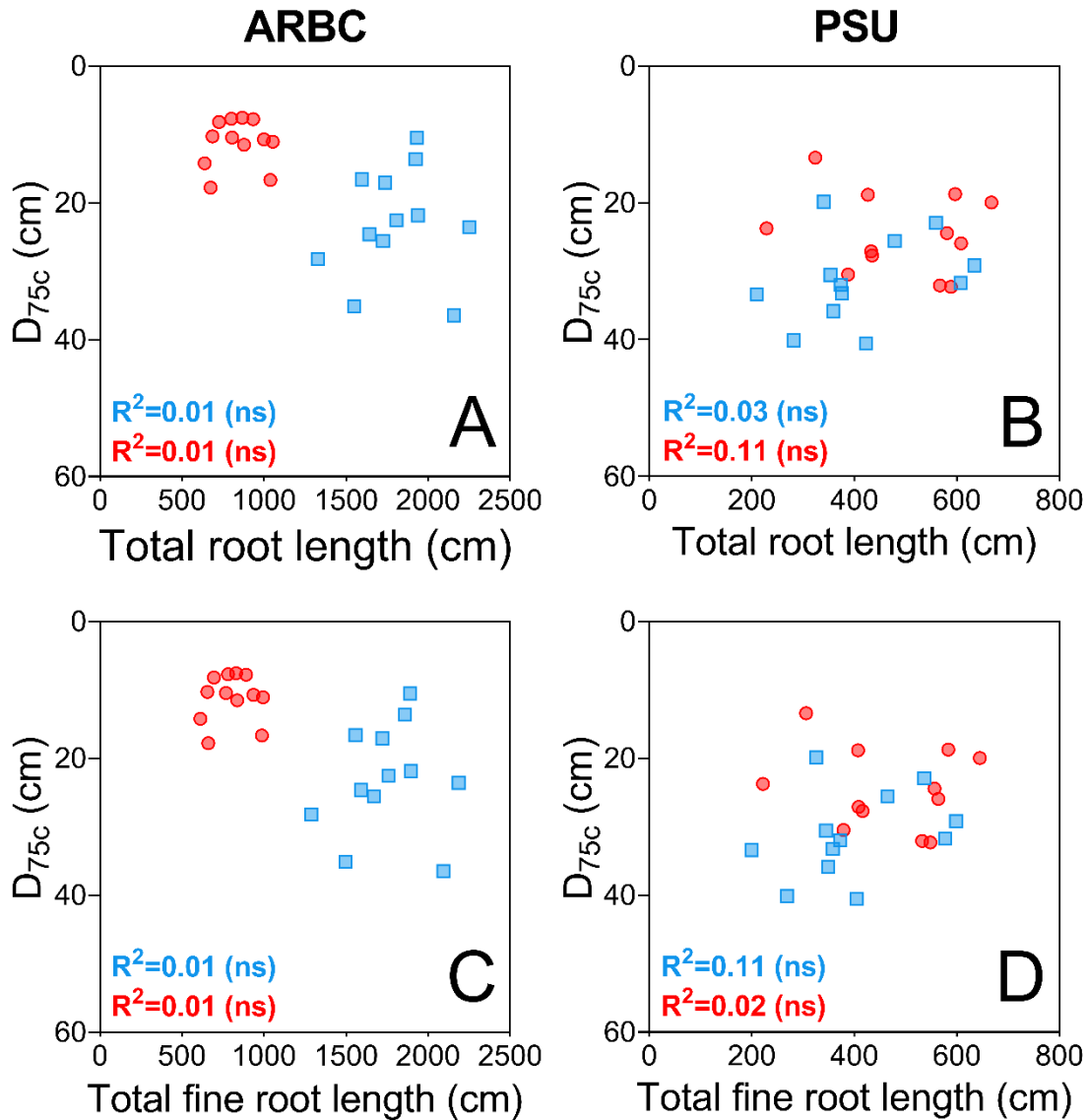
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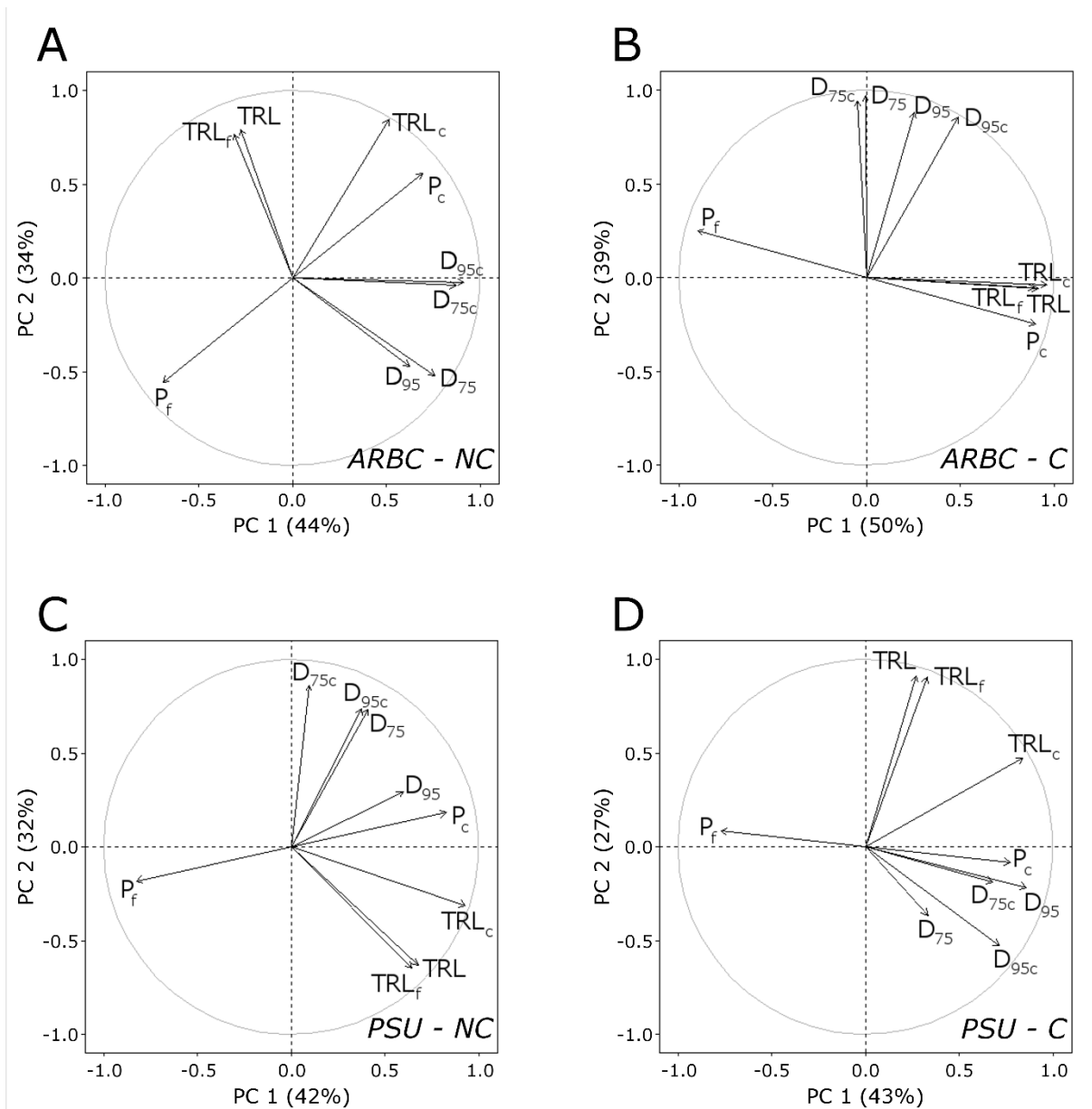
Figure S6 – Relationships between total rooting depth (D_{75}) and other root distribution variables across field sites and compaction treatments. Linear regression was used for A-D and beta-regression for E-F due to proportional data. Panels A,C and E represent field site ARBC (coarse-loam) and panels B, D and F represent field site PSU (silt-loam). Non-compacted data in blue, compacted data in red. One significant

1153 relationship was detected at significance level + $p \leq 0.10$, other relationships were non-
1154 significant (ns).



1155 **Figure S7** – Relationships between total rooting depth (D_{75c}) and other root distribution
1156 variables across field sites and compaction treatments. Panels A and C represent field
1157 site ARBC (coarse-loam) and panels B and D field site PSU (silt-loam). Non-
1158 compacted data in blue, compacted data in red. No significant (ns) linear relationships
1159 were detected.
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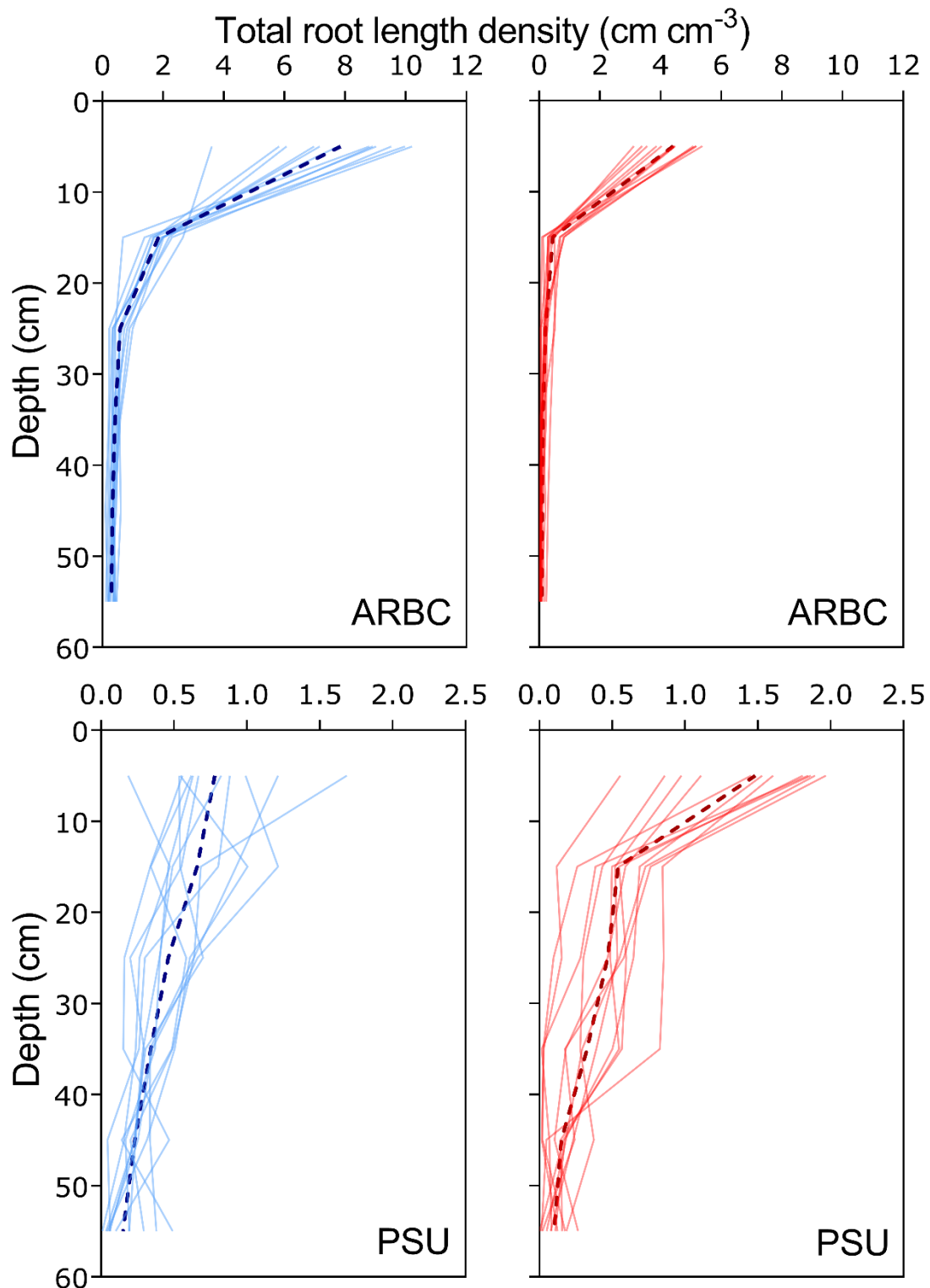
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1163 **Figure S8** – Principle component analysis per field site (ARBC (coarse-loam) or PSU
 1164 (silt-loam)) – compaction treatment (C – compacted; NC – non-compacted)
 1165 combination illustrating relationships between root distribution variables within
 1166 respective environmental conditions.

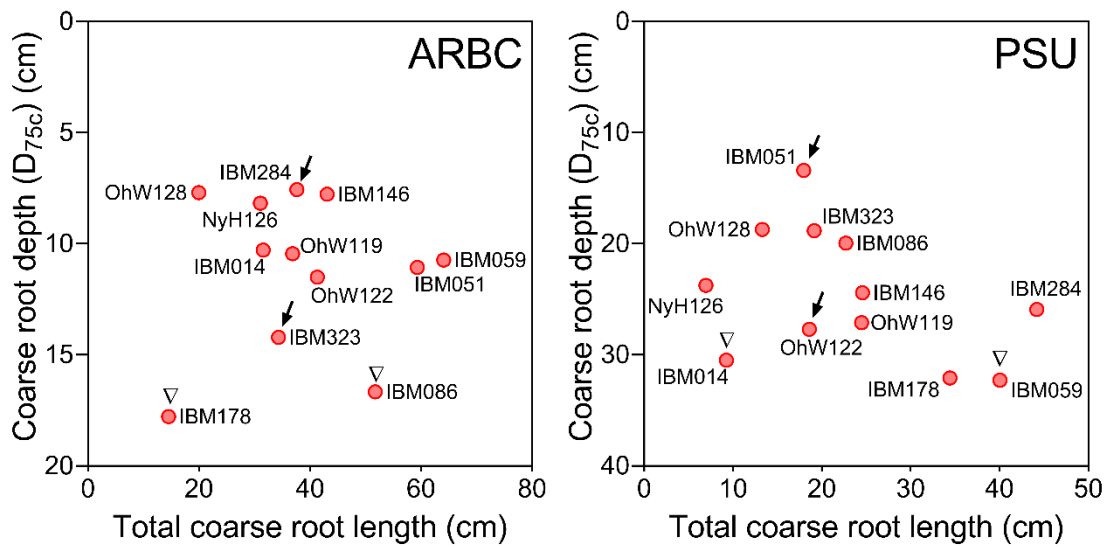
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1169 **Figure S9** – Genotypic variation in total root length density (cm cm⁻³) per depth
 1170 increment across two field sites and two compaction treatments. The ARBC field site
 1171 has a coarse-loam soil texture and the PSU field site has a silt-loam soil texture. Non-
 1172 compacted data in blue and compacted data in red. The striped line are the averages
 1173 across all genotypes, lighter coloured lines are the average for individual genotypes
 1174 tested.

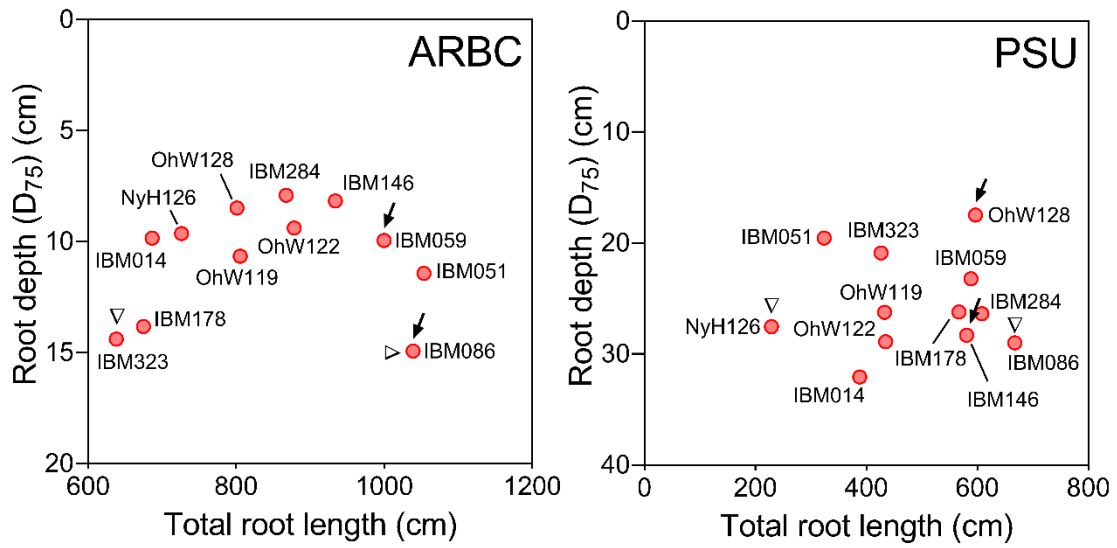
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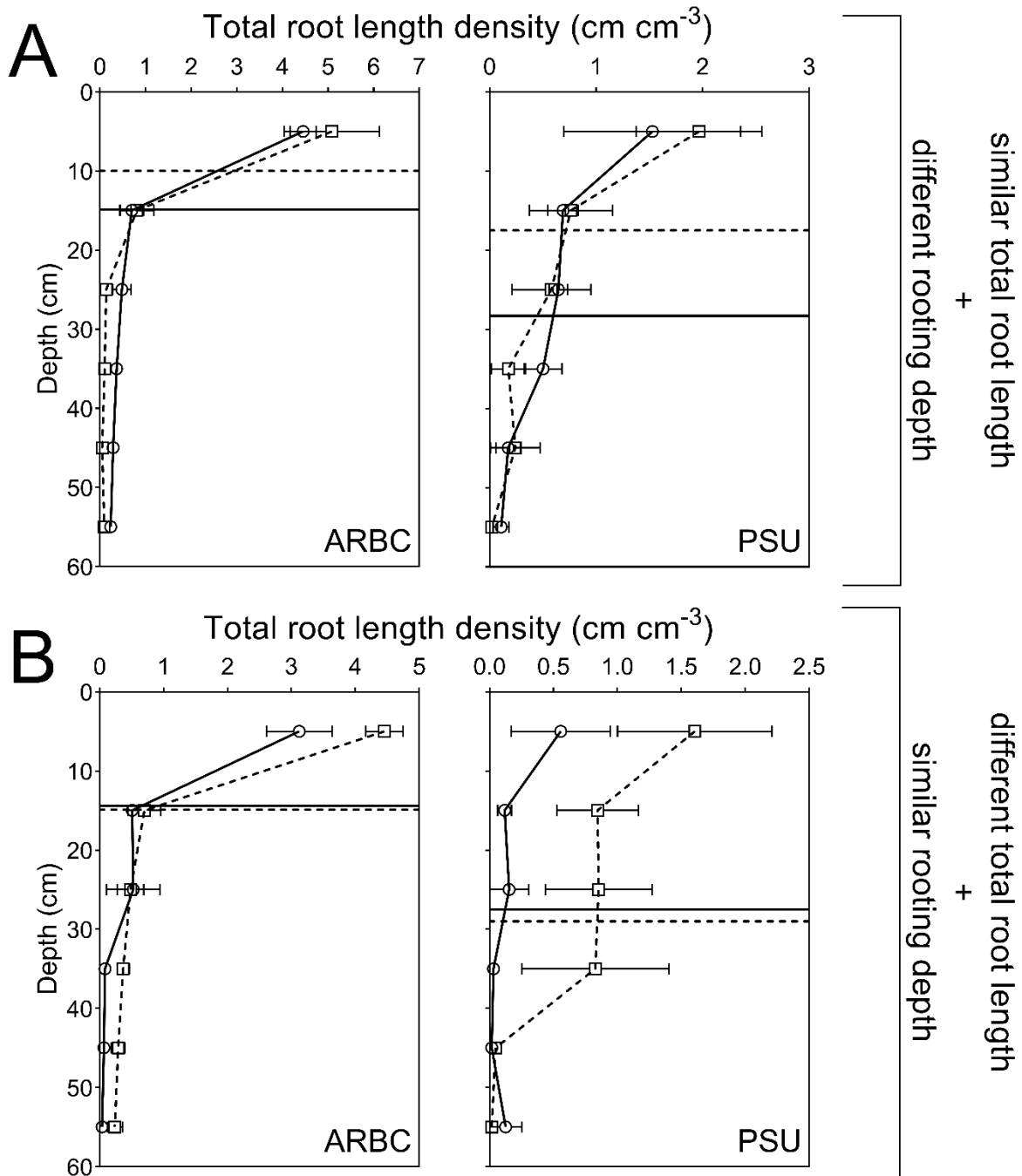
1177 **Figure S10** – Selection of genotypes to be compared based on their coarse rooting
 1178 depth and coarse total root length. Genotypes indicated with an arrow were selected
 1179 on the bases of similar coarse root length but different coarse rooting depths (shallow
 1180 versus deep) and genotypes indicated with a triangle were selected on the basis of
 1181 similar coarse rooting depth but are different according to total coarse root length (few
 1182 versus many roots for deeper rooting genotypes). . The ARBC field site has a coarse-
 1183 loam soil texture and the PSU field site has a silt-loam soil texture.

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Figure S11 – Selection of genotypes to be compared based on their total rooting depth and total root length. Genotypes indicated with an arrow were selected on the bases of similar coarse root length but different coarse rooting depths (shallow versus deep) and genotypes indicated with a triangle were selected on the basis of similar coarse rooting depth but are different according to total coarse root length (few versus many roots for deeper rooting genotypes). . The ARBC field site has a coarse-loam soil texture and the PSU field site has a silt-loam soil texture.



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1195 **Figure S12** - Total root length densities (cm cm^{-3}) \pm SE distributions with soil depth on
 1196 compacted plots comparing (A) two genotypes per field sites with similar total coarse
 1197 root length but with different associated rooting depths under compaction and (B) two
 1198 genotypes with similar rooting depths but with different total coarse root lengths under
 1199 compaction. For (A) solid lines stands for the deeper rooting genotype and associated
 1200 D_{75} , while the striped line stands for the shallower rooting genotypes and associated
 1201 D_{75} . For (B), the solid line is used for the genotype that produces less roots but reaches
 1202 equally deep then the genotype that produces more roots (striped lines). . The ARBC
 1203 field site has a coarse-loam soil texture and the PSU field site has a silt-loam soil
 1204 texture.

1205 **Table S1** – Field applications during the field season. Table adjusted from supplementary Table 1 from Vanhees *et al.* (2020).

Field applications						
Irrigation		Fertilizers			Pesticides	
coarse-loam	18/06/2016	0.94 mm	04/06/2016	ProSol (15 gallons/acre)	17/06/2016	Atrazine and S-metolachlor
	21/06/2016	0.60 mm	14/06/2016	ProSol (12.5 gallons/acre)	14/06/2016	Copper, Azoxystrobin and Chlorantraniliprole
	22/06/2016	1.20 mm	15/06/2016	UAN (38.3 lbs/acre)	23/06/2016	Chlorantraniliprole
	23/06/2016	0.32 mm	16/06/2016	ProSol (12.5 gallons/acre)		
	25/06/2016	1.60 mm				
	28/06/2016	0.30 mm				
	04/07/2016	0.24 mm				
	06/07/2016	0.20 mm				
	08/07/2016	0.50 mm				
	10/07/2016	0.72 mm				
	17/07/2016	0.75 mm				
	20/07/2016	0.50 mm				
	24/07/2016	0.50 mm				
	27/07/2016	0.50 mm				
	09/08/2016	0.50 mm				
silt-loam	<i>No irrigation applied as moisture content remained high enough during growing season</i>		urea Nitrogen (200 lbs/acre) applied prior to planting		<i>No pesticides were applied</i>	

1206

1207 **References in supplementary**

1208 Vanhees D.J., Loades, K.W., Bengough, A.G., Mooney, S.J., Lynch, J.P., 2020. Root
1209 anatomical traits contribute to deeper rooting of maize under compacted field conditions.
1210 J.Exp.Bot 71, 4243-4257. doi: 10.1093/jxb/eraa16

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