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1 **Genomic content of wheat has a higher influence than plant domestication status on the ability**
2 **to interact with *Pseudomonas* plant-growth promoting rhizobacteria**

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25 **Running title:** Wheat evolution and PGPR interaction

26 **Abstract**

27

28 Plant evolutionary history has had profound effects on belowground traits, which is likely to have
29 impacted the ability to interact with microorganisms, but consequences on root colonization and gene
30 expression by plant growth-promoting rhizobacteria (PGPR) remain poorly understood. Here, we
31 tested the hypothesis that wheat genomic content and domestication are key factors determining the
32 capacity for PGPR interaction. Thus, 331 wheat representatives from eight *Triticum* or *Aegilops*
33 species were inoculated under standardized conditions with the generalist PGPR *Pseudomonas ogarae*
34 F113, using an autofluorescent reporter system for monitoring F113 colonization and expression of *phl*
35 genes coding for the auxinic inducing signal 2,4-diacetylphloroglucinol. The interaction with *P.*
36 *ogarae* F113 was influenced by ploidy level, presence of genomes AA, BB, DD, and domestication.
37 While root colonization was higher for hexaploid and tetraploid species, and *phl* expression level
38 higher for hexaploid wheat, the diploid *Ae. tauschii* displayed higher *phl* induction rate (i.e.
39 expression:colonisation ratio) on roots. However, a better potential of interaction with F113 (i.e. under
40 non-stress gnotobiotic conditions) did not translate, after seed inoculation, into better performance of
41 wheat landraces in non-sterile soil under drought. Overall, results showed that domestication and
42 especially plant genomic content modulate the PGPR interaction potential of wheats.

43

44 **KEYWORDS**

45 Breeding, domestication, genomes, PGPR, phytostimulation, polyploidy, wheat.

46

47 1. INTRODUCTION

48

49 The rhizosphere harbors a diversified microbial community, which may contribute positively to plant
50 performance as it includes plant-growth promoting rhizobacteria (PGPR) and other symbiotic
51 microorganisms (Vacheron *et al.*, 2013). Therefore, it is important to understand selective pressures
52 governing PGPR ecology. One key factor is the plant genotype, as it modulates microbial diversity on
53 roots, for particular populations (Fromin *et al.*, 2001; Andreote *et al.*, 2009; Neiverth *et al.* 2014; Jack
54 *et al.* 2019), functional groups (Bouffaud *et al.*, 2016, 2018), or the whole microbial community (Berg
55 and Smalla, 2009; Philippot *et al.*, 2013). Plant genotype has also the potential to influence
56 rhizosphere colonization by individual PGPR strains (Johansson *et al.*, 2014; Vacheron *et al.*, 2016)
57 and the functioning of beneficial plant-microbe interactions (Salem *et al.*, 2018; Samain *et al.*, 2019).
58 However, current knowledge is insufficient to predict, for a given plant genotype, rhizosphere
59 colonization level and plant-beneficial effects by native or inoculated PGPR strain(s).

60 Environmental conditions put aside, trait variations between plant genotypes result from
61 differences in evolutionary history (Anderson *et al.*, 2011). In this context, plant domestication and
62 subsequent man-made dissemination and selection have had a profound impact on plant properties
63 (Pérez-Jaramillo *et al.*, 2016; Iannucci *et al.*, 2017; Abbasi and Eslahi, 2022). Consequences for root
64 colonization or the functioning of PGPR strains have started to receive research attention (Leff *et al.*,
65 2017; Martin-Robles *et al.*, 2017; Mendes *et al.*, 2018; Abdullaeva *et al.*, 2022). In bread wheat
66 (*Triticum aestivum*), Valente *et al.* (2020) showed that root colonization and expression of *phl* gene
67 (coding for 2,4-diacetylphloroglucinol [DAPG] synthesis) by the model PGPR *Pseudomonas ogarae*
68 (*ex-fluorescens*, *ex-kilonensis*) F113 were higher with landraces and old cultivars than with modern
69 cultivars. The choice of this PGPR strain was appropriate for different reasons. First, bacteria closely
70 related to *P. ogarae* F113 are widespread in arable soils (Mazzola *et al.*, 2004; Costa *et al.*, 2007).
71 Second, this strain can colonize various dicots including sugarbeet (Walsh *et al.*, 2003) - from which it
72 was isolated - and monocots including wheat (Couillerot *et al.*, 2011). Third, it produces DAPG, an
73 antimicrobial compound at high concentration (Keel *et al.*, 1992; Imperiali *et al.*, 2017), but at lower
74 concentration it triggers an ISR response through the jasmonate-ethylene pathway (Chae *et al.*, 2020)

75 and stimulates root branching via an auxin-dependent signaling pathway (Brazelton *et al.*, 2008),
76 which are general modes of action. Fourth, strain F113 enhances growth of various plants (Vacheron
77 *et al.*, 2018; Walker *et al.*, 2012) including wheat (Couillerot *et al.*, 2011). In Valente *et al.* (2020),
78 wheat accessions that displayed a strong interaction potential with *P. ogarae* F113 (i.e. determined
79 under gntobiotic, non-stress conditions) benefited the most from F113 inoculation. However, the work
80 focused on domesticated bread wheat, providing only a glimpse on the complex evolutionary history
81 of wheat. Much more drastic genetic changes occurred upstream from the formation of *T. aestivum*,
82 and it is likely that differences between wheat genotypes across a longer evolutionary time would give
83 more contrasted differences in wheat-PGPR relations in comparison with the intra-species differences
84 found by Valente *et al.* (2020).

85 The formation of current bread wheat (hexaploid; genome AABBDD) has involved several
86 genome hybridization events (Marcussen *et al.*, 2014; Glémin *et al.*, 2019; Pont *et al.*, 2019),
87 subsequent domestications (Salamini *et al.*, 2002; Feldman and Kislev, 2007; Özkan *et al.*, 2010;
88 Baidouri *et al.*, 2017) and human breeding (Gayon and Zallen, 1998; Bonjean *et al.*, 2001; Sramkova
89 *et al.*, 2009; Kiszonas and Morris, 2018) (summarized in Figure S1). Hybridization, which led to
90 polyploidization and a specific genome architecture for each wheat species, had a strong impact on
91 wheat adaptation (Soltis *et al.*, 2000, 2015). Wheat gene expression changes with genome architecture,
92 through epigenetic effects and alternative splicing (Yu *et al.*, 2020), causing sub-genome dominance
93 effects in bread wheat (Ramirez-Gonzales *et al.*, 2018; Chagué *et al.*, 2010; Leach *et al.*, 2014; Powell
94 *et al.*, 2017), which depend on growth stage and tissue. Root system architecture, root surface
95 properties and exudation patterns, which very likely should influence plant-microorganism
96 interactions in soil (Haichar *et al.*, 2008; Doornobos *et al.*, 2012), vary with plant genotype (Badri and
97 Vivanco, 2009), including in wheat (Shaposhnikov *et al.*, 2016; Iannucci *et al.*, 2017, 2021; Golan *et al.*
98 *et al.*, 2018; Gruet *et al.*, 2022). In particular, they are likely to be affected by wheat genomic content
99 (Leach *et al.*, 2014; Hao *et al.*, 2017; Ramirez-Gonzales *et al.*, 2018; Yu *et al.*, 2020; Juery *et al.*
100 2021).

101 Data on the impact of wheat genome architecture on interactions with microorganisms remain
102 scarce (Gruet *et al.*, 2022). They are mostly restricted to taxonomic information (Ito *et al.*, 2021; Wipf

103 *et al.*, 2021), with little attention so far on microbial functioning on wheat roots (Spor *et al.*, 2020).
104 Here, the objective was to take into account the breadth of wheat evolutionary history and test the
105 hypothesis that wheat genomic architecture is an overriding factor underpinning the ability for
106 molecular interactions with PGPR. To this end, we used the fluorescence screening protocol of
107 Valente *et al.* (2020) for molecular monitoring of root colonisation and *pht* expression in *P. ogarae*
108 F113-*mCherry*(*Ppht-egfp*) during interaction with 331 wheat lines from the *Aegilops* species *Ae.*
109 *speltoides* (BB{SS} genome), *Ae. tauschii* (DD genome), and *Triticum* species *T. urartu* (AA
110 genome), *T. dicoccoides*, *T. dicoccon*, *T. durum* (AABB genome), *T. spelta*, *T. aestivum* (AABBDD
111 genome). For selected lines, the approach was validated by qPCR, and a greenhouse experiment in
112 non-sterile soil was carried out to determine whether landraces from *T. aestivum* and *T. durum*
113 interacting better with *P. ogarae* F113 benefited better from F113 phytostimulation.

114

115 **2. MATERIALS AND METHODS**

116

117 **2.1. Plant material**

118 Molecular screening was performed with a total of 331 wheat lines, i.e. 20 lines for each of the six
119 wheat species *T. urartu*, *T. dicoccoides*, *T. dicoccon*, *T. spelta*, *Ae. tauschii* and *Ae. speltoides*, 19 lines
120 for *T. durum* (Table S1), as well as 192 lines for *T. aestivum* (35 landraces, 43 old varieties from the
121 19th century to 1960, and 114 modern genotypes developed after 1960 and carrying semi-dwarf *Rht*
122 alleles; Borojevic and Borojevic, 2005). All lines were selected from the wheat collection of the
123 Leibniz Institute of Plant Genetics and Crop Plant Research (Gatersleben, Germany) for their
124 contrasting characteristics in terms of geographic origin, registration date and intra-specific taxonomic
125 traits, except for *T. aestivum* lines obtained from the Center of Biological Resources ‘Céréales à
126 Paille’ (Clermont-Ferrand, France). Screening data for the 192 *T. aestivum* lines have been published
127 in Valente *et al.* (2020).

128

129 **2.2. Inoculum for the screening**

130 The screening experiment was performed with *P. ogarae* F113-*mCherry*(*Pphl-egfp*). This strain
131 carries the reporter gene *mCherry* (Rochat *et al.*, 2010; red fluorescence), under the control of the *tac*
132 promoter (*Ptac*), with a kanamycin-resistance cassette on its chromosome, giving a constitutive
133 expression of *mCherry*, and the promoter of the *phl* operon fused to the promoterless reporter gene
134 *egfp* (enhanced green fluorescent protein), on the plasmid pOT1e carrying a gentamycin-resistance
135 cassette (Vacheron *et al.*, 2016), giving an induced expression of *egfp*. The inoculum was prepared by
136 growing the strain 24 h in King's B medium (King *et al.*, 1954) supplemented with kanamycin (50 µg
137 mL⁻¹) and gentamycin (25 µg mL⁻¹) at 28°C and 180 rpm, then overnight in Minimal Medium (MM)
138 broth (Garcia de Salamone, 2001) supplemented with kanamycin and gentamycin, at 28°C and 180
139 rpm. The cells were washed and resuspended in 10-mM MgSO₄ and OD₆₀₀ was adjusted to 8.0
140 (corresponding to 10⁹ CFU mL⁻¹). Pre-germinated wheat seeds (described below) were inoculated with
141 50 µL of cell suspension containing 5 × 10⁷ CFU.

142

143 **2.3. Preparation of pre-germinated wheat seeds**

144 The 331 wheat lines were studied under the same gnotobiotic conditions, and data for the 192 *T.*
145 *aestivum* lines were already reported in Valente *et al.* (2020). Briefly, wheat seeds were surface-
146 disinfected by soaking for 30 min in a sodium hypochlorite solution (Na₂CO₃ 0.1 g, NaCl 3 g and
147 NaOH 0.15 g in 100 mL distilled water) supplemented with 10% commercial bleach and 0.01% of
148 Tween 20%. They were rinsed for five min (three times) in sterile demineralized water, and immersed
149 for one hour in sterile water. Seeds were pre-germinated on sterile agar plate containing plant agar
150 (Sigma-Aldrich, St Louis, MO, USA) at 8 g L⁻¹ for 24 h in the dark at 28°C, and the seedlings were
151 then transferred in 120 × 120 mm Petri dishes containing plant agar, with 3 seedlings per plate. Then,
152 9 seedlings were inoculated with the strain and 9 seedlings were not inoculated (receiving 50 µL of
153 MgSO₄), giving 6 plates for each line. The inoculated seedlings and the controls were grown in a
154 growth chamber for seven days, at 21°C, with a 16/8 h day/night cycle and 60% hygrometry.
155 Seedlings grew without touching/lifting the lid during the 7-day-incubation.

156

157 **2.4. Root sampling and fluorescence measurements**

158 At seven days of growth, three inoculated and three non-inoculated root systems of each line were cut
159 in 1-cm fragments and ten fragments from the same plant were introduced into a tube containing 1 mL
160 of 10-mM MgSO₄ and a steel bead (5 mm diameter). Roots were ground for 1 min (twice) with a
161 FastPrep-24 Classic Instrument (MP Biomedicals, Santa Ana, CA, USA) at maximum speed (6 m s⁻¹).
162 The tubes were centrifuged 2 min at 2000 rpm to pellet the biggest debris. 200 µL of each supernatant
163 were then transferred into black 96-well plates with a clear bottom, and plates were placed in an
164 Infinite M200 PRO microplate reader (Tecan, Männedorf, Switzerland) to read the fluorescence
165 intensities of supernatants (i.e. comparisons made for a same total root length). mCherry red
166 fluorescence level (corresponding to F113 colonization) was read with an excitation wavelength of
167 587 nm and an emission wavelength of 661 nm, and EGFP green fluorescence intensity
168 (corresponding to *phl* expression) was recorded with an excitation wavelength of 488 nm and an
169 emission wavelength of 530 nm. The mean fluorescence intensity of the three non-inoculated plantlets
170 was subtracted from the fluorescence intensity of each inoculated plantlet. As in Valente *et al.* (2020),
171 the ratio between green and red fluorescence was used as a proxy to determine the *phl* induction rate.

172

173 **2.5. Validation of the screening method**

174 In order to verify the correlation between fluorescence intensities and F113 colonization/*phl*
175 expression, the inoculant was also monitored by qPCR/qRT-PCR using a subset of 10 wheat lines with
176 contrasting results for each parameter (F113 colonization, *phl* expression and *phl* induction rate ;
177 Table S2), i.e. *T. dicoccoides* TRI 18506, *T. urartu* TRI 17143, *T. dicoccon* TRI 29817, *T. durum* TRI
178 10450, *Ae. tauschii* AE 1632, *Ae. tauschii* AE 235, *Ae. tauschii* AE 1038, *Ae. tauschii* AE 721, *Ae.*
179 *speltoides* AE 739 and *T. spelta* TRI 9883. Seed-surface disinfection and seedling inoculation were
180 performed as described above, to obtain for each line eight inoculated plantlets and eight non-
181 inoculated plantlets. Four non-inoculated plantlets served as controls for red fluorescence intensity and
182 the four others as controls for green fluorescence intensity. At seven days of growth, for each of the
183 ten lines, the root systems of four inoculated plantlets were treated as above to measure red
184 fluorescence intensity (F113 colonization), and the rest of the supernatant was centrifuged for 5 min at

185 5000 rpm to pellet the cells. DNA extraction was then performed on the pellet, with the NucleoSpin
186 Tissue kit (Macherey-Nagel, Illkirch, France) according to the manufacturer instructions, and
187 extracted DNA was quantified with the Qubit dsDNA Quantification high sensitivity assay kit
188 (ThermoFisher Scientific, Waltham, MA, USA). The root systems of the four other inoculated
189 plantlets were also ground but without a steel bead, for 5 min, twice. The supernatants were then used
190 to measure green fluorescence, as described above, and to perform RNA extraction with the RNeasy
191 Mini Kit (Qiagen, Hilden, Germany), following the manufacturer instructions. Any remaining DNA
192 was removed by treating 20 μ L of nucleic acid solution with 4 U of DNase I (ThermoFisher Scientific)
193 in 1 \times DNase I reaction buffer for 15 min at room temperature. The reaction was stopped by adding 1
194 μ L of 25-mM EDTA and incubating for 10 min at 65°C. The lack of DNA contamination was checked
195 by qPCR amplification (performed as described below). cDNA synthesis was made from 8 μ L of RNA
196 extract, with random hexanucleotide primers (Promega, Madison, WI, USA) and the Omniscript
197 reverse transcription kit (Qiagen), according to the manufacturer instructions.

198 The abundance of *P. ogarae* F113 was determined by qPCR from DNA samples using strain-
199 specific primers F113_1_for and F113_1_rev, targeting sequence-characterized amplified region
200 (SCAR), as described (Von Felten *et al.*, 2010). The number of *phlD* transcripts was estimated from
201 cDNA samples using primers B2BR3 and B2BF, as described (Almario *et al.*, 2013). See Figure S6
202 for PCR methodology.

203

204 **2.6. Greenhouse experiment**

205 A soil pot experiment was carried out to compare hexaploid bread wheat (genome AABBDD) and
206 tetraploid durum wheat (genome AABB), using for each wheat species 10 landraces that had shown
207 contrasted results in the screening experiment. The 10 landraces of *T. durum* were TRI 9517, TRI
208 10450, TRI 11430, TRI 12311, TRI 7871 (strong F113 interaction), and TRI 17796, TRI 16846, TRI
209 732, TRI 11542 and TRI 609 (weak F113 interaction) (Figure S5f) and the 10 landraces of *T. aestivum*
210 were Bordeaux 113, Blé Barbu de Murol, Rouge de Marchissy, Non Plus Extra and Candéal de
211 Arévalo (strong F113 interaction), and Chyaksila Epi Non Velu, Tau Bugda, Fruh Weizen, Blanc
212 Précoce and Rouge d'Altkirch (weak F113 interaction) (Figure S5h, Table S3).

213 For each line, six pots were inoculated with strain F113 and six others were not inoculated.
214 Wheat seeds were surface-disinfected as described above, and 4 seeds were placed in each pot
215 containing 680 g of sieved (6 mm) non-sterile loamy soil from the surface horizon of a luvisol (clay
216 16%, silt 44%, sand 40%; 2.1% organic matter, pH 7, cation exchange capacity 8.2 cmol kg⁻¹) from La
217 Côte Saint-André near Lyon (France). In the inoculated pot, each seed received 200 µL of a cell
218 suspension (obtained as described above) of *P. ogarare* F113, containing 2.5 × 10⁶ CFU, whereas in
219 the non-inoculated pots, seeds received 200 µL of 10-mM MgSO₄. Pots were placed in a greenhouse
220 with 16 h of light (25°C) and 8 h of darkness (18°C), and were organized following a randomized
221 block design and regularly moved around to minimize greenhouse heterogeneity effects. For the first
222 14 days of growth, water content was maintained at 22% w/w (i.e. 80% of the water-holding capacity).
223 At 10 days of growth, the number of plantlets was reduced to three per pot in order to have an equal
224 number in each pot, as three was the minimal number of seeds that had germinated. At day 14, water
225 stress was implemented by letting the soil dry to 12 % w/w (i.e. permanent wilting point) and
226 maintaining it at that level until the end of the experiment.

227 At one month of growth, one individual plant in each of the six inoculated pots and six non-
228 inoculated pots per wheat accession was sampled, except with lines Bordeaux 113, Rouge de
229 Marchissy, Chyaksila Epi Non Velu, Blanc Précoce, Rouge d'Altkirch, and TRI 9517 because of seed
230 germination problems (only five replicates available). These individual plants were used to evaluate
231 plant growth and F113 colonization. For plant growth, shoots were separated from the root system and
232 shoot biomass (fresh and later dry) was measured. Root systems were shaken to discard non-adhering
233 soil and then roots and adhering-soil were soaked into a NaCl 0.8% solution to separate root-adhering
234 soil from roots, by vortexing 5 min. Roots were put in a new tube containing NaCl solution and stored
235 at 4°C until measurement of root system architecture (number, length, diameter, surface and volume of
236 roots) using WinRhizo image analysis (Regent Instrument, Nepean, ON), and dry root biomass after
237 drying for 72 h at 60°C.

238

239 **2.7. Analysis of rhizosphere colonization by *P. ogarae* F113**

240 For root colonization by *P. ogarae* F113, root-adhering soil in NaCl solution was pelleted by
241 centrifugation for 5 min at 2000 rpm, lyophilised for 48 h and stored at -20°C. Total nucleic acid
242 extraction was performed on 500 mg of homogenized lyophilized soil with the FastDNA Spin Kit (MP
243 Biomedicals, Santa Ana, CA, USA), according to the manufacturer's instructions. DNA was eluted in
244 80 µL DNase-free water and DNA concentration was measured in a Nanophotometer NP80 (Implen
245 GmbH; Munich, Germany). Colonization by *P. ogarae* F113 was estimated by qPCR using primers
246 F113_1_for and F113_1_rev of Von Felten *et al.* (2010) (see above). Results obtained in g µL⁻¹ were
247 transformed into numbers of copies using the formula [DNA (g) × Avogadro's number (molecules
248 mol⁻¹)]/[number of DNA bp in amplified fragments × 660 (g mol⁻¹)], based on an average of 660 g
249 mol⁻¹ per base pair.

250

251 **2.8. Assessment of *phlD* expression on roots**

252 Five other plants of the two *T. aestivum* lines Bordeaux 113 and Tau Bugda and the two *T. durum*
253 lines TRI 7871 and TRI 732, under inoculated and non-inoculated conditions, were harvested to assess
254 *phlD* expression level by *P. ogarae* F113 (and resident *phl*⁺ pseudomonads) in the rhizosphere. The
255 plant root system was strongly shaken to dispose of non-adhering soil and root-adhering soil was then
256 separated from roots by scraping gently the roots using sterile tweezers. The root-adhering soil was
257 recovered in a 15 mL collection tube and flash frozen in liquid nitrogen before being stored at -80°C.
258 Nucleic acid extraction was done as described by Bouffaud *et al.* (2014) from 0.5 g of wet soil. DNA
259 was removed by treating 20 µL of nucleic acid solution with 4U of DNase I (ThermoFisher Scientific)
260 in 1× DNase I reaction buffer for 15 min at room temperature. The solution was then purified with the
261 RNeasy Mini Kit (Qiagen), using the RNA Clean Up protocol. RNA was eluted in 30 µL of RNase-
262 free water and an additional step of DNase treatment was done to remove any DNA remaining. The
263 reaction was stopped by adding 1 µL of 25-mM EDTA for 10 min at 65°C. DNA contamination was
264 checked by a lack of qPCR amplification. cDNA synthesis was made as described above from 8 µL of
265 RNA extract with the Omniscript reverse transcription kit (Qiagen). Quantification of *phlD* transcripts

266 was carried out by qPCR on cDNA, as described above, using the primers B2BR3/B2BF (Almario *et*
267 *al.*, 2013).

268

269 **2.9. Statistics**

270 All analyses were done at $P < 0.05$, using R 4.0.3 software (<https://www.r-project.org>). All
271 data and residuals were checked for normal distribution and homogeneity of variance. Variation
272 coefficients (i.e. based on standard deviation divided by the mean) were computed.

273 Comparison of red and of green fluorescence levels were made using an ANOVA on a nested
274 model, followed by Tukey's HSD tests, taking into account the variability between lines of a same
275 category. As genotype categories (*T. aestivum* landraces, old cultivars and modern cultivars) tested by
276 Valente *et al.* (2020) comprised respectively 35, 43 and 114 lines, the test was run 100 times with each
277 time a random subset of 20 genotypes of these three *T. aestivum* categories, in combination with the
278 20 genotypes of each of the seven other wheat species. When comparing red and green fluorescence
279 levels according to ploidy status, presence/absence of genome A, B or D, and domestication status,
280 ANOVA was carried out followed by Tukey's HSD tests for F113 colonization data. For data not
281 normally distributed (*phl* expression level and *phl* induction), Kruskal-Wallis tests were performed,
282 followed by Conover-Iman tests for pairwise comparisons. Analyses were run 500 times with, each
283 time, a different random subset of each category whose size was that of the category with the smallest
284 number of observations (i.e. 59, 40, 40, 99 and 80, respectively).

285 For validation of the screening method, the correlations between red-*mCherry* fluorescence
286 and the abundance of *P. ogarae* F113, as well as between green-*egfp* fluorescence and the number of
287 *phlD* transcripts were estimated using Pearson's correlation coefficient, and comparisons between the
288 wheat lines were made using a Kruskal-Wallis rank-sum test, followed by Conover-Iman tests.

289 To compare results from the greenhouse experiment, for each growth parameter investigated,
290 an ANOVA and Tukey's HSD tests were performed on a nested model with four factors, i.e.
291 inoculation status \times wheat genotype category \times level of molecular interaction with F113 \times individual
292 wheat line ('level of interaction' being nested into 'wheat category', and 'wheat line' into 'level of

293 interaction'). Moreover, a two-way ANOVA and Tukey's HSD tests were performed with the two
294 factors inoculation status \times level of interaction with F113.

295

296 3. RESULTS

297

298 3.1. Root colonization by *P. ogarae* F113 is higher for tetraploid and hexaploid wheats

299 Red *mCherry* fluorescence measured in the gnotobiotic screening experiment, to assess root
300 colonization by *P. ogarae* F113-*mCherry*(*Pphl-egfp*), ranged from 0 (for *T. dicoccoides* lines TRI
301 18531, TRI 18491, TRI 18508, TRI 18486, *T. urartu* line TRI 11563, *T. spelta* line TRI 3419, *Ae.*
302 *speltoides* line AE 348) to 931 arbitrary units (AU) for *T. durum* line TRI 9517 after 7 days of growth
303 (Figures 1a and S2).

304 When considering species, root colonization by the pseudomonad was higher on *T. durum*
305 (AABB genome), followed by *T. aestivum* (AABBDD genome) independently of the category
306 (landraces, old cultivars or modern cultivars), and then the other AABBDD wheat *T. spelta* and the
307 AABB-genome *T. dicoccoides* and *T. dicoccon*, whereas *Ae. tauschii* (DD genome) showed the lowest
308 root colonization (Figure 2a). Accordingly, wheat species containing the A or B genome displayed
309 higher root colonization by F113 than the DD-genome species *Ae. tauschii*, while the presence of the
310 D genome did not have a significant impact (Figure 3b,c,d). Overall, significantly-higher root
311 colonization was observed for tetraploid and hexaploid species compared with diploid species (See
312 Figure 3a), and for domesticated wheats in comparison with wild wheats (Figure 3e).

313 Significant variability in F113 colonisation was found between lines within species, with
314 variation coefficients ranging from 35% for *T. aestivum* landraces and recent cultivars to 100% for *Ae.*
315 *speltoides*, *T. dicoccoides*, *T. dicoccon* and *T. durum* (Figure S5). Among the 331 genotypes studied,
316 the 50 genotypes displaying the highest F113 colonisation levels included 21% of the *T. durum* lines
317 and 14-31% of the *T. aestivum* lines (depending on genotype category), whereas the 50 genotypes
318 displaying the lowest F113 colonisation levels included 21% of the *T. durum* lines but none of the *T.*
319 *aestivum* lines (Table 1). In comparison with *T. aestivum*, the 50 worst genotypes included as much as
320 25% of the *T. spelta* lines. Diploid wheats were little represented among the 50 best genotypes (0 to

321 5.0% of these wheats); in contrast, the 50 worst genotypes included 35% of the *T. urartu* lines (AA
322 genome) and 35% of the *Ae. speltooides* lines (BB {SS} genome), and as much as 80% of the *Ae.*
323 *tauschii* lines (DD genome).

324

325 **3.2. *phl* expression level of *P. ogarae* F113 is higher on roots of hexaploid *T. aestivum***

326 Among all the accessions tested during the screening experiment, some showed no *phl* expression on
327 roots, i.e. *T. dicoccoides* TRI 18531, TRI 18491, TRI 18508, TRI 18486, *T. urartu* TRI 11563, *T.*
328 *spelta* TRI 3419 and *Ae. speltooides* AE 348 (Figures 1b, S3, S5), whereas EGFP-green fluorescence
329 reached up to 1939 AU for *T. aestivum* recent cultivar D130-63 plants (Figures 1b, S3).

330 *T. aestivum* (AABBDD genome), regardless of the category (landraces, old and modern
331 cultivars) presented the highest *phl* expression level by *P. ogarae* F113-*mCherry*(*Pphl-egfp*) on roots
332 (Figure 2b), followed by *T. durum* (AABB genome). Levels with *T. durum* were not significantly
333 different from those with the AA-genome *T. urartu* and the BB {SS}-genome *Ae. speltooides*, but
334 exceeded levels with the DD-genome *Ae. tauschii*, the other AABB-genome species *T. dicoccoides*
335 and *T. dicoccon*, and *T. spelta* (AABBDD genome) (Figure 2b). When considering ploidy status, *phl*
336 expression level on roots was higher for hexaploid than diploid and tetraploid wheat species (Figure
337 3a). Moreover, the categories of wheat genotypes containing genome A, genome B or genome D
338 collectively displayed higher *phl* expression level by F113 when comparing with the categories of
339 genotypes devoid of respectively genome A, B or D (Figure 3b,c,d). Levels of *phl* expression were
340 higher with domesticated wheats than wild wheats (Figure 3e).

341 As for F113 colonization, *phl* expression level was highly variable within each species (i.e.
342 depending on the line), with variation coefficients from 42% for *T. aestivum* landraces to 100% for *T.*
343 *dicoccoides*, *T. dicoccon* and *T. durum* (Figure S5). Among the 50 genotypes showing the highest *phl*
344 expression level on their roots, 19% to 41% (depending on genotype category) of the *T. aestivum* lines
345 were found, but only 5% of the *T. dicoccon* and *T. durum* lines and none of the other species (Table 1).
346 The 50 worst genotypes included none of the *T. aestivum* lines but 40% of the other hexaploid wheat
347 *T. spelta*, 32% to 45% of the tetraploid wheats and 20 to 45% of the diploid wheats (Table 1).

348

349 **3.3. The *phl* induction rate in *P. ogarae* F113 is higher on roots of diploid *Ae. tauschii***

350 The *phl* induction rate (i.e. the green fluorescence: red fluorescence ratio) was not computed for *T.*
351 *urartu* TRI 11563, *Ae. speltooides* AE 348, *Ae. tauschii* AE 724, *T. dicoccoides* TRI 18531, TRI 18491,
352 TRI 18508, TRI 18486 and *T. spelta* TRI 3419, as red and green fluorescence were equal to zero. For
353 the other lines, it reached 0.21 (for *T. dicoccoides* TRI 16630) to 58 AU (for *Ae. tauschii* AE 1632)
354 (Figures 1c, S4).

355 *Ae. tauschii* presented the highest *phl* induction rate, followed by all three categories of *T.*
356 *aestivum*, and then the diploid *Ae. speltooides* and the hexaploid *T. spelta* (Figure 2c). The lowest *phl*
357 induction rate was found with the three tetraploid wheats *T. dicoccoides*, *T. dicoccon* and *T. durum*.
358 Therefore, the *phl* induction rate was lower overall for tetraploids than diploids and hexaploids (the
359 latter did not differ) (Figure 3a), whereas the difference between domesticated and wild wheats was
360 not significant (Figure 3e). The presence of the A genome or the B genome did not have a significant
361 effect (Figure 3b,d), but species with the D genome displayed a higher *phl* induction rate (Figure 3d).

362 The variation coefficient for the *phl* induction rate ranged from 17% for *T. aestivum* old
363 cultivars to 100% for *Ae. speltooides*, *Ae. tauschii* and *T. spelta* (Figure S5). The 50 genotypes
364 displaying the highest *phl* induction rate included 30% of the *Ae. tauschii* lines, 20% of the *T. urartu*
365 lines and 15% of the *Ae. speltooides* lines, but only 0 to 5% of the tetraploid wheat lines (Table 1). The
366 50 worst genotypes were comprised of 40% of the tetraploids *T. dicoccoides* and *T. dicoccon*, 53% of
367 *T. durum* lines and 70% of the hexaploid *T. spelta*, but none of the other hexaploid *T. aestivum*.

368

369 **3.4. Fluorescence screening results were validated statistically by qPCR and qRT-PCR data**

370 When the screening was repeated with 10 lines that had given contrasted results, correlation between
371 red-*mCherry* fluorescence and qPCR of F113 abundance was highly significant ($P = 1.1 \times 10^{-7}$, $n =$
372 40), but with a moderately-high r value of 0.72 (Figure S6a). Similarly, correlation between green-*egfp*
373 fluorescence and qRT-PCR of *phlD* transcripts was highly significant ($P = 1.5 \times 10^{-6}$, $n = 40$), with $r =$
374 0.68 (Figure S6b). When comparing means for the 10 lines, the same statistical relations between lines
375 were found with qPCR of F113 colonisation and with *mCherry*-red fluorescence (Figure S6c,d). In
376 addition, essentially the same statistical relations were obtained with qRT-PCR of *phlD* transcripts and

377 *egfp*-green fluorescence, but the difference between lines AE 1038 and TRI 10450 versus line AE
378 1632 was significant with *egfp*-green fluorescence (Figure S6f) but not with qRT-PCR (Figure S6e).

379

380 **3.5. Rhizosphere colonization by *P. ogarae* F113 in non-sterile soil is higher for *T. durum* than** 381 **for *T. aestivum***

382 In non-sterile soil, after one month of plant growth, SCAR markers corresponding to *P. ogarae* F113
383 were retrieved by qPCR (detection limit of 4.52 log SCAR copies per g of dry root) from 30 of 114
384 non-inoculated plants (13 for *T. aestivum* and 17 for *T. durum*), meaning that indigenous bacteria
385 genetically close to strain F113 were present. When the inoculant was used, SCAR markers were
386 evidenced in 62 of 110 plants (23 for *T. aestivum* and 39 for *T. durum*) (Table S4).

387 Overall, the number of SCAR copies was higher with *T. durum* roots than *T. aestivum* roots,
388 and for both species it was higher with inoculated plants than non-inoculated plants, as expected
389 (Figure S9a). When considering individual lines, the difference between inoculated and non-inoculated
390 plants was significant for *T. durum* lines TRI 11430, TRI 12311, TRI 609 and TRI 732 and for *T.*
391 *aestivum* line Chyaksila Epi Non Velu (Figure S9a). For *T. durum* and for *T. aestivum*, the difference
392 in number of SCAR copies between F113-stimulating and non-stimulating-genotypes was not
393 significant, regardless of whether the analysis was done with inoculated plants, non-inoculated plants,
394 or all plants together. Essentially similar results were found when comparisons were performed using
395 only individual plants for which SCAR copies had been detected (Table S4).

396 The number of *phlD* transcripts was measured for four wheat lines to estimate inoculant
397 functionality. For inoculated wheat, *phlD* transcripts varied from 1.1×10^2 to 1.4×10^6 copies per root
398 system, and for non-inoculated wheat from 4.4×10^1 to 4.5×10^5 copies per root system (Figure S9b),
399 pointing to the occurrence of resident *phl*⁺ pseudomonads, and the number of *phlD* transcripts was
400 higher for inoculated than non-inoculated plants.

401

402 **3.6. Inoculation benefits depend on wheat species and F113 interaction ability**

403 When considering individual lines as replicates (Table 2, Figure S8), using the means for each line
404 (detailed in Figure S7), the relative impact of inoculation was positive on the number of roots, root

405 volume, root surface, dry root biomass (useful to better explore a soil layer), fresh shoot biomass and
406 dry shoot biomass in *T. aestivum*, and on root length (useful to reach deeper soil layers) and root
407 surface in *T. durum*, but at the expense of shoot development (Figure 4a, Table S5). When comparing
408 F113-stimulating vs non F113-stimulating *T. aestivum* genotypes, the relative impact of inoculation
409 was respectively +25% vs +8.6% for dry root biomass, +0.5% vs -3.2% for root average diameter, and
410 +9.6% vs +2.7% for fresh shoot biomass, whereas it was +8.4% vs +22% for root surface, -0.6% vs
411 +50% (difference statistically significant at $P < 0.05$) for the number of roots, +3.3% vs +20% for root
412 volume, -8.4% vs +6.5% for root length, and +2.4% vs +6.6% for dry shoot biomass (Figure 4b). The
413 relative impact of inoculation for F113-stimulating lines, which was positive on root surface and dry
414 root biomass but negative on root length, and positive on fresh shoot biomass but neutral on dry shoot
415 biomass, could mean that the inoculant effect on root functioning benefitted the plant in terms of water
416 acquisition by shoots, without a negative trade-off on shoot development. In contrast, the relative
417 impact of inoculation for non F113-stimulating *T. aestivum* lines, positive (and of high magnitude) on
418 most root parameters, but essentially neutral ($< +10\%$) on fresh and dry shoot biomasses, meant that
419 positive effects on root development did not materialize on shoots.

420 When comparing F113-stimulating vs non F113-stimulating *T. durum* genotypes, the relative
421 impact of inoculation for root diameter was +0.6% in F113-stimulating genotypes vs -0.4% in non
422 F113-stimulating, whereas opposite trends were found for the other parameters (Figure 4b). The
423 relative impact of inoculation for F113-stimulating lines was hardly positive ($< +10\%$) on root length
424 and surface but negative on root number, and on dry shoot biomass, therefore inoculation was not
425 beneficial overall. In contrast, the relative impact of inoculation for non F113-stimulating *T. durum*
426 lines was positive on many root parameters, and essentially neutral (diminution less than 10%) on
427 fresh and dry shoot biomasses, which means beneficial effects were only on root development.

428

429 **4. DISCUSSION**

430

431 The consequences of wheat complex evolutionary history are the apparition of several taxa of wheat
432 differing in terms of (i) genomic content (chromosomes present and ploidy level), (ii) domestication

433 status, (iii) the genus and species they belong to, and (iv) natural and/or human-based selection history
434 (Salamini *et al.*, 2002; Kiszonas and Morris 2018; Pont *et al.*, 2019). In addition, most if not all wheat
435 taxa have diversified considerably afterwards, leading to a wide range of individual lines in each
436 species (Gruet *et al.*, 2022). Different wheat genotypes have different root properties when considering
437 root system architecture, root surface physico-chemical traits, defence mechanisms, and root exudation
438 (Goyal and Asthir 2010; Nakhforoosh *et al.*, 2014; Iannucci *et al.*, 2017; Szoboszlay *et al.*, 2015;
439 Roucou *et al.*, 2018; Gholizadeh *et al.*, 2022). This is likely to lead to contrasted patterns of plant-
440 microbe interactions, as suggested by microbial community-level data available so far, which show
441 that different wheats may select different microbial communities (Tkacz *et al.*, 2020; Iannucci *et al.*,
442 2021; Wipf *et al.*, 2021). However, this type of data is not appropriate to determine to which extent a
443 given type of microorganism will interact with contrasted wheats. On this basis, we focused on the
444 assessment of the model PGPR *P. ogarae* F113, a versatile PGPR capable of interaction with a broad
445 variety of wheat genotypes (Coullerot *et al.*, 2011; Valente *et al.*, 2020) and therefore suitable to
446 quantify the PGPR interaction ability of different wheats. Carbon sources known to be present in root
447 exudates can modulate DAPG production (Duffy and Défago 1999), including in *P. ogarae* F113
448 (Shananan *et al.*, 1992; Rieusset *et al.*, 2021).

449 Plant host genotype plays a significant role in the recruitment of *P. ogarae* F113 by roots and
450 in the expression of *phl* genes (Notz *et al.*, 2001; Landa *et al.*, 2006; de Werra *et al.*, 2008; Vacheron
451 *et al.*, 2016), including in wheats (Valente *et al.*, 2020). In particular, ancient bread wheat genotypes
452 have a higher capability of forming molecular interactions with PGPR in comparison with more recent
453 ones (Valente *et al.*, 2020), but this analysis was restricted to the case of *T. aestivum* and so only a
454 very small fraction of wheat diversity had been targeted. Since all *T. aestivum* genotypes display a
455 same AABBDD profile, these data did not enable to assess the significance of wheat genomic content.
456 In the current work, we tested the hypothesis that wheat genomic architecture was indeed an
457 overriding factor determining the ability for molecular interactions with PGPR.

458 The comparison of 331 wheat lines evidenced a high intra-species variability for F113
459 colonization, *phl* expression level and *phl* induction rate, i.e. contrasted levels of interaction with the
460 PGPR in each of the species. Not the same subset of individual lines could be used when assessing the

461 significance of individual genomes, ploidy level or domestication status, but when considering each
462 factor separately, the R-squared adjusted value in one-way ANOVA or Kruskal tests indicated that
463 individual genomes accounted for 21% of the variability for F113 colonization, 5% for *phl* expression
464 level and 18% for *phl* induction rate, but ploidy level as much as 38% for F113 colonization, 32% for
465 *phl* expression level and 29% for *phl* induction rate. Conversely, domestication status accounted for
466 only 11 % of the variability for F113 colonization, 12% for *phl* expression level and 0.08% for *phl*
467 induction rate. However, care is needed to interpret these metrics, as it must be kept in mind that the
468 particular evolutionary history of wheat species (leading to an unbalanced statistical ‘design’) makes it
469 hard to disentangle the effects of the different factors studied. When the analysis carried out in Figure
470 2 was repeated using only data from tetraploid wheats (i.e., the only genomic context for which both
471 domesticated and wild wheats were available), it gave the same differences shown in Figure 2 for *T.*
472 *durum*, *T. dicoccon* (domesticated) and *T. dicoccoides* (wild).

473 Under gnotobiotic conditions, colonization by F113 and expression level of the *phl* operon
474 varied according to presence/absence of the A, B and D genomes. *phl* expression level can be high
475 even at moderate levels of F113 colonization, and this is visible for wheats containing the D genome,
476 as presence of the D genome is associated with a high *phl* induction rate. Polyploids were better
477 colonized by *P. ogarae* F113 compared with diploid, and *phl* expression was higher on hexaploid
478 roots. Polyploidy confers ecological benefits and new characteristics to plants, enhancing adaptation
479 (te Beest *et al.*, 2012; Soltis *et al.*, 2015), and the current work suggests that it might include the ability
480 to recruit more PGPR and stimulate their functioning, at least in the case of strain F113 and perhaps
481 also closely-related *P. ogarae* genotypes. As for polyploidy, domestication resulted in stronger
482 interactions with PGPR in our study. Domestication has impacted root traits (Szoboszlay *et al.*, 2015;
483 Iannucci *et al.*, 2017; Roucou *et al.*, 2018), as found when assessing wild emmer *T. dicoccoides*,
484 cultivated emmer *T. dicoccon* (its domesticated descendant) and durum wheat. But in contrary to F113
485 colonization and *phl* expression level, *phl* induction rate was not significantly different when
486 comparing domesticated wheats or wild wheats, suggesting that domestication did not impact the
487 ability to trigger *phl* expression, but rather the recruitment of F113. Recent cultivars are mostly dwarf
488 or semi-dwarf varieties created under high fertilization during the Green Revolution (Berry *et al.*,

489 2015), and they display smaller root systems compared with landraces originating from the slow, early
490 selection carried out over several thousand years at low fertilization (Waines and Edhaie, 2007;
491 Roucou *et al.*, 2018). Valente *et al.* (2020) concluded that root colonization by *P. ogarae* F113 and *phl*
492 expression level were higher on ancient *T. aestivum* genotypes (landraces and old cultivars) than on
493 recent cultivars, and that wheat intensive breeding had not favoured the maintenance of plant genes
494 promoting PGPR interactions. Here, these differences between *T. aestivum* landraces, old cultivars and
495 recent cultivars were not significant anymore against the background of the larger variability found
496 with the other genotype categories. Breeding was shown to have a strong impact on the root
497 microbiome, as differences between *T. durum* landraces and recent cultivars were larger than between
498 *T. durum* landraces, *T. dicoccon* and *T. dicoccoides* (Spor *et al.*, 2020), but this did not show up here
499 when considering the interaction potential of the polyvalent PGPR *P. ogarae* F113 in the current
500 conditions.

501 Despite significant differences between genotype categories in their molecular interaction
502 level with *P. ogarae* F113, substantial variability was also found within each of these categories. Since
503 a stronger molecular interaction is likely to lead to better benefits for the plant (Barahona *et al.*, 2011;
504 Podile *et al.*, 2014; Zboralski and Filion, 2020), this observation raises the possibility that certain
505 individual lines may display the same level of benefits from *P. ogarae* F113 despite belonging to
506 different genotype categories. To test this hypothesis, a greenhouse experiment in non-sterile soil was
507 carried out using ten lines with strong F113 interaction in the screening experiment (five *T. aestivum*
508 and five *T. durum*) vs ten lines with a weak F113 interaction (five *T. aestivum* and five *T. durum*). This
509 was done under moderate stress (progressive drought), as (i) PGPR inoculation impact on plants is
510 stronger under stress conditions (Fasciglione *et al.*, 2015), (ii) *P. ogarae* F113 displays relevant traits
511 i.e. synthesis of the root system branching signal DAPG (Brazelton *et al.*, 2008) as well as ACC
512 deaminase activity, *etc.*, and (iii) strain F113 can be effective at alleviating drought stress in wheat
513 (Valente *et al.*, 2020). In addition, wheat response to drought varies according to the genotype
514 (Vassileva *et al.*, 2009; Budak *et al.*, 2013), and expression partitioning (i.e. different expression
515 patterns of homeolog genes) was observed during *T. aestivum* acclimation to drought (Liu *et al.*,
516 2015).

517 For F113-stimulating lines, the inoculant effect on root functioning benefitted the plant in
518 terms of water acquisition by shoots without a negative trade-off on shoot development in *T. aestivum*,
519 but inoculation was not beneficial overall in *T. durum*. For non F113-stimulating lines, the relative
520 impact of inoculation was positive on most (*T. aestivum*) or many (*T. durum*) root parameters, but it
521 was essentially neutral (<10%) on shoots. The negative inoculation impact in F113-stimulating *T.*
522 *durum* resulted perhaps from phytotoxic effects of DAPG if produced at too high concentration (Keel
523 *et al.*, 1992; Brazelton *et al.*, 2008), as data for highly-colonized TRI 12311 suggest. Therefore, the
524 assessment of PGPR interaction potential in simplified non-stress conditions need to be expanded to
525 include other types of plant-beneficial microorganisms occurring in soil and to consider more complex
526 soil conditions and the occurrence of stress. It is also worth keeping in mind that the current work
527 focused on phytostimulation only, and it would be of interest to consider also the biocontrol potential
528 of *P. ogarae* F113.

529

530 **5. CONCLUSION**

531

532 Wheat genomic content had a stronger influence than domestication on the interaction potential with
533 *P. ogarae* F113. Presence of the D genome was associated with a high *phl* induction rate whereas
534 polyploidy proved also significant, but the latter deserves further research as the experimental set-up
535 did not provide a sufficiently balanced design to assess this issue. This approach performed with a
536 model wheat-adapted PGPR establishes a proof of principle and could be useful to complement
537 microbiome-based strategies to identify PGPR-friendly genotypes for future wheat breeding strategies.

538

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542

543 **CONFLICT OF INTEREST**

544 The authors declare no conflict of interest.

545

546 **DATA AVAILABILITY STATEMENT**

547 All data are available in this manuscript.

548

549 **SUPPLEMENTARY MATERIAL**

550 The Supplementary Material for this article can be found online.

551

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808

809 **Legends**

810

811 **FIGURE 1.** Root colonization (A), *phl* expression level (B) and *phl* induction rate (C) of *P. ogarae*
812 F113-*mCherry*(*Pphl-egfp*) for individual accessions of eight wheat species. Root colonization and *phl*
813 expression were assessed based on red and green fluorescences (expressed in arbitrary units),
814 respectively, whereas the *phl* induction rate was the ratio between green fluorescence and red
815 fluorescence. Data are shown as means with standard deviations (n = 3), and those for *T. aestivum*
816 originate from Valente *et al.* (2020).

817

818 **FIGURE 2.** Root colonization (A), *phl* expression level (B) and *phl* induction rate (C) of *P. ogarae*
819 F113-*mCherry*(*Pphl-egfp*) according to wheat species and *T. aestivum* genotype category. Root
820 colonization and *phl* expression level were assessed based on red and green fluorescences (expressed
821 in arbitrary units; standardized to root length), respectively, whereas the *phl* induction rate was the
822 ratio between green fluorescence and red fluorescence. AA genome is represented in burgundy, BB
823 genome in salmon, DD genome in blue, AABB in green and AABBDD in purple. The ploidy status is
824 indicated. The horizontal stripes indicate domesticated species, while the others are wild species. Data
825 were computed using individual lines (in Figure 1) as replicates and are shown as means with standard
826 errors (n = 20 for *T. urartu*, *Ae. speltooides*, *Ae. tauschii*, *T. dicoccoides* and *T. dicoccon*, n = 19 for *T.*
827 *durum*, n = 35 for *T. aestivum* landraces, n = 42 for *T. aestivum* old cultivars and n = 115 for *T.*
828 *aestivum* modern cultivars), and those for *T. aestivum* originate from Valente *et al.* (2020). Statistical
829 differences are shown with letters a to e (nested ANOVA and Tukey's HSD tests, $P < 0.05$)

830

831 **FIGURE 3.** Root colonization, *phl* expression level and *phl* induction rate of *P. ogarae* F113-
832 *mCherry*(*Pphl-egfp*) depending on ploidy status (A), presence of the A genome (B), presence of the B
833 genome (C), presence of the D genome (D) and domestication status (E). Root colonization and *phl*
834 expression level were assessed based on red and green fluorescences (expressed in arbitrary units),
835 respectively, whereas the *phl* induction rate was the ratio between green fluorescence and red

836 fluorescence. Data were computed using individual lines (in Figure 1) as replicates and are shown as
837 means with standard deviations (successively from left to right: n = 60, 59 and 212 for ploidy status, n
838 = 291 and 40 for A genome presence or absence, n = 291 and 40 for B genome presence or absence, n
839 = 232 and 99 for D genome presence or absence, and n = 80 and 251 for domestication status), and
840 those for *T. aestivum* originate from Valente *et al.* (2020). Statistical differences are shown with letters
841 a and b (ANOVA and Tukey's HSD tests, $P < 0.05$).

842

843 **FIGURE 4.** Relative impact of seed inoculation with *P. ogarae* F113 on the growth of *T. aestivum*
844 and *T. durum*. Data are shown globally for *T. aestivum* and *T. durum* (A), as well as by considering
845 F113-stimulating genotypes (strong interaction scores) and non F113-stimulating genotypes (weak
846 interaction scores) of *T. aestivum* (B) and *T. durum* (C). For each of the eight plant parameters
847 investigated, the relative impact of inoculation was computed as (inoculated – non-inoculated) / non-
848 inoculated, using individual lines as replicates (see details in Figure S8 and Table S2). Differences
849 between *T. aestivum* and *T. durum* were not significant at $P < 0.05$. The relative impact on the number
850 of roots of *T. aestivum* was higher for non F113-stimulating genotypes than F113-stimulating
851 genotypes, whereas the other differences between F113-stimulating and non F113-stimulating
852 genotypes were not significant at $P < 0.05$ level, for *T. aestivum* and *T. durum*.

853

TABLE 1. Percentages of lines in each wheat species category showing the highest or lowest values for root colonization and *phl* expression by *P. ogarae* F113. The number of lines was n = 20 for *T. urartu*, *Ae. speltooides*, *Ae. tauschii*, *T. dicoccoides*, *T. dicoccon*, *T. spelta*, n = 19 for *T. durum*, n = 35 for *T. aestivum* landraces, n = 42 for *T. aestivum* old cultivars and n = 115 for *T. aestivum* modern cultivars.

	<i>T. urartu</i>	<i>Ae. speltooides</i>	<i>Ae. tauschii</i>	<i>T. dicoccoides</i>	<i>T. dicoccon</i>	<i>T. durum</i>	<i>T. spelta</i>	<i>T. aestivum</i> (landraces)	<i>T. aestivum</i> (old cultivars)	<i>T. aestivum</i> (modern cultivars)
Root colonization by F113										
50 best genotypes	0.0%	5.0%	0.0%	15.0%	10.0%	21.0%	20.0%	20.0%	31.0%	14.0%
50 worst genotypes	35.0%	35.0%	80.0%	25.0%	20.0%	31.5%	25.0%	0.0%	0.0%	0.0%
<i>phl</i> expression level in F113										
50 best genotypes	0.0%	0.0%	0.0%	0.0%	5.0%	5.3%	0.0%	25.7%	40.5%	19.1%
50 worst genotypes	25.0%	20.0%	45.0%	45.0%	45.0%	31.5%	40.0%	0.0%	0.0%	0.0%
<i>phl</i> induction rate in F113										
50 best genotypes	20.0%	15.0%	30.0%	5.0%	0.0%	0.0%	0.0%	11.4%	19.0%	19.1%
50 worst genotypes	25.0%	15.0%	10.0%	40.0%	40.0%	52.6%	70.0%	0.0%	0.0%	0.0%

TABLE 2. Relative impact of seed inoculation with *P. ogarae* F113 on the growth of ten *T. aestivum* and ten *T. durum* lines. For each of the eight parameters investigated, the relative impacts were computed as (inoculated - non-inoculated) / non-inoculated. This table details Figure 4. Significant differences between inoculated plant and controls are indicated in bold ($P < 0.05$; detailed in Figure S7). Differences between F113-stimulating genotypes and non F113-stimulating genotypes were not significant for *T. aestivum* and *T. durum*, except for the number of roots of *T. aestivum*, for which non F113-stimulating genotypes displayed a higher relative impact of seed inoculation than F113-stimulating genotypes.

	Dry root biomass	Fresh shoot biomass	Dry shoot biomass	Root surface	Root average diameter	Root length	Root volume	Number of roots
<i>T. aestivum</i>								
<i>F113-stimulating genotypes</i>								
BORDEAUX 113	-15.0%	3.1%	-2.7%	25.3%	0.0%	4.2%	7.1%	-29.8%
BLE BARBU DE MUROL	-6.7%	28.9%	36.5%	-1.6%	3.9%	-18.7%	-7.8%	5.5%
ROUGE DE MARCHISSY	-28.0%	-30.8%	-32.9%	-9.9%	8.0%	-11.1%	-6.9%	-20.4%
NON PLUS EXTRA	94.7%	9.9%	-5.4%	24.6%	-4.6%	-27.7%	17.1%	17.6%
CANDEAL DE AREVALO	81.3%	36.7%	16.7%	3.5%	-4.9%	11.2%	7.0%	23.9%
<i>Non F113-stimulating genotypes</i>								
CHYAKSILA EPI NON VELU	35.5%	-0.4%	19.9%	-6.3%	-7.1%	-6.3%	4.0%	26.4%
TAU BUGDA	-25%	-0.3%	-5.5%	40.9%	2.9%	12.8%	2.5%	-8.2%
FRUH WEIZEN	12.1%	-8.3%	1.6%	-19.5%	-13.6%	-28.9%	95.9%	32.1%
BLANC PRECOCE	53.6%	7.3%	6.2%	96.6%	11.4%	42.8%	3.9%	28.8%
ROUGE D'ALTKIRCH	-32.9	14.6%	10.9%	0.4%	-9.4%	11.4%	0.1%	134.2%
<i>T. durum</i>								
<i>F113-stimulating genotypes</i>								
TRI 9517	15.9%	-49.3%	-55.9%	-23.4%	3.7%	-13.8%	0.3%	-43.0%
TRI 10450	19.1%	28.1%	9.4%	17.9%	0.2%	21.8%	0.5%	9.0%
TRI 11430	0.0%	-24.2%	-7.5%	23.3%	-5.0%	38.1%	5.3%	1.3%
TRI 12311	-78.4%	-7.3%	-20.8%	34.2%	12.4%	19.3%	-17.5%	-49.8%
TRI 7871	9.9%	14.7%	17.3%	-30.9%	-8.3%	-36.5%	-1.1%	6.2%
<i>Non F113-stimulating genotypes</i>								
TRI 17796	33.3%	8.4%	12.8%	-21.9%	-3.4%	-27.4%	-4.3%	23.2%
TRI 16846	-33.3%	-17.9%	-16.3%	-2.1%	-2.2%	-13.6%	-9.1%	-36.4%
TRI 732	-35.7%	-16.7%	-13.0%	40.0%	-1.0%	61.8%	2.8%	10.8%
TRI 11542	42.8%	-5.3%	1.8%	18.1%	4.4%	24.7%	16.3%	40.5%
TRI 609	-0.2%	-3.4%	0.0%	31.8%	0.1%	0.4%	-0.1%	-0.2%