

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

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1	Genomic content of wheat has a higher influence than plant domestication status on the ability
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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. While root colonization was higher for hexaploid and tetraploid species, and *phl* expression level 37 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.

#### 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 and Smalla, 2009; Philippot et al., 2013). Plant genotype has also the potential to influence 55 rhizosphere colonization by individual PGPR strains (Johansson et al., 2014; Vacheron et al., 2016) 56 57 and the functioning of beneficial plant-microbe interactions (Salem et al., 2018; Samain et al., 2019). However, current knowledge is insufficient to predict, for a given plant genotype, rhizosphere 58 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., 2017; Martin-Robles et al., 2017; Mendes et al., 2018; Abdullaeva et al., 2022). In bread wheat 65 (Triticum aestivum), Valente et al. (2020) showed that root colonization and expression of phl gene 66 (coding for 2.4-diacetylphloroglucinol [DAPG] synthesis) by the model PGPR Pseudomonas ogarae 67 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), wheat accessions that displayed a strong interaction potential with P. ogarae F113 (i.e. determined 78 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 genome hybridization events (Marcussen et al., 2014; Glémin et al., 2019; Pont et al., 2019), 86 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 98 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 phl expression in P. ogarae 108 F113-mCherry(Pphl-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 19<sup>th</sup> century to 1960, and 114 modern genotypes developed after 1960 and carrying semi-dwarf Rht 121 122 alleles; Borojevic and Borojevic, 2005). All lines were selected from the wheat collection of the Leibniz Institute of Plant Genetics and Crop Plant Research (Gatersleben, Germany) for their 123 124 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).

#### 129 **2.2. Inoculum for the screening**

The screening experiment was performed with P. ogarae F113-mCherry(Pphl-egfp). This strain 130 131 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 expression of *mCherry*, and the promoter of the *phl* operon fused to the promotorless reporter gene 133 134 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 mL<sup>-1</sup>) and gentamycin (25 µg mL<sup>-1</sup>) at 28°C and 180 rpm, then overnight in Minimal Medium (MM) 137 138 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 MgSO<sub>4</sub> and OD<sub>600</sub> was adjusted to 8.0 (corresponding to 10<sup>9</sup> CFU mL<sup>-1</sup>). Pre-germinated wheat seeds (described below) were inoculated with 140 141 50 µL of cell suspension containing  $5 \times 10^7$  CFU.

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#### 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 (Na<sub>2</sub>CO<sub>3</sub> 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 (Sigma-Aldrich, St Louis, MO, USA) at 8 g L<sup>-1</sup> for 24 h in the dark at 28°C, and the seedlings were 150 151 then transferred in  $120 \times 120$  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  $\mu$ L of 153 MgSO<sub>4</sub>), 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. Seedlings grew without touching/lifting the lid during the 7-day-incubation. 155

#### 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 MgSO<sub>4</sub> and a steel bead (5 mm diameter). Roots were ground for 1 min (twice) with a FastPrep-24 Classic Instrument (MP Biomedicals, Santa Ana, CA, USA) at maximum speed (6 m s<sup>-1</sup>). 161 The tubes were centrifuged 2 min at 2000 rpm to pellet the biggest debris. 200 µL of each supernatant 162 163 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.

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#### 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 ten lines, the root systems of four inoculated plantlets were treated as above to measure red 183 184 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 plantlets were also ground but without a steel bead, for 5 min, twice. The supernatants were then used 189 190 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 µL 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 µL 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  $\mu$ 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.

The abundance of *P. ogarae* F113 was determined by qPCR from DNA samples using strainspecific primers F113\_1\_for and F113\_1\_rev, targeting sequence-characterized amplified region (SCAR), as described (Von Felten *et al.*, 2010). The number of *phlD* transcripts was estimated from cDNA samples using primers B2BR3 and B2BF, as described (Almario *et al.*, 2013). See Figure S6 for PCR methodology.

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#### 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 Candeal de Arévalo (strong F113 interaction), and Chyaksila Epi Non Velu, Tau Bugda, Fruh Weizen, Blanc 211 212 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 16%, silt 44%, sand 40%; 2.1% organic matter, pH 7, cation exchange capacity 8.2 cmol kg<sup>-1</sup>) from La 216 Côte Saint-André near Lyon (France). In the inoculated pot, each seed received 200 µL of a cell 217 218 suspension (obtained as described above) of *P. ogarare* F113, containing  $2.5 \times 10^6$  CFU, whereas in the non-inoculated pots, seeds received 200 µL of 10-mM MgSO4. Pots were placed in a greenhouse 219 220 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.

#### 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 F113\_1\_for and F113\_1\_rev of Von Felten et al. (2010) (see above). Results obtained in g µL<sup>-1</sup> were 246 247 transformed into numbers of copies using the formula [DNA (g)  $\times$  Avogadro's number (molecules  $mol^{-1}$ ]/[number of DNA bp in amplified fragments × 660 (g mol<sup>-1</sup>)], based on an average of 660 g 248 mol<sup>-1</sup> per base pair. 249

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#### 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*<sup>+</sup> 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  $1 \times$  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 RNA extract with the Omniscript reverse transcription kit (Qiagen). Quantification of *phlD* transcripts 265

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

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#### 269 **2.9. Statistics**

All analyses were done at P < 0.05, using R 4.0.3 software (https://www.r-project.org). All data and residuals were checked for normal distribution and homogeneity of variance. Variation 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), Kruskall-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).

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

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

interaction'). Moreover, a two-way ANOVA and Tukey's HSD tests were performed with the two
factors inoculation status × 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

Red *mCherry* fluorescence measured in the gnotobiotic screening experiment, to assess root colonization by *P. ogarae* F113-*mCherry*(P*phl-egfp*), ranged from 0 (for *T. dicoccoides* lines TRI 18531, TRI 18491, TRI 18508, TRI 18486, *T. urartu* line TRI 11563, *T. spelta* line TRI 3419, *Ae. speltoides* line AE 348) to 931 arbitrary units (AU) for *T. durum* line TRI 9517 after 7 days of growth (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 5.0% of these wheats); in contrast, the 50 worst genotypes included 35% of the *T. urartu* lines (AA
genome) and 35% of the *Ae. speltoides* lines (BB {SS} genome), and as much as 80% of the *Ae. tauschii* lines (DD genome).

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

Among all the accessions tested during the screening experiment, some showed no *phl* expression on roots, i.e. *T. dicoccoides* TRI 18531, TRI 18491, TRI 18508, TRI 18486, *T. urartu* TRI 11563, *T. spelta* TRI 3419 and *Ae. speltoides* AE 348 (Figures 1b, S3, S5), whereas EGFP-green fluorescence 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. speltoides, 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).

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

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

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

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

The variation coefficient for the *phl* induction rate ranged from 17% for *T. aestivum* old cultivars to 100% for *Ae. speltoides, Ae. tauschii* and *T. spelta* (Figure S5). The 50 genotypes displaying the highest *phl* induction rate included 30% of the *Ae. tauschii* lines, 20% of the *T. urartu* lines and 15% of the *Ae. speltoides* lines, but only 0 to 5% of the tetraploid wheat lines (Table 1). The 50 worst genotypes were comprised of 40% of the tetraploids *T. dicoccoides* and *T. dicoccon*, 53% of *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

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

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

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

401

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

When considering individual lines as replicates (Table 2, Figure S8), using the means for each line (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 species (Gruet et al., 2022). Different wheat genotypes have different root properties when considering 436 437 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 variety of wheat genotypes (Couillerot et al., 2011; Valente et al., 2020) and therefore suitable to 445 quantify the PGPR interaction ability of different wheats. Carbon sources known to be present in root 446 447 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.

The comparison of 331 wheat lines evidenced a high intra-species variability for F113 colonization, *phl* expression level and *phl* induction rate, i.e. contrasted levels of interaction with the 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 Kruskall 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 phl expression level and 29% for phl induction rate. Conversely, domestication status accounted for 465 only 11 % of the variability for F113 colonization, 12% for phl expression level and 0.08% for phl 466 467 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 expression level were higher on ancient T. aestivum genotypes (landraces and old cultivars) than on 492 493 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 recent cultivars were not significant anymore against the background of the larger variability found 495 496 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 was done under moderate stress (progressive drought), as (i) PGPR inoculation impact on plants is 509 510 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 patterns of homeolog genes) was observed during T. aestivum acclimation to drought (Liu et al., 515 516 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

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

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809 Legends

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

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FIGURE 2. Root colonization (A), phl expression level (B) and phl induction rate (C) of P. ogarae 818 819 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. speltoides, 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)

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FIGURE 3. Root colonization, *phl* expression level and *phl* induction rate of *P. ogarae* F113*mCherry*(P*phl-egfp*) depending on ploidy status (A), presence of the A genome (B), presence of the B genome (C), presence of the D genome (D) and domestication status (E). Root colonization and *phl* expression level were assessed based on red and green fluorescences (expressed in arbitrary units), respectively, whereas the *phl* induction rate was the ratio between green fluorescence and red fluorescence. Data were computed using individual lines (in Figure 1) as replicates and are shown as means with standard deviations (successively from left to right: n = 60, 59 and 212 for ploidy status, n = 291 and 40 for A genome presence or absence, n = 291 and 40 for B genome presence or absence, n = 232 and 99 for D genome presence or absence, and n = 80 and 251 for domestication status), and those for *T. aestivum* originate from Valente *et al.* (2020). Statistical differences are shown with letters a and b (ANOVA and Tukey's HSD tests, P < 0.05).

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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*.

**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. speltoides, 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.

	T urartu	Ae. speltoides	Ae. tauschii	T. dicoccoides	T. dicoccon	T. durum	T. spelta	T. aestivum	T. aestivum (old	T. aestivum
	<b>1</b> . <i>u</i> / <i>u</i> / <i>i</i> / <i>i</i>							(landraces)	cultivars)	(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%
phl 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%
phl 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
T. aestivum								
F113-stimulating genotypes								
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%
Non F113-stimulating genotypes								
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%
T. durum								
F113-stimulating genotypes								
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%
Non F113-stimulating genotypes								
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%