



**HAL**  
open science

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

Cécile Gruet, Maroua Alaoui, Florence Gerin, Claire Prigent-Combaret, Andreas Börner, Daniel Muller, Yvan Moënne-Loccoz

## ► To cite this version:

Cécile Gruet, Maroua Alaoui, Florence Gerin, Claire Prigent-Combaret, Andreas Börner, et al.. Genomic content of wheat has a higher influence than plant domestication status on the ability to interact with *Pseudomonas* plant growth-promoting rhizobacteria. *Plant, Cell and Environment*, 2023, 46 (12), pp.3933-3948. 10.1111/pce.14698 . hal-04245524

**HAL Id: hal-04245524**

**<https://hal.science/hal-04245524v1>**

Submitted on 14 Nov 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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**

3  
4

5 Cécile Gruet<sup>1</sup>, Maroua Alaoui<sup>1</sup>, Florence Gerin<sup>1</sup>, Claire Prigent-Combaret<sup>1</sup>, Andreas Börner<sup>2</sup>, Daniel  
6 Muller<sup>1</sup>, Yvan Moëgne-Loccoz<sup>1</sup>

7

8 <sup>1</sup>Univ Lyon, Université Claude Bernard Lyon 1, CNRS, INRAE, VetAgro Sup, UMR5557 Ecologie  
9 Microbienne, 43 bd du 11 Novembre 1918, 69622 Villeurbanne, France

10 <sup>2</sup>Genebank Department, Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Corrensstr.  
11 3, 06466 Seeland, OT Gatersleben, Germany

12

13 **Correspondence**

14 Yvan Moëgne-Loccoz, Université Claude Bernard Lyon 1, UMR5557 Ecologie Microbienne, 43 bd  
15 du 11 Novembre 1918, 69622 Villeurbanne, France

16 Email: yvan.moenne-locco@univ-lyon1.fr

17

18 **ORCID**

19 Cécile Gruet 0000-0001-8667-0838

20 Claire Prigent-Combaret 0000-0001-8968-0660

21 Andreas Börner 0000-0003-3301-9026

22 Daniel Muller 0000-0002-6619-4691

23 Yvan Moëgne-Loccoz 0000-0002-9817-1953

24

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 19<sup>th</sup> 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<sup>-1</sup>) and gentamycin (25 µg mL<sup>-1</sup>) 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 MgSO<sub>4</sub> and OD<sub>600</sub> was adjusted to 8.0  
140 (corresponding to 10<sup>9</sup> CFU mL<sup>-1</sup>). Pre-germinated wheat seeds (described below) were inoculated with  
141 50 µL of cell suspension containing 5 × 10<sup>7</sup> 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 (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  
150 (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  
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 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.  
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 MgSO<sub>4</sub> 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<sup>-1</sup>).  
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  $\mu$ 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  $\mu$ 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  $\mu$ 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.

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<sup>-1</sup>) 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 × 10<sup>6</sup> CFU, whereas in  
219 the non-inoculated pots, seeds received 200 µL of 10-mM MgSO<sub>4</sub>. 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<sup>-1</sup> were  
247 transformed into numbers of copies using the formula [DNA (g) × Avogadro's number (molecules  
248 mol<sup>-1</sup>)]/[number of DNA bp in amplified fragments × 660 (g mol<sup>-1</sup>)], based on an average of 660 g  
249 mol<sup>-1</sup> 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*<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× 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  $1.1 \times 10^2$  to  $1.4 \times 10^6$  copies per root  
398 system, and for non-inoculated wheat from  $4.4 \times 10^1$  to  $4.5 \times 10^5$  copies per root system (Figure S9b),  
399 pointing to the occurrence of resident *phl*<sup>+</sup> 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 (Couillerot *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

## 539 **ACKNOWLEDGMENTS**

540 This work made use of Serre and DTAMB platforms of FR3728 BioEnviS at Université Lyon 1. We  
541 thank D. Abrouk for help with statistics.

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

552 **REFERENCES**

553

554 Abdullaeva Y, Ambika Manirajan B, Honermeier B, Schnell S, Cardinale M. 2021. Domestication  
555 affects the composition, diversity, and co-occurrence of the cereal seed microbiota. *Journal of*  
556 *Advanced Research* 31: 75–86.

557 Almario J, Moëgne-Loccoz Y, Muller D. 2013. Monitoring of the relation between 2,4-  
558 diacetylphloroglucinol-producing *Pseudomonas* and *Thielaviopsis basicola* populations by real-  
559 time PCR in tobacco black root-rot suppressive and conducive soils. *Soil Biology and*  
560 *Biochemistry* 57: 144–155.

561 Anderson JT, Willis JH, Mitchell-Olds T. 2011. Evolutionary genetics of plant adaptation. *Trends in*  
562 *Genetics* 27: 258–266.

563 Andreote FD, Rossetto PB, Mendes R, Avila LA, Labate CA, Pizzirani-Kleiner AA, Azevedo JL,  
564 Araújo WL. 2009. Bacterial community in the rhizosphere and rhizoplane of wild type and  
565 transgenic eucalyptus. *World Journal of Microbiology and Biotechnology* 25: 1065–1073.

566 Badri DV, Vivanco JM. 2009. Regulation and function of root exudates. *Plant, Cell & Environment*  
567 32: 666–681.

568 Baidouri ME, Murat F, Veyssiere M, Molinier M, Flores R, Burlot L, Alaux M, Quesneville H, Pont  
569 C, Salse J. 2017. Reconciling the evolutionary origin of bread wheat (*Triticum aestivum*). *The*  
570 *New Phytologist* 213: 1477–1486.

571 Barahona E, Navazo A, Martínez-Granero F, Zea-Bonilla T, Pérez-Jiménez RM, Martín M, Rivilla R.  
572 2011. *Pseudomonas fluorescens* F113 mutant with enhanced competitive colonization ability and  
573 improved biocontrol activity against fungal root pathogens. *Applied and Environmental*  
574 *Microbiology* 77: 5412–5419.

575 Berg G, Smalla K. 2009. Plant species and soil type cooperatively shape the structure and function of  
576 microbial communities in the rhizosphere. *FEMS Microbiology Ecology* 68: 1–13.

577 Bonjean A. 2001. Histoire de la culture des céréales et en particulier de celle du blé tendre (*Triticum*  
578 *aestivum* L.). *Dossier de l'environnement de l'INRA* 21: 29-37.

579 Borojevic K, Borojevic K. 2005. The transfer and history of “reduced height genes” (Rht) in wheat  
580 from Japan to Europe. *Journal of Heredity* 96: 455–459.

581 Bouffaud M, Poirier M, Muller D, Moënne- Loccoz Y. 2014. Root microbiome relates to plant host  
582 evolution in maize and other Poaceae. *Environmental Microbiology* 16: 2804–2814.

583 Bouffaud M-L, Renoud S, Dubost A, Moënne-Loccoz Y, Muller D. 2018. 1-aminocyclopropane-1-  
584 carboxylate deaminase producers associated to maize and other Poaceae species. *Microbiome* 6:  
585 114.

586 Bouffaud M-L, Renoud S, Moënne-Loccoz Y, Muller D. 2016. Is plant evolutionary history impacting  
587 recruitment of diazotrophs and *nifH* expression in the rhizosphere? *Scientific Reports* 6: 1–9.

588 Brazelton JN, Pfeufer EE, Sweat TA, McSpadden Gardener BB, Coenen C. 2008. 2,4-  
589 diacetylphloroglucinol alters plant root development. *Molecular Plant-Microbe Interactions* 21:  
590 1349–1358.

591 Budak H, Kantar M, Yucebilgili Kurtoglu K. 2013. Drought tolerance in modern and wild wheat. *The*  
592 *Scientific World Journal* 2013: e548246.

593 Chae D-H, Kim D-R, Cheong MS, Lee YB, Kwak Y-S. 2020. Investigating the induced systemic  
594 resistance mechanism of 2,4-diacetylphloroglucinol (DAPG) using DAPG hydrolase-transgenic  
595 *Arabidopsis*. *Plant Pathology Journal* 36: 255–266.

596 Chagué V, Just J, Mestiri I, Balzergue S, Tanguy A, Huneau C, Huteau V, Belcram H, Coriton O,  
597 Jahier J, Chalhoub B. 2010. Genome- wide gene expression changes in genetically stable  
598 synthetic and natural wheat allohexaploids. *The New Phytologist* 187: 1181–1194.

599 Costa R, Gomes NCM, Krögerrecklenfort E, Opelt K, Berg G, Smalla K. 2007. *Pseudomonas*  
600 community structure and antagonistic potential in the rhizosphere: insights gained by combining  
601 phylogenetic and functional gene-based analyses. *Environmental Microbiology* 9: 2260–2273.

602 Couillerot O, Combes-Meynet E, Pothier JF, Bellvert F, Challita E, Poirier M-A, Rohr R, Comte G,  
603 Moënne-Loccoz Y, Prigent-Combaret C. 2011. The role of the antimicrobial compound 2,4-  
604 diacetylphloroglucinol in the impact of biocontrol *Pseudomonas fluorescens* F113 on  
605 *Azospirillum brasilense* phytostimulators. *Microbiology* 157: 1694–1705.



606 de Werra P, Baehler E, Huser A, Keel C, Maurhofer M. 2008. Detection of plant-modulated  
607 alterations in antifungal gene expression in *Pseudomonas fluorescens* CHA0 on roots by flow  
608 cytometry. *Applied and Environmental Microbiology* 74: 1339–1349.

609 Doornbos RF, van Loon LC, Bakker PAHM. 2012. Impact of root exudates and plant defense  
610 signaling on bacterial communities in the rhizosphere. A review. *Agronomy for Sustainable  
611 Development* 32: 227–243.

612 Duffy BK, Défago G. 1999. Environmental factors modulating antibiotic and siderophore biosynthesis  
613 by *Pseudomonas fluorescens* biocontrol strains. *Applied and Environmental Microbiology* 65:  
614 2429–2438.

615 Fasciglione G, Casanovas E, Quillehauquy V, Yommi A, Goñi M, Roura S, Barassi C. 2015.  
616 *Azospirillum* inoculation effects on growth, product quality and storage life of lettuce plants  
617 grown under salt stress. *Scientia Horticulturae* 195: 154–162.

618 Feldman M, Kislev ME. 2007. Domestication of emmer wheat and evolution of free-threshing  
619 tetraploid wheat. *Israel Journal of Plant Sciences* 55: 207–221.

620 Fromin N, Achouak W, Thiéry JM, Heulin T. 2001. The genotypic diversity of *Pseudomonas  
621 brassicacearum* populations isolated from roots of *Arabidopsis thaliana*: influence of plant  
622 genotype. *FEMS Microbiology Ecology* 37: 21–29.

623 García de Salamone IE, Hynes RK, Nelson LM. 2001. Cytokinin production by plant growth  
624 promoting rhizobacteria and selected mutants. *Canadian Journal of Microbiology* 47: 404–411.

625 Gayon J, Zallen DT. 1998. The role of the Vilmorin company in the promotion and diffusion of the  
626 experimental science of heredity in France, 1840-1920. *Journal of the History of Biology* 31:  
627 241–262.

628 Gholizadeh S, Mohammadi SA, Salekdeh GH. 2022. Changes in root microbiome during wheat  
629 evolution. *BMC Microbiology* 22: 64.

630 Glémin S, Scornavacca C, Dainat J, Burgarella C, Viader V, Ardisson M, Sarah G, Santoni S, David J,  
631 Ranwez V. 2019. Pervasive hybridizations in the history of wheat relatives. *Science Advances* 5:  
632 eaav9188.

633 Golan G, Hendel E, Espitia GEM, Schwartz N, Peleg Z. 2018. Activation of seminal root primordia  
634 during wheat domestication reveals underlying mechanisms of plant resilience. *Plant, Cell &*  
635 *Environment* 41: 755–766.

636 Goyal M, Asthir B. 2010. Polyamine catabolism influences antioxidative defense mechanism in shoots  
637 and roots of five wheat genotypes under high temperature stress. *Plant Growth Regulation* 60:  
638 13–25.

639 Gruet C, Muller D, Moëgne-Loccoz Y. 2022. Significance of the diversification of wheat species for  
640 the assembly and functioning of the root-associated microbiome. *Frontiers in Microbiology* 12:  
641 4000.

642 Haichar F el Z, Marol C, Berge O, Rangel-Castro JI, Prosser JI, Balesdent J, Heulin T, Achouak W.  
643 2008. Plant host habitat and root exudates shape soil bacterial community structure. *The ISME*  
644 *Journal* 2: 1221–1230.

645 Hao M, Li A, Shi T, Luo J, Zhang L, Zhang X, Ning S, Yuan Z, Zeng D, Kong X, Li X, Zheng H, Lan  
646 X, Zhang H, Zheng Y, Mao L, Liu D. 2017. The abundance of homoeologue transcripts is  
647 disrupted by hybridization and is partially restored by genome doubling in synthetic hexaploid  
648 wheat. *BMC Genomics* 18: 149.

649 Iannucci A, Canfora L, Nigro F, De Vita P, Beleggia R. 2021. Relationships between root  
650 morphology, root exudate compounds and rhizosphere microbial community in durum wheat.  
651 *Applied Soil Ecology* 158: 103781.

652 Iannucci A, Fragasso M, Beleggia R, Nigro F, Papa R. 2017. Evolution of the crop rhizosphere:  
653 Impact of domestication on root exudates in tetraploid wheat (*Triticum turgidum* L.). *Frontiers in*  
654 *Plant Sciences* 8: 2124.

655 Imperiali N, Chiriboga X, Schlaeppi K, Fesselet M, Villacrés D, Jaffuel G, Bender SF, Dennert F,  
656 Blanco-Pérez R, van der Heijden MGA, Maurhofer M, Mascher F, Turlings TCJ, Keel CJ,  
657 Campos-Herrera R. 2017. Combined field inoculations of *Pseudomonas* bacteria, Arbuscular  
658 Mycorrhizal Fungi, and entomopathogenic nematodes and their effects on wheat performance.  
659 *Frontiers in Plant Sciences* 8: 1809.

660 Ito N, Mori N, Miyashita NT. 2020. Rhizospheric bacterial community structure of *Triticum* and  
661 *Aegilops* revealed by pyrosequencing analysis of the 16S rRNA gene: dominance of the A  
662 genome over the B and D genomes. *Genes Genetic System* 95: 249–268.

663 Jack CN, Wozniak KJ, Porter SS, Friesen ML. 2019. Rhizobia protect their legume hosts against soil-  
664 borne microbial antagonists in a host-genotype-dependent manner. *Rhizosphere* 9: 47-55.

665 Johansson AH, Bejai S, Niazi A, Manzoor S, Bongcam-Rudloff E, Meijer J. 2014. Studies of plant  
666 colonisation by closely related *Bacillus amyloliquefaciens* biocontrol agents using strain specific  
667 quantitative PCR assays. *Antonie van Leeuwenhoek* 106: 1247–1257.

668 Juery C, Concia L, De Oliveira R, Papon N, Ramírez- González R, Benhamed M, Uauy C, Choulet F,  
669 Paux E. 2021. New insights into homoeologous copy number variations in the hexaploid wheat  
670 genome. *Plant Genome* 14: e20069.

671 Keel C, Schnider U, Maurhofer M, Voisard C, Laville J, Burger U, Wirthner P, Haas D, Défago G.  
672 1992. Suppression of root diseases by *Pseudomonas fluorescens* CHA0: Importance of the  
673 bacterial secondary metabolite 2,4-diacetylphloroglucinol. *Molecular Plant-Microbe Interactions*  
674 5: 4–13.

675 King EO, Ward MK, Raney DE. 1954. Two simple media for the demonstration of pyocyanin and  
676 fluorescin. *The Journal of Laboratory and Clinical Medicine* 44: 301–307.

677 Kiszonas AM, Morris CF. 2018. Wheat breeding for quality: a historical review. *Cereal Chemistry* 95:  
678 17–34.

679 Landa BB, Mavrodi DM, Thomashow LS, Weller DM. 2003. Interactions between strains of 2,4-  
680 diacetylphloroglucinol-producing *Pseudomonas fluorescens* in the rhizosphere of wheat.  
681 *Phytopathology* 93: 982–994.

682 Leach JE, Triplett LR, Argueso CT, Trivedi P. 2017. Communication in the Phytobiome. *Cell* 169:  
683 587–596.

684 Leff JW, Lynch RC, Kane NC, Fierer N. 2017. Plant domestication and the assembly of bacterial and  
685 fungal communities associated with strains of the common sunflower, *Helianthus annuus*. *The*  
686 *New Phytologist* 214: 412–423.

687 Liu Z, Xin M, Qin J, Peng H, Ni Z, Yao Y, Sun Q. 2015. Temporal transcriptome profiling reveals  
688 expression partitioning of homeologous genes contributing to heat and drought acclimation in  
689 wheat (*Triticum aestivum* L.). *BMC Plant Biology* 15: 152.

690 Marcussen T, Sandve SR, Heier L, Spannagl M, Pfeifer M, The International Wheat Genome  
691 Sequencing Consortium, Jakobsen KS, Wulff BBH, Steuernagel B, Mayer KFX, Olsen O-A.  
692 2014. Ancient hybridizations among the ancestral genomes of bread wheat. *Science* 345:  
693 1250092.

694 Martín-Robles N, Lehmann A, Seco E, Aroca R, Rillig MC, Milla R. 2018. Impacts of domestication  
695 on the arbuscular mycorrhizal symbiosis of 27 crop species. *The New Phytologist* 218: 322–334.

696 Mazzola M, Funnell DL, Raaijmakers JM. 2004. Wheat cultivar-specific selection of 2,4-  
697 diacetylphloroglucinol-producing fluorescent pseudomonas species from resident soil  
698 populations. *Microbial Ecology* 48: 338–348.

699 Mendes LW, Mendes R, Raaijmakers JM, Tsai SM. 2018. Breeding for soil-borne pathogen resistance  
700 impacts active rhizosphere microbiome of common bean. *The ISME Journal* 12: 3038–3042.

701 Nakhforoosh A, Grausgruber H, Kaul H-P, Bodner G. 2014. Wheat root diversity and root functional  
702 characterization. *Plant and Soil* 380: 211–229.

703 Neiverth A, Delai S, Garcia DM, Saatkamp K, de Souza EM, de Oliveira Pedrosa, F, Guimarães VF,  
704 dos Santos MF, Gruszka Vendruscolo EC, da Costa ACT. 2014. Performance of different wheat  
705 genotypes inoculated with the plant growth promoting bacterium *Herbaspirillum*  
706 *seropedicae*. *European Journal of Soil Biology* 64: 1-5.

707 Notz R, Maurhofer M, Schnider-Keel U, Duffy B, Haas D, Défago G. 2001. Biotic factors affecting  
708 expression of the 2,4-diacetylphloroglucinol biosynthesis gene *phlA* in *Pseudomonas fluorescens*  
709 biocontrol strain CHA0 in the rhizosphere. *Phytopathology* 91: 873–881.

710 Özkan H, Willcox G, Graner A, Salamini F, Kilian B. 2011. Geographic distribution and  
711 domestication of wild emmer wheat (*Triticum dicoccoides*). *Genetic Resources for Crop*  
712 *Evolution* 58: 11–53.

713 Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH. 2013. Going back to the roots: the  
714 microbial ecology of the rhizosphere. *Nature Reviews Microbiology* 11: 789–799.

715 Podile AR, Vukanti R, Ankati S, Kalam S, Dutta S, Durgeshwar P, Vaikuntapu P. 2014. Root  
716 colonization and quorum sensing are the driving forces of plant growth promoting rhizobacteria  
717 (PGPR) for growth promotion. *Proceedings of the Indian National Science Academy* 80: 407.

718 Pont C, Leroy T, Seidel M, Tondelli A, Duchemin W, Armisen D, Lang D, Bustos-Korts D, Goué N,  
719 Balfourier F, Molnár-Láng M, Lage J, Kilian B, Özkan H, Waite D, Dyer S, Letellier T, Alaux M,  
720 Russell J, Keller B, van Eeuwijk F, Spannagl M, Mayer KFX, Waugh R, Stein N, Cattivelli L,  
721 Haberer G, Charmet G, Salse J. 2019. Tracing the ancestry of modern bread wheats. *Nature*  
722 *Genetics* 51: 905–911.

723 Powell JJ, Fitzgerald TL, Stiller J, Berkman PJ, Gardiner DM, Manners JM, Henry RJ, Kazan K.  
724 2017. The defence-associated transcriptome of hexaploid wheat displays homoeolog expression  
725 and induction bias. *Plant Biotechnology Journal* 15: 533–543.

726 Rieusset L, Rey M, Gerin F, Wisniewski-Dyé F, Prigent-Combaret C, Comte G. 2021. A cross-  
727 metabolomic approach shows that wheat interferes with fluorescent *Pseudomonas* physiology  
728 through its root metabolites. *Metabolites* 11: 84.

729 Ramírez-González RH, Borrill P, Lang D, Harrington SA, Brinton J, Venturini L, Davey M, Jacobs J,  
730 van Ex F, Pasha A, Khedikar Y, Robinson SJ, Cory AT, Florio T, Concia L, Juery C, Schoonbeek  
731 H, Steuernagel B, Xiang D, Ridout CJ, Chalhoub B, Mayer KFX, Benhamed M, Latrasse D,  
732 Bendahmane A, International Wheat Genome Sequencing Consortium, Wulff BBH, Appels R,  
733 Tiwari V, Datla R, Choulet F, Pozniak CJ, Provart NJ, Sharpe AG, Paux E, Spannagl M,  
734 Bräutigam A, Uauy C. 2018. The transcriptional landscape of polyploid wheat. *Science* 361:  
735 eaar6089.

736 Rochat L, Péchy-Tarr M, Baehler E, Maurhofer M, Keel C. 2010. Combination of fluorescent  
737 reporters for simultaneous monitoring of root colonization and antifungal gene expression by a  
738 biocontrol pseudomonad on cereals with flow cytometry. *Molecular Plant-Microbe Interactions*  
739 23: 949–961.

740 Roucou A, Violle C, Fort F, Roumet P, Ecarnot M, Vile D. 2018. Shifts in plant functional strategies  
741 over the course of wheat domestication. *Journal of Applied Ecology* 55: 25–37.

742 Salamini F, Özkan H, Brandolini A, Schäfer-Pregl R, Martin W. 2002. Genetics and geography of  
743 wild cereal domestication in the near east. *Nature Reviews Genetics* 3: 429–441.

744 Salem G, Stromberger ME, Byrne PF, Manter DK, El-Feki W, Weir TL. 2018. Genotype-specific  
745 response of winter wheat (*Triticum aestivum* L.) to irrigation and inoculation with ACC  
746 deaminase bacteria. *Rhizosphere* 8: 1–7.

747 Samain E, Aussenac T, Selim S. 2019. The effect of plant genotype, growth stage, and  
748 *Mycosphaerella graminicola* strains on the efficiency and durability of wheat-induced resistance  
749 by *Paenibacillus* sp. strain B2. *Frontiers in Plant Science* 10: 587.

750 Shanahan P, O’Sullivan DJ, Simpson P, Glennon JD, O’Gara F. 1992. Isolation of 2,4-  
751 diacetylphloroglucinol from a fluorescent pseudomonad and investigation of physiological  
752 parameters influencing its production. *Applied and Environmental Microbiology* 58: 353–358.

753 Shaposhnikov AI, Morgounov AI, Akin B, Makarova NM, Belimov AA, Tikhonovich IA. 2016.  
754 Comparative characteristics of root systems and root exudation of synthetic, landrace and modern  
755 wheat varieties. *Agricultural Biology* 51: 68–78.

756 Soltis PS, Marchant DB, Van de Peer Y, Soltis DE. 2015. Polyploidy and genome evolution in plants.  
757 *Current Opinion in Genetics & Development, Genomes and Evolution* 35: 119–125.

758 Soltis PS, Soltis DE. 2000. The role of genetic and genomic attributes in the success of polyploids.  
759 *Proceedings of the National Academy of Sciences of the USA* 97: 7051–7057.

760 Spor A, Roucou A, Mounier A, Bru D, Breuil M-C, Fort F, Vile D, Roumet P, Philippot L, Violle C.  
761 2020. Domestication-driven changes in plant traits associated with changes in the assembly of the  
762 rhizosphere microbiota in tetraploid wheat. *Scientific Reports* 10: 12234.

763 Szoboszlay M, Lambers J, Chappell J, Kupper JV, Moe LA, Mcnear DH. 2015. Comparison of root  
764 system architecture and rhizosphere microbial communities of Balsas teosinte and domesticated  
765 corn cultivars. *Soil Biology and Biochemistry* 80: 34–44.

766 te Beest M, Le Roux JJ, Richardson DM, Brysting AK, Suda J, Kubešová M, Pyšek P. 2012. The more  
767 the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany* 109: 19–45.

768 Tkacz A, Pini F, Turner TR, Bestion E, Simmonds J, Howell P, Greenland A, Cheema J, Emms DM,  
769 Uauy C, Poole PS. 2020. Agricultural Selection of wheat has been shaped by plant-microbe  
770 interactions. *Frontiers in Microbiology* 11: 132.

771 Vacheron J, Combes-Meynet E, Walker V, Gouesnard B, Muller D, Moënne-Loccoz Y, Prigent-  
772 Combaret C. 2016. Expression on roots and contribution to maize phytostimulation of 1-  
773 aminocyclopropane-1-decarboxylate deaminase gene *acdS* in *Pseudomonas fluorescens* F113.  
774 *Plant and Soil* 407: 187-202.

775 Vacheron J, Desbrosses G, Bouffaud M-L, Touraine B, Moënne-Loccoz Y, Muller D, Legendre L,  
776 Wisniewski-Dyé F, Prigent-Combaret C. 2013. Plant growth-promoting rhizobacteria and root  
777 system functioning. *Frontiers in Plant Science* 4: 356.

778 Vacheron J, Desbrosses G, Renoud S, Padilla R, Walker V, Muller D, Prigent-Combaret C. 2018.  
779 Differential contribution of plant-beneficial functions from *Pseudomonas kilonensis* F113 to root  
780 system architecture alterations in *Arabidopsis thaliana* and *Zea mays*. *Molecular Plant-Microbe*  
781 *Interactions* 31: 212–223.

782 Valente J, Gerin F, Le Gouis J, Moënne-Loccoz Y, Prigent-Combaret C. 2020. Ancient wheat  
783 varieties have a higher ability to interact with plant growth-promoting rhizobacteria. *Plant, Cell &*  
784 *Environment* 43: 246–260.

785 Vassileva V, Simova-Stoilova L, Demirevska K, Feller U. 2009. Variety-specific response of wheat  
786 (*Triticum aestivum* L.) leaf mitochondria to drought stress. *Journal of Plant Research* 122: 445–  
787 454.

788 Von Felten A, Défago G, Maurhofer M. 2010. Quantification of *Pseudomonas fluorescens* strains  
789 F113, CHA0 and Pf153 in the rhizosphere of maize by strain-specific real-time PCR unaffected  
790 by the variability of DNA extraction efficiency. *Journal of Microbiological Methods* 81: 108–  
791 115.

792 Waines JG, Ehdaie B. 2007. Domestication and crop physiology: roots of green-revolution wheat.  
793 *Annals of Botany* 100: 991–998.

794 Walker V, Couillerot O, Von Felten A, Bellvert F, Jansa J, Maurhofer M, Bally R, Moënne-Loccoz Y,  
795 Comte G. 2012. Variation of secondary metabolite levels in maize seedling roots induced by

796 inoculation with *Azospirillum*, *Pseudomonas* and *Glomus* consortium under field conditions.  
797 *Plant and Soil* 356: 151–163.

798 Walsh UF, Moënne-Loccoz Y, Tichy H-V, Gardner A, Corkery DM, Lorkhe S, O’Gara F., 2003.  
799 Residual impact of the biocontrol inoculant *Pseudomonas fluorescens* F113 on the resident  
800 population of rhizobia nodulating a red clover rotation crop. *Microbial Ecology* 45: 145–155.

801 Wipf HML, Coleman-Derr D 2021. Evaluating domestication and ploidy effects on the assembly of  
802 the wheat bacterial microbiome. *PLoS ONE* 16: e0248030.

803 Yu K, Feng M, Yang G, Sun L, Qin Z, Cao J, Wen J, Li H, Zhou Y, Chen X, Peng H, Yao Y, Hu Z,  
804 Guo W, Sun Q, Ni Z, Adams K, Xin M. 2020. Changes in alternative splicing in response to  
805 domestication and polyploidization in wheat. *Plant Physiology* 184: 1955–1968.

806 Zboralski A, Filion M. 2020. Genetic factors involved in rhizosphere colonization by phytobeneficial  
807 *Pseudomonas* spp. *Computational and Structural Biotechnology Journal* 18: 3539–3554.  
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. 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,  $P < 0.05$ )

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)
<b>Root colonization by F113</b>										
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%
<b><i>phl</i> expression level in F113</b>										
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%
<b><i>phl</i> induction rate in F113</b>										
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
<b><i>T. aestivum</i></b>								
<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%	<b>-32.9%</b>	-9.9%	8.0%	-11.1%	-6.9%	-20.4%
NON PLUS EXTRA	<b>94.7%</b>	9.9%	-5.4%	24.6%	-4.6%	-27.7%	<b>17.1%</b>	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%	<b>-13.6%</b>	-28.9%	<b>95.9%</b>	32.1%
BLANC PRECOCE	53.6%	7.3%	6.2%	<b>96.6%</b>	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%	<b>134.2%</b>
<b><i>T. durum</i></b>								
<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	<b>-78.4%</b>	-7.3%	-20.8%	34.2%	<b>12.4%</b>	19.3%	<b>-17.5%</b>	<b>-49.8%</b>
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%