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Comparative Transcriptome Profiling Provides Insights into the Growth Promotion Activity of *Pseudomonas fluorescens* strain SLU99 in Tomato and Potato Plants

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14 **Keywords: PGPR, *Pseudomonas fluorescens*, *Serratia*, root traits, beneficial bacteria,**
15 **IAA, Ethylene.**

16 **Abstract**

17 The use of biocontrol agents with plant growth-promoting activity has emerged as an approach
18 to support sustainable agriculture. During our field evaluation of potato plants treated with
19 biocontrol rhizobacteria, four bacteria were associated with increased plant height. Using two
20 important solanaceous crop plants, tomato and potato, we carried out a comparative analysis
21 of the growth-promoting activity of the four bacterial strains: *Pseudomonas fluorescens*
22 SLU99, *Serratia plymuthica* S412, *S. rubidaea* AV10, and *S. rubidaea* EV23. Greenhouse and
23 *in vitro* experiments showed that *P. fluorescens* SLU99 promoted plant height, biomass
24 accumulation, and yield of potato and tomato plants, while EV23 promoted growth in potato

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25 but not in tomato plants. SLU99 induced the expression of plant hormone-related genes in
26 potato and tomato, especially those involved in maintaining homeostasis of auxin, cytokinin,
27 gibberellic acid and ethylene. Our results reveal potential mechanisms underlying the growth
28 promotion and biocontrol effects of these rhizobacteria and suggest which strains may be best
29 deployed for sustainably improving crop yield.

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30 ## 1 Introduction

31 The plant rhizosphere is a significant carbon sink (Strand et al., 2008; Drigo et al., 2010), and
32 represents an ecosystem hosting a diverse microbial community, including a variety of
33 phytopathogens. The co-evolution of plants and microbial communities has led to the formation
34 of complex symbiotic associations (Delaux and Schornack, 2021; Abdelfattah et al., 2022).
35 Several studies have indicated that plants recruit specific microbial communities through root
36 exudates, positively regulating the rhizosphere (Besserer et al., 2006; De Weert et al., 2007;
37 Rudrappa et al., 2008). Through secreting secondary metabolites such as pyrrolnitrin and
38 fusaricidin (Burkhead et al., 1994; Vater et al., 2017; Liu et al., 2020), outer membrane vesicles
39 (McMillan et al., 2021) and phytohormones (Tsukanova et al., 2017), microbial communities
40 assist plants in their defence against pathogens by priming plant defences while keeping severe
41 immune responses to a minimum (Van Wees et al., 2008). Termed biological control agents
42 (BCA), several bacterial genera including *Pseudomonas*, *Serratia*, *Bacillus*, and *Azospirillum*
43 compete in the rhizosphere environment with pathogens through siderophore biosynthesis,
44 antibiosis, lytic enzyme production and detoxification, thus protecting the plant (Loper, 1988;
45 Loper and Henkels, 1999; Compant et al., 2005). Some species of rhizospheric BCA, known
46 as plant growth-promoting rhizobacteria (PGPR), have long been known to enhance plant
47 growth through the secretion of auxin (Přikryl et al., 1985), cytokinin (Tien et al., 1979;
48 Timmusk et al., 1999), 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Glick et al.,
49 1994), nitrogen fixation (Bal and Chanway, 2012), volatile organic compound (VOC)
50 production (Tahir et al., 2017), and phosphate solubilization (Son et al., 2006; Olanrewaju et
51 al., 2017).

52 Many PGPR modulate root architecture, promote shoot elongation, and increase
53 chlorophyll content and photosynthetic efficiency (Diagne et al., 2020). One of the most
54 common alterations induced by PGPR in the root system architecture is the increased formation
55 of lateral roots (LR) and root hairs (RH), thus assisting in improved water and nutrient
56 acquisition from the soil. Changes in root system architecture (RSA) could be caused by PGPR
57 interference with the signalling in the main hormonal pathways regulating plant root
58 development, namely auxin and cytokinin (Ali et al., 2009; Dodd et al., 2010). PGPRs also
59 promote plant growth by reducing stress-related ethylene levels via ACC deaminase activity
60 (Glick et al., 1998; Hardoim et al., 2008; Amna et al., 2019). PGPR have been demonstrated to
61 be beneficial for several important crop species including tomato, apple, grapes, and cereals
62 such as rice, wheat and maize (Kumari et al., 2019).

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63 *Pseudomonas* spp. are Gram-negative, chemoheterotrophic, motile rod-shaped bacteria
64 that are adapted to a wide range of ecological niches. Extensive research has shown that several
65 *Pseudomonas* strains function as PGPR through diverse metabolic capabilities. *P. putida*
66 isolate WCS358 (Zamioudis et al., 2013) and *P. chlororaphis* subsp. *aurantiaca* strain JD37
67 (Fang et al., 2013) isolated from potato rhizosphere promote plant growth in *Arabidopsis*
68 *thaliana* and maize, respectively. *P. putida* isolate GR12-2 enhances root elongation through
69 the ethylene pathway (Glick et al., 1994) and root branching by producing cyclodipeptides that
70 modulate auxin responses (Ortiz-Castro et al., 2020). Furthermore, we have recently
71 demonstrated that *P. aeruginosa* encodes genes for tryptophan biosynthesis and indole-3-acetic
72 acid (IAA) synthesis, and promotes tomato growth (Ghadamgahi et al., 2022). *P. fluorescens*
73 strain WCS365 has been shown to colonize both tomato and potato rhizospheres (Mercado-
74 Blanco and Bakker, 2007). *P. fluorescens* strain WCS417 inhibits primary root elongation
75 while stimulating LR and RH development through auxin signalling (Zamioudis et al., 2013).
76 *Serratia* sp. are Gram-negative bacteria belonging to the family Enterobacteriaceae.
77 Several species of *Serratia* are reported to enhance plant growth, such as *S. fonticola* strain
78 AU-P3 and *Serratia* sp. SY5 that promote growth in pea and maize plants, respectively (Koo
79 and Cho, 2009; Devi et al., 2013). Recently, it was reported that *Serratia rubidaea* strain ED1
80 promotes seed germination in quinoa (Mahdi et al., 2021).
81 A shift in societal acceptance away from using harmful and often expensive chemical
82 fertilizers to a safer and natural alternative, combined with the increasing challenges of climate
83 change and the growing world population, has resulted in PGPR drawing increased attention.
84 The effects of PGPR-plant interactions on molecular mechanisms are complex and may vary
85 depending on the strain or consortia of strains, plant species, and receiving environment
86 (Tsukanova et al., 2017). Understanding how a beneficial bacterium improves the growth and
87 health of a specific crop in a specific environment is therefore critical. The strains used in this
88 study were isolated from potato and tomato rhizosphere soils. *In vitro* antagonistic analysis
89 indicated a strong antagonistic activity against plant pathogens, including *P. colocasiae*
90 (Kelbessa et al., 2022)*, P. infestans* and *R. solani* (unpublished). The aim of this study was to
91 conduct a holistic study on the effect of PGPR on potato and tomato growth and select the best-
92 performing PGPR to gain insights into their mechanism of action. To that end, we carried out
93 a field trial with six bacteria with biological control activity on potato plants in a high disease
94 pressure *P. infestans* infested field. Selected strains associated with increased potato growth
95 were then tested under greenhouse conditions for growth-promoting activity.

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96 The complex effects of PGPR on plant gene expression, including genes that play key roles
97 in signal transduction, metabolism, and catabolism of plant hormones have been reported in
98 several studies (Shen et al., 2013; Tsukanova et al., 2017; Wei et al., 2020). However, studies
99 on global transcriptomic changes induced by PGPR treatment in the context of plant growth
100 and development are limited. Moreover, to our knowledge, there is no report on the
101 transcriptome profiling of potato plants under PGPR treatment. Understanding how plants
102 including potato and tomato respond to PGPR treatment will greatly empower the usage of
103 PGPR towards enhancing sustainable agriculture. To that end, we carried out transcriptome
104 profiling of potato and tomato roots and leaves treated with the bacterial supernatant to gain
105 insight into the growth promotion mechanisms of *P. fluorescens*.
106

107 2 Materials and methods

108 2.1 Field trial

109 Field experiments were carried out in the summer of 2020 using the potato cultivar Kuras. A
110 total of six bacterial isolates that displayed antagonistic activity against *Phytophthora infestans*
111 under lab conditions were assessed for their plant growth promotion activity. These strains
112 include *Pseudomonas fluorescens* SLU99, *Serratia rubidaea* EV23 and AV10, *S. plymuthica*
113 S412 and AS13, and *S. proteamaculans* S4. One single colony of each bacterial strain was
114 cultured in Luria-Bertani (LB) liquid for 16 h at 28°C. Then the cultures were centrifuged at
115 3000 x g for 10 min and the bacterial cells were resuspended in 5 L sterile water to a final
116 OD_{600} 0.2. The bacterial suspension was transferred to a 5 liter pressure sprayer for field
117 application, water treatment were used as a control. The testing site was Mosslunda, near the
118 city of Kristianstad (55°58'00.3"N 14°07'03.0"E) where the average daily temperature ranged
119 between 12 and 18°C and average monthly precipitation was 42-64 mm, with an average
120 daylength was 17.5 hours. The experiment was carried out in a plot with four rows of 10 meters
121 in width and 15 meters in length. The experimental design consisted of randomized block
122 design with four blocks. Each block contained all eight treatments distributed randomly, with
123 10 plants per treatment. The potato plants were sprayed with six biocontrol bacteria (individual
124 treatments) once every two weeks for a period of 8 weeks.

125 2.2 Greenhouse and PGPR treatment

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126 To evaluate the effects of selected rhizobacteria on tomato and potato plant growth, a pot
127 experiment was conducted for each crop in two separate plant cultivation chambers (biotron).
128 Nine and ten biological replicates were used for tomato and potato, respectively. The tomato
129 seeds were surface sterilized using 3% bleach followed by washing with sterile water three
130 times before sowing in a 105-hole seed tray filled with nursery soil. At 25 days after sowing,
131 uniform four-leaf stage seedlings were transplanted into 1 L pots containing 325 g of nursery
132 soil (1 seedling/pot). For bacterial inoculations, strains SLU99, EV23, AV10 and S412 were
133 cultured as described in the previous section. Thirty-five milliliters of bacterial suspensions at
134 OD_{600} 0.2 prepared with 1 × phosphate-buffered saline (PBS) (Thermo Scientific, Waltham,
135 MA, USA) or only 1 × PBS (control treatment) was added to the roots of tomato seedlings
136 before they were covered with soil. For potato, all seed tubers were first cleaned with water,
137 treated with 100 ppm gibberellic acid, and dried for eight days to promote bud initiation. Prior
138 to planting in 2 L pots (containing 650 g nursery soil), the seed tubers were inoculated with
139 bacteria suspension at OD_{600} 0.2 prepared with 1 × PBS or with only 1 × PBS for 15 min.
140 The inoculation was repeated twice, once at 10 and 30 days after transplanting (DAT) for
141 tomato or days after planting (DAP) for potato with 35 ml bacterial suspension (OD_{600} 0.2) per
142 plant in both crops to ensure the growth of bacteria in the soil. The liquid was poured 2-3 cm
143 from each plant's base and 5 cm deep in the soil. For the duration of the experiments, the plants
144 were grown in two separate growth chambers in 16 h light/8 h dark photoperiods supplemented
145 with 250 µmol m-2 s-1 light, temperatures of 20-23˚C and 60% humidity for 60 days. The plant
146 positions within the growth chambers were randomly rearranged at least twice a week.

147 2.3 Phenotyping

148 To determine the effects of selected rhizobacteria on plant growth, parameters of plant height,
149 total plant dry weight and yield were measured. Plant height was measured from the soil surface
150 to the tip of the plant every ten days from planting until harvest. The yield of tomato and potato
151 were measured by total fruit or tuber number and total fresh weight. Firstly, fruit or tubers were
152 harvested, counted, and weighed. Then, the shoot and root systems were separated. Leaves
153 were separated from the plant by cutting the leaf petiole, and the stems were cut. The number
154 of leaves was counted and recorded. The intact roots were gently shaken to remove soil, briefly
155 washed with water, and gently blotted dry using paper towels. Then, immediately the roots,
156 leaves, stems, and fruits/tubers were separately placed in paper bags and oven-dried at 65˚C

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157 until they reached constant weight. Finally, the dry weight was measured using a precision
158 scale and recorded.

159 **2.4 Chlorophyll content index measurement**

160 The chlorophyll content of tomato and potato plants grown in the growth chamber were
161 measured at harvest using the MC-100 Chlorophyll Concentration Meter (Apogee Instruments
162 Inc., Logan, UT, USA). The MC-100 was calibrated to measure chlorophyll concentration with
163 units of chlorophyll content index (CCI) and zeroed before commencing measurement
164 according to the manufacturer's instructions (Apogee Instruments, 2018). The generic equation
165 was used in the measurement of the relative chlorophyll content of both crops. For tomato
166 plants, the measurements were made by clipping the sensor onto the second terminal leaflet on
167 the fifth fully expanded leaf from the top of each plant (Matsuda et al., 2014). For potato plants,
168 the measurements were made on the top point of the top leaflet of the 4th compound leaf (Li et
169 al., 2012).

170 **2.5 Soil sampling and analysis**

171 To evaluate the effects of rhizobacteria applications on soil nutrient content, soils were
172 collected and pooled from all pots of each bacterial treatment for analysis. For the control
173 treatment, soils were collected from eight randomly non-inoculated plants. The soil samples
174 were sent to the LMI AB testing laboratory (Helsingborg, Sweden) for analysis. The soils
175 sampled before planting and at harvest were analyzed for pH, soil organic matter (SOM),
176 electrical conductivity (EC), total nitrogen, available phosphorus (P), and available potassium
177 (K).

178 **2.6 *In vitro* growth conditions for plants**

179 Tomato seeds or potato explants were grown in half-strength Murashige and Skoog (MS)
180 culture medium (M0221; Duchefa Biochemie B.V, Haarlem, The Netherlands), pH 5.8,
181 supplemented with 0.25% (w/v) Phytagel (Sigma-Aldrich Co., St. Louis, MO, United States),
182 0.05% (w/v) 2-(N-morpholino)ethanesulfonic acid (MES) and 1% sucrose (w/v) (Duchefa
183 Biochemie B.V, Haarlem, The Netherlands). For SLU99 treatment, bacteria were cultured
184 overnight in LB until an OD_{600} of 2 was reached. Cell-free supernatant was obtained by
185 centrifuging at 3000 x g for 10 min, filtered through a 0.22-µm filter and mixed with ½ MS
186 medium at 1:10 ratio before plating. Tomato var Moneymaker seeds were obtained from

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187 Plantagen AB and were surface sterilized with 3% (v/v) sodium hypochlorite for 5 min and
188 washed three times with sterile water. Seeds were then plated either on control or SLU99
189 supernatant supplemented ½ MS plates and stratified for 48 h at 4°C. For potato plants, the
190 explants from sterile potato plants were grown either on mock treated or SLU99 supernatant
191 supplemented ½ MS media in plant tissue culture boxes. The plants were grown in a growth
192 chamber with 16 h light/8 h dark photoperiods and temperatures of 20-22°C.

193 2.7 Transcriptome analysis

194 For RNA-seq analysis, leaf or root samples were collected for each treatment and frozen in
195 liquid nitrogen. RNA was extracted using the RNeasy Mini Kit (Qiagen). The quality and
196 integrity of the RNA was measured using Agilent Bioanalyzer 2100 (Agilent, California,
197 USA). Library preparation was carried out using a TruSeq RNA poly-A selection kit (Illumina,
198 Inc.). Sequencing was performed at National Genomics Infrastructure (NGI), Stockholm on an
199 Illumina NovaSeq6000 S4 platform. Adapter sequences and poor quality reads (<Q30) were
200 removed using BBduk (Bushnell et al., 2017). Next, cleaned data were fed into STAR (Dobin
201 et al., 2013) for alignment against the reference genome. FeatureCounts (Liao et al., 2014) was
202 used for the quantification of aligned reads. Finally, R package DEseq2 (Love et al., 2014) was
203 used for the analysis of differential gene expression and normalization. For volcano plots, R
204 package ggplot2 (Ito and Murphy, 2013) was used. Pathway and enrichment analysis of
205 differentially expressed genes was carried out with the R package clusterProfiler (Wu et al.,
206 2021).

207 3 Results

208 3.1 Plant growth-promoting traits of *P. fluorescens* and *Serratia* species

209 We investigated six bacterial strains with biological control activity, *P. fluorescens* SLU99,
210 *Serratia rubidaea* EV23, AV10, *Serratia plymuthica* AS13, S412, and *Serratia*
211 *proteamaculans* S4. To evaluate the growth promotion activity of these bacteria, potato plants
212 grown in field conditions were subjected to treatment with these bacteria. Four out of the six
213 tested strains, SLU99, EV23, AV10 and S412 resulted in significantly increased plant height,
214 compared to the water treated control (Figure 1).
215 To examine the effectiveness of plant growth promotion, potato and tomato plants
216 grown under greenhouse conditions were inoculated with the four selected strains. Inoculation
217 with *P. fluorescens* SLU99 significantly increased plant height, total dry weight, and yield of

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218 tomato plants by 13.3%, 34.5%, and 183.9%, respectively, compared to non-inoculated plants.
219 Meanwhile, *S. rubidaea* AV10-treated tomato plants had 12.3% greater total dry weight than
220 non-inoculated plants. On the other hand, inoculation with *S. rubidaea* EV23 and *S. plymuthica*
221 S412 had no significant effect on all morphological parameters tested on tomato plants (Table
222 1, Figure 2A-F). Furthermore, inoculation with both SLU99 and EV23, individually,
223 significantly increased potato plant height, yield, and total plant dry weight (Table 1).
224 Inoculation with AV10 promoted plant growth as total plant dry weight but not plant height,
225 and vice versa for S412 on potato. Nevertheless, all inoculated plants had significantly higher
226 tuber yields compared to the controls. The highest increase in yield for potato was recorded for
227 EV23 (15%) and SLU99 (13.7%), followed by AV10 and S412 treated plants with 11.3%, and
228 10.7%, respectively (Table 1).

229 Plant height increased rapidly during the vegetative stage until fruit set (40 DAT), or
230 until the start of tuber initiation (30 DAP) for tomato and potato plants, respectively, and was
231 not significantly different among treatments. Thereafter, during the fruit growth stage (50-60
232 DAT), a significant effect of bacteria inoculation on tomato plant height was observed
233 (P=0.0431 and P=0.0131 at 50 and 60 DAT, respectively) (Table 1, Supp Figure 1B). In
234 contrast, a 4.2% reduction in tomato plant height was observed when plants were treated with
235 EV23 (Table 1). Applications of SLU99 resulted in increased tomato leaf (Figure 2E) and fruit
236 number (Figure 2F) compared to other treatments. Consequently, SLU99-treated tomato plants
237 had 39.7% and 191.2% more leaf and fruit dry weights, respectively, compared to non-
238 inoculated plants.

239 For potato plants at 30 DAP, swelling stolon tips were observed in all treatments
240 suggesting tuber initiation had started. The effect of bacteria inoculation on potato plant height
241 was only significant during the tuber bulking stage (40-60 DAP) (Table 1, Supp Figure 1). In
242 addition, all bacteria except S412 significantly increased tuber dry weight over control plants
243 (P=0.0003). However, the dry weight of other plant parts was not enhanced by bacteria
244 treatments (Figure 2G-I).

245 Relative chlorophyll content was significantly higher after SLU99 application in tomato
246 (P=0.0188) and potato plants (P=0.0287) but was not improved after EV23, AV10 and S412
247 treatments compared to the control (Figure 3).

248 Additionally, at harvest, inoculation with SLU99 resulted in 3.4% higher total nitrogen
249 (TN) in the tomato grown soil, while inoculation of EV23, AV10 and S412 resulted in 10.7%,
250 7.7% and 24.3% lower TN over control treatment, respectively (Supp. Table 1). The elements
251 of P & K were slightly increased in tomato grown soil after SLU99 treatment, whereas EC and

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252 SOM were decreased. In potato grown soil, all bacterial treatments increased available K over
253 the control by 22.2%-66.7%. TN in potato grown soil decreased in a small range after SLU99,
254 EV23 and AV10 treatments (2.1%-6.2%). Meanwhile, the available P, pH, EC, and SOM at
255 harvest of soils grown with potato were not affected by bacteria treatments (Supp. Table 1). In
256 summary, inoculation of SLU99 significantly promoted the growth of tomato and potato plants,
257 and EV23 promoted the growth of potato plants grown in a controlled environment as reflected
258 by high chlorophyll content, total plant biomass and yield.

259 3.2 Effects of rhizobacteria inoculation on growth of *in vitro* grown tomato and potato 260 plants

261 To gain insights into the mechanisms behind growth promotion, tomato and potato plants were
262 grown in MS media supplemented with the sterile-filtered bacterial culture supernatant. When
263 compared to the mock treatment, tomato seeds grown in the SLU99-supernatant supplemented
264 media showed a higher germination rate, increased root growth and shoot height, and enhanced
265 number of lateral roots (Figure 4A, B). Potato explants grown in the media supplemented with
266 SLU99 and EV23 supernatant resulted in increased shoot height by 24.6 % ($p = 0.02$) compared
267 to the control (Figure 4C, D). SLU99 treatment also increased root growth and resulted in the
268 formation of adventitious roots and secondary adventitious roots (SAR), which emerge from
269 aerial parts (Figure 4D).

270 3.3 Differentially expressed genes (DEGs) and KEGG pathway enrichment analysis

271 To gain insights into the mechanisms of SLU99-mediated growth promotion in tomato and
272 potato plants, RNA extracted from the roots and leaves grown in the media supplemented with
273 the supernatant of SLU99 was subjected to transcriptome profiling. A total of 1193 and 2226
274 genes were differentially expressed (log2FC >1.5, $p < 0.05$) in the roots of tomato and potato,
275 respectively, compared to the control samples (Table 2). Among them, 1076 and 996 genes
276 were upregulated, and 117 and 1230 genes were downregulated in the respective samples
277 (Table 2, Fig. 5A and B). In tomato leaves, a total of 1732 DEGs were detected (log2FC >1.5,
278 $p < 0.05$) with 1322 genes upregulated and 410 genes downregulated (Fig 5C). For potato
279 leaves, we identified 959 (log2FC >1.5, $p < 0.05$) when treated with SLU99 compared to the
280 control samples. Of the identified DEGs, 206 were upregulated, and 753 genes were
281 downregulated (Table 2 and Fig 5D).

282 We performed KEGG pathway enrichment analysis to gain a better understanding of
283 the functional categories of the DEGs in response to the PGPR culture supernatant treatment.

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284 In the treated root samples, a total of 300 and 753 genes were grouped into enriched pathways
285 in tomato and potato, respectively, and a total of 382 and 259 genes were grouped into enriched
286 pathways in the treated leaves of tomato and potato, respectively. Treatment resulted in
287 enrichment for genes involved in plant hormone signal transduction pathway (37 and 33 genes,
288 respectively), zeatin biosynthesis (15 and 13 genes), plant-pathogen interactions (37 and 25
289 genes) and MAPK signalling pathway (30 and 19 genes) in both tomato and potato leaves.
290 Additionally, a total of 40, 76, 44 and 25 genes related to the phenylpropanoid biosynthesis
291 pathway were enriched in the roots and leaves of tomato and potato upon treatment with SLU99
292 culture supernatant (Fig 6).

293 To compare the effects of the tomato and potato samples, we examined the overlap of
294 the DEG products among the roots and leaves. The analysis showed an overlap of 164 gene
295 products in the root samples, and 95 in the leaf samples upon SLU99 treatment in potato and
296 tomato plants (Fig. 7A and B). Within the species, there was an overlap of 515 gene products
297 between root and leaf samples of tomato, while 265 similar gene products were responsive in
298 the root and leaf samples of potato (Fig. 7C and D).

299 3.4 SLU99 regulates phytohormonal biosynthesis and signal transduction pathways

300 One of the major objectives of this study was to elucidate the changes in the host transcriptomes
301 that are important for PGP activity. Phytohormones, as a result of their complex interaction
302 and crosstalk, regulate various cellular processes involved in plant growth and development.
303 The gibberellins (GAs) play an important role in several developmental processes including
304 seed germination. Upon SLU99 treatment in tomato root, *gibberellin 3-beta-dioxygenase 1-*
305 like (*GA3OX1*), a gene involved in the biosynthesis of GA was upregulated (log2FC 1.9,
306 $p<0.05$). On the other hand, in tomato leaves, *gibberellin 2-beta-dioxygenase 8* (*GA2ox8*), a
307 gene involved in the deactivation of GA, was upregulated (log2FC 1.6, $p<0.01$) (Fig.8).

308 The hormones auxin and CK are major players in the regulation of signaling pathways
309 underlying plant growth and development. In tomato, *tryptophan synthase beta subunit*
310 *1* (*TSB1*)-like, responsible for increased in tryptophan biosynthesis, and *YUCCA8*, responsible
311 for the last enzymatic step from indole-3-pyruvic acid (IPA) to IAA were upregulated by 16
312 and 3 times (log2FC 4 and 1.6) in leaf and root samples, respectively. Additionally, in potato
313 roots, SLU99 treatment resulted in increased expression (log2FC 3.3) of *L-tryptophan-*
314 *pyruvate aminotransferase 1 (TAA1)*-like, which encodes an enzyme that converts L-
315 tryptophan to IPA (Fig. 8).

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316 The activation of auxin biosynthesis genes and production of IAA by SLU99 (Kelbessa
317 et al., 2022) prompted us to analyze the differences in the expression of genes involved in auxin
318 signaling pathways. Major auxin-responsive genes such as *Gretchen Hagen 3* (*GH3*) and *small*
319 *auxin up RNA* (*SAUR*) are transcriptionally regulated by auxin at early stages of signal
320 transduction. Following treatment with SLU99 culture supernatant, expression of the *IAA-*
321 *amido synthetase GH3.1 (GH3.1)*, important for maintaining auxin homeostasis increased
322 significantly (log2FC 6.8, 4.6 and 1.6 in tomato root, tomato leaf and potato root, respectively)
323 in comparison to the mock treatment. Within the SAUR family, five and seven genes were
324 differentially expressed in the tomato and potato plants, respectively. Additionally, *PIN2*, a
325 root-specific auxin transporter and *PIN8*, a constitutively active auxin transporter were also
326 upregulated in the potato plants (Fig.8).

327 The gene encoding CK hydroxylase, an enzyme that catalyzes the biosynthesis of trans-
328 zeatin (tZ), a biologically active CK, was strongly upregulated (log2FC 7.5) upon treatment
329 with SLU99 in tomato roots. On the other hand, in tomato leaf *CK dehydroxygenase 3* (*CKX3*),
330 involved in the degradation of CK was upregulated 4-fold (log2FC 2) compared to the mock
331 treatment. Furthermore, *zeatin O-glycosyltransferase* (*ZOG1*) and *zeatin O-xylosyltransferase*
332 (*ZOX1*) were upregulated in tomato leaves (log2FC 5.4 and 3.5), while only *ZOG1* was
333 upregulated in the tomato and potato roots (log2FC 2.1 and 1.6). *ZOG1* and *ZOX1* are involved
334 in the conversion of tZ to a stable and reversible O-glycosylzeatin and O-xylosylzeatin,
335 respectively.

336 The PGP activity of bacteria is also attributed to the changes in the plant hormone
337 ethylene (Poupin et al., 2016). Since SLU99 displayed ACC deaminase activity, we examined
338 changes in the expression of genes encoding the enzymes of the ethylene biosynthesis pathway.
339 *1-aminocyclopropane-1-carboxylate_synthase*-like (*ACS*) involved in the synthesis of ACC, a
340 direct precursor of ethylene, and *1-aminocyclopropane-1-carboxylate_oxidase* (*ACO*)
341 subsequently oxidizes ACC to ethylene. In tomato, *ACS* and *ACO1* were upregulated in roots
342 (Log2FC 5.1 and 1.8, respectively), while *ACO1* and *ACO4* were upregulated in leaves
343 (Log2FC 3.2 and 2.6, respectively). In potato, *ACS2* was upregulated in roots (log2FC 4.1),
344 while *ACS4* was upregulated in leaves (log2FC 2.2). *ACO* homologs were upregulated both in
345 the roots and leaves (log2FC 2.9 and 1.7, respectively), while *ACO1, ACO5* and *ACO11* were
346 upregulated in leaves (log2FC 2.1, 2.1 and 3.3, respectively). Lysine histidine transporters
347 (LHT) are associated with the transportation of ACC. When treated with SLU99 culture
348 supernatant, *LHT8* was upregulated in both tomato and potato roots and tomato leaves by 3.6,
349 2.5 and 2.5 times (log2FC), respectively, while *LHT1* was upregulated only in tomato leaves

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350 (log2FC 1.6). Taken together, these results indicate that treatment with the culture supernatant
351 from SLU99 stimulates the accumulation of phytohormones auxin, CK and ethylene.

352 3.5 Reprogramming of host transcriptional networks

353 The discovery of several DEGs involved in signal transduction pathways in response to SLU99
354 treatment suggests strong regulation of host transcription factor networks. To investigate the
355 interaction of SLU99 with the plant transcriptional network, DEGs encoding TFs were
356 identified and assigned to families using the plant transcription factor database. In total, DEGs
357 belonging to 24 different TF families were identified with the greatest number of DEGs
358 identified in the root samples compared to the leaf samples (Supp. Table 2). In the tomato and
359 potato roots, a total of 112 and 182 TF encoding DEGs were found, whereas 62 to 92 DEGs
360 were found in leaf samples, implying significant reprogramming of the host transcriptional
361 network. The HD-ZIP TF genes were exclusively upregulated in tomato plants (11 upregulated
362 and 2 downregulated), while 14 HD-ZIPs were downregulated in potato. Notably, the strongest
363 upregulation was found for *ATHB12* (log2FC 9.6) followed by *ATHB40-like* (log2FC 6.4), and
364 *ATHB7-like* (log2FC 3.4) in tomato leaves. *ATHB12* and *ATHB7*, considered paralogs, belong
365 to the class-I HD-ZIP TF family and were also upregulated in root samples (log2FC 2.1 and
366 2.0, respectively). *ATHB40*, on the other hand, is a class-II HD-ZIP TF that was upregulated in
367 the root (log2FC 3.7). *ATHB12* and *ATHB7* are associated with root elongation and leaf
368 development, albeit at different stages (Ré et al., 2014; Hur et al., 2015). *ATHB40* is a negative
369 regulator of primary root development (Mora et al., 2022).

370 In addition to the PGP-related TF encoding DEGs, we also identified several DEGs
371 encoding for TFs involved in defence-related pathways, namely, WRKY, MYB, MYC, HSF,
372 and NAC TFs. WRKY TFs are global regulators of host responses to phytopathogens.
373 Treatment with SLU99 culture supernatant triggered differential expression of 14 WRKY
374 genes in tomato and 11 genes in potato. Two of the WRKY TF encoding genes, *WRKY30* and
375 *WRKY45*, involved in defence against biotic and abiotic stresses, were upregulated in common
376 between tomato and potato. *WRKY6, WRKY55,* and *WRKY71* were uniquely upregulated in
377 tomato leaf and, along with *WRKY33B* and *WRKY75*, are involved in defence against
378 necrotrophic fungal pathogens. *WRKY40* and *WRKY41*, genes involved in abiotic stress
379 tolerance, were strongly upregulated in tomato leaves (log2FC 9.0 and 4.5, respectively), and
380 were downregulated in potato leaves upon SLU99 treatment (log2FC -2.1 to -2.7). The *MYC2*
381 TF upregulated (log2FC 5.1) in tomato roots upon SLU99 treatment indicates a role in JA-
382 mediated induced systemic resistance (ISR). Furthermore, treatment with SLU99 induced

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383 expression of several R-gene orthologs such as *Cf-2,2-like* (log2FC 2.2), *Cf-9* (log2FC 3.4),
384 *RPM1* (log2FC 1.7), *RPS5* (log2FC 4.1), *CSA1* (log2FC 4.8) and *Alternaria stem canker*
385 *resistance* (log2FC 1.6) in tomato leaves, *LEAF RUST 10 DISEASE-RESISTANCE LOCUS*
386 *RECEPTOR-LIKE PROTEIN KINASE-like 1.1* (*LRK10*) (log2FC 2.9 and 5.3 in root and leaf,
387 respectively), *TMV resistance protein N* gene (log2FC 6.0) in tomato root and *putative late*
388 *blight resistance protein homolog R1A-10* (log2FC 1.6) and *R1A-3* (log2FC 1.5) in potato
389 leaves.

390 ## 4 Discussion

391 Several soilborne rhizobacteria have long been known to promote plant growth across a wide
392 range of plant species. In this study, six bacterial strains were chosen for their biocontrol
393 potential and tested on potato plants in a late-blight hotspot field. Four of the strains that
394 directly impacted the height of the potato plant in the field were chosen for detailed
395 examination in a controlled environment to further evaluate their growth-promoting function.
396 These strains included *P. fluorescens* strain SLU99, *S. rubidaea* strains EV23, AV10, and *S.*
397 *plymuthica* S412.

398 In the growth chamber, all four strains enhanced at least two growth variables in potato
399 plants, indicating that all tested strains significantly impact potato growth, which is consistent
400 with the field evaluation. However, the effect of these strains on the dry matter accumulation
401 is only noticeable in the tuber, which accounts for more than 60% of the total dry weight,
402 suggesting that PGPR treatment promotes photosynthate translocation into tubers. In contrast,
403 growth-promotion activity in tomato plants is strain-dependent with SLU99 and AV10
404 improving plant height and total dry weight. Furthermore, SLU99 improved chlorophyll
405 content, total leaf number and leaf area, suggesting enhanced light interception and
406 photosynthesis rate explaining the obtained higher tomato fruit yield.

407 Intriguingly, although all four strains isolated from tomato rhizospheres are favorable to
408 potato yield, only SLU99 is significantly beneficial to tomato yield. Previous research found
409 that bacterial consortiums aid plant growth by enhancing stress tolerance (Silambarasan et al.,
410 2019; Yang et al., 2021; Kelbessa et al., 2023). Recently, results from our group demonstrated
411 that SLU99 is compatible with strains EV23 and AV10 (Kelbessa et al., 2022), implying that
412 these bacteria could co-exist as a consortium in the rhizosphere. Considering that all these
413 strains are potent biocontrol agents (Kelbessa et al., 2022), a bacterial consortium of these
414 strains could act synergistically to contribute to reducing disease under natural conditions.

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415 Moreover, plant exudates attract rhizobacteria to colonize the roots (Bais et al., 2006). It has
416 been demonstrated that the composition of root exudates varies between cultivars of the same
417 species (Zhang et al., 2020) and thus cultivar-specific traits might have contributed to a
418 negative regulatory effect of the colonization of *Serratia* species in the tomato variety used in
419 this study.

420 PGPR also enhances the mobilization of locally available nutrients for plant uptake by
421 solubilizing P, K, and Zn, and nitrogen fixation (Prasanna et al., 2016). N and K are the most
422 abundant nutrients in plant tissues (Sardans and Peñuelas, 2015). Potato cultivation takes up K
423 in large quantities and is very important to gain a higher yield of marketable tubers (Khan et
424 al., 2012). Our results suggest increased K in the soil following the treatment with PGPR,
425 consistent with a previous study that showed *Enterobacter cloacae*, a PGPR, led to a higher
426 amount of K in the soil (Ghadam Khani et al., 2019). However, further research validation is
427 required to assess the impact of PGPR on soil nutrient contents. On the other hand, in tomato,
428 TN, available P and K were slightly increased after SLU99 treatments, indicating that this strain
429 may have facilitated nutrient availability for plant uptake (Meena et al., 2014).

430 Phytohormone-mediated signal transduction and their interplay regulate several
431 physiological processes in plant growth and development. Phytohormones also mediate
432 cellular responses during abiotic and biotic stress. Rhizobacterial-stimulated plant growth is
433 intrinsically linked to the production of phytohormones, siderophores, and secretion of ACC-
434 deaminase that reduces ethylene biosynthesis (Yang et al., 2009). Accordingly, KEGG pathway
435 enrichment analysis suggested that treatment with SLU99 culture supernatant resulted in
436 significant differential expression of genes involved in plant hormone signal transduction.
437 Genes involved in the biosynthesis of zeatin, a naturally occurring CK that promotes cell
438 division in plants, were significantly differentially expressed in both potato and tomato leaves
439 upon SLU99 treatment. Strain SLU99 enhanced the expression of *CK hydroxylase* in tomato
440 root suggesting an increase in the biosynthesis of trans-zeatin, which is reported to be
441 transported through the xylem (Osugi et al., 2017). However, excess CK needs to be stored to
442 be protected against CK oxidases. Conversion of zeatin to O-glucosyl- and O-xylosyl-zeatin, a
443 reversible process, is important for the storage of CK. Our results show that *ZOG1* and *ZOX1*,
444 genes that encode enzymes in the glycosylation of zeatin are upregulated, suggesting the CK
445 is synthesized in excess and is stored in roots and leaves, upon SLU99 treatment in tomato.

446 The increase in the germination of the tomato seeds requires specific reprogramming of the
447 GA pathway (Groot and Karssen, 1987). Moreover, the presence of GA in the root meristem
448 and elongation zone is necessary for the normal growth of the root. *GA3OX* encodes a key

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449 enzyme involved in the last step in the biosynthesis of the GA and is reported to be expressed
450 in the root elongation zone (Barker et al., 2021). SLU99 culture supernatant treatment of tomato
451 plants resulted in an increased expression level of *GA3OX*, suggesting an increase in the GA
452 in the roots. GA homeostasis is necessary for plant growth and development (Richards et al.,
453 2003). GA 2-oxidation mediated by the *GA2ox* gene family is reported to be a major GA
454 inactivation pathway that functions throughout *Arabidopsis* development (Schomburg et al.,
455 2003; Rieu et al., 2008) and is necessary for maintaining GA levels in peach (Cheng et al.,
456 2021). Our results show that *GA2ox8* is upregulated in tomato leaves following treatment with
457 SLU99 culture supernatant, suggesting PGPR aid in maintaining GA levels. Our results of
458 increased expression of genes encoding DELLA-GAI and a slight increase of AP2/ERF
459 (log2FC 1.2, p 0.04) in tomato leaves are in line with reports showing lowered GA levels are
460 also associated with improved stress tolerance through DELLA-mediated activation of
461 AP2/ERF (Colebrook et al., 2014; Castro-Camba et al., 2022).
462 It is well-established that several auxin producing PGPR regulate auxin localization and
463 distribution in the plant (Tsukanova et al., 2017). Rhizobacterial-produced auxin has also been
464 shown to be important for PGPR-mediated morphological changes in plants (Spaepen et al.,
465 2014). Treatment with these PGPR also resulted in increased levels of endogenous auxin and
466 is associated with root growth. Indeed, local auxin maxima in the pericycle is necessary for the
467 formation of lateral root primordia and their subsequent development into lateral roots.
468 However, the effect of exogenous auxin on the root is concentration dependent. At higher
469 concentrations, exogenous auxin inhibits root growth (Ivanchenko et al., 2010). Consequently,
470 large amounts of auxin generated by some rhizobacteria strains, such as *Enterobacter* (Park et
471 al., 2015), *P. fluorescens* (Zamioudis et al., 2013) and *P. syringae* (Loper and Schroth, 1986)
472 inhibit primary root elongation in lettuce, *Arabidopsis*, and sugar beet, respectively. In short,
473 while auxin is an important contributing factor to root growth, regulating endogenous auxin
474 levels is also crucial. *GH3* genes, upon induction by IAA accumulation, encode enzymes
475 involved in the conjugation of free IAA to amino acids thereby maintaining auxin homeostasis
476 (Staswick et al., 2005). Our study is consistent with earlier reports of *P. fluorescens* producing
477 auxin and with increased lateral root formation (Chu et al., 2020; Ortiz-Castro et al., 2020).
478 Additionally, treatment with SLU99 also impaired primary root elongation in potato plants.
479 Taken together, our results support the hypothesis that treatment with SLU99, while increasing
480 the endogenous IAA levels through upregulation of *YUCCA8*, and utilizing necessary auxin

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481 for lateral root development, also aided in maintaining its homeostasis through GH3.1 mediated
482 conjugation of free auxin (Fig. 9).
483 Higher auxin levels are also associated with increased ethylene biosynthesis (Fa Yang and
484 Hoffman, 1984). Regulating cellular ethylene content is a critical aspect of plant growth and
485 development. Application of exogenous auxin is also reported to increase expression of *ACS*
486 genes that encode enzymes involved in the conversion of *S*-adenosylmethionine to ACC, the
487 ethylene precursor (Tsuchisaka and Theologis, 2004; Niu et al., 2022). Considering that PGPR
488 produce auxin, it can be hypothesized that the auxin produced by PGPR result in increased
489 expression of *ACS*, and thus might promote ACC production. Providing further evidence of
490 ethylene synthesis, *ACO1,* which encodes ACC oxidase, the enzyme required for the synthesis
491 of ethylene from ACC, is also upregulated upon SLU99 treatment. However, higher ethylene
492 levels not only inhibit root development but also trigger an adaptive response such as growth
493 inhibition and delayed flowering (Ravanbakhsh et al., 2018). PGPR belonging to diverse
494 genera are reported to produce ACC deaminase, an enzyme that lowers host ACC levels (Glick,
495 2005). It is important to note that although bacteria produce ACC deaminase, due to the higher
496 substrate affinity of ACC oxidase than ACC deaminase, the ethylene level in the plant cannot
497 be totally eliminated (Glick et al., 1998). Intriguingly, two differentially expressed genes, *LHT8*
498 and *LHT1*, belonging to the lysine histidine transporter family that was previously linked to
499 ACC transport (Shin et al., 2015; Vanderstraeten and van Der Straeten, 2017) are upregulated
500 in treated roots and leaves, respectively, suggesting that the excess ACC may be transported to
501 the shoot (Fig.9). Further research using ethylene biosynthetic and signalling mutants is
502 necessary to enhance our understanding of the involvement of PGPR in modulating ethylene
503 levels during plant development.
504 Plant hormone homeostasis is critical in plant growth and development. Since PGPR can
505 have a significant influence on hormone biosynthesis and signalling, plants need to cope with
506 such differences. Upregulation of *CKX3*, *GA2OX,* and *GH3* in PGPR-treated plants in our study
507 might thus be an adaptation mechanism to increased hormone levels.
508 All of the rhizobacteria strains tested here have previously been shown to have biocontrol
509 activity against the plant pathogen *Phytophthora colocasiae* (Kelbessa et al., 2022), both in
510 culture and *in planta*. The activation of plant metabolite pathways (growth and defence) by the
511 rhizobacteria, and their direct antagonistic activity against pathogens, suggests that these strains
512 will have utility in sustainable agriculture by controlling serious crop diseases and boosting
513 yield.
514

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515 **Data availability statement**

516 All the raw high quality (Q30), adapter trimmed fastq files were deposited into the NCBI SRA
517 database under Bioproject PRJNA851815. Accession numbers of BioSamples are
518 SAMN29251990, SAMN29251991, SAMN29251992, SAMN29251993.

519

520 **Author contributions**

521 Conceptualization and designing the experiment: PBK and RV. Methodology: NASH, FG, RV
522 and PBK. Data validation and analysis: NASH, FG, SG, RV and PBK. Investigation: NASH,
523 PBK and FG. Resources: RV, RO, and PBK. Writing - original draft preparation: NASH and
524 PBK. Writing - review and editing: NASH, RRV, SW, SG, RO, and PBK. Supervision and
525 project administration: PBK, RV, SW, and RO. Funding acquisition: PBK, RV and RO. All
526 authors contributed to the article and approved the submitted version.

527

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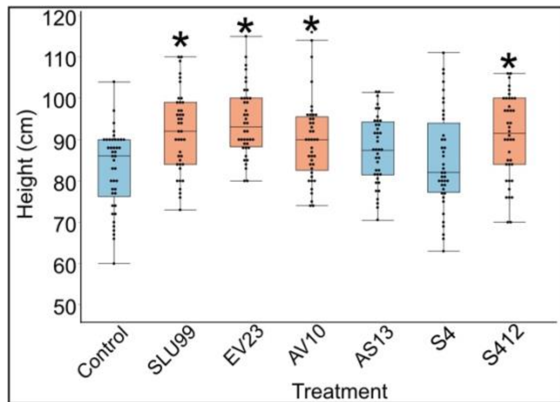

Fig. 1. Effects of bacterial inoculations on the height of potato plants grown under field conditions. Strains used were *Pseudomonas fluorescens* SLU99, *Serratia rubidaea* EV23 and AV10, *S. plymuthica* S412 and AS13, and *S. proteamaculans* S4. Asterisks indicated statistical significance (* $p < 0.001$).

Table 1. Plant height at 30 and 60 days after transplanting, yield, and total dry weight of tomato and potato plants inoculated with *P. fluorescens* SLU99, *Serratia rubidaea* EV23, AV10, *S. plymuthica* S412 and control (no inoculation).

Treatment	Plant height at 30 DAT (cm)		Plant height at 60 DAT (cm)		Yield/plant (g)		Total plant dry weight (g)	
	Tomato	Potato	Tomato	Potato	Tomato	Potato	Tomato	Potato
***P. fluorescens* SLU99**	44.43	62.78	70.50^{a}	66.80^{a}	73.3^{a}	149.0^{a}	44.8^{a}	48.5^{a}
***S. rubidaea* EV23**	42.30	62.44	59.57^{c}	66.12^{a}	32.0^{b}	150.7^{a}	34.6^{c}	47.8^{a}
***S. rubidaea* AV10**	47.83	59.00	65.90^{ab}	62.81^{bc}	30.7^{b}	145.8^{a}	37.3^{b}	47.2^{a}
***S. plymuthica* S412**	46.13	59.70	63.77^{bc}	64.76^{ab}	30.3^{b}	145.0^{a}	35.2^{bc}	46.4^{ab}
Control	45.57	58.37	62.20^{bc}	62.10^{c}	25.8^{b}	131.0^{b}	33.3^{c}	43.8^{b}
***p* value**	0.2420 (ns)	0.0709 (ns)	0.0131 (*)	0.0005 (**)	<0.0001 (***)	0.0103 (*)	<0.0001 (***)	0.0152 (*)

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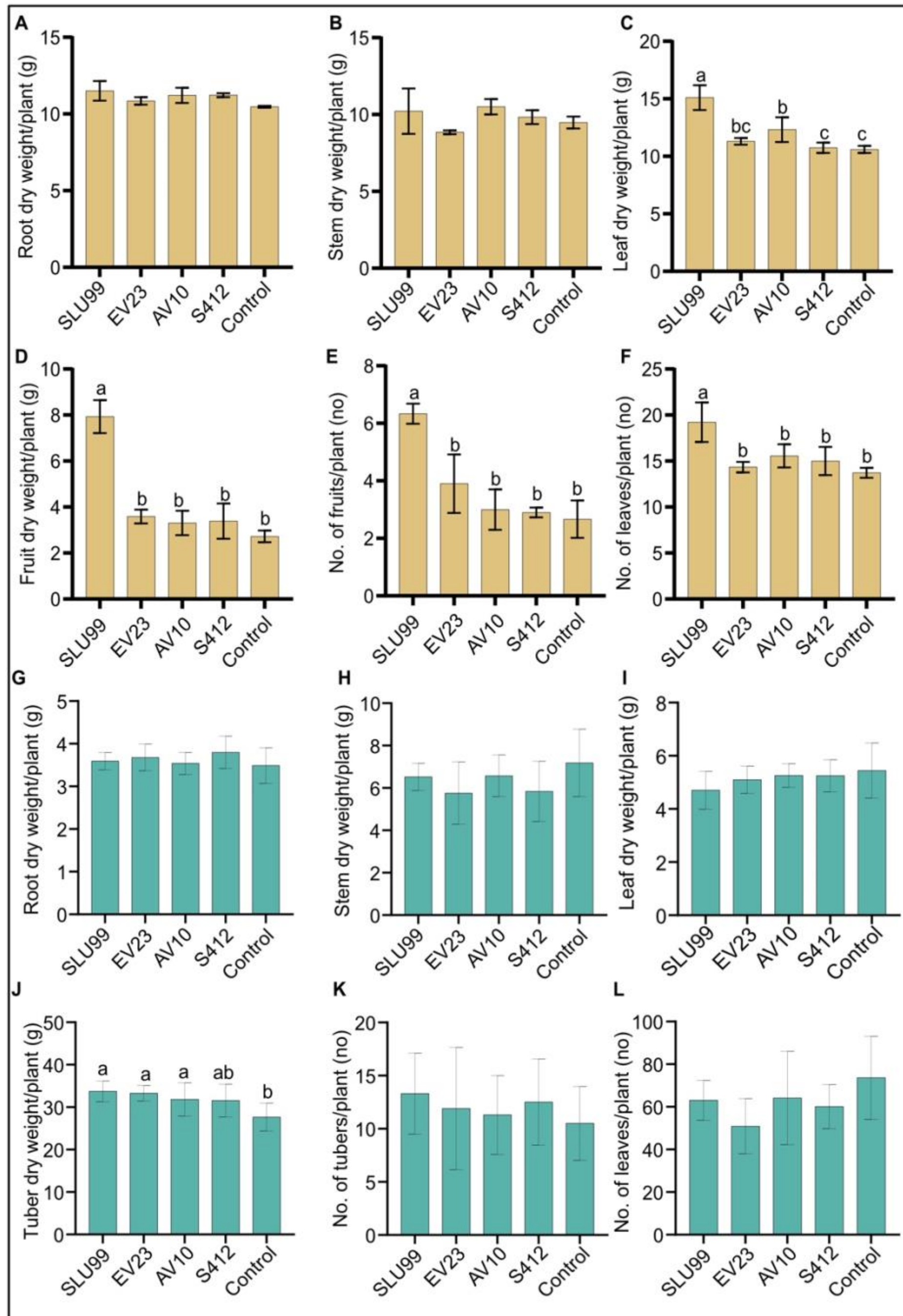

Fig. 2. Effects of bacteria inoculations on the phenotypic characteristics of tomato and potato plants. Dry weight of different tomato (A-D) and potato (G-J) plant parts, and fruit (E), tuber (K) and leaf (F, L) number per plant. Means of root and stem dry weight were not significantly different among treatments. Strains used were *Pseudomonas fluorescens* SLU99, *Serratia rubidaea* EV23 and AV10, *S. plymuthica* S412. Means within the same bar graph without a common letter are significantly different by LSD's test at 95% confidence level. Each value is the mean of nine and ten biological replicates per treatment for tomato and potato plants, respectively. Error bars represent standard deviations (SD).

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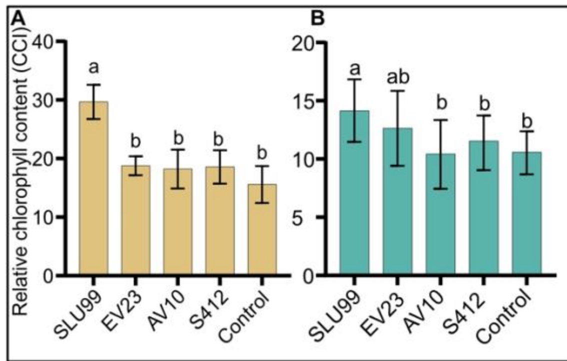

Fig. 3. Relative chlorophyll content of tomato and potato plants inoculated with rhizobacteria. The values presented are mean values of relative chlorophyll content in the unit of Chlorophyll Content Index (CCI) measured using an Apogee MC-100 Chlorophyll Concentration Meter at harvest. Each value is the mean of 90 readings from nine biological replicates for tomato and 100 readings from ten biological replicates for potato per treatment. Means within the same bar graph without a common letter are significantly different by LSD's test at 95% confidence level.

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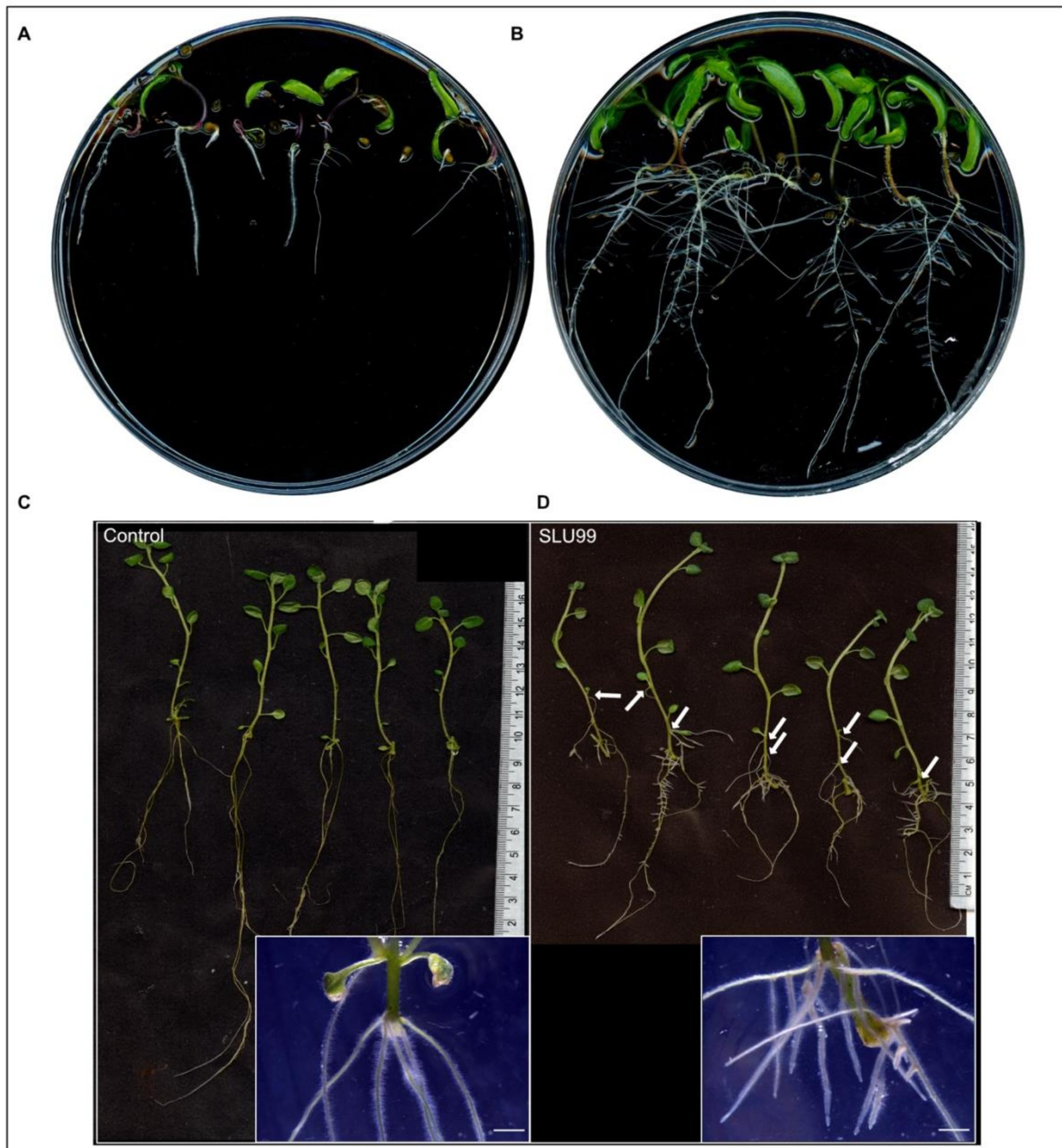

Figure 4. Effect of *Pseudomonas fluorescens* SLU99 on plants grown *in vitro*. Growth of tomato seedlings upon treatment with culture supernatant of SLU99 (B) compared to mock treatment (A). Growth of potato plants treated with *P. fluorescens* SLU99 (D) compared to control treatment (C). Arrows indicate secondary adventitious roots developed upon treatment with SLU99. Insets in C and D are representative stereo microscope images at root induction. The scale bar in the inset images represents 1 mm.

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Table 2. Characteristics of the DEGs in tomato and potato plants treated with *Pseudomonas fluorescens* SLU99 culture supernatant.

	Tomato		Potato	
	Root	Leaf	Root	Leaf
Upregulated	1675	2024	1787	411
Log2FC > 1.5	1094	1467	1012	209
p value < 0.05	1076	1322	996	206
Downregulated	319	841	2253	1112
Log2FC < 1.5	118	420	1251	772
p value < 0.05	117	410	1230	753

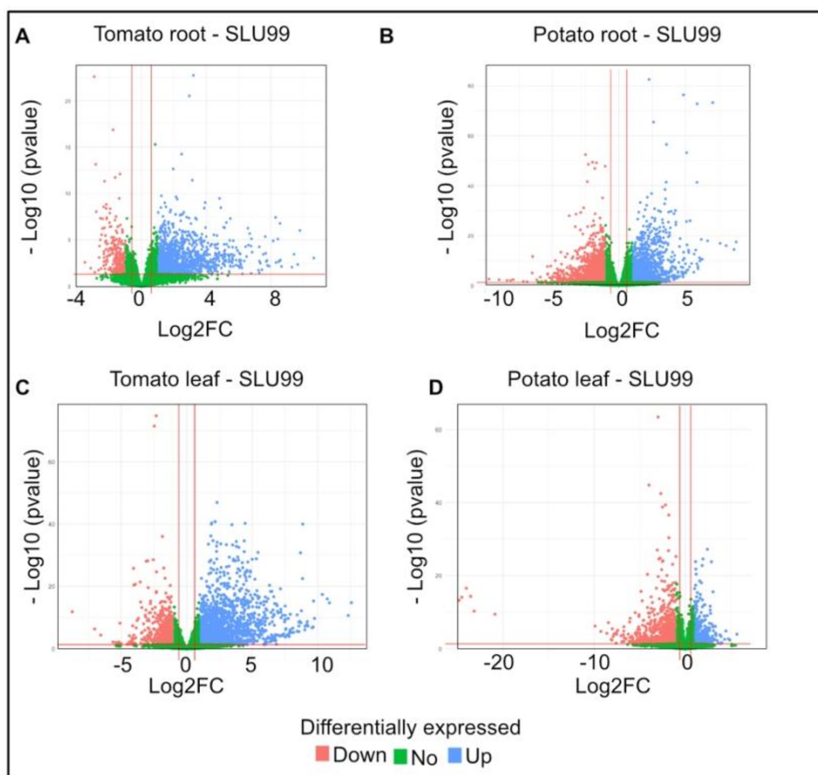

Figure 5. Volcano plot of differentially expressed genes (DEGs) for potato and tomato leaves and roots treated with the culture supernatant of *Pseudomonas fluorescens* SLU99, compared to the mock treatment. Upregulated genes are shown as blue dots at the right side of each plot; downregulated genes are shown as pink dots at the left side of each plot; non-differentially expressed genes are shown as green dots clustered at the centre (centred around Log2FC 0) of each plot.

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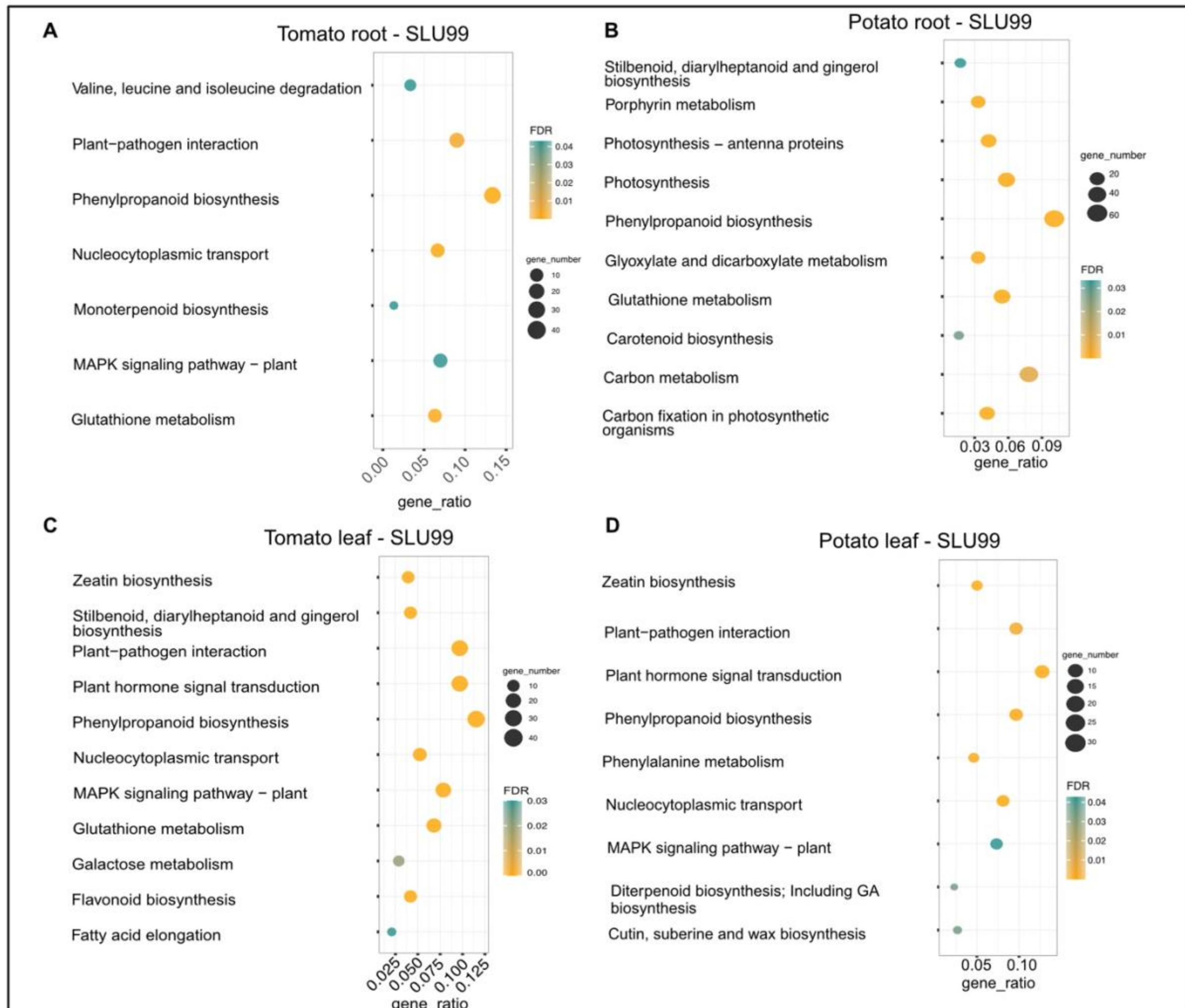

Fig. 6. KEGG enrichment analysis of DEGs in the transcriptomes of potato and tomato leaves and roots treated with the culture supernatant of *Pseudomonas fluorescens* SLU99, compared to the mock treatment. The size of the circles in each plot represents the number of DEGs annotated for that pathway or process. The gene ratio on the x-axis represents the ratio of the count of core enriched genes to the count of pathway genes.

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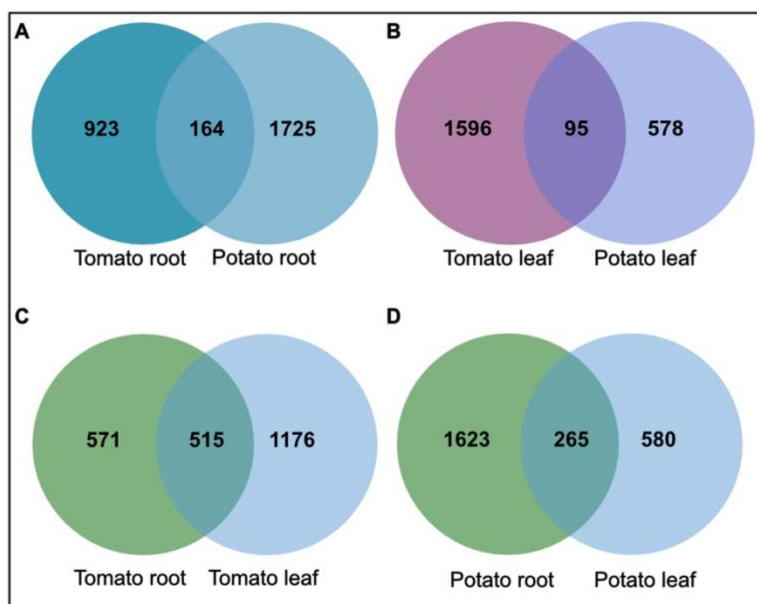

Fig. 7. The overlap of products of differentially expressed genes (DEGs) in potato and tomato leaves after treatments with *Pseudomonas fluorescens* SLU99 supernatant.

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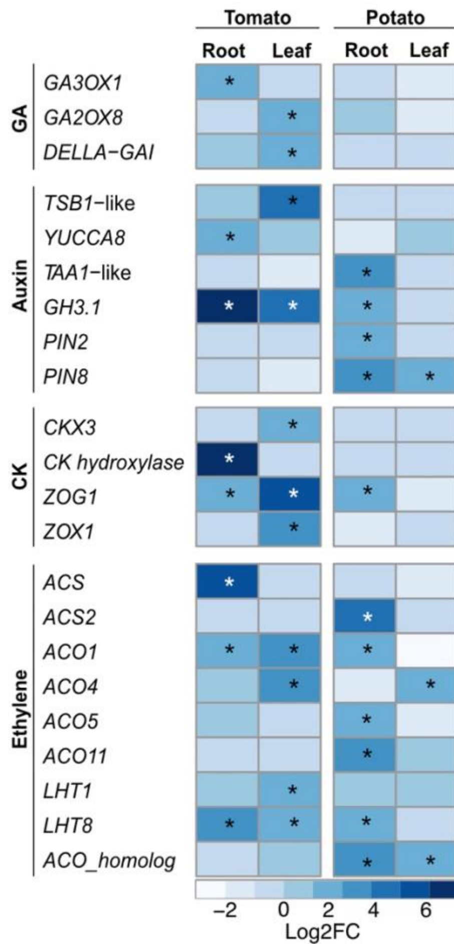

Figure 8. Heatmap of key differentially expressed genes (DEGs) involved in different phytohormonal pathways upon treatment with *Pseudomonas fluorescens* SLU99 culture supernatant. GA = gibberellic acid; CK = cytokinin. Asterisks indicated statistical significance (* $p < 0.05$).

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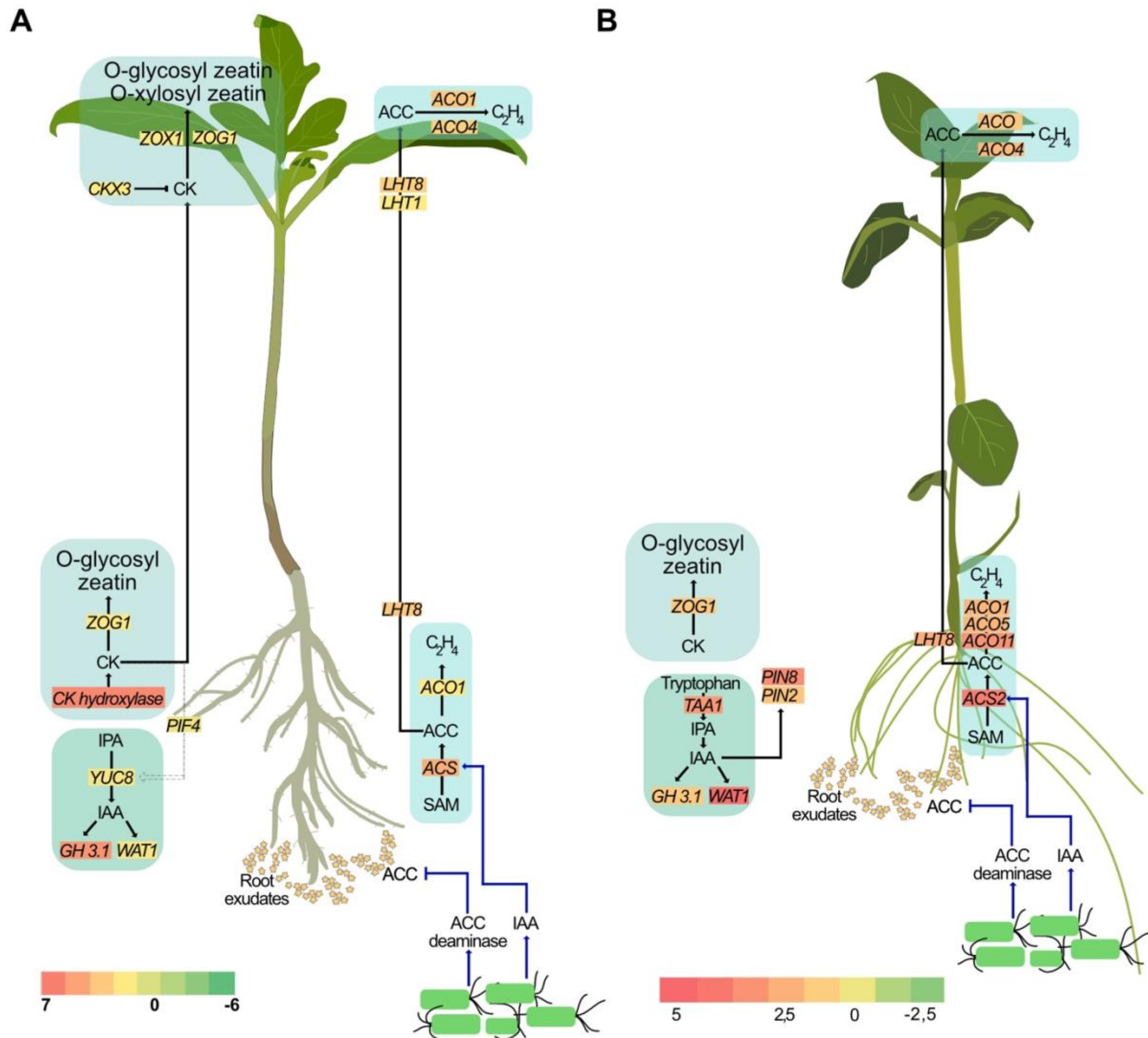

Figure 9. A proposed model illustrating the effect of *P. fluorescens* strain SLU99 on different phytohormonal pathways in tomato (A) and potato (B) plants.

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Supplementary Table 1. Analysis of soil nutrients and characteristics after amendment with selected rhizobacteria and growth of tomato and potato plants. TN: total nitrogen, P: phosphorus, K: potassium, EC: electrical conductivity, SOM: soil organic matter.

Treatment	TN (mg/kg)		Available P (mg/l)		Available K (mg/l)		pH		EC (mS/cm)		SOM (%)	
	Tomato	Potato	Tomato	Potato	Tomato	Potato	Tomato	Potato	Tomato	Potato	Tomato	Potato
***P. fluorescens* SLU99**	7080	5780	36	29	140	15	5.9	6.5	1.7	1.4	42.7	43
***S. rubidaea* EV23**	6190	6000	34	27	140	11	5.9	6.4	2.1	1.3	43.4	48
***S. rubidaea* AV10**	6360	6030	34	27	130	14	5.9	6.4	2.4	1.4	39.6	44
***S. plymuthica* S412**	5510	6190	34	28	150	11	5.8	6.5	2.3	1.3	41.0	44
Control	6850	6160	32	28	130	9	5.9	6.5	2.3	1.2	42.9	46

Supplementary Table 2. Overview of differentially expressed transcription factor (TF) families identified in tomato and potato plants upon treatment with culture filtrate of *Pseudomonas fluorescens* SLU99.

TF Family	Differentially Expressed TFs			
	Tomato Root	Potato Root	Tomato leaf	Potato leaf
AP2	0	5	0	0
ARR-B	1	0	2	2
B3	4	4	1	3
bHLH	11	23	19	8
bZIP	1	2	1	0
CO-like	0	6	1	3
DBB	0	5	5	0
ERF	16	18	15	4
GATA	2	6	5	3
GRAS	3	6	3	1
HD-ZIP	11	23	1	6
HSF	4	1	5	2
LBD	6	13	6	6
MIKC_MADS	14	8	1	2
MYB	21	16	16	8
MYB_related	3	8	2	5
NAC	2	12	3	8
NF-Y	4	4	3	1
TALE	2	4	1	1
TCP	0	5	0	2
Trihelix	1	1	1	1
WOX	1	1	0	0
WRKY	4	8	1	4
ZF-HD	1	3	0	0

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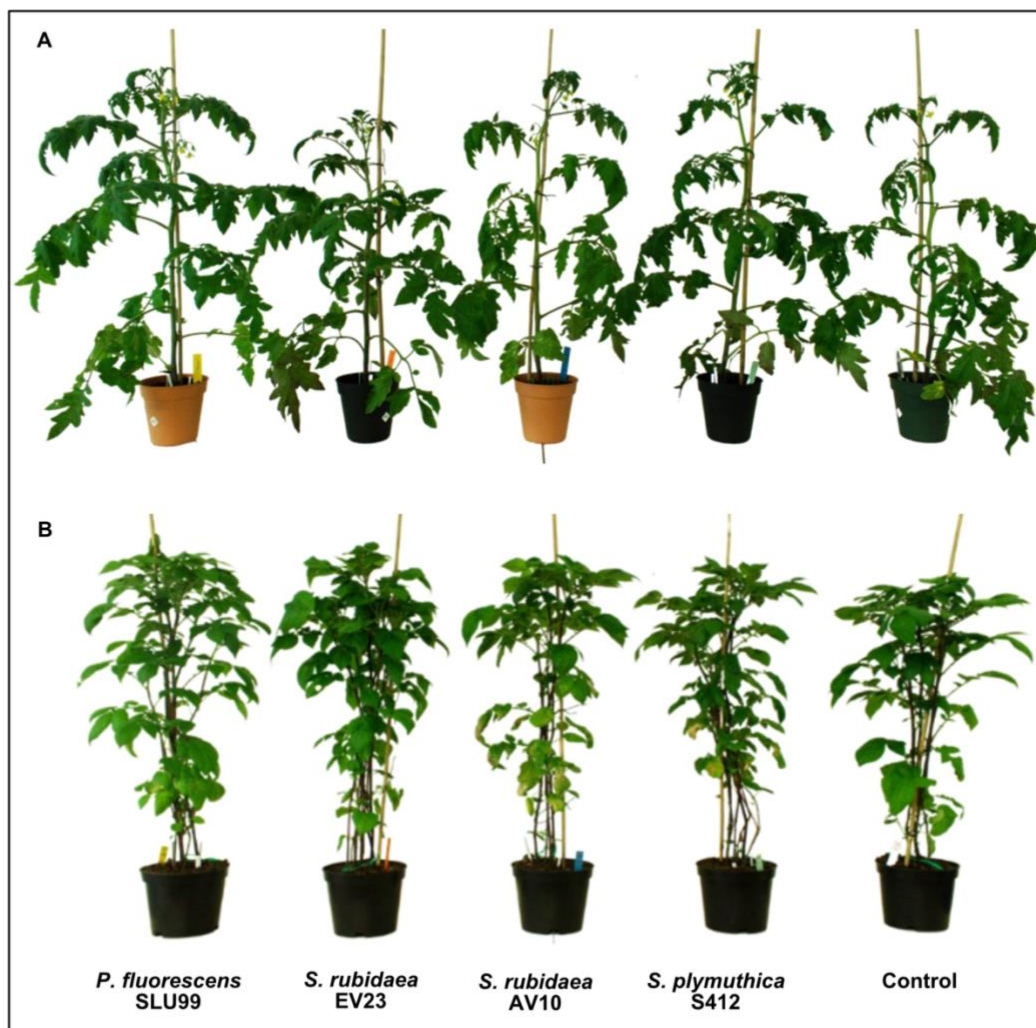

Supplementary Figure 1. Plant height after treatment with different bacteria. (A) Tomato plants 42 days after transplanting (B) Potato plants 53 days after planting.