# Unveiling the potato cultivars with microbiome interactive traits for sustainable agricultural production

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23

24 **ABSTRACT**

25 Root traits significantly shape rhizosphere microbiomes, yet their impact on microbes is
26 often overlooked in plant breeding programs. Here, we propose that selecting modern
27 cultivars based on microbiome interactive traits (MITs), such as root biomass and exudate
28 patterns, can enhance agricultural sustainability by interacting effectively with soil
29 microbiomes, which in turn, promotes plant growth and resistance to stress, thereby
30 reducing reliance on synthetic crop protectants. Through a stepwise selection process, we
31 chose 51 potato cultivars based on their plant growth matrices with distinct root exudate
32 patterns. In a greenhouse experiment, we verified their capacity to interact with the soil
33 microbiome. These were further clustered into functional groups based on their MITs and
34 leaf metabolites and further characterised by their rhizosphere microbiome (bacterial and
35 fungal communities). Our results indicate a positive correlation between microbial
36 community diversity and root biomass. A potential influence of leaf metabolites on the
37 composition of rhizosphere bacteria was observed, supporting the plant holobiont
38 framework. We highlight the significance of incorporating positive effects on
39 microbiomes into the breeding targets to advance the objectives of sustainable agriculture.
40 Finally, a set of 11 potato cultivars was selected to verify whether those with microbiome-

interactive traits could contribute to sustainable agricultural production under field conditions.

## 1 INTRODUCTION

Potato (*Solanum tuberosum* L.) cultivations rely heavily on conventional agricultural practices as a staple crop. Conventional management, which includes the widespread use of synthetic fertilisers and pesticides, is frequently used to enhance yields and protect crops from pests and diseases (Timsina, 2018). However, this dependency on synthetic compounds comes with substantial environmental issues. Overusing chemical inputs in conventional agriculture leads to water pollution, soil degradation, and soil microbial biomass and activity reduction, which are crucial in maintaining soil fertility and nutrient cycling (AL-Ani et al., 2019; Tripathi et al., 2020). Balancing the imperative for high yields with care for our environment is a critical challenge in the breeding of crops.

In conventional breeding, plants are bred for traits such as high yield, disease resistance, tolerance to environmental stresses, and improved agronomic traits (Breseghello and Coelho, 2013). While pivotal in crop development, conventional breeding has inadvertently led to the dissociation between plant and soil microbiomes, negatively affecting beneficial plant-microbiome interactions (Spor et al., 2020). Comparisons between domesticated cultivars and their ancestral plants revealed that the rhizosphere microbiome of the latter exhibited higher complexity and connectivity (da Silva et al., 2023; Rossmann et al., 2020). However, relying solely on ancestral or wild plants may not effectively address the challenge of optimising plant-soil microbiome interactions in

63 modern agricultural systems. Identifying specific genes associated with beneficial
64 microbiomes in ancestral plants, with the aim of a subsequent transfer to modern crops
65 (Clouse and Wagner, 2021), is complex due to environmental effects on gene expression
66 (Raaijmakers and Kiers, 2022). Despite the reduced focus on plant-microbiome
67 interactions during domestication (Wei and Jousset, 2017), multiple studies have
68 demonstrated that inoculating modern crop cultivars with beneficial microbes can
69 significantly enhance plant growth and stress resistance (Diagne et al., 2020; Fröhlich et
70 al., 2012; Rodriguez et al., 2019; Tiwari et al., 2017). This suggests that modern cultivars
71 retain the capacity for beneficial interactions with soil microbes, which can be leveraged
72 or strengthened. Therefore, it is critical to identify gene markers associated with
73 beneficial microbiomes in modern crops and apply this knowledge in real-world
74 agricultural systems, particularly in the context of climate change.

75 The connection between root traits and plant productivity in crops has long been
76 acknowledged (Lynch, 1995), and it is increasingly evident that our understanding of this
77 connection should extend to how root traits shape the composition and functionality of
78 the rhizosphere microbiome. While this aspect has received somewhat limited attention
79 within plant breeding (Herms et al., 2022), many studies highlight the role of root traits
80 in the rhizosphere microbiome. For instance, a study on maise revealed that wild maise
81 had a significant impact on the structure of the microbial community, which was
82 attributed to a high root-to-shoot biomass ratio (Szoboszlay et al., 2015). Plant root traits
83 influence the soil microbial community by modulating the fungi-to-bacteria ratio,
84 contributing to nutrient cycling (Wan et al., 2021). Moreover, a study involving beans
85 (Pérez-Jaramillo et al., 2017) indicated that root architecture is linked to increased

specific bacterial taxa, which could be connected to plant health. In addition to the root system, root exudates substantially impact the rhizosphere microbiome. As a survival strategy, plants secrete an abundance of compounds in their root exudates that can influence the diversity of the rhizosphere microbial community, promote the development of a more complex microbial network and enhance microbial carbon cycling, thereby facilitating the growth and survival of the host (Wang et al., 2022). A study on wheat has demonstrated that cultivars with a strong capacity for root exudates contribute to increased soil microbial diversity (Iannucci et al., 2021). These specific cultivars can be further explored for their resource utilisation potential in agricultural systems.

Here, we approach the challenge of identifying plant characteristics associated with soil microbes by exploring the microbiome interactive traits (MITs) of existing potato cultivars in the European potato germplasm bank. The root system architecture and exudate patterns, identified as pivotal MITs, guide our stepwise selection process for cultivars exhibiting high to low MITs. We hypothesise that cultivars with high MITs will select a more diverse rhizosphere microbiome, exhibiting superior growth to those with low MITs. A greenhouse experiment was conducted to investigate the relationship between the plant traits of 51 potato cultivars and the rhizosphere microbial community. We propose that MITs capable of recruiting beneficial microbes to the rhizosphere should be considered in the breeding and developing of new crop cultivars. By prioritising these interactive traits, we aim to contribute not only to the enhancement of crop performance but also to the interaction between plants and their microbiomes, unravelling valuable insights for innovative and sustainable agricultural practices.

## 2 MATERIALS AND METHODS

In this project, we initially narrowed down a selection of 148 late-season potato cultivars, including a commercial cultivar Desiree as a reference, selected from a pool of a thousand potato cultivars based on their resistance to pathogens, especially viruses (Table S1). The method for determining the resistance scale is detailed in the study by Michalak and Chrzanowska (2017), which offers a comprehensive overview of the procedure used to assess resistance to potato virus Y. Detailed information is available in The European Cultivated Potato Database (www.europotato.org). These 148 cultivars were then further selected based on the plant growth matrices (e.g., shoot and root length, dry weight, and root-to-shoot dry weight ratio) under sterile conditions using 6-week-old *in vitro* plants (cf. section 2.1). From those, 51 cultivars (including Desiree) were tested for their ability to interact with soil microbiome in a greenhouse experiment (cf. section 2.2). For the selected 51 cultivars, root exudate profiles from the *in vitro* experiment were also analysed.

### 2.1 *In vitro* experiment

Two-week-old potato plantlets grown from vegetative propagation in tissue culture (Bonin, Poland) were transplanted from agar tubes into 15 ml Eppendorf tubes, each containing 12 ml of sterile 0.5 x Hoagland solution. To ensure aseptic conditions, sterile cotton wool was wrapped around the above-ground part of the plantlets, which were then gently placed into the 15 ml tubes. The roots were submerged in the Hoagland medium, while the above-ground part remained above it. The plantlets were allowed to acclimate to their new environment during a one-week growth period in a controlled climate

130 chamber. The climate chamber maintained a temperature of 22 °C during the day and
131 18 °C at night, with a photoperiod of 16 hours of light and 8 hours of darkness.

132 Upon completion of the initial week, the plantlets were transferred to new sterile 15 mL
133 tubes, maintaining the 12 ml sterile 0.5 x Hoagland solution, as described in the previous
134 step. To compensate for the liquid lost during the experiment, sterile water was added to
135 maintain the volume at 12 ml.

136 After the third week, the plants were harvested for length and dry weight measurements.
137 Additionally, 1 ml aliquots of the growth medium were collected for root exudate
138 metabolite analysis. The samples were immediately stored at -80°C until further analysis.

139 **2.2 Greenhouse experiment**

140 Fifty-one potato cultivars (including Desiree) were selected for a greenhouse experiment
141 based on plant growth traits from the *in vitro* experiment, with the cultivars spread across
142 a range of growth parameters (Figure S1 and Table S2). The soil in this study originated
143 from a sugar beet field and was sieved with a 2 mm sieve. Before starting the experiment,
144 six bulk soil samples were kept for physicochemical analyses and DNA extraction.

145 Potato plantlets obtained from tissue culture from the Institute of Plant Breeding and
146 Acclimation in Bonin (Bonin, Poland) were transplanted from agar tubes to small pots
147 filled with homogenised soil. Three replicates were established for each cultivar.
148 Additionally, six control pots without plants were prepared. The greenhouse temperature
149 was 22 °C during the day and 18 °C at night, with a photoperiod of 14 hours of light and
150 10 hours of darkness.

151 After two weeks, the potato plants were transplanted into larger pots (1.45 L). Plant leaves,
152 specifically the second or third leaf from the shoot top, were harvested for metabolomics
153 analysis in the sixth week. The harvested leaves were snap-frozen in liquid nitrogen and
154 then transferred to a freezer at -80 °C. The rhizosphere soil was obtained by gently
155 brushing off adhering soil from the roots with a disposable toothbrush. Additionally, six
156 bulk soil samples were collected from pots without plants. These soil samples were frozen
157 at -20 °C until DNA extraction the following day. Shoot height and root length were
158 measured on the day of harvesting, and shoot and root dry weights were measured after
159 drying at 65 °C for 72 hours.

160 **2.3 Metabolite profiling of root exudates and leaf tissue**

161 Metabolite fractions enriched for primary metabolites were profiled by gas
162 chromatography and electron impact ionisation-time of flight mass spectrometry (GC/EI-
163 TOF-MS) (Lisec et al., 2006; Erban et al., 2020). Root exudate samples, i.e. equal debris-
164 free 1 mL volumes, of the *in vitro* experiment, cf. section 2.1, were freeze-dried directly
165 without further sample preparation. A polar metabolite fraction was prepared from 50
166 mg snap-frozen leaf samples of the greenhouse experiment, cf. section 2.2. The frozen
167 samples were extracted by a water-methanol-chloroform solvent mixture; a polar fraction
168 was prepared from the extracts by water-induced liquid-liquid phase separation and dried
169 in a speed-vacuum-concentrator, as described earlier (Erban et al., 2020). The dried
170 fractions were subjected to methoxyamination and trimethylsilylation prior to GC/EI-
171 TOF-MS analysis. $^{13}C_6$ Sorbitol was added to all leaf samples before metabolite extraction
172 (Erban et al., 2020). N-alkanes were added to each sample upon chemical derivatisation
173 for subsequent retention index (RI) calibration (Erban et al., 2020). The GC/EI-TOF-MS

174 chromatograms were obtained and baseline adjusted by ChromaTOF software (LECO
175 Instrumente GmbH, Mönchengladbach, Germany) and background corrected using non-
176 sample controls. Metabolite annotation was performed using TagFinder software
177 (Luedemann et al., 2008), the NIST17 mass spectral database (U.S. Department of
178 Commerce, Gaithersburg, USA), and the RI and mass spectral reference data of the Golm
179 Metabolome Database, http://gmd.mpimp-golm.mpg.de/ (Hummel et al., 2010; Kopka
180 et al., 2005). Compounds representing known contaminants and added internal
181 standards were removed from further analysis. Metabolites absent from more than 75%
182 of all analysed exudates or leaf tissue samples were excluded, resulting in 84 characterised
183 leaf metabolites (Data S1) and 49 metabolites (Data S2) that were robustly present in root
184 exudates.

185 Relative concentrations were normalised for further analyses to record the sample's fresh
186 weight and internal standard or exudate volume (Schaarschmidt et al., 2020). An ANOVA
187 tool was used to perform a batch correction of the metabolite data sets for different
188 measurement batches and the measurement sequence within batches (Lisec et al., 2011).
189 All presented metabolite data are relative metabolite abundances. Three replicate
190 samples per cultivar were analysed. The missing values were substituted by zero.

191 **2.4 Soil sample sequencing and processing**

192 DNA was extracted from 12 bulk soil samples and 153 rhizosphere samples with DNeasy
193 PowerSoil Kit (Qiagen, Hilden, Germany) on 0.25 g of soil. DNA extraction followed the
194 kit's instructions except for the initial stage of bead beating, which was conducted with a
195 FastPrep-24TM 5G Instrument at 6000 rpm/s for 40 s (MP Biomedicals, Santa Ana,

196 USA). For sequencing of the bacterial community, the V4 region of the 16S rRNA gene
197 was targeted using the primer sets 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R
198 (5′-GGACTACHVGGGTWTCTAAT-3′) (Caporaso et al., 2012, 2011). For the fungal
199 community, the ITS2 region was sequenced with the primer sets 5.8SR (5'-
200 TCGATGAAGAACGCAGCG-3') and reverse primer ITS4 (5'-
201 TCCTCCGCTTATTGATATGC-3') (White et al., 1990). The Illumina MiSeq platform was
202 used for paired-end sequencing (2 × 250bp for 16S, 2 × 300bp for ITS) at the PGTB
203 (Genome Transcriptome Platform of Bordeaux, Cestas, France).

204 The 16S rRNA gene sequencing data were processed using a QIIME2 (version 2020.8)
205 pipeline (Bolyen et al., 2019). Sequences were filtered, denoised, and dereplicated using
206 the default setting of the Divisive Amplicon Denoising Algorithm (DADA2) plugin (Calla-
207 han et al., 2016). 16S rRNA taxonomic classification was performed using the q2-feature-
208 classifier plugin (Bokulich et al., 2018) against the SILVA database (version 138) (Yilmaz
209 et al., 2014). ITS sequencing data was processed using the PIPITS / 2.4 pipeline (Gweon
210 et al., 2015). In brief, the PEAR plugin was used to join read pairs (Zhang et al., 2014).
211 The FASTX-Toolkit was utilised for quality filtering (Gordon and Hannon, 2010). The
212 fungal-specific ITS2 region was extracted via ITSx (version 1.1b) (Bengtsson-Palme et al.,
213 2013). The VSEARCH 2.13.3 plugin (Rognes et al., 2016) was used to dereplicate unique
214 sequences, clustering to 97% sequence identity, and the UNITE Uchime reference dataset
215 was used for chimera detection (Nilsson et al., 2015). Ultimately, the taxonomy was
216 assigned with the RDP Classifier against the UNITE database (version 8.0) (Kõljalg et al.,
217 2013).

218 **2.5 Statistical Analysis**

219 A one-way analysis of variance (ANOVA) was used to test variation in plant metabolite
220 diversity, plant performance (shoot and root growth), and rhizosphere microbial alpha
221 diversity (Data S1-S4). Post hoc comparisons were performed through Tukey's honest
222 significant differences or Duncan's multiple range tests.

223 Analysis of soil microbial community structure (bacteria and fungi) was performed in R
224 (version 4.2.0). Feature tables were rarefied at 14400 reads for bacterial 16S rRNA gene
225 and 6361 for fungal ITS sequences, resulting in 8970 amplicon sequence variants (ASVs)
226 for the bacterial community and 2006 operational taxonomic units (OTUs) for the fungal
227 community after excluding non-microbial OTUs (Data S4). The rarefactions of feature
228 tables were generated via 'rarefy' function in the package 'vegan' (Dixon, 2003). The same
229 package was used to calculate the alpha diversity metrics for microbial communities and
230 plant metabolites. Specifically, species richness indicates the number of unique species or
231 metabolites observed, evenness describes how evenly the abundances of different species
232 or metabolites are distributed, and the Shannon Diversity Index accounts for both the
233 number of species/metabolites and their relative abundances (Jost, 2006; Wagner et al.,
234 2018; Young and Schmidt, 2008).

235 The soil microbial community, root exudate and leaf metabolite compositions (Data S1,
236 S2 and S4) were visualised through Principal Coordinate Analysis (PCoA) based on Bray-
237 Curtis distance. This analysis used the 'ape' package in R (Paradis et al., 2004). PCoA
238 scores per axis were averaged for each sample to illustrate the distribution of distinct
239 cultivars in PCoA plots clearly. Permutational multivariate analysis of variance
240 (PERMANOVA) was conducted using the 'adonis' function within the 'vegan' package to

241 assess the impact of cultivars on soil microbial communities and metabolite profiles
242 (Dixon, 2003).

243 Principal Component Analysis (PCA) based on the covariance matrix was performed with
244 the R package 'FactoMineR' to reduce the dimensionality of the data and to visualise the
245 distribution of plant cultivars (Lê et al., 2008). The variables included in the analysis were
246 shoot and root length, shoot and root dry weight, metabolite diversity and composition of
247 plant leaf tissue and root exudates (Data S3). Due to the significant variation in root
248 exudate relative abundance observed in the *in vitro* experiment, median values were used
249 for PCA plotting. Normalisation of plant data and metabolite richness was performed
250 before analysis by calculating Z-scores. Subsequently, a PERMANOVA was conducted to
251 assess the influence of variables on the distribution of 51 cultivars. The cultivars were
252 classified into four functional groups based on their distribution across the first and
253 second principal components (PC1 and PC2). The classification was done by dividing the
254 PCA plot into four quadrants, each representing a distinct functional group of cultivars,
255 reflecting differences in growth characteristics and metabolite profiles. The summarised
256 group details can be found in Table S3.

257 To investigate the relationship between plant cultivars and rhizosphere microbiome
258 composition, we categorised the 51 potato cultivars into four distinct functional groups.
259 The category was determined by the distribution of cultivars and variables along the first
260 two axes in the PCA plot.

261 The correlation between plant growth and related omics datasets (Data S3) was calculated
262 using the Spearman correlation coefficient via the 'corr.test()' function from the 'psych'

263 package in R (Revelle, 2024). The resulting p-values were adjusted using the False
264 Discovery Rate (FDR) method to control for multiple comparisons and minimise false
265 positives. We used the Mantel test with Spearman's rank correlation to assess the
266 correlation between microbial community compositions and metabolite profiles, utilising
267 Bray-Curtis dissimilarity matrices. This analysis aimed to investigate the relationship
268 between plant leaf metabolites and rhizosphere soil community.

269 Using the 'ggsankey' R package (Sjoberg, 2023), a Sankey plot was generated based on
270 functional groups to summarise the selection of the 11 cultivars with the most potential
271 for future research. The distribution of rhizosphere bacterial and fungal community
272 compositions was illustrated for the 11 selected cultivars using Spearman correlation
273 analysis. The first axis of the PCoA plot of bacterial and fungal communities served as the
274 indicator of community composition (Data S3).

275

276 **3 RESULTS**

277 **3.1 Plant growth**

278 Plant growth varied across the 51 potato cultivars in the greenhouse experiment. Analysis
279 of variance (ANOVA) revealed that most of these cultivars' growth patterns differed
280 significantly according to their identity. Among them, the cultivars showed a more
281 pronounced effect on root biomass than root length (root biomass: $p$ = 0.001, F = 2.26;
282 root length: $p$ = 0.003, F = 1.91; Figure 1). Specifically, the cultivars Inwestor, Salto and
283 Szyper demonstrated higher root biomass than others. For shoot growth, the cultivars

had a more pronounced effect on shoot length than on shoot biomass (shoot length: $p$ = 0.001, F = 6.80; shoot biomass: $p$ = 0.009, F = 1.75; Figure S2). Astrid, Inwestor, and Tewadi cultivars were the top three in shoot biomass. Regarding the root-to-shoot ratio, the length ratio exhibited a significant response to distinct cultivars ($p$ = 0.001; Figure S3). Conversely, the ratio of root-to-shoot dry weight did not show a substantial response to different cultivars ($p$ = 0.36; Figure S3).

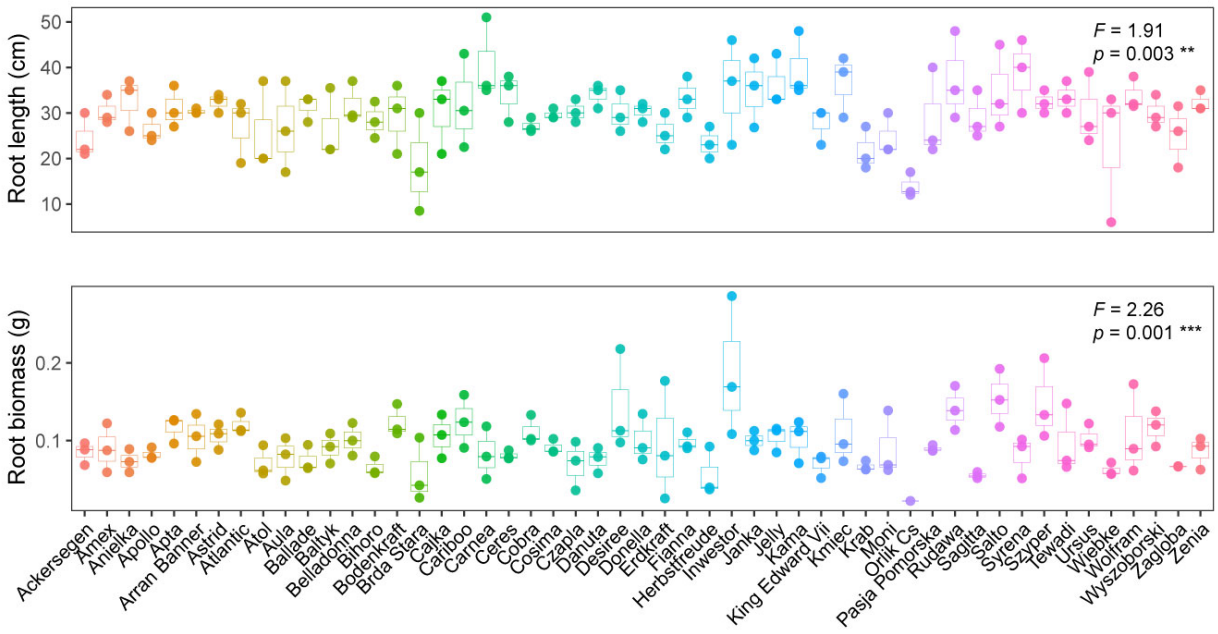


**Figure 1.** Root growth analysis of 51 potato cultivars. The upper panel displays root length, while the lower panel illustrates root dry weight. Each colour represents a distinct potato cultivar in alphabetical order. The upper right corner of each plot displays one-way ANOVA results, where the F-value explains the variation among different cultivars, and the $p$-value indicates the statistical relationship among cultivars. Significance levels are denoted as ** ($p$ = 0.01) and *** ($p$ = 0.001).

## 3.2 Plant leaf and root exudate metabolites

298 To understand the variation in metabolites produced and released by the 51 potato
299 cultivars, we conducted a Principal Coordinates Analysis (PCoA) and visualised the
300 distribution of metabolites among different cultivars (Figure 2). The cultivars differed
301 significantly in metabolite composition from both root exudates and leaves ($p_{\text{root exudate}}$ =
302 0.001 and $p_{\text{leaf}}$ = 0.001; Figure 2).

303 Notably, leaf metabolite structure responded more strongly to plant cultivar identity than
304 root exudate metabolites ($R^2_{\text{leaf metabolite}}$ = 0.66, and $R^2_{\text{root exudates}}$ = 0.55; Figure 2). The first
305 two axes of the PCoA plot explained more than 30% of the variation for both metabolites.
306 Although most cultivars tended to cluster together, several cultivars stood out, suggesting
307 a unique and pronounced influence on the metabolite profiles. Furthermore, we found
308 that the alpha diversity of plant metabolites was significantly affected by cultivars (Table
309 S4). These results indicate that different potato cultivars exhibit distinct metabolites,
310 contributing to variations in metabolite composition among cultivars.

311

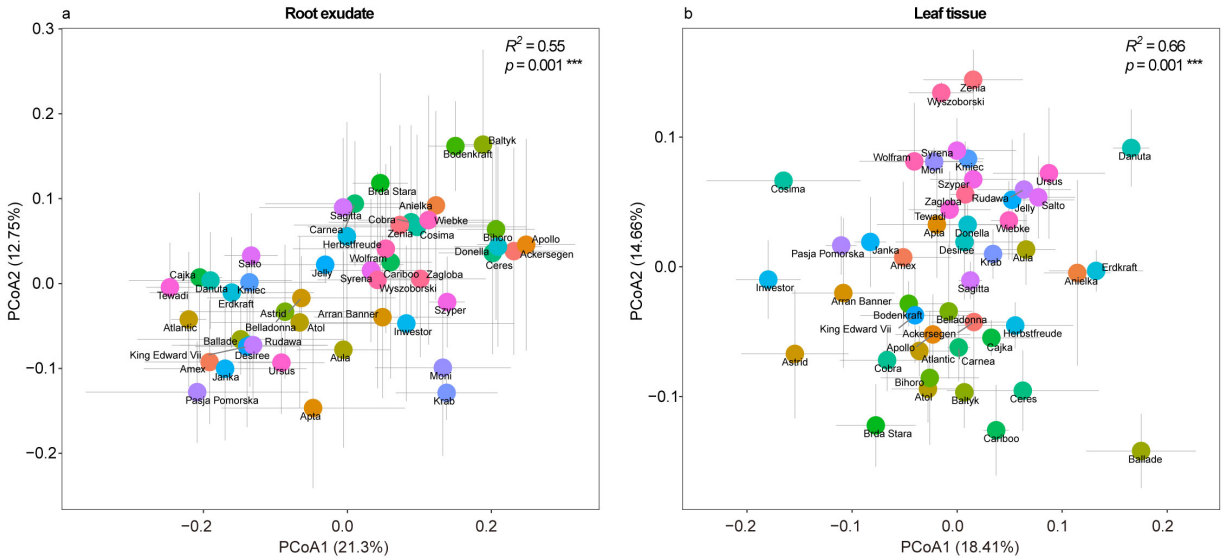


**Figure 2.** Distribution of metabolites in root exudates and leaves across different cultivars. Principal Coordinates Analysis (PCoA) based on mean Bray-Curtis dissimilarity of metabolite composition of root exudates (a) and leaves (b). Distinct potato cultivars are represented by different colours, with the error bars for each cultivar displayed in grey. PERMANOVA results are shown in the upper right corner of each panel, indicating variations in metabolite composition among different cultivars. $R^2$ quantifies the explained variation, and p-values are derived from 9999 permutations; *** denotes statistically significant p-values ($p$ = 0.001). Four outlier cultivars (Kama, Czapla, Fianna, Orlik Cs) were excluded to better illustrate the distribution of distinct cultivars. The distribution of the complete set of 51 potato cultivars is presented in Figure S4.

## 3.3 Plant cultivar functional groups

The analysis of plant cultivar growth characteristics, including shoot and root growth, leaf metabolites and root exudates, revealed that the distribution of these traits differed significantly among different potato cultivars, as evidenced by the results of the PERMANOVA analysis ($p$ = 0.001; Figure 3). Specifically, the first axis of the PCA biplot prominently reflected the impact of root exudate metabolite diversity and composition

328 (Figure 3). In contrast, plant performance metrics and leaf metabolite composition
329 mainly drove the second axis.

330 Based on the distribution of cultivars and variables across the first two axes, the 51 potato
331 cultivars were systematically categorised into four distinct functional groups (Figure 3).
332 Group A featured cultivars exhibiting high leaf metabolite diversity and plant biomass,
333 suggesting strong performance in leaf metabolic diversity and plant development. Group
334 B included cultivars with high root exudate diversity and plant length, indicating a focus
335 on below-ground metabolic processes and vertical growth of plants. Group C consisted of
336 cultivars characterised by complex leaf metabolite composition. These cultivars may have
337 a distinct composition of leaf metabolites compared to other groups, indicating specific
338 leaf metabolic profiles that differentiate them from other cultivars. Group D comprised
339 cultivars with low root exudate metabolite diversity and different metabolite
340 compositions. The summarised group details and cultivars can be found in Table S3.

341

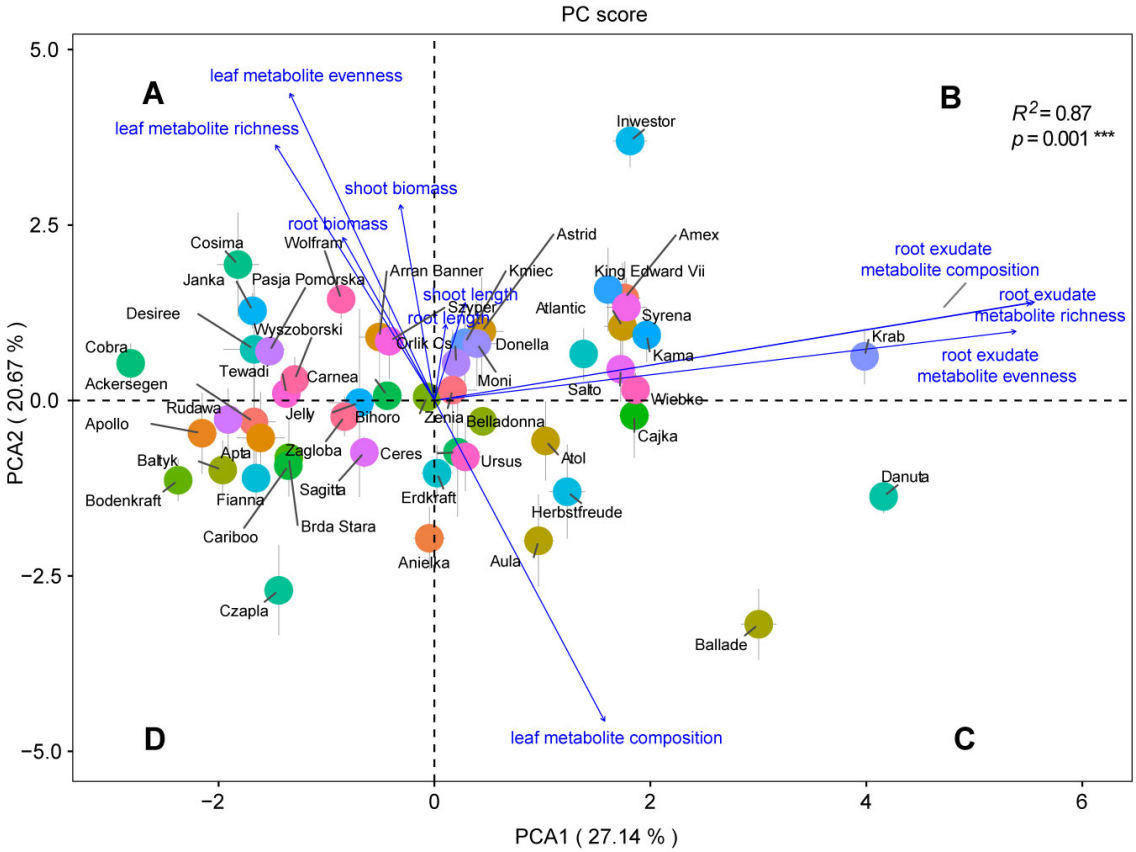


**Figure 3.** Distribution of 51 potato cultivars based on plant performance, root exudates and leaf metabolite profiles. Principal Component Analysis (PCA) based on the covariance matrix, highlighting variables impacting the distribution of potato cultivars. Distinct potato cultivars are represented by different colours, with the error bars for each cultivar displayed in grey. The result of PERMANOVA is shown in the upper right, elucidating the cultivar's influence on the distribution. $R^2$ quantifies the explained variation, and p-values, derived from 9999 permutations, are denoted with *** for statistically significant results (p = 0.001). Letters A, B, C and D represent the four distinct functional groups.

## 3.4 Soil microbial communities

The analysis of microbial communities in bulk and rhizosphere soil revealed a significant impact of plant presence on microbial communities. At the diversity level, there was a significant difference in bacterial evenness between different soil compartments ($p$ =

354 0.001; Figure S5), whereas no significant effect on fungal diversity was observed.
355 Regarding the composition level, bacterial and fungal communities responded to the
356 presence of plants (Figure S6). Specifically, all bulk soil samples were found to cluster
357 together in bacterial communities, separate from the rhizosphere samples (Figure S6a).
358 Some potato cultivars' rhizosphere fungal communities were grouped distinctly apart
359 from the bulk soil (Figure S6b).

360 Comparison across the 51 potato cultivars revealed considerable variation and no
361 significant effect of cultivar on bacterial and fungal alpha diversities, except for the
362 cultivar effect on fungal evenness ($p$ = 0.03; Figure S7). Plant cultivars showed no
363 significant impact at the composition level but a trend towards influencing bacterial
364 community distribution ($p$ = 0.093 and $R^2$ = 0.34; Figure 4a). However, cultivars
365 exhibited significant variation in fungal community composition ($p$ = 0.001 and $R^2$ = 0.37;
366 Figure 4b), indicating that cultivars can significantly influence the fungal community
367 composition within their rhizosphere.

368

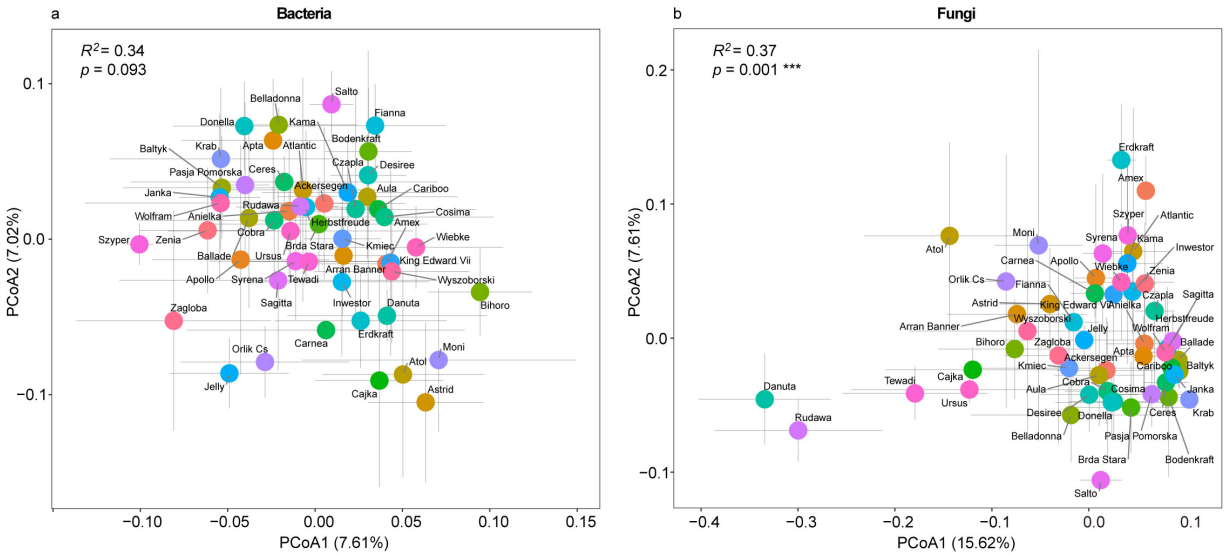


**Figure 4.** Rhizosphere microbial community composition. Principal Coordinates Analysis (PCoA) based on mean Bray-Curtis dissimilarity of community composition of bacteria (a) and fungi (b). Distinct potato cultivars are represented by different colours, with the error bars for each cultivar displayed in grey. PERMANOVA results in the upper left corner of each panel elucidate the influence of cultivars on community composition. $R^2$ quantifies the explained variation, and $p$-values are derived from 9999 permutations. The symbol *** denotes statistically significant $p$-values ($p$ = 0.001).

Grouping the cultivars in the functional groups determined by MIT revealed no significant differences in the alpha diversity of bacterial and fungal communities between the different functional groups ($p > 0.05$; Figure S8). Similarly, the composition of rhizosphere microbial communities did not vary among the functional groups ($p_{bacteria}$ = 0.49 and $p_{fungi}$ = 0.14; Figure S9).

## 3.5 Correlation between plant traits, metabolites and rhizosphere microbiome

To evaluate how different plant traits relate to root-associated microbes and metabolite release, we correlated plant shoot growth, MITs (i.e., root biomass and root exudate

385 metabolites) with leaf metabolites and rhizosphere microbial communities of the 51
386 potato cultivars. Positive correlations were observed between plant biomass and leaf
387 metabolite richness. In contrast, negative correlations were identified between plant
388 shoot growth and leaf metabolite composition (Figure 5). Regarding the microbiome, we
389 observed positive correlations between rhizosphere bacterial species richness, root
390 biomass, and root-to-shoot biomass ratio (Figure 5). Similarly, rhizosphere fungal species
391 richness positively correlated with the root-to-shoot biomass ratio. However, the
392 composition of the rhizosphere microbial community showed no significant correlations
393 with root growth. Notably, the bacteria-to-fungi species richness ratio (B/F) was
394 positively associated with root and root-to-shoot biomass ratios. Additionally, we did not
395 observe a pronounced correlation between root exudate metabolites and the rhizosphere
396 microbial community (Figure 5).

397 We performed Mantel tests based on Bray-Curtis dissimilarity matrices to further
398 investigate the relationship between plant leaf metabolites and soil microbial
399 communities. Our analysis revealed a subtle yet statistically significant correlation
400 between bacterial community compositions and leaf metabolite profiles ($r = 0.10$, $p =$
401 $0.02$). In contrast, the Mantel test for fungi showed no significant correlation between
402 fungal community compositions and leaf metabolite profiles ($r = 0.04$, $p = 0.22$).

403

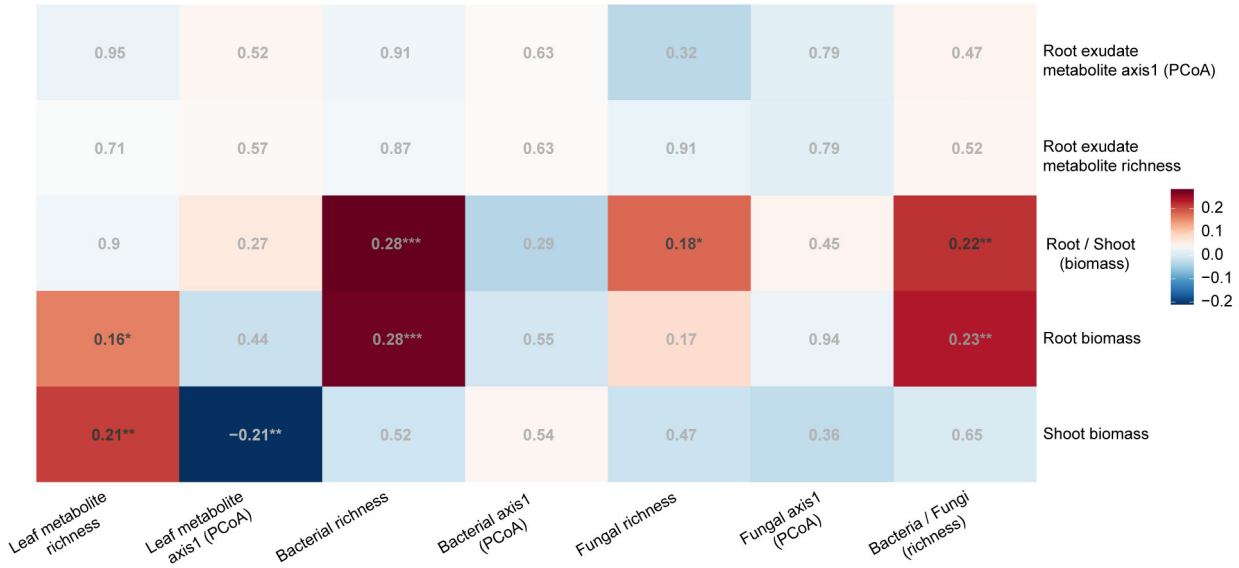


**Figure 5.** Correlation analysis between shoot biomass, MITs, leaf metabolite, and rhizosphere microbial community of the 51 potato cultivars. Correlations are based on the Spearman's rank correlation coefficient. Dark-coloured boxes indicate a significant correlation ($p < 0.05$), with the colour intensity reflecting the strength of the correlation coefficient. Red represents a positive correlation, while blue represents a negative correlation. The numbers displayed within the boxes represent the correlation coefficient. Significance levels are denoted as follows: * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

When examining the correlations between plant root biomass and rhizosphere bacterial community diversity across different functional groups, functional groups A and D showed significant positive correlations ($p < 0.05$; Figure S10). Functional groups B and C show no significant correlation between these variables. A positive correlation between leaf metabolite and bacterial Shannon index was found in functional group B ($p < 0.05$; Figure S11). No significant correlations were observed between leaf metabolite and fungal Shannon index regardless of functional groups ($p > 0.05$; Figure S11).

### 3.6 MIT-selected cultivars and their characterisation

420 The stepwise selection workflow and the chosen cultivars are visualised in Figure 6a. We
421 initially selected 148 potato cultivars, including the commercial cultivar Desiree as a
422 reference, from a pool of a thousand based on their resistance to pathogens *in silico*. These
423 148 cultivars were then further grown *in vitro*, from which 51 were selected based on plant
424 growth matrices for subsequent greenhouse experiments. For these 51 cultivars, plant
425 growth, leaf metabolites and root exudate metabolites were used to classify them into four
426 functional groups with distinct growth traits. This classification allowed us to identify ten
427 representative cultivars across four groups, covering a range of MIT values, including root
428 growth and exudate metabolites. This diverse range of MIT values allows us to better
429 understand how different combinations of these traits influence plant growth and
430 interactions in subsequent trials. Furthermore, we illustrated the distribution of the
431 rhizosphere community composition of the 51 cultivars in Figure 6b, which shows a
432 substantial separation in bacterial and fungal compositions among the MIT-selected
433 cultivars. These selected cultivars can undergo further exploration in real-world
434 conditions to evaluate their potential for interacting with beneficial soil microbiomes.

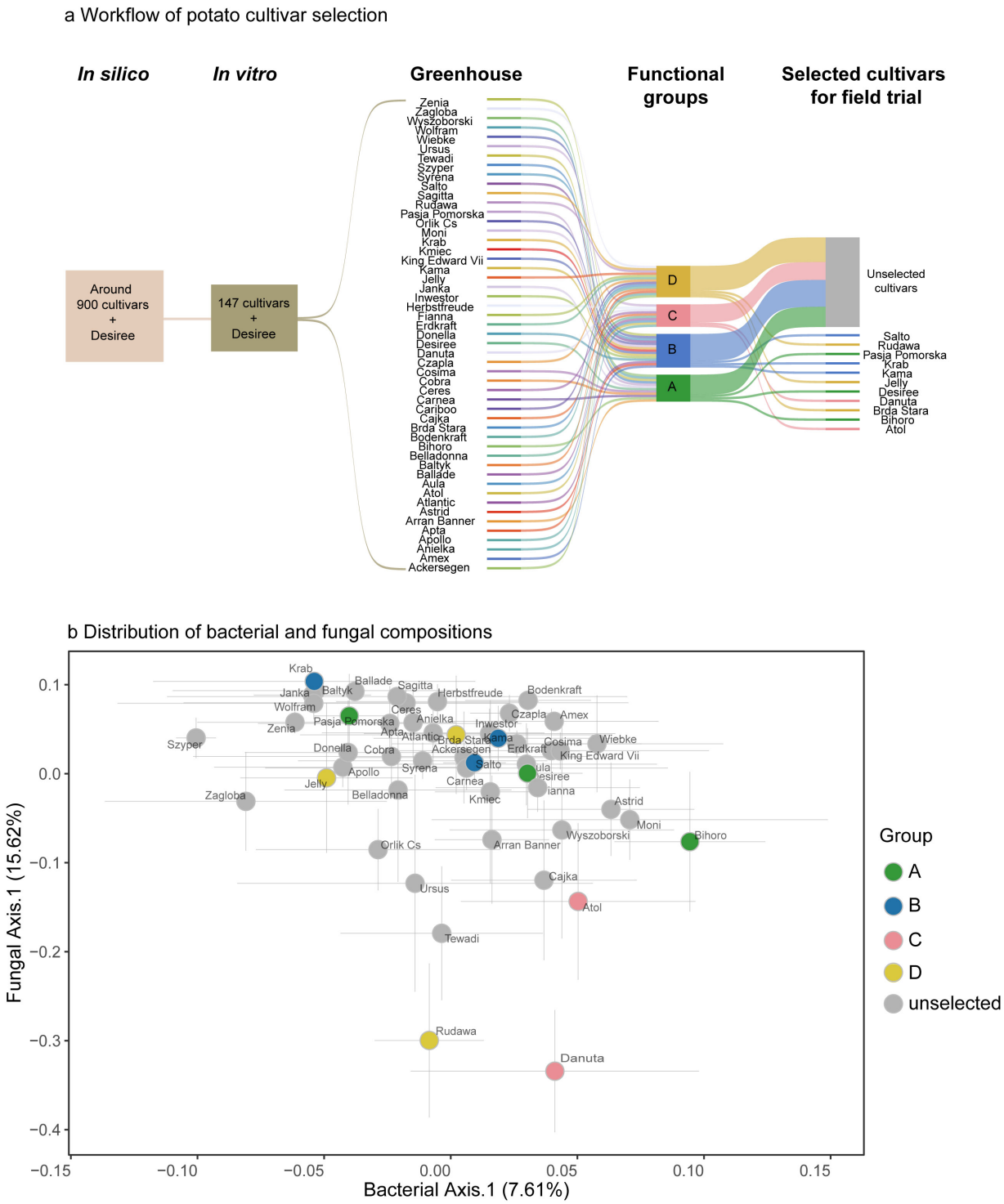


**Figure 6.** Workflow of the potato cultivar selection by Sankey plot (a) and distribution of rhizosphere bacteria and fungi community composition through Spearman correlation analysis (b). The first axis of principal coordinate analysis (PCoA1) of microbial community beta-diversity (bacteria and fungi) serves as

439 the indicator of community composition. The error bars for each cultivar are displayed in grey. The colour
440 of selected cultivars corresponds to the functional groups. The cultivars that were not selected are depicted
441 in grey (b).

442

443 We conducted a comprehensive characterisation of the MIT-selected cultivars (Figure 7).
444 The one-way ANOVA results revealed variations among the selected 11 cultivars in terms
445 of plant metabolites, root development, and rhizosphere microbial community richness.
446 Specifically, Desiree and Pasja Pomorska from group A demonstrated higher leaf
447 metabolite richness and microbial diversity (Figure 7a, c, d, g, h). In contrast, in group B,
448 Krab and Salto showed superior microbial diversity performance (Figure 7c, d, g, h). In
449 comparison, Danuta from group D exhibited lower plant metabolite richness, root growth,
450 and bacterial diversity (Figure 7a-c, e-g). At the compositional level, there were no
451 significant cultivar effects on metabolite or microbial profiles, except for root exudate
452 metabolite composition (Figure 7i-l).

453

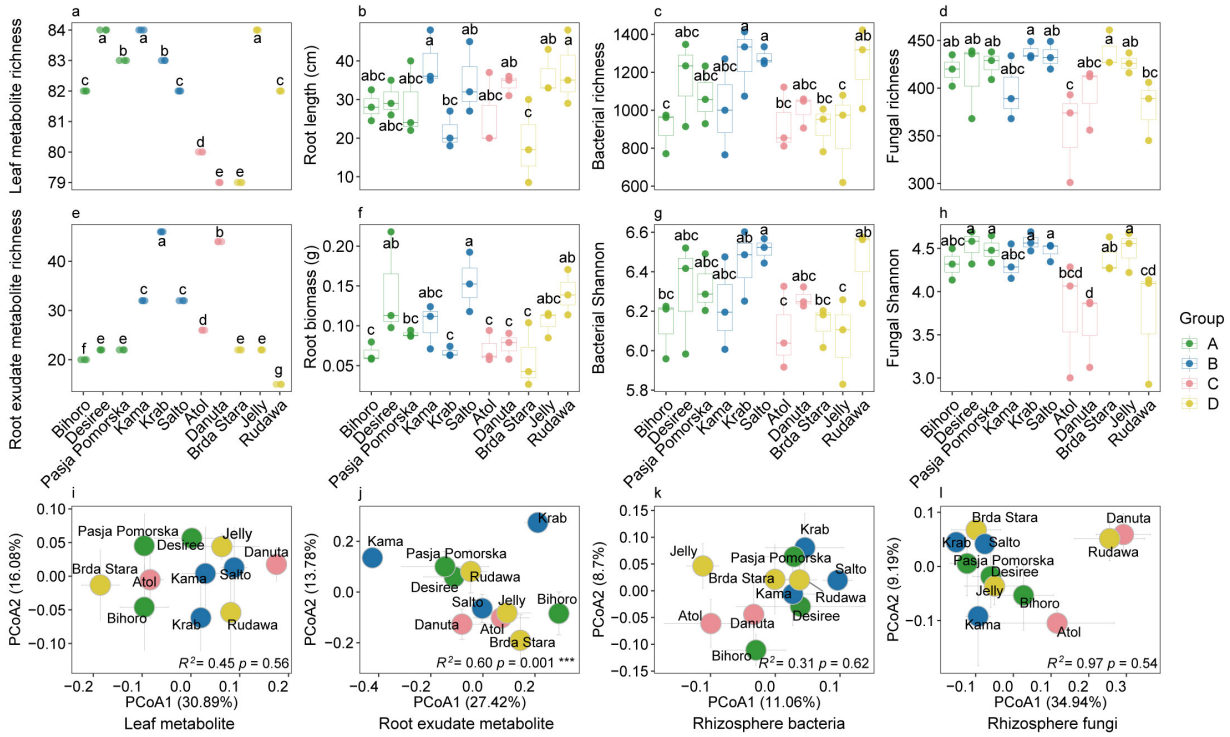


**Figure 7.** Characterisation of selected cultivars. Selected potato cultivars from different functional groups are represented by different colours, with the error bars for each cultivar displayed in grey. Letters in the upper two panels indicate significant differences across cultivars (Duncan post hoc test). In the lower right corner of the last panel plots, PERMANOVA results elucidate the influence of cultivars on community composition. $R^2$ quantifies the explained variation, and p-values are derived from 9999 permutations. A significance level is denoted as *** ($p < 0.001$).

## 4 DISCUSSION

Conventional breeding primarily harnesses genetic variation to achieve the desired traits of plants. However, the impact of a cultivar's genetic information on associated microbial organisms has yet to receive much consideration, particularly those associated with the rhizosphere. Here, we emphasise that modern breeding should consider the soil microbiome as a strategy to reduce its environmental footprint. Understanding the

468 importance of microbiome interactive traits (MITs), such as root traits and exudates, is
469 vital to comprehending how plants and microbiomes interact. In the future, this
470 understanding will contribute to informing the breeding process, providing valuable
471 insights for developing new microbiome-based cultivars.

472 **4.1 Correlation between plant traits, metabolites and rhizosphere**
473 **microbiome**

474 Our findings underscore the significant role of plant genetics in shaping both root exudate
475 and leaf metabolite profiles. We observed substantial cultivar-dependent variation in root
476 exudate metabolite composition consistent with previous studies. This genetic influence
477 also extends to leaf metabolites, aligning with earlier research on rice (Schaarschmidt et
478 al., 2020). These results collectively demonstrate that the genetic makeup of different
479 plant cultivars significantly influences the metabolite composition of different plant
480 tissues.

481 We observed a positive correlation between leaf metabolite richness and plant biomass, a
482 relationship that can be explained through considerations of resource availability and
483 plant growth strategies. Environmental conditions and functional traits influence
484 biomass allocation among plant organs, such as leaves and roots, influencing many
485 growth processes (Mensah et al., 2016; Poorter et al., 2012). In optimal environmental
486 conditions, biomass allocation (primarily above-ground to compete for light) can enhance
487 the diversity of leaf metabolites instead of root metabolites (Chapin et al., 2005). The
488 crucial role of plant secondary metabolites in host defence may also explain this
489 correlation. These compounds protect hosts against herbivores, pathogens, and (biotic)

490 stresses (Anjali et al., 2023; Divekar et al., 2022; Yadav et al., 2021; Zaynab et al., 2018).
491 Plants with higher biomass may invest more in defence mechanisms, producing a wider
492 range of leaf metabolites for protection. This establishes positive feedback loops, wherein
493 increased biomass boosts photosynthetic activity and energy production, consequently
494 supporting the synthesis of more diverse metabolites.

495 Previous studies have demonstrated that plant root traits are crucial in regulating
496 rhizosphere microbial communities (Szoboszlay et al., 2015; Wan et al., 2021). This
497 relationship is further supported by Eisenhauer et al. (2017), who showed that microbial
498 diversity increases with increasing root biomass and exudate amount. Our results align
499 with these findings, revealing positive correlations between plant root biomass and root-
500 to-shoot biomass ratio, rhizosphere bacterial diversity, and bacteria-to-fungi species
501 richness ratio (B/F). A more diverse microbial community, in turn, can enhance soil
502 nutrient cycling and availability (Jiao et al., 2021), potentially promoting plant growth.

503 Previous studies have demonstrated that root exudates significantly influence bacterial
504 and fungal communities in the rhizosphere (Hartmann et al., 2009). In contrast, our
505 study did not find a significant correlation between root exudate metabolites and the
506 rhizosphere microbial community. This unexpected result may be because we collected
507 root exudate metabolites from 51 potato cultivars under *in vitro* conditions, while the
508 microbial community data were obtained from a greenhouse experiment. The differences
509 in substrates between these environments may have influenced the root exudate profiles,
510 leading to variances that could explain the lack of correlation.

Given the complexity of collecting root exudates from soil plants, we collected leaf metabolites in our current experiment to explore the relationship between plant metabolites and the soil microbial community. The marginal but positive correlation observed between leaf metabolites and the rhizosphere bacterial community suggests a potential influence of leaf metabolites on the composition of rhizosphere bacteria. This finding indicates a possible link between above-ground plant tissues and below-ground microbial communities, aligning with the holobiont concept, in which plants and their associated microorganisms are viewed as a holistic ecological unit (Vandenkoornhuyse et al., 2015).

Recent studies further support this interconnection. Korenblum et al. (2020) demonstrated that the composition of the rhizosphere microbial community affects the metabolomes and transcriptomes of tomatoes' leaves and roots. Earlier research showed that rhizobacterium Bacillus strains can influence photosynthesis, leaf growth, and overall plant phenotypes by producing phytohormones or volatile organic compounds (Pang et al., 2021), potentially impacting leaf metabolomes. These findings collectively emphasise the concept of metabolites as primary mediators regulating plant-microbiome interactions within the holobiont framework (Carper et al., 2022). As described, the transport of leaf-produced metabolites to the roots via the phloem (Broussard et al., 2023) suggests a potential mechanism for how above-ground metabolites might influence root exudate patterns and, consequently, the rhizosphere microbiome. However, it's important to note that our study only demonstrates correlation, not causation. The complex interactions between leaf metabolites, root exudates, and microbial communities require further investigation to elucidate the holobiont concept fully.

534 **4.2 Enhancing plant-microbiome interactions for sustainable agriculture**

535 The soil microbiome promotes plant growth by promoting carbon, nutrient, and
536 phosphorus cycling (Hartmann and Six, 2022). It also contributes to plant resistance by
537 producing hormones that protect against abiotic and biotic stress (Eichmann et al., 2021).
538 Despite its critical functions, the soil microbiome has received limited attention in
539 conventional breeding (Mitter et al., 2019; Wei and Jousset, 2017). Compounding this
540 issue is the fact that conventional agricultural management not only negatively affects the
541 environment but also substantially impacts the soil microbiome (Longepierre et al., 2021).
542 This dual impact increases the decoupling between plants and soil microbiomes (Huang
543 et al., 2019; Spor et al., 2020).

544 Studies addressing the role of plants in regulating their associated microbiome remain
545 relatively limited (Wei and Jousset, 2017). More precisely, plant roots, serving as the
546 primary interface for interaction with soil microbes, are underexplored in plant breeding
547 (Herms et al., 2022; Reinhold-Hurek et al., 2015). Here, we consider morphological root
548 characteristics and root exudate metabolites as microbiome interactive traits (MITs) to
549 explore their interaction with the rhizosphere microbiome. We aim to supply a strategy
550 for breeding that considers plant-associated microbiota.

551 Indeed, the positive correlation between root growth and rhizosphere microbial diversity
552 indicates that MITs can aid in identifying plant cultivars with the potential to interact
553 effectively with root-associated microbiomes. Cultivars exhibiting high MITs are likely to
554 select for a more diverse rhizosphere microbiome, which in turn can lead to enhanced
555 plant growth through the support of beneficial microorganisms. Identifying the genes

556 associated with beneficial microbiomes in modern cultivars and using them in selective
557 breeding efforts to achieve microbial-assisted cultivars can serve as a new plant breeding
558 strategy. This approach represents a promising avenue for sustainable agriculture, as it
559 harnesses the power of beneficial microorganisms to improve crop performance while
560 reducing the need for chemical inputs.

561 **4.3 Integrating additional root traits and phyllosphere microbiome in future**
562 **studies**

563 We suggest expanding future research beyond the MITs examined in this study to include
564 a broader range of root phenotypic traits. While the current study focuses on root biomass
565 and length, future investigations should include root diameter, surface area, and root type.
566 Although less studied, evidence suggests that fine roots with smaller diameters have
567 larger surface areas, potentially recruiting a greater diversity and abundance of microbes
568 through enhanced nutrient and metabolite exchange (Saleem et al., 2018; Wan et al.,
569 2021). Pérez-Jaramillo et al. (2017) linked root types (thin or thick) to specific bacterial
570 phyla, highlighting the importance of root morphology in shaping microbial communities.
571 Additionally, the spatial distribution of microbial communities along the root should be
572 considered. Kawasaki et al. (2016) observed that the functional genes detected in
573 microorganisms near the root tip were distinct from those isolated near the root base.
574 Collectively, these various root phenotypic traits should be considered to improve plant-
575 microbiome interactions.

576 In addition to expanding our focus on root phenotypic traits, we propose incorporating
577 the phyllosphere microbiome into future studies. The phyllosphere microbiome, which

578 includes microorganisms inhabiting the above-ground parts of plants, plays a crucial role
579 in plant health and function (Thapa and Prasanna, 2018; Vorholt, 2012). Previous studies
580 have demonstrated that host genotypes significantly influence the composition of
581 phyllosphere microbial communities (Bodenhausen et al., 2014; Thapa et al., 2017). The
582 phyllosphere microbiome is involved in nitrogen fixation (Abadi et al., 2021), enhancing
583 stress tolerance (Etemadi et al., 2018; Stone et al., 2018), and suppressing plant diseases
584 (Fan et al., 2019; Das et al., 2023). Additionally, they can regulate plant growth through
585 the production of plant hormones (Stone et al., 2018). These diverse functions highlight
586 the importance of the phyllosphere microbiome in plant health and productivity.

587 By considering the phyllosphere microbiome together with the rhizosphere microbiome
588 and plant metabolites, we can establish a more comprehensive understanding of the plant
589 holobiont. This approach will allow us to bridge the gap between the plant's above- and
590 below-ground components. By harnessing the functions of phyllosphere and rhizosphere
591 microbiomes, we may enhance crop yields, improve plant resilience, and reduce reliance
592 on chemical inputs, ultimately contributing to more sustainable agricultural systems.

593

594 **5 CONCLUSION**

595 This study underscores the significant impact of plant cultivars on leaf metabolites and
596 root exudate metabolites. We also observe a positive correlation between leaf metabolites
597 and rhizosphere bacterial community; further studies are needed to verify the causation
598 and to involve root exudates to expand our knowledge of the holobiont framework. We
599 systematically selected potato cultivars to identify those with diverse microbiome

interactive traits (MITs). We lay the foundation for further studies to evaluate the performance of MIT-selected cultivars in field conditions. This is needed to provide a promising strategy for future breeding programs, including identifying gene markers associated with a beneficial microbiome and utilising these genes to increase plant-microbiome interactions. This breeding strategy could promote host growth while reducing the reliance on synthetic chemicals in conventional agriculture. Finally, we suggest integrating additional root phenotypic traits and the phyllosphere microbiome in future studies to establish a more comprehensive understanding of the plant holobiont, which can benefit plant-microbiome interactions.

## Availability of Data and Materials

The metadata and datasets used for the bioinformatic analyses are available at the following link: https://github.com/tianci-zhao/potatoMETAbiome-Greenhouse-Experiment.

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630

631 **Author contributions**

632 J.F.S., S.N.V., J.T.M.E., A.E., and E.A. designed the experiment; T.Z. and S.N.V.
633 performed the experiment, laboratory work and data analysis; X.J. participated in data
634 analysis; E.A. and R.G. contributed to plant sampling; D.M. and K.T. provided the potato
635 materials; A.E., S.S., J.K., and E.Z. measured and analysed plant metabolites. T.Z. drafted
636 the manuscript, with all authors contributing to its modification and approval of the final
637 version.

638

639 **Declaration of competing interest**

640 The authors declare that they have no known competing financial interests or personal
641 relationships that could have appeared to influence the work reported in this paper.

642

643 ## Supporting information

644 **Figure S1.** Root dry weight and root-to-shoot ratio of 51 potato cultivars *in vitro* experiment. Each
645 colour represents a distinct potato cultivar. The upper left corner of each plot displays one-way ANOVA
646 results, where the F-value explains the variation among different cultivars, and the *p*-value indicates the
647 statistical relationship among cultivars.

648 **Figure S2.** Shoot growth analysis of 51 potato cultivars. The upper panel displays the shoot length, while
649 the lower panel illustrates the shoot dry weight. Each colour represents a distinct potato cultivar. The upper
650 right corner of each plot displays one-way ANOVA results, where the F-value explains the variation among
651 different cultivars, and the *p*-value indicates the statistical relationship among cultivars.

652 **Figure S3.** Root-to-shoot ratio analysis of 51 potato cultivars. The upper panel displays the root-to-shoot
653 length ratio, while the lower panel illustrates the root-to-shoot dry weight ratio. Each colour represents a
654 distinct potato cultivar. The upper right corner of each plot displays one-way ANOVA results, where the F-
655 value explains the variation among different cultivars, and the *p*-value indicates the statistical relationship
656 among cultivars.

657 **Figure S4.** Impact of 51 potato cultivars on the composition of plant root exudates (a) and leaf (b)
658 metabolites. A Principal Coordinates Analysis (PCoA) based on Bray-Curtis dissimilarity was performed to
659 visualise the composition. The metabolite dissimilarities of root exudates and leaf are depicted separately
660 on the left and right. Distinct potato cultivars are represented by different colours, with the error bars for
661 each cultivar displayed in grey. PERMANOVA (Adonis) results in the upper right corner of each panel
662 elucidate the influence of cultivars on metabolite composition. $R^2$ quantifies the explained variation, and
663 *p*-values are derived from 9999 permutations.

664 **Figure S5.** The alpha-diversity of the bacterial community in bulk and rhizosphere soil, displayed by
665 species richness and evenness. Different colours represent bulk samples from the beginning of the

experiment (Bulk_D0), at harvest (Bulk_D36), and rhizosphere samples of 51 cultivars. The lower right corner of each plot displays one-way ANOVA results, where the F-value explains the variation among different soil compartments (bulk and rhizosphere), and the *p*-value indicates the statistical relationship.

**Figure S6.** The microbial community composition in bulk and rhizosphere soil. Principal Coordinates Analysis (PCoA) based on Bray-Curtis dissimilarity was performed to visualise the community composition of bacteria (a) and fungi (b). Different shapes represent different soil compartments (bulk and rhizosphere). Different colours represent bulk samples from the beginning of the experiment (Bulk_D0), at harvest (Bulk_D36), and different potato cultivars, with the error bars for each cultivar displayed in grey. PERMANOVA results in the lower left corner of each panel elucidate the influence of soil compartments on community composition. $R^2$ quantifies the explained variation, and *p*-values are derived from 9999 permutations.

**Figure S7.** Rhizosphere microbial community evenness of 51 potato cultivars. The upper panel is bacterial evenness, and the lower panel is fungal evenness. Different colours indicate different cultivars. The lower right corner of each plot displays one-way ANOVA results, where the F-value explains the variation among different cultivars, and the *p*-value indicates the statistical relationship among cultivars.

**Figure S8.** Rhizosphere microbial community species richness. The upper panel is bacterial richness, and the lower panel is fungal richness. Different colours indicate different cultivar functional groups. The "ns" indicates no significant influence of groups on microbial alpha diversity (one-way ANOVA).

**Figure S9.** Rhizosphere microbial community composition. Principal Coordinates Analysis (PCoA) based on Bray-Curtis dissimilarity was performed to visualise the community dissimilarities of bacteria (a) and fungi (b). Distinct potato cultivar functional groups are represented by different colours, with the error bars for each cultivar displayed in grey. PERMANOVA results in the upper right corner of each panel elucidate the influence of groups on community composition. $R^2$ quantifies the explained variation, and *p*-values are derived from 9999 permutations.

690 **Figure S10.** Correlation between plant root biomass and rhizosphere bacterial alpha diversity (species
691 richness and Shannon diversity) across different functional groups. Displayed by functional groups A, B, C
692 and D. The Spearman correlation assessed the relationship, with $R^2$ indicating the strength of the
693 correlation. Y is the regression equation, and a *p*-value < 0.05 represents a significant correlation between
694 the variables.

695 **Figure S11.** Correlation of leaf metabolite and microbial community Shannon index across different
696 functional groups. Displayed by functional groups A, B, C and D. The Spearman correlation assessed the
697 relationship, with $R^2$ indicating the strength of the correlation. Y is the regression equation, and a *p*-value
698 < 0.05 represents a significant correlation between the variables.

699 **Table S1.** Background information on 148 selected cultivars for the *in vitro* experiment.

700 **Table S2.** Plant growth data of 148 potato cultivars from *in vitro* experiment.

701 **Table S3.** Functional groups of potato cultivars categorised based on plant growth and metabolite profiles.

702 **Table S4.** The one-way analysis of variance (ANOVA) shows the influence of cultivar on the plant
703 metabolite alpha diversity.

704 **Data S1.** Leaf tissue metabolites data in greenhouse experiment

705 **Data S2.** Root exudate metabolites data *in vitro* experiment

706 **Data S3.** Plant performance in greenhouse experiment

707 **Data S4.** Rhizosphere microbial feature tables

708

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