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Increased exopolysaccharide production and microbial activity affect soil water retention and field performance of tomato under water deficit

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1 Increased exopolysaccharide production and microbial activity affect soil
2 water retention and field performance of tomato under water deficit

3 Summary

4 According to the literature, biological processes in the rhizosphere could play a role in the
5 adaptation of plants to droughts under a changing climate. A previous study has identified
6 significantly different productivity level and fruit quality for two tomato varieties under wa-
7 ter deficit conditions. We conducted a field study, with and without water deficit, with these
8 two varieties to examine whether microbiological activity and exopolysaccharides concen-
9 tration could affect soil hydrophysical properties. The rhizosphere soil had indeed distinct
10 bio-chemical and hydrophysical properties between the two cultivars and between the two
11 water-related conditions. The quantity of soil exopolysaccharide and/or nitrogenous sub-
12 stances, and the activity of microorganisms (fungi in particular) explains part of the soil wa-
13 ter retention measurements. In addition, these mechanisms are significantly accentuated for
14 the cultivar with the best productive capability under water-limited condition—i.e. with
15 commercial yield, fruit dry matter and water use efficiency which are respectively 35%, 28%,
16 and 31% higher for the productive cultivar.

17 Key words

18 Rhizosphere, Water deficit, Soil water retention, Exopolysaccharide, Microbial activity

19 Introduction

20 The current increase in temperature, evapotranspiration, and in the seasonal variation of
21 water regimes linked to climate change lead to a higher pressure on the water resources,
22 which affects the agricultural production (Jia et al., 2019, Boeck et al., 2011). This calls for
23 the development of more water-efficient agroecological systems, able to withstand more
24 frequent water deficit periods (Lipiec et al., 2013). The water retention capacity of soils has a
25 strong influence on their capacity to satisfy crops' water requirements and could thus miti-
26 gate the effects of extreme climatic events (Łabędzki, 2016).

27 The rhizosphere is the area of soil around the roots influenced by plant roots and where the
28 plant, the soil, and the associated microorganisms interact (Bargett et al., 2014; Hinsinger et
29 al., 2009; Angers et al., 1998). The rhizosheath is the portion of soil that is physically in con-
30 tact with the root system. The rhizosheath is part of the rhizosphere, but rhizosphere may
31 extend beyond the rhizosheath (Marasco et al., 2018; Pang et al., 2017). The rhizosphere is
32 both a "hot spot" of biological activity and metabolic processes in the soil (Zhang et al.,
33 2020), and the zone where root water and nutrient uptake takes place. Moreover, the rhizo-
34 sphere has specific physicochemical properties: soil aggregates are more stable; bulk densi-
35 ty, porosity, water and nutrients transfer as well as pH are modified with respect to the bulk
36 soil (Hinsinger et al., 2009). These properties are linked to the specific biochemical activities
37 of roots, such as rhizodeposition and exudation of organic compounds (Personeni et al.,
38 2017), which can then be consumed by the associated microbial communities (van Veelen et al.
39 2018). In addition, these microbial communities, stimulated by the rhizosphere environ-
40 ment, can also excrete similar organic molecules, including Exo-polymeric Substances (EPS),
41 such as Exo-PolySaccharides (EPSac) (Redmile-Gordon et al., 2014). EPSac may also consti-

42 tute the majority of root mucilage (Nazari, 2021). These polymeric substances contribute to
43 the stability of soil aggregates (Crouzet et al., 2019), improve soil water retention (Czarnes et
44 al., 2000), and present either hydrophilic or hydrophobic characteristics depending on their
45 state of hydration (Carminati and Vetterlein, 2013). Until now, few studies have focused on
46 the influence of both the physicochemical and biological properties of the rhizosphere on
47 plant water use efficiency (WUE) (Benard et al. 2019). However, since all the water tran-
48 spired by a plant must cross the rhizosphere soil layer, understanding its functioning and its
49 properties is critical (Bengough, 2012). Thus, acting on the functioning of the rhizosphere
50 could be a lever to maintain the productivity of crops suffering from water deficit (Ahmed et
51 al., 2018, Doussan et al., 2015).

52 Tomato (*Solanum lycopersicum*) is widely grown in the Mediterranean region and its produc-
53 tion is one of the most important worldwide in terms of market value and quantity (FAO-
54 STAT, n.d.). Understanding how this crop adapts to droughts is therefore of prime im-
55 portance. Under glasshouse conditions, water deficit negatively affects plant growth, leaf
56 water potential and gas exchange intensity during the early stages of tomato development
57 (Duan et al., 2016) as well as fruit mass and composition at the latter stages (Ripoll et al.
58 2016). The impact of water deficit was also observed in the field for industrial tomato culti-
59 vars (Arbex de Castro Vilas Boas et al., 2017). In particular, under water deficit, the cultivar
60 Terradou, compared to H1015, showed a higher dry yield (on average 76 kg.ha⁻¹ and 56.kg
61 ha⁻¹ respectively) and a higher Water Use Efficiency (WUE) (41 and 33 kg.m⁻³ respectively).
62 Terradou fruits had also a higher sugar content (Glucose, Fructose, higher SSC index) while
63 H1015 fruits had more acids (Malic, Citric). The fruit puree viscosity increased in general
64 when the plants underwent water deficit, but more markedly for H1015 than for Terradou.

65 As water deficit is one of the main factors limiting yield in tomatoes (Costa et al., 2007;
66 Patanè and Consentino, 2010), depending on its intensity, duration, and timing in the crop
67 cycle (Rinaldi et al., 2007), the response of these cultivars to water deficit deserves further
68 testing.

69 While several studies have investigated the influence of microbial activity, and in particular
70 mycorrhizae (Cavagnaro et al., 2006; Hallett et al., 2009; Bowles et al., 2016), on tomato
71 phenology and its yield components, it is worthwhile to investigate the influence of soil hy-
72 drophysical properties. Understanding this possible link between soil bio-chemical and hy-
73 drophysical parameters might broaden our understanding of the plants' responses to
74 drought. Our objective was therefore to observe in the field the links between different bio-
75 chemical parameters of the soil (i.e., microbial biomass and activities, EPSac amounts) and
76 the soil water retention (i.e. Field Capacity and Permanent Wilting Point). We took into ac-
77 count the influence of (i) the rhizosphere of tomatoes, (ii) the season stage of the plant de-
78 velopment, (iii) the tomato cultivars, and (iv) the water conditions (well irrigated or deficit).

79 We carried out a field experiment with the two cultivars Terradou and H1015 on the same
80 Mediterranean experimental site than previously used by Arbex de Castro Vilas Boas et al
81 (2017). We increased water deficit by limiting irrigation, and we measured the biophysical
82 parameters mentioned above both in the rhizosphere and in the bulk soil. Our hypothesis
83 was that the EPS exudation and microbial activities would be higher for Terradou compared
84 to H1015, and that these processes would allow for a better yield resilience to water deficit
85 conditions for Terradou. We also assumed that these processes would be relatively more
86 important in the rhizosphere and that their dynamics would follow the development stages
87 of the plant.

88 Materials and methods

89 Experimental set-up and sampling

90 The experimental site is an industrial tomato field of a SONITO (French interprofessional or-
91 ganisation of the tomato sector). It is located under a Mediterranean climate at Piolenc,
92 France (44°11'16.9 "N 4°48'10.8 "E), and is used for a varietal trial. The soil is a Stagnosol
93 (WRB classification; or Redoxisol in French classification) with a loam texture (main soil
94 properties are shown in Table 1). We studied two widely grown commercial cultivars of to-
95 mato (*Solanum lycopersicum* L.): Terradou (T) and H1015 (H), previously tested by Arbex de
96 Castro Vilas Boas et al. (2017). The cultivation practices applied on this field correspond to
97 current conventional practices (density of 3.3 plants.m⁻², fertilization and pesticides). During
98 this experimentation, two irrigation treatments were applied: from planting (May 18, 2018)
99 to fructification (July 23, 2018), all the plants received the same amount of irrigation water
100 via daily drip irrigation to compensate 87% of evapotranspiration losses, resulting in nearly
101 460 mm of total water input before the fructification (135 mm from rainfalls and 325 mm
102 from irrigation). Then, from fructification to harvest (August 9), half of the plots had water
103 deficit (WD) conditions i.e., 57% of the water input of the fully irrigated plots (well-watered
104 "WW"). Each cultivar was grown on two plots (42 m length each) of two rows (33 cm apart)
105 of tomato plants on cultivation ridges distributed on both sides of the main irrigation tube.
106 For each cultivar, one plot was WW and one plot was WD (Fig.S1).

107 Soil samples were collected at the beginning of the flowering stage (June 19, 2018) and later
108 at the fructification stage (August 2, 2018) before harvesting. Five sub-plots were randomly
109 chosen within the plots. In those sub-plots, we sampled two types of soil: the 'rhizosphere'

110 soil and the corresponding 'bulk' soil. For the rhizosphere soil sampling, three plants per cul-
111 tivar in each sub-plot were excavated with their proximal root system and surrounding soil
112 using a spading fork (to a depth of 20 cm maximum). The plants were then shaken vigorously
113 by hand, but without breaking roots, until no more soil aggregates could be detached from
114 roots. The soil remaining on root was collected and judged to be the rhizosphere soil. The
115 rhizosphere soil of the three selected plants was pooled (Göttlein, 2006). We selected three
116 subsamples of bulk soil located on the outside bare soil of the ridge facing the plants sam-
117 pled for the rhizosphere soil over 0-20 cm depth (Fig S1). These three subsamples of bulk soil
118 were also pooled. All soil samples were air-dried, sieved at 2 mm and stored at 4°C until
119 analysis.

120 Measurements of soil and plant parameters

121 *Soil microbial and fungal catabolic measurements*

122 Substrate Induced Respiration (SIR) of soil was assessed with the FungiResp, adapted from
123 the MicroResp™ colorimetric technique (Ben Sassi et al., 2012; Chapman et al., 2007), con-
124 sisting in a 96-deep-well microplate filled with soil subsamples. The soil water content was
125 preliminary adjusted to 40% of the water holding capacity (about 0.22 g/g gravimetric water
126 content). 25 µl of organic substrates (6.7 mg.g⁻¹ dw soil) were added in each deep-well. Each
127 filled soil plate was then sealed face to face with a CO₂ trap microplate including a pH dye
128 indicator, and an intercalated silicone joint to individualize the plate wells. The systems were
129 then incubated in the dark at (23°C±1) for six hours. Absorbance of the gel CO₂-trap was
130 measured at 570 nm, before and after incubation. A calibration curve of absorbance versus
131 head space equilibrium CO₂ concentration (measured by gas chromatography) was fitted to a
132 regression model, which was then used to compute the amounts of released CO₂ in µg C-

133 CO₂.g⁻¹ Dry Soil.h⁻¹. We measured the microbial basal respiration by adding 25 µL of demin-
134 eralised water instead of organic substrate (M.Bas). In order to address substrate-induced
135 respiration according to fungal communities, we applied a bacterial inhibitor (25 µL for a
136 final concentration of 78 µg Bronopol.g⁻¹ soil, concentration selected after performing a
137 dose/response curve on the respiration of this soil, Ben Sassi et al., 2012) to half of the soil
138 sub-samples distributed in the deep well-plate (the other half of the soil sub-samples re-
139 ceived 25 µL of demineralised water). Glucose-induced respiration was used as a proxy of
140 active total microbial biomass (MB) and fungal biomass (FB) in µg C.g⁻¹ DrySoil (Anderson
141 and Domsch, 1978). To access the catabolic profiles of fungal communities (F-CLPP) (F.Tre,
142 F.Cell, F.Ala, F.Gly, F.Mal, F.GlcN) and microbial communities (M-CLPP) (M.Tre, M.Cell, M.Ala,
143 M.Gly, M.Mal, M.GlcN) we used various organic substrates (trehalose, cellobiose, alanine,
144 glycine, malate, glucosamine, respectively) distributed in the deep well-plate, and at the
145 same amounts of glucose, with and without the addition of bacterial inhibitor (Bérard et al.,
146 2011).

147 *Soil water retention measurements*

148 The measurement of water retention was carried out for matric potentials of 0.3 bars (i.e.,
149 Field Capacity) and 15 bars (i.e., Permanent Wilting Point) on soil aggregates by using a pres-
150 sure plate system. The triplicates of initially saturated samples (about 10 g) were placed in
151 porous plate enclosures into which nitrogen gas was injected at a pressure of 0.3 or 15 bars.
152 Samples were left to drain excess water until equilibrium was reached, with no outflow. The
153 gravimetric water content (g water.g⁻¹ dry soil) was then measured by weighing the soil be-
154 fore and after drying at 105°C (24h).

155 *Soil exopolysaccharides measurements*

156 The ExoPolySaccharides (EPSac) that are principally involved in soil physical properties are
157 those tightly bound to the soil particles (Chen et al., 2014; Crouzet et al. 2019). We used the
158 physico-chemical Cation Exchange Resin (CER) technique (Redmile-Gordon et al., 2014; Bér-
159 ard et al., 2020) to extract the bound-ExoPolymeric Substance (bound-EPS) from the soil.
160 Before bound-EPS extraction, loosely bound EPS were extracted (each 0.5 g of soil sample)
161 using 5 mL CaCl_2 (10^{-2} M) under agitation (50 rpm) for one hour at laboratory temperature
162 (Redmile-Gordon et al., 2014; Bérard et al., 2020). The soil/ CaCl_2 mixtures were then centri-
163 fuge (8000 xg for 15 min at 10°C), and the supernatants were removed. The remaining cen-
164 trifuged soil pellets were then extracted by the CER extraction technique. The CER (Dowex
165 Marathon C Na^+ form, Sigma Aldrich, Steinheim, Germany) was previously washed with a
166 phosphate buffer (consisting of 2 mM $\text{Na}_3\text{PO}_4 \cdot 12\text{H}_2\text{O}$, 4 mM $\text{NaH}_2\text{PO}_4 \cdot \text{H}_2\text{O}$, 9 mM NaCl, 1
167 mM KCl, adjusted to pH 7 with 1M HCl and stored at 4°C) until the pH of the solution stabi-
168 lized to 7. In a centrifuge tube containing the soil pellet samples, the CER was added to ob-
169 tain a ratio of 70 g dry CER per 1 g of soil organic matter. Five mL of phosphate buffer pH 7
170 were then added to the soil and CER. After manual stirring, the samples were incubated for
171 sixteen hours overnight under agitation (50 rpm) at room temperature. Bound-EPSac were
172 measured as the total carbohydrate content of the bound-EPS extracted from soil, using the
173 phenol–sulphuric acid Dubois method (Dubois et al., 1956) with glucose as the standard.

174 *Plant and Fresh Fruit Measurements*

175 At harvest, for each cultivar and irrigation modality, five tomato plants were sampled. We
176 measured the commercial yield (CoY, in $\text{t}\cdot\text{ha}^{-1}$) corresponding to the tomato marketable
177 fresh yield for the industry (red and yellow ones), and harvest losses due to rotten tomatoes
178 (RoY, in $\text{t}\cdot\text{ha}^{-1}$). The dry mass of this commercial yield (DMY in $\text{kg}\cdot\text{ha}^{-1}$) was also measured.

179 We calculated the water use efficiency (WUE - $\text{kg}\cdot\text{m}^{-3}$) as the ratio between the commercial
180 yield (CoY) and the total water volume provided by irrigation and rainfall to the plant, for a
181 given surface. Some chemical analyses were also performed on the tomato fruits, such as
182 the soluble solid content (SSC, in °Brix), the titrable acidity and the pH (as in Arbex de Castro
183 Vilas Boas et al., 2017).

184 Data Analysis:

185 *Statistical analysis*

186 Four modalities were investigated in the experimental design: the type of soil—rhizosheath
187 or bulk (SOIL), the season—June or August (SEAS), the cultivar—Terradou or H1015 (CULT),
188 and the plots' water status modalities in August —WD or WW. 76 soil samples were ana-
189 lysed. Quantitative data were analysed using R (R core Team, 2017) with R Studio IDE (R Stu-
190 dio Team, 2020). We first observed the statistical differences between the three first modali-
191 ties (SOIL, SEAS, CULT) for each of the soil parameter studied (microbial, hydro-physical, and
192 chemical) at a level of significance of $p < 0.05$ with an ANOVA F-test (the R stat package and
193 anova() function). Table 2 shows the main effects and their interactions performed over the
194 whole dataset of soil parameters and on rhizosheath soil dataset. Table 2 also presents spe-
195 cific analyses for June, August-WD irrigation and August-WW irrigation datasets, allowing us
196 to compare the WW and WD data. Homoscedasticity of variances (Bartlett test) and normali-
197 ty (Shapiro test) were checked before data analyses. The mean and standard deviation for
198 the groups of data analysed are reported in Table S1.

199 *Principal Component Analysis*

200 Each substrate-induced respiration measurement was normalized to the sum of all SIR
201 measurements, to exclude the microbial biomass effect on the individual respirations (Ben
202 Sassi et al. 2012). Principal Component Analysis (PCA) was performed on these normalized
203 measurements of microbial and fungal catabolic profiles carried out on the seven organic
204 substrates: glucose, trehalose, cellobiose, alanine, glycine, malate, glucosamine. The *Fac-*
205 *toMineR* R package with the `fviz_pca_ind()` function (Lê et al., 2008) was used to perform
206 PCA analysis. A first global PCA analysis was performed on dataset including the 7 microbial
207 or fungal variables and the whole 76 observations (2 cultivars × 2 seasons × 2 soil types × 2
208 irrigation levels × 5 replicates, 4 data missing). Then, we performed PCA analyses on the June
209 data exclusively, as well as for the August-WW and the August-WD.

210 *Linear regression models*

211 Multiple linear regression models (Schielzeth, 2010; Whittingham et al., 2006) with the `lm()`
212 function in *stats* package were established to relate 0.3 bars and 15 bars water contents to
213 soil candidate predictor variables: EPSac, microbiological and fungal activity and biomass
214 measurements. A stepwise regression (Murtaugh, 2009) was used to select the best predic-
215 tor variables using the AIC information criterion (Hegyi and Gramszegi, 2011) with the func-
216 tion `ols_step_both_aic()` from the *o/ssa* R-package. The Variable Inflation Factor (VIF) was
217 computed with the function `ols_vif_tol()` from the same package. The VIF must be lower
218 than 10 for the variable to be selected (Dormann, 2013). This way, we obtained between
219 one and four predictor variables in the linear regression models.

220 **Results**

221 How soil type, season and cultivar influence soil indicators

222 Significant differences are observed between most of the bio-physicochemical properties of
223 the rhizosphere soil of tomato plants and the corresponding "bulk" soil far from roots (Tab.2
224 and S1). Microbial and fungal biomass and activity are almost constantly significantly higher
225 in rhizosphere. The same holds for water retention values at the Permanent Wilting Point
226 (W15b) (p -value = $1.26e-04$), the field capacity (W0.3b) showing the same trend (p -value =
227 $6e-2$). A higher EPSac amount is also denoted in the rhizosphere on this global dataset (mean
228 respectively equal to 780 and 760 $\mu\text{g.g}^{-1}$; p -value= $7e-2$) (Tab.2 and S1).

229 Microbiological activities, fungal activities, and the amount of EPSac are higher in August
230 compared to June (highly significantly) (Tab.2 and S1). Concerning hydraulic parameters,
231 W15b was also higher in August, but W0.3b is higher in June (p -value= $5.4e-2$ for both). This
232 temporal difference in hydraulic parameters increases when considering only the rhi-
233 zosphere soil (respectively p -value= $4.5e-3$ and $1.2e-7$). In June, some physicochemical and
234 microbial parameters show significantly higher values in the rhizosphere soil than in bulk
235 soil, but for August-WW irrigation, most of the microbial indicators exhibit significant higher
236 values in the rhizosphere soil compared to bulk soil (Tab.2 and S1).

237 Concerning the tomato cultivars, a number of microbial soil indicators are significantly high-
238 er for the T compared to the H cultivar (Tab.2 and S1). In June, we observe differences in
239 microbial indicators between H and T cultivars ($T>H$) only for the rhizosphere soils. The soil
240 indicators for these two varieties are then differentiated into two distinct behaviours accord-
241 ing to the type of irrigation. Moreover, the analyses of variance show interactions between
242 the factors season and soil, for the water retention variable W0.3b and for the microbial
243 variables F.GlcN, F.Ala, M.Cell. The season and cultivar factors also show interactions, for the

244 variables W15b, EPS, M.Mal and in the rhizosphere for the variables W15b, F.Ala, M.Gly,
245 M.Mal (Tab.2).

246 Differences between soil indicators exacerbated under water deficit

247 Moisture content of soil samples from August campaign sampling differed between WD and
248 WW, with higher water content in WW plots compared to less irrigated WD plots (respective
249 averages of 13.7 and 12.4 g.g⁻¹, p-value=0.031). In August-WD, we observe differences in
250 both W15b and W0.3b between rhizosphere and bulk soils, while only W15b values present
251 significant differences in August-WW (Tab.2). However, the trend is the same for the two
252 irrigation treatments: W15b values are higher in rhizosphere soils than in bulk soils while it is
253 the contrary for W0.3b. For August-WD, the soil of T cultivar exhibits parameters (W0.3b and
254 a number of microbial indicators) that are significantly higher than for H cultivar (for rhi-
255 zosphere soils alone and for rhizosphere and bulk soils together). In August-WW, the differ-
256 ences between cultivars are less pronounced than in August-WD and the ranking of cultivars
257 is inverted: Some microbial and fungal catabolic activities present higher values in H soils
258 compared to T soils (Tab.2 and S1).

259 Microbial and fungal catabolic profiles

260 The microbial and fungal catabolic profiles of the 76 soil samples were analysed with Princi-
261 pal Component Analysis (PCA). Considering the catabolic profiles from the global dataset, no
262 discrimination appears between cultivars (T/H) and soil types (R/B) for microbial (Supp. Fig.
263 2-b, 2-c) and fungal (Fig. 1-b, 1-c) catabolic profiles. However, PCA shows differences be-
264 tween August and June sampling seasons. In August catabolic activity of microbial communi-
265 ties show more homogeneity between samples, with points concentrated in the center of
266 the graph, compared to June (Supp. Fig.2, % total of variance=79.5). The fungal communities

267 show a discrimination between June and August catabolism, the later showing a higher dif-
268 ference in catabolism of nitrogen-containing organic substrates (alanine and glycine, glu-
269 cosamine) (Fig.1-a, % total of variance=73).

270 When considering only June data, no discrimination in the catabolism of both the microbial
271 and the fungal communities is denoted, either between the cultivars nor between rhi-
272 zosheath and bulk soils (Fig.2-a; Fig.3-a; Supp. Fig. 2-a; Supp. Fig. 3-a).

273 On the contrary, in August there are differences in catabolic profiles. Microbial catabolic
274 profiles separate H and T cultivars, with higher catabolism of trehalose and glucose in T
275 plots, whereas glycine and malate are preferentially catabolized in H plots (Fig. 2-b, 2-c). The
276 differences in Fungal catabolic profiles observed in August are marked between rhizosheath
277 and bulk soils (Fig.3 b, c), especially at WD irrigation, where fungal communities preferential-
278 ly catabolize nitrogen-containing organic substrates (glucosamine, glycine and alanine)
279 (Fig.3-c).

280 Relation between hydro-physicals, chemical and microbiological indicators

281 Figure 4 presents the relationship between EPSac amounts and the microbial or fungal bio-
282 masses. EPSac amounts increase with and correlate with microbial biomass ($R^2= 0.20$; p-
283 value = $4.09e-5$), as well as with fungal biomass ($R^2= 0.32$; p-value = $1.28e-7$).

284 Both for microbial and fungal biomasses, these correlations with EPSac amounts are strong-
285 er when considering bulk soil and weaker for rhizosheath soil solely (Tab. 3). When consider-
286 ing the data for June or August, no significant relationship appears (on global, rhizosheath or
287 bulk soils data), with the exception of a weak relationship for fungal biomass in June ($R^2=$
288 0.22 ; p-value = $1.6e-3$) (Tab. 3).

289 The best linear models explaining water retention variables (W0.3b and W15b) with the
290 measured EPSac and microbial/fungal data variables as predictors are shown Table 4 (for
291 global dataset and for June or August data). Whatever the dataset considered, a significant
292 correlation emerges between water retention and EPSac/microbial variables (R^2 from 0.16 to
293 0.74). Most often, the fungal indicators are the significant predictors and EPSac is linked to
294 W0.3b (except in August-WW irrigation). Fungal catabolism of alanine is also linked to W0.3b
295 (except in June). The link between water retention (W0.3b and W15b) and EPSac/microbial
296 variations is stronger in August ($R^2=0.3$ to 0.74) (and particularly in August-WD irrigation)
297 compared to June ($R^2=0.16$ to 0.23).

298 Aboveground productive characteristics and fruit quality measurement

299 There is no significant difference between the two cultivars productive characteristics when
300 well irrigated (WW) (Fig.5-a). However, under WD these characteristics show systematic
301 higher values for the T cultivar compared to H (Fig.5-b), with significant differences for CoY,
302 DMY and WUE (p-value= $1.9e-2$; $4.8e-2$ and $1.9e-2$ respectively) except for RoY, for which it
303 is the opposite (H>T). Titrable acidity and pH of fruits show no significant differences. The
304 soluble solid content (SSC) is slightly higher for H cultivar compared to T cultivar in context of
305 deficit irrigation (mean respectively equal to 6.40 and 6.07, in °Brix ; p-value= $3.4e-2$).

306 Discussion

307 Influence of the rhizosphere on soil parameters

308 We highlighted a quantitative effect of the rhizosphere on soil parameters, with higher wa-
309 ter retention values and higher amounts of exopolysaccharides in the rhizosphere compared
310 to the bulk soil. We also observed that total microbial and fungal biomass, as well as micro-

311 bial and fungal catabolic activities were significantly higher in the rhizosphere. This differen-
312 tiation was more pronounced at the fruit maturation stage in August (especially at WD)
313 compared to June (rhizosphere data: Tab. 2 and S1, interactions between season and soil
314 factors and also between season and variety factors). A phenology effect seems to occur
315 here and increases during the season within the rhizosphere (Bardgett et al., 2005). Between
316 June and August, the rhizosphere soil would have received a fresh carbon supply from the
317 roots (especially EPSac) of the developed tomato plants, stimulating microbial biomass and
318 activities and promoting water retention.

319 Qualitatively, these differences were more pronounced for the catabolic profile of fungal
320 communities at the fruit maturation stage and in water-deficit context (August-WD). Fungal
321 communities are linked to a higher catabolism of nitrogen containing organic substrates in
322 rhizosphere soils (Fig.1, Fig.2). We suggest the hypothesis that carbon exudation by roots
323 boosted by water stress (Henry et al., 2007), could induce a “priming effect” in relation with
324 the stimulation of microbial and fungal exo-enzymes involved in the degradation of soil or-
325 ganic nitrogen (Bardgett et al., 2014). Another possible cause would be that the develop-
326 ment of nitrogen-fixing bacteria was favoured by EPSac secreted by the roots (Nazari, 2021)
327 in case of water deficit. The contribution of organic nitrogen by diazotrophic bacteria could
328 then have favoured a higher catabolism of nitrogen containing organic substrates in rhi-
329 zosphere soils (Zuluaga et al., 2020). To confirm these hypotheses, additional measurements
330 on the N cycle (N₂ fixing activities, enzymatic activities, nitrogenous forms...) would be nec-
331 essary.

332 Biochemical activity of roots and their microbial communities. Relationship with
333 soil water retention

334 Several below ground processes, possibly interacting, can allow the plant to compensate for
335 water deficit. The particular hydro-physical properties of the rhizosheath are partly linked to
336 the physical presence of the roots themselves (Aravena et al. 2011, De León-González et al.
337 2007), and to the production of EPS by the roots and microorganisms (Chenu 1993; Czarnes
338 et al, 2000; Sher et al., 2020), which are also influenced by changes in moisture and nutrient
339 conditions (Alami et al. 2000, Henry et al. 2007, Lynch and Whipps 1990, Redmile-Gordon et
340 al. 2014, Roberson and Firestone 1992).

341 We observe that the amount of soil EPSac follows the same seasonal dynamics as soil micro-
342 bial and fungal biomass and their catabolic activity, increasing from spring to summer, espe-
343 cially in rhizosheath soils (Tab. 2, Tab.S1). Indeed, although low, the correlations were posi-
344 tive between EPSac and microbial and fungal biomasses (the correlation with fungal bio-
345 masses was higher - Tab. 3 and Fig. 4). In August, at the fruit maturation stage, water reten-
346 tion at 0.3 and 15 bars was mostly linked to physico-chemical and microbial variables, and
347 more significantly in case of water-deficit than with full irrigation (Tab. 4). In particular, the
348 EPSac was partially predictive of the water retention at field capacity (W0.3b) (Tab. 4).

349 The increase in root and microbial biological stimulation in the rhizosheath, notably by a
350 higher EPS production than their consumption (Redmile-Gordon et al. 2014) could explain
351 these results. This stimulation in the rhizosheath could have increased with the root density
352 and the intensification of exudation per unit of root length linked to a phenology effect and
353 a triggered by water deficit in case of deficit irrigation condition (Henry et al., 2007; Nazari et
354 al., 2020).

355 Furthermore, fungal biomass and catabolic parameters also seem to be important variables
356 explaining water retention: the fungal catabolism of alanine, an amino-acid, was almost sys-

357 tematically found as a predictor variable for water retention at field capacity (W0.3b). In
358 general, fungi are more tolerant to water stress than bacteria (Bérard et al., 2015). Rhizo-
359 sphere fungi (and mycorrhizae in particular) are known to act on soil aggregation (and water
360 retention) (Freschet et al., 2021) through the physical action of their hyphae and their pro-
361 duction of proteins (e.g. glomalin) and polysaccharides (e.g. scleroglucan), resulting in parti-
362 cle sticking actions (Poirier et al., 2018). Studies involving mycorrhizae and tomatoes show
363 that mycorrhizae promote plant resistance to drought by stimulating nutrient cycles (includ-
364 ing nitrogen) and root exudation (especially Amino Acids, which can play an osmoregulatory
365 role) (Bowles et al. 2016). Moreover, Cavagnaro et al. (2006) showed that mycorrhizae pro-
366 mote soil aggregation in tomatoes rhizosphere, especially in the presence of mineral N. One
367 hypothesis would be that tomatoes exude more organic compounds under water deficit
368 conditions, which would promote nitrogen catabolism (directly and/or through a “priming
369 effect” or diazotrophic bacteria stimulation as suggested above), fungal development (my-
370 corrhization) and its direct or indirect effects on water retention. Thus, these different chem-
371 ical and biological phenomena probably interact with the hydro-physical properties of the
372 soil (Hallett et al. 2009). However, our hypothesis is based on proxy measurements of bio-
373 mass and fungal catabolism (FungiResp method). It would have been interesting to measure
374 the intensity of root colonization by mycorrhizae to confirm this hypothesis, which we were
375 unable to do during this study and could thus be done in future investigations.

376 Nevertheless, it seems that the fungal catabolism of alanine is related to the hydraulic prop-
377 erties of the soil without water deficit, while in conditions of water deficit, there could be a
378 shift to other mechanisms explaining water retention, which would be related to EPSs,
379 among others. Indeed, in August, we found that the fungal catabolism of alanine explained
380 the water retention of the soils with higher R² values in the WW irrigated plots than in the

381 irrigation-limited plots (WD): in particular for the W0.3b retention at WW irrigation the in-
382 crease in R2 for F-Alanine was 0.33, while at WD irrigation it dropped to 0.2, with the ap-
383 pearance of the EPSac as an explanatory variable (increase in R2=0.18; Tab.5).

384 Possible relationships between aboveground cultivars characteristics and their
385 belowground bio-physico-chemical soil parameters

386 The T cultivar presents a higher production potential compared to the H cultivar in the water
387 deficit situation, and irrigation seemed to mitigate these differences (Fig. 5). Arbex de Casto
388 Vilas Boas et al. (2017) showed in a previous similar experiment that WUE was better for T
389 than H cultivar especially in WD conditions, ranging from 25 kg.m⁻³ for WW irrigation to 41
390 kg.m⁻³ for a WD situation in the field. Despite a much higher total water input in this 2018
391 field experiment and, thus, with lower mean WUE values (between 11 and 18 kg.m⁻³), the
392 WUE was still significantly higher for T than for H cultivar in WD situation (Fig. 5), indicating
393 that H seems more sensitive to WD.

394 It seems that our biochemical observations on the soils (microbial activities, especially fungal
395 activities and amounts of EPSac, Tab.2) leading to a local modification of soil water retention
396 (Tab.4) are in agreement with the production potential of tomato cultivars T and H, as a
397 function of their water efficiency (Fig. 5). In fact, cultivar H, which seems to have better ex-
398 pressed its productive potential under optimal irrigation conditions, presents in its rhi-
399 zosheath in August-WW a higher F.Ala catabolism, which contributes to explain the water
400 retentions W0.3b and W15b. On the contrary, cultivar T seems to have better expressed its
401 production potential under water deficit conditions, in correspondence with higher water
402 retention W0.3b, together with higher EPSac amounts and higher indicators of fungal activi-
403 ty and biomass in the T soil plots. Of course, if resistance/tolerance is also related to root

404 system characteristics (root density, root depth) (Fang et Xiong, 2015), our results point to
405 the fact that biochemical properties of the rhizosheath may also play a role.

406 The water retention properties of soils have a strong influence on crop development and
407 could factor in the crop's capacity to withstand droughts. A better understanding of the pos-
408 sible links between soil bio-physicochemical parameters and hydrophysical properties, par-
409 ticularly in the rhizosheath (Bengough, 2012), could help improve crop resistance to water
410 deficit. While creating water deficit conditions by limiting irrigation, we measured biophysi-
411 cal indicators of soil quality and rhizosheath functioning (in comparison to bulk soil). This
412 field study brings new information regarding the links between soil parameters and produc-
413 tivity of two tomato cultivars and two types of irrigation.

414 Conclusion

415 Our study suggests that rhizosheath affects the soil biophysical parameters measured and
416 this influence increased between the end of the vegetative phase and the fruit maturation
417 stage. Secondly, it seems that hydro-physical properties of the soil (e.g., water retention
418 capacities) are partly linked to two interacting phenomena: the presence in the rhizosheath
419 environment of specific substances such as exopolysaccharides and/or nitrogenous sub-
420 stances from roots and microorganisms, and the presence and activity of fungi (possibly my-
421 corrhizae). The importance of fungal activity stood out during the study and it would be in-
422 teresting to investigate their effects further by using tools dedicated to fungi and mycorrhi-
423 za.

424 In addition, these two aforementioned relationships could be a part of the adaptation
425 mechanisms of the Terradou cultivar to water deficit, enabling higher agricultural productivi-
426 ty via a higher plant WUE. This study confirms the observations made by Arbex de Castro

427 Vilas Boas et al (2017) and provides hypotheses related to the influence of the rhizosheath
428 on the responses of these cultivars to water deficit.

429 Our observations—i.e., correlations between the microbial biochemical and hydrophysical
430 parameters of the soil, which are different for the two cultivars—confirm the importance of
431 taking into account soil (and particularly rhizosheath soil) parameters when selecting culti-
432 vars for specific agroclimatic contexts (Nazari et al., 2020, Cattivelli et al., 2008). Finally, this
433 study, suggests some links between aboveground and soil parameters in relation with water
434 deficit and plant water use efficiency. This underlines the need of getting a more integrated
435 and quantitative view of the interactions between soil microbial-biochemical parameters
436 and soil hydrophysical properties when investigating agro-ecological solutions to water re-
437 lated yield gap.

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Figures and table

Table of abbreviations

Abbreviation	Description	Unit
A	Soil sampling date at the beginning of fructification stage (August 2. 2018).	-
AIC	Akaike Information Criterion	-
B (Bulk)	Soil sampling from bulk soil (without roots)	-
CoY	Fresh Commercial Tomato Yield (including red and yellow tomato)	kg/ha
DMY	Commercial Tomato Yield in Dry Matter (including red and yellow tomato)	kg/ha
EPSac	ExoPolySaccharides	mg eq glc / g DrySoil
F.Ala	Alanine induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
F.Bas	Basal respiration for fungi communities in soil	CO ₂ /gDrySoil/h
F.Cell	Cellulobiose induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
F.Gly	Glycine induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
F.GlcN	Glucosamine induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
F.Mal	Malate induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
F.Tre	Trehalose induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
H	Soil sampling from Heinz 1015 tomato cultivar	-
J	Soil sampling date at the beginning of flowering stage (June 19. 2018).	-
M.Ala	Alanine induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
M.Bas	Basal respiration for fungi communities in soil	CO ₂ /gDrySoil/h
M.Cell	Cellulobiose induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
M.Gly	Glycine induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
M.GlcN	Glucosamine induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
M.Mal	Malate induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
M.Tre	Trehalose induced respiration for fungi communities in soil	CO ₂ /gDrySoil/h
R (Rhizo)	Soil sampling from rhizosheath soil (root adhering)	-
RoY	Rotten Tomato Yield	t/ha
T	Soil sampling from Terradou tomato cultivar	-
VIF	Variable Inflation Factor	-
W0.3b	Water Retention Capacity at 0.3b (at Field Capacity)	g/g
W15b	Water Retention Capacity at 15b (at Permanent Wilting Point)	g/g
WD	Water deficit irrigation (57% of ETP losses)	-
WUE	Plant Water Use Efficiency	kg/m ³
WW	Well watered irrigation (87% of ETP losses)	-

Localisation	44°11'N/4°48'E
Texture	loam
Clay (g kg ⁻¹)	290
Loam (g kg ⁻¹)	331
Sand (g kg ⁻¹)	379
SOC (g kg ⁻¹)	12.5
TN (g kg ⁻¹)	1.1
C/N	11
CaCO ₃ (g kg ⁻¹)	484
Ca ²⁺ (cmol+ kg ⁻¹)	14.6
Mg ²⁺ (cmol+ kg ⁻¹)	0.595
CEC (cmol+ kg ⁻¹)	12.7
pH (water)	8.5
WSA (%)	36

Table 1: Main physical, chemical and microbial characteristics of the soils used for this study on the Piolenc experimental site. SOC: Soil Organic Carbon, TN: Total Nitrogen, C/N: carbon over nitrogen ratio CEC: Cation Exchange Capacity, WSA: Water Stable Aggregates

	W0.3b	W15b	EPSac	F.Glc	F.Tre	F.Cell	F.GlcN	F.Ala	F.Gly	F.Mal	FB	M.Bas	M.Glc	M.Tre	M.Cell	M.GlcN	M.Ala	M.Gly	M.Mal	MB
Global																				
SOIL	R>B	R>B***	R>B	R>B***	R>B**	R>B***	R>B***	R>B***	R>B***	R>B***	R>B***	R>B**	R>B***	R>B***	R>B***	R>B***	R>B***	R>B***	R>B***	R>B***
CULT	T>H	H>T	T>H	T>H	T>H	T>H	T>H	H>T	T>H	H>T	T>H**	T>H	T>H*	T>H**	T>H*	T>H	T>H	T>H	H>T	T>H*
SEAS	J>A	A>J	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***
SOIL:CULT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SOIL:SEAS	***	-	-	-	-	-	***	*	-	-	-	-	-	-	*	-	-	-	-	-
CULT:SEAS	-	*	**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-
Global Rhizo																				
CULT	T>H	H>T	T>H	T>H***	T>H	T>H	T>H	H>T	H>T	T>H	T>H**	T>H	T>H	T>H*	T>H	T>H	T>H	H>T	H>T	T>H
SEAS	J>A***	A>J**	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J*	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***	A>J***
CULT:SEAS	-	*	-	-	-	-	-	*	-	-	-	-	-	-	-	-	-	*	**	-
June																				
SOIL	R>B***	R>B	R>B**	R>B***	R>B	R>B*	R>B	R>B	R>B	R>B*	R>B***	R>B	R>B	R>B**	R>B*	R>B	R>B*	R>B*	R>B**	R>B
CULT	H>T	T>H	H>T	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H
SOIL:CULT	-	-	-	*	-	-	-	-	-	-	**	-	-	-	-	-	-	-	-	-
June Rhizo																				
CULT	H>T	T>H	T>H	T>H*	T>H	T>H	T>H	T>H	T>H	T>H	T>H*	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H	T>H
August WW																				
SOIL	B>R	R>B*	R>B	R>B**	R>B*	R>B*	R>B***	R>B**	R>B**	R>B*	R>B**	R>B*	R>B***	R>B***	R>B***	R>B***	R>B**	R>B***	R>B***	R>B***
CULT	T>H	H>T*	T>H*	T>H	T>H	H>T	T>H	H>T	H>T	H>T	T>H	T>H	T>H	T>H	T>H	T>H	H>T	H>T	H>T	T>H
SOIL:CULT	-	-	-	-	-	-	-	*	-	-	-	-	-	-	*	-	**	*	-	-
August WW Rhizo																				
CULT	T>H	H>T	T>H	T>H	H>T	H>T	T>H	H>T*	H>T	H>T	H>T	H>T	H>T	H>T	T>H	H>T	H>T	H>T	H>T**	H>T**
August WD																				
SOIL	B>R**	R>B***	R>B	R>B	R>B	R>B	R>B***	R>B***	R>B***	R>B*	R>B	R>B*	R>B***	R>B***	R>B***	R>B***	R>B***	R>B***	R>B***	R>B***
CULT	T>H***	T>H	T>H	T>H*	T>H	T>H	T>H*	H>T	H>T	T>H	T>H*	T>H	T>H	T>H	T>H	T>H	T>H	T>H	H>T	T>H
SOIL:CULT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
August WD Rhizo																				
CULT	T>H*	H>T	T>H	T>H*	T>H	T>H	T>H	T>H	H>T	T>H	T>H*	T>H	T>H	T>H	T>H	T>H	T>H	H>T	H>T	H>T

Table 2: Analyses of variance (ANOVAs) results for the soil parameters for the three factors : the type of soil rhizosphere or bulk (SOIL), the season (SEAS) and the cultivar (CULT). Main effect and their interactions are calculated on global dataset (whatever the rhizosphere or bulk soil, the season, the cultivar) and on rhizosphere soil dataset. Below are analysis for June, August-WD irrigation and August-WW irrigation dataset. X>Y signifies that the parameter X is greater than Y. Level of significance: *p<0.05; **p<0.01; ***p<0.001. See table of abbreviations for more information.

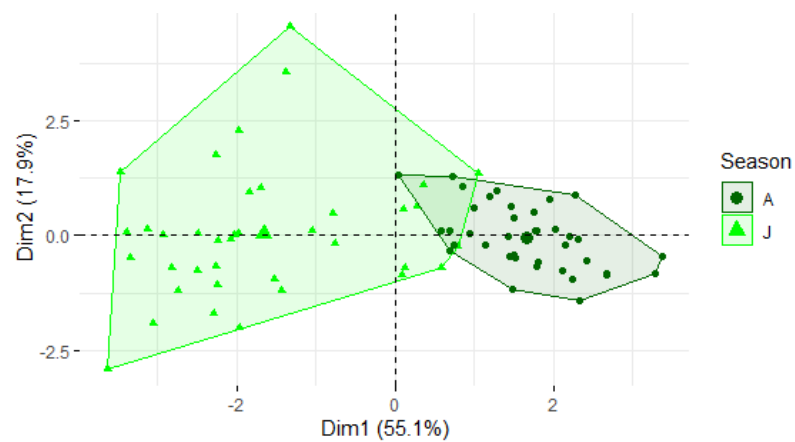
Dataset	Factor	R²	p-value	Sign. code
Global	MB	0.20	4.09E-05	***
n=76	FB	0.32	1.28E-07	***
Rhizo	MB	0.16	7.39E-03	**
n=38	FB	0.19	3.53E-03	**
Bulk	MB	0.21	2.38E-03	**
n=38	FB	0.39	1.71E-05	***
June	MB	-0.02	6.12E-01	
n=38	FB	0.22	1.60E-03	**
June rhizo	MB	-0.06	9.63E-01	
n=19	FB	0.11	9.07E-02	.
June bulk	MB	-0.03	4.79E-01	
n=19	FB	5E-4	3.29E-01	
August	MB	5E-4	3.19E-01	
n=38	FB	-0.03	7.83E-01	
August rhizo	MB	-0.06	8.48E-01	
n=19	FB	-0.03	5.05E-01	
August bulk	MB	0.07	1.50E-01	
n=19	FB	-0.005	3.54E-01	

Table 3: Results of linear regression between EPSac and the microbial or fungal biomasses (MB, FB). Considering global soil data or subsets of the soil data. a: slope ; b: intercept of linear regression. Level of significance: *p<0,05; **p<0,01;***p<0,001. See table of abbreviations for more information. See table of abbreviations for more information.

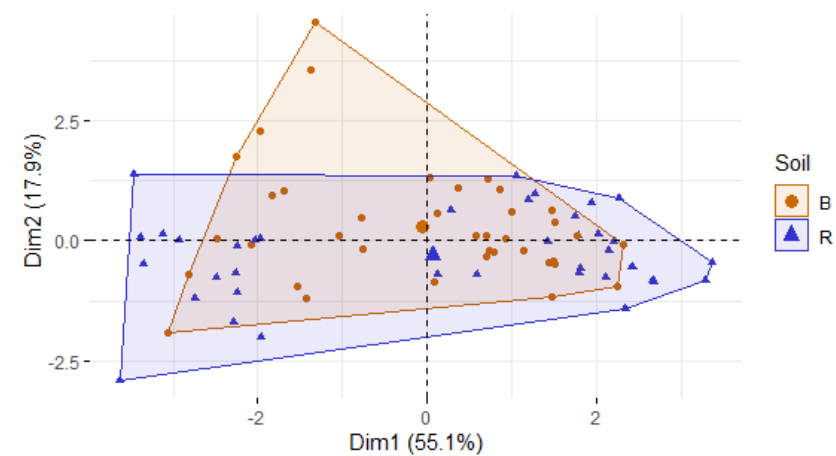
Variables selected	AIC	VIF	Final AIC	Final p-value	Signif. Code	Final R ²
W0.3b global			-445.06	3.69E-04	***	0.21
F.Ala	-433.78	5				
M.Ala	-441.62	3.06				
F.Cell	-444.49	5.43				
EPSac	-445.06	1.73				
W15b global			-562.14	6.14E-05	***	0.21
F.Tré	-548.36	3.67				
M.Tré	-550.61	3.67				
W0.3b June			-215.13	7.91E-03	**	0.23
EPSac	-212.62	1.13				
F.Cell	-212.71	5.09				
F.Tré	-215.13	4.87				
W15b June			-284.35	8.24E-03	**	0.16
M.Cell	-284.35	nn				
W0.3b August-WW			-122.85	4.15E-03	**	0.51
FB	-112.45	1.66				
M.Cell	-114.28	2.73				
F.Ala	-122.85	1.86				
W15b August-WW			-120.62	1.04E-02	*	0.3
F.Ala	-120.62	nn				
W0.3b August-WD			-129.78	3.94E-04	***	0.65
F.Ala	-115.33	2.61				
EPSac	-119.84	1.07				
M.Tré	-123.31	1.98				
F.Gly	-129.78	2.99				
W15b August-WS			-164.75	1.50E-05	***	0.74
F.D.Glc	-157.97	5.2				
M.Gly	-161.08	2.94				
M.D.Glc	-164.75	7.1				

Table 4: Multiple linear regression model between water retention (W0.3b and W15b) and both physico-chemical (EPSac) and microbial parameters (catabolic profile, biomass) for the global dataset and subsets. Best model issued from stepwise regression using AIC selection criteria. The final model include variable with VIF<10. restricted to a maximum 4 explanatory variables. Level of significance: *p<0.05; **p<0.01;***p<0.001. See table of abbreviations for more information.

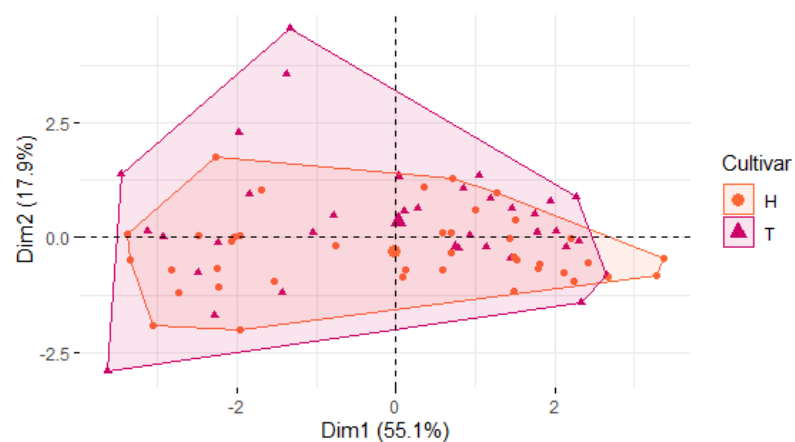
1-a: Season



1-c: Soil type



1-b: Cultivar



1-d: Correlation graph substrates

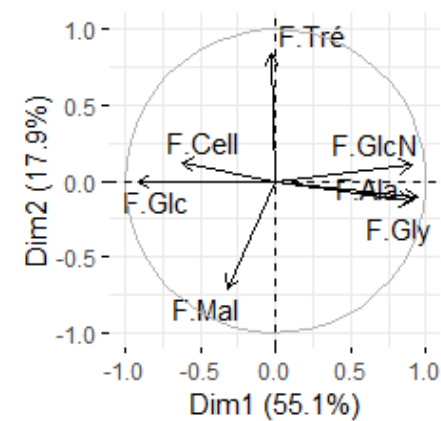


Figure 1: Principal Component Analysis (PCA) of fungal catabolic profile of the rhizosphere and bulk soil data. Projection on axes 1 and 2 (73% of variance). Distribution of individuals and correlations shown for cultivar (H and T), soil type (R and B) and sampling season (J and A).

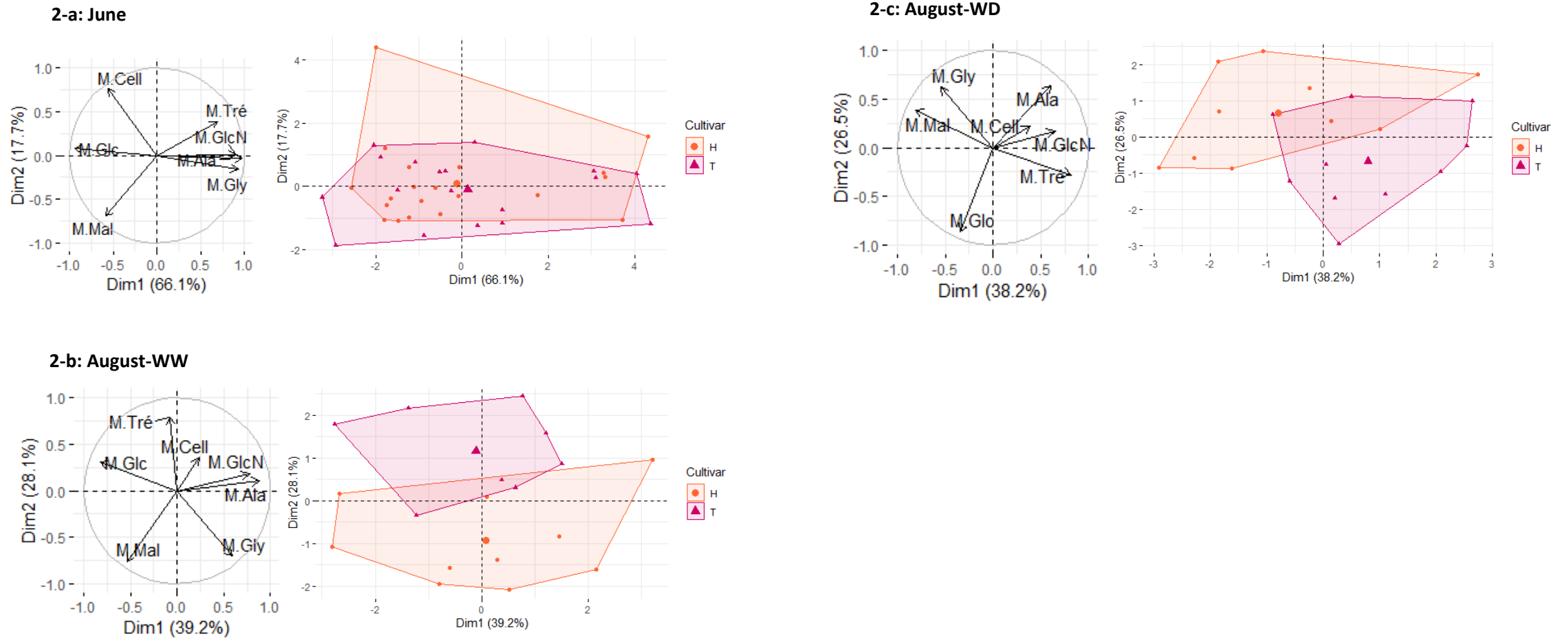


Figure 2: Principal Component Analysis (PCA) of microbial catabolic profile of the rhizosphere and bulk soil data. Projection on axes 1 and 2 (> 64% variance). Microbial catabolic profile for June, August-WW and August-WD data. Distribution of individuals and correlations shown for cultivar (H and T).

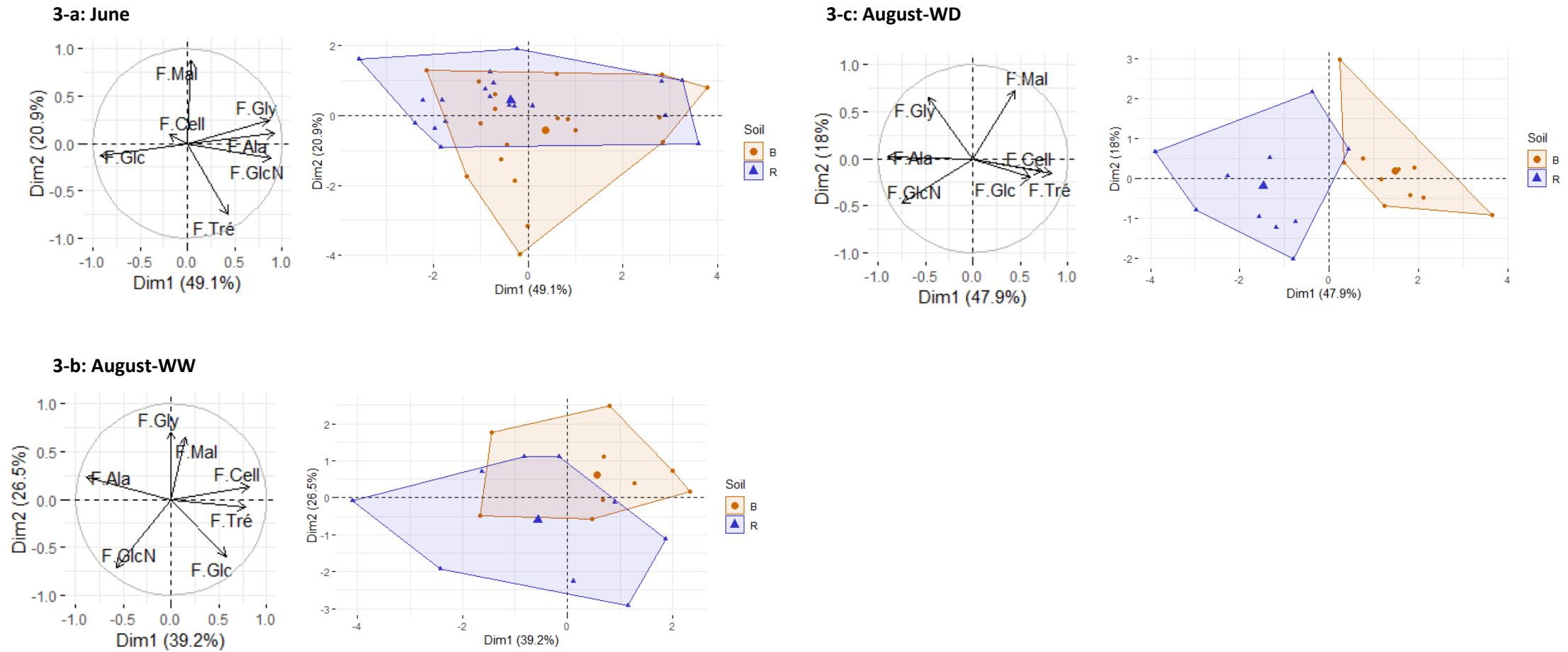


Figure 3: Principal Component Analysis (PCA) of fungal catabolic profile for June, August-WW and August-WD data. Projection on axes 1 and 2 (> 65% variance). Distribution of individuals and correlations shown for soil types (R and B).

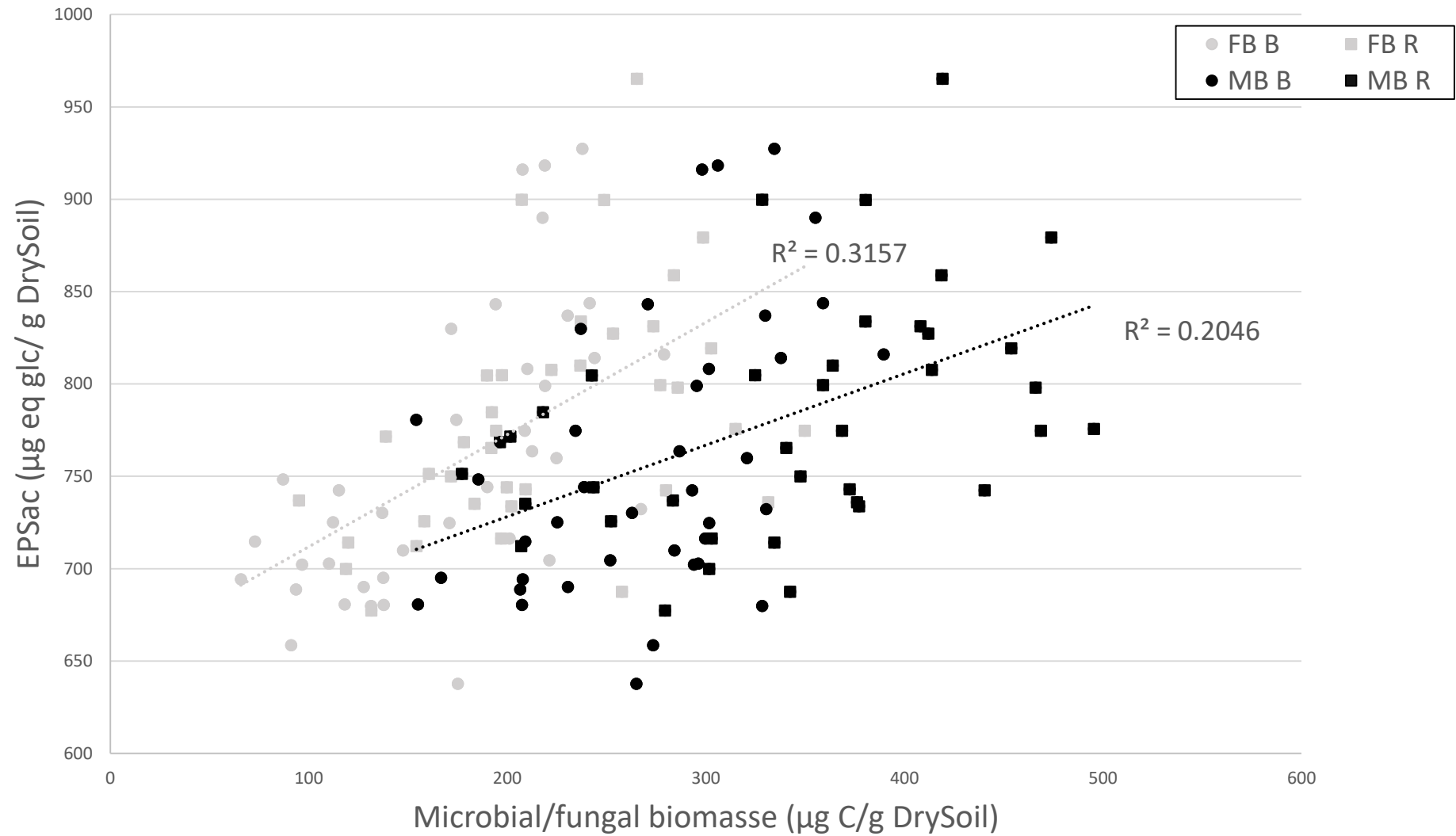


Fig. 4: Linear regression between EPSac amount and the microbial or fungal biomasses (MB, FB) for the global soil data set.

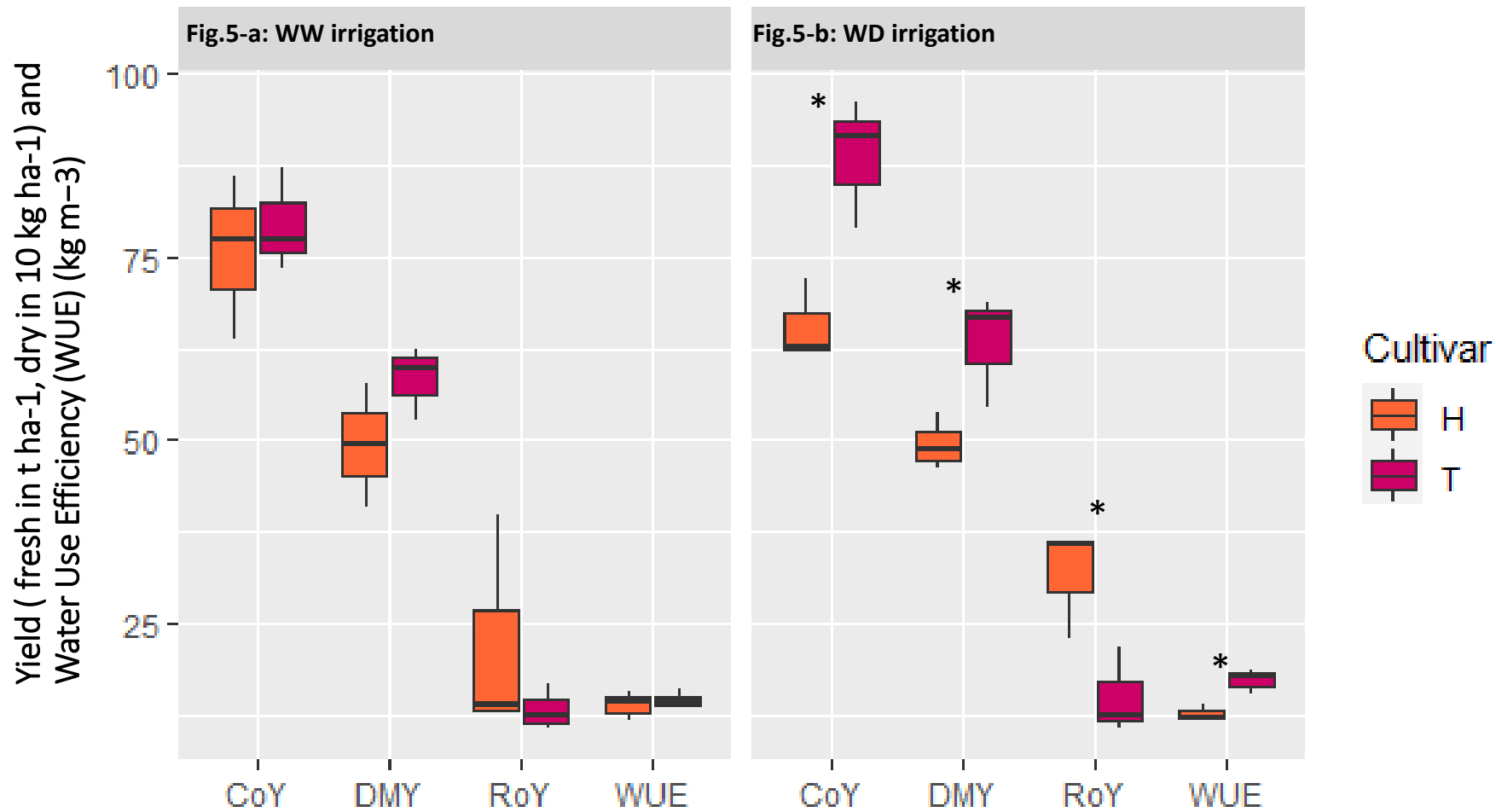


Figure 5: Box plots comparing H and T varieties for the WW irrigation dataset (Fig.5-a), and the WD irrigation dataset (Fig.5-b), with Rotten tomato Yield (RoY, in t ha-1), fresh Commercial Yield (CoY, in t ha-1) and Dry Matter Yield (DMY, in 10 kg ha-1) and Water Use Efficiency (WUE, in kg m-3). Level of significance: * $p < 0.05$. See table of abbreviations for more information.