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Summary

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

Key words

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

Introduction

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

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

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

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

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

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

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

Materials and methods

Experimental set-up and sampling

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

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

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

Measurements of soil and plant parameters

Soil microbial and fungal catabolic measurements

Substrate Induced Respiration (SIR) of soil was assessed with the FungiResp, adapted from the MicroResp^{TM} colorimetric technique (Ben Sassi et al., 2012; Chapman et al., 2007), consisting in a 96-deep-well microplate filled with soil subsamples. The soil water content was preliminary adjusted to 40% of the water holding capacity (about 0.22 g/g gravimetric water content). 25 µl of organic substrates (6.7 mg.g^{-1} dw soil) were added in each deep-well. Each filled soil plate was then sealed face to face with a CO_2 trap microplate including a pH dye indicator, and an intercalated silicone joint to individualize the plate wells. The systems were then incubated in the dark at (23°C±1) for six hours. Absorbance of the gel CO_2-trap was measured at 570 nm, before and after incubation. A calibration curve of absorbance versus head space equilibrium CO_2 concentration (measured by gas chromatography) was fitted to a regression model, which was then used to compute the amounts of released CO_2 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 fuged (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 Na3PO4. 12H2O, 4 mM NaH2PO4. H2O, 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 $t.ha^{-1}$) 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 $t.ha^{-1}$). The dry mass of this commercial yield (DMY in $kg.ha^{-1}$) was also measured.

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

Data Analysis:

Statistical analysis

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

Principal Component Analysis

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

Linear regression models

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

Results

How soil type, season and cultivar influence soil indicators

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

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

Concerning the tomato cultivars, a number of microbial soil indicators are significantly higher for the T compared to the H cultivar (Tab.2 and S1). In June, we observe differences in microbial indicators between H and T cultivars (T>H) only for the rhizosheath soils. The soil indicators for these two varieties are then differentiated into two distinct behaviours according to the type of irrigation. Moreover, the analyses of variance show interactions between the factors season and soil, for the water retention variable W0.3b and for the microbial variables F.GlcN, F.Ala, M.Cell. The season and cultivar factors also show interactions, for the

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

Differences between soil indicators exacerbated under water deficit

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

Microbial and fungal catabolic profiles

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

show a discrimination between June and August catabolism, the later showing a higher difference in catabolism of nitrogen-containing organic substrates (alanine and glycine, glucosamine) (Fig.1-a, % total of variance=73).

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

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

Relation between hydro-physicals, chemical and microbiological indicators

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

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

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

Aboveground productive characteristics and fruit quality measurement

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

Discussion

Influence of the rhizosheath on soil parameters

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

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

Qualitatively, these differences were more pronounced for the catabolic profile of fungal communities at the fruit maturation stage and in water-deficit context (August-WD). Fungal communities are linked to a higher catabolism of nitrogen containing organic substrates in rhizosheath soils (Fig.1, Fig.2). We suggest the hypothesis that carbon exudation by roots boosted by water stress (Henry et al., 2007), could induce a “priming effect” in relation with the stimulation of microbial and fungal exo-enzymes involved in the degradation of soil organic nitrogen (Bardgett et al., 2014). Another possible cause would be that the development of nitrogen-fixing bacteria was favoured by EPSac secreted by the roots (Nazari, 2021) in case of water deficit. The contribution of organic nitrogen by diazotrophic bacteria could then have favoured a higher catabolism of nitrogen containing organic substrates in rhizosheath soils (Zuluaga et al., 2020). To confirm these hypotheses, additional measurements on the N cycle (N_2 fixing activities, enzymatic activities, nitrogenous forms...) would be necessary.

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

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

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

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

Furthermore, fungal biomass and catabolic parameters also seem to be important variables 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 rhizosheath, 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 EPSacs,
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

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

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

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

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

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

The water retention properties of soils have a strong influence on crop development and could factor in the crop's capacity to withstand droughts. A better understanding of the possible links between soil bio-physicochemical parameters and hydrophysical properties, particularly in the rhizosheath (Bengough, 2012), could help improve crop resistance to water deficit. While creating water deficit conditions by limiting irrigation, we measured biophysical indicators of soil quality and rhizosheath functioning (in comparison to bulk soil). This field study brings new information regarding the links between soil parameters and productivity of two tomato cultivars and two types of irrigation.

Conclusion

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

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

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

Our observations—i.e., correlations between the microbial biochemical and hydrophysical parameters of the soil, which are different for the two cultivars—confirm the importance of taking into account soil (and particularly rhizosheath soil) parameters when selecting cultivars for specific agroclimatic contexts (Nazari et al., 2020, Cattivelli et al., 2008). Finally, this study, suggests some links between aboveground and soil parameters in relation with water deficit and plant water use efficiency. This underlines the need of getting a more integrated and quantitative view of the interactions between soil microbial-biochemical parameters and soil hydrophysical properties when investigating agro-ecological solutions to water related 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 inducted respiration for fungi communities in soil	CO2/gDrySoil/h
F.Bas	Basal respiration for fungi communities in soil	CO2/gDrySoil/h
F.Cell	Cellulobiose inducted respiration for fungi communities in soil	CO2/gDrySoil/h
F.Gly	Glycine inducted respiration for fungi communities in soil	CO2/gDrySoil/h
F.GlcN	Glucosamine inducted respiration for fungi communities in soil	CO2/gDrySoil/h
F.Mal	Malate inducted respiration for fungi communities in soil	CO2/gDrySoil/h
F.Tre	Trehalose inducted respiration for fungi communities in soil	CO2/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 inducted respiration for fungi communities in soil	CO2/gDrySoil/h
M.Bas	Basal respiration for fungi communities in soil	CO2/gDrySoil/h
M.Cell	Cellulobiose inducted respiration for fungi communities in soil	CO2/gDrySoil/h
M.Gly	Glycine inducted respiration for fungi communities in soil	CO2/gDrySoil/h
M.GlcN	Glucosamine inducted respiration for fungi communities in soil	CO2/gDrySoil/h
M.Mal	Malate inducted respiration for fungi communities in soil	CO2/gDrySoil/h
M.Tre	Trehalose inducted respiration for fungi communities in soil	CO2/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/m3
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
CaCO3 (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	T>H	H>T	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 rhizosheath or bulk (SOIL), the season (SEAS) and the cultivar (CULT). Main effect and their interactions are calculated on global dataset (whatever the rhizosheath or bulk soil, the season, the cultivar) and on rhizosheath soil dataset. Bellow 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.

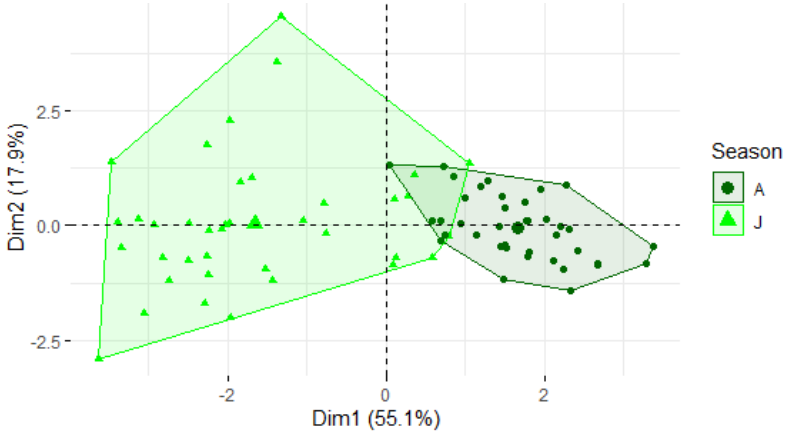
Dataset	Factor	R^2	p-value	Sign. code
Global	MB	0.20	4.09E-05	***
n=76	FB	0.32	1.28E-07	***
Rhizo	MB	0.16	7.39E-03	**
n=38	FB	0.19	3.53E-03	**
Bulk	MB	0.21	2.38E-03	**
n=38	FB	0.39	1.71E-05	***
June	MB	-0.02	6.12E-01	
n=38	FB	0.22	1.60E-03	**
June rhizo	MB	-0.06	9.63E-01	
n=19	FB	0.11	9.07E-02	.
June 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.

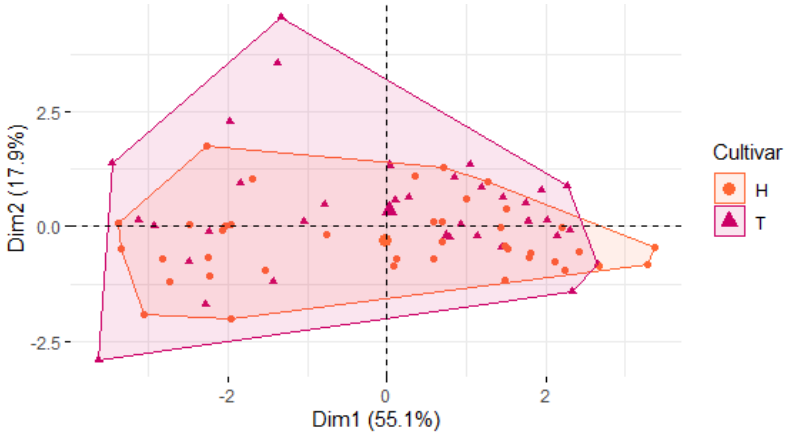
Variables selected	AIC	VIF	Final AIC	Final p-value	Signif. Code	Final R^2
W0.3b global			-445.06	3.69E-04	***	0.21
F.Ala	-433.78	5				
M.Ala	-441.62	3.06				
F.Cell	-444.49	5.43				
EPSac	-445.06	1.73				
W15b global			-562.14	6.14E-05	***	0.21
F.Tré	-548.36	3.67				
M.Tré	-550.61	3.67				
W0.3b June			-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.

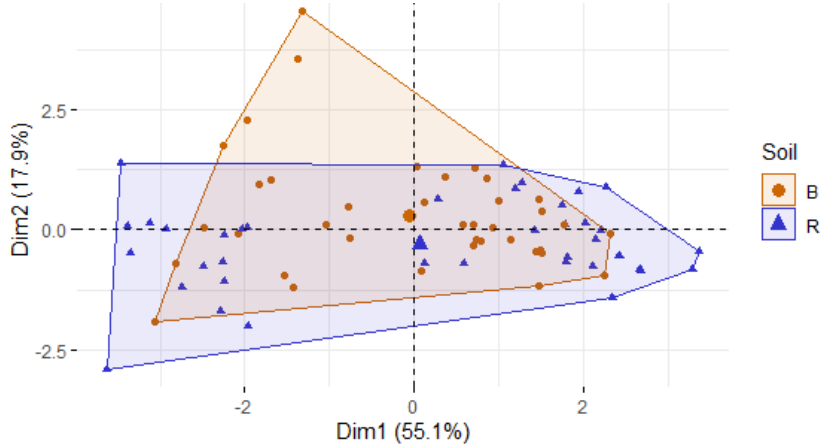
1-a: Season



1-b: Cultivar



1-c: Soil type



1-d: Correlation graph substrates

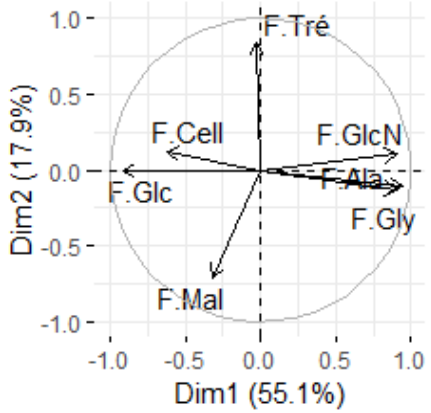


Figure 1: Principal Component Analysis (PCA) of fungal catabolic profile of the rhizosheath and bulk soil data. Projection on axes 1 and 2 (73% of variance). Distribution of individuals and correlations shown for cultivar (H and T). soil type (R and B) and sampling season (J and A).

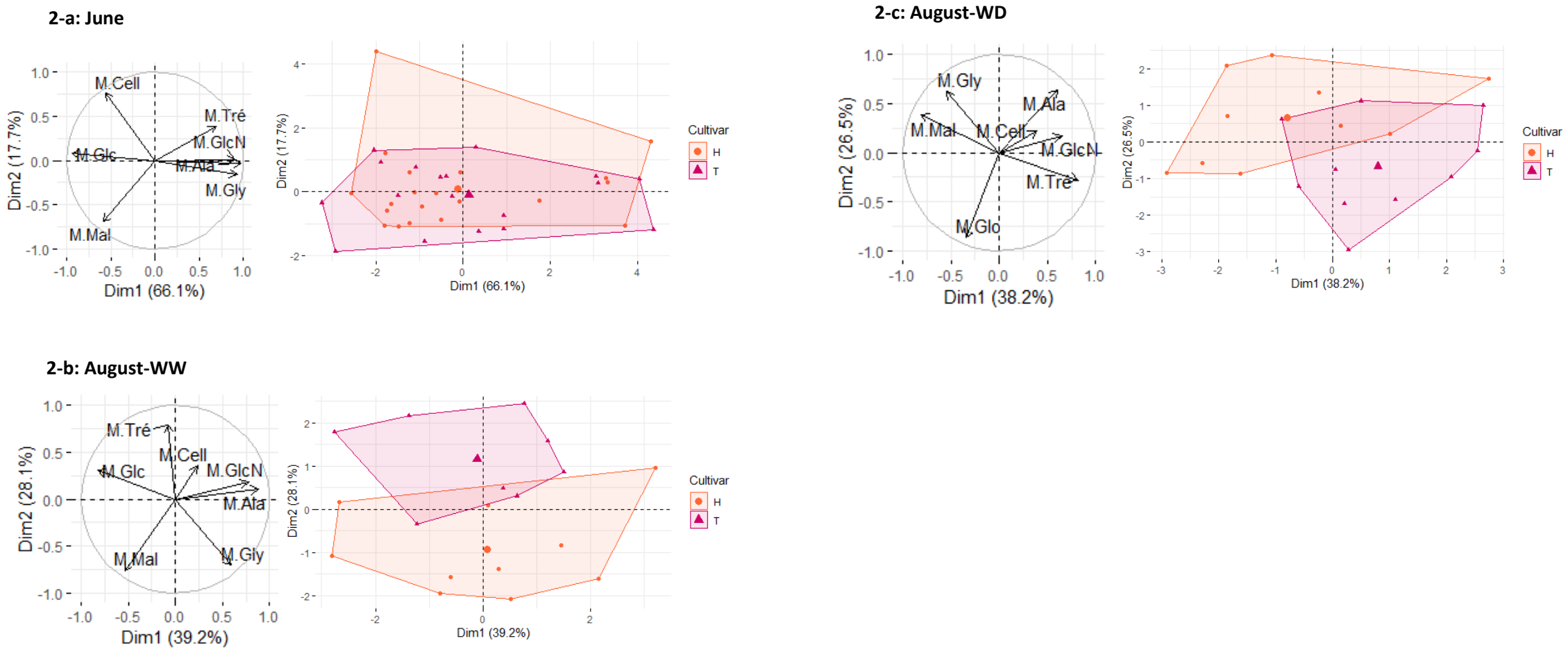
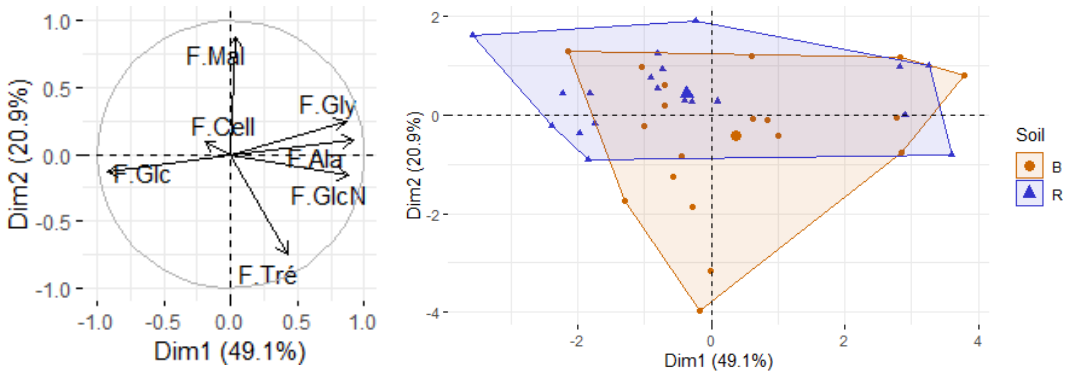
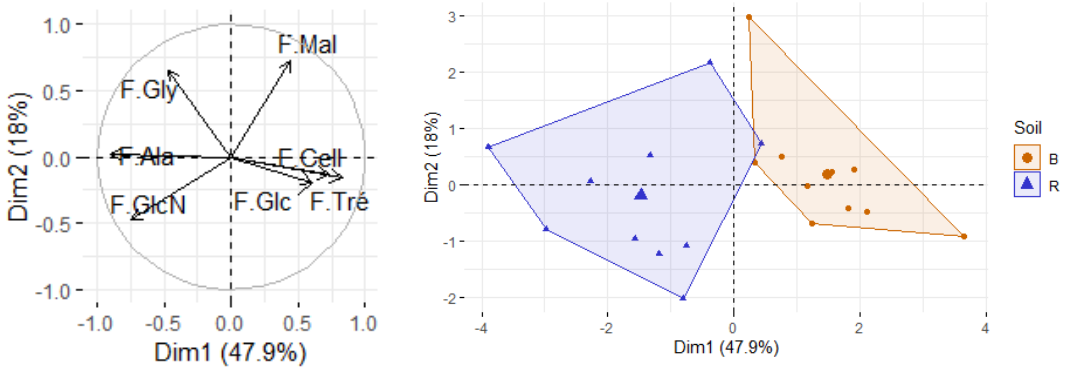


Figure 2: Principal Component Analysis (PCA) of microbial catabolic profile of the rhizosheath and bulk soil data. Projection on axes 1 and 2 (> 64% variance). Microbial catabolic profile for June. August-WW and August-WD data. Distribution of individuals and correlations shown for cultivar (H and T).

3-a: June



3-c: August-WD



3-b: August-WW

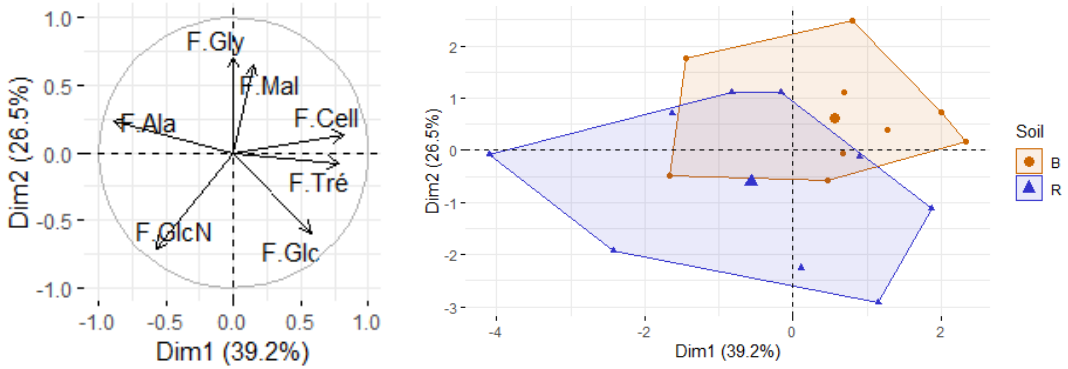


Figure 3: Principal Component Analysis (PCA) of fungal catabolic profile for June. August-WW and August-WD data. Projection on axes 1 and 2 (> 65% variance). Distribution of individuals and correlations shown for soil types (R and B).

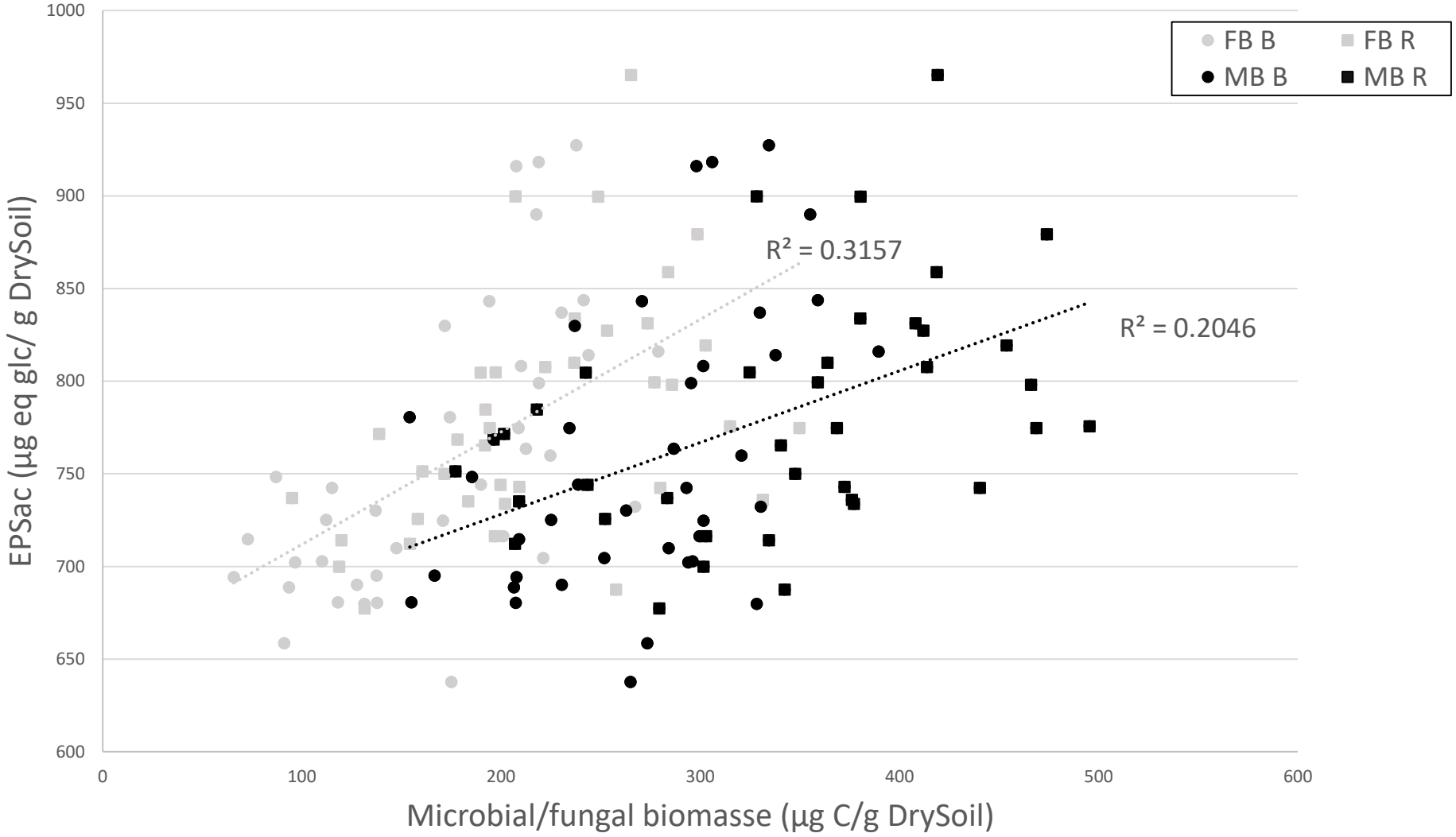


Fig. 4: Linear regression between EPSac amount and the microbial or fungal biomasses (MB, FB) for the global soil data set.

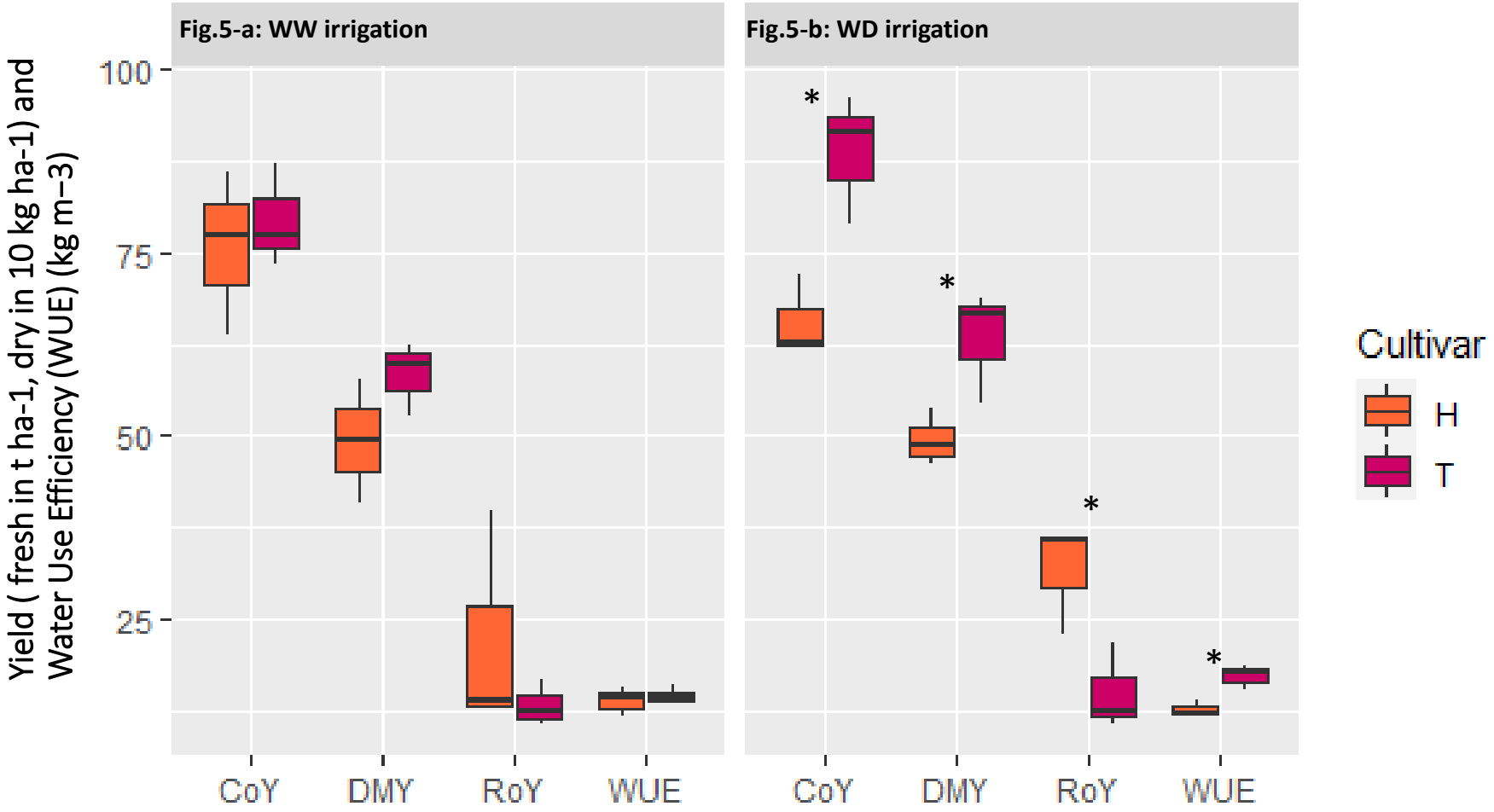


Figure 5: Box plots comparing H and T varieties for the WW irrigation dataset (Fig.5-a), and the WD irrigation dataset (Fig.5-b), with Rotten tomato Yield (RoY, in t ha-1), fresh Commercial Yield (CoY, in t ha-1) and Dry Matter Yield (DMY, in 10 kg ha-1) and Water Use Efficiency (WUE, in kg m−3). Level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