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Wheat rhizosphere effect on soil microbial structure and activities change with pedoclimatic conditions in Moroccan agroecosystems

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Abstract

Crop may select their microbiome by modifying soil physicochemical properties. However, the variation of this crop capability throughout variable agroclimatic conditions remain underexplored. This study examines how wheat growth affects soil microbiota structure and activities under contrasting Moroccan agroclimatic conditions qualified as unfavorable, moderate and favorable based on their mean annual temperature (MAT) and mean annual precipitation (MAP). For this purpose, microbial biomass, structure and catabolic activities were analyzed in rhizosphere and bulk soils sampled in wheat fields located in Safi (unfavorable), El-Jadida (moderate), Meknes and Beni-Mellal (favorable) regions. The results indicated that microbial structure varied between regions and was driven by soil edaphic properties and climatic variables (MAP, MAT, altitude) in bulk soils. In rhizosphere soils, the impact of climatic parameters was considerably reduced and physicochemical factors were the main drivers of microbial structure. Interestingly, we observed a higher soil catabolic activities in the rhizosphere than bulk soil of wheat only in Safi. Our study demonstrates that the wheat functional-based selection on soil microbiota is modulated through a modification of soil edaphic properties which balance the effect of climatic conditions and suggests a greater wheat potential to select catabolically active microbes in its rhizosphere when cultivated in unfavorable conditions.

Keywords: Wheat; rhizosphere effect; PLFA profiling; Catabolic activities; soil pedoclimatic variation; soil microbial biomass

1. Introduction

Soil microbiomes play a key role in several ecosystem functions within agroecosystems, including nutrient cycling, C storage and turnover, soil structure, water retention, plant growth (crop yield and quality), and abiotic stress tolerance (Creamer et al., 2016a; Hartmann and Six, 2023; Maron et al., 2018; Thiele-Bruhn et al., 2020). The diversity and community structure of the soil microbiome are key factors that affect these ecosystem functions (Philippot et al., 2023; Shu et al., 2022). As such, understanding the role that diversity and functions of plant- and soil-associated microbiome have in food production is vital to ensure sustainable food production and contribute to several sustainable development goals (SDG1, 2, 12 and 13).

Abiotic factors influence the development, complexity, and functionality of soil microbial communities. Examples of such abiotic factors include soil organic carbon content (SOC) (Naveed et al., 2016; Pignataro et al., 2012), moisture content (Diatta et al., 2020), pH (Grządziel et al., 2019; Shu et al., 2022), temperature (Yang et al., 2021) and nutrient content (Wang et al., 2018). In addition, biotic factors such as plant rhizosphere interactions (Ndour et al., 2017) and some management strategies like microbial inoculation (Mawarda et al., 2020) could influence microbial community development. At regional scale, several studies have reported an influence of pH, texture and SOC (Diatta et al., 2020; Liu et al., 2015, 2014) as well as climatic factors such as altitude, mean annual temperature (MAT), mean annual precipitation (MAP) in determining the soil microbial community diversity and/or structure (Cui et al., 2019; Pascual et al., 2018; Ren et al., 2021). However, large scale studies of soil microbiota structure and function as well as the role the potential of crops to modulate these soil physicochemical and geographical parameters specificities that drive microbial structure and functions in agroecosystems remain largely underexplored in Africa. Therefore, understanding soil microorganisms' patterns and their abiotic drivers in different pedoclimatic zones may enable the development of agroecological strategies to increase the resilience of food production in response to climate change. Moreover, it is crucial to know the extent to which different crops can modulate the soil physicochemical and microbiological status in variable pedoclimatic contexts to predict their potential for adaptation to climate change.

Morocco is characterized by contrasting climatic zones due to the influence of Sahara Desert on the south and the Mediterranean see on the north, along with a gradient of altitude between the coastal and Atlas Mountains regions where altitude can reach up to 30)00 m. Hence, the country presents an annual rainfall variation ranging from <100 mm to >1000 mm between arid

and favorable regions. Furthermore, crop production is dominated by winter cereals which occupy more than 55% of arable lands, with a predominance of wheat accounting for 75% of cereal cropped surface (Bouras et al., 2020). However, the agricultural sector is threatened by abiotic stresses, predominantly drought, and the subsequent reduced fertility of soil in south arid regions. Climate change is likely to exacerbate these problems as warmer drier seasons are predicted to reduce crop yields (Schilling et al., 2012).

This study evaluates soil microbial community structure (microbial biomass and phospholipid fatty acid profiles) and functions (substrates induced respiration profiles, enzyme activities) associated with bulk and rhizosphere soils sampled in field grown wheat under contrasting pedo-agroclimatic conditions across different regions in Morocco. We hypothesized that (i) wheat could modulate the soil microbial structure and functioning through the root exudation and (ii) the rhizosphere soil physicochemical characteristics and agroclimatic conditions would affect microbial community structure and functioning. Consequently, collected data will help to understand how climatic factors and soil edaphic properties drive soil microbial communities in Moroccan agroecosystems and to determine the potential of wheat to adapt to the changing climate by modulating its associated microbiota.

2. Material and methods

2.1. Soil sampling

Soil sampling was carried out in 16 sites localized in four Moroccan agroclimatic regions between March 16th and March 31st, 2021 **(Fig. 1).** The soils taxonomy were Leptosols, Luvisols, Kastanozems and Calcisols for respectively samples from Beni-Mellal, Meknès, El-Jadida and Safi regions. These environmental conditions were considered as favourable (Béni-Mellal and Meknès MAP > 400 mm), moderate (El-Jadida, 300 mm <MAP<400 mm), and unfavorable (MAP<300 mm) based on mean annual rainfall (MAP) derived from NASA POWER V2.3.1. Concordantly, the monthly rainfall in March 2021 for Safi, El-Jadida, Meknes and Béni-Mellal were 13 mm, 29 mm, 125 mm and 118 mm. In each site 5 transects of 25 m were marked out with a plant and soil sample being taken every 5m. The bulk soil samples as well as plant root samples for each transect were pooled (i.e., for each transect, bulk soil samples were generated from pooling the 5 bulk soil samples; for each transect root samples were pooled). Rhizosphere soils were isolated from root sample mechanically at the laboratory. All soils were sampled to a depth of 15 cm, transported on ice to the laboratory, and sieved (2 mm).

Soil was then either stored at 4°C for catabolic profiling and enzyme activities determinations, freeze-dried for PLFA, or air-dried for physicochemical characterization.

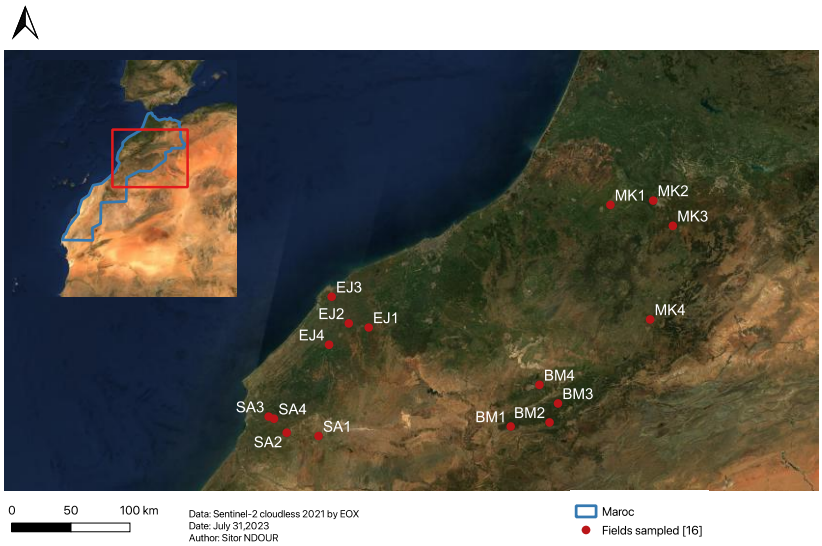


***Figure 1**: Wheat fields sampled across Moroccan territory; SA: Safi, EJ: El-Jadida, BM: Béni-Méllal and MK: Meknes*

2.2. Soil physicochemical and climatic parameters

The soil water content (SWC as %) was determined gravimetrically by oven drying at 105°C for 3 days. Soil pH and electric conductivity were determined using a ratio of 1:5 soil to water in a Seven Excellence Multiparameter Mettler Toledo. Conductivity will be termed EC and expressed in uS/cm. CEC was determined by the cobalt hexamine method according to the ISO 23470 _2018. Soils above pH 6.5 are extracted using calcite-saturated hexamminecobalt (III) chloride. Extractions were analyzed by inductively coupled plasma optical emission spectrometry (ICP-OES) in an Agilent 5900 SVDV (Agilent Technologies, Santa Clara, California, USA). Total carbon (C) was determined by dry combustion (Tiessen et al., 1981) using a Leco TruMac CN Combustion analyser (LECO Corporation, St Joseph, Michigan, USA) and Inorganic C by Inorganic Carbon Analyser- Skalar Primacs (Skalar Analytical BV, Breda, Netherlands). Soil Organic Carbon (SOC) was calculated as the difference between total C and total inorganic C. Total P was extracted by the Aqua Regia method as described in Acquah et al. (2022) and the total elemental concentration determined by ICP-OES. Available P was extracted according to Olsen et al. (1954) and determined by the phospho-molybdenum blue method in a continuous colorimetric flow analysis on a Skalar San++ System (Skalar Analytical BV, Breda, Netherlands). Soil texture analysis by laser diffraction according to

Thomas et al (2021). Soil samples were analysed in a Partica LA-960 (Horiba Ltd, Kyoto, Japan). The percentage of particles assigned to each diameter bin were grouped into the texture categories classed as: clay < 8 µm, silt 8–63 µm, sand > 63–2000 µm. Climatic data (mean annual temperature: MAT and mean annual precipitation: MAP) are derived from the NASA POWER V2.3.1 tool (https://power.larc.nasa.gov/data-access-viewer/) by considering data from 1981 to 2022.

2.3. Microbial biomass

Microbial biomass was estimated using the fumigation-extraction method (Vance et al., 1987). C and N were extracted using K_2SO_4 (0.025 M) and quantified using a TOC-L analyzer (Shimadzu). The microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were amended using K_{EC} correction factor of 0.45 (Wu et al., 1990).

2.4. Multiple Substrate Induced Respiration (MSIR)

The functional capability of soils was determined using the MicroResp^{TM} system (Bao et al., 2015; Campbell et al., 2003). Briefly, 96 well indicator detection plates contained 3% agar, KCl: 16,77 g.L^{-1}, NaOH: 0,315 g.L^{-1} and Cresol red: 18,75 mg. L^{-1}. Substrates (at room temperature) were added to soil (around 0.35 g/well) in the deep-well plates. Substrates included D-glucose, fructose, L-alanine, malic acid, gamma-aminobutyric acid, alpha ketoglutaric acid and citric acid, which were added to the soil at a concentration of 30 mg. g^{-1} H_2O. In addition, water (alone) was added to the soil. The absorbance (570 nm) of detection plates was determined at time zero and after 6 hours incubation (25°C), and CO_2 emissions calculated.

2.6. Phospholipid fatty acids profiling

Phospholipid fatty acid (PLFA) profiles of microbiota were determined using the method of (Frostegard et al., 1993), and modified by (Pawlett et al., 2013) using freeze-dried soils (8g). Briefly, lipids were extracted using chloroform, methanol and citrate buffer at a ratio of 1:2:8 (v/v/v). Phospholipids were fractionated by solid phase extraction, derivatized by mild alkaline methanolysis, and quantified (mol%) by gas chromatography (Agilent Technologies, Santa Clara, California, USA). The PLFA markers 15:0i, 15:0ai, 16:0i, 17:0i, ai17:0 17:0br and 18:0(10Me) were attributed to Gram-positive bacteria (Lewe et al., 2021; Orwin et al., 2018); 16:1ω7c, 18:1ω9c, 18:1ω7t and 18:1 ω 13 to Gram-negative bacteria (Lewe et al., 2021; Zelles, 1997); 14:0, 15:0, 16:0, 18:0 and 20:0 were identified as non-specific PLFA microbial markers

(Joergensen, 2022), 16:1ω5 and 18:2ω6,9 were used as fungal markers (Zhou et al., 2022); 18:0(10Me) for Actinobacteria; 16:1w5 for arbuscular mycorrhizal fungi (AMF) (Joergensen, 2022). The sum of (%) Gram-positive and (%) Gram-negative bacteria was considered as the total (%) of bacterial PLFA.

2.7. Data analysis

Data analysis was performed using R (version 4.3.0). The physico-chemical parameters (pH, EC, SOC, and SWC), and the soil microbial biomass (MBC and MBN) data were subjected to ANOVA to test for the effect of pedoclimatic conditions (*region fator)*. Thereafter, the Tukey pairwise comparison test ($p < 0.05$) was then applied to identify significant differences between regions. The soil *niche* (*rhizosphere vs bulk*) effect was tested in the same data using *paired t.test* ($p < 0.05$). Using *FactoMineR* and *Factoextra* packages, the MicroResp^{TM} and the PLFA data were subjected to Principal Component Analyses (PCA) to compare the catabolic profiles and the microbial community structure of soils from the different regions and the two niches. Permutational analysis of variance (PERMANOVA) were carried out to test for the effect of region and soil niches in catabolic profiles and microbial community structure using the *vegan* package (Oksanen et al., 2022). Redundancy analyses (RDA) were also carried out to test the effect of different environmental parameters (soil physicochemical and climatic data) on the structure of microbial communities assessed by PLFA profilg using “vegan” package in R. Variation partition analyses were performed to assess the contribution of climatic and soil physicochemical variables on soil microbial activities and structure.

3. Results and discussion

3.1. Soils physicochemical data and microbial biomass varied significantly between the different agroclimatic Moroccan regions

The soil water content (SWC) varied significantly between regions, with soils from El-Jadida being the driest, and soils from Béni-Mellal the wettest in both rhizosphere and bulk niches (**Table 1**). Moreover, SWC was greater overall in bulk compared to rhizosphere soils ($p < 0.001$). The pH was lower in soils from Meknes compared to those from Béni-Méllal and El-Jadida for both niches, while SOC were significantly higher in Meknes and Béni-Méllal soils compared to those sampled in Safi and El-Jadida. We also noticed a decreased pH in rhizosphere compared to bulk soils ($p < 0.05$). The electric conductivity (EC) was not affected by the soil niche while it varied significantly between regions in the following order: EC (Safi) > EC (Béni-Mellal) > EC (El-Jadida) > EC (Meknes). MBC and MBN varied significantly between regions in both rhizosphere and bulk soil **(Fig. 2).** Meknes and Béni-Méllal soils had greater MBC and MBN in both soil niches compared to Safi and El-Jadida. In addition, the MBC was greater in rhizosphere soils compared to bulk soils ($p < 0.001$) whereas there was no significant difference of MBN between these two soil niches (**Fig. 2**). Therefore, this reduced microbial biomass observed in the more arid regions could be explained by their lower SOC and SWC, and reduced rainfall as reported in other studies (Liu et al., 2021; Maestre et al., 2015). Similarly, microbial biomass variation across different European biogeographical zones has been correlated with variation in soil organic matter content (Francisco et al., 2016).

Table 1: *pH, electric conductivity (EC), soil organic carbon (SOC) and soil water content (SWC), determined in rhizosphere (rhiz) and bulk soils of wheat sampled in four Moroccan agroclimatic regions. The different letters indicate significant differences between region within each soil niche ($p < 0.05$, Tukey pairwise test). * (p-value < 0.05); *** (p-value <0.001), ns (no significant difference: p-value > 0.05) indicate the paired_t.test results between rhizosphere and bulk soils for each variable.*

Region	Niche	pH	EC (S/m)	SOC (%)	SWC (%)
Safi	Rhiz	8.47 *ab*	599.2 *d*	1.16 *a*	9.24 *b*
El-Jadida	Rhiz	8.67 bc	114.4 *b*	1.41 *ab*	5.64 *a*
Meknes	Rhiz	8.25 *a*	99.02 *a*	1.91 *b*	12.98 *c*
Béni-Méllal	Rhiz	8.77 c	174.3 *c*	1.73 *b*	17.45 *d*
Safi	Bulk	8.50 *a*	562.3 *d*	1.18 *a*	12.36 *b*
El-Jadida	Bulk	8.84 *b*	183.3 *b*	1.07 *a*	8.82 *a*
Meknes	Bulk	8.49 *a*	113.3 *a*	1.78 *b*	15.35 *cd*
Béni-Méllal	Bulk	8.80 *b*	204.5 *c*	1.73 *b*	19.15 *d*
Rhiz vs Bulk		*	*ns*	*ns*	***

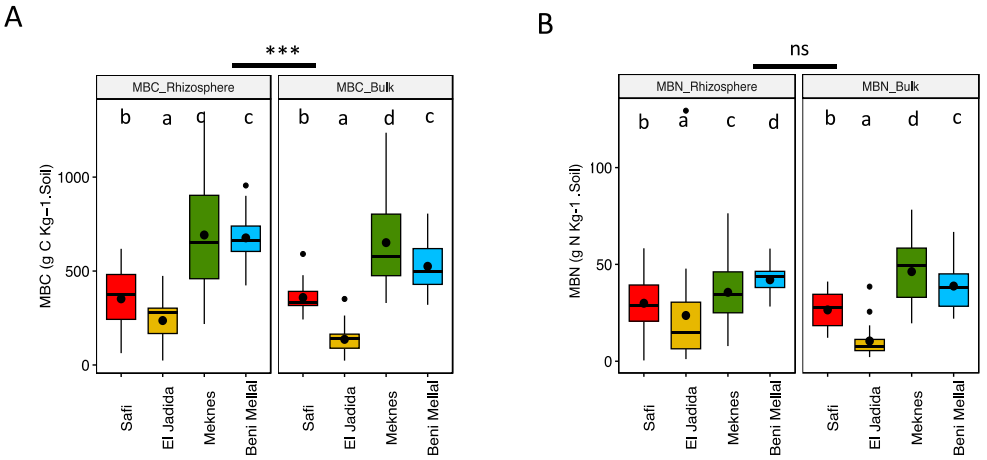


Figure 2**: (A) Microbial biomass carbon (MBC), (B) microbial biomass nitrogen (MBN), measured in rhizosphere and bulk soil sampled in the four agroclimatic regions. The different letters represent significant difference between regions within a soil niche using ANOVA and Tukey pairwise tests ($p < 0.05$). **** indicates significant difference between rhizosphere and bulk soil and **ns** indicates no significant difference.*

3.2. Environmental variations impact soil microbial structure and functioning in different Moroccan regions

Soil PLFA profiling is a relevant indicators which has been successfully used to monitor soil biodiversity patterns across different biogeographical zones in Europe (Lemanceau et al., 2016). In particular, PLFA biomass and specific biomarkers has allowed to distinguish different land use types and biogeographical zones (Francisco et al., 2016). In our study, the projections of the different individuals (soil samples) on the two first axes of the PCAs performed with bulk soils PLFA data showed a total inertia of 43.8% explained by the PC1 and PC2. Along the PC1, the soils sampled in Meknes region are clearly separated from those from El-Jadida (**Fig. 3A**). This difference in microbial structure could be mainly explained by composition in Gram- and Gram+ bacteria as the ratio $Gram^{+}/Gram^{-}$ is significantly higher ($p< 0.05$) in El-Jadida (R = 1.09) compared to Meknes soils (R = 0.62), but also the abundance of *Actinobacteria* and AMF that was higher in Meknes than in Safi (**Fig. S2**). The RDA analysis show significant effect of both soil physicochemical (SOC, texture, CEC, SWC) and environmental variables (MAT, MAP, Altitude) (**Table S1; Fig. 3B**). These results were concordant with numerous report finding an effect of soil physicochemical (pH, soil texture, SOC) and environmental variables (geographical distance, altitude) on the structure of microbial community (Diatta et al., 2020; Liu et al., 2015, 2014; Ren et al., 2021).

For rhizosphere soils, the two first axes explained 41.3 % of the variance. Along the PC1 (dim 1), we noticed clear opposite profiles between rhizosphere soils from Béni-Méllal and those sampled in Safi, meaning that their microbial composition was taxonomically different (**Fig. 3C**). Indeed, we observed a greater Fungi/Bacteria ratio and a higher *Actinobacteria* relative abundance in the rhizosphere soils of Béni-Méllal compared to those of Safi (**Fig. S2**). Furthermore, the RDA analysis showed significant effect for only physicochemical variables (texture, pH, CEC, SWC and EC) (**Table S2**; **Fig. 3D**). Therefore, we can advocate that the wheat root strengthened the influence of physicochemical determinant and this may reduce the role of the climatic parameters.

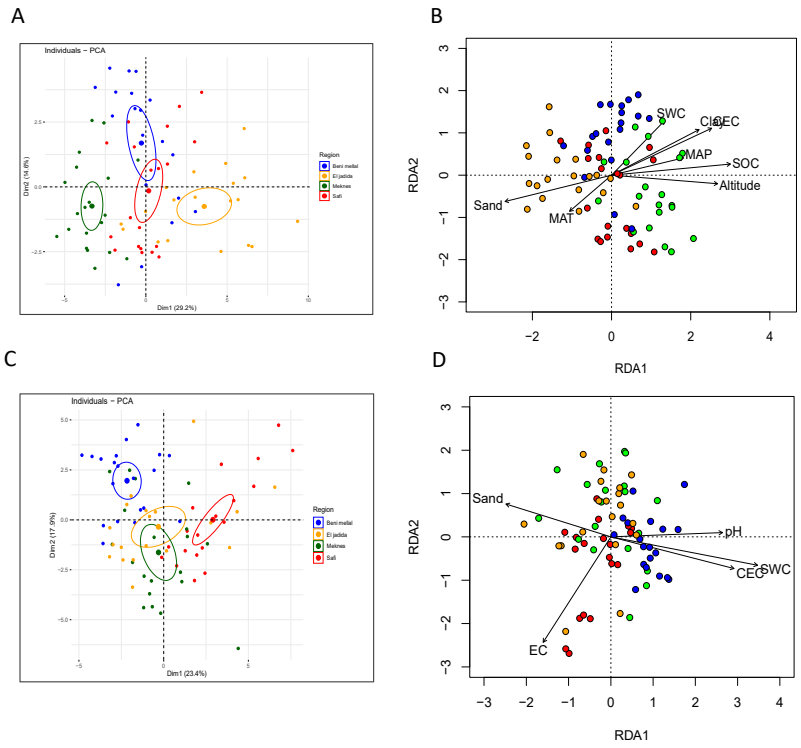


Figure 3: *(A) PCA Ordination and (B) RDA plot of PLFAs of bulk soils. (C) PCA ordination and (D) RDA plot of rhizosphere soils sampled in four Moroccan regions. The ellipses represent confidence intervals and the points in on their center represent the barycenter*

MicreoResp^{TM} was able to detect the variability of soil functioning across Europe and showed that soil microbial activity responded to land use type, soil pH and soil organic carbon variation (Creamer et al., 2016b). Here, the PCAs performed on the multiple substrates induced respiration (MSIR) data obtained from the MicroResp^{TM} assay on bulk soils sampled in the different Moroccan agroclimatic regions showed 77 % cumulative contribution of PC1 and PC2 **(Fig. 4).** Although we observed a positive correlation of glucose, fructose, citric acid, alpha-ketoglutaric acid and malic acid with the PC1 **(Fig. 4A)**, we didn't notice any clear separation

of bulk soils from the different regions along this axis **(Fig. 4B)**. For rhizosphere soils, the PC1 and PC2 explained 76.8% of total inertia and citric acid, fructose, alpha-ketoglutaric acid, malic acid and gamma-aminobutyric acid showed the greatest correlations with PC1 (**Fig. 4C**). Conversely, the projection of individual soil samples in the plan formed by PC1 (dim1) and PC2 (dim2) showed a significant effect of region (PERMANOVA, 23% of variation explained, p= 0.001) notably with rhizosphere soils from Meknes and Safi separated to those from Béni-Mellal on the dim1 of the PCA **(Fig. 4D).** Indeed, higher catabolic potential to mineralize substrates (citric acid, alpha-ketoglutaric acid, malic acid and gamma-aminobutyric acid) was observed in rhizosphere soil from Meknes and Safi compared to those from Béni-Mellal. Therefore, we hypothesize that the higher altitude and the related lower temperatures (MAT) in Béni-Méllal region could explain their lower microbial activities compared to the other regions. Similarly, a shift in soil microbial communities structure along with a decrease in soil enzymatic activities was previously reported along an elevation gradient (Ren et al., 2021). Along the PC2, which was correlated with alanine **(Fig. 4C),** we noticed a separation of rhizosphere soils from Safi (that showed a lower catabolic capacity for this substrate) from those of the three other regions (**Fig. 4D)**.

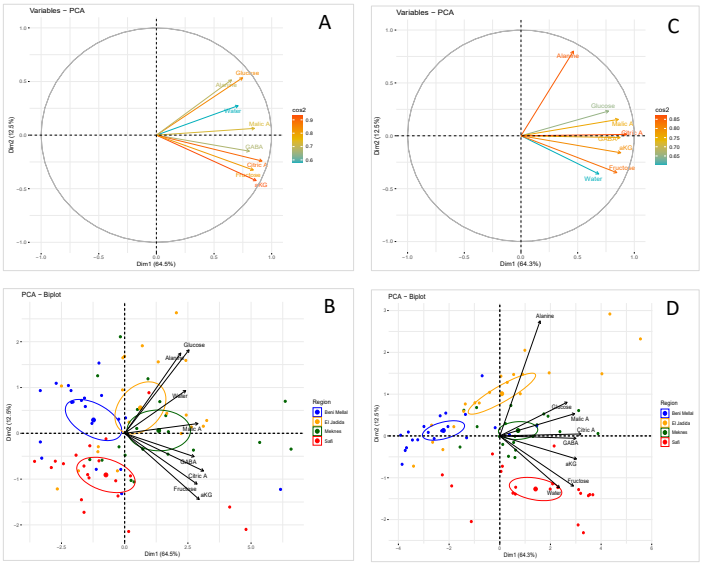


Figure 4*: PCAs of MSIR (MicroResp™) data measured in bulk and rhizosphere soils sampled in the four different regions. A and B: bulk soil; C and D rhizosphere soils*

3.3. Environmental context governs rhizosphere-driven changes in microbial activity rather than in community composition.

Beside the influence of climatic and edaphic parameters, the plant can influence the structure and the functions of soil microbial communities (Pascual et al., 2018). Root exudates which

represent a preferential source of organic carbon for rhizosphere microbiota impact significantly their diversity and activity (Ndour et al., 2022; Sasse et al., 2018; Wang et al., 2022; Zhalnina et al., 2018). Therefore, wheat roots may potentially influence the structure and functions of soil microbiota and the extent of such effect may depend on environmental conditions. Thus, we tested the influence of regions (climatic parameters) on wheat rhizosphere effect on soil microbial structure and functioning.

First, the PCA carried out on each region using PLFA data showed that the profiles of rhizosphere and bulk soils microbial communities are clearly distinct for all four regions (PERMANOVA, p = 0.001) (**Fig. 5 E-H**). This suggests that wheat root exert significant selective pressures on the rhizosphere microbial composition independently of regional pedoclimatic conditions. Such rhizosphere filtering is well-documented in various cropping systems and soil types (Bulgarelli et al., 2013; Philippot et al., 2013), and appears to represent a robust ecological mechanism allowing plants to recruit specific microbial for their growth and defense. However, the PCAs performed using catabolic activities data in rhizosphere and bulk soils for each region taken individually showed contrasting patterns. In Safi, the rhizosphere soils showed higher substrate induced respiration rates than bulk soils and these two niches were clearly separated in the PC1 (PERMANOVA, 30% of variance explained, p = 0.001) (**Fig. 5A**). In contrast, in the three other regions, no clear functional differentiation between rhizosphere and bulk soils was observed as the PCAs ordinations did not show any clear separation between these two niches (PERMANOVA, p> 0.05) (**Fig.5: B-D)**.

These findings suggest that, while structural differentiation of microbial communities between rhizosphere and bulk soil is conserved across environments**,** their translation into soil functioning is plastic and context-dependent (Allison and Martiny, 2008; Strickland et al., 2009). Several factors could explain this functional variability. First**,** soil resources availability**,** especially labile carbon inputs and nutrient levels can modulate microbial metabolic responses to root exudates (de Graaff et al., 2010). In addition, soil water potential could also have an indirectly effect on this rhizosphere effect on soil functioning through a modulation of soil organic carbon (SOC) flux. Indeed, Li et al. (2022) showed a greater rhizosphere effect on SOC content in desert area compared to more a humid area. Safi soils likely offers favorable physicochemical conditions (e.g., texture, moisture, nutrient availability) for microbial responsiveness to rhizodeposits. Indeed, Safi soils was characterized by lower SOC, SWC and MBC and a higher EC compared to the three other regions. This low fertility conditions may constrain microbes to mineralize more rapidly fresh and easily assimilable C provided by plant

roots. Concordantly, it was previously reported that soil with low SOM showed a faster microbial turnover and a higher decomposition of rhizodeposited C (*i.e.* assimilation by rhizosphere microbiota) compared to soils with higher SOM content (Zhu et al., 2017). Furthermore, Safi is an arid region characterized by a very low MAP (<300 mm). Importantly, a recent study have found that the positive effect of tomato root exudates on soil microbial and fungal catabolic activities was higher in water deficit compared to well-watered treatment (Le Gall et al., 2021). This suggests that the water scarcity in Safi may contribute to a greater responsiveness of soil microbiota and then to a greater effect of wheat root exudate on soil catabolic activities.

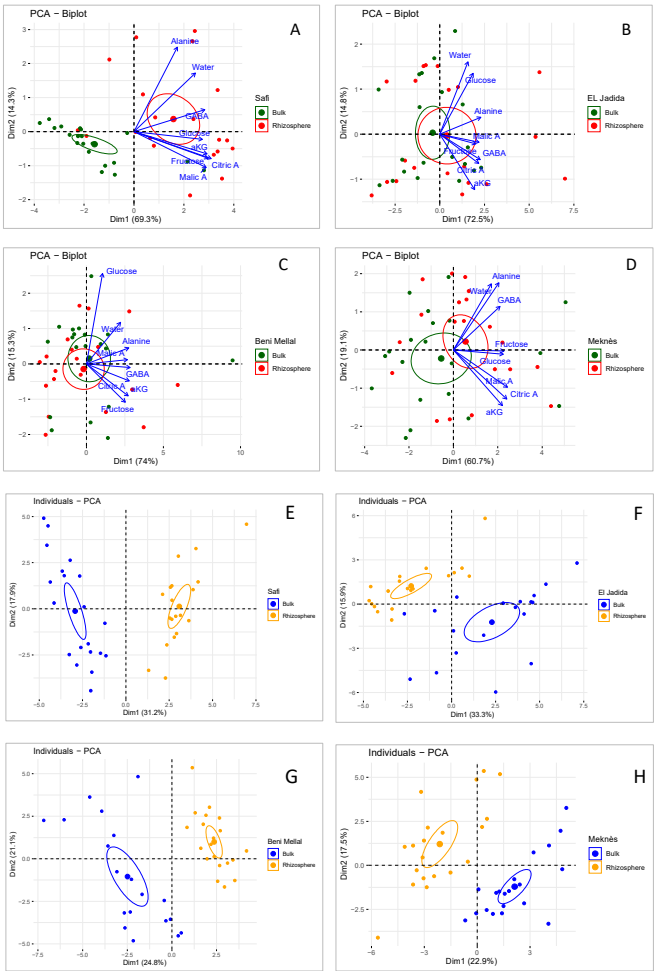


Figure 5*: PCA of Microresp and PLFA data comparing rhizosphere to bulk soils for each region taken solely. A: Safi, B: El-Jadida, C: Béni-Méllal and D: Meknes for MicroResp™. E: Safi, F: El-Jadida, G: Béni-Méllal and H: Meknes for PLFA. The ellipses represent confidence intervals and the points in their center represent the barycenters.*

3.4. The contribution of physicochemical and climatic variables on soil microbial structure and activities across the different regions

The variance partition analysis showed that soil physicochemical variables account for 6% in catabolic activities variance in bulk soils (**Fig. 6C**) whereas in rhizosphere soils, they explained 36% of the total variance (**Fig. 6D**). The influence of climatic variables on soil activities was very low (1% in bulk soils and 3% in the rhizosphere). For microbial structure, climatic variables were more determinant in bulk than in rhizosphere soils (5 vs 2%) whereas physicochemical variables were more important in rhizosphere than in bulk soils (24 vs 15%). These results were concordant with the strong influence of physicochemical variables on microbial community structure we observed in the RDA we carried out on PLFA data. Therefore, microbial composition and catabolic activities are likely influenced by wheat root exudation which has modulated the soil physicochemical parameters and this likely has lowered the effect of climatic variables in the rhizosphere. Concordantly the significant decrease of soil pH in rhizosphere compared to bulk soils supported this hypothesis as root exudate from wheat include a large quantity of compound (i.e., amino acids, polyalcohols and organic acids) with pH-decreasing effect (Iannucci et al., 2021). However, in our study, we did not observe a significant increase in SOC content in rhizosphere soils. A such result is not surprising as root exudates are reported to be rapidly metabolized by soil microorganisms for their energy and biomass (Bernard et al., 2007; Haichar et al., 2016). Importantly, we evidenced in our study an increase of MBC in rhizosphere compared to bulk soils which suggested that the C rhizodeposited was likely used by microbial communities for their metabolism (**Fig. 2A**).

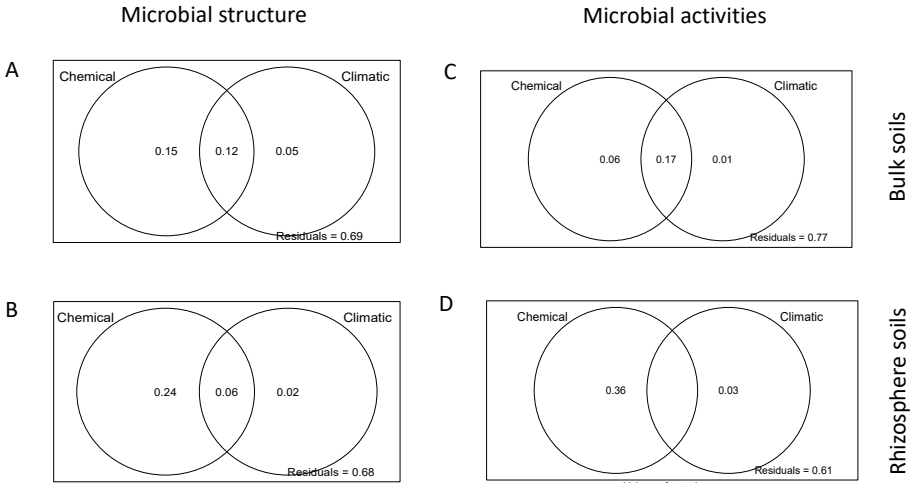


Figure 6*: Variation partition analyses showing the contribution of physicochemical (pH, CEC, EC, SWC, SOC, N, P, Silt, Clay and Sand content) and climatic variables (altitude, MAP, MAT) on the structure and the catabolic activities of microbial communities in bulk and rhizosphere soils.*

4. Conclusion

Our study investigated the influence of variable edaphic and climatic parameters on soil microbial abundance, structure and catabolic activities in rhizosphere and bulk soils of wheat in northern Morocco. The soil microbial biomass did not show clear relationships with microbial functioning as the favorable regions (Meknes and Béni-Mellal) with higher microbial biomass did not necessarily exhibit greater soil catabolic activities. Soil edaphic properties were the main drivers of microbial structure in bulk soils, followed by climatic variables (MAP, MAT, altitude). In the wheat rhizosphere, the physicochemical variables remain determinant whereas the influence of climatic factors were considerably reduced. The catabolic activities were mainly driven by soil physicochemical variable with an increased effect observed in the rhizosphere soils, suggesting a strong influence of wheat root on soil edaphic properties. Moreover, our study demonstrated that the rhizosphere effect of wheat on soil catabolic activities was greater in the unfavorable region (Safi with the lower MAP and SWC and the higher MAT) compared to Béni-Méllal (more favorable one) indicating a potential of wheat for the selecting resilient microbial species that can ensure soil agronomic functions (i.e., organic matter decomposition and nutrients recycling) with abiotic stress. Moreover, it suggests that the wheat functional-based selection of soil microbiota is modulated through modification of soil edaphic properties which could reduce the negative effect of harsh climatic conditions.

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Table S1: Permutation test for the evaluation of the environmental variables on bulk soils microbial structure

	Df	Sum Of Sqs	R2	F	Pr(>F)	Signif
SOC	1	0.11	0.16	18.88	0.001	***
Sand	1	0.05	0.07	8.22	0.002	**
CEC	1	0.03	0.04	4.64	0.002	**
Altitude	1	0.04	0.05	6.39	0.001	***
Clay	1	0.02	0.03	3.49	0.009	**
MAP	1	0.01	0.02	2.44	0.045	*
SWC	1	0.02	0.02	2.67	0.019	*
MAT	1	0.02	0.03	3.75	0.006	**
Residual	69	0.39	0.58			
Total	77	0.68	1.00			

Table S2: Permutation test for the evaluation of the environmental variables on rhizosphere soils microbial structure

	Df	Sum Of Sqs	R2	F	Pr(>F)	Signif
SWC	1	0.05	0.12	12.66	0.001	***
CEC	1	0.01	0.03	3.28	0.003	**
EC	1	0.03	0.06	6.12	0.001	***
pH	1	0.02	0.05	4.88	0.001	***
Sand	1	0.02	0.04	3.76	0.004	**
Residual	72	0.30	0.70			
Total	77	0.42	1.00			

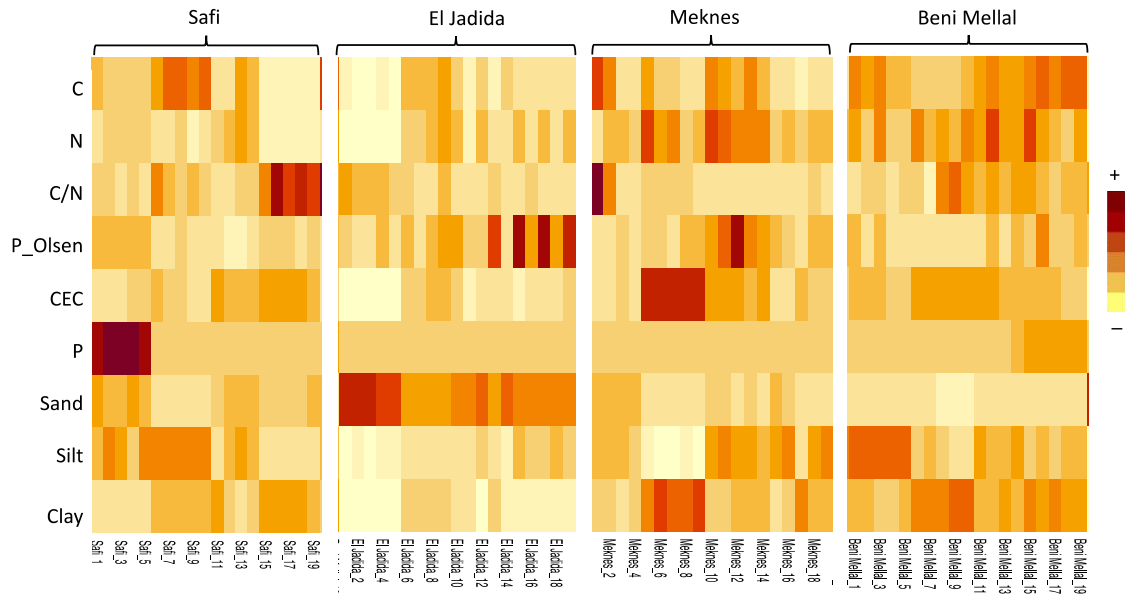


Figure S1: Heatmap of soil physicochemical characteristic in bulk soils sampled in the four regions

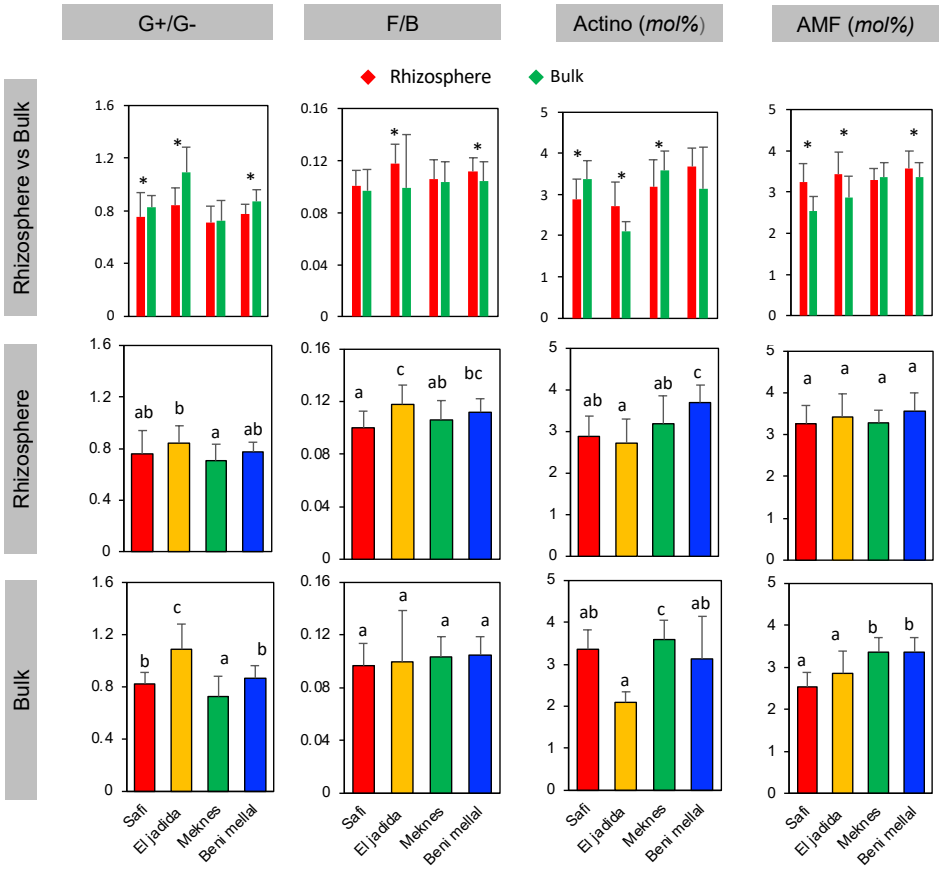


Figure S2: Rhizosphere and bulk soils PLFA biomarkers. Bars on the histograms represent the standard deviations. The (*) represent significant differences between rhizosphere and bulk soils within each region using the Kruskal-Wallis's test ($p < 0.05$). The different letters represent significant difference between regions using the Kruskal-Wallis's test coupled with Wilcoxon pairwise tests ($p < 0.05$).

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