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ORIGINAL PAPER

Quantifying the Respiratory Pattern of Rhizosphere Microbial Communities in Healthy and Diseased Tomato Plants Using Carbon Substrates

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Abstract

The sustainable production of tomatoes (*Solanum lycopersicum*) is important, and this can be achieved by determining the rate of respiration of microbes in the tomato plants' rhizosphere soil. This study aimed at the potential of microbes to utilize carbon substrates embedded in the rhizosphere soil thereby contributing to the healthy nature of the tomato plants. The potential soil physiochemical features and utilization of carbon substrate by soil microorganisms as a result of their respiration to reveal their functions in the ecosystem were evaluated. The soil samples were amassed from the healthy tomato plant rhizosphere, diseased tomatoes, and bulk soil in this study. The physiochemical features and carbon substrate utilization in the bulk soil samples, and rhizosphere samples of powdery diseased, and healthy tomato plants were assessed. The MicroRespTM procedure was used to determine the community-level physiological profiles (CLPP) employing fifteen (15) carbon (C) substrates selected based on their importance to microbial communities embedded in the soil samples. Our results revealed that various physiochemical properties, moisture content, water retention, and C substrates including sugar, amino acid, and carboxylic acid were greater in HR and the substrates were not significantly different ($p < 0.05$). The study reveals higher soil respiration in HR as a result of the microbial communities inhabiting HR utilizing more of the C-substrates. This investigation contributes to the tomato plant's healthy state as the microbial communities utilized carbon substrate compared to DR after employing the CLPP assays.

Keywords Carbon substrates · Community-level physiological profiles · MicroRespTM · *Solanum lycopersicum* · Sustainable agriculture

Abbreviations

BR	Bulk soil
CCA	Canonical correspondence analysis
CLPP	Community-level physiological profiles
DR	Diseased tomato plant rhizosphere
EUF	Electro-ultrafiltration
F	Filtered water
HR	Healthy tomato plant rhizosphere
MC	Moisture content
PPO	Polyphenol oxidase
SOM	Soil organic matter
WR	Water retention

Core ideas Physiochemical features of soil
Soil moisture content and water retention
Sequestration of carbon substrate

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1 Introduction

Crop growth and development are dependent on the nature of the soil employed for planting (Amare and Desta 2021; Lal et al. 2021; Omotayo and Babalola 2021). Over the years, crop production has increased tremendously with much importance in the feeding of humans and animals globally, alongside eradicating hunger (Adedayo et al. 2022a). Various challenges have been observed in the soil as the population of humans and animals increases, thereby causing the soil to lose its fertility. Biodiversity loss and soil degradation result from substantial changes observed in the soil (Hojjati et al. 2021; Qiu et al. 2021). The exudates produced by the plant root are the major constituents controlling

the existence of microorganisms dwelling in the rhizosphere soil (Badri et al. 2013; Chaparro et al. 2014; Savarese et al. 2022). Some studies have revealed how beneficial microbial communities were inhabited by natural disease rhizosphere soils (Ge et al. 2021; Noman et al. 2021; Zhao et al. 2021) and found their way into the soil via the root exudates thereby acting against phytopathogens in the soil. The populations of the microbial communities in these disease soils are not as much as in healthy rhizosphere soil which is why the microorganisms living in the healthy rhizosphere (HR) consumed carbon (C) substrates more than the microorganisms in the diseased rhizosphere (DR) (Wang et al. 2019).

Tomato (*Solanum lycopersicum* L.) is one of the essential fruits around the world consumed by humans because it contains important carotene, lycopene, vitamins, and minerals (Dorais et al. 2008). The cultivation of tomatoes and other crop plants has added more value to the soil used for agricultural purposes. Microbes living in the rhizosphere of tomato crops carry out an important function in soil structure formation, transformation, and decomposition of various organic compounds likewise removal of toxic compounds (Adedayo et al. 2022b; Ling et al. 2022). The microbes colonizing the soil can gather some compounds, alleviate the nutrient assimilation in plants through root hairs, improve plant growth, and improve defense processes and stress tolerance against biotic and abiotic factors (Dukare et al. 2022).

Carbon sequestration and nutrient cycling are major functions obtained in the soil that help maintain the balance of the sustainable ecosystem (Amoo et al. 2021a; Raj and Jhariya 2021; Zhao and Wu 2021). However, the decomposition of wastes, the profile of microbial functionality, and the cycling of nutrients required more knowledge as a result of soil usage for plantations. C cycling is one of the prominent functions carried out by the microbial communities in the ecosystem (Holmberg et al. 2019; Li et al. 2021a). Luo et al. (2022) indicated that the carbon found in the terrestrial biosphere is made of organic carbon. In a functioning ecosystem, the important function of soil organic matter (SOM) is to retain nutrients, stabilize soil structure, and preserve water-holding capacity (Amoo et al. 2021b). SOM decomposition enables the production of nutritive substances required for adequate plant development (Cardenas et al. 2021). Plants are known to be producers in the feeding hierarchy in the ecosystem which makes them special from other ecobiomes. Tomato plants have been reported by Li et al. (2022) to alter the quantity of C assimilated into the soil which may be prone to unfavorable effects on soil carbon in the atmosphere. As a result, the knowledge of soil C response accelerates the ability of microbes embedded in the soil to break down various C sources to acknowledge the specific changes observed in the soil (Amoo et al. 2021b). The high level of C substrate in soils contributes to a significant improvement in the diversity and functions of microbial communities in agricultural ecosystems, thereby enhancing sustainable agriculture (Adedayo et al. 2022a; Kaul et al. 2021). C source carries out functions like nutrient cycling and its availability to crop plants in rhizosphere soil (Kaul et al. 2021). Plants derive benefit from the microbial community activity in the rhizosphere soil when they assimilate C source as a nutrient, enhance microbe phytohormones regulation, inhibit the proliferation of spoilage organisms, and thus enhance plant health (Bogati and Walczak 2022).

The physicochemical features of the soil samples can control the associations between the microbial communities and the plants. The distribution of microbial species in the soil is associated with various soil properties like pH, organic carbon, ions (Mg^+, K^+, Ca^{2+}), and nitrogen concentration, among others (Li et al. 2021b). The role of the microbiome in the soil is their potential to respire in soil with certain C substrates that differ structurally to produce community-level physiological profiling (CLPP). The procedure of measuring the substrate required by the microbes in the soil is conducted by employing the CLPP assay (Nwachukwu et al. 2021).

Previous studies have reported the effect of the microbial communities and their functional diversity in the root region soil of tomatoes employing 16 s ribosomal RNA (16S rRNA) gene amplicon sequencing (Hu et al. 2020; Li et al. 2014), internal transcribed spacer (ITS) (Li et al. 2014; Wei et al. 2021), and shotgun metagenomic sequencing among others (Adedayo et al. 2022a, b). The results obtained in these previous studies revealed differences in taxonomical (that revealed the existence and abundance of the microbial communities including Actinobacteria, Planctomycetes, Chloroflexi, Cyanobacteria, Proteobacteria, Ntrospirae, Verrucomicrobia, Deinococcus-Thermus) in Supplementary Fig. 1 and functional diversity (Carbohydrates, Cell Division and Cell Cycle, Cofactors, Vitamins, Prosthetic Groups, Pigments, Fatty Acids, Lipids, Dormancy, and Sporulation, Isoprenoids, Miscellaneous, Nucleosides, and Nucleotides, Clustering-based subsystems, Stress Response, Cell Wall and Capsule, Nitrogen Metabolism, Regulation and Cell signaling, Motility and Chemotaxis, Potassium metabolism, and Photosynthesis) in the rhizosphere (Supplementary Fig. 2), but these studies have not reported respiration profile based as a specific function of improving the healthy status of the tomato plant. Although few reports have shown how microbiomes inhabiting soil consume C substrate for catabolic activity (Hamilton et al. 2021; Lu et al. 2016; Wolińska et al. 2020), yet, no distinct differences in the sequestration of carbon were observed by microbial communities in the soils. So, the multifarious dynamic that controls the microbial communities, their impact, and other functions involving C sequestration is not fully understood. Microbial communities revealed their impact on how to utilize C substrates inhabiting the rhizosphere soil of healthy

plants, in order to prevent the existence of negative factors as a result of C feedback (Amoo and Babalola 2019; Amoo et al. 2021b).

MicroResp assay has been employed in this study to differentiate between soil samples in a controlled laboratory environment. It helps to determine soil health, quality, and community-level physiological profiles. This assay considers quantifying microbial respiration through C sources to the point where the microbial population assimilated the C substrates (Enagbonma et al. 2021). This technique is employed to determine the entire soil community-level physiological profiles independent of the microbial population multiplication. Its application in various studies has proven its validity in other procedures (Amoo et al. 2021b; Enagbonma et al. 2021). The study however aimed to evaluate the ability of the rhizosphere microorganisms in the soil samples to utilize C substrates and we speculated that the microbes in HR will carry out higher catabolism by utilizing more C substrates compared to DR and BR.

2 Methodology

2.1 Experimental Location and Sampling

This study was investigated at the North-West University farm (Mmabatho, South Africa) (coordinates 25°47′19.1″S, 25°37′05.1″E; 25°47′17.0″S, 25°37′03.2″; 26°019′36.9″S, 26°053′19.0″E, altitude 159 m above sea level). Little rainfall of about 300 to 600 mm is often experienced with thunderstorms annually in the northwest region of South Africa between August and April summer. The region has a degree of hotness and coldness ranges between 20 and 40 °C. The temperature falls drastically during the winter to 5 °C or less and is experienced between the early months of May and July.

The Roma tomato variety (*S. lycopersicum* cv Roma VF) has been cultivated for more than six years, and soil has been managed with traditional nitrogen, phosphorus, and potassium (NPK) fertilization. The plantation of the tomato commenced in November 2020. From three plots, bulk and rhizosphere soil samples of tomatoes were collected in three replicates for HR, DR, and BR from an open field in March 2021. The portion of the first site was healthy tomatoes. On the second plot was a diseased tomato (powdery mildew) with the following features: yellow spots on the leaves followed by powdery nature on leaves and stems. The third region of the farmland was regarded as the bulk soil with no tomato plantation. The healthy and diseased plots were 40 m distant from each other, and the bulk plot was 50 m distant from the other plots.

The HR and DR were obtained after soil samples were collected from five different healthy and diseased tomato plants which were pooled together to produce a replicate. So, 3 replicates were produced from 15 tomato healthy and diseased plant rhizosphere soils after being pooled together. However, the same procedure was done for bulk soil too. In March 2021, the soil sampling was conducted, before the harvest season. A sterilized soil auger was employed for the collection of the soil samples around the roots of the plants. The soils were dug to a depth of 4–15 cm deep and were packed into sterile polythene sampling bags. The soil adhering to the roots was also jolted and collected into the plastic bag. The soil samples were kept at − 4 °C in cold boxes and conveyed to the cold room where they were kept at − 20 °C.

2.2 Physiochemical Properties of Soil Samples

The physical and chemical concepts of the tomato rhizosphere and bulk soils obtained were evaluated following standard procedures. Using a pH meter, the soil pH was quantified in the ratio of 1:2.5 (soil:water) while the total carbon was measured by the dry combustion procedure (Santi et al. 2006). Nitrogen forms in soils including nitrate and ammonium were confirmed by the potassium chloride (KCl) extraction method as reported by Bremner and Keeney (1966). Following the method of Mebius (1960), organic carbon was measured. Calcium, magnesium, and potassium ions are determined by the electro-ultrafiltration (EUF) procedure (Di Meo et al. 2003). The sulfur content of the soil samples was determined as explained by Kotkova et al. (2008). Following the method of Tandon et al. (1968), phosphorus was determined from the soil samples by applying an acid-free vanadate-molybdate reagent for spectrophotometry analysis. Soil organic matter was evaluated following the method of Terefe et al. (2008). Soil samples were subjected to high temperatures (100 °C) to reduce organic content in the soil. The temperature controls evapotranspiration, which impacts the water content of the soil, which is attributed degradation of soil organic matter (Davidson et al. 2000).

2.3 Community-Level Physiological Profile

The moisture content of the soil samples was observed to range from 30 to 60% according to the standard MicroResp method as reported by Campbell et al. (2003). For 7 days, the soil samples were incubated at − 20 °C so that the microorganisms in the soil could accumulate after sieving with a 5-mm sieve (Creamer et al. 2016). Some of the soil samples that contained more than 60% moisture content were air-dried in an incubator above 40 °C for 24 h until their moisture content ranged between 30 and 60% as explained in the MicroResp manual (Renault et al. 2013). The method of Benke and Kearfott

(1999) was used to detect the moisture content of soil samples after oven-drying them above 100 °C.

MC moisture content
X the weight of the soil sample before incubation
R the weight of the soil sample after incubation

$$MC = \frac{X - R}{X} \times 100 \quad (1)$$

Water retention (WR) also known as water holding capacity is the ability of the soil samples to hold the amount of water when saturated employing a suitable soil handling method to regulate the moisture content of the soil. In this study, the soil samples used were measured (25 g) and added to filter paper in the funnel. Fifty milliliters of distilled water was added (volume of water used) and allowed to stand for 20 min. The filtered water (F) was measured with the aid of a calibrated measuring cylinder, and the water retention capacity was calculated using the standard (OECD) method for soil water retention capacity as explained by Jakob et al. (2012) used in the study.

The standard MicroResp procedure was conducted by measuring 0.4 g of the soil samples with the calibrated weighing balance and adding them into 96 deep well plates. The deep well plates were covered with Parafilm and incubated in a dark cupboard for 3–5 days. After incubation days, 15 carbon sources were employed to assess the physiological activities together with a control well that contained the soil samples and distilled $H_2O_{(l)}$. These substrates employed in the study comprised 4 carbohydrates that include (glucose, lactose, galactose, and maltose), and 5 amino acids (glycine, L-cysteine, L-arginine, L-lysine, and methionine), 5 carboxylic acids that comprise (citric acid, D-malic acid, oxalic acid, pantothenic acid, and salicylic acid), alcohol (mannitol), and distilled water. The weight of the salts required for each soil is calculated as shown below:

W the weight of soil required
MC moisture content
WS the weight of the soil in 96 deep well = 0.4
K constant = 30

$$W = MC \times WS \times K = MC \times 0.4 \times 30 \quad (2)$$

After obtaining the salt required, 25 mL of distilled $H_20_{(l)}$ was added to dissolve the different carbon sources. From the solution of the carbon salts obtained, 25 µL of the solution is added into the deep wells containing 0.4 g of soil samples with the aid of a micropipette.

Colorimetric gel detection plates were prepared as follows: 3 g of agar was measured into a 200-mL conical flask, and 100 mL of distilled H_2O was added. The solution was shaken to dissolve undissolved agar powder and further heated in an oven for some minutes. Cresol red (18.75 mg), 0.315 g $Na(HCO_3)_2$, and 16.7 g KCl were dissolved in 1 L of distilled $H_2O_{(l)}$ to prepare an indicator solution. One hundred milliliters of the agar solution prepared was added to 200 mL of indicator prepared in the water bath at 60 °C at a ratio of 1:2. With the aid of an 8-channel micropipette, 25 µl aliquots were dispensed into a 96-well detection plate of 1.2 mL deep. The dispensed aliquots were allowed to solidify, and the detection plates were kept in a desiccator for 2 days before being used in a dark cupboard. The initial reading of the prepared detection plates at 0 h was measured on the MicroResp™ machine at wavelength 570 nm. It was noted that the initial reading should not exceed 5% after measuring the reading result on the Excel sheet package. This procedure was explained according to the MicroResp manual (Renault et al. 2013).

After the initial reading has been checked, the detection plate is assembled with the 96-deep well and incubated at 25 °C for 6 h. MicroResp™ microplate was employed again to check the final reading according to the manufacturer's guide (AccuReader M965 + , Taipei, Taiwan) after 6 h of incubation at 570 nm to obtain the absorbance figures. The percentage CO_2 and CO_2 rate were determined according to the equation below as used by Amoo et al. (2021b).

$$\%CO_2 = \frac{A + B}{1 + D} \times Ai \quad (3)$$

where $A = -0.2265$, $B = -1.606$, Ai = normalized absorbance data, and $D = -6.771$ according to the standard MicroResp manual.

$$CO_2 \text{rate} = \left\{ \frac{(\%CO_2/100) \times \text{vol} \times (44/22.4) \times (273/\text{T} + 273) \times (12/44)}{\text{soilfrhwt} \times (\text{soil\%drywt}/100)} \right\}/t \quad (4)$$

$\%CO_2$ percentage of carbon dioxide (%).
CO_2 rate carbodioxide rate (µg CO_2-cg^{-1} h^{-1}).
vol volume in the well (µL).
frh wt fresh weight of soil in the well (g).
dry wt % soil sample dry weight.
t incubation time.

2.4 Statistical Analyses

The mean value and standard error obtained in the properties of the soil and C substrate were worked out with Univariate analysis of variance (ANOVA). In the 96-well deep-well plate, the soil samples were replicated three times after adding different carbon sources, so that the mean of the three replicates of the samples was obtained and further employed for statistical analysis to confirm the significant differences ($p < 0.05$). The significance ($p < 0.05$) was tested employing Duncan's multiple range test employing IBM SPSS statistics software 27. Canonical correspondence analysis (CCA)

on CANOCO 5 (Microcomputer Power, Ithaca, NY) was adopted to compare the CLPPs among the soil sample properties and the ability to utilize the carbon source. Catabolic diversity was determined by investigating microbial functions after the addition of carbon sources (Brolsma et al. 2017; Enagbonma et al. 2021).

3 Result

3.1 Physiochemical Parameter of the Soil Samples

Changes observed in the soil samples are accompanied by physiochemical properties of the soil samples that include moisture content, soil organic matter (SOM), potassium (K), magnesium (Mg), phosphorus (P), nitrate (NO_3), and pH that may have certain effects on the soil as the result of carbon sequestration and nutrient cycling (Yin et al. 2014). Physiological profile modifications of the microbes embedded in the used soil samples were determined and presented as observed in Table 1. The depleted potential to utilize C sources can lead to depleted carbon sequestration with certain effects on the advancement of the planet's temperature change or global warming (Jiang et al. 2017). Various changes occurring in soil properties are usually associated with reduced functions in the soil. The rhizosphere and bulk soil employed in this study's physiochemical attributes were determined. The soil sample texture was sandy-loam in nature, which made the soils have high porosity and infiltration (Mortazavizadeh et al. 2022). The soil physicochemical analysis reveals that the soil pH, total C, organic carbon, organic matter, potassium ammonium, and soil nitrate were significantly different across the tomato rhizosphere soil samples and bulk soil as observed in Table 1.

3.2 Moisture Content and Water Retention

The result obtained for moisture content and water retention capacity of the soil samples (HR, DR, and BR) showed that HR has the highest moisture content as well as water retention capacity then DR and BR in order of HR > DR > BR. From the employed soil samples (HR, DR, and BR), the initial weight was measured before incubating the soil in the incubator. After incubation, the final weight was measured. The moisture content was obtained in percentage. The volume of distilled water obtained after the filtration method, and the percentage of water retention obtained as observed in Table 2. This study revealed that HR has the highest water retention compared to DR and BR. This shows the ability of HR to absorb water for crop plant consumption to improve the growth of the plants.

The data present the mean ± standard error. "HR" denotes the rhizosphere soil of a healthy tomato plant;

Table 1 Physiochemical properties of the soil samples (Olowe et al. 2023)

Soil sample	pH (H_2O)	SO_4^{2-}(mg kg^{-1})	Org. C (%)	Total C (%)	P (mg kg^{-1})	K (mg kg^{-1})	Mg (mg kg^{-1})	Total N(%)	NNO_3(mg kg^{-1})	NNH_4(mg kg^{-1})
HR	6.72 ± 0.12^{b}	8.38 ± 0.01^{c}	2.1 ± 0.02^{a}	2.17 ± 0.05^{a}	58 ± 0.02^{b}	900 ± 5.77^{a}	714 ± 3.46^{a}	0.1 ± 0.003^{b}	27.87 ± 0.02^{a}	6.27 ± 0.07^{b}
DR	7.58 ± 0.06^{a}	13.3 ± 0.06^{b}	1.1 ± 0.07^{c}	1.15 ± 0.04^{b}	7.16 ± 0.03^{c}	422 ± 4.33^{c}	389 ± 6.06^{c}	0.1 ± 0.003^{b}	12.84 ± 0.06^{b}	10.58 ± 0.09^{a}
BR	7.85 ± 0.04^{a}	16.6 ± 0.11^{a}	1.2 ± 0.03^{b}	1.28 ± 0.02^{b}	115.3 ± 0.5^{a}	779 ± 5.81^{b}	435 ± 8.14^{b}	0.26 ± 0.04^{a}	26.22 ± 1.04^{a}	4.84 ± 0.05^{c}

The data present the mean ± standard error. "HR" denotes rhizosphere soil of healthy tomato plant; "DR" denotes rhizosphere of the diseased plant; and "BR" is the bulk soil. According to Duncan's multiple range test ($n = 3$), values that have common letters are not different significantly ($p > 0.05$)

"DR" denotes the rhizosphere of the diseased plant; and "BR" is the bulk soil.

3.3 CLPP of Microorganisms—MicroPlate™

This study revealed consistent responses of C cycling in the HR, DR, and BR. Fifteen carbon substrates and distilled water were employed in the study to assess the activity of soil microbiomes in utilizing these substrates (Figs. 1, 2, and 3). The analyses of CLPP were observed from microbial respiration responses to the substrates. The microorganisms in HR were observed to consume the substrate in abundance unlike those in DR and BR. The substrate consumption is significantly higher in HR (p-values > 0.05) in the order HR > DR > BR with the following listed substrates: glucose, lactose, maltose, glycine, methionine, lysine, malic acid, citric acid, cysteine, oxalic acid, and salicylic acid. The substrates observed to be consumed higher in DR are galactose, arginine, and mannitol. However, pantothenic acid and distilled water were observed to be significantly higher in BR as shown in Supplementary Table 1.

3.4 The Soil Properties and Microbial Communities' Potential

CCA, as used in this study, revealed that total N, org C, Mg, K, N-NO_3, and P positively correlated with most of the C substrates that include glucose, maltose, lactose, glycine, lysine, methionine, cysteine, malic acid, salicylic acid, citric acid, and oxalic acid (Fig. 4; Table 1). N-NH_4, pH, total C, and SO_4^{2-} negatively correlated with galactose, arginine, mannitol, and distill H_2O, while pantothenic acid was abundant in DR and BR sites (Fig. 4; Table 1). The effect properties of the soil on the physiological potential of the microorganisms were unveiled by employing CCA as observed in Fig. 4. The association among various environmental

Table 2 Quantification of moisture content and water retention of the soil samples (Doerr and Thomas 2000)

Soil samples	Initial weight (g)	Final weight (g)	Moisture content (%)	Vol. of used distl H_2O (mL)	Vol. of obtained distl. H_2O (mL)	Water retention (%)
HR	5.043 ± 0.010	3.267 ± 0.13	35.2 ± 2.57	50.0 ± 0.0	36.0 ± 1.16	56.0 ± 4.62
DR	5.056 ± 0.004	3.421 ± 0.05	32.23 ± 0.95	50.0 ± 0.0	36.67 ± 0.88	53.33 ± 3.53
BR	5.049 ± 0.011	3.453 ± 0.05	31.68 ± 0.99	50.0 ± 0.0	35.67 ± 1.45	46.0 ± 6.43

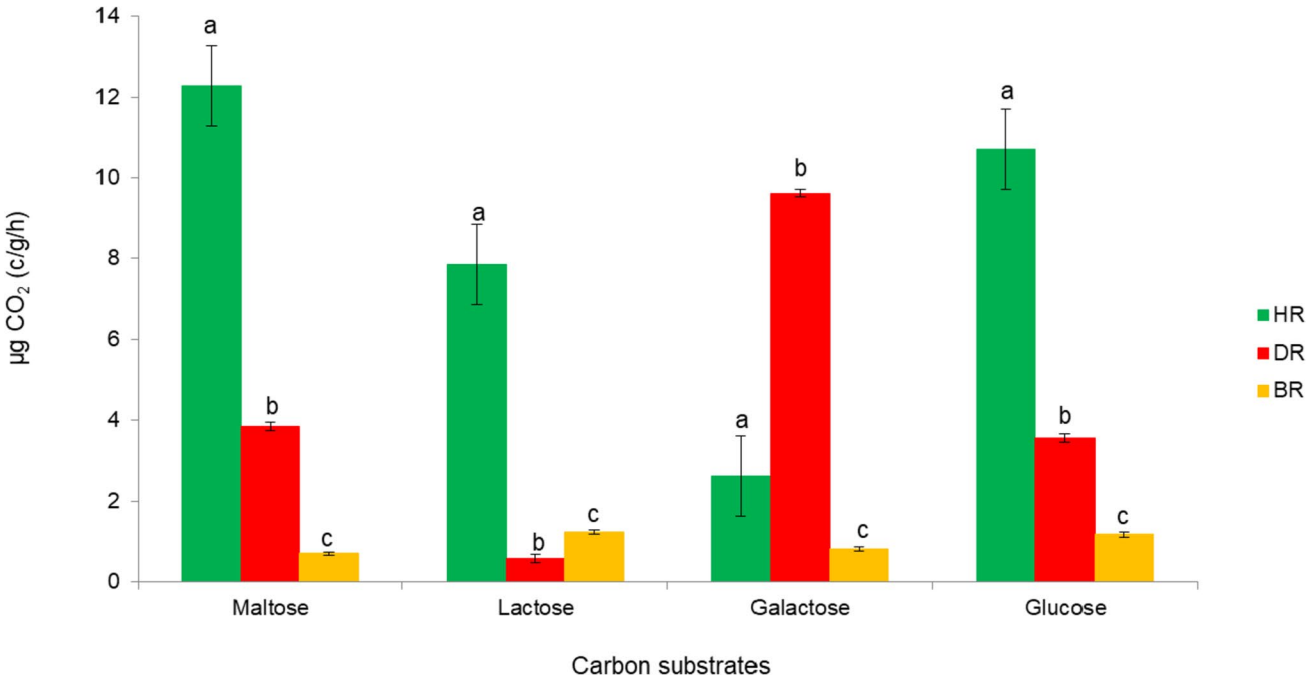

Fig. 1 Respiration responses of rhizosphere microbes in tomato to various carbohydrate substrates. Means ± standard error differs significantly. The plot is drawn with the aid of Microsoft Excel. "HR" denotes the rhizosphere soil of healthy tomato plants; "DR" denotes the rhizosphere of the diseased plant; and "BR" is the bulk soil

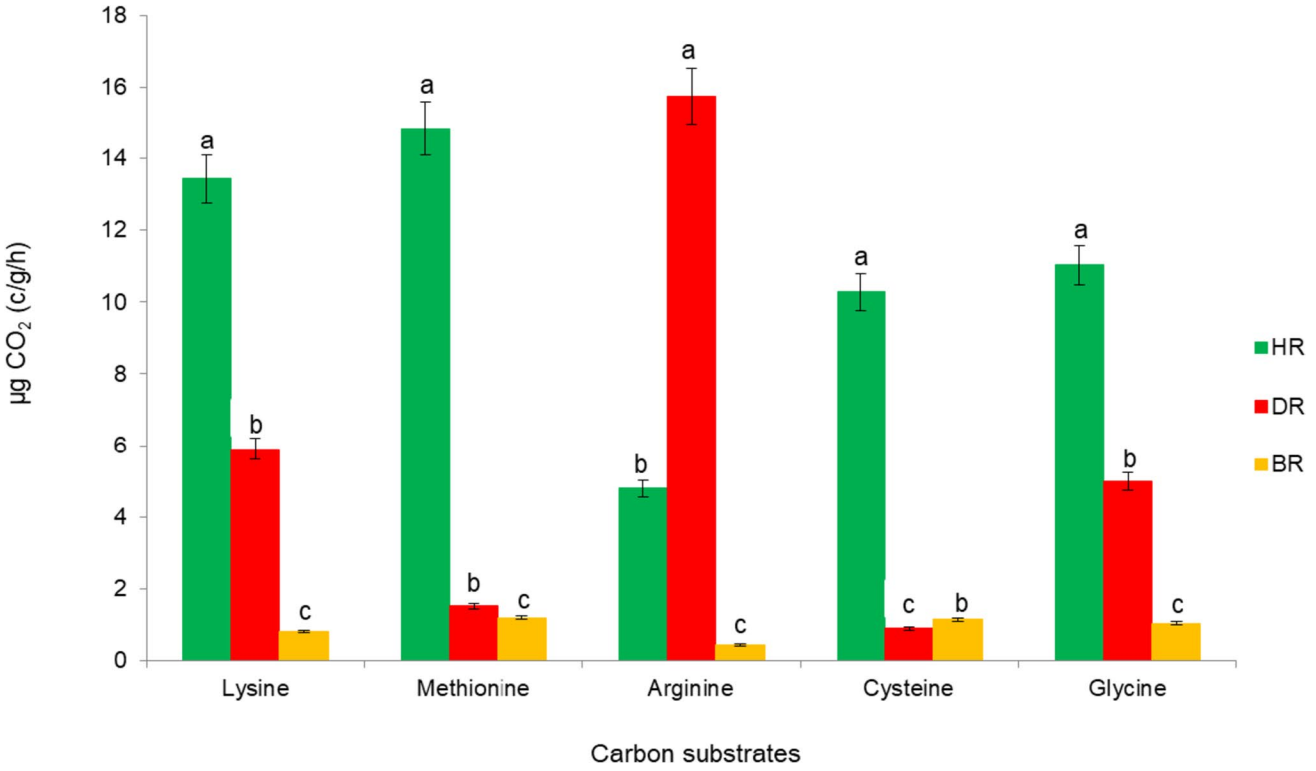

Fig. 2 Respiration responses of rhizosphere microbes in tomato various amino acid substrates. Means ± standard error differs significantly. The plot is drawn with the aid of Microsoft Excel. "HR" denotes the rhizosphere soil of healthy tomato plants; "DR" denotes the rhizosphere of the diseased plant; and "BR" is the bulk soil

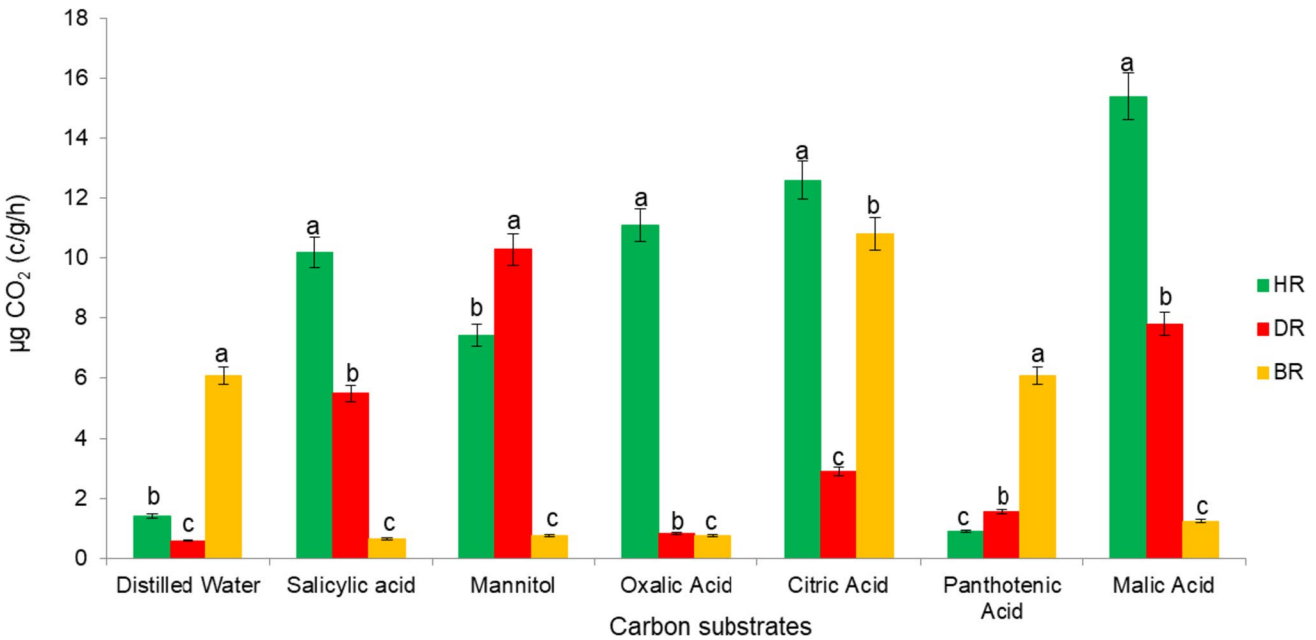

Fig. 3 Respiration responses of rhizosphere microbes in tomato to various carboxylic acid and mannitol substrates, as (%) of the substrate required. Means ± standard error differs significantly. The plot is drawn with the aid of Microsoft Excel. "HR" denotes the rhizosphere soil of a healthy tomato plant; "DR" denotes the rhizosphere of the diseased plant; and "BR" is the bulk soil

variables was revealed in the plot. CCA axis 1 explained 31.7% of the total variation and 20.1% on axis 2 of the environmental variables and the metabolic attributes of the soil microbes (Table 1; Supplementary Table S2).

4 Discussion

The application of the MicroResp™ assay to quantify community-level profiling of microbial activity in various soil samples has revealed the latent effects on the microbiomes to soil properties (Enagbonma et al. 2021). This present study affirmed the significant changes that take place in community-level physiological profiles (CLPP) of soil samples or the level of utilization of C substrate among HR, DR, and BR that coincides with the study of Venter et al. (2016). Tomato cultivation has a specific influence on soil structure and microbiomes embedded in its rhizosphere soil. In this study, CLPP assays were employed to compare and reveal the process of metabolism of the microbes in tomato plants' rhizosphere soil, and control soil, otherwise regarded as bulk soil. The basic concept of the CLPP defines the total amount of carbon consumed, revealing the microbial biomass that uses up a particular C source (Creamer et al. 2016). Pradhan et al. (2020) reported that the metabolic activities and functional diversity of microbiomes increase as a result of the huge amount of carbon source the microbiomes utilize.

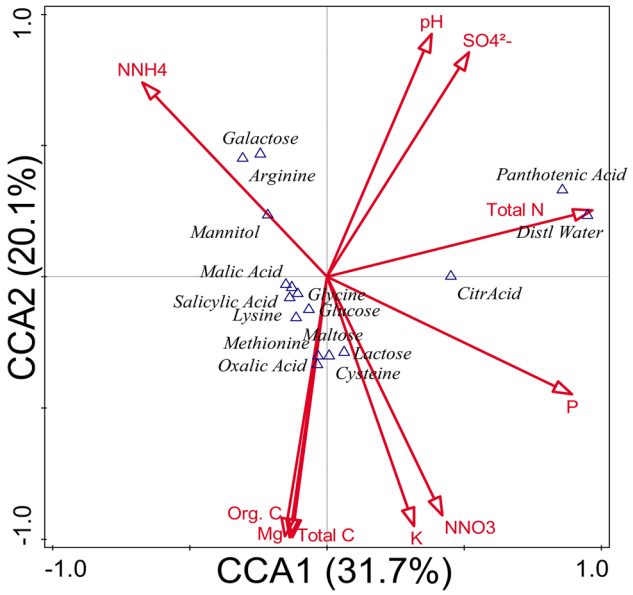

Fig. 4 CCA ordination plot of the carbon substrate and soil physicochemical features of the microbes. The plot is drawn with the aid of Canoco software. "HR" denotes the rhizosphere soil of a healthy tomato plant; "DR" denotes the rhizosphere of the diseased plant; and "BR" is the bulk soil

The pH of the soil contributes immensely to soil microbiomes' functions at different levels and soil structure (Ali et al. 2019a; Siedt et al. 2021). Narendra et al. (2015) reported how rhizosphere soil samples obtained from growing tomatoes with pH 6.5 biosynthesize an antioxidant peroxidase and polyphenol oxidase (PPO) contributing to the growth of tomato and further preventing early blight disease from attacking the tomato plant. The report coincides with our study with a pH value of 6.72 protecting the HR tomato plantation from powdery mildew diseases. Organic carbon, total carbon, and nitrogen contribute to the healthy status of tomatoes by preventing disease attacks on tomatoes. Islam and Toyota (2004) reported how organic carbon produced by different compost, nitrogen, ammonium nitrogen (NH_4^+-N), and nitrate-nitrogen (NO_3^--N) inhibition of phytopathogen *Ralstonia solanacearum* on tomatoes which was in line with our study. We likewise reported the effort of essential nutrients P, K, Mg, and SO_4^{2-} in preventing the invasion of powdery mildew diseases on tomato plants. These elements were greater in HR. Ali et al. (2019b) reported the effectiveness of organic fertilizer composed of Ca, Mg, N, P, and K in preventing disease and insect attacks on a tomato plant and improving environmental tolerance.

Rhizosphere soil respiration is affected by certain properties among which are temperature, moisture content, and pH. Soil respiration is not sensitive to low temperatures (< 5 °C) but sensitive in the high-temperature range (10–20 °C). When the moisture content of the soil samples was maintained at ≤ 60% of the water holding capacity as employed in this study, respiration will be controlled by SOM. However, the carbon substrates supplied likewise control the respiration level when they interact with other soil properties. While plants are photosynthesizing at high temperatures, soil respiration will increase because of carbon responsiveness to temperature changes when provided with enough carbon substrates (Hunt et al. 2002).

The degradation and rate of utilization of carbon substrate were higher in HR, unlike DR and BR. This is because of the health status of the tomato plant to carry out respiration activity, thereby requiring C sources for catabolic activity. Carbon substrates that include cysteine, glucose, lactose, maltose, glycine, methionine, lysine, malic acid, citric acid, oxalic acid, and salicylic acid were greater in HR; galactose, arginine, and mannitol in DR; and pantothenic acid and distilled water in BR. This showed how the microbial communities inhabiting the soil samples degrade the substrates provided in a control laboratory environment. Our report is in line with the report that explained how *Aspergillus tubingensis* utilized various C substrates, which include glucose, galactose, lactose, and maltose to inhibit *Fusarium solani* that brings about soft rot diseases affecting the tomato plant (Kriaa et al. 2015). In this study, various amino acid substrates reported were greater in HR and they include glycine, cysteine, methionine,

and lysine, supporting the healthy condition of the tomato plant growth while arginine is greater in DR. Our report corresponds with Alfosea-Simón et al. (2020) that reported how various amino acid impart to the development of tomato plant. Carboxylic acid substrates, including malic acid, citric acid, oxalic acid, and salicylic acid, were abundant in HR, while pantothenic acid is abundant in BR.

After the catabolic activity of soil microbiome profiling, significant differences were observed in the soil samples. The results presented in earlier studies revealed that the MicroResp assay is a proportional biological indicator procedure for analyzing the metabolic potential of soil microbiomes with different soil properties and C sources on different soil samples (Bérard et al. 2014).

The activities of microbes improve healthy plantations, limit the respiration rate in soil, and have the potential to break down C sources (Tahat et al. 2020; Wani et al. 2012). So, there is a rise in the involvement of the plantations' influences in sustainable agriculture. Healthy plant crops are well known to possess huge C substrates in their soil ecosystems, and they possess greater carbon sequestration rates (Akinola and Babalola 2021). Crop plants likewise modified the functional potential of soil microbiomes across sites. However, we confirmed that crop plants have limited potential to break down C sources in the soil during their degradation. Such C sources include alcohol, amino acids, carboxylic acids, and sugars of animal, microbial, and plant origins. The healthy tomato plants provide support to soil organisms to break down C source as observed by reducing the mechanisms obtainable in the soils to break down the soil organic matter.

The canonical correspondence analysis (CCA) plot is often used to show the relationship among environmental variables. Ter Braak and Verdonschot (1995) explain how CCA has been applied to various environmental samples that back up our study. CCA is a multivariate method to elucidate the relationships between biological assemblages of C substrates and the physicochemical properties of the soil samples employed in this study. The method is also employed to reveal environmental gradients from ecological data obtained via soil properties. The soil properties' effect on the physiological potential of the microbial communities was unveiled by employing CCA (Fig. 4). Most of the C substrates were more significant in the HR site. The important function of sugar in the rhizosphere has been revealed to preserve and stimulate activities of microbiomes for quality performance as explained by Gunina and Kuzyakov (2015). The soil properties do not impart to the microbial population growth in the soil as observed in this study. Other C substrates used in building microbial biomass are amino acids and various carboxylic acids (Gunina et al. 2014; McDaniel and Grandy 2016). The low content of nitrogen compounds ($N\text{-}NH_4$) and total C available in the soil explains how low amounts of the amino acid and carboxylic acid substrates were required for assimilation by the microbiome in the rhizosphere soils to build microbial population during the respiration process (Högberg and Read 2006; Lipson and Näsholm 2001).

5 Conclusion

Taken together, this is one of the foremost studies to show how soil microbes influence the utilization of C substrates in the rhizosphere soil of diseased and healthy tomato plants. We employed the MicroResp™ assay to quantify the community-level physiological profile of microbial functionality in diseased and healthy tomato rhizosphere soil and the bulk soil. The study revealed that the microbial communities in the healthy rhizosphere site utilized more carbon substrates due to the higher soil respiration in the healthy rhizosphere, as compared to diseased rhizosphere and bulk soil sites. This shows the impact of microbial catabolism during the respiration profiles of microbial communities in rhizosphere soil samples obtained from healthy, diseased rhizosphere, and bulk soil. More research should be conducted on the activity of C substrate enzymes to improve the healthy nature of tomato plants.

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Author Contribution AAA carried out the laboratory and fieldwork, handled the literature findings, executed all necessary analyses, interpreted the results, and prepared the manuscript. AEF provided technical input, assisted in result interpretation and OOB initiated the next-generation sequence research, helped shape the research, verified the analytical methods, secured funds for the study, proofread, commented on the manuscript at all stages, and supervised AAA and AEF.

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Declarations

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