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Post-Harvest Resilience of Microbial Activity in Bacterially Inoculated Soils Under Drought Stress

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Abstract

The effects of microbial inoculation strategies on plant development in agricultural ecosystems are widely known. However, the "legacy effects" left on the soil after the main crop is harvested are not fully known. This study was conducted to examine the permanent effects of different Bradyrhizobium japonicum inoculation methods (seed and soil) on microbial stability during the 10-day plant-free incubation period after soybean (Glycine max L.) harvest in soils with a history of drought stress. In the study, soil respiration (CO_2), dehydrogenase activity (DHA), microbial biomass carbon (MBC) and metabolic (qCO_2) and specific (qD) ecophysiological indices were evaluated with multivariate statistical analyzes (PCA and Correlation). The findings showed that the "nutrient shock" caused by the cessation of post-harvest root exudates led to severe metabolic stress and carbon wastage from cellular respiration in the uninoculated control group. While drought stress (WS) suppressed microbial biomass and enzyme activities, inoculation from soil under stress (WS+A2) compensated for these losses in an extraordinary way. While basal respiration (CO_2) decreased dramatically by approximately 40% in WS+A2 application in the post-harvest period; The increase in microbial biomass (MBC) and enzyme activity (DHA) by 119.4% and 91.3%, respectively, compared to the stress group, proved that the microbial community maintained its cellular potential by reducing unnecessary carbon expenditure. As a result, it has been determined that bacterial inoculation from the soil goes beyond the existence of the plant and creates a high ecological resistance (resilience) in the soil microbiota against post-harvest hunger and drought shocks and prepares the ecosystem for the next production season by preserving carbon with maximum efficiency.

Keywords: *Aftereffect, Microbial ecology, Bradyrhizobium japonicum, Drought stress, Ecophysiological indices.*

Introduction

Severe drought periods triggered by global climate change not only limit crop production but also put the soil microbiological health, which forms the basis of the agricultural ecosystem, under a long-term threat (Liu et al., 2022; Seleiman et al., 2021). It is widely reported in the literature that plant growth-promoting rhizobacteria (PGPR) improve growth parameters and physiological defense mechanisms in plants under drought stress (Glick, 2014; Vacheron et al., 2013). In our preliminary research conducted in this context, it was successfully demonstrated that Bradyrhizobium japonicum inoculation alleviates oxidative stress in soybean (Glycine max L.), protects photosynthetic capacity and significantly supports plant development, and the targeted study outcomes have been completed (Tuncer and Sarıoğlu., 2026, under review).

However, the sustainability of agricultural ecosystems directly depends not only on microbial interactions during the period when the plant exists, but also on the "legacy effects" remaining in the soil in the post-harvest period (de Vries et al., 2018; Matthews et al., 2023). When the plant is harvested, root exudates, which are the main source of energy and carbon for soil microorganisms, are suddenly cut off (Bais et al., 2006). This creates a secondary source of "nutrient shock" and metabolic stress for microbial communities, especially in soil conditions where abiotic stresses such as drought persist (Naylor & Coleman-Derr, 2018). Although the effects of PGPR applications on the plant have been extensively studied in the literature, there is still a large gap in how long and at what efficiency these bacteria applied after the plant is removed from the soil can maintain soil microbial dynamics (Ibarra et al., 2020; Wu et al., 2016).

The main aim of this study is to examine the permanent effects of drought stress and different inoculation methods (seed and soil) on soil microbial stability during the 10-day plant-free incubation period after soybean harvest. Current research goes beyond classical enzyme activities; It interrogates the "metabolic health" of the soil through ecophysiological coefficients such as microbial biomass carbon (MBC), microbial metabolic fraction (qCO_2) and specific dehydrogenase activity (qD). The findings aim to reveal the role of microbial interventions made directly in the soil in preparing the soil ecosystem for the next production season and its microbial resistance capacity, even after the main crop is withdrawn from the field.

Materials and Methods

This study was conducted to examine the legacy effects of drought stress and different Bradyrhizobium japonicum inoculation methods (seed and soil) on the rhizosphere of soybean (Glycine max L., cv. GAPSOY 16). The direct effects of the preliminary trial on plant physiology and growth parameters were reported in detail in the main study (Tuncer and Sarıoğlu., 2026, under review). The aforementioned preliminary experiment was set up according to the randomized block trial design in controlled greenhouse conditions, in pots filled with soil with high clay content, calcareous soil and pH value between 7.5-8.0. Two different irrigation regimes were applied throughout plant development: full irrigation (100% of field capacity) and water stress (50% of field capacity); The inoculation factor is designed as control, seed inoculation and pulverized inoculation directly into the soil.

Post-Harvest Incubation and Soil Sampling

After the soybean plants were harvested during the flowering period and their roots were carefully removed from the soil, the soil remaining in the pots constituted the main material of the current experiment. In this new period, when microorganisms were deprived of root secretions (the main carbon source), the soils were incubated in pots for 10 days in order to observe the permanent effects of stress and inoculation methods on the microbial flora. During this process, soil moisture was kept constant at harvest levels (according to the relevant irrigation regime). At the end of the incubation period, homogenized soil samples taken from each pot were prepared for laboratory analysis.

Examined Soil Microbiological Parameters

Soil Respiration (CO_2 Output): CO_2 output, which is a general indicator of soil microbial activity, was determined according to the closed jar incubation and titration method (Isermeyer, 1952). Soil Dehydrogenase Activity (DHA): It was determined by treating soil samples with TTC (triphenyltetrazolium chloride) and reading the formed formazan spectrophotometrically at 546 nm, in accordance with the method of Thalmann, (1968) for the determination of active microbial respiration and enzyme viability.

Microbial Biomass Carbon (MBC): MBC analysis in soil was performed according to the method of Öhlinger, (1996). A 50 g soil sample was taken and brought to field capacity. Samples were placed in a desiccator containing a beaker containing 50 mL of chloroform. The air in the desiccator was evacuated using a vacuum pump. After a 24-hour waiting period, the samples were removed. The extracted samples were mixed with potassium sulfate solution at a ratio of 1:5 and left to shake for 30 minutes. After shaking, the samples were filtered and organic matter was determined.

Microbial Metabolic Quotient (qCO_2): Calculated by dividing daily CO_2 output to microbial biomass carbon (CO_2-C/MBC) in order to determine the tolerance of soil microorganisms to environmental stress and energy use efficiency (Anderson & Domsch, 1990).

Specific Dehydrogenase Activity (qD): In order to determine the dehydrogenase enzyme activity per unit carbon of microbial biomass (microbial physiological state), it was calculated by dividing the measured DHA value to the microbial biomass carbon and incubation time ($\mu gTPF/mgC/h^{-1}$) (Anderson & Domsch, 1990).

Statistical Analysis

The data obtained were subjected to two-way (irrigation level x inoculation method) analysis of variance (ANOVA). Differences between applications were evaluated with Duncan's multiple comparison test ($p<0.05$). Additionally, Principal Component Analysis (PCA) was used to see the multidimensional relationship between microbial dynamics in the post-harvest period.

Results

Soil Respiration (CO_2) and Dehydrogenase Activity (DHA)

Following the 10-day incubation period after harvesting the soybean plant and removing the roots, statistically significant differences ($p<0.05$) were detected between the treatments in CO_2 release and dehydrogenase (DHA) enzyme activity, which are indicators of microbial activity in the soil.

In soils incubated under full irrigation conditions, Bradyrhizobium japonicum inoculations from seed (A1) and soil (A2) increased CO_2 output (Figure 1A) by 23.8% and 38.1%, respectively, compared to the control group. However, CO_2 output in pots with a history of drought stress (WS) decreased by 56.9% compared to the control group. Although bacterial inoculations performed under stress conditions increased CO_2 output by 22.6% in the WS+A1 application and 36.4% in the WS+A2 application compared to the WS group, they were statistically in the same group with WS.

When dehydrogenase (DHA) enzyme activity was examined (Figure 1B), a different picture emerged. Under normal irrigation conditions, A1 and A2 applications increased DHA activity by 12.5% and 14.6%, respectively, compared to the control. Water stress (WS) application caused a sharp decrease in enzyme activity by 51.9% compared to the control group.

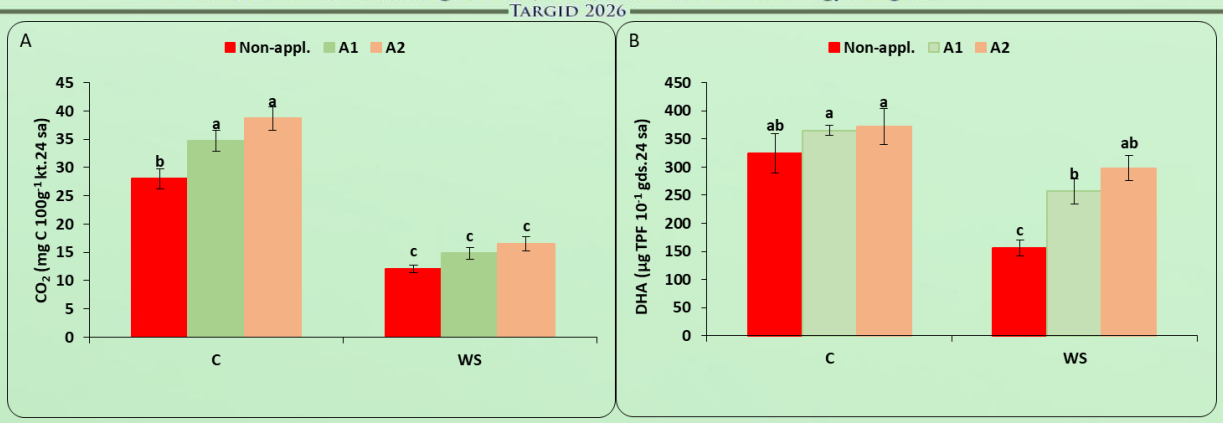

Figure 1: Soil respiration [CO_2 (A)] and Dehydrogenase enzyme activity [DHA (B)] Soybean plant under water stress (WS) of not inoculation (non-appl.), inoculation from seed (A1) and inoculation from soil (A2) application (Mean ± S.E.). C: treatment with water alone; WS: irrigation 50%

It was determined that vaccinations administered under drought stress kept DHA levels significantly higher during the 10-day incubation period. Seed grafting (WS+A1) increased the DHA value by 64.6% compared to the WS group. In the soil inoculated stress group (WS+A2), this increase was much higher and enzyme activity increased by 91.3% compared to the WS group. According to the statistical analysis results, the DHA activity of WS+A2 application was found to be no different (in the same statistical group) with the control soil that had not received any stress.

Microbial Biomass Carbon (MBC) and Ecophysiological Indices (qCO_2 and qD)

Statistically significant differences ($p<0.05$) were determined between applications in microbial biomass carbon (MBC) values, which express the size of the live microbial population in the soil. Bacterial inoculations applied from seed (A1) and soil (A2) under normal irrigation conditions increased the amount of MBC (Figure 2A) by 145.6% and 158.3%, respectively, compared to the control (C) group. In contrast, drought stress (WS) treatment reduced live microbial biomass by 36.2% compared to the control group. Grafting practices under drought stress significantly compensated for these biomass losses. While seed grafting (WS+A1) increases the MBC value by 99.7% compared to the stress group (WS); Soil inoculation (WS+A2) increased this increase to 119.4%. Remarkably, the biomass value reached by WS+A2 application under stress was found to be 39.9% higher than the MBC value of the control group without stress.

A different picture was observed when ecophysiological indices (qCO_2 and qD) reflecting the energy use efficiency and physiological state of the microbial population were examined. In microbial metabolic carbon (qCO_2) values (Figure 2B), the control group was statistically at the highest level. All remaining stress and inoculation treatments (A1, A2, WS, WS+A1 and WS+A2) exhibited significantly lower qCO_2 values compared to the control group.

The highest value in the specific dehydrogenase activity (qD) parameter (Figure 2C), which expresses the dehydrogenase enzyme activity per unit microbial biomass, was also measured in the control group. Drought stress (WS) and grafting applications under stress (WS+A1 and WS+A2) reduced qD values by 23.7%, 38.6% and 35.5%, respectively, compared to the control group. The lowest qD values were determined in A1 and A2 applications under normal irrigation conditions.

Multivariate Statistical Analyzes (Correlation and PCA)

As a result of Pearson correlation analysis (Figure 3), which was performed to determine the relationships between post-harvest soil microbial parameters, statistically significant ($p<0.05$ and $p<0.01$) relationships were detected between the variables. Strong positive correlations ($r = 0.880$ to 0.839) were found between CO_2, DHA and MBC, which are key activity indicators in soil. In contrast, a negative relationship was observed between microbial biomass (MBC) and ecophysiological stress indices; In particular, a statistically significant and very strong negative correlation ($r = -0.817$, $p<0.05$) was detected between MBC and specific dehydrogenase activity (qD). Additionally, a near-perfect positive relationship ($r=0.968$, $p<0.01$) was determined between qCO_2, which expresses microbial stress, and qD.

In the Principal Components Analysis (PCA) biplot plot (Figure 3), which was performed to visualize the holistic effect of treatments on microbial parameters, the first two principal components (PC1 and PC2) explained 97.3% of the total variance (70.7% and 26.6%, respectively). While the PC1 axis represents high biomass and enzyme activity (MBC, CO_2, DHA) in a positive direction; PC2 axis reflected metabolic stress indices (qCO_2, qD). In the PCA space, applications are clearly separated. Inoculation treatments (A1 and A2) under normal irrigation conditions exhibited the highest microbial health profile, positioned to the far right of PC1. While water stress (WS) application is isolated at the negative end of PC1; inoculums under stress (WS+A1 and WS+A2) shifted towards the center, showing that stress was alleviated. The control (C) group showed a sharp positive separation on the PC2 axis and was located in the same region as the qCO_2 and qD vectors.

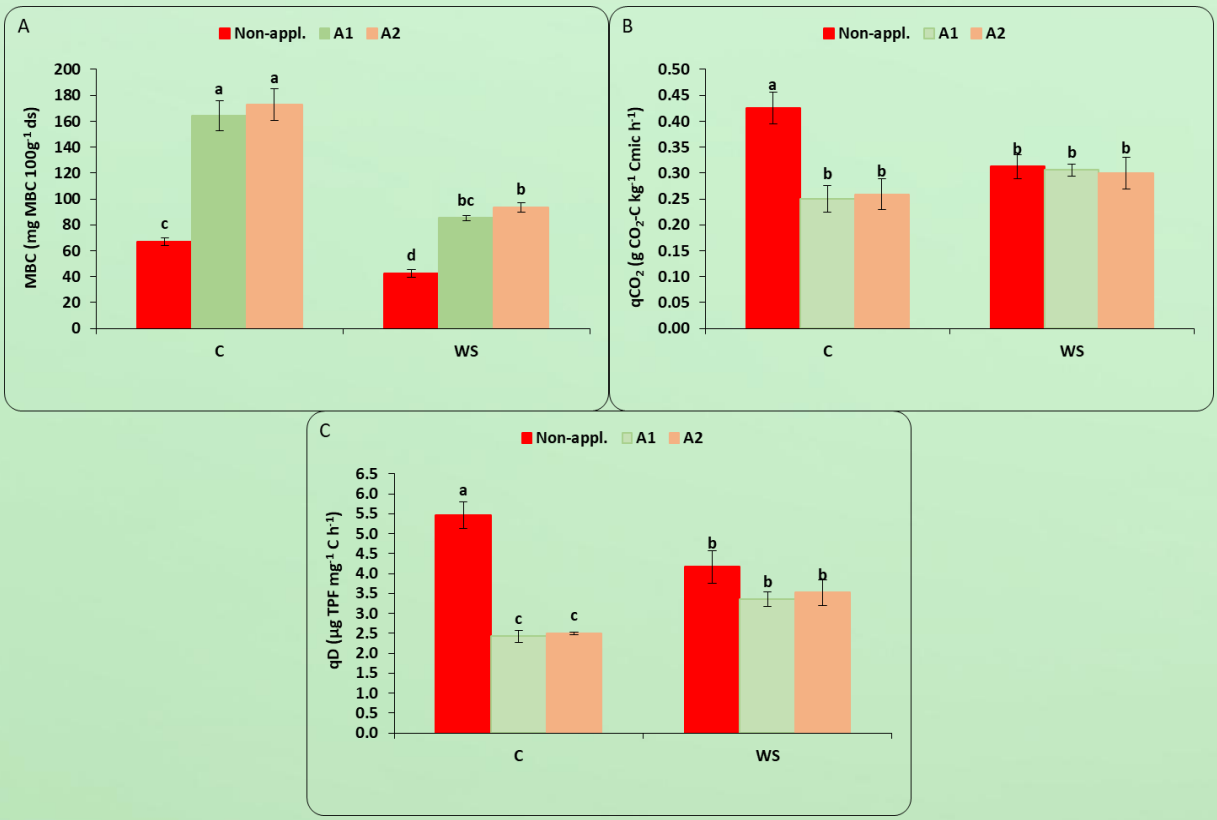

Figure 2: Microbial biomass carbon [MBC (A)], microbial metabolic coefficient [qCO2 (B)] and microbial biomass conversion [qD (C)] Soybean plant under water stress (WS) of not inoculation (non-appl.), inoculation from seed (A1) and inoculation from soil (A2) application (Mean ± S.E.). C: treatment with water alone; WS: irrigation 50%

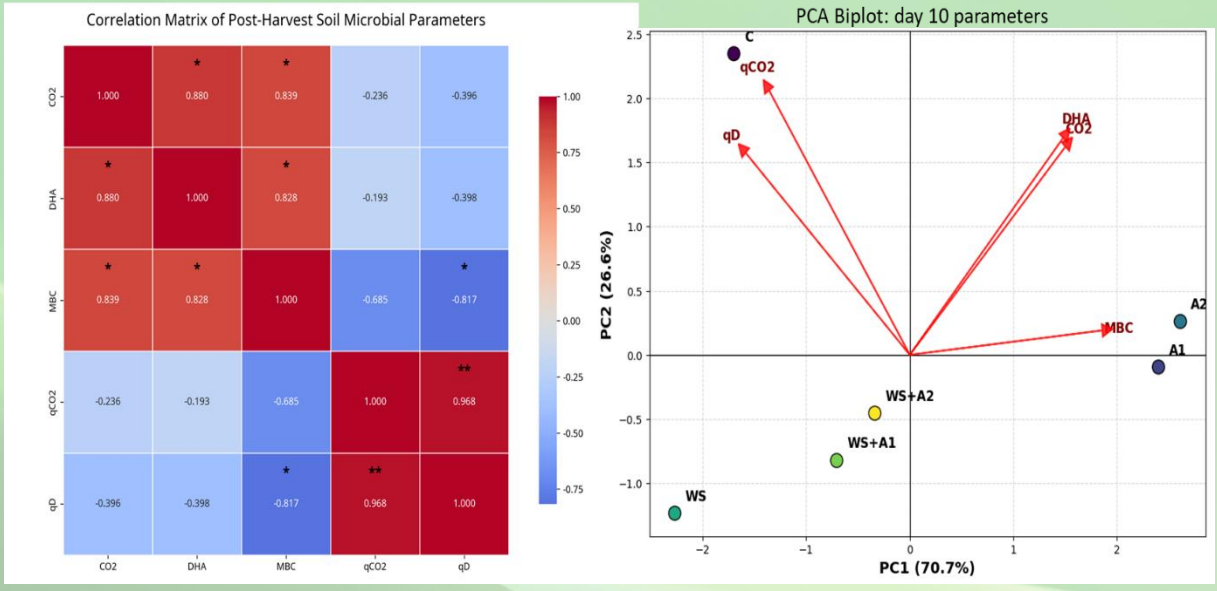

Figure 3: Correlation matrix and PCA analysis of the results

Discussion

The post-harvest period is a critical transitional phase for soil microbial communities when the flow of fresh carbon from plant roots is abruptly interrupted and existing populations face "nutrient shock." When the data obtained at the time of harvest in our main study (Tuncer and Sarıoğlu., 2026, under review) were compared with the findings obtained after 10 days of plant-free incubation, a clear ecological decoupling was detected in the responses of the applications to this shock.

As expected, removal of the plant from the field caused a general metabolic slowdown in all groups. In the (A2) group inoculated from soil under normal irrigation conditions, CO_2 output and DHA activity showed a balanced decrease of 12.1% and 13.5%, respectively, compared to the time of harvest. In contrast, the almost no decrease in CO_2 respiration in the unvaccinated control (C) group (minimal decrease of 0.9%) may seem like stability at first glance, but this actually reflects a severe metabolic stress. It is understood that the native flora, whose food source has been cut off, continues to engage in high rates of cellular respiration (carbon waste) in order to survive. As a matter of fact, Hartman & Richardson, (2013) reported that soil microorganisms under nutrient limitation increase basal respiration in order to maintain their energy balance, and this leads to a carbon loss that negatively affects ecosystem health in the long term. The peak of qCO_2 values in the control group also confirms this carbon waste.

The most striking finding of our study is the microbial adaptation strategy observed after harvest in inoculated soils (WS+A1 and WS+A2) with a history of drought stress. With the removal of plant roots, CO_2 output decreased dramatically by 40.7% in the WS+A2 application. However, this sharp decline does not represent microbial deaths, but rather a successful protection mechanism (survival state) developed by the inoculated Bradyrhizobium japonicum strains. In the same group, the decrease in specific enzyme activity (DHA), which is the main indicator of cellular viability and potential, was limited to only 8.8%. This proves that in extreme conditions where drought and nutrient shock are combined, the microbial community engages in respiratory-enzyme decoupling (CO_2 output) by stopping unnecessary carbon expenditure (CO_2 output) and successfully protects the main cellular metabolism.

Recent studies in the literature support this finding. (Xiao et al., 2023) reported that rhizosphere bacteria under severe drought and nutrient deficiency protect intracellular enzyme systems by suppressing general respiration and thus increase ecological resistance. Similarly, (Shi et al., 2025) emphasized that successful microbial inoculations maximize carbon use efficiency by reducing basal respiration during stress.

As a result, when the harvest period findings obtained in the main study and the 10th day results of the current study are integrated; It has been proven that soil inoculation (A2 and WS+A2) creates a strong legacy effect that can transfer cellular potential to the next season by promoting microbial activity in the presence of plants, while protecting the ecosystem from carbon waste in the absence of plants.

These specific physiological differences between treatments clearly outline the general framework of ecosystem dynamics in multivariate analyzes where all microbial parameters are evaluated together. The correlation and PCA results obtained in our research clearly explain the "nutrient shock" and microbial resistance mechanisms occurring in the post-harvest soil ecology. The strong negative relationships observed between microbial biomass (MBC) and metabolic stress indices (qCO_2 and qD) in the correlation matrix prove that microorganisms use energy (carbon) much more efficiently as the number of living cells in the environment increases. Daunoras et al., (2024) reported that enzyme activities in the soil microbiota play a critical role in maintaining ecosystem health and high biomass prevents metabolic waste; Our findings are in full agreement with this ecological principle.

The most striking ecological outcome of our study is the spatial distribution exhibited by the control (C) group in the PCA graph. It is extremely significant that the control group, which was reported to not experience any physiological stress in the presence of plants in our main study (Tuncer and Sarıoğlu., 2026, under review), shifted strongly towards qCO_2 and qD stress vectors during the post-harvest incubation period. The sudden cessation of root exudates (the main carbon source) by removing the soybean plant from the field created a severe "starvation stress" on the microbial flora in the uninoculated control soil. Darenova et al., (2023) state that in situations such as removal of vegetation or water deficit, soil microorganisms perform cellular respiration at a high rate to survive, and this increases the qCO_2 value. This high metabolic loss observed in our control group confirms the relevant literature.

On the other hand, Bradyrhizobium japonicum inoculation (A2 and WS+A2), especially applied from soil, created a serious buffer mechanism (afterprotection effect) that protected the microbial flora against this nutrient shock. The fact that A2 applications are located at the farthest point from the stress indices in the PCA graph, at the end of the MBC and DHA vectors, shows that the microorganisms directly injected into the soil form stable biofilms within the soil micro-aggregates. Bogati & Walczak, (2022) emphasized that increasing microbial activity is the most critical factor in strengthening ecosystem resilience after drought. In conclusion, even with a history of drought stress, rhizosphere flora inoculated from soil exhibit high carbon utilization efficiency (low qCO_2) and strong enzyme viability (high DHA), proving that inoculation not only protects the plant but also guarantees long-term soil microbial stability in the post-plant period.

Conclusion

This study clearly demonstrated the "legacy effects" of drought stress and different Bradyrhizobium japonicum inoculation methods on soil microbial ecology after soybean harvest. The nutrient shock caused by the removal of

the main crop from the field causes high carbon wastage (peaking qCO_2 values) and metabolic stress in the uninoculated native flora; The soil inoculation strategy (A2) has successfully buffered this ecological problem.

The most striking outcome of the research, which contributes to the literature, is the microbial adaptation and "respiration-enzyme decoupling" mechanism detected in soil-inoculated (WS+A2) pots with a history of drought. Microbial communities in this group have entered an ecological protection mode (survival state) by dramatically reducing unnecessary basal respiration (CO_2 output) by approximately 40% in the absence of plants and under stress; However, it maintained the main cellular workforce (MBC) and potential enzyme vitality (DHA) of the soil almost without loss.

The obtained ecophysiological coefficients (qCO_2 and qD) prove that direct microbial interventions in agricultural areas are not a short-term solution that only improves the plant physiology of the current season. Bacterial inoculation from soil makes the microbial flora highly resilient to hunger and drought shocks in the difficult post-harvest period, and safely transfers a stable soil ecosystem that uses carbon with maximum efficiency to the next production season. Within the context of sustainable agricultural practices, this potential of microbial inoculants to create long-term “soil memory” should be considered as an essential tool for future climate change adaptation strategies.

Declarations

Ethical Approval Certificate

Ethics committee approval was not required for this study.

Author Contribution Statement

Ali SARIOĞLU: Designed the study, prepared other necessary materials for the research, contributed to the setup of the experiment, analysis and article writing.

Emine Nur TUNCER: She contributed to the establishment and follow-up of the experiment and the analysis.

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Conflict of Interest

The authors declare no conflict of interest.

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