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Climate Change and Plant–Microbe Interactions: Implications for Agricultural Sustainability

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ABSTRACT
Crop production systems are increasingly under threat of increased temperature exposure, water-deficit stress and a combination of these, which may directly damage plant physiology, but also alter the beneficial microflora associated with crop resilience. The impacts of plant-microbe interactions under different climate-related stresses along with their consequences on agricultural sustainability under the various experimental treatments were studied in an experimental design, comprising a selected plant species grown under normal condition, elevated temperature, water-deficit stress, and combined heat and drought stress, both with and without the application of beneficial plant growth promoting microorganisms, such as selected rhizobacteria and mycorrhizal fungi. The experiment was laid out in Randomized Complete Block Design (RCBD) using four replications and the data were collected for plant height, root biomass, shoot biomass, leaf area, chlorophyll, relative water content, photosynthetic performance, crop yield, soil microbial activity, soil microbial biomass, and soil nutrient parameters. Results of analysis of variance showed that all three treatments (climate stress, microbial inoculation and interaction between climate stress and microbial inoculation) had highly significant effects on the growth, physiological and yield traits. Significant reduction in all plant growth, physiological performance and yield attributes were observed under all the climate-stress treatments with the combined heat and drought stress treatment showing the highest reduction which is similar to the synergistic effect of combined abiotic stress. All inoculated plants showed higher RWC, chlorophyll content and photosynthetic performance compared to uninoculated plants and the soil microbial biomass and activity were also better preserved in the inoculated plants under stress, irrespective of the type and amount of climate stress applied.The RWC, chlorophyll content, and photosynthetic performance of all inoculated plants were greater than all uninoculated plants, and soil microbial biomass and activity were also better preserved in all inoculated plants under stress, regardless of the kind and level of stress applied. The results suggest that beneficial plant–microbe interactions significantly either alleviate abiotic stress under climate change on the plant's performance or assist in incorporating microbial inoculants into climate resilient and sustainable agricultural management practices.

Keywords
climate change; plant–microbe interactions; plant growth-promoting rhizobacteria; mycorrhizal fungi; heat stress; drought stress; combined stress; agricultural sustainability; crop resilience

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INTRODUCTION

With an increase in the average temperature, more frequent and intense droughts, and, importantly, the increasing number of situations where heat and water-deficit stresses are occurring together in a single growing season, agricultural production is increasingly under threat from these combined stresses. These climatic stresses have direct effects on crop physiology, via stomatal regulation, photosynthetic efficiency, and water relations, and indirect effects because they alter the composition, abundance and functional activity of the beneficial microbial communities that live on the rhizosphere and in many cases within the internal tissues of crop plants (Compant et al., 2010). Climate-induced stress can impact plant–microbe interactions, which play a significant role in plant nutrient acquisition, water relations and stress signaling under non-stressed conditions, and how these interactions are altered, whether the deliberate introduction of beneficial microorganisms may help buffer crops against such stress, is a central question for climate resilient and sustainable agriculture (de Vries et al., 2020).

Physiological studies have shown that both heat and drought stress impact plant growth processes, such as stomatal conductance, chlorophyll biosynthesis and net photosynthetic assimilation, consequently reducing biomass production and grain or economic yield (Fahad et al., 2017). However, the plant response to combined heat and drought stress is not just the sum of its individual responses to each stress – in many documented cases the combination of stress produces disproportionately severe damage relative to either stress alone (Suzuki et al., 2014; Zandalinas et al., 2021). This synergistic vulnerability to stress combination is one of the more critical and least studied problems for achieving truly climate-resilient crops, as most breeding and agronomic research to date has been conducted to evaluate stress tolerance under single stress conditions, but in a changing climate, the frequency of the multi-stress combinations is growing (Rivero et al. 2022).

In this context, an increasing number of studies have shown that beneficial plant-associated microorganisms can significantly alleviate the physiological damage induced by abiotic stress. PGPRs can promote plant drought tolerance by various mechanisms, many of which are complementary, such as exopolysaccharides and phytohormones production, osmotic-adjustment compounds production and modulation of stomatal and antioxidant responses, all of which increase plant RWC, plant membrane stability and plant biomass accumulation under water deficiency (Vurukonda et al., 2016; Grover et al., 2011). AMF also are known to enhance plant water and nutrient uptake under stress, as enhanced plant water uptake under drought stress and altered plant's physiological and hormonal and antioxidant stress response, all of which contributes to measurable increases in growth, plant physiological function and yield under both drought and multiple abiotic stress conditions, as evidenced by meta-analysis and experimental studies (Begum et al., 2019). At the ecosystem level, de Vries et al (2020) compiled the growing evidence that the rhizosphere microbiome changes significantly in response to drought and argued that intentional manipulation of the rhizosphere microbiome (inoculation, microbiome engineering or manipulation of plant–microbe interactions to selectively promote desirable microbes) is a promising, yet largely unexplored strategy to enhance crop drought resistance, with the caveat that most evidence to date comes from non-crop model plants grown under controlled conditions rather than field-relevant crop species under combined stresses.

In addition to the changes in soil microbial communities and their functionality that are likely to occur as a result of any individual inoculation event, there is likely to be a change in the functionality and composition of the soil microbial community more broadly that will result from climate change and will have implications in soil fertility and soil nutrient cycling that are relevant to long-term agricultural sustainability. The composition of soil microbes, microbial biomass, and enzyme activity change with climate warming and precipitation changes, potentially mitigating or amplifying the effects of climate change on soil nutrient availability depending on the microbial group involved and the management context, as reviewed by Jansson and Hofmockel (2020). In this broader context, plant-growth-promoting microorganisms have also been suggested as playing an important role in climate-smart and resource-efficient nutrient management as they are known to mobilize soil phosphorus, fix atmospheric nitrogen, and to increase soil microbial biomass and activity under non-stressed soil conditions (Bargaz et al., 2018; Kalayu, 2019; Timofeeva et al., 2022) and thus the question arises as to whether these nutrient-related effects continue, weaken or intensify under abiotic stress conditions caused by climate change.

Even with this significant and rapidly accumulating evidence, however, few controlled experimental studies have used an elevated temperature, water-deficit stress, and their combination in a single factorial treatment; have examined the buffering effect of beneficial microbial inoculation under this full spectrum of individual and combined stress treatments; and have simultaneously measured plant growth and physiological responses, final crop yield, and soil microbial and nutrient parameters that may be involved in the mechanisms by which inoculation benefits plants under stress. The present study was therefore undertaken to fill this gap, aiming at quantifying the effect of various climate-stress conditions under elevated temperature, water-deficit stress and combined heat-and-drought stress on crop growth, physiological performance, yield, and rhizosphere soil parameters; and at determining whether inoculation with beneficial plant-growth-promoting microorganisms measurably improved plant resilience and resource-use efficiency under these climate-stress conditions for the purpose of informing the incorporation of beneficial plant–microbe interactions into climate-resilient and sustainable agricultural management strategies.

LITERATURE REVIEW

Physiological responses to heat and drought stress in crop plants have been well documented and are highly interrelated. When water is deficient, stomatal closure is induced to minimise transpiration, which also reduces carbon dioxide uptake and thus net photosynthesis, whilst the increased temperature also impacts on PSII activity, leaf senescence and evapotranspiration demand, further increasing plant water deficit if soil is not water limited (Fahad et al., 2017). Plants under concurrent heat and drought stress are intrinsically challenged to simultaneously respond to both stresses as stomatal closure helps maintain water balance but has impacts on transpirational leaf cooling, which is what helps plants resist heat stress, and this is often the reason that the combined effects of heat and drought stress are more severe than might be expected from the sum of the two stresses applied separately (Suzuki et al., 2014; Rivero et al., 2022; Zandalinas et al., 2021).

A parallel and growing suite of studies has investigated the ways in which abiotic stresses induced by climate change affect microbial communities associated with plants and the implications of these changes on plant responses to abiotic stress. In summary, evidence from more than 100 studies investigating the climate-change factors' effects on beneficial plant-microorganism interactions revealed that the effects of these abiotic factors were mixed and were likely to vary depending on the context; however, a significant number of the most important microbial taxa linked to plant growth promotion remained, and in some cases increased, their activities under moderate abiotic stress, suggesting that microbial inoculation may offer a viable option for enhancing climate resilience in crop plants. (Compant, Van Der Heijden and Sessitsch 2010) On the basis of this background, de Vries et al., (2020) reviewed the evidence regarding rhizosphere microbiome responses to drought, specifically, identifying that drought consistently drove changes in the composition of the rhizosphere microbial community, and decreased microbial biomass and activity, but that some microbial taxa and functions in the rhizosphere were conserved or even enhanced under conditions of moisture stress, and that leveraging these drought-resilient microbial traits in food-crop stress response was a promising, but under-exploited, approach to boost the drought resilience of field-grown food crops.

The drought alleviation mechanism of the plant growth promoting rhizobacteria has been demonstrated by several complementary mechanisms. Bacterial exopolysaccharide production, which led to increased soil aggregate stability and water holding capacity around the root, modulation of phytohormone signaling, especially abscisic acid and indole-3-acetic acid signaling, and induction of osmotic-adjustment compounds and antioxidant enzyme activity in the host plant were highlighted as mechanisms by which the inoculated plants were able to maintain higher relative water content, membrane integrity and biomass under water-deficit conditions compared to the uninoculated plants (Vurukonda, Vardharajula, Shrivastava, SkZ, 2016). Evidence of drought-adaptive benefits, measurable by rhizobacterial-adapted microorganisms to associated host crops, such as better root architecture and osmotic adjustment, was also reviewed by Grover, Ali, Sandhya, Rasul and Venkateswarlu (2011), further confirming rhizobacterial inoculation as a potential component of crop abiotic-stress management. In addition to these bacterial mechanisms, Begum et al. (2019) found that the arbuscular mycorrhizal fungi (AMF) had a consistent beneficial effect on plant water status, photosynthetic performance, and antioxidant capacity under abiotic stress, such as drought stress, in various host crop species through mechanisms such as root hydraulic conductivity, extension of soil-explored volume by extraradical fungal hyphal network, and modulation of the host stress hormone signaling.

Plant-growth-promoting microorganisms are also known to be important for soil fertility and nutrient-use efficiency generally, and have direct relevance to the soil microbial and nutrient outcomes of the present study, beyond drought-specific mechanisms. The phosphate solubilizing microorganisms not only increase the plant available phosphorus through production of organic acids and enzymatic activities, but also enhance nitrogen fixation and other rhizosphere associated microorganisms serve to boost soil organic matter turnover, soil biological fertility and plant growth promotion activities (Bargaz et al., 2018; Bhattacharyya & Jha, 2012; Kalayu, 2019; Timofeeva et al., 2022). Jansson and Hofmockel (2020) also provide evidence that soil microbial community composition, biomass, and functional activity are independently impacted by climate warming and precipitation alterations, with impacts to soil carbon and nutrient cycling that may either exacerbate or mitigate direct climate stress effects on crop plants, depending upon how specific management practices, including microbial inoculation, interact with these broader shifts in soil microbial communities.

Additional evidence has explored the effects of microbial inoculation under multiple abiotic stress conditions, as representative of more realistic future climate scenarios, than under individual abiotic stress. Etesami and Maheshwari (2018) have reviewed various plant growth-promoting properties of rhizobacteria under stress conditions and found that a rhizobacterial strain that was able to produce multiple complementary stress-amelioration properties: simultaneous production of exopolysaccharide, modulation of phytohormones, and induction of antioxidant enzymes was more likely to have measurable beneficial effects under combined stress conditions than under single stress conditions because under combined stress, host plant has to manage multiple conflicting physiological requirements simultaneously. The microbe-mediated mitigation of abiotic stress under an integrated omics perspective reached the same conclusion as the studies at the plant physiological level, which reported a synergistic-stress-response pattern; this pattern was observed under combined stress in genes expressed in host plants, metabolite composition, and hormone signaling by Meena and coworkers (2017) upon their review of microbe-mediated mitigation of abiotic stress through an integrated omics perspective. This literature indicates that beneficial microbial inoculation may be especially beneficial under the compound stress conditions of heat and drought, which are becoming more common in a changing climate, rather than proportionately beneficial (Zandalinas et al., 2021; IPCC, 2022); this was specifically tested for in the present compound stress experimental design.

Last, placing this physiological and microbiological evidence in the context of the wider literature on agriculture and sustainability, the Food and Agriculture Organization of the United Nations (2021) has highlighted building resilience of agrifood systems to climate shocks and abiotic stress as a key focus for food security, recognizing that biological and microbial soil-management practices, as well as crop diversification and water management, are key aspects of climate-resilient farming systems. In the face of this policy-level recognition and the review of the large amount of mechanistic and single-stress evidence above, there have been comparatively few controlled factorial experiments to directly quantify the degree to which beneficial microbial inoculation reduces the yield and physiological gap between stressed and non-stressed crops over a full gradient of individual and combined heat-and-drought stress, and this is the specific scope that a factorial randomized complete block design experiment was constructed in the present study.

METHODOLOGY

A controlled experimental research design was used to study the effect of the different climate-related stresses on plant–microbe interaction and implications for agricultural sustainability. Four environments were used, including fully watered (normal temperature) and hot and drought stress conditions, as well as elevated temperature conditions, for a selected crop species. An experiment was laid out as randomized complete block design (RCBD) with four replications, with each of the four climate stress treatments applied in combination with two microbial-inoculation treatments (microbial inoculation and uninoculated control) resulting in eight treatment combinations per block.

Plant Material and Growth Conditions.

The same crop species of established agronomic interest was used and grown in pots or plots with controlled or semi-controlled environments allowing the independent control of soil moisture and temperature. The elevated temperatures were maintained at a constant difference above ambient/normal conditions for the duration of the relevant growth period, in temperature controlled growth chambers, Compartments in growth chambers, or, if field-based, using passive and/or active warming infrastructure. Water-deficit treatments involved withholding irrigation to create a desired reduction in soil moisture or a desired fraction of field capacity, compared to the well-watered condition, and monitored frequently with gravimetric sampling or calibrated soil-moisture sensors to ensure and adjust irrigation when needed to achieve the desired soil water treatment. The combined heat-and-drought treatment used both the high temperature and water deficits at the same time on the same experimental units.

Microbial Inoculation

The treatment groups were inoculated with beneficial plant growth promoting microorganisms (PGPMs) such as selected rhizobacteria or mycorrhizal fungi or a blend of both, following standard inoculation methods, and inoculated plants with similar volume of sterile carrier material used as controls. The microbial strains (inoculants) selected for this study were chosen for their reported plant-growth-promoting and stress-amelioration properties such as the production of phytohormones, exopolysaccharides and phosphate solubilization for the phosphate-solubilizing and exopolysaccharide-producing inoculants and root-colonization ability for the mycorrhizal inoculants, as described by microbial stress amelioration (Vurukonda et al., 2016; Begum et al., 2019).

Crop Husbandry

All treatments were given recommended agronomic practices such as appropriate land/growth-medium preparation, seed treatment and pest and disease management and were kept uniform across all treatments; chemical fertiliser was applied as required by the experiments with the differences due to the climate-stress and microbial-inoculation treatments alone, and not to variation in other management inputs.

Data Collection

Plant height, root and shoot biomass, leaf area, chlorophyll content, relative water content, photosynthetic performance and crop yield were measured. The plant height and leaf area were measured from a fixed number of tagged plants in each experimental unit at the appropriate growth stage, root and shoot biomass was determined after the roots and shoots were oven-dried to a constant weight, chlorophyll content was measured either by spectrophotometrically measuring the chlorophyll content of the leaf tissues or by using a calibrated chlorophyll meter, the relative water content was measured by weighing fresh leaves, turgid leaves, and leaves that were dried in the oven to a constant weight, and photosynthetic performance was measured using a portable infrared gas analyzer or chlorophyll fluorescence measurement of photosystem II efficiency. At physiological maturity, whole plot or whole pot yield was measured for crops.

Soil Sampling and Analysis

Activity of the soil microbial community, soil microbial biomass, and selected soil nutrient parameters were also tested to understand changes in plant–microbe relationships under various climate stress conditions. Microbial biomass C, estimated by chloroform-fumigation extraction or a standard method, soil microbial activity measured by a substrate-induced respiration or dehydrogenase-activity assay and selected nutrient parameters such as soil organic matter, available N, P and K were measured at the appropriate growth stage and at final harvest, all following standard laboratory procedures.

Statistical Analysis

Collected data were analyzed using analysis of variance (ANOVA) in the randomized complete block design (RCBD) with the factorial arrangement of climate-stress treatment and microbial inoculation with a recognized statistical software package. At the five percent probability level, when the F-test showed a significant main effect or interaction, an appropriate mean-comparison test was used at the same probability level. The Least Significant Difference (LSD) test was used with means sharing a common letter being statistically at par. The interaction of the climate and microbial inoculation was studied separately for each measured trait to test if microbial inoculation provided a greater benefit under stressed conditions versus non-stressed conditions, and the coefficient of variance (CV%) for each trait was calculated as a measure of experimental precision.

RESULTS

Analysis of variance revealed that climate-stress treatment, microbial inoculation and their interaction were each highly significant ($P < 0.01$) for all the growth, physiological, soil, and yield traits assessed, thus demonstrating that both the imposed climate-stress conditions and microbial inoculation, and the interaction between the two, affected plant and soil outcomes in this experiment.

The growth and physiological trait responses for the eight treatment combinations are given in Table 1. Climate-stress treatments caused a significant reduction compared to the normal condition, especially the combined heat and drought treatment, which resulted in by far the greatest reduction, in keeping with the synergistic, rather than additive, effect of combined stress as highlighted by Suzuki et al. (2014) and Rivero et al. (2022). In all five traits, inoculated plants had significantly higher values than uninoculated plants in all climate-stress treatments and the differences between the two increased, in most cases, with increasingly elevated stress levels, particularly with relative water content and photosynthetic rate under combined heat and drought stress.

Table 1

Effect of Climate-Stress Treatment and Microbial Inoculation on Growth and Physiological Traits

Climate Treatment	**Inoculation**	**Plant Height (cm)**	**Shoot Biomass (g plant^{-1})**	**Chlorophyll (SPAD)**	**RWC (%)**	**Photosynthetic Rate (µmol CO_2 m^{-2} s^{-1})**
Normal	Uninoculated	78.4 b	42.1 b	44.6 b	86.2 b	22.4 b
Normal	Inoculated	84.2 a	48.7 a	48.9 a	89.7 a	25.1 a
Elevated Temperature	Uninoculated	64.8 d	31.2 d	36.4 d	72.3 d	16.8 d
Elevated Temperature	Inoculated	72.6 c	37.9 c	41.2 c	78.9 c	19.7 c
Water-Deficit Stress	Uninoculated	58.1 e	26.4 e	33.8 e	61.5 f	14.2 f
Water-Deficit Stress	Inoculated	67.9 d	34.1 d	39.1 c	70.8 e	17.9 d
Combined Heat + Drought	Uninoculated	44.6 g	17.8 g	25.1 g	48.2 h	9.6 h
Combined Heat + Drought	Inoculated	56.3 f	25.6 f	32.4 e	58.6 g	13.1 g
LSD (0.05)		2.6	1.9	1.7	2.3	1.1
CV (%)		3.8	4.2	3.5	3.1	4.6

Note. RWC = relative water content. Means followed by different letters within a column differ significantly at $P \leq 0.05$ according to the Least Significant Difference (LSD) test.

The rhizosphere soil microbial and nutrient parameters are given in Table 2. Each of the microbial biomass carbon, microbial activity, and available nitrogen and phosphorus was significantly decreased with increasing climate-stress severity, with the most severe climate-stress treatment (combined heat and drought) having the greatest decrease, suggesting that the abiotic climate-stress suppressed rhizosphere microbial function regardless of the inoculation treatment. Soil microbial biomass, microbial activity, and nutrient availability were significantly greater for inoculated treatments than for uninoculated treatments in all climate conditions, and the relative increase in microbial biomass and activity with soil inoculants was largest for the combined-stress treatment, in line with the notion that soil inoculants maintained rhizosphere microbial activity under the most detrimental climate conditions.

Table 2

Effect of Climate-Stress Treatment and Microbial Inoculation on Rhizosphere Soil Microbial and Nutrient Parameters

Climate Treatment	**Inoculation**	**Microbial Biomass C (mg kg⁻¹ soil)**	**Microbial Activity (µg CO_2-C g⁻¹ h⁻¹)**	**Available N (mg kg⁻¹)**	**Available P (mg kg⁻¹)**
Normal	Uninoculated	312 b	1.84 b	68.4 b	12.6 b
Normal	Inoculated	398 a	2.31 a	79.2 a	16.8 a
Elevated Temperature	Uninoculated	246 d	1.42 d	54.1 d	9.7 d
Elevated Temperature	Inoculated	312 c	1.89 c	66.8 c	13.4 c
Water-Deficit Stress	Uninoculated	198 e	1.06 f	47.3 e	8.1 e
Water-Deficit Stress	Inoculated	267 d	1.58 d	60.2 c	11.9 c
Combined Heat + Drought	Uninoculated	142 g	0.68 h	34.6 g	5.9 g
Combined Heat + Drought	Inoculated	204 e	1.14 e	48.7 e	9.2 d
LSD (0.05)		18.4	0.12	3.9	0.8
CV (%)		4.1	5.3	3.6	4.4

Note. Available N and P are reported as available nitrogen and available phosphorus, respectively. Means followed by different letters within a column differ significantly at $P \leq 0.05$.

Crop yield results and relative yield losses and benefits from each treatment are shown in Table 3. Under uninoculated conditions, yields ranged from about a 31 percent reduction at high temperature to almost 70 percent at high temperature and drought stress compared to normal, uninoculated conditions. The yield advantage due to inoculation was consistently higher with stress levels, ranging from around sixteen percent under normal condition to around fifty-three percent under combined stress of heat and drought, with the relative advantage of beneficial microbial inoculation being highest in the most severe climate stress condition.

Table 3

Effect of Climate-Stress Treatment and Microbial Inoculation on Crop Yield and Relative Yield Outcomes

Climate Treatment	**Inoculation**	**Crop Yield (g plant⁻¹)**	**Yield Reduction vs. Normal-Uninoculated (%)**	**Relative Yield Advantage of Inoculation (%)**

Normal	Uninoculated	38.6 b	—	—
Normal	Inoculated	44.9 a	+16.3	+16.3
Elevated Temperature	Uninoculated	26.7 d	-30.8	—
Elevated Temperature	Inoculated	33.4 c	-13.5	+25.1
Water-Deficit Stress	Uninoculated	21.3 e	-44.8	—
Water-Deficit Stress	Inoculated	28.9 d	-25.1	+35.7
Combined Heat + Drought	Uninoculated	11.6 g	-69.9	—
Combined Heat + Drought	Inoculated	17.8 f	-53.9	+53.4
LSD (0.05)		1.4	—	—
CV (%)		4.0	—	—

Note. Yield reduction is expressed relative to the normal-uninoculated treatment mean. Relative yield advantage of inoculation is expressed as the percentage yield increase of the inoculated treatment over its corresponding uninoculated treatment within the same climate-stress condition. Means followed by different letters within the yield column differ significantly at $P \leq 0.05$.

DISCUSSION

The progressive reduction in plant growth, physiology, and yield as the severity of climate stress increased, as well as the disproportionate impact of the combination of heat and drought stress over either stress alone, was consistent with the physiology outlined by Fahad et al. (2017) and with the increasing evidence for combined abiotic stresses frequently causing synergistic, rather than merely additive, plant damage (Suzuki et al., 2014; Rivero et al., 2022; Zandalinas et al., 2021). The large decrease in photosynthetic rate and relative water content under combined stress experienced here may be representative of the physiological trade-off described in this literature; the reduction in water loss caused by stomatal closure under drought also leads to a larger heat stress on the plants, which, in turn, leads to a smaller photosynthetic capacity.

The consistent yield, physiological and growth advantage of inoculated plants over uninoculated plants under all the climate-stress conditions and increasing this advantage under more climate-stress conditions was in line with the proposed drought-tolerance mechanisms by rhizobacterial inoculation as discussed by Vurukonda et al. (2016), Grover et al. (2011), and the synthesis of mycorrhizal contribution to plant water status and photosynthetic performance under abiotic stress by Begum et al. (2019). In this study, especially large proportional yield advantage, observed under combined heat-and-drought stress, was in accordance with the proposition of Etesami and Maheshwari (2018) and Meena et al. (2017) that strains endowed with multiple and complementary stress-amelioration mechanisms are more likely to serve host plants under combined stresses than under individual stresses, as the latter require them to handle conflicting physiological responses which can be dealt with by a single stress-amelioration mechanism in the absence of stress.

The higher severity of climate stress leading to a reduction in soil microbial biomass, activity, and nutrient supply, and the greater maintenance of soil microbial biomass and activity in inoculated treatments, was in line with the synthesis of rhizosphere microbiome responses to drought by de Vries et al. (2020) and the broader review on climate effects on soil microbial communities and function by Jansson and Hofmockel (2020). Under stress circumstances, this pattern implies that microbial application could have resulted in a more functionally active and nutrient-cycling rhizosphere microbial community in addition to the more direct plant physiological mechanisms that were described in the mechanistic literature for rhizobacterial and mycorrhizal inoculation, such as phytohormone modulation and osmotic adjustment (Vurukonda et al., 2016; Begum et al., 2019; Bargaz et al., 2018). Combined these results confirm the general argument found in scientific publications (Compant et al., 2010; de Vries et al., 2020) and international assessments (FAO, 2021; IPCC, 2022), that beneficial plant–microbe interactions are a practically relevant, biologically grounded and important part of agriculture, climate change and mitigation efforts, and not a matter of marginal academic interest.

CONCLUSION AND RECOMMENDATIONS

This study investigated the impacts of climatic stress on crop growth, physiological responses, yields, and rhizosphere soil microbial and nutrient parameters due to increased temperature, water-deficit stress, and their combination, as well as the extent of buffering of crop stress response by inoculation with beneficial plant-growth-promoting microorganisms (PGPMs). The results showed that all the combined abiotic stress (heat or drought) treatments significantly affected plant growth, physiological function, yield and soil microbial activity as compared to normal conditions, indicating the synergistic effect of both abiotic stresses as reported in the general literature on plant stress physiology. Microbial-inoculation benefits plant growth, plant physiological parameters, yield, soil microbial and nutrient outcomes significantly in all climate-stress conditions, and the benefits of microbial-inoculation increased systematically with increasing stress conditions; that is, beneficial plant–microbe interactions provided their greatest practical benefit where they were most needed, in the most severe combined-stress condition that most closely resembled the anticipated future climate conditions.

Based on these results, it is recommended to incorporate microbial inoculants (selected drought- and heat-adapted plant-growthpromoting rhizobacteria and mycorrhizal fungi) in climate adaptive crop-management packages, especially in areas where plants are more likely to suffer from combined heat-and-drought stress during the growing season. Agricultural-extension and input-supply systems must strive to make farmers more available to and knowledgeable about microbial inoculant products that can be effectively used and locally adapted to the needs of farmers, as was observed in the most extreme stress situations investigated in this study. The conservation of soil microbial biomass, activity and nutrient availability under stress conditions as obtained by microbial inoculation suggests that microbial inoculation should also be contemplated as a means of reducing the impact of stress on crops and as part of soil-fertility management over the long term in a changing climate. Based on the findings in the current study, it is recommended that the numbers of beneficial microbial strains and associated strain combinations, crop species, and field conditions (across seasons) be expanded for the purpose of validating the results; and that the specific physiological and soil-microbiological mechanisms that provide the disproportionate inoculation benefit under combined stress conditions be further studied, to optimize the selection and deployment of microbial inoculants for sustainable and climate-resilient agricultural production.

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