Pak. J. Bot., 57(4): DOI: http://dx.doi.org/10.30848/PJB2025-4(21)

CO-INOCULATION Of COMPOST WITH ARBUSCULAR MYCORRHIZAL FUNGI AND ENDOPHYTIC BACTERIA TO ALLEVIATE THE ADVERSE IMPACT OF DROUGHT STRESS IN MAIZE

LAHOUCINE ECH-CHATIR[1,2†], REDOUANE OUHADDOU[1,2†], CHAYMA IKAN[1,2], ABDERRAHIM BOUTASKNIT[3], ABEER HASHEM[4], GRACIELA DOLORES AVILA-QUEZADA[5], ELSAYED FATHI ABD_ALLAH[6] AND ABDELILAH MEDDICH[1,2,7*]

[1]*Center of Agrobiotechnology and Bioengineering, Research Unit Labelled CNRST, Cadi Ayyad University, Marrakesh 40000, Morocco*
[2]*Laboratory of Agro-Food, Biotechnologies and Valorization of Plant Bioresources, Department of Biology, Faculty of Science Semlalia, Cadi Ayyad University, Marrakesh 40000, Morocco*
[3]*Department of Biology, Multidisciplinary Faculty of Nador, Mohamed First University – Oujda, 62700 Nador, Morocco*
[4]*Botany and Microbiology Department, College of Science, King Saud University, P.O. Box. 2460, Riyadh 11451, Saudi Arabia*
[5]*Facultad de Ciencias Agrotecnológicas, Universidad Autónoma de Chihuahua, 31350, Chihuahua, Chihuahua, México*
[6]*Plant Production Department, College of Food and Agricultural Sciences, King Saud University, P.O. Box. 2460, Riyadh 11451, Saudi Arabia*
[7]*African Sustainable Agriculture Research Institute (ASARI), University Mohammed VI Polytechnic (UM6P), Laayoune 70000, Morocco*
[†]*These authors contributed equally to this work*
[*]*Corresponding author's email: a.meddich@uca.ma*

Abstract

Drought is a major abiotic factor limiting agricultural ecosystem productivity in arid and semi-arid areas. This study aims to evaluate the role of biostimulants in mitigating the adverse effect of water stress (well-watered (WW): 75% field capacity (FC) and drought-stressed (DS): 25% FC) through the application of single or combined biostimulants based on two microbial consortia (P: *Bacillus subtilis* and *Bacillus* sp., M: native arbuscular mycorrhizal fungi) and organic amendment (C) to *Zea mays* L. The metabolism of exposed plants to DS was negatively modified, affecting growth, mycorrhizal symbiosis, biochemistry, physiology, and mineral nutrition of the maize plants and also generated changes in the soil properties. Furthermore, biostimulants, particularly CM, improved shoot and root dry biomass by 179 and 275%, respectively, compared with control plants under DS. However, under 25% FC, shoot height and root length were stimulated by PC (68%) and P (37%) compared with the controls. Root mycorrhization was more intense when soil contained P and inhibited when it was amended with C under DS. The single/combined application of biofertilizers enhanced stomatal conductance, osmolytes (proline and total soluble sugars), antioxidant system (Polyphenol oxidase), and leaf mineral composition (K, Fe, S, Ca, Mn, and Zn) compared with untreated plants. On the other hand, stress markers content (malondialdehyde and hydrogen peroxide) were reduced by CMP treatment (67% and 18%, respectively). Biostimulants (C and/or P and/or M) modified soil quality by improving total organic matter, available phosphorus, nitrogen, K, Si, Ca, Fe, S, Mn, and Zn. In conclusion, the strategy of combining biostimulants could be an ecological solution in degraded agricultural soils in arid and semi-arid regions to protect maize crops against drought.

Key words: Drought stress; AMF; *Bacillus* sp.; *Bacillus subtilis*; Compost.

Introduction

On a global scale, and in (semi)arid climates in particular, irregular rainfall and elevated temperatures are the principal factors threatening and disrupting food security through pronounced drought. The greatest threat is that drought is expected to bring down the world's production of major crops by around fifty percent by 2050 and by ninety percent by 2100 (Malhi *et al.*, 2021). Due to climate change, crops of economic interest, in particular, are being adversely affected by extreme water shortages in terms of yield and fruit nutritional quality (Soares *et al.*, 2023). Several Researchers have reported that drought damages morpho-physiological aspects of plants, such as cells' membrane degradation, increased oxidative activity, and reduced photosynthesis rates (Boutasknit *et al.*, 2020; Manaa *et al.*, 2021). Drought disrupts the normal circulation of water in plant's different parts, resulting in physiological drought (Quiroga *et al.*, 2020). Many physiological parameters are negatively affected by severe drought, including water content, photosynthetic pigments, leaf water potential and stomatal conductance (Anli *et al.*, 2020; Ouhaddou *et al.*, 2023a). Similarly, at the biochemical level, water stress weakens immune system performance by accumulating reactive oxygen species (ROS), thus, generating oxidative stress (Hasanuzzaman *et al.*, 2020). Besides affecting the plant, this stress also impacts the physico-chemical properties of the soil (Benaffari *et al.*, 2022). In very water-limited conditions, it is the root that receives stress first, as it is in contact with changes in soil moisture (Shimazaki *et al.*, 2005). Access to mineral elements and water is, therefore, very limited in such conditions (Soufiani *et al.*, 2023). There are several reasons behind this, such as the slower release of mineral nutrients as they move from a mobile to an immobile state. On the other hand, lower soil water content leads to reduced leaching of nutrients into the soil solution and a lower mineral weathering rate (Schlesinger *et al.*, 2016; Slessarev *et al.*, 2016). This lack of access to mineral nutrients has direct repercussions on the photosynthetic machinery, whose functioning is closely linked to mineral elements and water, which in turn reduces biomass and plant yields (Zargar *et al.*, 2017).

Cereals are among the crops affected by drought, as in the case of maize (*Zea mays* L.) (Sood *et al.*, 2020). Around forty percent of global maize production decreased due to drought in 2013 (Daryanto *et al.*, 2016). As its name suggests, sweet corn (SC) has a high sugar content (polysaccharides) (Harakotr *et al.*, 2022). Worldwide, SC plays a key role, both directly and indirectly, by providing calories, proteins, and certain vitamins and minerals needed by humans (Xiang *et al.*, 2019). It is intended for human use, fodder, ethanol, and industrial sugar production. Corn is the world's most important cereal crop, accounting for 1.135 billion tonnes per year (Tinte *et al.*, 2022). In the context of climate change and population growth, the introduction of phytochemical products to intensify agricultural productivity has been the main solution. However, their massive application year-on-year threatens soil and human health (Rouphael & Colla, 2020; Mushtaq *et al.*, 2021). Saving and ensuring food security without compromising soil and human health is one of the ecological approaches most recommended by researchers (Nephali *et al.*, 2021; Krasilnikov *et al.*, 2022). Scientists are now suggesting that the use of biostimulants is one of the main strategies for boosting agricultural productivity, particularly during drought (Meddich, 2022). Several studies showed the biostimulants' ability to induce positive changes in plants' physiological, biochemical, and growth processes (Wu, 2017; Etesami & Maheshwari, 2018). The plant rhizosphere is a source of microorganisms such as plant growth-promoting bacteria (PGPR) whose role is the stimulation of the growth of plants through a number of mechanisms (Ouhaddou *et al.*, 2022a). They facilitate access to mineral elements through their direct action on roots. PGPR modulate the adverse impacts of oxidative stress generated by drought by strengthening the enzymatic antioxidant system (SOD, POX...etc). These bacteria stimulate the biosynthesis of phytohormone signalling pathways essential for plant development and growth under standard and stress conditions. They have a positive effect on the structure of soil via substances capable of binding soil particles together to form aggregates, notably exopolysaccharides (Raklami *et al.*, 2019; Slimani *et al.*, 2023). In addition, plants are also able to form symbiotic relationships with arbuscular mycorrhizal fungi (AMF), providing the plant with its needs, notably water and mineral elements, through their mycelial network (Han *et al.*, 2023). AMF can supply plants with a degree of resistance to abiotic stresses, such as drought, through some adaptive strategies: i) improving the plant's water status by stimulating genes encoding aquaporins (Cheng *et al.*, 2020), ii) increasing the efficiency of mineral uptake thanks to arbuscules such as the acquisition of phosphorus, potassium, and nitrogen in the plant (Meddich *et al.*, 2021b; Begum *et al.*, 2022), iii) improving gas exchange (Soussani *et al.*, 2023), iv) modulating osmotic stress by accumulating osmolytes (Begum *et al.*, 2022), v) regulating oxidative stress by boosting antioxidant activity (Ikan *et al.*, 2023b). In addition to rhizospheric microorganisms, soil enrichment with organic amendments such as compost is a good alternative for farmers (Mobaligh *et al.*, 2023). Thanks to its composition in organic matter and minerals, including phosphorus and nitrogen, it boosts crop productivity and yields (Meddich *et al.*, 2019; Ben-Laouane *et al.*, 2020). Numerous studies have confirmed compost's role in improving plant growth traits, physiology and biochemistry under conditions of water deficit (Kanwal *et al.*, 2017).

It has been demonstrated that the microorganisms mentioned above when combined or not with compost, enhance the growth of various crops (lettuce, alfalfa, wheat) in comparison with their singular applications (Gopal *et al.*, 2012; Begum *et al.*, 2022). However, research on the use of this new alternative combination in sweet corn (SC) in water stress conditions is still not well developed. In this respect, this study aims to test the efficacy of single or combined application of native biostimulants and compost on morphological, biochemical, physiological, and nutritional processes of SC plants under well-watered and drought-stressed conditions. Particularly to understand the role of mineral elements in plant tolerance through the application of biostimulants.

Material and Methods

Indigenous microorganisms and local compost: The microbial biostimulants used in this study were collected from the palm grove of Tafilalet's rhizosphere, which is situated in an arid area 500 kilometers southeast of Marrakech, Morocco. To obtain an optical density of about 1 at 600 nm (1×10^9 CFU/mL) for the PGPR (P)-based bacterial consortium, all strains were grown for 48 hours at 30°C in Tryptic Soy Broth (TSB) liquid medium with agitation. The mycorrhizal consortium (M) was obtained by multiplication using maize as a mycotrophic plant for 3 months. The M inoculum consisted of fragments of infected roots, vesicles, and hyphae. Both consortia were inoculated at the time of transplanting of maize seeds and the local compost was mixed with the soil. Table 1 lists all the characteristics of the biostimulants used.

Plant growth conditions, treatments, and study design: This work was carried out at Cadi Ayyad University, Faculty of Science, Marrakech, Morocco, in a culture room with a temperature of 24°C, photosynthetically active radiation (PAR) of 600 μmol $m^{-2}s^{-1}$, light/dark photoperiod of 16/8 h, and 65.5% relative humidity. The maize seeds (*Zea mays* L.) were disinfected with NaClO (10%) for ten minutes and rinsed with distilled water, then germinated in sterile sand for three days. After germination, seeds were moved and placed in plastic bags (3 seeds/pot) containing three kilograms of soil previously sterilized in an oven at 180°C for 4 hours. The following physico-chemical characteristics were observed in the soil used: sand: 50%, loam: 30%, clay: 20%, pH: 8.6 and EC: 0.2 mS/cm, available phosphorus: 12 ppm, organic matter: 1%, organic carbon: 0.60%, nitrogen: 0.09%, calcium: 0.86%, potassium: 0.24%, silicon: 0.4%, iron: 2.45%, sulfur: 0.03%, manganese: 0.04, zinc: 0.007%.

Table 1. Biostimulants characteristics.

	Origin	Properties	Applied amounts
Compost (C)	- Vermicompost	- pH: 7.7 - Phosphorus: 1.11 % - Nitrogen: 2.05 % - Potassium: 0.88 % - Calcium: 0,85 % - Magnesium: 0.90 % - Zinc: 5.1 ppm - Copper: 2.00 ppm - Iron: 5.9 ppm - Carbon: 18.02 $\%^{-1}$	5%
Mycorrhizal consortium (M)	- 15 species: *Acaulospora delicata, Acaulospora leavis, Acaulospora* sp,, *Claroideoglomus claroideum, Glomus aggregatum, G. clarum, G. claroides, G. deserticola, G. heterosporum, G. macrocarpum, G. microcarpum, G. versiforme, Glomus* sp., *Rhizophagus intraradices, Pacispora boliviana*	- Tolerance to water and salt stress - Promotes plant growth	15 g
Bacterial consortium (P)	- 2 species: *Bacillus subtilis, Bacillus* sp.	- Secretion of exopolysaccharides (EPS) - Solubilization of phosphorus, - Solubilization of potassium - Auxin synthesis - Resistance to polyethylene glycol 6000	10 ml (reminder after 15 days)

Two factors were investigated in the experiment in a completely arbitrary design: 1) water stress using two water regimes, well-watered (WW: 75% of field capacity (FC)) and drought-stressed (DS: 25% FC). 2) based on biofertilizers applied alone: i) plants without treatment (control), inoculated with the bacterial consortium (P), AMF consortium (M), or organic amendment (C), or mixed: ii) M+P, P+C, C+M, and C+M+P. All treatments were repeated 10 times. At the 4-leaf stage of the maize plants, DS was applied and the soil moisture was maintained according to the desired water regime.

Root mycorrhizal colonization and growth: After harvesting the maize plants, the roots were cleaned and subjected to an evaluation of colonization by mycorrhizal structures using the methodology developed by Phillips & Hayman (1970). The roots were chopped into short fragments (1 cm) and then treated with 10% KOH until total emergence and placed at 90°C for 40 min. To neutralize excess KOH, samples were subsequently treated for 10 minutes with 2% HCl. Roots were stained using trypan blue (90°C for 20 min). After microscopic observation (OPTIKA Microscopes, Italy), Two indexes for mycorrhization were measured: the frequency of mycorrhization (MF) and the intensity of mycorrhization (MI) as described by Trouvelot *et al*., (1986).

Morphological growth traits such as shoot dry weight (SDW), root dry weight (RDW), shoot height (SH), root length (RL), and leaves number (LN) were measured. After that, the root and above-ground sections were dehydrated at 80°C until their weights stabilized. Mineral elements content was assessed in leaves such as calcium (Ca), Silicon (Si), phosphorus (P), potassium (K), iron (Fe), manganese (Mn), sulfur (S), and zinc (Zn) by XRF analyzer Delta Handheld, Olympus, Germany. The kinetics of growth parameters and physiology were recorded during maize cultivation every two weeks (W).

Photosynthetic efficiency and gas exchange measurements: Gas exchange (gs) measurements were taken between 09:00 and 11:00 using a porometer (SC-1 LEAF POROMETER) on well-developed leaves along the leaf blade according to the procedure described by Harley *et al*., (1992).

Measurements of chlorophyll fluorescence were taken using a portable fluorometer: OPTI-SCIENCE, OS30p. The test surface was created by clamping a leaf and leaving it in the dark for half an hour. Following the light flash, the fluorescence signal was acquired at a speed of 10 µs for one second. The initial fluorescence (F_0), maximum fluorescence (F_m), and quantum yield were measured.

$(F_m\text{-}F_0)/F_m = F_v/F_m$, where F_v is the variable fluorescence (Straaer, 1995).

Protein quantification and antioxidant activity determination: To obtain fresh material protein extracts, 0.1 g was ground and placed in 4 mL of 1 M phosphate buffer (pH 7) together with 2.5% insoluble polyvinylpolypyrrolidone (PVPP) and 0.1 mM EDTA (ethylene diamine tetraacetic acid) (Bradford, 1976). These extracts were used for the determination of enzyme activities.

Using the method of Hori *et al*., (1997), polyphenol oxidase (PPO) activity was evaluated. 0.1 ml of the enzyme extract was added to two milliliters of catechol (10 mM). The activity of PPO was given in units of enzyme mg^{-1} of protein. The amount of enzyme causing an increase in absorbance of 0.001 min^{-1} at 420 nm is defined as one unit of PPO activity.

Osmolytes determination: The concentration of total soluble sugars (TSS) was measured after grinding a fresh 0.1 g sample in ethanol 80%. Once centrifuged, test tubes were filled with 0.2 ml of the extract, 0.2 mL of phenol and 1 mL of pure sulfuric acid. The concentration of TSS was assessed at 485 nm (Dubois *et al.*, 1956).

Proline concentration was assessed as described by Carillo *et al*., (2008). 0.1 g of the fresh material was ground in 4 ml of ethanol (40%). The extract was stored overnight at 4°C. Afterwards, a mixture of 1% ninhydrin, 60% acetic acid, and 20% ethanol was added in 1 ml to 0.5 ml of the ethanolic extract obtained. Optical density (OD) was read at 520 nm following placement of the reaction mixture at 90°C for 20 minutes.

Malondialdehyde and hydrogen peroxide content: Quantification of malondialdehyde (MDA) was done according to the method developed by Dhindsa & Matowe (1981). 1 mL trichloroacetic acid (TCA) 10% and 1 mL acetone (90%) were used to homogenize 0.05 g fresh material. After centrifugation, 0.5 mL of 0.6% thiobarbituric acid (TBA) and 0.5 mL of 0.1% phosphoric acid were combined with 0.25 mL of the supernatant. After 30 minutes of incubation at 100°C, the process was stopped with an ice bath, and 0.75 mL of 1-butanol was added. Measurements of OD were made at 532 and 600 nm.

Hydrogen peroxide (H_2O_2) levels in leaves were determined by grinding 0.1 g in 2 mL of 10% (w/v) TCA. After centrifugation, the OD of a mixture containing 0.5 mL of the supernatant, 1 mL potassium iodide (1 M), and 0.5 mL potassium phosphate buffer (10 mM, pH 7) was measured at 390 nm (Velikova *et al.,* 2000).

Soil analysis: After harvesting, rhizospheric soil samples were subjected to the following analyses: Nitrogen (N) (Kjeldahl method), available phosphorus (AP) (Olsen & Sommers, 1982), total organic carbon (TOC) and total organic matter (TOM) (Aubert, 1978), electrical conductivity (conductivity meter, HI-9033, Hanna Instruments, Padova, Italy) and pH in water (pH meter, HI 9025). Mineral elements were assessed, such as calcium (Ca), iron (Fe), potassium (K), silicon (Si), phosphorus (P), manganese (Mn), sulfur (S), and zinc (Zn) by X-ray fluorescence spectrometry (XRF) (Analyzer Delta Handheld, Olympus, Germany).

Statistical data analysis: Data analysis was carried out using RStudio (version 2023.9.1.494). For data analysis, two-way ANOVA based on Tukey's Honest Significant Difference (HSD) test with a significance value of 5% was employed. At the $p<0.05$ level, smaller values denote significant differences between treatments. In addition, in a heatmap, a Pearson correlation and Dendrograms were done between the physiological, morphological, nutritional, and biochemical characteristics of the maize plants in all treatments. For mycorrhization frequency and intensity, the non-parametric Scheirer–Ray–Hare test was used instead (Rohlf & Sokal, 1995), followed by the Dunn post hoc test.

Results

Effect on mycorrhizal symbiosis, growth and physiology: Microscopic examination of maize plant roots showed that untreated plants were not infected with AMF (M). Drought stress (DS) significantly reduced mycorrhization intensity (MI), with the highest value (59.3%) observed in plants supplemented with P compared with their control (M). Under the same conditions, this parameter showed an increase when C and P were applied to the soil (CMP). An almost total inhibition of root colonization (4.2%) was observed with the double combination of M and C (CM), regardless of watering conditions (Fig. 1A). On the other hand, mycorrhization frequency (MF) ranged between 60% and 100% under WW or DS conditions. The results showed that DS significantly reduced MF. Under 25% field capacity (FC), plants mycorrhized in the presence of bacterial consortium (MP) showed 100% mycorrhization compared with plants treated only with mycorrhizal consortium M. But this frequency was reduced in the presence of compost (C) under WW or DS conditions (Fig. 1B).

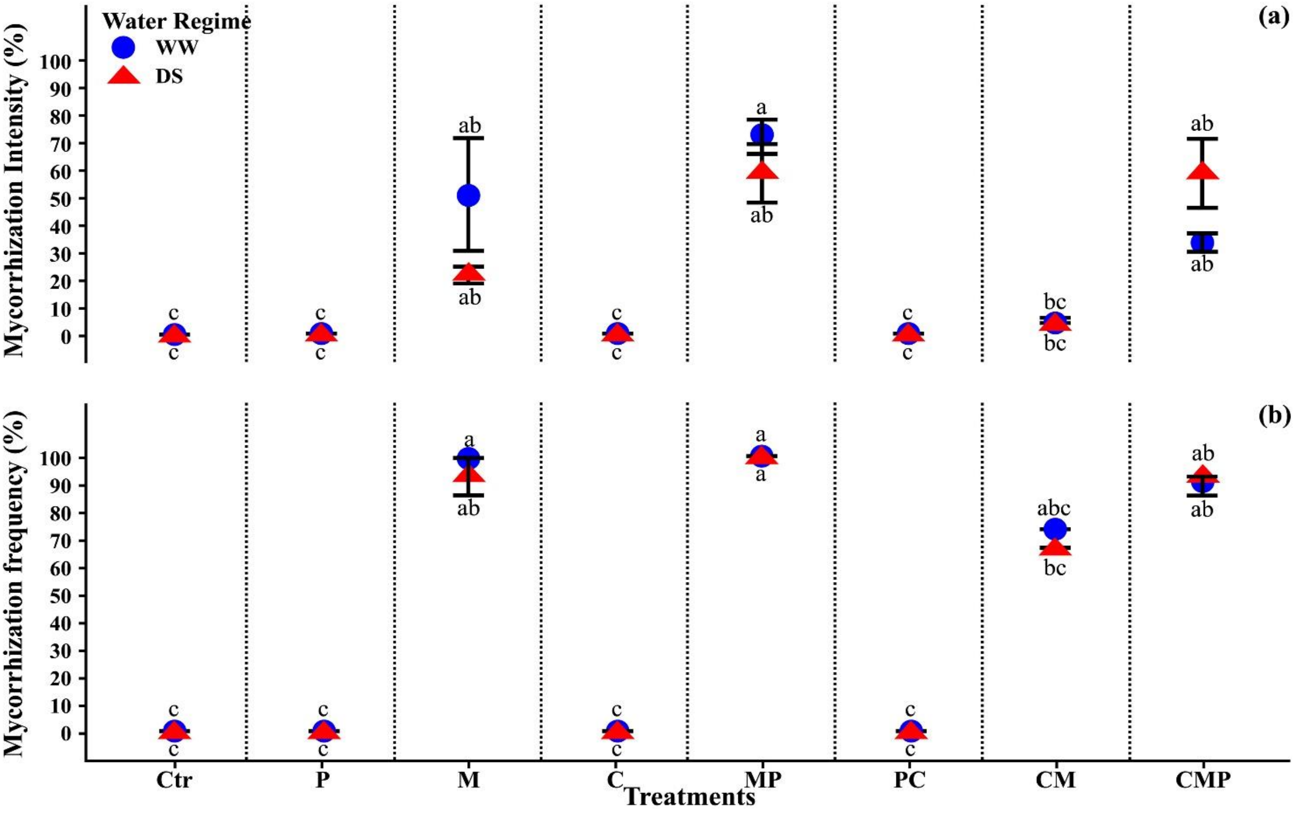

Fig. 1. Effect of biostimulants (P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM, and CMP) and water regimes (75 and 25% FC) on mycorrhization intensity (a) and frequency (b) in maize plants compared with controls (Ctr). The values of each column labeled with different letters indicate significant differences assessed by the Scheirer–Ray–Hare test, followed by the Dunn post hoc test.

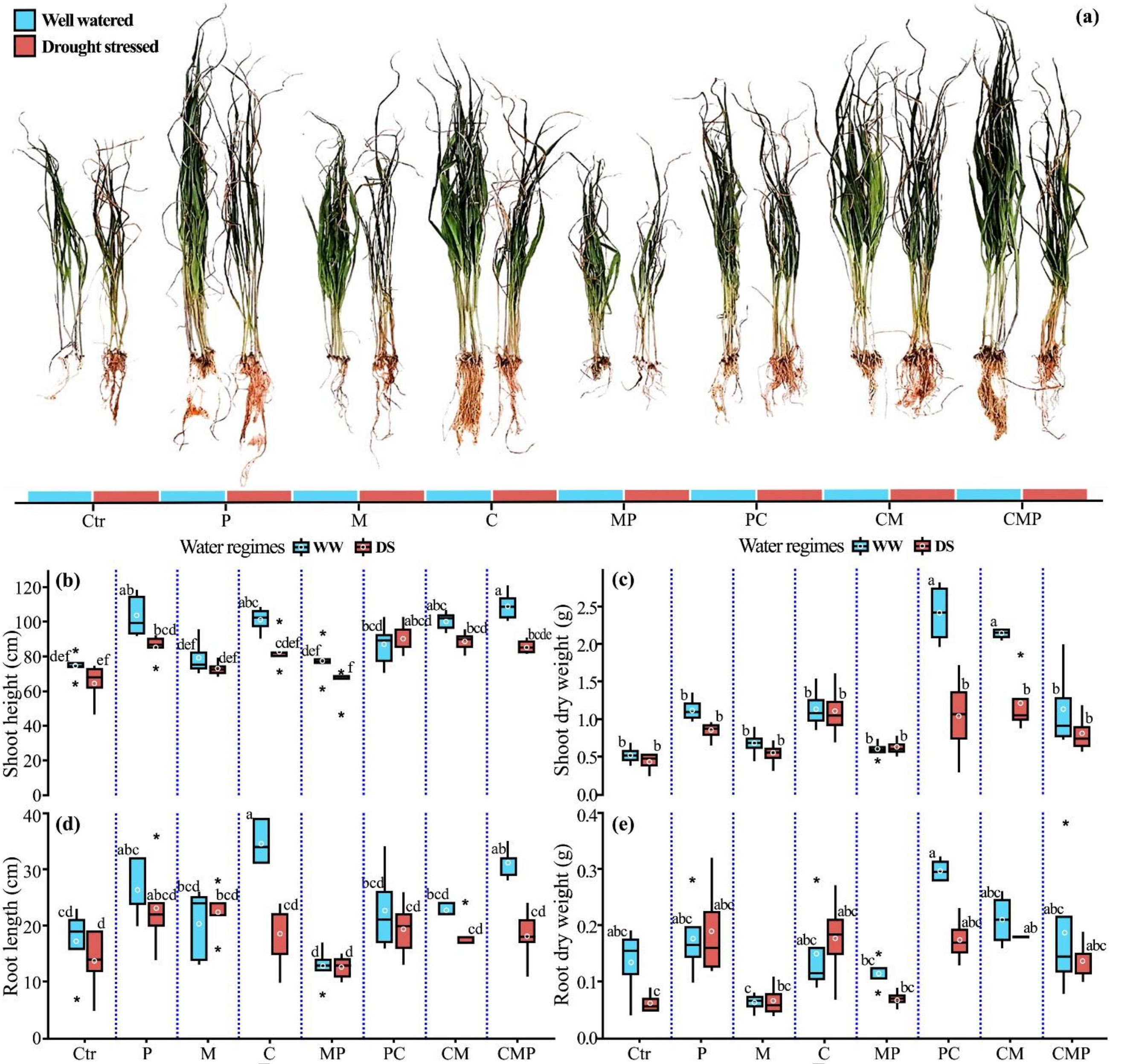

Fig. 2. Effect of biostimulants (P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM, and CMP) and water regimes (75 and 25% FC) on (a, b) shoot height, (c) shoot dry weight, (a, d) root length and (e) root dry weight in maize plants compared with controls (Ctr). The values of each column labeled with different letters indicate significant differences assessed by Tukey's test ($p < 0.05$). Boxplots show the median (horizontal line), quartiles (boxes), and mean (white circle).

Compared with control plants, the unfavorable water regime adversely affected morphological indicators such as shoot dry weight (SDW), root dry weight (RDW), shoot height (SH), root length (RL), and number of leaves formed (LN) (Fig. 2A, B, C, D, E). However, soil enrichment with biostimulants significantly improved these parameters, irrespective of the water regime imposed. SH was positively stimulated following the application of PC (37%) and CM (36%) under severe conditions compared with respective controls (Fig. 2A, B). The values of this parameter ranged between 20 and 100 cm over time depending on the stress and the biostimulants applied (Fig. 3). As soon as the stress was applied (W3 and W4), its values were lower in the untreated plants (64 ± 4.93). Moreover, biostimulants in association with microbes (PC) enhanced this parameter (90 ± 3.98) (Fig. 3). A remarkable and significant effect was noted on SDW of plants grown in the presence of 5% compost and/or P or M, e.g., 154.26%, 138.31%, and 179%, respectively, under 25% FC ($p < 0.05$, Fig. 2C). While, RL was improved by P (68%) compared with control plants (Fig. 2A, D). Among all treatments, plants treated with CM showed a high value of RDW compared with the control under a pronounced lack of water (Fig. 2E). It should also be noted that the number of leaves increased in plants receiving the 3 biostimulants at the same time under 25% FC. Over time, only 6 leaves were reached because of the delay generated by DS from W3, except for CM and CMP were 8 leaves were observed in comparison with control plants after the severe stress periods.

The physiology of maize plants was affected by DS and applied biostimulants. DS negatively affected stomatal conductance (gs) (Fig. 3). However, the addition of biostimulants improved this parameter, particularly in plants treated with C and/or M under reduced water levels (25% FC) as compared to control. With no water stress, inoculation of plants with the P significantly improved gs by 293% as compared to the control. During and after water stress application, gs began to decrease after 1 month of cultivation, essentially in plants neither amended nor inoculated. Therefore, during this period, a clear improvement was observed in the plants receiving CM at the same time, compared with their control. Tripartite application (CMP) helped to overcome the negative effect of DS on maize plants by improving photosynthetic apparatus (F_v/F_m) by 3.5% compared with the untreated, stressed control, but no significant difference was detected. From W1 to W4, the F_v/F_m of untreated maize plants decreased as the soil began to dry out (from 0.760 to 0.723). On the other hand, the F_v/F_m of the plants biostimulated by CMP decreased from 0.780 to 0.740 in comparison with the control plants (Fig. 3).

Effect on Biochemical Traits

Proteins and antioxidant activity: The water regimes applied (75 and 25% FC) and the biostimulants affected the protein content and antioxidant activity of the aerial part (Table 2). With no water stress, plants treated with P alone or with C and M (CMP) showed maximum protein contents ($p<0.05$) of 89 and 93%, respectively, in comparison with unstressed control. Moreover, under 25% FC, the combination of P with C enhanced protein composition (307%) compared with untreated and stressed plants. PPO recorded higher values ($p<0.05$) in stressed and untreated plants followed by those treated with M alone and RC in duplicate.

Osmolytes accumulation: Reducing soil moisture from 75 to 25% FC caused an increase in total soluble sugars (TSS) and proline levels in the leaves (Table 2). Whatever the water regime applied, the triple combination of biostimulants (CMP) increased TSS levels in comparison with control plants. With no water stress, sugars were reduced by half as compared with controls in plants inoculated with P or M. As for proline, the combined action of C and P significantly ($p<0.05$) increased proline levels (119.41 μmol/g) compared with all treated and untreated treatments under 25% FC. In addition, plants inoculated with bacterial suspension (P) showed higher amino acid accumulation irrespective of FC application, compared with stressed and unstressed controls.

Lipid peroxidation and hydrogen peroxide content: The level of hydrogen peroxide(H_2O_2) in leaves was significantly reduced as a result of biostimulant application compared with untreated plants in severely water-limited conditions (25%). A significant (52%) reduction ($p<0.05$) in H_2O_2 levels was observed for treatments with C and P (PC) followed by those mycorrhized and inoculated with MP (35%), CMP (19%) and CM (17%) under DS conditions compared with their respective controls (Table 2). Decreasing FC to 25% also induced an over-accumulation of the final by-product of cell membrane degradation (MDA) in the leaves. However, the triple combination (CMP) recorded very low and significant values (by 67%) in MDA compared to control plants under DS conditions (Table 2).

Effect of drought stress and biostimulants on mineral composition of leaves and soil: XRF results showed that the soil and maize leaves mineral content evolved positively during the biostimulant*DS interaction (Table 3). Soil desiccation (25% FC) caused a significant attenuation of (macro) microelements in the leaves. Potassium (K) and iron (Fe) were significantly improved in plants grown in compost-amended soils and infected with the fungi (CM) under severe conditions, compared with other treatments, including the untreated and non-inoculated controls. However, plants double-treated with PC revealed highly significant sulfur (S) and manganese (Mn) values compared with control plants under 25% FC. Zn and Ca reached maximum values in mycorrhizae-treated plants alone (M) or in combination with the bacterial consortium (P), respectively, in comparison with control plants. In the conditions of water stress, treatments with the triple combination (CMP), showed high values of phosphorus (P) in comparison with their controls.

The mineral elements evaluated (Ca, K, Si, Fe, P, S, Mn, and Zn) were also affected by the water regimes and biostimulants application. Under WW conditions, soils inoculated with CMP, MP, and P had high Ca contents of 15, 13.4, and 13.46%, respectively, compared with control soils. However, under DS conditions, Ca, S, and Fe levels in M-treated soil exceeded those in the control. Under the same conditions, the addition of C alone improved the composition of S (12.32%), Si (5.3%), P (2%), Mn (3%), and Zn (10.8%) compared with the control. The M and P treatments significantly improved soil K content at 21.23 and 15.52%, respectively, compared with their corresponding controls (Table 3).

Effect on soil physico-chemical properties: Positive changes in soil physicochemical properties were observed after harvesting maize plants under WW and DS conditions. Total organic matter (TOM), total organic carbon (TOC), available phosphorus (AP) and nitrogen (N) were significantly modified ($p<0.05$) in soils supplemented mainly with C singly or together with P and/or M (Table 4). Under DS conditions, the maximum values of TOM, and TOC were raised and improved significantly by PC (238%), C (211%), and CM (201%) compared to control soils. In addition, AP levels were significantly improved in the soil where all the biostimulants were combined (CMP), followed by soil treated with compost alone under DS conditions, compared with their controls. As for N, significantly high levels were noted in the soil that had received the three biofertilizers (CMP) in comparison with unstressed control. Under DS conditions, mycorrhizae-amended soil inoculation (CM) was the best treatment in terms of N content compared with the other treatments, including the stressed and unstressed control, but no significant differences were noted. Electrical conductivity and pH were modified by the effect of biostimulants and FC. Both DS and biostimulants caused a slight increase in these parameters.

Table 2. Effect of two water regimes (WW: well-watered and DS: drought stress) and biostimulants (P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM and CMP) on biochemical traits compared with controls (Ctr). Values are means ± SE. The values of each column labelled by different letters indicate significant differences assessed by Tukey's test (p<0.05).

	Protein (mg/g DM)		PPO (µmol de catechol. min^{-1} .mg^{-1} Prot)		TSS (mg/g DM)		Proline (µmol/g DM)		H_2O_2 (nmol/g DM)		MDA (nmol/g DM)	
	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS
Ctr	23.68±5.37 c-f	5.39±0.68 f	0.45±0.19 bc	2.10±0.28 a	152.41±4.70 b	186.58±2.76 a	45.17 ±1.84 h	43.08±1.12 h	0.007±0.00 g-i	0.011±0.00 b	87.23±9.23 cd	205.42±20.85 a-c
P	44.91±0.46 ab	9.39±4.69 ef	0.24±0.00 c	0.80±0.03 bc	72.00±3.24 c	186.33±2.77 a	96.78 ±2.90 a-c	98.12±5.62 ab	0.005±0.00 j	0.009±0.00 b-d	93.94±47.08 b-d	92.90±17.28 b-d
M	32.27±1.93 a-d	10.18±0.85 ef	0.40±0.02 bc	1.18±0.10 b	73.90±2.43 c	180.61±2.47 a	52.75±2.65 f-h	77.42 ±1.91 b-e	0.007±0.00 e-h	0.014±0.00 a	70.71±0.89 cd	231.74±37.84 a
C	36.33±3.61 a-c	16.73±0.30 d-f	0.33±0.04 bc	0.54±0.00 bc	134.08±1.04 b	185.18±3.93 a	69.09±6.03 d-g	83.36±3.63 b-d	0.006±0.00 h-j	0.010±0.00 bc	108.90±5.66 a-d	131.10±49.56 a-d
MP	26.52±2.05 b-e	16.82±0.32 d-f	0.52±0.04 bc	0.64±0.01 bc	132.63±2.82 b	185.37±2.24 a	43.68±0.27 h	70.49±7.48 d-g	0.008±0.00 d-g	0.007±0.00 f-h	169.29±2.38 a-d	175.23±35.01 a-d
PC	18.95±2.45 c-f	21.96±8.05 c-f	0.61±0.07 bc	1.07±0.53 bc	152.06±1.89 b	182.56±1.97 a	47.38±4.02 gh	119.41±3.96 a	0.008±0.00 d-g	0.005±0.00 ij	226.58±26.52 ab	191.48±30.09 a-d
CM	19.87±0.83 c-f	11.94±2.51 ef	0.82±0.03 bc	0.87±0.21 bc	179.67±6.30 a	172.51±9.10 a	77.42±8.12 b-e	74.40±3.65 c-f	0.007±0.00 e-h	0.009±0.00 c-e	72.77±2.08 cd	124.90±35.16 a-d
CMP	45.71±6.72 a	18.60±0.39 c-f	0.62±0.00 bc	0.20±0.02 c	186.03±2.86 a	191.42±0.22 a	54.86±0.41 e-h	84.60±1.44 b-d	0.006±0.00 h-j	0.009±0.00 c-f	64.00±1.19 d	66.06±2.38 d

Table 3. Effect of two water regimes (WW: well-watered and DS: drought stress) and biostimulants (P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM and CMP) on mineral composition of leaves and soil compared with controls (Ctr).

		Ca (%)		K (%)		Si (%)		Fe (%)		P total (%)		S (%)		Mn (%)		Zn (%)	
		Soil	Leaves	Soil	Leaves	Soil	Leaves	Soil	Leaves	Soil	Leaves	Soil	Leaves	Soil	Leaves	Soil	Leaves
WW	Ctr	1.04±0.007	0.81±0.005	0.27±0.004	0.76±0.005	0.46±0.012	0.35±0.010	3.04±0.021	0.25±0.003	0.13±0.005	0.10±0.004	0.03±0.003	0.02±0.002	0.05±0.003	0.04±0.002	0.009±0.000	0.004±0.000
	P	1.18±0.008	0.73±0.005	0.27±0.004	0.70±0.005	0.42±0.016	0.36±0.010	2.94±0.019	0.12±0.002	0.12±0.005	0.10±0.004	0.03±0.002	0.03±0.002	0.04±0.002	0.04±0.002	0.008±0.000	0.004±0.000
	M	1.00±0.007	0.64±0.004	0.24±0.004	0.68±0.005	0.40±0.011	0.35±0.010	3.01±0.020	0.10±0.002	0.11±0.004	0.09±0.004	0.02±0.004	0.03±0.002	0.04±0.003	0.02±0.001	0.008±0.000	0.004±0.000
	C	0.99±0.007	0.73±0.005	0.27±0.004	0.77±0.006	0.42±0.015	0.36±0.010	2.86±0.019	0.17±0.003	0.12±0.004	0.10±0.004	0.02±0.002	0.03±0.002	0.04±0.002	0.03±0.002	0.007±0.004	0.005±0.000
	MP	1.18±0.008	0.75±0.005	0.30±0.004	0.62±0.005	0.44±0.012	0.35±0.010	3.09±0.021	0.15±0.002	0.11±0.005	0.10±0.004	0.03±0.002	0.02±0.002	0.04±0.003	0.03±0.002	0.009±0.000	0.004±0.000
	PC	1.06±0.007	0.67±0.005	0.27±0.004	0.98±0.007	0.41±0.011	0.40±0.011	2.84±0.018	0.14±0.003	0.11±0.004	0.11±0.004	0.03±0.002	0.03±0.002	0.04±0.002	0.02±0.002	0.007±0.000	0.007±0.000
	CM	1.06±0.007	0.61±0.004	0.25±0.004	0.93±0.006	0.40±0.011	0.36±0.010	2.72±0.018	0.08±0.002	0.11±0.004	0.10±0.004	0.03±0.002	0.03±0.002	0.04±0.002	0.01±0.001	0.008±0.000	0.004±0.000
	CMP	1.20±0.008	0.56±0.004	0.30±0.004	0.64±0.005	0.44±0.012	0.36±0.010	3.14±0.021	0.04±0.001	0.13±0.005	0.10±0.004	0.03±0.002	0.02±0.002	0.04±0.002	0.01±0.001	0.009±0.000	0.006±0.000
DS	Ctr	1.20±0.008	0.55±0.004	0.28±0.004	0.37±0.004	0.43±0.012	0.37±0.010	2.96±0.020	0.10±0.002	0.13±0.005	0.10±0.004	0.03±0.003	0.02±0.002	0.04±0.003	0.02±0.001	0.008±0.000	0.007±0.000
	P	1.20±0.008	0.64±0.004	0.32±0.005	0.46±0.004	0.44±0.012	0.35±0.001	2.92±0.020	0.13±0.002	0.12±0.005	0.10±0.004	0.03±0.003	0.02±0.002	0.04±0.003	0.02±0.002	0.007±0.000	0.004±0.000
	M	1.26±0.008	0.37±0.003	0.34±0.005	0.13±0.003	0.44±0.012	0.33±0.009	3.10±0.021	0.09±0.002	0.13±0.005	0.09±0.003	0.04±0.003	0.01±0.002	0.04±0.002	0.00±0.002	0.008±0.000	0.006±0.000
	C	1.18±0.008	0.60±0.004	0.29±0.005	0.85±0.006	0.45±0.012	0.35±0.002	2.92±0.020	0.08±0.002	0.13±0.005	0.10±0.004	0.04±0.003	0.03±0.002	0.04±0.003	0.02±0.001	0.009±0.000	0.005 ± 0.000
	MP	1.09±0.008	0.66±0.005	0.26±0.004	0.57±0.005	0.40±0.011	0.35±0.010	3.03±0.022	0.25±0.003	0.11±0.005	0.10±0.004	0.03±0.002	0.02±0.002	0.03±0.002	0.02±0.001	0.008±0.000	0.003 ± 0.000
	PC	1.11±0.007	0.62±0.004	0.29±0.004	0.72±0.005	0.41±0.011	0.35±0.010	2.97 ± 0.019	0.19 ± 0.003	0.12 ± 0.005	0.10 ± 0.004	0.03 ± 0.002	0.02 ± 0.002	0.04 ± 0.002	0.03 ± 0.002	0.008 ± 0.000	0.005 ± 0.000
	CM	0.93±0.007	0.63±0.004	0.23±0.004	0.95±0.006	0.41±0.011	0.36±0.010	2.59±0.018	0.25±0.003	0.12±0.005	0.10±0.004	0.03±0.002	0.02±0.002	0.04±0.002	0.02±0.002	0.008±0.000	0.004±0.000
	CMP	1.09±0.007	0.62±0.004	0.28±0.004	0.73±0.005	0.41±0.011	0.34±0.010	2.87±0.019	0.19±0.003	0.11±0.005	0.10±0.004	0.03±0.002	0.02±0.002	0.04±0.002	0.02±0.001	0.008±0.000	0.004±0.000

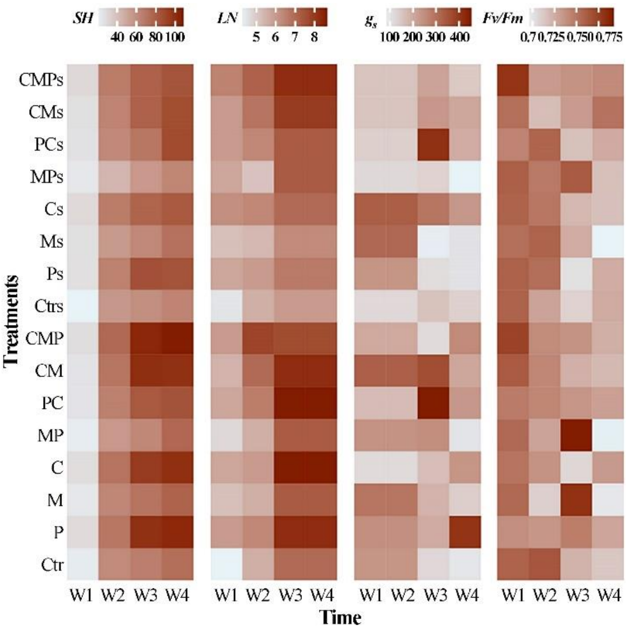

Fig. 3. Kinetics of growth and physiological parameters under the effect of biostimulants (P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM, and CMP) and water regimes (75 and 25% FC) every 15 days from the date of transplanting (W1, W2, W3, and W4) compared with controls. SH: shoot height, LN: leaf number, gs: stomatal conductance, Fv/Fm: chlorophyll fluorescence.

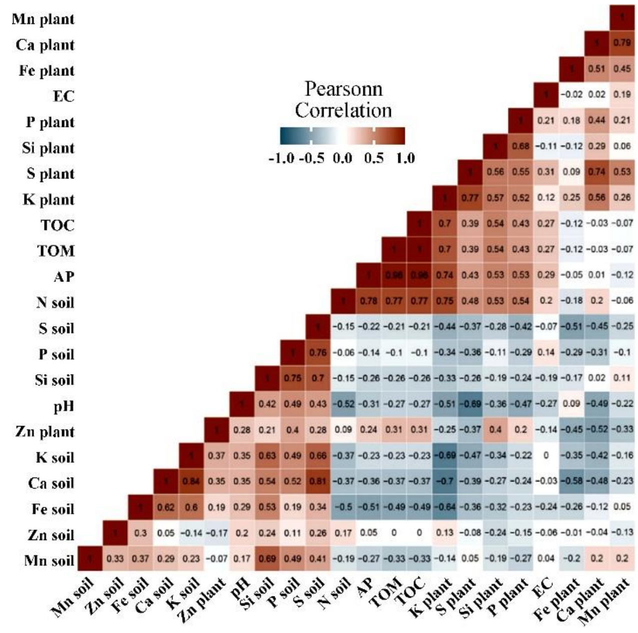

Fig. 4. Pearson correlation analysis for the effect of biostimulants (Ctr: control plants, P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM, and CMP) and water regimes (75 and 25% FC) on physicochemical characteristics of soil. TOM: total organic matter, TOC: total organic carbon, AP: available phosphorus, EC: electrical conductivity, Ca: calcium, K: potassium, Si: silicon, Fe: iron, P: phosphorus, S: sulfur, Mn: manganese, Zn: zinc.

Pearson correlation and principal component analysis: Fig. 4 shows the results of the correlation between the mineral elements of maize plants and the physicochemical characteristics of the soil. A highly positive correlation (coefficient tending towards 1) was revealed between the mineral composition of the plants and that of the soil. For example, between "N_{soil}, AP, TOM and TOC" and "K_{plant}, S_{plant}, Si_{plant} and P_{plant}". On the other hand, it is negative (values tending towards -1) between "Fe_{plant} and Ca_{plant}" and "Ca_{soil} and K_{soil}". Additionally, there is a significant correlation within the plant between "Ca_{plant}" and "S_{plant} and Mn_{plant}".

Principal component analysis (PCA) combined all the parameters studied at soil and plant level, in the presence or absence of biostimulants in conditions of water stress. A total variability of 47.9 (PC1 = 32.9%, PC2 = 15%) was detected (Fig. 5). A positive correlation was observed between the biostimulants applied (combined or not) and growth, physiological and nutritional parameters, as well as root mycorrhization under normal or stress conditions. The PCA of individuals showed that the PCs, CMs, CMPs, PC, CM, and CMP treatments were strongly positively correlated along the PC1 axis whatever the water regime imposed. This goes hand in hand with the strong contribution revealed in the PCA-Variables between growth parameters (RDW, SDW, SH, LN, and RL), physiology (Fv/Fm, gs), biochemistry (Prol and Ptn), nutrition (Si_{plant}, $P_{plant,}$ K_{plant}, S_{plant}, Ca_{plant}, Mn_{plant}, and Fe_{plant}), soil physicochemical characteristics (TOM, TOC, AP, N_{soil},). Moreover, the PCA of variables showed a clear positive correlation under water stress conditions between MDA, PPO, H_2O_2, TSS, and Zn_{plant}.

Dendrograms in a heatmap matrix and cluster analysis: This analysis makes it easier to read the data by showing the parameters with higher (red color) and lower (blue color) values and their grouping. For example, in the left half of the heatmap, growth parameters (LN, RL, SH, SDW, and RDW), leaf mineral elements (K_{plant}, $S_{plant,}$ P_{plant}, and Si_{plant}) and soil physicochemical properties (AP, TOM, TOC, and N_{soil}) were significantly increased and positively correlated by the action of biostimulants alone or in combination, in particular the combination of C with microorganisms (CM, PC, CMP), whatever the field capacity applied (Fig. 6). On the other hand, in the right half of the heatmap, a stronger positive correlation was observed concerning MDA, H_2O_2, PPO, TSS, and Zn_{plant} in untreated and M-treated plants under severe water stress conditions.

Discussion

Losses in agricultural yields are continuing at a spectacular rate, in parallel with climate change, especially the pronounced drought in (semi)arid climates (Paz *et al.*, 2016; del Pozo *et al.*, 2019). Moving away from intensive farming practices such as chemical fertilizers towards biological agriculture, such as the integration of biostimulants, is proving to be the best sustainable ecological solution (Castiglione *et al.*, 2021). Numerous studies have confirmed the serious consequences of drought on plant biochemistry, physiology and nutrition (Bogati & Walczak, 2022; Meddich, 2022). However, the use of biostimulants, including PGPR, AMF and organic amendments, modulate these adverse effects (Boutasknit *et al.*, 2020; Ouhaddou *et al.*, 2023a). In this study, moving from 75 to 25% FC caused many changes in the soil and plant. Mycorrhizal symbiosis was affected significantly by DS as mycorrhization frequency (MF) and mycorrhization intensity (MI) decreased from 100 to 93% and from 51 to 22%, respectively, in mycorrhized plants alone. This is explained by the delay in spore germination and degradation by drought (Zhang *et al.*, 2018). Whatever the water regime used, the presence of bacterial consortium (P) doubled the percentage of colonization of mycorrhizal structures within the root cortex (59%) compared with control or mycorrhizal plants alone (22%). The same results were obtained in several studies on different plant species, such as maize, rice, barley, and lettuce under abiotic stress (Aini *et al.*, 2019; Ouhaddou *et al.*, 2022a, 2023b; Silva *et al.*, 2023). This indicates that P stimulated the differentiation of AMF hyphae and vesicles (Gopal *et al.*, 2012). Studies in genetics have shown that this stimulation is due to the secretion of certain substances by the bacteria (Sangwan & Prasanna, 2022). On the other hand, these parameters fell sharply in the presence of compost (C), with a percentage of 5% (w/w). The same biostimulants in addition to P had a high MI value under DS conditions compared with their controls. This inhibition strategy is due to the fact that the plant has found sufficient nutrients in the C. Studies have explained this blockage of root colonization by the presence of sufficient phosphorus (Yazici *et al.*, 2021). It is also possible that excessive phosphorus input into the soil results in an increase in membrane phospholipids, which in turn enhances its rigidity (Aloui *et al.*, 2018). According to El Amerany *et al.*, (2020), the success of AMF colonization of maize roots depends also on the dose of applied compost. On the other hand, other studies have postulated that compost encourages root colonization by mycorrhizal structures (hyphae, vesicles, and arbuscules) (Paymaneh *et al.*, 2023). Humic substances are among the complex molecules that stimulate spore germination (Pinos *et al.*, 2019). A study on the effect of water stress (30% FC) and AMF on maize reported that root colonization by mycorrhizal structures was intensive under water stress conditions compared with normal conditions (80%) (Silva *et al.*, 2023). Similar findings were reported by Meddich et *al.*, (2021a) concerning drought stress's effect on root colonization. This ability to penetrate the periphery of the central root cylinder under water-limited conditions was reflected by the action of root exudates (Steinkellner *et al.*, 2007; Baumert *et al.*, 2018). Strigolactones and flavonoids are part of the root-secreted molecules in the event of increased water shortage and enter into dialogue with the spores to propagate the root (Nagata *et al.*, 2016). Plenty of researchers have documented the positive correlation that exists between mycorrhizal symbiosis and plant growth (Baslam & Goicoechea, 2012; Fall *et al.*, 2023). Moreover, in our study, the growth attributes of plants treated with M alone followed the same trend as the control plants despite the degree of colonization observed. The present work showed that growth parameters were negatively affected by water stress, such as shoot and root length and shoot and root dry weight. This damage might result from the over-accumulation of ROS in leaves like H_2O_2 and MDA in our case, or the accumulation of other ROS as demonstrated by Choudhury et *al.*, (2017). However, the application of biostimulants positively affected the plants, regardless of the water regime applied. As shown in our work, root and shoot biomass, shoot height, and root length correlated positively with mineral element content, in particular, potassium (K), nitrogen (N), iron (Fe), and available phosphorus (AP). In terms of high performance, our results affirm that P, CM, PC, and CMP showed their power to provide growth shelter under very low humidity (25% FC) compared to the respective control plants. Aroca *et al.*, (2008) demonstrated that the response to water stress via biostimulants is due to the regulation of the root's hydraulic properties, promoting water transport to the shoot and accelerating the plant's leaves rehydration. This response is probably linked to shoot stomatal conductance (gs) and root hydraulic conductivity being coordinated along with phosphorus content (Bitterlich *et al.,* 2018; Kranz *et al.,* 2020; Quiroga *et al.,* 2020). Numerous studies confirmed that the combination of biostimulants gives better results than their individual application thanks to synergistic dialogues (Pinos *et al.,* 2019; Raklami *et al.,* 2019; Halim *et al.,* 2021; Ouhaddou *et al.,* 2022b). The root is the organ that acts as an intermediary between the aerial parts and the soil, and its growth depends on soil physicochemical, and biological characteristics (Kulkarni *et al.*, 2017; Maqbool *et al.*, 2022). In light of our results, root biomass and length were improved in plants treated with P or CM. This can be explained by the growth hormones secreted by the bacteria, increasing root surface area and, therefore water and mineral salts uptake by the plant (Kumari *et al.*, 2019). The synergistic effect of CM possibly results from compost's advantageous properties, owing to its structure, porosity, water retention capacity, and mineral composition (Ouhaddou *et al.*, 2023a). This extraordinary matrix also provides a suitable surface for the maximum functioning of microbes, such as potassium and phosphate solubilization and the transfer of other mineral elements and water by AMF hyphae, for the benefit of plants (Wahid *et al.*, 2016; Anli *et al.*, 2022; Slimani *et al.*, 2022). One of the serious consequences of drought is that it adversely affects the normal transfer of mineral elements to the plant (Der, 2014). In our study, the mineral status of maize plants decreased or increased proportionally with soil moisture (75 and 25% FC). In contrast, the role played by the biostimulants used, appropriately modulated the effect of pronounced soil desiccation on foliar mineral content. Compost has been reported to provide macro- and micro-nutrients to plants (Kanwal *et al.*, 2017; Kakabouki *et al.*, 2020). For example, the CM treatment showed an enhancement in foliar K, Ca, and Fe under water stress (25% FC) compared with the control. These findings are consistent with the results obtained by Boutasknit *et al.*, (2021) on drought-stressed carob plants. Indeed, studies have pointed out the role of K in several physiological processes, in particular stomatal dynamics, under the control of abscisic acid (Sarwat & Tuteja, 2017; Ouledali *et al.*, 2019). In addition to its role in osmotic regulation, as reported by Ortuño *et al.*, (2018). This work shows that the presence of a bacterial consortium in the treatments increases the Fe content. This may be due to the capacity of this consortium to chelate Fe via siderophore secretions, which increases the bioavailability of this nutrient (Umair *et al.*, 2018). Symbiosis with M and/or P increased Ca levels under severe water conditions. In parallel with this postulate, He *et al.*, (2022) showed that the synergistic action of *Glomus mosseae* and endophytic bacteria (*Bacillus amyloliquefaciens*) significantly increased Ca and other mineral content in common bean seeds compared to normal plants. Ca plays a number of roles, particularly in cell wall rigidity.

Table 4. Effect of two water regimes (WW: well-watered and DS: drought stress) and biostimulants (P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM and CMP) on physic-chemical properties of soil compared with controls. Values are means ± SE. The values of each column labelled with different letters indicate significant differences assessed by Tukey's test (p<0.05).

	Ctr		P		M		C		MP		PC		CM		CMP	
	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS
N (%)	0.03±0.01 b-e	0.02±0.01 c-e	0.03±0.00 a-e	0.02±0.00 c-e	0.03±0.00 b-e	0.01±0.00 e	0.06±0.00 a-d	0.06±0.00 a-d	0.05±0.01 a-e	0.02±0.00 de	0.06±0.00 a-d	0.04±0.00 a-e	0.08±0.00 ab	0.07±0.01 ac	0.08±0.00 a	0.04±0.01 a-e
TOM (%)	1.18±0.20 de	0.86±0.28 e	1.34±0.07 c-e	1.02±0.23 e	1.50±0.23 b-e	1.26±0.36 de	2.61±0.15 ab	2.68±0.27 ab	1.10±0.15 de	0.62±0.07 e	3.48±0.28 a	2.92±0.49 a	2.53±0.07 a-c	2.61±0.20 ab	2.53±0.07 a-d	2.29±0.07 a-d
TOC (%)	0.68±0.12 de	0.50±0.16 e	0.77±0.04 c-e	0.59±0.13 e	0.86±0.13 b-e	0.73±0.21 de	1.51±0.09 ab	1.56±0.15 ab	0.63±0.09 de	0.36 ± 0.04 e	2.01±0.16 a	1.70±0.28 a	1.46±0.04 a-c	1.51±0.12 ab	1.46±0.04 a-d	1.33±0.04 a-d
AP (mg/Kg)	58.7±11.56 e	13.50±1.09 c	53.68±1.74 de	40.58±3.81 de	49.57±1.60 de	24.63±1.52 de	148.4±2.97 c	187±9.89 bc	39.32±2.15 de	21.1 ± 2.35 de	257.4±22.3 a	180.4±1.70 bc	177.97±4.03 bc	171.8±10.84 bc	158.9±14.86 bc	202.6±3.60 b
EC (mS/cm)	0.50±0.00 e	0.60±0.00 d	0.75±0.02 ab	0.70±0.00 bc	0.60±0.00 d	0.50±0.00 e	0.70±0.00 bc	0.65±0.02 cd	0.50±0.00 e	0.50 ± 0.00 e	0.50±0.00 e	0.70±0.00 bc	0.50±0.00 e	0.70±0.00 bc	0.70±0.00 bc	0.80±0.00 a
pH	7.95±0.02 b	8.06±0.00 a	7.71±0.04 e	7.84±0.02 cd	7.81±0.00 d	8.11±0.02 a	7.77±0.00 de	8.07±0.00 a	7.83±0.01 cd	7.97 ± 0.00 b	7.79 ± 0.00 de	7.96±0.00 b	7.71±0.00 e	7.90±0.00 bc	7.79±0.01 de	7.80±0.00 d

The reduction of water up to 30% FC was the main condition for *Glomus mosseae* to penetrate and colonize the root cells of barley to supply it with missing nutrients such as Ca and phosphorus (Meddich *et al.*, 2021b). Sulfur (S) is one of the essential microelements in plants, as it is essential for protein synthesis (Métayer *et al.*, 2008). It is an important factor in tolerating water stress in plants, as reported by Ahmad *et al*., (2016). In parallel to our results, maize plants treated with PC concentrated a lot of S under desiccated soil compared to control plants. Moreover, it has recently been reported that AMF can improve the mineral status of water-stressed Pistachio plants, particularly zinc (Zn) (Abbaspour *et al.*, 2012). This element acts as a catalyst for numerous enzymatic processes implicated in the synthesis of proteins and carbohydrate metabolism (Broadley *et al.,* 2012). In our study, Zn was significantly increased by M in parallel with the control under 25% FC. In addition, the use of compost in combination with the bacterial consortium (*Bacillus subtilis* and *Bacillus* sp.) increased leaf manganese (Mn) concentration under severe water stress (25% FC) in comparison with stressed control plants. In the same context, Delshadi *et al*., (2017) demonstrated that inoculating *Bromus tomentellus* plants with *Azotobacter vinelandii* improved mineral content, particularly Mn. This nutrient is necessary for the initiation of several metabolic reactions, in particular for the functioning of the photosynthetic apparatus (formation of chloroplasts), and plants' protection against oxidative stress in extreme environmental conditions (Shams, 2019; Messant *et al.*, 2023). Mn is the main key for the superoxide dismutase (SOD) enzyme to counteract reactive oxygen species (ROS) (Ye *et al.*, 2019). Studies have reported that photosystem II performance is linked to Mn. Furthermore, cell division and elongation depend on Mn variations in the plant (Broadley *et al.,* 2012). In this study, soil desiccation caused negative changes in the physiological traits of maize plants. Statistically, the observed improvements in mineral nutrition are directly correlated with maize plant physiology. Numerous studies have reported that most mineral elements are involved in several physiological processes, in particular, the photosynthetic machinery. In this regard, we have shown that stomatal conductance showed a significant improvement upon the treatment of maize plants with native biostimulants. Treatment C combined with P and/or M outperformed the other treatments, particularly the control, in terms of gas exchange efficiency. This was due to good assimilation and diffusion of CO_2, resulting in enhanced yield and plant growth. The improvement in stomatal conductance can also be explained by up-regulation of the genes coding for 5-bisphosphate carboxylase/oxygenase (Rubisco) in charge of CO_2 fixation (Erb & Zarzycki, 2018). Tolerance to water stress via biostimulants is also linked to the good photosynthetic efficiency of chlorophyll pigments (Goñi *et al.*, 2018). Chlorophyll fluorescence (F_v/F_m) is a parameter that gives information on the photosystem II state and functioning (Hernández-Herrera *et al.*, 2016). After taking F_v/F_m measurements, we found that the biostimulants applied improved this parameter. In particular, plants treated with C, the mycorrhizal consortium (CM), were the most distinctive in terms of photosynthetic performance under conditions of severe water shortage. One explanation for this is a good composition of photosynthetic pigments, in particular chlorophyll *a* and *b*, as well as the mineral elements essential for the photosynthetic apparatus, in particular Mn, Fe, etc. In a recent pot experiment, the chlorophyll content of maize leaves inoculated with *Funneliformis mosseae* and exposed to three levels of water stress (75%, 55% and 35%) was spectrally estimated (Sun *et al.*, 2021). Their findings revealed that at 35% FC, this species increased leaf chlorophyll content, thereby increasing photosynthetic net rate as well as transpiration rate (E), stomatal conductance (gs) and water use efficiency of maize plants (Sun *et al.*, 2021). Meddich *et al.*, (2021a) revealed that mycorrhized melon plants grown under water stress concentrated chl *a*, chl *b* and carotenoids very significantly. The cell structure is damaged by heavy water stress by reducing its protein composition. In addition, our results indicated an improvement in protein content in plants treated with both C and P (307%). In line with these results, Khan *et al.*, (2019) demonstrated that inoculation with a *Bacillus*-based consortium (*Bacillus thuringiensis*, *Bacillus subtilis,* and *Bacillus megaterium*) enhanced the protein composition and metabolic regulation of chickpea under water-limited conditions. There are many adaptation strategies in plants, including the enzymatic antioxidant system capable of neutralizing the effect of oxidative stress generated by ROS, particularly H_2O_2 (Kapoor *et al.*, 2019). Catalase (CAT), superoxide dismutase (SOD), peroxidase (POX) and polyphenoloxidase (PPO) are key enzymes responsible for defending various plants against biotic and abiotic stresses, irrespective of treatment with biostimulants. (He *et al.*, 2020; Ikan *et al.*, 2023a). Our findings show that treated and untreated plants exposed to water deficit (25% FC) have very high PPO values. According to Liu *et al*., (2019), this increase could be due to the overexpression of the transcription factor MnMYB3R1, which increases the transcription of the MnPPO1 gene that confers drought resistance to *Morus notabilis* plants. In the event of an exaggerated lack of water, plant cells turn their behaviour towards the accumulation of specific molecules known as osmolytes (osmotic adjustment), namely glycine betaine, proline and total soluble sugars (TSS) (Shafiq *et al.*, 2021; Slimani *et al.*, 2023). Proline is an amino acid that is stored in cell vacuoles and transported to the cytoplasm in the event of osmotic stress generated by drought (Lehmann *et al.*, 2010). These dehydrated cells, therefore, develop a strategy of drawing water from the external environment towards the internal environment, which further rehydrates the entire cellular system (Enebe & Babalola, 2018). The accumulation of this amino acid keeps also the cells well hydrated and stabilizes the chloroplast membrane integrity, helping to protect and restore the photochemical functioning of photosystem II (Maia Júnior *et al.*, 2020). In fact, our work showed that leaf proline has significantly accumulated, especially in those supplemented with compost and PGPR under conditions of pronounced water stress. Such accumulation could be justified by overexpression of the gene (p5cs) encoding the enzyme pyrroline-5-carboxylate synthetase (P5CS) (Adamipour *et al.*, 2020). The increase in proline levels in maize leaves exposed to DS gives an indication of the improvement in water status, in particular relative water content, water content, water potential and good hydraulic conductance within the roots. The improvement in root water uptake was explained by the expression of genes encoding fungal and plant aquaporins (Sharma *et al.*, 2021). High levels of proline are also known to stimulate antioxidant enzyme synthesis (Hayat *et al.*, 2013). Similarly to proline, our study showed that TSS also follows the severity of water shortage, i.e., as FC decreases, TSS accumulates to a greater extent in treated and untreated leaves. This is reflected in the osmotic regulation strategy employed by the maize plant to relieve the DS effect (Ortuño *et al.*, 2018). The present study shows that osmolyte concentration correlates directly with mineral element content. Osmolytes boost oxidative stress effect by lowering the concentration of ROS to normal values since they are necessary for cell signaling (Toscano *et al.*, 2023). H_2O_2 and MDA are among the stress markers that accumulate during abiotic or biotic stress in plants and cause deterioration of unsaturated fatty acid chains in membrane phospholipids (Ait Rahou *et al.*, 2021; Akensous *et al.*, 2022; Bogati and Walczak, 2022). These ROS are mainly produced by chloroplasts, mitochondria and peroxisomes when cells are very dehydrated (Pastore *et al.*, 2007; Sandalio *et al.*, 2013). ROS overproduction induces carbohydrates, proteins and genetic material (DNA) oxidation (Sharma *et al.*, 2012; Anjum *et al.*, 2015). The present work showed that the severe water stress imposed increased the concentration of the above-mentioned stress markers, especially in mycorrhizal and control plants in comparison with the other treatments. However, the maximum reduction was noted in plants treated with MP and PC under DS conditions. This reduction may be linked to good assimilation of mineral elements and improved water uptake. In addition, the mechanism involved in this attenuation was explained by the fact that antioxidant enzymes such as peroxidase (POX) reduce H_2O_2 to water and catalase (CAT) to oxygen and water (Rajput *et al.,* 2021). This also indicates that the cells are well protected and retain their integrity despite the drying out of the soil. These results are supported by Anli *et al*., (2020). Our results also showed that plants inoculated with P alone and CMP accumulated less MDA than the other treatments.

Biostimulants positively affect not only the physiological, biochemical, nutritional, and growth traits of plants but also the soil's physicochemical and biological properties (Bogati & Walczak, 2022; Raho *et al.*, 2022). Moreover, several researchers reported that plants raised in dry conditions suffer from the lack of mineral elements such as phosphorus, nitrogen, and potassium, etc., as well as suitable structure and texture for plant growth (Mu *et al.*, 2023; Quintana *et al.*, 2023). On the basis of our results, the 25% FC imposed generated radical changes in the soil physico-chemical properties. On the other hand, the use of biostimulants in the root zone appropriately modulated this effect, essentially by adding compost in combination with microorganisms. Numerous studies have shown that composts of various origins are a major source of mineral elements derived from organic matter degradation, which are essential for the development and growth of plants under extreme environmental conditions (Duong *et al.*, 2012; Mobaligh *et al.*, 2023). From the results obtained, it should be noted that soils amended with compost, whether or not combined with the two microbial consortia, improved their organic matter and carbon content. According to principal component analysis results, NPK, available phosphorus (AP), organic matter and physiological and growth parameters were influenced and positively correlated by the combined action of CM and PC along the PCA2 axis (32.9%) under conditions of increased soil dryness. Recently, we showed that soil enrichment with an organic amendment combined with rhizospheric microorganisms improved AP and OM for lettuce plants' tolerance to water stress conditions (33% FC) (Ouhaddou *et al.*, 2023a). The effectiveness of these combinations enables plants to absorb nutrients either directly from the compost or via micro-organisms by the action of solubilization or transport using AMF hyphae (Grobelak *et al.*, 2015; Kohler *et al.*, 2015). Moreover, it has been shown that when there is a phosphorus deficit, AMF express genes coding for specific phosphorus (Pi) transporters in their extracellular hyphae, which improves phosphorus nutrition and, therefore, plant growth (Giovannini *et al.*, 2020; Cao *et al.*, 2022). In addition, compost increases water retention and promotes plant rooting thanks to its porous structure and good root oxygenation (Xu *et al.*, 2018; Kranz *et al.*, 2020). Our study also revealed that biostimulants positively changed soil mineral composition compared with the control soil. For example, nitrogen (N) was maximized in soil supplemented with C and inoculated with AMF. This was accompanied and positively correlated with the growth of maize plants under water stress. These changes in the soil have positive repercussions in the aerial part, increasing the performance of the defense system against a pronounced lack of water.

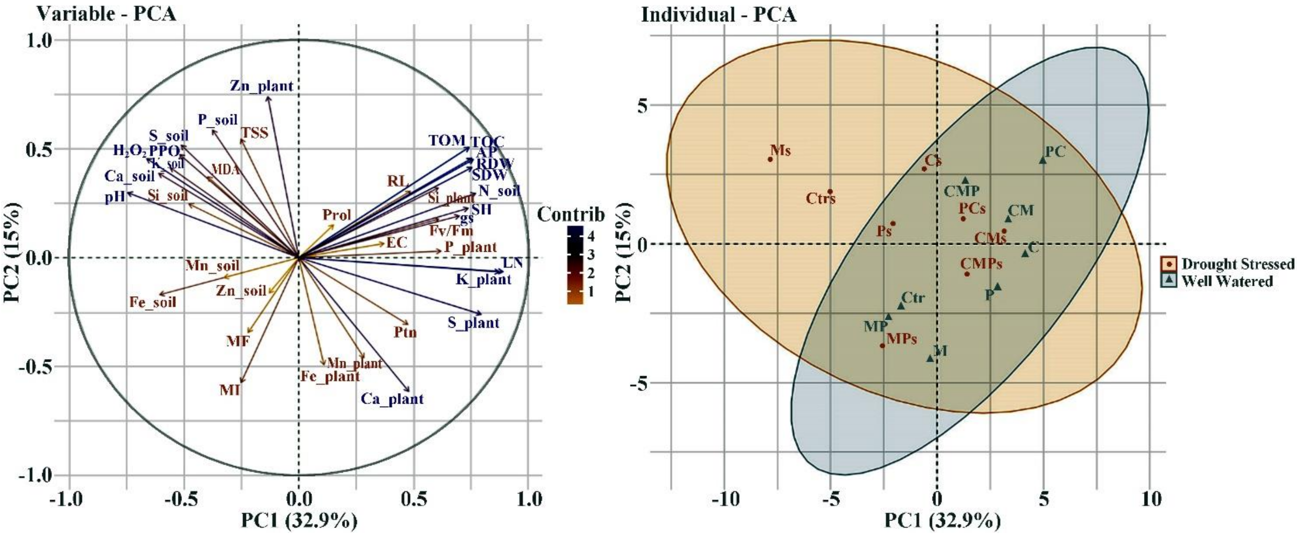

Fig. 5. Principal component analysis (PCA: individuals and variables) of all the parameters measured in the plant and in the soil for maize under the impact of biostimulants (Ctr: control plants, P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM and CMP) and water regimes (75 and 25% FC). SH: shoot height, RL: roots length, SDW: shoot dry weight, RDW: root dry weight, LN: leaf number, Fv/Fm: chlorophyll fluorescence, gs: stomatal conductance, MI: mycorrhizal intensity, MF: mycorrhizal frequency, H2O2: hydrogen peroxide, MDA: Malondialdehyde, PPO: polyphenoloxidase activity, TSS: total soluble sugars, Prol: proline, Ptn: proteins, EC: electrical conductivity, TOM: total organic matter, TOC: total organic carbon, AP: available phosphorus, Ca: calcium, K: potassium, Si: silicon, Fe: iron, P: phosphorus, S: sulfur, Mn: manganese, Zn: zinc.

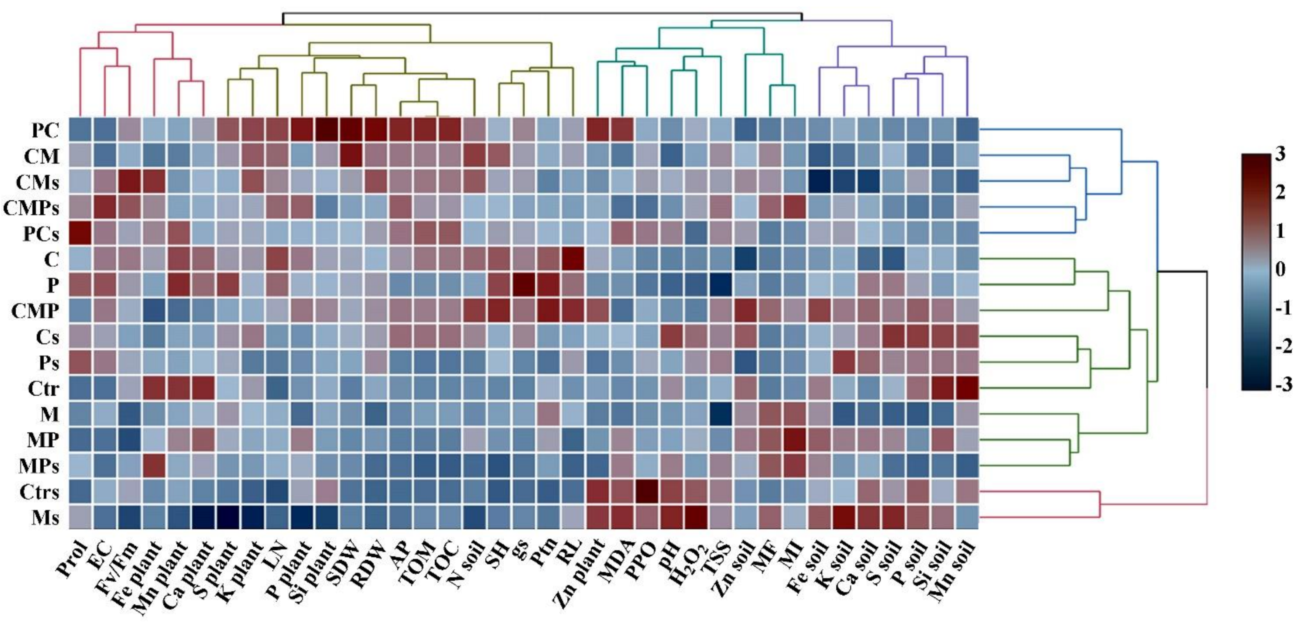

Fig. 6. Cluster and dendrogram analysis in a heatmap matrix for the impact of biostimulants (Ctr: control plants, P: bacterial consortium, M: mycorrhizal consortium, C: compost, PM, PC, CM, and CMP) and water regimes (75 and 25% FC). SH: shoot height, RL: roots length, SDW: shoot dry weight, RDW: root dry weight, LN: leaf number, Fv/Fm: chlorophyll fluorescence, gs: stomatal conductance, MI: mycorrhizal intensity, MF: mycorrhizal frequency, H2O2: hydrogen peroxide, MDA: Malondialdehyde, PPO: polyphenoloxidase activity, TSS: total soluble sugars, Prol: proline, Ptn: proteins, EC: electrical conductivity, TOM: total organic matter, TOC: total organic carbon, AP: available phosphorus, Ca: calcium, K: potassium, Si: silicon, Fe: iron, P: phosphorus, S: sulfur, Mn: manganese, Zn: zinc.

Conclusion

As already pointed out by several studies, drought is a worldwide challenge to food security. In light of the results obtained, it appears that water stress has adversely affected the morphological, physiological, biochemical, and nutritional traits of maize plants. Changes at the soil level were also generated after limiting water to 25% FC. However, the use of biostimulants modulated the effect of this constraint by improving the total biomass and root architecture of the maize plants. The application of biostimulants in combined mode proved effective in improving maize plants' tolerance to water stress. This beneficial effect stems from a multi-pathway strategy of mechanisms developed by biostimulants for overcoming the effects of water stress. These include i) improving photosystem II performance by increasing the F_v/F_m ratio and CO_2 fixation by increasing stomatal conductance, ii) improving leaf mineral status (K, Fe, Mn, Si, S, Ca, P and Zn), iii) dedicated osmotic adjustment through the accumulation of total soluble sugars and proline, iv) strengthening of the antioxidant system (high PPO activity) and reduction of stress markers (H_2O_2 and MDA). This tolerance is also attributable to biostimulants' positive effect on the soil, in particular, the enhancement in organic matter and mineral elements such as nitrogen, assimilable phosphorus, K, Fe, Mn, Si, S, Ca, P, and Zn. From a performance point of view, the bacterial consortium (*Bacillus subtilis*, *Bacillus* sp.) alone and the compost in association with the mycorrhizal consortium are considered distinctive compared with the other treatments, including the control. In order to provide plants with systemic drought tolerance, it is important to apply biostimulants in combined mode. Consequently, it would be interesting to exploit the indigenous microbial community of the rhizosphere for the restoration of degraded soils suffering from drought. Experiments under field conditions are important to confirm the results obtained.

Acknowledgment

The authors would like to extend their sincere appreciation to the Researchers Supporting Project Number (RSP2025R134), King Saud University, Riyadh, Saudi Arabia. Also, this project has received funding from the European Union's Horizon 2020 research and innovation program under grant agreement N° 862555.

References

Abbaspour, H., S. Saeidi-sar, H. Afshari and M.A. Abdel-wahhab. 2012. Tolerance of Mycorrhiza infected Pistachio (*Pistacia vera* L.) seedling to drought stress under glasshouse conditions. *J. Plant Physiol.*, 169: 704-709.

Adamipour, N., M. Khosh-Khui, H. Salehi, H. Razi, A. Karami and A. Moghadam. 2020. Metabolic and genes expression analyses involved in proline metabolism of two rose species under drought stress. *Plant Physiol. and Biochem.*, 155: 105-113.

Ahmad, N., M. Malagoli, M. Wirtz and R. Hell. 2016. Drought stress in maize causes differential acclimation responses of glutathione and sulfur metabolism in leaves and roots. *BMC Plant Biol.*, 16: 1-15.

Aini, N., W.S.D. Yamika and B. Ulum. 2019. Effect of nutrient concentration, PGPR and AMF on plant growth, yield and nutrient uptake of hydroponic lettuce. *Int. J. Agric. Biol.*, 21: 175-183.

Ait Rahou, Y., M. Ait-El-Mokhtar, M. Anli, A. Boutasknit, R. Ben-Laouane, A. Douira, R. Benkirane, C. El Modafar and A. Meddich. 2021. Use of mycorrhizal fungi and compost for improving the growth and yield of tomato and its resistance to *Verticillium dahliae*. *Arch. Phytopathol. Plant. Pro.*, 54: 665-690.

Akensous, F., M. Anli and A. Meddich. 2022. Biostimulants as innovative tools to boost date palm (*Phoenix dactylifera* L.) performance under drought , salinity , and heavy metal (Oid) s ' Stresses: A Concise Review. *Sustain. J. (Switzerland)*, 14: 15484.

Aloui, A., G. Recorbet, C. Lemaître-Guillier, A. Mounier, T. Balliau, M. Zivy, D. Wipf and E. Dumas-Gaudot. 2018. The plasma membrane proteome of *Medicago truncatula* roots as modified by arbuscular mycorrhizal symbiosis. *Mycorrhiza*, 28.

Anjum, N.A., A. Sofo, A. Scopa, A. Roychoudhury, S.S. Gill, M. Iqbal, A.S. Lukatkin, E. Pereira, A.C. Duarte and I. Ahmad. 2015. Lipids and proteins—major targets of oxidative modifications in abiotic stressed plants. *Environ. Sci. Pollut. Res.*, 22: 4099-4121.

Anli, M., A. Boutasknit, M. Ait-El-Mokhtar, R. Ben-Laouane, Y. Ait-Rahou, A. Fakhech and A. Meddich. 2022. Improving lettuce yield and quality of an agricultural soil using a combination of arbuscular mycorrhizal fungus and phosphate-green wastes compost. *Gesunde Pflanzen*, 74: 205-217.

Anli, M., M. Baslam, A. Tahiri, A. Raklami, S. Symanczik, A. Boutasknit, M. Ait-El-Mokhtar, R. Ben-Laouane, S. Toubali, Y. Ait Rahou, M. Ait Chitt, K. Oufdou, T. Mitsui, M. Hafidi and A. Meddich. 2020. Biofertilizers as strategies to improve photosynthetic apparatus, growth, and drought stress tolerance in the date palm. *Front. Plant Sci.*, 11: 1560.

Aroca, R., P. Vernieri and J.M. Ruiz-lozano. 2008. Mycorrhizal and non-mycorrhizal *Lactuca sativa* plants exhibit contrasting responses to exogenous ABA during drought stress and recovery. *J. Exp. Bot.,* 59: 2029-2041.

Aubert, G. 1978. Méthodes d'analyses des sols, 2ème Edn. Marseille: Centre régional de Documentation Pédagogique. *Open J. Ecol.*, 191.

Baslam, M. and N. Goicoechea. 2012. Water deficit improved the capacity of arbuscular mycorrhizal fungi (AMF) for inducing the accumulation of antioxidant compounds in lettuce leaves. *Mycorrhiza*, 22: 347-359.

Baumert, V.L., N.A. Vasilyeva, A.A. Vladimirov, I.C. Meier, I. Kögel-Knabner and C.W. Mueller. 2018. Root exudates induce soil macroaggregation facilitated by fungi in subsoil. *Front. Environ. Sci.*, 6: 140.

Begum, N., L. Wang, H. Ahmad, K. Akhtar, R. Roy, M.I. Khan and T. Zhao. 2022. Co-inoculation of arbuscular mycorrhizal fungi and the plant growth-promoting rhizobacteria improve growth and photosynthesis in tobacco under drought stress by up-regulating antioxidant and mineral nutrition metabolism. *Microb. Ecol.*, 83: 971-988.

Benaffari, W., A. Boutasknit, M. Anli, M. Ait-El-Mokhtar, Y. Ait-Rahou, R. Ben-Laouane, H. Ben Ahmed, T. Mitsui, M. Baslam and A. Meddich. 2022. The native arbuscular mycorrhizal fungi and vermicompost-based organic amendments enhance soil fertility, growth performance, and the drought stress tolerance of quinoa. *Plants*, 11: 393.

Ben-Laouane, R., M. Ait-El-Mokhtar, M. Anli, A. Boutasknit, Y. Ait Rahou, A. Raklami, K. Oufdou, S. Wahbi and A. Meddich. 2020. Green compost combined with mycorrhizae and rhizobia: A strategy for improving alfalfa growth and yield under field conditions. *Gesunde Pflanzen*, 73: 193-207.

Bitterlich, M., P. Franken and J. Graefe. 2018. Arbuscular mycorrhiza improves substrate hydraulic conductivity in the plant available moisture range under root growth exclusion. *Front. Plant. Sci.*, 9: 301.

Bogati, K. and M. Walczak. 2022. The impact of drought stress on soil microbial community, enzyme activities and plants. *J. Agron.*, 12: 1-26.

Boutasknit, A., M. Baslam, M. Ait-El-Mokhtar, M. Anli, R. Ben-Laouane, Y. Ait-Rahou, T. Mitsui, A. Douira, C. El Modafar, S. Wahbi and A. Meddich. 2021. Assemblage of indigenous arbuscular mycorrhizal fungi and green waste compost enhance drought stress tolerance in carob (*Ceratonia siliqua* L.) trees. *Sci. Rep.*, 11: 22835.

Boutasknit, A., M. Baslam, M. Ait-El-mokhtar, M. Anli, R. Ben-Laouane, A. Douira, C. El Modafar, T. Mitsui, S. Wahbi and A. Meddich. 2020. Arbuscular mycorrhizal fungi mediate drought tolerance and recovery in two contrasting carob (*Ceratonia siliqua* L.) ecotypes by regulating stomatal, water relations, and (in)organic adjustments. *Plants*, 9: 80.

Bradford, M.M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Crop J.*, 72: 248-254.

Broadley, M., P. Brown, I. Cakmak, Z. Rengel and F. Zhao. 2012. Chapter 8 - Beneficial elements. In: Marschner, P. Marschner's Mineral Nutrition of Higher Plants (Third Edition), Academic Press. pp. 249-269.

Cao, M.A., R.C. Liu, Z.Y. Xiao, A. Hashem, E.F. Abd_Allah, M.F. Alsayed, W. Harsonowati and Q.S. Wu. 2022. Symbiotic fungi alter the acquisition of phosphorus in *Camellia oleifera* through regulating root architecture, plant phosphate transporter gene expressions and soil phosphatase activities. *J. Fungi*., 8(8): 800.

Carillo, P., G. Mastrolonardo, F. Nacca, D. Parisi, A. Verlotta and A. Fuggi. 2008. Nitrogen metabolism in durum wheat under salinity: Accumulation of proline and glycine betaine. *Funct. Plant Biol.*, 35: 412-426.

Castiglione, A.M., G. Mannino, V. Contartese, C.M. Bertea and A. Ertani. 2021. Microbial biostimulants as response to modern agriculture needs: Composition, role and application of these innovative products. *Plants*, 10: 1533.

Cheng, H.Q., Y.E. Ding, B. Shu, Y.N. Zou, Q.S. Wu and K. Kuca. 2020. Plant Aquaporin responses to mycorrhizal symbiosis under abiotic stress. *Int. J. Agric. Biol.*, 23: 1-9.

Choudhury, F.K., R.M. Rivero, E. Blumwald and R. Mittler. 2017. Reactive oxygen species, abiotic stress and stress combination. *Plant Jl.*, 90: 856-867.

Daryanto, S., L. Wang and P.A. Jacinthe. 2016. Global synthesis of drought effects on maize and wheat production. *PLoS. One.*, 11: 1-15.

del Pozo, A., N. Brunel-Saldias, A. Engler, S. Ortega-Farias, C. Acevedo-Opazo, G.A. Lobos, R. Jara-Rojas and M.A. Molina-Montenegro. 2019. Climate change impacts and adaptation strategies of agriculture in Mediterranean-climate regions (MCRs). *Sustain J.*, 11(10): 2769.

Delshadi, S., M. Ebrahimi and E. Shirmohammadi. 2017. Effectiveness of plant growth promoting rhizobacteria on *Bromus tomentellus* Boiss seed germination, growth and nutrients uptake under drought stress. *S. Afr. J. Bot.*, 113: 11-18.

Der, T.B. 2014. Mineral nutrient content of sweet corn under deficit irrigation. 90.

Dhindsa, R.S. and W. Matowe. 1981. Drought tolerance in two mosses: Correlated with enzymatic defence against lipid peroxidation. *J. Exp. Bot.*, 32: 79-91.

Dubois, M., K. Gilles, J.K. Hamilton, P.A. Rebers and F. Smith. 1956. A colorimetric method for the determination of sugars. *Nature*, 168: 167.

Duong, T.T.T., C. Penfold and P. Marschner. 2012. Amending soils of different texture with six compost types: Impact on soil nutrient availability, plant growth and nutrient uptake. *Plant Soil J.*, 354: 197-209.

El Amerany, F., M. Rhazi, S. Wahbi, M. Taourirte and A. Meddich. 2020. The effect of chitosan, arbuscular mycorrhizal fungi, and compost applied individually or in combination on growth, nutrient uptake, and stem anatomy of tomato. *Sci. Hortic.*, 261: 109015.

Enebe, M.C. and O.O. Babalola. 2018. The influence of plant growth-promoting rhizobacteria in plant tolerance to abiotic stress: A survival strategy. *Appl. Microbiol. Biotechnol.*, 102: 7821-7835.

Erb, T.J. and J. Zarzycki. 2018. A short history of RubisCO: the rise and fall (?) of Nature's predominant CO_2 fixing enzyme. *Curr. Opin. Biotechnol.*, 49: 100-107.

Etesami, H. and D.K. Maheshwari. 2018. Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture: Action mechanisms and future prospects. *Ecotoxicol. Environ. Saf.*, 156: 225-246.

Fall, A.F., G. Nakabonge, J. Ssekandi, H. Founoune-Mboup, A. Badji, A. Ndiaye, M. Ndiaye, P. Kyakuwa, O.G. Anyoni, C. Kabaseke, A.K. Ronoh and J. Ekwangu. 2023. Combined effects of indigenous arbuscular mycorrhizal fungi (AMF) and NPK fertilizer on growth and yields of maize and soil nutrient availability. *Sustain. J. (Switzerland)*, 15: 1-12.

Giovannini, L., C. Sbrana, L. Avio and A. Turrini. 2020. Diversity of a phosphate transporter gene among species and isolates of arbuscular mycorrhizal fungi. *FEMS Microbiol. Lett.*, 367: 1-9.

Goñi, O., P. Quille and S.O. Connell. 2018. Plant physiology and biochemistry *Ascophyllum nodosum* extract biostimulants and their role in enhancing tolerance to drought stress in tomato plants. *Plant J. Physiol. Biochem.*, 126: 63-73.

Gopal, S., M. Chandrasekaran, C. Shagol, K.-Y. Kim and T.-M. Sa. 2012. Spore Associated bacteria (SAB) of arbuscular mycorrhizal fungi (AMF) and plant growth promoting rhizobacteria (PGPR) increase nutrient uptake and plant growth under stress conditions. *Korean J. Soil. Sci. Fert.*, 45: 582-592.

Grobelak, A., A. Napora and M. Kacprzak. 2015. Using plant growth-promoting rhizobacteria (PGPR) to improve plant growth. *Ecol. Eng.*, 84: 22-28.

Halim, L.S., L.O.S. Bande, Y.B. Pasolon, F.S. Rembon and S. Ginting. 2021. Improvement yield of sweet corn (*Zea mays* Saccharata (Sturt.) Bailey using arbuscular mycorrhiza fungi (AMF) and cow manure fertilizer (CMF) on ultisol. *World J. Adv. Res. Rev.*, 09: 304-308.

Han, S., L. Na, Z. Rongchao, H. Xiuqin, Z. Wenyu, Z. Bo, L. Xinpeng, W. Zhen and X. Jie. 2023. Study on signal transmission mechanism of arbuscular mycorrhizal hyphal network against root rot of *Salvia miltiorrhiza*. *Sci. Rep.*, 13: 1-19.

Harakotr, B., W. Sutthiluk and P. Rithichai. 2022. Changes on sugar and starch contents during seed development of synergistic sweet corn and implication on seed quality. *Int. J. Agron.*, 2022.

Harley, P.C., F. Loreto, G. Di Marco and T.D. Sharkey. 1992. Theoretical considerations when estimating the mesophyll conductance to CO_2 flux by analysis of the response of photosynthesis to CO_2. *Plant Physiol.*, 98: 1429-1436.

Hasanuzzaman, M., M.H.M.B. Bhuyan, K. Parvin, T.F. Bhuiyan, T.I. Anee, K. Nahar, M.S. Hossen, F. Zulfiqar, M.M. Alam and M. Fujita. 2020. Regulation of ROS metabolism in plants under environmental stress: A review of recent experimental evidence. *Int. J. Mol. Sci.*, 21: 1-44.

Hayat, S., Q. Hayat, M.N. Alyemeni and A. Ahmad. 2013. Proline enhances antioxidative enzyme activity, photosynthesis and yield of *Cicer arietinum* L., exposed to cadmium stress. *Acta. Bot. Croat.*, 72: 323-335.

He, J.D., Y.N. Zou, Q.S. Wu and K. Kuča. 2020. Mycorrhizas enhance drought tolerance of trifoliate orange by enhancing activities and gene expression of antioxidant enzymes. *Sci. Hortic.*, 262: 1-8.

He, W.X., Q.S. Wu, A. Hashem, E.F. Abd-Allah, P. Muthuramalingam, A.B.F. Al-Arjani and Y.N. Zou. 2022. Effects of symbiotic fungi on sugars and soil fertility and structure-mediated changes in plant growth of *Vicia villosa*. *Agriculture (Switzerland)*, 12: 1-12.

Hernández-Herrera, R.M., F. Santacruz-Ruvalcaba, J. Zañudo-Hernández and G. Hernández-Carmona. 2016. Activity of seaweed extracts and polysaccharide-enriched extracts from *Ulva lactuca* and *Padina gymnospora* as growth promoters of tomato and mung bean plants. *J. Appl. Phycol.*, 28: 2549-2560.

Hori, K., A. Wada and T. Shibuta. 1997. NII-Electronic Library Service. *Chem. Pharm. Bull.*, 32: 356-371.

Ikan, C., R. Ben-Laouane, R. Ouhaddou, C. Ghoulam and A. Meddich. 2023b. Co-inoculation of arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria can mitigate the effects of drought in wheat plants (*Triticum durum*). *Plant Biosyst.*, 0: 1-20.

Ikan, C., R. Ben-Laouane, R. Ouhaddou, M. Anli, A. Boutasknit, S. Lahbouki, A. Benchakour, A. Jaouad, M. Bouchdoug, A. El Moatasime, M. Ouhammou, Y. Jaouad, M. Baslam and A. Meddich. 2023a. Interactions between arbuscular mycorrhizal fungus and indigenous compost improve salt stress tolerance in wheat (*Triticum durum*). *S. Afr. J. Bot.*, 158: 417-428.

Kakabouki, I., A. Efthimiadou, A. Folina, C. Zisi and S. Karydogianni. 2020. Effect of different tomato pomace compost as organic fertilizer in sweet maize crop. *Commun. Soil Sci. Plant Anal.*, 51: 2858-2872.

Kanwal, S., N. Ilyas, N. Batool and M. Arshad. 2017. Amelioration of drought stress in wheat by combined application of PGPR, compost, and mineral fertilizer. *J. Plant Nutr.*, 40: 1250-1260.

Kapoor, D., S. Singh, V. Kumar, R. Romero, R. Prasad and J. Singh. 2019. Antioxidant enzymes regulation in plants in reference to reactive oxygen species (ROS) and reactive nitrogen species (RNS). *Plant Gene.*, 19: 100182.

Khan, N., A. Bano, M.A. Rahman, J. Guo, Z. Kang and M.A. Babar. 2019. Comparative physiological and metabolic analysis reveals a complex mechanism involved in drought tolerance in chickpea (*Cicer arietinum* L.) induced by PGPR and PGRs. *Sci. Rep.*, 9: 1-19.

Kohler, J., F. Caravaca, R. Azcón, G. Díaz and A. Roldán. 2015. The combination of compost addition and arbuscular mycorrhizal inoculation produced positive and synergistic effects on the phytomanagement of a semiarid mine tailing. *Sci. Total Environ.*, 514: 42-48.

Kranz, C.N., R.A. McLaughlin, A. Johnson, G. Miller and J.L. Heitman. 2020. The effects of compost incorporation on soil physical properties in urban soils – A concise review. *J. Environ. Manage.*, 261: 110209.

Krasilnikov, P., M.A. Taboada and Amanullah. 2022. Fertilizer use, soil health and agricultural sustainability. *Agriculture (Switzerland)*, 12: 16-20.

Kulkarni, M., R. Soolanayakanahally, S. Ogawa, Y. Uga, M.G. Selvaraj and S. Kagale. 2017. Drought response in wheat: Key genes and regulatory mechanisms controlling root system architecture and transpiration efficiency. *Front. Chem.*, 5: 1-13.

Kumari, B., M.A. Mallick, M.K. Solanki, A.C. Solanki, A. Hora and W. Guo. 2019. Plant growth promoting rhizobacteria (PGPR): modern prospects for sustainable agriculture. *Plant Health Under Biotic Stress: Volume 2: Microbial Interactions,* pp. 109-127.

Lehmann, S., D. Funck, L. Szabados and D. Rentsch. 2010. Proline metabolism and transport in plant development. *Amino Acids*, 39: 949-962.

Liu, D., S. Meng, Z. Xiang, G. Yang and N. He. 2019. An R1R2R3 MYB transcription factor, MNMYB3R1, regulates the polyphenol oxidase gene in mulberry (*Morus notabilis*). *Int. J. Mol. Sci.*, 20: 1-14.

Maia Júnior, de O.S., J.R. de Andrade, C.M. dos Santos, A.L.J. Silva, L. Endres, J.V. Silva and L.K. dos Santos Silva. 2020. Osmoregulators' accumulation minimizes the effects of drought stress in sugarcane and contributes to the recovery of photochemical efficiency in photosystem II after rewatering. *Acta Physiol. Plant.*, 42: 1-11.

Malhi, G.S., M. Kaur and P. Kaushik. 2021. Impact of climate change on agriculture and its mitigation strategies: A review. *Sustainability (Switzerland)*, 13: 1-21.

Manaa, A., R. Goussi, W. Derbali, S. Cantamessa, J. Essemine and R. Barbato. 2021. Photosynthetic performance of quinoa (*Chenopodium quinoa* Willd.) after exposure to a gradual drought stress followed by a recovery period. *Biochim. Biophys. Acta Bioenerg.*, 1862(5): 148383.

Maqbool, S., M.A. Hassan, X. Xia, L.M. York, A. Rasheed and Z. He. 2022. Root system architecture in cereals: Progress, challenges and perspective. *Plant J.*, 110: 23-42.

Meddich, A. 2022. Biostimulants for resilient agriculture—improving plant tolerance to abiotic stress: A concise review. *Gesunde Pflanzen*, 75(4): 709-727.

Meddich, A., K. Oufdou, A. Boutasknit, A. Raklami, A. Tahiri, R. Ben-Laouane, M. Ait-El-Mokhtar, M. Anli, T. Mitsui, S. Wahbi and M. Baslam. 2019. *Use of organic and biological fertilizers as strategies to improve crop biomass, yields and physicochemical parameters of soil*, 247-288.

Meddich, A., R. Ouhaddou, M. Anli and A. Boutasknit. 2021b. Role of phosphorus and arbuscular mycorrhizal fungi in the growth performances and tolerance of barley to water stress. *Plant Cell. Biotechnol. Mol. Biol.*, 45-67.

Meddich, A., Y. Ait Rahou, A. Boutasknit, M. Ait-El-Mokhtar, A. Fakhech, S. Lahbouki, W. Benaffari, R. Ben-Laouane and S. Wahbi. 2021a. Role of mycorrhizal fungi in improving the tolerance of melon (*Cucumus melo*) under two water deficit partial root drying and regulated deficit irrigation. *Plant Biosyst.*, 156(2): 469-479.

Messant, M., U. Hani, T. Hennebelle, F. Guérard, B. Gakière, A. Gall, S. Thomine and A. Krieger-Liszkay. 2023. Manganese concentration affects chloroplast structure and the photosynthetic apparatus in *Marchantia polymorpha*. *Plant Physiol.*, 192: 356-369.

Métayer, S., I. Seiliez, A. Collin, S. Duchêne, Y. Mercier, P.A. Geraert and S. Tesseraud. 2008. Mechanisms through which sulfur amino acids control protein metabolism and oxidative status. *J. Nutr. Biochem.*, 19: 207-215.

Mobaligh, M., M. Anli, A. Boutasknit, Y. Ait-rahou, A. Meddich and K. Fares. 2023. Roles of indigenous arbuscular mycorrhizal fungi and composts in improving tomato tolerance to water stress under controlled greenhouse conditions. *Catalysis Research*, 3(3): 1-22.

Mu, Z., D. Asensio, J. Sardans, R. Ogaya, J. Llusià, I. Filella, L. Liu, X. Wang and J. Peñuelas. 2023. Chronic drought alters extractable concentrations of mineral elements in Mediterranean forest soils. *Sci. Total Environ.*, 905: 167062.

Mushtaq, Z., H. Mushtaq, S. Faizan and M.A. Parray. 2021. Microbial degradation of organic constituents for sustainable development. *Microbiota and Biofertilizers, Vol 2: Ecofriendly Tools for Reclamation of Degraded Soil Environs*, 103-117.

Nagata, M., N. Yamamoto, T. Miyamoto, A. Shimomura, S. Arima, A.M. Hirsch and A. Suzuki. 2016. Enhanced hyphal growth of arbuscular mycorrhizae by root exudates derived from high R/FR treated *Lotus japonicus*. *Plant Signal. Behav.*, 11: e1187356.

Nephali, L., V. Moodley, L. Piater, P. Steenkamp, N. Buthelezi, I. Dubery, K. Burgess, J. Huyser and F. Tugizimana. 2021. A metabolomic landscape of maize plants treated with a microbial biostimulant under well-watered and drought conditions. *Front Plant. Sci.*, 12: 1-15.

Olsen, S. and L. Sommers. 1982. Methods of soil analysis. Part 2. Chemical and microbiological properties of phosphorus. *ASA Monograp.,* 9: 403-430.

Ortuño, M.F., B. Lorente, J.A. Hernández and M.J. Sánchez-Blanco. 2018. Mycorrhizal inoculation on compost substrate affects nutritional balance, water uptake and photosynthetic efficiency in *Cistus albidus* plants submitted to water stress. *Revista Brasil. Bot.*, 41: 299-310.

Ouhaddou, R., A. Meddich, C. Ikan, R. Lahlali, E. Ait Barka, M.R. Hajirezaei, R. Duponnois and M. Baslam. 2023b. Enhancing maize productivity and soil health under salt stress through physiological adaptation and metabolic regulation using indigenous biostimulants. *Plants,* 12.

Ouhaddou, R., L. Ech-chatir, M. Anli, R. Ben-Laouane, A. Boutasknit and A. Meddich. 2023a. Secondary metabolites, osmolytes and antioxidant activity as the main attributes enhanced by biostimulants for growth and resilience of lettuce to drought stress. *Gesunde Pflanzen,* 75: 1737-1753.

Ouhaddou, R., R. Ben-Laouane, A. Slimani, A. Boutasknit, M. Anli, K. Oufdou, M. Baslam and A. Meddich. 2022b. Autochthonous biostimulants as a promising biological tool to promote lettuce growth and development under salinity conditions. *Environ. Sci. Proc.,* 16: 41.

Ouhaddou, R., R. Ben-Laouane, R. Lahlali, M. Anli, C. Ikan, A. Boutasknit, A. Slimani, K. Oufdou, M. Baslam, E. Ait Barka and A. Meddich. 2022a. Application of indigenous rhizospheric microorganisms and local compost as enhancers of lettuce growth, development, and salt stress tolerance. *Microorganisms*, 10: 1625.

Ouledali, S., M. Ennajeh, A. Ferrandino, H. Khemira, A. Schubert and F. Secchi. 2019. Influence of arbuscular mycorrhizal fungi inoculation on the control of stomata functioning by abscisic acid (ABA) in drought-stressed olive plants. *S. Afr. J. Bot.,* 121: 152-158.

Pastore, D., D. Trono, M.N. Laus, N. Di Fonzo and Z. Flagella. 2007. Possible plant mitochondria involvement in cell adaptation to drought stress - A case study: Durum wheat mitochondria. *J. Exp. Bot.,* 58: 195-210.

Paymaneh, Z., M. Sarcheshmehpour, H. Mohammadi and M.A. Hesni. 2023. Vermicompost and/or compost and arbuscular mycorrhizal fungi are conducive to improving the growth of pistachio seedlings to drought stress. *Appl. Soil Ecol.,* 182: 104717.

Paz, S., M. Negev, A. Clermont and M.S. Green. 2016. Health aspects of climate change in cities with Mediterranean climate, and local adaptation plans. *Int. J. Environ. Res. Public Health,* 13: 438.

Phillips, J.M. and D.S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Trans. Br. Mycol. Soc.,* 55: 158-IN18.

Pinos, N.Q., R.L. Louro Berbara, S.S. Elias, T.A. van Tol de Castro and A.C. García. 2019. Combination of humic substances and arbuscular mycorrhizal fungi affecting corn plant growth. *J. Environ. Qual.,* 48: 1594-1604.

Quintana, J.R., J.P. Martín-Sanz, I. Valverde-Asenjo and J.A. Molina. 2023. Drought differently destabilizes soil structure in a chronosequence of abandoned agricultural lands. *Catena (Amst),* 222.

Quiroga, G., G. Erice, R. Aroca, Á.M. Zamarreño, J.M. García-Mina and J.M. Ruiz-Lozano. 2020. Radial water transport in arbuscular mycorrhizal maize plants under drought stress conditions is affected by indole-acetic acid (IAA) application. *J. Plant. Physiol.,* 246-247: 153115.

Raho, O., A. Boutasknit, M. Anli, R. Ben-laouane, Y. Ait Rahou, R. Ouhaddou, R. Duponnois, A. Douira, C. El Modafar and A. Meddich. 2022. Impact of native biostimulants / biofertilizers and their synergistic interactions on the agro-physiological and biochemical responses of date palm seedlings. *Gesunde Pflanzen*, 74(4): 1053-1069.

Rajput, V.D., Harish, R.K. Singh, K.K. Verma, L. Sharma, F.R. Quiroz-Figueroa, M. Meena, V.S. Gour, T. Minkina, S. Sushkova, and S. Mandzhieva. 2021. Recent developments in enzymatic antioxidant defence mechanism in plants with special reference to abiotic stress. *Biology*, 10: 267.

Raklami, A., N. Bechtaoui, A.I. Tahiri, M. Anli, A. Meddich and K. Oufdou. 2019. Use of rhizobacteria and mycorrhizae consortium in the open field as a strategy for improving crop nutrition, productivity and soil fertility. *Front. Microbiol.,* 10: 1-11.

Rohlf, F.J. and R.R. Sokal. 1995. Statistical tables. *Macmillan*.

Rouphael, Y. and G. Colla. 2020. Biostimulants in agriculture. *Front. Plant Sci.*, 11: 40.

Sandalio, L.M., M. Rodríguez-Serrano, M.C. Romero-Puertas and A. del Río Luis. 2013. Role of peroxisomes as a source of reactive oxygen species (ROS) signaling molecules. *Subcell. Biochem.,* 69: 231-255.

Sangwan, S. and R. Prasanna. 2022. Mycorrhizae helper bacteria: Unlocking their potential as bioenhancers of plant–arbuscular mycorrhizal fungal associations. *Microb. Ecol.,* 84: 1-10.

Sarwat, M. and N. Tuteja. 2017. Hormonal signaling to control stomatal movement during drought stress. *Plant Gene.,* 11: 143-153.

Schlesinger, W.H., M.C. Dietze, R.B. Jackson, R.P. Phillips, C.C. Rhoades, L.E. Rustad and J.M. Vose. 2016. Forest biogeochemistry in response to drought. *Glob. Chang. Biol.,* 22: 2318-2328.

Shafiq, S., N.A. Akram, M. Ashraf, P. García-Caparrós, O.M. Ali and A.A.H.A. Latef. 2021. Influence of glycine betaine (natural and synthetic) on growth, metabolism and yield production of drought-stressed maize (*Zea mays* L.) Plants. *Plants,* 10: 2540.

Shams, K. 2019. Alleviation of terminal drought stress in wheat by foliar application of zinc and manganese. *Soil Environ.,* 38: 103-111.

Sharma, K., S. Gupta, S.D. Thokchom, P. Jangir and R. Kapoor. 2021. Arbuscular mycorrhiza-mediated regulation of polyamines and aquaporins during abiotic stress: deep insights on the recondite players. *Front. Plant Sci.*, 12: 1072.

Sharma, P., A.B. Jha, R.S. Dubey and M. Pessarakli. 2012. Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *J. Bot.,* 2012: 1-26.

Shimazaki, Y., T. Ookawa and T. Hirasawa. 2005. The root tip and accelerating region suppress elongation of the decelerating region without any effects on cell turgor in primary roots of maize under water stress. *Plant Physiol.,* 139: 458-465.

Silva, A.M.M., D.L. Jones, D.R. Chadwick, X. Qi, S.R. Cotta, V.L.V.P. Araújo, F.P. Matteoli, G. V. Lacerda-Júnior, A.P.A. Pereira, P.I. Fernandes-Júnior and E.J.B.N. Cardoso. 2023. Can arbuscular mycorrhizal fungi and rhizobacteria facilitate 33P uptake in maize plants under water stress?. *Microbiol. Res.,* 271: 127350.

Slessarev, E.W., Y. Lin, N.L. Bingham, J.E. Johnson, Y. Dai, J.P. Schimel and O.A. Chadwick. 2016. Water balance creates a threshold in soil pH at the global scale. *Nature,* 540: 567-569.

Slimani, A., A. Raklami, B. Benmrid, K. Oufdou and A. Meddich. 2023. Salt-tolerant plant growth-promoting rhizobacteria mitigate salinity in barley by improving photosynthetic capacity, antioxidant activity, and soil fertility. *Biologia (Bratisl)*, 78(12): 3367-3379.

Slimani, A., A. Raklami, K. Oufdou and A. Meddich. 2022. Isolation and Characterization of PGPR and Their Potenzial for Drought Alleviation in Barley Plants. *Gesunde Pflanzen,* 1-15.

Soares, D., T.A. Paço and J. Rolim. 2023. Assessing climate change impacts on irrigation water requirements under mediterranean conditions—A review of the Methodological Approaches Focusing on Maize Crop. *Agronomy,* 13: 117.

Sood, G., R. Kaushal and M. Sharma. 2020. Alleviation of drought stress in maize (*Zea mays* L.) by using endogenous endophyte *Bacillus subtilis* in North West Himalayas. *Acta Agric. Scand. B. Soil Plant Sci.,* 70: 361-370.

Soufiani, M., A. Chakhchar, S. Aissam, A. Ferradous, A. Douira, A. Meddich and C. El Modafar. 2023. Can an indigenous consortium of arbuscular mycorrhizae effectively mitigate drought stress in argan trees (*Argania spinosa* L. Skeels) by modulating mineral nutrition and phosphatase activities?. *S. Afr. J. Bot.,* 159: 439-446.

Soussani, F.E., A. Boutasknit, R. Ben-Laouane, R. Benkirane, M. Baslam and A. Meddich. 2023. Arbuscular mycorrhizal fungi and compost-based biostimulants enhance fitness, physiological responses, yield, and quality traits of drought-stressed tomato plants. *Plants,* 12: 1856.

Steinkellner, S., V. Lendzemo, I. Langer, P. Schweiger, T. Khaosaad, J. Toussaint and H. Vierheilig. 2007. Flavonoids and strigolactones in root exudates as signals in symbiotic and pathogenic plant-fungus interactions. *Molecules*, 12(7): 1290-1306.

Straaer, B.J. 1995. *Measuring fast fluorescence transients to address environmental questions L: the JIP-test*. Photosynthesis: from light to biosphere. Dordrecht: Springer Netherlands.

Sun, J., L. Yang, X. Yang, J. Wei, L. Li, E. Guo and Y. Kong. 2021. Using spectral reflectance to estimate the leaf chlorophyll content of maize inoculated with arbuscular mycorrhizal fungi under water stress. *Front. Plant Sci.,* 12: 1-12.

Tinte, M.M., K. Masike, P.A. Steenkamp, J. Huyser, J.J.J. van der Hooft and F. Tugizimana. 2022. Computational metabolomics tools reveal metabolic reconfigurations underlying the effects of biostimulant seaweed extracts on maize plants under drought stress conditions. *Metabolites,* 12: 1-24.

Toscano, S., M.J. Gómez-Bellot, D. Romano and M.J. Sánchez-Blanco. 2023. Physiological and biochemical changes in response to *Moringa oleifera* biostimulant in petunia plants under water deficit. *Sci. Hortic.,* 319: 112187.

Trouvelot, A., J.L. Kough and V. Gianinazzi-Pearson. 1986. Mesure du taux de mycorhization VA d'un système radiculaire. Recherche de méthodes d'estimation ayant une signification fonctionnelle. *Mycorhizes: physiologie et génétique,* 217-220.

Umair, M., I.-H. Muhammad, S. Muhammad, A. Adeela, A. Farooq and H. Sikandar. 2018. A brief review on plant growth promoting rhizobacteria (PGPR): A key role in plant growth promotion. *Plant Protection,* 2(2): 77-82.

Velikova, V., I. Yordanov and A. Edreva. 2000. Oxidative stress and some antioxidant systems in acid rain-treated bean plants Protective role of exogenous polyamines. *Plant Sci.,* 151: 59-66.

Wahid, F., M. Sharif, S. Steinkellner, M.A. Khan, K.B. Marwat and S.A. Khan. 2016. Inoculation of arbuscular mycorrhizal fungi and phosphate solubilizing bacteria in the presence of rock phosphate improves phosphorus uptake and growth of maize. *Pak. J. Bot.,* 48: 739-747.

Wu, Q.S. 2017. *Arbuscular Mycorrhizas and Stress Tolerance of Plants,* Springer.

Xiang, N., C. Li, G. Li, Y. Yu, J. Hu and X. Guo. 2019. Comparative evaluation on vitamin E and carotenoid accumulation in sweet corn (*Zea mays* L.) seedlings under temperature stress. *J. Agric. Food Chem.*, 67: 9772-9781.

Xu, L.Y., M.Y. Wang, X.Z. Shi, Q.B. Yu, Y.J. Shi, S.X. Xu and W.X. Sun. 2018. Effect of long-term organic fertilization on the soil pore characteristics of greenhouse vegetable fields converted from rice-wheat rotation fields. *Sci. Total Environ.,* 631-632: 1243-1250.

Yazici, M.A., M. Asif, Y. Tutus, I. Ortas, L. Ozturk, H. Lambers and I. Cakmak. 2021. Reduced root mycorrhizal colonization as affected by phosphorus fertilization is responsible for high cadmium accumulation in wheat. *Plant Soil,* 468(1-2): 19-35.

Ye, Y., I.A. Medina-Velo, K. Cota-Ruiz, F. Moreno-Olivas and J.L. Gardea-Torresdey. 2019. Can abiotic stresses in plants be alleviated by manganese nanoparticles or compounds?. *Ecotoxicol. Environ. Saf.*, 184: 109671.

Zargar, S.M., N. Gupta, M. Nazir, R. Mahajan, F.A. Malik, N.R. Sofi, A.B. Shikari and R.K. Salgotra. 2017. Impact of drought on photosynthesis: Molecular perspective. *Plant Gene.,* 11: 154-159.

Zhang, F., Y.N. Zou and Q.S. Wu. 2018. Quantitative estimation of water uptake by mycorrhizal extraradical hyphae in citrus under drought stress. *Sci. Hortic.,* 229: 132-136.

(Received for publication 14 May 2024)