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Combined Application of Boron and Methyl Jasmonate Through Modulating Tolerance Responses Improves Maize Growth and Yield Traits Under Drought Stress

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Abstract

Maize, as one of the most important agricultural crops, is suffering from drought stress due to climate change, leading to a significant reduction in yields and thus food shortages worldwide. Foliar application of micronutrients and phytohormones has been introduced as an effective strategy to combat this condition. Therefore, this field study was conducted to evaluate the potential effect of application of boron (B) (0, 0.5%, 1%), methyl jasmonate (MeJA) (0, 50, 100 µM), and their combinations on maize morphological, physiological, and yield characteristics under irrigation deprivation at eight-leaf and ear emergence stages. Our results showed that water deficit during early and late developmental stages significantly ($p<0.05$) decreased almost all growth and yield traits compared to well-irrigated plants, while application of different concentrations of B and MeJA, especially B3M2 and B3M3, alleviated the dryness detrimental effects. These observations suggest that combined treatments with B and MeJA can reinforce drought tolerance responses in maize plant. Further, our data revealed that water-stressed plants treatment with a combination of B and MeJA in different ways increased total chlorophyll, chlorophyll a, chlorophyll b, carotenoid, free proline, and malondialdehyde (MDA) contents, quantum yield of photosystem II and activity of antioxidant enzymes superoxide dismutase (SOD) and catalase (CAT) compared to water-treated plants. It can be concluded that foliar spraying of B and MeJA, especially in a combined manner, can significantly reduce the damage caused by water stress to the quantity and quality of the maize crop by positively regulating and improving the drought tolerance response.

Keyword: Boron; Drought stress; Drought tolerance; maize; Methyl jasmonate

1. Introduction

Maize (*Zea mays* L.) as the third most important crop in the world after wheat and rice, plays an essential role in providing food for millions of people worldwide (FAOSTAT, 2012; Afshari et al., 2021). Furthermore, the world's population is growing rapidly, making food security crucial for sustainable human life (Myers et al., 2017). However, maize growth and productivity are severely limited through climate change consequences and stressful conditions (Balbaa et al., 2022). Drought is one of the most devastating impacts of climate disaster on agricultural production, threatening the global food supply (Ericksen 2008; Vurukonda et al., 2016). Water deficit stress generally influences the arid and semi-arid regions, covering one-third of the Earth's landmass (Anjum et al., 2017). In this state, plants experience disturbances in water and nutrients uptake, photosynthetic rate, phytohormone balance, and cells' oxidative status (Arora et al., 2002; Balbaa et al., 2022). The magnitude of yield loss depends on the plants' species, drought severity, the exposure time and the growth stage of the plant (Kamali et al., 2022). In response to drought stress, plants use different resistance strategies to overcome the negative effects of water limitation (Falahi et al., 2018). Therefore, developing sustainable methods to increase plant resistance to drought will be an effective and economical approach to prevent millions of people from facing hunger and food insecurity. Application of various chemicals with the potential to reduce the destructive effects of drought, can be a promising way to increase crops tolerance to abiotic stress (Van Nguyen et al., 2022).

Boron (B) is an essential micronutrient for optimal plant growth, development, and yield as well as crops quality. Its key roles have been demonstrated in the metabolism of carbohydrate and protein, structure and synthesis of cell wall, stability of membranes, function of phytohormones, transmission of water and nutrients from roots to the other plant parts, and metabolism of phenolic and indole acetic acid (Uluisik et al., 2018). This element is also important for root development, flowering, pollen germination, pollen tube growth, and seed formation (Shireen et al., 2018). Soil dryness disrupts B uptake by roots, leading to B deficiency and reduced plant growth and productivity (Aydin et al., 2019). According to some studies, exogenous application of B can counteract most of the destructive effects of water stress on strategic agricultural crops (Naeem et al., 2018; Shehzad et al., 2018; Aydin et al., 2019; Akhtar et al., 2022).

To acclimate to stressful conditions, plant defense system is regulated by various phyto-protectants that mediate the redox balance in a dynamic environment (Alhaithloul & Soliman 2021). Methyl jasmonate (MeJA), a compound derived from jasmonic acid (JA), is a plant hormone that, as a signaling molecule, plays a role in regulating various processes such as seed germination and seedling emergence, root system growth and development, fruiting and senescence. (Allagulova et al., 2020). In addition, MeJA plays an important role in intensifying the tolerance response against various biotic and abiotic stressors such as salinity, drought, osmotic shock, UV radiation, high temperature, and pathogens attack (Wei et al., 2021). The effect of this regulatory molecule on alleviating water stress in various plants has been investigated in the recent decades (Mohamed & Latif, 2017; Fugate et al., 2018; Xiong et al., 2020). Given the exposure of maize to drought stress during its growth and development period in arid and semiarid areas, and also the importance of having a sustainable yield in this situation, we carried out a field study to evaluate and understand whether and how applying different concentrations of B, MeJA, and B+MeJA act as adopting strategy to influence yield quantity and quality, and some resistance reactions of maize under various irrigation regimes.

2. Materials and methods

2.1. Field condition

This study was conducted at geographical coordinates of 51˚ 40'E and 35˚ 17'N in Varamin (Iran) at an altitude of about 1000 meters above sea level during the two crop years of 2020- 2021. According to the Koppen climate

category, this region is located in a semi-arid temperate zone with warm and dry summers. Based on the 40 years of data, the average annual precipitation in this area is 170 mm, generally distributed from the beginning of November to the middle of April. To determine the properties of farm soil, samplingmwas done from a depth of 0–30 cm and the texture, saturation percentage (SP), electrical conductivity (EC), acidity (pH), percentage of clay, sand and silt, organic carbon, total nitrogen, available phosphorus and
potassium of soil were measured (Table 1).

2.2. Experimental design and treatments

The experiment was designed as a split plots form over randomized complete block with three replications. Maxima hybrid maize seed was used as a usual seed in this area. After land preparation and seed planting, three irrigation treatments comprising I1) regular irrigation, I2) irrigation interruption at eight-leaf stage, and I3) irrigation interruption at ear emergence stage were applied to the main plots. Subplots treatments included three concentrations of B (0, 0.5, and 1%, mentioned B1, B2, and B3, respectively), MeJA (0, 50, and 100 μM, mentioned M1, M2, and M3, respectively), and their combination at the beginning of stem formation stage. Plant sampling was carried out at the end of reproductive stage.

2.3. Plant growth and crop production

Plant height, row number per ear, kernel number per row, kernel number per ear, 1000-kernel weight, grain yield, biological yield and harvest index were determined in 5 replicates at all treatments.

2.4. Grain oil and protein content

The oil percentage of 100 g seeds was calculated using N.M.R method and then, based on the seed oil percentage and seed yield, seed oil yield was calculated. Similarly, protein percentage of 100 g seeds was measured based on Kjeldahl method and then, according to seed protein percentage and seed yield, seed protein yield was calculated.

2.5. Photosynthetic pigments

The fresh samples were extracted whit 80% (v/v) acetone and the solution absorbance was measured at 470,645 and 663 nm via spectrophotometer to determine the contents of chlorophyll a, chlorophyll b, total chlorophyll and carotenoids using the equations described by Lichtenthaler (1987).

2.6. Quantum yield of photosystem II

To measure quantum yield of photosystem II, a fluorescence meter device (PEA, Walz, Germany) was used. The measurement was done in the seed filling stage from the end leaf in the early hours of the morning and after 30 minutes of darkness by special clips.

2.7. Free proline content

The free proline content was assayed according to Bates (1973) method. 0.2 g fresh leaf tissue was homogenized with 3 mL of 3% sulfosalicylic acid at 4 °C. The extract was centrifuged at 12,000 rpm for 15 min. Next, 2 mL of supernatant, 2 mL of ninhydrin agent, and 2 mL of glacial acetic acid were mixed and incubated at 100 °C for

1 h. After cooling, the reaction mixture was extracted with 4 mL of toluene. The chromophore-containing toluene was separated from the hydrated phase. Its absorbance was determined at 520 nm by spectrophotometry method. The proline concentration was calculated based on a standard curve and expressed as mg proline g-1 FW.

2.8. Antioxidant enzymes activity

Protein extraction and measurement were done based on Lowry (1951) method. SOD (EC 1.15.1.1) enzyme activity was assessed based on its capacity to inhibit the photochemical reduction of nitroblue tetrazolium salt (NBT). For this, 3 mL of reaction mixture containing 33 µM NBT, 10 mM L-methionine, 0.66 mM disodium EDTA, and 0.0033 mM riboflavin in 0.05 mM sodium phosphate buffer (pH 7.8), were incubated in the light for 15 min. The sample absorbance was recorded at 560 nm before and after exposure to light according to the method of Giannopolitis and Rie (1977). The SOD activity of each samples was expressed as unit enzyme in protein mg-1 min-1. For determination of CAT (EC 1.11.1.6) enzyme activity, the absorbance of reaction mixture containing 0.1 mL of protein extract and 0.05 M sodium phosphate buffer (pH 7.0) with 0.1 mM EDTA and 3% H2O2 was followed for 1 min at 240 nm. The activity of this enzyme was reported as ∆Abs 240 mg-1 protein min-1 (Cakmak & Marschner 1992).

2.9. Malondialdehyde (MDA) content

To determine the level of MDA, fresh leaf (0.2 g) was ground in liquid nitrogen with 1 mL of 0.5% (w/v) thiobarbituric acid in 20% (w/v) trichloric acid. After heating for 30 min at 95 °C, the samples were cooled to 4 °C, to stop the reaction. After centrifugation for 10 min at 10,000 rpm, the absorbances of the supernatants were determined at 532 and 600 nm. The extinction coefficient for MDA is 155 mM-1 cm-1. The results were expressed as nmol MDA g-1 FW (Stewart & Bewley 1980).

2.10. Statistical analysis

All the experiments were carried out in five replications. Data were analyzed using SPSS 24 software. Duncan post hoc test was applied to identify significant difference ($p \leq 0.05$) amongst different treatment groups.

3. Results

3.1. Plant Growth and crop production

The data presented in Table 2 revealed the effects of water regimes, B, MeJA, and B+MeJA treatments under water deficiency on the eight growth and productivity traits of maize. The results showed that irrigation cut-off significantly decrease all the measured parameters, including plant height, row number per ear, kernel number per row, kernel number per ear, 1000-kernel weight, grain yield, biological yield and harvest index. The time of stopping irrigation had different effects on the kernel number per row, kernel number per ear, 1000-kernel weight, grain yield, biological yield differently, so that its cut-off at the ear emergence stage caused a further decrease in these parameters. Spraying two concentrations of B in maize whose irrigation was interrupted caused an increase in plant height, row number per ear, kernel number per row, kernel number per ear, 1000-kernel weight compared to corresponding irrigated cut-off plants, while no positive effects were observed on grain yield, biological yield and harvest index. On the other hand, the results showed that MeJA exogenous application can positively influence row number per ear, kernel number per row, and kernel number per ear in plants exposed water restriction during early and late developmental stages, as well. The effects of different concentrations of B+MeJA on growth and productivity of maize under water stress also were investigated. The results indicated that these treatments can significantly ($p \leq 0.05$) increase the measured parameters except for grain yield, biological yield and harvest index at certain concentrations.

3.2. Grain protein and oil qualities

Analysis of the drought-exposed plants showed that irrigation cut-off at both early and late stages of development significantly ($p \leq 0.05$) increased percent of kernel protein, while yield of kernel protein increased only after stopping irrigation at eight-leaf stage. The irrigation interruption also decreased kernel oil percent and yield in both situations (Table 3). The effects of single application of B and MeJA on irrigated cut-off corns were investigated. The results showed that with the exception of yield of kernel protein, B spraying increased all measured parameters, whereas MeJA increased oil percent and yield after both phases of stopping irrigation. Different concentrations of B+MeJA increased the quality of seed oil and protein compared to non-irrigated MeJA-treated plants. On the other hand, compared to single treatments of B, these treatments increased the mentioned parameter only in the present of high concentration of B in combination with MeJA.

3.3. Photosynthetic pigments

The determination of photosynthetic pigments showed that irrigation cut-off led to a decrease in chlorophyll a, chlorophyll b, and total chlorophyll contents, especially at late stage of maize development (Table 4).Foliar application of B, MeJA, and B+MeJA improved the contents of these pigments in plants under water scarce conditions. The higher contents of chlorophyll a, chlorophyll b, and total chlorophyll in both irrigation cut-off levels were reported under B+MeJA treatment with high concentration of B. In contrast to chlorophylls contents, we observed an increase in the carotenoid level when irrigation was stopped (Table 4). Spraying B and B+MeJA intensified this enhancement, while individual MeJA treatment had no impact on carotenoid content. The highest content occurred in 1% B in combination with MeJA concentrations under irrigation cut-off at ear emergence stage.

3.4. Quantum yield of photosystem II

The quantum yield of photosystem II was also monitored in response to different treatments under irrigation cut-off patterns (Table 4). The results indicated that water deficiency significantly ($p \leq 0.05$) decreased the quantum yield of photosystem II, with a minimum value at ear emergence stage. Exogenous application of B and MeJA had different effects on this factor, so that B increased it and MeJA could not influence quantum yield of photosystem II under drought conditions. Similar to chlorophylls contents, B+MeJA treatments improved quantum yield of photosystem II at some concentrations, especially those with higher B content.

3.5. Free proline content

As shown in table 5, the irrigation cut-off resulted in a marked increase in free proline content. It was approximately 3 and 6 times higher than that of the normally irrigated sample at eight-leaf and ear emergence stages, respectively. The effect of spraying with different concentrations of B, MeJA and B+MeJA on free proline accumulation in plants exposed to water deficit was investigated, as well. The data showed that single application of B and MeJA increased the free proline content, with the exception of M2 at early dryness and B2 at late dryness. The B+MeJA treatments also showed an increasing trend in its level, so that the highest content occurred when combining a high concentration of B with both MeJAtreatments.

3.6. Antioxidant enzymes activity

The activity of two antioxidant enzymes CAT and SOD was measured in response to water deficiency, as well as the application of B, MeJA and B+MeJA treatments in these situations (Table 5). Both enzymes activity increased under irrigation cut-off, with a greater impact at ear emergence stage. Changing the time of irrigation interruption caused a 2-folds increase in SOD enzyme activity. In response to supplements application, only 1% B could increase the CAT activity at both irrigation withholding stages, while all statements of B+MeJA positively affected this enzyme activity. In contrast, SOD activity significantly increased in response to 100 µM MeJA, as well as all B+MeJA treatments, except B2M2.

3.7. MDA content

According to table 5, the content of MDA as a consequence of lipid peroxidation, increased significantly in response to limited irrigation with a maximum level at ear emergence stage. Lipid peroxidation diminished after spraying different concentrations of B, and B+MeJA, while individual treatment of MeJA did not affect the MDA level. Its largest decrease occurred in exposure to combined treatment of B and MeJA.

4. discussion

During last decades, climate change derived environmental stresses, particularly droughts, has disrupted the growth and productivity of plants globally, causing a drastic decrease in crops yield, including maize (Webber et al., 2018). In this condition, it is crucial to investigate practical agricultural strategies to improve crop productivity for ensuring substantial human life. Exogenous application of nutrients and regulatory molecules could be an efficient method to recover plant function under water deficit (Kapoor et al., 2020). Therefore, we conducted a study to evaluate the spray-enhancing effects of different concentrations of B, MeJA, and B+MeJA on the yield and resistance of maize subjected to irrigation interruption at different plant developmental stages. The results showed that irrigation cut-off at both early and late developmental stages leads to significant decrease in plants height. Treatment of water-stressed maize with B improves plant height across all irrigation cut-off regimes, while individual MeJA treatments had no significant impact. Likewise, in response to combined treatments B3M2 and B3M3 at both patterns of irrigation restriction, the plant height reached a level similar to well-watered plants. As has been proven, exposure to drought stress at different stages of plant growth significantly decreases the maize plant height (Zhu et al., 2021). Various studies indicated that drought stress can affect a variety of plant physiological and biochemical process such as tissues water potential, cell elongation, CO2 capture capacity, cell division, nutrient uptake, transpiration of assimilates, and photosynthetic efficiency, leading to reduced plant growth and function (Anjum et al., 2011). Spraying of B and MeJA possibly has a promoting effect on maize height by reducing the severity of these damages. The limited irrigation at early and late stages of plant development also led to a considerable decrease in the quantity of maize production including row number per ear, kernel number per row, kernel number per ear, and 1000-kernel weight. The effect of stage of drought application on all of these measured parameters was almost the same (10%) except for the weight of 1000 kernels, which was strongly affected by exposure to drought stress during the ear formation phase with a 40% decrease. However, row number of each ear increased in response to individual spray of B

and MeJA, but combination treatments I2B3M2, I2B3M3, I3B2M3, I3B3M2, and I3B3M3 revealed the maximum amount
which was also greater than that of the control sample. The number of kernel per each row and ear in maize plant exposed to water deficit was also improved by the application of B and MeJA, exceeding the control level in I2B3M2, I2B3M3, I3B2M3, I3B3M2, and I3B3M3 treatments. The maximal recovery effect of B and MeJA at both phases of the irrigation interruption occurred in B3M3 treatment for the crop parameters mentioned. As regards kernel weight, the dramatic effect of drought was moderated by application B and MeJA. We observed that B3M2 and B3M3 treatments result in an almost 5% increase in kernel weight in both irrigation restriction experiments compared to the drought stressed samples. It can be concluded that B and MeJA, specially in combination with each other, can mitigate drought-induced damages to ear characteristics. Previous studies have reported that B and MeJA alone can diminish negative effects of drought stress on agriculture production quantity (Anjum et al., 2016; Shehzad et al., 2018). Perhaps through reducing drought-induced B deficiency and also activating drought tolerance responses, they can improve maize productivity. However, their combined application appears to have a greater impact on maize production quantity. Besides, the values of grain yield, biological yield and harvest index were affected by drought as factors related to the grain quantity in one hectare of field. Similar to the results of grain weight, the data showed that grain yield and biological yield of maize were highly vulnerable in response to irrigation cut-off at the ear emergence stage, and showed a decrease of approximately 40%. Nevertheless, maize yield losses were significantly rectified by the use of B, MeJA, and B+MeJA treatments.In addition, the quality of maize grains was also determined and the results showed that drought stress at eight-leaf and ear emergence stages significantly increased the percentage of protein by 14 and 35%, respectively. Conversely, the grain protein yield had a negative relationship with protein content under limited irrigation at late stage of maize development. According to grain yield data, a decrease in grain protein yield by 16% occurred in response to drought stress at ear formation stage. In this situation, foliar application of B, MeJA and B+MeJA not only increased protein percent of maize grain beyond the normal irrigation sample, but also positively affected protein yield under both limited irrigation conditions. The
highest grain protein percentage was obtained in the I3B3M2 and I3B3M3 treatments, which was about 2 times its amount in the grains from well-irrigated plants. On the other hand, these combined treatments increased the yield of grain protein in plants exposed to drought stress at the end of growth to the extent that it was 26% more than the level in stressed plants, and 6% more than non-stressed plants. Besides, grain oil percent and yield decreased dramatically in response to drought stress, as well. Our data showed a 12 and 45% decrease in maize grain oil when exposed to drought during the early and late stages of development. Grain oil yield continued to decline further in response to water restriction. Both irrigation interruption patterns experienced a 20% and 65% drop in oil yield, respectively. Although spraying different concentrations of B, MeJA and their combination resulted in an increase in these parameters, the highest amount was still observed in the well-irrigated plants. Nevertheless, in both cases of irrigation restriction, the B3M2 and B3M3 treatments had the greatest effect on improving oil content and yield of maize grains. Once plants exposed to water scarcity, they exhibit a range of physiological changes that can affect their growth, yield and tolerance (Gao et al., 2015). Extreme environmental conditions such as water shortage, can weaken photosynthetic rate in plants. Under soil dryness and stomata closure, reduction of CO2 uptake leads to a decrease in the photosynthesis process (Khalvandi et

al., 2021). The limitation of photosynthesis can lead to the absorption of more light energy than its consumption during carbon fixation, which is an important source of reactive oxygen species (ROS) production in chloroplasts. High level of ROS and oxidative stress can directly damage membranes and their components in this susceptible organelle (Farooq et al., 2009). In our study, the contents of photosynthetic pigments in both early and late stages of maize development were significantly affected by the interruption of irrigation. Water limitation had a negative impact on the total chlorophyll, chlorophyll a, and chlorophyll b contents, while increased the carotenoids levels. Stopping watering at the ear emergence stage was 30% more destructive to the chlorophylls contents. The reduction in chlorophyll content in maize exposed to drought stress may be due to damage to the chloroplast membrane. Nevertheless, it was found that maize treated with B, MeJA, and their combinations had the higher chlorophyll pigments at both irrigation cut-off stages. The chlorophylls levels reached control plants under B3M2 and B3M3 treatments at limited irrigation during eight-leaf stage, implying that these treatments had a healing effect on stressed maize plants. Previous studies reported that B and MeJA individually stimulate the accumulation of photosynthetic pigments to tolerate drought stress (Anjum et al., 2019; Shehzad et al., 2018; Akhtar et al., 2022). It appears that changes in chlorophylls contents may also affect quantum yield of photosystem II as an indicator of the operational potential of photosystem II. We observed that quantum yield of photosystem II reduced significantly by 10 and 15%, respectively, in response to irrigation withholding at early and late developmental stages compared to well-irrigated plants.

In addition, the application of B and MeJA had a compensating effect on this parameter similar to that of the amounts of chlorophylls. Combined treatments B and MeJA had the most positive effect on quantum yield of photosystem II, increasing it by approximately 10%. On the other hand, carotenoids are pigments that, in addition to absorbing light photons, are also responsible for scavenging ROS molecules. These pigments have been shown to play important roles in the drought resistance in higher plants (Zhang et al., 2021). Drought-induced carotenoids enhancement in our study was consistent with previous studies (Talebi et al., 2013; Mibei et al., 2017). Irrigation disruption at early and late stages of maize development led to 40 to 90% carotenoid accumulation compared to well-irrigated plants. Moreover, foliar spraying of different concentrations of B, MeJA, and B+MeJA enhanced the positive effect of dryness on the amount of this pigment, so that it peaked under I3B3M2 and I3B3M3 conditions with a 125% enhancement compared to untreated plants. It can be concluded that the recovery of chlorophyll and quantum yield of photosystem II values, together with the sharp increase of carotenoids levels under foliar application of B and MeJA, especially their combinations, by increasing the photosynthesis rate and reducing ROS level, improve plant growth and productivity in dryness condition. Proline accumulation is one of the most important adaptation scenario in plants under drought stress, and allowing them to survive and recover by regulating cytosolic osmotic pressure, maintaining the structure of cellular proteins, removing ROS and regulating oxidation reactions (Balbaa et al., 2022). Our results showed that the content of proline in maize leaves accumulates in response to the termination of irrigation at both stages of development. Its values in dry condition at the early and late stages of plant development were approximately 3 and 6 times higher compared to the control sample, respectively. The cumulative effect of drought on proline content was also promoted by treating stressed plants with different concentrations of B and MeJA. Regarding this osmolyte, the B3M2 and B3M3 combination treatments showed the highest increase in the both limited irrigation stages, which were respectively 5 and 8 times more than the amount of normal irrigation. Our data suggest that high level of proline could be an efficient mechanism of osmotic regulation and cellular adaptation to water stress in maize plant, consistent with the findings of previous reports (Yadollahi Farsani et al., 2021; Akhtar et al., 2022). Therefore, it is likely that by stimulating proline biosynthesis, B and MeJA may lead to maintaining cell water potential and reducing the deleterious effect of drought on maize plants (Rahman et al., 2021; Salavati et al., 2021). Antioxidant enzymes are another key component of resistance system, protecting the plant from the destructive effects of oxidative stress induced by extreme environmental conditions (Khodamoradi et al., 2022). Our results showed that drought-exposed maize experienced significant increases in SOD and CAT enzyme activity at both early and late development stages. Similar photosynthetic pigments and proline contents, this study suggest that spray different concentrations of B+MeJA can have an additional effect on the activation of these enzymes under drought stress condition, peaking in I3B3M2 and I3B3M3 treatments (about 140-fold more than well- irrigated samples). Previously, Aydin et al. (2019) reported that exogenous B increased antioxidant enzymes activity and genes expression. There are also numerous studies stated that MeJA as a regulatory molecule induces antioxidant enzymes at the levels of gene expression and protein activation (Aftab et al., 2011; Serna-Escolano et al., 2021).

The protective effects of exogenous application of B and MeJA on drought-suffering maize plants can be confirmed considering the results of MDA in response to different treatments. The content of MDA as an indicator of cell membranes oxidation under oxidative stress, increased in plant exposed to drought at both developmental stages. The maximum value was recorded at the ear emergence stage for stressed plants. Also, as expected from our other mentioned results, B+MeJA treatments could alleviate drought-induced MDA production. Therefore, this data clarified that the combined treatments of B and MeJA greatly enhance maize ability to tolerate drought stress.

Conclusion

In general, it can be concluded that however maize is a drought-sensitive plant, especially during the ear formation stage, foliar spraying of B and MeJA in a combined manner compared to their separate application can significantly reduce the damage caused by drought on the growth and yield. The positive effects of B+MeJA supplementation on the growth and crop quantity and quality of maize exposed to drought stress were associated with the regulation of biochemical processes due to increased chlorophylls and carotenoids, accumulation of free proline, and activation SOD and CAT enzymes. Nevertheless, it turns out that 1% B supplement in combination with 50 and 100 µM MeJA are the best treatments to mitigate the drought stress adversities to improve maize yield and quality.

Conflicts of interest

The authors declare no conflicts of interest.

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Contributions

All authors contributed to this research paper. M.H. performed the experiments, methodology, analyzed the data, interpreted data, and wrote the manuscript. H.R.T.M. designed and supervised the study. F.G., P.K. and M.N. advised the study and edited final manuscript.

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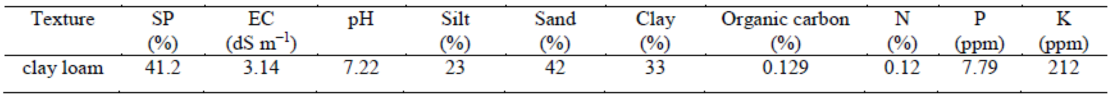
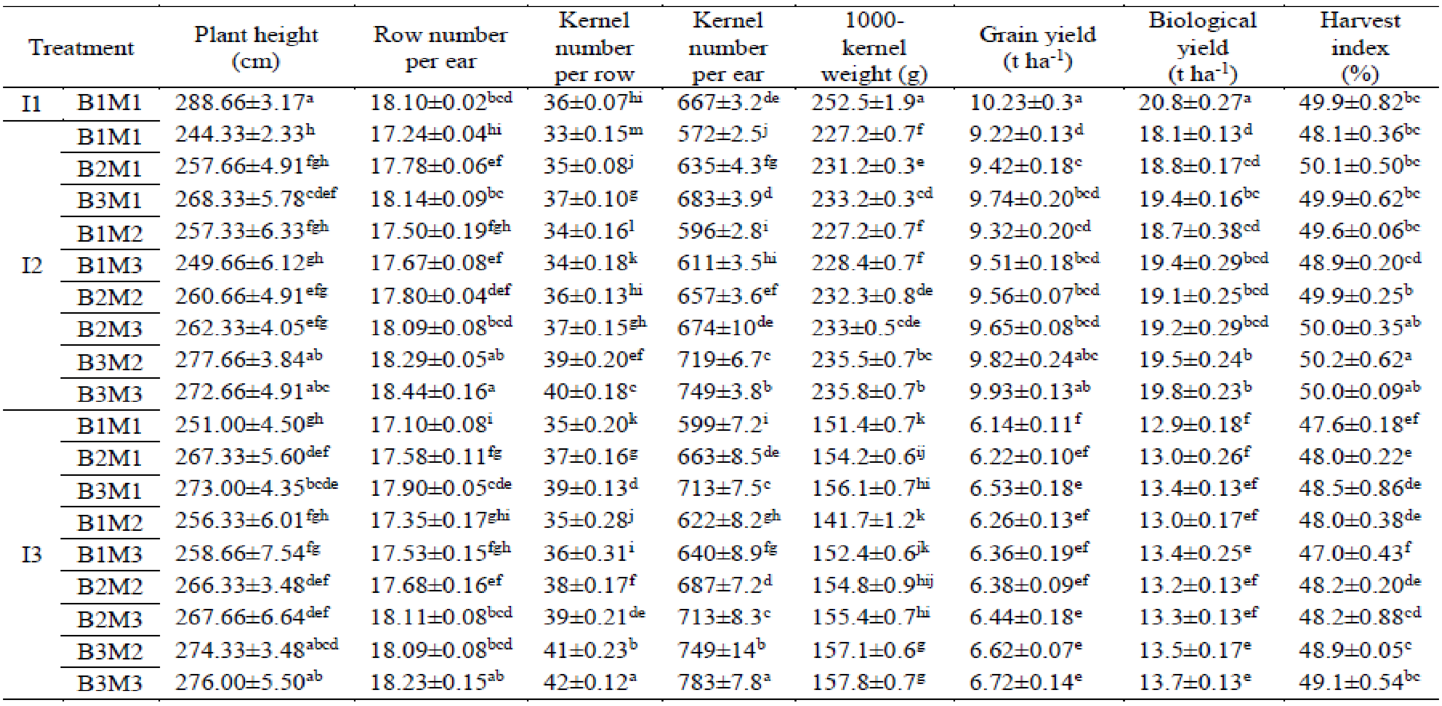
Table 1. Physicochemical properties of soil collected from site study.



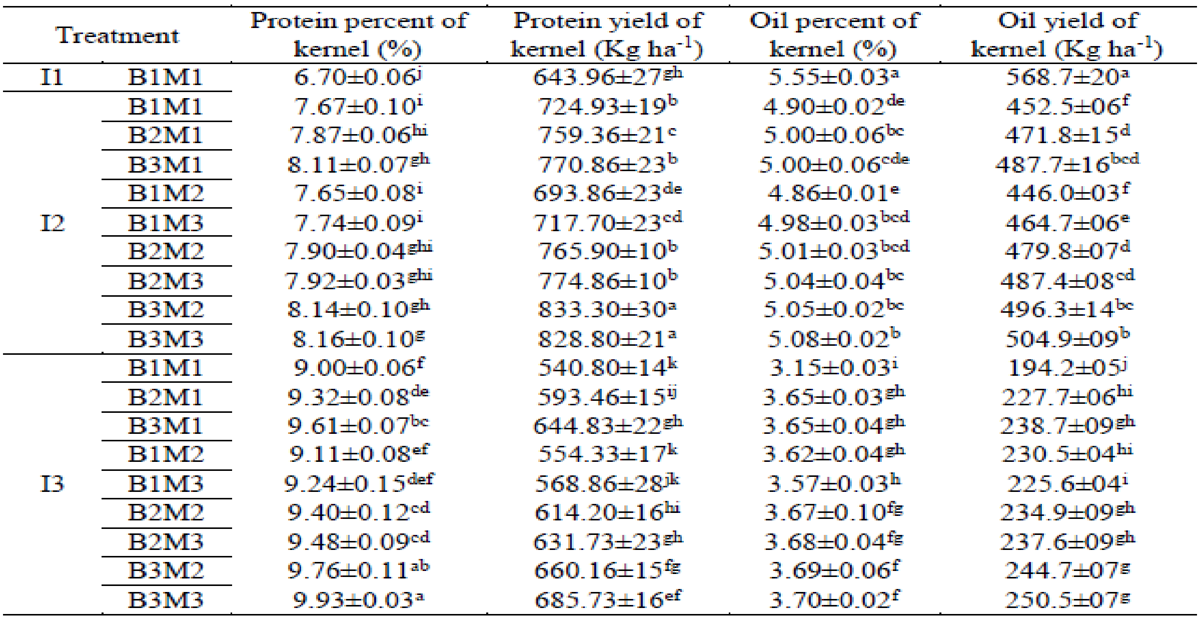
Texture	SP (%)	EC (dS m^{-1})	pH	Silt (%)	Sand (%)	Clay (%)	Organic carbon (%)	N (%)	P (ppm)	K (ppm)
clay loam	41.2	3.14	7.22	23	42	33	0.129	0.12	7.79	212

Table 2. The effect of B and MeJA foliar application on maize growth and productivity traits under irrigation cut-off at eight-leaf (I2) and ear emergence (I3) stages. Data represent means ± SD. Significant differences ($p \le 0.05$) are indicated by different letters.



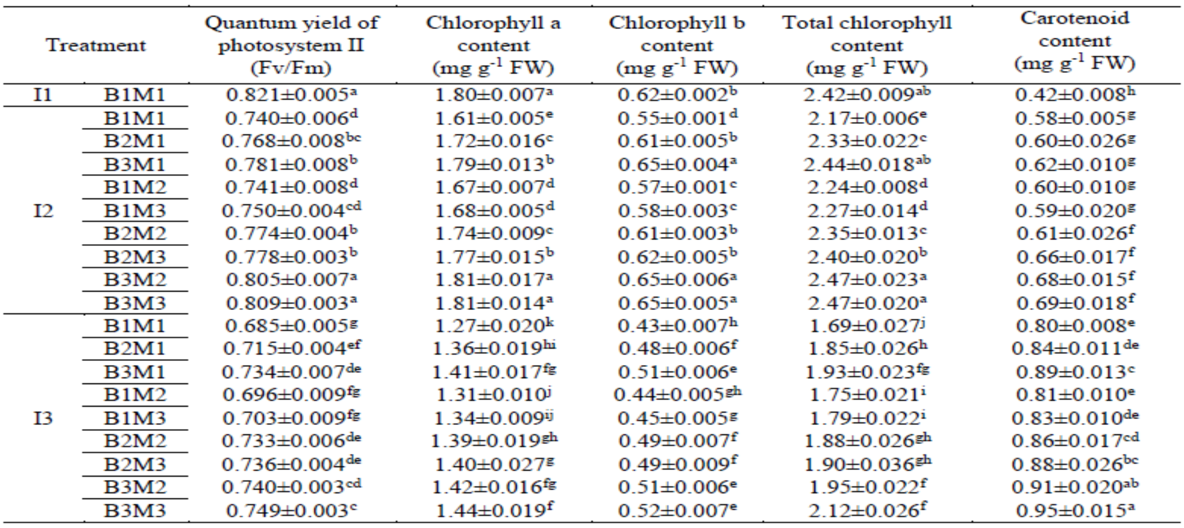
Treatment		Plant height (cm)	Row number per ear	Kernel number per row	Kernel number per ear	1000-kernel weight (g)	Grain yield (t ha^{-1})	Biological yield (t ha^{-1})	Harvest index (%)
I1	B1M1	288.66 ± 3.17^{a}	18.10 ± 0.02^{bcd}	36 ± 0.07^{hi}	667 ± 3.2^{de}	252.5 ± 1.9^{a}	10.23 ± 0.3^{a}	20.8 ± 0.27^{a}	49.9 ± 0.82^{bc}
I2	B1M1	244.33 ± 2.33^{h}	17.24 ± 0.04^{hi}	33 ± 0.15^{m}	572 ± 2.5^{j}	227.2 ± 0.7^{f}	9.22 ± 0.13^{d}	18.1 ± 0.13^{d}	48.1 ± 0.36^{bc}
	B2M1	257.66 ± 4.91^{fgh}	17.78 ± 0.06^{ef}	35 ± 0.08^{j}	635 ± 4.3^{fg}	231.2 ± 0.3^{e}	9.42 ± 0.18^{c}	18.8 ± 0.17^{cd}	50.1 ± 0.50^{bc}
	B3M1	268.33 ± 5.78^{cdef}	18.14 ± 0.09^{bc}	37 ± 0.10^{g}	683 ± 3.9^{d}	233.2 ± 0.3^{cd}	9.74 ± 0.20^{bcd}	19.4 ± 0.16^{bc}	49.9 ± 0.62^{bc}
	B1M2	257.33 ± 6.33^{fgh}	17.50 ± 0.19^{fgh}	34 ± 0.16^{l}	596 ± 2.8^{i}	227.2 ± 0.7^{f}	9.32 ± 0.20^{cd}	18.7 ± 0.38^{cd}	49.6 ± 0.06^{bc}
	B1M3	249.66 ± 6.12^{gh}	17.67 ± 0.08^{ef}	34 ± 0.18^{k}	611 ± 3.5^{hi}	228.4 ± 0.7^{f}	9.51 ± 0.18^{bcd}	19.4 ± 0.29^{bcd}	48.9 ± 0.20^{cd}
	B2M2	260.66 ± 4.91^{efg}	17.80 ± 0.04^{def}	36 ± 0.13^{hi}	657 ± 3.6^{ef}	232.3 ± 0.8^{de}	9.56 ± 0.07^{bcd}	19.1 ± 0.25^{bcd}	49.9 ± 0.25^{b}
	B2M3	262.33 ± 4.05^{efg}	18.09 ± 0.08^{bcd}	37 ± 0.15^{gh}	674 ± 10^{de}	233 ± 0.5^{cde}	9.65 ± 0.08^{bcd}	19.2 ± 0.29^{bcd}	50.0 ± 0.35^{ab}
	B3M2	277.66 ± 3.84^{ab}	18.29 ± 0.05^{ab}	39 ± 0.20^{ef}	719 ± 6.7^{c}	235.5 ± 0.7^{bc}	9.82 ± 0.24^{abc}	19.5 ± 0.24^{b}	50.2 ± 0.62^{a}
	B3M3	272.66 ± 4.91^{abc}	18.44 ± 0.16^{a}	40 ± 0.18^{c}	749 ± 3.8^{b}	235.8 ± 0.7^{b}	9.93 ± 0.13^{ab}	19.8 ± 0.23^{b}	50.0 ± 0.09^{ab}
I3	B1M1	251.00 ± 4.50^{gh}	17.10 ± 0.08^{i}	35 ± 0.20^{k}	599 ± 7.2^{i}	151.4 ± 0.7^{k}	6.14 ± 0.11^{f}	12.9 ± 0.18^{f}	47.6 ± 0.18^{ef}
	B2M1	267.33 ± 5.60^{def}	17.58 ± 0.11^{fg}	37 ± 0.16^{g}	663 ± 8.5^{de}	154.2 ± 0.6^{ij}	6.22 ± 0.10^{ef}	13.0 ± 0.26^{f}	48.0 ± 0.22^{e}
	B3M1	273.00 ± 4.35^{bcde}	17.90 ± 0.05^{cde}	39 ± 0.13^{d}	713 ± 7.5^{c}	156.1 ± 0.7^{hi}	6.53 ± 0.18^{e}	13.4 ± 0.13^{ef}	48.5 ± 0.86^{de}
	B1M2	256.33 ± 6.01^{fgh}	17.35 ± 0.17^{ghi}	35 ± 0.28^{j}	622 ± 8.2^{gh}	141.7 ± 1.2^{k}	6.26 ± 0.13^{ef}	13.0 ± 0.17^{ef}	48.0 ± 0.38^{de}
	B1M3	258.66 ± 7.54^{fg}	17.53 ± 0.15^{fgh}	36 ± 0.31^{i}	640 ± 8.9^{fg}	152.4 ± 0.6^{jk}	6.36 ± 0.19^{ef}	13.4 ± 0.25^{e}	47.0 ± 0.43^{f}
	B2M2	266.33 ± 3.48^{def}	17.68 ± 0.16^{ef}	38 ± 0.17^{f}	687 ± 7.2^{d}	154.8 ± 0.9^{hij}	6.38 ± 0.09^{ef}	13.2 ± 0.13^{ef}	48.2 ± 0.20^{de}
	B2M3	267.66 ± 6.64^{def}	18.11 ± 0.08^{bcd}	39 ± 0.21^{de}	713 ± 8.3^{c}	155.4 ± 0.7^{hi}	6.44 ± 0.18^{e}	13.3 ± 0.13^{ef}	48.2 ± 0.88^{cd}
	B3M2	274.33 ± 3.48^{abcd}	18.09 ± 0.08^{bcd}	41 ± 0.23^{b}	749 ± 14^{b}	157.1 ± 0.6^{g}	6.62 ± 0.07^{e}	13.5 ± 0.17^{e}	48.9 ± 0.05^{c}
	B3M3	276.00 ± 5.50^{ab}	18.23 ± 0.15^{ab}	42 ± 0.12^{a}	783 ± 7.8^{a}	157.8 ± 0.7^{g}	6.72 ± 0.14^{e}	13.7 ± 0.13^{e}	49.1 ± 0.54^{bc}

Table 3. The effect of B and MeJA foliar application on protein and oil qualities of maize grain under irrigation cutoff at eight-leaf (I2) and ear emergence (I3) stages. Data represent means ± SD. Significant differences ($p \le 0.05$) areindicated by different letters.



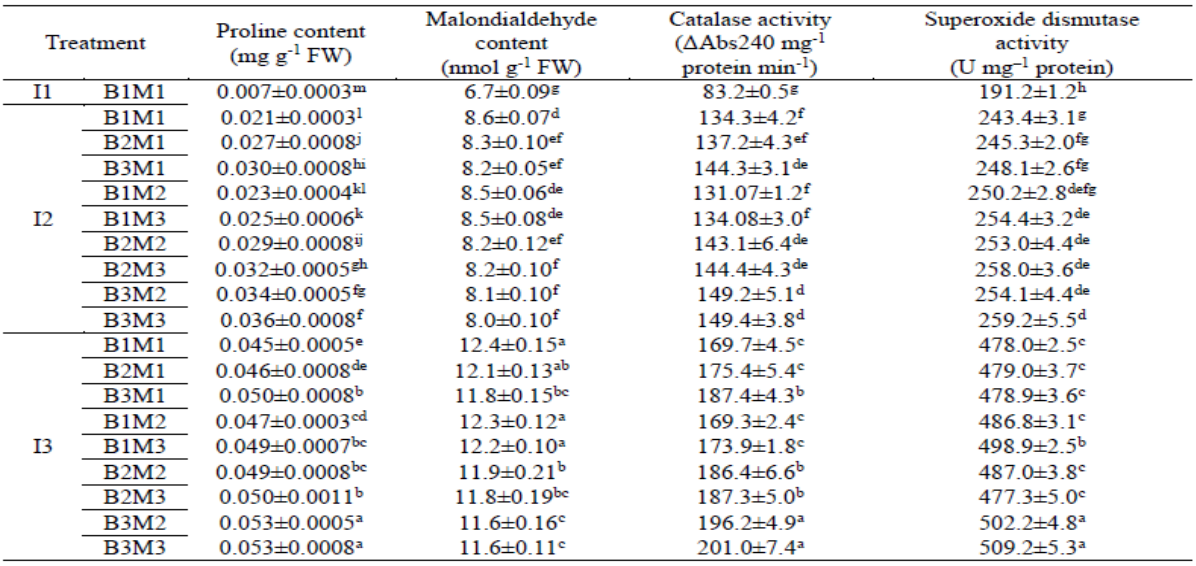
Treatment		Protein percent of kernel (%)	Protein yield of kernel (Kg ha^{-1})	Oil percent of kernel (%)	Oil yield of kernel (Kg ha^{-1})
I1	B1M1	6.70 ± 0.06^{j}	643.96 ± 27^{gh}	5.55 ± 0.03^{a}	568.7 ± 20^{a}
I2	B1M1	7.67 ± 0.10^{i}	724.93 ± 19^{b}	4.90 ± 0.02^{de}	452.5 ± 06^{f}
	B2M1	7.87 ± 0.06^{hi}	759.36 ± 21^{c}	5.00 ± 0.06^{bc}	471.8 ± 15^{d}
	B3M1	8.11 ± 0.07^{gh}	770.86 ± 23^{b}	5.00 ± 0.06^{cde}	487.7 ± 16^{bcd}
	B1M2	7.65 ± 0.08^{i}	693.86 ± 23^{de}	4.86 ± 0.01^{e}	446.0 ± 03^{f}
	B1M3	7.74 ± 0.09^{i}	717.70 ± 23^{cd}	4.98 ± 0.03^{bcd}	464.7 ± 06^{e}
	B2M2	7.90 ± 0.04^{ghi}	765.90 ± 10^{b}	5.01 ± 0.03^{bcd}	479.8 ± 07^{d}
	B2M3	7.92 ± 0.03^{ghi}	774.86 ± 10^{b}	5.04 ± 0.04^{bc}	487.4 ± 08^{cd}
	B3M2	8.14 ± 0.10^{gh}	833.30 ± 30^{a}	5.05 ± 0.02^{bc}	496.3 ± 14^{bc}
	B3M3	8.16 ± 0.10^{g}	828.80 ± 21^{a}	5.08 ± 0.02^{b}	504.9 ± 09^{b}
I3	B1M1	9.00 ± 0.06^{f}	540.80 ± 14^{k}	3.15 ± 0.03^{i}	194.2 ± 05^{j}
	B2M1	9.32 ± 0.08^{de}	593.46 ± 15^{ij}	3.65 ± 0.03^{gh}	227.7 ± 06^{hi}
	B3M1	9.61 ± 0.07^{bc}	644.83 ± 22^{gh}	3.65 ± 0.04^{gh}	238.7 ± 09^{gh}
	B1M2	9.11 ± 0.08^{ef}	554.33 ± 17^{k}	3.62 ± 0.04^{gh}	230.5 ± 04^{hi}
	B1M3	9.24 ± 0.15^{def}	568.86 ± 28^{jk}	3.57 ± 0.03^{h}	225.6 ± 04^{i}
	B2M2	9.40 ± 0.12^{cd}	614.20 ± 16^{hi}	3.67 ± 0.10^{fg}	234.9 ± 09^{gh}
	B2M3	9.48 ± 0.09^{cd}	631.73 ± 23^{gh}	3.68 ± 0.04^{fg}	237.6 ± 09^{gh}
	B3M2	9.76 ± 0.11^{ab}	660.16 ± 15^{fg}	3.69 ± 0.06^{f}	244.7 ± 07^{g}
	B3M3	9.93 ± 0.03^{a}	685.73 ± 16^{ef}	3.70 ± 0.02^{f}	250.5 ± 07^{g}

Table 4. The effect of B and MeJA foliar application on maize photosynthetic pigments and quantum yield of photosystem II under irrigation cut-off at eight-leaf (I2) and ear emergence (I3) stages. Data represent means ± SD. Significant differences (p≤0.05) are indicated by different letters.



Treatment		Quantum yield of photosystem II (Fv/Fm)	Chlorophyll a content (mg g^{-1} FW)	Chlorophyll b content (mg g^{-1} FW)	Total chlorophyll content (mg g^{-1} FW)	Carotenoid content (mg g^{-1} FW)
I1	B1M1	0.821 ± 0.005^{a}	1.80 ± 0.007^{a}	0.62 ± 0.002^{b}	2.42 ± 0.009^{ab}	0.42 ± 0.008^{h}
I2	B1M1	0.740 ± 0.006^{d}	1.61 ± 0.005^{e}	0.55 ± 0.001^{d}	2.17 ± 0.006^{e}	0.58 ± 0.005^{g}
	B2M1	0.768 ± 0.008^{bc}	1.72 ± 0.016^{c}	0.61 ± 0.005^{b}	2.33 ± 0.022^{c}	0.60 ± 0.026^{g}
	B3M1	0.781 ± 0.008^{b}	1.79 ± 0.013^{b}	0.65 ± 0.004^{a}	2.44 ± 0.018^{ab}	0.62 ± 0.010^{g}
	B1M2	0.741 ± 0.008^{d}	1.67 ± 0.007^{d}	0.57 ± 0.001^{c}	2.24 ± 0.008^{d}	0.60 ± 0.010^{g}
	B1M3	0.750 ± 0.004^{cd}	1.68 ± 0.005^{d}	0.58 ± 0.003^{c}	2.27 ± 0.014^{d}	0.59 ± 0.020^{g}
	B2M2	0.774 ± 0.004^{b}	1.74 ± 0.009^{c}	0.61 ± 0.003^{b}	2.35 ± 0.013^{c}	0.61 ± 0.026^{f}
	B2M3	0.778 ± 0.003^{b}	1.77 ± 0.015^{b}	0.62 ± 0.005^{b}	2.40 ± 0.020^{b}	0.66 ± 0.017^{f}
	B3M2	0.805 ± 0.007^{a}	1.81 ± 0.017^{a}	0.65 ± 0.006^{a}	2.47 ± 0.023^{a}	0.68 ± 0.015^{f}
	B3M3	0.809 ± 0.003^{a}	1.81 ± 0.014^{a}	0.65 ± 0.005^{a}	2.47 ± 0.020^{a}	0.69 ± 0.018^{f}
I3	B1M1	0.685 ± 0.005^{g}	1.27 ± 0.020^{k}	0.43 ± 0.007^{h}	1.69 ± 0.027^{j}	0.80 ± 0.008^{e}
	B2M1	0.715 ± 0.004^{ef}	1.36 ± 0.019^{hi}	0.48 ± 0.006^{f}	1.85 ± 0.026^{h}	0.84 ± 0.011^{de}
	B3M1	0.734 ± 0.007^{de}	1.41 ± 0.017^{fg}	0.51 ± 0.006^{e}	1.93 ± 0.023^{fg}	0.89 ± 0.013^{c}
	B1M2	0.696 ± 0.009^{fg}	1.31 ± 0.010^{j}	0.44 ± 0.005^{gh}	1.75 ± 0.021^{i}	0.81 ± 0.010^{e}
	B1M3	0.703 ± 0.009^{fg}	1.34 ± 0.009^{ij}	0.45 ± 0.005^{g}	1.79 ± 0.022^{i}	0.83 ± 0.010^{de}
	B2M2	0.733 ± 0.006^{de}	1.39 ± 0.019^{gh}	0.49 ± 0.007^{f}	1.88 ± 0.026^{gh}	0.86 ± 0.017^{cd}
	B2M3	0.736 ± 0.004^{de}	1.40 ± 0.027^{g}	0.49 ± 0.009^{f}	1.90 ± 0.036^{gh}	0.88 ± 0.026^{bc}
	B3M2	0.740 ± 0.003^{cd}	1.42 ± 0.016^{fg}	0.51 ± 0.006^{e}	1.95 ± 0.022^{f}	0.91 ± 0.020^{ab}
	B3M3	0.749 ± 0.003^{c}	1.44 ± 0.019^{f}	0.52 ± 0.007^{e}	2.12 ± 0.026^{f}	0.95 ± 0.015^{a}

Table 5. The effect of B and MeJA foliar application on the contents of free proline and malondialdehyde as well as activity of antioxidant enzymes in maize under irrigation cut-off at eight-leaf (I2) and ear emergence (I3) stages. Data represent means ± SD. Significant differences (p≤0.05) are indicated by different letters.



Treatment		Proline content (mg g^{-1} FW)	Malondialdehyde content (nmol g^{-1} FW)	Catalase activity (ΔAbs240 mg^{-1} protein min^{-1})	Superoxide dismutase activity (U mg^{-1} protein)
I1	B1M1	0.007 ± 0.0003^{m}	6.7 ± 0.09^{g}	83.2 ± 0.5^{g}	191.2 ± 1.2^{h}
I2	B1M1	0.021 ± 0.0003^{l}	8.6 ± 0.07^{d}	134.3 ± 4.2^{f}	243.4 ± 3.1^{g}
	B2M1	0.027 ± 0.0008^{j}	8.3 ± 0.10^{ef}	137.2 ± 4.3^{ef}	245.3 ± 2.0^{fg}
	B3M1	0.030 ± 0.0008^{hi}	8.2 ± 0.05^{ef}	144.3 ± 3.1^{de}	248.1 ± 2.6^{fg}
	B1M2	0.023 ± 0.0004^{kl}	8.5 ± 0.06^{de}	131.07 ± 1.2^{f}	250.2 ± 2.8^{defg}
	B1M3	0.025 ± 0.0006^{k}	8.5 ± 0.08^{de}	134.08 ± 3.0^{f}	254.4 ± 3.2^{de}
	B2M2	0.029 ± 0.0008^{ij}	8.2 ± 0.12^{ef}	143.1 ± 6.4^{de}	253.0 ± 4.4^{de}
	B2M3	0.032 ± 0.0005^{gh}	8.2 ± 0.10^{f}	144.4 ± 4.3^{de}	258.0 ± 3.6^{de}
	B3M2	0.034 ± 0.0005^{fg}	8.1 ± 0.10^{f}	149.2 ± 5.1^{d}	254.1 ± 4.4^{de}
	B3M3	0.036 ± 0.0008^{f}	8.0 ± 0.10^{f}	149.4 ± 3.8^{d}	259.2 ± 5.5^{d}
I3	B1M1	0.045 ± 0.0005^{e}	12.4 ± 0.15^{a}	169.7 ± 4.5^{c}	478.0 ± 2.5^{c}
	B2M1	0.046 ± 0.0008^{de}	12.1 ± 0.13^{ab}	175.4 ± 5.4^{c}	479.0 ± 3.7^{c}
	B3M1	0.050 ± 0.0008^{b}	11.8 ± 0.15^{bc}	187.4 ± 4.3^{b}	478.9 ± 3.6^{c}
	B1M2	0.047 ± 0.0003^{cd}	12.3 ± 0.12^{a}	169.3 ± 2.4^{c}	486.8 ± 3.1^{c}
	B1M3	0.049 ± 0.0007^{bc}	12.2 ± 0.10^{a}	173.9 ± 1.8^{c}	498.9 ± 2.5^{b}
	B2M2	0.049 ± 0.0008^{bc}	11.9 ± 0.21^{b}	186.4 ± 6.6^{b}	487.0 ± 3.8^{c}
	B2M3	0.050 ± 0.0011^{b}	11.8 ± 0.19^{bc}	187.3 ± 5.0^{b}	477.3 ± 5.0^{c}
	B3M2	0.053 ± 0.0005^{a}	11.6 ± 0.16^{c}	196.2 ± 4.9^{a}	502.2 ± 4.8^{a}
	B3M3	0.053 ± 0.0008^{a}	11.6 ± 0.11^{c}	201.0 ± 7.4^{a}	509.2 ± 5.3^{a}