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REVIEW

Crop Improvement and Abiotic Stress Tolerance Promoted by Moringa Leaf Extract

Md. Abir Ul Islam[1], Juthy Abedin Nupur[2], Charles T. Hunter[3], Abdullah Al Mamun Sohag[4], Ashaduzzaman Sagar[5], Md. Sazzad Hossain[6], Mona F. A. Dawood[7,*], Arafat Abdel Hamed Abdel Latef[8], Marián Brestič[9,10] and Md. Tahjib-Ul-Arif[4,*]

[1]Department of Genetics and Plant Breeding, Bangladesh Agricultural University, Mymensingh, 2202, Bangladesh

[2]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, AB T6G 2R3, Canada

[3]Chemistry Research Unit, United States Department of Agriculture-Agricultural Research Service, Gainesville, 32608, USA

[4]Department of Biochemistry & Molecular Biology, Bangladesh Agricultural University, Mymensingh, 2202, Bangladesh

[5]Department of Crop Botany, Bangladesh Agricultural University, Mymensingh, 2202, Bangladesh

[6]Department of Agronomy and Haor Agriculture, Sylhet Agricultural University, Sylhet, 3100, Bangladesh

[7]Botany and Microbiology Department, Faculty of Science, Assiut University, Assiut, 71516, Egypt

[8]Botany and Microbiology Department, Faculty of Science, South Valley University, Qena, 83523, Egypt

[9]Department of Botany and Plant Physiology, Czech University of Life Sciences Prague, Prague, 165 00, Czech Republic

[10]Institute of Plant and Environmental Sciences, Faculty of Agrobiology and Food Resources, Slovak University of Agriculture, Nitra, 94976, Slovakia

[*]Corresponding Authors: Mona F. A. Dawood. Email: mo_fa87@aun.edu.eg; Md. Tahjib-Ul-Arif. Email: tahjib@bau.edu.bd

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ABSTRACT

Moringa leaf extract (MLE) has been shown to promote beneficial outcomes in animals and plants. It is rich in amino acids, antioxidants, phytohormones, minerals, and many other bioactive compounds with nutritional and growth-promoting potential. Recent reports indicated that MLE improved abiotic stress tolerance in plants. Our understanding of the mechanisms underlying MLE-mediated abiotic stress tolerance remains limited. This review summarizes the existing literature on the role of MLE in promoting plant abiotic stress acclimation processes. MLE is applied to plants in a variety of ways, including foliar spray, rooting media, and seed priming. Exogenous application of MLE promoted crop plant growth, photosynthesis, and yield under both nonstress and abiotic stress conditions. MLE treatment reduced the severity of osmotic and oxidative stress in plants by regulating osmolyte accumulation, antioxidant synthesis, and secondary metabolites. MLE also improves mineral homeostasis in the presence of abiotic stress. Overall, this review describes the potential mechanisms underpinning MLE-mediated stress tolerance.

KEYWORDS

Abiotic stress; antioxidants; biostimulant; plant growth; moringa extract; osmotic stress; oxidative stress

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1 Introduction

Plant growth is hampered by abiotic stresses such as drought, extreme temperatures, flooding, salinity, ozone, ultraviolet radiation, and heavy metals that together cause crop yield losses estimated to be up to 50% worldwide [1]. Abiotic stresses disrupt normal growth, development, metabolism, and productivity. They impact plants throughout development, from seed germination to maturity, disrupting a multitude of physiological, biochemical, and molecular processes [2–6]. Drought- and saline-affected lands are becoming more common across the world, a trend that is expected to continue [7], and agricultural lands near urban centers continue to be polluted with heavy metals [8]. Approximately 21% of the agricultural land area is affected by salinity stress [9]. Some predict that 30% of arable land will be made ill-suited for agriculture by salinization by the end of 2028, and 50% by the middle of the twenty-first century [9]. Global temperature is expected to increase by approximately 3°C with CO_2 concentrations reaching approximately 500–1000 ppm by 2100 [10]. During abiotic stress, which is expected to be more common with changing climates, plants accumulate reactive oxygen species (ROS) that cause physiological harm [11,12]. For instance, salinity and drought [13,14], heavy metals [15] and cold stress [4] inhibit photosynthesis and disrupt plant water relations and metabolic homeostasis.

Moringa oleifera L. (drumstick) is a cultivated species that belongs to the *Moringaceae* family [16]. It originated in the sub-Himalayan region of India, Pakistan, Bangladesh, Afghanistan, and Egypt, but is now found in many of the world's tropical and subtropical regions [17]. Due to its exceptional nutritional and medicinal properties, moringa has been used in agriculture as a yield enhancer and in medicine as a nutritional supplement [18]. Extensive research into its chemical composition and medical applications has been conducted, but the use of moringa in crop treatment for abiotic stress tolerance is a relatively new research area. Moringa leaf extract (MLE) represents an organic and sustainable source of plant growth-promoting compounds, growth regulators, osmoprotectants, antioxidants, secondary metabolites, and mineral nutrients that promote plant resiliency to stress [19–21].

This review aims to discuss the use of MLE in protecting plants from environmental stress, summarizing recent results that have investigated the mitigating effects of MLE on abiotic stress. MLE-induced plant improvement under nonstressed conditions is also discussed. Finally, we present a mechanistic view of MLE-induced crop defense. The following paragraphs of this review address the benefits of MLE on osmolyte balance, antioxidant status, oxidative stress mitigation, mineral absorption, and phytohormone control in plants.

2 Moringa Leaf Extract: Chemical Composition

Moringa leaf extract contains high levels of plant growth hormones, antioxidants, vitamins, secondary metabolites, and minerals (Table 1) [22–24]. Growth hormones such as gibberellins, indole-3-acetic acid (IAA), abscisic acid (ABA), salicylic acid (SA), and cytokinins, minerals such as sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), zinc (Zn^{2+}), iron (Fe^{3+}), and manganese (Mn^{2+}), more than 40 natural antioxidants such as ascorbic acid (ASC), glutathione (GSH), β-carotene, tocopherols, vitamins A, B, C, D, and K, and many secondary metabolites occur at high levels in MLE [16,20,25–34]. Of particular note, plant growth-regulating cytokinins are present in the forms of zeatin, dihydrozeatin and isopentyladenine [35,36]. Among these, zeatin contents remain at very high concentrations between 5 and 200 $\mu g\ g^{-1}$ [37,38]. Additionally, there are high levels of several allelochemicals, including isothiocyanates and nitriles [39,40]. Of course, the chemical composition of MLE can vary with developmental stage, tissue, and growing conditions [41].

Table 1: Chemical constituents of moringa leaves

Name of chemicals	Type of chemicals	Amount	References
Nitrogen	Minerals (mg 100 g^{-1} DW)	1070	[16]
Calcium		364.5	[42]
Potassium		1500	[19]
Phosphorus		70.00	[16]
Manganese		9.58	[27]
Magnesium		76.6	[42]
Iron		7.00	[16]
Copper		4.40	[42]
Zinc		1.80	[42]
Sulfur		630	[19]
Sodium		1929.5	[43]
Amino acids	Osmolytes (mg g^{-1} DW)	142.2	[21]
Proline		32.1	
Total soluble sugars		198.6	
Ascorbic acid	Antioxidants (mg g^{-1} DW)	549.5	
Glutathione		301.2	
α-Tocopherol		0.035	
DPPH-radical scavenging activity	Antioxidant capacity (%)	79.6	
Indole-3-acetic acid	Phytohormones (mg g^{-1} DW)	0.83	[44]
Gibberellins		0.74	
Zeatin		0.96	
Abscisic acid		0.29	
Salicylic acid		0.078	[45]
Phytates	Phytochemicals and anti-nutrients (g 100 g^{-1} DW)	2.59	[20]
Oxalates		0.45	
Saponins		1.46	
Tannins		9.36	
Hydrogen cyanide		0.10	
Anthraquinone		11.68	
Alkaloids		3.07	
Steroids		3.21	
Terpenoids		4.84	
Carotenoids		1.16	

Note: DW, dry weight.

3 Exogenous Application of MLE to Alleviate Abiotic Stress

Abiotic stresses such as salinity, drought, flooding, heat, cold and heavy metals inhibit the growth and development of plants and reduce crop yield [46–48]. One possible solution to offset yield loss is the application of organic biostimulants such as MLE, which is considered a more ecofriendly and sustainable approach than chemicaclly synthesized fertilizers and protectants [49]. MLE can improve seedling emergence, plant growth, development and yield during periods of abiotic and biotic stresses [49]. In recent years, several studies have examined the mitigation of abiotic stress via exogenous application of MLE, the results from which are summarized in Table 2. In the following sections, we will discuss what is known regarding the impact of MLE on plants under various abiotic stresses.

Table 2: Plant responses to exogenous MLE application under abiotic stresses

Plant species	Type of stress	Exogenous MLE application	Plant responses to exogenous MLE	References
Zea mays (Maize)	Drought (75% & 50% FC)	1:30 dilution @ 25 mL plant^{-1} as foliar spray	↑ LA, PH, Chl *a* and *b* contents under 50% FC, RFW and RDW under 75% FC	[50]
Triticum aestivum (Wheat)	Drought (75% & 50% FC)	1:30 dilution @ 25 mL plant^{-1} as foliar spray	↑ POD, CAT, ASC and leaf K^+ contents under moderate drought, TPC under extreme drought	[24]
Cucurbita pepo (Squash)	Drought (60%, 80% & 100% FC)	3.0% as a foliar spray	↑ Harvest index, WUE, Chl fluorescence, RWC, and MSI, photosynthetic pigments, soluble sugars and proline	[51]
Glycine max (Soybean)	Drought (40%, 60%, & 80% FC)	1:30 dilution as a foliar spray	↑ SL, RL, SDW, RDW, photosynthetic pigments ↑ ASC, α-tocopherol, GSH, GR, SOD, APX, sugars, proline, and TPC ↓ MDA and ABA content ↑ IAA, GA_3, N, P, and K^+ content	[52]
Oryza sativa (Rice)	Drought (75% FC)	3% MLE as seed priming	↑ Germination, growth, yield, and photosynthetic pigments ↑ SOD, CAT, and APX activity ↓ H_2O_2 content	[53] [54]
Zea mays (Maize)	Full and deficit irrigation conditions	1:30 dilution as a foliar spray	↑ Growth, grain yield, photosynthetic pigments, RWC and proline accumulation and decrease MDA content	[55]
Phaseolus vulgaris (Common bean)	Salinity (90 mM NaCl)	10 kg L^{-1} fresh leaf as a foliar spray	↑ MSI and RWC, proline content and antioxidant enzyme activity.	[56]

(Continued)

Table 2 (continued)

Plant species	Type of stress	Exogenous MLE application	Plant responses to exogenous MLE	References
Phaseolus vulgaris (Common bean)	Salinity (100 mM NaCl)	500 g leaf crude extract in 2 L water as a presoaking solution	↑ Growth, higher osmoprotectant concentration, enzymatic and nonenzymatic antioxidant activity, increased K^+/Na^+	[48]
Phaseolus vulgaris (Common bean)	Salinity (200 mM NaCl)	1:30 dilution as a foliar spray	↑ Shoot and root length and weight, higher photosynthetic pigments and phytohormone content	[31]
Triticum aestivum (Wheat)	Salinity (4, 8 & 12 dSm^{-1})	1:30 dilution as a foliar spray on tillering, joining, booting and heading stage	↑ Grain weight and kernel yield, shoot K^+ content, SOD and POD activity. ↓ Shoot Na^+ and Cl^- content	[55]
	Salinity (0, 0.05, 0.1, 0.15, and 0.2 M NaC)	1:30 dilution (seed soaking or foliar spray)	↑ Shoot length, leaf number, leaf area, dry weight	[57]
Cucurbita pepo (Squash)	Deficit irrigation (100% , 80 or 60% of ETc)	3.0% as a foliar spray	↑ Growth and yield characteristics, harvest index, WUE, chlorophyll fluorescence, photosynthetic pigments, soluble sugars and free proline, RWC and MSI. ↓ EL	[51]
Helianthus annuus (Sunflower)	Salinity (EC, 6.42–6.48 dSm^{-1})	The MLE application was used as seed soaking or foliar spray.	↑ Growth and seed yield, seed oil and protein content, and antioxidant enzyme activity	[58]
Sorghum × *drummondii* (Sudan grass)	Salinity (EC, 3.01, 6.12 and 12.33 dSm^{-1})	3% of MLE as a foliar spray	↑ Chlorophyll content, nutrient uptake, available N and P, and fresh and dry weight	[59]
Ocimum basilicum cv. Cispum (Sweet basil)	Salinity (100 mM NaCl)	2.5%, 5.0%, 10% and 20% of MLE with irrigation water	↑ Leaf area, shoot length, shoot fresh weight, number of branches, root length and root dry weight, anthocyanin and total carbohydrates content, SOD, CAT, POD, APX and ascorbic acid oxidase activity	[60]
Trigonellafoenum-graecum (Fenugreek)	Salinity (0, 50, 100 and 200 mM NaCl)	25 times diluted MLF as a foliar spray	↑ Growth parameters	[61]

(Continued)

Table 2 (continued)

Plant species	Type of stress	Exogenous MLE application	Plant responses to exogenous MLE	References
Moringa oleifera (Moringa)	Salinity (3, 6, 10 and 14 dSm^{-1})	30 times diluted MLF as a priming agent	↑ Germination, growth, yield, Chl content, SOD, CAT, APX and POD activity, and ASC and TPC contents	[62]
Zea mays (Maize)	Heat (7°C–10°C higher than ambient temperature)	3% of MLF as a foliar spray	↓ H_2O_2 and MDA contents ↑ ASC, TPC, niacin and riboflavin contents	[46]
Phaseolus vulgaris (Common bean)	Heat (45°C) for 5 h for 2 days	1:30 of MLF as a foliar spray	↑ SL, RL, FW, DW, Chl *a* and *b* contents, phytohormone content (IAA, GA_3, ABA, kinetin and benzyl adenin) ↓ Oxidative stress markers ($O_2^{\bullet-}$, H_2O_2 and MDA)	[31]
Zea mays (Spring maize)	Cold (12 ± 1°C)	3% (w/v) of MLF as a priming agent	↑ Germination efficiency and seedling growth	[63]
Gossypium hirsutum (Cotton)	Heat (38/24°C and 45/30°C) for 7 days)	30 times diluted MLF as a foliar spray	↑ Growth, yield, SOD and CAT activities, leaf chlorophyll and photosynthetic efficiency	[64]
Zea mays (Maize)	Heavy metal (1 and 0.5 mg $HgCl_2$ kg^{-1} soil)	2.5% and 5% of MLE as a foliar spray	↑ Seed germination, growth, Chl pigment and TPC, Hg^{2+} phytoremediation potential	[47]
Phaseolus vulgaris (Common bean)	Heavy metal (1 mM $CdCl_2$)	30 times diluted MLE as a foliar spray	↑ MSI, RWC, proline content, the activity of antioxidant enzymes ↓ Cd^{2+} content	[56]
Sorghum bicolor, Penisetum typhoideum and Sorghum sudanese	Soil and water salinity in an arid environment	1:10, 1:20, 1:30, and 1:40 dilution as a foliar spray	↑ Growth and forage yields, inorganic elements, growth hormone content	[65]

Note: LA, leaf area; PH, plant height; FC, field capacity; RFW, root fresh weight; RDW, root dry weight; POD, peroxidase; CAT, catalase; ASC, ascorbic acid; WUE, water use efficiency; RWC, relative water content; RL, root length; SDW, shoot dry weight; GSH, glutathione; GR, glutathione reductase; SOD, superoxide dismutase; APX, ascorbate peroxidase; TPC, total phenolic compounds; MDA, malondialdehyde; ABA, abscisic acid; MSI, membrane stability index; IAA, indole-3-acetic acid; GA_3, gibberellic acid; FW, fresh weight; DW, dry weight; EL, electrolyte leakage.

3.1 MLE in Drought Stress

Water accounts for 80%–95% of the fresh biomass of plants and plays a vital role in physiological processes, including plant growth, development, and metabolism [66]. Thus, water scarcity or osmotic stress is considered the main environmental constraint for crops that could destabilize world food security

[67]. Drought stress typically leads to a reduction in leaf size, stem elongation, root growth, and water use efficiency (WUE) [50,55,68]. Other effects of drought include the reduction of photosynthetically active radiation, a curtailed harvest index (HI) [69], metabolic disruptions [70], the inhibition of certain enzymatic activities [24], the reduction of soil water potential, ionic imbalance and disturbances in solute accumulation [71,72]. MLE has been shown to be an effective plant growth modulator during drought stress events [73]. Foliar or root application of MLE led to the enhancement of leaf area, plant height (PH), biomass production, RWC, WUE, MSI, and chlorophyll content in maize (*Zea mays* L.) [50,55], *Glycine max* (soybean) [52] and *Cucurbita pepo* (Squash) [51] under drought stress. MLE application increased the accumulation of osmoprotectants and enzymatic and nonenzymatic antioxidants such as peroxidase (POD), catalase (CAT), ascorbate (ASC) and leaf K^+ contents in *Triticum aestivum* (wheat) under drought stress [24]. Moreover, MLE application increased total phenolic compounds (TPCs) in wheat plants under extreme drought [24]. Electrolyte leakage (EL) along with morphophysiological trait improvement was also observed after MLE application to drought-stressed squash plants [51]. Finally, exogenous MLE application enhanced the yield of maize under drought stress [55].

3.2 MLE in Salinity Stress

Soil salinity can negatively impact crop yield by affecting growth parameters [74,75]. Salinity affects plant growth by disrupting physiological and biochemical processes, particularly water relations and nutrient balance [76]. Salinity can have major impacts on germination by altering seed imbibition due to the lower osmotic potential of soil [77], changing nucleic acid metabolism and transcriptome profiles [78,79], altering protein metabolism [80], and disturbing hormonal balance [81].

To help alleviate the harmful effects of soil salinity on crops, several growth regulators, osmoprotectants and fertilizers have been successfully used [82], including MLE [83]. Previous research revealed that moringa leaves contain high levels of essential plant nutrients, hormones, and antioxidants [84]. Therefore, MLE application improved salt stress tolerance and grain yield in wheat by enhancing seed germination, protein synthesis, and antioxidant activities under salinity stress [28]. Foliar application of MLE to wheat modulated antioxidants, proteins, and essential mineral content in a way that helped ameliorate the negative effects of salinity stress [55]. Exogenous MLE application to salt stressed *Phaseolus vulgaris* (common bean) led to increased shoot and root length and weight, a response associated with higher photosynthetic pigments, membrane stability index (MSI), relative water content (RWC) and phytohormone content [56,61]. Enhanced fresh weight, dry weight, mineral uptake such as nitrogen (N) and phosphorus (P) uptake, and protection against photooxidative damage in chlorophylls under salt stress conditions were also found in MLE applied to salt stressed *Sorghum* × *drummondii* (Sudan grass) plants [59]. Salinity stress can trigger metabolic disruptions and arrest protein synthesis and these effects are prevented by exogenous MLE, and that can play a key role in the signaling of plant adaptive responses to salinity [61].

Seed priming with MLE improved salt tolerance in common bean by enhancing osmolyte accumulation, chlorophyll pigments, enzymatic and nonenzymatic antioxidants, and K^+ content [48]. Furthermore, pretreatment of *Moringa oleifera* seeds with MLE improved seedling emergence and growth characteristics, nutrient homeostasis, and superoxide dismutase (SOD) and catalase (CAT) activities under salt stress [62]. Both foliar application and seed presoaking with MLE led to increased growth, yield and changes in stem anatomy, including stem section diameter, average number of xylem vessels, average thickness of xylem vessels, and average diameter of xylem vessels, in salt-stressed *Helianthus annus* (sunflower) [58]. MLE-treated, salt-stressed sunflower plants showed higher antioxidant enzyme activity, proline and soluble sugar accumulation, and N, P, and K^+ contents than non-MLE-treated, salt-stressed plants [58]. Enhanced anthocyanin, total carbohydrate, and antioxidant potentials such as SOD, CAT, POD, ascorbate peroxidase (APX) and ASC oxidase were also observed in MLE-treated *Ocimum basilicum cv. Cispum* (sweet basil) plants under salt stress [60].

3.3 MLE in Temperature Stress

Global warming is posing a major concern for humanity by changing climate patterns and increasing temperature. Heat stress severely impacts plant growth and development, threatening crop production and food security [85]. Application of MLE has been shown to combat heat stress in maize plants by reducing oxidative damage markers (hydrogen peroxide, H_2O_2 and lipid peroxidation products, MDA) and enhancing antioxidant potentials such as ASC, TPCs, and niacin and riboflavin contents [46]. Additionally, MLE treatment enhanced growth and yield in heat-stressed *Gossypium hirsutum* (cotton) plants by improving photosynthetic efficiency, causing higher chlorophyll content, and promoting higher SOD and CAT activities [64]. MLE application also mitigated the growth inhibitory effects of heat stress in common bean by enhancing the levels of IAA, GA3, ABA, kinetin and benzyl adenine and reducing oxidative stress markers [31]. Finally, MLE has been shown to improve cold stress tolerance in spring maize by improving the germination rate and growth [62].

3.4 MLE in Heavy Metal Stress

Heavy metals in excessive concentrations can disturb plant growth, development, metabolism, and senescence [86]. Exogenous MLE has been found to increase the tolerance of plants to heavy metal stress. Howladar [56] showed that foliar application of MLE treatment improved cadmium stress tolerance; increased photosynthetic pigments, RWC, proline content, MSI and WUE; and decreased electrolyte leakage (EL) in common bean [56]. Moreover, MLE application enhanced antioxidant enzyme activities and reduced lipid peroxidation in cadmium-stressed common bean plants [56]. Bibi et al. [47] demonstrated that MLE improved the germination, growth and chlorophyll content of maize seedlings under mercury stress.

4 Possible Mechanisms of MLE-Mediated Abiotic Stress Tolerance

To explore the mechanisms underlying MLE-mediated abiotic stress tolerance, the following sections summarize recent reports on the interaction of MLE with major osmolytes, mineral nutrients, secondary metabolites, phytohormones, ROS signaling, and the modulation of antioxidants.

4.1 Influence of MLE on Osmolytes

The synthesis and accumulation of osmolytes, compounds that counterbalance osmotic pressure, are among the first responses of host plants to osmotic stress caused by environmental challenges [87]. The accumulation of solutes in plant cells undergoing stress conditions causes the osmotic potential of the cells to become highly negative and leads to endosmosis of water to maintain cell turgor. This osmotic adjustment is controlled by the accumulation of solutes/osmolytes [88] and is an important factor for combatting drought [89,90] salinity [91], osmotic [92], heavy metal [93], temperature [94], light, and pesticide stress [95] (Fig. 1). Upon perception of abiotic stress, signaling pathways induce transcription factors that upregulate stress responsive genes related to biosynthesis and accumulation of osmolytes, including free amino acids and their derivatives, carbohydrates and soluble sugars, polyols, polyamines, free amines, and other secondary metabolites [87].

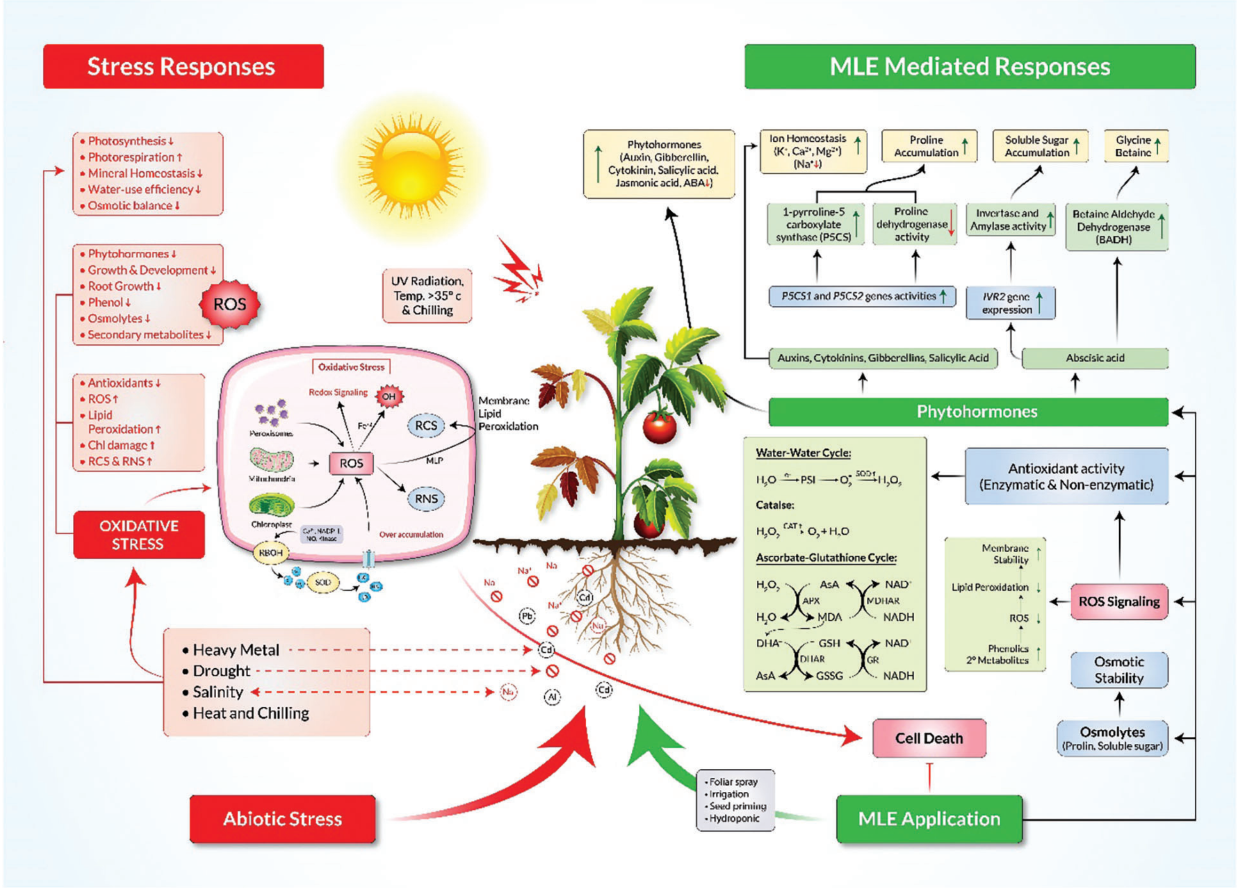

Figure 1: Potential mechanisms of MLE-mediated abiotic stress tolerance in plants. MLE consists of a complex blend of phytohormones, minerals, antioxidants and secondary metabolites that promote enhanced phytohormone production, osmolyte accumulation, ion homeostasis and scavenging of reactive oxygen species (ROS). MLE mediates the detoxification of ROS by triggering the water-water cycle and the ascorbate-glutathione cycle and by promoting the accumulation of secondary metabolites in cells. It also protects plants from overaccumulation of reactive carbonyl species (RCS) and reactive nitrogen species (RNS). MLE, Moringa leaf extract; ABA, abscisic acid; AsA, ascorbic acid; GSH, reduced glutathione; GSSG, oxidized glutathione; P5CS, Δ^1-pyrroline-5-carboxylate synthetase; BADH, betaine aldehyde dehydrogenase

A range of osmotically active molecules accumulate under drought stress. Among these, proline helps to adjust the cellular osmotic balance, protect biological membranes, and stabilize enzymes and proteins by detoxifying excess ROS [96]. Proline accumulation under stress conditions results from increasing synthesis and degradation of proteins [97,98]. Numerous reports show that exogenous application of MLE increases the abundance of proline and other osmolytes under various abiotic stresses (Table 3). Treatment of sunflower with MLE via seed soaking or foliar spray led to increased total soluble sugar and proline contents and resulted in improved sunflower growth, seed yield and oil content under salt stress [58]. Similarly, MLE application improved osmolyte status in salt stressed *Trigonellafoenum-graecum* (Fenugreek) [48], common bean [61], and Sudan grass [59], resulting in improved growth and development of plants. In addition, the application of MLE to drought-stressed *Zea mays* enhanced proline content [55]. MLE also induced proline and total soluble sugar contents in drought-stressed

Glycine max (Soybean) [52] and *Cucurbita pepo* (Squash) [51] leading to improved growth and development. Moreover, *Zea mays* subjected to chilling stress and treated with MLE showed an increase in proline content [63]. The increase in proline could be due to enhanced gene expression of biosynthetic genes that may be induced by MLE responsive phytohormones such as auxins, gibberellins, cytokinins, and abscisic acid (Table 1; Fig. 1) all of which have been shown to promote osmolyte accumulation [96]. The proline biosynthetic genes *P5CS1* and *P5CS2* are up-regulated by auxins, while cytokinin downregulates *P5CS1* but upregulates *P5CS2* in Arabidopsis [99–102] (Fig. 1). A gibberellic acid (GA)-responsive element, GARE, is present upstream of *SbP5CS*. Proline biosynthesis is also modulated by ABA-dependent pathways [100] (Fig. 1).

Table 3: Effects of exogenous MLE on various osmolytes under abiotic stress conditions

Plant species	Stress	Effects of MLE on osmolytes	References
Helianthus annuus (Sunflower)	Salinity	↑ Total soluble sugars (by 27.6%) and proline content (by 62.4%)	[58]
Phaseolus vulgaris (Common bean)	Saline, heat and gamma ray	↑ Total soluble sugar (by 24.97%)	[31]
Zea mays (Maize)	Water stress	↑ Free proline (by 88%)	[55]
Trigonellafoenum-graecum (Fenugreek)	Salinity	↑ Free proline (by 35.48%), soluble sugars (by 24.34%) and total amino acid (by 63.8%)	[61]
Glycine max (Soybean)	Drought	↑ Proline content (by 10.37%), total soluble sugars (by 4.38%)	[52]
Phaseolus vulgaris (Common bean)	Salinity and heavy metal	↑ Proline content (by 16.75%)	[56]
Zea mays (Maize)	Chilling	↑ Total soluble sugars (by 60%)	[63]
Cucurbita pepo (Squash)	Drought	↑ Proline content (by 6.25%) and total soluble sugar (by 5%)	[51]
Phaseolus vulgaris (Common bean)	Salinity	↑ Soluble sugars (by 21.24%), proline content (by 52.23%) and glycinebetaine (by 0.62%)	[48]
Sudan grass	Salinity	↑ Proline content (by 5.15%)	[59]

Application of MLE also promotes the accumulation of glycinebetaine, another important osmolyte [103]. Glycinebetaine is synthesized from choline in a two-step oxidation by a ferredoxin (Fd)-dependent choline monooxygenase (CMO) and a betaine aldehyde dehydrogenase (BADH) with a strong preference for nicotinamide adenine dinucleotide (NAD^+), typically via the unstable intermediate betaine [87]. Glycinebetaine biosynthesis is induced under abiotic stress after the application of the MLE component ABA, which activates the GB biosynthetic enzyme BADH [104,105].

4.2 *Influence of MLE on Mineral Nutrients*

Treatment of plants with MLE can help support mineral homeostasis, which is critical for plants to tolerate abiotic stresses [106]. Salinity stress is associated with the reduction of chlorophyll content caused by excessive Na^+ accumulation in leaves, which leads to reduced Mg^{2+} and downregulation of chlorophyll biosynthesis [107]. Mg^{2+} deficiency can also disrupt the vascular system, transportation of carbohydrates, and protein synthesis [108–110]. Moreover, salt stress can interrupt K^+ and Ca^{2+} uptake and transportation [111] and cause salt-sensitive plants to have lower K^+/Na^+ and Ca^{2+}/Na^+ under salinity conditions [112]. The K^+/Na^+ ratio is an important factor for estimating plant growth rates, and increasing the K^+/Na^+ and Ca^{2+}/Na^+ ratios leads to the activation of plant defenses [113–117]. However, antagonistic relationships between Na^+ and ions such as K^+, Ca^{2+} and Mg^{2+} have been observed in salt-tolerant crops [61,113,117,118]. These antagonisms were amplified in crops such as lettuce, wheat, okra, fenugreek and *Brassica juncea* after the application of MLE [24,111,115]. This amplification resulted from increased K^+, Ca^{2+}, Mg^{2+} and better maintenance of the K^+/Na^+ and Ca^{2+}/Na^+ ratios, which served to protect photosynthetic pigments [31]. It is possible that components of MLE, such as hormones like IAA, GAs, SA, and ABA, function to maintain ion homeostasis [21,119]. In plants under salinity stress, exogenous application of auxins, ABA and SA have all been shown to enhance Ca^{2+} and K^+ [120–122], while application of GA and IAA enhance Mg^{2+} [120,121]. Additionally, MLE contains high levels of Mg^{2+}, Ca^{2+} and K^+, which provides plants with greater exposure to these nutrients and promotes tolerance to abiotic stresses [19,42].

4.3 Influence of MLE on ROS Signaling and Antioxidants

Redox homeostasis is fundamental to cellular function and integrity, and its regulation includes control of ROS and modulation of the cellular redox state [123]. The equilibrium between the production and scavenging of ROS such as singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), superoxide ($O_2^{\bullet-}$), and hydroxyl radicals ($^{\bullet}OH$) is controlled by enzymatic and nonenzymatic antioxidants [123,124]. The enzymatic antioxidants responsible for scavenging ROS are SOD, CAT, the ASC-GSH cycle enzymes [APX, monodehydroascorbate reductases (MDHAR), dehydroascorbate reductases (DHAR), glutathione reductase (GR)], peroxiredoxins (PRX), glutathione peroxidase (GPX), and glutathione-*S*-transferase (GST), whereas the nonenzymatic antioxidants include more diverse compounds such as ASC, GSH, phenolic compounds, alkaloids, nonprotein amino acids, and α-tocopherols [123,125–128]. Upregulation of antioxidant enzymes occurs when plants are exposed to oxidative stress. This upregulation serves as a proactive acclimation response that results in lower ROS levels and higher tolerance to conditions that cause oxidative stress [123], and promoting this process can improve a plant's tolerance and adaptive capacity to abiotic stresses [129–131]. The primary mechanism by which plants balance ROS is the ASC-GSH pathway [128,132], which involves the successive oxidation and reduction of ascorbate, glutathione, and NADPH. The redox reactions are catalyzed enzymatically by APX, MDHAR, DHAR, and GR and nonenzymatically by tocopherol, carotenoids, and phenolic compounds [128,132–134] (Fig. 1).

Table 4: MLE modulates antioxidants in plants under abiotic stress conditions

Plant species	Stress	Effect of MLE on antioxidants	References
Trigonellafoenum-graecum	Salinity	↑ Activity of SOD by 19.37%, CAT by 66.85% ↓ POD activity by 52.35%	[61]
Helianthus annuus	Salinity	↑ SOD (70.2%), APX (100.4%), and GR (80.3%) activities	[58]
Triticum aestivum	Drought stress	↑ Activity of SOD by approximately 28%, CAT by 100%, ASC by 100% and POD by 81.8%	[24]
Triticum aestivum	Salinity	↑ Activity of SOD by 66.67%, POD by 31.58%, and CAT by 144.29%	[135]
Glycine max	Drought	↑ Content of ASC by 2.31%, GSH by 8.44% and activity of SOD by 7.67%, APX by 24.74%, GR by 0.47%	[52]

(Continued)

Table 4 (continued)

Plant species	Stress	Effect of MLE on antioxidants	References
Phaseolus vulgaris	Salinity and heavy metal	↑ Activity of CAT by 4.64%, POD by 10.68%, GR by 6.7% ↓ Activity of SOD by 18.92%	[56]
Phaseolus vulgaris	Salinity, heat and gamma ray	↑ GR activity by 36%	[31]
Phaseolus vulgaris	Salinity	↑ Contents of ASC by 14.49%, GSH by 17.21% and activities of SOD by 23.6%, APX by 20%, GR by 38.6% ↓ Activity of CAT by 11.68%	[48]

Note: SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; POD, peroxidase; GR, glutathione reductase; ASC, ascorbic acid; GSH, glutathione.

Exogenous application of MLE to plants under abiotic stress can supplement antioxidants such as ASC and GSH (Table 4). It is possible that MLE application directly supplements ASC and GSH and thereby helps to improve abiotic stress tolerance. In various salt-stressed plant species, MLE promoted the activities of SOD, CAT, APX, GR, and POD and led to higher ASC and GSH contents (Table 4). The enhanced activity of the abovementioned enzymes resulted in a decline in oxidative damage to cells and growth improvement, highlighting the direct involvement of MLE in stress mitigation [61]. The improved antioxidant system in MLE-treated plants helps lower oxidative stress and peroxidation of lipids [136], enhances biosynthesis of cysteine and GSH to maintain the GSH/GSSG ratio [137–139], increases the accumulation of osmolytes such as proline and glycinebetaine [137] and α-tocopherol [140], all of which help plants withstand abiotic stress.

The antioxidant α-tocopherol is a primary component of MLE (Table 1). Exogenous application of α-tocopherol to plants under drought and salt stress promotes stress tolerance, enhances tocopherol content, and decreases lipid peroxidation [141,142]. The upregulation of proline is also associated with H_2O_2 accumulation and the activity of antioxidant enzymes such as SOD, POD, APX and CAT under abiotic stress [143]. Taken together, MLE application supplements the plants with antioxidants present in MLE itself and increases endogenous antioxidant activity and production that ultimately helps plants withstand abiotic stresses (Fig. 1).

4.4 Influence of MLE on Major Secondary Metabolites

Plants produce and accumulate high levels of secondary metabolites such as phenylpropanoids, flavonoids, tannins, coumarins, and lignin precursors, a group of metabolites collectively known as phenolics that are involved in scavenging free radicals and enhancing membrane stability under stress conditions [98,144–146]. There are large quantities of phenolics in MLE (Table 1), and these have been suggested to be responsible for the prevention of membrane leakage and lipid peroxidation observed in MLE-treated, salt-stressed *Phaseolus vulgaris* plants [56]. MLE-treated *Phaseolus vulgaris* had higher levels of phenolics, which enhanced salt tolerance and membrane stability by ameliorating ROS [135] (Fig. 1). MLE application also enhanced carotenoids, which help protect proteins, DNA, and RNA from damage by quenching free radicals produced during photosynthesis [12,147,148]. Anthocyanin, another phenolic compound found in MLE, acts as an antioxidant under stress conditions [149–153]. Therefore, plants supplemented with MLE receive a wide range of secondary metabolites that may directly protect plants against abiotic stress-induced oxidative damage and thus enhance stress tolerance.

4.5 Influence of MLE on Phytohormones

Exogenous application of MLE can modulate phytohormone contents in plants. Supplementation with MLE increased auxins, gibberellins, and cytokinins but decreased ABA in common bean plants under salinity, heat and gamma ray stress conditions [31]. Similarly, fertilization of rocket plants with MLE enhanced auxin, gibberellin and cytokinin contents and reduced ABA content under nonstress conditions [154]. Spraying common bean with MLE increased the contents of benzoic acid, trans-cinnamic acid, SA, trans-jasmonic acid, IAA, indole-3-propionic acid, indole-3-butyric acid, trans-zeatin, trans-zeatin riboside, gibberellic acid (GA3), gibberellin A4 (GA4), gibberellin A7 (GA7), and decreased ABA content [155]. MLE contains high levels of phytohormones such as zeatin, dihydrozeatin and isopentyladenine [35–38], auxins, gibberellins and salicylates [154,155]. Hormones present in MLE may contribute to the improvement in abiotic stress tolerance and growth observed in MLE-treated plants (Fig. 1).

5 Role of MLE in Crop Improvement under Nonstress Conditions

Along with mitigating abiotic stresses, exogenous MLE can also provide benefits under nonstress conditions by improving plant growth, development, and agronomic characteristics (Table 5). For instance, seed priming with MLE can promote germination indices under nonstressed conditions in a wide range of plant species, including pea [156], wheat [135], okra [157], maize [158] and pepper [159]. Seed pretreatment with MLE solutions improved the rate of seed emergence, vigor of seedlings, and overall growth of wheat plants [135]. Moreover, seed priming with MLE enhanced germination, plant growth, α-amylase activity, and total soluble sugars in pea seedlings under nonstress conditions [156]. Numerous studies have reported that exogenous application of MLE improved the vegetative growth of plants and economic yield performance of several plant species, including snap bean [160], okra [157], *Freesia hybrida* [161], *Cyperous rotandous* [162], wheat [163,164], tomato [165,166], maize [167], soybean [168], pepper [169], sweet pepper [170], lettuce [171], sunflower [172], and gladiolus [173]. Both vegetative growth parameters such as PH, SL, SFW, SDW, and leaf number as well as yield components such as cob length, cob diameter, grains per cob, 100-grain weight, and grain weight per plant were improved after foliar application of MLE to maize [167]. Moreover, *Prunus salicina* trees sprayed with MLE exhibited higher fruit setting, total yield, fruit weight, firmness, color, TSS value, titrable acidity ratio, ascorbic acid content, anthocyanin content, antioxidant activity, reduced titrable acidity and less fruit drop compared to untreated plants [174].

Table 5: Effects of exogenous MLE on crops under nonstress conditions

Plant species	Exogenous MLE application	Response to exogenous MLE	References
Phaseolus vulgaris (Common bean)	1:1 (50%), 1:2 (33%), 1:4 (20%) and 1:8 (11%) MLE as a foliar spray	↑ PH, LA, leaf number, leaf Chl content, and yield	[160]
Triticum aestivum (Wheat)	3% MLE as a seed priming	↑ Biochemical parameters and yield	[175]
Solanum lycopersicum var. *cerasiforme* (Cherry tomato)	3.3% (w/v) of MLE in foliar and root applications	↑ Canopy biomass, floral shoot number, number of flowers and number of fruit per plant, lateral vegetative shoot number, PH, yield as grams of fruit per plant	[176]
Lycopersicon esculentum (Tomato)	20%, 40%, 60%, 80%, and 100% MLE as a foliar spray	↑ Growth and yield, erect stemming, number of fresh leaves, regular branching and healthy fruits and regular flowering	[165]

(Continued)

Table 5 (continued)

Plant species	Exogenous MLE application	Response to exogenous MLE	References
Lycopersicon esculentum (Tomato)	20% MLE as a foliar application	↑ SDW, RDW and PH	[166]
Zea mays (Maize)	1:30 MLE as a seed treatment	↑ Seed emergence, Chl *a* and Chl *b* contents, grain yield and harvest index	[158]
Triticum aestivum (Wheat)	3% solution of MLE as foliar spray	↑ Growth and yield	[177]
Triticum aestivum (Wheat)	1:5 (w/v) of MLE as a foliar spray	↑ 1000-grain weight along with biological yield	[163]
Triticum aestivum (Wheat)	1:32 (v/v) of MLE as a foliar spray	↑ Plant biomass, grain yield and fertilizer use efficiency	[164]
Abelmoschus esculentus (Okra)	2.5%, 5% and 10% of MLE as a pretreatment	↓ Possibility of fungal infection, ↑ Viability and vigor of the seed	[176]
Foeniculum vulgare (Fennel)	1:30 and 1:40 of MLE dilutions as a foliar spray	↑ PH, branch number per plant, FW, fruit weight, umbel number per plant, and fruit yield, photosynthetic pigments, total phenols, and oil content	[178]
Foeniculum vulgare (Fennel)	2.5% and 5% aqueous extract, 2.5% and 5% ethanolic extract of MLE as a foliar spray	↑ Vegetative growth, number of umbels per plant, fruit and oil yield per plant, total carbohydrate content in fruits, Chl *a*, Chl *b* and carotenoids contents, N, P and K^+ contents in leaves	[179]
Cyperus rotundus	25%, 50%, 75% and 100% of MLE as a soil application	↑ RL, SL, SFW and SDW	[162]
Prunus salicina	4%, 5%, and 6% of MLE as a foliar spray	↑ Fruit setting, yield, fruit weight, firmness, color, TSS value, titrable acidity ratio, ascorbic acid content, anthocyanin content, antioxidant activity ↓ Fruit drop	[174]
Freesia hybrida	1%, 2%, 5% and 10% of MLE as a foliar spray	↑ PH, 50% sprouting, leaves per plant, LA, total Chl content, stem diameter, number of flowers per stem, number of marketable stem, vase life, and flower diameter	[161]
Triticum aestivum (Wheat)	10 and 30 times dilution of MLE as a foliar spray	↑ Germination and seedling growth attributes	[73]

(Continued)

Table 5 (continued)

Plant species	Exogenous MLE application	Response to exogenous MLE	References
Abelmoschus esculentus (Okra)	10%, 20% and 30% of MLE as a foliar spray	↑ PH, number of branches plant^{-1}, number of leaves plant^{-1}, leaf area index, dry weight of leaves, stems, roots, total biomass, number of pods ha^{-1} and dry weight of pods	[157]
Zea mays (Maize)	1:32 (v/v) of MLE as a foliar spray	↑ Growth parameters like PH, SL, SFW, SDW, number of leaves plant^{-1}, and yield components like cob length, cob diameter, number of grains cob^{-1}, 100-grain weight, grain weight plant^{-1}	[167]
Gladiolus grandiflorus (Gladiolus)	30 times diluted of MLE as a foliar spray	↑ PH, stalk length, number of florets spike, vase life in sucrose solution, earlier spike emergence, corm weight and cormel diameter	[173]
Brassica napus (Canola)	2% of MLE a foliar sprays	↑ Seed yield, biological yield, harvest index, number of siliques, 1000-seed weight, higher leaf area indices, crop growth rates and net assimilation	[172]
Pisum sativum (Pea)	3% of MLE as a priming agent	↑ Germination indices, seedling vigor, root and shoot growth, α-amylase activity and total soluble sugar contents	[156]
Salvia officinalis (Sage)	2.5, 5.0 and 10 g L^{-1} of MLE as a foliar spray	↑ PH, number of leaves, number of branches, yield and essential oil contents	[180]
Glycine max (Soybean)	10%, 20% and 30% of MLE as a foliar spray	↑ Root development parameters and root exudates	[168]
Capsicum annuum (Pepper)	2%, 4%, and 6% of MLE as foliar application	↑ Germination indices, seedlings growth parameters, LA, yield contributing characters, carbohydrate, ASC, K^+ and Ca^{2+} contents	[159]
Capsicum annuum (Pepper)	1:10 and 1:20 of MLE as a foliar application	↑ Growth and yield parameters	[169]
Lactuca sativa (Lettuce)	30 times diluted MLE as a foliar application	↑ Vegetative growth, chemical characteristics and yield ↓ Nitrate content	[171]
Capsicum annum (Sweet bell pepper)	1:32 (v/v) of MLE as a foliar spraying	↑ PH, number of leaves, fruit weight and yield	[170]

(Continued)

Table 5 (continued)

Plant species	Exogenous MLE application	Response to exogenous MLE	References
Triticum aestivum (Wheat)	1%, 2%, 3%, and 4% of MLE at 40, 70, and 90 days foliar spraying	↑ Straw and grain yield, biological yield, 1000-grain weight, yield efficiency, protein content, and nutrient uptake	[59]
Eruca vesicaria subsp. sativa (Rocket)	1%, 2% and 3% of MLE as a foliar spraying	↑ Photosynthetic rates, stomatal conductance, chlorophyll a and b, carotenoids, sugars, proteins, phenols, ascorbic acid, N, P, K^+, Ca^{2+}, Mg^{2+}, and Fe^{2+} contents, auxins, gibberellins and cytokinins and the activities of SOD, CAT, and POD ↓ Lipid peroxidation and abscisic acid	[154]
Helianthus annuus (Sunflower)	5%, 10%, 15% and 20% of MLE as a foliar spraying	↑ Agronomic parameters and economic yields, achene protein and oil contents	[172]
‘Kinnow’ mandarin (*Citrus nobilis* × *Citrus deliciosa*)	3.0% of MLE as a foliar spray	↓ Fruit drop ↑ Fruit set, yield, fruit weight, juice weight, TSS value, ASC, sugars, and TPC, SOD and CAT activity	[181]
Allium sativum (Garlic)	2% of MLE as a foliar spray	↑ N, P and K contents in leaves and bulb, quality and total yield, average bulb weight, weight of leaves, total dry weight plant^{-1}, and TSS value of bulbs	[182]
Linum usitatissimum (Linola)	3.3% of MLE as a foliar spray	↓ Crop branching, flowering and maturity times, PH, number of branches, tillers, pods and seeds per pod	[44]
Cenchrus ciliaris, Panicum antidotale, and *echinochloa crusgalli*	1:10, 1:20, 1:30, and 1:40 of MLE as a foliar spray	↑ Seed germination, number of leaves, number of tillers, and shoot vigor	[62]
Chenopodium quinoa (Quinoa)	3% of MLE as a foliar spray	↑ Growth and yield parameters ↑ Photosynthesis and pigments ↑ Total free amino acid, total soluble proteins, anthocyanin, ASC and proline ↓ MDA content	[183]
Helianthus annuus (Sunflower)	Moringa leaf (25% and 50% solution)	↑ plant height, plant fresh and dry weights, root fresh and dry weight number of achenes per plant, 1000-achene weight, flower diameter, leaf area, and yield	[184]

(Continued)

Table 5 (continued)

Plant species	Exogenous MLE application	Response to exogenous MLE	References
Triticum aestivum (Wheat)	3% of MLE as a foliar spray	↑ Seed germination, growth, photosynthetic pigment contents and yield	[185]

Note: LA, leaf area; PH, plant height; RDW, root dry weight; POD, peroxidase; CAT, catalase; ASC, ascorbic acid; SDW, shoot dry weight; SOD, superoxide dismutase; TPC, total phenolic compounds; TSS, total soluble sugar.

Application of exogenous MLE can also boost nutrient content in a variety of plant species (as summarized in Table 3). Foliar spray of MLE enhanced N, P, K^+, Ca^{2+}, Mg^{2+}, and Zn^{2+} contents in leaves of Kinnow' mandarin [181]. Similarly, higher contents of N, P, K^+, Ca^{2+}, Mg^{2+}, and Fe^{2+} were observed in the rocket (*Eruca vesicaria* subsp. *sativa*) plants when sprayed with MLE [154]. Additionally, exogenous application of MLE can improve photosynthetic efficiency under nonstress conditions [154]. For instance, exogenous MLE application on rocket plants increased the photosynthetic rate, stomatal conductance, chl *a* and chl *b*, and carotenoid contents compared with untreated plants [154].

6 Conclusion and Future Prospects

Application of MLE has been shown to be an effective and eco-friendly approach to protect plants against abiotic stressors. The complex blend of antioxidants, metabolites, phytohormones, and minerals present in MLE appears to help protect plants by influencing many aspects of plant physiology, metabolism, hormone signaling, cellular homeostasis, redox potential, and developmental processes. Additional investigations into the precise nature of the protection offered by MLE are needed and may provide information important for crop plant protection and crop productivity, helping ensure food security. Future studies should aim to identify the particular MLE bioactive molecules that confer stress tolerance in plants and the underlying mechanisms.

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