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Melatonin: Role in Increasing Plant Tolerance in Abiotic Stress Conditions

Raziye Kul, Aslihan Esringü, Esin Dadasoglu, Üstün Sahin, Metin Turan, Selda Örs, Melek Ekinici, Guleray Agar and Ertan Yildirim

Abstract

Nowadays, due to the environmental stress factors that limit the production of crops, it has become very difficult to find suitable areas to enable the plant to reach its optimum product potential. Abiotic stress is very effective in decreasing agricultural production. Factors such as drought, salinity, high and low temperature, flood, radiation, heavy metals, oxidative stress, and nutrient deficiency can be considered as abiotic stress factors, and these sources of stress negatively affect plant growth, quality and productivity. Melatonin (MEL) was first identified in plants in 1995 and is increasingly becoming important for its role and effects in the plant system. MEL has been shown to have a substantial role in plant response to growth, reproduction, development, and different stress factors. In addition to its regulatory role, MEL also plays a protective role against different abiotic stresses such as metal toxicity, temperature, drought, and salinity. In plants, an important role of MEL is to alleviate the effects of abiotic stresses. In this review, the effects of MEL on plant growth, photosynthetic activity, metabolism, physiology, and biochemistry under abiotic stress conditions as a plant growth regulator will be examined.

Keywords: melatonin, plant development, physiology, abiotic stress

1. Introduction

Plants are exposed to various adverse conditions that limit their growth in areas where they are grown. Conditions that prevent growth, development, and metabolism in plants are called stress [1]. Due to the continuation of climate change and the increase in extreme climatic conditions, it is reported that the negative impact of environmental stress factors on plant production will increase in many regions of the world [2]. Stress factors can simultaneously show their effects on plants [3]. On the reducing amount of agricultural product, abiotic stress has reached a massive quantity of 71% although other stresses are on 29% [4]. It is estimated that only 10% of the arable land in the world is far from some forms of stress. It has been reported that abiotic stress factors are the main limiting factors of crop production in the world and cause more than 50% reduction in the yield of most products [5].

In the last decade, different irrigation techniques, soil improvement, and the use of suitable fertilizers have been intensified in order to reduce the impact of major stress factors. As a different approach, the use of some externally applied healers during plant growth has been tried in recent years, and it has been observed that the applications using MEL may have an effect of increasing stress tolerance in the plant.

MEL (N-acetyl-5-methoxytiprimamine) was discovered in 1958 in the cattle pineal gland [6]. MEL has been one of the most investigated biological molecules, which is extensively researched in animals. MEL was first explored in plants in 1995 and is an indoleamine neurohormone [7, 8]. There has been an increasing interest in MEL's roles and impacts on metabolic processes. It was found to play a major role in various plant reactions such as growth, flowering, development, and stress [9–11]. Most of the reports that provide information about these processes are based on analytical analysis to determine the internal MEL content in response to a stimulus, treatment, or mutation, whereas administration usually requires prolonged exposure or treatment of plants under in vitro or greenhouse conditions [9].

Several studies have reported that MEL can be considered a growth regulator because it plays a role in specific physiological events in plants. Indeed, MEL regulates the growth of leaf, shoots and explants, and the leaf senescence. The natural antioxidant capacity of MEL can be explained by its ability to increase tolerance in plants exposed to abiotic stresses such as drought, cold, heat, salinity, chemical pollutants, herbicides, and UV rays [12]. MEL's capability to behave as a plant biostimulator for biotic and abiotic stress conditions and the ability to regulate plant growth can regulate plant vegetative growth processes such as rooting, leaf aging, photosynthetic yield, and biomass yield, and it plays a potential regulatory role in flowering processes and the formation and maturation of fruit and seeds [10, 12, 13].

In this study, the effects of MEL on plant growth and physiology against some abiotic stress factors that have important impacts on plant growth and development have been given according to the findings of various researches.

2. MEL and its function in plant growth and physiology

MEL regulates various metabolic processes in animals and plants. MEL is an endogenously produced molecule in all plant species that have been investigated. Its concentration in plant organs varies in different tissues, e.g., roots versus leaves, and with their developmental stage [10].

MEL, tryptophan, tryptamine, and serotonin are structural biogenic indoleamine and also related to indole-3acetic acid (IAA) and indolic compounds, which are very important in plant physiology such as common auxin. Metabolic pathways of tryptophan in mammals and plants as proposed by Murch et al. [14] are shown in **Figure 1**. MEL was determined in the roots, leaves, fruits, and seeds of various plant species. Melatonin has been suggested to function as an auxin to promote vegetative growth in a number of plant species [15]. For instance, Murch et al. [16] used auxin, serotonin, and MEL inhibitors to demonstrate the role of MEL in plant growth and found that the high intrinsic MEL concentration promotes root growth in the *Hypericum perforatum* L. plant, while the increase in serotonin concentration, the precursor to MEL, promotes body development. It takes part in many different tasks in the metabolic processes in the plant. It has been shown to regularize proline metabolism [17]. It contributes root formation and water balance, thus keeping membrane and chlorophyll integrity [18, 19].

Earlier researchers have inspected the physiochemical effects of MEL on plants. These reports indicated that MEL has a role in various plant metabolic processes as the modulation of the flowering physiology and development. Furthermore, it also

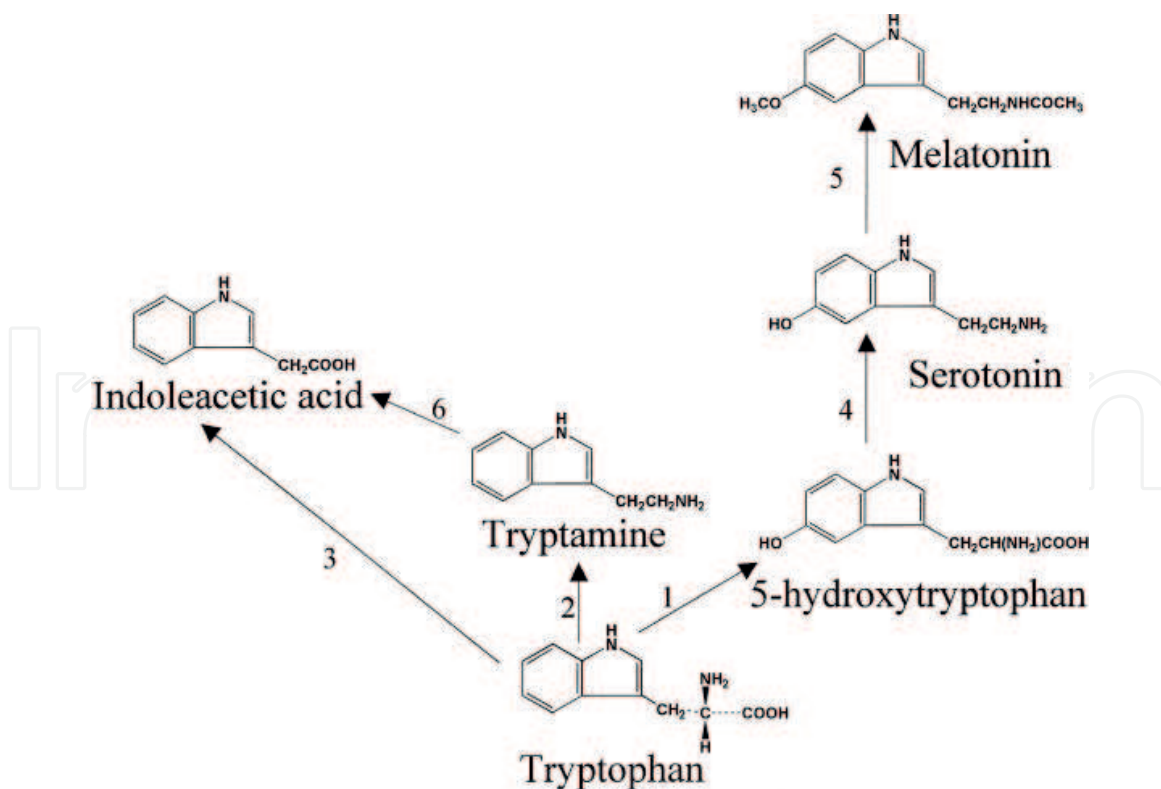


Figure 1.
 Metabolic pathways of tryptophan in mammals and plants as proposed by Murch et al. [14].

postpones flower formation, countenances plant growth and biomass production, and hinders chlorophyll degradation [20, 21]. It has been shown that MEL roles in plants could be: growth promoters as auxins, antioxidants for ROS, and other roles as signal molecules [15]. It acts in various plant cellular metabolic and biological processes, including rooting [22], chlorophyll catabolism [20], and stress tolerance [23, 24]. Plants can synthesize MEL, and it plays a role as an antioxidant or a modulator of growth and development in plants [25].

Similar effects (growth induction or inhibition at high levels because of auxin-stimulated ethylene biosynthesis) of MEL were determined in the monocotyledons [26]. Furthermore, MEL applications enhanced photosynthetic capacity, redox homeostasis, and root formation in various crops [22, 27, 28]. According to another report, a coating of soybean seed with MEL notably increased plant growth and seed yield [19].

It has been reported that MEL affects lateral root formation in lupin, and this effect is very similar to the effect of IAA [29]. In these studies, auxin-induced root and cytokinin-induced shoot organogeneses were inhibited by alterations in the endogenous concentration of MEL and inhibitors of the transport of serotonin and MEL [30]. MEL has been reported to regulate seed germination, growth of roots, shoots and explants, and leaf senescence [12]. In addition, Tan et al. [31] pointed out that high MEL content in plants increased the germination rate of seeds under adverse conditions, increasing the life expectancy and improving the quality of plant production. In lupin, MEL increased plant root and shoot biomass with similar results to IAA for root biomass in concentrations used [32]. Exogenous MEL was applied to etiolated wild mustard, and the effect on root growth and endogenous indole-3-acetic acid (IAA) levels was detected in wild mustard. Exogenous lower MEL concentrations also elevated the endogenous IAA content in roots, whereas higher levels did not significantly affect the IAA content. The specific mechanism which leads exogenous MEL to increase the IAA content in roots, associated with root formation, continues to emerge [21].

Increased MEL levels in plants have been suggested to mitigate various pollutant effects via behaving as a ROS scavenger and antioxidant. MEL can detoxify the OH^- , H_2O_2 , nitric oxide, ONOO^- , HNO_3 , and HClO , which are biosynthesized under stress conditions. Moreover, MEL treatments elevate antioxidant enzyme activities under abiotic stress conditions. One MEL molecule has the ability to scavenge up to 10 free radicals [33]. MEL has also been suggested to have a significant effect on nitrogen and carbohydrate metabolism and on transcription rearrangement [34]. Thus, it is suggested that MEL affects signal transduction and also has an important role in regulating physiological and biological processes. As a conclusion, MEL could be considered as a biological growth regulator to increase the production capacity in crops.

3. Role of melatonin in mitigating abiotic stresses

3.1 Salinity and MEL applications

Extreme salinity in soil solution is the major abiotic stress factor that drastically limits crop productivity worldwide. Salinity affects 110 million hectares in arid and semi-arid regions. According to FAO, an estimated 20–30 million ha area is severely deteriorated due to salinity [34]. In addition to the natural conditions, problems with salinity have increased with the fact that water tables have increased and concentrated in a large part of the land that has been recently irrigated [35]. Moreover, use of the treated and untreated wastewater at increasing proportions due to the insufficient clean water resources in the world can promote the soil salinity. Salinity causes osmotic stress by reducing the water potential and increasing the energy required for the intake of water and nutrients. Ionic stress is caused by the accumulation of sodium and chlorine ions in sensitive plant tissues [36–38]. Therefore, it has been reported that high concentrations of salt (especially NaCl) in soils or irrigation water disrupt the morphological and physiological processes in plants and prevent growth [39].

In addition, salinity conditions may lead to nutritional disorders and deficiencies [40]. In the short term, while the water availability reduces due to inducing osmotic stress under salty conditions, in the long term, the nutrient imbalances induce ion toxicity [41]. Salinity increases ROS formation and stimulates oxidative stress [42], which causes substantial injury to membranes and other cellular structures [43]. Salt stress affects plant physiology at both plant and cellular levels by osmotic and ionic stress. High salt concentrations may adversely affect seed germination, seedling growth, vegetative growth, flowering and fruit behavior, and photosynthetic activity and ultimately reduce economic yield and quality [44].

Lately, the positive roles of MEL in plant salt stress resistance have been progressively evolved by two ways: the exogenous application of MEL or genetic modification of the enzymes involved in MEL synthesis [45]. Indeed, exogenous MEL applications improved growth, photosynthetic capacity, antioxidant activity, and chlorophyll content, but decreased the ROS level and oxidative injury in cucumber grown under salinity stress conditions [46]. Dawood et al. [47] indicated that exogenous MEL applications enhanced plant biomass, relative water content, photosynthetic activity, phenolic matter, and plant nutrient uptake, and reduced the Na and Cl content in fava bean under salinity stress conditions. 500 mM of MEL was more effective than 100 mM on observed parameters.

Zhou et al. [48] investigated influences of MEL treatments on photosynthetic activity in tomato under salinity conditions. They concluded that MEL treatments mitigated the deleterious effects of salinity on growth and photosynthetic capacity. It was determined that MEL decreased the ROS levels and expedited the recovery

of the photosynthetic electron transport chain and protein biosynthesis, therefore improving photosynthetic capacity under salinity stress. Similarly, MEL treatments on roots of watermelon mitigated salt-stress damage in photosynthetic capacity and oxidative stress, improving redox homeostasis and antioxidant enzyme activity [28]. In another study, it was reported that MEL treatments improved the tolerance to salt stress and K^+/Na^+ homeostasis in potato, increasing K^+ and decreasing NaCl concentration [44].

In *Cucumis sativus*, especially after treatment with MEL under salinity conditions, an increase in seedling growth, nutrient intake, and nitrogen metabolism was observed [49]. Ke et al. [50] proved that MEL pretreatments alleviated the negative impact of salinity stress by regulating polyamine metabolism in wheat. They also suggested that MEL could induce enzyme activity, resulting in stimulating ROS scavenging antioxidant defense in response to salinity. In another study, it was concluded that 10–500 μ M MEL solutions enhanced germination and seedling growth in rice under salinity conditions. This enhancement was attributed to reducing the contents of Na^+ and Cl^- in roots and leaves [51]. The results of Jiang et al. [52] showed that exogenous MEL treatments on salt stressed maize plants caused a notable improvement in growth, photosynthetic capacity, antioxidant enzyme activity, and homeostasis. It was proven that MEL concentration in roots elevated because of stress conditions, increasing to six times the MEL concentration compared to the control. This raise can play an important role in the amelioration of stress conditions [20].

Exogenous MEL treatments showed a major effect of MEL related to lipid metabolism with K^+/Na^+ homeostasis in a potato grown under salinity stress [44]. MEL applications on roots mitigated the deleterious effects of salinity on photosynthetic capacity by reducing oxidative stress, improving antioxidant enzyme activity in watermelon. This effect was attributed to the inhibition of stomatal closure and enhanced light energy absorption and electron transport in photosystem II [28].

Liang et al. [23] treated plants with MEL to determine its effect on physiological and biochemical properties in rice grown under salinity stress. The results of the study showed that MEL treatments decreased or inhibited chlorophyll damage and the transcripts of senescence-associated genes, thus improving salinity tolerance. It was also determined that MEL postponed the leaf senescence and cell death by counteracting the ROS.

3.2 Drought and MEL applications

Water scarcity has been becoming a major problem worldwide due to population growth and social and economic development. A number of countries faced to water shortage is more than 100, and approximately two thirds of the world population will be exposed to be suffering from moderate to high water stress by 2025 [53]. Increasing domestic and industrial water demand and pollution of water threatens the water used in agriculture. Therefore, drought is one of the most important agricultural problems in the world. Two-fifths of world agriculture is carried out in arid areas [54]. Studies show that in the coming years, the effect of drought will increase further and this situation will affect the negative effects of agricultural production [55]. It is reported that global climate change, in addition to the expansion of arid and semi-arid areas, will increase the duration and intensity of drought, desertification processes, salinization, and erosion [56]. It has been shown in many studies that drought has an impact on all plant growth events from plant morphology to molecular levels [57]. Drought stress causes various physiological, biochemical, and molecular responses in different plants to help them adapt to such limiting environmental conditions [58, 59]. Arid

conditions have a negative effect on photosynthetic activity, cause changes in chlorophyll content and components in the cell, and damage photosynthetic parts [60]. It also inhibits photochemical activity and reduces the activity of enzymes in the Calvin circle [61].

Earlier studies pointed out that exogenous MEL treatments improved plant tolerance to water deficit stress. Increased antioxidant activity in different plants grown in drought stress has been associated with the MEL content [62]. The effect of MEL application on plant development and some biochemical properties of *Brassica napus* L. under dry conditions were determined. In the study, it was determined that exogenous MEL treatments (0.05 mmol/L) mitigated the deleterious effects of water deficit on plant growth. Moreover, MEL treatments caused decreased H_2O_2 and increased antioxidant enzyme activity and osmotic solutes [63].

It has been shown that a notable increase in photosynthetic capacity and stress-related phytohormones was associated with the endogenous MEL content under water deficit conditions. Indeed, Fleta-Soriano et al. [25] proved that MEL treatments enhanced photosystem II resulting in a preserving factor in maize under drought stress. MEL treatments helped to recover from drought stress by enhancing the Fv/Fm ratio, which could have a defensive effect in plants subjected to water deficit conditions.

Cui et al. [64] demonstrated that MEL applications alleviated the deleterious effects of drought stress in wheat by increasing antioxidant activity and decreasing ROS and membrane injury. They also showed that MEL caused a thicker epidermal cell, intact grana lamella of chloroplast and leaf structure, and higher photosynthetic activity. They explained these positive responses to MEL treatments in wheat with enhanced enzyme activity and gene expression. Moreover, Wang et al. [18] proved that MEL had an ameliorative effect on drought stress by increasing antioxidant activity. Similarly, mitigation of deleterious effects of drought stress could be attributed to its ROS scavenging functions by improving antioxidant enzyme activity and photosynthetic efficiency [65].

Ma et al. [66] showed that exogenous MEL treatments elevated ME biosynthesis gene (TDC1, SNAT1, and COMT) expression, resulting in mitigation of leaf senescence caused by water deficit in *Agrostis stolonifera*. In another study, it was determined that MEL applications in drought conditions reduced electrical leakage, decreased chlorophyll degradation, and increased photosynthetic activity in two different apple cultivars that are resistant to drought. MEL applications reduce the expression of the ABA synthetic gene (MdNCED3) and increase the expression of catabolic genes (MdCYP707A1 and MdCYP707A2), thus reducing the level of ABA under dry conditions [67]. Exogenous MEL treatments have resulted in enhanced photosynthetic capacity and water use efficiency due to increased indole acetic acid (IAA) and zeatin and decreased H_2O_2 and aminocyclopropane-1-carboxylic acid (ACC) production [68].

It was determined in plants that drought increased the expression of genes related to drought stress and decreased the production of abscisic acid (ABA), which leads to the closure of stomata [69]. In addition to reducing the effect of drought stress, MEL also helps to heal the plants after drought has occurred and water is re-fed [33, 65, 69, 70].

3.3 Heavy metal stress and MEL applications

The increment in mining, factories, and industrialization leads to the contamination of larger areas with heavy metals. It is reported that heavy metals are included in the food chain by accumulation by plants [71]. Studies on heavy metal accumulation and its effects on plants have shown that heavy metals are a potent

phytotoxic and cause growth inhibition and, in some cases, death [72, 73]. Metals are the elements necessary for normal survival of plants. However, the presence of some metals in the root region has a toxic effect on the plants. These metals, which have a negative effect on growth and yield in plants, are mostly cadmium (Cd), chromium (Cr), zinc (Zn), copper (Cu), lead (Pb), and nickel (Ni) [74]. They can easily accumulate in plants and prevent plant growth and nutrient uptake [75]. The metals in question prevent the uptake of necessary minerals by making a toxic effect and by replacing the necessary minerals such as iron for the plants. Heavy metals, by activating active oxygen species in plants, cause a decrease in chlorophyll and thus photosynthesis rate. As in other stress conditions, heavy metal stress also increases the level of plant ethylene, slows down the growth of roots and shoots, reduces CO₂ fixation, and limits the transport of sugar [76]. Many researchers have reported that heavy metals stimulate ROS formation, leading to oxidative stress [77–79].

The plants exposed to heavy metals (lead, zinc, cadmium, etc.) have been shown to induce MEL biosynthesis for alleviating stress effects [80]. Tan et al. [32] pointed out that MEL treatments elevated the phytoremediation capacity of pea under copper stress. Many studies have shown that exogenous MEL treatments reduced the toxic impact of various heavy metals such as cadmium, aluminum, copper, vanadium, nickel, etc. by enhancing root growth, antioxidant activity, photosynthetic capacity, and organic acid anion exudation, reducing metal concentration, and regulating MEL biosynthesis and antioxidant-related gene expression in various crops [24, 81, 82].

Tang et al. [83] reported that foliar MEL applications improved the photosynthetic capacity of eggplant under cadmium stress. They suggested that increased MEL concentration elevated photosynthetic capacity in stressed plants, and a concentration of 150 $\mu\text{mol}\cdot\text{L}^{-1}$ was the best for alleviating cadmium stress. Cadmium (Cd), one of the most dangerous heavy metal pollutants, is toxic to animals and plants. A significant increase in antioxidant enzyme activity and low ROS contents were related to treatment of MEL-stimulated Cd tolerance in tomato. MEL treatments induce Cd sequestration and transfer of cadmium from cytosol to the vacuole and cell wall [84]. Similarly, MEL applications mitigated Cd-stimulated oxidative stress by increasing the levels of nonenzymatic and enzymatic antioxidants. Gu et al. [85] determined that Cd stress conditions enhanced endogenous MEL concentrations in alfalfa. It was determined in their research that exogenous MEL treatments mitigated the negative effect of Cd on plant growth by reducing Cd accumulation and reestablishing the micro RNA-mediated redox homeostasis. They suggested that MEL could regulate expression of ion-channel genes in crops against Cd stress. Moreover, Safari et al. [86] concluded that excessive boron (B) decreased photosynthesis and dry matter in pepper. However, they pointed out that exogenous 1 μM MEL treatments eliminated visible B toxicity symptoms due to B, increased nutrient uptake, photosynthetic activity, antioxidant capacity, and accumulation of carbohydrates, and decreased ROS and membrane permeability.

Zhang et al. [24] tested whether exogenous MEL treatments could mitigate aluminum induced phytotoxicity in *Glycine max*. They pointed out that the effect of MEL on Al stress was dose-dependent. While 0.1 and 1 mM doses of MEL improved root growth and reduced H₂O₂ content, 100 and 200 mM doses affected negatively. 1 mM MEL root application increased antioxidant enzyme activity under Al stress conditions. Ni et al. [87] demonstrated that Cd stimulated the expression of MEL-related genes and enhanced the endogenous MEL content in wheat. Exogenous MEL treatments mitigated Cd toxicity on plant growth and increased ascorbate peroxidase (APX) and superoxide dismutase (SOD) activity. They reported that MEL had an important role in keeping H₂O₂ homeostasis by modulating antioxidant activity. Restricted growth properties, chlorophyll and carotenoid content, photosynthetic

activity, and increased lipid peroxidation were alleviated by MEL treatments in spinach via enhancing antioxidant activity and reducing ROS levels [88].

3.4 Temperature extremes and MEL applications

Plants are affected at the maximum level from the environmental temperature from seed germination to product acquisition. Plants require an optimum temperature request for every stage of growth, and this requirement may vary between species and even varieties. The temperatures below the optimum negatively affect plant growth and ultimately yield. Low and high temperatures slow the seed germination and emergence, limit the intake of water and nutrients, increase the damage of diseases, negatively affect flowering, seed and fruit formation, and finally cause death of the plant [89]. Hot climate plant species are very sensitive to low temperatures [90]. It has been reported that low temperature affects the whole metabolic system of the cell and even causes water stress [91]. It has also been reported that low temperature causes damage in cell membranes, which also affects sugars, phenolics, phospholipids, protein, and ATP [92]. Low temperature is one of the most limiting abiotic stresses for crop yield and geographical distribution in plants [93, 94]. Low temperature stimulates the overproduction of ROSs in plant cells such as superoxide radical ($O_2^{\cdot-}$), H_2O_2 , and hydroxyl radical ($OH^{\cdot-}$). ROS may lead to lipid peroxidation and oxidative modifications in proteins and nucleic acids [95, 96].

However, the plants have developed a specific protective mechanism to alleviate and repair damage induced by oxidative stress. The most important oxidative stress cleaning mechanisms are enzymatic systems consisting of SOD, POD, CAT, APX, and GR and nonenzymatic acetyl salicylic acid and glutathione (GSH) [97, 98]. Tolerance to low temperature in plants is positively related to activation of ROS cleaning systems. Research has shown that antioxidant activity has a substantial role in preserving plants to oxidative injury caused via stress [93].

High temperature stress is one of the most harmful stress conditions that damage the growth and yield of cool season plants. High temperature can negatively affect germination and output in many plant species. In the vegetative development period, it was reported that high temperature decreases photosynthesis capacity, CO_2 assimilation, and metabolic processes [99, 100]. High temperatures can also deteriorate membrane stability, resulting in necrotic spots similar to water stress symptoms in leaves, eventually leading to premature deaths [101]. Temperature stress negatively affects the food intake in plants [102]. In the generative development period, high temperature, flower dust germination, fertilization, flowering, and seed and fruit formation can cause a significant decrease in yields [103, 104]. Like other stresses, high temperature stress also has a significant negative impact on product yield. High temperature causes oxidative stress, lipid peroxidation, membrane damage, protein degradation, enzyme inactivation, pigment bleaching, and degradation of DNA strands in plants [105].

Temperature extremes were shown to increase MEL biosynthesis. Moreover, it has been reported that exogenous MEL treatments helped to protect plants from temperature extremes [106]. Several studies indicated that antioxidant capacity of MEL could strengthen plants subjected to abiotic stresses such as cold and heat [107, 108]. There are reports showing that supplementation with MEL induced MEL biosynthesis and upregulated genes under cold stress conditions [109, 110]. Studies have also shown that MEL treatments alleviated the deleterious impact on plants by upregulating or downregulating genes and proteins related to high or low temperature stresses, scavenging ROS, modulating polyamine metabolism, increasing chlorophyll and heat shock protein synthesis, and affecting the ABA and cytokinin pathway [33, 110–113].

Lei et al. [114] suggested that MEL enhanced carrot cell survival due to induced putrescine and spermidine biosynthesis under cold stress. Similarly, Balabusta et al.

[115] determined that osmo-primed cucumber seeds with MEL had lower ROS levels and higher superoxide dismutase (SOD) activity, detoxifying ROS under chilling stress. It is evidenced that exogenous MEL treatments reduced photoinhibition by enhancing nonphotochemical quenching via induction of violaxanthin de-epoxidase activity in tomato plants under chilling stress [116]. Alam et al. [117] concluded that MEL-treated tall fescue plants under high temperature stress had lower ROS electrolyte leakage and malondialdehyde levels and higher chlorophyll, total protein, and antioxidant enzyme activities compared to nontreated plants. They also showed that exogenous MEL treatments improved thermo-tolerance.

In another study, maize seeds were primed with MEL (50 and 500 μM) to determine the priming-induced changes under chilling stress. Priming with MEL regulated MEL-associated proteins in seeds exposed to lower temperature and enhanced plant tolerance to chilling [118]. Foliar MEL-treated *Lolium perenne* plants had greater biomass, chlorophyll content, and photosynthetic capacity compared to nontreated ones under heat stress. MEL also caused increased endogenous MEL and reduced ABA content. Genes related to ABA were downregulated by MEL treatments [113].

MEL applications decreased the H_2O_2 and MDA content of pepper seedlings, but increased the SOD and CAT enzyme activities in pepper under chilling stress. The decrease in the peroxidation of lipids in the tissues caused an increase in the levels of antioxidant enzyme activities, thus increasing the germination and seedling emergence performance of pepper seeds [119]. Xu et al. [120] reported that external MEL applications caused a significant increase in enzymatic antioxidants such as SOD, POX, CAT, and APX peroxidase and nonenzymatic antioxidants such as ascorbic acid and vitamin E, resulting in decreased ROS levels and lipid peroxidation in cucumber under high temperature stress. Lei et al. [114] reported that MEL applications improved attenuates cold-induced apoptosis root cell suspensions in a process that does not relate to reactive oxygen species generation in carrot.

Posmyk et al. [121] investigated osmo- and hydropriming with MEL application on germination in cucumber (*Cucumis sativus*) in order to improve germination under cold stress conditions. Seed germination increased to 50–60% at 15°C and the addition of 25–100 μM MEL increased the germination percentage. Following these results, it was reported that MEL treatments protected cell membranes against peroxidation in cucumber seeds during chilling stress but high levels of MEL caused oxidative changes in proteins. The mitigating role of MEL in two bermudagrass (*Cynodon dactylon*) genotypes under lower temperatures was reported. The effects of MEL differed between genotypes, which were attributed to differential adaptive responses to lower temperatures due to differentiation of antioxidant enzyme activity, photosystem capacity, and metabolic homeostasis [122].

4. Conclusion

Based on literature knowledge, MEL, which is considered a plant growth regulator candidate and known as tolerance to stress in plants, can be used to increase the plant productivity positively under the abiotic stress conditions. It enhances plant growth such as shoot and root biomass, induces root formation, and increases seed germination under unfavorable conditions. These positive attributes could be caused by (1) improving photosynthetic capacity, (2) reducing oxidative stress, (3) enhancing antioxidant activity, (4) downregulating or upregulating stress-related genes, and (4) elevating osmotic metabolites. There are still many unanswered questions about MEL and more areas for further research. The mechanisms by which MEL is produced are still largely unresolved and need to be elucidated by different plant cells in different situations.

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