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ROLE OF PLANT PROTECTIVE AGENTS IN THE ALLEVIATION OF VARIOUS ABIOTIC STRESSES IN CROP PLANTS

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ROLE OF PLANT PROTECTIVE AGENTS IN THE ALLEVIATION OF VARIOUS ABIOTIC STRESSES IN CROP PLANTS

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1. INTRODUCTION

1.1 Justification of the study

Crop productivity faces formidable challenges from abiotic stresses such as drought, soil salinity, heat, and cold, leading to significant constraints on the quantity and quality of agricultural output (Bashir et al., 2019). Projections suggest that these challenges will worsen due to climate change and the escalating demands of a steadily expanding global population. It is crucial to prioritize mitigating environmental impacts on agriculture, with the population of world standing at approximately 8 billion and estimated to rise to over 8.5 billion by 2030 and 9.7 billion by 2050 (United Nations, 2023). Most of the arable land is sadly prone to adverse environmental challenges (Cramer et al., 2011). Abiotic stress often results in a reduction in yields of around 60% relative to optimal yields (Boyer, 1982). The increasing frequency of more intense climatic changes, majorly in polar regions, points up the significance of understanding and mitigating the effects of these stresses globally (Zhang et al., 2022). In immediate research using regional agricultural yield data and advanced machine learning algorithms has reported that extreme climate significantly influences up to 50% of the observed variability in crop yields worldwide (Vogel et al., 2019). Climate shift poses significant threats to living organisms, including humans, due to rising temperatures, thawing glaciers, and polar ice melting. Climatic variations increase the vulnerability of floods in coastal regions, lead to desertification and poses threat to food security. To find solution and drawing attention towards climate change needs collaborative and immediate actions to reduce greenhouse gas emissions, adaptation to changing conditions and promote global resilience.

To combat with the rising concerns of global warming scientific community plays an important role in finding the solution to deal with its effects in the form of various abiotic stresses faced by agricultural sector. The main concern of the agricultural sector is to find the solution to combat abiotic stresses faced by crop plants via recognizing the tolerant crops to changing climates, to cut down resource use in agriculture and to find the easily available and applicable beneficial plant protective agents to abiotic stresses. These protective agents need to be sustainable, improve plants resilience towards abiotic stresses as well as provide the essential nutrients to support human health during environmental challenges. In our research, we aimed to explore various known plant protective agents for their beneficial

effects under abiotic stresses mainly focusing on water deprivation, a critical challenge to agricultural crop productivity. In this research, we explore the effect of well-known organic acid acetic acid, phytohormone melatonin and polyamine spermine in sweet corn genotypes under water deprivation, as well as effect of different light qualities in general and water deprivation in case of spinach was examined to uncover the novel strategies for enhancing stress tolerance in crop plants. Exposure to different light qualities may have various physiological responses in pants, including the varied responses towards water deficit, while acetic acid treatment has been reported to enhance plant tolerance by improving nutrient uptake and photosynthesis. Melatonin earlier associated with sleeping pattern in animals, now well known plant hormone with distinct plant functions, has been reported as effective agents under various abiotic stresses. Similarly, spermine, a polyamine is associated with regulation of various physiological processes, including antioxidant defence mechanisms and osmotic regulation, so that improving plant resilience to abiotic stresses.

This research investigates the significance of plant protective agents in alleviating the negative effects of water deprivation in sweet corn plants, suggesting the sound solutions to enhance agricultural productivity and tolerance. Understanding mechanisms by looking into the interactions between environmental challenges like water deficit and protective agents including acetic acid, melatonin and spermine or effect of light qualities, the research goals are to fill the vital knowledge gaps, paving the way for targeted strategies to boost crop tolerance to water deprivation. With increasing population and food demand and depleting water resources under extreme climate change, results of this research hold promise for growing resilient crop varieties and sustainable cultivation methods. The interdisciplinary approach of this research spanning through physiology, biochemistry and agronomy provides a comprehensive interpretation of plant responses to water deprivation, effective for shaping agricultural practices and policy decisions. Eventually amidst of environmental challenges, this study may contribute to global efforts to ensure food security and agricultural sustainability.

1.2 Objectives

- Our research aims to make a significant contribution to plant stress physiology by thoroughly exploring the efficacy of foliar applications of acetic acid, melatonin, and spermine in modulating water deficit-induced morpho-physiological and biochemical responses.
- Although these plant protective agents have been reported to confer stress tolerance in various crop plants, their integrative effects on sweet corn, particularly under water deficit conditions, remain largely unexplored.
- This research aims to explore an adaptable approach to study the roles of these protective agents in enhancing osmotic adjustment, antioxidant defense, and other vital physiological processes that improve resilience to water deprivation, thereby paving the way for novel agricultural practices aimed to mitigate the negative effects of climate induced water scarcity.
- In parallel, this study will explore the physiological and morphological impacts of water deprivation on the germination and early developmental stages of spinach.
- Additionally, we aim to study the influence of varying light qualities on the morphophysiological traits of spinach, both under optimal and water deficit conditions, with the goal of identifying light mediated mechanisms that can be harnessed to optimize growth and enhance stress adaptation.
- By bridging these research dimensions, the study aims to generate a comprehensive understanding of how these treatments and environmental stresses interact to influence plant performance under abiotic stress conditions, ultimately contributing to the development of more resilient crop systems.

2. LITERATURE REVIEW

This chapter seeks to provide an in-depth examination of the existing knowledge regarding how plants react to water deprivation. It will explore the significance of protective agents like melatonin, acetic acid, and spermine, which have been recognized as vital in alleviating abiotic stress and improving water deficit tolerance. Additionally, the economic aspects and challenges of sweet corn cultivation will be examined and emphasizing the significant impact of light quality on the growth and development of the spinach plants.

Through this exploration, we aim to clarify the intricate ways in which plants respond to water deprivation and highlight the urgent need for innovative strategies to bolster agricultural resilience amid growing environmental challenges. As we explore the complex relationship between water deprivation and plant physiology, it becomes evident that enhancing our knowledge in this field is crucial for maintaining sustainable food production and ecosystem health during a time of significant environmental changes.

2.1 Water deprivation and its effect on plant growth and development

Water, an essential element for biochemical activities in all known life forms, plays a vital role in the growth and sustenance of plant cells. The critical aspect of this role is the phenomenon of turgor pressure generated by water, which serves as a driving force for cell expansion (Xiong and Zhu, 2002). However, the optimal functioning of plant cells relies heavily on maintaining a precise balance within a specific range of water status, quantified by the free energy state of water molecules, known as water potentials (ψw). Within the complex environment of a cell, water potential predominantly encompasses pressure and osmotic potential. Plant cells dynamically regulate their osmotic potential to uphold a positive turgor pressure, fulfilling the overall water budget requirements of the entire plant (Xiong and Zhu, 2002). In severe cases, osmotic stress can be a significant threat to plants, disturbing normal cellular functions and leading to cell death and plant mortality. High salinity and drought are the two prominent environmental challenges contributing to osmotic stress in plants (Xiong and Zhu, 2002). As osmotic stress induced by water deprivation alters water availability and disrupts cellular mechanisms, it is essential to have comprehensive research on the response of plants to water deprivation.

Plants face various environmental stressors throughout their growth and development, which may occur in natural and agricultural settings. Drought is a severe phenomenon that

significantly impacts plant productivity due to multiple stressors. Water is vital for several physiological processes, including growth, development, and metabolism, since it accounts for around 80-95% of total fresh biomass in plants (Brodersen et al., 2019; Abbasi et al., 2010). In drought-prone areas, drought is often considered the primary environmental stress affecting several plant species (Anjum et al., 2011; Diatta et al., 2020). It is generally recognized as the main threat to global food security and has historically been a major cause of significant famines (Emmanuel et al., 2021). The leading cause of water scarcity is the absence or diminished rainfall, which reduces the soil moisture content, decreases water potential in the aerial plant parts, such as stems, and leaves (Ristvey et al., 2019). Plants need an ideal level of water availability to grow and flourish; any fluctuation in the ideal threshold for soil moisture can have detrimental effects on grain quality and production. On the other hand, inadequate water availability in the rhizosphere hinders plant development, which in turn prevents the absorption of nutrients (Elemike et al., 2019). Besides drought, the ongoing climatic variability and global warming make the conditions more difficult, further decreasing grain crop productivity (Bal and Minhas, 2017; Hafez and Seleiman, 2017). Drought at early development stages increases the risk of damage because it affects the processes of cell division and differentiation (Anjum et al., 2003). Drought-induced osmotic stress significantly reduced water absorption in maize seeds, which in turn caused insufficient germination and hindered seedling development (Achakzai, 2009). Reduced water absorption and seed moisture content due to drought-induced osmotic stress affect biomass production, growth, vigor index, and seed germination (Li et al., 2017). Under water scarcity conditions, plants often generate abundant reactive oxygen species (ROS) such as hydrogen peroxide and superoxide anion radicals. The excessive generation of reactive oxygen species (ROS) hampers the growth process, impairs the photosynthetic system (Deeba et al., 2012), leads to lipid peroxidation, and enhances programmed cell death mechanisms (Gill and Tuteja, 2010).

However, plants employ various methodologies and tactics to alleviate the adverse effects of drought-induced stress; avoidance, escape, and tolerance are the primary survival strategies. Responses can be seen both at the molecular and plant levels. The biosynthesis and accumulation of secondary metabolites are crucial in the plant stress response (Espinosa et al., 2022). Alkaloid compounds, phenolics, and terpenes were quantified in several plant species under drought. For example, Li et al. (2016) found that the amount of hydrophilic

phenolics increased when *Salvia castanea* was subjected to drought stress. Likewise, in *Silybum marianum*, phenolic compound content increased in response to stress concentrations (Zahir et al., 2014). In addition, plants stimulate enzymatic antioxidants such as superoxide dismutase, peroxidase, catalase, glutathione reductase, and ascorbate peroxidase to remove excessive reactive oxygen species (ROS) (Gill and Tuteja, 2010). Modifications in the functioning of these enzymes significantly affect the ability of plants towards water stress (Denaxa et al., 2020).

Throughout Hungarian history, drought has been a recurring issue, often leading to reduced agricultural yields, livestock losses, and increased risks of hunger and epidemics (Buzási et al., 2021). In recent years, frequency of drought like conditions has risen sharply in Hungary, experiencing a moderate drought every two years and a severe drought every three years (Buzási et al., 2021). Droughts are expected to become more frequent, last longer, cover larger areas, and result in more severe impacts due to due to the intensifying effects of climate change (Mezősi et al., 2014).

2.2 Polyethylene glycol induced water deprivation

Over half a century ago, concerns about the negative impacts of water shortages on agricultural output were heightened by worries about the growing global population and the increasing consequences of climate change (Broecker, 1975). Thus, understanding how plants' response towards water scarcity emerged as a key area of scientific research. Early investigations into water deprivation involved gradually subjecting plants to reducing soil moisture or transplanting them into pots with reduced water availability (Saunier et al., 1968; Boyer, 1971). However, these methods were considered inadequate due to the challenges associated with managing stress levels and their incompatibility for large-scale plant cultivation.

New methods for investigating water deficit response were developed during the 1970s and 1980s, initially focusing on cell cultures and then expanding to encompass whole plants (Kaufmann and Eckard, 1971). By adding specific chemical compounds into the growth medium decreased the water potential, hindering the ability of plants to uptake water from the substrate. Sodium chloride (NaCl), polyethylene glycol (PEG), mannitol, and sorbitol are commonly utilized chemical compounds as mimetics of water deprivation (Verslues et al., 2006; Claeys et al., 2014b). Despite their diverse chemical properties, these compounds

stimulate distinct responses in plants, with a common characteristic being their ability to instigate osmotic adjustment within plant cells. Consequently, they are often categorized as inducers of water deprived osmotic stress alongside drought and freezing stressors. Polyethylene glycol is a widely used chemical that has shown significant utility in inducing stable, long-term low water potential stress (Verslues et al., 2006; Claeys et al., 2014b).

Cellular responses as observed under drought stress, polyethylene glycol offers the advantage of inducing similar responses. In drought stress, cytorrhysis occurs, characterized by the cell wall and protoplast shrinkage due to exosmosis (Haswell and Verslues, 2015). Studies conducted by Kaufmann and Eckard, (1971), as well as by Heyser and Nabors, (1981), have demonstrated that PEG molecules with a high molecular mass, such as PEG6000 or greater, are unable to permeate the cell membrane and induce cytorrhysis like drought stress.

Polyethylene glycol is a versatile chemical for studying plant responses to water deficit in hydroponic systems. It allows accurate regulation of stress levels, simplifies application, mimics drought stress, avoids physical damage, uniformly distributes stress, and can be used in various setups and designs (Dubois et al., 2020). Its ease of application enhances reproducibility and efficiency in experimental setups and ensures consistent exposure of plant specimens to stress, enhancing experimental reliability and accuracy.

2.3 Role of plant protective agents under stress

Plant protective agents include various chemical compounds, serving as a shield against many abiotic and biotic stresses in plants. Under this umbrella term, various substances are naturally present in plants and utilized for defense mechanisms. These include several secondary metabolites with diverse protective functions, including phytohormones (auxin, jasmonic acid, melatonin, abscisic acid, cytokinins, gibberellins), signaling molecules (hydrogen peroxide), polyamines (spermine, spermidine, and putrescine), additionally, organic acids, like acetic acid, citric acid and malic acid which are naturally present in plants, and are being recognized for their emerging role as protective agents (Godoy et al., 2021). These agents enhance plant resilience to environmental stresses such as drought, extreme temperatures, salinity, pathogen attacks, and herbivore damage (Godoy et al., 2021). For instance, the critical physiological role of vitamin C (ascorbic acid) in animal and plant metabolism has long been known in connection with the Hungarian scientist Albert Szent

Györgyi. Stressed plants often produce excessive reactive oxygen species (ROS) and can deal with this problem by producing ROS-neutralizing molecules like non-enzymatic and enzymatic antioxidants. Ascorbic acid (AsA) is a universal non-enzymatic antioxidant with substantial potential for scavenging ROS and impacting several important plant functions in stressful and non-stressful conditions. Likewise, melatonin (MEL) (N-acetyl-5-methoxy tryptamine), a naturally occurring hormone in animals and plants, has been found to have significant effect on plant growth and development (Hattori et al.,1995; Shida et al.,1994). Research confirms that melatonin can act as a growth promoter and rooting agent, improving plant growth and root development (Sarrou et al., 2014). Melatonin has also been found to impact plant stress significantly, reducing the negative effects of various environmental stressors such as drought, salt, temperature, heavy metals, and more (Zhang et al., 2014). Melatonin helps to mitigate plant stress by generating reactive oxygen species (ROS). These ROS molecules serve as signaling molecules and are important for plant responses to stress. Melatonin enhances ROS production and trigger plant antioxidant defense mechanisms enabling plants to manage stress and its effects (Zhang et al., 2014). In *Arabidopsis*, the overexpression genes involved in acetic acid synthesis leads to improved drought tolerance. Research suggests that manipulating the expression of genes associated with acetic acid metabolism can enhance the ability of plants to cope with water scarcity (Rasheed et al., 2018). Proline may help maintain the structural stability of proteins and plays a role in balancing the redox equilibrium by acting as a suppressor of singlet oxygen (Alcántara et al., 1994; Das et al., 1997). Polyamines (PAs) are small nitrogenous bases produced by cellular metabolism that regulate plant growth and responses to abiotic stress. They protect against environmental challenges and generate hydrogen peroxide on oxidation, which plays a significant role in signal transduction and plant responses (Liu et al., 2007; Chen et al., 2019). Transgenic plants overexpressing polyamines biosynthetic enzymes have demonstrated their protective roles under abiotic stress conditions.

2.3.1 Role of exogenously applied plant protective agents under abiotic stress

Agricultural practitioners are employing numerous approaches to enhance stress tolerance, which include the use of intragenic, transgenic, and cisgenic crops (genetically modified organisms), conventional breeding programs, novel breeding technologies like CRISPR/Cas editing, and the application of plant biostimulants (Godoy et al., 2021). However, the

application of all these methods is somehow hindered. For example, genetically modified organisms (GMOs) engineered to withstand abiotic stress depend on the regulatory landscape of individual nations, and the approval process involves rigorous scrutiny, leading to prolonged timelines before cultivation and commercialization. Despite the authorization of over 500 transgenic crops, only a few are tailored explicitly for abiotic stress tolerance, reflecting the complex nature of this trait (Kumar et al., 2020). Moreover, negative public perceptions and protracted regulatory procedures challenge GMO cultivation. Regulatory compliance for GMOs entails substantial costs, averaging around USD 35 million, with a development timeline spanning approximately 13 years from inception to market entry (McDougall, 2011; Kumar et al., 2020). Genetic modification of crops facilitated by advancements in CRISPR technology, for example commercialization of CRISPR-edited mushrooms (Waltz, 2016). However, regulatory frameworks for these crops are still progressing in many jurisdictions. Unlike GMOs, conventional crop breeding is not subject to rigorous environmental and biosafety regulations. However, developing a new variety takes a long time, ranging from ten to twenty years, depending on the species (Ahmer et al., 2020).

Instead, the exogenous application of plant protective agents, a non-genetic approach to improve crop yield under stress, is relatively convenient to implement in a short period. Plants, microbes and fungi have been known to produce over two million chemicals that may either be primary or secondary metabolites (Geilfus, 2019). Primary metabolites such as proteins, carbohydrates and lipids are essential building block of an organism which determine its growth and development. Moreover, plants synthesize another group of secondary metabolites which include terpenoids, phenolics and alkaloid as main groups and are localized in different cellular compartments (Geilfus, 2019) that suggests the defense against biotic or abiotic stressors causing damage to the crops (Godoy et al., 2021). Several metabolic pathways give rise to these compounds such as the tricarboxylic acid, shikimate and acetate-malonate pathway or side reactions from glycolysis (Godoy et al., 2021). Plant metabolites display enhanced abiotic stress tolerances, especially salinity, heavy metal and drought tolerance in greenhouse as well as field conditions when applied exogenously. This method highlights the substantial influence of plant metabolites on various facets of crop development, including growth, physiological traits, and overall productivity. Employing the external use of these protective agents is an easy and practical approach for manufacturers

because of its simplicity. However, the time during which these positive effects are shown is influenced by many parameters, including the administered dose, the timing of treatment, and the type of crop (Godoy et al., 2021). External application of glutathione has proved to improve multiple characteristics of plants, such as the effectiveness of photosynthesis, levels of chlorophyll a and b, carotenoids, root and shoot length, fresh and dry weight of plant biomass, yield, and fruit weight per plant (Khalid et al., 2022). Furthermore, research revealed that applying ascorbic acid to cauliflower seedlings enhanced their ability to withstand drought stress in two specific varieties. This was achieved by improving the activity of catalase (CAT) and superoxide dismutase (SOD) enzymes in the plants (Latif et al., 2016). Applying Indol-3-acetic acid (IAA) exogenously to crops via foliar treatment or other methods result in improved plant growth and development, ultimately leading to increased yield. The morphology of wheat, such as plant height, flag leaf area, spike length, number of spikes, and grain in spikes, were significantly enhanced on treatment with IAA (Hanaa et al., 2019). An external application of 24-epibrassinolide under drought stress led to the improved growth factors and increased crop output in maize (Anjum et al., 2011). Talaat et al. (2015) observed an increased quantity of grains produced per plant after EBL treatment. Anjum et al. (2011) claim that plants cultivated in arid conditions and treated with EBL led to enhanced maize yield.

2.3.2 Acetic acid and abiotic stress

Acetic acid (CH_3COOH) is a widely used organic acid that plays a crucial role in plants to cope with water deprivation. Acetic acid can boost the efficiency of photosynthesis and the absorption of essential nutrients. Research has extensively reported that acetic acid can improve drought tolerance in various plant species, such as maize, cassava, and wheat (Kudo et al., 2023; Kim et al., 2017; Rahman et al., 2019). It is important to note that the exogeneous treatment with acetic acid in cassava has been found to improve drought resistance by increasing gene expression in the abscisic acid (ABA) signaling pathway (Utsumi et al., 2019). In the case of Arabidopsis, it is known that upregulation of these genes will increase the plant's drought tolerance through the activation of the jasmonate signaling system under enhanced histone H4 acetylation, which promotes a metabolic shift from glycolysis to acetate synthesis (Kim et al., 2017) suggesting that plants can develop increased resistance to water scarcity through alterations in gene expression linked to acetic acid metabolism.

Acetic acid exhibits a complex network of interactions with other phytohormones, such as jasmonic and abscisic acid (Kim et al., 2017) affecting chromatin structure which can influence gene expression. In addition to drought, the application of acetic acid in lentils was reported to be effective in mitigating the adverse effects of copper toxicity (Hossain et al., 2020). This treatment recorded reduced oxidative damage and copper absorption.

Enhancing agricultural output holds great potential in addressing global food challenges, and utilizing acetic acid in water deprivation can offer advantages because of its great potential in addressing the issue of desertification, which is becoming increasingly urgent due to the impacts of climate change.

2.3.3 Melatonin and abiotic stress

The low molecular weight indole-based hormone melatonin (N-acetyl-5-methoxy tryptamine), discovered in the late 1990s as a ubiquitous by-product of tryptophan, has been reported to enhance plant tolerance to abiotic stresses (Zhang et al., 2015; Kabiri et al., 2018). The significance of melatonin as an important antioxidant and plant growth regulator has been recorded in various plants, regulating various processes such as root and bud development, leaf senescence, photoprotection, and seed germination (Arnao and Hernandez, 2015; Simlat et al., 2018). Melatonin functions as an inherent scavenger of free radicals and a powerful antioxidant, therefore assisting plants in regulating redox homeostasis and mitigating the impacts of environmental challenges (Huang et al., 2019; Sun et al.,2021). Melatonin content varies based on stress and the environment, although a higher concentration in unfavorable conditions was recorded (Arnao and Hernández, 2013). Melatonin content in the roots and leaves of plants grown in the sun are three times higher than those grown in artificial light (Zhang et al., 2014). In pepper fruits, melatonin levels were lower in shaded fruit than in un-shaded fruit, indicating that MEL levels are controlled by sun exposure (Riga et al., 2014). Under stress, plants produce more melatonin as an adaptive response (Zargar et al., 2022). Water hyacinth contains melatonin and its metabolite AFMK (N-acetyl-N-formyl-5-methoxykynuramine), to withstand wastewater contamination from commercial and agricultural sources, including arsenic, mercury, nitrogen, and phosphorus, as well as the pesticide ethion (Tan et al., 2007a). When temperature and heavy metals, including cadmium, lead, and zinc, were present, the MEL content in the *Ulva* species of green microalgae increased (Tal et al., 2011). Improved

endogenous MEL content in UV-B-treated *Glycyrrhiza uralensis* highlights its protective role against UV-induced oxidative damage (Afreen et al., 2006).

Exogenous melatonin treatment may reduce the levels of reactive oxygen species (ROS) in plants, increase the activity of antioxidant enzymes, and mitigate the damage in ultrastructure of grape plants caused by drought (Meng et al., 2014). According to research by Liang et al. (2019), kiwifruit seedlings under water deficit treatment with melatonin exogenously reduced lipid peroxidation and protect cell membranes. According to Kaya et al. (2020), in pepper plants (*Capsicum annuum* L.) external melatonin treatment improved photosynthesis by increased chlorophyll (Chl), notably Chl-a and -b, and improved photosystem II (Fv/Fm) quantum efficiency. These effects become most evident in iron deficiency, salt stress, or both are present. Zhang et al. (2013) reported that applying melatonin to cucumber seedlings increased photosynthetic activity rates, reducing the adverse effects of water stress. Melatonin pretreatment decreases reactive oxygen species (ROS) burst, lowers malondialdehyde levels, a marker of oxidative damage, and increases the activities of antioxidant enzymes, such as superoxide dismutase, ascorbate peroxidase, catalase, and peroxidase, according to research on tea plants subjected to cold, salt, and drought stress (Li et al., 2019).

Furthermore, by raising the quantity of chlorophyll and the rate of photosynthesis, resulting in improved performance of photosystem II (PSII), and exogenous melatonin treatment has been shown to enhance seedlings resistance to osmotic stress (Zhang et al., 2019; Zou et al., 2019). When applied as a pretreatment, melatonin improves photosynthetic rates and minimizes membrane damage in wheat seedlings, increasing resistance to drought (Cui et al., 2017). According to Yang et al. (2018), tomato plants may be successfully protected from the detrimental effects of low temperatures by applying melatonin directly to roots and foliar spraying, allowing the photosynthetic organs to remain intact. Studies have highlighted that the exogenous treatment of melatonin can improve plant growth under cadmium stress in mustard (Zargar et al., 2022). Additionally, it can alleviate various abiotic stressors, such as water scarcity, iron deficiency, salt stress, and their combinations, across multiple crop species (Lee and Back, 2018). All these research studies show that melatonin may have valuable uses in horticulture and agriculture, where it may assist in boosting crop productivity and enhance plant survival under adverse conditions.

2.3.4 Spermine and abiotic stress

Polyamines (PAs) are small nitrogenous bases formed during cellular metabolism, and while not classified as hormones, they have been proposed as a special class of plant growth regulators due to their involvement in various growth processes and responses to environmental stress (Liu et al., 2007; Chen et al., 2019; Pal et al., 2021). Initially, the biological functions of polyamines were thought to depend on their ability to interact with anionic macromolecules, suggesting a structural role similar to that of polycations (Seiler and Raul, 2005; Alcázar et al., 2010; Igarashi and Kashiwagi, 2010). However, further research has shown that PAs regulate critical biological processes such as cell division, differentiation, DNA and protein synthesis, and gene expression. Physiological processes such as fruit ripening, reproductive system development, organ maturation, and leaf aging are also influenced by PAs (Capell et al., 2004; Yamaguchi et al., 2006; Kusano et al., 2007). The three main low-molecular-weight polyamines putrescine (PUT), spermidine (SPD), and spermine (SPM) are aliphatic nitrogenous bases found across various life forms. These compounds play vital roles in numerous physiological and developmental processes, including flower formation, leaf senescence, cell division, embryogenesis, and responses to environmental stress.

Spermine (SPM) is particularly important for a wide range of biological activities, including shoot and root development, the initiation of flowering, fruit production, leaf senescence, DNA synthesis, osmolyte regulation, chlorophyll maintenance, gene transcription, and protein translation. Moreover, spermine enhances defenses against environmental stressors such as heat, cold, drought, and heavy metals. Studies on spermine-treated plants and drought-resistant tomato genotypes have shown increased levels of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT), which improve resistance to oxidative stress caused by dehydration (Sánchez and Rodríguez et al., 2016). In stressed pea plants, spermine treatment increased antioxidant enzyme activity and reduced chlorophyll degradation (Todorova et al., 2016).

Additionally, plants treated with spermine exhibited elevated levels of non-enzymatic antioxidants such as glutathione and ascorbic acid, along with increased activities of enzymes like catalase, superoxide dismutase, glutathione S-transferase, and glutathione reductase (GR). This led to a reduction in the accumulation of reactive oxygen species (ROS) (Nahar et al., 2016a, b). Spermine enhances GR activity and decreases metal-induced ROS

production, thus reducing oxidative damage caused by heavy metals in wheat leaves (Groppa et al., 2007). In soybean leaves under osmotic stress, SPM treatment reduced the degradation of proteins, carotenoids, and chlorophyll, while boosting antioxidant enzyme activities (Radhakrishnan and Lee, 2013). Likewise, SPM treated seedlings subjected to combined drought and heat shocks showed stress tolerance and increased expression of heat shock proteins, along with increased CAT, SOD, and peroxidase activities (Fu et al., 2014).
These results suggest that SPM increases tolerance to oxidative damage caused by various environmental factors by activating enzymatic and non-enzymatic antioxidant pathways.

2.4 Economic importance and challenges in sweet corn cultivation

Corn, or maize, is a staple cereal grain that is grown all over the globe because of its environmental tolerance. As the world's most important cereal crop, it is ranked third in terms of importance to human consumption, after rice and wheat (Swapna et al., 2020). Farmers increasingly turn to specialty corn production, such as sweet corn, for higher returns and job opportunities, particularly in urban areas. Sweet corn (*Zea mays* var. saccharate*)* boasts immense market potential and genetic diversity, offering scope for enhancing its nutritional value (Swapna et al., 2020). Its popularity among consumers stems from its unique taste, pleasant flavor, and sweetness. Specifically bred to enhance sugar content, sweet corn matures 75 to 90 days after sowing (Schultheis, 1994). Sweet corn has diverse physiological constituents, including sugars, starch, water-soluble polysaccharides, proteins, vitamins, and minerals, which contribute to its nutritional value (Szymanek, 2012). Due to its elevated fiber content and reduced cholesterol levels, it is a beneficial inclusion in a nutritious diet. Sweet corn is becoming recognized as a superfood for health-conscious persons due to its nutritional profile, which is equivalent to high-priced vegetables such as cauliflower and cabbage (Swapna et al., 2020). Sweet corn may be used in a broad range of cuisines throughout the globe, such as salads, pizzas, soups, syrups, candies, jams, and pastes.

Despite its high-calorie content, sweet corn offers a plethora of health benefits, mainly when cooked. Contrary to widespread assumption, cooked sweet corn maintains antioxidant qualities even after losing vitamin C (Dewanto et al., 2002). As a grass family member, sweet corn is harvested at the milk stage of endosperm development, ensuring its kernels are soft, succulent, and sweet (Pajic et al., 2004). Unlike field corn, harvested when fully mature,

sweet corn is picked when immature, offering a vegetable rather than grain (Schultheis, 1994). There are many kinds of sweet corn available, and regional tastes vary. The most well-known sort of sweet corn is still the conventional yellow type. Genetic variables influencing starch synthesis are thought to be responsible for variations in sweetness; genes such as sugary (SU) and shrunken (SH) modify the amounts of sugar and starch in kernels (Swapna et al., 2020).

Prior to France in European Union, Hungary is one of the determinant producers of sweet corn. Sweet corn here is grown as a field vegetable in high quantity and largest area (Felföldi and Kerekes, 2016). In Hungary constant depletion of rain in summers and frequent rise in temperature will lead to intense summer droughts (Szeles et al., 2023). Sweet corn production faces significant challenges due to the adverse impacts of drought (Hirich et al., 2016). Water scarcity, exacerbated by climate change and erratic weather patterns, seriously threatens the growth and development of sweet corn plants. With water accounting for a substantial portion of a plant's biomass and being essential for various physiological processes, including growth and metabolism, prolonged periods of drought can severely hamper sweet corn productivity.

2.5 Economic importance and challenges in spinach cultivation

Spinach *(Spinacia oleracea* L. cv. Matador) is one of the economic vegetables with a minimum growth cycle and is grown annually (Ribera et al.,2020). The increasing consumption of fresh (in salads) and processed spinach demonstrates its rising popularity worldwide. When fresh, steamed or barely cooked, spinach has a high biological value and is particularly abundant in antioxidants (Ribera et al., 2020). It has high levels of fibres, minerals (Mn, Fe, K, Mg, Ca, Se), and vitamins (A, E, K, C, B2, B6, B9, folic acid) (Roberts and Moreau, 2016). Spinach is also known for its anti-inflammatory, antitumoral, anti-obesity and lipid-lowering effects. Consuming more antioxidant-rich fruits and vegetables, like spinach, may halt the deterioration of antioxidant defence mechanisms that occur with ageing (Hassan et al., 2022). Spinach crops must be improved in quality and yield by finding new approaches. Moreover, efforts to reduce the potential environmental impact on the production and consumption of spinach are essential. Light and water are two crucial needs of plants regulating their survival, morpho-physiology, and productivity (McElrone et al., 2013; Bayat et al., 2018; Klem et al., 2019), and abundance or scarcity of any of them

imposes deleterious effects on plants and limit crop productivity (Fahad et al., 2017). In nature, plants are exposed to a combination of stresses, and their impact differs from the individual impact of stress (Francini and Sebastiani, 2019). Combinatorial stresses may be antagonistic or synergistic to each other. For instance, heat and drought stress acts synergistically and cause more damage than their individual treatments (Pandey et al., 2017). In contrast, some stresses in combination (drought and ozone, drought and pathogen) acts antagonistically. Some stress combinations have a net neutral or beneficial effect on plants because they cancel out one another (Pandey et al., 2017). Selecting appropriate light intensity is one of the major challenges in the plant factories in the production of green leafy vegetables as most of the studies are based on same crops while the response and performance of various crops stay limited. In spinach, being highly economical to study the response towards different light qualities and their effect under water deprivation hence become crucial, to find weather these two factors when act antagonistically or synergistically.

2.6 Role of different light qualities in plant growth regulation

Among various environmental factors, light is one of the most crucial abiotic factors that regulate plant growth, photosynthesis, survival, and adaptation. Light quality affects plant development, photomorphogenesis, and tissue composition; in addition to light quantity, factors like intensity and length (photoperiod) also influence plant productivity (Ouzounis et al., 2015). Red and blue light, for instance, are the colours most effectively used for photosynthesis, and red light promotes the development of the photosynthetic apparatus (Paradiso et al., 2011). Far-red light encourages blooming in long-day plants, whereas blue light impacts stomatal opening, plant height, and chlorophyll biosynthesis. The red/far red ratio controls stem and branching length, leaf area, and reproduction (Zheng et al., 2019). Seedlings grown under a combination of green, red, and blue lights were taller than those grown under monochromatic red or blue lights in *Arabidopsis thaliana* (Folta, 2004) and increased fresh and dry weight of tomato plants and fruit in combination with red and blue light is recorded (Kaiser et al., 2019). By raising the expression of synthesis pathway genes, blue and UV wavelengths have been demonstrated to promote the accumulation of bioactive chemicals in plant tissues (Hasan and Bae, 2017). Bian et al. (2015) highlighted the positive effects of blue, UV-A, and UV-B on forming phenolic compounds in general and

anthocyanins and the positive impacts of blue, red, and UV-B on carotenoids in various vegetables. Researchers have shown that UV-C-induced effects depend on radiation dose and developmental stage (Poiroux et al., 2010). There is mounting evidence that plants may benefit from UV-C light (Urban et al., 2016). These may result in changes to various primary and secondary metabolites, such as chlorophyll, carotenoids, phenolics, and glucosinolates (Katerova et al., 2012; Vandenbussche et al., 2018; Mewis et al., 2012; Heinze et al., 2018). When exposed to UV radiation, flavonoid accumulation was seen in epidermal cells, leaf hairs, and leaf wax (Harborne and Williams, 2000). UV light greatly stimulates the production of carotenoids such as violaxanthin, neoxanthin, antheraxanthin, luteoxanthin, and lutein (Molnar et al., 2010). UV-C radiation exposure increased carotenoids (Bravo et al., 2013). So, knowing what light quality leads to which plant response becomes crucial. During the daytime, sunlight is the only source of different light qualities, but plants only need some for proper growth. We need to understand and find what kinds of light in plants lead to the proper growth, leaf extension, or stem elongation and yield. This information could be used in greenhouse horticulture to improve crop yield, quality, and production schedules (Paradiso et al., 2021).

3. MATERIAL AND METHODS

3.1 Study Location and Growth Conditions

The experiments were conducted from 2021 to 2024 at the Institute of Crop Sciences, Department of Applied Plant Biology, University of Debrecen, Hungary. All studies were performed in a controlled climatic environment room under hydroponic conditions (Fig. 1). The relative humidity was maintained between 65 and 75%, with a 16-8-hour light/dark cycle with a respective 24-20 ^{0}C temperature and 300 µmol m^{-2} s^{-1} light intensity during daytime.

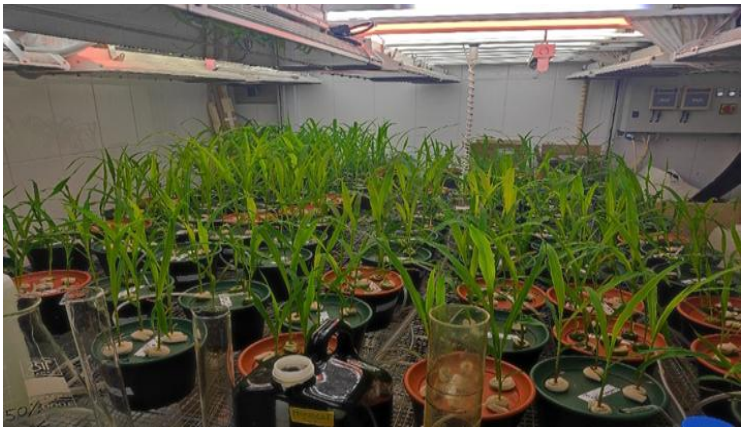


Figure 1. Sweet corn genotypes grown in controlled climatic environmental room under hydroponic conditions.

3.1.1 Nutrient Solution Preparation

The nutrient solution used in hydroponic systems to provide essential elements for plant growth was a modified Hoagland solution for monocot and dicot plants, as Marschner et al. (1990) indicated. The nutrient mixture included 0.7 mM K_2SO_4, 0.5 mM $MgSO_4$, 0.1 mM KH_2PO_4, 0.1 mM KCl, 0.5 µM $MnSO_4$, 0.5 µM $ZnSO_4$, 10 µM H_3BO_3, and 0.2 µM $CuSO_4$ along with 2.0 mM Ca $(NO_3)_2$. Additionally, iron was given in the form of 10^{-4} M Fe-EDTA. The nutrient solution was changed every three days.

3.2 Effect of Acetic Acid Foliar Application on Sweet Corn Under Water Deprivation

Objective

To study the effect of acetic acid foliar application on morphophysiological and biochemical traits in sweet corn genotypes under water deprivation.

Plant Material

The study focused on three genotypes of sweet corn (*Zea mays* L. var. saccharata): Messenger, GSS 8529, and Tyson.

Seed Sterilization and Germination

The seeds were washed with tap water multiple times and sterilized by soaking in 6% H_2O_2. After 15 minutes, the seeds were washed with distilled water and soaked in a 0.01 M $CaSO_4$ solution for two hours, followed by another thorough wash with distilled water. The seeds were then germinated geotropically between moistened filter papers at a temperature of 22 ± 2°C.

Transplantation and Growth

One week after sowing, seedlings (Zadoks scale 10-11) with good vigor were transplanted into plastic pots (1.7L) under hydroponic conditions. Each genotype had 18 pots (4 plants per pot), with the nutrient being changed every third day.

Treatments

Two weeks after sowing, when the seedlings had entered the early vegetative phase (Zadoks scale 13-14), 5% polyethylene glycol (PEG 6000, VWR International bvba, Geldenaaksebaan, Leuven, Belgium) was used to osmotically simulate water deprivation for 9 of the 18 pots per genotype. The one-week treatment with PEG induced mild symptoms of water deficiency which were checked by relative chlorophyll measurements (SPAD values) and stomatal conductance to assess the effectiveness of water deficiency.

Subsequently, on the 25th day after sowing, an acetic acid (VWR International S.A.S., France) foliar treatment was applied for five consecutive days using two different concentrations: 20 mM and 10 mM, control plants were sprayed with DDW. Each plant was sprayed thrice. The nozzle of spray was adjusted to spray 1mL of solution in a single sprinkle. Thus, we have six different treatments:

1. Control with optimal conditions for growth (Distilled water foliar Spray)
2. 10 mM Acetic acid foliar spray.
3. 20 mM Acetic acid foliar spray.
4. 5% PEG (Water deprivation control).
5. 10 mM Acetic acid + 5% PEG.

6. 20 mM Acetic acid + 5% PEG.

Pots were arranged following a randomized complete block design with three independent replicates for each treatment.

Measurements

After the 30th day of sowing, relative chlorophyll content (SPAD values), stomatal conductance, and fast phase of the chlorophyll fluorescence induction curve were recorded. Furthermore, the plants were harvested on the 35th day after sowing to analyze various physio-morphological parameters.

Statistical Analysis

A completely randomized block design with three replications and four plants per replica was used to arrange the pots. Analysis of variance (two-way ANOVA) and Fisher's protected least significant difference test was used by GenStat Release 12.1 to analyze the differences and statistical significance between treatments and genotypes.

3.3 Effect of Melatonin Foliar Application on Sweet Corn Under Water Deprivation

Objective

To study the effect of melatonin foliar application on morphophysiological and biochemical traits in sweet corn genotypes under water deprivation

Plant Material

The study focused on four sweet corn genotypes (*Zea mays* var. saccharata): Messenger, Dessert, Royalty, and Tyson.

Seed Sterilization and Germination

Seeds were sterilized, soaked in 0.01 M $CaSO_4$, and germinated as described previously (Experiment 1).

Transplantation and Growth

Seedlings at the VE growth stage (Zadoks scale 09) with good vigor were transplanted into plastic pots (1.7 L) under hydroponic conditions. Each genotype had 18 pots, with 4 plants per pot, resulting in a total of 72 pots (4 genotypes ×6 treatments×3 replications). The nutrient solution was replaced every three days.

Treatments

After two weeks of sowing, when plants reached the V4-V5 (Zadoks scale 14-15) vegetative stage, polyethylene glycol (PEG 6000, VWR International bvba Geldenaaksebaan, Leuven, Belgium) was used to induce water deprivation. The different concentrations of PEG used include 8% and 12% in 6 replicates each. After two weeks of PEG treatments, besides visual symptoms, like leaf rolling and leaf tip burn, at the V6-V7 vegetative stage, nondestructive parameters, relative chlorophyll content (SPAD values), and stomatal conductance were measured to confirm the presence of water scarcity (Fig. 2). At this stage, foliar application of 100 µM melatonin (Cayman chemical company) treatment was given to each of three replicates of control, 8% and 12% PEG-treated plants for seven consecutive days. Each plant was sprayed thrice. The nozzle of spray was adjusted to spray 1mL of solution in a single sprinkle. Thus, we have six different treatments:

1. Control with optimal conditions for growth (Distilled water foliar Spray)
2. 100µM melatonin
3. 8% PEG (Moderate water deprivation control)
4. 12% PEG (Severe water deprivation control)
5. 8% PEG + 100 µM Melatonin.
6. 12% PEG + 100 µM Melatonin.

Pots were arranged following a randomized complete block design with three independent replicates for each treatment.

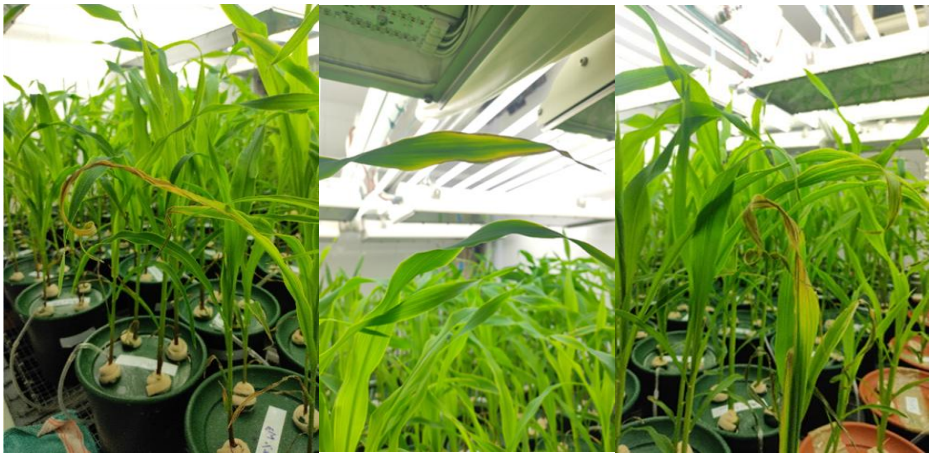


Figure 2. Visible symptoms of PEG-induced water deprivation (rolling and yellowing of leaf tips in sweet corn genotypes).

Measurements

After melatonin treatment for one week at the V8-V9 vegetative stage (Zadoks scale 18-19), samples were taken to evaluate several morphological, physiological, and biochemical parameters.

Statistical Analysis

A completely randomized block design with three replications and four plants per replica was used to arrange the pots. Analysis of variance (two-way ANOVA) and Fisher's protected least significant difference test was used by GenStat Release 12.1 to analyze the differences and statistical significance between treatments and genotypes.

3.4 Effect of Spermine Foliar Application on Sweet Corn Under Water Deprivation

Objective

To study the effect of spermine foliar application on morphophysiological and biochemical traits in sweet corn genotypes under water deprivation

Plant Material

The same four genotypes were used: Messenger, Dessert, Royalty, and Tyson.

Seed Sterilization and Germination

Seedlings were grown and prepared as described in previous experiments.

Transplantation and Growth

Seeds were transplanted and grown as described previously in previous experiments.

Treatments

After two weeks of sowing, when plants reached V4-V5 (4 to 5 established leaves, Zadoks scale 14-15), vegetative stage polyethylene glycol (PEG 6000 VWR International bvba Geldenaaksebaan, Leuven, Belgium) was used to introduce water deprivation. The different concentrations of PEG used include 8% and 12%. After two weeks of PEG treatments, besides visual symptoms, like leaf rolling and leaf tip burn, at the V6-V7 vegetative stage, nondestructive parameters, relative chlorophyll content (SPAD), and stomatal conductance were measured to confirm the effect of water scarcity. At this stage, for seven consecutive days, the foliar application of 0.2 mM spermine (Sigma-Aldrich Kft. Budapest) treatment was given to each of three replicates of control, 8%, and 12% PEG-treated plants. Each plant was sprayed thrice. The nozzle of spray was adjusted to spray 1mL of solution in a single sprinkle. Thus, we have six different treatments:

1. Control with optimal conditions for growth (Distilled water foliar Spray)
2. 0.2 mM spermine
3. 8% PEG (Moderate water deprivation control)
4. 12% PEG (Severe water deprivation control)
5. 8% PEG + 0.2 mM spermine
6. 12% PEG + 0.2 mM spermine

Pots were arranged following a randomized complete block design with three independent replicates for each treatment.

Measurements

After spermine treatment for one week at the V8-V9 vegetative stage (Zadoks scale 18-19), samples were taken to evaluate several morphological, photosynthetic, and biochemical parameters.

Statistical Analysis

A completely randomized block design with three replications and four plants per replica was used to arrange the pots. Analysis of variance (two-way ANOVA) and Fisher's protected least significant difference test was used by GenStat Release 12.1 to analyze the differences and statistical significance between treatments and genotypes.

3.5 Effect of Water Deprivation and Light Quality on Spinach Growth

Objective 1

To study the effect of water deprivation on germination parameters in spinach

Experimental Design

Spinach Seeds (*Spinacia oleracea* var. Matador) were surface sterilized using 6% [v/v] H_2O_2 for 20 minutes and washed and rinsed extensively with deionized water. The treatment of 2.5% PEG 6000 [VWR international bvba Geldenaaksebaan, Leuven, Belgium] solution was applied to the seeds in three replicates, and for control treatment, the nutrient solution was applied (Marschner et al., 1990). The seeds were germinated geotropically between moistened filter papers at 22 ± 2°C. Each roll contained 30 seeds. Seed germination was counted every day, and from the germination counts, the germination parameters were determined after 7 days of sowing.

Objective 2

To study the effect of different light qualities on morphophysiological traits in spinach in general and under water deprivation

Experimental Design

The spinach seeds were surface sterilized with 6% [v/v] H_2O_2 for 20 minutes before being properly washed and rinsed with deionized water. The seeds were grown geotropically at 22 ± 2°C between moist filter sheets. After they developed two true leaves, seedlings of the same size were transplanted into plastic pots (1.7L) in a hydroponic environment. The racks on which pots were placed were equipped with LED lamp sets (Tungsram Ltd. Hungary) with 300 µmol m^{-2} s^{-1} and three different light qualities: Light 1 with a higher percentage of

blue light (Blue >>Red), Light 2 with normal white light taken as control and Light 3 with higher red light (Red > Blue >) along with flashes of UV-C once a week (Table 1).

Table 1. Percentage of different light qualities used in the experiment

Light quality							
LED lamps	Blue	Green	Red	Far-red	UV-C	Total PPF	Explanation
Light 1	20%	40%	66%	10%	0%	245 µmol/s	Blue >>Red
Light 2	35%	48%	15%	1%	0%	350 µmol/s	Normal White
Light 3	12%	4%	75%	10%	1%	308 µmol/s	Red > Blue > Flashes of UV-C radiations once a week for 5 minutes.

Treatments

In the experiment, six pots were set up for each LED lamp set, each containing four spinach plants. Among these pots, three were filled with a nutrient solution, and the other three were filled with a nutrient solution mixed with 2.5% polyethylene glycol (PEG) to induce water deprivation. Throughout the experiment, the nutrient solution was replaced every three days until harvest.

Measurements

On the 25th day after sowing, two plants were harvested from each pot containing only the nutrient solution to examine the impact of various light qualities on spinach growth. For further investigation, the remaining two plants from each pot (with only nutrient solution) were allowed to grow until the 35th day after sowing, serving as the control group to compare against the plants grown with the nutrient solution mixed with 2.5% PEG under different light qualities. These plants were harvested on the 35th day (Full harvest) to analyze the effects of water deprivation and different light qualities on spinach growth and development.

Statistical Analysis

Treatments were arranged in a randomized complete-block design with three independent replications and 30 seeds per replicate for the germination experiment. A randomized complete block design with three replications and four plants per replica was used to arrange the pots in an experiment with spinach under different light qualities and water deprivation. Analysis of variance (ANOVA) and the Tukey Post Hoc test were used by the SPSS program (Version 26, IBM, USA) to indicate significantly different means of each treatment.

3.6 Methodology

3.6.1 Germination traits

From the germination counts, the following germination parameters were determined after seven days of sowing:

1. Germination percentage :

   $G(\%) = \frac{\sum_{i=1}^{k} n_i}{N}$ x 100

2. Mean germination time:

   $\bar{t} = \frac{\sum_{i=1}^{k} n_i\, t_i}{\sum_{i=1}^{k} n_i}$ (Ellis and Roberts, 1981)

3. Mean germination rate:

   $\bar{v} = \frac{1}{\bar{t}}$ (Ranal et al., 2009)

4. Coefficient of variation of germination time:

   $CV_t = \frac{S_t}{\bar{t}}\ x\ 100$ (Ranal et al., 2009)

5. Germination index:

   $GI = \sum_{i=1}^{k} n_i / t_i$ (Wiesner L., 1990)

6. Coefficient of velocity of germination:

   $CVG = \frac{\sum_{i=1}^{k} n_i\, t_i}{\sum_{i=1}^{k} n_i}\ x\ 100$ (Jones and Sanders, 1987)

7. Mean daily germination percent:

   $\bar{G} = \frac{GP}{T_n}$ (Adams and Farrish, 1992)

8. Germination value:

   GV = MDG × PV (Czabator, 1962)

   Where MDG = mean daily germination, PV = peak value

3.6.2 Root and shoot length

The length of the roots and shoots were measured using a ruler. This straightforward method involves physically measuring the distance from the base of the plant to the tip of the root or shoot using a ruler. Specific root (SRL) and shoot length (SSL) were calculated as follows: SRL = Root length / Root dry weight (Li et al., 2021), SSL = Shoot length / Shoot dry weight.

3.6.3 Root volume

The water displacement technique was used, where the initial and final water levels were measured to calculate the difference, representing the volume of the roots. (Archimedes' principle: Birouste et al., 2013)

3.6.4 Fresh and dry weight

An electronic scale (Ohaus, Switzerland) was used to measure the fresh weights of both roots and shoots. Three replicate samples from each treatment were dried in an oven set at 70°C for four days to obtain dry weights. The samples were dried until a consistent weight was achieved and weighed on an electronic scale with a precision of 0.001g (Ohaus, Switzerland).

3.6.5 Total dry biomass and Shoot-to-root ratio

Total dry biomass was calculated as the total dry weight of the plant, which is the sum of shoot and root weight. Shoot: root is calculated as follows: SRR = Shoot dry weight / Root dry weight.

3.6.6 Specific leaf area

Five leaf discs with known surface area were used for SLA measurement. The fresh samples were dried at 104.5°C until a constant weight. The dry weight of all 5 leaf discs was then measured using an electronic scale with a precision of 0.001g (OHAUS, Swiss). Finally, the SLA of each leaf was calculated by dividing the leaf area by the corresponding leaf dry weight (Garousi et al., 2016).

3.6.7 Relative chlorophyll content

Relative chlorophyll content was measured using a SPAD-502Plus device (Konica Minolta, Japan). Three readings per repetition were taken from each treatment's last fully developed leaves.

3.6.8 Qualitative and quantitative measurement of photosynthetic pigments

Photosynthetic pigments, including chlorophyll-a and -b and total carotenoid contents, were extracted following the methodology described by Moran and Porath, (1980) and determined using the Wellburn, (1994) method. Samples were soaked in darkness in the N, N dimethylformamide solvent for 48 hours at room temperature. After 48 hours, the supernatant was measured using UV-VIS spectrophotometry (Metertech SP-830 PLUS, Taiwan) at specific wavelengths.

Analysis of antheraxanthin, lutein, zeaxanthin, and violaxanthin concentration was measured using the High-Performance Liquid Chromatography (HPLC) method. The separation was performed using a Nucleosil C18 column. The eluents consisted of a solution composed of acetonitrile and water in a ratio of 9:1, which included 0.01% triethylamine and ethyl acetate. The HPLC system employed a UV/VIS detector (JASCO, Japan). To determine the highest peaks in the chromatogram and quantify the levels of pigments, zeaxanthin was consistently introduced as a reference throughout the process (Mészáros et al., 1995). This method facilitated the quantification of antheraxanthin, zeaxanthin, lutein, and violaxanthin levels in the leaf extract, and the total amount of these four compounds was computed to determine the xanthophyll pool.

3.6.9 Stomatal conductance

AP4 porometer (Delta-T, UK) was used to measure stomatal conductance in three repetitions from the youngest fully expanded leaves.

3.6.10 Chlorophyll fluorescence

The measurements of the fast phase of chlorophyll fluorescence induction curve parameters were taken from the youngest fully developed leaves using a portable chlorophyll fluorometer-PAM-2100 (Walz Gmbh, Germany) in three replicates. Maximum, minimal, and variable fluorescence were recorded to calculate potential photosynthetic capacity (Fv/Fo) by dividing the variable fluorescence (Fv) by the minimal fluorescence (F0), maximum photochemical efficiency of PSII (Fv/Fm) was calculated by dividing the difference between the maximum fluorescence (Fm) and the minimal fluorescence (Fo) by the maximum fluorescence (Fm). Also, the actual photochemical efficiency of PSII

($\Delta F/Fm'$), also referred as Yield, was recorded (Kitajima and Butler, 1975; Schreiber et al., 1996).

3.6.11 Malondialdehyde content

An extraction buffer containing trichloroacetic acid (TCA) was utilized for lyophilized leaf samples. The extract was centrifuged, the solid particles and liquid supernatant were separated. The supernatant was transferred to a tube with TCA and thiobarbituric acid (TBA). The reaction between thiobarbituric acid and MDA leads to the formation of a colored complex that can be quantified. The mixture was heated at a high temperature of 95 °C for 30 minutes to promote the reaction and then rapidly cooled to stop any further reactions. Another round of centrifugation was performed to eliminate any remaining precipitates. At last, the absorbance of the resulting solution was measured at 532 nm using a spectrophotometer (Metertech SP-830 PLUS, Taiwan). The absorbance value at this wavelength corresponds to the concentration of the colored complex, indicating the MDA content in the original lyophilized leaf sample (Baryla et al., 2000).

3.6.12 Peroxidase activity

Lyophilized leaf samples were homogenized in a phosphate buffer. The extract was then transferred into an Eppendorf tube and centrifuged for 10 minutes. In the cuvette, sodium acetate buffer, hydrogen peroxide, and o-anisidine were added to prepare the reaction mixture, and the prepared sample extract was added to the cuvette. Contents were mixed carefully. Afterwards, the absorbance of the reaction mixture was measured at 460 nm using a spectrophotometer (Metertech SP-830 PLUS, Taiwan). Readings were taken every 10 seconds for a total duration of one minute. This enabled monitoring changes in absorbance over time (Roxas et al., 1997).

4. RESULTS AND DISCUSSION

4.1 Morphophysiological Responses to Acetic Acid under Water Deprivation

4.1.1 Modulation of Specific Root and Shoot Length

The results of specific root length (SRL) and specific shoot length (SSL) under various treatments reveal a complex interaction between acetic acid concentrations, water deprivation, and different sweet corn genotypes (Table 2). PEG-induced water deprivation significantly decreased SRL and SSL across all genotypes. Our results align with previous studies on water stress impacts on plant growth (Mahmud et al., 2023). The reductions are attributed to the disruption of water equilibrium, affecting cell turgor, growth, and division (Zia et al., 2021).

Application with 10 mM acetic acid decreased SRL in Messenger and GSS 8529, while in Tyson substantial increase was recorded. With 20 mM acetic acid, SRL was further reduced in Messenger and GSS 8529, whereas SRL continued to increase in Tyson. Similarly, 10 mM acetic acid enhanced SSL in all genotypes, but 20 mM acetic acid showed varied effects: decreasing SSL in Messenger but increasing it in Tyson and GSS 8529 genotypes.

When acetic acid was applied in combination with PEG treatments, the results varied. Acetic acid mitigated the adverse effects of water deprivation on plant growth (Table 2). For instance, with 10 mM acetic acid under 5% PEG, SRL significantly increased in Messenger and Tyson compared to PEG treatment alone, while GSS 8529 recorded a decrease. At 20 mM acetic acid under 5% PEG, all genotypes showed increased SRL. Similarly, SSL significantly increased in all three genotypes with 10 mM acetic acid under water deprivation, while 20 mM acetic acid showed significant increases in Messenger and Tyson, with no effect on GSS 8529.

Table 2. Effect of foliar spray of acetic acid on the specific root and shoot length (cm g^{-1}) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Messenger	Tyson	GSS 8529
Specific root length	Control	100.57^{aA}	80.08^{dB}	75.05^{aC}
	10 mM acetic acid	97.78^{bA}	137.50^{aB}	64.62^{cC}
	20 mM acetic acid	91.12^{cA}	99.99^{bB}	71.69^{bC}
	5% PEG (Water deficit control)	46.11^{fA}	34.50^{eB}	35.84^{eB}
	10 mM acetic acid + 5% PEG	49.85^{eB}	87.12^{cA}	32.15^{fC}
	20 mM acetic acid + 5% PEG	69.59^{dB}	79.75^{dC}	38.85^{dA}
Specific shoot length	Control	29.31^{cA}	20.67^{dB}	19.18^{bcC}
	10 mM acetic acid	42.25^{aA}	28.64^{bB}	19.67^{bC}
	20 mM acetic acid	25.57^{dA}	25.50^{cA}	20.73^{aB}
	5% PEG (Water deficit control)	22.88^{eA}	18.27^{eB}	14.96^{eC}
	10 mM acetic acid + 5% PEG	25.76^{dB}	31.22^{aA}	16.99^{dC}
	20 mM acetic acid + 5% PEG	39.21^{bC}	27.03^{cB}	14.96^{eA}

Messenger and GSS 8529 generally recorded reduced growth parameters with individual acetic acid treatments, but the combination with water deprivation revealed a more nuanced interaction, where acetic acid mitigated stress effects to varying degrees. Messenger exhibited significant increases in both SRL and SSL when acetic acid was applied under water deprivation, indicating a moderate level of adaptability. In contrast, Tyson consistently exhibited enhanced growth parameters under all conditions, including acetic acid treatment alone and with water deprivation. Results suggest that genotype Tyson has a distinctive physiological mechanism aiding it to benefit from acetic acid treatment even under water deprivation. Response of genotype Tyson highlights its best adaptability to water deprivation and combination treatments with acetic acid.

Our results align with research reporting the beneficial effects of acetic acid under drought like conditions (Kim et al., 2017; Kudo et al., 2023). Specifically, mitigation of osmotic stress by acetic acid treatment may involve regulation of stress related genes and maintaining cellular homeostasis, as reported by Zia et al. (2021).

4.1.2 Alterations in Root Volume and Total Biomass Accumulation

Treatment with 10 mM acetic acid under normal conditions significantly reduced root volume for both Messenger and GSS 8529 genotypes (Table 3). While genotype Tyson

recorded a significant increase in root volume under the same treatment. At higher concentration of acetic acid (20 mM), Tyson recorded a slight decrease in root volume, while in GSS 8529 substantial reduction was observed.

All three studied genotypes recorded a significant decrease in root volume under PEG (5%) induced water deprivation. However, treatment with 10 mM acetic acid under water deprivation improved root volume in all three genotypes (Messenger, Tyson, and GSS 8529) compared to water deprivation. Likewise, the treatment with 20 mM acetic acid under water deprivation increased root volume, with significant increase in genotype Tyson.

The recorded results highlight the significant reduction in root volume across all genotypes due to water deprivation, consistent with the expected effects of reduced water supply on root growth. The decrease in root volume under PEG treatment can be attributed to a decrease in specific root length, which ultimately affects overall root volume (Hussain et al., 2020). However, the application of acetic acid under water deprivation appears to mitigate its negative effects, suggesting a potential role for acetic acid in alleviating the adverse impacts of water deficit on root growth.

Table 3. Effect of foliar spray of acetic acid on the root volume (cm^3) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes		
	Messenger	Tyson	GSS 8529
Control	4.33^{aB}	4.67^{cB}	9.33^{aA}
10 mM acetic acid	2.21^{aC}	5.33^{bA}	4.00^{cB}
20 mM acetic acid	4.33^{aA}	4.33^{cA}	3.67^{cdB}
5% PEG (Water deficit control)	3.48^{aA}	1.67^{eB}	3.00^{dA}
10 mM acetic acid + 5% PEG	4.67^{aA}	3.00^{dA}	5.00^{bA}
20 mM acetic acid + 5% PEG	4.00^{aA}	6.67^{aB}	3.67^{cdA}

The findings reveal a genotypic-dependent response to acetic acid application under water deprivation. For genotype Messenger and GSS 8529, 10 mM acetic acid application under water deprivation increased root volume than water deprivation alone. While, for Tyson, the 20 mM acetic acid treatment was more effective, suggesting that both the concentration of acetic acid and the genotype specific response to treatments. The genotype-specific response highlights Tyson as the genotype with the best adaptability to water deprivation and combination treatments with acetic acid, showing significant increases in root volume under

stress conditions. These results align with previous studies reported by Mahmud et al. (2023) that acetic acid treatment in maize and *Arabidopsis* under PEG-induced osmotic stress-maintained root volume similar to control plants, further supporting the role of acetic acid in mitigating the effects of water deprivation.

The effect of acetic acid and water deprivation on total biomass reveals intricate interactions that vary across different sweet corn genotypes (Table 4). Foliar application of acetic acid alone, at both concentrations, reduced total biomass for all genotypes compared to the control. This suggests that, under non-stress conditions, acetic acid may act as an inhibitor of biomass accumulation, potentially due to its effects on metabolic processes or plant growth regulation.

When subjected to water deprivation induced by 5% PEG, the genotypes exhibited differential responses. Genotype GSS 8529 recorded an increase in total biomass by 10.5%, suggesting an inherent resilience to water-deficit conditions. This response could be accredited to genetic or physiological adaptations that allow GSS 8529 to manage water deprivation better, as indicated by studies like those of Ribaut et al. (2009) and Farooq et al. (2009) that response to water deprivation can vary among cultivars based on genetic or physiological differences. In contrast, Messenger and Tyson recorded a decrease in biomass under water deprivation, suggesting high sensitivity to water deficit, consistent with a reduction in physiological processes critical for biomass production under water-limited conditions, as reported by Achakzai, (2009).

Table 4. Effect of foliar spray of acetic acid on total biomass (g) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes		
	Messenger	Tyson	GSS 8529
Control	2.98^{cA}	3.52^{dA}	4.77^{abB}
10 mM acetic acid	1.75^{aA}	2.43^{aA}	4.22^{aB}
20 mM acetic acid	2.72^{bcA}	3.00^{cA}	4.10^{aB}
5% PEG (Water deficit control)	2.17^{abA}	2.94^{bcA}	5.27^{bB}
10 mM acetic acid + 5% PEG	3.08^{cA}	2.75^{abcA}	6.23^{cB}
20 mM acetic acid + 5% PEG	1.88^{aA}	2.53^{abA}	4.65^{abB}

Messenger and GSS 8529 recorded a significant increase in total biomass when 10 mM acetic acid was applied under water deprivation. The biomass of Messenger increased by

41.9%, while GSS 8529 recorded an increase of 18.2%. It appears that acetic acid may have a protective effect when it comes to water deprivation, particularly at lower concentrations. This could be due to its ability to enhance stress tolerance mechanisms or improve water use efficiency. Recorded results support the hypothesis that acetic acid may help plants reduce the negative impact of water scarcity, potentially allowing them to maintain their biomass production at levels similar to control. On the other hand, when 20 mM acetic acid was applied during the water deficit, a reduction in total biomass for all genotypes was recorded. It appears that when it comes to acetic acid, lower concentrations may have positive effects in stressful situations, but higher concentrations could be harmful. This indicates that acetic acid might have a threshold effect, where it could potentially cause additional stress or toxicity, disrupting important physiological functions (Kim et al., 2017).

4.1.3 Adjustment in Shoot-to-Root Ratio

Shoot: Root (SRR) increased in Messenger and Tyson (9.3% and 64.8%), while decreased in GSS 8529 (8.6%) on treatment with 10 mM acetic acid compared to control (Table 5). At higher concentrations of acetic acid in Messenger and Tyson, an increase in shoot: root was recorded, while in GSS 8529, a decrease was recorded compared to the control. Upon treatment with 5% PEG, a significant decrease in two genotypes (45.6% and 23.2% in Messenger and GSS 8529, respectively) was recorded, while in Tyson, an increase was recorded. On treatment with 10 mM acetic acid under PEG, a decrease in all three genotypes was recorded (15.0%,28.9%, and 8.2% in Messenger, Tyson, and GSS 8529, respectively). Likewise, a higher concentration of acetic acid under PEG decreased shoot: root compared to PEG (17.3%, 19.9%, and 12.4% in Messenger, Tyson, and GSS 8529, respectively). The shoot-to-root ratio (SRR) results revealed that water deprivation decreased SRR in Messenger and GSS 8529, which coincided with the results for the above growth traits. The results in these genotypes demonstrate that the SRR based on dry weight decreased in the presence of water deprivation, indicating that shoot growth is more sensitive than root growth, as also described by Ashraf and Foolad, (2007). In Tyson, SRR increased under water deprivation, indicating genotype-specific response, as reported that different genotypes of durum wheat responded differently under PEG-induced water deficit (Bajii et al., 2000). Several studies (Rahman et al., 2019a; Utsumi et al., 2019; Rahman et al., 2020) have reported that both PEG-induced osmotic stress and water deficiency can lead to the

suppression of shoot and root growth, along with a reduction in various growth parameters. Individual treatment, especially with lower concentration of acetic acid, increased SRR in Messenger and Tyson. In contrast, in combination treatment with water deprivation, a decrease was reported compared to water deficit conditions, indicating the possibility of the beneficial effects of acetic acid or detrimental interactions between acetic acid and water deprivation. These results indicate that acetic acid treatment can affect plant growth differently depending on concentration, genotype, and combination with water deprivation.

Table 5. Effect of foliar spray of acetic acid on the shoot-to-root ratio (g g^{-1}) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes		
	Messenger	Tyson	GSS 8529
Control	4.75^{aB}	3.43^{cdC}	6.29^{aA}
10 mM acetic acid	5.19^{aA}	5.63^{aA}	5.75^{abA}
20 mM acetic acid	4.93^{aB}	4.77^{abB}	6.09^{abA}
5% PEG (Water deficit control)	2.58^{bB}	4.51^{bcA}	4.83^{bcA}
10 mM acetic acid + 5% PEG	2.20^{bC}	3.20^{dB}	4.44^{cA}
20 mM acetic acid + 5% PEG	2.14^{bA}	3.61^{cdB}	4.23^{cB}

4.1.4 Regulation of Specific Leaf Area and Relative Chlorophyll Content

Specific leaf area (SLA) decreased in Messenger and GSS 8528 on treatment with 10 mM acetic acid concentration, while in Tyson, an increase was recorded compared to control. An increase at 20 mM acetic acid application in Messenger and Tyson was recorded, while in GSS 8529, a decrease of 31.2% was recorded in comparison to the control (Fig. 3). Under 5% PEG treatment, SLA decreased in all three genotypes (48.5%, 21.8%, and 40.0% in Messenger, Tyson, and GSS 8529 respectively). In combination, treatment of 10 mM acetic acid and 5% PEG increase in all three genotypes were recorded (22.4%, 2.6%, 15.3% in Messenger, Tyson, and GSS 8529 respectively) compared to PEG treatment. In 20 mM acetic acid treatment under PEG, an increase was also recorded compared to PEG treatment (72.0%, 10.6%, and 18.6% in Messenger, Tyson and GSS 8529, respectively).

Osmotic stress reduces the surface leaf area by reducing leaf expansion as water deficit restricts cell division and expansion, resulting in smaller and narrower leaves with reduced leaf area (Chaves et al., 2002). Our results align with this study, as SLA was reduced in all genotypes under PEG-induced water deprivation. The lack of moisture leads to a decrease

in both the number and size of leaves. The leaf growth is often influenced by turgor pressure and the availability of assimilates. Under dry environmental conditions, the primary factors that restrict leaf growth are decreased turgor pressure and a reduced rate of photosynthesis (Rucker et al., 1995). Foliar application of acetic acid under water deprivation increased the SLA in all genotypes with a pronounced increase under 20 mM acetic acid application. Aligning with our results, in mung bean plants under salt stress, an increase in leaf area per trifoliate was recorded on foliar application of acetic acid (Rahman et al., 2019a).

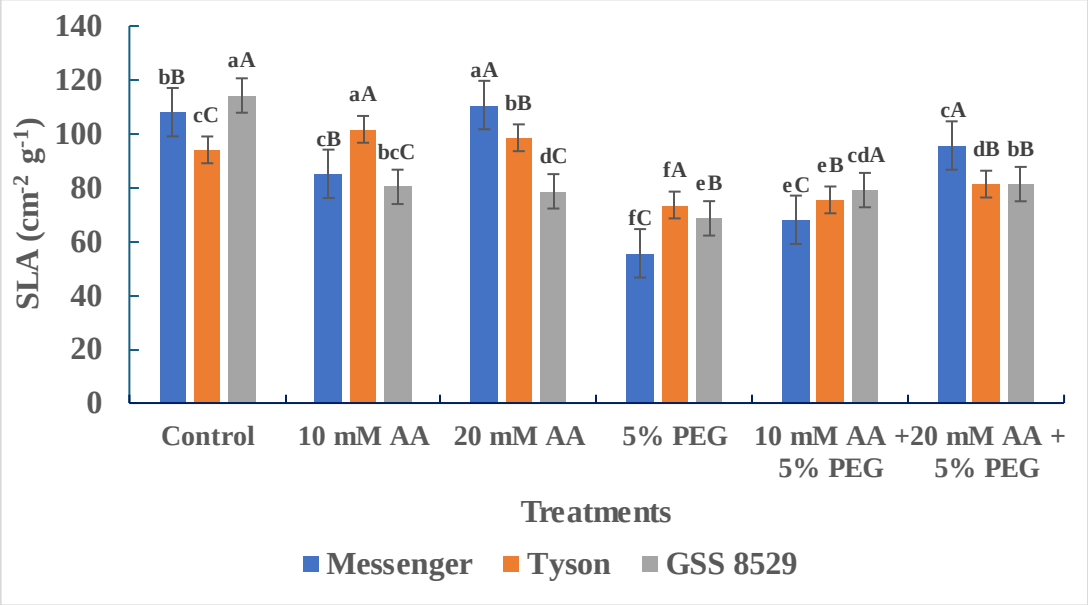


Figure 3. Effect of foliar spray of acetic acid (AA) on specific leaf area ($cm^{-2}\ g^{-1}$) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

The effect of acetic acid and water deprivation on relative chlorophyll content (SPAD) in three different types of sweet corn: Messenger, Tyson, and GSS 8529 was examined (Table 6). In individual treatment with 10 mM acetic acid under normal conditions, Messenger and GSS 8529 recorded an increase in SPAD by 12.9% and 21.2% respectively, compared to the control. This suggests that acetic acid might have a stimulating effect on chlorophyll synthesis or help protect chlorophyll content, as reported by Rehman et al. (2019a). However, Tyson recorded a slight decrease of 2.7% showing varied response among different genotypes, possibly because of differences in metabolic pathways. In the treatment with 20 mM acetic acid, the SPAD levels increased in all genotypes: 8.9% in Messenger,

18.5% in Tyson, and 21.2% in GSS 8529. This suggests that higher levels of acetic acid have a more positive effect on chlorophyll preservation.

Under 5% polyethylene glycol induced water deprivation, SPAD values decreased. Messenger recorded a decrease of 15.4%, Tyson recorded a reduction of 22.4%, and GSS 8529 recorded a reduction of 6.3%. This indicates that water deprivation negatively affects the chlorophyll content in the plants, most likely because it impairs the function of the chloroplasts (Fahad et al., 2017). Treatment of acetic acid under water deprivation resulted in a noticeable increase in SPAD values compared to using PEG alone. When 10 mM acetic acid was applied under water deprivation, the SPAD levels increased by 24.5% in Messenger, 32.7% in Tyson, and 24.2% in GSS 8529. The increases were even more significant at 20 mM acetic acid treatment under water deprivation. In Messenger, the increase was 28.3%, in Tyson it was 38.3%, and in GSS 8529 it was 21.9%. The results suggest that acetic acid can help to reduce the negative effects of water deprivation via increase in chlorophyll content and potentially improve the photosynthetic performance when plants are experiencing water deficit conditions (Rehman et al., 2019a).

Table 6. Effect of foliar spray of acetic acid on relative chlorophyll content (SPAD values) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes		
	Messenger	Tyson	GSS 8529
Control	27.52^{bA}	27.65^{dA}	27.80^{cA}
10 mM acetic acid	31.07^{eB}	26.91^{dC}	33.68^{aA}
20 mM acetic acid	29.97^{dC}	32.77^{aB}	33.68^{aA}
5% PEG (Water deficit control)	23.27^{aB}	21.47^{eC}	26.05^{dA}
10 mM acetic acid + 5% PEG	28.97^{cB}	28.50^{cB}	32.35^{bA}
20 mM acetic acid + 5% PEG	29.85^{dB}	29.67^{bB}	31.75^{bA}

4.2 Photosynthetic and Stomatal Responses to Acetic Acid under Water Deprivation

4.2.1 Photosynthetic Pigment Composition: Chlorophyll, Total Carotenoid and Xanthophyll Profiles

The results indicate the complex interactions between genotype-specific responses, treatments, and the regulation of photosynthetic pigments (Table 7). The varied responses of chlorophyll-a (Chl-a), chlorophyll-b (Chl-b), and total carotenoids to acetic acid and water deprivation across the genotypes Messenger, Tyson, and GSS 8529 provide insights into the

mechanisms underlying stress adaptation. In genotype Messenger, the recorded reduction in Chl-a content in all treatments, specifically with acetic acid, suggests a sensitivity to water deprivation and acetic acid treatment. This aligns with findings by Anjum et al. (2011) and Din et al. (2011), who reported that drought stress could damage thylakoid membranes and reduce chlorophyll levels. The lack of significant change under the water deficit implies that Messenger may have a limited capacity to modulate Chl-a synthesis or degradation under PEG-induced water deprivation. In Tyson, Chl-a content decreased under individual acetic acid and PEG treatments, which is consistent with drought's detrimental effects on chlorophyll synthesis. However, the significant increase in Chl-a content under combined acetic acid and PEG treatments (68.6% and 46.4% for 10 mM and 20 mM acetic acid, respectively) suggests an ameliorative role of acetic acid in mitigating water deficit effects. This is supported by Rehman et al. (2020), who reported that acetic acid could help maintain photosynthetic pigments under drought stress. In GSS 8529, the Chl-a content improved across acetic acid concentrations, and PEG treatment suggests a robust mechanism to cope with water deprivation, possibly through enhanced chlorophyll synthesis or reduced degradation. The ability of genotype GSS 8529 to increase Chl-a content under water deprivation aligns with reports of increased chlorophyll levels in cereals under moisture stress, emphasizing the impact of crop species and variety (Estill et al., 1991).

The varied responses of Chl-b content to treatments across genotypes further illustrate the complexity of genotype-specific responses. The decrease in Chl-b content in Messenger and Tyson under 10 mM acetic acid and significant reductions under 20 mM acetic acid and PEG treatments suggest a similar sensitivity to stress as seen with Chl-a content. However, the substantial increase in Chl-b content in Tyson under combined acetic acid and PEG treatments (146.6% for 10 mM acetic acid and 114.7% for 20 mM acetic acid) highlights the potential of acetic acid to mitigate PEG-induced stress more effectively in this genotype. In GSS 8529, the increase in Chl-b content across all treatments reinforces its resilience and ability to modulate chlorophyll production under stress. This genotype-specific response underscores the role of genetic factors in determining stress tolerance and the capacity to maintain or enhance photosynthetic pigments under adverse conditions.

The total carotenoid content results explain the protective responses of different genotypes to water deprivation. The decrease in total carotenoids in Messenger (38.6% for 10 mM acetic acid, 50.6% for 20 mM acetic acid, and 32.2% for PEG) suggests a decline in

photosynthetic activity or increased chlorophyll degradation (Khoyerdi et al., 2016). Conversely, the increase in total carotenoids in Tyson (1.9% under 10 mM acetic acid, 9.6% under 20 mM acetic acid, and 55.5% under PEG treatment) and GSS 8529 (16.4% for 10 mM acetic acid, 22.7% for 20 mM acetic acid, and 34.3% for PEG) under acetic acid and PEG treatments indicates a protective mechanism against oxidative stress, as carotenoids are known to protect thylakoid membranes and photosystems (Latowski et al., 2011). However, like Tyson, a decrease was noted under combined acetic acid and PEG treatments compared to PEG alone, indicating a complex interaction that might lead to stress-induced pigment degradation or impaired pigment synthesis under combined conditions (Rehman et al., 2019b).

Table 7. Effect of foliar spray of acetic acid on photosynthetic pigments (mg g^{-1}) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Messenger	Tyson	GSS 8529
Chlorophyll- a	Control	13.69^{aA}	12.95^{aB}	9.83^{aC}
	10 mM acetic acid	12.17^{bA}	10.13^{cB}	11.81^{aA}
	20 mM acetic acid	10.14^{cB}	10.16^{cB}	12.49^{aA}
	5% PEG (Water deficit control)	12.50^{bA}	7.93^{dB}	12.38^{aA}
	10 mM acetic acid + 5% PEG	12.00^{bA}	13.37^{aA}	12.19^{aA}
	20 mM acetic acid + 5% PEG	12.47^{bA}	11.61^{bA}	11.75^{aA}
Chlorophyll- b	Control	5.89^{aA}	6.48^{aA}	2.93^{aB}
	10 mM acetic acid	5.19^{abA}	3.32^{cB}	3.60^{aB}
	20 mM acetic acid	3.03^{cB}	3.156^{cB}	4.05^{aA}
	5% PEG (Water deficit control)	4.29^{bcA}	1.91^{dB}	3.98^{aA}
	10 mM acetic acid + 5% PEG	3.82^{bcA}	4.71^{bA}	3.95^{aA}
	20 mM acetic acid + 5% PEG	4.45^{abcA}	4.10^{bcA}	4.29^{aA}
Total carotenoids	Control	3.89^{aA}	2.09^{cB}	2.07^{aB}
	10 mM acetic acid	2.39^{bA}	2.13^{cA}	2.41^{aA}
	20 mM acetic acid	1.92^{bB}	2.29^{bcA}	2.54^{aA}
	5% PEG (Water deficit control)	2.62^{bA}	3.25^{aA}	2.78^{aA}
	10 mM acetic acid + 5% PEG	2.50^{bA}	2.93^{abA}	2.64^{aA}
	20 mM acetic acid + 5% PEG	2.59^{bA}	2.49^{bcA}	2.58^{aA}

The results demonstrate significant genotype-dependent responses to treatments, highlighting the intricate relationship between stress conditions and xanthophyll

accumulation (Fig. 4). In Messenger, xanthophyll content decreased under individual application of acetic acid (10.0% with 10 mM and 24.6% with 20 mM) and in PEG (11.1%) treatment, compared to the control, suggesting an adverse impact on xanthophyll synthesis or stability under these conditions. However, when combined with PEG, acetic acid treatments improved xanthophyll content by 4.2% (10 mM) and 12.3% (20 mM) compared to PEG alone. This indicates that acetic acid may play a role in improving xanthophyll synthesis or protecting against degradation under water deprivation, potentially through mechanisms that stabilize chloroplasts or improve antioxidant capacity (Latowski et al., 2011). Genotype Tyson recorded a decrease in xanthophyll content under 10 mM acetic acid (3.3%) and PEG (12.8%), suggesting a sensitivity to these treatments that might result in reduced xanthophyll synthesis or increased degradation. However, the combination of acetic acid with PEG increased xanthophyll content by 49.2% (10 mM) and 38.5% (20 mM) compared to PEG alone, emphasizing a pronounced protective effect of acetic acid in this genotype. These findings suggest that acetic acid can alleviate the adverse effects of water deprivation on xanthophyll levels, possibly by enhancing the plant's antioxidant defenses or maintaining the structural integrity of chloroplasts (Khoyerdi et al., 2016). GSS 8529, on the other hand, showed an increase in xanthophyll content under all treatments. Acetic acid treatments led to increases of 8.4% (10 mM) and 2.4% (20 mM), and PEG treatment increased 34.3% compared to the control. Under combined treatments with acetic acid and PEG, xanthophyll content increased, indicating a robust response to both individual and combined treatments. The ability of the genotype to accumulate more xanthophylls under stress suggests an inherent resilience, possibly due to efficient mechanisms for xanthophyll synthesis or enhanced antioxidative capabilities that protect against stress-induced damage (Muller and Conklin, 2002).

These results indicate the significant variation in xanthophyll accumulation responses among the sweet corn genotypes under similar treatments. While Messenger and Tyson showed decreases in xanthophyll content under individual treatments, GSS 8529 demonstrated an ability to increase xanthophyll levels, indicating superior stress resilience. The combination of acetic acid with PEG significantly improved xanthophyll content in all genotypes, suggesting that acetic acid may enhance the protective role of xanthophylls under water deprivation conditions.

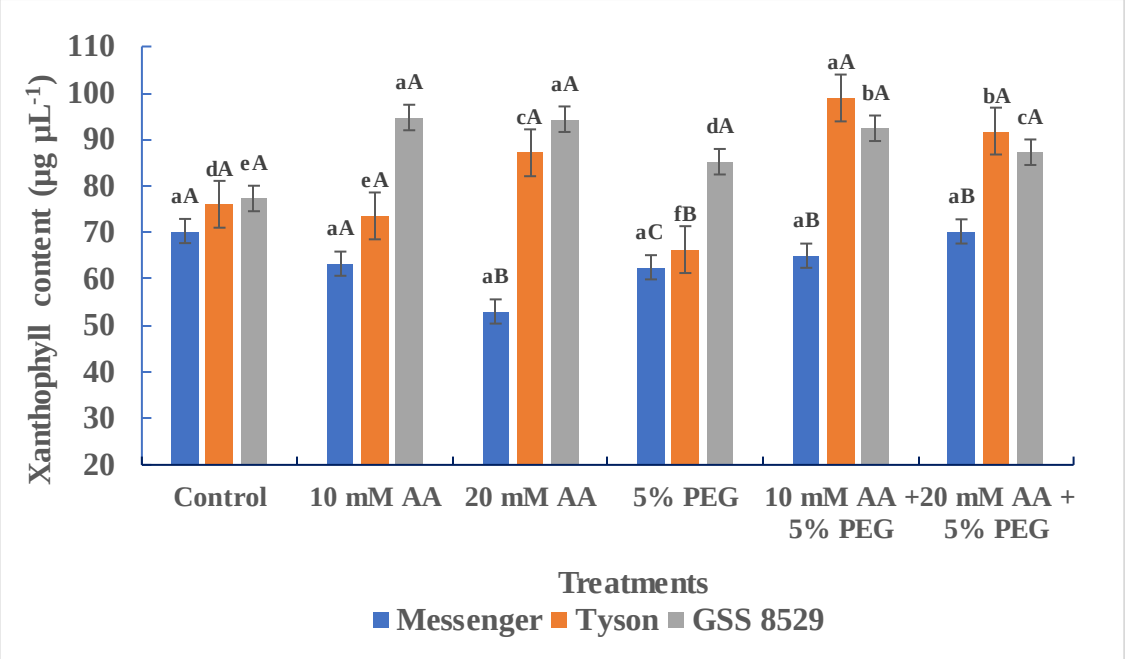


Figure 4. Effect of foliar spray of acetic acid (AA) on xanthophyll content (µg µL^{-1}) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.2.2 Stomatal Conductance and Chlorophyll Fluorescence Dynamics

The results suggest significant genotype-specific responses to applied treatments, highlighting variations in how each genotype manages water loss and gas exchange under stress conditions (Table 8). When treated with 10 mM acetic acid, stomatal conductance recorded a reduction in Messenger and Tyson, while GSS 8529 showed a slight increase of 10.6%. This indicates that acetic acid can have a differential impact on stomatal behavior depending on the genotypes, potentially due to differences in their physiological mechanisms for regulating water loss and maintaining internal water balance (Li et al., 2021). In contrast, treatment with 20 mM acetic acid resulted in an 86.3% increase in stomatal conductance in Messenger, suggesting a potential enhancement in gas exchange and water regulation under higher acetic acid concentration. However, a decrease in stomatal conductance was observed in Tyson and GSS 8529, indicating a reduction in water loss through stomatal closure as a response to higher acetic acid levels (Rehman et al., 2019a). Under water deprivation induced by 5% PEG, a significant decrease in stomatal conductance was recorded across all genotypes, with reductions of 67.2% in Messenger, 85.3% in Tyson, and 28.9% in GSS 8529. This reduction reflects a typical plant response to drought stress,

where stomata are close to minimizing water loss, consequently reducing carbon dioxide intake and negatively impacting photosynthesis (Farooq et al., 2009). The pronounced decrease in Tyson indicates a stomatal closure response, which might be part of its adaptive strategy to conserve water under severe stress conditions.

In combination with acetic acid and PEG treatments, significant increases in stomatal conductance were recorded in Messenger and Tyson. With 10 mM acetic acid combined with PEG, there was a significant increase of 321.4% in Messenger and 265.8% in Tyson compared to PEG treatment alone, suggesting that acetic acid can alleviate the restrictive effects of water deprivation on stomatal conductance, possibly by enhancing stomatal opening or improving osmotic balance within the plant. Similar increases were noted with 20 mM acetic acid and PEG treatment, with 105% in Messenger and 96.1% in Tyson, further indicating the ameliorative role of acetic acid under combined treatments. Conversely, in GSS 8529, a decrease in stomatal conductance was observed under the combined treatment with 20 mM acetic acid and PEG compared to PEG alone, indicating that in this genotype, higher acetic acid concentrations under water deprivation may lead to further reduction in water loss, possibly as a protective mechanism against excessive transpiration. Previous research also recorded reduced stomatal conductance on acetic treatment in mung beans and cotton plants (Rehman et al., 2019a; Li et al., 2021).

Table 8. Effect of foliar spray of acetic acid on stomatal conductance (mmol H_2O m^{-2} s^{-1}) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes		
	Messenger	Tyson	GSS 8529
Control	18.80^{cB}	32.80^{aA}	15.33^{aC}
10 mM acetic acid	7.77^{eC}	11.03^{cB}	16.96^{aA}
20 mM acetic acid	35.03^{aA}	9.80^{dB}	7.98^{cB}
5% PEG (Water deficit control)	6.17^{fB}	4.83^{eC}	10.90^{bA}
10 mM acetic acid + 5% PEG	26.00^{bA}	17.67^{bB}	10.33^{bC}
20 mM acetic acid + 5% PEG	12.70^{dA}	9.47^{dB}	5.80^{dC}

The chlorophyll fluorescence parameters studied include the actual photochemical efficiency of photosystem II ($\Delta F/Fm'$), also known as yield, potential photosynthetic capacity (Fv/Fo), and maximum photochemical efficiency of PSII (Fv/Fm), all of which are essential indicators of photosynthetic efficiency and plant stress tolerance (Krause and

Weiss, 1991; Percival and Sheriffs, 2002) (Table 9). Studies have shown that these parameters strongly correlate with whole-plant mortality in response to environmental stresses and are reliable stress indicators (Hakam et al., 2000; Percival and Sheriffs, 2002; Krause and Weiss, 1991).

Actual Photochemical Efficiency of Photosystem II ($\Delta F/Fm'$): The genotypes showed different responses to the treatments regarding actual photochemical efficiency ($\Delta F/Fm'$). In Messenger and GSS 8529, no significant differences were recorded across all treatments. This suggests that these genotypes maintain a consistent PSII efficiency, regardless of acetic acid or PEG application. Nevertheless, in Tyson, there were notable increases in $\Delta F/Fm'$ when exposed to 10 mM acetic acid (6.2%) and 20 mM acetic acid (5.1%) compared to the control. In addition, a study found that when 10 mM acetic acid was combined with PEG treatment, there was a 3.1% increase in PSII efficiency compared to PEG treatment alone. This suggests that acetic acid may improve energy conversion efficiency within the photosynthetic apparatus, particularly under water deprivation.

Potential Photosynthetic Capacity (Fv/Fo): Potential photosynthetic capacity (Fv/Fo) also showed significant responses to treatments, indicating the ability of genotypes to maintain or improve photosynthetic potential under stress. Messenger recorded a 16.3% increase with 10 mM acetic acid, while Tyson recorded a 19.3% increase with the same treatment. Under PEG treatment alone, Fv/Fo increased by 34.7% in Tyson, but this increase dropped slightly to 30% with the combined treatment of 10 mM acetic acid and PEG. In GSS 8529, an increase of 7.7% in Fv/Fo was recorded with the combined treatment of 20 mM acetic acid and PEG compared to PEG alone, suggesting a slight enhancement in potential photosynthetic efficiency under combined treatments.

Maximum Photochemical Efficiency (Fv/Fm): The maximum photochemical efficiency (Fv/Fm) varied among the different genotypes in response to the treatments. In Messenger, there was a 3.3% increase in Fv/Fm with 10 mM acetic acid and a 4.4% increase with PEG. However, when 10 mM acetic acid and PEG were combined, there was a slight decrease of 1.3% compared to PEG alone. Acetic acid can improve PSII efficiency, but the combination with PEG may not consistently produce additional benefits. Tyson exhibited slight variations in Fv/Fm, except for a 2.7% increase with 20 mM acetic acid and an 8.1% increase with PEG. These findings suggest a moderate enhancement in PSII efficiency when exposed to higher concentrations of acetic acid and water deprivation. The GSS 8529 consistently

recorded increases in all treatments, with rises of 2.2%, 3.9%, and 4.0% for 10 mM acetic acid, 20 mM acetic acid, and PEG, respectively. There were slight improvements observed when the treatments were combined, compared to using PEG alone, suggesting that photosynthetic efficiency remains robust even under stressful conditions.

Table 9. Effect of foliar spray of acetic acid on actual photochemical efficiency of photosystem II ($\Delta F/Fm'$), potential photosynthetic capacity (Fv/Fo), maximum photochemical efficiency (Fv/Fm) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Genotypes		
		Messenger	Tyson	GSS 8529
$\Delta F/Fm'$	Control	0.73^{aAB}	0.71^{cB}	0.75^{aA}
	10 mM acetic acid	0.74^{aA}	0.75^{abA}	0.74^{aA}
	20 mM acetic acid	0.74^{aA}	0.75^{abA}	0.74^{aA}
	5% PEG (Water deficit control)	0.74^{aA}	0.73^{bA}	0.73^{aA}
	10 mM acetic acid + 5% PEG	0.75^{aA}	0.76^{aA}	0.75^{aA}
	20 mM acetic acid + 5% PEG	0.74^{aA}	0.75^{abA}	0.73^{aA}
Fv/F0	Control	3.38^{bA}	3.00^{aA}	3.16^{cA}
	10 mM acetic acid	3.93^{aA}	3.58^{aB}	3.44^{bcB}
	20 mM acetic acid	3.46^{bA}	3.23^{aA}	3.72^{abA}
	5% PEG (Water deficit control)	4.13^{aA}	4.04^{aA}	3.73^{abB}
	10 mM acetic acid + 5% PEG	3.86^{aA}	3.90^{aA}	3.93^{aA}
	20 mM acetic acid + 5% PEG	4.11^{aA}	3.75^{aA}	4.02^{aA}
Fv/Fm	Control	0.77^{bA}	0.74^{aA}	0.76^{aA}
	10 mM acetic acid	0.80^{aA}	0.75^{aA}	0.77^{abA}
	20 mM acetic acid	0.78^{bA}	0.76^{aA}	0.79^{bcA}
	5% PEG (Water deficit control)	0.81^{aA}	0.80^{aA}	0.79^{bcB}
	10 mM acetic acid + 5% PEG	0.79^{aA}	0.80^{aA}	0.80^{cA}
	20 mM acetic acid + 5% PEG	0.80^{aA}	0.89^{aA}	0.80^{cA}

4.3 Oxidative Stress and Antioxidant Enzyme Activity under Acetic Acid Treatment

4.3.1 Lipid Peroxidation Assessed via Malondialdehyde Levels

Malondialdehyde, a byproduct of lipid peroxidation, is widely known as a reliable marker for oxidative stress in plants (Sairam et al. 2000). MDA increased in all three genotypes,

Messenger, Tyson, and GSS 8529, by 6.3%, 14.0% and 3.2%, respectively, compared to the control under 10mM acetic acid foliar spray (Fig. 5). 20 mM acetic acid increased MDA in Messenger and GSS 8529 by 5.4% and 3.6%, respectively, but decreased in Tyson by 9.2% compared to control. Under PEG-induced water deprivation, MDA accumulation increased in all genotypes (Messenger, Tyson, and GSS 8529, by 36.1%, 27.5% and 18.5%, respectively), compared to control indicating the rise of reactive oxygen species under stress and oxidative damage. Treatment with acetic acid resulted in a decrease in MDA accumulation under water deprivation, resulting in a reduction of reactive oxygen species and subsequently reduced MDA accumulation. Combining 10 mM acetic acid with 5% PEG reduced MDA by 10.7%, 32.4% and 10.4%, respectively, in Messenger, Tyson and GSS 8529 compared to PEG. 20 mM acetic acid with 5% PEG reduced MDA by 10.6%, 31.6% and 9.7% compared to the 5% PEG treatment in Messenger, Tyson, and GSS 8529.These results align with the previous study in soyabean where acetic acid reduced the MDA levels under drought stress by increase in the activity of antioxidant enzymes (Rehman et al., 2020).

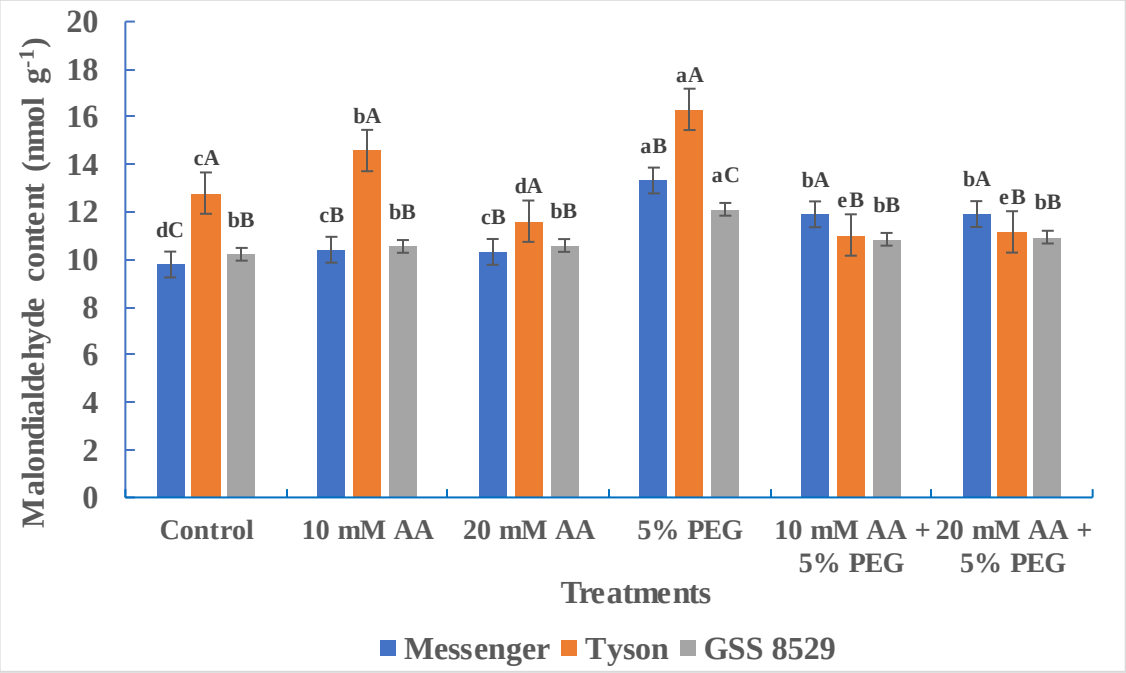


Figure 5. Effect of foliar spray of acetic acid on malondialdehyde content (nmol g^{-1}) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.3.2 Peroxidase Enzymatic Activity

Peroxidase (POD) is an essential antioxidant enzyme that mitigates oxidative stress and counteracts reactive oxygen species (ROS). The peroxidase activity increased in all genotypes under water deprivation, with an increase of 18.1% in Messenger, 51.0% in Tyson, and 13.5% in GSS 8529. This indicates a robust antioxidant reaction to regulate oxidative damage caused by increased amounts of reactive oxygen species (ROS), which is consistent with previous study during water stress (Srivalli et al., 2003; Kukreja et al., 2005). The genotypes Tyson and GSS 8529, when treated with acetic acid alone, exhibited increased peroxidase (POD) activity at concentrations of 10 mM and 20 mM. This indicates that acetic acid may improve the antioxidant defenses in these genotypes. Conversely, in genotype Messenger POD activity dropped when treated with acetic acid, suggesting a possible decrease in the enzyme's activity. The same trend was reported in soybean (Rehman et al., 2020). Under water deprivation, the activity of POD was found to be decreased in the presence of 10 mM and 20 mM acetic acid in Messenger, however, Tyson and GSS 8529 exhibited 20.9% and 91.7% respectively increase in peroxidase (POD) activity when exposed to 20 mM acetic acid during water deprivation. This suggests that these genotypes had an improved ability to reduce oxidative stress. The results highlight the potential of acetic acid to regulate stress responses and enhance resilience in different sweet corn genotypes additionally; they emphasize the intricate and genotype-specific impacts of water deprivation and acetic acid on the activity of antioxidant enzymes (Table 10).

Table 10. Effect of foliar spray of acetic acid on peroxidase activity (µmol min^{-1} g^{-1}) of three sweet corn genotypes under water deprivation. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes		
	Messenger	Tyson	GSS 8529
Control	50.56^{cA}	20.69^{dC}	23.78^{dB}
10 mM acetic acid	44.69^{eA}	31.56^{bC}	34.76^{bB}
20 mM acetic acid	44.61^{eA}	29.35^{cC}	33.37^{bB}
5% PEG (Water deficit control)	59.71^{aA}	31.25^{bcB}	26.98^{cC}
10 mM acetic acid + 5% PEG	48.30^{dA}	19.03^{dC}	32.90^{bB}
20 mM acetic acid + 5% PEG	54.76^{bA}	37.78^{aB}	51.72^{aA}

4.4 Morphophysiological Responses to Melatonin under Water Deficit

4.4.1 Modulation of Root and Shoot Length Parameters

The statistical analysis of shoot and root length across four sweet corn genotypes (Dessert, Messenger, Tyson, and Royalty) recorded a significant variation in response to treatments involving melatonin and polyethylene glycol (PEG), indicating a pronounced effect of water deprivation and the alleviative potential of melatonin (Table 11,12). The application of melatonin significantly enhanced shoot length in the Dessert genotypes by 6.7% compared to the control, while PEG treatments reduced shoot length substantially, with an 8% PEG treatment causing a 10.5% reduction and a 12% PEG treatment resulting in a 50.6% decrease. However, melatonin mitigated the negative effects of PEG, increasing shoot length by 16.2% under 8% PEG and 70.1% under 12% PEG conditions. This trend was consistent across all genotypes, with melatonin improving shoot length despite PEG-induced water deprivation. For instance, in Messenger, melatonin under 8% PEG led to a 27.9% increase in shoot length, although a marginal decrease was observed with 12% PEG. Similarly, in Tyson and Royalty, melatonin applications resulted in significant shoot length increases of 28.8% and 69.1% under 8% and 12% PEG for Tyson and 34.9% and 76.6% for Royalty, respectively.

Table 11. Effect of melatonin and PEG treatments on average shoot length (cm) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes			
	Dessert	Messenger	Tyson	Royalty
Control	95.00^{dA}	91.33^{dB}	87.33^{dC}	61.50^{cD}
MEL	101.33^{fA}	86.00^{cC}	89.44^{dB}	66.67^{cD}
8% PEG	85.00^{cA}	74.00^{bB}	46.33^{bC}	36.07^{aD}
12% PEG	46.96^{aB}	67.33^{aA}	35.67^{aC}	29.92^{aD}
8% PEG + MEL	98.80^{eA}	94.67^{eA}	59.67^{cB}	48.67^{bC}
12% PEG + MEL	79.90^{bA}	65.67^{aB}	60.33^{cC}	52.83^{bD}

Root length analysis revealed that melatonin increased root growth across all genotypes. In the Dessert, root length improved by 19.5% with melatonin treatment, while PEG treatments induced a reduction of 21.8% (8% PEG) and 49.6% (12% PEG). However, applying melatonin in PEG treatments significantly mitigated these reductions, with root lengths increasing by 21.5% under 8% PEG and 75.3% under 12% PEG. Messenger, Tyson, and

Royalty genotypes also exhibited improved root lengths with melatonin, although the extent of improvement differed. For instance, in Messenger, root length increased by 32.6% and 32.5%, with melatonin under 8% and 12% PEG, respectively. Tyson, however, showed significant mitigation only under 8% PEG, with no significant difference under 12% PEG, suggesting a genotype-specific response. Royalty also recorded increased root lengths of 10.5% and 22%, with melatonin under 8% and 12% PEG, respectively.

The recorded varied responses across genotypes can be attributed to genetic diversity and inherent variability in stress tolerance and melatonin metabolism, as reported by Krasensky and Jonak, (2012). The role of melatonin in improving plant tolerance to osmotic stress by improving antioxidant defenses and cell membrane stability has been well-documented (Li et al., 2012), aligning with our findings of improved root and shoot growth. Furthermore, the interaction of melatonin with auxin signaling pathways, crucial for root development, supports the observed increase in root lengths, particularly in the Dessert genotype, as reported by Zhang et al. (2013). The adverse impact of water deprivation on shoot and root lengths, leading to reduced cell expansion and dehydration, aligns with the findings of Verslues et al. (2006). However, the mitigative effects of melatonin across treatments underscore its potential to enhance plant resilience to abiotic stress by maintaining cell integrity and supporting growth under unfavorable conditions, consistent with the study by Li et al. (2015).

Table 12. Effect of melatonin and PEG treatments on average root length (cm) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes			
	Dessert	Messenger	Tyson	Royalty
Control	55.34^{eB}	57.36^{dB}	55.00^{dB}	87.00^{bcA}
MEL	66.00^{fB}	58.79^{eC}	56.67^{dC}	97.00^{cA}
8% PEG	43.30^{bB}	42.85^{cB}	44.67^{bB}	73.00^{abA}
12% PEG	27.90^{aB}	31.43^{aB}	34.33^{aB}	61.33^{aA}
8% PEG + MEL	52.60^{dC}	56.80^{dB}	49.98^{cC}	80.67^{bA}
12% PEG + MEL	48.90^{cB}	41.63^{bC}	32.89^{aD}	74.83^{abA}

4.4.2 Root Volume and Biomass Allocation Adjustments

The analysis of root volume in sweet corn genotypes under melatonin and PEG treatments revealed significant interactions, highlighting the role of melatonin in mitigating the effects

of water deprivation (Table 13). Individual treatment with Melatonin reduced root volume under normal conditions, with significant decreases in Dessert (18.4%) and Tyson (22.6%). However, melatonin notably increased root volume under water deprivation, reversing the substantial reductions caused by water deficit. For example, melatonin improved root volume in Dessert by 38.9% under 8% PEG and 171.6% under 12% PEG. In Messenger, melatonin under 8% and 12% PEG increased root volume by 122.9% and 116.8%, respectively, despite significant water deficit-induced reductions. Tyson, sensitive to PEG, showed 72.9% and 100% increases in root volume under 8% and 12% PEG with melatonin. Royalty recorded the most significant melatonin-induced increases, improving root volume by 116.7% under 8% PEG and 219.9% under 12% PEG. These findings suggest that melatonin enhances root growth under stress by improving water retention and osmotic balance (Arnao and Hernández, 2017; Tan et al., 2012), with genotype-specific responses potentially due to genetic diversity (Krasensky and Jonak, 2012).

Table 13. Effect of melatonin and PEG treatments on average root volume (cm^3) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes			
	Dessert	Messenger	Tyson	Royalty
Control	9.67^{cdB}	9.50^{dB}	13.33^{dA}	6.33^{bC}
MEL	7.89^{bcA}	9.51^{dA}	10.32^{cA}	11.67^{cA}
8% PEG	7.56^{bA}	4.49^{bB}	3.99^{aB}	2.00^{aB}
12% PEG	2.39^{aA}	2.78^{aA}	1.50^{aB}	1.67^{aB}
8% PEG + MEL	10.50^{dA}	10.00^{dA}	6.90^{bB}	4.33^{abB}
12% PEG + MEL	6.50^{bA}	6.03^{cA}	3.00^{aB}	5.33^{abAB}

The analysis of fresh and dry root-shoot weights under melatonin and PEG-induced water deprivation in four sweet corn genotypes (Dessert, Messenger, Tyson, and Royalty) revealed significant interactions and varied responses. Melatonin alone generally decreased fresh root weights but significantly increased under water deprivation, particularly in the Dessert genotype, where it mitigated PEG-induced reductions by 49.7% under 8% PEG and 88.0% under 12% PEG. This aligns with Arnao and Hernández (2015), who noted the role of melatonin in alleviating water deprivation by improving water retention and osmotic balance. Messenger and Tyson also recorded substantial increases in fresh root weights under water deprivation, with Tyson displaying a significant 421.2% increase under 12%

PEG, highlighting the potential of melatonin in stress adaptation, as suggested by Zhang et al. (2013). Royalty recorded a 71.4% increase under 12% PEG despite a decrease with melatonin alone, indicating genetic variability in response to melatonin (Hardeland, 2016).

Table 14. Effect of melatonin and PEG treatments on average fresh root and shoot weight (g) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Genotypes			
		Dessert	Messenger	Tyson	Royalty
Fresh root weight	Control	11.07^{dC}	13.03^{dB}	15.46^{cA}	15.34^{cA}
	MEL	9.11^{cB}	15.42^{eA}	18.30^{dA}	10.84^{bcB}
	8% PEG	5.90^{bA}	8.74^{cA}	8.54^{bA}	8.40^{abA}
	12% PEG	3.33^{aB}	4.16^{aA}	1.89^{aC}	3.78^{aAB}
	8% PEG + MEL	8.83^{cBC}	12.99^{dAB}	14.30^{cA}	6.65^{abC}
	12% PEG + MEL	6.27^{bB}	6.95^{bB}	9.85^{bA}	6.48^{abB}
Fresh shoot weight	Control	36.71^{cdB}	35.53^{eB}	40.29^{eA}	25.20^{bC}
	MEL	38.60^{dA}	27.88^{dB}	35.77^{dA}	40.97^{cA}
	8% PEG	22.54^{bB}	22.81^{cB}	26.44^{bA}	19.56^{abC}
	12% PEG	12.80^{aA}	11.32^{aA}	4.43^{aB}	13.12^{aA}
	8% PEG + MEL	34.56^{cA}	27.32^{dAB}	31.32^{cA}	20.00^{abB}
	12% PEG + MEL	24.90^{bA}	14.71^{bC}	8.21^{aD}	19.83^{abB}

For fresh shoot weights, melatonin improved weight under water deprivation in all genotypes, with significant increases in Dessert (94.5% under 12% PEG) and Tyson (85.3% under 12% PEG) (Table 15). This is consistent with Li et al. (2015), who reported that melatonin enhances plant tolerance to drought by bolstering antioxidant defenses and improving cell stability. Messenger and Royalty also benefited significantly, although Royalty recorded a decrease under normal conditions. Melatonin's role in mitigating water deprivation was evident across all genotypes, enhancing root and shoot weights and indicating improved stress resilience, supporting findings by Tan et al. (2012).

Likewise, dry root and shoot weights improved under melatonin treatment in water-deficit conditions. Dessert recorded a substantial increase in dry root weight by 307.1% under 8% PEG, and dry shoot weight also increased significantly. Tyson, most susceptible to water deprivation, recorded a significant recovery with melatonin, particularly in dry root weight (274.2% under 12% PEG), consistent with findings by Arnao and Hernández, (2017). Messenger and Royalty also exhibited notable improvements, confirming melatonin's role

in stress mitigation and aligning with research by Li et al. (2015) that melatonin helps maintain cellular integrity under stress.

Table 15. Effect of melatonin and PEG treatments on average dry root and shoot weight (g) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Genotypes			
		Dessert	Messenger	Tyson	Royalty
Dry root weight	Control	0.98^{cBC}	1.56^{bAB}	0.66^{eC}	1.94^{bA}
	MEL	1.42^{dA}	1.67^{bA}	0.59^{deB}	0.54^{aB}
	8% PEG	0.29^{aB}	0.61^{aA}	0.26^{abB}	0.24^{aB}
	12% PEG	0.17^{aB}	0.34^{aA}	0.12^{aB}	0.19^{aB}
	8% PEG + MEL	0.89^{cB}	1.63^{bA}	0.37^{bcC}	0.35^{aC}
	12% PEG + MEL	0.52^{bA}	0.59^{aA}	0.44^{cdAB}	0.36^{aB}
Dry shoot weight	Control	4.56^{cdA}	2.08^{bB}	4.66^{cA}	4.69^{cA}
	MEL	4.74^{dB}	2.11^{bB}	6.44^{dA}	3.55^{bBC}
	8% PEG	2.84^{bA}	1.08^{aB}	2.44^{bA}	1.93^{aAB}
	12% PEG	1.20^{aA}	0.98^{aA}	0.28^{aA}	0.95^{aA}
	8% PEG + MEL	5.79^{dA}	2.16^{bC}	4.34^{cB}	1.74^{aC}
	12% PEG + MEL	3.15^{bcA}	1.14^{aB}	0.28^{aB}	1.48^{aB}

4.4.3 Regulation of Specific Leaf Area and Relative Chlorophyll Content

The result analysis of specific leaf area (SLA) under melatonin and PEG-induced water deprivation across the sweet corn genotypes: Dessert, Messenger, Tyson, and Royalty showed significant genotype-specific responses and notable differential effects (Table 16). The treatment with melatonin under non-stress conditions resulted in a slight decrease in SLA for Dessert (2.3%) and Tyson (5.9%), suggesting a minor impact on leaf morphology under normal conditions. Conversely, in genotypes Messenger and Royalty showed increases in SLA by 6.1% and 9.3%, respectively, indicating that melatonin may enhance leaf area or leaf thickness, potentially improving light capture and water retention in these genotypes (Arnao and Hernández, 2015).

Underwater deprivation induced by PEG, a consistent trend of decreased SLA was recorded across all genotypes, with reductions being more pronounced at higher PEG concentration. For example, in the Tyson genotype, SLA dropped significantly by 55.5% with 8% PEG and 73.8% with 12% PEG, indicating a high susceptibility to water deprivation. This aligns with studies showing that osmotic stress reduces leaf expansion to conserve water (Altaf et al.,

2022). Messenger and Royalty also experienced considerable reductions in SLA under 8% and 12% PEG treatments, illustrating their vulnerability to water-deficit conditions.

However, the application of melatonin under water deprivation recorded a substantial ameliorative effect, significantly increasing SLA across all genotypes. Notably, in the Dessert genotype, melatonin combined with 12% PEG resulted in a significant 224.2% increase in SLA, while Messenger recorded a 121.8% increase under similar conditions. This suggests the role of melatonin in improving leaf expansion and water retention under stress (Tiwari et al., 2021). Despite being the most susceptible to water deprivation, Tyson showed the highest SLA improvement with melatonin treatment, increasing 77.2% under 8% PEG and an impressive 224.6% under 12% PEG. Royalty also recorded a significant SLA increase of 94.6% under 8% PEG and 124.7% under 12% PEG, indicating melatonin's broad efficacy in dealing with water deprivation by enhancing leaf morphology and functionality (Zhang et al., 2013).

Table 16. Effect of melatonin and PEG treatments on average specific leaf area ($cm^2\ g^{-1}$) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Treatment	Genotypes			
	Dessert	Messenger	Tyson	Royalty
Control	69.22^{cA}	68.14^{dA}	75.72^{cA}	91.41^{eA}
MEL	67.63^{cA}	72.29^{eA}	71.29^{cA}	99.88^{fA}
8% PEG	58.77^{bA}	52.53^{bAB}	33.71^{abC}	38.77^{bBC}
12% PEG	44.05^{aA}	32.16^{aB}	19.85^{aC}	28.24^{aB}
8% PEG + MEL	73.72^{cA}	66.14^{cA}	59.72^{bcA}	75.46^{dA}
12% PEG + MEL	142.81^{dA}	71.32^{eB}	64.44^{bcB}	63.45^{cB}

The analysis of relative chlorophyll content (SPAD) under melatonin and PEG-induced water deprivation across the sweet corn genotypes: Dessert, Messenger, Tyson, and Royalty revealed significant genotype-specific responses and notable differential effects (Fig. 6). Melatonin treatments generally increased SPAD values, suggesting a stabilizing effect on chlorophyll and enhanced photosynthetic performance, except in the Tyson genotype, which showed a 26.6% decrease in SPAD under melatonin alone. This anomaly may reflect complex physiological interactions unique to Tyson, deviating from the typical effects of melatonin in other genotypes (Arnao and Hernández, 2015; Muhammad et al., 2022).

In water deprivation, a significant decrease in SPAD values was observed in all genotypes, with higher PEG concentrations exacerbating the reduction. For instance, 12% PEG in the Dessert reduced SPAD by 48%, whereas 8% PEG led to an 18.7% reduction. Similar trends were observed in Messenger and Royalty, where SPAD values decreased significantly under 12% PEG by 52.1% and 37%, respectively. These findings are consistent with Ashraf and Harris (2013), who reported that osmotic stress reduces chlorophyll content by limiting water availability and hindering photosynthesis.

However, the application of melatonin under water deprivation recorded a substantial ameliorative effect across all genotypes. In Dessert, melatonin increased SPAD values by 27.5% under 8% PEG and by 70.8% under 12% PEG, reflecting the role of melatonin in protecting chlorophyll against oxidative damage and stabilizing photosynthesis under stress (Ahmad et al., 2021; Tan et al., 2012). Messenger recorded similar enhancement, with SPAD increasing by 8.5% under 8% PEG and by 100.8% under 12% PEG, highlighting the potential of melatonin in mitigating stress effects.

In Tyson, despite the initial decrease in SPAD with individual melatonin treatment, the treatment with melatonin under water deprivation led to significant improvements, with SPAD values increasing by 62.8% under 8% PEG and a remarkable 232.5% under 12% PEG. While Tyson is highly susceptible to water deprivation, melatonin effectively enhances chlorophyll content under severe stress conditions (Muhammad et al., 2022). Royalty also exhibited significant increases in SPAD values with melatonin under water deficit, showing a 56.8% increase under 8% PEG and a 50% increase under 12% PEG, which supports the protective role of melatonin in preserving chlorophyll content across varying stress levels (Arnao and Hernández, 2015).

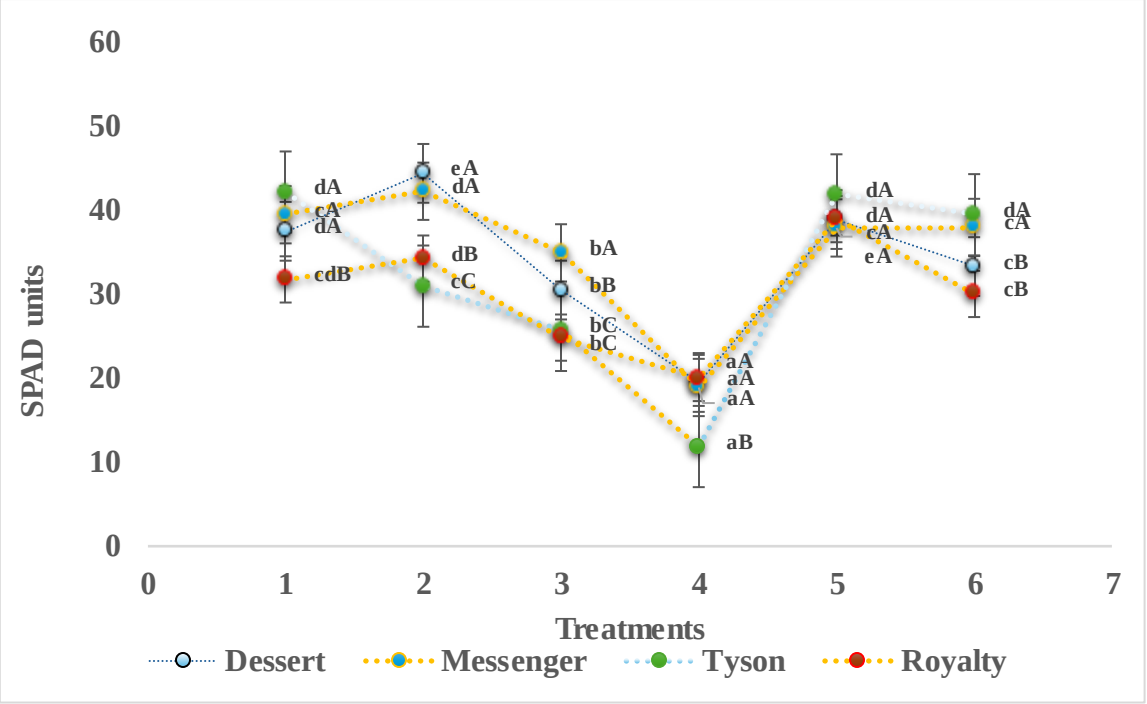


Figure 6. Effect of melatonin and PEG treatments [1(Control), 2 (MEL), 3 (8% PEG), 4 (12% PEG), 5 (8% PEG + MEL), 6 (12% PEG + MEL)] on average relative chlorophyll content (SPAD) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.5 Photosynthetic Pigments and Stomatal Responses to Melatonin under Water Deprivation

4.5.1 Photosynthetic Pigment Analysis: Chlorophyll, Total Carotenoids and Lutein Profiles

The effect of melatonin and PEG-induced water deprivation on chlorophyll-a, chlorophyll-b, and total carotenoid content in sweet corn genotypes: Dessert, Messenger, Tyson, and Royalty recorded significant variations and genotype-specific responses (Table 17). The analysis revealed that melatonin altered pigment concentrations differently across genotypes, highlighting its potential role in enhancing photosynthetic performance and plant resilience under stress.

For chlorophyll-a, individual treatment with melatonin led to a slight decrease of 2.3% in Dessert but increased levels by 9.5% in Tyson, suggesting the stabilizing effect of melatonin on chlorophyll is influenced by the genotypic variations. In contrast, Messenger and Royalty exhibited moderate increases of 4.9% and a decrease of 9.3%, respectively, indicating complex interactions possibly related to genetic differences (Muhammad et al., 2022). Under PEG-induced water deprivation, chlorophyll-a content significantly declined across all

genotypes, particularly with higher PEG concentrations. For instance, 12% PEG was reduced to 33.9% in Dessert, 29.6% in Messenger, 25.9% in Tyson, and 47.1% in Royalty. This highlights the negative effects of water deprivation on chlorophyll synthesis, consistent with findings by Ashraf and Harris, (2013). However, melatonin application under water deficit conditions mitigated these reductions, with notable increases recorded, such as a 27.4% increase in Dessert under 8% PEG and a 31.8% increase in Tyson under 12% PEG, underscoring the protective role of melatonin against chlorophyll degradation (Ahmad et al., 2021).

Regarding chlorophyll-b, melatonin alone decreased content by 24.4% in Dessert but significantly increased it by 37.3% in Messenger, suggesting genotype-dependent responses to melatonin treatment. Tyson recorded a slight decrease of 5.2%, whereas Royalty recorded a significant reduction of 51.2%, suggesting variability in chlorophyll-b regulation among the genotypes (Nawaz et al., 2016). Water deprivation led to substantial reductions in chlorophyll-b across all genotypes, particularly under 12% PEG, with decreases up to 65.5% in Messenger and 57.5% in Tyson, emphasizing the stress-induced inhibition of chlorophyll-b synthesis (Tan et al., 2012). Role of melatonin in ameliorating these effects was evident, with significant increases recorded when combined with PEG treatments. Melatonin treatment increased chlorophyll-b by 160.9% in Messenger under 12% PEG and by 187.0% in Tyson under the same conditions, suggesting its efficacy in enhancing pigment stability under unfavorable conditions (Zhang et al., 2019).

Total carotenoid content recorded varying responses to treatments. Individual treatment with melatonin slightly increased carotenoid levels in Dessert (2.6%) and Messenger (25.3%), while Tyson recorded a 13.3% increase, suggesting a role of melatonin in enhancing carotenoid synthesis and protecting against oxidative damage (Muhammad et al., 2022). Water deprivation caused significant decreases, particularly under 12% PEG, with reductions of 61.2% in Dessert and 60.3% in Tyson, highlighting the detrimental effects of water deprivation on carotenoid content. However, melatonin significantly mitigated these reductions, notably increasing carotenoid content by 44.7% in Dessert under 8% PEG and by 148.3% in Royalty under 12% PEG, supporting the role of melatonin in enhancing the synthesis of protective pigments and mitigating stress-induced damage (Zhang et al., 2019). Among the genotypes, Tyson emerged as the most susceptible to water deprivation, showing the most significant decreases in chlorophyll and carotenoid content under PEG treatments.

However, Tyson also benefited the most from melatonin application, showing the highest increases in pigment content under water deficit conditions. This highlights the critical role of melatonin in improving chlorophyll and carotenoid stability and enhancing photosynthetic efficiency under stress in sweet corn genotypes (Nawaz et al., 2016; Tan et al., 2012).

Table 17. Effect of melatonin and PEG treatments on average photosynthetic pigments (mg g^{-1}) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Genotypes			
		Dessert	Messenger	Tyson	Royalty
Chlorophyll-a	Control	16.32^{eA}	17.10^{deA}	15.08^{bcdB}	14.83^{dB}
	MEL	15.94^{eB}	17.94^{eA}	16.51^{dB}	13.45^{cC}
	8% PEG	11.89^{bB}	13.66^{bA}	13.70^{bA}	9.23^{bC}
	12% PEG	10.79^{aC}	12.04^{aA}	11.17^{aB}	7.85^{aD}
	8% PEG + MEL	15.15^{dAB}	14.59^{cB}	15.45^{cdA}	13.70^{cC}
	12% PEG + MEL	13.73^{cA}	16.48^{dA}	14.72^{bcAB}	15.12^{dAB}
Chlorophyll-b	Control	6.70^{dA}	7.83^{cA}	4.35^{cB}	6.82^{cdA}
	MEL	5.07^{bcB}	10.75^{dA}	4.12^{bcB}	3.33^{aB}
	8% PEG	5.60^{cA}	4.43^{bA}	3.04^{abB}	4.52^{abA}
	12% PEG	4.44^{abB}	2.70^{aC}	1.85^{aC}	7.75^{dA}
	8% PEG + MEL	4.06^{aC}	7.90^{cA}	5.76^{dB}	4.85^{abBC}
	12% PEG + MEL	5.08^{bcB}	7.04^{cA}	5.31^{cdB}	5.27^{bcB}
Total carotenoids	Control	5.42^{dA}	4.07^{bB}	4.42^{dB}	2.49^{bC}
	MEL	5.56^{dA}	5.10^{cA}	5.01^{eA}	3.35^{cB}
	8% PEG	2.10^{aC}	3.98^{bA}	2.92^{bB}	2.84^{bcB}
	12% PEG	2.28^{aB}	3.15^{aA}	1.76^{aC}	1.39^{aD}
	8% PEG + MEL	3.04^{cC}	4.72^{cA}	3.91^{cB}	2.97^{bcC}
	12% PEG + MEL	2.70^{bC}	4.01^{bA}	3.81^{cA}	3.44^{cB}

Lutein content showed a varied response among treatments and genotypes. Melatonin increased lutein content in Dessert (25.0%) and Messenger (30.3%), while a decrease was recorded in Tyson (13.4%) and Royalty (9.6%) under normal conditions. In Dessert and Messenger, lutein content could increase because of melatonin potential in enhancing carotenoid biosynthesis (Arnao and Hernández, 2015; Zhang et al., 2013). The variation among genotypes could be attributed to differences in regulatory mechanisms of antioxidant defenses or secondary metabolites biosynthesis (Foyer and Noctor, 2005; Ashraf, 2010).

Under water deprivation, varied responses were also recorded among genotypes; the increase in lutein content in Messenger 15.6% and 34.8% for 8% and 12% PEG, respectively can be attributed to stress-induced enhancement of the antioxidant defense system (Fig. 7). Moderate PEG-induced stress often leads to upregulation of secondary metabolites like lutein, which function as ROS scavengers, thereby protecting the plant cells from oxidative damage (Farooq et al., 2009; Yang et al., 2014). Combined application of melatonin and water deprivation at a higher concentration of PEG, increased lutein content in Dessert (86.1%), and Tyson (21.1%), suggesting potential of melatonin to further activate stress tolerance mechanisms and antioxidant pathways under high-stress conditions (Zhang et al., 2015; Wei et al., 2015).

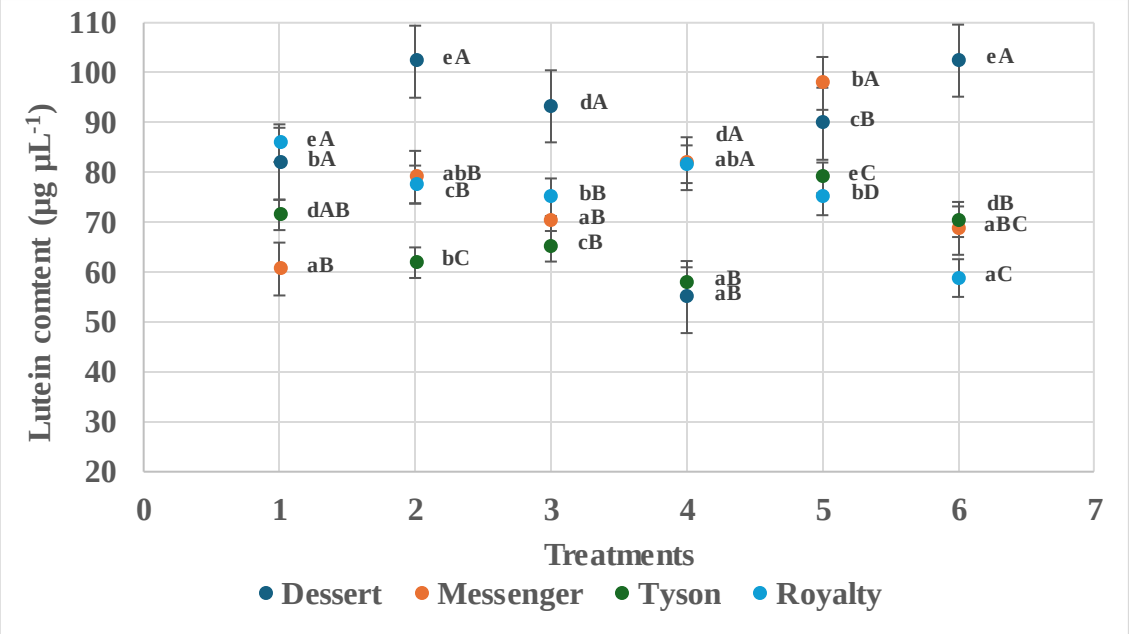


Figure 7. Effect of melatonin and PEG treatments [1(Control), 2 (MEL), 3 (8% PEG), 4 (12% PEG), 5 (8% PEG + MEL), 6 (12% PEG + MEL)] on average lutein (µg μL^{-1}) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.5.2 Stomatal Conductance and Chlorophyll Fluorescence Parameters

Stomatal conductance plays an important role in regulating gas exchange and water loss in plants, and the responses observed indicate a significant impact of melatonin and PEG treatments on stomatal conductance. Statistical analysis of variance about stomatal conductance revealed significant variances in gas exchange across distinct treatments (Fig.

8). Within the Dessert genotype, treatment with melatonin exhibited a increase of approximately 79.1% in stomatal conductance relative to the control. Conversely, PEG concentrations induced declining trends, with 12% PEG showing a substantial decrease of 45.2% and 8% PEG exhibiting a significant reduction of 12.6% compared to the control. The concurrent application of PEG with melatonin demonstrated variable effects, implying a potential ameliorative impact of melatonin on PEG-induced reductions in stomatal conductance. Notably, significant differences were recorded between treatments with 8% PEG and those with 12% PEG, manifesting an increase of approximately 50.7% and 33.1%, respectively, upon the introduction of melatonin.

Converse trends were recorded in the Messenger genotype, where treatment with melatonin exhibited a marginal decrease (approximately 2.5%). In contrast, compared to control, PEG treatments yielded significant decreases in stomatal conductance, by 27.0% and 67.2%, respectively. Concurrent applications with melatonin also yielded mixed effects, suggesting a potential role of melatonin to alleviate PEG-induced water deficit. Significant differences were noted with 8% PEG and 12% PEG, displaying a 15.9% and 139.3% increase upon melatonin application.

In the Tyson genotype, treatment with melatonin increased stomatal conductance by 35.6% compared to the control. However, PEG treatments led to substantial decreases. Stomatal conductance exhibited reductions of 1.8% and 35.8% under 8% and 12% PEG treatments, respectively, compared to the control, suggesting a more pronounced impact of higher PEG concentrations on inhibiting stomatal conductance. Application of melatonin with 8% PEG led to a 27.6% increase in stomatal conductance compared to PEG treatment alone, though a significant increase of 168.4% was recorded in the 12% PEG treatment.

In the Royalty genotype, melatonin treatment enhanced stomatal conductance (by 19.1%); however, like other genotypes, both PEG treatments led to decreased stomatal conductance (16.7% and 21.2%), with significant decreases recorded at higher PEG concentrations compared to the control. Application of melatonin under 8% PEG increased stomatal conductance by 15.1% and 68.3% under the 12% PEG treatment compared to their respective PEG treatments.

Melatonin increased stomatal conductance in Dessert, Tyson and Royalty under normal conditions indicating melatonin potential to promote stomatal openings. This will help plants conduct gas exchange efficiently and enhance photosynthesis even in stressful conditions.

Our results align with a previous study in maize, where melatonin increases stomatal conductance in drought stress by protecting the photosynthetic system and reducing oxidative stress, thus maintaining efficient water use and carbon dioxide uptake (Muhammad et al., 2022). PEG treatment, especially at higher concentrations, significantly decreased stomatal conductance, indicating the impact of water deficit induced by PEG, which mimics the drought by reducing the water potential and forcing plants to close stomata for water conservation. Similar results were recorded under salinity stress, resulting in decreased stomatal conductance to prevent excess water loss (Li et al., 2021). Treatment with melatonin under water deficit enhances stomatal conductance in all genotypes, suggesting melatonin can help efficiently manage water deprivation. Under drought in maize, melatonin enhanced water use efficiency by improving stomatal conductance and photosynthetic capacity (Muhammad et al., 2022). This could be due to the potential of melatonin to upregulate the expression of stress-protective genes or its antioxidant nature, which helps protect stomata under stress.

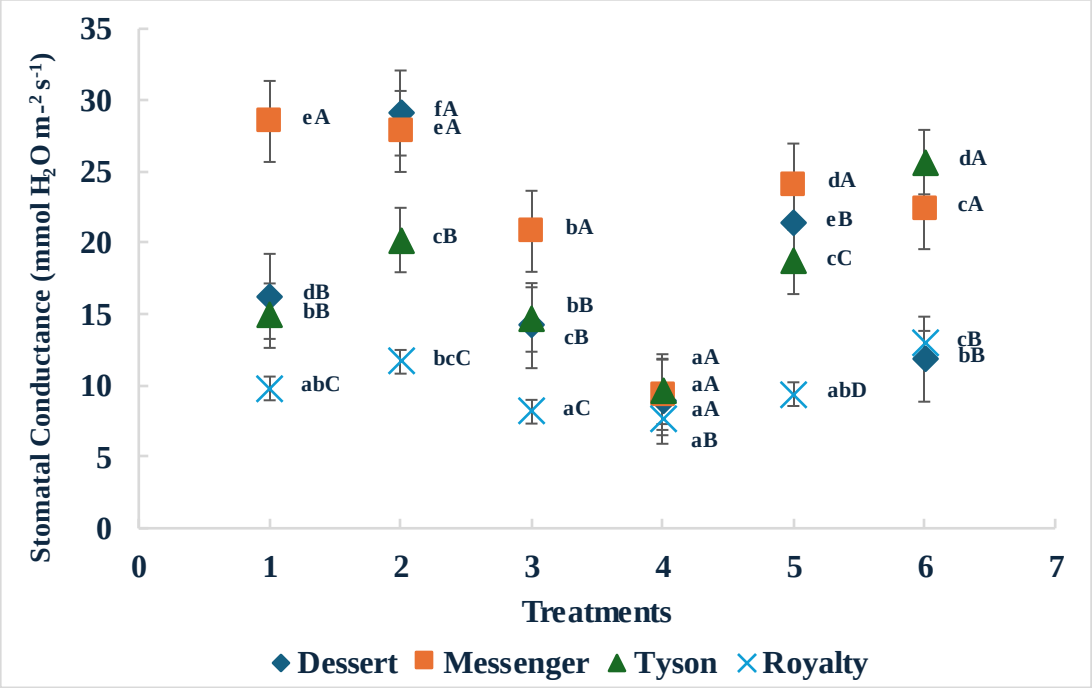


Figure 8. Effect of melatonin and PEG treatments [1(Control), 2 (MEL), 3 (8% PEG), 4 (12% PEG), 5 (8% PEG + MEL), 6 (12% PEG + MEL)] on average stomatal conductance (mmol H_2O m^{-2} s^{-1}) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

This study investigated the effects of melatonin and PEG treatments on maximum photochemical efficiency (Fv/Fm), potential photosynthetic capacity (Fv/F0), and actual photochemical efficiency (Yield/ΔF/Fm') in four genotypes (Dessert, Messenger, Tyson, and Royalty) (Table 18). Melatonin was potentially an ameliorative agent against PEG-induced water deprivation in these genotypes.

The maximum photochemical efficiency (Fv/Fm') recorded a slight increase in the Dessert and Tyson genotypes (1.6% and 3.2%, respectively) on application with melatonin. In contrast, it resulted in a decrease in the Messenger genotype (2.5%) and no effect in Royalty. PEG treatments consistently decreased Fv/Fm across all genotypes, with the most substantial reduction recorded in Tyson (20.4% under 8% PEG and 21.6% under 12% PEG). However, when combined with melatonin, Fv/Fm values increased significantly, suggesting that melatonin mitigates the adverse effects of PEG-induced water deprivation. Tyson, for instance, exhibited a remarkable increase of 29.9% and 26.0% under 8% and 12% PEG, respectively, when treated with melatonin, indicating its higher sensitivity to water deprivation but also pronounced improvement with melatonin treatment.

Potential photosynthetic capacity (Fv/F0) also recorded a similar trend, with melatonin enhancing Fv/F0 in Dessert and Tyson (8.6% and 16.9%, respectively) but decreasing it slightly in Messenger in normal conditions. PEG treatments led to significant decreases in Fv/F0 across all genotypes, with the highest decreases recorded in Tyson (52.8% and 55.9% under 8% and 12% PEG, respectively). Nevertheless, melatonin mitigated these reductions, with Tyson recording an increase in Fv/F0 by 149.2% under 8% PEG and 118.7% under 12% PEG. This suggests that while Tyson is particularly vulnerable to water deprivation, it benefits significantly from melatonin treatment, highlighting the role of melatonin in improving non-photochemical energy dissipation and possibly altering the xanthophyll cycle, as discussed by Maxwell and Johnson, (2000).

Actual photochemical efficiency (Yield/ΔF/Fm') revealed a slight increase in the Dessert genotype with melatonin treatment (0.8%), while the Messenger and Tyson genotypes recorded a decrease (by 6.2% and 11.5%, respectively). PEG treatments caused significant reductions in yield across all genotypes; with Tyson again recording the high sensitivity, (15.9% and 32.9% decreases under 8% and 12% PEG, respectively). However, melatonin application significantly improved yield in the presence of PEG, with Tyson showing an increase of 64.3% under 12% PEG treatment. This aligns with previous findings that

melatonin can enhance mitochondrial electron efficiency in plants (Liu et al., 2015; Wang et al., 2012).

The results suggest that despite being the most susceptible to water deprivation, the Tyson genotype exhibits the highest benefit from melatonin treatment across all measured parameters. Conversely, the Royalty genotype, although showing the least susceptibility to PEG-induced stress, also demonstrated variable responses to melatonin, indicating it may be the most stable under water deficit but less responsive to external ameliorative treatments.

Table 18. Effect of melatonin and PEG treatments on average maximum photochemical efficiency (Fv/Fm), potential photosynthetic capacity (Fv/F0), actual photochemical efficiency (ΔF/Fm') in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Genotypes			
		Dessert	Messenger	Tyson	Royalty
Fv/Fm	Control	0.80^{cA}	0.80^{aA}	0.78^{bA}	0.81^{cA}
	MEL	0.81^{cA}	0.78^{aA}	0.81^{bA}	0.81^{cA}
	8% PEG	0.76^{bA}	0.73^{aA}	0.62^{aA}	0.74^{bA}
	12% PEG	0.71^{aA}	0.71^{aA}	0.61^{aB}	0.64^{aB}
	8% PEG + MEL	0.81^{cA}	0.80^{aA}	0.81^{bA}	0.68^{abB}
	12% PEG + MEL	0.80^{cA}	0.81^{aA}	0.77^{bA}	0.82^{cA}
Fv/F0	Control	3.92^{cA}	3.91^{bcA}	3.63^{bcA}	4.19^{cA}
	MEL	4.25^{cA}	3.67^{bcA}	4.24^{cdA}	4.19^{cA}
	8% PEG	3.18^{bA}	2.96^{abA}	1.71^{aA}	2.81^{bA}
	12% PEG	2.46^{aA}	2.49^{aA}	1.60^{aB}	1.81^{aB}
	8% PEG + MEL	4.34^{cA}	3.97^{bcA}	4.27^{dA}	2.18^{aB}
	12% PEG + MEL	4.06^{cA}	4.34^{cA}	3.50^{bA}	4.41^{cA}
ΔF/Fm'	Control	0.75^{cA}	0.75^{cA}	0.84^{bcA}	0.76^{cA}
	MEL	0.75^{cA}	0.75^{cA}	0.74^{bA}	0.78^{cA}
	8% PEG	0.66^{bB}	0.70^{bA}	0.70^{abA}	0.64^{bB}
	12% PEG	0.56^{aB}	0.63^{aA}	0.56^{aB}	0.53^{aB}
	8% PEG + MEL	0.76^{cA}	0.76^{cA}	0.75^{bA}	0.77^{cA}
	12% PEG + MEL	0.75^{cA}	0.77^{cA}	0.92^{cA}	0.77^{cA}

4.6 Oxidative Stress and Antioxidant Enzyme Activity under Melatonin Treatment

4.6.1 Peroxidase Activity

The effects of melatonin on peroxidase (POD) activity across four genotypes under water deprivation were recorded, melatonin generally increased POD activity, aligning with its role in enhancing plant antioxidant defenses (Wang et al., 2016).

Melatonin significantly increased POD activity in Dessert (115.9%) and Messenger (134.5%), suggesting strong antioxidant responses (Fig. 9). This aligns with findings by Wang et al. (2016) that melatonin enhances antioxidant enzyme activity. In contrast, Tyson showed a significant decrease in POD activity (63.4%), reflecting a complex response. Royalty exhibited a moderate increase (7.7%), suggesting a stable but less pronounced response. PEG treatments alone had variable effects. Dessert and Messenger showed significant increases in POD activity under 12% PEG concentrations. Genotype Tyson recorded varied response with a decrease under 8% PEG and an increase under 12% PEG, indicating sensitivity to water deficit (Wang et al., 2012). Royalty recorded significant decreases in POD activity, indicating a less effective stress response mechanism.

Combining melatonin with PEG generally enhanced POD activity across genotypes. Dessert and Messenger recorded the most significant increases, indicating synergistic effect of melatonin in boosting antioxidant defenses (Wang et al., 2016). Tyson exhibited modest improvements under 8% PEG but decreased POD activity at higher PEG concentrations, reflecting its high stress sensitivity. Royalty recorded moderate improvements with melatonin under PEG treatments, indicating role of melatonin in mitigating stress-induced reductions in POD activity.

Overall, Dessert and Messenger genotypes benefited most from melatonin, showing substantial increases in POD activity. Tyson and Royalty were less responsive, with Tyson particularly sensitive to water deprivation. Dessert emerged as the most suitable for melatonin application due to its significant increase in POD activity under combined treatments, aligning with known role of melatonin in enhancing plant stress responses (Wang et al., 2016).

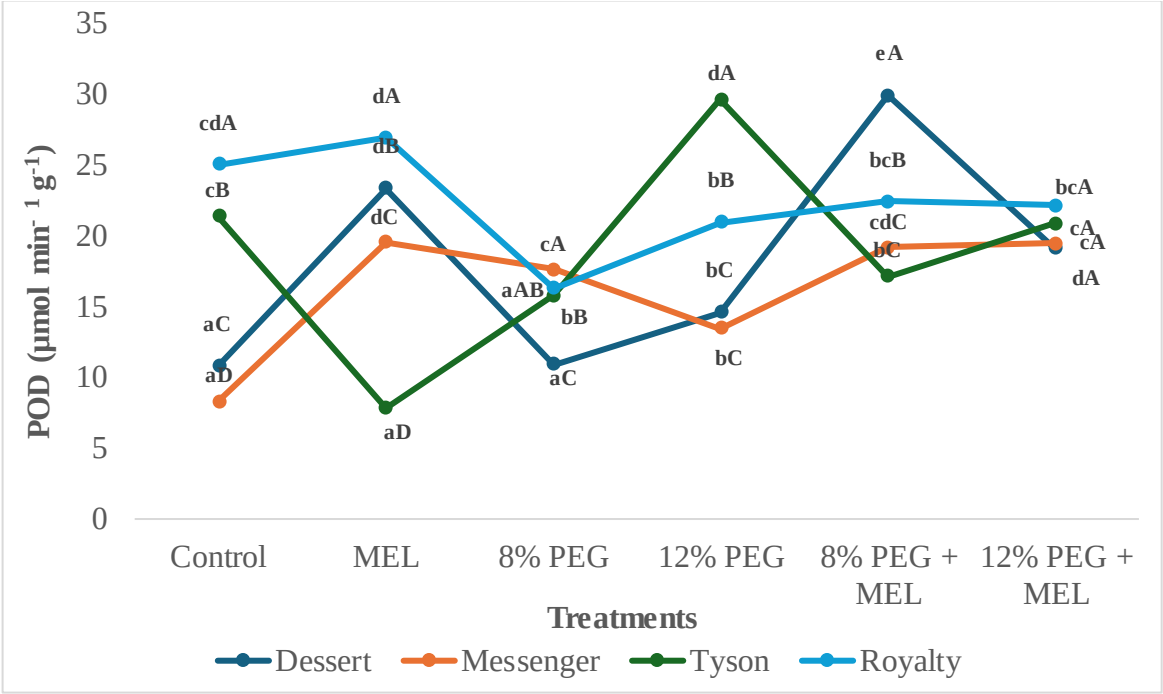


Figure 9. Effect of melatonin and PEG treatments on average peroxidase activity (µmol min^{-1} g^{-1}) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.6.2 Assessment of Lipid Peroxidation via Malondialdehyde Content

The results indicate that PEG treatments increased MDA content in all genotypes, suggesting heightened lipid peroxidation under water-deprived conditions, consistent with findings by Zhang et al. (2024). Conversely, melatonin reduced MDA content, highlighting its potential in alleviating oxidative damage (Muhammad et al., 2022). PEG treatments alone led to substantial increases in MDA content across all genotypes, reflecting heightened lipid peroxidation and oxidative damage under water deprivation. In Dessert, MDA content increased by 23.6% and 52.6% under 8% and 12% PEG, respectively, indicating a significant response to water deprivation. Messenger also showed significant increases of 26.3% and 37.1% under 8% and 12% PEG, respectively. Tyson exhibited the highest sensitivity to water deprivation, with MDA content rising by 77.6% under 8% PEG and 140.4% under 12% PEG, underscoring its susceptibility to water deficit conditions. Royalty recorded more moderate increases in MDA content, with elevations of 10.7% and 31.8% under 8% and 12% PEG, respectively, indicating a less severe but still significant response. Melatonin

alone had varied effects on MDA content across the genotypes. In Dessert, melatonin reduced MDA content by 6.4%, indicating its efficacy in mitigating oxidative damage. Messenger recorded a slight decrease of 1.3%, suggesting a moderate protective effect. Interestingly, Tyson displayed an increase in MDA content by 4.9% with melatonin, possibly due to complex interactions with its stress response mechanisms. In Royalty, melatonin decreased MDA content by 5.1%, indicating a stabilizing effect on lipid peroxidation (Fig. 10).

Combining melatonin with PEG treatments generally reduced MDA content, demonstrating melatonin's mitigating effect against PEG-induced oxidative damage. In Dessert, melatonin reduced MDA content by 16.7% under 8% PEG and 34.0% under 12% PEG, highlighting its significant protective role. Similarly, in Messenger, melatonin application led to decreases of 20.4% and 21.0% in MDA content under 8% and 12% PEG, respectively, underscoring its effectiveness in reducing lipid peroxidation. Tyson exhibited the most substantial reductions, with melatonin decreasing MDA content by 56.9% under 8% PEG and 42.0% under 12% PEG, suggesting that while Tyson is highly susceptible to water deprivation, it highly benefits from melatonin treatment. Royalty also recorded significant decreases in MDA content with melatonin, with reductions of 20.3% under 8% PEG and 26.5% under 12% PEG, indicating the role of melatonin in mitigating oxidative stress. These results align with findings by Muhammad et al. (2022) that melatonin effectively reduces oxidative damage and enhances cellular integrity under stress.

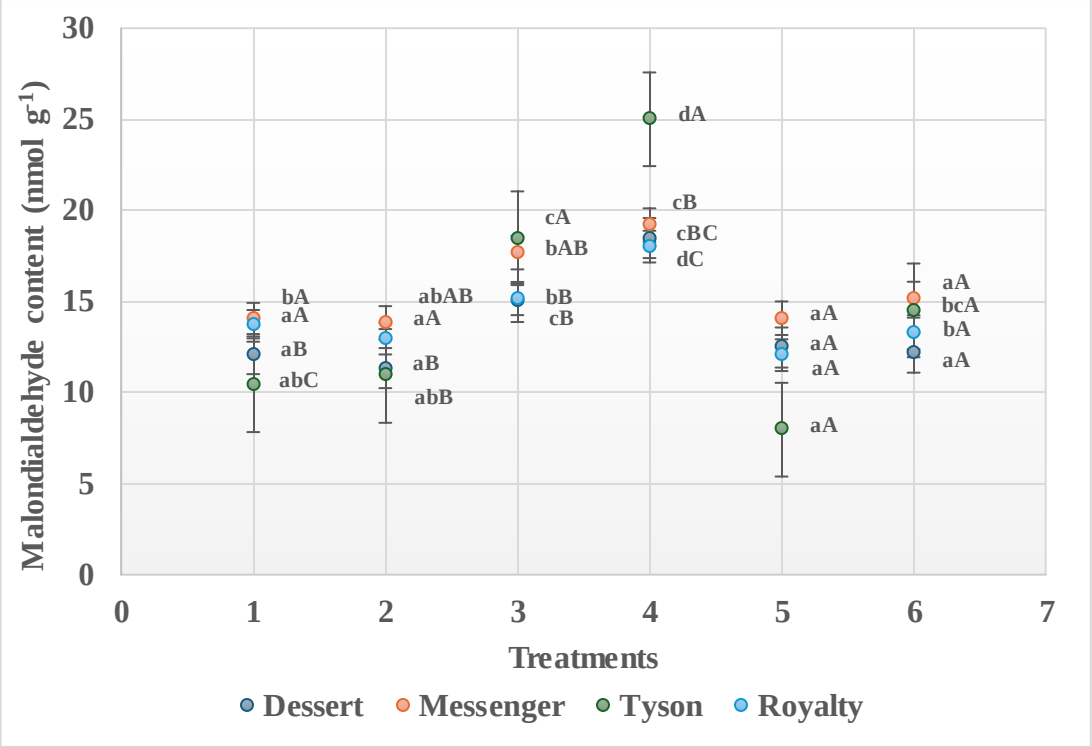


Figure 10. Effect of melatonin and PEG treatments [1(Control), 2 (MEL), 3 (8% PEG), 4 (12% PEG), 5 (8% PEG + MEL), 6 (12% PEG + MEL)] on average malondialdehyde content (nmol g^{-1}) in various sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

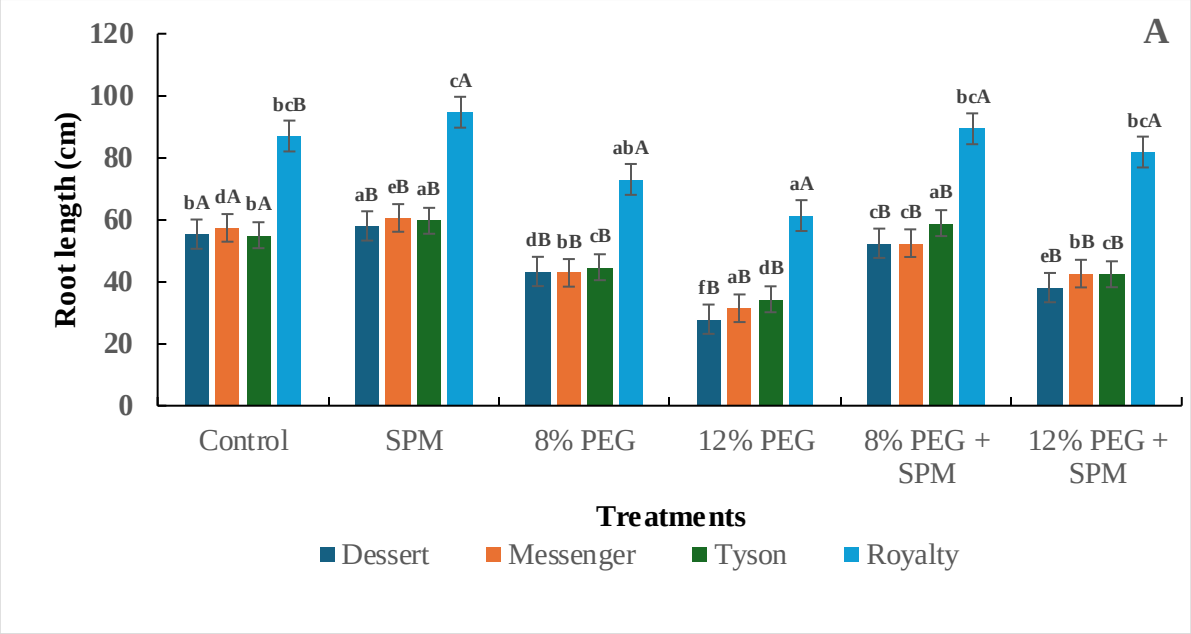
4.7 Morphophysiological Responses to Spermine under Water Deprivation

4.7.1 Variations in Root and Shoot Length Metrics

This study explores the impact of PEG-induced water deprivation and spermine foliar spray (SPM) on root and shoot length in four genotypes (Fig. 11). PEG treatments significantly reduced root and shoot length, highlighting the detrimental effects of water deprivation. In contrast, the spermine application mitigated these reductions and promoted growth. In the Dessert genotype, spermine application recorded a 4.8% increase in root length, whereas PEG treatments resulted in significant decreases (49.6% at 12% PEG). This response was consistent across the Messenger, Tyson, and Royalty genotypes, where spermine effectively counteracted the adverse impact of PEG-induced water deprivation, indicating its potential to promote root growth. In Messenger, an increase of 35.6% was recorded under 12% PEG, with spermine application, while in Tyson, it was 23.5%, and in Royalty, it was 33.4%. This aligns with previous studies highlighting the ability of spermine to stabilize cell membranes

and enhance osmotic balance, thereby supporting root development under stress (Seifi and Shelp, 2019).

Likewise, positive affect on shoot length was recorded with spermine treatment. For instance, in genotype Dessert an increase of 8.3% in shoot length was recorded, while PEG treatments alone led to a significant decline. Spermine treatment under water deficit conditions significantly mitigated reductions, with significant increases in shoot length recorded in all genotypes. Significant differences were recorded between the 8% and 12% PEG treatments when spermine was applied, with increases of 21.6% and 28.6% in shoot length, respectively in Dessert, 39.6% and 15.4% in Messenger, by 19.4%, and by 90.6% in Tyson and 32.2% and 34.8% in Royalty were observed. This suggests spermine helps maintain shoot growth by protecting against water deficit-induced damage, essential for sustaining plant biomass and productivity under drought conditions (Liu et al., 2018).



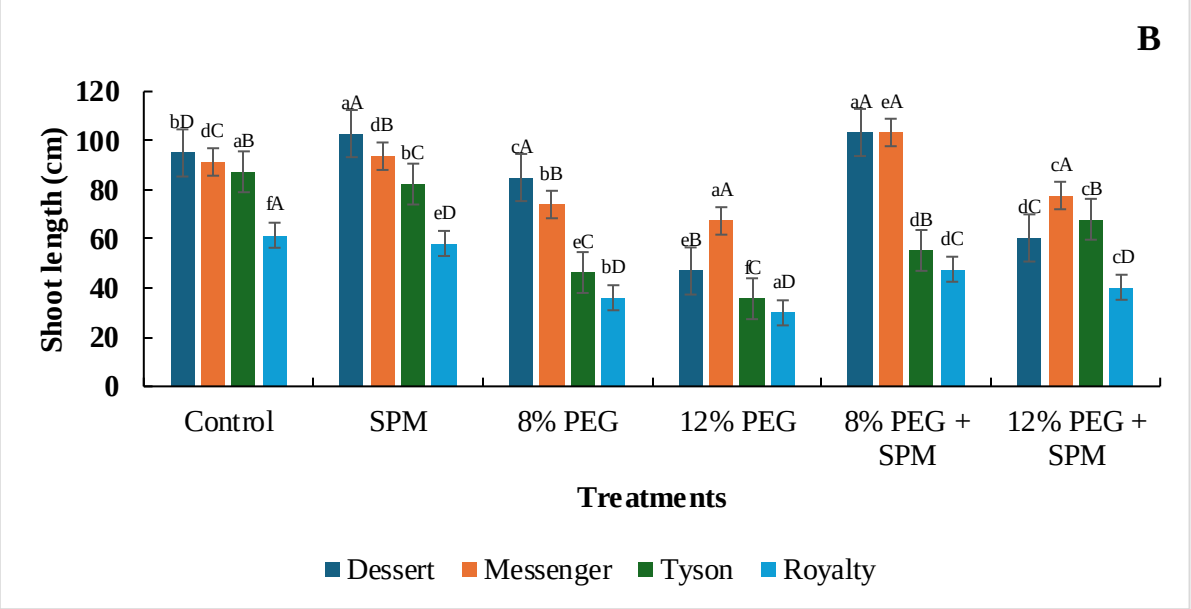


Figure 11. Effect of spermine and PEG-induced water deprivation on average root [A] and shoot [B] length (cm) on sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.7.2 Root Volume and Biomass Distribution Analysis

Water deprivation induced by PEG treatments significantly reduced root volume across all genotypes, indicating severe stress impacts. Root volume decreased 21.8% under 8% PEG and 75.2% under 12% PEG in Dessert. Messenger recorded reductions of 52.8% and 70.7%

under 8% and 12% PEG, respectively. Tyson exhibited the most significant decreases, reducing root volume by 70.1% and 88.7% under 8% and 12% PEG. Royalty recorded decreases of 68.4% and 73.7% under the same treatments. These findings confirm that water deprivation leads to substantial root volume reductions, consistent with previous studies that water scarcity and osmotic stress result in high concentrations of reactive oxygen species (ROS), damaging plant tissues and impairing root growth (Seifi and Shelp, 2019).

Spermine foliar spray generally improved root volume in water deprivation. In Dessert, spermine alone decreased root volume but mitigated water deficit-induced reductions with increases of 27.0% and 64.4% under 8% and 12% PEG. Messenger recorded a 9.4% increase with spermine alone and significant improvements of 98.3% and 127.3% under 12% and 8% PEG. Tyson decreased with spermine alone but increased root volume by 32.8% under 8% PEG and 100.0% under 12% PEG with combined treatments. Royalty exhibited significant increases of 216.7% under 8% PEG and 199.9% under 12% PEG with spermine (Fig. 12). These results indicate the role of spermine in enhancing stress resilience by improving antioxidant defenses, osmoregulation, and interaction with phytohormones and other stress-responsive molecules (Liu et al., 2004; Zhao and Yang, 2008).

The differential response among genotypes suggests varying stress tolerance and benefits from spermine. Dessert and Messenger recorded significant root volume reductions under PEG but substantial improvements with Spermine. With the most severe decreases due to water deprivation, Tyson demonstrated marked recovery with spermine, highlighting its high susceptibility and significant benefit from treatment. Royalty also recorded substantial increases with spermine, indicating a robust response to stress mitigation.

The observed variations in response to spermine and PEG treatments can be explained by the role of polyamines in plant stress responses. Polyamines like spermine stabilize cell membranes and scavenge free radicals, reducing oxidative damage (Liu et al., 2004; Zhao and Yang, 2008). Furthermore, polyamine interaction with phytohormones enhances plant growth and stress tolerance (Liu et al., 2011).

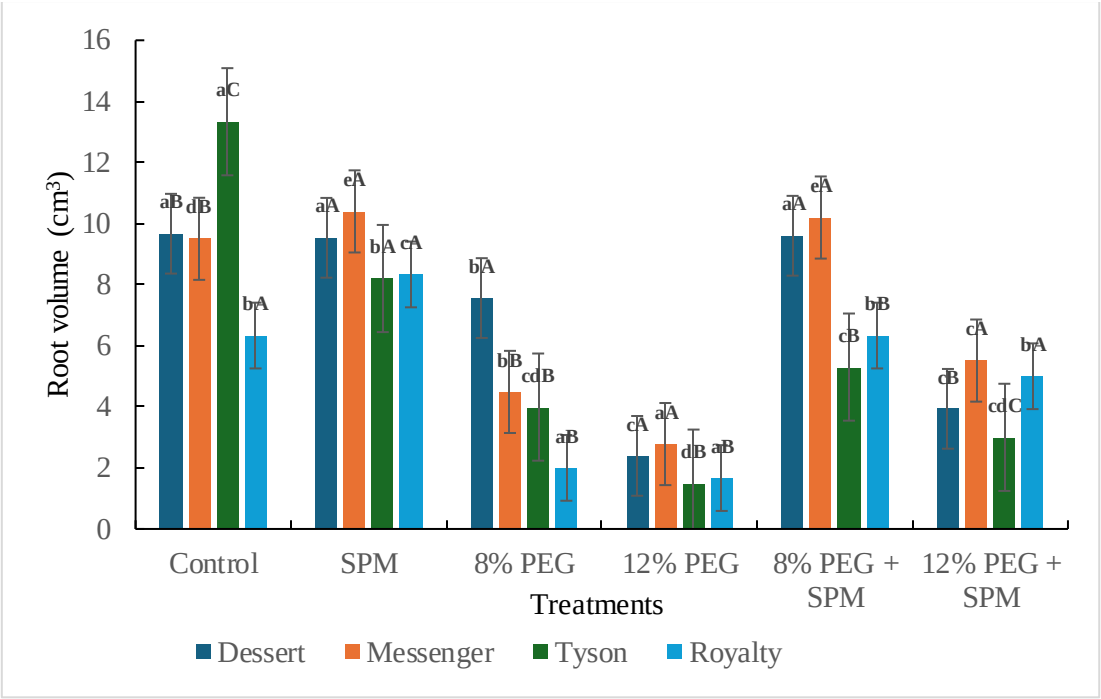


Figure 12. Effect of spermine and PEG-induced water deprivation on average root volume (cm^3) on sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

This study investigates the effects of PEG-induced water deprivation and spermine foliar spray on root and shoots weights (fresh and dry) across four genotypes (Table 19). Water deprivation significantly reduced root and shoot weights due to reduced water availability and increased reactive oxygen species (ROS), causing cellular damage and impaired growth (Seifi and Shelp, 2019). However, the spermine application mitigated these reductions, enhancing growth under stress conditions.

In the Dessert genotype, fresh root weight decreased by 46.7% under 8% PEG and 69.9% under 12% PEG. Spermine application mitigated these reductions, increasing weights by 186.4% and 69.4%, respectively. Similarly, fresh shoot weight in Dessert decreased by 38.6% and 65.1% under 8% and 12% PEG, respectively, with spermine mitigating these effects and increasing weights by 125.4% and 44.5%. Dessert recorded 70.4%, and 82.7% decreases for dry root weight under 8% and 12% PEG, respectively, while spermine increased weights by 362.1% and 292.4%. Dry shoot weight decreased by 37.7% and 73.8%, with spermine increasing weights by 121.5% and 124.9%.

In the Messenger genotype, fresh root weight decreased by 32.9% and 68.1% under 8% and 12% PEG, respectively. Spermine application increased weights by 174.1% and 64.7%. Fresh shoot weight in Messenger decreased by 35.8% and 68.1%, with spermine increasing weights by 100.3% and 116.6%. Dry root weight showed 60.6% and 78.2% reductions, with spermine increasing weights by 297.4% and 114.7%. Dry shoot weight decreased by 48.3% and 52.9%, with spermine increasing weights by 416.5% and 118.9%.

The Tyson genotype recorded the most pronounced reductions, with fresh root weight decreasing by 44.8% and 87.8% under 8% and 12% PEG, respectively. Spermine increased weights by 58.1% and 234.9%. Fresh shoot weight decreased by 34.4% and 89.0%, with spermine increasing weights by 67.2% and 176.1%. For dry root weight, Tyson experienced 60.4% and 82.2% decreases, with spermine increasing weights by 106.4% and 191.3%. Dry shoot weight showed reductions of 47.6% and 93.9%, with spermine increasing weights by 45.1% and 497.2%.

In the Royalty genotype, fresh root weight decreased by 45.2% and 75.4% under 8% and 12% PEG, respectively. Spermine application increased weights by 92.9% and 249.2%. Fresh shoot weight in Royalty decreased by 22.4% and 47.9%, with spermine increasing weights by 57.2% and 77.0%. Dry root weight showed reductions of 87.5% and 90.2%, with spermine increasing weights by 341.6% and 151.1%. Dry shoot weight decreased by 58.9% and 79.7%, with spermine increasing weights by 66.6% and 101.2%.

These results highlight the role of polyamines like spermine in improving antioxidant defenses, enhancing osmoregulation, and stabilizing cellular structures under stress (Liu et al., 2004; Zhao and Yang, 2008; Liu et al., 2011; Shi et al., 2010). Genotype, Royalty and Tyson benefited most from spermine application under water deficit, with Royalty recording the highest improvements in root and shoot weights, making it the most suitable for spermine treatment. Despite high sensitivity towards water deficit, genotype Tyson recorded substantial improvement with spermine, suggesting the effectiveness of polyamines in enhancing plant resilience under stress (Seifi and Shelp, 2019).

Table 19. Effect of spermine on fresh and dry root-shoot weights (g) in water deprived sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatments	Genotypes			
		Dessert	Messenger	Tyson	Royalty
Fresh root weight	Control	11.07^{cA}	13.03^{dB}	15.46^{aC}	15.34^{cdC}
	SPM	24.10^{aA}	24.09^{eA}	15.77^{aB}	25.20^{eA}
	8% PEG	5.90^{dA}	8.74^{cA}	8.54^{cA}	8.40^{bA}
	12% PEG	3.33^{eB}	4.16^{aA}	1.89^{eC}	3.78^{aAB}
	8% PEG + SPM	16.90^{bB}	23.96^{eA}	13.50^{bC}	16.20^{dB}
	12% PEG + SPM	5.64^{dB}	6.85^{bB}	6.33^{dB}	13.20^{cA}
Fresh shoot weight	Control	36.71^{bB}	35.53^{cB}	40.29^{bA}	25.20^{cC}
	SPM	49.30^{aA}	38.27^{cB}	49.55^{aA}	28.99^{dC}
	8% PEG	22.54^{cB}	22.81^{bB}	26.44^{cA}	19.56^{bC}
	12% PEG	12.80^{eA}	11.32^{aA}	4.43^{eB}	13.12^{aA}
	8% PEG + SPM	50.80^{aA}	45.69^{dB}	44.22^{bB}	30.75^{dC}
	12% PEG + SPM	18.50^{dB}	24.52^{bA}	12.23^{dC}	23.22^{cA}
Dry root weight	Control	0.98^{cAB}	1.56^{cBC}	0.66^{aA}	1.94^{bC}
	SPM	1.89^{dAB}	2.45^{dA}	0.67^{aB}	2.50^{bA}
	8% PEG	0.29^{aB}	0.61^{abA}	0.26^{bcB}	0.24^{aB}
	12% PEG	0.17^{aB}	0.34^{aA}	0.12^{cB}	0.19^{aB}
	8% PEG + SPM	1.05^{cB}	1.82^{cA}	0.28^{bcC}	0.83^{aB}
	12% PEG + SPM	0.67^{bAB}	0.73^{bA}	0.34^{bC}	0.48^{aBC}
Dry shoot weight	Control	4.56^{cB}	2.08^{bA}	4.66^{aB}	4.69^{cB}
	SPM	5.99^{cdA}	3.20^{cA}	4.89^{aA}	3.21^{bA}
	8% PEG	2.84^{bA}	1.08^{aB}	2.44^{bA}	1.93^{aAB}
	12% PEG	1.20^{aA}	0.98^{aA}	0.28^{cA}	0.95^{aA}
	8% PEG + SPM	6.29^{dA}	5.56^{dA}	3.54^{abB}	3.21^{bB}
	12% PEG + SPM	2.69^{abA}	2.15^{bAB}	1.69^{bcB}	1.92^{aB}

4.7.3 Regulation of Specific Leaf Area and Relative Chlorophyll Content

The impact of spermine application and water deprivation induced by polyethylene glycol (PEG) on specific leaf area (SLA) across four genotypes: Dessert, Messenger, Tyson, and Royalty, highlighted the genotypic differences in response to different treatments.

The spermine application increased SLA in the Dessert and Messenger genotypes, aligning with previous research that polyamines promote cell growth (Liu et al., 2015), under optimal conditions. While in genotype Tyson and Royalty, decrease was recorded which might be attributed to their unique physiological characteristics (Liu et al., 2015).

PEG induced water deprivation at both concentrations resulted in a significant decrease in SLA across all genotypes, consistent with the known adverse effects of drought on leaf growth (Farooq et al., 2009). In genotype Dessert, SLA decreased by 15.1% under 8% PEG and 36.4% under 12% PEG. In Messenger, SLA reduced by 22.9% and 52.8%, under 8% and 12% PEG, respectively. Tyson recorded a more severe reduction in SLA, with reduction of 55.5% and 73.8% under 8% and 12% PEG. Likewise, Royalty recorded SLA reductions of 57.6% and 69.1% under the same conditions. These decreases highlight the substantial impact of water deprivation on leaf development across all genotypes.

Applying spermine under water deficit conditions significantly mitigated the reduction in SLA. In the Dessert, spermine increased SLA by 71.7% and 85.2% under 8% and 12% PEG, respectively, compared to individual PEG treatments. Messenger recorded even more pronounced improvements, with SLA increasing by 112.5% and 173.7% under the same conditions. Tyson, which recorded the most severe initial reductions, exhibited significant increases in SLA by 192.8% and 272.6%, with spermine application under 8% and 12% PEG. Royalty also demonstrated substantial improvements, with SLA increasing by 197.3% and 190.0% under 8% and 12% PEG with spermine treatment (Table 20). These results suggest that polyamine effectively mitigates the adverse effects of water deprivation, likely through enhancing osmotic adjustment and activating stress-responsive signaling pathways (Talaat et al., 2015; Gill and Tuteja, 2010).

The study underscores the complex nature of plant stress responses and the significant potential of polyamine in enhancing stress tolerance. While all genotypes benefited from spermine application under stress conditions, the degree of improvement varied, reflecting genotypic differences. Tyson and Royalty recorded the highest improvements, highlighting their potential for spermine treatment to enhance resilience under water deprivation. These findings align with existing research that indicates polyamines play crucial roles in improving cell growth, protecting cellular structures, and strengthening overall plant resilience under stress conditions (Liu et al., 2015; Gill and Tuteja, 2010).

Table 20. Effect of spermine on specific leaf area ($cm^2\ g^{-1}$) in water deprived sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatments	Genotypes			
		Dessert	Messenger	Tyson	Royalty
SLA	Control	69.22^{cA}	68.14^{dA}	75.72^{aA}	91.41^{fA}
	SPM	82.14^{dAB}	72.29^{eB}	48.96^{abC}	88.81^{eA}
	8% PEG	58.77^{bA}	52.53^{bAB}	33.71^{bC}	38.77^{bBC}
	12% PEG	44.05^{aA}	32.16^{aB}	19.85^{bC}	28.24^{aB}
	8% PEG + SPM	100.90^{eA}	59.08^{cC}	64.99^{aBC}	76.48^{cB}
	12% PEG + SPM	81.60^{dA}	88.01^{fA}	73.96^{aA}	81.90^{dA}

It is well documented that PEG induces water deficit conditions, reducing chlorophyll content due to osmotic stress, as observed in rice (Farooq et al., 2019). Our results align with these findings, showing significant decrease in SPAD values across all genotypes under water deprivation. However, spermine application improved SPAD under these conditions, suggesting its potential role in protecting chloroplast structure and mitigating water deficit effects (Talaat et al., 2016; Parveen et al., 2019).

Spermine treatment alone had mixed effects, with Dessert and Royalty increase in SPAD values by 18.4% and 11.2%, respectively was recorded, while Messenger and Tyson exhibited decreases of 15.0% and 10.1% (Fig.13). PEG treatments significantly reduced chlorophyll content, with 8% and 12% causing decrease of 18.7% and 48.0% in Dessert, 11.5% and 52.1% in Messenger, 39.1% and 71.9% in Tyson, and 21.8% and 37.0% in Royalty. However, spermine application in water deficit mitigated these effects, significantly increasing SPAD values in all genotypes. Under 8% PEG with spermine, SPAD values increased by 51.9% in Dessert, 13.1% in Messenger, 44.0% in Tyson, and 32.3% in Royalty. Similarly, 12% PEG with spermine resulted in SPAD increases of 103.1% in Dessert, 28.4% in Messenger, 225.4% in Tyson, and 43.3% in Royalty. These findings suggest that spermine can counteract the adverse effects of water deprivation, enhancing chlorophyll content and potentially protecting chloroplast structure, with Tyson showing significant increases under severe water deficit, indicating its unique ability to utilize polyamine for stress mitigation (Talaat et al., 2016; Parveen et al., 2019).

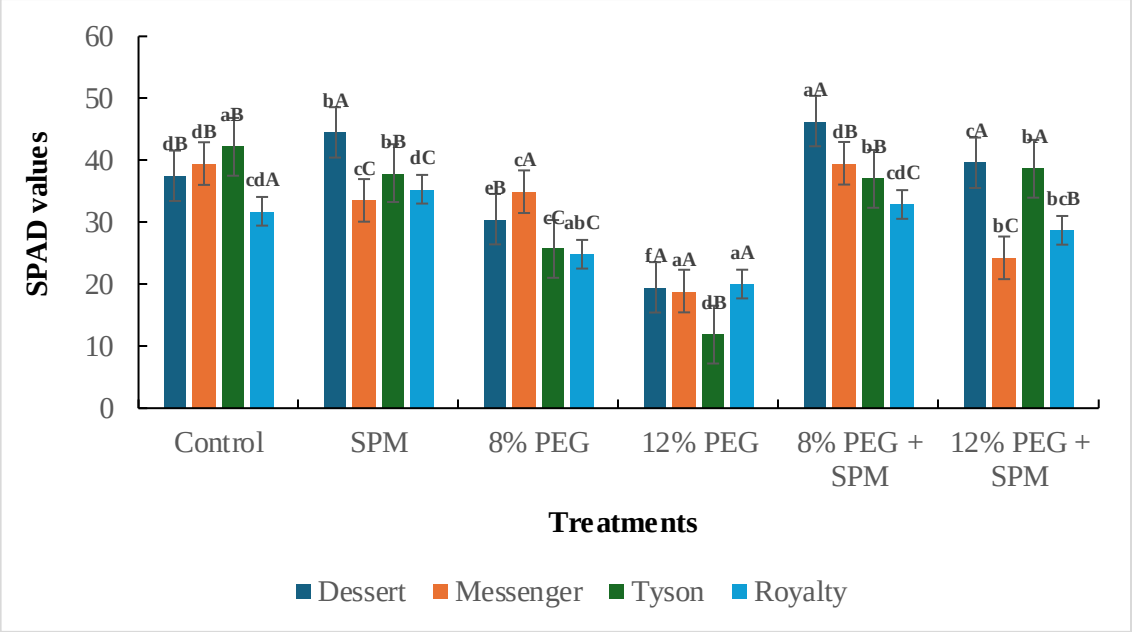


Figure 13. Effect of spermine on relative chlorophyll content (SPAD) in water deprived sweet com genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.8 Photosynthetic and Stomatal Responses to Spermine under Water Deprivation

4.8.1 Photosynthetic Pigment Analysis: Chlorophyll, Total Carotenoids and Lutein Profiles

The effects of polyethylene glycol (PEG)-induced water deprivation and spermine application on photosynthetic pigments in four genotypes, Dessert, Messenger, Tyson, and Royalty were recorded (Table 21). The results demonstrate significant variations in pigment content due to different treatments, highlighting the protective role of spermine in water-deficit conditions.

Under normal conditions, the spermine application produced varied responses among the genotypes. In Dessert, spermine increased chlorophyll-a by 8.3% and total carotenoids by 13.5% while decreasing chlorophyll-b by 42.3%. Conversely, in Messenger, spermine treatment decreased chlorophyll-a and chlorophyll-b by 5.2% and 10.1%, respectively, but increased total carotenoids by 12.9%. Tyson exhibited increases in chlorophyll-a (14.2%), chlorophyll-b (5.0%), and total carotenoids (22.5%). In Royalty, chlorophyll-a and chlorophyll-b decreased by 9.2% and 32.6%, respectively, while total carotenoids increased significantly by 49.7%. These variations suggest that spermine can enhance photosynthetic efficiency in some genotypes while promoting photoprotection in others, reflecting potential

genotypic differences in spermine metabolism and its effects on photosynthetic pigment composition (Liu et al., 2015).

Water deprivation induced by PEG significantly decreases in all photosynthetic pigments across all genotypes. In Dessert, chlorophyll-a, chlorophyll-b, and total carotenoids decreased by 27.1%, 16.5%, and 61.2% under 8% PEG, and by 33.9%, 33.8%, and 57.8% under 12% PEG, respectively. Similarly, in Messenger, these pigments decreased by 20.1%, 43.4%, and 2.4% under 8% PEG, and by 29.6%, 65.5%, and 22.6% under 12% PEG treatment. Tyson recorded reductions of 9.2%, 30.1%, and 33.9% under 8% PEG and 25.9%, 57.5%, and 60.3% under 12% PEG treatment. Royalty recorded decreases in chlorophyll-a and chlorophyll-b by 37.8% and 33.7% under 8% PEG, while total carotenoids increased by 14.3%: under 12% PEG, chlorophyll-a decreased by 47.1%, chlorophyll-b increased by 13.7%, and total carotenoids decreased by 44.2%. These reductions are consistent with the negative impacts of osmotic stress, such as increased chlorophyllase activity and ROS-induced damage to chloroplast structures (Santos, 2004; Li et al., 2015).

Spermine application under water-deprived conditions led to significant improvements in photosynthetic pigments. In Dessert, spermine increased chlorophyll-a by 24.1% under 8% PEG and by 28.5% under 12% PEG and increased total carotenoids by 61.5% and 16.4%, respectively, while chlorophyll-b decreased by 26% under 8% PEG and increased by 33.1% under 12% PEG. In Messenger, spermine treatment increased chlorophyll-a by 7.0% and 32.2%, chlorophyll-b by 62.0% and 327.5%, and total carotenoids by 11.8% and 37.5% under 8% and 12% PEG, respectively. Tyson recorded a 3.8% decrease in chlorophyll-a, a 60.3% increase in chlorophyll-b, and a 13.3% decrease in total carotenoids with 8% PEG, but with 12% PEG, increases of 25.1%, 173.9%, and 61.5% in these pigments were recorded. Royalty exhibited increases of 38.7% and 48.4% in chlorophyll-a, decreases of 6.3% and 50.9% in chlorophyll-b, and increases of 8.2% and 118.2% in total carotenoids under 8% and 12% PEG, respectively.

These findings underscore the protective role of spermine in enhancing plant resilience to water deprivation by supporting photosynthetic pigment stability and activating stress-responsive pathways. The substantial increases in chlorophyll-b and total carotenoids in Tyson and Royalty under higher PEG concentrations suggest that these genotypes might possess unique mechanisms for better utilizing spermine for stress mitigation. This aligns with research indicating that polyamines enhance osmotic adjustment, protect chloroplast

structures, and activate stress-responsive signaling pathways (Da Silva et al., 2022; Hassan et al., 2020). Polyamine application under stress conditions significantly improved photosynthetic pigments, highlighting its potential in protecting the photosynthetic machinery, supporting cell division, and maintaining the antioxidant system (Liu et al., 2015; Santos, 2004; Li et al., 2015; Talaat et al., 2016; Hassan et al., 2020; Khatri and Rathore, 2022).

Table 21. Effect of spermine on photosynthetic pigments (mg g^{-1}) in water deprived sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Genotypes			
		Dessert	Messenger	Tyson	Royalty
Chlorophyll-a	Control	16.32^{cB}	17.10^{eB}	15.08^{cA}	14.83^{eA}
	SPM	17.68^{dA}	16.21^{dB}	17.22^{dA}	13.47^{dC}
	8% PEG	11.89^{aB}	13.66^{bA}	13.70^{bA}	9.23^{bC}
	12% PEG	10.79^{aC}	12.04^{aA}	11.17^{aB}	7.85^{aD}
	8% PEG + SPM	14.75^{bA}	14.62^{cA}	13.18^{bA}	12.80^{dA}
	12% PEG + SPM	13.86^{bB}	15.92^{dA}	13.97^{bcB}	11.65^{cC}
Chlorophyll-b	Control	6.70^{cB}	7.83^{bB}	4.35^{cA}	6.82^{bB}
	SPM	3.86^{aB}	7.04^{bA}	4.57^{cB}	4.59^{aB}
	8% PEG	5.60^{abcA}	4.43^{aA}	3.04^{bB}	4.52^{aA}
	12% PEG	4.44^{abB}	2.70^{aC}	1.85^{aC}	7.75^{bA}
	8% PEG + SPM	4.14^{aA}	7.18^{bA}	4.88^{cA}	4.23^{aA}
	12% PEG + SPM	5.90^{bcB}	11.53^{cA}	5.06^{cB}	3.81^{aC}
Total carotenoids	Control	5.42^{dC}	4.07^{bcB}	4.42^{dB}	2.49^{bA}
	SPM	6.15^{eA}	4.60^{dC}	5.42^{eB}	3.72^{dD}
	8% PEG	2.10^{aC}	3.98^{bA}	2.92^{cB}	2.84^{bcB}
	12% PEG	2.28^{abB}	3.15^{aA}	1.76^{aC}	1.39^{aD}
	8% PEG + SPM	3.39^{cB}	4.44^{cdA}	2.53^{bC}	3.07^{cBC}
	12% PEG + SPM	2.66^{bC}	4.33^{bcdA}	2.84^{bcBC}	3.03^{cB}

Lutein is an essential antioxidant and plays a significant role in safeguarding photosynthetic machinery by quenching reactive oxygen species (ROS) produced under stress (Gill and Tuteja, 2010). The results indicate significant variations due to different treatments, highlighting the role of spermine in enhancing stress tolerance. Under normal conditions, spermine application led to varied responses in lutein content among the genotypes. In the Dessert genotype, spermine treatment decreased lutein content by 25.0% compared to the

control, indicating that lutein synthesis or stability might be differentially regulated. Conversely, in the Messenger, spermine increased lutein content by 41.1%, suggesting an enhancement of the antioxidative defense system (Alcázar et al., 2010). In Tyson, spermine increased lutein content by 26.2%, indicating improved protection against oxidative damage. However, in Royalty, spermine decreased lutein values by 15.9%, which might reflect a complex interaction between spermine and lutein metabolism (Groppa and Benavides, 2008).

Water deprivation led to different responses in lutein content across the genotypes. In Dessert, 8% PEG treatment increased lutein by 14.1%, while 12% PEG treatment decreased it by 32.7%. This suggests that moderate stress might enhance lutein levels, whereas severe stress reduces it. Spermine application under 8% PEG increased lutein by 9.2%, and under 12% PEG, increase of 42.3% was recorded, suggesting an enhanced antioxidative response under higher stress (Gill and Tuteja, 2010).

In Messenger, 8% and 12% PEG treatments increased lutein content by 15.6% and 34.8%, respectively (Table 22). However, spermine application under 8% PEG led to a significant increase of 102% in lutein content, while with 12% PEG, it resulted in a decrease of 28.0%. This variation suggests that the effectiveness of spermine might be influenced by the stress level and genetic factors (Groppa and Benavides, 2008).

In Tyson, water deprivation decreases lutein content, with 8% PEG resulting in a decrease of 8.8% and 12% PEG treatment to a further drop of 19.0%. However, spermine application under 8% PEG resulted in a substantial increase of 95.8% in lutein content compared to PEG treatment alone, indicating its protective role in moderate stress but not in severe stress.

In Royalty, both PEG treatments decreased lutein content significantly, with decreases of 12.6% and 4.9% for 8% and 12% PEG, respectively. Spermine application under 8% PEG increased lutein content by 102%, while under 12% PEG, it decreased by 27.4%. These results suggest that spermine enhances lutein levels under moderate stress but may not provide the same benefit under severe stress, possibly due to the overwhelming oxidative damage that exceeds protective capacity of spermine.

The increase in lutein content after spermine treatment, particularly at lower PEG concentrations, suggests an improved antioxidative defense system. Lutein is essential for protecting photosystem II (PSII) from oxidative damage and ensuring better photosynthetic performance, which likely contributes to the observed increases in photosynthetic efficiency

and yield (Alcázar et al., 2010). However, the decrease in lutein content at higher PEG concentrations even after spermine application in some genotypes, such as Royalty, raises the possibility that high stress levels may overcome its protective benefits. This variation within each genotype underscores that the effectiveness of spermine is mostly determined by genetic factors and innate stress tolerance mechanisms (Groppa and Benavides, 2008).

Table 22. Effect of spermine on lutein content ($\mu g\ \mu L^{-1}$) in water deprived sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatments	Genotypes			
Lutein		Dessert	Messenger	Tyson	Royalty
	Control	81.72^{dB}	60.63^{aA}	71.50^{bAB}	85.86^{eB}
	SPM	61.27^{bC}	85.55^{aAB}	90.22^{aA}	72.25^{bBC}
	8% PEG	93.25^{eA}	70.10^{aB}	65.19^{cB}	75.01^{cB}
	12% PEG	55.01^{aB}	81.75^{aA}	57.91^{eB}	81.64^{dA}
	8% PEG + SPM	101.86^{fA}	71.53^{aBC}	62.44^{dC}	76.51^{cB}
	12% PEG + SPM	78.27^{cA}	58.83^{aA}	50.10^{fA}	59.26^{aA}

4.8.2 Stomatal Conductance and Chlorophyll Fluorescence Metrics

Under normal conditions, spermine application showed varied responses among genotypes. In the Dessert, spermine treatment resulted in a significant 23.7% increase in stomatal conductance compared to the control, suggesting improved gas exchange and potential improvements in photosynthetic efficiency. In contrast, in the Messenger, spermine treatment slightly decreased stomatal conductance by 1.5%. Tyson recorded a substantial increase of 87.0%, while Royalty exhibited a 32.3% increase. These differences in responses reflect potential genotypic differences in how spermine affects stomatal behavior and gas exchange under non-stress conditions.

Water deprivation induced by PEG led to significant decline in stomatal conductance across all genotypes. In Dessert, stomatal conductance decreased by 12.6% under 8% PEG and by 67.2% under 12% PEG. Messenger exhibited reductions of 27.0% and 67.2% under the same conditions. Tyson experienced slight and severe decreases of 1.8% and 35.8%, respectively, while Royalty showed reductions of 16.6% and 21.2%. These reductions are consistent with the expected response to osmotic stress, where decreased specific leaf area, reduced photosynthetic pigments, and impaired photosystem II efficiency contribute to lower

stomatal conductance (Talat, 2020). Similar trends have been observed in maize plants under osmotic stress (Talat, 2020).

When spermine was applied under water deficit conditions, significant improvements in stomatal conductance were recorded across all genotypes, aligning with previous research that exogenous polyamine application enhances photosynthetic efficiency under environmental stress (Yousefi et al., 2019). In Dessert, spermine application increased stomatal conductance by 59.7% and 56.0% under 8% and 12% PEG, respectively, compared to PEG treatments alone. In Messenger, spermine increased stomatal conductance by 22.9% under 8% PEG and by 80.7% under 12% PEG. Tyson recorded increases of 50.2% and 29.7% under the same conditions, while Royalty exhibited improvements of 36.2% and 44.2% (Table 23). These findings suggest that polyamine helps to mitigate the negative effects of water deficit conditions, enhancing gas exchange and maintaining stomatal function (Zhang et al., 2009).

The decrease in stomatal conductance under water deprivation in all genotypes is consistent with findings in other crops and is attributed to factors such as reduced specific leaf area, impaired photosynthetic pigments, and decreased photosystem II efficiency (Talat, 2020). However, the ability of spermine to increase stomatal conductance under these conditions highlights its protective potential, supporting previous studies that show polyamines can enhance photosynthetic functions and improve plant resilience to stress (Yousefi et al., 2019; Zhang et al., 2009).

Table 23. Effect of spermine on stomatal conductance (mmol H_2O m^{-2} s^{-1}) in water deprived sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait		Genotypes			
Stomatal Conductance		Dessert	Messenger	Tyson	Royalty
	Control	16.25^{cB}	28.51^{eC}	14.90^{cB}	9.80^{abcA}
	SPM	20.10^{dB}	28.09^{eA}	27.87^{aA}	12.97^{cC}
	8% PEG	14.20^{bB}	20.81^{cA}	14.63^{cB}	8.17^{abC}
	12% PEG	8.90^{aA}	9.36^{aA}	9.56^{dA}	7.72^{aB}
	8% PEG + SPM	22.68^{eA}	25.58^{dA}	21.97^{bA}	11.13^{bcB}
	12% PEG + SPM	13.88^{bB}	16.91^{bA}	12.40^{cdBC}	11.13^{bcC}

This study explores the effects of polyethylene glycol (PEG)-induced water deprivation and spermine application on various chlorophyll fluorescence parameters (Fv/Fm, Fv/F0, and yield) across four genotypes: Dessert, Messenger, Tyson, and Royalty. The results indicate significant variations due to different treatments, highlighting the role of spermine in mitigating stress effects (Table 24).

Water deprivation decreases the maximum photochemical efficiency of photosystem II (Fv/Fm) in all genotypes. In the Dessert, 8% PEG decreased Fv/Fm by 4.5%, and 12% PEG decreased by 10.7%. However, spermine application under these conditions increased Fv/Fm by 5.8% and 12.4%, respectively. Messenger exhibited decreases of 8.8% and 11.3% with 8% and 12% PEG, respectively, while spermine increased Fv/Fm by 101.4% and 12.7% under the same conditions. In Tyson, 8% and 12% PEG reduced Fv/Fm by 20.4% and 21.6%, respectively, but spermine significantly increased Fv/Fm by 129.8% and 27.7%. Royalty recorded decreases of 8.7% and 20.8%, with spermine increasing Fv/Fm by 89.8% and 24.7% under 8% and 12% PEG, respectively. These results suggest that spermine mitigates the adverse effects of water deprivation on PSII efficiency, enhancing stress tolerance in plants (Talaat et al., 2015).

The potential photosynthetic capacity (Fv/F0) also decreased under water deprivation in all genotypes. In Dessert, 8% and 12% PEG reduced Fv/F0 by 18.7% and 37.3%, respectively. Spermine application increased Fv/F0 by 28.5% and 62.1% under these conditions. Messenger recorded reductions of 24.3% and 36.4%, with spermine increasing Fv/F0 by 96.9% and 61.8%. Tyson experienced substantial decreases of 52.8% and 55.9%, but with spermine application, increases of 248.9% and 130.0% were observed. In Royalty, Fv/F0 decreased by 33.1% and 56.7% with 8% and 12% PEG, while spermine increased it by 71.4% and 116.4% (Table 25). These findings suggest that polyamine helps maintain photosynthetic capacity under stress conditions, possibly by enhancing electron transport and stabilizing photosynthetic machinery (Gill and Tuteja, 2010).

Water deprivation also decreased yield (actual photochemical efficiency) across all genotypes. In Dessert, 8% PEG reduced yield by 12.0%, and 12% PEG by 25.6%. Spermine increased yield by 11.7% and 37.1% under these conditions. Messenger showed yield reductions of 6.2% and 16.2%, with spermine increasing yield by 96.7% and 22.3%. Tyson experienced decreases of 15.9% and 32.9%, but spermine led to increases of 107.2% and 43.2%. Royalty recorded yield decreases of 16.0% and 29.6%, with Spermine increasing

yield by 99.4% and 39.6%. The improvement in yield with spermine under water deficit conditions is attributed to its positive effects on photosynthetic efficiency and overall physiological performance (Farooq et al., 2009).

The consistent decrease in photosynthetic efficiency (Fv/Fm and Fv/F0) and yield under water deprivation in all genotypes can be attributed to impaired electron transport and reduced photosynthetic activity due to water shortage, as documented in previous studies (Gill and Tuteja, 2010). However, the spermine application mitigated these reductions, suggesting its role in enhancing photosystem II efficiency and stress tolerance. Polyamine's ability to improve these photosynthetic parameters correlates with increased actual photochemical efficiency (yield), indicating better physiological performance under stress (Talaat et al., 2015). For instance, in Tyson, spermine treatment led to significant improvements in Fv/Fm, Fv/F0, and yield, demonstrating a robust protective effect even under severe stress conditions (Liu et al., 2015).

Table 24. Effect of spermine on maximum photochemical efficiency (Fv/Fm), potential photosynthetic capacity (Fv/F0), actual photochemical efficiency ($\Delta F/Fm'$) in water deprived sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

Trait	Treatment	Genotypes			
		Dessert	Messenger	Tyson	Royalty
$\Delta F/Fm'$	Control	0.75^{cA}	0.75^{cdA}	0.84^{aA}	0.76^{cA}
	SPM	0.76^{cA}	0.74^{cdA}	0.76^{aA}	0.78^{cA}
	8% PEG	0.66^{bB}	0.70^{bcA}	0.70^{abA}	0.64^{bB}
	12% PEG	0.56^{aB}	0.63^{aA}	0.56^{bB}	0.53^{aB}
	8% PEG + SPM	0.73^{cA}	0.68^{abAB}	0.75^{aA}	0.63^{bB}
	12% PEG + SPM	0.76^{cA}	0.77^{dA}	0.80^{aA}	0.75^{cA}
Fv/F0	Control	3.92^{cA}	3.91^{bcA}	3.63bA	4.19^{cA}
	SPM	4.11^{cA}	4.06^{cA}	3.91^{abA}	3.83^{cA}
	8% PEG	3.18^{bA}	2.96^{abA}	1.71^{cA}	2.81^{bA}
	12% PEG	2.46^{aA}	2.49^{aA}	1.60^{cB}	1.81^{aB}
	8% PEG + SPM	4.09^{cA}	2.87^{abB}	4.27^{aA}	2.00^{aC}
	12% PEG + SPM	3.98^{cA}	4.03^{cA}	3.68^{bA}	3.92^{cA}
Fv/Fm	Control	0.80^{cA}	0.80^{aA}	0.78^{aA}	0.81^{cA}
	SPM	0.80^{cA}	0.80^{aA}	0.80^{aA}	0.79^{cA}
	8% PEG	0.76^{bA}	0.73^{aA}	0.62^{bA}	0.74^{bA}
	12% PEG	0.71^{aA}	0.71^{aA}	0.61^{bB}	0.64^{aB}
	8% PEG + SPM	0.80^{cA}	0.74^{aB}	0.81^{aA}	0.66^{aC}
	12% PEG + SPM	0.80^{cA}	0.80^{aA}	0.78^{aA}	0.80^{cA}

4.9 Oxidative Stress and Antioxidant Enzyme Activity under Spermine Treatment

4.9.1 Peroxidase Activity

Peroxidase activity is a key indicator of the antioxidant defense system, which helps mitigate oxidative stress in plants. The results indicate significant variations due to different treatments, highlighting the diversity of plant responses to abiotic stresses (Fig. 14).

Under normal conditions, spermine application led to varied responses in peroxidase activity among the genotypes. Spermine significantly increased peroxidase activity by 100.8% and 134.9% in genotype Dessert and Messenger, along with an increase in Royalty genotype suggesting robust activation of the antioxidant defense system and improved tolerance to oxidative stress (Gill and Tuteja, 2010; Alcázar et al., 2010; Talaat et al., 2015). On the other hand, in genotype Tyson, decrease in peroxidase activity by 55.6% was recorded, reflecting a potential suppression of antioxidative defense under non-stress conditions, which might induce a compensatory mechanism under higher stress levels (Liu et al., 2015).

Varied responses in peroxidase activity were recorded under water deprivation among genotypes. In Dessert, peroxidase activity increased by 34.9% under 12% PEG, and spermine treatment, further boosted peroxidase activity by 104.0% and 34.3% under 8% and 12% PEG, respectively. This suggests that polyamine enhances the antioxidative defense system under stress, reducing oxidative damage (Gill and Tuteja, 2010). Messenger exhibited increases in peroxidase activity by 111.3% and 61.6% under 8% and 12% PEG, respectively (Fig. 14). Spermine application further increased these values by 47.4% and 68.6%, demonstrating its role in strengthening oxidative defenses under stress conditions (Alcázar et al., 2010).

In Tyson, peroxidase activity decreased by 26.0% under 8% PEG but increased by 38.6% under 12% PEG. In Royalty, peroxidase activity decreased by 34.9% and 16.2% under 8% and 12% PEG, respectively. However, spermine treatment increased peroxidase activity by 28.5% and 18.8% under the same conditions, indicating its role in enhancing antioxidative defense during stress (Talaat et al., 2015).

The varied effect of spermine on peroxidase activity among genotypes under optimal and water deficit conditions underscores the diversity of plant responses to abiotic stresses. In Dessert and Messenger, spermine significantly improved peroxidase activity under optimal and water deficit conditions, suggesting a robust activation of the antioxidant defense system

crucial for reducing oxidative damage. In Tyson, spermine increased peroxidase activity under severe 12% PEG induced water deprivation but decreased it under optimal conditions and 8% PEG stress, indicating a complex interaction where spermine might suppress the antioxidative defense initially but induce a compensatory mechanism under severe water deficit. In Royalty, spermine boosted peroxidase activity under optimal conditions and countered the decrease in activity during water deprivation, highlighting its role in improving antioxidative defense under stress.

These results align with previous research recording that polyamines can enhance the antioxidant defense system, mitigate oxidative stress, and improve stress tolerance in plants (Gill and Tuteja, 2010; Alcázar et al., 2010; Talaat et al., 2015; Liu et al., 2015). The varying responses among the genotypes indicate genotypic differences in how plants manage oxidative stress, with some genotypes showing more pronounced benefits from spermine application under water deprivation.

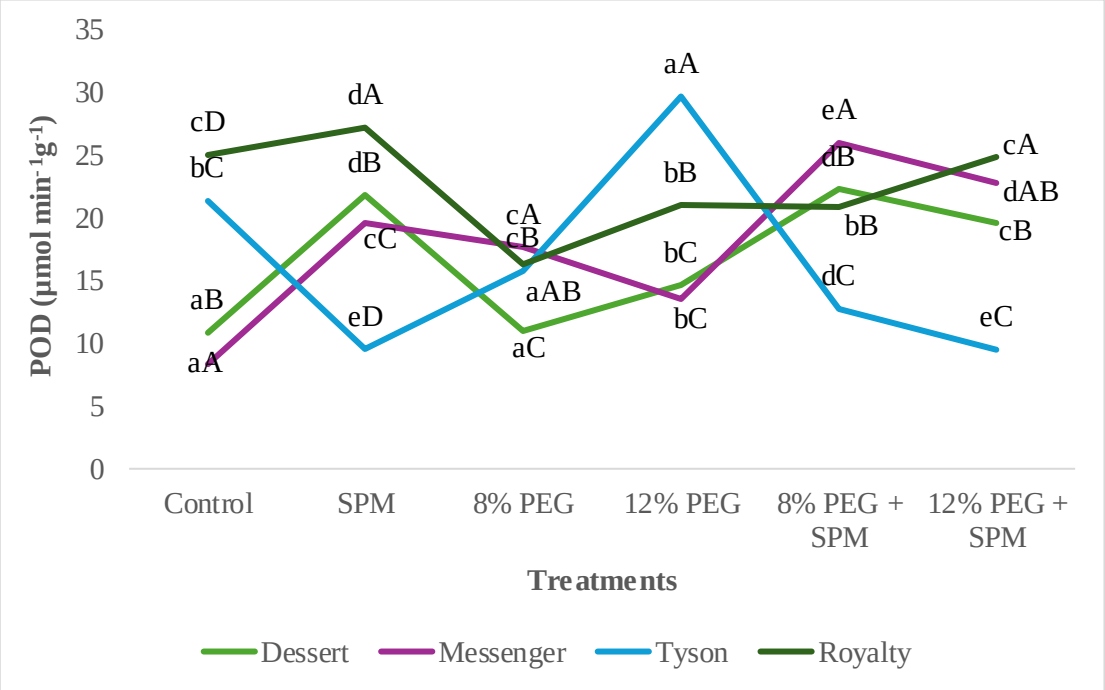


Figure 14. Effect of spermine on peroxidase activity (µmol min^{-1} g^{-1}) in water deprived sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.9.2 Assessment of Lipid Peroxidation via Malondialdehyde Content

Malondialdehyde serves as an indicator of lipid peroxidation and oxidative stress, providing insight into the level of stress in plants. Under normal conditions, the application of spermine

decreased MDA content in the Dessert, Messenger, and Royalty genotypes suggesting reduction in oxidative stress. The MDA content decreased by 10.2% in Royalty and 2.9% in Messenger (Fig. 15). However, a more significant decrease was recorded in Dessert. Results suggest that spermine has a positive effect on antioxidant defenses and cell membrane stability, leading to a decrease in lipid peroxidation and oxidative damage (Da Silva et al., 2022; Hassan et al., 2020). Nevertheless, the application of spermine in Tyson increases MDA content highlighting a distinct genotypic response that might include several metabolic pathways that influence oxidative stress markers.

The presence of water deprivation led to a significant increase in MDA content in all genotypes. This increase indicates oxidative damage and stress caused by the limited availability of water. The MDA content in Dessert increased by 23.6% under 8% PEG and by 52.6% when exposed to 12% PEG, compared to the control. Messenger recorded comparable patterns with rise of 26.3% and 37.1%, respectively. Tyson recorded the most significant increase, with MDA recording a 77.6% increase under 8% PEG and 140.4% increase under 12% PEG. Royalty recorded an increase of 10.7% and 31.8% when subjected to PEG levels of 8% and 12%, respectively. The observed increases align with the reported consequences of water deprivation, which result in heightened levels of reactive oxygen species (ROS) and consequent lipid peroxidation, causing damage to cell membranes (Farooq et al., 2009).

When spermine was applied under water deprivation, a notable decrease in MDA level was recorded in all genotypes, indicating its protective function. When spermine was applied in Dessert at concentrations of 8% and 12% PEG, it resulted in a decrease of 19.0% and 41.5% in MDA levels, respectively, compared to treatments with PEG alone. Messenger had decreases of 22.4% and 22.1% under the same conditions. Tyson recorded a reduction of 28.2% and 48.7% in MDA levels when spermine was applied in the presence of 8% and 12% PEG, respectively. Royalty also recorded positive effects from spermine, as observed by a reduction in MDA content by 19.4% and 37.0% when exposed to 8% and 12% PEG, respectively (Fig. 15). The results indicate that spermine aids in reducing oxidative stress by strengthening antioxidant mechanisms and maintaining cellular membranes, hence decreasing lipid peroxidation (Da Silva et al., 2022; Hassan et al., 2020).

The different responses recorded in genotypes to water deprivation and spermine application indicate variations in how oxidative stress is regulated based on genotype. For instance, in

the context of Dessert and Royalty, the decline in MDA levels due to the presence of spermine after water deprivation highlights its effectiveness in mitigating oxidative damage. In Tyson, while spermine initially increased MDA levels under normal settings, its beneficial benefits became apparent after water deprivation, as of reduced MDA levels compared to treatments with PEG alone.

This study demonstrates that water deprivation has a substantial impact on oxidative damage in all genotypes, as evidenced by elevated levels of MDA content. Nevertheless, the application of spermine during water deprivation successfully mitigates the damage, emphasizing its function in augmenting plant resistance by safeguarding against oxidative stress and fortifying cellular structures. Our results are consistent with previous research in other crops, which supports the idea that polyamines can enhance stress tolerance in plants (Da Silva et al., 2022; Hassan et al., 2020).

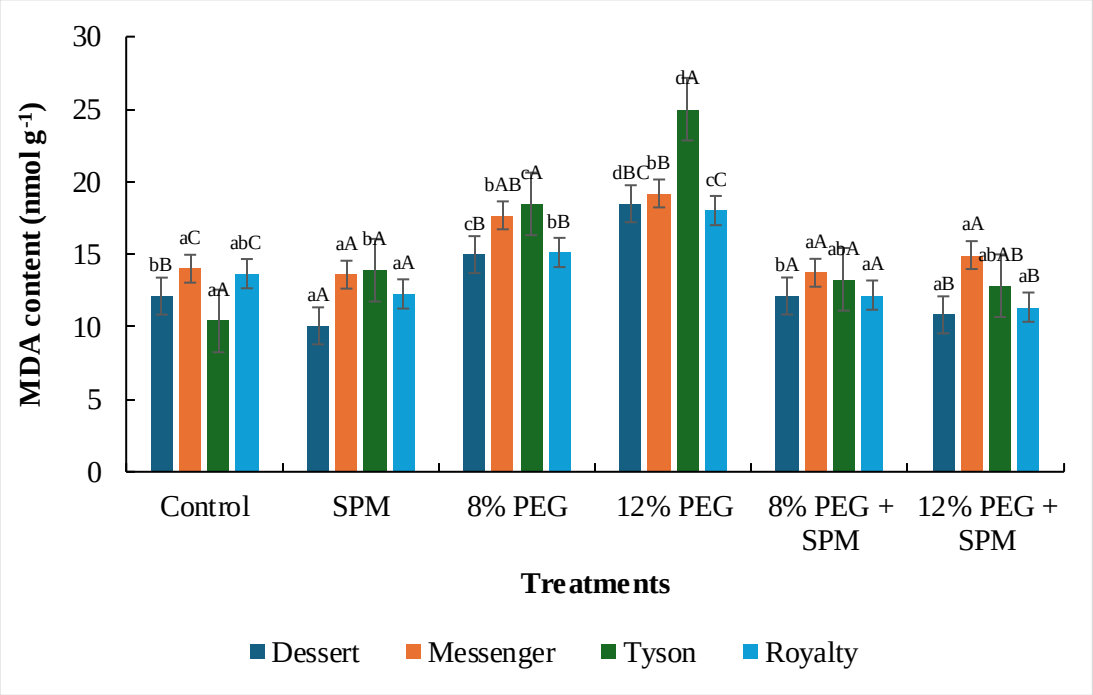


Figure 15. Effect of spermine on malondialdehyde content (nmol g^{-1}) in water deprived sweet corn genotypes. Different small letters indicate significant differences *($p \leq 0.05$)* among the treatments of each genotype, and different capital letters indicate significant differences *($p \leq 0.05$)* among genotypes within each treatment.

4.10 Effect of water deprivation on spinach germination parameters

The results of this study revealed the significant effects of PEG-induced water deprivation on various germination parameters of spinach seeds (Table 25). The germination percentage of PEG-treated seeds was markedly lower at 63% compared to 79% in the control group, showing a significant decrease of 20%. These results align with previous findings that drought stress reduces the ability of seeds to germinate effectively due to insufficient water uptake, which is important for initiating the germination process (Lu et al., 2022).

The mean germination time (MGT) was reduced by 27.1% in PEG-treated seeds. Conversely, the mean germination rate (MGR) increased by 34.62%; this suggests that while the onset of germination was delayed under water deficit conditions, once germination began, it proceeded at a faster rate. This could be due to the seeds' compensatory mechanisms to accelerate germination under stressful conditions to ensure survival.

The coefficient of variation of germination time (CVt) recorded an 18.14% decrease in PEG-treated seeds (42.61%) compared to control (52.07%); in contrast, the coefficient of the velocity of germination (CVg) increased by 35.83% from 26.28% in control to 35.69% in treated seeds.

A decrease in Germination Index (GI) was observed by 5.9% in PEG treatment compared to the control, while the mean daily germination percent (MDG) decreased by 19.7%. The germination value (GV), which combines both the speed and completeness of germination, decreased by 17.99%, from 194.19 in control to 159.26 in PEG-treated seeds (Table 25).

Water deficit conditions can cause late and reduced germination during the germination phase or may completely prohibit germination (Hegarty, 1977). Reducing water potential reduces germination by interrupting water uptake (Delachiave et al., 2003). During germination, water is required for various metabolic activities the physical process of water absorption increases germination rate, enzyme synthesis, protein synthesis and hydration (Zhu et al., 2006). Hydrolytic enzymes like a-amylase, proteases, and lipases are responsible for hydrolysing cotyledon reserves required to provide energy in the early stages of seed growth by respiration (Dahal et al., 1996; Zayed et al., 1997). A decrease in the activity of such enzymes due to a reduction in seed water content under low water potential is observed (Dahal et al., 1996; Zayed et al., 1997). The water deprivation treatment delayed the germination and affected the final germination percentages. Slower decomposition of

endosperm or slower transport of decomposed materials to the seedlings is one of the factors for reducing the germination percentage under drought stress (Falleri et al., 2004).

Table 25. The effect of PEG-induced water deprivation on the various germination parameters of spinach seeds. Different letters indicate significant *($p \leq 0.05$)*. differences between treatments.

Traits	Treatments	
	Control	PEG
Germination percentage (%)	79.00[a]	63.00[b]
Mean germination time (day)	3.91[a]	2.85[a]
Mean germination rate (day^{-1})	0.26[a]	0.35[a]
Coefficient of variation of germination time (%)	52.07[a]	42.61[a]
Coefficient of velocity of germination (%)	26.28[a]	35.69[a]
Germination index (day)	9.06[a]	8.52[a]
Mean daily germination Percent (%)	11.27[a]	9.04[b]
Peak value for germination (day^{-1})	16.66[a]	17.5[a]
Germination value	194.19[a]	159.26[a]

4.11 Effect of different light qualities on the growth parameters of spinach

The study showed significant differences in growth parameters, such as root and shoot length, root volume, and fresh and dry mass of the roots and shoots, in spinach plants subjected to different light qualities (Light 1, Light 2, and Light 3) during both harvest phases (Table 26). Various parameters decrease when comparing Light 3 to Light 2 at the first and full harvest phases. During the first harvest, a significant decrease in root length by 48.8%, shoot length by 73.6%, root volume by 93.8%, fresh root weight by 95.7%, fresh shoot weight by 93.5%, dry root weight by 93.7%, and dry shoot weight by 91.6% were recorded. The trend recorded at the full harvest showed a decline in shoot length (32.0%), fresh root weight (84.4%), and fresh shoot weight (71.2%). In addition, there was a 9.5% increase in root length but a decrease in root volume (55.2%), dry root weight (9.2%), and dry shoot weight (28.7%) when comparing Light 3 to Light 2. The recorded declines in growth parameters under Light 3 suggest that the quality of light has a significant impact on the physiological and morphological characteristics of spinach. The comparison between Light 3 (higher red light with flashes of UV-C radiation) and Light 2 (normal white light) emphasizes the harmful consequences of excessive red light and UV-C radiation on plant growth (Table 26). These findings support previous research suggesting UV-C radiation can harm chloroplasts, mitochondria, and cell membranes in higher plants (Shavit and Avron, 1963). The decrease in chlorophyll content observed under Light 3 provides evidence that

an overabundance of red light and UV-C radiation can interfere with photosynthetic efficiency, resulting in stunted growth (Wituszyńska et al., 2014).

Under light 1, the results recorded a slight improvement. During the first harvest, there was a significant decrease in root length, while the dry shoot weight recorded a notable increase. During the full harvest, root volume was significantly increased by 91.7% and fresh root weight by 37.5% compared to Light 2. In addition, there was a noticeable increase in shoot length, root volume, fresh root weight, fresh shoot weight, and dry root weight at both harvest times. Based on the results, Light 1, which had a higher amount of blue light, demonstrated more favorable outcomes in terms of promoting growth when compared to Light 2. Based on the findings, blue light has a beneficial effect on root development and the overall biomass of plants, as evidenced by the increase in root volume and fresh root weight at the full harvest. Research has shown that blue light positively affects stomatal opening, plant height, and chlorophyll biosynthesis, explaining the observed improvements in different growth parameters (Folta, 2004; Kaiser et al., 2019).

Table 26. Effect of different light qualities on the growth parameters of spinach. Different letters among light qualities within a specific harvest indicate significant differences *($p \leq 0.05$)*.

Traits	First Harvest (25th day after sowing)			Full Harvest (35th day after sowing)		
	Light 1	Light 2	Light 3	Light 1	Light 2	Light 3
Root Length (cm)	33.8^{b}	45.6^{a}	23.3^{b}	30.4^{a}	35.7^{a}	39.1^{a}
Shoot Length (cm)	12.9^{a}	12.4^{a}	3.2^{b}	15.7^{a}	17.4^{a}	11.8^{b}
Root volume (cm^3)	6.58^{a}	6.1^{a}	0.3^{b}	33.6^{a}	17.5^{b}	7.8^{a}
Fresh root weight (g)	5.26^{a}	4.4^{a}	0.19^{b}	29.4^{a}	21.4^{b}	3.3^{c}
Fresh shoot weight (g)	6.77^{a}	5.8^{a}	0.38^{b}	20.5^{a}	19.5^{a}	5.6^{b}
Dry root weight (g)	0.23^{a}	0.1^{a}	0.01^{b}	0.71^{a}	0.6^{a}	0.5^{a}
Dry shoot weight (g)	0.60^{a}	0.4^{b}	0.04^{c}	1.83^{a}	1.9^{a}	1.36^{a}

4.11.1 Effect of different light qualities on the relative chlorophyll content and photosynthetic pigments in spinach leaves

The relative chlorophyll content (SPAD) recorded a significant decrease of 44.5%, 38.5%, 25.5%, 30.6%, and 22.0% in Light 3 compared to Light 2 on each measurement day (Fig. 16A). During the first and second days of measurement under Light 1, there was a slight decrease; however, on the fourth and fifth days, there was a significant increase of 12.8% and 25.8% compared to Light 2. The chlorophyll-a content recorded a significant decrease of 49.4% under Light 3, while it increased by 12.0% under Light 1 compared to Light 2 (Fig.

16B). The chlorophyll-b content showed a similar trend, with a significant decrease of 56.8% under Light 3 and an increase of 25.7% under Light 1, compared to Light 2 (Fig. 16C). Likewise, total carotenoid content recorded a significant decrease of 47.1% under Light 3, while an increase of 18.1% under Light 1 compared to Light 2 (Fig. 16D). The results show that red light and UV-C radiation (Light 3) have a detrimental effect on the levels of photosynthetic pigments, leading to a reduction in chlorophyll and carotenoid content, which can be attributed to the oxidative stress and damage caused to the structures of chloroplasts (Wituszyńska et al., 2014). On the other hand, an increase in blue light (Light 1) can improve photosynthetic pigments, resulting in improved photosynthetic efficiency and overall well-being of the plants (Folta, 2004).

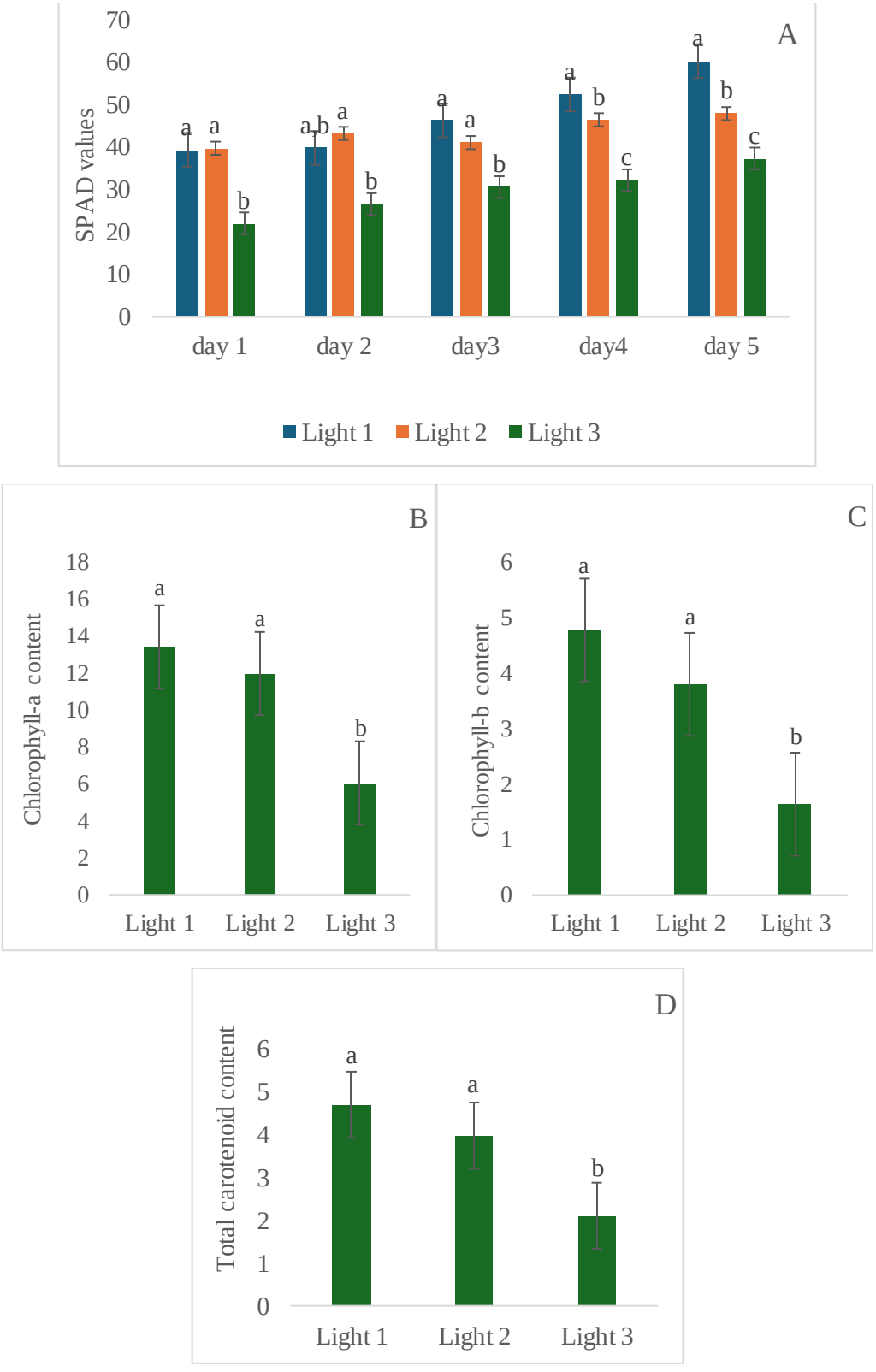


Figure 16. Relative chlorophyll content (A), photosynthetic pigments [chlorophyll- a (B), chlorophyll-b (C), and total carotenoids (D) (mg g^{-1})] in spinach leaves grown under different light qualities provided by LED Lamps. Different letters correspond to significant differences *($p \leq 0.05$)* among lights in a particular trait. n=3, ± S.E.

4.11.2 Effect of different light qualities on xanthophyll content in spinach

Under Light 3 a higher concentration of antheraxanthin (24.8%) and a modest increase in lutein (1.3%) and violaxanthin (1.9%) content compared to Light 2 was recorded. Under Light 1, there were significant increases in antheraxanthin (24.5%), lutein (43.4%), and violaxanthin (16.4%) compared to Light 2. The recorded increase in xanthophyll levels, particularly antheraxanthin, lutein, and violaxanthin, under Light 3 highlights a protective response against the harmful effects of UV-C radiation (Table 27). As noted by Palmer et al. (2002), xanthophyll synthesis helps mitigate oxidative damage. The increase in lutein levels under Light 1 suggests its role in enhancing light absorption and protecting against phototoxic effects, ultimately promoting improved growth and development under blue light (Jahns and Holzwarth, 2012).

4.11.3 Effect of different light qualities in the malondialdehyde content in spinach

The MDA content slightly increased under light 3 compared to light 2 (Table 27). The observed increase in MDA content under Light 3 suggests a potential rise in lipid peroxidation and membrane damage caused by the oxidative stress triggered by UV-C radiation and red light. Previous studies have demonstrated that exposure to UV-C radiation can result in elevated MDA levels, indicating the presence of oxidative damage in plants (Heath and Packer, 1968). Light 1, which had a higher concentration of blue light, resulted in the lowest MDA levels, indicating a decrease in oxidative stress and improved stability of the cell membranes (Jahns and Holzwarth, 2012).

Table 27. Xanthophyll content (antheraxanthin, lutein, and violaxanthin) and MDA content under different light qualities. Different letters correspond to significant differences *($p \leq 0.05$)*.

Trait	Light 1	Light 2	Light 3
Antheraxanthin (µg µL^{-1})	3.19^{a}	4.23^{a}	5.2^{a}
Lutein (µg µL^{-1})	136.2^{a}	94.9^{a}	96.2^{a}
Violaxanthin (µg µL^{-1})	57.0^{a}	49.0^{a}	49.0^{a}
Malondialdehyde (nmol g^{-1})	11.9^{a}	13.2^{a}	13.3^{a}

4.12 Effect of water deprivation under different light qualities on growth parameters of spinach

Under Light 1 and in the presence of 2.5% PEG, there was a significant decrease in growth parameters. The root length, shoot length, root volume, fresh root weight, fresh shoot weight, dry root weight, and dry shoot weight all recorded reductions compared to the control.

Similarly, when exposed to Light 2, the presence of 2.5% PEG led to a notable reduction in various growth parameters (Table 28). When exposed to Light 3 with flashes of UV-C radiation and PEG treatment, the plants could not survive. The results highlight the negative impact on growth parameters across different light qualities under water deprivation. The most significant effects were observed under Light 3, suggesting that combining UV-C radiation and water deprivation is fatal to plant survival. Results support the idea that when plants experience drought and light stress can negatively affect their growth and biomass (Qaderi et al., 2007; Jaleel et al., 2008). It is interesting to note that plants exposed to Light 1 and Light 2 show a higher resistance to water deprivation compared to those under Light 3. This observation hints at the potential of blue light in mitigating the adverse effects of drought stress. One possible explanation for this could be the positive influence of blue light on root development and water use efficiency, as suggested by Kaiser et al. (2019).

Table 28. Effect of water deprivation under different light qualities on growth parameters of spinach. Different letters indicate the significant difference at $p \leq 0.05$ within treatments in a different light and the different numbers indicate the significant difference at $p \leq 0.05$ within treatments in a particular light.

Trait	Light 1		Light 2	
	Control	2.5% PEG	Control	2.5% PEG
Root length (cm)	$33.83^{b,1}$	$21.60^{a,2}$	$45.67^{a,1}$	$21.33^{a,2}$
Shoot length (cm)	$12.92^{a,1}$	$3.58^{b,2}$	$12.42^{a,1}$	$5.92^{b,2}$
Root volume (cm^3)	$6.58^{a,1}$	$3.08^{a,2}$	$6.17^{a,1}$	$0.37^{a,2}$
Fresh root weight (g)	$5.26^{a,1}$	$0.13^{a,2}$	$4.47^{a,1}$	$0.44^{a,2}$
Fresh shoot weight (g)	$6.77^{a,1}$	$0.15^{a,2}$	$5.88^{a,1}$	$0.60^{a,2}$
Dry root weight (g)	$0.23^{a,1}$	$0.01^{a,2}$	$0.16^{a,1}$	$0.03^{a,2}$
Dry shoot weight (g)	$0.60^{a,1}$	$0.05^{a,2}$	$0.48^{b,1}$	$0.15^{a,2}$
SPAD day 1	$39.4^{a,1}$	$21.2^{a,1}$	$39.7^{a,1}$	$41.9^{a,1}$
SPAD day 2	$39.8^{a,1}$	$14.6^{b,2}$	$43.2^{a,1}$	$39.3^{a,1}$
Malondialdehyde (nmol g^{-1})	$13.20^{a,1}$	$16.22^{a,1}$	$11.95^{a,1}$	$16.41^{a,2}$

5. CONCLUSION AND RECOMMENDATIONS

5.1 Foliar application of acetic acid under water deprivation

Under water deficit conditions, this research examined the effects of acetic acid's foliar application on three sweet corn genotypes (Messenger, Tyson, and GSS 8529). The results showed that acetic acid could reduce the adverse effects of water deprivation by improving many physiological and biochemical traits. In a genotype-dependent manner, acetic acid treatment improved particular root and shoot lengths, root volume, specific leaf area, chlorophyll content, photosynthetic efficiency, and antioxidant defense mechanisms. With the Tyson genotype recording the evident favorable response, the main conclusions include improved growth parameters, stomatal conductance, chlorophyll content improvements, and lowered oxidative stress indicators.

These results indicate that more studies on optimizing acetic acid concentrations for sweet corn genotypes should concentrate on maximizing stress resilience and growth performance. Field trials will validate the effectiveness of acetic acid under natural growing conditions, and its practical relevance in agricultural practices will be evaluated. Furthermore, offering a complete strategy to improve water deprivation in sweet corn involves

- investigating the possibilities of additional organic acids,
- doing molecular investigations to grasp the fundamental processes and
- combining acetic acid treatment with other agronomic methods.

Following these suggestions is expected to increase sweet corn's resilience to water deprivation significantly, promoting sustainable agriculture methods among the problems related to world water scarcity.

5.2 Foliar application of melatonin under water deprivation

The study focused on the effects of foliar application of melatonin on improving the resistance of sweet corn to water deprivation caused by polyethylene glycol. Four different genotypes were tested using two different polyethylene glycol (PEG) concentrations and melatonin treatment. The recorded results revealed that the application of melatonin effectively mitigates the adverse effect of water deprivation, resulting in enhancements in a range of morphological, physiological, and biochemical traits.

Notable observations involve morphological parameter enhancements like substantial root and shoot length growth, fresh and dry weights, and root volume among various genotypes.

These findings suggest improved growth and increased biomass accumulation in stressful conditions. The physiological parameters significantly improved, including increased relative chlorophyll content, photosynthetic pigments (chlorophyll-a, chlorophyll-b, and total carotenoids), and stomatal conductance. These improvements suggest better water retention and improved photosynthetic efficiency due to melatonin application.

Results suggest that melatonin significantly reduced the malondialdehyde content, suggesting a decrease in lipid peroxidation and oxidative stress. In specific genotypes, the increased peroxidase activity suggests melatonin's role in reducing oxidative damage. Moreover, the photosynthetic performance recorded an improvement, as the maximum efficiency of photosystem II (Fv/Fm) and specific leaf area (SLA) significantly increased under melatonin treatments showing an apparent enhancement in both photosynthetic performance and leaf structure. Overall, the research findings support the idea that melatonin has the potential to act as a plant protective agent, improving the ability of sweet corn to withstand water deprivation.

The study suggests that more research on optimizing melatonin for sweet corn genotypes should concentrate on conducting thorough field trials to validate the effectiveness of melatonin in real-world conditions and different environmental challenges, along with exploring the most effective dosage and timing of melatonin application to improve stress-relieving benefits in various plant varieties and growth stages.

Investigating the potential of melatonin in sustainable agricultural practices, particularly in areas susceptible to water deprivation, to improve crop yield and resilience and exploring the molecular mechanisms that underlie the protective role of melatonin should also be considered. Also encouraging policymakers to prioritize research and development efforts that explore creative solutions, like the application of melatonin, to tackle the pressing issues of climate change and water scarcity in agriculture.

5.3 Foliar application of spermine under water deprivation

The research explored the impact of the foliar application of spermine on four sweet corn genotypes (Dessert, Messenger, Tyson, and Royalty) to reveal if it could enhance their capacity to tolerate water deficits. The results reveal that spermine significantly alleviates the adverse effects of water deprivation across various morphological and physiological traits, with notable genotypic variations in response. More precisely, spermine application

improved root and shoot growth, and increased biomass accumulation. Moreover, ameliorative effect of spermine towards photosynthetic pigments, stomatal conductance, and enhanced antioxidant activity when plants were exposed to water deficit conditions shows positive effects of its application. In genotypes like Dessert and Tyson, growth and biomass improved significantly, whereas the Messenger and Royalty genotypes moderate improvements were observed. Additionally, the spermine treatment reduced oxidative stress in all genotypes, as shown by decreased malondialdehyde (MDA) content. Among the genotypes, significant reduction was recorded in Dessert. Yield and lutein content also increased in all genotypes, with the most significant improvements recorded in Royalty and Tyson. This suggests the potential of spermine to boost the antioxidant capacity and overall resilience in plants.

The study also revealed the contrasting effects of two different concentrations of PEG (8% and 12%) used to induce water deprivation. A higher concentration of PEG (12%) resulted in more significant reduction in root and shoot lengths, biomass accumulation, and photosynthetic pigments compared to lower concentration of PEG, indicating that high PEG concentrations increase the severity of water deprivation. Spermine treatment reduced these adverse effects at both concentrations of PEG. The benefits were more evident at the higher concentration of PEG, suggesting that spermine can offer significant protective advantages even under severe stress.

Especially in areas prone to drought, to enhance the tolerance of sweet corn under water deprivation, we can recommend using spermine by foliar treatment as a realistic agricultural method. Moreover, additional research is required to adjust the dosage and frequency of spermine treatment for various genotypes and environmental challenges. Furthermore, exploring the positive effects of spermine in other crops could broaden its utilization in agriculture. By combining the use of spermine with other stress management methods, such as adequate irrigation and the cultivation of stress-tolerant varieties, it is possible to produce synergistic results. Regular assessment of crops treated with spermine in field trials is important to confirm laboratory results and verify practical viability.

5.4 Germination and water deprivation in spinach

Water deprivation significantly affects the germination of spinach seeds. The findings indicate the importance of ideal water accessibility for seed germination and early growth and development.

5.5 Light quality and water deprivation in spinach

Plant growth is significantly influenced by various environmental factors, including the quality and quantity of light. These factors play a vital role in determining the morphology of plants, such as root, shoot length, root volume, fresh root and shoot weight, as well as dry root, and shoot weight. Plants facing unfavourable light conditions, such as scarce or poor-quality light, have negative effects on growth and development. This study reflect the significance of blue light in plant growth and the effect of different light qualities on several aspects of plant development. The percentage of blue light along with presence and absence, may affect root, shoot length, fresh, and dry weight, root volume, photosynthetic pigment contents, and malondialdehyde (MDA) levels. According to the study, when using LED technology, spinach develops better when exposed to more blue light than red light. UV-C rays, on the other hand, may harm plants, especially when combined with water deprivation. It was found that under such circumstances, water deprivation could exacerbate the negative effects of different light qualities. The correct UV-C treatment may increase the carotenoid content of spinach, but determining the appropriate doses and knowing how it interacts with the environment will be challenging problems to solve in the future. The findings emphasize the need to consider UV-C radiation and the light spectrum when designing lighting systems for indoor plant growth.

6. NEW SCIENTIFIC RESULTS

1. Acetic Acid Enhances Root Growth and Photosynthetic Pigments Under Water Deficit

In the Tyson genotype of sweet corn, acetic acid foliar spray (10 mM and 20 mM) under water deficit conditions significantly increased specific root length by 152.2% and 131.2%, respectively, compared to untreated plants. Total biomass exhibited genotype-specific responses, with notable increases under water deficit conditions at 10 mM acetic acid: 41.9% in Messenger and 18.2% in GSS 8529. Photosynthetic pigments in Tyson showed marked improvements, with 10 mM acetic acid increasing Chl-a by 68.6% and Chl-b by 146.6%, while 20 mM acetic acid increased Chl-a by 46.4% and Chl-b by 114.7%, indicating enhanced photosynthetic efficiency. Additionally, acetic acid reduced oxidative damage, as evidenced by decreased MDA levels across genotypes: 10.7%, 32.4%, and 10.4% reductions at 10 mM in Messenger, Tyson, and GSS 8529, respectively, and 10.6%, 31.6%, and 9.7% reductions at 20 mM in the same genotypes. These findings highlight the concentration-dependent efficacy of acetic acid in mitigating water stress.

2. Melatonin Increases Leaf Area and Antioxidant Activity Under Water Deficit

Application of 100 µM melatonin under PEG-induced water deprivation (8% and 12%) significantly increased specific leaf area, with the highest improvements observed in the Messenger and Tyson genotypes. Melatonin also enhanced photosynthetic performance under 12% PEG, with the Tyson genotype showing a 64.3% increase in actual photochemical efficiency ($\Delta F/Fm'$), indicating improved photochemical and photosynthetic capacity. Additionally, melatonin treatment increased peroxidase activity across all genotypes under 8% PEG water deprivation and significantly reduced MDA content under both 8% and 12% PEG conditions, highlighting its role in mitigating oxidative stress and enhancing water deficit tolerance.

3. Spermine Stimulates Plant Growth and Reduces Oxidative Stress

Application of 0.2 mM spermine foliar spray significantly enhanced the tolerance of sweet corn genotypes to PEG-induced water deprivation by promoting growth and reducing oxidative stress. Spermine increased root and shoot lengths across all genotypes,

with the Tyson genotype showing a significant 90.6% increase in shoot length under 12% PEG water deprivation. It also improved fresh and dry root and shoot weights, countering the reductions caused by water deprivation. Additionally, spermine enhanced relative chlorophyll content and photosynthetic pigments, with the Messenger genotype displaying a significant 327.5% increase in chlorophyll-b content under 12% PEG and the Dessert genotype showing a 41.5% reduction in MDA content, reflecting decreased oxidative damage. These findings demonstrate spermine's potent role in improving plant growth, photosynthetic efficiency, and resilience under water deficit conditions.

4. *Blue Light Promotes Plant Growth While Higher Red Light With UV-C Flashes Hinders Plant Development*

Blue light (Light 1) significantly promoted root volume and fresh root weight in spinach, enhancing overall plant growth. In contrast, red light combined with UV-C radiation (Light 3) severely inhibited growth parameters, including root and shoot lengths and biomass. The combination of Light 3 and 2.5% PEG-induced water stress proved fatal to the plants.

7. PRACTICAL UTILIZATION OF RESULTS

1. The results indicate that using foliar acetic acid can be a viable approach to enhance the ability of sweet corn to withstand water deprivation via increased crop output and the plant's ability to tolerate stressful conditions. Tailoring treatments based on specific genotypes maximize development by improving photosynthetic efficiency and enhancing antioxidant defenses to minimize oxidative damage. The foliar acetic acid application provides a cost-efficient and environmentally friendly approach to enhance resistance to water deprivation. Field applications should optimize the concentration of acetic acid by considering the genotype.
2. Acetic acid at both concentrations (10 mM and 20 mM) had beneficial effects in alleviating the negative consequences of water deprivation. However, the concentration of 10 mM in genotype Tyson often yielded comparable outcomes in terms of specific root length, specific shoot length, root volume, chlorophyll content, and oxidative stress indicators, particularly when used in conjunction with 5% PEG. This concentration also exhibited a consistent defensive reaction across several genotypes in the presence of water deprivation. Hence, the 10 mM acetic acid concentration may be the optimal and well-rounded option for improving the potential of sweet corn to withstand water scarcity.
3. Foliar application of melatonin can be utilized in agricultural practices to improve crop resilience, particularly in water deficit areas. All four genotypes (Messenger, Dessert, Royalty, and Tyson) reflect improved resilience to water deprivation when treated with melatonin. The study suggests that these genotypes are suitable for cultivation, especially in water-deficit environments, with the application of melatonin to enhance stress tolerance.
4. Foliar application of 0.2 mM spermine significantly enhances stress tolerance in sweet corn genotypes by mitigating the adverse effects of PEG-induced water deprivation. The results suggest that spermine can be effectively used to enhance crop resilience and productivity in water-limited environments, making it a valuable addition to agricultural practices, particularly in controlled hydroponic systems making hydroponic farming more resilient to environmental stressors.
5. Under LED lamps, improving the growth and quality of spinach plants requires optimized light qualities, ensuring a balanced blue-to-red ratio, and avoiding

exposure to harmful UV-C radiation. Using tools such as SPAD meters and spectrophotometry, farmers can effectively monitor relative chlorophyll content and photosynthetic pigments to make precise adjustments to lighting and watering in controlled environment agriculture settings, like vertical farming and hydroponics to control environmental factors effectively and consistently produce high-quality spinach.

8. SUMMARY

With the rapid progression of climate change, we are witnessing an increase in both the frequency and intensity of abiotic stresses like drought, which present considerable obstacles to global agricultural output and food security. The challenges of water scarcity, exacerbated by erratic weather patterns, have a significant impact on plant growth and productivity, particularly during critical developmental stages. Given the urgent need to enhance crop resilience under stress conditions, this study addresses a critical issue in agricultural research: identifying effective, sustainable strategies to improve plant performance during periods of water scarcity. This research focuses on the use of protective agents and the optimization of growth conditions to bolster plant resilience.

The primary aim of the study was to evaluate the effects of various plant protective agents acetic acid, melatonin, and spermine on enhancing water deficit tolerance in sweet corn genotypes under controlled hydroponic conditions. Additionally, the study examined the impact of different light qualities on spinach growth, both under normal and water-deprived conditions. Three separate experiments on sweet corn assessed the effects of foliar applications of acetic acid, melatonin, and spermine on morphophysiological and biochemical traits under water deficit conditions induced by polyethylene glycol (PEG). Spinach trials focused on germination parameters under PEG-induced water deprivation and the effects of different light spectra on plant traits.

Under water deficit conditions, the effects of acetic acid foliar application were examined on three sweet corn genotypes (Messenger, Tyson, and GSS 8529). The results indicated that acetic acid could mitigate the adverse impacts of water deprivation by enhancing key physiological and biochemical traits. The treatment led to genotype-dependent improvements in root and shoot lengths, root volume, specific leaf area, chlorophyll content, photosynthetic efficiency, and antioxidant defense mechanisms. The Tyson genotype showed the most pronounced response, with notable enhancements in growth parameters, stomatal conductance, chlorophyll content, and reduced oxidative stress markers.

To assess the effect of melatonin foliar treatment under two PEG concentrations, four sweet corn genotypes (Dessert, Messenger, Tyson, and Royalty) were evaluated. The findings suggest that applying 100 µM melatonin effectively alleviates the negative effects of water deficit by enhancing morphophysiological and biochemical traits. Significant improvements

in root and shoot growth, fresh and dry weights, root volume, and specific leaf area were observed, indicating better growth and biomass accumulation under water-deprived conditions. Melatonin treatment also led to significant enhancements in relative chlorophyll content, photosynthetic pigments, and stomatal conductance, suggesting improved water retention and photosynthetic efficiency. The increased photosynthetic performance, coupled with improved maximum efficiency of photosystem II, supports the hypothesis that melatonin acts as a potent plant hormone, boosting the resilience of sweet corn to water deprivation.

In terms of biochemical responses, melatonin treatment reduced lipid peroxidation and oxidative damage, as shown by lower malondialdehyde (MDA) levels and enhanced peroxidase activity across the genotypes.

Similarly, spermine treatment exhibited ameliorative effects under PEG-induced water deficit in the four sweet corn genotypes, showing comparable improvements to those observed with melatonin. Spermine application enhanced root and shoot growth, biomass accumulation, photosynthetic pigment content, and stomatal conductance, while also increasing antioxidant enzyme activity. Notably, significant increases in growth and biomass were recorded in the Dessert and Tyson genotypes, while the Messenger and Royalty genotypes displayed moderate improvements. Additionally, spermine reduced oxidative stress markers, with a particularly significant decrease in MDA levels in the Dessert genotype, underscoring its potential to bolster antioxidant capacity and plant resilience.

The study also investigated the impact of different PEG concentrations used to simulate water deprivation. As PEG levels increased, a marked decline in growth parameters and photosynthetic pigments was observed, highlighting the direct relationship between PEG concentration and the severity of water deprivation. However, treatments with spermine and melatonin consistently provided protective effects across both PEG concentrations, with spermine showing more pronounced benefits under higher stress levels.

Water is crucial for seed germination, and its absence significantly impacted spinach seed performance. Results for germination parameters under water deprivation emphasized the critical role of adequate water availability in seed germination and early growth stages.

In experiments involving different light qualities, spinach demonstrated varied responses depending on the wavelength of light exposure. Blue light promoted growth and photosynthetic traits, while red light had a lesser effect. However, exposure to UV-C

radiation, especially in combination with water deficit conditions, led to severe physiological damage and reduced growth. These findings suggest that optimizing light quality is vital for supporting plant growth and stress resilience, particularly in controlled environments like greenhouses.

Overall, this study highlights the effectiveness of acetic acid, melatonin, and spermine in enhancing water deficit tolerance by improving growth, photosynthetic efficiency, and oxidative stress mitigation in sweet corn. The results indicate genotype-specific responses, suggesting that targeted applications of these protective agents can be an effective strategy for increasing crop resilience. Moreover, optimizing light conditions can further enhance plant development under stress, providing valuable insights for practical crop management strategies aimed at improving productivity in the face of climate-induced water scarcity.

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10. PUBLICATION LIST

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List of publications related to the dissertation

Foreign language international book chapters (1)

1. **Zargar, T. B.**, Basal, O., Veres, S.: Exogenous application of plant metabolites to enhance abiotic stress tolerance in plants.
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11. DECLARATION

STATEMENT

I wrote this thesis in the framework of the University of Debrecen Kerpely Kálmán Doctoral School for the purpose of obtaining a doctoral degree (Ph.D.) at the University of Debrecen.

Debrecen, 13/02/2025

…….....

signature of the candidate

Tahoora Batool Zargar

STATEMENT

I hereby certify that the doctoral candidate Tahoora Batool Zargar has carried out her work under my supervision within the framework of the above-mentioned Doctoral School between 2020-2024. The candidate has made a decisive contribution to the results of the thesis through her independent creative work, and the thesis is the candidate's independent work. I recommend that the thesis be accepted.

Debrecen, 13/02/2025

…….....

signature of the supervisor

Dr. Szilvia Veres

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