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Genotype-dependent resilience mediated by melatonin in sweet corn

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Abstract

Background Water deficits, exacerbated by climate change and unpredictable weather, have become a significant global challenge to agricultural productivity. In this context, exogenous melatonin treatment is well documented as a stress alleviator; however, its effects on various biological processes, particularly in less-explored genotypes, remain understudied. This study aimed to enhance water deficit resilience in sweet corn by applying foliar melatonin to four genotypes-Messenger, Dessert, Royalty, and Tyson under two levels of water deprivation induced by polyethylene glycol at 8% and 12% concentrations in a hydroponic, controlled environment.

Results The melatonin treatments were assessed for their impact on various morphological, physiological, and biochemical parameters under both normal and water-deficit conditions. Under severe water deprivation (12% PEG), melatonin increased root length by 75%, peroxidase activity by 31% while reducing malondialdehyde content by 34% in genotype Dessert indicating enhanced antioxidant defense and reduced oxidative damage. Likewise in genotype Royalty, stomatal conductance increased by 68%, with increasing specific area by 125% on melatonin treatment under severe water deprivation. The treatment also improved chlorophyll-a content by 93% in Royalty and 37% in Tyson, while decrease in malondialdehyde levels by 42% in Tyson, indicating reduced oxidative damage under severe water deprivation. In addition, melatonin increased photosystem II efficiency (Fv/Fm) in all genotypes with 27% increase in Royalty and improved quantum yield across all genotypes, regardless of the water deficit level.

Conclusion Overall, melatonin treatment showed genotype-specific and dose-dependent effects in mitigating water deficit effects, offering a promising strategy to improve crop resilience and productivity in limited water environments. These results suggest the practical application for integrating melatonin treatments into sustainable agricultural practices, such as improving water deficit tolerance in sweet corn and potentially other crops, to maintain productivity under adverse climatic conditions.

Keywords Phytohormone, Abiotic stress, Water deprivation, Genotypes

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Introduction

Plants are exposed to a variety of environmental stresses during growth and development in both natural habitats and agricultural settings. Among the many stressors, drought stands out as a severe phenomenon that has a significant impact on plant productivity. The presence of water is crucial in different physiological processes, including growth, development, and metabolism, since it makes up approximately 80–95% of the total fresh biomass of the plant [1, 2]. Hence, it is widely held that drought is the prime environmental determinant impacting many plant species, especially in drought-prone regions of the world, and the most important threat to future food security worldwide [3, 4]. Water deficit conditions arise because of less or lack of rainfall resulting in reduced soil water content and low water potential in shoot, for example, leaves and stems [5]. It is crucial to maintain an ideal amount of water for suitable growth and development of plants. Going beyond such an optimal level of soil moisture variability could be detrimental to grain yield and quality. Likewise, insufficient water availability within the rhizosphere curtails plant development, which in turn prevents the absorption of nutrients [6]. Grain crop productivity has lately dropped significantly because of insufficient water supply, and the prevailing effects of global warming and climate change are anticipated to exacerbate the situation [7, 8].

Agricultural practitioners are introducing numerous approaches to enhance drought stress tolerance, among them focusing on the use of exogenous regulators, chemicals, synthetic hormones, and compounds. These protective agents hold considerable potential in enhancing drought resistance across different stages of plant development [9].

Melatonin (N-acetyl-5-methoxytryptamine) is an indole-based molecule, byproduct of tryptophan and belongs to a class of low molecular weight phytohormones that serve to enhance plant tolerance to abiotic stresses [10–12]. Since the late 1990s, when melatonin was identified in plants, this molecule has been characterized as a very potent antioxidant and an effective plant growth regulator with very significant roles in crops under stress, such as wheat, barley, corn, and rice [13]. It regulates critical processes such as root and bud growth, leaf aging, photoprotection, and seed germination. Acting as a free radical scavenger, melatonin helps in the maintenance of redox homeostasis, alleviating the impact that environmental stressors on plants [14, 15]. Exogenous melatonin treatment has been reported to alleviate various stresses in plants by reducing reactive oxygen species (ROS) levels, enhancing antioxidant enzyme activity, and protecting cellular structures [16]. Melatonin also strengthens plant stress tolerance in grape, mustard, kiwifruit, maize, and, among other species of plants, to alleviate the effects of heavy metal, drought, cold, and salt stress by boosting antioxidant defenses [17–21]. Melatonin enhances the level of chlorophyll and the efficiency of photosystem II while decreasing oxidative damage to improve plant tolerance against stress [22].

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 [23]. Farmers are increasingly turning 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. Its popularity among consumers stems from its unique taste, pleasant flavor, and sweetness. Specifically bred to enhance sugar content, sweet corn matures in just 75 to 90 days after sowing [24]. Sweet corn has a diverse array of physiological constituents, including sugars, starch, water-soluble polysaccharides, proteins, vitamins, and minerals, which contribute to its nutritional value. Due to its elevated fiber content and reduced cholesterol levels, it is a beneficial inclusion in a nutritious diet [25]. Sweet corn is becoming recognized as a superfood for health-conscious persons due to its nutritional profile, which is equivalent to that of high-priced vegetables such as cauliflower and cabbage. 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, particularly when cooked. Contrary to popular assumption, cooked sweet corn maintains antioxidant qualities even after losing vitamin C [26]. Being a member of the grass family, sweet corn is harvested at the milk stage of endosperm development, ensuring its kernels are soft, succulent, and sweet. Unlike field corn, which is harvested when fully mature, sweet corn is picked when immature, offering a vegetable rather than grain. There are many kinds of sweet corn available, and regional tastes vary. The most well-known kind of sweet corn is still the conventional yellow type. Variations in sweetness among sweet corn genotypes can be attributed to genetic differences influencing starch synthesis; genes such as sugary (SU) and shrunken (SH) modify the amounts of sugar and starch in kernels [23].

Water shortages, intensified by climate change and unpredictable weather, pose a significant threat to the growth and development of sweet corn plants [27]. Water is essential for a large part of biomass in plants and is essential for various physiological processes, including growth and metabolism. Extended periods of water scarcity can significantly reduce sweet corn productivity. Exploring the role of melatonin in mitigating the adverse

effects of water scarcity on sweet corn is crucial. Melatonin, a powerful phytohormone and antioxidant, has demonstrated promising results in enhancing plant tolerance to various abiotic stresses, including drought [9]. Even in maize seedlings under drought melatonin reduced oxidative damage, improved overall plant growth [9]. By understanding how melatonin treatment affects sweet corn plants under water deficit conditions, we can develop effective strategies to improve its resilience and productivity in drought-prone areas. Our research aims to explore the potential of melatonin treatment in alleviating the effects of water scarcity on sweet corn by applying melatonin externally to four different sweet corn genotypes that have not been previously examined in this context and subjecting them to two levels of water deficit induced by polyethylene glycol (PEG). In hydroponics, PEG works osmotically by reducing water potential, leading to water being drawn out of plant tissues. This results in water stress due to depletion of water from the tissues. This experimental setup is commonly used to simulate drought stress in plants for scientific studies [28]. By applying melatonin and inducing water deprivation using controlled concentrations of polyethylene glycol (PEG), we will systematically assess the physiological and biochemical responses of each genotype under both well-watered and water-deficit conditions. Our aim is to determine whether the effects of melatonin differ among genotypes and how it may contribute to improved water deficit resilience. In this experiment, four sweet corn genotypes (*Zea mays* var. saccharata) were evaluated: Dessert, Messenger, Tyson, and Royalty. Messenger is a late-maturing genotypes, while Tyson and Royalty are mid-season, and Dessert ranges from early to mid-early maturity. Messenger and Dessert are versatile, suitable for both fresh consumption and processing, whereas Tyson is primarily cultivated for fresh market sales. These genotypes exhibit distinct resistance traits: Messenger is highly wind-resistant, making it suitable for regions prone to heavy winds; Tyson offers broad-spectrum disease resistance; Dessert varieties are well-suited for early planting with strong resistance to multiple diseases; and Royalty is notable for its stress tolerance and resistance to specific viruses and rust. In terms of kernel characteristics, Tyson and Dessert are valued for their sweet, smooth kernels, while Royalty produces robust kernels with high yield stability [29–31]. Despite these well-documented traits, data on the water deficit tolerance of these genotypes remain limited or unavailable. Based on previous research suggesting the range of PEG concentrations used to induce water deprivation, the effects of a small difference in PEG concentrations, specifically 8% and 12%, were studied to examine plant responses across a narrow spectrum of moderate to severe water deprivation [32–35]. This study was designed to address this gap by examining their responses to water deficit conditions and melatonin treatment, leveraging their diverse characteristics to provide a comprehensive understanding of genotype-specific resilience mechanisms and offer potential strategies for optimizing sweet corn production in water-limited environments.

Materials and methods

Plant material

The experiment was carried out at the Faculty of Agricultural and Food Sciences and Environmental Management, Department of Applied Plant Biology, University of Debrecen, Hungary. This study was conducted in a controlled climatic room focused on four sweet corn genotypes (*Zea mays* var. saccharata): Messenger, Dessert, Royalty, and Tyson with maintained relative humidity between 65 and 75%, 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. The seeds were rinsed several times with tap water before being sterilized with a 6% hydrogen peroxide solution. After 15 min, the seeds are washed with distilled water and immersed in a 0.01 M calcium sulphate solution for two hours, then thoroughly rinsed with distilled water. Healthy and regular sized seeds were then germinated geotropically between moistened filter sheets at 22 °C. Seedlings (VE growth stage) (Zadok's scale 09) [36] with good vigor, were transplanted into plastic pots (1.7 L) under hydroponic conditions having the nutritional solution composition indicated by Marschner et al. [37] and is changed in every three days with fresh one.

Experimental procedure and treatment pattern

After two weeks, 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, 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. At this stage, foliar application of 100µM 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 once a day in the morning hours, using a nozzle adjusted to dispense 1 mL of solution per spray. Each session consisted of three sets of sprays per plant. Thus, we have six different treatments: control treatment with optimal conditions for growth (with foliar application of double distilled water), 100µM melatonin, 8% PEG, 12% PEG, 8% PEG+100µM melatonin, and 12% PEG+100µM

melatonin each with three replicates. The total number of pots was 72 (4 genotypes ×6 treatments×3 replications). 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.

Morphological parameters

To assess morphological parameters, we measured several key parameters, each in three replicates. Root and shoot lengths were determined using a standard scale. Root volume was gauged through the water displacement method. The specific leaf area (SLA) of each plant's last fully grown leaves was analyzed by punching out five leaf discs with known surface area and were dried at 104.5 °C for 24 h till constant weight was achieved [38]. The SLA of each leaf was calculated by dividing the leaf area by the corresponding leaf dry weight [38].

Physiological and biochemical parameters

Relative chlorophyll content (SPAD) values were recorded at V8-V9 vegetative stage using a SPAD-502Plus (Konica Minolta, Japan) to evaluate the relative chlorophyll content each in three repetitions for each treatment, from the last fully developed leaves.

Photosynthetic pigments, including chlorophyll-a, chlorophyll-b, and total carotenoids, were analyzed from the last fully developed leaves using the extraction methods outlined by Moran and Porath [39] and the spectrophotometric measurement techniques described by Wellburn [40]. The leaf samples were immersed in N, N-dimethylformamide (DMF) solvent for 48 h to extract the pigments. The concentrations of the pigments were then quantified using UV–VIS spectrophotometry with a Metertech SP-830 PLUS (Taiwan) at specific wavelengths as detailed by Wellburn [40].

The HPLC method was used to analyze Lutein content in leaf extract using a Nucleosil C18 column and a UV/VIS detector (JASCO, Japan). Zeaxanthin was injected as a standard compound to identify peaks and calculate pigment contents [41].

The chlorophyll-fluorescence measurements were carried out with PAM-2100 portable chlorophyll fluorometer (Walz Gmbh, Germany). The youngest fully developed leaves were dark-adapted for 20 minutes. After dark adaptation, the initial fluorescence (Fo) was excited by weak light (0.1 µmol m^{-2} s^{-1}). The maximal fluorescence (Fm) was induced by white saturating flash (8000 µmol m^{-2} s^{-1}) (fast phase of chlorophyll fluorescence). 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 (ΔF/Fm'), also referred as Yield, was recorded [42].

Stomatal conductance was measured with an AP4 porometer (Delta-T, UK) after the calibration under the present temperature from the last fully expanded leaves in three repetitions at V8-V9 vegetative stage.

To determine the malondialdehyde (MDA) content of lyophilized leaf samples trichloroacetic acid (TCA) was used as an extraction buffer. The process involved mixing crushed leaf powder with 0.1% TCA, centrifuging, and transferring the supernatant to a tube containing 20% TCA and 0.5% thiobarbituric acid. The mixture was heated, cooled, and centrifuged again. The absorbance of the solution was measured at 532 nm, indicating the MDA content in the original leaf sample [43].

For peroxidase activity lyophilized leaf sample was homogenized in phosphate buffer, then centrifuged to generate a clean supernatant. A reaction mixture was prepared using sodium acetate buffer, hydrogen peroxide, and o-anisidine, and a spectrophotometer was used to measure absorbance at 460 nm, allowing tracking of absorbance variations over time [44].

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 the GenStat Release 12.1 to analyze the differences between treatments and genotypes. Origin Pro was used for principal component analysis. (PCA).

Results

Morphological responses to water deprivation and melatonin treatment

Osmotically stimulated water deprivation via PEG elicited pronounced reductions in both root and shoot lengths across the evaluated sweet corn genotypes, with distinct genotypic variability (Table 1). Genotype Tyson significantly ($p \leq 0.05$) exhibited the most severe reduction in root volume, experiencing a decrease of 70.1% under 8% PEG and 88.7% under 12% PEG, underscoring its heightened susceptibility to osmotic water deprivation. In contrast, the treatment with melatonin conferred significant ameliorative effects across all genotypes, with 100% improvement in Tyson under severe water deprivation. Specifically, in Dessert, melatonin treatment resulted in a statistically ($p \leq 0.05$) significant enhancement of root length by 21.5% under moderate water deprivation (8% PEG) and an unprecedented 75.3% increase under severe water deprivation (12% PEG). Messenger, another genotype, demonstrated consistent

Table 1 Effects of individual and combined treatments of melatonin (MEL) and PEG (8% and 12%) on the average ($n=3$) root length (cm), shoot length (cm), root volume (ml), and specific leaf area ($cm^2\ g^{-1}$) in various sweet corn genotypes (Dessert, Messenger, Tyson, Royalty)

Trait	Treatment	Dessert	Messenger	Tyson	Royalty
Root length	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}
Shoot length	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 Volume	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}
Specific leaf area	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}

*Note: Different small letters indicate significant differences ($p \le 0.05$) among the treatments within each genotype, and different capital letters indicate significant differences ($p \le 0.05$) among genotypes within each treatment

improvements with melatonin, recording increases of 32.6% and 32.5% in root length under moderate and severe water deprivation conditions, respectively.

Shoot lengths were similarly influenced by melatonin, with Dessert recording a notable increase of 16.2% under moderate water deprivation and a substantial 70.1% increase under severe water deficit. Royalty recorded even more pronounced improvements in shoot length, with increases of 34.9% under moderate and 76.6% under severe water deprivation, highlighting the genotype's responsive interaction with melatonin under water deficit. The less robust melatonin-mediated improvement in genotypes like Tyson stems from genetic variability affecting stress tolerance, hormonal signaling, antioxidant activity, and root system integrity. Understanding these differences can help improve genotype-specific strategies for improving water deficit resilience.

Specific Leaf Area (SLA), an important indicator of leaf morphology, showed a marked decrease under PEG treatments, yet was significantly ($p \le 0.05$) improved with melatonin treatment (Table 1). In Dessert, melatonin induced a 25.4% increase in SLA under 8% PEG and a significant 224.2% increase under 12% PEG. Messenger and Royalty also recorded substantial amelioration in SLA, further corroborating melatonin's pivotal role in mitigating water deficit-induced morphological impairments.

Light-harvesting pigments and photochemical conversion efficiency

Chlorophyll-a retention under PEG-induced water deficit revealed distinct genotype-specific responses, with melatonin significantly ($p \le 0.05$) enhancing chlorophyll-a levels across the board. Dessert, a genotype previously uncharacterized for its water deprivation tolerance, exhibited a 27.2% increase in chlorophyll-a content under severe water deprivation (12% PEG) with melatonin, whereas Messenger demonstrated a robust 36.9% increase, indicative of its strong photosynthetic resilience (Table 2). Results of Tyson and Royalty were also noteworthy, where melatonin treatment resulted in chlorophyll-a level increases of 31.8% and a remarkable 92.6%, respectively, under severe water deprivation, underscoring melatonin's broad-spectrum efficacy in enhancing photosynthetic pigment stability under water deprivation.

Chlorophyll-b, essential for the light-harvesting complex in photosynthesis, revealed a substantial variability among the genotypes (Table 2). Messenger displayed a pronounced 160.9% increase in chlorophyll-b content under severe water deprivation with melatonin treatment, suggesting a unique photoprotective mechanism facilitated by melatonin in this genotype. Tyson also demonstrated a significant ($p \le 0.05$) increase of 187.0% in chlorophyll-b, further reinforcing the differential genotypic response to melatonin. Conversely, Royalty exhibited a reduction in chlorophyll-b, indicating potential genotype-specific limitations in melatonin's efficacy in modulating this pigment.

The analysis of total carotenoid and lutein content, both critical for photoprotection and antioxidative defence, revealed significant reductions under PEG induced water deprivation, with an improvement upon melatonin treatment. Tyson recorded a 60.3% decrease in carotenoid content under severe water deprivation, which was remarkably reversed by a 116.7% increase with melatonin treatment, highlighting melatonin's restorative potential. Dessert exhibited a 44.7% increase in carotenoid content under moderate water deprivation with melatonin, indicative of a strong antioxidative response. Messenger and

Table 2 Effects of individual and combined treatments of melatonin (MEL) and PEG (8% and 12%) on the average ($n=3$) chlorophyll-a, chlorophyll-b, total carotenoids content (mg g^{-1}) and lutein content (µg $µL^{-1}$) in various sweet corn genotypes (Dessert, Messenger, Tyson, Royalty)

Trait	Treatment	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	Control	81.27^{bA}	60.63^{aB}	71.5^{dAB}	85.86^{eA}
	MEL	102.2^{eA}	79.02^{abB}	61.90^{bC}	77.59^{cB}
	8% PEG	93.25^{dA}	70.10^{aB}	65.19^{cB}	75.01^{bB}
	12% PEG	55.01^{aB}	81.75^{abA}	57.91^{aB}	81.64^{dA}
	8% PEG + MEL	89.75^{cB}	97.82^{bA}	78.91^{eC}	75.20^{bD}
	12% PEG + MEL	102.4^{eA}	68.72^{aBC}	70.11^{dB}	58.82^{aC}

*Note: Different small letters indicate significant differences ($p \le 0.05$) among the treatments of each genotype, and different capital letters indicate significant differences ($p \le 0.05$) among genotypes within each treatment

Tyson recorded a significant ($p \le 0.05$) increase in lutein content, with levels increasing by 39.6% and 21% respectively, under moderate water deprivation with melatonin treatment, while in Dessert decrease was observed suggesting a genotype-specific enhancement of antioxidative capacity not previously documented in sweet corn. Further, decrease in lutein content in Messenger and Royalty was recorded under severe water deprivation with melatonin treatment.

Stomatal conductance, a key physiological trait influencing water use efficiency, varied significantly across genotypes, with melatonin treatment improving this trait under water deprivation. Messenger exhibited a significant ($p \le 0.05$) 139.3% increase in stomatal conductance under severe water deprivation with melatonin, suggesting an enhanced ability to maintain water retention and gas exchange efficiency under adverse conditions (Fig. 1). Similarly, Tyson and Royalty displayed substantial increases in stomatal conductance 168.4% and 68.3%, respectively validating melatonin's role in modulating this critical physiological response across diverse genetic backgrounds.

Relative chlorophyll content, as indicated by SPAD values, demonstrated significant ($p \le 0.05$) genotype-specific responses to water deprivation and melatonin treatment (Fig. 2). The significant results were recorded in Messenger, where SPAD values increased by 100.8% under severe water deprivation with melatonin, reflecting a significant stabilization of chlorophyll content under water deficit.

The maximum photochemical efficiency of photosystem II (Fv/Fm) was adversely affected by PEG-induced water deprivation across all genotypes, yet melatonin treatment facilitated a notable recovery (Table 3). Tyson exhibited a 26.0% increase in Fv/Fm under severe water deprivation with melatonin, suggesting a protective effect of melatonin on PSII efficiency. The potential photosynthetic capacity (Fv/F0) also varied significantly among genotypes, with Royalty displaying a 143.0% increase under severe water deprivation with melatonin, a finding that suggests melatonin not only protects but may also enhance the recovery potential of photosynthetic machinery in less resilient genotypes. Similarly, actual photochemical efficiency (Yield/ΔF/Fm') was enhanced across all genotypes with melatonin, with Dessert showing a 34.6% increase under severe water deprivation, indicating melatonin's efficacy in mitigating declines in photosynthetic performance under water deprivation.

Oxidative biomarkers and antioxidative enzyme dynamics

Malondialdehyde (MDA) content, a reliable marker of lipid peroxidation and oxidative stress, was significantly increased under PEG-induced water deprivation, reflecting extensive cellular damage (Fig. 3). However, melatonin treatment effectively mitigated these increases across all genotypes. In Dessert, melatonin reduced MDA levels by 16.7% under moderate water deprivation (8% PEG) and by 34.0% under severe water deprivation (12% PEG), demonstrating a significant reduction in oxidative damage. Similarly, Tyson, which exhibited the highest sensitivity to oxidative water deprivation with a 140.4% increase in MDA under severe water deprivation, recorded a significant 42.0% reduction in MDA levels with melatonin, highlighting melatonin's strong antioxidative protective effect. Royalty exhibited a more moderate increase in MDA (31.8% under severe water deprivation), with melatonin reducing this by 26.5%, further confirming melatonin's broad-spectrum efficacy across different genotypes.

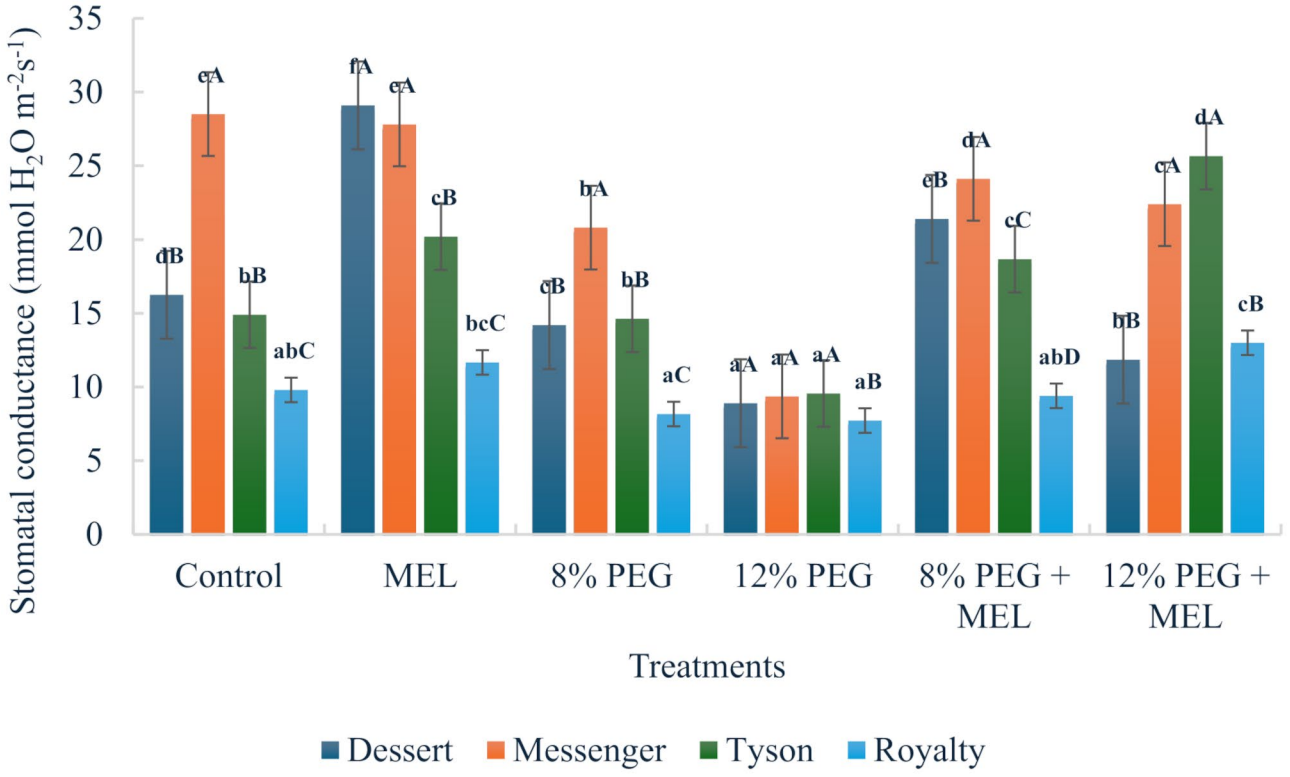

Fig. 1 Stomatal conductance (mmol H_2O m^{-2} s^{-1}) of sweet corn genotypes (Dessert, Messenger, Tyson, Royalty) under control, melatonin (100 µM), PEG (8% and 12%), and combined treatments. Error bars represent the standard error (SE). 12% PEG significantly reduced stomatal conductance ($p \leq 0.05$), while melatonin treatment increased, with Messenger recording the highest improvement, Tyson recovered well under severe stress, and Royalty had the weak but positive response. Different small letters indicate significant differences ($p \leq 0.05$) among the treatments within each genotype, and different capital letters indicate significant differences ($p \leq 0.05$) among genotypes within each treatment

Peroxidase (POD) activity, a crucial component of the antioxidative defence system, displayed significant genotypic variability in response to PEG water deprivation and melatonin treatment (Table 4). In Dessert, melatonin treatment enhanced POD activity by 115.9% compared to control conditions, with even greater increases observed under combined PEG water deprivation, where POD activity increased by 174.1% under moderate water deprivation. Messenger recorded a similar pattern, with melatonin boosting POD activity by 134.5%, further increasing under combined water deprivation conditions, indicating a robust antioxidative response. In contrast, Tyson exhibited a more complex response, with melatonin decreasing POD activity by 63.4% under control conditions but increasing it by 8.5% under moderate water deprivation and decreasing by 29.7% under severe water deprivation suggesting a nuanced interaction between melatonin and the antioxidative defence mechanisms in this genotype. Royalty, with a 37.7% increase in POD activity under moderate water deprivation with melatonin, also demonstrated melatonin's efficacy in restoring antioxidative capacity under water deprivation.

Discussion

Climate change with projection in temperate regions signifies a rise in temperature and a decrease in precipitation, which will negatively impact water availability shortly [45]. A rise in temperature will decrease maize's growing season and water requirements. However, with the temperature rise, there is a projected rise in evapotranspiration, resulting in an overall decrease in yield [45].

In our experiment, the main objective was to evaluate the alleviating effect of melatonin under water deprivation in four different sweet corn genotypes. Melatonin as a phytohormone is crucial in enhancing plant tolerance by mitigating abiotic stresses [10].

Malondialdehyde (MDA), a marker of lipid peroxidation, increased under PEG-induced water deprivation across all genotypes, with the highest content observed under 12% PEG treatment. Increased MDA content reflects high oxidative stress caused by osmotic imbalance. Similar results were recorded under drought, which increased oxidative stress in plant cells [46].

However, melatonin treatment under PEG-induced water deprivation decreased the MDA content in all genotypes, highlighting the potential of melatonin in

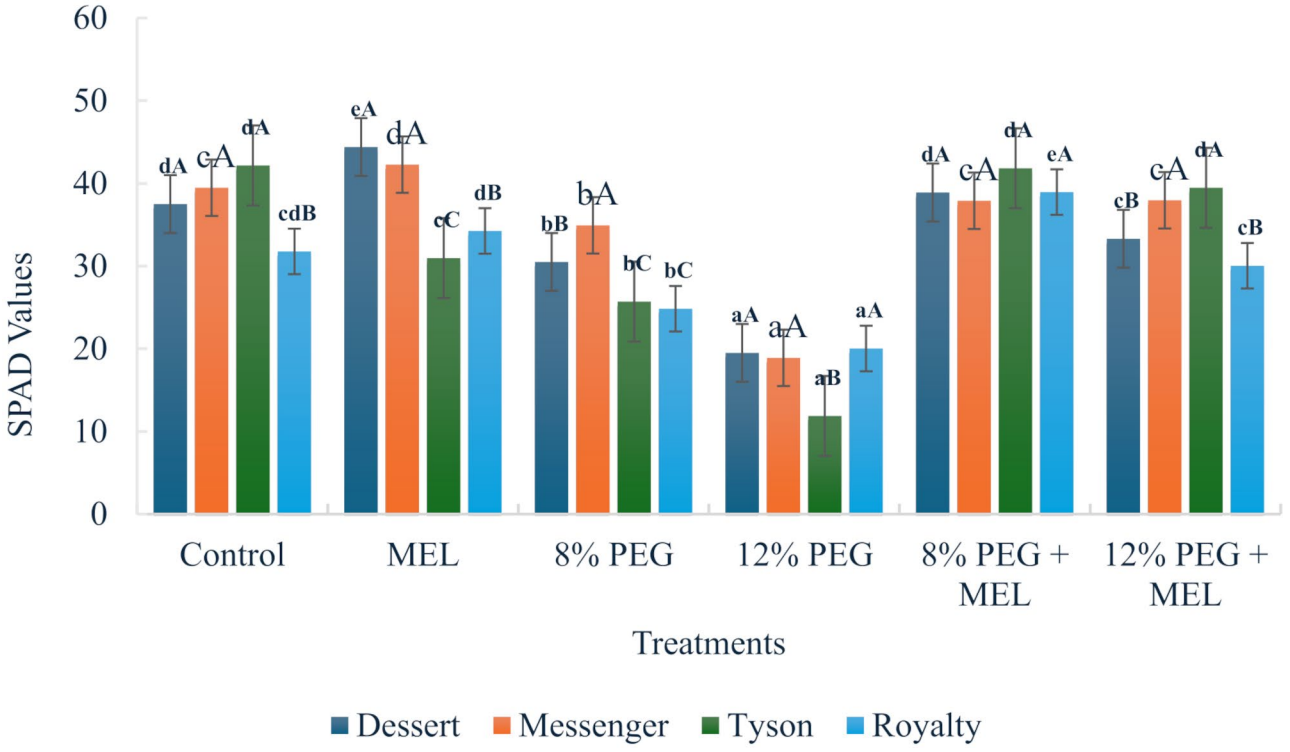

Fig. 2 SPAD values of sweet corn genotypes (Dessert, Messenger, Tyson, Royalty) under control, melatonin (100 µM), PEG (8% and 12%), and combined treatments. Error bars represent the standard error (SE). PEG significantly reduced SPAD values ($p \leq 0.05$), with the lowest values observed under 12% PEG. Melatonin improved SPAD values under both stress levels ($p \leq 0.05$), with Tyson showing highest improvement under combined treatments. Different small letters indicate significant differences ($p \leq 0.05$) among the treatments within each genotype, and different capital letters indicate significant differences ($p \leq 0.05$) among genotypes within each treatment

alleviating lipid peroxidation. According to Mahmoud et al. [9], melatonin significantly reduced MDA content under drought, improving cellular integrity and stability. Melatonin may regulate antioxidant defenses, helping to mitigate damage from reactive oxygen species [9]. The reduction in MDA content relates to increase in peroxidase activity with melatonin treatment, suggesting the activation of antioxidative defense systems to scavenge reactive oxygen species and prevent cellular damage. According to Wang et al. [47], melatonin upregulates the expression of genes related to antioxidant enzymes, including peroxidase.

For example, in genotype Royalty, the POD activity under 8% PEG+MEL treatment coincided with a notable reduction in MDA levels, indicating a robust antioxidative response.

In our study, potential photosynthetic capacity, maximum photochemical efficiency and the actual photochemical efficiency of PSII decreased under water deficit in all genotypes; however, the treatment with melatonin alleviated the adverse effect at both concentrations of PEG used. This could be possible as melatonin treatment can improve non-photochemical energy dissipation to enhance or change the xanthophyll cycle. Also, it is reported that melatonin can increase the efficiency of mitochondrial electrons in plants [47, 48]. The enhanced POD activity under reduced oxidative stress is likely responsible for stabilizing photosynthetic machinery, as reflected in improved chlorophyll fluorescence and pigment stability in all genotypes under severe water deprivation with melatonin treatment.

Under normal conditions, melatonin increased relative chlorophyll content (SPAD) in Dessert, Messenger, and Royalty, indicating its role in stabilizing chlorophyll and enhancing photosynthetic performance [49]. In contrast, Tyson showed a decrease in treatment with melatonin under normal conditions, which may reflect a complex interaction between environmental or physiological factors not directly related to melatonin's usual effects. Water deprivation, simulated with PEG, reduced SPAD values, particularly at higher PEG concentrations, due to decreased chlorophyll content and photosynthesis under drought stress [50]. Melatonin counteracted this effect by increasing SPAD across all genotypes, demonstrating its ability to protect chlorophyll from oxidative damage [51]. These findings align with studies highlighting melatonin's role in boosting photosynthetic capacity by enhancing chlorophyll biosynthesis and reducing degradation under stress conditions [9, 52].

Table 3 Effects of individual and combined treatments of melatonin (MEL) and PEG (8% and 12%) on the average ($n = 3$) Fv/Fm′, Fv/F0, ΔF/Fm in various sweet corn genotypes (Dessert, Messenger, Tyson, Royalty)

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}

*Note: 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

Table 4 Effects of individual and combined treatments of melatonin (MEL) and PEG (8% and 12%) on the average ($n = 3$) peroxidase activity (μmol min^{-1} g^{-1}) in various sweet corn genotypes (Dessert, Messenger, Tyson, Royalty)

Trait	Treatment	Genotypes			
		Dessert	Messenger	Tyson	Royalty
Peroxidase activity	Control	10.83^{aC}	8.33^{aD}	21.39^{cB}	25.01^{cdA}
	MEL	23.38^{dB}	19.53^{dC}	7.83^{aD}	26.94^{dA}
	8% PEG	10.92^{aC}	17.60^{cA}	15.82^{bB}	16.28^{aAB}
	12% PEG	14.61^{bC}	13.46^{bC}	29.64^{dA}	20.95^{bB}
	8% PEG + MEL	29.93^{eA}	19.17^{cdC}	17.16^{bC}	22.41^{bcB}
	12% PEG + MEL	19.09^{cA}	19.49^{dA}	20.85^{cA}	22.17^{bcA}

*Note: 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

Likewise, the effect of melatonin and PEG on total carotenoids, chlorophyll-a, and chlorophyll-b suggest that melatonin enhances plant resilience to water deficit conditions by supporting antioxidant systems and photosynthetic machinery. The results recorded for genotypes to melatonin treatment for improved carotenoid and chlorophyll content are consistent with the previous study by Nawaz et al. [53], who reported that melatonin treatment can decrease oxidative damage by stabilizing photosynthetic pigments and improving antioxidant

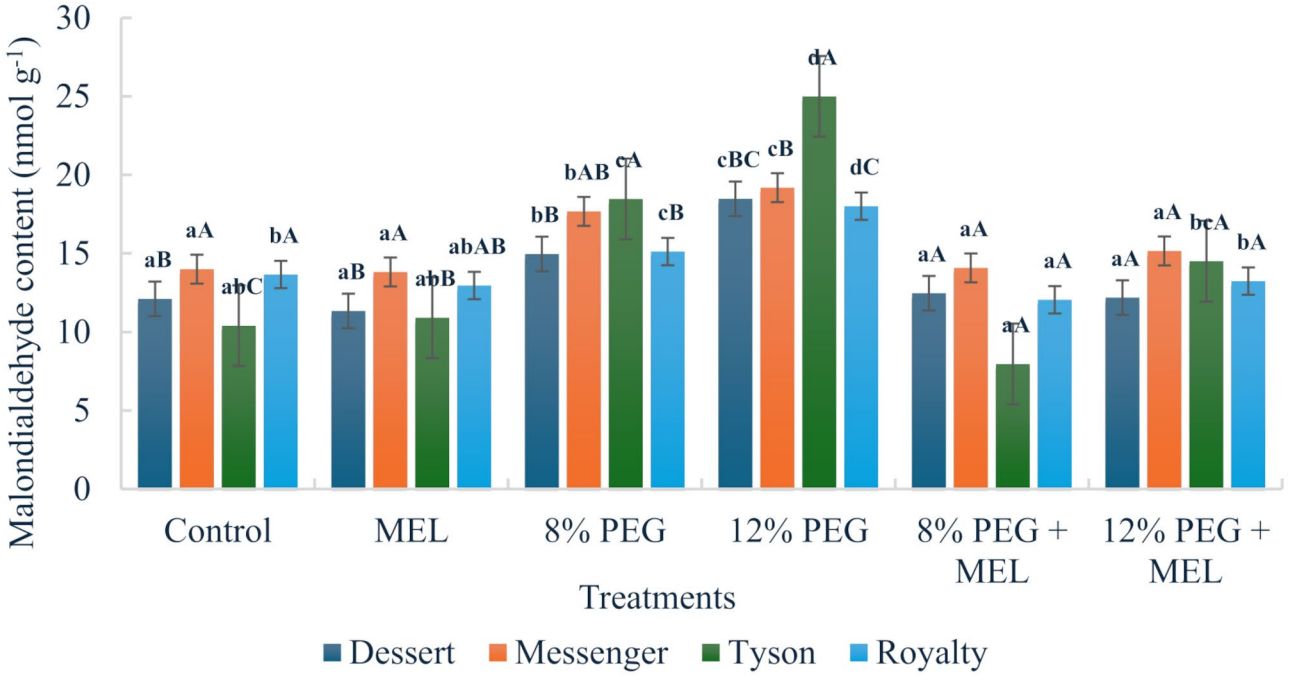

Fig. 3 Malondialdehyde content (nmol g^{-1}) in sweet corn genotypes (Dessert, Messenger, Tyson, Royalty) under control, melatonin (100 μM), PEG (8% and 12%), and combined treatments. Error bars represent the standard error (SE). PEG treatments significantly increased MDA content ($p \leq 0.05$), with the highest levels observed under 12% PEG, particularly in Tyson. Melatonin significantly reduced MDA levels under stress conditions ($p \leq 0.05$), with Tyson showing the strongest reduction under combined treatments. Different small letters indicate significant differences ($p \leq 0.05$) among the treatments within each genotype, and different capital letters indicate significant differences ($p \leq 0.05$) among genotypes within each treatment

enzyme activities. Under water deprivation, melatonin mitigates the adverse effects on pigment concentration, assisting plants in adjusting to stress by preserving essential pigments for defense and photosynthesis.

Conversely, the pigment level decline after PEG treatments, suggesting how water deficit may decrease or inhibit carotenoids and chlorophyll content. This aligns with the study of Mahmoud et al. [9], that drought stress affects photosynthetic machinery and promotes enzymes that damage chlorophyll pigments.

Moreover, an improvement in total carotenoids after melatonin treatment under high PEG concentration, particularly in the Tyson and Royalty genotypes, highlights that melatonin may improve the biosynthesis of protective pigments that function as photo protectants and antioxidants. This is consistent with findings by Zhao et al. [54], that melatonin stimulates the synthesis of carotenoids to minimize oxidative stress and stress-induced photodamage.

Lutein content recorded a varied response among treatments and genotypes. Melatonin treatment increased lutein content in Dessert and Messenger, while a decrease was recorded in Tyson and Royalty under normal conditions. In Dessert and Messenger, lutein content increased because of melatonin potential in improving carotenoid biosynthesis [49, 55]. The variation among genotypes could be attributed to differences in regulatory mechanisms of antioxidant defenses or secondary metabolites biosynthesis [56, 57]. Under water deprivation, varied responses were recorded among genotypes; the increase in lutein content in Messenger and Dessert can be attributed to stress-induced enhancement of the antioxidant defense system. 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 [58, 59]. Application of melatonin at a higher concentration of PEG, increased lutein content in Dessert and Tyson, suggesting melatonin's potential to further activate stress tolerance mechanisms and antioxidant pathways under high-stress conditions [12, 60].

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 [9]. 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, like osmotic stress, resulting in decreased stomatal conductance to prevent excess water loss [61]. Similar results were recorded in maize, where melatonin enhanced water use efficiency by improving stomatal conductance and photosynthetic capacity [9].

Decrease in oxidative stress and enhanced photosynthetic efficiency translated into enhanced morphological traits, such as root volume, shoot length, root length and specific leaf area. Melatonin improved root growth, which aligns with the previous research suggesting that melatonin can improve root architecture through different mechanisms like hormonal interactions, especially auxin. In *Arabidopsis*, melatonin improved root development by influencing auxin signaling pathways, supporting our results of increased root length within the Dessert genotype on melatonin treatment [55]. Contrariwise, the treatment with PEG to induce water deficit results in a significant decrease in root length, consistent with the observation of Verslues et al. [62], that absence of ideal amount of water can cause cell dehydration and reduce cell expansion in root tissues. In Tyson under 12% PEG, melatonin did not show a mitigative effect, suggesting responses may vary among genotypes, which could be genetic differences and how they respond to melatonin metabolism and water deficit, as genetic diversity plays a significant role in how plants respond to abiotic stresses [63].

Similarly, melatonin increased the shoot length compared to the control, suggesting its ability to enhance growth by hormonal regulation via interaction with auxins and gibberellins, which play an essential role in shoot growth [55]. Water deprivation reduced the shoot length in all genotypes, with a significant reduction at higher concentrations of PEG, which aligns with the known fact that osmotic stress limits water availability and hinders nutrient uptake, leading to stunted growth [62]. The SLA results recorded showed a general trend where SLA showed a slight decrease in genotype Dessert and Tyson but an increase in Royalty and Messenger on application with melatonin under normal conditions. These results suggest the potential role of melatonin in modifying leaf morphology to improve water retention or enhance light capture under varying environmental conditions. Water deficit treatments reduced SLA; a higher reduction was recorded at higher concentrations of PEG. Reduction in SLA due to water deprivation may be attributed to water conservation through reduced leaf expansion. This aligns with the previous study that osmotic stress has an adverse effect on plant growth and development [64]. However, on the application of melatonin under water deficit, SLA increased in all genotypes, with a higher percentage at higher concentrations of PEG, suggesting

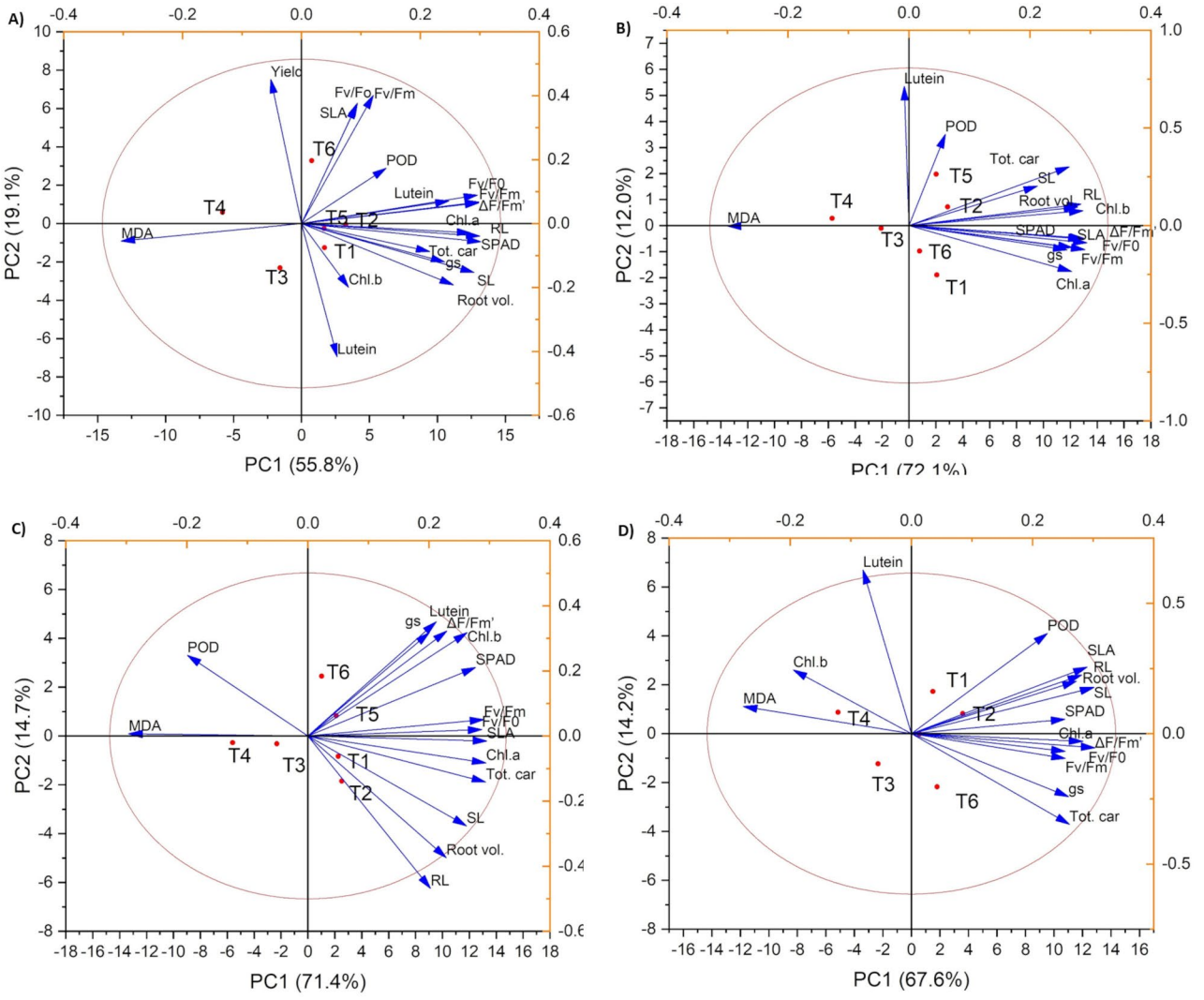

Fig. 4 (**A**) (Dessert), (**B**) (Messenger), (**C**) (Tyson), (**D**) (Royalty), PCA analysis. T1, Control; T2, Melatonin; T3, 8% PEG: T4, 12% PEG; T5, 8% PEG + Melatonin; T6, 12% PEG + Melatonin

melatonin regulatory and protective role of melatonin under osmotic stress [65].

The PCA analysis (Fig. 4A–D) underscores the distinct differences among the four genotypes (Dessert, Messenger, Tyson, and Royalty) in their physiological and biochemical responses to PEG-induced water deprivation and melatonin treatments. In genotype Dessert (Fig. 4A), water deprivation treatments (T3, T4) are strongly linked with high oxidative stress (MDA), highlighting its vulnerability to water deprivation, and melatonin treatments (T2, T5, T6) showed limited improvements in photosynthetic traits (Fv/Fm, SPAD) and antioxidative markers (POD, lutein). In genotype Messenger (Fig. 4B) moderate tolerance to water deprivation, clustering closer to MDA under water deprivation, but demonstrates better improvement of photosynthetic efficiency and antioxidative capacity with melatonin treatments. Tyson (Fig. 4C), recorded better resilience, exhibits clear water deficit mitigation under combined PEG and melatonin treatments (T5, T6), with strong associations with photosynthetic traits (Fv/Fm, SPAD), root volume, and antioxidative markers (POD, carotenoids). In contrast, genotype Royalty (Fig. 4D) emerges as the most tolerant genotype, showing the weakest association with MDA under water deprivation and the strongest correlations with yield-related traits (root volume, SLA, total carotenoids) and antioxidative markers (lutein, POD), particularly under combined treatments (T5, T6). The PCA biplots also reveal that Tyson and Royalty integrate stress mitigation and productivity more effectively, with tight clustering of melatonin treatments near yield-related traits, while Dessert and Messenger show weaker but still positive responses to melatonin. Overall, the PCA results highlight clear genotypic differences in water deprivation

responses, with Tyson and Royalty demonstrating superior resilience.

Future research

The findings of this study offer significant insights into role of melatonin in alleviating water deprivation, although numerous limitations should be addressed. The experiment was performed under controlled conditions, which may not entirely reflect the complexity of field environment. Subsequent trials should emphasize field studies to ascertain the effectiveness of melatonin treatment under diverse environmental conditions. These studies should explore the connections between melatonin and environmental factors, including soil composition, irrigation schedules, and regional climatic patterns. Moreover, integrating molecular methodologies, including transcriptome and proteomic analysis, should reveal the fundamental genetic and metabolic processes stimulated by melatonin. Identifying critical stress-responsive genes and regulatory networks will enhance deeper understanding of genotype-specific responses and facilitate the development of targeted interventions.

Conclusion

This study reveals the significant potential of exogenous melatonin treatment in enhancing sweet corn resilience to severe water deprivation. By investigating the responses of four different sweet corn genotypes-Messenger, Dessert, Royalty, and Tyson this research highlights the genotype-specific effects of melatonin treatment, with noticeable improvement in root and shoot growth, chlorophyll content, photosystem II efficiency, and oxidative stress markers. Genotype Royalty recorded the high resilience, driven by robust antioxidative defenses and efficient resource allocation. Tyson relied on pigment stability and enhanced photosynthetic performance for water deficit tolerance. Messenger recorded moderate improvements, with photosynthetic recovery and morphological adaptations as key mechanisms. Dessert exhibited limited responses, benefiting mainly from partial oxidative stress alleviation. These findings emphasize the need for genotype-specific strategies and further research to validate effectiveness of melatonin under field conditions and uncover molecular pathways for stress mitigation.

Abbreviations

DMF	N, N-dimethylformamide
Fv/F0	Potential photosynthetic capacity
Fv/Fm	Maximum photochemical efficiency of Photosystem II
HPLC	High Performance Liquid Chromatography
MDA	Malondialdehyde
MEL	Melatonin
PEG	Polyethylene glycol
POD	Peroxidase activity
SLA	Specific leaf area
TCA	Trichloroacetic acid
ΔF/Fm'	Actual photochemical efficiency of Photosystem II

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Author contributions

Conceptualization, S.V and T.B.Z.; methodology, T.B.Z.; material preparation, data collection, and analysis, T.B.Z.; original draft preparation, T.B.Z.; supervision, S.V.; review and editing, M.S, O.B and S.V. All authors commented on previous versions of the manuscript and approved the final version.

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Data availability

All data generated or analysed during this study are included in this manuscript.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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