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ORIGINAL ARTICLE / ORIGINALBEITRAG

Melatonin Concentration and Treatment Technique Influenced the Increase of Cereal Plant Biomass and Antioxidant Defence System Under Salinity Stress. A Meta-Analysis

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Abstract

Salinity stress is one of the primary issues with cereal crops (CR) such as corn, rice, and wheat. Melatonin has been shown to enhance CR's growth and physiological activity under salinity stress. Therefore, we performed a meta-analysis to quantitatively evaluate the effect of melatonin treatment (MT) on salinity stress tolerance on growth and physiological activity of CR and to determine the parameters modulated by melatonin. The meta-analysis approach combines all related experiments found in the relevant literature to accomplish this. A total of 325 datasets from 28 published articles were entered into the database. MT used seed priming (SP), water solution (WS), foliar (FOL) and soil drench (SD). Due to the limited number of studies, the melatonin concentration entered in the database was limited to the 0–200 µM level. Meanwhile, the salinity levels determined in this study ranged from 0 to 51.30 dSm^{-1}. The analysis was based on a linear mixed model methodology. Different studies were considered random effects, and properties related to melatonin application (either on CR or MT) were treated as fixed effects. Our findings revealed that overall, more significant increases in melatonin concentration were associated with increases in shoot dry biomass (SDB), root dry biomass (RDB), photosynthetic rate (Pn), stomatal conductivity (gs), superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and soluble protein content (SPC) ($p<0.05$). The results of the meta-analysis showed that the relationship between CR (maize, rice and wheat) with increased melatonin concentrations resulted in higher increases in SDB, RDB, Pn, SOD, CAT, POD and SPC in corn and higher increases in gs in wheat ($p<0.05$). The relationship between MT (SP, WS, FOL, and SD) with an increase in melatonin concentration resulted in a higher increase in SDB and RDB in the SP technique and a higher increase in Pn, gs, SOD, CAT, and POD in the SD technique ($p<0.05$). It was concluded that applying melatonin to CR with various types of MT could reduce oxidative damage by increasing the antioxidant defence system and photosynthetic and stomatal activity.

Keywords Corn · Melatonin application · Photosynthetic rate · Rice · Superoxide dismutase · Wheat

Introduction

Cereal crops (CR) are among the most important crops grown as the primary sources of energy and food. Almost half of the world's population uses CR, such as corn, rice, and wheat. Increased crop production, particularly CR, will be crucial in satisfying future food demands as the world's population approaches 9 billion by 2050 (Cole et al. 2018). However, deteriorating environmental quality owing to human-caused environmental stress might limit its growth and productivity. CR will respond to environmental changes by altering its metabolism, growth, and productivity. The abiotic stress most detrimental to CR productivity is salt stress. Naturally, salinity issues arise when minerals and salty rocks are eroded and ion concentrations in the soil accumulate (Athar and Ashraf 2009). In addition, high temperatures, flooding, and wind erosion can be considered natural causes of salinity because of the accumulation of minerals and salts from one region to another. On the other hand, large-scale agricultural activities, poor irrigation, unbalanced use of fertilizers, soil degradation, and poor drainage are the anthropogenic causes of salinity (Shrivastava and Kumar 2015). More than 954 million hectares of land are affected by salinity, increasing daily

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and involving more than 20% of agricultural land (Okur and Örçen 2020).

In earlier research, salinity stress negatively affected germination and growth, leaf chlorophyll content, leaf mineral content, enzymatic activity, reactive oxygen species (ROS), and gas exchange activity (Wang et al. 2018a, b; Feghhenabi et al. 2020; Liu et al. 2020; Sezer et al. 2021). To tackle the salinity problem, the development of salinity-tolerant plants by genetic approaches has been given priority (Ayyam et al. 2019), however this will take time. When hypersalinity arises, unpredictable environmental conditions also reduce the tolerance of most rice, wheat, and corn varieties. Several growth regulators, including salicylic acid (Rasheed et al. 2020), proline (de Freitas et al. 2019), gibberellins (Álvarez-Méndez et al. 2022), and melatonin (Sezer et al. 2021), have been used in recent years to mitigate the negative effects salinity stress. Recent studies have revealed that the application of growth regulators such as melatonin by using external treatments such as seed priming (SP) (Johnson and Puthur 2021), water solution (WS) (Zhu et al. 2019), foliar (FOL) (Wei et al. 2021), and soil drench (SD) (Ahmad et al. 2021a) have been widely used to increase germination and yield under salinity stress.

Melatonin is an environmentally friendly biomolecule that can penetrate cell compartments due to its small size and high solubility in water and lipids. Therefore, melatonin is an alternative and inexpensive strategy to increase plant tolerance to abiotic stressors such as salinity. Melatonin (N-acetyl-5-methoxytryptamine) is the product of the synthesis of phytomelatonin from tryptophan under the activation of several enzymes (Tripathi et al. 2021). The enzyme of tryptophan decarboxylase (TDC) first catalyzes 5-hydroxytryptophan to serotonin or tryptophan into tryptamine in the phytomelatonin biosynthetic pathway (Hardeland 2017). Then, the enzyme tryptophan 5-hydroxylase (T5H) catalyzes tryptophan to 5-hydroxytryptophan and N-acetyl tryptamine to N-acetyl serotonin reactions. After that, serotonin N-acetyltransferase (SNAT) catalyzes the movement of the acetyl group from acetylcoenzyme A to different biomolecules. Lastly, phytomelatonin is synthesized through the catalysis of N-acetylserotonin via the 5-hydroxyindole O-methyltransferase enzyme (Hardeland 2017).

Under salinity stress, melatonin treatment (MT) using SP, WS, FOL, and SD techniques increased growth, leaf chlorophyll content, leaf mineral content, enzymatic activity, ROS, and gas exchange activity in corn (Jiang et al. 2016c; Guo et al. 2021), rice (Wei et al. 2021; Yan et al. 2021a), and wheat (Ke et al. 2018; Zafar and Anwar 2019). Several studies found that the SP (Sezer et al. 2021), SD (Ahmad et al. 2019), and FOL (Wang et al. 2018a) techniques for applying melatonin to corn increased biomass and photosynthetic efficiency. In addition to rice, different MT techniques have been demonstrated to boost enzymatic activity and ROS, such as Superoxide Dismutase (SOD), Catalase (CAT), and Peroxidase (POD) (Li et al. 2017a; Huangfu et al. 2020; Chen et al. 2021). In addition, several MT techniques considerably impact plant biomass and gas exchange in wheat (Sadak and Sh Sadak 2016; Ke et al. 2018; Zafar and Anwar 2019). Based on the above, it shows that melatonin can play various roles that protect plants by various mechanisms such as protecting the photosynthetic machinery from oxidative damage, increasing antioxidant activity, maintaining the integrity of biological membranes, increasing permeability and reducing lipid peroxidation so as to reduce toxicity and increase plant growth.

Although there have been several studies on the effect of melatonin and its application technique on CR growth, leaf chlorophyll content, leaf mineral content, enzymatic activity, ROS, and gas exchange activity under salt stress, none summarize or synthesize the results. Furthermore, there are contradictory results about whether melatonin can increase or decrease CR's growth, development, and physiological activity. This necessitates an evaluation of the facts about the properties of melatonin applied to cereals in the limited trials conducted to date. It was hypothesized that melatonin would enhance growth, leaf chlorophyll content, leaf mineral content, enzymatic activity, ROS, and gas exchange activity on CR and MT. In addition, different types of CR and MT will result in different responses to salinity stress in terms of growth, leaf chlorophyll content, leaf mineral content, enzymatic activity, reactive oxygen species (ROS), and gas exchange activity.

This meta-analysis aimed to (1) correlates melatonin's effect on growth, leaf chlorophyll content, leaf mineral content, enzymatic activity, ROS, and gas exchange activity in CR and MT under salinity stress, (2) Investigate how certain experimental variables are affected by melatonin? (3) How can melatonin be used practically to increase crop productivity?

Materials and methods

Database development

A database is developed from multiple sources that measure the effects of melatonin on the growth, leaf chlorophyll content, leaf mineral content, enzymatic activity, ROS, and gas exchange activity of corn, rice, and wheat. The included literature is retrieved from the databases Scopus, Web of Science, Wiley, Crossref, Pub Med, Science Direct, and Springer using the specific keywords "Melatonin", "Salinity", "Rice", and "Corn" and "Wheat." After that, 32 articles from around the globe were identified. The following research criteria are included in the database: (a) Melatonin concentration levels are reported, (b) MT is reported, (c) growth parameters, leaf chlorophyll content, leaf mineral content, enzymatic activity, reactive oxygen species (ROS), and gas exchange activity are reported, and (d) English-language articles are reported. Unlike a standard literature review, a meta-analysis is guided by a specialized search strategy that includes inclusion and exclusion criteria and a filtering process that further establishes the study's feasibility. Following the inspection of the abstract and the full text, 4 articles were deleted because they were unsuitable as article reviews or were not written in English. After analyzing the substance, including data presentation, melatonin concentration, MT type, observed parameters, and proper statistical criteria, 28 papers are included in the database for meta-analysis.

Data extraction and description

The author's name, publication year, kind of CR, MT, melatonin concentration, and salinity levels are summarized from 28 selected papers in Table 1. While the parameters arranged in the database are plant growth and biomass (plant height (PH), stem diameter (SD), number of leave (NoL), leaf area (LA), shoot fresh biomass (SFB), shoot dry biomass (SDB), root fresh biomass (RFB), root dry biomass (RDB), plant dry biomass (PDB)), leaf chlorophyll content (chlorophyll (Chl) a, chlorophyll (Chl) b, chlorophyll (Chl) total and carotenoid (CAR)), leaf mineral content (Cu^{2+}, Mn^{2+}, Zn^{2+}, Na^{2+}, K^{+}, Ca^{2+}, K/Na, Ca/Na, N content, P content, and relative water content (RWC)), enzymatic activities and ROS (proline, malondialdehyde (MDA), superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), soluble sugar content (SSC), soluble protein content (SPC), H_2O_2 content, and O_2 content), gas exchange activity (photosynthetic rate (Pn), transpiration rate (Tr) and stomata conductivity (gs)). The data for the parameters above were extracted from the scientific literature. The GetData Graph Digitizer 2.26 program extracted the data displayed in graphical format. Each parameter data is transformed to a similar unit of measurement before data processing.

Table 1 Studies included in the meta-analysis of the effects of melatonin treatment on CR

No	Referance	Plants	Melatonin Treatment (MT)	Salinity level (dSm-1)	Melatonin level (µM)
1	(Sezer et al. 2021)	Corn	Seed priming	0.27–10.52	0–200
2	(Jiang et al. 2016c)	Corn	Seed priming	10	0–80
3	(Ahmad et al. 2019)	Corn	Soil drench	10.52	0–90
4	(Ahmad et al. 2020)	Corn	Seed priming and Foliar	8	0–75
5	(Jiang et al. 2016b)	Corn	Water solutions	9.8	0–50
6	(Wang et al. 2018a)	Corn	Foliar	9.8	0–100
7	(Chen et al. 2018)	Corn	Water solutions	14.7	0–100
8	(Zhang et al. 2020)	Corn	Water solutions	9.8	0–100
9	(Ahmad et al. 2021b)	Corn	Foliar	8	0–75
10	(Guo et al. 2021)	Corn	Seed priming	3.92–15.68	0–10
11	(Liu et al. 2021b)	Corn	Foliar	3.92–15.68	0–5
12	(Ren et al. 2020)	Corn	Water solutions	0–9.8	0–10
13	(Chen et al. 2021)	Rice	Foliar	17.1–51.3	0–200
14	(Wei et al. 2021)	Rice	Foliar	0–9.8	0–200
15	(Yan et al. 2021b)	Rice	Foliar	0–14.7	0–200
16	(Yan et al. 2021a)	Rice	Foliar	0–14.7	0–200
17	(Li et al. 2017a)	Rice	Water solutions	0–11.76	0–75
18	(Wei et al. 2021)	Rice	Foliar	0–9.8	0–200
19	(Huangfu et al. 2020)	Rice	Seed priming	0–9.8	0–100
20	(Liu et al. 2020)	Rice	Seed priming	0–9.8	0–20
21	(Ke et al. 2018)	Wheat	Water solutions	0–9.8	0–100
22	(Sadak and Sh Sadak 2016)	Wheat	Seed priming	0.23–7.69	0–100
23	(Zafar and Anwar 2019)	Wheat	Foliar	0–9.8	0–100
24	(Talaat 2021b)	Wheat	Foliar	0.1–12	0–70
25	(Zhang et al. 2022)	Wheat	Water solutions	0–9.8	0–100
26	(Hussain et al. 2021)	Wheat	Foliar	0–9.8	0–100
27	(Al-Behadili and Al-Hayani 2019)	Wheat	Foliar	0–9.8	0–100
28	(Talaat 2021a)	Wheat	Foliar	0–12	0–70

The articles listed in Table 1 were published between 2016 and 2022. This study utilized 3 types of cereals: corn (42.85%), rice (28.5%), and wheat (28.5%). MT utilized SP, WS, FOL, and SD. Due to the limited number of studies, the concentration of melatonin included in the database was limited to 200 µM. The salinity levels determined by this study ranged from 0 to $51.30\,dSm^{-1}$.

Statistic analysis

Data analysis was carried out according to a meta-analysis technique based on a linear mixed model methodology (Sauvant et al. 2008). Different experiments were considered random effects, and factors related to melatonin application (either on CR or MT type) were treated as a fixed effect. Assessment of the effect of melatonin concentration and type of CR (corn, rice, wheat) or MT (SP, WS, FOL and SD) on the observed parameters was carried out using the following statistical model:

$$Y_{ijk} = \mu + s_i + \tau_j + s\tau_{ij} + B_1 1X_{ij} + b_i X_{ij} + B_j X_{ij} + e_{ijk}$$

where Y_{ijk} = dependent variable, μ = overall mean, s_i = random effect of the i the experiment, τ_j = fixed effect of the j the level of factor τ, $s\tau_{ij}$ = random interaction between the i the experiment and the j the level of factor τ, B_1 = linear regression coefficient of Y on X (fixed effect), X_{ij} = value of the continuous predictor variable (melatonin concentration), b_i = random effect of experiment i on the regression coefficient of Y on X in experiment i, B_j = effect of j the level of the discrete factor τ on the regression coefficient (fixed effect), and e_{ijk} = the unexplained residual error. The model used is weighted observations with the number of replications. The variables "experimental", "CR", and "MT" are stated in the class statement because these variables do not contain quantitative information. *p*-Values and root mean square errors (RMSE) were used as model statistics. Significance of an effect was stated at $p < 0.05$. All statistical analyses were performed with SAS Software version 9.1 (SAS Institute 2008).

Results

According to the meta-analyses, an increase in melatonin concentration was not related with parameters in LA, SFB, and PDB (Table 2). Nonetheless, higher melatonin concentrations were related with increased SDB and RDB in CR and MT types ($p < 0.05$; Fig. 1a,b and Fig. 2a,b). The increase in melatonin concentration in corn's SDB and RDB shows higher yields than in rice and wheat (Fig. 1a,b). In MT, the SP technique is more effective than other techniques for increasing SDB and RDB (Fig. 2a,b). Higher melatonin concentrations were correlated ($p < 0.05$) with linear increases in PH, SD, NoL, and RFB (Table 2). In general, there were no significant differences between the various forms of CR and MT in plant growth and biomass parameters, except for SD and NoL on MT, where the increase in these parameters was greater with the FOL technique than with the FOL technique other techniques.

Higher melatonin concentrations were related to higher Chltot, Pn, and gs concentrations at CR ($p < 0.05$) (Table 3). Other parameters such as Chl a, Chl b, CAR, and Tr were unaffected by the addition of melatonin. The intensity of the relationship between corn, rice, and wheat at the concentrations of Pn and gs varied significantly ($p < 0.05$). High melatonin concentrations were more efficient at increasing Pn in corn (Fig. 3a), whereas they were more effective at increasing gs in wheat (Fig. 3b). In MT, the SD technique was more effective than other techniques at increasing Pn (Fig. 4a) and gs (Fig. 4b).

There was no significant difference in leaf mineral content parameters between CR and MT types. However, higher melatonin concentrations ($p < 0.05$) correlated

Table 2 Regression equation on the influence of melatonin concentration (µM; independent factor) on plant growth and biomass

Response variable	Unit	n	Parameter estimates				Model statistics			
			Intercept	SE intercept	Slope	SE Slope	*p*-Value	RMSE	CR	MT
PH	cm	77	45.216	5.147	0.0721	0.0146	<0.0001	11.686	0.724	0.390
SD	mm	21	249.070	242.950	0.0038	0.0028	0.0183	1.448	Na	0.009
NoL	Pcs	28	5.035	0.767	0.0043	0.0030	0.0161	1.793	0.153	0.020
LA	cm^2	50	210.300	92.928	0.3109	0.4845	0.5245	204.556	0.808	0.404
SFB	gr	47	27.492	12.522	0.0009	0.0479	0.986	36.208	0.294	0.468
SDB	gr	100	2.936	0.734	0.0066	0.0026	0.0136	2.718	0.029	0.038
RFB	gr	41	6.442	2.989	0.0199	0.0117	0.0397	8.372	0.132	0.138
RDB	gr	103	0.591	0.189	0.0015	0.0009	0.0103	0.936	0.038	0.026
PDB	gr	103	29.136	28.805	0.0861	0.1444	0.5525	119.785	0.137	0.602

PH Plant height, *SD* Stem diameter, *NoL* Number of Leave, *LA* Leaf Area, *SFB* Shoot fresh biomass, *SDB* Shoot dry biomass, *RFB* Root fresh biomass, *RDB* Root dry biomass, *PDB* Plant dry biomass, *n* number of observation, *CR* Types of Cereals, *MT* Melatonin Treatments, *RMSE* root mean square error, *SE* standard error

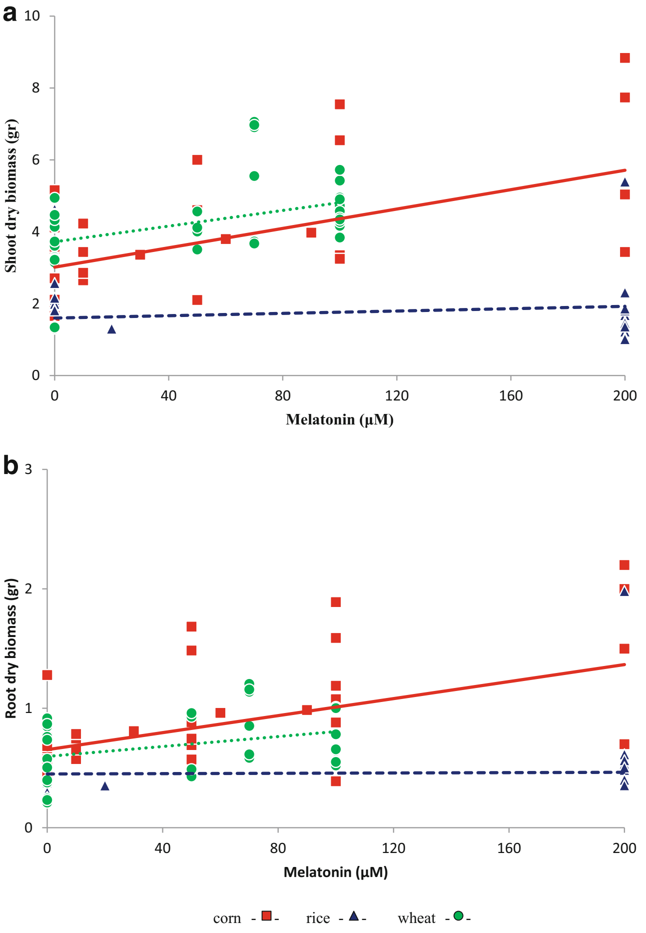

Fig. 1 **a** Relationship between shoot dry biomass (SDB, gr) and melatonin (µM) of corn (-■-), rice (-▲-), and wheat (-●-). Corn: SDB (gr) = 3.016 + 0.0135 melatonin (µM), ($n = 28$; $p < 0.0136$; $R^2 = 0.988$); Rice: SDB (gr) = 1.599 + 0.0016 melatonin (µM), ($n = 28$; $p < 0.0426$; $R^2 = 0.848$); Wheat: SDB (gr) = 3.720 + 0.0109 melatonin (µM), ($n = 44$; $p < 0.0142$; $R^2 = 0.823$). **b** Relationship between root dry biomass (RDB, gr) and melatonin (µM) of corn (-■-), rice (-▲-), and wheat (-●-). Corn: RDB (gr) = 0.653 + 0.0036 melatonin (µM), ($n = 37$; $p < 0.0103$; $R^2 = 0.851$); Rice: RDB (gr) = 0.449 + 7E-05 melatonin (µM), ($n = 28$; $p < 0.0472$; $R^2 = 0.976$); Wheat: RDB (gr) = 0.596 + 0.0021 melatonin (µM), ($n = 38$; $p < 0.0174$; $R^2 = 0.898$)

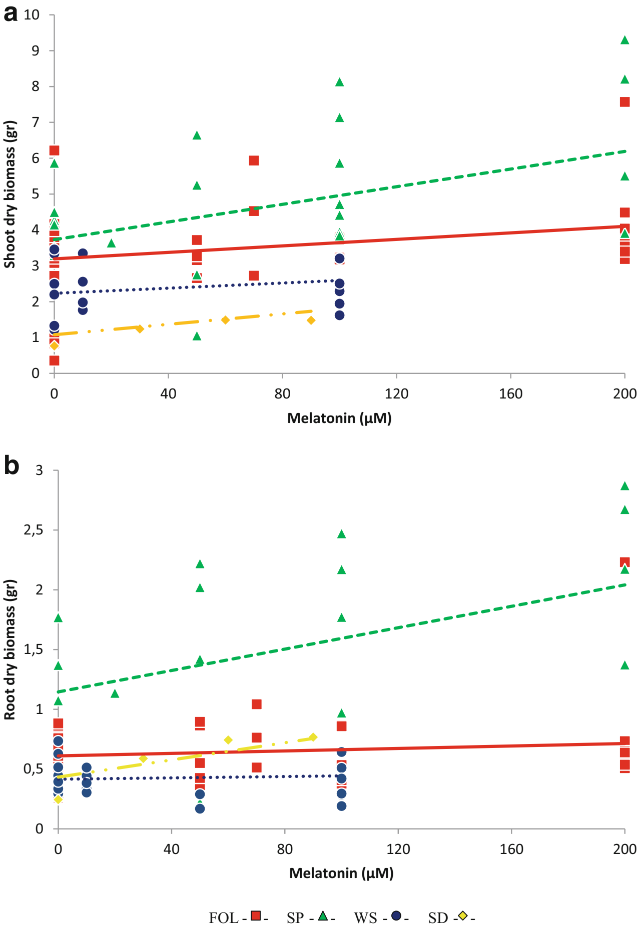

Fig. 2 **a** Relationship between shoot dry biomass (SDB, gr) and melatonin (µM) of FOL (-■-), SP (-▲-), WS (-●-), and SD (-◆-). FOL: SDB (gr) = 3.192 + 0.0045 melatonin (µM), ($n = 54$; $p < 0.0225$; $R^2 = 0.715$); SP: SDB (gr) = 3.730 + 0.0123 melatonin (µM), ($n = 26$; $p < 0.0123$; $R^2 = 0.923$); WS: SDB (gr) = 2.233 + 0.0036 melatonin (µM), ($n = 16$; $p < 0.0374$; $R^2 = 0.834$); SD: SDB (gr) = 1.078 + 0.0073 melatonin (µM), ($n = 4$; $p < 0.0411$; $R^2 = 0.861$). **b** Relationship between root dry biomass (RDB, gr) and melatonin (µM) of FOL (-■-), SP (-▲-), WS (-●-), and SD (-◆-). FOL: RDB (gr) = 0.610 + 0.0005 melatonin (µM), ($n = 57$; $p < 0.0312$; $R^2 = 0.715$); SP: RDB (gr) = 1.145 + 0.0045 melatonin (µM), ($n = 20$; $p < 0.0182$; $R^2 = 0.923$); WS: RDB (gr) = 0.415 + 0.0003 melatonin (µM), ($n = 22$; $p < 0.0113$; $R^2 = 0.834$); SD: RDB (gr) = 0.433 + 0.0036 melatonin (µM), ($n = 4$; $p < 0.0165$; $R^2 = 0.861$)

with linear increases in Cu^{2+} and Mn^{2+} (Table 4). Higher melatonin concentrations showed significant differences between CR types in SOD, CAT, POD, and SPC parameters. While, SOD, CAT, and POD parameters in MT types showed statistically significant differences ($p < 0.05$). (Table 5). Other parameters such as MDA, proline, H_2O_2, O_2, and SSC were unaffected by the addition of melatonin. Nonetheless, increased melatonin levels were related to a linear ($p < 0.05$) increase in APX activity (Table 5). The intensity of the relationship between corn, rice, and wheat at SOD, CAT, POD, and SPC activity varied significantly ($p < 0.05$). The increase in the high melatonin concentration was more effective in increasing the SOD, CAT, POD, and SPC activity in corn (Fig. 5a–d). Compared to other techniques, the SD technique increased the activity of SOD, CAT, and POD in MT (Fig. 6a–c).

These results showed that melatonin increased biomass growth (SDW and RDW), photosynthetic activity (Pn and gs), and antioxidant enzyme activity (SOD, CAT, and POD) in CR and MT under salinity pressure. However, interestingly, there was no significant change in the activity of ROS (MDA and H_2O_2) formation, which means that ROS forma-

Table 3 Regression equation on the influence of melatonin concentration (µM; independent factor) on leaf chlorophyll content and leaf gas exchange

Response variable	Unit	n	Parameter estimates				Model statistics			
			Intercept	SE intercept	Slope	SE Slope	*p*-Value	RMSE	CR	MT
Chl a	mg g^{-1} FW	55	1.316	0.270	0.0010	0.0015	0.5047	1.423	0.866	0.570
Chl b	mg g^{-1} FW	55	0.532	0.126	0.0004	0.0004	0.3571	0.420	0.755	0.800
Chl tot	mg g^{-1} FW	102	3.062	0.749	0.0023	0.0019	0.0225	1.512	0.355	0.339
CAR	mg g^{-1} FW	48	0.902	0.584	0.0003	0.0008	0.7089	0.777	0.990	0.999
Pn	mmol H_2O m^{-2}s^{-1}	109	12.921	1.813	0.0167	0.0096	0.0483	9.963	0.047	0.031
Tr	mmol H_2O m^{-2}s^{-1}	42	2.910	0.632	0.0042	0.0039	0.2870	1.791	0.247	0.469
Gs	mmol H_2O m^{-2}s^{-1}	58	0.143	0.030	0.0018	0.0002	0.0307	0.134	0.021	0.003

Chl a Chlorophyll a; *Chl b* Chlorophyll b; *Chl tot* Chlorophyll total; *CAR* Carotenoid; *Pn* Photosynthetic rate; *Tr* Transpiration rate; *gs* Stomata conductivity; *n* number of observation; *FW* Fresh Weight; *CR* Types of Cereals; *MT* Melatonin Treatments; *RMSE* root mean square error; *SE* standard error

tion is an important part of the antioxidant defense system in mitigating plants under salinity stress. Here, we selected antioxidant enzyme activity as a representative parameter to comprehensively analyze melatonin's mitigating capacity to reduce oxidative stress under salinity stress indirectly.

Discussion

The increase in SDB and RDB with increasing melatonin concentrations indicated that these compounds positively affected CR under salinity stress (Fig. 1a,b). Several studies have shown that the application of melatonin can perform as a concentration-dependent potential modulator of plant growth and development and reduce the inhibitory effect of salt stress. Melatonin induces root growth as regulated by auxin-modulating physiological mechanisms that affect water uptake and trigger irreversible cell wall elongation, contributing to the increase in plant growth and development (Bleiss and Ehwald 1993). This is consistent with (Sezer et al. 2021), which state that 200 µM of melatonin can increase the SDB and RDB of corn by 48.21% and 51.52%, respectively. Moreover, melatonin can directly increase carbon assimilation, enhancing photosynthesis's capacity to increase biomass accumulation (Subrata et al. 2022). Interestingly, although melatonin can promote development in the root system (Fig. 1b), it had no significant effect in our findings on mineral absorption (Zn^{2+}, Na^{2+}, K^{+}, and Ca^{2+}) (Table 4). Nutrient uptake is generally influenced by plant species, plant tissue, soil salinity, melatonin concentration, growth conditions and growth stage (Tuna et al. 2008). The complex relationship between salinity and nutrient uptake causes salt stress to increase or decrease nutrient uptake in plants or may not have any effect at all.

Our meta-analysis shows that MT type increases SDB and RDB significantly. On SDB and RDB, the SP technique demonstrated greater significance than other techniques (Fig. 2a,b). It has been shown that the SP technique can increase seed germination and plant growth under high salt stress. During seed soaking, the moisture level is controlled to activate the seed's metabolism, resulting in the hydrolysis of complex carbohydrates into simpler forms that are readily available for uptake by the embryo (Ali and Elozeiri 2017). This was made possible by the early completion of pre-germination metabolic activity during priming, which stimulated seed development and the emergence of radicles. It has been shown that soaking seeds in melatonin increase the biomass of corn, rice, and wheat (Qiao et al. 2019; Li et al. 2021; Yu et al. 2022).

Furthermore, the application of melatonin to salt stress significantly increased Pn and gs in CR (Fig. 3a,b). This result was validated by (Zhan et al. 2019), which showed that gs and Pn were higher in melatonin-treated than untreated corn under salt stress conditions. Under salt stress, wheat (Zhang et al. 2022) and rice (Huangfu et al. 2020) treated with 100–200 µM melatonin significantly increased Pn and gs. Melatonin can promote plant recovery by increasing the photosynthetic process and optimizing stomata movement via regulation of guard cell membrane anion channel proteins and dehydrins (Arnao and Hernández-Ruiz 2019). In addition, the presence of melatonin can increase PS II light absorption and electron transport (Chang et al.

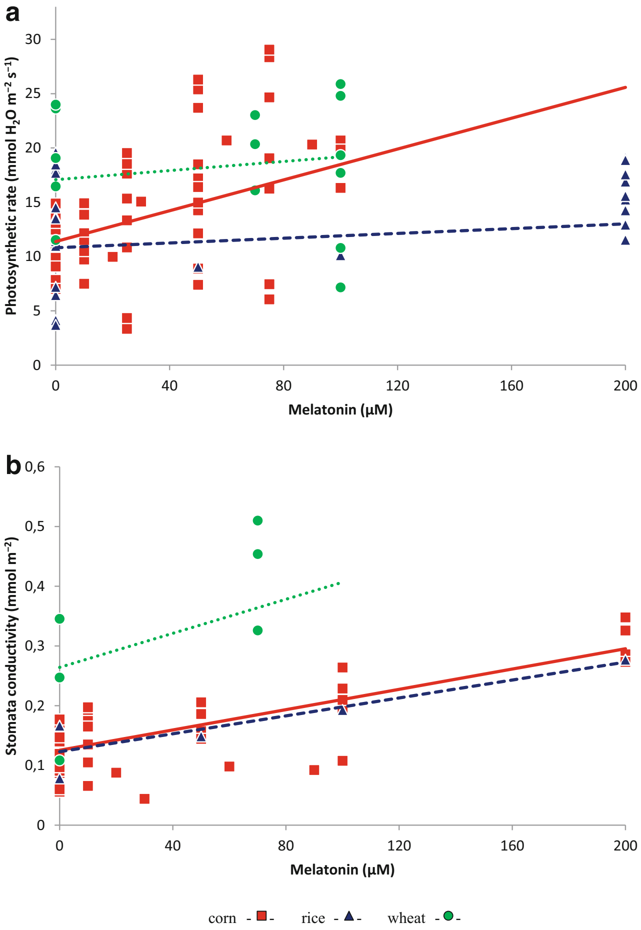

Fig. 3 **a** Relationship between photosynthetic rate (Pn, mmol H_2O m^{-2} s^{-1}) and melatonin (μM) of corn (-■-), rice (-▲-), and wheat (-●-). Corn: Pn (mmol H_2O m^{-2} s^{-1}) = 11.379 + 0.071 melatonin (μM), ($n = 66$; $p < 0.0061$; $R^2 = 0.954$); Rice: Pn (mmol H_2O m^{-2} s^{-1}) = 10.812 + 0.011 melatonin (μM), ($n = 29$; $p < 0.0137$; $R^2 = 0.921$); Wheat: Pn (mmol H_2O m^{-2} s^{-1}) = 17.077 + 0.021 melatonin (μM), ($n = 14$; $p < 0.0098$; $R^2 = 0.734$). **b** Relationship between stomata conductivity (gs, mmol m^{-2}) and melatonin (μM) of corn (-■-), rice (-▲-), and wheat (-●-). Corn: gs (mmol m^{-2}) = 0.125 + 0.0008 melatonin (μM), ($n = 47$; $p < 0.0223$; $R^2 = 0.912$); Rice: gs (mmol m^{-2}) = 0.123 + 0.0008 melatonin (μM), ($n = 5$; $p < 0.0453$; $R^2 = 0.823$); Wheat: gs (mmol m^{-2}) = 0.264 + 0.0014 melatonin (μM), ($n = 6$; $p < 0.0512$; $R^2 = 0.856$)

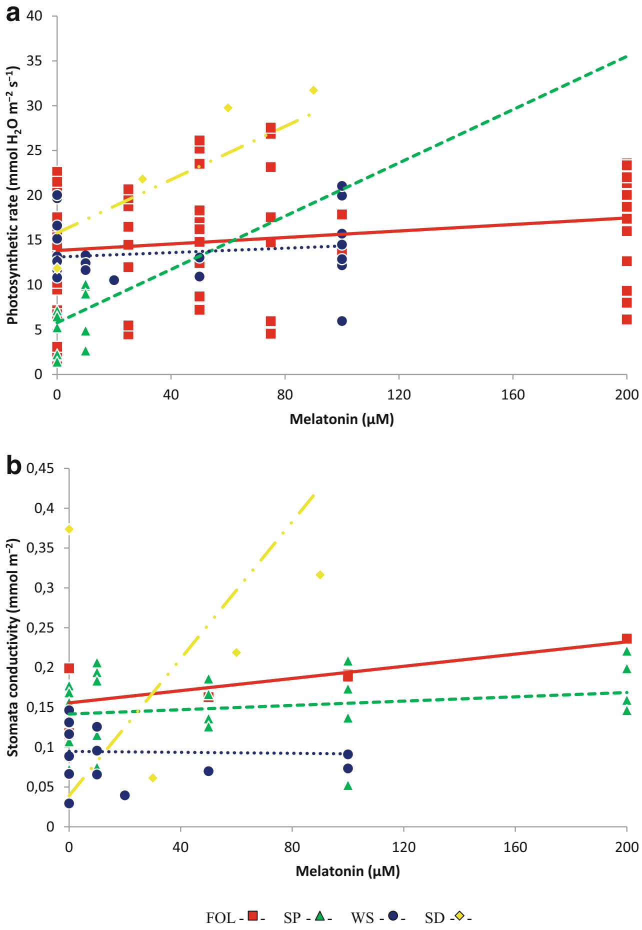

Fig. 4 **a** Relationship between photosynthetic rate (Pn, mmol H_2O m^{-2} s^{-1}) and melatonin (μM) of FOL (-■-), SP (-▲-), WS (-●-), and SD (-◆-). FOL: Pn (mmol H_2O m^{-2} s^{-1}) = 13.844 + 0.0181 melatonin (μM), ($n = 70$; $p < 0.0013$; $R^2 = 0.938$); SP: Pn (mmol H_2O m^{-2} s^{-1}) = 5.784 + 0.1486 melatonin (μM), ($n = 10$; $p < 0.0325$; $R^2 = 0.856$); WS: Pn (mmol H_2O m^{-2} s^{-1}) = 13.112 + 0.0123 melatonin (μM), ($n = 25$; $p < 0.0241$; $R^2 = 0.542$); SD: Pn (mmol H_2O m^{-2} s^{-1}) = 15.812 + 0.1486 melatonin (μM), ($n = 4$; $p < 0.0008$; $R^2 = 0.952$). **b** Relationship between stomata conductivity (gs, mmol m^{-2}) and melatonin (μM) of FOL (-■-), SP (-▲-), WS (-●-), and SD (-◆-). FOL: gs (mmol m^{-2}) = 0.155 + 0.0004 melatonin (μM), ($n = 14$; $p < 0.0421$; $R^2 = 0.789$); SP: gs (mmol m^{-2}) = 0.141 + 0.0001 melatonin (μM), ($n = 26$; $p < 0.0015$; $R^2 = 0.853$); WS: gs (mmol m^{-2}) = 0.094 + 3E-05 melatonin (μM), ($n = 14$; $p < 0.0652$; $R^2 = 0.617$); SD: gs (mmol m^{-2}) = 0.039 + 0.0043 melatonin (μM), ($n = 4$; $p < 0.0043$; $R^2 = 0.937$)

2020). Melatonin modulates the production of RuBisCO, glyceraldehyde-3-phosphate dehydrogenase, and carbohydrate interconversion enzymes in the Calvin cycle so that photosynthesis is not inhibited (Arnao and Hernández-Ruiz 2019). Our meta-analysis showed that the application of melatonin to CR using the SD technique resulted in a significant increase in Pn and gs compared to other techniques (Fig. 4a,b). The differences in melatonin effect between the MT types may be due to the absorption mechanism at play in plants. The SD technique is more effective because the roots can absorb amino acids through specialized transporters (Näsholm et al. 2009), making melatonin more readily available throughout the day when combined with a growth system. In contrast, the FOL technique is a passive process mediated by climatic factors such as wind and humidity levels, affecting plant biological responses like stomatal opening and cuticle thickness (Pecha et al. 2012) and affecting melatonin absorption when the FOL technique is applied. The above explanation is supported by research results (Cristofano et al. 2021), which indicate that giving biostimulants to lettuce through their roots is significantly more effective than through their leaves. This process in-

Table 4 Regression equation on the influence of melatonin concentration (µM; independent factor) leaf mineral content

Response variable	Unit	n	Parameter estimates				Model statistics			
			Intercept	SE intercept	Slope	SE Slope	*p*-Value	RMSE	CR	MT
Cu^{2+}	ppm	22	10.327	6.427	0.0519	0.0158	0.0039	8.555	0.520	0.520
Mn^{2+}	ppm	16	41.954	3.588	0.1503	0.0313	0.0003	16.044	Na	Na
Zn^{2+}	ppm	22	26.886	3.304	0.0608	0.0338	0.0877	19.650	0.893	0.893
Na^{2+}	%	74	0.878	0.209	–0.001	0.0008	0.9189	0.782	0.930	0.811
K^{+}	%	84	1.733	0.424	0.0012	0.0007	0.1070	0.706	0.310	0.353
Ca^{2+}	%	46	3.251	1.773	0.0010	0.0018	0.5889	1.496	0.104	0.939
K/Na	(no unit)	74	4.842	1.382	0.0018	0.0076	0.8124	7.606	0.801	0.351
Ca/Na	(no unit)	46	7.719	4.280	0.0023	0.0108	0.8320	8.841	0.289	0.941
N Content	mmol g^{-1} DW	40	7.240	4.409	0.0070	0.0091	0.4473	6.179	0.392	0.864
P Content	mmol g^{-1} DW	30	1.102	0.764	0.0007	0.0012	0.5831	0.830	0.171	0.997
RWC	%	40	78.705	4.150	0.0315	0.0275	0.2619	14.418	0.563	0.790

RWC Relative Water Content; *DW* Dry Weight; *CR* Types of Cereals; *MT* Melatonin Treatments; *RMSE* root mean square error; *SE* standard error

Table 5 Regression equation on the influence of melatonin concentration (µM; independent factor) on enzym activities and ROS

Response variable	Unit	n	Parameter estimates				Model statistics			
			Intercept	SE intercept	Slope	SE Slope	*p*-Value	RMSE	CR	MT
MDA	µmol g^{-1} FW	75	12.490	3.923	–0.010	0.0124	0.4156	8.994	0.860	0.842
Proline	mg g^{-1} FW	55	90.930	32.917	0.0945	0.2368	0.6918	132.842	0.304	0.828
SOD	U g^{-1} FW	157	37.026	11.145	0.0456	0.0292	0.0215	34.836	0.001	0.026
CAT	U g^{-1} FW	137	54.646	15.076	0.0565	0.0254	0.0282	29.329	0.002	0.013
POD	U g^{-1} FW	152	29.423	5.690	0.0703	0.0209	0.0010	24.867	0.007	0.050
APX	U g^{-1} FW	37	4.792	2.709	0.0034	0.0021	0.0134	1.581	0.176	0.156
H_2O_2	µmol g^{-1} FW	62	49.501	19.772	–0.062	0.0405	0.1263	32.308	0.940	0.958
O_2	µmol g^{-1} FW	62	49.501	19.772	–0.062	0.0405	0.1263	32.308	0.981	Na
SSC	mg g^{-1} FW	108	30.646	10.808	0.0295	0.0362	0.4182	29.708	0.238	0.935
SPC	mg g^{-1} FW	95	24.138	5.755	–0.011	0.0089	0.0197	6.866	0.013	0.917

MDA Malondialdehyde; *SOD* Superoxide dismutase; *CAT* Catalase; *POD* Peroxidase; *APX* Ascorbate peroxidase; *SSC* Soluble sugar content; *SPC* Soluble protein content; *FW* Fresh Weight; *DW* Dry Weight; *CR* Types of Cereals; *MT* Melatonin Treatments; *RMSE* root mean square error; *SE* standard error

volves an increase in signaling molecules, such as the protein kinase cascade, which is a typical melatonin compound, to increase photosynthetic activity in response to melatonin application through the roots (Back 2021).

Our meta-analysis showed that melatonin treatment in CR had no significant effect changes in MDA and H_2O_2, which are markers of ROS formation (Table 5). The possible production of lower lipid peroxidation levels and less loss of electrolytes in some types of CR refers to these plants inherent salt tolerance features. Likewise, for H_2O_2, it is possible that melatonin-mediated plant resistance to salinity does not occur through the H_2O_2 regulatory pathway. Because in another perspective, melatonin treatment in CR is associated with higher activity of antioxidant enzymes such as POD, CAT and SOD indicating better protection from oxidative damage by preserving cellular membranes under various levels of salinity stress. The increase in antioxidant enzymes (POD, CAT, and SOD) in CR although there was no significance in the formation of ROS (MDA and H_2O_2) indicates that melatonin has an indirect role in reducing oxidative stress. Furthermore, substantial evidence has shown that melatonin can indirectly scavenge H_2O_2 and O2 (Fowler et al. 2003; Bonnefont-Rousselot et al. 2011), thus regulating redox homeostasis by melatonin results from its ability to induce antioxidant enzymes.

The insignificant H_2O_2 content in melatonin treatment may be due to the efficient absorption of H_2O_2 by antioxidant defence enzymes such as POD, CAT, and SOD. In plant cells, O_2 can be rapidly converted to H_2O_2 by the action of SOD, whereas H_2O_2 can be absorbed by the CAT regeneration cycle (Noctor and Foyer 1998). We report that melatonin induces the activity of several antioxidant enzymes such as POD, CAT, and SOD under salt stress (Fig. 5a–c). These results suggest that melatonin can improve cellular redox homeostasis by activating antioxidant enzymes in plants to protect cells from oxidative stress induced by salt stress. Furthermore, the antioxidant enzyme expressed strongly under melatonin treatment could prevent

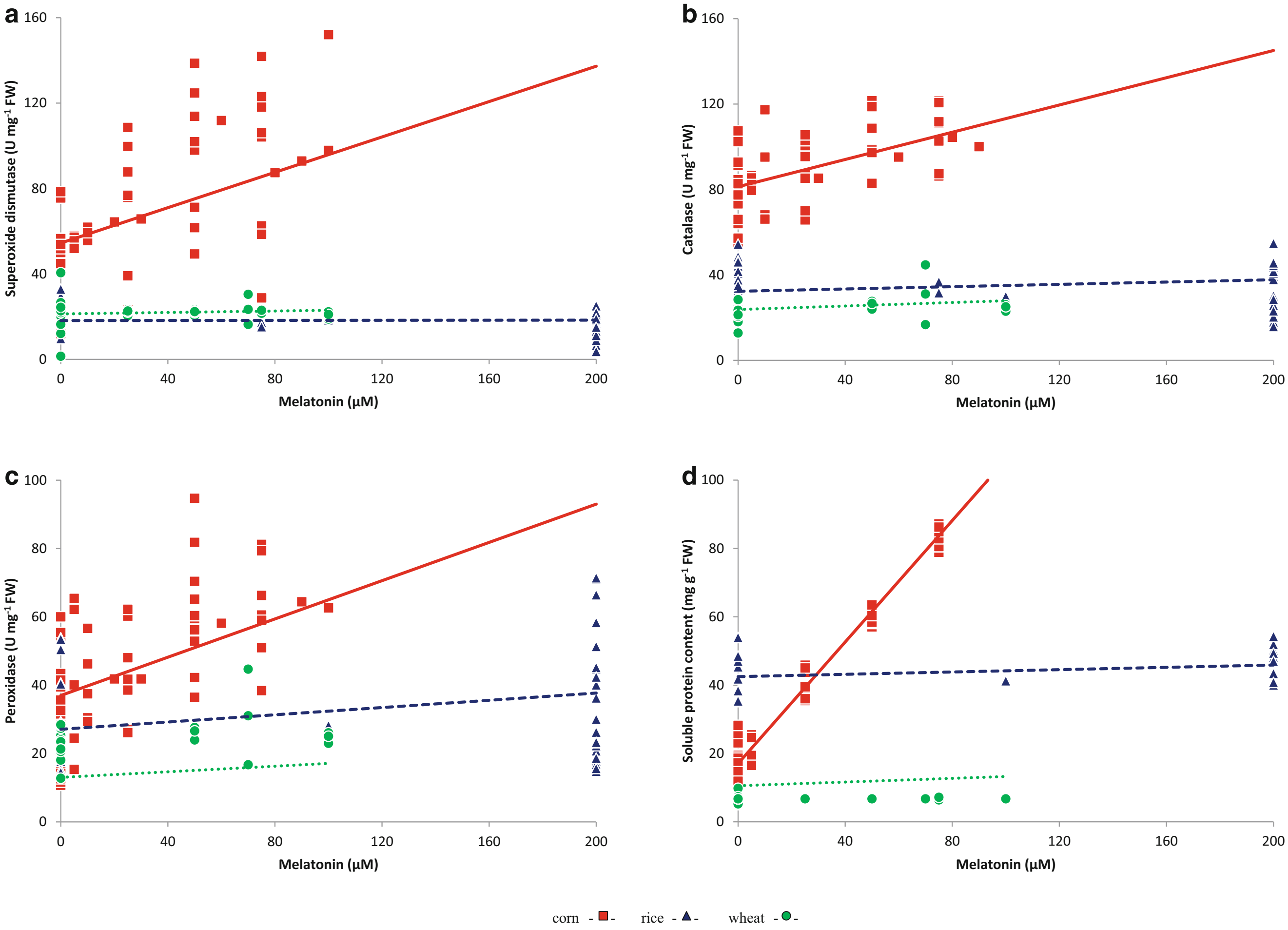

Fig. 5 **a** Relationship between superoxide dismutase (SOD, U mg^{-1} FW) and melatonin (μM) of corn (-■-), rice (-▲-), and wheat (-●-). Corn: SOD (U mg^{-1} FW) = 54.476 + 0.4143 melatonin (μM), ($n = 59$; $p < 0.0017$; $R^2 = 0.869$); Rice: SOD (U mg^{-1} FW) = 18.192 + 0.0009 melatonin (μM), ($n = 51$; $p < 0.0380$; $R^2 = 0.831$); Wheat: SOD (U mg^{-1} FW) = 21.286 + 0.0174 melatonin (μM), ($n = 47$; $p < 0.0297$; $R^2 = 0.912$). **b** Relationship between catalase (CAT, U mg^{-1} FW) and melatonin (μM) of corn (-■-), rice (-▲-), and wheat (-●-). Corn: CAT (U mg^{-1} FW) = 81.289 + 0.319 melatonin (μM), ($n = 62$; $p < 0.0027$; $R^2 = 0.834$); Rice: CAT (U mg^{-1} FW) = 32.333 + 0.027 melatonin (μM), ($n = 51$; $p < 0.0678$; $R^2 = 0.812$); Wheat: CAT (U mg^{-1} FW) = 23.796 + 0.041 melatonin (μM), ($n = 24$; $p < 0.0888$; $R^2 = 0.912$); **c** Relationship between peroxidase (POD, U mg^{-1} FW) and melatonin (μM) of corn (-■-), rice (-▲-), and wheat (-●-). Corn: POD (U mg^{-1} FW) = 36.998 + 0.282 melatonin (μM), ($n = 63$; $p < 0.0094$; $R^2 = 0.962$); Rice: POD (U mg^{-1} FW) = 27.106 + 0.053 melatonin (μM), ($n = 45$; $p < 0.0587$; $R^2 = 0.859$); Wheat: POD (U mg^{-1} FW) = 13.021 + 0.041 melatonin (μM), ($n = 44$; $p < 0.0493$; $R^2 = 0.752$); **d** Relationship between soluble protein content (SPC, mg g^{-1} FW) and melatonin (μM) of corn (-■-), rice (-▲-), and wheat (-●-). Corn: POD (U mg^{-1} FW) = 17.061 + 0.889 melatonin (μM), ($n = 42$; $p < 0.0037$; $R^2 = 0.988$); Rice: POD (U mg^{-1} FW) = 42.487 + 0.017 melatonin (μM), ($n = 21$; $p < 0.0435$; $R^2 = 0.946$); Wheat: POD (U mg^{-1} FW) = 10.557 + 0.027 melatonin (μM), ($n = 32$; $p < 0.0493$; $R^2 = 0.866$)

oxidative damage to plants as evidenced by the insignificant level of MDA. Activation of defence mechanisms in suppressing the level of lipid peroxidation is carried out by maintaining membrane functionality which may be due to the adequate response of antioxidant enzymes to oxidative damage. This mechanism is manifested by increased POD, CAT and SOD which is closely related to melatonin treatment and the ability of the antioxidant system to scavenge free radicals and suppress lipid peroxidation.

Many studies have shown that one of the main effects of melatonin is increasing the activity of antioxidant enzymes, which helps reduce oxidative damage caused by salt stress (Moustafa-Farag et al. 2020; Ali et al. 2021; Zahedi et al. 2021). Consistently, we showed that increasing melatonin levels enhanced POD, CAT, and SOD activity in CR stressed with salt stress (Fig. 5a–c). Antioxidant enzymes play a significant role in defence mechanisms. This system aids in cellular ROS balance maintenance, delays membrane lipid peroxidation, and resists stress (Wang et al. 2018a). In corn and rice, it has been shown that the treatment of up to 200 μM melatonin protects against membrane damage caused by salt stress by increasing the activity of antioxidant enzymes (Jiang et al. 2016a; Li et al. 2017b; Ahmad et al. 2020; Chen et al. 2021). On the other hand, in

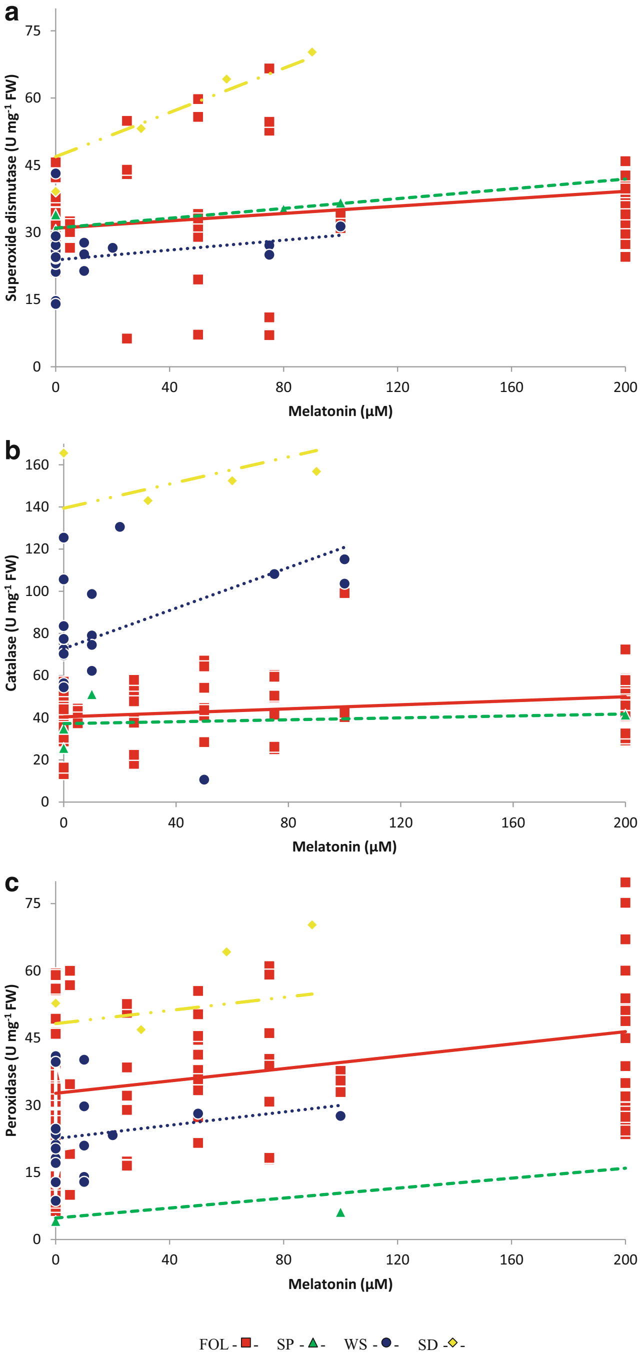

Fig. 6 **a** Relationship between superoxide dismutase (SOD, U mg^{-1} FW) and melatonin (µM) of FOL (-■-), SP (-▲-), WS (-●-), and SD (-◆-). FOL: SOD (U mg^{-1} FW) = 30.929 + 0.0412 melatonin (µM), (n = 115; $p < 0.0374$; $R^2 = 0.931$); SP: SOD (U mg^{-1} FW) = 30.976 + 0.0547 melatonin (µM), (n = 15; $p < 0.0865$; $R^2 = 0.861$); WS: SOD (U mg^{-1} FW) = 23.847 + 0.0552 melatonin (µM), (n = 23; $p < 0.0543$; $R^2 = 0.873$); SD: SOD (U mg^{-1} FW) = 46.897 + 0.2467 melatonin (µM), (n = 4; $p < 0.0021$; $R^2 = 0.984$); **b** Relationship between catalase (CAT, U mg^{-1} FW) and melatonin (µM) of FOL (-■-), SP (-▲-), WS (-●-), and SD (-◆-). FOL: CAT (U mg^{-1} FW) = 40.423 + 0.0477 melatonin (µM), (n = 102; $p < 0.0021$; $R^2 = 0.931$); SP: CAT (U mg^{-1} FW) = 37.211 + 0.0228 melatonin (µM), (n = 8; $p < 0.0256$; $R^2 = 0.861$); WS: CAT (U mg^{-1} FW) = 72.766 + 0.4812 melatonin (µM), (n = 23; $p < 0.0471$; $R^2 = 0.873$) SD: CAT (U mg^{-1} FW) = 139.442 + 0.3042 melatonin (µM), (n = 4; $p < 0.0086$; $R^2 = 0.984$), **c** Relationship between peroxidase (POD, U mg^{-1} FW) and melatonin (µM) of FOL (-■-), SP (-▲-), WS (-●-), and SD (-◆-). FOL: POD (U mg^{-1} FW) = 32.644 + 0.0688 melatonin (µM), (n = 125; $p < 0.0021$; $R^2 = 0.931$); SP: POD (U mg^{-1} FW) = 4.8321, +0.0556 melatonin (µM), (n = 3; $p < 0.0256$; $R^2 = 0.861$); WS: POD (U mg^{-1} FW) = 22.545 + 0.0741 melatonin (µM), (n = 20; $p < 0.0471$; $R^2 = 0.8734$); SD: POD (U mg^{-1} FW) = 48.236 + 0.0733 melatonin (µM), (n = 4; $p < 0.0086$; $R^2 = 0.984$)

wheat, the increase in antioxidant enzyme activity was linear to the melatonin concentration, up to 100 µM (Ke et al. 2018; Huangfu et al. 2020). A general comparison of the antioxidants examined revealed that the SOD, CAT and POD activities (Fig. 5a–c) were significantly higher for maize than rice and wheat. This difference indicates that maize (C4 plant) has a mechanism of resistance to secondary oxidative stress resulting from increased ROS formation under higher salinity stress than rice and wheat (C3). Our results confirm those described by other authors who explained that the administration of melatonin could tolerate salt to enhance the high constitutive antioxidant defenses in maize. Furthermore, it has been shown that increasing the concentration of melatonin increases SPC activity in CR (Fig. 5d). According to (Huang et al. 2019), melatonin can influence protein synthesis under environmental stress conditions. Under salinity stress, melatonin can improve PS II by maintaining the availability of protein in corn (Cao et al. 2019), rice (Han et al. 2017), and wheat (Talaat 2021a).

Our meta-analysis showed that the SD technique was more effective than the other techniques at increasing POD, CAT, and SOD activities (Fig. 6a–c). Therefore, we can assume that this technique can induce mild stress so that enzyme activity can continue to increase under salinity conditions. It has been shown that the SD technique increases the absorption of melatonin from plant growth media by increasing the surface area of the root hairs and the plant's hydration status (Liu et al. 2021a). Our analysis results agree with the previous studies (Ahmad et al. 2021a), the SD technique at a concentration of 50 µM was much more effective than the FOL technique at a concentration of 100 µM for increasing antioxidant enzyme activity. According to (Puglisi et al. 2022), the SD technique is more effective at acting directly on the Krebs cycle due to a simultaneous increase in the enzymes CS (cytrate synthase) and MDH (malate dehydrogenase), which positively correlates with the antioxidant enzymes POD, CAT, and SOD. The increased accumulation of antioxidant enzymes due to the Krebs cycle may be because melatonin effectively reduces oxidative stress and plays a crucial role in plant defence in saline conditions (Mukherjee et al. 2015; Naaz et al. 2020; Samanta et al. 2020).

Conclusion

The present meta-analysis compiled experimental evidence for the observation that under cereal crops and melatonin treatment salinity stress conditions, melatonin has differing effects on biomass, the antioxidant defence system, and photosynthetic activity. Various parameters, such as shoot dry biomass, root dry biomass, photosynthetic rate, superoxide dismutase, catalase, peroxidase, and soluble protein content, increased significantly in maize ($p < 0.05$), while stomatal conductivity increased significantly in wheat ($p < 0.05$). The seed priming technique with melatonin has the highest shoot dry biomass and root dry biomass weights compared to other techniques ($p < 0.05$). Furthermore, the soil drench technique increased the activity of photosynthetic rate, stomatal conductivity, superoxide dismutase, catalase, and peroxidase on cereal crops significantly more effectively ($p < 0.05$). Our results infer that melatonin can perform various activities under salinity stress and that melatonin modification may boost cereal crops stress tolerance via increased antioxidant activity. The research also revealed that melatonin treatment by the soil drench technique was more effective at increasing photosynthetic and antioxidant activities, whereas the seed priming technique was more effective at increasing cereal crops biomass.

Declarations

Conflict of interest B. Anggarda Gathot Subrata, I. Sezer, Z. Mut and H. Akay declare that they have no competing interests.

Ethical standards For this article no studies with human participants or animals were performed by any of the authors. All studies mentioned were in accordance with the ethical standards indicated in each case. This manuscript represents original research, and has not been submitted in full or in part to any other journals for publication.

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