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Original research

Meta-analysis of the protective effect of trehalose on *Triticum aestivum* under drought and high-temperature stress

Yuriy E. Kolupaev[1, 2, 3*], Maksym A. Shkliarevskyi[4], Dmytro A. Taraban[1, 2], Ivan V. Shakhov[1, 2], Alexander I. Oboznyi[1], Tetiana O. Yastreb[1]

[1] Yuriev Plant Production Institute, National Academy of Agrarian Sciences of Ukraine, Heroiv Kharkova Str. 142, 61060 Kharkiv, Ukraine
[2] State Biotechnological University, Alchevskih Str. 44, 61022 Kharkiv, Ukraine
[3] Poltava State Agrarian University, Skovorody Str. 1/3, 36003 Poltava, Ukraine
[4] Intego Group, Manizera Str. 8, 61002 Kharkiv, Ukraine
*Corresponding author. E-mail: plant_biology@ukr.net

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Abstract

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Currently, exogenous trehalose is considered a potential tool for inducing plant resistance to various types of stressors. However, the mechanisms underlying the stress-protective action of trehalose remain largely unclear, and data on the phenomenology of its effects are contradictory and poorly analysed. To obtain objective information on the stress-protective effect of trehalose on wheat (*Triticum aestivum* L.) exposed to drought or high-temperature conditions, a meta-analysis of scientific publications was conducted. As a result of an initial search on Google Scholar, 46 publications were collected on the effect of trehalose on wheat resistance to major abiotic stressors. After careful screening, 15 studies were selected, containing 65 pairs of observations characterising the effect of trehalose on integral physiological indicators (plant growth, relative water content, and chlorophyll content), 61 pairs of observations on the effect of trehalose on the level of oxidative stress and membrane condition, and 115 pairs of observations on the effect of trehalose on the functioning of antioxidant and osmoprotective systems. The results showed that trehalose treatment significantly improved plant growth and increased relative water content and chlorophyll content under drought conditions, but not under high temperatures. However, a decrease in lipid peroxidation products and the release of electrolytes through membranes under the influence of trehalose in wheat plants was observed under both types of stress. Trehalose treatment had little effect on the activity of all antioxidant enzymes studied in plant tissues, but it increased the content of ascorbate, reduced glutathione, and sugars during drought. The results obtained indicate the promise of trehalose as a stress-protective agent and the advisability of further studying its action specificity, depending on the nature of the stress factors.

Keywords: antioxidant system, data meta-analysis, stress-protective effect, trehalose, *Triticum aestivum* L.

INTRODUCTION

Trehalose (α-D-glucopyranosyl-[1,1]-α-D-glucopyranoside) is a disaccharide formed by a 1,1-bond between two glucose molecules. It has been first discovered in rye (*Secale cereale* L.) and certain fungal species (Richards et al., 2002). Currently, researchers consider this disaccharide to be widespread in vari-

ous organisms, including bacteria, yeast, fungi, and algae, as well as in some insects, invertebrates, and the plant kingdom (Han et al., 2024). Among soluble carbohydrates, trehalose is considered a unique plant stress metabolite. This is due to its ability to stabilise biomolecules and their complexes, exert direct antioxidant effects, and participate in cell signalling (Iturriaga et al., 2009; Raza et al., 2024; Eh et al., 2025).

Under optimal conditions, angiosperms synthesise insignificant amounts of trehalose. However, under stressful conditions, its concentration in plants increases substantially (Lunn et al., 2014; Kosar et al., 2019; Hassan et al., 2023). Trehalose biosynthesis in plants occurs in two stages. First, under the influence of trehalose-6-phosphate synthase, uridine diphosphate glucose and glucose-6-phosphate form the intermediate product trehalose-6-phosphate. The latter is then converted to trehalose by dephosphorylation with the participation of trehalose-6-phosphate phosphatase (John et al., 2017). In recent decades, genes encoding these trehalose biosynthesis enzymes from plants and prokaryotes have been successfully used to create transgenic plants of various species that are resistant to drought and other stress factors (Yatsyshyn et al., 2017). For instance, the overexpression of the *ScTPS1* yeast trehalose-6-phosphate synthase gene in potato and tomato plants has resulted in trehalose accumulation and resistance to salt stress, drought and cold (Sah et al., 2016; Kosar et al., 2019).

Trehalose plays a particularly important role in stresses associated with cell dehydration, such as drought, salt stress and exposure to sub-zero temperatures, which are accompanied by the formation of extracellular ice. Even at low concentrations, trehalose prevents the fusion of membrane vesicles and maintains lipids in a liquid-crystal state (Ohtake et al., 2006). Trehalose has a high hydration potential during drying or freezing, stabilising proteins and biological membranes by replacing surface-bound water (Luzardo et al., 2000). Furthermore, it forms hydrogen bonds with the hydroxyl (OH) groups and polar groups of proteins, as well as with the phosphate groups of membranes (Kosar et al., 2019). Another important property of trehalose is its ability to bind reactive oxygen species (ROS), thereby protecting biomacromolecules from oxidative damage (Luo et al., 2008; Raza et al., 2024). Finally, data have been obtained on trehalose's ability to influence the expression of many genes associated with protective responses to stress, including those of antioxidant enzymes. These effects are caused by the involvement of trehalose in cellular signalling networks and its influence on the synthesis of plant stress hormones, including abscisic acid (Choudhary et al., 2025). However, the mechanisms underlying effects of trehalose remain poorly understood.

The accumulation of fundamental knowledge about the unique role of trehalose in plant resistance to dehydration-causing stresses has naturally stimulated research into the effect of exogenous trehalose on the drought, salt, and heat tolerance of cultivated plants (Kosar et al., 2019). Data obtained to date show increased drought resistance in fenugreek, rapeseed, radish, corn, sunflower, and several other crops (Ali & Ashraf, 2011; Akram et al., 2016; Sadak, 2016; Kosar et al., 2019, 2022; Choudhary et al., 2025). These effects are associated with the activation of antioxidant enzymes and the accumulation of low-molecular-weight antioxidants and other stress-protective compounds under the influence of trehalose (Raza, 2021; Choudhary et al., 2025). The phenomenology of the exogenous effect of trehalose on plants under heat stress is less well studied. However, trehalose has been shown to mitigate heat-induced oxidative damage in corn (Li et al., 2014) and to enhance photosynthetic efficiency in wheat under heat stress (Raza et al., 2024).

Wheat has become one of the most important crops and is currently used as a model for studying the protective effects of exogenous trehalose against various stresses (Aldesuquy & Ghanem, 2015; Kosar et al., 2019). Herewith, wheat is classified as 'very sensitive' in terms of its response to water-deficit conditions (Asseng et al., 2012). Furthermore, 50% of the land used for wheat cultivation is subject to drought (Hasanuzzaman et al., 2018). Like drought, high temperatures affect virtually all stages of wheat growth and development, including seed germination, root and leaf emergence, stem growth, flower formation, pollination, fertilisation, grain yield, and grain quality (Lal et al., 2021). Drought and high temperatures cause significant oxidative damage to wheat plant cells and tissues (Kirova et al., 2021; Kolupaev et al., 2023a; 2023b; 2024c). Conversely, wheat responds quite strongly to exogenous plant hormones,

antioxidants, osmoprotectants, and signalling molecules (Lal et al., 2021). Trehalose is one of the compounds that exhibits most of these properties (Kosar et al., 2019; Han et al., 2024). Wheat responds to trehalose by activating components of the antioxidant system and accumulating osmolytes. This is usually accompanied by a mitigation of stress-induced disturbances to basic functions, such as photosynthesis, the water regime, growth, and productivity (Heshmat et al., 2018a; Luo et al., 2021a).

However, the available data on the effect of trehalose on wheat resistance to drought and high temperatures cannot be considered unequivocally positive. Some studies have noted inhibition of plant growth in the presence of trehalose (Luo et al., 2021b). Despite active research into the effects of trehalose on the resistance of cultivated plants for almost two decades, the analysis of this subject remains incomplete. This is particularly true for wheat. To objectively analyse the impact of exogenous trehalose on wheat's resistance to drought and heat stress, we conducted a meta-analysis of the literature. To date, positive experience has been accumulated using meta-analysis to evaluate the stress-protective effects of several other compounds on plants, such as melatonin and nitric oxide (Muhammad et al., 2022; Tahjib-Ul-Arif et al., 2022). Such analysis is typically conducted within the context of the target compound's effect on a specific crop species (Muhammad et al., 2024, 2025).

This study aimed to determine, using meta-analysis tools, the extent to which exogenous trehalose significantly influences wheat resistance to drought and heat stress and to assess, based on a mathematical analysis of a pool of published data, whether the stress-protective effects of trehalose are associated with changes in the functioning of the antioxidant and osmoprotective systems.

MATERIALS AND METHODS

Data search and collection

The data were collected in October 2025 through a search of the Google Scholar database, which is considered the most comprehensive. The search included the terms 'trehalose AND (drought OR "heat stress") AND (wheat OR "Triticum aestivum")' and identified 475 documents. After reviewing the titles and abstracts, 46 articles investigating the impact of trehalose on wheat's resistance to drought or heat stress were initially selected. For further processing, duplicate data in reviews and papers were excluded, and publications were selected for direct meta-analysis. The selection criteria were: 1) the experiment included variants involving the treatment of plants with trehalose at a certain concentration, as well as corresponding control variants and variants involving exposure to drought or heat stress; 2) the conditions for growing the plants in a laboratory (e.g. a phytotron or a greenhouse) were described, including the conditions and the level of stress (e.g. the moisture regime or the concentration of polyethylene glycol for laboratory experiments, or the temperature); 3) the data on experiment repetitions and the standard error or standard deviation of the mean values were available; and 4) the quality of the graphs was satisfactory for data extraction. Data presented graphically in the articles were extracted from the texts using the WebPlotDigitizer programme (Burda et al., 2017).

In most studies included in meta-analyses, a single effective concentration of trehalose was used. Where data on the effect of trehalose at several concentrations were available, only the data on the optimal concentration (which exhibited the maximum stress-protective effects) were used for the meta-analysis. When studying the effects of stress factors on temporal dynamics, each time point was treated as a separate pair of observations (untreated and trehalose-treated variants). If the study used different wheat genotypes, the data for each genotype were considered independent paired observations (untreated and trehalose-treated variants, respectively). Therefore, several pairs of variants (control and trehalose-treated) reported in a single article were evaluated as independent observations, as is commonly practised in meta-analyses of plant biology studies (Klümper & Qaim, 2014; Sun et al., 2020; Renzetti et al., 2024). After thorough screening of publications, 15 articles were selected, comprising a total of 241 pairs of studies (identical variants without treatment and with trehalose treatment) across various indicators. These data are presented in Appendix I–4, with the corresponding references listed in the list of references.

When analysing the articles, the indicators were divided into several groups. The group of integral

physiological indicators included: (1) growth indicators (since various articles used different growth indicators, data on the accumulation of raw and (or) dry biomass of organs or whole plants, linear growth, and leaf area were summarised into one category) (2) relative water content in leaves, and (3) chlorophyll content (total chlorophylls *a* and *b*). The group of indicators of oxidative stress and membrane damage included data on hydrogen peroxide and malondialdehyde (a product of lipid peroxidation) in tissues, as well as on the release of electrolytes from tissues. Data on the functioning of the antioxidant system were represented by the activity of the following enzymes: superoxide dismutase, guaiacol peroxidase, catalase, and glutathione reductase, as well as the content of the main low-molecular-weight antioxidants: ascorbic acid and reduced glutathione. Additionally, data on the content of main cellular osmolytes, proline and sugars, were processed.

To evaluate the effect of trehalose, a generalised assessment was carried out on all pairs of indicators in the control group (without trehalose treatment) and the experimental group (with trehalose treatment), for both groups experiencing stress and those that did not. Groups of variants experiencing drought (osmotic stress) or heat stress were categorised separately. All paired data (control and trehalose) were divided into categories based on the plant development phase – vegetative or generative. Only indicators with at least two independent observations were used to analyse the data for a given category.

Statistical analyses

A meta-analysis was performed using a random-effects model due to anticipated heterogeneity across studies. First, an overall analysis was conducted across the entire dataset. Subgroup analyses were then conducted for each category.

The effect sizes were estimated by calculating the natural logarithm (lnR) of the ratio of the mean value of the corresponding indicator under trehalose treatment (Xe) to the control value (the variant without trehalose treatment – Xc): $\ln R = \ln (Xe/Xc)$ (Wang et al., 2022). REML (restricted maximum likelihood estimator) was used to estimate the model parameters. REML is a standard method in many advanced statistical software packages and enables the relatively accurate detection of patterns with limited data. Heterogeneity was assessed using three complementary metrics: τ^2 estimated via restricted maximum likelihood (Viechtbauer, 2005), Cochran's Q test, and the I^2 statistic (Higgins & Thompson, 2002). These metrics were selected as they are commonly used in meta-analysis and together provide comprehensive information on heterogeneity: τ^2 estimates between-study variance, Q tests for its significance, and I^2 quantifies the fraction of total variability caused by heterogeneity. The effect of trehalose was considered significant if the 95% confidence intervals did not cross the zero line. All data transformations, analyses, and visualisations were performed using the R programming language (version 4.5.1) and the metafor package (Viechtbauer, 2010).

RESULTS

Data heterogeneity

The meta-analysis revealed that the data were normally distributed, with significant heterogeneity observed across most moderators (Table 1). This is probably due to differences in experimental conditions, despite the presence of certain criteria in data selection (see "Materials and methods"). In particular, plant age varied substantially across studies, as did the duration and intensity of stress treatments and the concentrations of exogenous trehalose.

The effect of trehalose on integral physiological indicators in wheat plants

When the entire data set was evaluated (Ma et al., 2013; Luo et al., 2014, 2021a; Ahmed et al., 2016; Heshmat et al., 2018a; Qaid, 2020; Li et al., 2023b), a small but significant at $p \leq 0.05$ increase in growth parameters was observed in the trehalose-treated variants compared to the control ones (Fig. 1A, Appendix I). In the group without stress, the effect of trehalose was weak. However, this effect was significantly greater in the variants exposed to drought (osmotic stress). Conversely, no notable impact of trehalose on plant growth parameters was evident under heat stress. Overall, growth parameters increased when plants were treated with trehalose during both the vegetative and generative phases of development.

Table 1. Heterogeneity analysis of growth response, relative water content, chlorophyll, H_2O_2, malondialdehyde content, electrolyte loss, enzymatic activity, ascorbate, glutathione, and osmolytes contents in wheat

Indicator	Variant	Cochran's Q	df	*p*-value	τ^2	I^2
Growth response	Total	322.56	45	< 0.001	0.00895	91.92
	non-stress	33.55	20	0.029	0.00092	45.12
	drought	88.31	17	< 0.001	0.00614	78.58
	heat	138.81	6	< 0.001	0.03252	98.86
	vegetative	140.79	29	< 0.001	0.00762	83.76
	generative	181.58	15	< 0.001	0.01401	96.68
Relative water content	Total	269.75	8	< 0.001	0.00180	98.51
	non-stress	4.18	4	0.382	0.00001	27.07
	drought	63.14	3	< 0.001	0.00172	97.99
	vegetative	52.70	4	< 0.001	0.00316	87.53
	generative	217.03	3	< 0.001	0.00085	98.71
Chlorophyll content	Total	129.16	9	< 0.001	0.00818	95.89
	non-stress	20.54	2	< 0.001	0.00777	92.35
	drought	0.85	1	0.358	~ 0	~ 0
	heat	40.47	4	< 0.001	0.00139	86.58
	vegetative	58.42	5	< 0.001	0.01411	96.26
	generative	1.13	3	0.769	~ 0	~ 0
H_2O_2 content	Total	262.77	8	< 0.001	0.02268	98.28
	non-stress	17.18	4	0.002	0.00324	89.66
	drought	2.90	3	0.408	0.00011	17.42
	vegetative	262.77	8	< 0.001	0.02268	98.28
Malondialdehyde content	Total	534.55	35	< 0.001	0.02581	97.53
	non-stress	82.61	12	< 0.001	0.01944	95.67
	drought	207.29	15	< 0.001	0.01193	93.93
	heat	4.89	6	0.558	0.00018	14.74
	vegetative	504.30	27	< 0.001	0.02979	98.10
	generative	11.35	7	0.124	~ 0	0.03
Electrolyte leakage	Total	86.20	15	< 0.001	0.00773	79.13
	non-stress	25.03	7	< 0.001	0.01048	74.79
	drought	41.51	5	< 0.001	0.00718	86.23
	heat	0.01	1	0.923	~ 0	~ 0
	vegetative	74.78	11	< 0.001	0.00973	81.70
	generative	8.54	3	0.036	0.00441	69.14
Superoxide dismutase activity	Total	165.67	13	< 0.001	0.00640	94.54
	non-stress	2.05	4	0.726	~ 0	~ 0
	drought	17.64	3	< 0.001	0.02379	94.65
	heat	7.86	4	0.097	~ 0	1.29
	vegetative	21.18	9	0.012	~ 0	0.69
	generative	1.57	3	0.666	~ 0	~ 0
Guaiacol peroxidase activity	Total	1257.01	21	< 0.001	0.10110	99.06
	non-stress	182.26	8	< 0.001	0.05428	96.98
	drought	352.83	7	< 0.001	0.26175	99.29
	heat	3.79	4	0.435	0.00009	16.06
	vegetative	934.56	17	< 0.001	0.11676	98.58
	generative	3.26	3	0.354	0.00009	21.22
Catalase activity	Total	688.65	21	< 0.001	0.10043	98.45
	non-stress	65.59	8	< 0.001	0.01652	89.35
	drought	525.75	7	< 0.001	0.20525	99.29
	heat	3.88	4	0.423	~ 0	~ 0
	vegetative	663.18	17	< 0.001	0.12052	98.56
	generative	0.51	3	0.917	~ 0	~ 0

Indicator	Variant	Cochran's Q	df	*p*-value	τ^2	I^2
Glutathione reductase activity	Total	115.45	7	< 0.001	0.01643	96.50
	non-stress	45.71	3	< 0.001	0.02351	96.07
	drought	65.39	3	< 0.001	0.00877	94.90
	vegetative	115.45	7	< 0.001	0.01643	96.50
Ascorbate content	Total	12.23	7	0.093	0.00117	35.23
	non-stress	9.77	3	0.021	0.00790	77.20
	drought	2.35	3	0.502	~ 0	~ 0
	vegetative	12.23	7	0.093	0.00117	35.23
Reduced glutathione content	Total	29.97	13	0.005	0.00276	61.11
	non-stress	9.02	3	0.029	0.00219	70.35
	drought	12.19	9	0.203	0.00154	32.98
	vegetative	29.97	13	0.005	0.00276	61.11
Proline content	Total	923.78	17	< 0.001	0.09238	98.53
	non-stress	61.55	5	< 0.001	0.10142	99.02
	drought	277.38	11	< 0.001	0.05780	96.30
	vegetative	773.38	13	< 0.001	0.03311	96.81
	generative	16.51	3	< 0.001	0.08509	85.59
Sugars content	Total	51164.86	8	< 0.001	0.15119	99.93
	non-stress	48922.16	4	< 0.001	0.27443	99.98
	drought	16.13	3	0.001	0.00343	81.59
	vegetative	5850.68	4	< 0.001	0.24589	99.83
	generative	1.04	3	0.791	~ 0	~ 0

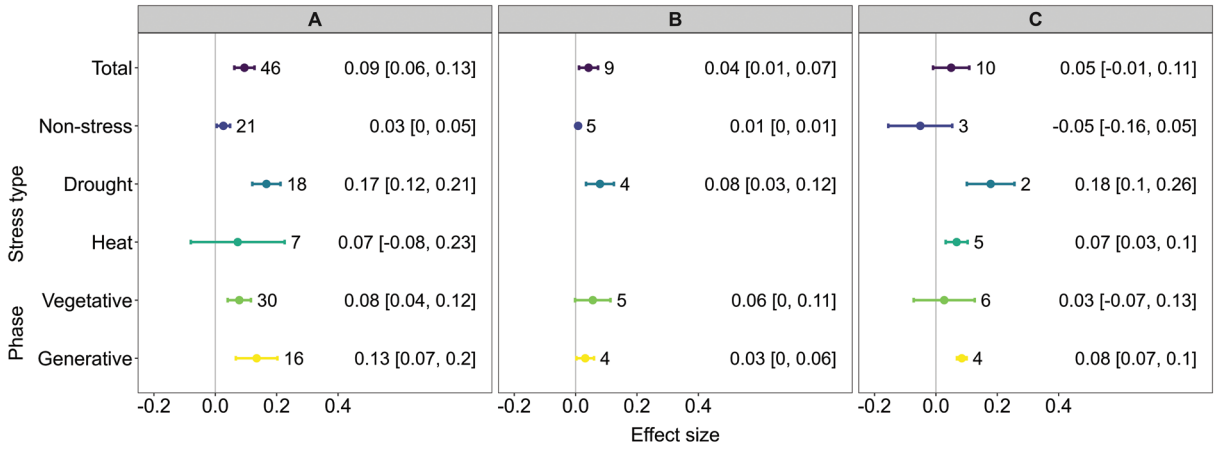

Fig. 1. Effect of exogenous trehalose on growth parameters (A), relative water content (B) and total chlorophyll content (C) in wheat plants. The vertical line indicates no difference between the control and trehalose-treated plants (effect size = 0). Numbers near the symbols specify the number of data points, and the error bars indicate 95% confidence intervals. The mean values of the effects and their confidence intervals are also shown in the fields to the right of the figures.

Higher trehalose effects were observed in the generative phase, though this difference from the vegetative phase effects was not statistically significant at $p \leq 0.05$ (Fig. 1A).

Treating plants with trehalose generally increased the relative water content of their tissues only slightly (Luo et al., 2014; Heshmat et al., 2018a; Qaid, 2020), and this effect was not observed in the absence of stress (Fig. 1B, Appendix I). However, under drought conditions, trehalose increased the relative water content index.

In the absence of stress factors, no effect of trehalose on total chlorophyll content was observed (Luo et al., 2014; Ahmed et al., 2016; Mohsin et al., 2022; Li et al., 2023b) (Fig. 1C, Appendix I). However, under both types of stress, chlorophyll content increased in leaves of plants treated with trehalose, with effect more pronounced under drought. Overall, however,

no increase in chlorophyll content was observed under trehalose treatment during the vegetative phase, when evaluating variants with and without stress effects. During the generative phase of development, this effect was significant at $p \leq 0.05$, albeit small.

The effect of trehalose on oxidative stress indicators and biomembrane condition

The impact of trehalose on hydrogen peroxide levels in plant tissues was not substantial when the dataset was analysed as a whole (Ma et al., 2013; Luo et al., 2018; Mohsin et al., 2022) (Fig. 2A, Appendix II). At the same time, trehalose treatment caused a slight but significant ($p \leq 0.05$) increase in H_2O_2 content in wheat plants in the absence of stress factors. Conversely, under osmotic stress, hydrogen peroxide content decreased following trehalose treatment.

The effect of exogenous trehalose on the level of one of the main products of lipid peroxidation, malondialdehyde, was clearer. The amount of this oxidative stress marker decreased slightly but significantly in the trehalose-treated variants at $p \leq 0.05$ in the overall assessment of all observations (Ma et al., 2013; Aldesuquy & Ghanem, 2015; Ahmed et al., 2016; Luo et al., 2018, 2021a; Qaid, 2020; Mohsin et al., 2022; Li et al., 2023b; Ahsan et al., 2024) (Fig. 2B, Appendix II). However, under optimal conditions, the effect of trehalose on malondialdehyde content was not apparent. At the same time, the malondialdehyde content in plant tissues treated with trehalose was lower than in the control group during both drought and heat stress. The effects of malondialdehyde reduction were observed in both the vegetative and generative phases of plant development.

Trehalose treatment helped preserve the integrity of plant cell membranes (Qaid, 2020; Aldesuquy & Ghanem, 2015; Ahmed et al., 2016; Luo et al., 2022). This is evidenced by a significant decrease in electrolyte leakage from tissues in the trehalose variants, for both types of stress exposure and for the group of variants without stress (Fig. 2C, Appendix II). This effect was found to be virtually identical in the vegetative and generative phases of plant development.

The effect of trehalose on the activity of antioxidant enzymes

In general, superoxide dismutase activity of wheat plants changed very little when treated with trehalose (Ma et al., 2013; Luo et al., 2018; Mohsin et al., 2022; Li et al., 2023b) (Fig. 3A, Appendix III). A slight increase in enzyme activity was observed only in the group of variants under heat stress and in the group of observations at the generative phase of development under trehalose.

In general, and in the group of variants without stress influences, the activity of guaiacol peroxidase remained almost unchanged in response to trehalose treatment (Ma et al., 2013; Ahmed et al., 2016; Luo et al., 2018; Qaid, 2020; Mohsin et al., 2022; Li et al., 2023b) (Fig. 3B, Appendix III). However, sig-

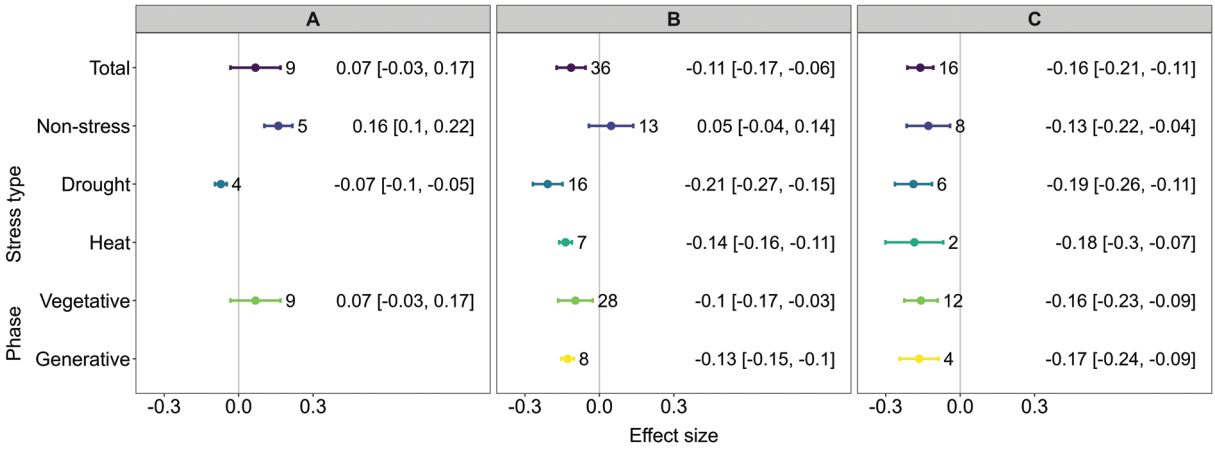

Fig. 2. Effect of exogenous trehalose on hydrogen peroxide (H_2O_2) content (A), malondialdehyde content (B), and electrolyte leakage (C) in wheat plants. The vertical line indicates no difference between the control and trehalose-treated plants (effect size = 0). Numbers near the symbols specify the number of data points, and the error bars indicate 95% confidence intervals. The mean values of the effects and their confidence intervals are also shown in the fields to the right of the figures.

nificant ($p \leq 0.05$) but opposite changes in enzyme activity were observed under drought and heat stress: trehalose treatment caused a slight decrease in guaiacol peroxidase activity under drought conditions, but an increase under heat stress conditions. Changes in guaiacol peroxidase activity at different developmental phases were also opposite in sign: a decrease during the vegetative phase and an increase during the generative phase (Fig. 3B).

There were no big changes in catalase activity when wheat plants were treated with trehalose (Ma et al., 2013; Ahmed et al., 2016; Luo et al., 2018; Qaid, 2020; Mohsin et al., 2022; Li et al., 2023b). No significant effect of trehalose on enzyme activity was found at $p \leq 0.05$ when the entire dataset was evaluated, including data obtained during drought and during the vegetative phase of plant development (Fig. 3C, Appendix III). However, under heat stress and during the generative phase, trehalose slightly increased catalase activity.

Glutathione reductase activity is represented by a small number of studies (only eight), which complicates the conclusions that can be drawn (Ma et al., 2013; Mohsin et al., 2022). Overall, no changes in glutathione reductase activity were recorded in the group of variants without stress effects (Fig. 3D). However, a small but significant ($p \leq 0.05$) increase in the enzyme activity was observed in the presence of trehalose under drought conditions.

The effect of trehalose on the levels of low-molecular-weight antioxidants and osmolytes

The effects of trehalose on ascorbic acid content have been little studied (only eight observations) (Ma et al., 2013; Mohsin et al., 2022), which does not provide sufficient grounds for a comprehensive analysis. However, there is reason to suggest a tendency towards increased ascorbate level in general, particularly under drought stress (Fig. 4A, Appen-

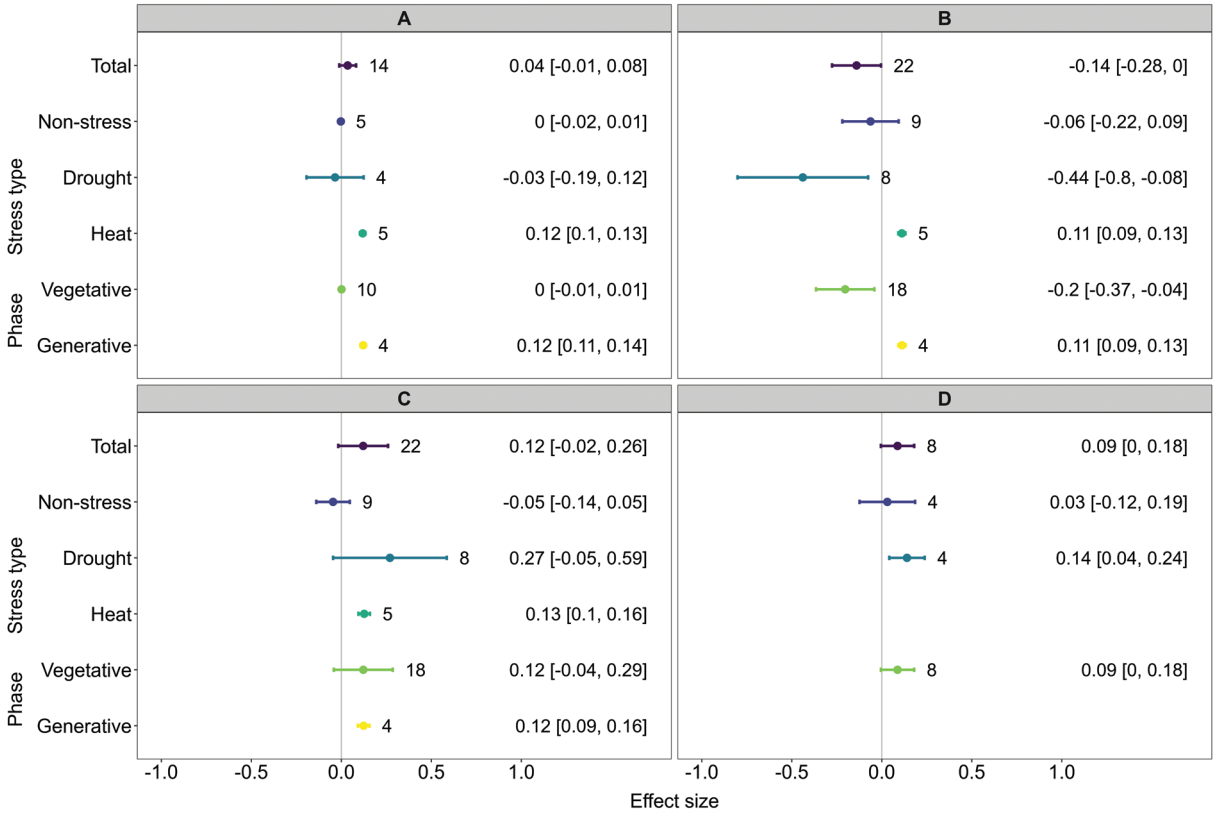

Fig. 3. Effect of exogenous trehalose on the activity of superoxide dismutase (A), guaiacol peroxidase (B), catalase (C) and glutathione reductase (D) in wheat plants. The vertical line indicates no difference between the control and trehalose-treated plants (effect size = 0). Numbers near the symbols specify the number of data points, and the error bars indicate 95% confidence intervals. The mean values of the effects and their confidence intervals are also shown in the fields to the right of the figures.

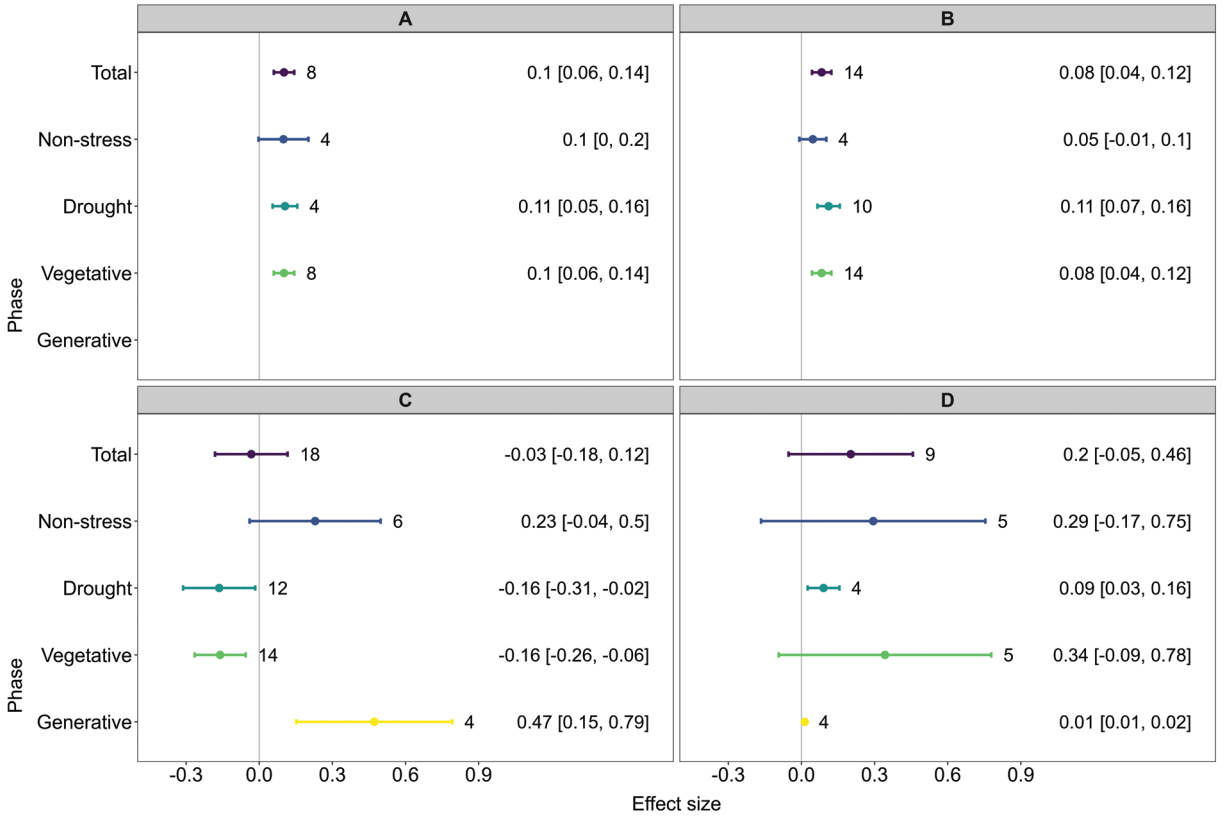

Fig. 4. Effect of exogenous trehalose on the content of ascorbic acid (A), reduced glutathione (B), proline (C), and sugars (D) in wheat plants. The vertical line indicates no difference between the control and trehalose-treated plants (effect size = 0). Numbers near the symbols specify the number of data points, and the error bars indicate 95% confidence intervals. The mean values of the effects and their confidence intervals are also shown in the fields to the right of the figures.

dix IV). In this case, all of the available studies at the time of the meta-analysis were conducted during the vegetative phase of plant development.

The level of another key antioxidant, glutathione, increased significantly under the influence of trehalose, although this effect was not observed in the absence of stress (Ma et al., 2013; Mohsin et al., 2022; Ahsan et al., 2024) (Fig. 4B, Appendix IV). Under drought stress, the glutathione content increased markedly in the presence of trehalose. It should be noted that the effect of trehalose on this indicator was only studied during the vegetative phase of plant development.

The proline content changed minimally under trehalose treatment (Ahmed et al., 2016; Heshmat et al., 2018b; Qaid, 2020; Ahsan et al., 2024) (Fig. 4C, Appendix IV). In the absence of stress factors, trehalose treatment had no significant effect on proline content. However, under drought conditions, a small but significant decrease in proline content was observed ($p \leq 0.05$). Conversely, a decrease in proline content was observed when trehalose was applied during the vegetative phase, whereas an increase was noted during the generative phase (Fig. 4C).

The total content of soluble carbohydrates did not change significantly in response to trehalose treatment in either the overall set of results (Qaid, 2020; Heshmat et al., 2018b; Zhang et al., 2022) or the group without stress effects. However, it increased a little in response to drought stress (Fig. 4D, Appendix IV).

DISCUSSION

As is well known, the most integral indicator of a plant's physiological state is its growth ability. The meta-analysis of data shows that trehalose can enhance plant growth, even in the absence of stress factors (Fig. 1A). It is currently believed that one of the main mechanisms through which trehalose positively

affects plant growth, development and productivity is by modulating carbohydrate metabolism (Han et al., 2024). In particular, it has been demonstrated that in *Arabidopsis thaliana* (L.) Heynh., trehalose induces NADPH-dependent thioredoxin reductase C expression during the day and inhibits its expression at night. This affects the activity of ADP-glucose pyrophosphorylase, thereby promoting starch accumulation (Noroozipoor et al., 2020). The influence of trehalose on the formation of both leaves and flowers has also been demonstrated. Plants with impaired trehalose synthesis enzyme genes (encoding trehalose-6-phosphate synthase or trehalose-6-phosphate phosphatase) have been shown to have smaller leaves, shorter roots, and delayed flowering (Wahl et al., 2013; Kataya et al., 2020). However, under certain conditions, trehalose may inhibit rather than stimulate growth processes. For example, it can inhibit seed germination by enhancing abscisic acid synthesis (Han et al., 2024). It should be noted that most of the information on the effect of trehalose on plant growth has been obtained using the model organism *Arabidopsis thaliana*, and this information can only be extrapolated cautiously to other plant species.

In wheat, enhanced growth processes under trehalose treatment were observed during the vegetative phase, as indicated by various indicators such as plant height, root and leaf biomass, and dry matter accumulation (Ahmed et al., 2016; Qaid, 2020; Luo et al., 2021a). Several data were also obtained during the generative phase. In particular, an increase in seed formation under trehalose treatment was observed (Heshmat et al., 2018a; Luo et al., 2022).

In general, the growth-promoting effects of trehalose are more pronounced under stressful conditions. For example, under drought conditions, trehalose has been shown to promote the growth of the above-ground parts and roots of *Helianthus annuus* L. (Kosar et al., 2021), *Raphanus sativus* L. (Shafiq et al., 2015), and *Ocimum basilicum* L. (Zulfiqar et al., 2021). Wheat plants under drought conditions also exhibited significant improvements in growth parameters (Fig. 1A). However, no such effect was observed under heat stress conditions. This may be due to insufficient data to obtain statistically significant results (only seven observations) and to the specific characteristics of the stress itself or the research objects used.

The more noticeable effect of trehalose on growth processes under drought conditions may be due to its positive impact on water metabolism. It is known that water deficiency inhibits photosynthesis and plant growth (Shao et al., 2022). Water loss can be reduced by trehalose, which involves the main regulator of the stomatal apparatus, abscisic acid, in this process (Lin et al., 2020; Han et al., 2024). A significant increase in the relative water content index in wheat under drought conditions under the influence of trehalose is shown in the data analysed (Fig. 1B). This effect may, of course, be associated not only with trehalose's influence on abscisic acid-mediated stomatal regulation, but also with osmolyte accumulation, which will be discussed below.

It is well known that the ability to maintain a pool of photosynthetic pigments under stressful conditions is one of the markers of plant resistance to stress factors (Santos, 2004). The positive effect of trehalose on chlorophyll content in wheat leaves was not evident in the absence of stress. Still, it was significant under heat and, in particular, drought stress (Fig. 1C). These effects may be associated with reduced oxidative damage in the presence of trehalose (Han et al., 2024). Thus, under drought and heat stress, the content of malondialdehyde, a key marker of oxidative stress, decreased significantly in wheat plants under the influence of trehalose (Fig. 2B), potentially preserving the native state of membrane lipids (Fig. 2C). Furthermore, when plants were treated with high concentrations of trehalose immediately before exposure to stress, it cannot be ruled out that trehalose may have directly stabilised the membranes by forming hydrogen bonds with membrane components (Crowe, 2007; Raza et al., 2024; Choudhary et al., 2025).

A somewhat unexpected effect of treating plants with trehalose was an increase in hydrogen peroxide content in tissues in the absence of stress factors (Fig. 2C), especially considering trehalose's demonstrated ability to act as a scavenger of superoxide anion radicals and hydrogen peroxide (Luo et al., 2008). However, it is also well known that hydrogen peroxide is a key signalling mediator that activates many adaptive responses and 'preparing' plants for stressors (Kolupaev et al., 2013; Rao et al., 2025). It is an essential signalling mediator for the protective effects of many stress metabolites, such as gamma-

aminobutyric acid and melatonin (Ahammed et al., 2024; Kolupaev et al., 2024a, 2024b). Currently, there is little data on hydrogen peroxide as a signalling mediator in relation to trehalose. However, it has recently been demonstrated that trehalose's protective effect on melon plants (*Cucumis melo* var. *makuwa* Makino) under cold stress is mediated by the induction of apoplastic H_2O_2 production (Han et al., 2025). Therefore, like many other compounds with stress-protective effects, the trehalose signal may be mediated by one of the main participants in redox regulation: hydrogen peroxide.

The effect of trehalose on the activity of one of the key antioxidant enzymes, superoxide dismutase, was generally insignificant. However, it is worth noting a significant increase in activity under heat stress, but not under drought (Fig. 3A). The literature also reports that trehalose contributes to the preservation of wheat superoxide dismutase activity under denaturing heating conditions (Luo et al., 2008). Data on the effect of trehalose on superoxide dismutase activity under stress conditions from other plant species are also available. For instance, an increase in superoxide dismutase SOD activity has been observed in *Raphanus sativus* (Shafiq et al., 2015; Akram et al., 2016) and *Linum usitatissimum* L. (Abid & Shahbaz, 2022) under drought conditions. Exogenous trehalose has also been shown to increase the activity and expression of superoxide dismutase genes in cucumber plants under drought conditions (Li et al., 2023a). An increase in superoxide dismutase activity induced by trehalose was also observed in maize plants subjected to salt stress (Rohman et al., 2019). Conversely, trehalose treatment was found to slightly reduce enzyme activity in *Oryza sativa* L. under salt stress conditions (Mostofa et al., 2015). These effects may be due to various factors, such as influence of trehalose on enzyme stability, changes in gene expression of the corresponding genes, and peculiarities in cellular redox homeostasis under specific experimental conditions. Superoxide dismutase (SOD) in plants is represented by three different forms (Cu/Zn-SOD, Fe-SOD, and Mn-SOD), which differ in cellular localisation and sensitivity to various factors (Alscher et al., 2002; Kolupaev et al., 2020). However, sufficient differentiated studies on the effect of trehalose on the activity of different superoxide dismutase forms have yet to be conducted.

Although trehalose treatment had little effect on guaiacol peroxidase activity, it should be noted that enzyme activity decreased significantly during drought and increased during heat stress (Fig. 3B). Literature data on the effect of trehalose on non-specific peroxidase activity, often referred to as guaiacol peroxidase activity, are also inconclusive. However, in sunflowers (*Helianthus annuus* L.) (Kosar et al., 2019), cowpeas (*Vigna unguiculata* L.) (Khater et al., 2018) and sweet basil (*Ocimum basilicum*) (Zulfiqar et al., 2021), trehalose has been shown to positively affect guaiacol peroxidase activity during drought. Additionally, okra (*Abelmoschus esculentus* L.) plants treated with trehalose exhibited increased guaiacol peroxidase activity in response to salinity and drought (Wang et al., 2025). However, Alhudhaibi et al. (2024) have found that trehalose has no effect on guaiacol peroxidase activity in wheat under salt stress. Conversely, a decrease in this enzyme's activity has been observed in cotton (*Gossypium hirsutum* L.) under salinity conditions (Shahzad et al., 2020). The ambiguous effect of trehalose on peroxidase activity may be due to its multifunctionality. Available data indicate that the activity and function of non-specific peroxidases may vary depending on the composition of the phenolic reducing agents used (Cségény & Rácz, 2023). Evidence suggests that phenolic compounds can form a synergistic regeneration cycle with ascorbic acid, enabling non-specific peroxidases to convert significant quantities of H_2O_2 (Zhao et al., 2021). Conversely, it is known that non-specific peroxidases can exhibit oxidase activity, transferring electrons from reducing agents (e.g. NADH) to molecular oxygen (Chen & Schopfer, 1999). This peroxidase action results in the formation of superoxide anion radicals and hydrogen peroxide. These functions may be important at certain (but not all) stages of stress adaptation. Excessive activity of non-specific peroxidase can lead to excessive ROS generation and oxidative damage (Kolupaev et al., 2020). In this regard, the effect of trehalose on various forms of the enzyme at different stress intensities warrants further study.

Changes in the activity of two other antioxidant enzymes (catalase and GR) under the influence of trehalose were very small. This fact, along with the small number of observations on these enzymes, does not allow any definitive conclusions to be drawn.

Ascorbate and glutathione are the most important low-molecular-weight antioxidants. They interact with pro-oxidants both directly and through their participation in the ascorbate-glutathione cycle, one of the most important antioxidant cascades (Kolupaev et al., 2020). Notably, the treatment of wheat plants with trehalose under drought conditions was found to significantly increase ascorbate content and reduce glutathione levels (Fig. 4). An increase in ascorbate content during drought due to trehalose has also been observed in sunflowers (Kosar et al., 2021) and flax (*Linum usitatissimum*) (Abid & Shahbaz, 2022). Trehalose treatment has also been shown to increase the levels of reduced glutathione and ascorbate, as well as the activity of enzymes in the ascorbate-glutathione cycle, in wheat plants exposed to elevated temperatures at the booting stage (Liang et al., 2021). In *Vigna radiata* L. plants exposed to chromium toxicity, the addition of exogenous trehalose increased the ascorbate content (Elkelish et al., 2024). In rice seedlings under salt stress, trehalose normalised the balance between the oxidised and reduced forms of low-molecular-weight antioxidants (Mostofa et al., 2015). In radishes (*Raphanus sativus*) under osmotic stress, trehalose increased the content of not only ascorbate, but also several other low-molecular-weight antioxidants, including the total content of phenolic compounds, glycine betaine, and total tocopherols (Shafiq et al., 2015). Therefore, it can be concluded that trehalose positively affects the levels of low-molecular-weight antioxidants in plants of various taxonomic groups when subjected to abiotic stress. The mechanisms of these effects remain poorly understood. In particular, it would be interesting to clarify whether an increase in the content of these compounds is associated with a general change in redox homeostasis, or whether it is specifically influenced by trehalose acting as a signalling compound on the expression of genes involved in regulating the antioxidant system.

It is known that one of the strategies for plants to adapt to drought and other stresses causing dehydration is the accumulation of compatible osmolytes (Chaum et al., 2019; Ozturk et al., 2021), in particular, proline (Forlani et al., 2019). It is one of the proteinogenic amino acids necessary for protein biosynthesis, while also acting as an osmoprotectant, stabilising macromolecules (chaperone effect), functioning as a free radical scavenger (direct antioxidant action), and participating in maintaining redox homeostasis (Raza, 2021; Ghosh et al., 2022). Overall, the meta-analysis showed that trehalose mitigated drought-induced proline accumulation (Fig. 4C). However, this effect was observed only during the vegetative phase of plant development. In contrast, in the generative phase, there was an increase in drought-induced proline content in the leaves of plants treated with trehalose. This significant effect was observed not only in the four studies included in the meta-analysis, but also in studies excluded due to a lack of data on experimental error. For instance, Ibrahim and Abdellatif (2016) have demonstrated that a threefold treatment of wheat plants with trehalose during the vegetative phase increases proline content in the leaves of 45-day-old plants. An increase in proline content has also been recorded in studies not included in the meta-analysis due to technical issues. For instance, Dawood et al. (2022) have demonstrated an increase in proline content in wheat leaves under the influence of trehalose, even in the absence of stress factors. Similar effects have been observed in other plant species. For example, trehalose enhance drought-induced proline accumulation in cowpea and radish plants (Akram et al., 2016; Khater et al., 2018). Enhanced drought-induced proline accumulation under trehalose influence has also been reported in *Zea mays* L. (de Novais Portugal et al., 2021) and *Linum usitatissimum* (Abid & Shahbaz, 2022). Hyperaccumulation of proline has been observed in response to trehalose treatment in *Ocimum basilicum* plants under drought conditions (Karamzehi & Einali, 2024). However, some plant species (e.g. *Abelmoschus esculentus*) have been shown to reduce stress-induced proline accumulation when treated with trehalose (Sadak et al., 2019).

Despite the universality of proline accumulation during drought, it should be noted that this reaction is not always associated with increased resistance. For instance, a meta-analysis of proline accumulation data in wheat during the vegetative stages of development reveals no significant differences in the manifestation of this effect between drought-resistant and sensitive cultivars (Kolupaev & Shkliarevskyi, 2025). It is believed that an increase in proline content under stress serves not only an osmoprotective function, but also a regulatory function, associated with direct and (or)

indirect involvement in signalling networks (Kaur & Asthir, 2015). The relationship between proline and redox regulation, as well as its involvement in various metabolic pathways, suggests that proline acts not only as a protective compound, but also as a metabolic signal that controls cellular homeostasis in response to changes in environmental conditions (Alvarez et al., 2022; Kolupaev & Shkliarevsky, 2025). Given this complexity, interpreting the links between the quantitative content of proline in tissues and a plant's actual drought resistance is challenging.

It is quite natural that proline is far from being the only osmoprotectant, and the effects of compounds that induce the development of resistance, including trehalose, can be realised by the content of other osmolytes being modulated, in particular sugars (Paul et al., 2017). However, meta-analysis data showed that trehalose had a relatively small effect on wheat sugar content during drought (Fig. 4D). Overall, these results are difficult to interpret unambiguously due to the limited number of studies investigating the effect of trehalose on sugar content in wheat during drought. Nevertheless, it should be noted that overexpression of the trehalose-6-phosphate phosphatase gene (*AtTPPF*), which catalyses the final stage of trehalose formation in plants, led to an increase in the content of not only trehalose, but also sucrose and the total amount of soluble carbohydrates in *Arabidopsis* plants under drought conditions (Lin et al., 2019). Transforming maize plants with the rice trehalose-6-phosphate phosphatase gene increased sugar content in ear spikelets and improved drought resistance during the generative phase (Nuccio et al., 2015). A link between trehalose-6-phosphate metabolism and sugar content has also been established for wheat genotypes (Paul et al., 2017). However, it remains unclear how exogenous trehalose affects tissue sugar content.

CONCLUSION

The meta-analysis of 241 pairs of observations across 15 articles indicates that, in general, exogenous trehalose has a positive effect on wheat's resistance to drought and heat. However, noticeable improvements in growth indicators were observed only under drought, not heat, stress. At the same time, trehalose treatment helped maintain membrane integrity and chlorophyll pools under both types of stress by reducing lipid peroxidation. Exogenous trehalose can likely exert a direct protective effect through antioxidant activity and hydration of membrane components, as well as an indirect effect due to its involvement in complex cellular signalling processes. The volume of research results does not yet allow us to develop a comprehensive understanding of protective effect of trehalose during drought and heat stress in wheat. Nevertheless, the meta-analysis indicates the need for specialised studies on the specific features of the action of trehalose under different types of stress and across different taxonomic groups of plants.

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YEK https://orcid.org/0000-0001-7151-906X
MAS https://orcid.org/0000-0001-7781-4481
DAT https://orcid.org/0000-0002-4891-2100
IVS https://orcid.org/0009-0009-6378-9866
AIO https://orcid.org/0000-0001-9558-2768
TOY https://orcid.org/0000-0003-3604-9028

Appendix I

The effect of trehalose on integrative physiological parameters in wheat plants. Notes: n – number of studies; SE – standard error.

Indicator	Reference	Phase	Variant	Stress type	n control	Value control	SE control	n trehalose	Value trehalose	SE trehalose
Growth	Qaid, 2020	vegetative	non-stress		3	643.67	20.11	3	635.66	22.33
		vegetative	non-stress		3	757.37	22.96	3	814.70	23.04
		vegetative	non-stress		3	67.00	2.40	3	65.95	2.21
		vegetative	non-stress		3	76.80	1.95	3	79.87	1.99
		vegetative	non-stress		3	14.20	0.78	3	14.63	0.40
		vegetative	non-stress		3	18.11	0.14	3	18.87	0.30
		vegetative	stress	drought	3	501.00	17.96	3	559.89	16.16
		vegetative	stress	drought	3	555.90	23.56	3	642.93	25.65
		vegetative	stress	drought	3	53.38	2.19	3	59.80	1.48
		vegetative	stress	drought	3	57.42	2.82	3	66.17	3.15
		vegetative	stress	drought	3	11.09	0.32	3	12.72	0.56
		vegetative	stress	drought	3	12.27	0.37	3	14.62	0.51
	Heshmat et al., 2018a	generative	non-stress		10	4.42	0.287	10	4.49	0.184
		generative	non-stress		10	2.95	0.403	10	3.53	0.169
		generative	non-stress		10	2.00	0.137	10	2.09	0.112
		generative	non-stress		10	1.54	0.09	10	1.82	0.125
		generative	non-stress		10	10.90	0.112	10	11.14	0.157
		generative	non-stress		10	10.10	0.112	10	10.44	0.189
		generative	stress	drought	10	2.59	0.173	10	3.49	0.134
		generative	stress	drought	10	1.89	0.025	10	2.19	0.313
		generative	stress	drought	10	0.476	0.094	10	1.41	0.088
		generative	stress	drought	10	0.87	0.142	10	0.996	0.153
		generative	stress	drought	10	13.16	0.160	10	13.70	0.137
		generative	stress	drought	10	12.10	0.187	10	12.80	0.379
	Ma et al., 2013	vegetative	non-stress		6	10.4	0.15	6	10.6	0.20
		vegetative	non-stress		6	10.9	0.2	6	12.0	0.1
		vegetative	non-stress		6	12.6	0.2	6	12.2	0.2
		vegetative	stress	drought	6	7.53	0.10	6	8.48	0.10
		vegetative	stress	drought	6	7.21	0.3	6	9.23	0.4
		vegetative	stress	drought	6	7.95	0.3	6	10.5	0.1
	Ahmed et al., 2016	vegetative	non-stress		3	52.17	1.89	3	55.77	1.02
		vegetative	non-stress		3	14.92	0.51	3	14.35	0.58
		vegetative	non-stress		3	20.81	0.39	3	19.92	0.55
		vegetative	stress	drought	3	34.57	1.11	3	39.25	1.50
		vegetative	stress	drought	3	9.18	0.37	3	11.97	0.39
		vegetative	stress	drought	3	12.43	0.76	3	15.53	0.85

Indicator	Reference	Phase	Variant	Stress type	n control	Value control	SE control	n trehalose	Value trehalose	SE trehalose
Growth	Li et al., 2023b	generative	stress	heat	3	15.4	0.0	3	16.3	0.1
		generative	stress	heat	3	5.28	0.1	3	6.65	0.15
		generative	stress	heat	3	17.2	0.1	3	19.0	0.2
		generative	stress	heat	3	8.25	0.15	3	11.0	0.15
	Luo et al., 2014	vegetative	non-stress		3	0.22	0.01	3	0.22	0.01
		vegetative	stress	heat	3	0.23	0.02	3	0.22	0.02
	Luo et al., 2021a	vegetative	non-stress		3	0.55	0.25	3	0.79	0.3
		vegetative	non-stress		3	12.9	2.5	3	11.2	2.7
		vegetative	stress	heat	3	0.67	0.2	3	0.23	0.22
		vegetative	stress	heat	3	12.5	0.7	3	9.2	1.0
Relative water content	Qaid, 2020	vegetative	non-stress		3	90.75	1.11	3	93.26	2.18
		vegetative	non-stress		3	89.67	1.67	3	92.54	5.71
		vegetative	stress	drought	3	77.07	4.28	3	84.25	0.66
		vegetative	stress	drought	3	68.92	0.78	3	78.8	0.95
	Heshmat et al., 2018a	generative	non-stress		3	88.28	0.2	3	88.73	0.2
		generative	non-stress		3	90.99	0.2	3	92.12	0.2
		generative	stress	drought	3	74.77	0.2	3	80.18	0.2
		generative	stress	drought	3	80.63	0.2	3	83.78	0.2
	Luo et al., 2014	vegetative	non-stress		3	86.92	0.25	3	86.98	0.69
Chlorophyll content	Mohsin et al., 2022	vegetative	non-stress		3	14.2	0.26	3	12.26	0.23
		vegetative	stress	drought	3	8.67	0.37	3	9.96	0.4
	Ahmed et al., 2016	vegetative	non-stress		3	1.43	0.04	3	1.49	0.03
		vegetative	stress	drought	3	1.06	0.04	3	1.31	0.05
	Li et al., 2023b	generative	stress	heat	3	44.01	0.37	3	47.82	0.41
		generative	stress	heat	3	38.95	0.5	3	43.26	0.75
		generative	stress	heat	3	43.88	0.51	3	47.48	0.45
		generative	stress	heat	3	39.94	0.55	3	43.18	0.8
	Luo et al, 2014	vegetative	non-stress		5	2.41	0.01	5	2.31	0.04
		vegetative	stress	heat	5	2.26	0.01	5	2.27	0.02

Appendix II

The effect of trehalose on oxidative stress markers and membrane stability in wheat plants. Notes: n – number of studies; SE – standard error.

Indicator	Reference	Phase	Variant	Stress type	n control	Value control	SE control	n trehalose	Value trehalose	SE trehalose
H_2O_2 content	Ma et al., 2013	vegetative	non-stress		6	9.92	0.1	6	11.5	0.1
		vegetative	non-stress		6	10.4	0.1	6	11.8	0.1
		vegetative	non-stress		6	10.2	0.2	6	12.2	0.2
		vegetative	stress	drought	6	13.8	0.2	6	13.1	0.1
		vegetative	stress	drought	6	16	0.5	6	15	0.1
		vegetative	stress	drought	6	14.4	0.2	6	13.1	0.2
	Mohsin et al., 2022	vegetative	non-stress		3	255	3	3	283	5
		vegetative	stress	drought	3	416	10	3	383	3
	Luo et al., 2018	vegetative	non-stress		5	109	10	5	169	1
Malondialdehyde content	Qaid, 2020	vegetative	non-stress		3	2.75	0.12	3	2.5	0.1
		vegetative	non-stress		3	3.08	0.12	3	3.15	0.1
		vegetative	stress	drought	3	3.62	0.15	3	3.21	0.15
		vegetative	stress	drought	3	4.29	0.15	3	3.61	0.15
	Ahsan et al., 2024	vegetative	stress	drought	3	12.6	0.5	3	10	0.5
		vegetative	stress	drought	3	14	0.5	3	11.1	0.5
		vegetative	stress	drought	3	15.9	0.5	3	12.6	0.5
		vegetative	stress	drought	3	19	0.5	3	16.7	0.5
		vegetative	stress	drought	3	22.9	0.5	3	20	0.5
		vegetative	stress	drought	3	25.9	0.5	3	23.4	0.5
	Aldesuquy, Ghanem, 2015	generative	non-stress		3	0.51	0.07	3	0.46	0.01
		generative	non-stress		3	0.89	0.07	3	0.58	0.07
		generative	stress	drought	3	0.56	0.07	3	0.52	0.07
		generative	stress	drought	3	0.98	0.07	3	0.62	0.07
	Ma et al., 2013	vegetative	non-stress		6	11.8	0.75	6	15.2	0.75
		vegetative	non-stress		6	14.1	0.75	6	18.8	0.75
		vegetative	non-stress		6	16.9	0.75	6	19.6	0.75
		vegetative	stress	drought	6	30.1	0.75	6	22.2	0.75
		vegetative	stress	drought	6	39.7	0.75	6	27.4	0.75
		vegetative	stress	drought	6	35.7	0.75	6	22.4	0.75
	Mohsin et al., 2022	vegetative	non-stress		3	36.8	2	3	40.6	2
		vegetative	stress	drought	3	64.8	2	3	54.6	1

Indicator	Reference	Phase	Variant	Stress type	n control	Value control	SE control	n trehalose	Value trehalose	SE trehalose
Malondialdehyde content	Ahmed et al., 2016	vegetative	non-stress		3	2.6	0.02	3	2.7	0.02
		vegetative	non-stress		3	3.4	0.02	3	3.3	0.02
		vegetative	stress	drought	3	3.5	0.04	3	3.1	0.02
		vegetative	stress	drought	3	4	0.02	3	3.7	0.02
	Li et al., 2023b	generative	stress	heat	3	25.4	0.1	3	22	0.7
		generative	stress	heat	3	38.7	0.7	3	34.4	0.2
		generative	stress	heat	3	20.5	0.7	3	18	0.4
		generative	stress	heat	3	32.5	0.7	3	29	0.5
	Luo et al., 2018	vegetative	non-stress		5	4.6	0.1	5	4.8	0.7
		vegetative	stress	heat	5	7	0.1	5	5.9	0.1
	Luo et al., 2021a	vegetative	non-stress		3	2.95	1	3	2.1	0.2
		vegetative	non-stress		3	2	0.1	3	2.4	0.1
		vegetative	stress	heat	3	5.1	1.74	3	3.7	0.73
		vegetative	stress	heat	3	2.5	0.5	3	1.8	0.3
Electrolyte leakage	Qaid, 2020	vegetative	non-stress		3	31.06	1.31	3	31.13	0.61
		vegetative	non-stress		3	37.12	2.78	3	35.97	1.24
		vegetative	stress	drought	3	42.43	2.08	3	34.03	0.66
		vegetative	stress	drought	3	59.21	1.02	3	42.74	0.59
	Aldesuqu, Ghanem, 2015	generative	non-stress		3	27.27	0.81	3	22.62	0.66
		generative	non-stress		3	23.48	0.81	3	17.82	0.86
		generative	stress	drought	3	35.65	0.71	3	30.5	0.81
		generative	stress	drought	3	25.2	0.86	3	23.82	0.87
	Ahmed et al., 2016	vegetative	non-stress		3	34.54	1.59	3	32.04	0.57
		vegetative	non-stress		3	38.63	0.68	3	35.68	1.59
		vegetative	stress	drought	3	54.77	0.68	3	44.54	1.02
		vegetative	stress	drought	3	49.09	1.13	3	42.95	1.59
	Luo et al., 2022	vegetative	non-stress		3	12.88	1.43	3	8.58	0.43
		vegetative	non-stress		3	8.3	1.57	3	8.58	1.15
		vegetative	stress	heat	3	59.53	3.15	3	49.8	3.43
		vegetative	stress	heat	3	52.95	2.57	3	43.79	2.86

Appendix III

The effect of trehalose on the activity of antioxidant enzymes in wheat plants. Notes: n – number of studies; SE – standard error.

Indicator	Reference	Phase	Variant	Stress type	n control	Value control	SE control	n trehalose	Value trehalose	SE trehalose
Superoxide dismutase activity	Ma et al., 2013	vegetative	non-stress		6	18.6	0.15	6	18.67	0.19
		vegetative	non-stress		6	18.86	0.3	6	18.89	0.37
		vegetative	non-stress		6	19.16	0.15	6	19.05	0.09
		vegetative	stress	drought	6	20.56	0.19	6	20.87	0.26
		vegetative	stress	drought	6	17.34	0.5	6	18.4	0.54
		vegetative	stress	drought	6	17.72	0.69	6	18.67	0.19
	Mohsin et al., 2022	vegetative	non-stress		3	3.78	0.44	3	4.18	0.29
		vegetative	stress	drought	3	18.38	0.99	3	13.36	0.87
	Li et al., 2023b	generative	stress	heat	3	199	2.53	3	229	2.88
		generative	stress	heat	3	181.66	2.17	3	205.15	2.16
		generative	stress	heat	3	214.54	2.17	3	241.27	2.17
		generative	stress	heat	3	196.48	2.12	3	219.6	2.89
	Luo et al., 2018	vegetative	non-stress		5	62.65	0.2	5	57.82	4.3
		vegetative	stress	heat	5	60.97	1.89	5	60.13	2.62
Guaiacol peroxidase activity	Qaid, 2020	vegetative	non-stress		3	0.092	0.001	3	0.097	0.001
		vegetative	non-stress		3	0.087	0.003	3	0.103	0.001
		vegetative	stress	drought	3	0.131	0.004	3	0.115	0.001
		vegetative	stress	drought	3	0.125	0.005	3	0.12	0.006
	Ma et al., 2013	vegetative	non-stress		6	8.48	0.2	6	6.47	0.26
		vegetative	non-stress		6	8.52	0.31	6	6.12	0.31
		vegetative	non-stress		6	8.6	0.3	6	5.69	0.31
		vegetative	stress	drought	6	9.47	0.31	6	8	0.18
		vegetative	stress	drought	6	10.7	0.35	6	8.32	0.39
		vegetative	stress	drought	6	9.81	0.32	6	7.64	0.24
	Mohsin et al., 2022	vegetative	non-stress		3	0.56	0.02	3	0.5	0.02
		vegetative	stress	drought	3	0.23	0.02	3	0.03	0.01
	Ahmed et al., 2016	vegetative	non-stress		3	0.065	0.002	3	0.088	0.003
		vegetative	non-stress		3	0.114	0.004	3	0.12	0.004
		vegetative	stress	drought	3	0.163	0.002	3	0.073	0.002
		vegetative	stress	drought	3	0.256	0.009	3	0.187	0.002
	Li et al., 2023b	generative	stress	heat	3	119.25	1.49	3	136.85	1.66
		generative	stress	heat	3	100.37	2.03	3	112.4	3.34
		generative	stress	heat	3	136.11	1.29	3	151.48	1.85
		generative	stress	heat	3	107.22	0.92	3	118.14	1.48
	Luo et al., 2018	vegetative	non-stress		5	8.79	0.27	5	8.46	0.75
		vegetative	stress	heat	5	8.46	0.81	5	8.79	0.27

Indicator	Reference	Phase	Variant	Stress type	n control	Value control	SE control	n trehalose	Value trehalose	SE trehalose
Catalase activity	Qaid, 2020	vegetative	non-stress		3	0.78	0.02	3	0.76	0.02
		vegetative	non-stress		3	0.82	0.02	3	1.03	0.07
		vegetative	stress	drought	3	0.42	0.01	3	0.64	0.01
		vegetative	stress	drought	3	0.18	0.01	3	0.47	0.02
	Ma et al., 2013	vegetative	non-stress		6	0.342	0.007	6	0.304	0.008
		vegetative	non-stress		6	0.336	0.008	6	0.293	0.007
		vegetative	non-stress		6	0.338	0.006	6	0.283	0.01
		vegetative	stress	drought	6	0.365	0.009	6	0.328	0.008
		vegetative	stress	drought	6	0.392	0.005	6	0.346	0.009
		vegetative	stress	drought	6	0.374	0.004	6	0.336	0.01
	Mohsin et al., 2022	vegetative	non-stress		3	383	11	3	350	16
		vegetative	stress	drought	3	217	10	3	256	11
	Ahmed et al., 2016	vegetative	non-stress		3	0.74	0.024	3	0.84	0.011
		vegetative	non-stress		3	1.055	0.066	3	0.892	0.014
		vegetative	stress	drought	3	0.204	0.016	3	0.53	0.016
		vegetative	stress	drought	3	0.653	0.016	3	0.672	0.016
	Li et al., 2023b	generative	stress	heat	3	24.96	0.58	3	28.53	0.29
		generative	stress	heat	3	17.92	0.29	3	19.95	0.48
		generative	stress	heat	3	35.56	0.97	3	40.48	0.67
		generative	stress	heat	3	22.55	23.32	3	25.06	0.38
	Luo et al., 2018	vegetative	non-stress		5	22.07	3.25	5	22.53	3.05
		vegetative	stress	heat	5	19.48	3.11	5	30.13	1.68
Glutathione reductase activity	Ma et al., 2013	vegetative	non-stress		6	0.11	0.002	6	0.115	0.002
		vegetative	non-stress		6	0.104	0.004	6	0.12	0.003
		vegetative	non-stress		6	0.107	0.002	6	0.122	0.001
		vegetative	stress	drought	6	0.135	0.001	6	0.136	0.002
		vegetative	stress	drought	6	0.123	0.002	6	0.148	0.002
		vegetative	stress	drought	6	0.116	0.001	6	0.137	0.002
	Mohsin et al., 2022	vegetative	non-stress		3	0.286	0.008	3	0.233	0.009
		vegetative	stress	drought	3	0.099	0.006	3	0.126	0.006

Appendix IV

The effect of trehalose on the content of low-molecular antioxidants and osmolytes in wheat plants. Notes: n – number of studies; SE – standard error.

Indicator	Reference	Phase	Variant	Stress type	n control	Value control	SE control	n trehalose	Value trehalose	SE trehalose
Ascorbate content	Ma et al., 2013	vegetative	non-stress		6	1.1	0.02	6	1.2	0.01
		vegetative	non-stress		6	1	0.05	6	1.2	0.01
		vegetative	non-stress		6	1	0.07	6	1.2	0.01
		vegetative	stress	drought	6	1.4	0.04	6	1.5	0.08
		vegetative	stress	drought	6	1.2	0.05	6	1.4	0.01
		vegetative	stress	drought	6	1.1	0.005	6	1.2	0.05
	Mohsin et al., 2022	vegetative	non-stress		3	3225	190	3	2992	140
		vegetative	stress	drought	3	1992	140	3	2060	160
Reduced glutathione content	Ahsan et al., 2024	vegetative	stress	drought	3	364.1	15	3	367.3	15
		vegetative	stress	drought	3	328.5	17	3	351.1	19
		vegetative	stress	drought	3	296.1	15	3	331.7	20
		vegetative	stress	drought	3	312.3	20	3	315.5	20
		vegetative	stress	drought	3	212	20	3	279.9	22
		vegetative	stress	drought	3	139.2	21	3	153.7	15
	Ma et al., 2013	vegetative	non-stress		6	672.8	10	6	706.3	10
		vegetative	non-stress		6	674.6	14	6	734.4	20
		vegetative	non-stress		6	667.5	18	6	732.7	18
		vegetative	stress	drought	6	560.1	10	6	611.2	10
		vegetative	stress	drought	6	472	20	6	567.1	14
		vegetative	stress	drought	6	581.2	18	6	685.1	10
	Mohsin et al., 2022	vegetative	non-stress		3	53.2	1.5	3	51.2	1
		vegetative	stress	drought	3	28.8	3	3	33	2
Proline content	Qaid, 2020	vegetative	non-stress		3	3	0.05	3	3.2	0.05
		vegetative	non-stress		3	3.8	0.05	3	3.6	0.05
		vegetative	stress	drought	3	6.2	0.05	3	3.8	0.05
		vegetative	stress	drought	3	6.6	0.2	3	4.5	0.2
	Ahsan et al., 2024	vegetative	stress	drought	3	4.1	0.4	3	3.6	0.4
		vegetative	stress	drought	3	6.3	0.7	3	5.2	0.5
		vegetative	stress	drought	3	9.7	0.3	3	7.1	0.3
		vegetative	stress	drought	3	2.3	0.1	3	2	0.25
		vegetative	stress	drought	3	2.7	0.75	3	2.3	0.2
		vegetative	stress	drought	3	5.8	0.3	3	4.8	0.2
	Ahmed et al., 2016	vegetative	non-stress		3	1.7	0.05	3	1.8	0.05
		vegetative	non-stress		3	2.8	0.05	3	3.1	0.05
		vegetative	stress	drought	3	3.1	0.15	3	2.7	0.15
		vegetative	stress	drought	3	5.2	0.05	3	3.9	0.08
	Heshmat et al., 2018b	generative	non-stress		3	1.2	0.1	3	2.8	0.4
		generative	non-stress		3	2.5	0.6	3	4.7	0.1
		generative	stress	drought	3	1.9	0.1	3	2.9	0.1
		generative	stress	drought	3	5.9	0.6	3	6.5	0.2

Indicator	Reference	Phase	Variant	Stress type	n control	Value control	SE control	n trehalose	Value trehalose	SE trehalose
Sugars content	Qaid, 2020	vegetative	non-stress		3	9.48	0.23	3	10.72	0.7
		vegetative	non-stress		3	14.11	0.31	3	15.31	0.35
		vegetative	stress	drought	3	8.67	0.14	3	9.76	0.13
		vegetative	stress	drought	3	12.28	0.28	3	14.39	0.14
	Heshmat et al., 2018b	generative	non-stress		3	35.1	0.5	3	36	0.3
		generative	non-stress		3	31.6	0.1	3	32	0.1
		generative	stress	drought	3	37.9	2	3	39.8	0.1
		generative	stress	drought	3	36.5	0.8	3	37.2	0.6
	Zhang et al., 2022	vegetative	non-stress		3	26.03	0.08	3	88.7	0.14