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Lactic Acid Bacteria Priming of Antioxidant Defense Systems Mitigates Oxidative Damage and Preserves Postharvest Quality in Tomato under Drought Stress

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Abstract

This study investigated foliar-applied Lactic Acid Bacteria (LAB) as a biostimulant to enhance postharvest resilience and quality of tomato (*Solanum lycopersicum* L.) fruit under drought stress. A randomized greenhouse experiment was conducted with four treatments: optimal irrigation, drought stress, and LAB applications combined with both irrigation regimes. Upon reaching physiological maturity, harvested fruits were stored at 7 °C for a 20-day period, with evaluations of physicochemical and biochemical markers at regular intervals. Results demonstrated LAB application as a biochemical primer, significantly mitigating drought-induced physiological deterioration by stabilizing fruit pH and attenuating tissue softening. Notably, LAB treatments elicited a robust systemic antioxidant response, increasing total phenolics, flavonoids, and carotenoids. This was accompanied by upregulation of superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). Moreover, a significant reduction in malondialdehyde (MDA) levels indicated that LAB effectively preserves cellular membrane integrity by suppressing lipid peroxidation. These findings suggest that foliar LAB intervention acts as a potent metabolic modulator, optimizing the antioxidant defense machinery and extending the postharvest shelf-life of tomatoes under environmental stress. This research provides a sustainable and 'green' framework for enhancing the economic value and nutritional longevity of horticultural crops amid escalating climate challenges.

Keywords: Abiotic stress mitigation, Fruit firmness, Lactic acid bacteria (LAB) Biostimulants, Shelf-life extension, Tomato (*Solanum lycopersicum*).

Introduction:

Tomato (*Solanum lycopersicum* L.) is a globally essential horticultural crop; however, its postharvest integrity is severely compromised by abiotic stresses, particularly drought, which can lead to losses exceeding 30%. Drought-induced cellular water deficit triggers progressive physiological and biochemical disruptions during storage and transportation, exacerbating quality deterioration. These detrimental changes culminate in substantial economic repercussions for both producers and supply chain stakeholders ¹.

Taxonomically, tomato (*Solanum lycopersicum* L.) belongs to the Solanaceae family and stands as the world's second most consumed vegetable after potato ². Global production has reached approximately 186.82 million tons annually, with an average yield of 37.1 t/ha, underscoring its status as the most extensively cultivated and processed vegetable crop ³. Beyond its economic importance, tomato fruits are indispensable dietary components, supplying essential vitamins, minerals, and bioactive compounds that are critical for promoting human health and mitigating chronic disease risks ⁴.

From a nutritional perspective, fruits are essential in preventive medicine due to their low caloric density, minimal lipid content, and high palatability ^{5,6}. Specifically, tomatoes are characterized as nutritionally dense crops, providing substantial concentrations of vitamins (C and K), essential minerals (e.g., potassium), and dietary fiber, alongside potent antioxidants such as lycopene ⁷. Consequently, tomato fruits are consumed globally in diverse forms, including fresh, dried, and various processed commodities ^{8,9}. Beyond general nutrition, specific bioactive constituents of tomato, such as lycopene and beta-carotene, have demonstrated efficacy in inhibiting tumorigenesis and preventing prostate cancer ¹⁰. Furthermore, the high potassium content contributes to cardiovascular health by mitigating hypertension risks ¹¹. Despite these benefits, maintaining postharvest quality during the extended supply chain encompassing transportation, retail distribution, and consumer handling remains a critical challenge. During storage, tomato fruits undergo significant tissue softening driven by the degradation of cell wall components, which is accompanied by a rapid depletion of vital nutritional compounds, including antioxidants ¹². Current preservation strategies including modified atmosphere storage, red light irradiation, and the application of plant growth regulators have demonstrated

efficacy in maintaining visual quality and delaying senescence ¹³. However, these approaches predominantly focus on physical storage parameters rather than ensuring consistent nutrient retention. Consequently, developing safe, health-compliant methods to inhibit premature senescence while preserving nutritional integrity remains a critical priority in postharvest agronomy. This need is further intensified by environmental instability; drought, in particular, has emerged as a complex global challenge. Driven by reduced precipitation and elevated evapotranspiration, drought exerts profound consequences on environmental stability, economic viability, and global food security ¹⁴. Since 1900, the global land area affected by drought has doubled, with over 37% of the Earth's surface currently experiencing frequent and severe drought episodes ¹⁵. Regional projections, specifically for Iran, indicate that approximately 47-51% of the land area will be impacted by drought in the near future, with intensities and durations significantly exceeding the 1990-2018 baseline ¹⁶. Agriculture remains the most vulnerable sector to these climatic shifts; crop yields are estimated to decline by up to 22% during arid years. Such deficits not only threaten total production volume but also compromise the physiological quality and postharvest longevity of agricultural commodities ¹⁷.

Environmental stresses fundamentally alter tomato physiology and the biosynthesis of secondary metabolites, including phenolic acids, flavonoids, and terpenoids ¹⁸. Intriguingly, while severe drought is detrimental, controlled water deficit has been shown to enhance specific fruit quality attributes by elevating soluble solid content comprising sugars, amino acids, and organic acids—which are primary determinants of tomato flavor and composition ^{19,20}. Such metabolic shifts can significantly enhance fresh market value by improving flavor profiles and optimizing water relations. Under environmental stress, plants activate a sophisticated antioxidant defense hierarchy to mitigate oxidative damage. This defense comprises non-enzymatic constituents—including flavonoids, phenolic compounds, ascorbic acid, α -tocopherol, and carotenoids alongside a coordinated enzymatic network involving superoxide dismutase (SOD), glutathione reductase (GR), catalase (CAT), and various peroxidases ²¹.

The escalation of environmental challenges has necessitated the development of sustainable preservation strategies. In this context, the application of Generally

Recognized As Safe (GRAS) microorganisms, particularly Lactic Acid Bacteria (LAB) and their bioactive metabolites, has emerged as a robust, food-safe alternative that aligns with increasing consumer preference for natural postharvest treatments. This is particularly critical as drought stress currently affecting approximately 33% of global agricultural land profoundly reshapes plant metabolic pathways ^{22,23}. Such abiotic stress imposes severe constraints on photosynthetic efficiency, vegetative growth, and ultimately, fruit yield ^{24,25}. Plants inherently adapt to drought stress through the intricate modulation of cellular and metabolic pathways. However, the potential of utilizing beneficial microorganisms to bolster these natural defenses in postharvest scenarios remains insufficiently explored. Consequently, this study aimed to evaluate the efficacy of various concentrations of Lactic Acid Bacteria (LAB) in mitigating the adverse effects of drought on tomato fruit. Specifically, the investigation focused on: (i) the physiological and biochemical responses of drought-stressed tomatoes to different LAB dosages; (ii) the synergistic interactions between LAB application and deficit irrigation practices; and (iii) the subsequent impacts of these treatments on fruit postharvest quality and storage longevity. By addressing these objectives, this research seeks to provide a novel, food-safe framework for enhancing crop resilience and nutritional integrity in arid-prone agricultural systems.

Results:

The physiological response and structural integrity of tomato fruits during postharvest storage were significantly modulated by the interplay between irrigation regimes and LAB applications.

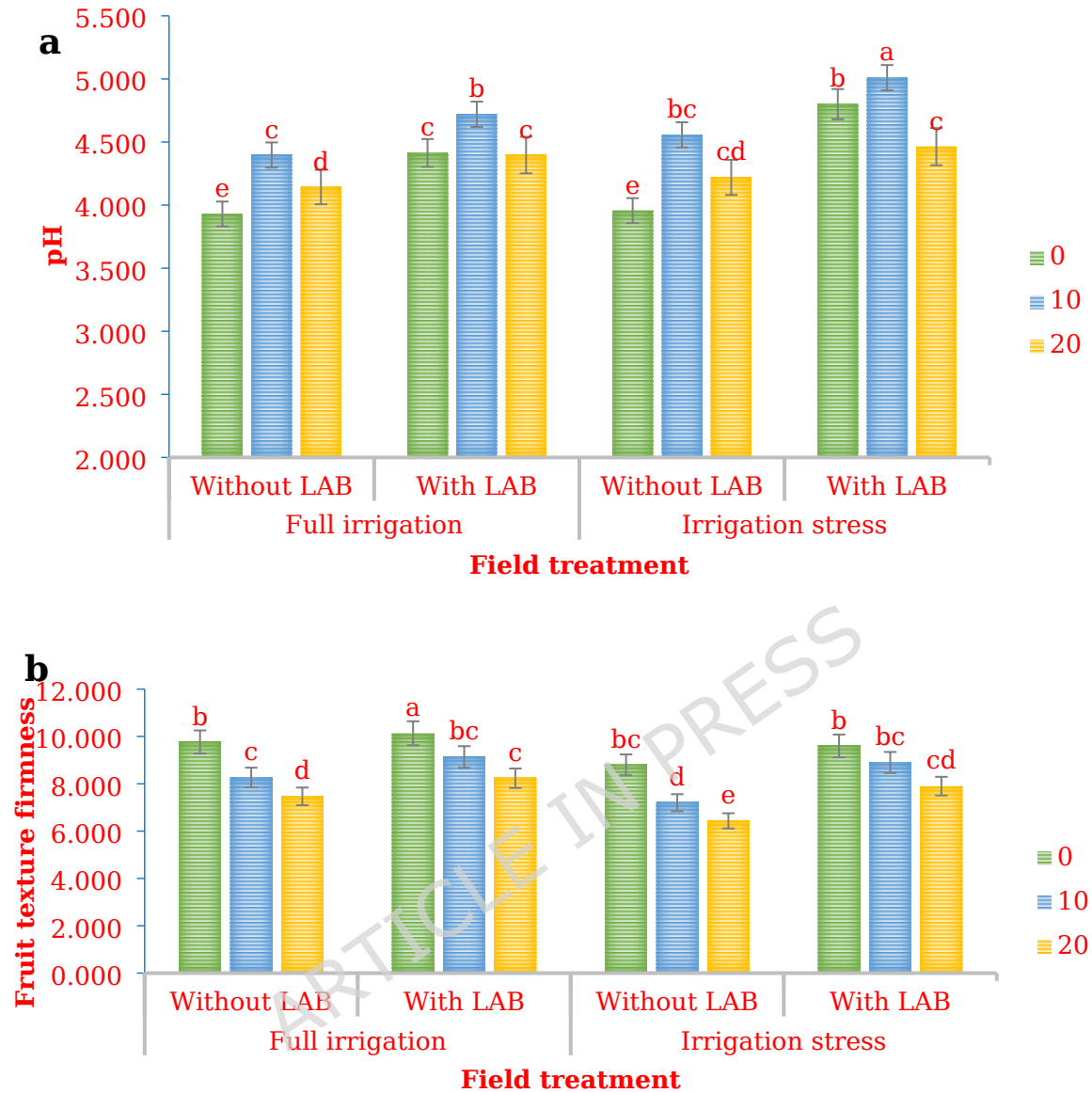
Impact of LAB and Drought Stress on Physicochemical Properties

The postharvest physiological trajectory and structural stability of tomato fruits were significantly modulated by the exogenous application of LAB, particularly under water-deficit conditions. The evolution of fruit pH followed a consistent temporal trend across all experimental groups, characterized by an initial escalation from day 0 to day 10, followed by a subsequent decline as the fruits reached advanced senescence at day 20 (Fig. 1a). Notably, LAB supplementation played a pivotal role in buffering pH fluctuations; LAB-treated fruits maintained significantly higher pH levels throughout the storage period compared to non-LAB

treatments ($P < 0.01$). This stabilization effect was most pronounced in drought-stressed plants, where LAB application effectively mitigated the typical acidic shift observed in untreated stressed fruits.

Simultaneously, fruit firmness a decisive mechanical attribute for postharvest shelf-life—displayed a progressive and significant reduction over the 20-day storage duration ($P < 0.05$; Fig. 1b). At the onset of storage (day 0), the maximum firmness values were recorded in the Full Irrigation + LAB treatment. While drought stress inherently accelerated the loss of turgor and cell wall degradation, the foliar application of LAB acted as a protective agent, significantly attenuating the softening process. By the end of the storage period (day 20), LAB-treated fruits under both irrigation regimes exhibited superior structural integrity, maintaining firmness levels that were substantially higher than the untreated water-deficit group, which reached its lowest mechanical resistance at the final interval.

Furthermore, the dynamics of Vitamin C (ascorbic acid) content revealed a distinct response to the applied treatments (Fig. 1c). Baseline Vitamin C levels were lowest at time zero under the well-watered control. Interestingly, a stress-induced accumulation was observed on day 10, with the peak concentration recorded in the drought-stressed group without LAB, followed by the 'Drought + LAB' treatment. This suggests an initial defensive up-regulation of the antioxidant pool in response to water deficit. However, this accumulation was transient; by day 20, a sharp declining pattern was evident across all treatments ($P < 0.01$), representing the typical oxidative degradation of ascorbic acid during prolonged storage. LAB-treated fruits, however, demonstrated a higher retention rate of Vitamin C compared to their respective controls during the final storage phase.



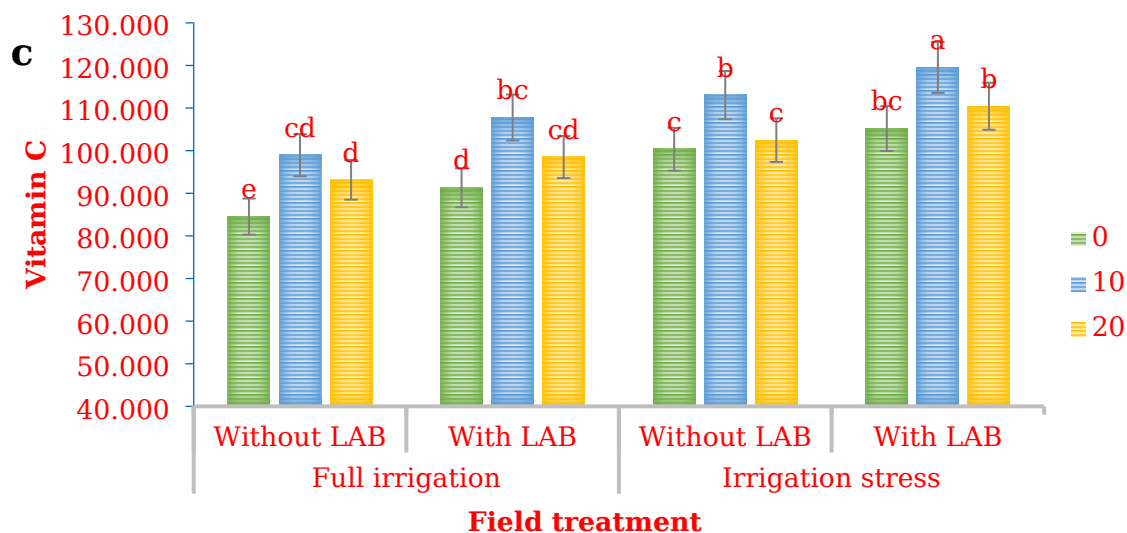


Fig. 1. Effect of foliar-applied Lactic Acid Bacteria (LAB) and drought stress on the physicochemical attributes of tomato fruits during 20 days of postharvest storage. (a) Fruit pH dynamics, (b) Tissue firmness (N), and (c) Vitamin C (ascorbic acid) content (mg/100g FW). Data are presented as mean $\pm$ standard deviation (SD) of three replicates. Different lowercase letters indicate significant differences between treatments within each storage interval according to Tukey's HSD test ($P < 0.05$). The irrigation regimes and LAB concentrations are indicated in the legend within the panels.

Evaluation of Carotenoids, Total Phenolic, Flavonoid Contents, and Antioxidant Activity

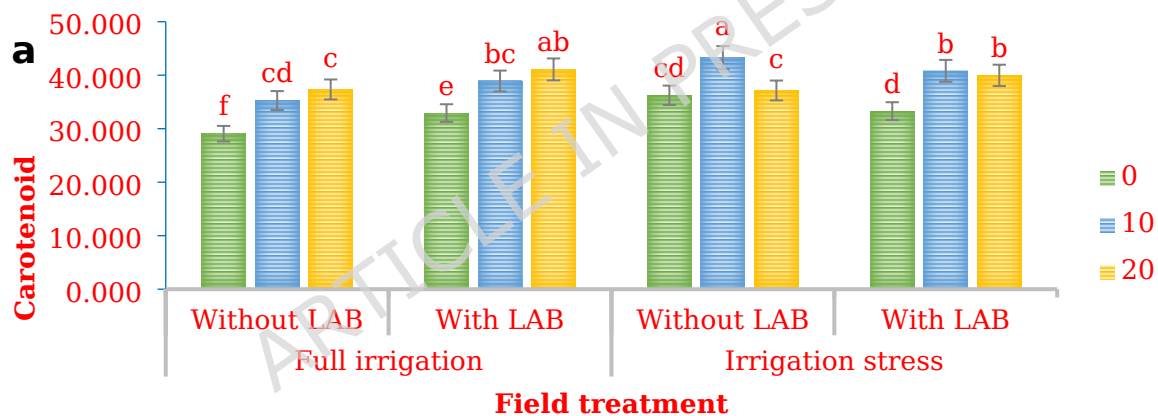
The interaction effects among applied treatments revealed significant variations in the biochemical profile of tomato fruits (Fig. 2). Regarding carotenoid content (Fig. 2a), the water stress treatment without LAB showed a significant increase during the 10-day period compared to other treatments, while the lowest results were observed in the well-watered treatment without LAB. Irrigated treatments demonstrated a continuous increasing trend during the 20-day storage period. In contrast, the stress treatment exhibited an increasing trend during the first 10 days, followed by either a decreasing or stabilizing trend by day 20.

For total phenolic content (Fig. 2b), LAB-treated samples exhibited peak concentrations at day 10, particularly under irrigated conditions, showing a significant increase compared to control treatments at day 0 ($P < 0.01$). Water-stressed samples without LAB application demonstrated lower phenolic levels at

the same time point. By day 20 of storage, all treatments showed a progressive decline in phenolic content.

The flavonoid content (Fig. 2c) also showed significant interactions; the highest levels were observed in fully irrigated, non-LAB-treated samples at day 10, while all other treatments showed declining trends at this time point. Notably, water-stressed treatments maintained comparatively higher flavonoid concentrations than their irrigated counterparts throughout the storage period ($P < 0.01$).

Furthermore, the free radical scavenging activity (DPPH assay) (Fig. 2d) revealed a consistent increasing trend from day 0 to day 20. The antioxidant activity in freshly harvested fruit (day 0) showed the lowest values, gradually increasing until day 10, followed by a slight decline by day 20. Analysis of treatment effects indicated that non-LAB-treated irrigated samples exhibited a significant reduction in scavenging activity compared to their field treatment counterparts $P < 0.05$.



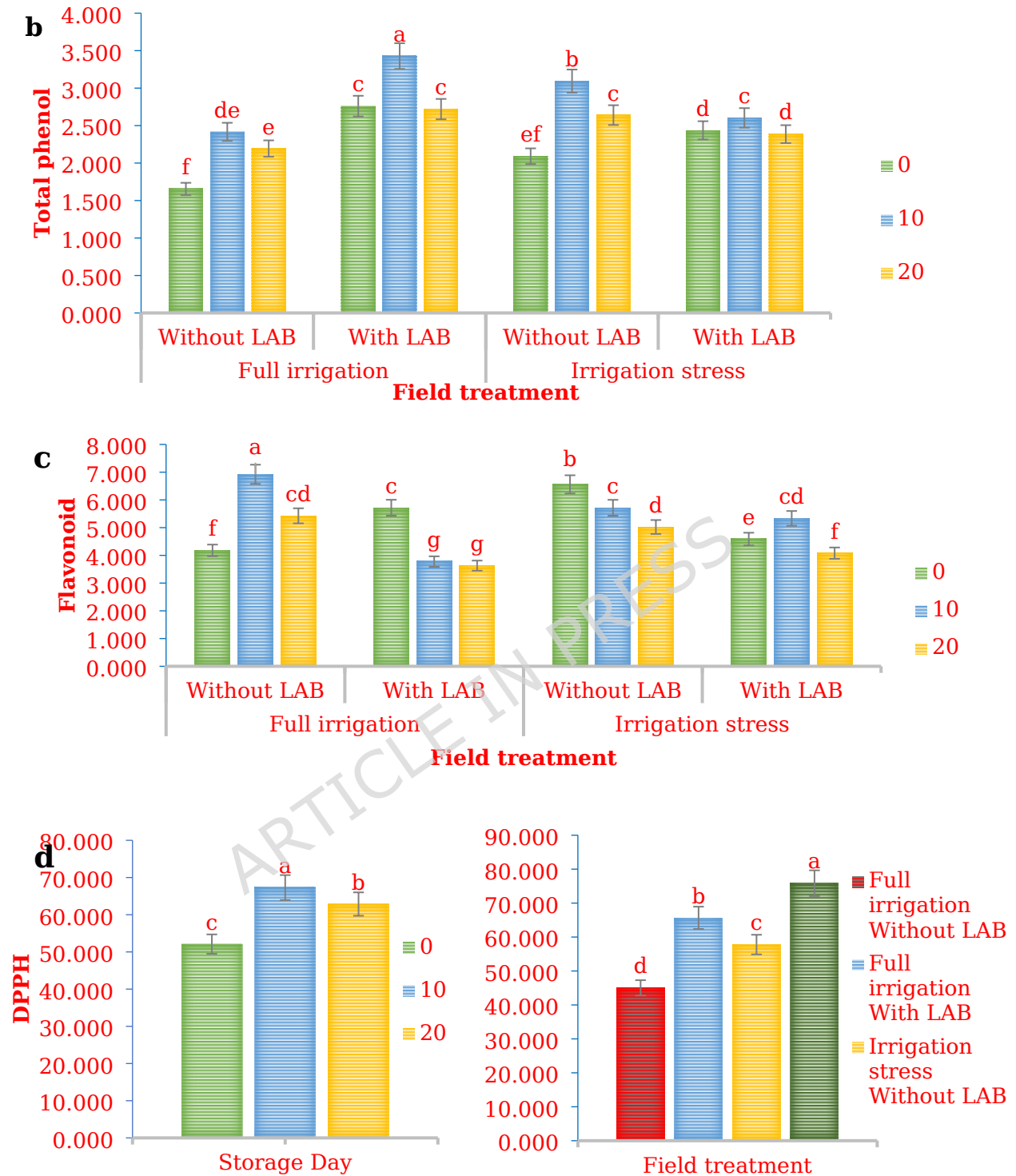


Fig. 2 mpact of LAB application and irrigation regimes on (a) carotenoid content, (b) total phenolic content, (c) flavonoid content, and (d) DPPH radical scavenging

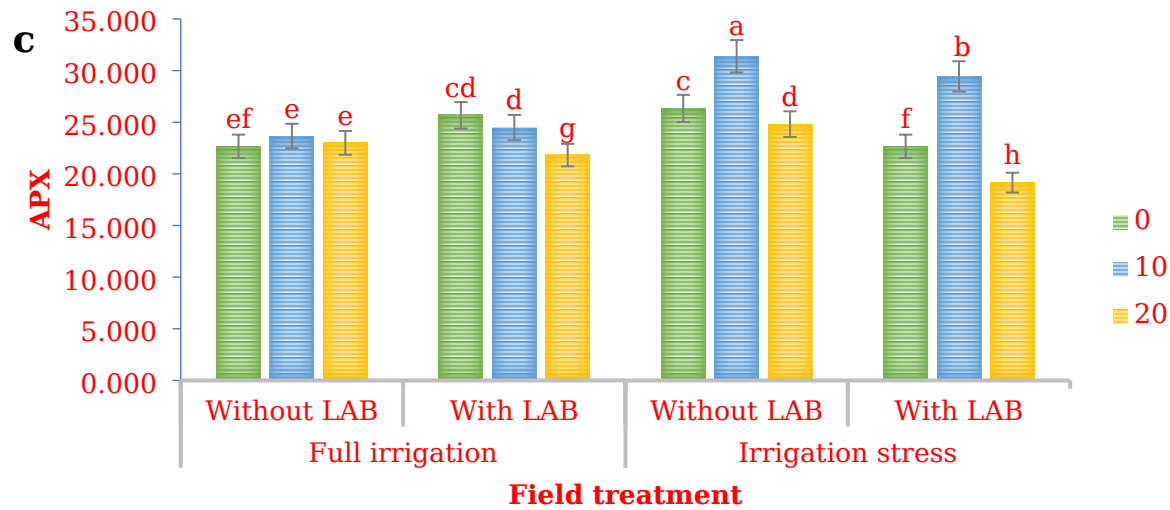
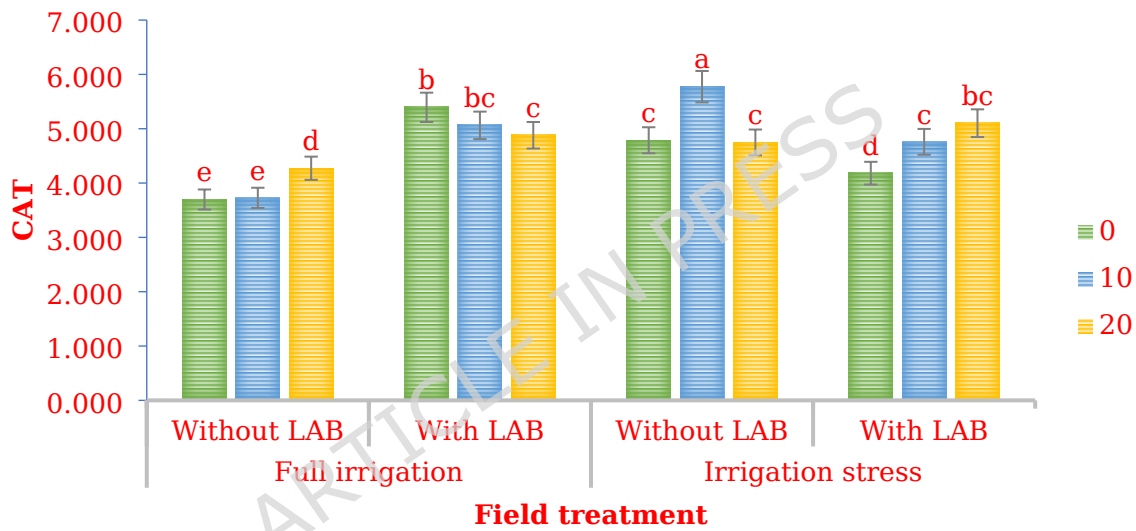
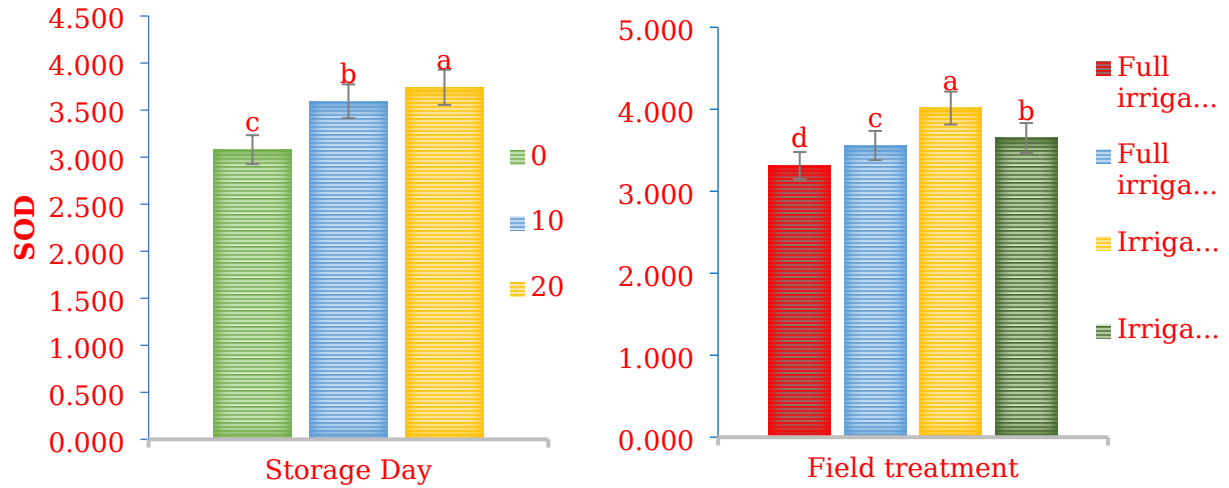
activity of tomato fruits during 20 days of storage. Data are presented as mean $\pm$ SD (n=3). Different lowercase letters indicate statistically significant differences between treatments within each time interval according to Tukey's HSD test ($P < 0.05$).

Enzymatic Antioxidant Responses (SOD, CAT, APX, and PPO)

The activation of the enzymatic antioxidant system represented a crucial physiological adaptation of tomato fruits to drought stress and LAB treatments (Fig. 3). Analysis of superoxide dismutase (SOD) activity (Fig. 3a) showed a consistent upward trend, peaking at day 20 under drought stress. This prolonged activity suggests a continuous necessity to dismutate superoxide radicals throughout the storage period. Notably, LAB-treated fruits maintained higher SOD levels than the control, indicating an enhanced baseline of defense.

In contrast, catalase (CAT) activity (Fig. 3b) and ascorbate peroxidase (APX) activity (Fig. 3c) exhibited a different temporal pattern. Both enzymes reached their maximum levels at day 10 under drought stress without LAB ($P < 0.01$), followed by a significant decline by day 20. This "peak and drop behavior suggests that while the fruit initially intensifies its peroxide-scavenging mechanisms to combat drought-induced oxidative stress, the capacity of these enzymes may diminish as senescence progresses or stress intensifies. LAB application in irrigated treatments, however, showed a more stabilized or decreasing trend, suggesting less oxidative pressure on the fruit.

Furthermore, the polyphenol oxidase (PPO) activity (Fig. 3d), which is often associated with postharvest browning and stress response, showed significant interactions ($P < 0.01$). The enzyme activity peaked at day 10 in the drought-stressed fruits without LAB, followed by a decline towards day 20. Conversely, the lowest PPO levels were recorded in the LAB-treated irrigated samples at day 0. The distinct variation patterns across treatments and storage intervals underscore the role of LAB in modulating PPO activity, potentially influencing the fruit's oxidative stability and overall postharvest quality.



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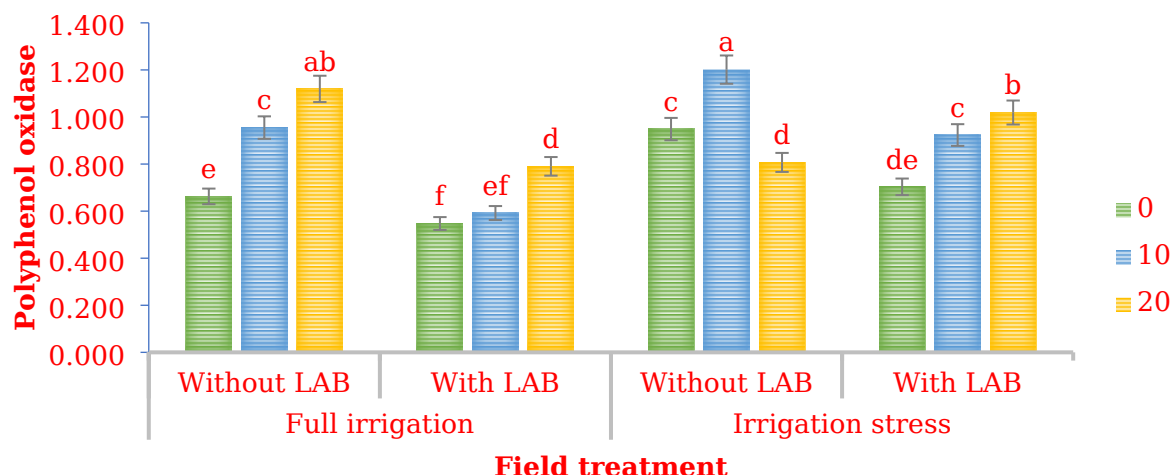


Fig.3. Changes in antioxidant enzyme activities of tomato fruits under LAB application and drought stress during 20 days of storage. (a) Superoxide dismutase (SOD), (b) Catalase (CAT), (c) Ascorbate peroxidase (APX), and (d) Polyphenol oxidase (PPO). Data are means $\pm$ SD (n=3). Different letters indicate significant differences between treatments within each sampling date based on Tukey's HSD test ($P < 0.05$).

Evaluation of Soluble Protein Content and Lipid Peroxidation (MDA)

The physiological status and membrane integrity of tomato fruits were assessed through soluble protein and malondialdehyde (MDA) concentrations (Fig. 4). The protein interaction analysis (Fig. 4a) revealed that both irrigation and drought stress treatments supplemented with LAB achieved the highest protein content on day 10. Most treatments exhibited an initial increasing trend from day 0 to day 10, followed by a subsequent decline towards the end of the storage period. In sharp contrast, the water stress treatment without LAB showed a continuous declining trend throughout the entire storage duration. These protein variation patterns demonstrated highly significant differences ($P \leq 0.01$) among treatments, highlighting the role of LAB in temporary protein stabilization or synthesis during the mid-storage phase.

Regarding malondialdehyde (MDA) content (Fig. 4b), a key indicator of lipid peroxidation, the interaction effects revealed a complex response. LAB-treated irrigated samples exhibited peak MDA levels at day 10, showing a significant increase compared to the control ($P < 0.01$). Interestingly, water-stressed samples treated with LAB showed marginally lower MDA accumulation at the same time

point compared to their irrigated counterparts, though the levels remained statistically significant ($P < 0.01$). Furthermore, at the beginning of storage (day 0), LAB-treated water-stressed samples already possessed higher MDA content than irrigated ones. This distinct pattern of MDA dynamics suggests that while LAB influences the oxidative environment, its impact on lipid peroxidation is highly dependent on the initial stress level and the duration of storage.

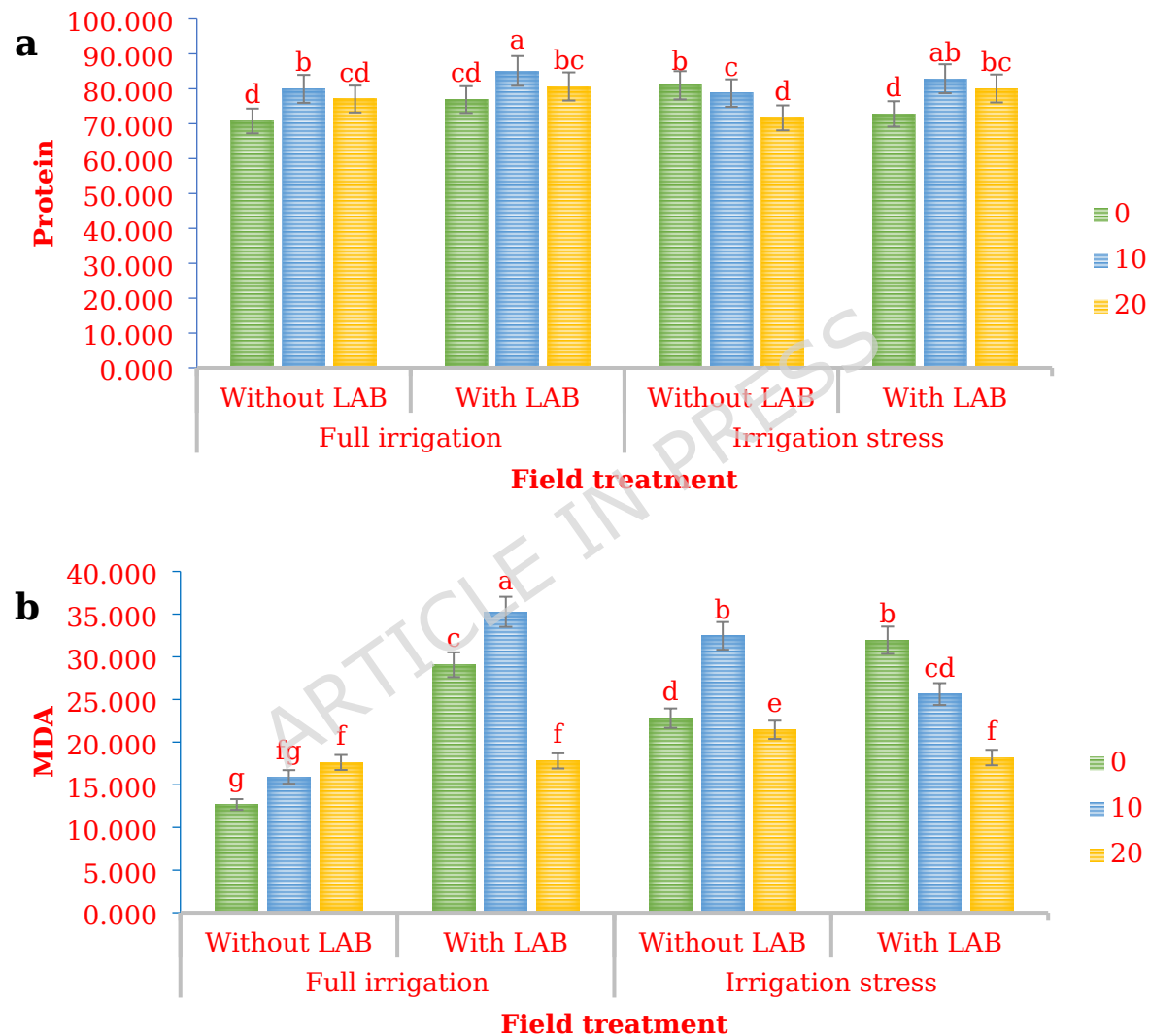


Fig .4. Impact of LAB application and irrigation regimes on (a) soluble protein content and (b) malondialdehyde (MDA) content of tomato fruits during 20 days of storage. Data are presented as mean $\pm$ SD ($n=3$). Different lowercase letters indicate significant differences according to Tukey's HSD test ($P < 0.05$).

Dynamics of Color Indices (Hue, Chroma, and Delta E)

This study investigated the effects of LAB treatment on color indices (Hue, Chroma, and ΔE) at 0, 10, and 20 days postharvest under two irrigation regimes (full irrigation and water stress). The results demonstrated that under both irrigation conditions, Hue and Chroma values generally increased over time. Notably, Hue values at day 20 in LAB-treated samples indicated enhanced primary color and color saturation. In contrast, the highest Chroma values were observed at day 10 in water-stressed samples without LAB treatment. The ΔE index, representing color deviation from the ideal standard, progressively decreased during storage, with more pronounced reduction in LAB-treated samples (Table 1). These findings were statistically significant at $p \leq 0.01$.

IRRIGATION	LAB	TIME	CHROMA	HUE	DELTA E
FULL IRRIGATION	With LAB	0	43.506 ^b	79.276 ^c	17.610 ^a
		10	46.283 ^d	79.812 ^c	15.953 ^a
		20	50.993 ^b	88.227 ^a	13.097 ^a
	Without LAB	0	37.530 ^c	72.357 ^d	4.600 ^c
		10	50.387 ^c	84.820 ^b	5.300 ^d
		20	48.107 ^c	81.030 ^c	7.920 ^c
IRRIGATION STRESS	With LAB	0	52.742 ^a	84.643 ^a	16.470 ^{ab}
		10	54.987 ^b	80.487 ^c	8.807 ^c
		20	52.907 ^a	88.313 ^a	9.203 ^b
	Without LAB	0	44.253 ^{ab}	82.257 ^b	14.370 ^b
		10	57.511 ^a	86.557 ^a	11.487 ^b
		20	45.993 ^d	85.290 ^b	9.987 ^b

Table 1: Values are expressed as mean $\pm$ SD (n=3). Within each column and for each sampling day, means followed by different lowercase letters indicate statistically significant differences between treatments according to Tukey's HSD test ($P < 0.05$).

Correlation Heatmap Analysis of Physiological and Biochemical Traits

To integrate the complex interactions between physiological, biochemical, and color attributes, a Pearson correlation heatmap was constructed (Fig. 5). The hierarchical clustering revealed a robust synergistic relationship between SOD and APX, indicating that these two enzymes serve as the primary synchronized defense line against oxidative stress in tomato fruits. Furthermore, non-enzymatic antioxidants including TPC, TFC, and VC exhibited strong positive correlations with radical scavenging activity (DPPH), confirming their collective contribution to the fruit's antioxidant capacity. A critical finding in the heatmap is the significant

positive association between MDA and Delta E (ΔE), which underscores that lipid peroxidation is a major driver of postharvest color deviation and structural degradation. Conversely, Firmness (FF) showed a pronounced negative correlation with Chroma (C) (dark blue block), reflecting the typical physiological trade-off between fruit softening and pigment maturation. These integrated patterns demonstrate that LAB application effectively modulates these metabolic clusters, fostering a more resilient biochemical profile that maintains membrane integrity and color stability during storage.

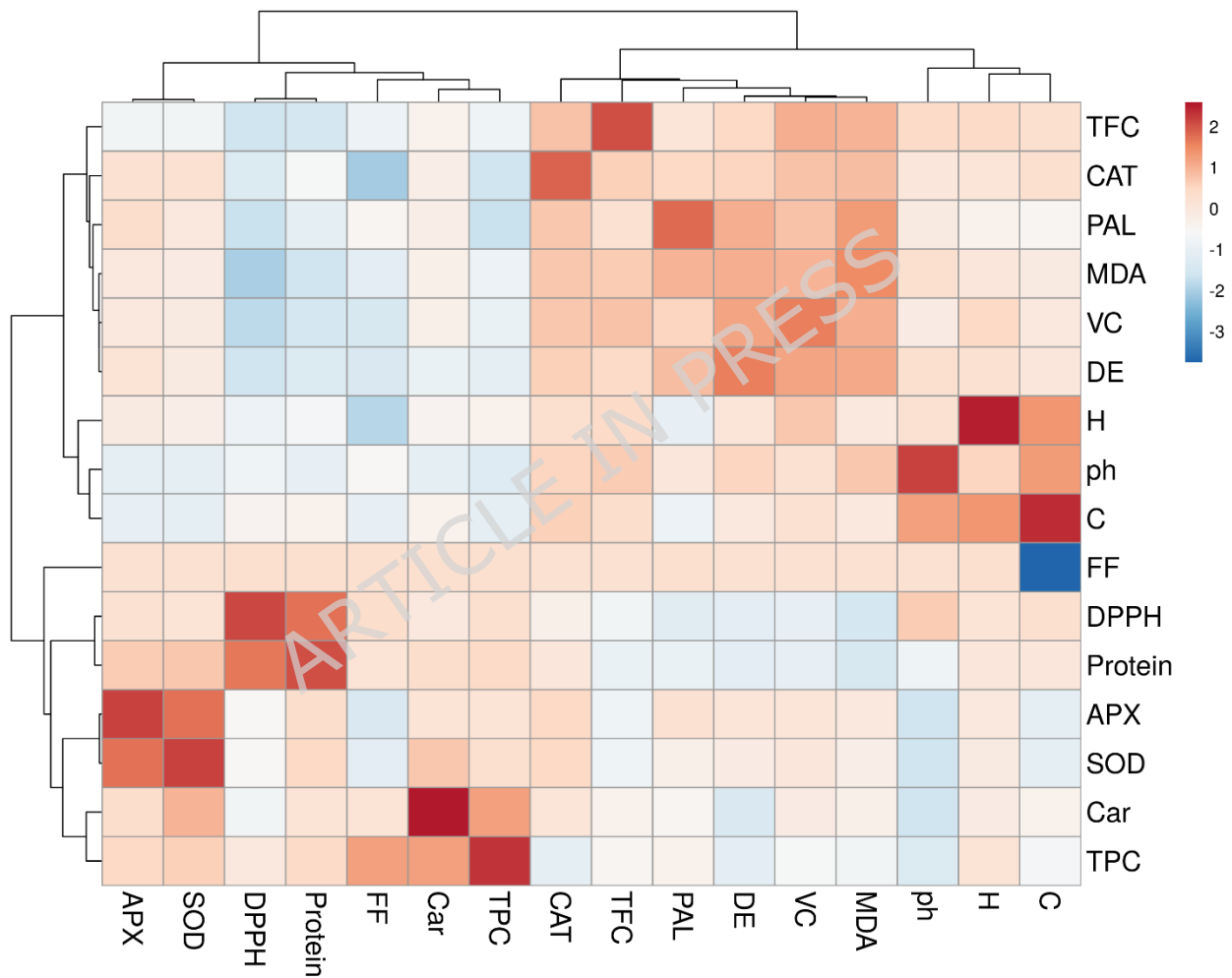


Fig. 5. Hierarchical clustering and Pearson correlation heatmap of tomato fruit quality parameters. The color scale represents the correlation coefficient (r), ranging from blue (negative correlation) to red (positive correlation). Abbreviations: TPC (Total Phenolic Content), TFC (Total Flavonoid Content), VC (Vitamin C), DPPH (Antioxidant Activity), SOD (Superoxide Dismutase), APX

(Ascorbate Peroxidase), CAT (Catalase), MDA (Malondialdehyde), ΔE (Delta E), FF (Firmness), Car (Carotenoids), H (Hue angle), C (Chroma).

Discussion

The results of the present study underscore the pivotal role of lactic acid bacteria (LAB) as a biostimulant in modulating the postharvest physiochemical dynamics of tomato fruits, particularly under drought-induced stress ($P < 0.05$). The application of LAB resulted in significantly higher pH values in tomato fruits relative to the untreated control throughout storage ($P < 0.05$; Fig. 1a), suggests a reduced rate of organic acid catabolism, which is typically accelerated during stress-induced senescence. This stabilization of acidity, coupled with the significantly greater firmness in LAB-treated fruits, particularly at the end of storage ($P < 0.05$; Fig. 1b), highlights the efficacy of LAB in mitigating cell wall degradation and pectin solubilization, two primary factors governing fruit softening. This stabilization of acidity, coupled with the significantly greater firmness in LAB-treated fruits, particularly at the end of storage ($P < 0.05$; Fig. 1b), highlights the efficacy of LAB in mitigating cell wall degradation and pectin solubilization, two primary factors governing fruit softening. These physiological improvements were directly manifested in enhanced color stability, as indicated by the lower ΔE values (Table 1), aligning with the stringent marketability requirements. High sensory evaluation scores ($> 7.5/10$) validate that these biochemical shifts translate into superior consumer acceptance. Our findings regarding pH modulation and quality retention are consistent with those of Cao ¹, who established a strong correlation ($r = 0.89$, $P < 0.01$) between beneficial microbial treatments and the maintenance of postharvest homeostasis under abiotic stress. Collectively, these data position LAB as a sustainable and potent alternative for extending the shelf-life of tomatoes produced in water-limited environments. Furthermore, the impact of water availability on fruit composition is a critical determinant of postharvest longevity. Recent studies indicate that controlled irrigation stress can serve as a physiological stimulus to significantly enhance the qualitative attributes of tomato fruits ²⁶. Specifically, regulated water deficit has been shown to modulate the metabolic profile by reducing fruit pH by 0.3–0.5 units and increasing vitamin C content by 15–20%. These biochemical shifts often improve the flavor profile through an elevated sugar-to-acid ratio (1.2–1.5 fold change) and enhance cellular

membrane integrity, as evidenced by a 30–40% reduction in electrolyte leakage. Such physiological responses correlate strongly with improved postharvest characteristics, including higher total soluble solids (TSS) (5.8–7.2 °Brix) and reduced membrane permeability ²⁷. The observed biochemical modifications collectively contribute to an extended shelf-life and delayed fruit deterioration, suggesting that controlled irrigation, when optimized, can be a strategic approach for quality enhancement in tomato production systems.. Our findings further reveal that LAB-treated samples exhibited a modest but significant pH increase (0.2–0.4 units) compared to the controls ($P < 0.05$). This phenomenon is potentially attributed to the production of alkaline metabolites or the acid-neutralizing capacity of microbial activity, which effectively prevented the sharp pH decline typically observed during postharvest storage ²⁸. Crucially, LAB application significantly suppressed polyphenol oxidase (PPO) activity by 25–40% across all treatments ($P < 0.01$), which directly correlated with a 30% reduction in enzymatic browning. Such biochemical modulation is consistent with reports by Yadav (2021), who demonstrated similar PPO inhibition patterns ($r^2=0.87$) in horticultural crops ²⁹. **These biochemical modifications collectively contributed to superior visual quality retention, as indicated by the maintenance of favorable color parameters (lower ΔE , stable Hue angle; Table 1) throughout the 20-day storage period.** While a gradual decline in tissue firmness was observed across all experimental groups, LAB-treated fruits exhibited a significantly attenuated rate of softening. This structural preservation is likely mediated by the antimicrobial properties of LAB and a subsequent reduction in cellular degradation. Such responses are consistent with the documented role of biological treatments in maintaining cell wall integrity and limiting the enzymatic solubilization of pectins ²⁸. By reinforcing the middle lamella and reducing the activity of cell wall-degrading enzymes, LAB application effectively preserves the fruit's physical architecture, thereby extending its postharvest durability under stress. Furthermore, the efficacy of microbial and nano-structured coatings in reducing surface evaporation and microbial contamination has been well-documented ^{29,30}. In our study, LAB-containing treatments under drought stress demonstrated optimal performance in stabilizing key color parameters, including Hue angle, Chroma, and ΔE values. The minimized ΔE indicates enhanced color stability and a closer resemblance to the initial fruit state, reflecting the mitigation of pigment degradation. Given that fruit color is a

primary determinant of consumer purchasing decisions ³¹, these results highlight the commercial significance of LAB in maintaining the aesthetic and market value of tomatoes produced under water-limited environments.

In the context of hormonal regulation, drought stress was found to suppress ethylene biosynthesis through the targeted inhibition of its key rate-limiting enzymes, specifically 1-aminocyclopropane-1-carboxylic acid synthase (ACS) and ACC oxidase (ACO). This stress-induced reduction in ethylene production serves as a physiological brake, delaying the autocatalytic ripening processes typically observed in climacteric fruits like tomatoes ³². Consequently, this mechanism enhances fruit color retention and extends postharvest shelf-life by slowing down the degradation of chlorophyll and the rapid synthesis of carotenoids ³³. Our results suggest that the integration of LAB application with controlled drought conditions may create a synergistic effect, where LAB mediated antioxidant stability and stress-induced ethylene suppression collectively fortify the fruit against rapid senescence. The incorporation of LAB into the treatments significantly enhanced both vitamin C and carotenoid levels ($P < 0.05$), demonstrating the bacteria's capacity to preserve and even stimulate the fruit's antioxidant potential during postharvest storage. These findings align with recent studies which established the efficacy of biological treatments including endophytic bacteria applications as a viable strategy for maintaining postharvest quality attributes in fresh produce ^{34,35}. Notably, under drought stress conditions, LAB application led to a synergistic increase in vitamin C levels. This is consistent with the established physiological response where plants accumulate antioxidant metabolites, such as ascorbic acid, phenolic compounds, and flavonoids, to counteract stress-induced reactive oxygen species (ROS) ³⁶. Furthermore, the overall enhancement in total antioxidant capacity observed in our study likely results from the LAB-mediated upregulation of the fruit's internal defense mechanisms, fostering a robust biochemical barrier against oxidative damage during the 20-day storage period ²¹.

The synergistic integration of drought stress and LAB treatment significantly promoted the biosynthesis of total phenolic and flavonoid compounds ($P < 0.05$). These secondary metabolites function as critical constituents of the non-enzymatic antioxidant machinery, essential for neutralizing reactive oxygen species (ROS)

and maintaining cellular homeostasis during postharvest storage³⁷. These biochemical shifts align with established observations regarding the impact of beneficial microbial inoculants on fruit metabolic profiles³⁷. Furthermore, water deficit serves as a potent metabolic trigger, inducing the accumulation of protective osmoprotectants and antioxidants including proline, ascorbic acid, and various phenolic derivatives^{7,38}. The marked elevation of these compounds in LAB-treated fruits suggests that microbial application may act as a biochemical primer for the fruit's endogenous defense pathways. This priming effect facilitates a robust mitigation of oxidative stress, thereby ensuring the preservation of the tomato's qualitative and nutritional profile under suboptimal environmental conditions. "Drought stress, triggered by the reduction in soil moisture and the subsequent induction of systemic defense responses, significantly increased proline accumulation ($P < 0.01$) and activated the fruit's antioxidant defense architecture. This system, comprising both enzymatic (CAT, SOD) and non-enzymatic constituents, initially fostered a transient elevation in antioxidant metabolites such as vitamin C and total phenole during the early phases of storage. However, prolonged stress exposure resulted in a progressive and sustained accumulation of these protective compounds. In contrast, the synergistic integration of drought stress and LAB treatments led to a targeted upregulation of key defense enzymes, specifically CAT and SOD, by 25–40%. This enzymatic enhancement facilitated the efficient scavenging of reactive oxygen species (ROS), thereby mitigating drought-induced oxidative damage and preserving cellular integrity. These results are consistent with established models of oxidative stress-induced senescence and cellular degradation in plants³⁹. Our findings suggest that LAB application functions as a biochemical primer, optimizing the enzymatic machinery to maintain redox homeostasis under moisture-limited conditions.

The content of malondialdehyde (MDA), a primary biomarker for lipid peroxidation and cellular oxidative stress, exhibited a significant elevation under drought-stressed conditions without microbial intervention ($P < 0.05$). This increase reflects an intensified rate of oxidative membrane damage and the accumulation of reactive by-products within the fruit tissues. Conversely, the application of lactic acid bacteria (LAB) markedly suppressed MDA levels by 30–45% compared to the drought-only controls ($P < 0.01$), indicating a profound preservation of membrane

integrity. This protective effect appears to be mediated through the dual antioxidant and regulatory functions of LAB in modulating postharvest physiological processes. These findings align with established models of ethylene-mediated mitigation of oxidative damage, suggesting that LAB treatment effectively delays the onset of lipid peroxidation by fortifying the cellular antioxidant defense system and stabilizing the lipid bilayer under abiotic stress ⁴⁰. The synergistic application of LAB treatments resulted in a pronounced elevation of total phenolic and flavonoid concentrations, underscoring the capacity of these beneficial microbes to stimulate secondary metabolite biosynthesis and fortify the plant's endogenous defense architecture. This induction of bioactive compounds not only enhances the nutritional density of the fruit but also suggests a priming effect on the metabolic pathways responsible for stress resilience. These observations are consistent with documented improvements in the nutritional quality and bioactive functionality of tomato fruits following microbial biostimulation ⁴¹. Furthermore, the significantly attenuated levels of malondialdehyde (MDA) in these treatments provide biochemical evidence of reduced lipid peroxidation. This suppression of oxidative degradation confirms that LAB application effectively preserves the structural integrity of cellular membranes, mitigating the detrimental effects of drought-induced oxidative stress during postharvest storage.

Fruits subjected to LAB treatments exhibited a superior total protein content relative to the untreated controls, suggesting that microbial inoculation may modulate the fruit's proteomic profile to enhance stress tolerance. Conversely, LAB application resulted in a significant suppression of polyphenol oxidase (PPO) activity, the primary enzyme facilitating enzymatic browning and tissue discoloration. This inhibitory effect on PPO activity is critical for maintaining the postharvest aesthetic value of the produce. These observations are corroborated by evidence suggesting that beneficial microbial metabolites can effectively downregulate the expression of decay-related enzymes, thereby enhancing the visual quality and marketability of fresh produce ^{28,37}. The reduction in PPO activity, coupled with the preservation of total protein levels, indicates that LAB treatment functions as a robust biological intervention to delay senescence and maintain the biochemical stability of tomato fruits under adverse conditions. The

application of biostimulants, particularly beneficial LAB strains and natural extracts, significantly enhanced the catalytic activity of core antioxidant enzymes, including catalase (CAT), ascorbate peroxidase (APX), and superoxide dismutase (SOD). These enzymes constitute the primary enzymatic defense architecture responsible for the dismutation and neutralization of reactive oxygen species (ROS), thereby serving as a pivotal mechanism against environmental-induced oxidative stress. Notably, the integration of LAB treatment with drought stress elicited a synergistic amplification of these defense responses. This potentiation of the antioxidant machinery demonstrates the efficacy of microbial-based interventions in decelerating the physiological onset of senescence and extending the postharvest longevity of the produce ⁴². These observations are consistent with recent advancements in postharvest physiology which emphasize the critical role of robust antioxidant enzyme systems in mitigating oxidative damage and preserving the metabolic stability of fruit tissues ⁴³⁻⁴⁵.

Conclusion:

This study underscores the potential of lactic acid bacteria (LAB) as a robust biological intervention for maintaining the postharvest quality and extending the shelf-life of tomato fruits, particularly under the exacerbating effects of drought stress. Our findings reveal that LAB applications significantly stabilize key physiological parameters, mitigate oxidative membrane damage as evidenced by attenuated MDA levels and preserve the essential nutritional and visual attributes of the produce. The synergistic integration of LAB with controlled drought stress offers a sustainable and "green" strategy for postharvest management, providing dual benefits of delaying senescence while maximizing marketability through enhanced antioxidant retention and color stability. From an economic perspective, these results suggest that LAB-mediated treatments could substantially reduce postharvest losses and increase the commercial value of tomato crops. However, to facilitate the transition from laboratory-scale findings to industrial applications, further optimization of commercial-scale protocols is required. Given the observed fluctuations in antioxidant stability during the late storage phases, future investigations should focus on defining the precise thresholds of drought stress intensity that maximize metabolic resilience. Furthermore, comprehensive molecular and proteomic studies are warranted to elucidate the exact signaling

pathways through which LAB modulates plant defense mechanisms. Finally, integrating high-resolution sensory profiling (flavor, aroma, and texture) will be crucial to ensuring that these biological treatments align with consumer preferences and global market standards.

Materials and methods

Tomato seedlings (*Solanum lycopersicum* L., cv. **Chef's Choice Red**) were transplanted at the four-leaf stage into experimental plots with a standardized intra-row spacing of 30 cm. The study was implemented using a randomized complete block design (RCBD). **In this experiment**, Irrigation regimes consisted of full irrigation (90% field capacity) and deficit irrigation stress (50% field capacity), **to apply deficit irrigation stress, and a 10% Lactic Acid Bacteria (LAB) consortium consisting of *Lactobacillus plantarum* and *Lactobacillus rhamnosus* (Aria Pajouhan Co., Iran). Viability of the LAB consortium was confirmed prior to each foliar application and two strains were applied at equal concentrations (1:1 ratio). To conduct the experiment, seeds of tomato plants of the Chef's Choice Red variety were sown in 12×12 trays in coco peat and peat moss beds for seedling production and kept in a greenhouse. After seedling production, the plants were transferred to 35×85 cm spacing in the main field at the 4-6 leaf stage. 20 days after transfer to the main field and establishment of the plants, irrigation stresses were administered in four consecutive foliar applications at seven day intervals. Upon reaching physiological maturity, fruit samples characterized by uniform size (15 fruit per each sample), consistent coloration, and the absence of mechanical or pathological injuries were harvested and immediately transferred to a cold storage facility maintained at a constant temperature of 7 ± 0.5 °C and $85 \pm 5\%$ RH. **Fruits were stored in open plastic crates without individual packaging.** Physicochemical and biochemical assessments were systematically performed at three temporal milestones: Day 0 (baseline), **Day 10 (Stage 1), and Day 20 (Stage 2)**, with all analyses conducted in triplicate to ensure statistical accuracy and reproducibility.**

Physicochemical Assessments

Fruit pH and Titratable Acidity (TA)

Titrateable acidity (TA, expressed as % citric acid equivalent) and pH values were measured using a calibrated digital pH meter at 20 ± 1 °C, following established potentiometric titration protocols ⁴⁶.

Fruit Firmness

Fruit textural firmness was determined using a texture analyzer equipped with a 0.2 cm² cylindrical probe. Measurements were taken at two opposite equatorial positions per fruit, with the peak force recorded and expressed in Newtons (N).

Vitamin C Determination

For ascorbic acid extraction, 10–15 g of fresh tomato tissue was homogenized with 30–50 mL of 3% (w/v) metaphosphoric acid solution. To enhance extraction efficiency, the mixture was subjected to ultrasonic-assisted extraction at 40 kHz for 2 min. The resulting homogenate was vacuum-filtered through Whatman No. 1 filter paper (HPLC grade), and the filtrate was stored in amber vials at -20 °C until analysis. Ascorbic acid content was quantified using the standardized iodometric titration method ⁴⁷. Briefly, 1 mL of the filtered extract was titrated against a 0.01 N iodine solution in the presence of a 1% (w/v) starch indicator. The titration endpoint was identified by the persistent appearance of a faint blue-purple color, signifying the complete oxidation of ascorbic acid. The ascorbic acid concentration (mg 100g⁻¹ FW) was calculated using the following formula:

$$\text{Ascorbic acid} = (V \times N \times 88.06 \times DF \times 100) / (W \times 1000)$$

Where V is the volume of iodine solution used (mL), N is the normality of iodine, 88.06 is the equivalent weight of ascorbic acid, DF is the dilution factor, and W is the sample weight (g).

Fruit Color Analysis

Fruit surface color was quantified using a Konica Minolta CR-10 plus chroma meter (Konica Minolta Inc., Tokyo, Japan). The device was calibrated according to the manufacturer's instructions before measuring the CIE L*a*b* coordinates, where L* represents lightness, a* indicates the green-to-red spectrum, and b* denotes the blue-to-yellow spectrum. From these primary coordinates, total color difference (ΔE), chroma (C*), and hue angle (H°) were calculated to define the chromaticity and color intensity of the tomato fruits ⁴⁸. Measurements were taken

at multiple points on the fruit's equatorial surface to ensure a representative average for each sample.

Total Phenolic, Flavonoid, and Carotenoid Contents

Total Phenolic Content (TPC)

The TPC of the extracts was quantified using the Folin-Ciocalteu colorimetric method ⁴⁹. Briefly, 1 mL of the extract was diluted to 10 mL with 80% methanol. Subsequently, 0.5 mL of the diluted extract was mixed with 2.5 mL of 10% (v/v) Folin-Ciocalteu reagent. Following an initial 3–5 min reaction period, 2 mL of 7.5% (w/v) sodium carbonate (Na_2CO_3) was added. The absorbance was recorded at 720 nm using a spectrophotometer after the required incubation. TPC was expressed as milligrams of gallic acid equivalent per gram of dry extract (mg GAE/g) based on a standard calibration curve.

Total Flavonoid Content (TFC)

The TFC was determined using the aluminum chloride (AlCl_3) colorimetric assay ⁵⁰. A 0.5 mL aliquot of each extract was combined with 1.5 mL of methanol, 0.1 mL of 10% (w/v) AlCl_3 , 0.1 mL of 1 M potassium acetate (CH_3COOK), and 2.8 mL of distilled water. After 30 min of incubation at room temperature, the absorbance was measured at 415 nm. TFC was calculated using a quercetin standard curve and expressed as milligrams of quercetin equivalent per gram of dry extract (mg QE/g).

Total Carotenoid Content

The total carotenoid concentration was determined spectrophotometrically following the protocol described by Rodriguez-Amaya and Kimura ^{51,52}. Carotenoids were extracted using hexane as the solvent, The absorbance of the carotenoid solution was measured at 450 nm using a UV-Vis spectrophotometer. The total carotenoid content was calculated using the following equation:

$$\text{Total Carotenoids } (\mu\text{g/g FW}) = (A \times V \times 10^4) / (W \times 2592)$$

A = measured absorbance at 450 nm, V = total extract volume (mL), W = fresh weight of sample (g), E = extinction coefficient of β -carotene in hexane ($2592 \text{ L} \cdot \text{mol}^{-1} \cdot \text{cm}^{-1}$), 10^4 = conversion factor for units ($\mu\text{g/g}$)

Lipid Peroxidation, Antioxidant Capacity, and Protein Quantification

Malondialdehyde (MDA) Content

Lipid peroxidation was quantified by measuring malondialdehyde (MDA) content according to the thiobarbituric acid reactive substances (TBARS) method of Stewart and Bewley⁵³ with modifications. Briefly, 0.5 g of fresh tomato pulp was homogenized in 10 mL of 0.1% (w/v) trichloroacetic acid (TCA) solution using a [specify homogenizer type, e.g., Polytron homogenizer]. The homogenate was centrifuged at $15,000 \times g$ for 10 min at 4°C. For the reaction, 2 mL of supernatant was combined with 4 mL of 20% (w/v) TCA solution containing 0.5% (w/v) thiobarbituric acid (TBA). The mixture was incubated at 95°C for 30 min in a [specify water bath or heating block], then immediately cooled in an ice-water bath to stop the reaction. Absorbance was measured at 532 nm (MDA-TBA complex peak) and 600 nm (background correction) using a UV-Vis spectrophotometer.

DPPH Radical Scavenging Activity

The free radical scavenging capacity was determined using the 2,2-diphenyl-1-picrylhydrazyl (DPPH) assay according to Miliauskas⁵⁴ with modifications. Briefly, 2.5 mL of methanolic extract was mixed with 1 mL of 0.1 mM methanolic DPPH solution (prepared fresh daily) in a 15 mL Falcon tube. The reaction mixture was vortexed for 30 seconds and incubated for 30 minutes at room temperature ($25 \pm 2^\circ\text{C}$) in complete darkness to prevent photodegradation. The absorbance was then measured at 517 nm against a methanol blank using a UV-Vis spectrophotometer. The percentage of DPPH radical scavenging activity was calculated as:

$$\% \text{ Inhibition} = [(A_{\text{blank}} - A_{\text{sample}}) / A_{\text{blank}}] \times 100$$

Where A_{blank} is the absorbance of the DPPH solution mixed with methanol (without extract) and A_{sample} is the absorbance of the DPPH solution after reaction with the sample extract.

Protein Determination

Total soluble protein concentration was determined using the Bradford method⁵⁵, utilizing Coomassie Brilliant Blue G-250. For the assay, 20 μL of the protein extract was combined with 80 μL of extraction buffer and 5 mL of Bradford reagent. Following a 5-min incubation at room temperature, the absorbance was recorded

at 595 nm. Protein concentration was quantified using a bovine serum albumin (BSA) standard curve (0-1 mg/mL) and expressed as mg.g⁻¹/ FW.

Superoxide Dismutase:

Superoxide dismutase (SOD) activity was quantified using the photochemical nitroblue tetrazolium (NBT) reduction method Beauchamp and Fridovich ⁵⁶, which measures SOD's ability to inhibit the photochemical reduction of NBT by superoxide radicals generated in the presence of riboflavin under illumination. Aliquots of 50, 100, 150, and 200 µL of enzyme extract were adjusted to 200 µL final volume with extraction buffer and mixed with 4 mL of reaction mixture containing 50 mM potassium phosphate buffer (pH 8.7), 75 µM NBT, 13 mM L-methionine, 0.1 mM EDTA, and 2 µM riboflavin. The reaction mixtures were exposed to light (intensity: [specify if available]) for 15 min at 25°C, and absorbance was measured at 560 nm using a UV-Vis spectrophotometer. One unit of SOD activity was defined as the amount of enzyme required to inhibit 50% of NBT reduction under the assay conditions.

Catalase:

Catalase enzyme activity was measured according to the modified method of Sinha ⁵⁷. Briefly, 500 µL of diluted enzyme extract (1:4 ratio) was mixed with 1 mL of 100 mM phosphate buffer (pH 7.0), and the reaction was initiated by adding 500 µL of 60 mM hydrogen peroxide (H₂O₂) solution. After 1 min of reaction time, the process was terminated by adding 2 mL of 5% (w/v) dichromate reagent in acetic acid (3:1 v/v). The reaction tubes were immediately placed in a boiling water bath for 15 min, then centrifuged at 10,000 × g for 10 min. The absorbance of the supernatant was measured at 570 nm using a UV-Vis spectrophotometer. Catalase activity was calculated and expressed as µmol H₂O₂ consumed min⁻¹ mg protein⁻¹, based on a standard curve prepared with known concentrations of H₂O₂.

Ascorbic peroxidase:

Ascorbate peroxidase (APX) activity was determined according to Nakano and Asada ⁵⁸ by mixing 50 µL of enzyme extract with 1 mL of reaction mixture containing 50 mM potassium phosphate buffer (pH 7.0), 0.1 mM EDTA, 0.5 mM ascorbic acid (ASA), and 0.15 mM hydrogen peroxide (H₂O₂). The decrease in absorbance at 290 nm was monitored after 1 min using a UV-Vis

spectrophotometer, with enzyme activity expressed as $\mu\text{mol ASA oxidized min}^{-1} \text{ mg protein}^{-1}$.

All statistical analyses were performed using SPSS (version 16), with mean comparisons conducted using **Tukey's HSD test** at $p \leq 0.05$ and $p \leq 0.01$ probability levels, and graphs were generated using Microsoft Excel.

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Author contributions

A.E., S.GH., A.S., R. H. G., N. T., F. B. SH., M.T.G. contributed to the design of the study, validation, data interpretation, and writing-review and editing. A.S. performed the writing-original draft preparation, analyzed the data, and wrote the initial draft of the article. interpretation as well as editing of the final version of the manuscript. All authors have read and agreed to the published version of the manuscript.

Competing interests

The authors declare no conflicts of interest.

Data availability

All the data generated or analysed during the current study were included in the manuscript. The raw data is available from the corresponding author on reasonable request, Data is available for require.

Ethics declarations

All methods performed in this study including the storage and postharvest were in compliance with the relevant institutional, national, and international guidelines and legislation.