

Greenhouse spectral quality affects the post-digestive phenolic levels of tomatoes and probiotic growth

Samikshya Bhattarai

Vegetable and Fruit Improvement Center

Deepak K. Jha

Vegetable and Fruit Improvement Center

Sangeeta Balyan

Vegetable and Fruit Improvement Center

Shuyang Zhen

Texas A&M University

Bhimanagouda S. Patil

`bhimanagouda.patil@ag.tamu.edu`

Vegetable and Fruit Improvement Center

Article

Keywords: gut microbiota, phenolics, prebiotics, supplemental lighting, tomato

Posted Date: July 8th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9644386/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Scientific Reports on October 3rd, 2026. See the published version at <https://doi.org/10.1038/s41598-026-73221-3>.

Abstract

Although light quality influences tomato phenolic biosynthesis, its impact on the bioaccessibility and probiotic growth remains unclear. Thus, bioaccessibility, phenolic profiles of *in vitro* digested tomatoes, and their effects on *Lactobacillus plantarum* growth were assessed using greenhouse-grown Plum Regal (PR) and TAM Hot-Ty (THT) varieties under supplemental blue (B), ultraviolet-B (UV-B), combined (B + UV-B), and no supplemental light (control). Supplemental lighting modulates phenolic bioaccessibility in a genotype-dependent manner. While UV-B may promote structural binding of hydroxycinnamic acids, blue light tends to favor soluble phenolics accumulation in tomatoes. Growth kinetics modeling revealed predominantly sigmoidal growth patterns, whereas UV-B-treated PR digesta exhibited a distinct double-sigmoidal response. The elevated caffeic and ferulic acid content in UV-B samples suggests their partial contribution to the double-sigmoidal growth pattern observed in *L. plantarum*. Thus, this study demonstrates how horticultural practices could be leveraged to enhance the functional potential of tomatoes as a prebiotic source.

1. Introduction

Tomato (*Solanum lycopersicum* L.) fruits are abundant in bioactive metabolites such as phenolic acids, flavonoids, and carotenoids. These metabolites have been linked to health benefits, including antioxidant properties, anti-inflammatory effects, and gut microbiome-modulating activities (Visioli et al., 2011; Luna-Guevara et al., 2018). Improving the nutritional quality of tomatoes through genetic manipulation, breeding strategies, or changes in the plant growth environment has therefore been a subject of interest recently (Wang et al., 2025; Wang et al., 2019).

Light is an important environmental factor that influences the accumulation of health-promoting compounds in plants. The light spectral quality significantly affects the biosynthesis and accumulation of phytochemicals by triggering biosynthetic pathways, including the phenylpropanoid pathway (Castagna et al., 2014; Kaiser et al., 2019; Rácz & Hideg, 2021; Tissot & Ulm, 2020; Wang et al., 2022). Supplemental lighting, particularly blue (400–500 nm) and UV-B (280–315 nm), upregulates shikimate and phenylpropanoid metabolism, leading to increased accumulation of phenolic antioxidants such as hydroxybenzoic acids (HBAs) and hydroxycinnamic acids (HCAs) (Kim et al., 2021; Liu et al., 2023; Bhattarai et al., 2025b).

Numerous studies have focused on the influence of supplemental lighting on polyphenol composition, but the abundance of these compounds in raw fruits does not always translate to beneficial effects on human health (Toor et al., 2009; Cárdenas-Castro et al., 2021). After being consumed, tomatoes are digested; this affects the stability and release of bioactive compounds in the gut (Lippolis et al., 2023). Thus, the fraction of these compounds released from the fruit matrix during digestion and made available for absorption in the gastrointestinal tract affects their biological functionality, often referred to as bioaccessibility. Although the effect of supplemental lights on the concentration of polyphenols in tomato fruits has been examined, the effects on their bioaccessibility remain to be fully explored.

Polyphenols have been reported to exert prebiotic effects by influencing the growth, activity, and composition of gut microbiota, such as *Lactobacillus plantarum* (Cardona et al., 2013; Mithul Aravind et al., 2021; Wan et al., 2021). Beneficial gut microbiomes use dietary polyphenols for growth modulation, redox balancing, and biofilm formation (Dissanayake et al., 2025; Leonard et al., 2021; Rodríguez et al., 2009; Wan et al., 2021). HBAs and HCAs can be transformed by *L. plantarum* in the human gut post-digestion through a series of enzymatic reactions that modify their chemical structure and lead to the production of compounds with different biological activities (Esteban-Torres et al., 2015; Izzo et al., 2022; Lippolis et al., 2023). However, no prior studies have linked the functional impact of the digested products of light-treated tomatoes to microbial growth dynamics, particularly in the context of whole fruit matrices. Therefore, this study investigated the effect of *in vitro* digestion on the polyphenol profile of blue and UV-B-treated greenhouse-grown tomatoes and assessed the growth response of *L. plantarum* to the post-digestion product, exploring the implications for gut health. To our knowledge, this is the first study to directly connect pre-harvest light spectral treatments with microbial growth response through post-digestive phenolic acids profile of whole tomatoes.

2. Materials and methods

2.1. Plant materials and growth conditions

Two tomato varieties, Plum Regal (PR) and TAM-Hot-Ty (THT), were used for this study due to their contrasting genetic makeup and stress responses. The plants were grown under controlled greenhouse conditions at Texas A&M University, College Station, TX (**Figure S2**). The cultivation practices, including soil preparation, irrigation, fertigation, and environmental controls, were carried out as described in our previous study (Bhattarai et al., 2025a). At the flowering stage, plants were exposed to one of four light treatments:

1. a. Blue light (B, peak wavelength at 444 nm; intensity of $238 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 40 cm below the light fixtures, near the top of the plant canopy for 8 h per day from 8:00 am–4:00 pm).
2. b. Ultraviolet-B light (UV-B, peak wavelength at 309 nm; intensity of $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 46 cm below the light fixtures, near the top of the plant canopy for 4 h per day from 8:00 pm–12:00 am).
3. c. Combination of B and UV-B light (B + UV-B): For the B + UV-B treatment, plants received blue light from 8:00 am to 4:00 pm, followed by UV-B light from 8:00 pm to 12:00 am every day using the same intensity as that of the individual treatments.
4. d. No supplemental lighting (control).

The intensity and duration of these treatments were determined based on the difference in photon flux density between the inside and the outside of the greenhouse (**Figure S1**). Details about the varieties and light bars are provided in Tables S1 and S2.

2.2. Reagents

Formic acid (98%–100%), chlorogenic acid (purity $\geq$ 98%), caffeic acid (purity $\geq$ 98%), sinapic acid (purity $\geq$ 98%), and all the chemicals used for *in vitro* digestion were purchased from Sigma-Aldrich (St. Louis, MO, USA). Other reagents used were acetonitrile (HPLC grade, VWR), water (HPLC grade, VWR), methanol (HPLC grade, VWR), *p*-coumaric acid (purity $\geq$ 98%, Cayman Chemical Company), and ferulic acid (purity $\geq$ 98%, Cayman Chemical Company).

2.3. Sample preparation

After harvesting at the red-ripe stage, five fruits from each biological replication with similar CIE Lab values were washed with Nanopure water, cut into pieces, and blended for 30 seconds. The tomato puree was then stored at -80°C until further analysis.

2.4. In vitro digestion of tomato samples

Tomato puree was subjected to *in vitro* digestion using a gastrointestinal tract (GIT) model that simulates the mouth, gastric, and intestinal phases following a previously published method with slight modifications (Balyan et al., 2025).

Simulated Mouth Phase: To mimic the mouth phase of digestion, Simulated Saliva Fluid (SSF) was prepared by dissolving NaHCO_3 (25.0 mM), MgCl_2 (0.15 mM), KCl (15.1 mM), KH_2PO_4 (3.7 mM), and $(\text{NH}_4)_2\text{CO}_3$ (0.06 mM) in one liter of deionized water and adjusting the pH of the solution to 7.0 using HCl. An equal volume of tomato puree and SSF was mixed, and the final pH was adjusted to 6.8. The mixture was then stirred constantly at 100 rpm for 10 minutes at 37°C .

Simulated Gastric Phase: Simulated Gastric Fluid (SGF) was prepared by dissolving NaHCO_3 (25.0 mM), NaCl (47.2 mM), MgCl_2 (0.1 mM), KCl (6.91 mM), KH_2PO_4 (0.896 mM), and $(\text{NH}_4)_2\text{CO}_3$ (0.50 mM) in one liter of deionized water and then adjusting the pH to 2.5 with HCl. After that, pepsin (2000 U/mL) was added to the SGF solution, and an equal volume of the mixture from the mouth phase was combined with the SGF. The final pH of the mixture was adjusted to 2.5 with HCl, and then it was stirred continuously at 37°C for 2 hours at 100 rpm.

Simulated Small Intestine Phase: Simulated Small Intestinal Fluid (SSIF) was prepared by dissolving NaHCO_3 (85.0 mM), NaCl (38.4 mM), MgCl_2 (0.33 mM), KCl (6.8 mM), and KH_2PO_4 (0.801 mM) in one liter of deionized water and then adjusting the pH to 7.0. Bile salt (10 mM) and pancreatin (1:3000) were added to the SSIF solution, and an equal volume of the mixture from the gastric phase was combined with the SSIF. The final pH of the solution was then adjusted to 7.0. The mixture was stirred constantly at 37°C for two hours at 100 rpm.

2.5. Bacterial growth

To evaluate the potential prebiotic activity, *L. plantarum* was selected because it is a well-known probiotic that naturally occurs in the human gut and helps break down food components and improve nutrient availability (Muñoz et al., 2017). The bacterial culture was first activated by inoculating it into de Man, Rogosa, and Sharpe (MRS) broth and incubating for 24 h at 37°C . After activation, the inoculum was diluted to a 10^{-6} concentration. The tomato digesta from different light treatments and diluted inoculum were added to tubes containing MRS medium, and the mixture was dispensed into sterile 96-well plates. The remaining samples in the tubes were incubated at 37°C for 48 hours. To study the growth kinetics, the optical density (OD) at 600 nm was monitored every hour for 48 hours using a spectrophotometer. The temperature was maintained at 37°C .

2.6. Ultra-high performance liquid chromatography (UHPLC) for analysis of phenolic acids and bioaccessibility calculation

The phenolic acid extraction was performed according to Bhattarai et al. (2025b) with slight modifications. Briefly, samples from *in vitro* digestion and prebiotic study were extracted with an equal volume of methanol. The mixture was homogenized for 1 minute, sonicated in ice-cold water for 30 minutes, and centrifuged for 16 minutes at $3,214 \times g$. The supernatant was collected in a 15-ml microfuge tube, and the final volume was recorded. The methanolic extract was then analyzed by UHPLC (Milford, MA, USA) for HBAs and HCAs using an Agilent Eclipse Plus RRHD C18 column (2.1 mm $\times$ 100 mm, 1.8 μm). Water with 0.1% formic acid (solvent A) and acetonitrile with 0.1% formic acid (solvent B) were used for gradient elution as follows: 0–3 min: 2%–10% B, 3–7 mins: 10%–18% B, 7–9 min: 18%–18% B, 9–11.5 min: 18%–20% B, 11.5–14 min: 20%–30% B, 14–17 min: 30%–45% B, 17–19 min: 45%–2% with 0.3 ml/min flow rate. The concentrations of individual compounds were determined using the external calibration curve of their respective commercial standards. Results are expressed as μg per g fresh weight of tomato.

Bioaccessibility percentage of each phenolic acids were calculated by dividing the individual phenolics content in digesta divided by their respective content in raw tomato fruit (published in Bhattarai et al., 2025b).

2.7. Statistical analysis

Six replications per variety were evaluated for each light treatment. The values of individual HBAs and HCAs obtained were expressed as the average of replicates $\pm$ standard error. All the variables were assessed for normality and homogeneity of variance. Then, the phenolic acids dataset was subjected to one-way analysis of variance (ANOVA) with Origin software, and the treatment means within each variety were compared using Fisher's Least Significant Difference (LSD) when there was no significant interaction effect between the light treatment and variety (**Table S3**). However, for others, a two-way analysis of variance (ANOVA) was conducted, and the treatment means between varieties were compared using Tukey's Honestly Significant Difference (HSD). Bacterial growth kinetics were subjected to global curve fitting, and Pearson correlation analysis was conducted between variables using Origin software. The data related to bioaccessibility were used to calculate z-scores, and the results are shown as z-ratios, representing the number of standard deviations each measurement is above (positive z-score) or below (negative z-score) the mean, as previously described in (Cheadle et al., 2003). A z-score is a method of standardizing data, where each variable has a mean of zero and a standard deviation of one. For each value in a dataset, the z-score tells how many standard deviations it is from the mean.

2.8. Computational

The growth of *L. plantarum* followed a 4-parameter logistic growth model for all samples, except PR-UV-B. The 4-parameter logistic growth curve can be represented by the Eq. (1):

$$y(t) = A_1 - \left[\frac{A_1 - A_0}{1 + \left(\frac{t}{c}\right)^p} \right] \# (1)$$

Where $y(t)$ = OD at time t ; A_0 = initial OD; A_1 = maximum OD; t = time; p = hill slope; c = time at which the OD reaches halfway between A_0 and A_1 .

2.8.1. Derivation of maximum growth rate (μ_{max}):

$$\frac{dy}{dt} = \frac{d}{dt} \left(A_1 - \frac{A_1 - A_0}{1 + \left(\frac{t}{c}\right)^p} \right) \# (2)$$

$$\text{Let, } u(t) = \left(\frac{t}{c}\right)^p \# (3)$$

$$\Rightarrow 1 + u(t) = 1 + \left(\frac{t}{c}\right)^p \# (4)$$

Rewriting Eq. (2),

$$\frac{dy}{dt} = \frac{d}{dt} \left(A_1 - \frac{A_1 - A_0}{1 + u(t)} \right) \# (5)$$

$$\Rightarrow \frac{dy}{dt} = -(A_1 - A_0) \cdot \frac{d}{dt} \left(\frac{1}{1 + u(t)} \right) \# (6)$$

Using the chain rule,

$$\frac{d}{dt} \left(\frac{1}{1 + u(t)} \right) = -\frac{1}{(1 + u)^2} \cdot \frac{du}{dt} \# (7)$$

Computing the derivative of Eq. (3),

$$\frac{du}{dt} = \frac{p}{c} \cdot \left(\frac{t}{c}\right)^{p-1} \# (8)$$

Therefore,

$$\frac{dy}{dt} = -(A_1 - A_0) \cdot \left[-\frac{1}{(1 + u)^2} \cdot \frac{du}{dt} \right] \# (9)$$

$$\Rightarrow \frac{dy}{dt} = (A_1 - A_0) \cdot \frac{p}{c} \cdot \frac{\left(\frac{t}{c}\right)^{p-1}}{\left(1 + \left(\frac{t}{c}\right)^p\right)^2} \# (10)$$

Since the maximum growth rate occurs at the inflection point (where $t = c$), we have $\frac{t}{c} = 1$. Replacing this value in Eq. (10), we get:

$$\mu_{max} = \left. \frac{dy}{dt} \right|_{t=c} = \frac{(A_1 - A_0) \cdot p}{4c} \# (11)$$

2.8.2. Calculation of lag time (λ):

The lag time is defined as the time when the extrapolation of the tangent at the inflection point ($t = c$) intersects the initial OD (A_0). The lag time can be calculated using the point-slope equation of a tangent line to the growth curve at the inflection point: $y - y_1 = m(x - x_1)$, where $y = A_0$; $y_1 = y(c)$; slope = μ_{max} ; $x = \lambda$; $x_1 = c$. $y - y_1 = m(x - x_1) \# (12)$

Substituting the values,

$$A_0 - y(c) = \mu_{max} (\lambda - c) \# (13)$$

$$\Rightarrow A_0 - \frac{A_1 + A_0}{2} = \frac{(A_1 - A_0) \cdot p}{4c} (\lambda - c) \# (14)$$

$$\Rightarrow \frac{-(A_1 - A_0)}{2} = \frac{(A_1 - A_0) \cdot p}{4c} (\lambda - c) \# (15)$$

Solving for λ ,

$$\lambda = c \left(1 - \frac{2}{p} \right) \# (16)$$

2.7.3. 7-parameter double-logistic growth model (for PR-UV-B)

$$y(t) = A_2 - \left[\frac{A_1 - A_0}{1 + \left(\frac{t}{c_1}\right)^{p_1}} + \frac{A_2 - A_1}{1 + \left(\frac{t}{c_2}\right)^{p_2}} \right] \# (17)$$

Where, $y(t)$ = OD at time t ; A_0 = initial OD; A_1, A_2 = maximum OD of phases I & II, respectively; t = time; p_1, p_2 = hill slope for phases I & II, respectively; c_1, c_2 = time at which the OD reaches halfway between minimum and maximum OD at phases I & II, respectively.

2.7.4. Calculating maximum growth rate (μ_{max1}, μ_{max2}) using Eq. (11)

Phase I:

$$\mu_{max1} = \frac{(A_1 - A_0) \cdot p_1}{4c_1} \# (18)$$

Phase II:

$$\mu_{max2} = \frac{(A_2 - A_1) \cdot p_2}{4c_2} \# (19)$$

2.7.5. Calculation of lag time (λ_1, λ_2) using Eq. (15)

Phase I:

$$\lambda_1 = c_1 \left(1 - \frac{2}{p_1} \right) \# (20)$$

Phase II:

$$\lambda_2 = c_2 \left(1 - \frac{2}{p_2} \right) \# (21)$$

3. Results and discussion

3.1. Bioaccessibility and post-digestive content of HBAs and HCAs in blue and UV-B light-exposed tomatoes

The profiles of HBAs and HCAs in *in vitro* digested tomato samples were significantly influenced by supplemental lighting in a genotype-dependent manner (Fig. 1). The digesta obtained from *in vitro* digestion of supplemental light-exposed THT samples had higher ($p < 0.0001$) gallic acid content compared to the control (Fig. 1A). However, in PR, the gallic acid content was higher only in the samples treated with blue light. Likewise, 4-hydroxybenzoic acid (4-HBA) content was higher in B and B + UV-B, whereas it was unchanged in UV-B digesta (Fig. 1B).

The *in vitro* digestion of THT samples obtained from exposure to B, UV-B, and B + UV-B had significantly ($p < 0.0001$) higher levels of *p*-coumaric acid, ferulic acid, and chlorogenic acid compared to the control (Fig. 2). However, in PR, only caffeic acid and ferulic acid were significantly ($p < 0.0001$) higher in UV-B digesta, and *p*-coumaric acid and chlorogenic acid contents were slightly higher in B + UV-B digesta than those of the control.

A comparison of the bioaccessibility of individual HBAs and HCAs in light-treated versus control samples using the z-ratio shows a genotype-dependent effect of light (Fig. 3). Overall, the bioaccessibility of these phenolic acids was positively influenced by light treatments in THT, but negatively influenced in PR. In Plum Regal, only caffeic acid bioaccessibility among all the studied phenolic compounds was significantly higher (z-ratio ≥ 1.96) in UV-B-exposed tomatoes. On the other hand, the bioaccessibility of chlorogenic acid and *p*-coumaric acid was significantly reduced (z-ratio ≤ -1.96) under UV-B exposure in PR. In THT, the bioaccessibility of gallic acid from UV-B-exposed samples was significantly higher (z-ratio ≥ 1.96). Similarly, blue light-exposed THT tomatoes had higher accessibility for chlorogenic acid, *p*-coumaric acid, and ferulic acid. On the other hand, the bioaccessibility of caffeic acid was significantly reduced (z-ratio ≤ -1.96) under B + UV-B exposure in THT.

Past studies have shown that HCAs are rapidly released in the stomach and duodenum during *in vitro* digestion, but their stability tends to decrease in later stages of digestion (Lee et al., 2014).

The potential health benefits of HCAs, including antioxidant activity and disease prevention, depend on their accessibility and absorption in the body (Di Pede et al., 2024). Among different HCAs, *p*-coumaric acid is generally more bioavailable than ferulic acid, caffeic acid, and chlorogenic acid (Zhao & Moghadasian, 2010). HCAs undergo significant changes during *in vitro* digestion; their levels change during the oral, gastric, and intestinal phases of digestion because they break down or transform into other metabolites, which may or may not retain the same bioactivity as the original compounds (Izzo et al., 2022). For example, chlorogenic acid shows only about 25.8% bioaccessibility after *in vitro* digestion. This suggests that most of the original compound is not available for absorption, thereby limiting its health benefits (Izzo et al., 2022).

Light exposure is known to regulate the biosynthesis of phenolics, including HBAs and HCAs in plants (Bhattarai et al., 2025b; Wu et al., 2025). UV-B and blue light activate distinct photoreceptors, which upregulate genes in the phenylpropanoid pathway, and ultimately, enhance phenolic acid content (Podolec &

Ulm, 2018). The phenolic acids in tomatoes are either present as free soluble, esterified, or cell-wall bound forms (Perea-Domínguez et al., 2018). During the digestion, low pH in the gastric phase can facilitate the hydrolysis of some esterified phenolics, and the pancreatin and bile salts can cause matrix disintegration and micellization (Wojtunik-Kulesza et al., 2020). However, phenolic acids that are bound to the cell wall or dietary fiber are poorly released (Wojtunik-Kulesza et al., 2020). Therefore, the positive or negative z-ratios reflect how light treatments shifted phenolics among the different forms rather than simply changing their concentration.

Figure 3: Bar graphs showing z-ratio of phenolics bioaccessibility from fruits of Plum Regal and TAM Hot-Ty tomato varieties grown under different pre-harvest light settings (Blue, B + UV-B, and UV-B) compared to the control treatment.

In PR, negative z-ratios for most phenolics, particularly in UV-B-exposed samples, suggests that UV-B exposure likely promoted structural incorporation of HCAs into cell wall polysaccharides as a photoprotective response. HCAs can form ester or ether linkages with cell wall polysaccharides, serving both as UV screens and as cross-linking agents that reinforce the plant cell wall under stress conditions (Jenkins, 2017). Phenolic acids can also form non-covalent complexes with proteins, which might reduce their solubilization and limit their extraction into the aqueous fraction of digesta, thus reducing their bioaccessibility during digestion (Wang et al., 2022). Therefore, the negative z-scores in PR likely indicate towards the enhanced structural binding of phenolics induced by UV-B stress. On the other hand, the significant increase in z-ratio for caffeic acid bioaccessibility in PR under UV-B can likely be explained by digestive hydrolysis of chlorogenic acid, an ester of caffeic acid and quinic acid. Previous digestion studies have shown similar results where chlorogenic acid partially degraded into caffeic acid during gastrointestinal digestion (Sato et al., 2011).

In contrast to PR, THT variety showed predominantly positive z-ratios, indicating improved release of phenolic acids during digestion. Blue light exposure particularly increased the bioaccessibility of chlorogenic acid, *p*-coumaric acid, and ferulic acid, demonstrating light-induced synthesis of soluble phenolics that remain bioaccessible rather than in a structurally bound form. However, the significant decrease in caffeic acid bioaccessibility in B + UV-B treated THT suggests light-induced changes in phenolic localization and interactions within the fruit matrix rather than reduced synthesis. Combined light stress may promote structural incorporation, oxidative polymerization, or stronger binding of caffeic acid within the cell wall and fiber, limiting its release during digestion.

3.2. Growth dynamics of *L. plantarum* with tomato digesta supplementation

The growth of *L. plantarum* followed a 4-parameter logistic growth model for all samples ($R^2 \geq 0.9$), except PR-UV-B, which followed a 7-parameter double-logistic growth model ($R^2 \geq 0.9$) (Fig. 4). In both varieties, the maximum OD was observed in UV-B, followed by blue, B + UV-B, and control. Tomato digesta from THT exposed to UV-B light exhibited the highest *L. plantarum* growth, reaching A_1 of 1.266 and μ_{max} of 0.069 h^{-1} (Table 1). Blue light closely followed the response shown in UV-B, with A_1 of 1.213 and μ_{max} of 0.067. However, the combination of blue and UV-B had lower values for A_1 (1.165) and μ_{max} (0.056) than the individual blue and UV-B exposures, but was still higher than that of the control ($\mu_{max} = 0.043$ and $A_1 = 0.945$). Furthermore, the lag times in UV-B (10.89 h) and blue (11.95 h) light were moderately short compared to the control (12.42 h); however, a longer lag time was observed in the B + UV-B-exposed samples.

The results suggest that the digesta of tomatoes grown with supplemental light favored bacterial growth, possibly due to an altered metabolite composition enriched with bacterial growth-promoting compounds compared to those without supplemental lighting. Although the combined exposure showed slightly lower growth compared to the individual blue or UV-B treatments, the higher maximum growth rate and OD compared to the control indicate that both light wavelengths, individually or in combination, contribute positively to enhance the prebiotic benefits from the tomato matrix. However, a lower growth in response to combined exposure compared to individual light exposures could potentially result from metabolic trade-offs as tomato metabolism shifts from nutrient production to defense metabolite biosynthesis in response to intense oxidative stress. Such trade-offs reduce the availability of substrates, such as sugars and amino acids, required for bacterial growth. Among all the light treatments, UV-B exposure appears to result in the accumulation of more microbiome-accessible nutrients, such as simple sugars and phenolics. The shortest lag time suggests a more rapid adaptation and uptake of these nutrients by the bacteria.

In contrast, the digesta from PR under UV-B produced a double-sigmoidal growth pattern in *L. plantarum* (Fig. 4A). The first phase exhibited a slight increase in biomass ($A_1 = 0.701$) and a very short lag time ($\lambda_1 = 5.0 \text{ h}$), accompanied by a high maximum growth rate ($\mu_{max1} = 0.123 \text{ h}^{-1}$), indicating a faster initial uptake of easily accessible nutrients (Table 1). However, this was followed by a second lag phase, potentially due to limited access to the preferred substrate (a limiting factor), resulting in the induction of machinery desired to support growth by utilizing other substrates. This short secondary lag phase was followed by a second growth phase ($A_2 = 1.404$, $\mu_{max2} = 0.068 \text{ h}^{-1}$, $\lambda_2 = 15.59 \text{ h}$), which may be due to the microbial accessibility of more complex or bound metabolites such as polyphenol conjugates or fiber digestion products. This biphasic response could also be due to the UV-B-induced accumulation of defensive or stress-related compounds that are initially inhibitory or poorly fermentable but are metabolized by microbial enzymes over time. In the B and B + UV-B samples, A_1 and μ_{max} were higher than those of the control, indicating that the bacteria multiplied at a greater rate than in the control samples. The lag time for the blue light sample was similar to that of the control samples, but was longer in the B + UV-B sample. OD was lower than the control in B + UV-B until 24 hours, after which the growth was higher than the control (Fig. 4A).

Table 1
The values obtained for different parameters in the bacterial growth model upon feeding the bacteria with the digesta of light-exposed tomatoes from TAM Hot-Ty and Plum Regal varieties.

Variety	Parameters	Control	Blue	B + UV-B	UV-B
TAM Hot-Ty	A_0	0.270	0.276	0.278	0.302
	A_1	0.945	1.213	1.165	1.266
	c	20.21	18.99	20.77	17.88
	p	5.187	5.396	5.249	5.117
	$\mu_{\max}$	0.043	0.067	0.056	0.069
	λ	12.42	11.95	12.85	10.89
Plum Regal	A_0	0.303	0.306	0.274	0.281
	A_1	1.016	1.14	1.122	0.701
	c_1	19.10	18.47	20.85	6.711
	p_1	4.942	5.174	5.349	7.86
	$\mu_{\max 1}$	0.046	0.058	0.054	0.123
	λ_1	11.37	11.33	13.06	5.00
	A_2				1.404
	c_2				20.79
	p_2				7.989
	$\mu_{\max 2}$				0.068
	λ_2				15.59

Phenolic compounds, including HBAs and HCAs, share a common structure consisting of an aromatic ring with one or more hydroxyl groups. These compounds exhibit diverse biological activities, but their absorption in the human body is often limited by their chemical structures and interactions within the food matrix. *L. plantarum* plays an important role in modifying these phenolic acids found in tomatoes by using enzymes like esterases, decarboxylases, and reductases. Esterases first break the ester bonds in HBA-derivatives by hydrolysis and release free acids (Landete et al., 2021; Muñoz et al., 2024). Decarboxylases then remove carboxyl groups from these acids and form decarboxylated products (Barthelmebs et al., 2001; Gaur & Gänzle, 2023). These enzymatic actions make complex phenolic compounds more easily metabolizable, thereby enhancing the nutritional and sensory qualities of fermented foods.

Similar to HBAs, HCAs can exist as free acids or in bound form (e.g., esterified as chlorogenic acids). Free forms are generally easier to absorb, whereas bound forms require an enzymatic breakdown for release and absorption (Stalmach, 2014; Zhao & Moghadasian, 2010). *L. plantarum* uses specific genes and enzymes for HCA metabolism. It utilizes a heterodimeric NADH-dependent coumarate reductase (HcrAB), which acts on the carbon-carbon double bond to reduce HCAs, such as *p*-coumaric, caffeic, and ferulic acids, to phenylpropionic acids (Santamaría et al., 2018). The genes *lp_1424* and *lp_1425* encode the reductase components, HcrA and HcrB, respectively. HcrB exhibits hydroxycinnamate reductase activity, and HcrA stabilizes the enzyme complex (Santamaría et al., 2018). Another gene, *est_1092*, encodes an esterase enzyme that can hydrolyze phenolic esters, including hydroxycinnamic esters such as methyl ferulate and methyl caffeate. It exhibits both feruloyl esterase and tannase activities, helping the bacteria to break down complex phenolic compounds (Esteban-Torres et al., 2015).

The genetic basis for hydroxycinnamic acid metabolism in *L. plantarum* mainly involves *hcrAB* genes for reductase activity and the *est_1092* gene for esterase activity. These genes are not common in other lactic acid bacteria and, thus, indicate that *L. plantarum* has a specialized ability to process these compounds (Santamaría et al., 2018). Genomic studies have also found other possible phenolic acid reductases, such as Par1 and HcrF, in different *Lactobacillus* species. This suggests there are multiple metabolic ways for reducing HCAs across different strains (Gaur et al., 2020). Thus, the ability to metabolize phenolic acids varies between strains, depending on their genetic makeup and the structural properties of phenolic acids themselves (Rogozinska et al., 2021).

3.3. Correlation analysis between growth parameters and phenolics

A correlation analysis was conducted between the bacterial growth model parameters and the individual phenolic acid profiles in digesta to understand the impact of available HBAs and HCAs on *Lactobacillus* growth (Table 2). The positive association of A_1 with p and $\mu_{\max}$ indicated that conditions that support higher bacterial biomass also promote rapid and steep transitions from lag to exponential phase. A high hill slope indicates rapid bacterial proliferation due to readily available energy sources and the presence of minimal inhibitory factors. The strong positive correlation of A_1 with caffeic and ferulic acid reflects

the importance of these phenolic acids in bacterial growth. *L. plantarum* can metabolize HCAs like caffeic acid to enhance its energy metabolism and resilience to oxidative stress, using HCAs as electron acceptors to regenerate NAD⁺ during fermentation (Filannino et al., 2014; Rodríguez et al., 2009). Similarly, the positive correlations of *p* with caffeic and ferulic acid suggest that these compounds are probably essential for helping bacteria rapidly adjust their metabolism during the exponential growth phase.

Table 2
Correlation between the model parameters and polyphenols. The green-colored cells indicate a significant ($p < 0.05$) positive correlation, whereas the orange cells indicate a significant negative correlation among the parameters. The values in gray correspond to the *p*-values.

<i>A</i> ₀	<i>A</i> ₁	<i>c</i>	<i>p</i>	μ_{max}	λ	<i>amplitude</i>	<i>gallic</i>	<i>4-HBA</i>	<i>chlorogenic</i>	<i>caffeic</i>	<i>p-coumaric</i>	<i>ferulic</i>	<i>sinapic</i>
	0.0647	-0.765	-0.241	0.133	-0.561	0.142	0.515	-0.364	-0.0756	-0.263	-0.0756	0.198	-0.231
	0.879	0.027	0.566	0.754	0.148	0.738	0.192	0.375	0.859	0.529	0.859	0.638	0.582
	<i>A</i> ₁	-0.0011	0.725	0.926	0.496	0.348	-0.0785	-0.0094	0.318	0.701	0.318	0.807	-0.0785
		0.998	0.0419	0.0009	0.211	0.399	0.853	0.982	0.442	0.0429	0.442	0.015	0.853
		<i>c</i>	0.448	-0.281	0.801	-0.436	-0.717	-0.0556	-0.334	0.347	-0.334	0.0654	0.0208
			0.265	0.5	0.0169	0.28	0.045	0.896	0.418	0.399	0.418	0.878	0.961
			<i>p</i>	0.468	0.893	-0.361	-0.69	-0.35	-0.26	0.973	-0.26	0.828	-0.346
				0.242	0.0028	0.379	0.058	0.396	0.534	0.00004	0.534	0.011	0.401
				μ_{max}	0.192	0.607	0.208	0.194	0.558	0.493	0.558	0.625	0.0421
					0.649	0.11	0.622	0.645	0.15	0.214	0.15	0.098	0.921
					λ	-0.435	-0.812	-0.243	-0.322	0.826	-0.322	0.583	-0.213
						0.281	0.014	0.563	0.436	0.011	0.436	0.13	0.613
						<i>amplitude</i>	0.756	0.604	0.844	-0.352	0.844	-0.12	0.452
							0.029	0.113	0.008	0.393	0.008	0.778	0.26
							<i>gallic</i>	0.551	0.633	-0.67	0.633	-0.27	0.542
								0.157	0.092	0.069	0.0922	0.518	0.165
								<i>4-HBA</i>	0.835	-0.301	0.835	-0.252	0.918
									0.009	0.468	0.0099	0.548	0.001
									<i>chlorogenic</i>	-0.211	1	-0.048	0.709
										0.615	< 0.0001	0.911	0.049
										<i>caffeic</i>	-0.211	0.762	-0.368
											0.615	0.028	0.37
											<i>p-coumaric</i>	-0.048	0.709
												0.911	0.049
												<i>ferulic</i>	-0.133
													0.754

This observation is consistent with earlier research, which demonstrated that HCAs have a significant impact on the redox balance and energy availability in lactic acid bacteria (Filannino et al., 2014). The strong negative correlation between *c* and λ with gallic acid suggests its effectiveness in reducing adaptation time and enhancing active growth. Gallic acid is a potent antioxidant and can reduce oxidative stress in lactic acid bacteria or act as an easily metabolizable component in the digesta. In contrast, the positive correlation between λ and caffeic acid suggests that the bacteria do not readily metabolize it and may require specific enzyme activation for its utilization (Rodríguez et al., 2009). The net microbial growth (denoted by “*amplitude*”: $A_1 - A_0$) showed positive correlation with gallic acid, chlorogenic acid, and *p*-coumaric acid. This suggests that these phenolic acids promote the proliferation of the bacterial population, either by acting as substrates or functioning as signaling molecules that stimulate growth (Cardona et al., 2013). The strong intercorrelations among phenolic acids (e.g., 4-HBA with chlorogenic acid, *p*-coumaric acid, and sinapic acids; caffeic acid with ferulic acid) reflect their common biosynthetic pathway.

4. Conclusion

This study demonstrates that supplemental lighting has a significant effect on the post-digestive phenolic composition and bioaccessibility of phenolic compounds in tomatoes, and therefore, modulates the growth of *L. plantarum*. Supplemental lighting significantly altered the levels of most hydroxybenzoic

acids and hydroxycinnamic acids in tomato digesta, and their bioaccessibility but in a genotype-dependent manner. UV-B may promote structural binding of hydroxycinnamic acids and reduce digestive release whereas blue light tends to favor accumulation of soluble phenolic acids. UV-B-treated tomatoes supported the highest *L. plantarum* growth, followed by B and B + UV-B light. Notably, UV-B samples produced a unique double-sigmoidal pattern in Plum Regal, possibly due in part to the higher levels of caffeic and ferulic acids, along with the availability of simple sugars and amino acids in the digesta. These findings indicate that pre-harvest light strategies affect the phenolic composition of the post-digestion product of tomatoes and subsequently modulate the growth and proliferation of gut microbes. Therefore, this research demonstrates the potential of supplemental lighting to enhance the prebiotic properties of tomatoes and lays the foundation for integrating horticultural innovation with nutrition and gut health outcomes.

Declarations

Acknowledgments

The authors would like to acknowledge Dr. Kevin Crosby for providing seeds of the TAM Hot-Ty variety.

Funding sources

This work was partially supported by USDA-NIFA-2024-51181-43464, USDA-NIFA-AFRI 2023-67013-39616 through the Vegetable and Fruit Improvement Center and Institute for Advancing Health Through Agriculture of Texas A&M University.

Author contribution statement

Samikshya Bhattarai: Methodology, Investigation, Formal analysis, Data curation, Software, Visualization, Validation, Writing - original draft, review & editing. **Deepak K. Jha:** Writing - review & editing. **Sangeeta Balyan:** Methodology. **Shuyang Zhen:** Writing - review & editing. **Bhimanagouda S. Patil:** Conceptualization, Resources, Funding acquisition, Supervision, Validation, Writing- review & editing.

Data availability

All relevant data supporting the findings of this study are available in this article, as well as the supporting information.

Declaration of competing interests

The authors declare no competing interests.

References

1. Balyan, S., Dadwal, V., Bhattarai, S., Jha, D. K. & Patil, B. S. *Lactobacillus*-derived exopolysaccharide nanoemulsions for essential oils Delivery: Improving bioaccessibility, gastrointestinal stability, and prebiotic function. *Food Bioscience*. **69**, 106891. <https://doi.org/10.1016/j.fbio.2025.106891> (2025).
2. Barthelmebs, L., Diviés, C. & Cavin, J. F. Molecular characterization of the phenolic acid metabolism in the lactic acid bacteria *Lactobacillus plantarum*. *Le Lait*. **81** (1–2), 161–171. <https://doi.org/10.1051/laite:2001120> (2001).
3. Bhattarai, S., Jha, D. K., Singh, J., Zhen, S. & Patil, B. S. Supplemental greenhouse lighting enhances the abundance of *cis*-lycopene isomers in tomato fruits. *J. Food Compos. Anal.* **142**, 107534. <https://doi.org/10.1016/j.jfca.2025.107534> (2025a).
4. Bhattarai, S. et al. UV-B and Blue Light Supplementation Improves Tomato Quality and Antioxidant Dynamics: A Novel Approach for Sustainable Greenhouse Production. *J. Agric. Food Res.* 102054. <https://doi.org/10.1016/j.jafr.2025.102054> (2025b).
5. Cárdenas-Castro, A. P. et al. *In vitro* gastrointestinal digestion and colonic fermentation of tomato (*Solanum lycopersicum* L.) and husk tomato (*Physalis ixocarpa* Brot.): Phenolic compounds released and bioconverted by gut microbiota. *Food Chemistry*, 360, 130051. (2021). <https://doi.org/10.1016/j.foodchem.2021.130051>
6. Cardona, F., Andrés-Lacueva, C., Tulipani, S., Tinahones, F. J. & Queipo-Ortuño, M. I. Benefits of polyphenols on gut microbiota and implications in human health. *J. Nutr. Biochem.* **24** (8), 1415–1422. <https://doi.org/10.1016/j.jnutbio.2013.05.001> (2013).
7. Castagna, A., Dall'Asta, C., Chiavaro, E., Galaverna, G. & Ranieri, A. Effect of Post-harvest UV-B Irradiation on Polyphenol Profile and Antioxidant Activity in Flesh and Peel of Tomato Fruits. *Food Bioprocess Technol.* **7** (8), 2241–2250. <https://doi.org/10.1007/s11947-013-1214-5> (2014).
8. Cheadle, C., Vawter, M. P., Freed, W. J. & Becker, K. G. Analysis of Microarray Data Using Z Score Transformation. *J. Mol. Diagnostics: JMD*. **5** (2), 73–81. [https://doi.org/10.1016/S1525-1578\(10\)60455-2](https://doi.org/10.1016/S1525-1578(10)60455-2) (2003).
9. Di Pede, G. et al. A Systematic Review and Comprehensive Evaluation of Human Intervention Studies to Unravel the Bioavailability of Hydroxycinnamic Acids. *Antioxid. Redox. Signal.* **40** (7–9), 510–541. <https://doi.org/10.1089/ars.2023.0254> (2024).
10. Dissanayake, I. H. et al. Lactic acid bacterial fermentation as a biotransformation strategy to enhance the bioavailability of phenolic antioxidants in fruits and vegetables: A comprehensive review. *Food Res. Int.* **209**, 116283. <https://doi.org/10.1016/j.foodres.2025.116283> (2025).
11. Esteban-Torres, M. et al. A *Lactobacillus plantarum* Esterase Active on a Broad Range of Phenolic Esters. *Appl. Environ. Microbiol.* **81** (9), 3235–3242. <https://doi.org/10.1128/AEM.00323-15> (2015).
12. Filanino, P., Gobetti, M., De Angelis, M. & Di Cagno, R. Hydroxycinnamic Acids Used as External Acceptors of Electrons: An Energetic Advantage for Strictly Heterofermentative Lactic Acid Bacteria. *Appl. Environ. Microbiol.* **80** (24), 7574–7582. <https://doi.org/10.1128/AEM.02413-14> (2014).
13. Gaur, G. & Gänzle, M. G. Conversion of (poly)phenolic compounds in food fermentations by lactic acid bacteria: Novel insights into metabolic pathways and functional metabolites. *Curr. Res. Food Sci.* **6**, 100448. <https://doi.org/10.1016/j.crf.2023.100448> (2023).

14. Gaur, G. et al. Genetic Determinants of Hydroxycinnamic Acid Metabolism in Heterofermentative Lactobacilli. *Appl. Environ. Microbiol.* **86** (5), e02461–e02419. <https://doi.org/10.1128/AEM.02461-19> (2020).
15. Izzo, L. et al. Bioaccessibility and Antioxidant Capacity of Bioactive Compounds From Various Typologies of Canned Tomatoes. *Frontiers in Nutrition*, **9**. (2022). <https://doi.org/10.3389/fnut.2022.849163>
16. Jenkins, G. I. Photomorphogenic responses to ultraviolet-B light. *Plant. Cell. Environ.* **40** (11), 2544–2557. <https://doi.org/10.1111/pce.12934> (2017).
17. Kaiser, E. et al. Adding Blue to Red Supplemental Light Increases Biomass and Yield of Greenhouse-Grown Tomatoes, but Only to an Optimum. *Frontiers in Plant Science*, **9**. (2019). <https://doi.org/10.3389/fpls.2018.02002>
18. Kim, M. J. et al. Blue and UV-B light synergistically induce anthocyanin accumulation by co-activating nitrate reductase gene expression in Anthocyanin fruit (Aft) tomato. *Plant Biol.* **23** (S1), 210–220. <https://doi.org/10.1111/plb.13141> (2021).
19. Landete, J. M. & Plaza-Vinuesa Laura, Montenegro, Cinthya, Santamaría, Laura, Reverón, Inés, de las Rivas, Blanca, & and Muñoz, R. The use of *Lactobacillus plantarum* esterase genes: A biotechnological strategy to increase the bioavailability of dietary phenolic compounds in lactic acid bacteria. *International Journal of Food Sciences and Nutrition*, **72**(8), 1035–1045. (2021). <https://doi.org/10.1080/09637486.2021.1900078>
20. Lee, H. J., Cha, K. H., Kim, C. Y., Nho, C. W. & Pan, C. H. Bioavailability of Hydroxycinnamic Acids from *Crepidiastrum denticulatum* Using Simulated Digestion and Caco-2 Intestinal Cells. *J. Agric. Food Chem.* **62** (23), 5290–5295. <https://doi.org/10.1021/jf500319h> (2014).
21. Leonard, W., Zhang, P., Ying, D. & Fang, Z. Hydroxycinnamic acids on gut microbiota and health. *Compr. Rev. Food Sci. Food Saf.* **20** (1), 710–737. <https://doi.org/10.1111/1541-4337.12663> (2021).
22. Lippolis, T., Cofano, M., Caponio, G. R., De Nunzio, V. & Notarnicola, M. Bioaccessibility and Bioavailability of Diet Polyphenols and Their Modulation of Gut Microbiota. *Int. J. Mol. Sci.* **24** (4). Article 4. <https://doi.org/10.3390/ijms24043813> (2023).
23. Liu, Y., Singh, S. K., Pattanaik, S., Wang, H. & Yuan, L. Light regulation of the biosynthesis of phenolics, terpenoids, and alkaloids in plants. *Commun. Biology.* **6** (1), 1–14. <https://doi.org/10.1038/s42003-023-05435-4> (2023).
24. Luna-Guevara, M. L., Luna-Guevara, J. J., Hernández-Carranza, P., Ruíz-Espinosa, H. & Ochoa-Velasco, C. E. Chapter 3 - Phenolic Compounds: A Good Choice Against Chronic Degenerative Diseases. In Atta-ur-Rahman (Ed.), *Studies in Natural Products Chemistry* (Vol. 59, pp. 79–108). Elsevier. (2018). <https://doi.org/10.1016/B978-0-444-64179-3.00003-7>
25. Mithul Aravind, S., Wichienchot, S., Tsao, R., Ramakrishnan, S. & Chakkaravarthi, S. Role of dietary polyphenols on gut microbiota, their metabolites and health benefits. *Food Res. Int.* **142**, 110189. <https://doi.org/10.1016/j.foodres.2021.110189> (2021).
26. Muñoz, R. et al. Biotransformation of Phenolics by *Lactobacillus plantarum* in Fermented Foods. In J. Frias, C. Martinez-Villaluenga, & E. Peñas (Eds.), *Fermented Foods in Health and Disease Prevention* (pp. 63–83). Academic Press. (2017). <https://doi.org/10.1016/B978-0-12-802309-9.00004-2>
27. Muñoz, R. et al. Food phenolics and *Lactiplantibacillus plantarum*. *Int. J. Food Microbiol.* **412**, 110555. <https://doi.org/10.1016/j.ijfoodmicro.2023.110555> (2024).
28. Perea-Domínguez, X. P. et al. Phenolic composition of tomato varieties and an industrial tomato by-product: Free, conjugated and bound phenolics and antioxidant activity. *J. Food Sci. Technol.* **55** (9), 3453–3461. <https://doi.org/10.1007/s13197-018-3269-9> (2018).
29. Podolec, R. & Ulm, R. Photoreceptor-mediated regulation of the COP1/SPA E3 ubiquitin ligase. *Curr. Opin. Plant. Biology Cell. Signal. Gene Regul.* **45**, 18–25. <https://doi.org/10.1016/j.pbi.2018.04.018> (2018).
30. Rácz, A. & Hideg, É. Narrow-Band 311 nm Ultraviolet-B Radiation Evokes Different Antioxidant Responses from Broad-Band Ultraviolet. *Plants* **10** (8). Article 8. <https://doi.org/10.3390/plants10081570> (2021).
31. Rodríguez, H. et al. Food phenolics and lactic acid bacteria. *Int. J. Food Microbiol.* **132** (2), 79–90. <https://doi.org/10.1016/j.ijfoodmicro.2009.03.025> (2009).
32. Rogozinska, M., Korsak, D., Mroczek, J. & Biesaga, M. Catabolism of hydroxycinnamic acids in contact with probiotic *Lactobacillus*. *J. Appl. Microbiol.* **131** (3), 1464–1473. <https://doi.org/10.1111/jam.15009> (2021).
33. Santamaría, L., Reverón, I., López de Felipe, F., de las Rivas, B. & Muñoz, R. Unravelling the Reduction Pathway as an Alternative Metabolic Route to Hydroxycinnamate Decarboxylation in *Lactobacillus plantarum*. *Appl. Environ. Microbiol.* **84** (15), e01123–e01118. <https://doi.org/10.1128/AEM.01123-18> (2018).
34. Sato, Y. et al. *In vitro* and *in vivo* antioxidant properties of chlorogenic acid and caffeic acid. *International Journal of Pharmaceutics*, **403**(1), 136–138. (2011). <https://doi.org/10.1016/j.ijpharm.2010.09.035>
35. Stalmach, A. Chapter 42—Bioavailability of Dietary Anthocyanins and Hydroxycinnamic Acids. In R. R. Watson, V. R. Preedy, & S. Zibadi (Eds.), *Polyphenols in Human Health and Disease* (pp. 561–576). Academic Press. (2014). <https://doi.org/10.1016/B978-0-12-398456-2.00042-6>
36. Tissot, N. & Ulm, R. Cryptochrome-mediated blue-light signalling modulates UVR8 photoreceptor activity and contributes to UV-B tolerance in *Arabidopsis*. *Nat. Commun.* **11** (1), 1323. <https://doi.org/10.1038/s41467-020-15133-y> (2020).
37. Toor, R. K., Savage, Geoffrey, P., Lister, C. E. & and Release of antioxidant components from tomatoes determined by an in vitro digestion method. *Int. J. Food Sci. Nutr.* **60** (2), 119–129. <https://doi.org/10.1080/09637480701614121> (2009).
38. Visioli, F. et al. Polyphenols and Human Health: A Prospectus. *Crit. Rev. Food Sci. Nutr.* **51** (6), 524–546. <https://doi.org/10.1080/10408391003698677> (2011).
39. Wan, M. L. Y., Co, V. A. & El-Nezami, H. Dietary polyphenol impact on gut health and microbiota. *Crit. Rev. Food Sci. Nutr.* **61** (4), 690–711. <https://doi.org/10.1080/10408398.2020.1744512> (2021).
40. Wang, J. et al. Manipulating the Light Systemic Signal HY5 Greatly Improve Fruit Quality in Tomato. *Adv. Sci.* **12** (23), 2500110. <https://doi.org/10.1002/advs.202500110> (2025).

41. Wang, Q. et al. Cryptochrome-mediated blue-light signal contributes to lignin biosynthesis in stone cells in pear fruit. *Plant Sci.* **318**, 111211. <https://doi.org/10.1016/j.plantsci.2022.111211> (2022).
42. Wang, T., Zhang, H. & Zhu, H. CRISPR technology is revolutionizing the improvement of tomato and other fruit crops. *Hortic. Res.* **6** (1), 77. <https://doi.org/10.1038/s41438-019-0159-x> (2019).
43. Wang, Y. et al. Insights into interactions between food polyphenols and proteins: An updated overview. *J. Food Process. Preserv.* **46** (5), e16597. <https://doi.org/10.1111/jfpp.16597> (2022).
44. Wojtunik-Kulesza, K. et al. Influence of In Vitro Digestion on Composition, Bioaccessibility and Antioxidant Activity of Food Polyphenols—A Non-Systematic Review. *Nutrients* **12** (5). <https://doi.org/10.3390/nu12051401> (2020).
45. Wu, W. et al. Light regulates the synthesis and accumulation of plant secondary metabolites. *Frontiers in Plant Science*, 16. (2025). <https://doi.org/10.3389/fpls.2025.1644472>
46. Zhao, Z. & Moghadasian, M. H. Bioavailability of hydroxycinnamates: A brief review of in vivo and in vitro studies. *Phytochem. Rev.* **9** (1), 133–145. <https://doi.org/10.1007/s11101-009-9145-5> (2010).

Figures

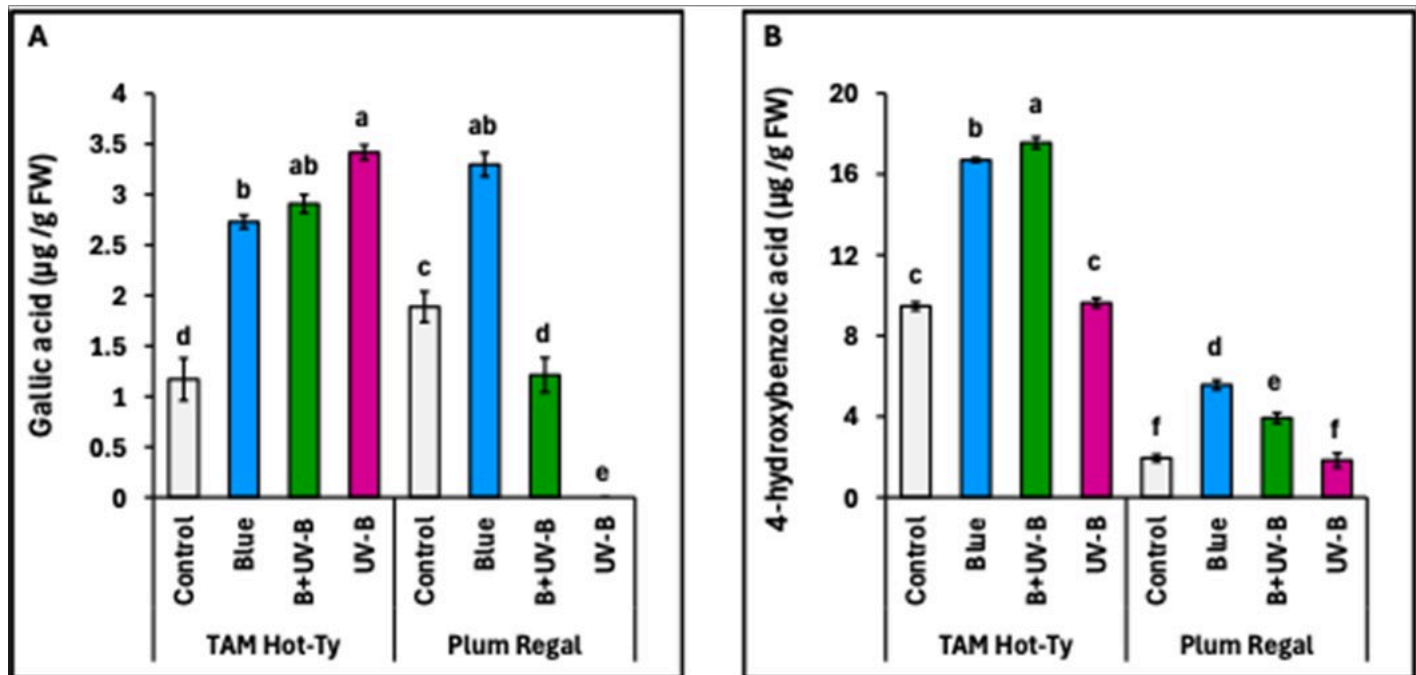


Figure 1

Bar graphs showing concentrations of hydroxybenzoic acids: (A) gallic acid, and (B) 4-hydroxybenzoic acid, in the digesta of fruits from two tomato varieties, TAM Hot-Ty and Plum Regal, grown under different pre-harvest light treatments: Control (white), Blue (blue), B+UV-B (green), and UV-B (magenta). Error bars represent the standard error of the mean. Different letters above error bars indicate significant differences (p < 0.05) among treatments between the varieties based on Tukey's HSD test.

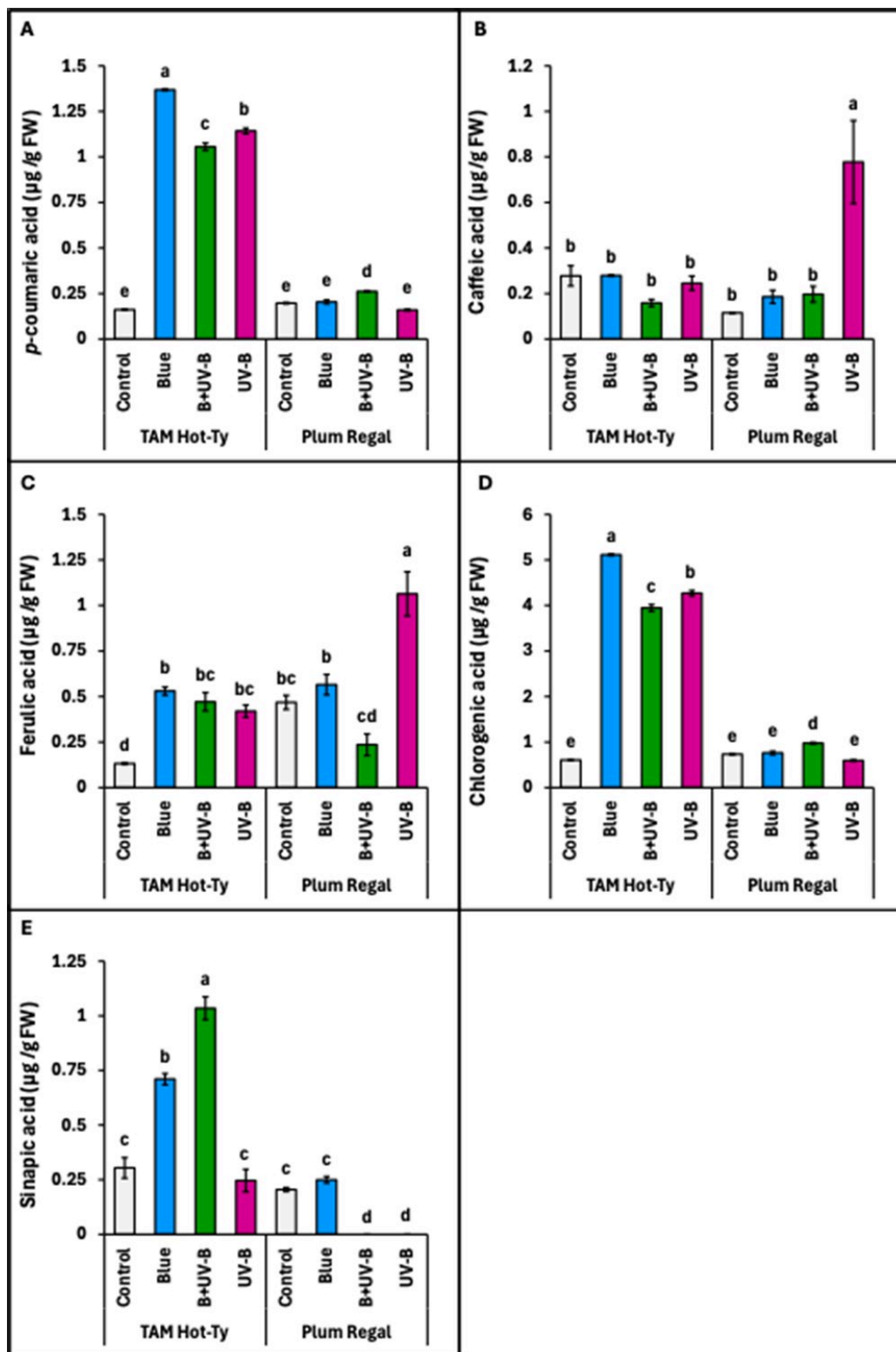


Figure 2

Bar graphs showing concentrations of hydroxycinnamic acids: (A) p-coumaric acid, (B) caffeic acid, (C) ferulic acid, (D) chlorogenic acid, and (E) sinapic acid, in the digesta of fruits from two tomato varieties, TAM Hot-Ty and Plum Regal, grown under different pre-harvest light treatments: Control (white), Blue (blue), B+UV-B (green), and UV-B (magenta). Error bars represent the standard error of the mean, and different letters above error bars indicate significant differences ($p < 0.05$) among treatments between the varieties based on Tukey's HSD test.

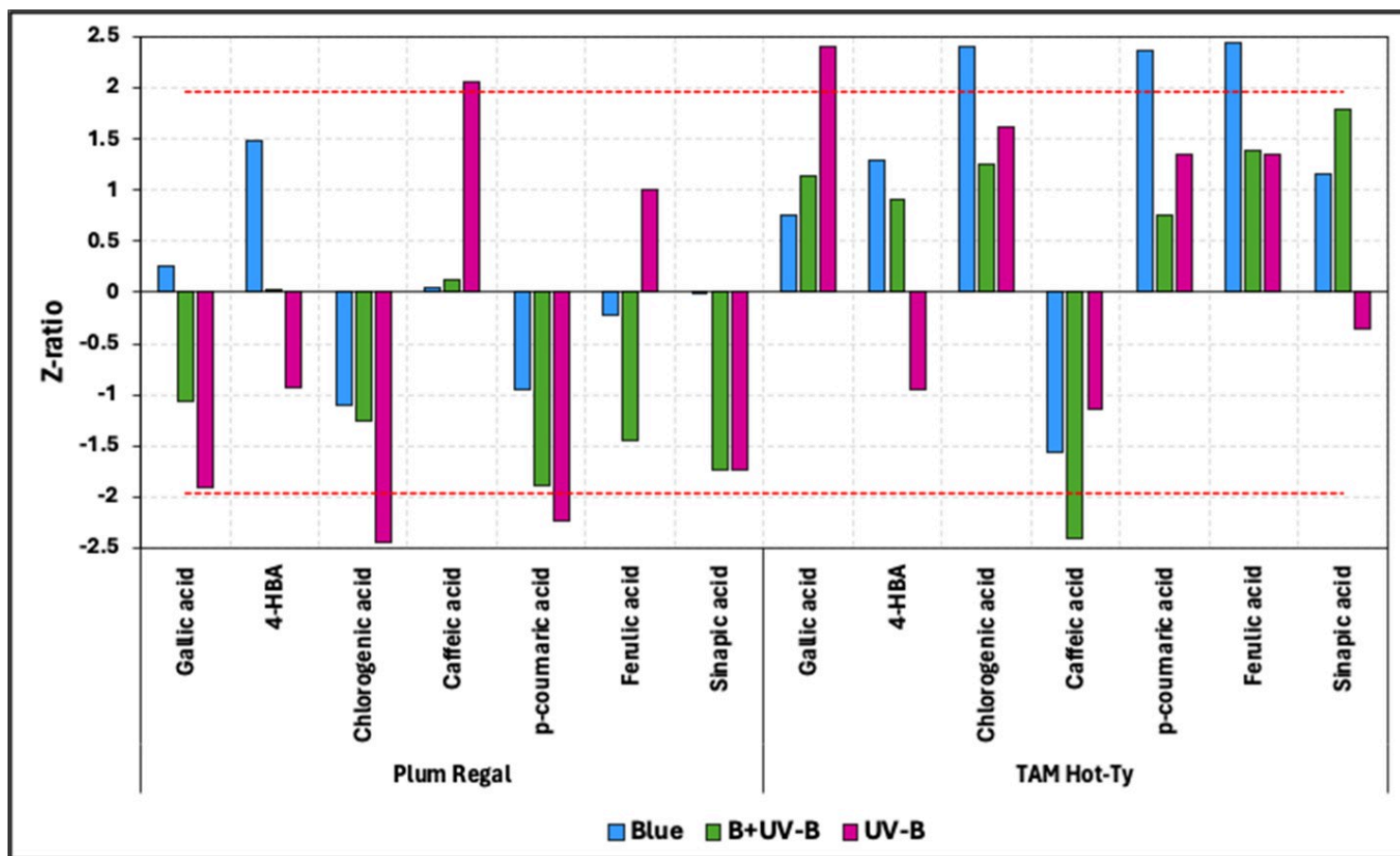


Figure 3
Bar graphs showing z-ratio of phenolics bioaccessibility from fruits of Plum Regal and TAM Hot-Ty tomato varieties grown under different pre-harvest light settings (Blue, B+UV-B, and UV-B) compared to the control treatment.

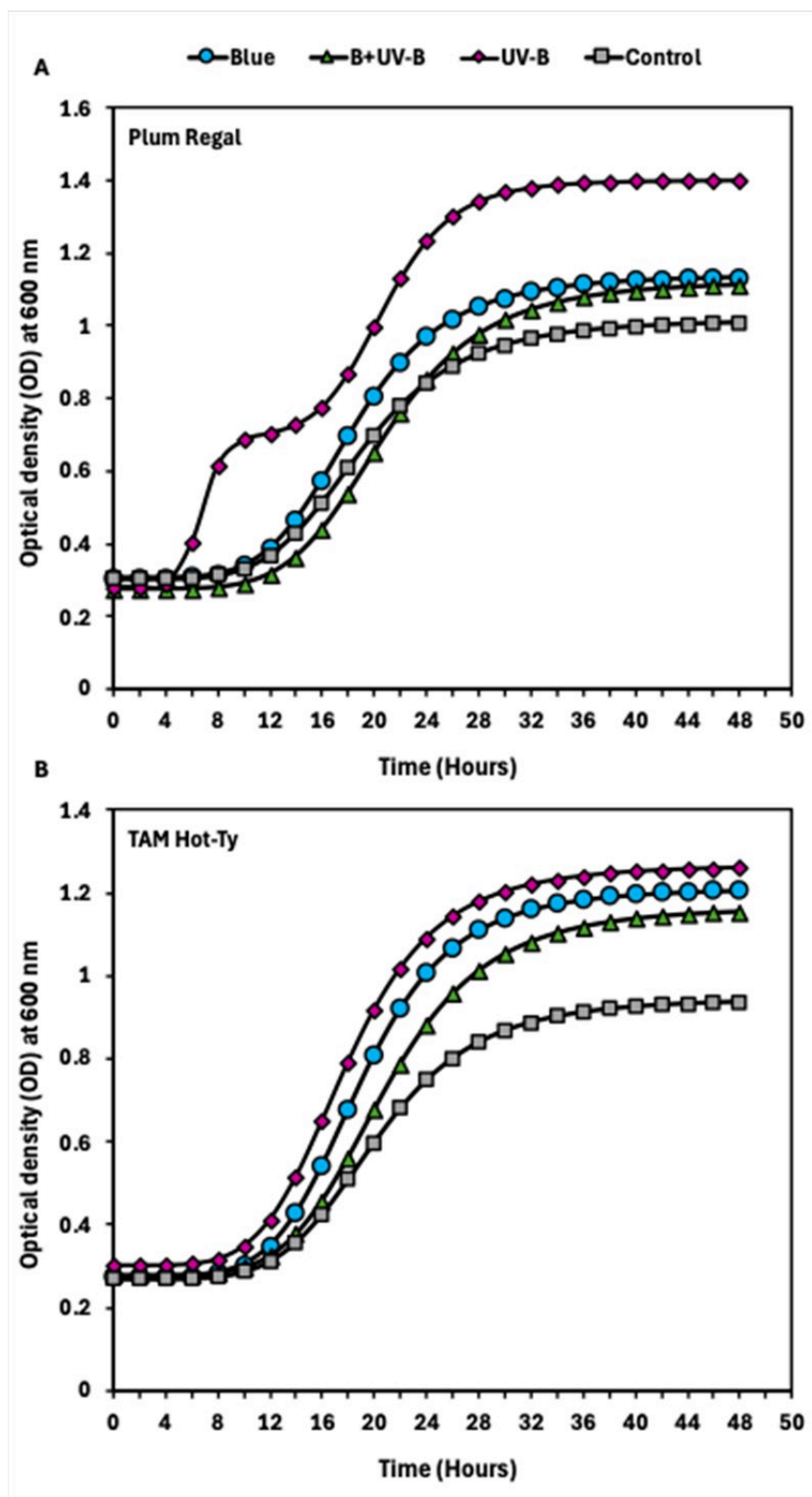


Figure 4
Growth kinetics of *Lactobacillus plantarum* in MRS broth supplemented with in vitro digested tomato samples from two varieties, Plum Regal (top) and TAM Hot-Ty (bottom), exposed to different pre-harvest light treatments: Control (gray), Blue (blue), B+UV-B (green), and UV-B (magenta). Optical density (OD) at 600 nm was monitored over 48 hours to assess bacterial growth response to digested tomato supplementation.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [BhattaraiChaper6supplementaryfile.docx](#)