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Humic Substances and LED Lighting Improved Tomato Transplant Growth, with Limited Carryover Effects on Fruit Yield and Quality

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Abstract. **Humic substances (HS) and light-emitting diode (LED) light applications have shown beneficial effects on plant growth, nutrition, and yield in various vegetable crops. However, their carryover effects on fruit yield and quality, when applied to the growing media before transplanting, have not been widely explored in tomatoes. This study evaluated tomato transplant growth in response to the application of solid HS (1% v/v, control) and varying LED light qualities [10 blue (B):90 red (R), 50B:50R, 100B, and fluorescent] in growth chamber conditions (25/19 °C, 16-hour days/8-hour nights, 100 μmol·m^{-2}·s^{-1} photosynthetic photon flux density, 60% relative humidity), followed by a post-transplant study assessing fruit yield and quality. Round-type 'Celebrity' and cherry-type 'Chadwick' tomato seedlings were transplanted into 16-L pots 5 weeks after sowing (WAS), and fruit were harvested for 10 weeks. Transplant growth components measured at 5 WAS were significantly greater in seedlings treated with HS compared with control plants, including improved shoot and root dry weight, stem diameter, leaf area, and total root length and surface area. Seedlings grown under 50B:50R light showed a greater increase in shoot and root growth when treated with HS compared with other light treatment groups, whereas plants grown under 10B:90R light exhibited the greatest growth without HS. However, the enhanced seedling growth under HS and specific LED light treatments did not translate fully into increased fruit yield and quality after transplanting. There were no significant increases in fruit yield in response to HS application, except for 'Chadwick' under 50B:50R and 100B light. No clear correlation was observed between high-quality transplants and tomato quality traits, such as total soluble solids and secondary metabolites, although the 100B light treatment increased lycopene and total phenolic content. In conclusion, the application of HS to the transplant growing media, combined with specific LED wavelengths, particularly 50B:50R, enhanced shoot and root growth significantly in young tomato seedlings. However, these benefits largely diminished after transplanting and did not result consistently in increased fruit yield or quality.**

Tomatoes (*Solanum lycopersicum* L.) are among the most valuable vegetable crops in the world, with an estimated global production of 186.1 million tons in 2022 (FAOSTAT 2024). In numerous vegetable production systems, including tomatoes, transplanting with containerized seedlings is the standard practice for crop establishment as it increases stand establishment and survival rates, shortens the growth period, and improves plant uniformity (Leskovar 2020). High-quality vegetable transplants grown under optimal conditions, such as appropriate cell size, growing media, irrigation management, and light quality, are characterized by vigorous shoot and root systems with compact and nonelongated stems (Balliu et al. 2017; Leskovar 2020). These traits help reduce transplant shock, enabling plants to adapt quickly to their new environment. Previous studies have shown that the quality of vegetable transplants improve plant growth and fruit production significantly after transplanting (Javanmardi and Emami 2013; Moncada et al. 2020; Qin and Leskovar 2020b; Zaller 2007), although the results were highly dependent on species and cultivars (Campolongo et al. 2020; Kerbiriou et al. 2013; Qin and Leskovar 2020b).

Humic substances (HS), the largest constituent of soil organic matter, are high-molecular mass (100–300 kDa) heterogeneous aggregates composed of sugars, fatty acids, polypeptides, aliphatic chains, and aromatic rings (Trevisan et al. 2010). Although the precise structure of HS is complex and not fully characterized, they are broadly classified into humin, humic acid, and fulvic acid based on their solubility across varying pH levels (Stevenson 1994). HS have demonstrated beneficial effects in vegetable production, including increased shoot and root biomass, water and nitrogen use efficiency, and crop yield (Arancon et al. 2006; Choi et al. 2024; Qin and Leskovar 2020a, 2020b; Qin et al. 2023a, 2023b; Selim and Ali Mosa 2012). These benefits are attributed to the ability of HS to improve soil aggregation and structure, increase cation exchange capacity and soil pH buffering, and enhance water retention and nutrient bioavailability through both physical and chemical interactions with soil substrates and molecules (MacCarthy 2001; Rose et al. 2014). However, the compositional diversity of HS, resulting from varied chemical functional groups (Enev et al. 2014) and different source materials (Bezuglova and Klimenko 2022), can lead to entirely different outcomes in vegetable production. Furthermore, even identical HS products may exhibit different effects depending on growth environments and crop species (Rose et al. 2014), particularly under abiotic stress conditions (Kaya et al. 2020; Qin and Leskovar 2020b).

Light quality (i.e., wavelength composition) is one of the key environmental factors regulating plant growth and development in controlled environment agriculture. Light-emitting diodes (LEDs) have been widely used in vegetable production because of their advantages, including the ability to provide targeted wavelengths, greater energy efficiency, and reduced cost compared with traditional light sources such as high-intensity discharge lamps and fluorescent lamps (Dou et al. 2017). In addition to providing energy for photosynthesis, different wavelengths of light function as signaling cues in plants, regulating their physiology and metabolism (Trivellini et al. 2023). Red (620–700 nm) and blue (400–490 nm) light are considered most effective wavelengths for photosynthesis (McCree 1971), with combined red and blue wavelengths enhancing plant growth and yield compared to monochromatic red or blue light (Paradiso and Proietti 2022). Red light has been reported to promote stem and root elongation, chlorophyll biosynthesis, and the development of photosynthetic apparatus, whereas blue light regulates stomatal opening, inhibits cell division and extension, and promotes secondary metabolite biosynthesis (Paradiso and Proietti 2022; Trivellini et al. 2023). In tomato plants, combining blue and red light with a 90:10 optical power ratio [i.e., photosynthetically active radiation (PAR)] improved the net photosynthetic rate compared with higher blue light ratios (Nanya et al. 2012; Naznin et al. 2019), whereas a 25:75 ratio demonstrated greater plant growth and fruit yield compared with 50:50 or higher ratios (Liang et al. 2021; Son et al. 2018). However, some studies reported conflicting findings, showing that a 50:50 ratio led to a greater

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plant biomass than a 25:75 ratio (Hernández et al. 2016; Liu et al. 2018).

The benefits of individually applying HS and varying LED light quality have been widely reported in many vegetable studies, but research on their combined effects for optimizing transplant quality in tomato plants is lacking. Also, most HS studies have used the foliar spraying method with liquid HS (Qin and Leskovar 2020b), and research on treatment carryover effects post-transplanting remains limited, despite their importance (Rose et al. 2014). Therefore, this study aimed to evaluate the effects of solid HS application and LED light quality with varying blue-to-red light ratios on transplant growth of 'Celebrity' and 'Chadwick' tomatoes, followed by an assessment of fruit yield and quality in the absence of treatments after transplanting. We hypothesized that the combined pretransplant application of HS and mixed red and blue LED light enhances tomato transplant quality, with these improvements carrying over to fruit yield and quality traits, such as total soluble solids (TSS) and secondary metabolite content, after transplanting.

Materials and Methods

Plant materials, growth conditions, and experimental design

Round-type 'Celebrity' (Clifton Seed Company, Faison, NC, USA) and cherry-type 'Chadwick' (Atlee Burpee & Co., Warminster, PA, USA) tomato seeds were sown in 200-cell trays (32 cm^3 per cell; TR200A model, Speedling Inc., Ruskin, FL, USA) filled with growth media consisting of 90% sphagnum peatmoss and 10% perlite and vermiculite (LM-CB; Lambert Peat Moss Inc., Rivière-Ouelle, Quebec, Canada), and the seedlings were grown in a growth chamber (GEN1000; Conviron Ltd., Winnipeg, Manitoba, Canada) set at 25/19 °C (16-h days/8-h nights), 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density (PPFD) and 60% relative humidity. The experiment followed a factorial experimental design, incorporating the application of lignite-derived solid HS (32% humic acid, 24% humin, 3% fulvic acid; Novihum GmbH, Dresden, Germany) in the growth media (1% v/v) and LED light (LX601G; Heliospectra AB, Gothenburg, Sweden) with three different blue (peak wavelength, 450 nm) and red (peak wavelength, 660 nm) optical power ratios [10 blue (B):90 red (R), 50B:50R, and 100B]. These ratios were designed using the Heliospectra System Assistant software (V. 1.3.0) to produce different spectra with equivalent total PAR. The selected LED model was chosen based on its proven ability to modulate plant growth and development under controlled environments (Granström and Jansson 2017; Spall and Lopez 2023), and its high photon efficiency (1.7 $\mu mol \cdot J^{-1}$) (Nelson and Bugbee 2014). The control group used fluorescent light (FL; 4100 K) and growth media without HS. Seedlings were irrigated daily until saturation and fertigated once a week with a 50-$mg \cdot L^{-1}$ P water-soluble fertilizer (11–56–3; Vital Fertilizers LLC, Mission, TX, USA) starting from 14 d after sowing (DAS). Seedling growth was measured at 35 DAS with six plant replicates.

After 35 d in the growth chamber, the seedlings were transplanted into 16-L pots (27.5-cm diameter × 27.5-cm height) filled with clay soil (hyperthermic Aridic Calciustolls of the Uvalde series; 31% sand, 28% silt, and 41% clay; pH, 8.2; electrical conductivity 0.08 $dS \cdot m^{-1}$) obtained from the field. The field soil was used to simulate the growth conditions in the field effectively while minimizing biotic and abiotic variability in the experiment (Fageria 2005). Also, the alkaline clay soil is representative of soil conditions found in arid regions worldwide, including the western United States, thereby enhancing the reproducibility of the study (Bockheim and Hartemink 2013; Dawood et al. 2001; Hoffmeister 1947; McLachlan et al. 2023; Senbayram et al. 2019). Transplanted seedlings were grown in a high tunnel with a semicontrolled environment (Fig. 1) accompanied by a mini weather station (WatchDog® 2400; Spectrum Technologies Inc., Aurora, IL, USA) at Texas A&M AgriLife Research and Extension Center in Uvalde, TX, USA (lat. 29.21N, long. 99.79W). HS and LED light applications were discontinued in the post-transplant growth environment. A randomized complete block design was used with four blocks and three plant replicates per treatment (totaling 12 plants per treatment group), with pots spaced 0.3 m apart in rows and 0.6 m apart in columns. The plants were trellised using twines suspended from a support wire; axillary shoots were pruned regularly. Irrigation was provided daily using a drip irrigation system until saturation, and fertigation was conducted once a week with 150 to 250 $mg \cdot L^{-1}$ N Peters Professional 20–20–20 water-soluble fertilizer (ICL Specialty Fertilizers Ltd., Tel Aviv, Israel). The concentration increased as developmental stages progressed, with additional micronutrients added at a rate of 10 $mg \cdot L^{-1}$ Mg (Microplex; Miller Chemical & Fertilizer LLC, Hanover, PA, USA). 'Chadwick' and 'Celebrity' tomatoes were harvested twice a week from 19 Aug and 1 Sep 2022, respectively, to 28 Oct 2022 at the fully "red" stage with more than 90% red coloration on the fruit surface (US Department of Agriculture–Agricultural Marketing Service 1991). Tomato weight and quality were measured on the same day as harvesting, and shoot fresh weight (FW) was measured on the final day of harvest. The yield was divided into three harvest periods (early, mid, and late) by splitting the entire harvest period equally by the number of days.

Measurements

Seedling growth. In addition to seedling height (measured in centimeters), stem diameter was measured in millimeters using a digital caliper. Soil plant analysis development (SPAD) was measured with a portable chlorophyll meter (SPAD-502 Plus; Konica Minolta, Tokyo, Japan) to estimate the leaf chlorophyll content, with the average value of three readings per seedling taken. Canopy leaf area was measured using image-processing software ImageJ (V. 1.53k; US National Institutes of Health, Bethesda, MD, USA) (Schneider et al. 2012). Total root length and surface area were measured using WinRHIZO software (WinRHIZO Pro V. 2002c; Regent Instruments Inc., Quebec City, Quebec, Canada) after washing and scanning the entire root system with a flatbed scanner (Epson Perfection V700 PHOTO; Epson America Inc., Long Beach, CA, USA). Shoot and root dry weight (DW) were measured in grams after the samples were oven-dried at 70 °C for 48 h.

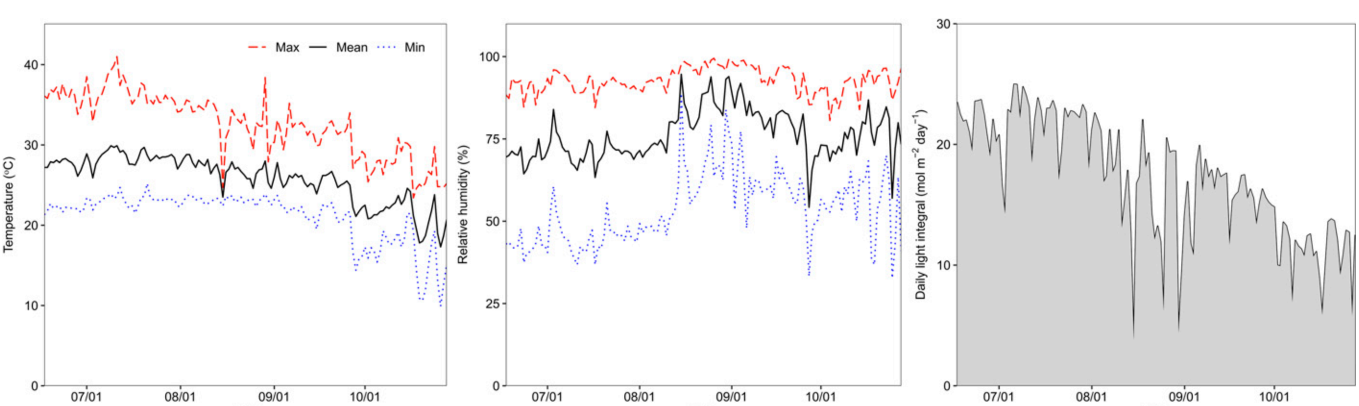

Fig. 1. Temperature (**left**), relative humidity (**middle**), and daily light integral (**right**) in the high tunnel during the post-transplant growth period.

Tomato quality. Tomato quality was measured using 36 fruit replications per treatment, with one replicate comprising three fruit of the cherry-type 'Chadwick' for biochemical measurements. Tomato fruit weight and diameter were measured in grams and millimeters, respectively, for all harvested fruit. The harvest index (measured as a percentage) was calculated as total fruit FW divided by the sum of total fruit and shoot FW.

Tomatoes were homogenized with a hand blender and a tissue homogenizer (Polytron PT10/35; Kinematica Inc., Bohemia, NY, USA), and filtered through a 1-mm sieve to remove large pulp pieces. TSS and titratable acidity (TA) were measured as °Brix and a percentage, respectively, using a portable Brix-acidity meter (PAL-BX IACID3; Atago Co. Ltd, Tokyo, Japan), and the TSS:TA ratio was calculated by dividing TSS by TA. The rest of the filtered samples were stored at –80 °C and used for lycopene, β-carotene, ascorbate, and total phenolics analyses.

Lycopene and β-carotene contents were determined using a modified method of Nagata and Yamashita (1992). Briefly, 0.5 g of blended tomato pulp was homogenized with 3 mL of acetone:hexane (4:6, v/v) using a paint shaker (Harbil® Next Gen; Fast & Fluid Management BV, Sassenheim, Netherlands). The absorbance of the upper phase of the extract was measured at 663, 645, 505, and 453 nm using a microplate spectrophotometer (Multiskan GO; Thermo Scientific, Waltham, MA, USA). Lycopene and β-carotene contents were calculated as follows:

$$\text{Lycopene}\left(\text{mg}\cdot\text{L}^{-1}\text{ extract}\right) = -0.458 \times A_{663} + 2.04 \times A_{645} + 3.72 \times A_{505} - 0.806 \times A_{453}.$$

$$\beta-\text{Carotene}\left(\text{mg}\cdot\text{L}^{-1}\text{ extract}\right) = 2.16 \times A_{663} - 12.2 \times A_{645} - 3.04 \times A_{505} + 4.52 \times A_{453}.$$

Ascorbate content was determined using the method of Kapur et al. (2012) with slight modifications. One gram of tomato sample was homogenized with a 10-mL extraction solution containing 3% metaphosphoric acid and 8% acetic acid using a paint shaker and centrifuged at 3500 rpm for 10 min at 4 °C using a benchtop swinging-bucket centrifuge (Sorvall Legend XTR; Thermo Scientific). A total of 0.6 mL of the supernatant was mixed with 34.5 µL of 3% bromine water, 19.5 µL of 10% thiourea, and 0.15 mL of 2,4-dinitrophenolhydrazine (DNPH) solution (1 g of 2,4-DNPH dissolved in 5 mL of sulfuric acid). After 3 h of incubation at 37 °C, followed by 30 min cooling on ice, 0.75 mL of 85% sulfuric acid was added to the sample solution. The absorbance of the solution was measured at 521 nm using a microplate spectrophotometer, and the standard curve was obtained with ascorbate.

Total phenolic content was measured using a modified method of Singleton and Rossi (1965). One gram of tomato sample was homogenized with distilled water (3 mL for 'Celebrity' and 7 mL for 'Chadwick') in a paint shaker and centrifuged at 3500 rpm for 10 min at 4 °C. In a 96-well microplate, 30 µL of the supernatant was mixed with 60 µL of 20% Folin-Ciocalteu reagent and 230 µL of 8% (w/v) sodium carbonate. After incubation at room temperature in the dark for 1 h, the absorbance was measured at 765 nm, and the standard curve was obtained using gallic acid.

Statistical analysis

All experimental data were subjected to a two-way analysis of variance (ANOVA) to examine the individual and interactive effects of HS and LED light quality within each cultivar using R software (ver. 4.2.0; R Foundation for Statistical Computing, Vienna, Austria). In this study, ANOVA was conducted separately for each tomato cultivar to account for significant variability among the cultivars, providing cultivar-specific insights into the responses to HS and LED light quality treatments.

Differences between treatment means were compared using Tukey's honestly significant difference (HSD) at a $P = 0.05$ significance threshold using the agricolae package in R (De Mendiburu 2014). Tukey's HSD is a robust post hoc test for determining significant pairwise differences among treatment means while effectively controlling the family-wise Type I error rate (Midway et al. 2020). This method was considered appropriate for comparing HS and LED light quality treatments, the data of which satisfied the assumptions of normality and homoskedasticity.

Pearson's correlation coefficient method, which measures the linear association between two normally distributed random variables (Schober et al. 2018), was used to assess the relationships between various fruit quality traits using the Hmisc package in R (Harrell and Dupont 2020).

Results

Seedling growth. The application of HS resulted in a highly significant increase in seedling growth compared with the control soil treatment (Figs. 2 and 3). Both 'Celebrity' and 'Chadwick' plants in all LED light treatments demonstrated an increase in plant height, stem diameter, canopy leaf area, shoot and root DW, total root length, and surface area in response to HS treatments. The only exceptions without significant differences were the total root surface area in 'Celebrity' seedlings under FL, and total root length and surface area in 'Chadwick' seedlings under 100B light (Figs. 2H, 3G, and 3H). The LED light treatment groups showed variations in plant growth depending on the soil treatments and the cultivars. Seedlings under FL, 10B:90R, and 50B:50R showed overall comparable growth in 'Celebrity', regardless of the soil treatments (Supplemental Fig. 1A and C). In contrast, 'Chadwick' seedling growth was the most vigorous under 10B:90R in the control soil, whereas that under 50B:50R was the greatest in HS treatments (Supplemental Fig. 1B and D).

Both 'Celebrity' and 'Chadwick' tomato seedlings under FL and 10B:90R had significantly greater heights than those under 50B:50R and 100B, regardless of the soil treatments, except for 'Chadwick' seedlings under 100B in HS treatments (Figs. 2A and 3A). Similarly, stem diameter was significantly greater under FL and 10B:90R compared with the 100B treatment groups regardless of the soil treatments in both cultivars, except for 'Chadwick' seedlings treated with HS, which showed no significant differences between the LED light treatments (Figs. 2B and 3B). In 'Celebrity' plants, the 50B:50R treatment group had similar or smaller stem diameter than those under FL and 10B:90R, but was larger than under 100B.

In the control soil treatment, seedlings under 50B:50R showed the highest SPAD values in 'Celebrity' and a higher value than those under 10B:90R in 'Chadwick' (Figs. 2C and 3C). In HS treatments, both FL and 50B:50R treatment groups had a significantly higher SPAD value than the 10B:90R and 100B treatment groups in both 'Celebrity' and 'Chadwick' seedlings. The canopy leaf area was the largest in seedlings under FL in 'Celebrity' in the control soil, whereas those under 10B:90R were higher than 50B:50R and 100B in both 'Celebrity' and 'Chadwick' (Figs. 2D and 3D). In HS treatments, seedlings under 100B showed significantly less canopy leaf area than those under FL in 'Celebrity', and under FL and 50B:50R in 'Chadwick'. Shoot DW was greater in seedlings under 10B:90R than in those under 50B:50R and 100B in 'Celebrity' and all other LED treatment groups in 'Chadwick' in the control soil (Figs. 2E and 3E). However, there were no significant differences between the LED treatments in HS treatments.

There were no significant differences between the LED treatment groups in root DW, total root length, and surface area in 'Celebrity' seedlings, regardless of the soil treatments (Fig. 2F–H). In 'Chadwick' seedlings, the 10B:90R treatment groups had a similar or greater root DW and morphology in the control soil, whereas in HS treatments, the 50B:50R treatment groups demonstrated similar or greater results compared with the other LED treatment groups (Fig. 3F–H).

Tomato yield and quality. The total tomato yield showed no significant differences between the soil treatments in 'Celebrity' plants (Fig. 4A), whereas 'Chadwick' plants under 50B:50R and 100B demonstrated a significant yield increase under HS treatments (Fig. 4B). The early yield increased with HS applications in 'Celebrity' plants under 10B:90R, and both the early and mid yields increased in 'Chadwick' plants under 50B:50R. There were no significant yield differences between the LED light treatments in 'Celebrity' plants, whereas 'Chadwick' plants under FL had a greater total yield than those under 100B, but only in the control soil. The harvest index increased with HS applications in both 'Celebrity' and 'Chadwick' plants under 100B, but

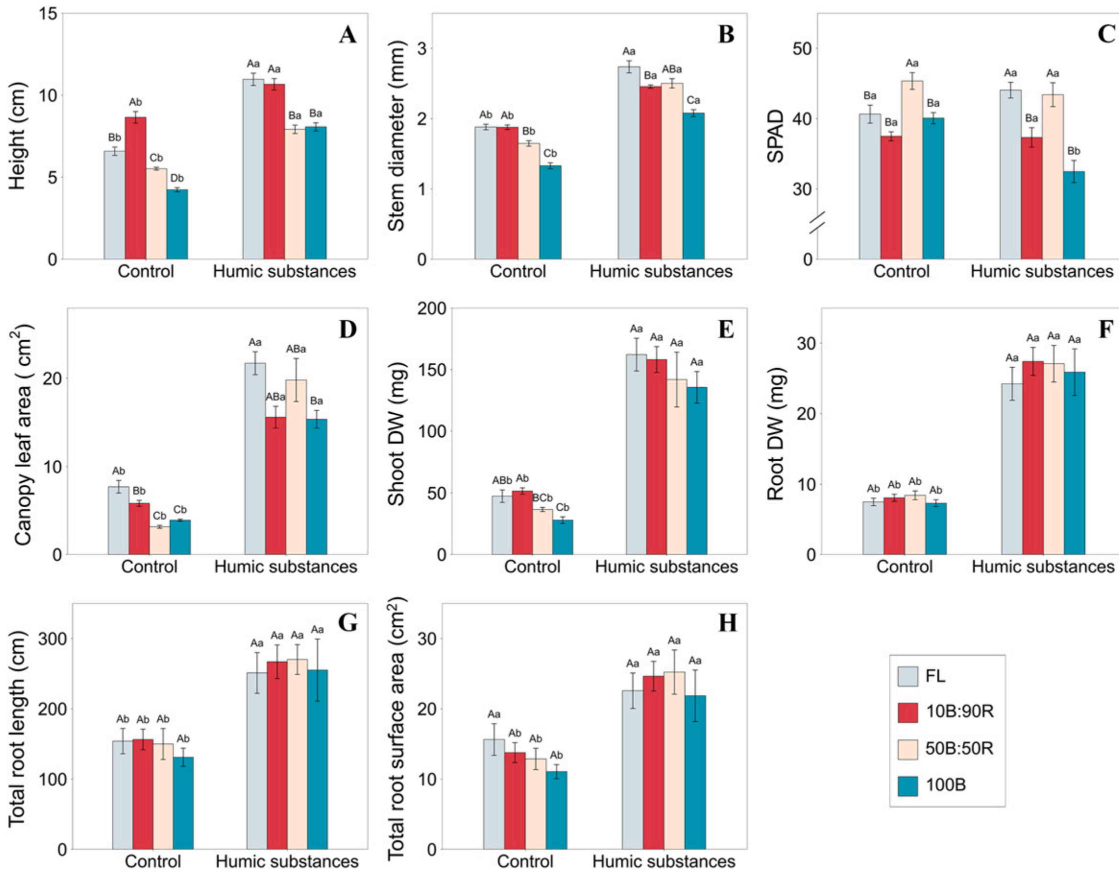

Fig. 2. Effects of humic substances and light-emitting diode (LED) light quality on height (**A**), stem diameter (**B**), soil plant analysis development (SPAD) (**C**), canopy leaf area (**D**), shoot dry weight (DW) (**E**), root DW (**F**), total root length (**G**), and total root surface area (**H**) in 'Celebrity' tomato seedlings at 35 d after sowing. Different uppercase letters indicate significant differences between the LED light treatments within the same soil treatment; different lowercase letters indicate significant differences across the soil treatments within the same LED light treatments at $P \leq 0.05$. Error bars represent the standard error of the mean. B = blue; FL = fluorescent light; R = red.

this was not observed in the other LED light treatment groups (Supplemental Fig. 2).

The number of harvested tomato fruit did not show significant differences among soil and LED light treatments in either 'Celebrity' or 'Chadwick' plants (Fig. 5A and B). In 'Celebrity' plants grown in control soil, the fruit diameter was the smallest in the 10B:90R treatment group (Fig. 5C), whereas fruit diameters under control soil in 'Chadwick' were comparable between the LED treatments, with the largest value in the FL treatment group (Fig. 5D). In HS treatments, 'Celebrity' plants exposed to 50B:50R had a significantly larger fruit diameter compared with those under 100B. The 10B:90R treatment group showed similar values to other LED light treatment groups, with a significant increase under HS application. In 'Chadwick' plants, contrasting responses were observed in fruit diameter, as the fruit diameter of the FL treatment group decreased with HS application, whereas that of the 10B:90R and 50B:50R groups increased. This resulted in a larger fruit diameter in the 10B:90R and 50B:50R treatment groups compared with the rest of the LED light treatment groups under HS application. The average fruit weight showed similar trends in treatment differences to the fruit diameter results in both tomato cultivars (Fig. 5E and F).

Tomatoes reared under different LED light qualities showed no significant differences in TSS contents or TA within the soil treatments in both 'Celebrity' and 'Chadwick' cultivars (Fig. 6A–D). However, significant HS effects were detected in TSS, with a decrease in 10B:90R-treated 'Celebrity' and an increase in FL-treated 'Chadwick' tomatoes under HS application. Because the magnitude of treatment differences in TA was less than in TSS, the TSS:TA ratio followed the trends of the differences found in the TSS results (Fig. 6E and F).

The ascorbate content in fruit showed similar trends in treatment differences to the TSS results (r = 0.41 in 'Celebrity', r = 0.59 in 'Chadwick', $P < 0.001$) in both tomato cultivars (Fig. 7A and B), with completely matching responses to HS application observed in 'Celebrity' plants under 10B:90R and 'Chadwick' plants under FL. The lycopene content increased significantly with HS application in the 10B:90R-treated 'Celebrity', and the FL- and 100B-treated 'Chadwick' tomatoes (Fig. 7C and D). With regard to β-carotene content, no significant differences were observed among soil and LED light treatments, except for 100B-treated 'Chadwick' tomatoes, which had a greater value than those under the FL treatment (Fig. 7E and F). Similarly, total phenolic content was significantly greater in 100B-treated 'Chadwick' tomatoes than in the 10B:90R and 50B:50R treatments. Also, the 100B treatment group demonstrated a significant increase in total phenolic content under HS application in both 'Celebrity' and 'Chadwick' tomatoes (Fig. 7G and H).

Discussion

Effects of humic substances on seedling growth. Tomato seedlings treated with HS showed significantly greater shoot and root growth compared with control plants, with a more than 3-fold increase in canopy leaf area, and shoot and root DW on average in both 'Celebrity' and 'Chadwick' (Figs. 2 and 3). Although the beneficial effects of HS on vegetable transplant growth have been widely studied (Çimrin et al. 2010; Gulser et al. 2010; Osman and Rady 2014), the magnitude of the effects observed in our study was substantially greater than the typical HS effects, which generally enhance shoot and root growth by ∼15% to 25% (Rose et al. 2014).

The particularly pronounced effects of HS in our study may be attributed to the suboptimal light intensity (100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD) for tomato plants (Zheng et al. 2023), which was the maximum intensity available from the monochromatic blue LED described in

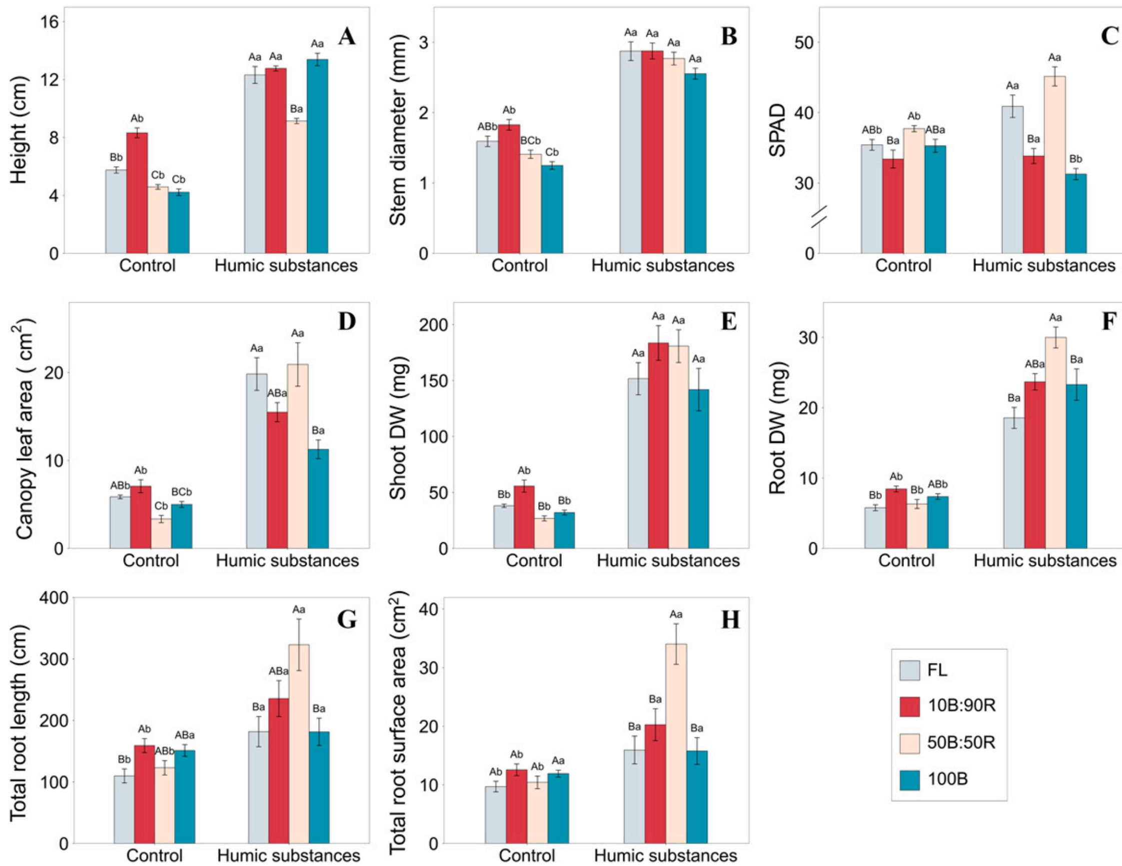

Fig. 3. Effects of humic substances and light-emitting diode (LED) light quality on height (**A**), stem diameter (**B**), soil plant analysis development (SPAD) (**C**), canopy leaf area (**D**), shoot dry weight (DW) (**E**), root DW (**F**), total root length (**G**), and total root surface area (**H**) in 'Chadwick' tomato seedlings at 35 d after sowing. Different uppercase letters indicate significant differences between the LED light treatments within the same soil treatment; different lowercase letters indicate significant differences across the soil treatments within the same LED light treatments at $P \leq 0.05$. Error bars represent the standard error of the mean. B = blue; FL = fluorescent light; R = red.

"Plant Materials, Growth Conditions, and Experimental Design." Given the beneficial effects of HS on enhancing photosynthetic capacity (Chen et al. 2022; Fan et al. 2014), it is speculated that seedlings under HS treatments were more capable of compensating for the insufficient light conditions than those in the control soil, possibly as a result of synergistic effects between increased photosynthesis and HS-promoted root development (Shah et al. 2018), ultimately resulting in highly significant differences between the control and HS treatment groups.

In addition, the outstanding HS effects might be attributed to the relatively low fertilization rate (50 $mg \cdot L^{-1}$ P) during the seedling stage. The beneficial effects of HS in soil, such as improving nutrient bioavailability and serving as a micronutrient reservoir, are most pronounced in nutrient-limited conditions

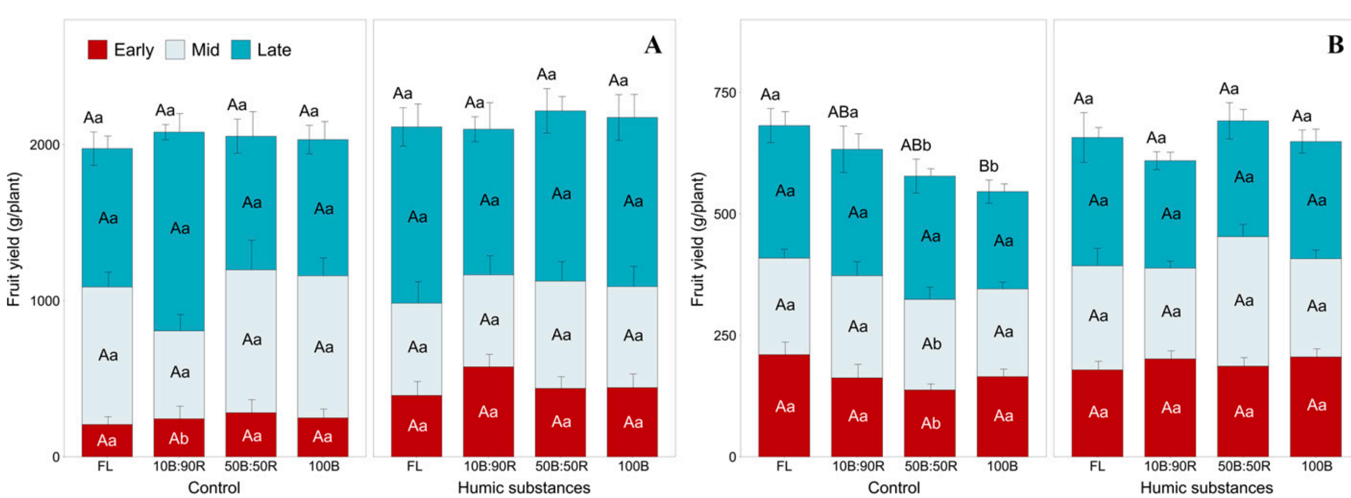

Fig. 4. Tomato yield (early, mid, and late) in 'Celebrity' (**A**) and 'Chadwick' (**B**) plants in response to humic substances application and different light-emitting diode (LED) light qualities. Different uppercase letters indicate significant differences between the LED light treatments within the same soil treatment; different lowercase letters indicate significant differences across the soil treatments within the same LED light treatments at $P \leq 0.05$. Error bars represent the standard error of the mean. Letters within the bar and the error bars positioned at the center represent the yield of each term (early, mid, and late); and letters above the bar and the error bars positioned below the letter represent the total yield. B = blue; FL = fluorescent light; R = red.

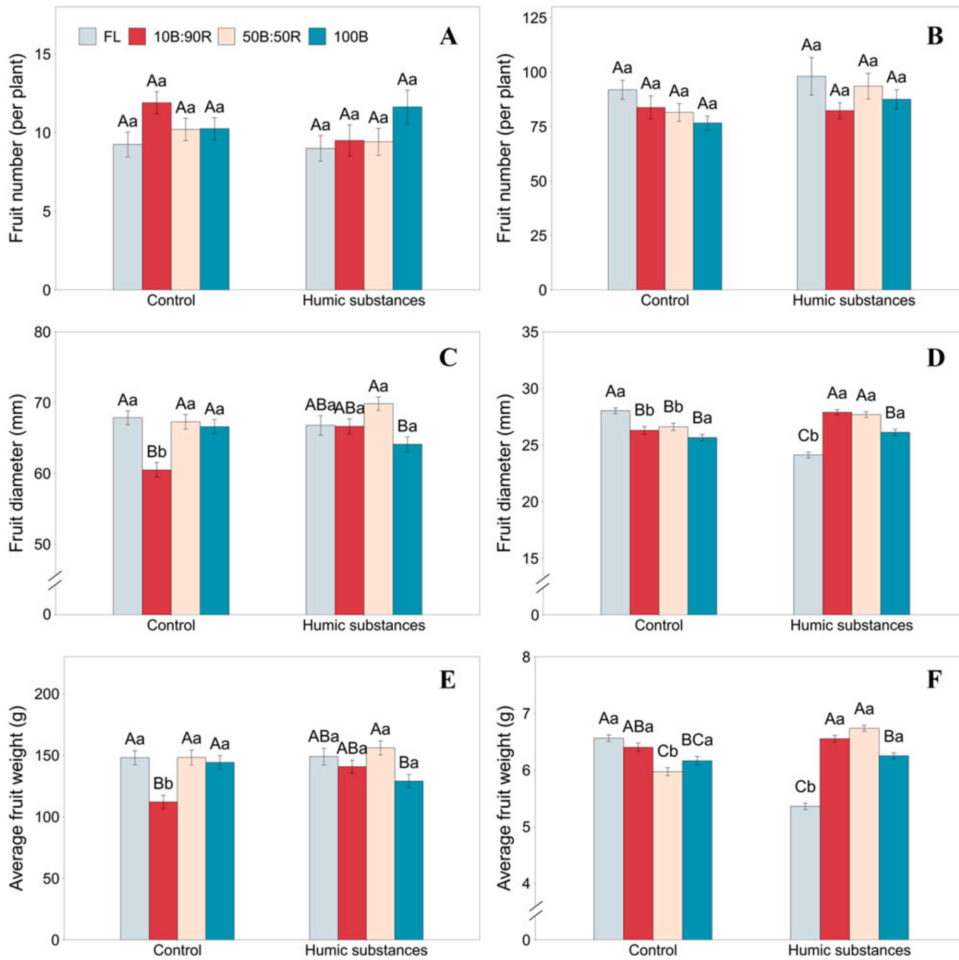

Fig. 5. Tomato fruit number, diameter, and average weight in ‘Celebrity’ (**A**, **C**, **E**) and ‘Chadwick’ (**B**, **D**, **F**) plants in response to humic substances application and different light-emitting diode (LED) light qualities. Different uppercase letters indicate significant differences between the LED light treatments within the same soil treatment; different lowercase letters indicate significant differences across the soil treatments within the same LED light treatments at $P \leq 0.05$. Error bars represent the standard error of the mean. B = blue; FL = fluorescent light; R = red.

(Garcia et al. 2016; MacCarthy 2001). The growth differences observed at the early stage of the seedlings before fertilization also support the HS function as a growth promoter. However, these benefits are likely not the result of the direct nutritional contribution of HS, as they were applied in very low quantities (Nardi et al. 2021). Also, commercial growth media already contain a certain level of extractable nutrients (Kingston et al. 2017; Qin and Leskovar 2020b), which may have mitigated the direct nutritional effect of HS.

Effects of LED light on seedling growth. Seedlings treated with FL and 10B:90R light in ‘Celebrity’, and 10B:90R light in ‘Chadwick’ showed overall greater performance compared with the other light treatment groups in control soil, but the benefits of 10B:90R light reduced under HS treatments in both cultivars (Figs. 2 and 3, Supplemental Fig. 1). In control soil, seedlings under 10B:90R had a significantly greater stem diameter, canopy leaf area, and shoot DW than those under 50B:50R and 100B in both ‘Celebrity’ and ‘Chadwick’, as well as greater root DW than those under FL and 50B:50R in ‘Chadwick’. However, with HS application, 10B:90R-treated seedlings did not show significantly greater results than the other light treatment groups in those parameters, except for stem diameter in ‘Celebrity’, implying that the beneficial effects of HS were not additive to those already existing in 10B:90R light. Conversely, under HS treatments, FL-treated ‘Celebrity’ seedlings were able to maintain their beneficial traits in stem diameter and canopy leaf area along with an increased SPAD value.

In ‘Chadwick’ seedlings, 50B:50R light exhibited the most pronounced synergistic effect with HS application (Fig. 3, Supplemental Fig. 1D). Under HS application, plants exposed to 50B:50R light showed a numerically greater or comparable increase in all shoot and root growth parameters except for plant height, resulting in the overall greatest transplant quality among all treatment combinations. According to Leskovar (2020), high-quality vegetable transplants are characterized by a thick, nonelongated stem and a balanced root–shoot system—traits that matched those of ‘Chadwick’ seedlings grown under 50B:50R light and HS treatments. Notably, their root growth was enhanced under HS treatments (Fig. 3F–H), possibly as a result of a synergistic effect between the auxin-like activities of HS (Shah et al. 2018; Trevisan et al. 2010) and the upregulation of plant growth hormones such as auxin and gibberellin in roots under combined red and blue light (Li et al. 2021). However, this response was not observed in ‘Celebrity’ seedlings, suggesting that the synergistic effect may be cultivar specific. Further studies are necessary to confirm the underlying mechanism.

Regardless of cultivar and soil treatments, seedlings under 100B light demonstrated similar or reduced growth across all shoot and root parameters, except plant height, compared with the other light treatments. This outcome is likely attributed to the low photosynthetic efficiency of blue light, which is 25% to 35% less than that of red light (McCree 1971). These results align with previous LED studies on monochromatic blue light (Gao et al. 2022; Guo et al. 2023; Kim et al. 2004), which reported significant reductions in plant growth parameters such as shoot and root biomass, leaf area, and net photosynthetic rate compared with combined red and blue light. In addition, 100B-treated seedlings showed no synergistic effect with HS, but rather a decline in SPAD (Figs. 2C and 3C), indicating that 100B light is undesirable for tomato seedling growth in combination with HS treatments compared with the other light treatments. However, given that monochromatic light induces distinct physiological responses compared with

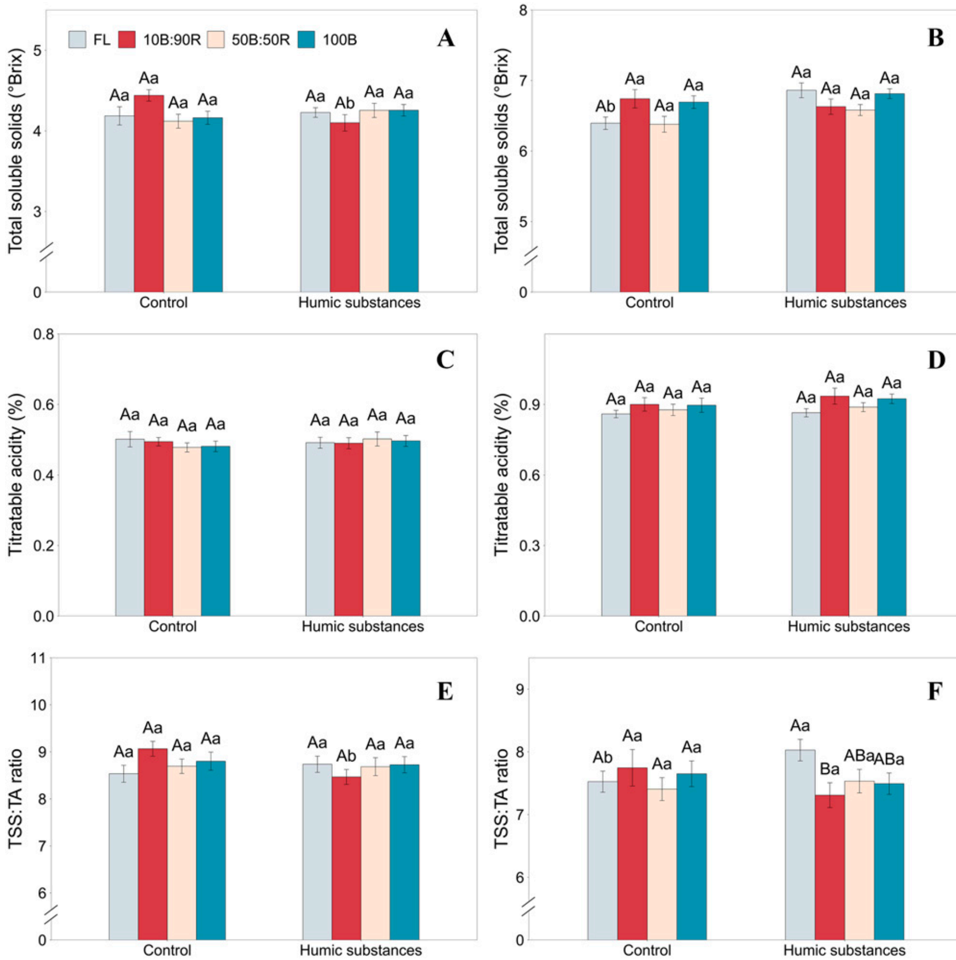

Fig. 6. Tomato total soluble solids (TSS), titratable acidity (TA), and TSS:TA in 'Celebrity' (**A**, **C**, **E**) and 'Chadwick' (**B**, **D**, **F**) plants in response to humic substances application and different light-emitting diode (LED) light qualities. Different uppercase letters indicate significant differences between the LED light treatments within the same soil treatment; different lowercase letters indicate significant differences across the soil treatments within the same LED light treatments at $P \leq 0.05$. Error bars represent the standard error of the mean. B = blue; FL = fluorescent light; R = red.

combined red and blue light, further studies incorporating low levels of red LED light alongside blue light are needed for a more comprehensive evaluation of high blue-light effects on tomato seedlings.

In summary, FL and 50B:50R light demonstrated the greatest synergistic effect with HS application on 'Celebrity' transplant quality, and 50B:50R light also showed a superior interaction effect with HS in 'Chadwick' transplants. However, the magnitude of differences in seedling growth between the LED light treatments was relatively smaller than the HS effects, indicating the limited impact of modifying light quality compared with the soil environment. Also, the interaction effects between LED light and HS treatments were cultivar specific (Supplemental Table 1), suggesting the need to explore a wider range of cultivars to understand more fully the combined effects of LED light and HS application on transplant quality.

Carryover effects of transplant quality on tomato production. The enhanced seedling growth under LED light and HS treatments just described did not result in consistently improved performance during the fruiting stage after transplanting. Among all treatment combinations, only the 'Chadwick' plants exposed to 50B:50R and 100B light showed increased total fruit yield under HS application, whereas the rest of the treatment groups showed no benefits of HS application (Fig. 4). Similarly, no significant yield differences were detected between the LED light treatments, except for a greater total yield in 'Chadwick' seedlings under FL compared with those under 100B light in control soil. Even the LED treatment groups with the greatest transplant quality, such as 50B:50R-treated 'Chadwick' plants in HS treatments, had similar yields compared with those with the lowest transplant quality, such as 100B-treated seedlings. Furthermore, post-transplant shoot FW did not differ significantly among treatment groups (data not shown), indicating that improved transplant quality did not lead to enhanced net photosynthate accumulation in the shoot after transplant.

The fruit quality results also did not correspond to the treatment differences in seedling growth. Although a few significant effects of LED light and HS on fruit quality were detected (Figs. 5–7), they did not align with those observed at the seedling stage (Figs. 2 and 3). For example, TSS content was not enhanced in HS treatment groups in 'Celebrity' tomatoes despite advantageous HS effects on seedling growth (Fig. 6A); 'Chadwick' tomatoes with 50B:50R light and HS treatments, which had the greatest transplant quality (Supplemental Fig. 1D), showed similar secondary metabolite contents to those of other light treatment groups (Fig. 7).

The limited carryover effects of transplant quality on post-transplant growth and fruit production suggest that producing high-quality vegetable transplants may not lead to significantly enhanced crop production, especially in an uncontrolled environment where initial growth differences can be diminished by various biotic and abiotic factors (Fig. 1). For example, tomato TSS content showed significant differences among experimental blocks (Supplemental Fig. 3), with values increasing with distance from the evaporative cooling system, implying a greater effect of temperature on TSS content compared with that of LED light (Fig. 6A and B). In addition, the restricted root growth of transplanted plants in pots may have reduced the benefits of a

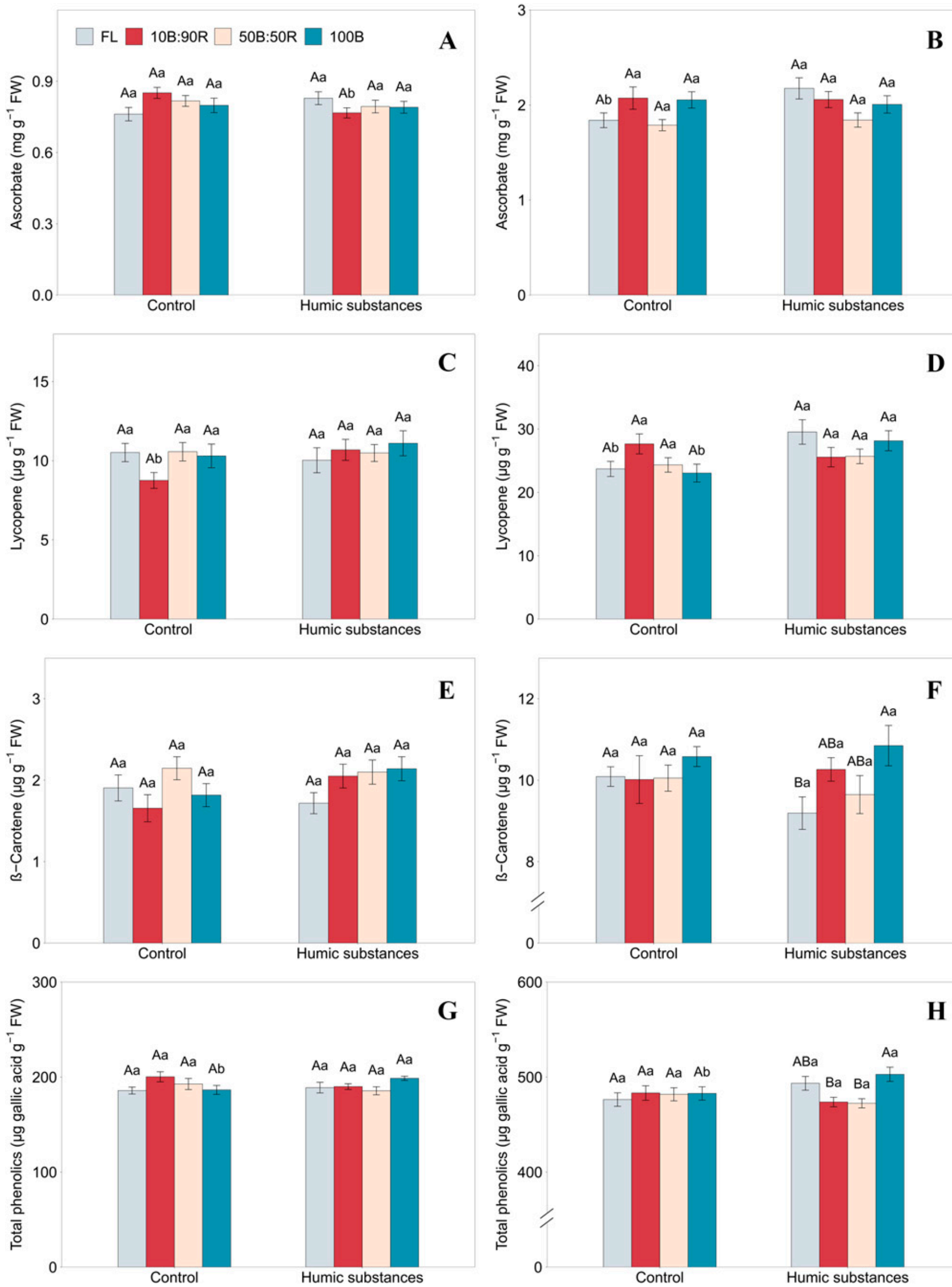

Fig. 7. Tomato ascorbate, lycopene, β-carotene and total phenolics contents in 'Celebrity' (**A**, **C**, **E**, **G**) and 'Chadwick' (**B**, **D**, **F**, **H**) plants in response to humic substances application and different light-emitting diode (LED) light qualities. Different uppercase letters indicate significant differences between the LED light treatments within the same soil treatment; different lowercase letters indicate significant differences across the soil treatments within the same LED light treatments at $P \leq 0.05$. Error bars represent the standard error of the mean. B = blue; FL = fluorescent light; FW = fresh weight; R = red.

vigorous root system that existed in high-quality seedlings, limiting their enhanced ability to absorb nutrients once the root zone was confined to the pot. A vegetable transplant study by Qin and Leskovar (2020b) supports the adverse effect of restricting the root zone when using high-quality transplants, reporting that the benefits of HS application on tomato seedlings were maintained after transplant and during fruit production when grown in an open-field environment. Moreover, the post-transplant cultivation period in our study (19 weeks) was longer than the seedling growth period under experimental treatments (5 weeks), which likely provided sufficient time for lower quality transplants to compensate for their initial disadvantages in growth.

Beneficial effects of humic substances on tomato production. Vigorous seedling growth under HS treatments did not lead to enhanced fruit yield and quality in most treatment groups. However, some groups benefited from HS in certain parameters, including early yield and secondary metabolites, indicating that the beneficial effects of HS could partially extend to the fruiting stage, depending on the cultivar and LED light treatments. In addition to the total yield increase described in the previous section, early yield increased under HS treatments in 'Celebrity' and 'Chadwick' plants exposed to 10B:90R and 50B:50R light, respectively, and the values were numerically greater in all 'Celebrity' plants under HS treatments (Fig. 4, Supplemental Table 1). As early harvest can increase market profitability (Leskovar 2020; O'Sullivan et al. 2019) and help avoid growing seasons with high environmental stresses (Toivonen and Hodges 2011), our results suggest that HS application may be advantageous for tomato producers operating in challenging growth environments. In addition, as transplants grown in larger cell volumes or with greater maturity are known to produce greater early yields (Leskovar 2020), HS application could potentially compensate for smaller cell volumes or younger seedling ages, which can increase time and space efficiency for tomato transplant production.

HS application also selectively increased secondary metabolite content of tomatoes, depending on the treatment combinations (Fig. 7). Plants exposed to 100B light showed the greatest synergistic effect with HS application among the LED treatments, having a significant increase in lycopene content in 'Chadwick' and total phenolic content in both 'Celebrity' and 'Chadwick' tomatoes under HS. Blue light is known to promote the accumulation of antioxidants, such as carotenoids and phenolic compounds, by upregulating their biosynthetic pathways (Hasan et al. 2017; Kim et al. 2014). In our study, 100B-treated plants showed similar secondary metabolite contents to the other LED treatment groups in the control soil, but demonstrated significantly greater β-carotene content than FL-treated plants and greater total phenolic contents than 10B:90R- and 50B:50R-treated plants in 'Chadwick' tomatoes under HS treatments. This suggests that the effect of blue light on upregulating antioxidant biosynthesis could extend to fruit production when treated with HS at the seedling stage. However, lack of antioxidant analysis at the seedling stage limits the ability to confirm this mechanism, and further study is required.

The ascorbate content in tomatoes (Fig. 7) correlated positively with the TSS content (Fig. 6) at a moderate level (r = 0.41 in 'Celebrity', r = 0.59 in 'Chadwick', $P < 0.001$), which aligns with the role of ascorbate as a sugar acid synthesized from sugar molecules, such as glucose (Wheeler et al. 1998). Also, TSS content had a moderate and weak negative correlation with the average fruit weight in 'Celebrity' (r = –0.45, $P < 0.001$) and 'Chadwick' plants (r = –0.25, $P = 0.016$), respectively, the relationship of which aligns with other tomato quality studies (Adeniji et al. 2020; Bernousi et al. 2011; Zemach et al. 2023). Similarly, ascorbate content showed a weak negative correlation with the average fruit weight (r = –0.32, $P = 0.004$ in 'Celebrity', r = –0.24, $P = 0.022$ in 'Chadwick'). The overall correlation between average fruit weight, TSS, and ascorbate content suggests that the differences observed in ascorbate may not be a direct effect of HS, but could be an indirect effect caused by changes in average fruit weight, which may also depend on the number of fruit per plant (Adeniji et al. 2020; Yeshiwas et al. 2016). For example, the lowest average fruit weight of 10B:90R-treated 'Celebrity' plants within the control soil treatments (Fig. 5E), potentially resulting from the numerically highest fruit number (Fig. 5A, r = –0.33, $P = 0.002$), may have led to significantly greater TSS (Fig. 6A) and ascorbate (Fig. 7A) contents in control soil compared with those under HS treatments, which could be misinterpreted as a direct HS effect. Because the underlying mechanisms of HS effects on fruit number and average fruit weight were not identified in our study, caution is needed in concluding the direct carryover effects of HS on tomato secondary metabolite contents.

Conclusion

Our study demonstrated that the application of solid HS in growing media significantly enhanced both shoot and root growth of tomato seedlings. Among the LED light treatments, a 50B:50R light ratio provided the greatest synergistic effect with the HS in enhancing transplant quality, whereas the 10B:90R treatment yielded the most vigorous growth without HS. However, these improvements in transplant quality did not translate into corresponding changes in fruit yield and quality. In particular, the beneficial effects of HS observed at the seedling stage were markedly reduced at the post-transplant fruiting stage, with benefits limited to fruit yield and secondary metabolite content in specific treatments. These findings suggest that the combination of HS and optimized LED light treatments could help tomato transplant nursery growers save time and costs by achieving the desired quality more quickly with enhanced seedling vigor, though these treatments need to be continued post-transplanting to achieve additional benefits in fruit production.

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