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Harnessing LED Technology for Consistent and Nutritious Production of Large-fruited Tomatoes

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***Abstract.* Tomatoes have traditionally been cultivated in greenhouses, where the combination of natural light and semicontrolled environmental conditions supports high yields and fruit quality. In contrast, the cultivation of large-fruited tomato varieties in fully enclosed, light-emitting diode (LED)–based plant factories remains limited, mainly due to technical and physiological challenges. This study demonstrates the successful cultivation of the large-fruited tomato cultivar CF Momotaro Fight in an LED-based plant factory, marking a significant advancement in controlled-environment agriculture. Then, we compared environmental conditions, growth parameters, photosynthetic performance, and fruit characteristics between plant factory and greenhouse systems. Tomatoes grown in the plant factory exhibited enhanced vegetative growth, including increased plant height, stem diameter, and soil–plant analysis development values, likely due to the stable light and temperature conditions. However, photosynthetic efficiency was lower, as indicated by reduced maximum quantum efficiency of PSII (F_v/F_m), effective quantum yield of PSII [Y(II)], electron transport rate (ETR), and fraction of open PSII reaction centers (qL) values. Fruits produced in the plant factory were smaller, had lower Brix values, but exhibited higher ascorbic acid content, suggesting altered resource allocation under uniform environmental conditions. In contrast, tomatoes cultivated in greenhouses, where plants are exposed to high and fluctuating light conditions, exhibited higher photosynthetic efficiency and superior fruit quality, including increased fruit weight, larger size, and higher Brix values. These findings highlight the complementary advantages of each system. While plant factories provide precise environmental control and stable year-round production, greenhouses leverage abundant natural sunlight to enhance fruit quality and yield. This study offers new insights into tomato cultivation under contrasting controlled environments and contributes to the development of sustainable, high-value horticultural production systems.**

As the global population continues to rise, the demand for horticultural products is expected to increase substantially. To meet this growing need, the development of innovative and efficient cultivation systems is essential. Among current technologies, greenhouse cultivation and plant factory systems have emerged as leading solutions (Graamans et al. 2018). Each system offers distinct advantages and faces specific challenges, particularly in terms of light utilization, temperature regulation, and energy efficiency. Greenhouses are generally more cost-effective due to their reliance on natural sunlight but may suffer from limited temperature control and lower energy efficiency (Cuce et al. 2016; Soussi et al. 2022). In contrast, plant factories provide highly controlled environments with optimized conditions and efficient resource use, although they typically require significant energy inputs (Goto 2012; Graamans et al. 2018; Shamshiri et al. 2018). Balancing the strengths and limitations of these systems remains a critical focus in advancing sustainable agricultural production.

Greenhouse cultivation offers a semienclosed environment that shields crops from adverse weather, pests, and diseases. It has a long history and remains widely practiced worldwide. By regulating temperature, humidity, and light, greenhouses can support plant growth and yield across seasons and geographic locations (Nemali 2022). Most greenhouses use solar energy for lighting and heating (Panwar et al. 2011), with supplementary heating or cooling systems compensating for energy deficits or surpluses. However, their transparent and conductive structures inherently create a trade-off between solar energy utilization and environmental control (Soussi et al. 2022; Vanthoor et al. 2011). The cost–benefit balance of greenhouse production is highly dependent on latitude and external climate. In high-latitude regions, solar radiation may be insufficient to offset energy losses, whereas in low-latitude areas, excessive heat buildup may require active cooling (Kozai 2012).

Compared with greenhouses, plant factories represent a more technologically advanced cultivation method. These fully enclosed systems are designed to maximize production density, yield, and resource use efficiency (Graamans et al. 2018; Hatfield and Walthall 2015; Kozai 2013). Often employing vertical farming techniques, plant factories enable multilayered crop production within a compact footprint (Kozai et al. 2019). Their urban deployment potential reduces transportation distances and environmental impacts (Shamshiri et al. 2018). However, plant factories rely heavily on artificial energy to maintain precise control over lighting, nutrient delivery, temperature, humidity, and CO_2 levels (Bantis et al. 2018; Orsini et al. 2020). While this fine-tuned environment ensures high productivity and consistency (Zou et al. 2024), it also incurs significantly higher operational costs (Zhuang et al. 2022).

From a physiological perspective, photosynthetic efficiency is a key driver of crop productivity (Yamori et al. 2016; Zhu et al. 2010) and is highly sensitive to environmental conditions. Environmental factors—such as light intensity, CO_2 concentration, humidity, and temperature—directly affect photosynthesis and are in turn shaped by the cultivation system (Hayashi et al. 2024; Katsuhama et al. 2025; Levine et al. 2023; Qu et al. 2021, 2025). In greenhouses, natural sunlight is the primary light source, with artificial lighting used as a supplement. Variations in weather, seasonal changes, solar altitude, and shading can cause fluctuations in light intensity, leading to inconsistent photosynthetic performance (Baille et al. 2001; Kimura et al. 2020; Yamori et al. 2020). Moreover, greenhouse systems often lack effective control over humidity, CO_2, and temperature, which may further limit plant growth and yield (Mat et al. 2018). Conversely, plant factories use only artificial light, allowing precise adjustment of intensity and spectrum to optimize photosynthesis, thereby enhancing both efficiency and yield (Darko et al. 2014; Kozai 2013; Li et al. 2025). Control over other environmental variables further supports consistent and accelerated plant development (Kozai 2012).

Tomato (*Solanum lycopersicum*) is a globally important crop, valued both for its economic impact and for its nutritional content, with annual production exceeding 180 million metric tons (Food and Agriculture Organization 2021). While greenhouse cultivation of tomatoes is well established, commercial-scale production in plant factories is still emerging (Zhuang et al. 2024). Consequently, the comparative impacts of these systems on tomato growth are not yet fully understood. Moreover, since tomatoes are primarily consumed as fresh fruits, fruit quality is a critical factor in evaluating cultivation performance. Quality parameters include physical traits such as size, color, and firmness, as well as chemical attributes such as sugar content, acidity, and nutrient levels (Felföldi et al. 2022). These characteristics are influenced by cultivation conditions, including light spectrum, nutrient availability, and environmental stressors (Bacelar et al. 2024). Prior studies suggest that greenhouse-grown tomatoes may benefit from natural light for flavor and aroma, while plant factory–grown tomatoes may exhibit improved nutritional content and uniformity due to controlled conditions (Bian et al. 2015; Palmitessa et al. 2021; Pennisi et al. 2019; Zhuang et al. 2024).

Despite the unique advantages offered by each system, their comparative influence on tomato photosynthetic efficiency and fruit quality remains underexplored. This study aims to evaluate and contrast the physiological performance and fruit characteristics of tomatoes grown in greenhouses and plant factories. By doing so, we aim to clarify the benefits and limitations of each approach and offer practical insights for growers, researchers, and policymakers seeking to optimize tomato production in diverse cultivation environments.

Materials and Methods

Plant material and cultivation. The experiment used the large-fruited tomato cultivar CF Momotaro Fight (Takii & Co., Ltd., Kyoto, Japan). Cultivation was carried out under two controlled-environment systems: a greenhouse with soil-based cultivation and a fully enclosed plant factory using hydroponics. In the greenhouse system, tomatoes were cultivated in soil amended with cow manure compost, which was applied as a basal fertilizer following conventional cultivation practices, and illuminated by natural daylight only. The environment of greenhouse was passively controlled with shading and ventilation in summer when temperature rose above 25 °C and actively warmed up by a kerosene burner in the winter when temperature dropped below 15 °C. In the plant factory system, the plants were grown hydroponically using the OAT House Fertilizer Series A formulation (OAT House No. 1 and No. 2; OAT Agrio Co., Ltd., Osaka, Japan) as a nutrient solution with a N–P–K ratio of 10–8–27, and this system employed fully artificial lighting and environmental controls to maintain stable growth conditions. Plants were illuminated by white light light-emitting diode (LED) with a 16-h/8-h light–dark circle, and the temperature was actively maintained at 25 °C with an air conditioning system. All cultivation trials were conducted concurrently from Jan to Apr 2024 at the Institute for Sustainable Agro-ecosystem Services, Graduate School of Agricultural and Life Sciences, University of Tokyo, Tokyo, Japan.

Determination of photosynthetic parameters. Chlorophyll fluorescence was measured to evaluate photosynthetic efficiency in leaves from the upper, middle, and lower canopy layers of tomato (*Solanum lycopersicum* L. cv. CF Momotaro Fight) plants. Measurements were conducted in situ using a Micro-PAM fluorometer (Heinz Walz GmbH, Effeltrich, Germany) under the growth conditions. A range of actinic light intensities (0 to 1500 μmol photons $m^{-2}\cdot s^{-1}$) was applied sequentially to each selected leaf. At each light level, measurements were recorded after 5 min of illumination to ensure steady-state photosynthetic activity (Yoshiyama et al. 2024). The following fluorescence parameters were obtained: initial fluorescence (F_0), maximum fluorescence (F_m), variable fluorescence ($F_v = F_m - F_0$), maximum quantum yield of Photosystem II (PSII) (F_v/F_m), effective quantum yield of PSII [Y(II)], electron transport rate (ETR), photochemical quenching (qP), nonphotochemical quenching (qN), fraction of open PSII reaction centers (qL), nonphotochemical quenching (NPQ), quantum yield of nonregulated energy dissipation [Y(NO)], and quantum yield of regulated nonphotochemical quenching [Y(NPQ)]. Measurements were conducted on at least three biologically independent plants per treatment, and representative fully expanded leaves were selected from each canopy layer.

Determination of growth parameters. Growth parameters, including plant height, stem diameter, and soil–plant analysis development (SPAD) values, were recorded weekly for each plant throughout the cultivation period. The shoot apex was operationally defined as the base of the youngest fully expanded leaf nearest to the stem apex. To track vertical growth, training strings were used, and the position of the growing point was marked weekly with dated tape. Weekly stem elongation was determined by measuring the distance between consecutive tape markers. Total stem length was calculated cumulatively by adding each week's elongation to the initial stem length measured at the beginning of the observation period. Stem diameter was measured using digital calipers at the thickest point of the stem corresponding to the previous week's growing point position. Chlorophyll content was estimated using a SPAD meter (SPAD-502Plus; Konica Minolta, Tokyo, Japan). SPAD measurements were taken from the leaf immediately above the flower truss bearing at least three open flowers and located closest to the growing point. Three readings were taken per leaf and averaged for each plant.

Determination of fruit quality. Tomato fruits were harvested sequentially at full maturity. For each truss, three representative fruits were selected for analysis. Fresh weight was measured immediately after harvest using an electronic balance. The same fruits were then used for subsequent analysis of sugar content, titratable acidity, ascorbic acid, and lycopene concentration. Fruits were cut longitudinally, and one half was used for immediate measurements, while the other half was frozen at –20 °C for later lycopene analysis. Soluble sugar content (°Brix) and titratable acidity were measured using a digital sugar–acid meter (PAL-BX|ACID F5; ATAGO Co., Ltd., Fukaya, Japan). Sugar content was determined by pressing the cut surface directly onto the sensor to extract juice, while for acidity measurement, 1 mL of juice was collected from each fruit, diluted with deionized water according to the manufacturer's protocol, and analyzed (Yoshiyama et al. 2024). Each measurement was conducted in triplicate, and the mean value was used for analysis. Ascorbic acid content was quantified using ascorbic acid test strips and reflectometer (RQ Flex plus; Merck, Darmstadt, Germany) as described by Yamori et al. (2022): Juice was extracted from the fruit, and the strips were immersed according to the manufacturer's instructions. The reduced ascorbic acid content was expressed in mg/100 g of fresh tomato juice.

Statistical analysis. The data were analyzed and visualized in R 4.2.3 (R Core Team 2023). Here, we use "fruit value" to evaluate the general quality of fruit product, which is calculated from fruit weight, fruit Brix value, and ascorbic acid content, which were considered to be important parameters related with customer's preference and market value (Causse et al. 2010). The data were analyzed by one-way analysis of variance to evaluate the influence of cultivation methods on tomatoes photosynthetic efficiency and fruit value ($\alpha = 0.05$).

A principal component analysis (PCA) was performed to reveal the relations among all collected traits with the "ggbiplot" package in R. Mantel analysis was used to determine the factors' contribution to fruit value. In this analysis, fruit value was calculated by the following equation:

$$\text{Fruit value} = \sum_{i1}^{n}(x_i \times w_i) \qquad [1]$$

where x_i is the value of the ith trait, w_i is the weight of the ith trait, and n is the total number of traits. To reduce redundancy, three fruit indexes including fruit weight, fruit Brix value, and ascorbic acid content were used for the calculation in the analysis. The weights

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Ningzhi Qiu and Hao Shen contributed equally to this work.

W.Y. and N.Q. designed the experiments. W.Y. and S.K. set hydroponic systems in a LED plant factory. N.Q., H.S., D.I., K.Y., and Y.Q. grew the plants, performed the experiments, and analyzed the data. N.Q. and H.S. prepared figures. N.Q., H.S., Y.Q., and W.Y. prepared the manuscript. All authors have read and approved the final version of this manuscript.

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of each trait were calculated using the entropy weight method.

Results

Tomatoes growth and photosynthesis in greenhouse and plant factory. The environmental conditions in the greenhouse and the plant factory showed various differences. During the tomato cultivation period, although temperature fluctuations were greater in the greenhouse, the overall average temperature in the greenhouse (24.0 ± 1.8 °C) was similar to that in the plant factory (25.9 ± 1.1 °C) (Fig. 1A). On the other hand, light intensity in the greenhouse exhibited substantial fluctuations, peaking at 2053 μmol·m^{-2}·s^{-1} due to natural sunlight variability (Fig. 1C). In contrast, the plant factory maintained a stable light environment, with LED illumination providing a constant intensity of 276 μmol·m^{-2}·s^{-1} from 4:00 AM to 8:00 PM daily (Fig. 1E). In addition, light distribution differed markedly between the greenhouse and the plant factory (Supplemental Fig. 1).

Tomato plants exhibited significantly different growth patterns under the two cultivation systems. Plants grown in the plant factory showed a higher daily stem elongation rate compared with those in the greenhouse (Fig. 1B). Similarly, stem diameter expansion was significantly greater in the plant factory (Fig. 1D). In addition, leaf SPAD values, which reflect chlorophyll content, were consistently higher in plant factory–grown plants (Fig. 1F), indicating enhanced nitrogen status or chlorophyll accumulation under stable, controlled conditions.

Tomato leaves from different canopy positions exhibited distinct photosynthetic efficiencies in both the greenhouse and plant factory systems (Fig. 2). In both environments, lower canopy leaves consistently displayed reduced Y(II), ETR, and qL compared with middle and upper leaves (Fig. 2A, 2D, and 2E). In the greenhouse, these lower leaves also showed significantly elevated Y(NPQ) and NPQ, indicating enhanced photoprotective responses (Fig. 2B and 2F). In contrast, plant factory–grown tomatoes exhibited the highest Y(NPQ) and NPQ values in the lower canopy, while the middle canopy showed the lowest values, suggesting a different pattern of energy dissipation across the canopy.

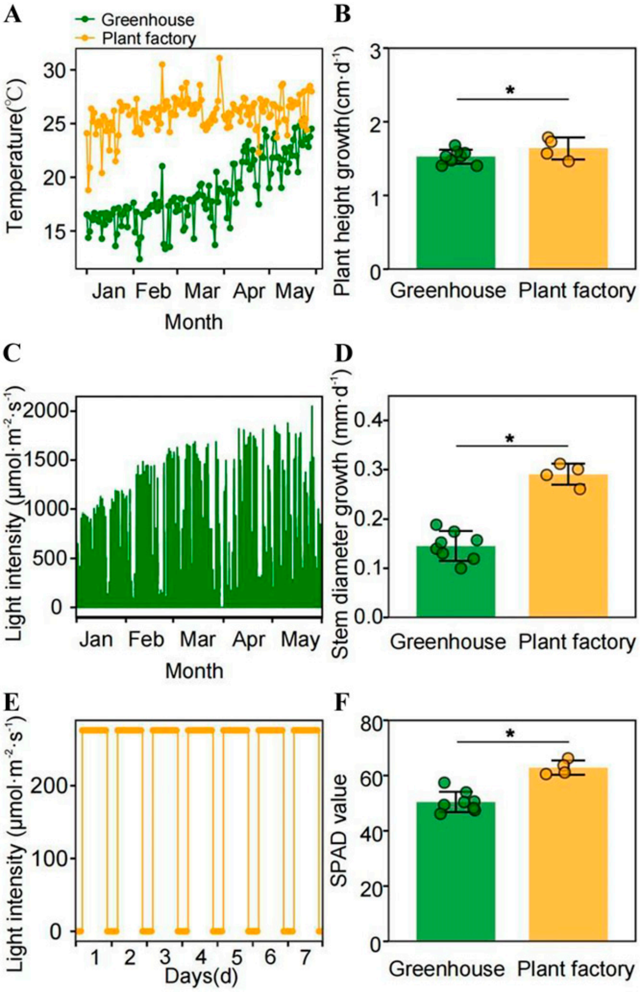

Fig. 1. Tomato growth status in greenhouse and plant factory. Different lowercase letters indicate significant difference at the $P < 0.05$ level. (**A**) Average temperature during the cultivation period in the greenhouse and plant factory. (**B**) Plant height growth. (**C**) Light intensity during the cultivation period in the greenhouse. It was calculated by the following equation: Photosynthetic photon flux density ~solar radiation × 0.45 × 4.6 (Thimijan and Heins 1983). Note: Data for 30 and 31 Mar 2024 are missing. (**D**) Stem diameter growth. (**E**) Light intensity during the cultivation period in the plant factory. Note: A representative 7-d period light intensity fluctuation was presented here to avoid redundant visualization. (**F**) Soil–plant analysis development (SPAD) value. * indicates significant difference at the $P < 0.05$ level.

Variation in the Y(NO) across canopy layers was relatively modest in both systems; however, greater variability was observed among plant factory–grown leaves (Fig. 2C). Overall, tomatoes cultivated in the greenhouse demonstrated consistently higher values for Y(II), ETR, qL, Y(NPQ), and NPQ, alongside lower Y(NO) values compared with those grown in the plant factory. Correlation analysis indicated a positive association between light intensity and ETR, NPQ, and Y(NPQ) in both systems, with no distinct differences observed in the interparameter relationships across systems (Supplemental Fig. 2).

To further quantify photosynthetic responses under actual light conditions, light-response curves were fitted to chlorophyll fluorescence parameters measured at different canopy layers (Fig. 3). Greenhouse-grown plants exhibited significantly higher F_v/F_m in the middle and lower canopy layers compared with the plant factory ($P < 0.05$), with overall higher mean F_v/F_m values across all layers (Fig. 3A). Y(II) was significantly higher in the middle canopy layer of the plant factory, while in the lower canopy, higher values were observed in the greenhouse ($P < 0.05$; Fig. 3B). Greenhouse plants also showed significantly higher Y(NPQ) in both the upper and middle canopy layers, and overall, than those in the plant factory ($P < 0.05$; Fig. 3C). No significant differences in Y(NO) were detected between systems (Fig. 3D). ETR values were significantly greater in the greenhouse at all canopy levels, particularly in the upper and middle layers (Fig. 3E). Similarly, qL and NPQ followed this trend, with no significant differences in the lower canopy but overall higher values in the greenhouse (Fig. 3F and 3G).

Tomatoes quality and yield in the greenhouse and plant factory. Significant differences in fruit yield and quality parameters were observed between tomatoes cultivated in the greenhouse and those grown in the plant factory (Fig. 4). Tomatoes produced in the greenhouse exhibited significantly greater average fruit weight, fruit size, total yield, and soluble solids content (Brix value) compared with those from the plant factory ($P < 0.05$; Fig. 4A–D). In contrast, fruit acidity did not differ significantly between the two cultivation systems (Fig. 4E). Notably, the ascorbic acid content of fruits was significantly higher in the plant factory–grown tomatoes than in those cultivated in the greenhouse ($P < 0.05$; Fig. 4F), suggesting enhanced nutritional value under controlled environmental conditions.

Relations between all collected traits of tomatoes in greenhouse and plant factory. PCA effectively differentiated tomato plants cultivated in the greenhouse from those grown in the plant factory (Fig. 5). The two groups formed distinct clusters, indicating clear

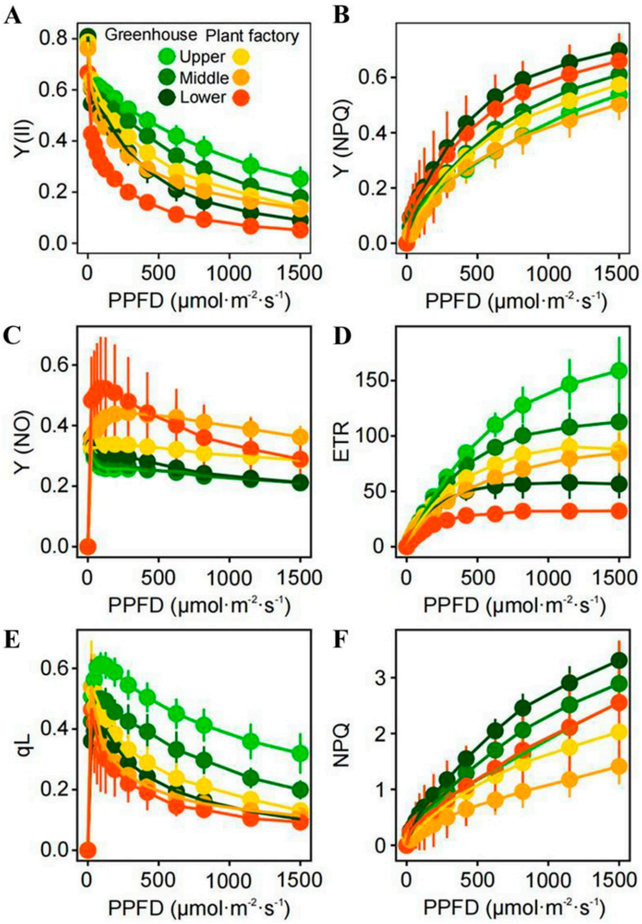

Fig. 2. Chlorophyll fluorescence response of different level tomato leaves in greenhouse and plant factory. (**A**) Effective quantum yield of Photosystem II (PSII) [Y(II)]. (**B**) Quantum yield of regulated nonphotochemical quenching [Y(NPQ)]. (**C**) Quantum yield of nonregulated energy dissipation [Y(NO)]. (**D**) Electron transport rate (ETR). (**E**) Fraction of open PSII reaction centers (qL). (**F**) Nonphotochemical quenching (NPQ). PPFD = photosynthetic photon flux density.

differences in physiological and quality-related traits associated with their respective growing environments. Greenhouse-grown tomatoes, which experienced greater environmental variability, exhibited a stronger association with high fruit quality parameters. Variables such as F_v/F_m, ETR, qL, NPQ, Y(NPQ), fruit size, fruit weight, and Brix value were positively correlated and grouped closely, suggesting that photosynthetic efficiency is closely linked to fruit quality traits. In contrast, parameters including ascorbic acid content, SPAD value, Y(NO), plant height growth, and stem diameter growth formed a separate cluster, also showing positive intercorrelation. These growth- and stress-related traits were generally negatively correlated with the fruit quality cluster, indicating a trade-off between vegetative growth and fruit quality under the tested conditions.

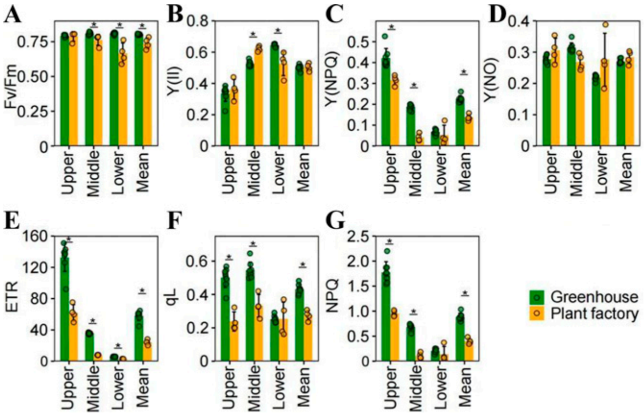

Fig. 3. Tomato photosynthetic efficiency in the greenhouse and plant factory. The parameters were calculated according to the light distribution characteristics in the greenhouse and plant factory. After fitting the light response curve, the chlorophyll fluorescence parameters of tomato leaves at different canopy levels were calculated based on different light intensity levels: in the greenhouse: upper, 888 μmol·m^{-2}·s^{-1}; middle, 154 μmol·m^{-2}·s^{-1}; lower, 24 μmol·m^{-2}·s^{-1}; and in the plant factory: upper, 418 μmol·m^{-2}·s^{-1}; middle, 33 μmol·m^{-2}·s^{-1}; lower 14 μmol·m^{-2}·s^{-1}. ETR = electron transport rate; F_v/F_m = maximum quantum efficiency of PSII; NPQ = nonphotochemical quenching; PSII = Photosystem II; qL = fraction of open PSII reaction centers; Y(II) = effective quantum yield of PSII; Y(NO) = quantum yield of nonregulated energy dissipation; Y(NPQ) = quantum yield of regulated NPQ.

Factors affecting tomatoes' fruit value. To further explore the relationship between environmental and physiological factors and fruit quality in tomatoes, a Mantel test was conducted for both cultivation systems (Fig. 6). The analysis revealed that greenhouse-grown tomatoes exhibited higher overall fruit value compared with those cultivated in the plant factory. Specifically, fruit value was positively correlated with fruit size and the maximum quantum yield of PSII (F_v/F_m), indicating that both fruit development and photosynthetic performance contribute significantly to quality. Conversely, SPAD values were negatively correlated with fruit value, suggesting that excessive chlorophyll content may not necessarily align with optimal fruit quality in this context.

Discussion

The comparative analysis between greenhouse and plant factory cultivation systems underscores the distinct strengths and limitations inherent in each approach (Fig. 7). Greenhouse-grown tomatoes demonstrated enhanced photosynthetic efficiency and superior fruit quality, reflecting the advantages of using natural light conditions and more moderate environmental fluctuations. These traits are particularly beneficial for maximizing resource-use efficiency and achieving high marketable quality. Conversely, plant factory–grown tomatoes exhibited accelerated vegetative growth under precisely controlled environmental settings, highlighting the system's potential for rapid production cycles and year-round cultivation. Although photosynthetic efficiency and yield were lower compared with greenhouse conditions, the plant factory system offers opportunities for tailored nutrient management and consistent production irrespective of external weather conditions. Collectively, these findings emphasize that each system offers unique benefits that can be strategically leveraged depending on production goals—whether emphasizing quality and sustainability in greenhouses or consistency and control in plant factories.

Greenhouse and plant factory influence tomato growth and photosynthetic parameters differently. In this study, tomato plants cultivated in the plant factory exhibited superior vegetative growth, as evidenced by greater increases in plant height and stem diameter compared with those grown in the greenhouse (Fig. 1). This enhanced growth performance is likely attributable to the highly controlled environment of the plant factory, which ensures consistent light exposure, stable temperature, and precise nutrient delivery—

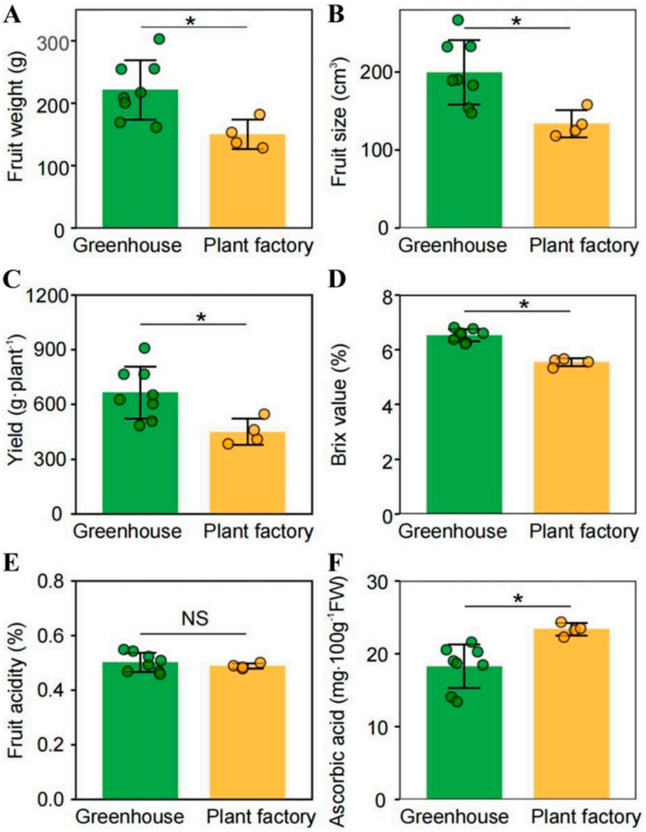

Fig. 4. Tomatoes quality parameters. (**A**) Fruit weight. (**B**) Fruit size. (**C**) Fruit yield. (**D**) Brix value. (**E**) Fruit acidity. (**F**) Fruit ascorbic acid. Asterisks indicate significant difference at $P < 0.05$ level. Fruit size was calculated by the following equation: V (cm^3) = $4\pi/3 \times (L/2)(W/2)(H/2)$, where L indicates length, W indicates width, and H indicates height (Taheri-Garavand et al. 2011). NS = not significant.

conditions known to optimize plant growth (Hayashi et al. 2024; Kozai et al. 2019; Kubota et al. 2012; Li et al. 2025). Meanwhile, despite their slower growth, greenhouse-grown tomatoes demonstrated significantly higher photosynthetic efficiency (Figs. 2 and 3). This was reflected in elevated values of photochemical parameters such as Y(II), ETR, qL, and F_v/F_m under steady light intensities. The superior efficiency observed in greenhouse plants may result from exposure to natural sunlight, which offers a full spectrum of light wavelengths not entirely replicable by artificial lighting (Lanoue et al. 2018; Savvides et al. 2012). Moreover, the dynamic nature of light in greenhouses—characterized by temporal and spatial fluctuations—could promote the development of more responsive and efficient photosynthetic mechanisms (Kaiser et al. 2015; Vialet-Chabrand et al. 2017; Yamori 2016). In contrast, the constant light conditions typical of plant factories, while consistent, may lack the necessary variability to trigger optimal adjustment of the photosynthetic apparatus.

The layered analysis of photosynthesis further underscores the importance of canopy light distribution (Figs. 2 and 3; Supplemental Fig. 1). In both cultivation systems, the upper canopy leaves displayed higher ETR and qL values, indicative of more active photochemistry (Ellsworth and Reich 1993; Lichtenthaler et al. 2007; Niinemets and Kull 2001). Meanwhile, the patterns in NPQ revealed contrasting light-use strategies between the systems (Figs. 2 and 3). In greenhouses, upper leaves had the lowest NPQ and Y(NPQ), suggesting efficient use of available light even at high intensities (Murchie and Niyogi 2011). In contrast, the higher NPQ values in lower canopy leaves indicate an increased reliance on thermal dissipation mechanisms to manage excess light energy (Takahashi and Badger 2011), likely due to inconsistent light penetration in the greenhouse canopy. Conversely, in the plant factory, the lower leaves again exhibited the highest NPQ and Y(NPQ), but surprisingly, middle canopy leaves showed the lowest values (Figs. 2 and 3). This may reflect a more even vertical distribution of light, allowing for reduced light stress on upper leaves and more homogeneous photosynthetic activity throughout the canopy. Additionally, the generally lower need for photoprotective responses in the plant factory could be attributed to its consistent light regime.

Interestingly, greenhouse-grown plants maintained higher F_v/F_m values in the lower canopy (Fig. 3), suggesting sustained photochemical efficiency even in older leaves. This may be due to moderated microclimatic conditions—such as reduced heat stress—within the lower canopy of greenhouse environments (Poorter et al. 2019; Zheng et al. 2020). Conversely, in the plant factory, older leaves had significantly lower F_v/F_m values, potentially resulting from accumulated light stress or less optimal temperature management over time (Joshi et al. 2017; Saengtharatip et al. 2021; Trouwborst et al. 2010; Zhang et al. 2015).

Despite the higher photosynthetic activity observed in greenhouse-grown tomatoes (Figs. 2 and 3), this did not lead to enhanced vegetative growth (Fig. 1). This discrepancy may be attributed to a greater allocation of assimilated carbon toward fruit development and sugar accumulation, rather than to vegetative tissues (Figs. 1 and 4). In contrast, plant factory–grown tomatoes exhibited lower photosynthetic efficiency yet achieved more vigorous growth. This may be due to a shift in carbon allocation away from fruit and sugar production, coupled with the benefits of a controlled environment—such as constant light intensity and optimal temperature—which promoted steady vegetative development (Figs. 1 and 4).

Greenhouse and plant factory influence tomato yield and fruit quality differently. Although improved plant growth serves as a good parameter for our scientific study, it does not necessarily equal with superior fruit quality or yield (Gómez and Mitchell 2015; Poorter et al. 2012). Our results showed that greenhouse cultivated tomatoes generally had higher fruit weight, Brix value, and fruit size compared with those grown in the plant factory (Fig. 4). These fruit quality parameters are crucial for consumer acceptance and market value, with fruit size/weight directly affecting pricing, while Brix (sugar content) is a key determinant of flavor perception (Causse et al. 2010). According to previous studies, the superior fruit value we observed in greenhouses could be possibly attributed to the natural light spectrum and intensity, which may contribute to flavor development and fruit growth (Fanwoua et al. 2012; Ouzounis et al. 2015; Zoratti et al. 2014). As described in previous studies, the difference between day and night temperatures serves as a inducing factor for increased accumulation of sugar and other nutrients in tomato (Yang et al. 2014). It is also possible that the fluctuating environmental conditions in the greenhouse serves as stress signals, which were just enough to stimulate organic material reallocation during the process of fruit development, thereby improving fruit quality. However, interestingly, tomatoes cultivated in the plant factory exhibited higher ascorbic acid concentrations compared with those grown in the greenhouse (Fig. 4). Ascorbic acid is known to accumulate in response to various plant stresses (Ioannidi et al. 2009). Although the upper parts of the plants in the plant factory showed vigorous growth under precisely controlled and seemingly optimal environmental conditions (Figs. 1 and 3), it is possible that the lower canopy received insufficient light, potentially triggering localized stress responses within the plant (Figs. 2 and 3). This internal stress may have contributed to the increased ascorbic acid levels observed in the fruit (Fig. 4). These findings suggest that despite the overall stability of the plant factory environment, its light distribution may not be fully optimized for uniform plant development. Further

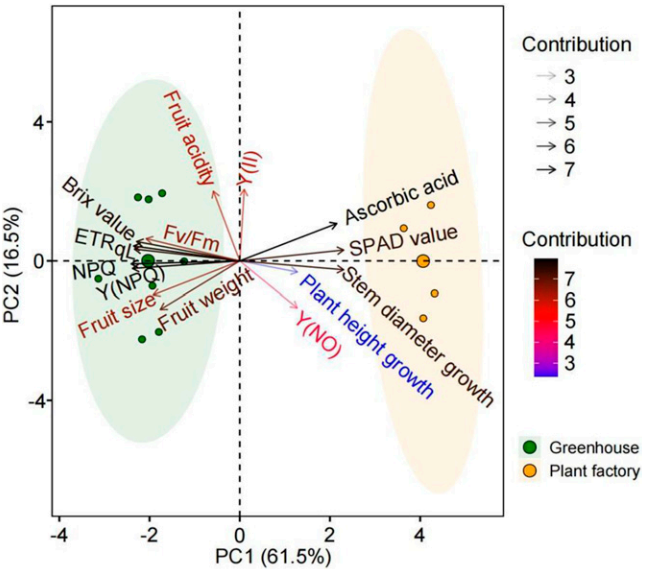

Fig. 5. Principal component analysis of all collected traits. The length and color of a variable vector in the representation space is indicative of the variable's level of contribution. The angles of the arrows indicate the respective strength of the relationship of all variables. Sample points are depicted as green and orange dots, with their proximity indicating similarity in the PC space. The angle between variable vectors reflects the correlation between variables. The smaller the angle, the stronger the positive correlation. An angle close to 90 degrees indicates that the variables are almost uncorrelated, while an angle close to 180 degrees indicates a strong negative correlation. ETR = electron transport rate; F_v/F_m = maximum quantum efficiency of PSII; NPQ = nonphotochemical quenching; PC = principal component; PSII = Photosystem II; SPAD = soil–plant analysis development; qL = fraction of open PSII reaction centers; Y(II) = effective quantum yield of PSII; Y(NO) = quantum yield of nonregulated energy dissipation; Y(NPQ) = quantum yield of regulated NPQ.

studies are warranted to explore improved light delivery strategies in plant factory systems.

Factors affecting tomato fruit value. This study aimed to elucidate the key physiological and morphological factors influencing tomato fruit value, a composite parameter devised to simplify and quantify fruit quality and yield outcomes. Mantel analysis revealed that F_v/F_m, fruit size, and SPAD value were significantly correlated with fruit value (Figs. 5 and 6). Among these, F_v/F_m and fruit size exhibited positive correlations, whereas SPAD value showed a negative correlation (Fig. 6).

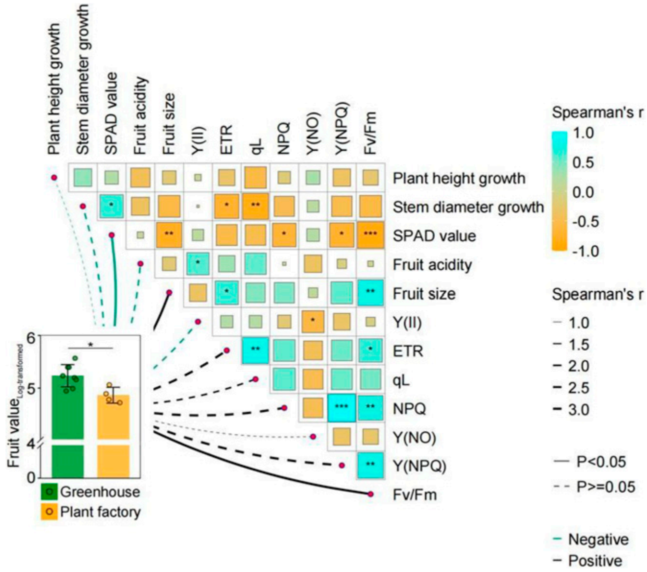

Fig. 6. Mantel test analyzes the factors affecting tomato fruit value. *, **, and *** indicate significant correlation at $P < 0.05$, $P < 0.01$, and $P < 0.001$ level, respectively. Green represents negative correlation, and cyan represents positive correlation. Black lines represent positive correlation, gray lines represent negative correlation, dashed lines represent nonsignificant, and solid lines represent significant ($P < 0.05$). ETR = electron transport rate; F_v/F_m = maximum quantum efficiency of PSII; NPQ = nonphotochemical quenching; PSII = Photosystem II; SPAD = soil–plant analysis development; qL = fraction of open PSII reaction centers; Y(II) = effective quantum yield of PSII; Y(NO) = quantum yield of nonregulated energy dissipation; Y(NPQ) = quantum yield of regulated NPQ.

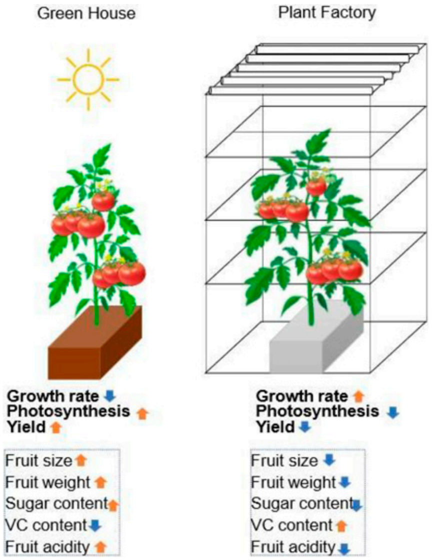

Fig. 7. Conceptual figure of tomato grown in greenhouse and plant factory. VC = ascorbic acid, vitamin C.

In the greenhouse, tomato plants displayed significantly higher F_v/F_m values (Figs. 3 and 6), indicating superior photosynthetic capacity. This enhanced capacity was positively associated with greater fruit weight and elevated Brix values (Fig. 6)—both critical indicators of fruit quality. The higher F_v/F_m likely facilitated more effective carbon assimilation, promoting the accumulation of sugars and other metabolites essential for optimal fruit development (Dorais et al. 2002; Gruda 2005). These findings align with previous reports that link photochemical efficiency with improved fruit metabolic profiles and flavor quality (Fanwoua et al. 2019; Li et al. 2015). Fruit size, another key driver of fruit value identified in the analysis, was also significantly greater in greenhouse-grown tomatoes (Fig. 6). The correlation between fruit size and fruit value reinforces the notion that both metabolic (e.g., sugar accumulation) and morphological traits contribute jointly to overall fruit quality. These results suggest that the higher fruit value observed in greenhouse conditions can be largely attributed to improved photosynthetic performance and increased fruit size (Fig. 6). Conversely, SPAD values—higher in plant factory–grown plants—were negatively correlated with fruit value (Fig. 6). Although SPAD values are commonly used as a proxy for chlorophyll content and potential photosynthetic capacity (Uddling et al. 2007; Xiong et al. 2015), excessive chlorophyll accumulation does not necessarily translate to better fruit quality. This inverse relationship may reflect a physiological trade-off, wherein higher chlorophyll content supports vegetative growth at the expense of reproductive development and metabolic accumulation in fruits. Previous studies have similarly noted that an overemphasis on vegetative vigor can detract from fruit set, sugar loading, and secondary metabolite synthesis (Dorais et al. 2008; Heuvelink 1997; Matsuda et al. 2011). Despite the advantages of the plant factory's controlled environment in promoting rapid vegetative growth, it did not foster equivalent fruit quality. The consistently higher SPAD values and accelerated growth observed in the plant factory were not accompanied by improved F_v/F_m or fruit size. Lower F_v/F_m in this system suggests suboptimal photosynthetic efficiency, potentially due to the spectral limitations of artificial lighting or insufficient light variability. This constraint likely impaired carbon fixation and reduced the synthesis of sugars and flavor-related compounds, culminating in smaller fruits and diminished fruit value.

In conclusion, this study highlights the importance of integrating both physiological efficiency and morphological traits when targeting high-value tomato production. Optimizing F_v/F_m and ensuring sufficient fruit size are key to maximizing fruit value. While greenhouse cultivation naturally supports these conditions through its dynamic light environment and full-spectrum radiation, plant factory systems may require targeted adjustments, such as spectral tuning of LED lights or light regime modifications, to boost photosynthetic efficiency and enhance fruit development. Future research should further investigate the nuanced role of chlorophyll content and its interaction with photosynthesis and carbon allocation, particularly in controlled-environment agriculture.

Optimizing management for improving tomato fruit value. This study successfully demonstrated the feasibility of cultivating large-fruited tomatoes in a fully controlled LED-based plant factory system (Fig. 7). This achievement represents a significant step forward, as fruiting vegetables have traditionally posed challenges for commercial production in plant factories, which have largely focused on leafy greens.

While the stable environmental conditions in the plant factory facilitated rapid vegetative growth (Fig. 1), our findings suggest that such uniformity may limit the plant's ability to optimally allocate resources toward fruit development and quality enhancement. In contrast, moderate environmental fluctuations—such as those observed in greenhouse cultivation (Fig. 1)—were associated with improved fruit yield and quality (Fig. 4). These results highlight the importance of balancing environmental consistency with beneficial variability to stimulate favorable physiological responses in the plant. Rather than aiming for absolute environmental stability, incorporating controlled fluctuations in light intensity and temperature may enhance key fruit quality traits such as sugar accumulation, pigment synthesis, and fruit size. For greenhouse systems, improvements in light distribution and temperature management could enhance the function of lower and older leaves, thereby maintaining high photosynthetic efficiency across the entire canopy (Tewolde et al. 2016, 2018). In plant factory systems, innovations should focus on developing lighting strategies that more closely replicate the spectral composition and diurnal rhythms of natural sunlight (Li et al. 2025). Furthermore, microclimate management—such as regulating leaf temperature in the lower canopy—may help mitigate age-related declines in photosynthetic capacity.

In summary, this study underscores the complementary advantages and limitations of both greenhouse and plant factory systems. Greenhouses leverage natural variability to support photosynthetic optimization and fruit quality, while plant factories provide unparalleled control over growth conditions. Future research should explore hybrid or integrative approaches that combine the strengths of both systems, enabling more sustainable and efficient tomato production with enhanced yield and fruit value.

Conclusions

This study successfully demonstrated that large-fruited tomatoes can be cultivated in an LED-based plant factory system, marking a significant advancement in controlled-environment agriculture. While fruiting vegetables have traditionally been considered difficult to grow in fully enclosed systems, our findings confirm the feasibility of tomato production under tightly controlled conditions.

Tomatoes grown in the plant factory benefited from stable environmental parameters, including consistent temperature and light, which supported rapid vegetative growth, thicker stems, and higher SPAD values. These features highlight the plant factory's potential for efficient biomass production, predictable scheduling, and year-round cultivation, especially in areas with limited arable land or harsh climates. In contrast, greenhouse-grown tomatoes, cultivated under more variable light and temperature conditions, exhibited superior photosynthetic efficiency and produced fruits with higher quality. These advantages were reflected in elevated chlorophyll fluorescence, larger fruit size, increased yield, and higher Brix values, suggesting a more favorable allocation of assimilates toward reproductive organs under naturally fluctuating conditions. Overall, this comparative study underscores the unique strengths and limitations of both systems. Plant factories offer precise control and production stability, while greenhouses leverage natural variability to enhance photosynthetic efficiency and fruit quality. Future strategies should explore hybrid cultivation models that integrate the benefits of both systems to achieve sustainable, high-value tomato production under diverse environmental and economic constraints.

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