HortScience 60(7):1065–1074. 2025. https://doi.org/10.21273/HORTSCI18568-25

Effects of Different Cultivation Facilities and Planting Densities on Tomato Seedling Production

Haoyu Zhang
College of Ecological Technology and Engineering, Shanghai Institute of Technology, Shanghai 201418, China

Chen Miao, Cuifang Zhu, and Xiaotao Ding
Shanghai Key Laboratory of Protected Horticultural Technology, Horticultural Research Institute, Shanghai Academy of Agricultural Sciences, Shanghai 201403, China

Shaojun Yang
Shanghai Youyou Agricultural Technology Co., Ltd., Yuanqu South Road No. 1000, Chongming District, Shanghai 202150, China

Liying Chang
School of Agriculture and Biology, Shanghai Jiao Tong University, Shanghai 200240, China

Yuping Jiang
College of Ecological Technology and Engineering, Shanghai Institute of Technology, Shanghai 201418, China

Keywords. artificial lights, cultivation densities, glasshouses, plant factories, tomato nursery

Abstract. **Plant factories with precise control systems create a stable microenvironment, making them essential for cultivating stronger, more uniform seedlings needed for high-quality production. Among the various factors influencing seedling quality, planting density plays a critical role as a key management practice. To explore this relationship, the combined effects of cultivation facilities and planting densities on tomato (*Solanum lycopersicum* L.) seedlings were investigated in this study. Two facilities were compared: a plant factory with artificial light (PFAL) and a glasshouse with natural light (GHNL). The results revealed that the specific leaf area, health index, ratio of dry weight to fresh weight, and radiation use efficiency (RUE) were predominantly affected by planting density, whereas plant height, leaf area, chlorophyll content, and epicotyl and hypocotyl lengths were mainly influenced by the cultivation facilities. The stem diameter was minimally affected by these conditions. The epicotyl and hypocotyl lengths were significantly greater in the GHNL, while the stem diameter remained unchanged. Seedlings grown in the GHNL had a higher fresh weight, but similar dry weight compared with those grown in the PFAL, with the lowest leaf-to-stem weight ratio observed in the GHNL for both fresh and dry weights. Among treatments, natural light with low planting density (NL, 80 seedlings per tray) produced the highest dry weight, whereas artificial light with high planting density (AH, 240 seedlings per tray) resulted in the lowest. Both the health index and the ratio of dry weight to fresh weight were enhanced with low planting density. The PFAL significantly increased the chlorophyll and carotenoid levels. Furthermore, the RUE of seedlings with high planting density was significantly greater than seedlings with low planting density. The combination of a higher planting density and the PFAL appears to offer certain benefits for seedling production, including graft suitability and production costs.**

Received for publication 10 Mar 2025. Accepted for publication 10 Apr 2025.
Published online 13 Jun 2025.
This research was funded by the Shanghai Agricultural Science and Technology Innovation Project (2024-02-08-00-12-F00001). The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.
H.Z. and C.M. contributed equally to this work.
Y.J. is the corresponding author. E-mail: yupingjiang@sit.edu.cn.

With the rapid development of urbanization, modern cities have reduced agricultural land area and introduced new demands for agriculture, with a particularly significant increase in the year-round demand for fresh produce such as vegetables (Kil et al. 2023). However, traditional agricultural practices often struggle to provide a stable supply throughout the year, especially during winter. As a result, intensive and efficient modern agricultural production has become an inevitable trend (Lambin and Meyfroidt 2011). Among various vegetables, tomatoes are one of the most popular worldwide. According to FAOSTAT data, the cultivated area of tomatoes (*Solanum lycopersicum* L.) globally reached 5,412,458 ha in 2023, representing an increase of 168,357 ha compared with the previous year (https://www.fao.org/faostat). As the cultivated area expands, traditional open-field cultivation faces increasing challenges in providing sufficient high-quality seedlings consistently, which poses new challenges for modern agriculture.

At the same time, global climate change has become increasingly evident, characterized by rising temperatures and reduced precipitation, which have complex effects on tomato growth. On the one hand, higher temperatures may accelerate the growth rate of tomatoes; on the other hand, this acceleration is often accompanied by reduced yields and decreased efficiency in water and nitrogen utilization (Cammarano et al. 2020). In seedling production, temperature is one of the critical environmental factors affecting growth (Niu et al. 2022). Studies have shown that high temperatures reduce photosynthetic performance, decrease chlorophyll content, and accelerate leaf senescence (Twala et al. 2022). Furthermore, urbanization exacerbates the "urban heat island effect," where reduced vegetative cover in and around cities leads to more severe and frequent combined stress from drought and heat (Hao et al. 2018). This phenomenon, along with its derived effects such as heat stress and water deficit, severely impairs the normal growth of tomato seedlings and leads to problems such as overgrowth, weak root systems, and high mortality rates, which are three primary obstacles to tomato seedling production (Bae et al. 2024; Kabano et al. 2021). In recent years, the highest daily temperature in summer in Shanghai often exceeded 40 °C, which is a great challenge for seedling cultivation. The seedlings grown in traditional greenhouses reduced biomass accumulation due to excessive respiration from high temperature and high light intensity, eventually leading to a decrease in yield and quality (Bae et al. 2024). Traditional greenhouses consume a lot of energy in summer temperature control, which was obviously against sustainable agricultural production (Ahmadbeyki et al. 2023). Therefore, in modern agriculture, localized climate control is essential to create optimal growing conditions for crops. The plant factory with artificial light (PFAL) can shield the external environment, which can greatly reduce the temperature control pressure during summer seedling cultivation.

Plant factories are enclosed or semi-enclosed cultivation systems that rely on artificial control to minimize dependence on natural conditions. These systems achieve resource and energy efficiency by recycling water and fertilizers (Montero et al. 2017; Parada et al. 2021), using artificial lighting, and supplementing carbon dioxide (Dannehl et al. 2012; Du et al. 2023). Such features are difficult to achieve in conventional agriculture (Kikuchi et al. 2018; Li et al. 2020; Liu et al. 2016). In recent years, plant factories have become important in the field of plant production, offering more advantages in the field of seedling cultivation. Plant factories use advanced monitoring and regulation systems to maintain optimal growing conditions (Liu et al. 2021). For grafted plants, these systems provide a controlled environment that facilitates healing and recovery (Lang et al. 2020). Light-emitting diodes (LEDs) are widely used in plant factories given their high photo-electric conversion efficiency, adjustability, and compact size (Yeh and Chung 2009). Positioned directly above seedlings, LEDs provide consistent light that promotes uniform growth (Balázs et al. 2023). However, plant factories still lack optimal control strategies tailored to specific crops, which limits their ability to maximize efficiency (Xu et al. 2021). By combining vertical planting, resource recycling, and heat management, plant factories enhance resource use efficiency and reduce their environmental impact (Kikuchi et al. 2018). Moreover, their integration with advanced technologies contributes to urban economic and technological development (Jaeger 2024; Liaros et al. 2016; Van Delden et al. 2021). Grafting is a very important technique in tomato production, which helps to improve water and nutrient uptake and virus resistance (Duan et al. 2024; Morais et al. 2024; Zhou et al. 2022). The PFAL can control the environmental conditions as the requirements of seedlings for grafting to enhance the recovery of grafted seedlings in modern agriculture (Dong et al. 2015). Studies have shown that PFAL has positive effects on the survival rate and energy use efficiency of tomato grafted seedlings (Zheng et al. 2021), so PFAL plays a key role in producing high-quality seedlings that need grafting. In this process, electricity consumption for illumination and temperature control was an important part of the cost and the primary barrier to achieving sustainability (Ahamed et al. 2023; Dauchot et al. 2024). These unique advantages of PFAL can solve the obstacles of traditional greenhouse summer seedlings productions and achieve energy-efficient and cheaper sustainable production. The multilayer structure of a plant factory increases the number of plants per unit area, improves the yield per unit area, and solves the reduction of agricultural land due to urbanization. As a hallmark of modern agriculture, plant factories offer significant development potential.

Planting density significantly affects light interception and competition among plants. Research has shown that planting density influences seedling quality (Wang et al. 2019) but has minimal effect on fruit yield (Rodriguez et al. 2007). Lower planting densities can increase the biomass and leaf area of individual seedlings (Yasutake et al. 2014). In addition, as planting density decreases, the nitrogen content in plants increases while evapotranspiration decreases, leading to greater biomass accumulation (Bates et al. 2019). However, high planting densities often reduce the production of secondary metabolites (Sandhu et al. 2021). Different plant species display varying degrees of sensitivity to planting density (Li et al. 2024; Lichtenthaler et al. 2007; Qiu et al. 2013). For tomatoes grown in greenhouses, total yield increases with plant density up to a certain limit, while yield per plant decreases slightly (Katsoulas et al. 2015; Lichtenthaler et al. 2007). Intensive high-density cultivation has become essential in modern agriculture to meet production demands and conserve land resources, consistent with the goal of increasing production per unit area through multilayer structures. However, most studies on planting density have focused on open-field conditions, with limited attention paid to its effects in plant factories.

Plant factories are important for the production of high-quality seedlings under the impact of global climate change and civilization. Although there is some research on tomatoes, most studies have focused on the reproduction period or fruit production. Studies have rarely focused on the interaction between cultivation facilities and planting density, which both affect seedling quality and subsequent production. As previously mentioned, planting density significantly influences plant growth and production costs by affecting the land area used for cultivation. The plant factory reduces environmental costs and improves land use efficiency. Consequently, it is essential to investigate the combined impact of planting density and plant factory on seedling development to optimize seedling production. However, studies on the influence of planting density on seedling rearing in plant factories are limited. Therefore, this study focused on the interaction between cultivation facilities and planting density, as well as the influence of these two factors on the growth characteristics of tomato seedlings, in order to provide a theoretical basis for improving plant factory seedling cultivation. This research can enrich the related theories of plant factory seedling rearing, guide production practice, improve the production efficiency and quality of summer tomato seedling rearing, and promote the sustainable development of agricultural production.

Materials and Methods

Plant material, growing conditions, and treatments. The experiment was conducted in a solar glasshouse and a PFAL at the Shanghai Youyou Agricultural Technology Co., Ltd. in Chongming District, Shanghai, China (E 121°51′, N 31°34′).

The hybrid tomato cultivar Saopolo (*Solanum lycopersicum* L.), a high-quality cherry tomato variety, was used in the present research. Seeds were sown in 240-hole plug trays (length × width × height = 59 cm × 40.5 cm × 4.8 cm) filled with rock wool (a cylinder with 20 mm diameter and 27 mm height) in Aug 2024, then saturated with nutrient solution, and covered with vermiculite. The seeds germinated in a germination chamber and the daily temperature range was controlled to be 25.5 ± 1.5 °C, and the relative humidity was 100%. After germination, the seedlings were transferred to a PFAL (Shanghai Sansi Electronic Engineering Co., Ltd., Shanghai, China). The LED light tubes had a length of 121.4 cm and a diameter of 3 cm, 25 cm above the tray, each layer had 12 LED light tubes with 20-cm interval (Fig. 1A). The environmental conditions in the plant factory were set as follows: temperatures of 24 to 27 °C, 24-h average temperature of 25.5 °C, relative humidity of 70% to 90%, illumination of 190 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density (PPFD) for 12 h daily before the first true leaf expanded. Once the first true leaf unfolded, the illumination was adjusted to 230 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD for 12 h daily. The LED lighting situation is shown in Fig. 2. The illumination parameters at the plant canopy were measured using a broadband spectroradiometer (specbos 1211, JETI Technische Instrumente GmbH, Jena, Germany) and temperature data were recorded with data loggers DL-W111 (HangZhouGsome Technology Co., Ltd., Hangzhou, China). The environmental parameters of the glasshouse were recorded using the greenhouse management system Priva (Priva, Zijlweg 3, De Lier, Netherlands). Information on electricity consumption was obtained from the partitioned independent electricity meters, and the difference between the meter readings on the day of the start and end of the experiment was the electricity consumption of a certain area.

Half of the seedlings were transferred to a GHNL. The environmental conditions in the glasshouse were as follows: a temperature of 20 to 42 °C, a 24-h average temperature of 27 °C, relative humidity of 70% to 90%, and

Fig. 1. Tomato seedlings grown in the plant factory with artificial light (**A**) and glasshouse with natural light (**B**).

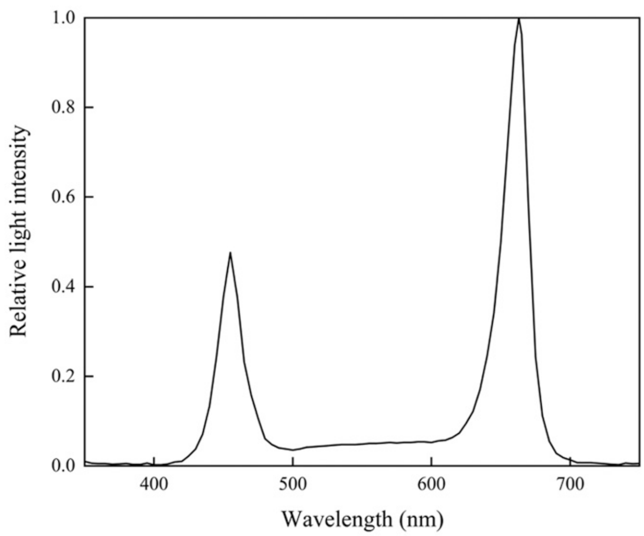

Fig. 2. The spectral relative light intensity composition of the light-emitting diode tube in the plant factory with artificial light measured at the height in the middle of the plant canopy.

light conditions representative of eastern China in August (Fig. 3). When the cooling system was not able to reduce the temperature for adequate tomato seedling growth (very high outside temperature, almost reaching 40 °C in extreme weather), shading curtains were used. Under these conditions, the greenhouse illumination was ~500 to 700 μmol·m^{-2}·s^{-1} PPFD, and the shading curtains were closed between 10:00 AM and 3:00 PM as necessary on sunny days. Solar radiation in the glasshouse was measured in horizontal level at the height of the plant canopy using the LI-250A light meter (LI-COR Biosciences, Lincoln, NE, USA). In both the PFAL and GHNL, trays were irrigated daily using a commercial nutrient solution (composition of nutrient solution stock solution: $Ca(NO_3)_2·4H_2O$, 175 g·L^{-1}; EDTA-Fe, 1.5 g·L^{-1}; KNO_3, 55 g·L^{-1}; KH_2PO_4, 25 g·L^{-1}; K_2SO_4, 10 g·L^{-1}; $MgSO_4·7H_2O$, 60 g·L^{-1}; $MnSO_4·H_2O$, 180 mg·L^{-1}; $ZnSO_4·7H_2O$, 125 mg·L^{-1}; $Na_2B_4O_7·10H_2O$, 240 mg·L^{-1}; $CuSO_4·5H_2O$, 25 mg·L^{-1}; $Na_2MoO_4·2H_2O$, 15 mg·L^{-1}, when using, diluted with water to EC 0.8 dS·m^{-1} before the first true leaf opening, then upgraded to 1.5 dS·m^{-1} until the end of the experiment). The experimental protocol was based on the factorial combination of two facility types (PFAL and GHNL) and two seedling densities (high planting density at 240 seedlings per tray with ~1000 seedlings/m^2 and low planting density at 80 seedlings per tray with ~333 seedlings/m^2). The planting density was consistent with the typical commercial practices in this area. A treatment design was used that included three replicates.

Morphological and physiological parameter measurements. Five samples were selected from the three replicates, and the remaining five samples were measured after the larger and smaller ones were removed. Morphological parameters including plant height, stem diameter, and the length and width of every leaf were measured daily using nondestructive methods after the first true leaf had expanded and the second leaf had appeared on some plants (Katsoulas et al. 2015). The plant height of the shoots was measured from the base of the stem to the peak of the plants, and the stem diameter was measured at 10 mm below the cotyledons. The leaf length was measured from the petiole base to the tip of terminal leaflets, and the distance between two points perpendicular to the blade axis was regarded as the leaf width. When counting leaves, a threshold of 5 mm in unfolded leaf width was used. Seedlings were destructively sampled to measure the leaf area and fresh and dry weights. Seedlings' leaves were flattened with a clear glass plate, and photos were taken vertically. The photographs were processed and analyzed using ImageJ to obtain leaf area data. The fresh weight and dry weight of leaves and stems were measured using an electronic balance.

The specific leaf area (SLA) was determined using the following equation:

$$\mathrm{SLA} = \frac{\text{Leaf area (cm}^{-2})}{\text{Leaf dry weight (g)}} \quad [1]$$

The health index was determined using the following equation (Ding et al. 2023):

$$\text{Health index} = \frac{\text{Stem diameter (mm)}}{\text{Plant height (mm)}} \times \text{Dry weight (g)} \quad [2]$$

The RUE was determined using the following equation (Larsen et al. 2020):

$$\mathrm{RUE} = \frac{(\mathrm{GP}_i - \mathrm{GP}_0) \times \text{Planting density (plants/m}^2)}{\sum_{i=0}^{i} R_i\ (\text{mol·m}^{-2})}, \quad [3]$$

where GP_i is the growth parameter on day i, such as plant height on day i, GP_0 is the growth parameter on day 0, R_i is cumulative radiation from day 1 to day i.

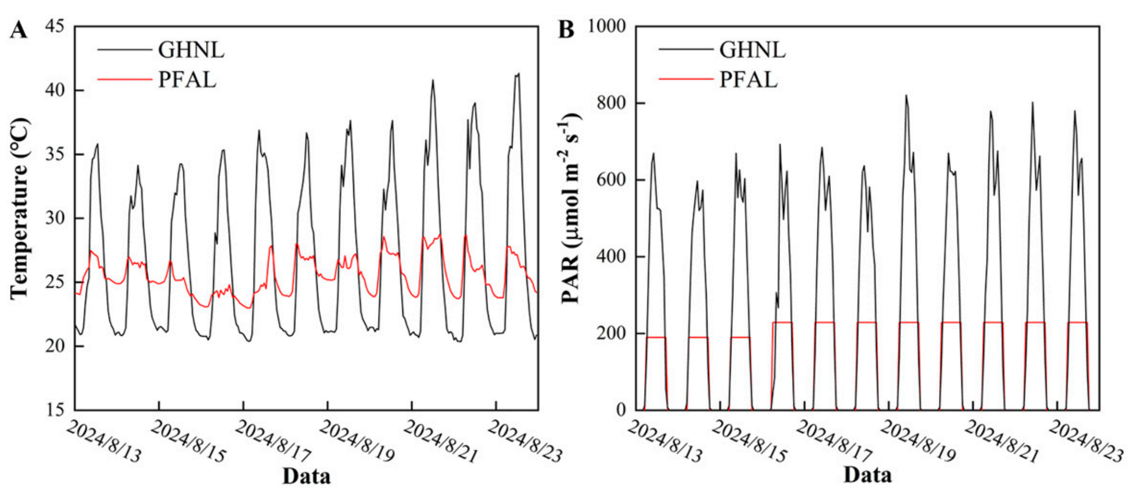

Fig. 3. Temperature (**A**) and radiation (**B**) in the glasshouse with natural light (GHNL) and plant factory with artificial light (PFAL) during the seedling stage. PAR = photosynthetically active radiation.

Pigment measurements. Chlorophyll and carotenoid contents were measured using the absorbance method. Briefly, 0.1 g of the largest leaf without veins was taken and its area was measured. Shredded leaf samples were stored in ethyl alcohol (95%) and kept in the dark until they were completely discolored. The ethanol solutions were filtered into a volumetric bottle, and the volume was increased to 25 mL. Absorbance was measured at 470, 649, and 665 nm to measure the chlorophyll a, chlorophyll b, and carotenoid contents, respectively. The chlorophyll a, chlorophyll b, and carotenoid contents were calculated using the equations below:

$$C_a = 13.95A_{665} - 6.88A_{649} \quad [4]$$

$$C_b = 24.96A_{649} - 7.32A_{665} \quad [5]$$

$$C_c = \frac{1000A_{470} - 2.05C_a - 114.8C_b}{245} \quad [6]$$

$$C_{ps} = \frac{C \times V \times N}{S}, \quad [7]$$

where C_a, C_b, and C_c are concentrations ($mg{\cdot}L^{-1}$) of chlorophyll a, chlorophyll b, and carotenoid in the extract, respectively, and A665, A649, and A470 are absorbances at 665, 649, and 470 nm wavelength, respectively. C_{ps} is the content ($\mu g{\cdot}cm^{-2}$) of certain pigment per unit area of leaves, C is the concentration of pigment in the extract, V is the volume (mL) of extract, N is the dilution ratio, and S is the area (cm^2) of the sample.

Statistical analysis. The results were statistically analyzed using analysis of variance with SPSS software version 19.0 (SPSS Inc., Chicago, IL, USA), and differences between means were tested using Duncan's multiple range test ($P < 0.05$). Data are represented as the means ± standard deviation (n = 5 replicates). All graphs were generated using Origin 2018 (OriginLab Corporation, Northampton, MA, USA).

Results

Temperature and radiation parameters. Temperature and radiation are important factors affecting plant growth. In this study, data for both factors were recorded in 5-min increments using sensors at the same height as the seedling. As shown in Fig. 3, temperature and radiation both had a larger variation range in the GHNL than the PFAL. Extremely elevated temperatures above 40 °C were also observed in the GHNL in a narrow time window from 11:00 AM to 1:00 PM when vertical sunlight was dominant. The temperature and radiation were not always synchronous and acutely changed due to variations in weather and glasshouse conditions. The PFAL data were relatively stable. The temperature was consistently around 25 °C, and the radiation was almost consistent during the daytime (Fig. 3). The radiation in the GHNL was significantly higher than that in the PFAL. After 10:00 AM, the curtains were closed to avoid the high temperature caused by the excessive light intensity in the greenhouse, so the radiation intensity suddenly decreased after this point. The illumination period that can satisfy seedling growth, was similar in both the GHNL and PFAL, ∼12 h, with the GHNL exhibiting significantly higher radiation intensity compared with the PFAL (Fig. 3B).

Morphology and growth characteristics. To evaluate the effects of different cultivation facilities and different planting densities on the morphology of tomato seedlings, we photographed seedlings 10 d after treatment. The differences were comprehensively displayed from horizontal- and top-view perspectives. As shown in Fig. 4, planting density had different effects on seedlings in different cultivation facilities. In addition, the stems and leaves of seedlings grown in the GHNL were a lighter green than those of seedlings grown in the PFAL. Although the relationship between planting density and seedling growth in the PFAL was not readily apparent, seedlings grown in the GHNL under low planting density exhibited larger leaves and stronger shoots compared with those grown under high planting density (Fig. 4).

As shown in Fig. 5, the leaf area was mainly affected by growing conditions, whereas the SLA was mainly affected by planting density. Plant height in the PFAL was relatively unaffected by planting density, whereas seedlings in the GHNL exhibited large differences between planting densities. However, the stem diameter remained similar regardless of growing conditions and planting densities. Specifically, plant heights of seedlings grown under NH and natural light (NL) conditions increased by more than 95% and 45%, respectively, compared with those grown in the PFAL. High planting density in the GHNL resulted in taller seedlings (Fig. 5A). The average daily growth rates of plant height over the whole cycle for NH, NL, AH, and artificial light (AL) were 13.89 ± 0.53 mm/d, 9.5 ± 0.59 mm/d, 5.63 ± 0.33 mm/d, and 5.87 ± 0.26 mm/d, respectively. The difference in stem diameter was not obvious among the four treatments (Fig. 5B). Overall, a linear increase in plant height and stem diameter was noted regardless of treatment (Fig. 5A and B). The characteristics of leaf area and SLA are presented in Fig. 5C and D, seedlings grown in the GHNL exhibited larger leaf areas compared with those grown in the PFAL (Fig. 5C). Exponential growth was shown in the leaf area growth process (Fig. 5C). The SLA demonstrated characteristics dependent on planting density rather than environmental conditions (Fig. 5D). Specifically, the SLA of seedlings at high planting density on 10 DAT (days after treatment) was similar to that before treatment. In contrast, seedlings grown at low planting density exhibited a general trend with a greater than 20% reduction in SLA over the same period (Fig. 5D). In summary, the cultivation facilities had distinct effects on different morphological and growth parameters of the seedlings, and the influence of planting density on plant height was strongly dependent on the cultivation facilities.

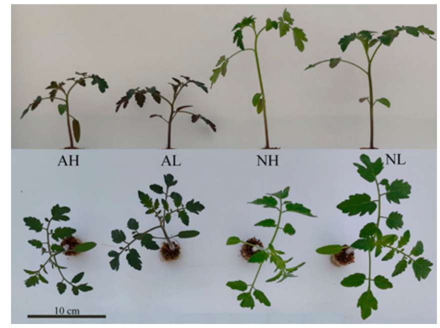

Fig. 4. Photographs of tomato seedlings grown in the plant factory with artificial light (PFNL) and glasshouse with natural light (GHNL). Photograph showing 10 d after treatment. AH = PFAL with high planting density; AL = PFAL with low planting density; NH = GHNL with high planting density; NL = GHNL with low planting density.

Epicotyl and hypocotyl lengths and diameters. The epicotyl and hypocotyl are critical regions for grafting; thus, we studied the effects of different growing conditions and densities on the embryonic axis. Differences between the epicotyl and hypocotyl shown in Fig. 6 indicate that the cultivation facilities and density significantly affect epicotyl diameter but not hypocotyls. In terms of embryonic axis length, seedlings in the PFAL were more similar, while those grown in the GHNL were more affected by planting density (Fig. 6). Although the hypocotyl diameters did not significantly differ under the four environmental conditions, the epicotyl diameter exhibited directional characteristics such that a lower planting density and solar glasshouse conditions both thickened the epicotyl (Fig. 6A). Interestingly, the epicotyl diameter of seedlings in the PFAL was thinner than the corresponding hypocotyl diameter, whereas it was similar to seedlings grown in the GHNL (Fig. 6A). Regarding stem length, seedlings grown in the PFAL showed consistency irrespective of planting density, whereas significant differences were observed in seedlings grown in GHNL (Fig. 6B). The epicotyl length, hypocotyl length, and plant height of NH were all significantly greater than the others (Fig. 6B). In addition, all stem segments of seedlings grown in the GHNL were longer than those of seedlings grown in the PFAL (Fig. 6B). The length of the epicotyl is markedly shorter than that of the hypocotyl, with the exception of NH, which exhibits a nearly equivalent length (Fig. 6B). In conclusion, the cultivation facilities significantly influenced epicotyl diameter but not hypocotyl diameter. Furthermore, the PFAL demonstrated a positive effect in maintaining consistent epicotyl and hypocotyl lengths across different planting densities.

Biomass and health index. Fresh and dry weights, along with their distribution, are important indicators of seedling quality. Both the cultivation facilities and planting density significantly affected dry and fresh weights,

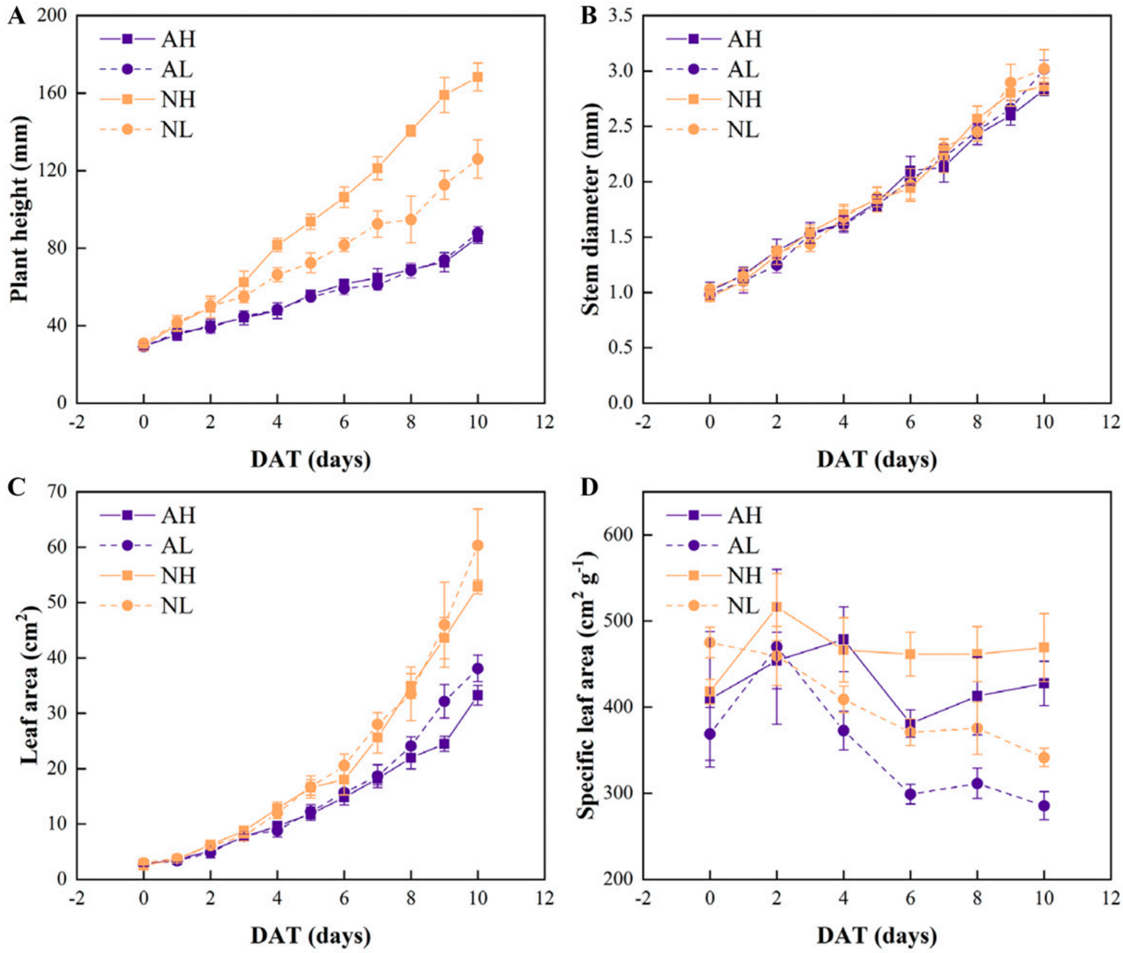

Fig. 5. Plant height (**A**), stem diameter (**B**), leaf area (**C**), and specific leaf area (**D**) of the seedlings over time. DAT = days after treatment; AH = plant factory with artificial light (PFAL) with high planting density; AL = PFAL with low planting density; NH = glasshouse with natural light (GHNL) with high planting density; NL = GHNL with low planting density. Vertical bars represent standard deviations.

as well as biomass allocation. In terms of shoot fresh weight, seedlings grown in the PFAL exhibited significantly lower values than those grown in the GHNL. High planting density significantly inhibited the fresh weight of seedling shoots in the PFAL. This was also reflected in the fresh weight of leaves (Fig. 7A). The fresh weight of seedling stems in the GHNL exhibited a significant increase compared with seedlings grown in the PFAL (Fig. 7A). Regarding dry weight, seedlings grown under AL and NH conditions exhibited similar shoot dry weight, but the stem dry weight of seedlings grown under NH conditions significantly increased compared with seedlings grown under AL conditions (Fig. 7B). The total shoot dry weight of seedlings grown under NL conditions exhibited a remarkable increase among the four treatments (Fig. 7B). Seedlings grown in the PFAL had the highest leaf-to-stem ratios for both fresh and dry weights, whereas those grown under NH conditions had the lowest leaf-to-stem ratio (Fig. 7). In summary, GHNL and low planting density promoted biomass accumulation, whereas PFAL increased the leaf-to-stem ratio for both fresh and dry weights. Notably, the ratio of dry weight to fresh weight in seedlings grown at low planting density exceeded 10%, whereas the ratio of dry weight to fresh weight of seedlings grown at high planting density were lower than 10% (Fig. 8). In addition, the health index of seedlings grown at low planting density was significantly higher than that of seedlings grown at high planting density, with similar values observed for both greenhouse and plant factory conditions (Fig. 8). These results indicated that the cultivation facilities and planting density both affect the biomass distribution and water content in the leaf and stem. The application of the PFAL enhanced the ratio of leaf biomass to stem biomass, whereas low planting density improved the ratio of dry weight to fresh weight.

Chlorophyll and carotenoid content. Based on actual observations as well as photographs shown in Fig. 4, we observed a large variation in seedling color. Significant interactions were observed between chlorophyll and carotenoid content and cultivation conditions by measuring the content of pigments. The chlorophyll and carotenoid contents were only related to the cultivation facilities. The seedlings grown in the PFAL had significantly higher chlorophyll and carotenoid levels, and these levels were independent of planting density (Fig. 9A). Low planting density increased the ratio of chlorophyll a/b in plants grown in both the PFAL and GHNL and seedlings grown in the PFAL had a significantly higher ratio of total chlorophyll content to carotenoid content compared with those grown in the GHNL (Fig. 9B). The results indicated that the seedlings cultivated in the PFAL had higher chlorophyll and carotenoid levels.

RUE of tomato seedlings. To evaluate RUE, the increase in specific parameters per unit of radiation was calculated. The results are presented in Table 1. Although certain morphological and physiological parameters of seedlings grown in the GHNL were significantly increased, the RUE characteristics exhibited an opposite situation due to the low radiation of the PFAL. In general, the high-density planting group exhibited higher RUE. The AH demonstrated superior RUE across most parameters, except for plant height. Specifically, the efficiency of plant height in the NH was significantly higher than that of other treatments. Although no significant difference was observed in the light utilization efficiency of fresh weight between the AH and NH groups, the dry weight efficiency in the AH group was significantly

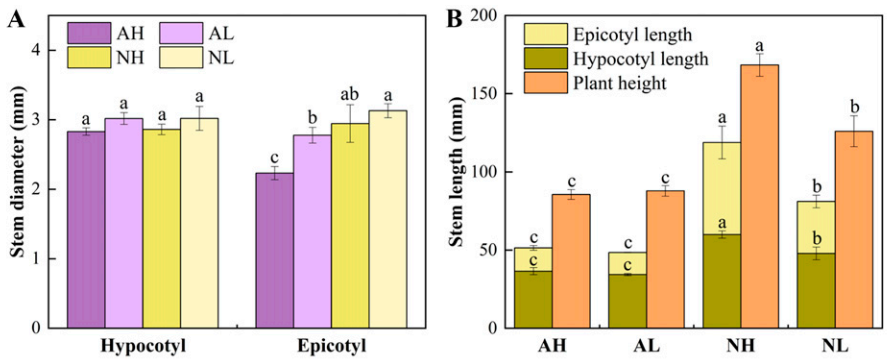

Fig. 6. Epicotyl and hypocotyl diameter (**A**) and length (**B**) of stems of seedlings grown under different cultivation facilities. AH = plant factory with artificial light (PFAL) with high planting density; AL = PFAL with low planting density; NH = glasshouse with natural light (GHNL) with high planting density; NL = GHNL with low planting density. Vertical bars represent standard deviations. Different letters indicate statistical significance at the $P < 0.05$ level (n = 5).

higher (Table 1). When comparing the two factors, high-density planting demonstrated clear advantages in enhancing RUE.

Electricity consumption. Electricity was the largest component of energy consumption in summer seedling production, primarily used for cooling and lighting, and its cost largely determined the total cost. The electricity consumption per unit area in PFAL was higher than in GHNL, as the PFAL needs extra electricity for lighting compared with GHNL. However, the vertical multistory structure of plant factories allows more plants per unit area of land; in addition, PFAL is isolated from the outside environment to reduce the pressure of temperature control, and the internal LED lighting produces less heat, so the electricity consumption per plant was less than that of GHNL. Higher planting density clearly reduced electricity consumption per plant, indicating that high-density intensive production is energy-efficient and cost-effective. NH consumed 3.5 times more energy than AH, whereas NL used 10 times more (Fig. 10).

Discussion

Tomato seedlings, like most crops, have a comprehensive set of environmental requirements. Therefore, the quality of seedlings cannot be improved when certain environmental parameters are unsuitable. High-quality seedlings can be consistently produced only in growth environments with optimal conditions (He et al. 2022).

The results of this study demonstrated that the cultivation facilities, planting density, and their interaction significantly influenced tomato seedling growth. Although seedlings cultivated in GHNL at high density exhibited greater height and larger shoots (Figs. 4 and 5), they did not fulfill the criteria for high-quality nursery seedlings. This was due to the stems of overgrown seedlings exhibiting reduced mechanical strength (Figs. 7B and 8B), which ultimately led to lower yields (Wu et al. 2023) and diminished resistance to insects and pathogens (Qin et al. 2023). The results in Fig. 5 show that the morphological characteristics of seedlings were affected by planting facilities and planting density. This finding indicates that altering planting facility and planting density can meaningfully change plant morphology. In this study, the average temperatures in two types of plant environments were similar; however, temperatures above 34 °C were recorded almost daily at noon in the GHNL (Fig. 3A). This consistent exposure to elevated temperatures may contribute to overgrowth (Kim et al. 2023). Notably, seedlings in the GHNL with low planting density exhibited both the largest canopy size and the highest health index (Figs. 4 and 8), indicating superior seedling quality, but it had lower chlorophyll and carotenoid contents compared with seedlings in the PFAL (Fig. 9A). It should be noted that these advantages pertain specifically to seedlings that do not require grafting; this section will be covered later. Conversely, high planting density has been shown to enhance auxin and cytokinin biosynthesis, thereby promoting stem growth (Küpers et al. 2023). This phenomenon may partially explain the increased performance of seedlings grown in the GHNL under conditions of low planting density.

The findings of this study indicate that the canopy volume of tomato seedlings cultivated at high planting densities was relatively substantial for the given plant density, resulting in contact with and compression of the leaves of neighboring seedlings. Previous research has demonstrated that such contact could lead to a reduction in leaf enzymatic activity and photosynthetic capacity (Li et al. 2019). In addition, the shading and alteration of the light spectrum caused by the canopies of adjacent seedlings can modify the content and distribution of leaf hormones, further affecting leaf growth (Küpers et al. 2023). Conversely, lower planting densities have been shown to enhance leaf expansion and decrease SLA (Fig. 5), indicating a thickening of the leaf and an increase in biomass per unit leaf area; a higher SLA is associated with improved light interception capacity (Yao et al. 2016). When analyzed in conjunction with environmental parameters (Fig. 3), it appears that the morphological characteristics were primarily influenced by temperature conditions, whereas the physiological characteristics were predominantly affected by the radiation captured by the leaf surface. Furthermore, high planting density significantly inhibited plant biomass, irrespective of whether the seedlings were grown in the GHNL or PFAL (Fig. 7) but increased the

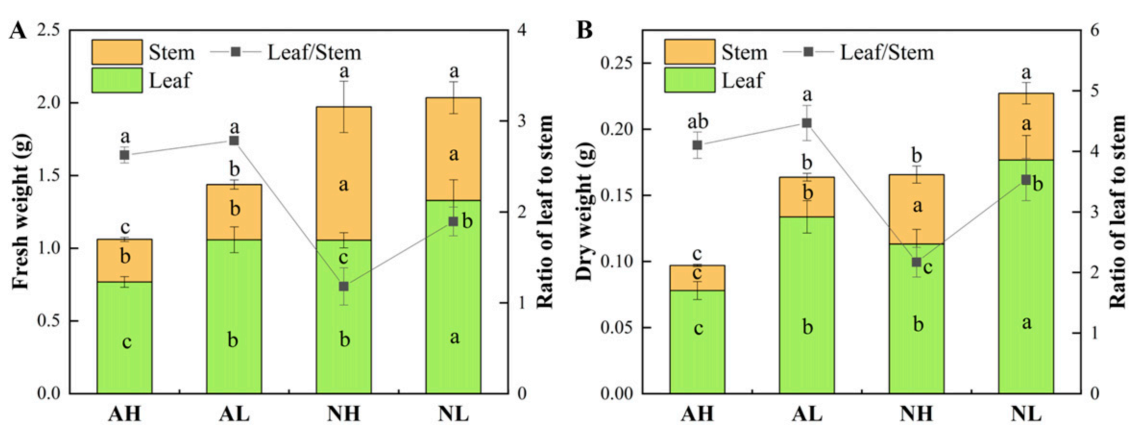

Fig. 7. Fresh weight (**A**), dry weight (**B**), and leaf-to-stem ratio of seedlings grown in different cultivation facilities. AH = plant factory with artificial light (PFAL) with high planting density; AL = PFAL with low planting density; NH = glasshouse with natural light (GHNL) with high planting density; NL = GHNL with low planting density. Vertical bars represent standard deviations. Different letters indicate statistical significance at the $P < 0.05$ level (n = 5).

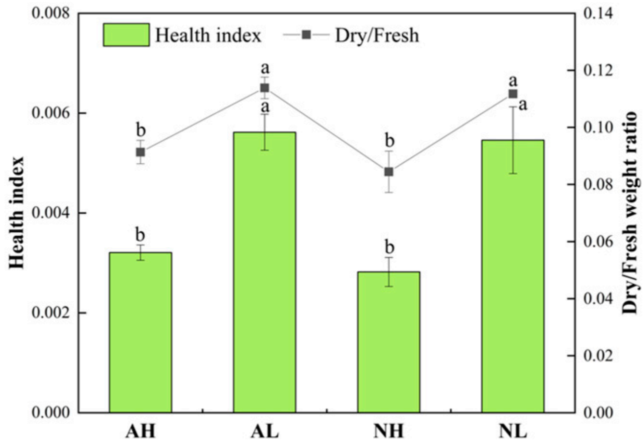

Fig. 8. Health index and dry weight to fresh weight ratio of seedlings grown in different cultivation facilities. AH = plant factory with artificial light (PFAL) with high planting density; AL = PFAL with low planting density; NH = glasshouse with natural light (GHNL) with high planting density; NL = GHNL with low planting density. Vertical bars represent standard deviations. Different letters indicate statistical significance at the $P < 0.05$ level (n = 5).

total biomass of a tray, corroborating findings from other studies (Yan et al. 2024). This finding is contrary to the requirements for high-quality seedlings.

In plant factories, temperature and light conditions can be artificially controlled, ensuring consistent and uniform production during the critical seedling phase, even under unfavorable weather conditions (Zhou et al. 2022). In addition, plant factories can even fulfill specific requirements such as temperature inversion (Kim et al. 2023). A significant distinction in illumination between the PFAL and GHNL is the provision of constant light in the PFAL. In contrast, the movement of the sun reduced the light energy captured by individual leaves compared with global horizontal radiation (Burgess and Cardoso 2023). For seedlings cultivated in the PFAL, the lighting conditions remain stable throughout the photoperiod. Consequently, the PFAL facilitates uniformed plant growth by comprehensively regulating temperature and light, thereby mitigating the adverse effects associated with high planting density, such as overgrowth and shading. The primary advantage of the PFAL includes its ability to produce relatively high-quality seedlings at high planting densities while disregarding external weather conditions, thereby enhancing land use efficiency and energy saving (Kikuchi et al. 2018). However, the initial investment required to build plant factories along with the energy cost during operation, is difficult for most small and medium-sized agricultural producers to afford. Government subsidies may be necessary to promote plant factories and improve local production capacity and competitiveness of agricultural products.

According to Fig. 9, seedlings grown in the PFAL had higher chlorophyll and carotenoid levels. In addition, different planting densities did not affect these levels. The ratios of chlorophyll a/b and the ratio of chlorophyll to carotene were significantly influenced by planting density and cultivation facilities. The PFAL was characterized by lower radiation and temperature levels in comparison with the GHNL. Elevated temperatures reduced chlorophyll a and b concentrations as well as the chlorophyll to carotene ratio (Feng et al. 2014). Conversely, higher light intensity enhanced the chlorophyll a/b ratio (Faik et al. 2016), while shading caused by higher planting density increased the chlorophyll content per unit area of leaves. This has also been observed in other plant species (Lichtenthaler et al. 2007; Song and Li 2016). The higher proportion of blue light in plant factories promotes chlorophyll synthesis (Liang et al. 2021). Under the combined action of factors such as temperature and light, seedlings in plant factories have higher chlorophyll content. Plants with higher levels of photosynthetic pigments exhibited stronger biomass production capacity, as reflected in other studies (Chen et al. 2024; Marković et al. 2021).

Many crops require grafting to enhance nutrition absorption, stress tolerance, and yields; this is also true for tomatoes. In plant factories, light, temperature, humidity, and fertilizer are regulated to benefit grafting (Lang et al. 2020). Seedlings cultivated in the GHNL exhibited a relatively thicker epicotyl, which may hinder a secure fit with the stems of rootstocks, thereby presenting challenges for grafting as observed in practical applications (Fig. 6). In the PFAL seedlings, the larger difference in the diameters of the hypocotyl and epicotyl and the shorter epicotyl may also cause some difficulties in grafting. Thus, for grafting, a combination of the PFAL and GHNL might produce better results; however, this needs to be further studied. In addition, GHNL seedlings demonstrated a larger canopy, and their morphology varied significantly when subjected to different planting densities (Fig. 4). Seedlings characterized by excessively large leaves or an abundance of leaves were more prone to developing aerial roots, which negatively impacts seedling quality (Meyer et al. 2017). Moreover, variations in the conditions of the scion complicate large-scale grafting efforts, rendering GHNL seedlings unsuitable for this purpose.

Light and temperature conditions are often considered critical environmental factors influencing plant growth (Li et al. 2022; Song et al. 2022; Wang et al. 2024). Some researchers have described plant growth based on the product of thermal energy obtained from the average temperature and accumulative radiation (Hang et al. 2019; Yan et al. 2023; Zhou et al. 2019). Despite the significant differences in temperature and radiation between two distinct cultivation facilities, morphological and physiological parameters did not exhibit large disparities. According to the RUE of specific parameters (Table 1), seedlings grown in the AH demonstrated notably high efficiencies in most parameters and high-density planting demonstrated clear advantages in enhancing RUE. The optimal temperature range for tomato cultivation was reported to be between 15 and 32 °C (Lu et al. 2017); however, the temperatures of GHNL exceeded this optimal range (Fig. 3A), mainly because of the high radiation and outside temperature. Thus, the grower needs to use a shading curtain and cooling system

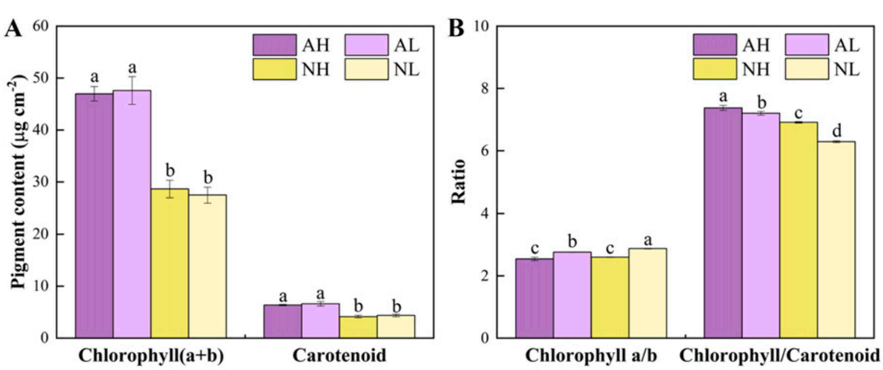

Fig. 9. Chlorophyll and carotenoid contents (**A**) and their ratios (**B**) in seedlings grown in different cultivation facilities. AH = plant factory with artificial light (PFAL) with high planting density; AL = PFAL with low planting density; NH = glasshouse with natural light (GHNL) with high planting density; NL = GHNL with low planting density. Vertical bars represent standard deviations. Different letters indicate statistical significance at the $P < 0.05$ level (n = 5).

Table 1. Radiation use efficiency of plant height, leaf length, and fresh and dry weight.

Treatment	Plant ht ($cm\cdot mol^{-1}$)	Leaf length ($cm\cdot mol^{-1}$)	Leaf area ($cm^2\cdot mol^{-1}$)	Shoot fresh wt ($g\cdot mol^{-1}$)	Shoot dry wt ($g\cdot mol^{-1}$)
AH	59.64 ± 3.85 b	219.75 ± 12.14 a	346.38 ± 23.83 a	11.07 ± 0.67 a	1.00 ± 0.097 a
AL	20.16 ± 2.05 c	89.56 ± 4.41 c	135.12 ± 9.12 c	5.14 ± 0.51 b	0.59 ± 0.055 c
NH	70.92 ± 4.38 a	136.79 ± 8.95 b	275.03 ± 7.07 b	10.38 ± 1.22 a	0.87 ± 0.085 b
NL	15.45 ± 1.42 c	49.53 ± 2.77 d	104.84 ± 12.12 d	3.56 ± 0.46 c	0.40 ± 0.047 d

Note: Different letters indicate statistical significance at the $P < 0.05$ level (n = 5). AH = plant factory with artificial light (PFAL) with high planting density; AL = PFAL with low planting density; NH = glasshouse with natural light (GHNL) with high planting density; NL = GHNL with low planting density.

(air-conditioning system and high-pressure water mist) to cool the greenhouse. In addition, the shading curtain and high temperature decreased the RUE for tomato seedlings grown in the GHNL. The heat increases the activity of whiteflies, which spreads the yellow leaf curl virus that wreaks havoc on tomato production (Wang et al. 2022; Yan et al. 2021), potentially leading to detrimental effects on seedling growth. Consequently, producers were compelled to allocate substantial resources and funding to regulate environmental conditions, representing a significant expense associated with model greenhouses. In contrast, PFAL systems offer distinct advantages in this context (Graamans et al. 2018). Figure 10 illustrates the power savings advantage of PFAL. Although the electricity consumption per unit area of PFAL was higher, the electricity consumption per plant was decreased, as vertical multilayer planting reduces the land area and coupled with the enclosed environment, reduces the electricity consumption per plant. Although the greenhouse has a large space with intense radiation heat effects and single layer cultivation, resulting in significant cooling demands and high electrical energy consumption per plant.

Decreasing planting density might enhance seedling quality; however, this approach might lead to an expansion of the site area, resulting in elevated land, management, and energy costs associated with environmental control. In addition, a separate study conducted by Deng et al. (2012) suggested that the limitations imposed by planting density were less obvious at the seedling stage. Consequently, the advantages of reduced planting density might not outweigh these increased expenses. Furthermore, the results indicated that the influence of planting density on seedlings grown in the PFAL was minimal. In addition to the advantages of seedlings cultivation in the PFAL for grafting and electricity saving, a combination of higher planting density and growth in the PFAL appears to offer certain benefits in the context of seedling nurseries.

This study focused on soilless cultivation in modern glasshouses and plant factories. However, a significant proportion of traditional soil-based plastic film greenhouse cultivation and field cultivation systems exist that lack multiple environmental control methods. In addition, the light conditions differ due to the variations in coverage. Therefore, the results of this study may not be applicable to these situations but can be used as a reference for seedling cultivation. Further research is needed to explore the applicability and specificity of these findings under other cultivation conditions.

Conclusions

This study demonstrated that planting density significantly influenced the morphological and physiological parameters of tomato seedlings. A low planting density notably enhanced canopy growth, particularly under GHNL conditions, and significantly enhanced dry weight accumulation. Due to high temperature, seedlings cultivated in the GHNL were taller and had larger leaves compared with those in the PFAL; moreover, they contained lower levels of chlorophyll and carotenoid content and exhibited reduced RUE. In contrast, seedlings grown in PFAL were characterized by higher chlorophyll and carotenoid content, greater RUE, and a more uniform morphology, making them particularly suitable for tomatoes requiring grafting. These findings highlight the importance of optimizing planting density and environmental conditions for improving seedling production. From the perspective of tomato seedling production, introducing plant factories into modern greenhouse cultivation can lead to higher-quality seedlings and more energy-efficient, sustainable production. The combination of high planting density and the use of plant factories potentially represents a better choice for tomato seedling production.

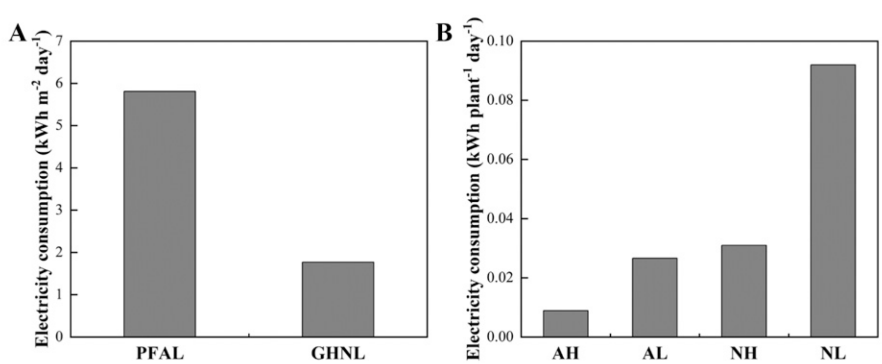

Fig. 10. Electricity consumption per unit area (**A**) and per plant (**B**) of seedlings grown in different cultivation facilities. AH = plant factory with artificial light (PFAL) with high planting density; AL = PFAL with low planting density; NH = glasshouse with natural light (GHNL) with high planting density; NL = GHNL with low planting density.

References Cited

Ahamed MS, Sultan M, Monfet D, Rahman MS, Zhang Y, Zahid A, Bilal M, Ahsan TMA, Achour YA. 2023. Critical review on efficient thermal environment controls in indoor vertical farming. J Clean Prod. 425:138923. https://doi.org/10.1016/j.jclepro.2023.138923.

Ahmadbeyki A, Ghahderijani M, Borghaee A, Bakhoda H. 2023. Energy use and environmental impacts analysis of greenhouse crops production using life cycle assessment approach: A case study of cucumber and tomato from Tehran province, Iran. Energy Reports. 9:988–999. https://doi.org/10.1016/j.egyr.2022.11.205.

Bae HJ, Kim SH, Jeong Y, Park S, Ochar K, Hong Y, Seo YA, Ko B, Bae JH, Lee DS, Choi I. 2024. Optimal planting time for summer tomatoes (*Lycopersicon esculentum* Mill.) cropping in Korea: Growth, yield, and photosynthetic efficiency in a semi-closed greenhouse. Plants. 13(15):2116. https://doi.org/10.3390/plants13152116.

Balázs L, Kovács GP, Gyuricza C, Piroska P, Tarnawa Á, Kende Z. 2023. Quantifying the effect of light intensity uniformity on the crop yield by pea microgreens growth experiments. Horticulturae. 9(11):1187. https://doi.org/10.3390/horticulturae9111187.

Bates GM, McNulty SK, Amstutz ND, Pool VK, Cornish K. 2019. Planting density and growth cycle affect actual and potential latex and rubber yields in Taraxacum kok-saghyz. HortScience. 54(8):1338–1344. https://doi.org/10.21273/HORTSCI13986-19.

Burgess AJ, Cardoso AA. 2023. Throwing shade: Limitations to photosynthesis at high planting densities and how to overcome them. Plant Physiol. 191(2):825–827. https://doi.org/10.1093/plphys/kiac567.

Cammarano D, Ronga D, Di Mola I, Mori M, Parisi M. 2020. Impact of climate change on water and nitrogen use efficiencies of processing tomato cultivated in Italy. Agr Water Manage. 241:106336. https://doi.org/10.1016/j.agwat.2020.106336.

Chen R, Chen Y, Lin K, Ding Y, Liu W, Wang S. 2024. Growth, quality, and nitrogen metabolism of *Medicago sativa* under continuous light from red–blue–green LEDs responded better to high nitrogen concentrations than under red–blue LEDs. Int J Mol Sci. 25(23):13116. https://doi.org/10.3390/ijms252313116.

Dannehl D, Huber C, Rocksch T, Huyskens-Keil S, Schmidt U. 2012. Interactions between changing climate conditions in a semi-closed greenhouse and plant development, fruit yield, and health-promoting plant compounds of tomatoes. Sci Hortic Amsterdam. 138:235–243. https://doi.org/10.1016/j.scienta.2012.02.022.

Dauchot G, Aubry C, Crème A, Dorr E, Gabrielle B. 2024. Energy consumption as the main challenge faced by indoor farming to shorten supply chains. CLCB. 9:100127. https://doi.org/10.1016/j.clcb.2024.100127.

Deng J, Ran J, Wang Z, Fan Z, Wang G, Ji M, Liu J, Wang Y, Liu J, Brown JH. 2012. Models and tests of optimal density and maximal yield for crop plants. Proc Natl Acad Sci USA. 109(39):15823–15828. https://doi.org/10.1073/pnas.1210955109.

Ding X, Miao C, Li R, He L, Zhang H, Jin H, Cui J, Wang H, Zhang Y, Lu P, Zou J, Yu J, Jiang Y, Zhou Q. 2023. Artificial light for improving tomato recovery following grafting: Transcriptome and physiological analyses. Int J Mol Sci. 24(21):15928. https://doi.org/10.3390/ijms242115928.

Du B, Shukla MK, Yang X, Du T. 2023. Enhanced fruit yield and quality of tomato by photosynthetic bacteria and CO_2 enrichment under reduced irrigation. Agr Water Manage. 277:108106. https://doi.org/10.1016/j.agwat.2022.108106.

Duan Y, Zhang F, Meng X, Shang Q. 2024. Spatio-temporal dynamics of phytohormones in the tomato graft healing process. Hortic Plant J. 10(6):1362–1370. https://doi.org/10.1016/j.hpj.2022.11.014.

Dong W, Zhou ZC, Bu YL, Zhuo JQ, Chen LZ, Li YZ. 2015. Research and application of grafted seedlings healing room. Acta Hortic. 1056:51–57. https://doi.org/10.17660/ActaHortic.2015.1086.4.

Faik A, Popova AV, Velitchkova M. 2016. Effects of long-term action of high temperature and high light on the activity and energy interaction of both photosystems in tomato plants. Photosynthetica. 54(4):611–619. https://doi.org/10.1007/s11099-016-0644-5.

Feng B, Liu P, Li G, Dong ST, Wang FH, Kong LA, Zhang JW. 2014. Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. J Agron Crop Sci. 200(2):143–155. https://doi.org/10.1111/jac.12045.

Graamans L, Baeza E, van den Dobbelsteen A, Tsafaras I, Stanghellini C. 2018. Plant factories versus greenhouses: Comparison of resource use efficiency. Agr Syst. 160:31–43. https://doi.org/10.1016/j.agsy.2017.11.003.

Hang T, Lu N, Takagaki M, Mao H. 2019. Leaf area model based on thermal effectiveness and photosynthetically active radiation in lettuce grown in mini-plant factories under different light cycles. Sci Hortic. 252:113–120. https://doi.org/10.1016/j.scienta.2019.03.057.

Hao L, Huang X, Qin M, Liu Y, Li W, Sun G. 2018. Ecohydrological processes explain urban dry island effects in a wet region, southern China. Water Resour Res. 54(9):6757–6771. https://doi.org/10.1029/2018WR023002.

He Z, Su C, Cai Z, Wang Z, Li R, Liu J, He J, Zhang Z. 2022. Multi-factor coupling regulation of greenhouse environment based on comprehensive growth of cherry tomato seedlings. Sci Hortic-Amsterdam. 297:110960. https://doi.org/10.1016/j.scienta.2022.110960.

Jaeger SR. 2024. Vertical farming (plant factory with artificial lighting) and its produce: Consumer insights. Curr Opin Food Sci. 56: 101145. https://doi.org/10.1016/j.cofs.2024.101145.

Kabano P, Lindley S, Harris A. 2021. Evidence of urban heat island impacts on the vegetation growing season length in a tropical city. Landscape Urban Plan. 206:103989. https://doi.org/10.1016/j.landurbplan.2020.103989.

Katsoulas N, Peponakis K, Ferentinos KP, Kittas C. 2015. Calibration of a growth model for tomato seedlings (TOMSEED) based on heuristic optimisation. Biosyst Eng. 140:34–47. https://doi.org/10.1016/j.biosystemseng.2015.09.004.

Kikuchi Y, Kanematsu Y, Yoshikawa N, Okubo T, Takagaki M. 2018. Environmental and resource use analysis of plant factories with energy technology options: A case study in Japan. J Clean Prod. 186:703–717. https://doi.org/10.1016/j.jclepro.2018.03.110.

Kil SH, Park HM, Park M, Kim YI, Lee E. 2023. Location selection of urban rooftop greenhouses in Seoul based on AHP and GIS. Land. 12(12):2187. https://doi.org/10.3390/land12122187.

Kim YH, Yang HC, Bae YH, Hyeon SJ, Hwang SJ, Kim DH, Jang DC. 2023. Preventing overgrowth of cucumber and tomato seedlings using difference between day and night temperature in a plant factory with artificial lighting. Plants. 12(17). https://doi.org/10.3390/plants12173164.

Küpers JJ, Snoek BL, Oskam L, Pantazopoulou CK, Matton SEA, Reinen E, Liao C-Y, Eggermont EDC, Weekamp H, Biddanda-Devaiah M, Kohlen W, Weijers D, Pierik R. 2023. Local light signaling at the leaf tip drives remote differential petiole growth through auxin-gibberellin dynamics. Curr Biol. 33(1):75–85. e75. https://doi.org/10.1016/j.cub.2022.11.045.

Lambin EF, Meyfroidt P. 2011. Global land use change, economic globalization, and the looming land scarcity. Proc Natl Acad Sci USA. 108(9):3465–3472. https://doi.org/10.1073/pnas.1100480108.

Lang KM, Nair A, Litvin AG. 2020. An alternative healing method for grafted tomato transplants: The effect of light exclusion and substrate temperature on plant survival and growth. HortTechnology. 30(6):677–684. https://doi.org/10.21273/HORTTECH04626-20.

Larsen DH, Woltering EJ, Nicole CCS, Marcelis LFM. 2020. Response of basil growth and morphology to light intensity and spectrum in a vertical farm. Front Plant Sci. 11:597906. https://doi.org/10.3389/fpls.2020.597906.

Li H, Mao Y, Wang Y, Fan K, Shi H, Sun L, Shen J, Shen Y, Xu Y, Ding Z. 2022. Environmental simulation model for rapid prediction of tea seedling growth. Agronomy. 12(12):3165. https://doi.org/10.3390/agronomy12123165.

Li J, Martin A, Carver L, Armstrong S, Givens S, Walters K. 2024. Optimizing sowing density for parsley, cilantro, and sage in controlled environment production: Balancing productivity and plant quality. HortTechnology. 34(3): 305–312. https://doi.org/10.21273/HORTTECH05381-23.

Li M, Schmidt JE, LaHue DG, Lazicki P, Kent A, Machmuller MB, Scow KM, Gaudin ACM. 2020. Impact of irrigation strategies on tomato root distribution and rhizosphere processes in an organic system. Front Plant Sci. 11:360. https://doi.org/10.3389/fpls.2020.00360.

Li T, Zhang Y, Dai J, Dong H, Kong X. 2019. High plant density inhibits vegetative branching in cotton by altering hormone contents and photosynthetic production. Field Crop Res. 230:121–131. https://doi.org/10.1016/j.fcr.2018.10.016.

Liang Y, Kang C, Kaiser E, Kuang Y, Yang Q, Li T. 2021. Red/blue light ratios induce morphology and physiology alterations differently in cucumber and tomato. Sci Hortic. 281:109995. https://doi.org/10.1016/j.scienta.2021.109995.

Liaros S, Botsis K, Xydis G. 2016. Technoeconomic evaluation of urban plant factories: The case of basil (*Ocimum basilicum*). Sci Total Environ. 554-555:218–227. https://doi.org/10.1016/j.scitotenv.2016.02.174.

Lichtenthaler HK, Ac A, Marek MV, Kalina J, Urban O. 2007. Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. Plant Physiol Biochem. 45(8):577–588. https://doi.org/10.1016/j.plaphy.2007.04.006.

Liu X, Feike T, Shao L, Sun H, Chen S, Zhang X. 2016. Effects of different irrigation regimes on soil compaction in a winter wheat–summer maize cropping system in the north China plain. CATENA. 137:70–76. https://doi.org/10.1016/j.catena.2015.08.014.

Liu Y, Mousavi S, Pang Z, Ni Z, Karlsson M, Gong S. 2021. Plant factory: A new playground of industrial communication and computing. Sensors. 22(1). https://doi.org/10.3390/s22010147.

Lu T, Meng Z, Zhang G, Qi M, Sun Z, Liu Y, Li T. 2017. Sub-high temperature and high light intensity induced irreversible inhibition on photosynthesis system of tomato plant *(Solanum lycopersicum* L.). Front Plant Sci. 8:365. https://doi.org/10.3389/fpls.2017.00365.

Marković SM, Živančev D, Horvat D, Torbica A, Jovankić J, Djukić NH. 2021. Correlation of elongation factor 1A accumulation with photosynthetic pigment content and yield in winter wheat varieties under heat stress conditions. Plant Physiol Biochem. 166:572–581. https://doi.org/10.1016/j.plaphy.2021.06.035.

Meyer LJ, Kennelly MM, Pliakoni ED, Rivard CL. 2017. Leaf removal reduces scion adventitious root formation and plant growth of grafted tomato. Sci Hortic. 214:147–157. https://doi.org/10.1016/j.scienta.2016.11.019.

Montero JI, Baeza E, Heuvelink E, Rieradevall J, Muñoz P, Ercilla M, Stanghellini C. 2017. Productivity of a building-integrated roof top greenhouse in a mediterranean climate. Agr Syst. 158:14–22. https://doi.org/10.1016/j.agsy.2017.08.002.

Morais MC, Torres LF, Kuramae EE, Andrade S, Mazzafera P. 2024. Plant grafting: Maximizing beneficial microbeplant interactions. Rhizosphere. 29:100825. https://doi.org/10.1016/j.rhisph.2023.100825.

Niu C, Wang G, Sui J, Liu G, Ma F, Bao Z. 2022. Biostimulants alleviate temperature stress in tomato seedlings. Sci Hortic-Amsterdam. 293: 110712. https://doi.org/10.1016/j.scienta.2021.110712.

Parada F, Gabarrell X, Rufí-Salís M, Arcas-Pilz V, Muñoz P, Villalba G. 2021. Optimizing irrigation in urban agriculture for tomato crops in rooftop greenhouses. Sci Total Environ. 794: 148689. https://doi.org/10.1016/j.scitotenv.2021.148689.

Qin C, Li Y-H, Li D, Zhang X, Kong L, Zhou Y, Lyu X, Ji R, Wei X, Cheng Q, Jia Z, Li X, Wang Q, Wang Y, Huang W, Yang C, Liu L, Wang X, Xing G, Hu G, Shan Z, Wang R, Li

H, Li H, Zhao T, Liu J, Lu Y, Hu X, Kong F, Qiu L-J, Liu B. 2023. PH13 improves soybean shade traits and enhances yield for high-density planting at high latitudes. Nat Commun. 14(1):6813. https://doi.org/10.1038/s41467-023-42608-5.

Qiu R, Song J, Du T, Kang S, Tong L, Chen R, Wu L. 2013. Response of evapotranspiration and yield to planting density of solar greenhouse grown tomato in northwest China. Agr Water Manage. 130:44–51. https://doi.org/10.1016/j.agwat.2013.08.013.

Rodriguez JC, Shaw NL, Cantliffe DJ. 2007. Influence of plant density on yield and fruit quality of greenhouse-grown Galia muskmelons. HortTechnology. 17(4):580–585. https://doi.org/10.21273/HORTTECH.17.4.580.

Sandhu RK, Boyd NS, Zotarelli L, Agehara S, Peres N. 2021. Effect of planting density on the yield and growth of intercropped tomatoes and peppers in Florida. HortScience. 56(2):286–290. https://doi.org/10.21273/HORTSCI15567-20.

Song J, Chen Z, Zhang A, Wang M, Jahan MS, Wen Y, Liu X. 2022. The positive effects of increased light intensity on growth and photosynthetic performance of tomato seedlings in relation to night temperature level. Agronomy. 12(2):343. https://doi.org/10.3390/agronomy12020343.

Song X, Li H. 2016. Effects of building shade on photosynthesis and chlorophyll fluorescence of *Euonymus fortunei*. Acta Ecol Sin. 36(5):350–355. https://doi.org/10.1016/j.chnaes.2016.05.008.

Twala TC, Witkowski ETF, Fisher JT. 2022. The effects of heat and drought stress on the ecophysiological responses and growth of *Afrocarpus falcatus* and *Podocarpus henkelii* seedlings. S Afr J Bot. 149:258–268. https://doi.org/10.1016/j.sajb.2022.06.011.

van Delden SH, SharathKumar M, Butturini M, Graamans LJA, Heuvelink E, Kacira M, Kaiser E, Klamer RS, Klerkx L, Kootstra G, Loeber A, Schouten RE, Stanghellini C, van Ieperen W, Verdonk JC, Vialet-Chabrand S, Woltering EJ, van de Zedde R, Zhang Y, Marcelis LFM. 2021. Current status and future challenges in implementing and upscaling vertical farming systems. Nat Food. 2(12):944–956. https://doi.org/10.1038/s43016-021-00402-w.

Wang H, Ding Y, Yao Q, Ma L, Ma Y, Yang M, Qin S, Xu F, Zhang Z, Gao Z. 2024. Modeling of cotton yield estimation based on canopy sun-induced chlorophyll fluorescence. Agronomy. 14(2):364. https://doi.org/10.3390/agronomy14020364.

Wang P, Wang ZK, Sun XC, Mu XH, Chen H, Chen FJ, Lixing Y, Mi GH. 2019. Interaction effect of nitrogen form and planting density on plant growth and nutrient uptake in maize seedlings. J Integr Agr. 18(5):1120–1129. https://doi.org/10.1016/S2095-3119(18)61977-X.

Wang X, Wang B, Zhu X, Zhao Y, Jin B, Wei X. 2022. Exogenous nitric oxide alleviates the damage caused by tomato yellow leaf curl virus in tomato through regulation of peptidase inhibitor genes. Int J Mol Sci. 23(20):12542. https://doi.org/10.3390/ijms232012542.

Wu Y, Si W, Yan S, Wu L, Zhao W, Zhang J, Zhang F, Fan J. 2023. Water consumption, soil nitrate-nitrogen residue and fruit yield of drip-irrigated greenhouse tomato under various irrigation levels and fertilization practices. Agr Water Manage. 277:108092. https://doi.org/10.1016/j.agwat.2022.108092.

Xu D, Ahmed HA, Tong Y, Yang Q, van Willigenburg LG. 2021. Optimal control as a tool to investigate the profitability of a Chinese plant factory - lettuce production system. Biosyst Eng. 208:319–332. https://doi.org/10.1016/j.biosystemseng.2021.05.014.

Yan Y, Duan F, Li X, Zhao R, Hou P, Zhao M, Li S, Wang Y, Dai T, Zhou W. 2024. Photosynthetic capacity and assimilate transport of the lower canopy influence maize yield under high planting density. Plant Physiol. 195(4):2652–2667. https://doi.org/10.1093/plphys/kiae204.

Yan Z, Cheng J, Wan Z, Wang B, Lin D, Yang Y. 2023. Prediction model of pumpkin rootstock seedlings based on temperature and light responses. Agronomy. 13(2):516. https://doi.org/10.3390/agronomy13020516.

Yan Z, Wolters A-MA, Navas-Castillo J, Bai Y. 2021. The global dimension of tomato yellow leaf curl disease: Current status and breeding perspectives. Microorganisms. 9(4):740. https://doi.org/10.3390/microorganisms9040740.

Yao H, Zhang Y, Yi X, Zhang X, Zhang W. 2016. Cotton responds to different plant population densities by adjusting specific leaf area to optimize canopy photosynthetic use efficiency of light and nitrogen. Field Crop Res. 188:10–16. https://doi.org/10.1016/j.fcr.2016.01.012.

Yasutake D, Kiyokawa C, Kondo K, Nomiyama R, Kitano M, Mori M, Yamane S, Maeda M, Nagare H, Fujiwara T. 2014. Characteristics of nutrient salt uptake associated with water use of corn as a catch crop at different plant densities in a greenhouse. Pedosphere. 24(3):339–348. https://doi.org/10.1016/S1002-0160(14)60020-5.

Yeh N, Chung JP. 2009. High-brightness LEDs-energy efficient lighting sources and their potential in indoor plant cultivation. Renew Sust Energ Rev. 13(8):2175–2180. https://doi.org/10.1016/j.rser.2009.01.027.

Zheng J, Gan P, Ji F, He D, Yang P. 2021. Growth and energy use efficiency of grafted tomato transplants as affected by LED light quality and photon flux density. Agriculture. 11(9):816. https://doi.org/10.3390/agriculture11090816.

Zhou T, Wu Z, Wang YC, Su X, Qin C, Huo H, Jiang FL. 2019. Modelling seedling development using thermal effectiveness and photosynthetically active radiation. J Integr Agr. 18(11):2521–2533. https://doi.org/10.1016/S2095-3119(19)62671-7.

Zhou Z, Feng S, Gai S, Gao P, Xu C, Xia M, Tang W, Lu X. 2022. Affordable phosphor-converted LEDs with specific light quality facilitate the tobacco seedling growth with low energy consumption in industrial seedling raising. J Photochem Photobiol B. 235:112564. https://doi.org/10.1016/j.jphotobiol.2022.112564.

Zhou Z, Yuan Y, Wang K, Wang H, Huang J, Yu H, Cui X. 2022. Rootstock-scion interactions affect fruit flavor in grafted tomato. Hortic Plant J. 8(4):499–510. https://doi.org/10.1016/j.hpj.2022.01.001.