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The Positive Effects of Increased Light Intensity on Growth and Photosynthetic Performance of Tomato Seedlings in Relation to Night Temperature Level

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Abstract: Light and temperature are related to the growth and development of plants as well as their energy consumption in plant factories. However, most of the studies to date have focused on light and temperature extremes, while the adaptive responses and underlying mechanisms of plants to non-stress light intensity (LI) and night temperature (NT) largely remain elusive. Here, we investigated the growth and physiological responses of tomatoes grown under three LI regimes of 250 (L_L), 300 (L_M), and 350 (L_H) μmol m^{-2} s^{-1}, respectively, combined with two NT conditions. The results revealed that increased LI comprehensively improved tomato growth and physiological status at lower NT levels, but the growth stimulations induced by increasing LI were limited by higher NT. In addition, the lower NT at L_M and L_H conferred a relatively better endogenous physiological condition and significantly promoted tomato growth, but the higher NT significantly accelerated shoot growth at L_L, indicating a compensation of higher NT for low light induced growth restriction. Taken together, the current study suggests that the adaptation mechanism of tomato plants to higher NT varied with LI levels, and higher LI plus lower NT would be an effective strategy to improve tomato growth.

Keywords: cherry tomato; controlled environment; growth; light quantity; night temperature; distribution of light energy

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1. Introduction

Plant factories can avoid unfavorable external environmental factors during crop production, so growing and nourishing vegetables is very stable throughout the year, letting an uninterrupted supply of vegetables at a constant price, regardless of weather conditions. However, in an artificially controlled plant factory, one of the biggest challenges is the massive energy consumption due to the maintenance and regulation of light and temperature environments [1]. Light and temperature are the two most crucial environmental stimuli that regulated plant growth and development [2], and not only serve as cues to initiate multiple developmental processes, but are also required for optimal performances of biochemical and physiological cascades in the normal plant life cycle [3]. Thus, understanding the responses in the growth and development of the plants to different light and temperature levels is an essential prerequisite for deciphering appropriate strategies to regulate environmental parameters in plant factories.

The effects of sole light or temperature on plant growth and development, including light intensity (LI) and night temperature (NT) have been studied extensively. Plants have

evolved a wide range of growth and survival mechanisms, including plant morphological and physiological changes, to adapt to light and temperature environments [1,2,4,5]. In general, an improvement in photosynthetic capacity is positively correlated with an increase in LI, but excessive light can directly lead to a decrease in the net photosynthetic rate [6]. While low irradiation often induces some adaptive responses at the foliage level in plants, such as an expansion of leaf area and increment of leaf angle, and these adaptive behaviors improve light availability and photosynthesis [7]. In contrast, many acclimatizing morpho-physiological characteristics, like reduced leaf area and plant height, and increased leaf thickness, have occurred to mitigate the harmful effects of excessive light, ensuring optimum photosynthetic rate [4]. Moreover, plants have evolved multiple receptors to perceive new environmental signals and changes in environmental conditions as well, and transform the information into downstream metabolic or biochemical changes to facilitate plants to survive under given LI conditions [2].

Temperature, like light stimuli, also regulates almost all stages of plant growth and development [8]. Essential processes such as plant respiration, repair of damaged photosystems, and carbohydrate translocation are significantly activated during the dark period [5]. Besides, the biological process of the plant during the nighttime, including photosynthate translocation can influence photosynthetic efficiency of the leaves and other physiological metabolism in the subsequent daytime [5,9]. Therefore, NT is particularly essential for the growth and development of higher plants, acting as a stimulus to control the timing of the developmental transitions [2,5]. It has been reported that high NT increased respiration, resulting in a reduction of ATP levels and carbohydrate contents in cotton leaf [9], which inhibits the photosynthesis processes of plants in the daytime [10]. Analogously, excessively low NT is also associated with the reduction of CO_2 net assimilation in the subsequent daytime [11], but the physiological basis of this phenomenon is still under debate [5].

Previous studies have demonstrated a complex cross-talk between light and temperature signals in regulating germination, plant architecture, flowering, and enhancing freezing tolerance [12,13], but most of the studies have so far focused on high/poor light and temperature stress only [6] and hardly investigated the plant responses in physiological acclimation to the combination of non-stress LI and NT. The environments of the plant factory are precisely controllable, so extreme light and temperature do not occur, but massive energy inputs are needed to maintain the proper light-temperature environments. Therefore, it is necessary to develop new energy saving strategies based on the current energy usage models. In general, moderate LI and cool-night temperature adequately allow a proper growth condition for the cultivation of most vegetables. Tomato is a widely distributed crop in the world and is cultivated in China throughout the year. The individual effects of LI or temperature on growth and photosynthesis of tomato have been well understood [4,14,15], and the previous studies have demonstrated under controlled environments, 300 μmol m^{-2} s^{-1} of red and blue composite light and red, blue, and green composite light can ensure sound growth of tomato seedlings [4,16]. The interactive influences of different lights and daily/nighttime temperatures on tomato growth have been also investigated as well [17,18], demonstrating that tomato plants are better acclimated to the combined effects of high light and temperature rather than exposed to a single stimulus. Nevertheless, the light and temperature used in the study are still two stress factors [17], and tomato responses to different LI accompanied with different cool-night temperatures have received relatively little attention at the same daily temperature. A cool-night temperature, usually defined as non-stress NT between 15–20 °C, is a near-optimal NT for photosynthate transport, biomass accumulation, and fruit formation in tomatoes [1,19].

The research concerning the responses of seedlings exposed to different moderate LI and non-stress NT in a plant factory are very essential based on energy saving, which also has implications for providing insight into the LI and NT relationships during the early weeks of vegetable growth. To this end, in the present study, three levels of moderate light intensities referred to previous studies and two NTs in the range of cool-night temperatures were used to investigate the effects of LI and NT on the growth, photosynthetic performance,

and energy utilization of cherry tomato seedlings, accompanied with an understanding the interactive regulatory mechanism between LI and NT for tomato seedling growth.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Cherry tomato (*Lycopersicon esculentum* Mill. 'Qianxi') seeds were sterilized and incubated at 28 °C and then sown and grown in pots (8-cm diameter) containing a mixture of peat and vermiculite (3:1, v/v). The seedlings have grown to two true-leaf stages in an open ambient climate under natural light condition before being subjected to six combinations of three LI levels (250, 300, and 350 μmol m^{-2} s^{-1}, recorded as L_L, L_M, and L_H, respectively) and two NT regimes [(15 ± 1) °C and (18 ± 1) °C, recorded as NT_L and NT_H, respectively] for 30 days. Herein, a combination of red (peak at 660 nm), blue (peak at 445 nm), and green (peak at 550 nm) LEDs light (Opt-run Biotechnology Co., Nanjing, China) was used as a light source, and the full width at half maximum of all LEDs was 30 nm. The photosynthetic photon flux density (PPFD) ratio of red to blue LEDs was 1:1, and 30 μmol m^{-2} s^{-1} of green LEDs was precisely added. Each treatment contained 40 uniform seedlings, and 6 groups were exposed at a day temperature of (26 ± 1) °C with 12 h photoperiod (lighting from 08:00 to 20:00). In addition, the CO_2 concentration and relative humidity were the same as outdoor.

2.2. Growth Parameters and Photosynthetic Pigment Measurements

Tomato seedlings were collected for the measurement of growth indices along with subsequent chemical investigations. At least 3 young plants were randomly selected for each treatment. Plant height, stem diameter, and dry weight were measured in accordance with the standard procedure. Leaf area was measured by the disc method. In brief, 1-cm^2 partial leaves were cut from the intact leaves with a puncher to measure the dry weight, and the number of 1-cm^2 partial leaves was recorded as N. Leaf area was determined according to the formula: leaf area = (Dry weight of all leaves × N)/Dry weight of N pieces 1-cm^2 partial leaves. The health index was determined using the following formula: (Stem diameter/Plant height + Root dry weight/Shoot dry weight) × Plant dry weight.

The chlorophyll (Chl) and carotenoid (Car) contents were extracted from 0.1 g of fresh leaves and immersed in 10 mL of 80% acetone (v/v) until the leaves turned white, and then the optical density was measured using a UV-1200 spectrophotometer (MAPUDA instrument, Shanghai, China) and the photosynthetic pigment contents were calculated as described by Fan et al. [20].

2.3. Determination of Carbon and Nitrogen Nutritional Status

The carbon and nitrogen nutritional status of plants were estimated by non-structural carbohydrates (NSC), defined as the sum of soluble sugar and starch, and by main nitrogenous compounds including soluble protein and free amino acid, respectively. Briefly, the starch and soluble sugar contents were measured using the anthrone method, and the sucrose concentration was calculated by the resorcinol method in accordance with the method of Li et al. [21]. Soluble protein was extracted from fresh samples and determined using Coomassie Brilliant Blue G-250 [21]. Free amino acid was determined according to the published method of Li et al. [21].

2.4. The Determinations of Malondialdehyde (MDA) and Ascorbic Acid (AsA) Contents, and Antioxidant Enzyme Activities

The MDA content was determined using a thiobarbituric acid solution according to Li et al. [21]. For the measurements of the antioxidants, the radical scavenger AsA was extracted by 4.5% aqueous phosphoric acid and quantified as described [22]. Antioxidant enzymes including superoxide dismutase (SOD), catalase, and peroxidase were quantified by previously described procedures [21].

2.5. Photosynthesis and Chl Fluorescence Traits Measurements

The net photosynthetic rate (P_N), stomatal conductance (G_S), and intercellular CO_2 concentration (C_i) of the fully expanded third leaves were measured during the daytime between 9:30 and 11:30 using a photosynthesis measurement system (LI-6400XT; LI-COR, Lincoln, NE, USA). Measurements were performed under a PPFD of 250, 300, and 350 μmol m^{-2} s^{-1} provided by a mixture of red and blue LEDs for data measurements of L_L, L_M, and L_H treatments, respectively. The leaf temperature, ambient CO_2 concentration (C_a), and relative humidity were 26 °C, (390 ± 10) μmol mol^{-1}, and 60–70%, respectively. Stomatal limitation (L_S) was estimated by the following formula: $1 - C_i/C_a$.

The Chl fluorescence parameters were also measured using LI-6400XT. The initial Chl fluorescence yield (Fo) was determined in standard modulated excitation intensity, and a 0.8 s saturation pulse was applied to measure the maximum fluorescence yield (Fm) after the plants were kept in darkness for 30 min. The maximal photochemistry efficiency of PSII (Fv/Fm), where Fv = Fm − Fo, the minimal (Fo′) and maximum (Fm′) fluorescence level during illumination were also estimated. The fluorescence traits of light-adapted leaves were evaluated when the steady state fluorescence (Fs) level was reached. The actual photochemical efficiency of PSII (PhiPS2) was determined as (Fm′ − Fs)/Fm′, photochemical fluorescence quenching (qP) was calculated as (Fm′ − Fs)/(Fm′ − Fo′), non-photochemical fluorescence quenching (NPQ) was recorded as (Fm − Fm′)/Fm′, and efficiency of open PSII center (Fv′/Fm′) was determined as (Fm′ − Fo′)/Fm′. The electron flow through PSII (ETR) was calculated as follows: ETR = 0.5 × PhiPS2 × PPFD × 0.84. The relative restriction in photosynthetic performance (L_{PFD}) of seedlings was calculated as described by Schreiber et al. [23] as follows: $L_{PFD} = 1 - qP \times Fv'/Fm'/0.83$. The instantaneous fluorescence decline ratio in light (R_{FD}) was calculated as follows: $R_{FD} = (Fm - Fs)/Fs$. The excitation pressure (E_P) of PSII, measured as the relative redox state of QA, was calculated from: $E_P = 1 - qP$.

The distribution coefficient of excitation energy of PSI (α) was calculated as qP/(1 + qP), and the distribution coefficient of excitation energy of PSII (β) was calculated as 1/(1 + qP). The imbalance of excitation energy distribution between two photosystems is expressed by $\beta/\alpha - 1$. According to the method of Demmig-Adams et al. [24]. The fraction of absorbed light energy used for photochemical reaction (P) was determined as (Fv′/Fm′) × qP; the fraction of non-photochemical dissipation (E_X) was determined as $E_P \times$ (Fv′/Fm′); the fraction of antenna thermal dissipation (D) was estimated from D = 1 − Fv′/Fm′. Three plants were randomly measured in each treatment, and each plant was repeated twice to take the average value.

2.6. Measurement of Dark Respiration Rate and Photorespiration Rate

The fully expanded third leaves were used to measure the light response curve and CO_2 response curve using LI-6400XT. The measurement procedures and fitting models were referred to in a previous study [25]. During the measurements of the light response curve, leaf temperature was 25 °C, CO_2 concentration was 390 μmol mol^{-1}, and the PPFD gradients were set as 15 levels (1600, 1400, 1200, 1000, 800, 600, 400, 200, 150, 125, 100, 75, 50, 25, 0 μmol m^{-2} s^{-1}). The P_N was measured after 2 min adaptation to each PPFD level. During the measurements of the CO_2 response curve, the leaf temperature was 25 °C, and the CO_2 concentration gradients were set as 9 levels (1200, 1000, 800, 600, 400, 200, 150, 100, 50 μmol mol^{-1}). The P_N was measured after 2 min adaptation to each CO_2 concentration. Using a mechanistic model to fit the two response curves and finally calculate dark respiration rate and photorespiration rate (http://photosynthetic.sinaapp.com/calc.html, accessed on 6 December 2021) [25].

2.7. Measurement of Leaf Anatomy and Stomatal Density

The fully expanded leaf of each treatment with the same leaf position was cut vertically with two razor blades pressed together into thin slices, and the slices were then gently put on a glass slide, added a drop of distilled water, and covered with another glass slide. The

temporary slices were used to observe the anatomical structure by an optical microscope (DP71; Olympus Inc., Tokyo, Japan), and cross-sections of leaves were measured for leaf thickness, upper epidermis, palisade tissue, spongy tissue, and lower epidermis thickness. Twelve images from three plants per treatment were analyzed.

For the observation of stomata, the imprinting method was adopted according to Yao et al. [26]. A colorless and transparent nail polish was applied evenly to the lower epidermis of the leaf samples, allowed it to solidify for 8 min at room temperature, and subsequently, dried coating layers were torn with tweezers. After the coating layers were unfolded in the glycerol layer on glass slides and squeezed to remove air bubbles, filter paper was used to drain the surrounding glycerin. Temporary slides of epidermal fingerprints were processed using an optical microscope (DP71; Olympus Inc., Tokyo, Japan) connected to an imaging analysis system. The number of stomata per field of view in the leaf epidermis was used to calculate the stomatal density, and stomatal length, width, and area were also measured. Eight images per leaf, one leaf per plant, and three plants per treatment were analyzed.

2.8. Observation and Measurement of Chloroplast Ultrastructure

Leaf samples were collected after illumination for approximately 3 h, and the ultrastructure of chloroplast was examined using the methods of Yao et al. [26]. Briefly, the leaves were immerged in 0.2 mol L^{-1} of phosphate buffer (pH 7.2) containing 2.5% glutaraldehyde, followed by vacuum-pumping. The pre-treated samples were fixed for 2 h in 1% osmium tetroxide, dehydrated in a series of graded ethanol, immersed in acetone, and embedded in Epon-812 epoxide resin. Ultrathin sections (100 nm thickness), which were sectioned with an ultra-microtome (Powertome XL, RMC Products; Boeckeler Instruments Inc., Tucson, AZ, USA), were put on copper grids (one-slot 1 mm) and stained with 2% uranyl acetate and lead citrate. The sections were observed and photographed with an electron microscope (H-7650; Hitachi Ltd., Tokyo, Japan). Eight images per leaf, one leaf per plant, and three plants per treatment were analyzed.

2.9. Statistical Analysis

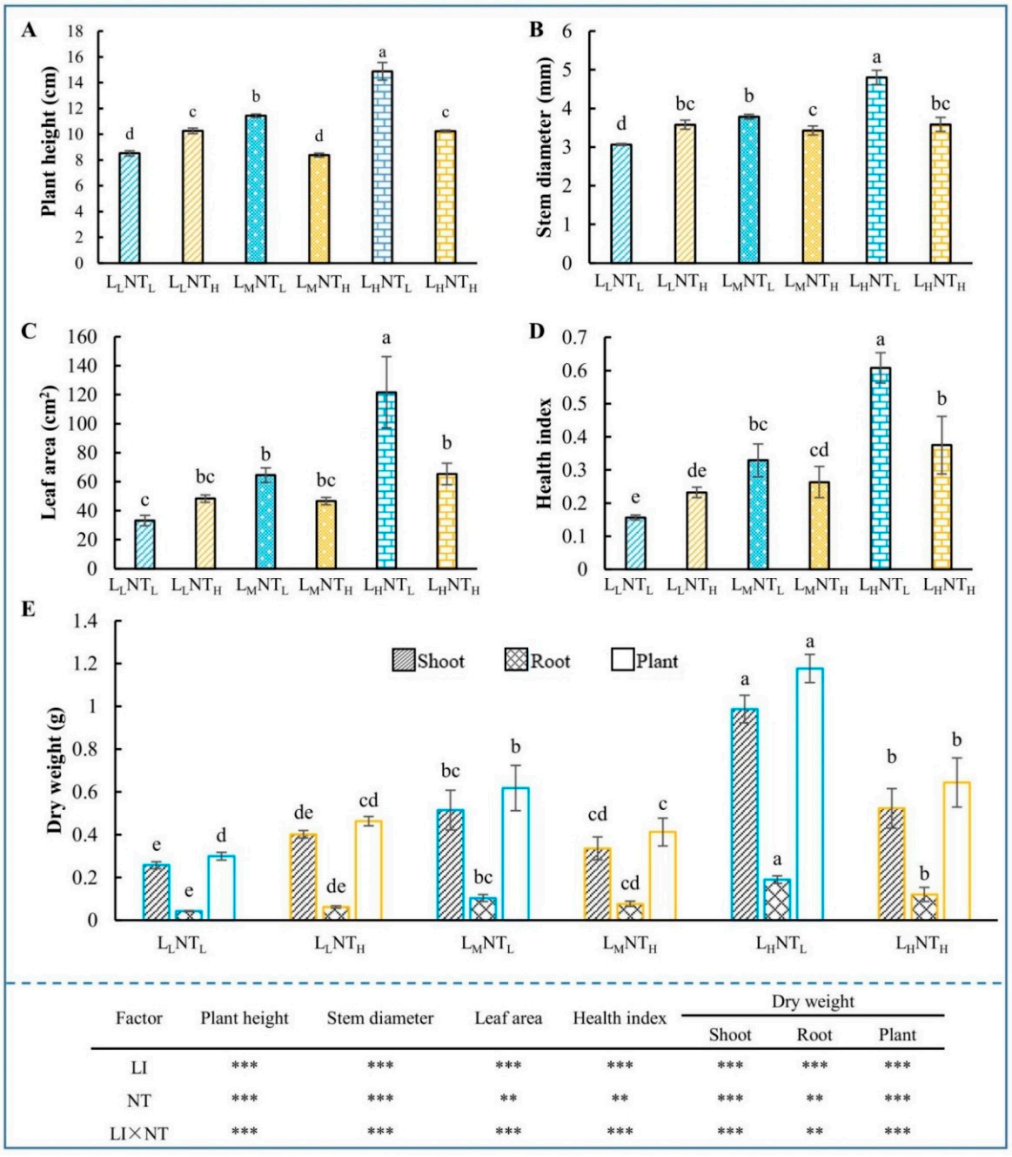
The experiment was repeated three times. Statistical analyses were carried out using Statistical Product and Service Solutions for Windows, ver. 19.0 (SPSS Inc., Chicago, IL, USA). Two-way ANOVA was performed using Fisher's LSD test to assess the interactive effects of LI and NT and differences between means were tested using Duncan's multiple range test ($p < 0.05$). The correlations among the parameters used in the study were determined by Pearson's correlation coefficient. Differences were considered to be statistically significant for *p*-values below 0.05.

3. Results

3.1. Growth Traits

F-test indicated that LI and NT as well as their interaction significantly affected tomato seedling growth (Figures 1 and 2A–E). At the NT_L level, an increase in LI significantly promoted plant growth and increased plant height, stem diameter, leaf area, health index, and dry weight of tomato seedlings. In contrast, at the NT_H level, the increased LI from L_L to L_M did not promote growth, but the significant promotion still remained in biomass accumulation and health index when increasing LI from L_L to L_H or from L_M to L_H. Under L_L conditions, higher NT greatly increased plant height, stem diameter, and shoot and plant dry weights. Conversely, a lower NT significantly propelled tomato growth under L_M and L_H conditions. The healthiest tomato seedlings were observed under L_HNT_L conditions. These results indicated that the growth promotion by increasing LI is limited by higher NT and the influence of NT on tomato growth is significantly affected by the LI levels.

Figure 1. The phenotype of cherry tomato seedlings grown under different light intensity (LI) and night temperature (NT) conditions for 30 days. The LI and NT conditions of different treatments as follows: L_LNT_L, 250 μmol m^{-2} s^{-1} and 15 ± 1 °C; L_LNT_H, 250 μmol m^{-2} s^{-1} and 18 ± 1 °C; L_MNT_L, 300 μmol m^{-2} s^{-1} and 15 ± 1 °C, L_MNT_H, 300 μmol m^{-2} s^{-1} and 18 ± 1 °C; L_HNT_L, 350 μmol m^{-2} s^{-1} and 15 ± 1 °C; L_HNT_H, 350 μmol m^{-2} s^{-1} and 18 ± 1 °C.

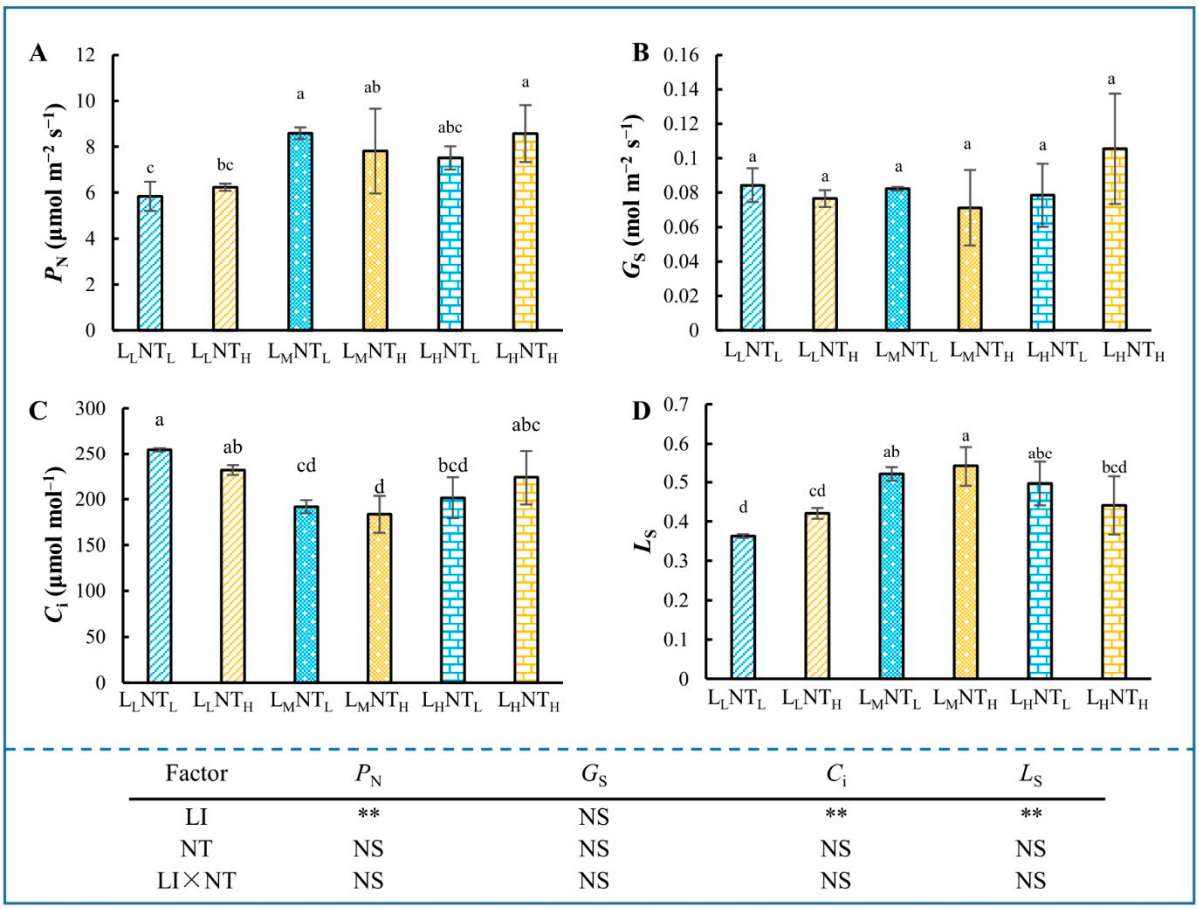


Factor	Plant height	Stem diameter	Leaf area	Health index	Dry weight		
					Shoot	Root	Plant
LI	***	***	***	***	***	***	***
NT	***	***	**	**	***	**	***
LI×NT	***	***	***	***	***	**	***

Figure 2. Effect of different light intensity (LI) and night temperature (NT) on plant height (**A**), stem diameter (**B**), leaf area (**C**), health index (**D**) and dry weight (**E**) of cherry tomato seedlings. Abbreviations of different treatments were as described in Figure 1. The symbol "**" and "***" indicate significant level at $p < 0.01$ and $p < 0.001$ by Duncan's test, respectively. Different letters on bars for the same parameter indicate statistically significant differences ($p < 0.05$).

3.2. Photosynthetic Traits, Dark Respiration Rate (R_d) and Photorespiration Rate (R_p)

F-test showed that LI had a significant effect on P_N, C_i, and L_S, while the LI and NT, as well as their interaction, did not significantly affect the G_S (Figure 3A–D). Under the same NT condition, the P_N and L_S at L_M and L_H levels were greater than those at L_L levels, while C_i had an opposite result. The P_N, L_S, and C_i at L_M and L_H levels had no significant difference at NT_L, while, at NT_H, the C_i decreased but the L_S increased significantly at L_M level compared with L_H level. At the same LI level, NT had no significant influence on photosynthetic traits. The correlation analysis showed that the P_N had no significant positive linear correlation with tomato growth parameters (Table S1).



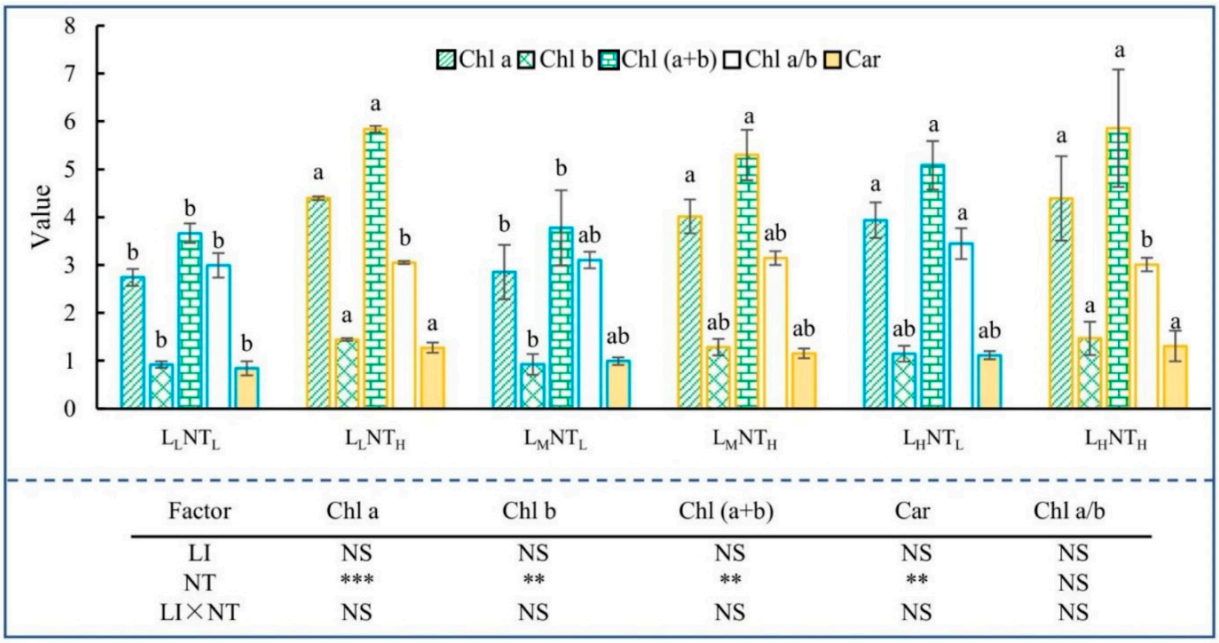
Factor	P_N	G_S	C_i	L_S
LI	**	NS	**	**
NT	NS	NS	NS	NS
LI×NT	NS	NS	NS	NS

Figure 3. Effect of light intensity (LI) and night temperature (NT) on photosynthetic traits including P_N, net photosynthetic rate (**A**) G_S, stomatal conductance (**B**) C_i, intercellular CO_2 concentration (**C**) and L_s, stomatal limitation (**D**) of cherry tomato seedlings. Abbreviations of different treatments were as described in Figure 1. The symbol "NS" and "**" indicate no significance at $p < 0.05$, and significant level at $p < 0.01$ by Duncan's test, respectively. Different letters on bars for the same parameter indicate statistically significant differences ($p < 0.05$).

We also measured the R_d and R_p using the method of Ye et al. [26] to determine rates of respiration in the dark and in the light (Table S2). The data showed that the values of R_p were much larger than R_d, and R_d at NT_L was higher than that at NT_H, and conversely, the R_p at NT_L was lower than that at NT_H. The differences of R_d at L_L and L_H were more obvious than that at L_M. At NT_L level, the R_d was the greatest under L_L conditions, while the R_d was the greatest under L_M conditions at NT_H level. The highest R_p was found under two L_M treatments.

3.3. Photosynthetic Pigments

To better define how LI and NT jointly affect photosynthesis, we measured photosynthetic pigments. *F*-test showed that LI and its interaction with NT had no significant effect on Chl and Car accumulations (Figure 4). Under NT_L conditions, the Chl a and Chl (a + b) contents in L_L and L_M conditions were significantly lower than those in L_H condition; the Chl a/b increased with an increase of LI (Figure 4). Under NT_H conditions, LI alterations had no significant influence on photosynthetic pigment contents and Chl a/b. NT plays a great role in Chl and Car accumulations, and elevated NT significantly increased the contents of Chl and Car under L_L conditions; under L_M condition, elevated NT also significantly increased the contents of Chl a and Chl (a + b); while under L_H condition, elevated NT had no significant effect on Chl and Car contents, but significantly decreased the Chl a/b. The results show that enhancing pigments contents induced by improved LI is closely related to lower NT, while the promotion of high NT on photosynthetic pigment are limited by high LI. The correlation analysis showed that the photosynthetic pigments had no significant linear correlation with the P_N, but Chl a/b was highly positive linear correlated with tomato growth parameters shown in Table S1.



Factor	Chl a	Chl b	Chl (a+b)	Car	Chl a/b
LI	NS	NS	NS	NS	NS
NT	***	**	**	**	NS
LI×NT	NS	NS	NS	NS	NS

Figure 4. Effect of different light intensity (LI) and night temperature (NT) on photosynthetic pigment content of cherry tomato seedlings. Car, carotenoid; Chl, chlorophyll. The unit of photosynthetic pigments is (mg/g). Abbreviations of different treatments were as described in Figure 1. The symbol "NS", "**" and "***" indicate no significance at $p < 0.05$, significant level at $p < 0.01$ and $p < 0.001$ by Duncan's test, respectively. Different letters on bars for the same parameter indicate statistically significant differences ($p < 0.05$).

3.4. Chl Fluorescence Parameters

We measured Chl fluorescence parameters to better understand the light energy utilization and distribution of tomato seedlings grown under different LI and NT conditions. *F*-test showed that LI, as well as LI and NT interactions, significantly affected most of the Chl fluorescence parameters (Table 1). Under NT_L conditions, PhiPS2 and ETR increased while the L_{PFD} decreased with an increase of LI, and the highest NPQ and Fv'/Fm' occurred in L_M conditions; the D decreased significantly in L_M and L_H conditions compared to that in L_L condition. Under NT_H conditions, PhiPS2 and qP tended to decrease while L_{PFD} increased with an increase of LI, while NPQ significantly increased; the ETR first increased and then decreased, the ETR at L_M level was significantly higher than that at L_H level; the

E_P, β, $\beta/\alpha - 1$ and E_X at L_H level were significantly higher than those at other two light levels. Compared with NT_L, NT_H significantly promoted PhiPS2 but decreased L_{PFD} at L_L level, while NT_H significantly decreased PhiPS2 and Fv′/Fm′ at L_M and L_H levels at L_H level; NT_H also significantly decreased the qP and ETR under L_H condition. Besides, under L_H condition, NT_H resulted in greater E_P, β and $\beta/\alpha - 1$, L_{PFD} as well as higher E_X and D, but caused a lower α and p, showing that the excitation pressure and energy distribution of PSII were increased by the combination of higher LI and NT.

Table 1. Effect of light intensity (LI) and night temperature (NT) on Chl fluorescence parameters of cherry tomato seedlings and LI and NT interaction analysis.

Parameter	Treatment						*F*-Test		
	L_LNT_L	L_LNT_H	L_MNT_L	L_MNT_H	L_HNT_L	L_HNT_H	LI	NT	LI × NT
Fv/Fm	0.800a	0.799a	0.811a	0.810a	0.809a	0.812a	*	NS	NS
PhiPS2	0.41bc	0.50a	0.46ab	0.40c	0.48a	0.36c	NS	NS	***
qP	0.86ab	0.90a	0.82b	0.83ab	0.87ab	0.71c	**	NS	**
NPQ	1.36cd	1.18d	1.86a	1.41c	1.55bc	1.65b	***	**	**
Fv′/Fm′	0.51c	0.52c	0.56a	0.53bc	0.55ab	0.51c	*	*	*
ETR	48.85d	54.28bcd	57.32bc	59.34b	66.12a	52.62cd	**	NS	**
L_{PFD}	0.57b	0.46d	0.55bc	0.60b	0.50cd	0.69a	**	*	***
R_{FD}	3.37a	3.35a	3.36a	3.38a	3.39a	3.18a	NS	NS	NS
E_P	0.14bc	0.10c	0.18bc	0.17bc	0.13bc	0.29a	**	NS	**
α	0.46a	0.47a	0.45a	0.45a	0.47a	0.41b	**	NS	**
β	0.54b	0.53b	0.55b	0.55b	0.53b	0.59a	**	NS	**
$\beta/\alpha - 1$	0.16b	0.11b	0.22b	0.21b	0.15b	0.42a	*	NS	**
P (%)	43.63a	46.80a	45.65a	43.51a	47.82a	36.24b	NS	*	**
E_X (%)	6.87bc	5.01c	9.92b	9.10b	6.98bc	14.89a	**	NS	**
D (%)	49.50a	48.20a	44.43c	47.39ab	45.19bc	48.88a	*	*	*

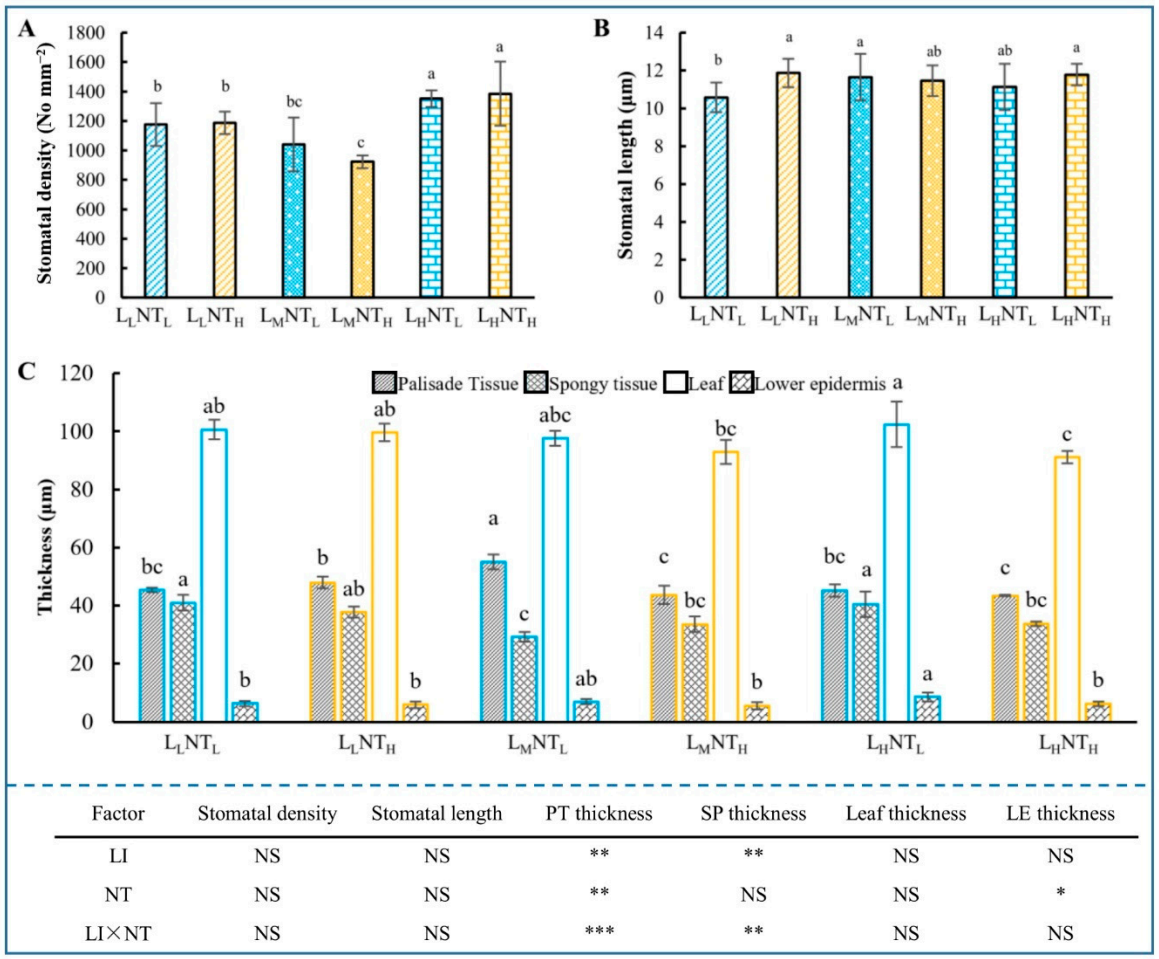
Note: The LI and NT conditions of different treatments as follows: L_LNT_L, 250 μmol m^{-2} s^{-1} and 15 ± 1 °C; L_LNT_H, 250 μmol m^{-2} s^{-1} and 18 ± 1 °C; L_MNT_L, 300 μmol m^{-2} s^{-1} and 15 ± 1 °C, L_MNT_H, 300 μmol m^{-2} s^{-1} and 18 ± 1 °C; L_HNT_L, 350 μmol m^{-2} s^{-1} and 15 ± 1 °C; L_HNT_H, 350 μmol m^{-2} s^{-1} and 18 ± 1 °C. α, Excitation energy distribution coefficient of PSI; β, Excitation energy distribution coefficient of PSII; $\beta/\alpha - 1$, unbalanced distribution of coefficient deviation on excitation energy between two photosystems; D, quotient of absorbed luminous energy used for antenna heat dissipation; E_P, excitation pressure of PSII; ETR, electron flow through PSII; E_X, quotient of absorbed luminous energy used for non-photochemical dissipation; Fv/Fm, maximum photochemical efficiency of PSII; Fv′/Fm′, antenna conversion efficiency; L_{PFD}, relative restriction in photosynthetic performance; NPQ, non-photochemical fluorescence quenching coefficient of PSII; PhiPS2, practical photochemical efficiency; qP, photochemical fluorescence quenching coefficient; R_{FD}, instantaneous fluorescence decline ratio in light. The symbol "NS", "*", "**" and "***" indicate no significance at $p < 0.05$, significant level at $p < 0.05$, $p < 0.01$ and $p < 0.001$ by Duncan's test, respectively. Different letters within the same parameter indicate statistically significant differences ($p < 0.05$).

The correlation analysis showed that Chl fluorescence parameters were significantly correlated with the P_N. Therein, the L_{PFD}, Fv/Fm, NPQ, E_P, β, $\beta/\alpha - 1$, and E_X were strongly positively correlated with the P_N, while the P_N was highly negatively correlated with the qP and α. In addition, the Fv′/Fm′ and ETR were significantly positively correlated with the growth parameters shown in Figure 2, while the D was significantly negatively correlated with growth parameters (Table S1).

3.5. Leaf Anatomical Structure and Stomatal Traits

Leaf growth has a feedback effect on photosynthesis. *F*-test showed that LI and NT as well as their interaction did not significantly affect stomatal parameters and leaf thickness but affected the thicknesses of palisade tissue, spongy tissue, and lower epidermis with varying significant levels (Figure 5A–C, Figures S1 and S2A–D). The stomatal density reduced at L_M level but significantly increased at L_H level compared with L_L level regardless of NT; while the stomatal length increased with an increasing LI under NT_L condition, and the stomatal length of the L_MNT_L treatment was significantly longer than that of the L_LNT_L treatment. Under NT_L condition, the stomatal width and lower epidermis thickness had a trend to increase with increasing LI, and the palisade tissue and PTT/SPT in the L_M

condition were significantly greater than that in the other two light levels. Under NT_H conditions, the stomatal width had a trend to decrease with increasing LI, and the thickness of leaf and palisade tissue decreased with the increase of LI. The effects of NT on stomatal and leaf development depend on LI. At L_L levels, elevated NT significantly increased the stomatal length but slightly reduced the stomatal width. At L_M level, the thickness of palisade tissue and PTT/SPT decreased while upper epidermis thickness decreased with an increase of NT; while under L_H condition, a much thinner leaf, sponge tissue, and lower epidermis were observed at NT_H levels.



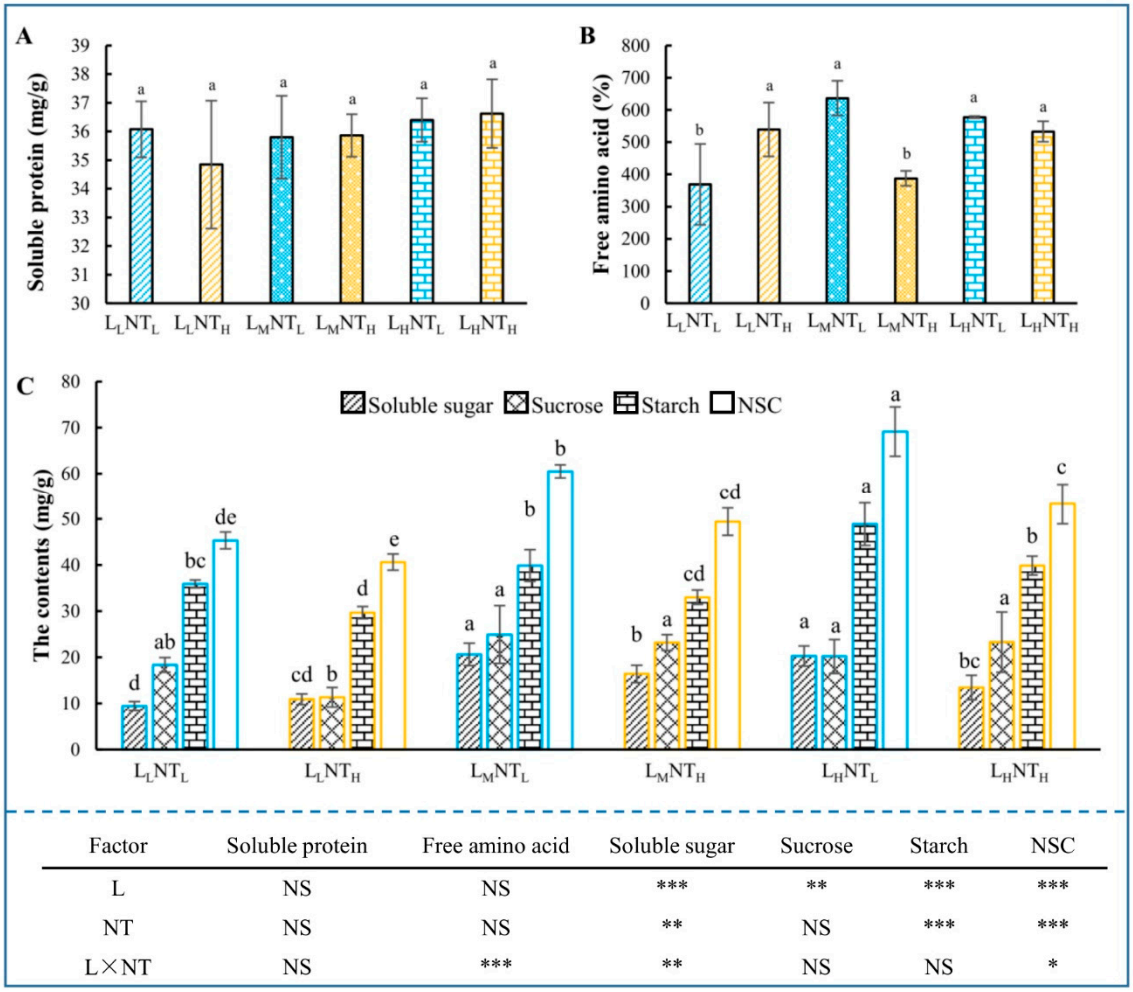
Factor	Stomatal density	Stomatal length	PT thickness	SP thickness	Leaf thickness	LE thickness
LI	NS	NS	**	**	NS	NS
NT	NS	NS	**	NS	NS	*
LI×NT	NS	NS	***	**	NS	NS

Figure 5. Effect of light intensity (LI) and night temperature (NT) on the stomata traits including stomatal density (**A**) and stomatal length (**B**) and the thickness of different tissues in leaf anatomical structure (**C**) of cherry tomato seedlings. LE, lower epidermis; PT, palisade tissue; SP, spongy tissue. A.; B.; C. Thickness. Abbreviations of different treatments were as described in Figure 1. The symbol "NS", "*", "**" and "***" indicate no significance at $p < 0.05$, significant level at $p < 0.05$, $p < 0.01$ and $p < 0.001$ by Duncan's test, respectively. Different letters on bars for the same parameter indicate statistically significant differences ($p < 0.05$).

The correlation analysis showed that the PTT/SPT was significantly positively correlated with the P_N, while spongy tissue thickness was significantly negatively correlated with the P_N; the lower epidermis thickness was highly positively correlated with growth parameters shown in Figure 2. In addition, leaf thickness was significantly correlated with most of the Chl fluorescence parameters (Table S1).

3.6. Carbon and Nitrogen Nutrition Status

The LI and NT as well as their interaction didn't significantly affect soluble protein content but affected the accumulations of carbohydrates and free amino acid (Figure 6A–C). Under NT_L conditions, the content of free amino acid, soluble sugar, and NSC contents were significantly higher at L_M and L_H levels, when compared to those at L_L level, and the contents of sucrose, starch, and NSC also remained at a significantly high level at L_H under NT_H condition. Under L_M conditions, free amino acid content decreased significantly at NT_H conditions, and the contents of soluble sugar, starch and NSC also decreased with an increase of NT under L_M and L_H conditions, which indicated that higher NT hindered the accumulation of carbon and nitrogen in the plant at relatively high LI levels. Compared with other treatments, L_HNT_L gained higher contents of free amino acid, soluble sugar, starch, and NSC. The results showed that higher LI plus lower NT increased the accumulation of carbohydrates and free amino acids.



Factor	Soluble protein	Free amino acid	Soluble sugar	Sucrose	Starch	NSC
L	NS	NS	***	**	***	***
NT	NS	NS	**	NS	***	***
L×NT	NS	***	**	NS	NS	*

Figure 6. Effect of light intensity (LI) and night temperature (NT) on the carbon and nitrogen nutrition status including soluble protein (**A**), free amino acid (**B**) and sugar (**C**) contents of cherry tomato seedlings. NSC, non-structural carbohydrates. Abbreviations of different treatments were as described in Figure 1. The symbol "NS", "*", "**" and "***" indicate no significance at $p < 0.05$, significant level at $p < 0.05$, $p < 0.01$ and $p < 0.001$ by Duncan's test, respectively. Different letters on bars for the same parameter indicate statistically significant differences ($p < 0.05$).

The correlation analysis showed that the contents of soluble sugar, starch, NSC, and free amino acid were significantly correlated with growth parameters shown in Table S1, while the sucrose content was significantly positively correlated with the P_N. In addition,

the nitrogen and carbon nutrition status were also significantly correlated with most of the Chl fluorescence parameters (Table S1).

3.7. Chloroplast Ultrastructure

Electron microscopy revealed an increase in LI, regardless of NT, significantly increased starch granules accumulation and gradually altered chloroplast shape (Figure 7). The chloroplasts exhibited a long shuttle shape under the two lower LI conditions but some chloroplasts have shown a similar trapezoid shape under L_H conditions. Besides, increased LI plus lowered NT level induced larger and more starch granules.

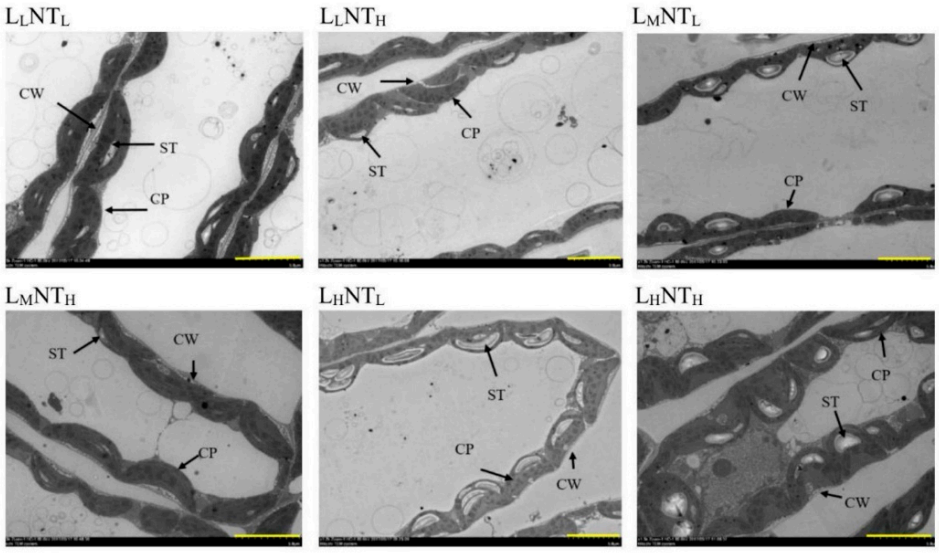


Figure 7. Electron microscopy of chloroplast in palisade tissue of cherry tomato grown under different light intensity (LI) and night temperature (NT). CP, chloroplast; CW, cell wall; ST, starch granule. Abbreviations of different treatments were as described in Figure 1. Scale bar is 5 μm.

3.8. Antioxidants and MDA Content

We measured MDA and antioxidants enzymes activity to evaluate oxidative damage and antioxidant ability. *F*-test showed that LI and NT as well as their interactions had no significant effect on CAT activity and MDA content, but affected the activities of SOD, POD, and AsA content (Table 2). At the same NT level, SOD and POD activities were increased with an increase of LI, and their activities under L_HNT_L were the highest; the AsA content at L_M and L_H levels was significantly higher than those of L_L level under NT_L condition, but that at L_M level was significantly lower than at L_L and L_H levels under NT_H condition. At the same LI level, the SOD activity significantly decreased with an increase of NT, while the POD activity also reduced with an increase of NT at L_H level. The results showed that increasing NT or decreasing LI would partly reduce the antioxidant capacity, and increasing LI plus lowering NT would significantly improve the antioxidant capacity.

The correlation analysis showed that the activities of SOD and POD and AsA content were strongly positively correlated with growth parameters shown in Table S1, soluble sugar, starch, NSC, free amino acid, and lower epidermis thickness. The SOD activity was also positively correlated with the ETR and NPQ, and the activity of POD was positively correlated with the ETR. In addition, the AsA was highly negatively correlated with the D (Table S1).

Table 2. Effect of light intensity (LI) and night temperature (NT) on the antioxidants and MDA of cherry tomato seedlings and LI and NT interaction analysis.

Parameter		SOD (U g^{-1} FM)	POD (U min^{-1} g^{-1} FM)	CAT (mmol min^{-1} g^{-1} FM)	AsA (mg g^{-1})	MDA (μmol g^{-1})
Treatment	L_LNT_L	359.45cd	10.42cd	4.30a	11.85b	0.06a
	L_LNT_H	182.41e	7.92d	4.50a	18.56a	0.05a
	L_MNT_L	547.89ab	10.00cd	4.37a	23.11a	0.05a
	L_MNT_H	259.25de	12.13bc	4.57a	13.73b	0.05a
	L_HNT_L	610.89a	19.79a	4.63a	21.80a	0.05a
	L_HNT_H	452.98bc	14.96b	4.13a	20.61a	0.05a
F-test	L	***	***	NS	**	NS
	NT	***	NS	NS	NS	NS
	L × NT	NS	*	NS	***	NS

Note: Abbreviations of different treatments were as described in Table 1. AsA, ascorbic acid; CAT, catalase; FM, fresh mass; MDA, malondialdehyde; POD, peroxidase; SOD, superoxide dismutase. The symbol "NS", "*", "**" and "***" indicate no significance at $p < 0.05$, significant level at $p < 0.05$, $p < 0.01$ and $p < 0.001$ by Duncan's test, respectively. Different letters within the same columns indicate statistically significant differences ($p < 0.05$).

4. Discussion

4.1. The Growth Promotion Induced by Increasing LI Was Obviously Limited by Higher NT

The present study showed that continuously increased LI, especially at lower NT level, comprehensively improved plants growth quality and physiological traits (Figures 1, 2, 5 and 6, Table 1), which is consistent with the previous results that increased LI allows better performances of Chinese red radish and rape seedlings [26,27]. In this study, however, the promotion induced by the increased LI was obviously limited by higher NT. At NTH conditions, an increase in LI only slightly boosted the health index and dry weights of seedlings (Figure 2).

Under both NT_L and NT_H conditions, an increase of LI boosted carbohydrate accumulation (Figure 6C). High levels of NT are considered to be one of the leading environmental factors resulting in lower yield in cotton, which has been attributed to a negative effect of respiration on carbohydrate accumulation [9]. Our result confirmed the point that the tomato growth limitation under higher NT was strongly correlated with lower carbohydrate accumulation and stronger photorespiration but not dark respiration (Tables S1 and S2). Higher NT significantly decreased starch accumulation, increased R_p, changed the shape, and reduced quantity of starch granule, leading to an obvious reduction in NSC, especially under L_M and L_H conditions (Figures 6C and 7 and Table S2).

Previous results showed that the leaves became thinner in higher temperature environments [28]. It was supported by our findings that when the NT increased, the leaves' thickness gradually became less, which was significantly obvious under high LI.

4.2. Reversible Inactivation of PSII Reaction Center and Photorespiration Caused Tomato Growth Limitation Induced by Higher NT at L_H Condition

The Chl is the fundamental material of plant photosynthesis, participating in the absorption, transmission, and distribution of light energy [29]. Under natural conditions, the light environments are continuously fluctuating resulting in unstable light interception of plant leaves. One of the physiological mechanisms that allows plants to quickly adapt to the fluctuation of both light intensity and light quality is regulating the Chl a/b ratio in leaves [26,30]. Higher Chl a/b is a typical character of plants grown under high LI conditions [26]. The current study showed similar results that, under NT_L conditions, with the increase of LI, the Chl a/b ratio of the treatments gradually increased (Figure 4). The Chl a/b ratio was also affected by light quality (mainly the blue and red light). Exactly, blue light boosted the formation of Chl a, and thus led to a higher Chl a/b ratio, whereas red light induced more Chl b and lower Chl a/b ratio [31]. In this study, the NTs affected

the contents of Chl a and Chl b, as well as the Chl a/b ratio. Especially at L_H condition, the increasing NT significantly reduced the Chl a/b ratio of tomato leaves (Figure 4). It was deduced that the tomato plants grown under L_HNT_H might absorb more red light than blue light compared to the plants grown under L_HNT_L. The plant morphological differences between L_HNT_H and L_HNT_L treatments might be related to the light energy absorbed by plants under the two treatments, because the absorption of blue light excites the electrons to a higher energy state than red light [32].

Correlation analysis showed that Chl a/b was not only highly positively correlated with morphology and dry weight of tomato plants, but also correlated with the Fv'/Fm', ETR, and D (Table S1). Within the pigment molecules, the absorbed light energy excites electrons to a higher state, which is then transferred to the proteins located on the thylakoid membrane, therefore entering into the electron transport chain. In this study, elevated NT at L_H level caused a significant reduction in PhiPS2, qP, Fv'/Fm', and ETR, but a significant increase in the excitation pressure of PSII (E_P), implying a reduction in the utilization of excitation energy through photosynthetic electron transport chain and the excessive accumulation of light energy in PSII. In addition, L_HNT_H also led to more distribution of excitation energy at PSII (higher β) and less excitation energy distribution at PSI (less α), resulting in an imbalance of excitation energy distribution between the two photosystems, which was indicated by a larger $\beta/\alpha - 1$ (Table 1). High PSII excitation energy pressure (namely high E_P and high β) would induce reversible inactivation of the reaction center, and even destroy the structure of PSII and thylakoid membrane, so as to hinder electron transfer and seriously restrict the efficient operation of photosynthetic apparatus. However, the excess excitation energy in the L_HNT_H treatments did not seem to destroy the photosynthetic apparatus but tended to cause relative reversible inactivation of the PSII reaction center, because of no differences in Fv/Fm, R_{FD}, and MDA content between the L_HNT_L and L_HNT_H treatments (Tables 1 and 2). In addition, under NT_H conditions, a higher photorespiration rate indicated that photorespiration also consumed excess energy in order to protect the reaction center of PSII from being damaged by strong light. These reasons ultimately led to relative limitation for photosynthetic function (reflected by the highest L_{PFD}) and lower light energy utilization, and resulted in a growth inhibition of plants in the L_HNT_H treatment (Table 1) [33,34].

4.3. Higher NT at L_M Condition Limited Tomato Growth but Exerted No Excess Excitation Pressure on PSII

Unlike L_H levels, elevated NT at L_M levels did not lead to an imbalance of excitation energy distribution between the two photosystems and excess excitation pressure of PSII, but merely significantly reduced the PhiPS2 and Fv'/Fm', and increased the quotient of absorbed luminous energy used for antenna heat dissipation (D) (Table 1). This result suggested that the enhancement of PSII antenna heat dissipation, in order to maintain the normal excitation pressure of PSII in plants, was one of the main mechanisms of self-protection of photosynthetic apparatus during photosynthesis when increased the NT under L_M condition.

A previous study indicated that AsA also stimulated electron flow and photochemical quenching [35]. In this study, AsA was positively correlated to Fv'/Fm', and when increased NT under L_M, AsA content was also reduced by 75.12%, implying that the restriction in the utilization of excitation energy under L_MNT_H condition was in relation to the reduction in the AsA content (Tables 2 and S1). In addition, AsA and SOD confer higher free radical scavenging ability in plants [36]. At L_M levels, the increased NT significantly reduced AsA content and SOD activity, indicating that increasing NT weakened the antioxidant capacity of plants, thus somewhat limiting the plant growth.

Moreover, significantly less free amino acid was observed under L_MNT_H than that under L_MNT_L, indicating that plants could respond to NT alteration via nitrogen metabolism. The limitation of tomato growth at L_MNT_H is also partly due to some NADPH and ATP consumed in nitrogen reduction [23]. In addition, under L_MNT_H condition, stronger pho-

torespiration increased the inclusion losses in the leaf and slowed down the growth process of plants.

4.4. Elevated NT Performed Compensatory Effect on Plant Growth under Insufficient Light Conditions

In contrast to L_M and L_H levels, elevated NT significantly reduced the relative restriction of photosynthetic performance (L_{PFD}) and could comprehensively improve tomato shoot growth at L_L levels (Figure 1 and Table 1). The dry weight of shoot and plant grown under higher NT was both significantly increased by about 50% compared to those under lower NT (Figure 1). Fan et al. [4] indicated that red and blue composite light of 300 μmol m^{-2} s^{-1} was fit for the culture of young tomato plants, so red, blue, and green composite light of 250 μmol m^{-2} s^{-1} in this study was slight insufficient for tomato growth. However, under L_LNT_H condition, the R_d was largely lower than that under L_LNT_L condition, while the R_p was only slightly higher than that under L_LNT_L condition, suggesting that elevated NT decreased the energy consumption for respiration. The results implied that elevated NT had a compensatory effect on plant growth and the photosynthesis process when LI was not sufficient for tomato growth.

To Cope with the shortage of light, free amino acid, and AsA contents were significantly increased to create a relatively better endogenous environment for energy consumption, electron transfer, and radical scavenging ability, and plants grown under L_LNT_H improved Chl and Car contents (Figures 2C, 3 and 6B, Table 2) [23,36]. An increase of Chl content broadened the light absorption bands (mainly at green and the far-red regions), so we deduced that the plants grown under higher NT might absorb more green light than that grown lower NT at L_L level [24]. The green light sensory systems adjusted growth and development interacting with red and blue sensors [37], and green light can penetrate further into the leaf than red or blue light to promote leaf photosynthesis more efficiently [38]. Correspondingly, at L_L levels, the PhiPS2 of the higher NT treatment was significantly increased (Table 1). Similarly, at L_M levels, higher NT may display a similarly positive effect, but it was overwhelmed by other limiting factors.

5. Conclusions

In summary, different combinations of LI and NT induced differential growth response in tomato seedlings, and the promotion induced by increased LI was limited by higher NTs. The responsive mechanism of tomato plants to higher NT varied with LI levels. At L_H level, higher NT inhibited tomato growth via reducing the leaf area, changing the Chl a/b and chloroplast shape, regulating excitation energy utilization and distribution, and carbon metabolism; while, reducing antioxidant capacity mainly responsible for growth constraints caused by higher NT at L_M level. Whereas, elevated NT has a growth compensation for tomato seedlings under the lowest LI, and higher NT improved tomato growth mainly by improving light energy utilization in low light and physiological indicators, primarily by increasing stomatal length, pigments, free amino acid, and AsA contents, and decreasing R_d. Comprehensive analysis showed that higher LI plus lower NT would be an effective strategy to improve tomato growth, while lower LI plus higher NT might be worth considering as a strategy for tomato production in hot season in view of energy consumption cost in a controlled environment.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy12020343/s1, Figure S1: Electron microscopy of stomata in lower epidermis of cherry tomato grown under different light intensity (LI) and night temperature (NT), Figure S2: Effect of light intensity (LI) and night temperature (NT) on the stomata characteristics, upper epidermis thickness and PTT/SPT of cherry tomato seedlings, Table S1: Correlation analysis among growth, photosynthetic, leaf development and antioxidants parameters, Table S2: Fitted photosynthetic parameters via light/CO_2 response curves under different light intensity and night temperature conditions.

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