Interaction of Supplementary Light and CO₂ Enrichment Improves Growth, Photosynthesis, Yield, and Quality of Tomato in Autumn through Spring Greenhouse Production

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Abstract. During the autumn/spring “off” season, yield and quality of tomatoes are often affected by insufficient CO₂ and low light in greenhouse production. Although tomato is one of the most widely cultivated vegetables, few studies have investigated the interactive effects of supplementary light and CO₂ enrichment on its growth, photosynthesis, yield, and fruit quality in greenhouse production. This study investigates the effects of supplementary light ($200 \pm 20 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and CO₂ enrichment (increases to about $800 \mu\text{mol}\cdot\text{mol}^{-1}$), independently and in combination, on these parameters in autumn through spring tomato production. Compared with tomatoes grown under ambient CO₂ concentrations and no supplementary light (CaLn), supplementary light (CaLs) and supplementary light and CO₂ enrichment (CeLs) significantly promoted growth and dry weight accumulation. Meanwhile, CO₂ enrichment (CeLn) and CaLs significantly improved photosynthetic pigment contents and net photosynthetic (Pn) rates, whereas CeLs further improved these and also increased water use efficiency (WUE). CeLn, CaLs, and CeLs significantly increased single fruit weight by 16.2%, 28.9%, and 36.6%, and yield per plant by 19.0%, 35.6%, and 60.8%, respectively. The effect of supplementary light on these parameters was superior to that of CO₂ enrichment. In addition, CaLs and CeLs improved nutritional quality significantly. Taken together, CeLs promoted the greatest yield, WUE, and fruit quality, suggesting it may be a worthwhile practice for off-season tomato cultivation.

Tomato (*Solanum lycopersicum* Mill.) is one of the most widely cultivated food plants in the world. It enjoys a wide range of uses in the kitchen and contains an abundance of dietary nutrients, including antioxidants (Mamatha et al., 2014). Tomato fruit yield and quality are affected by a large number of environment factors, including the levels of CO₂ and light (Mamatha et al., 2014; Tewolde

et al., 2016). How these two factors can be regulated to maximize fruit yield and quality has been the subject of considerable research. This work should help us meet the increasing food demands of a growing world population.

Atmospheric CO₂ concentration has increased considerably since the beginning of the Industrial Revolution (in 1825, $285 \mu\text{mol}\cdot\text{mol}^{-1}$). By the middle of the past century, it had risen by about 15% (in 1950, $320 \mu\text{mol}\cdot\text{mol}^{-1}$); by the beginning of this century, it had risen by 30% (in 2000, $375 \mu\text{mol}\cdot\text{mol}^{-1}$), and it is now rising faster than ever. The CO₂ level is about $400 \mu\text{mol}\cdot\text{mol}^{-1}$, and this value is projected to double by the end of 21st century (Urban et al., 2014).

However, in a closed greenhouse, as plants absorb CO₂ for photosynthesis, CO₂ levels may fall to as low as $150 \mu\text{mol}\cdot\text{mol}^{-1}$ in bright sunlight (Kläring et al., 2007). Because CO₂ is the key substrate for photosynthesis, CO₂ fertilization is widely accepted as a key technique for enhancing photosynthesis, thus increasing yield and

commercial revenue (Chalabi et al., 2002; Kläring et al., 2007). Numerous studies have shown that CO₂ enrichment can increase growth, affect physiology, and increase both yield and quality in tomatoes (Mamatha et al., 2014; Nilsen et al., 1983; Yelle et al., 1990). Atmospheric CO₂ enrichment can also increase the numbers of branches and leaves, the average leaf area, and the rate of dry matter accumulation in tomatoes (Fierro et al., 1994; Mamatha et al., 2014). Moreover, it may increase photosynthetic rate, while also reducing transpiration, hence significantly increasing WUE (Bencze et al., 2011; Mamatha et al., 2014; Pazzagli et al., 2016; Wei et al., 2018a, 2018b).

However, photosynthetic acclimation may also occur after prolonged periods of CO₂ enrichment (Yelle et al., 1990). Also, although elevated CO₂ levels can promote fruit yield and have positive effects on fruit quality, it can also have negative effects (Mamatha et al., 2014; Zhang et al., 2014). Because regulation of the CO₂ environment in a greenhouse is technically demanding and expensive, the use of CO₂ fertilization is rather limited in China. Therefore, studies on how and to what extent CO₂ enrichment can improve yield of tomatoes in greenhouses seems well worth investigating.

Light is the primary energy source for photosynthesis, so light intensity is one of the key environmental factors driving plant growth (Fukuda et al., 2008). Many studies have reported on the effects of light intensity on the growth of tomatoes (Fan et al., 2013; Hao et al., 2017; O’Carrigan et al., 2014). In general, increasing light intensity increases dry weight gain and stem diameter, but decreases height (Fan et al., 2013). Meanwhile, within certain limits, increases in light intensity result in increases in photosynthesis (Fan et al., 2013), although excessive light intensities cause photoinhibition (Carvalho and Amancio, 2002; O’Carrigan et al., 2014). Because growth and yield of plants is so strongly affected by photosynthetic rate (Yamori, 2013, 2016; Yamori and Shikanai, 2016; Yamori et al., 2016), in greenhouse horticulture, the provision of supplementary lighting significantly increases growth and yield by increasing photosynthesis (Jiang et al., 2017). However, Tewolde et al. (2016) showed that supplementary daytime lighting with light-emitting diodes significantly increased photosynthesis and yield of tomato during winter but not in summer. In winter and early spring, sunlight intensity is low in the early morning and late afternoon. Under these conditions, supplementary lighting significantly enhances growth and yield in tomato.

Previous research has focused largely on the effects of individual factors of supplementary light or supplementary CO₂ on plant growth, yield, and quality (Hikosaka et al., 2013; Mamatha et al., 2014; Yelle et al., 1990; Zou et al., 2016). Urban et al. (2014) reported that the enhancement of photosynthesis under CO₂ enrichment is strongly affected by light intensity. Kaiser et al.

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(2017) reported that CO₂ enrichment can stimulate photosynthesis under conditions of fluctuating irradiance. Bencze et al. (2011) reported that CO₂ enrichment can enhance photosynthesis in tomatoes and peppers even under low-light conditions. Interestingly, combinations of CO₂ enrichment and supplementary lighting can result in greater positive effects on plant growth and yield than enhancement of either factor on its own (Labeke and Dambre, 1998; Naing et al., 2016). To the best of our knowledge, the effects of the combination of supplementary lighting and CO₂ enrichment in winter and spring on the growth of tomatoes have not been thoroughly investigated. The aims of this study were 1) to investigate the effects of supplementary lighting and CO₂ enrichment on tomato yield and quality under the irradiance conditions in northwest China and 2) to seek a practicable method for providing supplemental lighting and CO₂ enrichment for local greenhouse tomato growers, particularly for use in winter and springtime. We also sought to test the hypothesis that there is a positive interaction between supplementary lighting and CO₂ enrichment on the growth and yield of tomatoes.

Materials and Methods

Location and plant materials. The experiment was conducted from 1 Nov. 2016 to 30 Mar. 2017 at the North Experimental Station of Northwest Agriculture and Forestry University, Yangling, China (lat. 34°20'N, long. 108°24'E; altitude, 443.6 m). The region enjoys an average temperature of 12.9 °C, 211 frost-free days, an average annual photoperiod of 2163.8 h, annual solar radiation of 4810 MJ·m⁻², and annual precipitation of 635.1 mm. We used tomato *Lycopersicon esculentum* Mill., cv. Jinpeng No.1. Uniform seedlings with four leaves were cultivated in polyethylene bags filled with a commercial peat-based compost (Yufeng Seed Industry Co., Ltd., Yangling, China) with two seedlings per bag. The plastic bags were 45 × 60 cm, 24 L in volume, and white internally and gray externally.

Experimental design. There were four treatments: 1) ambient CO₂ and no supplementary light (CaLn), 2) elevated CO₂ (about 800 μmol·mol⁻¹) and no supplementary light (CeLn), 3) ambient CO₂ and supplementary light of 200 ± 20 μmol·m⁻²·s⁻¹ (CaLs), and 4) elevated CO₂ and supplementary light (CeLs). Four identical and adjacent 4 × 4 × 2.5-m open-top chambers were established with an aluminum frame and 0.25-mm-thick polythene (ultraviolet proof) in a greenhouse. Each chamber had side and top windows of 0.8 × 1.5 m and contained 60 tomato seedlings. The apical growth was stopped 115 d after transplanting (DAT). CO₂ enrichment was from steel cylinders containing liquid CO₂ (Qinhong gas Co. Ltd., Xianyang, China) and was controlled by a CO₂ infrared (IR) gas analyzer (JSA5-Gas; Shenzhen, China). Supplementary light was provided by high-pressure sodium lamps (HPS1000;

Zhuhai Meiguangyuan, Co. Ltd., Zhushai, China) (see Supplemental Fig. 1 for spectral distribution). These were all controlled by a central control system during the two daily periods 0800 to 1000 HR and 1600 to 1800 HR from 1 Nov. 2016 to 1 Mar. 2017. Irrigation was by dripper, and this and other management occurred according to local commercial practice.

Indices measurement and methods. Environmental data in the chambers were recorded every 30 min from the beginning of the experiment to the end of the treatments. CO₂ concentrations were recorded by a CO₂ analyzer (TPJ-26-I; Zhejiang, China). Photosynthetically active radiation (PAR) at a height of 1.5 m was recorded by a quantum sensor (MQ-100; Apogee, Logan, UT), and temperature and humidity were recorded by a dual external sensor (PDEI-2-2X; Heilongjiang, China).

Before treatment, four plants were selected from the same position in each chamber and marked. At 110 DAT, we measured plant height, stem diameter, and leaf number per plant. The leaf area was determined using a leaf area meter (Li-3000; LI-COR, Lincoln, NE). The plants were then each divided into leaves, stem, and roots, and these fractions were oven-dried to a constant weight (80 °C, 72 h) and weighed.

The gas exchange parameters, including Pn, stomatal conductance (g_s), and transpiration rate (Tr) were measured from 1030–1200 HR on two consecutive sunny days at four stages: seedling, flowering, initial fruiting, and fruiting at 15, 45, 75, and 105 DAT, respectively. Measurements were made with a portable IR photosynthesis analyzer (Li-6400, LI-COR) (n = 6). The light density was set at 800 μmol·m⁻²·s⁻¹, with the block temperature, flow rate, relative humidity, and CO₂ concentration set at 25 ± 1 °C, 500 μmol·s⁻¹, 50% to 65%, and 400 μmol·mol⁻¹, respectively. WUE was calculated as WUE = Pn/Tr (Rasineni et al., 2011).

Leaf pigments were assayed according to Jia et al. (2010), with some modifications (n = 6). Briefly, leaf samples (0.05 g) were ground and placed into 10-mL centrifuge tubes along with 95% ethyl alcohol, then incubated in darkness for 24 h, during which the tubes were shaken up and down gently by hand three times for 30 s each time. The chlorophyll a (Chla) content, chlorophyll b (Chlb) content, and carotenoid content were assayed using a ultraviolet spectrophotometer (ultraviolet-1800; Shimadzu, Kyoto, Japan) at A₆₆₅, A₆₄₉, and A₄₇₀ and calculated according to Lichtenthaler and Wellburn (1983).

Ten plants were selected for uniformity from the middle and sides of each treatment and were tagged before harvest to determine yield characteristics. Ripe fruits were harvested every 5 d during harvest, and fruit number per plant, single fruit weight, and yield per plant were measured. Yield was calculated as tons per hectare.

At harvest, five ripe fruit were selected randomly from each treatment to determine quality index. Soluble sugar content was

measured as follows: Fruit samples (2 g) were homogenized with 5 mL 80% ethyl alcohol, incubated for 30 min in an 80 °C water bath, and centrifuged at 3500 rpm for 10 min. Then, the supernatant was transferred to a 25-mL volumetric flask and the sediment was homogenized and extracted twice. Next, all the supernatants were combined and volumed to 25-mL with extract solution. Then, 2 mL of the solution was transferred to a 10-mL centrifuge tube and dried. After this, 10 mL of distilled water was added and centrifuged at 3500 rpm for 10 min before being diluted 20 times. Last, the mixture, which contained 5 mL of anthrone sulfuric acid and 2 mL of the dilute solution, was boiled for 10 min and measured at A₆₂₀ using a spectrophotometer (ultraviolet-1800, Shimadzu).

The lycopene content was determined using the method of Marković et al. (2006). Briefly, fruit samples (5 g) were homogenized and placed in 200-mL flasks wrapped with aluminum foil. They were then agitated for 10 min after addition of a 100-mL mixture of hexane/acetone/ethanol (2/1/1, v/v/v). After this, 15 mL of distilled water was added to each flask and agitated for another 5 min. The contents were then divided into distinct polar and nonpolar layers. Last, the nonpolar layer containing lycopene was filtered through 0.2-mm filter paper before the filtrate was diluted with the hexane/acetone/ethanol mixture and measured at an absorbance of 470 nm.

Ascorbic acid content was measured according to Kampfenkel et al. (1995). Briefly, fruit samples (0.15 g) were homogenized with 5% (w/v) aqueous trichloroacetic acid and centrifuged for 10 min at 4 °C. The mixtures containing 0.05 mL of the supernatant, 0.1 mL 0.2 M phosphate buffer (pH 7.4), and 6 mM DL-dithiothreitol (DTT) were held in a water bath at 42 °C for 15 min. The excess DTT was then removed by the addition of 0.05 mL 0.5% (w/v) aqueous N-ethylmaleimide for 2 min at room temperature. Last, the mixtures containing 1 mL 10% (w/v) trichloroacetic acid (TCA), 0.8 mL of 42% (v/v) o-phosphoric acid, 0.8 mL of 4% (w/v) a,a'-dipyridyl, and 0.1 mL of 3% (w/v) FeCl₃ were incubated at 42 °C for 40 min and measured at A₅₂₅.

The soluble solids content and organic acid content were measured using a digital refractometer (DG-NXT; ARKO India Ltd., India). Before each measurement, the refractometer was zeroed with distilled water and wiped with mirror paper. Data were recorded as percent Brix and percent organic acid content, respectively.

Data analysis. Data except environmental factors were measured in triplicate and are presented as means ± SE. SPSS 20.0 (IBM Corp., Armonk, NY) was used to examine significant differences among treatments (*P* < 0.05). GraphPad Prism 6 (GraphPad Software Inc., La Jolla, CA) was used to draw graphs.

Results

Environmental factors. The environmental factors during the experimental period are shown in Fig. 1 in terms of the daytime

Fig. 1. Values of CO_2 concentration, light intensity, temperature, and air relative humidity in the greenhouse during the experimental period. (A) Daytime course of CO_2 concentration from 0800 to 1800 HR. The solid line, dotted solid line, dotted line, and circle dotted line represent the four treatments of ambient CO_2 and no supplementary light (CaLn), CO_2 enrichment and no supplementary light (CeLn), ambient CO_2 and supplementary light (CaLs), and CO_2 enrichment and supplementary light (CeLs), respectively. (B) Daytime course of light intensity during a typical sunny day (dotted line) and cloudy day (solid line). (C) Temporal changes in average daytime (solid line) and nighttime (dotted line) temperatures. (D) Temporal changes in air relative humidity (solid line) and average daily light intensity (dotted line). PAR = photosynthetically active radiation; DAT = days after transplanting.

course of CO_2 concentration (Fig. 1A), daytime course of light intensity on sunny days and cloudy days (Fig. 1B), average daytime and nighttime temperatures (Fig. 1C), and air relative humidity and average daily light intensity (Fig. 1D). Under no CO_2 enrichment (treatments CaLn and CaLs), the CO_2 concentration ranged from 382 to 530 $\mu\text{mol}\cdot\text{mol}^{-1}$ during 0800 to 1000 HR and 1600 to 1800 HR each day, whereas under CO_2 enrichment (treatments CeLn and CeLs) CO_2 concentrations were increased significantly to about 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ (Fig. 1A). Meanwhile, the PAR intensity on sunny and cloudy days during the period was low, with maximum light intensities of about 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ on sunny days (Fig. 1B). Average daytime ($\approx 18^\circ\text{C}$) and nighttime ($\approx 12^\circ\text{C}$) temperatures fluctuated first down and then up, then bottomed at the end of Jan. 2017 (Fig. 1C). Average daily light intensity followed the same general pattern as temperature, whereas air relative humidity showed an inverse trend (Fig. 1D).

Effects of CO_2 enrichment and supplementary light on growth and dry weight. All growth parameters, except stem diameter, were significantly increased by CaLs and CeLs, but not significantly by CeLn (Fig. 2). Compared with CaLn, CaLs and CeLs

significantly increased plant height by 12.7% and 14.3%, respectively (Fig. 2A); leaf area was increased by 19.0% and 21.2%, respectively (Fig. 2C); and leaf number by 12.8% and 17.7%, respectively (Fig. 2D). CeLs had the most significant effects on plant height, leaf area, and leaf number, whereas CaLs was ranked second, indicating that CO_2 enrichment enhanced the effects of supplementary light on growth.

Compared with CaLn, CeLn and CaLs significantly increased the dry weight of leaves, roots, and shoots, whereas CeLs increased them further (Table 1). CeLs significantly increased the dry weight of leaves, stems, and roots by 40.0%, 102.1%, and 98.4%, respectively. Hence, it also increased the shoot dry weight and the ratio of root dry weight to shoot dry weight by 57.6% and 26.7%, respectively. Overall, CO_2 enrichment and supplementary light promoted accumulation of dry weight during the vegetative period, and the interaction between CO_2 enrichment and supplementary light was positive.

Effects of CO_2 enrichment and supplementary light on gas exchange and photosynthetic pigment content. Leaf gas exchange parameters including P_n , g_s , and Tr changed significantly with time—first increasing, then

decreasing, and finally increasing. Meanwhile, WUE showed a gradual downward trend (Fig. 3). At the seedling, flowering, and initial fruiting stages, compared with CaLn, CeLn and CaLs increased P_n by 9.2% to 26.8% and by 20.5% to 38.9%, respectively, whereas CeLs increased P_n by 28.1% to 49.5% (Fig. 3A). The value of g_s in CeLn was significantly less than in CaLn, and was less in CeLs than in CaLs, indicating CO_2 enrichment decreased g_s (Fig. 3B). A similar response was observed for Tr , with CaLs having the greatest effect, followed in descending order by CeLs, CaLn, and CeLn (Fig. 3C). On average, in comparison with CaLn, CeLs enhanced WUE by 22.7% to 52.6% before fruiting stage, whereas CeLn and CaLs improved WUE by 16.9% to 49.4% and 9.0% to 24.8%, respectively. However, at fruiting stage, treatment effects were reduced, with CeLn having the greatest WUE (Fig. 3D).

Photosynthetic pigment contents were increased by supplemental light and by CO_2 enrichment to different degrees (Table 2). The content of Chla was greatest under CaLs, followed in descending order by CeLs, CeLn, and CaLn, with significant differences between CaLs, CeLs, CeLn, and CaLn. The content of Chl a+b was most affected by

Fig. 2. Effects of CO₂ enrichment and supplementary lighting on (A) plant height, (B) stem diameter, (C) leaf area, and (D) leaf number of tomato plants grown in a greenhouse. Values represent the means ± SE (n = 4). Different letters indicate significant differences at $P < 0.05$ according to Duncan's multiple range test. CaLn = ambient CO₂ and no supplementary light; CeLn = CO₂ enrichment and no supplementary light; CaLs = ambient CO₂ and supplementary light; CeLs = CO₂ enrichment and supplementary light.

Table 1. Effects of CO₂ enrichment and supplementary light on dry weight distribution of greenhouse-grown tomato plants.

Treatments	Leaf dry wt (g)	Stem dry wt (g)	Root dry wt (g)	Shoot dry wt (g)	R/S ratio
CaLn	22.73 ± 1.33 c	8.97 ± 0.71 c	1.41 ± 0.06 c	31.70 ± 0.87 d	0.05 ± 0.00 b
CeLn	26.88 ± 0.69 b	9.95 ± 0.19 c	1.70 ± 0.09 b	36.83 ± 0.75 c	0.05 ± 0.00 b
CaLs	28.19 ± 1.23 b	15.17 ± 1.69 b	2.12 ± 0.14 a	43.35 ± 2.59 b	0.05 ± 0.00 b
CeLs	31.83 ± 0.85 a	18.13 ± 0.61 a	2.80 ± 0.89 a	49.97 ± 1.39 a	0.06 ± 0.02 a

Values shown represent the means ± SE (n = 4). Different letters in the same column indicate significant differences at $P < 0.05$ according to Duncan's multiple range tests.

R/S ratio = ratio of root dry weight to shoot dry weight; CaLn = ambient CO₂ and no supplementary light; CeLn = CO₂ enrichment and no supplementary light; CaLs = ambient CO₂ and supplementary light; CeLs = both CO₂ enrichment and supplementary light.

CaLs, followed in descending order by CeLn, CeLs, and CaLn. Overall, CaLs had the most significant positive effect on all photosynthetic pigments, promoting Chla, Chlb, and Chla+b contents by 42.28%, 40.50% and 40.84%, respectively. Next for overall photosynthetic pigment content was CeLs.

Effects of CO₂ enrichment and supplementary light on yield characteristics and fruit quality of tomatoes. Single fruit weight, yield per plant, and yield per hectare were significantly increased by CeLn, followed in increasing order by CaLs and CeLs; fruit number per plant, compared with CaLn, was significantly enhanced only by CeLs (Table 3). Compared with CaLn, single fruit weight was significantly increased in CeLn, CaLs, and CeLs by 16.2%, 28.9%, and 36.6%, respectively. Yield per plant (the same as yield per hectare) was also increased in CeLn, CaLs, and CeLs by 19.0%, 35.6%, and 60.8%, respectively. Summarizing, among all treatments, CeLs had the greatest fruit number per plant and greatest single fruit weight, combining to create the greatest fruit yield per plant and total yield. The

results indicate CO₂ enrichment and supplementary light can each significantly improve single fruit weight and yield of tomato, whereas supplementary light was more effective than CO₂ enrichment. Moreover, this result indicates there is a positive interactive effect between these treatments on yield characteristics.

Nutritional qualities were promoted by CaLs and CeLs, but were slightly reduced by CeLn (Table 4). Compared with CaLn, CaLs affected nutrient contents the most, with increases in soluble sugars, lycopene, ascorbic acid, soluble solids, and sugar-to-acid ratio by 42.4%, 17.3%, 38.7%, 7.3%, and 13.1%, respectively. In addition, CeLs markedly increased the contents of soluble sugar, lycopene, and ascorbic acid. There were no significant differences between CeLn and CeLs for lycopene or organic acid. CeLn significantly decreased soluble sugar and lycopene by 25.5% and 21.6%, respectively, but increased ascorbic acid and organic acid by 11.8% and 9.1%, respectively. There were no significant differences in organic acid content among CaLn, CaLs, and CeLs.

Discussion

Previous studies in this area are few (Fierro et al., 1994; Hikosaka et al., 2013; Nilsen et al., 1983). Here we investigate the effects of CO₂ enrichment and supplementary light on photosynthesis, growth, yield, and quality of tomatoes.

Light is the primary source of energy, the intensity and spectral composition (light quality) of which play crucial roles in plant growth, morphological establishment, and physiology (Fukuda et al., 2008; Hernández et al., 2016; Li and Kubota, 2009; Zou et al., 2016). Enhanced light intensity can promote the previously mentioned parameters by optimizing stomatal morphology, enhancing enzyme activity (e.g., Rubisco and 1,6-diphosphate fructose phosphatase) (Li et al., 2017), and affecting the distribution of dry weight (Fan et al., 2013). Appropriate spectral composition may promote the growth and yield of plants (Tsujita and Dutton, 1983). A composite spectrum could enhance photosynthesis compared with red-blue light (Bergstrand et al., 2016). The spectral composition of the high-pressure sodium lamps used in this study was different from that used by others (Hikosaka et al., 2013; Jiang et al., 2017), so it is possible some results will also be different. Because CO₂ is the key substrate for photosynthesis, a high CO₂ concentration may significantly enhance photosynthesis of tomato and pepper (Bencze et al., 2011). However, the effects of CO₂ enrichment are usually modulated by light conditions (Bencze et al., 2011; Kaiser et al., 2017; Urban et al., 2014). Hence, supplementary light should be combined with CO₂ enrichment (Bergstrand et al., 2016), and our research supports this (Fig. 3; Table 3).

In this research, CeLn and CaLs significantly enhanced plant height, leaf area, and leaf number whereas CeLs further enhanced them, suggesting CO₂ enrichment and supplementary lighting exert positive interactive effects on plant growth (Fig. 2). This result agrees with previous studies (Madhana et al., 2014; Naing et al., 2016). Compared with CaLn, dry weight components (leaf, stem, and roots) were significantly affected by CeLn and CaLs, but the greatest affect was with CeLs (Table 1). We found CeLn, CeLn, and CeLs increased dry weight accumulation in shoots and roots, which agrees with the result of Fierro et al. (1994), but they also shifted dry weight to the roots, resulting in a higher root-to-shoot ratio compared with CaLn. This result is consistent with the effects of CO₂ enrichment in grape (Wu and Lin, 2013) and in Rhodes grass (Ksiksi and Youssef, 2010), indicating supplementary light and CO₂ enrichment may promote the uptake of nutrients from culture substrate by altering the distribution of dry weight and thus increasing yields.

We found both photosynthetic pigments (Table 2) and gas exchange parameters (Fig. 3) were increased significantly by CeLn, CaLs and CeLs, which may be the result of enhanced photosynthesis-related enzyme activity (Nilsen et al., 1983; Yu and Wang, 2010). The gas exchange parameters fluctuated with time, which may be the result of the combined

Fig. 3. Effects of CO₂ enrichment and supplementary light on (A) net photosynthetic rate (Pn), (B) stomatal conductance (g_s), (C) transpiration rate (Tr), and (D) water use efficiency (WUE; calculated as Pn/Tr) of tomato plants grown in a greenhouse, with values shown representing means $\pm$ SE (n = 6). DAT = days after transplanting; CaLn = ambient CO₂ and no supplementary light; CeLn = CO₂ enrichment and no supplementary light; CaLs = ambient CO₂ and supplementary light; CeLs = both CO₂ enrichment and supplementary light.

Table 2. Effects of CO₂ enrichment and supplementary light on photosynthetic pigment content in tomato leaves.

Treatments	Chla (mg·g ⁻¹ FW)	Chlb (mg·g ⁻¹ FW)	Carotenoid (mg·g ⁻¹ FW)	Chla+b (mg·g ⁻¹ FW)	Chl a/b
CaLn	1.28 $\pm$ 0.02 d	0.43 $\pm$ 0.01 c	0.29 $\pm$ 0.01 b	1.72 $\pm$ 0.02 c	3.11 $\pm$ 0.13 a
CeLn	1.57 $\pm$ 0.04 c	0.48 $\pm$ 0.02 b	0.32 $\pm$ 0.02 ab	1.99 $\pm$ 0.09 b	3.16 $\pm$ 0.05 a
CaLs	1.82 $\pm$ 0.04 a	0.61 $\pm$ 0.02 a	0.34 $\pm$ 0.01 a	2.423 $\pm$ 0.05 a	3.01 $\pm$ 0.04 a
CeLs	1.68 $\pm$ 0.03 b	0.49 $\pm$ 0.03 b	0.31 $\pm$ 0.02 ab	1.97 $\pm$ 0.05 b	3.06 $\pm$ 0.06 a

Values shown represent the means $\pm$ SE (n = 6). Different letters in the same column indicate significant differences at $P < 0.05$ according to Duncan's multiple range tests.

Chla = chlorophyll a; Chlb = chlorophyll b; Chla+b = the sum of chlorophyll a and chlorophyll b; Chl a/b = ratio of chlorophyll a to chlorophyll b; CaLn = ambient CO₂ and no supplementary light; CeLn = CO₂ enrichment and no supplementary light; CaLs = ambient CO₂ and supplementary light; CeLs = both CO₂ enrichment and supplementary light.

influences of growth status and fluctuating temperature and humidity (Fig. 1). Transpiration of tomato increases with decreasing humidity (Jolliet et al., 1993), which is consistent with our study. g_s and Tr were inhibited by CO₂ enrichment, which may be a result of increased resistance to gas diffusion in mesophyll cells, hence reducing transpiration and increasing WUE. This was consistent with previous studies (Jin et al., 2014; Nabity et al., 2012). In our study, CeLs had the greatest WUE, indicating it can balance water use and carbon assimilation of plants (Wang and Feng, 2012). However, WUE decreased with time, which may be the result of decreasing water uptake and use as a result of decreased temperatures. This mechanism deserves further investigation.

Table 3. Effects of CO₂ enrichment and supplementary light on tomato fruit yield characteristics.

Treatments	Fruit no./plant	Single fruit wt (g)	Yield (kg/plant)	Yield (t/ha)
CaLn	13.28 $\pm$ 0.32 b	116.18 $\pm$ 2.59 d	1.54 $\pm$ 0.04 d	57.72 $\pm$ 1.56 d
CeLn	13.55 $\pm$ 0.48 b	134.97 $\pm$ 2.94 c	1.83 $\pm$ 0.06 c	68.68 $\pm$ 2.34 c
CaLs	13.96 $\pm$ 0.39 b	149.73 $\pm$ 2.29 b	2.09 $\pm$ 0.09 b	78.28 $\pm$ 3.19 b
CeLs	15.53 $\pm$ 0.51 a	158.68 $\pm$ 3.23 a	2.47 $\pm$ 0.09 a	92.79 $\pm$ 3.49 a

Values shown represent the means $\pm$ SE (n = 10). Different letters in the same column indicate significant differences at $P < 0.05$ according to Duncan's multiple range tests.

CaLn = ambient CO₂ and no supplementary light; CeLn = CO₂ enrichment and no supplementary light; CaLs = ambient CO₂ and supplementary light; CeLs = both CO₂ enrichment and supplementary light.

Fruit yield and quality parameters are the primary focus of farmers. Therefore, all kinds of methods have been investigated to achieve them, ranging from agricultural management to gene manipulation (Ho, 2003; Simkin et al., 2015). In the current study, CO₂ enrichment and supplementary light, and the

hypothesis of a positive interaction between them on yield is confirmed (Table 3). This is consistent with previous studies (Ma et al., 2015; Yelle et al., 1990). Nutritional quality is one of the most important factors affecting consumer choice, with lycopene and ascorbic acid being antioxidants that are particularly

Table 4. Effects of CO₂ enrichment and supplementary light on tomato fruit quality.

Treatments	Soluble sugar content (mg·g ⁻¹ FW)	Lycopene content (mg·100 g ⁻¹ FW)	Ascorbic acid content (mg·g ⁻¹ FW)	Soluble solid content (%)	Organic acid content (%)	Sugar-to-acid ratio
CaLn	26.44 ± 2.05 c	7.47 ± 0.56 b	49.95 ± 4.96 c	4.77 ± 0.05 b	0.55 ± 0.03 ab	8.75 ± 0.51 b
CeLn	19.69 ± 1.86 d	5.85 ± 0.08 c	55.84 ± 2.19 b	4.73 ± 0.05 b	0.60 ± 0.11 a	8.19 ± 1.40 b
CaLs	37.64 ± 0.88 a	8.76 ± 0.14 a	69.27 ± 3.96 a	5.12 ± 0.04 a	0.52 ± 0.03 b	9.90 ± 0.55 a
CeLs	31.51 ± 1.38 b	8.35 ± 0.31 a	58.55 ± 1.86 b	4.52 ± 0.08 c	0.57 ± 0.04 ab	7.99 ± 0.54 b

Values shown represent the means ± SE (n = 6). Different letters in the same column indicate significant differences at $P < 0.05$ according to Duncan's multiple range tests. Sugar-to-acid ratio is the ratio of soluble solids content to organic acid content.

CaLn = ambient CO₂ and no supplementary light; CeLn = CO₂ enrichment and no supplementary light; CaLs = ambient CO₂ and supplementary light; CeLs = both CO₂ enrichment and supplementary light.

beneficial for human health (Hooper and Cassidy, 2006). In addition, the soluble solid content, organic acid content, and sugar-to-acid ratio are also important nutritional indexes that affect flavor (Li et al., 2017; Mamatha et al., 2014). CaLs and CeLs improved all these quality parameters except for soluble solid content, whereas CeLn slightly decreased some quality parameters (Table 4). This too is consistent with previous studies (Helyes et al., 2015; Li et al., 2017). This result may be because supplementary light increases the primary and secondary metabolites of photosynthesis, thus enhancing quality, whereas a greater CO₂ concentration may result in greater fruit water content, hence diluting the quality-determining contents (Di, 1999; Li et al., 2017; Mamatha et al., 2014). In this study, it is clear that supplementary light had a greater effect than CO₂ enrichment on growth, yield, and quality. This could be explained by heating effects and should be investigated further. Also, because different CO₂ concentrations and/or different light intensities may exert varying effects on tomato growth and yield, much work should be conducted in the future to explore the optimal combination of CO₂ concentration and light intensity to obtain the greatest yield and quality of tomatoes.

Conclusions

Supplementary light and CO₂ enrichment during winter and spring each enhanced significantly shoot dry weight growth, photosynthesis, and fruit yield of tomatoes grown under greenhouse conditions. The effect of supplementary light on these parameters was superior to that of CO₂ enrichment. The combination of CO₂ enrichment and supplementary light further increased the growth, photosynthesis, yield, and quality of tomatoes. The practice proposed to increase the yield and quality of greenhouse-grown tomatoes in northwest China in winter and spring (November to March) is simultaneous CO₂ enrichment (to 800 μmol·mol⁻¹) and supplementary lighting (to 200 ± 20 μmol·m⁻²·s⁻¹) during the mornings (0800–1000 HR) and afternoons (1600–1800 HR).

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Supplemental Fig. 1. The spectral distribution of high pressure sodium lamps.