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 ± 20 μmol·m⁻²·s⁻¹) and CO₂ enrichment (increases to about 800 μmol·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 (CaLs), 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 and is one of the most widely cultivated food plants in the world. It enjoys a wide range of uses and 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 ± 20 μmol·m⁻²·s⁻¹) and CO₂ enrichment (increases to about 800 μmol·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 (CaLs), 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.

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Commercial revenue (Chalabi et al., 2002; Klarås 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 Amâncio, 2002; O’Carrigan et al., 2014).

Because growth and yield of plants is so strongly affected by photosynthetic rate (Yamori, 2013; Yamori and Shikanai, 2016; Yamori et al., 2012), 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.
(2017) reported that CO$_2$ enrichment can stimulate photosynthesis under conditions of fluctuating irradiance. Bencze et al. (2011) reported that CO$_2$ enrichment can enhance photosynthesis in tomatoes and peppers even under low-light conditions. Interestingly, combinations of CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 *Lycopersicum 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 CO$_2$ and no supplementary light (CaLn), 2) elevated CO$_2$ (about 1200 μmol·m$^{-2}$·s$^{-1}$) and no supplementary light (CeLn), 3) ambient CO$_2$ and supplementary light (CaLn), 4) elevated CO$_2$ and supplementary light (CeLn). Four identical and adjacent 4 × 4 2.5-m open-top chambers were established with an aluminum frame and 0.25-mm-thick polyethylene (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). CO$_2$ enrichment was from steel cylinders containing liquid CO$_2$ (Qinhong gas Co. Ltd., Xianyang, China) and was controlled by a CO$_2$ infrared (IR) gas analyzer (JSAS-Gas; Shenzhen, China). Supplementary light was provided by high-pressure sodium lamps (HPS1000; Zuhuai 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. CO$_2$ concentrations were recorded by a CO$_2$ analyzer (TPJ-26-l; 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 (gs), 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, Lincoln, NE). The light density was set at 800 μmol·m$^{-2}$·s$^{-1}$, with the block temperature, flow rate, relative humidity, and CO$_2$ concentration set at 25 ± 1 °C, 500 μmol·m$^{-2}$·s$^{-1}$, 50% to 65%, and 400 μmol·mol$^{-1}$, respectively. WUE was calculated as WUE = Pn/Tr (Rasenini 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 an 80 °C water bath for 40 min and measured at A$_{470}$ 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 1 mL of 2% (w/v) ascorbic acid and 2 mL of the dilute solution, was boiled for 10 min and measured at A$_{520}$ using a spectrophotometer (ultraviolet-1800, Shimadzu).

The lycopene content was determined using the method of Markovič 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 Kamphoenkel 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 mL 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% (w/v) o-phosphoric acid, 0.8 mL of 4% (w/v) acetic acid, and 0.1 mL of 3% (w/v) FeCl$_3$ were incubated at 42 °C for 40 min and measured at A$_{255}$.

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
course of CO₂ 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 CO₂ enrichment (treatments CaLn and CaLs), the CO₂ concentration ranged from 382 to 530 μmol·mol⁻¹ during 0800 to 1000 HR and 1600 to 1800 HR each day, whereas under CO₂ enrichment (treatments CeLn and CeLs) CO₂ concentrations were increased significantly to about 800 μmol·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 μmol·m⁻²·s⁻¹ on sunny days (Fig. 1B). Average daytime (≥18 °C) and nighttime (≥12 °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 CO₂ 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 CO₂ 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, CO₂ enrichment and supplementary light promoted accumulation of dry weight during the vegetative period, and the interaction between CO₂ enrichment and supplementary light was positive.

Effects of CO₂ enrichment and supplementary light on gas exchange and photosynthetic pigment content. Leaf gas exchange parameters including Pn, gs, 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 Pn by 9.2% to 26.8% and by 20.5% to 38.9%, respectively, whereas CeLs increased Pn by 28.1% to 49.5% (Fig. 3A). The value of gs in CeLn was significantly less than in CaLn, and was less in CeLs than in CaLs, indicating CO₂ enrichment decreased gs (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 CO₂ enrichment to different degrees (Table 2). The content of Chl a 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
CeLn = CO₂ enrichment and no supplementary light; CaLs = ambient CO₂ and supplementary light; CeLs = CO₂ enrichment and supplementary light.

R/S ratio = ratio of root dry weight to shoot dry weight; CaLn = ambient CO₂ and no supplementary light; CaLs, CeLn, and CeLs increased dry weight accumulation in shoots and roots (Table 1). We found CaLn, 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 (Kisiksi and Youssef, 2010), indicating supplemental 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, CaLn, and CeLs, which may be the result of the combined effects of CO₂ enrichment and supplementary lighting 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; Urbán 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 effect was with CeLs (Table 1). We found CaLn, 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 (Kisiksi and Youssef, 2010), indicating supplemental 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 the combined effects of CO₂ enrichment and supplementary light on dry weight distribution of greenhouse-grown tomato plants.

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       | 28.68 ± 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 indicate significant differences at P < 0.05 according to Duncan’s multiple range tests.

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. 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.
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 $T_r$ were inhibited by CO$_2$ 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 2. Effects of CO$_2$ 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 ± 0.02 d          | 0.43 ± 0.01 c          | 0.29 ± 0.01 b                | 1.72 ± 0.02 c           | 3.11 ± 0.13 a |
| CeLn       | 1.57 ± 0.04 c          | 0.48 ± 0.02 b          | 0.32 ± 0.02 ab               | 1.99 ± 0.09 b           | 3.16 ± 0.05 a |
| CaLs       | 1.82 ± 0.04 a          | 0.61 ± 0.02 a          | 0.34 ± 0.01 a                | 2.43 ± 0.05 a           | 3.01 ± 0.04 a |
| CeLs       | 1.68 ± 0.03 b          | 0.49 ± 0.03 b          | 0.31 ± 0.02 ab               | 1.97 ± 0.05 b           | 3.06 ± 0.06 a |

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.

Table 3. Effects of CO$_2$ 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 ± 0.32 b  | 116.18 ± 2.59 d     | 1.54 ± 0.04 d    | 57.72 ± 1.56 d |
| CeLn       | 13.55 ± 0.48 b  | 134.97 ± 2.94 c     | 1.83 ± 0.06 c    | 68.68 ± 2.34 c |
| CaLs       | 13.96 ± 0.39 b  | 149.73 ± 2.29 b     | 2.09 ± 0.09 b    | 78.28 ± 3.19 b |
| CeLs       | 15.53 ± 0.51 a  | 158.68 ± 3.23 a     | 2.47 ± 0.09 a    | 92.79 ± 3.49 a |

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

Table 2. Effects of CO$_2$ enrichment and supplementary light on photosynthetic pigment content in tomato leaves.

Table 3. Effects of CO$_2$ enrichment and supplementary light on tomato fruit yield characteristics.

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, CO$_2$ 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...
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 sugar 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 h) and afternoons (1600–1800 h).

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