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ORIGINAL PAPER

The impact of elevated CO_2 concentration on fruit size, quality, and mineral nutrient composition in tomato varies with temperature regimen during growing season

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Abstract
The negative effects of high temperature on the number of flowers and fruit set of tomato (*Solanum lycopersicum* L.) plants may be mitigated by elevated CO_2 concentration (eCO_2). Moreover, eCO_2 and high temperature have the potential to modify fruit size and nutritional composition in horticultural crops. However, the effects of the combination of both factors are less well understood. Here, we show that eCO_2 increases tomato fruit yield but reduces nutrient content of the fruits of plant grown at a temperature regimen of 27/22 °C day/night compared with 23/18 °C. Fruit concentrations of zinc, magnesium, lycopene, β-carotene, and vitamin C were reduced by warmer temperature, with a more pronounced decrease under eCO_2 than under ambient CO_2 (aCO_2) concentration. The temperature regimen of 27/22 °C also led to a lower soluble sugars concentration in fruits, regardless of CO_2 levels. In addition, we found higher concentrations of boron, manganese, and calcium in fruit of tomato plants at 27/22 °C relative to 23/18 °C, but this effect was less pronounced under eCO_2. Remarkably, the reductions of fruit minerals by eCO_2 at 27/22 °C occurred without a change in the concentrations of macronutrients and micronutrients in leaves, suggesting that eCO_2 and warmer temperature affect mineral transport from source to sink tissues in tomato. Overall, our results revealed that many of the effects of high CO_2 in tomato fruit size and composition are also affected by the temperature regimen during the growing season.

Keywords Climate change · Tomato fruit composition · *Solanum lycopersicum* · Specific leaf area · Warming

Introduction

Atmospheric CO_2 is expected to reach between 550 and 1000 µmol mol^{-1} by the end of century, leading to average air temperature increases of 1 to 4 °C (Ciais et al. 2013). In this context, the ongoing increase of atmospheric CO_2 has the potential to increase tomato (*Solanum lycopersicum*) fruit size, measured as either weight or diameter, via a positive effect on whole-plant photosynthesis, which increases carbohydrate availability for fruits (Jiao et al. 2019). On the other hand, warmer temperatures may reduce flower number and fruit set of tomato plants, thus leading to decreased plant productivity (Harel et al. 2014). For instance, the rates of flower opening and fruit set were lower in tomato plants grown at 26 °C compared with those from plants grown at 22 °C (Adams et al. 2001). It has recently been shown that the inhibitory effect of high temperature on number of flowers and fruit set was overcome when tomato plants were grown under elevated CO_2 (eCO_2), thereby increasing fruit yield (Rangaswamy et al. 2021). These results suggest a certain developmental flexibility of tomato plants under eCO_2, which could improve the yield of plants grown at increasing temperature. However, responses underlying the interaction between CO_2 and temperature are still not fully understood. Since plants grown in natural conditions are exposed to frequent fluctuations in temperature, it is important to test whether the growth flexibility of tomato plant under eCO_2 is affected by the temperature regimen during the growing season.

The combination of eCO_2 and elevated air temperature not only influences productivity, but also affects nutritional

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composition of agricultural crops (Beach et al. 2019; Dusenge et al. 2019). In tomato fruit, total soluble solids (Brix – a measure used in the fruit industry for total soluble solids), ascorbic acid, and lycopene were increased by eCO_2 and decreased by elevated temperature (Rangaswamy et al. 2021; Yang et al. 2020). Thus, physiological studies have shown that high CO_2 and elevated air temperature may have opposing effects on the fruit composition of tomato. In many cases, however, the combined effect of eCO_2 and elevated temperature on tomato fruit composition has been investigated in moderately limiting temperature. For instance, high (700 µmol mol^{-1} air) CO_2 in combination with an elevation of 2 °C above that of the canopy temperature reduced Brix and concentrations of reducing sugars, ascorbic acid, and lycopene in tomato fruit (Rangaswamy et al. 2021).

Brix is a particularly important factor for tomato fruit quality used in the processing industry as it is positively correlated with the amount of product that can be extracted from a fixed quantity of freshly harvested fruit (Liabeuf and Francis 2017). Most tomato cultivars used by the processing industry have determinate growth habit to allow mechanical harvesting (Robbins et al. 2011). Their fruits ripen simultaneously, but tend to have a lower Brix value than indeterminate varieties (Rosseaux et al. 2005). As high CO_2 may affect tomato fruit composition in an opposite manner to elevated temperature, it is possible that the ability of high CO_2 to regulate fruit quality in tomato plants is dependent on the temperature regimen during the growing season. However, it remains unclear how the combination of high CO_2 and increasing temperature between different growing seasons influence the fruit quality of tomato.

Elevated CO_2 and elevated temperature regimen affect mineral composition in the edible parts of the plant, as demonstrated by meta-analyses, mainly on seed crops (Loladze 2014; Myers et al. 2014). For instance, high CO_2 (600 µmol mol^{-1} air) resulted in a lower concentration of minerals in soybean (*Glycine max*) seeds, which, however, was restored by warm temperature (Köhler et al. 2019). The tomato fruit is a source of macro- and micronutrients important for human health (Guil-Guerrero et al. 2009). In tomato plants, eCO_2 reduced the concentrations of Mg, N, Zn, and Mn in the fruit, but increased the concentrations of Ca, Fe, and Cu at 35/14 °C day/night temperature regimen (Khan et al. 2013). In this temperature range, there were no differences in concentrations of K in tomato fruit under eCO_2 (Khan et al. 2013). On the other hand, K, Ca, and Mg showed higher accumulation in the fruit of tomato plants grown under ambient CO_2 (aCO_2) at 25/15 °C day/night temperature regimen (Inthichack et al. 2013). These results suggest that, when assessing fruit mineral composition of tomato plants, the combined effects of eCO_2 and growth temperature should be taken into account. However, information on the interaction of eCO_2 and growth-season air temperature on mineral composition of tomato fruits is hitherto limited. In this study, we test the hypothesis that effects of high CO_2 on tomato fruit size and nutrient composition are dependent on temperature during the growing season.

Materials and methods

Plant material and experimental setup

All experiments were conducted using tomato (*Solanum lycopersicum* L.) cultivar 'Teteia', a landrace with determinate growth donated by tomato producers from the State of Goias, Brazil. It is currently stocked as accession UFV-605125 in the Federal University of Viçosa's (UFV) Plant Biology Department germplasm collection. Seeds were sown into trays containing commercial substrate (Tropstrato HT, Mogi Mirim, Brazil) and germinated in a greenhouse at the UFV (20º 45'S, 42º 15'W, 650 m altitude), Viçosa, Minas Gerais, Brazil. When the first true leaf appeared, seedlings were planted singly in 3.5 L pots containing commercial substrate supplemented with 1 g L^{-1} 10:10:10 NPK and 4 g L^{-1} dolomite limestone. After five days, plants were selected for uniformity and moved to six open-top chambers (1.2 m diameter and 1.4 m high; 8 plants per chamber) with either aCO_2 (410 ± 20 µmol mol^{-1} air) or eCO_2 (650 ± 50 µmol mol^{-1} air) as described by Brito et al. (2020). Treatment with eCO_2 was designed to represent the likely climate scenario in the second half of this century (Ciais et al. 2013). Routine practices for tomato cultivation were used, including 2 g N (as urea), 1.5 g P (as single super phosphate) and 5 g K (as KCl) fertilization applied with irrigation water. Experiments were carried out over two consecutive growth seasons (2019 and 2020) in open-top chambers in the greenhouse of the UFV under natural photoperiod to investigate the combined effect of rising CO_2 and warming growing-season temperature on fruit size and composition of tomato. The daily light integrals, vapor pressure deficit and air temperature inside the chambers during the two growing seasons are shown in Table S1. The mean day/night air temperature over the 2020 growing season was on average 4 °C higher than the 2019 season, with natural fluctuations but no difference between CO_2 treatments within each season (Fig. 1a, b and Table S1).

Phenotypic measurements

Tomato plants were harvested 45 days after germination to determine growth traits. Leaf area was determined using a LI-3100 area meter (Li-Cor, Lincoln, NE, USA). Roots, stems, and leaves were then oven-dried at 70 °C until constant mass to determine dry mass. Specific leaf area was

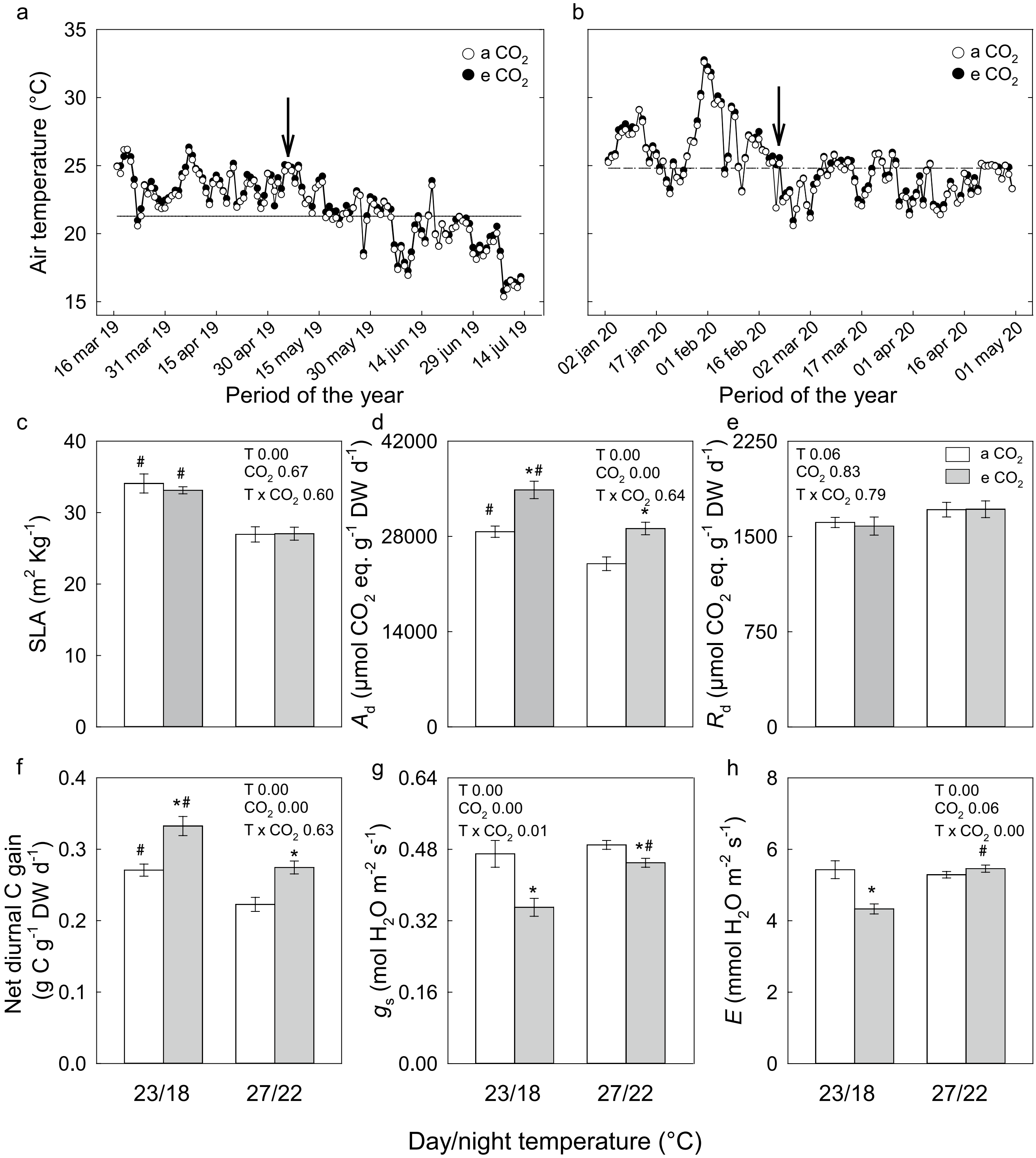


Fig. 1 Effects of CO_2 conditions and temperature during development of tomato plants. **a-b** Fluctuation of daily air temperature inside the open-top chambers supplemented with ambient (open circle) or elevated (filled circle) CO_2 during the course of experiments. Solid and dashed lines represent data at 23/18 °C and 27/22 °C day/night temperature regimens throughout March to July 2019 and January to May 2020, respectively. Arrows indicate days after planting that the first flower appears. The number of days needed for tomato plants to start to flower was as follows: 51.2 ± 0.6 days and 51.5 ± 0.5 days at 23/18 °C in plants grown under aCO_2 and eCO_2, respectively; 51.4 ± 0.4 days and 51.3 ± 0.6 days at 27/22 °C in plants grown under aCO_2 and eCO_2, respectively. **c** Specific leaf area. **d** Rate CO_2 assimilation on a per day basis. **e** Nighttime respiration rate on a per day basis. **f** Net diurnal carbon gain. **g** Stomatal conductance. **h** Transpiration rate. Asterisks indicate statistically different means between plants grown under ambient and elevated CO_2 within the same temperature regimen ($P < 0.05$). Hashtags indicate statistically different means between plants grown under 23/18 °C and 27/22 °C temperature regimens within the same CO_2 concentration ($P < 0.05$). Values are means ± SEM ($n = 10$)

calculated through the relationship between leaf area and dry mass.

Individual flowers were tagged on the day of anthesis, and fruit set percentage of tomato plants was calculated as the ratio of number of fruits to total number of flowers. The number of fruits per plant, yield, average weight per fruit, and Brix in fruits were assessed 100 days after germination. Fresh fruit weight was calculated by dividing the total fruit weight by the total fruit number on each plant. For determination of fruit dry weight, slices of fruits were oven-dried at 70 °C until constant weight. Brix was measured with a digital refractometer (model RTD 45, Instrutherm®, São Paulo, Brazil).

Gas exchange measurements

Gas exchange analyses were performed in tomato plants at 45 days after germination. The measurements were made on the third fully expanded leaf between 9:00 and 11:30 h using an open-flow gas exchange system infrared gas analyzer (LI-6400XT, LICOR, Lincoln, NE, USA). The analyses were performed under photon flux density of 1000 μmol photons m^{-2} s^{-1} at the day growth temperature of the plants and the reference CO_2 concentration was maintained at 410 μmol mol^{-1} air (for plants under aCO_2) and 650 μmol mol^{-1} air (for plants under eCO_2) using a CO_2 injector and compressed CO_2 cartridge. Dark respiration was measured between 1:00 and 3:00 am at the respective night growth temperature of the tomato plants. The rate of CO_2 assimilation and nighttime respiration rate on a per day basis as well as the net diurnal carbon gain were calculated as described by Pyl et al. (2012).

Biochemical analysis

Six fruits from each treatment were harvested at red ripe stage (56 days after anthesis) and then fruit pericarp samples were ground to a fine powder in liquid nitrogen and stored at − 80 °C until analysis. The procedure of extraction and assay of sucrose, glucose, fructose, and total amino acids was performed according to the method described by Cross et al. (2006), with 100 mg frozen fruit material. Ascorbic acid content was determined as described by Stevens et al. (2008) and total phenolics compounds as described by Fu et al. (2011). For carotenoids measurements, frozen fruit material was extracted and analyzed for concentration of lycopene, β-carotene, and lutein using high performance liquid chromatography (HPLC, Agilent 1200, New York, equipped with an Eclipse XDB-C_{18} column) as described by Zhang et al. (2014). The pericarp structural carbon content was determined as described by Prudent et al. (2009).

Mineral analysis

Six fruits from each treatment were harvested at red ripe stage (56 days after anthesis) and fruit pericarp samples were dried at 65 °C until a constant weight, ground to a fine powder using a pestle and mortar, and then digested in concentrated nitric acid. Concentrations of P, K, Ca, Mg, S, Cu, B, Fe, Mn, Zn, and Mo were analyzed by inductively coupled plasma-optical emission spectroscopy (ICP-OES, Perkin-Elmer, Shelton, CT) as described by Wheal et al. (2011). Concentrations of N in fruit pericarp samples were determined by the Dumas combustion method (Jung et al. 2003).

Statistical analysis

The experiments were designed in a completely randomized distribution. Two-way analysis of variance (ANOVA, $P < 0.05$) was applied to compare the means of the measured parameters with the factors temperature and CO_2 concentration. The F-test was used to assess the differences between CO_2 concentrations within each temperature regimen and vice versa. All statistical analyses were performed using the R program version 4.0.2.

Results

Growth and fruit yield of tomato plants in response to $CO_2$and temperature

To characterize the responses of vegetative and reproductive development in tomato plants to changes in CO_2 concentration and temperature, tomato plants were grown in a 2 × 2 factorial design of aCO_2 (410 μmol mol^{-1} air) and eCO_2 (650 μmol mol^{-1} air) at both 23/18 °C and 27/22 °C day/night temperature regimens (Fig. 1a, b). Specific leaf area decreased by 20% in plants grown at 27/22 °C compared with those grown at 23/18 °C, when averaged across CO_2 conditions (Fig. 1c). The temperature regimen of 27/22 °C also led to lower daily CO_2 assimilation. In this context, the cumulative amount of carbon that was assimilated in the light (A_d) decreased by 17% and 16% at 27/22 °C compared with plants grown at 23/18 °C under aCO_2 and eCO_2, respectively (Fig. 1d). No differences between CO_2 and temperature treatments were found in night-time respiration (R_d) (Fig. 1e). The net diurnal carbon gain of tomato plants is the difference between A_d and R_d (Fig. 1f). Compared with 23/18 °C, net carbon gain decreased by 18% under aCO_2 and 17% under eCO_2 in the 27/22 °C regimen. Stomatal conductance (g_s) and transpiration rate (E) increased at 27/22 °C compared with plants at 23/18 °C under eCO_2 but not under aCO_2, leading to T × CO_2 interaction (Fig. 1g, h). No differences were found on time to flowering between temperature and CO_2 treatments (indicated by arrows on Fig. 1a, b). We next examined the effect of CO_2 and temperature on agronomic traits during reproductive development. Plants grown at 27/22 °C displayed increased number of flowers compared with plants at 23/18 °C under both CO_2 conditions, but with a reduction in fruit set percentage (Fig. 2a, b). Moreover, the number of fruits per plant was not significantly different between the treatments (Fig. 2c).

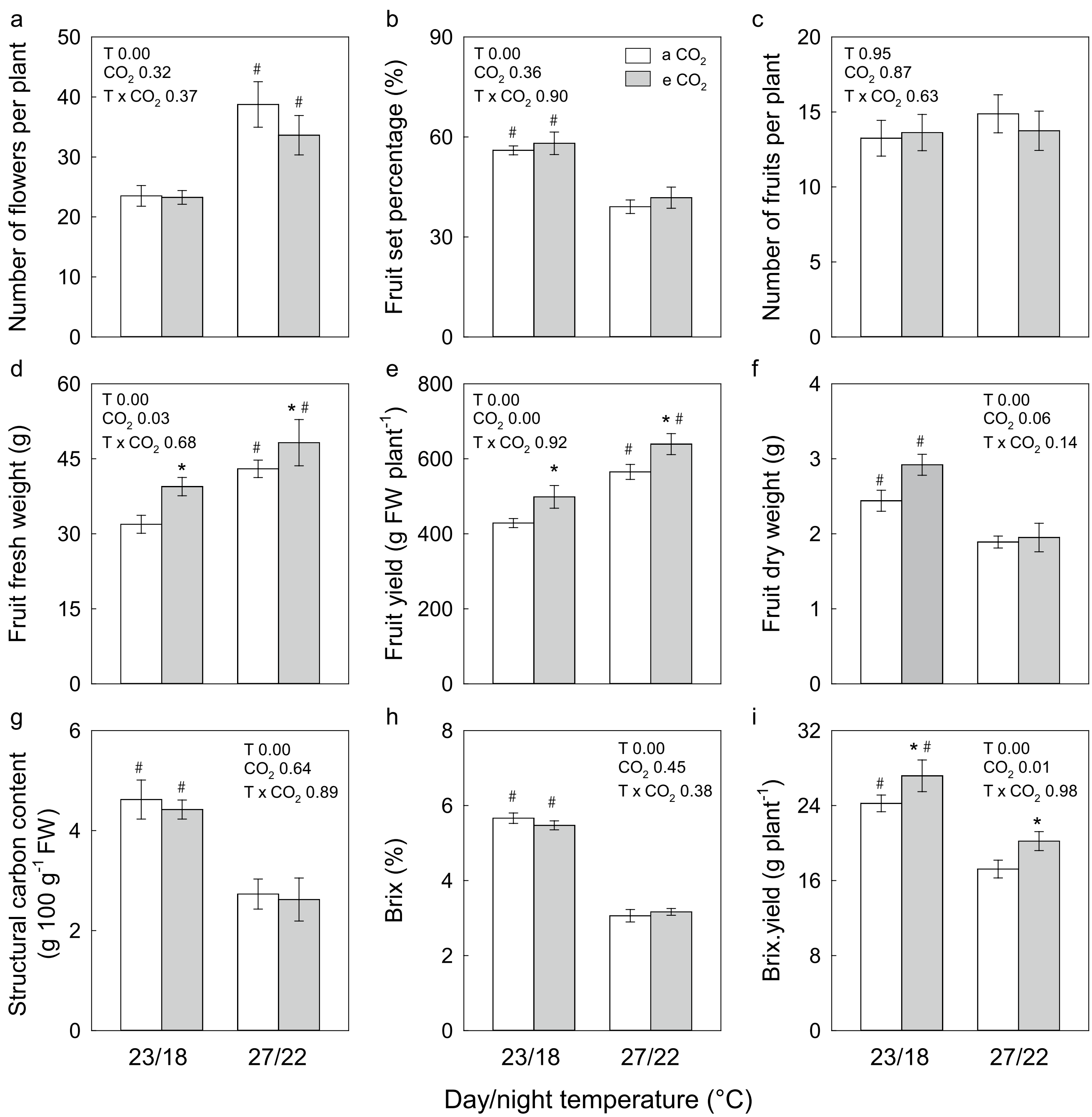


Fig. 2 Changes in physiological parameters observed in tomato plants in response to CO_2 and temperature treatments. **a** Number of flowers per plant. **b** Fruit set percentage. **c** Number of fruits per plant. **d** Fruit fresh weight. **e** Fruit yield. **f** Fruit dry weight. **g** Pericarp structural carbon content. **h** Brix. **i** The product of Brix × ripe yield. Asterisks indicate statistically different means between plants grown under ambient and elevated CO_2 within the same temperature regimen ($P < 0.05$). Hashtags indicate statistically different means between plants grown under 23/18 °C and 27/22 °C temperature regimens within the same CO_2 concentration ($P < 0.05$). Values are means ± SEM ($n = 10$)

Compared with 23/18 °C, individual fruit fresh weight increased by 25% under aCO_2 and 18% under eCO_2 at 27/22 °C (Fig. 2d). Tomato plants grown at 27/22 °C displayed higher fruit yield (24% at aCO_2; 22% at eCO_2) when compared with plants at 23/18 °C (Fig. 2e). There was a slight upward trend for fruit fresh weight and fruit yield under eCO_2 compared with aCO_2 at both temperature regimens (Fig. 2d, e). The fruit dry weight did not differ between CO_2 conditions within each temperature treatment (Fig. 2f). However, fruit dry weight decreased by 27% in plants grown at 27/22 °C compared with those at 23/18 °C, when averaged across CO_2 conditions. The pericarp structural carbon content was lower in 27/22 °C than 23/18 °C across CO_2 conditions (Fig. 2 g). Additionally, Brix in tomato fruits was lower at 27/22 °C than at 23/18 °C regardless of CO_2 conditions (Fig. 2h). The product of Brix × ripe yield (BxY), also called 'horticultural yield', a key agronomic parameter in processing tomato, decreased by 29% under aCO_2 and 25% under eCO_2 at 27/22 °C compared with 23/18 °C (Fig. 2i). Moreover, B × Y of mature fruits was slightly higher under eCO_2 compared with aCO_2 at both temperature regimens.

Effects of CO_2 and temperature on tomato fruit nutritional composition

Concentrations of total phenols, glucose, fructose, and sucrose were affected by temperature but not by CO_2 treatment (Fig. 3a–d). In this context, concentrations of total phenols, glucose, fructose, and sucrose decreased in fruits of plants grown at 27/22 °C compared with 23/18 °C regardless of the CO_2 level (Fig. 3a–d). On the other hand, concentrations of lutein, lycopene, β-carotene, total amino acids, and ascorbic acid in fruit were significantly affected by both temperature and CO_2 treatments (Fig. 3e–i). Compared with 23/18 °C, concentrations of lutein and lycopene in fruit decreased by 35% and 14% under ambient CO_2 and 41% and 34% under elevated CO_2 at 27/22 °C, respectively (Fig. 3e, f). There was a significant T × CO_2 interaction for concentrations of lycopene, β-carotene, total amino acids, and ascorbic acid (Fig. 3f–i). Concentrations of β-carotene and total amino acids in fruits were lower at 27/22 °C than at 23/18 °C across the CO_2 treatments (Fig. 3g, h). Ascorbic acid (vitamin C) concentration was 34% lower under elevated eCO_2 in fruits of plants grown at 27/22 °C compared with 23/18 °C (Fig. 3i).

Changes in the fruit mineral accumulation in response to CO_2 and temperature

Irrespective of CO_2 conditions, temperature of 27/22 °C resulted in a positive effect on concentration of P in the tomato fruits but a negative effect on the concentration of N and K (Fig. 4a-c). The fruit Ca concentration was increased by eCO_2 at 23/18 °C (Fig. 4d). On the other hand, temperature of 27/22 °C increased fruit Ca concentration irrespective of CO_2 conditions. Elevated CO_2 decreased concentrations of Mg in fruits of plants grown at 27/22 °C compared with 23/18 °C (Fig. 4e). The ability of the tomato fruit to accumulate S and B depended both on the temperature and CO_2, but the effects of these environmental factors were independent, *i.e.*, eCO_2 increased S and B at both temperature regimens (Fig. 4f, g). There was a significant T × CO_2 interaction for concentrations of Zn and Mn in tomato fruits (Fig. 4h, i). Under eCO_2, fruit Zn concentration decreased by 27% at 27/22 °C compared with 23/18 °C (Fig. 4h). Under aCO_2, fruit Mn concentration increased by 37% at 27/22 °C compared with 23/18 °C (Fig. 4i). On the other hand, temperature regimen of 27/22 °C decreased fruit Mn concentration by 20% under eCO_2 compared with aCO_2. Elevated CO_2 itself significantly increased the concentration of Fe in fruits, when compared with fruits that developed under aCO_2 in both growing seasons (Fig. 4j). The main effect of the environmental treatments (T and CO_2) was significant for fruit Cu concentration, showing a decrease at 27/22 °C compared with 23/18 °C but an increase under eCO_2 compared with aCO_2 (Fig. 4k). There were no differences in fruit Mo concentration across treatments (Fig. 4l).

Discussion

The ongoing increases of atmospheric CO_2 concentration and temperature are expected to have strong effects on agronomic parameters of crops (Dusenge et al. 2019; Moore et al. 2021). However, little is known about how plants respond to eCO_2 in conjunction with increased temperature. Here, we investigated the effect of eCO_2 on fruit size and composition of tomato plants grown at 23/18 °C and 27/22 °C day/night temperature regimens. The results showed that eCO_2 and temperature regimen of 27/22 °C had a synergistic effect increasing tomato yield, but simultaneously leading to a decrease in the concentration of some of the key nutrients found in the fruit. This finding has implications for horticultural production in the face of rising CO_2 and global warming.

The effects of temperature and CO_2 on tomato development and phenology

Temperature and CO_2 are important environmental factors influencing the timing of the vegetative-to-reproductive transition in tomato plants (Raza et al. 2019). Our results revealed that the temperature regimen of 27/22 °C combined with eCO_2 did not alter the timing of developmental transitions in tomato plants, as evidenced by the unchanged number of days needed for tomato plants to reach the flowering

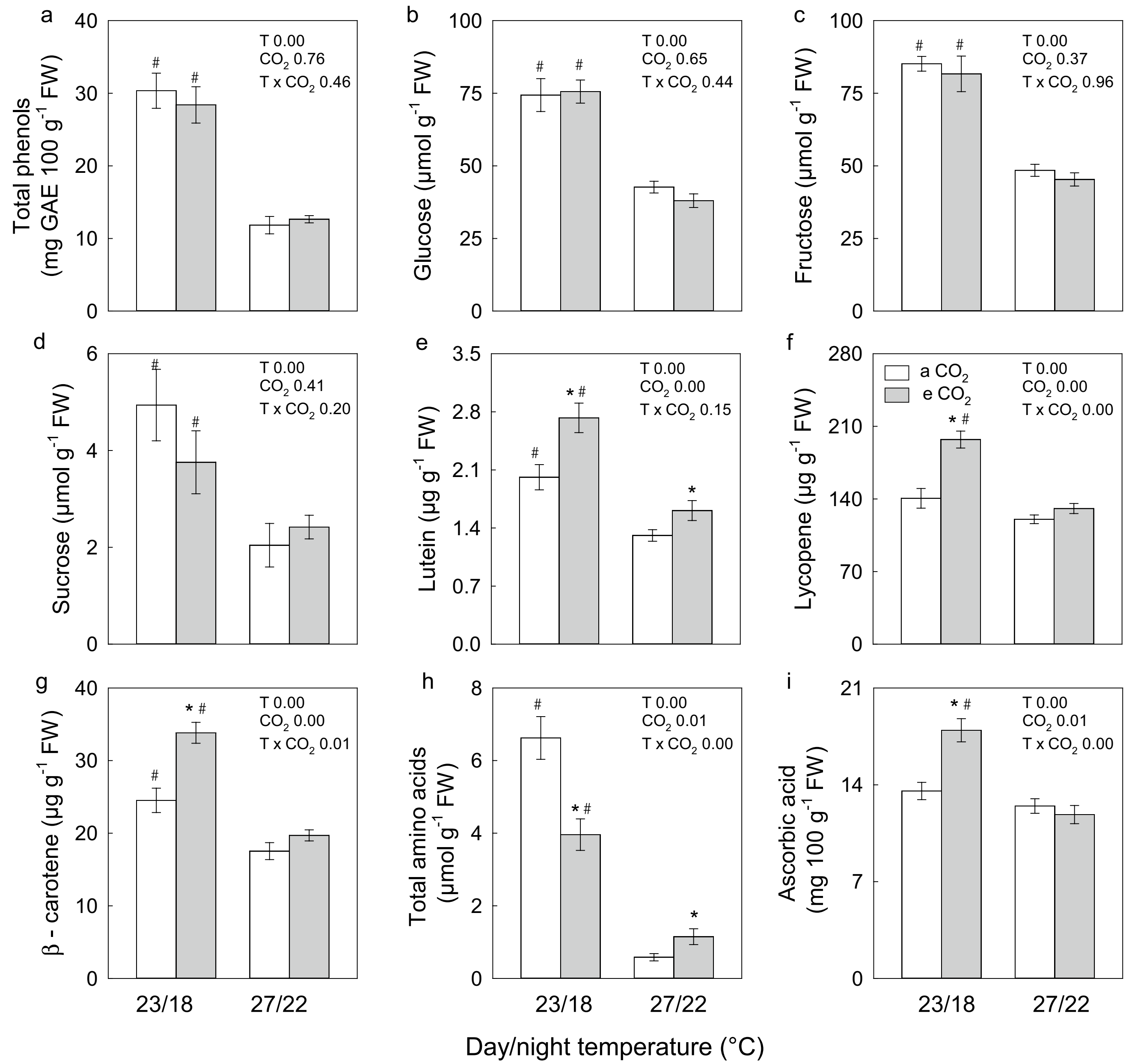
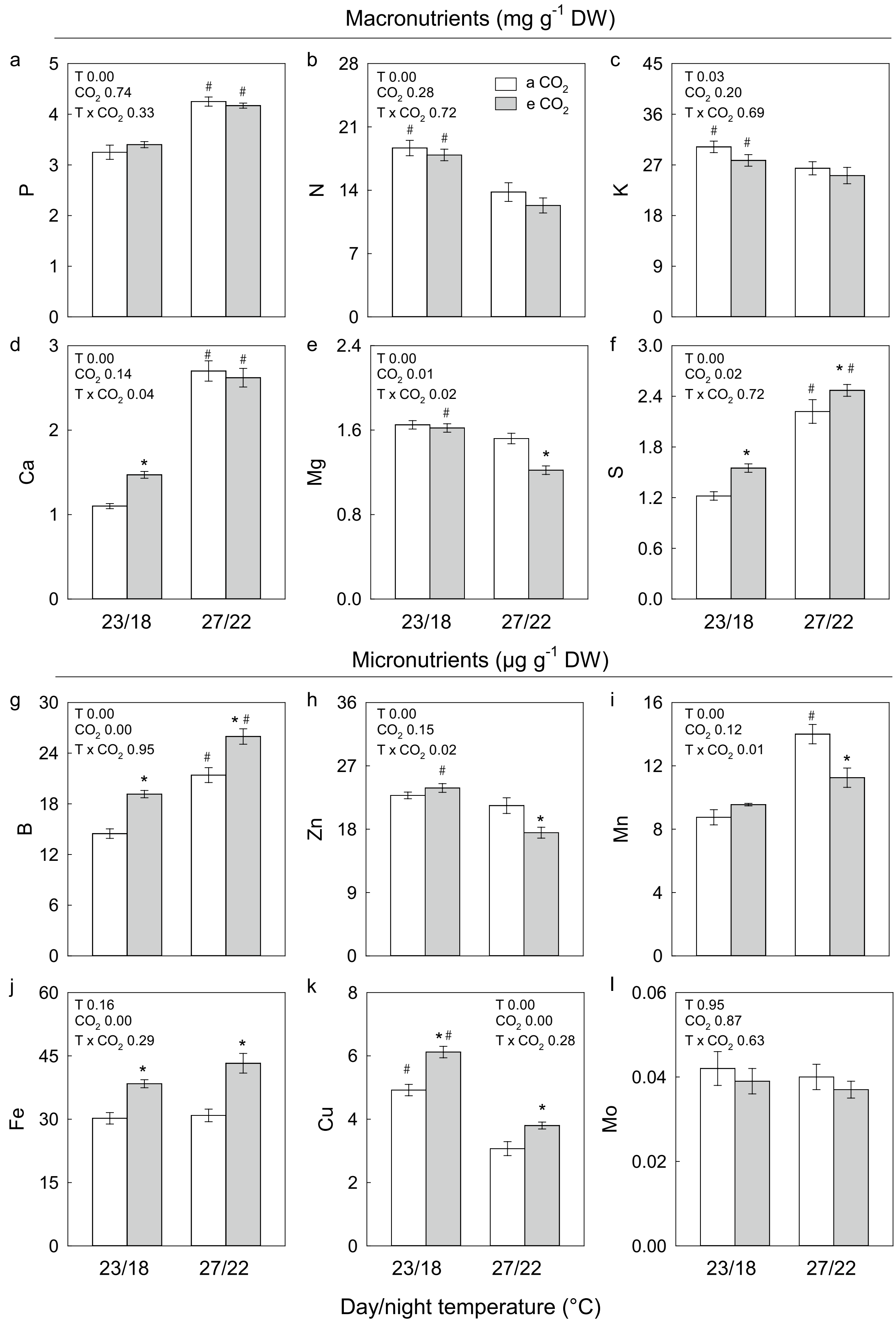


Fig. 3 Changes in tomato fruit composition in response to CO_2 and temperature treatments. **a** Total phenols. **b** glucose. **c** Fructose. **d** Sucrose. **e** Lutein. **f** Lycopene. **g** β-Carotene. **h** Total amino acids. **i** Ascorbic acid. Asterisks indicate statistically different means between plants grown under ambient and elevated CO_2 within the same temperature regimen ($P<0.05$). Hashtags indicate statistically different means between plants grown under 23/18 °C and 27/22 °C temperature regimens within the same CO_2 concentration ($P<0.05$). Values are means ± SEM ($n=6$). GAE, Gallic acid equivalents

stage (Fig. 1). Interestingly, the number of flowers and the rate of fruit set in the tomato plants were not affected by CO_2 condition (Fig. 2), whereas an optimum temperature for early reproductive development was observed. Thus, the increase in average of number of flowers per plant at 27/22 °C appears to be balanced by reduced fruit set, so that there is no significant difference in mean fruit number between treatments (Fig. 2). Experiments manipulating source-sink relationships have previously demonstrated that carbon limitation is a major component of flower and fruit abortion in horticultural crops (Osorio et al. 2014). Temperature regimen of 27/22 °C led to a decrease in the net diurnal carbon gain in tomato plants, irrespective of the CO_2 conditions (Fig. 1). This finding has two implications. First, flowering in tomato plants appears to be buffered against changes in carbon availability. Second, temperature is the primary signal that controls fruit set within a given atmospheric CO_2 concentration.


Macronutrients (mg g-1 DW)
a
T 0.00
CO2 0.74
T x CO2 0.33
P
b
T 0.00
CO2 0.28
T x CO2 0.72
a CO2
e CO2
N
c
T 0.03
CO2 0.20
T x CO2 0.69
K
d
T 0.00
CO2 0.14
T x CO2 0.04
Ca
e
T 0.00
CO2 0.01
T x CO2 0.02
Mg
f
T 0.00
CO2 0.02
T x CO2 0.72
S
23/18
27/22
Micronutrients (µg g-1 DW)
g
T 0.00
CO2 0.00
T x CO2 0.95
B
h
T 0.00
CO2 0.15
T x CO2 0.02
Zn
i
T 0.00
CO2 0.12
T x CO2 0.01
Mn
j
T 0.16
CO2 0.00
T x CO2 0.29
Fe
k
T 0.00
CO2 0.00
T x CO2 0.28
Cu
l
T 0.95
CO2 0.87
T x CO2 0.63
Mo
23/18
27/22
Day/night temperature (°C)

◂**Fig. 4** Macro and microelement concentrations in fruits of tomato plants grown under aCO_2 and eCO_2 at both 23/18 °C and 27/22 °C temperature regimens. **a** Phosphorus. **b** Total nitrogen. **c** Potassium. **d** Calcium. **e** Magnesium. **f** Sulphur. **g** Boron. **h** Zinc. **i** Manganese. **j** Iron. **k** Copper. **l** Molybdenum. Asterisks indicate statistically different means between plants grown under ambient and elevated CO_2 within the same temperature regimen ($P<0.05$). Hashtags indicate statistically different means between plants grown under 23/18 °C and 27/22 °C temperature regimens within the same CO_2 concentration ($P<0.05$). Values are means ± SEM ($n=4$)

Floral development and fruit set of tomato plants are also known to be at least partly under the control of essential nutrients availability in source leaves (Quinet et al. 2019). For example, B concentration in source leaves plays an important role in the flowering process, whereas K concentration is important to support fruit set (Sainju et al. 2003). We observed that temperature regimen of 27/22 °C had a positive effect on B concentration and a negative effect on K concentration in tomato leaves under both CO_2 conditions (Fig. S1), which may also explain why the temperature regimen of 27/22 °C increased the number of flowers but reduced the rate of fruit set (Fig. 2). Together, these results imply that temperature regimen of 27/22 °C lead to changes in early fruit development in tomato plants that are independent of changes in atmospheric CO_2 concentration.

Temperature regimen of 27/22 °C and eCO_2 increase tomato fruit yield

The later stages of tomato fruit development rely on a continuous supply of carbohydrates from source leaves (Ho et al. 2019). Our study revealed that the increase in fruit size, measured as fresh weight, depended on both temperature regimens and concentrations of CO_2, but the effects of these factors were independent, *i.e.*, eCO_2 increased slightly fruit growth for both temperature regimens (Fig. 2). In fact, eCO_2 increased the amount of carbon that was accumulated in the light period and remobilized at night in tomato plants grown at both temperature regimens (Fig. 1). However, the increase in leaf protein concentration under eCO_2 at both temperature regimens (Fig. S1) is likely to result in higher growth costs because the assimilation of inorganic nitrogen into amino acids and the subsequent metabolic conversion of amino acids into protein are energetically expensive processes (Pyl et al. 2012). In addition, temperature regimen of 27/22 °C led to a decrease in specific leaf area and amount of carbon fixed per day in plants grown under either CO_2 conditions (Fig. 1). Thus, one potential explanation for the increase in fruit fresh weight at 27/22 °C would be that there is a decrease in structural components of the fruits. Our finding that there is a decrease in pericarp structural carbon content and dry weight of the fruit at 27/22 °C is consistent with this hypothesis (Fig. 2). This resembles a previous study with tomato plants, in which higher fruit fresh weight was associated with a decreased structural carbon content under high fruit load conditions (Prudent et al. 2009).

Despite the differences in fruit fresh weight and structural carbon content, the fruit number per plant was similar in all temperature and CO_2 conditions investigated (Fig. 2). Thus, a central feature of our results is that temperature regimen of 27/22 °C had a larger effect on amount of carbon fixed per day than carbon competition. This is accompanied by lower concentrations of sugars on a fresh weight basis and decreased in Brix in fruits of plants at 27/22 °C grown under both CO_2 conditions (Figs. 2, 3). Reduced irrigation regimen combined with high CO_2 cause an increase in soluble solid content in tomato fruit (Yang et al. 2020). Therefore, interactions of temperature with soil water content that lead to altered fruit quality must be considered in the context of climate change. This is indeed realistic when considering the temperature regimen of 27/22 °C coupled to the significant drop in B × Y, an important agronomic parameter for tomato plants, under different CO_2 conditions (Fig. 2).

Detrimental effects of temperature and CO_2 on tomato fruit nutrient content

Tomato fruits are important source of minerals elements and functional metabolites that are important for human nutrition (Guil-Guerrero et al. 2009). In this context, antioxidants in tomato fruits such as lycopene, β-carotene, ascorbic acid, and phenolic compounds play a significant role in their nutritional quality for humans (Ali et al. 2021). Earlier results showed that eCO_2 led to an increase in concentrations of carotenoids and ascorbic acid in tomato fruit on a fresh weight basis (Zhang et al. 2014). However, temperature regimen of 27/22 °C counteracted the increase in concentrations of lycopene, β-carotene, and ascorbic acid in fruits driven by the combination of eCO_2 with 23/18 °C temperature regimen (Fig. 3). Thus, temperature is an important factor in determining the concentrations of carotenoids and ascorbic acid in tomato fruit on a fresh weight basis. Temperature regimen of 27/22 °C was also shown to have a negative effect on the concentration of total phenols and lutein (Fig. 3). The decrease in concentrations of antioxidant compounds may be related to an increase in fruit fresh weight of tomato plants grown at a temperature regimen of 27/22 °C under both CO_2 conditions. Our finding of a negative correlation of fruit fresh weight and total antioxidant content defined as the sum of lycopene, β-carotene, lutein, ascorbic acid, and total phenols is consistent with this hypothesis (Fig. S2). These results suggest that growth of tomato plants under eCO_2 at 27/22 °C is not an effective means of increasing the antioxidant capacity of fruits. Therefore, it may be expected that the cultivation of tomato plants under future climate conditions will be positively affected for fruit size, but with a negative effect in terms of nutrition via decrease in antioxidant capacity.

Concentrations of Mg and Zn were significantly lower under eCO_2 compared with aCO_2 at 27/22 °C (Figs. 4, 5). The amounts of minerals in tomato fruits are the result of the balance between uptake by roots, distribution and partition to the fruits (Barickman et al. 2019). Elevated CO_2 combined with temperature regimen of 27/22 °C did not cause Mg and Zn deficiency in leaves of tomato plants (Fig. S1). Therefore, we think it is reasonable to assume that the effect eCO_2 at 27/22 °C on concentrations of Mg and Zn (on a dry weight basis) are associated with reduced import from the phloem. Variations in concentrations of B, Mn and Ca were also noted, *e.g.* a smaller increases in concentrations

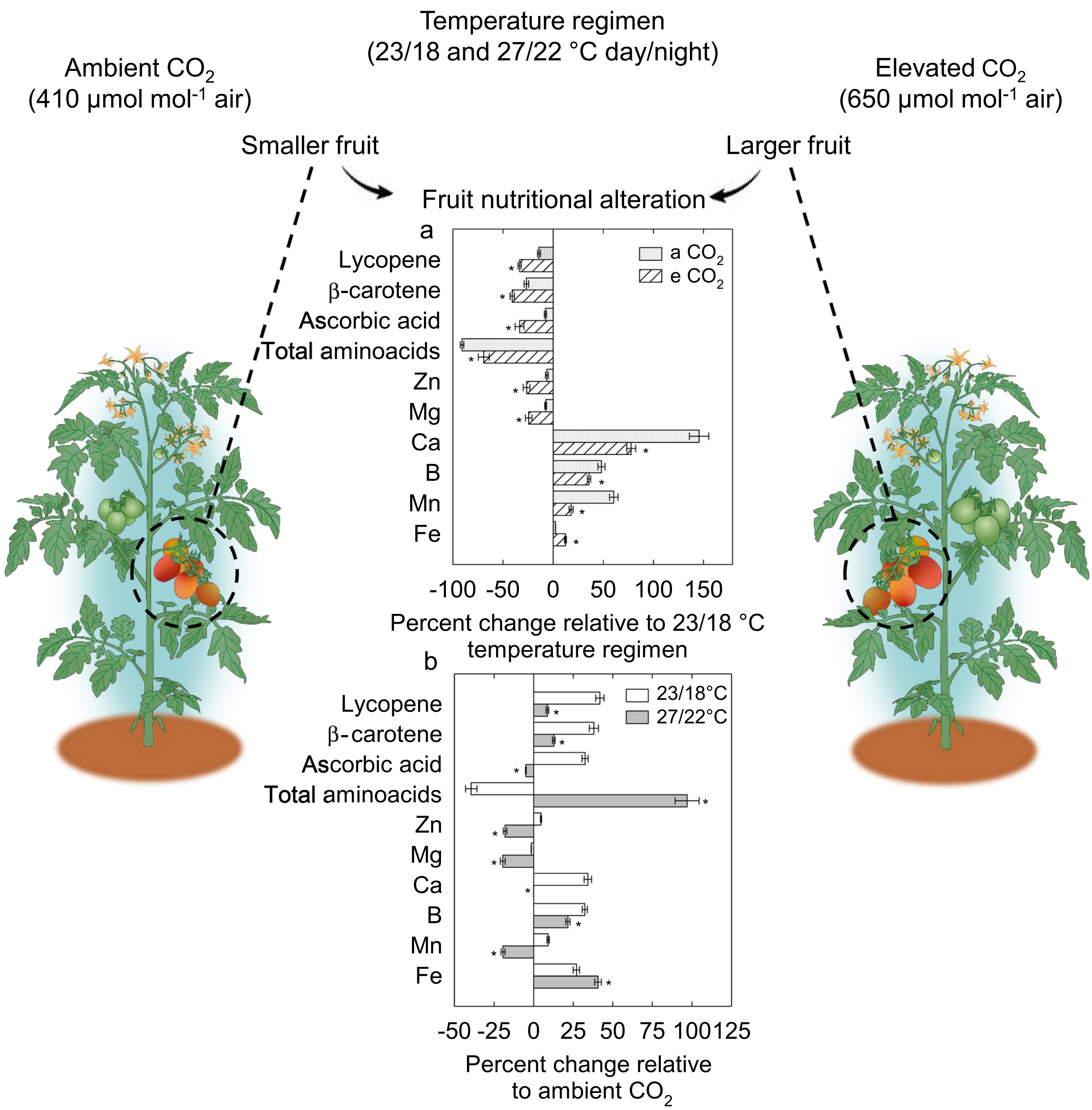


Fig. 5 Summary of CO_2 and temperature effects on fruit size and fruit nutritional quality. Overall, temperature regimen of 27/22 °C and eCO_2 increased fruit size and yield of tomato plants, independently. The combined effect of eCO_2 and temperature regimen of 27/22 °C affect the fruit nutritional quality of tomato plants. **a** Percent change in fruit nutritional composition of tomato plants grown at 27/22 °C relative to 23/18 °C temperature regimen. Asterisks indicate statistically different means between plants grown under aCO_2 and eCO_2 ($P < 0.05$). **b** Percent change in fruit nutritional composition of tomato plants grown under eCO_2 relative to aCO_2. Asterisks indicate statistically different means between plants grown at 27/22 °C and 23/18 °C ($P < 0.05$). Data are derived from Figs. 3, 4. Values are means ± SEM

of these minerals in fruits of tomato plants under eCO_2 at 27/22 °C relative to 23/18 °C (Fig. 5). Since concentrations of macronutrients and micronutrients in tomato leaves were not affected by eCO_2 at 27/22 °C, it seems feasible that eCO_2 alters the balance between transport and nutrient-use efficiency. This observation is somewhat at odds with a previous study showing that increasing temperature counteracted the reductions of minerals in soybean seeds under eCO_2 (Köhler et al. 2019). Several factors could explain this contrasting trend, including the fact that the dynamics of nutrient accumulation is different between fruits and grains. Irrespective of the reason underlying the different conclusion of this study, our work indicates that eCO_2 and temperature regimen of 27/22 °C have a negative effect on tomato fruit quality as a result of reduced concentration of important minerals. The exception being Fe, which was higher in fruits of tomato plants grown under eCO_2 at both temperature regimens (Figs. 4, 5).

Conclusions

We found that eCO_2 may increase tomato yield via increases in fresh fruit weight, but with a negative effect on nutrient contents at a growth temperature of 27/22 °C day/night compared with 23/18 °C. Acclimation of tomato plants to temperature regimen of 27/22 °C involved changes in fruit composition, including a decrease in concentrations of the main tomato antioxidant compounds (lycopene, β-carotene, and ascorbic acid) and essential minerals (Zn and Mg) in fruits, with a more pronounced decrease under eCO_2 than under aCO_2 (Fig. 5). In addition, eCO_2 results in lower accumulation of Ca, B, and Mn in fruits of tomato plants at 27/22 °C relative to 23/18 °C (Fig. 5). The eCO_2 treatment only partially compensates the negative effect of temperature regimen of 27/22 °C on concentrations of total amino acids (Fig. 5). Interestingly, concentrations of ascorbic acid, Zn, and Mn increase in eCO_2 treatment at 23/18 °C but decrease at 27/22 °C (Fig. 5), indicating that temperature and CO_2 conditions should be evaluated concurrently when assessing tomato fruit nutritional value. Together, these findings raise a concern about ongoing increases in atmospheric CO_2 and temperature, since most processing tomato varieties, such as the one assessed in this study, are cultivated in non-controlled conditions in the field, making their fruits susceptible to significant reductions in nutritional value.

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Author contributions TMP, GAdS, JMH, FALB, LST and RSA conducted experiments and statistical analysis. TMP, GAdS and AZ performed literature survey. TMP, AZ and DMR designed the research and interpreted the results. All authors contributed to the writing of the manuscript and all authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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