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Impact of Elevated CO_2 and Temperature on Growth, Development and Nutrient Uptake of Tomato

Tejaswini C. Rangaswamy [1], Shankarappa Sridhara [1,*], Konapura Nagaraja Manoj [1], Pradeep Gopakkali [1], Nandini Ramesh [1], Shadi Shokralla [2,3], Tarek K. Zin El-Abedin [4], Khalid F. Almutairi [5] and Hosam O. Elansary [5,*]

1 Center for Climate Resilient Agriculture, University of Agricultural and Horticultural Sciences, Shivamogga 577204, Karnataka, India; cr.tejaswini9@gmail.com (T.C.R.); manojrajagri@gmail.com (K.N.M.); g.pradeep76@gmail.com (P.G.); nandinianuram@gmail.com (N.R.)
2 Centre for Biodiversity Genomics, University of Guelph, Guelph, ON N1G 2W1, Canada; sshokral@uoguelph.ca
3 Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada
4 Department of Agriculture and Biosystems Engineering, Faculty of Agriculture (El-Shatby), Alexandria University, Alexandria 21545, Egypt; drtkz60@gmail.com
5 Plant Production Department, College of Food and Agriculture Sciences, King Saud University, Riyadh 11451, Saudi Arabia; almutairik@ksu.edu.sa
* Correspondence: sridharas1968@gmail.com (S.S.); helansary@ksu.edu.sa (H.O.E.)

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Abstract: Elevated carbon dioxide (EC) can increase the growth and development of different C_3 fruit crops, which may further increase the nutrient demand by the accumulated biomass. In this context, the current investigation was conceptualized to evaluate the growth performance and nutrient uptake by tomato plants under elevated CO_2 (EC_{700} and EC_{550} ppm) and temperature (+2 °C) in comparison to ambient conditions. Significant improvement in the growth indicating parameters like leaf area, leaf area index, leaf area duration and crop growth rate were measured at EC_{700} and EC_{550} at different stages of crop growth. Further, broader and thicker leaves of plants under EC_{700} and EC_{550} have intercepted higher radiation by almost 11% more than open field plants. Conversely, elevated temperature (+2 °C) had negative influence on crop growth and intercepted almost 7% lower radiation over plants under ambient conditions. Interestingly, earliness of phenophases viz., branch initiation (3.0 days), flower initiation (4.14 days), fruit initiation (4.07 days) and fruit maturation (7.60 days) were observed at EC_{700} + 2 °C, but it was statistically on par with EC_{700} and EC_{550} + 2 °C. Irrespective of the plant parts and growth stages, plants under EC_{700} and EC_{550} have showed significantly higher nutrient uptake due to higher root biomass. At EC_{700}, the tune of increase in total nitrogen, phosphorus and potassium uptake was almost 134%, 126% and 135%, respectively compared to open field crop. This indicates higher nutrient demand by the crop under elevated CO_2 levels because of higher dry matter accumulation and radiation interception. Thus, nutrient application is needed to be monitored at different growth stages as per the crop needs.

Keywords: elevated CO_2; elevated temperature; tomato; phenophases; nutrient uptake

1. Introduction

Climate change has become a main focus of social and scientific attention. It is one of the most critical threats faced by the world today. The rise in atmospheric carbon dioxide (CO_2) concentration is one of the most prominent and undesirable indicators of global climate change. Greenhouse gases are the primary source of cause for rising temperature levels in the atmosphere. According to the Intergovernmental Panel on Climate Change (IPCC), the CO_2 level has risen at a pace of 1.9 ppm per year over the last twelve years and is expected to exceed 570 ppm by the middle of this century [1]. As a result, global surface temperature is expected to rise by 3–4.5 °C [1]. In addition, crop development is highly

influenced by predicted climate changes globally, such as CO_2 levels, surface temperatures, and rainfall patterns [2].

Crop growth and production are influenced by climate change, mainly through the changes in photosynthetic carbon assimilation [3]. Under elevated conditions, as a carbon fertilizer, CO_2 enhances the growth and development of crops [4]. A higher rate of photosynthetic carbon fixation by leaves is the primary effect of increased atmospheric CO_2 on plants [5]. Crop growth and development at higher CO_2 levels (475–600 ppm) enhanced photosynthetic rate by almost 40% in different plant species under several Free-air carbon dioxide enrichment (FACE) experiments [6]. Increased photosynthetic rate enables more photosynthates and thereby more dry matter buildup at elevated CO_2 conditions. Elevated CO_2 levels increased the leaf area, leaf area index (LAI), leaf thickness, leaf area duration (LAD) and amount of dry biomass production in tomatoes [7,8]. On the other hand, higher dry matter accumulation under elevated CO_2 conditions also increases radiation interception by the plants. A linear association between solar radiation interception and total dry matter buildup was earlier noticed in rice and chickpea [9,10]. LAI and LAD will primarily influence the radiation interception by the crop. However, these parameters were higher under elevated CO_2 conditions and intercepted more radiation in different crop species [11,12]. Higher CO_2 levels are generally characterized by an increase in ambient temperature, and as a result, temperature influences the various phenological phases and crop duration [13,14]. Previous studies also documented a shorter crop cycle and early initiation of different phenophases in rice, wheat, maize and mungbean at higher temperature conditions [15–17]. Elevated temperature negatively influences the net photosynthesis in the leaves by affecting photorespiration and ribulose-1,5-bisphosphate carboxylase activity in addition to heat injury and physiological disorders and thereby reduces crop yield [18,19].

The impact of increased CO_2 on plants will differ based on other climatic factors. Under elevated conditions, the prevailing air temperature and moisture stress will influence plant growth and development. However, it directly impacts plant metabolism by photosynthesis, where carbon enters the biosphere [20]. Thus, higher CO_2 levels are expected to promote photosynthetic rate, while the magnitude of increase was unclear as it relies on leaf air temperature, moisture availability, and soil nutrient status [21,22]. Although increased CO_2 allows carbon to be more accessible to plants, they also need other resources from the soil, such as mineral nutrients. The nutrient requirement by the crops also will vary under elevated CO_2 levels to put forth higher dry matter. Previous studies have also shown that nitrogen, phosphorus and potassium play a prominent role in regulating the magnitude of the crop's response to increased CO_2 and that their higher uptake will negatively impact soil nutrient dynamics [23,24]. Under lower nutrient availability, plants' ability to react to increased CO_2 with higher photosynthetic rate and biomass accumulation can be reduced [25]. Lower nutrient conditions decreased the enhancement in dry matter accumulation under elevated CO_2 in many crop species [26]. Wheat and rice also showed significant improvement in nutrient uptake under elevated CO_2 [13,27,28].

Tomato is one of the commonly grown vegetable crops on the planet, and it is known to be a heavy fertilizer feeder. Like other C_3 species, tomato growth, development, and nutrient demand will vary according to the CO_2 concentration and temperature variations. The enhanced photosynthetic rate was earlier reported in vegetable crops under higher CO_2 levels [7,29]. The elevated temperature also influences vegetative growth like biomass production, its partitioning to different plant parts and development regarding the branch, flower, and fruit initiation. Besides, it also affects the fruit maturation of tomatoes at the cost of crop growth rate and development [30,31]. However, proper documentation on the combined influence of elevated CO_2 and temperature levels on growth indicating parameters, nutrient uptake and requirement by tomato crop is very meager. At this juncture the current investigation was aimed to determine the effect of elevated CO_2 and temperature at their individual level and particularly in their combination on different growth indicating parameters such as leaf area, leaf area index, leaf area duration, crop growth

rate etc. and different developmental stages of tomato crop such as branch initiation, flower initiation, fruit initiation, fruit maturation. Since biomass accumulation has a strong influence on nutrient uptake patterns, we also aimed to study the effect of elevated CO_2 and temperature on nutrient uptake patterns in the tomato crop under sub-tropical climatic situations of the Indian context.

2. Materials and Methods

2.1. Experimental Details

The field investigation was carried out during rainy season of 2019 (June–October) in the Open Top Chambers (OTC) at Centre for Climate Resilient Agriculture, University of Agricultural and Horticultural Sciences, Navile, Shivamogga, Karnataka, India. The experimental site is located between 13°58′ North latitude and 75°34′ East longitude at an elevation of 615 m above the mean sea level. The climate of the site is tropical and semi-arid. The soil was Sandy loam in texture with neutral in reaction (6.60 pH), normal in electrical conductivity (103 dS/m) and medium in organic carbon (0.63%). Further, the soil was low in available nitrogen (248 kg/ha), high in available phosphorus (30.82 kg/ha) and medium in potassium (261.58 kg/ha). During the cropping period (August to December), the actual precipitation received was 940.5 mm, which was above the usual rainfall (435.8 mm). The mean maximum and minimum temperature of 30.7 °C and 17.6 °C were recorded during November and December months. The relative humidity was varied from 75% in November to 88% in August.

The experiment was formulated in two factors randomized complete block design with three replications. The treatment details are furnished in Table 1. OTCs of size 5 m × 5 m × 3 m were constructed of an aluminum frame covered by panels of polyvinyl chloride with an open top without chimney and were utilized for the experiment. As per the treatments, pure CO_2 gas was provided to the OTCs and maintained at desired levels utilizing sensor based Non-dispersive infrared (NDIR) CO_2 gas analyzer. The supply of CO_2 was controlled by Supervisory Control and Data Acquisition (SCADA) system coupled to a computer. A week after transplanting of seedlings to a week prior to crop maturity, CO_2 gas was injected from the CO_2 cylinders every day from 7.30 a.m. to 5.30 p.m. to maintain the desired level inside the OTCs. Similarly, infrared heaters were installed all over the periphery of the OTCs to maintain the desired temperature of +2 °C above the normal air temperature every day from 7.30 a.m. to 5.30 p.m. The automated temperature controller could detect both inside and outside temperatures, and if the temperature rose by more than +2 °C, the heaters would automatically turn off. Prevailed CO_2 and temperature values under different treatments were presented in Table 2 along with actual weather conditions.

Table 1. Treatment details of the experiment.

Treatment No.	Treatment	Description
T_1	C_0T_0	Ambient CO_2 and ambient temperature at OTC
T_2	C_1T_0	Elevated CO_2 (550 ± 20 ppm) and ambient temperature
T_3	C_1T_1	Elevated CO_2 (550 ± 20 ppm) and elevated temperature of +2 °C
T_4	C_2T_0	Elevated CO_2 (700 ± 20 ppm) and ambient temperature
T_5	C_2T_1	Elevated CO_2 (700 ± 20 ppm) and elevated temperature +2 °C
T_6	C_0T_1	Ambient CO_2 and elevated temperature +2 °C
T_7	C_0T_0	Ambient CO_2 and ambient temperature at open field

Table 2. Average CO_2, Temperature values recorded under each of the OTCs and the actual weather conditions prevailed during the study.

Description	Average CO_2 Concentration (ppm)	Mean Temperature (°C)
Ambient CO_2 and ambient temperature at OTC	-	25.8 (1.1)
Elevated CO_2 (550 ± 20 ppm) and ambient temperature	554 (29)	-
Elevated CO_2 (550 ± 20 ppm) and elevated temperature of +2 °C	552 (33)	27.2 (1.1)
Elevated CO_2 (700 ± 20 ppm) and ambient temperature	701 (32)	-
Elevated CO_2 (700 ± 20 ppm) and elevated temperature +2 °C	702 (36)	27.4 (1.4)
Ambient CO_2 and elevated temperature +2 °C	-	26.8 (1.1)
Ambient CO_2 and ambient temperature at Open field	414 (25)	24.9 (1.1)
Actual Weather		
T_{mean}	24.6 (0.6)	
$T_{maximum}$ (°C)	30.7 (1.3)	
$T_{minimum}$ (°C)	17.6 (1.5)	
RH_{mean} (%)	81.8 (5)	
Mean sunshine hours	5.5 (2.1)	
Total Rainfall (mm)	940.5 (197)	

Note: Values in parenthesis represents standard deviation between the daily values.

Prior to transplanting, land in normal condition and within the OTCs was manually dug up to a depth of about 30 cm and the soil was brought to the fine tilth. Following land preparation, farmyard manure was incorporated at the rate of 25 tones ha-1 and mixed into the soil 15 days prior to transplanting. About 30 days old, vigorous and uniform height seedlings of Arka Rakshak hybrid were transplanted at 90 cm × 90 cm spacing in each OTCs. The selected hybrid was not a self-pruned cultivar, so it was grown in vertical tied up to wooden poles. In each OTC, 25 plants were accommodated with five plants each in five raised beds. In which, three beds were considered as three replications in each OTC and remaining plants in two beds were utilized for destructive sampling purpose (3 plants at each observation). Fertilizers (urea, single super phosphate and muriate of potash) were applied at the rate of 250 kg N, 250 kg P_2O_5 and 250 kg K_2O per ha in three split doses with basal dose of 50% N, 25% P and K applied four days after transplanting (DAT). Remaining was given at 30 DAT (25% N, 50% P and K) and 50 DAT (25% N, P and K), respectively. Foliar spray of Arka vegetable special at 4 g/L (Zinc: 225 ppm, Iron: 105 ppm, Boron: 50 ppm, Manganese: 42.5 ppm and Copper: 5 ppm) was given at 25 DAT, flower initiation and fruit initiation to supplement the micronutrients. To raise the seedlings, all the management practices were uniformly followed under both OTCs and open field conditions.

2.2. Growth Indicating Parameters

2.2.1. Leaf Area (cm^2)

By using standard LI-COR leaf area meter (Model LI-3100, LICOR Inc., Lincoln City, NE, USA) total leaf area per plant was measured at three growth stages (50% flowering, peak fruiting, and harvest) in five randomly picked plants in each treatment and expressed in cm^2.

2.2.2. Leaf Area Index

Leaf area index (LAI) is the green leaf area per unit ground area covered by the plant. It was determined using the following formula [32].

$$\text{LAI} = \frac{\text{Leaf area } (\text{cm}^2)}{\text{Land area}(\text{cm}^2)}$$

2.2.3. Leaf Area Duration (Days)

Leaf area duration (LAD) denotes the capability of crop plant to produce green leaf area on unit ground area during crop cycle. It was worked out as per the Power et al. [33].

$$LAD = \frac{LAI_i + LAI_{i+1}}{2} \times (t_2 - t_1)$$

where,

LAI_i = Leaf area index at ith stage
$LAI_i{+}_1$ = Leaf area index at $(i + 1)^{th}$ stage
$t_2 - t_1$ = Time interval (days)

2.2.4. Crop Growth Rate ($g/m^2/day$)

Crop growth rate (CGR) signifies amount of drymatter accumulation per unit ground area and time, it was determined at different growth stages by the formula outlined by Watson [32].

$$CGR = \frac{W_2 - W_1}{t_2 - t_1} \times \frac{1}{P}$$

where,

W_1 = Dry matter of the plant (g) at time t_1
W_2 = Dry matter of the plant (g) at time t_2
P = Unit land area occupied by the plant (m^2)

2.2.5. Radiation Interception (MJ/m^2)

To determine the amount of radiation intercepted by crop canopy, the incoming Photosynthetically Active Radiation (PAR) at both above and below the crop canopy was measured by using line quantum sensor (LI-COR, Lincoln City, NE, USA). The measurements were made at mid-day in order to avoid the effect of solar radiation on PAR interception [34]. Light transmission and proportion of PAR interception were calculated by using the following formulae given by Charles-Edwards and Lawn [35].

$$\text{Light transmission } (T_n) = \frac{I_L}{I_o}$$

where,

I_L = PAR values below the crop canopy (i.e., LAI)
I_O = PAR values above the crop canopy
The proportion of intercepted PAR by the crop at noon was calculated as

$$Q_n = (1 - T_n)$$

The total incident solar radiation ($MJ/cm^2/day$) as measured from Agro meteorological observatory was converted to PAR ($MJ/m^2/day$) using a constant of 0.042 by assuming 45 per cent of incident solar radiation as PAR [36,37]. The cumulative intercepted radiation was computed for three growth stages of tomato (50% flowering, peak fruiting and at harvest).

2.3. Phenological Observations

The different phenophases—days to first branch initiation, days taken for flower initiation, days taken for fruit initiation and days taken for fruit maturation—were determined from five initially identified and labeled plants during entire crop cycle through visual observations by counting the number of days taken from the time of seedlings transplanting to the particular above mentioned phenophases [13,16].

2.4. Nutrient Uptake (kg/ha)

The crop samples (leaf and stem) were collected, oven dried, fine grinded and analyzed for total nitrogen, phosphorous and potassium content (%) at three different stages of the crop (50% flowering, peak fruiting and at harvest) as per the procedure described by Jackson [38]. Later, nutrient uptake by leaf and stem portion of the plant was worked out separately for each sample using the following formula.

$$\text{Nutrient uptake by leaf (kg/ha)} = \frac{\text{Nutrient concentration in leaf (\%)}}{100} \times \text{Leaf dry matter (kg/ha)}$$

$$\text{Nutrient uptake by stem (kg/ha)} = \frac{\text{Nutrient concentration in stem (\%)}}{100} \times \text{Stem dry matter (kg/ha)}$$

2.5. Root Dry Weight

Three plants from each treatment were uprooted at the time of observation and separated into leaves, stems and root, then dried in hot air oven at 65 °C until constant weight is attained. Later oven dry weight of roots was taken and dry weight per plant was worked out.

2.6. Data Analysis

The data obtained on various parameters was statistically analyzed by using SPSS software version 20. Two-way analysis followed by Duncan's Multiple Range Test (DMRT) is used for mean comparison apart from Least Significant Difference (LSD). The significance at p = 0.05 level was used for the comparison. Correlation was studied to know the association between growth indicating parameters, radiation interception and nutrient uptake by tomato plants. Pearson correlation coefficients were computed and correlograph was plotted using corrplot package version 0.87 in R studio version 3.6.2.

3. Results

3.1. Effect on Growth Indicating Parameters

The elevated levels of temperature and CO_2 significantly influenced the different growth indicating parameters as shown by variation in leaf area, LAI, LAD and CGR at 50% flowering, peak fruiting and at harvest stages of tomato. The plants showed significant (p = 0.05) increase in leaf area and LAI up to peak fruiting stage and then declined at harvest stage due to senescence of the crop. Compared to ambient levels in reference OTC and open field condition, improvement in leaf area and LAI was recorded at both elevated levels of CO_2. Significantly higher total leaf area at 50% flowering (4829.93 cm^2/plant), peak fruiting (9110.68 cm^2/plant) and at harvest of tomato (4201.54 cm^2/plant) was recorded in EC_{700} and the magnitude of increase was 21%, 42% and 241%, respectively over the open field plants. Subsequent maximum leaf area was noticed in EC_{550} (4431.26, 8660.76 and 4193.75 cm^2/plant, respectively). LAI followed the same trend as that of the leaf area and recorded significantly improved LAI at EC_{700} (0.60, 1.12 and 0.52), which was closely followed by EC_{550} (0.55, 1.07 and 0.52) at 50% flowering, peak fruiting, and at harvest, respectively (Table 3). Meanwhile, crops grown under elevated temperature of +2 °C have shown reduced leaf area by 11–54% and LAI by 7–55% than crop grown under ambient conditions at open field situation across the different stages. Contrastingly, when crop was exposed to both elevated CO_2 (EC_{550} and EC_{700}) and temperature, the crop performed well than temperature alone in terms of leaf area and LAI at all stages of the crop growth and development.

The LAD and CGR were significantly influenced by the elevated CO_2 levels and temperature rather than ambient conditions at all growth stages of the crop and are presented in Table 4. Increasing trend of LAD and CGR was noticed up to 50% flowering to peak fruiting stage, however it was reduced at peak fruiting to harvest stage due to reduced leaf area. But, the tune of variation was significantly higher than ambient conditions. The LAD of tomato plants at EC_{700} was improved by about 21%, 34% and

75% at 0 to 50% flowering, 50% flowering to peak fruiting and peak fruiting to harvest period, respectively over open field crop. Similarly, the tune of increase was 23%, 49% and 103%, respectively compared to ambient CO_2 and temperature at reference OTC. Similarly, enhanced CGR of 59–83% and 29–70% have witnessed at EC_{700} and EC_{550}, respectively than open field crop. On the other hand, elevated temperature of +2 °C has shown negative influence on LAD and CGR across the crop growth stages. However elevated temperature coupled with elevated CO_2 levels masked the adverse effects of temperature and reflected in the improvement of LAD and CGR than open field condition with maximum at EC_{550} + 2 °C combination. Subsequent total LAD and average CGR of all the growth stages was also observed under EC_{700} (37% and 67%) and EC_{550} (29% and 46%) over open field crop (Table 4).

Table 3. Effect of elevated CO_2 and temperature on leaf area and leaf area index (LAI) of tomato at different growth stages.

	Leaf Area (cm^2/Plant)			LAI		
Treatments	**50% Flowering**	**Peak Fruiting**	**at Harvest**	**50% Flowering**	**Peak Fruiting**	**at Harvest**
			(Mean ± SE)			
T_1	3943.44 ± 60.23 ^{c}	5382.56 ± 82.221 ^{e}	1184.46 ± 18.090 $^{c, d}$	0.49 ± 0.009 ^{c}	0.66 ± 0.012 ^{d}	0.15 ± 0.003 ^{c}
T_2	4431.26 ± 92.236 ^{b}	8660.76 ± 180.280 ^{b}	4193.75 ± 87.299 ^{a}	0.55 ± 0.012 ^{b}	1.07 ± 0.021 ^{a}	0.52 ± 0.012 ^{a}
T_3	4193.89 ± 87.303 $^{b, c}$	7488.56 ± 155.887 ^{c}	3524.27 ± 73.358 ^{b}	0.52 ± 0.012 $^{b, c}$	0.92 ± 0.018 ^{b}	0.44 ± 0.009 ^{b}
T_4	4829.93 ± 73.774 ^{a}	9110.68 ± 139.178 ^{a}	4201.54 ± 64.192 ^{a}	0.60 ± 0.009 ^{a}	1.12 ± 0.019 ^{a}	0.52 ± 0.007 ^{a}
T_5	4167.54 ± 104.891 $^{b, c}$	6764.23 ± 170.229 ^{d}	1274.69 ± 32.076 ^{c}	0.51 ± 0.012 $^{b, c}$	0.84 ± 0.022 ^{c}	0.16 ± 0.003 ^{c}
T_6	3572.29 ± 94.510 ^{d}	4149.21 ± 109.772 ^{f}	1112.68 ± 29.438 ^{d}	0.44 ± 0.012 ^{d}	0.51 ± 0.012 ^{e}	0.14 ± 0.003 ^{c}
T_7	4002.58 ± 105.898 ^{c}	6398.35 ± 169.293 ^{d}	1231.72 ± 32.591 $^{c, d}$	0.49 ± 0.012 ^{c}	0.79 ± 0.021 ^{c}	0.15 ± 0.006 ^{c}
SEM±	87.97	145.32	51.95	0.01	0.02	0.01
LSD (p = 0.05)	271.07	447.77	160.08	0.03	0.06	0.02

Note: According to DMRT, values with same alphabet(s) do not differ statistically at the 0.05 level; Refer Table 1 for the description of the treatments.

Table 4. Effect of elevated CO_2 and temperature on leaf area duration (LAD) and crop growth rate (CGR) of tomato at different growth stages.

	LAD (Days)				CGR (g/m^2/day)			
Treatments	**0–50% Flowering**	**50% Flowering-Peak Fruiting**	**Peak Fruiting-Harvest**	**Total LAD**	**0–50% Flowering**	**50% Flowering-Peak Fruiting**	**Peak Fruiting-Harvest**	**Average CGR**
				(Mean ± SE)				
T_1	10.95 ± 0.165 ^{c}	25.91 ± 0.394 ^{e}	6.08 ± 0.092 ^{d}	42.94 ± 0.657 ^{e}	0.78 ± 0.012 ^{f}	2.13 ± 0.034 ^{e}	1.04 ± 0.015 ^{c}	1.32 ± 0.019 ^{f}
T_2	12.31 ± 0.255 ^{b}	36.37 ± 0.756 ^{b}	11.90 ± 0.247 ^{a}	60.58 ± 1.261 ^{b}	1.72 ± 0.035 ^{b}	3.05 ± 0.066 ^{b}	2.26 ± 0.045 ^{a}	2.35 ± 0.048 ^{b}
T_3	11.65 ± 0.244 $^{b, c}$	32.45 ± 0.675 ^{c}	10.20 ± 0.211 ^{b}	54.30 ± 1.130 ^{c}	1.33 ± 0.027 ^{c}	2.88 ± 0.062 ^{b}	2.24 ± 0.047 ^{a}	2.15 ± 0.047 ^{c}
T_4	13.42 ± 0.205 ^{a}	38.72 ± 0.593 ^{a}	12.33 ± 0.190 ^{a}	64.47 ± 0.984 ^{a}	1.85 ± 0.027 ^{a}	3.87 ± 0.058 ^{a}	2.32 ± 0.036 ^{a}	2.68 ± 0.039 ^{a}
T_5	11.58 ± 0.290 $^{b, c}$	30.37 ± 0.764 ^{d}	7.44 ± 0.188 ^{c}	49.39 ± 1.242 ^{d}	1.12 ± 0.027 ^{d}	2.62 ± 0.067 ^{c}	2.21 ± 0.057 ^{a}	1.99 ± 0.050 ^{d}
T_6	9.92 ± 0.261 ^{d}	21.45 ± 0.567 ^{f}	4.87 ± 0.129 ^{e}	36.24 ± 0.959 ^{f}	0.46 ± 0.012 ^{g}	1.66 ± 0.044 ^{f}	1.38 ± 0.038 ^{b}	1.17 ± 0.030 ^{g}
T_7	11.12 ± 0.294 ^{c}	28.89 ± 0.764 ^{d}	7.06 ± 0.188 ^{c}	47.07 ± 1.247 ^{d}	1.01 ± 0.026 ^{e}	2.37 ± 0.065 ^{d}	1.46 ± 0.041 ^{b}	1.61 ± 0.044 ^{e}
SEM±	0.24	0.65	0.18	1.07	0.03	0.06	0.04	0.04
LSD (p = 0.05)	0.75	1.99	0.55	3.29	0.08	0.17	0.13	0.12

Note: According to DMRT, values with same alphabet(s) do not differ statistically at the 0.05 level; Refer Table 1 for the description of the treatments.

3.2. Effect on Cumulative Radiation Interception (MJ/m^2)

The radiation interception of tomato plants improved significantly under higher CO_2 levels and their combination with elevated temperature (Table 5). Plants grown at EC_{700} intercepted maximum cumulative radiation at different growth stages (50% flowering (143.61 MJ/m^2), peak fruiting (365.77 MJ/m^2) and at harvest (479.41 MJ/m^2)) of tomato and the magnitude of increase was about 7%, 7% and 15%, respectively over open field crop. We also observed a similar kind of higher radiation interception even with the combination of elevated CO_2 levels and temperature in our study. Conversely, a decrease

in the cumulative radiation interception was observed when crop grown at elevated temperature of +2 °C alone (10%, 8% and 5%, respectively) and combination of ambient CO_2 and temperature in OTC (9%, 3% and 1%, respectively) over open field crop.

Table 5. Effect of elevated CO_2 and temperature on cumulative radiation interception and phenological stages initiation of tomato.

Treatments	Cumulative Radiation Interception (MJ/m^2)			Days Taken for First Initiation			
	50% Flowering	Peak Fruiting	at Harvest	Branch Initiation	Flower Initiation	Fruit Initiation	Fruit Maturation
	(Mean ± SE)						
T_1	122.75 ± 1.876 ^{c}	333.20 ± 5.089 $^{c, d}$	410.91 ± 6.276 ^{b}	23.37 ± 0.387 $^{a, b}$	38.00 ± 0.255 $^{a, b}$	48.60 ± 0.417 ^{a}	75.20 ± 1.149 $^{a, b}$
T_2	141.03 ± 2.935 $^{a, b}$	365.40 ± 7.607 ^{a}	481.49 ± 10.024 ^{a}	23.00 ± 0.479 ^{b}	36.95 ± 0.540 ^{b}	47.67 ± 0.436 $^{a, b, c}$	74.00 ± 0.804 $^{a, b, c}$
T_3	139.24 ± 2.899 $^{a, b}$	355.40 ± 7.399 $^{a, b}$	466.71 ± 9.716 ^{a}	22.80 ± 0.348 $^{b, c}$	35.93 ± 0.749 $^{c, d}$	46.13 ± 0.961 $^{b, c, d}$	72.33 ± 1.504 $^{b, c, d}$
T_4	143.61 ± 2.194 ^{a}	365.77 ± 5.589 ^{a}	479.41 ± 7.324 ^{a}	22.77 ± 0.239 $^{b, c}$	35.80 ± 0.547 $^{c, d}$	45.47 ± 0.693 $^{c, d}$	70.80 ± 1.081 $^{c, d}$
T_5	137.10 ± 3.448 $^{a, b}$	353.07 ± 8.884 $^{a, b, c}$	455.96 ± 11.472 ^{a}	21.63 ± 0.282 ^{c}	35.06 ± 0.570 ^{c}	45.20 ± 1.138 ^{d}	69.40 ± 1.746 ^{d}
T_6	121.12 ± 3.204 ^{c}	316.40 ± 8.369 ^{d}	393.76 ± 10.419 ^{b}	23.33 ± 0.720 $^{a, b}$	37.33 ± 0.673 $^{a, b, c}$	48.13 ± 0.955 $^{a, b}$	74.33 ± 1.646 $^{a, b, c}$
T_7	134.54 ± 3.557 ^{b}	342.35 ± 7.428 $^{b, c}$	416.18 ± 11.013 ^{b}	24.63 ± 0.676 ^{a}	39.20 ± 0.719 ^{a}	49.27 ± 0.136 ^{a}	77.00 ± 1.406 ^{a}
SEM±	2.87	7.20	9.45	0.44	0.61	0.79	1.40
LSD (p = 0.05)	8.83	22.19	29.12	1.35	1.87	2.44	4.31

Note: According to DMRT, values with same alphabet(s) do not differ statistically at the 0.05 level; Refer Table 1 for the description of the treatments.

3.3. Effect on Phenological Phases

At elevated CO_2 levels, a remarkable change in the different phenological phase's initiation during crop development was noticed in the tomato (Table 5). Crops took 21.63 days for first branch initiation, 35.06 days for flower initiation, 45.20 days for fruit formation and 69.40 days for fruit maturation under EC_{700} + 2 °C condition, but it was found statistically at par with EC_{700}, EC_{550} + 2 °C. Conversely, tomato plants grown under open field conditions have taken 3.0, 4.14, 4.07 and 7.60 days longer for branch initiation, flower initiation, fruit formation and fruit maturation, respectively than plants grown at EC_{700} + 2 °C. However, plants grown at ambient conditions (CO_2 and temperature) and elevated temperature (+2 °C) under OTCs have not shown earliness in the different phenophases initiation and were found on par with open field condition.

3.4. Effect on Nutrient Uptake

Elevated CO_2 and temperature alone and their combinations have statistically influenced the nutrient uptake by the tomato plant parts (leaf, stem and fruit) at different growth stages. Irrespective of plant parts and growth stages, EC_{700} have shown statistically higher nitrogen (N), phosphorus (P) and potassium (K) uptake followed by EC_{550} (Figures 1–3). The magnitude of increase in nutrient uptake under EC_{700} was 261%, 173%, 246% in leaf and 99%, 102%, 77% in stem, respectively at 50% flowering, peak fruiting and at harvest stages of the crop than open field crop. Similarly, the increase was 122% and 78% in fruit at peak fruiting and harvest stages, respectively. Similar to the N, higher P and K uptake was noticed in plants grown under EC_{700} followed by EC_{550} than open field conditions. Irrespective of the growth stages, higher P uptake by 2.60, 1.32, 1.03 folds and K uptake by 2.37, 1.29, 1.26 folds was observed under EC_{700} in leaf, stem and fruit of tomato plants, respectively. However, plants grown under elevated temperature of +2 °C and at ambient conditions of CO_2 and temperature have shown lower NPK uptake over the open field grown plants. On the other hand, combined effect of elevated temperature and CO_2 levels resulted in improved nutrient uptake with maximum uptake at EC_{550} + 2 °C by 1.82, 2.81 and 1.51 folds followed by EC_{700} + 2 °C (1.40, 2.05 and 1.02 folds) than temperature alone. Among the stages, at harvest higher uptake of nutrients was observed in all the treatments. Total nutrient uptake was also noticed higher under EC_{700} and which was 134%, 126% and 135% higher than NPK uptake by the plants grown under ambient conditions (Figure 4).

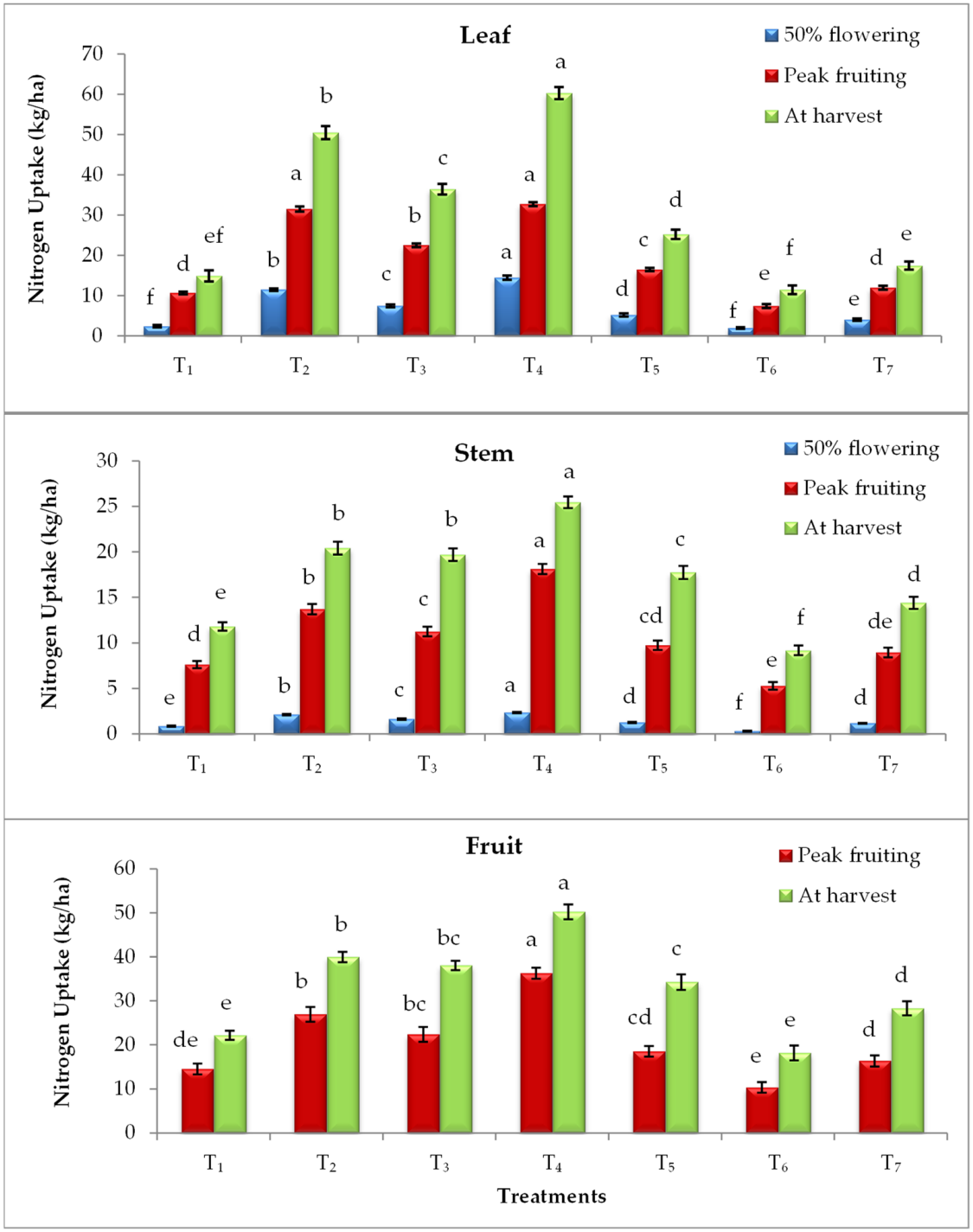

Figure 1. Nitrogen uptake by leaf, stem and fruit of tomato plants as influenced by elevated CO_2 and temperature at 50% flowering, peak fruiting and at harvest stages (n = 15). Note: According to DMRT, values with same alphabet(s) do not differ statistically at the 0.05 level; Refer Table 1 for the description of the treatments.

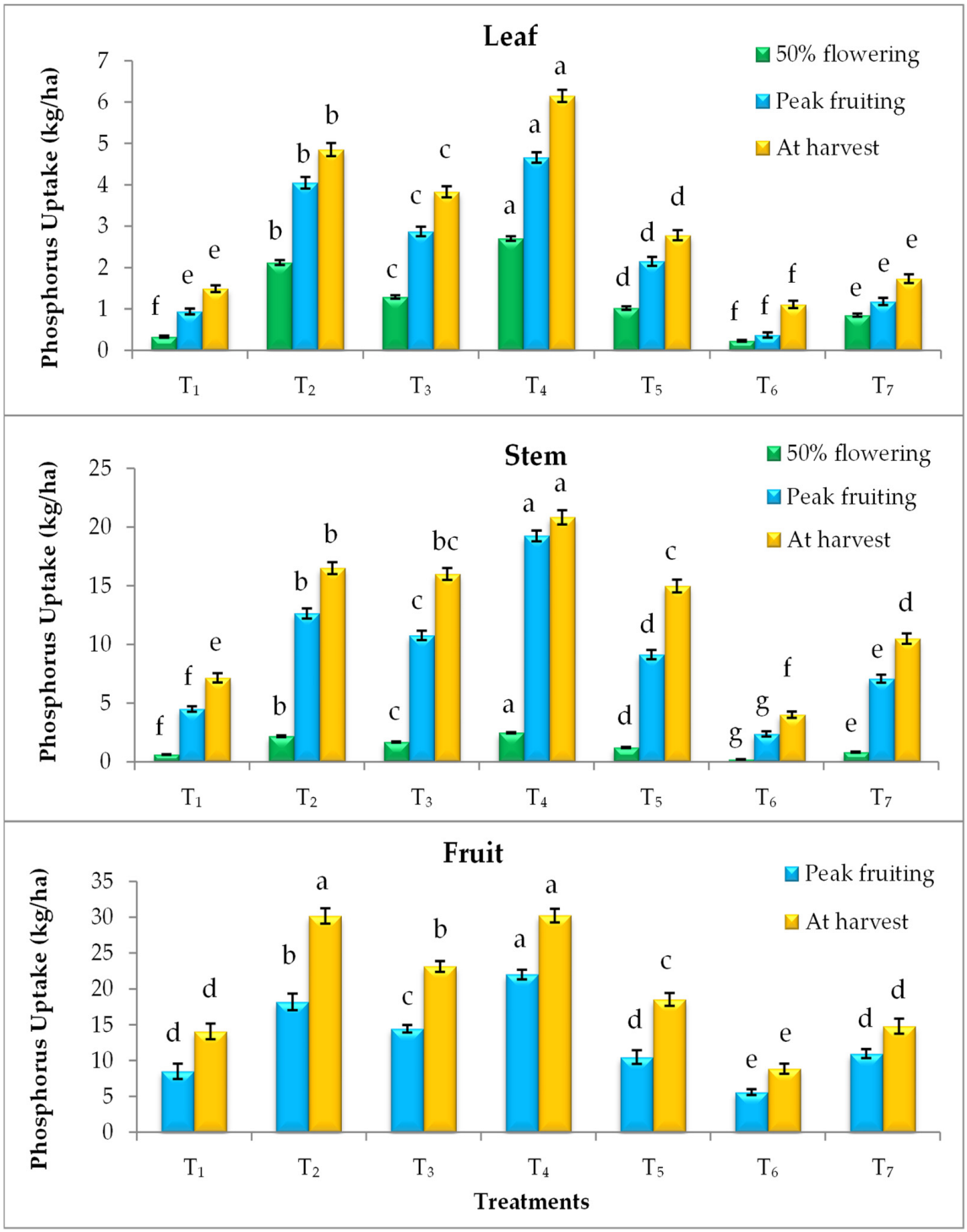

Figure 2. Phosphorus uptake by leaf, stem and fruit of tomato plants as influenced by elevated CO_2 and temperature at 50% flowering, peak fruiting and at harvest stages (n = 15). Note: According to DMRT, values with same alphabet(s) do not differ statistically at the 0.05 level; Refer Table 1 for the description of the treatments.

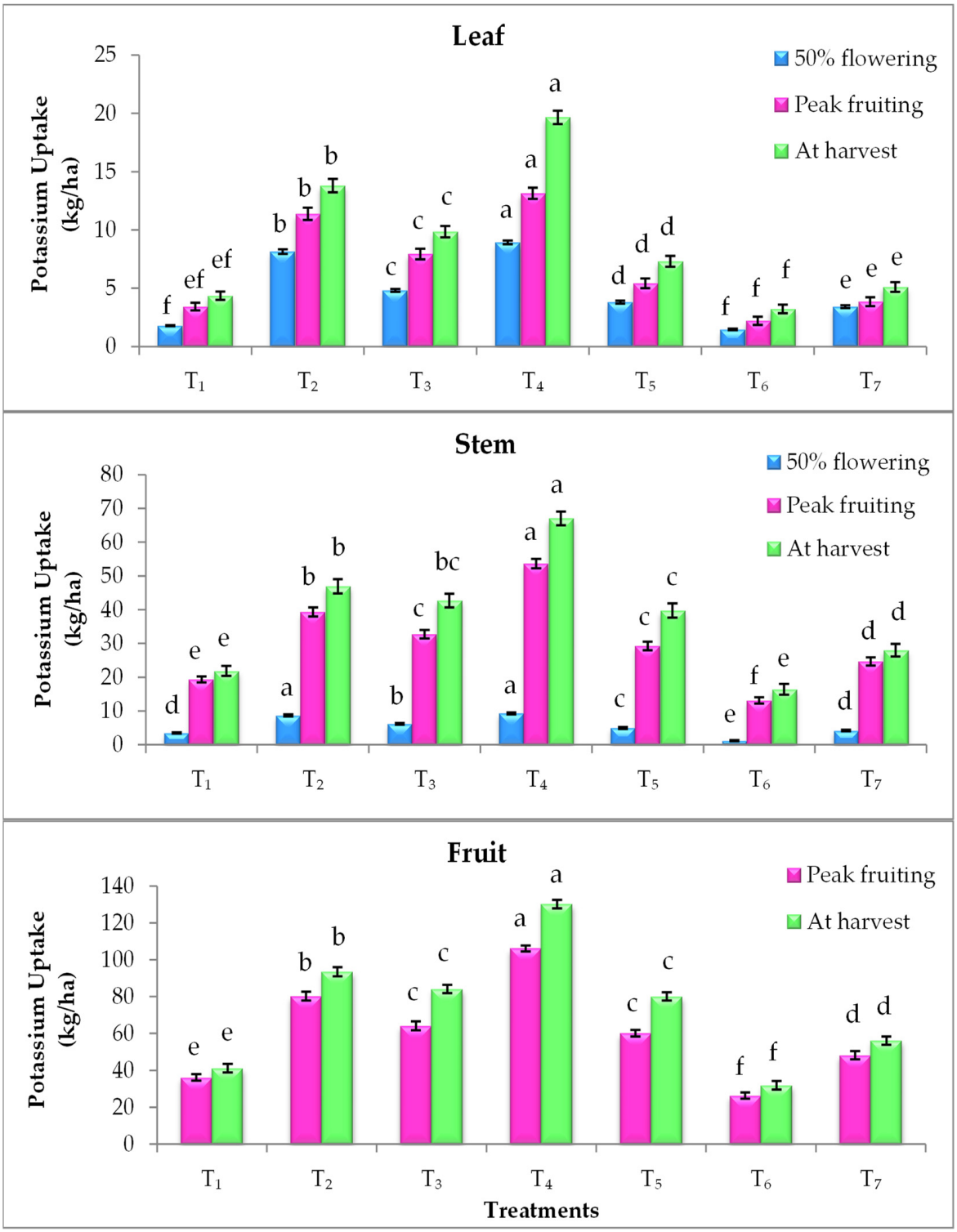

Figure 3. Potassium uptake by leaf, stem and fruit of tomato plants as influenced by elevated CO_2 and temperature at 50% flowering, peak fruiting and at harvest stages (n = 15). Note: According to DMRT, values with same alphabet(s) do not differ statistically at the 0.05 level; Refer Table 1 for the description of the treatments.

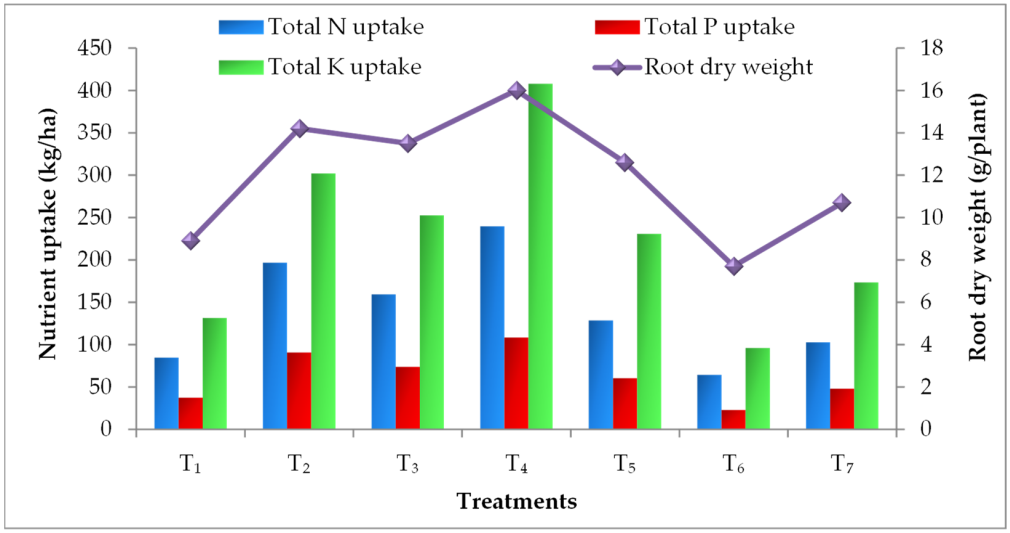

Figure 4. Total NPK uptake and root dry weight of tomato plants as influenced by elevated CO_2 and temperature (n = 15). Refer Table 1 for the description of the treatments.

3.5. Correlation Studies

The relationship between growth indicating parameters, radiation interception and nutrient uptake by tomato plants under elevated CO_2 and temperature levels alone and in combination was interpreted through correlation studies (Figure 5). Correlation values revealed strong positive relationship between all the parameters. The higher root biomass favored higher nutrient availability and thereby nutrient uptake under elevated CO_2 conditions. Further, higher uptake has resulted in increased dry matter accumulation and growth indicating parameters. These above-mentioned statements were strongly evident by the higher correlation values (>0.93) in our current study.

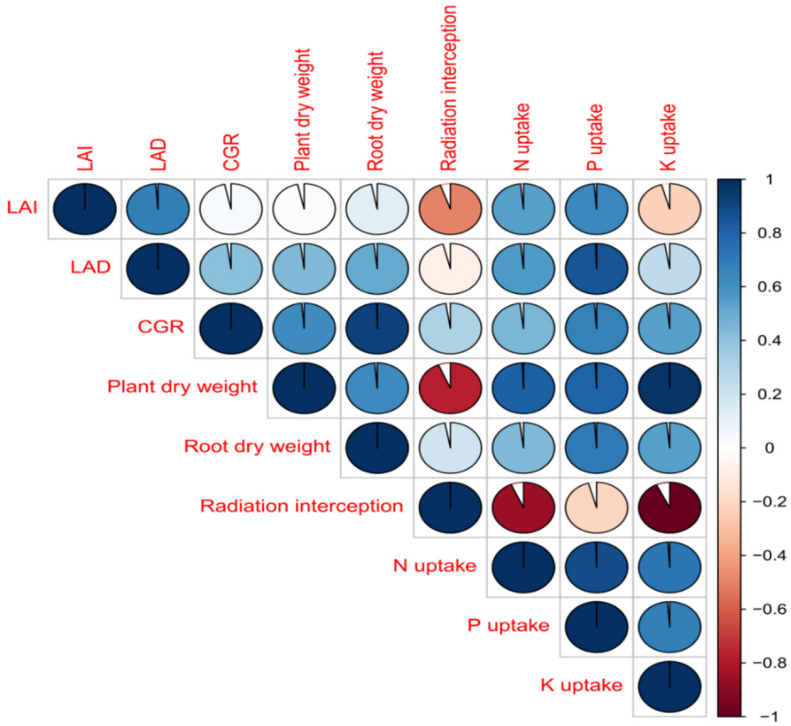

Figure 5. Relationship between growth parameters, radiation interception and nutrient uptake of tomato under elevated CO_2 and temperature.

4. Discussion

The insights of elevated CO_2 and temperature impact on crop growth, development and nutrient uptake at individual level and in their combination is presented in this study in tomato. The EC_{700} and EC_{550} have enhanced all growth indicating parameters (leaf area, LAI, LAD, CGR) than ambient conditions under both open field and OTCs. Broader leaves resulted from increased photosynthetic rate, cell division, cell differentiation and leaf number lead to increased leaf area under elevated CO_2 condition. Elevated CO_2 levels increase net photosynthesis by boosting substrate availability for Rubisco's activity while reducing photorespiration [39] and habitually display improved leaf traits (leaf area, leaf number and leaf thickness) [40]. Supplementary light (200 ± 20 µmol/m^2/s) and enriched CO_2 (800 µmol/mol) increased the leaf area of tomato by 21.2% at 110 DAT [8]. Elevated CO_2 (900 ± 5 ppm) favored to achieve higher biomass production through higher leaf area in tomato than ambient CO_2 of 450 ppm [41]. A significant association between intercepted photosynthetically active radiation and biomass accumulation in wheat was also earlier noticed [42]. Contrastingly, higher leaf area of about 44.4% was observed [7] at EC_{550} than at EC_{700} in tomato but, it was 64.4% higher than ambient CO_2 of 380 ppm. Similar to our results, elevated CO_2 levels of 550 µmol/mol, 720 µmol/mol and 900 µmol/mol have resulted in increased leaf area by 50% in maize [43], 30% in sugarcane [44] and 25% in sorghum [45], respectively. The higher LAI at both CO_2 concentrations compared to ambient CO_2 is because of the positive relationship between LAI and leaf area. Improved LAI at tasseling (17.5%) and silking stage (14.8%) at elevated CO_2 (550 ± 20 ppm) and decreased LAI by 5.4 to 13.2% at elevated temperature (+1.5 to 3.0 °C) was noticed in maize [15]. Irrespective of the cultivars, increased LAI of about 23% at both vegetative and flowering stages of wheat at elevated CO_2 (550 ppm) was revealed by Yadav et al. [46]. In safflower, elevated CO_2 of 1000 µmol/mol maximized the LAI by 28% at anthesis stage over ambient CO_2 of 400 µmol/mol [47]. The current results also corroborate the findings of Bray and Reid [48]; Nasser et al. [49].

Higher LAD at higher levels of CO_2 has been noticed at all growth stages of the study. Irrespective of growth stages 21–75% higher LAD was observed under EC_{700}. The higher leaf area of the plants resulted in higher LAD when they grow under elevated CO_2 [50]. At initial pod filling to full seed stage in soybean, increased LAD by 4.3 fold at the upper nodes and 2.4 fold on branches under elevated CO_2 (580 ppm) was revealed by Jin et al. [51]. Similarly, higher LAD of castor at EC_{700} and EC_{550} was earlier noticed by Vanaja et al. [52]. The improved leaf area and LAD have accelerated the photosynthesis under elevated CO_2 levels and showed a significant increase in CGR of tomato crop. Increased dry matter accumulation of about > 27% due to higher photosynthetic rate of 20–28% was reported under elevated CO_2 (~750 µmol/mol) condition by Usuda [53]. Aein et al. [54] and Sujatha [55] also reported a significant increase in CGR under elevated CO_2 in potato and rice, respectively. A linear association has been reported between biomass, LAI, LAD, and intercepted photosynthetically active radiation (IPAR) in different cereal, oilseed and pulse crops [56–58]. In contrast to elevated CO_2 levels, lower growth parameters (leaf area, LAI) have lowered the LAD and CGR under elevated temperature alone (+2 °C). At higher temperatures, because of reduced solubility of CO_2 and reduced specificity of Rubisco enzyme, the photorespiratory loss of CO_2 will be more, and have lower affinity for photosynthetic carbon fixation. In addition, reduced electron transport rate at elevated temperature further restricts photosynthesis and reduces crop growth [59,60]. However, elevated CO_2 levels reduce photorespiratory loss because of carbon fixation through photosynthetic carbon reduction cycle and thereby results in increased photosynthetic rate [61]. However, elevated carbon masked the higher temperature effects and showed increased growth parameters under their combination in our study. Even though we have not studied the photosystem-II (PS-II) efficiency, improved PS-II thermostability leading to higher crop growth at both elevated CO_2 and temperature was evident from the other studies [62]. CO_2 enrichment increased leaf photosynthetic rate by 66%, 43% and 39% at temperature regimes of 28/18, 34/24 and 40/30°C, respectively [63]. Similarly, enhanced

photosynthetic rate due to elevated CO_2 levels at higher temperatures was also earlier reported in groundnut [64,65].

The combined effect of elevated CO_2 levels and temperature have altered the different phenophases of the tomato and showed earliness in branch initiation, flower initiation, fruit formation and fruit maturation than ambient levels under open field conditions and under OTCs. Enhanced crop growth and development determining parameters like plant height, leaf area, dry matter, LAI, LAD, CGR, and net photosynthetic rate indirectly influence the earliness of different phenophases at elevated CO_2 through canopy temperature modification [66]. Temperature and CO_2 levels are important determines of plant growth and duration of various developmental stages [67,68]. Higher canopy temperature at elevated CO_2 conditions may indirectly lead to early phenological stages in the crops [14]. Furthermore, altered source to sink relationship due to imbalance translocation of photosynthates was the key factor for earliness in the crop maturity at elevated CO_2 and temperature [69,70]. Elevated CO_2 of 500 µmol/mol and temperature of 1.5–2.0 °C shortened pre-heading stage by 12 days in wheat [13]. Advanced maturity of wheat by 10–13 days was reported [17,71] by increasing daily mean canopy temperature (1.5–2.0 °C). In rice, increasing daily mean temperature by 1.1–2.0 °C has reduced pre-heading stage by 3.3 days [72]. Irrespective of mungbean genotypes, earliness in first flowering by 3.8 days and first pod maturity by 5.19 days was noticed at elevated CO_2 (570 ± 20 ppm) under OTCs [16]. Maize grown under ambient CO_2 and elevated temperature (+3.0 °C) have shortened the 50% tasseling by 5.3 days followed by elevated temperature (+3 °C) and CO_2 (550 ± 20 ppm) by 4.2 days compared to the ambient situation [15].

Higher growth and biomass accumulation under elevated CO_2 levels led to higher nutrient uptake than ambient conditions. Irrespective of the plant parts (leaf, stem and fruit) and growth stages (50% flowering, peak fruiting and at harvest) enhanced NPK uptake was observed at EC_{700} followed by EC_{550}. About 134%, 126% and 135% higher total NPK uptake was observed under EC_{700} over ambient conditions. Increased root biomass and nutrient demand by accumulated biomass are critical factors for increased nutrient uptake under elevated CO_2 conditions [73]. Higher root biomass due to higher allocation of photosynthates and carbon to the roots under higher atmospheric CO_2 was earlier reported by Pendall et al. [74]. We also observed increased root dry weight by 50% under EC_{700} and 33% under EC_{550} compared to plants grown under open field conditions. However, decreased root weight by 28% and 17% was also noticed under elevated temperature (+2 °C) and ambient conditions of CO_2 and temperature at OTC over the open condition. Increased root weight by 36–48% and nitrogen uptake by 17% in dry seasons under elevated CO_2 (≈490 µmol/L) in rice was reported by Satapathy et al. [75]. The strong positive relationship between root biomass and N uptake (0.97) and between N uptake and total dry matter accumulation (0.96) was also reported earlier by Kim et al. [76] and Carvalho et al. [77]. Increased N uptake in both straw and grain of rice due to increased grain and straw yield under elevated CO_2 (550 ± 20 ppm) was noticed by Raj et al. [23]. Increased N uptake by wheat and rice up to the milking stage and maturity stage, respectively was also reported by Cai et al. [13] at elevated CO_2 of 500 µmol/mol. They also observed reduced N uptake at elevated temperature (1.5–2.0 °C) alone. However, in our study we have observed increased NPK uptake up to the harvesting stage of the crop. The rate of N supply will play a prime role in N uptake by the crop in the form of higher dry-matter accumulation. The evident association between N application rate and CO_2 treatment towards N uptake by the crop was earlier revealed and reported that increase in N uptake by 2% with low N (4 g N/m^2) and 20% with high N (12 g N/m^2) under free-air CO_2 enrichment in rice [76].

With respect to P, the external supply of P through fertilizers and the native soil P pool are the key determinants of P-use efficiency, but this varies by species [24]. With enhanced plant growth under elevated CO_2, the external P demand is likely to rise. Increased CO_2 levels are likely to influence the crop's ability to obtain P from soil profiles by altering root architecture and morphology. Altering the composition and quantity of root exu-

dates can also affect rhizosphere properties and helps in P acquisition [78]. According to a meta-analysis, elevated CO_2 increased the total rhizodeposits by 38% and total root biomass by 29% in various crops [79]. Similarly, higher efflux rates of total soluble sugars (47%), citrate compounds (16%) and carboxylates (111%) under elevated CO_2 were also reported by Dong et al. [80]. All these compounds will play a prime role in enhancing the microbial population in the rhizosphere soil, which are responsible for better nutrient availability in the soil. Under elevated CO_2, an increase in active Pseudomonas bacteria population in the rhizosphere capable of solubilizing sparingly soluble inorganic P compounds was observed [81,82]. Positive correlation between improved P uptake by shoot and root biomass was observed by Yang et al. [83]. In rice, higher P uptake under elevated CO_2 (550 µmol/mol) in shoot (29%), root (28%) and grain (22%) due to higher root and shoot biomass than control chamber was reported by Bhattacharyya et al. [27] and revealed that enhanced soil P solubilization in the rhizosphere soil due to improved phosphatase enzyme activity have favored the more uptake of P under elevated CO_2. Similar to N and P, a significant increase in the K uptake at elevated CO_2 of 700 µmol/mol in rice was evident by Seneweera [28]. At elevated CO_2, altered stomatal conductance and transpiration rates might have had a significant influence on mass flow of water to the root surface, as well as ion transport and thereby nutrient uptake. In relation to our results, a high correlation between shoot biomass, root biomass, LAI, nitrogen uptake and radiation interception was evident by Roy et al. [84] and Weerakoon et al. [10].

5. Conclusions

The elevated CO_2 levels and temperature have influenced the growth and nutrient uptake by the tomato plants similar to the other C_3 crops at different growth stages in the current study. The growth indicators were found statistically higher under EC_{700} followed by EC_{550} than plants under ambient conditions in the open field. However, crop under elevated temperature (+2 °C) alone and ambient conditions under OTC have showed lower growth than open field plants at all stages. Interestingly, elevated temperature in combination with elevated CO_2 have showed higher growth parameters than elevated temperature alone. Among the different stages, maximum growth was noticed during peak fruiting stage. The combination of elevated CO_2 (700 ppm) and temperature (+2 °C) have showed earliness in different phenophases such as branch initiation, flower initiation, fruit initiation and fruit maturation, and thereby reduced the crop cycle. Broader and thicker leaves under EC_{700} and EC_{550} showed higher cumulative radiation interception and favored for rapid growth of the plants. The increased drymatter accumulation and root foraging area under elevated CO_2 levels (700 and 550 ppm) have resulted in higher NPK uptake by the leaf, stem and fruit of the tomato plants. Thus, to maximize fruit yield under elevated CO_2, adequate NPK must be supplied during the crop growing season to sustain the increase in dry matter production. Moreover, adequate quantities of NPK availability must be coordinated with the crop's growth stages to optimize yield. However, detailed studies on physiological changes under elevated CO_2 and temperature is further needed for better understanding of their interactive effect.

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