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Growth parameters contributing to increased drought tolerance responses in tomato (*Solanum lycopersicum* L.) under elevated carbon dioxide

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Abstract
Based on reports by the IPCC (Intergovernmental Panel on Climate Change), atmospheric CO_2 concentration is rising. Plant growth is nearly always stimulated by elevation of CO_2 and it has been found to ameliorate water stress in the majority of species studied. A pot culture experiment was conducted with three varieties of tomato i.e, Manulakshmi, Vellayani Vijay, Anagha with the objective to study the growth parameters contributing to increased drought tolerance responses in tomato (*Solanum lycopersicum* L.) under elevated Carbon dioxide using the Open Top Chambers (OTC) system. One month old potted tomato plants after shifting to OTC were subjected to water stress and then were allowed to recover. Various growth parameters like root weight, shoot weight, root shoot ratio, specific leaf area, total dry matter content were analysed both after stress and recovery. Elevated CO_2 was found to increase growth parameters like root weight, shoot weight, specific leaf area and total dry matter production. Significantly higher values were recorded for root weight (0.92 g), shoot weight (6.88 g), total dry matter production (5.74 g) under elevated CO_2 compared to open control. The challenges extended by the changing climate situations along with the global warming and reducing water availability, studies on drought tolerance responses as modified by elevated CO_2 environments is highly significant. The results of this study will also help to design improved production technologies with suitable varieties for a changing climatic scenario.

Keywords: climate change, global warming, elevated CO_2, water stress, drought tolerance

Introduction
Agricultural productivity is decreasing worldwide due to detrimental effects of various biotic and abiotic stresses. Drought, which is the most important environmental stress, severely impairs plant growth and development, limits plant production and the performance of crop plants more than any other environmental factor. According to the Intergovernmental Panel on Climate Change (IPCC) [1], by the year 2050, the current atmospheric CO_2 level of 384 µmol l^{-1} (800 Gt) is predicted to rise to 1000 Gt. Increase in global average temperatures would further result in drastic shifts in the annual precipitation with a 20% reduction per year and about 20% loss in soil moisture and can increase potential evapotranspiration, leading to a more severe water deficit in arid and semiarid areas [2].
Carbon dioxide is the ‘food’ that sustains essentially all plants on the face of the earth as well as those in the sea. Carbon dioxide being a primary substrate for photosynthesis, a rising concentration will have a direct effect on plant growth by enhancing the production of assimilates although not proportional. Rising CO_2 generally stimulates C_3 photosynthesis more than C_4. Doubling of the current ambient CO_2 concentration stimulated the growth of C_4 plants to the tune of 10–20% whereas that in C_3 plants was about 40–45% [3]. Elevated CO_2 increases photosynthesis, dry matter production and yield, substantially in C_3 species which is mainly attributed by the competitive inhibition of photorespiration [4].
Elevated CO_2 levels may enhance plant diversity and productivity in an entire ecosystem by decreasing stomatal conductance (g_s) and consequently increasing water use efficiency (WUE) and soil water availability [5, 6, 7]. Thus, plant growth and leaf area increase due to the improvement in water status by CO_2 enrichment under moderate drought conditions.
Tomato (*Solanum lycopersicum*) is the widely cultivated vegetable in India and 2nd most important vegetable crop next to potato. Current world production is about 100 million ton fresh fruits from 3.7 million ha. Considering the role of elevated CO_2 in the drought tolerance responses, the present investigation will help to understand the growth performance, productivity and water stress tolerance capacitiy of tomato and the results of this study will also help to design improved production technologies with suitable varieties for a changing climatic scenario.

Materials and Methods

A pot culture experiment was conducted with three varieties of tomato i.e, Manulakshmi, Vellayani Vijay, Anagha at the Department of Plant Physiology, College of Agriculture, Vellayani, under Kerala Agricultural University. The technology used for CO_2 enrichment was Open Top Chamber (OTC) system [Figure 1]. Two Open Top Chambers were used, one with CO_2 level of 600 ppm (T1) and a second control chamber with control chamber level for assessing chamber effect (T2). A set of experimental plants was maintained in the open field as control (T3). One month old potted plants of amaranthus were shifted to the CO_2 treatment conditions. Plants were maintained under well irrigated conditions for one week. Water stress conditions were imposed by withdrawing irrigation for two days after shifting and stress observations were taken. Thereafter plants were re-watered and on the 5^{th} day of re-watering, recovery observations were taken. The experiment was laid out in CRD with three treatments three replications and two stress levels.

Open Top Chambers (OTC) are square type chambers constructed to maintain near natural conditions and elevated CO_2 conditions for experimental purposes. The basic structure of OTC was built of metal frame and installed in the experimental field. OTCs were covered with a 200 micron UV poly sheet. The chamber was constructed with 3 x 3 x 3 dimension, 45^0slope and $1m^2$ opening at the top. Two such chambers were built in the experimental field; one serves to impose CO_2 enrichment and the other serves as control chamber to study the chamber effects. Elevated CO_2 was released into the chamber from a CO_2 cylinder in a controlled manner. Measurements of microclimatic parameters (temperature, humidity and light) were done within and outside the OTCs with the help of sensors on a real time basis. On an average basis, mean temperature of 46.15^OC relative humidity of 65.96% were recorded inside the chambers during the experimental period. Potted plants were kept within these chambers for a period of two months and observations were taken.

For calculating specific leaf area, fully expanded third leaf (from main stem apex) was collected from each plant. Leaflets were separated, petioles were discarded and area was measured. Leaflets were oven dried at 80^0C for 2 days and the dry weight was taken. SLA was calculated using the formula;

$$SLA(cm^2/g) = \frac{leaf\ area}{dry\,weight}$$

The roots of plants were cut at the base level and washed free of adhering soil with water. The roots were then oven dried and dry weight was recorded. Shoot weight was measured by weighing the above ground part of the plants in a weighing balance. Ratio of weights of dried roots and shoots of sample plants were calculated and mean values were calculated. The sum of root and shoot dry weights were taken as the total dry matter yield.

Fig 1: Open Top Chamber for CO_2 enrichment

Results

Specific leaf area

Stress induced reduction in specific leaf area was observed less in treatment T1 compared to treatment T2 and treatment T3 [Table 1]. Reduction in specific leaf area was found under elevated CO_2 (294.10 cm^2 g^{-1}) compared to open control (319.73 cm^2 g^{-1}) and control chamber (346.09 cm^2 g^{-1}). Among the varieties, highest specific leaf area was observed for variety Manulakshmi (347.77 cm^2 g^{-1}) and lowest was observed for variety Vellayani Vijay (280.75 cm^2 g^{-1}). After re-watering also specific leaf area was observed highest for control chamber (368.33 cm^2 g^{-1}) followed by open control (365 cm^2 g^{-1}) and elevated CO_2 (334.16 cm^2 g^{-1}). Among the varieties, highest specific leaf area was observed for variety Manulakshmi (422.22 cm^2 g^{-1}) and lowest was observed for variety Vellayani Vijay (308.27 cm^2 g^{-1}) [Table 2].

Root weight

Reduction in root weight due to water stress was observed in varieties under all the treatments after stress. After stress, higher root weight was maintained under treatment T1 (1.32 g) followed by treatment T2 (1.28 g) and treatment T3 (0.87 g) [Table 1]. Among the varieties, Vellayani Vijay recorded higher root weight (1.55 g) compared to Anagha (1.06 g) and it was significantly higher compared to Manulakshmi. after re-watering, higher root weight was observed under elevated CO_2 (1.30 g) compared to open control (1.11 g) and among the varieties, Vellayani Vijay was found to maintain higher root weight (1.64 g) followed by Anagha (1.17 g) and Manulakshmi (1.13 g).

Shoot weight

Higher shoot weight was observed under treatment T1 (4.42 g) followed by treatment T2 (3.98 g) and treatment T3 (3.54 g) after stress and among the varieties, higher shoot weight was observed for the variety Vellayani Vijay (4.56 g) followed by Manulakshmi (3.85 g) and Anagha (3.53 g). After re-watering, higher shoot weight was observed under elevated CO_2 (4.09 g) followed by control chamber (3.02 g) and open control (2.04 g). Among the varieties, higher shoot weight was observed for Vellayani Vijay (3.54 g). Extent of re-gain in shoot weight from water stress was observed more for variety Vellayani Vijay under treatment T1 compared to treatment T3 [Table 2].

Root shoot ratio

Root shoot ratio under elevated CO_2 (0.40) was observed higher compared to treatment open control (0.35) after stress [Table 1]. Among the varieties, higher root shoot ratio was recorded for Vellayani Vijay (0.47) compared to Anagha (0.37) and Manulakshmi (0.40). After re-watering, lower root shoot ratio was observed under treatment T1 (0.34) followed by treatment T3 (0.56) and treatment T2 (0.62). Among the varieties, higher root shoot ratio was observed for the variety Manulakshmi (0.70) compared to Vellayani Vijay (0.64) and it was found significantly higher compared to Anagha (0.47).

Dry matter production

After stress, water stress induced reduction in dry matter production under elevated CO_2 was found to be less compared to open control. Dry matter production was recorded significantly higher under treatment T1 (5.74 g) compared to treatment T3 (4.41 g) and lower compared to treatment T2 (5.94 g) [Table 1]. Among the varieties, dry matter production was recorded significantly higher for Vellayani Vijay compared to both Manulakshmi and Anagha. After re-watering, highest recovery in dry matter production from stress was observed under elevated CO_2 for the variety vellayani vijay. Dry matter production was observed significantly higher under elevated CO_2 (5.40 g) compared to treatment open control (3.16 g). Among the varieties, highest dry matter production was recorded for the variety Vellayani Vijay (5.19 g) followed by Anagha (4.21 g) and Manulakshmi (3.72 g) [Table 2].

Table 1: Effect of elevated CO_2 on growth parameters after stress and re-watering in tomato

Parameter	Elevated CO_2(T1)		Ambient CO_2(T2)		Open control(T3)		CD(0.05)	
	Stress	Recovery	Stress	Recovery	Stress	Recovery	Stress	Recovery
Specific leaf area ($cm^2\ g^{-1}$)	294.10	334.16	346.09	368.33	319.73	365.00	59.72	63.89
Root weight (g)	1.32	1.30	1.28	1.53	0.87	1.11	0.52	0.47
Shoot weight (g)	4.42	4.09	3.98	3.02	3.54	2.04	1.41	1.50
Root shoot ratio	0.40	0.34	0.49	0.62	0.35	0.56	0.19	0.20
Dry matter production (g)	5.74	5.40	5.94	4.56	4.41	3.16	1.85	1.63

Table 2: Varietal variation in growth parameters under elevated CO_2 after stress and re-watering in three varieties of amaranthus

Parameter	Manulakshmi		Vellayani Vijay		Anagha		CD(0.05)	
	Stress	Recovery	Stress	Recovery	Stress	Recovery	Stress	Recovery
Specific leaf area ($cm^2\ g^{-1}$)	347.77	422.22	280.75	308.27	304.40	337.00	59.72	63.89
Root weight (g)	0.85	1.13	1.55	1.64	1.06	1.17	0.52	0.47
Shoot weight (g)	3.85	2.58	4.56	3.54	3.53	3.04	1.41	1.50
Root shoot ratio	0.37	0.70	0.47	0.64	0.40	0.47	0.19	0.20
Dry matter production (g)	4.71	3.72	6.78	5.19	4.60	4.21	1.85	1.63

Discussion

Plant development and morphogenesis is governed by the effects of several environmental conditions super imposed upon genetic constraints. Thus genetically identical plants can exhibit very different structural features when subjected to different environmental conditions. Number of leaves, leaf size and anatomy are often altered under elevated CO_2 but the magnitude of these changes often decreases as leaves mature and hinges upon plant genetic plasticity, nutrient availability, temperature and phenology [8].

Specific leaf area (SLA) is an indicator of leaf thickness and density. Exposure to elevated CO_2 can increase number of palisade cells, which contributes to increase in leaf thickness [9]. High accumulation of starch and lower rate of leaf expansion can also lead to the reduction in specific leaf area under elevated CO_2. In tomato, 8% and 8.44% Reduction in specific leaf area was found under elevated CO_2 compared to open control after stress and re-watering respectively. The result was in accordance with a study conducted in *Jatropha curca* where drought stress decreased specific leaf area under elevated CO_2 [10].

An extensive root system is advantageous to support plant growth during the water limited conditions in early crop growth stage to extract water from shallow soil layers that is otherwise easily lost by evaporation. Root physiology and morphology can be affected by elevated CO_2. Previous studies have shown that elevated CO_2 increased the root density by influencing both mass and unit root length per volume of soil and this is most evident in roots located in the upper layers of soil [11].

In the present study on tomato, highest root weight was maintained under elevated CO_2 than open control after stress and re-watering. A per cent increase in root weight by 34.09 and 14.61 was recorded under elevated CO_2 compared to open control after stress and re-watering respectively. This is in agreement with many studies conducted in winter wheat [12] and many annual plant species [13].

Shoot growth can be stimulated by exposure of plant canopies to high CO_2 concentration. Photosynthesis and Carbon allocation to plant shoots increases as atmospheric CO_2 rises which leads to an increase in above plant biomass.

In the present study, increase in shoot weight was recorded for all the varieties of tomato under carbon dioxide enriched treatment compared to open control both after stress and re-watering. An increment by 19% and 50% in shoot weight after stress and recovery was observed respectively under elevated CO_2 compared to open control. This result was in agreement with former reports in *Fagus sylvatica* [14] and *Larrea tridentate* [15]. Root/shoot ratio is the simple calculation of the ratio of root dry mass to shoot dry mass and should serve as a measure of the preferential allocation of C to roots or shoots [16]. In this experiment, no significant difference in root shoot ratio was observed after stress where as 39% reduction in root shoot ratio was observed after re-watering under elevated CO_2 compared to open control.

Elevated CO_2 stimulates photosynthesis in various intensities during different phenological phases [17] and its direct consequence is increased dry matter production [18, 19]. In present study on tomato, water stress induced reduction in dry matter production under elevated CO_2 was found to be less compared to open control. Dry matter production under elevated CO_2 was found 23.17% and 41.48% superior after stress and re-watering respectively which was found in agreement was in agreement with findings in soybean [20] dry bean [21], peanut and cowpea [22, 23].

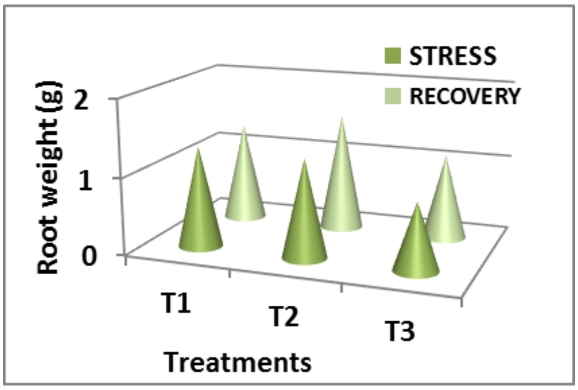

Fig 2: Effect of elevated CO2 on root weight of tomato after water stress and recovery

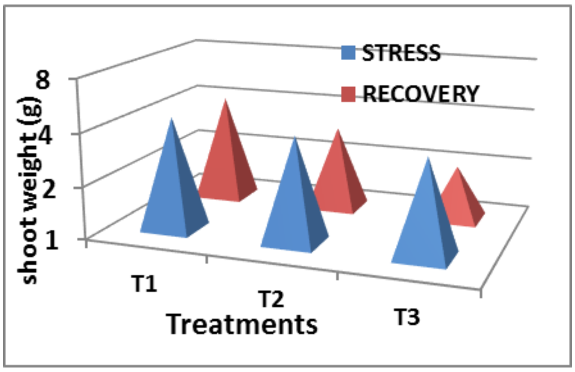

Fig 3: Effect of elevated CO2 on shoot weight of tomato after water stress and recovery

Conclusion

The present investigation was carried out with the objective to study the physiological basis of varietal responses of tomato to water stress conditions and to study their modifications under elevated CO_2 environments. Considering all the growth parameters, it can be concluded that carbon dioxide enrichment has a positive role in improving water stress tolerance and recovery responses in the case of tomato. High shoot weight and total dry matter content for the variety Vellayani Vijay in tomato was achieved in elevated CO_2 under water stress conditions because of activation of drought tolerance mechanisms like maintaining high root weight which helps in efficient water absorption under water limited conditions. Varietal variation was found existing in Carbon dioxide enrichment induced drought tolerance responses which gives better scope for the selection of suitable varieties for a changing climatic scenario.

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