Response of C_4 (maize) and C_3 (sunflower) crop plants to drought stress and enhanced carbon dioxide concentration

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ABSTRACT

Sunflower (*Helianthus annuus* L.) and maize (*Zea mays* L.) were chosen as C_3 and C_4 crop plants and assessed for the impact of enhanced CO_2 (700 ppm) and its interaction with drought stress in open top chambers (OTCs). The ameliorative effect of higher CO_2 concentration (eCO_2) under drought stress was quantified. It is interesting to note that the C_3 crop responded significantly and positively with eCO_2 under both well-watered and drought stress treatments for root: shoot ratio while C_4 crop showed a better response only with the drought stress environment. Root volume showed a positive significant response with CO_2 concentration enhanced over ambient level and the increment in root volume was 146% and 340% in sunflower and maize crops, respectively. The leaf water potential, stomatal conductance and transpiration showed a decreasing trend in both the crops with drought stress and eCO_2 showed an ameliorative effect leading to higher P_n rates in sunflower crop under drought stress treatment. The findings reveal that improvement of root traits is worth attempting for the future crop behavioral responses under eCO_2 and drought stress environments. The study confirmed the beneficial effect of eCO_2 in maize and sunflower by ameliorating the adverse affects of drought stress.

Keywords: leaf area; root and shoot characteristics; leaf water potential; gas exchange

The rising atmospheric CO_2 may cause global warming as well as alterations in precipitation patterns. Rising temperature and altered soil moisture due to climate change is believed to decrease the yield of food crops over next 50 years and elevated CO_2 concentration is expected to enhance the crop yield and mitigate the detrimental effects of climate change. Controlled environment studies revealed that CO_2 fertilization factors simulate the enhancements of net CO_2 assimilation rate and yield in both C_3 and C_4 crops (Kimball et al. 2002, Reddy et al. 2010). Drought is the main environmental factor limiting plant growth and the productivity of many crops. In most of the tropical and equatorial regions of the world and across large areas outside the tropics, the yield of agricultural crops is limited more with the amount of water received in and stored within the soil than by air temperature.

It is now well known that C_3 and C_4 plants respond differently to atmospheric CO_2 enrichment. Early controlled environment experiments with plants grown in pots demonstrated that C_3 species would produce more biomass than C_4 species, when grown individually under enhanced CO_2. The differential response of C_3 and C_4 crops may lead to changes in areas sown under different crops. When atmospheric CO_2 content is increased, one might expect C_3 crops to generally perform better than C_4 crops (Reddy et al. 2010). It may, for example, accelerate the recent trend in India toward wheat, rice and barley and away from maize and millets, a trend that has largely been driven by the promise of greater increases in yield.

Maize is an important staple C_4 food crop in many countries of the world and it accounts for around 712 million metric tones in 2006. Sunflower (*Helianthus annuus* L.) is one of the important oilseed crop grown in the world and the edible oil contains more vitamin E than any other vegetable oil. Sunflower seed production was 33.3 million tons in 2008–2009, and accounts around 8.5% of the total oilseeds production of world.

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Independently, the impact of increased atmospheric CO_2 and drought stress on crop growth and productivity was well documented, however the interaction between these two are not well understood. The present study was aimed at assessing the influence of enhanced CO_2 under both well watered and drought stress conditions on plant water status, gas exchange and various root and shoot parameters of maize (C_4) and sunflower (C_3) crop plants.

MATERIALS AND METHODS

Sunflower (*Helianthus annuus* L.) cv. KBSH-1 and maize (*Zea mays* L.) cv. Harsha were chosen as C_3 and C_4 crops to evaluate their response to enhanced CO_2 (eCO_2) and its interaction with moisture stress. The plants were raised in open top chambers (OTCs) having 3 m × 3 m × 3 m dimensions lined with transparent PVC (polyvinyl chloride) sheet having 90% transmittance of light. The eCO_2 of 700 ppm was maintained in two OTCs throughout the study and other two OTCs without any additional CO_2 supply which served as ambient control with 380 ppm (aCO_2). The desired CO_2 concentrations within the OTCs were maintained and monitored continuously throughout the experimental period as illustrated by Vanaja et al. (2006).

The plants were raised in 5 liter capacity pots filled with approximately 6.5 kg of red soil (Alfisol) having 16% moisture content at field capacity. The soil was sandy loam in texture, neutral in pH (6.8), low in available N (210 kg/ha), P (10 kg/ha) and medium to high in available K (170 kg/ha). The recommended dose of fertilizers was applied and the plants were maintained free from pests and diseases.

Each OTC contained 48 pots with each pot containing one plant. The pots were spaced 20 cm apart in all directions in order to minimize competition for light and rows were oriented in a north-south direction. After raising the plants for 21 days in OTCs, half of them were subjected to moisture stress by withholding the irrigation. The two water regimes 80% and 50% of soil water content at field capacity served as well watered (WW) and drought stressed (DS) conditions, respectively. The soil water content was determined by weighing the pots daily and calculated based on the pot weight, soil dry weight and the expected soil water content. Water was added at the time of weighing to maintain the predetermined water content in each pot. Additionally in the last stage of the experiment, the wet weight per seedling was estimated and added to the pot weight. Each treatment i.e. elevated CO_2 + WW (EW); elevated CO_2 + DS (ED); ambient CO_2 + WW (AW); ambient CO_2 + DS (AD) have 12 pots in each OTC and total 24 pots per treatment. The effect of moisture stress on gas exchange and growth components was analyzed at the end of the stress period of five days in each treatment.

Plant water and gas exchange measurements

Plant water status was assessed at the end of the stress period by measuring the leaf water potential (Ψ_w) of the youngest fully expanded leaf using the Scholander pressure chamber (PMS Instruments, Model 600, Corvallis, USA). The net photosynthetic rate (P_n), stomatal conductance (g_s) and transpiration rate (T_r) were measured using LI-COR-6400 photosynthesis system (LI-COR, Lincoln, USA) under field condition. A CO_2 cartridge was used in order to get stable CO_2 concentrations and to maintain CO_2 concentration of the growth conditions into the leaf chamber.

Growth measurements

Plants were harvested at the end of the stress period and plant parts were separated into leaves, stem, and roots. The leaf area was measured with L1-3100 leaf area meter (LI-COR, Lincoln, USA) and expressed as cm^2/plant. Root length was recorded on the main root of each plant and root volume was measured as mL of water displaced and expressed as mL/plant. After thorough drying of the plant material in hot air oven at 65°C till constant weights were obtained, the dry weights of stem, root and leaf were recorded and expressed as g/plant.

The data were analyzed statistically using a two-way analysis of variance (ANOVA) to test the significance of treatments namely crops, CO_2 levels, moisture levels and their interactions.

RESULTS AND DISCUSSION

Plant water status and gas exchange

Leaf water potential (Ψ_w) decreased significantly ($P \leq 0.01$) with moisture stress in both maize and sunflower crops with ED and AD treatments (Figure 1). The CO_2 levels and their interaction

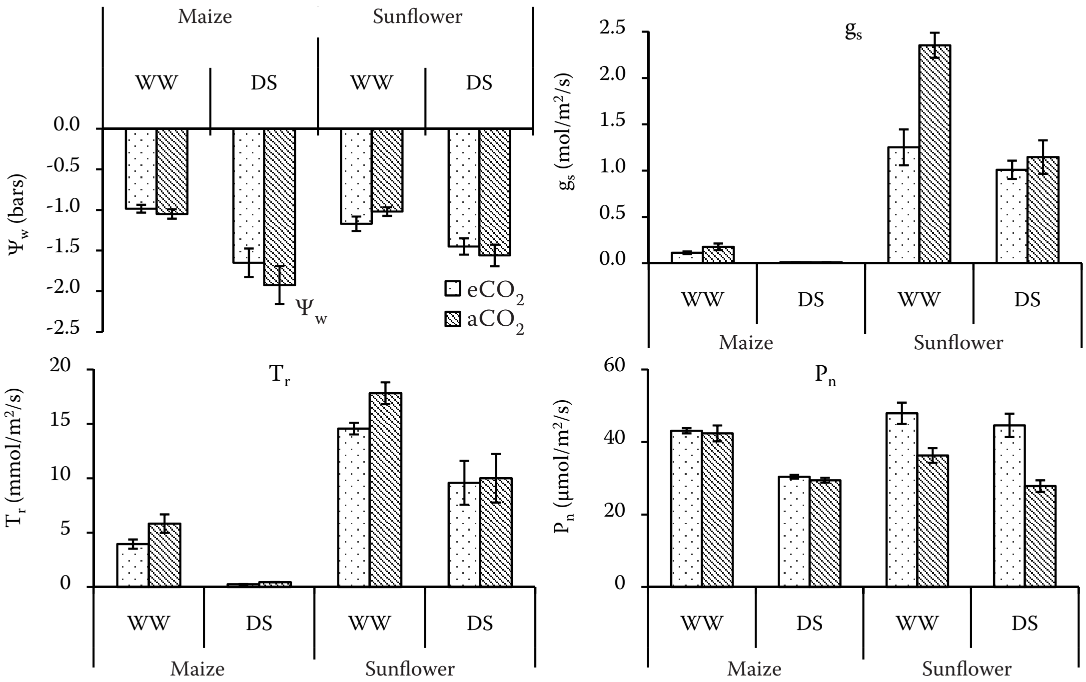

Figure 1. Leaf water potential (Ψ_w), stomatal conductance (g_s), transpiration rate (T_r) and net photosynthetic rate (P_n) of maize (C_4) and sunflower (C_3) under well watered (WW) and drought stress (DS) conditions at elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) concentrations

with moisture status were non-significant in both the crops for change in Ψ_w response. However, the Ψ_w decreased slowly under ED conditions which improved Ψ_w by 7% in sunflower and 14% in maize over ambient. Increased atmospheric CO_2 concentrations ameliorates, mitigates or compensates for the negative impacts of drought on plant growth (Wullschleger et al. 2002) and enables the plants to remain turgid and functional for longer period (Centrito et al. 1999). Maintenance of better Ψ_w in plants grown at eCO_2 could be a consequence of stomatal control.

Stomatal conductance (g_s) of both ambient and elevated CO_2 grown sunflower and maize plants were influenced by drought stress ($P \leq 0.01$). Stomatal conductance of well watered sunflower (46.8%) and maize (35.6%) plants was significantly reduced by growth under elevated CO_2 conditions ($P \leq 0.01$). There was also a significant difference ($P \leq 0.01$) in g_s between CO_2 treatments when sunflower plants were subjected to drought. However, under similar situation the response of maize was very small (Figure 1). The reduction of stomatal conductance is the primary impact of increased atmospheric CO_2 concentration on plants (Wall 2001). Considerably lower stomatal conductance at elevated CO_2 was reported in some other crops such as sugarcane (Vu and Allen 2009), barley (Robredo et al. 2007), rice (Uprety et al. 2002) and wheat (Wall 2001).

Transpiration was significantly ($P \leq 0.01$) influenced by water availability in both maize and sunflower. Elevated CO_2 reduced transpiration by 18% and 32% in sunflower and maize under well watered condition. The reduction in transpiration due to increased CO_2 under drought stress was at higher magnitude in maize (42%) than sunflower (4%). Reduction in stomatal conductance under eCO_2 decreased transpirational water losses through plant stomata. It appears eCO_2 exposure tends to enhance soil moisture conservation, which can improve overall plant water relations and facilitate higher biomass production.

Elevated CO_2 significantly ($P \leq 0.01$) improved the P_n in both well watered and moisture stressed sunflower plants. Under drought stress the sunflower P_n values were significantly ($P \leq 0.01$) higher (60%) in elevated compared with ambient CO_2 (32%). In contrast, the impact of elevated CO_2 on P_n in maize was not significant in both well watered and moisture stress conditions, though significant ($P \leq 0.01$) reduction in P_n with drought stress was observed under both elevated and ambient CO_2. As per Ward et al. (1999), the reduction in the rates of net photosynthesis under water stressed conditions was less in C_4 plants as compared with greater reduction in P_n values and leaf area for C_3 plants resulting in higher reduction in biomass production. Relatively less negative effect of soil drying on P_n under eCO_2 was observed in C_4 maize as compared with C_3 sunflower and it could be due to better Ψ_w and the photosynthesis more readily saturated even at normal atmospheric conditions.

Growth measurements

The growth response of both maize (C_4) and sunflower (C_3) crops to eCO_2 and its interaction with moisture stress was categorized as (i). The improvement of different biomass components due to eCO_2 in which the most responsive growth parameter to eCO_2 in each crop was identified under both irrigated and stress conditions. (ii) The reduction due to moisture stress and its interaction with eCO_2 in which the most affected growth parameter due to moisture stress at eCO_2 and aCO_2 and the range of ameliorating capability of eCO_2 in each crop was identified. The per se values of different growth parameters of both maize and sunflower crops at eCO_2 and aCO_2 were presented in Figure 2.

The ANOVA results for different growth characters indicated that CO_2 levels and moisture levels are significant for leaf area, total biomass and its components such as leaf, stem and root biomass of both crops; however the interaction of CO_2 and moisture levels were non-significant (Table 1). The response of shoot length was significant in sunflower for both CO_2 levels as well as moisture levels whereas in maize it was significant only with moisture levels. The root length in sunflower and root volume in maize was significant for CO_2 levels. Highly significant response was observed for maize with the interaction of CO_2 and moisture levels. The root: shoot weight ratio response was highly significant in maize with moisture levels.

(i) Response of biomass components to eCO_2 in sunflower and maize

Leaf characters. An increase in the leaf area in response to eCO_2 ranged from 7% and 86% in

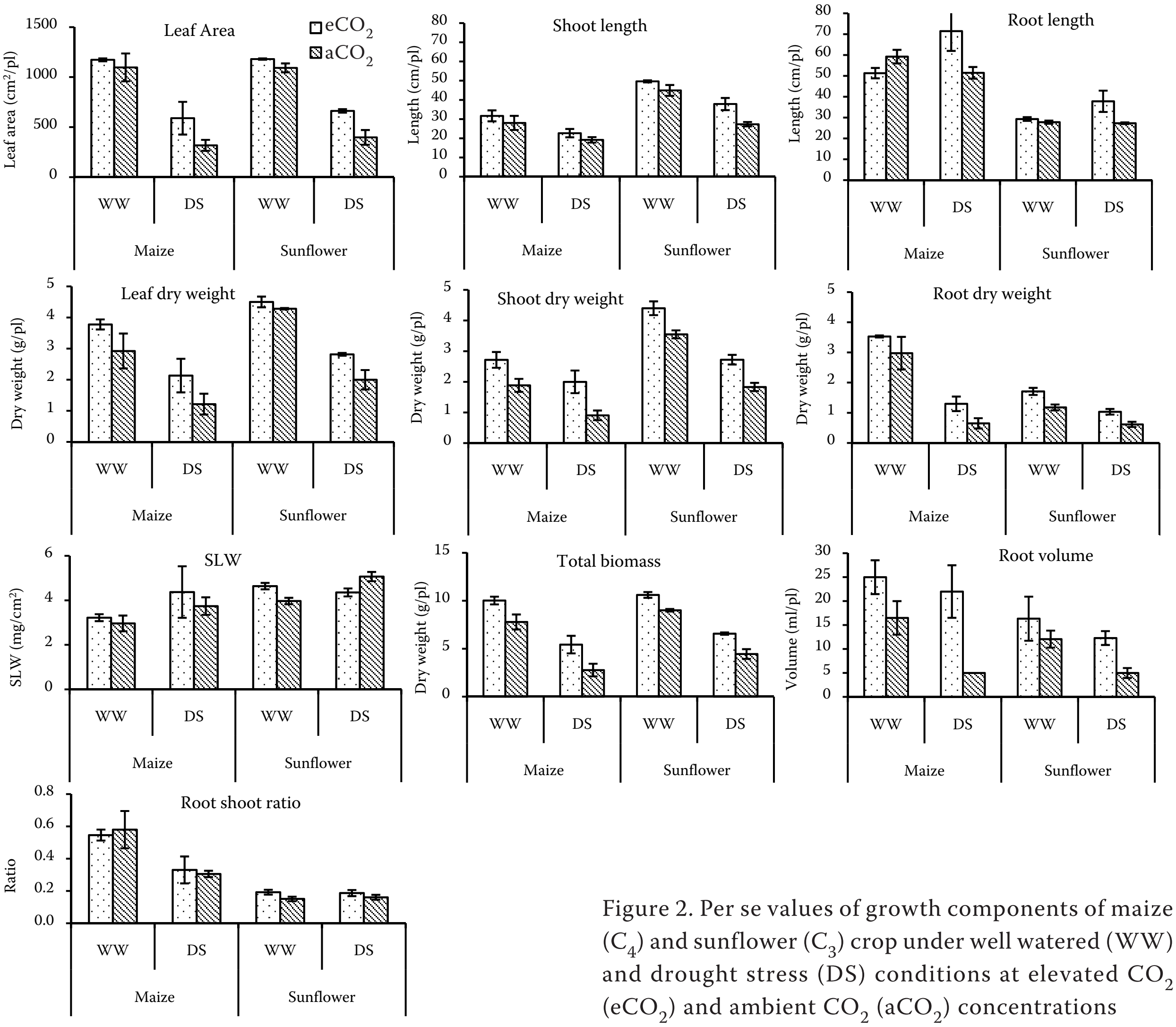

Figure 2. Per se values of growth components of maize (C_4) and sunflower (C_3) crop under well watered (WW) and drought stress (DS) conditions at elevated CO_2 (eCO_2) and ambient CO_2 (aCO_2) concentrations

Table 1. ANOVA of root and shoot characters with (aCO_2) and (eCO_2) under well-watered and drought stressed conditions in maize and sunflower

Characters	Mean sum square					
	CO_2 levels		moisture levels		CO_2 × moisture levels	
	maize	sunflower	maize	sunflower	maize	sunflower
Shoot length	ns	174.04*	238.52*	649.74**	ns	ns
Root length	ns	105.02*	ns	ns	584.50**	ns
Root volume	487.69*	ns	ns	ns	ns	ns
Leaf area	90584*	93810**	1394432**	1105954**	ns	ns
Leaf dry weight	2.36*	0.805*	8.44**	11.84**	ns	ns
Stem dry weight	2.78**	2.28**	2.15*	8.65**	ns	ns
Root dry weight	1.07*	0.678**	15.57**	1.152**	ns	ns
Total dry weight	18.00**	10.43**	69.23**	55.56**	ns	ns
Root shoot weight ratio	ns	ns	0.137**	ns	ns	ns
Photosynthesis	ns	806.557**	656.643**	139.234**	ns	26.016*
Stomatal conductance	ns	1.538**	0.033**	2.103**	0.024**	0.931**
Transpiration	ns	ns	82.174**	163.904	ns	ns
Leaf water potential	ns	ns	2.372**	0.672**	ns	ns

**P < 1%, *P < 5%; ns – not significant

maize and 8% and 67% in sunflower under EW and ED conditions, respectively (Table 2). The leaf dry weight improved by 29% in maize and 5% in sunflower with elevated CO_2 under well watered condition and 76% and 41% under drought stress for maize and sunflower, respectively. The eCO_2 conditions improved the specific leaf dry weight (SLW) of maize under both irrigated (9%) and moisture stressed (17%) conditions. Sunflower showed a different trend as eCO_2 improved the SLW under irrigated condition (17%) and decreased under moisture stress condition (–14%). This clearly indicates that in sunflower crop, eCO_2 facilitated more in maintenance of leaf area under moisture stress than leaf dry weight.

Plasticity in leaf area is an important means by which a drought stressed crop maintains control over water use (Blum 1996). Leaf area averaged slightly more per plant of sorghum and soybean under elevated CO_2 (Dugas et al. 1997). Increased CO_2 tends to accelerate the growth and leaf area per plant, which may increase the total transpiration. Uprety et al. (2000) reported that the leaf area increased by 46% compared to ambient grown rice plants. Rogers et al. (1992) reported that there was about 56% increase in the leaf area of soybeans (*Glycine max* L.) at 700 ppm of CO_2. The maintenance of leaf area under drought stress is crucial to sustain the photosynthesis and thereby crop productivity (Wu et al. 2004).

Stem characters. The improvement in shoot length of maize with elevated CO_2 was 13% under well watered conditions which increased to 18% under drought stress. The response of sunflower was 11% and 38% under similar conditions. The increase in dry weight of stem was 44% and 121% under EW and ED in maize while in sunflower it was 24% and 49%, respectively. This clearly indicates that maize stem dry weight response at eCO_2 was higher as compared with that of sunflower under both irrigated and moisture stress conditions. Zhao et al. (2006) observed a positive effect of high CO_2 concentration on shoot biomass growth of *Cinnamomum camphora* under three soil water levels. Higher shoot growth and stem dry weight were observed in *Phaseolus acutifolius* at 700 ppm than at ambient CO_2 (Salsman et al. 1999). Similarly, increased shoot length and dry weight were recorded with enhanced level of CO_2 in *Ricinus communis* (Vanaja et al. 2008). The plant height was unaffected in *Commelina benghalensis*; however leaf, stem and shoot dry weight tended to increased when exposed to enhanced level of CO_2 (Price et al. 2009).

Root characters. The response of root characters such as root length, root volume and root

Table 2. Increase (%) of root and shoot characters due to (eCO_2) over (aCO_2) in maize and sunflower under well-watered (WW) and drought stressed (DS) conditions

	Maize		Sunflower	
	WW	DS	WW	DS
Root characters				
Root length	–13.4	38.8	5	54
Root volume	51.5	340	35	146
Root dry weight	18.6	98.6	45	68
Shoot characters				
Shoot length	13.1	18.3	11	38
Stem dry weight	44.3	120.5	24	49
Leaf area	6.9	85.8	8	67
Leaf dry weight	29.2	75.6	5	41
Root and shoot characters				
Total dry weight	28.8	95.8	18	48
Root shoot ratio	0.58	8.2	28	16

dry weight with ED recorded higher values as compared with EW in both the crops. In maize the response was –13%, 52% and 19% for root length, root volume and root dry weight, respectively for EW when compared with AW and the values for the same parameters under AD were 39%, 340% and 99% (Table 2). In sunflower the response was 5.4% and 38% for root length, 35% and 146% for root volume and 45% and 68% for root dry weight under EW and ED, respectively. A significant improvement in root volume with eCO_2 was evident with both the crops under both conditions. The response of these root characters was more prominent with maize under stressed condition. Under ED the response of root length was significantly higher in sunflower whereas the response of root volume was higher in maize. Elevated CO_2 concentration significantly increased the soybean root volume and root: shoot ratio (Rogers et al. 1994) as a result of increase in root diameter, length, volume and weight.

Total biomass. Total dry weights of both maize (C_4) and sunflower (C_3) crops showed a significant positive response under both EW and ED conditions. Increase in the total biomass of maize was 29% under EW and 96% under ED and the response was 18% and 48% in sunflower, respectively. Earlier studies on a number of crop plants at eCO_2 revealed a positive response in biomass of C_4 crops, although to a smaller extent as compared with C_3 plants (Kimball 1993). In potato an increase in biomass was observed with irrigation at enhanced CO_2 (Fleisher et al. 2008) and even under severe water stress it led to increased dry matter production in groundnut (Clifford et al. 1993). A significant and positive response in total biomass was observed in *Vigna radiata* L. (Srivastava et al. 2001) and in *Vigna mungo* L. (Vanaja et al. 2007) under enhanced levels of CO_2 at vegetative, reproductive and harvest stages. At early vegetative growth stage in *Vigna mungo* L. and sunflower the total biomass increased with elevated CO_2 with concomitant increase in stem, root and leaf biomass. The root: shoot ratio depends upon the partitioning of photosynthates which may be influenced by environmental stimuli. Rogers et al. (2006) observed large variability in root: shoot ratio regardless of photosynthetic pathway.

(ii) Drought stress and its interaction with eCO_2 in maize and sunflower

The reduction of total biomass due to drought stress in maize was lower under eCO_2 (46%) compared to aCO_2 (64%) (Table 3) and similar trend was observed with sunflower and the values were 38% (eCO_2) and 51% (aCO_2).

The extent of reduction in different total plant biomass components namely leaf, stem and root biomass due to moisture stress differed significantly ($P \leq 0.01$) with CO_2 levels and the range of reduction was also found to be dissimilar in maize (C_4) and sunflower (C_3) crops. At aCO_2 the maximum

Table 3. Decrease (%) in root and shoot characters under drought stressed (DS) conditions at (eCO_2) and (aCO_2) in maize and sunflower

	Maize		Sunflower	
	aCO_2	eCO_2	aCO_2	eCO_2
Root characters				
Root length	13.1	–39.3 (400)	30.5	–1.16 (104)
Root volume	69.7	12.0 (83)	58.6	24.7 (58)
Root dry weight	78.2	63.2 (19)	47.8	39.5 (17)
Shoot characters				
Shoot length	31.5	28.4 (10)	39.2	23.8 (39)
Stem dry weight	50.4	26.5 (47)	48.4	38.1 (21)
Leaf area	71.1	49.8 (30)	63.6	44.0 (31)
Leaf dry weight	58.3	43.4 (26)	53.4	37.4 (30)
Root and shoot characters				
Total dry weight	64.3	45.9 (29)	50.7	38.1 (25)
Root shoot ratio	39.9	39.6 (1)	–6.6	3.1 (147)

The values in parenthesis are the % improvement due to (eCO_2) under moisture stress

impact of moisture stress was observed with root volume, root dry weight, leaf area and leaf dry weight in both maize and sunflower though the extent of reduction varied between these parameters. However, eCO_2 helped in amelioration of adverse effects to a larger extent in both the crops.

Leaf, stem, root dry weights of maize decreased due to moisture stress by 58%, 50% and 78% under aCO_2; however, eCO_2 helped the plants to ameliorate the adverse affects by improving them to the extent of 26%, 47% and 19%, respectively over aCO_2 (Table 3). The decrease in these parameters due to moisture stress in sunflower was 53%, 48% and 48% under aCO_2; however, eCO_2 improved leaf, stem, root dry weights to the extent of 30%, 21% and 17%, respectively. In both crops the impact of eCO_2 was found to be highest under drought stress for root length followed by root volume. The improvement in root length was 400% in maize and 104% in sunflower under the ED over AD. The root volume decreased by 70% in maize and 59% in sunflower under AD, which was ameliorated to the extent of 83% and 58%, respectively, by eCO_2. This enhancement in root length and root volume under ED in both crops makes the plants to explore soil moisture more efficiently and maintain growth under drought stress.

Drought stress led to a decrease in leaf area by 71% and 64% in maize and sunflower, respectively under aCO_2, and the detrimental effects were ameliorated to the tune of around 30% in both crops when subjected to eCO_2 condition. Elevated CO_2 also induces other changes in plant development besides enhancing dry matter production. In the present study it was observed that eCO_2 did not influence the P_n rates of maize crop both under WW and DS conditions as compared with sunflower where this condition led to improvement in the P_n rates under both WW and DS conditions. In contrast to this the g_s and T_r were very low in maize under WW condition as compared to sunflower and they further declined under DS condition. An increase in atmosphere CO_2 concentration mitigates drought stress directly by reducing stomatal conductance which reduces transpiration enabling the plant to avoid drought (Wall 2001). Investigations have revealed that elevated CO_2 reduces the rate of drying of plants as water is withheld, consistent with their lower stomatal conductance and lower transpiration rate (Bunce 1998). Elevated CO_2 might enhance the drought tolerance of plant by lowering osmotic potential (Tyree and Alexander 1993).

The study confirmed the beneficial effects eCO_2 in both maize (C_4) and sunflower (C_3) crops more so under drought stress conditions. The root: shoot ratio in sunflower improved under EW and ED conditions by 28% and 16%, respectively over AW and AD. Nevertheless, in maize the response was 8% under ED compared to AD and it was not substantial under irrigated conditions. The higher root: shoot ratio indicates higher partitioning of photosynthates to below-ground parts with enhanced root length and root volume which helps the plants to thrive better under limited moisture environments.

It is interesting to note that the quantum of response of maize (C_4) to eCO_2 was better under both irrigated and moisture stress as compared with sunflower (C_3) crop. This could be due to the responses to eCO_2 that are genotype dependent rather than photosynthetic pathway. However, to conclude the findings, a higher number of representative genotypes from each group of these crops need to be evaluated.

The results of the present study suggest that elevated CO_2 may mitigate drought impact and improve water relations thus abating the ill effects of drought stress on growth of both maize and sunflower. These findings would facilitate the comprehension of how the crop plants would respond to eCO_2 and how would change precipitation patterns in future with changed climatic conditions.

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