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Differential improvement in transpiration efficiency of C_3 and C_4 crop plants under elevated CO_2 conditions

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Atmosphere CO_2 concentration has increased from 280 ppm to the present 393 ppm after industrial revolution. The rate of increase is currently 1.9 ppm per year and CO_2 at the end of this century may reach 500–1000 ppm (IPCC 2007). An increase in CO_2 concentration causes partial closure of stomata, thereby decreasing leaf conductance to CO_2 and H_2O vapour (Morison 1987) and reducing leaf transpiration (Kimball and Idso 1983) while increasing net carbon assimilation. Reduced leaf conductance reduces evapotranspiration (ET, water evaporated from plants and soil per unit land area (Allen 1990).This reduction in transpiration, coupled with increased photosynthesis, can contribute to increased water use efficiency (WUE, production of dry matter per unit of water consumed in ET) and decrease in water requirement (WR, water consumed/ dry matter produced). With respect to agricultural crops, it is reported that atmospheric CO_2 enrichment increased plant WUE in C_3 species (wheat, potato, cotton and soybean) and C_4 species (sorghum and corn).

Elevated CO_2 increased the WUE in wheat by 9.9% and 13.8% under well watered and drought conditions (Qiao *et al*. 2010) and by 20% and 10% under high and low soil nitrogen regimes (Hunsaker *et al*. 2000) and in other C_3 crops, viz. cotton (Hunsaker *et al*. 1994), potato (Magliulo *et al*. 2003), and soybean (Bernacchi *et al*. 2007). In C_4 crops, WUE under elevated CO_2 was higher (7.8-10.4 g/l) than that of ambient CO_2 (5.7-7.0 g/l) under long term moderate and severe water limitation conditions in maize (Chun *et al*. 2011) and it was 9% and 19% under well watered and stressed conditions in sorghum (Conley *et al*. 2001).

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Above studies have reported that elevated CO_2 increased water use efficiency (WUE) of C_3 and C_4 crop plants, but information on transpiration efficiency (TE) a relevant trait related to WUE is lacking. WUE is biomass produced per unit of water consumed in ET while TE is biomass produced per unit of water transpired (T). TE excludes amount of water lost by soil evaporation. This paper presents the water use and transpiration efficiency of sunflower (*Helianthus annuus* L.) (a C_3 crop) and pearl millet (*Rennisetum glaucum* L.) (a C_4 crop) grown simultaneously under ambient and elevated CO_2 (550 ppm) in the open top chambers

Transpiration efficiency was determined by a high throughput gravimetric method (Xin *et al*. 2008). Briefly, 7L capacity plastic pots was filled with potting mix (mixture of vermiculite, Irish peat mass and perlite) and watered until dripping from bottom. When saturated, each pot can hold approximately 1.5 kg of available water which is sufficient to support the growth of seedlings to the initial 20 days. NPK water soluble fertilizer was used for pearl millet and sunflower. The experiment was carried out from January to April 2012. Two seeds were sown in each pot. One week after emergence, each pot thinned to one plant, and the pot was covered from both ends with poly bags. A slit cut in the top bag to permit seedling growth was further sealed with a piece of clear adhesive tape and covered with a layer of dry potting mix to minimize water loss through the slit. The poly bags were tightly fixed onto the pots with an elastic band. The initial weight of the pot was taken. The plastic bagging effectively minimized the water loss from the soil surface. Six pots were kept for each crop (sunflower, KBSH-1 and pearl millet var ICTP 8203) in each chamber (ambient and elevated CO_2). Desired CO_2 concentration of 550 ppm was maintained and monitored continuously throughout the experimental period as illustrated by Vanaja *et al*. (2006). The other OTC without any additional CO_2 supply served as a control chamber (ambient level). The pots were weighed every 3 days (from 15 days after covering with poly bags) and water was supplemented. A small tube (0.4cm diameter) was placed through the poly bag and sealed with adhesive tape on the top. Measured quantity of of water was supplied through a funnel placed on this tube and again sealed with a tape after watering. The plants were maintained till maturity. The plants were cut at the base of the stem at maturity and final pot weight (including roots) was taken. Total water used was calculated by subtracting the final pot weight from the initial weight and then adding the amount of that has been applied at regular intervals. Roots were collected, weighed and then washed to clean the potting mix core. Dry weight measurement of roots and shoots were taken. $TE_{biomass}$ was calculated by dividing the above ground dry biomass by the amount of water transpired; TE_{grain} was calculated by dividing the grain yield by the amount of water used. Transpiration Ratio (TR) was calculated as the ratio of amount of water used (transpired) by a plant during its growing season to the weight of dry matter produced.

Sunflower plants grown under elevated CO_2 conditions, produced significantly more biomass and seed yield and also used more water (not significantly) compared to ambient. The sunflower plants used 11.0% extra water and produced 22.8% extra biomass and 26.8% extra yield under elevated CO_2 conditions compared to ambient thereby increasing the $TE_{biomass}$ and TE_{grain} by 10.5% and 14.1% respectively under elevated CO_2 (Table 1). This is consistent with higher WUE attained with elevated CO_2 in wheat (Chaudhuri *et al*. 1990, Hunsaker *et al*. 2000 and Qiao *et al*. 2010). The high TE_{grain} than $TE_{biomass}$ under elevated CO_2 resulted from high HI. Water used increased from sowing to harvest as the CO_2 increased is in agreement with Chaudhuri *et al*. (1990) where he reported that water transpired increased in wheat (a C_3 crop) as the level of CO_2 increased from ambient to 825ppm. In the present study, TR or the water transpired decreased from 370 g H_2O/g biomass at ambient to 334.2 g H_2O/g biomass at elevated CO_2 and from 1 099.5 g/g grain at ambient to 962 g/g grain at elevated CO_2 supports the previous study demonstrating that water requirement of wheat reduced by 29% when the CO_2 level was raised (Chaudhuri *et al*. 1990). In other C_3 crops it has been reported that higher yield and lower ET under elevated CO_2 lead to substantial increase in WUE in soybean (Bernacchi *et al*. 2007) and potato (Magliulo *et al*. 2003) while WUE increased with the increase in growth caused by elevated CO_2 in cotton (Hunsaker *et al*. 1994) and wheat (Qiao *et al.* 2010) without change in ET.

Pearl millet plants grown under elevated CO_2 produced more biomass (non significantly) and grain yield and used significantly reduced amount of water compared to ambient. The pearl millet plants used 11.9% lesser amount of water and produced 7.1% and 3.8% additional biomass and seed yield, respectively under elevated CO_2 conditions compared to ambient thereby increasing the $TE_{biomass}$ and TE_{grain} by 21.9% and 17.8% respectively (Table 1). The low TE_{grain} than $TE_{biomass}$ at elevated CO_2 conditions resulted from low HI than ambient conditions. Transpiration ratio (TR) or the water transpired decreased from 224.4 g H_2O/g biomass at ambient to 183.7 g H_2O/g biomass at 550 ppm and 483 g H_2O/g grain at ambient to 409.3 g H_2O/g grain at 550 ppm. These results are in agreement with those of Conley *et al*. (2001) and Chun *et al*. (2011). Conley *et al*. (2001) reported that the elevated CO_2 reduced ET (10%) and increased WUE (16%) in sorghum. Chun *et al*. (2011) found that approximately 13-35% less water was used under elevated CO_2 conditions for the water stressed and well watered conditions respectively in maize.

Integrated TE determined by the gravimetric method can be improved either through decreased transpiration or increased biomass production integrated over a period of

Table 1 Effect of elevated CO_2 on total biomass, grain yield and transpiration efficiency of sunflower and pearl millet

Parameters	Sunflower (C_3 crop)			Pearl millet (C_4 crop)		
	380 ppm	550 ppm	CD (P=0.05)	380 ppm	550 ppm	CD (P=0.05)
Total biomass (g/pl)	61.78	75.84 (22.8%)	9.09	85.61	91.7 (7.1%)	NS
Grain yield (g/pl)	20.81	26.38 (26.8)	3.74	39.87	41.38 (3.8%)	NS
Total water used (kg/pl)	22.87	25.40 (11.1%)	NS	19.15	16.86 (–11.9%)	1.95
$TE_{biomass}$(g biomass/kg H_2O)	2.70	2.99 (10.5%)	0.12	4.47	5.45 (21.9%)	0.447
TE_{grain} (g grain/kg H_2O)	0.91	1.04 (14.1%)	0.027	2.08	2.45 (17.8%)	0.236
HI	33.7	34.8	NS	46.5	45.1	NS
Root wt. (g/pl)	6.78	7.50	NS	7.90	9.16	NS
TR_{grain} (g H_2O/g grain)	1099.5	962.0 (–12.5%)	20.94	483.0	409.3 (–15.3%)	46.53
$TR_{biomass}$(g H_2O/g biomass)	370.0	334.2 (–9.7%)	14.24	224.4	183.7 (–18.1%)	20.14

time. Sunflower plants grown under elevated CO_2, produced significantly more biomass and also used more water (not significantly) compared to ambient indicating that increased biomass contributed to the increase TE under elevated CO_2 in C_3 crop. Since the TR or the water transpired (g H_2O/g biomass) decreased under elevated CO_2, decreased transpiration also contributed to increase TE under elevated CO_2 in this C_3 crop. In pearl millet, the plants grown under elevated CO_2 produced more biomass (non significantly) and used significantly reduced amount of water compared to ambient indicating that decreased transpiration contributed to increase TE under elevated CO_2 in this C_4 crop. These results are consistent with Rogers and Dahlman (1993) where he reported, increased photosynthesis as well as reduced transpiration contributes to determination of increased WUE in C_3 plants, whereas decreased transpiration contributes in C_4 plants under elevated CO_2 conditions.

SUMMARY

Sunflower plants (C_3) transpired more water than pearl millet (C_4) from seedling to maturity under ambient conditions. The transpiration (water use) at elevated CO_2 was lesser for pearl millet and higher for sunflower compared to ambient. Elevated atmospheric CO_2 increased TE more in pearl millet (21.9%) than in sunflower (10.5%) and decreased the TR or water transpired to produce dry mass by 18.1% in pearl millet and 9.7% in sunflower compared to ambient. As the CO_2 content of the air continues to rise, both sunflower (C_3) and pearl millet (C_4) agriculture crops will respond favorably by exhibiting increases in TE.

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