Effects of elevated CO_2 and moisture stress on *Brassica juncea*

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Abstract

The interactive effect of elevated CO_2 (EC) and moisture stress (MS) on *Brassica juncea* cv. Pusa Bold was studied using open-top chambers. The EC markedly increased net photosynthetic rate and internal CO_2 concentration and reduced variable and maximal chlorophyll fluorescence. Under MS, EC increased water potential and relative water content, and reduced transpiration rate. The greater allocation of biomass to the roots, which serve as a strong sink for assimilated carbon under EC, helped in better root growth.

Additional key words: chlorophyll fluorescence; dry mass; leaf area; leaf water potential; open-top chamber; relative water content; seed mass and yield; stomatal conductance; transpiration; water potential.

Introduction

The rise in atmospheric CO_2 concentration is one of the important changes which might influence the productivity of future crop plants (for review see Saralabai *et al.* 1997). There is no consensus on the quantitative effects of EC on plants due to differences among species and other limiting environmental factors such as moisture stress (MS), temperature, and salinity (Conroy *et al.* 1986, Uprety *et al.* 1995, 1998). We studied a C_3 plant *Brassica juncea* cv. Pusa Bold which experiences intermittent drought at different stages of growth. Study was done in open top chambers (OTC) to characterize the possible interactive effect of EC and MS.

Materials and methods

Brassica juncea L. cv. Pusa Bold plants were grown in OTCs of 2.6 m diameter,

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Abbreviations: AOTC = ambient CO_2 open-top chamber; C_i = internal CO_2 concentration; DAS = days after sowing, DM = dry mass; E = transpiration rate; EOTC = elevated CO_2 open-top chamber; F_m = maximum fluorescence; F_v = variable fluorescence; g_s = stomatal conductance; LA = leaf area; LWP = leaf water potential; P_N = net photosynthetic rate; PS = photosystem; R_D = dark respiration rate; RWC = relative water content.

lined with transparent PVC sheet (for details see Uprety 1998). The MS was induced at pre-flowering (35 d after sowing, DAS), flowering (45 DAS), or post flowering (70 DAS) stages. Only the values at flowering stage are reported in this paper due to the similarity in response at all the stages. The irrigation was withheld for 8 d between first flower initiation to 50 % flowering to reach an 8 to 10 % moisture in soil. Control plants were grown in soil with 23 to 25 % moisture. CO_2 enrichment of 600±20 μmol mol^{-1} was done in some OTC (EOTC) by continuously injecting 100 % CO_2 in the input blower, where it was mixed with ambient air before entering the chamber. The flow of gas was regulated using solenoid valve and pressure gauge. Thermohygrograph was also kept in each OTC.

P_N, intercellular CO_2 concentration (C_i), and respiration rate (R_D) were measured in the uppermost fully expanded leaf of the main branch by portable infra-red gas analyser *Licor 6200* (Lincoln, Nebraska, USA). R_D was determined near the end of the 10-min dark period. The chlorophyll fluorescence was measured in attached leaves using a portable fluorometer (*CF-1000*, Morgan, USA). The values on maximal fluorescence (F_m), variable fluorescence (F_v), and photochemical efficiency of PS2 (F_v/F_m) were recorded. The leaf temperature was 23 to 24 °C under irrigated condition and 25 °C under MS in OTC-grown plants, whereas irradiance was 1250 to 1300 μmol m^{-2} s^{-1} during P_N, R_D, and fluorescence measurements. The E and stomatal conductance (g_s) were recorded using *Licor-1600* Steady State Porometer (Lincoln, Nebraska, USA). Relative water content (RWC) of leaf was estimated by the method of Weatherly (1950). Leaf water potential (LWP) was measured using a *PMS* (Oregon, USA) pressure chamber (Tyree and Richter 1981). Leaf area (LA) measurements were made by *Licor-3000* (Lincoln, USA) leaf area meter. Seed yield, siliqua mass, and 100 seed mass were recorded from harvested plants. All the observations were made with four replicates. Values were analysed statistically following the analysis of variance (Snedecor and Cochran 1981).

Results

Elevated CO_2 concentration in EOTC significantly increased P_N in *B. juncea* measured *in situ*. The increase was 30 or 34 % compared to field and ambient OTC plants (AOTC), respectively. Moisture stress significantly decreased the P_N, by 41.0, 38.8, and 29.7 % in field, AOTC, and EOTC grown plants, respectively (Table 1).

The EC enhanced internal C_i in plants by 33 % compared to AOTC and field grown plants. The MS treatment decreased the C_i by 35, 30, and 17 %, under field, AOTC, and EOTC, respectively (Table 1).

The EC brought about a significant reduction in the leaf R_D (29 %). The reduction in R_D caused by MS was 64.6, 61.0, and 55.0 % under field, AOTC, and EOTC conditions, respectively (Table 1). The EC treatment significantly increased the P_N/R_D ratio. It was 78 to 83 % higher than in field and AOTC grown plants. The MS decreased the P_N/R_D ratio (Table 1).

The F_m was reduced with EC by 20 to 22 % in relation to AOTC and field grown plants. The MS significantly increased the F_m, by 20 and 29 % under field and

AOTC, respectively, whereas under EC the increase remained only at 5.4 % (Table 1). The EC caused a significant reduction in F_v, while the MS increased it: by 12 % under field, by 21 % under AOTC, and by only 4 % under EOTC (Table 1). The F_v/F_m ratio (an index of photochemical efficiency of photosystem 2) significantly increased under EC (by 15 % in relation to the field plants and by 11 % compared to AOTC). The MS treatment significantly reduced F_v/F_m, by 6 % in field and AOTC, and by only 1.8 % under EOTC treatment (Table 1).

Table 1. Effect of elevated CO_2 concentration (EC) and moisture stress (MS) on net photosynthetic rate (P_N) [μmol m^{-2} s^{-1}], respiration rate (R_D) [μmol m^{-2} s^{-1}], internal CO_2 concentration (C_i) [μmol m^{-3}], and chlorophyll fluorescence parameters F_m and F_v in *Brassica juncea*. AOTC - open-top chambers with ambient CO_2, EOTC - open-top chambers with elevated CO_2. NS - non-significant.

	MS	P_N	R_D	P_N/R_D	C_i	F_m	F_v	F_v/F_m
field	-	27.24	5.24	5.2	340	262	138	0.527
	+	15.81	1.86	8.5	220	315	155	0.492
AOTC	-	25.50	5.10	5.0	330	256	139	0.545
	+	15.60	1.95	8.0	230	330	169	0.511
EOTC	-	32.87	3.46	9.5	458	222	132	0.592
	+	23.10	1.54	15.0	380	235	137	0.583
CD at $p = 0.05$	EC	2.66	0.39	0.84	41.8	6.30	7.77	0.019
	MS	1.68	0.32	0.69	34.1	5.14	6.34	0.016
	EC×MS	NS	0.56	1.19	NS	8.91	10.99	0.027

The EC significantly decreased the g_s of leaves, by 42 and 33 % compared to the field and AOTC grown plants. The MS caused a marked reduction in g_s, by 37, 41, and 21 % in field, AOTC, and EOTC grown plants, respectively (Table 2).

The transpiration rate (E) was considerably reduced under EC, by 31 and 35 % compared to field and AOTC plants, respectively. The MS also reduced E by 26, 29, and 50 % under field, AOTC, and EOTC, respectively. The EC brought about significant increase in the RWC of leaves, by 14.7 and 12.0 % compared to field and AOTC grown plants. The MS treatment decreased the RWC, however, the decrease was 28 and 25 % at field and AOTC, compared to 13 % under EOTC (Table 2).

The LWP was significantly increased under EOTC condition, by 37 and 29 % in relation to field and AOTC. The MS significantly reduced the LWP, however, less under EOTC (Table 2).

The EC significantly increased leaf area, leaf, stem, and root dry masses, but the MS significantly depressed it. The reduction was similar in all the conditions. The MS caused significant reduction in the DM of leaf, stem, and roots; the reduction was significantly less under EOTC compared to AOTC and field conditions (Table 3).

The EC increased the seed yield (by 55 and 44 %), siliqua mass (by 85 and 45 %), and hundred seed mass (by 27 and 21 %) compared to field and AOTC grown plants, respectively. The EC treatment also brought about early flowering. The MS treatment

Table 2. Effect of elevated CO_2 concentration (EC) and moisture stress (MS) on the stomatal conductance (g_s) [mmol m^{-2} s^{-1}], transpiration rate (E) [mmol m^{-2} s^{-1}], relative water content (RWC) [%], and leaf water potential (LWP) [MPa] in *Brassica juncea*. AOTC - open-top chambers with ambient CO_2, EOTC - open-top chambers with elevated CO_2. NS - non-significant.

	MS	g_s	E	RWC	LWP
field	-	760	4.5	82.5	-0.60
	+	480	3.3	61.0	-1.55
AOTC	-	670	4.8	84.0	-0.50
	+	390	3.4	62.8	-1.42
EOTC	-	410	3.6	88.2	-0.40
	+	300	1.7	76.5	-0.95
CD at $p = 0.05$	EC	18.5	1.05	3.44	0.056
	MS	22.7	0.85	2.81	0.046
	EC×MS	27.0	0.21	NS	0.079

decreased the seed yield, siliqua mass, and hundred seed mass: the reduction was significantly less in EOTC grown plants (Table 3).

Table 3. Effect of elevated CO_2 concentration (EC) and moisture stress (MS) on growth and yield components in *Brassica juncea:* leaf area (LA) [cm^2], dry mass (DM) of leaves, stem, and roots [g $plant^{-1}$], time to 50 % flowering [d], seed yield and siliqua mass [g $plant^{-1}$], and 100 seed mass [g]. AOTC - open-top chambers with ambient CO_2, EOTC - open-top chambers with elevated CO_2. NS - non-significant.

	MS	LA	DM_{leaf}	DM_{stem}	DM_{root}	Time to flowering	Seed yield	Siliqua mass	1000 seed mass
field	-	413.50	2.92	3.20	2.10	46	27.35	39.25	5.96
	+	320.45	1.70	1.95	1.60	44	12.73	16.50	4.91
AOTC	-	430.62	2.80	3.50	2.54	44	29.74	46.56	6.52
	+	334.00	1.95	2.10	1.62	43	14.26	24.34	4.95
EOTC	-	768.25	3.85	4.90	3.25	41	36.12	60.28	7.02
	+	584.60	3.10	3.79	2.48	40	26.82	42.48	6.86
CD at $p = 0.05$	EC	16.4	0.190	0.285	0.252	1.25	3.70	6.51	0.483
	MS	13.1	0.155	0.179	0.146	0.85	3.02	5.31	0.375
	EC×MS	22.7	NS	NS	NS	NS	5.23	9.20	NS

Discussion

The CO_2 enrichment brought about a marked increase in P_N and C_i. The enhancement in P_N in *B. juncea* at EC was also reported by Andreeva *et al.* (1989) and Maevskaya *et al.* (1990). They attributed it to the decrease in photorespiratory loss of CO_2. The larger increase in P_N in the present investigation was accompanied by relatively small decrease in g_s. Turner (1974) demonstrated that g_s of leaves under EC was not reduced as rapidly during stress as it did under ambient CO_2 concentration. This may limit the water loss through transpiration and may prove as adaptation of plants to EC. The lower P_N under MS was greatly ameliorated by EC indicating that stomata were the main limiting factor for carbon uptake under MS.

Fluorescence parameters F_v, F_m, and F_v/F_m decreased under EC insignificantly. Thus the electron transport capacity did not change with EC enrichment but was sufficient to sustain high P_N.

We observed a great decline in R_D in *B. juncea* leaves at EC. According to Imai (1995) the suppressed R_D at EC may generally increase the net production in rice unless it is not too low to adversely affect the energetic processes. In our experiments the additional establishment of structural and storage tissue was not affected by reduced respiration. The decline in R_D under MS was greater at AC than EC.

The EC affected the dry matter production under MS. The CO_2 impact on the production of new sinks became marked before the stress effect lead to greater leaf area and root growth. The additional foliage from greater leaf area stimulated by EC helped to fix more carbon, thereby substantially magnifying the growth enhancement induced by increased P_N per unit area. Under MS the fruiting size may be source-limited at AC. However, continuous higher source activity under EC reduced the limitation of the source for photoassimilate transport to siliqua and seed growth, thereby reducing the stress effect on productivity.

The EC induced changes in g_s, reduction in E, and increases in LWP and RWC in *Brassica* helped to maintain congenial water balance for maximal physiological functions and dry matter production in water stressed plants. The below-ground biomass and the root/shoot ratio were higher under EC than AC. Clough *et al.* (1981) suggest that such selective translocation of photosynthates to the roots is necessary to keep saccharides at minimum level in the leaves to prevent reduction in P_N. Thus the present study shows that in *B. juncea* plants the EC induced remobilization of dry matter by increasing the proportion of roots and readjustment of plant water component in favour of its lesser loss. This made congenial photosynthetic balance through change in light reactions and light-harvesting capacity to enable plants to adjust to MS condition.

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