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Yield response of durum (*Triticum durum*) and bread wheat (*T. aestivum*) varieties to carbon dioxide enrichment

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ABSTRACT

In an experiment conducted during the winter season of 1996–97 and 1997–98, 2 varieties ('HD 4502' and 'B 4409') of durum wheat (*Triticum durum* Desf.) and 2 ('Kalyansona' and 'Kundan') of bread wheat (*T. aestivum* L. emend. Fiori & Paol.) were grown in field at atmospheric and elevated CO_2 (650 ± 50 ppm) concentrations inside open top chambers to examine yield components at maturity. The CO_2 enrichment enhanced the grain yield mostly through an increase in the number of ear-bearing tillers. Individual ear weight was also increased in plants grown under elevated CO_2 concentration. Varieties however differed in the manner, the individual ear weight was increased. In 'B 449' and 'Kalyansona', the increase in grain yield of individual ear of plants grown under elevated CO_2 concentration was due to an increase in individual grain weight. In 'HD 4502', an increase in grain yield of individual ear of plants grown under elevated CO_2 concentration was due to higher grain number/ear as a result of increase in spikelets/ear. Genotypic differences in response to elevated CO_2 were observed. Varieties having greater sink capacity in terms of higher grains/ear showed a greater yield response in both tetraploid and hexaploid wheat.

Key words: Wheat species, Yield components, CO_2 enrichment

The concentration of atmospheric CO_2 has risen from pre-industrial concentration of 280 ppm to more than 360 ppm and is rising at a rate of over 1.5 ppm/year (Keeling and Whorf 1992, Bowes 1996). Attempts are therefore being made to analyse how crop plants are going to respond to such changes in CO_2 level (Bowes 1996, Drake *et al.* 1997). However, a meagre information is available on the effect of CO_2 enrichment on plant species in a tropical environment (*Ziska et al.* 1991). CO_2 is a substrate limiting photosynthesis particularly in C_3 plants in the present atmosphere (Bowes 1993, Drake *et al.* 1997, Ghildiyal *et al.* 1998). Photosynthetic productivity is therefore expected to increase under higher CO_2 level. However, long-term exposure to elevated CO_2 down regulates photosynthesis because of imbalance in the supply and demand of carbohydrates (Bowes 1996, Sharma-Natu *et al.* 1997). In order to utilize the beneficial effect of high CO_2 on photosynthesis, sink capacity of the system should be efficient enough to utilize assimilates, otherwise photosynthesis could be limited by sink demand. The yield response to elevated CO_2 therefore, may depend on capacity of economic sinks to utilize assimilates. There are large variations in economic sink capacity in terms of number of potential grains in wheat varieties. Furthermore, a negative correlation between the grain number and grain size has been frequently observed and it is usually ascribed to a limitation in availability of assimilates per grain (Slafer *et al.* 1996, Sunita Kumari and Ghildiyal 1997). Hence an experiment was conducted to analyse the effect of elevated CO_2 on yield in wheat varieties differing in sink potential.

MATERIALS AND METHODS

The study was carried out during the winter season of 1996–97 and 1997–98 at New Delhi, with 4 varieties of wheat, 2 of durum wheat ('HD 4502' and 'B 449') and 2 of bread wheat ('Kalyansona' and 'Kundan'). 'HD 4502' is a small grain type with higher grains/ear, whereas 'B 449' is of bold grain types with less grains/ear. 'Kalyansona' has smaller grains than 'Kundan' with former having more grains/ear than the latter. These wheat varieties were grown in the field inside open top chambers (200 cm × 160 cm). The construction of the open top chambers was based on the design of Leadley and Drake (1993). Two chambers having ambient CO_2 level served as the control, whereas CO_2 concentration in other 2 chambers was elevated to 650 ± 50 ppm. The regular monitoring of CO_2 concentration in the chamber was done by Infra-red gas analyser (ADC 225 MK 3). Spacing of

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Table 1 Yield components in varieties of durum and bread wheat grown under ambient and elevated CO_2 concenteration

Character		Durum wheat		Bread wheat	
		'HD 4502'	'B 459'	'Kalyansona'	'Kundan'
Grain yield (g/plant)	CA	6.03	5.03	5.66	5.02
	CE	8.09	5.96	7.08	5.60
	Increase (%)	34.16	18.49	23.09	11.55
Ears/plant	CA	3.17	3.23	2.90	3.40
	CE	3.40	3.50	3.20	3.75
	Increase (%)	7.25	8.36	10.34	10.29
Grain number	CA	42.84	30.51	58.50	30.00
	CE	52.48	30.95	63.54	30.49
	Increase (%)	23.34	1.44*	8.61	1.63*
1 000-grain weight (g)	CA	44.50	50.94	33.38	49.25
	CE	45.03	55.01	34.84	48.95
	Increase (%)	1.19*	7.99	4.37	-0.61*
Total dry-matter (g/plant)	CA	14.72	11.25	11.59	10.77
	CE	19.49	13.77	14.44	12.10
	Increase (%)	32.40	22.40	24.59	12.35
Harvest index (%)	CA	40.96	44.71	48.83	46.61
	CE	41.50	43.28	49.03	46.28
	Increase (%)	1.32*	−3.20*	0.41*	−0.71*

*NS; CA, ambient CO_2; CE, elevated CO_2

the plants was 20 cm between rows and 2.5 cm within a row. Fertilizers were applied @ 120, 60 and 60 kg/ha of N, P and K respectively. Nitrogen was supplied in 2 split doses, at sowing and ear emergence stage whereas P and K were given only at the time of sowing.

Plants were harvested at maturity and total dry-matter and yield components of main shoot and tillers expressed as per plant were determined. The effect of CO_2 enrichment on the grain weight/spikelet as well as growth of grains at different positions (from basal to apical) in a spikelet were examined in the main shoot ear. In each ear, the apical, middle and basal spikelets were excized. In each of these spikelets, the grains at different positions (from basal to apical) were separated and their dry weights were determined. Data were analysed statistically to determine the CD value. Since the response trends were more or less similar, the data of 1996–97 alone are presented.

RESULTS AND DISCUSSION

Plants grown under elevated CO_2 showed 11.5–34.16% enhancement in grain yield compared to plants grown under atmospheric CO_2 concentration (Table 1). The maximum enhancement of 34.16% in grain yield was in 'HD 4502' durum wheat and a minimum enhancement of 11.55% in 'Kundan' bread wheat. Within a species, a variety having more grains/ear showed a greater enhancement in grain yield by elevated CO_2 than lesser grain type in both tetraploid and hexaploid wheats. One of the components that significantly contributed to the enhancement in grain yield is an increase in ears/per plant owing to an increase in ear-bearing tillers. In 'HD 4502' grains/ear were increased significantly under elevated CO_2 by 23–24% compared to plants grown under ambient CO_2 concentration. 'B 449' showed an increase in 1 000-grain weight by elevated CO_2. An increase in grain yield was observed in plants along with total dry-matter production in all the genotypes, hence there was no significant effect of this treatment on harvest index.

The increase in grain yield expressed on per plant basis in wheat varieties grown under elevated CO_2 was not entirely owing to an increase in ear-bearing tillers. The effect of elevated CO_2 on yield of main shoot ear was therefore determined. The grain yield of main shoot ear increased in plants grown under elevated CO_2 compared with ambient grown plants in all the varieties. The increase however, was not significant in 'Kundan' (Table 2). Varieties differed in the manner in which this increase was brought about. In 'B 449' and 'Kalyansona', the increase in grain yield of main shoot ear was owing to an increase in individual grain weight. In 'HD 4502', the increase in grain yield of main shoot ear of plants grown under elevated CO_2 appeared to be due to an increase in grains/ear as a result of higher number of spikelet/ ear.

The grain weight/apical, middle and basal spikelets in 'HD 4502' and 'Kundan' was not significantly affected by elevated

Table 2 Yield components of main shoot ear in varieties of durum and bread wheat grown under ambient and elevated CO_2

Character		Durum wheat		Bread wheat	
		'HD 4502'	'B 459'	'Kalyansona'	'Kundan'
Grain yield (g/plant)	CA	2.50	1.80	2.53	2.12
	CE	2.79	2.13	2.89	2.32
	Increase (%)	11.60	18.33	14.23	9.43
Grains/ ear	CA	54.00	30.33	76.00	42.70
	CE	60.67	33.00	76.70	46.30
	Increase (%)	12.35	8.80*	0.92*	8.43*
1000-grain weight (g)	CA	46.26	59.06	33.24	49.76
	CE	46.03	64.28	37.65	50.07
	Increase (%)	–0.50*	8.84	13.27	0.62*
Spikelets/ ear	CA	19.50	15.17	19.80	16.60
	CE	23.00	16.33	19.30	17.40
	Increase (%)	17.95	7.65*	–2.52*	4.82
Grains/ spikelet	CA	2.77	2.01	3.84	2.57
	CE	2.64	2.02	3.97	2.66
	Increase (%)	–4.69*	0.50*	3.38*	3.50*
Grain weight (mg/spiklet)	CA	128	119	128	128
	CE	121	130	149	133
	Increase (%)	–5.47*	9.24	16.41	3.91*

*NS; CA, ambient CO_2; CE, elevated CO_2

Table 3 Grain weight (mg/spikelet) of apical, middle and basal spikelets of ear in durum and bread wheat varieties grown under ambient and elevated CO_{2a} concentration

Character	Variety	Treatment	Basal	Middle	Apical
Durum wheat	'HD 4502'	CA	106.33	169.97	94.58
		CE	104.50	168.00	93.17
		Increase (%)	–1.72*	–1.16*	–1.06*
	'B 449'	CA	121.00	161.16	86.66
		CE	133.99	193.09	89.00
		Increase (%)	10.73*	19.81	2.70*
Bread wheat	'Kalyansona'	CA	119.33	144.67	83.83
		CE	124.67	164.93	91.99
		Increase (%)	4.47*	14.00	9.73
	'Kundan'	CA	115.66	167.99	78.00
		CE	116.99	167.34	81.42
		Increase (%)	0.87*	–0.39*	4.38*

*NS; CA, ambient CO_2; CE, elevated CO_2

Table 4 Grain weight (mg/grain) of different positions in the apical, middle and basal spikelets of main shoot ear in durum wheat varieties grown under ambient and elevated CO_2

Wheat	Variety	Treatment	Grain position in a spikelet				
			1	2	3	4	5
Durum wheat				*Apical spikelet*			
	'HD 4502'	CA	40.33	39.25	15.00		
		CE	41.00	38.17	14.00		
		CE/CA	1.02*	0.97*	0.93*		
				Middle spikelet			
		CA	52.00	52.80	44.92	20.25	
		CE	53.83	53.42	45.42	15.33	
		CE/CA	1.03*	1.01*	1.01*	0.76*	
				Basal spikelet			
		CA	45.83	46.92	13.58		
		CE	45.58	47.92	11.00		
		CE/CA	0.99*	1.02*	0.81*		
				Apical spikelet			
	'B 449'	CA	46.33	40.33			
		CE	47.67	41.33			
		CE/CA	1.03*	1.02*			
				Middle spikelet			
		CA	59.12	62.08	39.96		
		CE	68.67	70.42	54.00		
		CE/CA	1.16	1.13	1.35		
				Basal spikelet			
		CA	52.00	55.00	14.00		
		CE	52.66	54.33	27.00		
		CE/CA	1.01*	0.99*	1.93		
Bread wheat							
				Apical spikelet			
	'Kalyansona'	CA	31.50	33.33	19.00		
		CE	33.66	33.33	25.00		
		CE/CA	1.07*	1.00*	1.31		
				Middle spikelet			
		CA	39.00	39.00	31.67	21.00	14.00
		CE	40.92	41.08	36.83	28.00	18.00
		CE/CA	1.05*	1.05*	1.16	1.33	1.28
				Basal spikelet			
		CA	36.00	36.33	29.00	18.00	
		CE	36.67	37.00	29.00	22.00	
		CE/CA	1.02*	1.02	1.00*	1.22	
				Apical spikelet			
	'Kundan'	CA	47.75	27.25			
		CE	48.17	33.25			
		CE/CA	1.01*	1.22			
				Middle spikelet			
		CA	59.33	58.66	50.00		
		CE	58.67	62.00	46.67		
		CE/CA	0.99*	1.06*	0.93*		
				Basal spikelet			
		CA	50.33	51.00	14.33		
		CE	51.33	46.32	19.33		
		CE/CA	1.02*	0.91*	1.35		

*NS; CA, ambient CO_2; CE, elevated CO_2

CO_2 (Table 3). The grain weight of middle and basal spikelets in 'B 449' increased in plants grown under elevated CO_2 due to an increase in the weight of individual grains of middle spikelet and third grain of basal spikelet compared with ambient CO_2 grown plants (Tables 3, 4). In 'Kalyansona' grain weight of middle and apical spikelets was significantly higher in elevated CO_2 grown plants than ambient CO_2 concentration grown plants owing to an increase in weight of 3rd grain from base in apical spikelet 3rd, 4th and 5th grain from base of middle spikelet in elevated CO_2 compared to ambient CO_2 grown plants (Table 3, 4).

The results showed that CO_2 enrichment enhances grain yield differentially in wheat varieties. The enhancement in yield was mostly through an increase in the number of ear bearing tillers. Individual ear weight was also increased in plants grown under elevated CO_2 concentration. Varieties however differed in the manner, the individual ear weight was increased. In 'B 449' and 'Kalyansona', the increase in grain yield of main shoot ear was owing to an increase in individual grain weight. In 'HD 4502', an increase in grain yield of main shoot ear of plants grown under elevated CO_2 concentration appeard to be owing to higher grains/ear as a result of increase in spikelets/ear.

CO_2 is a substrate limiting photosynthesis in C_3 plants in the present atmosphere, an increase in CO_2 level therefore, increases photosynthesis (Kimball 1983). This advantage could be sustained by the plants only if there is considerable sink capacity to utilize the assimilates, otherwise, photosynthesis may be limited by sink demand (Sharma-Natu 1993, Ghildiyal and Sirohi 1986, Ghildiyal 1991. A variety having greater sink in terms of higher grain number showed greater response in the present study, is in line with the above concept.

The enhancement in yield under elevated CO_2 was attributed to a considerable extent to ears/plant because of increase in ear-bearing tillers. Ethylene production enhances under elevated CO_2 (Grodzinski 1992). The increase in tiller production may therefore, possibly be mediated through ethylene production. This has also been observed in rice (*Oryza sativa* L.) where tiller number largely accounted for higher productivity under elevated CO_2 (Baker *et al.* 1990, Seneweera *et al.* 1994). Tillering is expressed more in widely spaced plants and ear-bearing tillers decrease in a denser crop stand (Mc Master 1997). It was observed that yield response of field-grown wheat to elevated CO_2 was considerably less than the pot-grown plants as ear bearing tillers did not show a proportionate increase in a denser crop stand in field possibly due to a greater inter-and intra-plant competition (Ghildiyal M C *unpublished*). The tiller associated yield response to elevated CO_2 therefore, would vary depending on the density of the stand. The individual ear weight however, also increased under elevated CO_2. In 'Kalyansona' and 'B 449' there was an increase in individual grain weight, whereas in 'HD 4502' grains/ear was increased owing to greater number of spikelets/ear. Such a response to elevated CO_2 would possibly be sustained even under a denser crop stand.

The fact that CO_2 is a greenhouse gas makes high global temperatures an important consideration in the rising CO_2 debate. It may however be mentioned that the temperature and rainfall prediction are uncertain (Bowes 1993). Nevertheless photosynthetic response to elevated CO_2 concentration is expected to increase under high temperature. A rise in temperature lowers the ratio of $CO_2 : O_2$ in solution, shifts the specificity of Ribulose-1, 5-bisphophate carboxylase-oxygenase (Rubisco) enzyme towards oxygenase and enhances photorespiration. Since elevated CO_2 concentration would inhibit oxygenase activity of Rubisco, the photosynthesis response to CO_2 at high temperature would be higher (Bowes 1996). The future-increases in atmospheric CO_2 and day-temperatures therefore have the potential for positive interactive effect on photosynthesis and vegetative growth of many C_3 species. Rawson (1995) showed that grain yield in C_3 cereals are likely to be substantially increased by rising level of atmospheric CO_2 concentration in areas where temperature is moderate. However, in areas where the temperature is already marginal for yield, further increase in temperature will decrease yield because of greatly accelerated crop development and flower abortion. There are however, differences between species and even between genotypes in their response to high CO_2 at different temperatures (Conroy *et al.* 1994). The heat tolerant varieties therefore would do better under such conditions (Ahmed *et al.* 1993).

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