

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 CO₂ (650 ± 50 ppm) concentrations inside open top chambers to examine yield components at maturity. The CO₂ 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 CO₂ 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 CO₂ 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 CO₂ concentration was due to higher grain number/ear as a result of increase in spikelets/ear. Genotypic differences in response to elevated CO₂ 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, CO₂ enrichment

The concentration of atmospheric CO₂ 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 CO₂ level (Bowes 1996, Drake *et al.* 1997). However, a meagre information is available on the effect of CO₂ enrichment on plant species in a tropical environment (Ziska *et al.* 1991). CO₂ is a substrate limiting photosynthesis particularly in C₃ plants in the present atmosphere (Bowes 1993, Drake *et al.* 1997, Ghildiyal *et al.* 1998). Photosynthetic productivity is therefore expected to increase under higher CO₂ level. However, long-term exposure to elevated CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ level served as the control, whereas CO₂ concentration in other 2 chambers was elevated to 650 ± 50 ppm. The regular monitoring of CO₂ 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 CO₂ concentration

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 CO₂; CE, elevated CO₂

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 CO₂ 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 excised. 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 CO₂ showed 11.5-34.16% enhancement in grain yield compared to plants grown under atmospheric CO₂ 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 CO₂ 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 CO₂ by 23-24% compared to plants grown under ambient CO₂ concentration. 'B 449' showed an increase in 1 000-grain weight by elevated CO₂. 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 CO₂ was not entirely owing to an increase in ear-bearing tillers. The effect of elevated CO₂ on yield of main shoot ear was therefore determined. The grain yield of main shoot ear increased in plants grown under elevated CO₂ 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 CO₂ 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 CO₂

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 CO₂; CE, elevated CO₂Table 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 CO₂; CE, elevated CO₂

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 CO₂

Wheat	Variety	Treatment	Grain position in a spikelet				
			1	2	3	4	5
<i>Durum wheat</i>							
	'HD 4502'			<i>Apical spikelet</i>			
		CA	40.33	39.25	15.00		
		CE	41.00	38.17	14.00		
		CE/CA	1.02*	0.97*	0.93*		
				<i>Middle spikelet</i>			
		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*	
				<i>Basal spikelet</i>			
		CA	45.83	46.92	13.58		
		CE	45.58	47.92	11.00		
		CE/CA	0.99*	1.02*	0.81*		
	'B 449'			<i>Apical spikelet</i>			
		CA	46.33	40.33			
		CE	47.67	41.33			
		CE/CA	1.03*	1.02*			
				<i>Middle spikelet</i>			
		CA	59.12	62.08	39.96		
		CE	68.67	70.42	54.00		
		CE/CA	1.16	1.13	1.35		
				<i>Basal spikelet</i>			
		CA	52.00	55.00	14.00		
		CE	52.66	54.33	27.00		
		CE/CA	1.01*	0.99*	1.93		
<i>Bread wheat</i>							
	'Kalyansona'			<i>Apical spikelet</i>			
		CA	31.50	33.33	19.00		
		CE	33.66	33.33	25.00		
		CE/CA	1.07*	1.00*	1.31		
				<i>Middle spikelet</i>			
		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
				<i>Basal spikelet</i>			
		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	
	'Kundan'			<i>Apical spikelet</i>			
		CA	47.75	27.25			
		CE	48.17	33.25			
		CE/CA	1.01*	1.22			
				<i>Middle spikelet</i>			
		CA	59.33	58.66	50.00		
		CE	58.67	62.00	46.67		
		CE/CA	0.99*	1.06*	0.93*		
				<i>Basal spikelet</i>			
		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 CO₂; CE, elevated CO₂

CO₂ (Table 3). The grain weight of middle and basal spikelets in 'B 449' increased in plants grown under elevated CO₂ due

to an increase in the weight of individual grains of middle spikelet and third grain of basal spikelet compared with

ambient CO₂ grown plants (Tables 3, 4). In 'Kalyansona' grain weight of middle and apical spikelets was significantly higher in elevated CO₂ grown plants than ambient CO₂ 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 CO₂ compared to ambient CO₂ grown plants (Table 3, 4).

The results showed that CO₂ 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 CO₂ 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 CO₂ concentration appeared to be owing to higher grains/ear as a result of increase in spikelets/ear.

CO₂ is a substrate limiting photosynthesis in C₃ plants in the present atmosphere, an increase in CO₂ 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 CO₂ was attributed to a considerable extent to ears/plant because of increase in ear-bearing tillers. Ethylene production enhances under elevated CO₂ (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 CO₂ (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 CO₂ 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 CO₂ therefore, would vary depending on the density of the stand. The individual ear weight however, also increased under elevated CO₂. 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 CO₂ would possibly be sustained even under a denser crop stand.

The fact that CO₂ is a greenhouse gas makes high global temperatures an important consideration in the rising CO₂

debate. It may however be mentioned that the temperature and rainfall prediction are uncertain (Bowes 1993). Nevertheless photosynthetic response to elevated CO₂ concentration is expected to increase under high temperature. A rise in temperature lowers the ratio of CO₂:O₂ in solution, shifts the specificity of Ribulose-1, 5-bisphosphate carboxylase-oxygenase (Rubisco) enzyme towards oxygenase and enhances photorespiration. Since elevated CO₂ concentration would inhibit oxygenase activity of Rubisco, the photosynthesis response to CO₂ at high temperature would be higher (Bowes 1996). The future-increases in atmospheric CO₂ and day-temperatures therefore have the potential for positive interactive effect on photosynthesis and vegetative growth of many C₃ species. Rawson (1995) showed that grain yield in C₃ cereals are likely to be substantially increased by rising level of atmospheric CO₂ 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 CO₂ 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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