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REVIEW ARTICLE

Rising atmospheric carbon dioxide on grain quality in crop plants

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Abstract There is a general concern that changes in plant productivity and composition caused by increase in atmospheric CO_2 concentration will alter the chemical composition of the grain. This review describes the impact of rising atmospheric CO_2 on the grain characteristics in wheat, rice, brassica, mungbean and soybean, which are significantly responsive to the elevated CO_2 for their growth, physiology and biochemical processes. The synthesis of the CO_2 induced changes in the chemical composition and nutritional qualities of their grains has been discussed. It was demonstrated that the rise in atmospheric CO_2 affects the nutritional and industrial application properties of the grains of crop plants. The grain proteins and other nutritionally important constituents significantly reduced, adversely affecting the nutritional and bread making quality in wheat. However, there are evidences suggesting the sustenance of the bread making properties by fertilizer application. Similarly, the CO_2 induced changes in the composition of starch in rice grains, result into easy gelatinization and higher viscosity on cooking. These grains bring firmness due to increase in amylose content. Adequately larger size of grains was the outcome of the elevated CO_2 effects, in Brassica species. It increased the oil content due to greater acetyl Co A enzyme activity and also help in regulating fatty acid biosynthesis. Some of the nutritionally undesirable fatty acids were significantly reduced in this process, making this oil less harmful for heart patients. The adequate use of fertilizer application and selection pressure of breeders may significantly contribute in developing cultivars, which will counter the adverse effect of rising atmospheric CO_2 on grain quality.

Keywords Carbon dioxide · Grain quality · Fatty acids · Wheat · Rice · Brassica

Introduction

The atmospheric CO_2 and temperature affect plant growth and development and both have changed in recent past and are predicted to change further. Carbon dioxide has increased from 270 to 380 μ mol mol^{-1} since industrial revolution and is still increasing at the rate of 1.5 to 1.8 μ mol mol^{-1} yr^{-1}. It is expected to be between 470 and 570 μ mol mol^{-1} by the year 2050 (IPCC 2007). Model projections also suggest an increase of 1.4 to 4.5°C in earth's temperature by 2100. A significant amount of literature is available on the response of crop plants to elevated CO_2 for their growth, productivity, physiological and biochemical processes and the impact assessment analysis of CO_2 and temperature on these processes in crop plants indicates possibilities of considerable changes in biochemical composition of grains and their nutritional quality (Stafford 2007; Uprety and Reddy 2008; Uprety et al. 2009). This review will describe the impact of rising atmospheric CO_2 on the grain characters of wheat, rice, brassica, mungbean and soybean, which are significantly responsive to the elevated CO_2 for their growth and productivity (Kimball 1983).

Wheat

Wheat (*Triticum aestivum* L.) is one of the world's important food sources. The potential impact of elevated

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CO_2 on wheat yield and grain quality will influence the supply and nutritional value of wheat products. Rawson (1995) reported little change in the thousand grain weight in wheat due to the effect of elevated CO_2 and concluded that the increase in the yield was based on the development of the number of grains (more ears per m^2) rather than heavier kernels. Kimball et al. (2001) observed that the CO_2 induced increase in the grain weight was greater under average phosphorus treatment compared to higher phosphorus level. This influence of CO_2 and phosphorus supply was attributed to the increase in the number of cells in the endosperm which was the consequence of the enhanced rate of cell division during grain development or by greater grain filling during ripening phase. Hogy and Fangmeier (2008) surveyed the effect of elevated CO_2 on the grain quality parameters of wheat varieties grown in different CO_2 enrichment facilities. Accordingly they observed an over all increase in the thousand grain weight in all the treatments except for the observations in Open Top Chambers (OTC), when experiments were conducted in pots. Thousand grain weight was significantly increased by 6.9% (P=0.034) in larger pot experiment and 3.5%, when the plants were grown in field at Free Air CO_2 Enrichment (FACE).

Hogy and Fangmeier (2008) observed that elevated CO_2 brought about higher starch content in wheat grains due to increase in carbohydrate translocation from the source (leaves and stem) to sink (grain). However, the significant increase in starch content was restricted to wheat grains under high nitrogen conditions. They demonstrated a significant CO_2 induced increase in the concentration of starch in wheat grains ranging from 0.9% to 7.6%. Wheat starch is made up of approximately 25% amylose and 75% amylopectin and CO_2 induced increase was greater in the proportion of amylose than that of amylopectin. This increase was found to be associated with the greater seed weight (Mulchi et al. 1995; Hogy et al. 1998). A high proportion of B type starch granules are usually formed when the carbohydrate supply to developing grains is high. The amount of B type of starch granules decreased with elevated CO_2, while desirable large A type starch granules increased proportionally (Bluementhal et al. 1996). Elevated CO_2 treatments brought about reduction in the concentrations of total and non starch lipids by 7.0% and 11.5% respectively while starch lipids were increased by 3.2%. Lipids are also essential for bread making quality, although they compose only 1.5%–3.5% of the total wheat grain mass. They are closely associated with starch granules and gluten proteins and involve in the binding of gliadin and glutelin in gluten and gluten to starch within dough. Williams et al. (1993; 1995) observed that the concentration of non starch lipids decreased by 21.5% under high CO_2 condition in the range of 700 μ mol mol^{-1} compared to ambient levels. The changes in lipid composition such as increase in palmate with corresponding decrease in linoliate, have been identified in plants, exposed to elevated CO_2 (Williams et al. 1994). Uprety et al. (2009) observed significantly greater CO_2 induced increase in mass, length and breadth of grains of hexaploid compared to tetraploid and diploid wheat species in a FACE study (Table 1). They have attributed this variation to the enhanced flow of carbohydrates in hexaploids due to their greater sink capacity.

Elevated CO_2 resulted in reduced nitrogen concentrations irrespective of the exposure techniques and the condition applied (Conroy 1992; Conroy and Hocking 1993; Conroy et al. 1994). The CO_2 induced decrease in nitrogen concentration is largely the result of the accumulation of carbohydrates and other organic compounds in leaves and possibly in other organs as a result of the stimulation of photosynthesis (Korner 2000; Fangmeier and Jager, 2001; Kimball 2004). In addition, elevated CO_2 predominantly reduces the amount and activity of Rubisco (Ainsworth and Long 2005) and the levels of transcripts of small subunit of Rubisco and other photosynthetic genes (Moore et al. 1999). The reallocation of nitrogen away from Rubisco to light harvesting and sucrose synthesis will increase nitrogen use efficiency (Conroy and Hocking 1993) and grain protein concentration is generally decreased (Lawlor and Mitchell 2001; Jablonski et al. 2002; Kimball 2004). A striking feature of CO_2 enrichment experiments is that the nitrogen concentration of the foliage is reduced by up to 50% (Conroy 1992; Conroy and Hocking 1993). The protein synthesis in wheat is limited by

Table 1 Effect of increased CO_2 conditions on length and breadth of seeds of diploid, tetraploid and hexaploid wheat species (Uprety et al. 2009)

Wheat species	CO_2 condition	Length (microns)	Breadth (microns)
Diploid	Ambient	5989.35±156.84	2485.73±21.44
	Elevated	6180.06±74.29	2507.55±30.23
Tetraploid	Ambient	7785.39±183.54	2192.59±80.61
	Elevated	7794.36±107.46	2306.26±36.53
Hexaploid	Ambient	5181.04±53.92	2532.95±37.05
	Elevated	5680.78±62.33	2863.80±90.49
CD at 5% CO_2 Cond.		191.54	91.55

the size of amino acid export pool in the leaves, resulting in the lower levels of nitrogen and protein in the grains (Hocking and Meyer 1991). Conroy et al. (1994) observed the reduction in nitrogen and protein in flour produced from grains of high CO_2 grown plants. Reduced nitrogen concentrations in wheat grown under CO_2 enrichment suggested that future changes in atmospheric composition may affect wheat processing quality (Manderscheid et al. 1995; Bluementhal et al. 1996; Fangmeier et al. 1997). Such relationship exists between grain protein content and protein linked quality parameters such as the Zeleny value and gluten content (Tables 2 and 3). Bread making quality mainly depends upon the gluten content, its strength and extensibility (Jennings and Morton 1963). The proportions and properties of two main classes of storage proteins (glutelin and gliadin) are primarily responsible for grain processing quality. In particular the gliadins are associated with dough viscosity and extensibility and the glutelins, with dough strength. The ratio of gliadin and glutelin and proportions of large glutelin polymers are therefore, widely used as indicators of dough strength (Shewry et al. 1992). Both of these proteins are adversely affected by elevated CO_2 conditions (Wieser et al. 2008). They observed marked CO_2 induced reduction in protein of wheat grains by 14% under high nitrogen treatment (N 100) and 9% under low nitrogen conditions (N 50). Gliadin was reduced by 20% and 13% and glutelin by 15% and 15% respectively under these conditions. A greater reduction was observed in omega -5- gliadins (35–22%) and omega-1, 2 gliadins (27–14%) compared to alfa gliadins (21–13%) and gama gliadins (16–12%). Within glutelin, high molecular weight subunits were more affected (23–18%) than those of low molecular weight subunits (12–15%). Thus flour from high CO_2 grown grains will have a diminishing baking quality. Erda et al. (2005) in a study on the impact of climate change on wheat crop in China, observed that elevated CO_2 significantly reduced the protein content of flour and the sedimentation value of ZhongYu five wheat cultivars, thereby reducing their baking quality. Piikki et al. (2007) observed that elevated CO_2 increased the protein yield but reduced the grain protein concentration and the Zeleny value in spring wheat. Smith and Gooding (1999) stated that the grain protein in wheat were below 10% due to CO_2 enrichment in FACE, which was unacceptable by UK millers. Hogy (2002) observed CO_2 induced reduction in the protein concentration of wheat grains to the level of protein value of 9.1% to 10.8% which is much below to the minimum quality standard, required for bread making. The adequate fertilizer is necessary to attain good quality of grain under high CO_2 condition.

Studies showed that grain protein concentration was decreased between 3.9 and 14.1% due to elevated CO_2 depending upon exposure system and rooting volume (Kimball et al. 2002). Carbon dioxide exposure to plants grown in small pots resulted in a reduction of 9.8% in the lysine content of their harvested grains but the reduction was 3.1% in the harvested grains from the larger pots (Hogy and Fangmeier 2008).The largest decrease in grain protein concentration was observed in OTC experiments with restricted rooting volume, which can be attributed to a feed back inhibition of the photosynthetic CO_2 response and accumulation of non structural carbohydrates (Weigel and Manderscheid 2005). Metabolic proteins (albumin and globulin) that make about 15–20% of total protein have only minor impact on dough properties and bread making quality. They are rich in sulphur-containing amino acids cystine, methonine and lysine, resulting in a high nutritive value. Consequent of protein response, elevated CO_2 reduced the concentration of total amino acids in wheat grains by 6.1%–23.9% and the reduction in the concentration of essential amino acids such as threoline, valine, isoleucine, leucine and phenylalanine was 20.9%, 7.7%, 21.8%, 19.7% and 14.2% respectively; however, there was no change in histidine.

Unfortunately the CO_2 induced reduction in grain protein may not easily be overcome by increase in nitrogen fertilization since this may translate into high biomass and yield production rather than into enhanced redistribution of nitrogen to the grains (Weigel and Manderscheid 2005). Therefore, CO_2 enrichment is likely to decrease wheat grain

Table 2 Effects of Levels of CO_2 on baking and dough quality* of wheat species (Bluementhal et al. 1996)

Wheat species	CO_2 level	Loaf volume (ml)	Dough Extensibility (cm)	Dough development Time (sec)
Hartog	Ambient	695	17.7	8.8
	Elevated	598	15.9	1.8
Late Hartog	Ambient	633	16.4	3.3
	Elevated	583	14.8	1.8
Both genotypes	Ambient	664	17.1	6
	Elevated	591	15.4	1.8
P values for elevated	CO_2	0.02	0.01	<0.001

* From trial 3 only. All values represent means of triplicate determinations

Table 3 Grain quality attributes: averages comparing CO_2 levels (Bluementhal et al. 1996)

	Ambient	Trial3 Elevated	Significance
TKW (g)[a]	39.5	37.8	$P<0.01$
% Protein	12.3	10.4	$P<0.01$
Mix time (sec)	269	336	$P<0.05$
Peak resistance[b]	180	151	$P<0.01$
Breakdown (%)	16.8	15.6	ns
% B granule	24.9	20.6	$P<0.05$
Glu-Gli ratio	0.81	0.8	ns[c]

[a] 1,000 kernel weight

[b] Arbitary units

[c] Not significant

quality in the future. In contrast, Kimball et al. (2001) concluded that negative impacts of high CO_2 levels may be alleviated by additional application of nitrogen fertilizers. There may be an inverse relationship between increasing grain yield and decreasing grain protein in wheat (Pleijel et al. 1999), resulting in benefits for starch based industries, while protein based industries may suffer from future CO_2 elevation. It was observed that the increase in temperature (2–4°C) had a larger effect than elevated CO_2 on grain quality (Tester et al. 1995; Williams et al. 1995). Moreover, the effects of elevated CO_2 on grain quality may be partially balanced because temperature increase can enhance grain protein content (Randall and Moss 1990; Wrigley et al. 1994).

Most of the nutrients in grains originate from redistribution from vegetative pools during grain filling. Carbon dioxide enrichment also causes alterations in the concentrations of other macro and microelements in the wheat grains, decreasing their nutritional value. Reductions in macro elements such as Na, Ca, Mg, and S due to CO_2 elevation were consistent for different cultivars. Among the micro elements, the concentrations of Fe, Zn and Mn were predominantly reduced by elevated CO_2 (Manderscheid et al. 1995) (Table 4). Hogy and Fangmeier (2008) reported that the effect of CO_2 enrichment brought about significant reduction in the concentration of macro elements ranging from 0.7–19.5% except for K and P in wheat grains. In addition, Ca and Mg were decreased by 9.7% and 4.8% respectively. Similarly the concentration of Na, Ca, Mg, and S were reduced by 5.5%, 14.5%, 7.2% and 12.3% respectively. Elevated CO_2 also reduced the concentrations of all the microelements by 3.7%–18.3% where Fe and Zn were declined by 18.3% and 13.1% respectively. Elevated CO_2 resulted in the reduction in concentrations of mineral nutrients such as N, P, K, and Zn in mature grains (Dong-Xiu et al. 2004). This was probably caused by the dilution effect, induced by increased concentration of carbohydrates in grains. An overall decrease in essential elements due to CO_2 enrichment is likely to aggravate the already acute micronutrient malnutrition in the world, however, the total quantity of mineral nutrients, accumulated in grains per hectare were still larger under high CO_2 due to increase in grain yield.

There may be a combination of the beneficial effect of CO_2 on yield and adverse effect on grain constituents such as proteins, their fractions, and nutritionally important macro and microelements. The magnitude of the CO_2 induced effect on quality will depend on future atmospheric CO_2 concentration and agronomic practices such as nitrogen supply, cultivars choice and growing conditions. Current application rates of nitrogen fertilizers may be inadequate in many situations to achieve the standards of bread making quality; there is evidence to suggest whether additional fertilizer supply can satisfy the quality requirement for wheat under elevated CO_2. Future research is needed to understand and quantify the impacts of elevated CO_2 and also their interactions with other biotic and abiotic stresses on grain quality. This is important for the production of improved varieties by breeding and to develop appropriate crop management systems

Rice

Studies on the response of rice cultivars to the elevated CO_2 in OTC and FACE facilities demonstrated significant increase in their grain yield (Imai et al. 1985; Baker et al. 1990; Uprety et al. 2000, 2003, 2007b). Elevated CO_2 impact on rice cultivars in general showed that their development was accelerated throughout the vegetative phase, and flowering commenced seven days earlier, which contributed to the higher grain yield and change in the chemical composition of the rice grains.

Unlike wheat, rice is generally consumed as cooked whole grain; therefore, the properties of grain itself, rather than the flour, determine the quality. Average grain weight, amylose concentration, relative paste viscosity and nutrient concentrations determine the grain quality of rice. The other determinants of rice quality are appearance, milling and cooking (Blakeney 1992; Juliano 1992; Blakeney et al. 1994).

Increase in the atmospheric CO_2 is likely to increase the firmness of cooked grain because of higher amylose content. Reinke (1993) reported 27% amylose content in high CO_2 grown rice compared to 24% under ambient condition. Carbon dioxide enrichment brought about increase in amylose and calcium contents in rice grains under high phosphorus treatment (Seneweera et al. 1996). However, the relationship of these changes between calcium and amylose content is not known. According to

Table 4 Effect of CO_2 enrichment on nutrient concentration in grains of wheat plants (Manderscheid et al. 1995)

Nutrient	Observed/adjusted means		*P* CO_2	*P* COV	Ratio
	384 p.p.m CO_2	718 p.p.m CO_2			
K (mg per g)					
W1	4.49	4.61	n.s.	n.s.	1.03
W2	4.17	4.43	***	n.s.	1.06
Ca (ug per g)					
W 1	369	265	***	n.s.	0.72
W 2	326	288	***	n.s.	0.88
Mg (mg per g)					
W 1	1.05	0.966	***	n.s.	0.92
W 2	1.21	1.05	***	n.s.	0.87
N (mg per g)					
W 1	24.2	17.5	***	n.s.	0.72
W 2	26.7	18.8	***	n.s.	0.7
P (ug per g)					
W 1	543	436	n.s.	*	1
W 2	867/798	860/929	***	n.s.	0.91
S (mg per g)					
W 1	1.82	1.43	***	n.s.	0.79
W 2	1.82	1.44	***	n.s.	0.79
Fe (ug per g)					
W 1	52.2	39.9	***	n.s.	0.76
W 2	49.7	37	***	n.s.	0.74
Mn (ug per g)					
W 1	42.2	39.7	n.s.	n.s.	0.94
W 2	50.1/49.2	46.2/47.0	n.s.	**	0.96
Zn (ug per g)					
W 1	44	33.2	***	n.s.	0.75
W 2	45.4	35.3	***	n.s.	0.78

**P*<0.05; ***P*<0.01; ****P*<0.001

Francis (1992) the cell division may be faster at high CO_2 because of greater soluble carbohydrate concentrations within the meristematic cells. The growth of sucrose deprived cells, which was arrested at the G 1 phase of the cell cycle, was regulated by CO_2, induced increase in SPS (Sucrose Phosphate Synthase) activity (Masle et al. 1993).

Wang et al., (1995) demonstrated that the amylose content in rice endosperm is related to the post transcriptional regulation of the waxy (Wx) gene; rice cultivars with higher amylose content produce large amount of Wx mRNA and Wx protein. Therefore, an understanding of the waxy gene regulation in response to CO_2 enrichment could be important in predicting how cooking quality may change under future CO_2 scenario.

Measurements of relative paste viscosity demonstrated that cooked grains from high-CO_2 grown cultivars would be firmer (Yang et al. 2007). The setback value, which is calculated from the differences between the peak heights at 12 and 6 min, were 30 and 65 for the ambient and high CO_2 treatments respectively. Higher setback values are correlated with firmer cooked grains (Juliano 1992). In contrast to the amylose measurements, the paste viscosity curves indicate that cooking quality will be influenced by high CO_2 at both low and high phosphorus supplies (Seneweera and Conroy 1997). Lieffering et al. (2004) found a CO_2 induced decrease in the rice grain N concentration and observed no change in the content of any other elements. Rice grain also showed CO_2 induced reduction in N similar to wheat grain (Conroy et al. 1994); however, the quality of rice is based on the amylose content (Juliano 1992) which significantly improved its cooking property under elevated CO_2 conditions. Significant reduction in the protein content of rice grains grown under CO_2 enrichment facilities was also observed (Conroy et al. 1994; Seneweera, and Conroy 1997; Uprety and Reddy 2008). However, the decline in protein content was compensated by increase in yield. Thus the overall protein yield may not be reduced by elevated CO_2 although the amount of protein on a consumption basis was reduced. Terao et al. (2005) concluded that this change in protein content resulted in an increase in maximum viscosity and breakdown of starch that improves the eating quality of rice. In addition, they have also observed that elevated CO_2 reduced the milling degree and increased the whiteness of both brown and milled rice grains.

Higher atmospheric CO_2 concentrations are also likely to influence the nutritive value of rice grain by changing both protein and mineral concentrations. Protein is located in protein bodies, distributed throughout the starch granules in the endosperm and constitutes about 10% of the dry weight of polished grain. The protein content of brown rice is slightly higher because of protein rich embryo and aleurone layer (Nanda and Coffman 1978). Although the phosphorus (P) concentration was also reduced by CO_2 enrichment due to greater starch accumulation, the total P content per grain was higher. This indicated that, in contrast to N, more P was sequestered in each grain, possibly as phytate under high CO_2 conditions. Much of the P in cereal grain is present in this form and binds ions such as Mg (Batten, 1994). This may explain the strong correlation between Mg and P concentrations in grains. Accumulation of phytate can cause dietary problems in the areas where Mg and other mineral supplies in the diet are low. The total P per grain increases at high CO_2 to minimize the problem of magnesium binding to phytate through the optimum supply of phosphorus fertilizers.

Uprety (2007) in a study on the response of rice varieties Pusa Sugandh–2 (PS–2) and Pusa rice hybrid (PRH-10) observed that CO_2 enrichment modified the quality of rice grains significantly. The reducing, non-reducing, total sugars and starch content significantly increased in the grains of CO_2 enriched plants which ultimately increased the grain mass (Table 5). Amylose content of the grain in PRH-10 variety increased to optimum levels, improving the grain quality. In PS-2, the amylose content was greatly increased to a level that will make the grains hard after cooking, thus decreasing the quality of the grain (Juliano 1992) (Table 5). Elevated temperature decreased all these parameters which were ameliorated by the CO_2 enrichment. Similarly, the increased temperature conditions also reduced the N, Ca and K content in the grain. This adverse effect was ameliorated by elevated CO_2. Ziska et al. (1997) showed no significant change of Ca and K content in the grains at elevated CO_2, whereas Conroy et al. (1994) in contrast found an increase in Ca content of rice grains under similar conditions.

Okada et al. (2001) in a FACE experiment observed that CO_2 improves palatability by affecting proteins and amylose levels, in rice grains. Seneweera et al. (1994) reported CO_2 induced increase in amylose content in grains, under various levels of phosphorus application. However, Terao et al. (2005) did not observe any change in the palatability of rice grains with the reduction in the protein content under elevated CO_2 condition.

Seneweera et al. (1994) observed 4% increase of amylose content due to elevated CO_2 under phosphorus-deficient conditions, which is much higher than the decrease in protein content that was less than 2.5%. This increase in amylose content was not simply because of the decreased protein content, but also because of the change in the starch composition.

Terao et al. (2005) also reported that CO_2 enrichment changed the starch pasting properties affecting the texture and stickiness of cooked rice. However, CO_2 induced change in the amylose content did not affect the viscosity of starch. The higher maximum viscosity and breakdown (i.e., the difference between the maximum and minimum

Table 5 Effect of elevated CO_2 on the grain quality parameters of the rice varieties in FACE (Uprety 2007)

	PRH-10		PS-2		CD at 5%		
	Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2	Variety (V)	CO_2	V x CO_2
Grain weight (g/100grains)	1.81	2.07	1.61	1.89	0.060	0.042	ns
Reducing sugars*	88.33	137.12	82.71	131.36	2.856	2.856	4.039
Non-reducing* sugars	122.34	134.14	118.32	139.63	ns	4.875	6.894
Total sugars*	210.43	274.14	200.32	270	ns	28.79	ns
Amylose (%)	24.81	25.41	25.70	27.73	0.813	0.813	1.149
TNC*	441.36	568.81	424.69	551.01	18.96	18.96	ns
Nitrogen (%)	1.62	1.59	1.55	1.49	0.039	0.039	ns
Calcium (%)	0.081	0.093	0.079	0.090	0.002	0.002	ns
Potassium (%)	0.180	0.250	0.16	0.23	0.005	0.005	ns

*mg g−1 DW

TNC-Total Nonstructural Carbohydrates

viscosity) suggests that the starch in rice grains grown under elevated CO_2 gelatinizes more easily and exhibits higher viscosity when cooked. It is to be noted that higher protein content is associated with reduced viscosity and elasticity (Yamashita and Fujimoto 1974).

Brassica

Uprety et al. (2007a; b) studied the interactive effects of elevated CO_2 and soil moisture stress on the chemical composition of harvested grains of *Brassica* cultivars. They demonstrated significant increase in the seed mass and an altered chemical composition of seeds of *Brassica campestries* and *Brassica juncea* cultivars (Table 6; Fig. 1). Reducing, non reducing and total sugar as well as starch contents were significantly higher in the seeds of CO_2 enriched *Brassica* plants. Carbon dioxide enrichment also reduced crude fiber content which was related to CO_2 induced changes in C/N ratio (Uprety et al. 2007a, b) (Table 6). Decrease in crude fiber content may increase grain mass, which was correlated with oil and carbohydrate contents (Uprety et al. 1997). The reduced crude fiber content will also minimize lignin content in meal, which adversely affects the protein and amino acid digestibility in non ruminant animals (Clandinin and Robblee 1981). Crude fiber content is mainly cellulose and hemi cellulose, which bring about overall reduction of the feed value and consequently a lower metabolic energy value for animals, fed on rape seed meal

Uprety et al. (2007a; b) demonstrated the accumulation of greater carbohydrates in *Brassica* seeds due to CO_2 enrichment; however, moisture stress adversely affected the reducing, non reducing, total sugar and starch contents (Table 6). The stress-induced reduction in carbohydrate was mitigated in elevated CO_2 condition, possibly due to the greater transfer of photosynthates and redistribution of carbon from the vegetative parts to the seeds in *Brassica* species. The additional carbon made these plants metabolically flexible to compensate the adverse moisture stress effect on seed carbohydrate components. Although, oil content in *Brassica* seeds was significantly reduced by moisture stress but this reduction was markedly ameliorated by elevated CO_2. This result was in accordance with the findings of Uprety et al. (1997) in *Brassica juncea* seeds, which they attributed to sequestration of carbon and improved water status. The accumulation of carbohydrates possibly resulted in the reduction of nitrogen concentration due to dilution effect. The increase in oil content was attributed to the participation of additional CO_2 in stimulating the activity of acetyl Co A enzyme (Uprety et al. 1997) which increases the formation of abundant malonyl Co A under elevated CO_2 condition and plays a positive role in regulating fatty acid biosynthesis. This increase in seed oil content possibly is at the expense of either carbohydrate or protein. Under elevated CO_2 greater oil content appears to be due to larger accumulation of carbohydrate (Uprety et al. 2007a, b). However, carbohydrate requirement for this conversion to oil will be greater compared to that for protein (Mitra and Bhatia 1974). Elevated CO_2 altered the fatty acid composition of seeds (Uprety et al. 2007a, b). The palmitic, stearic, linolenic and erucic acids were significantly reduced and the linoleic acid and oleic acid contents were increased (Table 7).

It was demonstrated that the elevated CO_2 brought about a reduction in the saturated fatty acids namely palmitic, and stearic acid content, indicating that most of the fatty acids undergo desaturation and produced unsaturated fatty acids due to lower O_2: CO_2 ratio. Significantly higher quantity of linoleic acid and oleic acid was found in the seeds of CO_2 enriched plants. The conversion of linoleic acid to linolenic acid requires sufficient quantity of O_2 that was not available due to higher intercellular concentration of CO_2, which, in turn, resulted in the reduction of polyunsaturated fatty acid. Although the synthesis of linoleic acid was also a desaturation process, optimum level of O_2 may be available for desaturation in that step. After large consumption of O_2 in this step, sufficient intercellular O_2 was not available for the subsequent desaturation (Fig. 1). Moreover, at this point the ratio of CO_2/ O_2 increased significantly due to the high consumption of O_2, which ultimately reduced the rate of desaturation process. Another possibility of reduction of linolenic acid was that most of the linolenic acid was used for chloroplast membrane organization (Thies and Nitsch 1974). Linolenic acid oxidizes easily and may not be a desirable fatty acid. Oleic acid is the direct metabolic precursor of erucic acid and the reduced level of erucic acid may explain the accumulation of oleic acid, which is possibly not being used for the synthesis of erucic acid and linolenic acid (Bartkowiak-Brada, and Krzymanski 1983). The increase in oleic acid content due to elevated CO_2 is a positive effect, as its thermo stability is desirable from the cooking and nutritional point of view.

Reduction of the saturated fatty acid pool and some unsaturated fatty acids like linolenic and erucic acid are also important because most of these fatty acids increase blood cholesterol in the human body. However, saturated and monounsaturated fatty acids were less involved in this process. Linoleic acid is considered an essential fatty acid because human body can not synthesize it. This acid was significantly increased (about 20%) in the seeds of CO_2 enriched plants. The main function of linoleic acid is to lower blood cholesterol, help in the growth and development of human cells, reduce roughness of skin etc. (Shenolikar 1980). Linolenic acid is also nutritionally desirable but it gets easily oxidized resulting in unpleasant taste. The nutritional value of mustard oil could be

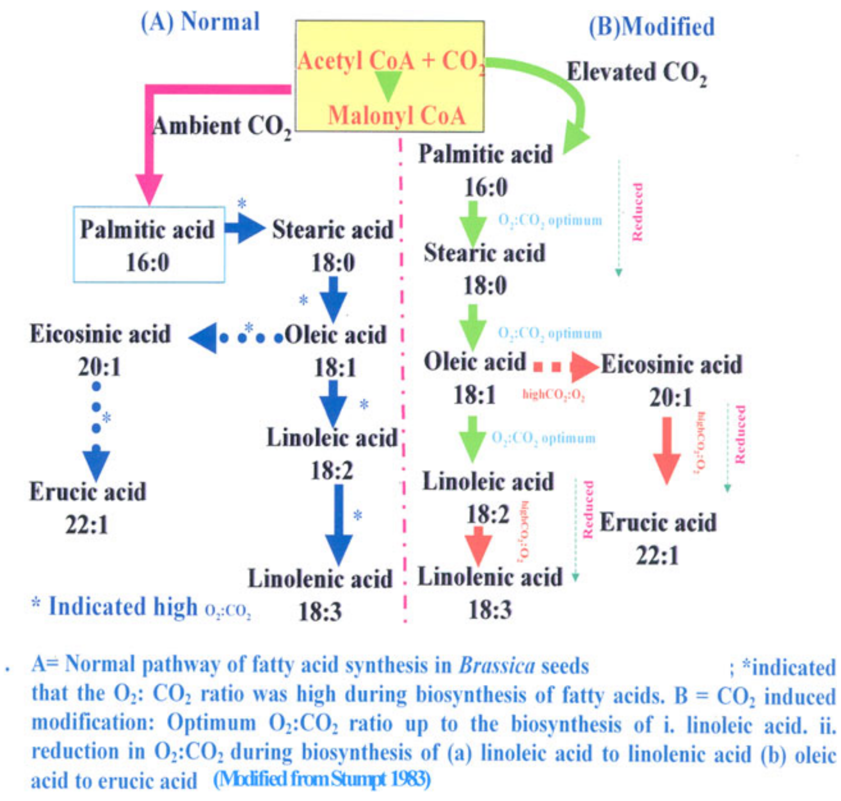
Table 6 Interactive effect of elevated CO_2 and moisture stress on seed quality of *Brassica* species (Uprety et al. 2007a, b)

Treatment	1000 Seed weight (g)		Nitrogen (%)		Oil content (%)		Carbon mg/g dw		C/N Ratio		*Non reducing sugars		*reducing sugars		*Total sugar		*Starch		*Crude fiber	
a	V !	V 2	V !	V 2	V !	V 2	V !	V 2	V !	V 2	V 1 b	V 2	V 1	V 2	V 1	V 2	V 1	V 2	V 1	V 2
Ambient CO_2																				
Control	4.5	6.4	6.7	6.3	37.69	35.92	25.2	30.2	4.0	4.7	17.5	22.7	11.8	15.2	29.3	37.9	63.3	73.8	89.0	103.0
Moisture-stress	3.2	4.9	4.2	5.1	28.70	26.15	15.9	22.7	3.7	4.4	11.3	16.2	7.4	11.3	18.7	27.5	41.9	51.7	86.0	97.0
Elevated CO_2																				
Control	5.1	6.9	4.3	5.2	42.79	40.10	31.9	37.4	7.4	7.4	22.3	28.3	14.8	19.6	37.1	47.9	78.4	94.3	79.0	89.0
Moisture-stress	4.5	6.2	4.2	5.0	37.06	34.80	22.8	29.5	5.3	5.8	16.9	23.4	11.2	15.7	28.1	39.1	59.3	73.4	74.0	83.0
CD at 5%																				
Variety	0.53		0.56		ns		3.44		ns		4.24		2.15		7.74		8.44		7.32	
Treatment CO_2	0.20		0.44		1.14		1.77		1.11		2.12		1.09		3.56		5.21		4.44	
Moisture-stress	0.12		0.48		1.34		1.99		0.67		1.89		1.84		2.12		3.34		NS	
Var. x CO_2											3.03		1.54		4.78		7.44		8.12	
Var. x MS											2.12		2.60		3.67		5.77		NS	
CO_2 x MS											3.44		2.81		5.44		7.79		NS	
Var x CO_2 x MS											4.12		3.67		5.12		10.44		NS	

*mg/g dry weight

V1-Pusa Gold V2-RH-30

Fig. 1 The impact of elevated CO_2 on the normal pathway of fatty acid synthesis in *Brassica* seeds (Uprety et al. 2007a, b)



enhanced if erucic acid content is reduced to <5% (Walker et al. 1970). Uprety et al. (2007a; b) observed that about 13% erucic acid was reduced due to CO_2 enrichment in *Brassica juncea* grains. They concluded that elevated CO_2 was involved in the alteration of fatty acid composition in seeds by regulating the CO_2:O_2 ratio at different stages of fatty acid synthesis.

Other crops

Ziska et al. (2007) studied the impact of rising atmospheric CO_2 on the nutritional quality of mung bean (*Vigna mungo*) seeds. They observed that elevated CO_2 increased the absolute amount of omega 3 fatty acid (Table 8), but decreased palmitic and omega -6- fatty

Table 7 Interactive effect of elevated CO_2 and water stress on the fatty acid composition of *Brassica* seed (Uprety et al. 2007a, b)

Treatment	Stearic acid (%)		Palmitic acid (%)		Linoleic acid (%)		Linolenic acid (%)		Erucic acid (%)		Oleic acid (%)	
	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
Ambient CO_2												
Control	1.40	1.30	2.80	2.79	12.2	10.7	6.37	7.99	52.4	55.4	5.24	6.66
Moisture-stress	1.20	1.20	2.30	2.74	11.9	10.4	6.29	7.84	51.7	55.2	5.21	6.70
Elevated CO_2												
Control	0.98	0.92	2.00	2.70	14.1	12.9	5.24	6.66	47.7	47.3	6.37	7.99
Moisture-stress	0.92	0.94	2.10	1.94	13.8	12.7	5.20	6.70	47.1	48.2	6.29	7.84
CD at 5%												
Variety	ns		ns		1.63		1.43		ns		1.43	
Treatment CO_2	1.19		0.54		1.02		0.58		2.31		0.58	
Moisture-stress	ns		ns		ns		ns		ns		ns	

V1-Pusa Gold V2-RH-30

Table 8 Effect of elevated CO2 on the fatty acid percentage in mung bean (*Vigna radiate* L. Wilczek) seeds (Ziska et al. 2007)

Fatty acids (%)	CO2 concentration (ppm)		*P*- values CO2
	413	667	
Palmitic	18.7	17.1	0.04*
Palmitoleic	1.9	1.7	0.22 ns
Stearic	4.9	5.2	0.38 ns
Vaccinic	1.4	1.3	0.37 ns
Oleic	1.6	1.7	0.56 ns
Omega-6	13.0	10.2	0.001***
Omega-3	47.8	52.6	0.008**

$*P<0.05$; $**P<0.01$; $***P<0.001$

acids. The significant increase in ratio of omega 3 to omega 6 fatty acids suggests an over all improvement in the potential of mungbean to provide significant sources of omega 3 fatty acids under elevated CO_2 condition. There is increasing evidence that omega 3 fatty acids in human diets may be associated with a reduction in cardiovascular diseases as well as being anti-thrombotic and anti-inflammatory (Covington 2004). It is thought that omega 3 fatty acids lower plasma triglyceride levels, particularly in persons exhibiting hypertriglyceridemia, by inhibiting the synthesis of very low density lipoprotein (VLDL) cholesterol and triglycerides in the liver. Conversely, omega 6 fatty acids which are readily available from a number of processed foods can compete with omega 3 fats, and reduce any positive cardiovascular benefits (Covington 2004). It has been suggested to balance the intake of both fats by reducing fat consumption in processed foods and maximizing fat coming from omega 3 fatty acids. It is thus clear that future increases in atmospheric CO_2 are likely to alter qualitatively and quantitatively the composition of mungbean seeds. Elevated CO_2 can alter the content of essential fatty acids. There is significant potential in future atmospheric CO_2 to alter food quality. The correlations of these changes in the fatty acid composition of mungbean grains with the nutrition of human has been ignored and overlooked the aspect of rise in CO_2 in plant biology.

Tomas et al. (2003) studied the interactive effects of elevated temperature and CO_2 on soybean seed composition. As growth temperature of field-grown soybean increased up to a mean of 28°C, oil concentration increased and protein concentration decreased from 14°C to a minimum at 22°C (Piper and Boote 1999). In addition to changes in the concentration of oil produced in seeds, the ratio of fatty acids in soybean oil changes when seeds develop under elevated temperature. For example, oleic acid concentration increased with increasing temperatures while linoleic acid decreased (Carver et al. 1986; Rennie and Tanner 1989; Rebetzke et al. 1996). Heagle et al. (1998) observed a positive, significant effect of CO_2 enrichment on soybean seed oil and oleic acid concentration.

Presumably high temperature or CO_2 induced changes in seed composition are mediated at the level of gene expression. In soybean, however, studies on temperature or CO_2 effects on seeds have not yet been associated with expression of specific genes related to seed storage compounds. The ratio of polyunsaturated to monounsaturated fatty acids in soybean oil is known to decrease with high temperature (Rebetzke et al. 1996; Wolf et al. 1982); however, the abundance of transcripts encoding fatty acid desaturase did not change (Heppard et al. 1996).

Tomas et al. (2003) observed substantial differences in seed composition due to growth temperatures for plants grown at temperatures increasing from 28/18 to 44/34°C and there was no effect due to elevated CO_2 level. Oil concentration increased with increasing temperature up to 32/22°C than decreased. These observations were complementary to the findings of Piper and Boote (1999) who observed increase in oil with rise in temperature up to 28° C. The degree of fatty acid saturation in soyabean oil was significantly increased by increasing temperature but there was no effect of elevated CO_2. Similarly the oleic acid concentration of oil increased and linolenic acid decreased with increasing temperature. Changes in fatty acid composition such as concentration of oleic acid are associated with nutritional aspects as well as longevity of soybean oil (O'Byrrne 1995). Nitrogen concentration increased with temperature up to 40/30°C above which it decreases. Tomas et al. (2003) hypothesizes that increasing protein concentrations with decreasing oil, may actually be a mathematical side effect caused by rising temperature. Soybean protein concentration in general is negatively correlated to seed oil. Phosphorus concentration in seed was also increased and 50% of this phosphorus in soybean is in phytate form.

Heagle et al. (1998) found a significant effect of elevated CO_2 on soybean oil in cultivars Essex, Holladay and NK6955. The oleic acid concentration was positively affected by CO_2 and the effect of cultivar was also highly significant. There was no effect of CO_2 on protein concentration. Thus it can be contended that higher temperature significantly affected seed composition with the effects of elevated CO_2 being comparatively small and insignificant. However, elevated temperature will have considerable impact on seed composition and will be accompanied by changes in transcript abundance. Additional study is necessary to understand the biochemical basis of this phenomenon.

Future directions

The magnitude of the CO_2 induced effect on grain quality will depend on the future atmospheric concentration of CO_2, and its interactions with the biotic and abiotic stresses, agronomic practices, cultivars choice & growing conditions. Unfortunately our knowledge on these interactions is limited and needs to be thoroughly studied and judiciously recorded for the development of plant types for future. It is also important to note that grain quality is not only determined by the contribution of chemical constituents such as proteins, starch, lipids to dough strength in wheats, rice cooking properties & the fatty acid balance of oil seeds but also by the interaction between these components, which needs to be investigated and utilized for quality improvement. Most of the studies with crop plants demonstrate reduction in the concentration of nutrient constituents like Ca, S, Mg, Fe & Zn. Depending in the magnitude of the dilution effect, this has the potential to contribute to health problems caused by micro element deficiencies in population, where these crops provide a large part of dietary needs. The possible negative effects of this elemental dilution on micronutrient deficiencies needs to be mitigated either by selecting suitable cultivars or by nutrient management. The introduction of new experimental methods such as the use of stable isotopes, proteomics & metabolomics as well as identification of qualitative trait loci (QTL) will be important steps to identify & quantify CO_2 effects on grain quality parameter. Research is required to sustain the CO_2 induced positive balance of desired fatty acids in oil seeds and to transfer such characters to other compatible species using biotechnology & plant breeding. The challenge for plant breeders & biotechnologists to take advantage of the inevitable increase in atmospheric CO_2 concentration by selecting genotypes that will produce more & yet maintain desirable quality characteristics under future CO_2 scenario.

Conclusion

Thus it is clear that the changes in the atmospheric CO_2 are not only affecting the productivity and physiological processes in crops like wheat, rice and B*rassica* but also altering their composition and grain structure. These changes in grain quality may affect their uses as food ingredients and may prove a threat to their application. Reduction in the protein and gluten content and change in gleidin and glutelin ratio indeed may degrade the baking and chapatti making properties of wheat cultivars. The changes in CO_2 affected rheological properties of gluten due to its adverse effect on gleidin and glutelin ratio may further suggest changes in their uses. Whereas, in case of rice, the eating quality and the palatability are determined by the ratio of amylose and amylopectin, may bring CO_2 induced changes leading to compactness among cooked rice although, there was significant increase in the size of grain even after cooking. However, the level of protein remained low to bring a negative constituent in its nutritional properties. The transcriptional regulation of waxy gene (Wx) in CO_2 induced higher amylose containing rice grains may be important in predicting, how cooking quality may change in future high CO_2 environment. *Brassica,* an oil seed crop has been found to increase in their grain weight and grain size, and brings improvement in their fatty acid composition (reduction in the erucic acid) under elevated CO_2 conditions, thus increasing the possibility of its use for the heart patients. The alteration of the quality of grains of various crops suggests that the current application of nitrogen fertilizers may be increased to achieve the improvement in their protein quality and nutrient composition. Further the new experimental approaches of the use of stable isotopes, proteomics and metabolimics as well as the identification of QTL may help in improving the grain quality of these crops under future high CO_2 environment protecting security of these food grains for their application purpose. Plant breeders also may have to impose selection pressure for higher protein concentration in grains to offset decreases that may accompany the increases in atmospheric $CO_{2.}$ Overall elevated atmospheric CO_2 and subsequent global climate changes will provide opportunities that may be exploited by plant breeders to increase productivity and improve the quality of crops for the industrial and application purposes which may otherwise be adversely affected in twenty first century.

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