International Journal of Chemical Studies

P-ISSN: 2349–8528 E-ISSN: 2321–4902 IJCS 2019; 7(4): 517-524 © 2019 IJCS Received: 07-05-2019 Accepted: 09-06-2019

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Effect of elevated Co₂ on physiological, biochemical and nutritional changes in crop growth: A review

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Abstract

Reforestation and combustion of fossil fuels result in release of large amount of CO₂ into the atmosphere, and thus the concentration of atmospheric CO₂ has greatly been increasing, especially in the past half century and, as is predicted will be double the concentration of the preindustrial era around the mid -21^{st} century. Now it was already upto 373 μ mol mol⁻¹ in the year 2002. Increase in atmospheric CO₂ concentration has the potential to affect terrestrial ecosystems by influencing plant photosynthesis and productivity. This review is undertaken to know the effect of elevated levels of CO₂ on crop growth, yield, nutrient content, nutrient uptake, physiological and biochemical characters.

Keywords: Elevated levels of CO₂, crop growth, yield, nutrient content, nutrient uptake, physiological characters, biochemical characters

Introduction

The CO₂ concentration has increased approximately 25 % from ~ 280 ppm to 350 ppm, since the beginning of the industrial revolution and continues rising at a rate of approximately 0.5% per year. The Intergovernmental Panel on Climate Change (IPCC) Projects, based on climate model results show that the global mean temperature may increase by about 0.3 °C per decade over the next century and the precipitation and possibly wind patterns may be altered as well (IPCC, 1990) ^[28]. These projected climate change and increases in CO₂ could have significant impact on agriculture. The detrimental effect of CO₂ and other green house gases can be avoided by sequestering carbon into soil and plant.

Biosequestration of carbon both by soil and biota is a truly win-win situation. Indirect plant carbon sequestration occurs as plant photosynthesizes atmospheric CO_2 into plant biomass. Subsequently, some of this plant biomass is indirectly sequestered as soil organic carbon during decomposition process. Further, there is an additional potential of carbon sequestration in biomass especially by forest and other biota. This potential is considerable in terms of the negotiation under the provision of Clean Development Mechanisms under IPCC and for trading carbon in the national and international markets.

With increasing levels of atmospheric CO_2 concentration, much research has been attracted to finding insight into the response of plants to elevated CO_2 . Information on the CO_2 exchange processes (eg photosynthesis and respiration) between the atmosphere and terrestrial ecosystems, which are affected by the ongoing dramatic enrichment of atmospheric CO_2 is necessary for understanding the feedback effects from CO_2 elevation on global vegetation and carbon budget. Plants which are able to produce high yield and increase SOC in soil under high concentration of green house gases especially CO_2 should be known to improve carbon sequestration through plants.

Keeping these in mind, in this review paper an overview is discussed on impact of enriched CO_2 levels on crop growth attributes, yield and yield components, nutrient availability in soil, nutrient uptake, physiological and biochemical characters in plant.

Effect of elevated CO2 on growth attributes of crops

Elevated CO₂ increased plant height, tillering and dry weight per stem in hybrid rice cultivars (Yang *et al.* 2009 and Liu *et al.* 2008) ^[71, 37]. Studies on rice under controlled environments have found that elevated CO₂ usually has little effect on individual leaf area but generally increases tiller number, resulting in greater leaf area per plant (Ziska *et al.*, 1997) ^[74].

Increased CO₂ concentration showed that 'N' nutrition and water has significant effects on the tillering of spring wheat (Li *et al.*, 2004) ^[35]. Different spring wheat cultivars introduced in Germany between 1890 and 1988 were exposed to normal and elevated CO₂ concentration. CO₂ enrichment resulted in a greater growth stimulation of the older cultivars than the modern cultivars (Manderschield and Weigel, 1997) ^[41].

Kimball *et al.* (2002) ^[33] reported that aboveground biomass of cotton was 85 per cent greater in the CO₂ enriched treatment than in the ambient air treatment, while the aboveground biomass of sorghum was 2 per cent lower in the CO₂ enriched air than in the ambient air. CO₂ enriched air on amply irrigated sorghum, did not enhance the total biomass (Ottman *et al.*, 2001) ^[51]. Growth at elevated CO₂ did not stimulate photosynthesis and biomass production of maize crops. There was no significant effect of growth at elevated CO₂ on stover biomass and grain biomass (Leakey *et al.*, 2006) ^[34].

Ghannoum *et al.* (1998) ^[24] reported that under conditions of high soil nitrogen, atmospheric CO_2 enrichment increased total plant dry mass by 27 per cent for *Panicum coloratum* (C₄) and 28 per cent for both *Panicum laxum* (C₃) and *Panicum antidotale* (C₄). However, under conditions of low soil nitrogen, elevated CO₂ had no significant effect on the dry mass of *Panicum laxum* and *Panicum antidotale* while dry mass actually decreased by 25 per cent in *Panicum Coloratum*.

Effect of elevated CO₂ on yield and yield components of crops

Under elevated CO_2 to maximize rice grain yield it is important to supply sufficient nitrogen over the whole season, in order to maintain the enhancement in dry matter production as well as grain yield (Kim *et al.*, 2001)^[32]. The considerable variation in the magnitude of the response of grain yield can be attributed to differences in experimental conditions and indicated that factors such as air temperature, nutrient supply and cultivars can affect the response of rice to elevated CO_2 (Baker *et al.*, 1996)^[4].

Elevated CO₂ substantially enhanced grain yield (+34 per cent) in three-line hybrid *indica* rice. CV. *Shangou* 63. The magnitude of yield response to CO₂ was independent of 'N' fertilization, but varied among different years (Liu *et al.*, 2008) ^[37]. Elevated CO₂ increased panicle number per unit land area by 8 per cent due to an increase in maximum tiller number, while productive tiller ratio remained unaffected, spikelet number per panicle showed an average increase of 10 per cent due to elevated CO₂, which was also supported by increased plant height and dry weight per stem (Yang *et al.*, 2009) ^[71]. Grain yield was stimulated by an average of 13 per cent by Free-Air *Carbon dioxide* Enrichment (*FACE*) in a Japonica rice cultivar, due to increased total dry matter production rather than any changes in partitioning to the grain (Yang *et al.*, 2006) ^[70].

Effect of elevated CO₂ on physiological characters of crops Chlorophyll meter readings (SPAD values)

Spring wheat cv. Minaret was grown in open-top chambers at four sites across Europe. The effect of CO_2 enrichment on the chlorophyll content of the flag leaf was investigated using the MINOLTA SPAD-502 meter. No significant effect of elevated CO_2 was observed at anthesis. Leaf senescence, indicated by the chlorophyll breakdown after anthesis, was relatively constant in the control chambers. Elevated CO_2 caused a faster decline in chlorophyll content indicating a faster rate of plant development at two experimental sites (Ommen *et al.*, 1999)^[49].

Potato cv. *Bintje* was grown in open top chambers and free air enrichment system at 7 sites across Europe for 2 years (1998-99). Season long chlorophyll average were 9.3 per cent lower in the CO₂ treatment. From tuber initiation onward the leaves of plants grown under elevated CO₂ showed progressively lower chlorophyll content (-4.8 per cent) indicating a faster senescence of leaves that increased during the late growth period (-12.8 per cent) (Bindi *et al.*, 2012)^[8]

Under future atmospheric environment, it seems that expected increases in the concentration of atmospheric CO_2 will play a very important role in their regulation acting on the leaf chlorophyll content (Evans, 1989). Miglietta *et al.* (1998) ^[19, 44] stated that high nitrogen demand under elevated CO_2 of the tuber determines faster leaf senescence. The redistribution of nitrogen from chlorophyll binding proteins is considered to be the main cause of chlorophyll degradation.

Parameters of plant water relations

A primary response of C_3 plants to elevated atmospheric CO_2 concentrations is an increase in the net assimilation rate and associated decrease in the transpiration rate per unit leaf area (Morrison, 1987) ^[45]. Numerous experiments have demonstrated that in many C_3 species high atmospheric CO_2 leads to increase in photosynthetic rate, whole plant growth and water use efficiency. It also decreases stomatal conductance, transpiration rate and photosynthesis which is the most sensitive process to CO_2 enrichment (Jiang, 1995) ^[31].

With elevation of CO_2 concentration, stomata do not appear to limit photosynthesis any more than they do at ambient CO_2 concentration, even though stomatal conductance usually decreases under these conditions (Drake and Meler, 1997)^[18]. In most plant species, it has been reported that elevated CO_2 concentration reduces the stomatal conductance by 33 - 50 per cent and leaf transpiration rate by 20 - 27 per cent (Samarakoon *et al.*, 1995)^[57].

In rice crop, leaf stomatal conductance exhibited favorable responses, being reduced in the CO₂ enriched chambers by 15 - 52 per cent in the *maha* season (Jan-Mar) and by 13 - 19 per cent in the *yala* season (May - Aug). These responses led to significant reductions in leaf transpiration rate per unit leaf area in both growing seasons (De Costa *et al.*, 2003) ^[17]. In spring wheat elevated CO₂ induced decrease in transpiration almost compensated for the increase in evapotranspiration brought by the higher leaf area under adequate N and water supply, CO₂ enrichment had limited effect on either leaf growth or evapotranspiration (Li *et al*, 2004) ^[35].

Averaged over the two years of experimentation in sorghum plants, elevated CO_2 reduced cumulative crop evapotranspiration by 10 per cent and 4 per cent under well watered and water stressed conditions, respectively (Conley *et al.*, 2001). Yashimoto *et al.* (2005) ^[13, 73] reported that elevated CO_2 reduced stomatal conductance by 13 per cent in upper leavers and by 40 per cent in lower leaves at the panicle initiation stage, but that reduction declined thereafter and CO_2 induced reduction in total evaporation by 8.2 per cent.

Jenny *et al.* (2000) ^[30] analyzed the impact of elevated CO₂ on sorghum plants and found that the ratio of quantum yield of CO₂ fixation to PS II efficiency was lower in plants grown at elevated CO₂ but only when leaf internal was below 50 μ l 1⁻¹. This suggests a reduction in the efficiency of the C₄ cycle

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when CO_2 is low and also implies increased electron transport to acceptors other than CO_2 .

Effect of elevated CO₂ on biochemical characters of crops Chlorophyll content

Nie *et al.* (1995) ^[47] observed that the decline in chlorophyll concentration during senescence was accelerated due to CO_2 enrichment. Leaf Chlorophyll content were significantly greater in the CO_2 enriched chambers ranging from 1-9 per cent higher in both maha (Jan-Mar) and yala (May to Aug) seasons in rice crop (De Costa *et al.*, 2003) ^[17]. Chlorophyll content was highest at the time of flowering and thereafter it started to decline in rice crop under elevated CO_2 concentration. The rate of decline in chlorophyll content was faster in plants grown under elevated CO_2 mostly in later part of growth. Irrespective of treatment difference, flag leaf contained the highest amount of chlorophyll than penultimate and third leaf (Moynul Huque *et al.*, 2006) ^[46].

CO₂ enrichment, in spring wheat did not affect light saturated rate of photosynthesis or protein and total chlorophyll. However, single flag leaf area and fresh weight per leaf area were increased by elevated CO₂. This increase was possibly responsible for a significant decrease in the chlorophyll a/b ratio (Manderscheid and Weigel, 1997)^[41].

Soluble protein content

About 50 per cent of soluble protein is occupied by an enzyme namely RUBISCO (Ribulose 1-5 biphosphate carboxylase oxygenase). It is the key enzyme which catalyses the fixation of CO_2 in C_3 plants. Pleijel *et al.* (1999) ^[53] observed the negative impact of atmospheric CO_2 enrichment on grain protein concentration would probably be alleviated by higher applications of nitrogen fertilizers.

Rice plants have relatively limited potential for developing additional carbon sinks grown at an atmospheric CO₂ concentration of 700 ppm exhibited increased leaf carbohydrate contents, which likely reduced leaf RUBISCO protein contents (Gesch *et al.*, 1998) ^[23]. The soluble protein, RUBISCO and its activase contents decreased significantly in rice plants grown under elevated CO₂ (Yong *et al.*, 2005) ^[72]. Elevated CO₂ increased net photosynthetic rates by 28 and 49 per cent in potato grown at 530 and 700 ppm, in spite of the fact that the plants experienced photosynthetic acclimation, as indicated by 13 and 21 per cent reductions in total RUBISCO activity (Sicher and Bunce 1999) ^[60].

The meta analysis investigated over 40 studies and reported the effects of high levels of CO₂ on five crops (barley, rice, wheat, soybean and potato). All of these crops had lower protein concentrations when grown at the higher CO₂ levels projected for the end of the 21st century. For wheat, barley, rice and potatoes elevated CO₂ cut protein concentration by 10-15 percent. Soybean showed a smaller reduction of 1.4 percent (Taub *et al.*, 2008) ^[62]. Increase in the air's CO₂ content leads to greater decreases in the concentration of protein in the foliage of C₃ grasses as compared to C₄ grasses (Wand *et al.*, 1999) ^[66]. Doubled CO₂ concentration of 740 ppm for two months decreased foliage protein concentration by 20 per cent in the C₃ grass, but by only 1 per cent in the C₄ grass (Berbehenn *et al.*, 2004) ^[7].

Ribulose 1-5 biphosphate carboxylase oxygenase (RUBISCO) - C₃ plants

RUBISCO known as the most abundant protein in the world because of its widespread occurrence in plants and its relatively higher concentration in the soluble protein fraction of leaves (>70 per cent). Plants grown in elevated CO_2 environments, exhibit some degree of photosynthetic acclimation or down regulation which is typically characterized by reduced amounts of RUBISCO (Farage *et al.*, 1998)^[22].

Mc Kee and Woodward (1994) ^[43] observed a carbohydrate accumulation and a decline in RUBISCO activity of wheat plants grown in high CO₂ concentration. A lower RUBISCO capacity and an increase in leaf starch concentration under CO₂ elevation has also been reported by Tuba et al. (1994) ^[65]. Elevated CO₂ reduced the amount of RUBISCO required to sustain enhanced rates of photosynthesis, which lead to a significant increase in plant nitrogen use efficiency of spring wheat (Theobald et al., 1998) [64]. Elevated CO₂ induced reductions in foliar RUBISCO concentrations occurred in a depth dependent manner, with the reductions increasing with depth in the canopy of wheat plants (Osborne et al., 1998)^[50]. Elevated CO₂ had no effect on leaf RUBISCO content in the younger leaves composing the upper canopy, but significantly reduced it in older leaves located lower within the canopy in sunflower crop (Sims et al., 1999). Prasad et al. (2004) [61, 54] reported that midday leaf photosynthetic rates of elevated CO₂ grown kidney bean plants at the highest temperature (40 / 30° C) were 35 per cent greater than those of the ambient CO₂ plants at the lowest temperature (28 / 18°C). Even with a down regulation, the activity and content of RUBISCO protein were still adequate to maintain greater photosynthesis at elevated CO₂. Reid *et al.* (1998) ^[56] stated that in soybean elevated CO₂ only reduced the activity of RUBISCO but not its amount.

Phosphoenol pyruvate carboxylase (PEP case) - C₄ plants

This enzyme is involved in fixation of CO_2 in C_4 plants. Sorghum, maize and sugarcane are some of C_4 plants. They have high affinity to CO_2 molecules. The reaction catalysed by this enzyme is given below.

	PEP case
Phosphoenol pyruvate (PEP) + CO_2	Oxaloacetic acid

In C₄ plants, PEP case fixes CO₂ in the mesophyll cells of the leaf and the resulting four carbon compound, malate, is shuttled into the bundle sheath cells where it releases CO₂ for fixation by RUBISCO. Thus, two processes are separated spatially, allowing for RUBISCO to operate in a low – oxygen environment to circumvent photorespiration. Photorespiration occurs due to the inherent oxygenase activity of RUBISCO in which the enzyme uses oxygen instead of carbon-di-oxide without incorporating carbon into sugars or generating ATP. As such, it is wasteful reaction for the plant. By comparison, C₄ carbon fixation via PEPcase is more efficient. So, estimation of amount and activity PEPcase enzyme is important in case of C₄ plants.

Elevated CO₂ (1100 ppm) increased photosynthesis in maize by about 15 per cent relative to that measured in plants grown at 350 ppm CO₂, inspite of the fact that photosynthetic down regulation occurred for both RUBISCO and PEP case (Maroco *et al.*, 1999) ^[42]. Maroco *et al.* (1998) found that no change in RUBISCO content for heterozygous PEP case mutant of *Amaranthus edulis* (C₄ dicot) with a reduction in PEP case content.

Elevated CO_2 reduced sorghum photosynthesis rates by about 16 per cent, contrary to the results of an earlier study conducted by the authors, where photosynthetic rates nearly doubled with atmospheric CO_2 enrichment (Watling and

Press, 1997) ^[67]. C_4 species has the ability to acclimate to elevated CO_2 in much the same way most C_3 plants do. They can reduce their investment in their primary CO_2 fixing enzyme (PEP case) and other related components (bundle sheath cell walls) and use the saved resources for processes that are more limiting to growth (Watling *et al.*, 2000) ^[68].

Elevated CO_2 had no effect on the cell-specific localization of RUBISCO or PEP case at any stage of leaf development, and the relative ratios of RUBISCO to PEP case remained constant during leaf development. However, in the oldest tissue at the tip of the leaf the total activities of Rubisco and PEP case decreased under elevated CO_2 in C₄ plants implying that young C₄ photosynthetic plant tissue may acclimate to growth under elevated CO_2 (Cousins *et al.*, 2003).

Antioxidants

During abiotic and biotic stresses production of reactive oxygen species is encountered. The scavenging enzymes called as antioxidant enzymes *viz.*, peroxidase, catalase and super oxide dismutase, they remove the free radicles and prevent the membranes and DNA from oxidative damage. Catalase enzyme is more related to abiotic stress and peroxidase for biotic stress.

Elevated CO₂ concentration in wheat cultivars increased the H_2O_2 levels slowly. Thus, to remove this H_2O_2 antioxidative enzyme concentration viz., catalase content increased (Lin and Wang 2002)^[36]. In maize crop, activities of catalase and ascorbate peroxidase were not affected by the elevated CO₂ concentration (Baczek-Kwinta and Koscielniak, 2003)^[3]. In soybean elevated CO₂ reduced the activities of catalase and super oxide dismutase by 15 and 24 per cent, respectively (Pritchard *et al.*, 2000)^[55].

Elevated CO₂ increased the activity of ascorbate peroxidase which is the first line of enzymatic defence that has diffused into plant tissues, by an average of 150 per cent. Similarly, elevated CO₂ increased the activity of catalase, which breaks down toxic hydrogen peroxide into water and oxygen molecules by 80 per cent. Thus atmospheric CO₂ enrichment increased the activities of these two enzymes in sugar maple that function to keep cells from experiencing oxidative particularly damage, to their membranes (Niewiadomska et al., 1999)^[48]. In poplar species, elevated CO₂ concentration increased the antioxidative enzyme content in leaves (Schwanz and Polle, 2011)^[58].

Effect of elevated CO2 on nutrient availability in soil

Active pool carbon increased in elevated CO₂ chambers relative to ambient CO₂ chamber treatments systematically over the first 3 years of exposure to elevated CO₂ in top soils and to a lesser degree in subsoils in semi-arid grasslands (Pendall and King, 2007) ^[52]. Allard et al. (2005) ^[2] reported that aboveground pasture biomass and leaf litter production were not altered by elevated CO₂, but that root growth rate and turnover were strongly stimulated by CO₂ particularly at low soil moisture contents during summer. As a result of the root responses, they also found that significantly more plant material was returned to the soil under elevated CO2 leading to an accumulation of coarse (>1 mm) particulate organic matter (POM), together with a similar but not yet significant trend in fine POM. In addition, they found there was a CO₂ induced lowering of POM carbon/nitrogen ratio, which they attributed to the higher proportion of legumes in the pasture under elevated CO₂.

Williams *et al.* (2000) ^[69] calculated that the CO₂-induced increase in soil carbon sequestration would amount to an

additional 1.3 Pg of carbon being sequestered in just the top 15 cm of the world's grassland soils over the next century. Hu *et al.* (2001) found that a doubling of the air's CO_2 content in grassland soils increased both soil microbial biomass and plant nitrogen uptake.

An increased retention of carbon in older SOC pools might be expected under elevated relative to ambient CO₂. Hence, not only does atmospheric CO₂ enrichment lead to higher rates of carbon input to soils, it apparently leads to slower rates of carbon withdrawal from them as well (Cardon *et al.*, 2011) ^[11]. Increased CO₂ typically increases photosynthetic rates, since photosynthesis consists of an assimilation of atmospheric CO₂ by the plant. This makes the elements assimilated through photosynthesis, like carbon, more available to plants, but does not in itself increase the availability of the elements that plants obtain from soils, like nitrogen (Taub, 2008) ^[63].

Microbial biomass N, extractable soil NH4⁺ N and NO3⁻ N were generally not affected by elevated CO₂ in the grassland ecosystems after several years of elevated CO₂ environment (Barnard et al., 2004)^[5]. Under elevated CO₂ availability of soil N and P increased, particularly P and application of N and P should be adjusted to need for rice at tillering and jointing and for wheat at whole growth stages (Ma et al., 2007) [38]. Elevated CO₂ increased phosphatase activity in wheat roots grown under continuous, but not transient, phosphorous deficiency, with the largest percentage stimulation (30 to 40 per cent) occurring in the most phosphorus deficient treatment. Furthermore, because these increases in phosphatase activity were also observed under sterile growing conditions, this observation indicates that this response can be mediated directly by plant roots without involving soil microorganisms, which are already known to aid in phosphorus mineralization (Barrett et al., 1998)^[6].

Effect of elevated CO₂ on nutrient content and uptake of crops

Macro nutrients (N, P and K)

A reduction of leaf nitrogen concentration owing to a downward regulation of photosynthesis to adjust the assimilate production to the demand of the plant's sink (Bowes, 1991)^[9]. Plant nitrogen concentration depends on the developmental stage (Greenwood *et al.*, 1990)^[25] and recently Coleman *et al.* (1993)^[12] have demonstrated that CO₂ induced reduction in tissue nitrogen concentration was due to accelerated plant growth under CO₂ enrichment. Jablonski *et al.* (2002)^[29] found that there is no reduction in grain nitrogen (protein) concentration in response to atmospheric CO₂ enrichment in rice crop. Likewise, they found no CO₂ induced decrease in seed nitrogen concentration on the studies of *legumes*. Uptake of nitrogen reduced in rice at high CO₂ due to lower transpiration rates (Conroy and Hocking, 1992)^[14].

Free-Air Carbon dioxide Enrichment (FACE) increased N uptake at panicle initiation but not at maturity in medium and high N treatments in rice crop. For the total dry matter, spikelet number and grain yield positive interactions between CO₂ and N uptake were observed (Kim *et al.*, 2001) ^[32]. Wheat exposed to elevated CO₂ experienced reduced leaf nitrogen content and this effect was exacerbated by elevated CO₂, eventhough the low nitrogen pot grown plants received more total nitrogen over the duration of the experiment (Farage *et al.*, 1998) ^[22]. Additional nitrogen can then be used to support larger reproductive structures, thereby enabling them to produce and sustain the larger yields that are

commonly reported for crops exposed to elevated levels of atmospheric CO₂ (Osborne *et al.*, 1998) ^[50].

Atmospheric CO₂ enrichment in grew wheat (*Triticum aestivum*) led to a 28 per cent reduction in leaf nitrogen without affecting leaf chlorophyll content. These decreases are not due to dilution of N caused by a relative increase in the plant mass but are the result of a decrease in N allocation to leaves at the level of the whole plant (Makino and Mae, 1999) [^{39]}. The CO₂ enrichment usually produced a decrease in nutrient concentrations, which was already detectable at the booting stage and was further enhanced until plant maturity. Nutrient concentrations of straw were more affected than those of grains. The decrease in concentration was greatest for N followed by K and the maximum decrease as compared with ambient CO₂ amounted to 43 per cent and 21 per cent for straw, and 30 per cent and -6 per cent for grains (Manderscheid *et al.*, 1995) ^[41].

The positive effects of elevated CO_2 on biomass, N and P uptake of wheat were greater than that of rice (Ma *et al.*, 2007) ^[38]. A reduction in nutrient uptake was noticed due to the CO_2 induced decrease in transpiration rate (Conroy, 1992) ^[15]. Cao and Tibbitts (1997) ^[10] found reductions in nitrogen and phosphorus concentrations in potato, which were not solely attributable to increases in starch content; no effect on potassium concentration was observed. Heagle *et al.* (2003) ^[26] found decreased concentrations of P in potato tubers grown in elevated CO_2 . Allard *et al.* (2003) ^[11] reported that under elevated CO_2 in mixed forage crops, leaves of the individual species exhibited lower nitrogen concentrations but higher water soluble carbohydrate (WSC) concentrations.

Secondary and micronutrients (Ca, Mg, S, Fe, Mn, Zn and Cu)

Two cultivars each of spring wheat (*Triticum aestivum* L., cv. Star and cv. Turbo) and spring barley (*Hordeum vulgare* L., cv. Alexis and cv. Arena) were exposed season-long above ambient CO₂ concentrations in open top chambers. The CO₂ enrichment usually produced a decrease in nutrient concentrations, which was already detectable at the booting stage and was further enhanced until plant maturity. Nutrient concentrations of straw were more affected than those of grains. The decrease in concentration was greatest for Mg followed by Ca, and the maximum decrease as compared with ambient CO₂ amounted to 35 per cent and 33 per cent for straw, and 13 per cent and 28 per cent for grains. Concentrations of micronutrients were also found to be partially decreased by about 10 - 30 per cent (Manderscheid *et al.*, 1995) ^[41].

Potato crops were grown at seven sites across Europe to test the effects of elevated atmospheric carbon dioxide. Under elevated CO₂, nearly all nutrient elements tended to decrease in concentration. At maximum leaf area, a significant reduction was observed for the concentrations of calcium in tubers. Since CO₂ enrichment promoted early tuber growth, these effects could in part be attributed to tuber developmental stage. At maturity, potato grown under CO₂ enrichment exhibited significantly lower concentrations of manganese and iron in aboveground organs, and magnesium in tubers which means a reduction of tuber quality (Fangmeier *et al.*, 2002) ^[20].

Elevated CO₂ decreased the concentrations of Ca, S, Mg, Fe and Zn in the grain at wheat (Manderscheid *et al.*, 1995) ^[41] while Fangmeier *et al.* (1999) ^[21] reported decreases in Ca, S and Fe. Seneweera and Conroy (1997) ^[59] found that under elevated CO₂ the concentration of Zn in brown rice grains

decreased on an average about 15 per cent while that of Fe decreased over 60 per cent.

Conclusion

Current evidence suggests that the concentrations of atmospheric CO₂ predicted for the year 2100 will have major implications for plant physiology and growth. Under elevated CO₂ most plant species show higher rates of photosynthesis, increased growth, decreased water use and lowered tissue concentrations of nitrogen and protein. Rising CO₂ over the next century is likely to affect both agricultural production and food quality. The effects of elevated CO₂ are not uniform; some species, particularly those that utilize the C₄ variant of photosynthesis, show less of a response to elevated CO₂ than do other types of plants. Rising CO₂ is therefore likely to have complex effects on the growth and composition of natural plant communities.

The effects of an enriched CO_2 atmosphere on crop productivity, in large measure, as positive, leaving little doubt as the benefits for global food security. Now, after more than a century, and with the confirmation of thousands of scientific reports, CO_2 gives the most remarkable response of all nutrients in plant bulk, is usually in short supply, and is nearly always limiting for photosynthesis. The rising level of atmospheric CO_2 is a universally free premium, gaining in magnitude with time, on which we can all reckon for the foreseeable future.

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