Carbon Dioxide Enrichment and Crop Productivity

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Abstract

Photorespiration (oxidative photosynthetic carbon cycle) is a process in which photosynthates burn down due to oxidative action of RUBISCO. This led to 25% reduction in photosynthetic output. However, e[CO_2] can inhibit this reaction resulting to the minimum loss of carbon also known as CO_2 fertilization.

Keywords

Carbon dioxide (CO_2) · Free-Air Carbon dioxide Enrichment (FACE) · Photorespiration · CO_2 fertilization

3.1 Introduction

Carbon dioxide (CO_2) is one of the important components of life on planet earth as it helps in the process of photosynthesis. Human activities in the form of deforestation, urbanization, industrialization, fossil fuel burning, and mechanization in agricultural practices resulted to the increased level of CO_2. Mauna Loa Observatory (MLO) which is a premier research facility at Hawaii, USA, monitors and collects data related to atmospheric changes in CO_2. The data in Fig. 3.1 shows that

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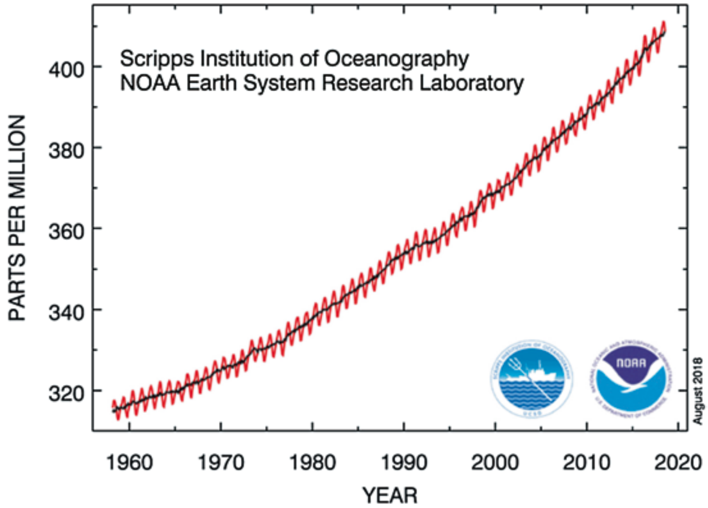

Fig. 3.1 Concentration of carbon dioxide (CO_2) from 1960 to 2020. (Source: Mauna Loa Observatory)

concentration of CO_2 is increasing at faster rate since after 1960. This situation is alarming for the world as CO_2 is main greenhouse gas. Forster et al. (2007) stated that elevated CO_2 is major driving factor of global warming and climate change. According to A1B emissions scenario of Intergovernmental Panel on Climate Change (IPCC) the carbon dioxide concentration (CO_2) might reach to 550 μLL^{-1} till 2050 (50% increase from 370 μLL^{-1} at the turn of century and 75% increase from 315 μLL^{-1} measured in 1960) (Carter et al. 2007). Such a big change in the substrate of photosynthesis and fundamental resource of plant life will have direct impacts on plant metabolism and ultimately on all agriculture and natural ecosystem (Tausz et al. 2013). Many studies have been conducted earlier in enclosure system, but after the advent of Free-Air Carbon dioxide Enrichment (FACE) technology, now elevated atmospheric [CO_2] (e[CO_2]) can be studied easily without constraints (Nösberger et al. 2006). Since managed ecosystem provide most of our food, wood, fiber, and source of renewable energy. Increased temperature and decreased soil moisture will lower the crop yield in future but that can be offset by e[CO_2] could be called as CO_2 fertilization. However, this impact will be different across the globe. FACE is a technique which can be used effectively to study the impact of e[CO_2] on crop parameters without altering the environment. FACE experiments have been effectively going on at Maricopa, Arizona, USA, since 1989. Ainsworth et al. (2008a, b) stated that FACE experiments provide good platform to do genetic screening and explain the genetic differences in crop productivity under e[CO_2]. They proposed new generation of large-scale, low-cost per unit area FACE experiments to identify CO_2-responsive genotypes which can be a starting line for future breeding program. In previous studies, it has been concluded that e[CO_2] could be easily capitalized by C3 crops by increasing photosynthesis rate, growth,

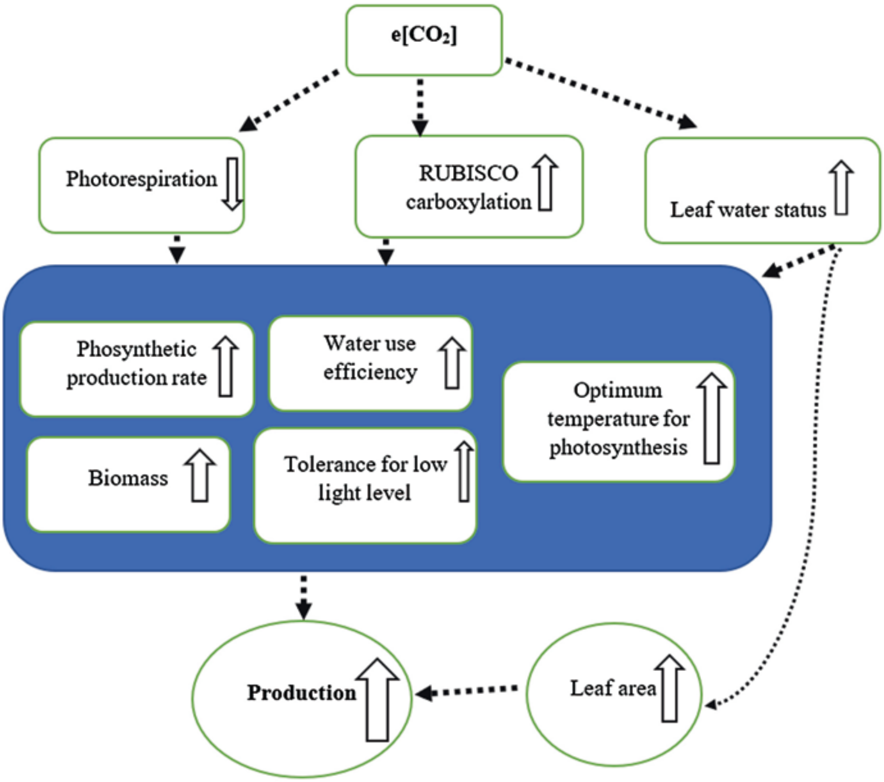

Fig. 3.2 Conceptual diagram of the direct initial effects of e[CO_2] on C3 crop production

and yield (Ainsworth and Long 2005; Long et al. 2006; Ainsworth and Rogers 2007; Ainsworth et al. 2008a, b; Leakey et al. 2009). Since e[CO_2] resulted to the increase rate of carboxylation at RuBisCO while inhibiting the oxygenation reaction. This resulted to the minimum loss of carbon due to photorespiration. Higher leaf water status and leaf area resulted to the maximum production (Fig. 3.2).

CO_2 fertilization effect is getting more attention as compared to secondary climate change factors (increasing temperatures or drought) as it is obvious that increase in CO_2 will continue to affect the planet (Ziska 2008). Therefore, to feed billions across the globe, positive effects of e[CO_2] should be harvested to offset the negative effect of drought and high temperature. Different agronomic and breeding efforts could be used to achieve this goal. Different crop traits need to be given attention through biotechnological means as they can optimize crop responses to e[CO_2]. The traits could be divided into two categories, vegetative growth traits (VGT) and regenerative growth traits (RGT). The VGT includes stress tolerance traits (thermal energy dissipation, antioxidant defense), nutrient use efficiency traits (nutrient (N,P) uptake, nutrient assimilation, stem nutrient storage), source traits (photosynthesis, RuBP regeneration, electron transport), and sink traits (tillering, root traits, stem carbohydrate storage). RGT includes stress tolerance traits (thermal energy dissipation and antioxidant defense traits in heads, nutrient use efficiency traits (nutrient (N,S) remobilization from leaf and stem and translocation, nutrient assimilation), source traits (photosynthetic traits in heads, remobilization of carbohydrates from stem and electron transport), and sink traits (seed numbers and seed weight potentials). Similarly, application of FACE facilities on major crop species needs time to have better future planning. Some of the FACE facilities are already going on soybeans (SoyFACE) (Rogers et al. 2006), rice (Rice FACE) (Okada et al. 2001), and wheat (AGFACE) (Mollah et al. 2009). These experiments have identified traits which potentially governs the growth and yield response under e[CO_2]. However, still they have to look for traits particularly for nutrient and water-use efficiency, stress tolerance, and grain quality.

IPCC (Intergovernmental Panel on Climate Change) projections reported continuous rise of CO_2 from 500 to 1000 ppm by the end of the century (IPCC 2007). This elevated level of CO_2 has direct effect on growth, physiology, and chemistry of plants. Photosynthesis which is heart of nutritional metabolism of plants has been directly affected due to elevated level of CO_2. However, ability of plants to responds to elevated level of CO_2 have interactions with mineral availability and it has been well documented in case of nitrogen (Ainsworth and Long 2005). Cure and Acock (1986) in their findings identified strengths and weakness for modeling plant responses to CO_2. They have collected published data of ten leading crops and studied response of net carbon exchange rate (NCER), net assimilation rate (NAR), biomass accumulation (BA), root-shoot ratio (RSR), harvest index (HI), conductance (C), transpiration rate (TR), and yield (Y) to elevated CO_2. There results depicted that doubling of CO_2 resulted to 52% increase in NCER and 41% increase in grain yield. However, TR decreased 23% on average. Similarly, it has been reported by Pandey et al. (2018) that hexaploid wheat is more responsive to e[CO_2] than tetraploid. Further details of overall crop responses to CO_2 doubling, CO_2 doubling and water stress interactions, CO_2 doubling and nutrient stress interactions, and CO_2 doubling and light interactions have been presented in Table 3.1.

3.2 Elevated CO_2 and Nutrients

Nutrient availability is linked with plant photosynthetic rates. CO_2 is the main substrate for carbon (C) assimilation in photoautotrophic organisms. Therefore, its higher concentration will significantly affect the nutrients availability and uptake by the plants. Nitrogen (N) is the nutrient required in largest quantities, and plant generally takes N as nitrate (NO_3^-) and ammonium (NH_4^+) form. Root N uptake affects plant productivity, but root N uptake to elevated CO_2 depends on N source (Cohen et al. 2018). Rhizosphere priming (RP) was used to enhance plant nitrogen uptake under elevated CO_2 and results showed that RP effects on soil organic matter (SOM) decomposition and N availability (Nie and Pendall 2016). Phosphorus (P) is a major macronutrient of plant. Mechanism of P-acquisition in C3 plants under changing climate needs to be studied to have crop adaptability to future climate change. Since P-reserves are declining, thus it might limit crop growth, while on the other hand

Table 3.1 Impact of elevated CO_2 on different crop parameters

Crop species	M	STCER	ACER	INAR	LTNAR	BA	RSR	HI	C	Tr	Y
Overall crop CO_2 doubling response to different plant parameters											
Wheat (*Triticum aestivum* L.)	C3	41	27	11	6	31	1.4	2.4	−22	−17	35
Barley (*Hordeum vulgare* L.)	C3	50	14	14	11	30	6.4	1.3	−52	−19	70
Rice (*Oryza sativa*)	C3	42	46	26	_-	27	−4	1.9	−33	−16	15
Corn (*Zea mays*)	C4	26	4	9	3	9	3.1	4.3	−37	−26	29
Sorghum (*Sorghum bicolor*)	C4	−3	6	–	20	9	−8.5	–	−27	−27	–
Soybean (*Glycine max* L.)	C3	78	42	35	23	39	1.1	−5	−31	−23	29
Alfalfa (*Medicago sativa* L.)	C3	139	–	–	–	57	−5	–	–	–	–
Cotton (*Solanum hirsutum* L.)	C3	60	13	-_	40	84	3.2	-_	−15	−18	209
Potato (*Solanum tuberosum* L.)	C3	105	–	–	54	−15	−2.1	1.9	−59	−51	51
Sweet potato (*Ipomoea batatas*)	C3	–	–	–	11	59	34.9	–	–	–	83
CO_2 doubling and water stress interactions											
Wheat (*Triticum aestivum* L.)	C3	–	–	–	–	35	−4.1	2.8	–	–	25
Barley (*Hordeum vulgare* L.)	C3	–	–	–	–	107	1	–	–	–	–
Rice (*Oryza sativa*)	C3	–	–	–	–	51	−3	–	–	–	–
Corn (*Zea mays*)	C4	–	–	–	–	0	−26	–	–	–	–
Sorghum (*Sorghum bicolor*)	C4	–	–	–	–	26	−8	–	–	–	–
Soybean (*Glycine max* L.)	C3	–	65	–	–	–	–	1.6	−23	−14	60
Alfalfa (*Medicago sativa* L.)	C3	–	–	–	–	130	2	–	–	–	–
Cotton (*Gossypium hirsutum* L)	C3	–	–	–	–	0	10	-_	–	–	–
Potato (*Solanum tuberosum* L.)	C3	–	–	–	–	–	–	–	–	–	–
Sweet potato (*Ipomoea batatas*)	C3	–	–	–	–	–	–	–	–	–	–
CO_2 doubling and nutrient stress interactions											
Wheat (*Triticum aestivum* L.)	C3	–	–	–	25	39	1	2.7	–	–	–
Barley (*Hordeum vulgare* L.)	C3	–	–	–	–	–	–	–	–	–	–

(continued)

Table 3.1 (continued)

Crop species	M	STCER	ACER	INAR	LTNAR	BA	RSR	HI	C	Tr	Y
Rice (*Oryza sativa* L.)	C3	–	–	–	–	32	–	–	–	–	_-
Corn (*Zea mays* L.)	C4	–	32	5	–	14	−1.9	–	–	–	–
Sorghum (*Sorghum bicolor* L.)	C4	–	–	–	–	–	–	–	–	–	-_
Soyabean (*Glycine max* L.)	C3	–	39	35	19	52	−0.3	−5.1	−37	–	–
Alfalfa (*Medicago sativa* L.)	C3	-_	–	–	–	13	−9.6	–	–	–	–
Cotton (*Gossypium hirsutum* L.)	C3	76	35	-_	–	146	–	–	–	–	–
Potato (*Solanum tuberosum* L.)	C3	_-	–	–	–	–	–	–	–	–	–
Sweer potato (*Ipomea batatas*)	C3	_-	–	–	–	–	–	–	–	–	–
CO_2 doubling and light interaction											
Wheat (*Triticum aestivum* L.)	C3	37	–	–	–	15	–	–	–	–	–
Barley (*Hordeum vulgare* L.)	C3	_-	11	9	7	20	–	–	–	–	–
Rice (*Oryza sativa*)	C3	–	–	39	_	28	–	–	–	–	–
Corn (*Zea mays*)	C4	21	–	8	−3	16	2	–	–	–	–
Sorghum (*Sorghum bicolor*)	C4	-_	–	–	–	–	–	–	–	–	–
Soybean (*Glycine max* L.)	C3	52	84	23	–	44	−2	–	–	–	–
Alfalfa (*Medicago sativa* L.)	C3	_-	–	–	–	–	–	–	–	–	–
Cotton (*Gossypium hirsutum* L.)	C3	67	–	–	–	–	–	–	–	–	–
Potato (*Solanum tuberosum* L.)	C3	–	–	–	–	–	–	–	–	–	–
Sweet potato (*Ipomoea batatas*)	C3	_	_	_	_	_	_	_	_	_	_

Where *M* Metabolism, *STCER* short-term carbon exchange rate, *ACER* acclimatized carbon exchange rate, *INAR* initial net assimilation rate, *LTNAR* long-term net assimilation rate, *BA* biomass accumulation, *RSR* root-shoot ratio, *HI* harvest index, *C* conductance transpiration rate, *Y* yield

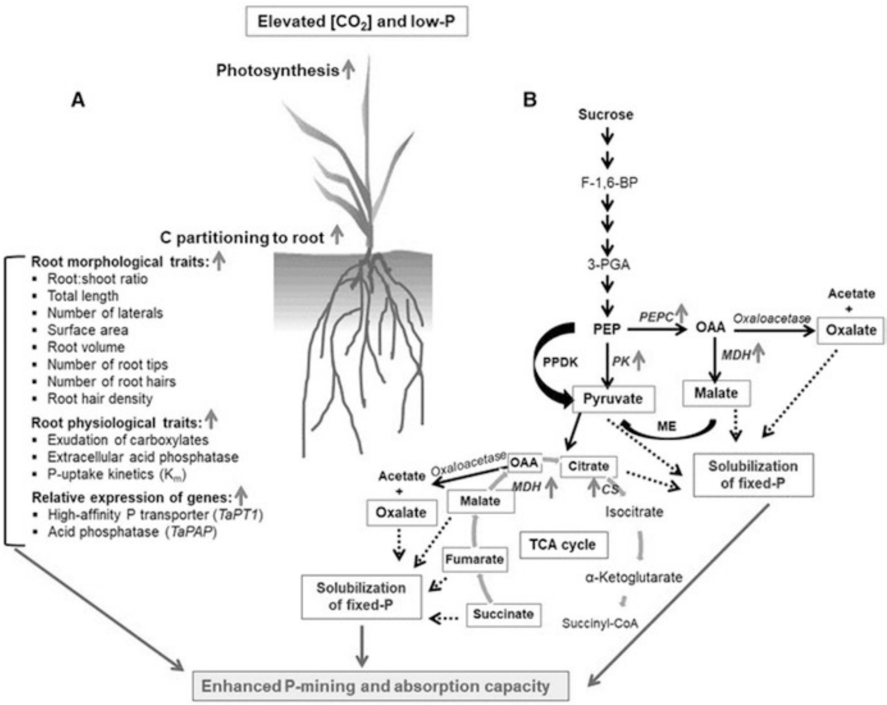

Fig. 3.3 Proposed P-model under elevated CO_2. (Source: Pandey et al. 2018)

elevated CO_2 increases growth rates by altering physiological processes. Norby et al. (2010) reported that growth stimulation under elevated CO_2 depends on the availability of nutrients and water. Interactive effect of P and e[CO_2] were studied on different plant processes. Results showed that e[CO_2] resulted to increased root biomass, volume, and surface area. e[CO_2] might also influence exudation of C compounds in the rhizosphere which is good adaptation strategy to coup with P deficiency (Krishnapriya and Pandey 2016). Model for e[CO_2] facilitated by P-mining and absorption by plants under P starvation was proposed by Pandey et al. (2018). Model depicted that e[CO_2] resulted to increased photosynthesis, high C partitioning to root, and improved root traits. This further increase extracellular acid phosphatase activity and P-absorption due to expression of phosphatase enzymes. The model also proposed bypass reaction under P starvation (Fig. 3.3).

3.3 Elevated CO_2 and Soil Microbiome

Significant effect of elevated CO_2 has been reported on soil mycorrhizae. Terrestrial ecosystems (type of ecosystem found only on biomes also known as beds) have connection with CO_2 through photosynthetic fixation of CO_2, C-sequestration, and release of CO_2 through respiration and decomposition. Previous studies depicted impact of CO_2 enrichment on terrestrial ecosystems in the form of organic C dynamics. Since majority of life in soil is heterotrophic and dependent on photosynthesis (plant-derived organic carbon), therefore, activity and functioning of soil organism have strong association with elevated CO_2. Studies showed that main effect of elevated CO_2 on soil microbiota is through plant metabolism and root secretion. Figure 3.4 illustrates that increased photosynthetic C-allocation due to elevated CO_2 is directed to mycorrhizae and root tissue. Mycorrhizae then translocate C into the soil microbial community (bacteria and fungi) which resulted to the change in the

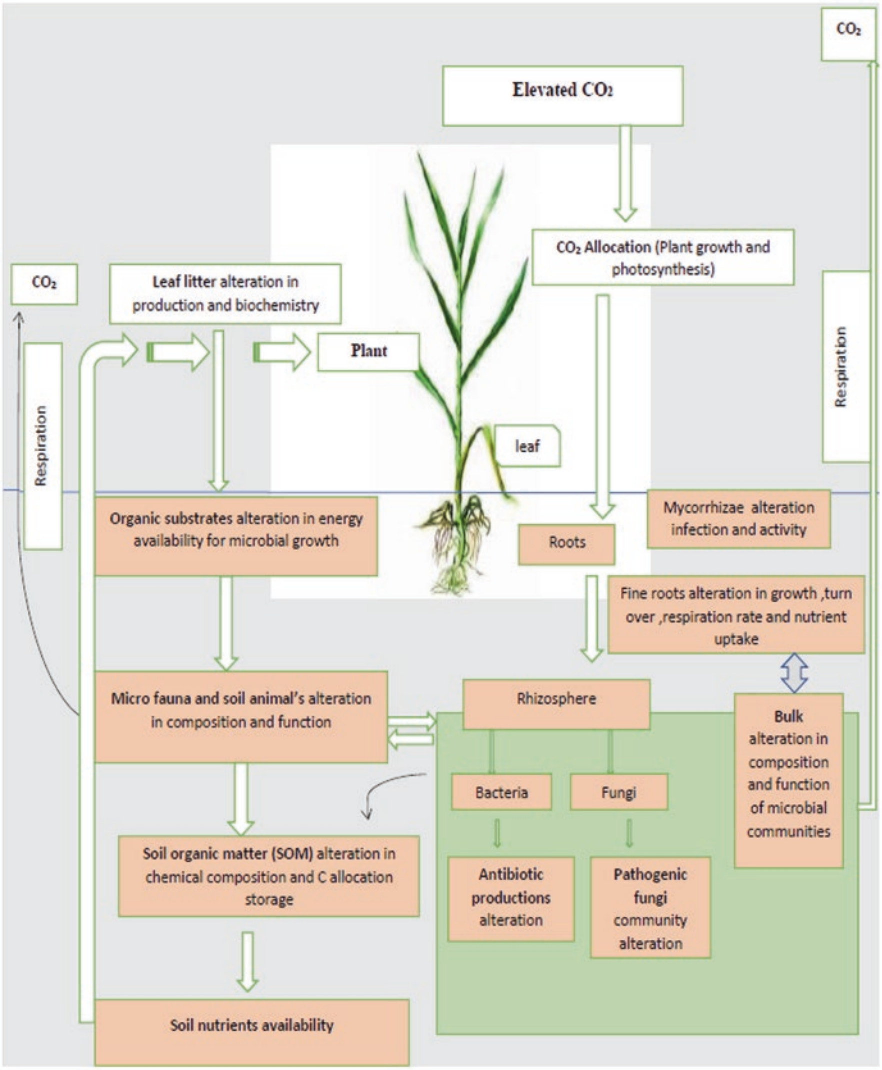

Fig. 3.4 Effects of elevated atmospheric CO_2 on microbial community

structure, size, and activity of the community. It further mediates ecosystem feedbacks that regulate the cycling of C and N (Phillips et al. 2006; Drigo et al. 2008; Nguyen et al. 2011; Xiong et al. 2015; Calvo et al. 2017). Sulieman et al. (2015) reviewed the benefits of elevated CO_2 on N_2-fixing leguminous symbioses. They concluded on the basis of previous results that elevated CO_2 have beneficial effect on symbiotic legumes. The effect will be on leaves, root, nodules, and rhizosphere as shown in Fig. 3.5. e[CO_2] affect soil nitrogen (N) cycling by altering N-losses from terrestrial ecosystems. Soil organic matter dynamics were also affected by elevated CO_2. Nevada Desert Free-Air Carbon dioxide Enrichment (FACE) Facility (NDFF) reported greater ecosystem C and N concentrations as it was exposed to elevate CO_2 for 10 years (Tfaily et al. 2018).

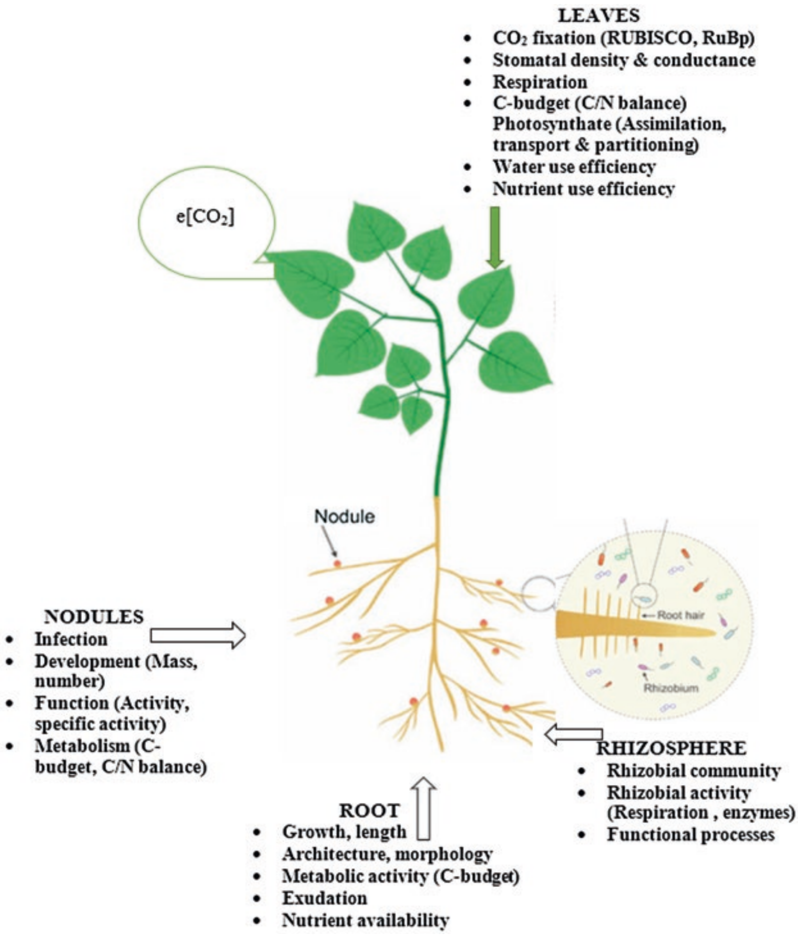

Fig. 3.5 Elevated carbon dioxide concentration and different morphological, physiological, and biochemical parameters in legume crop

3.4 e[CO_2] and Plant Enzymes

The effect of e[CO_2] has been also seen at enzymatic level. The enzyme used in C_3 pathway is ribulose 1,5-bisphosphate carboxylase/oxygenase (RuBisCO) which is capable of performing two distinct reactions; one leads to formation of two molecules of PGA provided that CO_2 is the substrate, while the other leads to one molecule of PGA and phosphoglycolate provided O_2 is the substrate. When CO_2 is deficient, RuBP performs oxygenase reaction resulting in less CO_2 fixation and release of CO_2 in process called photorespiration. The photosynthetic activity of C3 plants decreases considerably with decrease in CO_2 because of RuBisCO sensitivity to O_2, whereas it increases under elevated CO_2 levels since RuBisCO gets saturated with CO_2 and is forced to perform carboxylation (Ainsworth and Rogers 2007). RuBisCO of C4 plants is almost 12–20 times greater than that for C3 plants. Information from IPCC suggests that CO_2 concentration will change from 6.3 to 15 mM at active site of RuBisCO of C_3 plants by the end of the century. This scenario will result in an increase in C3 photosynthesis because of increase in the rate of carboxylation reaction as RuBisCO will get substrate saturated at elevated CO_2 levels. Moreover, oxygenation reaction of RuBisCO will be inhibited reducing CO_2 loss (Long et al. 2004). To study the effect of elevated CO_2 on C3 plants photosynthesis and stomatal conductance, usually FACE experiments are used. FACE experiments help to simulate the impact of future elevated CO_2 levels by providing more realistic conditions (Ainsworth et al. 2006). Guard cells sense CO_2 because of their inherent property as they are more responsive to intercellular CO_2 as compared to CO_2 at leaf surface. Assmann (1999) reported that if the membrane potential of guard cells is made less negative or in other words is depolarized, it will result in stomatal closure. The activity of inward rectifying K+ channels is decreased under increased CO_2 levels, whereas the activity of outward rectifying K+ channels increases as observed through electrophysiological studies. The greater the depolarization of membrane potential of guard cells, the greater will be the reduction in stomatal aperture. It is yet not clear as controversies still continue whether or not photosynthetic metabolites and processes have an effect on the response of guard cells to elevated CO_2 levels. Calcium sensitive and insensitive phases may also be used as response mechanism by guard cells against elevated CO_2 levels. Zheng et al. found that long-term exposure to elevated CO_2 levels resulted in reduced stomatal conductance in soybean. They reported that reduced rate of transpiration as a result of decreased stomatal conductance (gs) was partially responsible for poor N translocation. Furthermore, CO_2-induced downregulation of leaf photosynthesis was observed by the consistently declined leaf net photosynthetic rate (An) with elevated CO_2 concentrations. This could also be due to dramatic decrease in carboxylation rate (Vcmax) and the maximum electron transport rate (Jmax). Moreover, leaf photosynthesis downregulation was also partially attributed with reduced gs due to number of features such as declined stomatal density and stomatal area and changes in the spatial patterns of stomata. Since stomatal conductance is controlled by the integration of environmental and endogenous signals, Habermann et al. (2019)

studied the combined effect of e[CO_2] and +2oC warming on stomatal properties. Their results showed that under alone effect of elevated CO_2, transpiration rate was reduced with increased leaf temperature and maintenance of soil moisture which was due to reduced stomatal density, stomatal index, and stomatal conductance (gs). However, warming alone resulted to the enhanced PSII photochemistry and photosynthesis. The combined effect of warming and elevated CO_2 revealed that leaf temperature was increased compared to alone effects. This showed that stomatal opening under elevated CO_2 was not changed by warmer environment but in combination (e[CO_2] x warming) can significantly improve the whole plant functioning. Zheng et al. (2019) reported that elevated CO_2 concentrations exceeding the optimal not only reduced the stomatal conductance but also changed the spatial distribution pattern of stomata on leaves. It was observed that the maximum photosynthetic efficiency was 4.6% for C3 photosynthesis but 6% for C4 photosynthesis. This advantage over C3 will expire as atmospheric [CO_2] reaches 700 ppm. There is 60% increase in maximum photosynthetic efficiency in C4 plants compared to C3 plants. The C4 plants can photosynthesize with ~50% greater water-use efficiency, as C4 photosynthesis has the potential to assimilate an equal amount of CO_2 with only half the stomatal conductance.

3.5 e[CO_2] and Nutritional Quality

Elevated CO_2 have significant impact on nutritional quality of crop. Dong et al. (2018) reported that e[CO_2] resulted to the increased concentration of carbohydrates (glucose (13.2%), fructose (14.2%), total soluble sugar (17.5%)), total antioxidant capacity (59.0%), phenols (8.9%), flavonoids (45.5%), ascorbic acid (9.5%), and calcium (Ca) (8.2%). However, decreased concentration of protein (9.5%), nitrate (NO_3^{-1}) (18.0%), magnesium (Mg) (9.2%), iron (Fe) (16.0%), and Zn (9.4%) have been observed (Fig. 3.6). The increased concentration of sugars and decreased N content have been observed due to elevated CO_2 in different studies (Webber et al. 1994; Sun et al. 2012). Guo et al. (2015) work on rice revealed that elevated CO_2 increases the contents of Ca (61.2%), Mg (28.9%), Fe (87.0%), Zn (36.7%), and Mn (66.0%) in panicle. However, in stem Ca, Mg, Fe, Zn, and Mn were increased by 13.2, 21.3, 47.2, 91.8, and 25.2%, respectively. Similarly, they concluded that elevated CO_2 had positive effects on the weight ratio of mineral/biomass in stem and panicle. Grain quality of rice genotypes was investigated by Jena et al. (2018) and they reported that elevated CO_2 resulted to higher yield but lower nutrient harvest index and use efficiency values. Reduction in grain protein (2–3%) and Fe (5–6%) was observed in their findings under elevated CO_2. Analysis on dietary intake of iron, zinc, and protein under elevated CO_2 concentrations revealed that future human population will be zinc and protein deficient. Therefore there would be more chances of anemia prevalence. This risk will be more in South and Southeast Asia, Africa, and the Middle East (Smith and Myers 2018).

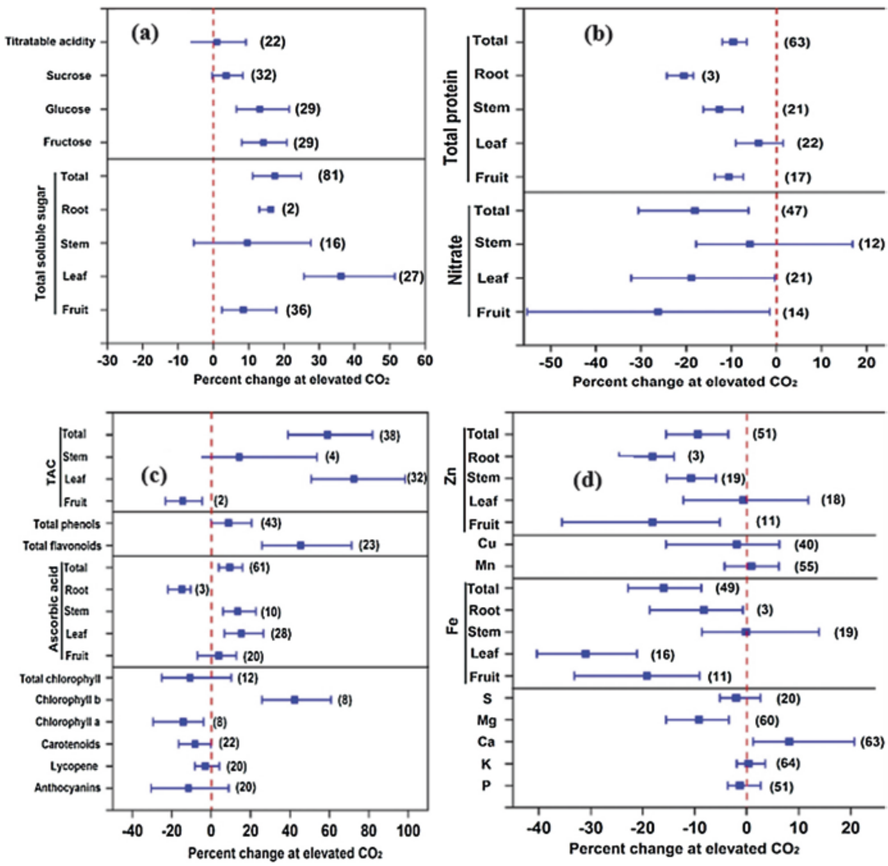

Fig. 3.6 Effect of e[CO_2] on (**a**) carbohydrates and acidity, (**b**) total protein and nitrate (NO_3^{-1}), (**c**) antioxidants, and (**d**) minerals in plants. (Source: Dong et al. 2018)

3.6 e[CO_2] and Modeling

In today's world models are the useful tools to study the impact of climate change on crop production and food security. Mechanistic eco-physiological models are being increasingly used for climate change impact on crop production (Tubiello and Ewert 2002). There is great emphasis on improvement of crop models so that climate change impact on crop production could be worked out. At first the crop models were being used for study of climate change impact on a small field. Far ahead efforts were made to evaluate the impact of climate variation on larger areas such as nations and large watersheds (Rosenzweig 1985; Hoogenboom et al. 1995; Parry et al. 2004; Rosenzweig and Tubiello 2007; Rosenzweig et al. 2013; Ruane et al. 2013). The CROPGRO model was used to stimulate the impact of increased CO_2 concentration on maize and to predict the climate change impact on maize production in the future (2080–2100). Model showed that yield of the crop reduced due to rise in temperature, but it increases at the same time due to enhanced CO_2 concentration and precipitation thus causing the counter balance. Change in CO_2 concentration greatly effects the plant growth and development, and this has been demonstrated by different scientists (Tubiello et al. 2007). The APSIM-Wheat model was used for studying the effect of elevated CO_2 on crop growth. Meanwhile, multimodel ensemble approach could be used to study the sole effect of elevated CO_2 (Ahmed et al. 2019). O'Leary and his co-workers have also used APSIM to study the impact of elevated CO_2 on crop growth and its interaction with RUE and TE (Anwar et al. 2007; O'Leary et al. 2015). This equation shows the light limited photosynthetic response to CO_2 concentration at 350 micro mol per mole.

$$\phi P = \frac{\left(CO_2 - T\right)\left(350 + 2T\right)}{\left(CO_2 + 2T\right)\left(350 - T\right)}$$

T temperature dependent CO_2 compensation point is given by

$$TE = \frac{\left(163 - T\right)}{\left(5 - 0.1T\right)}.$$

The experiment showed that under elevated CO_2 the transpiration efficiency (TE) increases. The APSIM-Wheat model showed 21% increase in wheat biomass in response to elevated CO_2.

3.7 e[CO_2] and Breeding Traits

Breeder in the future should focus on traits like plant architecture, branching geometry, root architecture, and stay-green traits to harvest the impact of elevated CO_2. Thus, to improve water-use efficiency (WUE) knowledge of genes should be utilized and a consolidated good implementing functional characterization of promising QTLs, high-throughput phenotyping, field validation of traits, improvements in photosynthetic efficiency and WUE by introducing C4-like characteristics in C3 cells, pyramiding and stacking of these traits into WUE coupled with modeling, providing important information for trait base selection-like root architecture model, water transport model and soil water model for improving crop water management under elevating atmospheric CO concentrations should be done.

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