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Effects of elevated carbon dioxide on plant physiology, nutritional quality and plant biotic factors: A review

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Abstract

Carbon dioxide, methane, and nitrous oxide are some of the important greenhouse gases among which CO₂ ranks first in percent contribution to promote global warming. CO₂ may contribute to the global warming but it is also a very important gas for plants to carry out photosynthesis. Furthermore, how a plant reacts to Increased CO₂ levels assist to determine future breeding strategies. Increased CO₂ concentrations are expected to boost plant physiological responses in general. A thorough perusal of current literatures on the effects of increasing CO₂ on crops has helped in understanding that an increased CO₂ levels can have both positive and negative impacts on the plant system. Elevated CO₂ conditions not only affect metabolic activities like photosynthesis, quality of protein produced in plants but also influence defense mechanism in plants against biotic (pest and plant pathogen) and abiotic stress; interaction of plant roots with soil microbes.

Keywords: Global warming, carbon dioxide, metabolic activities, biotic and abiotic stress

Introduction

Climate change has emerged as a significant hazard to the natural environment. The fundamental cause of climate change is a rise in carbon dioxide levels in the atmosphere. Prior to industrialization, the atmospheric CO₂ level was 260 ppm, but it has now surpassed 400 ppm (May 2021). It is anticipated to reach 550 parts per million within the next decade (IPCC 2013) [15]. The increase in atmospheric carbon dioxide levels has a substantial impact on plant growth and development. The effects of elevated CO₂ levels on plants and trees can be examined in confined environments such as greenhouse chambers and controlled environment chambers (CECs), where the experimental conditions can be closely monitored. It can also be evaluated in open top chambers (OTCs) and free air CO₂ enrichment facilities (FACE) which promote natural field conditions without altering the microclimate or biotic interactions. However, Screen Aided CO₂ Control Systems are being offered as a medium ground between OTC and FACE facilities, as OTC does not guarantee appropriate microclimate and FACE is expensive due to the high amount of CO₂ required, rising costs (Leadley *et al.*, 1997; Machacova 2010). In this review, we have discussed about effects of elevated carbon dioxide on various parameters like plant physiology, nutritional quality and biotic factors.

Effect of eCO₂ on plant physiological responses

Elevated CO₂ has beneficial effects on plant productivity, biomass, and yield (Reddy *et al.*, 2010, Tausz Posch *et al.*, 2020) [37, 44]. It helps in increasing photosynthetic rates (Drake *et al.*, 1997) [8] decreasing stomatal conductance (Drake *et al.*, 1997, Ainsworth and Rogers 2007, Lee *et al.*, 2020) [8, 1, 24], thereby improves water uptake and nutrient uptake efficiency (Drake *et al.*, 1997, Leakey *et al.*, 2009, Kant *et al.*, 2012) [8, 23]. In contrast to the previously stated general notion, several research have shown that increasing eCO₂ enhances stomatal conductance in stress conditions such as dry and warm drought occur (Purcell *et al.*, 2018, Konrad *et al.*, 2008, Medlyn *et al.*, 2013) [36, 21, 32]. Photosynthesis, the fundamental determinant of plant biomass and production, is regulated by a variety of factors, the most important of which is atmospheric carbon dioxide concentration. The increase in net photosynthetic rate caused by eCO₂ is principally attributable to a decrease in photorespiration and an increase in RuBisCO carboxylation activity. However, this rise in photosynthetic rate does not correspond to a continuous increase in eCO₂. Plants exhibit photosynthetic acclimation after extended eCO₂ exposure, resulting in a decrease in photosynthetic activity (Drake *et al.*, 1997, Kirschbaum 2010) [8, 20] due to a limitation of maximum carboxylation rate (V_{cmax}) by decreasing RuBisCO activity (Leakey *et al.*, 2009) [23], limited regeneration of RuBP

(Tausz *et al.*, 2013) [43]. This downregulation of photosynthetic potential is well described in an experiment performed at the Poplar Free Air CO₂ Enrichment (PopFACE) facility, where there is an initial increase in the rate of photosynthesis under eCO₂ (38 percent increase in A_{sat}) that later decreases due to the concurrent decrease in maximum capacity for carboxylation (V_{cmax}) and maximum rates of electron transport (J_{max}), which is related to the activity of RuBisCO and regeneration of RuBP (Long, 2003) [27]. Similarly, Zheng *et al.* 2019 [53] observed a decrease in photosynthesis in a soybean crop cultivated under eCO₂ circumstances, which is corroborated by a decrease in net photosynthetic rate (A_n). The reduction in maximum carboxylation rate (V_{cmax}) at 600 ppm and maximum electron transport rate (J_{max}) at 400 ppm of eCO₂ was linked to the downregulation of photosynthetic rate. Other factors that contribute to the decrease in A_n include changes in stomatal conductance (G_s), stomatal density, stomatal area, and stomatal distribution, reduced mesophyll tissue, and lower nitrogen availability (Zheng *et al.*, 2019) [53]. Kirschbaum *et al.* (2010) [20] observed that increasing photosynthesis (+30%) increased the relative growth rate by up to 10%, which can translate into an increase in absolute growth during the plant's exponential development phase. A meta-analytic review by Zhang *et al.* (2021) [52] has shown increased photosynthetic rates up to 28.6% under elevated carbon dioxide conditions (+670ppm) along with improved water use efficiency up to 58.6%. C3 plants were shown to be more responsive than C4 plants, as C3 plants do not exhibit a saturation effect for carbon fixation under ambient circumstances. eCO₂ conditions improve overall net photosynthetic rate in *Brassica juncea* by 50% (Ruhil *et al.*, 2014) [38], while decreasing stomatal conductance and transpiration rate, hence improving photosynthetic water use efficiency. As a result of the increased leaf area index, it also resulted in more biomass and seed output. Higher carbon uptake by plants under eCO₂ conditions is ascribed to increased biomass and yield. A favorable association occurs between increased biomass, yields, and photosynthetic rate in CO₂ enrichment experiments (Ghini *et al.*, 2015, Kellner *et al.*, 2019, Tausz Posch *et al.*, 2020) [10, 19, 44, 43]. Pandey *et al.* (2017) [34] revealed that eCO₂ wheat crop had a good effect on belowground biomass (+24%) and aboveground biomass (+15%), as well as an increase in grain production (+35%), inflorescence weight (+27%), and harvest index (+11.4%). Similarly, under eCO₂ there was an increase in belowground biomass of up to 22 to 38 percent in poplar trees, and overall biomass increase was greater than under ambient conditions (Calfapietra *et al.*, 2003) [5]. Ainsworth and Long (2020) [2] observed an 18% increase in yield of 18 C3 crop species in the presence of adequate water and nutrients in a meta-analytic review. Ghini *et al.* (2015) [10] investigated the effects of eCO₂ on two cultivated coffee varieties, Catuaí and Obatã, and observed an increase in growth metrics such as plant height and stem girth. It was also found that the fertilising impact of eCO₂ increased crop yields by up to 14.6 percent for Catuaí and 12 percent for Obatã.

Effect of eCO₂ on nutritional quality

In general, increased CO₂ has a detrimental impact on plant nutritional quality since it leads to a decrease in nitrogen, protein, and mineral content (Lee *et al.*, 2020, Loladze 2014) [24, 26]. The mechanisms responsible for reduced nitrogen and

protein content could be the diluting impact of eCO₂ caused by carbohydrate buildup or the limited plant uptake of minerals (Taub *et al.*, 2008) [42]. Other factors that may be responsible for the decrease in nutritional quality include a restriction in transpirational flow in xylem vessels or an altered distribution of nutrients in plant tissues (McGrath and Lobell 2013) [31]. Reduced nitrogen assimilation as a result of carbon dioxide acclimatization results in the depletion of organic N compounds such as proteins, which eventually impacts food quality (Bloom *et al.*, 2010) [3]. The increase in the C:N ratio caused by increased carbon assimilation under eCO₂ resulted in a 39.7 percent decrease in nitrogen concentration, whereas magnesium, phosphorous, and chlorophyll content were negatively affected (Lee *et al.*, 2020) [24]. Reductions in zinc and iron content have been found in C3 and legume crops, with C3 crops showing a higher reduction than legume crops and C4 plants showing only a loss in iron content. Reduction of protein content is less influenced in leguminous crops due to increased nitrogen (N₂) fixation, whereas non-leguminous C3 crops are severely affected due to lower N₂ fixation (Myers *et al.*, 2014). Leguminous crops do not show significant protein reduction owing to their increased nodulation activity (Ainsworth and Long 2020) [2]. Similarly, Loladze (2014) [26] observed that eCO₂ had a detrimental influence on plant mineral content up to 8%, with a considerable drop in key minerals such as Ca, K, Zn, and Fe, as well as an increase in carbohydrate to minerals ratio. Zhu *et al.* (2018) [54] investigated the effects of eCO₂ on grain quality in 18 cultivated rice lines and observed a significant decrease in proteins, minerals such as Fe and Zn, vitamin B (B1, B2, B5, and B9), but a rise in vitamin E content. Broberg *et al.* (2017) [4] reported a decrease in mineral concentrations such as N, Fe, S, Zn, and Mg in a meta-analysis report. In contrast, eCO₂ has favourable benefits such as improved strawberry flavour due to an increase in glucose, fructose, sucrose, and other total sugars content (Wang *et al.*, 2004) [45]. Almuhyawi *et al.* (2020) investigated the effects of eCO₂ on three broccoli sprout cultivars and observed an increase, not only in biomass and photosynthesis but also in amino acid derived glucosinolates and other nutritional aspects, which improved the anti-cancer and anti-inflammatory properties of the broccoli sprout cultivars. Jing *et al.* (2020) observed an improved taste of rice as well as improvements in grain characteristics such as grain length and width under eCO₂. The oil content of soyabean seed increased with an increase in oleic acid content, but protein and amino acid content decreased (Li *et al.*, 2018). Strawberries cultivated with eCO₂ showed higher amounts of polyphenols, flavonoids, and anthocyanins, which improved the overall appearance, aroma, and nutritional quality of the fruits (Wang & Bunce., 2004) [45].

Effects of eCO₂ on plant biotic factors

Pests

The performance of insect herbivores is influenced by eCO₂ as it affects the growth and development of insect herbivores and their feeding habits, fecundity, reproduction, survival rate and mortality. (Senthil-Nathan., 2021) [40]. The consumption rate of insects increases as the plant nutrient quality declines owing to the dilution effect caused by eCO₂ on proteins, nutrients, increased C:N ratio and secondary metabolites (Chen *et al.*, 2005) [6]. When exposed to eCO₂ conditions

plant-pest interactions are influenced by the changes in C:N ratio, production of primary and secondary metabolites which plays a key role in plant defense mechanisms (Zavala *et al.*, 2016) [50]. Plants grown under eCO₂ had higher carbohydrate content and lower nitrogen content due to improved photosynthetic rate (Reddy *et al.*, 2010, Xu *et al.*, 2019) [37]. In order to compensate for nutritional requirements, insects feed more in plants exposed to eCO₂ (Ainsworth and Rogers 2020) [2], extending their time of growth and development (Xu *et al.*, 2019). Plant defence mechanisms against insects are controlled by phytohormonal pathways such as Jasmonic acid (JA), salicylic acid (SA), and ethylene signalling (Wu *et al.*, 2010). Johnson *et al.* (2020) found that eCO₂ suppressed the jasmonic acid pathway in *Medicago sativa*, while simultaneously increasing the relative growth rate in *Helicoverpa armigera* by up to 66 percent when they feed on plants exposed to eCO₂. Xu *et al.* (2019) investigated the effects of eCO₂ on maize and found an increase in defensive chemicals such as jasmonic acid content and total phenolics content, as well as an increase in defensive enzyme activity of peroxidase, polyphenol oxidase, phenyl alanine ammonia lyase, and proteinase inhibitors, which confers resistance to the chewing insect *Ostrinia furnacali*. Plant vulnerability to biotic agents changes as eCO₂ alters the generation of biotic stress-induced defence hormones including jasmonic acid (JA), which confers resistance to *Spodoptera litura* in tobacco but not in melon (Zhang *et al.*, 2020) [51]. Guo *et al.* (2012) [12] observed that tomato plants grown in eCO₂ conditions have reduced resistance to *Helicoverpa armigera* due to decreased levels of JA and JA-induced defensive enzymes. Ghini *et al.* (2015) [10] found a considerable reduction in the incidence of leaf miners in two Coffee cultivars throughout the critical time of pest occurrence under eCO₂.

Diseases

Many studies have revealed that eCO₂ has an impact on plant pathogen interactions (Luck *et al.*, 2011, Itagaki *et al.*, 2015) [28, 16]. Phytohormones such as salicylic acid (SA), jasmonic acid (JA), and ethylene affect plant defence systems (Gimenez- Ibanez and Solano 2013) [11]. SA controls systemic acquired resistance (SAR) against biotrophic infections in plants, whereas JA controls induced systemic resistance (ISR) against necrotrophic pathogens and herbivores (Pieterse *et al.*, 2012) [35]. Plants exposed to increased CO₂ levels have varying effects on SA and JA concentrations, activating plant defence mechanisms via increased transcript expression of pathogenesis related proteins (Eastburn *et al.*, 2011, Sun *et al.*, 2013) [9, 41], as seen in mustard crop grown in eCO₂ conditions, where the transcript levels of PR-1, PR-2, and NPR-1 were higher due to the increased SA levels. Despite increasing JA levels under eCO₂, NPR-1 inhibition of PR-12 and PR-13 lowered transcript levels of JA-induced pathogenesis associated genes (PR-12 and PR-13). The increased PAL activity is responsible for the considerable increase in SA concentrations in non-infected plants cultivated under eCO₂. However, after *Alternaria brassicae* pathogen infection in mustard crop, SA concentrations reduced dramatically while JA concentrations increased in eCO₂ conditions. The combination of these phytohormonal alterations and induced PAL activity reduced the disease severity of alternaria blight in mustard by up to 29.57 percent (Mathur *et al.*, 2017). Due to increased total phenol concentrations, higher PAL activity, and high epicuticular

wax, Mathur *et al.* (2013) [29] observed that mustard plants cultivated in eCO₂ exhibited a decreased incidence and severity of *Alternaria* blight produced by *Alternaria brassicae* and Downy mildew induced by *Hyaloperonospora brassicae*. However, white rust caused by *Albugo candida* increased in mustard cultivated in eCO₂, possibly due to increased sugar availability (Mathur *et al.*, 2013) [29].

Soil microbes

C3 crops cultivated in high CO₂ conditions have significantly higher levels of non-structural carbohydrates, resulting in carbohydrate-rich soil exudates that promote crop-microbe symbiosis (Ainsworth and Long 2020) [2]. Microbe activity is limited due to a lack of labile C and energy (Schimel and Weintraub 2003) [39]. Microbial activity in the rhizosphere can be boosted by the emission of carbon-rich soil exudates (Kuznyakov and Blagodatskaya, 2015) [22]. He *et al.* (2013) studied the impact of eCO₂ on soil microbial activity in a soyabean crop and observed an increase in functional genes involved in C fixation, C degradation, and other nitrogen cycling processes. The enhanced availability of C aided in efficient nitrification under eCO₂ circumstances, enhancing the *Novosphingobium* genera microbial activity and nitrogen fixing capabilities (He *et al.*, 2013). Similarly, eCO₂ circumstances increased the microbial communities of Bacilli and Betaproteobacteria (Da Costa *et al.*, 2018) [7]. The rhizosphere of *Robinia pseudoacacia* was negatively impacted by heavy metal toxicity produced by Cd and Pb, leading in a decrease in microbial abundance and activity. However, eCO₂ increased soil fertility and rhizospheric conditions, resulting in an increase in organic compounds as well as an improvement in microbial abundance, biomass, and activity (Huang *et al.*, 2017) [17]. Williams *et al.* (2018) [46] studied the effects of eCO₂ in *Arabidopsis*, resulting in higher rhizosphere colonization of *Pseudomonas simia* WCS417 due to better rhizosphere deposits. eCO₂ circumstances had no significant effect on soil microbial populations or the rhizosphere of *Bothriochloa ischaemum*, according to Xiao *et al.* (2017) [48].

Conclusion

Carbon dioxide emissions have risen to over 400ppm, up from 250ppm as predicted in the 1960s, and it may can rise to atmospheric 550ppm in the coming decade (IPCC 2013) [15]. The rise in CO₂ levels has become a major driving force with long-term effects on plant physiology, nutrition, and pathogen interactions. A thorough study on works of elevated CO₂ on plant system suggested that genes governing photosynthesis, carbohydrate metabolism, plant defence pathways, and secondary metabolite production have been upregulated (Eastburn *et al.*, 2011) [9]. eCO₂ conditions influence photosynthetic rate and water use efficiency to boost plant productivity. Plant defence system against biotic or abiotic stress has been found to be stimulated by eCO₂ conditions by manipulating phytohormone concentrations, as well as phytohormonal crosstalk. Consequently, we can say that a thorough understanding of the underlying mechanisms by which eCO₂ affects plant defence pathways will aid in the development of crops that are resistant to adverse conditions. However, the nutritional aspects of plants grown in eCO₂ must be emphasised in order to improve crop quality in the face of adversely changing climate scenarios. Integrating genomics, transcriptomics, proteomics, and metabolomics

with eCO₂ analysis over plant ecosystems would aid in understanding morphological, biochemical, and physiological changes in plants as well as evaluating crop responses to climate change.

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