International Journal of Plant and Environment
Vol. 3, No. 2 (2017), 73-77

Carbon Di Oxide Fertilization: Effects on Plant Productivity

Supriya Tiwari* and N.K. Dubey

Department of Botany, Institute of Science, Banaras Hindu University, Varanasi-221005, INDIA

Publication Info

***Article history*:**
Received : 14.05.2017
Accepted : 30.06.2017
DOI : https://doi.org/10.18811/ijpen.v3i02.10440

***Key words*:**
Biofuels
C_3 plants
C_4 plants
Carbon dioxide (CO_2)
Photosynthesis
Productivity

Corresponding author:
Dr. Supriya Tiwari
Ph. +91 9453886448
Email: supriyabhu@gmail.com

Abstract

Increasing Carbon dioxide (CO_2) is an important component of global climate change that has drawn the attention of environmentalists worldwide in the last few decades. Besides acting as an important greenhouse gas, it also produces a stimulatory effect, its instantaneous impact being a significant increase in the plant productivity. Atmospheric CO_2 levels have linearly increased from approximately 280 parts per million (ppm) during pre-industrial times to the current level of more than 390 ppm. In past few years, anthropogenic activities led to a rapid increase in global CO_2 concentration. Current Intergovernmental Panel on Climate Change (IPCC) projection indicates that atmospheric CO_2 concentration will increase over this century, reaching 730-1020 ppm by 2100. An increase in global temperature, ranging from 1.1 to 6.4°C depending on global emission scenarios, will accompany the rise in atmospheric CO_2. As CO_2 acts as a limiting factor in photosynthesis, the immediate effect of increasing atmospheric CO_2 is improved plant productivity, a feature commonly termed as "CO_2 fertilization". Variability in crop responses to the elevated CO_2 made the agricultural productivity and food security vulnerable to the climate change. Several studies have shown significant CO_2 fertilization effect on crop growth and yield. An increase of 30 % in plant growth and yield has been reported when CO_2 concentration has been doubled from 330 to 660 ppm. However, the fertilization effect of elevated CO_2 is not very much effective in case of C_4 plants which already contain a CO_2 concentration mechanism, owing to their specific leaf anatomy called kranz anatomy. As a result, yield increments observed in C_4 plants are comparatively lower than the C_3 plants under similar elevated CO_2 concentrations. This review discusses the trends and the causes of increasing CO_2 concentration in the atmosphere, its effects on the crop productivity and the discrepancies in the response of C_3 and C_4 plants to increasing CO_2 concentrations.

1. Introduction

Global food security is a topic of concern for the environmentalists, agriculturalists and economists in near future. With the current trends of population growth, the world food production will have to be doubled to feed the total population by 2025 (FAO, 2009). As the arable land is limited and cannot be expanded beyond a certain limit, increasing population imposes huge pressure upon the food production. Although global food production in the last half century has increased, one in seven people do not have enough food to eat, and further a billion people lack sufficient protein and energy in their diets (Godfray *et al.,* 2010). In addition to the escalating population and changing food habits (higher consumption of meat and dairy products), increased food demand, increased non-food applications such as biofuels, urbanization, soil erosion and climate change are potential constraints to food security (Parry and Lea, 2009; Tilman *et al.,* 2011). Therefore, a key challenge to achieve food security for the present as well as future generations is to increase the global food production.

Climate change has affected the food security either directly or indirectly. A substantial body of literature shows that the earth's climate has changed since the middle of the nineteenth century (Screen and Simmonds, 2010; Rohde *et al.,* 2013). The major components of climate change include elevated atmospheric carbon dioxide concentrations (elevated CO_2), warming, and altered precipitation patterns, as well as their interactions within and with other environmental factors (IPCC, 2013). Based on updated information, with increase in global atmospheric CO_2 concentrations by 43% from the pre-industrial level of 280 ppm in 1750 to the present level of 400 ppm (an annual increase of 1.35%), the global CO_2 concentration has increased by about 1.55 ppm CO_2 per year over the past 55 years. It continues to be elevated at an unprecedented pace of ~1.0 ppm per year, as a result of further increase in the cumulative emissions of CO_2 to the atmosphere during the 21st century (400 ppm in 2011 vs 936 ppm in 2100 (IPCC, 2013; NASA, 2014).

2. CO_2 Fertilization

Photosynthesis is one of the fundamental biological processes of the plants that play a crucial role in determining the productivity of the plants. Several studies have shown that elevated CO_2 has a positive effect on the rate of photosynthesis in plants (Kant *et al.,* 2012; Xu *et al.,* 2015; Kumar, 2016). Elevated CO_2 can stimulate plant growth by providing additional carbon, the phenomenon termed as CO_2 fertilization effect. The CO_2 fertilization assist the plants by mitigating wide-ranging abiotic stresses including O_3 stress through certain mechanisms which are still under investigation (AbdElgawad *et al.,* 2016). Researchers have shown that elevated CO_2 brings about a few modifications in targeted plant's physiological and biochemical processes which help in partial amelioration of O_3 injury (Xu *et al.,* 2015; Hager *et al.,* 2016). Plants growing under stress generally accumulate unnecessary ROS, which is in excess of the scavenging capacity of the plant's intrinsic defense system (enzymatic and non enzymatic antioxidants) (Sharma *et al.,* 2012; Tripathy and Oelmuller, 2012). It has been suggested that elevated CO_2 helps in detoxifying ROS produced under O_3 stress (Kumari *et al.,* 2013). Effect of elevated CO_2 in mitigating other environmental stresses is also well documented (Kant *et al.,* 2012; Xu *et al.,* 2015). In addition to providing extra C, elevated CO_2 induces stomatal closing. This improves water use, protects against drought stress, and helps to explain efficiency reduced impact of ozone stress (reduced uptake). However, reduced oxidative damage and ROS levels under elevated CO_2, probably involves so called non-stomatal factors (Ghannoum, 2009), including metabolic changes. More specifically, increased C availability, possibly resulting in an increased supply of defense (antioxidant) molecules, is often held primarily responsible for improved protection against oxidative damage in elevated CO_2.

The stimulation of light saturated photosynthetic CO_2 assimilation rate is a general response of plants to CO_2 enrichment with an average 31 % increase observed by Ainsworth and Rogers (2007). However, the magnitude of response varies with different plant functional types (PFTs), with maximum for trees and C_3 grasses, moderate for shrubs, C_3 and C_4 crops and legumes and minimum for C_4 grasses (Ainsworth and Rogers, 2007; Xu *et al.,* 2015). Robinson *et al.* (2012), through the meta-analysis of 152 plant species, found the largest and most consistent differences between C_3 and C_4 plant groups. Plants with a C_4 photosynthetic mechanism are adapted for low CO_2 environments and contain a biochemical pump that concentrates CO_2 at the site of carboxylation, thus reducing carbon loss through photorespiration. At current levels of CO_2, the carboxylation function of RuBisCO in C_4 plants is thought to be near saturation. C_3 plants do not possess this CO_2 concentrating ability, and carbon gains are expected under elevated CO_2 as the concentration gradient of CO_2 from the air to the site of carboxylation increases. Of 365 C_3 plant responses and 37 C_4 plant responses to elevated CO_2 measured, on average, plant biomass was significantly increased in C_3 species but was unchanged in C_4 species (Robinson *et al.,* 2012). In another study, meta-analysis of C_3 and C_4 responses restricted to the Poaceae found that while C_3 plant biomass increased by 44 % in response to elevated CO_2, C_4 biomass increased by 33 % (Wand *et al.,* 1999).

3. C_3 and C_4 Photosynthetic Mechanism

Atmospheric CO_2 is fixed in the plants *via* two pathways, on the basis of which the plants as categorized as C_3 or C_4 plants. Atmospheric CO_2 is fixed either directly *via* RuBisCO (Ribulose 1,5 bisphosphate carboxygenase/oxygenase (C_3 photosynthesis), or indirectly after primary fixation by phosphoenol pyruvate carboxylase (PEPC). C fixed through this mechanism is subsequently re-released into adjacent cells which are not in direct communication with atmospheric CO_2 (C_4 photosynthesis).The majority of crop species (rice, wheat, grain legumes, canola, and all root crops) and ~ 85% of terrestrial plants use C_3 photosynthesis, while C_4 crops are a minority, represented predominantly by maize, sorghum, and sugarcane among economically important crops (Ehleringer *et al.,* 1991).

The photosynthetic efficiency of C_4 plants is approximately 50 % higher than those of C_3 plants due to difference in their respective mechanisms of carbon fixation (Kajala *et al.*, 2011). C_3 plants use only the Calvin cycle for fixing CO_2 which takes place inside the chloroplasts of the mesophyll cells. In C_4 plants, however, the photosynthetic activities are partitioned between mesophyll and bundle sheath cells and which are anatomically and biochemically distinct. The most important enzyme of photosynthesis, ribulose 1, 5 bisphosphate carboxygenase/ oxygenase (RuBisCO), is the fundamental C fixation enzyme which shows high affinity towards oxygen and CO_2. Due to the similar affinity of RuBisCO towards both these molecules, it is unable to distinguish O_2 from the CO_2 molecule resulting in unnecessary O_2 uptake, especially under hot and arid conditions. This oxygenation activity produces phosphoglycolate molecules, which are then broken down in a process referred to as photorespiration, an energy-consuming and wasteful process (Kajala *et al.,* 2011). Photorespiration has been identified as the bottleneck preventing C_3 plants from achieving full photosynthetic potential due to competition between CO_2 and O_2 at the C fixation site on the RuBisCO enzyme. C_4 photosynthesis evolved to ameliorate photorespiration by utilizing two distinct cell types namely, mesophyll cells and bundle sheath cells. These cells are arranged concentrically relative to the surrounding vascular tissue, a structure characteristic of C_4 plants known as 'Kranz anatomy' (Muhaidat *et al.,* 2007; Sage *et al.,* 2012). When atmospheric CO_2 is assimilated into the mesophyll cells, PEP carboxylase fixes C molecules as oxaloacetate. This reaction does not show any affinity to O_2 and is highly efficient (Sheen, 1999). The resulting C_4 compound is de-carboxylated within the bundle sheath cells, delivering higher concentrations of CO_2 directly to the RuBisCO enzyme while minimizing the oxygenation of RuBisCO. The increased concentration of CO_2 at the site of RuBisCO activity maximizes photosynthetic efficiency. These evolutionary adaptations in C_4 plants provide an advantage over C_3 photosynthesis while potentially improving water and nutrient use (Kajala *et al.,*, 2011). This CO_2 concentration mechanism prevalent in C_4 plants gives them an edge over the C_3 plants as far as the plant productivity is concerned. Zhu *et al.* (2008) reported a 60% increase in maximum photosynthetic efficiency in C_4 plants compared to C_3 plants. C_4 plants can photosynthesize with ~50% greater water use efficiency, as C_4 photosynthesis can assimilate an equivalent amount of CO_2 with only half the stomatal conductance (Sage and Kubien, 2003).

4. Effect of Elevated CO_2 on Plants

As discussed above, the positive effects of elevated CO_2 plants can be attributed to the fertilization effects of CO_2. Further, high CO_2 inhibits the oxygenation reaction in leaves, which results in carbon loss through photorespiration (Bowes, 1991). Additionally, elevated CO_2 decreases the stomatal conductance which effectively reduces water use per unit of CO_2 assimilated by the plant, thereby increasing the water productivity of both C_3 and C_4 species. Theoretically, at 25°C, an increase in CO_2 up to 550 ppm has the potential to enhance C_3 crop yields by 29 and 39 % at 700 ppm (Leakey *et al.,* 2009). On the contrary, the response of C_4 crops to elevated CO_2 has been the subject of debate among researchers. Since C_4 plants are photosynthetically saturated at current CO_2 conditions; predicted rises in atmospheric CO_2 would have no major impact on their C fixation rate, biomass production, and yield (Ainsworth and Long, 2005). In contrast, as C_3 plants are not photosynthetically saturated at present CO_2 levels, photosynthesis, biomass, and subsequent yields should increase with elevated atmospheric CO_2.

Recent evidence from free-air CO_2 enrichment (FACE) experiments suggests that high CO_2 does not stimulate C_4 photosynthesis and thus have no effect on productivity (Ainsworth and McGrath, 2010). Although C_4 crops may not exhibit an increase in photosynthetic activity, improvement of water use efficiency *via* reduction in stomatal conductance may still increase its yield under drought condition (Long *et al.,* 2004). However, no yield increase would be expected for well irrigated crops. Laboratory and field studies have shown that photosynthetic rates of C_3 plants were approximately doubled when plants grown at about 380 ppm CO_2 were exposed to 700 ppm CO_2 (Ainsworth and Long, 2005). Hager *et al.* (2016) also reported that C_3 grasses were more responsive than C_4 ones under elevated CO_2 as far as their productivity is concerned. In addition to this, photosynthetic nitrogen-use efficiency (PNUE) has also been found to increase in C_3 crops grown at high CO_2, which in turn optimize the allocation of nitrogen to maximize carbon gain (Leaky *et al.,* 2009). In addition, the evidences from FACE and chamber experiments suggest that stomatal conductance decreases at high CO_2 (Ort *et al.,* 2006; Ainsworth and Rogers, 2007), which results in the reduction of evapotranspiration (ET). The effect of decreased ET under high CO_2 environment results in a boost in soil moisture, as found in cotton (Hunsaker *et al.,* 1994), wheat (Hunsaker *et al.,* 1996), sorghum (Conley *et al.,* 2001) and maize (Leakey *et al.,* 2006). However, when plants are exposed to high CO_2 for extended period, the photosynthetic rates slow down due to the so called "acclimation" response (Long *et al.,* 2004; Reich *et al.,* 2006). This is thought to result from direct effects of sucrose on the transcription of genes encoding proteins involved in CO_2 fixation and electron transport activity (Moore *et al.*, 1999).

5. Conclusion

Positive effects of CO_2 on plants can be useful in finding a solution to the threats imposed on the plant productivity due to the global climate change. Global warming caused due to increasing atmospheric CO_2 concentration brings about certain changes in the meteorological conditions of the atmosphere which may cause some negative effects on plant performance. Increased temperature and altered precipitation pattern are two important parameters which adversely affect the plant productivity. CO_2 fertilization increases the plant productivity, not only by providing extra C for fixation, but also mitigates the negative effect of increased temperature and altered precipitation pattern on plant productivity. Elevated CO_2 increases the productivity of C_3 plants and also enhance the yield of C_4 plants grown under other environmental stresses.

References

AbdElgawad, H. Zinta, G. Beemster, T.S.G. Janssens, I.A. and Asard, H. 2016. Future Climate CO2 Levels Mitigate stress Impact on Plants: Increased Defense or Decreased Challenge? *Frontiers in Plant Science* **7**: 556.

Ainsworth, E.A. and Long, S.P. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist* **165**: 351-372.

Ainsworth, E.A. and Mcgrath, J.M. 2010. Direct effects of rising atmospheric carbon dioxide and ozone on crop yields. In: Climate Change and Food Security (pp. 109-130). Springer Netherlands.

Ainsworth, E.A. and Rogers, A. 2007. The response of photosynthesis and stomatal conductance to rising (CO_2): Mechanisms and environmental interactions. *Plant Cell and Environment* **30**:258-270.

Bowes G. 1991. Growth at elevated CO_2: photosynthetic responses mediated through Rubisco. *Plant Cell Environment* **14**: 795-806.

Conley, M.M. Kimball, B.A. Brooks, T.J. Pinter Jr, P.J. Hunsaker, D.J. and Wall, G.W. 2001. CO_2 enrichment increases water-use efficiency in sorghum*. New Phytologist* **151(2)**: 407-412.

Ehleringer, J.R. Sage, R.F. Flanagan, L.B. and Pearcy, R.W. 1991. Climate change and the evolution of C_4 photosynthesis. *Trends in Ecology and Evolution* **6**: 95-99.

FAO. 2009. The state of food insecurity in the world. Rome: FAO

Ghannoum, O.2009. C4 photosynthesis and water stress. *Annals of Botany* **103**:635–644.

Godfray, H.C.J. Beddington, J.R. Crute, I.R. Haddad, L. Lawrence, D. Muir, J.F. Pretty, J. Robinson, S. Thomas, S.M. and Toulmin, C. 2010. Food security: the challenge of feeding 9 billion people. *Science* **327**: 812-818.

Hager, H.A. Ryan, G.D. Kovacs, H.M. and Newman, J.A. 2016. Effects of elevated CO_2 on photosynthetic traits of native and invasive C_3 and C_4 grasses. *BMC Ecology* **16**:28-40.

Hunsaker, D.J. Hendrey, G.R. Kimball, B.A. Lewin, K.F. Mauney, J.R. and Nagy, J. 1994. Cotton evapotranspiration under field conditions with CO_2 enrichment and variable soil-moisture regimes. *Agricultural and Forest Meteorology* **70(1-4)**: 247-258.

Hunsaker, D.J. Kimball, B.A. Pinter, P.J. LaMorte, R.L. and Wall, G.W. 1996. Carbon dioxide enrichment and irrigation effects on wheat evapotranspiration and water use efficiency. *Transactions of ASAE* **39(4)**: 1345-1355.

IPCC. 2013. Summary for policy-makers. In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, editors. Climate Change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

Kajala, K. Covshoff, S. Karki, S. Woodfield, H. Tolley, B.J. Dionora, M. J.A. Mogul, R.T. Mabilangan, A.E. Danila, F.R. Hibberd, J.M. and Quick, W.P. 2011. Strategies for engineering a two-celled C_4 photo synthetic pathway in to rice. *Journal of Experimental Botany* **62**: 3001-3010.

Kant, S. Seneweera, S. Rodin, J. Materne, M. Burch, D. Rothstein, S.J. and Spangenberg, G. 2012. Improving yield potential in crops under elevated CO_2: integrating the photosynthetic and nitro- gen utilization efficiencies. *Frontiers in Plant Science* **3**:162- 170.

Kumar, A. 2016. Impact of climate change on crop yield and role model for achieving food security. *Environmental Monitoring and Assessment* **188**: 465- 478.

Kumari S, Agrawal M, Tiwari S. 2013. Impact of elevated CO_2 and elevated O_3 on *Beta vulgaris* L.: pigments, metabolites, antioxidants, growth and yield. Environ Poll. 174, 279-288.

Leakey, A.D.B. Ainsworth, E.A. Bernacchi, C.J. Rogers, A. Long, S.P. and Ort, D.R. 2009. Elevated CO_2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of Experimental Botany* **60**:2859-2876.

Leakey, A.D.B. Uribelarrea, M. Ainsworth, E.A. Naidu, S.L. Rogers, A. Ort, D.R. and Long, S.P. 2006. Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO_2 concentration in the absence of drought. *Plant Physiology* **140(2)**: 779-790.

Long, S.P. Ainsworth, E.A. Rogers, A. and Ort, D.R. 2004. Rising atmospheric carbon dioxide: plants FACE the future. *Annual Review of Plant Biology* **55**: 591-628.

Moore, B.D. Cheng, S.H. Sims, D. and Seemann, J.R. 1999. The biochemical and molecular basis for photosynthetic acclimation to elevated atmospheric CO_2. *Plant Cell Environment* **22**: 567-582.

Muhaidat, R. Sage, R.F. and Dengler, N.G. 2007. Diversity of Kranz anatomy and biochemistry in C_4 eudicots. *American Journal of Botany* **94**: 362-381.

NASA. 2014. *Global Climate Change: Vital Signs of the Planet.* Available at: http:// climate.nasa.gov/400ppmquotes[accessedDecember4,2014].

Ort, D.R. Ainsworth, E.A. Aldea, M. Allen, D.J. Bernacchi, C.J. and Berenbaum, M.R. 2006. SoyFACE: the effects and interactions of elevated [CO_2] and [O_3] on soybean. In J. Sberger, S. P. Long,R. J. Norby, M. Stitt, G. R.Hendry,&H. Blum (Eds.), Managed ecosystems and CO2 (pp. 71-86). Berlin, Heidelberg: Springer

Parry, M.A.J. and Lea, P.J. 2009. Food security and drought. *Annals of Applied Biology* **55(3)**: 299-300.

Reich, P.B. Hobbie, S.E. Lee, T. Ellsworth, D.S. West, J.B. Tilman, D. Knops, J.M. Naeem, S. and Trost, J. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO_2. *Nature* **440**: 922-925.

Robinson, E.A. Ryan, G.D. and Newman, J.A. 2012. A meta-analytical review of the effects of elevated CO_2 on plantarthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytologist* **194**:321-336.

Rohde, R. Muller, R.A. Jacobsen, R. Muller, E. Perlmutter, S. and Rosenfeld, A. 2013. A new estimate of the average earth surface land temperature spanning 1753 to 2011. *Geoinformatics & Geostatistics: An Overview* **1:** 1000101

Sage, R.F. and Kubien, D.S. 2003. *Quo vadis* C_4? An ecophysiological perspective on global change and the future of C_4 plants. *Photosynthetic Research* **77**:209-25.

Sage, R.F. Sage, T.L. and Kocaci- nar, F. 2012. Photorespiration and the evolution of C_4 photosynthesis. *Annual Review of Plant Biology* **63**:19-47.

Screen, J.A. and Simmonds, I. 2010. The central role of diminishing sea ice in recent Arctic temperature amplification. *Nature* **464** (7293): 1334-1337.

Sharma, P. Jha, A.B. Dubey, R.S. and Peesarakli, M. 2012. Reactive Oxygen Species, Oxidative damage, and Antioxidative Defense Mechanism in Plants under Stressful Conditions. *Journal of Botany* **2012:** 1- 26. Article ID 217037.

Sheen J. 1999. C_4 gene expression. *Annual Review of Plant Physiology and Plant Molecular Biology* **50**: 187-217.

Tilman, D. Balzer, C. Hill, J. and Befort, B.L. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences* **108**(50): 20260-20264.

Tripathy, B.C. and Oelmuller, R. 2012. Reactive oxygen species generation and signaling in plants. *Plant Signalling and Behaviour* **7**(12): 1621–1633.

Wand, S.J.E. Midgley, G.F. Jones, M.H. and Curtis, P.S. 1999. Responses of wild C_2 and C_3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology* **5**:723-741.

Xu, Z. Jiang, Y. and Zhou, G. 2015. Response and adaptation of photosynthesis, respiration, and antioxidant systems to elevated CO_2 with environmental stress in plants. *Frontier in Plant Science* **6**:701- 717.

Zhu, X.G. Long, S.P. and Ort, D.R. 2008.What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Current Opinion in Biotechnology* **19**:153-159.