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Elevated CO_2–Does it Really Matter for Plants That Are Already Experiencing Higher than Ambient Levels?

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Abstract: Atmospheric concentration of CO_2 has increased significantly over the past few decades and so have the concerns about the greenhouse effect and global warming. One of the extensively explored aspects is the response of ecosystem components in terms of performance and productivity. A host of information thus generated suggests a positive effect of elevated CO_2 on functioning of plants from seed germination through maturation vis-à-vis rhizospheric microbial functions. Amazingly, most (if not all) of the researches deal with plant responses to CO_2 at levels twice that of ambient with a view that fossil fuel burning and increased agricultural activity are adding substantially to the atmospheric CO_2. As such, hardly any attention has been paid to the contribution of soil respiration (includes that of microbes and plant roots) to CO_2 concentration within the soil matrix as well as above the soil surface. This study presents an analysis of the available literature to demonstrate that by default the plant communities are already functioning at elevated levels of CO_2. Any further increase due to human intervention (especially fossil fuel burning) may not have a significant effect on plant functions and productivity. Hence the potential dangers of elevated CO_2 resulting from fossil fuel burning should not be considered as alleviated through increased plant productivity.

Key words: Ambient CO_2, crop productivity, dark photosynthesis, global warming, greenhouse effect, rhizodeposition, soil organic matter, soil respiration

INTRODUCTION

Atmospheric concentration of CO_2 has increased significantly over the past few decades mainly because of increased fossil fuel burning vis-à-vis human development. In <50 years, CO_2 concentration has increased from 316 to 370 ppm with a current increase of about 1.8 ppm per annum[1]. The concentration of CO_2 is likely to double in the present century[2], especially if the pace of development continues; finding alternative ways of fuel/energy notwithstanding. This increase will enhance the global greenhouse effect and in changed distributions of rainfall and other weather components. These changes will have a significant bearing on terrestrial plants at both individual and ecosystem levels.

The research on effects of rising atmospheric CO_2 on plants and ecosystems took off in the late 1980s. A wealth of information now available shows a significant stimulation by elevated CO_2 of growth and development of plants, particularly of those with a C_3 photosynthetic system. A positive response of plants to elevated CO_2 is present in all types of vegetation [3]. Lawlor and Mitchell[4] concluded that crop yields would be 30-40 and 9% greater for C_3 and C_4, respectively, at 700 compared to that at 350 mmol mol^{-1} CO_2 if all other climatic factors were unchanged. A review of 430 individual experiments showed 30% increase in the productivity of most herbaceous plants in response to doubling of CO_2 [5]. Analysis of 55 experiments by Idso and Idso[6] revealed an increase of >200% in productivity at additional 600 ppm CO_2 under water limiting conditions. Not only the terrestrial plants, but those growing under submerged conditions also show a positive response to elevated CO_2[7,8]. The effect of CO_2 has been more when environmental factors are affecting the plant growth and development severely[9]. According to Bowes [10], the CO_2-enriched atmosphere of 21st century does not look to be a bleak prospect for most plants, or for agriculture. Instead, it might usher in a greener planet, though the species mix will change. Wittwer[11] summed up his observations by saying “rising level of atmospheric CO_2 is a universally free premium, gaining in magnitude with time, on which we can reckon for the future”.

There is no denying the fact that above-ambient levels of CO_2 have a positive effect on plant processes and rhizospheric microbial functions leading to improvement in plant/crop productivity. However, most of the information comes from studies conducted under

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controlled levels (ambient or above-ambient) of CO_2 and hardly any attention has been paid to CO_2 originating from soil respiration and its implications. The data being presented here is aimed at suggesting that rhizorespiration may significantly raise the levels of CO_2 within the plant canopy/stand. Hence, any further increase in atmospheric CO_2 through fossil fuel burning may or may not have a significant bearing on plant functions.

RESPONSE OF PLANTS AND PLANT PROCESSES TO INCREASING LEVELS OF CO_2

Remaining within the limits of expected rise in atmospheric CO_2 levels during the current century, most of the studies have been conduced at CO_2 levels twice that of ambient with a generalized but significantly positive response of plants and plant processes. Incidentally, however, the rate of CO_2 assimilation does not show a linear increase with the level of CO_2 as to result in increased plant productivity with unlimited increase in the latter. Presented below are few of the abundant examples suggesting that the plants and plant processes respond positively to CO_2 levels up to a certain limit beyond which the response is non-existent.

- Osmond *et al.*[12] reported quantum yield to increase significantly up to CO_2 600 ppm CO_2 only, any further increase in CO_2 had no effect.
- Frank and Bauer[13] studied the effect of 300 and 600 ppm CO_2 above ambient on dry matter yield of wheat under growth chamber conditions. In 5 of the 6 instances, increase in biomass was less at 600 than that at 300 ppm CO_2 above ambient.
- Cheng and Fuchigami[14] reported 50% increase in CO_2 assimilation at twice the ambient levels but only 11-19% increase at 1200 ppm of intercellular CO_2 in apple leaves.
- In *Sorghum bicolor*, Walting *et al.*[15] studied the effect of elevated CO_2 on the key elements of photosynthesis. Their results show that increase in intercellular CO_2 beyond a minimum did not have any effect.
- In *Amaranthus* and *Chenopodium*, the rate of C assimilation increased with intercellular CO_2 concentration and leaf temperature[16], the increase being significant at 31°C while no increase was observed >300 ppm at <23°C. Their results showed that gross photosynthesis will not increase beyond 400 ppm CO_2 at higher temperatures; while at lower temperatures the increase was virtually non-existent.
- The results presented by Gunderson *et al.*[17] support the contention that elevated CO_2 will have an effect on plants when they are CO_2 limited. They observed that elevated CO_2 had greater effect on photosynthetic parameters of upper parts of the plant canopy (where efflux from soil would not have made a major difference) than the lower canopy.
- In sunflower, Tezara *et al.*[18] measured the response of net photosynthetic CO_2 assimilation to intercellular levels of CO_2 (C_i) of up to 800 μmol mol^{-1} at 3 water stress regimes. Beyond 300 μmol mol^{-1} there was some positive effect in stressed plants, but almost no effect in unstressed plants.

The examples quoted above suggest that increase in CO_2 beyond twice the ambient levels will not lead to additional benefits. Hence, plants already experiencing twice the ambient levels of CO_2 or more may not benefit any further from the CO_2 being dumped into the atmosphere through fossil fuel burning or increased agricultural activity. An analysis of reported literature presented in the next section suggests that under normal agricultural conditions the plants may indeed be facing several times the ambient levels of CO_2.

SOIL AS A SOURCE OF CO_2

Soil represents the largest reservoir of organic C that is estimated at 1500 Pg to a depth of one meter. Hence fluxes between soil organic C and the atmosphere are important, the former showing a depletion with time unless augmented with organic amendments at regular intervals. However, the role of organic matter in elevating CO_2 concentrations at the leaf level has seldom been considered. This is important as CO_2 efflux of 727 mg m^{-2} will be sufficient to double its concentration in a cubic meter of the atmosphere. This calculation is based on the fact that I) atmospheric concentration of CO_2 is approximately 0.037% at present and ii) one m^3 (1000 L) of the atmosphere over 1 m^2 of land will contain 370 ml of CO_2, 727 mg CO_2, or 231 mg CO_2-C. This measure has been taken as most of the C_3 agricultural crops attain an average height of 1 m. The free movement of air across a crop stand can be considered as minimum while a decrease with height in the CO_2 gradient within the crop stand can develop depending upon the rate and extent of rhizorespiration (respiration by soil microorganisms and plant roots). Since, the rate of plant assimilation may not be commensurate with the rate of efflux, a temporary or prolonged build-up of CO_2 within the crop stand well above the levels saturating photosynthesis can be expected. Examples that follow suggest that soil respiration can be expected to elevate the CO_2 levels several folds. Indeed, the plants start experiencing elevated levels ever since the seed is sown as the CO_2 content of soil atmosphere is several times greater than that above the soil[19]. While reviewing the examples presented, it will be pertinent to mention that a gross CO_2 efflux of 727 mg m^{-2} will double its concentration in a cubic meter of the atmosphere as mentioned earlier.

- Kowalenko *et al.*[20] studied the effect of N fertilization on CO_2 evolution from soil in 3 consecutive years and reported an efflux of 16.5-26.8 kg CO_2 ha^{-1} day^{-1} which is equivalent to 1650-2680 mg m^{-2} day^{-1}.
- Huntjens[21] reported an efflux of 220 mg CO_2-C m^{-2} h^{-1} (5280 mg m^{-2} day^{-1}) from pasture soil profiles; efflux from arable soil being 1/3rd of this.
- Using ^{14}C-labelled plant residues and components, Azam *et al.*[22] showed 50% of the C applied as glucose, cellulose and wheat straw was respired as CO_2 within a week of incubation.
- Tans *et al.*[23] reported CO_2 efflux from soil equivalent to 60 Pg C yr^{-1}.
- Hanson *et al.*[24] reported an efflux of 3-22 g m^{-2} day^{-1} from different forest communities.
- Biedederbeck *et al.*[25] reported C mineralization equivalent to 1000-2700 m^{-2} day^{-1} to a depth of 0-7.5 cm.
- Lessard *et al.*[26] reported CO_2 efflux of 2.3 to 14.8 g m^{-2} day^{-1}
- Gorissen *et al.*[27] applied ^{14}C-labelled root material to soil at 0.1% and found CO_2 evolution from soil organic matter to be >600 mg m^{-2} day^{-1}; that from added root material was >450 mg m^{-2} day^{-1}.
- Edwards and Norby[28] reported CO_2 efflux of 0.4-0.75 μmols m^{-2} sec^{-1} from soil bearing Acer saplings.
- Curtin *et al.*[29] applied wheat straw at 2.8 tons ha^{-1}; after 70 days, 25% of the straw was lost i.e., 700 kg ha^{-1}. Assuming 50% C in straw and 50% of this being converted to CO_2 (rest transformed into microbial biomass and metabolites), 175 kg C would have been released as CO_2 ha^{-1} in 70 days. This amounts to 917 mg CO_2 m^{-2} day^{-1}. Roughly an equivalent amount was lost from the native soil organic matter giving a total of 1834 mg CO_2 being produced m^{-2} day^{-1}. A greater proportion of the respired C will end up in the atmosphere where a definite sink is available especially during the day time.
- Saggar *et al.*[30] studied basal respiration from 14 soils containing 3-10% organic C and found CO_2 evolution to vary between 9700-17000 mg m^{-2} day^{-1}.
- Knoepp *et al.*[31] studied CO_2 efflux from 5 forest stands and found the values to range between 186 and 310 mg C m^{-2} h^{-1}.
- Calderon *et al.*[32] reported CO_2 efflux of 30-120 mg m^{-2} hr^{-1} from soil surface.
- Prieme and Christensen[33] studied the effect of natural perturbations on CO_2 emissions from organic soils containing 20-49% C. CO_2 flux was around 1000-2000 mg m^{-2} day^{-1} from three different soils.
- Weiske *et al.*[34] studied efflux of CO_2 from fields cropped to barley, vetch/maize or wheat. The data presented showed an efflux of 100 to 240 kg CO_2-C ha^{-1} day^{-1} or 10-24 g CO_2 m^{-2} day^{-1}. The efflux was in the order wheat > barley > vetch/maize; maize showed the minimum efflux during a similar study period and was more during the summer months.
- Certini *et al.*[19] reported an efflux of CO_2 from soil under two types of forest trees to the atmosphere to vary between 0.1 and 1 g m^{-2} h^{-1} depending upon the month of determination. Concentration of CO_2 in the soil air increased with depth and could be up to 1.28% as compared to 0.03% in the air and upper soil layers. This gradient could play a significant role in CO_2 diffusion out of the soil into the atmosphere. Basal respiration could be as high as 220 mg CO_2 kg^{-1} dry soil day^{-1} from the top soil layer; average being *ca* 125 mg kg^{-1} day^{-1} (equivalent to 5500 mg m^{-2} day^{-1}) over a period of 42 days.
- Baggs *et al.*[35] showed CO_2-C efflux of 600-900 mg m^{-2} day^{-1} that is equivalent to 2200-3300 mg CO_2.

The examples given above are mainly from studies on unplanted soils. This situation will be different for planted soils that continuously receive C as rhizodeposits. It is a common knowledge that almost all organic C found in soil is primarily derived from plants in the form of root/shoot residues and root exudates. Kuzyakov and Domanski[36] reported that of the total C translocated below ground, 7-13% is ultimately found in roots, 2-5% exuded and 7-14% used up in root respiration. They reported a net C input by wheat into the soil of 1.5 to 2.4 tons ha^{-1} yr^{-1} depending on the method of measurement used. Keith *et al.*[37] reported rhizodeposition (dumping of carbonaceous materials into the rhizosphere) of 1000-1500 kg C ha^{-1} equivalent to 15-30% of that assimilated by plants. In some arable annual plants, 30-50% of the photosynthetic C is transported below-ground during their life cycle[38,39] leading to an increase in soil organic matter content[40]. The transport process is fairly rapid and within 30 minutes of applying ^{14}C pulse, the newly synthesized compounds can be detected below-ground[41].

A significant proportion (51 to 89% of the total CO_2 efflux from soil) of the rhizodeposits is lost through rhizospheric respiration; half of this coming from root respiration alone[42]. Huge amounts of rhizodeposits (1000-2500 kg ha^{-1}; 250-1250 kg C ha^{-1}) and the ease with which they are decomposed, will suggest their significant contribution to the build-up/maintenance of elevated CO_2 levels within the plant stand/canopy. Assuming that 90% of the C in rhizodeposits will be converted into CO_2, the net efflux of the latter could be 1650-4125 kg ha^{-1} or 165-413 g m^{-2} over one crop season that may last for 70-120 days. These are indeed high amounts of CO_2 (compared to 727 mg CO_2 m^{-3}) being released during the crop growth; residues left as root matter after harvest notwithstanding.

There is no doubt about the real raise in CO_2 concentration of the atmosphere due to fossil fuel burning and increased agricultural activity over the past few decades. This is also a fact that this increase will add to the greenhouse effect and global warming. However, in view of the above assertions, it would appear that the effect of predicted doubling of CO_2 on plant performance vis-à-vis different physiological and biochemical functions is probably much too over-emphasized. The fact remains that under natural conditions of organic matter dynamics, the plants are living in an environment with CO_2 levels much higher than those found in the atmosphere. Determinations made during the light hours may not give realistic picture of CO_2 levels within the plant stand/canopy, while during the night a major proportion of the CO_2 may represent microbial respiration. High levels of CO_2 thus expected within the crop stand will have implications not only to the so-called positive effects of twice the ambient levels of CO_2, but to the dark and photo-respiration as well. At CO_2 concentration of 1000 µmol mol^{-1}, for example, the dark respiration may be inhibited by 46%[43]; by extrapolation, the inhibition could be 95% at 3500 µmol mol^{-1} i.e., 10 times ambient. Under natural conditions of CO_2 concentrations that are several times higher than ambient, dark respiration may already be non-existent. Likewise, photo-respiratory losses of fixed C that may amount to 25% of the total[44] will be minimized to a significant extent. In the overall perspective, the crops growing on soils with high organic matter content (and thus more productive) may not respond to doubling of CO_2; reverse may be true for those growing under arid and semi-arid conditions and on soils with meager quantities of organic matter. Hence, for ecosystems with high soil organic matter content, the vegetation may not mitigate the negative environmental impact of elevated levels of CO_2 resulting from burning of fossil fuels.

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