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Elevated CO₂ and Stress Tolerance in Crop Plants with Particular Reference to Agro-climatic Conditions of Pakistan

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Abstract: One of the dramatic observations on response of plants to elevated CO₂ is their enhanced tolerance to stresses like light, temperature, salinity and nutrients. High temperatures and light intensity (like that in Pakistan) have generally a depressing effect on growth of plants, especially those having C₃ photosynthetic system. These plants have a lower optimum temperature for photosynthesis that is raised at elevated CO₂ thereby protecting the plants from being over-heated. In addition, the photorespiratory activities of C₃ plants at higher temperatures are curtailed in the presence of high CO₂ concentrations, thereby helping the plants conserve C and energy. Low as well as high light intensities are reported to limit photosynthesis at ambient concentrations of CO₂, while elevated CO₂ levels have a mitigating effect. Elevated CO₂ levels allow plants to live under light conditions insufficient to meet photosynthetic requirements, while under high light intensities photorespiratory activities are curtailed. Similarly, positive effect of elevated CO₂ on plant performance under conditions of limited water availability (e.g., because of soil salinity, drought) has consistently been reported. It is believed that the on-going rise in air's CO₂ content will protect trees from debilitating water stress. The water stress may not necessarily be that of drought, excessive irrigation may have negative effect as well and is reported to be mitigated by elevated CO₂. Plants growing under soil salinity stress have also been reported to benefit from elevated CO₂. The benefit is reported to be derived from the availability of more solutes for osmoregulation by reducing the transpirational intake of salts or by improving RUBISCO activity. In C₄ plants, elevated CO₂ helps overcome the leakiness induced by salt stress. In addition, positive effect of elevated CO₂ on root proliferation and root-induced microbiological and biochemical changes may help plants withstand salinity stress. One of the reasons for a more positive effect of elevated CO₂ on plants under growth limiting conditions is the enhanced root proliferation. Thus at low level of N availability that would generally limit plant growth, elevated CO₂ helps plants extract more N from soil by exploring a greater soil volume and stimulation of photosynthetic rates. This paper gives an overview of the available information on the subject vis-à-vis agroclimatic conditions prevailing in Pakistan.

Key words: Elevated CO₂, environmental stresses, drought, rhizodeposition, photosynthesis, salinity

Introduction

Pakistan is located between latitudes 23° 35 north and 37° 05 north and extends from longitude 61° east to 76° east with four distinctly different seasons that vary widely in humidity, temperature, and light intensity. The climate is mostly arid or semiarid with humid conditions restricted to some northern areas. The rainfall decreases from the Himalayas towards the south i.e. from 750 mm to 100 mm per annum. The terrain consists of Indus plain in the east, mountainous in the north and northwest, and Baluchistan plateau in the west. The temperature is highly variable ranging from several degrees below Celsius in the north to as high as 55 °C in the south and south-west regions. In the mainly agricultural areas i.e., plains that traverse the country from north to south, the extremes of temperature, humidity and light intensity are not uncommon. Likewise, a significant proportion of the agricultural lands (about 6.3

million hectares) are affected by salinity of different extent and the problem is getting aggravated due to rapid salinization of originally productive soils mainly because of the agroclimatic conditions including high temperatures and surface irrigation. Although irrigation has resulted in tremendous increase in crop yields on the short term, this has contributed to soil salinization and water-logging. This has been of considerable significance to agriculture in Pakistan where about 30% of the salt-affected area is canal irrigated. These environmental extremes have exerted a significantly negative effect on the agricultural productivity in the country.

The major reason for reduced agricultural productivity is the highly negative effect of environmental extremes/stresses on the photosynthetic activity of the plants. As a result it is not only the net accumulation of dry matter in the above-ground plant parts that is affected

negatively, but partitioning of photosynthates to the below-ground parts is reduced to a significant extent. The latter effect has a significantly negative bearing on the rhizospheric microbial functions and hence the nutrient acquisition by plants. Increase in the CO₂ concentration in the atmosphere is reported to mitigate the negative effects of environmental extremes/stresses on plant productivity. Under agricultural conditions of Pakistan, the major source of atmospheric or leaf level CO₂ is the soil organic matter that decomposes fairly rapidly. Therefore, in spite of the fact that increase in humus content is not visible under these conditions, a rapid build up of CO₂ levels in the crop canopy could help plants do better in terms of productivity. This paper reviews the causes of reduced agricultural productivity under stress situations and the role of elevated CO₂ in mitigating some of these effects vis-à-vis the agro-climatic conditions in Pakistan.

History of changes in atmospheric levels of CO₂ vis-à-vis growth and development of human population

Views about the composition of earlier atmospheres are conflicting, but the last 30 million years seem to have faced typically low levels of CO₂. Carbonate concentrations and $\delta^{13}\text{C}$ values in the mineral goethite suggest that the first terrestrial plants, living about 420 million years ago, faced CO₂ partial pressures that were 16-fold higher than the present (Yapp and Poths, 1992). Although major atmospheric changes are not novel, previously they occurred over thousands to millions of years, not decades. For the past two millennia, the CO₂ content of the earth's atmosphere has been fairly constant averaging 280 ppm. With rapid industrialization, however, this equilibrium has been disturbed over the last 250 years (Fig. 1). Presently, it stands at around 370 ppm, showing an increase of 100 ppm since 1700. During the last 25 years alone, a rise of *ca* 60 ppm in CO₂ concentration has been recorded, while an increase of *ca* 25 ppm occurred between the years 1900 and 1950. Hence, in less than 50 years, CO₂ concentration has increased from 316 to the present levels of 370 ppm with a current increase of about 1.8 ppm per annum (Kimball, 1997). According to King *et al.* (1992), without Divine intervention, the concentration of CO₂ is likely to double in the present century, especially if the current pace of development continues, finding alternative ways of fuel/energy notwithstanding.

The CO₂ concentration of the air started increasing as humanity embarked upon a course of unprecedented economic development that coincided with the increase in the burning of fossil fuels such as coal, gas and oil, expansion of agriculture, urbanization and deforestation

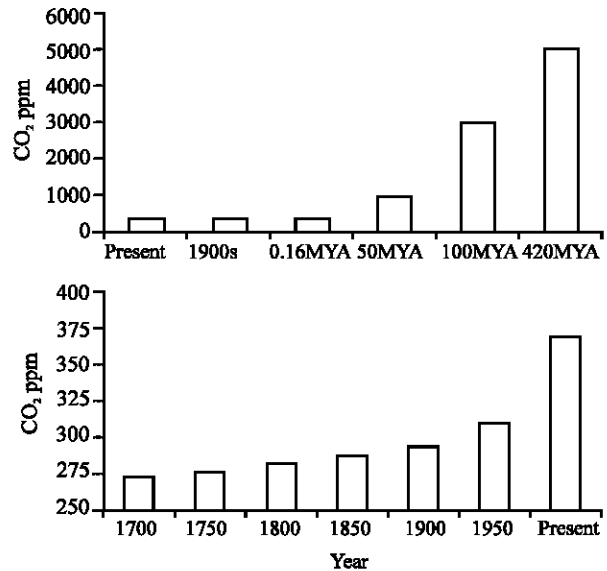


Fig. 1: Changes in CO₂ concentration over time

(Fig. 2). It is the human activities generating 5-8 Gt C yr⁻¹ that has made all the difference to the atmospheric CO₂ concentration over the past few decades. Interestingly, the increase in atmospheric CO₂ levels has coincided with human development that is bound to improve, especially in the present day developing countries with fast growing populations. As high population countries such as Nigeria, India, Pakistan, China, and Indonesia increase their standard of living, the energy consumption (90% produced by burning fossil fuels) will have a major implications for global CO₂ levels. The fossil fuel contributes 11.4 Gt ha⁻¹ of CO₂ whereas deforestation adds 4.6 Gt to the atmosphere. Of this, 9.4 Gt is being absorbed by oceanic and terrestrial biota, while about 6.6 Gt ha⁻¹ of CO₂ remains in the atmosphere leading to the increase mentioned. Thus in the foreseeable future with consistent population growth (Fig. 2) and drive towards higher standards of living, an increase in CO₂ concentration would appear inevitable.

Elevated CO₂ and the process of photosynthesis

During a greater part of the planet's history, terrestrial vegetation lived in an atmosphere that saturated photosynthesis. In contrast, present CO₂/O₂ regime restricts most vegetation to only 60-70% of its photosynthetic potential. Therefore, an increase in CO₂ concentration is bound to increase the photosynthetic efficiency of plants and hence an enhanced productivity vis-à-vis increase in below-ground plant activities (Fig. 3). Studies with a number of species have demonstrated that responses at the plant level translate into enhanced photosynthesis and growth at the canopy and community

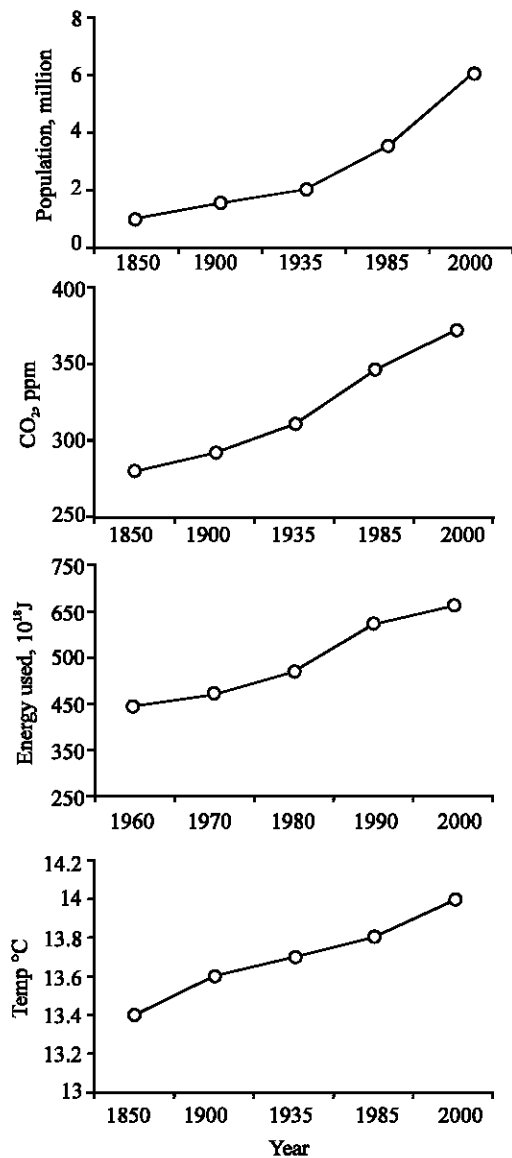


Fig. 2: Relationship between population growth, energy consumption, CO₂ levels and atmospheric temperature (a synthesis from literature)

level (Drake and Leadley, 1991). However, the response of plants to elevated CO₂ depends to a great extent on the photosynthetic system. The plants could be i) C₃ having a 3-carbon compound i.e., phosphoglyceric acid as the first product of photosynthesis, ii) C₄, having a 4-carbon compound i.e., malate or malic acid as the first product, or iii) CAM i.e., having crassulacean acid metabolism. A comparison of the three plant types is presented in Table 1. Approximately 95% of the terrestrial plants are C₃ species, 1 % C₄ and the remaining 4% have crassulacean acid metabolism (CAM plants). The C₄ and CAM plants

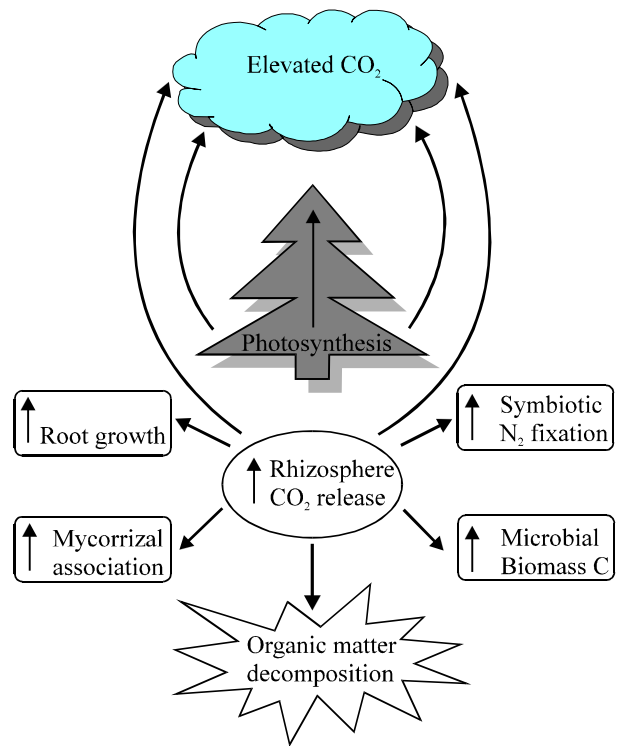


Fig. 3: Elevated CO₂, photosynthesis and rhizospheric microbial functions.

differ from C₃ plants in having the mechanism to maintain extra carbon at the enzyme responsible for C reduction. In all photoautotrophs, the key enzyme responsible for photosynthetic C reduction is RUBISCO (ribulose, 1-6, biphosphate carboxylase oxygenase). This enzyme catalyzes the first and major rate-limiting step in the C reduction cycle. The present CO₂/O₂ regime restricts most vegetation to only 70% of its photosynthetic potential, because of kinetic constraints imposed by RUBISCO. Three characteristics of RUBISCO are pertinent with regard to the composition of atmosphere i.e., i) for optimum functioning, it requires high CO₂ concentrations compared to those normally available, ii) the carboxylation reaction is competitively inhibited by O₂ and iii) it acts as mono-oxygenase, using O₂ to initiate the photorespiratory C oxidation. In the current atmosphere, C₃ chloroplast stroma contains about 5 μM CO₂, which is far less than that required (8-25 μM) for optimal functioning of RUBISCO. Thus the problem of low substrate (CO₂) availability together with high O₂ concentrations constrains photosynthesis. Contrary to C₃ plants, those with a C₄ system have developed a CO₂ concentrating mechanism to provide a steady-state level of *ca* 70 μM at RUBISCO which is localized in special bundle sheath cells. In C₄ plants, therefore, the inherently elevated levels

Table 1: Photosynthetic pathways in C₃, C₄, and CAM plants

Characteristics	C ₃	C ₄	CAM
CO ₂ acceptor	RuBP	PEP	In light: RuBP In dark: PEP
First product of photosynthesis	C ₃ acids (PGA)	C ₄ acids	In light: PGA In dark: Malate
C isotope ratio in photosynthate ($\delta^{13}\text{C}$)	-21 to -40 ‰	-10 to -20 ‰	-10 to -35 ‰
CO ₂ compensation level	3-50 ppm	>10 ppm	In light: 0-200 ppm In dark: <5 ppm
Photosynthetic capacity	Slight to high	High to very high	In light: slight In dark: medium
Dry matter production	Medium	High	Low

of CO₂ at the site of fixation offset the competitive effects of O₂ on RUBISCO. The plants with CAM mechanism have also specialized in providing elevated levels of CO₂ at the RUBISCO level. In these plants the stomata remain closed during the daytime and hence gaseous exchange is at its minimum. During the dark period (at night), however, the stomata are open and the CO₂ entering into the leaf cells is assimilated into oxaloacetate. The malate formed from oxaloacetate is decarboxylated during the daytime and CO₂ thus produced is further reduced by the normal photosynthetic system involving RUBISCO. In CAM plants, therefore, complete or partial closure of stomata under stress situations has practically no bearing on the RUBISCO activity.

With the background provided above and the fact that C₃, C₄ and CAM plants differ in CO₂ conditions at RUBISCO level, changes in the concentration of atmospheric CO₂ will have a different impact on the process of photosynthesis and rate of their growth. An assimilation of data presented in Fig. 4 depicts an effect of elevated CO₂ under different conditions on some of the photosynthetic aspects of C₃ and C₄ plants. Akita and Tanaka (1973) were among the pioneers to report a substantial gain in dry matter yield of C₃ but not of C₄ plants. In a comprehensive survey of agricultural plants, Kimball (1983) reported a 33% yield increase in C₃ plants. In a most comprehensive review of over 1000 laboratory and field experiments, Idso (1992) documented a mean productivity enhancement of 52% in C₃ plants in response to doubling of CO₂. Compared to C₃ plants, those with a C₄ system respond differently to elevated CO₂, generally with no to negligible effect being observed (Akita and Tanaka, 1973; Cure and Acock, 1986; Allen, 1990). For CAM plants, variable response to elevated CO₂ has been reported. Pineapple showed no response, while several growth attributes of *Aechmea magdalanæ* improved (Hogan *et al.*, 1991). In view of the fact that overwhelming majority of plant species (>95%) belongs to the C₃ category which are the main beneficiaries of elevated CO₂, further discussion will focus on these plants only.

Environmental stresses, photosynthesis and elevated CO₂

The plants may face both atmospheric (above-ground) and rhizospheric (below-ground) stress situations at some stage of their growth. These stresses may be biotic or abiotic in nature both of which could be imposed from the atmosphere as well as the rhizosphere. The dominant abiotic stresses from the atmosphere include extremes of temperature, light intensity, fog, air-borne solid particles and CO₂ etc., while those from the rhizosphere arise because of drought/water-logging, deteriorated soil structure (air/water balance), excessive salts, and insufficient nutrients. The prevalent biotic stresses could be attributed to air-borne and soil-borne plant pathogens imposed from atmosphere and rhizosphere, respectively. In addition, mutual competition for nutrients and other requirements may impose a stress on one or the other plant growing in an ecosystem. Hence, plant survival and crop productivity are strictly dependent on the capability of plants to adapt to different environments; adaptation being the result of the interaction among roots and biotic and abiotic components of soil.

The effect of CO₂ has been much more pronounced when environmental factors (like those narrated above) are severely affecting the plant growth and development (Koch and Monney, 1996). In fact, the effect of elevated CO₂ becomes irrelevant at optimum or high nutrient availability, but more relevant for plants growing under stress situations. This is one reason that elevated CO₂ is reported to have negligible effect under optimum plant growth conditions but significantly better effect under stress situations. Under conditions that limit ecosystem productivity, elevated CO₂ has been reported to help plants overcome some of the restrictions. For example, in a cotton crop showing lower growth because of high root-zone moisture (compared to those with optimum moisture and good growth), Pinter *et al.* (1996) reported a greater CO₂-induced increase in growth in two different years. In the case of Kansas grass prairie, doubling the CO₂ concentration enhanced vegetative productivity by 5-10%

under normal conditions, while the increase was up to 80% under growth limiting conditions (Owensby, 1996). A common response of the plants facing abiotic stresses is the partial or complete closure of the stomata depending upon the intensity and duration of the stress. As a result not only the transpiration-mediated uptake of water and nutrients is hindered but partial pressure of CO₂ relative to O₂ within the leaf atmosphere and ultimately at RUBISCO level is significantly reduced. Elevated CO₂ mitigates some of these effects and increases the tolerance of plants to the stresses listed above. This is particularly true for C₃ plants, which are in fact the main beneficiary of elevated CO₂ because of their characteristic photosynthetic system which is under-fed with CO₂ especially when facing extremes of environmental conditions that lead to partial or complete closure of stomata. When environmental factors are such as to curtail plant growth and development severely, the effects of elevated CO₂ have been much more prominent (Koch and Monney, 1996). High temperatures have generally a depressing effect on growth of C₃ plants because of their lower optimum temperature for photosynthesis. In addition, the photorespiratory activities of C₃ plants induced/enhanced by higher temperatures are curtailed at elevated levels of CO₂, thereby helping the plants conserve C and energy. This is made possible through increased partial pressure of CO₂ at RUBISCO level thereby reducing the oxygenase function (responsible for deterioration of photosynthetic apparatus) of the enzyme. Elevated CO₂ raises the optimum temperature (Berry and Bjorkman, 1980; Osmond *et al.*, 1980; McMurtrie and Wang, 1993) thus protecting the plants from being overheated as well as altering the CO₂/O₂ specificity of RUBISCO in favour of CO₂. This is supposed to be one of the reasons that global warming resulting from elevated CO₂ may not have a major effect on most of the C₃ plants (Bowes, 1993). Faria *et al.* (1996) believe that life-sustaining function of increased concentrations of CO₂ at high air temperatures may be partially due to a stabilization of enzymes susceptible to heat through increased photosynthesis and thus elevated sugar content. Fig. 4 shows a positive effect of elevated CO₂ on rate of photosynthesis under the influence of increasing temperature. In wheat and barley, Bunce (1998) reported a significantly positive effect of increasing temperature on photosynthesis at elevated CO₂ levels. Similar results were obtained by Hakala (1998).

As mentioned earlier, both CO₂ and O₂ compete for a site on RUBISCO. In C₃ plants with low partial pressure of CO₂ at the RUBISCO level, O₂ becomes the dominant competitor and has a deleterious effect on photosynthetic

apparatus. This is especially true under high light intensities when more light is absorbed than can be used for the CO₂ fixation. This leads to transfer of energy to more abundant O₂ molecules. The resulting short-lived activated oxygen species react non-specifically with organic molecules e.g. membrane lipids, and destroy (oxidative photodestruction or photodynamic effect) them thus disrupting the photosynthetic activity. Proteins, nucleic acids and chlorophylls may meet a similar fate. The plants do possess mechanisms to escape from deleterious effects of oxygen radicals mainly by removing them via superoxide dismutase. However, it is not only the negative effects of oxygen species, but the present CO₂:O₂ ratio in the atmosphere, and the RUBISCO specificity factors (Jorden and Ogren, 1983) also translate into photorespiratory losses of fixed C that may amount to 25% of the total (Keys, 1986). A presumed doubling of atmospheric CO₂ in the this century should more than halve this deleterious effect of O₂ on C₃ plants, but would have negligible effect on C₄ plants which have already the mechanism to concentrate CO₂ at the RUBISCO level. Rising CO₂ concentration will also protect the plants from increasing O₃ concentrations (McKee *et al.*, 2000). Under normal CO₂ levels, however, partial or complete closure of stomata during stress situations may be an effective measure to lower the negative effects of oxygen radicals. Low light intensities are reported to limit photosynthesis at ambient concentrations of CO₂, while elevated CO₂ levels have a mitigating effect. In a review, Idso and Idso (1994) reported a doubling of photosynthesis at 600 ppm CO₂. Several subsequent studies demonstrate that low light intensities do not negate the beneficial effects of elevated CO₂ (Wang, 1996; Kubiske and Preziger, 1997). Osborne *et al.* (1997) found that elevated CO₂ levels allowed plants to live under light conditions insufficient to meet photosynthetic requirements. They concluded that the potential range of habitats that such species could occupy will expand considerably with rising atmospheric CO₂. In addition, elevated CO₂ increases the quantum yield (Fig. 4), stabilizes photochemical efficiency of C₃ plants, and thus leads to gains in C accumulation at relatively lower levels of energy consumption.

Positive effect of elevated CO₂ on plant performance under conditions of limited water availability has consistently been reported (Hudak *et al.*, 1999; Li *et al.*, 2000; Wall 2001). Fig. 5 clearly depicts the effect of drought on relative growth rate of C₃ plants at two levels of CO₂. Intermittent drought stress leads to closure of stomata and decreased photosynthesis, while death of plant parts or whole plants may occur during prolonged drought (Boyle and Hellenbrand, 1991; Bryla

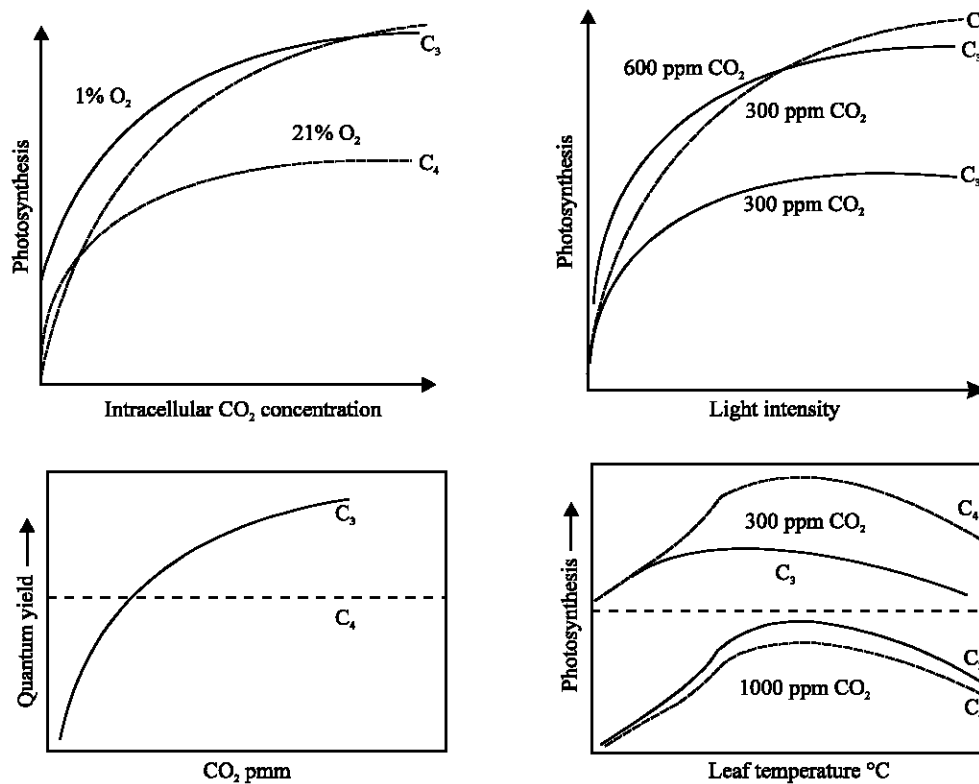


Fig. 4: Diagrammatic representation of the response of photosynthesis to elevated CO₂ under different conditions (source: Osmond *et al.*, 1980)

and Duniway, 1997). In addition, root growth may be reduced as cell expansion rates at the root tip decline in dry soil (Sharp and Davies, 1979) and root exudation of water-soluble compounds decreased by up to 80% under drought stress with serious impact on rhizospheric microbial functions (Marschner *et al.*, 2002; Neumann and Romheld, 2001). Elevated CO₂ is reported to mitigate such effects, especially by increasing root proliferation and hence improved acquisition of nutrients, the mobility of which is curtailed under water deficient environments. Polley *et al.* (1996) reported increased survival of seedlings subjected to water stress at elevated CO₂. Brassica species responded positively to the elevated CO₂ under drought (Upriety *et al.*, 1995). Thornley and Cannell (1996) concluded that the on-going rise in air's CO₂ content will protect trees from debilitating water stress. Similar views have been expressed by Idso and Idso (1994) who reviewed the results of 55 independent experiments. A general response to doubling of CO₂ concentration is 30-60% reduction in stomatal conductance and leaf stomatal density. As a result, improvements in water use efficiency have often been reported (Allen, 1990; Hogan *et al.*, 1991). Not only this,

but the damaging effects of ozone can also be relieved as a result of reduced stomatal opening at higher than ambient levels of CO₂. In addition, under moderately elevated levels of ozone, increase in CO₂ concentration improves the efficiency of carboxylation. However, the water stress may not necessarily be that of drought, excessive irrigation may have negative effect as well and is reported to be mitigated by elevated CO₂. In a cotton crop, it was the high irrigation regime with growth limiting effect at which elevated CO₂ proved beneficial (Pinter *et al.*, 1996).

Plants growing under soil salinity stress have also been reported to benefit from elevated CO₂ (Rozema *et al.*, 1991; Idso and Idso, 1994; Azam *et al.*, 1998; Azam and Farooq, 2001). The benefit is reported to be derived from the availability of more solutes for osmoregulation by reducing the transpirational intake of salts (Bazzaz, 1990), or by improving RUBISCO activity. In C₄ plants, elevated CO₂ helps overcome the leakiness induced by salt stress (Wong and Osmond, 1991). In C₃ plants, the positive effect is mediated mainly through enhanced photosynthesis as discussed above for other stresses. In addition, positive effect of elevated CO₂ on root

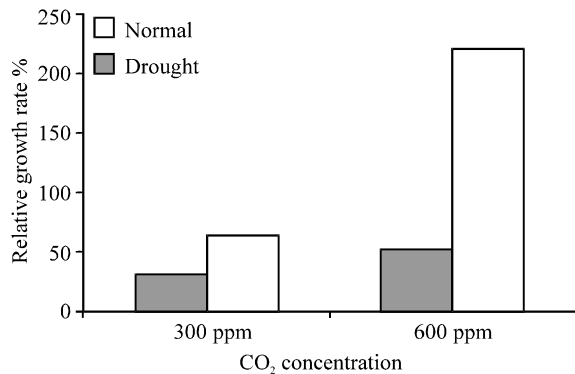


Fig. 5: Effect of elevated CO₂ on relative growth rate of plants grown under normal and drought situations

proliferation and root-induced microbiological and biochemical changes (discussed elsewhere in this paper) may help plants withstand salinity stress.

Elevated CO₂ and rhizodeposition: An important factor that might determine the overall response of plants is the ability of the root system to adjust nutrient acquisition capacity to meet variations in shoot demand caused by environmental changes including elevated CO₂. They do this by adjusting their physiological, longevity, morphological and/or architectural characteristics (Chapin, 1980; Clarkson, 1985). The capacity to adjust is an important characteristic that determines variable response of different plant types to environmental changes. Tingey *et al.* (2000) have reported changes in growth and morphology of roots induced by elevated CO₂. This is in turn determined by soil nutrient availability and soil factors affecting nutrient transport to the root surface (Bassirirad, 2000). A number of studies have shown both a short-term stimulation of growth and increased supply of root respiratory substrates (Cruz *et al.*, 1993; Tschaplinski *et al.*, 1993).

In most studies dealing with stress tolerance of plants, attention has been given to responses of plant tops and the processes therein to elevated CO₂. This happened in spite of the fact that a more positive effect of elevated CO₂ on plants under growth-limiting compared to optimum conditions is due to the enhanced root proliferation. The morphology, proliferation, distribution and density of the roots may be the critical component of a plant's positive response to elevated CO₂ that is generally exhibited in terms of increased soil volume being explored for nutrient acquisition (Rogers *et al.*, 1992; Bernston *et al.*, 1993). Indeed the below-ground component is positively affected and the plants grown at elevated CO₂ are reported to have more extensive and active root system (Day *et al.*,

1996; Curtis *et al.*, 1990; Kubiske *et al.*, 1997). Thus at low levels of N availability (for example) that would generally limit plant growth, elevated CO₂ helps plants extract more N from soil and stimulate rate of photosynthesis (Norby *et al.*, 1992). This happens also because uptake of nutrients requires energy and elevated CO₂ accelerates the process of photosynthesis and flow of photosynthates (energy rich materials) into the rhizosphere thus helping the plants meet the extra energy demands. Enhanced rates of photosynthesis should also allow greater partitioning of carbohydrates belowground, thereby enhancing root growth and enabling plants to better explore the soil for precious water supplies during times of drought (Wall, 2001).

It would appear that at ambient CO₂ levels, carbon starvation is a more pertinent factor limiting nutrient uptake in spite of the fact that 30-50% of the photosynthetic C is transported below-ground during the life cycle of arable annual plants (Swinnen *et al.*, 1994; Domanski *et al.*, 2001). In fact, almost all organic C found in soil is primarily plant-derived in the form of root/shoot residues and root exudates (Kuzyakov and Domanski, 2000,2002). A significant proportion of the rhizodeposits is lost through rhizospheric respiration that may represent 51 to 89% of the total CO₂ efflux from soil; half of this coming from root respiration (Kuzyakov *et al.*, 1999). Kuzyakov and Domanski (2000,2002) 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 for the maintenance, root growth and ion uptake. They also 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.* (1986) 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; a decrease in the amount being noted with plant age. Elevated CO₂ is reported to significantly enhance the transfer of photosynthates to the rhizosphere (Hungate *et al.*, 1997). There is typically an increase in soil organic matter (Wood *et al.*, 1994) which usually produces even further benefits. These benefits include stimulation in earthworm activity (Rogers *et al.*, 1994) leading to the creation of much new soil and improvement in soil fertility parameters including structure, aeration and drainage.

Enhancement in the activity of rhizospheric microorganisms because of increased supply of photosynthates as rhizodeposits (root exudates and sloughed off root material) under conditions of elevated CO₂ is another common observation. The enhanced microbial activity in turn stimulates a multiplicity of

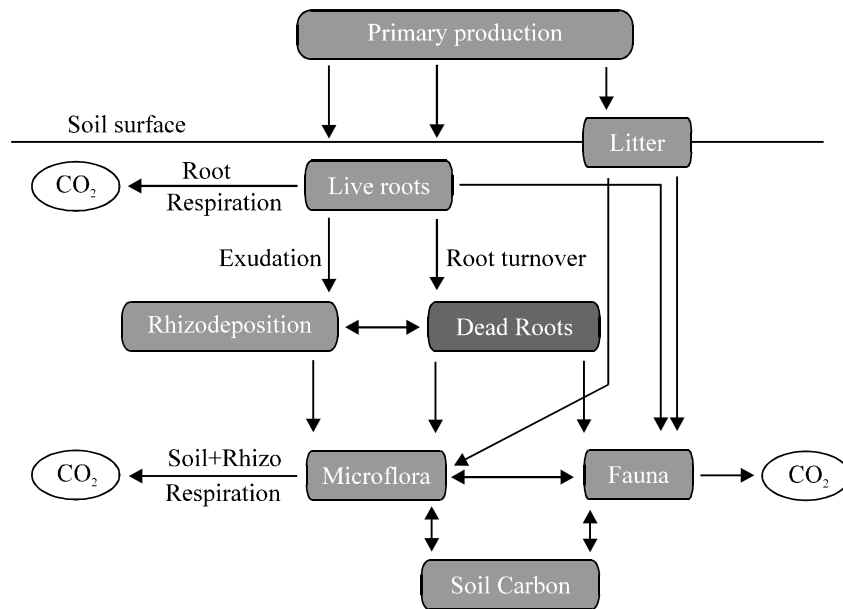


Fig. 6: A conceptual model of carbon allocation to below-ground components of an ecosystem.

growth promoting effects in the rhizosphere including root growth stimulation and production of abundant lateral roots and root hairs (Zak *et al.*, 1993; Simmons and Pope, 1988). Of all different kinds of microbial activities, increase in the number and performance of nitrogen fixers (Murphy, 1986) is of immense significance. This is particularly important in view of the role of N_2 fixation in meeting a substantial proportion of the plant requirement for combined N. The process of N_2 fixation being highly energy intensive, good quantities of photosynthates will have to be transported to the rhizosphere. In addition, N_2 fixation (especially the rhizobial fixation in legumes) imposes some sort of stress on plants (Azam, 2001) inducing them to transport more energy rich materials. Elevated CO_2 should enhance the process of N_2 fixation mainly through increased supply of photosynthates.

Soil aggregation is a critical regulator of ecosystem functioning. It determines the distribution of soil pore sizes, and thus water infiltration, microbial predation, aeration, root growth and the heterogeneity of redox conditions in the soil. These factors, in turn, greatly influence biogeochemical cycles (Oades, 1984). In Pakistan, most of the salt-affected soils lack productivity because of less than optimum content of stable aggregates and thus a deteriorated soil structure. The modifications of soil aggregation could therefore have important consequences for the functioning of ecosystems. Many factors influence soil aggregate stability, including microbial EPS (Roberson *et al.*, 1995), fungal hyphae (Tisdall, 1991), soil microbial biomass, rhizodeposits and humus (Evrin and Chapin, 2002).

Elevated CO_2 increased soil aggregation at field sites (Rilling *et al.*, 1999). Many key pedological processes such as soil organic matter turnover and the maintenance of soil structure are determined by the nature and efficiency of mutualistic associations between micro- and macroorganisms. Associations between soil organisms can have significant influence on plant growth and *vice versa* and the effect they have on soil structure and function. This is one of the reasons that interactions between the roots, the mineral soil matrix and soil microbes lead to a different C allocation and sequestration by roots as compared with the nutrient solution culture or sterile soil (Meharg and Killham, 1990, 1991).

Status of CO_2 at the canopy level in upland crops and the measures for its increase: At the level of crop canopies, the concentration of CO_2 is expected to be higher relative to that in the atmosphere around. This increase results from the CO_2 originating from the soil as a result of rhizospheric respiration (from roots and microbial biomass). Fig. 6 gives a summary of the processes leading to the evolution of CO_2 from soil. As mentioned above, a significant proportion of the C in the rhizodeposits is returned to the atmosphere thereby augmenting the ambient concentrations of CO_2 . Since a major portion of the additional CO_2 comes from microbial respiration, anything that enhances the activities of aerobic microorganisms is bound to increase the process. Ecological conditions in the soil, particularly temperature and moisture, will have a significant bearing on the process vis-à-vis availability of organic carbon. In

Pakistan, the higher root-zone temperature together with intermittent changes in moisture regime will have a positive effect on the decomposition of organic matter and release of CO₂. In addition, these and other factors like stresses imposed by nutrients and salinity etc. will have a positive bearing on rhizodeposition and consequently the dynamics of CO₂ and its impact on photosynthesis. Thus, in a way, higher respiratory activities may have a net positive effect on the ecosystem functioning.

In most studies, the role of soil organic matter as a source of additional CO₂ within the plant canopies has generally received less attention relative to build-up of humus and its implications to plant productivity. It is logical to assume, however, that amendment of soils with organic manures will have a significant bearing on ecosystem functioning through increased levels of CO₂. Normally, 15-30% or even more of the organic C (1000-1500 kg ha⁻¹ in case of wheat) in plant residues would be expected to be released within a cropping season thus significantly improving the CO₂ status at the canopy level. Leaving plant residues on the soil surface (incorporation may have serious negative side effects on the standing crop) has the potential to increase by several folds the level of CO₂ in the atmosphere of a standing crop. For example, wheat crop with grain yield of 2000 kg ha⁻¹, will roughly add 3000 kg (if not more) of carbonaceous materials in or on the soil. Assuming that i) the residues contain 50% C and thus 1500 kg C ha⁻¹ and ii) a minimum of 75% of the C being released as CO₂ i.e., 1125 kg C will be lost from each hectare of the soil into the atmosphere. This amount is equivalent to Ca 3.5 g CO₂-C day⁻¹ per m² (100 days of active cropping period). This amount is sufficient to raise the CO₂ level of one cubic meter of the atmosphere at least by 50%. The argument here is that at the maximum rate of return of plant residues (plus rhizodeposits), wheat ecosystem has the ability to significantly raise the atmospheric CO₂ concentration. This ability will be more in systems with higher yields. However, this normally does not happen under prevalent agricultural conditions since a significant part of the surface residues is removed. It is possible, therefore, to increase the CO₂ supplies to the crop stand by adopting organic manuring/mulching practices and hence harvest the benefit emerging there from, especially under stress situations.

Conclusion

Indeed, the on-going rise in the air's CO₂ is enhancing agricultural productivity the world over. According to Bowes (1993), "the CO₂-enriched atmosphere of 21st century does not look to be a bleak prospect for most plants, or for agriculture. It might usher in a greener planet, though the species mix will change. For good or ill,

change always has been an inextricable part of our world". Wittwer (1995) sums up his observations by saying "rising level of atmospheric CO₂ is a universally free premium, gaining in magnitude with time, on which we can reckon for the future". Organic amendments could further improve the yields of crop plants exposed to short- or long-term environmental stresses.

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References

- Akita, S. and I. Tanaka, 1973. Studies on the mechanism of differences in photosynthesis among species. IV. The differential response in dry matter production between C₃ and C₄ species to atmospheric carbon dioxide enrichment. Proc. Crop Sci. Soc. Jpn., 42: 288-295.
- Allen, L.H.Jr., 1990. Plant responses to rising carbon dioxide and potential interactions with air pollutants. J. Environ. Qual., 19: 15-34.
- Azam, F., 2001. Legume-bacterium (*Rhizobium*) association - symbiosis, a marriage of convenience, necessary evil OR bacterium taken hostage by the legume. Pak. J. Biol. Sci., 4: 757-761.
- Azam, F. and S. Farooq, 2001. Impact of elevated atmospheric CO₂ on crop plants - an overview. Pak. J. Biol. Sci., 4: 220-224.
- Azam, F., A. Lodhi and H.M. Helal, 1998. Improvement of saline soils through biological means - Organic matter dynamics and plant productivity. In: Sustainable Agriculture for Food, Energy and Industry - Strategies toward achievement (El-Bassam N, Behl RK and Prochnow B, eds). James and James (Science Publishers) Ltd, London, UK, pp: 287-291.
- Bassirirad, H., 2000. Kinetics of nutrient uptake by roots: Responses to global change. New Phytol., 147: 155-169.
- Bazzaz, F.A., 1990. The response of natural ecosystems to the rising global CO₂ levels. Annu. Rev. Ecol. Sys., 21: 167-196.
- Bernston, G.M., K.D.M. McConnaughay and F.A. Bazzaz, 1993. Elevated CO₂ alters deployment of roots in small growth chambers. Oecologia, 94: 558-564.
- Berry, J. and O. Bjorkman, 1980. Photosynthetic response and adaptation to temperature in higher plants. Ann. Rev. Plant Physiol., 31: 491-543.
- Bowes, G., 1993. Facing the inevitable: Plants and increasing atmospheric CO₂. Ann Rev Plant Physiol. Plant Mol. Biol., 44: 309-332.

- Boyle, C.D. and K.E. Hellenbrand, 1991. Assessment of the effect of mycorrhizal fungi on drought tolerance of conifer seedlings. *Can. J. Bot.*, 69: 1764-1771.
- Bryla, D.R. and J.M. Duniway, 1997. Effects of mycorrhizal infection on drought recovery in sunflower and wheat. *Plant Soil*, 197: 95-103.
- Bunce, J.A., 1998. The temperature dependence of the stimulation of photosynthesis by elevated carbon dioxide in wheat and barley. *J. Exp. Bot.*, 49: 1555-1561.
- Chapin, F.S. III., 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. System*, 11: 233-260.
- Clarkson, D.T., 1985. Factors affecting mineral nutrient acquisition by plants. *Ann. Rev. Plant Physiol.*, 36: 77-115.
- Cruz, C., S.H. Lips and M.A. Martins Loução, 1993. The effect of nitrogen source on photosynthesis of carob at high CO₂ concentrations. *Physiol. Plant.*, 89: 552-556.
- Cure, J.D. and B. Acock, 1986. Crop responses to carbon dioxide doubling: a literature survey. *Agric. Meteorol.*, 8: 127-145.
- Curtis, P.F., L.M. Balduman, B.G. Drake and D.F. Whigham, 1990. Elevated atmospheric CO₂ effects on below ground processes in C₃ and C₄ estuarine marsh communities. *Ecology*, 71: 2001-2006.
- Day, F., W.P. Weber, C.R. Hinkle and B.G. Drake, 1996. Effects of elevated atmospheric CO₂ on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. *Global Change Biol.*, 2: 143-148.
- Domanski, G., Y. Kuzakov, S.V. Siniakina and K. Stahr, 2001. Carbon flows in the rhizosphere of ryegrass (*Lolium perenne*). *J. Plant Nutr. Soil Sci.*, 164: 381-387.
- Drake, B.G. and P.W. Leadley, 1991. Canopy photosynthesis of crops and native plant communities exposed to long-term elevated CO₂. *Plant Cell Environ.*, 14: 853-860.
- Evnir, V.T. and F.S. Chapin III, 2002. The influence of plant species, fertilization and elevated CO₂ on soil aggregate stability. *Plant Soil*, 246: 211-219.
- Faria, T., D. Wilkins, R.T. Besford, M. Vaz, J.S. Pereira and M.M. Chaves, 1996. Growth at elevated CO₂ leads to down-regulation of photosynthesis and altered response to high temperature in *Quercus suber* seedlings. *J. Exp. Bot.*, 47: 1755-1761.
- Hakala, K., 1998. Growth and yield potential of spring wheat in a simulated changed climate with increased CO₂ and higher temperature. *Eur. J. Agron.*, 9: 41-52.
- Hogan, K.P., A.P. Smith and L.H. Ziska, 1991. Potential effects of elevated CO₂ and changes in temperature on tropical plants. *Plant Cell Environ.*, 14: 763-768.
- Hudak, C., J. Bender, H.J. Weigel and J. Miller, 1999. Interactive effects of elevated CO₂, O₃ and soil water deficit on spring wheat (*Triticum aestivum* L. cv. Nandu). *Agronomie*, 19: 677-687.
- Hungate, B.A., E.A. Holland, R.B. Jackson, F.S. Chapin III, H.A. Mooney and C.B. Field, 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature*, 388.
- Idso, K.E. and S.B. Idso, 1994. Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agric. Meteorol.*, 69: 153-203.
- Idso, S.B., 1992. Plant responses to rising levels of atmospheric carbon dioxide: A compilation and analysis of the results of a decade of international research into the direct biological effects of atmospheric CO₂ enrichment. Tempe, AZ, Office of Climatology, Arizona State University, AZ, USA.
- Jorden, D.B. and W.L. Ogren, 1983. Species variation in kinetic properties of ribulose 1,5-bisphosphate carboxylase/oxygenase. *Arch. Biochem. Biophys.*, 227: 425-433.
- Keith, H., J.M. Oades and J.K. Martin, 1986. Input of carbon to soil from wheat plants. *Soil Biol. Biochem.*, 18: 445-449.
- Keys, A.J., 1986. Rubisco: its role in photorespiration. *Philos. Trans. R Soc. London*, 313: 325-336.
- Kimball, B.A., 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agron. J.*, 75: 779-788.
- Kimball, B.A., 1997. Influence of increasing CO₂ concentration on photosynthetic stimulation of selected weeds. *Photosynth. Res.*, 54: 199-208.
- King, A.W., W.R. Emanuel and W.M. Post, 1992. Projecting future concentrations of atmospheric CO₂ with global carbon cycle models: the importance of simulating historical changes. *Environ. Manage.*, 16: 91-108.
- Koch, G.W. and H.A. Mooney, 1996. Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, CA, USA.
- Kubiske, M.E. and K.S. Pregitzer, 1997. Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO₂. *Functional Ecol.*, 11: 24-32.
- Kubiske, M.E., K.S. Pregitzer, C.J. Mikan, D.R. Zak, J.L. Maziasz and J.A. Teen, 1997. *Populus tremuloides* photosynthesis and crown architecture in response to elevated CO₂ and soil N availability. *Oecologia*, 110: 328-336.
- Kuzyakov, Y. and G. Domanski, 2000. Carbon input by plants into the soil. Review. *J. Plant Nutr. Soil Sci.*, 163: 421-431.

- Kuzyakov, Y. and G. Domanski, 2002. Model for rhizodeposition and CO₂ efflux from planted soil and its validation by ¹⁴C pulse labeling of ryegrass. *Plant Soil*, 239: 87-102.
- Kuzyakov, Y., A. Kretschmar and K. Stahr, 1999. Contribution of *Lolium perenne* rhizodeposition to carbon turnover of pasture soil. *Plant Soil*, 213: 127-136.
- Li, A.G., Y.S. Hou, G.W. Wall, A. Trent, B.A. Kimball and P.J. Printer Jr., 2000. Free air CO₂ enrichment and drought stress effects on grain filling rate and duration in spring wheat. *Crop Sci.*, 40: 1263-1270.
- Marschner, P., W. Marino and R. Lieberei, 2002. Seasonal effects pm microorganisms in the rhizosphere of two tropical plants in a polyculture agroforestry system in Central, Brazil. *Biol. Fertil. Soils*, 35: 68-71.
- McKee, I.F., B.J. Mulholland, J. Craigon, C.R. Black and S.P. Long, 2000. Elevated concentrations of atmospheric CO₂ protect against and compensate for O₃ damage to photosynthetic tissues of field-grown wheat. *New Phytol.*, 146: 427-435.
- McMurtie, R.E. and Y.P. Wang, 1993. Mathematical models of the photosynthetic response of tree stands to rising CO₂ concentrations and temperatures. *Plant Cell Environ.*, 16: 1-13.
- Meharg, A.A. and K. Killham, 1990. Carbon distribution within the plant and rhizosphere in laboratory and field grown *Lolium perenne* at different stages of development. *Soil Biol. Biochem.*, 22: 471-477.
- Meharg, A.A. and K. Killham, 1991. A new method of quantifying root exudation in the presence of soil microflora. *Plant Soil*, 133: 111-116.
- Murphy, P.M., 1986. Effect of light and atmospheric carbon dioxide concentration on nitrogen fixation by herbage legumes. *Plant Soil*, 95: 399-409.
- Neumann G. and V. Romheld, 2001. The release of root exudates as affected by the plant's physiological status. In: *The rhizosphere: Biochemistry and organic substances at the soil-plant interface* (PintonR, Varanini Z and Nannipieri P, eds), Dekker, New York, pp: 91-94.
- Norby, R.J., C.A. Gunderson, S.D. Wullschleger, E.G. O'Neill and M.K. McCracken, 1992. Productivity and compensatory responses of yellow-poplar trees in elevated CO₂. *Nature*, 357: 322-324.
- Oades, J., 1984. Soil organic matter and structural stability: mechanisms and implications for management. *Plant Soil*, 76: 319-337.
- Osborne, C.P., B.G. Drake, J. LaRoche, S.P. Long, 1997. Does long-term elevation of CO₂ concentration increases photosynthesis in forest floor vegetation? *Plant Physiol.*, 114: 337-344.
- Osmond, C.B., O. Bjorkman and D.J. Anderson, 1980. *Physiological Processes in Plant Ecology - Toward a Synthesis with Atriplex*. Springer-Verlag, Berlin, pp: 468.
- Owensby, C.E., J.M. Ham, A.K. Knapp, C.W. Rice, P.I. Coyne and L.M. Auen, 1996. Ecosystem level response of tallgrass prairie to elevated CO₂. In: *Carbon dioxide and terrestrial ecosystems* (Koch, G.W. and H.A. Monney, eds), Academic Press, San Diego, CA, USA, pp: 175-193.
- Pinter, Jr. P.J., B.A. Kimball, R.L. Garcia, G.W. Wall, D.J. Hunsaker and R.L. LaMorte, 1996. Free-air CO₂ enrichment: response of cotton and wheat crops. In: *Carbon dioxide and terrestrial ecosystems* (Koch, G.W. and H.A. Monney, eds), Academic Press, San Diego, CA, USA, pp: 215-249.
- Polley, H.W., H.B. Johnson, H.S. Mayeux, C.R. Tischler and D.A. Brown, 1996. Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (*Prosopis glandulosa*) seedlings. *Tree Physiol.*, 16: 817-823.
- Rilling, M., S. Wright, M. Allen and C. Field, 1999. Rise in carbon dioxide changes soil structure. *Nature*, 300: 628.
- Roberson, E., S. Sarig, C. Sherman and M. Firestone, 1995. Nutritional management of microbial polysaccharide production and aggregation in an agricultural soil. *Soil Sci. Soc. Am. J.*, 59: 1587-1594.
- Rogers, H.H., C.M. Petterson, J.N. McCrimmon and J.D. Cure, 1992. Response of plant roots to elevated atmospheric carbon dioxide. *Plant Cell Environ.*, 15: 749-752.
- Rogers, H.H., G.B. Runion and S.V. Krupa, 1994. Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environ. Poll.*, 83: 155-189.
- Rozema, J., F. Dorel, R. Janissen, G. Lenssen, R. Broeman, W. Arp and B. G. Drake, 1991. Effect of elevated atmospheric CO₂ on growth, photosynthesis and water relations of salt marsh grass species. *Aquat. Bot.*, 39: 45-55.
- Sharp, R.E. and W.J. Davies, 1979. Solute regulation and growth by roots and shoots of water stressed maize plants. *Planta*, 147: 43-50.
- Simmons, G.L. and P.E. Pope, 1988. Influence of soil compaction and vesicular-arbuscular mycorrhizae on root growth of yellow poplar and sweet gum seedlings. *Can. J. Res.*, 17: 970-975.
- Swinnen, J., J.A. Van Veen and R. Merckx, 1994. ¹⁴C pulse-labelling of field-grown spring wheat, an evaluation of its use in rhizosphere carbon budget estimations. *Soil Biol. Biochem.*, 29: 161-170.

- Thornley, J.H.M. and M.G.R. Cannell, 1996. Temperate forest responses to carbon dioxide, temperature and nitrogen: a model analysis. *Plant Cell Environ.*, 19: 1331-1348.
- Tingey, D.T., D.L. Phillips and M.G. Johnson, 2000. Elevated CO₂ and conifer roots: effects on growth, life span and turnover. *New Phytol.*, 147: 87-103.
- Tisdall, J., 1991. Fungal hyphae and structural stability of soil. *Austr. J. Soil Res.*, 29: 729-743.
- Tschaplinski, T.J., R.J. Norby and S.D. Wullschlegel, 1993. Responses of loblolly pine seedlings to elevated CO₂ and fluctuating water supply. *Tree Physiol.*, 13: 283-296.
- Upreti, D.C., R.S. Mishra and Y.P. Abrol, 1995. Effect of elevated CO₂ and moisture stress on the photosynthesis and water relation in *Brassica* species. *J. Agron. Crop Sci.*, 175: 231-237.
- Wall, G.W., 2001. Elevated atmospheric CO₂ alleviates drought stress in wheat. *Agric. Ecosys. Environ.*, 87: 261-271.
- Wang, K.Y., 1996. Canopy CO₂ exchange of Scots pine and its seasonal variation after four-year exposure to elevated CO₂ and temperature. *Agric. Meteorol.*, 82: 1-27.
- Wittwer, S.H., 1995. Food, climate and carbon dioxide: The global environment and world food production. CRC Press, FL, USA.
- Wong, S.C. and C.B. Osmond, 1991. Elevated atmospheric partial pressure of CO₂ and plant growth. III. Interactions between *Triticum aestivum* (C₃) and *Echinochloa frumentacea* (C₄) during growth in mixed culture under different CO₂, N nutrition and irradiance treatments, with emphasis on below-ground responses estimated using $\delta^{13}\text{C}$ value of root biomass. *Aust. J. Plant Physiol.*, 18: 137-152.
- Wood, C.W., H.A. Torbert, H.H. Rogers, G.B. Runion and S.A. Prior, 1994. Free-air CO₂ enrichment effects on soil carbon and nitrogen. *Agric. Meteorol.*, 70: 103-116.
- Yapp, C.J. and H. Poeths, 1992. Ancient atmospheric CO₂ pressures inferred from natural goethites. *Nature*, 355: 342-344.
- Zak, D.R., K.S. Pregitzer, P.S. Curtis, J.A. Teen, R. Fogel and D.L. Randlett, 1993. Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles. *Plant Soil*, 151: 105-117.