The impact of global elevated CO_2 concentration on photosynthesis and plant productivity†

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The alarming and unprecedented rise in the atmospheric concentration of greenhouse gases under global climate change warrants an urgent need to understand the synergistic and holistic mechanisms associated with plant growth and productivity. Photosynthesis is a major process of sequestration and turnover of the total carbon on the planet. The extensive literature on the impacts of climate change demonstrates both positive and negative effects of rising CO_2 on photosynthesis in different groups of higher plants. Significant variation exists in the physiological, biochemical and molecular responsiveness to elevated CO_2 atmosphere, among terrestrial plant species including those with C_3, C_4 and crassulacean acid metabolic (CAM) pathways. However, the regulatory events associated with the inter- and intraspecific metabolic plasticity governed by genetic organization in different plants are little understood. The adaptive acclimation responses of plants to changing climate remain contradictory. This review focuses primarily on the impacts of global climate change on plant growth and productivity with special reference to adaptive photosynthetic acclimative responses to elevated CO_2 concentration. The effects of elevated CO_2 concentration on plant growth and development, source–sink balance as well as its interactive mechanisms with other environmental factors including water availability, temperature and mineral nutrition are discussed.

Keywords: Climate change, elevated CO_2, interactions, photosynthesis, plant productivity, rubisco.

RECENT interest in understanding plant responses to changing global climate makes this review timely. Increase in atmospheric CO_2 concentrations and the associated rise in temperature and precipitation patterns will have profound effects on terrestrial plant growth and productivity in the near future. According to the Intergovernmental Panel on Climate Change (IPCC)[1], the pre-industrial levels of carbon in the atmosphere rose from 285 μmol l^{-1} (600 gigatonnes (Gt)) to the current level of 384 μmol l^{-1} (800 Gt) and the predicted rise in the atmospheric CO_2 would approach 1000 Gt by the year 2050. Such an abnormal rise in the levels of atmospheric CO_2 would result in direct and indirect global climate changes. The increase in CO_2 concentrations as well as other greenhouse gases, due to anthropogenic intensification, will result in an increase in global average temperatures which would further result in drastic shifts in the annual precipitation[2,3]. IPCC report projects the average rise in the global temperatures to be as high as 6.4°C by 2100, associated with an annual 20% reduction in precipitation, and about 20% loss in soil moisture[4]. The Kyoto Protocol of 1997 had a focus on reducing CO_2 emission and stabilization of atmospheric CO_2 concentration by a combination of limitation on the use of fossil fuel and creation of carbon sinks within a specified time frame. Deep oceans were predicted to be potential sinks for the global carbon mitigation but later it was realized that CO_2 absorption rate by the oceans is slow and would take several centuries to reach effective equilibrium with the atmosphere, and, thus we face a growing concern on how to sequester the increasing atmospheric CO_2 (ref. 5).

Climate change affects plant growth and development primarily due to changes in photosynthetic carbon assimilation patterns. The acclimatory responses of plants to the rapidly changing environment and understanding the potential impacts of multiple interacting factors (water availability, temperature, soil nutrition and ozone) have become a subject of debate over the past two decades. Conflicting reports on plant responses to elevated CO_2, and several such differential photosynthetic responses, could be attributed to differences in experimental technologies, plant species used for the experiments, age of the plant as well as duration of the treatment[6,7]. The direct and indirect effects of climate change on plants have been significant sources of uncertainty in the impact assessments and parameterization which are crucial for modelling plant growth and productivity. Further, the sensitivity of photosynthesis to each of the environmental variables

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†This is the fourth article on the theme ‘Photosynthesis and the Global Issues’ being guest-edited by Govindjee, George C. Papageorgiou and Baishnab C. Tripathy. The first article by Lars Olof Björn and Govindjee discussed the evolution of photosynthesis and the chloroplasts and was published in 2009 (vol. 96, pp. 1466–1474); the second article, by Maria Ghirardi and Prasanna Mohanty, discussed hydrogen production by algae, and was published in 2010 (vol. 98, pp. 499–507); the third article by Gernot Renger reviewed ‘Light reactions of photosynthesis’, and was published in 2010 (vol. 98, pp. 1305–1319).

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including high temperature, low water availability, vapour pressure deficit and soil salinity, associated with the inevitable rise in atmospheric CO_2, has not been well documented in assessing plant responses to the new changing environment[8]. It is estimated that the current average annual net primary productivity is ~ 107 PgC $year^{-1}$ with ~ 51% coming from land, whereas oceans contribute the rest, ~ 49% (ref. 9). Capturing atmosphere CO_2 by photosynthesis is crucial for the production of food, fibre and fuel for the humanity; future changes in global climate should play an essential role in modifying the key processes involved in photosynthetic productivity[9]. The specific objective of this review is to evaluate the recent studies on plant responses to global climate change with a critical assessment on photosynthesis research to offset the effects of the predicted future increase in atmospheric CO_2.

Photosynthesis in the changing climate

C_3 plants

The bulk of vegetation belongs to the C_3 photosynthesis group. This group is called C_3 because the 'first' product of carboxylation is a 3-carbon acid, phosphoglyceric acid (PGA)[10,11]. Out of 15 crops which supply 90% of the world's calories, 12 have the C_3 photosynthetic pathway. C_3 photosynthesis is known to operate at less than optimal CO_2 levels and can show dramatic increase in carbon assimilation, growth and yields. A classical experiment of Kimball[12] showed biomass increase of 10–143% in several C_3 crops in response to doubling of the ambient CO_2. A literature survey (1994–2009; Table 1) on the influence of elevated CO_2 among certain C_3, C_4 and crassulacean acid metabolism (CAM) species suggests that most of the C_3 plants showed a significant positive response to photosynthetic acclimation, *Sorghum* and *Panicum* (two C_4 plants) exhibited negative response, whereas *Ananas*, *Agave* and *Kalanchoe* (CAM plants) showed positive responses to increased CO_2 concentration during growth (Table 1)[13–56].

The advantage of efficient CO_2 assimilation in C_3 plants has been related to the availability of increased substrate in the atmosphere and in the fact that they do not have to bear the metabolic costs of CO_2 concentrating mechanism at the site of carboxylation[8]. Photosynthesis in C_3 plants is usually influenced by RuBP (ribulose bisphosphate) carboxylase–oxygenase (rubisco) (EC 4.1.1.39) and by the accumulation of carbohydrates during carbon assimilation. This activity of the enzyme would cause the combination of CO_2 with RuBP followed by dismutation into two molecules of 3-PGA, which is known as the first committed step in the Calvin–Benson–Bassham cycle[57]. As rubisco is substrate-limited by the current atmospheric CO_2 levels, this enzyme has the potential to respond to increases in CO_2 concentration; and have a metabolic control to alter the CO_2 flux during carbon assimilation[8,58]. Elevated CO_2 is known to be advantageous to the kinetic characteristics of rubisco as it increases the velocity of carboxylation and at the same time competitively inhibits the oxygenase reaction[59]. Most of the studies on pot-grown C_3 plants under elevated CO_2 have indicated photosynthetic acclimation, which might be due to soil and nutrient limitation associated with reduced root volume. However, experiments conducted in open top chambers (OTCs) and free atmospheric CO_2 enrichment (FACE) environment showed significant increases in light-saturated rates of photosynthesis in several C_3 plants grown at elevated CO_2 (ref. 56). The marked increase in net assimilation rates has been explained to be due to increased intercellular CO_2 concentrations (C_i). Increased photosynthetic rates, as observed in such studies, fit into C_3 leaf model photosynthesis as proposed by Farquhar *et al.*[60], wherein increase in photosynthetic rates under high CO_2 levels was determined by the activity of rubisco when RuBP regeneration was not limiting[8,61].

As implied above, elevated CO_2 atmosphere increases the carboxylation efficiency relative to oxygenation, resulting in reduced photorespiration. Strong reduction in photosynthetic rates under elevated CO_2 conditions has been associated with reduction in the initial slope of A/C_i (A, photosynthetic rate and C_i, internal CO_2 concentration) response curve due to reduced rubisco activity[8]. Decrease in rubisco catalytic activity has been attributed to the repression of transcription of small subunit gene, which will be discussed later in this review.

The activity of carbonic anhydrase (CA) (EC 4.2.1.1) was also thought to be crucial in photosynthetic acclimation. CA activities were predicted to enhance the rate of photosynthesis by catalysing the rapid equilibration of inorganic carbon and thus increasing the supply of CO_2 across the stroma in the chloroplast[62]. CA was low in most of the plants exposed to elevated CO_2 (ref. 63), but enhanced CA activities were noticed in *Arabidopsis* and *Zea mays* (maize or corn), grown at elevated CO_2, indicating difficulties in the interpretation of the role of CA in photosynthetic acclimation[64,65]. However, research on the response of different isoforms of CA and their polyfunctionality in concentrating CO_2 near the carboxylation site should provide useful evidence for the positive role of CA as a regulator for photosynthetic acclimation. The role of other enzymes including sucrose phosphate synthase (EC 2.4.1.14), ADPG pyrophosphorylase (EC 2.7.7.9), rubisco activase and phosphoenolpyruvate carboxylase (PEP-Case) (EC 4.1.1.31) in regulating carbon assimilation under elevated CO_2 has now received greater attention[7].

Changes in photosynthetic rates and acclimatory responses in C_3 plants grown under elevated CO_2 concentration could also be attributed to the feedback metabolic control wherein large accumulation of foliar starch and other carbohydrates could inhibit CO_2 assimilation rates,

Table 1. Literature survey (1994–2009) on the influence of elevated CO_2 among different plant species

Plant species	Treatment	Response	Reference
Eucalyptus pauciflora	Open-top chamber	Positive response	Atwell *et al.*[13]
Alfalfa	Controlled environmental chamber	Positive response	Aranjuelo *et al.*[14]
Acacia nigrescens	Controlled environmental chamber	No response	Possell and Hewitt[15]
Gossypium hirsutum	Controlled environmental chamber	Positive response	Yoon *et al.*[16]
Cucumis sativus	Controlled environmental chamber	Positive response	Kosobryukhov[17]
Oryza sativa	FACE	Positive response	Shimono *et al.*[18]
Pinus taeda	FACE	Positive response	Crous *et al.*[19]
Quercus ilex	Natural CO_2 spring	Positive response	Paoletti *et al.*[20]
Phleum pratense	Natural CO_2 spring	Positive response	Pfanz *et al.*[21]
Betula papyrifera	Controlled environmental chamber	No response	Zhang *et al.*[22]
Glycine max	Open-top chamber	Positive response	Srivastava *et al.*[23]
Panderosa pine	Open-top chamber	No response	Johnson *et al.*[24]
Temperate forest trees	FACE	No response	Korner *et al.*[25]
Populus species	FACE	Positive response	Wittig *et al.*[26]
Beta vulgaris	Controlled environmental chamber	Positive response	Ignatova *et al.*[27]
Trifolium alexandrium	Open-top chamber	Positive response	Madan *et al.*[28]
Lolium perenne	FACE	Positive response	Ainsworth *et al.*[29]
Citrus reticulata	Controlled environmental chamber	Negative response	Vu *et al.*[30]
Sorghum vulgare	FACE	No response	Ottman *et al.*[31]
Solanum tuberosum	Open-top chamber	Acclimatory response	Lawson *et al.*[32]
Quercus ilex	Natural CO_2 spring	Positive response	Polle *et al.*[33]
Pinus koraiensis	Open-top chamber	Positive response	Shi-Jie *et al.*[34]
Liquidambar styraciflua	FACE	Positive response	Norby *et al.*[35]
Solanum tuberosum	Open-top chamber	Acclimatory response	Schapendonk *et al.*[36]
Picea sitchensis	Open-top chamber	Positive response	Centritto *et al.*[37]
Luehea seemannii	Open-top chamber	No response	Lovelock *et al.*[38]
Dactylis glomerata	Controlled environmental chamber	Positive response	Gunn *et al.*[39]
Bellis perennis			
Trifolium repens			
Schima superba	Controlled environmental chamber	Acclimatory response	Sheu and Lin[40]
Ananas comosus	Controlled environmental chamber	Positive response	Zhu *et al.*[41]
Lolium perenne	FACE	Negative response	Rogers *et al.*[42]
Gossypium hirsutum	Controlled environmental chamber	Positive response	Reddy *et al.*[43]
Betula pendula	Open-top chamber	Acclimatory response	Rey and Jarvis[44]
Havea brasiliensis	Poly bag environmental chamber	Positive response	Dev kumar *et al.*[45]
Panicum antidotale	Controlled environmental chamber	No response	Ghannoum *et al.*[46]
Mokara spp.	Controlled environmental chamber	Positive response	Gouk *et al.*[47]
Citrus aurantium	Open-top chamber	Positive response	Idso and Kimball [48]
Kalanchoe pinnata	Controlled environmental chamber	Positive response	Winter *et al.*[49]
Agave deserti	Controlled environmental chamber	Positive response	Graham and Nobel[50]
Agave salmiana	Controlled environmental chamber	Positive response	Nobel *et al.*[51]
Stenocereus queretaroensis	Controlled environmental chamber	Positive response	Nobel[52]
Fagus sylvatica	Open-top chamber	Positive response	Mousseau *et al.*[53]
Quercus alba	Open-top chamber	Positive response	Norby *et al.*[54]
Populus euramericana	Controlled environmental chamber	Positive response	Bosac *et al.*[55]
Gossypium hirsutum	FACE	Positive response	Mauney *et al.*[56]

whereas the plants with potential sinks for carbohydrate translocation and accumulation may not show any down-regulation of photosynthetic capacity suggesting that imbalances in source–sink could be attributed to the variations in the photosynthetic acclimation in different plants[8]. The relationship between carbohydrate accumulation rates and concomitant increase in respiration in plants under enriched CO_2 is still a matter of controversy. Higher dark respiration rates were recorded in several C_3 plants grown in high CO_2 environment whereas certain C_4 plants did not show any changes in foliar respiration[66]. Further, the reallocation of resources away from the non-limiting processes including rubisco into limiting ones might also result in the acclimation of the photosynthetic apparatus resulting in down-regulation of carbon assimilation rates under elevated CO_2 growth regimes[67]. The role of starch and sucrose accumulation during photosynthetic acclimation in the leaves grown under elevated CO_2 is still a subject of debate. Some evidence suggests that monosaccharides rather than starch and sucrose activate the signal for photosynthetic acclimation in plants[68].

A two-season (spring and summer) experiment conducted in our experimental field at the University of Hyderabad (Hyderabad, India) for three consecutive years (2006–2008), using a tree species *Gmelina arborea* Roxb (Verbenaceae) under CO_2-enriched atmosphere in open

Table 2. Phenotypic characteristics and biomass yields as influenced by CO_2 (ambient – 360 μmol mol^{-1}; elevated – 460 μmol mol^{-1}) in *Gmelina arborea* recorded at the end of two growth seasons (Rasineni and Reddy, unpublished data)

Character	Ambient CO_2	Elevated CO_2
Plant height (cm)	209.45 ± 2.12	359.92 ± 2.78***
Basal diameter (cm)	13.21 ± 0.59	28.40 ± 0.80***
Number of branches	26.20 ± 0.72	44.20 ± 1.19***
Total shoot length (m)	30.73 ± 1.05	59.62 ± 1.43**
Number of leaves/longest shoot	52.70 ± 2.00	108.60 ± 3.12***
Leaf length (cm)	28.10 ± 0.98	37.62 ± 1.12**
Relative plant height growth rate (g day^{-1})	2.97 ± 0.45	4.08 ± 0.72**
Leaf size expansion rate	3.89 ± 0.57	9.75 ± 1.02***
Root weight (kg)	3.96 ± 0.89	5.97 ± 0.85**
Leaf weight (kg)	10.81 ± 1.03	15.54 ± 2.12***
Stem weight (kg)	14.86 ± 0.75	22.13 ± 3.12***
Aerial biomass (kg)	25.67 ± 2.32	37.67 ± 2.98**
Plant biomass (kg)	29.63 ± 1.67	43.64 ± 3.12***

Values are mean ± SD. Values were tested by paired *t*-test, $***p < 0.001$, $**p < 0.01$

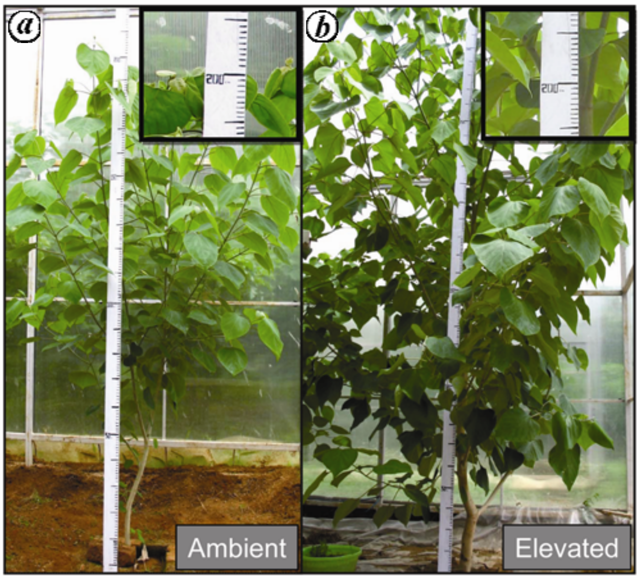

Figure 1. Five-month-old *Gmelina arborea* plants grown in open top chambers under ambient (***a***) and elevated (***b***) CO_2 concentrations. CO_2 was supplied from a high pressure CO_2 cylinder, injected through pressure regulator and was monitored by a CO_2 analyser. The height of ambient CO_2 grown plant was ~ 210 cm, while that of the plant grown under elevated CO_2 was ~ 360 cm. The other growth characteristics of these plants are shown in Table 2. After screening several tree species for their growth characteristics under elevated CO_2, we have selected *G. arborea* as its growth was found to be very fast in response to increased CO_2 concentrations.

top chambers (4 × 4 × 4 m, Figure 1), demonstrated a significant up-regulation of photosynthesis throughout the growing season (Table 2). Plants grown under high CO_2 (460 μmol l^{-1}) showed high rates of photosynthesis compared to those grown under ambient CO_2 levels (360 μmol l^{-1}). After the harvest during all seasons, the biomass yields were markedly higher (48%) in the plants grown under elevated CO_2. Unlike many other reported plant species, growth of *Gmelina* in elevated CO_2 resulted in increased root volume, stem diameter, altered branching pattern and significant increase in plant height. We attribute the positive correlation between photosynthesis and the morphological characteristics of *Gmelina* to be due to potential sink capacity which is crucial to the understanding of the physiological, biochemical, genetic and environmental limitations for the productivity in plants grown in CO_2-enriched atmosphere. These potential changes in the growth and development of *Gmelina* under elevated CO_2 may also be ascribed to increased cell division, cell expansion, cell differentiation and organogenesis, stimulated by increased carbon and more efficient water use[69]. We believe that optimal utilization of resources and well-balanced source–sink activity might enhance carbon gain in plants grown under elevated CO_2. However, the ability of exploiting the extra carbon by any plant species might largely be a function of its inherent structural and physiological attributes, integrated with the plasticity of morphological and anatomical characteristics.

Other factors which can influence plant responses to elevated CO_2 are the growth environment, soil nutrition and the genetic organization of the plant species. The direct effects of rising CO_2 on plant growth and metabolism are a modulation of stomatal conductance, changes in carboxylation capacity, and accumulation of photoassimalates. These three regulatory mechanisms will have a wide range of indirect effects on growth and development of plants, as shown in Figure 2. Davey *et al.*[7] postulated that fast growing perennial species would have a greater advantage of having a better sink strength which could result in the up-regulation of carbon metabolism unlike the annual species wherein photosynthetic acclimation has been frequently recorded due to less efficient sink capacity. Different experiments on the effects of elevated CO_2 on photosynthetic capacity in C_3 plants indicate either up- (or) down-regulation, which varies with genetic and interactive environmental factors.

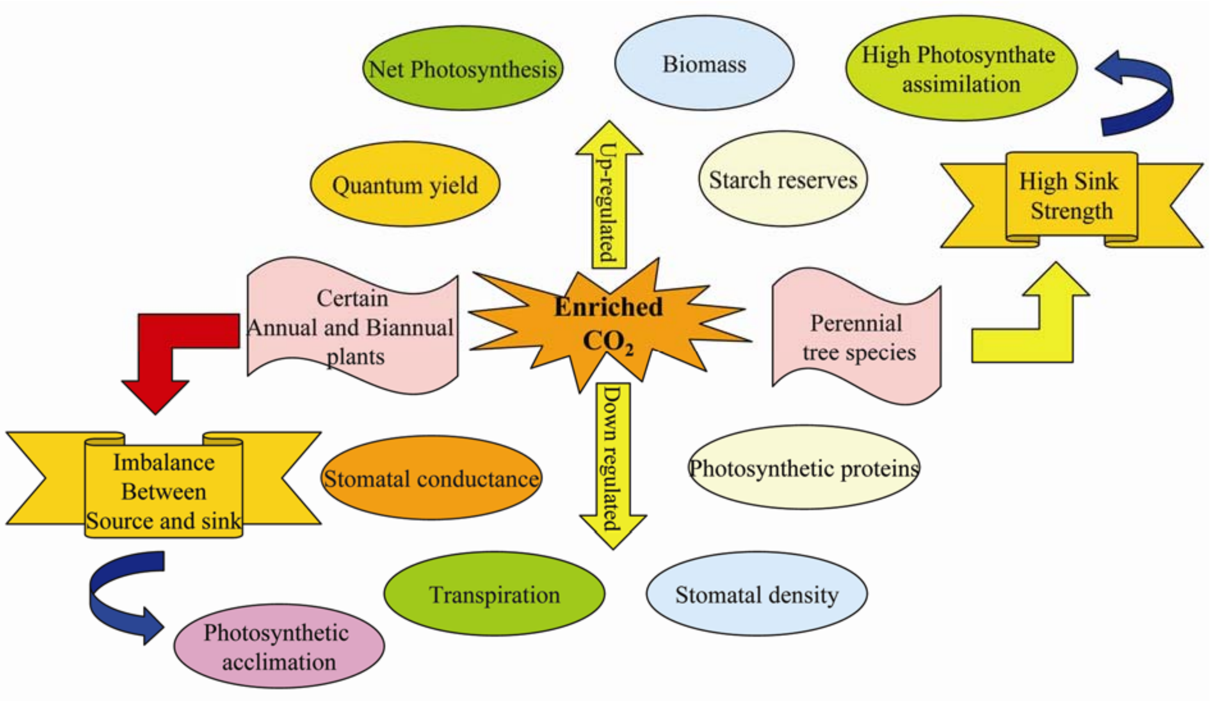

Figure 2. Schematic representation of the effects of elevated CO_2 on the regulation of plant growth and metabolism. Factors affecting up- or down-regulation of photosynthesis in annual and perennial plant species are shown.

C_4 plants

Most of the research on plant responses to elevated CO_2 has been carried out with C_3 species, whereas C_4 plants have received very little attention. These plants are called C_4 plants because the 'first' product of carboxylation is a 4-C acid (e.g. malic acid); the C-4 pathway, is also called the Hatch–Slack pathway[70]. The lower attention on C_4 plants in the studies of the effects of increased CO_2 has been attributed to the assumption that the inherent CO_2 concentrating mechanism in C_4 plants renders these plants insensitive to elevated CO_2 atmosphere. Under natural atmospheric conditions, the biochemistry of C_4 photosynthesis elevates CO_2 concentration in the bundle sheath cells approximately to 2100 $\mu mol\ l^{-1}$, which is at least 10 times more than that present in the mesophyll cells of the C_3 plants. This substantially higher CO_2 level saturates the carboxylase reaction and abolishes photorespiration[71]. Moreover, photosynthesis in C_4 plants is more readily saturated at the normal atmospheric CO_2 concentrations, which reflects that PEPCase is insensitive to changes in the ratio of $CO_2 : O_2$ due to lack of binding of O_2 to the catalytic site of PEPCase. However, several reports indicate that C_4 plants also significantly respond to elevated CO_2 concentration by showing enhanced carbon uptake[72,73].

Some C_4 plants grown under FACE exhibited increased photosynthetic rates only during drought or under the conditions of atmospheric vapour pressure deficits[74,75]. Ghannoum *et al.*[76] reported that C_4 plants, grown under high irradiance, showed enhanced photosynthesis under elevated CO_2 conditions, whereas there was not much response in the growth of C_4 species under low irradiance. Doubling of the current ambient CO_2 concentration stimulated the growth of C_4 plants to the tune of 10–20% whereas that in C_3 plants was about 40–45% (ref. 76). It is also well known that the growth stimulation of C_4 weeds is much larger compared to that of C_4 crops.

Although certain C_4 plants showed positive response to elevated CO_2, the underlying mechanisms for the enhanced growth responses are still not clear. In addition to improved photosynthetic rates under elevated CO_2, C_3 plants exhibited reduced mitochondrial respiratory rates, which could contribute to increased biomass yield. However, little is known about the impact of elevated CO_2 on the respiratory rates of C_4 plants. The positive responses of certain C_4 plants to elevated CO_2 were believed to be due to differences in bundle sheath leakiness, biochemical subtype, and direct CO_2 fixation in the bundle sheath cells as well as C_3-like photosynthesis in young and developing leaves of C_4 species[77]. Further, the lack of photosynthetic acclimation in C_4 plants (in contrast to several C_3 plants) could be attributed to relatively less rubisco protein and more active carbonic anhydrase and PEPcase. Although there are several studies on the interactive effects of increased air temperature, nutrients, water availability and elevated CO_2, very little is known about such interactive influence of elevated CO_2 with the environmental variables during growth of C_4 plants[75].

Crassulacean acid metabolism

CAM photosynthesis is known to occur in approximately 7% of the vascular plants[78,79]. CAM is one of the three types of photosynthesis used by vascular plants in which nocturnal CO_2 fixation results in the formation of malate, which is decarboxylated during day time releasing CO_2, which in turn is assimilated into carbohydrates[80]. Compared to the studies on the effects of elevated CO_2 in C_3 and C_4 plants, very little is known about the response of CAM plants to increasing atmospheric CO_2 concentrations. CAM plants are known for their considerable inherent photosynthetic plasticity associated with environmental conditions during different developmental stages[78,81]. The characteristic features of nocturnal CO_2 fixation in CAM plants and variation in responses of carboxylating enzymes (both rubisco and PEPCase) make generalization of their response more complex than those of C_3 and C_4 plants. Although certain CAM plants show stimulated rates of photosynthesis and 20–40% increase in biomass production, under elevated atmospheric CO_2 concentrations, with no acclimation during growth, contradictory range of responses of these plants to elevated CO_2 have been reported, which include increase and/or decrease in nocturnal CO_2 uptake, daytime CO_2 fixation patterns as well as in water use efficiency[82].

The lack of acclimation in CAM plants under elevated CO_2 has been attributed to the succulence which could be a diffusional constraint to CO_2 as well as to accommodate large amount of photosynthate to avoid feedback inhibition. The significant increase in biomass production in CAM plants under elevated CO_2 atmosphere, on marginal arid and semi-arid lands, suggests that CAM plants could also be exploited for terrestrial sequestration of atmospheric CO_2 in the changing global environment. Further, the exceptional degree of stress tolerance in CAM plants to water-deficit regimes, high temperatures and high light intensities should render these plants robust to the predicted harsh impacts of the future global climate change. The lack of acclimation of CAM species under elevated atmospheric CO_2 concentrations could enhance the importance of several economically important CAM plants worldwide in improving the photosynthetic productivity.

Interactions between elevated CO_2 and other environmental factors

The literature survey (1994–2009), shown in Table 3, demonstrates that the responses of different plant species are due to interaction of elevated CO_2 with other environmental variables including temperature, nutrients, water availability and ozone levels in the atmosphere[24,40,83–105]. The majority of the experiments (Table 3) demonstrate positive response to elevated CO_2 when grown under controlled conditions. The positive response was primarily due to improved photosynthetic rates which were associated with increased biomass yields. Most of the climate change-related plant growth models have been based on predicted estimates of future emissions of greenhouse gases and the simulation of their influence on plant growth and development[9]. Thus, several simulated crop growth models have limitations, and certain uncertainties, as there is no integrated approach in considering the interactions of variable climate factors along with the impact of greenhouse gas emissions. The relative importance of other factors including water availability, soil nutrition, temperature, relative humidity and ozone, which could possibly interact with the effects of elevated CO_2, need to be better understood.

Temperature

Available literature indicates that semi-arid plants will greatly benefit from a rise in the atmospheric CO_2 concentration, such crops show greater percentage increase in yield under elevated CO_2. Morison and Lawlor's[106] classical explanation is that the specificity of rubisco for CO_2 relative to O_2 declines with increasing temperature. C_3 plants exhibit stimulated rates of photosynthesis with increase in temperature under elevated atmospheric CO_2 concentration. Theoretical calculations on the interactive effects of elevated CO_2 concentration and temperature were based on the carboxylation to oxygenation ratios. Such studies confirm that the predicted positive CO_2 uptake may be increased by an increase in the temperature at least by 2–4°C at elevated atmospheric CO_2 concentration. Ainsworth and Long[107] reported that light-saturated rates of photosynthesis under elevated CO_2 concentrations in FACE experiments were enhanced by 19% at 25°C and below, whereas those conducted above 25°C showed 30% increase in photosynthetic rates. High temperatures might also affect/alter the carbon utilization rates of the fast growing metabolic sinks, reducing carbohydrate accumulation, which in turn enhances the up-regulation of photosynthesis under high CO_2. High (e.g. 36°C) and low (e.g. 18°C) temperatures are known to reduce carbohydrate export through phloem resulting in downward acclimation in CO_2-enriched atmosphere[43]. However, the actual consequences of rise in temperature (above 35°C), associated with increase in atmospheric CO_2 concentration, are difficult to predict as these interactive effects are still to be established in combination with other environmental variables including drought stress and nutrient availability.

Soil nitrogen

Nitrogen (N) is required in relatively very large quantities for growth and development of plants, especially for plants grown under elevated CO_2 atmosphere. Plant N

Table 3. Literature survey (1994–2009) on the interactive influence of elevated CO_2 with different environmental variables among different plant species

Plant species	Treatment	Interacting factors	Response	References
Gossypium hirsutum	Controlled environmental chamber	Temperature (high)	Positive response	Yoon *et al.*[83]
Citrus *reticulata*	Controlled environmental chamber	Temperature (high)	No response	Allen and Vu[84]
Betula albosinensis	Controlled environmental chamber	Planting density	Acclimatory response	Zhang *et al.*[85]
Betula papyrifera	Controlled environmental chamber	Nitrogen (high)	Positive response	Cao *et al.*[86]
Solanum tuberosum	SPAR chamber	Water stress	Positive response	Fleisher *et al.*[87]
Quercus mogolica	Controlled environmental chamber	Temperature (high)	Positive response	Wang *et al.*[88]
Hordeum vulgare	Controlled environmental chamber	Dry soil condition	Positive response	Robredo *et al.*[89]
Daucus carota	Controlled environmental chamber	High irradiance	Positive response	Thiagarajan *et al.*[90]
Molinia caerulea	Controlled environmental chamber	Nutrients (increased)	No response	Franzaring *et al.*[91]
Betula papyrifera	Controlled environmental chamber	Nutrients (increased)	Positive response	Zhang *et al.*[92]
Pinus ponderosa	Open-top chamber	Nitrogen (high)	No response	Johnson *et al.*[24]
Brassica napus	Controlled environmental chamber	High temperature drought	Positive response	Qaderi *et al.*[93]
Gossypium hirsutum	Controlled environmental chamber	Potassium fertilizer	Positive response	Reddy and Zhao[94]
Oryza sativa	Controlled environmental chamber	Drought	Positive response	Widodo *et al.*[95]
Citrus reticulata	Controlled environmental chamber	Temperature (high)	Positive response	Vu *et al.*[96]
Acacia farnesiana *Gleditsia triacanthos* *Leucaena leucocephala* *Parkinsonia aculeate* *Prosopis glandulosa*	Controlled environmental chamber	Drought	Positive response	Polley *et al.*[97]
Andropogon gerardii	Open-top chamber	Dry season	Positive response	Adam *et al.*[98]
Cucumis sativus	Controlled environmental chamber	Heat stress	Positive response	Taub *et al.*[99]
Larrea tridentate	Controlled environmental chamber	Heat stress	Positive response	Hamerlynck *et al.*[100]
Schima superba	Controlled environmental chamber	Temperature (high)	Positive response	Sheu and Lin[40]
Quercus suber	Controlled environmental chamber	Low soil moisture	Positive response	Faria *et al.*[101]
Glycine max	Open-top chamber	Ozone (high)	Positive response	Reid *et al.*[102]
Oryza sativa	Controlled environmental chamber	Ozone	Positive response	Olszyk and Wise[103]
Eucalyptus macrorhyncha *Eucalyptus rosii*	Controlled environmental chamber	Low soil moisture	Negative response	Roden and Ball[104]
Betula populifolia *Betula alleganiensis* *Acer pennsylvanicum*	Controlled environmental chamber	Heat stress	Negative response	Bassow *et al.*[105]

productivity (g dry weight increase per unit plant N content) is known to increase under elevated CO_2 to sustain the photosynthetic rates similar to those observed at ambient CO_2, but with a reduced investment in leaf N[108]. Rubisco acclimation in plants grown under elevated CO_2 results in substantial saving in leaf N, which would be greater in crop species compared to tree species. FACE experiments have proven that plants grown with low N accumulate more foliar carbohydrates associated with greater rubisco acclimation compared to those grown with high N supply[75]. Perhaps, more N is to be provided for the plants grown under elevated CO_2 to offset the N-limited biochemical events.

A recent analysis showed a positive interaction between elevated CO_2 and N, indicating that limitation of soil N might progressively suppress the positive responses in photosynthetic carbon acquisition and biomass to elevated CO_2 (refs 109 and 110). Such limitation of CO_2 fertilization under reduced N availability may not be noticed under N-rich soils. Most of the elevated CO_2 studies have considered soil N as the limiting factor with relatively less attention to other essential mineral nutrients. Possible molecular reprogramming/genetic manipulation of N use efficiency under excess sugar environment would be highly favourable to plants grown under elevated CO_2. For example, genetic manipulation of nitrogen metabolism, specifically over-expression of rate limiting enzymes of nitrogen assimilation, could improve the capacity of nitrogen sink for overloaded sugar. Further research is needed to establish the role of other nutrients to understand the mechanisms of their effects on the acclimation of plants under elevated CO_2. Photosynthetic acclimation to elevated CO_2 would be more pronounced under nutrient-limited conditions whereas adequate nutrient supply is believed to mitigate the elevated CO_2-mediated acclimation, at least in crop species.

Water availability

Interactive studies on water availability and elevated CO_2 show that there will be a partial closure of stomata due to increased CO_2 concentration in the substomatal cavity decreasing partial pressure of CO_2 in the leaf and this CO_2-dependent amplification of stomatal response could improve water use efficiency at the leaf and whole plant level[8]. In a wide range of experiments, plants grown under elevated CO_2 had substantial decrease in stomatal conductance (g_s) showing acclimation of g_s to elevated CO_2. Decreased g_s might increase leaf temperature, which could increase the rates of transpiration. However, different experimental techniques used by Wullschleger *et al.*[111] led to the conclusion that plants grown under elevated CO_2 possessed increased root surface and root volume due to increased allocation of carbon to root growth. Such increase in the surface area of roots enables the plants grown under elevated CO_2 to exploit more water even from deep soil layers. However, the decrease in stomatal conductance may also be offset by increased leaf area in plants grown under elevated CO_2 and thus water use by the whole plant may not be proportional to stomatal conductance.

For the actual determination of water use efficiency in plants under CO_2-enrichment, rates of transpiration on plant basis and/or on ground area basis are essential. It is believed that decreased stomatal conductance is an interactive factor and low water availability might be beneficial for plant productivity under increased CO_2 concentration in the atmosphere. The availability of water as an interactive environmental factor suggests that the reduced leaf level stomatal conductance under elevated CO_2 might also influence the whole canopy conductance to water than mitigating the water loss and conserving the available soil moisture.

Expression of photosynthetic genes in plants under CO_2-enrichment

The molecular processes of high CO_2-driven photosynthetic gene expression in plants are not completely understood. As variable acclimation responses have been reported in plant species grown under elevated CO_2, it is crucial to understand the extent of variation among different plants which exhibit up- or down-regulation of photosynthesis to accurately predict the impact of global CO_2 rise on growth and productivity of plants. The up- and down-regulation of photosynthates under elevated CO_2 is a complex process regulated by morphophysiological changes associated, during plant growth and development, with particular reference to carbon allocation between source and sink tissues of either annual or perennial plants as shown in Figure 2. Van Oosten and Besford[112] showed a rapid down-regulation of rubisco small subunit (rbcS) transcript in high CO_2-grown tomato plants when the sink demand was low. Steady state level of carbonic anhydrase mRNA increased in *Arabidopsis* grown under elevated CO_2 (ref. 64). It was speculated that the progressive accumulation of sugars due to insufficient sink strength renders nuclear genes more sensitive than the chloroplastic genes[112]. Transcript abundance differences were recorded wherein chloroplast-related functions were down-regulated and increased expression was associated with development and signalling functions[113–115].

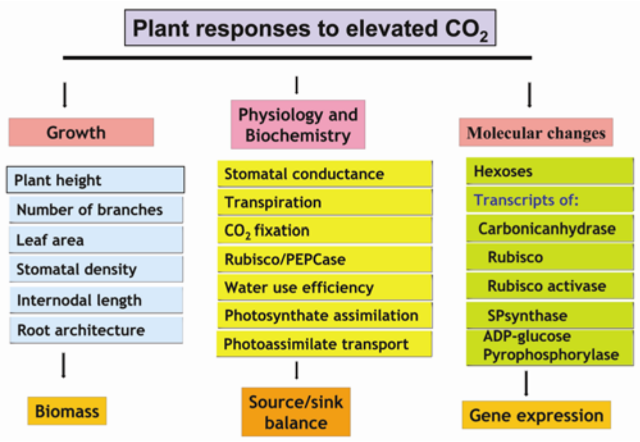

Figure 3. A summary of morphological, physiological, biochemical and molecular characteristics in plants affected by rising atmospheric CO_2 concentrations.

Significant increase in the levels of soluble sugars in the high CO_2-grown leaves was associated with increased activities of hexokinase (EC 2.7.1.1) to be a sensor of sugars in plant cells. Phosphorylated glucose was shown to signal the sugar-sensitive genes in the nucleus, which suppressed biosynthesis of the rubisco small subunit[116]. The varying responses in gene expression to elevated CO_2 among different plants indicate that response of plants to elevated CO_2 is species-specific. Elevated CO_2 also increased the transcript level of genes encoding glycolytic pathway and tricarboxylic acid (TCA) cycle in soybean[114].

Developmental changes associated with the use of different types of growth chambers were also known to significantly affect the profile of transcripts in the leaves of ambient and high CO_2-grown plants. Nitrogen deficiency resulted in reduced expression of genes for chlorophyll protein complex (*cab*)[117]. Fukayama *et al.*[118] have reported down-regulation of genes associated with CO_2 assimilation and up-regulation of genes encoding RuBP regeneration and starch synthesis in the leaves of rice grown under elevated CO_2. Interestingly, the expression of gene for rubisco activase was up-regulated suggesting a compensatory regulation of photosynthesis, which could be present between rubisco and rubisco activase[118].

Figure 3 summarizes morphological, physiological, biochemical and molecular responses in plants affected by elevated atmospheric CO_2. Increased or decreased biomass yields in plants grown under elevated CO_2 would certainly depend upon the source–sink balance which in turn would be associated with changes in activities of key photosynthetic enzymes and the expression of photosynthetic genes.

Conclusions and future strategies

The exact consequences of alarming rise in atmospheric CO_2 concentration are difficult to predict due to the existence of its interactive relationships with many of the environmental variables including temperature, radiation, water availability, visible and ultraviolet sunlight, salinity and soil nutrition. Therefore, the interactive effects of multiple environmental factors on plant responses to rising CO_2 require a careful study. Such information should demonstrate how the multiple environmental factors, when altered in a changed climate, could interact with each other resulting in increase or decrease in the growth and metabolism of several plants.

An immediate and significant increase in photosynthesis can be exploited as a major strategic adaptation to mitigate the global rise in atmospheric CO_2. The veracity of information on morphological, physiological, biochemical and molecular responses of different plants to elevated CO_2 suggests that photosynthetic acclimation and the resulting down-regulation of plant metabolism is due to imbalances between the source–sink capacity.

Future genetic studies on sugar management for biomass production in green plants, exposed to increased CO_2 concentration in the atmosphere, would be extremely important. Genetic transformation of plants for efficient nitrogen assimilation under elevated CO_2 could be highly useful in improving the capacity of nitrogen sink to mitigate excessive accumulated sugars. It would also be useful to understand the impact of elevated CO_2 on primary photosynthetic reactions including photosystem II (PS II)[119] photochemical performance. Evolution of plants from C_3 to C_4 indicates that elimination of photorespiration was due to high level concentration of CO_2 around rubisco. Studies on single cell photosynthesis to substantially increase the concentration of CO_2 around the carboxylating system(s), by engineering C_4 genes into C_3 plants, could lead to producing C_4-like environment in these plants.

The intensity of photosynthetic acclimatory responses to rising CO_2 is species-specific. Significant positive photosynthetic acclimation responses would be noticed if a large sink is available to accommodate excess carbon as seen in the tree species, *G. arborea*. The up-regulation of photosynthesis under elevated atmospheric CO_2 in *G. arborea* suggests that this tree could potentially become a dominant species with better net primary productivity under future global climate change scenario. If photosynthetic acclimation can be decreased either through breeding or by potential recombinant DNA technology, many of the C_3 and C_4 food crops could profit more from the constant increase in the atmospheric CO_2 concentrations and the concomitant changes in the global climate.

Quantification of trade-offs between certain key physiological traits among various plant types is highly essential for the understanding of the potential effects of physiological adjustments as well as the competition between individual plants. A major challenge would be to develop a whole plant for optimal acclimation responses for increasing atmospheric CO_2 concentrations and its interactions with various growth environments. It would also be interesting to evaluate the genetic variability among plants for acclimatory adaptive responses within a specific interactive environmental context. We believe that genetic manipulation of crop plants for positive acclimatory responses is an extremely useful strategy to obtain optimal crop yields under predicted changing global climate.

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