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GROWTH AND DEVELOPMENT OF PLANTS IN A CO_2 ENRICHED WORLD

A. S. DEVAKUMAR AND JAMES JACOB
Plant Physiology Division, Rubber Research Institute of India,
Kottayam - 686 009, Kerala, India

The never ending wants of human race for a better life has forced to discover as well as exploit the natural resources. The material comforts that man has realized so far are highly energy dependant. Globally, the lion share of the human energy needs is met by fossil fuels which leads to emission of CO_2 apart from CO, SO_2 and N_2O into the atmosphere. There is an environmental cost to be paid for the energy that we consume.

Industrial revolution and urbanization has led to clearing of large areas of forests. Forests are reported to contribute 70% of the terrestrial carbon fixation, there by making them a major sink for atmospheric CO_2 (Waring and Schlesinger, 1985). Because of deforestation and burning of fossil fuel an imbalance between the sources and sinks for CO_2 occurs, leading to the build up of CO_2 in the atmosphere. Estimates of CO_2 concentrations for a period of 200 years between 1750 - 1950 have indicated the rate at which CO_2 was building up in the atmosphere (Neftal *et al*, 1985). Between 1750 - 1850 a small increase in the atmospheric CO_2 was estimated to occur from-280 ppm to-285-290 ppm at the rate of 0.05-0.1 ppm year^{-1}. However, between 1850 - 1950, due to industrial revolution accompanied by population pressure, the concentration increased from-290 to-315 ppm which accounts for an average rate of increase of-0.35 ppm year^{-1}. In the last forty five years or so it has increased to more than 350 ppm, the average rate of increase being 0.83 ppm year^{-1}. Currently the CO_2 concentration is increasing at a rate of 1.8 ppm year^{-1} (John and Lloyd, 1992). Unless radical steps are taken to contain fossil fuel burning, the atmospheric CO_2 concentration may reach 50% above the pre-industrial concentrations in the next 20 years. Photosynthesis being the only process through which plants absorb atmospheric CO_2 it plays an important role in the carbon cycle. There is growing interest to know how plants and ecosystems would respond to continued increases in atmospheric CO_2 concentrations.

In the past two decades, quite a good amount of research has gone in to the analysis of plant response to higher concentrations of CO_2. Though there is much to be understood, it is evident from the majority of these studies that there will be increased growth rates, especially in plants with the C_3 type of photosynthetic metabolism. The primary plant process that is affected due to higher concentrations of CO_2 is photosynthesis. It is well established that photosynthetic rates of C_3 plants are limited by the existing atmospheric CO_2 levels (Farquhar,1980; Sharkey, 1985) and therefore, photosynthetic rates in these plants are expected to increase under elevated CO_2 concentrations. Plant stomatal dynamics is another character which plays a key role in allowing CO_2 to enter the plant system and at the same time transpire moisture from the plant body, hence regulating the water use efficiency. How these two processes are co-ordinated under elevated CO_2 becomes important. Respiration is the major catabolic process through which plant looses nearly 50% of the carbon fixed in the process of photosynthesis. Therefore, regulation of respiration under elevated CO_2 levels can alter the carbon balance of plants. Allocation of carbon between various plant organs, reproductive development and senescence are other important issues that are altered due to growth in a CO_2 enriched atmosphere. Response of individual plants to elevated CO_2 will affect various ecosystem processes in the long term. This review is an attempt to cover the responses of plants to elevated CO_2 at different levels of organization of the ecosystem.

PHOTOSYNTHESIS

Plants respond to atmospheric CO_2 through photosynthesis. The primary carboxylase enzyme, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) present in C3 plants is sensitive to atmospheric CO_2 concentration (Bowes, 1993). This enzyme has the dual role of carboxylase and oxygenase. At the prevailing CO_2 concentration, the carboxylase activity is not saturated and it is estimated that almost 30% or even more of the carbon assimilated by the plant is released back into the atmosphere through the processes of photorespiration resulting from the oxygenase activity of this enzyme. An increase in the atmospheric CO_2 concentration will decrease the oxygenase activity and increase the carboxylase activity resulting in increased photosynthesis in a CO_2 enriched atmosphere. A doubling of atmospheric CO_2 concentration from the present level will inhibit photorespiration by 50% (Sharkey 1988). The immediate and marked response of plants to elevated CO_2 owes to the biochemical properties of Rubisco (Long, 1991).

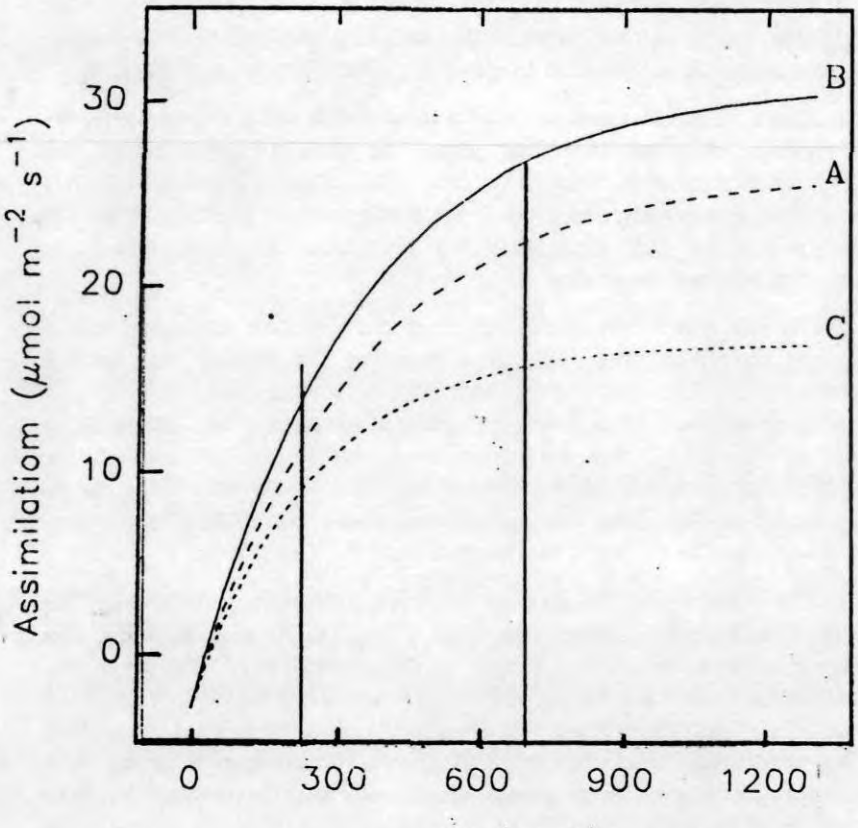

Figure 1. Three hypothetical curves to show various types of photosynthetic acclimation responses. Curve A represents a plant grown in normal ambient CO_2. Curves B and C represent plants grown at elevated CO_2 concentration; B shows a positive acclimation and C shows a negative acclimation. The vertical lines indicate the C_i corresponding to a C_a of 300 ppm and 700 ppm CO_2.

Table 1: The following studies have shown significantly higher photosynthetic rates in plants grown at elevated CO_2 than those grown at normal ambient CO_2 when compared at their respective growth CO_2 concentration

Species	Reference
Scripus olneyi	Jacob et al., 1994
Ranunculuc glacialis	Kroner and Diemer, 1994
Loblolly pine	Tissue et al., 1993
White oak, yellow poplar	Gunderson et al., 1993
Populas grandidentata	Curtis and Teir, 1992
White oak, yellow poplar	Wullschleger et al., 1992
Scirpus olneyi	Arp and Drake, 1991
Soybean	Ziska et al., 1990; Campbell et al., 1988; Clough et al., 1981; Havelka et al., 1984; Cure et al., 1989
Potato	Sage et al., 1989
Cotton (grown with high N)	Wong, 1979
Vine	Kriedman et al., 1976
Pinus taeda	Lewis et al., 1996

The following studies have shown lower (or smaller)rates of photosynthetic ratesin plants grown at elevated CO_2 than those grown at normal ambient CO_2 when compared at their respective growth CO_2 concentrations:

Species	Reference
Phaseolus vulgaris	von Caemmerer and Farquhar 1984; Sage et al., 1989
Brassica oleracia	Sage et al., 1989
Chenopodium album,	
Cotton	Thomson and Strain, 1991
Water Hyacinth	Spencer and Bowes, 1986
Cotton (Grown with low N)	Wong, 1979
Tomato	Yelle et al., 1989a; Besford, 1993
Eriophorum vaginatum	Tissue and Oechel 1987
Tobacco	Raper and Peedin 1978
Cucumber	Peet et al., 1986
Eucalyptus	Roden and Ball, 1996a, 1996b
tomato	Van ooster and Besford, 1995

Many studies have shown that photosynthesis will increase with CO_2 enrichment. (see above Table 1 for a summary). In a study with six different C3 species, a significant increase in the photosynthetic rates was found at elevated CO_2 levels (Ziska, *et al.*, 1991). In soybean 1.5 fold increase of assimilation was seen with CO_2 enrichment (Wong 1990). Long and Drake (1992) has reviewed the photosnythetic response to elevated CO_2 in more details and concluded that there is considerable stimulation in photosynthesis with CO_2 enrichment.

However, there are also reports which are contradictory to the above type of plant response. Photosynthetic rates of plants grown in elevated CO_2 can be often lower than the rates of plants in normal ambient CO_2 when measured at the same back ground CO_2 (DeLucia *et al.*, 1985). This is generally termed photosynthetic acclimation.

The relevant question for a future world rich in CO_2 is that whether plants would adjust their photosynthetic response to elevated CO_2 in the long run. Would they undergo acclimation? If so what would be the extent of photosynthetic aclimation? And will the degree of acclimation vary with the plant type? Three hypothetical scenarios of no acclimation and a positive or negative acclimation are demonstrated in Figure 1.

It has been shown that prolonged exposure to elevated CO_2 results in a gradual reduction in the photosynthetic capacity of these plants. The photosynthetic rate at a given background CO_2 level will be less in a plant exposed to elevated CO_2 for long periods of time than a plant grown at the normal ambient CO2. This is often reflected in the reduced initial slope of the A/Ci response function (carboxylation efficiency). This reduction in the carboxylation efficiency was found to be related to a reduction in the total soluble protein pool, including Rubisco of the leaves grown at elevated CO_2 (Jacob *et al.*, 1994; Stitt, 1991) However, seldom was the photosynthetic rates of the plants grown and measured at elevated CO_2 less than that of plants grown and measured at normal ambient CO_2. In other words, at the operational CO_2 levels plants grown at elevated CO_2 did maintain a higher photosynthetic rate than their counter parts grown at normal ambient CO_2 (Stitt, 1991; Long abd Drake, 1992).

Indirect measurements of Rubisco protein by binding with 14C carboxyarabinitol 1-5, Bisphosphate (CABP) indicated that there was loss of Rubisco protein in cabbage grown in elevated CO_2 (Sage *et al.*, 1989). There was an initial increase in photosynthetic rates, followed by a decrease over days or weeks to a rate similar to that observed in plants grown at ambient CO_2 (Delucia *et al.*, 1985). The decrease in Rubisco content has been attributed to the reallocation of nitrogen to the other more limiting enzyme systems (Woodrow 1994). Because carboxylation is favored through higher CO_2 availability in plants grown at elevated CO_2, decreased Rubisco content appears to be the major factor leading to photosynthetic acclimation (Sage *et al.*, 1989; Arp *et al.*, 1991).

There are also some reports of a reduction in the photosynthetic rate of elevated CO_2 grown plants below the rates of those grown and measured at normal ambient CO_2 (Diaz *et al.*, 1994). This kind of down regulation is generally observed in pot studies and in annuals. There are few reports of such negative down regulation in photosynthesis in perennial and in field studies.

Thomas and Strain (1991) demonstrated a decline in photosynthetic capacity in potted cotton plants because of the smaller size of the containers in which they were grown. The decline in photosynthesis was rapidly reversible if plants were transplanted to larger pots. According to Cure and Acock (1986) a high metabolic or storage sink activity is required for sustained photosynthetic response to elevated CO_2. Long and Drake (1992) found out that photosynthetic stimulation to elevated CO_2 was less (23%) in pot studies than field (65%) studies.

The source-sink balance is a major factor in determining the acclimation of photosynthesis to high CO_2. Variabilities affecting this balance may influence the extent of the reduction of photosynthetic capacity in high CO_2 (Arp, 1991). Arp and Drake (1991) concluded from a long term experiment that after four years of exposure to elevated CO_2, the photosynthetic capacity of Scripus olneyi grown in the field was not decreased. Field grown crops and natural ecosystems, may continue to respond positively to increasing atmospheric levels of CO_2 (Gunderson *et al.*, 1993).

It is proposed that the source sink relationship of the plant plays a key role in the degree of acclimation to elevated CO_2 and this is brought about by alterations in the rates of supply and utilization of photosynthates. In annuals and in plants grown in pots, probably the sink demand for more photosynthates is not high enough to maintain a steady high rate of photosynthesis at elevated CO_2. This results in accumulation of carbohydrates in the source organs which will down regulate photosynthesis through various feed back regulatory mechanisms.

Accumulation of starch and soluble sugars in plants grown at elevated CO_2 is commonly observed (Long and Drake, 1992). Starch accumulation can lead to reduced availability of light to chloroplast (Neals and Nicholls, 1978) tie up inorganic phosphate in metabolic intermediaries and even rupture chloroplast (Stitt, 1991; Cave*et al.*, 1981; Woulf and Strain, 1982).

It has been shown that accumulation of soluble sugars may be involved in down regulating the expression of Rubisco genes and possibly other photosynthetic genes and thus regulate photosynthesis resulting in acclimation of the photosynthetic apparatus (Nie *et al.*, 1995b). A review by Long and Drake (1992) shows that in plants grown in pots, starch and sucrose increased by more than 300% and 150%, respectively. It is possible that organs such as rhizomes, hard wood, stem etc may act as a repository for phoptosynthates and thus increase the demand for photoassimilates more in perennials than annuals. It may be noted that a complete negation of the stimulatory effect of elevated CO_2 on photosynthesis was never seen in perinnials or in field grown plants, but was observed only in a few cases of pot culture experiments with annual crop plants.

Diurnal changes in the stimulation in photosynthesis to elevated CO_2 was affected by end product accumulation and faster movement of photoassimilates from the leaves to the sink was necessary to maintain the continued stimulation in photosynthesis (Zhang and Nobel 1996). Nie *et al.*, (1995b) have reported increased leaf soluble carbohydrates concentration and decreased mRNA transcripts for genes coding for some photosynthetic enzymes and in particular, rbcS and rbcL coding for Rubisco small unit and large subunits, respectively. Feeding glucose to leaves repressed the expression of many Calvin cycle genes (Jones *et al.*, 1996; Sheen 1990). But Riviere-Rolland *et al.*, (1996) reported that Rubisco is not down regulated beyond a threshold supply of N even if soluble carbohydrates accumulate. Activities and transcript levels of Rubisco and carbonic anhydrase were less in plants grown at elevated CO_2 (Majeau and Coleman, 1996). Exposed leaves did not down regulate Rubisco, but shaded leaves did in response to elevated CO_2 (Nie *et al.*, 1995b). It has been suggested that Rubisco is down regulated to tune the rate of photosynthesis in equilibrium with the sink activity of the plant (Stitt, 1991). The capacity for sucrose synthesis may also limit the plants' ability to respond to elevated CO_2. Flaveria plants with less fructose-1,6-bisphopshatase had less response to elevated CO_2 (Micallef *et al.*, 1996). Acclimation of photosynthesis to elevated CO_2 appears to be a classical case of source sink dynamics mediated through end product induced down regulation of events at the molecular and physiological levels.

STOMATA AND TRANSPIRATION

Irrespective of the degree of acclimation in photosynthesis, stomatal conductance and transpiration rates are less in plants exposed to elevated CO_2. This is largely true in short and long term experiments. This results in higher water use efficiency in plants grown at elevated CO_2. If stomata behave in such a way to keep the Ci/Ca ratio constant at nearly 0.7, it is estimated that the stomatal conductance should be decreased by 40% when the CO_2 concentration is increased from 350 to 700 ppm (Long and Drake 1992). However, what is observed in terms of reduction in stomatal conductance and increase in WUE at the single leaf level may not be fully translated into canopy levels, because, plants grown at elevated CO_2 tend to have more leaf area and biomass and thus end up loosing more water than what is predicted from single leaf measurements. But, for comparable leaf area and biomass there is definitely less requirement of water in plants grown at elevated CO_2 than normal ambient CO_2.

A reduction in the transpiration rates has immense implications to the plants, soil and atmosphere. Less transpiration means that the leaf tends to remain slightly warmer. This will affect the leaf metabolism including the response to elevated CO_2. The activity of many enzymes including Rubisco are temperature sensitive. Photosynthesis is highly sensitive to temperature (Long, 1991). It may be noted that Rubisco may become more of an oxygenase and less of a carboxylase as temperature increases, because temperature alters the CO_2/O_2 specificity of Rubisco and the solubilities of CO_2 and O_2 in water (Jordan and Ogren, 1984). Growth and development of organs are extremely temperature dependent. Reduced water loss from the leaf will improve the water status of the leaves and the plant in general. This helps to conserve soil moisture and thus helps in managing drought to some extent. Reduced transpiration will alter the microclimate, particularly the relative humidity in the immediate environment of plants which will have implications for other living organisms sharing the same ecosystem with the plants. Reduced stomatal conductance may eventually result in less canopy conductance leading to substantial reduction in the transpiration rates of plants in large geographical areas and thus affecting the local weather markedly. eg. increased atmospheric temperature or reduced precipitation (Field *et al.*, 1995).

Kimball and Idso (1983) have shown that doubling CO_2 levels decreased transpiration by 30% each in soybean and cotton and 10% in wheat, but by 45% in maize. Allen, (1990) showed 23% decrease in transpiration in maize.-So the range is large and variable. There was 30% decrease in transpiration in Eucalyptus at 680 ppm of CO_2 and at saturating light intensity compared to normal ambient CO_2 (Wong and Dunin, 1987). Jones *et al.*, (1985) reported a significant decrease in transpiration rate of soybean plants at elevated CO_2. Wong and Dunin (1987) noticed 80% reduction in transpiration ratio which was due to a 50% increase in photosynthetic rates and a 30% reduction in transpiration. Elevated CO_2 induced increase in WUE has been reported in many plant species (Oberbauer *et al.*, 1985; Picon *et al.*, 1996). There was 63% improvement in the canopy WUE and a three fold increase in single leaf WUE at elevated CO_2 levels in white clover (Nijs *et al.*, 1989). Data obtained for tropical plants indicate that the WUE increases substantially under elevated CO_2 conditions (Ziska *et al.*, 1991). This higher WUE is attributable to the combined effect of reduced transpiration along with increased photosynthetic rates. This trend was noticed in both C3 and C4 species (Morrison, 1985). For tropical tree species, Reekie and Bazzaz, (1989) report a tendency towards a lower rate of water loss, with increasing CO_2 concentrations.

RESPIRATION

One would expect that the increased supply of photosynthates would stimulate respiration in plants grown at elevated CO_2, because photosynthates are the basic substrates which when oxidized during respiration provide the carbon skeleton and the energy for growth and maintenance of the plant. Respiration has been shown to increase in response to short term increases in the concentration of exogenously applied sugars (Azcon-Bieto 1983). But there is considerable reduction in the respiration rates of plants grown at elevated CO_2 (Amthor, 1991; Bunce, 1990) in spite of increased availability of sugars. This decrease is particularly observed in mature tissues exposed to elevated CO_2 (Bunce, 1990). In young tissues, increased photosynthetic rates stimulated respiration rates under elevated CO_2 (Hrubec *et al.*, 1985; Poorter *et al.*, 1988).

Effects of elevated CO_2 on respiration can be classified into two categories. The first one is the direct effect of elevated CO_2. This is the immediate reduction in the respiratory rate when plants are exposed to elevated CO_2 in the short term and this is often completely reversible. The second is a long term residual effect which is related to changes in the tissue biochemistry and it is less reversible. In this case the respiratory rates of plants grown at elevated CO_2 will be less than the rates of plants grown at normal ambient CO_2 when both set of plants are measured at the normal ambient CO_2 level. This type of respose is related to the long term acclimatrory changes that have occurred to the biochemical composition of the respiring tissue (Farrar and Williams,. 1991).-The most important of them are the changes in the total soluble protein content of the tissues leading to a significant reduction in the tissue N content (Bowes, 1993). A reduction in the tissue N content may explain only part of the reduction in the respiration at elevated CO_2 (Azcon-Bieto *et al.*, 1994). They have found that reduction in the respiration at elevated CO_2 was correlated with reduction in the activities of mitochondrial enzymes, particularly Cytochrome c oxidase. Elevated CO_2 has a direct effect on the mitochondrial respiration (cytochrome c oxidase pathway) and not on the cyanide resistant alternative pathway (Gonzalez-Meler, 1996).

Inhibition in the respiratory rates of plants may contribute substantially to the over all biomass production of plants grown at elevated CO_2 over and above what might be expected from the enhanced photosynthetic rates (Reuvei & Gale 1985).

PRODUCTION AND PARTITIONING OF DRY MATTER BETWEEN ORGANS

Reasonably good number of plant species were studied for their response to rising levels of CO_2 concentration. To quote a few, CO_2 enrichment increased dry matter (DM) production in cereal crops like wheat (Gifford, 1979, Sehonfeld *et al.*,1989; Chaudhuri *et al.*, 1990), rice (Baker *et al.*, 1990), vegetable crops like cucumber, cabbage and carrot (Slack and Hand, 1985; Heij *et al.*, 1984; Wheeler *et al.*, 1994) and fruit crops like oranges and tomatoes (Downtown *et al.*, 1987; Calvert, 1975; Idso & Kimball, 1994), tuber crops like cassava, sweet potato and potato (Imai *et al.*, 1984; Biswas and Hileman, 1985; Ku and Edwarids, 1977) and fibre crops like cotton (Hendrix *et al.*, 1994). Extensive work on oil seeds like soybean also indicated the increased production of DM at elevated CO_2 concentration (Havelka, *et al.*, 1984a). Not just the food crops or crops of commercial importance that would gain from enriched CO_2 concentrations; even weeds like water hyacinth and Echinochloa crusgalli accelerated their growth rates and produced more DM under elevated than normal ambient CO_2 (Poorter *et al.*, 1988; Potvin and Strain, 1985). Increased biomass in plants grown at elevated CO_2 has been reported by Schenk *et al.*, 1995; Rogers *et al.*, 1996a; 1996b; Nobel *et al.*, 1996; Hunt *et al.*, 1996; Roden and Ball, 1996b).

Leaves

Elevated CO_2 levels increase the leaf area (LA) either by increasing the leaf number or by higher expansion rates. Such an increase in LA under elevated CO_2 condition was recorded in soybean (Rogers *et al.*, 1983) and many tree species (Devakumar, 1994). Increase in LA is largely due to more extensive branching in dicotyledonous plants (Rogers *et al.*, 1984) and tillering in grasses (Sionit *et al.*, 1981). Increase in LA is also attributed to increase in expansion rates and a small increase in maximum leaf size (Cure *et al.*, 1989). However, Biswas and Hileman (1985) found increase in LA in sweet potato was primarly due to an increase in branching and greater leaf size. Increase in total number of main stem, leaf nodes and the area of the main stem trifoliate leaves in soybean is shown by Miglietta *et al.*, (1993). Marginal increase in the rate of leaf initiation due to CO_2 enrichment was seen in soybean (Baker *et al.*, 1989; Cure *et al.*,1989), winter wheat (Sehonfeld *et al.*,1989) and weed species Pueraria lobata (Sesak and Strain, 1989).

Specific leaf weight (SLW) increased in response to elevated CO_2 in soybean (Leadley and ·Raynolds, 1988; Leith *et al.*, 1986; Rogers *et al.*, 1983) and sweet potato (Biswas and Hileman, 1985). The increase in SLW was presumably due to the increase in starch content (Huber *et al.*, 1984). Increase in leaf thickness was also attributed to the increased number of palisade cells as seen in soybean (Thomas and Harvey, 1983). On the other hand, maize plants grown in elevated CO_2 did not show any remarkable increase in SLW (Rogers *et al.*, 1983). Elevated CO_2 seemed to have little effect on increasing palisade cells in maize (Thomas and Harvey, 1983).

Roots

In various field and pot experiments with different crops root growth was found to increase when plants are exposed to elevated CO_2 concentrations (Del castillo *et al.*, 1989). In soybean plants root length was found to increase. The elongation rate of individual root axis was not affected, but there was a significant increase in the number of actively growing roots (Del castillo *et al*, 1989).

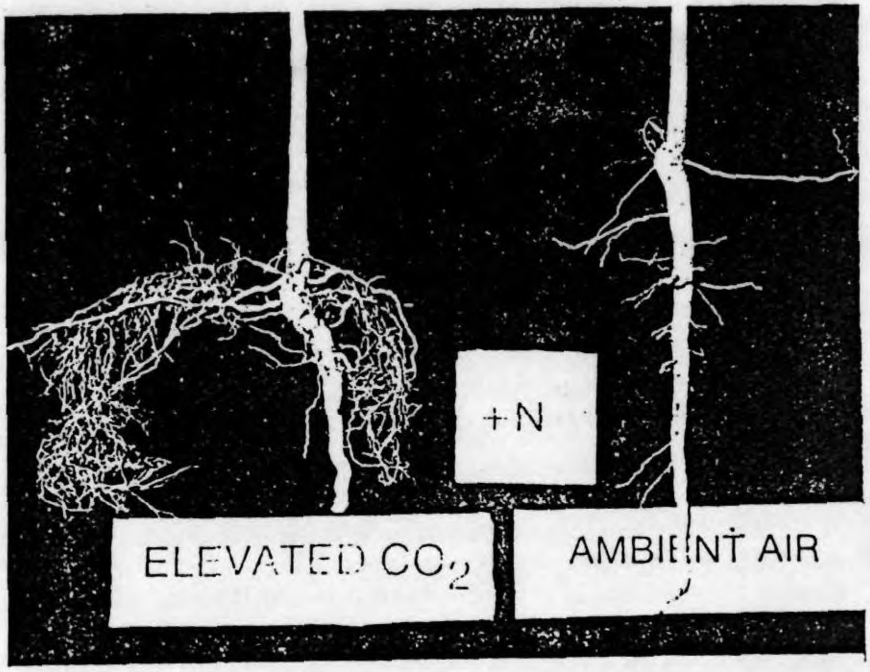

Fig. 2. Allocation of biomass to root growth in seedlings of *Hevea braziliensis* grown under elevated CO_2 concentration and at ambient air. Seedlings were grown with normal dose of nitrogen (+N) fertilizer in the nursery bed.

CO_2 enrichment was found to increase both root biomass at all depths and maximum depth reached by the roots (Baker *et al.*, 1990, Chaudhuri *et al.*, 1990). Similar type of response was seen in sour oranges (Idso and Kimball, 1992). In native vegetation also elevated CO_2 increased root production (Day *et al.*, 1996). Under moisture stress conditions, root growth was found to increase when higher CO_2 concentration was provided indicating that CO_2 can compensate for decreased root growth under drought (Del Castillo *et al.*, 1989). However, the root dry matter of sweet potato increased more with elevated CO_2 in well watered than in droughted plants (Bhattacharaya *et al.*, 1990). In one of our studies where seedlings of Hevea brasiliensis were grown in the nursery beds without any restriction of soil volume, and with normal dose of N, there was a substantial increase in root growth of plants grown under elevated CO_2 (Fig. 2) leading to high root to shoot ratio (Devakumar *et al.*, 1996).

Varying trends were evident from control environment studies on the effect of elevated CO_2 on the distribution of dry matter between organs. For example, no significant effect of elevated CO_2 was seen on the harvest indices and root:shoot ratios (Cure and Acock, 1986). However, in crops where tubers form the bigger proportion of DM, the response was different.

In field grown sweet potato increased divertion of total dry matter to tubers was observed at higher concentrations of CO_2 (Biswas and Hileman,1985; Bhattacharaya *et al.*,1990). Similar results were found in carrot and radish (Idso *et al.*, 1988), but there was little effect of elevated CO_2 on the root:shoot ratio in cotton and soybean (Idso *et al.*, 1988: Radin *et al.*, 1987). An increase in harvest index due to elevated CO_2 was observed in cowpea (Biswas and Hileman, 1985), but there was no effect on the winter wheat (Havelka *et al.*, 1984b). There were no significant changes in the partitioning of dry matter between leaves, stems or pods due to elevated CO_2 in one study on soybean (Ackerson *et al.*,1984), although there was a slight decline in harvest index with increasing CO_2 in another (Rogers *et al.*, 1986). The pattern of biomass distribution between various organs may be influenced by experimental conditions and availability of nutrients.

Reproductive Development

Elevated CO_2 influences the reproductive biology of plants. Floral initiation was observed to be 1-3 days earlier in wheat and sunflower due to higher CO_2 concentration, while the rate of primordial initiation was reduced (Marc and Gifford, 1984). Similarly, flowering was 1-3 days earlier in faba bean, wheat and leucerne (Goudrian and de Rutier, 1983). However, no effect of elevated CO_2 concentration on the timing of reproductive stages was found in soybean (Havelka *et al.*, 1984a; Rogers *et al.*, 1986). Lawlor and Mitchell (1990) are of the opinion that these small changes in reproductive stages with CO_2 are not a direct influence of CO_2 concentration on development.

Economic Yield

Apart from increasing the total dry matter, CO_2 enrichment has also been shown to increase the economic yield. This increase in yield due to CO_2 enrichment is often attributed to an increase in the number of structures rather than in their mean size. In soybean, yield increased almost entirely as a result of more number of seeds (Ackerson *et al.*, 1984; Havelka *et al.*, 1984a; Rogers *et al.*, 1983). However, the number of seeds per pod decreased as a result of CO_2 enrichment (Ackerson *et al.*, 1984). The number of seeds per pod decreased at elevated CO_2 with a concomitant increase in the number of pods in Phaseolus vulgaris (Gustafson, 1984).

Interestingly, in some cases, CO_2 enrichment did not affect the mean seed weight. The number of panicles per plant was almost entirely responsible for a 47% increase in grain yield due to a doubling of CO_2 concentration in rice (Baker *et al.*, 1990) and in wheat (Havelka *et al.*, 1984b). However, Krenzer and Moss (1975) concluded that increase in spring wheat yield was due to an increase in grain weight. Sweet potato yields increased as a result of more tubers rather than mass per tuber (Biswas and Hileman, 1985). The effect of CO_2 enrichment on yield is dependent on the stage of growth at which it is applied. CO_2 enrichment at the early pod development stage did not increase soybean yield, while enrichment from the early pod development until maturity and from the emergence to maturity increased yields by 27 and 36% respectively (Ackerson *et al.*, 1984). A 20% increase in grain yield was recorded in wheat grown at elevated CO_2 under controlled environmental conditions (Mitchell *et al.*, 1996). In wheat Havelka *et al.*, (1984b) showed that exposure to 1200 ppm had maximum effect during the period upto anthesis, while CO_2 enrichment increased yields of spring wheat most during tillering (Krenzer and Moss, 1975).-Kimball (1983) compiled more than 430 observations from 37 species and concluded that increasing CO_2 concentration to double the existing ambient levels will probably increase the yield of plant species. It is suggested that the additional carbohydrates formed with CO_2 enrichment are required during early flower and seed development and are not used during grain filling. Presumably the availability of energy and substrates determines how reproductive organs develop and the abundance of assimilate may allow young tillers and growing primordia to survive and produce more reproductive structures. Lack of proper understanding of factors determining the distribution of carbohydrates and nitrogenous compounds into sinks precludes prediction of the effects of CO_2 enrichment under a range of conditions.

TISSUE COMPOSITION

The biochemical composition of plants undergo changes when grown at elevated CO_2 for a long period. Wheat accumulated double the amounts of sucrose and starch under elevated CO_2 (Havelka *et al.*, 1984b). Sweet potato had greater cellulose content in stems when grown under elevated CO_2, but hemicellulose of leaves together with lignin in stems decreased (Bhattacharaya *et al.*, 1990). The tubers developed under elevated CO_2 contained less protein, total carotenoids and fibre and had a smaller percentage of nitrogen and protein. On the other hand, water content of tissues decreased at high CO_2 (Biswas and Hileman, 1985). Sweet potato grown in elevated CO_2 had more starch in storage tubers and leaves, but not in stems when compared with those grown under ambient CO_2 both under well watered and stress conditions (Bhattacharaya *et al.*, 1990).

There was no effect of water stress under CO_2 enrichment on the elemental composition of maize plants (Loomis and Lafitte, 1987). Similarly no CO_2 enrichment effect was observed on the moisture content, fibre, oil, proteins or fatty acid composition of maize and soybean seeds (Rogers *et al.*,1983; 1986). Havelka *et al.*, (1984b) found no change in the nitrogen content per unit dry matter in leaves, stems or grain due to CO_2 enrichment in winter wheat. However, there are reports that the C:N ratio of cereals decreases, because of accumulation of carbohydrates and reduction in protein content. In experiments with

Scirpus, total soluble proteins, including Rubisco were decreased by 30-50% (Jacob *et al.*, 1994) which may have been the reason for the 15-20% reduction in the tissue N content (Curtis *et al.*, 1989). Similar results were obtained in rice by Rowland-Bamford *et al.*, 1991). Reduced tissue protein and N contents were also observed by workers (Thompson and Drake, 1994; Stitt, 1991; Hunt *et al.*, 1996). Changes in the tissue biochemical composition may affect the grain quality (Willimas *et al.*, 1995). Several studies have shown significant accumulation of carbohydrates in plants grown at elevated CO_2 (Rogers *et al.*, 1996a; 1996b; Stitt, 1991; Nie *et al.*, 1995a; Roden and Ball, 1996a).

Contradictory reports were made by Biswas and Hileman (1985) who noticed an increase in nitrogen content at elevated CO_2 conditions in cowpea. CO_2 had little effect on the water content of a range of plants including carrot, cotton, radish and soybean except under conditions which led to starch accumulation (Idso *et al.*,1988). Changes in the tissue composition will alter the fodder quality of plants, nutritive value of grains and affect the foraging habits of herbivores, microbial decomposition, and therefore, the nutrient cycling through litter decomposition.

SENESCENCE

Leaves grow faster and slightly earlier under elevated than normal ambient CO_2. Therefore, leaves grown under elevated CO_2 conditions attain maturity faster than leaves grown at normal ambient CO_2. There are report showing high concentration of CO_2 decreasing the senescence process. Curtis *et al.*, (1989) reported slower rates of senescence and continued production of new shoots in Scirpus olneyi under elevated CO_2. Mature Bartlett pea fruits when stored under a continuous flow of air with 10% CO_2 for 4 days showed reduced respiration and ethylene evolution rate and fruits remained greener and firmer than fruits stored in ambient air (Kerbel *et al.*, 1988). On the contrary, Bhattacharya *et al.*, (1985) found early leaf senescence in sweet potato grown at 675 ppm CO_2. Senescence was not affected in soybean and wheat (Havelka *et al.*, 1984a; 1984b) and in White oak (Gunderson *et al.*, 1993) grown at elevated CO_2. However, leaves of wheat plants grown in high CO_2 have been seen to senesce three to foour days earlier (Sionet *et al.*, 1981). Recently Mc Connaughy *et al.* (1996) also found no change in senescence in two forest species.

High CO_2 probably has little direct effect on leaf senescence. The mechanism by which CO_2 might affect senescence is not clear. High levels (> 2000 ppm) inhibit the action of ethylene. Early senescence under elevated CO_2 may be correlated with the timing of other phenological events such as flowering (St. Omer and Horvath, 1983) or tuber maturation (Bhattacharya *et al.*, 1985).

INTERACTION OF ATMOSPHERIC CO_2 WITH ENVIRONMENTAL FACTORS

Physiological or developmental responses of plants to increased CO_2 will depend strongly on other environmental factors. Global climate change is largely due to rising temperatures and uncertainty surrounding cloud formation and rainfall pattern. These will intern alter the soil microbial activity which will alter the soil nutrient status and thus influence the response of plants to elevated CO_2.

Temperature

Elevated CO_2 will increase photosynthesis while high temperature will increase photorespiration. For a given atmospheric CO_2, an increase in temperature will increase the oxygenase activity of Rubisco relative to its carboxylase activity and thus the proportion of photosynthesis lost to photorespiration will be more at high temperature (Long 1991). Thus reduction in oxygenase by elevated CO_2 and hence increase in phtosynthesis will have greater effect at high CO_2 rather than temperatures (Long 1991). Photosynthetic stimulation to elevated CO_2 has been more in summer than in winter (Lewis *et al.*, 1996). In the artic tundra, doubling the atmospheric CO_2 only had a transient stimulation on photosynthesis (Oechel and Strain, 1985). But in a warm temperate climate, elevated CO_2 continued to stimulate photosynthesis and biomass production in Scirpus olneyi (Drake, 1992). Ziska *et al.*, (1990) showed that in this species, the relative effect of high CO_2 on photosynthesis was enhanced with a small temperature increase of 4 °C. This geographical variation in the results can be largely explained on the basis of the temperature differences. It is even predicted that boreal forests and tundra will emit CO_2, but tropics will assimilate carbon in a future world rich in CO_2 (Wang and Polgalse, 1995). However, Udayakumar and Prasad (1993) have argued that the benificial effects of elevated CO_2 on photosynthesis will be nullified at high temperatures. In this context it may be noted that Sionet *et al.*, (1987) reported increased leaf photosynthetic rates of soybean in response to elevated CO_2 more at 22/16 oC than at 26/20 °C.

Increased temperature enhanced the growth at elevated CO_2 in various species such as the tropical aquatic plant. Eichornia crassipes (Idso *et al.*,1987), cassava (Imai *et al.*, 1984) and soybean (Sionit *et al.*, 1987). Temperature and CO_2 had opposite effects on growth of determinate crops such as wheat (Mitchell *et al.*, 1996).

Elevated CO_2 concentrations can affect plant growth and development at subtropical temperatures. Orange trees grown at 800 ppm CO_2 before anthesis, showed an increase in fruit set (Downton *et al.*,1987). Growth at elevated CO_2 reduced chilling inhibition of carbohydrate transport in two species of temperate C4 grasses (Potvin, 1985).-At sub-optimal temperature, okra was found to have higher survival, growth and reproduction at elevated CO_2 than normal ambient CO_2 levels (Sionit *et al.*,1981). Rogers *et al.*, (1984) noticed a marginal decrease in seed yield of soybean at 660 ppm CO_2 with temperature range of 23 to 33°C, however seed yield increased with temperature at 330 ppm CO_2. Ryle *et al.*, (1992) found that combined effect of CO_2 and temperature reduced the root to shoot ratio of white clover.

Light

Higher photosynthetic rates under elevated CO_2 are highly dependent on light. Light saturation is usually increased under elevated CO_2 compared with ambient CO_2 (Valle *et al.*, 1985; Wong and Dunin, 1987; Campbell, 1988). Soybean plants grown at high CO_2 exhibited better capability to utilise radiation effectively throughout all light levels than plants grown at low CO_2 (Valle *et al.*, 1985). Light compensation point was reduced from 35 μmoles photons m-2 s-1 at 300 ppm CO_2 to 27 23 μmoles photons m-2 s-1 at 660 ppm CO_2. Sharon and Mitchel (1988) found lettuce leaf growth to respond most to a combination of high light intensities and CO_2 enrichment. Plants exposed to eleavted CO_2 can utilize low light better than those grown at normal ambinet CO_2 (Long and Drake, 1991). The apparent quantum yield for photosynthesis increased by 93% in Quercus plants grown at elevated CO_2 (Scarasciia-Mugnozza *et al.*, 1996). In tropical forests where photon flux and water availability are high (Chazdon and Fetcher, 1984; Becker *et al.*, 1988) plants may be able to express their full physiological potential when exposed to elevated concentration of CO_2.

Nutrients

Plant responses to elevated CO_2 can vary depending on the nutrient status of the soil. One opinion is that plants can perform better under elevated CO_2 levels even if the soil nutrient status is relatively poor, while another view is that continued response of plants to elevated CO_2 needs higher nutrients as biomass production increases drastically at elevated CO_2 (Wong *et al.*, 1992).-

Wong *et al.* (1979) have shown that the response to N fertilizer under elevated CO_2 is species specific. In their experiment with four different Eucalyptus species they have shown a positive interaction with N. Number of leaves per plant increased substantially with high CO_2 when combined with high N. Nevertheless, the nature of allocation of nutrients to different plant parts depends on the nutrient status. Nutrient rich condition will call for less root to service a given shoot mass, with a consequent increase in shoot:root ratio (Wilson, 1988; Wong, *et al.*,1992). Shoot biomass increased by 30% at elevated CO_2 irrespective of N supply, but growth effects closely matched changes in sink development mediated through N supply (Rogers *et al.*, 1996a; 1996b). In rice photosynthesis and growth response to elevated CO_2 were highly dependent on N supply and was mediated through sink development (Ziska *et al.*, 1996). Elevated CO_2 increased photosynthesis in K deficient needles of Norway Spruce (Barnes *et al.*,1995).

Moisture Stress

Under elevated CO_2 conditions stomatal conductance decreases, and therefore, water loss through stomata decreases.-It is clear from several studies on temperate species that increased CO_2 can substantially reduce water loss primarily through stomatal closure (Rogers *et al.*, 1983; 1984). Tolly and Strain (1985) found that for the temperate tree Liquidamber styraciflua and Pinus taeda, elevated CO_2 delayed the onset of water stress effects and allowed the plants to maintain high photosynthetic rates for a longer period of time. The leaf water potentials at which photosynthesis was inhibited in ambient air grown plants was not affected by the CO_2 treatment, indicating that the effect was most likely due to CO_2 effects on conductance, and therefore, on transpiration. In a similar study, Gifford (1979) also noted that water stress enhanced the positive effect of elevated CO_2 on plant biomass.

Elevated CO_2 increased the leaf water potential in Eucalyptus during drought and alleviated the effects of drought (Roden and Ball, 1996a; Scarascia-Mugnozza *et al.*, 1996). Growth at elevated CO_2 reduced the oxidative stress (Schwanz *et al.*, 1996) and even improved the PSII activity which is very sensitive to drought in plants exposed to elevated CO_2 (Scarascia-Mugnozza *et al.*, 1996). C4 photosynthesis responded positively to elevated CO_2 during drought but not under well watered conditions (Samarakoon *et al.*, 1996a). Elevated CO_2 increased the WUE more in drying than well watered cotton plants (Samarakoon *et al.*, 1996b). Irrigation requirements for wheat have been predicted to decline with rising CO_2 concentration (Senock *et al.*, 1996).

ELEVATED CO_2 AND ECOSYSTEM PROCESSES

Biomass

The higher rates of photosynthesis and lower rates of respiration observed in single leaf measurements were translated into field level measurable effects. Measurements of ecosystem carbon uptake rate and respiration showed a considerable increase and decrease, respectively, in plants grown at elevated CO_2 in the field for several years (Long and Drake, 1992). This led to increased biomass produced per unit land area as discussed earlier. Reduced stomatal conductance and transpiration led to better water use efficiency in term of the amount of water consumed to produce a given amount of biomass on a land area basis compared to plants grown at normal ambient CO_2.

Continuous growth at elevated CO_2 in the field for several years led to sustained stimulation in canopy photosynthesis and increased net primary production of both shoot and root systems in plant communities dominated by C3 plants which resulted in accumulation of carbon in the soil (Drake 1992). Increased soil carbon might have increased the soil microbial activity leading to increased production of methane in plots exposed to elevated CO_2 for several years (Dacey *et al.*, 1994). Increased soil microbial biomass carbon due to elevated CO_2 has been reported by Schenk *et al.*, (1995).

Insects and Fungi

Increased availability of photosynthates and decrease in the tissue protein content leads to changes in the C:N ratio which is an important factor determining the forage quality and degradebility of the tissue during microbial decomposition. A reduction in the nutritive value of the plants from the reduction in their protein contents (and thus, of tissue N) may affect the foraging habits of herbivores and fungi in a future world rich with CO_2 (Thompson and Drake, 1994). Insect larvae have been shown to increase the tissue consumption to maintain their total N uptake when fed with N poor tissue (Scriber and Slansky, 1981). However, their growth is often markedly reduced (Price, 1984). Many types of larvae exhibited increased consumption of plant tissues grown at elevated CO_2 (Lincoln *et al.*, 1986; 1989; Fajer *et al.*, 1989) and showed early instar development (Fajer *et al.*, 1989). Thompson and Drake (1994) found that fewer plants grown in elevated CO_2 were attacked by insects and even in those plants infested by the insects less tissue was eaten by the larvae and that the tissue N content correlated positively with the insect infestation. Due to poor nutrient status, the female larvae of beech weevil ate in a compensatory manner, but the male larvae were not affected (Docherty *et al.*, 1996).

Reduced tissue N content has been cited as the reason for reduced fungal infection of wheat grown at elevated CO_2 (Thompson *et al.*, 1993). However in the same study they found that wheat plants grown at elevated CO_2 and subjected to water stress did not reduce their tissue N content but increased the tissue water content and that caused increased fungal attack. Thompson and Drake (1994) reported a significant reduction in the severity of fungal infestation of plants grown at elevated CO_2 only when the tissue N content was less. In some C4 plants where the tissue N did not decrease, better relative water content of the tissue led to increased fungal attack (Thompson and Drake, 1994). Thus the degree of fungal infestation may depend on the tissue composition and water content. Also, changes in the microhabitat, particularly relative humidity resulting from changed stomatal conductance and transpiration may also play a role in fungal and insect population dynamics and hence on the extent of damage that plants may suffer from insects and fungus in a future world with elevated CO_2. It is possible that the microbial population also may show a tissue sensitive response which may affect the rate of litter decomposition and nutrient cycling in forests and agricultural ecosystems.

INFLUENCE OF ELEVATED CO_2 ON PLANT-PLANT INTERACTION

In order to know the plant community response to elevated CO_2, it is necessary to understand how interactions among neighboring plants in a plant community would alter the growth and reproduction of individual species.

In a study where a community of plant species comprising of both C3 and C4 species was exposed to elevated CO_2 concentration, the C3 species showed higher growth rates than C4 species (Carter and Paterson, 1983). Such a species response was later shown to be mainly due to the differences in their photosynthetic response to elevated CO_2 (Paterson *et al.*,, 1984). C3 plants being more sensitive to changes in ambient CO_2 concentration may out grow C4 species in a community (Drake,1992). Due to differences in the species response to elevated CO_2, community structure may change in the native ecosystems (Leadley and Stocklin, 1996) such as grass lands and forests.-

Changes in growth rate can create a competition among the various species of a community for natural resources like light, moisture, nutrients, pollinators and microclimatic conditions like humidity, temperature and wind (Bazzaz and carlson, 1984; Zangler and Bazzaz, 1984). Therefore, apart from photosynthetic responses of C3 and C4 species, the competition for natural resources will bring in plant-plant interaction (Bazaz *et al.*, 1992) and may lead to composition changes in the community.

Another possible way through which elevated CO_2 concentration might affect the plant-plant interaction is through the changes that it brings about in the tissue composition. We have seen that CO_2 affects C:N ratio significantly in addition to other tissue components. This can lead to differential preference of insects and pests and there by some species become more susceptable in multiple species stands. Pollinators that frequent a species might also change based on the nectar secreting ability the nutritive value of which may be again altered due to growth in elevated CO_2. This can affect the reproductive fitness of certain species. As a cumulative effect, after a few generations this can lead to changes in the species composition of a community.-When such a differential growth response occurs, certain species may become locally extinct after several generations following the Darwinian laws of natural selection.

CONCLUSIONS

This review reveals how molecular, physiological and environmental factors regulate carbon metabolism in vegetation grown at elevated concentrations of CO_2 and how that will have a strong impact on global carbon cycle. Annually, global photosynthesis and respiration cycles more than 100 GT of CO_2 between the atmosphere and the pools of carbon in terrestrial ecosystems (Gifford, 1994; Goudriaan, 1993). Analysis of the major sources and sinks for carbon in the biosphere suggests that a net 0.4-2.4 Gt/year uptake into terrestrial ecosystems may be the result of CO_2 fertilization caused by increasing atmospheric CO_2 since 1958 (Gifford, 1994; Goudrian, 1993). The mechanisms regulating carbon flow in ecosystems in response to rising CO_2 and climate change will determine the future levels of atmospheric CO_2.

Majority of the CO_2 experiments have been conducted in controlled environments, and the lack of agreement between various studies is mainly because of the varying conditions under which the experiments were conducted. Different types of systems such as closed structures, open top chambers, free air CO_2 enrichment (FACE) system etc are used in CO_2 experiments. In majority of the CO_2 experiments potted plants are used.-A major inadequacy of pot experiments is the small volume of soil available to roots which necessitates frequent watering and application of nutrient. The small soil volume in pots may restrict the growth for many reasons which cannot be over come by application of water and nutrients in more split doses (Lawlor & Mitchell, 1991; Arp,1991; Radin *et al.*, 1987; Arp and Drake,1991; Campball *et al.*,1988). One must take all these factors in to consideration while comparing or making any conclusions from the different CO_2 studies conducted by different researchers under different growth conditions.

There are a number of models developed to predict future growth and yield of plants in the agricultural and natural ecosystems and the changes in ecosystem and climate processes that are associated with the increasing atmospheric CO_2 concentrations. Predictions using models that are based on valid scientific data, both metereological and biological will be useful to develop guidelines for future planning.

Productivity of vegetation is an outcome of highly complicated interactions of many environmental, soil, water, nutrient and plant factors. Interaction of environmental factors plays a key role in regulating the physiological processes of plants to elevated atmpspheric

CO_2 concentration. The compositional changes in the tissue .due to elevated CO_2 concentration can bring in changes in the plant community making some plants more vulnerable and some less to insect/pest damage. In addition to this, the varying species response to elevated CO_2 concentration in terms of growth may cause changes in the composition of the plant community in a few generations of a species growth at elevated concentrations of atmospheric CO_2.

There is a general expectation that rising CO_2 and increasing global temperature will be accompanied by increased production of plant biomass. This is largely based on the well known kinetic responses of photosynthesis, growth and water use efficiency to increased atmospheric CO_2 concentration. Changes in respiration rates can also contribute significantly in the overall carbon budget of a plant. Because more than 50% of the carbon assimilated through photosynthesis is lost in respiration in the life time of a plant. The physiological and biochemical processes of vegetations have a pivotal role in global carbon cycle. The ability of plants to put on more biomass under elevated atmospheric CO_2 concentration can be expected to have a positive impact on enhancing growth rates of crop plants and agricultural productivity.

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