EFFECT OF ENHANCED LEVELS OF CARBON DIOXIDE ON PRIMARY PRODUCTIVITY

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To
My family

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CERTIFICATE

The research work embodied in this dissertation entitled "Effect of enhanced levels of carbon dioxide on primary productivity" has been carried out in the School of Environmental Sciences, Jawaharlal Nehru University, New Delhi. This work is original and has not been submitted so far, in part or full, for any other degree or diploma of any University.

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CONTENTS

PART II:EFFECT OF ENHANCED LEVEL OF CO_2 ON SPINACEA OLERACEA

Materials and Methods
Results
Discussion

ABSTRACT

REFERENCES

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

2. Schematic diagram of open top chamber system used in the experiment
3. S. oleracea cv. All Green plants after ten days exposure to A. Ambient CO_2 B. Elevated CO_2 (600 $\pm$ 50 ppm)
4. S. oleracea cv. Banerjee's Giant plants after ten days exposure to A. Ambient CO_2 B. Elevated CO_2 (600 $\pm$ 50 ppm)

PART I:EFFECT OF ENHANCED LEVEL OF CO_2 ON PLANTS

Carbon dioxide is one of the natural constituents, comprising 0.03% of the earth's atmosphere. Plants take up CO_2 and assimilate carbon by the process of photosynthesis creating reduced carbon ($C_nH_{2n}O$). The reduced carbon is stored in biota, in dead organic matter in soil and in the top layers of the sediments, in coal, oil and gas reserves, and as highly dispersed carbon in the lithosphere. Expanding human activities involving fossil fuel combustion and large scale deforestation have resulted in increased levels of CO_2 in the atmosphere.

The atmospheric concentration of CO_2 is now 25% higher than during the first half of the last century. (Houghton and Woodwell, 1989). Direct sampling of air at the South Pole and Mauna Loa, Hawaii, has shown that the CO_2 concentration of the atmosphere has risen from about 314 ppm in 1958 to over 345 ppm today (Keeling et al., 1989). This change is due to, the burning of fossil-fuels which is ejecting approximately 5-6 g T (1 giga tonne = 10^9 tonne) of carbon into the atmosphere yearly, and deforestation which may account for another 1-2gT (Moore and Bolin, 1986/87 ; Detwiler and Hall,1988). Future projections indicate that by the year 2065, atmospheric CO_2 levels will reach 600 ppm (IPCC, 1990).

In addition to carbon dioxide other atmospheric trace gases such as methane, ozone, nitrous oxide and chlorofluorocarbons (CFC_{11} and CFC_{12}) are transparent to incoming solar radiation but absorb the out going infra-red radiation from the earth. This phenomenon is known as the 'greenhouse effect 'and the gases causing it are known as the greenhouse gases (Jager, 1986). Increasing levels of greenhouse gases are expected to bring serious changes in global climate (Jager, 1986). The focus of this review is to evaluate the effect of enhanced levels of CO_2, on plants at individual and ecosystem levels.

Rising levels of CO_2 can affect plants in two ways, (i) directly due to higher concentration of ambient CO_2 on plant growth and development or (ii) indirectly due to global climate change triggered by rising levels of CO_2 manifested as rise in average ambient temperature, alteration in precipitation regimes and associated changes (Warrick et al., 1984). In general, higher ambient CO_2 stimulates greater net photosynthesis, the so called CO_2 fertilization effect. High CO_2 levels suppress transpiration through partial closure of stomata, resulting in greater water use efficiency (Warrick et al., 1984). However, the extrapolation from individual plants to dynamic ecosystems is highly tenuous. Competetion between plants, and

consequent interaction between plants, animals and microbes are likely to change drastically (Warrick et al., 1984).

A cursory, global survey of natural systems reveals an unmistakable correspondence between the broad features of regional climates and the major characteristics of world's biomes. Major changes in the global climate will bring about major changes in natural biomes which will be particularly more dramatic in transtion zones or ecotones (Warrick et al.,1984).

A. SPECIES LEVEL RESPONSE:

Species level responses to elevated CO_2 have been discussed in relation to herbaceous, tree and aquatic plant species.

A.1 HERBACEOUS SPECIES

Predictions of crop growth and yield under elevated CO_2 are incomplete if based solely on photosynthetic response at the level of primary CO_2 fixation mechanism. Other primary and secondary responses (like stomatal conductance and morphological development) and feedbacks interpose between photosynthetic metabolism and crop yield and must be taken into consideration in assessing the effects of higher atmospheric CO_2 in particular a CO_2 doubling (Warrick et al., 1984).

Growth and Development:

Leaf area : In several C_3 species, leaf area has been found to increase under elevated CO_2 conditions in response to improved photosynthate supply (Rogers et al., 1984; Delucia et al., 1985). Soybean (Glycine max) grown at twice normal CO_2 showed an increased leaf area (Rogers et al., 1984). Elevated CO_2 had a small accelerating effect on the rate of leaf initiation and also caused a faster expansion of the G. max leaves (Rogers et al., 1986). In cotton, (Gossypium hirsutum) CO_2 enrichment caused a significant increase in leaf area (Delucia et al, 1985) in the first 20 days, following emergence, (Mauney et al., 1978). CO_2 enrichment resulted in increased total canopy area, 36% greater than controls on day 22, in soybean (Cure et al., 1987). In sugarbeet (Beta vulgaris) (Wyse, 1980) increased CO_2 also increased leaf number in addition to leaf area increase. In bean (Phaseolus vulgaris) plants (Porter and Grodzinski, 1984), there was an increase in leaf area only after 14 days of CO_2 enrichment. On 14th day in ambient treatment leaf area was 144.3 cm^2/plant compared to 183.6 cm^2/plant under high CO_2. Rice (Oryza sativa) does not increase leaf area appreciably under CO_2 enrichment even though dry weight growth responds (Yoshida, 1972; Morison and Gifford, 1984).

Conversely, several C_4 species that did not show a response of net CO_2 fixation per unit leaf area or per unit of intercepted radiation, neverthless responded with an increase in leaf area (Patterson and Flint, 1980; Morison and Gifford, 1984b). Growth analysis of both maize (Zea mays) and itchgrass (Rottboellia exaltata) (Patterson and Flint, 1980) showed that leaf area increased while NAR (net assimilation rate) was unaffected by CO_2 enrichment to above 600 ppm. Similarly with a doubling of normal CO_2, Morison and Gifford (1984b) observed increases in leaf area of the C_4 species Amaranthus edulis (15%), Sorghum bicolor (29%), and Zea mays (40%), NAR remaining unchanged by high CO_2. Thus, the increase in growth by higher CO_2 in these C_4 species was attributable to greater interception of light because of bigger leaf area, not to increased photosynthesis per unit leaf area, implying that CO_2 was acting on leaf area development in some way other than via CO_2 effects on photosynthesis rate (Morison and Gifford, 1984).

The mechanisms involved in CO_2 - stimulated leaf area expansion have not been widely investigated. Depending on the species, the component of leaf area increase varies between axillary growth, faster rate of leaf emergence and development of larger leaves (Goudriaan and de Ruiter, 1983).

Growth rate : Increased growth rates at high CO_2 levels may be caused by a number of factors (Mott, 1990). These could be, an increased supply of photosynthetically fixed carbon, increased plant water potential and turgor due to stomatal closure, increased osmoregulation under water stress due to improved carbon supply, decreased dark respiration rates or direct effect of CO_2 on rates of cell division or enlargement (Mott, 1990).

Growth rates are generally enhanced when elevated CO_2 is given in the early stages of growth (Thomas et al., 1975; Mauney et al., 1978). But with small grain cereals like wheat (Triticum aestivum), interesting results have been obtained. An increase in grain yield (36%) with a doubling of CO_2 is nearly twice the increase in biomass of immature crops (20%) (Kimball, 1983). The effects of high CO_2 on wheat seedlings is small (Neales and Nicholls, 1978) compared to the effects once tillering and grain formation occur (Gifford, 1977; Sionit et al., 1981a).

Despite decreases in photosynthetic rates and relative growth rates during long-term CO_2 enrichment, plants grown at high CO_2 concentration usually continue to grow at a faster absolute rate and maintain higher dry weight over control plants throughout the enrichment period. This has been attributed to the fact that increases

in growth rate during the early period of growth increase the leaf area over that of controls. This allows higher rates of photosynthesis per plant and a higher growth rate, despite similar rates of photosynthesis per leaf area (Spencer & Bowes, 1986; Curtis et al., 1989a; Mauney et al., 1978).

Biomass : Cure and Acock (1986) calculated that the average increase in biomass for C_3 grasses grown under twice normal CO_2 concentration was 28% but increases of 100% or more in biomass have been reported for some C_3 plants (Delucia et al., 1985; Mauney et al., 1978; Wong, 1979). Sage et al. (1989) found that in five C_3 species, they studied, growth at high CO_2 significantly increased leaf dry weight per area, probably due to accumulation of starch. Clough et al. (1981), experimenting with soybean plants, observed that under high CO_2 vegetative dry weights and per pod dry weights were higher compared to those under ambient CO_2. Bean (P. vulgaris) plants exposed to high CO_2, (Porter and Grodzinski, 1984) after 14 days, showed a 71% increase in dry weight, and specific leaf weight was also found to increase. Fresh and dry weights of whole cowpea (Vigna unguiculata) plants increased at elevated CO_2 (640 ppm) concentrations (Mbikayi et al., 1988) as compared to plants grown at ambient CO_2. Patterson and

Flint (1980) studied dry matter production in two C_3 species (G. max and Abutilon theophrasti) and two C_4 species (Z. mays and R. exaltata). C_3 dry weight growth responded to CO_2 concentrations above 350 ppm whereas C_4 species did not respond. In Pisum sativum (Paez et al., 1980) not much difference in total plant dry weights was observed at high CO_2 (1000 ppm) and ambient CO_2 (350 ppm) even after 39 days of exposure. In B. vulgaris , Wyse (1980) observed a 180% increase in total dry weight over a 10 day exposure to 1000 ppm CO_2 compared to ambient. Delucia et al. (1985) found a similar increase in dry weight in G. hirsutum plants grown at 675 ppm (72% increase) and 1000 ppm CO_2 (115% increase) over that of plants grown at 350 ppm CO_2. Cure et al. (1987) observed a 69% increase in dry weight of high CO_2 (700 pmm) grown G. max plants over a 3-week period. It seems probable that the increase in dry weight in C_3 plants under elevated CO_2 is largely the result of increased photosynthetic assimilation whereas C_4 plants do not respond to elevated CO_2 in this respect.

Flowering : No particular trend in the onset of flowering in relation to elevated CO_2 concentration is discernible. Amaranthus retroflexus flowered significantly earlier at 700 ppm CO_2 than at 350 ppm, whereas Setaria faberii flowered significantly later at 700 ppm CO_2 (Garbutt et al., 1990). A. theophrasti and Ambrosia

artemisiifolia showed a trend towards earlier flowering at high CO_2 (Garbutt et al., 1990). A slowing in the rate of flower development in Sorghum under elevated CO_2 without any change in dry weight growth (Marc & Gifford, 1983) has been observed. There is no conclusive evidence that dry weight is preferentially allocated to reproductive structures as fruits and flowers. Calculated yield increases for CO_2 enrichment of agricultural species (Kimball, 1983; Cure & Acock, 1986) are not different from increases in total biomass with CO_2 enrichment indicating that carbon is allocated more or less equally among reproductive and vegetative portions of the plant. However investigations in this area would be most interesting. Study of effects of CO_2 enrichment on morphology and functioning of floral parts would provide us with a better insight into the mechanism(s) underlying the observed responses.

Senescence : An increased rate of senescence (aging) due to CO_2 enrichment, has been widely reported in the literature. Accelerated senescence has been observed in G. hirsutum (Chang, 1975), under 850 and 1000 ppm CO_2. But Carter and Peterson (1983) observed delayed senescence in Sorghum at 600 ppm CO_2. Curtis et al. (1989a) observed a decreased rate of senescence in the C_3 sedge Scirpus olneyi. Although the observed senescence effect is minor, and is not

always detected (eg. no effect in wheat; Gifford, 1977), it could possibly be pervasive due to increase in ethylene, a natural growth regulator in plants which accelerates senescence. High CO_2 concentrations caused H. annus shoots to produce more ethylene, (Dhawan et al., 1981). In addition, the CO_2 source for enriching the air might also contain unsuspected traces of ethylene which could promote early senescence (Morison and Gifford, 1984a). Early senescence under elevated CO_2 may also be correlated with the timing of other phenological events such as flowering (St. Omer and Horvath, 1983).

Physiology and Biochemistry

Stomatal conductance : The presence of a CO_2 - impermeable cuticle on most aerial surfaces of land plants makes the direct sensing of atmospheric CO_2 unlikely. Most of the known responses to atmospheric CO_2 can be attributed to changes in intercellular CO_2 (C_i) concentration (Mott 1988) and more specifically to the effect of changes in C_i on stomatal conductance (Mott, 1990). Changes in ambient CO_2 concentration will cause changes in C_i, such that the ratio of ambient CO_2 to C_i remains approximately constant (Bell, 1982). The general trend in response of stomatal conductance to increasing CO_2 concentrations is that of a decreasing one (Cure and Acock, 1986). In soybean (Rogers et

al., 1984), stomatal conductance measurements have been shown to decrease significantly, from 1.0 cm s^{-1} (300 ppm) to 0.25 cm s^{-1} (900 ppm). In cotton (Delucia et al., 1985) , a short term exposure to CO_2 caused stomatal conductance to decline from 0.6 cm s^{-1} (350 ppm) to 0.4 cm s^{-1}(100 ppm). In V. unguiculata (Mbikayi et al., 1988), stomatal conductance on adaxial surface was lower than abaxial surface in leaves, but decreased in both cases at 655 ppm CO_2 compared to 354 ppm. During long-term exposures to elevated CO_2, a further decline in stomatal conductance values has been observed (Spencer & Bowes, 1986). There is no difference between C_3 and C_4 plants with respect to the sensitivity of stomatal conductance to change in CO_2 concentration (Morison and Gifford, 1983). A reasonable approximation is that, for most species and environmental conditions, a CO_2 doubling will cause about a 34% decrease in stomatal conductance (Cure and Acock, 1986).

The mechanism for stotmatal responses to CO_2 is unknown at present (Mott, 1990). The existence and functioning of the photosynthetic carbon reduction cycle in guard cell chloroplasts is controversial (Tarczynski et al., 1989), however it is possible that stomatal sensitivity to CO_2 may depend on the response of photosynthesis to CO_2 in stomatal guard cells (Mott, 1990). Stomatal responses to C_i have evolved to compensate for changes in C_i caused by

changes in mesophyll demand for CO_2, they may not regulate gas exchange optimally for changes in C_i caused by an increase in ambient CO_2 (Mott, 1990). Other aspects of stomatal physiology including the effects of CO_2 enrichment on stomatal responses to light and humidity, are areas which have to be probed in order to define an optimal response of stomata to enriched ambient CO_2 concentrations (Mott, 1990).

Chlorophyll content : A generally decreasing trend in chlorophyll content with increasing CO_2 concentration has been observed for most of the species studied. Madsen (1968) reported, no variation in chlorophyll content in tomato (Lycopersicum esculentum) when measured on a leaf area basis, but on a fresh weight basis reduction in chlorophyll was observed at elevated level of CO_2. In G. hirsutum (Chang, 1975), about 42% decrease in chlorophyll content on fresh weight basis was observed at 1000 ppm CO_2 compared to ambient CO_2. In Trifolium subterraneum (Cave et al., 1981), total chlorophyll, calculated on a dry weight basis, in immature leaves was 34% lower in 1000 ppm treatment compared to 350 ppm. Mature leaves showed a 30% decrease in chlorophyll. Chlorophyll a : b ratio also decreased for high CO_2 plants, 22% decrease in immature leaves and a 33% decrease in mature leaves (Cave et al., 1981). Delucia et al. (1985) also reported a 61% decrease in total

chlorophyll on dry weight basis and a decreased Chl a:b ratio in cotton at elevated CO_2 (1000 ppm) compared to 350 ppm grown plants. Sage et al. (1989) reported a decline in chlorophyll content at 950 ppm CO_2 in Chenopodium album (14%) and Brassica oleracea (34%) compared to ambient.

The decrease in chlorophyll content associated with increasing atmospheric CO_2 could be due to chloroplast degeneration as a result of excess starch accumulation (Madsen, 1968). The electron micrographs offer additional evidence that increasing starch accumulation in plants growing in enriched CO_2 atmospheres affects chloroplast structure and whole plant chlorophyll content, contributing to chlorosis of leaves. (Cave et al., 1981). The lower chlorophyll a:b ratio is primarily accounted for by a reduction in chlorophyll (a) content and not an increase in chlorophyll (b) (Cave et al., 1981). Decline in chlorophyll content could thus place serious limitations on the photosynthetic capacity of plants in the long run.

Photosynthesis : Photosynthesis plays a central role in the physiology of plants. Thus, it is likely that many responses exhibited by plants to elevated CO_2 are, infact, mediated by response of photosynthesis to elevated CO_2. C_3 and C_4 plant photosynthesis has been reported to respond to elevated CO_2 in a strikingly different manner (Pearcy and Ehleringer, 1984).

Short term exposure of C_3 plants to elevated CO_2 typically causes an increase in the rate of net photosynthesis. In contrast several studies have shown that long term exposure can result in a subsequent decline in net carbon assimilation when measured on a leaf area basis. Cure and Acock (1986) calculated that photosynthesis is initially stimulated at an average of 52% after doubling the CO_2 concentration. But this average increase is only 29% after plants acclimate to new CO_2 concentration. Tobacco (Nicotiana tabacum) plants grown at 1000 ppm CO_2 for a period of 35 days showed a 20% decline in the rate of net photosynthesis. (Raper and Peedin, 1978). In another study, long term exposure (4 weeks) of cotton plants to 1000 ppm CO_2 caused a decline in net photosynthesis after an initial increase. The 350 ppm plants consistently had higher rates of photosynthesis than the 675 ppm or 1000 ppm CO_2 plants. (Delucia et al., 1985). In the C_3 species G. max and A. theophrasti (Patterson and Flint, 1980) increasing CO_2 concentration from 350 to 600 ppm increased the NAR (Net assimilation rate) by 35%. In C_4 species, Z. mays and R. exaltata, elevated CO_2 did not affect the NAR, (Patterson and Flint, 1980). In a C_3 sedge, Scirpus olneyi (Ziska et al, 1990), however, increased photosynthetic rates were maintained throughout the two years of experiment, without an acclimation to high CO_2.

The observed increase in net photosynthesis in C_3 plants under CO_2 enrichment could be due to an improved competitive advantage of CO_2 molecules over O_2 molecules for the active sites on rubisco. The reduced carbon flow through the photorespiratory cycle leads to less photorespiratory CO_2 loss as well. Hence C_3 plants are expected to respond positively to elevated CO_2 atmospheres (Warrick et al., 1984). In contrast, the primary carboxylase in C_4 plants is PEP carboxylase which is not competitively inhibited by O_2. Photorespiration is therefore negligible. PEP caboxylase has a higher effective affinity for CO_2 than does rubisco in the absence of O_2, so the enzyme is close to CO_2 saturation at the present atmospheric CO_2 concentration. Also in C_4 plants rubsico is located in the bundle sheath cells, where the CO_2 concentration largely saturates carboxylation and inhibits oxygenation. Therefore, one would not expect a significant enhancement of C_4 crop growth from increased CO_2 in so far as the primary carboxylase properties are concerned (Warrick et al., 1984).

The mechanism (s) responsible for the decrease in photosynthetic rate over long term exposure have not been established clearly. Under long term exposures, the activity of growth sinks and the associated ability to utilise the increased supply of photosynthate plays an important role (Clough et al., 1981). If sink demand is insufficient,

assimilates can accumulate in source leaves, resulting in end product inhibition of photosynthesis. Soybean plants in which pod set had taken place were taken and trimmed to either 21 pods (high sink) or 6 pods (low sink) (Clough et al., 1981). Comparing plants from the same CO_2 treatment, high sink plants had greater rates of photosynthesis at 1000 ppm CO_2 than the low sink plants. Thus, high source : sink ratios are associated with lower rates of photosynthesis. The more rapidly storage tissues are filled the more rapidly rates of photosynthesis decline. Mechanism for feedback inhibition of photosynthesis is supported by measurements showing increased levels of starch and sucrose in many plants subjected to prolonged CO_2 enrichment (Spencer and Bowes, 1986). The degree of starch accumulation in plants grown in high CO_2 is often so great that distortion of chloroplasts by starch grains has been suggested as a mechanism for decreasing the rate of photosynthesis (Madsen, 1968, Cave et al., 1981).

A decline in rubisco activity under elevated CO_2 could be another factor in acclimation of plants to high CO_2. At normal ambient CO_2 concentration, photosynthesis is limited significantly by RUBP regeneration capacity, and sucrose synthesis capacity (Von Caemmerer and Farquhar, 1984). When ambient CO_2 is increased, however, the

apparent maximum catalytic capacity of rubisco is also increased and the balance among limitations is upset RUBP regeneration and sucrose synthesis become more limiting and carboxylation capacity (Rubisco) becomes less limiting (Von Caemmerer and Farquhar, 1984). In view of the altered balance among these three limiting elements, it has been hypothesized (Sage et al, 1989) that acclimation of the photosynthetic system to high CO_2 should involve re-allocation of protein nitrogen from rubisco to the enzymes of light harvesting RUBP regeneration and starch and sucrose synthesis. The effects of such a re-allocation would be to restore the balance among limiting factors. Since rubisco constitutes the single largest sink for N in the photosynthetic apparatus, changes in its content will have greatest effect on N partitioning within the leaf. Rubisco activity does decline following long term exposure to high CO_2. In B. oleracea and in C. album, (Sage et al., 1989) leaf rubisco content was lower in plants grown at high CO_2 (950 ppm). The percent of leaf N invested in rubsico was lower in plants grown at high CO_2, particularly C. album. The rubisco activation state was also lower in leaves of all five species grown at high CO_2 (Sage et al, 1989). In P. vulgaris too, rubisco activity dropped by 40% under elevated CO_2. Thus, a decline in rubsico activity under elevated CO_2 plays an important role in acclimation of plants under high

CO_2. There is no evidence, however, to suggest that plants re-allocate nitrogen to relieve limitations by starch and sucrose synthesis. Sucrose synthase and sucrose - P - synthase activities in plants grown at high CO_2 were found to be similar to those in plants grown at normal CO_2 (Peet et al, 1986).

Photosynthate partitioning: Ambient CO_2, level seems to play a definite role in photosynthate partitioning (Wyse, 1980). Reports on biomass partitioning under elevated CO_2 have shown mixed results.

In soybean (Cure et al, 1987) by day 22 of exposure to 700 ppm CO_2, dry weight of leaves increased 60%, stems 73% and roots 88% above the controls indicating preferential allocation to roots. In B. vulgaris (Wyse, 1980), the additional photosynthate resulting from enhanced photosynthesis at elevated CO_2 (1000 ppm), was allocated preferentially to root sink. In Bromus mollis root: shoot ratio increased at elevated CO_2 mainly due to increase in root biomass (Larigauderie et al., 1990). The partitioning of biomass between roots and shoots was not affected by CO_2 concentration in the C_4 species, Z. mays and R. exaltata (Patterson and Flint, 1980) However, in the C_3 species, (G. max, A. theophrasti) the root : shoot ratios tended to increase with increasing CO_2 concentration (Patterson and

Flint, 1980). These effects of CO_2 enrichment on dry matter partitioning between roots and shoots may have implications for weed - crop competitive interactions. C_3 weeds will become more competitive with crops having C_4 pathway. Weeds with C_4 pathway may become less competitive with crops having C_3 pathway (Patterson and Flint, 1980). In another study on soybean (Finn and Brun, 1982), it was observed that additional photosynthate provided by CO_2 enrichment was being utilized predominantly by shoot material for growth and storage, with relatively little being partitioned to the roots and nodules. This result is contrary to observations on soybean noted above. In cotton (Delucia et al., 1985) too, biomass partitioning was preferential to the leaf sink followed by stems and least to the roots.

Biomass partitioning thus seems to be guided by individual plant characterstics and requirements and does not seem to follow a general pattern under CO_2 enrichment.

Starch content : Elevated CO_2 treatment has a profound effect on the diurnal pattern of leaf starch accumulation (Delucia et al., 1985). Under ambient CO_2 levels, starch concentration gradually increases throughout the light period and declines to the previous morning's levels by the end of the dark period (Delucia et al., 1985). In elevated CO_2 (675 and 1000 ppm) grown cotton plants

(Delucia et al., 1985), the rate of increase and maximum starch concentration during the light period was considerably greater. Due to insufficient translocation and or degradation of carbohydrates in high CO_2 grown plants, the starch pool did not return to the previous morning's level by the end of dark period. A similar behaviour was observed in tomato plants by Madsen (1968). At elevated CO_2 concentrations starch content maxima is reached within 1-2 hr after sunrise, whereas for control plants, it is reached only at noon. Cave et al. (1981) observed that, in T. subterraneum leaves, there was a significant increase in starch content in late afternoon as compared to early morning. In high CO_2 plants the increase was 135% whereas in control plants it was 46.7% only. In soybean (Finn and Brun, 1982). majority of the additional carbohydrates provided by CO_2 enrichment were stored in the shoots as leaf starch, resulting in 46% increase in foliar starch content.

In most C_3 plants, CO_2 enrichment produces a large increase in starch concentrations, causing a disruption of equilibrium in the starch pool size on a diurnal basis. This disequilibrium in pool size would grow with each day, unless and until degradation and/or translocation to sinks, of this additional starch takes place. CO_2 enrichment has been found to have little or no effect on concentration of soluble sugars resulting from

degradation of additional starch (Madsen, 1968). Sink size and number has been found to increase under CO_2 enrichment for few plants like wheat, rice, soybean (Gifford, 1979; Cock and Yoshida, 1973; Finn and Brun, 1982).

Starch accumulation can limit the rate of photosynthesis by feedback inhibition during long term exposure, thus putting constraints on the increase in productivity under high CO_2.

Respiration : Experiments on the effects of high CO_2 concentrations on respiration show mixed results. It has been proposed that mitochondrial respiration may increase in plants under high CO_2 in response to sucrose accumulation in leaves (Tolbert et al., 1983). A mechanism for this is thought to act via the alternative pathway of respiration, that may function to dissipate excess photosynthesized energy (Lambers, 1982). Hrubec et al. (1984), reported increased respiration rates of soybean leaves grown in high CO_2. However, the converse result was found for wheat (Gifford et al., 1985) plants grown in 590 ppm CO_2, which experienced up to 45% reduction in respiration by both roots and whole plants. The operation of the alternative pathways of respiration actually declined for continuously CO_2 enriched plants. For V. radiata (Gifford et al., 1985) high CO_2 caused no significant change in root respiration per

unit root dry weight. H. annus (Gifford et al., 1985) had another pattern of response. Here root respiration per unit dry weight was increased, this increase was not attributable to the alternative pathway but to the cytochrome oxidase pathway. Increasing CO_2 from 350 to 950 ppm for a short term reduced the rate of dark respiration of Medicago sativum (Reuveni and Gale, 1985), the suppression being greater for roots than tops. The above short term effect of high CO_2 was confirmed for longer periods. High CO_2 at night (~ 1000 ppm) reduced respiration and increased the 24 hr net carbon gain and calculated dry weight growth. In these, as for short term experiments, the percentge reduction of respiration was greater when the plant was in a low photosynthate "maintenance respiration" condition (28% vs 11%) (Reuveni and Gale, 1985).

The mechanism of action of high CO_2 on dark respiration is not clear. Either high CO_2 directly affects respiration or CO_2 might affect rate of an energy requiring process whose ATP or NADPH demand affects respiration. These results suggest that even a small depression of respiration may have a significant effect on growth if two conditions are met (Reuveni and Gale, 1985):

(1) that the plant is growing under conditions in which the net daily carbon gain is low and

(2) reduction of respiration is not deleterious.

Thus this effect will be especially pronounced in regions and under conditions in which the daily net carbon gain is low or negative, for example in areas receiving low insolation at high latitudes or low water availability in arid regions (Reuveni and Gale, 1985).

Carbon and nitrogen ratio : Elevated CO_2 levels are expected to have an impact on the elemental composition of plant tissues, particularly the carbon and nitrogen content. C/N ratios under high CO_2 are likely to increase.

Curtis et al. (1989b) exposed three plant communities on a brackish marsh of Rhode river, to elevated CO_2 concentrations for an entire growing season. Two communities were monospecific one of S. olneyi (C_3) other of Spartina patens (C_4), the third was a mixed community of S. olneyi, S. patens and Distichlis spicata(C_4). A clear dichotomy was observed in the effects of elevated CO_2 on shoot % N in the C_3 and C_4 species. Elevated CO_2 reduced green tissue % N in the C_3 sedge S.olneyi but had no effect on the C_4 grasses S. patens or D. spicata. Percent carbon varied only slightly. This decrease in tissue % N in Scirpus caused a significant increase in C/N ratio of about 20-40% in pure as well as mixed community. There was no difference in % C or % N of seeds from Scirpus between elevated and ambient treatments. The enveloping bracts,

however, had significantly less % N under elevated CO_2. Total litter N, while unaffected by CO_2 in Scirpus in pure stand, increased significantly in Scirpus from mixed community (Curtis et al., 1989b).

Chang (1975) while working on G. hirsutum found that under elevated CO_2 ,protein content declined in the leaves with no accompanying increase in ninhydrin positive compounds. This observation evidenced that high CO_2 decreases the content of protein ,not by degradation, but by curtailing protein synthesis. Mbikayi et al. (1988), found that in V. unguiculata, after 41 days of exposure in elevated CO_2 there was no effect on protein content of either shoots or roots. After 79 days of exposure protein nitrogen content of both shoot and seeds was not affected by increasing levels of CO_2, but that of roots decreased significantly.

Sage et al. (1989) studied five C_3 species, (C. album, P. vulgaris, Solanum tuberosum, Solanum melongena and B. oleracea) for various parameters under elevated CO_2. With respect to leaf nitrogen content per unit area, they found that it increased in two Solanum species but was little changed in the other three. Nitrogen per unit weight fell in all species following exposure to high CO_2, but this was largely a consequence of the increase in leaf weight per

area. Leaf N content was found to decline under elevated CO_2 (500 and 700ppm) in all five annuals studied: A. theophrasti, A. retroflexus, A. artemisiifolia, C.album and S. faberii (Garbutt et al., 1990). B. mollis also showed a decreased leaf N content under 650 ppm CO_2 (Larigauderie et al., 1988). Declining N content under elevated CO_2 would thus mean a poorer tissue quality which could have a profound impact on herbivory, nutrient cycling and fertilizer use.

Water use efficiency : Higher atmospheric CO_2 concentration reduces stomatal aperture thereby reducing transpiration. This decrease in tranpiration rate, together with the typical high-CO_2-enhancement of net photosynthesis, accounts for the greater water use efficiency (ratio of carbon exchange rate to transpiration rate) in dry matter production under CO_2 enrichment (Warrick et al., 1984). Jones et al. (1984) observed that in soybean canopies grown under enriched-CO_2, water use efficiency was enhanced 1.6 times than in ambient CO_2, the absolute water requirements remaining the same in all treatments. Rogers et al. (1984) while experimenting with soybean (G. max) plants found that, transpiration per plant decreased with increasing CO_2 concentration inspite of increased leaf area per plant, leading to a decrease in water use per unit leaf area. B. mollis also showed an increased water use efficiency under

650 ppm CO_2 compared to 350 ppm CO_2 (Larigauderie et al., 1990).

Increased efficiency of water use alongwith decreased transpiration rates, could have far reaching effects on dry matter production in enhanced-CO_2 atmospheres especially under water-stressed conditions.

A.2. TREE SPECIES

Forests account for as much as two thirds of global photosynthesis (Kramer, 1981) and thus play a dominant role in the conversion of atmospheric CO_2 to fixed forms of carbon that have slow decomposition rates. The complexity of forest ecosystems and the technical challenges of quantifying their behaviour are few factors which have confined the number of studies on forest ecosystems. The studies available have been conducted with CO_2 enrichment of small trees and seedlings (Jarvis, 1989).

Studies on Gymnosperms : Growth chamber studies, on Douglas fir (Pseudotsuga menzeii) seedlings exposed to CO_2 (1000ppm) for 90 days, showed increased growth as a result of increased leaf photosynthesis (Purohit and Tregunna, 1976). Similar results have been obtained for seedling growth of lodgepole pine (Pinus contorta) and Sitka spruce (Picea sitchensis) (Canham and Mc Cavish, 1981). Under many

water and nutrient - stress conditions, seedling growth may be enhanced with elevated atmospheric CO_2 levels, [Pinus radiata, Pinus virginiana (Conroy et al., 1986, 1988)]. One open - top chamber experiment on long term CO_2 exposure was conducted with sapling of ponderosa pine (Pinus ponderosa) for 2.5 years (Surano et al., 1986). This pilot study showed that tree growth was enhanced upto a CO_2 level of 500 ppm but at 650 ppm growth was inhibited, an effect attributed to heat stress.

Studies on Angiosperms : A similar range of responses has been identified for seedlings of angiosperm deciduous species exposed to CO_2 enrichment [Quercus alba (Norby et al., 1986a), Liriodendron tulipifera (O'Neill, 1987)]. Long term growth responses of forest species to CO_2 enrichment remain speculative.

In the nutrient-cycling dynamics of forests, litter quality is another factor that could change with CO_2 enrichment. Litter produced at high CO_2 was predicted to be carbon rich and nitrogen poor (Norby et al., 1986b), leading to slower rates of decomposition.

Responses of mature trees to CO_2 enrichment have been evaluated using tree ring chronologies (Kienast and Luxmoore, 1988). Trees in temperate zones form distinct

annual growth rings. Since tree growth responds to CO_2 enrichment, it is expected that the historical change in CO_2 is recorded in tree-ring chronologies. Findings from modern tree-ring records indicate increases in growth that correlate with the increase in atmospheric CO_2 in recent decades (Kienast and Luxmoore, 1988).

Forest ecosystems thus need greater attention as the studies that have been carried out are restricted to few species specifically of Pinaceae family. The information gathered is insufficient to predict the responses of forest ecosystems to elevated CO_2 levels.

A.3. AQUATIC SPECIES

Aquatic plant species that have been studied for their responses under elevated CO_2 are Eichhornia crassipes (Spencer and Bowes, 1986, Idso et al., 1987) Nymphaea marliac (Allen et al.,1990), Vallisneria americana (Titus et al., 1990) and Azolla pinnata (Idso et al., 1987, Allen et al., 1988), which is a pteridophyte. Among these E. crassipes is the most well investigated species. In E. crassipes (Spencer and Bowes, 1986), leaf number, as also the leaf area per plant increased under elevated CO_2 (600 ppm). A 32% increase in dry matter production in high CO_2 plants over ambient plants was noted. Flower production

increased substantially at 600 pm CO_2. Net photosynthesis increased by 40%, but this was not maintained as plants acclimated to high CO_2 over a 4-week period. Rubisco activity was 40% less after 4 weeks in 600 ppm CO_2. Dark respiration rates of leaves, reduced by about one third in enriched plants. Transpiration rate of 600 ppm plants declined over the course of experiment especially on adaxial leaf surfaces. After four weeks in elevated as compared to ambient CO_2, soluble protein content was 49% less, chlorophyll 26% less, and starch content 40% greater. Net photosynthesis of N. marliac (Allen et al., 1990) in 640 ppm CO_2 under conditions of high light and high temperature was 60% greater than in ambient CO_2 treatment. In A. pinnata an aquatic fern (Allen et al., 1988), net photosynthesis was influenced by significant interactions between CO_2 level and short wave solar radiation as well as air temperature. Under the favorable conditions of high light intensity and high temperature, the net photosynthesis rate of Azolla under 640 ppm CO_2 was 70% greater than for those in ambient CO_2 treatment. In V. americana, at pH 5 biomass increased 2.8 times at elevated CO_2 (770 ppm) compared to ambient (Titus et al., 1990). The information on response of aquatic plants to elevated CO_2 is limited. It is thus extremely difficult to assess their responses under CO_2 enrichment.

TABLE 1: A COMPARISON OF C_3 AND C_4 PLANT RESPONSE TO THE DOUBLING OF CO_2
(BASED ON LITERATURE SURVEY FROM 1968-1990)

PARAMETER	RESPONSE UNDER ELEVATED CO_2	
	C_3	C_4
CARBON EXCHANGE		
Stomatal conductance	-	-
Net photosynthesis	+	0
Plant respiration	-	?
Decomposition of dead shoots	-	?
GROWTH		
Leaf area	+	+
Biomass	+	0
Photosynthate partitioning	M	?
Root/shoot ratio	+	0
TISSUE COMPOSITION		
Tissue N concentration	-	0
C/N ratio	+	0
Starch content	+	0

DEVELOPMENT/REPRODUCTION		
Tillering	+	?
Flowering time	M	?
Number of seeds	?	?
WATER USE		
Transpiration	-	-
Leaf water potential	+	+
Water use efficiency	+	+

+	Increase
-	Decrease
M	Mixed response
0	No response
?	No information

A comparison of C_3 and C_4 plant response to the doubling of CO_2 levels (Table 1) shows that in relation to stomatal conductance, and transpiration, both plant groups show a decreasing trend. But with respect to leaf area, leaf water potential and water use efficiency , both C_3 and C_4 show an increasing trend. There are other parameters where a clear dichotomy in response of C_3 and C_4 has been observed. Net photosynthesis increases under enhanced CO_2 in C_3 while C_4 plants do not respond. Biomass and starch content increases in C_3 but not in C_4. Tissue N concentration decreases in C_3 but is not affected in C_4 species. Many aspects like photosynthate partitioning, respiration, flowering time, seed number, decomposition rates under elevated CO_2 have not been studied well in case of C_4 species. Thus a comprehensive study of effect of elevated CO_2 on growth determining developmental, physiological and biochemical parameters of plants is required to predict their responses.

Enhanced CO_2 in Relation to Environmental Factors

Interactions between the atmospheric CO_2 and other growth limiting environmental variables and their effects on plant growth are complex and not studied well. Experimental studies indicate that elevated CO_2 concentration can reduce the deleterious impacts on growth, because of water -

shortages, low light intensity, temperature extremes or certain mineral deficiencies, notably nitrogen deficiency.

Temperature : A global warming of about $3^{o}C$ is predicted for the year 2030 A.D. due to increasing levels of greenhouse gases in atmosphere (Jager, 1986). In this context, plant response to enriched CO_2 under higher temperature is important. It appears that in general the positive effect of higher CO_2 in stimulating photosynthesis is increased with higher temperature. Growth of C_3 plants is expected to increase by as much as 56% with a rise in surface air temperature of $3^{o}C$ and atmoshpheric concentration of 640 ppm CO_2 (Cure and Acock, 1986). However, the effect of increasing temerature on the kinetic properties of rubisco, and solubility of CO_2 (relative to O_2), which declines, could cause a negative feedback (Jordan and Ogren, 1984). Also temperature is important in determining the rate of growth of metabolic sinks (such as developing fruits) and high temperature adversely affect sink growth. All these factors would thereby feed back onto leaf photosynthesis and modulate the CO_2 response.

At low temperatures too, high CO_2 has been shown to have positive effects, by reducing the minimum temperature at which a plant grows and completes its life cycle (Sionit et al., 1981b). Okra plants (Abelmoschos

esculentor) were unable to complete their life-cycle in normal CO_2 at temeperature below 23° (day)/17°C (night), while plants grown in 1000 ppm CO_2 at 20/14°C matured and produced fruit (Sionit et al., 1981). Thus with increasing atmospheric CO_2 levels the cultivation of okra may spread into cooler areas. Interaction of air temperature and elevated CO_2 would thus play an important role in determining growth and reproductive success of a species in the altered environment.

Water : Elevated CO_2 levels decrease transpiration rates and stomatal conductance of plants hence increasing their water use efficiency (Warrick et al., 1984). Wheat plants growing in elevated CO_2 under water stress (Sionit et al., 1981c) have been shown to osmoregulate more effectively. In wheat, Gifford (1979) reported that under extreme aridity, there was relative enchancement of yield due to CO_2 enrichment, because it allowed some grain growth where none occurred without extra CO_2. Water-stressed soybean plants (Rogers et al., 1984) showed greater leaf tissue damage, lower leaf water potential, and higher stomatal resistance in low CO_2 than in high CO_2 grown plants. Starch accumulated in water stressed leaves of plants grown in CO_2 enriched environment. Under water stress coupled with elevated CO_2, there was a significant increase in assimilate partitioning to roots in wheat (Gifford, 1979). This could be an

important response under field conditions if it were to allow roots to probe deeper layers of moist soil under CO_2 enriched conditions (Gifford, 1979).

Under growth-limiting water supply, growth of C_3 crops responds to higher CO_2 because of both photosyntetic and stomatal effects (Gifford, 1979) while growth of C_4 species resonds because of stomatal effects alone. Thus for both C_3 and C_4 species, the less the availability of water, the greater the 'relative enhancement' of growth by high CO_2 concentrations (Gifford 1979).

Nutrients

Nitrogen : Low nitrogen supply reduces growth of all species, under ambient CO_2. With doubling of CO_2 concentration, however, C_3 non leguminous plant species will still register a relative enhancement in dry weight growth even under nitrogen stess. The weight of cotton plants almost doubled, both under 2mM or 24mM nitrate in the nutrient solution when CO_2 concentration was increased from 330 to 640ppm, whereas for corn, a C_4 non legume, the increase was only 20% (Wong, 1979). In wheat, Sionit et al. (1981) found that the stimulation of dry-matter accumulation by 675 ppm plants compared to 350 ppm CO_2 plants increased with increasing nutrient availability. In legumes such as

soybeans or peas, high CO_2 leads to greater biological nitrogen fixation which could be attributed to the production of more nodules on an elaborate root system, rather than to greater specific activity of nodules (Finn and Brun, 1982). Under CO_2 enriched conditions, N-use efficiency of a plant tends to increase. The increased efficiency could be due to a reduced investment in photosynthetic machinery (which has a high N-requirement) per unit of photosynthetic assimilate produced (Sage et al., 1989).

Phosphorus : P-deficient plants of Z. mays, S. bicolor and G. max (Pettigrew et al., 1990) under CO_2 saturating condition had lower net photosynthetic rates than P-sufficient plants. This could be because inorganic phosphate (Pi) plays an important role in regulating transport of triose - phosphate sugars out of chloroplasts via the phosphate translocator; in P-deficient plants this mechanism being disrupted could have lead to end-product inhibition of photosynthesis (Pettigrew et al., 1990). On the contrary P-deficient bean (Vicia faba) plants have been found to be even more responsive to high CO_2 than were plants grown with adequate P (Goudriaan and de Ruiter, 1983). Further studies are required to elucidate the actual mechanism of interaction of high CO_2 and P.

Potassium : There is little information on interaction of potassium with atmospheric CO_2 enrichment on plants. In potato, Goudriann and de Ruiter (1983) noted negative effect of increased CO_2.

Sodium : Sodium is an essential element for C_4 photosynthesis. The signs of sodium deficiency in the C_4 species, Amaranthus tricolor and Atriplex spongiosa were alleviated when the species were grown in conditions of high CO_2 concentration (1500 ppm) (Johnston et al., 1984). Sodium sufficient C_4 plants were relatively unaffected by the CO_2 treatments (Johnston et al., 1984). Schwarz and Gale (1984), on the other hand have shown that tolerance of saline (excess sodium) conditions is increased by CO_2 enrichment to 2500 ppm. This effect was ascribed to, a shortage of photosynthate in salt stressed plants, made up by enhanced CO_2, or to reduced demand for saline water because of CO_2 reduced transpiration under enhanced CO_2.

Light : CO_2 enrichment increases crop growth and yield at low light intensities which are otherwise growth limiting under conditions of ambient CO_2. The relative enhancement of growth can even be greater than at high light level, as has been found for wheat (Gifford, 1979). The mechanism of growth response to CO_2 depends on two factors under photosynthetically limiting light intensities. One is

that the quantum yield of leaf photosynthesis close to light compensation point (the light intensity at which CO_2 uptake by a leaf is just balanced by respiratory release of CO_2) is CO_2 dependent in C_3 species, but not in C_4 species (Ehleringer and Bjorkman, 1977). If the whole plant respiration is less under high CO_2, then the light compensation point is lowered and some growth is achieved at light intensities that otherwise would prove insufficient for photosynthesis, which explains the pattern shown by wheat under high CO_2 and low intensity (Gifford, 1979). In case of soybean, which has shown increased respiration under high CO_2, the relative enhancement of growth by high CO_2 appears equal at low and high light intensities (Sionit et al., 1982).

B. ECOSYSTEM LEVEL RESPONSES

The knowledge about effects of CO_2 at community and ecosystem level is very limited. Recently, the following two natural ecosystems have been studied at Toolik lake, Alaska and Chespeake Bay, to gain some insight into ecosystem functioning in response to CO_2 enrichment.

(1) Moist tussock tundra at Toolik lake in the foothills of the Brooks Range in Alaska (Oechel and Riechers, 1986, Tissue and Oechel, 1987). Temperature controlled greenhouses were used to maintain elevated CO_2 levels

(510 and 680 ppm). The arctic tundra ecosystem was floristically diverse and comprised of C_3 species. Dominant plant species was cotton grass, Eriophorum vaginatum.

(2) Coastal salt-marsh on the Chespeake Bay (Curtis et al., 1989a, 1989b, 1990, Drake et al., 1989, Ziska et al., 1990). Here open-top chambers were used to create test atmospheres of normal ambient & elevated CO_2 (normal ambient + 340ppm). The coastal marsh system was comprised of two higher plants, S. olneyi (C_3) and S. patens (C_4), both often occuring in monospecific stands, and a mixed community of S. olneyi, S. patens and D. spicata (C_4).

Significant ecosystem level effects were noted in both the arctic and salt marsh.

Net carbon storage : In arctic ecosystem short-term exposure to elevated CO_2 resulted in immediate postive ecosystem carbon gain while ambient CO_2 chambers achieved it 6 d later. Over a 74 d growing season the tussock tundra under ambient CO_2 had a net carbon loss (-53.4 g C m^{-2} y^{-1},) whereas elevated CO_2 chambers showed net carbon acquisition (206.5 g C m^{-2} y^{-1}). Homeostatic adjustment of whole ecosystem carbon flux was complete within three years

(Grulke et al., 1990). The marsh increased carbon storage under elevated CO_2 but no changes in nutrient relations were observed. The C_4 S. patens stands showed results similar to S. olneyi, except there was no increase in ecosystem carbon storage (Ziska et al., 1990).

Biomass : In tussock tundra root biomass and root : shoot ratio generally decreased at elevated CO_2 (Tissue and Oechel, 1987). Growth under elevated CO_2 resulted in an 83% increase in root dry mass in Scirpus community. S. patens community and C_4 component of mixed community showed no increase in root growth under elevated CO_2 (Curtis et al, 1990).

Dark respiration : Elevated CO_2 concentration had no significant effects on tundra ecosystem dark respiration rates (Grulke et al., 1990). Net ecosystem respiration decreased in salt marsh system (Curtis et al., 1989a).

Nitrogen content: In the arctic tundra, elevated CO_2 tended to decrease nitrogen content and increase C/N ratio (Tissue and Oechel, 1987). Nitrogen content (%) of roots of S. olneyi was lower under elevated CO_2 compared to ambient grown plants. No effect on nitrogen content was observed in S. patens or D. spicata (Curtis et al.,1990).

Water relations: There was little long term effect on evapotranspiration, or water-use (Tissue and Oechel, 1987) in tussock tundra system. In coastal marsh system stands of C_3 S. olneyi, showed improvements in water relations under elevated CO_2. Evapotranspiration decreased by 30% in both C_3 and C_4 stands in the salt marsh system, resulting in 80-100% increase in water use efficiency.

A list of species (Table 2) and families (Table 3) studied for their response to CO_2 doubling shows that the study is spread over fifty four species belonging to eighteen families. Table 2 clearly indicates that a greater emphasis has been placed on response of crop plants (39% of studis) and their associated weeds (20% of studies) to elevated CO_2. However, in relation to uncultivated herbaceous species, tree species as well as aquatic species not many studies have been done. Leguminosae is the most well studied family among angiosperms while among gymnosperms studies have been limited to Pinaceae family and specifically to genus Pinus (Table 3). Among trees only short term experiments using tree seedlings have been done. Only one long term study 2.5 yr) using saplings of Pinus ponderosa (Surano et al., 1986).

Information on aquatic plants is limited to four species only, one of them being a fern, Azolla pinnata.

TABLE 2 : LIST OF PLANT SPECIES STUDIED FOR ELEVATED CO_2 RESPONSE
(BASED ON LITERATURE SURVEY FROM 1968 TO 1990)

Plant Species	Meta-bolism	Method of Study*	Duration of Study**	Cate-gory***	Family	Reference
HERBACEOUS SPECIES						
Abelmoschus esculentus	C_3	GC	L	C	Malvaceae	Sionit et al., 1981.
Abutilon theophrasti	C_3	GC	S,L	UC	Malvaceae	Patterson and Flint, 1980, Garbutt et al., 1990.
Amaranthus tricolor	C_4	GC	L	UC	Amaranthaceae	Johnston et al., 1984
Amaranthus retroflexus	C_4	GC	S	UC	Amaranthaceae	Garbutt et al., 1990
Ambrosia artemisiifolia	C_3	GC	S	UC		Garbutt et al., 1990
Atriplex hastata	C_3	GC	L	UC	Chenopodiaceae	Johnston et al., 1984
Atriplex spongiosa	C_4	GC	L	UC	Chenopodiaceae	Johnston et al., 1984
Beta vulgaris	C_3	GC	S	C	Chenopodiaceae	Wyse, 1980
Brassica oleracea	C_3	GC	L	C	Cruciferae	Sage et al., 1989
Bromus mollis	C_3	GC	L	UC	Gramineae	Larigauderie et al., 1988
Cassia obtusifolia	C_3	GC	S,L	UC	Leguminosae	Pattern son Flint, 1982
Chenopodium album	C_3	GC	L	UC	Chenopodiaceae	Sage et al., 1989, Garbutt et al., 1990
Crotalaria spectablis	C_3	GC	S,L	UC	Leguminosae	Patterson and Flint, 1984
Daucus carota	C_3	OTC	L	C	Umbelliferae	Idso et al., 1987
Distichlis spicata	C_4	OTC	L	UC	Gramineae	Curtis et al., 1989, Curtis and Balduman, 1990.
Eriophorum vaginatum		GC	L	UC		Tissue and Oechel, 1987; Grulke et al., 1990
Glycine max	C_3	GC	S,L	C	Leguminosae	Patterson and Flint, 1980; Clough et al., 1981; Finn and Brun, 1982; Patterson and Flint, 1982; Jones et al., 1984; Cure et al., 1987; Rogers et al., 1984,1986
		OTC	L			

TREE SPECIES

Acer macrophyllum	C_3	GC	S		Aceraceae	Bailey et al., 1991
Liquidamber styraciflua	C_3	GC	S		Hamamelidaceae	Tolley and Strain, 1984; Fetcher et al., 1988
Liriodendron tulipifera	C_3	GC	S		Magnoliaceae	O'Neill, 1987
Picea sitchensis	C_3	GC	S		Pinaceae	Canham and Mc Cavish, 1981
Pinus contorta	C_3	GC	S		Pinaceae	Canham and Ma Cavish, 1981
P. ponderosa	C_3	GC	S,L		Pinaceae	Green and Wright, 1977; Surano et al., 1986
P. radiata	C_3	GC	S		Pinaceae	Conroy et al., 1986,1988
P. strobus	C_3	GC	S		Pinaceae	Funsh, 1970
P. taeda	C_3	GC	S		Pinaceae	Tolley and Strain 1984; Fetcher et al., 1988
P. virginiana		GC	S		Pinaceae	Conroy et al., 1986, 1988
Pseudotsuga menzeii	C_3	GC	S		Pinaceae	Purohit and Tregunna, 1976
Quercus alba	C_3	GC	S		Fagaceae	Norby et al., 1986

AQUATIC SPECIES

Azolla pinnata	C_3	OTC	L	UC	Salviniaceae	Idso, 87, Allen et al., 1988
Eichhornia crassipes	C_3	GC OTC	L	UC	Pontederiaceae	Spencer and Bowes, 1986 Idso, et al., 1987
Nymphaea marliac	C_3	OTC	L	UC	Nymphaeaceae	Allen et al., 1990
Vallisneria americana	C_3	GC	L	UC	Hydrocharitaceae	Titus et al., 1990

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* GC - Growth Chamber/Environment Chamber/Greenhouse
/Controlled Environment Rooms/Glasshouse/Plant Chamber
OTC- Open top Chamber

** S- Short term study
L- Long term study

*** UC - Uncultivated
C - Cultivated

TABLE 3 :LIST OF PLANT FAMLIES AND SPECIES STUDIED IN RELATION TO CO_2 ENRICHMENT
(BASED ON LITERATURE SURVEY FROM 1968 TO 1990)

Family	No. of species studied
Leguminosae	9
Gramineae	8
Pinaceae	8
Chenopodiaceae	4
Solanaceae	4
Malvaceae	3
Amaranthaceae	2
Compositae	2
Cyperaceae	2
Umbelliferae	1
Aceraceae	1
Hamamelidaceae	1
Magnoliaceae	1
Fagaceae	1
Salviniaceae	1
Pontederiaceae	1
Nymphaeceae	1
Hydrocharitaceae	1

TABLE 4 :STUDIES ON PLANT RESPONSES TO DIFFERENT CONCENTRATIONS OF CO_2 RANGING FROM 300 - 1500 ppm (BASED ON LITERATURE SURVEY FROM 1968 TO 1990)

CO_2 CONCENTRATION RANGE (ppm)	NO. OF STUDIES
300 - 399	66
400 - 499	9
500 - 599	8
600 - 699	43
700 - 799	8
800 - 899	2
900 - 999	14
1000- 1099	14
1100- 1199	1
1200- 1299	1
1500	5

This survey shows that database to comprehend and predict plant responses to elevated CO_2 is rather limited. Another aspect relates to the fact that in most of the species plant responses have been studied in relation to doubling of CO_2 (600-650 ppm). The impact of intermediate levels of CO_2 concentrations ranging from 400-500 ppm, likely to be encountered in next few years, is yet to be studied at individual and community level.

Species level studies provide valuable specific information but it is of little help in comprehending their response in a community under field conditions .The plant responses in a community or natural ecosystems are likely to be much different.Species composition in communities and natural ecosystems is likely to change depending on their relative competitive ability and reproductive success under altered CO_2 regime. Changes in mineral composition of plants under elevated CO_2 might play an important role in changing pest and herebivore preferences. Litter decomposition under high CO_2 could be slower due to a likely increase in C/N ratio. This would result in a slow nutrient release which may further complicate nutrient status of soil and affect plant response. Studies of intra- and inter-specific competition in relation to elevated CO_2 on various types of economically important and other wild

plants are important to anticipate responses of agro-ecosystems and natural ecosystems.

Detailed studies under elevated CO_2 at species and ecosystem level are required in relation to local variations of climatic, edaphic and anthropogenic factors. Such primary data on plants would provide a sound basis for assessing impact of elevated CO_2 at local and regional levels.

PART II: EFFECT OF ENHANCED LEVELS OF CO_2 ON SPINACEA OLERACEA

Materials and Methods:

Exposure Chamber : An open-top type of exposure chamber of 2.5 m height and 2 m diameter was constructed using locally available materials (Plate 1, 2) based on design given by Rogers et al., 1983. The chamber frame consisted of eight bamboo poles placed equidistant forming a circle of 2 m diameter. Poles were tied with one another with a thick cotton tape woven around them at a height of 0.5 m and 1.5 m from the ground to provide support and stability. This prevented the caving in of the chamber due to strong winds or under its own weight. The chamber was covered with transparent PVC plastic sheet. An entry point to the chamber was provided by leaving the plastic sheets unsealed. The entry was kept covered by overlapping plastic flaps when not in use.

Inside the chamber, at a height of 0.3 m from the ground, an inflatable plastic air-delievery tube of 0.114 m diameter was fixed along the inner wall of the exposure chamber. Equally placed holes (0.5 cm diameter) were punched on the inside of the air delievery tube in such a manner that the flow of CO_2 enriched air into the chamber keeps it fully inflated, and distributes it uniformly inside the chamber.

Plate 1 Open top chamber used in the experiment

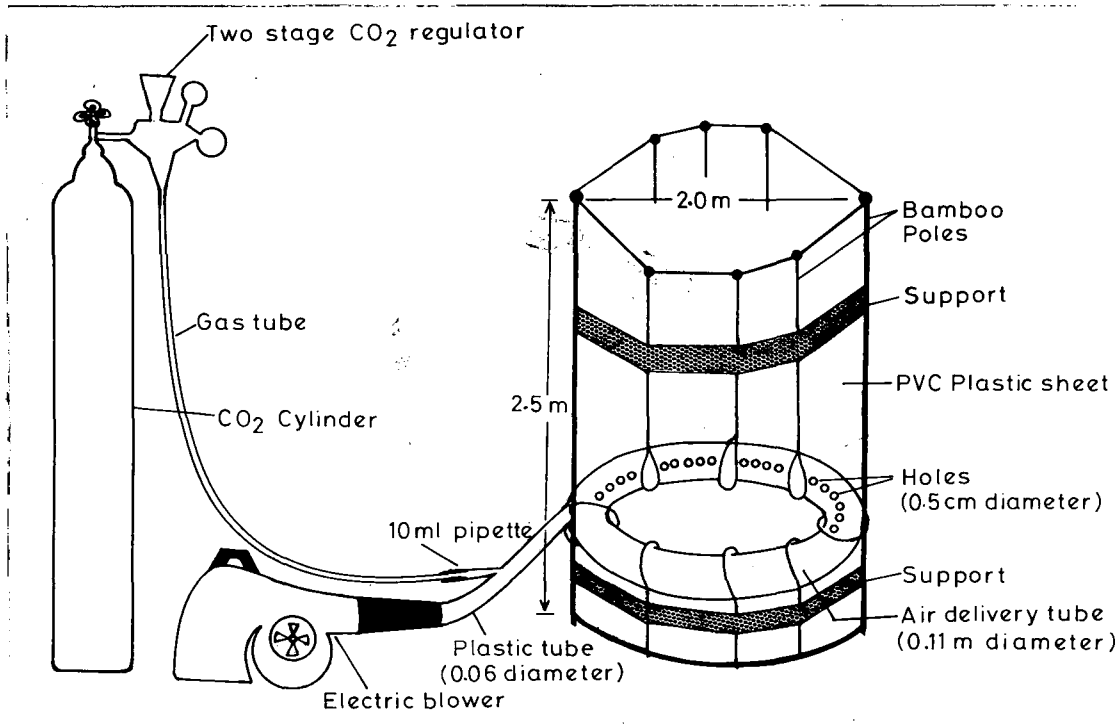

Plate 2 Schematic diagram of open top chamber system used in the experiment

CO_2 supply : The source of carbon dioxide was compressed CO_2 cylinders (27 kg) fitted with a double stage CO_2 regulator. The gas cylinder was connected to an electric blower (flow rate = 1.5 l/min). The blower was connected to the air delievery tube by a thick plastic pipe (diameter = 0.06m). A 10 ml pipette, connected with help of a gas tube to the CO_2 cylinder, released CO_2 gas into the plastic pipe connected to blower. This ensured through mixing of air and CO_2 which was finally released into the air delievery tube. The open top of the chamber acted as the outlet.

CO_2 levels inside the exposure chamber were monitored every three hr with the help of a Portable Photosynthetic System (LICOR LI-6000), which has an in built IR analyzer. CO_2 levels inside the chamber were maintained at 600 $\pm$ 50 ppm.

An identical open top chamber was constructed to keep control plants, the only difference being that the air supplied to this chamber was not enriched with CO_2. The chambers were constructed in an open, unshaded area in the ecology lab garden.

Plant Materials : The following two cultivars of Spinacea oleracea (C_3) were chosen for the experimental

study:

i cv. `All green'

ii cv. `Banerjee's giant'

Thirty earthern pots of 15 cm height, 20 cm diameter were filled with well manured garden soil. Plants of both varieties were raised from seeds in labelled pots. Eighteen days after planting, ten pots of each variety having similar size plants were chosen. Thinning was done and only 3 plants per pot were maintained. Out of the ten pots of each variety, five were kept in CO_2 - enriched chamber and rest five were kept in the chamber supplied with ambient air only. The plants in experimental pots were properly labelled and were continuously exposed to elevated CO_2 for ten days from 19.4.91 to 29.4.91. The plants were watered regularly, and 0.1 % aqueous solution of malathion was sprayed once in five days as a prophylactic measure to protect the experimental plants from pests.

Leaf Area : Length (l) and breadth (b) of each leaf was measured and leaf area was calculated by : l x b x multiplying factor. The multiplying factor was calculated as follows. Fifty leaves of Spinacea oleracea were taken and their length (l) and breadth (b) was recorded. L x b gave apparent leaf area. The actual leaf area was determined with the help of graph paper. Actual leaf area divided by

apparent leaf area gave the multiplying factor, which in this case was 0.660. Leaf area of each plant before the experiment and after terminating the experiment was estimated.

Chlorophyll Estimation: 0.5 g of fresh leaf tissue was homogenized in 10 ml of 80% acetone. The homogenate was centrifuged at 2000 g for 5 minutes. The clear green supernatant was taken and kept in a tube covered with aluminium foil. The pellet was re-extracted with another 10 ml of 80% acetone, centrifuged again and the supernatants from both steps were pooled together and the final volume made to 25 ml. The absorbance was measured at 645 and 663 nm (for chlorophyll estimation), at 480 and 510 nm (for carotene estimation) using Spectronic - 20. Chlorophyll a,b and carotene content was calculated according to following formulae (in mg/0.5g)

$$\text{Chlorophyll (a)} = \frac{12.7A_{663} - 2.69A_{645}}{a \times 1000 \times w}$$

$$\text{Chlorophyll (b)} = \frac{22.9A_{645} - 4.68A_{663}}{a \times 1000 \times w}$$

$$\text{Total Chlorophyll (mg/o.5g)} = \frac{20.2A_{645} + 8.02A_{663}}{a \times 1000 \times w} \times v$$

$$\text{Carotene} = \frac{7.6A_{480} - 1.49A_{510}}{a \times 1000 \times w} \times v$$

All values in mg/0.5 g leaf tissue were converted to mg/g.

A = Absorbance at that particular wavelength

a = Length of light path in the cell (usually 1 cm)

v = Volume of sample

w = weight of leaf tissue taken.

Biomass: After 10 days of exposure plants were harvested along with the root system. Each plant was carefully washed to remove the soil particles with a fine brush. Root and shoot were separated and put in pre weighed labelled beakers. For dry weight determination plant material was kept in an electric oven at 85° C for 48 hr and root : shoot ratios were calculated.

Starch Content: Starch content was determined using a simpler version of Pucher's method (Pucher et al., 1948). 250 mg of dry ground plant material was taken in a test tube. To this 200 mg of fine sand and 5 ml distilled water was added and mixed. The tube was heated in a boiling waterbath for 15 min to gel the starch. After cooling the

test tube 5 ml 60% $HClO_4$ was added whilst mixing. The tissue was grounded against the side of test tube for 20 min then transferred to a 100 ml volumetric flask and diluted to volume. Allowed to settle. An aliquot of 5 ml was transferred to a 50 ml volumetric flask. To this few drops of indicator solution (0.1% Phenol red, in 90% ethyl alcohol) were added, then NaOH (M) was added until solution turns red. Acetic acid (10% v/v) was added to destroy colour and then added further 2.5 ml. To this 0.5 ml KI solution (10% w/v), 5.0 ml KIO_3 solution (0.0125 M) were added. Shook well and diluted to volume. Absorbance was measured at 680 nm. A calibration curve was prepared using a range of standard starch solutions, and used to obtain mg starch in the sample aliquot. Percentage of starch content was calculated according to the following formula:

If C = mg starch obtained from calibration curve then,

$$\text{Starch (\%)} = \frac{C\text{(mg)} \times \text{solution volume (ml)}}{10 \times \text{aliquot (ml)} \times \text{sample wt (g)}}$$

Results

Effect of elevated CO_2 (600 ± 50 ppm) on leaf area in Spinacea oleracea : (Table 5, Fig 1,2) Average leaf area per plant registered an increase under elevated CO_2 in both cultivars after ten days of exposure continuously. In S. oleracea cv. All Green average leaf area per plant (ambient CO_2) was 30.21 cm^2 and 58.68 cm^2 (elevated CO_2) amounting to a 94.2% increase over control. In S. oleracea cv. Banerjee's Giant average leaf area per plant was 26.36 cm^2 (ambient CO_2) and 36. 94 cm^2 (elevated CO_2) resulting in 40.14% increase over control.

Effect of elevated CO_2 (600±50 ppm) on chlorophyll content in S. oleracea : (Table 6, Fig 3,4). There was a reduction in chlorophyll and carotene content in both cultivars under elevated CO_2. In S. oleracea cv. All Green a 23.97% reduction in Chl (a), 39.47% in Chl (b) over control was observed. Total chlorophyll decreased from 1.005 mg/g leaf tissue (ambient CO_2) to 0.706 mg/g (elevated CO_2), a 29.75% reduction. Carotene content decreased to 34.85% over control. Chl a/b ratio increased from (ambient CO_2) to 2.11 (elevated CO_2). In S. oleracea cv. Banerjee's Giant Chl (a) did not show any reduction whereas Chl (b) decreased by 23.2% over control. Total Chl decreased from 0.732 mg/g (ambient CO_2) to 0.681 (elevated CO_2), amounting

to 6.97% reduction. Carotene content decreased by 8.53%. Chl a/b ratio increased from 2.3 to 3.05 under elevated CO_2.

Effect of elevated CO_2 (600 ± 50 ppm) on biomass in S. oleracea : (Table 7, Fig 5,6) In S. oleracea cv. All Green root biomass showed a 296% increase whereas shoot biomass a 83.5% increase over control. Root/Shoot ratio increased from 0.161 (ambient CO_2) to 0.348 (elevated CO_2). In S. oleracea cv. Banerjee's Giant root biomass showed a 188.8% increase whereas shoot biomass a 73.5% increase over control. Root/Shoot ratio increased from 0.096 (ambient CO_2) to 0.160 (elevated CO_2).

Effect of elevated CO_2 on foliar starch content in Spinacea oleracea : (Table 8, Fig 7) Foliar starch content increased from 2.3% (ambient CO_2) to 4.0% (elevated CO_2) in S. oleracea cv. All Green. In S. oleracea cv. Banerjee's Giant it increased from 1.2% (ambient CO_2) to 2.3% (elevated CO_2).

TABLE 5: EFFECT OF ELEVATED CO_2 (600 ±50 ppm) ON LEAF AREA IN SPINACEA OLERACEA

Sample	Period of Exposure (days)	Average Leaf Area Plant^{-1} (cm^2) 0	10	Increase (%) in Leaf Area over Control
S. oleracea (cv.All Green)	Control	21.48	30.21	
	Elevated CO_2	23.91	58.68	94.2
S. oleracea (cv. Banerjee's Giant)	Control	16.34	26.36	
	Elevated CO_2	16.29	36.94	40.14

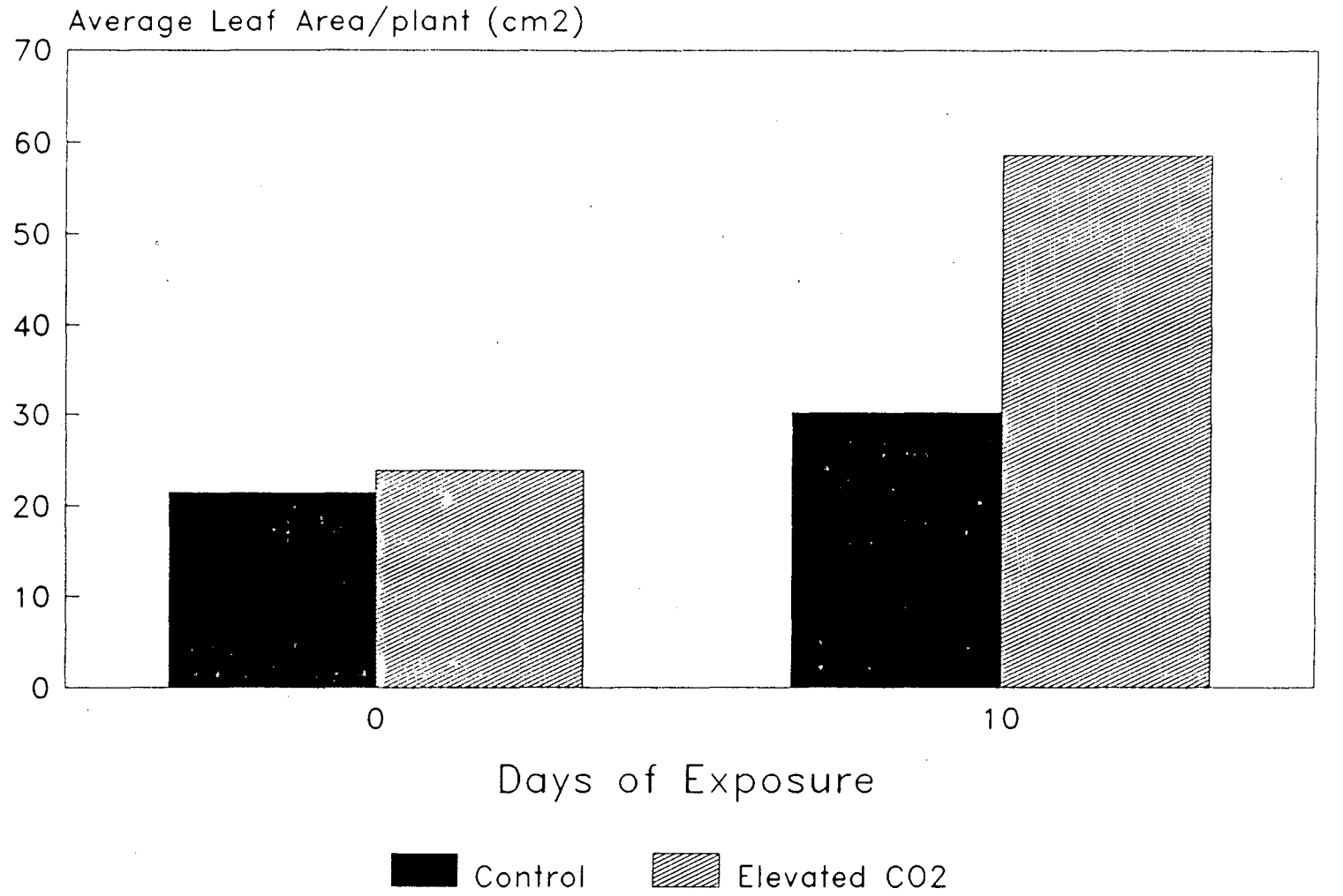

Fig 1 Increase in leaf area (S oleracea cv. All green) after ten days exposure to elevated CO_2 (600 ± 50 ppm)

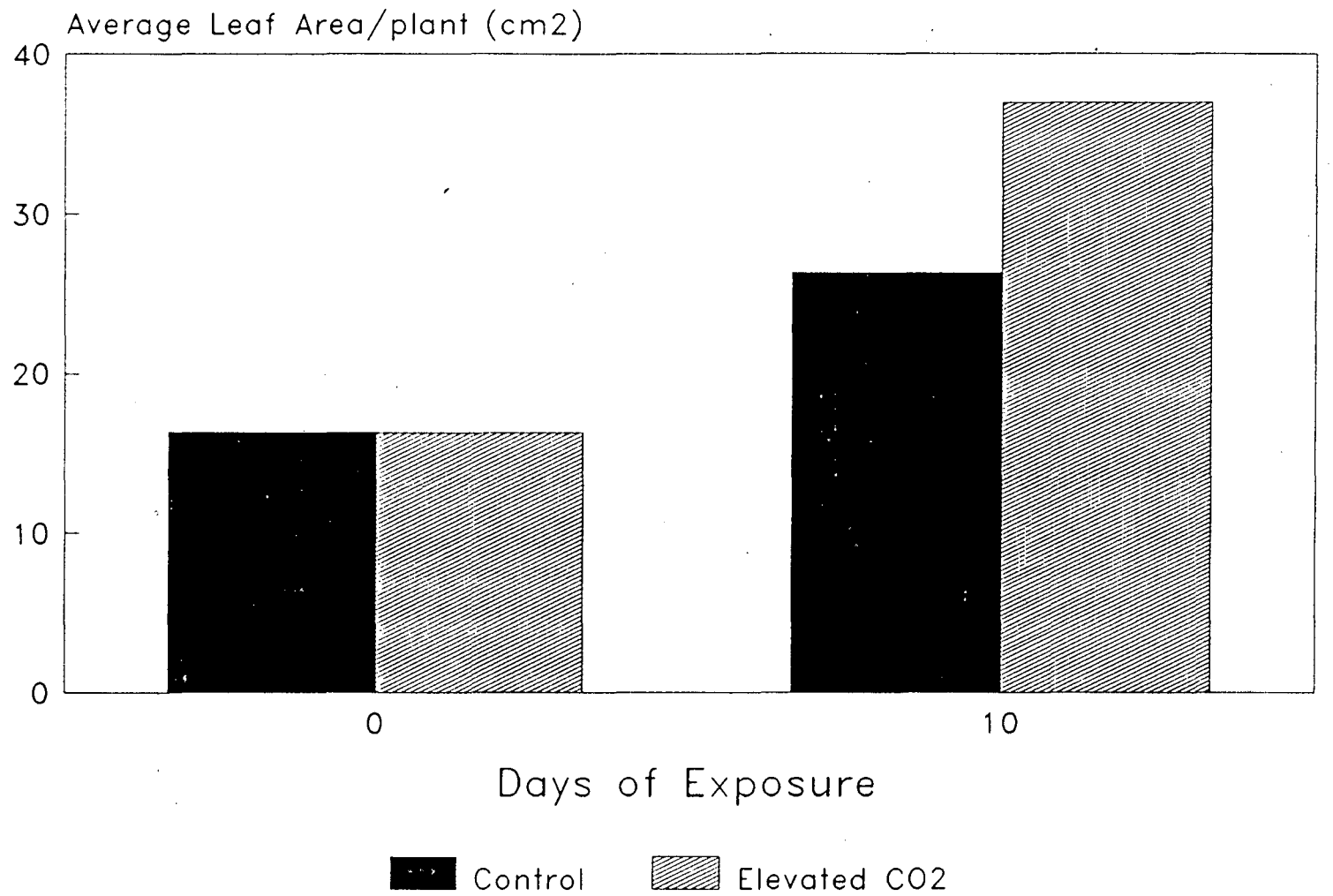

Fig 2 Increase in leaf area (S. oleracea cv. Banerjee's Giant) after ten days exposure to elevated CO_2 (600 ± 50 ppm)

TABLE 6: EFFECT OF ELEVATED CO_2 (600 ±50 ppm) ON CHLOROPHYLL CONTENT IN SPINACEA OLERACEA

Sample		Chl(a)*	Reduction (%)over control	Chl(b)*	Reduction (%)over control	Total Chl*	Reduction (%)over control	Carotene*	Reduction (%)over control	Chl a/b ratio
S. oleracea (cv.All Green)	Control	0.630		0.375		1.005		0.396		1.68
	Elevated CO_2	0.479	23.97	0.227	39.47	0.706	29.75	0.258	34.85	2.11
S. oleracea (cv.Banerjee's Giant)	Control	0.513		0.219		0.732		0.293		2.3
	Elevated CO_2	0.513	0.00	0.168	23.2	0.681	6.97	0.268	8.53	3.05

* Value expressed in mg/g leaf tissue

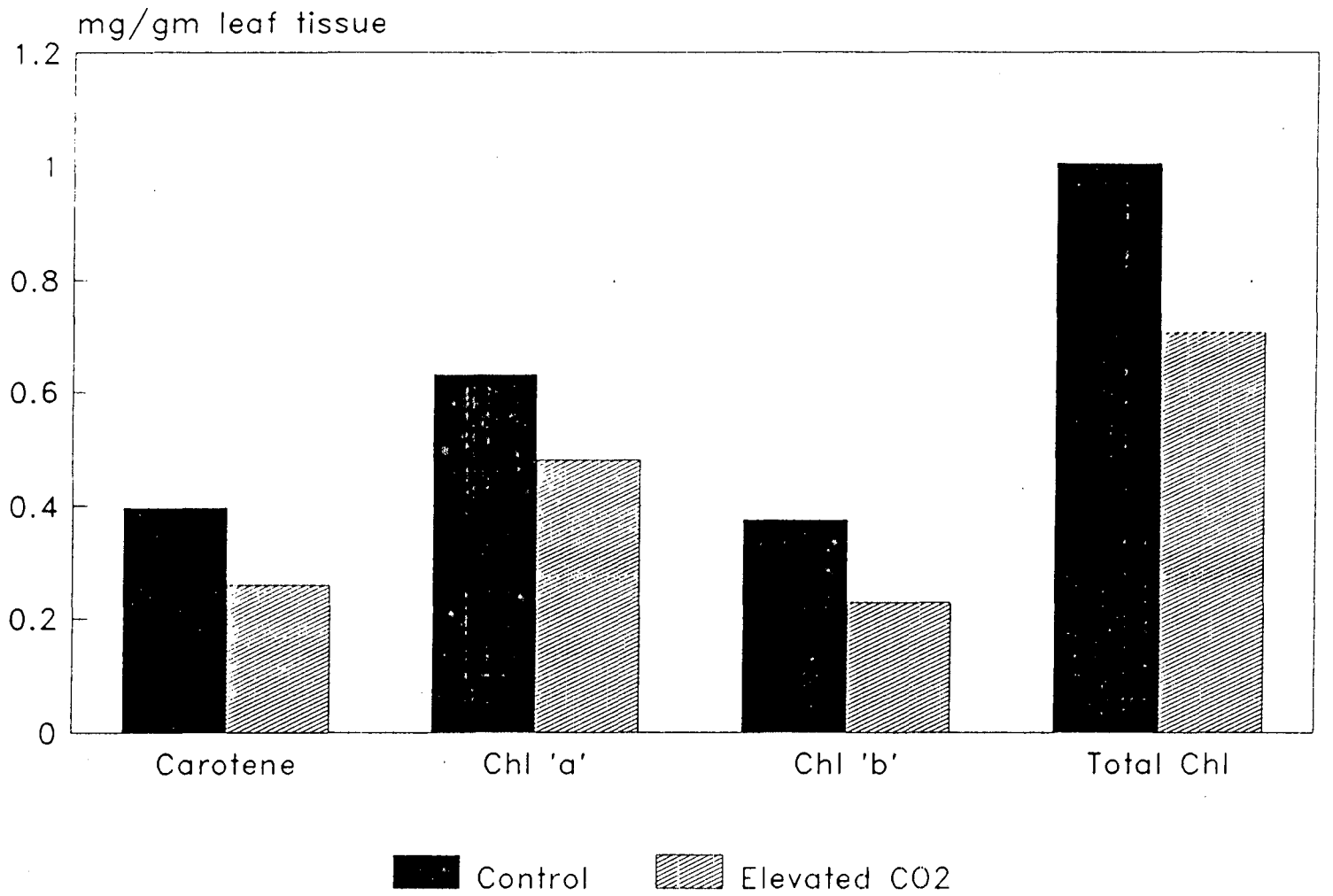

Fig 3 Decrease in chl (a), chl (b), total chl and carotene (S. oleracea cv. All Green) after ten days exposure to elevated CO_2 (600 ± 50 ppm)

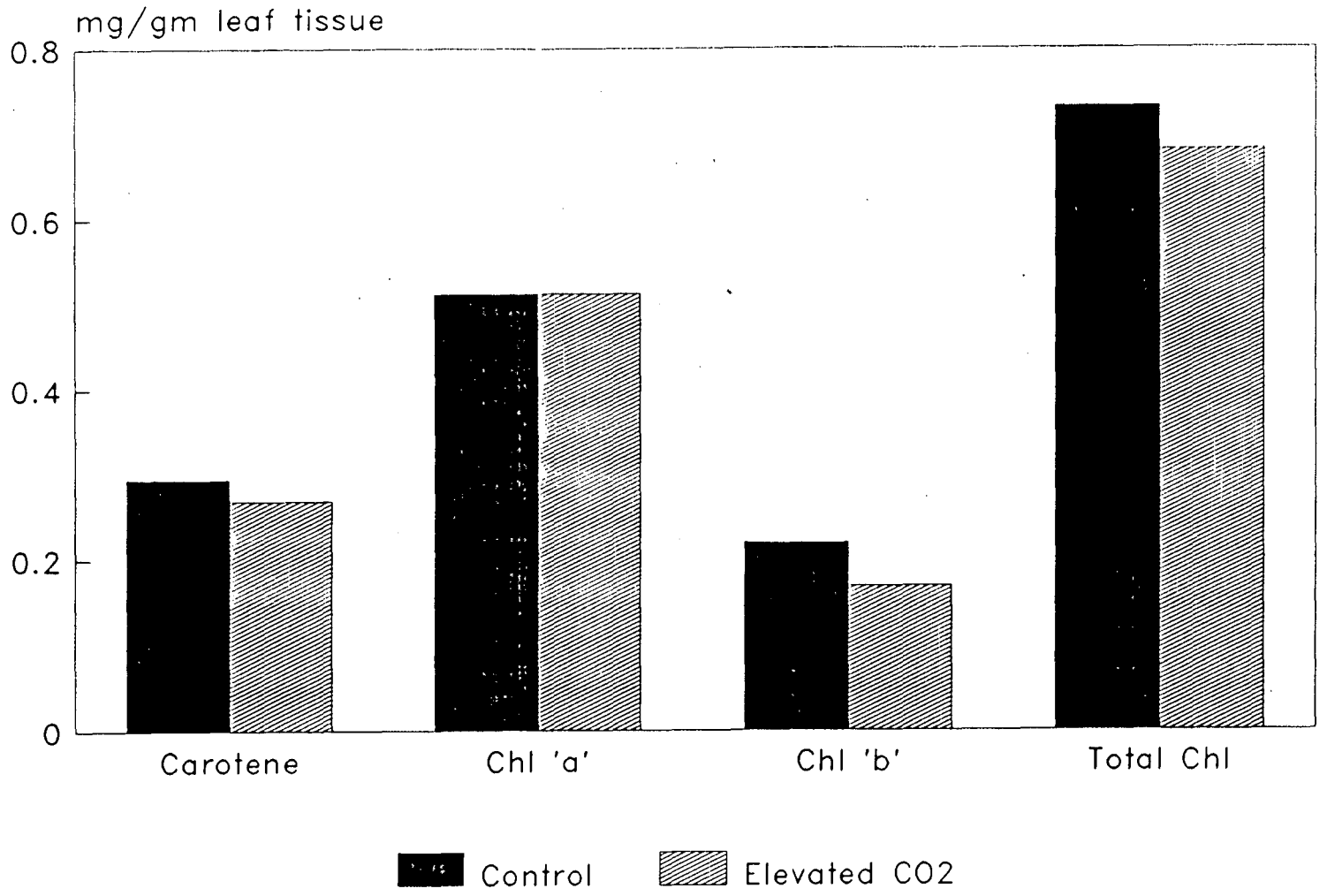

Fig 4 Decrease in chl (a), chl (b), total chl and carotene (S. oleracea cv. Banerjee's Giant) after ten days exposure to elevated CO_2 (600 ± 50 ppm)

TABLE 7: EFFECT OF ELEVATED CO_2 (600 ±50 ppm) ON BIOMASS IN SPINACEA OLERACEA

Sample		Root Biomass (g)	Increase (%) over control	Shoot Biomass (g)	Increase (%) over control	Root/Shoot
S. oleracea (cv.All Green)	Control	0.051		0.316		0.161
	Elevated CO_2	0.202	296	0.580	83.5	0.348
S. oleracea (cv. Banerjee's Giant)	Control	0.009		0.094		0.096
	Elevated CO_2	0.026	188.8	0.163	73.5	0.160

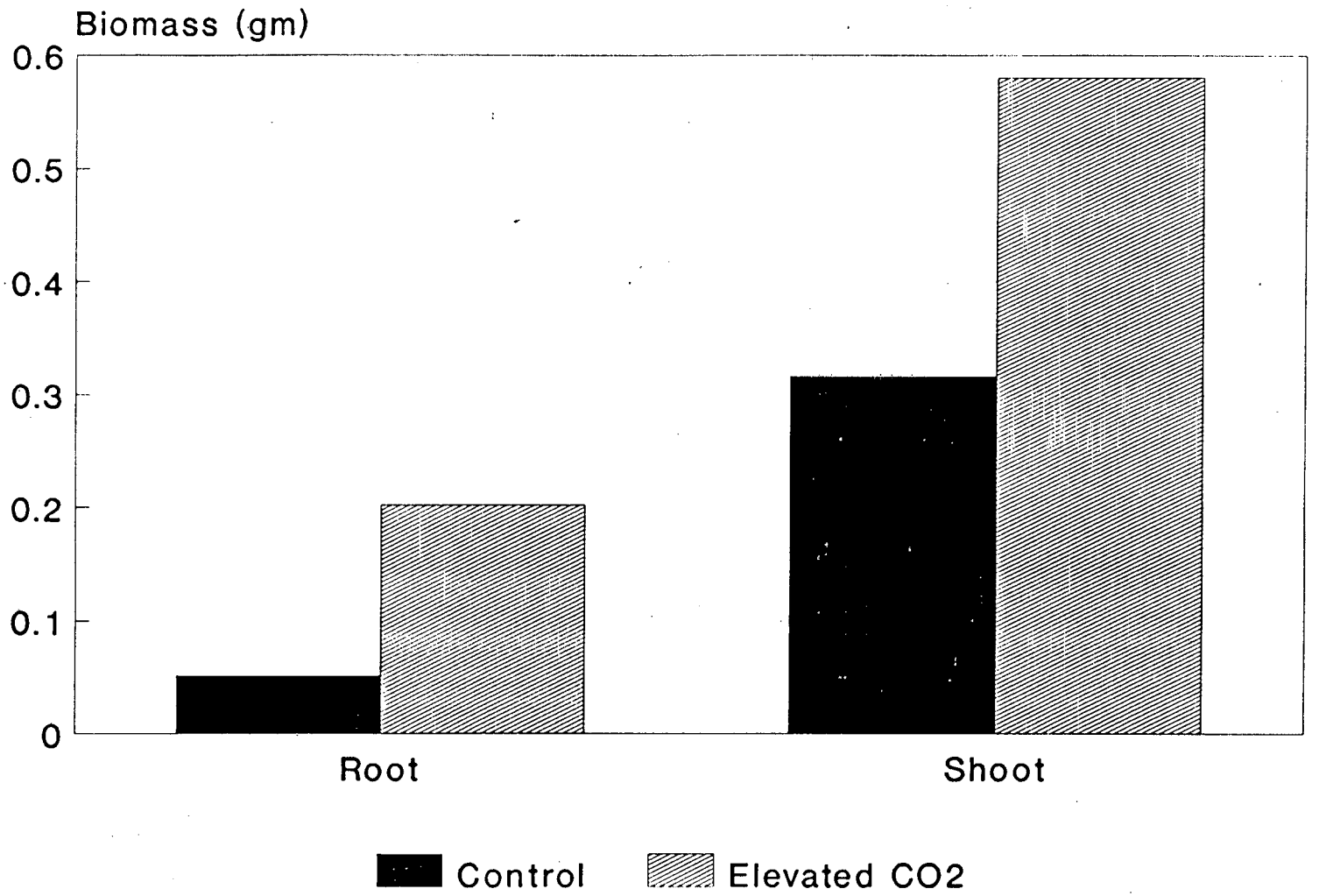

Fig 5 Increase in root and shoot biomass (S. oleracea cv. All Green) after ten days exposure to elevated CO_2 (600 ± 50 ppm)

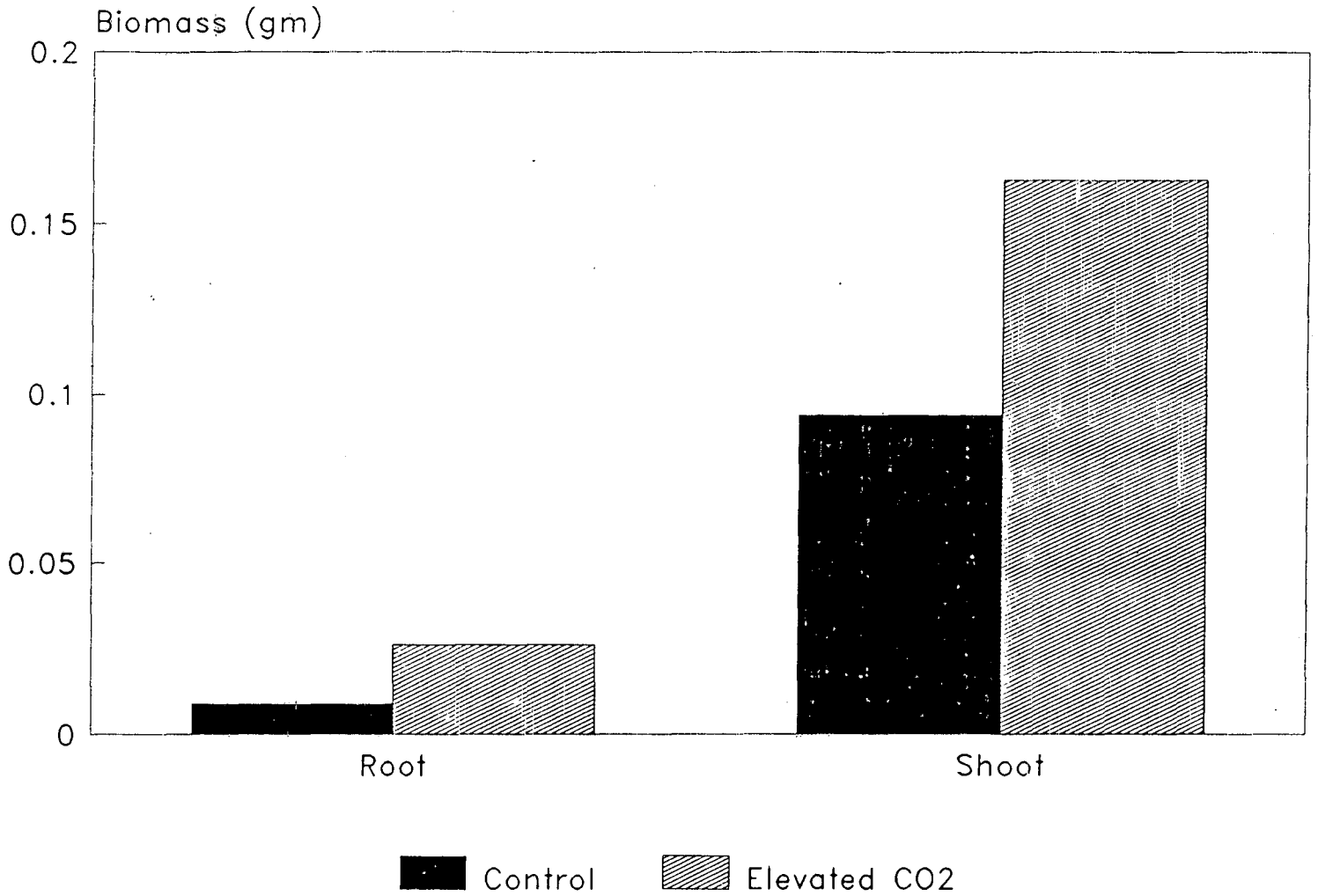

Fig 6 Increase in root and shoot biomass (S. oleracea cv. Banerjee's Giant) after ten days exposure to elevated CO_2 (600 ± 50 ppm)

TABLE 8: EFFECT OF ELEVATED CO_2 (600 ±50 ppm) ON FOLIAR STARCH CONTENT IN SPINACEA OLERACEA

Sample		Starch Content (%)
S. oleracea (cv. All Green)	Control	2.3
	Elevated CO_2	4.0
S. oleracea (cv. Banerjee's Giant)	Control	1.2
	Elevated CO_2	2.3

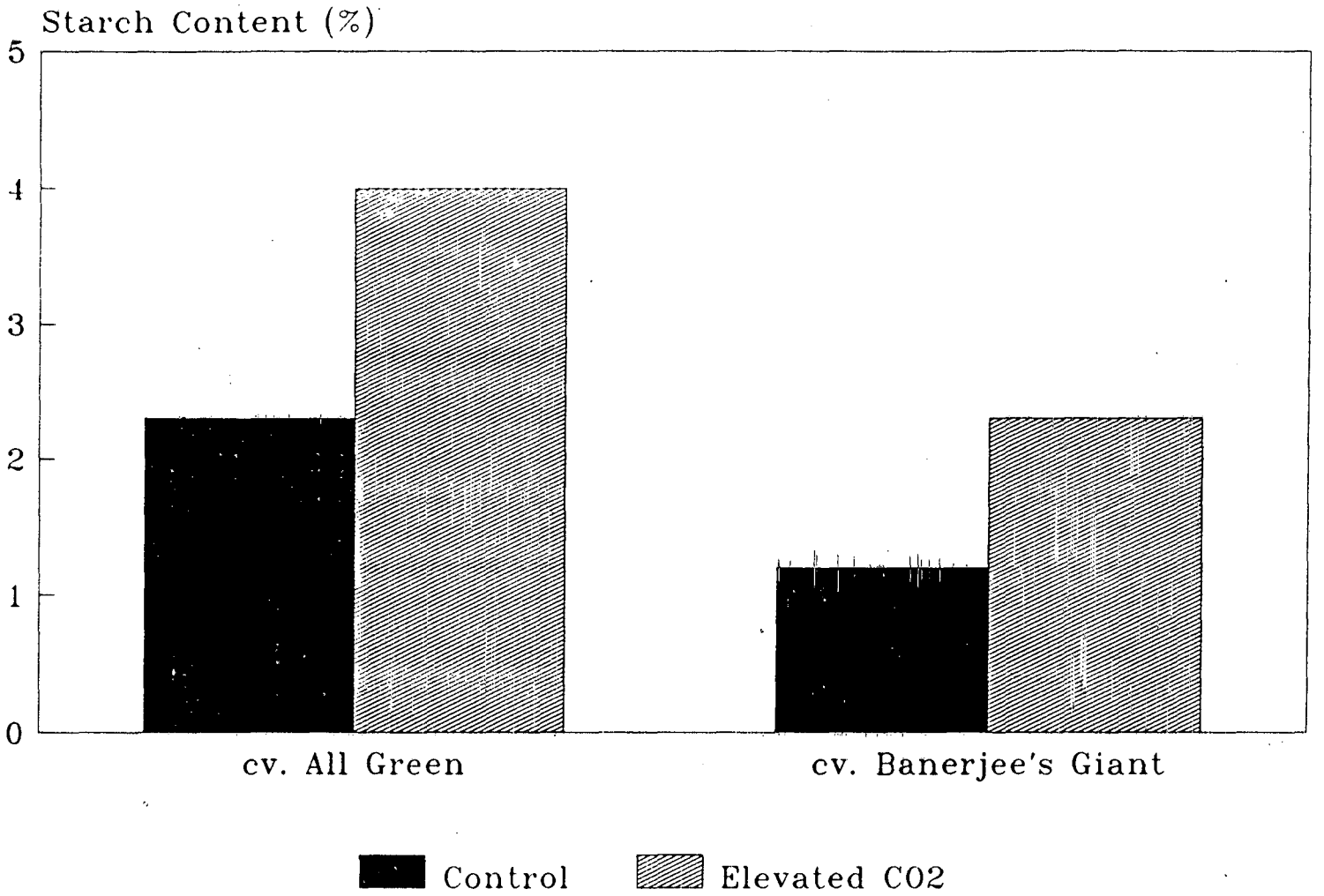

Fig 7 Percentage increase in foliar starch content after ten days exposure to elevated CO_2 (600 ± 50 ppm)

Discussion

The leaf area in Spinacea oleracea plants exposed to elevated CO_2 (600 ± 50 ppm) for ten days continuously exhibit a marked increase over control plants. The percentage increase in leaf area in S. oleracea cv. All Green under elevated CO_2 was 94.2%, and in S. oleracea cv. Banerjee's Giant it was 40.14%, over control. Under elevated CO_2 enhanced photosynthetic rates promoted the growth of additional leaf area. Individual plants vary with respect to % increase in leaf area under elevated CO_2. Increase in leaf area has also been recorded for other C_3 species as G. max (Rogers et. al., 1986), G. hirsutum (Delucia et.al, 1985). P. vulgaris, plants (Porter and Grodzinski, 1984) showed a 28% increase in leaf area under CO_2 enrichment (1200 ppm) compared to control over a 14-day exposure period.

Total chlorophyll content declined under elevated CO_2, 29.75% reduction in S. oleracea cv. All Green, 6.97% in S. oleracea cv. Banerjee's Giant, over control. Total chlorophyll has been reported to decline under CO_2 enrichment in other plants too. A, 42% reduction has been reported in G. hirsutum (Chang, 1975), 30% in T. subterraneum (Cave et al., 1981), 61% in G. hirsutum (Delucia et al., 1985), 14% in C. album (Sage et al., 1989) and 34% in B. oleracea (Sage et al., 1989). Reduction in

chlorophyll content at elevated CO_2 is attributed to chloroplast degeneration as a result of excess starch accumulation (Madsen, 1968). Chl a:b ratio increased under elevated CO_2 in S. oleracea cv. All Green from 1.68 to 2.11 and from 2.3 to 3.05 in S. oleracea cv. Banerjee's Giant. This result is in contrast to values reported in literature where chl a:b ratio has been found to decrease under elevated CO_2 (Cave et al., 1981; Delucia et al., 1985). The reason for the observed increase in chl a:b ratio could be, a greater % reduction in chl (b) compared to chl (a), under CO_2 enrichment. Carotene was also found to decrease under CO_2 enrichment. The information about response of carotene under enhanced CO_2 is practically non existent.

An increase in root and shoot biomass was observed in plants exposed to elevated CO_2. Percentage increase in root biomass was more than shoot biomass in both cultivars, with S. oleracea cv. All Green exhibiting greater % increase than S. oleracea cv. Banerjee's Giant. Similar results have been obtained in G. max (Cure et al., 1987) where, by day 22 of exposure to 700 ppm CO_2 biomass of roots increased by 88% over control as compared to 60% in leaves and 73% in stems. But contrasting results have been obtained in G. hirsutum (Delucia et al., 1985) where biomass partitioning was preferential to leaf sink followed by stems and least to roots. Root/Shoot ratio was found to increase under elevated

CO_2 from 0.161 to 0.348 (S. oleracea cv. All Green) and from 0.096 to 0.160 (S. oleracea cv. Banerjee's Giant). The results indicate that there is a preferential partitioning of photosynthates to root system. Ambient CO_2 thus, seems to have a definite control over photosynthate partitioning. Generalizations are not possible since the response seems to be species specific.

Foliar starch content increased in both cultivars with cv. All Green exhibiting a greater % starch content (4%) under elevated CO_2 (4%) compared to control (2.3%) than in cv. Banerjee's Giant (2.3 & 1.2%). In G. max, Finn and Brun (1982), reported a 46% increase in leaf starch content. In T. subterraneum (Cave et al., 1981), the percentage increase in starch content under elevated CO_2 was 135% compared to control (46.7%). The reason for lower leaf starch content in S. oleracea under elevated CO_2 could be, that additional photosynthate is present as sugars rather than starch.

The results clearly indicate that S. oleracea being a C_3 plant responds positively to elevated CO_2 as expected. But distinct intervarietal difference in response of S. oleracea to elevated CO_2 are evident (Plate 3,4). S. oleracea cv . All Green is more responsive to elevated CO_2 levels than S. oleracea cv. Banerjee's Giant, as the

Plate 3 S. oleracea cv. All Green plants after ten days exposure to A. Ambient CO_2 B. Elevated CO_2 (600 ± 50 ppm)

Plate 4 S. oleracea cv. Banerjee's Giant plants after ten days exposure to A. Ambient CO_2 B. Elevated CO_2 (600 ± 50 ppm)

former showed a greater % increase in leaf area, biomass and starch content under elevated CO_2. Percentage reduction in chlorophyll and carotene content was also greater in S. oleracea cv. All Green under elevated CO_2.

Studies using open top chamber have not been done in India so far. In absence of any previous experience, chamber construction and standardization took a major part of the time available. In addition to this CO_2 was monitored rigorously every three hr. Due to these demanding conditions and limited time available the exposure period could not be extended beyond ten days and replicates also could not be obtained. As a result the data could not be subjected to statistical analysis. Inspite of these limitations definite trends in response of S. oleracea to enhanced CO_2 were quite discernible. These results can only be treated as indicative rather than being conclusive in characterisation of response of S. oleracea to elevated CO_2. In future, long term studies on response of local plants to enhanced CO_2 levels using standard open top chambers are important. Such studies are required to obtain basic information for making a more realistic evaluation of impact of elevated CO_2 on plants.

ABSTRACT

Eighteen - day old Spinacea oleracea cv. All green and S. oleracea cv. Banerjee's Giant plants were exposed to ambient (350 ± 25 ppm) and elevated (600 ± 50 ppm) CO_2 in open - top chambers over a ten day period continuously. Leaf area increased by 94.2% (S. oleracea cv. All Green) and 40.14% (S.oleracea cv. Banerjee's Giant), under elevated CO_2 over ambient CO_2 plants. Root and shoot biomass inceased in both cultivars under elevated CO_2, 296 and 83.5% (S. oleracea cv. All Green), 188.8 and 73.5% (S. oleracea cv. Bannerjee's Giant) respectively. Root : Shoot ratio increased from 0.161 to 0.348 (S. oleracea cv. All Green) and from 0.096 to 0.160 (S. oleracea cv. Banerjee's Giant) under elevated CO_2. Foliar starch content increased slightly. Total chlorophyll content decreased by 29.75% (S. oleracea cv. All Green) and 6.97% (S. oleracea cv. Banerjee's Giant) compared to control. Chl a:b ratio increased under CO_2 enrichment. Enhanced photosynthetic rates leading to greater dry matter production under elevated CO_2 seem to be responsible for the observed increases in leaf area, biomass and starch. Decline in chlorophyll content could be due to disruption of chloroplasts by excess starch accumulation (Madsen, 1968). Out of the two cultivars of S. oleracea, studied, S. oleracea cv. All Green seems to be more responsive to

elevated CO_2 levels than S. oleracea cv. Banerjee's Giant. Overall positive responsive of S. oleracea many well enhance the market value of this leafy vegetable under enriched CO_2 atmospheres. The present study was of preliminary, short-term investigatory nature. Long-term, indepth study is needed to substantiate the results obtained above.

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