

**INFLUENCE OF CO₂ ENRICHMENT ON SEEDLING
GROWTH AND GAS EXCHANGE PARAMETERS
IN A FEW FOREST TREE SPECIES**

NATARAJA KARABA. N.

**DEPARTMENT OF CROP PHYSIOLOGY
UNIVERSITY OF AGRICULTURAL SCIENCES
BANGALORE
1991**

ಕೃಷಿ ವಿಶ್ವವಿದ್ಯಾನಿಲಯ
ವಿಶ್ವವಿದ್ಯಾನಿಲಯ ಕ್ರಾಂತಿ ಅಯ
ಗಾ. ಪಿ. ವಿ. ಕೆ., ಮಂಗಳೂರು-೬೨.
9DEC1991
Th. 2667
ಅವಕಾಶ ಸಂ.
ವ ಸಂ.

**INFLUENCE OF CO₂ ENRICHMENT ON SEEDLING
GROWTH AND GAS EXCHANGE PARAMETERS
IN A FEW FOREST TREE SPECIES**

NATARAJA KARABA. N.

Thesis submitted to the
University of Agricultural Sciences, Bangalore
in partial fulfilment of the requirements
for the award of the Degree of
MASTER OF SCIENCE (AGRICULTURE)
in
CROP PHYSIOLOGY

BANGALORE

NOVEMBER 1991

To

My Beloved Parents

DEPARTMENT OF CROP PHYSIOLOGY
UNIVERSITY OF AGRICULTURAL SCIENCES
BANGALORE

Certificate

This is to certify that the thesis entitled
"INFLUENCE OF CO₂ ENRICHMENT ON SEEDLING GROWTH AND GAS
EXCHANGE PARAMETERS IN A FEW FOREST TREE SPECIES"
submitted in partial fulfilment of the requirement for the
degree of **MASTER OF SCIENCE (AGRICULTURE)** in CROP
PHYSIOLOGY to the University of Agricultural Sciences,
Bangalore is a record of research work carried out by **Mr.**
NATARAJA KARABA. N. under my guidance and supervision and
that no part of the thesis has been submitted for the
award of any other degree, diploma, associateship,
fellowship or other similar titles.

Bangalore
November, 1991

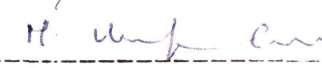

(T. G. PRASAD)
Major Advisor

APPROVED BY:

Chairman:


(T. G. Prasad)

Members: 1.


(M. Udaya Kumar)

2.


(R. Devendra)

3.

(V. Bhaskar)

4.


(C. K. Mathai)

ACKNOWLEDGEMENT

I take pleasure in acknowledging the following personalities who have helped me in shaping my career during the my M.Sc. degree programme.

Firstly, I sincerely thank Dr. T. G. Prasad, my guide, guru, freind and philosopher, who suggested me this line of research, guided the course of investigation and helped me in bringing out this thesis.

Dr. M. Udaya Kumar, Professor and Head, who is a constant source of inspiration beyound cliché, has taken immense trouble in channelising this research in the right direction and in correcting the earlier drafts. I thank him.

I thank the members of my advisory committee Dr. R. Devendra Assoc. Prof., Department of Crop Physiology, Dr. V. Bhaskar, Assoc. Prof., Department of Farm Forestry and Dr. C. K. Mathai, Scientist, IIHR, Hesaraghatta, who have critically evaluated the manuscript.

Dr. A. G. Shankar who is the main source of inspiration for all of us in the department needs a special mention here. Dr. Uma Shaanker, Mr. Aftab Huisen, Dr. Shashidhar and other staff members and non-teaching staff have extended their full co-operation and encouragement to me. I also thank them sincerely.

My sincere thanks to Dev, Shiv, Shesha, Jhansi, Patil, Uma, Anitha, Prakash, Kitty, Anks, KV, JP, Hebbar, Murali, - my seniors, who have stood with me in bringing out this thesis.

My classmates Kumuda, Manju, M³, Mohanraju and Vijaya have tolerated me and also helped me in several field and late night stays in the Lab.

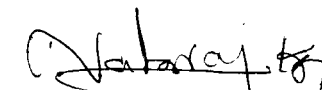
I am very much thankful to all my friend community for their needful suggestions and comments during this investigation.

I thank my brothers NNK, Dev & Krishnaraj and relatives Venkatesh, Sripathy, Sumathi, Srinivas Udupa, Dr. Mithyantha, M. V. Shastri, Janardhan Adiga, B. M. Somayaji, Bhadri and Vinodhini who helped in many ways through this study.

I thank ICAR for granting me Junior Research Fellowship during this investigation.

Finally, I thank all those who helped me while typing the thesis.

Bangalore
November, 1991.


(NATARAJA KARABA. N.)

C O N T E N T S

CHAPTER	TITLE	PAGE NO.
I.	INTRODUCTION	1-4
II.	REVIEW OF LITERATURE	5-28
III.	MATERIAL AND METHODS	29-52
IV.	EXPERIMENTAL RESULTS	53-105
V.	DISCUSSION	106-124
VI.	SUMMARY	125-129
VII.	REFERENCES	130-142

LIST OF TABLES

Table	Title	Page No.
1a.	Plant height, branch number and leaf number as affected by CO ₂ concentration and soil nutrient status.	55
1b.	Influence of CO ₂ enrichment and high soil nutrient status with regards to plant height, leaf and branch number in seedlings of forest tree species.	57
2a.	Effect of elevated CO ₂ concentration and soil nutrient status on leaf area, leaf weight and specific leaf weight.	60
2b.	Influence of elevated CO ₂ concentration and nutrient status on leaf area, leaf area and SLW in seedlings of tree species.	63
3a.	Effect of elevated CO ₂ concentration and soil nutrient status on the leaf weight ratio, shoot weight ratio, root weight ratio and root to shoot ratio.	66
3b.	Influence of elevated CO ₂ concentration and soil nutrient status on LWR, SWR, RWR and Root to shoot ratio in seedlings of different tree species.	68
4a.	Effect of elevated CO ₂ concentration and soil nutrient status on total biomass and biomass accumulation during the experimental period (DM).	70
4b.	Influence of elevated CO ₂ concentration and soil nutrient status on total dry matter and DM in seedlings of different tree species.	73
5a.	Influence of CO ₂ enrichment on plant height of the seedlings of different age groups in <u>Grevelia</u> and <u>Eucalyptus</u> .	75
5b.	Effect of CO ₂ on leaf number.	75

LIST OF TABLES
(Contd.)

Table	Title	Page No.
5c.	Effect of CO ₂ on branch number.	75
6a.	Response of different aged seedlings to CO ₂ enrichment with regard to leaf area (cm ²)	77
6b.	Influence of elevated CO ₂ on leaf area.	77
6c.	Effect of CO ₂ on leaf weight of different aged seedlings of <u>Grevelia</u> and <u>Eucalyptus</u> .	79
6d.	Effect of CO ₂ on specific leaf weight (SLW)	79
7a.	Differential response of different aged seedlings of <u>Grevelia</u> and <u>Eucalyptus</u> to CO ₂ with regards to leaf weight ratio.	81
7b.	Effect of CO ₂ on shoot weight ratio.	81
8a.	Root weight ratio of different aged seedlings of <u>Eucalyptus</u> and <u>Grevelia</u> as affected by CO ₂ .	83
8b.	Influence of CO ₂ on root to shoot ratio (R/S ratio).	83
9a.	Response to CO ₂ enrichment with regards to shoot weight in different aged seedlings.	85
9b.	Influence of CO ₂ on root weight of different aged seedlings of <u>Eucalyptus</u> and <u>Grevelia</u> .	85
10a.	Influence of CO ₂ concentration on total dry matter.	87
10b.	Influence of CO ₂ on DM.	87
10c.	Gas exchange characteristics in seedlings of different forest tree species.	90

LIST OF TABLES
(Contd.)

Table	Title	Page No.
11.	Assimilation rates ($\mu\text{Mols.m}^{-2}.\text{s}^{-1}$) at 330 and 660 Ci (ppm) in four seedlings of different tree species.	93
12.	Stomatal and mesophyll limitations to assimilation in seedlings of few tree species.	95
13.	Photorespiration ($\mu\text{Mols.m}^{-2}.\text{s}^{-1}$) in seedlings of different forest species.	100
14.	Maintenance respiration rates of seedlings of different tree species.	102
15.	Leaf chlorophyll content (mg/g Fwt.)	105
16.	Per cent increase in leaf area and biomass in highly responsive and low responsive species due to CO_2 enrichment.	122

LIST OF FIGURES

Figure	Title	Between Page No.
1.	Set up used for CO ₂ enrichment studies.	33-34
2.	Setting up of instrument (ADC- LCA-2)	38-39
3.	Set up to obtain different CO ₂ concentration for A/Ci curves using ADC- LCA-2.	39-40
4.	Hypothetical CO ₂ response curve showing initial slope of the curve, stomatal and mesophyll limitations.	41-42
5.	Set up to study maintenance respiration in plants using ADC IRGA model GS-225B.	49-50
6.	The change in the CO ₂ concentration in trenches covered with polythene structures.	53-54
7.	Responses of (a) <u>Acacia</u> , (b) <u>Casuarina</u> , (c) <u>Eucalyptus</u> , (d) <u>Derris</u> , (e) <u>Spathodea</u> , (f) <u>Leucaena</u> and (g) <u>Grevelia</u> to CO ₂ enrichment and high soil nutrient status, two months after the initiation of the experiment.	58-59 60-61 63-64 64-65
8.	Responses of different aged seedlings of (a) <u>Eucalyptus</u> and (b) <u>Grevelia</u> to CO ₂ enrichment two months after initiation of second experiments.	86-87
9.	CO ₂ response curves (A/Ci) for (a) <u>Acacia</u> , (b) <u>Derris</u> , (c) <u>Eucalyptus</u> , (d) <u>Spathodea</u> seedlings grown under two different CO ₂ levels.	91-92
10a.	Light response curve (A/PFD) for (a) <u>Acacia</u> , (b) <u>Derris</u> , (c) <u>Eucalyptus</u> , (d) <u>Spathodea</u> seedlings grown under two different CO ₂ levels.	96-97
10b.	Light response curve (gs/PFD) for (a) <u>Acacia</u> , (b) <u>Derris</u> , (c) <u>Eucalyptus</u> , (d) <u>Spathodea</u> seedlings grown under two different CO ₂ levels.	97-98

LIST OF FIGURES
(Contd...)

Figure	Title	Between Page No.
11a.	VPD response curve (A/VPD) for (a) <u>Acacia</u> , (b) <u>Derris</u> , (c) <u>Eucalyptus</u> , (d) <u>Spathodea</u> seedlings grown under two different CO ₂ levels.	98-99
11b.	VPD response curve for (gs/VPD) for (a) <u>Acacia</u> , (b) <u>Derris</u> , (c) <u>Eucalyptus</u> , (d) <u>Spathodea</u> seedlings grown under two different CO ₂ levels.	98-99
12.	Differential responses of different aged seedlings to elevated CO ₂ concentration.	115-116

LIST OF ABBREVIATIONS USED

'A'	CO ₂ assimilation rate
APQY	Apparent quantum yield
APS	Apparent photosynthesis
ADP	Adenosine diphosphate
ATP	Adenosine triphosphate
C	Degree celcius
CA	Carbonic anhydrase
CAP	Carboxy arabinnitol-1-phosphate
Ca	Ambient carbon dioxide concentration
CE	Carboxylation efficiency
CGR	Crop growth rate
Chl	Chlorophyll
Ci	Intercellular carbon dioxide concentration
cm	Centi meter
CO ₂	Carbon dioxide
DNS	Dinitro salicylate
DMSO	Dimethyl sulphoxide
E	Transpiration rate
En	Einstein
g _m	Mesophyll conductance
'g _s '	Stomatal conductance
g	Grams
HI	Harvest Index
IRGA	Infra red gas analyser
K _m	Affinity constant of the enzyme

Contd...

K_{cat}	Turn over number of the enzyme
LCA	Leaf chamber analyser
LSU	Large subunit
Mg^{+2}	Megnesium ion
M	Molar solution
m	Meter
ml	Milliliter
μM	Micro molar concentration
mg	Milligram
$\mu Mol.$	Micro moles
Na_2CO_3	Sodium carbonate
NADPH	Nicotinamide adenine dinucleotide phosphate
NAR	Net assimilation rate
nm	Nano meter
O_2	Oxygen
OD	Optical density
P	Phosphorus
PBL	Photochemical and biochemical limitations
PGA	3-Phosphoglycerate
PFD	Photon flux density
pH	Negative log of hydrogen ion concentration
Pi	Inorganic phosphate
P_{max}	Maximum photosynthetic rate
P_n	Net biomass gain
PPM	Parts per million
PR	Photorespiration
PSI	Photosystem I

Contd...

PSII	Photosystem II
PSU	Photosynthetic unit
P ₇₀₀	Reaction center of photosystem I
Q	Quantity of incident light
QY	Quantum yield
R	Respiratory losses
RH	Relative humidity
RNA	Ribonucleic acid
mRNA	Messenger RNA
RuBP	Ribulose-1,5-Bisphosphate
Rubisco	Ribulose-1,5-bisphosphate-carboxylase/oxygenase
s	Second
TP	Triose phosphate
TPS	True photosynthesis
TCA	Trichloro acetic acid
VPD	Vapor pressure deficit
V _{max}	Maximum velocity of an enzyme catalysed reaction
Zn	Zinc

INTRODUCTION

INTRODUCTION

The forest area in India is declining at an alarming rate and now it is about 14 to 19 per cent of the total geographical area. The annual rate of loss of forest works out about 47,500 ha. However, for the stability of ecosystem, it is believed that about 33 per cent of the geographical area should be covered by undisturbed forest.

Many evidences from different sources indicate that the atmospheric CO₂ concentrations is steadily rising (Woodward et al., 1991). This rise in CO₂ concentrations is strongly correlated with increase in global consumption of fossil fuels and the clearing of forests, especially in the tropics. This increase in CO₂ concentrations may have the potential to bring about long-term and perhaps irreversible alteration to our physical and biological environment. The realisation that mankind is playing a major role in bringing about changes in the global environment is one of the most significant features of biological thinking of the last decade. Because of this awareness, afforestation programme is assuming a great importance, especially in tropical countries where the forest degradation is occurring at a faster rate.

In India, to reduce the pressure on natural forests, social forestry programmes like farm forestry,

agroforestry etc, are being popularised in order to meet the basic demands like fuel, fodder, wood and other forest products. For the successful afforestation programmes, a continuous supply of healthy saplings is a must. Under normal condition to obtain tall and healthy transplantable seedlings we have to maintain them in the nursery at least for two to three years. This is mainly because of their poor initial growth rates.

The tree species that are used for afforestation programme are generally propagated by seeds or by cuttings in the forest nursery. The initial growth rate mainly depends on the stored food materials, initial leaf expansion rate and assimilation potential. In general woody species have very low leaf expansion rate.

Plant growth and development in a given environment depend upon the genetic as well as environmental factors. Amongst the environmental factors light, temperature, relative humidity (RH), soil moisture and nutrient status and CO_2 concentration play a major role. High nutrients in the restricted rooting medium favours the growth and development of the seedlings. Under high relative humidity there will be reduction in vapour pressure deficit (VPD) which will increase the leaf expansion rate as well as assimilation.

Further, plant growth and development are mainly governed by the process of photosynthesis. One of the

major environmental factor which affects the assimilation and so the biomass production is the ambient CO_2 concentration. Evidences from many sources show that it is possible to increase the biomass by more than two fold by CO_2 fertilization. This technique of CO_2 fertilization is being followed in commercial production of fruits, vegetable and ornamental plants. The increase in biomass under high CO_2 concentrations is mainly due to enhanced apparent photosynthesis and reduced photorespiration. In addition to this, stomatal conductances are known to decrease at elevated CO_2 concentrations. So, by using this technique it is also possible to enhance the seedling growth rate of forest tree species in the nursery. Identification of tree species highly responsive to elevated CO_2 concentrations and using them in afforestation programme can help in reducing the increase in global CO_2 concentration. It is also necessary to identify highly responsive seedling growth stage to elevated CO_2 concentration in the nursery to achieve maximum initial growth rate. Although in literature increase in dry matter at high CO_2 concentration has been worked out, the factors responsible for high assimilation in forest tree species has to be worked out.

Keeping the above view, the experiments were conducted with the following objectives :

1. to study the influence of high CO₂ concentrations on seedling growth rate of a few forest tree species.
2. to identify the most responsive seedling growth stage to elevated CO₂ concentration, and
3. to study the possible reasons for differential responses in different tree species to CO₂ by studying the gas exchange parameters, including the maintenance respiration.

REVIEW OF LITERATURE

II. REVIEW OF LITERATURE

Plant growth and development depend on a number of endogenous as well as exogenous factors like temperature, RH, light intensity and its duration. Since, CO₂ is one of the substrates for the process of photosynthesis, this also influences the growth rates and development of plant species.

It is universally accepted that CO₂ concentration of the earth's atmosphere is rising at an alarming rate (Idso, 1989). Many plant scientists believe that elevated CO₂ in earth's atmosphere enhances photosynthesis and thus growth and development (Lemon, 1983). Carbon dioxide is one of the substrates for photosynthesis and carbon constitutes the major portion of the biomass in plant. Recently, lot of interest is being shown to study the influence of increased CO₂ concentration on growth and development of plant with a primary objective to select plant types which are highly efficient in utilizing the CO₂.

In this investigation an attempt has been made to study the relative response of a few forest tree seedlings to elevated CO₂ concentrations. In this chapter, the general effect CO₂ enrichment on plant growth and development and gas exchange parameters are given.

Influence of elevated CO₂ concentration on growth and development

Influence of elevated CO₂ concentration on growth and productivity in crop plants has been studied by a number of workers. Increasing CO₂ concentration in the growth medium increases the growth rates in all species, and increase was maximum in C₃ species. Elevated CO₂ concentrations were known to increase biomass production in cereal crops like wheat (Gifford, 1979), vegetable crops like cucumber and cabbage (Heij *et al.*, 1984) and fruit crops like oranges and tomatoes (Downton *et al.*, 1987; Calverts, 1975). Amongst oil seed crops a number of reports indicate that soybean is highly responsive to elevated CO₂ concentration resulting in higher biomass production (Havelka *et al.*, 1984a).

In herbaceous C₃ crops, doubling of CO₂ concentration resulted in increase in yield. Baker *et al.*, (1990) claimed 32 per cent increase in grain yield in rice by doubling CO₂ concentration. Lamarks *et al.* (1984) showed higher growth rates in natural vegetation due to rise in global CO₂ concentration using ring analysis technique. Similar results were shown in tree species under doubled CO₂ concentrations. Ramus and Jarvis (1989) claimed that there was 40 per cent increase in the growth rates of tree species at around 600 ppm CO₂ concentration. Recently, Sasek and Strain (1991) observed 76 and 135 per cent

increase in biomass of Japanese honey suckle at 675 and 1000 μ lit/lit of CO_2 . Similarly doubling of biomass was reported after 54 days of growth in sweet oranges at elevated CO_2 level (Idso et al., 1991). Idso and Kimball (1991) showed biomass enhancement to an extent of 175 per cent in CO_2 enriched seedlings of sour orange. Seed yield per plant was increased with high CO_2 treatment (1000 μ lit/lit) applied at seed filling period in groundnut (Chen and Sung, 1990). Total biomass of Ochroma lagopus and Pentaclethra macroloba significantly increased in the elevated CO_2 levels of 675 μ lit/lit. The total dry weight of citrus seedling maintained at high CO_2 levels was increased by 100 per cent (Koch et al., 1986). Conroy et al. (1990) reported increased wood production in Pinus radiata under elevated CO_2 levels upto 30-90 per cent. Roger et al. (1983) have shown an increase in dry weight up to 157 per cent in Pinus taeda grown in open top chamber in the field for 3 months at 910 ppm of CO_2 .

These informations indicate that CO_2 enrichment/fertilization increases the growth rate of all the plant species. The increase in biomass at elevated CO_2 concentrations could be due to increase in photosynthetic surface area or due to increase in assimilation rate or due to reduction in photorespiration and dark respirations.

Allocation of biomass

Elevated CO_2 concentration has been shown to increase the rate of biomass accumulation as well as a change in the pattern of allocation of biomass to different parts of plant. Ramus and Jarvis (1989) suggested that primary effect of elevated CO_2 is increased growth rate and any change in allocation just reflect a change in timing of development. There is some evidence for this contention (Bazzaz et al., 1989). However, many other observation indicates that the pattern of allocation of assimilates changes at high CO_2 concentration for example, an increased allocation towards root has been shown at elevated CO_2 (Bazzaz et al., 1985).

An increase in the CO_2 concentration may significantly affect the tree anatomy and physiology. Stimulation of carbon assimilation rates resulting from higher internal carbon dioxide concentration (C_i) in the leaves in an enriched environment lead to several morphological changes. Campagna et al. (1989), Sionit et al. (1985), Jarvis (1989), Curtis (1989), Higginbotham et al. (1985) showed increased stem and foliar biomass, surface area, number of branches and foliage nutrition under CO_2 fertilization treatment and Sionit et al. (1985), Campagna et al. (1989), Oberbauer (1985) and Norby (1986) noticed greater root biomass and volume under elevated CO_2 concentration. Oberbauer et al. (1985) observed increased seed size and weight under high CO_2

level. According to Sasek and Strain (1991) the main effect of CO_2 enrichment was to triple the number of branches and to increase total branch length six times. Enhanced and accelerated branching increased total leaf area to an extent 50 per cent at elevated concentration of CO_2 (0.75 ul/lit). The main stem lengths was increased by 36 per cent at 1000 ul/lit of CO_2 in honey suckle vine. Sionit et al. (1985) observed increase in branch number under high CO_2 level in Pinus taeda and Liquidambar styraciflua seedlings.

In general higher CO_2 levels results in greater amount of starch accumulation in leaves and that extra carbon in leaves induced by high CO_2 concentrations results in an increase in leaf size, number of branches, plant height etc., which will ultimately leads to increased dry matter.

Influence of elevated CO_2 concentration on photosynthesis

Plants are always CO_2 limited for photosynthesis. CO_2 can enhance photosynthetic rate of C_3 plants over a wide range of concentrations when all other environmental factors are optimum. Photosynthetic quantum efficiency of C_3 plants at all irradiation levels increases markedly with CO_2 (Ehleringer and Bjorkman, 1977). This indicates that growth responses may be enhanced at low light intensity and elevated concentrations of CO_2 as observed in wheat (Mac Dowell, 1972). In species with C_4

metabolism there was little or no response of photosynthesis on quantum efficiency to an increase in CO₂ (Pearcy and Bjorkman, 1983).

In all short term experiments when the leaves were exposed to elevated CO₂ levels for a short period, increase in photosynthetic rates has been clearly demonstrated. Short term experiments with ponderosa pine, Quercus coccinea Pinus radiata, Populus deltoides, Eucelia farinosa and Ceanothus megacarpus have shown a clear increase in photosynthetic rate upto 40-80 per cent under high CO₂ levels of 600 ppm (Green and Wright, 1977; Sionit and Kramer 1986). Downton et al. (1990) in mangosteen (Garcinia mangostana L.) noticed increase in CO₂ fixation rate by 40-60 per cent under elevated CO₂ levels of 800 ppm. In soybean, photosynthetic rates, measured during seed filling stage were upto 150 per cent greater with leaflets grown at 660 compared to 330 μ lit/lit of CO₂ when measured across a range of intercellular CO₂ concentration and irradiance (Campbell et al., 1988). CO₂ enriched chrysanthemum leaves were more efficient than ambient grown leaves at irradiation below 400 μ mol/m²/lit because of greater photosynthetic efficiencies (Peet et al., 1991).

RuBISCO characteristics and carboxylation efficiency

The instantaneous response of C leaf to the ambient

1980; Von Caemmerer and Farquhar, 1981; Sharkey, 1985). At low Ca the rate of photosynthesis is limited by RuBISCO activity and in this phase, raising CO₂ concentration results in an increased rate of net CO₂ assimilation. In the second phase of response curve, at high Ca, photosynthesis is no longer limited by RuBISCO activity and it was thought that protein RuBISCO activase controls this (Salvucci, 1989) probably by controlling the level of ribulose biphosphate (RuBP) at the site of catalytic activity on RuBISCO.

CO₂ is involved in the activation of RuBISCO by reacting with lysine group at a locus distinct from the enzymatic site (Edwards and Walker, 1983; Hartman *et al.*, 1986). Inadequate recycling of inorganic phosphorus limits the assimilation rate at elevated CO₂ levels even in short term experiments. When the capacity to regenerate Pi declines, the rate of electron transport also declines (Sharkey *et al.*, 1989). It is well established that the rate of RuBP production and consumption and rate of triose phosphate utilization has been the major factor determining the extent of limitation imposed by inadequate Pi recycling. At high CO₂, triose phosphate utilization is alleviated (Sage, *et al.*, 1989), which presumably results from the stimulation of starch and sucrose synthesis. The rate of sucrose and starch synthesis increases linearly with CO₂ concentrations in short term (Sharkey, 1985). But in Vicia faba grown at

high CO₂ (550 $\mu\text{mol s}^{-1}\text{.mol s}^{-1}$) triose-phosphate utilization became the main limitation of CO₂ assimilation. In long term experiments when the plants were continuously exposed to enriched CO₂ levels, the results have been contradictory. There were evidences that the enhanced rates of photosynthesis observed during short term exposure to high CO₂ but not in long term exposure. After growth for a number of weeks in high CO₂, photosynthetic rates declined in cucumber (Clough, et al., 1981), tobacco (Raper and Peedin, 1978) and tomato (Yell,et al., 1989). After long term exposure to high CO₂, there was a loss of RuBISCO activity in a number of crops like soybean (Vu,et al., 1983), tomato (Yelle, et al., 1989). Indirect measurements of RuBISCO protein by finding with ¹⁴C carboxyarabinitol biphosphate indicated that there was loss of RuBISCO protein in cabbage grown in elevated CO₂ (Sage,et al., 1989). There was an initial increase in photosynthetic rate, followed by a fall in photosynthetic rates over days or week often to a rate similar to that observed in plants grown at ambient CO₂ (DeLucia, et al., 1985). A decrease in photosynthetic rates for plants grown at higher CO₂ concentration and measured at growth CO₂ concentration have been reported in water hyacinth (Spencer and Bowes, 1986), in Desmodium paniculatum (Wulff and Strain, 1982) and in cotton (Sasek et al., 1985).

The decrease in photosynthetic rate has been attributed to many reasons such as decreased carboxylation

efficiency or increased mesophyll resistances as in case of tomato (Bruggunik, 1984) or decrease in stomatal conductances as in case of cucumber (Peet et al., 1986). End product inhibition of photosynthesis has been attributed as a major reason (AzconBeito and Osmond, 1983). Starch accumulation has been stated as a major reason for inhibition in several studies (Šasek and Strain, 1985; Peet et al., 1986; Wulff and Strain, 1982; Cave et al., 1981; Oberbauer et al., 1985).

Several reasons are attributed for the observed decrease in assimilation due to starch accumulation. A reduction in chlorophyll content and grana formation due to starch accumulation has been reported by Wulff and Strain (1982) and Cave et al. (1981). The other inhibitory effect of starch accumulation was reduction in light reaching the chloroplast or increase in diffusive path length or interference of intercellular CO₂ transport due to large starch grains (Nafziger and Koller, 1976). Physical distortion of chloroplast due to starch grain were observed in plants grown at elevated CO₂ (Caves et al., 1981), leading to suggestion that the decline in 'A' at high CO₂ results from either feed back inhibition or damage to chloroplast (De Lusia et al., 1985). Peet et al. (1991) noticed feed back inhibition of photosynthesis in tomato plants under CO₂ enrichment.

In plants acclimated to saturated CO₂ and light,

decline in the RuBISCO activity and content has been noticed. The decrease is 'A' (assimilation rate) in high CO₂ acclimated water hyacinth was due to substantial decrease in RuBISCO activity and also soluble protein content. Sage et al. (1986) noticed reduction in RuBISCO content and activation state in plants acclimated to 950 CO₂ partial pressure. The decrease in RuBISCO content has been attributed to reallocation of N to the other enzyme systems because carboxylation is favoured through higher substrate levels.

In contrast Riechers (1984) did not notice any starch accumulation in C₄ grassland species under CO₂ enrichment. Increase in assimilation rate at higher CO₂ concentration in long term experiments has been observed in several plant species by Havelka et al. (1984), Campbell (1988), Nijis et al., 1989). Long term experiments up to 2 years with Pinus radiata have shown a higher photosynthetic rate at higher CO₂ levels (600 ppm) and the photosynthetic response increased as the tree aged. However, high photosynthetic rates at elevated CO₂ level did not sustain faster growth rates after 34 weeks (Conroy et al., 1990).

CO₂ and stomatal conductances

It is an accepted fact that stomatal conductances decreases, when the ambient CO₂ concentration (Ca) increases. Lowering of Ca can lead to stomatal opening, even in darkness but the width of stomatal aperture will

be even as great in the dark as in the light. There was reduction in stomatal conductance in cotton (Sasek et al., 1985), in rice and maize (Morison and Gifford, 1983) under elevated CO_2 concentrations. Alan et al. (1990) noticed 34 per cent reduction in leaf conductances under 600 $\mu\text{mol/lit}$ of carbon dioxide concentration in maize. Peet and Willits (1985) observed an increase in stomatal resistances in CO_2 enriched plants of tomato, but in cucumber, stomatal conductance was not affected by CO_2 concentrations. Potvin and Strain (1985) reported that stomatal conductances (gs) of two C_4 species, Eleusine indica and Echinochloa crusgalli was not changed when grown at elevated CO_2 concentration.

In most of the C_3 and C_4 plants, stomatal conductance changes in response to a change in Ca in such a way that the ratio of Ci to Ca remains more or less constant (Dubbe et al., 1978; Farquhar et al., 1978; Lowwerse, 1980; Morison and Gifford, 1983). Decrease in stomatal conductance has been shown in cotton (Sasek et al., 1985) and in rice and maize (Morison and Gifford, 1985) but few species particularly boreal confers, showed an insensitive response (Woodward, 1988; Eamus and Jarvis, 1989). According to Akita and Moss (1972) C_3 are less sensitive to elevated CO_2 concentration compared to C_4 plants but Morison and Gifford (1983) found no such evidences and Ci/Ca ratio was constant in C_3 and C_4 species at all concentrations of Ca . There was reduction in stomatal

conductances at $655 \mu\text{CO}_2/\text{l}$ in cowpea (Mbikayiet et al., 1988). Sasek et al. (1985) reported that g_s increases as the ambient CO_2 level reduces, but the decrease in g_s was permanent in water hyacinth and it did not increase when the plants were shifted back to lower CO_2 levels (Spencer and Bowes, 1986).

From the above observations it is clear that ' g_s ' decreases with increase in CO_2 concentration, where as, C_i increase with increase in C_a despite of decrease in ' g_s '.

CO_2 and photorespiration

Photosynthesis in C_3 species is relatively low because of competition between O_2 and CO_2 for RuBISCO. According Bjorkman (1966) CO_2 uptake in ambient air may be reduced by upto 40 per cent by photorespiration. Therefore increased CO_2 concentrations will reduce the O_2 uptake by photorespiration and increase CO_2 uptake (Farquhar et al., 1980) at least in the short term (Pearcy and Bjorkman, 1983). The mechanisms of enhancement of photosynthetic rates during short term exposure to raised CO_2 is mainly due to increase in RuBP carboxylation and the suppression of RuBP oxygenation (Besford, et al., 1985). Besford (1984) reported that the $K_m(\text{CO}_2)$ for tomato leaf was $4.7 \mu\text{M}$ at 20°C in the absence of O_2 and it was $7.1 \mu\text{M}$ in the presence of ambient levels of O_2 .

There was a decrease in oxygen inhibition of quantum yield in Eucalyptus species from 7.2 per cent at 88 μbar

internal CO_2 concentration (C_i) to 6 per cent at 1510 ubar C_i (Ehleringer and Bjorkman, 1977). According to Valle et al. (1985) there was a significant decrease in CO_2 compensations point in soybean leaves adapted to high CO_2 levels indicating a decrease in photorespirations. Foch et al. (1979) noticed a reduction in photorespiration to total photosynthesis ratio with increasing CO_2 concentrations. Mortensen (1984) has shown that elevated CO_2 concentrations caused a significant reduction in photorespiration of Picea abies. From these reports we can conclude that higher concentrations of CO_2 competes with O_2 to bring down the photorespiration.

CO_2 and dark respiration

Enhancement of photosynthesis under elevated CO_2 concentrations may lead to increased respiration because of the increased availability of substrate for respiration. Such a response might be reported if there is increased sucrose accumulation in leaves grown at high CO_2 (Tolbert and Zelitch, 1983), leading to enhanced rates of mitochondrial respiration. This expected enhancement was found in soybean leaves (Hrubec, et al., 1984). Several arctic tundra species showed a substantial increase in dark respiration under elevated CO_2 concentrations (Oechel and Strain, 1985). However, the dark respiration rates of wheat was reduced by 45 per cent following a doubling of CO_2 (Gifford et al., 1985). There

was no influence of elevated CO₂ on dark respiration or on light compensation in Desmodium paniculatum (Wulff and Strain, 1982). There was no significant difference in dark respiration in mungbean whereas in sunflower respiration was enhanced (Gifford et al., 1985) and Potvin and Stain (1985) reported an increase in respiration rates at elevated CO₂ concentrations in Gleusine indica and Echinochloa crusgalli. Shoot respiration was hardly affected by CO₂ enrichment in Plantago major where as root respiration was stimulated by CO₂ enrichment in young plants (Hrubec et al., 1985). The dark respiration was visually constant over a range of CO₂ concentrations from 50 to 1000 u bars (Kirschbaum and Farquhar, 1987) in eucalypts. However Bunce and Caulfield (1991) in a investigation on long-term effects of elevated carbon dioxide concentration on respiration in Dactylis glomerata, Lolium perenne and Medicago sativa in controlled environment chambers, and in D. glomerata and M. sativa in field plots showed reduced CO₂ efflux at elevated carbon dioxide concentrations. In field, Medicago sativa plots at high CO₂ had 15 per cent less carbon dioxide efflux per unit ground area. Reduction in whole plant respiratory carbon dioxide efflux per unit of mass during long-term exposure to carbon dioxide at 70 Pa as compared to 35 Pa was also reported by Bunce (1990) in two annual species.

From these reports we can conclude that the

respiration rates differs with species and plant parts under elevated carbon dioxide concentrations.

CO₂ and transpiration

As stomatal conductance decreases in response to elevated CO₂, transpiration decreases in proportion, provided the leaf temperature and the relative humidity of the air remain constant. Huber *et al.* (1984) noticed a reduction in transpiration in soybean. The decrease was from 140 mg H₂O/m²/sec at ambient level to 80 mg H₂O/m²/sec at 300 ppm above ambient level. There was 30 per cent decrease in transpiration in eucalypts at 680 u bars ambient potential pressure of CO₂ and at saturating light intensity (Wong and Dunin, 1987). In *Zea mays* L. doubling CO₂ (600 u mol/mol) caused an overall reduction of 23 per cent in transpiration rate (Alan, *et al.*, 1990). Jones *et al.* (1985b) reported an inverse relationship between transpiration rates and CO₂ levels in soybean. However, Valle *et al.* (1985b) reported a significant decrease in transpiration rate of soybean plants grown at elevated CO₂ concentrations.

From these reports it can be that the transpiration rate decreases at higher CO₂ levels but the extent of response varies.

CO₂ and H₂O use efficiency

Elevated CO₂ concentration increases photosynthetic

rate and is likely to cause reduction in stomatal conductance and this will reduce the rate of transpiration which will leads to an increase in WUE. Tolley and Strain (1985) and Norby et al. (1986) noticed a higher WUE at elevated CO₂ concentration in seedling of sweetgum and Quercus alba. Valle et al. (1985) showed a doubling of WUE in soybean leaves at 660 ppm of CO₂, but there was no significant decrease in transpiration rate. Wong and Dunin (1987) noticed 80 per cent reduction in transpiration ratio which was due to a 50 per cent increase in photosynthetic rates and a 30 per cent reduction in transpiration. Morison (1985) reported increase in WUE in the range of 60-160 per cent with a doubling of CO₂ concentrations both in C₃ and C₄ species. Enhancement of plant water use efficiency was also observed in plants grown in the field (Rogers et al., 1983). In Nerium oleander and Gossypium hirsutum (C₃) doubling WUE in the enriched CO₂ atmosphere as compared to the normal atmosphere was resulted due to 25 per cent decline in leaf conductances and 50 per cent increase in photosynthesis (Downton et al., 1980). In C₄ species Zea mays, the increase in photosynthesis was much smaller, but the conductances declined by 33 per cent so that overall photosynthetic WUE nearly doubled (Wong, 1979). Carlson and Bazzaz (1980) and Downton et al. (1980) have shown doubling of WUE in woody plants under enriched CO₂ atmosphere. There was a 63 per cent improvement in canopy WUE and three fold increase in single leaf WUE at

elevated CO_2 levels ($600 \text{ parts}/10^{-6} \text{ CO}_2$) in white clover (Nijs et al., 1989) stomatal conductance of Pentaclethra macroloba and Ochroma lagopus decreased with CO_2 enrichment resulting in significant increase in WUE (Oberbauer et al., 1985).

CO_2 and moisture stress

Increase in CO_2 concentration can compensate for stress induced reduction in growth. There was complete compensation for stress in Liquidambar styraciflua and partial compensation in Pinus taeda grown in low photon flux densities and doubled CO_2 concentrations (Tolley and Strain, 1984a). Full compensation for water stress by a doubling of the CO_2 concentration was also shown in Liquidambar styraciflua and partial compensation in Pinus taeda by Tolley and Strain (1984b), although Sionit et al. (1982) showed only partial compensation in older seedling of L. styraciflua. Conroy et al. (1986) also showed compensation for water stress in Pinus radiata. Sionit et al. (1981) suggested that increasing CO_2 concentration may induce wheat plants to osmoregulate more effectively and possibly enable them to adapt better to subsequent water stress. Marks and Starin's (1989) work on asters (C_3) and broomsedge (C_4) shows that C_3 plants would be better competitors during well watered as well as water limited condition under elevated CO_2 concentrations. The increase in WUE was greater in water stressed plants than in non-

stressed plants of Liquidambar styraciflua and Pinus taeda under CO₂ enrichment (Tolley, 1982).

CO₂ - ripening and senescence

CO₂ is an ethylene action inhibitor. Quazi and Freebairn (1970) noticed a delay in ripening of banana at high CO₂ concentration in the absence of ethylene. Mature Bartlett pea fruits when stored under a continuous flow of air with 10 per cent CO₂ for 4 days showed reduced respiration and ethylene evolution rate and remained greener and firmer than fruits stored in air (Kerbel et al., 1988).

High CO₂ probably has little direct effect on leaf senescence. There are varying reports about effect of high CO₂ on senescence. Hardy and Havelka (1975) reported delayed senescence in soybean but in the studies conducted by Havelka et al. (1984a) and Havelka et al. (1984b), senescence was not affected in soybean and wheat grown at elevated CO₂ levels. However, leaves on wheat plants grown in high CO₂ have been seen to senesce 3-4 days earlier (Sionit et al., 1981).

Interaction of CO₂ with other environmental factors:

CO₂ and nutrient supply:

The issue of plant response to elevated CO₂ under nutrient limiting condition have been shown by several workers. Brown and Higginbotham (1986) showed increase in

growth in response to an increase in CO₂ concentration at each amount of added nitrogen in seedling provided with a range of nitrogen concentration in sand culture with Populus tremuloides and Pinus glauca. Conroy et al. (1986) observed similar results in Pinus radiata at different phosphorus level. In the both the cases, plant weight, leaf weight and plant height were increased particularly at the higher addition of nutrients and root weight at the lower additions. Norby et al. (1986) and Luxmore et al. (1987) noticed greater proliferation of fine roots in response to an increase of CO₂ concentration which was associated with increase in the amount of nutrient uptake. Norby et al. (1986) observed 85 per cent increase in growth under CO₂ enrichment (690 u lit/lit) in a nutrient deficit forest soil although all of the seedling became severely nitrogen deficient. The uptake of nutrients like P, K increased with CO₂ concentrations but the uptake of N, S, B was not affected by CO₂. Larigauderie et al. (1988) reported a reduction in leaf nitrogen content at both high and low nitrogen levels and under low nitrogen level, low leaf nitrogen resulted in lower photosynthetic rates measured at 650 ul/lit compared to photosynthetic rates measured at 350 ul/lit for the non-enriched plants. Nodulated Alnus rubra seedlings showed greater whole plant photosynthesis and nitrogenase activity under high CO₂ compared to nodulated plants grown at ambient CO₂ and non-nodulated plants grown at both CO₂ levels. However,

whole plant dry weight, increased similarly with CO₂ enrichment in plants provided with additional mineral nutrients and in unfertilized plants although the fertilized plants grew 10 fold longer (Norby and O'Neill, 1991).

Brown and Higginbotham (1986) Goudriaan and de Ruiter (1983), Zangerl and Bazzaz (1984) have shown that the enhancing effects of CO₂ disappear under nitrogen and phosphorus limitations. Hocking and Meyer (1991) conducted a glass house experiment in which wheat, a C₃ species and maize, a C₄ species, were grown for eight weeks at high CO₂ (1500 cm³.m⁻³) on nitrogen supplies ranging from deficient (0.5 mols.m⁻³) to more than adequate for maximum growth (25 mols.m⁻³) and noticed the response of wheat to both carbon dioxide enrichment and nitrogen supply, but maize only to nitrogen supply. CO₂ enriched wheat produced about twice the dry matter of control plants at all the levels of nitrogen supply. Carbon dioxide enriched wheat plants accumulated more N than the control plants but the proportional increase in N content was not as great as that in dry matter, with the result that the concentrations of total-N and nitrate-N were lower in all enriched plants, including ears. Nitrate reductase activity was lower in enriched plants than in control. N-use efficiency in wheat was increased by CO₂ enrichment. In a study with the C₃ annual, Chenopodium album L. Sage et al. (1991) said that the initial slope of the

photosynthetic CO_2 response curve and the CO_2 saturated rate of photosynthesis depends linearly on organic leaf nitrogen content. However elevated atmospheric CO_2 (640 ubars) stimulated shoot growth of Triticum aestivum and the stimulation was greatest in plants provided with low NO_3 (Wong and Osmond, 1991).

The results indicate that a growth response to CO_2 enrichment is possible in nutrient limited system, but still there is some uncertainty as to whether CO_2 enrichment stimulate the growth of nutrient-stressed plants (Kramer 1981; Gifford, 1989).

CO_2 and light

Photosynthesis enhancement under elevated CO_2 highly depends on the light. Light saturation is usually higher under elevated CO_2 than under ambient CO_2 (Valle et al., 1985), Wong and Dunin (1987) in eucalypts and, Campbell (1988) in soybean noticed a high light saturation point under high CO_2 . Soybean plants adapted to high CO_2 exhibited capability to utilize radiation more effectively at elevated CO_2 throughout all light levels than leaflet grown at low CO_2 (Valle et al., 1985) and light compensation point was reduced from 35 $\mu\text{mol} \cdot \text{photon} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ at 330 $\mu\text{mol}^{-1} \cdot \text{mol}^{-1}$ to 27 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ at 660 $\mu\text{mol}^{-1} \cdot \text{mol}^{-1}$. Sharon and Mitchell (1988) said that lettuce leaf growth is most responsive to a combination of high light intensities and CO_2 enrichment.

CO₂ and temperature

The interaction of CO₂ with temperature is critical to the response of plants to climate change. Acock (1980) and Acock and Allen (1985) showed higher optimal temperature for photosynthesis at high CO₂ level than at ambient CO₂ level. Sionit et al. (1988a) observed that the reduction in dry weight of plant parts at lower temperature was ameliorated by increase atmospheric CO₂ levels. Imai et al. (1984) noticed a greater enhancement of leaf area and whole plant dry weight in casava at higher CO₂ and high temperature compared to higher CO₂ and lower temperature. Sionit et al. (1986) showed that plant height and number of branches, pod number and seed increased with CO₂ enrichment and more significantly with increasing temperature. Kimball (1985) reported that the per cent increase in growth caused by CO₂ enhancement was about the same over the range of temperature and Cure (1985) concluded that a doubling of CO₂ generally caused greater increase in growth at high temperature. However, Sionit et al. (1987) reported increased leaf photosynthetic of soybean in response to CO₂ enrichment more at 22/16°C than at 26/20°C. Backer et al. (1989) showed that seed yield of soybean at 660 ppm CO₂ decreased slightly with temperature over range of 23 to 33°C but it increased slightly with temperature at 330 ppm of CO₂. But Idso et al. (1987) found negative effect of 300 ppm

elevated CO_2 for temperature less than 19°C for five species (carrot, radish, cotton, water hyacinth, waterfern) and a somewhat linear increase of growth at elevated CO_2 with increasing temperature over the range of 19 to 34°C for all the species. The plants of okra at ambient CO_2 did not survive at day/night temperatures below $26/20^\circ\text{C}$, whereas plants thrived at $20/14^\circ\text{C}$ when CO_2 concentrations was 450, 675 and 1000 ppmv (Sionit et al., 1981).

From the above reports we can say that the extent of plants response to elevated CO_2 depends greatly on the temperature.

CO_2 and vapour pressure deficit (VPD)

VPD affects the photosynthesis by altering the stomatal conductances. Increased vapour pressure deficit is mainly caused by an increase in air temperature (Allen, 1990 and Allen et al., 1990). An increase air temperature from 28 to 33°C caused a 20 per cent increase in soybean canopy transpiration at both 330 and 800 ppm CO_2 (Jones et al., 1985). Higher VPD if reduces the stomatal conductances than it should also alter the C_i/C_a ratio. Morison and Gifford (1983) in two C_3 and C_4 species showed similar C_i/C_a ratio (0.8 - 0.9) at small VPD's but at large VPD's it was 0.7 and 0.5 in C_3 and C_4 species respectively and the response of conductance to VPD was maximum at low CO_2 and vice-versa. However, the relative

response of g_s either to CO_2 and VPD was unaffected by the other variables. In general, the response of plants to elevated CO_2 depends greatly on the VPD to which the plants are exposed and the response of plants to VPD, in turn depends on the other environmental factors.

MATERIAL AND METHODS

III. MATERIAL AND METHODS

Experiments were conducted to study the effect of high CO₂ concentration on seedling growth rates of few forest tree species and also to identify highly responsive tree species to elevated CO₂ concentrations. The reasons for differential response of the tree species at elevated CO₂ concentrations were further looked into by studying gas exchange characteristics of the species at elevated CO₂ concentrations. In addition to this, experiments were also conducted to study the influence of high soil nutrients on growth rates under elevated CO₂ concentration. Experiments were also conducted to identify the highly responsive growth stages of seedling of tree species for elevated CO₂ concentrations in terms of increase in leaf area and biomass.

The experiments were conducted in the Department of Crop Physiology, University of Agricultural Sciences, Bangalore, which is situated at a latitude of 12°58' north, longitude of 17°35' east and at an altitude of 930 MSL. The average annual rainfall of the experimental area was about 890.9 mm. The material used in this study and the experimental procedures adopted to achieve the objectives are given briefly in this chapter.

Experiment-I: The influence of elevated CO₂ concentration and soil nutrient status on seedling growth rates of few forest tree species

The main objective of this experiment was to identify responsive species for elevated CO₂ concentration and to study the influence of additional mineral nutrients on growth rates of seedlings under CO₂ enriched environment.

Design : Factorial CRBD

Treatments : (A) Species

- a. Eucalyptus hybrid
- b. Grevelia robusta (Silver oak)
- c. Spathodea campanulata
- d. Casuarina equisetifolia
- e. Derris indica (pongamia)
- f. Acacia auriculiformis
- g. Leucaena leucocephala (Subabul)

(B) CO₂ concentrations and nutrient levels:

- a. CO₂-1 :-ambient CO₂ level (340ppm)
- b. CO₂-2 :-700-800 ppm of CO₂

(C) Nutrient status in the rooting medium:

- a. N1- Rooting mixture :- sand, soil and FYM (1:1:0.5)
- b. N2- Rooting mixture+NPK :-25 mg of urea, 80 mg of superphosphpate and 13 mg of muriate of potash per seedling

The nutrients were added at the time of initiation of experiment and five more times at 15 days intervals from the start of the experiment.

Replications : Twenty

Duration of the experiment : 90 days

Observations recorded

1. Plant height
2. Branch number
3. Leaf number
4. Leaf area
5. Leaf biomass
6. Root weight
7. Final total dry matter
8. Total dry matter accumulated during the experimental period
9. Root/shoot ratio (R/S)
10. Specific leaf weight (SLW)
11. Leaf weight/dry matter (LWR)
12. Total increment in leaf area during experimental period (Δ LA)
13. Root weight ratio (RWR)
14. Shoot weight ratio (SWR)
15. Total leaf chlorophyll content
16. Gas exchange characteristics

Experiment-II: Influence of seedling age on growth response of forest tree seedlings to elevated CO₂ concentrations

The main objective of this experiment was to identify highly responsive seedling growth stages of tree species to elevated CO₂ concentrations.

Design : Factorial RCBD

Treatments : (A) Species

1. Eucalyptus seedlings of age 2, 5 and 10 months old
2. Grevelia robusta (Silver oak) seedlings of age group of 2, 5 and 10 months.

(B) CO₂ concentrations:

1. C1 - CO₂-1.
2. C2 - CO₂-2.

Replications : Ten

Duration of the experiment: 90 days

Observations recorded

1. Plant height
2. Branch number
3. Leaf number
4. Leaf area
5. Leaf biomass
6. Root weight
7. Final total dry matter
8. Total dry matter accumulated during the experimental period (DM)
9. Root/shoot ratio (R/S)
10. Specific leaf weight (SLW)
11. Leaf weight/dry matter (LWR)
12. Total increment in leaf area during experimental period (delta LA)
13. Root weight ratio (RWR)
14. Shoot weight ratio (SWR)

Seedling procurement

Uniform sized seedlings of required age were procured from the forest nursery, Department of Farm Forestry, University of Agricultural Sciences, Bangalore to assess the effect of CO_2 on growth rate and gas exchange characteristics.

Preparation of the seedlings

Procured seedlings from the forest nursery were carefully transplanted into polythene bags containing 2.2 kg of soil, sand and FYM mixture (1:1:0.5). The transplanted seedlings were kept under the shade for a period of 50 days for acclimatization. During this period they were watered thrice a day to maintain the soil water at field capacity.

Set up of experiment

Methods adopted to enhance CO_2 concentration.

The main treatment consisted of exposing the seedlings to two levels of CO_2 , CO_2 -1 (ambient CO_2 levels) and CO_2 -2 (700-800ppm of CO_2). Trenches of 4 x 1 x 0.6 mtrs were dug for the set up of experiment. Eight such trenches were dug, two each for four different treatments. Four trenches constituted CO_2 treatment (fig. 1).



Fig. 1. Setup used for CO₂ enrichment

Healthy seedlings in the polythene bags were transferred to trenches. Four trenches which constituted CO₂-2 treatment were covered with polythene sheets from 4.00 PM to 10.30 AM. Sheets were supported by metallic frame measuring 12 feet length, 4 feet width and 2 feet height. The trench was made air tight by burrying the free end of the polythene sheet into the soil. By covering, CO₂ released by dark respiration and soil respiration was trapped during night for making it available to plants during morning hours upto 10.30 AM.

Before initiation of the treatments, five plants from each treatments were taken for initial observations. At the time of initiation of the treatments, nutrients, nitrogen, phosphorus and potassium in the form of urea, superphosphates and muriate of potash were added (25 mg of urea, 80 mg of superphosphate and 13 mg of muriate of potash per seedling), to the treatment combination of CO₂ (700-800) + NPK and ambient CO₂ + NPK. The nutrient were added four more times at an interval of 15 days during experimental period at the same rate.

Methods adopted for collection of data

Plant height

Plant height was measured from soil surface to base of the youngest leaf on the main stem and expressed in cm.

Number of leaves and branches

The number of leaves and branches were counted in the seedling before the harvest and expressed as number/seedling.

Leaf area

LICOR leaf area meter (Model LI-3000) was used to measure the leaf area and expressed as $\text{cm}^2/\text{seedling}$. Leaves were detached from the plant to take the leaf area at the time of harvest for dry matter estimation.

Delta leaf area (ΔLA)

It is a reflection of total photosynthesising area that is developed during the experimental period.

$$\Delta\text{LA} = \text{Final LA} - \text{Initial LA}$$

Where; LA = Leaf area (cm^2 per plant.)

Estimation of biomass.

Total biomass accumulated was estimated at the beginning and at the end of the experiment. At the time of harvesting, plants were removed from the soil along with the roots. The polythene covers were cut open and the soil mass adhering to root was removed by washing with running water to get almost all the root system intact. The seedlings were separated into root, shoot and leaves and oven dried at 80°C for 48 hrs. After drying, root

weight, stem weight and leaf weights were taken separately. The total dry matter, leaf, stem, and root biomass was expressed as g DM/seedling. Total dry matter accumulated during the experimental period (DM) was computed by taking the differences between the initial and final dry matter of seedlings.

Specific leaf weight

Specific leaf weight is the ratio of the average leaf biomass per seedling to the average leaf area per seedling and expressed as g/cm².

$$SLW = \frac{\text{Leaf weight}}{\text{Leaf area}}$$

Leaf weight ratio.

Leaf weight ratio gives the ratio of leaf biomass to total biomass.

$$LWR = \frac{\text{Leaf biomass(g)}}{\text{Total dry matter(g)}}$$

The ratios was computed using the data on final leaf biomass, leaf area and total dry matter.

Shoot weight ratio (SWR)

SWR indicates the ratio of the dry matter that is allocated to the above ground portion to that of total biomass produced by the plant.

$$SWR = \frac{\text{Shoot weight (g)}}{\text{Total dry matter (g)}}$$

Root to shoot ratio (R/S ratio)

This ratio gives an idea about the pattern of partitioning of biomass between root and shoot system. This was calculated using the final harvest data on root and shoot biomass.

Root weight ratio (RWR)

RWR is the reflection of ratio of dry matter allocated to below ground portion to that of dry matter accumulated per plant.

$$\text{RWR} = \frac{\text{Root weight (g)}}{\text{Total dry matter (g)}}$$

Total dry matter accumulated during the experimental period (Δ DM)

It is the total amount of dry matter accumulated during the experimental period.

$$\Delta \text{DM} = \text{Final DM} - \text{Initial DM}$$

Gas exchange characteristics

The growth rates as measured by the increase in biomass and leaf area is a reflection of the species to the enhanced CO_2 , RH and temperature which will alter the assimilation rate and stomatal conductances. In this investigation an attempt was made to study the gas exchange characteristics to know the cause for the differences in response. The following parameters were studied.

1. Assimilation rate
2. Light response curves
3. CO₂ response curves
4. Gas exchange parameters at different VPD and VPD response curves.

All the gas exchange parameters were measured using portable ADC photosynthesis system (ADC-IRGA) (fig.2). This instrument can be used to measure the following parameters.

1. Photosynthetic rate (A) in $\mu\text{moles m}^{-2}\text{sec}^{-1}$
2. Stomatal conductances (gs) in $\text{mmoles m}^{-2}\text{sec}^{-1}$
3. Transpiration (E) in $\text{mmoles m}^{-2}\text{sec}^{-1}$
4. Intercellular CO₂ concentration (Ci) in ppm
5. Vapour pressure deficit (VPD) in milli bars.

All gas exchange traits were measured under ambient conditions by maintaining VPD between 30-35 milli bars. Leaf was clamped in the Parkinson's leaf chamber of ADC LCA-2 and once 'A' and gs values were stabilized the data were recorded.

Development of CO₂ response curves (A/Ci curves)

A/Ci curves refer to the pattern of increase in carbon assimilation rate (A) of leaves with increase in internal CO₂ concentrations. These are developed by plotting 'A' against CO₂ concentration at mesophyll cell surfaces (Ci). These curves follow a hyperbolic pattern. Such a A/Ci response curves can be used to quantify and

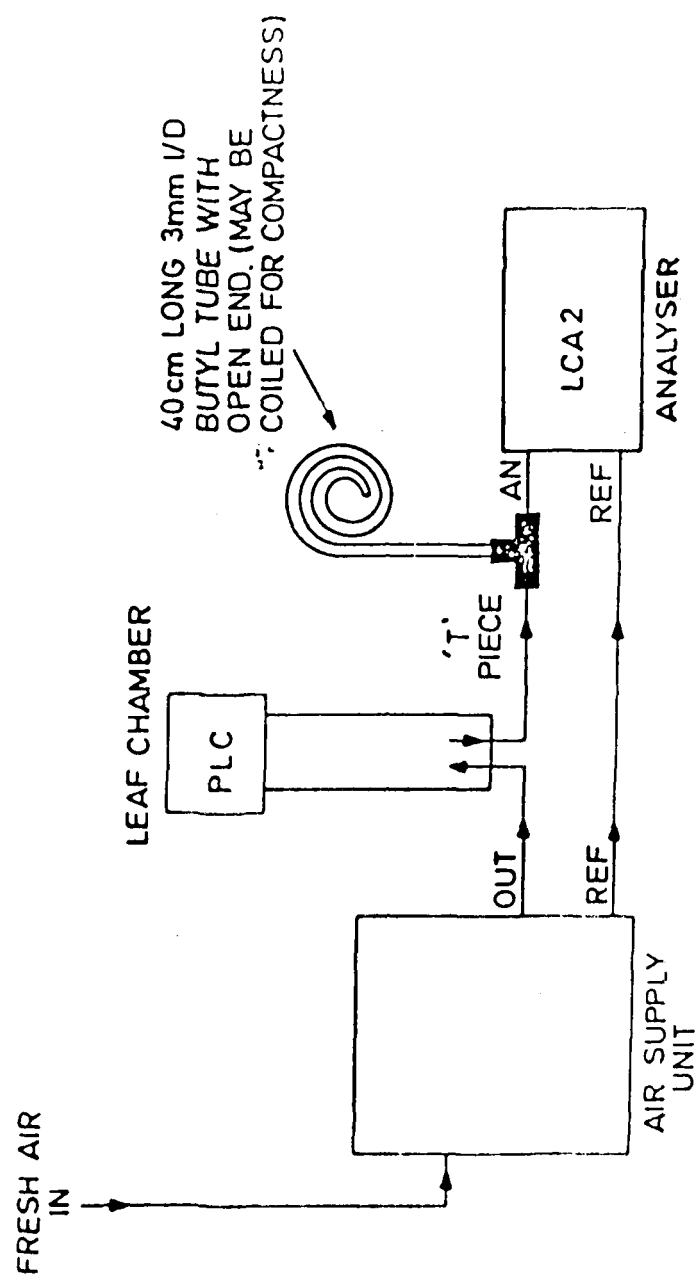
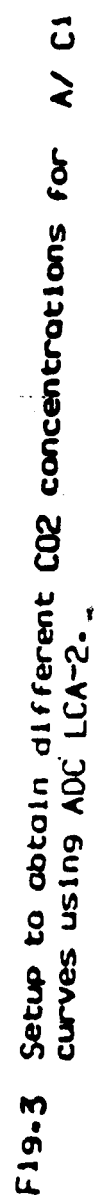


Fig. 2. Setting up of instrument (ADC- LCA-2).

separate the stomatal and mesophyll limitations and to quantify the carboxylation efficiency. The initial slope of this hyperbolic equation is often considered to represent the carboxylation efficiency of the systems.

Methodology

As shown in fig.3, the aluminium drums of 25 litres capacity were placed inverted over water in a plastic bucket of 50 litres capacity. Drums float over water in the inverted position when filled with air and slide down when air was removed slowly. Then proportionately decreasing the volume of air in the drum. An iron frame was used to position the aluminium drum over the water and also to facilitate easy up and down sliding. The connections into the drum were given in such a way that the air with known CO_2 concentration could be pumped into it and when once it was full, the air would be easily drawn at, without alteration in the composition of the air maintained in the drum. The air was pumped into the drum using an air pump. To obtain CO_2 levels lower than the atmospheric concentration the ambient air was pumped through KOH-soda lime trap and to increase CO_2 concentration above ambient CO_2 level a known amount of enriched CO_2 ($\text{CaCO}_3 + \text{HCl}$) was pumped into the drums. Air enriched with CO_2 was generated in a Kipp's apparatus by reacting 10 g of CaCO_3 with 20 ml of 1 N HCl. A known volume of this CO_2 enriched air was taken in a syringe and connected to the pumping system. The enriched air was



- 1-CO2 Scrubber 2-3-Way valve 3-Syringe 4-CO2 Source 5-Pump
6-Weight 7-Inverted drum. 8-Plastic waterbath 9-Inlet pipe
10-Outlet pipe 11-Water level (6.7-8.9.10.11) Aspirator.

pumped into the drum using an air pump. The pumping of atmospheric air dilutes the enriched air resulting in a known concentration of CO_2 higher than the atmospheric CO_2 concentrations. By altering the volume of CO_2 taken for dilution, different concentrations of CO_2 were generated. Six concentrations, three below and three above the atmospheric CO_2 concentrations were generated. †

The drums were sequentially connected to the air supply unit (ASU) of portable IRGA, ADC-LCA-2.

The CO_2 assimilation rates were measured using the youngest fully expanded leaves at saturated light intensities ($2000 \mu \text{Ein/m}^{-2}\text{sec}^{-1}$) and observations were taken between 9 AM and 12 noon. The selected leaf was clamped to the Parkinson's leaf chamber of area 6.25 cm^2 and held perpendicular to the incident light. The RH in the leaf chamber was maintained at a steady state level around the existing ambient RH by manipulating the rate of flow of dry air through air supply unit of portable IRGA, gas exchange parameters were recorded after 'A' and gs stabilized to a steady state condition. The assimilation rates at all seven CO_2 concentrations were recorded on the same exposed leaf area within 20 min of clamping.

The intercellular CO_2 concentration (C_i) was calculated using the formula given by

$$C_i = \frac{C_a (1/D_2 - E/2) - A}{(1/D_2 + E/2)}$$

Where;

$$D_2 = 1.585 r_s + 1.37 r_b$$

r_b = Boundary layer resistance

C_a = Ambient CO_2 concentration (ppm)

A = Photosynthetic rate (μ moles $m^{-2}sec^{-1}$)

The A/C_i curves were developed based on the principle of least squares with the help of a personal computer.

Estimation of stomatal and mesophyll limitations of photosynthesis

The modified method proposed by Farquhar and Sharkey (1982) was used to quantify the stomatal limitations of photosynthesis (fig.4). On the A/C_i response curve the following points were marked to assess the limitations.

A = Observed photosynthetic rates at any given time.

A_o = Potential photosynthetic rate when stomatal factors are not limiting and mesophyll factors are limiting.

A_g = Potential photosynthetic rate when mesophyll factors are not limiting and stomatal factors are limiting.

A_T = Potential maximum photosynthetic rate when mesophyll factors and stomatal factors are not limiting.

Using these values the limitations were calculated using the following formula.

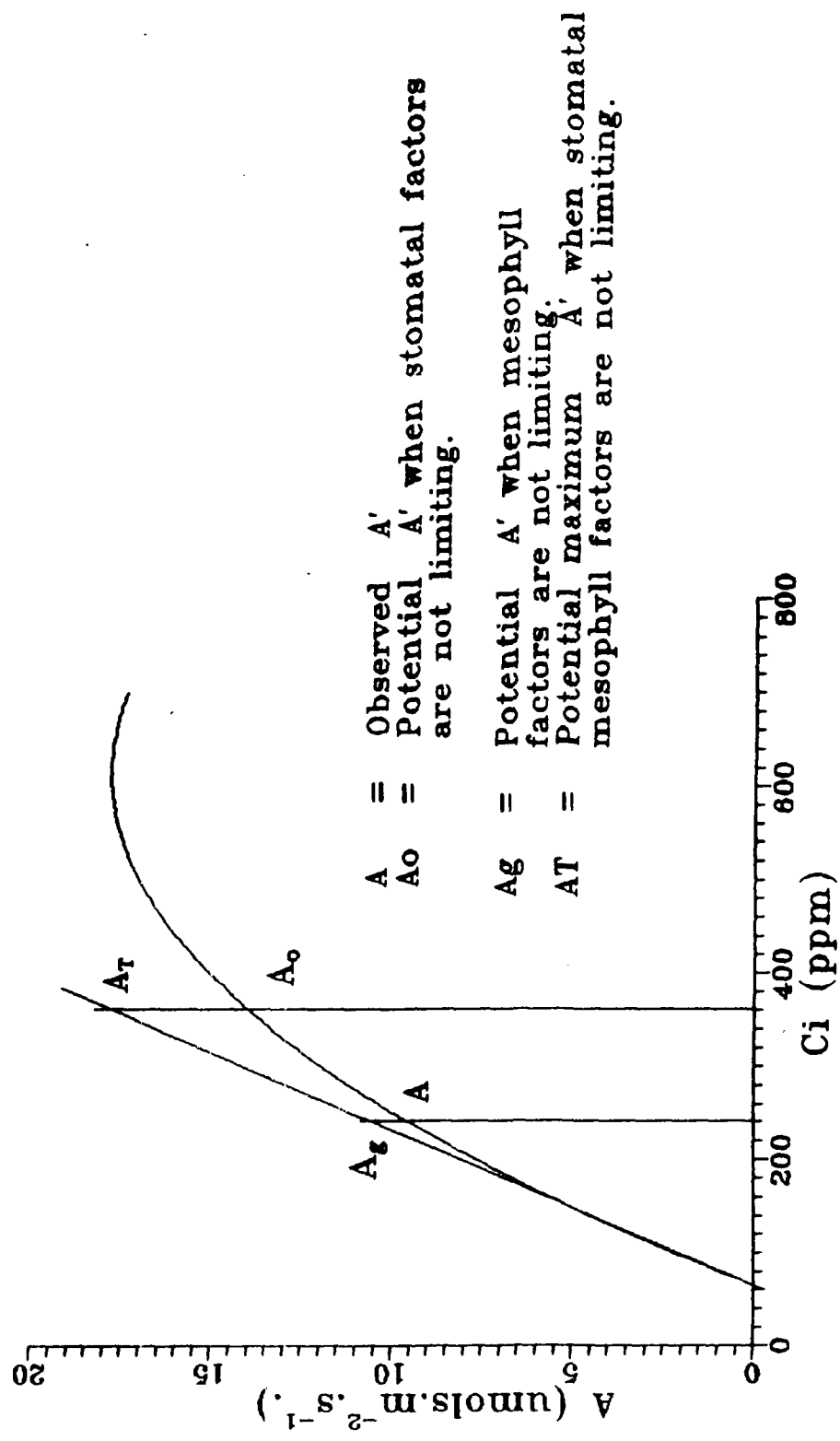


Fig.4: Hypothetical CO₂ response curve showing initial slope of the curve, stomatal and mesophyll limitations.

$$ls = \frac{A_o - A}{A_o} \times 100$$

Where;

ls = Stomatal limitation

$$lm = \frac{A_g - A}{A_g} \times 100$$

Where;

lm = Mesophyll limitations of observed photosynthetic rate.

$$ML = \frac{A_T - A_o}{A_T} \times 100$$

Where;

ML = Mesophyll limitation to the potential photosynthesis (A_T) when there is no stomatal limitation

Measurement of 'A' and g_s at ambient and elevated CO_2 levels

'A' and g_s measurements were taken at two different CO_2 concentrations, one at ambient and one at 700-800 ppm of CO_2 . A single leaf was clamped in Parkinson's leaf chamber of ADC. Gas exchange parameters were first measured at ambient CO_2 concentration and later at higher CO_2 concentrations. Readings were recorded after stabilization of 'A' and g_s values. Air containing 700-800 ppm of CO_2 was obtained following the same method as in A/Ci response curves.

Development of light response curves

Light response curves were developed to assess the saturating light intensity to photosynthesis by plotting light intensity against assimilation(A).

Methodology

Assimilation rates were measured at different light intensities. Different layers of polythene sheets were used to reduce the light intensity to a desired level. The assimilating leaf was covered with these filtes at a distance 2-4 cm above the leaf chamber to decrease the light intensity.

Light response curves were developed on a bright sunny day with a PFD of around 2000-2200 $\mu\text{mol m}^{-2}\text{sec}^{-1}$. The gas exchange characteristics (A , g_s , C_i , E) were measured using broad leaf Parkinson's leaf chamber of ADC-LCA-2; at different light intensities, after connecting the four components, ADC-IRGA, ASU, and leaf chamber with leaf clamped into the chamber. The assimilation rates were measured at a given light intensity by using specific filters. Initially the clamped leaves were exposed to low light intensity, keeping the filters to reduce approximately 80 per cent of the natural PFD. After stabilization g_s the gas exchange traits were recorded. The RH , g_s and A were continuously monitored using data logger and only after reaching a stable condition, data were logged. Later on, light intensities were increased gradually by using different filters and gas exchange characteristics were recorded after stabilization of g_s . During the measurements care was taken to maintain the RH of the leaf chambers equal to the ambient RH to minimize

the effect of VPD on gas exchange traits. Since, light has profound effect on g_s , the RH within the chamber decreases with low light. By using flow rate and bypass valve, required RH was monitored in the leaf chamber. By this procedure, light saturation curves were developed within 20-25 minutes. Light reflectors were used to enhance the light intensity approximately upto 2900-3000 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$. These light response curves used to assess the light saturation assimilation rate and to identify the PFD level for A-max measurements.

VPD response curves

VPD depends mainly on environmental factors like air temperature and RH. Under covered condition in the trenches, the micro-environment around the plant changes. The polythene covers not only prevent the diffusion of CO_2 but also traps the water vapour released by plants and soil surface. So in the evening RH increases leading to reduction in VPD. But in morning hours because of increase in temperature, the VPD inside the closed trench increases irrespective of the high RH. However, the VPD will be much less in covered trenches compared to non-covered trenches. Stomatal movement is regulated by VPD (at high VPD stomata tend to close) which will alter the gas exchange characteristics. By keeping all this in mind, VPD response curves were developed by determining the gas exchange traits of seedlings at different VPD's using ADC-IRGA, LCA-2.

The effect of VPD on 'A' and g_s was measured by instantaneously altering the VPD by changing the RH in the cuvette. In ADC, RH can be altered by manipulating the by-pass throttle valve and the flow rates. When the bypass throttle valve is opened, part of the air moves into the leaf chamber without passing through the desiccant. The extent of undried air passing through the valve could be reduced by reducing the extent of opening of the bypass valve and can be fully stopped when the valve is fully closed. By ASU (air supply unit) the inflow of air into the leaf chamber can be monitored. The working range is 200 to 600 ml of air per minute when the flow rates are small, the rate of dry air entering the leaf chamber would be lower, so RH in the leaf chamber would be at a higher level, depending upon the transpiration rates of the clamped leaf. Under high flow rates the air inside the leaf chambers would be flushed out, so the RH would be low. So it is possible to manipulate the VPD in the leaf chambers by altering the bypass valve opening and flow rates.

A fully expanded young leaf was clamped in the leaf chambers. The bypass valve was fully opened and flow rates was kept minimum to maintain the RH in the cuvette and thus minimum VPD. After allowing the leaf for acclimatization and when g_s and RH stabilized in the cuvette, the observations were recorded. Later bypass

valve was closed to desired level and flow rate was increased to get minimum RH and maximum VPD and observations were recorded after standardization of readings. The observations were recorded between 15 to 35 milli bars of VPD. Using these data, A/VPD , gs/VPD , T/VPD response curves were developed with the help of IBM compatible computer (PC-XT).

Measurements of photorespiration based on TPS and APS measurements

Photorespiration is nothing but release of fixed CO_2 by photosynthesis in the presence of light and this can be detected in C_3 plants by a number of methods. Since, in light photosynthesis and photorespiration are occurring simultaneously, it is difficult to measure the absolute values of photorespiration. Determination of CO_2 compensation point, rate of release of $^{14}CO_2$ from labelled glycine and the difference between true photosynthesis (TPS) and apparent photosynthesis (APS) are the few techniques to measure photorespiration. Photorespiration based on TPS and APS measurements is often used under steady state condition.

Apparent photosynthesis is the net exchange of CO_2 between leaf and atmosphere whereas true photosynthesis is the total CO_2 uptake at the site of carboxylation. The difference between the APS and TPS gives the photorespiratory loss of CO_2 . Accurate measurement of TPS can not be done, however, by inhibiting photorespiration

by giving 2 per cent O_2 it is possible to approximate TPS.

In spite of this drawback, the difference between TPS and APS is still a very reliable method for assessing the photorespiration under steady state condition. At 2 per cent ambient O_2 condition the photorespiratory release of CO_2 is negligible. The difference between photosynthetic rate at 2 per cent O_2 (TPS) and 21 per cent O_2 (APS) along with normal 330 ppm CO_2 concentration has been used to estimate photorespiration rate. O_2 stimulates photorespiration and inhibits the photosynthesis, therefore, difference in photosynthetic rate at 2 per cent and 21 per cent O_2 provide only an extreme upper limit of photorespiration.

METHODOLOGY:

A source of air with 2 per cent O_2 and ambient CO_2 level is the pre-requisite for determination of photorespiration. To achieve this, a gas cylinder with 2 per cent O_2 and 98 per cent N_2 is needed. A simple device was developed to achieve 2 per cent O_2 and 330 ppm CO_2 in an aluminium drum of 20 litres capacity as shown in fig. Required CO_2 concentration was obtained by mixing a given volume of 100 per cent CO_2 from the Kipp's apparatus with 2 per cent O_2 from oxygen cylinder. First CO_2 was pumped into the drum and then O_2 from the oxygen cylinder was pumped into it till the required concentration was reached. The gas cylinder was connected to the inverted

aluminium drum in such a manner that air from the cylinder with 2 per cent O_2 is fed into the drum and required amount of CO_2 gas from CO_2 source into a syringe and pushed into the drum through three way valve. Approximately 2 ml of CO_2 in 20 liters will rise CO_2 level by 100 ppm. The CO_2 concentration inside the drum was measured using IRGA and approximate volume of CO_2 was added to bring the CO_2 concentration near to ambient CO_2 concentration.

Measurement of 'A' at 21 per cent and 2 per cent oxygen:

The gas exchange characteristics like 'A', 'gs', C_i and transpiration rate were measured using broad leaf parkinson chamber suitably connected to ADC-IRGA and Air supply unit. After clamping the leaf into the chamber the assimilation traits were determined by drawing air from air mast with ambient CO_2 and 21 per cent O_2 . Next, air from the drum having 2 per cent O_2 and 330 ppm CO_2 was fed to the same leaf in the leaf chamber through ASU. After stabilization of RH and 'gs', the readings were recorded. RH inside the leaf chamber was maintained nearly same when either the air with 2 per cent or 21 per cent O_2 was fed. The difference between assimilation rates at 2 per cent and 21 per cent O_2 was calculated and expressed in terms of $\mu\text{Moles.m}^{-2}.\text{s}^{-1}$.

Measurement of maintenance respiration :

Dark and maintenance respiration rates in plants exposed to ambient and high CO_2 concentration may vary. Enhancement of photosynthesis may lead to increased respiration because of the increased availability of substrate for respiration. Effect of enriched CO_2 on respiration is important to understand the carbon gain. Genotypes with low maintenance respiration have been shown to have higher growth rates. Under CO_2 enrichment increased biomass may be due to reduction in respiration. To know this an experiment was conducted by selecting four plant species having least response as well as high response to elevated CO_2 .

Several techniques are employed to determine the dark respiration. The rate of CO_2 released by the matured plant tissue has been used to assess the differences in maintenance respiration. In recent years, IRGA open system is used to determine maintenance respiration.

IRGA maintenance respiration setup :

There are six chambers for placing plant material, Latex tubes, plastic T connectors, adjustable pinch cock, T valve and an external pump to ensure the flow of ambient air at constant pressure to each chamber. Connections are such that, there is a constant flow of ambient air through the chamber always [fig.5]. Volume of the chambers and

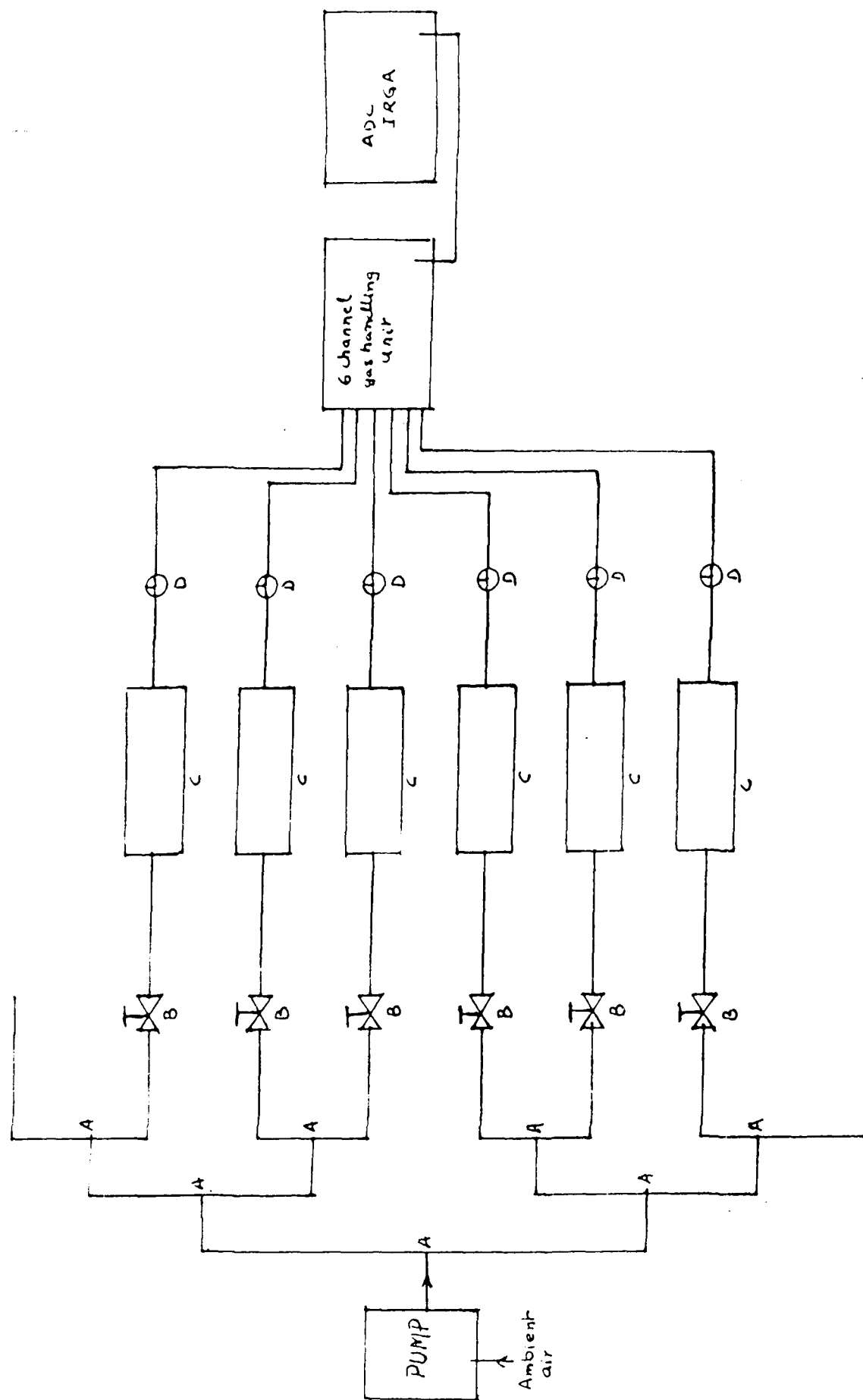


Fig. 5. Setup to study maintenance respiration in plants using
 ADC- IRGA model GS-225B.
 A-3-Way connector B. Throttle valve C-Chamber D. 3-Way valve

the length of tubing is maintained same for all the six lines. Last two connections were left open to ensure the pressure drop through the gas handling unit which measures the flow rates and feeds the air from one chamber at a time into the IRGA (ADC,UK.). CO_2 concentration was measured in the absolute mode. Adjustable pinch cock regulates the air flow into the chamber and gas handling unit. The flow of air into the gas handling unit or to atmosphere is regulated by T valve. In this set up, steady state was maintained in 5 sample chambers as there was continuous flow of air through the chambers leading out either to atmosphere or to IRGA. Thus, there was no build up of CO_2 inside the chambers. CO_2 levels were regulated by controlling the flow rates or by changing the amount of respiring tissue in the chamber. Flow rates through the chamber was maintained to get maximum differences in the CO_2 levels between control chamber and chambers with the respiring tissue.

Methodology

Intact seedlings were brought to laboratory and kept under darkness for 24 hours. During the dark treatment plants were kept under turgid condition by putting adequate water. Twentyfour hours after dark pre-treatment in the laboratory condition, well matured leaves were excised from the seedlings and placed in the sample chamber of IRGA. Leaf area and leaf weight of the sample leaves were recorded. Change in CO_2 concentrations

(ΔCO_2) was measured at steady state condition at a constant flow rate using the IRGA. Respiration rate was calculated using the following formula.

$$\text{Respiration rate} = (\Delta\text{CO}_2 \text{ in ppm})(w) \\ (\mu\text{mols.g}^{-1}.\text{h}^{-1}.)$$

where;

$$w = \frac{\text{Flow rate}}{\text{weight of the tissue}} \times \frac{60 \times 0.9872}{22.4}$$

$$w = \text{mass flow (mol.g}^{-1}.\text{h}^{-1}.)$$

Flow rate in ml/min.

Estimation of total chlorophyll content in the leaf

In addition to the measurements of gas exchange traits total leaf chlorophyll content was estimated in four plant species namely Eucalyptus, Spathodea, Derris and Acacia at the end of the experiments by DMSO method (Hiscox and Iorolestan, 1979).

Leaf discs weighing 100 mg was incubated overnight in 10 ml of DMSO (Dimethyl sulphoxide) and Acetone (1:1) mixture. After the period of incubation the samples were bioled in a water bath for 5 minutes. Then the extract was made up to 10 ml and optical density was read at 663 and 645 nm using double beam spectrophotometer. The total chlorophyll, chlorophyll 'a' and chlorophyll 'b' were calculated using the following formulae,

$$\begin{array}{l} \text{mg of chlorophyll} \\ \text{'a' / g of tissue} \end{array} = \frac{12.7(D \text{ at } 663) - 2.69 (D \text{ at } 645)}{a \times 1000 \times W} \times V$$

$$\begin{array}{l} \text{mg of chlorophyll} \\ \text{'b' / g of tissue} \end{array} = \frac{22.9 (D \text{ at } 645) - 4.68 (D \text{ at } 663)}{a \times 1000 \times W} \times V$$

$$\begin{array}{l} \text{Total chlorophyll} \\ \text{(mg/g)} \end{array} = \frac{20.2 (D \text{ at } 645) + 8.02 (D \text{ at } 663)}{a \times 1000 \times W} \times V$$

where,

D = Optical density.

V = Final volume of extract made

W = Fresh weight of leaf discs.

a = Path length in the photocell (1cm).

EXPERIMENTAL RESULTS

VI. EXPERIMENTAL RESULTS

The present investigation was conducted to know the effect of elevated CO_2 concentration on seedling growth of few tree species. The influence of increased soil nutritional status on growth rate under elevated CO_2 concentration was also studied. In addition, experiments were conducted to identify the highly responsive growth stages of the seedlings of tree species to elevated CO_2 concentrations.

The response of different forest species to elevated CO_2 concentration was studied by examining the following main parameters:

- a) determining the increment growth rate under elevated CO_2 concentration.
- b) studying the gas exchange traits at higher CO_2 levels.

To study the response of seedling of tree species to elevated CO_2 two separate experiments were conducted. As explained in the earlier chapter the methodology of CO_2 enrichment remain same in both the experiments. There was a considerable increase in CO_2 inside the enclosed trench. The build of CO_2 during evening hours and depletion of CO_2 during morning hours represented in the fig.6.

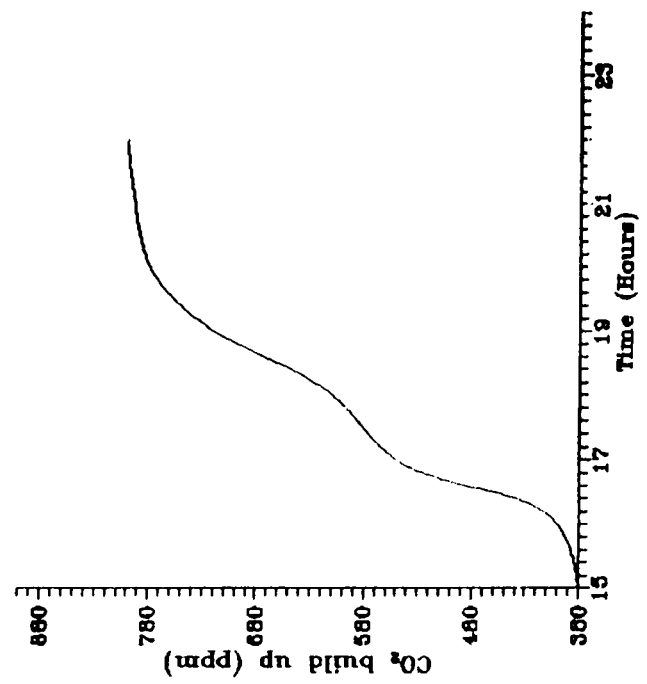
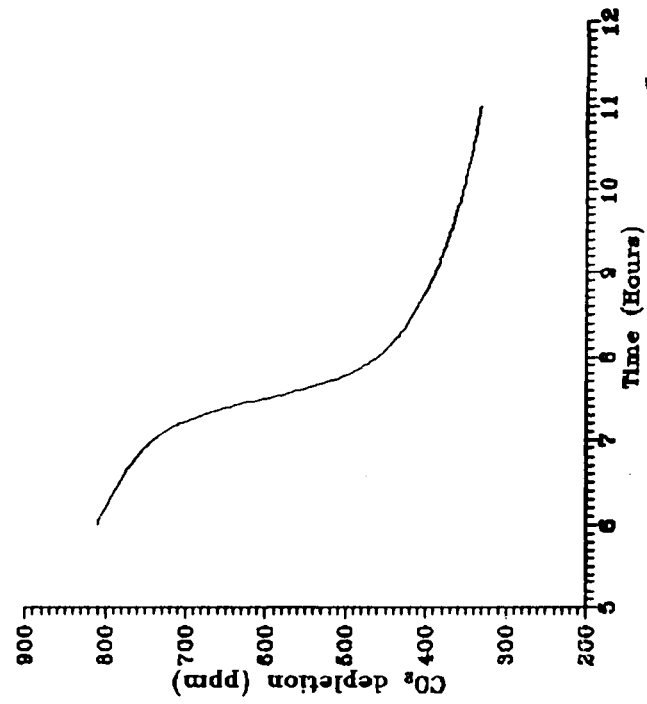


Fig. 6. The changes in the in the CO₂ concentration in trenches covered with polythene structures.

4.1 The influence of elevated CO₂ concentration and soil nutrient status on seedling growth rate of a few forest tree species

Experiment was conducted with seedlings of seven tree species to study the effect of elevated CO₂ concentrations on growth and also to identify highly responsive species to elevated CO₂ concentration. The influence of soil nutrient status was also studied to know the effect of nutrients on growth at two concentrations of CO₂. The seedlings were kept at different CO₂ levels for a total duration of 90 days and change in the growth parameters were assessed at the end of the experiment. In order to assess the influence of high CO₂ levels and nutrient status on growth rates, the data on leaf area, leaf biomass, root biomass, stem biomass and total biomass were recorded and biomass accumulated during the experimental period was calculated.

4.1.1 Influence of CO₂ enrichment and soil nutrient status on morphological characters

The plant height, the number of branches and number of leaves of the seedlings grown in four different treatments ie C1, C2, C1+N and C2+N are given in the Table 1(a) and Table 1(b).

The plant height at the end of the experiment showed significant increase due to CO₂ enrichment as well as due to soil nutrient status. Increasing the soil nutrient

Table i (a) : Plant height, branch number and leaf number
as affected by CO₂ concentration and
soil nutrient status.

Treatments	Plant height (cm)	Branch number (No/plant)	Leaf number (No/plant)
C1	42.29	1.80	31.69
C1+N	49.90	2.37	36.46
C2	58.73	3.31	49.71
C2+N	62.65	4.09	55.31
CD at 5%	1.59	0.26	3.24

status increased the plant height by 17.9 per cent. Enrichment of CO₂ resulted in 38.87 per cent increase in plant height over the plants grown at ambient CO₂ levels. High CO₂ and high soil nutrient status increased the plant height further, to an extent of 48.14 per cent over the plants grown at ambient CO₂ levels without high soil nutrient status. In all the seven species tested, there was increase in plant height when the soil nutrient status was higher. However the increase was marked only in Grevelia, Derris and Casuarina in which the increase in plant height was more than 30 per cent compared to the plants grown at ambient CO₂ level with low soil nutrient status. CO₂ enrichment increased the plant height in all the species studied and the increase ranged from 17 to 97 per cent. In Grevelia and Derris the response was very marked. In plants exposed to high CO₂ concentration and high soil nutrient status the plant height was maximum compared to the plants grown at high CO₂ concentration only. In Grevelia and Derris the response to high CO₂ along with high nutrient was more compared to high CO₂ treatment alone.

Branch number

Number of branches per plant at the end of the experiment was significantly more due to increase in the soil nutrient status as well as due to CO₂ enrichment. The per cent increase in branch number due to the increase in the soil nutrient status alone or at enriched CO₂ alone

Table 1 (b) : Influence of CO₂ enrichment and high soil nutrient status with regards to plant height, leaf and branch number in seedlings of forest tree species.

Species	Plant height (cm)				Branch number(No/plant)				Leaf number(No/plant)			
	C1	C1+N	C2	C2+N	C1	C1+N	C2	C2+N	C1	C1+N	C2	C2+N
<u>Acacia</u>	63.72 (12.6)	71.80 (17.8)	75.03 (19.4)	76.06	2.0	3.0 (50)	4.0 (100)	4.2 (110)	36.2 [*] (8.8)	39.4 (30.9)	47.4 (46.9)	53.2
<u>Casuarina</u>	47.08 (30.2)	61.28 (57)	73.96 (67.7)	79.44	2.8	4.0 (42)	4.8 (71)	6.0 (114)	85.6 (7.9)	92.4 (67)	143.0 (89)	162.2
<u>Eucalyptus</u>	69.00 (3.6)	71.47 (23)	84.87 (27)	87.97	2.2	3.6 (63)	4.4 (100)	6.4 (190)	30.4 (49)	45.2 (64)	50.4 (92)	58.4
<u>Derris</u>	25.40 (36)	34.50 (89)	47.97 (102)	51.40	0.0	0.0	0.0	1.0	10.2 (2)	10.4 (69)	17.2 (73)	17.6
<u>Spathodea</u>	29.20 (21)	35.2 (24)	36.09 (37)	40.03	0.0	0.0	1.2	1.0	10.6 (-2)	10.4 (42)	15.0 (34)	14.2
<u>Leucaena</u>	46.83 (4)	48.48 (37)	63.97 (34)	62.60	4.4	4.0 (-9)	6.2 (41)	6.4 (45)	27.0 (7)	29.0 (25)	33.7 (50)	40.6
<u>Grevelia</u>	14.80 (79)	26.48 (97)	29.20 (177)	41.05	1.2	2.0 (66)	2.6 (116)	3.6 (200)	21.8 (30)	28.4 (91)	41.6 (88)	41.0
CD at 5%	4.2				0.695				0.57			

* Values in the parenthesis indicate per cent increase/decrease over control.

were 31.6 and 84 per cent, respectively over the plant grown at ambient CO₂ concentration (Table 1b).

Five out of seven species tested showed more number of branches due to enriched soil nutrient status as well as due to high CO₂ concentration. Increase in the number of branches was more in Grevelia, Eucalyptus, Acacia and Casuarina. In Eucalyptus and Grevelia elevated CO₂ concentration along with high soil nutrient status enhanced the branch number significantly more than that in enriched CO₂ concentration alone.

Leaf number

The average number of leaves per plant at the end of the experiment was significantly more due to increase in the soil nutrient status as well as due to elevated CO₂ concentrations. Average per cent increase in leaf number due to high nutrient status in the rooting medium and elevated CO₂ concentration were 15.1 and 56.9 compared to the plant grown under ambient CO₂ levels and low level of nutrients in the rooting medium.

Leaf number per plant at the end of the experiment was 48.7 and 30.3 per cent more due to high nutrient status at ambient CO₂ levels in Eucalyptus and Grevelia respectively. Increase in CO₂ concentration resulted in 24.8 to 90.8 per cent increase in the leaf number in different species. Increase in leaf number due to CO₂



Acacia

Fig. 7. Responses of seedling of different tree species to CO₂ enrichment and high soil nutrient status two months after initiation of the experiments.



Casuarina

enrichment was more than 50 per cent in Grevelia, Derris, Eucalyptus and Casuarina. In plants exposed to elevated CO₂ concentration and high nutrient status in the soil medium the number of leaves retained at the end of the experiment was maximum in all the species except in Spathodea and Grevelia (Table 1b)

Leaf area

Influence of CO₂ enrichment and soil nutrient status on leaf area development was substantial. The mean leaf area of all the species in C1 treatment was 285 cm² per plant and it increased to 710.9 cm² per plant at elevated CO₂ concentration. The leaf area showed marked increase due to high soil nutrient status. Maximum leaf area was observed in C2+N treatment. The increase in leaf area due to increased soil nutrient status was 42.2 per cent. CO₂ enrichment treatment increased the leaf area by 149.3 per cent. Elevated CO₂ concentration with high nutrient status in rooting medium resulted in further increase in average leaf area to an extent of 154.49 per cent (Table 2a).

Seedlings of tree species showed significant variation in their response to elevated CO₂ concentration and high nutrient status in terms of leaf area development. Increase in the soil nutrient status resulted in increase in leaf area in six out seven species. The increase was marked in Spathodea and Acacia. In Leucaena

Table 2(a) : Effect of elevated CO₂ concentration and soil nutrient status on leaf area, leaf weight and specific leaf weight.

Treatment	Leaf area (cm ² /plant)	Leaf weight (gm/ plant)	Specific leaf weight (g/cm ²)	LA (cm ²)
C1	285.28	3.89	0.018	156.45
C1+N	405.81 (42.22)	4.49 (45.55)	0.020 (11.11)	277.13 (77.15)
C2	710.94 (149.27)	8.09 (161.95)	0.017 (-5.5)	582.28 (272.17)
C2+N	725.84 (154.49)	8.04 (160.51)	0.016 (-11.11)	597.21 (281.72)
CD at 5%	40.86	0.467	0.003	

* Values in parenthesis indicate per cent increase over control.



Eucalyptus



Derris

there was a marginal reduction in leaf area at higher nutrient status in the rooting media. Significant species variation was observed in increase of leaf area to elevated CO₂ concentration. Maximum response to high CO₂ was observed in Grevelia, followed by Derris (table 2b). In other three species Casuarina, Leucaena and Spathodea also the increase in leaf area at elevated CO₂ was more than 100 per cent. In Eucalyptus increase was to an extent of 46.2 per cent. High CO₂ along with high nutrient status although increased leaf area in many species more than that of elevated CO₂ alone, the differences were not marked. Only in Grevelia there was substantial increase in leaf area in C2+N treatment compared to C2 alone.

Differential leaf area (Δ LA)

The influence of different treatments on increase in leaf area during 90 days experimental period was assessed. The absolute increase in average leaf area per plant indicated that both elevated CO₂ concentration and higher nutritional status in the rooting medium increases the leaf area development significantly. The per cent increase in the leaf area during the experimental period was to an extent of 77.1 per cent due to increase in nutrient status in the rooting media and 272.2 per cent due to elevated CO₂ concentration. The plants raised under elevated CO₂ and high nutrient status showed a further increase of 9 per cent leaf area compared to the plants raised under elevated CO₂ alone.

Increase in the soil nutrient status resulted in increased leaf area development in six out of the seven species tested and the increase was to an extent of 31.5 per cent in Derris to 390.2 per cent in Spathodea. In Acacia and Grevelia also the increase in leaf area was substantial to an extent of 257.1 and 107.4 per cent respectively. Increase in the CO₂ concentration resulted in substantial increase in leaf area in all the species studied. The increase ranged from 54 to 1750 per cent in different species. In Grevelia there was nearly 18 fold increase in leaf area development. In Acacia, Spathodea, Derris and Leucaena there was five, four, three and three fold increase in leaf area development due to elevated CO₂ concentration respectively. In plants raised with high nutrient status as well as elevated CO₂ concentration resulted an increase in leaf area development ranged from 52.92 to 2280 per cent in different treatments. Substantial increase in leaf area development due to high nutrient status along with elevated CO₂ concentration compared to elevated CO₂ concentration alone was observed only in Grevelia (Table 2b).

Leaf biomass:

The influence of CO₂ enrichment and nutrient status on leaf biomass was significant. High nutrition status in the rooting medium resulted in a significant increase in mean leaf biomass of all the species. The increase due to higher nutrient status was to an extent of 45.25 per cent.

Table 2(b) : Influence of elevated CO₂ concentration, and nutrient status on leaf area, Δ leaf area and SLW in seedling of tree species.

Species	Leaf area (cm ² /plant)			Delta Leaf area (cm ² /plant)			Leaf biomass(g/plant)			Specific leaf weight(g/cm ⁻²)			
	CI	CI+N	C2	C2+N	CI	CI+N	C2	C2+N	CI	CI+N	C2	C2+N	
<u>Acacia</u>	225.5	408.4 (81)	615.0 (173)	544.3 (141)	70.9	253.5 (257)	460.4 (548)	389.3 (448)	3.56	4.71 (32)	7.80 (119)	8.38 (135)	0.016 (-25) (-18)
<u>Casuarina</u>	57.4	80.0 (39)	162.9 (184)	167.8 (192)	48.4	70.9 (47)	154.1 (218)	159.1 (229)	2.95	4.40 (49)	8.33 (182)	7.34 (148)	0.056 (10.7) (-5) (-21)
<u>Eucalyptus</u>	509.2	668.1 (31)	744.8 (46)	737.1 (45)	430.9	589.7 (37)	666.4 (55)	650.7 (53)	4.58	6.00 (31)	8.54 (86)	9.29 (103)	0.009 (33) (44)
<u>Derris</u>	449.4	546.9 (22)	1451.2 (223)	1441.4 (221)	309.1	406.5 (32)	1310.8 (324)	1301.1 (321)	2.50	3.20 (28)	9.52 (281)	9.03 (261)	0.006 (17)
<u>Spathodea</u>	356.7	724.4 (103)	741.3 (108)	761.4 (113)	94.2	461.9 (390)	478.9 (408)	498.9 (429)	2.92	4.92 (68)	6.04 (107)	6.09 (109)	0.008 (-12.5)
<u>Leucaena</u>	294.3	280.6 (-4.6)	680.6 (131)	704.0 (139)	114.4	100.7 (-12)	500.7 (338)	524.1 (358)	3.37	4.35 (29)	8.20 (143)	8.27 (145)	0.013 (23) (-7.6) (-7.6)
<u>Grevelia</u>	103.0	132.3 (28)	580.4 (463)	724.9 (604)	27.3	56.6 (107)	504.7 (1750)	649.2 (2200)	1.72	4.49 (161)	8.09 (369)	8.04 (367)	0.017 (76) (-17) (-35)
CD at 5%		100.115				110.155				1.236			0.00886

* Values in the parenthesis indicate per cent increase/decrease over control.



Spathodea



Leucaena

CO₂ enrichment resulted in an increase in the leaf biomass to an extent of 8.09 g per plant compared to 3.09 g per plant in control plant. Elevated CO₂ with high soil nutrient status also resulted in an increase in the leaf biomass to the extent as that of elevated CO₂ alone. The per cent increase in leaf biomass was 45.5 due to high nutrient level and 161.9 per cent due to elevated CO₂.

Increase in soil nutrient status resulted in significant increase in leaf biomass in Spathodia, Casuarina, Eucalyptus and Grevelia. The increase was maximum in Grevelia which registered an increase of 160.7 per cent due to higher nutrient status in the soil. In other three species Acacia, Derris and Leucaena, although the leaf biomass increased due to high soil nutrient status the differences were not significant. High CO₂ in the growth medium increased leaf biomass significantly in all species. In Grevelia and Derris increase in leaf biomass was to an extent of 369 and 281 per cent respectively. In Casuarina, Leucaena, Acacia and Spathopdea the increase in leaf biomass was more than 100 percent. In Eucalyptus, it was 86 per cent. The effect of elevated CO₂ and increased nutrient status although increased leaf biomass in four out of seven species the difference between C2 and C2+N were not significant.

Specific leaf weight (SLW):

The specific leaf weight (SLW) did not showed any



Grevelia

difference between control and other treatments. However the SLW was maximum in the treatment with ambient CO_2 level at high soil nutrient status and it was least in high CO_2 and high nutrient status. In Acacia, Casuarina, Leucaena and Grevelia, there was a marginal reduction in SLW under elevated CO_2 concentration (Table 2b).

Leaf weight ratio (LWR)

The mean leaf weight ratio of all the species showed a marginal increase due to high soil nutrient status.

Seedling raised in ambient CO_2 concentration with high nutrient status in the soil resulted in 2.9 to 24 per cent increase in LWR in different species. Elevated CO_2 concentration as well as high nutrient status in the rooting medium resulted in marked increase in the leaf weight ratio in Acacia, Leucaena and Derris (Table 3b).

Shoot weight ratio (SWR)

The mean ratio of biomass allocated to shoot in relation to total biomass at the end of the experiment showed a marginal increase due to higher nutritional status in the soil. Increase in CO_2 concentration had no effect on shoot weight ratio (Table 3a).

Increasing CO_2 concentration resulted in marginal increase in SWR in Acacia, Spathodea, Derris and Grevelia. In Leucaena, Eucalyptus and Casuarina there was a slight

Table 3(a) : Effect of elevated CO₂ concentration and soil nutrient status on Leaf weight ratio, Shoot weight ratio, root weight ratio and root to shoot ratio.

Treatments	LWR	SWR	RWR	R/S ratio
C1	0.311	0.601	0.399	0.710
C1+N	0.358 (15.11)	0.646 (7.48)	0.354 (-11.7)	0.585 (-17.6)
C2	0.334 (7.39)	0.616 (2.49)	0.384 (-3.7)	0.656 (-7.6)
C2+N	0.317 (1.93)	0.622 (3.49)	0.380 (-4.76)	0.647 (-8.8)
CD at 5%	NS	0.0248	0.0249	0.0258

* Values in parenthesis are per cent increase over control.

reduction in SWR with elevated CO₂ concentration. When CO₂ concentration was increased in the medium with high soil nutrient status, marginal increase in SWR was observed in six out of seven species tested.

Root weight ratio (RWR)

The mean root weight ratio reduced due to CO₂ concentration as well as due to increase in nutrient status. The reduction was significant due to high soil nutrient status (Table 3a).

Amongst several species tested RWR was relatively high in Leucaena, Spathodea and Acacia. In Grevelia the RWR was relatively less (Table 3b).

Root weight ratio showed marginal reduction due to high nutrient status in rooting media in all species. The reduction was marked in Grevelia, Casuarina, Acacia and Spathodea. The influence of elevated CO₂ on RWR was marginal and insignificant. Only in Acacia there was 13.5 per cent reduction in RWR due to high CO₂ treatment.

Root shoot ratio (RSR)

A significant reduction in root shoot to ratio was noticed due to high nutrient status as well as due to high CO₂ concentration. Reduction in RSR was more due to increase in nutrient status in rooting medium than elevated CO₂ concentration.

Table 3(b) : Influence of elevated CO₂ concentration and nutrient status on LWR, SWR, RWR & R/S ratio in seedlings of different tree species.

Species	LWR			SWR			RWR			R/S ratio						
	Cl	Cl+H	C2	C2+H	Cl	Cl+H	C2	C2+H	Cl	Cl+H	C2	C2+H				
<u>Acacia</u>	0.212	0.263	0.298	0.294	0.517	0.586	0.582	0.559	0.483	0.414	0.418	0.441	0.943	0.734	0.727	0.792
<u>Casuarina</u>	0.408	0.492	0.381	0.322	0.696	0.752	0.690	0.712	0.304	0.248	0.310	0.288	0.443	0.336	0.454	0.424
<u>Eucalyptus</u>	0.306	0.315	0.304	0.342	0.620	0.640	0.611	0.647	0.380	0.360	0.389	0.369	0.615	0.592	0.636	0.570
<u>Peris</u>	0.327	0.360	0.364	0.340	0.612	0.648	0.646	0.646	0.388	0.382	0.354	0.354	0.641	0.619	0.559	0.550
<u>Spathodea</u>	0.234	0.261	0.222	0.227	0.528	0.592	0.552	0.514	0.472	0.408	0.488	0.486	0.923	0.704	0.828	0.949
<u>Leucaena</u>	0.215	0.231	0.264	0.258	0.500	0.549	0.498	0.523	0.492	0.451	0.502	0.447	1.012	0.829	1.014	0.913
<u>Grevelia</u>	0.475	0.508	0.505	0.432	0.727	0.783	0.751	0.758	0.273	0.217	0.269	0.242	0.390	0.280	0.370	0.330
CD at 5%	NS			0.06576			0.0659			NS						

Root to shoot ratio was markedly high in Leucaena, Spathodea and Acacia, and it was less in Casuarina and Grevelia. CO₂ enrichment resulted in reduction in RSR in Acacia, Derris, Spathodea and Grevelia. However, the reduction was more than 20 per cent only in Acacia. The treatment in which plants were exposed to elevated CO₂ with high soil nutrient status, the RSR was relatively less in Spathodea, Acacia and Derris. The reduction in these species ranged from 14.22 to 16.00 per cent. In Leucaena, Eucalyptus and Casuarina, the reduction was less than 10.0 per cent as shown in the Table 3(b).

Total biomass

The influence of CO₂ enrichment and nutrient status on total biomass was significant. Final dry matter increase was 26.78, 125.22 and 130.6 per cent, over control in the treatments C1+N, C2 and C2+N, respectively. CO₂ enrichment resulted in an average increase in dry matter to an extent of 25.37 g/plant compared to 11.2 g/plant in control (table 4a). Elevated CO₂ concentration with high soil nutrient status resulted in further increase in total dry matter to an extent of 4 per cent.

The total dry matter at the end of the experiment in plants raised under ambient CO₂ concentration was high in Acacia, Leucaena and Eucalyptus, and it was least in Grevelia. High soil nutrient status and high CO₂ resulted in significant increase in biomass in four out of seven

Table 4(a) : Effect of elevated CO₂ concentration and soil nutrient status on final biomass accumulated and amount of biomass accumulated during the experimental period.(△DM)

Treatments	Final dry matter (g/plant)	△ DM (g/plant)
C1	11.27	9.48
C1+N	14.29 (26.8)	12.49 (31.8)
C2	25.37 (125.2)	23.58 (148.8)
C2+N	25.99 (130.6)	24.20 (155.3)
CD at 5%	0.879	0.98

* Values in the parenthesis indicate the per cent increase over control.

species tested. The increase was more than 50 per cent in Spathodea and Grevelia. Increase in CO₂ concentration resulted in significant increase in biomass in all the species and the increase ranged from 56.1 per cent in Acacia to 322.5 per cent in Grevelia. More than two fold increase in biomass was observed in Grevelia, Casuarina, Derris, Spathodea and Leucaena. Elevated CO₂ with high nutrient status although increased the final dry matter in five out of seven species tested, the increase was marginal and hence insignificant (Table 4b).

Diferential dry matter (ΔDM).

The mean amount of biomass accumulated during the experimental period showed significant increase due to high nutrient status as well as due to elevated CO₂ concentration. The mean increase in biomass accumulation due to nutrient alone was 31.8 per cent (table 4a). Elevated CO₂ concentrations resulted in increase in the biomass accumulation to a extent of 148.8 per cent. In C2+N treatment the increase was 155.3 per cent and this was nearly 7 per cent more than elevated CO₂ treatment alone.

All the seven species studied in this experiment showed increase in biomass accumulation due to higher soil nutrient status. However, significant increase in biomass accumulation was observed only in four out of seven species tested. Enrichment of CO₂ resulted in increase in

biomass accumulation in all the species and the increase ranged from 72.6 to 437 per cent. Biomass increase during the experimental period was four and three fold in Grevelia and Derris, respectively. Casuarina registered two fold increase, in Spathodea and Leucaena the biomass doubled during the experimental period. High soil nutrient status with elevated CO_2 concentration increased the biomass accumulated during the experimental period further in five out of seven species, but the increase was not statistically significant (Table 4b).

Experiments conducted to study the influence of elevated CO_2 concentration for a brief period during morning hours on growth of seedling of tree species indicated that in all the seven species studied there was substantial increase in growth due to elevated CO_2 concentration. The experimental methodology followed to increase the CO_2 concentration resulted in parallel increase in relative humidity. This suggests that the observed increase in morphological and growth parameters may be due to the combined effect of high CO_2 and high relative humidity.

Out of seven species tested in this experiment, increase in the amount of biomass accumulated during the experimental period was more than 100 per cent in Derris, Spathodea, Leucaena, Casuarina and Grevelia, under high CO_2 as well as high CO_2 along with high nutrient status in the rooting media. In Derris and Grevelia, the increase in

Table 4 (b) : Influence of elevated CO₂ conc. and soil nutrient status on total dry matter and Δ DM in seedlings of different tree species.

Species	Final Dry matter(g)				Δ DM	
	C1	C1+N	C2	C2+N	C1	C1+N
<u>Acacia</u>	16.88	18.14	26.36	28.59	13.05	14.31
		(7.5)	(56)	(69.4)		(9.7)
						(72.6)
						(89.8)
<u>Casuarina</u>	7.24	9.2	21.98	22.52	7.08	9.05
		(27)	(203.6)	(211)		(27.7)
						(208)
						(216)
<u>Eucalyptus</u>	14.91	19.06	28.13	27.27	13.96	18.11
		(28)	(88)	(83)		(30)
						(95)
						(88)
<u>Derris</u>	7.67	8.90	26.16	26.59	5.99	7.22
		(16)	(241)	(247)		(20)
						(307)
						(315)
<u>Spathodea</u>	12.73	19.23	27.38	26.79	11.23	17.73
		(51)	(115)	(110)		(58)
						(130)
						(125)
<u>Leucaena</u>	15.61	18.79	31.39	32.07	12.19	15.38
		(20.4)	(101)	(105)		(26)
						(129)
						(135)
<u>Grevelia</u>	3.83	6.49	16.20	18.08	2.83	5.68
		(69.3)	(323)	(372)		(101)
						(438)
						(504)
CD at 5%	2.3259					2.61556

*Values in the parenthesis indicate per cent increase/decrease over control.

biomass due to CO₂ concentration was to an extent of 307.7 and 437.6 per cent respectively. The per cent increase in biomass during the experimental period was less than 100 per cent in Acacia and Eucalyptus. These results indicate that Casuarina, Derris, Spathodea, Leucaena and Grevelia are highly responsive to elevated CO₂ concentration compared to Acacia and Eucalyptus in terms of growth.

4.1.2 Experiment II: Influence of seedling age on growth response of forest tree seedlings to elevated CO₂ concentration

The main objective of this experiment was to identify the most responsive stage of seedling for elevated CO₂ concentrations. This experiment was conducted with seedlings of two tree species of age two, five and ten months. The seedlings were maintained at two CO₂ levels as explained in materials and methods. The duration of the experiment was 90 days. The influence of CO₂ enrichment on increase in growth rate were studied.

4.1.2.1 Influence of CO₂ on morphological characters Plant height

Plant height at the end of experiment showed significant increase at elevated CO₂ concentration. In both the species response to CO₂ reduced with age of the seedlings. In both the species seedlings of two month age showed high response to elevated CO₂ concentration (Table 5a).

Table 5(a) : Influence of CO₂ enrichment on Plant height (cm) of the seedlings of different age groups in Grevelia and Eucalyptus.

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	51.80	71.0	106.0	26.0	35.8	55.4
C2	78.6	95.2	111.4	45.6	54.0	73.6
CD at 5%	6.85079					

Table 5(b) : Effect of CO₂ on leaf number (No./Plant)

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	26.4	40.8	34.8	26.2	28.6	32.4
C2	25.8	44.6	36.0	26.6	37.2	33.0
CD at 5%	11.94					

Table 5(c) : Effect of CO₂ on branch number (No./Plant)

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	1.2	3.4	3.8	0.0	0.4	1.2
C2	2.8	3.2	2.8	0.0	1.6	1.8
CD at 5%	1.4117					

Branch number.

The number of branches per plant at the end of experiment was significantly more in Eucalyptus compared to Grevelia. The branch number per plant was not influenced by CO₂ enrichment (Table 5b).

Leaf number.

Number of leaves per plant at the end of the experiment did not differ significantly due to CO₂ enrichment (Table 5b). In Eucalyptus, two month old seedlings retained more number of leaves at the end of the experiment at ambient and elevated CO₂ concentration.

Leaf area.

There was a positive response in terms of leaf area to CO₂ enrichment in seedlings of all age groups in both the species. The increase in leaf area due to CO₂ enrichment in Eucalyptus was to an extent of 37.1, 15.87 and 87.83 per cent in two, five and ten months old seedlings respectively. In Grevelia, young seedlings of two months age showed maximum response to CO₂ enrichment and least response was noticed in five months old seedlings (Table 6a).

Differential leaf area (Δ LA).

Leaf area development during the experimental period was maximum in ten month old seedlings of both the species

Table 6(a) : Response of different aged seedlings to CO₂ enrichment with regard to leaf area (cm²)

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	427.65	535.02	440.37	717.43	975.32	998.24
C2	586.09 (37.1)	619.98 (15.87)	827.19 (87.83)	1166.65 (62.6)	1236.89 (26.82)	1371.39 (37.38)
CD at 5%	0.841					

* Values in the parenthesis indicate % increase over control.

Table 6(b) : Influence of elevated CO₂ on ΔLA

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	340.66	286.28	80.74	661.52	644.67	318.84
C2	503.12 (47.68)	349.13 (21.95)	498.64 (517.5)	1162.7 (75.7)	920.14 (42.73)	648.34 (103.3)
CD at 5%	32.60					

* Values in the parenthesis indicate per cent increase over control.

under high CO₂ concentration and least in five month old seedlings. The increase in leaf area ranged from 21.95 to 517.6 per cent over control in five and ten month old seedlings of Eucalyptus respectively. In Grevelia the increase in leaf area was 75.7, 42.73 and 103.3 in two, five and ten month old seedlings respectively under CO₂ enrichment treatment (Table 6b).

Biomass allocation

Leaf weight

Biomass in leaves at the end of the experiment was more in plants grown at elevated CO₂ concentration in both the species when the age of the seedlings was two and five months. Ten months old seedlings of Grevelia showed significant increase in leaf biomass at elevated CO₂ concentration.

Maximum response to elevated CO₂ concentration was observed in two months old seedlings and the increase in leaf biomass was to an extent of 76.3 and 63.7 per cent in Eucalyptus and Grevelia respectively (Table 6c).

Specific leaf weight (SLW).

Specific leaf weight showed a marginal increase at elevated CO₂ concentration in two and five months old seedlings of Eucalyptus. However, a marked reduction in SLW was noticed in ten month old seedlings of Eucalyptus at elevated CO₂ concentration. In Grevelia elevated CO₂

Table 6(c) : Effect CO₂ on leaf weight (g) of different aged seedlings of Grevelia and Eucalyptus.

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	4.48	6.5	9.3	6.8	9.4	12.6
C2	7.9 (76.34)	8.0 (23.1)	9.1 (-2.15)	11.13 (63.67)	10.90 (15.95)	15.14 (20.15)
CD at 5%	1.8345					
* The values in the parenthesis indicate per cent increase over control						

Table 6(d) : Effect of CO₂ on specific leaf weight (SLW)

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	0.011	0.012	0.012	0.010	0.010	0.013
C2	0.014	0.014	0.011	0.010	0.009	0.011
CD at 5%	0.003					

levels reduced specific leaf weight marginally in five and ten month old seedlings. However, the differences were not statistically significant (Table 6d).

Leaf weight ratio (LWR)

The ratio of biomass accumulated in the leaf in relation to total biomass showed marginal increase at elevated CO₂ concentration in young seedlings of two months age in both the species. However, in five and ten month old seedlings there was marginal reduction in leaf weight ratio in both the species (Table 7a).

Shoot weight ratio (SWR)

Shoot weight ratio in Eucalyptus increased due to elevated CO₂ concentrations particularly in two months old seedlings. In five and ten months old seedlings of Eucalyptus there was a marginal reduction in SWR at elevated CO₂ concentration. In Grevelia, CO₂ enrichment resulted in marginal reduction in shoot weight ratio in two and ten months old seedling. However, in five months old seedlings there was 7.4 per cent increase in shoot weight ratio (Table 7b).

Root weight ratio (RWR)

Root weight ratio reduced due to CO₂ enrichment in two months old seedlings of Eucalyptus. However, Eucalyptus seedling of five and ten months showed 9.4 and 17.2 per cent increase in RWR at elevated CO₂ levels as

Table 7(a) : Differential response of different aged seedlings of Eucalyptus and Grevelia to CO₂ with regards to Leaf weight ratio.

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	0.289	0.283	0.289	0.450	0.354	0.357
C2	0.329	0.263	0.233	0.527	0.341	0.328
CD at 5%	-NS-					

Table 7(b) : Effect of CO₂ on shoot weight ratio

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	0.537	0.662	0.668	0.778	0.635	0.730
C2	0.631	0.633	0.613	0.739	0.682	0.663
CD at 5%	0.0486					

shown in the Table 8(a). In Grevelia, the RWR increased due to elevated CO₂ concentration in two and ten months old seedlings, the increase was to an extent of 18.5 and 26.6 per cent respectively. Five months old seedlings of Grevelia showed 12.8 per cent reduction in root weight ratio at CO₂ enriched atmosphere.

Root to shoot ratio (R/S)

In young two months old seedlings of Eucalyptus root to shoot ratio was high at ambient CO₂ concentration. Seedlings grown at elevated CO₂ concentration showed a significant reduction in root to shoot ratio, when the seedling age was two months. However, in five and ten months old seedlings, CO₂ enrichment increased the root to shoot ratio by 12.5 and 28.3 respectively. In Grevelia, CO₂ enrichment enhanced root to shoot ratio in two and ten months old seedlings. Five months old Grevelia seedlings showed 18.5 per cent reduction in root to shoot ratio at elevated CO₂ concentration (Table 8b).

BIOMASS

Root biomass

Plants raised under elevated CO₂ concentrations showed significant increase in root biomass. In Eucalyptus, the per cent increase in root biomass was to an extent of 19.2, 45.5 and 47.1 per cent in two, five and ten months old seedlings respectively. In Grevelia, the

Table 8(a) : Root weight ratio of different aged seedlings of Eucalyptus and Grevelia as affected by CO₂.

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	0.457	0.338	0.332	0.222	0.365	0.267
C2	0.369 (-19.25)	0.370 (9.4)	0.389 (17.17)	0.263 (18.46)	0.318 (-12.8)	0.338 (26.5)

CD at 5% 0.04861

* Values in the parenthesis indicate the per cent increase over control

Table 8(b) : Influence of CO₂ on root to shoot ratio (R/S ratio)

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	0.851	0.519	0.501	0.288	0.578	0.371
C2	0.599 (-29.6)	0.584 (12.5)	0.644 (28.3)	0.357 (23.95)	0.470 (-18.68)	0.510 (37.47)

CD at 5% 0.1164

* Values in the parenthesis indicate per cent increase/decrease over control.

increase in root biomass at elevated CO₂ concentration in two, five and ten months old seedlings were 69.9, 6.2 and 60.8 per cent, respectively (Table 9b).

Shoot biomass

Shoot biomass also registered significant increase due to CO₂ enrichment. In Eucalyptus, the increase in shoot biomass in two, five and ten months old seedlings were to an extent of 77.8, 24.7 and 13.2 per cent respectively. In Grevelia, the per cent increase in shoot biomass at elevated CO₂ concentrations were 33.6, 28.8 and 17.8 per cent in two, five and ten months old seedlings respectively compared to the seedlings maintained at ambient CO₂ concentrations (Table 9a).

Total biomass

The total biomass at the end of the experiment was significantly high in seedlings of all ages due to high CO₂ treatment. The response of seedlings to high CO₂ concentrations reduced with age of seedlings. In Eucalyptus the response of two, five and ten months old seedlings were to an extent of 49.5, 31.2 and 24.1 per cent respectively. Similar trend was observed in Grevelia seedlings also (Table 10a).

Differential dry matter (Δ DM)

Biomass accumulation during the experimental period showed the positive influence of CO₂ enrichment. In

Table 9(a) : Response to CO₂ enrichment with regards to shoot weight (g) in different aged seedlings.

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	8.58	15.40	21.20	11.70	17.00	26.00
C2	15.20 (77.8)	19.20 (24.7)	24.00 (13.2)	15.63 (33.6)	21.9 (28.8)	30.64 (17.8)
CD at 5%	0.783					

* Values in the parenthesis indicate the per cent increase over control.

Table 9(b) : Influence of CO₂ on root weight (g) of different aged seedlings of Eucalyptus and Grevelia

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	7.3	7.7	10.4	3.3	9.6	9.7
C2	8.7 (19.2)	11.2 (45.45)	15.3 (47.12)	5.6 (69.69)	10.2 (6.25)	15.6 (60.82)
CD at 5%	1.833468					

* Values in the parenthesis indicate the per cent increase over control.

Eucalyptus the response of seedlings of different age groups for elevated CO₂ concentrations were marked. With increase in the age of the seedlings the per cent increase in biomass due to high CO₂ concentration reduced markedly. In Grevelia, the per cent increase in biomass accumulation during the experimental period was more in two months old seedlings followed by five and ten months old seedlings. However, the difference in DM between the seedlings of different age groups of Grevelia were relatively less compared to Eucalyptus.

Experiments were conducted to identify highly responsive seedling growth stage to CO₂ enrichment using two, five and ten months old seedling of Grevelia and Eucalyptus. Two months old seedlings were found to be more responsive to CO₂ enrichment in case of Eucalyptus. The response to CO₂ enrichment in terms of total biomass was to an extent of 49.5, 31.16 and 24.1 per cent increase over control in two, five and ten months old seedlings of Eucalyptus respectively. Seedlings of Grevelia also showed a similar trend.

The total biomass accumulated during the experimental period was 64.5, 33.67 and 30.56 per cent more over control in two, five and ten months old seedlings of Eucalyptus respectively. In Grevelia seedlings also, the percent increase in DM was more in young seedlings. But the differences in the dry matter accumulated during the



Eucalyptus



Grevelia

Table 10(a) : Influence of CO₂ concentration on total drymatter (g)

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	15.99	23.10	31.60	15.00	26.00	35.80
C2	23.90 (49.50)	30.30 (31.16)	39.20 (24.10)	21.20 (41.30)	32.10 (23.50)	46.18 (22.50)
CD at 5%	3.86065					

* Values in the parenthesis indicate per cent increase over control

Table 10(b) : Influence of CO₂ on Δ DM.

Treatment	<u>Eucalyptus</u>			<u>Grevelia</u>		
	I	II	III	I	II	III
C1	13.99	20.65	26.18	13.82	21.52	28.12
C2	23.02 (64.50)	27.60 (33.67)	34.18 (30.56)	19.19 (38.85)	28.68 (33.38)	36.72 (30.58)
CD at 5%	1.25					

* Values in the parenthesis indicate the per cent increase over control.

experimental period was less compared to Eucalyptus (table 10b) .

4.2 Gas exchange characteristics

Experiments conducted to study the influence of elevated CO_2 concentration on growth indicated that all the seven species showed positive response in terms of leaf area development as well as biomass accumulation. In the methodology adopted to increase CO_2 concentration there was concomitant increase in RH also. Variation in RH influences VPD and thus 'gs'. The influence of 'gs' on assimilation rate is well known. In order to study the intrinsic capacity for assimilation in different species 'A', 'gs' and A/gs were assessed in plants grown at ambient as well as elevated CO_2 levels. All gas exchange measurements were made at saturating light intensity in intact leaves at ambient condition. Gas exchange parameters were assessed in broad leaved species, two of which were showing more than 100 per cent increase in biomass accumulation due to CO_2 enrichment and two with less than 100 per cent increase in total biomass.

Species variation in assimilation rate

Assimilation rate at saturated light intensity showed significant variation among the species. Assimilation rates were measured at relatively high vapour pressure deficit (VPD) which ranged between 26 to 37.4 milli bars. Since, the assimilation rates were measured at saturating

light intensity and almost similar VPD, the species differences in 'A' and g_s are comparable.

In plants grown at ambient CO_2 concentration the P_{max} showed significant variation between the species. Eucalyptus had high P_{max} and least was in Spathodea. In plants grown at elevated CO_2 concentration when the P_{max} was assessed at ambient CO_2 concentration there was significant increase in 'A' and the increase was maximum in Acacia. The per cent increase in P_{max} in plants grown at elevated CO_2 concentration were to an extent of 77.8, 21.99, 15.9 and 9.8 per cent in Acacia, Spathodea, Eucalyptus and Derris respectively. Plants raised under high soil nutrient status showed high 'A' in all the species. It was quite interesting to see that plants raised under high CO_2 and high soil nutrient status had relatively high P_{max} compared to all other treatments. When the increase in P_{max} was compared between high CO_2 and high nutrient treatment, high CO_2 increased P_{max} to a greater extent than high nutrient treatment (table 10c).

Stomatal conductances (g_s)

Amongst the four species studied, g_s of Acacia and Eucalyptus was relatively high compared to Derris and Spathodea. Plants grown at high CO_2 had significantly high g_s in all the species. The effect of high nutrient status in the soil on g_s was also more particularly in plants which were exposed to elevated CO_2 concentration. When

Table 10(c): Gas exchange characteristics in seedlings of different forest tree species.

		Species				CD at 5%
		Acacia	Eucalyptus	Derris	Spathodea	
PAR ($\mu\text{Ein.m}^{-2}.\text{s}^{-1}$)	C1	1779	1676	1658	1602	
	C1+N	1760	1877	1821	1781	
	C2	2060	1678	1638	1630	
	C2+N	1701	1935	1713	1644	
Ca (ppm)	C1	334.94	338.40	340.26	339.21	
	C1+N	342.42	336.90	341.72	336.88	
	C2	354.86	335.02	337.88	337.28	
	C2+N	335.08	330.24	336.56	337.96	
Ci (ppm)	C1	260.90	245.02	247.00	246.40	
	C1+N	264.40	247.62	265.02	239.86	
	C2	286.40	250.32	265.88	252.86	
	C2+N	264.80	267.74	253.58	251.20	
RH (%)	C1	41.40	36.68	29.40	28.30	
	C1+N	38.56	41.80	34.52	28.14	
	C2	53.02	42.32	36.72	33.70	
	C2+N	45.74	60.28	36.30	38.18	
VPD (mBar)	C1	26.46	27.64	27.80	37.40	
	C1+N	30.18	30.14	35.48	30.06	
	C2	28.86	24.38	28.16	29.80	
	C2+N	23.22	27.60	30.82	30.10	
gs ($\mu\text{mol.m}^{-2}.\text{s}^{-1}$)	C1	230.82	280.54	188.66	177.32	25.88
	C1+N	219.64	329.28	255.72	175.96	
	C2	471.88	381.90	284.10	246.68	
	C2+N	402.90	539.50	280.00	246.62	
'A' ($\mu\text{mol.s.m}^{-2}.\text{s}^{-1}$)	C1	8.160	13.044	8.410	7.964	0.637
	C1+N	10.660	13.370	9.144	3.356	
	C2	14.508	15.120	9.238	9.716	
	C2+N	15.310	15.334	10.764	10.236	
A/gs	C1	0.0354	0.0400	0.0445	0.0449	
	C1+N	0.0485	0.0410	0.0350	0.0470	
	C2	0.0300	0.0390	0.0320	0.0390	
	C2+N	0.0310	0.0280	0.0380	0.0410	

compared to g_s values in the leaves of the plants exposed to ambient CO_2 concentration the per cent increase in g_s values in leaves of plants with high CO_2 and high nutrients were 109.1, 92.3, 48.5 and 39.1 in Acacia, Eucalyptus, Derris and Spathodea, respectively.

A/g_s values which gives an indication of water use efficiency at single leaf level also showed a marked variation due to CO_2 enrichment as well as higher soil nutrient status. Plants grown at elevated CO_2 concentration had low ' A '/ g_s values. In plants grown with high soil nutrient status the ' A '/ g_s was relatively more in Acacia and Spathodea. In Eucalyptus and honge ' A '/ g_s decreased with increase in soil nutrient status (table 10c).

CO_2 response curve : A/C_i curves.

CO_2 response curves (' A '/ C_i curves) were developed by plotting ' A ' against C_i in plants grown at ambient as well as elevated CO_2 concentrations. These curves were developed only in four species namely Derris, Acacia, Eucalyptus and Grevelia. This curve indicates the response of ' A ' to elevated CO_2 concentrations. The results indicated that the ' A ' for a given C_i is always more in plants exposed to elevated CO_2 concentrations (Fig. 9)

The pattern of the curve indicated that in Derris, there is a steep raise in ' A ' with increase in C_i up to

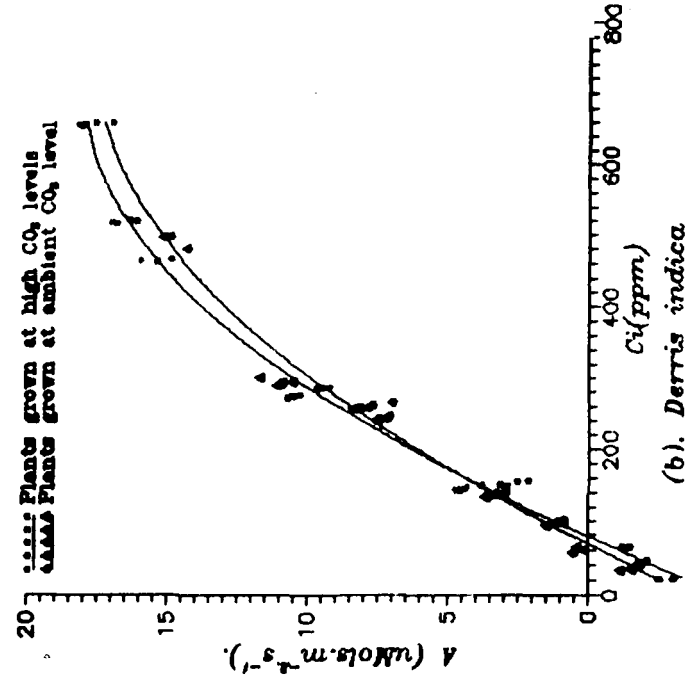
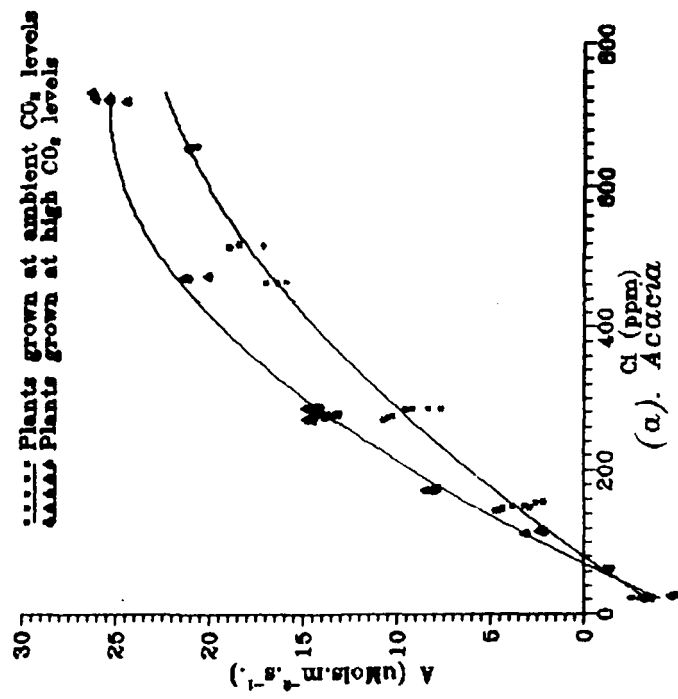


Fig. 9 CO_2 response curves for the seedlings grown under two different CO_2 levels.

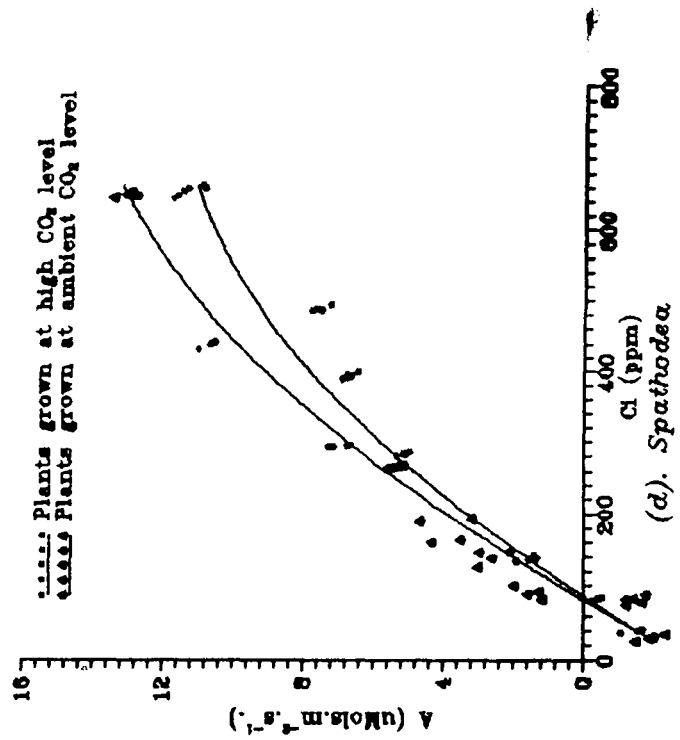
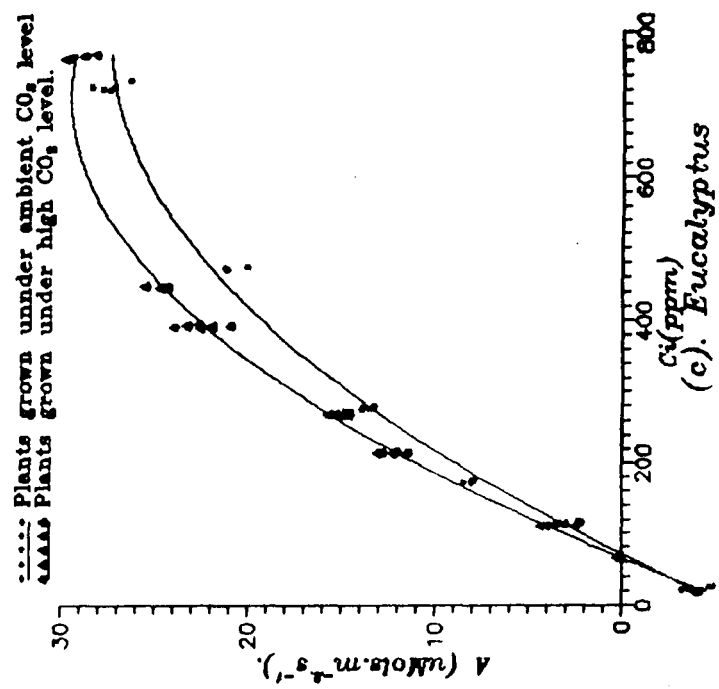


Fig. 9 CO_2 response curves for the seedlings grown under two different CO_2 levels.

660 ppm indicating that this species responses very much in terms of 'A' for increasing C_i . However, the differences in 'A' for a given C_i between the plant grown under ambient and high CO_2 concentrations were marginal.

In Spathodea also 'A' increased with increasing C_i up to 660 ppm. However, the 'A' per given C_i in this species was significantly less compared to all the other three species studied. Plants grown at elevated CO_2 concentration showed relatively high 'A' at a given C_i compared to plants raised at ambient CO_2 levels.

In Eucalyptus, 'A' increased with increase in C_i but the rate of increase in 'A' for a given C_i showed a decreasing trend after 400 ppm of C_i (internal CO_2 concentration). A marked increase in 'A' was observed in Eucalyptus seedlings grown at elevated CO_2 concentration. Acacia also showed same trend as that of Eucalyptus. However, 'A' per given C_i was always less in Acacia compared to Eucalyptus.

The influence of elevated CO_2 concentration on 'A' was computed using 'A'/ C_i curves. The data is presented in the Table 11. This table gives the data on the short term influence of high CO_2 concentration on assimilation rate in plants grown at ambient and elevated CO_2 concentrations. In Acacia and Eucalyptus plants grown at ambient CO_2 concentration were exposed to high CO_2 levels, there was marked increase in assimilation rate. When the

Table 11: Assimilation rates (uMols.m ⁻² .s ⁻¹) at 330 and 660 Ci (ppm) in four seedlings of different tree species.				
Species/Treatments		330	660	% increase
<u>Acacia</u>				
C1		12.00	21.5	79.16
C2		16.50(37.5)	25.0(16.2)	51.51
<u>Eucalyptus</u>				
C1		15.50	24.5	54.83
C2		19.00(22.5)	29.5(17.5)	55.12
<u>Spathodea</u>				
C1		6.80	9.5	39.70
C2		7.60(11.76)	13.0(36.8)	71.00
<u>Derris</u>				
C1		10.75	17.3	60.40
C2		11.50(9.5)	18.0(4.34)	56.52
* Values in the parenthesis indicate per cent increase over control.				

C_i was increased from 330 to 660 ppm, the increase in assimilation rate in Acacia grown at ambient CO_2 was 79 per cent more and in Eucalyptus it was 54.83 per cent more. However, in plants of the same species grown at elevated CO_2 concentration when exposed to 660 ppm C_i the increase in 'A' was less. Spathodea and Derris plants grown at elevated CO_2 concentration maintained high assimilation rate at high CO_2 concentration. For example, when it was increased from 330 to 660 ppm, the assimilation rate increased by 71 per cent in Spathodea and 56.5 per cent in Derris, indicating that these plants maintained high 'A' for long time even under elevated CO_2 concentration.

Limitations to assimilation

To understand the differences in 'A' between the species under ambient CO_2 concentration as well as under elevated CO_2 concentration various limitations offered for assimilation were computed. An attempt has been made to quantify relative stomatal limitations and mesophyll limitations to assimilation in plants grown under ambient as well as elevated CO_2 concentrations.

In plants grown at ambient as well as elevated CO_2 concentrations stomata exerts major limitation for assimilation rate. Only in Acacia stomatal limitations reduced markedly in plants grown at elevated CO_2 concentration. The mesophyll limitations also did not show

Table 12 : Stomatal and mesophyll limitations to assimilation in seedling of few tree species.

Species	A	Ag	Ao	AT	ls	lm	dA/dCi
<u>Eucalyptus</u>							
C1	8.5	9.5	12.75	15.50	33.33	10.50	0.0554
C2	11.7	13.0	17.50	21.50	32.85	9.62	0.0722
<u>Derris</u>							
C1	7.0	9.0	11.50	14.00	39.13	22.22	0.050
C2	7.8	8.8	12.00	14.50	35.40	11.40	0.056
<u>Acacia</u>							
C1	8.0	9.0	13.00	16.50	38.46	11.11	0.0563
C2	12.5	14.0	17.50	21.50	28.57	10.77	0.0657
<u>Spathodea</u>							
C1	5.0	6.0	8.00	9.25	37.50	16.66	0.0333
C2	4.8	5.3	7.00	8.25	32.14	9.50	0.0334
AO = $\mu\text{mols.m}^{-2}.\text{s}^{-1}$ dA/dCi = $\mu\text{mols.m}^{-2}.\text{s}^{-1}.\text{ul.l}^{-1}$.							

any variation in plants grown at ambient and elevated CO_2 concentration in Eucalyptus and Acacia. However, in Derris and Spathodea, marked reduction was observed in relative stomatal limitations in plants grown at elevated CO_2 concentration (Table 12).

Limitations to potential photosynthesis was more Acacia and minimum in Spathodia. Altering CO_2 concentration in the growing atmosphere did not alter the limitation for potential photosynthesis to a greater extent in all the species tested. The data on dA/dC_i indicated that there was a slight increase in carboxylation efficiency in plants grown under elevated CO_2 concentrations. Amongst four species tested the dA/dC_i ratio was more in Eucalyptus followed by Derris and Acacia (Table 11).

Light response curves

The influence of varying light intensity on gas exchange parameters were studied to know the light saturation point in different species. Plants grown both at ambient as well as elevated CO_2 concentration were used. The responses of 'A' to increase in light intensity indicated that the response is curvilinear and biphasic (Fig 10a).

In Acacia 'A' reached a maximum value at about $1800 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$ PFD. In other three species namely,

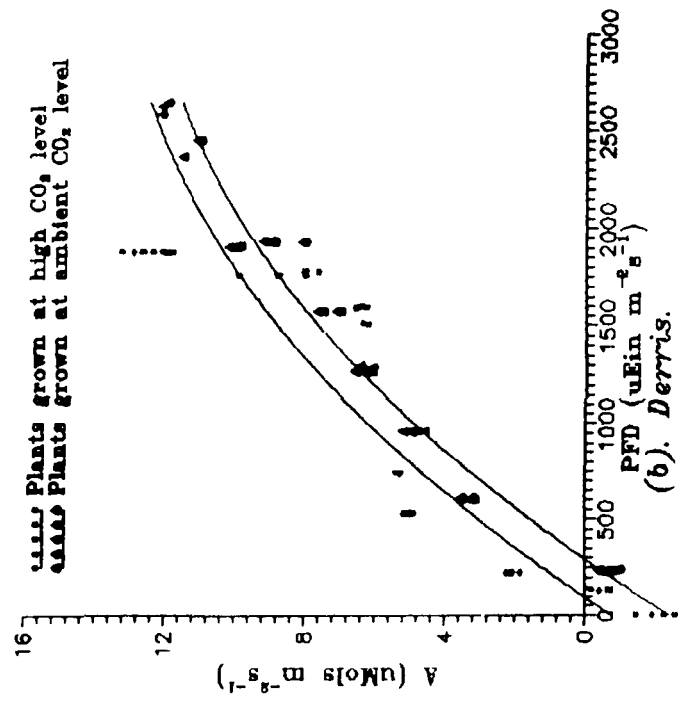
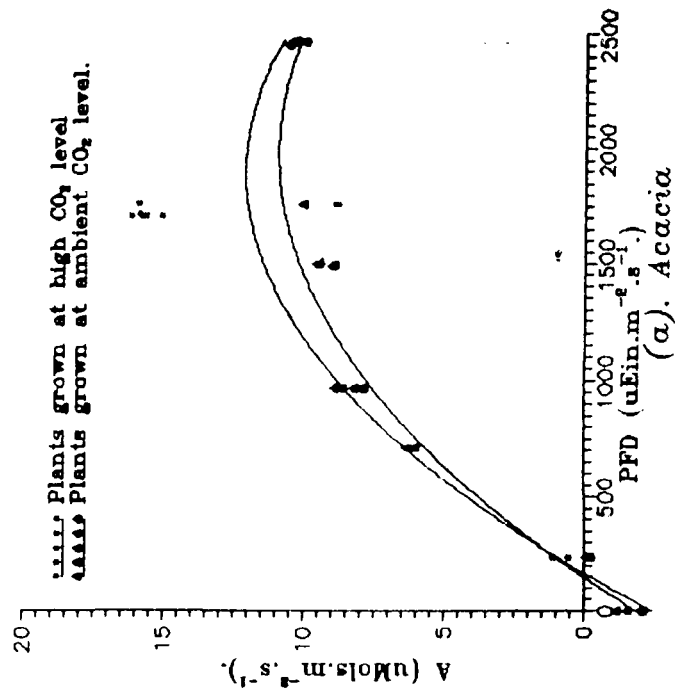


Fig. 10a Light response curves (A/PFD) for the seedlings grown under two different CO₂ levels.

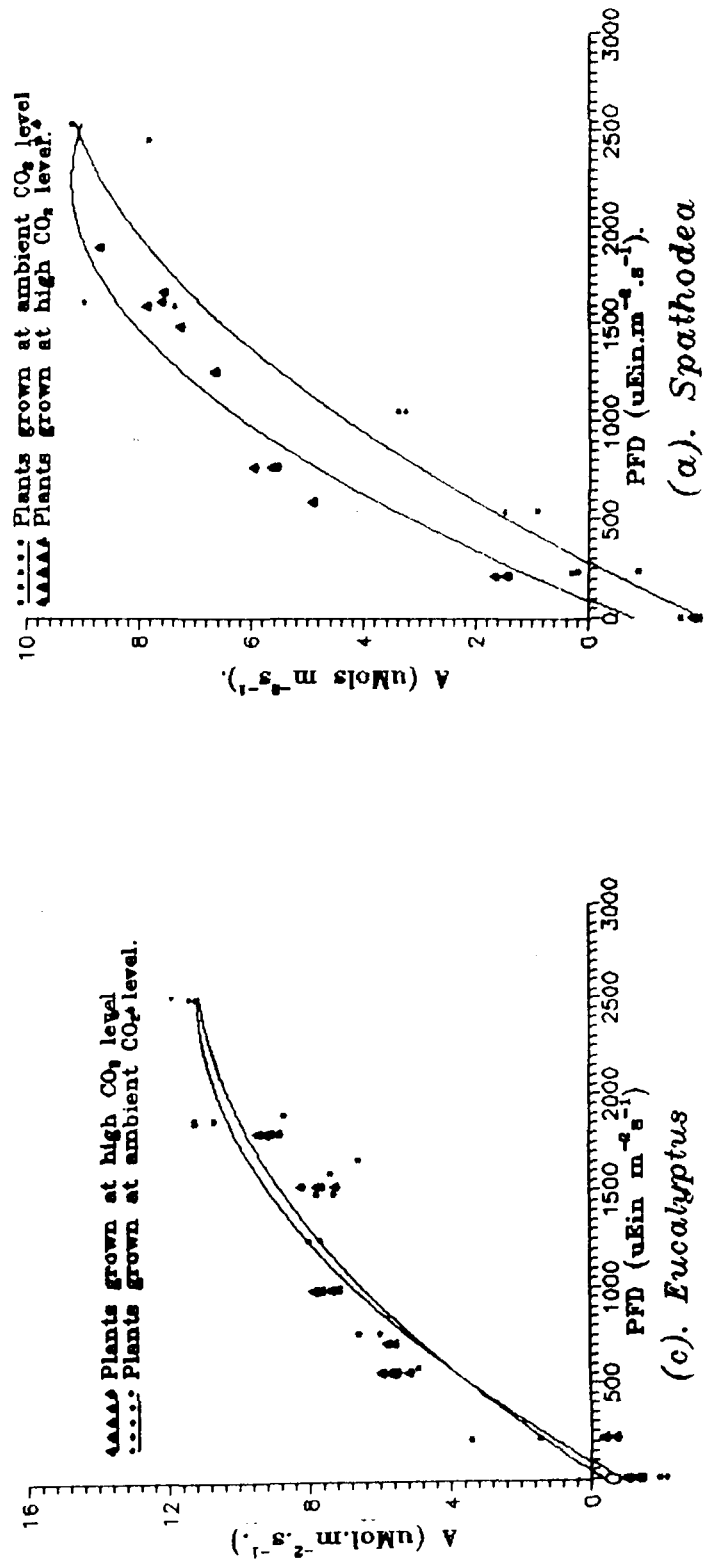


Fig.10a Light response curves (A/PFD) for the seedlings grown under two different CO_2 levels.

Eucalyptus, Spathodea and Derris 'A' increased with increase in PFD up to $2500 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$.

Plants grown at elevated carbon dioxide concentration always had high 'A' for a given PFD in Derris, Spathodea and Acacia. The differences between plants grown at ambient and elevated CO_2 concentration was more marked in Spathodea. In Eucalyptus, there was no difference in 'A' in response to varying PFD between the plants grown at ambient and elevated carbon dioxide concentration.

gs/PFD curves

Influence of varying levels of PFD on 'gs' was studied. Different species showed varied response to PFD. In the four species studied, 'gs' per given PFD was always more in plants grown at elevated CO_2 concentration (Fig.11b) In Derris 'gs' reached its maximum value at $1500 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$, further increase in PFD did not alter the 'gs' very much. In this species 'gs'/PFD curve did not differ much between the plants grown at elevated or ambient CO_2 levels.

In Spathodea 'gs' increased with PFD up to $2000 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$ in plants grown at high CO_2 and up to $2500 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$ PFD in plants grown at ambient CO_2 concentration. The differences in 'gs' responses to PFD was more in plants grown at elevated CO_2 concentration.

In Acacia 'gs' increased linearly with increase in

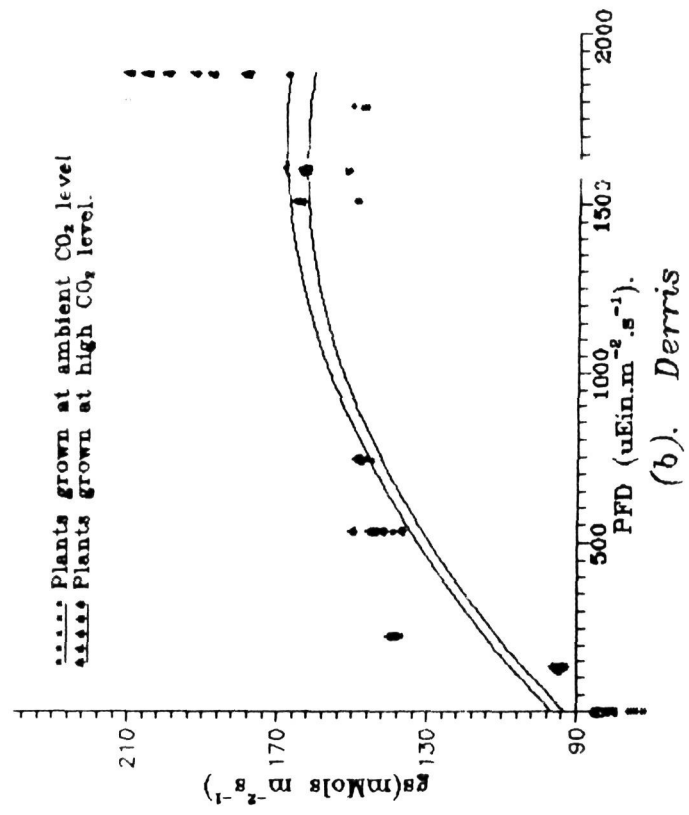
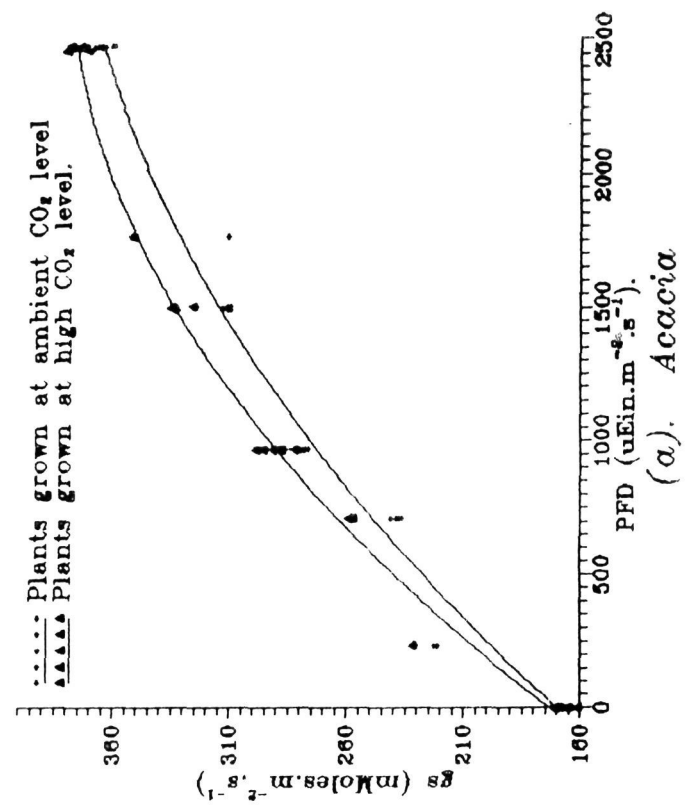


Fig.10b Light response curves (gs/PFD) for the seedlings grown under two different CO₂ levels.

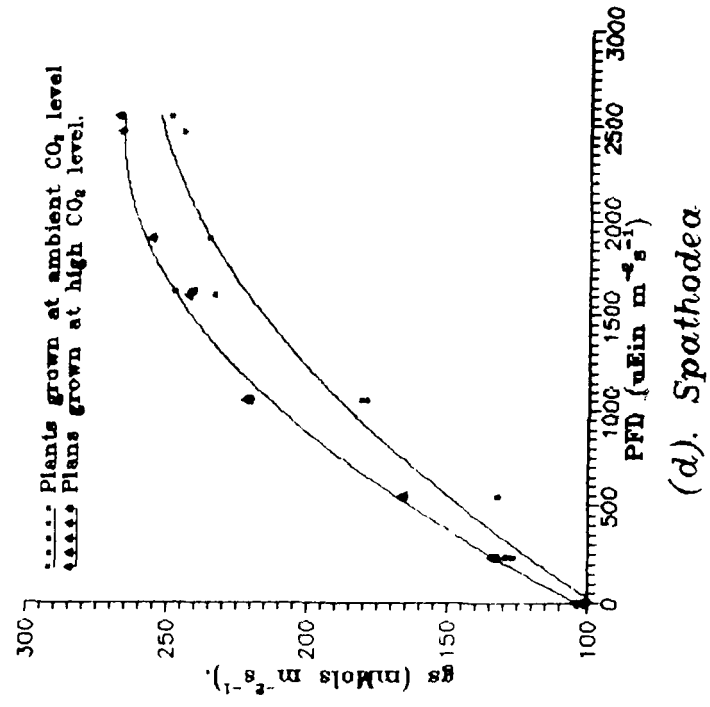
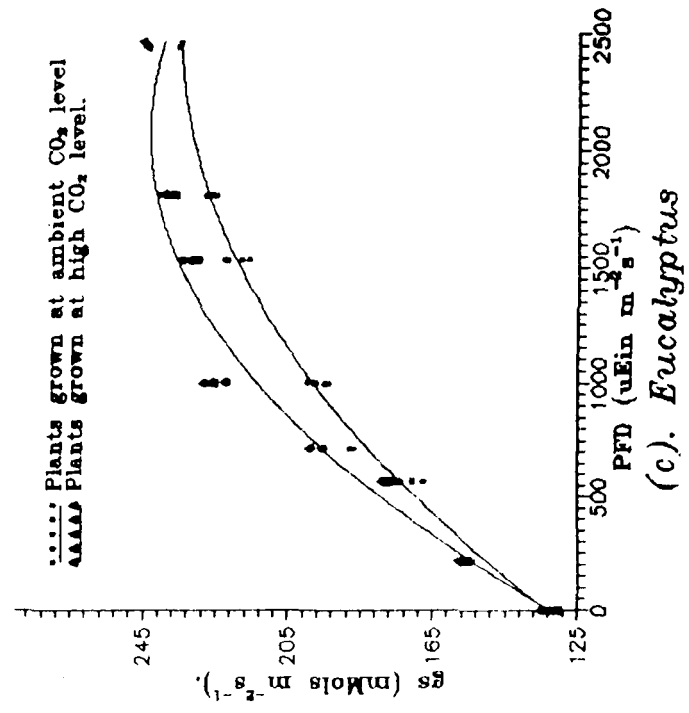


Fig.10b Light response curves (gs/PFD) for the seedlings grown under two different CO₂ levels.

PFD upto $2000 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$. Plants grown at ambient and elevated CO_2 levels showed differences in 'gs' when the light intensity was more than $1000 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$.

In Eucalyptus, 'gs' increased with increase in PFD of $1500 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$ in plants grown at elevated CO_2 and $1760 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$ in plants grown at ambient CO_2 concentration. The differences between the plants grown at ambient and elevated CO_2 levels in 'gs' was not observed when the PFD was more than 700 or more than $2250 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$ (Fig.10b)

VPD response curves

Gas exchange characteristics as influenced by range was studied in four species namely Derris, Spathodea, Eucalyptus and Acacia. In all the species with increase in VPD there was a marked reduction in 'A' as well as 'gs' (Fig.11a and 11b). In Spathodea and Derris the 'A' remained constant from 14 to 18 mbars of VPD respectively. Drastic reduction in 'A' was observed on when the VPD increased beyond 18 and 20 mbars in Spathodea and Derris respectively. However, 'gs' showed linear reduction with increase in VPD over a range of 15 to 40 mbars. In Eucalyptus even a marginal increase in VPD from 12 to 14 mbars resulted in marked reduction in 'A'. Similar trend was noticed in 'gs' also. In Eucalyptus increase in VPD beyond 18 mbars had little effect on 'gs' and 'A'. In Acacia VPD in the range of 16 to 20 mbars had a similar 'A' value. A further increase in VPD beyond 20 mbars

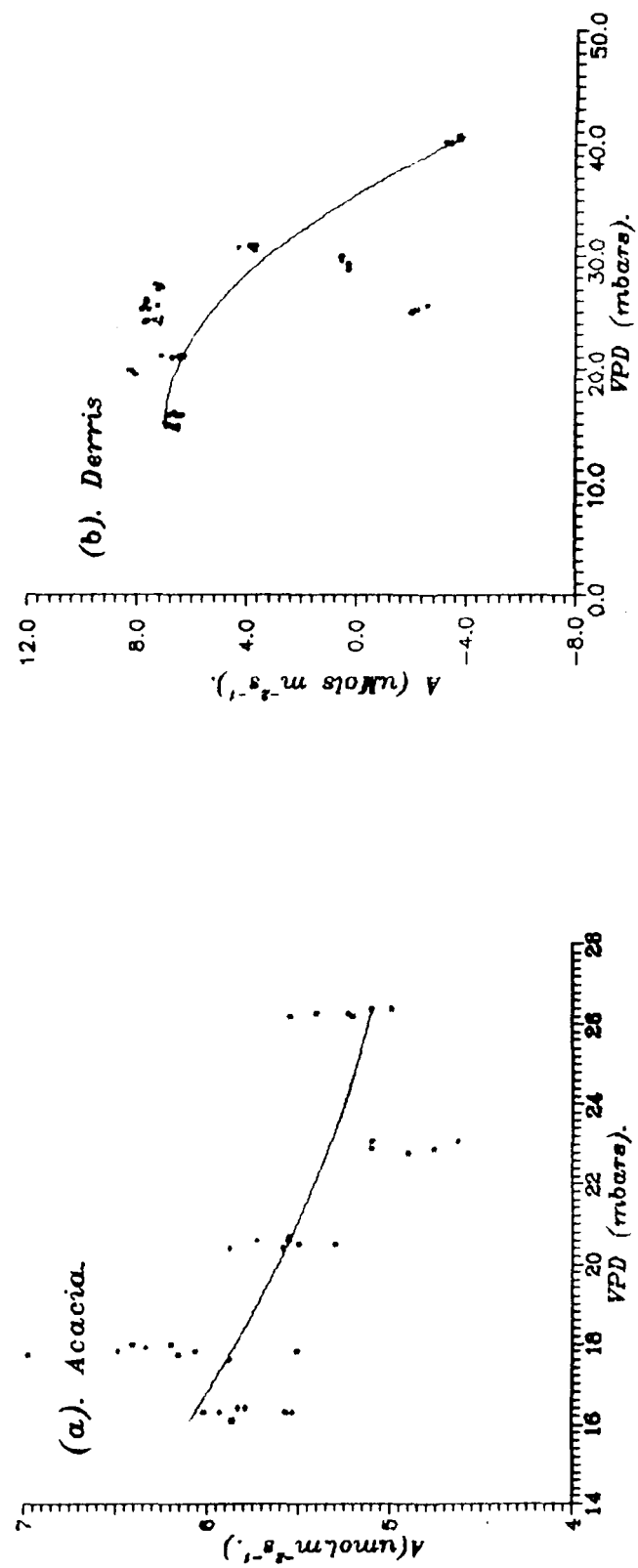


Fig.11a VPD response curves (A/VPD) for the seedlings grown under different CO₂ levels.

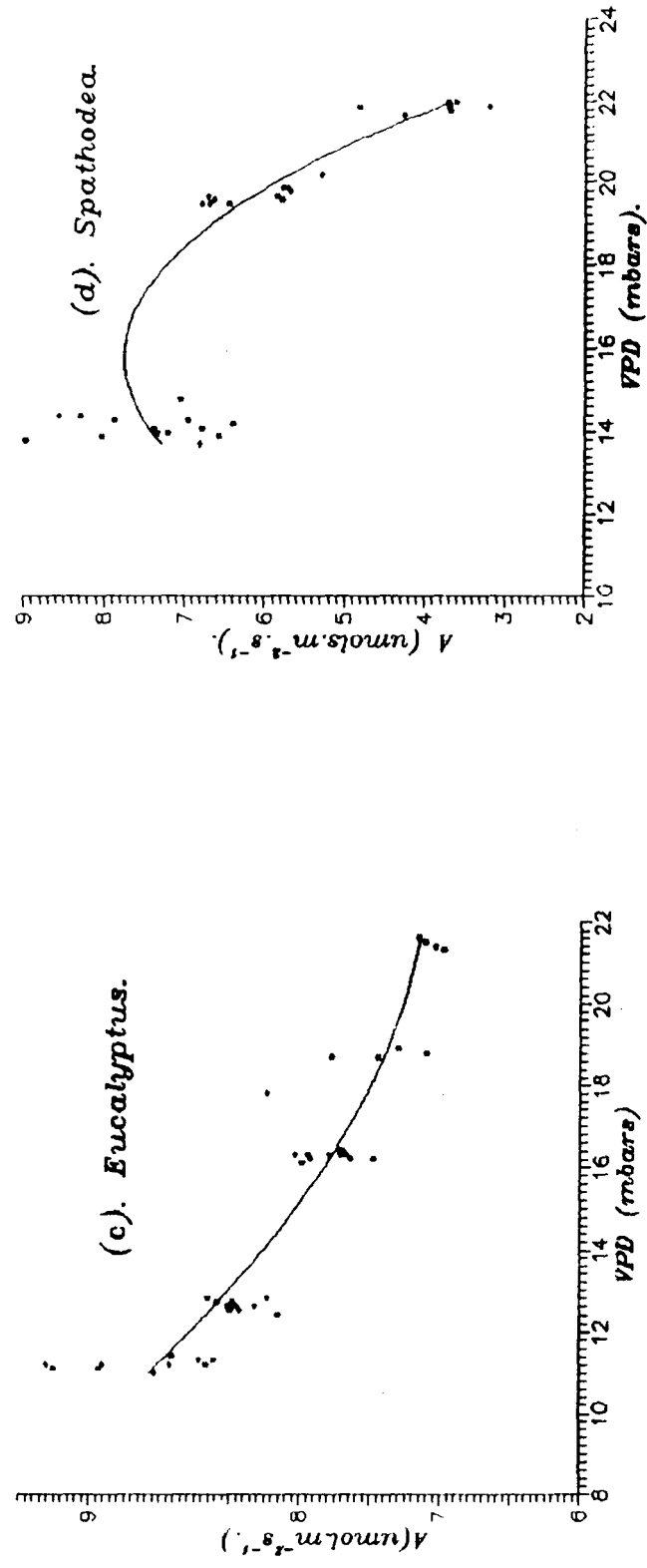


Fig. 11a VPD response curves (A/VPD) for the seedlings grown under different CO_2 levels.

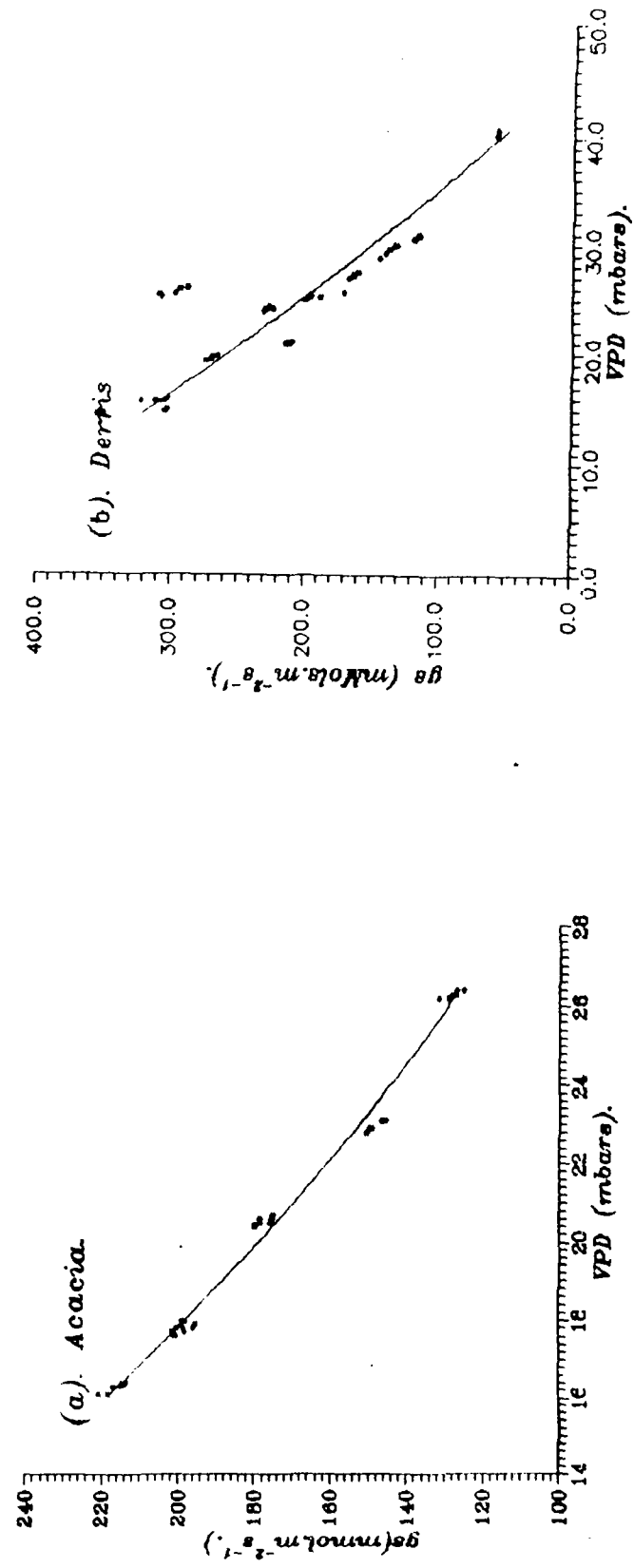


Fig. 11b VPD response curves (gs/VPD) for the seedlings grown under different CO₂ levels.

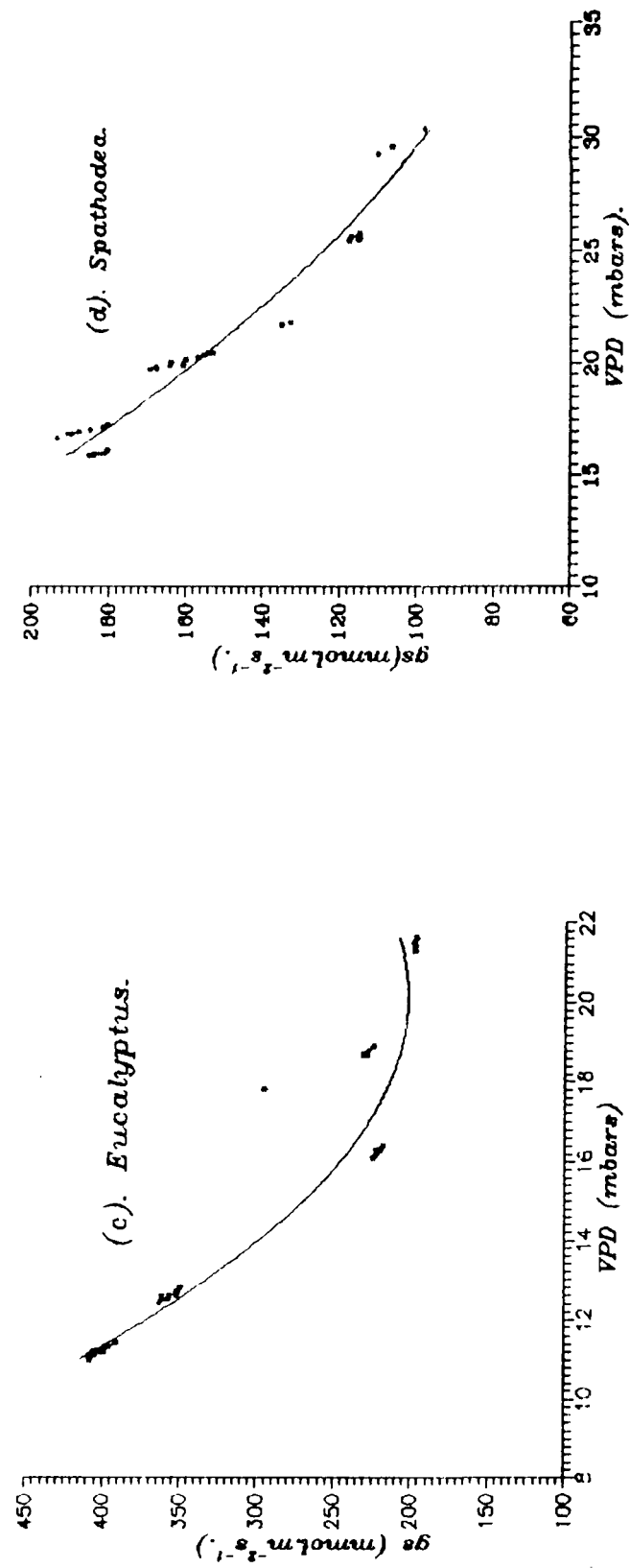


Fig. 11b VPD response curves (gs/VPD) for the seedlings grown under different CO₂ levels.

resulted in marked reduction in 'A'. However, 'gs' showed a linear reduction with increase in VPD from 16 to 26 mbars.

Photorespiration

Photorespiration rates were determined by studying apparent and total photosynthesis by allowing the plants to photosynthesize at ambient CO₂ plus 21 or 2 per cent oxygen. The difference between the photosynthetic rate at 21 and 2 per cent oxygen was calculated and represented as photorespiration (Table 13). The absolute values of photorespiration indicated that the photorespiration is highest in Eucalyptus followed by Spathodea. Pongamia had lowest photorespiration. When compared to Derris the photorespiration was seven times more in Eucalyptus.

Maintenance respiration

Species variation in maintenance respiration rate was studied to understand the reasons for differential response of species in terms of biomass to elevated carbon dioxide concentration. Amongst the four species studied Eucalyptus had the highest maintenance respiration expressed either on fresh weight basis or on leaf area basis (Table 14). The maintenance respiration rate was least in Derris followed by Spathodea.

In Derris indica and Spathodea the maintenance respiration rate per unit fresh weight was 24.1 and 31.8

Table 13 : Photorespiration ($\mu\text{mols.m}^{-2}.\text{s}^{-1}$) in seedlings of different forest species.

Species.	APS*	TPS*	PR*
<u>Derris</u>	3.71	4.85	1.14
<u>Eucalyptus</u>	11.88	19.91	8.11
<u>Spathodea</u>	3.08	6.74	3.66
<u>Acacia</u>	6.92	9.72	2.80

* = $\mu\text{Mols.m}^{-2}.\text{s}^{-1}$

APS = Apparent Photosynthesis (at 21 per cent oxygen)

TPS = True Photosynthesis (at 2 per cent oxygen)

PR = Photorespiration.

per cent less compared to Eucalyptus. similarly, the per cent differences in maintenance respiration in Spathodia companulata and Derris compared to Acacia auriculiformis per unit fresh weight basis was lesser by 22.6 and 30.22 per cent respectively. The trend remained same when the maintenance respiration rate was expressed in terms of dry weight basis or per unit leaf area as shown in the Table 14.

Experiments conducted to study the influence of elevated CO_2 concentration showed a marked increase in biomass accumulation in all the seven species tested. Out of seven species four broad leaved species namely, Derris, Eucalyptus, Acacia and Spathodea were selected for the measurement of gas exchange characteristic to study the possible reasons for varied response to elevated CO_2 concentration. There was a considerable variation in P_{max} in the plants grown at elevated CO_2 concentration. Lowest per cent increase in P_{max} was noticed in Derris (9.8 per cent) where as Acacia showed to an extent of 77.8 per cent under CO_2 enrichment. Plants raised under high soil nutrient status showed high 'A' in all species. Acacia and Eucalyptus showed high 'gs' compared to Derris and Spathodea. In all the species the 'gs' was high under CO_2 enrichment as well as high CO_2 with high soil nutrient status.

CO_2 response curves developed by plotting the 'A' against C_i in plants grown at ambient as well as elevated

Table 14 : Maintenance respiration rates of seedlings of different tree species.

Species	Maintenance respiration rate	
	uMols.g Fwt ⁻¹ .hr ⁻¹	uMols.cm ⁻² .hr ⁻¹
<u>Acacia</u>	9.519	0.16980
<u>Eucalyptus</u>	9.750	0.17600
<u>Spathodea</u>	7.400	0.09866
<u>Derris</u>	6.642	0.0972

CO₂ concentration indicated that the 'A' for a given Ci is always more in plants exposed to elevated CO₂ concentrations. In Derris there was a steep raise in 'A' with increase in Ci up to 660 ppm indicating that this species responds very much in terms of 'A' for increasing Ci. Spathodia also followed the same trend where as in Eucalyptus and Acacia 'A' increased with increase in Ci, but the rate of increase in 'A' for given Ci showed a decreasing trend after 400 ppm of Ci. In general Derris and Spathodea plants grown at elevated CO₂ concentration maintained high assimilation rate at high CO₂ concentration. In plants grown at ambient as well as elevated CO₂ concentration various limitations offered for assimilation were computed. Stomatal limitations were found to be a major limitation for these plants. Only in Acacia stomatal limitation reduced markedly under CO₂ enrichment. The light response curves that were developed for these species indicated that the response is curvilinear and biphasic. Under CO₂ enrichment Spathodea, Derris and Acacia always had high 'A' for a given PFD. Stomatal conductance also increased with increase in PFD. In all species tested increase in VPD decreased 'gs' as well as 'A'. In Eucalyptus marginal increase in VPD from 12 to 14 mbars resulted in drastic reduction in 'A'. The maintenance respiration measurements conducted suggests that, low responsive species like Eucalyptus and Acacia have high maintenance respiration compared to Derris.

Similarly Eucalyptus had high photorespiration compared to Derris.

Leaf chlorophyll content

The influence of elevated carbon dioxide concentration and high soil nutrient status on chlorophyll content in the leaf was determined at the end of the experiment. Amongst the four species studied Acacia had the lowest total chlorophyll content and it was relatively high in Derris and Spathodea. High nutrient status in the rooting media resulted in the marked increase in chlorophyll content in Acacia, Derris and Spathodea. Plants grown under elevated CO₂ concentration showed marked increase in total chlorophyll content in all the species. The total chlorophyll content in the leaves of the plants grown at elevated CO₂ concentration compared to the plants grown at ambient CO₂ concentration were 37.4, 132.3, 40.1 and 43.4 per cent in Acacia, Derris, Eucalyptus and Spathodea respectively (Table 15).

Chlorophyll a/b ratio was relatively less in plants grown at ambient carbon dioxide concentration. The differences in chlorophyll a/b ratio between the plants raised under ambient and high carbon dioxide concentration were marked in Derris compared to all other species tested.

Table 15 : Leaf chlorophyll content (mg g Fwt⁻¹)

Treatment	Acacia			Derris			Eucalyptus			Spathodia						
	Chlo. Chlo. Total a/b			Chlo. Chlo. Total a/b			Chlo. Chlo. Total a/b			Chlo. Chlo. Total a/b						
	a	b	chlo.	a	b	chlo.	a	b	chlo.	a	b	chlo				
C1	0.538	0.197	0.733	2.73	1.153	0.319	1.473	3.63	1.246	0.541	1.787	2.51	1.557	0.610	2.166	2.55
C1+N	0.702	0.315	1.010	2.23	2.229	1.125	3.422	2.04	1.814	0.689	2.504	2.63	2.147	0.962	3.108	2.23
C2	0.748	0.250	0.998	2.99	2.138	0.834	2.970	2.57	1.219	0.384	1.602	3.18	1.965	0.853	2.818	2.30
C2+N	0.768	0.287	1.055	2.67	2.247	1.560	3.810	1.44	1.517	0.537	2.053	2.83	1.899	0.789	2.690	2.41

DISCUSSION

DISCUSSION

The seedling growth rate of tree species which are recommended for afforestation programme is usually less. Although silviculturist identified tree species with higher growth rate for afforestation programme, the initial growth rate of these species seems to be poor. In many tree species recommended for planting, to get sapling of transplantable size the duration required varies from 24 to 36 months.

Plant growth and development is influenced by internal as well as by environmental factors. The growth rate of a plant species is influenced very much by its genetic potential. The environmental condition under which the plant grows also influences the growth rate of the plant species. Moisture availability, light intensity, temperature and relative humidity are some of the environmental factors which govern the expression of the genetic potential.

Plant biologists have shown some of the effects of high CO_2 levels on plants. In green houses CO_2 fertilisation is used to increase the growth and yield of many crop plants, vegetables and flowering plants.

In the present investigation an attempt has been made to know the influence of elevated CO_2 concentration on seedling growth rate of a few forest tree species.

An another factor which influences the early growth rate and seedling vigour is nutrient status of the soil. This factor becomes more important in seedlings raised in polybags, since the root growth and root spread is restricted because of space. Increase in the nutrient status in the restricted root medium will help in supplying the required nutrients for maximum growth of the seedlings. With these point of view alteration in the soil nutrient status was also done in the first experiment.

The major objectives of the present investigation were,

- 1) to study the influence of high CO_2 concentrations on seedling growth rate of few forest tree species.
- 2) to identify the most responsive seedling growth stage to elevated CO_2 concentration.
- 3) to study the possible reasons for differential responses in different tree species by studying the gas exchange parameters including the maintenance respiration.

5.1 Experiment I : Influence of elevated CO_2 concentration and soil nutrient status on seedling growth rate of few forest tree species.

A simple method was developed to increase the CO_2 concentration near the seedlings of few forest tree

species. In this method CO_2 released during dark respiration and soil respiration was trapped by enclosing the seedlings kept in trenches by covering with the polythene structures. Plants were enclosed between 4 pm to 10 am. CO_2 concentration which was increased to 700-800 ppm was used by the plants in photosynthesis process between 6.30 to 10 am. The polythene structures were removed at 10 am and plants were allowed to photosynthesis under ambient CO_2 concentration. In this method in addition to the increase in CO_2 concentration there was also substantial increase in relative humidity. This indicated that the observed response in the plant is due to the combination of elevated CO_2 as well as high RH for a brief period during a 24 hour cycle.

Response of forest species to soil nutrient status

Influence of high soil nutrient status on growth parameters were assessed at ambient as well as elevated CO_2 concentration. Increased soil nutrient status resulted in increased plant height, branch number and leaf area development.

Increase in the soil nutrient status resulted in significant increase leaf area development in six out of seven species studied. In plants maintained at ambient CO_2 concentration increase in the nutrient status in the nutrient medium resulted in 31.5 to 390.2 per cent increase in leaf area development during the experimental

period. A substantial increase in leaf area, development was observed due to increased nutrient status in soil in Spathodea, Acacia and Grevelia. In these three species increase in leaf area development during the experimental period was more than 100 per cent due to increased nutrient status.

In the plants grown at elevated CO_2 concentration high soil nutrient status resulted in significant increase in leaf area in two out of seven species studied, namely Leucaena and Grevelia.

At ambient CO_2 concentration the amount of biomass accumulated during the experimental period showed an increase to an extent of 9.6 to 101.1 per cent. Silver oak showed a very high response to increased soil nutrient status. In Spathodea seedlings the increase in biomass during the experimental period due to high CO_2 concentration was to an extent of 57.8 per cent. In Eucalyptus, Casuarina, Leucaena and Derris increase in biomass accumulated during the experimental period ranged from 20 to 30 per cent whereas in Acacia it was only 9.6 per cent.

At elevated CO_2 concentration increase in soil nutrient status increased the biomass accumulation during the experimental period in five out of seven species studied. The increase in biomass due to high soil nutrient status at elevated CO_2 concentration in relation to elevated CO_2 concentration treatment alone ranged from 5.5

to 66.6 per cent. High nutrient status increased biomass accumulation at elevated CO₂ concentration substantially in Grevelia. In Acacia also there was marked increase in biomass due to high soil nutrient status. In other species the effect was not substantial.

The influence of high nutrient status on biomass accumulation indicated that increasing the nutrient availability in the restricted rooting medium is effective in increasing the biomass accumulation in seedlings. This is primarily achieved by increase in photosynthetic capacity of the leaves. In species like Spathodia, Acacia and Grevelia high soil nutrient status increased the leaf area at ambient CO₂ concentration. At elevated CO₂ concentration, the total photosynthetic surface area increased substantially in Grevelia. High soil nutrient status was shown to increase the leaf area development and total biomass in many tree species (Sasek and Strain 1991) and crop plants (Hocking and Meyer 1991 ; Sage et. al 1991).

5.1.1 Response of seedlings of forest tree species to elevated CO₂ concentrations

Growth characteristics

Influence of elevated CO₂ concentration on the amount of biomass accumulated during the experimental period was assessed in plants grown at two levels of nutrients. All the seven species have responded positively to increased CO₂ concentrations.

When the soil nutrient status was relatively less, increase in CO₂ concentration resulted in substantial increase in biomass accumulation in all the species studied. The increase in biomass due to elevated CO₂ concentration ranged from 72.6 to 437.6 per cent. Silver oak and Derris showed maximum response to elevated CO₂ concentration followed by Casuarina. Spathodia and Leucaena showed moderate response in terms of biomass accumulation. In Acacia and Eucalyptus increase in biomass accumulation was relatively less (to an extent of 72.6 to 94.6 per cent respectively).

In plants grown at high soil nutrient status also increase in CO₂ concentration was effective in increasing the biomass accumulation substantially. The increase in biomass accumulation at elevated CO₂ and high nutrient status in the soil ranged from 88.5 to 504 per cent. Even at high soil nutrient status, response due to elevated CO₂ concentration was more in Grevelia, Derris and Casuarina compared to other species.

Increase in CO₂ concentration was shown to increase the biomass accumulation in number of plant species. Baker et.al (1990), noticed 32 per cent increase in grain yield in rice by doubling CO₂ concentration. Eamus and Jarvis claimed 40 per cent increase in growth rates under CO₂ enrichment (600 ppm CO₂) in tree species. Recently, Sasek and Strain (1991) in Japanese honey suckle, Idso et.al

(1991) in sweet oranges and Idso and Kimball (1991) in sour oranges showed a marked biomass enhancement under CO₂ enrichment. Increased wood production in Pinus radiatus was also reported by Conroy et.al (1990) under CO₂ enrichment. These findings suggest that increased CO₂ concentration has a profound effect on plant growth and development.

Increase in CO₂ concentration could result in increased biomass by increasing the biomass partitioned for leaf area development and/or by increasing the photosynthetic rate per unit area. In this set of experiments CO₂ altered the biomass partitioning to a certain extent. For example, leaf weight ratio increased to an extent of 2.9 to 24 per cent at elevated CO₂ concentration (at low nutrient levels) and the increase was more in Acacia, Derris and Leucaena suggesting that there was more allocation of biomass towards leaf area development. A marginal increase in shoot weight ratio was also observed in Acacia, Derris and Grevelia. This was achieved primarily by increased plant height, high leaf biomass and reduced root weight ratio. Root to shoot weight ratio reduced due to elevated CO₂ concentration in most of the species and reduction was substantial in Derris, Acacia, Spathodea and Grevelia. These results indicate that allocation of biomass for shoot and leaf area development increases at elevated CO₂ concentration. Increased CO₂ was shown to alter the allocation of

biomass in several plant species (Eamus and Jarvis, 1989). Greater allocation of biomass towards root has been shown at elevated CO_2 concentration by several workers (Acock and Allen ; Bazzaz et. al 1985). Most of the studies have shown that there is generally an increase in allocation to roots, especially when nutrients and water are limiting (Larigauderie et.al 1988; Mousseau and Enoch 1989; Norby et.al 1986). Several studies, especially with woody seedlings, have shown that branching increases with elevated CO_2 concentration (Sionit et. al 1985). There is also strong evidence that specific leaf area decreases with increasing CO_2 (Garbutt at. al 1990).

The salient findings of this experiments are as follows :-

- a. Enclosing the plants during dark hours in polythene structures results in substantial increase in CO_2 and RH near the seedlings.
- b. Elevated CO_2 concentration and RH increased the growth rate in all the seven species studied.
- c. Species showed differential responses in terms of growth to elevated CO_2 concentration.
- d. Increased nutrient status in the rooting medium also increased the leaf area and biomass. However, the response to nutrient was marginal compared to the response to elevated CO_2 concentration.

- e. Pongamia, Spathodea, Grevelia, Leucaena, and Casuarina showed more than 100 per cent increase in biomass accumulation at elevated CO₂ concentration.

5.2 EXPERIMENT II : Influence of seedling age on growth responses of few forest tree species seedlings to elevated CO₂ concentration.

Experiments were conducted to study the influence of elevated CO₂ concentration on seedling growth rate suggested that all the seven species tested responded positively to elevated CO₂ concentration, although the extent of response differed between the species. The age of the seedlings used in the first experiment were eight months. In another experiment, the influence of elevated CO₂ concentration on growth responses of seedlings were tested to identify the highly responsive growth stage for elevated CO₂ concentration. The experimental methodology was similar to that of first experiment and the influence of elevated CO₂ concentration on seedlings of two species namely, Eucalyptus and Grevelia were studied. The age of the seedlings used in this experiments was two, five and ten months. An increase in CO₂ concentration and RH resulted in a marked increase in growth of the seedlings of all age groups in both the species studied.

Plant height, shoot biomass and total biomass accumulated during the experimental period showed

significant increase with increase in CO_2 concentration and RH. The per cent increase in plant height and total biomass accumulated during the experimental period reduced with age of the seedlings. For example, in Eucalyptus the biomass accumulated during the experimental period showed an increase of 64.5, 33.67 and 30.56 per cent in seedling of age group two, five and ten months respectively. In Grevelia the corresponding values were 38.2, 33.27 and 30.58 per cent respectively (fig.12). These results clearly indicated that young seedlings of two months old are highly responsive in terms of growth to elevated CO_2 concentration and RH. Careful analysis of biomass partitioning to various organs indicated that in young two months old seedlings more amount of dry matter is partitioned into leaf area development, so that there is development of more photosynthesising tissue which further increases the photosynthetic production and thus biomass. Plants which partition the assimilates more towards leaf area development at early stages of growth were shown to have more crop growth rates under elevated CO_2 concentration (Sasek and Strain 1991; Koch et.al 1986; Nijs et.al 1989).

The experiment conducted to identify the highly responsive stage of seedlings for elevated CO_2 indicated the followings,

- a. Seedlings in the age groups of two, five and ten months old showed positive response to elevated CO_2 concentration.

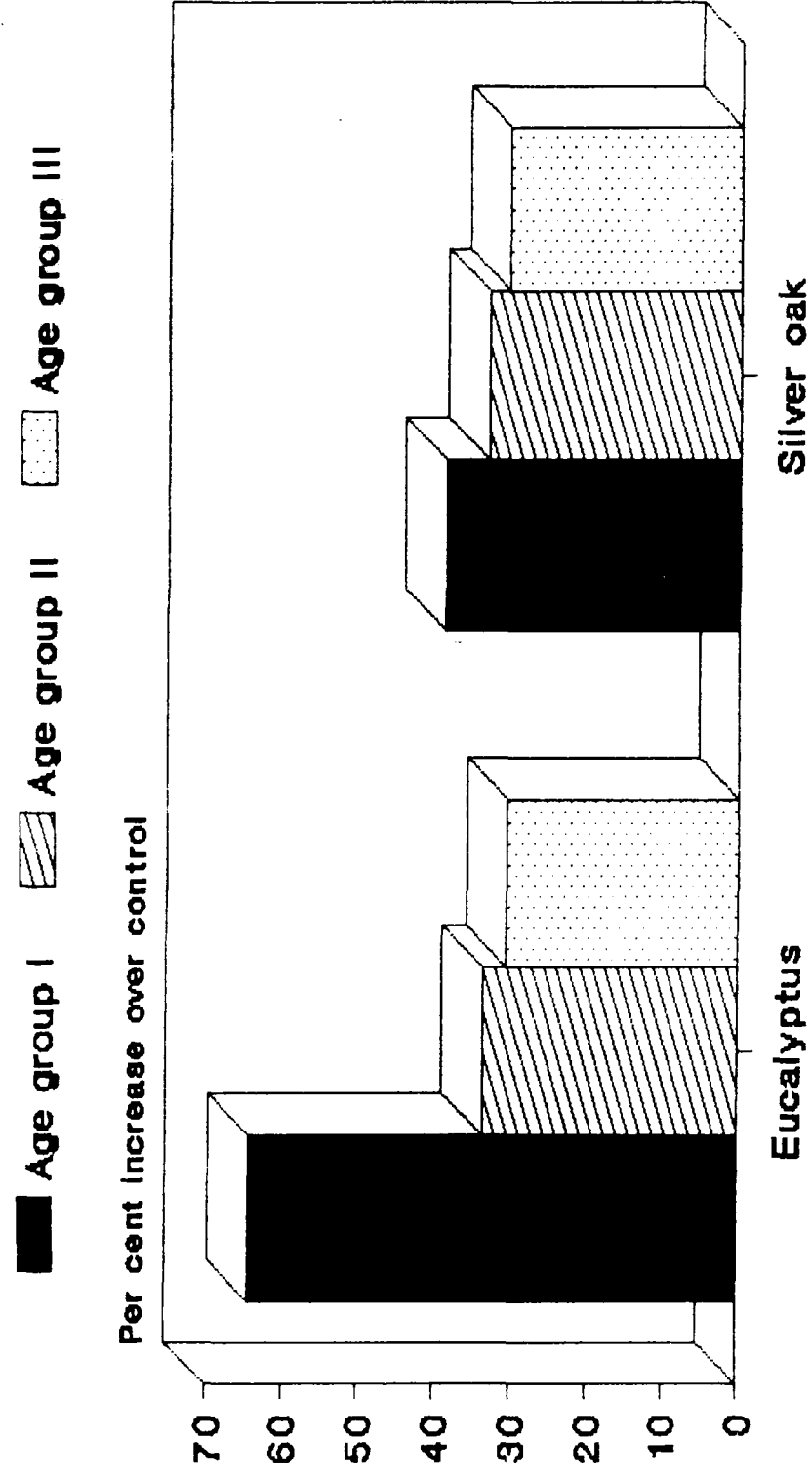


Fig.12. Differential responses of different aged seedlings to elevated CO₂ concentration (DM).

- b. Two months old seedlings showed high response in growth and biomass accumulation.
- c. In two months old seedlings more biomass was partitioned to leaf which increased the photosynthetic surface area.

Although seedlings of all age groups showed positive response to elevated CO_2 concentrations in the second experiment, the per cent increase in biomass was very much less compared to that of first experiment. The second experiment was conducted during middle of June to middle of September. This season coincides with more cloudy days and the total amount of radiation intercepted by the plant is less compared to the first which was conducted during middle of March to middle of June. This might be one of the reason for low response to elevated CO_2 concentration in the second experiment.

5.3 Gas exchange characteristics

In this series of experiments, influence of increase in CO_2 concentration on 'A' were measured to identify the species response to elevated CO_2 concentration. Instantaneous response of 'A' and 'gs' to varying CO_2 concentration at single leaf level was studied using an open system IRGA in intact leaves.

Initially gas exchange parameters were studied in plants grown at ambient and elevated CO_2 concentration

with and without high soil nutrient status. Eucalypt had intrinsically high response in terms of 'A' and in all other three species 'A' was more or less similar. However, in plants raised under elevated CO₂ concentration when 'A' was measured at ambient CO₂ concentration, substantial increase in 'A' was observed in Acacia. In other species the increase ranged from 9.8 to 22 per cent.

Elevated CO₂ concentration as well as high nutrient status increased 'A' in all the species. Stomatal conductances at 330 ppm of CO₂ was relatively high in Eucalyptus and Acacia and was low in Spathodea and Derris. The 'gs' at 330 ppm was also high in the plants grown at elevated CO₂ concentration. 'A'/'gs' ratio reduced significantly at high CO₂ concentration suggesting that water use efficiency at single leaf level increases at elevated CO₂ concentrations.

CO₂ response curve.

With increase in Ci the 'A' increased in Derris, indicating that, this species responds very much for increase in Ci. Spathodea also showed similar trend. However, 'A' per given Ci was markedly less in Spathodea compared to other species. In Eucalyptus and Acacia 'A' increased upto 400 ppm Ci, thereafter increase in 'A' with increase in Ci was not linear. These informations suggest that amongst the four species studied 'A' increased significantly in Derris. In all other species, although

'A' responded to increase in C_i , the response was not to the extent of Derris.

The CO_2 response curves also indicates that availability of CO_2 is the main limitation for 'A' in all these species. 'A' per given C_i was always more in plants raised under elevated CO_2 concentration. The dA/dC_i values also indicated the same trend. This was observed even when the C_i was less than 330 ppm indicating that carboxylation efficiency is high in plants grown under elevated CO_2 concentration.

Influence of light intensity on 'A'

Light response curves were taken in four broad leaved species namely, Acacia, Eucalyptus, Derris and Spathodea. 'A'_{max} values differed markedly amongst the four species studied. 'A'_{max} was high in Acacia and Eucalyptus followed by Derris. 'A' per unit PFD was also more in Acacia and Eucalyptus. Increase in PFD increased 'A' in all the species. In Eucalyptus, Derris and Spathodea light saturation was achieved at a PFD of about 2500 $\mu\text{Ein.m}^{-2}.\text{s}^{-1}$. Amongst the four species tested, low light saturation point was recorded in Acacia. With increase in PFD, 'gs' increased in all the species and maximum 'gs' was achieved at a PFD of 2500 $\mu\text{Ein.m}^{-2}.\text{s}^{-1}$ in Acacia.

In many C_3 species, light saturation for photosynthesis was shown to achieve at light intensity of about 660 $\mu\text{Ein.m}^{-2}.\text{s}^{-1}$. Tree species in general were shown

to have low light saturation point. Zelitch (1971) showed that deciduous tree species like oak and maple get saturated at $350 \mu\text{Ein.m}^{-2}.\text{s}^{-1}$. Similar values for many tree species have been reported by Kozlowski (1949) and Kramer and Dukes (1944).

A very high light saturation point in our situation for the tree species indicate that in tropics with very high available light intensities, the plants get adopted to enhanced light harvesting capability to achieve the 'A' especially, when all other factors are not limiting the photosynthesis. Plants growing under higher light intensities were shown adopt themselves for high light intensities by morphological, physiological, anatomical and biochemical modifications. Changes in the leaf anatomy, the ultrastructure of chloroplast and capability of chloroplast components were shown to alter the photosynthetic functional characteristics (Besford 1986; Chow et.al 1988). Plants raised under elevated CO_2 concentration always had high 'A' for a given PFD as shown in Derris, Spathodia and Acacia. This suggests that in these plants the light saturation point shifts to higher side under CO_2 enrichment.

Influence of VPD on gas exchange characteristics.

Method adopted in this investigation to elevate CO_2 concentration resulted in parallel increase in relative humidity. Particularly RH was very high in morning hours

near the plants which were enclosed under the polythene structures. High RH and low VPD were shown to increase 'A' by increasing the 'gs' and water relations of the leaves. In this study, experiments were also conducted to know the influence of VPD on gas exchange characteristics in four different species. This observation will help in understanding the influence of increased RH on seedling growth rates. The effect of varying VPD on gas exchange were assessed by studying the instantaneous response of 'A' and 'gs' to change in VPD.

In Spathodea and Derris 'A' reduced only when VPD increased beyond 18 and 20 mbars. However, in Eucalyptus drastic reduction in 'A' was observed when VPD increased from 12 to 14 mbars. However, at very high VPD, 'A' and 'gs' was affected to a little extent in Eucalyptus. In Acacia VPD beyond 20 mbars reduced 'A' and 'gs' significantly. These observations indicate that VPD has varying effect on 'A' in different species. Eucalyt seems to be highly sensitive to the change in VPD particularly, in the range of VPD between 14 to 18 mbars. In other species, the VPD above 18 or 20 mbars had a marked effect in reducing the 'A'. Maintenance of relatively higher 'A' at high VPD might one of the reason for high growth rate in Eucalyptus. In the experimental methodology followed in our experiment, plants were at low VPD from 6 pm to 10-30 am. During 10-30 am to 6 pm because of high temperature, the VPD increases and might be

reducing the 'A' in all other species, but not in Eucalyptus.

5.4 Relationship between the growth parameters and gas exchange characteristics.

Based on the results of the first experiment, four species were selected two species namely, Derris and Spathodea were grouped under highly responsive species, since the increase in biomass accumulation during the experimental period at elevated CO₂ concentration was more than 100 per cent. Two other species, namely, Eucalyptus and Acacia were grouped under low responsive type, since the increase in biomass was less than 100 per cent. The per cent increase in biomass and leaf area produced during the experimental period at elevated CO₂ concentration is given in the Table 16.

Per cent increase in assimilation rates in plants grown at ambient and elevated CO₂ concentration when exposed to a Ci of 660 ppm is given in the table 11. In species which showed low response in terms of growth rate for elevated CO₂ concentration, per cent increase in 'A' was 78 per cent at Ci of 660ppm. This indicated that in Acacia and Eucalyptus (low responsive in terms of growth to elevated CO₂ concentration) plants kept under elevated CO₂ concentration the increase in assimilation rate is relatively less.

Table 16: Per cent increase in leaf area and biomass in highly responsive and low responsive species due to CO₂ enrichment.

Species	% increase in total biomass	% increase in DM	% increase in total LA	% increase in LA
Highly responsive type:				
<u>Derris</u>	241.03	307.7	222.29	324.13
<u>Spathodea</u>	114.96	130.34	107.85	408.20
Low responsive type:				
<u>Acacia</u>	56.14	72.61	172.75	548.55
<u>Eucalyptus</u>	88.60	94.65	46.25	54.67

In Spathodea and Derris (high responsive types) instantaneous increase in 'A' at 660 ppm C_i in plants grown at ambient CO_2 concentration was relatively less. However, plant which was maintained at elevated CO_2 concentration showed large increase in 'A' at C_i of 660. This indicates that Derris and Spathodea maintained high 'A' even at elevated CO_2 concentration. A large increase in growth rates were observed in species which maintained high 'A' for a long period at enriched CO_2 concentration (Sage et.al 1991; Idso, et.al 1991; Chen and Sung 1990).

Spathodea and Derris showed very low maintenance respiration rate compared to Eucalyptus which had the highest maintenance respiration rate. In these two species the maintenance respiration rate was lesser by 31.8 and 24.1 per cent (on Fwt. basis) compared to Eucalyptus. Species with low maintenance respiration were shown to produce high biomass in several plant species (Volenec, et.al 1984). Maintenance respiration in nonphotosynthetic cell in the stems, branches and roots of large trees usually represent a large demand for carbohydrates, particularly in warm climate. Maintenance respiration plays a major role in regard to carbon gain and biomass accumulation.

Observation recorded on apparent photosynthetic rate and true photosynthetic rate to calculate the photorespiration (PR) also indicated that photorespiration

is high in Eucalyptus and low in Spathodea and Derris. Increase in light intensity resulted in continuous increase in 'A' in Derris and Spathodia to a certain extent. This might be another reason for higher growth rate at high CO₂ concentration. In low responsive type like Eucalyptus and Acacia light saturation is achieved at about 1800 and 2500 $\mu\text{Ein.m}^{-2}.\text{s}^{-1}$, respectively.

Results of the gas exchange studies indicates the following :

- a. Plants grown under high CO₂ concentration maintained high 'A' and 'gs' at all CO₂ levels.
- b. In Derris and Spathodea which showed high growth response to elevated CO₂ concentration the per cent increase in 'A' at elevated CO₂ concentration was more compared to low responsive species Eucalyptus and Acacia.
- c. The maintenance respiration rate was comparatively less in high responsive species Derris and Spathodea.
- d. In high responsive species Derris and Spathodea assimilation rate was affected by marginal variation in VPD above 18 or 20 mbars.
- e. Plants grown under high CO₂ levels always had high 'A' for a given PFD and with increase in PFD 'gs' also increased in all the species.

SUMMARY

VI SUMMARY

The main objective of the present investigation was to study the influence of elevated CO_2 concentration on seedling growth rate of a few forest tree species. In addition to this, influence of high soil nutrient status on seedling growth rate at two CO_2 levels was also studied. Second set of experiment was also conducted to identify the most responsive seedling growth stage to CO_2 fertilization. The response to elevated CO_2 and RH was studied by adopting a technique, in which CO_2 released by the plants and soil respiration was trapped by covering the trenches containing seedlings with polythene structures from 4 P.M. to 10 A.M. The increase in CO_2 concentration and RH was substantial within a few hours after covering the trenches.

Two separate set of experiments were conducted to study the response of plants in terms of growth rate in altered environmental condition. To understand the possible reasons for differential response to elevated CO_2 concentrations, gas exchange measurements including maintenance respiration rate were done in four different species differing in their growth responses to elevated CO_2 concentrations.

The results of the experiments conducted to study the influence of elevated CO_2 concentrations for a brief

period during morning hours on growth of seedlings of tree species indicated that in all the seven species studied there was substantial increase in growth rate. In addition to this, influence of high soil nutrient status on growth of the seedling at ambient and elevated CO₂ concentrations were also studied. There was significant increase in growth and biomass accumulation due to increase in the nutrient status in rooting medium as well as due to CO₂ enrichment. High soil nutrient status along with high CO₂ concentrations resulted in more growth than that of increased soil nutrient status alone. Under high CO₂ and high soil nutrient status the amount of biomass accumulated was more than 100 per cent in Derris, Leucaena, Casuarina and Grevelia whereas it was less than 100 per cent in Acacia and Eucalyptus.

Experiments conducted to identify highly responsive seedling growth stage to elevated CO₂ concentrations using two, five and ten months old seedlings of Eucalyptus and Grevelia showed that two months old seedlings were more responsive in terms of growth. There was substantial increase in plant height, leaf number and leaf area due to CO₂ enrichment. The total dry matter accumulated during the experimental period was to an extent of 64.5, 33.67, 30.56, and 38.85, 33.27, 30.50 per cent in two, five, ten months old seedling of Eucalyptus and Grevelia, respectively.

The total leaf chlorophyll content in four species namely Acacia, Spathodea, Eucalyptus and Derris was also determined. Plants grown under elevated CO₂ concentrations showed marked increase in total chlorophyll in all the species. The chlorophyll a/b ratio was relatively less in plants grown at ambient CO₂ levels.

In order to assess the possible reasons for the differential responses in terms of growth to elevated CO₂ concentrations, two highly responsive (Derris and Spathodea) species which were showing more than 100 per cent increase in dry matter (DM) and two slow responsive species (Acacia and Eucalyptus) which were showing less than 100 per cent increase in DM were selected. The salient findings of the gas exchange studies are :

1. There was a marked variation in assimilation at saturated light intensities in the four species tested. Plants grown at ambient CO₂ concentrations had low P_{max}. compared to the plants maintained at elevated CO₂ concentrations. The per cent increase in P_{max}. at elevated CO₂ concentrations varied from 9.8 per cent in Derris to 77.8 per cent in Acacia. Plants raised under high nutrient status and elevated CO₂ concentrations had relatively high P_{max}. compared to the plants in all other treatments. The 'gs' of the plants maintained under

high CO_2 concentrations was always high. Amongst the four species studied Acacia had relatively high 'gs'.

2. The 'A'/Ci curves developed in four species indicated that 'A' for a given Ci was always more in plants exposed to high CO_2 concentrations. There was steep increase in 'A' with increase in Ci up to 660 ppm in Derris and Spathodea. However, in Eucalyptus 'A' increased with increase in Ci but, the rate of increase for a given Ci showed a decreasing trend beyond about 400 ppm of Ci. This suggested that Spathodea and Derris maintained relatively high 'A' at elevated CO_2 concentrations which resulted more growth and biomass accumulation.
3. The maintenance respiration rate in low responding species like Eucalyptus and Acacia was more compared to Derris.
4. The photorespiration rate was high in Eucalyptus compared to Derris. This also seems to be one of the reasons for low response to elevated CO_2 concentrations.
5. The response of VPD on 'A' was also studied in these four species. The results suggested that in high responsive species like Derris and Spathodia, 'A' reduced when VPD increased beyond 18 and 20 mbars

respectively, but in Eucalyptus, drastic reduction in 'A' was observed when VPD increased from 12 to 14 mbars.

6. Light response curves were also taken in these four species. The Pmax varied amongst these four species. Increase in PFD increased 'A' and 'gs' in all the four species. Plants raised under high CO₂ concentrations always had high 'A' for a given PFD. In Acacia, Pmax was reached at about PFD of 1800 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, whereas in Derris Spathodia and Eucalyptus it was about 2500 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

REFERENCES

VII REFERENCES

- Acock, B., 1980, Analysing and predicting the response of the glass house crop to environmental manipulation. Hurd, R.G., Biscoe, P.V. and Dennis, C. (Ed.), In: Opportunities for increasing crop yield. (pp. 131-148). London: Pitman.
- Acock, B., and Allen, L.H.J., 1985, Crop response to elevated Carbon dioxide. In Strain, B.R. and Cure, J.D., (Ed.), In: Direct effect of increasing carbon dioxide on vegetation. (pp. 53-98). Washington, DC.
- Akita, S and Moss, D.N., 1972, Differential stomatal response between C3 and C4 species to atmospheric CO₂ concentration and light. Crop Sci., 12: 789-793
- Alan, G.B., King, K.M., Thurtell, G.W. and Graham, M.E.D., 1990, Humidity and soil water influence the transpiration response of maize to CO₂ enrichment. Can. J. Plant Sci., 70: 941-948.
- Allan, G. B., King, K. M., Thurtell, G. W. and Graham, M. E. D., 1990, Humidity and soil water influence the transpiration response of maize to CO₂ enrichment. Can. J. Plant Sci., 70: 941-948.
- Allan, L. H. Jr., Idso, S. B. and Kimball, B. A. 1990, Interaction effect of CO₂ and environment on net photosynthesis of water lily. Agric. Ecosyst. Environ. 30: 81-88.
- Allen, L. H. Jr., 1990, Plant responses to rising carbon dioxide and potential interactions with air pollutants. J. Environ. Qual., 19: 15-34.
- Anne, L., Hilbert, D. W. and Oechel, W. C., 1988, Effect of CO₂ enrichment and nitrogen availability on resource acquisition and resource allocation in a grass, *Bromus mollis*. Oecologia, 77: 544-549.
- Arnold III, J. A. and Gordon, J. C., 1990, Effect of nodulation, nitrogen fixation and CO₂ enrichment on the physiology, growth and dry mass allocation of seedlings of *Alnus rubra* Bong. New Phytol., 116: 55-66.
- AzconBeito, J and Osmond, B.C., 1983, Relationship between photosynthesis and respiration. Plant physiol., 71: 574-581.
- Baker, J. T., Allen, L. H., Boote, K. J., Jones, P. and Jones, J. W., 1989, Response of soybean to air

- temperature and carbon dioxide concentration. Crop Sci., 29: 98-105.
- Baker, J. T., Allen, L. H., Jr. and Boot, K. J., 1990, Growth and responses of rice to CO₂ concentrations.. J. Agric. Sci., 115: 313-320.
- Bazzaz, F.A., 1990, The response of natural ecosystem to the rising global CO₂ levels.. Annu. Rev. Ecol. Syst., 21: 176-196.
- Bazzaz, F. A. and Williams, W. E. 1985, Effect of increased atmospheric CO₂ concentration on plant communities. Strain, B. R. and Cure, J. D. (Ed.), In: Direct effects of increasing CO₂ on vegetation (pp. 155-170) US Department of Energy, Washington, DC.
- Bazzaz, F. A., Garbutt, K., Reekie, E. G. and Williams, W. E., 1989, Using growth analysis to interpret competition between a C₃ and a C₄ annual under ambient and elevated CO₂. Oecologia, 79: 223-33.
- Besford, R. T., 1984, Some properties of Rubisco extracted from tomato leaves. J. Expt. Bot., 35: 495-504.
- Besford, R. T. and Withers, A. C., 1985, Rubisco activity and photosynthesis during leaf development in the tomato. J. Expt. Bot., 36: 1530-1541.
- Björman, O., 1966, The effect of oxygen concentration on photosynthesis in higher plants.. Physiol. Plant., 19: 618-633.
- Brown, K., and Higginbotham, K.O., 1986, Effect of carbon dioxide enrichment and nitrogen supply on growth of boreal tree seedlings. Tree Physiology, 2: 223-232.
- Bruggink, G. T., 1984, Effect of CO₂ concentration on growth and photosynthesis of young tomato and carnation plants. Acta Horticulturæ, 162: 279.
- Bunce, J. A., 1990, Short- and long-term inhibition of respiratory carbon dioxide efflux by elevated carbon dioxide.. Annals of Bot., 65: 637-642.
- Bunce, J. A. and Caulfield, F., 1991, Reduced respiratory CO₂ efflux during growth at elevated carbon dioxide in three herbaceous perennial species.. Annals of Bot., 67: 325-330.
- Calvert, A and Slack, G., 1975, Effects of CO₂ enrichment on growth, development and yield of green house tomatoes. I Response to controlled conditions. J. Hort. Sci., 50: 61-71.

- Campagna, M. A. and Marglis, H. A., 1989, Influence of short-term CO₂ enrichment on growth, allocation patterns, and biochemistry of black spruce seedlings at different stages of development. Can. J. For. Res., 19: 773-782.
- Campbell, W. J., Allen, L. H. and Bowes, G., 1988, Effects of CO₂ concentration on Rubisco activity, amount and Photosynthesis in soybean leaves.. Plant Physiol., 88: 110-1316.
- Carlson, R. W. and Bazzaz, F. A., 1980, Effects of elevated CO₂ concentration on growth, photosynthesis, transpiration and water use efficiency of plants. In Singh, J. J. and Deepak, A. (Ed.), In: Environmental and climatic impact of coal utilisation (pp. 609-623) Academic Press New York.
- Cave, G., Tolley, L. C. and Strain, B. R., 1981, Effect of CO₂ enrichment on chlorophyll content, starch content and starch grain structure in Trifolium leaves. Plant Physiol., 88: 1310-1316.
- Chen, J.J. and Sung, M.J. 1990, Gas exchange rate and yield responses of Virginia-type peanut to carbon dioxide environment. Crop Science, 30: 1085-1089.
- Clough, J.M, Peet, M.M and Kramer, P.J., 1981, Effects of high atmospheric CO₂ and sink size on rates of photosynthesis of a soybean cultivar. Plant Physiol., 67: 1007-1010.
- Conroy, J., Burlow, E. W. R. and Bevege, D. I., 1986, Response of Pinus radiata seedlings to carbon dioxide enrichment at different levels of water and phosphorus: growth, morphology and anatomy. Ann. Bot., 57: 165-177.
- Conroy, J. P., Milham, P. J., Mazur, M. and Barlow, E. W. R., 1990, Growth, dry weight partitioning and wood properties of Pinus radiata after 2 years of CO₂ fertilisation. Plant cell and environment, 13: 39-337.
- Cure, J. D., 1985, Carbon dioxide responses: a crop survey. In Strain, B. R. and Cure, J. D. (Ed.), In: Direct effects of increasing carbon dioxide on vegetation (pp. 19-116). Washington: US Department of energy.
- Cure, J. D. and Acock, B., 1986, Crop responses to carbon dioxide doubling : a literature survey.. Agricultural and Forest Meteorology., 38: 127-145.

- Curtis, P. S., Drake, B. G., Leadley, P. W., Arp, W. J. and Whigham, D. F., 1989, Growth and senescence in plant communities exposed to elevated CO₂ concentrations on an estuarine marsh. Oecologia, 78: 20-26.
- DeLucia, E.H., Sasek, T.W. and Strain, B.R., 1985, Photosynthesis inhibition after long term exposure to elevated levels of atmospheric carbon dioxide. Photosynthesis Research, 7: 175-184.
- Downton, W. J. S., Bjorkman, O. and Pike, C., 1980, Consequences of increased atmospheric conc. of CO₂ for growth and photosynthesis of higher plants, Pearman, G. I. (Ed.), In: Carbon dioxide and climate: Australian Research. (pp. 143-153.), Canberra, Australian Academy of Science.
- Downton, W.J.S, Grant, W.J.R and Loveys, B.R., 1987, CO₂ enrichment increases yield of valencia orange. Aust. J. Plant Physiol., 14: 493-501.
- Downton, W. J. S., Grant, W. J. R. and Chacko, E. K., 1990, Effect of elevated CO₂ on photosynthesis and early growth of mangosteen (*Gracina mangostena* L.). Sci. Hortic., 44: 2115-225.
- Dubbe, D. D., Farquhar, G. D. and Raschke, K., 1978, Effect of ABA on the gain of feedback loop involving CO₂ and stomata. Plant Physiol., 62: 413-417.
- Eamus, D. and Jarvis, P.G., 1989, The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests. Advances in Ecological Research, 19: 1-55.
- Edward, G. and Walker, G., 1983, C₃, C₄ : Mechanisms, and Cellular and Environmental Regulation, of Photosynthesis., Black-well, Oxford.
- Ehleringer, J. and Bjorkman, O., 1977, Quantum yield for CO₂ uptake in C₃ and C₄ plants depends on temperature, CO₂ and O₂ uptake. Plant. Physiol., 59: 86-90.
- Farquhar, G. D., Dubbe, D. D. and Raschke, K., 1978, Gain of the feedback loop involving CO₂ and stomata. Plant Physiol., 62: 406-412.
- Farquhar, G.D., Von Caemmerer, S. and Berry, J.A., 1980, A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species.. Planta, 149: 78-90.
- Foch, H., Klug, K and Canvin, D.T., 1979, Effect of CO₂ and temperature on photosynthetic CO₂ uptake and photorespiratory CO₂ evolution in sunflower leaves. Planta, 145: 21-23.

- Garbutt, K., William, W. E. and Bazzaz, F. A., 1990, Analysis of differential responses of five annuals to elevated CO₂ during growth. Ecology, 71:
- Gifford, R.M., 1979, Growth and yield of CO₂ enriched wheat under water limited conditions. Aust. J. plant Physiol., 6: 367-368.
- Gifford, R. M., 1987, Global photosynthesis, atmospheric CO₂ and man's requirements.. Giovannozzi-Sermanni, G. and Nannipieri, P. (Ed.), In : Current Perspectives in Environmental Biogeochemistry. (pp. 413-43).
- Gifford, R. M., 1989, The effect of the build-up of carbon dioxide in the atmosphere on crop productivity. Proceedings of the Fifth Australian Agronomy Conference.. Pert, Western Australia.
- Gifford, R. M., Lambers, H. and Morison, J. I. L., 1985, Respiration of crop species under CO₂ enrichment . Physiol. Plant., 6: 367-368.
- Gourdriaan, J. and de Ruiter, H.E., 1983, Plant growth in response to CO₂ enrichment , at two levels of nitrogen and phosphorus supply. I. Dry matter, leaf area and development. Neth. J. Agric. Sci., 31: 157-169.
- Green, K. and Wright, R., 1977, Field response of photosynthesis to CO₂ enrichment in ponderosa pine. Ecology, 58: 687-692.
- Hardy, R. W. F. and Havelka, U. D., 1975, Photosynthesis as a major factor limiting nitrogen fixation by field grown legumes with emphasis on soybean. Nutman, P. S. (Ed.), In: Symbiotic nitrogen fixation in plants. International Biology Programme Series (Vol. 7, pp. 421-439) Cambridge University Press, London.
- Hartman, F. C., Stringer, C. D., Milanez, S. and Lee, E. H. 1986, The active site of Rubisco. Philosophical Transactions of the Royal Society of London, Series B, 313: 379-395.
- Havelka, U. D., Ackerson, R. C., Boyle, M. G. and Wittenbach, L. A., 1984a, CO₂ enrichment effect on soybean physiology I. Effects of long-term exposure. Crop Sci., 24: 1146-1168.
- Havelka, U. D., Wittenbach, V. A. and Boyle, M. G., 1984b, CO₂ enrichment effects on wheat yield and physiology. Crop Sci., 24: 1163-1168.

- Heij, G., Uffelen, J.A.M and Van., 1984, Effects of $c\text{CO}_2$ concentration on growth of glass house cucumber . Acata Horticulturae, 162: 29-36.
- Higginbotham, K. O., Mayo, J. M., L'Hirondelle, S. and Krystoflak. D. K. 1985, Physiological ecology of lodge pole pine (Pinus contorta) in an enriched CO_2 environment. Can. J. For. Res., 15: 417-421.
- Hocking, P. J. and Meyer, C. P., 1991, Effects of CO_2 enrichment and nitrogen stress on growth and partitioning of dry matter and nitrogen in wheat and maize. Aust. J. Plant Physiol., 18: 339-56.
- Hrubec, T.C., Robinson, J. and Donaldson, R.P., 1984, Effect of CO_2 enrichment on soybean leaf and mitochondrial respiration. Plant. Physiol., 75: 158.
- Hrubec, T. C., Robinson, J. M. and Donaldson, R. P., 1985, Effect of CO_2 enrichment and carbohydrate content on the dark respiration of soybeans. Plant Physiol., 79: 684-689.
- Huber, S.C., Rogers, H. and Israel, D.W., (1984). Effect of CO_2 enrichment on photosynthesis and photosynthate partitioning in soybean (Glycine max) leaves . Physiol. Plant., 62: 95-101.
- Idso, I.B. and Kimbell, B.A., 1991, Effects of two and a half years of atmospheric CO_2 enrichment on the root density distribution of tree-year-old sour orange trees. Agricultural and Forest Meteorology., 55: 345-349.
- Idso, S. B., 1989, Carbon dioxide and global change: Earth in Transition. IBR Press, Tempe, AZ.
- Idso, S. B., Kimball, B. A., Anderson, M. G. and Mauney, J. R., 1987, Effects of atmospheric CO_2 enrichment on plant growth: the interactive role of air temperature. Agric. Eosyst. Environ., 20: 1-10.
- Idso, S.B., Kimbell, B.A. and Allen, S.G., 1991, Net photosynthesis of sour orange trees maintained in atmospheres of ambient and elevated CO_2 concentrations. Agricultural and Forest Meteorology., 54: 95-101.
- Imai, K., Coleman, D. F. and Yagagisava, T., 1984, Elevated atmospheric partial pressure of CO_2 and dry matter production of casava (Monihot esulenta, Crantz.). Japanese J. Crop Sci., 53: 479-485.

- Jacob, J., 1988, Quantification of stomatal and mesophyll limitations of photosynthesis under stress- A mathematical approach . Ph.D. thesis, Submitted to University of Agricultural Sciences, Bangalore.
- Jarvis, P.G., 1989, Atmospheric carbon dioxide and forests.. Philosophical Transactions of the Royal Society of London, Series B, 324: 369-392.
- Jones, B., Allen, L.H. Jr. and Jones, J.W., 1985a, Responses of soybean canopy photosynthesis and transpiration to whole day temperature changes in different CO₂ enrichment . Agron. J., 77: 242-249.
- Jones, P. Jones, J. W. and Allen, L. H. Jr., 1985b, CO₂ effects on photosynthesis and transpiration during vegetative growth in soybeans.. In : Proceedings of soil and Crop Science Society of Florida, 44: 129-134.
- Kerbel, E. L., Kader, A. A. and Romani, R. J., 1988, Effects of elevated CO₂ concentrations on glycolysis in intact 'Bartlett' pear fruits . Plant Physiol., 86: 1205-1209.
- Kimball, B. A., 1985, Adaptation of vegetation and management practice to a higher CO₂ world. In Strain, B. R. and Cure, J. D. (Ed.), In: Direct effects of increasing CO₂ on vegetation (pp. 185-204). Washington, DC: US Department of Energy.
- Kirschbaum, M. U. C. and Farquhar, G., 1987, Investigation of CO₂ dependence quantum yield and respiration in Eucalyptus pauciflora. Plant Physiol., 83: 1032-1036.
- Koch, K.E., Jones, P.H., Avigne, W.T. and Allan, L.H. Jr., 1986, Growth, dry matter partitioning and diurnal activities of RuBP carboxylase in citrus seedlings maintained at two levels of CO₂. Physiol. Plant., 67: 477-484.
- Kozlowski, T. F., 1949, Light and water in relation to growth and competition of predominant forest tree species. Ecol. Monogr. 19: 207-231.
- Kramer, P. J. and Decker, J. P., 1944, Relationship between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. Physiol. Plant., 19: 3350-3358.
- Kramer, P. J., 1981, Carbon dioxide concentration, Photosynthesis and dry matter production.. BioScience, 31: 29-33.
- Lamark, V.J., Graybill, D.A., Fritts, H.C. and Rose, M.R., 1984, Increasing atmospheric carbon dioxide : Tree

- ring evidence or growth enhancement in natural vegetation. Science, 225: 1019-1021.
- Lemon, E. R. (Editor), 1983, CO₂ and Plants. Am. Ass. Adv. Sci., Selected symp. Westview Press, Boulder, CO.
- Louwerse, W., 1980, Effect of CO₂ concentration and irradiance on stomatal behaviour of maize, barley and sunflower plants in the field. Plant cell and Envi, 3: 391-398.
- MacDowell, F.D.H., 1972, Growth of Marquis wheat II. Carbon dioxide dependence. Can. J. Bot., 50: 883-889.
- Marks, S. and Strain, B.R., 1989, Effects of drought and CO₂ enrichment on competition between two old field perennials. New Phytol., 111: 181-186.
- Mbikayi, N. T., Hileman, D. R., Bhattacharya, N. C., Ghosh, P. P. and Biswas, P. K., 1988, Effects of CO₂ enrichment on the physiology and biomass production in cowpea (Vigna unguiculata L.) grown in open top chambers. In Proceedings of the international congress on plant physiology, held at New Delhi, Sinha, S. K., Sane, P. V. and Bhargava, S. C. (Eds.) pp. 640.
- Morison, J. I. L. and Gifford, R. M., 1983, Stomatal sensitivity to CO₂ and humidity. A comparison of two C₃ and two C₄ grass species. Plant Physiol., 71: 789-796.
- Morison, J.L., 1985, Sensivity of stomata and water use efficiency to high CO₂. Plant, Cell and Environment, 8: 789-796.
- Mortensen, L. M., 1984, Photosynthetic adaptations in CO₂ enriched air and the effect of intermittent CO₂ application on green house plants. Acta Horticulturae, 162: 153-158.
- Natziger, E. D. and Koller, H. R., 1976, Influence of leaf starch concentration on CO₂ assimilation in soybean. Plant Physiol., 57: 560-563.
- National Academy of Science., 1988, Towards an understanding of global change. Washington, DC: NAS.
- Nijs, I., Impens and Behaeghe, T., 1989, Effect of different CO₂ environments on the photosynthesis-yield relationships and the carbon and water balance of a white clover sward. J. Expt. Bot., 40: 353-359.
- Norby, R. J. and O'Neill, E. G., 1991, Leaf area compensation and nutrient interactions in CO₂ enriched

- seedlings of yellow-poplar (Liriodendron tulipifera L.). New Phytol., 117: 515-528.
- Norby, R. J., O'Neill, E. G. and Luxmoore, R. J., 1986, Effects of atmospheric CO₂ enrichment on the growth and mineral nutrition of Quercus alba seedlings in nutrient poor soil. Plant Physiol., 82: 83-89.
- Norby, R. J., Pastor, J. and Melillo, M. A., 1990, Carbon-nitrogen interactions in CO₂ enriched white oak: Physiological and long term perspectives. Tree Physiol., 2: 223-241.
- Oberbauer, S., Strain, B. R. and Fetcher, N., 1985, Effect of CO₂ enrichment on seedling physiology and growth of two tropical tree species. Physiol. Plant., 65: 352-356.
- Oechel, W. C. and Strain, B. R., 1985, Native species response to increased CO₂ concentration. Strain, B. R. and Cure, J. D. (Ed.), In Direct effects of increasing CO₂ on vegetation. (pp. 117-154) US Dept. of Energy, NTIS, Springfield, Virginia.
- Pearcy, R.W. and Bjorkman, O., 1983, The response of plants to rising levels of atmospheric carbon dioxide, In Lemon, E.R. (Ed.), Westview Press, Boulder, USA.
- Peet, M. and Willits, D., 1985, Photosynthetic and stomatal responses of tomatoes and cucumbers to long-term CO₂ enrichment. Plant Physiol. (Supplement), 77: 61.
- Peet, M. M., Huber, S. C. and Patterson, D. T., 1986, Acclimation to high CO₂ in monoecous cucumbers II carbon exchange rates, enzyme activities and starch and nutrient concentrations. Plant Physiol., 80: 63-67.
- Peet, M. M., Willits, D. H., Tripp, K.E. Kroen, W. K., Pharr, D. M., Depa, M. A. and Nelson, P.V., 1991, CO₂ enrichment responses of chrysanthemum, cucumber and tomato: Photosynthesis, growth nutrient concentration and yield. In Global climatic changes on photosynthesis and plant productivity. -Proceedings (pp. 193-212). New Delhi, India.
- Potvin, C. and Strain, B. R., 1985, Photosynthetic responses to growth temperature and CO₂ enrichment in two species of C₄ plants. Can. J. Bot., 63: 483-487.
- Quazi, H. M. and Freebairn, H.T., 1970, Influence of ethylene, oxygen and carbon dioxide on the ripening of bananas. Bot. Gaz., 131: 5-14.

- Raper, C.D. Jr. and Peedin, G.F., 1978, Photosynthetic rate during steady state growth as influenced by CO₂ concentration. Bot. Gaz., 139: 147-149.
- Reekie, E.G. and Bazzaz, F.A., 1989, Competition and pattern of resource use among seedlings of five tropical trees grown at ambient and elevated carbon dioxide.. Oecologia, 79: 212-222.
- Riechers, G. H., 1984, The effects of CO₂ enrichment on the C₄ grass land species. Dissertation Abstracts, International B (Science and Engineering), 44(12):.
- Rogers, H. H., Bingham, G.E., Cure, J. D., Smith, J. M. and Surano, K. A., 1983, Responses of selected plant species to elevated CO₂ in the field. J. Environ. Qual., 12: 569.
- Rogers, H. H., Thomas, J. F. and Bingham, G. E. (1983). Response of agronomic and forest species to elevated atmospheric carbon dioxide. Science, 22: 428.
- Rogers, H. M., Thhomas, J. F. and Bingham, G. M., 1983, Response of agronomic and forest species to elevated atmospheric carbbon dioxide. Science, 220: 428-430.
- Sage, R.F. and Sharkey, T.D., 1989, Acclimation of photosynthesis to elevated CO₂ in five C₃ species. Plant. Physiol., 89: 590-596.
- Sage, R. F., Sharkey, T. D. and Pearcy, R. W., 1990, The effect of leaf nitrogen and temperature on the CO₂ response of photosynthesis in the C₃ dicot Chenopodium album L. Aust. J. Plant Physiol., 17:, 135-48.
- Sage, R. F., Sharky, T. D. and Seeman, J. R., 1989, The acclimation of Photosynthesis to elevated carbon dioxide in five C-3 species.. Plant Physiol.
- Salvucci, M. E., 1989, Regulation of Rubisco activity in vivo. Physiol. Plant., 77: 164-171.
- Sasek, T. W. and Strain, B. R. 1991, Effects of CO₂ enrichment on the growth and morphology of a native and an introduced honey suckle vine.. American J. Bot., 78: 69-75.
- Sasek, T. W., DeLucia, E. V. and Strain, B. R., 1985, Reversibility of photosynthetic inhibition in cotton after long term exposure to elevated CO₂ concentrations. Plant Physiol., 78: 619-622.
- Sharkey, T.D., 1985, Photosynthesis in intact leaves of C₃ plants : physics, physiology and rate limitations.. Botanical Review, 51: 53-105.

- Sionit, N. and Kramer, P. J., 1986, Woody plants reactions to CO₂ enrichment. Enoch, H. Z. and Kimball, B. A. (Ed.), In Carbon dioxide enrichment of green house crops, Vol. II. (pp. 69-85) CRS Press.
- Sionit, N. and Patterson, D. T., 1985, Responses of C₄ grasses to atmospheric CO₂ enrichment II. Effect of water stress. Crop Sci., 25, 533-537.
- Sionit, N., Hellmers, H. and Strain, B.R., 1980, Growth and yield of wheat under carbon dioxide enrichment and water stress.. Crop Sci., 20: 687-690.
- Sionit, N., Strain, B. R. and Besford, R. A., 1981, Environmental control on growth and yield of okra I. Effect of temperature and CO₂ enrichment at cool temperature. Crop Sci., 21: 885-888.
- Sionit, N., Strain, B. R. and Flint, E. P., 1988b, Interaction of temperature and CO₂ enrichment on soybean : Photosynthesis and seed yield. Can. J. Plant Sci., 67: 629-636.
- Sionit, N., Strain, B. R. and Flint, E. P., 1982, Interactions of temperature and CO₂ enrichment on soybean: Growth and DM Partitioning. Can. J. Plant Sci., 67: 59-67.
- Sionit, N. Strain, B. R. and Hellmers, H., 1981, Effects of different concentrations of atmospheric CO₂ on growth yield components of wheat.. J. Agric. Sci., 79: 335-339.
- Sionit, N., Strain, B. R., Hellmers, H. and Kramer, P. J., 1981, Effects of atmospheric CO₂ concentration and water stress on water relations of wheat . Bot. Gaz., 142: 191-196.
- Sionit, N., Strain, B. R., Hellmers, H., Riechers, G. H. and Jaeger, C. H., 1985, Long-term atmospheric carbon dioxide enrichment effects and the growth and development of Liquidamber styraciflua and Pinus taeda seedlings. Can. J. For. Res., 15: 468-71.
- Slack, G. and Hand, D.W., 1985, The effect of water and summer CO₂ enrichment on the growth and fruit yield of glass house cucumber. J. Hort. Sci., 60: 507-516.
- Spencer, W. and Bowes, G., 1986, Photosynthesis and growth of water hyacinth under CO₂ enrichment . Plant Physiol., 82: 528-533.
- Tolbert, N. E. and Zelitch, I., 1983, Carbon metabolism. Lemon, B.R. (Ed.), In CO-2 and Plants : Response of

- plants to rising levels of atmospheric CO₂ (pp. 21-26) Westview Press, Boulder, USA.
- Tolley, L. C., 1982, The effects of atmospheric CO₂ enrichment, irradiance and water stress on seedling growth and physiology of Liquidambar styraciflua and Pinus taeda. Ph.D. Dissertation, Duke University Durham, N.C.
- Tolley, L. C. and Strain, B. R., 1984a, Effect of CO₂ enrichment on growth of Liquidambar styraciflua and Pinus taeda seedlings under different irradiance levels. Can. J. For. Res., 14:343-350.
- Tolley, L. C. and Strain, B. R., 1984b, Effects of CO₂ enrichment and water stress on growth of Liquidambar styraciflua and Pinus taeda seedlings. Can. J. Bot., 62: 2135-2139.
- Tolley, L. C. and Strain, B. R., 1985, Effects of CO₂ enrichment and water stress on gas exchange of Liquidambar styraciflua and Pinus taeda seedling grown under different irradiance. Oecologia, 65: 166-72.
- Valle, R., Mishoe, J.W., Campbell, W. J., Jones, J. W. and Allen L. H. Jr., 1985, Photosynthetic response of Bragg soybean leaves adapted to different carbon dioxide environments. Crop Sci., 25:333-339.
- Volennec, J.J., Nguyen, H. T., Nelson, C. J. and Sleper, D.A., 1984, Potential for genetically modifying dark respiration of Tall Fescue leaves. Crop Science, 24: 938-943.
- Von Caemmerer, S. and Farquhar, G.D., 1981, Some relationship between the biochemistry of photosynthesis and gas exchange of leaves. Planta, 153: 376-387.
- Vu, C. V., Allen, L. H. Jr. and Bowes, G., 1983, Effect of light and elevated atmospheric carbon dioxide on the Rubisco activity and RuBP level of soybean leaves. Plant Physiol., 73: 729-734.
- Warren, W. J., 1966, An analysis of plant growth and its control in artificial environments. Ann. Bot., 30: 383-402.
- Whiteman, P. C. and Koller, D., 1967, Interactions of CO₂ concentrations, light intensity and temperature on plant resistances to water vapour and CO₂ diffusion. New Phytologist, 66: 463-473.

- Wong, S. C., 1979, Elevated atmospheric partial pressure of CO₂ and plant growth, I. Interactions of nitrogen nutrition and photosynthesis capacity in C₃ and C₄. Oecologia, 44: 68-74.
- Wong, S. C. and Dunin, F. X., 1987, Photosynthesis and transpiration of trees in a Eucalyptus forest stand: Light and humidity responses. Aust. J. Plant Physiol., 14: 619-632.
- Wong, S.C. and Osmond, C. B., 1991, Elevated atmospheric partial pressure of CO₂ and Plant growth.III Interactions between Triticum and Echinochloa during growth in mixed culture . Aust. J. Plant Physiol., 18: 137-52.
- Wong, S. C., Cowan, I. R. and Farquhar, C. D., 1978, Leaf conductances in relation to assimilation in Eucalyptus pauciflora Subex spring. Plant Physiol., 62: 670-674.
- Woodward, F. F., Thompson, G.B. and McKee, I.F., 1991, The effect of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. Annals of Botany, 67: 23-38.
- Woodward, F. F., 1988, The response of stomata to changes in atmospheric levels of CO₂. Plants Today, 1: 132-135.
- Wulff, R. and Strain, B. R., 1982, Effect of CO₂ enrichment on growth and photosynthesis in Desmodium paniculatum. Can. J. Bot., 60: 1086-91.
- Yalle, S., Beeson, R. C., Trudel, M. J. and Gosselin, A., 1989, Acclimation of two tomato species to high atmospheric CO₂. I Sugar and starch accumulation . Plant Physiol., 90: 1465-1472.
- Zangerl, A. R. and Bazzaz, F. A., 1984, The response of plants to elevated CO₂. II. Competitive interactions among annual plants under varying light and nutrients. Oecologia, 62: 412-17.
- Zelitch, I., 1971, Environmental and physiological control of net photosynthesis, photorespiration and plant productivity (Ed. Academic Press), pp. 243-263.